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RESEARCH ARTICLE SUMMARY

PALEOBOTANY

Eocene Fagaceae from Patagonia and Gondwanan legacy in Asian rainforests

Peter Wilf*, Kevin C. Nixon, Maria A. Gandolfo, N. Rubén Cúneo

INTRODUCTION: The flowering plant family Fagaceae includes all oaks, beeches, chestnuts, stone oaks, and allies across 10 genera and >900 species. The family stands out for its very high biomass and its domination of forests from the northern temperate zone to the tropics, especially the Southeast (SE) Asian tropics. Numerous Fagaceae are keystone species that define forest structure, supply substantial food reserves through their famously nutritious fruits, and hold considerable economic and cultural importance. Until now, no living or fossil member of Fagaceae had been found south of the Malay Archipelago, and, accordingly, the Southern Hemisphere has not been seriously considered in the family's history (the southern beech, *Nothofagus*, belongs to a separate family).

RATIONALE: We discovered two fossil infructescences of Fagaceae, one mature and one

immature with >110 fruits preserved, along with abundant fagaceous leaves in the early Eocene (52-million-year-old) Laguna del Hunco flora of Chubut, southern Argentina. The highly diverse fossil assemblage represents rainforest vegetation from the terminal phase of Gondwana; South America, Antarctica, and Australia had not yet separated, and global warmth allowed floral and faunal interchange among those landmasses. Subsequently, Australia moved northward and eventually collided with SE Asia, initiating new biotic exchanges. The Laguna del Hunco flora reflects these Earth processes in preserving numerous taxa that survive in Australasia and SE Asia, among which several characteristically associate with tropical Fagaceae today and provide rich biogeographic context for the discovery. Examples include *Eucalyptus* (gum), *Gymnostoma* (rhu), engelhardtioid Juglandaceae (walnut family), *Ceratopetalum* (coachwood),

Lauraceae (laurels), *Ripogonum* (supplejack), *Agathis* (kauri), diverse podocarps (yellowwoods), *Papuacedrus* (a New Guinean cypress), and *Todea* (king fern).

RESULTS: We place the new fossil infructescences in Fagaceae and the living Asian genus *Castanopsis*, a close relative of the chestnuts, because of their preservation of cupule-fruit complexes with lateral, solitary placement on

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their spikelike infructescence axes; complete enclosure of the (single) nut; (two) asymmetrical valves; scaly ornamentation; lobed perianth; and three linear styles with unexpanded stigmas. The fossil leaves are also consistent with *Castanopsis* and in all likelihood represent the same source plant as the infructescences; both occur in the same strata with the just-listed taxa that are local associates of living *Castanopsis*, especially in New Guinea's montane rainforests. The new fossils represent a major southern extension of the historical range of Fagaceae, as well as the oldest record, by ~8 million years, of the genus *Castanopsis*, which has ~120 living species and is dominant at lower montane elevations from New Guinea to the Himalaya and Japan.

CONCLUSION: The fossils' diagnostic characters, early Eocene age, and occurrence in floral associations markedly similar to today's all suggest that *Castanopsis* evolved in the Southern Hemisphere, most likely from an ancestor that had dispersed earlier from North America, and followed the southern route to Asia along with the associated survivor taxa. This discovery substantially increases the known Gondwanan legacy in Asia and Malesia and shows the persistence of the survivor lineages, which tracked their preferred cool-wet rainforest environments through time and space from Gondwana to Asia. The modern analog forests, often located in biodiverse watershed areas, are now threatened by anthropogenic change that is occurring orders of magnitude more rapidly than in the geologic past. The abundant fossil leaves with feeding marks from diverse insects, the large nuts, and the associated flora all indicate that the ancient trees were keystone species in early Eocene "oak-laurel" forests of Patagonia, much like *Castanopsis* is today in Asia. Subsequently, *Castanopsis* and many other rainforest taxa appear to have gone extinct in Patagonia with the earliest phases of Antarctic separation and drying regional climates. ■



Discovering Argentina's lost *Castanopsis* rainforest. (Top) Early Eocene fossil lake beds at Laguna del Hunco. (Bottom) Left to right: Field-discovery photos of the *Castanopsis* mature (large nut length, 17 mm) and immature (length, ~15 cm) infructescence segments, a fagaceous leaf (length, 18.5 cm), a *Eucalyptus caldericola* infructescence (length, 8.2 cm), and a *Papuacedrus prechilensis* leafy branch (length, 10.2 cm).

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RESEARCH ARTICLE

PALEOBOTANY

Eocene Fagaceae from Patagonia and Gondwanan legacy in Asian rainforests

Peter Wilf^{1*}, Kevin C. Nixon², Maria A. Gandolfo², N. Rubén Cúneo³

The beech-oak family Fagaceae dominates forests from the northern temperate zone to tropical Asia and Malesia, where it reaches its southern limit. We report early Eocene infructescences of *Castanopsis*, a diverse and abundant fagaceous genus of Southeast Asia, and co-occurring leaves from the 52-million-year-old Laguna del Hunco flora of southern Argentina. The fossil assemblage notably includes many plant taxa that associate with *Castanopsis* today. The discovery reveals novel Gondwanan history in Fagaceae and the characteristic tree communities of Southeast Asian lower-montane rainforests. The living diaspora associations persisted through Cenozoic climate change and plate movements as the constituent lineages tracked post-Gondwanan mesic biomes over thousands of kilometers, underscoring their current vulnerability to rapid climate change and habitat loss.

Fagaceae sensu stricto (s.s.) (i.e., excluding *Nothofagus*) is one of the highest-biomass and most economically important plant families; it is the only angiosperm group that consistently dominates forests from the northern temperate zone to the tropics, especially the Southeast (SE) Asian and Malesian tropics, where it ranges into low southern latitudes (1–5). Among its 10 genera and >900 species, numerous Fagaceae are keystone species that define forest structure in biodiverse areas and produce abundant protein-rich, animal-dispersed fruits (6, 7). The family's fossil record is extensive but entirely restricted to the Northern Hemisphere (8–15); likewise, biogeographic hypotheses for the living genera do not consider the Southern Hemisphere (16–22). The southernmost occurrences of Fagaceae are in New Guinea, where a few species of the castaneoid genera *Castanopsis* and *Lithocarpus* are abundant (1, 23, 24).

