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PAPUACEDRUS (CUPRESSACEAE) IN EOCENE PATAGONIA: A NEW FOSSIL LINK TO AUSTRALASIAN RAINFORESTS¹

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The 51.9 Ma Laguna del Hunco (LH) and 47.5 Ma Río Pichileufú (RP) floras from Patagonia, Argentina are unusually rich, angiosperm-dominated assemblages with living relatives in the low-latitude West Pacific, neotropics, and temperate southern latitudes. The diverse gymnosperms in these floras are important for Gondwanan biogeographic history and paleoclimatic interpretations. “*Libocedrus*” *prechilensis* Berry 1938 (Cupressaceae), previously known only from the holotype (RP), a vegetative branch, is revised here based on new material from both localities, including a seed cone attached to a shoot with cuticle (LH). Characters of these fossils are diagnostic of monotypic *Papuacedrus* (highlands of New Guinea and Moluccas). Living *P. papuana* is most abundant in cloud forests receiving up to 4 m rainfall annually, whereas *Austrocedrus* (*Libocedrus*) *chilensis*, the basis of comparison when the fossil species was named, inhabits dry, cold steppe margins to mediterranean climates in southern South America. We establish *Papuacedrus prechilensis* comb. nov., which simultaneously invalidates a southern South American connection for the fossil floras and reveals a link to West Pacific montane rainforests. Combined evidence indicates a biome similar to extant subtropical, or tropical montane, rainforests that persisted for at least 4.4 Myr, linking elevated floral richness to abundant rainfall.

Key words: *Austrocedrus*; Cupressaceae; Eocene; Laguna del Hunco; *Libocedrus*; paleoclimate; *Papuacedrus*; Patagonia; Río Pichileufú; subtropical rainforest.

Fossil Cupressaceae from the southern hemisphere have far-reaching importance for Gondwanan biogeographic and paleoclimatic interpretations as well as gymnosperm evolutionary history (Brodrribb and Hill, 1997, 1998; Hill and Brodrribb, 1999; Farjon, 2005; Stockey et al., 2005; Crisp et al., 2009). The current record from Patagonia is sparse but includes important discoveries from Argentina such as *Austrohamia minuta* Escapa et al. (2008) from the Jurassic of Chubut Province and

Athrotaxis ungeri (Halle) Florin from several late Early Cretaceous sites of Santa Cruz Province (Halle, 1913; Florin, 1960; Del Fueyo et al., 2008).

Here, we revise “*Libocedrus*” *prechilensis* Berry (1938), previously known only from the holotype specimen, a part and counterpart of vegetative branches from the Río Pichileufú flora (RP), middle Eocene of Río Negro Province, Argentina (Fig. 1; Wilf et al., 2005a). The species was named for its perceived similarity to *Austrocedrus* (*Libocedrus*) *chilensis* (D. Don) Pic. Serm. & Bizarri, a South American conifer whose range includes steppe-margin habitats near Berry’s type locality. We have collected abundant, well-preserved new material equivalent to “*L.*” *prechilensis* from RP and from Laguna del Hunco (LH; Fig. 1), a prolific early Eocene site in Chubut Province (Berry, 1925a; Wilf et al., 2003, 2005a). The fossils mostly consist of vegetative branches with fragmentary cuticle and other organic preservation, and one specimen from LH bears an immature seed cone, attached to a shoot with well-preserved leaves.

The affinities of “*L.*” *prechilensis* have systematic, biogeographic, and paleoclimatic implications. Monotypic *Austrocedrus* Florin and Boutelje (1954) is one of three closely related genera of Cupressaceae within Libocedrinae (Farjon, 2005) that produce very similar, notably dimorphic foliage, the others being *Libocedrus* Endlicher (1847) and monotypic *Papuacedrus* H. L. Li (1953). However, *Austrocedrus* is the only dry- and cold-adapted genus and the only South American member of this group, whereas *Libocedrus* and *Papuacedrus* are restricted to Australasian rainforests (Table 1; discussed later). Determination of wet vs. dry affinities for the fossils studied here is directly relevant for explaining the elevated richness of the

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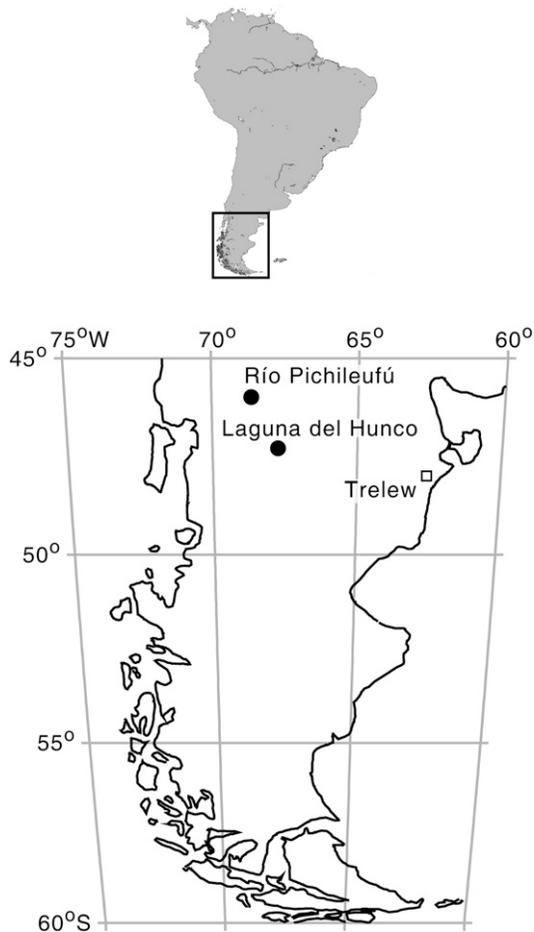


Fig. 1. Map showing 50 Ma positions, with modern coastlines and inset from modern South America, of the Laguna del Hunco and Río Pichileufú sites and the city of Trelew, redrawn from Wilf et al. (2005a). Reconstruction made using the Plate Tectonic Reconstruction Service of the Ocean Drilling Stratigraphic Network (<http://www.odsn.de/odsn/services/paleomap/paleomap.html>) based on data from Hay et al. (1999). South America graphic was generated using Online Map Creation (<http://www.aquarius.ifm-geomar.de>) (Wessel and Smith, 1995).

Laguna del Hunco and Río Pichileufú floras: environmental moisture has a first-order positive effect on biodiversity in modern ecosystems (Clinebell et al., 1995; Kreft and Jetz, 2007), especially where frost is not considered a constraint, as in these Eocene fossil floras (Wilf et al., 2005a).

“*Libocedrus*” prechilensis and similar extant taxa—Berry (1938) emphasized that the name “*Libocedrus*” *prechilensis* reflected the fossil’s similarity to, and proximity to the extant range of, *Austrocedrus* (*Libocedrus*) *chilensis*. The taxonomic concepts and fossil record of Libocedrinae (Farjon, 2005: *Austrocedrus*, *Libocedrus*, *Papuacedrus*, and *Pilgerodendron*) have since progressed considerably (Li, 1953; Florin and Boutelje, 1954; Johns, 1995; Farjon, 2005; Table 1). In light of the new fossil material, a full comparison is warranted of “*L.*” *prechilensis* to the three morphologically similar genera in Libocedrinae, *Austrocedrus*, *Libocedrus*, and *Papuacedrus*, which all have valvate seed cones and, usually, highly dimorphic foliage. However, as discussed later, there are character combinations that distinguish them reliably, first established by Li

(1953) for seed cones and by Florin and Boutelje (1954) for foliage. *Pilgerodendron*, which has no fossil record to date, is morphologically distinct from the fossils discussed here, especially in having monomorphic leaves.

Austrocedrus, *Libocedrus*, and *Papuacedrus* have highly dispersed, relict distributions and diverse habitat preferences (Wade and McVean, 1969; Hope, 1980; Enright and Hill, 1995; Johns, 1995; Veblen et al., 1995; Villalba and Veblen, 1997; Hill and Brodribb, 1999; Hill, 2004; Farjon, 2005). All are confined to the southern hemisphere, though *Papuacedrus* is found to $<1^{\circ}\text{S}$ latitude. *Austrocedrus chilensis* is restricted to southern Chile and Argentina, growing in dry, cold, premontane steppe margins on the eastern front of the Andean Cordillera (near the fossil sites), ca. 43.5°S , to Mediterranean climates with dry summers on the western front, ca. 32.5°S . *Austrocedrus* also occurs in mesic environments, including in several *Nothofagus* associations, and rarely in the Coastal Range rainforest in Chile. *Libocedrus* has five, exclusively rainforest species, two in New Zealand (*L. bidwillii*, *L. plumosa*) and three in New Caledonia (*L. austrocaledonica*, *L. chevalieri*, *L. yateensis*); *L. plumosa* and *L. yateensis* are lowland species, whereas the others are montane to subalpine in distribution. *Papuacedrus papuana* (F. Muell.) H. L. Li occurs only in New Guinea and the Moluccas, from lower montane (600–900 m a.s.l.) rainforests to subalpine scrub at more than 3500 m a.s.l.; it is maximally abundant in cloud forests at ca. 1500 m a.s.l. and higher, receiving up to 4 m per year of seasonally distributed rainfall (Wade and McVean, 1969; Van Royen, 1979; Johns, 1995; Farjon, 2005).

Reliable fossil occurrences of *Austrocedrus*, *Libocedrus*, and *Papuacedrus* are usually distant from their present ranges and are overwhelmingly concentrated in Tasmania; very few represent *Austrocedrus* and *Papuacedrus* (Table 1). Besides “*L.*” *prechilensis*, the only other South American record is material from the Miocene Navidad Formation of Chile, assigned to *Austrocedrus* (Troncoso and Romero, 1993).

Laguna del Hunco and Río Pichileufú floras—The Cupressaceae fossils presented here are best understood within the context of their source assemblages. These are two rich and well-preserved Eocene floras from fossil caldera-lake deposits located in the modern steppe biome of Patagonia, Argentina: the early Eocene Laguna del Hunco (LH) flora, Chubut Province, and the middle Eocene Río Pichileufú (RP) flora, Río Negro Province (Fig. 1). Both floras were the subject of historic descriptions by E. W. Berry (1925a, 1935a–c, 1938) and a handful of subsequent studies (Appendix 1). The assemblages rank among the most diverse compression-impression floras ever found in the fossil record, including more than 200 plant organ morphotypes representing at least 170 species at LH (Wilf et al., 2003, 2005a; authors’ unpublished data). Insect damage on fossil leaves is also extraordinarily diverse (Wilf et al., 2005b; Sarzetti et al., 2008, 2009), and many new insect taxa are being described (Petrulevičius and Nel, 2003, 2005; Petrulevičius, in press). Bedded tuffs intercalated stratigraphically with the fossil plant quarries yielded high-precision ^{40}Ar – ^{39}Ar ages of 51.91 ± 0.22 Ma for the LH flora and 47.46 ± 0.05 Ma for the RP flora (Wilf et al., 2003; 2005a). Paleoelevation for LH and RP is very poorly constrained, but the available evidence indicates that significant uplift, erosion, and burial occurred in the region from the Eocene to the Miocene (Pankhurst et al., 1999; Thomson, 2002).

Because the floras predate the deepwater opening of the Tasman Strait, ca. 32 Ma, and the Drake Passage, ca. 31 Ma (Lawver and Gahagan, 2003), biotic interchange occurred with

TABLE 1. Previous fossil record and extant diversity and ranges of *Austrocedrus*, *Libocedrus*, and *Papuacedrus*.

