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TABLE OF CONTENTS

TABLE OF CONTENTS CONTINUED

AJB Primer Notes & Protocols in the Plant Sciences

AJB Primer Notes & Protocols in the Plant Sciences is an online-only section of the Journal.

The articles for this issue can be accessed at http://www.amjbot.org/content/99/3.toc.

Corrigendum

Volume 98(8): 1299–1308. Becklin et al.—"Soil fungal effects on floral signals, rewards, and aboveground interactions in an alpine pollination web." In Figure 3, the second sentence of the legend was unclear. It has been changed from "Relationship between mycorrhizal fungal colonization and (A) total fragrance emission rate and (B) the number of floral volatiles produced by krummholz (open symbols) and tundra (closed symbols) plants. Triangles represent control plants and circles represent fungicide-treated plants. Vertical lines show mean AMF colonization of control (dashed) and fungicide-treated (solid) plants at the krummholz (gray) and tundra (black) sites. Negative relationships were significant at the tundra site ($R^2 = 0.29$, $P = 0.006$ and $R^2 = 0.28$, $P = 0.007$)." to "Relationship between mycorrhizal fungal colonization and (A) total fragrance emission rate and (B) the number of floral volatiles produced by krummholz (open symbols) and tundra (closed symbols) plants. Control (circles) and fungicide (triangles) treatments were pooled to provide the greatest range of colonization. Vertical lines show mean AMF colonization of control (dashed) and fungicide-treated (solid) plants at the krummholz (gray) and tundra (black) sites. Negative relationships were significant at the tundra site ($R^2 = 0.29$, $P = 0.006$ and $R^2 = 0.28$, $P = 0.007$)."

The online article has been corrected.

Abbreviations

Miscellaneous: AFLP, amplified fragment length polymorphisms; a.s.l., above sea level; bp, base pair; BP, before present; BSA, bovine serum albumin; cpDNA, chloroplast DNA; CTAB, hexadecyltrimethylammonium bromide; cv., cultivar; ddH$_2$O, double-distilled water; dNTP, deoxyribonucleotide E.C., Enzyme Commission; EDTA, ethylene diamine tetra-acetic acid; f. sp., forma specialis; indels, insertions and deletions; ITS, internal transcribed spacer; LM, light microscopy; mya, million years ago; PAGE, polyacrylimide gel electrophoresis; PCR, polymerase chain reaction; RAPD, random amplified polymorphic dimorphism; SDS, sodium dodecyl sulfate; SEM, scanning electron microscopy; s.l., sensu lato; s.s., sensu stricto; subsp., subspecies; TEM, transmission electron microscopy

Genetics: *A*, mean number of alleles per locus; *D*, mean genetic distance; CI, consistency index; *F*, fixation index; F_{IT}, total deviation from Hardy-Weinberg expectations; F_{ST}, genetic diversity among populations; F_{IS}, inbreeding within populations; G_{ST}, the proportion of genetic diversity among populations; H_e, Hardy–Weinberg expected heterozygosity; H_o, observed heterozygosity; MP, most parsimonious tree; *n*, individual chromosome number; Nm, mean number of migrants per generation; P_p, percentage of polymorphic loci; RI, retention index; *x*, base chromosome number

Statistics and math: ANOVA, analysis of variance; CV, coefficient of variation; df, degrees of freedom; *N*, number of individuals; *p*, probability; *P*, level of significance; PCA, principal components analysis; *r*, coefficient of correlation; SE, standard error; SD, standard deviation

Botany

RAINFOREST CONIFERS OF EOCENE PATAGONIA: ATTACHED CONES AND FOLIAGE OF THE EXTANT SOUTHEAST ASIAN AND AUSTRALASIAN GENUS DACRYCARPUS (PODOCARPACEAE)[1]

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- *Premise of the study:* Eocene caldera-lake beds at Laguna del Hunco (LH, ca. 52.2 Ma) and Río Pichileufú (RP, ca. 47.7 Ma) in Argentine Patagonia provide copious information about the biological history of Gondwana. Several plant genera from these sites are known as fossils from southern Australia and New Zealand and survive only in Australasian rainforests. The potential presence of *Dacrycarpus* (Podocarpaceae) holds considerable interest due to its extensive foliage-fossil record in Gondwana, its remarkably broad modern distribution in Southeast Asian and Australasian rainforests, its high physiological moisture requirements, and its bird-dispersed seeds. However, the unique seed cones that firmly diagnose *Dacrycarpus* were not previously known from the fossil record.
- *Methods:* I describe and interpret fertile (LH) and vegetative (LH and RP) material of *Dacrycarpus* and present a nomenclatural revision for fossil *Dacrycarpus* from South America.
- *Key results: Dacrycarpus puertae* sp. nov. is the first fossil occurrence of the unusual seed cones that typify living *Dacrycarpus*, attached to characteristic foliage, and of attached *Dacrycarpus* pollen cones and foliage. *Dacrycarpus puertae* is indistinguishable from living *D. imbricatus* (montane, Burma to Fiji). *Dacrycarpus chilensis* (Engelhardt) comb. nov. is proposed for Eocene vegetative material from Chile.
- *Conclusions:* Modern-aspect *Dacrycarpus* was present in Eocene Patagonia, demonstrating an astonishingly wide-ranging paleogeographic history and implying a long evolutionary association with bird dispersers. *Dacrycarpus puertae* provides the first significant Asian link for Eocene Patagonian floras, strengthens the biogeographic connections from Patagonia to Australasia across Antarctica during the warm Eocene, and indicates high-rainfall paleoenvironments.

   Key words: bird dispersal; caldera lake; conifers; *Dacrycarpus*; Eocene; Laguna del Hunco; Patagonia; Podocarpaceae; Río Pichileufú; rainforest.

The southern hemisphere fossil record of living conifer genera has attained great significance (von Ettingshausen, 1887; Halle,

1913; Florin, 1940a; Hill and Scriven, 1998a; Hill and Brodribb, 1999; Hill, 2004; Stockey et al., 2005). Due to apparent morphological conservatism and fortuitous preservation, many extant genera can be well diagnosed as fossils, providing novel information about biogeographic histories and ages of lineages on the Gondwanan land masses (e.g., Hill and Brodribb, 1999; Paull and Hill, 2009; Carpenter et al., 2011; Crisp et al., 2011). Moreover, several genera provide important paleoenvironmental constraints when found as fossils because much is known about their physiological drought limitations (Brodribb and Hill, 1998, 2004).

In many cases, southern hemisphere conifer fossils give compelling evidence for much greater lineage distributions in the past than the present and for large latitudinal shifts over time. Striking examples come from southeastern Australia and Patagonia, which until ca. 31–32 Ma were adjacent to Antarctica, without deepwater separation (Lawver and Gahagan, 2003). *Acmopyle* (Podocarpaceae), *Araucaria* sect. *Eutacta* (Araucariaceae), and *Papuacedrus* (Cupressaceae) have all been found in Paleogene sediments from southern Australia and Patagonia (Berry, 1938; Florin, 1940a, b; Hill and Carpenter, 1991; Hill and Brodribb, 1999; Wilf et al., 2009); the Patagonian occurrences are from two prolific, Eocene caldera-lake floras, Laguna del Hunco (LH) and Río Pichileufú (RP) (Fig. 1; see Materials and Methods). These lineages are only extant in Australasian, tropical, often montane rainforests, indicating former distributions across Antarctica during the warm Paleogene and a long and complex history of range shifts in response to climate change
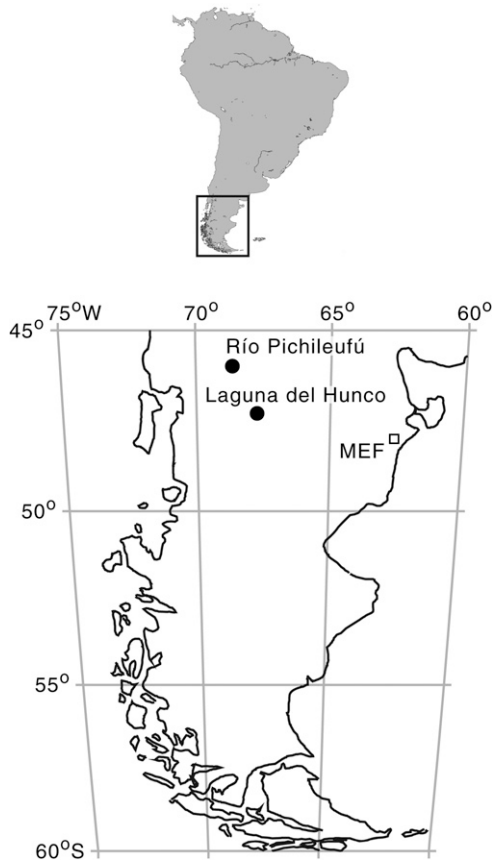
Fig. 1. Map showing 50 Ma positions, with modern coastlines and inset from modern South America, of the Laguna del Hunco (ca. 52.2 Ma) and Río Pichileufú (47.7 Ma) fossil sites and Museo Paleontológico Egidio Feruglio (MEF) in the city of Trelew, the repository for most specimens reported here. Redrawn from Wilf et al. (2005a, 2009). Reconstruction made using the Plate Tectonic Reconstruction Service of the Ocean Drilling Stratigraphic Network, www.odsn.de/odsn/services/paleomap/paleomap.html, using data from Hay et al. (1999). South America graphic generated using Online Map Creation, www.planiglobe.com (Wessel and Smith, 1995).

and plate movements. On the other hand, *Austrocedrus* and *Fitzroya* (Cupressaceae) have been found as fossils in Paleogene sediments of southeast Australia but not (reliably) in South America (Hill and Carpenter, 1989; Hill and Whang, 1996; Paull and Hill, 2008, 2010). These genera are both extinct in Australia and survive in southern South America, suggesting late dispersal into their current ranges and source extinction (or inadequate sampling in South America).

Dacrycarpus (Bennett) de Laubenfels (Podocarpaceae) is a genus of medium-sized to giant (to 50–60 m height), evergreen rainforest trees with a rich macrofossil record in southeast Australia and Patagonia, starting from the Eocene, and younger records in New Zealand (Table 1). Now extinct in both Australia and South America, *Dacrycarpus* remains successful, with nine living species, most of which are tropical montane. These occur across a vast area on both sides of Wallace's Line, from New Zealand to northern Burma (Table 2), up to ca. 27°N latitude and 18 000 km modern distance from central Patagonia. *Dacrycarpus* is one of the least drought-tolerant of all conifers physiologically (Brodribb and Hill, 1998, 2004) and is consistently

associated with high rainfall environments, very limited dry seasons, and wet or waterlogged soils (Wasscher, 1941; de Laubenfels, 1969); thus, the genus is a robust indicator of very wet paleoenvironments. According to a climatic compilation for six of the species (Biffin et al., 2011), grand means of mean annual and cold month mean temperatures (MAT and CMMT) and of mean annual precipitation (MAP) where *Dacrycarpus* occurs range from ca. 11–21°C, ca. 2–14°C, and ca. 1700–2900 mm, respectively (with considerable variance around these values), though only *D. dacrydioides* (New Zealand) is associated with CMMTs less than ca. 6°C.

The entire previous macrofossil record of *Dacrycarpus* is based on vegetative branches and cuticles, and a single, Miocene occurrence of dispersed pollen cones (Table 1). These fossils preserve many foliar, including cuticular, characters that associate them with *Dacrycarpus*; however, without the attachment of the highly distinctive, ovulate reproductive structures of the genus (Richard, 1832; Sinnott, 1913; de Laubenfels, 1969; Fountain et al., 1989; Tomlinson, 1992), doubt remains as to whether *Dacrycarpus* is truly ancient or whether the vegetative features are plesiomorphic to a larger clade, such that some fossils could represent extinct lineages outside *Dacrycarpus*.

Dacrycarpus seed cones (= bract, epimatium, and ovule; Figs. 2–8) arise terminally on short, leafy branches (Figs. 2, 6), which often curve to erect the cones once development begins (Tomlinson et al., 1991), and on which two to five distal leaves greatly enlarge and fuse to form a warty, fleshy, edible, brightly colored podocarpium that is targeted by birds (Figs. 2, 3). Additional modified leaves emerge distally from the podocarpium as elongate, fertile bracts, of which many abort. On the one or two that do not, a resinous epimatium develops, fused to the adaxial surface of the bract, and then relocated distally via intercalary bract growth; within the epimatium, an inverted ovule develops, specialized for pollen capture on the podocarpium surface (Tomlinson et al., 1991; Tomlinson, 1992: figs. 41–51). The bract forms a distinctive crest along its external midline, and the bract and epimatium remain fully fused, except that the bract remains free apically so as to project beyond the ovule and epimatium, quite markedly during immature stages, but only as a reduced, projecting tip or beak at maturity (Figs. 4, 7, 8). In addition to the cone features, living *Dacrycarpus* is usually easy to recognize from sterile material, especially those species having sharply dimorphic foliage (Table 2; Figs. 6, 7), comprised of bifacially flattened "adult" leaves primarily deployed on long shoots and bilaterally flattened, keeled, often distichous "juvenile" leaves on feather-like, determinate short shoots (there are also reduced scale leaves on the long shoots, with low preservation potential as fossils).