In 1925, E. W. Berry (25) assigned two fossil leaves of interest from the “Mirhoja” site in Argentine Patagonia to Dilleniaceae and the species “*Tetracera*” patagonica. Mirhoja, now Laguna del Hunco, has produced one of the most diverse Eocene floras [at 52.2 million years (Ma) old] worldwide (26, 27). The site captures a distinctive, high-resolution snapshot of the last ecosystems of Gondwanan South America, coinciding with the early Eocene climatic optimum (28). At that time, frost-free climates and diverse

biotas prevailed, and substantial dispersal took place across middle and high latitudes of both the Northern and Southern hemispheres; deep-water separation of South America, Antarctica, and Australia had not yet occurred (28–30).

Laguna del Hunco preserves fossils of numerous paleo-Antarctic rainforest lineages (PARLs) (31) whose living relatives characteristically associate with tropical Fagaceae in perhumid, lower-montane rainforests of Malesia (1, 2, 23, 24, 32–37). These taxa include two members of Fagales, *Gymnostoma* (Casuarinaceae) and *Alatonicula* (extinct engelhardioid Juglandaceae); the additional angiosperms *Eucalyptus* (Myrtaceae), *Ceratopetalum* (Cunoniaceae), and *Ripogonum* (Ripogonaceae); conifers in Cupressaceae (*Papuacedrus*), Araucariaceae (*Agathis* and *Araucaria* Section *Eutacta*), and Podocarpaceae (*Dacrycarpus*, *Podocarpus*, and a species similar to those of *Phyllocladus*); and the fern *Todea* (Osmundaceae) (27, 38–45). New Guinea, in particular, has all the listed lineages in its living flora in associations with *Castanopsis* and *Lithocarpus* (23, 24, 36, 37, 46–48). Leaves of Lauraceae, which also co-occur today with Fagaceae throughout SE Asia's lower-montane “oak-laurel” or “montane oak” forests (5, 49) (the term includes non-oak Fagaceae such as *Castanopsis*), are abundant at Laguna del Hunco but not identifiable to the genus level (27).

Most of the Laguna del Hunco PARLs are also known as fossils in Australia and elsewhere in Gondwana; nearly all went extinct in South America but survived in the Old World, especially on post-Gondwanan, northward-moving Australia (Sahul) (29, 31, 50, 51). Their dispersal to Asia (Sunda) began with the late Oligocene (52) onset of Sahul-Sunda collision. The notable persistence of PARL associations over time and space is considered to result from a convergence

of individualistic responses to climatic and tectonic change mediated by niche conservatism and physiological drought intolerance (31, 53, 54). Because of the presumed Northern Hemisphere origins of all Fagaceae, the modern-day co-occurrences of Fagaceae and PARLs in Malesia have been considered a mix of Laurasian and Gondwanan influences, respectively (5, 55–57).

The rich biogeographic context of the Laguna del Hunco flora and the widespread associations of its diverse living relatives with tropical Fagaceae have foreshadowed the potential discovery of fossil Fagaceae at the site. Here, we report two infructescences and abundant “*Tetracera*” leaves as the first reliable evidence of Fagaceae from Gondwana or the extratropical Southern Hemisphere. We refer the infructescences to *Castanopsis*, which today has ~120 species from the Himalaya to New Guinea and Japan (2, 58, 59), and the leaves to a fagaceous organ genus. These fossils reveal a new southern component of Fagaceae biogeography and substantially increase the known Gondwanan legacy in Asian tropical rainforests. We propose and critically discuss a biogeographic hypothesis to explain our observations.

Systematic paleontology

Family Fagaceae Dumortier, 1829. Genus *Castanopsis* (D. Don) Spach, 1841

Castanopsis rothwellii Wilf, Nixon, Gandolfo et Cúneo sp. nov.

Holotype here designated MPEF-Pb 6433a and MPEF-Pb 6433b (part and counterpart) (Fig. 1). Paratype: MPEF-Pb 8198a and MPEF-Pb 8198b (Fig. 2). Museo Paleontológico Egidio Feruglio (MEF), Trelew, Argentina (repository acronym MPEF-Pb).

Type locality: Laguna del Hunco, Tufolitas Laguna del Hunco, La Huitrera Formation, early Eocene (~52.2 Ma). Holotype from quarry LH13, paratype from quarry LH27 of (26, 39), collected 7 December 2002 and 8 December 2016, respectively.

Etymology: Honoring G. W. Rothwell, paleobotanist, for his eminence in research, teaching, and mentoring.

Diagnosis

Cupules numerous on the infructescence axis; two asymmetrical valves per cupule, abaxial valve larger than the adaxial, apices of open valves recurved; cupule ornamentation of imbricate, helically arranged, flattened, triangular scales; cupule fully enclosing a single nut.

Description

The holotype (Fig. 1) is a bent infructescence segment bearing four maturing fruits and several fruit scars, and the paratype (Fig. 2) is a bent, ~15-cm-long, unbranched, spikelike infructescence segment with >110 immature fruits. Fruits are solitary, lateral, and alternate on the infructescence axis, most of them strongly directed toward the axis apex but some nearly perpendicular, leaving ellipsoid scars of ~1.6 mm major axis length (Fig. 1H); fruits consist of solitary nuts