Taxon	Organ(s)	Locality	Age	Reference
<i>Austrocedrus</i> (1 species, southern Argentina and Chile)				
<i>A. australis</i>	L (S ^a)	Lea River, Tasmania	Early Oligocene	Paull and Hill, 2008
<i>A. tasmanica</i>	S	Monpeelyata, Tasmania	Late Oligocene-early Miocene	Hill and Carpenter, 1989
"A." sp.	L	Matanzas, Chile	Miocene	Troncoso and Romero, 1993
<i>Libocedrus</i> (2, New Zealand; 3, New Caledonia)				
<i>L. acutifolius</i>	L	Lake Bungarby, New South Wales	Late Paleocene	Whang and Hill, 1999
<i>L. balfourensis</i>	L	Balfour, Tasmania	Early Oligocene-early Miocene	Paull and Hill, 2009
<i>L. jacksonii</i>	L	Little Rapid River, Tasmania	Oligocene	Hill and Carpenter, 1989
<i>L. leaensis</i>	L, S	Lea River, Tasmania	Early Oligocene	Paull and Hill, 2009
<i>L. mesibovii</i>	S	Little Rapid River, Tasmania	Oligocene	Hill and Carpenter, 1989
<i>L. microformis</i>	L	Regatta Point, Tasmania	Early Eocene	Paull and Hill, 2009
<i>L. morrisonii</i>	L	Pioneer, Tasmania	Late Oligocene-early Miocene	Hill and Carpenter, 1989
<i>L. obtusifolius</i>	L	Lake Bungarby, New South Wales	Late Paleocene	Whang and Hill, 1999
"L." <i>prechilensis</i>	L	Río Pichileufú, Argentina	Middle Eocene	Berry, 1938
<i>L. sp. cf. L. bidwillii</i>	L	Mt. Somers coal mine, New Zealand	Early-middle Paleocene	Pole, 1998
<i>Libocedrus</i> sp.	L	Gore Lignite Measures, New Zealand	Oligocene-early Miocene	Pole, 2007
<i>Papuacedrus</i> (1, New Guinea, Moluccas)				
<i>P. australis</i>	L	Cethana and Pioneer, Tasmania	Early Oligocene and late Oligocene-early Miocene	Hill and Carpenter, 1989
<i>P. shenii</i> Zhou	L	Fossil Hill, King George Island, Antarctica	Eocene	Zhou and Li, 1994
<i>Papuacedrus</i> sp.	L	St. Bathans Paleovalley, New Zealand	Early Miocene	Pole, 2007

Notes: L = leaves, S = seed cone. Quotations indicate generic assignment needing revision. "*L.*" *prechilensis* is transferred to *Papuacedrus* in this paper, and its temporal range is expanded to include the early Eocene Laguna del Hunco flora.

^a Paull and Hill (2008) described a seed cone associated with, but not attached to the Lea River leaves as similar to *Austrocedrus*, but they did not place it in the genus.

Australasia via Antarctica as well as with northern South America (e.g., Hill, 1994). To date, the LH and RP floras have three distinct modern biogeographic components, detailed in Appendix 1: Australasian subtropical and tropical rainforest (Florin, 1940a; Romero and Hickey, 1976; Gandolfo et al., 1988, 2006; Zamaloa et al., 2006), reflecting formerly widespread distributions across Gondwana via Antarctica and subsequent northward retreat with cooling and aridification of middle and high latitudes; neotropical rainforest (González et al., 2007; Gandolfo et al., 2007), reflecting a different path of northward retreat; and humid temperate forests of South America, Australia, and New Zealand (Schodde, 1969; Romero et al., 1988; González et al., 2007), probably reflecting adaptation and survival of lineages more or less in situ, in wet, equable refugia. Subtropical and tropical Australasian relationships are by far the best established, though hundreds of species are not yet described or revised.

Paleoclimatic characterization of the floras has been inconsistent (Berry, 1925a, b, 1938; Aragón and Romero, 1984; Romero, 1986; Markgraf et al., 1996; Hinojosa, 2005). Morley (2000) suggested that tropical rainforest conditions occurred in the region during the globally warm early and middle Eocene (e.g., Zachos et al., 1994, 2008), but this was based on little direct evidence (see also Wolfe, 1985; Frakes et al., 1992; Beerling and Woodward, 2001; Ziegler et al., 2003). According to Morley (2000), true tropical rainforest requires a minimum mean monthly temperature above 18°C, annual precipitation above 2 m, and no four consecutive months below 0.1 m of rainfall per month.

Recent analyses of the LH flora from our greatly expanded collections, using leaf-margin (Wolfe, 1979) and leaf-area (Wilf et al., 1998) analyses, indicate a mean annual precipitation (MAP) of at least ~1.1 m and a mean annual temperature (MAT) ca. 16–17°C (Wilf et al., 2003, 2005a). The latter matches coeval sea surface temperature estimates from the South Atlantic (Zachos et al., 1994) and is more suggestive of subtropical than

tropical climates. Frost is unlikely due to the presence of numerous cold-intolerant lineages in both floras (Wilf et al., 2005a; Zamaloa et al., 2006). The continuing recognition of extant rainforest genera at LH and RP (Appendix 1) suggests MAP far higher than the ~1.1 m minimum estimate from leaf area. The podocarpaceous genera *Acmopyle* (Florin, 1940a), *Dacrycarpus*, and *Retrophyllum*, under separate investigation from new material, are particularly relevant because they are noted for drought intolerance and affinities with extremely wet habitats (Brodribb and Hill, 1998, 2004; Hill and Brodribb, 1999).

Berry's "*Libocedrus*" *prechilensis*, because of the explicit link he made to the dry- and cold-adapted *Austrocedrus* (*Libocedrus*) *chilensis*, presents a legacy challenge to the emerging rainforest interpretations of Eocene Patagonia. Further, Berry's (1938) interpretation suggests that the *Austrocedrus* lineage has been in Patagonia since the Eocene (although in Berry's time the RP flora was considered Miocene, as was the LH flora). In this paper, we transfer "*Libocedrus*" *prechilensis* and equivalent new material from the Laguna del Hunco and Río Pichileufú floras to *Papuacedrus*. We discuss the consequences of this new combination for the evolution and biogeography of Libocedrinae as well as the paleoclimatic implications for the Eocene Patagonian floras and their elevated diversity.

MATERIALS AND METHODS

The holotype and only formally referred specimen of "*Libocedrus*" *prechilensis* is a part and counterpart from the type Río Pichileufú collection (Berry, 1938), housed in the Division of Paleobotany of the Smithsonian National Museum of Natural History (USNM), Washington D.C. (USNM 40387, Figs. 2–9). The exact source coordinates of the type collection are unknown, although the entire fossiliferous exposure at RP is restricted to a single, small drainage. The most informative, stratigraphically constrained, and complete specimens equivalent to "*L.*" *prechilensis* (Figs. 10–65) came from our recent field reinvestigations of the Laguna del Hunco and Río Pichileufú floras (Wilf et al., 2003, 2005a). The Laguna del Hunco collections are curated at Museo Paleontológico

Egidio Feruglio (MEF), in Trelew, Chubut, Argentina, and the Río Pichileufú specimens are housed at Museo de Paleontología, San Carlos de Bariloche, Río Negro, Argentina. Specimen numbers for this material have the repository prefixes MPEF-Pb and BAR, respectively, with letter suffices indicating parts and counterparts. The Laguna del Hunco material is more abundant and complete, including a seed cone and better preservation of foliar characters and variation.

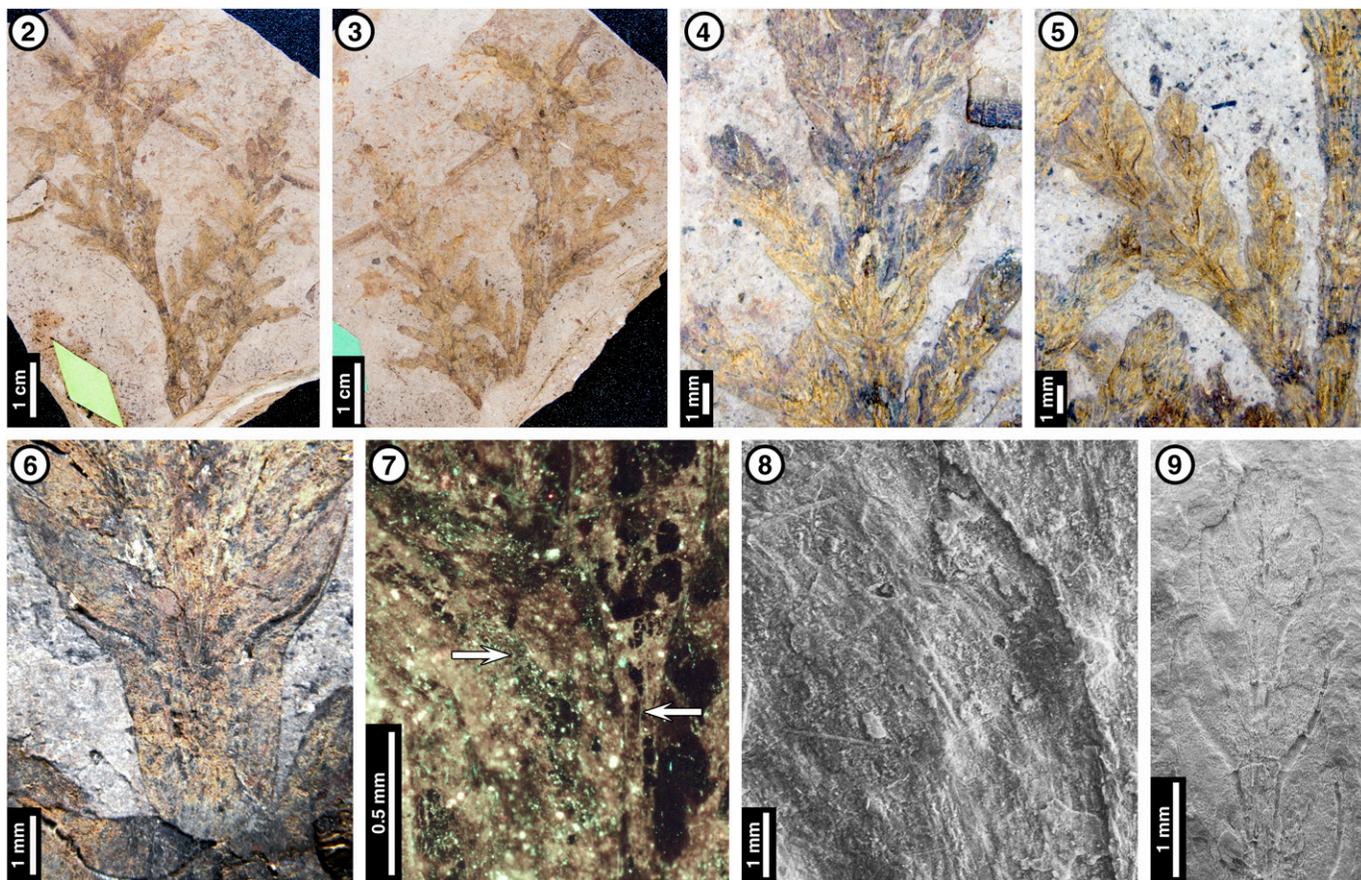
Laguna del Hunco specimens came from quarry sites LH1, LH2, LH4, LH6, LH13, and LH15 of Wilf et al. (2003); LH13 has the highest overall abundance of conifers among the LH quarries, also including Araucariaceae and several Podocarpaceae (Wilf et al., 2005a). The fossils studied here are rare, comprising only 25 of 4303 quantitatively collected specimens at Laguna del Hunco overall, and 16 of these are from LH13. Additional material was collected at two new localities 5 km south of the principal Laguna del Hunco exposures and at a lower stratigraphic level within the lake sequence, here designated AL1 and AL2 (for the nearby Puesto Alvarez). From Río Pichileufú, foliar material came from the RP3 quarry site of Wilf et al. (2005a), comprising five of 1107 specimens. Geographic coordinates for quarries not published by Wilf et al. (2003) are available from PW or from MEF Collections Management. In addition, five specimens (three from LH, two from RP) were discovered and examined in the collections of Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires (FCENCB-PB). Observations of fossils that we report here are based on all collections listed.

