

Tansley insight

Green Web or megabiased clock? Plant fossils from Gondwanan Patagonia speak on evolutionary radiations

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Summary

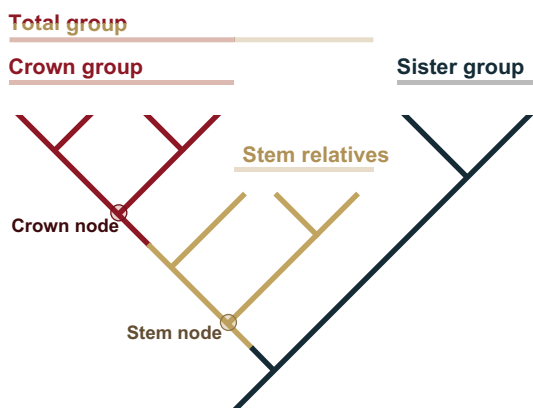
Evolutionary divergence-age estimates derived from molecular ‘clocks’ are frequently correlated with paleogeographic, paleoclimatic and extinction events. One prominent hypothesis based on molecular data states that the dominant pattern of Southern Hemisphere biogeography is post-Gondwanan clade origins and subsequent dispersal across the oceans in a metaphoric ‘Green Web’. We tested this idea against well-dated Patagonian fossils of 19 plant lineages, representing organisms that actually lived on Gondwana. Most of these occurrences are substantially older than their respective, often post-Gondwanan molecular dates. The Green Web interpretation probably results from directional bias in molecular results. Gondwanan history remains fundamental to understanding Southern Hemisphere plant radiations, and we urge significantly greater caution when using molecular dating to interpret the biological impacts of geological events.

I. Introduction

A shared goal of biology and paleontology is the correlation of evolutionary events with the timeline of Earth history. All dates for deep-time events ultimately come from geochronologic analyses of the radioisotopic ‘Earth clocks’ found in certain minerals. Geochronologic precision has improved massively in recent years (Gradstein *et al.*, 2012), and analytical uncertainties of absolute ages are now often < 0.05% (e.g. Burgess *et al.*, 2014).

Evolutionary paleobiology is a principal driver and beneficiary of advances in geochronology. As paleontologists who frequently

collaborate with geochronologists, we expect that molecular ‘timetrees’ (Hedges & Kumar, 2009) will help fill gaps in the fossil record. However, we find molecular divergence-age estimates (‘dates’) difficult to evaluate, and not only because many results differ strikingly from the fossil data. Molecular dates are extremely sensitive to placements of calibrating fossils at stem vs crown nodes (see Box 1) and to choices of methods and calibration scenarios (Sauquet *et al.*, 2012; Magallón, 2014). Perhaps most significantly, molecular dates usually cannot be tested adequately with fossils. If molecular estimates are truly too old, they cannot be falsified because the required fossils never existed. If they are younger than

Box 1 Basic terminology of phylogenetic relationships

A crown group (red) consists of the most recent common ancestor (at the crown node) of a living clade and all the living and extinct descendants of that ancestor. A stem node represents the evolutionary divergence of all members of a monophyletic group from a common ancestor, including extinct lineages that diverge below crown groups (stem relatives, pale brown).

comparable fossils, they are still ‘not wrong’ because they represent minimum ages. We dispute this logic because dated fossils also represent minimum ages of their lineages (clades). Arguments in support of molecular dating tend to emphasize the perceived similarities of results from different genes and models, thus lacking any geological validation, or they present small sets of clock-rock comparisons without any supporting stratigraphic discussion (de Queiroz, 2014).

It is now commonplace to compare molecular age estimates directly with the geologic time scale in ‘chronograms’ (e.g. Biffin *et al.*, 2010a; Nagalingum *et al.*, 2011). However, just as there are detailed requirements for taxonomic nomenclature, the International Commission on Stratigraphy defines rigorous criteria for assigning numerical ages and geologic time periods (Gradstein *et al.*, 2012; www.stratigraphy.org). Generations of scientists have developed the geologic timescale to its unprecedented current precision, using several, intensively cross-validated radioisotopic systems in conjunction with a diverse suite of complementary techniques (Gradstein *et al.*, 2012). Significant geochronologic errors are extremely rare and mostly stem from uncritical use of obsolete stratigraphic data, not from modern procedures for grain selection, preparation, and analysis. By contrast, the relatively new field of molecular dating does not yet have standards that define comparisons with the geologic timescale.