I here report new (and some historic) material bearing numerous diagnostic characters of *Dacrycarpus*, primarily found during ongoing paleontological and geological investigations of Laguna del Hunco and Río Pichileufú (Fig. 1). Along with numerous sterile specimens (Figs. 9–17), this notably includes unique attachments of seed and pollen cones to typical *Dacrycarpus* foliage (Figs. 18–56). I propose that this Eocene material from Argentina be placed into a new species, *Dacrycarpus puertae*. I resolve several nomenclatural issues related to *D. puertae* and for a species from the Eocene of Chile (Engelhardt, 1891; Florin, 1940a) that here receives the new combination *Dacrycarpus chilensis* (Engelhardt). I compare the two taxa to living species, and I discuss the contribution of *D. puertae*, confirmed as a modern-aspect *Dacrycarpus* species due to the fortuitously preserved
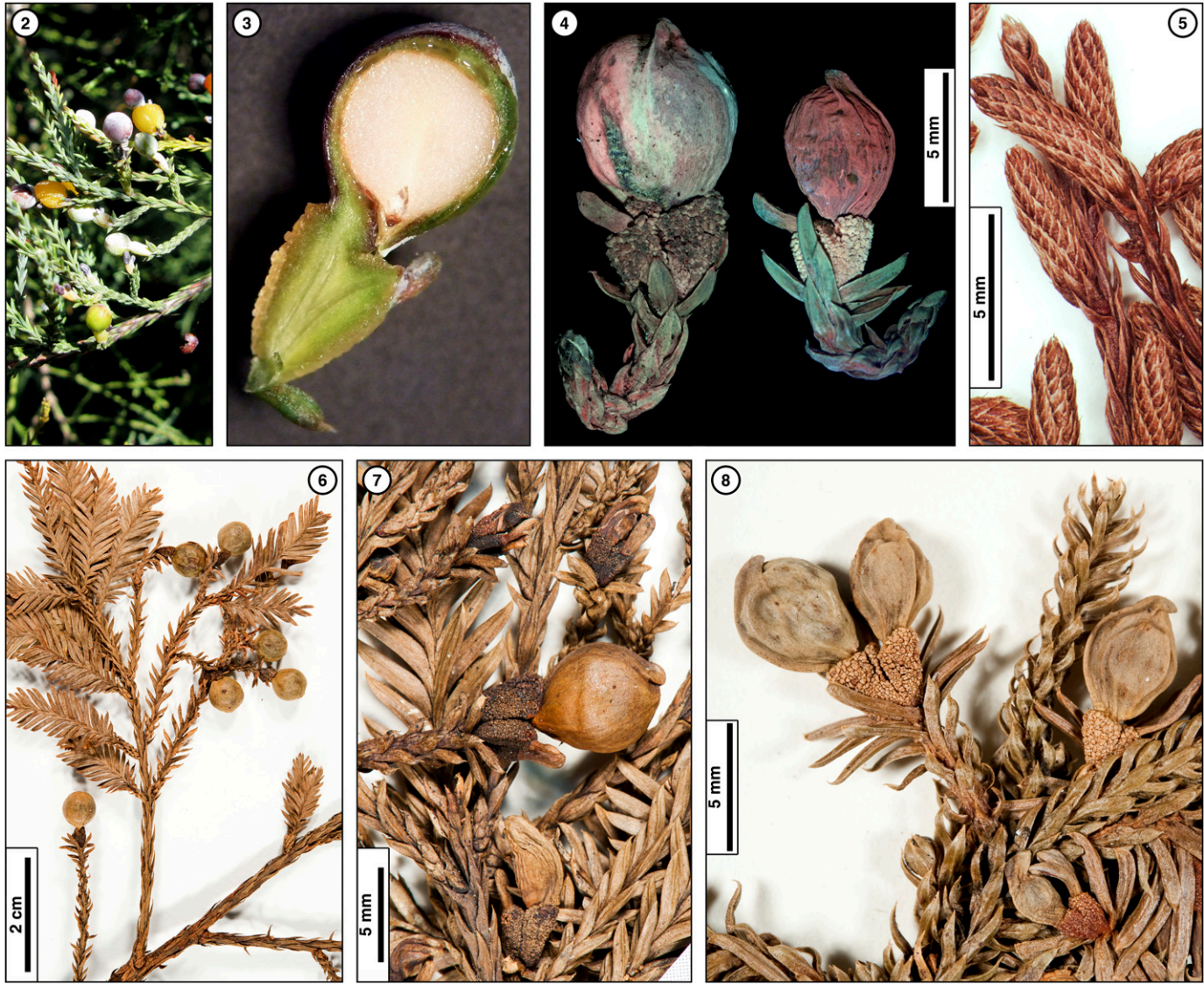
Figs. 2–8.   Extant *Dacrycarpus*, showing reference characters for the fossil *D. puertae* sp. nov. Note that podocarpia of herbarium specimens are significantly smaller than in life, due to desiccation; see Appendix 1 for additional voucher data. **2.** *D. dacrydioides*, showing seed cones in various developmental stages. Note curving fertile shoots with erect ovules, developing and expanded podocarpia, numerous aborted ovules, and spreading involucral leaves (the latter contra *D. puertae*). Width of frame, ca. 4 cm. Specimen tree, Royal Botanic Gardens, Melbourne. **3.** *D. dacrydioides*, longitudinal section of mature podocarpium and seed cone, showing: spreading involucral leaf (contra *D. puertae*) with two parallel rows of stomata; warty podocarpium showing prominent zones of marginal fusion between three constituent leaves (cf. Figs. 23, 24); aborted ovule; fertile bract (not extending beyond epimatium due to maturity) subtending distally thickened epimatium with large resin ducts; inverted seed; extended integument forming the micropyle; and the enclosing extension of the epimatium (cf. Figs. 43–45). Scale not available, but typical seed length for this species is 3.5–5 mm (Table 2). Photo by C.E.C. Gemmill. **4.** Ovulate shoots of *D. imbricatus* var. *curvulus*, the living taxon with greatest similarity to the fossils (see text), bearing mature (left) and submature (right) seed cones, positioned approximately orthogonal to the cleavage plane of the fossils. Note fertile bracts fused to the epimatia with keels and prolonged apices, curving subtending shoots, clasping involucral leaves, and warty podocarpia. Epifluorescence. North Sumatra, US 2897270. **5.** *D. imbricatus*, long shoot with laterally inserted pollen cones. Note the numerous, spirally inserted, imbricate, keeled, ovate, sharp-pointed microsporophylls, and the recurved, sharp-pointed bifacial leaves. Fiji, MEL 2344582, photo by H. Barnes. **6.** *D. imbricatus* var. *patulus*, with ovulate shoots and sharply dimorphic foliage, bearing close overall resemblance to the holotype of *D. puertae* (Figs. 18, 19), though all cones are mature and well rounded, unlike the fossil. Papua New Guinea, NSW 527532. **7.** *D. imbricatus*, detail of seed-cones in a range of developmental stages, and dimorphic foliage. The immature cone at bottom center is very similar to fossil cone c3 (Figs. 41, 42). Papua New Guinea, CANB 360480. **8.** *D. expansus*, detail of seed cones in a range of developmental stages, and the spreading bifacial leaves typical of this species (contra *D. puertae*). The three large cones at top show three orientations. The leftmost cone is in lateral view and shows the fertile bract with keel and beak and the micropyle perched just above the bract and against the podocarpium; the middle cone shows the obverse to the surface presented in the fossils, the view being only of the bract and its keel and beak, and the subtended epimatium and seed are out of view; the rightmost cone is positioned very similarly to most of the fossils and is in a similar developmental stage, and the relief of the inverted ovule shows well within the epimatium. The immature cone at bottom right is very similar to fossil cone c3 (Figs. 41, 42). Papua New Guinea, CANB 85921.

TABLE 1.   Macrofossil record of *Dacrycarpus*.

Species	Organ(s)	Localities, age	References
Dacrycarpus arcuatus Wells & R. S. Hill	bf, cut	Tasmania: Little Rapid River, Oligocene; Pioneer, late Oligocene-early Miocene	Wells and Hill, 1989a
D. chilensis (Engelhardt) Wilf, comb. nov.	bf, bl, cut	Chile: Coronel, Lota, Curanilahue, Peumo, and Minas Conquil, Eocene	Engelhardt, 1891, 1905; Florin, 1940a; this paper
D. crenulatus Wells & R. S. Hilll	bf, cut	Tasmania: Pioneer, late Oligocene-early Miocene	Wells and Hill, 1989a
D. cupressiformis Wells and R. S. Hill	bf, cut	Tasmania: Little Rapid River, Oligocene	Wells and Hill, 1989a
D. dacrydioides (A.Rich.) de Laub.	bf, bl, cut	New Zealand: Manuherikia Group, early Miocene	Pole, 1992b, 2007
D. elandensis R.S.Hill & S.S.Whang	bf, bl, cut, pc+p	New South Wales: Elands, Miocene	Hill and Whang, 2000
D. geminus Pole	bl, cut	Tasmania: Hasties, middle-late Eocene	Pole, 1992a
D. lanceolatus Wells & R.S.Hill	bf, cut	Tasmania: Monpeelyata, late Oligocene-early Miocene	Wells and Hill, 1989a
D. latrobensis R. S. Hill & R. J. Carp.	bf, bl, cut	Victoria: Yallourn and Morwell, late Oligocene-Pliocene; Bacchus Marsh, ?Oligocene	Cookson and Pike, 1953; Hill and Carpenter, 1991; Mill and Hill, 2004
D. linearis Wells & R.S.Hill	bf, cut	Tasmania: Little Rapid River, Oligocene	Wells and Hill, 1989a
D. linifolius Wells & R.S.Hill emend. R.S.Hill & R. J. Carp.	bf, cut	Tasmania: Regatta Point, early Eocene; Little Rapid River, Oligocene	Wells and Hill, 1989a; Hill and Carpenter, 1991
D. microfolius G.J.Jord., R.J.Carp., Bannister, D.E.Lee, Mildenh. & R.S.Hill	bf, bl, cut	New Zealand: Newvale Mine, late Oligocene-early Miocene	Jordan et al., 2011
D. mucronatus Wells & R.S.Hill emend. R.S.Hill & R. J. Carp.	bf, bl, cut	Tasmania: Regatta Point, early Eocene; Loch Aber and Hasties, middle-late Eocene; Cethana, early Oligocene; Little Rapid River, Oligocene	Wells and Hill, 1989a; Hill and Carpenter, 1991; Pole, 1992a
D. patulus R.S.Hill & Merrifield	bf, cut	Western Australia: West Dale, middle Eocene-Oligocene	Hill and Merrifield, 1993
D. praecupressinus (Ettingsh.) D. R. Greenw. ex R. R. Mill & R. S. Hill	bl	New South Wales: Vegetable Creek, late Eocene	von Ettingshausen, 1887; Greenwood, 1987; Hill and Carpenter, 1991; Mill and Hill, 2004
D. puertae Wilf, sp. nov.	bf+bl+sc, bf+pc	Argentina: Laguna del Hunco (Chubut), early Eocene; Río Pichileufú (Río Negro), middle Eocene	Berry, 1938; Florin, 1940a; this paper
Dacrycarpus sp.	bf, cut	Victoria: Berwick Quarry, late Oligocene-early Miocene	Pole et al., 1993
Dacrycarpus sp.	?bf, cut	Western Australia: Lefroy and Cowan Paleodrainages, middle Eocene	Carpenter and Pole, 1995

Notes: Abbreviations: bf, bifacially flattened ("adult") leaves; bl, bilaterally flattened ("juvenile") leaves; cut, cuticle; p, pollen; pc, pollen cones; sc, seed cones; +, reproductive attachment. Records restricted to dispersed cuticles not included. Additional names previously rejected as not belonging naturally to *Dacrycarpus* and relevant citations: *D. carpenterii* G. J. Jord. (Jordan, 1995; Pole, 1998; Hill and Brodribb, 1999), *D. acutifolius* Wells and R. S. Hill (Wells and Hill, 1989a; Pole, 1998; Hill and Brodribb, 1999), *D. involutus* Wells and R. S. Hill (Wells and Hill, 1989a; Pole, 1998; Hill and Brodribb, 1999), *D. eocenica* D. R. Greenw. (Greenwood, 1987; Hill and Scriven, 1998b; Mill and Hill, 2004), *D. setiger* (Townrow) D. R. Greenw. (Greenwood, 1987; Hill and Carpenter, 1991; Mill and Hill, 2004).

reproductive structures, to the fossil record and evolution of the genus and to biogeographic and paleoenvironmental knowledge of Gondwana.

MATERIALS AND METHODS

Laguna del Hunco and Río Pichileufú—The fossil assemblages that bear *Dacrycarpus puertae* sp. nov. are the early Eocene (ca. 52.2 Ma) Laguna del Hunco flora, from Chubut Province, and the middle Eocene (ca. 47.7 Ma) Río Pichileufú flora, from Río Negro Province, Argentina (Fig. 1). First reported in the 1920s and 1930s and considered Miocene (Berry, 1925, 1935a–c, 1938), several additions and revisions to these angiosperm-dominated floras and associated insect, fish, and frog taxa were made during the 20th century, as reviewed recently elsewhere (Wilf et al., 2005a, 2009). Among these, the presence of *Dacrycarpus* was noted from sparse material of vegetative branches at Río Pichileufú (Florin, 1940a), but under an erroneous name (see Systematics and Results). Whole-rock K-Ar analyses of associated volcanic strata, but not of the fossiliferous lake beds themselves, suggested a Paleocene or Eocene age for the LH and RP assemblages (Archangelsky, 1974; González Díaz, 1979; Mazzoni et al., 1991).

Significant field reinvestigations of the LH and RP sites have been conducted since 1999, leading to precise ^{40}Ar–^{39}Ar dating for both floras and detailed lithostratigraphy and paleomagnetic stratigraphy at LH; the discovery of highly elevated floral and insect-damage richness; and the description or revision of several plant, insect, vertebrate, and ichnotaxa (Wilf et al., 2003, 2005a, b, 2009; Petrulevičius and Nel, 2005; Zamaloa et al., 2006; González et al., 2007; Sarzetti et al., 2008, 2009; Petrulevičius, 2009; Barreda et al., 2010; Petrulevičius et al., 2010; Azpelicueta and Cione, 2011; Gandolfo et al., 2011; Gómez et al., 2011).

The most reliable ^{40}Ar–^{39}Ar results came from analyses of single sanidine crystals recovered from primary ashfall tuffs in the lake beds that are very closely associated stratigraphically with the fossil plants. At LH, tuff 2211A, stratigraphically located within the most densely sampled, highly fossiliferous interval (Wilf et al., 2003, 2005a), yielded an early Eocene (Ypresian) age of 52.13 ± 0.32 Ma (J. Obradovich in Wilf et al., 2003) and a subsequent reanalyzed age of 51.91 ± 0.22 Ma (M. Smith in Wilf et al., 2005a). At RP, three different tuffs found immediately above fossil plant horizons (tuffs RP1, T2, and RP3) yielded a concordant early middle Eocene (Lutetian) age of 47.46 ± 0.05 Ma (M. Smith in Wilf et al., 2005a). The ^{40}Ar–^{39}Ar ages from Wilf et al. (2005a) were here kindly recalculated by M. Smith, Sonoma State University (personal communication, 2011) relative to the astrochronologically calibrated, revised 28.201 Ma age for the Fish Canyon tuff sanidine (Kuiper et al., 2008), using the liquid-scintillation derived decay constants of Renne et al. (2010) and the uncertainty equations of Renne et al. (1998) and Kuiper et al. (2008). The recalculated ages, which do not affect marine stage assignments, are 52.22 ± 0.22 (analytical 2σ), ± 0.29 (full 2σ) Ma for tuff 2211A at Laguna del Hunco, and 47.74 ± 0.05, ± 0.18 for the three combined tuffs at Río Pichileufú.

Although a large number of plant species (>>100) from LH and RP remain undescribed or unrevised, a particularly notable feature of these assemblages is the strong biogeographic affinities of several genera both to extant Australasian, commonly montane, subtropical and tropical rainforests, and to southern

TABLE 2. *Dacrycarpus puertae* sp. nov. compared to the nine living *Dacrycarpus* species. Boldfaced font indicates a shared character state; for measurements, this is based on overlap with the maximum fossil value at the given precision. All measurements in millimeters.

Species	Bifacial/"adult" lvs			Bilaterally flattened and distinct	Bilateral/"juvenile" lvs			Shoot subtending pc			Involucral lvs				
	Clasp twig tightly (ct) or loosely (cl), or spreading (s)	len	wid		Distichous	len	wid	len	leaf len	len	Spreading (s) or clasping (c) part or all of pc (pc), part of sc (psc), or all of sc (asc)	pc len	sc len	%Match	Range
D puertae sp. nov.	**ct (cl, s)**	**2.1–4.9**	**0.3–1.0**	y	y	**3.1–17.4**	**0.6–2.0**	**6.4–8.1**	**1.9–2.3**	**2.3–2.7**	**c, pc**	**5.9–6.3**	**5.4**	—	Patagonia, Eocene
D. cinctus (Pilg.) de Laub.	s	1.5–4	0.4–0.6	n	y/n	≤12	≤0.8	5–20	2–4	6–11	c, psc	3–4	**4–7**	23	Sulawesi to NG, 1800–3000 m
D. compactus (Wassch.) de Laub.	cl	2–3	**0.6–1.0**	n	n	2–2.5	~0.6	6–18	**1.6–3**	4–10	**c, pc**	3–5	6–8.5	31	NG, 3000–4300 m
D. cumingii (Parl.) de Laub.	cl	**3–6**	0.6–0.8	y	y	≤12	~1.2	6–10	7–13	**2–13**	c, psc or asc	2–4	**3.5–6**	46	Philippines, Borneo, Sumatra, 1850–2650 m
D. dacrydioides (A. Rich.) de Laub.	**ct (cl, s)**	1–2	0.6–0.8	y	y	4–7	0.5–1	5–10	2–3	1.5–2	s	**3–7**	**3.5–5**	54	New Zealand, 0–500 m
D. expansus de Laub.	s	1.5–3	0.6–0.8	y/n	y (or 4r)	≤12	1.5	4–5	**2–3**	**3–6**	**c, pc**	2–4	**5–6**	31	NG, 2000–2750 m
D. imbricatus (Blume) de Laub.	**ct (cl, s)**	**0.8–6**	**0.4–1.0**	y	y	10–17	**1–2**	3–10	3–5	**1–5**	s or **c, pc**	**3–7**	**5–7**	92	Burma to Fiji, 700–2700 m
D. kinabaluensis (Wassch.) de Laub.	s	2–4	**0.8–1.0**	y	y (or nearly 4r)	10–15	1–1.2	5–16	5–8	5–8	c, psc	2–5	**5–7**	23	Mount Kinabalu, Borneo, 2100–4000 m
D. steupii (Wassch.) de Laub.	s	2–4	0.4–0.6	y	y	4–8	0.6–1	3–16	**3–5**	3–5	s	2–4	**4–6**	38	Borneo, Sulawesi, NG, 1500–2500 m
D. vieillardii (Parl.) de Laub.	s (cl)	2–4	0.4–0.6	y	y	3–10	0.5–1.0	6–12	**1–2**	1–2	s	2–3	**5–6**	38	New Caledonia, 150–750 m