All MEF and BAR specimens were manually prepared with air scribes, carbide rods, and fine brushes to remove extraneous matrix. Specimens were studied at MEF and at the Paleobotany Laboratory, Pennsylvania State University, primarily using nondestructive techniques. At Penn State, these consisted of standard and epifluorescent light microscopy with a Nikon SMZ-1500 stereoscope and a Nikon LV100 compound microscope (Nikon, Melville, New York,

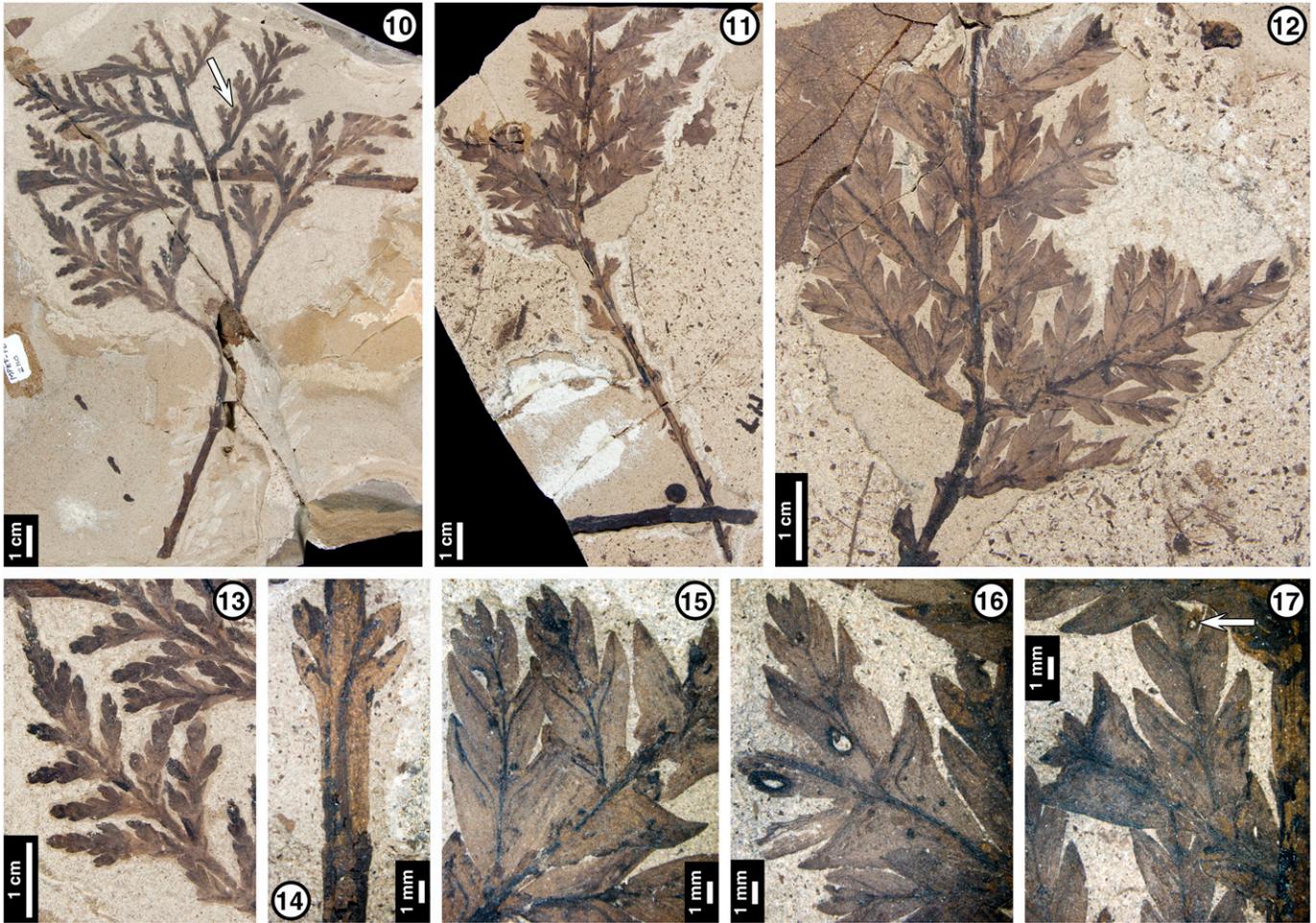
USA), sharing an X-Cite 120 epifluorescence illumination unit (EXFO Electro-Optical Engineering, Quebec City, Quebec, Canada), a Nikon DXM-1200F camera, and Nikon NIS Elements v. 2.1 software with extended depth of focus capability. The brightest fluorescence imaging was produced using an Endow GFP Longpass Emission green filter: exciter HQ470/40×, dichroic Q495LP BS, emitter HQ500LP, Chroma Technology Number 41018 (Chroma Technology, Rockingham, Vermont, USA). A Nikon Coolpix 8800 camera was used for most nonmicroscope photography. Environmental scanning electron microscope (ESEM) observations were done in the Materials Characterization Laboratory, Pennsylvania State University, with uncoated specimens under low vacuum and low voltage, usually 20 kV; backscatter detection yielded the best results.

Cuticle, when present, was thin, fragile, fragmented, and often degraded with fungal hyphae present (Fig. 63). Most observations were made in situ, on unprepared specimens, using epifluorescence. Cuticle isolation was extremely difficult because of fusion to amorphous organic matter in the matrix; application of acids and oxidizing agents for cuticle isolation caused degradation. One specimen prepared with 20% CrO₃ solution for 3 h was sufficiently clear of coaly residue for some ESEM imaging directly on the rock (Figs. 35–37), but further treatments failed to isolate any intact cuticle from the matrix. Bleach treatment successfully removed coal from one RP specimen, revealing epidermal cells but no stomata (Figs. 64, 65). Other preparation attempts on small rock fragments either did not sufficiently remove matrix or overly degraded the fragile cuticle, including HF, HCl, 5% KOH, 10% sodium pyrophosphate (Na₄P₂O₇), and additional CrO₃ treatment.

Extant herbarium specimens of *Austrocedrus*, *Libocedrus*, and *Papuacedrus* were examined, photographed, and measured at Royal Botanic Gardens, Kew (K); the National Herbarium of New South Wales, Botanic Gardens Trust,



Figs. 2–9. Holotype of “*Libocedrus*” *prechilensis* Berry 1938, from Río Pichileufú, USNM 40387, here transferred to *Papuacedrus prechilensis* comb. nov. Figs. 2, 4, 9, part (illustrated by Berry 1938: plate 12, fig. 1); Figs. 3, 5, 6–8, counterpart. 2, 3. Complete specimen. 4, 5. Selected details of branching and foliage. 6. Fused lateral leaf pair with convex bases, darkened margins, spreading free tips with sharp apices, and prominent resin canal molds. 7. Lateral leaf pair showing vein/resin duct (left arrow), raised zone of fusion (right arrow), and longitudinally oriented epidermal cells (under epifluorescence). 8. Detail of longitudinally oriented epidermal cells on a lateral leaf (ESEM). 9. Terminal shoot portion showing resin canal molds and organic matter (ESEM).



Figs. 10–17. Large foliage sprays of *Papuacedrus prechilensis* comb. nov., from Laguna del Hunco (quarry LH13). Figs. 10, 13, MPEF-Pb 2110. Figs. 11, 14, 16, 17, MPEF-Pb 971b. Figs. 12, 15, MPEF-Pb 971a. **10.** Spray with five orders of branching (arrow at 5th), alternate at lowest order with long lateral leaves addressed to the axis (e.g., Fig. 14), and opposite at higher orders. **11, 12.** Spray showing three orders of opposite branching, flattened transitional-form foliage, and long lateral leaves addressed to lowest-order axis (see Fig. 14), with axillary buds and branches visible above their free tips. **13.** Detail, showing relatively reduced lateral leaves of late-transitional to mature form foliage. **14.** Detail of elongated lateral leaves addressed to low-order axis, free tips subtending incipient axillary branches with first facial leaves. **15–17.** Details of distal branching and the expanded transitional-form foliage with convex bases (portion below the free tips), darkened margins, spreading, sharp-pointed free tips, prominent veins/resin canals; and faintly visible, longitudinal stomatal bands subparallel to the veins. Note dimorphism with facial leaves. Three instances of insect hole-feeding with dark reaction rims are visible, two in Fig. 16 and one in Fig. 17 (arrow).

Royal Botanic Gardens, Sydney (NSW); the National Herbarium of Victoria, Royal Botanic Gardens, Melbourne (MEL); and the United States National Herbarium, Smithsonian Institution, Washington, D.C. (US). From review of these specimens and the literature, we summarize the character states of these genera that are informative for the fossil material in Table 2 and partly illustrate them for extant *P. papuana* (Figs. 66–77). Additionally, Z. Zhou kindly provided original photographs of *Papuacedrus shenii* Zhou (Zhou and Li, 1994), from the Eocene of Antarctica, that are clearer than the published illustrations.

While acknowledging recent phylogenetic studies based on molecular data (Gadek et al., 2000; Quinn and Price, 2003), we follow the taxonomic framework in Farjon's (2005) Cupressaceae monograph because of his comprehensive, evolutionary treatment of morphology across the family. Terminology for foliage forms follows Offerl (1984; see also Figs. 66–69).

SYSTEMATICS AND RESULTS

Family—Cupressaceae Gray, A Natural Arrangement of British Plants 2: 222, 225 (1821).

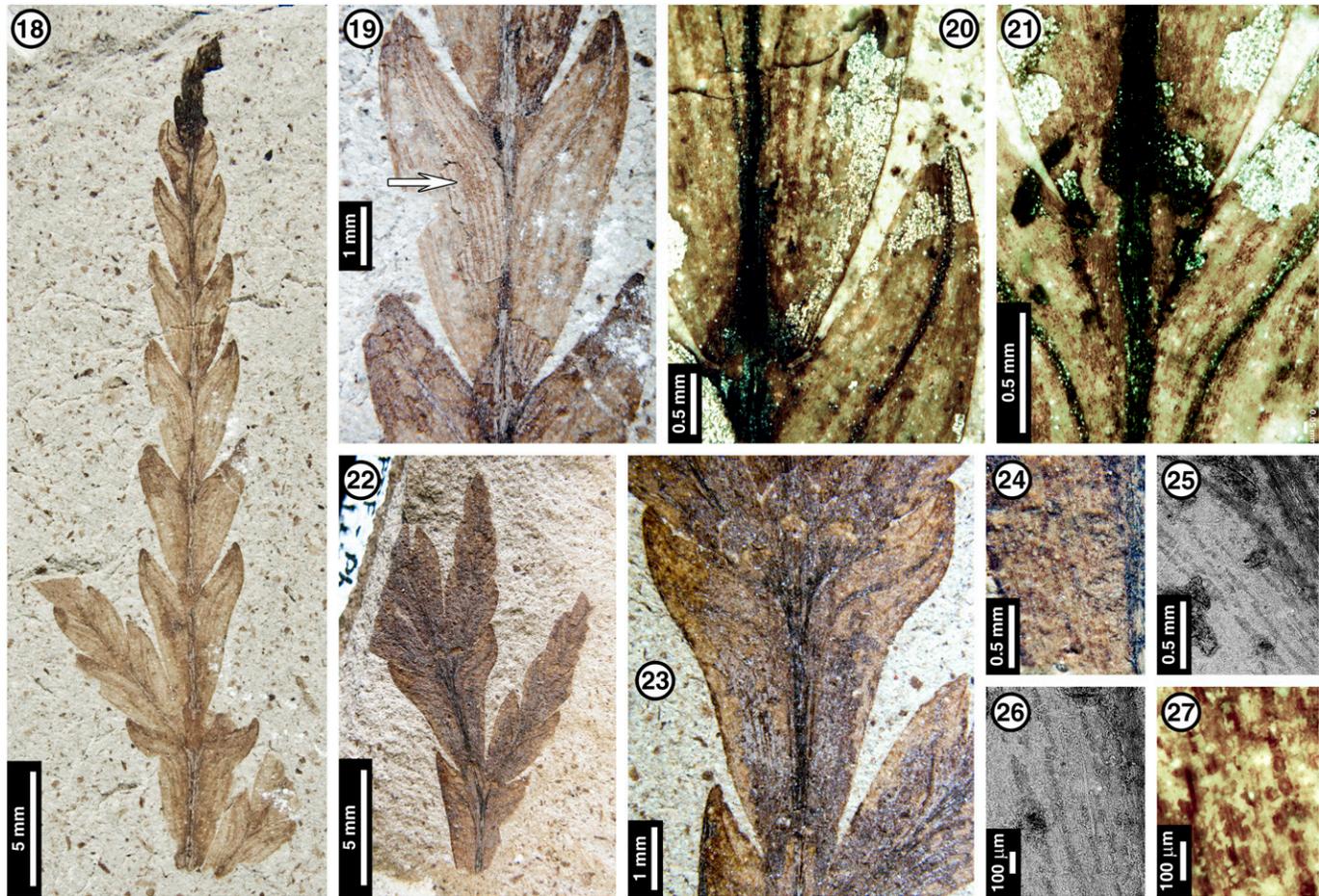
Genus—*Papuacedrus* H. L. Li, Journal of the Arnold Arboretum 34: 25 (1953).

