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Comment on “Eocene Fagaceae from Patagonia and Gondwanan legacy in Asian rainforests”

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Wilf *et al.* (Research Articles, 7 June 2019, eaaw5139) claim that *Castanopsis* evolved in the Southern Hemisphere from where it spread to its modern distribution in Southeast Asia. However, extensive paleobotanical records of Antarctica and Australia lack evidence of any Fagaceae, and molecular patterns indicate shared biogeographic histories of *Castanopsis*, *Castanea*, *Lithocarpus*, and *Quercus* subgenus *Cerris*, making the southern route unlikely.

In a recent paper (1), Wilf *et al.* described fossils belonging to the north hemispheric family Fagaceae (oak family) from sediments of Patagonia dated to 52.2 million years (Ma) ago, the early Eocene. The fossils comprise one immature (pistillate) infructescence and four mature fruits attached to an axis and are assigned to the extant genus *Castanopsis* on the basis of a DNA-scaffold analysis using seven scored morphological traits. Wilf *et al.* state that “the new fossils represent ... the oldest record, by ~8 million years, of the genus *Castanopsis*” and conclude that “*Castanopsis* evolved in the Southern Hemisphere” and, moving along a “southern route,” provided the stock for the modern survivors of *Castanopsis*, ~120 to 130 tree species ranging from northwestern India to New Guinea and Japan. They speculate that this ancestral *Castanopsis* represents one of several paleo-Antarctic plant genera that are today in Southeast Asian rainforests. Consequently, numerous younger fossils from North America and Eurasia previously assigned to *Castanopsis* must represent “more distant relatives of the extant genus” than the Patagonian fossils.

We acknowledge the importance of the fossil that geographically extends the record of Fagaceae but suggest an alternative evolutionary and biogeographic interpretation that takes into account genetic differentiation patterns of modern genera.

We (i) show that the character suite that links the Patagonian fossil to modern *Castanopsis* is plesiomorphic, making its generic assignment ambiguous. We (ii) use the extensive pollen and macrofossil record (Australia, Antarctica) to demonstrate that a southern route of Fagaceae to Southeast Asia currently lacks any fossil evidence. Finally, (iii) molecular data reject geographically isolated early evo-

lutionary histories of the castaneoid genera *Castanea*, *Castanopsis*, and *Lithocarpus* and link them to the Eurasian *Quercus* subgenus *Cerris*.

Regarding (i), we note that slightly younger infructescences from Tennessee described as *Castanopsoidea* (2) share features with the fossil from Patagonia but differ by three-flower cupules, a condition also present in modern *Castanopsis*; *Castanopsis rothwellii* from Patagonia shows a character suite that is distinctly primitive within the paraphyletic Castaneoideae [Fig. 1 and Table 1; character 7, inflorescence sexuality, was coded as unisexual for extant *Castanopsis* and *Lithocarpus*; this should be unisexual and mixed instead (3)]. On the basis of the available data, it is impossible to decide whether *Castanopsoidea* and *Castanopsis rothwellii* represent stem Castaneoideae/Fagaceae, are extinct sister lineages of *Castanea-Castanopsis*, or belong to the modern genus.

Regarding (ii), the southern route of *Castanopsis* to Asia, we note that evidence for such a pathway is currently missing. First, the genus was present in North America in the late early Eocene (4) less than 4 Ma after *C. rothwellii*. The revised age of the Nut Beds flora in Oregon is 48.32 Ma (5). In addition, the genus was present in Europe during the Eocene. Second, despite extensive paleopalynological and macrofossil work in Antarctica and Australia/Tasmania, dispersed pollen, leaves, or reproductive structures of Castaneoideae or any other Fagaceae, common in the Northern Hemisphere during the Paleogene, have never been recovered from Late Cretaceous to Oligocene strata across Gondwana. Instead, these regions were inhabited by temperate rainforests dominated by podocarps, Araucariaceae, Nothofagaceae, Proteaceae, and tree ferns (6, 7), which occupied

niches potentially suitable for Fagaceae since the Late Cretaceous. Hence, the southern route hypothesis would require that generations of palynologists had overlooked the characteristic pollen of Castaneoideae in Gondwanan records. Third, Wilf *et al.* argue that the Patagonian fossil plant assemblages are similar to modern assemblages with “substantial Gondwanic history.” We note that a large part of modern *Castanopsis* distribution occurs outside living plant communities with substantial Gondwanan history. Modern plant communities with *Castanopsis* differ considerably in New Guinea, the Himalayas, and Japan (8).