There is no more high-profile case that encompasses all these issues than the relationship between Gondwanan breakup and the biogeography of disjunct Southern Hemisphere lineages. Molecular data, calibrated using selected fossils, are used extensively to estimate whether particular groups evolved before (Gondwanan vicariance) or after (dispersal) the separations of the

continents where they live naturally today (e.g. Sanmartín & Ronquist, 2004; Barker *et al.*, 2007; Mao *et al.*, 2012). The increasing number of molecular age estimates that are younger than the respective separation dates favors the hypothesis that post-Gondwanan, oceanic dispersal of young lineages is the dominant mechanism that explains southern disjunctions. Recently, Alan de Queiroz (2014) made a detailed case for dispersal, metaphorically invoking the hypothesized trajectories of plants through time as a ‘Green Web’ across the oceans. The consequences of the Green Web hypothesis are far-reaching. The idea affects our fundamental understanding of the origins, persistence, associations, and dispersal capabilities of Southern Hemisphere plants, and their potential to survive and reassemble in the face of current climate change and disturbance.

The rapidly emerging paleobotanical record from Patagonia, Argentina (Wilf *et al.*, 2013), offers a rare, outstanding opportunity to test the Green Web hypothesis specifically, and the more general practice of using molecular divergence estimates in the framework of geologic time, by comparing fossils and clocks empirically. Before *c.* 50 Myr ago (Ma), the final separation of South America from Antarctica, and on to Australia, had not begun (Lawver *et al.*, 2011); deepwater barriers to biotic interchange developed gradually over the next several million years. The fossils we discuss (Table 1) are recently studied remains of ferns, cycads, conifers and angiosperms that lived on Gondwana, and the lineages they represent, by definition, evolved before Gondwana last separated.

II. Data: fossils and clocks

The Patagonian fossil occurrences represent a critical mass of diverse reports, originating from a single Gondwanan region, that are directly comparable with molecular studies of the same lineages because they are precisely dated geologically and well-understood taxonomically (Table 1, Fig. 1). The fossils are in varying stages of phylogenetic resolution, and we assigned them to stem or crown positions as indicated (Table 1, notes). The more ambiguous placements are compared with both stem- and crown-age estimates. We chose the most recent, comparable molecular studies available (Table 1), excluding those that: clearly had significant methodological errors; used the respective fossil as a calibration; or used other fossils to fix the node in question (unless there were no other recent studies of a clade). We did not tabulate the uncertainties on molecular age estimates because they were inconsistently reported; we acknowledge that these uncertainties are often large, and this does not affect our conclusions. Please see Table 1 for the geologic dates and literature citations that support the following discussion.

III. Results

The osmundaceous fern *Todea amissa* (52.2 Ma) resolved in the crown of *Todea*, and it is younger than the *Todea*–*Leptopteris* divergence (75.4 Ma). Although this result appears harmonious, a combined morphological and molecular analysis of *T. amissa* and numerous fossil and extant related species (Carvalho *et al.*, 2013) showed that this divergence must date to at least 265 Ma. For cycads, many recent molecular dates have been surprisingly young,