Species—*Papuacedrus prechilensis* (Berry) Wilf et al., comb. nov.

Basionym—*Libocedrus prechilensis* Berry, Geological Society of America Special Paper 12: 61 (1938). Holotype: USNM 40387 (Figs. 2–9).

Other material here referred—Río Pichileufú, Ventana Formation, middle Eocene, Río Negro Province, Argentina (type locality of "*Libocedrus prechilensis*"). From quarry RP3: BAR 4741–4745. From near RP1: FCENCBPB 186 and 187.

Laguna del Hunco, Tufolitas Laguna del Hunco, early Eocene, Chubut Province, Argentina. From quarry LH1: MPEF-Pb 2100 and 2101. From LH2: MPEF-Pb 2102 and 2103. From



Figs. 18–27. Transitional-form foliage of *Papuacedrus prechilensis* comb. nov., from Laguna del Hunco. Figs. 18–21, MPEF-Pb 2100 (LH1). Figs. 22–27, MPEF-Pb 2117 (LH13). **18.** Complete specimen with expanded lateral leaves and keeled facial leaves with elongate, acuminate apices. Lateral leaves have convex bases, darkened margins, spreading, sharp-pointed free tips, prominent veins/resin canals, and conspicuous longitudinal bands of stomata subparallel to veins. The reduced, darkened terminal foliage is comprised of scale-like leaves like those subtending a seed cone (e.g., Fig. 38), not preserved here. **19.** Detail showing keeled facial leaves with elongate-acuminate apices. Arrow indicates a sand cast with bands of stomatal impressions. **20, 21.** Details under epifluorescence. Bright areas are sand-cast fragments. Note the longitudinal, discontinuous stomatal bands spread across the lateral leaves and the elongate, four-sided, irregular polygonal epidermal cells on both lateral and facial leaves. **22.** Complete specimen, showing branching and expanded lateral leaves. **23.** Detail of largest lateral leaves from Fig. 22, with convex bases and dark margins; spreading, sharp-pointed, free tips; and prominent veins/resin canals; three facial leaves at branching point above. **24–27.** Discontinuous bands of stomata of the basalmost lateral leaf in Fig. 22, visible under normal light at base (Fig. 24), under ESEM at base (Fig. 25), under ESEM in distal portion (Fig. 26), and under epifluorescence in distal portion, showing elliptical Florin rings (Fig. 27).

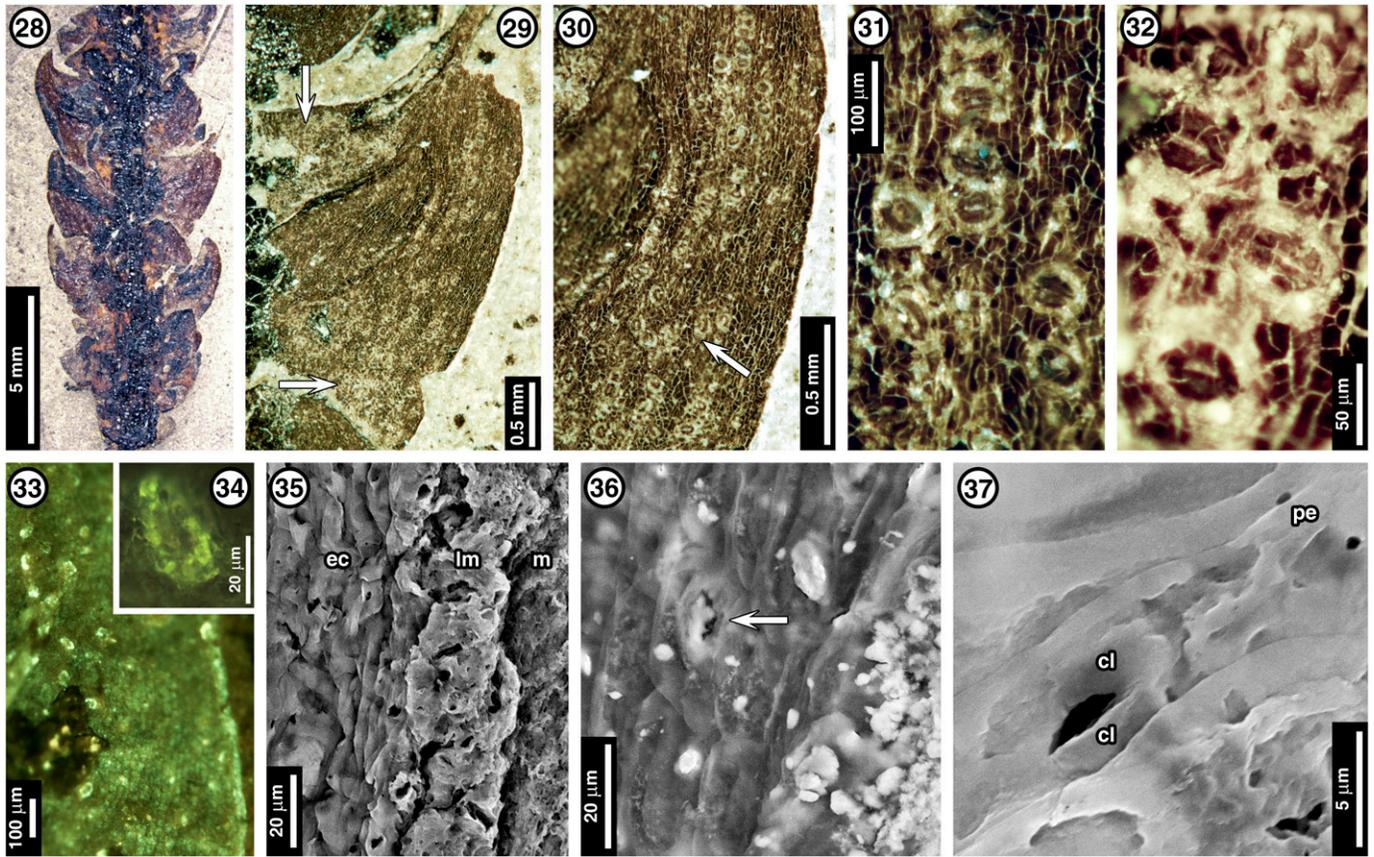
LH4: MPEF-Pb 3617. From LH6: MPEF-Pb 2104–2106. From LH13: MPEF-Pb 971 (“callitroid Cupressaceae” of Wilf et al., 2003: 122) and 2107–2120. From LH15: MPEF-Pb 2121. Laguna del Hunco, exact location unknown: FCENCBPB 180. From AL1: MPEF-Pb 3618–3622. From AL2: MPEF-Pb 3623.

Emended description—See Figs. 2–65. **Branching** (e.g., Figs. 10–12) in a single plane, up to five branch orders preserved, alternate or opposite on the lowest branching order, regularly opposite on higher-order branches. Branching initiates in axils of lateral leaves; facial leaves are the first produced (e.g., Fig. 14).

Foliage flat along branching plane, strongly dimorphic in transitional foliage (e.g., Figs. 18, 38), to less dimorphic (Fig. 10) or nearly monomorphic (Figs. 46, 47) in more mature forms. Leaves opposite-decussate or whorled (not distinguishable because facial leaf bases obscured by laterals), lateral leaves en-

larged, bilaterally flattened, facial leaves reduced, bifacially flattened.

Lateral leaves length to 11.0 mm, up to 15.7 mm in some leaves adpressed to low-order axes, with a single vein and prominent associated resin canal. Resin canal molds often filled with amber (Figs. 56, 57, 60). Outer leaf margins thickened, waxy (Fig. 35) and usually darker than adjacent lamina. Leaf pairs fused along the full inner margin that is adjacent to the axis (e.g., Figs. 7, 43, 54, 64); the outer margin of the leaf base (below the free tips) typically convex, rarely cuneate (Fig. 49). Free leaf tips spread up to 3.8 mm from the axis. Apex acute, sharp-pointed, oriented laterally to apically in relation to the axis, rarely recurved except in terminal leaves. **Facial leaves** basally covered by subtending lateral leaf pairs, visible length to 3.9 mm, width to 1.3 mm, conspicuously keeled (e.g., Figs. 18, 19, 48). Leaf shape rhomboid, broadly rounded to ovate, or ovoid, many having an elongated acuminate apex (Figs. 18,



Figs. 28–37. Transitional-form foliage of *Papuacedrus prechilensis* comb. nov., from Laguna del Hunco, with cuticle and coalified mesophyll, MPEF-Pb 2106 (LH6). Cuticle is fused to the organic-rich matrix; chemical isolation causes extensive degradation. Figs. 28–32, part 2106a, unprepared. Figs. 33–37, counterpart chip 2106c after clearing of coal with CrO_3 solution. **28.** Branch showing transitional leaves. **29, 30.** Arrangement of stomatal apparatus in discontinuous, subparallel to diagonally oriented (e.g., arrow in Fig. 30) bands. Note elliptical coalified structures preserving the shape of the thickened Florin rings on the far (outer) leaf surface; light areas within rings correspond to stomatal apertures. Arrows in Fig. 29 indicate regions of densely arrayed stomata visible as closely spaced light areas surrounding Florin rings. **31, 32.** Details of elliptical Florin ring coalifications (under epifluorescence). **33.** Inner view (epifluorescence) of elliptical, randomly oriented Florin rings glowing from outer surface of cuticle, elongate epidermal cells, and bright, thick, waxy zone on leaf margin at right. **34.** Detail (epifluorescence) of previous specimen, single elliptical Florin ring. **35.** Inner view (ESEM) of thick, waxy zone on leaf margin (lm), degraded epidermal cells (ec) at left and matrix (m) at right. **36.** Inner view (ESEM) of rectangular, striated epidermal cells with a single degraded stoma visible (arrow), margin torn adjacent to matrix (lower right), with thin cuticle (ESEM). **37.** Inner view (ESEM) of aperture surrounded by cuticular ledges (cl) and guard cell remnants including polar extension (pe) (ESEM).

19); shape usually incompletely preserved and partially obscured by lateral leaves.