Notes: Abbreviations—lvs, leaves; pc, podocarpium; sc, seed cone (bract, epimatium, and ovule); len, length; wid, width; 4r, 4-ranked; NG, New Guinea. For the fossil *D. puertae*, leaf measurements were taken as the maximum per shoot, and for sc len, only the most mature seed cone, c4 (Figs. 39, 40), is included. Extant species data primarily from Eckenwalder (2009) with extreme (parenthetical) values omitted, combined with Wasscher (1941), de Laubenfels (1969, 1988), and Farjon (2010) when these differed (usually only slightly). Additional sources consulted: de Laubenfels (1972, 1978), Van Royen (1979), Offler (1984), Beaman and Beaman (1998), and Sunarno et al. (1995).
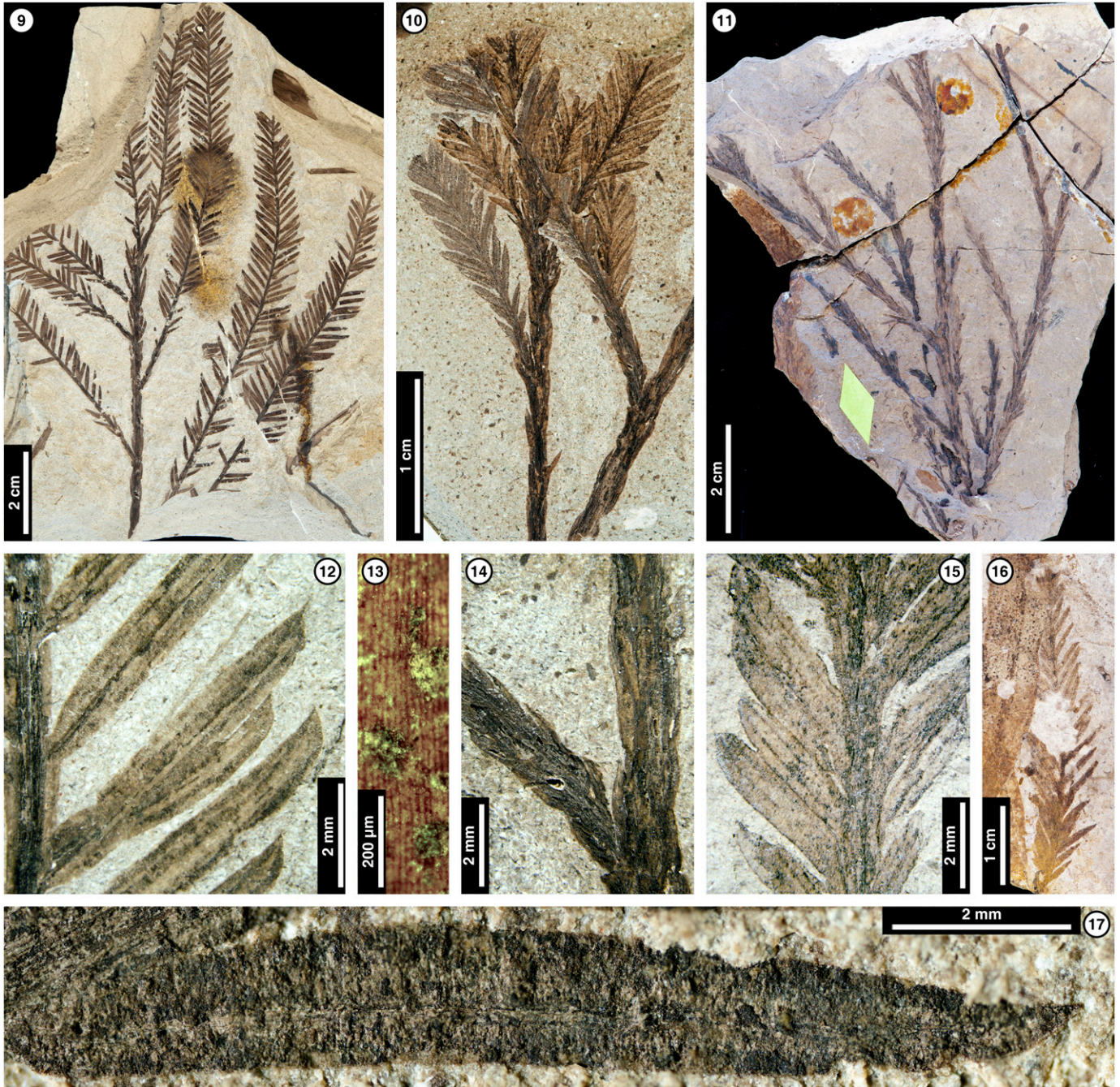
Figs. 9–17.   *Dacrycarpus puertae* sp. nov., selected foliar material from Laguna del Hunco and Río Pichileufú. **9.** Large spray showing sharply dimorphic foliage, including eight elongate short shoots with bilateral leaves. MPEF-Pb 973 (also Figs. 12, 13), from quarry LH15. **10.** Specimen showing sharply dimorphic foliage. MPEF-Pb 4990 (also Fig. 14), from LH13. **11**. Specimen figured by Berry (1938: pl. 12, fig. 2) as "*Fitzroya tertiaria*," here placed in *Dacrycarpus puertae* sp. nov. (see text), consisting of long shoots with bifacial leaves. USNM 40381a. **12.** Detail of bilateral leaves, MPEF-Pb 973 (Fig. 9), showing: twisting of the spirally inserted, decurrent leaf bases into a distichous deployment; single vein per leaf paralleled by two dark lines indicating compressed, coalified rows of stomata; and finely mucronate apices. **13.** Detail of longitudinally oriented epidermal cells on a bilateral leaf. MPEF-Pb 973 (Fig. 9), epifluorescence. **14.** Detail of bifacial leaves tightly clasping the axis, with finely mucronate apices. MPEF-Pb 4990 (Fig. 10). **15.** Detail of a short shoot with bilateral leaves, each showing two dark lines of compressed, coalified stomata. MPEF-Pb 4972, from LH13. **16.** Short shoot (with angiosperm leaves) found in the historic Río Pichileufú collection (Berry, 1938), demonstrating the presence of bilateral foliage in that collection. USNM 543561a, previously unfigured. **17.** Detail of a single bilateral leaflet, showing single midvein and coalified, fine mesophyll compressions preserving general orientation perpendicular to the midvein. MPEF-Pb 4982, from LH13.
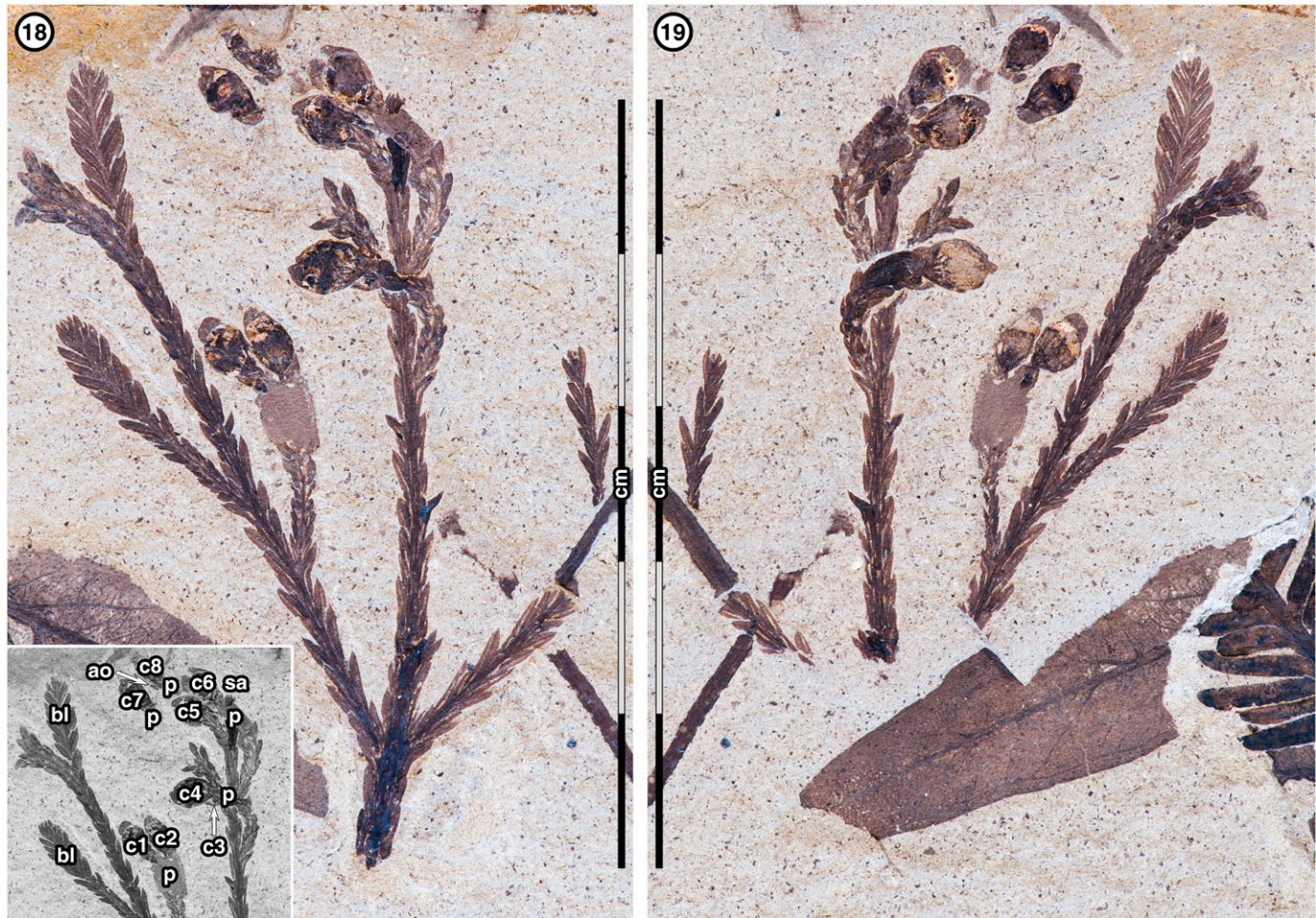
Figs. 18–19.   Holotype of *Dacrycarpus puertae* sp. nov., MPEF-Pb 4983, from Laguna del Hunco, quarry LH13, with inset notational key at lower left. Note: sharply dimorphic foliage, with bifacially flattened leaves on long shoots and bilaterally flattened leaves (bl) on feather-like short shoots, both with amber-filled resin-canal molds visible as white streaks; a long-shoot apex of loosely aggregated leaves (sa; also Fig. 22); curving leafy branches subtending erected seed cones; expanded podocarpia (p); and the eight terminal seed cones (c1–c8) in various maturation stages, from a very immature (c3, adjoining c4; also Figs. 21, 41, and 42) to a nearly mature cone (c4), as well as an aborted ovule (ao) on the podocarpium subtending c8 (also Fig. 45). Also visible are an angiosperm leaf and a specimen of *Acmopyle engelhardti* (Fig. 19, lower right), showing the large bilateral leaves that allow this closely related podocarp to be easily distinguished from *D. puertae* as in living counterparts (see text). **18.** MPEF-Pb 4983a (part) and **19.** MPEF-Pb 4983b (counterpart).

Australian fossil floras. Thus, the LH and RP assemblages comprise the primary macrofossil evidence from South America for significant Eocene floral continuity from Patagonia to Australia across Antarctica. In addition to the conifers mentioned above, angiosperms from LH and RP also support this pattern, including *Akania* (Akaniaceae), *Gymnostoma* (Casuarinaceae), and *Eucalyptus* subgenus *Symphyomyrtus* (Romero and Hickey, 1976; Gandolfo et al., 1988, 2011; Zamaloa et al., 2006). The increasing number of water-demanding genera being recognized, particularly *Papuacedrus*, *Acmopyle*, and *Gymnostoma*, supports Morley's (2000) hypothesis of rainforest environments in Eocene Patagonia; in turn, high-rainfall paleoenvironments, and mild winters without frost, are likely explanatory factors for the elevated species richness of the sites (Wilf et al., 2009).

Provenance and repositories—The majority of *Dacrycarpus* specimens described here from Argentina came from the recent field reinvestigations of LH and RP mentioned above and in particular the collections made in 1999 (LH) and 2002 (LH and RP) reported by Wilf et al. (2003, 2005a) as well as a 2005 collection at RP and a 2009 collection at LH. The Laguna del Hunco collections are curated at Museo Paleontológico Egidio Feruglio (MEF, repository prefix MPEF-Pb), in Trelew, Chubut, Argentina, and the Río Pichileufú specimens are housed at Museo de Paleontología, San Carlos de Bariloche, Río Negro, Argentina (BAR). Letter suffices (a, b) indicate parts and counterparts. The Laguna del Hunco material is more abundant and complete, including both of the fertile

specimens. Historic collections from Río Pichileufú (Berry, 1938) were also studied, housed at the Smithsonian Institution, National Museum of Natural History (USNM); these were originally sent to Berry by their discoverer, J. R. Guiñazu. Historic collections from LH, also at USNM, do not include any conifer material (Berry, 1925).

Laguna del Hunco specimens came from quarry sites LH2, LH6, LH13, and LH25 of Wilf et al. (2003) and from quarry LH27, at the same stratigraphic level as LH6 (Gandolfo et al., 2011). *Dacrycarpus* comprises 1% of quantitatively collected specimens for Laguna del Hunco overall (Wilf et al., 2005a: morphotype TY121). Quarry LH13 has the highest relative abundance of conifers for LH, and similarly, most *Dacrycarpus* specimens were found at LH13, comprising 3% of total specimens there (Wilf et al., 2005a). In total, the Laguna del Hunco material cited here includes 15 specimens that can be determined as long shoots (one of these bearing pollen cones), 43 of short shoots, and nine showing dimorphic foliage (one of these with attached seed cones).