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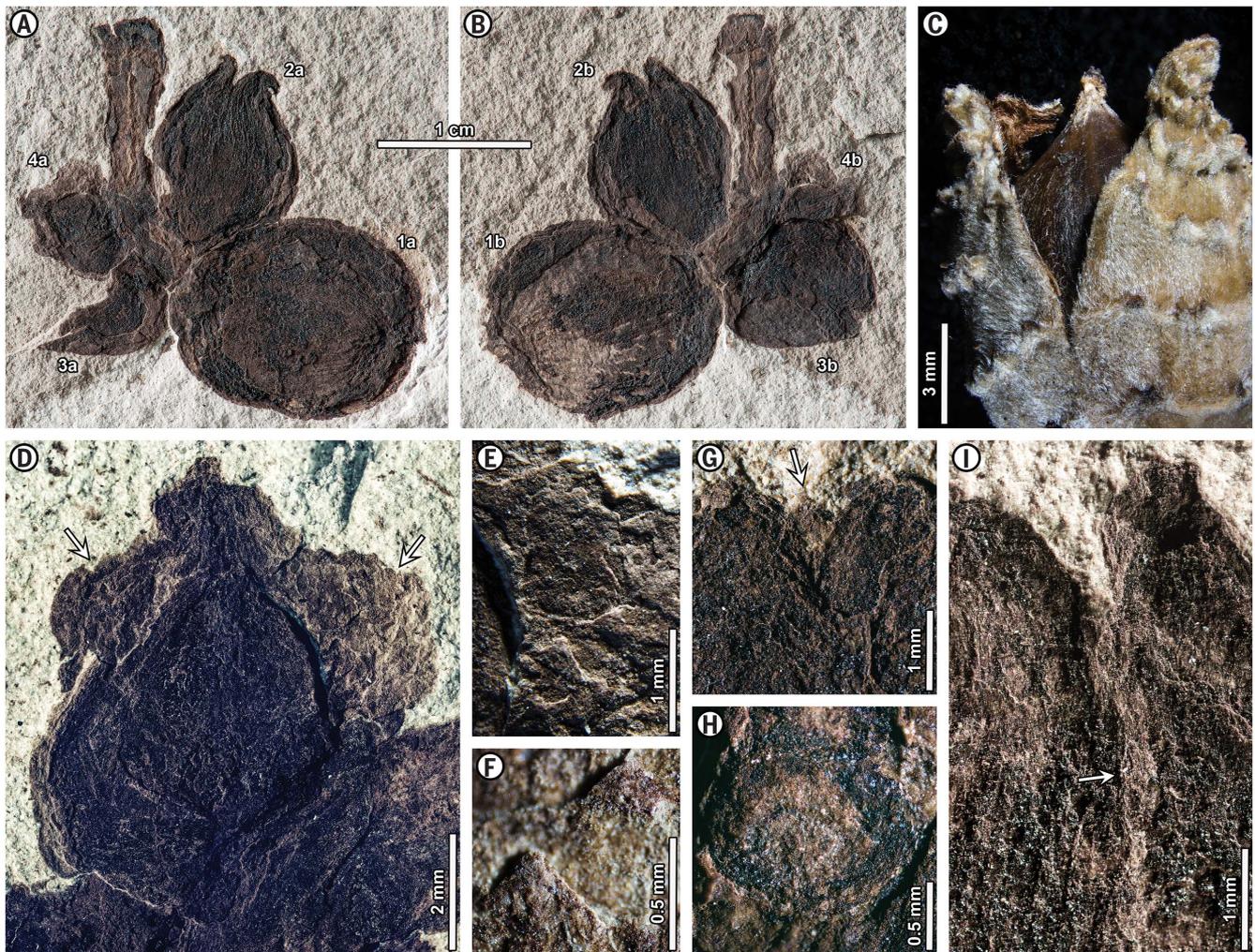


Fig. 1. *Castanopsis rothwellii* sp. nov. holotype. (A and B) *C. rothwellii* holotype, MPEF-Pb 6433, showing the infructescence segment (A) part and (B) counterpart with four fruits labeled 1 to 4. Fruit 1 preserves a longitudinally striated nut seated in abraded cupule remnants. Fruits 2 and 3 are cupules splitting into two unequal valves [also shown in (G) and (I)]. Recurved valve apices are well developed in fruit 2; fruit 3b preserves the nut apex exposed between the valve tips [also shown in (G)]. Fruit 4a has an ovate nut exposed and seated in cupule remnants with imbricate scaly ornamentation [see also (D) to (F)]. (C) *C. cuspidata* litter specimen,

Kyoto, Japan, similar to fossil fruit 2 [see (A), (B), and (I)], with the cupule splitting into two unequal valves with recurved apices; a single nut; and banded, scaly ornamentation. (D) Detail of fossil fruit 4a (A), showing a coalified, ovate nut with scaly cupule remnants (arrows) [also shown in (E) and (F)]. (E and F) Cupule scale details from (D). (G) The apex of cupule 3b [also shown in (B)] splitting into two valves, exposing the nut apex (arrow). (H) Fruit scar from the infructescence axis, located immediately distal to fruit 2b (B). (I) Detail of opening valves and extensive suture zone (arrow) of fruit 2b [also shown in (B)].

(Fig. 1D) fully enclosed by sessile to shortly pedicellate, two-valved, ovate to ellipsoid, asymmetrical cupules. Cupules are ornamented with imbricate, flattened, triangular, symmetrical, helically arranged scales with straight to acuminate apices (Figs. 1, D to F, and 2, B and J); cupules lack spines or tubercles. Maturing fruits (Fig. 1) are asymmetrical and two-valved, the inferred abaxial valve larger and more convex than the adaxial. Cupules are ovate or ellipsoid, the largest 17 mm long and 13.4 mm wide, splitting into two valves along a distinct suture zone (Fig. 1I), the freed valve apices recurved (Fig. 1, A, B, and I). Nuts are ovate (Fig. 1D), not visibly angled, with longitudinal striations; the scale length (visible portion) is ~0.75 mm. Immature

fruits (Fig. 2) have ellipsoid cupules on smaller (younger) fruits (Fig. 2H) and ovate-acuminate cupules with a thickened wall on more developed fruits (Fig. 2F). The perianth is lobed, the lobes apparently numbering six according to symmetry (Fig. 2E). The three styles are slender and undivided, with unexpanded stigmas (Fig. 2, B and E to I).

Remarks

Castanopsis rothwellii sp. nov. has cupule-fruit complexes, a synapomorphy of Fagaceae (17, 60–62). The maturing fruits have asymmetrical, valved and sutured, solitary cupules that fully enclose a single nut; this configuration is specific to *Castanopsis* among living Fagaceae (2, 58, 59, 63–65).

The immature fruits preserve the distinctive lobed perianth of Fagaceae and three linear styles with unexpanded stigmas, as seen only in the castaneoids *Castanopsis* and *Lithocarpus* among extant Fagaceae; however, the low insertion angle of most fruits to the axis is more typical of *Castanopsis* (2, 58, 59, 61, 63, 66). The spikelike, unbranched infructescence with laterally inserted fruits is also distinctive for *Castanopsis* and other Castaneoideae, although the total number of fruits per infructescence (as seen in the paratype) (Fig. 2, A and D) is much higher than in living *Castanopsis*; this may be a plesiomorphic condition relative to modern *Castanopsis*. Thus, both specimens of *C. rothwellii* have diagnostic characters of extant *Castanopsis*, and the two fossils

