



INVITED REVIEW

Monocot fossils suitable for molecular dating analyses

WILLIAM J. D. ILES^{1,2*}, SELENA Y. SMITH³, MARIA A. GANDOLFO⁴ and SEAN W. GRAHAM¹

¹*Department of Botany, University of British Columbia, 3529-6270 University Blvd, Vancouver, BC, Canada V6T 1Z4*

²*University and Jepson Herbaria, University of California, Berkeley, 3101 Valley Life Sciences Bldg, Berkeley, CA 94720-3070, USA*

³*Department of Earth & Environmental Sciences and Museum of Paleontology, University of Michigan, 2534 CC Little Bldg, 1100 North University Ave., Ann Arbor, MI 48109-1005, USA*

⁴*LH Bailey Hortorium, Plant Biology Section, School of Integrative Plant Science, Cornell University, 410 Mann Library Bldg, Ithaca, NY 14853, USA*

Received 6 June 2014; revised 3 October 2014; accepted for publication 7 October 2014

Recent re-examinations and new fossil findings have added significantly to the data available for evaluating the evolutionary history of the monocotyledons. Integrating data from the monocot fossil record with molecular dating techniques has the potential to help us to understand better the timing of important evolutionary events and patterns of diversification and extinction in this major and ancient clade of flowering plants. In general, the oldest well-placed fossils are used to constrain the age of nodes in molecular dating analyses. However, substantial error can be introduced if calibration fossils are not carefully evaluated and selected. Here we propose a set of 34 fossils representing 19 families and eight orders for calibrating the ages of major monocot clades. We selected these fossils because they can be placed in particular clades with confidence and they come from well-dated stratigraphic sequences. As more fossils are discovered or re-examined, these criteria can also be applied to expand the list of the fossils that are most suitable for dating the early branches of monocot phylogeny. © 2015 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2015, **178**, 346–374.

ADDITIONAL KEYWORDS: Alismatales – Arecales – Asparagales – calibration fossil – Dioscoreales – Liliales – Monocotyledonae – Pandanales – Poales – Zingiberales.

INTRODUCTION

The monocots represent a substantial fraction of extant angiosperm species (~22%, Stevens, 2001+), and define and dominate some of the most widespread and productive ecosystems, including grasslands and seagrass meadows (Larkum, Orth & Duarte, 2006; Strömberg, 2011). Despite their diversity and ecological ubiquity, they have often been viewed as having a meagre and confusing fossil record, primarily because of preservation biases associated with their predominantly herbaceous habit (Herendeen & Crane, 1995; Smith, 2013), but also due to the lack of morphological synapomorphies that can be assessed in fossils

(Gandolfo, Nixon & Crepet, 2000). A substantial expansion in our understanding of fossil monocots has come about through synthetic review (Doyle, 1973; Daghljan, 1981; Collinson, Boulter & Holmes, 1993; Herendeen & Crane, 1995; Gandolfo *et al.*, 2000; Greenwood & Conran, 2000; Stockey, 2006; Smith *et al.*, 2010; Friis, Crane & Pedersen, 2011; Smith, 2013), phylogenetic inference (e.g. Doyle, Endress & Upchurch, 2008) and new fossil discoveries. Recently described fossils include the first unequivocal orchids (Ramírez *et al.*, 2007; Conran, Bannister & Lee, 2009a) and the oldest known grasses (Prasad *et al.*, 2005, 2011). A parallel revolution has happened in our understanding of higher-order monocot relationships, due primarily to molecular systematic data (summarized in Stevens, 2001+). These different lines of

*Corresponding author. E-mail: will.jd.iles@gmail.com

evidence have provided new insights into the tempo and mode of diversification in monocots. However, a monocot-wide framework for assessing which fossils are most suitable for calibrating molecular dating analyses is still lacking. Our major goal here is to explore this issue in detail.

The fossil record provides the only physical evidence of past biological events, but many lineages have a poor or non-existent fossil history. Molecular dating approaches (e.g. Sanderson, 2003; Drummond *et al.*, 2006; Dos Reis & Yang, 2011; Heath, Huelsenbeck & Stadler, 2014) allow the integration of phylogenetic and fossil data to estimate divergence times across lineages lacking a fossil record, in addition to improving estimates for fossil-rich lineages. These inferred dates can be used in further downstream analyses, for example to estimate rates of extinction and speciation (e.g. Magallón & Sanderson, 2001), to reconstruct biogeographical patterns (e.g. Donoghue & Moore, 2003; Iles *et al.*, 2014) and to date the origin of specific ecosystems of interest (e.g. Davis *et al.*, 2005; Edwards *et al.*, 2010; Couvreur, Forest & Baker, 2011). Although there are multiple sources of error in molecular dating (e.g. Magallón, 2004; Rutschmann, 2006; Lepage *et al.*, 2007; Gandolfo, Nixon & Crepet, 2008; Parham & Irmis, 2008; Ho & Phillips, 2009; Clarke, Warnock & Donoghue, 2011; Parham *et al.*, 2012; Dos Reis & Yang, 2013; Paradis, 2013; Sauquet, 2013), the largest ones may be the mis-specification of fossil placement in the phylogenetic tree and the associated age of the fossil (Yang & Rannala, 2006; Sauquet *et al.*, 2012). This underlines the need for the careful selection of fossil calibrations on the basis of accurate and up-to-date assessment of fossil ages and phylogenetic placements (Magallón, 2004; Gandolfo *et al.*, 2008; Parham & Irmis, 2008; Parham *et al.*, 2012; Pirie & Doyle, 2013) and continued research on the fossil record.

Here, we attempt to identify and justify those monocot fossils that have the potential to be the most useful for dating monocot phylogenetic trees. Fossils suitable for calibration should have a well-justified age and phylogenetic placement, sufficient to constrain the age of an associated node in a molecular phylogenetic tree reliably. Typically the calibration is effectively applied as the minimum age for the associated node. Note that it is not accurate to say that the fossil originated at the node (see below). Our use of ‘calibration’ here is more general than that of Sanderson (1997) and Sanderson & Doyle (2001) and corresponds approximately to their use of the term ‘constraint’. We focus on two major requirements noted by several recent authors (Magallón, 2004; Gandolfo *et al.*, 2008; Parham & Irmis, 2008; Parham *et al.*, 2012; Sauquet *et al.*, 2012): (1) establishing the correct age of the strata where fossils were collected,

which defines the minimum age of an associated calibrated node in a phylogenetic tree; and (2) establishing the phylogenetic placement of the fossil, i.e. associating a fossil with a particular node in a tree as a calibration point. This may mean reviewing multiple candidate fossil records and taxa. Below we lay out the selection criteria in more detail and then apply them to the identification of fossils suitable for dating monocot phylogeny. When necessary, for clarity we use ‘fossil’ to refer to a particular specimen and ‘fossil taxon’ for a taxonomic entity comprising single or multiple specimens, possibly of widely varying geographical and temporal range.

EVALUATING FOSSIL AGE

The description of the locality where the fossil(s) was collected should ideally contain detailed information about the site, including the geological formation and the stratigraphic layer. This allows for independent confirmation of the proposed age of the stratum, which can change as relevant knowledge is gained. A relatively narrow age range for the fossil-bearing horizon may be inferred using marine biostratigraphy (if it is bracketed by marine incursions), terrestrial biostratigraphy (e.g. land mammal ages for North America, Europe, South America and Asia or palynozones) and/or absolute ages obtained from radiometric dating (if appropriate minerals are included in the sediments, e.g. volcanics, detrital zircons) (Fig. 1). Ideally, multiple methods of dating should be used to arrive at a narrowly constrained age, but in practice this is not always possible, due to particular techniques not being applicable to some sediment types. Conversely, stratigraphic data may be relatively uninformative and an absence of radiometrically dated material may suggest only a relatively broad age range (e.g. ‘middle Eocene’) for the fossil-bearing horizon. Note that a broad age range for a fossil does not imply that the fossil taxon was present in the whole temporal range; narrow ranges for fossils are desirable because they allow a more refined calibration, but are not always available. Our age estimates for fossils include: (1) ranges, which may correspond to the beginning and ending of stages or more precisely dated marine incursions and radiometrically dated volcanics; and (2) single point estimates, where the fossil horizon has been dated or an overlying horizon is dated (see Table 1 for details).

It is possible to use the entire known fossil history (i.e. all specimens across all fossil taxa) that are assignable to a clade (or lineage) in a molecular dating analysis (e.g. Marshall, 2008; Wilkinson *et al.*, 2011; Nowak *et al.*, 2013; Heath *et al.*, 2014). However, these analyses are technically complex and have mostly been carried out in small clades with

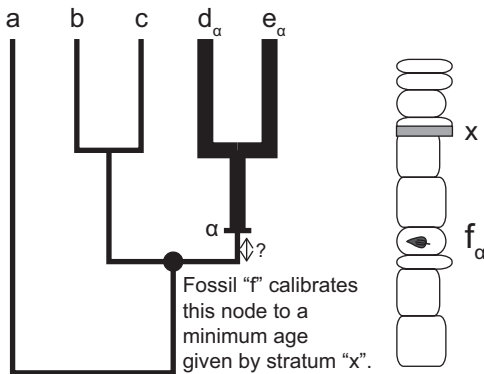


Figure 1. Key steps in using a fossil to calibrate a node in a molecular dating analysis. The right-hand panel is a diagram of a stratigraphic formation that includes a fossil ‘f’ closely overlain by a dated stratum. The left-hand panel shows a well-supported phylogenetic tree with extant taxa labelled ‘a’–‘e’. The fossil has an apomorphy (‘α’) shared here with two extant taxa ‘d’ and ‘e’ (presence of apomorphy indicated with a subscript); the thick line indicates multiple equally parsimonious placements of the fossil. The date of origin of the apomorphy is unknown (indicated by a question mark), and so the fossil conservatively dates the node indicated by the filled circle. The dated stratum ‘x’ that overlies the fossil (the oldest securely placed one with the apomorphy) provides a minimum age for the fossil and this node; when there is an age range for a stratum, the youngest age should be used in a molecular dating analysis, to be conservative. The vertical axis of the phylogenetic tree is in arbitrary time units terminating in the present at the top.

well-defined fossil records. Typically only a single fossil representative or a horizon-specific collection of fossils is used for calibrating a specified node. As a review of the monocot fossil record in its entirety is beyond the scope of this contribution, we focus only on those single fossil records most suitable for dating particular nodes. The oldest fossil clearly assigned (see below) to a clade should ideally be used for calibration, as this defines the minimum (youngest) possible age of the associated stem node.

PHYLOGENETIC PLACEMENT OF FOSSILS

Accurately placing a fossil taxon within a phylogenetic tree is more difficult than placing extant taxa. Fossils lack molecular data, may have poor preservation or lack preservation of key characters, and are often limited in number and fragmentary in nature. Plant organs and parts tend to be shed or preserved independently (as isolated leaves, flowers, pollen, stems etc.), which may each contain relatively few phylogenetically informative characters. The reliance on single organs to represent a species provides us

with fewer total characters for phylogenetic inference compared with whole plant data for extant taxa. In addition, the ability to recognize key characters in fossils can be hindered by our often limited knowledge of the morphology and anatomy of modern species (Smith, 2013).

In a molecular dating analysis it is not always clear which node in a phylogenetic tree should be associated with an individual fossil (taxon). We briefly review the logic behind this process here (see also Magallón, 2004). If we consider a fossil taxon, ‘f’, with an apomorphy, ‘α’, that it shares with an extant clade (labels ‘d’ and ‘e’ in Fig. 1), ‘f’ can be placed anywhere within that clade, or along the subtending branch (‘stem’) of the clade with equal cost in parsimony (see thick lines in Fig. 1). The fossil ‘f’ should conservatively be placed to the deepest possible point (at the origin of the apomorphy ‘α’), because shallower placements would tend to increase the age of the whole tree arbitrarily. In general, the exact timing of origin of the apomorphy along the stem is also unknown (see Fig. 1). To be conservative, the apomorphy ‘α’ is effectively assumed to originate immediately after the stem node, for the purposes of calibration. Thus, the minimum age of fossil ‘f’, defined by overlaying stratum layer ‘x’, effectively calibrates the stem node (filled circle in Fig. 1) that precedes the clade defined by apomorphy ‘α’ (Fig. 1). An underlying/deeper stratum, not marked in Figure 1, may also provide a maximum age for the fossil, but this would not provide a maximum age for the associated stem node, as older fossils with the apomorphy ‘α’ may be found. When a range is given for an age, the youngest (uppermost) age should be used in a molecular dating analysis, to be conservative.

If a fossil could be placed confidently along a single branch of the phylogenetic tree (e.g. in a phylogenetic analysis) to the exclusion of descendant branches, the same logic would apply: the minimum age of the fossil calibrates the stem node of that branch. Most researchers will use fossils as minimum age constraints for associated nodes (Sanderson, 1997; Sanderson & Doyle, 2001; see Yang & Rannala, 2006, who considered the use of soft minimum ages). The example discussed here assumes that the reference tree (Fig. 1) is accurate. Errors in the topology of the reference tree may lead to errors in the distribution of character states, and therefore in the placement of fossil calibrations within the tree. Well-supported phylogenetic trees covering the breadth of taxa under consideration should be used to evaluate the placement of fossil calibrations as far as possible, to minimize this possibility. Some fossil taxa that lack obvious apomorphies may still be useful for calibration, so long as a suite of characters unambiguously support the placement of the fossil in a described

Table 1. Monocot fossils for molecular dating

Fossil		Node assignment			Geology			
Fossil taxon	Organ	Specimen(s)	Node	Justification	Locality	Stratigraphy	Age (Ma)	Justification
MONOCOTS								
<i>Liliacitites</i> sp. A of Doyle & Hickey 1976 (= <i>Retimonocolpites</i> sp. C of Doyle, 1973)	Pollen	Specimen: 3215, slide no. 71-8-1d (USNM)	Stem node of monocots	Phylogenetic analysis (Doyle <i>et al.</i> , 2008)	Trent's Reach, VA, USA	Patuxent Fm	113–125	Aptian, biostratigraphy (Doyle, 1973; Hochuli <i>et al.</i> , 2006; Doyle <i>et al.</i> , 2008)
ALISMATALES: ALISMATACEAE								
<i>Caldesia brandoniana</i> Haggard & Tiffney 1997	Fruit and seeds	Holotype: 51406 (Paleobotanical C, Harvard U)	Stem node of <i>Caldesia</i> (Alismataceae)	Suite of characters (Haggard & Tiffney, 1997)	Forest Dale, VT, USA	Brandon Lignite	20	Terrestrial biostratigraphy (Tiffney, 1994; Traverse, 1994)
ALISMATALES: APONOGETONACEAE								
<i>Aponogon harrvi</i> Grimsson, Zetter, Halbritt, & G. Grimm 2014	Pollen	Holotype: IPUW 2012-0008 (Dept. Palaeontology, U Vienna)	Stem node of Aponogonaceae	Suite of characters (Grimsson <i>et al.</i> , 2014)	Elk Basin, Park County, WY, USA	Upper Eagle Beds, Eagle Fm	81.13	⁴⁰ Ar/ ³⁹ Ar radiometry (Hicks, 1993)
ALISMATALES: ARACEAE								
SUBFAMILY AROIDEAE								
<i>Montrichardia aquatica</i> F.A.Herrera, C.A.Jaram, Dilcher, S.L.Wing & C.Gómez Nav. 2008	Leaves	Holotype: ING-0904 (Colombian Geological I, INGEOMINAS)	Stem node of <i>Montrichardia</i> (Aroideae)	Suite of characters (Herrera <i>et al.</i> , 2008)	Pt Tobacco Extension and Tobacco 1 localities, Cerrejón mine, Colombia	Cerrejón Fm	58–60	Terrestrial biostratigraphy and carbon isotope analysis (Jaramillo <i>et al.</i> , 2007)
<i>Nitophyllites zaisanicus</i> Iljinsk. 1963 emend. Fedotov 1975 (see Wilde <i>et al.</i> , 2005 for English translations)	Leaves	Lectotype: 449g-8, (LE)	Stem node of <i>Typhonodorum</i> clade <i>sensu</i> Cusimano <i>et al.</i> (2011)	Suite of characters (Wilde <i>et al.</i> , 2005)	Kim Kerish Mountain, Zaysan Basin, Kazakhstan	Tayzhuzgen Fm	56.0 to –66.0	Palaocene, terrestrial biostratigraphy (Lucas <i>et al.</i> , 2012)
SUBFAMILY LASIOIDEAE								
<i>Keratospirma allenbyense</i> Cevallos-Ferriz & Stockey 1988 emend. S.Y.Sm. & Stockey 2003	Fruit and seeds	Holotype: P4268 D bot and E (Paleobotanical C, U. Alberta)	Stem node of Lasioideae	Suite of characters (Cevallos-Ferriz & Stockey, 1988; Smith & Stockey, 2003)	Similkameen River, ~8.4 km south of Princeton, BC, Canada	'Princeton Chert', Princeton Group, Allenby Fm	48.7	K/Ar radiometry (Smith & Stockey, 2003)
SUBFAMILY LEMNOIDEAE								
<i>Limonophyllum scutatum</i> (Dawson) Krassilov 1973 [Johnson, 2002]	Vegetative plants	Specimen: 6083 and others (YPM)	Stem node of Lemnoideae (Araceae)	Phylogenetic analysis and suite of characters (Kvaček, 1995; Stockey <i>et al.</i> , 1997; Bogner, 2009)	Five localities, ND & SD, USA	Hell Creek and lower Fort Union Fms	66.0	Multiple stratigraphic controls (Hicks <i>et al.</i> , 2002; Johnson, 2002)
SUBFAMILY MONSTEROIDEAE								
<i>Aracophyllites tertarius</i> (Engelh.) V.Wilde, Kvaček & Bogner 2005	Leaves	Holotype: ME 477 (HLMDD)	Stem node of Monstereae (Monsteroideae)	Suite of characters (Wilde <i>et al.</i> , 2005)	Messel Pit, near Darmstadt, Germany	Messel Fm	47	⁴⁰ Ar/ ³⁹ Ar radiometry and sedimentation rate (Franzen, 2005; Mertz & Renne, 2005)