From Río Pichileufú, foliar material came from: the RP3 quarry site of Wilf et al. (2005a), two specimens; a single specimen discovered in older collections at BAR, exact quarry site unknown; and two specimens from historic collections at USNM, exact quarry site unknown. The USNM material was described by Berry (1938) as "*Fitzroya tertiaria*" and by Florin (1940a) as *Podocarpus* "*tertiarius*" sect. *Dacrycarpus* (see Systematics and Results; quotations are used throughout to indicate either technically invalid or botanically doubtful names). In total, the Río Pichileufú material cited here includes one specimen
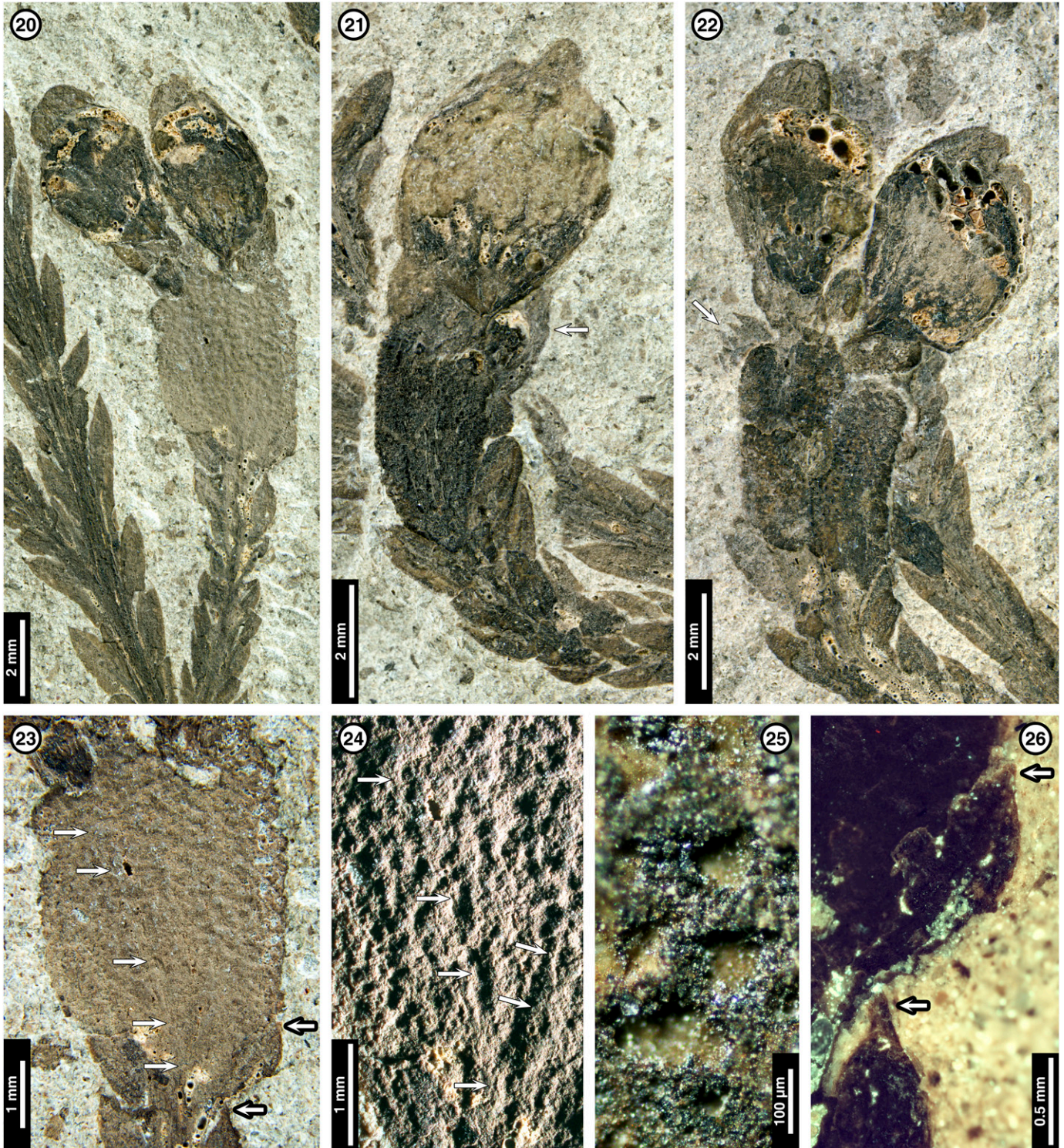
Figs. 20–26.   Holotype of *Dacrycarpus puertae* sp. nov., MPEF-Pb 4983, from Laguna del Hunco. See inset to Fig. 18 for notational key. Figs. 20–22, selected ovuliferous shoot portions; Figs. 23–26, details of the podocarpium in Fig. 20. Figs. 20, 23, 24, 26, part (a); Figs. 21, 22, 25, counterpart (b); Fig. 24, low-angle light from right side only; Fig. 26, epifluorescence. In all cones, the inverted ovule, resinous epimatium, and leafy bract are visible, as detailed in Figs. 27–42. **20.** Ovuliferous shoot terminating in c1 and c2, emerging from a single podocarpium. Note finely extended mucros on all foliage, abundant amber, involucral leaves clasping the podocarpium, and the warty, bumpy texture of the podocarpium, which is composed of at least three expanded, fused leaves (Figs. 23, 24). **21.** Ovuliferous shoot, with clasping involucral leaves subtending basal half of a probable two-leaved podocarpium (coalified, branch axis visible), from which emerge immature c3 (arrow; also Figs. 41, 42) adjoining nearly mature c4. **22.** Ovuliferous shoot, including a podocarpium, probably of three or more leaves, with warty, bumpy texture, subtending c5 and c6. Arrow indicates a long-shoot apex of loosely aggregated leaves (also Fig. 18). **23-26.** Podocarpium details: warty, bumpy texture (Figs. 23–25); two zones of fusion joining podocarpium leaves, curving away from the axis (Figs. 23, 24, light arrows); and well-preserved, clasping involucral leaves with fine, acuminate apices (Figs. 23, 26, heavy arrows).
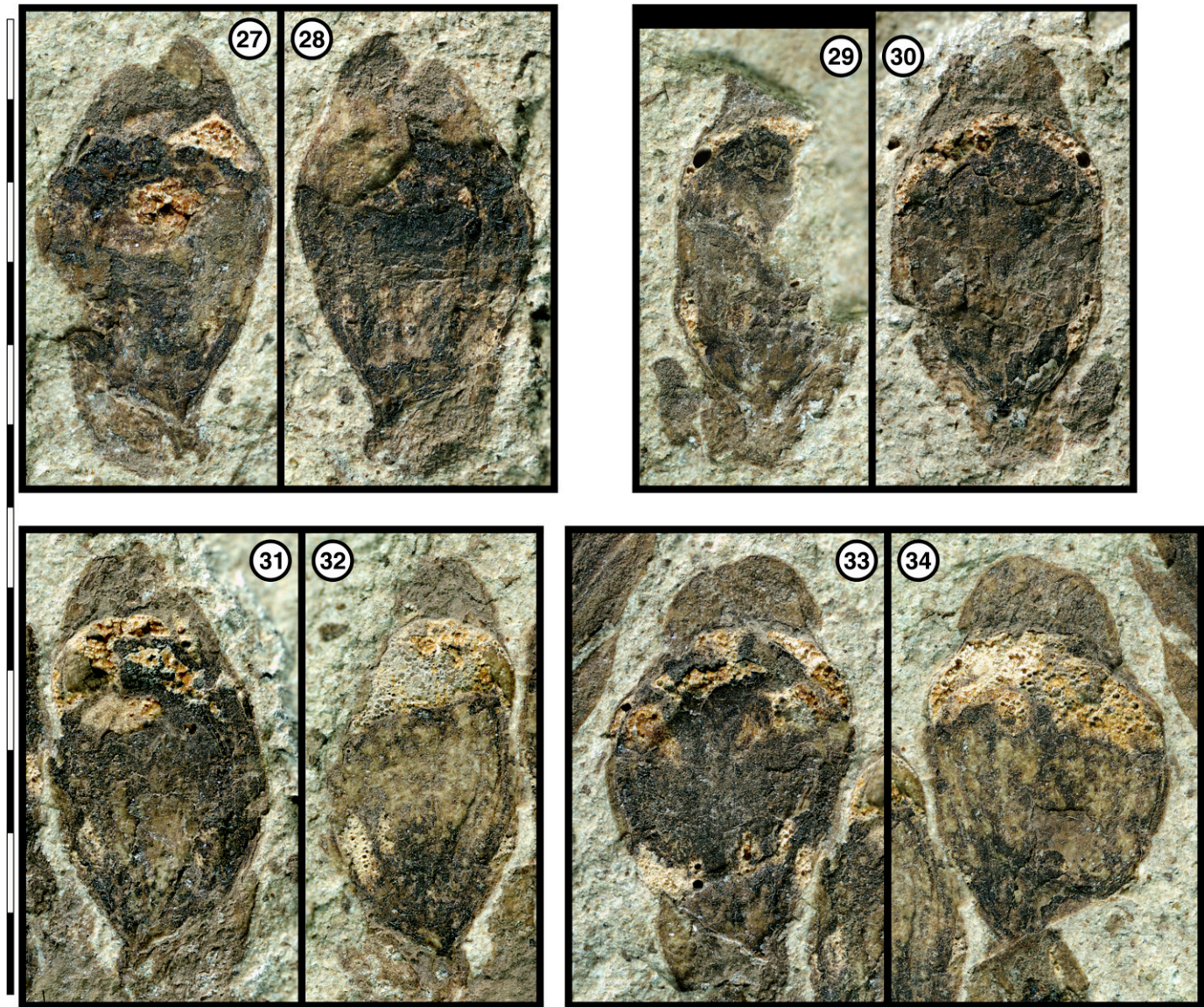
Figs. 27–42.   Holotype of *Dacrycarpus puertae* sp. nov., MPEF-Pb 4983, from Laguna del Hunco. Seed cones in part (a)–counterpart (b), left–right pairs, in approximate order of increasing size and at same scale, except Figs. 41, 42. See Fig. 18 inset for notational key. Each scale increment, black or white, equals 1 mm; scale in Fig. 41 also equals 1 mm and applies to Figs. 41 and 42 only. In all cones, the subtending podocarpium remnant, inverted ovule, resinous epimatium, and fertile bract are visible and easily distinguished: the podocarpia are bumpy in texture, and the ovules are mostly coalified and dark. The epimatia contain numerous resin ducts radiating from the base (e.g., Figs. 39–42) and many conspicuous, lightly colored amber vesicles. Amber is thickest and generally most visible in the areas immediately distal to the ovules; it is also visibly preserved along the basal and lateral margins of the ovules and in remnant patches on top of or underneath the ovules. The fertile bracts preserve with intermediate darkness, most easily seen projecting distally from the epimatia (Figs. 27–38), containing faintly visible resin ducts (Figs. 33, 34), and where the ovules and epimatia are preserved preferentially on the part (left, in this view) of the compression, leaving much of the bract visible on the counterpart (Figs. 32, 34, 40). **27, 28.** Cone c7 (also Fig. 44). **29, 30.** Cone c8. Note aborted ovule (also Fig. 45). **31, 32.** Cone c2 (also Fig. 43). **33, 34.** Cone c1 and adjacent, finely mucronate bilateral leaves. **35, 36.** Cone c6. **37, 38.** Cone c5. **39–42.** Cone c3 adjacent to base of the much larger c4 (also Fig. 21). In c3, note the dark ovule compression at base, the thick, resinous epimatium remnant distal to the ovule, and the long, acute bract apex typical of an immature cone (cf. Figs. 7, 8). The appearance of an extended bract tip in c4 (Fig. 40) is preservational: the cone is laterally flattened or deformed along its distal margin, and remnants of the true bract tip are visible distal to the ovule.

that can be determined as a long shoot, three of short shoots, and one of a possible short shoot. Geographic coordinates for LH and RP quarries not previously published (Wilf et al., 2003) are available from myself or from MEF Collections Management.

Fossil preparation and imaging—Fossil specimens were manually prepared with air scribes (mostly Paleo-Aro and Micro-Jack #2, Paleotools, Brigham City, Utah, USA), pin vises with carbide rods, and gentle air hoses to remove extraneous matrix. All detailed specimen work took place in the Paleobotany Laboratory, Pennsylvania State University, using nondestructive techniques. Reflected-light and epifluorescence microscopy were done on a Nikon SMZ-1500 stereoscope and a Nikon LV100 compound microscope (Nikon, Melville, New York, USA), sharing an X-Cite 120 epifluorescence illumination unit (EXFO Electro-Optical Engineering, Quebec City, Quebec, Canada), Nikon DXM-1200F and DS-Ri1 cameras, and Nikon NIS Elements v. 2 and 3 software. Fluorescence imaging used an Endow GFP Longpass Emission green filter: exciter HQ470/40, dichroic Q495LP BS, emitter HQ500LP, Chroma Technology Number 41018 (Chroma Technology Corp., Rockingham,
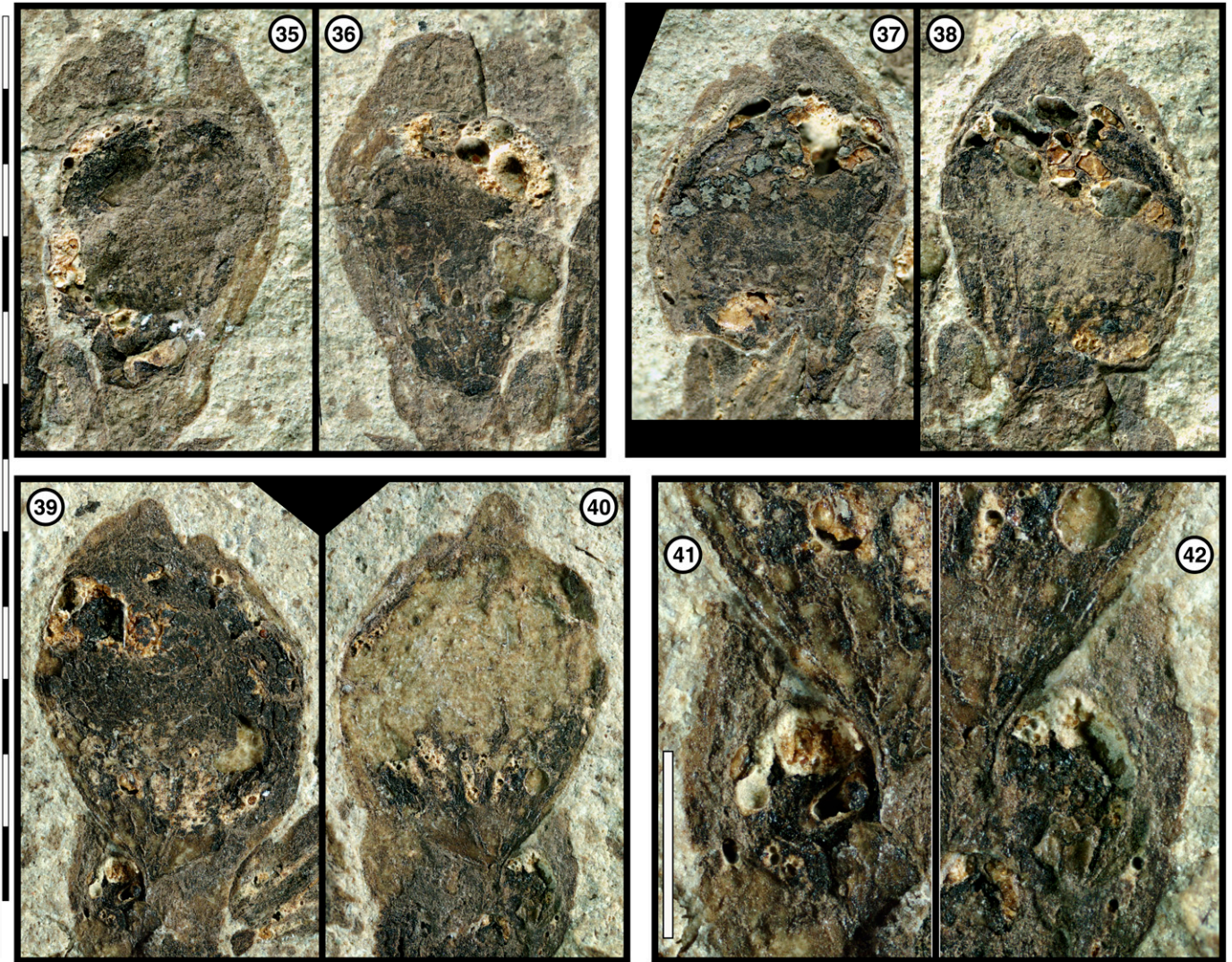
Figs. 35–42.

Vermont, USA). A Nikon D700 camera was used for most macrophotography, with 60 mm and 105 mm Micro-Nikkor macro lenses and polarizing filters. Because of uneven surfaces, high-quality images showing critical features often could not be obtained from single photographs, nor could these features be observed well at single focal planes under the microscope. Therefore, photographs were composited in many cases, especially those of fertile material, to obtain very sharp images with high depth of field (e.g., Kerp and Bomfleur, 2011). This was done both vertically, using manual *z*-stacking and the Adobe (San Jose, California, USA) Photoshop CS5 Align and Blend functions, and laterally, using the Photoshop CS5 Photomerge macro. Careful checks for artifacts were made at every step, and these occurred only very rarely. Reversible, whole-image linear processing to equilibrate color temperature, contrast, etc., was done using the Adobe Camera Raw Editor. All photographs are by the author unless otherwise noted.

Cuticle was usually coalified, including all areas where stomatal apparati might be preserved (Figs. 12, 15), or was found only in tiny, thin fragments that could not be extracted; no attempts were made following the difficulties previously encountered with better-preserved conifer cuticle from the same localities (Wilf et al., 2009). However, some epidermal cells could be observed using epifluorescence (Fig. 13), and coalified stomatal rows revealed position and orientation (Figs. 12, 15).

Status of Chilean material described by Engelhardt—Engelhardt's (1891) classic work on Paleogene floras of Chile included the original description of "*Sequoia*" *chilensis*, the basionym for *Dacrycarpus chilensis* comb. nov. Engelhardt originally received the specimens for this monograph from the famed geologist Carl Ochsenius (e.g., Ochsenius, 1888), who brought them from Chile to Germany; Engelhardt later returned them to Ochsenius. According to collection records at Senckenberg Natural History Collections Dresden, Germany, Museum of Mineralogy and Geology, Section Palaeobotany (MMG; T. Wappler, Universität Bonn, and L. Kunzmann, Senckenberg Naturhistorische Sammlungen Dresden, personal communication), in 1892 Ochsenius gave three of the pieces to Engelhardt as a gift, and Engelhardt donated these to MMG in 1894, where they remain housed. Fortuitously, this included the block containing the lectotype eventually designated by Florin (1940a) and a few other specimens (Fig. 57). However, the fate of the other "*Sequoia*" *chilensis* specimens referenced by Engelhardt (1891), as well as the great volume of other material described in that important work, is unknown, despite an energetic attempt to locate them within Germany by T. Wappler (personal communication). Additionally, Engelhardt (1905) illustrated a specimen of "*Sequoia*" *chilensis* from Curanilahue, Chile, but no material from this publication is confirmed to survive either (T. Wappler, personal communication).

Extant material and characters—The nine living species of *Dacrycarpus* were examined, photographed (using the same techniques described above), and measured from material housed at the United States National Herbarium, Smithsonian Institution, Washington, DC (US); the Australian National Herbarium, Canberra (CANB); the National Herbarium of New South Wales, Royal

Botanic Gardens, Sydney (NSW); and the National Herbarium of Victoria, Royal Botanic Gardens, Melbourne (MEL) (Appendix 1). From review of these specimens and the literature, a summary of the character states that are informative for the fossil material is presented in Table 2 and partly illustrated for extant examples (Figs. 2–8). When not otherwise cited, character discussions of living species are based on the literature cited in Table 2, especially Wasscher (1941), de Laubenfels (1969, 1988), Eckenwalder (2009), and Farjon (2010). Although work has been done to incorporate many *Dacrycarpus* species into phylogenetic analyses (Kelch, 1997, 1998, 2002; Sinclair et al., 2002; Biffin et al., 2011), there is, so far, no phylogenetic treatment involving all nine species in the genus that could provide a framework for analyzing the fossils.

SYSTEMATICS AND RESULTS

Family—Podocarpaceae Endlicher, Synopsis Coniferarum: 203 (1847).

Genus—*Dacrycarpus* (J. J. Bennett) de Laubenfels, Journal of the Arnold Arboretum 50: 315 (1969).

Species—*Dacrycarpus puertae* Wilf, sp. nov.
Dacrycarpus tertiarius (Berry) Fontes and Dutra, Revista Brasileira de Paleontologia 13: 199 (2010), cited Río Pichileufú material only.
"Species no. TY121, Coniferales, Podocarpaceae" (Wilf et al., 2005a: Table A2, citing MPEF-Pb 973, here shown: Figs. 9, 12, 13).
"Podocarpaceae" (Wilf et al., 2003: Fig. 1C, showing MPEF-Pb 973, here shown: Figs. 9, 12, 13).
Dacrycarpus? *tertiarius* (Berry) Zastawniak, Palaeontologia Polonica 55: 133 (1996), cited Río Pichileufú material only.
Podocarpus tertiarius (Berry) Florin, sect. *Dacrycarpus*, Kungliga Svenska Vetenskapsakademiens Handlingar 19: 39 (1940), cited Río Pichileufú material only.
Fitzroya tertiaria Berry, Geological Society of America Special Paper 12: 60 (1938), cited Río Pichileufú material only.