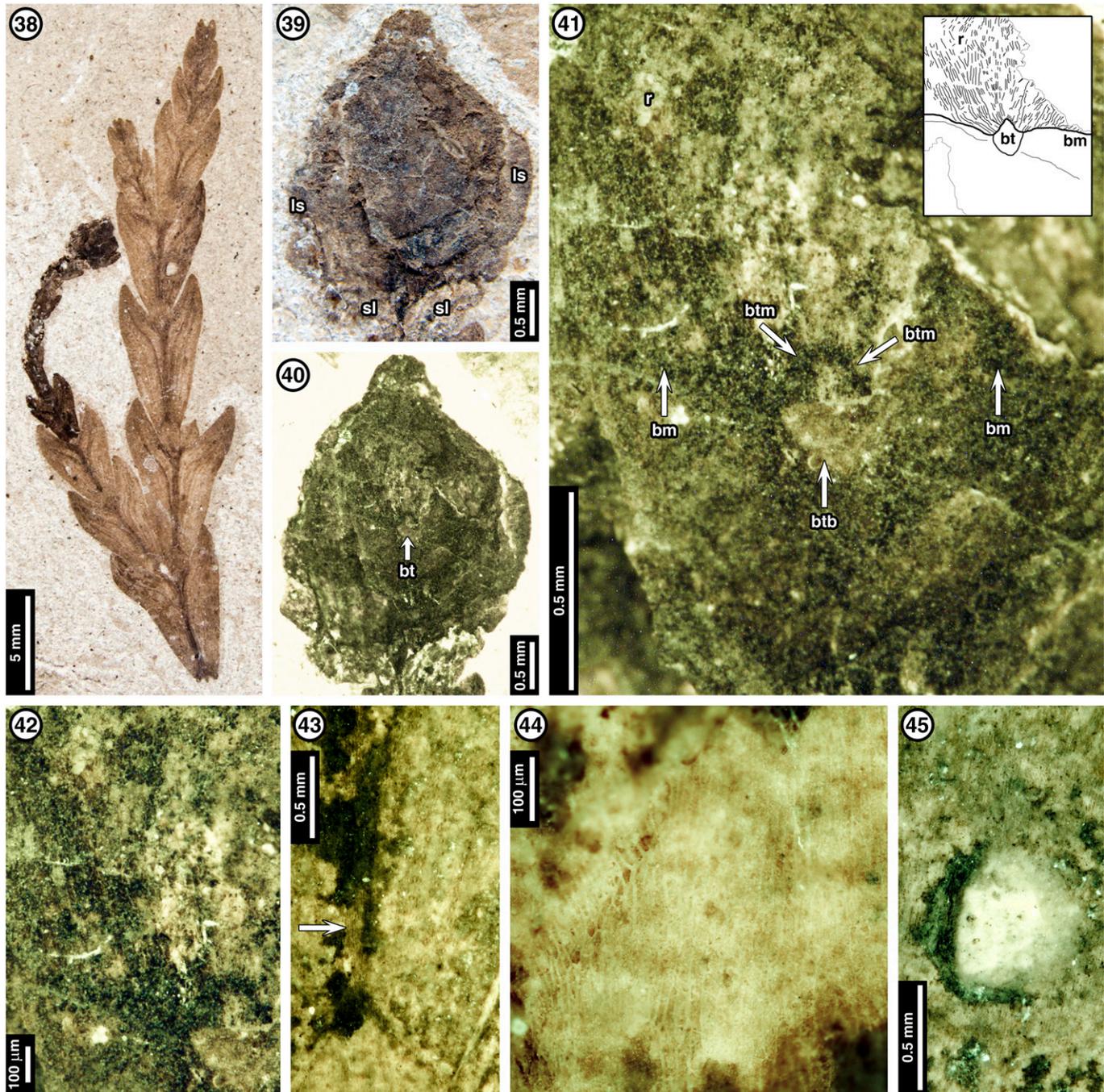
Epidermal cells (e.g., Figs. 8, 33, 36, 44, 45) elongate, striated, irregularly shaped, usually four-sided polygons. On apical margins of facial leaves, epidermal cells form a comb-like flange oriented approximately perpendicular to the margin, lacking scariose, individually projecting cells (Figs. 44, 53, 61, 62). *Stomata* (e.g., Figs. 19–27, 29–34, 43) occur on the largest lateral leaves, arranged in conspicuous, discontinuous, subparallel to diagonally (Fig. 30) oriented bands. Bands occur across most of the leaf width and are separated by clearly delineated nonstomatal areas. Stomatal apparatus often densely spaced, randomly or longitudinally oriented; Florin rings (Figs. 27, 31–34) elliptical, length 30–36 μm ; guard cell polar extensions visible (Fig. 37).

Immature seed cone (Figs. 38–42) oblong, 3.5 mm long, 2.9 mm wide, borne terminally on a shoot with ca. nine subtending, thickened, scale-like leaf pairs. The scale-like leaves become reduced and subtriangular toward the cone, and the terminal pair is adpressed to the cone (Figs. 38–40). Bract-scale complexes in two decussate pairs, preserved with the lower scales in lateral view

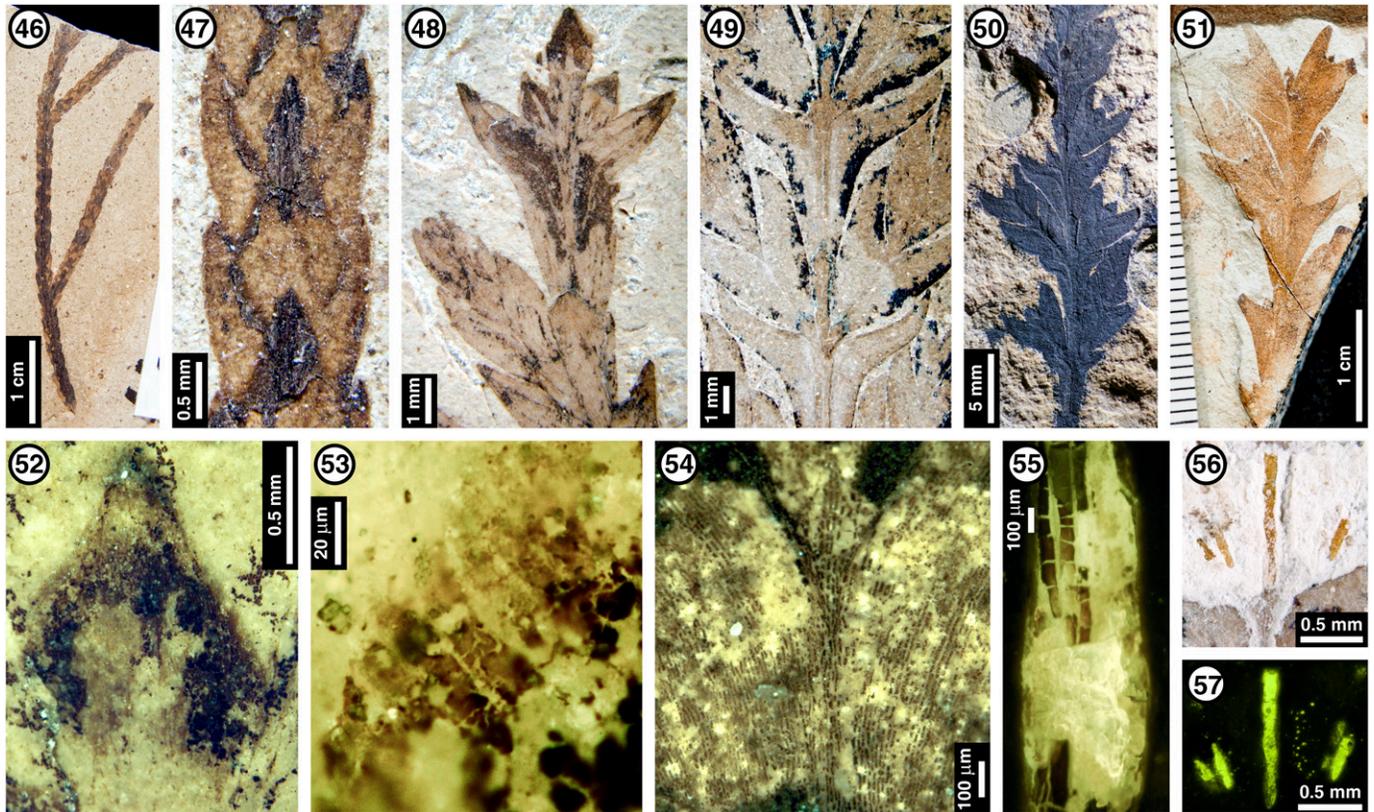
and one much larger upper scale complex occupying most of the facing view; upper scale apex rounded (Figs. 39, 40). Lower scale length about two-thirds that of the upper scale. Bract tip located at center of upper bract-scale complex, subtriangular, with convex and symmetrical margins and rounded base (Figs. 40–42). Scale rugosities radiate apically in subparallel, irregular arcs oriented away from the thickened margin of the bract (Figs. 40–42).

DISCUSSION

Assignment to Papuacedrus—The most relevant characters and supporting references for generic identification are outlined in Table 2 and partly illustrated in Figs. 66–77. The fossils are clearly members of Cupressaceae based on a combination of characters diagnostic of the family, especially the distinctively flattened, highly dimorphic foliage with one resin canal, and the valvate, oblong cone with decussate pairs of bract-scale complexes (e.g., Farjon, 2005). Among genera with these characters, only *Austrocedrus*, *Libocedrus*, and *Papuacedrus* have



Figs. 38–45. Immature seed cone of *Papuacedrus prechilensis* comb. nov. attached to transitional-form foliage, from Laguna del Hunco, MPEF-Pb 2121 (LH15). Figs. 40–45, epifluorescence. **38.** Branching shoot with dark, modified scale-like leaves subtending the attached seed cone, apex concealed under a lateral margin. The transitional-form leaves have the typical features described in text. **39, 40.** Seed cone, apex mechanically prepared (see Fig. 38), lateral leaf remnant visible at top. Most of the image is filled by the abaxial surface of an upper bract-scale complex in face view, having an apex with a rounded tip. Visible in both images (labeled in Fig. 39) are uppermost scale-like leaves (sl) addressed to the lower scales (ls) in lateral view; scale at right is better preserved. Visible only under epifluorescence are the central, subtriangular, flattened bract tip (bt), the lateral bract margin (as labeled in Fig. 41), and the large area of rugose folds radiating apically from the bract margin (as labeled in Fig. 41). **41.** Detail and schematic (inset) of center of upper bract-scale complex, showing the rounded bract tip base (btb), the darkened bract tip margins (btm), the darkened lateral bract margin (bm), and arcs of rugose folds (r) radiating apically from the bract margin. Gray lines in inset indicate fractures. **42.** Portion of same area taken at higher resolution, showing bract tip, bract margin, and curving, rugose folds (as labeled and diagrammed in Fig. 41) at higher contrast. **43.** Detail of fused lateral leaves subtended by a facial leaf, showing discontinuous bands of Florin rings spread across the width of a lateral leaf, epidermal cells comprising the zone of leaf fusion (arrow), and a prominent marginal flange on the facial leaf at bottom (see Fig. 44). **44.** Detail of flanged facial leaf in Fig. 43. Epidermal cells on most of the leaf are longitudinally elongate and irregularly rectangular, contrasting with the angled epidermal cells of the flange at left. Flange is smooth and comb-like, without scariosse projections. **45.** Detail of lateral leaf with hole-feeding insect damage. Note the three-dimensional preservation of dark reaction tissue at left and the field of epidermal cells surrounding the wound.



Figs. 46–57. Foliage of *Papuacedrus prechilensis* comb. nov. from Laguna del Hunco, selected photographs. Figs. 52–55 and 57, epifluorescence. **46**, **47**. Nearly monomorphic foliage form. MPEF-Pb 2116b (LH13). **48**. Branching detail at shoot apex, transitional foliage form, showing apical set of keeled facial leaves at initiation of opposite branches in lateral leaf axils. MPEF-Pb 2102 (LH2). **49**. Transitional-form foliage showing lateral leaves along lower-order axis having cuneate bases and widely spreading tips, suggestive of first transitional leaves of seedlings, and convex bases on the diverging lateral leaves (compare to Fig. 66). MPEF-Pb 2105 (LH6). **50**. Transitional-form specimen from Puesto Alvarez, ~5 km south of Laguna del Hunco. MPEF-Pb 3619 (AL1). **51**. Transitional-form specimen from Laguna del Hunco, University of Buenos Aires collections. FCENCBPB 190. **52**, **53**. Facial leaves with smooth, comb-like (nonscarious) marginal flanges. MPEF-Pb 2102 (LH2). **54**. Lateral leaves joined by epidermal cells visibly fused across the axis; facial leaf emerging top center at divergence point of lateral leaves from axis. MPEF-Pb 2112b (LH13). **55**. Amber visible in a stem fracture. MPEF-Pb 2120a (LH13). **56**, **57**. Branching and amber preservation within three-dimensional tissue replacement by silica. MPEF-Pb 2101b (LH1).

exactly two pairs of unequal-sized, decussate cone scales as in the fossils (Li, 1953; Farjon, 2005). *Calocedrus* Kurz has weakly dimorphic foliage and oblong seed cones with cone scales of unequal length, but the cones are dissimilar to those of Libocedrinae, having three (sometimes four) pairs of scales: the lower pair reduced, the middle pair spreading, the upper pair fused, and the middle and upper pairs of nearly equal length and width (Kvaček, 1999; Farjon, 2005).