Table 1. *Continued*

Fossil			Node assignment			Geology		
Fossil taxon	Organ	Specimen(s)	Node	Justification	Locality	Stratigraphy	Age (Ma)	Justification
ALISMATALES: HYDROCHARITACEAE								
<i>Stratiotes</i> L. sp. (Bone, 1986)	Seeds	Private collection, M. Collinson, Royal Holloway U'London	Stem node of <i>Stratiotes</i> (Hydrocharitaceae)	Suite of characters (Sille <i>et al.</i> , 2006)	Felpham, West Sussex, UK	Felpham Lignite Bed, Reading Fm	55.9	Terrestrial biostratigraphy and carbon isotope excursion (Bone, 1986; Collinson, 2000; Collinson & Cleal, 2001; Collinson <i>et al.</i> , 2003)
Thalassites								
<i>Thalassites parksonenses</i> Benzey & Brack-Hanes 2008	Vegetative plants	Holotype: AP Series 267A & B, & APS Series 267A (Eckerd College H.)	Stem node of <i>Erihalis</i> + <i>Halophila</i> + <i>Thalassia</i>	Suite of characters (Benzey & Brack-Hanes, 2008)	Gulf Hammock Quarry, FL, USA	Avon Park Fm	38.0–47.8	Middle Eocene, marine biostratigraphy (Miller, 1986)
ARECALES: ARECACEAE								
SUBFAMILY ARECOIDEAE								
<i>Triphylocarpa aestuaria</i> Gandolfo & Futey 2012 (in Futey <i>et al.</i> , 2012)	Fruits	Holotype: Pb-3766 (MPEF-Pb)	Stem node of Aitaleinae (Cocoseae: Arecoideae)	Apomorphy (Futey <i>et al.</i> , 2012)	Las Violetas, Patagonia, Argentina	Salamanca Fm	63.49–64.67	Magnetostratigraphy, Chron C28n (Clyde <i>et al.</i> , 2014)
SUBFAMILY CALAMOIDEAE								
<i>Mauritiidites crassi-baculatus</i> van Hoeken-Klinkenberg, 1964 (Schrank, 1994)	Pollen	Plates 6: figs 4–10; Plate 12: figs 6–10 (not deposited)	Stem node of Mauritiinae (Lepidocarpaceae: Calamoideae)	Apomorphy (Harley, 2006; Dransfield <i>et al.</i> , 2008)	Hed-Hed locality, Somalia	Yesomma Fm	66.0–~72.1	Maastrichtian–?Campanian, biostratigraphy (Schrank, 1994; Fantozzi & Kassim Mohamed, 2002)
SUBFAMILY CORYPHOIDEAE								
<i>Arengapolitenites achinattus</i> R.K.Kar 1985	Pollen	Holotype: slide no. 8236/2 (Birbal Sahni I. Palaeobotany) M. Ethiopia	Stem node of Corypoteae (Coryphoideae)	Suite of characters (Kar, 1985; Harley, 2006; Dransfield <i>et al.</i> , 2008)	Panandhro, India	Panandhro Lignite, Naredi Fm	47.8–56.0	Ypresian (Ilerdian' stage, marine biostratigraphy (Saraswati <i>et al.</i> , 2012)
<i>Hyphaene kappelmannii</i> A.D.Pan, B.F.Jacobs, J.Dransf. & W.J.Baker 2006	Petioles	Holotype: CH8-6 (N. M. Ethiopia)	Stem node of <i>Hyphaene</i> (Hyphaeninae: Borasseae)	Suite of characters (Pan <i>et al.</i> , 2006)	Chilga Woreda, Ethiopia	Guang River Flora	27.23	²⁰⁶ Pb/ ²⁰⁸ U radiometry (Pan, 2010)
<i>Sabalites carolinensis</i> E.W.Berry 1914	Leaves	Syntype: PAL 175717/P 38208 (USNM)	Stem node of Coryphoideae (Arecaceae)	Suite of characters (Berry, 1914)	Near Langley locality, SC, USA	Middendorf Fm	83.6–86.3	Santonian, marine biostratigraphy (Gohn <i>et al.</i> , 1992)
ASPARAGALES: ASPARAGACEAE								
<i>Paracordyline kerguelensis</i> Conran 1997	Leaves	Holotype: v.23718 (BMNH)	Stem node of <i>Cordylina</i> (Lomandroideae: Asparagaceae)	Apomorphy (Conran, 1997)	Port Jeanne d'Arc, La Grande Terre, Kerguelen Islands	Basaltic interbedded ash and fluvial sediments	22–26	Rb/Sr radiometry of basaltic flows (Gret <i>et al.</i> , 1989)
<i>Protouyca shadishii</i> Tidwell & L.R.Parker 1990	Vegetative plants	Holotype: 3245 (BYU)	Stem node of <i>Yucca</i> (Agavaceae)	Suite of characters (Tidwell & Parker, 1990)	Humbolt County, NV, USA	Virgin Valley Fm	14.5–16.2	⁴⁰ Ar/ ³⁹ Ar radiometry (Perkins <i>et al.</i> , 1998)
ASPARAGALES: ASTELIACEAE								
<i>Astelia antioua</i> Macinnes, Conran, Bannister, R.Paul & D.E.Lee 2011	Leaves	Holotype: FH617 (OU32892) (Geology M., U. Otago)	Stem node of <i>Astelia</i> (Asteliaceae)	Suite of characters and phylogenetic analysis (Macinnes <i>et al.</i> , 2011)	Near Middlemarch, South Island, New Zealand	Foulden Maar Diatomite	23.2	⁴⁰ Ar/ ³⁹ Ar radiometry (Lindqvist & Lee, 2009)

ASPARGALES: ORCHIDACEAE SUBFAMILY EPIDENDROIDEAE <i>Dendrobium wilkophyllum</i> Conran, Bannister & D.E.Lee 2009a	Leaves	Holotype: OU32218 (Geology M., U. Otago)	Crown node of <i>Dendrobium</i> (Dendrobiae: Orchidaceae)	Suite of characters and apomorphies (Conran <i>et al.</i> , 2009a)	Near Middlemarch, South Island, New Zealand	Foulden Maar Diatomite	23.2	⁴⁰ Ar/ ³⁹ Ar radiometry (Lindqvist & Lee, 2009)
<i>Earina fouldenensis</i> Conran, Bannister & D.E. Lee 2009a	Leaves	Holotype: OU32221 (Geology M., U. Otago)	Stem node of <i>Earina</i> (Agrostophyllinae: Epidendroideae: Orchidaceae)	Suite of characters and apomorphies (Conran <i>et al.</i> , 2009a)	Near Middlemarch, South Island, New Zealand	Foulden Maar Diatomite	23.2	⁴⁰ Ar/ ³⁹ Ar radiometry (Lindqvist & Lee, 2009)
SUBFAMILY ORCHIDOIDEAE <i>Meliorchis caribea</i> S.R.Ramirez, Gravand, R.B.Singer, C.R. Marshall & Pierce 2007	Pollinium	Holotype: 31141 (MCZ)	Stem node of Goodyerinae (Orchidoideae)	Phylogenetic analysis (Ramirez <i>et al.</i> , 2007)	Near Santiago, Dominican Republic	Dominican Amber	15–20	Marine and terrestrial biostratigraphy (Turraide-Vinent & MacPhee, 1996)
ASPARGALES: XANTHORRHOACEAE <i>Dianellophyllum saecenicum</i> Conran, Christophel & L.K.Cunn. 2003	Leaves	Holotype: L050 (ADU)	Stem node of Hemerocallidoideae (Xanthorrhoeaceae)	Suite of characters (Conran <i>et al.</i> , 2003)	Nelly Creek locality, Australia	Eyre Fm	38.0–47.8	Middle Eocene, terrestrial biostratigraphy (Alley <i>et al.</i> , 1996)
DIOSCOREALES: DIOSCOREACEAE <i>Dioscorea wilkinsonii</i> A.D.Pan, B.F.Jacobs & Curran 2014	Leaves	Holotype: CH40-110 (N. M. Ethiopia)	Stem node of <i>Dioscorea</i> sect. <i>Lasiophyton</i> (<i>Dioscorea</i> : Dioscoreaceae)	Suite of characters (Pan <i>et al.</i> , 2014)	Chilga Woreda, Ethiopia	Guang River Flora	27.23	²⁰⁶ Pb/ ²³⁸ U radiometry (Pan, 2010)
LILIALES: ALSTROEMERIACEAE <i>Luzuriaga peterbannisteri</i> Conran, Bannister, Mildenh. & D.E.Lee 2014 (in Conran <i>et al.</i> , 2014)	Leaves and possibly floral remains	Holotype: FH 437 (OU32666) (Geology M., U. Otago)	Stem node of <i>Luzuriaga</i> (= <i>Luzuriagoideae</i> : Alstroemeriaceae)	Apomorphy and additional characters (Conran <i>et al.</i> , 2014)	Near Middlemarch, South Island, New Zealand	Foulden Maar Diatomite	23.2	⁴⁰ Ar/ ³⁹ Ar radiometry (Lindqvist & Lee, 2009)
LILIALES: RIPOGONACEAE <i>Ripogonum tasmanicum</i> Conran, R.J.Carp. & G.J.Jord. 2009	Leaves	Holotype: LR42 (School of Plant Science, U. Tasmania)	Stem node of Ripogonaceae	Phylogenetic analysis (Conran <i>et al.</i> , 2009b)	Lowana Road Harbour, Tasmania, Australia	Maquarie Harbour Fm	51–52	Mid-Ypresian, marine and terrestrial biostratigraphy (Carpenter <i>et al.</i> , 2007)
PANDANALES: CYCLANTHACEAE <i>Cyclanthus messelensis</i> S.Y.Sm., M.E.Collinson & Rudall 2008	Fruits	Holotype: SM.B.Me 2005 (SMF)	Stem node of <i>Cyclanthus</i> (= Cyclanthaceae)	Apomorphy (Smith <i>et al.</i> , 2008b)	Messel Pit, near Darmstadt, Germany	Messel Fm	47	⁴⁰ Ar/ ³⁹ Ar radiometry and sedimentation rate (Franzen, 2005; Mertz & Renne, 2005)
PANDANALES: TRIURIDACEAE <i>Mabelia conatifolia</i> Gandolfo, Nixon & Crepet 2002	Flowers	Holotype: CUPC 1255 (BH, Cornell University)	Stem node of Triuridaceae	Phylogenetic analysis (Gandolfo <i>et al.</i> , 2002)	Old Crossman Clay Pit locality, Sayreville, NJ, USA	South Amboy Fire Clay, Raritan Fm	86.3	Coniacian–Santonian boundary marine and terrestrial biostratigraphy (Christopher, 1979; Massoni <i>et al.</i> , 2014)
POALES: CYPERACEAE <i>Volkeria messelensis</i> S.Y.Sm., M.E.Collinson, D.A.Simpson, Rudall, Marone & Stamppanoni 2009	Infructescences	Holotype: Sm.B.Me 16474 (SMF)	Stem node of Mapanioideae (= Cyperaceae)	Suite of characters (Smith <i>et al.</i> , 2009)	Messel Pit, near Darmstadt, Germany	Messel Fm	47	⁴⁰ Ar/ ³⁹ Ar radiometry and sedimentation rate (Franzen, 2005; Mertz & Renne, 2005)

Table 1. Continued

Node assignment			Geology				
Fossil	Specimen(s)	Node	Justification	Locality	Stratigraphy	Age (Ma)	Justification
POALES: POACEAE SUBFAMILY EHRHARTOIDEAE <i>Changii indicum</i> V.Prasad, Strömberg, Leaché, B.Samant, R.Patnaik, L.Tang, Mohabey, S.Ge & A.Sahni 2011 <i>Leersia seiffenhensdorffensis</i> H.Walther 1974							
Organ	Specimen(s)	Node	Justification	Locality	Stratigraphy	Age (Ma)	Justification
Epidermis and phylloliths	Holotype: slide 13160, coordinates: Q-14-3 (Birbal Sahni I. Palaeobotany)	Stem node of Oryzeae (= Ehrhartoideae: Poaceae)	Phylogenetic analysis (Prasad <i>et al.</i> , 2011)	Pisdura, India	Red Clay, Lameta Fm, Deccan Traps	66.0	Radiometry and magnetostratigraphy (Courtilot & Renne, 2003)
Inflorescence	Holotype: MMG, Sf. 12a; others: Sf. 154/71, Sf. 156/71 (MIMG)	Stem node <i>Leersia</i> (Oryzeae)	Suite of characters (Walther, 1974; Walther & Kváček, 2007)	Seiffenhensdorf, Germany	Seiffenhensdorf Diatomite	30.44	K/Ar radiometry (Bellon <i>et al.</i> , 1998)
SUBFAMILY POOIDEAE <i>Sipa florissanti</i> (Knowlt.) MacGinitie 1953							
Fruits	Syntypes: 34750, 34751 (USNM)	Stem node of Stipeae (Pooideae)	Suite of characters (MacGinitie, 1953; Manchester, 2001)	Florissant and Florissant Fossil Beds National Monument, CO, USA	Florissant Fm	34.07–36.7	⁴⁰ Ar/ ³⁹ Ar radiometry (Evanoff <i>et al.</i> , 2001)
POALES: RESTIONACEAE <i>Restiocarpum latericum</i> M.E.Dettmann & Clifford 2000							
Seeds	Holotype: M110/S10, QMF50038 (Queensland Museum, Brisbane, Australia)	Stem node of Centropodiaceae + Restionaceae	Suite of characters (Dettmann & Clifford, 2000; Briggs & Linder, 2009)	Rockhampton 1 locality, Queensland, Australia	Casuarina Beds	27.7	K/Ar radiometry and terrestrial biostratigraphy (Sutherland <i>et al.</i> , 1977; Noon, 1980; Dettmann & Clifford, 2000)
POALES: TYPHACEAE <i>Typha</i> L. sp. [Grande, 1984]							
Inflorescence	Specimen: PP33654 (FMNH)	Stem node of <i>Typha</i> (= Typhaceae)	Suite of characters (Grande, 1984)	Near Fossil Butte National Monument, Fossil Lake, WY, USA	'18 inch' layer, Fossil Butte Mb, Green River Fm	51.66	⁴⁰ Ar/ ³⁹ Ar radiometry of the K-feldspar tuff (Smith <i>et al.</i> , 2008a; Buchheim <i>et al.</i> , 2011)
ZINGIBERALES: ZINGIBERACEAE <i>Sprematospermum chandlerae</i> E.M.Friis 1988							
Seeds	Holotype: 401634 (USNM)	Stem node Zingiberaceae	Suite of characters (S.Y.S., J. Benedict & C. Specht, unpublished data)	Neuse River, Goldsboro, NC, USA	Tar Heels Fm	72.1–83.6	(Early) Campanian, marine biostratigraphy (Owens & Sohl, 1989; Sohl & Owens, 1991; Mitra & Mickte, 2007)

Fossil taxa that we consider to be suitable for molecular dating are listed with taxonomic authority, date of publication and organ type. If more than three authors are associated with a taxon it is abbreviated using 'primary author *et al.*'. If an older fossil belonging to this taxon is known from a different reference, it is listed in square brackets after the taxonomic authority. Specimen and geological information follow the oldest fossil record (i.e. the authority publication or, in some cases, the publication noted separately in square brackets), but node assignment information can come from any relevant publication that considered the fossil taxon. Fossil taxa are assigned to the shallowest reliable node, following the criteria outlined in the main text (placements in more inclusive named clades that may be informative in sparsely sampled dating analyses are mentioned in parentheses, all crown-node placements unless explicitly mentioned; clades noted after an equal sign are named crown nodes that are probably equivalent to the preceding stem node). A brief summary of the criteria used to justify the node assignment is given along with the relevant reference(s). Locality and stratigraphic information, age and a brief summary of the justification for the age are provided for the oldest fossil for each fossil taxon. Authority abbreviations follow IPNI Consortium (2012); institutional acronyms follow Sabaj Perez (2013) for museums and palaeobiological collections and Thiers (continuously updated) for herbaria, except when explicitly noted. C, Collection(s); Fm, Formation; H, Herbarium; I, Institut(-ions); M, Museum; Mb, Member; N, National; U, University.

taxon (even in the absence of a formal phylogenetic analysis); in these cases the suite may be functionally equivalent to an apomorphy, and may therefore be used to calibrate the stem node of the corresponding clade (Gandolfo *et al.*, 2008). We include these taxa with the caveat that additional phylogenetic reconstructions would be useful to clarify the status of individual characters in associated suites (some of these characters may act as apomorphies individually).

SELECTION OF FOSSILS FOR CALIBRATING MONOCOT PHYLOGENIES

We consulted recent reviews (Stockey, 2006; Doyle *et al.*, 2008; Doyle & Endress, 2010; Smith *et al.*, 2010; Clarke *et al.*, 2011; Friis *et al.*, 2011; Smith, 2013) and associated primary literature (see below) to identify candidate fossils to serve as calibrations for monocot molecular dating analyses. Our attention was focused on the oldest fossils associated with families (or subfamilies in some cases). We targeted fossil taxa that can be placed based on phylogenetic analyses, by the possession of apomorphies known to define particular clades or by the possession of a suite of characters that satisfactorily align them with well characterized clades. We chose fossils that are available as vouchered specimens curated in museum or university collections, to ensure that fossil identity and description can be verified (e.g. Gandolfo *et al.*, 2008; Parham *et al.*, 2012); in a few cases, noted in Table 1, the fossil belongs to a private collection or exists only as figures. We used these criteria to justify the suitability of individual fossils below (summarized in Table 1). We define the node that each fossil is suitable for calibrating, and the current age estimate of the fossil. In practice, taxon sampling in molecular dating analyses may not be dense enough to use the most refined placement of the fossil, and so we also list the next most inclusive named clades. We consulted recent reviews of fossil angiosperm localities (Clarke *et al.*, 2011; Friis *et al.*, 2011) and associated primary literature (see below) to evaluate the minimum age of calibration fossils. The chronostratigraphy follows the International Commission on Stratigraphy (Cohen, Finney & Gibbard, 2013). In total we propose 34 fossils that we consider to be suitable for dating the major lineages of monocot phylogeny, which span 19 families and eight orders (summarized in Table 1).

MONOCOTYLEDON FOSSILS

ACORALES

This monogeneric order is often recovered as the sister group of the rest of the monocots (e.g. Graham

et al., 2006). The order is represented by a single genus, *Acorus* L., which is geographically widespread in the Northern Hemisphere, but has low species diversity. There are several relevant fossils reported from the Eocene onward (Smith, 2013), of which the oldest record is the spadix *Acorites heeri* (E.W.Berry) Crepet from North America (Crepet, 1978). Several features of these fossils (inflorescence structure, paracytic stomata and trilocular ovaries) are seen in modern *Acorus* and some Araceae (Crepet, 1978; Grayum, 1987; Mayo, Bogner & Boyce, 1997). The fossils lack diagnostic characters to place them within extant species diversity and therefore they are not suitable for calibrating the crown or stem node of *Acorus*.

ALISMATALES: ALISMATAACEAE

Fossils with similarities to Alismataceae (including Limnocharitaceae) occur from the Late Cretaceous onward (Stockey, 2006; Smith, 2013). The best characterized of these are *Cardstonia tolmanii* M.G.Riley & Stockey, *Haemanthophyllum* Budantzev and *Heleophyton helobiaeoides* D.M.Erwin & Stockey (Erwin & Stockey, 1989; Golovneva, 1997; Riley & Stockey, 2004). These fossils show strong similarities to extant Alismataceae. However, the preserved characters do not reliably allow their placement in the crown clade of the family. Additionally, some of these genera also share characters with other alismatalean families (such as Aponogetonaceae and Butomaceae). The earliest fossils that can be unequivocally placed in the crown clade are fossil fruits from the late Oligocene to early Miocene of Eurasia and North America (reviewed by Haggard & Tiffney, 1997). Haggard & Tiffney (1997) described fossil fruits assignable to the extant genus *Caldesia* Parl. from the Brandon Lignite of Vermont based on 'horseshoe'-shaped seeds, thin exocarp and thick exocarp consisting of one layer of radially aligned lignified cells and ribs on the pericarp. *Caldesia* is well embedded in the Alismataceae clade (G. Ross, University of British Columbia, and S.W.G., unpubl. data). In terms of seed and fruit characters it may be closest to *Limnophyton* Miquel (Haggard & Tiffney, 1997), which has yet to be sampled in a molecular analysis. The age of the lignite is middle early Miocene (20 Ma) based on terrestrial biostratigraphy (Tiffney, 1994; Traverse, 1994). Fossils from the Isle of Wight, collected from the Bembridge Marl Member, Bouldnor Formation, late Eocene (33.8–34.0 Ma; Collinson, 1983; Hooker *et al.*, 2009), were placed within Alismataceae but are not particularly close to any extant genera, and they may represent stem Alismataceae. Therefore, we consider the Brandon Lignite fossil fruit taxon, *Caldesia brandoniana* Haggard & Tiffney, to be suitable for

calibrating the stem node of *Caldesia*, or more inclusively the crown node of Alismataceae. Additional fossils from the Eurasian Neogene have been assigned to modern species (e.g. *Alisma plantago* L., from the Miocene of Germany; Mai, 2000) and may be relevant as calibrations, once the original material has been re-examined and their identifications confirmed.

ALISMATALES: APONOGETONACEAE

Several fossil leaves have been considered to have affinity with Aponogetonaceae, but alternative assignments to other alismatalean families are often possible (Smith, 2013). The pollen of Aponogetonaceae is distinctive, being monosulcate with an echinate reticulum, and recently was recovered from Cretaceous and Eocene sediments from North America (Wyoming, USA, and British Columbia, Canada) and Greenland (Grimsson *et al.*, 2014). Grimsson *et al.* (2014) described three species from the three localities and ascribed them to different pollen subtypes within *Aponogeton* L.f. The oldest of these fossils is *Aponogeton harryi* Grimsson, Zetter, Halbritt. & G.Grimm from the Upper Eagle Beds, Eagle Formation, Elk Basin of Wyoming, USA (Grimsson *et al.*, 2014), with the pollen-bearing stratum dated to at least 81.13 Ma by an overlying bentonite layer (Hicks, 1993). Although the existence of pollen subtypes within *Aponogeton* suggests that it may be possible to place *A. harryi* within the context of extant diversity (i.e. to date the genus crown or shallower node), the taxonomic distribution of pollen subtypes in the genus is complex and our understanding of their evolutionary history is problematic (Les, Moody & Jacobs, 2005; Grimsson *et al.*, 2014). As a result, the fossil is best used to calibrate the stem node of *Aponogeton* (= Aponogetonaceae).