Etymology—In honor of Pablo Puerta, Head Technician of MEF and renowned field paleontologist, for his outstandingly successful efforts sustained over more than a decade so far, working with the author and many others to locate, quarry, prepare, and curate large numbers of superb fossil plant specimens in Patagonia and thus to make core contributions to paleobotany. Without Sr. Puerta's labors, much that is known would remain hidden in stone. Two Late Cretaceous dinosaur genera from Patagonia were previously named after Sr. Puerta (Novas, 1997; Novas et al., 2005). *Dacrycarpus puertae* is here the first plant taxon so defined.

Holotype—MPEF-Pb 4983a,b (Figs. 18–45), from Laguna del Hunco, Tufolitas Laguna del Hunco, early Eocene, Chubut Province, Argentina, quarry LH13 of Wilf et al. (2003), collected 7–8 December 2002 by P. Wilf, K. R. Johnson, L. Canessa, J. L. Carballido, B. Cariglino, and C. C. González.

Paratypes—Laguna del Hunco, Tufolitas Laguna del Hunco, early Eocene, Chubut Province, Argentina. From quarry LH2: MPEF-Pb 4950–4953. From LH6: MPEF-Pb 4954–4957. From LH13: MPEF-Pb 4958–4982 and 4984–4997 (see Fig. 15 for MPEF-Pb 4972; Fig. 17 for MPEF-Pb 4982; Figs. 10, 14 for MPEF-Pb 4990). From LH15: MPEF-Pb 973 (Figs. 9, 12, 13), 4998, and 5005—5008. From LH23: MPEF-Pb 4999, 5000, 5001 (Figs. 46–56), and 5002. From LH25: MPEF-Pb 5009. From LH27: MPEF-Pb 5010–5016. Float specimens, exact stratigraphic level unknown: MPEF-Pb 5003 and 5017.

Río Pichileufú, Ventana Formation, middle Eocene, Río Negro Province, Argentina. Original, historic collection, exact quarry sites unknown: the material referred to "*Fitzroya tertiaria*" by Berry (1938) and subsequently to *Podocarpus* "*tertiarius*" by Florin (1940a). Berry's (1938: pl. 12, fig. 2) illustrated specimen is USNM 40381a,b (Fig. 11), and an additional found specimen, not previously figured, is assigned USNM 543561a,b (Fig. 16). From quarry RP3: BAR 4746 and 4747. Exact quarry site unknown: BAR 5001-20.

Description—Descriptions encompass all studied material. *Branches* (Figs. 9–11, 18, 19) in distinct indeterminate long and determinate short shoots, the short shoots 11–127 mm long. *Foliage* spirally inserted, decurrent on the axis (Figs. 12, 14, 15), and strongly dimorphic (Figs. 9, 10, 16, 18, 19), consisting of bifacially flattened "adult" leaves on long shoots and bilaterally flattened "juvenile" leaves on feather-like short shoots that emerge from long shoots or, rarely, from other short shoots. Resting buds of long shoots a loose aggregation of terminal leaves overtopping the shoot apex (Figs. 22, 46, 47). All foliage with a single midvein (Figs. 12, 17), resin ducts (e.g., Fig. 47), a long, fine, mucro (Figs. 12, 14, 20), and longitudinally elongate epidermal cells (Fig. 13).
Bifacially flattened leaves (Figs. 11, 14, 18, 19) acicular, clasping the twig and recurved toward the axis (Fig. 14), or slightly spreading 0.7 to 2.9 mm from the axis (Fig. 9); maximum length per shoot 2.1–4.9 mm, maximum width per shoot 0.3–1.0 mm; mucro length 0.1–0.4 mm. *Bilaterally flattened leaves* (Figs. 9, 10, 12, 13, 15–19) twisted at the base so as to spread distichously from the axis; asymmetrical, falcate, straight to slightly apically curved; maximum length per shoot 3.1–17.4 mm, reaching maximum length at 25–80% of the short-shoot length, maximum width per shoot 0.6–2.0 mm, mucro length 0.1–0.3 mm. Stomatal bands linear, two per leaf, deployed for the full leaf length at equal distance to and parallel to midvein (Figs. 12, 15), individual stomatal complexes coalified, details not preserved. Mesophyll coalified, preserving cellular orientation perpendicular to midvein (Fig. 17).
Ovuliferous shoots (Figs. 18–22) arising from long shoots, each consisting of a subtending leafy branch, involucral leaves, a podocarpium, and seed cone(s). *Subtending branches* slightly to strongly curved, length 6.4–8.1 mm, leaves slightly spreading with maximum length per shoot 1.9–2.3 mm and an extended, fine mucro (Figs. 20, 21). *Involucral leaves* (Figs. 20, 21, 23, 26) length 2.3-2.7 mm, with an extended, fine mucro, clasping the basal half of the podocarpium. *Podocarpia* (Figs. 20–25) each consisting of two, three, or possibly more greatly expanded, fleshy leaves fused along their curved margins (Figs. 23, 24); surface distinctly warty, bumpy (Figs. 24, 25); length 5.9–6.3 mm, width 2.0-3.6 mm; some terminal leaves emerging distally as the fertile bracts of the seed cones or to enclose an aborted ovule (e.g., Figs. 29, 30, 45).
Seed cones (Figs. 18–22, 27–45) terminal, elliptical, obovate, or subrounded, deployed singly or doubly on a podocarpium, length 4.8–5.4 mm, width 2.6–3.6 mm, each consisting of fertile bract, epimatium (fertile scale), and ovule. *Fertile bracts* each emerging from podocarpium and subtending an epimatium and ovule, in full contact with and presumably fused to the epimatium, then free and projecting at the apex, apex broadly rounded (e.g., Figs. 27–38). *Epimatia* each enclosing an ovule, with numerous resin canals of variable thickness radiating from the base (Figs. 41, 42, 44), much resin preserved as vesicular amber, thickest and most prominently visible between distal

(chalazal) end of the ovule and the projecting fertile bract apex (Figs. 20, 22, 27–42), curving and narrowing proximally to enclose the micropyle (Figs. 43–45). *Ovules* (Figs. 20, 22, 27–39) inverted, curving and narrowing proximally to open onto the podocarpium, with an approximately hexagonal texture on the preserved surface; it is not clear if this is a taphonomic feature or if it represents one of the integumentary layers.

Pollen cones (Figs. 46–56) lateral or terminal, elliptic to ovate, length 2.5–3.6 mm, width 0.8–1.3 mm; receptacle short; microsporophylls numerous, spirally inserted, imbricate, and ovate, bases convex, apices acuminate and sharp-pointed, apparently mucronate. Pollen sacs and pollen not preserved.

Nomenclatural notes, **Dacrycarpus puertae** *sp. nov.—*There are several confusing issues regarding the vegetative branches from Río Pichileufú (Figs. 11, 16) that Berry (1938) assigned to "*Fitzroya*" *tertiaria* Berry 1928, whose holotype, USNM 37859, comes from Río Chalia in Santa Cruz, Argentina. The holotype, and Berry's (1928: pl. 2, figs. 2–4) drawings of it, show distinctly ovate, imbricate, bifacially flattened conifer foliage that in no way resembles the acicular, clasping, bifacial leaves (Fig. 11) nor the distichously spreading bilateral leaves (Fig. 16) of the Río Pichileufú specimens, which he misidentified (A. Iglesias, Universidad Nacional de La Plata, P. Wilf, joint personal observation). It is also noteworthy, as discussed by Frenguelli (1953, who further illustrated the Río Chalia species), that the Río Chalia beds are not Cenozoic but rather Late Cretaceous in age, and they are now referable to the Cenomanian Mata Amarilla Formation (Iglesias et al., 2007; Varela et al., 2012), which is more than twice as old as the Río Pichileufú flora.

Florin (1940a: p. 39) correctly noted that the Río Pichileufú "*Fitzroya tertiaria*" designated by Berry (1938) represented Podocarpaceae rather than Cupressaceae, noted its similarity to adult foliage of *Podocarpus* (now *Dacrycarpus*) *dacrydioides*, and revised it to the new combination *Podocarpus* "*tertiarius*" (Berry) Florin, sect. *Dacrycarpus* (that section is now synonymous with the genus *Dacrycarpus*: de Laubenfels, 1969). However, by making a new combination rather than a new species, and thus continuing to use the 1928 Río Chalia basionym, Florin retained Berry's identification error. Florin stated that he agreed with Berry in considering the Río Píchileufú and Río Chalia specimens to represent the same taxon, and like Berry he was unaware of the significant age disparity.

Decades later, the combinations *Dacrycarpus*? "*tertiarius*" (Berry) Zastawniak and *Dacrycarpus* "*tertiarius*" (Berry) Fontes and Dutra were fixed on the same Berry 1928 basionym, "*Fitzroya*" *tertiaria*, and applied to Paleogene conifer material from King George Island and Seymour Island, Antarctica (Zhou and Li, 1994; Doktor et al., 1996; Fontes and Dutra, 2010). Of relevance here, these combinations also cited the material from Río Pichileufú and therefore retained the erroneous species epithet for those specimens that Berry (1938) and Florin (1940a) had applied (there are no convincing macrofossil records of *Dacrycarpus* from Antarctica so far; for example, some of the Antarctic material, consisting of bifacial, ovate foliage, does not have the leaf morphology expected in *Dacrycarpus*, e.g., acicular bifacial leaves as in all living species).

The new species designation, *Dacrycarpus puertae*, is needed to separate the Eocene material presented here from the Cretaceous holotype of "*Fitzroya*" *tertiaria* (Berry, 1928), which clearly represents a different taxon. The new species is motivated first and foremost because attached cones (of both sexes) and foliage are preserved, a first for the fossil record of *Dacrycarpus*.

The additional sterile material from Laguna del Hunco records a sufficient range of variation (e.g., Figs. 9, 10, 15), encompassing that seen in the holotype, that it may be conservatively placed in the same single taxon as the fertile material. Including the younger and entirely vegetative Río Pichileufú specimens in the same species could be contested, but I observed no differences from the Laguna del Hunco material, and a single name is used to avoid proliferation and to be consistent with the large number of other species that are shared between these environmentally similar, caldera-lake sites (Berry, 1938; Wilf et al., 2005a, 2009).

Species—Dacrycarpus chilensis (Engelhardt) Wilf, comb. nov.

Podocarpus inopinatus Florin, Kungliga Svenska Vetenskapsakademiens Handlingar 19: 15 (1940).

Podocarpus engelhardti Berry, Geological Society of America Special Paper 12: 63 (1938), in part (Engelhardt's cited Chilean material only).

Sequoia chilensis Engelhardt, Bemerkungen zu Chilenischen Tertiärpflanzen: 71 (1905).

Basionym: *Sequoia chilensis* Engelhardt, Ueber Tertiärpflanzen von Chile: 646 (1891).

*Lectotype—*As designated by Florin (1940a: p. 15): "the specimen illustrated in Engelhardt 1891, Pl. II; Fig. 15 (right hand figure). Dep. of Coronel, Coronel. Eocene" (Chile), MMG PB SAT 1e (Fig. 57, arrow).

*Syntypes—*MMG PB SAT 1b–d, Coronel, Chile (Fig. 57). These three fossil short shoots that occur on the same block as the lectotype, illustrated by Engelhardt (1891: pl. 2, figs. 14, 15 left) as "*Sequoia*" *chilensis*, comprise the only other surviving protologue material that can be confirmed (see Materials and Methods). The specimens are syntypes because no holotype was designated in the protologue (Engelhardt, 1891), and that status continues even though Florin (1940a) later designated a lectotype, absent any formal provision for changing their status (McNeill et al., 2006). If eventually found, any of the remaining protologue specimens illustrated by Engelhardt (1891: pl. 2, figs. 11–13) would automatically be syntypes.

*Additional material—*The specimens designated and illustrated by Florin (1940a: p. 15), from Curanilahue, Lota, Minas Conquil, and Peumo, Chile, held at the Swedish Museum of Natural History, Stockholm (S): this material, collected by P. Dusén in 1896 and T. G. Halle in 1908, has all been verified and documented with recent photographs (S. McLoughlin, Swedish Museum of Natural History, personal communication). The specimen numbers of figured material (Florin, 1940a) are S160125, S160314, S160315 (designated by Florin as a "hypotype," having no nomenclatural status), S160664-01, S160664-02, S165205-02, and S165211. Six specimens housed at USNM that were collected by E. W. Berry from Curanilahue (Ríos Mine), Lota, and near Coronel (Puchocho Mine), Chile but not figured in his 1922 monograph, though the species is mentioned therein as "*Sequoia*" *chilensis* (Berry, 1922): USNM 545362–545367.

Nomenclatural notes, **Dacrycarpus chilensis** *comb. nov.—*In summary, Engelhardt's basionym is here restored in a new combination under *Dacrycarpus*. The original assignment was to "*Sequoia*" *chilensis* (Engelhardt, 1891). Through various publications over nearly five decades reviewed by Florin (1940a),

paleobotanists, including Berry, considered these Chilean fossils as good evidence that *Sequoia* once occupied South America (no reliable fossils indicate that this ever occurred: Stockey et al., 2005).

Later, Berry (1938, p. 63) regarded Engelhardt's (1891, 1905) "*Sequoia*" *chilensis* specimens as representing *Podocarpus*, and he transferred the Chilean material to the new species "*Podocarpus*" *engelhardti* Berry, which also included certain specimens from Río Pichileufú (Berry, 1938). Soon after, Florin (1940b) recognized that the "*P.*" *engelhardti* specimens from Río Pichileufú have distinctive features of *Acmopyle*, especially the very large leaves, and transferred them to the new combination *Acmopyle engelhardti* (Berry) Florin, while relocating Engelhardt's fine-needled Chilean material to the new species *Podocarpus inopinatus* Florin, Section *Dacrycarpus*. Both "*P.*" *engelhardti* and *P. inopinatus* were designated to avoid conflict with extant *Podocarpus chilinus* Rich., now synonymous with *P. salignus* D. Don.

Florin (1940a) described *Podocarpus inopinatus* using Engelhardt's (1891, 1905) works, from which he designated a lectotype (Fig. 57), and first-hand using several additional, more complete specimens from Swedish expeditions to Chile, some of which yielded excellent cuticle slides. He stated, with robust support from his superb descriptions and illustrations, that this species, based predominantly on short shoots of bilateral leaves and known entirely from Chile, "undoubtedly belong[s] to sect. *Dacrycarpus*" (Florin, 1940a: p. 16). When *Dacrycarpus* was later elevated to generic status (de Laubenfels, 1969), the original conflict for the species epithet became moot. Thus, Engelhardt's basionym is here restored by priority in the present new combination, *Dacrycarpus chilensis* (Engelhardt).

In a synoptic compilation of southern hemisphere conifer fossils, Hill and Brodribb (1999: p. 658) listed the Chilean fossils studied by Engelhardt and Florin as "*Dacrycarpus inopinnatus* (Florin) Greenwood," referring to Greenwood (1987). In addition to the misspelling and the localities being listed as in Argentina (rather than Chile), Greenwood never made the stated combination. The name *Podocarpus inopinatus* has also been applied to several ?latest Cretaceous (more likely Paleocene) to Eocene fossils from Chile that are not reviewed here, though all merit reinvestigation (Menéndez, 1972; Troncoso, 1992; Hünicken, 1995; Suárez et al., 2000; Troncoso et al., 2002).

The new combination *D. chilensis* is needed to stabilize the status of the important Chilean material cited and illustrated by Engelhardt (1891) and Florin (1940a), which represents the first *Dacrycarpus* fossils reported from South America. Due to the consistently smaller leaf dimensions in *D. chilensis* than in *D. puertae* (as reported by Florin and confirmed on the USNM specimens and on photographs), the occurrences of well-preserved, attached reproductive structures only in *D. puertae*, and the very different paleoenvironments, namely coastal swamps for *D. chilensis* and volcanic calderas for *D. puertae* (Collao et al., 1987; Aragón and Mazzoni, 1997), it is logical to maintain *D. chilensis* and *D. puertae* as separate species. Thus, my proposal is for two fossil species of *Dacrycarpus* in South America, *D. puertae* sp. nov., all recognized material being from Eocene caldera-lake deposits of Argentina, and *D. chilensis* (Engelhardt) comb. nov., all recognized material being from Eocene coastal swamp deposits of Chile.