Table 1 Patagonian plant fossils and related molecular age estimates

Taxon (organs)	Citation(s)	Placement	Oldest, site	Molecular stem	Molecular crown
Ferns					
Osmundaceae: <i>Todea amissa</i> Carvalho (F, FF)	Carvalho <i>et al.</i> (2013)	Crown ¹ <i>Todea</i>	52.22 ± 0.22 Ma, L. Hunco	<i>Leptopteris</i> – <i>Todea</i> split: 75.4 Ma, Schuettpelz & Pryer (2009)	n/a
Gymnosperms					
Cycadales: <i>Kurtzia</i> <i>Frenguelli</i> , spp. (F w/C)	Artabe & Stevenson (1999); Hermesen <i>et al.</i> (2006)	Stem ¹ Zamiaceae	> 201 Ma, Late Triassic, several sites	<i>Zamia</i> – <i>Stangeria</i> split: c. 140 Ma, Crisp & Cook (2011); 67.4 Ma, Nagalingum <i>et al.</i> (2011)	n/a
Araucariaceae: <i>Araucaria mirabilis</i> (Spegazzini) Windhausen (SC, S, E, F, W)	Stockey (1975); Escapa & Catalano (2013)	Crown ¹ Araucariaceae	Middle Jurassic, c. 172–162 Ma, Cerro Cuadrado	Variable, not shown	Araucariaceae crown: 65 Ma, Biffin <i>et al.</i> (2010a); 36 Ma, Crisp & Cook (2011)
Araucariaceae: <i>Araucaria grandifolia</i> Feruglio (F w/C, W)	Del Fueyo & Archangelsky (2002)	Stem ² A. Section <i>Araucaria</i>	114.67 ± 0.18 Ma, Punta del Barco Fm.	Sec. <i>Araucaria</i> stem: c. 25 Ma, Biffin <i>et al.</i> (2010a); 20.7 Ma, Leslie <i>et al.</i> (2012)	Sec. <i>Araucaria</i> crown: 9.8 Ma, Leslie <i>et al.</i> (2012); c. 5 Ma, Biffin <i>et al.</i> (2010a)
Araucariaceae: <i>Araucaria</i> <i>pichileufensis</i> Berry (F, PC, SC)	Berry (1938); Florin (1940a); Wilf <i>et al.</i> (2014)	Crown A. Section <i>Eutacta</i>	52.22 ± 0.22 Ma, L. Hunco	Sec. <i>Eutacta</i> stem: 57.4 Ma, Leslie <i>et al.</i> (2012); c. 46 Ma, Biffin <i>et al.</i> (2010a)	Sec. <i>Eutacta</i> crown: 22.8 Ma, Leslie <i>et al.</i> (2012); c. 20 Ma, Biffin <i>et al.</i> (2010a)
Araucariaceae: <i>Agathis zamunerae</i> Wilf (F, PC, SC, S)	Wilf <i>et al.</i> (2014)	Crown ² <i>Agathis</i>	52.22 ± 0.22 Ma, L. Hunco	<i>Agathis</i> – <i>Wollemia</i> split: 66.4 Ma, Leslie <i>et al.</i> (2012); 18 Ma, Crisp & Cook (2011)	<i>Agathis</i> crown: 23.9 Ma, Leslie <i>et al.</i> (2012); 23 Ma, Biffin <i>et al.</i> (2010a)
Podocarpaceae: <i>Acmopyle</i> <i>engelhardtii</i> (Berry) Florin (F)	Florin (1940b); Wilf (2012)	Stem or crown <i>Acmopyle</i>	52.22 ± 0.22 Ma, L. Hunco	<i>Acmopyle</i> stem: 92 Ma, Leslie <i>et al.</i> (2012); 80 Ma, Biffin <i>et al.</i> (2011)	<i>Acmopyle</i> crown: 36.9 Ma, Leslie <i>et al.</i> (2012); 34 Ma, Biffin <i>et al.</i> (2011)
Podocarpaceae: <i>Dacrycarpus puertae</i> Wilf (F, PC, SC)	Wilf (2012)	Crown ² <i>Dacrycarpus</i>	52.22 ± 0.22 Ma, L. Hunco	<i>Dacrycarpus</i> stem: 62 Ma, Biffin <i>et al.</i> (2011)	<i>Dacrycarpus</i> crown: 15 Ma, Biffin <i>et al.</i> (2011); 10 Ma, Keppel <i>et al.</i> (2011)
Cupressaceae: <i>Athrotaxis ungeri</i> (Halle) Florin (F w/C, SC)	Del Fueyo <i>et al.</i> (2008)	Stem or crown <i>Athrotaxis</i>	Aptian–Albian, many localities	<i>Athrotaxis</i> stem: 145.2 Ma, Leslie <i>et al.</i> (2012)	<i>Athrotaxis</i> crown: 3.7 Ma, Leslie <i>et al.</i> (2012)
Cupressaceae: <i>Papuacedrus</i> <i>prechilensis</i> (Berry) Wilf <i>et al.</i> (F, SC)	Wilf <i>et al.</i> (2009)	Sister to <i>P. papuana</i> ²	52.22 ± 0.22 Ma, L. Hunco	<i>P. papuana</i> lineage: 126.3 Ma, Yang <i>et al.</i> (2012); c. 68.1 Ma, Crisp & Cook (2011)	n/a
Angiosperms: noneudicots					
Arecaceae: <i>Tripylocarpa</i> <i>aestuaris</i> Gandolfo & Futsey (Fr)	Futsey <i>et al.</i> (2012)	Stem ¹ Subtribe Attaleinae	64.7–63.5 Ma, Las Violetas	Attaleinae stem: 50–60 Ma, Gunn (2004); 60 Ma, Meerow <i>et al.</i> (2009), fixed constraint	n/a
Potamogetonaceae: <i>Baibiancarpus</i> <i>chubutensis</i> Gandolfo (Fr)	Gandolfo <i>et al.</i> (2009)	Stem Potamogetonaceae	56–42 Ma, Baibian Beds	Potamogetonaceae stem: c. 50 Ma, Nauheimer <i>et al.</i> (2012); 46.3 Ma, Chen <i>et al.</i> (2012)	n/a
Ripogonaceae: <i>Ripogonum</i> <i>americanum</i> Carpenter <i>et al.</i> (F)	Carpenter <i>et al.</i> (2014)	Stem or crown <i>Ripogonum</i>	52.22 ± 0.22 Ma, L. Hunco	Ripogonaceae stem: 76 Ma, Janssen & Bremer (2004); 47 Ma, Vinnersten & Bremer (2001)	n/a