ALISMATALES: ARACEAE

The fossil record of Araceae has been reviewed extensively, with several general reviews (Friis *et al.*, 2011; Smith, 2013), recent ones on fossil pollen (Hesse & Zetter, 2007) and fossil leaves (Wilde, Kvaček & Bogner, 2005), and a comprehensive review for a genus-level molecular dating study of the family (Nauheimer, Metzler & Renner, 2012). When considering phylogenetic placement within Araceae, we used the phylogenetic tree of Cusimano *et al.* (2011; see also Henriquez *et al.*, 2014) as a reference. We provide a brief overview of the record here, starting with the oldest records, and then consider records for individual subfamilies.

Friis, Pedersen & Crane (2004) describe two pollen types from the Aptian–early Albian (Early Creta-

ceous) of Portugal (Doyle & Endress, 2014). The first, *Mayoa portugallica* E.M.Friis, K.R.Pedersen & P.R.Crane, was described as having affinities with extant *Holochlamys* Engl. and *Spathiphyllum* Schott in subfamily Monsteroideae. A possible relationship with Gnetales was raised, but rejected due to differences in infratectal structure. This discovery prompted Hesse & Zetter (2007) to review the ephedroid fossil pollen record (an artificial assemblage). They concluded that two additional taxa, *Ephedripites vanegensis* Hammen & Garcia de Mutis (Palaeocene) and *E. elsikii* Herengreen (Late Cretaceous), also belong to *Spathiphyllum*. More recently, Hofmann & Zetter (2010) proposed a strong likeness of *Mayoa* to *Lagenella martinii* (Leschik) W.Klaus, a fossil pollen morphotype of uncertain affinities with an extensive record from the Triassic to the Cretaceous, casting doubt on its relationship with Araceae and pointing to the need to reinvestigate both taxa in detail. Although it seems likely that some or all of these fossils represent members of Monsteroideae (especially the younger fossils), the close similarity with other extinct and extant lineages precludes their use as fossil calibrations. The second putatively araceous fossil pollen illustrated by Friis *et al.* (2004) shows strong similarities to the zona-aperturate pollen taxon *Proxapertites operculatus* Hammen (Hesse & Zetter, 2007). Zetter, Hesse & Frosch-Radivo (2001) established that *P. operculatus* is similar to pollen from two unrelated subfamilies in Araceae, Zamioiculcoideae and Monsteroideae. *Proxapertites operculatus* has an extensive record extending from the latest Cretaceous to early Oligocene, although more recent records are rarer (Zetter *et al.*, 2001). If the record of Friis *et al.* (2004) proves reliable, this would almost double the known age of the taxon (Hesse & Zetter, 2007). We currently reserve judgment concerning the identity of the Friis *et al.* (2004) fossil, and accept that Late Cretaceous records of *P. operculatus* probably reflect members of Monsteroideae or Zamioiculcoideae (Zetter *et al.*, 2001; Hesse & Zetter, 2007). However, because these subfamilies are distantly related and intervening subfamilies have different pollen types, this fossil taxon is not suitable for molecular dating (e.g. Nauheimer *et al.*, 2012, did not consider this taxon in their study). More complete araceous material from the Early Cretaceous (Albian) is represented by two fossil inflorescences, ‘Araceae fossil sp. A’ and ‘Araceae fossil sp. B’, which are also from Portugal (Friis, Pedersen & Crane, 2010). Based on floral and inflorescence characters these fossils were assigned to Aroideae and Pothoideae, respectively (Friis *et al.*, 2010); Araceae fossil sp. A is more plesiomorphic than extant members of Aroideae in having pollen with a reticulate-columellar exine, and is therefore probably a stem relative of Aroideae, if it is related at all

(J. A. Doyle, University of California, Davis, pers. comm.). However, these fossils need to be described formally and critically compared with other taxa, before use as fossil calibrations (see also Nauheimer *et al.*, 2012).

Additional records of Araceae to consider are those of Late Cretaceous or younger age, which in general can be placed to subfamily or shallower taxonomic levels reliably (Nauheimer *et al.*, 2012; Smith, 2013). Within Aroideae, Herrera *et al.* (2008) assigned Palaeocene fossil leaves from the Carrejón Mine of Colombia (Carrejón Formation, 58–60 Ma; Jaramillo *et al.*, 2007) to the extant genus *Montrichardia* Creug. on the basis of multiple shared leaf morphological characters between the fossil and extant species. *Montrichardia* is phylogenetically isolated within Aroideae and the fossil *M. aquatica* F.A.Herrera, C.A.Jaram., Dilcher, S.L.Wing & C.Gómez Nav. could therefore be used to calibrate the stem node of *Montrichardia* or, more inclusively, the crown node of Aroideae. Other fossils clearly assignable to clades within Aroideae are the leaves *Nitophyllites zaisanicus* Iljinsk. and *N. bohemicus* V.Wilde, Kvaček & Bogner. These are similar to each other and have multiple morphological similarities to tribes Peltrandeae and Arophyteae (Wilde *et al.*, 2005). These two tribes are sister taxa and the resulting clade is termed the ‘*Typhonodorum* clade’ by Cusimano *et al.* (2011). *Nitophyllites zaisanicus* is the older of the two species; it dates from the Palaeocene of Kazakhstan and could be used to calibrate the stem node of the *Typhonodorum* clade. Several other fossil leaves described by Wilde *et al.* (2005) also have affinities to Aroideae (*Araciphyllites schaarschmidti* V.Wilde, Kvaček & Bogner and *Caladiosma messelense* V.Wilde, Kvaček & Bogner), but their placement within the subfamily is unclear, and because they are younger than the fossils mentioned above they are not considered further here. It is also worth mentioning that the Campanian and Maastrichtian (Late Cretaceous) floating aquatic species *Cobbania corrugata* (Lesq.) Stockey, G.W.Rothwell & K.R.Johnson was originally described as an extinct *Pistia* L. (Stockey, Rothwell & Johnson, 2007) and has been used as a calibration in some analyses (e.g. Bremer, 2000). Although it is araceous and probably placed within Aroideae, its exact affinities are unknown, but it remains intriguing as an additional fully aquatic lineage of Araceae (Stockey *et al.*, 2007).

Within Lasioideae, the best characterized fossils are seeds from the Princeton Chert locality (Princeton Member, Allenby Formation) of British Columbia, which is of early Eocene age (Smith & Stockey, 2003). Older fossil pollen from the Late Cretaceous is known from Siberia and is assigned to the genus *Lasioideacidites* C.-C.Hofm. & Zetter (Hofmann & Zetter, 2010).

Its similarity to Lasioideae is based on thickened endexine in the sulcus region and similarity in morphology (Hofmann & Zetter, 2010). However, Hesse (2002) emphasized the need for transmission electron microscopy (TEM) sections in identifying the unique, synapomorphic two-layered endexine of Lasioideae. As TEM sections are lacking for *Lasioideacidites*, we do not consider it suitable for molecular dating at present. The fossil seeds *Keratosperma allenbyense* Cevallos-Ferriz & Stockey emend. S.Y.Sm. & Stockey are more suitable to calibrating the stem node of Lasioideae (as it does not appear to be closely related to any of the extant genera) (Cevallos-Ferriz & Stockey, 1988; Smith & Stockey, 2003). Fossils were found in multiple layers below and above ash layer 22 of the Princeton Chert, British Columbia, which has been dated radiometrically to 48.7 Ma (Smith & Stockey, 2003).

Fossil members of Lemnoideae were reviewed recently by Bogner (2009), who noted the presence of fossil seeds and plants of the extant genus *Lemna* L. from the Oligocene onwards. In particular, he focused on the extinct *Limnobiophyllum scutatum* (Dawson) Krassilov, found from the latest Cretaceous of Asia and North America. Morphological and palynological work suggests that *Limnobiophyllum* is closely related to subfamily Lemnoideae, although it is less reduced morphologically (Kvaček, 1995; Stockey, Hoffman & Rothwell, 1997; Hesse & Zetter, 2007; Bogner, 2009). A morphology-based phylogenetic analysis was used to place the genus as the sister group to extant Lemnoideae, although taxon sampling was scanty (Stockey *et al.*, 1997). The best preserved material, which includes *in situ* pollen (originally described as *Pandaniidites* Elsik; see Stockey *et al.*, 1997; Hesse & Zetter, 2007) is from Alberta and is of middle Palaeocene age (Stockey *et al.*, 1997). Slightly older material corresponding to the Cretaceous–Palaeogene boundary is known from Asia (Krassilov, 1973) and North America (Johnson, 2002). The North American material is represented by 99 specimens from five localities in south-western North Dakota and north-western South Dakota from the Hell Creek and lower Fort Union Formations (Johnson, 2002). These localities closely straddle the Cretaceous–Palaeogene boundary (Hicks *et al.*, 2002; Johnson, 2002) and we can therefore confidently calibrate the stem node of Lemnoideae to 66 Ma.

Araciphyllites tertarius (Engelh.) V.Wilde, Kvaček & Bogner, represented by leaves, comes from the famous Messel Pit of Germany, an Eocene maar lake. Wilde *et al.* (2005) re-evaluated it and placed it within Monsteroideae based on multiple leaf venation characters. They consider it most similar to tribe Monstereae, corresponding most closely to the ‘*Rhaphidophora* clade’ of Cusimano *et al.* (2011). *Araciphyllites tertarius* can be used for calibrating

the stem node of the *Rhaphidophora* clade, or more inclusively the crown node of Monsteroideae. The age of the Messel Pit is considered to be middle Eocene (47 Ma; Franzen, 2005; Mertz & Renne, 2005).

Within Orontioideae, Nauheimer *et al.* (2012) recognized several fossil calibration candidates from the Late Cretaceous, including the infructescence *Albertarum* Bogner, G.L.Hoffman & Aulenback, and fossil leaves assigned to *Lysichiton* Schott, *Orontium* L. and *Symplocarpus* Salisb. (Kvaček & Herman, 2004; Bogner, Hoffman & Aulenback, 2005; Bogner, Johnson & Upchurch, 2007). The three fossil taxa based on leaf remains lack distinguishing characters (Smith, 2013) and are therefore not reliable for molecular dating. *Albertarum* consists of an infructescence complete with seeds from the Late Cretaceous of Alberta that has multiple characters showing affinity to Orontioideae (*Albertarum pueri* Bogner, G.L.Hoffman & Aulenback; Bogner *et al.* 2005). However, *Albertarum* has a thick ribbed testa, a character not seen in living Orontioideae or Gymnostachyoideae and we therefore do not currently consider it suitable for calibration purposes. Additional leaf fossils from the Early Cretaceous of Brazil have been described as *Spixiarum kipea* Coiffard, B.A.R.Mohr & Bernardes-de-Oliveira and have been compared with subfamily Orontioideae, but the authors stopped short of definitively placing it within the subfamily (Coiffard, Mohr & Bernardes-de-Oliveira, 2013) and consequently we do not consider it further.

Nauheimer *et al.* (2012) recently used *Petrocardium* F.A.Herrera, C.A.Jaram., Dilcher, S.L.Wing & C.Gómez Nav. from the Palaeocene of Colombia (Herrera *et al.*, 2008) as a calibration fossil within Pothoideae. However, as Herrera *et al.* (2008) pointed out, *Petrocardium* is characterized by a suite of characters suggesting similarities to members of two distantly related subfamilies, Pothoideae (especially *Anthurium* Schott) and Lasioideae, and consequently it cannot be assigned with confidence to any particular clade or taxon within Araceae (Herrera *et al.*, 2008).

ALISMATALES: HYDROCHARITACEAE

Seeds recognizable as belonging to extant genera of Hydrocharitaceae first appear in the late Palaeocene and increase in diversity and frequency onwards. The oldest of these belong to *Stratiotes* L. (Stockey, 2006; Smith, 2013), which extends into the Palaeocene of England (Sille *et al.*, 2006). As *Stratiotes* may be the sister taxon of the rest of the family (Iles, Smith & Graham, 2013; but see Les, Moody & Soros, 2006), the oldest known *Stratiotes* fossil can most confidently be utilized for calibrating the stem node of *Stratiotes*, or potentially the crown node of Hydrocharitaceae. The

oldest *Stratiotes* comes from the Felpham Lignite Bed, Reading Formation, England (Bone, 1986), and has been dated to 55.9 Ma (Bone, 1986; Collinson & Cleal, 2001; Collinson, Hooker & Gröcke, 2003). Additional Eocene to Miocene fossils have also been assigned to modern genera (summarized by Smith, 2013) and may prove useful after they have been re-examined and their affiliations confirmed.

ALISMATALES: POTAMOGETONACEAE/RUPPIACEAE

There is a particularly rich record of fossil fruits assigned to what has been called the *Potamogeton-Ruppia* complex which spans from the Cretaceous to the present (Collinson, 1982; Zhao, Collinson & Li, 2004; Gandolfo *et al.*, 2009; Smith, 2013). *Potamogeton* L. (Potamogetonaceae) and *Ruppia* L. (Ruppiaceae) are quite distantly related to each other. They belong to a diverse clade that includes four or five families, including several seagrass families (Cymodoceaceae, Posidoniaceae and Zosteraceae) (Les, Cleland & Waycott, 1997; Iles *et al.*, 2013). Until these fossil taxa are examined in a more comprehensive context, the true affinities of these fossil taxa remain unclear.

ALISMATALES: 'SEAGRASSES'

Because of the close morphological and anatomical similarity (Stockey, 2006; van der Ham, van Konijnenburg-van Cittert & Indeharberge, 2007; Benzecry & Brack-Hanes, 2008; Smith, 2013) among distantly related seagrass families (Les *et al.*, 1997; Iles *et al.*, 2013) we consider them here together, rather than under separate family headings (Cymodoceaceae, Hydrocharitaceae *p.p.*, Posidoniaceae, Zosteraceae, but see above for Ruppiaceae fruits). Extensive convergence and simplification due to adaptation to a submerged aquatic environment (Les *et al.*, 1997) make taxonomic placement of seagrass fossils difficult in the absence of reproductive material. Well-preserved fossil seagrasses are known from the Avon Park Formation of Florida (middle Eocene; Miller, 1986), which have been assigned to extant genera (Lumbert *et al.*, 1984), but explicit justification for these placements is lacking. However, Benzecry & Brack-Hanes (2008) convincingly showed that the fossil *Thalassites parkavonenses* Benzecry & Brack-Hanes, from the same locality, is related to the hydrocharit seagrass clade (nested within Hydrocharitaceae) based on several characters, making *Thalassites* the best fossil for calibrating the stem node of hydrocharit seagrasses, to the middle Eocene (38.0–47.8 Ma).

ALISMATALES: TOFIELDIACEAE

Tofieldiaceae do not have a reliable fossil record. Bremer (2000) used a fossil pollen record, *Dicolpopollis*

Pflanzl, from the Campanian–Maastrichtian boundary or earliest Maastrichtian of California (Chmura, 1973) for calibrating Tofieldiaceae. Although disulcate pollen occurs in Tofieldiaceae, *Dicolpopollis* is usually referred to calamoid palms (e.g. Crepet, Nixon & Gandolfo, 2004; Smith, 2013) and at least some of the characters Chmura (1973) provided as evidence for affinity to Tofieldiaceae (e.g. small size and aspects of sculpturing) are also found in the palm genus *Calamus* Auct. ex L. (Dransfield *et al.*, 2008). Until further investigations are done that confirm the identity of this pollen, it is not suitable for calibration.

OTHER PUTATIVE ALISMATALES

Friis, Pedersen & Crane (2000) described a suite of reproductive organs (pollen, stamens and pistils) belonging to several closely related species from the Vale de Agua and Buarcos localities of Portugal (Albian; Heimhofer *et al.*, 2007; Dinis *et al.*, 2008); the reconstructed taxon is called the *Pennipollis* plant, after the form genus name for the pollen (*Pennipollis* E.M.Friis, K.R.Pedersen & P.R.Crane). Friis *et al.* (2000) most closely compared the plant with members of Araceae and Potamogetonaceae and suggested an affinity within Alismatales. Phylogenetic analyses of early lineages of angiosperms (Doyle *et al.*, 2008; Doyle & Endress, 2014) instead found an association of the *Pennipollis* plant with Chloranthaceae and *Ceratophyllum* L. We therefore do not consider the *Pennipollis* plant suitable for calibration of monocots.

ARECALES: ARECACEAE

The fossil record of palms is probably the most conspicuous of any monocot family and possibly extends back to the Turonian of France (*Palmoxylon andegavense* Crié, *P. ligerianum* Crié; Kvaček & Herman, 2004; Dransfield *et al.*, 2008). There have been several recent general reviews (Harley, 2006; Dransfield *et al.*, 2008), reviews of fossil pollen (Harley & Baker, 2001; see also Dransfield *et al.*, 2008) and a comprehensive review for a genus-level molecular dating of the family (Couvreur *et al.*, 2011). When considering fossil taxon placement we used the reference phylogenetic trees of Baker *et al.* (2009) and Dransfield *et al.* (2008). We review the fossil record here for each subfamily.

In Arecoideae, *Cocos* L.-like fruits have an extensive record, extending to the Maastrichtian Deccan Intertrappean beds of India (Harley, 2006; Shukla, Mehrotra & Guleria, 2012). However many of these records are poorly preserved or the locality information is incomplete (Patil & Upadhye, 1984; Mehrotra, 1987; Tripathi, Mishra & Sharma, 1999; Shukla *et al.*,

2012) and as a result we do not consider them further. In the New World, fossil fruits from the Palaeocene of Colombia and Argentina are known with strong similarities to *Cocos* and other members of subtribe Attaleinae (Gómez-Navarro *et al.*, 2009; Futey *et al.*, 2012). The Argentinian material is slightly older than the Colombian material and comes from the Estancia Las Violetas locality, Salamanca Formation, Chubut Province (Futey *et al.*, 2012). The permineralized fruits were placed within a new fossil species, *Tripylocarpa aestuaria* Gandolfo & Futey, the taxonomic position of which was explored using phylogenetic analyses of molecular sequences combined with morphological data. The results of these analyses confirmed the taxonomic placement suggested by the morphological and anatomical characters preserved in the fossils (Futey *et al.*, 2012). *Tripylocarpa* is the first confirmed record for subtribe Attaleinae worldwide and can confidently be used to calibrate the stem node of Attaleinae (or equivalently the crown node of Cocoseae, see Baker *et al.*, 2009); more inclusively it could date the crown node of Arecoideae. Palaeomagnetic data from several sections of the Salamanca Formation have been assigned to Chrons C28n and C29n; specifically, the diverse palaeoflora has been determined as belonging to Chron C28n, indicating that the age of the flora is between 63.49 and 64.67 Ma (Clyde *et al.*, 2014).

In Calamoideae, two groups of fossil pollen, *Dicolpopollis* and *Mauritiidites crassibaculatus* van Hoeken-Klinkenberg, have been described. The first, *Dicolpopollis*, is characterized by two opposite equatorial sulci (i.e. disulcate pollen). This character is seen in eight genera of tribe Calameae, and derived forms (e.g. diporate, zonosulcate, inaperturate) characterize most of the rest of the tribe (Harley, 2006; Dransfield *et al.*, 2008). Equatorial disulcate pollen grains are therefore an apomorphy for Calameae. The earliest reliable *Dicolpopollis* fossils are from the Yesomma Formation of Somalia (Schrank, 1994). The Yesomma Formation is overlain by the late Maastrichtian to early Eocene marine Aurabu Formation, and is considered to be late Maastrichtian (possibly as old as Campanian) in age (~72.1–66.0 Ma; Schrank, 1994; Fantozzi & Kassim Mohamed, 2002). The other group, *Mauritiidites*, is characterized by intectate monosulcate pollen with spines ‘embedded’ in the foot layer, causing a bulge below the spine in the pollen wall (van Hoeken-Klinkenberg, 1964; Harley, 2006). This pollen type also characterizes *Mauritia* L.f., and is similar to the pollen of the remaining members of subtribe Mauritiinae (tribe Lepidocaryeae) (Harley, 2006; Dransfield *et al.*, 2008). It can therefore be considered to be an apomorphy for this subtribe. The earliest known occurrences of *M. crassibaculatus* are from the Maastrichtian of Nigeria and the slightly

older Yesomma Formation (van Hoeken-Klinkenberg, 1964; Schrank, 1994). (There have also been reports of the genus from the Campanian to Eocene of Sudan; Eisawi & Schrank, 2008.) As Calameae and Lepidocaryeae are sister taxa, the crown-node placement of *Mauritiidites* in Lepidocaryeae (i.e. the stem node of subtribe Mauritiinae) makes it more informative than the stem-node placement of *Dicolpopollis* in tribe Calameae. We agree with Couvreur *et al.* (2011) and consider *Mauritiidites* to be appropriate for calibrating the stem node of subtribe Mauritiinae.