DISCUSSION

***Affinities of* Dacrycarpus puertae *sp. nov.*—**—*Dacrycarpus puertae* can be placed with high confidence in Podocarpaceae and *Dacrycarpus* due to preservation of numerous apomorphic characters. Placement in Podocarpaceae is clear due to several features restricted to the family (though not present in all genera), including bilaterally flattened leaves with spiral phyllotaxy and distichous deployment, and especially the solitary, reduced seed cones, each having a single inverted ovule surrounded by an epimatium and inserted on a single fertile bract, emerging from a distinctly swollen, fleshy receptacle of fused leaves.

Assignment to *Dacrycarpus* can be made from either the foliage or the seed cones, which are attached in the holotype (Figs. 18–45). The most distinctive foliar characteristic, unique to *Dacrycarpus* among living podocarp genera, is the sharp dimorphism into long shoots with bifacially flattened "adult" leaves and short shoots with expanded, bilaterally flattened, distichous "juvenile" leaves (Figs. 9, 10, 18, 19; de Laubenfels, 1969). The only genera with similar short shoots are *Acmopyle*, and to a much lesser extent *Falcatifolium*, but these entirely lack the bifacially flattened leaf type (though scale leaves are present). Moreover, extant *Acmopyle* bilateral leaves are typically much wider than those of *Dacrycarpus* (1.5–4.0 mm vs. 0.5–2 mm; Table 2 and sources cited therein), and this difference holds for fossil *Acmopyle engelhardti* (under separate study) and *Dacrycarpus puertae* at LH and RP, usually allowing them to be distinguished when only a short shoot is preserved (Fig. 19). Additional foliar features of the fossils that strongly associate them with *Dacrycarpus* include: resting buds a loose cluster of leaves overtopping the long-shoot meristem (Figs. 22, 46, 47), and stomatal bands generally deployed in linear pairs at equal distance from the midvein (Figs. 12, 15).

The terminal seed cones on short, curving branches, which erect the ovules and thus reveal the approximate (due to compression) life orientation of the holotype, are stereotypical for *Dacrycarpus* (Figs. 18–22). A warty podocarpium (e.g., Figs. 23–25) is only found today in *Dacrycarpus* and *Acmopyle*, but *Dacrycarpus* and the fossils share many attributes not found in *Acmopyle*, including: branches subtending the seed cones borne on long shoots and bearing little modified leaves (Figs. 6, 18–22), in contrast to the short subtending branches in *Acmopyle* that emerge from the tips of short shoots and bear reduced, scaly leaves; distinct involucral leaves (Figs. 4, 21, 26), lacking in *Acmopyle*; a well-fused podocarpium generally of 2–5 leaves (Figs. 3, 20–24), in contrast to the *Acmopyle* podocarpium of 5–8 leaves that typically remain separately visible externally; the typical presence only in *Dacrycarpus* of aborted ovules emerging from the podocarpium (Figs. 3, 4, 29, 30, 45); and a leafy bract that extends well beyond the ovule during development, as seen in *Dacrycarpus* and not *Acmopyle* (Figs. 4, 7, 8, 27–42). The sizes of the cones, and their increasingly rounded shape with increasing size, are also consistent with living *Dacrycarpus* (Figs. 27–42; Table 2), whereas *Acmopyle* cones are distinctly larger.

The typical bract crest of *Dacrycarpus* is not preserved here: the bract crest in living species runs down the midline of the bract, where it fuses to the epimatium (Figs. 4, 7, 8), and thus would only be expected in fossil cones preserved in precisely lateral view, which is not the case here (Figs. 18, 19). Also of note, in most mature *Dacrycarpus* cones, the projecting bract apex is reduced to a small beak (Figs. 7, 8), whereas the fossils
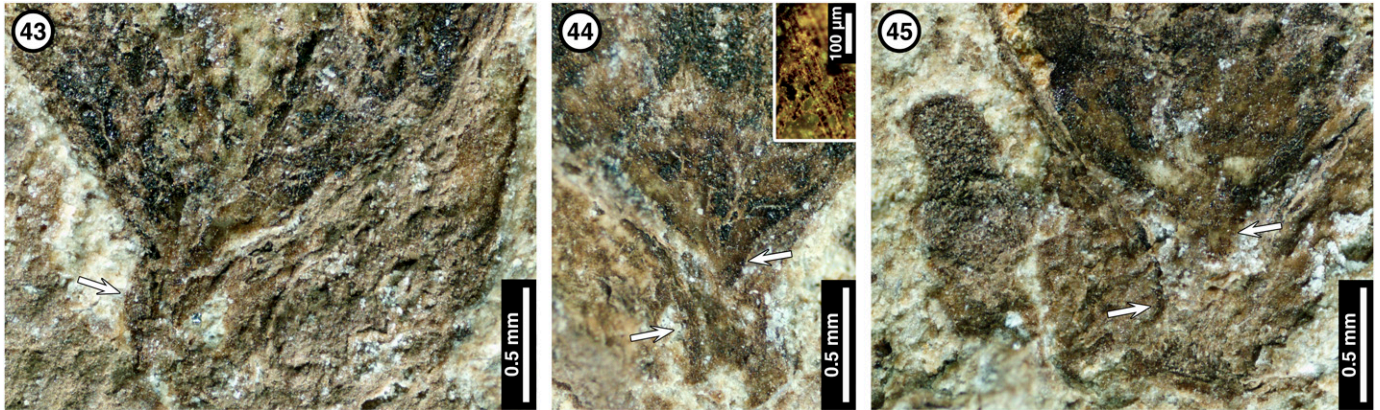
Figs. 43–45.   Holotype of *Dacrycarpus puertae* sp. nov., MPEF-Pb 4983a, from Laguna del Hunco. Selected details of seed-cone micropylar areas. Fig. 44 inset, epifluorescence. See inset to Fig. 18 for notational key. **43.** Cone c2 (Fig. 31) on its warty podocarpium, showing the basal epimatium (arrow) curving to surround the micropylar area. **44.** Cone c7 (Fig. 27) on its podocarpium, showing curving base of epimatium (lower arrow) subtending micropyle portion (upper arrow) and numerous fine, radiating resin ducts, enlarged under epifluorescence (inset). **45.** Cone c8 (Fig. 29) on its podocarpium, showing curving basal epimatium (lower arrow) enclosing micropyle portion (upper arrow) and numerous fine, radiating resin ducts; aborted ovule emerging at left.

(as expected due to the fact of their preservation prior to abscission), all appear to be immature to submature and thus preserve a broader, projecting bract apex that is stereotypical for immature cones (Figs. 7, 8, 27–38) (de Laubenfels, 1969). Although it is tempting to consider the narrowed apex preserved in one seed cone (Fig. 40) to represent a projecting beak, this is instead a preservational feature due to lateral compression at the apex and the loss of some projecting bract tissue.

The fossil pollen cones are consistent with living *Dacrycarpus* but have a generalized morphology that is not diagnostic. However, they are attached to branches bearing the typical *Dacrycarpus* bifacial foliage, including a large, loosely aggregated, resting bud (Figs. 46, 47).

As summarized in Table 2, the fossil *D. puertae* preserves most of the characters that are used to discriminate among the nine living species of *Dacrycarpus* (e.g., Wasscher, 1941; de Laubenfels, 1969; Eckenwalder, 2009; Farjon, 2010). Of these, by far the greatest similarity is to *D. imbricatus*, the most widespread and large-leaved species, typically found in low to middle montane tropical rainforests (Table 2), at MAT of 18 ± 4.3°C, CMMT of 11.7 ± 4.6°C, and MAP of 2569 ± 630 mm (Biffin et al., 2011). Several character states are restricted to *D. dacrydioides* and *D. imbricatus*, including distinct adult leaves that usually clasp the twig tightly, thus accentuating the sharp break between juvenile and adult foliage, and a large podocarpium (e.g., Figs. 9-10, 14; though the life dimensions may have been somewhat altered by saturation and compression during preservation). The large bilateral leaf dimensions of the fossils are shared with *D. imbricatus*, the second largest being *D. kinabaluensis* (which shares relatively few other characters with the fossils), whereas *D. dacrydioides* bilateral leaves are much smaller (Table 2). Even omitting a single fossil specimen with bilateral leaf length >17 mm, there are several more with leaf length >10 mm and one of 13.9 mm, still exceeding all living species other than *D. imbricatus* and *D. kinabaluensis*. In addition, the prolonged, fine mucro found on all foliage forms in the fossils is typical of *D. imbricatus* (Figs. 12, 14, 20; Wasscher, 1941; de Laubenfels, 1969), and several additional characters observed in the fossils are shared with *D. imbricatus* and other species (Table 2), notably including obligately distichous juvenile leaves and involucral leaves that clasp the base of the podocarpium (Figs. 21, 23, 26). The only observable difference between *D. puertae* and *D. imbricatus* is very minor and may be due to preservation: the leaves of the branches subtending the fossil cones are very slightly shorter (by <1 mm) than is currently recorded for the living species (Farjon, 2010). Despite the numerous similarities of its preserved characters to living *D. imbricatus*, *D. puertae* is presented as a separate species because a large amount of other whole-plant data is not yet known. This logic was recently applied to the fossil *Papuacedrus prechilensis* from LH and RP, which has no observed differences from living *Papuacedrus papuana* (Wilf et al., 2009).

Of the four varieties of *D. imbricatus*, *D. puertae* most closely resembles *D. imbricatus* var. *curvulus* (Miquel) de Laubenfels (Fig. 4), which is found on volcanic soils in high-relief environments of western Indonesia (Wasscher, 1941; de Laubenfels, 1969, 1988). This variety has, like the fossils (de Laubenfels, 1969, 1988; Eckenwalder, 2009; Farjon, 2010): adult leaves up to 1 mm wide (var. *curvulus* and var. *robustus*), the other two varieties being narrower; adult leaves usually clasping the twig tightly (var. *curvulus* and var. *imbricatus*); and involucral leaves clasping the base of the podocarpium, the other three varieties having spreading involucral leaves, or if clasping (var. *robustus*), being considerably longer than those observed in the fossils. However, *D. puertae* does not appear to have the characteristic curving, drooping branches of var. *curvulus* (Wasscher, 1941).

Dacrycarpus fossil record, implications—*Dacrycarpus puertae* is by far the most complete representation of its genus in the fossil record, strongly validating evolution of the *Dacrycarpus* crown group in Gondwana by the Eocene. Abundant apomorphic features of the leaves and cones of the living genus are found in a single fossil specimen, the holotype (Figs. 18–45). This specimen is the first ever found preserving the unique seed cones, emerging from podocarpia that remained swollen in, or were rehydrated in, the aqueous preservational environment, remaining much more true to life dimensions (Figs. 2, 3) than those preserved shrunken on herbarium sheets (Figs. 4, 6–8). For this remarkable preservation of such delicate structures to have occurred, the source tree for the holotype presumably
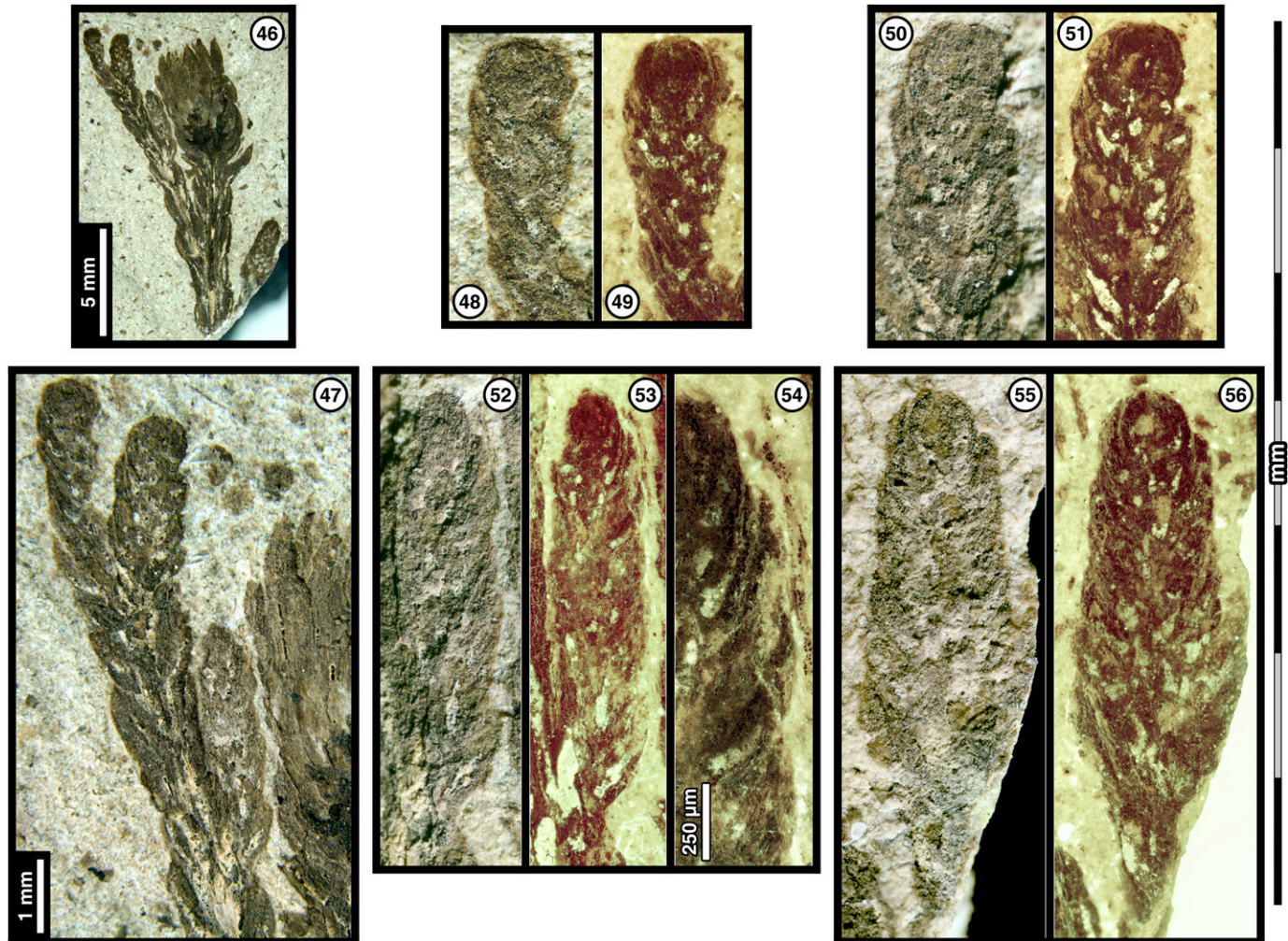
Figs. 46–56.　*Dacrycarpus puertae* sp. nov., MPEF-Pb 5001, from Laguna del Hunco, quarry LH23. Specimen with four pollen cones (pc; here pc1–4, left to right in Fig. 46) attached to characteristic bifacial foliage, including a large apical resting cluster of loosely aggregated leaves; pc1 and pc4 are apparently terminal, whereas pc2 and pc3 are lateral. All cones and leaves show abundant amber. Scale bar at right (each increment is 1 mm) applies to all panels except those with separate scale bars. Figs. 48–49, 50–51, 52–53, and 55–56 are identical view pairs under reflected light and epifluorescence, respectively. Fig. 54, also epifluorescence. **46.** Full specimen. **47.** Detail of pc1–3 and resting leaves. **48–49.** Details of pc1. **50–51.** Details of pc2. **52–54.** Details of pc3, Fig. 54 showing closeup of well-preserved microsporophylls from cone upper right. **55–56.** Details of pc4.

grew in very close proximity to, and probably overhanging, the Eocene caldera lake. Another specimen is the first record of *Dacrycarpus* pollen cones attached to vegetative branches (Figs. 46–56) and is much older than the dispersed *Dacrycarpus* pollen cones from the Miocene Elands locality in New South Wales (Hill and Whang, 2000). The Argentine foliar material lacks preservation of stomatal complexes, though the coalified remnants preserve the characteristic deployment pattern of the stomata in two lines parallel to the midvein (Figs. 12, 15).

The Australian fossil record of *Dacrycarpus* (Table 1), while prolific and impressive, in my view is in need of some revision because stomatal configuration has been relied on to define some fossil species whose foliar macromorphology does not closely resemble the living genus (see also Pole, 1998). The stomatal configuration typical of *Dacrycarpus* is certainly distinctive (Florin, 1931, 1940a; Wells and Hill, 1989b; Pole, 1998), but the fact that it appears in fossil foliage that does not fit the morphology of extant *Dacrycarpus* suggests that it may be a plesiomorphic character and thus insufficient for generic

diagnosis in the absence of suitable corroborative data (Pole and Vajda, 2009). Moreover, the stomatal configuration itself is prone to misinterpretation, as seen in several examples noted by Pole (1998) and others.