Table 1 (Continued)

Taxon (organs)	Citation(s)	Placement	Oldest, site	Molecular stem	Molecular crown
Monimiaceae: <i>Monimiophyllum</i> <i>callidentatum</i> C.L. Knight (F)	Knight & Wilf (2013)	Stem or crown <i>Wilkiea</i> clade	52.22 ± 0.22 Ma, L. Hunco	Stem <i>Wilkiea</i> clade: c. 36 Ma, Renner <i>et al.</i> (2010)	Crown <i>Wilkiea</i> clade: c. 33 Ma, Renner <i>et al.</i> (2010)
Angiosperms: eudicots					
Asteraceae: <i>Raiguenrayun cura</i> Barreda <i>et al.</i> (Fl, P)	Barreda <i>et al.</i> (2012)	Stem ² Asteraceae, above split of Barnadesioideae– Asteraceae	47.74 ± 0.05 Ma, Río Pichileufú	Split of Barnadesioideae– Asteraceae: 40 Ma, Kim <i>et al.</i> (2005)	n/a
Casuarinaceae: <i>Gymnostoma</i> , 3 species (F, Fr, P, PC)	Zamaloa <i>et al.</i> (2006)	Crown <i>Gymnostoma</i>	52.22 ± 0.22 Ma, L. Hunco	<i>Gymnostoma</i> stem: 48 Ma, Crisp <i>et al.</i> (2004)	<i>Gymnostoma</i> crown: c. 41 Ma, Crisp <i>et al.</i> (2004)
Fabaceae: <i>Paracioxylon</i> <i>frenquellii</i> Brea <i>et al.</i> (W)	Brea <i>et al.</i> (2008)	Stem Mimosoideae	64.7–63.5 Ma, P. Loros	Mimosoideae stem 55 Ma, Lavin <i>et al.</i> (2005), fixed constraints	n/a
Myrtaceae: <i>Eucalyptus</i> <i>caldericola</i> ⁺ Hermsen <i>et al.</i> (F, Fl, Fr)	Gandolfo <i>et al.</i> (2011); Hermsen <i>et al.</i> (2012)	Crown ¹ Eucalypteae	52.22 ± 0.22 Ma, L. Hunco	n/a	Crown Eucalypteae: c. 40 Ma, Biffin <i>et al.</i> (2010b)
Proteaceae: <i>Orites</i> <i>bivascularis</i> Romero <i>et al.</i> (Fr)	Romero <i>et al.</i> (1988); González <i>et al.</i> (2007)	Stem or crown <i>Orites</i>	52.22 ± 0.22 Ma, L. Hunco	<i>Orites</i> stem: 45.1 Ma, Barker <i>et al.</i> (2007); 15.3 Ma, Mast <i>et al.</i> (2008)	n/a