Papuacedrus bears all the leaf and cone characters observed in the fossils (Table 2). Regarding the leaves, the unique transitional foliage of *Papuacedrus* (Figs. 67, 70–73; Florin and Boutelje, 1954; Friis, 1977; Offler, 1984) is clearly evident in most of the fossils (e.g., Figs. 18, 38), and it was from these specimens that we first recognized the genus. The large transitional lateral leaves in the fossils, whose tips extend nearly 4 mm from the axis, are in the size range of living *P. papuana* var. *papuana* (de Laubenfels, 1988; Farjon, 2005). As in extant plants, the transitional-form fossils have lateral leaves with thickened outer margins that are usually convex below the free tips; tips that spread apically, but can be recurved; sharp apices; inner margins that are fused along the length that is addressed to the axis; stomata in characteristic subparallel to diagonally oriented bands separated by nonstomatous areas; and a single vein with a resin canal (as is typical of

Cupressaceae; Farjon, 2005). Transitional facial leaves are large and keeled, often with an acute or elongated acuminate apex bearing a smooth, comb-like flange that lacks projecting cells as seen in *Austrocedrus* and *Libocedrus* (Figs. 44, 53, 61, 62, 72, 73; see Florin and Boutelje, 1954). Late transitional and mature foliage forms of living *Papuacedrus* have reduced lateral leaves, becoming imbricate and sometimes monomorphic with facial leaves (Fig. 69); stomata tend to be suppressed (Offler, 1984). Thus, some of the fossils appear to represent late transitional to mature foliage forms (e.g., Figs. 2–5, 10, 13, 58), and one shows nearly monomorphic leaves (Figs. 46, 47). We note that the linear juvenile leaf form of *Papuacedrus*, only present on the seedling main axis in living plants (Fig. 66; Offler, 1984), was not found in the fossils, but one specimen has lateral leaves with cuneate bases on its lowest branch order that are suggestive of transitional leaves on the first branches of seedlings (Figs. 49, 66; see also Offler, 1984: figs. 25g, 26a).

The seed cone from LH (Figs. 38–42) is borne terminally on one of the best-preserved and most diagnostic examples of transitional foliage. Subtending leaves are modified and scale-like, a subtriangular, nonspiny bract tip is located in the central area of the upper bract-scale complex, and the scale bears rugose ornamentation, radiating from the bract margin. This suite of charac-

TABLE 2. Character state comparisons of Patagonian fossils to the relevant extant genera. Boldfaced text indicates a shared character state; for leaf dimensions, shared status is based on overlap with the maximum fossil value.

Character	Fossils	<i>Papuacedrus</i>	<i>Libocedrus</i>	<i>Austrocedrus</i>
Facial leaves				
Length (mm)	≤ 3.9	1–8	1–5	1–2
Marginal flange scarioso	No	No	Yes	Yes
Lateral leaves				
Length (mm)	≤ 15.7	2–20	2–7	≤ 15
Fused across axis	Yes	Yes	No	No
Margin marked	Yes	Yes	Yes	No
Margin shape below free tip	Convex	Convex	Variable	Concave/decurrent
Apex sharp or blunt	Sharp	Sharp, rarely blunt	Variable	Blunt, rarely sharp
Resin canal prominent	Yes	Yes	No	No
Stomata on lateral leaves (lower surface)				
Confined to medial strips	No	No	Yes	Yes
Discontinuous, clearly separated rows	Yes	Yes	No	No
Orientation	Longitudinal or random	Longitudinal or random	Longitudinal or random	Longitudinal
Ovulate cone				
Bract tip position near scale center	Yes	Yes	Yes in <i>L. austrocaledonica</i>, <i>L. bidwillii</i>, <i>L. chevalieri</i>	No, at apex
Bract tip an elaborated spine	No	No	Yes	No
Abaxial bract-scale surface	Rugosities, radiate apically from bract margin	Rugosities, radiate apically from bract margin	Slightly rugose in <i>L. bidwillii</i> , <i>L. chevalieri</i>	Striated longitudinally, full length
Subtending leaves reduced, scale-like	Yes	Yes	Yes	No

Notes: Principal sources: Florin and Boutelje (1954); Offler (1984); Farjon (2005); Paull and Hill (2008); authors' observations. Supplemental sources: Friis (1977); Van Royen (1979); de Laubenfels (1988); Hill and Carpenter (1989); Johns (1995); Kvaček (1999); Whang and Hill (1999).

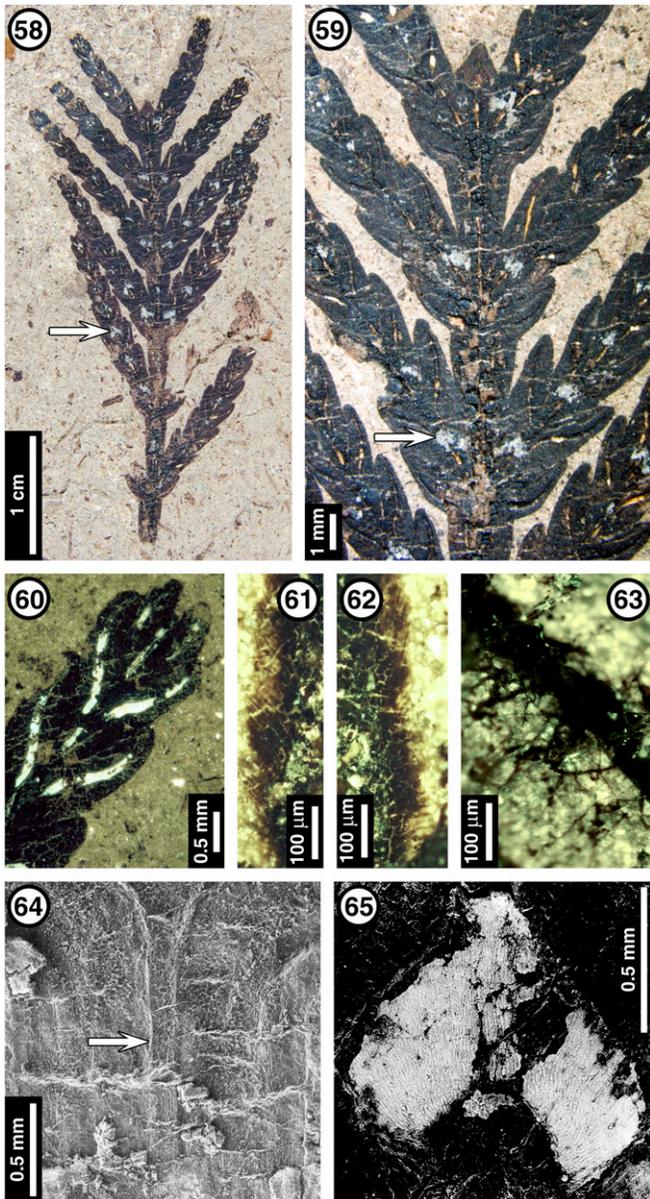
ters is diagnostic of *Papuacedrus*. Indeed, Li (1953) emphasized the importance of the centrally located, thickened, shield-like (vs. spiny as in *Libocedrus*, see later), triangular bract-tip in his original diagnosis of *Papuacedrus*. The fossil compares well with immature *Papuacedrus* cones (Fig. 77), in which the length ratio of the lower to the upper scale is much higher than in adult cones (Figs. 74, 75; 2:3 vs. 1:3–1:2; Farjon, 2005) from incomplete development and enlargement of the upper scale (Gibbs, 1917). In addition, the bract tip is more adpressed to the scale in immature cones (compare Figs. 75 and 77), which appears to be the case in the fossil cone (Figs. 40–42). The length of the fossil cone is less than those of adult cones of *Papuacedrus*, *Austrocedrus*, and *Libocedrus* (3.5 mm vs. 8–18 mm for *Papuacedrus* and *Libocedrus* and 7–14 mm for *Austrocedrus*; Farjon, 2005). Moreover, the fossil cone scales are fused, unlike mature, dehiscent, cones (Fig. 74). This combined evidence indicates that the fossil cone was immature at the time of preservation.

In contrast to *Papuacedrus*, *Libocedrus* and especially *Austrocedrus* share few character states with the fossils and can be eliminated via either leaf or cone characters (see Table 2). With regard to the leaves, both *Austrocedrus* and *Libocedrus* have stomata on lateral leaves that are confined to medial bands, where they are closely packed and not spread out into partial, separated bands as in the fossils (Florin and Boutelje, 1954; Friis, 1977; Paull and Hill, 2008). In addition, marginal flanges on the facial leaves in these genera have scarioso ornamentation, whereas the fossils have a smooth, comb-like flange (see also Florin and Boutelje, 1954: text fig. 2, plate IV; Paull and Hill, 2009: fig. 8f). Moreover, *Libocedrus* lateral leaves are not fused to each other, are shorter and less spreading than the fossils, and they are imbricate in many species, even in transitional-form foliage and unlike the fossils (Table 2). *Austrocedrus* lateral leaves, unlike the fossils, are unfused, their margins are not well demarcated ("marked" sensu Florin and Boutelje, 1954) due to their rounded shape in the lateral plane (authors'

observations), the margin below the free tip is typically concave/decurrent, and the apex is blunt. The stomata are consistently longitudinally oriented, whereas the fossils show longitudinal, subparallel, and diagonal orientations (Figs. 27, 29–33). In addition, *Austrocedrus* facial leaves are smaller than those of the fossils (Table 2).

Regarding the seed cone, *Austrocedrus* has very few character states in common with the fossil (Table 2; Li, 1953; Farjon, 2005; Paull and Hill, 2008). A conspicuous character in *Austrocedrus* is that the upper bract is much larger in relation to its subtended scale, and thus the bract tip is located close to the scale apex rather than centrally as in the fossil and extant *Papuacedrus*. Subtending leaves of *Austrocedrus* cones are not modified and thickened, in contrast to the modified leaves in extant *Papuacedrus* and the fossil. *Libocedrus* seed cones, like the fossil, have modified subtending leaves, and in two extant species the upper scales bear slightly rugose abaxial surfaces (*L. bidwillii*, *L. chevalieri*). In three species (*L. austrocaledonica*, *L. bidwillii*, *L. chevalieri*), the bract tip is more or less centrally positioned on the scale (e.g., Farjon, 2005). However, all *Libocedrus* bract tips, even in immature cones so long as these have developed their valvate morphology, are elaborated into projecting spines on both pairs of scales (Li, 1953; Tomlinson et al., 1993; Farjon, 2005). These spines do not occur in *Austrocedrus*, *Papuacedrus*, nor the fossil cone, where the bract tip is symmetrical and has an intact, thickened margin, demonstrating that it is not a broken remnant of a long spine (Figs. 40–42). There are also no projections arising laterally from the lower cone scales of the fossil.

The holotype of "*L.*" *prechilensis* (Figs. 2–9, from RP) does not preserve many of the characters in Table 2 but still can be linked to the other fossils and to extant *Papuacedrus*. The holotype has fused lateral leaves with darkened margins, convex margins below the sharp apices, and prominent resin canals. The specimen also lacks the imbricate leaves typical of *Libocedrus*



Figs. 58–65. Foliage of *Papuacedrus prechilensis* comb. nov., from Río Pichileufú. BAR 4742a (RP3). Specimen is coalified with patches of facial leaf cuticle visible (light areas). Figs. 60–63, epifluorescence; Figs. 64, 65, ESEM. **58, 59.** Branching and foliage. Note opposite branching; light-colored cuticles of facial-leaves overlying coal (some indicated by arrows); and light-colored amber in resin canals. **60.** Detail of amber fluorescing in resin canals at a shoot tip. **61, 62.** Left and right margins of the most apical facial leaf preserved on the lowest-order axis (see Fig. 59), with comb-like flange. **63.** Fungal hyphae on leaf surface. **64.** Well-preserved zone of fusion (arrow; in relief) between lateral leaves at base of specimen, joining the inner margins where they are adjacent to the axis; divergence at top (light bleach treatment; stomatal areas not well preserved). **65.** Facial leaf cuticle with elongate epidermal cells, flange not preserved.

and the decurrent lateral-leaf bases and reduced facial leaves of *Austrocedrus*. We interpret the “*L.*” *prechilensis* holotype as late transitional- to mature-form foliage of *Papuacedrus*.