Paleoenvironmental implications—The presence of modern-aspect *Dacrycarpus* in Eocene Patagonia strongly corroborates the evidence for high-rainfall, possibly montane paleoenvironments (Wilf et al., 2009). All living species of *Dacrycarpus* are characteristically associated with very wet habitats, including wet to waterlogged soils and many types of montane, and some lowland, rainforests (Kirk, 1889; Wasscher, 1941; de Laubenfels, 1969). Richard's (1832, p. 359) original description of *D. dacrydioides*, the tallest tree species in New Zealand and the type species of the genus, noted "un arbre magnifique, qui se plaît surtout dans les lieux bas et humides, le long des torrents." Similarly, de Laubenfels (1978) began his account of *Dacrycarpus* with: "trees or shrubs of very humid environments." The simple fact that *Dacrycarpus* has one of

Fig. 57. Lectotype and surviving syntypes of *Dacrycarpus chilensis* (Engelhardt) comb. nov., from Coronel, Chile, figured by Engelhardt (1891: pl. 2, figs. 14, 15), MMG PB SAT 1b-e. Photograph by L. Kunzmann. Arrow indicates the lectotype designated by Florin (1940a), MMG PB SAT 1e; the other short shoot to its immediate left is MMG PB SAT 1d; this pair was originally illustrated by Engelhardt (1891: pl. 2, fig. 15), in this orientation. The pair of short shoots at slab top right, from left to right, are MMG PB SAT 1b and 1c, both illustrated by Engelhardt (1891: pl. 2, fig. 14), in this orientation. Also visible are an uncatalogued, fragmentary short shoot at center, and angiosperm leaves.

the most extensive fossil records of any Southern conifer genus (Table 1; Hill and Brodribb, 1999) indicates its occupation through time of wet, topographically low areas that favor fossil preservation.

Experimental data firmly support interpretations of abundant moisture where fossil *Dacrycarpus* is found (Fountain et al., 1989; Brodribb and Hill, 1998, 2004). *Dacrycarpus* and *Acmopyle* have the lowest physiological drought tolerance known among the southern conifers, and areal decrease of high- and aseasonal-rainfall areas over time presumably was the principal reason these genera became extinct in both Patagonia and Australia (Brodribb and Hill, 1998). The seed of extant *D. dacrydioides* and its podocarpium, which maintains a water supply for the seed before and after abscission, both hold extremely high water content throughout a seasonal crop of ca. 800 kg of seeds per tree, and seed viability drops precipitously when water content lowers (Fountain et al., 1989). This massive, sustained investment of water into reproductive tissues occurs in a trade-off with the transpirational needs of the plant (Fountain et al., 1989) via the moisture-sensitive, expanded, single-veined leaves (Brodribb and

Hill, 1998), all of which does not appear possible with any significant interruption of the water supply. Many of the fossil bilateral leaves of *D. puertae* show mesophyll compressions indicating cellular long-axis orientation perpendicular to the midvein (e.g., Fig. 17), such that water transport from midvein to margin took place through modified mesophyll tissue at high resistance, as in *D. imbricatus* (T. Brodribb, personal communication 2010).

It is noteworthy that Florin (1940a: p. 17), partly on the basis of leaf size, compared *D. chilensis* (then *Podocarpus inopinatus*) most closely to *D. dacrydioides* and specifically pointed out that the *D. chilensis* leaves (unlike *D. puertae*) were too small to support affinity to *D. imbricatus*. *Dacrycarpus dacrydioides* is most abundant below 500 m elevation, in wet substrates (Richard, 1832; Wardle, 1974; Eckenwalder, 2009) comparable to the paleoenvironment of *D. chilensis* as also noted by Florin (Collao et al., 1987).

On the other hand, the paleoenvironments of *D. puertae* at LH and RP would have included much better drainage due to the relief of the caldera rim, and probably at least moderate elevation, as suggested by other living analogs of the fossils (Wilf et al., 2009) and the available geologic evidence (Pankhurst et al., 1999; Thomson, 2002; Ziegler et al., 2003; Aragón et al., 2011). This is consistent with *D. imbricatus*, which is notably successful on rapidly weathering, montane, volcanic soils (de Laubenfels, 1988).

Based on the other fossils found at Laguna del Hunco quarry LH13, where it is most common, *D. puertae* grew in association with a rich variety of other conifer groups that today are most characteristic of montane rainforests, including *Acmopyle*, *Podocarpus*, *Retrophyllum*, *Papuacedrus*, and *Araucaria* sect. *Eutacta* (Wilf et al., 2005a, 2009). The rainforest associations (also including extremely diverse angiosperms) appear to have stood alongside areas that were recently cleared by volcanic activity, dominated by *Eucalyptus* (Gandolfo et al., 2011). Many of the conifer taxa today produce canopy dominant and emergent trees. It is likely that very tall forests, shading a rich understory, were present in areas of the caldera experiencing intervals of volcanic quiescence.

Biogeographic and evolutionary implications—*Dacrycarpus puertae* is a case study of the extreme distances and latitudinal shifts seen in Gondwanan biogeography. The diagnostic fossil reproductive structures broadly validate the foliar record (Table 1) and thus an ancient distribution of *Dacrycarpus* by the Eocene at least from Patagonia to southeast Australia across a well-forested Antarctica. Today, four species occur on the Asian side of Wallace's Line (Table 2), and *D. imbricatus* is the most widely distributed, occurring over a 10 000 km distance from northern Burma (ca. 27°N latitude) to Fiji. Thus, *D. puertae* represents the first significant Asian link for the Patagonian fossil floras, while also being a robust Australasian component like several previously studied taxa.

Additional data on the history of the *Dacrycarpus* lineage come from the temporally and spatially widespread palynomorph *Dacrycarpites australiensis* Cookson and Pike (identical to that produced by living *Dacrycarpus*), which is reported from the Campanian to Maastrichtian of the Antarctic Peninsula, southeastern Australia, and New Zealand (Dettmann and Thomson, 1987; Dettmann and Jarzen, 1990; Macphail et al., 1994). I also note a possible precursor macrofossil species from the Early Cretaceous Baqueró Group in Patagonia: *Trisacocladus tigrensis*, comprised of leafy shoots attached to ovuliferous

structures and to male cones with pollen, and which has many noted similarities to *Dacrycarpus*, *Dacrydium*, and *Podocarpus* (Archangelsky, 1966; Baldoni and Taylor, 1982). Since the Eocene, the Patagonian wet, frost-free biome was lost through cooling and eventual erosion of possible elevated areas that had orographic rainfall, prior to the major Miocene uplift of the current southern Andes. Antarctica became completely inhospitable, and southern Australia cooled and dried while the continent moved far to the north. The youngest records of *D. australiensis* pollen from areas where *Dacrycarpus* is now extinct are from the Miocene for Patagonia (Barreda, 1996), from the late Eocene for East Antarctica (Truswell and MacPhail, 2009), and from the Pleistocene for Australia (e.g., Sniderman et al., 2007). Palynological occurrences at tropical latitudes begin in the Miocene (New Guinea: Khan, 1976) and show crossing of Wallace's Line into the Celebes Sea area and Borneo by the late Pliocene, possibly aided by local island uplifts at the time (Muller, 1966; van der Kaars, 1991; Morley, 2002).

The extensive modern distribution of *Dacrycarpus* is presumably attributable in large part to bird dispersal, especially via the brightly colored (typically orange, red, or purple in living species), edible, succulent podocarpium. Although the few known living consumers mostly have limited ranges (Beveridge, 1964; Beehler, 1983; Fountain et al., 1989; Robertson and Hackwell, 1995; Mill, 2003), significant animal dispersal must have occurred given the long periods of time available, and single bird dispersals of other taxa have been credited with major range expansions (Popp et al., 2011). There is some historical resonance because Wallace's Line originally derived from observations of large differences in avifauna on either side (Wallace, 1860).

Further, Biffin et al. (2011) attributed Cenozoic diversifications of nine living podocarp genera with flattened foliage (including *Dacrycarpus*) primarily to competition with angiosperms. However, the role of birds deserves much more study. Most of the podocarp genera with flattened foliage are primarily bird-dispersed (de Laubenfels, 1988), and the rapidly improving bird-fossil record shows no evidence for capable lineages until well after the end-Cretaceous extinction (e.g., Clarke et al., 2005; Longrich et al., 2011; McKellar et al., 2011). Moreover, there is also no fossil evidence until the Cenozoic for very large, fleshy podocarpia as seen here (Leslie, 2011), and a broader, long-noted, paleobiological pattern shows significant post-Cretaceous increases in specialized, frugivorous lineages of mammals and birds as well as angiosperm fruit and seed size (e.g., Wing and Tiffney, 1987). Thus, it seems likely that the combination of flattened foliage and fleshy reproductive tissues arose via adaptations to a suite of factors additional to possible angiosperm competition, such as the widespread southern rainforest environments of the Paleogene, which originally supported both these water-demanding traits, seasonally variable light at middle and high latitudes, the evolution of suitable animal dispersers, and large-scale ecological shifts following the end-Cretaceous extinction.

The famously warm global temperatures of the Eocene featured mild winters and thermophilic biota occurring well into high latitudes of both hemispheres (e.g., Estes and Hutchison, 1980; Greenwood and Wing, 1995; Zachos et al., 2001). Floral and faunal migrations at this time are well known across the warmed northern high latitudes (Gingerich, 1989; Manchester, 1994, 1999; Bowen et al., 2002; Smith et al., 2006), often followed by lineage retreat to much lower latitudes with cooling and regional drying. The Eocene plant occurrences from Patagonia provide abundant evidence that a similar phenomenon

occurred across Gondwana and suggest that the faunal record should be further explored for evidence of this pattern (Gómez et al., 2011). So far, although several mammalian lineages have been found from Eocene sediments both in Patagonia and the Antarctic Peninsula (Woodburne and Zinsmeister, 1984; summarized by Sigé et al., 2009), the relevant fossil record from Australia is very limited in comparison to the plant data (Beck et al., 2008; Megirian et al., 2010).

Conclusions—I report *Dacrycarpus* compression fossils from Eocene caldera-lake beds of Patagonia, Argentina, and assign them to *Dacrycarpus puertae* sp. nov. Nearly all material is vegetative branches, but a single specimen preserves eight seed cones in several developmental stages, attached to the characteristic dimorphic foliage and comprising the first fossil record of the delicate, specialized seed-cone structures of *Dacrycarpus*. A second specimen includes four pollen cones attached to a vegetative branch, the first record of attached pollen cones for the genus. I also propose *Dacrycarpus chilensis* (Engelhardt) comb. nov. for the Eocene Chilean material reported by Engelhardt (1891, 1905) and Florin (1940a). The most similar living species to *D. puertae* is tropical montane *D. imbricatus* (Burma to Fiji), whereas *D. chilensis* closely matches *D. dacrydioides* (Florin, 1940a), a tall lowland species restricted to New Zealand.

Living *Dacrycarpus* is characteristically associated with, and physiologically limited to, extremely wet habitats, and thus its presence strongly corroborates the hypothesis of rainforest environments in Patagonia during the Eocene (Morley, 2000), supporting the high species richness found there (Wilf et al., 2009). *Dacrycarpus puertae* grew on the margins of an ancient, possibly montane caldera-lake system, where it probably occupied slopes and ridges with rapidly weathering volcanic soils. *Dacrycarpus* and the associated conifer groups from the Argentine fossil sites are most characteristic of montane rainforests with tall canopies.

The findings of attached, diagnostic reproductive structures and dimorphic foliage validate the presence of modern-aspect *Dacrycarpus* at middle latitudes of Gondwana during the Eocene, presumably extending across Antarctica as well. *Dacrycarpus* now thrives over a vast, mostly tropical range on both sides of Wallace's Line, to ca. 27°N latitude and 18 000 km from the fossil sites in Patagonia, and bird dispersal is presumably a major factor contributing to this large range. Thus, *D. puertae* represents the first significant Asian link for the Patagonian fossil sites, especially because of its close resemblance to *D. imbricatus*. *Dacrycarpus puertae* further contributes to the array of taxa found as Eocene fossils in both Patagonia and Australia that are now extant in Australasia, indicating extensive biogeographic connections across high latitudes during this globally warm interval that can be directly compared to long-observed northern hemisphere floral and faunal continuity and biotic migrations across the Eocene Arctic.

Its extraordinary and well-recorded history, and its importance as a reliable indicator of rainforest environments through time, establish *Dacrycarpus* as a biogeographic icon deserving of intensified study as well as conservation focus for the most rare species and vulnerable populations. In addition to paleobotanical work, it seems certain that new, detailed molecular (Su et al., 2010), physiological, and ecological data from the living species, varieties, and populations of *Dacrycarpus* will yield important insights.

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Appendix 1. Herbarium vouchers seen.

Taxon. **COUNTRY. Region:** *voucher*, locality, year, herbarium/herbaria. CANB = Australian National Herbarium, Canberra, MEL = National Herbarium of Victoria, Royal Botanic Gardens, Melbourne, NSW = National Herbarium of New South Wales, Royal Botanic Gardens, Sydney, US = United States National Herbarium, Smithsonian Institution, Washington, District of Columbia.

Dacrycarpus cinctus **(Pilg.) de Laub. PAPUA NEW GUINEA.** *W.R. Barker and T. Umba LAE 67229*, Tel Basin, West Sepik District, 1975, US 2894655. *J.R. Croft et al. LAE 65036*, Mt. Kenive, Central District, 1974, US 2898233. *D. Foreman and P. Wardle NGF 45549*, Murray Pass, Central District, 1969, US 2935540. *D. Frodin NGF 28138*, Tari, Southern Highlands, 1966, NSW s.n. *R.D. Hoogland 9386*, Mannasat, Morobe District, 1964, US 3440170. *R.D. Hoogland 9478*, Mannasat, Morobe District, 1964, US 3438955. *P. Katik LAE 77816*, Mount Cromwell Range, Morobe District, 1984, NSW 272951. *R. Pullen 313*, ridge above Kuaki River, Eastern Highlands, 1957, US 2335975. *R. Pullen 5052*, Kubor Range, Western Highlands, 1963, US 3454211. *C.J. Quinn 4288*, Marifunga, Eastern Highlands, 1974, NSW s.n. *J.S. Womersley LAE 55322*, Kagoba, Southern Highlands, 1972, US 2929618. *J.S. Womersley NGF 24569*, Fatima River Valley, Eastern Highlands, 1965, NSW 527535.

Dacrycarpus compactus **(Wassch.) de Laub. PAPUA NEW GUINEA.** *L.J. Brass 29861*, Mt. Wilhelm, Eastern Highlands, 1959, US 2391220. *L.J. Brass 29935*, Mt. Wilhelm, Eastern Highlands, 1959, US 2391254. *J.R. Croft and L. Craven LAE 61463*, Mt. Albert Edward, Central District, 1974, US 2741712. *J.R. Croft and Y. Lelean 65898*, Mt. Scorpion, West Sepik District, 1975, US 3453364. *T.G. Hartley 12958*, Mt. Dickson, Northern District, 1964, US 3490404. *R.D. Hoogland and R. Pullen 5703*, Mt. Wilhelm, Eastern Highlands, 1956, US 2315044. *J. Jacobs s.n.*, Mt. Wilhelm, 1965, NSW 527531. *J.F. Veldkamp and P.F. Stevens 5585*, Mt. Suckling, Northern District, 1972, US 2758453.

Dacrycarpus cumingii **(Parl.) de Laub. PHILIPPINES.** *Anon.*, Mt. Banajao, Laguna Province, Luzon, 1911, US 3509005. *H. Curran and L. Merritt FB 7886*, Mt. Banajao, Laguna Province, Luzon, 1907, US 709132. *A.D.E. Elmer 11684*, Mt. Apo, Davao, Mindanao, 1909, US 712055, NSW s.n. *H.N. Whitford 951*, Tayabas Province, Luzon, 1904, NSW 527536, US 851845. **MALAYSIA. Borneo:** *Jacobs 5017*, Mt. Penrissen, Sarawak, 1958, US 2377263.

Dacrycarpus dacrydioides **(A. Rich.) de Laub. NEW ZEALAND. North Island:** *P.H. Buddle s.n.*, Waitakere Range, 1939, US 2038551. *T.F. Cheeseman s.n.*, 1884, US 206741. *R. Cooper and N. Nickerson 6124*, Omahuta State Forest, 1979, US 2975206. *R. Cooper and N. Nickerson 6224*, Mangamuka Forest, 1979, US 2947678. *J.H. Davis and R.B. Cooper s.n.*, Waitomo Caves Region, 1950, US 2037547. *J.H. Davis and R.B. Cooper s.n.*, Titirangi, 1950, US 2037548. *J.H. Davis and R.B. Cooper s.n.*, Waitakere Range, 1950, US 2037549. *F.R. Fosberg 30248*, Waitakere Range, 1949, US 2580020. *R.O. Gardner 271*, Mt. William, 1972, CANB 7806870. *R.O. Gardner 2347*, near Warkworth, 1979, US 2936696. *R.O. Gardner 5139*, Mangaotuku Valley, 1987, US 3208192. *Hynes s.n.*, Orini, 1952, US 2394844. *T. Kirk 499*, undated, US 809013. *D. Petrie s.n.*, 1917, US 1507877. *S.A. Rose and R. Cooper 22288*, Waitakere Range, 1946, US 2038679. *E.H. Walker 5309*, north of Waipoa Kauri Forest, 1949, US 1994477. *E.H. Walker 5315*, near Kaikohe, 1949, US 1994484. **South Island:** *A. Campbell s.n.*, Lincoln (cult.), 1973, CANB 00524082, NSW 527529. *F.R. Fosberg 30627*, Lee River, 1949, US 2696384. *P. Hind 4151 and G. Chapple*, near Waimangaroa, 1985, NSW 235470. *E.H. Woods 87/47 and B.H. Macmillan*, Jackson River, 1987, CANB 481308. **Unknown:** *J. Banks and D.C. Solander s.n.*, 1768-1771, US 1276797. *M. Vedel s.n.*, 1847, US 98231.