See cited papers for full details and additional literature, plus Césari *et al.* (2011) and Clyde *et al.* (2014) for geochronology of Punta del Barco and P. Loros/Las Violetas floras, respectively. The radiometric dates (uncertainties < ±0.3 million yr (Ma)) are from volcanic primary airfall tuffs that are intimately associated stratigraphically with the fossils; they most directly date the igneous events. Molecular age estimates shown as means, without uncertainties.

C, cuticle; E, embryos; F, foliage incl. leafy twigs; FF, fertile foliage; Fl, flower/inflorescence; Fr, fruit; L. Hunco, Laguna del Hunco; n/a, not available or not applicable; P. Loros, Palacio de los Loros; P, pollen; PC, pollen cone; SC, seed cone; S, seed; W, wood.

¹Position from cladistic analysis.

²Position suggested in cited literature without cladistic analysis. Other fossils provisionally considered under both stem and crown scenarios, unless they clearly belonged to extinct genera (stem) or preserved numerous reproductive characters of the living groups (crown).

⁺Also includes other *Eucalyptus* species that apply to the leaves and flowers.

including a Jurassic crown age for all cycads and a c. 67 Ma estimated divergence of *Zamia* and *Stangeria* (Nagalingum *et al.*, 2011). However, several Triassic genera represent crown-group cycads, including *Kurtzia* from Patagonia (Artabe & Stevenson, 1999). It is difficult to make fine comparisons for cycads because morphological and molecular phylogenies hypothesize very different relationships among the extant genera. With this caveat, we note that morphological phylogenies resolved both *Kurtzia* and *Ticoa* (Early Cretaceous, Patagonia) to positions allied with *Zamia*, indicating that the *Zamia*–*Stangeria* split dates to at least 200 Ma (Hermsen *et al.*, 2006; Martínez *et al.*, 2012).

The conifer fossil record in Patagonia is especially rich and informative, including Cupressaceae, Podocarpaceae, and Araucariaceae among the groups with living representatives. The Patagonian Cupressaceae include the oldest member of the crown family, Early Jurassic *Austrohamia minuta* (Escapa *et al.*, 2008). From the Early Cretaceous, *Athrotaxis ungeri* is extremely similar to extant *A. cupressoides*, even in ultrastructural details. It is likely that *A. ungeri* had an evolutionary position well above the stem and closer to the crown genus, which has a very young molecular-age estimate (3.7 Ma). *Papuacedrus prechilensis* (52.2 Ma) is indistinguishable from living *P. papuana*; this fossil species is much younger than the Cretaceous divergence estimates for the genus,

which were calibrated to Paleocene occurrences of its close relative *Libocedrus*.

In Podocarpaceae, *Acropyle engelhardti* (52.2 Ma) lies between stem (92 and 80 Ma) and crown (36.9 and 34 Ma) estimates for its genus. This fossil species has not yet been found with reproductive organs, which would be of great interest because the fossil is much older than the estimated crown node. *Dacrycarpus puertae* (52.2 Ma) is based on multiple organs and is indistinguishable from extant *D. imbricatus*. There is no doubt that it belongs in the *Dacrycarpus* crown, which was placed considerably younger (15 and 10 Ma) in molecular analyses that used other Eocene *Dacrycarpus* fossils as stem constraints.