Coryphoideae have the oldest systematically assignable fossil palms. These are keeled costapalmate leaves from the Late Cretaceous of eastern North America. The oldest of these is *Sabalites carolinensis* E.W.Berry, from the Near Langley locality, Middendorf Formation, South Carolina (Berry, 1914), which dates to the Santonian (83.6–86.3 Ma; Gohn, Dowsett & Sohl, 1992). *Sabalites magothiensis* E.W.Berry is known from the 'Deep Cut' at Summit Bridge, Delaware, and Grove Point, Maryland, localities, which are considered to be comparable to the Cliffwood beds of the Magothy Formation (Berry, 1905, 1911), which are also of Santonian age (Christopher, 1979). Costapalmate induplicate leaves are an apomorphy of subfamily Coryphoideae, and we therefore consider *S. carolinensis* to calibrate the stem node of Coryphoideae to the Santonian. As it is the oldest crown clade member of Arecaceae, it can also be used to calibrate the crown node of Arecaceae. There are also several plausible crown clade members of Coryphoideae. Several fossil petioles assignable to the modern genus *Hyphaene* Gaertn. were recently discovered in Ethiopia (Pan *et al.*, 2006). The fossils are characterized by features of the spines and are described as *Hyphaene kappelmannii* A.D.Pan, B.F.Jacobs, J.Dransf. & W.J.Baker. The age of the associated fossil flora is dated to the late Oligocene (27.23 Ma; Pan, 2010). *Hyphaene kappelmannii* can be utilized for calibrating the stem node of *Hyphaene* (see also Couvreur *et al.*, 2011) or, more inclusively, the crown node of tribe Borasseae. Additional evidence for crown Coryphoideae fossils comes from *Arengapollenites* R.K.Kar, which comprises intectate pollen with spines interlocking over the sulcus (Kar, 1985; Kar & Bhattacharya, 1992). This pollen type is most similar in structure and exine ornamentation to modern *Arenga* Labill. (tribe Caryoteae) (Kar, 1985; Kar & Bhattacharya, 1992). Nonetheless, all genera of Caryoteae have intectate pollen with either spines or clavae, which may interlock over the sulcus (Harley, 2006; Dransfield *et al.*, 2008). The age of the type locality Panandhro, India (Naredi Formation), is early Eocene (= Ypresian, 47.8–56.0 Ma; Kar, 1985; Saraswati, Sarkar & Banerjee, 2012). As the characters of the fossil are found in all genera of Caryoteae,

we consider *Arengapollenites* to calibrate the stem node of tribe Caryoteae. More inclusively, it can also calibrate the crown node of Coryphoideae.

In Nypoideae, fossil pollen grains (*Spinizonocolpites* Jan Muller) and fruits assigned to the subfamily are known from the Maastrichtian and Palaeocene, respectively (Harley, 2006; Gómez-Navarro *et al.*, 2009). However, as Nypoideae are monotypic, these fossils would effectively constrain the stem node of Nypoideae. A more informative (i.e. older) fossil for this same node is *Sabalites carolinensis*, mentioned above for subfamily Coryphoideae. As a result, we do not consider fossil Nypoideae further here.

ASPARAGALES: ASPARAGACEAE

Several macrofossils representing disparate woody lineages of Asparagaceae *s.l.* have been found in Australia, Antarctica, Asia and North America. Fossil leaves similar to those of extant *Cordyline* Comm. ex R.Br. have been recovered from the Oligocene and Eocene of the Kerguelen Islands in the southern Indian Ocean and Australia (Conran, 1997; Conran & Christophel, 1998). The older of these, *Paracordyline aureonemorialis* Conran & Christophel, comes from the early Eocene (Golden Grove, 56.0–47.8 Ma) of Australia (Conran & Christophel, 1998), whereas the younger, *P. kerguelensis* Conran, is from ash sediments between basalt flows (26–22 Ma; Giret *et al.*, 1989) on La Grande Terre in the Kerguelen Archipelago (Conran, 1997). Although these fossils are in general similar to each other and to *Cordyline*, and the younger fossil shares a cuticular sculpturing apomorphy with a subclade of *Cordyline*, other assignments are also possible (Conran, 1997; Conran & Christophel, 1998). Additional fossil material for *Cordyline* comes from the early Miocene Foulden Maar of New Zealand, which has yet to be formally described (Lee *et al.*, 2012). As *P. kerguelensis* shares an apomorphy with some members of *Cordyline* it can be used to calibrate the stem node of *Cordyline* to 22 Ma. More inclusively, it can be used to calibrate the crown node of subfamily Lomandroideae (see Steele *et al.*, 2012 for a reference phylogenetic tree).

Stems, roots and leaves that appear to be of an arborescent monocot are known from the Miocene Virgin Valley Formation of Nevada (Tidwell & Parker, 1990). Tidwell & Parker (1990) compared these anatomically preserved fossils with extant groups of woody monocots, and on that basis suggested a close relationship to *Yucca* L., especially *Y. brevifolia* Engelm. (Joshua tree), describing them as *Protoyucca shadishii* Tidwell & L.R.Parker. We agree with their assessment and suggest that *Protoyucca* be used to calibrate the stem node of *Yucca* or, more inclusively, the crown node of subfamily Agavoideae. The Virgin

Valley Formation has been radiometrically dated to 14.5–16.2 Ma (Perkins *et al.*, 1998).

Denk, Güner & Grimm (2014) recently reported on fossil leaves from the Miocene of Anatolia and suggested that they have affinities with the dragon tree group of *Dracaena* Vand. ex L. Individual fossil leaves and leaf rosettes were recovered (described as *D. tayfunii* Denk, H.T.Güner & G.Grimm), some with preserved cuticular features (e.g. the arrangement of stomata in rows that form bands and the presence of 'bone-like' papillate epidermal cells). These were interpreted as most similar to the Macaronesian *D. draco* (L.) L and *D. tamaranae* Marrero Rodr., R.S.Almeida & Gonz.-Mart. (Denk *et al.*, 2014). However, these leaves were not evaluated broadly against a large range of comparable taxa, and so we do not consider them currently as suitable for calibration.

ASPARAGALES: ASTELIACEAE

Fossil leaves from the Foulden Maar of New Zealand were recently described as having affinities to a subclade of *Astelia* Banks & Sol. ex R.Br., based on a phylogenetic analysis of cuticular characters (Maciunas *et al.*, 2011). The Foulden Maar has been radiometrically dated to 23.2 Ma (Lindqvist & Lee, 2009) and palaeontological studies also suggest a late Oligocene or early Miocene age. Consequently, *Astelia antiquua* Maciunas, Conran, Bannister, R.Paull & D.E.Lee can be used to calibrate the stem node of *Astelia* (or equivalently the crown node of Asteliaceae, see Birch, Keeley & Morden, 2012); more inclusively it can be used to date the stem node of Asteliaceae.

ASPARAGALES: ORCHIDACEAE

There have been several recent fossil finds of Orchidaceae from subfamilies Orchidoideae and Epidendroideae (Ramírez *et al.*, 2007; Conran *et al.*, 2009a). *Meliorchis caribea* S.R.Ramírez, Gravend., R.B.Singer, C.R. Marshall & Pierce is a pollinium mass attached to its pollinator preserved in Dominican amber (Ramírez *et al.*, 2007). Phylogenetic analysis of pollinia characters suggested a placement with subtribe Goodyerinae (subfamily Orchidoideae) and the age of the amber is mid-to-latest early Miocene (15–20 Ma; Iturralde-Vinent & MacPhee, 1996). Consequently, *M. caribea* could be used for calibrating the stem node of Goodyerinae. Additional evidence for early Miocene (or late Oligocene) fossil leaves (Conran *et al.*, 2009a) comes from the early Miocene Foulden Maar of New Zealand (23.2 Ma; Lindqvist & Lee, 2009). Conran *et al.* (2009a) assigned these fossils to two extant genera in subfamily Epidendroideae based on multiple morphological characters. However, the

higher-order phylogeny of Epidendroideae is largely unresolved and assigning these genera to subclades is therefore problematic (e.g. Cameron, 2004; Freudenstein *et al.*, 2004; van den Berg *et al.*, 2005; Neubig *et al.*, 2008; Górniak, Paun & Chase, 2010). Conran *et al.* (2009a) also noted that *Dendrobium winikaphyllum* Conran, Bannister & D.E.Lee is comparable to the indigenous extant New Zealand species *Dendrobium cunninghamii* Lindl., and they therefore consider it to belong to the Australasian *Dendrobium* clade (Conran *et al.*, 2009a; Adams, 2011). Conservatively, this can be used to date the stem node of *Dendrobium* Sw. (see Adams, 2011 for a reference phylogenetic tree). *Earina fouldenensis* Conran, Bannister & D.E.Lee was compared with extant species of *Earina* Lindl. from New Zealand to which it was found to be closely similar based on the shared presence of unique stomatal characters and general morphology (Conran *et al.*, 2009a). Here we consider it suitable to calibrate the stem node of *Earina*, or more inclusively, the stem of subtribe Agrostophyllinae (see van den Berg *et al.*, 2005 for a reference phylogenetic tree).

ASPARAGALES: XANTHORRHOEACEAE

A single fossil leaf, *Dianellophyllum eocenicum* Conran, Christophel & L.K.Cunn., from the Nelly Creek locality, Eyre Formation, Australia, has multiple characters that suggest an affinity with subfamily Hemerocallidoideae, particularly with the modern genera *Dianella* Lam. ex Juss. and *Thelionema* R.J.F.Hend. (Conran, Christophel & Cunningham, 2003). The Eyre Formation is dated to the middle Eocene (38.0–47.8 Ma) based on biostratigraphy (Alley, Krieg & Callen, 1996). Additional fossils similar to *Dianella* and *Phormium* J.R.Forst. & G.Forst. (subfamily Hemerocallidoideae) have been recovered from the early Miocene of New Zealand (Lee *et al.*, 2012). However, these lack a formal description and so are not considered further here. *Dianellophyllum eocenicum* can be used to calibrate the stem node of subfamily Hemerocallidoideae, or more inclusively, the crown node of Xanthorrhoeaceae (see Seberg *et al.*, 2012 for a reference phylogenetic tree).

DIOSCOREALES: DIOSCOREACEAE

Reliable fossil records of this family are known from the Eocene onwards; earlier records from the Cretaceous are less securely placed (Smith, 2013). A three-winged fruit assignable to *Dioscorea* L., based on the presence of a thick pedicel, retained perianth and fine venation on the wings, is known from the late Eocene of Colorado (Manchester, 2001; Manchester & O'Leary, 2010), but its placement with respect to extant species is unclear, and it may belong along the

stem lineage of *Dioscorea*. The fossil leaf *D. wilkinii* A.D.Pan, B.F.Jacobs & Currano from the Guang River flora (27.23 Ma; Pan, 2010; Pan, Jacobs & Currano, 2014) of Ethiopia is closely related to extant species of *Dioscorea* section *Lasiophyton* Uline (Pan *et al.*, 2014). We therefore assign *D. wilkinii* to the stem node of *Dioscorea* section *Lasiophyton* (for phylogenetic placement, see Wilkin *et al.*, 2005). Pan *et al.* (2014) also described *Tacca umerii* A.D.Pan, B.F.Jacobs & Currano from the early Miocene Mush Valley of Ethiopia (21.7 Ma). This fossil is thought to have greater similarities to the Malagasy, Asian and Malesian species than to the sole extant continental African species, *T. leontopetaloides* (L.) Kuntze, but Pan *et al.* (2014) stopped short of placing it definitively within the extant diversity of the genus. Considering its possible stem lineage placement with *Tacca* J.R.Forst. & G.Forst. and young age, we do not consider it informative for calibration purposes and do not consider it further here.

LILIALES: ALSTROEMERACEAE

Fossil leaves assigned to the extant genus *Luzuriaga* Ruiz & Pav. along with associated reproductive material (Lee *et al.*, 2012; Conran *et al.*, 2014) have been recovered from the early Miocene Foulden Maar of New Zealand (23.2 Ma; Lindqvist & Lee, 2009). Recognition of the extinct taxon *Luzuriaga peterbannisteri* Conran, Bannister, Mildenh. & D.E.Lee was based on the presence of resupinate leaves, venation patterns and cuticular details that closely agree with *Luzuriaga* (Conran *et al.*, 2014). The associated fossil flower was not organically connected to the leaves and was excluded from the species description. However, its characters also suggest association to *Luzuriaga* (Conran *et al.*, 2014). The placement of *L. peterbannisteri* was further explored within Alstroemeriaceae using phylogenetic approaches, where it was found to be either sister to extant *Luzuriaga*, or nested in *Luzuriaga*. We follow Conran *et al.* (2014) and conservatively consider that this fossil may be sister to extant members of the genus and therefore useful for calibrating the stem node of *Luzuriaga*. Note that Conran *et al.* (2014) performed molecular dating analyses, but in both cases used it to constrain nodes within the crown of extant *Luzuriaga*.

LILIALES: RIPOGONACEAE

Fossil leaves, *Ripogonum tasmanicum* Conran, R.J.Carp. & G.J.Jord., from the Macquarie Harbour Formation of Tasmania were assigned to *Ripogonum* J.R.Forst. & G.Forst. based on leaf venation and stomatal patterns (Pole, 2007a; Conran, Carpenter & Jordan, 2009b). A phylogenetic analysis placed *R. tas-*

manicum within the crown clade of *Ripogonum* (Conran *et al.*, 2009b). However, bootstrap support for this relationship is poor (< 50%) and so we only consider it suitable for calibrating the stem node of *Ripogonum*. Marine and terrestrial biostratigraphy date the Macquarie Harbour Formation to the mid-Ypresian (early Eocene, 51–52 Ma; Carpenter, Jordan & Hill, 2007). Additional fossils similar to *Ripogonum* have recently been recovered from the early Miocene of New Zealand (Pole, 2007b; Lee *et al.*, 2012), but await formal description; we do not consider them further here.

PANDANALES: CYCLANTHACEAE

Recent evaluation of infructescences and seeds from the Messel Pit of Germany (47 Ma; Franzen, 2005; Mertz & Renne, 2005) and the re-evaluation of isolated seeds from several Ypresian–Lutetian (early Eocene) localities in the UK demonstrated that they are most closely related to modern *Cyclanthus* Poit. ex A.Rich. (Smith, Collinson & Rudall, 2008b). Although the isolated seeds designated as *C. lakensis* (Chandler) S.Y.Sm., M.E.Collinson & Rudall probably represent *Cyclanthus*, they lack the apomorphies of the fossil infructescences *C. messelensis* S.Y.Sm., M.E.Collinson & Rudall, which directly link the latter to *Cyclanthus*. Therefore, *C. messelensis* can be used to calibrate the stem node of *Cyclanthus* or, more inclusively, the crown node of Cyclanthaceae.

PANDANALES: PANDANACEAE

Pandanoid fossil leaves are known from Cretaceous deposits onwards (e.g. Kvaček & Herman, 2004; Herman & Kvaček, 2010). However, these could be confused with certain members of Cyperaceae (i.e. some mapanioid sedges); fossil pandans are recognized by strap-shaped, parallel-veined leaves that are M-shaped in transverse section, armed with non-vascularized spines (e.g. as discussed by Kvaček & Herman, 2004; S.Y.S., pers. obs.), characters that also occur in some mapanioids (S.Y.S., pers. observ.) that are now recognized as being widespread in Europe in the early Cenozoic (Smith *et al.*, 2009). Confusion even with modern collections was apparent in investigating mapanioid material in herbarium, which had often been initially identified or accessioned as *Pandanus* (S.Y.S., pers. observ.). Therefore, we consider the records of fossil leaves to be unreliable markers of the family until significant distinguishing characters can be identified (Smith, 2013).

Fossil infructescences described as *Gruenbachia pandanoides* J.Kvaček & A.B.Herman were recently recovered from the early Campanian Grünbach Formation of Austria (Herman & Kvaček, 2010). These

fossils were found in association with pandanoid leaves and are similar to some members of Pandanaceae, particularly to *Pandanus* Parkinson, with which the fossils purportedly share the character of polydrupes (also termed 'phalanges' in the literature). However, several of the extant *Pandanus* spp. used for comparisons with the fossils are now segregated as *Benstonea* Callm. & Buerki and do not produce polydrupes (Callmander *et al.*, 2012), even though one is illustrated and labelled as such (see *P. gibbsianus* Martelli, plate 16 fig. 6 in Herman & Kvaček, 2010). Thus, although we consider that the fossils probably represent Pandanaceae and possibly even *Benstonea* or *Pandanus*, they are in need of further comparison with extant pandan fruits and we do not currently consider them appropriate for calibration purposes.

In the earlier literature certain fossil pollen types were considered evidence for Pandanaceae. The most widespread of these pollen types is the near cosmopolitan *Pandaniidites* (Jarzen, 1983), which was originally described as having an affinity to Pandanaceae based on shared monoporate echinate grains (Elsik, 1968; Hotton, Leffingwell & Skvarla, 1994). Sweet (1985) subsequently noted similarities to the pollen of subfamily Lemnoideae of Araceae. Evidence that at least some records belong to Lemnoideae came from *in situ* pollen in plants of *Limnobiophyllum*, an araceous fossil with affinities to Lemnoideae (Stockey *et al.*, 1997; see above for discussion on *Limnobiophyllum*). As a result, records of *Pandaniidites* are not reliable indicators of fossil Pandanaceae. Maastrichtian '*Pandanus tectoria*'-type pollen described by Jarzen (1978) and reported in Muller (1981) has been used by various authors as calibrations for Pandanaceae (e.g. Bell, Soltis & Soltis, 2010; Zanne *et al.*, 2014). However, this pollen type was reinterpreted as *Pandaniidites* (e.g. Nichols, 1987) and is therefore also not reliable for calibrating the family.

In the Palaeogene of Australia and New Zealand two fossil pollen types have been compared with *Freycinetia* Gaudich.: *Dryptopollenites semilunatus* Stover and *Lateropora glabra* Pocknall & Mildenh. The former was originally published by Stover & Partridge (1973) who mentioned a general similarity to Magnoliaceae, Arecaceae and Dioscoreaceae. *Dryptopollenites* was then tentatively compared with *Freycinetia* by Macphail *et al.* (1994) or more broadly with Pandanaceae (Macphail, 1999). In addition, the description of the pollen grains as having a large sulcus and often occurring in pairs (Stover & Partridge, 1973; Truswell, 1997) is unlike extant *Freycinetia* or Pandanaceae (Furness & Rudall, 2006). *Lateropora* (which ranges from the Palaeogene to Miocene) has also been associated with *Freycinetia* (Couper, 1953; Pocknall & Mildenhall, 1984). The characters used to place it (a relatively smooth

tectum that is punctate under scanning electron microscopy; a single pore) are found in *Freycinetia* (Furness & Rudall, 2006), but are homoplasious in angiosperms and may therefore not support this association. We therefore do not consider *Dryptopollenites* or *Lateropora* to be suitable for calibration.