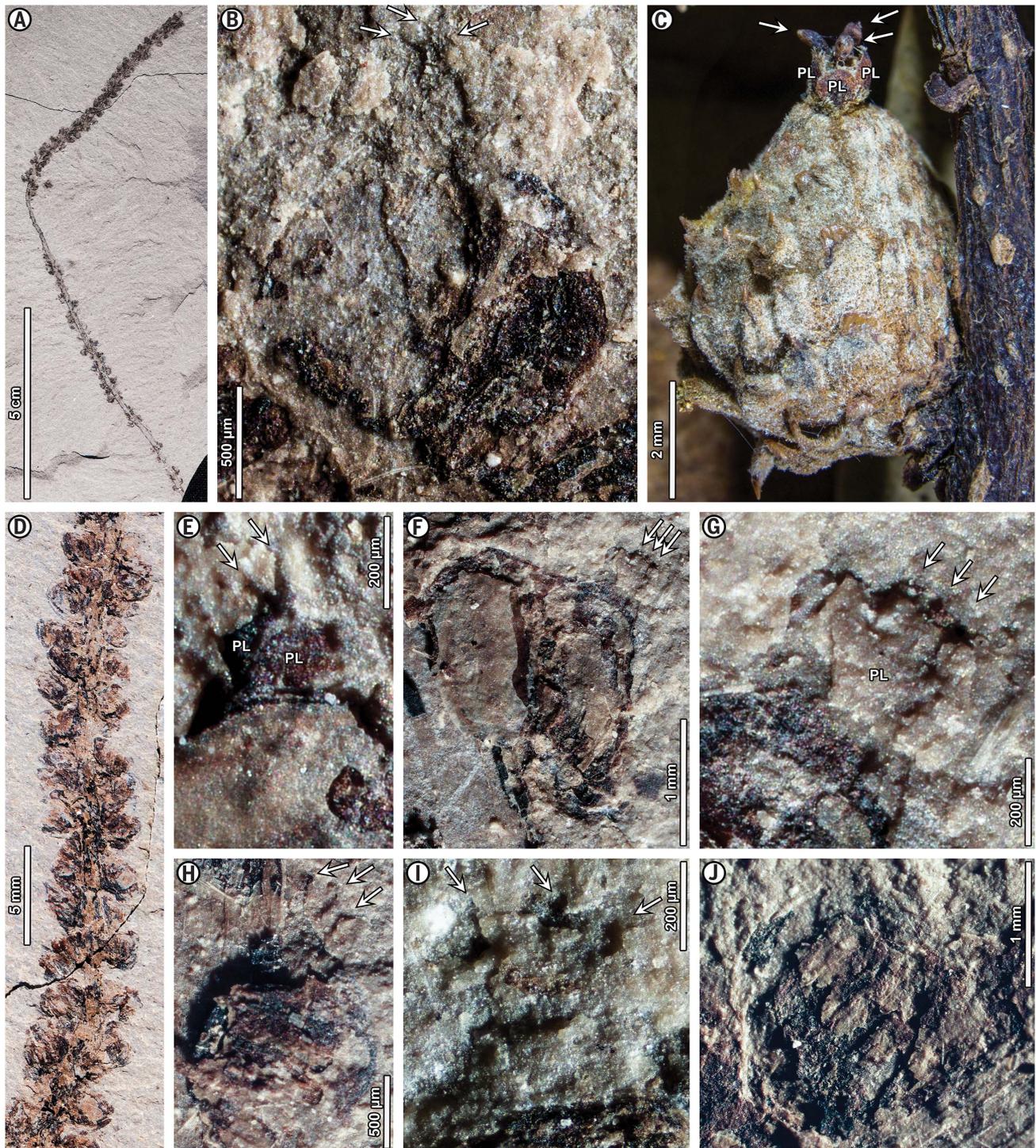


Fig. 2. *Castanopsis rothwellii* sp. nov. paratype. (A, B, and D to J) MPEF-Pb 8198; [(A), (B), and (D) to (G) part; [(I) and (J)] counterpart. (A) Spikelike infructescence segment with >110 immature cupules preserved [also shown in (D)]. (B) Single cupule ornamented with triangular, imbricate, helical scales, preserving three slender styles. (C) *C. acuminatissima*, US 3256853 (Papua New Guinea), young fruit similar to the fossil fruits, with comparable scale ornamentation, rounded perianth lobes, and three styles. (D) Detail from (A), across the hairline rock fracture, showing densely packed

cupules at variable orientations to the axis. (E) Fruit apex with two perianth lobes preserved, indicating an original configuration of six lobes by symmetry, and with two of three original styles (as indicated by symmetry). (F) Ovate cupule, nearly perpendicular to the axis, with three styles [see (G)]. (G) Detail of the cupule apex from (F), with a partially preserved perianth lobe and three styles. (H) Small cupule at an acute angle to the axis, with three styles. (I) Fruit apex with three styles. (J) Cupule with well-preserved ornamentation of triangular, imbricate, helical scales. Arrows, styles; PL, perianth lobe.

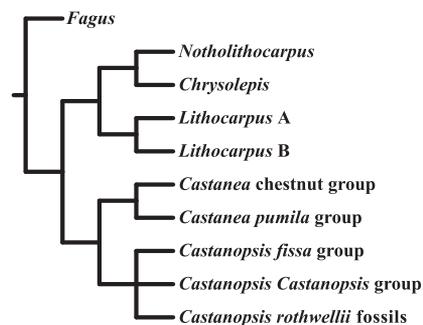


Fig. 3. Phylogenetic analysis. Consensus of the two most parsimonious trees, based on a matrix of seven morphological characters (Table 1), with the fossil infructescence, *C. rothwellii*, allowed to float on a scaffold according to the results of Manos *et al.* (98). See the text and Table 1 for additional details.

share several features, especially their deployment on a single infructescence axis of solitary, single-fruited, lateral cupules that entirely enclose the nut with ornamentation of helically arranged, imbricate scales. On the basis of the available information, we consider the two *C. rothwellii* specimens as an ontogenetic series of the same species.

Several extant *Castanopsis* species are similar to the fossils, although none is identical. Most living *Castanopsis* species have spiny or tubercular cupules; however, scaly ornamentation, often deployed in bands but sometimes imbricate, also occurs in various growth stages of several species (1, 2, 58, 59, 65). Young cupules of *Castanopsis acuminatissima* (New Guinea) (Fig. 2C) are very similar to the fossils; they are two-valved and one-fruited, with imbricate, triangular, helical scales. However, they are unlike the fossils in that their valve apices are not recurved, and their scales become more irregular and exerted with maturity. Cupules of *Castanopsis cuspidata* (Japan and Korea) (Fig. 1C) have a single nut and two or more valves with apices that are recurved and liplike when the valves are opened, closely resembling one of the mature fossil fruits (Fig. 1, A, B, and D); they also have flattened, helically arranged, triangular scales, like those of the fossils but separated into bands instead of helical. Because of the biogeographic interest of *Nothofagus* (67), we briefly note critical differences in this genus (1), including its single-fruited infructescences, symmetrical cupules, and expanded, strap-shaped stigmas.