Araucariaceae show the richest fossil conifer diversity in Patagonia, extensively documenting the radiations of several lineages. *Araucaria grandifolia* (114.7 Ma) is considered a basal member of *A. Section Araucaria* (molecular divergence 25 and 20.7 Ma) due to its distinctive leaves and leaf arrangement, although its cuticular micromorphology differs somewhat from the living species. *Araucaria pichileufensis* (52.2 Ma) has long been assigned to *A. Section Eutacta* based on its vegetative and cone-scale morphology that both closely resemble living *Eutacta* species (e.g. *A. columnaris*). We consider it to be a likely member of the crown *Eutacta* clade that is much older than molecular crown estimates

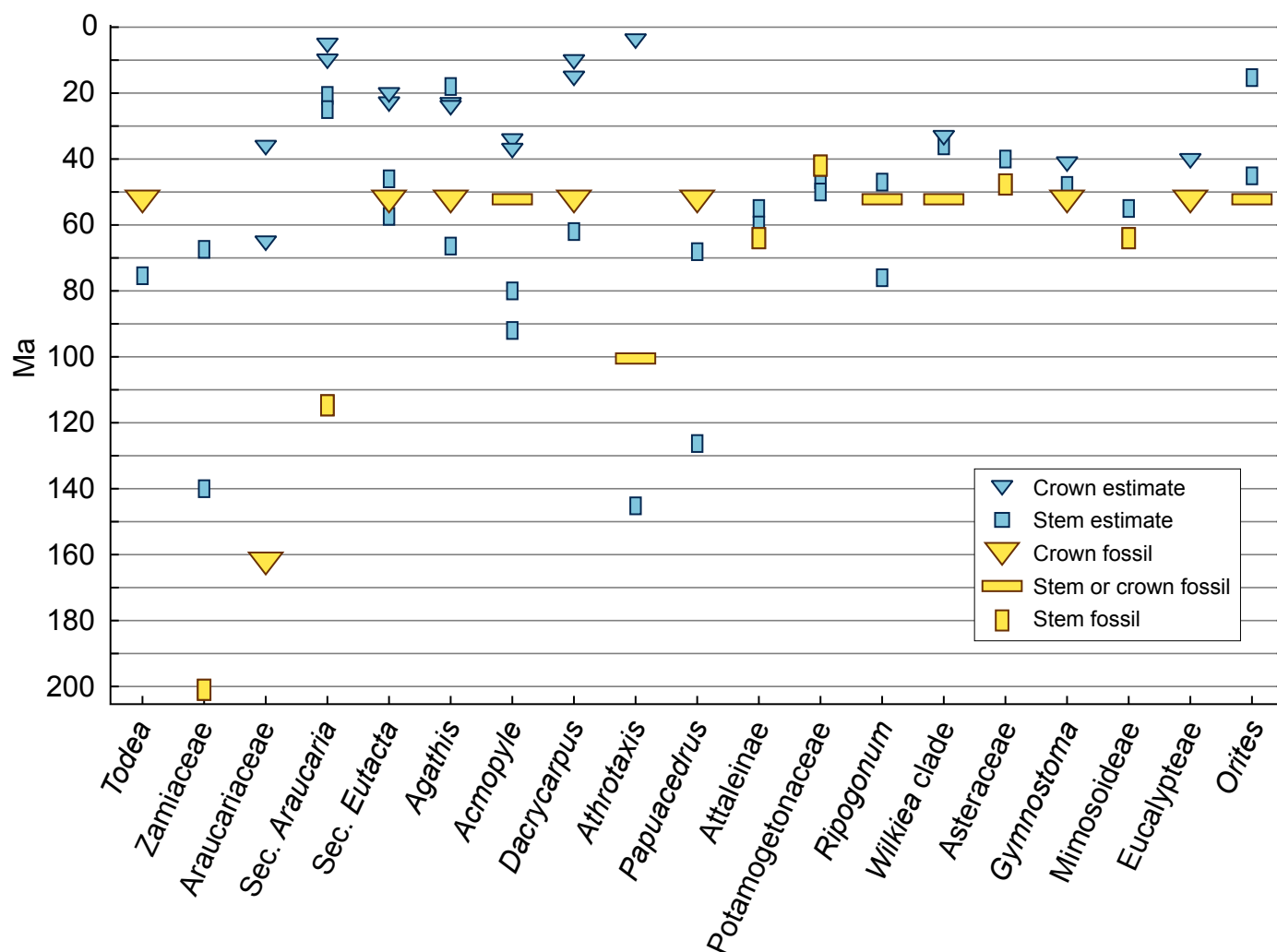


Fig. 1 Graphic summary of data in Table 1. Fossils with a range of potential ages are plotted using the youngest age, with reference to Gradstein *et al.* (2012, as updated at www.stratigraphy.org). Ma, million years ago.

(22.8 and 20 Ma). *Agathis zamunerae* (52.2 Ma) is based on multiple organs that show it must belong to the crown of *Agathis*, probably in a derived position. This fossil species is considerably older than recent estimates of the *Agathis* crown (23.9 and 23 Ma).

Middle Jurassic *Araucaria mirabilis* provides convincing evidence for the antiquity of crown Araucariaceae. This species is represented from exquisitely preserved seed cones and associated leaves and wood. Numerous morphological and anatomical features of its cones, seeds, and embryos support its affinity to *Araucaria* rather than the *Agathis*–*Wollemia* sister clade (Stockey, 1975; Escapa & Catalano, 2013). In striking contrast with these examples and many other fossils that demonstrate the Mesozoic divergences of *Araucaria*, its sections, and the *Agathis*–*Wollemia* clade (Stockey, 1994; Dettmann *et al.*, 2012; Escapa & Catalano, 2013), two recent molecular studies estimated very young ages for crown Araucariaceae (65 and 36 Ma).