PANDANALES: TRIURIDACEAE

Gandolfo and colleagues (Gandolfo *et al.*, 1998; Gandolfo, Nixon & Crepet, 2002) described well-preserved male flowers from the Late Cretaceous of North America and assigned them to three species (*Mabelia connatifila* Gandolfo, Nixon & Crepet, *M. archaia* Gandolfo, Nixon & Crepet, and *Nuhliantha nyanzaiana* Gandolfo, Nixon & Crepet). Phylogenetic analysis based on the morphology data set of Stevenson & Loconte (1995) suggested a sister relationship between these fossils (treated as a single taxon) and Triuridaceae (Gandolfo *et al.*, 2002). Further phylogenetic analysis focusing on members of Triuridaceae suggested a closer relationship between the fossils and tribe Triurideae than with tribe Sciaphileae (Gandolfo *et al.*, 2002). Rudall (2003) suggested other possible placements within Pandanales, and Friis *et al.* (2011) posited similarities with magnoliid families, especially Myristicaceae; these suggestions were not based on phylogenetic analyses of additional taxa or characters. However, tribe Kupeaeae (Triuridaceae) was not included in the second analysis of Gandolfo *et al.* (2002) and some character states (e.g. reticulate pollen tectum) are not found among current members of Triuridaceae (although reticulate pollen is found in some members of Pandanales; Furness & Rudall, 2006). The most complete specimen is represented by *M. connatifila* and we therefore consider it conservative to use it as a stem node calibration for Triuridaceae, which may also be supported by the good preservation of flowers in the fossil material (these are ephemeral in living members of the family; J. A. Doyle, University of California, Davis, pers. comm.; however, the fossil flowers are charcoaled and may represent pre-anthetic material). This fossil (along with the others) was collected from the Old Crossman Clay Pit locality, Sayreville, New Jersey, part of the South Amboy Fire Clay of the Raritan Formation, which is considered mid-Turonian to possibly Coniacian in age (Christopher, 1979), although the mesofossils are similar to eastern North American localities of Santonian or Campanian age (Friis *et al.*, 2011). The age of estimation of this sequence is complex; we follow Massoni, Doyle & Sauquet (2014) who suggest an age corresponding to the Coniacian–Santonian boundary. A complication to including Triuridaceae and associated fossils in a molecular dating analysis is that

heterotrophic taxa often have highly elevated rates of evolution in plastid, nuclear and mitochondrial genes (demonstrated in Triuridaceae by Mennes *et al.*, 2013, for the latter two genomes), which may prove challenging in molecular dating analyses.

POALES: CYPERACEAE

Isolated fossil fruits assigned to Cyperaceae are common from the Eocene onwards, but potentially extend back to the Palaeocene (Smith *et al.*, 2010). However, it is unclear if these records are all reliable, as a review of English fossil fruits assigned to *Scirpus* L. revealed them to be fossil seeds of Cyclanthaceae (Smith *et al.*, 2008b). Recently, *Volkeria messelensis* S.Y.Sm., M.E.Collinson, D.A.Simpson, Rudall, Marone & Stampanoni was described from the Messel Pit of Germany (47 Ma; Franzen, 2005; Mertz & Renne, 2005), and is represented by complete infructescences with pollen and fruits that can be unambiguously assigned to subfamily Mapanioideae (Smith *et al.*, 2009). Therefore, *V. messelensis* can be used to calibrate the stem node of Mapanioideae, or equivalently the crown node of Cyperaceae, as Mapanioideae are the sister group of the rest of the family (Simpson *et al.*, 2006).

POALES: JUNCACEAE

The vegetative fossil record of Juncaceae is generally doubtful (Smith *et al.*, 2010). More secure records come from seeds comparable to *Juncus* L. from the Eocene–Oligocene boundary of England (Collinson, 1983). Although seed characters can be useful taxonomically (Balslev, 1998), seed character evolution has not been studied within the family and uncertainty concerning the monophyly of *Juncus* relative to the rest of the family complicates this issue further (Drábková, 2010). Therefore, without further study of fruit or seed morphology, these fossils cannot currently be placed within the crown clade of the family and the relatively young age of the fossils suggests that they would not be informative if used as a stem node calibration for the family.

POALES: POACEAE

Although grasses are often ecologically dominant, their herbaceous habit and the dry habitat that they are often associated with makes for poor fossil preservation (Strömberg, 2011). There are several recent reviews of the grass fossil record (Jacobs, Kingston & Jacobs, 1999; Smith *et al.*, 2010; Friis *et al.*, 2011; Strömberg, 2011), and the family has repeatedly been the focus of molecular dating studies (Strömberg, 2005; Bouchenak-Khelladi *et al.*, 2008, 2014;

Vicentini *et al.*, 2008; Prasad *et al.*, 2011). Note that Poaceae (and some other Poales) have extensive rate elevation in plastid and other genes (e.g. Saarela & Graham, 2010), and it is possible that current dating methods do not fully accommodate this phenomenon (see the related discussion of elevated rates in heterotrophic taxa, in the section on Triuridaceae), a possible caveat for dating analyses of the family.

Strömberg (2011) provided the most comprehensive bibliography so far of possible grass fossils from the Cretaceous to the present. The most common grass fossils are pollen, which purportedly extend to the Maastrichtian (Jacobs *et al.*, 1999). However, the gross morphology of grass pollen is indistinguishable from that of many members of related poalean families (Anarthriaceae, Ecdiocoleaceae, Flagellariaceae, Joinvilleaceae and Restionaceae; Linder & Ferguson, 1985) and although TEM sections can be used to distinguish Poaceae pollen from relatives (Linder & Ferguson, 1985) they are rarely done on fossil pollen (Jacobs *et al.*, 1999). More systematically useful evidence comes in the form of bio-opaline phytoliths (silica bodies) and macrofossil evidence, which can often be assigned to subfamilies of Poaceae (e.g. Strömberg, 2004; Prasad *et al.*, 2005; Smith *et al.*, 2010). Although more work needs to be done to fully characterize phytolith morphologies in Poales and other groups, the available data (which includes examination of all families of Poales) demonstrate that there is no convergence between the specialized short-cell morphotypes found in Poaceae with any other plant families, and some poacean morphotypes are even diagnostic to a species level; however, it is not yet clear how diagnostic of the different subfamilies and tribes the different morphotypes are (Prychid, Rudall & Gregory, 2004; Piperno, 2006; Prasad *et al.*, 2011). A more conservative approach is to use phytoliths as fossil constraints when they are preserved in conjunction with other characters (see below).

Here we consider several putatively deeply nested fossils. Poinar (2011) evaluated phytoliths from a Late Cretaceous fossil leaf, *Programinis laminatus* Poinar, preserved in Burmese amber (98.8 Ma; Shi *et al.*, 2012). Based on the presence of rondel phytoliths, he suggested an affinity with Pooideae. However, their three-dimensional shape is hard to distinguish, and thus we reserve judgement about the affinity of the fossil within Poales. The oldest convincing macrofossils of Poaceae are spikelets from the Palaeocene–Eocene boundary (Crepet & Feldman, 1991). The presence of spikelets suggests an affinity to the core subfamilies of Poaceae (i.e. all subfamilies except Anomochlooideae; Crepet & Feldman, 1991; Grass Phylogeny Working Group, 2001; Saarela & Graham, 2010). Because these fossil spikelets possess two florets, Vicentini *et al.* (2008) considered them for

constraining the stem node of all subfamilies except Anomochloideae and Pharoideae (which have single flowered spikelets). As floret number is labile (Grass Phylogeny Working Group, 2001), we consider it more conservative for the fossil to calibrate the stem node of the clade comprising all grass subfamilies excluding Anomochloideae (i.e. the crown node of grasses). However, there are older more deeply nested fossils available to use, and so we do not consider these spikelets further.

Among the species-poor earliest diverging subfamilies, Anomochloideae lack a fossil record. A phytolith from the Maastrichtian of India, *Pipernoia pearsalla* V.Prasad, Strömberg, Alimohammadian & A.Sahni, was suggested to have some affinity with Puelioideae, but its placement with this subfamily is not certain (Prasad *et al.*, 2005). A spikelet attached to mammalian hair recovered from Dominican amber (15–20 Ma; Iturralde-Vinent & MacPhee, 1996) was considered to have affinity to *Pharus* P.Brown (Pharoideae) based on the comparison of eight characters (Poinar & Columbus, 1992). Further work on this fossil, *Pharus primuncinatus* Judz. & Poinar, indicates an association with *P. mezii* Prodoehl, although a phylogenetic analysis was not performed (Poinar & Judziewicz, 2005). We accept that *P. primuncinatus* belongs in *Pharus*, but are hesitant to consider it part of the genus crown clade. It could potentially be used to calibrate the crown node of Pharoideae. However, the monophyly and phylogeny of Pharoideae (including *Pharus*, *Leptaspis* R.Br. and *Scrotochloa* Judz.) has not been adequately evaluated (Judziewicz & Clark, 2007; Christin *et al.*, 2013), and the relatively young age of the fossil (15–20 Ma) makes it unsuitable for dating the stem node of Pharoideae. Another putative fossil member of Pharoideae is represented by leaves described as *Leptaspis* cf. *zeylanica*, from the Miocene Ngororoa Formation, Tugen Hills, Kenya (Jacobs & Kabuye, 1987; Jacobs, Judziewicz & Kabuye, 2014). However, as it is not figured or formally described in the literature, we do not consider it further here.

The oldest definitive fossils of Poaceae are from the Maastrichtian–Danian Deccan beds of India (Prasad *et al.*, 2005, 2011). These are phytoliths formed in the short cells of grass leaf epidermis, belonging to ten form species with affinities to a number of clades and subfamilies of Poaceae (Prasad *et al.*, 2005, 2011). Two of these phytolith form species, *Changii indicum* V.Prasad, Strömberg, Leaché, B.Samant, R.Patnaik, L.Tang, Mohabey, S.Ge & A.Sahni and *Tateokai deccana* V.Prasad, Strömberg, Leaché, B.Samant, R.Patnaik, L.Tang, Mohabey, S.Ge & A.Sahni, have been placed with tribe Oryzae, subfamily Ehrhartoideae, using a Bayesian phylogenetic approach (Prasad *et al.*, 2011); the remainder have not been analysed in this manner and so we do not consider

them further. The epidermal fragment of the holotype of *C. indicum* is exceptionally well preserved and we consider it to be suitable in dating the stem node of Oryzae or, equivalently, the crown node of Ehrhartoideae (the former tribe is the sister group of the remainder of the latter subfamily; Grass Phylogeny Working Group II, 2012). The age of the Deccan beds has been contentious. Here we follow Courtillot & Renne (2003) who reviewed the radiometric and magnetostratigraphic evidence over the extent of the basaltic flows and suggest that the bulk of the flows closely straddled the Cretaceous–Palaeogene boundary. As *C. indicum* was recovered from dinosaur coprolites in horizons containing dinosaur bones (Prasad *et al.*, 2011), we consider this fossil to be latest Maastrichtian (66 Ma). Phytoliths that have been recovered from the Eocene to Miocene of North America, South America and Asia putatively have affinity to Bambusoideae, Chloridoideae, Danthanoideae, Pooideae and other clades (Strömberg, 2004, 2005; Strömberg *et al.*, 2007, 2013; Zucol, Brea & Bellosi, 2010), but they have not been phylogenetically analysed like *C. indicum* and *T. deccana*, and the distribution of phytolith characters in Poaceae is not yet comprehensively known. Therefore, we do not consider them further here. Additional fossil evidence for subfamily Ehrhartoideae comes from the distal end of an inflorescence assignable to *Leersia* Sw., from the Seiffenhensdorf locality, Saxony, Germany (Walther, 1974; Walther & Kvaček, 2007). This locality has been dated by overlying basalts to the Oligocene (30.7 Ma; Bellon *et al.*, 1998). Therefore, the fossil *L. seiffenhensdorfensis* H.Walther can be used to calibrate the stem node of *Leersia* or, more inclusively, the crown node of Oryzae (Grass Phylogeny Working Group II, 2012). Non-phytolith evidence for Bambusoideae comes from spikelets preserved in Miocene Dominican amber (Poinar & Columbus, 2013) that show similarities to the climbing bamboo *Arthrostylidium* Rupr. However, the fossil is not definitely placed within the phylogeny of Bambusoideae, and so we do not consider it further here. Whole fossil grasses with Kranz anatomy are known from the Miocene of California, and were compared with *Paspalum* L. (Panicoideae) (Nambudiri *et al.*, 1978; Whistler *et al.*, 2009). Nevertheless, they were not rigorously evaluated and are not considered further here.

In Pooideae grass fruits described as *Stipa florissanti* (Knowlt.) MacGinitie are known from the Eocene Florissant Formation of Colorado (MacGinitie, 1953; Manchester, 2001). These fossils were compared closely with the extant Mexican species *Nassella mucronata* (Kunth) R.W.Pohl and other New World members of Stipeae [MacGinitie, 1953; Manchester, 2001; note that extant *Stipa* L. s.s. is considered to be restricted to the Old World (Romaschenko *et al.*,

2010), and so this fossil may not necessarily fit the modern circumscription of *Stipa*]. The age of the Florissant Formation is constrained by radiometric dating to 34.07–36.70 Ma (Evanoff, Mcintosh & Murphey, 2001). As tribe Stipeae is clearly nested in Pooideae (Grass Phylogeny Working Group II, 2012), we consider *Stipa florissanti* from Colorado to constrain the stem node age of Stipeae or, more inclusively, the crown age of Pooideae. In addition to this macrofossil evidence there exist *Stipa*-like phytoliths spanning the Eocene to Miocene from North America, South America and Asia (Strömberg, 2005; Strömberg *et al.*, 2007, 2013). However, these phytoliths have not been phylogenetically evaluated, and so we do not consider them further.

POALES: RESTIONACEAE

Fossil pollen widely ascribed to Restionaceae, *Milfordia* Erdtman emend. A.D.Partr., has a record extending back to the Maastrichtian (Smith *et al.*, 2010). However, its placement is not considered secure as there are several other poalean families with similar pollen (Linder & Ferguson, 1985; Linder, 1987). More convincing are fruits from the Eocene–Oligocene boundary in Queensland, Australia, assigned to the extinct genus *Restiocarpum* M.E.Dettmann & Clifford and co-occurring with *Milfordia* pollen (Dettmann & Clifford, 2000). These are unilocular fruits with a single, pendulous ovule with thin seed coat and tannins, much like extant Restionaceae (Dettmann & Clifford, 2000). Some of the fossil seed characters suggest placement in the crown clade of Restionaceae, but some of these characters (e.g. unilocular fruits) are homoplasious in the family (Briggs, Marchant & Perkins, 2010) and may not be systematically informative. Centrolepidaceae share many embryological features with Restionaceae (Briggs & Linder, 2009) and may either be phylogenetically embedded in Restionaceae or sister to it (Briggs *et al.*, 2010; Briggs, Marchant & Perkins, 2014). Because of the uncertainty in the phylogenetic placement of Centrolepidaceae, we consider *Restiocarpum* suitable for constraining the stem node of Centrolepidaceae + Restionaceae [we list the type species *R. latericum* M.E.Dettman & Clifford (Dettmann & Clifford, 2000) in Table 1, but any of these fossils would be suitable]. Palynological correlations of the locality Rockhampton 1, Casuarina Beds, Queensland, Australia (Noon, 1980), with radiometrically constrained strata indicate a minimum age of 27.7 Ma (Sutherland, Stubbs & Green, 1977; Dettmann & Clifford, 2000).

POALES: TYPHACEAE

As currently circumscribed Typhaceae contain two genera, *Sparganium* L and *Typha* L. (APG III, 2009).

Both genera have an extensive and distinctive record of fossil fruits from the Palaeogene onwards, with the record for *Typha* potentially extending to the Late Cretaceous (Smith *et al.*, 2010). *Typha* seeds are characterized as being elongate with a mucronate lid-like operculum that is one cell thick, a thin, membranous seed coat with only two layers, longitudinally orientated integumentary cells and a small cone-shaped chalazal chamber (Dettmann & Clifford, 2000; M. E. Collinson, Royal Holloway University of London, pers. comm., 2014). The chemistry of *Typha* and *Sparganium* seed coats is distinctive and could also be used to strengthen the identity of fossil seeds (Collinson & van Bergen, 2004). The European Cretaceous (Maastrichtian) *Typha* specimens (Knobloch & Mai, 1986) are probably Typhaceae, but require additional study to demonstrate key features (Crepet *et al.*, 2004; Friis *et al.*, 2011). Although somewhat younger, one of the best preserved specimens consists of a complete inflorescence (cattail) from the early Eocene of Wyoming (Grande, 1984). The Fossil Lake locality is part of the Green River Formation and the fossil-bearing stratum ('18 inch' layer) is overlain by a K-feldspar tuff that has been radiometrically dated to 51.66 Ma (Smith, Carroll & Singer, 2008a; Buchheim, Cushman & Biaggi, 2011). This unnamed *Typha* cattail is considered suitable for calibrating the stem node of *Typha* or, equivalently, the crown node of Typhaceae.

ZINGIBERALES

Spirematospermum M.Chandler, which has been variously assigned to Musaceae and Zingiberaceae, has an extensive fossil record covering Eurasia and North America from the Late Cretaceous nearly to the present day (Fischer *et al.*, 2009; Friis *et al.*, 2011). The oldest occurrence of the genus, *S. chandlerae* E.M.Friis, is from the early Campanian Tar Heels Formation of Neuse River, North Carolina (Friis, 1988; Owens & Sohl, 1989; Sohl & Owens, 1991; Mitra & Mickle, 2007; Friis *et al.*, 2011). Its placement in a particular family has been contentious, but current evidence tends to point to an association with crown Zingiberaceae (S.Y.S., M. Collinson, Royal Holloway University of London, J. Benedict, University of Michigan & C. Specht, University of California, Berkeley, unpubl. data). Despite the uncertainty in its systematic placement, we consider this fossil useful for calibrating the stem of Zingiberaceae to the Campanian (72.1–83.6 Ma).

UNPLACED MONOCOT FOSSILS

Until recently the earliest records of monocots were restricted to *Liliacidites* Couper pollen grains and a vegetative shoot, *Acaciaephyllum* Fontaine (Doyle

et al., 2008; Friis *et al.*, 2011). Like many fossil form-genera, *Liliacidites* has a complex history. The genus was first described for pollen grains from the Late Cretaceous of New Zealand (*L. kaitangataensis* Couper; Couper, 1953) that are monosulcate boat-shaped grains with a reticulate tectum that has graduated fining of the lumina towards the ends of the grain. This combination of features is only known from monocots (e.g. some members of Alismatales, Dioscoreales, Liliales, Asparagales and Poales; Doyle, 1973; Walker & Walker, 1984; Doyle *et al.*, 2008). However, fossil pollen grains without these characters have been called '*Liliacidites*' in the literature (Gandolfo *et al.*, 2000); some of these are demonstrably not of monocot affinity (Doyle *et al.*, 2008), and as a result care must be taken when considering whether a particular record actually represents monocot fossil evidence. The earliest records of *Liliacidites* with clear monocot affinity (showing the above mentioned features) are from the Trent's Reach locality of Virginia (Doyle, 1973; Doyle & Hickey, 1976; Doyle & Robbins, 1977; Doyle *et al.*, 2008), part of the Patuxent Formation and corresponding to the base of Zone I, (early?) Aptian (113–125 Ma; Doyle, 1973; Hochuli, Heimhofer & Weissert, 2006). These were originally described as *Retimonocolpites* sp. C by Doyle (1973) and later reinterpreted as *Liliacidites* sp. A by Doyle & Hickey (1976). A phylogenetic analysis placed these fossils either on the stem of monocots or equally parsimoniously anywhere in the included monocots (Doyle *et al.*, 2008). Vegetative material from the Dutch Gap locality of Virginia (Patuxent Formation) was described by Fontaine (1889) as *Acaciaephyllum* Fontaine and compared with *Acacia* Mill. phyllodes. Doyle (1973) subsequently reinterpreted them as monocot leaves based on venation patterns. This placement was challenged by Gandolfo *et al.* (2000) who re-examined the original fossils and discarded the placement in monocots based on the poor preservation of some of the fossils and the lack of apomorphic characters for monocot leaves. Doyle *et al.* (2008) revisited the issue with a phylogenetic analysis that affirmed his earlier placement. As *Liliacidites* sp. A *sensu* Doyle & Hickey (1976) provides an equivalent age constraint and is unambiguously associated with monocots, we consider that it represents the best early evidence for monocots in the fossil record and is therefore useful for calibrating the stem node of monocots.

CONCLUSION

Table 1 provides a summary of the fossils that we think are most reliably placed within extant monocot diversity, and that best satisfy the additional criteria for using fossils as calibrations in molecular dating

analyses (i.e. they have well-characterized phylogenetic placements and ages, and exist as voucher specimens). This review should serve as a guide for molecular dating studies, especially those focused on monocots. It is clear that there are many more monocot fossils still to be re-examined or discovered. We hope that our summary here will spur additional research into clarifying the systematic relationships of monocot fossils, and studies of the morphology and anatomy of modern relatives that are often needed for identifying synapomorphic characters that can be recognized in the fossil record.

ACKNOWLEDGEMENTS

We thank James Doyle and an anonymous reviewer for helpful comments. This work was supported by a University of British Columbia Graduate Scholarship to W.J.D.I., an NSERC (Natural Sciences and Engineering Research Council of Canada) Discovery Grant to S.W.G., US National Science Foundation grants DEB 0830020, DEB 091832 and DEB 0919071 and the Franklin Award from the American Philosophical Society to M.A.G., and US National Science Foundation grant DEB 1257080 to S.Y.S.

REFERENCES

- Adams PB. 2011.** Systematics of Dendrobiinae (Orchidaceae), with special reference to Australian taxa. *Botanical Journal of the Linnean Society* **166**: 105–126.
- Alley NF, Krieger GW, Callen RA. 1996.** Early Tertiary Eyre Formation, lower Nelly Creek, southern Lake Eyre Basin, Australia: palynological dating of macrofloras and silcrete, and palaeoclimatic interpretations. *Australian Journal of Earth Sciences* **43**: 71–84.
- APG III. 2009.** An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Botanical Journal of the Linnean Society* **161**: 105–121.
- Baker WJ, Savolainen V, Asmussen-Lange CB, Chase MW, Dransfield J, Forest F, Harley MM, Uhl NW, Wilkinson M. 2009.** Complete generic-level phylogenetic analyses of palms (Arecaceae) with comparisons of super-tree and supermatrix approaches. *Systematic Biology* **58**: 240–256.
- Balslev H. 1998.** Juncaceae. In: Kubitzki K, ed. *The families and genera of vascular plants. IV. Flowering plants. Monocotyledons: Alismatanae and Commelinanae (except Gramineae)*. Berlin: Springer, 252–260.
- Bell CD, Soltis DE, Soltis PS. 2010.** The age and diversification of the angiosperms re-revisited. *American Journal of Botany* **97**: 1296–1303.
- Bellon H, Bůžek Č, Gaudant J, Kvaček Z, Walther H. 1998.** The České Středohoří magmatic complex in Northern Bohemia ^{40}K – ^{40}Ar ages for volcanism and biostratigraphy of the Cenozoic freshwater formations. *Newsletters on Stratigraphy* **36**: 77–103.

- Benzecry A, Brack-Hanes SD. 2008.** A new hydrocharitacean seagrass from the Eocene of Florida. *Botanical Journal of the Linnean Society* **157**: 19–30.
- van den Berg C, Goldman DH, Freudenstein JV, Pridgeon AM, Cameron KM, Chase MW. 2005.** An overview of the phylogenetic relationships within Epidendroideae inferred from multiple DNA regions and recircumscription of Epidendreae and Arethuseae (Orchidaceae). *American Journal of Botany* **92**: 613–624.
- Berry EW. 1905.** A palm from the mid-Cretaceous. *Torreya* **5**: 30–33.
- Berry EW. 1911.** Contributions to the Mesozoic flora of the Atlantic coastal plain – VII. *Bulletin of the Torrey Botanical Club* **38**: 399–424.
- Berry EW. 1914.** *The Upper Cretaceous and Eocene floras of South Carolina and Georgia*. Washington, DC: United States Geological Survey.
- Birch JL, Keeley SC, Morden CW. 2012.** Molecular phylogeny and dating of Asteliaceae (Asparagales): *Astelia s.l.* evolution provides insight into the Oligocene history of New Zealand. *Molecular Phylogenetics and Evolution* **65**: 102–115.
- Bogner J. 2009.** The free-floating aroids (Araceae) – living and fossil. *Zitteliana* **48/49**: 113–128.
- Bogner J, Hoffman GL, Aulenback KR. 2005.** A fossilized aroid infructescence, *Albertarum pueri* gen. nov. et sp. nov., of Late Cretaceous (Late Campanian) age from the Horseshoe Canyon Formation of southern Alberta, Canada. *Canadian Journal of Botany* **83**: 591–598.
- Bogner J, Johnson KR, Upchurch GR. 2007.** New fossil leaves of Araceae from the Late Cretaceous and Paleogene of western North America. *Zitteliana* **47**: 133–147.
- Bone DA. 1986.** The stratigraphy of the Reading Beds (Palaeocene), at Felpham, West Sussex. *Tertiary Research* **8**: 17–32.
- Bouchenak-Khelladi Y, Salamin N, Savolainen V, Forest F, Van Der Bank M, Chase MW, Hodkinson TR. 2008.** Large multi-gene phylogenetic trees of the grasses (Poaceae): progress towards complete tribal and generic level sampling. *Molecular Phylogenetics and Evolution* **47**: 488–505.
- Bouchenak-Khelladi Y, Slingsby JA, Verboom GA, Bond WJ. 2014.** Diversification of C₄ grasses (Poaceae) does not coincide with their ecological dominance. *American Journal of Botany* **101**: 300–307.
- Bremer K. 2000.** Early Cretaceous lineages of monocot flowering plants. *Proceedings of the National Academy of Sciences of the United States of America* **97**: 4707–4711.
- Briggs BG, Linder HP. 2009.** A new subfamilial and tribal classification of Restionaceae (Poales). *Telopea* **12**: 333–345.
- Briggs BG, Marchant AD, Perkins AJ. 2010.** Phylogeny and features of Restionaceae, Centrolepidaceae and Anarthriaceae (restiid clade of Poales). In: Seberg O, Petersen G, Barfod AS, Davis JI, eds. *Diversity, phylogeny and evolution in the monocotyledons*. Aarhus: Aarhus University Press, 357–388.
- Briggs BG, Marchant AD, Perkins AJ. 2014.** Phylogeny of the restiid clade (Poales) and implications for the classification of Anarthriaceae, Centrolepidaceae and Australian Restionaceae. *Taxon* **63**: 24–46.
- Buchheim HP, Cushman RA, Biaggi RE. 2011.** Stratigraphic revision of the Green River Formation in Fossil Basin, Wyoming: overfilled to underfilled lake evolution. *Rocky Mountain Geology* **46**: 165–181.
- Callmender MW, Lowry PP, Forest F, Devey DS, Beentje H, Buerki S. 2012.** *Benstonea* Callm. & Buerki (Pandanaeae): characterization, circumscription, and distribution of a new genus of screw-pines, with a synopsis of accepted species. *Candollea* **67**: 323–345.
- Cameron KM. 2004.** Utility of plastid *psaB* gene sequences for investigating intrafamilial relationships within Orchidaceae. *Molecular Phylogenetics and Evolution* **31**: 1157–1180.
- Carpenter RJ, Jordan GJ, Hill RS. 2007.** A toothed Lauraceae leaf from the Early Eocene of Tasmania. *International Journal of Plant Sciences* **168**: 1191–1198.
- Cevallos-Ferriz S, Stockey RA. 1988.** Permineralized fruits and seeds from the Princeton Chert (Middle Eocene) of British Columbia: Araceae. *American Journal of Botany* **75**: 1099–1113.
- Chmura CA. 1973.** Upper Cretaceous (Campanian–Maastrichtian) angiosperm pollen from the western San Joaquin Valley, California, USA. *Palaeontographica Abteilung B: Paläophytologie* **141**: 89–171.
- Christin PA, Osborne CP, Chatelet DS, Columbus JT, Besnard G, Hodkinson TR, Garrison LM, Vorontsova MS, Edwards EJ. 2013.** Anatomical enablers and the evolution of C₄ photosynthesis in grasses. *Proceedings of the National Academy of Sciences of the United States of America* **110**: 1381–1386.
- Christopher RA. 1979.** *Normapolles* and triporate pollen assemblages from the Raritan and Magothy Formations (Upper Cretaceous) of New Jersey. *Palynology* **3**: 73–121.
- Clarke JT, Warnock RCM, Donoghue PCJ. 2011.** Establishing a time-scale for plant evolution. *New Phytologist* **192**: 266–301.
- Clyde WC, Wilf P, Iglesias A, Slingerland RL, Barnum T, Bijl PK, Bralower TJ, Brinkhuis H, Comer EE, Huber BT, Ibañez-Majia M, Jicha BR, Krause JM, Schueth JD, Singer BS, Raigemborn MS, Schmitz MD, Sluijs A, del Carmen Zamaloa M. 2014.** New age constraints for the Salamanca Formation and lower Rio Chico Group in western San Jorge Basin, Patagonia, Argentina: implications for K/Pg extinction recovery and land mammal age correlations. *Geological Society of America Bulletin* **126**: 289–306.
- Cohen KM, Finney S, Gibbard PL. 2013.** International Chronostratigraphic Chart v 2013/01. *International Commission on Stratigraphy*. Available at: <http://www.stratigraphy.org>
- Coiffard C, Mohr BAR, Bernardes-de-Oliveira MEC. 2013.** The Early Cretaceous aroid, *Spixiarum kipea* gen. et sp. nov., and implications on early dispersal and ecology of basal monocots. *Taxon* **62**: 997–1008.
- Collinson ME. 1982.** A reassessment of fossil Potamogetonaceae fruit with description of new material from Saudi Arabia. *Tertiary Research* **4**: 83–104.

- Collinson ME. 1983.** Palaeofloristic assemblages and palaeoecology of the Lower Oligocene Bembridge Marls, Hamstead Ledge, Isle of Wight. *Botanical Journal of the Linnean Society* **86**: 177–225.
- Collinson ME. 2000.** Fruit and seed floras from the Palaeocene/Eocene transition and subsequent Eocene in southern England: comparison and palaeoenvironmental implications. *GFF* **122**: 36–37.
- Collinson ME, van Bergen PF. 2004.** Evolution of angiosperm fruit and seed dispersal biology and ecophysiology: morphological, anatomical and chemical evidence from fossils. In: Hemsley AR, Poole I, eds. *The evolution of plant physiology*. London: Elsevier, 344–377.
- Collinson ME, Boulter MC, Holmes PL. 1993.** Magnoliophyta ('Angiospermae'). In: Benton MJ, ed. *The fossil record* 2. London: Chapman and Hall, 809–841.
- Collinson ME, Cleal CJ. 2001.** The palaeobotany of the Palaeocene and Palaeocene-Eocene transitional strata in Great Britain. In: Cleal CJ, Thomas BA, Batten DJ, Collinson ME, eds. *Mesozoic and Tertiary palaeobotany of Great Britain*. Peterborough: Joint Nature Conservation Committee, 155–184.
- Collinson ME, Hooker JJ, Gröcke DR. 2003.** Cobham Lignite Bed and penecontemporaneous macrofloras of southern England: a record of vegetation and fire across the Paleocene-Eocene Thermal Maximum. In: Wing SL, Gingerich PD, Schmitz B, Thomas E, eds. *Causes and consequences of globally warm climates in the Early Paleogene*. Boulder, CO, Geological Society of America Special Paper 369, 333–349.
- Conran JG. 1997.** *Paracordyline kerguelensis*, an Oligocene monocotyledon macrofossil from the Kerguelen Islands. *Alcheringa* **21**: 129–140.
- Conran JG, Bannister JM, Lee DE. 2009a.** Earliest orchid macrofossils: early Miocene *Dendrobium* and *Earina* (Orchidaceae: Epidendroideae) from New Zealand. *American Journal of Botany* **96**: 466–474.
- Conran JG, Bannister JM, Mildenhall DC, Lee DE, Chacon J, Renner SS. 2014.** Leaf fossils of *Luzuriaga* and a monocot flower with in situ pollen of *Liliacidites contortus* Mildenh. & Bannister sp. nov. (Alstroemeriaceae) from the Early Miocene. *American Journal of Botany* **101**: 141–155.
- Conran JG, Carpenter RJ, Jordan GJ. 2009b.** Early Eocene *Ripogonum* (Liliales: Ripogonaceae) leaf macrofossils from southern Australia. *Australian Systematic Botany* **22**: 219–228.
- Conran JG, Christophel DC. 1998.** *Paracordyline aureonemoralis* (Lomandraceae): an Eocene monocotyledon from South Australia. *Alcheringa* **22**: 349–357.
- Conran JG, Christophel DC, Cunningham L. 2003.** An Eocene monocotyledon from Nelly Creek, Central Australia, with affinities to Hemerocallidaceae (Lilianaes: Asparagales). *Alcheringa* **27**: 107–115.
- Couper RA. 1953.** Upper Mesozoic and Cainozoic spores and pollen grains from New Zealand. *New Zealand Geological Survey Paleontological Bulletin* **22**: 1–77.
- Courtillot VE, Renne PR. 2003.** On the ages of flood basalt events. *Comptes Rendus Geoscience* **335**: 113–140.
- Couvreur TLP, Forest F, Baker WJ. 2011.** Origin and global diversification patterns of tropical rain forests: inferences from a complete genus-level phylogeny of palms. *BMC Biology* **9**: 44.
- Crepet WL. 1978.** Investigations of angiosperms from the Eocene of North America: an aroid inflorescence. *Review of Palaeobotany and Palynology* **25**: 241–252.
- Crepet WL, Feldman GD. 1991.** The earliest remains of grasses in the fossil record. *American Journal of Botany* **78**: 1010–1014.
- Crepet WL, Nixon KC, Gandolfo MA. 2004.** Fossil evidence and phylogeny: the age of major angiosperm clades based on mesofossil and macrofossil evidence from Cretaceous deposits. *American Journal of Botany* **91**: 1666–1682.
- Cusimano N, Bogner J, Mayo SJ, Boyce PC, Wong SY, Hesse M, Hettterscheid WLA, Keating RC, French JC. 2011.** Relationships within the Araceae: comparison of morphological patterns with molecular phylogenies. *American Journal of Botany* **98**: 654–668.
- Daghlian CP. 1981.** A review of the fossil record of monocotyledons. *Botanical Review* **47**: 517–555.
- Davis CC, Webb CO, Wurdack KJ, Jaramillo CA, Donoghue MJ. 2005.** Explosive radiation of Malpighiales supports a mid-Cretaceous origin of modern tropical rain forests. *American Naturalist* **165**: E36–E65.
- Denk T, Güner HT, Grimm GW. 2014.** From mesic to arid: leaf epidermal features suggest preadaptation in Miocene dragon trees (*Dracaena*). *Review of Palaeobotany and Palynology* **200**: 211–228.
- Dettmann ME, Clifford HT. 2000.** Monocotyledon fruits and seeds, and an associated palynoflora from Eocene–Oligocene sediments of coastal central Queensland, Australia. *Review of Palaeobotany and Palynology* **110**: 141–173.
- Dinis JL, Rey J, Cunha PP, Callapez P, Pena dos Reis R. 2008.** Stratigraphy and allogenic controls of the western Portugal Cretaceous: an updated synthesis. *Cretaceous Research* **29**: 772–780.
- Donoghue MJ, Moore BR. 2003.** Toward an integrative historical biogeography. *Integrative and Comparative Biology* **43**: 261–270.
- Dos Reis M, Yang Z. 2011.** Approximate likelihood calculation on a phylogeny for Bayesian estimation of divergence times. *Molecular Biology and Evolution* **28**: 2161–2172.
- Dos Reis M, Yang Z. 2013.** The unbearable uncertainty of Bayesian divergence time estimation. *Journal of Systematics and Evolution* **51**: 30–43.
- Doyle JA. 1973.** Fossil evidence on early evolution of the monocotyledons. *Quarterly Review of Biology* **48**: 399–413.
- Doyle JA, Endress PK. 2010.** Integrating Early Cretaceous fossils into the phylogeny of living angiosperms: Magnoliidae and eudicots. *Journal of Systematics and Evolution* **48**: 1–35.
- Doyle JA, Endress PK. 2014.** Integrating Early Cretaceous fossils into the phylogeny of living angiosperms: ANITA lines and relatives of Chloranthaceae. *International Journal of Plant Sciences* **175**: 555–600.
- Doyle JA, Endress PK, Upchurch GR. 2008.** Early Cretaceous monocots: a phylogenetic evaluation. *Acta Musei*

- Nationalis Pragae: Series B – Historia Naturalis* **64**: 59–87.
- Doyle JA, Hickey LJ. 1976.** Pollen and leaves from the mid-Cretaceous Potomac Group and their bearing on early angiosperm evolution. In: Beck CB, ed. *Origin and early evolution of angiosperms*. New York: Columbia University Press, 139–206.
- Doyle JA, Robbins EI. 1977.** Angiosperm pollen zonation of the continental Cretaceous of the Atlantic Coastal Plain and its application to deep wells in the Salisbury Embayment. *Palynology* **1**: 43–78.
- Drábková LZ. 2010.** Phylogenetic relationships within Junaceae: evidence from five regions of plastid, mitochondrial nuclear ribosomal DNA, with notes on morphology. In: Seberg O, Petersen G, Barfod AS, Davis JI, eds. *Diversity, phylogeny, and evolution in the monocotyledons*. Aarhus: Aarhus University Press, 389–416.
- Dransfield J, Uhl NW, Asmussen CB, Baker WJ, Harley MM, Lewis CE. 2008.** *Genera Palmarum: the evolution and classification of palms*. Kew: Royal Botanic Gardens.
- Drummond AJ, Ho SYW, Phillips MJ, Rambaut A. 2006.** Relaxed phylogenetics and dating with confidence. *PLoS Biology* **4**: e88.
- Edwards EJ, Osborne CP, Strömberg CAE, Smith SA; C₄ Grasses Consortium. 2010.** The origins of C₄ grasslands: integrating evolutionary and ecosystem science. *Science* **328**: 587–591.
- Eisawi A, Schrank E. 2008.** Upper Cretaceous to Neogene palynology of the Melut Basin, southeast Sudan. *Palynology* **32**: 101–129.
- Elsik WC. 1968.** Palynology of a Paleocene Rockdale Lignite, Milam County, Texas. I. Morphology and taxonomy. *Pollen et Spores* **10**: 263–314.
- Erwin DM, Stockey RA. 1989.** Permineralized monocotyledons from the Middle Eocene Princeton chert (Allenby Formation) of British Columbia: Alismataceae. *Canadian Journal of Botany* **67**: 2636–2645.
- Evanoff E, McIntosh WC, Murphey PC. 2001.** Stratigraphic summary and ⁴⁰Ar/⁶⁹Ar geochronology of the Florissant Formation, Colorado. In: Evanoff E, Gregory-Wodzicki KM, Johnson KR, eds. *Fossil flora and stratigraphy of the Florissant Formation, Colorado*. Denver: Proceedings of the Denver Museum of Nature and Science, Series 4, Number 1, 1–16.
- Fantozzi P, Kassim Mohamed A. 2002.** Geological mapping in northeastern Somalia (Midjiurtinia region): field evidence of the structural and paleogeographic evolution of the northern margin of the Somalian plate. *Journal of African Earth Sciences* **34**: 21–55.
- Fedotov VV. 1975.** On systematic assignment of the genus *Nitophyllites*. *Paleontologicheskii Zhurnal* **1**: 133–136.
- Fischer TC, Butzmann R, Meller B, Rattei T, Newman M, Hölscher D. 2009.** The morphology, systematic position and inferred biology of *Spirematospermum* – an extinct genus of Zingiberales. *Review of Palaeobotany and Palynology* **157**: 391–426.
- Fontaine WM. 1889.** *The Potomac or younger Mesozoic flora: United States Geological Survey Monograph 15*. Washington, DC: Government Printing Office.
- Franzen JL. 2005.** The implications of the numerical dating of the Messel fossil deposit (Eocene, Germany) for mammalian biochronology. *Annales de Paléontologie* **91**: 329–335.
- Freudenstein JV, van der Berg C, Goldman DH, Kores PJ, Molvray M, Chase MW. 2004.** An expanded plastid DNA phylogeny of Orchidaceae and analysis of jackknife branch support strategy. *American Journal of Botany* **91**: 149–157.
- Friis EM. 1988.** *Spirematospermum chandlerae* sp. nov., an extinct species of Zingiberaceae from the North American Cretaceous. *Tertiary Research* **9**: 7–12.
- Friis EM, Crane PR, Pedersen KR. 2011.** *Early flowers and angiosperm evolution*. Cambridge: Cambridge University Press.
- Friis EM, Pedersen KR, Crane PR. 2000.** Fossil floral structures of a basal angiosperm with monocolpate, reticulate-acolumellate pollen from the Early Cretaceous of Portugal. *Grana* **39**: 226–239.
- Friis EM, Pedersen KR, Crane PR. 2004.** Araceae from the Early Cretaceous of Portugal: evidence on the emergence of monocotyledons. *Proceedings of the National Academy of Sciences of the United States of America* **101**: 16565–16570.
- Friis EM, Pedersen KR, Crane PR. 2010.** Diversity in obscurity: fossil flowers and the early history of angiosperms. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **365**: 369–382.
- Furness CA, Rudall PJ. 2006.** Comparative structure and development of pollen and tapetum in Pandanales. *International Journal of Plant Sciences* **167**: 331–348.
- Futey MK, Gandolfo MA, Zamalao MC, Cúneo R, Cladera G. 2012.** Arecaceae fossil fruits from the Paleocene of Patagonia, Argentina. *Botanical Review* **78**: 205–234.
- Gandolfo MA, Nixon KC, Crepet WL. 2000.** Monocotyledons: a review of their Early Cretaceous record. In: Wilson KL, Morrison DA, eds. *Monocots: systematics and evolution*. Collingwood: CSIRO, 44–51.
- Gandolfo MA, Nixon KC, Crepet WL. 2002.** Triuridaceae fossil flowers from the Upper Cretaceous of New Jersey. *American Journal of Botany* **89**: 1940–1957.
- Gandolfo MA, Nixon KC, Crepet WL. 2008.** Selection of fossils for calibration of molecular dating models. *Annals of the Missouri Botanical Garden* **95**: 34–42.
- Gandolfo MA, Nixon KC, Crepet WL, Stevenson DW, Friis EM. 1998.** Oldest known fossils of monocotyledons. *Nature* **394**: 532–533.
- Gandolfo MA, Zamalao MdelC, Cúneo NR, Archangelsky A. 2009.** Potamogetonaceae fossil fruits from the Tertiary of Patagonia, Argentina. *International Journal of Plant Sciences* **170**: 419–428.
- Giret A, Lameyre J, Beaux JF, Gautier I, Verdier O, Chotin P, Cantagrel JM. 1989.** Géologie, deux siècles de recherche dans les Îles Kerguelen. In: Laubier L, ed. *Actes du Colloque sur la recherche Française dans les Terres Australes (Kerguelen, Crozet, Saint-Paul et Amsterdam) et à*

- partir des navires qui les desservent, Strasbourg 1987*. Paris: Comité National Français des Recherches Antarctiques, 345–355.
- Gohn GS, Dowsett HJ, Sohl NF. 1992.** Biostratigraphy of the Middendorf Formation (Upper Cretaceous) in a corehole at Myrtle Beach, South Carolina. *U.S. Geological Survey Bulletin* **2030**: 1–12.
- Golovneva LB. 1997.** Morphology, systematics and distribution of the genus *Haemanthophyllum* in the Paleogene floras of the Northern Hemisphere. *Paleontologicheskii Zhurnal* **31**: 197–207.
- Gómez-Navarro C, Jaramillo C, Herrera F, Wing SL, Callejas R. 2009.** Palms (Arecaceae) from a Paleocene rainforest of northern Colombia. *American Journal of Botany* **96**: 1300–1312.
- Górniak M, Paun O, Chase MW. 2010.** Phylogenetic relationships within Orchidaceae based on a low-copy nuclear coding gene, *Xdh*: congruence with organellar and nuclear ribosomal DNA results. *Molecular Phylogenetics and Evolution* **56**: 784–795.
- Graham SW, Zgurski JM, McPherson MA, Cherniawsky DM, Saarela JM, Horne EFC, Smith SY, Wong WA, O'Brien HE, Biron VL, Pires JC, Olmstead RG, Chase MW, Rai HS. 2006.** Robust inference of monocot deep phylogeny using an expanded multigene plastid data set. In: Columbus JT, Friar EA, Porter JM, Prince LM, Simpson MG, eds. *Monocots: comparative biology and evolution (excluding Poales)*. Claremont: Rancho Santa Ana Botanic Garden, 3–20.
- Grande L. 1984.** Paleontology of the Green River Formation, with a review of the fish fauna, second edition. *Geological Survey of Wyoming Bulletin* **63**: 1–333.
- Grass Phylogeny Working Group. 2001.** Phylogeny and subfamilial classification of the grasses (Poaceae). *Annals of the Missouri Botanical Garden* **88**: 373–457.
- Grass Phylogeny Working Group II. 2012.** New grass phylogeny resolves deep evolutionary relationships and discovers C_4 origins. *New Phytologist* **193**: 304–312.
- Grayum MH. 1987.** A summary of evidence and arguments supporting the removal of *Acorus* from the Araceae. *Taxon* **36**: 723–729.
- Greenwood DR, Conran JG. 2000.** The Australian Cretaceous and Tertiary monocot fossil record. In: Wilson KL, Morrison DA, eds. *Monocots: systematics and evolution*. Collingwood: CSIRO, 52–59.
- Grimsson F, Zetter R, Halbritter H, Grimm GW. 2014.** *Aponogeton* pollen from the Cretaceous and Paleogene of North America and West Greenland: implications for the origin and palaeobiogeography of the genus. *Review of Palaeobotany and Palynology* **200**: 161–187.
- Haggard KK, Tiffney BH. 1997.** The flora of the Early Miocene Brandon Lignite, Vermont, USA. VIII. *Caldesia* (Alismataceae). *American Journal of Botany* **84**: 239–252.
- van der Ham RWJM, van Konijnenburg-van Cittert JHA, Indeherde L. 2007.** Seagrass foliage from the Maastrichtian type area (Maastrichtian, Danian, NE Belgium, SE Netherlands). *Review of Palaeobotany and Palynology* **144**: 301–321.
- Harley MM. 2006.** A summary of fossil records for Arecaceae. *Botanical Journal of the Linnean Society* **151**: 39–67.
- Harley MM, Baker WJ. 2001.** Pollen aperture morphology in Arecaceae: application within phylogenetic analyses, and a summary of record of palm-like pollen. *Grana* **40**: 45–77.
- Heath TA, Huelsenbeck JP, Stadler T. 2014.** The fossilized birth–death process for coherent calibration of divergence-time estimates. *Proceedings of the National Academy of Sciences of the United States of America* **111**: E2957–E2966.
- Heimhofer H, Hochuli PA, Burla S, Weissert H. 2007.** New records of Early Cretaceous angiosperm pollen from Portuguese coastal deposits: implications for the timing of the early angiosperm radiation. *Review of Palaeobotany and Palynology* **144**: 36–76.
- Henriquez CL, Arias T, Pires JC, Croat TB, Schaal BA. 2014.** Phylogenomics of the plant family Araceae. *Molecular Phylogenetics and Evolution* **75**: 91–102.
- Herendeen PS, Crane PR. 1995.** The fossil history of the monocotyledons. In: Rudall PJ, Cribb PJ, Cutler DF, Humphries CJ, eds. *Monocotyledons: systematics and evolution*. Kew: Royal Botanic Gardens, 1–21.
- Herman AB, Kvaček J. 2010.** *Late Cretaceous Grünbach Flora of Austria*. Vienna: Naturhistorisches Museum Wien.
- Herrera FA, Jaramillo CA, Dilcher DL, Wing SL, Gómez-Navarro C. 2008.** Fossil Araceae from a Paleocene rainforest in Colombia. *American Journal of Botany* **95**: 1569–1583.
- Hesse M. 2002.** The uniquely designed pollen aperture in Lasioideae (Araceae). *Aroideana* **25**: 51–59.
- Hesse M, Zetter R. 2007.** The fossil pollen record of Araceae. *Plant Systematics and Evolution* **263**: 93–115.
- Hicks JF. 1993.** Chronostratigraphic analysis of the Foreland Basin sediments of the latest Cretaceous, Wyoming, U.S.A. Unpublished PhD Thesis, Yale University.
- Hicks JF, Johnson KR, Obradovich JD, Tauxe L, Clark D. 2002.** Magnetostratigraphy and geochronology of the Hell Creek and basal Fort Union Formations of southwestern North Dakota and a recalibration of the age of the Cretaceous–Tertiary boundary. In: Hartman JH, Johnson KR, Nichols DJ, eds. *The Hell Creek Formation and the Cretaceous–Tertiary boundary in the northern Great Plains: an integrated continental record of the end of the Cretaceous*. Boulder, CO, Geological Society of America Special Paper 361, 35–55.
- Ho SYW, Phillips MJ. 2009.** Accounting for calibration uncertainty in phylogenetic estimation of evolutionary divergence times. *Systematic Biology* **58**: 367–380.
- Hochuli PA, Heimhofer U, Weissert H. 2006.** Timing of early angiosperm radiation: recalibrating the classical succession. *Journal of the Geological Society* **163**: 587–594.
- van Hoeken-Klinkenberg PMJ. 1964.** A palynological investigation of some Upper-Cretaceous sediments in Nigeria. *Pollen et Spores* **6**: 209–231.
- Hofmann CC, Zetter R. 2010.** Upper Cretaceous sulcate pollen from the Timerdyakh Formation, Vilui Basin (Siberia). *Grana* **49**: 170–193.

- Hooker JJ, Grimes ST, Matthey DP, Collinson ME, Sheldon ND. 2009.** Refined correlations of the UK Late Eocene–Early Oligocene Solent Group and timing of its climate history. In: Koeberl C, Montanari A, eds. *The Late Eocene earth – hothouse, icehouse, and impacts*. Boulder, CO, Geological Society of America Special Paper 452, 179–195.
- Hotton CL, Leffingwell HA, Skvarla JJ. 1994.** Pollen ultrastructure of Pandanaceae and the fossil genus *Pandaniidites*. In: Kurmann MH, Doyle JA, eds. *Ultrastructure of fossil spores and pollen*. Kew: Royal Botanic Gardens, 173–191.
- Iles WJD, Lee C, Sokoloff DD, Remizowa MV, Yadav SR, Barrett MD, Barrett RL, Macfarlane TD, Rudall PJ, Graham SW. 2014.** Reconstructing the age and historical biogeography of the ancient flowering-plant family Hydatellaceae (Nymphaeales). *BMC Evolutionary Biology* **14**: 102.
- Iles WJD, Smith SY, Graham SW. 2013.** A well-supported phylogenetic framework for the monocot order Alismatales reveals multiple losses of the plastid NADH dehydrogenase complex and a strong long-branch effect. In: Wilkin P, Mayo SJ, eds. *Early events in monocot evolution*. Cambridge: Cambridge University Press, 1–28.
- Ijinskaja IA. 1963.** Fossil flora of the Mountain Kiin-Kerish of the Zaisan Basin. II. *Palaeobotanica (Komarov)* **4**: 141–187.
- IPNI Consortium. 2012.** *The International Plant Names Index*. Available at: <http://www.ipni.org/>
- Iturralde-Vinent MA, MacPhee RDE. 1996.** Age and paleogeographical origin of Dominican amber. *Science* **273**: 1850–1852.
- Jacobs BF, Judziewicz EJ, Kabuye CHS. 2014.** A Miocene pharoid grass (Poaceae: Pharoideae) from Kenya and implications for mid-Miocene paleoecology. *Paleontological Society Special Publications (10th North American Paleontological Convention Abstract Book)* **13**: 135.
- Jacobs BF, Kabuye CHS. 1987.** A middle Miocene (12.2 my old) forest in the East African Rift Valley, Kenya. *Journal of Human Evolution* **16**: 147–155.
- Jacobs BF, Kingston JD, Jacobs LL. 1999.** The origin of grass-dominated ecosystems. *Annals of the Missouri Botanical Garden* **86**: 590–643.
- Jaramillo CA, Bayona G, Pardo-Trujillo A, Rueda M, Torres V, Harrington GJ, Mora G. 2007.** The palynology of the Cerrejón Formation (Upper Paleocene) of northern Colombia. *Palynology* **31**: 153–189.
- Jarzen DM. 1978.** Some Maestrichtian palynomorphs and their phytogeographical and paleoecological implications. *Palynology* **2**: 29–38.
- Jarzen DM. 1983.** The fossil pollen record of the Pandanaceae. *Gardens. Bulletin Singapore* **36**: 163–175.
- Johnson KR. 2002.** Megafloora of the Hell Creek and lower Fort Union Formations in the western Dakotas: vegetational response to climate change, the Cretaceous-Tertiary boundary event, and rapid marine transgression. In: Hartman JH, Johnson KR, Nichols DJ, eds. *The Hell Creek Formation and the Cretaceous-Tertiary boundary in the northern Great Plains: an integrated continental record of the end of the Cretaceous*. Boulder, CO, Geological Society of America Special Paper 361, 329–391.
- Judziewicz EJ, Clark LG. 2007.** Classification and biogeography of new world grasses: Anomochloideae, Pharoideae, Ehrhartoideae, and Bambusoideae. In: Columbus JT, Friar EA, Porter JM, Prince LM, Simpson MG, eds. *Monocots: comparative biology and evolution – Poales*. Claremont: Rancho Santa Ana Botanic Garden, 303–314.
- Kar RK. 1985.** The fossil floras of Kachchh – IV. Tertiary palynostratigraphy. *Palaeobotanist* **34**: 1–279.
- Kar RK, Bhattacharya M. 1992.** Palynology of Rajpardi lignite, Cambay Basin and Gujra Dam and Akri lignite, Kutch Basin. *Palaeobotanist* **39**: 250–263.
- Knobloch E, Mai DH. 1986.** Monographie der Früchte und Samen in der Kreide von Mitteleuropa. *Rozprawy Ústředního ústavu Geologického* **47**: 1–219.
- Krassilov V. 1973.** Cuticular structure of Cretaceous angiosperms from the far east of the USSR. *Palaeontographica Abteilung B: Paläophytologie* **142**: 105–116.
- Kvaček J, Herman AB. 2004.** Monocotyledons from the early Campanian (Cretaceous) of Grünbach, Lower Austria. *Review of Palaeobotany and Palynology* **128**: 323–353.
- Kvaček Z. 1995.** *Limnobiophyllum* Krassilov – a fossil link between the Araceae and the Lemnaceae. *Aquatic Botany* **50**: 49–61.
- Larkum AWD, Orth RJ, Duarte CM. 2006.** *Seagrasses: biology, ecology and conservation*. Berlin: Springer.
- Lee DE, Conran JG, Lindqvist JK, Bannister JM, Mildenhall DC. 2012.** New Zealand Eocene, Oligocene and Miocene macrofossil and pollen records and modern plant distributions in the Southern Hemisphere. *Botanical Review* **78**: 235–260.
- Lepage T, Bryant D, Philippe H, Lartillot N. 2007.** A general comparison of relaxed molecular clock models. *Molecular Biology and Evolution* **24**: 2669–2680.
- Les DH, Cleland MA, Waycott M. 1997.** Phylogenetic studies in Alismatidae, II: evolution of marine angiosperms (seagrasses) and hydrophily. *Systematic Botany* **22**: 443–463.
- Les DH, Moody ML, Jacobs SWL. 2005.** Phylogeny and systematics of *Aponogeton* (Aponogetonaceae): the Australian species. *Systematic Botany* **30**: 503–519.
- Les DH, Moody ML, Soros CL. 2006.** A reappraisal of the phylogenetic relationships in the monocotyledon family Hydrocharitaceae (Alismatidae). In: Columbus JT, Friar EA, Porter JM, Prince LM, Simpson MG, eds. *Monocots: comparative biology and evolution (excluding Poales)*. Claremont: Rancho Santa Ana Botanic Garden, 211–230.
- Linder HP. 1987.** The evolutionary history of the Poales/Restionales: a hypothesis. *Kew Bulletin* **42**: 297–318.
- Linder HP, Ferguson IK. 1985.** On the pollen morphology and phylogeny Restionales and Poales. *Grana* **24**: 65–76.
- Lindqvist JK, Lee DE. 2009.** High-frequency paleoclimate signals from Foulden Maar, Waipiata Volcanic Field, southern New Zealand: an Early Miocene varved lacustrine diatomite deposit. *Sedimentary Geology* **222**: 98–110.
- Lucas SG, Bray ES, Emry RJ, Hirsch KF. 2012.** Dinosaur eggshell and the Cretaceous–Paleogene boundary in the

- Zaysan Basin, eastern Kazakstan. *Journal of Stratigraphy* **36**: 417–435.
- Lumbert SH, den Hartog C, Phillips RC, Olsen FS. 1984.** The occurrence of fossil seagrasses in the Avon Park Formation (Late Middle Eocene), Levy County, Florida (U.S.A.). *Aquatic Botany* **20**: 121–129.
- MacGinitie HD. 1953.** *Fossil plants of the Florissant Beds, Colorado*. Washington, DC: Carnegie Institution of Washington Publication 599.
- Maciunas E, Conran JG, Bannister JM, Paull R, Lee DE. 2011.** Miocene *Astelia* (Asparagales: Asteliaceae) macrofossil from southern New Zealand. *Australian Systematic Botany* **24**: 19–31.
- Macphail MK. 1999.** Palynostratigraphy of the Murray Basin, inland southeastern Australia. *Palynology* **23**: 197–240.
- Macphail MK, Alley NF, Truswell EM, Sluiter IRK. 1994.** Early Tertiary vegetation: evidence from spores and pollen. In: Hill RS, ed. *History of the Australian vegetation: Cretaceous to recent*. Cambridge: Cambridge University Press, 189–261.
- Magallón S, Sanderson MJ. 2001.** Absolute diversification rates in angiosperm clades. *Evolution* **55**: 1762–1780.
- Magallón SA. 2004.** Dating lineages: molecular and paleontological approaches to the temporal framework of clades. *International Journal of Plant Sciences* **165**: S7–S21.
- Mai DH. 2000.** The middle and upper miocene floras of Meuro and Rauno sequences in the Lusatica region. Part I: water ferns, conifers, monocotyledons. *Palaeontographica Abteilung B: Paläophytologie* **256**: 1–68.
- Manchester SR. 2001.** Update on the megafossil flora of Florissant, Colorado. *Denver Museum of Nature and Science* **4**: 137–216.
- Manchester SR, O'Leary EL. 2010.** Phylogenetic distribution and identification of fin-winged fruits. *Botanical Review* **76**: 1–82.
- Marshall CR. 2008.** A simple method for bracketing absolute divergence times on molecular phylogenies using multiple fossil calibration points. *American Naturalist* **171**: 726–742.
- Massoni J, Doyle JA, Sauquet H. 2014.** Fossil calibration of Magnoliidae, an ancient lineage of angiosperms. *Palaeontologia Electronica* **17.3**: 2FC.
- Mayo SJ, Bogner J, Boyce PC. 1997.** *The genera of Araceae*. Kew: Royal Botanic Gardens.
- Mehrotra RC. 1987.** Some new palm fruits from the Deccan Intertrappean beds of Mandla District, Madhya Pradesh. *Geophytology* **17**: 204–208.
- Mennes CB, Smets EF, Moses SN, Merckx VSFT. 2013.** New insights in the long-debated evolutionary history of Triuridaceae (Pandanales). *Molecular Phylogenetics and Evolution* **69**: 994–1004.
- Mertz DE, Renne PR. 2005.** A numerical age for the Messel fossil deposit (UNESCO World Heritage Site) derived from $^{40}\text{Ar}/^{39}\text{Ar}$ dating on a basaltic rock fragment. *Courier Forschungsintitut Senckenberg* **255**: 67–75.
- Miller JA. 1986.** Hydrogeologic framework of the Floridan Aquifer System in Florida and in parts of Georgia, Alabama, and South Carolina. *US Geological Survey Professional Paper* **1403-B**: B1–B91.
- Mitra M, Mickle JE. 2007.** Palynological age assessment of localities (Tar Heel Formation) in North Carolina. *Journal of the North Carolina Academy of Science* **123**: 60–64.
- Muller J. 1981.** Fossil pollen records of extant angiosperms. *Botanical Review* **47**: 1–142.
- Nambudiri EMV, Tidwell WD, Smith BN, Hebbert NP. 1978.** A C4 plant from the Pliocene. *Nature* **276**: 816–817.
- Nauheimer L, Metzler D, Renner SS. 2012.** Global history of the ancient monocot family Araceae inferred with models accounting for past continental positions and previous ranges based on fossils. *New Phytologist* **195**: 938–950.
- Neubig KM, Whitten WM, Carlswald BS, Blanco MA, Endara L, Williams NH, Moore M. 2008.** Phylogenetic utility of *ycf1* in orchids: a plastid gene more variable than *matK*. *Plant Systematics and Evolution* **277**: 75–84.
- Nichols DJ. 1987.** Palynology of the Vermillion Creek coal bed and associated strata. In: Roehler HW, Martin PL, eds. *Geological investigations of the Vermillion Creek coal bed in the Eocene Niland Tongue of the Wasatch Formation, Sweetwater County, Wyoming: U.S. Geological Survey Professional paper 1314A-L*. Washington: United States Government Printing Office, 47–73.
- Noon TA. 1980.** Stratigraphic drilling report GSQ Rockhampton 1. *Queensland Government Mining Journal* **81**: 261–266.
- Nowak MD, Smith AB, Simpson C, Zwickl DJ. 2013.** A simple method for estimating informative node age priors for the fossil calibration of molecular divergence time analyses. *PLoS ONE* **8**: e66245.
- Owens JP, Sohl NF. 1989.** *Carolina Geological Society field trip guidebook: October 28–29, 1989: Campanian and Maastriichtian depositional systems of the Black Creek Group of the Carolinas*. Raleigh, NC: North Carolina Geological Survey.
- Pan AD. 2010.** Rutaceae leaf fossils from the Late Oligocene (27.23 Ma) Guang River flora of northwestern Ethiopia. *Review of Palaeobotany and Palynology* **159**: 188–194.
- Pan AD, Jacobs BF, Currano ED. 2014.** Dioscoreaceae fossils from the late Oligocene and early Miocene of Ethiopia. *Botanical Journal of the Linnean Society* **175**: 17–28.
- Pan AD, Jacobs BF, Dransfield J, Baker WJ. 2006.** The fossil history of palms (Arecaceae) in Africa and new records from the Late Oligocene (28–27 Mya) of north-western Ethiopia. *Botanical Journal of the Linnean Society* **151**: 69–81.
- Paradis E. 2013.** Molecular dating of phylogenies by likelihood methods: a comparison of models and a new information criterion. *Molecular Phylogenetics and Evolution* **67**: 436–444.
- Parham JF, Donoghue PCJ, Bell CJ, Calway TD, Head JJ, Holroyd PA, Inoue JG, Irmis RB, Joyce WG, Ksepka DT, Patané JSL, Smith ND, Tarver JE, van Tuinen M, Yang Z, Angielczyk KD, Greenwood JM, Hipsley CA, Jacobs L, Makovicky PJ, Müller J, Smith KT, Theodor JM, Warnock RCM, Benton MJ. 2012.** Best practices for justifying fossil calibrations. *Systematic Biology* **61**: 346–359.

- Parham JF, Irmis RB. 2008.** Caveats on the use of fossil calibrations for molecular dating: a comment on Near *et al.* *American Naturalist* **171**: 132–136.
- Patil GV, Upadhye EV. 1984.** *Cocos* like fruit from the Mahgaonkalan and its significance towards the stratigraphy of the Mahgaonkalan Intertrappean Beds. In: Sharma AK, Mitra GC, Banerjee M, eds. *Proceedings of the symposium on evolutionary botany and biostratigraphy*. New Delhi: Today & Tomorrows Printers and Publishers, 541–554.
- Perkins ME, Brown FH, Nash WP, Williams SK, McIntosh W. 1998.** Sequence, age, and source of silicic fallout tuffs in middle to late Miocene basins of the northern Basin and Range province. *Geological Society of America Bulletin* **110**: 344–360.
- Piperno DR. 2006.** *Phytoliths: a comprehensive guide for archaeologists and paleoecologists*. Lanham: Altamira Press.
- Pirie MD, Doyle JA. 2013.** Dating clades with fossils and molecules: the case of Annonaceae. *Botanical Journal of the Linnean Society* **169**: 84–116.
- Pocknall DT, Mildenhall DC. 1984.** Late Oligocene-early Miocene spores and pollen from Southland, New Zealand. *New Zealand Geological Survey Paleontological Bulletin* **51**: 5–58.
- Poinar G. 2011.** Silica bodies in the Early Cretaceous *Programinis laminatus* (Angiospermae: Poales). *Palaeodiversity* **4**: 1–6.
- Poinar G, Columbus JT. 2013.** *Alarista succina* gen. et sp. nov. (Poaceae: Bambusoideae) in Dominican amber. *Historical Biology* **25**: 691–696.
- Poinar G, Judziewicz EJ. 2005.** *Pharus primuncinatus* (Poaceae: Pharoideae: Phareae) from Dominican amber. *Sida* **21**: 2095–2103.
- Poinar GO, Columbus JT. 1992.** Adhesive grass spikelet with mammalian hair in Dominican amber: first fossil evidence of epizoochory. *Experientia* **48**: 906–908.
- Pole M. 2007a.** Early Eocene dispersed cuticles and mangrove to rainforest vegetation at Strahan-Regatta Point, Tasmania. *Palaeontologia Electronica* **10**: 16A.
- Pole M. 2007b.** Monocot macrofossil from the Miocene of southern New Zealand. *Palaeontologia Electronica* **10**: 15A.
- Prasad V, Strömberg CAE, Alimohammadian H, Sahni A. 2005.** Dinosaur coprolites and the early evolution of grasses and grazers. *Science* **310**: 1177–1180.
- Prasad V, Strömberg CAE, Leaché AD, Samant B, Patnaik R, Tang L, Mohabey DM, Ge S, Sahni A. 2011.** Late Cretaceous origin of the rice tribe provides evidence for early diversification in Poaceae. *Nature Communications* **2**: 480.
- Prychid CJ, Rudall PJ, Gregory M. 2004.** Systematics and biology of silica bodies in monocotyledons. *Botanical Review* **69**: 377–440.
- Ramírez SR, Gravendeel B, Singer RB, Marshall CR, Pierce NE. 2007.** Dating the origin of the Orchidaceae from a fossil orchid with its pollinator. *Nature* **448**: 1042–1045.
- Riley MG, Stockey RA. 2004.** *Cardstonia tolmarii* gen. et sp. nov. (Limnocharitaceae) from the Upper Cretaceous of Alberta, Canada. *International Journal of Plant Sciences* **165**: 897–916.
- Romaschenko K, Peterson PM, Soreng RJ, Garcia-Jacas N, Susanna A. 2010.** Phylogenetics of Stipeae (Poaceae: Poideae) based on plastid and nuclear DNA sequences. In: Seberg O, Petersen G, Barfod AS, Davis JI, eds. *Diversity, phylogeny and evolution in the monocotyledons*. Aarhus: Aarhus University Press, 511–537.
- Rudall PJ. 2003.** Monocot pseudanthia revisited: floral structure of the mycoheterotrophic family Triuridaceae. *International Journal of Plant Sciences* **164**: S307–S320.
- Rutschmann F. 2006.** Molecular dating of phylogenetic trees: a brief review of current methods that estimate divergence times. *Diversity and Distributions* **12**: 35–48.
- Saarela JM, Graham SW. 2010.** Inference of phylogenetic relationships among the subfamilies of grasses (Poaceae: Poales) using meso-scale exemplar-based sampling of the plastid genome. *Botany* **88**: 65–84.
- Sabaj Pérez MH. 2013.** *Standard symbolic codes for institutional resource collections in herpetology and ichthyology: an online reference version 4.0*. Washington, DC: American Society of Ichthyologists and Herpetologists, available at: <http://www.asih.org/>
- Sanderson MJ. 1997.** A nonparametric approach to estimating divergence times in the absence of rate constancy. *Molecular Biology and Evolution* **14**: 1218–1231.
- Sanderson MJ. 2003.** r8s: inferring absolute rates of molecular evolution and divergence times in the absence of a molecular clock. *Bioinformatics* **19**: 301–302.
- Sanderson MJ, Doyle JA. 2001.** Sources of error and confidence intervals in estimating the age of angiosperms from *rbcl* and 18S rDNA data. *American Journal of Botany* **88**: 1499–1516.
- Saraswati PK, Sarkar U, Banerjee S. 2012.** *Nummulites solitarius* – *Nummulites burdigalensis* lineage in Kutch with remarks on the age of Naredi Formation. *Journal of the Geological Society of India* **79**: 476–482.
- Sauquet H. 2013.** A practical guide to molecular dating. *Comptes Rendus Palevol* **12**: 355–367.
- Sauquet H, Ho SYW, Gandolfo MA, Jordan GJ, Wilf P, Cantrill DJ, Bayly MJ, Bromham L, Brown GK, Carpenter RJ, Lee DM, Murphy DJ, Sniderman JMK, Udovicic F. 2012.** Testing the impact of calibration on molecular divergence times using a fossil-rich group: the case of *Nothofagus* (Fagales). *Systematic Biology* **61**: 289–313.
- Schrank E. 1994.** Palynology of the Yesomma Formation in northern Somalia: a study of pollen, spores and associated phytoplankton from the Late Cretaceous Palmae Province. *Palaeontographica Abteilung B: Paläophytologie* **231**: 63–112.
- Seberg O, Petersen G, Davis JI, Pires JC, Stevenson DW, Chase MW, Fay MF, Devey DS, Jørgensen T, Sytsma KJ, Pillon Y. 2012.** Phylogeny of the Asparagales based on three plastid and two mitochondrial genes. *American Journal of Botany* **99**: 875–889.
- Shi G, Grimaldi DA, Harlow GE, Wang J, Wang J, Yang M, Lei W, Li Q, Li X. 2012.** Age constraint on Burmese amber based on U–Pb dating of zircons. *Cretaceous Research* **37**: 155–163.

- Shukla A, Mehrotra RC, Guleria JS. 2012.** *Cocos sahnii* Kaul: a *Cocos nucifera* L.-like fruit from the Early Eocene rainforest of Rajasthan, western India. *Journal of Biosciences* **37**: 769–776.
- Sille NP, Collinson ME, Kucera M, Hooker JJ. 2006.** Morphological evolution of *Stratiotes* through the Paleogene in England: an example of microevolution in flowering plants. *Palaios* **21**: 272–288.
- Simpson DA, Muasya AM, Alves MV, Bruhl JJ, Dhooge S, Chase MW, Furness CA, Ghamkhar K, Goetghebeur P, Hodkinson TR, Marchant AD, Reznicek AA, Nieuwborg R, Roalson EH, Smets E, Starr JR, Thomas WW, Wilson KL, Zhang X. 2006.** Phylogeny of Cyperaceae based on DNA sequence data – a new *rbcL* analysis. In: Columbus JT, Friar EA, Porter JM, Prince LM, Simpson MG, eds. *Monocots: comparative biology and evolution (excluding Poales)*. Claremont: Rancho Santa Ana Botanic Garden, 72–83.
- Smith ME, Carroll AR, Singer BS. 2008a.** Synoptic reconstruction of a major ancient lake system: Eocene Green River Formation, western United States. *Geological Society of America Bulletin* **120**: 54–84.
- Smith SY. 2013.** The fossil record of non-commelinid monocots. In: Wilkin P, Mayo SJ, eds. *Early events in monocot evolution*. Cambridge: Cambridge University Press, 29–59.
- Smith SY, Collinson ME, Rudall PJ. 2008b.** Fossil *Cyclanthus* (Cyclanthaceae, Pandanales) from the Eocene of Germany and England. *American Journal of Botany* **95**: 688–699.
- Smith SY, Collinson ME, Rudall PJ, Simpson DA. 2010.** Cretaceous and Paleogene fossil record of Poales: review and current research. In: Seberg O, Petersen G, Barfod AS, Davis JI, eds. *Diversity, phylogeny and evolution in the monocotyledons*. Aarhus: Aarhus University Press, 333–356.
- Smith SY, Collinson ME, Simpson DA, Rudall PJ, Marone F, Stampanoni M. 2009.** Elucidating the affinities and habitat of ancient, widespread Cyperaceae: *Volkeria messelensis* gen. et sp. nov., a fossil mapanioid sedge from the Eocene of Europe. *American Journal of Botany* **96**: 1506–1518.
- Smith SY, Stockey RA. 2003.** Aroid seeds from the Middle Eocene Princeton Chert (*Keratoperma allenbyense*, Araceae): comparisons with extant Lasioideae. *International Journal of Plant Sciences* **164**: 239–250.
- Sohl NF, Owens JP. 1991.** Cretaceous stratigraphy of the Carolina coastal plain. In: Horton JW, Zullo VA, eds. *The geology of the Carolinas: Carolina Geological Society, 50th anniversary volume*. Knoxville: University of Tennessee Press, 191–220.
- Steele PR, Hertweck KL, Mayfield D, McKain MR, Leebens-Mack J, Pires JC. 2012.** Quality and quantity of data recovered from massively parallel sequencing: examples in Asparagales and Poaceae. *American Journal of Botany* **99**: 330–348.
- Stevens PF. 2001+.** *Angiosperm Phylogeny Website, version 12, July 2012 (and more or less continuously updated since)*. Available at: <http://www.mobot.org/MOBOT/research/APweb/>
- Stevenson DW, Loconte H. 1995.** Cladistic analysis of monocot families. In: Rudall PJ, Cribb PJ, Cutler DF, Humphries CJ, eds. *Monocotyledons: systematics and evolution*. Kew: Royal Botanic Gardens, 543–578.
- Stockey RA. 2006.** The fossil record of basal monocots. In: Columbus JT, Friar EA, Porter JM, Prince LM, Simpson MG, eds. *Monocots: comparative biology and evolution (excluding Poales)*. Claremont: Rancho Santa Ana Botanic Garden, 91–106.
- Stockey RA, Hoffman GL, Rothwell GW. 1997.** The fossil monocot *Limnobiophyllum scutatum*: resolving the phylogeny of Lemnaceae. *American Journal of Botany* **84**: 355–368.
- Stockey RA, Rothwell GW, Johnson KR. 2007.** *Cobbania corrugata* gen. et. comb. nov. (Araceae): a floating aquatic from the Upper Cretaceous of Western North America. *American Journal of Botany* **94**: 609–624.
- Stover LE, Partridge AD. 1973.** Tertiary and Late Cretaceous spores and pollen from the Gippsland Basin, southeastern Australia. *Proceedings of the Royal Society of Victoria* **285**: 237–286.
- Strömberg CAE. 2004.** Using phytolith assemblages to reconstruct the origin and spread of grass-dominated habitats in the great plains of North America during the late Eocene to early Miocene. *Palaeogeography, Palaeoclimatology, Palaeoecology* **207**: 239–275.
- Strömberg CAE. 2005.** Decoupled taxonomic radiation and ecological expansion of open-habitat grasses in the Cenozoic of North America. *Proceedings of the National Academy of Sciences of the United States of America* **102**: 11980–11984.
- Strömberg CAE. 2011.** Evolution of grasses and grassland ecosystems. *Annual Review of Earth and Planetary Sciences* **39**: 517–544.
- Strömberg CAE, Dunn RE, Madden RH, Kohn MJ, Carlini AA. 2013.** Decoupling the spread of grasslands from the evolution of grazer-type herbivores in South America. *Nature Communications* **4**: 1478.
- Strömberg CAE, Werdelin L, Friis EM, Saraç G. 2007.** The spread of grass-dominated habitats in Turkey and surrounding areas during the Cenozoic: phytolith evidence. *Palaeogeography, Palaeoclimatology, Palaeoecology* **250**: 18–49.
- Sutherland FL, Stubbs D, Green DC. 1977.** K–Ar ages of Cainozoic volcanic suites, Bowen-St Lawrence Hinterland, North Queensland (with some implications for petrologic models). *Journal of the Geological Society of Australia* **24**: 447–460.
- Sweet AR. 1985.** The Cretaceous–Tertiary boundary in the central Alberta Foothills. II: miospore and pollen taxonomy. *Canadian Journal of Earth Sciences* **23**: 1375–1388.
- Thiers B. Continuously updated.** Index Herbariorum: a global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. Available at: <http://sweetgum.nybg.org/ih/>
- Tidwell WD, Parker LR. 1990.** *Protoyucca shadishii* gen. et sp. nov., an arborescent monocotyledon with secondary growth from the middle Miocene of northwestern Nevada, U.S.A. *Review of Palaeobotany and Palynology* **62**: 79–95.

- Tiffney BH. 1994.** Re-evaluation of the age of the Brandon Lignite (Vermont, USA) based on plant megafossils. *Review of Palaeobotany and Palynology* **82**: 299–315.
- Traverse A. 1994.** Palynofloral geochronology of the Brandon Lignite of Vermont, USA. *Review of Palaeobotany and Palynology* **82**: 265–297.
- Tripathi RP, Mishra SN, Sharma BD. 1999.** *Cocos nucifera* like petrified fruit from the Tertiary of Markantak, M. P., India. *Palaeobotanist* **48**: 251–255.
- Truswell EM. 1997.** Palynomorph assemblages from marine Eocene sediments on the west Tasmanian continental margin and the South Tasman Rise. *Australian Journal of Earth Sciences* **44**: 633–654.
- Vicentini A, Barber JC, Aliscioni SS, Giussani LM, Kellogg EA. 2008.** The age of the grasses and clusters of origins of C₄ photosynthesis. *Global Change Biology* **14**: 2963–2977.
- Walker JW, Walker AG. 1984.** Ultrastructure of Lower Cretaceous angiosperm pollen and the origin and early evolution of flowering plants. *Annals of the Missouri Botanical Garden* **71**: 464–521.
- Walther H. 1974.** Ergänzung zur Flora von Seifhennersdorf/Sachsen. II. Teil. *Abhandlungen des Staatlichen Museums für Mineralogie und Geologie zu Dresden* **21**: 143–185.
- Walther H, Kvaček Z. 2007.** Early Oligocene Flora of Seifhennersdorf (Saxony). *Acta Musei Nationalis Pragae: Series B – Historia Naturalis* **63**: 85–174.
- Whistler DP, Tedford RH, Takeuchi GT, Wang X, Tseng ZJ, Perkins ME. 2009.** Revised Miocene biostratigraphy and biochronology of the Dove Spring Formation, Mojave Desert, California. In: Albright LB, ed. *Papers on geology, vertebrate paleontology, and biostratigraphy in honor of Michael O. Woodburne*. Flagstaff, AZ, Museum of Northern Arizona Bulletin 65, 331–362.
- Wilde V, Kvaček Z, Bogner J. 2005.** Fossil leaves of the Araceae from the European Eocene and notes on other aroid fossils. *International Journal of Plant Sciences* **166**: 157–183.
- Wilkin P, Schols P, Chase MW, Chayamarit K, Furness CA, Huysmans S, Rakotonasolo F, Smets E, Thapayai C. 2005.** A plastid gene phylogeny of the yam genus, *Dioscorea*: roots, fruits and Madagascar. *Systematic Botany* **30**: 736–749.
- Wilkinson RD, Steiper ME, Soligo C, Martin RD, Yang Z, Tavaré S. 2011.** Dating primate divergences through an integrated analysis of palaeontological and molecular data. *Systematic Biology* **60**: 16–31.
- Yang Z, Rannala B. 2006.** Bayesian estimation of species divergence times under a molecular clock using multiple fossil calibrations with soft bounds. *Molecular Biology and Evolution* **23**: 212–226.
- Zanne AE, Tank DC, Cornwell WK, Eastman JM, Smith SA, FitzJohn RG, McGlenn DJ, O'Meara BC, Moles AT, Reich PB, Royer DL, Soltis DE, Stevens PF, Westoby M, Wright IJ, Aarssen L, Bertin RI, Calaminus A, Govaerts R, Hemmings F, Leishman MR, Oleksyn J, Soltis PS, Swenson NG, Warman L, Beaulieu JM. 2014.** Three keys to the radiation of angiosperms into freezing environments. *Nature* **506**: 89–92.
- Zetter R, Hesse M, Frosch-Radivo A. 2001.** Early Eocene zona-aperturate pollen grains of the *Proxapertites* type with affinity to Araceae. *Review of Palaeobotany and Palynology* **117**: 267–279.
- Zhao LC, Collinson ME, Li CS. 2004.** Fruits and seeds of *Ruppia* (Potamogetonaceae) from the Pliocene of Yushe Basin, Shanxi, northern China and their ecological implications. *Botanical Journal of the Linnean Society* **145**: 317–329.
- Zucol AF, Brea M, Bellosi ES. 2010.** Phytolith studies in Gran Barranca (central Patagonia, Argentina): the middle-late Eocene. In: Madden RH, Carlini AA, Vucetich MG, Kay RF, eds. *The paleontology of Gran Barranca: evolution and environmental change through the Middle Cenozoic of Patagonia*. Cambridge: Cambridge University Press, 317–340.