Dacrycarpus expansus **de Laub. PAPUA NEW GUINEA.** *R.D. Hoogland and R. Schodde 7440*, Yobobos grassland area, Western Highlands, 1960, CANB 85645. *R.D. Hoogland and R. Schodde 7463*, Yobobos grassland area, Western Highlands, 1960, CANB 85921 (Fig. 8), 85922 (isotype). *R.D. Hoogland and R. Schodde 7682*, Yobobos grassland area, Western Highlands, 1960, CANB 87026. *R.G. Robbins 3214*, Yobobos grassland area, Western Highlands, 1960, CANB 88066. *J. Vandenberg, J.S. Womersely, and Galore NGF 39953*, near Kopiago, Western Highlands, 1968, NSW s.n., US 2935543. *W. Vink 17499*, Mt. Ambua, Southern Highlands, 1966, CANB 201846. *W. Vink 17502*, Mt. Ambua, Southern

Highlands, 1966, CANB 201847. *J.S. Womersley LAE 55286*, near Kagoba, Southern Highlands, 1972, CANB 316492, NSW s.n., US 2919711. *J.S. Womersley and K. Woolliams NGF 37020*, Ialibu, Southern Highlands, 1967, CANB 180651.

Dacrycarpus imbricatus (Blume) de Laub. var. *imbricatus*. INDONESIA. Bali: *Kostermans, Kuswata, Soegene, and Soepadmo 138*, Bedugul Forest region, 1958, CANB 107920. *McDonald and Ismail 4941*, Bali Timur, 1994, CANB 481351. Flores: *I. Rensch 1307*, 1927, US 1559286. Java: *W. Palmer and O. Bryant 988*, Mount Pangranggo, 1909, US 652518. Sumbawa: *J. Elbert 4191*, 1910, CANB 27281. *H. Hallier 191*, 1910, US 2245720.

Dacrycarpus imbricatus (Blume) de Laub. var. *curvulus* (Miq.) de Laub. INDONESIA. Sumatra: W.J.J.O. de Wilde and B.E.E. de Wilde-Duyfjes 13272, Gunung Bandahara, 1972, US 2897270 (Fig. 4). W.J.J.O. de Wilde and B.E.E. de Wilde-Duyfjes 15181, Gunung Bandahara, 1975, US 2984499. W.J.J.O. de Wilde and B.E.E. de Wilde-Duyfjes 15534, Gunung Bandahara, 1975, US 2995746.

Dacrycarpus imbricatus (Blume) de Laub. var. *patulus* de Laub. FIJI. *O. Degener 14315*, near Nandarivatu, 1941, US 1943687. *A.C. Smith 4901*, near Nandarivatu, 1947, US 1965607. *A.C. Smith 6245*, near Nandarivatu, 1947, US 1966486. VANUATU. *S.F. Kajewski 849*, Aneityum Island, 1929, US 1597456, 1699621. MALAYSIA. Borneo: *F.R. Fosberg 44128*, Mt. Kinabalu, Sabah, 1963, US 2638768. *F. Sadau s.n.*, Pinosok Plateau, Sabah, 1965, US 2900820. INDONESIA: Sumatra: *R.S. Boeea 10697*, Aek Si Oelak, Asahan, 1936, US 3223124. *W. Meijer 7267*, Gunung Tudjuh, 1956, CANB 66234. Papua: *H.R. Karstel BW 5441*, Cycloop Mountains, 1957, CANB 116083. PAPUA NEW GUINEA. *D. Frodin NGF 26889*, Mt. Tangis, New Britain, 1966, CANB 169891, NSW s.n., US 2917515. *O. Gideon LAE 77177*, Hans Meyer Range, New Ireland, 1984, CANB 375693. *J.S. Womersley NGF 24928*, Okasa, Eastern Highlands, 1967, CANB 191679, NSW 527532 (Fig. 6).

Dacrycarpus imbricatus (Blume) de Laub. var. *robustus* de Laub. PHILIPPINES. *E.A. Mearns 4405*, Benguet Province, Luzon, 1907, NSW 527533, US 625854. *R.S. Williams 1298*, Mt. Santo Tomas, Benguet Province, Luzon, 1904, US 707540. MALAYSIA. Borneo: *Melegrito 471*, Tenompok Hill, Sabah, 1949, US 3224478. INDONESIA. Papua: *G. Iwanggin BW 9059*, Sidoarsi Mts., 1959, CANB 359814. *Rappard BW 698*, Enarotali, 1955, CANB 51733. *Chr. Versteegh and Ch. Koster BW 14*, Cycloop Mountains, 1952, CANB 152514. West Papua: *R.P. Mangold BW 2263*, Ransiki, 1957, CANB 65723. *Stefels BW 2038*, Anggi Lake, 1955, CANB 52184. *P. van Royen 3895*, Kebar Valley, 1954, CANB 65198. *Chr. Versteegh BW 10411*, Kebar Valley, 1960, CANB 118487. *Chr. Versteegh BW 250*, Anggi Gita Lake, 1954, CANB 152515. *Sleumer and Vink BW 14261*, Mt. Gwamongga, 1962, CANB 359775. PAPUA NEW GUINEA. *L.J. Brass 22582*, Mt. Dayman, Milne Bay District, 1953, CANB 83586, US 2830550. *L.J. Brass 23393*, Mt. Dayman, Milne Bay District, 1953, CANB 83585, US 2374252. *L.J. Brass 29577*, Mt. Kaindi, Morobe District, 1959, US 2391062. *L.J. Brass 29598*, Mt. Kaindi, Morobe District, 1959, CANB 102127, US 2391077. *L.J. Brass 29599*, Mt. Kaindi, Morobe District, 1959, CANB 102128, US 2391078. *L.J. Brass 30568*, Mt. Wilhelm, Eastern Highlands, 1959, CANB 101687 (isotype). *L.J. Brass 30570*, Mt. Wilhelm, Eastern Highlands, 1959, CANB 101686, US 2391562. *L.J. Brass 31660*, Purosa, Eastern Highlands, 1959, CANB 103201, US 2392274. *L.J. Brass 31852*, Purosa, Eastern Highlands, 1959, US 2392382. *J. Cavanaugh NGF 3322*, Mt. Hagen, Western Highlands, 1980, CANB 152519, 152520. *J.R. Flenley ANU 2176*, Lake Inim, Western Highlands, 1964, CANB 156083.1, 156082.2. *J.R. Flenley ANU 2613*, Yogonda, Western Highlands, 1965, CANB 157488.1, 157489.2. *D.B. Foreman and Y. Lelean NGF 48385*, Murray Pass, Central District, 1970, CANB 216896, US 2901100. *D. Frodin NGF 28460*, Habono, Southern Highlands, 1966, US 3293783. *R.D. Hoogland and L.A. Craven 9353*, Mt. Rawlinson, Morobe District, 1964, CANB 144238.1, 144239.2, US 3436403. *R.D. Hoogland and L.A. Craven 9354*, Mt. Rawlinson, Morobe District, 1964, CANB 144237, US 3436400. *R.D. Hoogland and L.A. Craven 9355*, Mt. Rawlinson, Morobe District, 1964, CANB 144236, US 3436401. *R.D. Hoogland and R. Pullen 5868*, southeast of Mt. Hagen, Western Highlands, 1956, CANB 152499, 152500, US 2315098, 2315099. *R. Pullen 5914*, Sibium Range, Northern District, 1964, CANB 154129. *R. Pullen 5930*, Sibium Range, Northern District, 1964, CANB 153080.1, 153081.2. *C.J. Quinn 4242*, near Margarima, Southern Highlands, 1974, NSW s.n. *C.J. Quinn 4273*, near Kandep, Enga Province, 1974, CANB

359768. *C.J. Quinn 4292*, Kaisenik logging area, Morobe District, 1974, CANB 359810. *C.J. Quinn 4302*, Mt. Kaindi, Morobe District, 1974, CANB 359809. *R.G. Robbins 1078*, Divide between Tomba and Tambil, Western Highlands, 1957, CANB 46211. *R.G. Robbins 1084*, Upper Kaugel Valley, Western Highlands, 1957, CANB 46219. *J.C. Saunders 823*, Chimbu Subdistrict, Eastern Highlands, 1957, CANB 44027. *J.C. Saunders 861*, Goroka Subdistrict, Eastern Highlands, 1957, CANB 44028.1, 44029.2. *J.C. Saunders 865*, Goroka Subdistrict, Eastern Highlands, 1957, CANB 44030. *J.C. Saunders 1007*, Wabag-Kompiam Road, Western Highlands, 1960, CANB 88956. *J.C. Saunders 1048*, near Sari, Western Highlands, 1960, CANB 88911. *C.D. Sayers NGF 21613*, Wagau, Morobe District, 1965, CANB 172513. *R. Schodde 5523*, Mt. Simpson Range, Milne Bay District, 1969, CANB 204274. *R. Schodde 5528*, Mt. Simpson Range, Milne Bay District, 1969, CANB 204279. *H.U. Stauffer 5652*, Mt. Wilhelm, Western Highlands, 1964, NSW s.n. *A. Vinas and J. Wiakabu LAE 59469*, Silinmogu, West Sepik District, 1975, US 2934150. *L.K. Wade ANU 7686*, Keglsugl area, Eastern Highlands, 1967, US 2914731. *J.S. Womersley NGF 11067*, Merimanta, Western Highlands, 1959, CANB 71932, MEL 2355234A, 2355235A. *J.S. Womersley NGF 14013*, Upper Asaro Valley, Eastern Highlands, 1961, CANB 99733. *J.S. Womersley NGF 5338*, Al River Mountains, Western Highlands, 1953, CANB 152524, NSW s.n. *J.S. Womersley NGF 5353*, Al River Mountains, Western Highlands, 1953, CANB 152525. *J.S. Womersley and A. Millar NGF 8324*, Wau-Salamaua Road, Morobe District, 1956, CANB 152493.

Dacrycarpus imbricatus (Blume) de Laub., variety not determined. FIJI. *E. Damanu FD 770*, Nabukavesi, 1963, MEL 2344582 (Fig. 5), 2355232A. *E. Damanu FD 854*, Nausori Highlands, 1963, MEL 2355233A. *J.W. Parham and E. Parham 14519*, Toninaiwau, 1965, US 2603375. VANUATU. *G. McPherson et al. 19472*, Espiritu Santo Island, 2006, US 3524187. MALAYSIA. Borneo: *W.A. Brooke 10507*, Bakelalan, Sarawak, 1955, US 2332052. INDONESIA. Java: *F.R. Fosberg 44614*, Mt. Gedeh, 1963, US 2638455. *J.J. Smith s.n.*, Mt. Gedeh, 1899, CANB 129258. West Papua: *A.P. Davis 804*, Kebar Valley, 1995, CANB 532077. *G. Hope ANU 19041*, Otomono Valley, 1972, CANB 229908. PAPUA NEW GUINEA. *B. Craig 95*, Sirius Ridge, West Sepik District, 1965, CANB 215330. *J.R. Croft and Y. Lelean NGF 34742*, Kagi Gap area, Central District, 1973, NSW s.n. *J.R. Croft et al. LAE 71061*, Mt. Kilkerran, Milne Bay District, 1976, CANB 342505, US 3321047. *D. Frodin NGF 28460*, near Habono, Southern Highlands, 1966, CANB 360480.1 (Fig. 7). *Goode, Sands, Y. Lelean NGF 46095*, Danfu River area, New Ireland, 1970, CANB 217578. *Heads 267*, Wau, Morobe District, 1981, CANB s.n. *E.E. Henty NGF 29018*, Lake Trist, Morobe District, 1966, CANB 203012. *G. Hope ANU 10642*, Mt. Wilhelm, Chimbu Province, 1970, CANB 241229. *W. MacGregor s.n.*, Mt. Knutsford, 1889, MEL 600760. *W. MacGregor s.n.*, Mt. Suckling, 1891, MEL 619402. *G.F.B. McVeagh NGF 7581*, near Bululo, Morobe District, 1957, MEL 2355230A. *A.N. Miller 1294*, Koisipe, Central District, 1971, NSW s.n. *R. Pullen 7847*, Mt. Wadimana, Milne Bay District, 1969, CANB 223554. *R. Pullen 7847A*, Mt. Wadimana, Milne Bay District, 1969, CANB 223553. *T. Reeve 2906*, Maiyingkaitakembo, East Sepik District, 1980, NSW s.n. *T. Reeve 3178*, Mt. Diwai, Central District, 1980, NSW s.n. *T. Reeve 4022*, Mt. Sapau summit, West Sepik District, 1981, NSW s.n. *T. Reeve 4960*, Upugosa Ridge, Morobe District, 1982, NSW s.n. *T. Reeve 6504*, Trauna Ridge, Western Highlands, 1983, CANB s.n. *R.G. Robbins 1232*, Upper Asaro Valley, Eastern Highlands, 1957, CANB 46066. *W.A. Sayer s.n.*, Mt. Obree, 1887, MEL 600759. *P.F. Stevens LAE 54072 and J.F. Veldkamp*, Paori, Milne Bay District, 1972, CANB 244027. *J. Wheeler ANU 6323*, Mt. Hagen, Western Highlands, 1967, CANB 178730.

Dacrycarpus kinabaluensis (Wassch.) de Laub. MALAYSIA. Borneo: *J.H. Beaman 8305*, Mt. Kinabalu, Sabah, 1984, US 3532539. *W.L. Chew and E.J.H. Corner RSNB 8887*, Mt. Kinabalu, Sabah, 1964, CANB 159393. *B.E. Weber SAN 54689*, Mt. Kinabalu, Sabah, 1966, US 3310103.

Dacrycarpus steupii (Wassch.) de Laub. INDONESIA. West Papua: *V.W. Moll BW 12820*, Upper Aifat Valley, 1961, CANB 359817. *V.W. Moll BW 12876*, Upper Aifat Valley, 1961, CANB 359816. PAPUA NEW GUINEA. *S. Clemens 7562a*, Sattelberg, Morobe District, 1937, CANB 159721. *L.A. Craven 2835*, Kosipi, Central District, 1974, CANB 268709. *J.R. Flenley ANU 2175*, Lake Inim, Western Highlands, 1964, CANB 156080.1. *J.R. Flenley ANU 2769*, near Lake Inim, Western Highlands, 1965, CANB 158186. *D. Foreman and P. Wardle NGF 45586*, near Woitape, Central District, 1969, CANB 206774, NSW s.n. *T.G.*

Hartley 11194, Mt. Salawaket, Morobe District, 1963, CANB 151156. *K. Paijmans 735*, Kosipi, Central District, 1970, CANB 219217. *R. Pullen 2716*, Lake Bunch, Southern Highlands, 1961, CANB 98856.1, 98857.2. *R. Pullen 2716A*, Lake Bunch, Southern Highlands, 1961, CANB 98854.1, 98855.2. *R. Pullen 2849*, near Tenggor, Southern Highlands, 1961, CANB 98449.1. *C.J. Quinn 4217*, Hagen-Wabag Road, Western Highlands, 1974, NSW s.n. *C.J. Quinn 4272*, Jibbibby River, Tengo, 1974, NSW s.n. *C.J. Quinn 4287*, Lake Inim, Western Highlands, 1974, NSW s.n. *R.G. Robbins 1263*, Aiyura, Eastern Highlands, 1957, CANB 46022.1, 46021.2. *R.G. Robbins 2940*, Lai Valley, Western Highlands, 1960, CANB 87756. *R.G. Robbins 3209*, near Kepilum, Western Highlands, 1960, CANB 88073. *J.S. Womersley NGF 4428*, Aiyura, Eastern Highlands, 1951, CANB 232394.

Dacrycarpus vieillardii (Parl.) de Laub. NEW CALEDONIA. *G. McPherson 1981*, Rivière Bleue Reserve, 1981, CANB (CBG 8701838). *G. McPherson 5040*, Ouinné River Valley, 1982, NSW 527530. *G. McPherson 5041*, Ouinné River Valley, 1982, CANB 351178. *J. Veillon 1922*, Dothio Region, 1969, CANB 504517.