In noneudicot angiosperms, the anatomically preserved cocosoid palm fruits referred to *Tripylocarpa aestuaria* (64 Ma) slightly antedate the prior stem-age estimate for their subgroup, Attaleinae (Gunn, 2004). Several more recent estimates for Attaleinae were

calibrated to cocosoid palms from the late Paleocene of Colombia, *c.* 59 Ma (Gómez-Navarro *et al.*, 2009), and *Tripylocarpa* is older than these as well. *Baibiancarpus chubutensis* is an extinct genus of Potamogetonaceae that can be constrained only to 56–42 Ma, a span that well matches stem-node estimates of the family. A new species of *Ripogonum* (52.2 Ma) is based on compressed leaves that are not distinguishable from the living species; it is younger than one (76 Ma) but similar to another (47 Ma) stem-divergence estimate for the genus. *Monimiophyllum callidentatum* (Monimiaceae, 52.2 Ma) is based on a single leaf that shows a closer affinity to *Wilkiea hugeliana* than any other extant species. The fossil species is significantly older than stem or crown estimates of the *Wilkiea* clade (*c.* 36 and 33 Ma, respectively).

Among eudicots, *Raiguenrayun cura* (47.7 Ma) is the only fossil capitulum of Asteraceae known. This spectacular fossil was placed in the basal Asteraceae above their split from Barnadesioideae, pre-dating the molecular estimate of this node (*c.* 40 Ma). Several species of *Gymnostoma* (52.2 Ma) are known from multiple organs that in all regards match the living genus. These occurrences are older than the stem and crown estimates of Crisp *et al.* (2004), who

estimated the stem of *Gymnostoma* at *c.* 48 Ma using an Oligocene *Gymnostoma* as a crown constraint. Sauquet *et al.* (2012, not shown) generated eight molecular-dating scenarios of Fagales based on 21 fossil calibrations. Among these, the stem divergence of Casuarinaceae ranged from 89 to 38 Ma. The scenarios that used a late Paleocene, Australian *Gymnostoma* fossil for calibration gave much older stem divergence results (89–87 Ma) than those that used other constraints (63.3–38 Ma).