In summary, the *C. rothwellii* infructescences have numerous distinctive features of extant *Castanopsis* and differ substantially from the living genus only in having large numbers of fruits per infructescence, which we consider insufficient cause to erect a new genus. We find the available evidence compelling to assign the new infructescences to *Castanopsis*. Phylogenetic analysis strongly supports our taxonomic assignment, placing the fossils either as sister to living *Castanopsis* or within the *Castanopsis* crown group (Fig. 3 and Table 1). The new fossils imply

Table 1. Character scores for phylogenetic analysis. Scores were assigned for characters, shown left to right in the following order. Style number: three = 0; six = 1. Cupule appendages: scaly = 0; spinose = 1. Cupule dehiscence: valvate = 0; hemispheric indehiscent = 1. Female flowers per node: solitary = 0; clustered = 1. Flowers per cupule: one = 0; three = 1; more than three = 2; nonadditive. Valve dehiscence: complete = 0; partial = 1; none = 2; nonadditive. Inflorescence sexuality: unisexual = 0; unisexual and mixed = 1. Brackets indicate polymorphisms. Cupule appendages were scored according to the predominant state in mature cupules. Female flowers per node is inapplicable in *Fagus* because there is only a single node (this is indicated in the score by a dash). Figure 3 shows the consensus tree from the phylogenetic analysis.

Taxon	Score
<i>Castanopsis rothwellii</i> fossils	0000010
<i>Fagus</i>	000-000
<i>Castanea</i> chestnut group	110[01]101
<i>Castanea pumila</i> group	1101001
<i>Castanopsis fissa</i> group	00[01]00[12]0
<i>Castanopsis Castanopsis</i> group	01[01]0[01][012]0
<i>Chrysolepis</i>	0101201
<i>Lithocarpus A</i>	001[01]020
<i>Lithocarpus B</i>	0011020
<i>Notholithocarpus</i>	0011021

a minimum age of 52.2 Ma for the *Castanea-Castanopsis* divergence, older than recent molecular-dating estimates (68), which are usually constrained by *Castanopsis crepetii* from the middle Eocene (~43.8 Ma) of Oregon (11). The oldest known *Castanea* fossil is from the middle Eocene of Tennessee (69, 70).

Family Fagaceae Dumortier, 1829. Genus *Castaneophyllum* Jones et Dilcher, 1988
Castaneophyllum patagonicum (Berry) Wilf, Nixon, Gandolfo et Cúneo comb. nov.

Basionym: *Tetracera patagonica* Berry, *Johns Hopkins University Studies in Geology*, vol. 6, p. 219 (1925) (25). Lectotype here designated USNM 201951 (Fig. 4, A to C), drawn in fig. 4 of plate I of (25), Paleobotanical Division, National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM). Syntype: USNM 201952 (Fig. 4, D and E), drawn in figs. 5 and 6 of plate I of (25).

Type locality: Laguna del Hunco, Tufolitas Laguna del Hunco, La Huitrera Formation, early Eocene (~52.2 Ma). The precise location is unknown, but the matrix and secondary mineral staining in the paratype (Fig. 4D) are specific to the bed containing quarry LH04 of (26). Additional material: MPEF-Pb 8200 to 8202, 8204, and 8205, from Laguna del Hunco quarry LH02 of (26, 39); 8209, 8222, 8224, 8227, 8228 (Fig. 4J), 8230, 8235, 8236, 8238, 8242 to 8245, 8248, 8249, and 8252 (LH04); 8255 (Fig. 4G), 8257 (Fig. 4H), 8259, 8262, and 8263 (LH13); 8266 (Fig. 4, F and I) (LH15); 8268 and 8269 (LH16); 8271 (LH18); 8272 (LH20); 8274 (LH23); 8275 (Fig. 4K) (LH26); 8278 (LH27); and 1453 and 1454 (precise location unknown).

Emended species description

Leaf organization inferred simple. Petiole insertion marginal, petiole length to >55 mm, petiole

width to 4 mm. Lamina unlobed and margin prominently serrate, the teeth present over most of the blade and nearly to the leaf base. Lamina size microphyll to mesophyll, reconstructed leaf area to ~8150 mm², length to 185 mm, width to 70 mm, length:width ratio 2.2 to 3.6:1. Lamina shape elliptical to ovate, with medial symmetry and asymmetrical basal insertion. Base and apex angle acute; base shape variably subrounded, convex, concavo-convex, or cuneate; apex shape straight to acuminate. Venation well organized, rank 4. Primary venation pinnate. Secondary veins craspedodromous, robust, subopposite to alternate and excurrent on midvein, up to 17 pairs observed on the largest leaves, spacing and angle regular to slightly irregular, rarely forking well inside the margin. Secondary course nearly straight, gently then increasingly curving apically on approach to and within the tooth, entering the tooth in the basal longitudinal half as the tooth's principal vein. Fimbrial vein present throughout blade, intermittently weakened or irregularly expressed as loops of exterior tertiaries. Intersecondary veins absent. Intercostal tertiary veins thin and closely spaced, course mixed percurrent but deflected by strong quaternaries, appearing ladderlike at a distance but less distinct when viewed closely because of deflections, angle obtuse to midvein and nearly perpendicular to the secondaries at departure. Epimedial tertiaries mixed percurrent and deflected as for intercostals, proximal course perpendicular to midvein, distal course basiflexed and parallel to intercostal tertiaries. Exterior tertiary course looped or terminating at the fimbrial vein. Quaternary and quinary vein fabric regular reticulate, areoles at fifth order, freely ending veinlets zero-, one-, or two-branched. Teeth in one order (simple); tooth spacing regular, ~2 teeth/cm, with one tooth per secondary. Tooth apical flank concave, straight, or flexuous; basal flank the same