Regarding (iii), molecular data reject the notion that “North American and European fossils assigned to *Castanopsis* [are] more distant relatives of the extant genus than are the new Argentine fossils” and are at odds with the southern route hypothesis. Nuclear data (9) show a sister relationship of *Castanopsis* with *Castanea*. *Castanea-Castanopsis* are close relatives of oaks, genus *Quercus*. *Quercus* was evolved and started to radiate by the early Eocene (10). *Castanea-Castanopsis* were already diverged when the North and South American *Castanopsis*-like fossils were deposited. Isolated biogeographic history inevitably would have left imprints in plastome signatures of *Castanopsis*; for instance, South American Nothofagaceae (subgenus *Nothofagus*) have different plastid signatures than their New Guinean–New Caledonian sister (subgenus *Brassospora*) despite potential long-distance dispersal (11). Within *Nothofagus*, three divergent, old plastid lineages indicate chloroplast capture and a larger distribution area in the past (12). Nuclear-plastid incongruence and strong geographic signal in the plastids is also found in core Fagaceae, which include all Castaneoideae and *Quercus*. If the Patagonian fossil represented the already diverged genus *Castanopsis* and if it were a precursor of modern-day Asian *Castanopsis*, one should find a divergent and genus-diagnostic plastid signature in at least some *Castanopsis*, with closer affinity to New World than to Old World Fagaceae. Shared plastid histories and near-identical plastid plant barcodes (*matK*, *rbcl*, *atpB-rbcL*, *trnH-psbA*) reflect shared biogeographic histories in the eastern hemispheric *Quercus* subgenus *Cerris*, *Lithocarpus*, *Castanea*, and *Castanopsis* (13–15) and set them apart from the western hemispheric *Quercus* subgenus *Quercus*, *Notholithocarpus*, and *Chrysolepis*. On the basis of all available genetic data, modern *Castanopsis* evolved near *Castanea*, *Lithocarpus*, and the mainly subtropical Eurasian oaks (subgenus *Cerris*), all of which lack a fossil record outside Eurasia but existed during the Paleogene of Eurasia. Therefore, the range expansion into South America was a dead end in the biogeographic history of the Fagaceae.

In sum, we are excited by the finding of Wilf and colleagues, but without fossil (Antarctic Castaneoideae) and molecular (distinct plastid signature of *Castanopsis*) evi-

dence, we do not see any evidence for the southern route as proposed by them.

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further information regarding the fossil record of Castaneoideae, please contact the corresponding author.

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Table 1. Emended and corrected seven-character matrix. Boldface entries are corrected from the Wilf *et al.* matrix.

	Style number	Cupule appendages	Cupule dehiscence	Female flowers per node	Flowers per cupule	Valve dehiscence	Inflorescence sexuality
<i>“Castanopsis” rothwellii</i>	Three	Scaly	Valvate	Solitary	One	Partial	Unisexual*
<i>Castanopsoidea</i> UCPC B627a	Three	Scaly	Valvate	Solitary?	Three	Partial?	Unisexual*
<i>Castanopsoidea</i> UCPC B849	Three	Spinose	Valvate	Solitary?	Three	Partial?	Unisexual*
<i>Fagus</i>	Three	Scaly	Valvate	–	Two	Complete	Unisexual
<i>Castanea</i> chestnut group	Six	Spinose	Valvate	Solitary/clustered	Three	Complete	Unisexual/mixed
<i>Castanea</i> pumila group	Six	Spinose	Valvate	Clustered	One	Complete	Unisexual/mixed
<i>Castanopsis</i> fissa group	Three	Scaly	Valvate/hemispheric indehiscent	Solitary	One	Partial/none	Unisexual/mixed
<i>Castanopsis</i> group	Three	Spinose	Valvate/hemispheric indehiscent	Solitary	One/three	Complete/partial /none	Unisexual/mixed
<i>Chrysolepis</i>	Three	Spinose	Valvate	Clustered	More than three	Complete	Unisexual/mixed
<i>Lithocarpus</i> A	Three	Scaly	Hemispheric indehiscent	Solitary/clustered	One	None	Unisexual/mixed
<i>Lithocarpus</i> B	Three	Scaly	Hemispheric indehiscent	Clustered	One	None	Unisexual/mixed
<i>Notholithocarpus</i>	Three	Scaly	Hemispheric indehiscent	Clustered	One	None	Unisexual/mixed
<i>Quercus</i>	Three	Scaly	Hemispheric indehiscent	Solitary	One	None	Unisexual
<i>Colombobalanus</i>	Three	Scaly	Valvate	Solitary	One to many	Complete	Unisexual
<i>Formanodendron</i>	Three	Scaly	Valvate	Solitary	One to many	Complete	Unisexual/mixed
<i>Trigonobalanus</i>	Three	Scaly	Valvate	Clustered	One to many	Complete	Unisexual/mixed

*Difficult to assess on the basis of limited material.