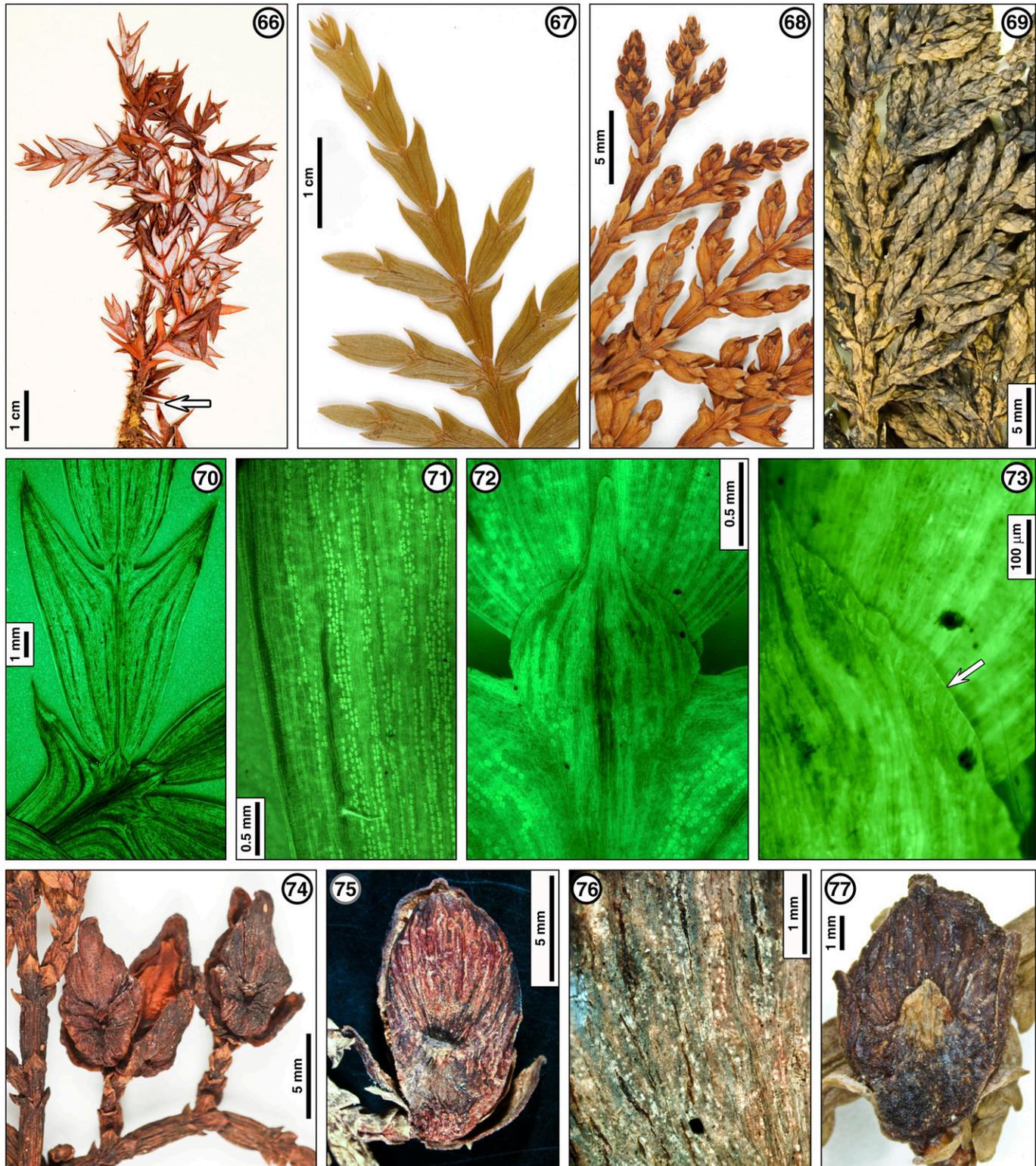
One of the new specimens from RP3 (BAR 4742; Figs. 58–65) further links Berry’s holotype to extant *Papuacedrus* and to

the specimens from Laguna del Hunco. This specimen represents a foliage form similar to the holotype. It preserves the fusion zone between lateral leaves, as well as large facial leaves with some cuticle and comb-like flanges without scariose projections, best preserved on the most terminal preserved facial leaf.

We note that Paull and Hill (2008, 2009) have described extant lateral leaves of both *Austrocedrus* and *Libocedrus* as fused basally (below the free tips). This contrasts with previous literature describing the lateral leaves of these genera in close contact only, and not fused with tissue continuous along the full inner margin that is adjacent to the axis, typical for *Papuacedrus* (Florin and Boutelje, 1954; Friis, 1977; Hill and Carpenter, 1989; Whang and Hill, 1999) and well displayed in the Patagonian fossils (Figs. 7, 43, 54, 64). Likewise, we have not encountered any extant specimens of *Austrocedrus* or *Libocedrus* with lateral leaf fusion except perhaps at the basalmost point, covered by facial leaves and similarly obscured in the fossils. At least some of the Oligocene leaf specimens from Lea River, Tasmania that Paull and Hill (2008: fig. 8) placed in *Austrocedrus australis* have lateral leaf fusion along the full inner margin that is adjacent to the axis as well as distinctly convex lateral leaf bases, and these should be re-examined for possible affinity to *Papuacedrus*.

In summary, all the Patagonian fossils considered here can be confidently assigned to *Papuacedrus*, which is revealed as a component of Eocene forests in the region for at least 4.4 Myr, the temporal separation of Laguna del Hunco and Río Pichileufú. All observable character states of the fossils are shared with extant *Papuacedrus*, including the seed cone characters Li (1953) originally used to diagnose the genus and several foliar characters noted by Florin and Boutelje (1954) that independently confirmed Li’s segregation of *Papuacedrus* from *Libocedrus*. It should be noted that while the importance of these seed-cone and leaf characters is still recognized (e.g., Johns, 1995; Farjon, 2005), the phylogenetic significance that Li (1953) ascribed to spirally arranged microsporophylls in *Papuacedrus* was rejected by Florin and Boutelje (1954), who sectioned pollen cones and found them to be arranged in whorls of four and not spirally; the arrangement has been subsequently described as whorled (when crowded on the axis) or decussate as in *Austrocedrus* and *Libocedrus* (de Laubenfels, 1988; Farjon, 2005). Thus, the absence of male strobili in our material is not critical to diagnosis in the context of Li’s circumscription of *Papuacedrus*.

Species assignment—We propose *Papuacedrus prechilensis* comb. nov. with two caveats directed to future studies. First, *P. prechilensis* has no currently known character states that are distinguishable from extant *P. papuana*. However, there are not sufficient whole-plant data, for example, from additional organs, developmental stages, or anatomical preservation, to justify a synonymy (e.g., Rothwell and Stockey, 1991). Future discoveries may clarify this issue by revealing more characters (e.g., Stockey et al., 2001). Second, the fossils from Laguna del Hunco preserve more diagnostic characters than those from Río Pichileufú, the type locality (strata 4.4 Myr younger than LH), due to preservation of the only known, attached seed cone and the most typical, greatly enlarged transitional foliage. It is possible that further discoveries will show that the specimens from the two localities differ, which may warrant a separate species for each site. However, based on current data, there are no criteria to separate two fossil species. More generally, the two



Figs. 66–77. Extant *Papuacedrus papuana* (New Guinea), showing reference characters for the fossils. **66.** Seedling. Note linear juvenile leaves emerging from main axis (one at arrow). This juvenile foliage form, not seen in the fossils, is restricted to the seedling main axis. Note that many of the transitional lateral leaves on the earliest branches have cuneate-decurrent bases, which we also found on other seedlings examined. Compare to Fig. 49. MEL 620556, photo by C. Gallagher. **67.** Transitional-form shoot, showing expanded, fused lateral leaves similar to most of the fossils (and characteristic of *P. papuana* var. *papuana*), with convex bases; spreading, sharp-pointed, free tips; and prominent veins/resin canals. NSW 522585. **68.** Late-transitional to mature foliage form, showing reduced lateral leaves, especially on higher-order axes. NSW 522581. Compare to Figs. 2–5, 10, 13, 58. **69.** Nearly monomorphic adult foliage form. Dimorphism and spreading lateral leaf tips are only well expressed on the lower-order axis and at branch points. K ex A s.n., L. J. Brass 9242.

floras share many other gymnosperm and angiosperm species (Appendix 1; Wilf et al., 2005a: table A4), and thus the con-specificity of the fossils is not unrealistic.

Other fossil occurrences of *Papuacedrus* and apparent stasis in *Libocedrinae*—The few other examples of *Papuacedrus* in the fossil record (Table 1), while from more fragmentary specimens than *P. prechilensis*, also display no recognizable differences from extant *P. papuana*. *Papuacedrus australis* Hill and Carpenter (1989), known from vegetative shoots with cuticle from the early Oligocene Cethana and Oligocene-Miocene Pioneer localities of northern Tasmania (see Carpenter et al., 1994 for additional site information), was reported by the authors to be indistinguishable from the three living species of *Papuacedrus* valid at the time; all three are now synonymized as two varieties of *P. papuana* (Johns, 1995; Farjon, 2005). *Papuacedrus shenii* (Zhou and Li, 1994), from the early middle Eocene Fossil Hill Formation, Fildes Peninsula, King George Island, Antarctica (Shen, 1999), about 2300 km SSE of Laguna del Hunco, is based on fragmentary vegetative shoots. The original photographs of *P. shenii* that we examined show lateral leaf characters that are diagnostic of *Papuacedrus* (especially for Zhou and Li, 1994: plate 3, figs. 4 and 4a), including the prominent ridge of fusion along the full contact zone between lateral leaves, and the faint but distinct longitudinal bands of stomatal impressions across the full widths of the leaves. In addition, *P. shenii* lateral leaves have darkened, well-defined margins, sharp apices, and prominent resin canal molds. Zhou and Li (1994: p. 216) justified separating *P. shenii* from the three, then-valid, species of *Papuacedrus* and from the fossil *P. australis* “by the long and narrow marginal leaves of the young shoots.” However, the illustrated leaf proportions of *P. shenii* fall well within the range of variation of *P. papuana* and of the Patagonian fossils, especially for long lateral leaves addressed to lower-order axes (Figs. 10, 11, 14). *Papuacedrus* sp., from the early Miocene St. Bathans Paleovalley outcrops of central Otago, New Zealand (Pole, 2007), based on vegetative branches with cuticle, has characteristic fused lateral leaves with convex bases, as in extant *Papuacedrus*.

In addition to *Papuacedrus*, many other fossil *Libocedrinae* also do not have informative character differences from extant species (although several clearly extinct species have been found, e.g., Hill and Carpenter, 1989). For example, Paull and Hill (2009: p. 381) remarked that “*Libocedrus* leaf morphology has remained much the same for 30 Myr.” Seed cones of *Austrocedrus tasmanica* and another probable species of *Austrocedrus* have been described from Tasmania (Table 1; Hill and Carpenter, 1989; Paull and Hill, 2008). These differ from extant

A. chilensis mainly in their smaller size and a proportionally larger lower vs. upper cone scale in *A. tasmanica*; both of these characteristics could be due to immaturity, as discussed earlier for *Papuacedrus*.

From these examples, including *P. prechilensis*, a question for future work is whether there is indeed a long history of morphological stability within the crown lineages of *Libocedrinae* or if significant character evolution can be detected following new discoveries and improved whole-plant concepts.

Biogeography and biome interpretation—Recognizing *Papuacedrus* in the early and middle Eocene of Patagonia has several implications. The link to dry and cold environments of southern South America that was suggested by Berry’s (1938) analysis of “*Libocedrus*” *prechilensis* is removed: the climatic range of *Austrocedrus chilensis* is completely separate from that of *Papuacedrus*, consisting of areas with significant water deficits, cool to freezing winters, or both (e.g., Veblen et al., 1995; Paruelo et al., 1998). Simultaneously, a new connection is established to tropical west Pacific, montane forests, providing further evidence for the severe contraction of numerous, formerly widespread Gondwanan plant lineages to Australasian rainforests due to Cenozoic climate change (e.g., Hill and Carpenter, 1991; Hill, 2004; Zamalao et al., 2006). The temporally and spatially expanded fossil history of *Papuacedrus*, demonstrated here, further highlights the biological importance of the New Guinea highlands, which contain vast numbers of endemic and relict taxa still being discovered (e.g., Diamond, 1985; Sekhran and Miller, 1996; Beehler et al., 2007).

The current fossil record for *Austrocedrus*, *Libocedrus*, and *Papuacedrus* (Table 1 and the present paper) outlines biogeographic hypotheses that can be tested, and no doubt modified, with future fossil discoveries. The first occurrence of *Papuacedrus* in Australia is early Oligocene (Hill and Carpenter, 1989), and its absence, so far, from Australian Paleocene and Eocene floras includes a late Paleocene locality that contains several other cupressaceous genera (Whang and Hill, 1999). *Papuacedrus* is also absent from well-collected early Paleocene localities in Patagonia (Iglesias et al., 2007). Thus, *Papuacedrus* may have evolved by the Eocene in Antarctica or southern South America and subsequently entered Australia, most likely before the ~32 Ma deepwater opening of the Tasman Strait (Lawver and Gahagan, 2003). Arrival in New Zealand by the Oligocene-Miocene (Pole, 2007) probably occurred via a dispersal event because New Zealand had long been separated (>75 Ma) from other Gondwanan land masses and may have been partially submerged during the Oligocene (Cooper and Millener, 1993).