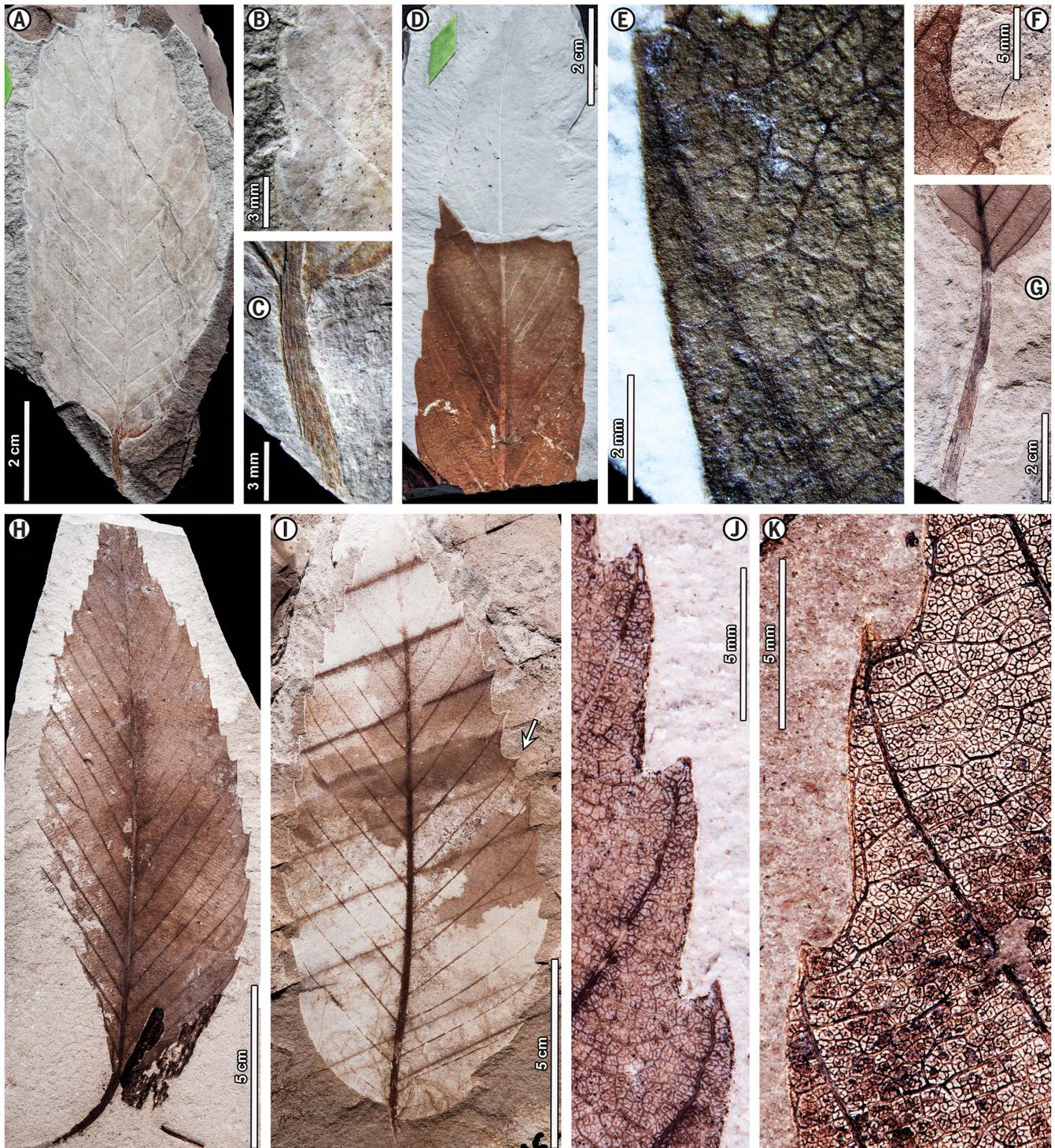


Fig. 4. *Castaneophyllum patagonicum* (Berry) comb. nov. (A to C) Lectotype, USNM 201951, with details of (B) the margin and (C) base, showing a long petiole and asymmetrical lamina insertion. (D and E) Syntype, USNM 201952 (with secondary iron staining); the base of (D), at left, expands to (E) detail of vein preservation. (F) MPEF-Pb 8266, margin detail with bristle-tipped tooth at lower right [also shown in (I)]. (G) MPEF-Pb 8255a, with a long petiole segment. (H and I) MPEF-Pb 8257 (H) and MPEF-Pb 8266 (I), large leaves with representative architecture including asymmetrical lamina insertion (I); robust, regular secondary

veins each terminating in a conspicuous tooth; ladderlike tertiary veins; a fimbrial vein; and teeth with long-arcuate sinuses and pointed to bristled apices. Deeply bifurcating secondary veins occur at center left and center right of (H). Parallel lineations in (H) are rock fractures. Arrow for (I), bristle shown in (F). (J and K) MPEF-Pb 8228 (J) and MPEF-Pb 8275 (K), marginal venation of leaves with strongly (J) and weakly (K) expressed teeth, showing characteristic fimbrial vein, deflected-percurrent tertiary veins, freely ending veinlets, deflected principal veins, and nonglandular apices.

plus convex; sinus usually long and arcuate. Principal vein deflected within the tooth at junctions with tertiary veins, terminating at the nonglandular tooth apex or extending beyond it in a bristle. Stipules, cuticles, and trichomes not preserved. Insect-feeding damage is diverse; a previous report (71) included damage types (DTs) (72) on “*Tetracera*” leaves from hole and surface feeding (DTs 1 to 5, 7, 8, 29, and 57), margin feeding (DTs 12 to 15), skeletonization (DTs 16, 19, and 22), galling (DT32), and mining (DT90).

Remarks

Jones and Dilcher’s (10) diagnosis of *Castaneophyllum* (“isolated leaves resembling, in general form, those of modern *Castanea*”), their generic description (even in the absence here of fossil cuticle), and their intent that *Castaneophyllum* “serve as a repository for isolated *Castanea*-like fossil leaves” make this genus ideal for taxonomic placement of the Patagonian leaf fossils. The only difference, deemed negligible, is that the original description of *Castaneophyllum* (10) included no more than one branching of the freely ending veinlets. Berry’s type specimens (25) (Fig. 4, A to E) preserve sufficient details to establish that they represent the same entity as the new leaf material, including a long petiole, basal insertion asymmetry, tooth configuration, and total venation pattern.

The leaf architecture of the fossils is definitely fagaceous, seen in the characteristic combination of robust, regular, craspedodromous secondary veins that each terminate at the apex of a single tooth and only rarely branch, far from the margin (Fig. 4H); thin, closely spaced, percurrent, ladderlike tertiary veins; and simple teeth with long-arcuate sinuses and nonglandular, pointed to bristle-tipped apices. These features are widespread among Fagaceae, especially in species of *Castanea*, *Castanopsis*, and *Quercus* (8–10, 58, 73), and the fossils would undoubtedly be assigned to Fagaceae if found in Northern Hemisphere deposits. The only angiosperm family with closely comparable leaves is Dilleniaceae, as historically identified (25). However, the toothed Dilleniaceae (e.g., some *Dillenia*, *Tetracera*, and *Davilla* species) feature prominent, expanded glands at the tooth apices (74) that do not occur in the fossil specimens. The toothed *Nothofagus* species, though variable, have a suite of features that do not conform to the fossils (75), including the prevalence of markedly asymmetrical leaves, plications, compound teeth, zig-zagging or curved primary veins, and irregular secondary veins that fork near the margin or include agrophich veins. In *Castanopsis*, leaves very similar to the fossils occur in several serrate-margined species of the Asian mainland, especially *Castanopsis indica*, from which the fossils differ only in their much longer petioles and their more deflected tertiaries and tooth principal veins (Fig. 4). Long petioles like those of the fossils are unusual in living *Castanopsis* but occur in some species (e.g., *Castanopsis ouonbiensis*, China).

The isolated *Castaneophyllum* leaves occur at the same localities as the *Castanopsis rothwellii*

infructescences and are likely to represent the same source plant, given the lack of evidence for other fossils of fagaceous fruit or leaf species. However, the leaves’ nomenclatural priority and lack of clear generic affinities within extant Fagaceae, when taken alone, require their maintenance under a separate name in the absence of organic attachment.

Berry (76) also included “*T.*” *patagonica* in his 1938 monograph on the ~47.8-Ma-old (27, 40) Río Pichileufú flora from Río Negro province; however, he did not illustrate material or cite specimens. Nevertheless, Berry determined “*T. patagonica*” on handwritten tags for three specimens (USNM 219128 to 219130), which we found markedly dissimilar to the types and more likely to represent sapindalean leaflets. We have not seen any fossils resembling Fagaceae from Río Pichileufú in either the historical (76) or our ongoing (27) collections. Jones and Dilcher (10) considered some of Berry’s 1938 (76) fossils from Río Pichileufú to be “somewhat similar to *Castaneophyllum*” but did not indicate which fossils these were.

Gondwanan “oak-laurel” forest

Castaneophyllum patagonicum leaves frequently occur at Laguna del Hunco, where they are the third most common leaf species, with a census count of 9.8% of total leaves (27). Moreover, most of the leaf specimens (84%) came from the same two quarries (LH02 and LH04) where leaves of Lauraceae are most abundant (27). This notable pattern indicates a Gondwanan iteration of the “oak-laurel” associations that now dominate lower-montane rainforests from the eastern Himalaya to New Guinea (5) and include many other PARLs known as fossils from Laguna del Hunco. Like living *Castanopsis*, which is abundant and insect pollinated (6), the Eocene trees presumably were keystone species that provided forest structure, nutritious nuts, and substantial pollinator rewards.

Southern Route to Asia hypothesis

The discovery of Gondwanan fossil Fagaceae raises important biogeographic questions. We outline and critically discuss a “Southern Route to Asia” hypothesis that arises from our findings, as follows: An ancestral castaneoid lineage dispersed from North America into Gondwanan South America and joined the widespread paleo-Antarctic rainforest biome (31). *Castanopsis* evolved in the Southern Hemisphere by the Eocene, followed the Sahul pathway along with the associated PARLs to the Asian collision, and diversified through the Neogene in Sahul and eventually in Sundaland.

There is ample precedent for Late Cretaceous or early Paleogene dispersal from North to South America. At Laguna del Hunco itself, other Fagales with northern connections co-occur with the new fossils, such as engelhardioid Juglandaceae (47) and members of the family Casuarinaceae (*Gymnostoma* spp.) (46), a close relative of the Laurasian family Betulaceae (68). The faunal record is rich with Late Cretaceous dis-

persals from North America to Patagonia and on to Antarctica, including hadrosaurs and diverse mammal groups (77–79). A postulated latest Cretaceous, ephemeral land connection or island chain along the Antillean Arc (80) would have been comparatively accessible to higher-latitude organisms because of Maastrichtian cooling (81), and the dispersing mammals themselves could have taken part in bringing castaneoids to South America. The alternative to dispersal, in situ evolution in South America, is unlikely because of the robust North American record of Late Cretaceous Fagaceae (12, 82) and the lack of any Mesozoic or other South American fossils of the family.

The idea of southern origins and biogeographic history for *Castanopsis* can be tested in at least three ways. First, the oldest Asian *Castanopsis* fossils should not predate the late Oligocene (52) onset of the Sahul-Sunda collision, and this condition is met so far (20). The earliest reliable Asian fossils of the genus are diagnostic fruits from late Miocene sediments of SE China (83). If North America and Europe were instead the sources of Asian *Castanopsis*, the genus apparently did not take advantage of numerous opportunities to reach Asia earlier (84).

Second, early *Castanopsis* fossil associations should be similar to living *Castanopsis* assemblages with substantial Gondwanic history, and this is overwhelmingly the case for the new fossils, which are the oldest known of the genus despite much more extensive collection of Northern Hemisphere than of Patagonian Paleogene floras. Local *Castanopsis* associations with the same paleo-Antarctic lineages seen at Laguna del Hunco (as listed earlier), and usually with several of them at a time, are extensively documented in Malesia (1, 2, 23, 24, 32–37). Northern Hemisphere fossils assigned to *Castanopsis* are younger and never co-occur with PARLs (11, 15, 85). We find the marked spatial and temporal stability of the old southern associations, requiring a high degree of biome conservatism over time (31, 53, 54), to be especially compelling evidence of a direct connection from Laguna del Hunco to SE Asia for *Castanopsis*. Although some Northern Hemisphere *Castanopsis* fossils co-occur with a different set of extant Malesian taxa, as seen in the Eocene of Oregon (11), comparatively few examples are known of those genera associating locally, collectively, and repeatedly with living *Castanopsis* (86).

Third, the hypothesis requires that the North American and European fossils assigned to *Castanopsis* be more distant relatives of the extant genus than are the new Argentine fossils. This issue is challenging, but the close affinity of the new Patagonian fossils to living *Castanopsis* is well supported by our morphological analysis (Fig. 3). Among Laurasian fossils, *Castanopsis kaulii*, a spectacular pistillate inflorescence from late Eocene Baltic amber, is clearly consistent with the living genus (15); however, fruits that would confirm its relationships with extant lineages are not yet known. European fruit fossils referred to *Castanopsis* are nuts that are never found in cupules, making their systematic placement

uncertain (85). *C. crepetii* fruits from the middle Eocene of Oregon include cupules and several anatomical characters consistent with living *Castanopsis* (11), although they do not preserve infructescence structure, perianth, or styles. Otherwise, the diverse North American reproductive fossils that are similar to *Castanopsis* belong to extinct genera (17, 87, 88).

We favor a southern origin for *Castanopsis* on the basis of the preservation of diagnostic infructescence and fruit characters in the new fossils from Argentina, their early Eocene age, and the marked similarities of fossil Patagonian and living Malesian plant associations. If *Castanopsis* is instead older than the postulated north-south dispersal and has both northern and southern history, older Laurasian *Castanopsis* fossils and a corresponding deep split in the genus' phylogeny, both so far unknown, would supply the necessary evidence. Notably, *C. acuminatissima* is a dominant living species in New Guinea (1, 24), where it associates with more Laguna del Hunco "survivor" taxa (e.g., *Eucalyptus* and *Araucaria*) than any other *Castanopsis* species; *C. acuminatissima* might be a true relict of Sahul rather than an immigrant from Asia as conventionally assumed. Genetic data from across that species' range, which extends to India (2), could be used to test this idea.

Concluding remarks

The discovery of *Castanopsis* in Eocene Patagonia adds a novel element to our understanding of late-Gondwanan rainforest vegetation, for which Malesian lower-montane rainforests provide a more robust analog than previously thought. New Guinea offers especially compelling similarities to Eocene Patagonia because of a large number of shared living-fossil genera. *Castanopsis* history now shows unexpected alignment with the austral genus *Nothofagus*, whose co-occurrence with *Castanopsis* and *Lithocarpus* in New Guinea historically puzzled biogeographers before the separation of Nothofagaceae from Fagaceae s.s. (57, 67, 89). However, despite their biogeographic parallels, we note that *Castanopsis* and *Nothofagus* are distant relatives within Fagales (82, 90). Adding further complexity, indisputably Laurasian Fagaceae, such as *Quercus* (14), also inhabit Malesia (but not New Guinea) (2). Thus, we propose that the classical idea of the region's montane rainforests as a meeting ground of Laurasian and Gondwanan lineages (55, 57) now applies within Fagaceae s.s.

Living *Castanopsis* is diverse, with high standing biomass and an extensive range reaching to Japan and the Himalaya. Thus, the fossils reported here substantially increase the recognized Gondwanan footprint in Asian forests. The marked conservatism of paleo-Antarctic lineages (31, 54), which have tracked their preferred biomes over time and space instead of adapting to climate change in situ, highlights their vulnerability to rapid anthropogenic disturbance (91, 92). In Patagonia, the lack of Fagaceae in the 47.8-Ma-old Río Pichileufú flora adds to a growing list of dissimilarities between the two iconic as-

semblages (29). The loss in such a geologically short time (52.2 to 47.8 Ma) of abundant angiosperms such as *Castanopsis*, *Eucalyptus*, and *Gymnostoma* suggests that the earliest phases of Antarctic separation and concurrent cooling and drying had substantial effects in southern South America.

Materials and methods

The Tufolitas Laguna del Hunco are fossiliferous caldera-lake deposits of La Huitrera Formation in northwest Chubut, Argentina, paleolatitude ~47°S (27, 93). Berry (25) first reported the fossil flora in 1925 from a small collection. The flora is now known to be highly diverse (26) and to hold the only South American (or global) records of a variety of extant Australasian, Asian, and neotropical plant genera (29, 44, 94). The stratigraphy of the 170-m-thick lake-bed sequence and its fossil quarries (LHO1 to LH28) is reported elsewhere (26, 27, 40). In summary, three ⁴⁰Ar-⁴⁰Ar ages and two paleomagnetic reversals, especially a 52.22 ± 0.22 Ma ⁴⁰Ar-⁴⁰Ar age on sanidine from the middle of the sequence, constrain all the fossil beds to a ~52.2-Ma age.

We studied the fossils at MEF and the Penn State Paleobotany Laboratory by using the same procedures for specimen preparation and imaging detailed in several previous papers (40, 43), with the addition of a Nikon DSFi3 camera and L4 control unit on the MEF Nikon Eclipse 50i microscope. Herbarium material of a majority of the *Castanopsis* species was examined at Herbarium Bogoriense (BO, Java, Indonesia), the L. H. Bailey Hortorium Herbarium (BH, Cornell University), the Singapore Herbarium (SING), and the U.S. National Herbarium (US, Smithsonian Institution). Several hundred images were downloaded from online herbaria, including the consortium sites JStor Global Plants (95) and the Chinese Virtual Herbarium (96). Fruit litter of living *C. cuspidata* (Fig. 1C) was collected in Kyoto and kindly provided by Y. Onoda. Leaf descriptive terminology is from Ellis *et al.* (97).

Phylogenetic analyses of the *C. rothwellii* infructescences used a scaffold tree for living Fagaceae subfamily Castaneoideae on the basis of the published molecular results of Manos *et al.* (98), which remain among the most comprehensive for the family. That phylogeny (98) was rooted on *Fagus* as a sister to all other Fagaceae, which divided into two clades, *Trigonobalanus* sensu lato and all remaining genera. Among these, *Quercus* was a sister to the Castaneoideae, wherein *Castanopsis* and *Castanea* formed a sister clade to the other genera (*Lithocarpus*, *Chrysolepis*, and *Notholithocarpus*). We note that many topologies have been published for Fagaceae, and Castaneoideae often resolve as paraphyletic (68, 90, 99). A matrix of seven morphological characters was developed on the basis of relevancy in the fossils (Table 1). The genus *Fagus* was used as the outgroup. *Castanea* and *Castanopsis* were split into subgroups according to results from (98), and *Lithocarpus* was split into artificial subgroups based on the consistency of cupule morphology characters.

This approach allows testing of whether the fossil would fall within a crown group of the genera but does not imply that all the subgroups are monophyletic. Parsimony analyses were performed using TNT version 1.2 (100) [see (101) for updates]. Thorough tree searches of the molecular [internal transcribed spacer (ITS)] scaffold tree, allowing the fossil to float, were done by using the parsimony ratchet with 500 replications, followed by tree fusion and tree drift (102, 103). Two most parsimonious trees resulted, one with the fossil species as a sister to the entire genus *Castanopsis* and a second with the fossil species as a sister to the *Castanopsis* subgroup within *Castanopsis* (the consensus tree is shown in Fig. 3). Additional analyses using more recent molecular data (99) similarly placed the fossils as a sister to extant *Castanopsis*. Further phylogenetic resolution within *Castanopsis* is not methodologically possible because sufficient diagnostic characters of the *Castanopsis* subgroups are not available in the fossils; moreover, no comprehensive phylogeny of the diverse castaneoid Fagaceae has been done that would justify the development of a large-scale morphological character matrix. Although refinement of the phylogenetic position of the fossils may become possible with additional studies of the living species, the placement within subfamily Castaneoideae is unequivocal with the currently available data.

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Eocene Fagaceae from Patagonia and Gondwanan legacy in Asian rainforests

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Fossil Fagaceae from Patagonia

The oak family Fagaceae is thought to have its evolutionary origins in northern temperate forests and Southeast Asia. Wilf *et al.* now report 52-million-year-old fossils from the Southern Hemisphere belonging to the still-living genus *Castanopsis*. Hypotheses of Fagaceae origins have focused only on the Northern Hemisphere. Ancestral *Castanopsis* may represent one of numerous paleo-Antarctic plant genera that are found with *Castanopsis* today in Southeast Asian rainforests.

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