The mimosoid wood *Paracacioxylon frenguelli* (64 Ma) antedates a prior fixed constraint of 55 Ma for the divergence of Mimosoideae. *Eucalyptus caldericola* (52.2 Ma) fruits and associated flowers and leaves have been cladistically resolved to the crown of Eucalypteae, older than molecular estimates (*c.* 40 Ma, using a 48 Ma constraint). In all likelihood, these fossils belong in a derived position within *Eucalyptus* (Gandolfo *et al.*, 2011). In Proteaceae, *Orites bivascularis* (52.2 Ma) fruits have characters that are consistent with living *Orites* and antedate estimated stem divergence (45.1 and 15.3 Ma).

IV. Discussion

Phylogenetically diverse, conservatively interpreted Gondwanan fossils (Table 1) are for the most part significantly older than their most comparable molecular dates, of which many are post-Gondwanan (i.e. younger than *c.* 45 Ma; Fig. 1). Clock estimates were most in tune when closely related fossils of similar or older age were already used as calibrations or fixed constraints (e.g. *Papuacedrus*, *Tripylocarpa* and Mimosoideae). Comparable results emerged from the recent study of Fagales (Sauquet *et al.*, 2012), wherein many nodes resolved younger when closely related fossils were removed from the various calibration scenarios.

We cannot fully explain the sources of directional bias, but we highlight two issues that should be addressable. First, several clock studies ignored previously known fossils that, if used as calibrations, would probably have made several estimates older (Table 1). These oversights mostly affected cycads and araucarians. Second, the convention of placing calibrations at stem nodes, unless they are explicitly resolved into a crown group, seems to cause significant directional bias. This procedure is methodologically conservative, but it forces crown nodes to be younger than the calibration fossil, whose real evolutionary position was either in the crown or along its subtending branch, not at a stem node.

Default stem placements should cause increased 'young bias' in younger strata, simply because younger fossils are more likely to represent crown groups. This logic could partly explain why 'young bias' appears for geologically younger lineages in this study and others (Carvalho *et al.*, 2011; Sauquet *et al.*, 2012) but is not usually present in work on older divergences, which may be biased by other issues (Magallón, 2010, 2014). One example is the young crown ages for *Agathis* and *Dacrycarpus* (Table 1). These were partly based on stem placements for Australian fossils of these taxa. However, given the recent discoveries of *A. zamunerai* and *D. puertae* in Patagonia, the similarly aged but less complete Australian fossils probably also represent derived species, of crown conifer genera that were widespread across Gondwana. Improving this situation may require a methodological innovation, perhaps

one that allows calibration placements at simulated nodes between stems and crowns (see Magallón, 2010).

V. Conclusions

Our results strongly suggest that the recent emphasis in the literature on post-Gondwanan dispersal, including the Green Web hypothesis, is partly based on megabiased clocks. The inherently large uncertainties of molecular dating do not compensate for the overall directional pattern of 'young bias' across plant clades. Even without any consideration of molecular dates, the record from Patagonia convincingly demonstrates that Gondwanan history remains fundamental to the evolutionary radiations, distributions, survival, and conservation of Southern Hemisphere plants and plant associations. If our findings apply to a broader spectrum of organisms, there would be profound consequences for the general understanding of evolutionary rates. Notably, like Gondwanan plants, some molecular dates for important human pathogens are surprisingly young and postdate fossil evidence (e.g. Lee *et al.*, 2012; Bos *et al.*, 2014).

We urge significantly greater caution when using molecular dates in the explicit context of geologic time and Earth history. The fossil record is always incomplete, but its exciting potential is only beginning to develop in many parts of the world. Future improvements in molecular dating seem very likely, but for now, fossils and geochronology provide the only rigorous, enduring temporal framework for evolutionary radiations.

Acknowledgements

Many highly relevant papers could not be cited here due to space constraints, and we regret these omissions. We gratefully acknowledge NSF grant DEB-0919071 for partial support of this work, R. Bateman and A. Leslie for helpful reviews, and M. Carvalho and R. Wilf for earlier comments on the manuscript.

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