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Compare to Figs. 46, 47. **70–73.** US 3440120, transitional foliage form, under epifluorescence. **70.** Leaf undersides showing branching, typical transitional leaf form, and stomatal distribution across leaves (bright areas are numerous, close rows of Florin rings). Compare to Figs. 29, 43, others. **71.** Detail of previous, showing bright Florin rings in characteristic partial, discontinuous bands. Compare to Figs. 18–27, 29–31, 43, others. Note thickened, waxy margin at left (compare to Figs. 33, 35). **72.** Single facial leaf with keel, extended acuminate apex, stomata (also visible on adjacent lateral leaves), and the characteristic comb-like marginal flange (see Fig. 73). Compare to Figs. 18–21, 43, 48, 52. **73.** Detail of previous, showing the smooth flange margin (arrow), lacking scariose projections. Compare to Figs. 44, 53, 61, 62. **74.** Pair of mature, dehisced seed cones borne terminally on shoots with reduced, scale-like leaves. Note the unequal sizes of the two pairs of decussate bract-scale complexes; bracts covering ca. half the upper scales; exerted bract tips near centers of upper bract-scale complexes; rugose upper-scale surfaces distal to and radiating from the bract margin; and seed wings visible inside the right half of the left cone. NSW 522580. **75–77.** US 3130489. **75.** Single mature, dehisced seed cone, showing subtending shoot with reduced scale-like leaves, rounded apex tip, exerted bract tip, and rugose folds emanating apically from bract margin. **76.** Epifluorescence detail of rugose area in previous, showing folds and bright bands of stomata. **77.** Immature seed cone, ca. twice the length of the fossil cone (7.4 vs. 3.5 mm; Figs. 38–42). Compared to adult cones (Figs. 74, 75), note the much greater proportional length of lower to upper bract-scale complexes, the proportionally wider apex of the upper scale, and the flattened, central bract tip; all these characters are shared with the fossil cone (Figs. 38–42). Also note bract margin, rugose upper-scale surface distal to the bract margin, and part of subtending shoot with reduced, scale-like leaves at bottom right.

Papuacedrus eventually suffered extinction in all areas but the New Guinea and Moluccan highlands. The history of *Austrocedrus* (Table 1), here excluded from the Paleogene of South America, suggests that late dispersal and source extinction in Australia could explain its currently restricted distribution in southern South America, whereas *Libocedrus* so far appears to have had a more limited geographic range within Australasia throughout its history.

Papuacedrus prechilensis contributes to an increasingly convincing case for a biome similar to extant subtropical, or tropical montane, rainforests in the Eocene of Patagonia. Although drought-tolerance of *Papuacedrus* has not yet been studied, the taxon has thin-walled foliar transfusion tracheids that are expected to collapse under mild leaf water deficits (T. Brodribb, University of Tasmania, personal communication), leading to early vascular failure during drought following the model shown for *Podocarpus* (Brodribb and Holbrook, 2005). The fossils have extremely thin cuticle incompatible with limited water availability (Figs. 35, 36). Along with the physiological tolerances and habitat preferences of the other rainforest conifers discussed earlier (Brodribb and Hill, 1998; Appendix 1), 2.5 m is a minimum estimate, with limited rainfall seasonality, of Eocene mean annual precipitation (MAP) for Laguna del Hunco and Río Pichileufú. Abundant rainfall and absence of frost, sustained over millions of years, are highly plausible explanations for the elevated plant, insect, and insect-feeding richness of these sites, which are premier examples of high biodiversity on the South American continent occurring early in the Cenozoic (Berry, 1938; Wilf et al., 2003, 2005a, b; Petrusevičius, 2009; Sarzetti et al., 2009).

In this context, the leaf-area estimate of 1.1 m minimum MAP for Laguna del Hunco (Wilf et al., 2005a) bears discussion. Although taphonomic filtering of large leaves probably accounts in part for the low value (Roth and Dilcher, 1978; Greenwood, 1992), another factor highlighted by our results is the lack of subtropical, Gondwanan rainforest floras in the leaf-area calibration data (Wilf et al., 1998). This point is well illustrated by a brief examination of Australian vegetation, wherein subtropical rainforests generally have much smaller leaves than tropical rainforests (Webb, 1959). For example, the Simple Nothophyll Vine Forest (SNVF) of northeastern New South Wales, at ca. 150–800 m a.s.l., has high plant diversity, similar climate to the Eocene paleoclimates inferred here (mean annual temperature ca. 17.5°C, no frost, MAP 2–2.5 m), and similarity to the fossil floras at the family level (Webb et al., 1984; Kooyman, 2005; Royer et al., 2009). A preliminary leaf-area analysis of 183 woody SNVF species from this area (R. Kooyman, Macquarie University, unpublished data), using the calibration of Wilf et al. (1998), generates an MAP estimate of 1.4 m, >30% below the actual value and very similar to the leaf-area estimate of MAP for the Laguna del Hunco flora. Clearly a full quantitative investigation of leaf area vs. rainfall in Gondwanan vegetation, and its variation with temperature, would be very useful for future paleoclimate studies of Gondwanan fossil floras.

Papuacedrus currently grows up to ca. 50 m tall, though more often up to ca. 20 m, and it is an emergent even in cloud forests (e.g., Wade and McVean, 1969; Van Royen, 1979; Farjon, 2005). We note that the *Papuacedrus* foliage studied here is mostly of the transitional form, indicating the likely preferential fossilization of young, lake-margin plants growing at the forest edge. Presumably, Eocene *Papuacedrus* occupied the upper forest strata, along with other probable emergents from the fossil floras such as *Araucaria* and the Podocarpaceae. These taxa currently

associate with *Papuacedrus*, especially in the highest, wettest parts of its range, where it is most abundant (Wade and McVean, 1969; Farjon, 2005). The relatively high abundance and richness of fossil *Papuacedrus*, *Araucaria*, and Podocarpaceae at quarry LH13 (Wilf et al., 2005a) may represent a similar, extremely wet association, consistent with some topographic relief being present during the Eocene. Alternatively, extant montane lineages may have changed or narrowed altitudinal ranges since the Eocene as their geographic ranges contracted.

Conclusions—We have recovered abundant fossils equivalent to “*Libocedrus*” *prechilensis* Berry (1938), from the early Eocene Laguna del Hunco and middle Eocene Río Pichileufú floras of Patagonia, Argentina. This species was previously only known from the holotype, from Río Pichileufú. The original identification stemmed from perceived similarity to extant *Austrocedrus* (*Libocedrus*) *chilensis*, whose current range includes dry, cold, Patagonian steppe margins near the fossil sites. Berry’s species presents a legacy challenge to emerging data favoring a frost-free, rainforest biome interpretation of the fossil floras and demonstrating little compositional affinity to plants now living near the fossil localities.

The new fossil specimens from Patagonia are better preserved than the holotype, and the Laguna del Hunco material includes an immature seed cone and the best preservation of foliar characters. Numerous diagnostic characters, including the distinctive transitional foliage form and stomatal distribution patterns as well as cone morphology, allow confident assignment of all the Patagonian fossils to *Papuacedrus*, a montane rainforest conifer currently restricted to New Guinea and the Moluccas. *Papuacedrus prechilensis* comb. nov. has no currently known character states that are distinguishable from extant *P. papuana*, and the expanded lateral transitional leaves of the fossils closely resemble *P. papuana* var. *papuana*. However, more organ discoveries are needed before a synonymy could be considered.

These results, including the first occurrence of *Papuacedrus* in South America and the first fossil cone of the genus, add to the developing record of fossil Cupressaceae from South America and have diverse implications. First, a modern, southern South American link for the fossil Patagonian floras is removed and replaced by a new tropical West Pacific connection, joining a growing list (Appendix 1) and greatly expanding the biogeographic history of *Papuacedrus*. Second, one of the few possible dry-biome indicators for the Patagonian fossil floras is now eliminated and replaced by a rainforest indicator. Along with an expanding group of other high-rainfall specialist lineages in the flora and previous temperature proxies, this study further improves the case for conditions similar to subtropical, or tropical montane, rainforest in Eocene Patagonia that had not been clear from leaf physiognomic analysis alone. Third, high precipitation and a lack of frost, combined with biotic interchange both with Antarctica (and beyond to Australasia) and the neotropics, emerge as the most logical explanations for the extraordinary diversity of plants, insects, and insect-feeding damage found at Laguna del Hunco and Río Pichileufú.

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APPENDIX 1. Biogeographic discussion of the Laguna del Hunco (LH) and Río Pichileufú (RP) floras.

The nonanalog combination of tropical and Gondwanan, including apparently cold-temperate, elements led to Romero's (1978, 1986, 1993) characterization of these and some other regional Paleogene assemblages as a "mixed paleoflora" (*paleoflora mixta*). Although Romero's classic concept is still valid in a broad sense and continues to be the topic of biogeographic analyses (Hinojosa and Villagrán, 1997, 2005; Villagrán and Hinojosa, 1997; Gayó et al., 2005), it was justified with extensive use of Berry's original taxonomic determinations, which cannot currently be considered reliable (e.g., Dilcher, 1973; present paper). Furthermore, the "mixing" of characteristically tropical and temperate extant lineages in Eocene mid-latitude floras is a well-known phenomenon globally that reflects the intense global warmth, equable and moist mid- and high-latitude climates, and poleward biotic migration of the time period, rather than a regional property of South American floras (Reid and Chandler, 1933; Greenwood and Wing, 1995; Pole and Macphail, 1996; Wilf, 2000). Thus, most mid-latitude Eocene floras are "mixed," and the term no longer serves to distinguish patterns in studies of Gondwanan biogeography.

The floras are better understood as having three distinct biogeographic components: Australasian subtropical and tropical rainforest, neotropical rainforest, and Gondwanan temperate rainforest. The Australasian component is the best known. Including some recently discovered material and that listed by Wilf et al. (2005a), this includes a number of groups now restricted to tropical, primarily rainforest regions, including *Acmopyle* (Podocarpaceae, previously known from RP: Florin, 1940a, and recognized by us at LH and RP; see also Hill and Brodribb, 1999),

extant in New Caledonia and Fiji; *Dacrycarpus* (Podocarpaceae, recently recognized at LH; Wilf et al., 2007), extant from Burma to New Zealand; *Akania* (Akaniaceae, LH, RP; Romero and Hickey, 1976; Gandolfo et al., 1988), extant in subtropical rainforests along the New South Wales–Queensland border; and three species of *Gymnostoma* (Casuarinaceae, LH; Zamalao et al., 2006), extant in New Caledonia, Fiji, Malesia, and northeastern Queensland. The neotropical relationships to date are less clear, despite indications from past literature that are mostly based on obsolete identifications. Reliable examples of one neotropical rainforest endemic, *Bixa* (Bixaceae, LH; Gandolfo et al., 2007), have emerged from recent collections. Purported leaves of *Roupala* (Proteaceae), another neotropical endemic, have been described from LH (Durango de Cabrera and Romero, 1988; González et al., 2007), but this genus has highly variable foliage, and the identification must be regarded as tentative. *Retrophyllum* (Podocarpaceae, recently recognized at LH and RP; Wilf et al., 2007) is disjunct between the neotropics and New Caledonia, Fiji, and the Moluccas. Both *Dacrycarpus* and *Retrophyllum* are known from other, possibly Eocene deposits in Chile and Argentina (Florin, 1940b; Greenwood, 1987; Hill and Brodribb, 1999). Taxa with temperate Gondwanan affinities include a "*Laurelia*" considered to belong in *Laureliopsis* (Atherospermataceae, LH, RP; Berry, 1935c, 1938; Schodde, 1969; Renner et al., 2000), extant in southern Argentina and Chile; *Orites* (Proteaceae, LH; Romero et al., 1988; González et al., 2007), extant in Australia and southern South America; and *Lomatia* (Proteaceae, LH, RP; Berry, 1938; González et al., 2007) leaves highly similar to *L. ferruginea*, extant in southern South America (the genus is also in Australia).