



Global biogeography and diversification of palms sheds light on the evolution of tropical lineages. I. Historical biogeography

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ABSTRACT

Aim Palms (Arecaceae/Palmae) are a model group for evolutionary studies in the tropics. Family-wide data on taxonomy, phylogenetics and distribution are now available, but a general framework of palm evolution is still lacking. The overall aim of this study, published in two companion papers, is to seek evolutionary explanations for the geographical distribution of palm lineages and species diversity patterns at global and regional levels. In this first paper we undertake a detailed analysis of palm biogeography for all major lineages in a global context, comparing our results to the fossil record, molecular dating studies and previously established biogeographical hypotheses for the family.

Location Global.

Methods A dated phylogeny of all palm genera and distributional data were used to infer ancestral areas. A global model of area evolution for tropical lineages was formulated and ancestral areas were reconstructed using a maximum likelihood approach under the dispersal–extinction–cladogenesis model.

Results The crown node divergence of palms and divergences of all five subfamilies occurred before the end of the Cretaceous within Laurasian regions. Early range expansions into South America took place in the stem lineages of subfamilies Arecoideae and Ceroxyloideae, and into Africa and South America in Cretaceous lineages within subfamily Calamoideae. The largest subfamily Arecoideae underwent its early diversification history in South America and has been an important source of lineages expanding into other regions, notably in the major Indo-Pacific tribe Areceae. In contrast, the history of subfamily Coryphoideae was primarily Laurasian, supporting earlier boreotropical hypotheses for the group. Dispersals across Wallace's Line are prevalent in major groups of Arecoideae, Calamoideae and Coryphoideae, both before and after the Miocene geological evolution of the Malesian Archipelago.

Main conclusions We present the first robust biogeographical hypothesis for the evolution of palms in space and time. Although palms show evidence of dispersal limitation, our findings highlight the role of long-distance dispersal events in the establishment of major biogeographical patterns of palm clades. This is consistent with the growing evidence for long-distance dispersal as a major mechanism underpinning the distribution of tropical lineages.

Keywords

Ancestral area reconstruction, Arecaceae, boreotropical hypothesis, historical biogeography, molecular dating, Palmae, tropical rain forests.

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INTRODUCTION

Palms (Arecaceae/Palmae) are a model plant family for evolutionary and ecological studies in the tropics (Svenning *et al.*, 2008; Couvreur *et al.*, 2011a; Kissling *et al.*, 2012a). They are distributed throughout tropical and subtropical regions, with the majority of the family's *c.* 2400 species restricted to the tropical rain forest biome (Couvreur *et al.*, 2011a) due to functional constraints in their structural biology that limit their presence in cooler and more arid areas (Tomlinson, 2006; Kissling *et al.*, 2012a). They display high species richness at a range of spatial scales (Eiserhardt *et al.*, 2011a), and often function as keystone species, providing ecosystem services (Fadini *et al.*, 2009) and shaping their environment (Peters *et al.*, 2004). Unrivalled data resources are now available for comparative research on palms: a complete species checklist of the family (Govaerts & Dransfield, 2005), a family-wide phylogeny of all genera (Baker *et al.*, 2009), a comprehensive, genus-level family monograph (Dransfield *et al.*, 2008) and an extensive, well-documented fossil record dating back to the Late Cretaceous (Harley & Baker, 2001; Harley, 2006; Dransfield *et al.*, 2008). With these resources, fundamental questions may be addressed concerning the origin and diversification history of the family and, using palms as a model, their implications for the evolution of tropical lineages in general.

Previous palm biogeographical analyses were based primarily on distribution patterns and hypotheses of primitive morphological character states (Moore & