



## **Fossil calibration of Magnoliidae, an ancient lineage of angiosperms**

**Julien Massoni, James Doyle, and Hervé Sauquet**

### **ABSTRACT**

In order to investigate the diversification of angiosperms, an accurate temporal framework is needed. Molecular dating methods thoroughly calibrated with the fossil record can provide estimates of this evolutionary time scale. Because of their position in the phylogenetic tree of angiosperms, Magnoliidae (10,000 species) are of primary importance for the investigation of the evolutionary history of flowering plants. The rich fossil record of the group, beginning in the Cretaceous, has a global distribution. Among the hundred extinct species of Magnoliidae described, several have been included in phylogenetic analyses alongside extant species, providing reliable calibration points for molecular dating studies. Until now, few fossils have been used as calibration points of Magnoliidae, and detailed justifications of their phylogenetic position and absolute age have been lacking. Here, we review the position and ages for 10 fossils of Magnoliidae, selected because of their previous inclusion in phylogenetic analyses of extant and fossil taxa. This study allows us to propose an updated calibration scheme for dating the evolutionary history of Magnoliidae.

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## INTRODUCTION

Among the first diverging lineages of angiosperms (outside monocots and eudicots), Magnoliidae are the largest clade, comprising about 10,000 species divided among 20 families and four orders: Magnoliales, Laurales, Canellales, and Piperales (APG III, 2009). Although Magnoliidae have a global distribution extending into the temperate zones of both hemispheres, most of their diversity occurs in tropical areas. This group has been supported as monophyletic by the great majority of molecular phylogenetic studies (Qiu et al., 1999, 2000, 2005, 2006, 2010; Soltis et al., 1999, 2000a, 2000b, 2007, 2011; Mathews and Donoghue, 1999, 2000; Savolainen et al., 2000; Graham and Olmstead, 2000; Zanis et al., 2002, 2003; Nickrent et al., 2002; Borsch et al., 2003; Hilu et al., 2003; Jansen et al., 2007; Moore et al., 2007, 2010; Burleigh et al., 2009). Although the majority of the relationships among families of Magnoliidae are well established, the exact positions of Hydnoraceae and Magnoliaceae and the relationships among Hernandiaceae, Lauraceae, and Monimiaceae are still debated (Figure 1; Massoni et al., 2014). This group has a rich fossil record starting in the Early Cretaceous. Cretaceous fossils assigned to Magnoliidae have been found in many parts of the world: South America (e.g., Mohr and Bernardes-Oliveira, 2004; Mohr et al., 2013), North America (e.g., Dilcher and Crane, 1984; Crepet et al., 2005), Europe (e.g., Friis et al., 2010, 2011), Asia (e.g., Takahashi et al., 2001, 2008), Africa (e.g., Doyle et al., 1990), Australasia (e.g., Dettmann et al., 2009), and Antarctica (e.g., Poole and Gottwald, 2001; Eklund, 2003). Fossil Magnoliidae come in a variety of forms, from wood (e.g., Herendeen, 1991; Poole and Gottwald, 2001; Schöning and Bandel, 2004) and leaves (e.g., Upchurch and Dilcher, 1990; Kvaček, 1992) to flowers (e.g., Dilcher and Crane, 1984; Drinnan et al., 1990; Takahashi et al., 2008; Friis et al., 2011), fruits (e.g., Friis et al., 2010, 2011), seeds (e.g., Knobloch and Mai, 1986; Frumin and Friis, 1996), and pollen (e.g., Doyle et al., 1990; Macphail et al., 1994). Because the number of characters observed in such fossils is often limited, establishing their phylogenetic relationships to extant taxa is not always straightforward. However, among fossils assigned to Magnoliidae, several are characterized by good to exceptional preservation and a large number of systematically useful characters, such as the lignitized and charcoalfied flowers considered here.

Investigating the evolutionary history of organisms often requires a temporal context, which until recently was based almost exclusively on the fossil record. Insofar as fossils can be placed in a phylogenetic tree, a paleontological approach can provide minimum ages and, to a lesser extent, maximum ages for clades. Over the past two decades, this method has been supplemented with molecular dating approaches, which generate estimates of absolute divergence times throughout the tree (i.e., not just in the neighborhood of a particular fossil). The first such studies were based on the concept of a molecular clock, but the development of new methods has helped to relax the assumption of a strict clock across the tree.

In molecular dating analyses, the fossil record provides minimum bounds to calibrate the trees. These calibration points are not only used to convert the time scale of relative ages into one of absolute ages, but they also serve as anchors for modeling molecular rate variation across the tree (e.g., Sanderson, 1997; Sauquet et al., 2012). In this context, calibration is being recognized as a critical point and can have a drastic influence on results (Inoue et al., 2010; Meredith et al., 2011; Sauquet et al., 2012). Because of re-evaluation of the boundaries of geological time units, and sometimes re-dating of fossil beds, the accepted age of a fossil can change through time (Gandolfo et al., 2008). Therefore, an exhaustive geological review is essential in order to provide an accurate minimum age (Parham et al., 2012). Except for recently developed total evidence dating approaches that combine the phylogenetic analysis of extant and fossil taxa with the estimation of divergence times (Pyron 2011; Ronquist et al., 2012), a review of the phylogenetic position of a fossil is a second crucial point in the calibration process (Gandolfo et al., 2008; Parham et al., 2012; Sauquet et al., 2012). Molecular scaffold approaches (analyzing morphological data with the topology of living taxa fixed by a backbone constraint tree; Springer et al., 2001) or total evidence approaches (using both molecular and morphological data; Kluge, 1989) can provide a genuine test for the phylogenetic position of extinct taxa. A decision regarding the identity of the node calibrated by a fossil has to take into account the uncertainty of its phylogenetic position and the uncertainty of the relationships among extant species. A number of fossil taxa of Magnoliidae have already been included in morphological data matrices and analyzed with a phylogenetic approach taking into account both morphological and molecular data (e.g., Doyle and Endress, 2010; von

**TABLE 1.** Summary of the calibration points provided in the present paper. Abbreviations: Ma, million anni.

Fossil Taxon	Node	Minimum Age
<i>Endressinia brasiliana</i>	Crown-group Magnoliaceae (Doyle and Endress, 2010; Mohr et al., 2013)	112.6 Ma
<i>Schenkeriphyllum glanduliferum</i>	Crown-group Magnoliaceae (Mohr et al., 2013)	112.6 Ma
<i>Archaeanthus linnenbergeri</i>	Stem Magnoliaceae (Doyle and Endress, 2010)	96.5 Ma
<i>Virginianthus calycanthoides</i>	Crown-group Laurales (Doyle et al., 2008)	107.7 Ma
<i>Lovellea wintonensis</i>	Crown-group Laurales (Dettmann et al., 2009)	100.1 Ma
<i>Jerseyanthus calycanthoides</i>	Crown-group Calycanthoideae (Crepet et al., 2005)	85.8 Ma
<i>Cohongarootonia hispida</i>	Crown-group core Laurales (von Balthazar et al., 2011)	107.7 Ma
<i>Mauldinia mirabilis</i>	Crown-group core Laurales (Doyle and Endress, 2010)	95.5 Ma
<i>Walkeripollis gabonensis</i>	Crown-group Canellales (Doyle and Endress, 2010)	125.9 Ma
<i>Saururus tuckeræ</i>	Stem node of extant <i>Saururus</i> (Smith and Stockey, 2007)	44.3 Ma

Balthazar et al., 2011). These previous studies should, in principle, allow firm calibration of a molecular time scale, which is currently lacking for Magnoliidae (Forest and Chase, 2009).

The purpose of the present study is to provide a reliable calibration scheme for the Magnoliidae, usable as a starting point for any molecular dating study of Magnoliidae or subgroups of this clade, as well as higher-level angiosperm divergence time studies. To do so, we have reviewed the geologic age and phylogenetic relationships of all fossils of Magnoliidae that have been included in at least one phylogenetic analysis (10 fossils, Table 1). For this paper, we did not re-examine the fossil specimens. Instead, our argumentation is based on previously published descriptive and phylogenetic studies. Nine of these are represented by fossil flowers, in four cases with associated vegetative parts, but one (*Walkeripollis gabonensis*) is based on dispersed pollen grains that have a particularly diagnostic combination of characters. Following a strict minimum age philosophy, we propose to calibrate the most recent common ancestor of all most parsimonious assignments of previous analyses, and we provide associated synapomorphies when they were mentioned in the original study.

Most of the fossils treated here are from continental deposits that contain neither marine fossils that would allow direct correlation with the marine-based relative time scale, nor minerals suitable for absolute radiometric dating. In most cases, their ages are based on indirect palynological correlations with pollen and spore sequences that are dated by marine fossils. For example, for the US Atlantic Coastal Plain, these reference sections are in the US Western Interior and Gulf Coast (Hedlund and Norris, 1968; Ward, 1986; Ludvigson et al., 2010) and western Europe (Góczán et al., 1967; Kemp, 1970; Laing, 1975; Hughes, 1994;

Heimhofer et al., 2005, 2007; Hochuli et al., 2006), which belonged to the same Southern Laurasian phytogeographic province of Brenner (1976; see Doyle, 1969a, 1977, 1992; Wolfe and Pakiser, 1971; Doyle and Hickey, 1976; Doyle and Robbins, 1977; Christopher, 1979; Christopher et al., 1999; Christopher and Prowell, 2010). Some of these fossils, or others from the same localities, have been used for calibration in previous molecular dating studies (Doyle et al., 2004; Magallón and Castillo, 2009; Clarke et al., 2011; Pirie and Doyle, 2012). In some cases, Clarke et al. (2011) proposed much younger minimum ages than those recommended here because of conflicting conclusions of earlier authors on the phylogenetic position of fossils or on stratigraphic correlations. We argue that these minimum ages can be improved with critical examination. Our treatment includes a review of the age of units in the Atlantic Coastal Plain, the source of four of the fossils treated here, and several non-magnoliid taxa used in other dating analyses, which has been a subject of recent discussion (Hochuli et al., 2006).

Absolute ages used here follow Ogg and Hinnov (2012). This chapter of the revised Geologic Time Scale of Gradstein (2012) is the most recent comprehensive synthesis of absolute dates for the Cretaceous, including estimated ages for each substage, which we derive here from the charts in figure 27.6 of Ogg and Hinnov (2012). When possible, use of substage boundaries is preferable to the use of stage boundaries only, which can be overly conservative when dealing with stages as long as the Albian (ca. 12.5 Ma). In their table 27.2, Ogg and Hinnov (2012) included the estimated uncertainty for the boundaries of stages (2-sigma), but not for the boundaries of substages. In order to be conservative and to take into account existing estimates of uncertainty, those of our recommended

minimum ages that correspond to stage boundaries are the point estimates of Ogg and Hinnov (2012) minus the associated two standard deviations. Many radiometric dates are available for the Late Cretaceous, thanks particularly to the abundance of bentonites. There are fewer radiometric dates for the Early Cretaceous, but there has been much progress in integrating these with sequence stratigraphy, magnetostratigraphy, isotope stratigraphy, and cyclostratigraphy (which relates cyclic sedimentation to astronomical cycles of the earth's orbit and tilt). Significantly younger ages and shorter durations for several stages were proposed by Fiet et al. (2006) based on K/Ar glauconite dates and cyclostratigraphy. Scott et al. (2009) suggested that these ages may be too young due to argon leakage, a problem in glauconites, and Fiet et al. (2006) recognized that they require testing with studies on bentonites. By contrast, Huang et al. (2010), also using cyclostratigraphy, obtained ages for the Aptian and Albian very close to those of Ogg and Hinnov (2012) and suggested that the shorter durations of Fiet et al. (2006) were due to incompleteness of the sections studied. The dates of Ogg and Hinnov (2012) still involve considerable extrapolation, but use of this single comprehensive scheme should make correction of the calibrations presented here easier if this becomes necessary in the future.

We organized the present text by sections on calibrated nodes. When several fossil species were available to calibrate the same node, we used the oldest (reported as the "preferred fossil" section in the text) to define the age associated with the calibration. The remaining extinct species that could be used to calibrate the same node are reported as "additional fossils." We organized the "additional fossil" sections following the same structure used for the "preferred fossil" section. We proceeded in this way because future phylogenetic and stratigraphic studies may refine or modify the position or the age of the fossils, leading to future improvement of the current scheme. This is especially relevant when the older fossils are less completely known than the younger ones. We also believe that reporting the complete details of redundant fossils identified as suitable calibrations is useful to increase confidence in the proposed calibration of the corresponding nodes.

## NODE 1: CROWN-GROUP MAGNOLIINEAE

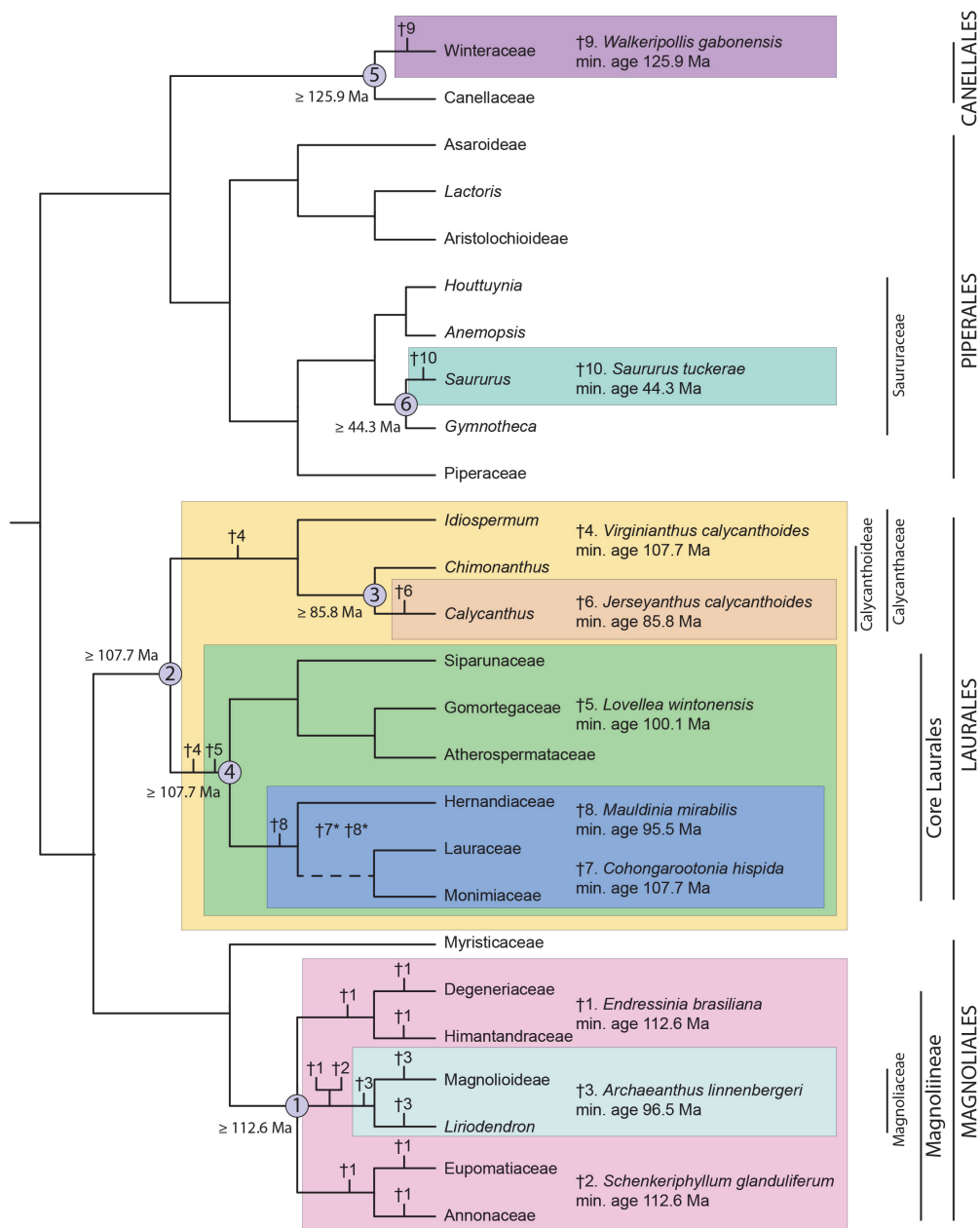
### Fossil Taxon 1 (preferred, given current knowledge)

*Endressinia brasiliiana* Mohr and Bernardes-de-Oliveira, 2004

**Node Calibrated.** Crown-group Magnoliineae (Doyle and Endress, 2010; Mohr et al., 2013)

**Reference Specimen.** MB. PB. 2001/1455 in Museum of Natural History, Institute of Paleontology, Berlin, Germany (holotype; branching axis with attached leaves and flowers).

**Phylogenetic Justification.** A molecular scaffold analysis by Doyle and Endress (2010), including 64 extant taxa sampled across angiosperms and 142 morphological characters, placed *Endressinia* in seven different most parsimonious positions: all positions within the crown group of the clade Himantandraceae + Degeneriaceae + Eupomatiaceae + Annonaceae (each represented as one terminal), or as the sister group of this clade. These relationships were supported by one unequivocal synapomorphy, the presence of glands on the stamens or staminodes (Doyle and Endress, 2010). A more recent molecular scaffold analysis (Mohr et al., 2013), which used a modified version of the morphological data set of Doyle and Endress (2010) reduced to Magnoliales, Laurales, and Canellales (as outgroup), placed *Endressinia* as the sister group of *Schenkeriophyllum glanduliferum* (another fossil from the same deposit, discussed below), with the clade of the two fossils being the sister group of Magnoliaceae. *Endressinia* and *Schenkeriophyllum* were united by sessile leaf blade (a new character) and linked with Magnoliaceae by sheathing leaf base and dry fruit wall. As noted by Mohr et al. (2013), Doyle and Endress (2010) did not score *Endressinia* as having a sheathing leaf base. This was probably because the sheath was formed from the unusual sessile leaf blade, rather than a leaf base separated from the blade by a petiole, but this difference does not rule out homology of the character. We have not attempted to resolve this conflict with a new analysis. The implications for dating are complicated by the fact that the position of Magnoliaceae within Magnoliales is still debated. Two alternative positions have been supported by most analyses: either as the sister group of a clade of Degeneriaceae + Himantandraceae (Soltis et al., 1999, 2007; Qiu et al., 2000, 2005, 2006; Savolainen et al., 2000; Zanis et al., 2002, 2003), or sister to a clade of Degeneriaceae + Himantandraceae + Eupomatiaceae + Annonaceae (Doyle and Endress, 2000; Sauquet et al.,



**FIGURE 1.** Simplified phylogenetic tree of Magnoliidae, after Massoni et al. (2014). Hydnoraceae (Piperales) are excluded, because the family was not included in original publications positioning the 10 fossils considered here. Colored boxes summarize the positions of fossils reviewed in the present paper. Their specific positions are figured by small branches with the number of the corresponding fossil at the tip. These correspond to the most parsimonious position(s) found for each fossil in previous phylogenetic analyses (see text for details). The minimum ages provided by the fossils are presented at the nodes they calibrate. The dashed branch refers to the phylogenetic uncertainty about relationships among Hernandiaceae, Lauraceae, and Monimiaceae (the position of Fossil 7 is on a branch not represented here, corresponding to a different set of relationships among these three families). Fossils are numbered following their order in the text. Abbreviations: Ma, million anni.

2003). However, the results of both Doyle and Endress (2010) and Mohr et al. (2013) support a position of *Endressinia* within the crown group of Magnoliineae, the well-supported clade of five families that is sister to Myristicaceae (Sauquet et al., 2003), and each study alone leads to use of this fossil to calibrate the crown node of this clade. Therefore, *Endressinia* provides a safe minimum age for the crown node of Magnoliineae (Figure 1).

**Minimum Age.** Aptian-Albian boundary, 112.6 Ma (113 ±0.4 Ma)

**Age Justification.** The fossil considered here was collected from the Crato Formation in the Araripe sedimentary basin of northeastern Brazil (Mohr et al., 2013). Mohr and Bernardes-de-Oliveira (2004) assumed that the Crato Formation is late Aptian or early Albian in age, based on numerous previous estimates (e.g., Pons et al., 1996). Because of this uncertainty, Clarke et al. (2011) proposed a minimum age for the Crato of 98.7 Ma, the top of the Albian. However, evidence has been accumulating in favor of a late Aptian age (Coimbra et al., 2002). Most recently, using gymnosperm pollen and dinoflagellates to correlate with better-dated sections, Heimhofer and Hochuli (2010) concluded that the Aptian-Albian boundary lies above the Crato Formation, and this was accepted by Mohr et al. (2013). We therefore propose a minimum age of 112.6 Ma for *Endressinia*, the Aptian-Albian boundary (113 ±0.4 Ma; Ogg and Hinnov, 2012).

**Previous Use as Calibration.** *Endressinia* has been used in several molecular dating studies with different ages and as a calibration for different nodes than recommended in the present study. In order to estimate divergence times within angiosperms, Magallón and Castillo (2009) used *Endressinia* with a similar age (112 Ma) but applied this age to the stem lineage of Magnoliineae. The same age was used by Pirie and Doyle (2012) to fix the age of the stem node of the clade of Eupomatiaceae and Annonaceae, sister to Magnoliaceae in their study. Surveswaran et al. (2010) used the fossil to provide a minimum age for the same stem lineage corresponding, in their study, to the same node recommended here (crown node Magnoliineae). However, they used an age of 115 Ma. Finally, Couvreur et al. (2011) calibrated the same node (crown node Magnoliineae) with the same age but using it as a fixed age constraint.

#### Fossil Taxon 2 (additional)

*Schenkeriophyllum glanduliferum* Mohr, Coiffard, and Bernardes-de-Oliveira, 2013

**Node Calibrated.** Crown-group Magnoliineae (Mohr et al., 2013)

**Reference Specimen.** MB. Pb. 1999/2356 in Museum of Natural History, Institute of Paleontology, Berlin, Germany (holotype; branching axis with leaves and flowers).

**Additional Specimens.** MB Pb. 2008/350. Paratype (branching axis with leaves and flowers; will be deposited at the Geosciences Institute of the University of São Paulo, Brazil, and is being stored with the number GP/3T2442).

MB.Pb. 2002/1336 (specimen with poorly preserved flowers).

MB. Pb. 1997/1219 (twigs with attached leaves).

MB. Pb. 1999/575, 1999/577A plus 1999/577B (dispersed leaves).

**Phylogenetic Justification.** As discussed for *Endressinia* (Fossil 1), the molecular scaffold analysis of Mohr et al. (2013) placed *Schenkeriophyllum glanduliferum* in a single most parsimonious position, together with *Endressinia brasiliiana*, as sister to the Magnoliaceae. This result implies that *Schenkeriophyllum* provides a minimum age for the stem node of Magnoliaceae or the crown node of Magnoliineae, which are the same in the reference backbone tree used by Mohr et al. (2013). Because the position of Magnoliaceae with respect to Himantandraceae + Degeneriaceae and Eupomatiaceae + Annonaceae remains unresolved, as discussed under *Endressinia* (Soltis et al., 1999, 2007; Doyle and Endress, 2000; Qiu et al., 2000, 2005, 2006; Savolainen et al., 2000; Zanis et al., 2002, 2003; Sauquet et al., 2003), and the position of *Endressinia* is debated (see phylogenetic justification for *Endressinia*; Doyle and Endress, 2010; Mohr et al., 2013), we propose to use the age of *Schenkeriophyllum* conservatively as a minimum age for crown group Magnoliineae (Figure 1).

**Minimum Age.** Aptian-Albian boundary, 112.6 Ma (113 ±0.4 Ma)

**Age Justification.** *Schenkeriophyllum* was collected from the same sedimentary unit as *Endressinia*, the Crato Formation in the Araripe basin of northeastern Brazil (Mohr et al., 2013). As discussed for *Endressinia* (Fossil 1), we propose a minimum age of 112.6 Ma, the Aptian-Albian boundary (113 ±0.4 Ma; Ogg and Hinnov, 2012), for this fossil, based especially on palynological correlations by Heimhofer and Hochuli (2010).

**Previous Use as Calibration.** None to our knowledge.

### Fossil Taxon 3 (additional)

*Archaeanthus linnenbergeri* Dilcher and Crane, 1984

**Node Calibrated.** Stem Magnoliaceae (Doyle and Endress, 2010)

**Reference Specimen.** UF 15703-4152 in University of Florida, Gainesville, USA (holotype of *Archaeanthus linnenbergeri* Dilcher and Crane; multifollicular fruit and proximal reproductive and vegetative portions of the same axis).

**Additional Specimens.** UF 15703; 2300, 2317, 2318, 2590, 3022, 3837, 3907, 4105, 4112, 4134-4150, 4152, 4153, 4155-4158, 4163, 4164, 4166-4170, 4198, 4532-4534: other specimens of *Archaeanthus linnenbergeri* examined in Dilcher and Crane (1984).

UF 15703-3179 (holotype of *Archaeopetala beekeri* Dilcher and Crane; perianth parts).

UF 15703-3882. Other specimen of *Archaeopetala beekeri* examined in Dilcher and Crane (1984).

UF 15703-2266 (holotype of *Archaeopetala obscura* Dilcher and Crane; perianth parts).

UF 15703-2747 (holotype of *Kalymnanthus walkeri* Dilcher and Crane; bud-scales).

UF 15703-4114, UF 15703-4115. Other specimens of *Kalymnanthus walkeri* examined in Dilcher and Crane (1984).

UF 15703-2272 (holotype of *Liriophyllum kansense* Dilcher and Crane; leaves).

UF 15703; 2267, 2271-2277, 2309, 2456, 2463-2466, 2469-2471, 2473, 2475-2477, 2479, 2480, 2482, 2484, 2485, 2487, 2488, 2492, 2493, 2679, 2948, 3443, 2813, 3816-3818, 3823, 3826, 3827, 3836, 3839, 3859, 3885, 3886, 3890, 3894, 3895, 3992, 4028, 4029, 4051, 4120. Other specimens of *Liriophyllum kansense* examined in Dilcher and Crane (1984).

**Phylogenetic Justification.** The position of *Archaeanthus linnenbergeri* was investigated by Doyle and Endress (2010), in a molecular scaffold analysis in which the family Magnoliaceae (ca. 227 species) was split into two taxa: Magnolioideae, often treated by recent authors as the single genus *Magnolia*, and *Liriodendron*. This analysis placed *Archaeanthus* in three different most parsimonious positions: one as the sister group of Magnoliaceae as a whole, and two within crown-group Magnoliaceae, either sister to *Liriodendron* or sister to Magnolioideae. The clade of *Archaeanthus* and Magnoliaceae was supported by three unambiguous synapomorphies: sheathing leaf base, bilobed stipules, and elongate receptacle, while the positions within the family were supported by bilobed leaf apex (shared with *Liriodendron*) or dehiscent

fruit (shared with Magnolioideae). By contrast, a recent cladistic analysis by Romanov and Dilcher (2013) positioned *Archaeanthus* sister to the Late Cretaceous seed genus *Liriodendroidea* (Frumin and Friis, 1996) and identified the clade made up of these two extinct genera as the sister group of *Liriodendron*, supported by four synapomorphies. This would imply that *Archaeanthus* provides a minimum age for crown-group Magnoliaceae. However, the taxonomic sampling of this analysis was very limited, as the extant taxa included only Magnoliaceae s.s. (= Magnolioideae) as a supra-specific terminal, *Liriodendron*, and *Illicium* (Austrobaileyales), which is many nodes more distant from Magnoliaceae than are other members of the order Magnoliales. In addition, one of the four proposed synapomorphies of *Archaeanthus* and *Liriodendron*, whorled perianth phyllotaxis, vs. spiral in *Illicium* and *Magnolia*, appears to be a symplesiomorphy in Magnoliales, where the perianth is basically whorled and trimerous (Endress and Doyle, 2009). Furthermore, although the perianth is spiral in some species of *Magnolia* s.l., in many species it is whorled (e.g., *M. denudata*: Erbar and Leins, 1981). Two other proposed synapomorphies, bilobed leaf apex and leaf lobation, are not independent characters, since the only lobation in the leaf of *Archaeanthus* is that of the apex; its origin requires only one change, not two. The status of the fourth synapomorphy, fruitlets shed from the receptacle, is uncertain, since *Degeneria* and most Annonaceae also have this feature (van Setten and Koek-Noorman, 1992). These observations imply that there are no more acceptable synapomorphies of *Archaeanthus* and *Liriodendron* in the Romanov and Dilcher (2013) data set than in Doyle and Endress (2010).

Even though we cannot dismiss the possibility that future analyses, based on denser taxon sampling and better knowledge of the phylogenetic position of Magnoliaceae, may eventually support a position of *Archaeanthus* within crown-group Magnoliaceae, we prefer to be conservative and recommend the use of *Archaeanthus* to serve as a minimum age constraint for the stem node of Magnoliaceae. In the current consensus tree presented in Figure 1, this is the same node as crown-group Magnoliinae (the larger clade of five families found by Doyle and Endress, 2010; Sauquet et al., 2003). However, this is not the case in one of the resolved trees of Massoni et al. (2014) on which this consensus tree is based, in which Magnoliaceae are the sister group of the clade consisting of *Degeneria* (Degeneriaceae) and *Galbulimima* (Himantand-

raceae). Furthermore, maintaining a distinction between the two nodes may be useful because the association of *Archaeanthus* with Magnoliaceae appears to be more strongly supported than that of *Endressinia* (and *Schenkeriphyllum*) and less likely to change in future analyses.

**Minimum Age.** Early-middle Cenomanian boundary, 96.5 Ma

**Age Justification.** All the specimens used to describe *Archaeanthus linnenbergeri* come from the Dakota Formation at the Linnenberger Ranch in Russell County, central Kansas, USA (Dilcher and Crane, 1984). This formation lies between the underlying Kiowa Shale of Albian age and the overlying Graneros Shale (Retallack and Dilcher, 2012) of Cenomanian age. It has been traditionally divided into two members, the Terra Cotta Clay Member below and the Jansen Clay Member above (Plummer and Romary, 1942). The beds containing the specimens considered here were assigned to the Jansen Clay Member (Dilcher and Crane, 1984). Dilcher and Crane (1984) considered the age of this locality to be latest Albian to earliest Cenomanian. However, D.L. Dilcher (pers. comm. in Doyle and Endress, 2010) argued that it is more likely latest Albian, based on a carbon isotope and sequence stratigraphic study by Gröcke et al. (2006) at the Rose Creek locality in Nebraska, where a flora described by Upchurch and Dilcher (1990) lies just below the Albian-Cenomanian boundary, plus the fact that the Dakota is transgressive toward the east and sites such as Russell County are among its most western exposures. A latest Albian age was accepted by Doyle and Endress (2010) and reaffirmed without discussion by Romanov and Dilcher (2013). However, although the Rose Creek and Linnenberger Ranch floras were both assigned to the Jansen Clay Member and considered roughly coeval by Farley and Dilcher (1986), their equivalence needs reexamination in light of detailed sequence stratigraphic and palynological analyses of the Dakota Formation in Kansas, Nebraska, and Iowa by Ludvigson et al. (2010). This study showed that the Dakota does not represent a simple transgressive sequence but rather three transgressive-regressive cycles. The first two cycles (equivalent to Palynostratigraphic Units 1 and 2) are late Albian, while the third (Units 3 and 4) is early and middle Cenomanian; the boundary recognized by Gröcke et al. (2006), between the second and third cycles, falls within beds formerly assigned to the Jansen Clay Member. Unfortunately, this analysis did not extend as far west as Russell County, although in Lincoln

County, just to the east, the lower part of the third cycle is represented by Dakota continental beds that interfinger with marine rocks to the west. Because we cannot exclude the possibility that the Linnenberger flora is from the lower part of the third cycle, which Ludvigson et al. (2010) dated as early Cenomanian, we propose a conservative minimum age of 96.5 Ma for *Archaeanthus*, the early-middle Cenomanian boundary (no uncertainty provided; Ogg and Hinnov 2012).

**Previous Use as Calibration.** *Archaeanthus* has been used to provide calibration points within Magnoliidae in studies focused on angiosperms (Magallón and Castillo, 2009) and on Annonaceae (Doyle et al., 2004; Richardson et al., 2004; Pirie et al., 2006; Couvreur et al., 2008; Erkens et al., 2009; Su and Saunders, 2009; Pirie and Doyle, 2012). The great majority of these analyses used this fossil as a minimum age constraint of 98 Ma for the node recommended in the present study (stem Magnoliaceae; Doyle et al., 2004; Richardson et al., 2004; Pirie et al., 2006; Couvreur et al., 2008; Erkens et al., 2009; Su and Saunders, 2009). Only Magallón and Castillo (2009) used the age we recommend (96.5 Ma), whereas Pirie and Doyle (2012) used an age of 100 Ma.

## NODE 2: CROWN-GROUP LAURALES

### Fossil Taxon 4 (preferred, given current knowledge)

*Virginianthus calycanthoides* Friis, Eklund, Pederesen and Crane, 1994

**Node Calibrated.** Crown-group Laurales (Doyle et al., 2008)

**Reference Specimen.** PP43703 in Field Museum of Natural History, Chicago (holotype; flower).

**Phylogenetic Justification.** Friis et al. (1994) assigned *Virginianthus calycanthoides* to the stem lineage of Calycanthaceae because it resembles extant Calycanthaceae (including *Idiospermum*) but is more plesiomorphic in characters such as monosulcate rather than disulcate pollen. This assignment was questioned by Crepet et al. (2005) based on a combined (total evidence) analysis of a data set of Renner (1999), which included 15 morphological characters, sequences of six molecular markers, 25 taxa of Laurales, and three outgroups. This analysis identified *Virginianthus* as the sister group of either Laurales as a whole or all Laurales other than Calycanthaceae. A molecular scaffold analysis by Doyle et al. (2008), incorporating 65 morphological characters and using the same backbone trees as Doyle and Endress (2010),



found two alternative most parsimonious positions for this fossil, one sister to Calycanthaceae, the other sister to the clade formed by all remaining Laurales. The first position was supported by extended anther connective and the second by embedded pollen sacs. Positions sister to Laurales as a whole and nested within Calycanthaceae were one step less parsimonious. Here we follow the result of Doyle et al. (2008) because it is based on a data set that included far more characters than Crepet et al. (2005), many derived from in-depth analyses of gynoecial morphology (e.g., Igersheim and Endress, 1997). Both most parsimonious positions imply that *Virginianthus* provides a minimum age for the crown node of Laurales (Figure 1).

**Minimum Age.** Middle-late Albian boundary, 107.7 Ma

**Age Justification.** The fossil flower described by Friis et al. (1994) comes from the Potomac Group at the Puddledock locality in the Tarmac Lone Star Industries sand and gravel pit 9 km southwest of Hopewell, Prince George County, Virginia, USA. Friis et al. (1994, 1995) and von Balthazar et al. (2011) considered this locality early or middle Albian, based on palynological correlation by R.A. Christopher (in Dischinger, 1987) with the basal part of Potomac Subzone II-B of Brenner (1963) and Doyle and Robbins (1977) and the suggestion of Doyle (1992) that Subzone II-B may begin in the early Albian. However, an early Albian age for Subzone II-B (and II-A) now appears unlikely in light of palynological correlations by Hochuli et al. (2006) with the well-dated marine Lower Cretaceous of Portugal and earlier work of Kemp (1970) on the marine Albian of England (cf. Doyle et al., 2008). These studies support correlation of upper Zone I with the basal early Albian of Portugal and the early Albian of England, based on the appearance in all these intervals of reticulate tricolpate pollen and *Clavatipollenites rotundus* (aff. *Retimonocolpites dividuus* of Doyle and Robbins, 1977), as argued by Doyle and Robbins (1977), but not striate tricolpates, which appear later in the early Albian of Portugal (Hochuli et al., 2006). Consistent with this, the Zone II index spore species *Apiculatisporis babsae* of Brenner (1963) appears at the base of the middle Albian in England (Kemp, 1970). The conclusion of Doyle (1992) that the Zone I/II boundary lies well down in the Aptian was based largely on comparisons with *Pennipollis* (*Brenneripollis*) species and *Schrankipollis* in Africa that appear to have involved too indirect cor-

relations and incompletely controlled species ranges, as argued by Hochuli et al. (2006).

Clarke et al. (2011) proposed a much younger minimum age for Puddledock, 92.7 Ma, or the top of the Cenomanian, based on the suggestion of Hochuli et al. (2006) that Zone II extends into the Cenomanian and the presence of late Cenomanian ammonites in the next younger unit, the Raritan Formation of New Jersey (Cobban and Kennedy, 1990). Hochuli et al. (2006) argued convincingly that there is a significant break between Zones I and II in the Potomac sequence, since the early to middle Albian interval in Portugal shows continuing higher diversity of angiosperm monosulcates than tricolpates, whereas tricolpates are already more diverse at the base of Zone II. They argued that Subzone II-B is late rather than middle Albian, based on the higher diversity of tricolpates than in the Portuguese middle Albian and the presence through Subzone II-B of the smooth tricolpate species *Cupuliferoidaepollenites* (*Tricolpopollenites*) *parvulus*, which they noted has not been reported in dated sequences until the late Albian. However, the reliability of *C. parvulus* is uncertain, since this species is rare in Subzone II-B and easy to overlook (for example, it was not reported by Brenner, 1963). Furthermore, its first occurrences cited by Hochuli et al. (2006) are in Canada, in the Northern Laurasia province of Brenner (1976), where angiosperms were less abundant than in Southern Laurasia, and in deep sea cores. It is also possible that the higher diversity of angiosperms observed in the Potomac is partly a facies effect of comparing continental and marginal marine sequences. If angiosperms were locally dominant in some lowland habitats but subordinate to ferns and gymnosperms at the regional scale (cf. Pierce, 1961; Doyle and Hickey, 1976), more angiosperms (including rare species) might be detected in a fluvial sequence such as the Potomac Group than in marine deposits like those in Portugal, where they would be diluted by the higher regional production of fern spores and gymnosperm pollen. It is also likely that the contrast between diversity curves from the two sequences is exaggerated by the fact that the Portuguese curves were based on number of species per sample, whereas the Potomac curves were based on a range chart (Doyle and Robbins, 1977), so that species whose ranges pass through the horizon of a given sample but were not found in that sample were treated as present.

More positive evidence that much of Subzone II-B is middle Albian comes from palynological cor-

relations with well-dated sequences in the US Gulf Coast and Western Interior, which were not considered by Hochuli et al. (2006). Doyle (1977) showed that the diverse angiosperm flora in the middle of Subzone II-B is especially similar at the species level to that described by Hedlund and Norris (1968) in the “Walnut” Clay and Antlers Sand (Fredericksburgian) of Oklahoma, which lies below the middle-late Albian boundary defined by ammonites in the overlying Goodland Limestone (Hedlund and Norris, 1968; Mancini and Puckett, 2005). Doyle and Robbins (1977) dated Subzone II-C as latest Albian, but Hochuli et al. (2006) argued that it is Cenomanian, based on the psilate tricolporate species *Tricolporoidites (Tricolporopollenites) distinctus* and *Tricolporoidites (Tricolporopollenites) triangulus*, which they stated first appear in the Cenomanian. However, most of the studies that Hochuli et al. (2006) cited considered only Cenomanian beds, not the latest Albian. More important, Ludvigson et al. (2010) listed psilate tricolporates (as *Psilatricolporites* sp.) in the latest Albian (Paly-nostratigraphic Unit 2) of the Dakota Formation (see discussion of *Archaeanthus*, Fossil 3), and Laing (1975) recorded triangular grains similar to *T. triangulus* as *Psilatricolpites rectilatibus* in the marine upper Albian of France (Laing distinguished *P. rectilatibus* from *T. triangulus* on lack of pores, but the bent shape of the colpi in the Cenomanian grain illustrated in his plate 90, figures 11-12 suggests that rudimentary pores were present). Together, these correlations lead us to consider that *Virginianthus* is of middle Albian age. Therefore, we use the middle-late Albian boundary, 107.7 Ma (no uncertainty provided; Ogg and Hinnov, 2012), as a minimum age for *Virginianthus*.

**Previous Use as Calibration.** *Virginianthus* has been used in several large-scale studies (Magallón and Sanderson, 2005; Moore et al., 2007; Soltis et al., 2008; Bell et al., 2010). With the exception of Magallón and Sanderson (2005), who used this fossil to calibrate the crown node of Laurales with a minimum age of 110 Ma, all these analyses used it to calibrate the most recent common ancestor of Laurales and Magnoliales (i.e., the stem node of Laurales). Moore et al. (2007) used it to define a minimum age of 113 Ma, Soltis et al. (2008) an age fixed between 98 and 113 Ma, and Bell et al. (2010) a minimum age of 98 Ma. In order to date divergence times within Calycanthaceae, Zhou et al. (2006) used this species to calibrate the age of the stem node of the family as at least 112 Ma.

### Fossil Taxon 5 (additional)

*Lovellea wintonensis* Dettmann, Clifford, and Peters, 2009

**Node Calibrated.** Crown-group Laurales (Dettmann et al., 2009)

**Reference Specimen.** QMF51133 in the Palaeontological Collection of the Queensland Museum, Queensland, Australia (Holotype, originally a complete specimen, now consisting of portions of a permineralized (silicified) flower/fruit in rock matrix cut longitudinally into two slices and two thin sections: QMF51133 a-d).

**Additional Specimens.** QMF51134, QMF51135, QMF51132. Other specimens used for the description (flowers/fruits).

**Phylogenetic Justification.** A morphological parsimony analysis using the matrix of Doyle and Endress (2000), with the exclusion of several taxa (eudicots, Piperales, Nymphaeales, monocots, *Austrobaileya*, Schisandraceae, and *Illicium*), placed *Lovellea wintonensis* in one most parsimonious position sister to all Laurales excluding Calycanthaceae (Dettmann et al., 2009). This “core Laurales” clade was well supported in previous studies (Soltis et al., 1999, 2000a, 2000b, 2007, 2011; Qiu et al., 1999, 2000, 2005, 2006, 2010; Renner, 1999, 2004; Doyle and Endress, 2000; Savolainen et al., 2000; Zanis et al., 2002, 2003; Nickrent et al., 2002; Hilu et al., 2003). Relationships within the clade based on the morphological analysis were not identical to those found in molecular or combined morphological and molecular analyses (Doyle and Endress, 2000), but they are consistent in supporting the monophyly of the Hernandiaceae-Lauraceae-Monimiaceae clade (though with the addition of Siparunaceae) and the position of Atherospermataceae and Gomortegaceae as outgroups to this clade (though as two successive branches rather than a clade). We consider *Lovellea wintonensis* to provide a minimum age for crown-group Laurales, or the stem node of all Laurales except Calycanthaceae (Figure 1).

**Minimum Age.** Albian-Cenomanian boundary, 100.1 Ma (100.5 ± 0.4 Ma)

**Age Justification.** *Lovellea wintonensis* comes from the basal part of the the Winton Formation, 48 km WNW of Winton, western Queensland, Australia (Dettmann et al., 2009). Dettmann et al. (2009) placed the sediments containing these fossils in the *Coptospora paradoxa* or *Phimopollenites pannosus* spore-pollen Zones of Helby et al. (1987) based on the co-occurrence of *Cicatricosisporites*, *Crybelosporites*, *Clavatipollenites*, and *Phimopollenites*, indicating that they are no older than mid-

dle Albian. Because the Winton Formation overlies the late Albian Mackunda Formation but no palynomorph taxa indicative of a Cenomanian or younger age are present, Dettmann et al. (2009) suggested a latest Albian age. Here we accept this age for *Lovellea wintonensis* and therefore use the upper boundary of the Albian, 100.1 Ma (100.5 ±0.4 Ma; Ogg and Hinnov, 2012), as a safe minimum age for this fossil.

**Previous Use as Calibration.** None to our knowledge.

### NODE 3: CROWN-GROUP CALYCANTHOIDEAE

#### Fossil Taxon 6

*Jerseyanthus calycanthoides* Crepet, Nixon and Gandolfo, 2005

**Node Calibrated.** Crown-group Calycanthoideae (Crepet et al., 2005)

**Reference Specimen.** CUPC 1483 in the Paleobotany Collection of the L.H. Bailey Hortorium, Cornell University (holotype / flower).

**Additional Specimens.** CUPC 1484–1502. Paratypes (flowers).

**Phylogenetic Justification.** Using the combined morphological and molecular data set described for *Virginianthus* (Fossil 4), in which Calycanthaceae were represented by *Idiospermum*, *Chimonanthus*, and *Calycanthus*, Crepet et al. (2005) found one most parsimonious position for *Jerseyanthus calycanthoides*, as the sister group of *Calycanthus*. Addition of the fossil *Virginianthus calycanthoides* did not influence the position of *Jerseyanthus*. The relationships among the three extant genera of Calycanthaceae are well supported in the literature, with *Idiospermum* sister to *Chimonanthus* and *Calycanthus* (Renner, 1998, 1999; Zhou et al., 2006; Massoni et al., 2014). *Jerseyanthus calycanthoides* therefore provides a minimum age for crown-group Calycanthoideae, the clade that is sister to *Idiospermum* and contains *Chimonanthus* and *Calycanthus* (Figure 1).

**Minimum Age.** Coniacian-Santonian boundary, 85.8 Ma (86.3 ±0.5 Ma)

**Age Justification.** These fossils were collected from the South Amboy Fire Clay Member of the Raritan Formation at the Old Crossman clay pit in Sayreville, New Jersey, USA (Crepet et al., 2005). This unit was first studied palynologically by Groot et al. (1961), who considered it Turonian based on preliminary studies on European sequences, and subsequently by Doyle (1969b), Wolfe and Pakiser (1971), Doyle and Robbins (1977), and Christopher (1979). Building on the palynological zonation

of the Potomac Group by Brenner (1963), to which Doyle (1969a) added Zone III (uppermost Potomac) and Zone IV (lower Raritan), Sirkin (1974) assigned South Amboy palynofloras to a new Zone V. This unit was renamed the *Complexiopollis exigua-Santalacites minor* Zone by Christopher (1979) and redefined by Christopher et al. (1999) as the lowest of three subzones of the *Sohlipollis* Taxon Range Zone. Wolfe and Pakiser (1971) and Sirkin (1974) considered the South Amboy late Cenomanian, not much younger than underlying Woodbridge Clay Member (Zone IV), but Doyle (1969b) and Doyle and Robbins (1977) argued that it is no older than middle Turonian, based on the presence of Normapolles genera that appear at that level in Europe (Góczán et al., 1967). Doyle and Robbins (1977) and Christopher (1979) allowed that it was “possibly Coniacian,” but Crepet and Nixon (1994) and Crepet et al. (2005) accepted a late Turonian age. By contrast, Clarke et al. (2011) suggested a minimum age of the Santonian-Campanian boundary, 82.8 Ma. However, correlations by Christopher et al. (1999) and Christopher and Prowell (2010) with better-dated rocks in South Carolina imply that the Crossman locality is not this young; they correlate the *C. exigua-S. minor* Zone with calcareous nannofossil zones CC13 and CC14, which extend from late Turonian through Coniacian (Burnett, 1998; Ogg and Hinnov, 2012). We therefore believe there is enough evidence to consider that *Jerseyanthus* was at least of Coniacian age, which translates into a conservative minimum age of 85.8 Ma, the Coniacian-Santonian boundary (86.3 ±0.5 Ma; Ogg and Hinnov, 2012).

**Previous Use as Calibration.** None to our knowledge.

### NODE 4: CROWN-GROUP CORE LAURALES

#### Fossil Taxon 7 (preferred, given current knowledge)

*Cohongarootonia hispida* von Balthazar, Crane, Pedersen, and Friis, 2011

**Node Calibrated.** Crown-group core Laurales (the clade consisting of Laurales except Calycanthaceae) (von Balthazar et al., 2011)

**Reference Specimen.** PP53716 in the Field Museum of Natural History, Chicago (holotype, flower).

**Phylogenetic Justification.** A molecular scaffold analysis by von Balthazar et al. (2011), using the morphological data set from Doyle and Endress (2010) and one of the same backbone trees, in

which Lauraceae and Hernandiaceae form a clade sister to Monimiaceae, placed *Cohongarootonia hispida* in a single most parsimonious position as the sister group of Lauraceae + Hernandiaceae. Synapomorphies of the three taxa were whorled tepals, whorled stamens, and one carpel. As a result, von Balthazar et al. (2011) unequivocally assigned the fossil to the order Laurales. However, although all recent analyses agree that Lauraceae, Hernandiaceae, and Monimiaceae form a well-supported clade within Laurales, the relationships among these three families are still debated. In analyses by Doyle and Endress (2000), a sister group relationship of Lauraceae and Hernandiaceae was strongly supported by morphological data and by combined morphological and molecular data, but analyses of molecular data alone have linked either Monimiaceae and Lauraceae or Monimiaceae and Hernandiaceae (Qiu et al., 1999, 2000, 2005, 2006, 2010; Renner, 1999; Doyle and Endress, 2000; Savolainen et al., 2000; Renner and Chanderbali, 2000; Hilu et al., 2003; Zanis et al., 2003; Soltis et al., 2011; Massoni et al., 2014). Until this conflict is resolved, we consider that *Cohongarootonia hispida* provides a minimum age for the stem node of the clade including Lauraceae, Monimiaceae, and Hernandiaceae, in other words the crown node of the clade of Laurales excluding Calycanthaceae (Figure 1).

**Minimum Age.** Middle-late Albian boundary, 107.7 Ma.

**Age Justification.** *Cohongarootonia* was collected from the Potomac Group at the same Puddledock locality, 9 km southwest of Hopewell, Virginia, as *Virginianthus calycanthoides* (Fossil 4). As discussed for that species, this locality has been correlated palynologically by R.A. Christopher (in Dischinger, 1987) with the lower part of Subzone II-B of Brenner (1963), which we argue is of middle Albian age. Therefore, we use the middle-late Albian boundary, 107.7 Ma (no uncertainty provided; Ogg and Hinnov, 2012), as a minimum age for *Cohongarootonia*.

**Previous Use as Calibration.** None to our knowledge.

#### Fossil Taxon 8 (additional)

*Mauldinia mirabilis* Drinnan, Crane, Friis and Pedersen, 1990

**Node Calibrated.** Crown-group core Laurales (the clade consisting of Laurales except Calycanthaceae) (Doyle and Endress, 2010)

**Reference Specimen.** PP35297 in Field Museum of Natural History, Chicago, USA (holotype of *Mauldinia mirabilis*; inflorescence).

**Additional Specimens.** PP34733, PP34794, PP34796, PP34797, PP35002-PP35006, PP35008, PP35056, PP35061, PP35141, PP35295-PP35305, PP35338-PP35340. Other specimens of *Mauldinia mirabilis* cited in Drinnan et al. (1990) (inflorescence fragments with flowers). PP34709-PP34715, PP34728-PP34732, PP34779, PP34780, PP34926, PP34927, PP34929, PP35007, PP35016-PP35019, PP35051-PP35055, PP35057-PP35060, PP35140, PP35150, PP35151, PP35306-PP35309, PP35315-PP35319. Other specimens of *Mauldinia mirabilis* cited in Drinnan et al. (1990) (flowers).

PP34903-PP34925, PP35009, PP35050, PP35144. Other specimens of *Mauldinia mirabilis* cited in Drinnan et al. (1990) (dispersed stamens).

PP34781-PP34783, PP34795, PP34928, PP34930, PP34931, PP35010-PP35012, PP35142, PP35143. Other specimens of *Mauldinia mirabilis* cited in Drinnan et al. (1990) (dispersed carpels).

PP34932, PP34933, PP35024, PP35025, PP35026, PP42982, PP42983. Other specimens of *Mauldinia mirabilis* cited in Drinnan et al. (1990) (cuticle preparations).

PP42981. Other specimens of *Mauldinia mirabilis* cited in Drinnan et al. (1990) (unsorted fragments). PP35023 (holotype of *Paraphyllanthoxylon marylandense* Herendeen, 1991; mature wood).

PP43591, PP43592, PP43617, PP43619, PP43620, PP43621, PP43622, PP43624, PP43625, PP43627, PP43629, PP43630, PP43631, PP43632, PP43636. Paratypes of *Paraphyllanthoxylon marylandense* Herendeen, 1991 (mature wood).

**Phylogenetic Justification.** Because of identical features in the first formed wood of *Paraphyllanthoxylon marylandense* (Herendeen, 1991) and inflorescence axes of *Mauldinia mirabilis* (Drinnan et al., 1990), Doyle and Endress (2010) combined these two taxa in their analyses. Their molecular scaffold analysis, which used a backbone tree in which Lauraceae and Hernandiaceae formed a clade sister to Monimiaceae, placed this fossil in a single most parsimonious position, as the sister group of Lauraceae + Hernandiaceae. The three taxa were united by the following unequivocal synapomorphies: solitary vessels, inflorescences with lateral cymes, whorled tepals, whorled stamens, and one carpel. The basal position of *Mauldinia* rel-

ative to the two living taxa was supported by the absence of well-developed paratracheal parenchyma in the wood, the superior position of the ovary, and the presence of endosperm in the seed, while Lauraceae and Hernandiaceae are united by paratracheal parenchyma, an inferior ovary (reversed within Lauraceae: Rohwer and Rudolph, 2005), and lack of endosperm in the mature seed. A position sister to Lauraceae alone was four steps less parsimonious. However, as discussed for *Cohongarootonia* (Fossil 7), Lauraceae and Hernandiaceae are included together with Monimiaceae in a well-supported clade, but different analyses have found all possible relationships among the three families. When Doyle and Endress (2010) used a molecular backbone in which Monimiaceae were sister to Lauraceae, the single most parsimonious position of *Mauldinia* was sister to the whole clade of Hernandiaceae + Lauraceae + Monimiaceae. Doyle and Endress (2010) did not test the third alternative present in the literature (Lauraceae sister to the remaining two families), but using their data set we find that the most parsimonious position for *Mauldinia* under this arrangement is also sister to the three living taxa. Until this conflict is resolved, we consider *Mauldinia mirabilis* to provide a minimum age for the stem node of the clade of Lauraceae, Hernandiaceae, and Monimiaceae, in other words the crown node of the clade of Laurales excluding Calycanthaceae (Figure 1).

**Minimum Age.** Middle-late Cenomanian boundary, 95.5 Ma

**Age Justification.** *Mauldinia mirabilis* and *Paraphyllanthoxylon marylandense* were described from the Mauldin Mountain locality in the upper Potomac Group (“Maryland Raritan”) of northeastern Maryland, USA (Drinnan et al., 1990; Herendeen, 1991). These beds contain a palynoflora assigned to the lower part of Zone III of the Potomac sequence, which Doyle and Robbins (1977) dated as early Cenomanian. The age of Zone III is bracketed above by the appearance of triporate Normapolles pollen (*Complexiopollis* spp.) in the lower Raritan Formation of New Jersey (Zone IV) and the upper part of the Peruc Formation of Bohemia (Pacltová, 1971; Doyle and Robbins, 1977), and by late Cenomanian ammonites in the lower Raritan (Cobban and Kennedy, 1990). The Peruc Formation underlies marine sediments with late Cenomanian mollusks, and its upper part was correlated palynologically by Pacltová (1977) with late middle Cenomanian marine beds that contain the first Normapolles in England and France (Azéma et

al., 1972; Laing, 1975); this agrees with studies of sequence stratigraphy in the Bohemian section by Uličný et al. (1997). The probable latest Albian age of Potomac Subzone II-C is discussed under *Virginanthus*. Because these data imply that the Zone III-IV boundary may lie within the middle Cenomanian, and the length of time between the base and top of Zone III is uncertain, it appears safest to conclude that *Mauldinia* could be of either early or middle Cenomanian age. Therefore, we propose the middle-late Cenomanian boundary, 95.5 Ma (no uncertainty provided; Ogg and Hinnov, 2012), as a conservative minimum age for *Mauldinia*.

**Previous Use as Calibration.** None to our knowledge.

## NODE 5: CROWN-GROUP CANELLALES

### Fossil Taxon 9

*Walkeripollis gabonensis* Doyle, Hotton, and Ward, 1990

**Node Calibrated.** Crown-group Canellales (Doyle and Endress, 2010)

**Reference Specimen.** Single-pollen grain preparation 2963-27 (holotype of *Walkeripollis gabonensis*). Doyle et al. (1990) stated that this specimen is deposited in the Elf-Aquitaine collection, but it is on loan to J.A. Doyle at the University of California, Davis. Because the company Elf-Aquitaine no longer exists, it will be deposited at the University of California (Berkeley) Museum of Paleontology (UCMP).

**Additional Specimens.** Sections, uncut block, and negatives, from Elf-Aquitaine preparation 2963, TM.1 (N'Toum No. 1) well, core 8, 939-944 m, Subzone C-VIIc, Gabon.

**Phylogenetic Justification.** Use of fossil pollen for calibration can be questioned because it usually lacks sufficient characters for secure phylogenetic placement, but this taxon has such a unique combination of features that it could be unambiguously placed in a large-scale phylogenetic analysis. A molecular scaffold analysis placed *Walkeripollis gabonensis* in a single most parsimonious position as sister to Winteraceae (Doyle and Endress, 2010), one of the two families of Canellales. Synapomorphies supporting this sister-group relationship were permanent tetrads and round aperture shape. The sculpture on the pore, forming a ring around a central thin area, also suggests a close relationship between the fossil species and Winteraceae (Doyle and Endress, 2010). However, this character was not included in the Doyle and Endress (2010) data set because it was not appli-

cable to most taxa. The sister-group relationship between living Winteraceae and Canellaceae is very well supported in the literature (e.g., Chase et al., 1993; Zanis et al., 2002, 2003; Qiu et al., 2005, 2006; Marquinez et al., 2009). We therefore consider *Walkeripollis gabonensis* to provide a minimum age for crown-group Canellales (Figure 1).

**Minimum Age.** Barremian-Aptian boundary, 125.9 Ma (126.3 ±0.4 Ma)

**Age Justification.** *Walkeripollis gabonensis* comes from the upper part of Elf-Aquitaine palynological Zone C-VII (Subzone C-VIIc) in the Cocobeach sequence (Doyle et al., 1990), near the town N'Toum in northern Gabon. The age of Zone C-VII is bracketed by late Aptian marine fossils in overlying units (Doyle et al., 1977, 1990). Doyle et al. (1977, 1982) dated Zone C-VII as early Aptian, but Doyle et al. (1990) and Doyle (1992) suggested it may be late Barremian, based on the occurrence of other taxa that appear in Zone C-VII, correlative rocks in Brazil, and better-dated Barremian rocks elsewhere, notably *Afropollis* and the first reticulate tricolpates (Doyle et al., 1982; Gübeli et al., 1984; Penny, 1989; Regali and Viana, 1989; Doyle, 1992). Additional evidence that favors a pre-Aptian age is the absence in Zone C-VII of two groups that appear in the overlying Zones C-VIII and C-IX and the Aptian of Egypt, namely striate tricolpates, which are not known until the Albian in Southern Laurasia but occur earlier in Northern Gondwana (Penny, 1988a; Hochuli et al., 2006; Heimhofer et al., 2007; Heimhofer and Hochuli, 2010), and the non-columellar reticulate monosulcate genus *Penipollis* ("*Retimonocolpites*" *peroreticulatus*, etc.), which appears just above the base of the marine Aptian of England and has never been reported from well-dated pre-Aptian rocks (Penny, 1988b; Doyle, 1992; Hughes, 1994; Hochuli et al., 2006). We therefore believe it is safe to accept a late Barremian age for *Walkeripollis gabonensis* and thus propose 125.9 Ma, the upper boundary of the Barremian (126.3 ±0.4 Ma; Ogg and Hinnov, 2012), as a minimum age for this fossil.

**Previous Use as Calibration.** Magallón (2010) and Magallón et al. (2013) used *Walkeripollis* to provide a minimum age of 125 Ma for the same node recommended here (crown-group Canellales). Marquinez et al. (2009) used this fossil to fix the age of the crown node of Winteraceae at 120 Ma.

## NODE 6: STEM NODE OF EXTANT SAURURUS

### Fossil Taxon 10

*Saururus tuckerae* Smith and Stockey, 2007

**Node Calibrated.** Stem node of extant *Saururus* (Smith and Stockey, 2007)

**Reference Specimen.** P1631 Bbot a in the University of Alberta (Edmonton) Paleobotanical Collections (UAPC) (holotype; inflorescence).

**Additional Specimens.** P1631 Btop a, Btop b, Btop f, Btop h, Bbot c, Cbot e; P5831 Bbot; P5839 A; P5937 Gbot b; P5991 B. Paratypes (isolated flowers).

**Phylogenetic Justification.** A morphological parsimony analysis using 24 morphological characters modified from matrices of Tucker et al. (1993), Tucker and Douglas (1996), and Meng et al. (2003) placed *Saururus tuckerae* in a single most parsimonious position within the family Saururaceae, as the sister group of a clade formed by the two extant species of *Saururus* (Smith and Stockey, 2007). The relationship of the fossil with extant *Saururus*, one of four genera in Saururaceae, was supported by the following synapomorphies: basally connate carpels, 1-2 ovules per carpel, and marginal placentation (Smith and Stockey, 2007). This study indicated that the genus *Saururus* was sister to *Gymnotheca*, and *Anemopsis* was sister to *Houttuynia*, relationships supported by other molecular and morphological studies (Meng et al., 2002, 2003; Jaramillo et al., 2004; Neinhuis et al., 2005; Wanke et al., 2007b; Massoni et al., 2014). Outside the Saururaceae, the relationships are compatible with molecular studies (e.g., Qiu et al., 2005, 2006; Soltis et al., 1999, 2000a, 2000b, 2007, 2011; Mathews and Donoghue, 1999, 2000; Qiu et al., 1999, 2000; Doyle and Endress, 2000; Savolainen et al., 2000; Zanis et al., 2002, 2003; Borsch et al., 2003; Hilu et al., 2003; Kelly and González, 2003; Jaramillo et al., 2004; Wanke et al., 2007a, 2007b; Massoni et al., 2014). We thus consider *Saururus tuckerae* to provide a minimum age for the stem node of the extant genus *Saururus*, which is also the crown node of *Gymnotheca* + *Saururus* (Figure 1).

**Minimum Age.** 44.3 Ma

**Age Justification.** Fossils described by Smith and Stockey (2007) come from the Princeton Chert, 8.4 km south of Princeton, British Columbia, Canada, which is part of the Princeton Group, Allenby Formation (Boneham, 1968). The Princeton Chert consists of a series of alternating layers of coal and chert. The paleontological record supports a middle Eocene age, such as an amiid fish correlated

with the occurrence of comparable fossils in British Columbia and in the Klondike Mountain Formation of Washington State (Wilson, 1982), and teeth of the mammal group Tillodontia (Russell, 1935). In addition, potassium-argon dating studies have provided comparable ages for the Allenby Formation:  $48 \pm 2$  Ma (Rouse and Mathews, 1961; Mathews, 1964), between  $47 \pm 2$  and  $50 \pm 2$  Ma (Hills and Baadsgaard, 1967), and  $46.2 \pm 1.9$  Ma and  $49.4 \pm 2$  Ma (Read, 2000). With a different method (U–Pb age from zircons), Moss et al. (2005) suggested an age of  $52.08 \pm 0.12$  Ma for the Allenby Formation. Finally, Smith and Stockey (2007) report a personal communication from H. Baadsgaard (University of Alberta, 1999) that supports an age of 48.7 Ma for the ash of Layer #22 of the Princeton Chert. Because the 7.5 m of the Princeton Chert sequence (incorporating the layer where the fossil was collected) may have accumulated in 15,000 years or less (Mustoe, 2011), this latter age is probably the closest to the real age of the fossil. However, in order to be conservative regarding the uncertainty of the age of this formation, and the fact that no uncertainty is associated with the latter age, *Saururus tuckerae* provides a safe minimum age of 44.3 Ma (the youngest age given by potassium-argon dating minus the associated error of 1.9 Ma).

**Previous Use of this Fossil.** González et al. (2014) used *Saururus tuckerae* to constrain the same node as recommended here, but with a minimum age of 48.5 Ma.

## DISCUSSION

The 10 fossils reviewed in this study provide minimum age constraints on six internal nodes in the phylogeny of Magnoliidae (Table 1, Figure 1). Considered together, one of these age constraints (the crown node of Laurales) is uninformative because it is implied by an equal minimum age constraint nested higher in the tree. Six of these fossils have not yet been used to provide calibration points in any molecular dating studies. The four remaining have been used in several previous studies, often with different ages and to calibrate different nodes (see “Previous Use as Calibration” sections). Several other fossils have been used in the literature to set minimum age calibrations, some of which are different from those recommended here. In the majority of these papers the justification for a specific age and position used in association with these fossils was not provided. The present review is intended to be a reliable

source of information for readers about the bases underlying the use of these calibration points.

The positions of *Archaeanthus linnenbergeri*, *Endressinia brasiliensis*, *Virginianthus calycanthoides*, *Mauldinia mirabilis*, *Cohongarootonia hispida*, and *Walkeripollis gabonensis* have been evaluated using similar backbone trees and either the data set of Endress and Doyle (2009) or the data set of Doyle and Endress (2010) (see fossil sections 1, 3, 4, 7, 8, and 9 for details). These studies investigated the position of the fossils in a broad context of basal angiosperms compatible with current knowledge of angiosperm phylogeny, and using a compromise between ‘exemplar’ and ‘compartmentalized’ approaches to taxon representation. When a supra-specific group did not have a homogeneous morphology, the authors of these studies filled the matrix with ancestral states deduced from knowledge of basal relationships in the taxon supported by other studies. Relationships within the compartments of Magnoliidae used by Endress and Doyle (2009) and Doyle and Endress (2010) to deduce plesiomorphic traits of these supra-specific terminals have not been contradicted by subsequent studies focused on particular families (Marquinez et al., 2009; Michalak et al., 2010; Renner et al., 2010; Chatrou et al., 2012). For all these reasons, we argue that the positions of the fossils supported in these studies are up-to-date and can be used with some confidence. Regarding other calibration points, the phylogenetic analyses we have used as a reference for fossil relationships in this paper represent solid advances. However, future analyses with denser taxon sampling and updated morphological and molecular data sets will be required to challenge further, and hopefully confirm, the relationships summarized in this paper. For instance, the analysis of *Saururus tuckerae* by Smith and Stockey (2007) could be improved by adding key taxa of Piperales not included in their analysis (Hydnoraceae, *Thottea*, *Saruma*, *Manekia*, and *Verhuellia*).

All the fossil species incorporated in our calibration scheme presented the advantage of having enough informative characters to allow accurate phylogenetic placement. However, because such fossils are not well represented in the fossil record, the delay between the time of divergence of the taxon and the fossilization event of the specimen used in the present study is difficult to estimate. Bayesian relaxed clock methods allow calibrations to be modeled with parametric distributions (uniform, exponential, lognormal, and gamma priors). These various priors are often used to model the

probability that the node calibrated is older than the fossil used. However, given the difficulty in objectively setting parameters for these models in many empirical situations, as well as the phylogenetic uncertainty often associated with fossil relationships (leading to conservative calibration of the lowest safe node on the tree), Sauquet et al. (2012) recommended the use of uniform priors. For the present calibration scheme we agree with this point of view and recommend that our age constraints be used as strict minimum ages only. This issue, resulting from the sporadic preservation of extinct species in the fossil record, is exacerbated by the fact that different events of fossilization do not necessarily conserve the same part of the plant. Fortunately, in some cases, such as *Archaeanthus linnenbergeri*, morphological features have allowed safe identification of separate organs as parts of the same plant species. The association of different parts could lead to an older age associated with a fossil taxon. For instance, it is likely that *Mauldinia* or related plants extend down below the Albian-Cenomanian boundary, as leaves described as *Pandemophyllum* from the latest Albian Rose Creek locality in the Dakota Formation of Nebraska (Upchurch and Dilcher, 1990; Gröcke et al., 2006) may represent plants like those that produced fossils described as *Prisca* by Retallack and Dilcher (1981) from the Hoisington and Linnenberger Ranch localities in Kansas (see *Archaeanthus*), which are probably inflorescences of *Mauldinia* (Drinnan et al., 1990). In other cases, there are slightly younger fossils that are even more like the putative extant relatives of the fossils used here. This is true for *Walkeripollis*, where tetrads with similar aperture structure but more open reticulate sculpture, approaching modern Winteraceae, are known from Aptian-Albian beds of Israel (Walker et al., 1983; Schrank, 2013) and the late Albian-Cenomanian of Argentina (Barreda and Archan-gelsky, 2006).

In addition to the 10 fossils listed here many more fossil taxa have been described as belonging to Magnoliidae, and a number of them could complement the current calibration set, pending further work on their phylogenetic relationships. There are species that are or bear flowers preserved in the form of compressions (e.g., Mohr and Eklund, 2003; Frumin et al., 2004), in three dimensions as charcoal (e.g., Kvaček and Eklund, 2003; Viehofen et al., 2008), or in amber (e.g., Poinar and Chambers, 2005). In addition to fossil flowers, there are fossil woods (e.g., Poole and Gottwald, 2001) and leaves (e.g., Rüffle and Knappe, 1988). Finally, pol-

len grains, seeds, and fruits referred to the group are also common in the fossil record (e.g., Friis, 1985; Carpenter et al., 1994; Friis et al., 1995). Among these extinct species several could be very useful to supplement our set of calibration points; those based on isolated organs may have too few characters for unambiguous placement, but the situation might improve with better understanding of character distributions in the living flora or association with other organs. In our scheme, the Piperales have only one minimum age constraint, in contrast to several for Laurales and Magnoliales. For Aristolochiaceae there are several fossil leaf and wood taxa described from the Late Cretaceous (e.g., Kulkarni and Patil, 1977) and the Cenozoic (e.g., MacGinitie, 1974), which if confirmed could provide a minimum age of Late Cretaceous for the Piperales. *Lactoripollenites africanus*, a fossil pollen type of monoporate tetrads from Turonian-Campanian sediments of the southern coast of southern Africa, was associated with the monotypic extant genus *Lactoris* by Zavada and Benson (1987). This fossil could also support the origin of the Aristolochiaceae in the Late Cretaceous. The 10 fossils reviewed in the present paper are generally close to the first reports of their taxonomic groups in the fossil record. However, *Saururus nipponensis* (Stopes and Fujii, 1911), interpreted as a fossilized stem of Saururaceae, from the Upper Cretaceous of Hokkaido (Japan), could provide much an older minimum age for the stem node of Saururaceae than the one used in the present review. Several fossils containing pollen grains in situ and sometimes branching axes bearing floral organs and leaves (e.g., Crepet and Nixon, 1998; Mohr and Eklund, 2003) would be good candidates for accurate phylogenetic placement. The latter cases are very interesting because they provide characters from different parts of the plant, without the uncertainty of association of two separate structures found in the same fossil bed. Several other fossils that are exceptionally well preserved could provide enough characters for an accurate phylogenetic placement within families. For instance, *Lauranthus futabensis* is a complete flower described from the lower Coniacian of the Futaba Group in northeastern Japan that has been interpreted as a member of Lauraceae (Takahashi et al., 2001).

Our new set of calibration points is a first step toward investigating the time scale of evolution of Magnoliidae as a whole more accurately than has been done before. Previous molecular dating analyses of Magnoliidae have been carried out either at



an intra-ordinal level (e.g., Chanderbali et al., 2001; Doyle et al., 2004; Pirie et al., 2006; Smith et al., 2008; Marquínez et al., 2009; Pirie and Doyle, 2012) or at the level of angiosperms and higher (e.g., Bell et al., 2005, 2010; Moore et al., 2007; Soltis et al., 2008; Magallón and Castillo, 2009; Magallón, 2010; Smith et al., 2010). A maximum of six calibration points have been used so far within the group (Magallón and Castillo, 2009). In terms of taxonomic sampling, the most complete molecular dating studies including Magnoliidae as a whole incorporated about 11 percent of the generic diversity of Magnoliidae (Wikström et al., 2001; Moore et al., 2007; Soltis et al., 2008). Previous dating analyses have provided dates for the origin of the Magnoliidae ranging from the Early Jurassic to the Early Cretaceous (Wikström et al., 2001; Bell et al., 2005, 2010; Moore et al., 2007, 2010; Soltis et al., 2008; Magallón and Castillo, 2009; Magallón, 2010; Smith et al., 2010). Among subgroups of Magnoliidae, several published ages are not compatible with minimum calibration points provided here. For instance, Bell et al. (2010) found younger ages for the diversification of Canellales (50–111 Ma) and Magnoliales (50–96 Ma), which are dated as at least 125.9 Ma and 112.6 Ma, respectively, by the present calibration scheme. A new molecular dating study of Magnoliidae, using this calibration scheme and denser taxonomic sampling, will certainly provide new insights on the tempo of the evolutionary history of this important group of angiosperms. In the future, a new morphological data set capturing the whole diversity of Magnoliidae would be very useful for filling in and improving the present calibration scheme. Such a data set, which we are currently assembling, will allow us to test and refine the phylogenetic placements of the fossils presented here and to evaluate the phylogenetic position of other described fossils.

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