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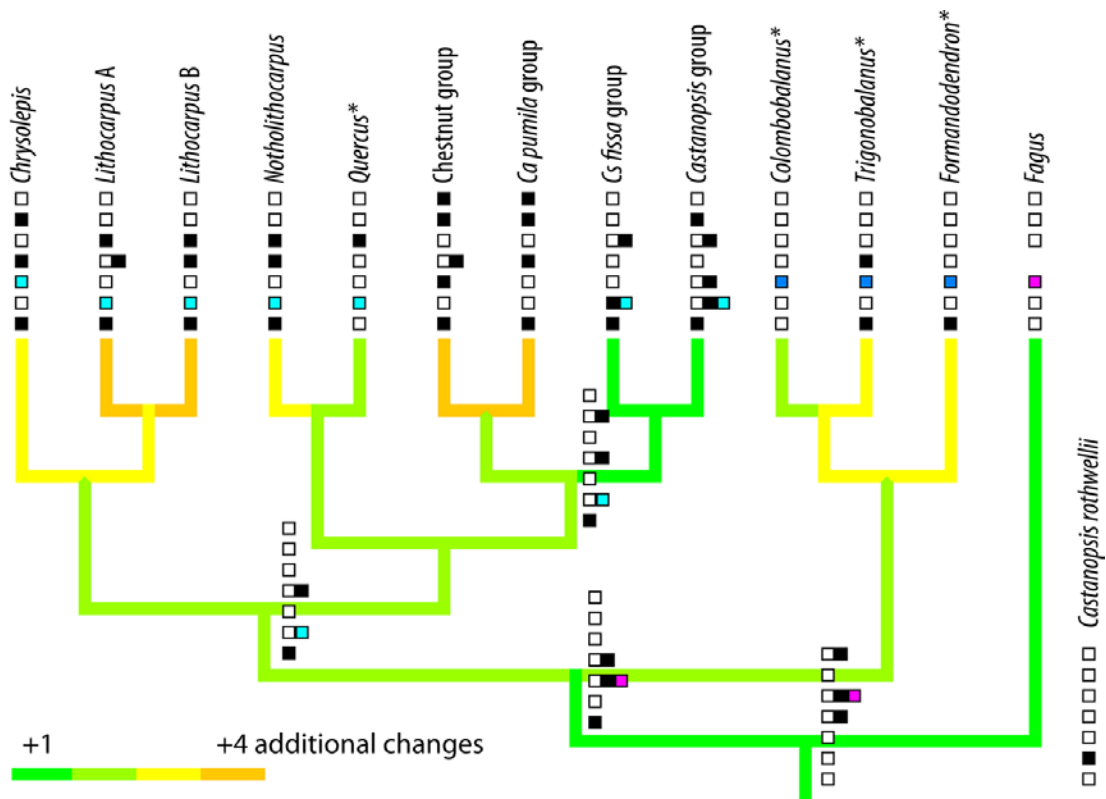


Fig. 1. Phylogenetic information content of the seven-character matrix used by Wilf *et al.* when using parsimony. Phylogenetic framework is from Oh and Manos (9) with a paraphyletic Castaneoideae. Character 7 was incorrectly coded in Wilf *et al.* for *Castanopsis* and *Lithocarpus*; character 5 was incorrectly coded for *Fagus*. Character states for characters 1 to 7 are indicated by open or solid squares (top to bottom) for terminal taxa; reconstructed character suites (using the standard parsimony model implemented in Mesquite version 3.6) are shown for selected hypothetical common ancestors. Tree length is 20. Colors of branches indicate numbers of additional steps (evolutionary changes) required by placing the fossil(s) on the corresponding branch. Note that the number of steps does not change whether *C. rothwellii* is placed as sister to all Fagaceae, sister to *Fagus*, sister to trigonobalanoids and quercoids, or as part of *Castanopsis*. Asterisks indicate genera not included in Wilf *et al.*'s analysis.

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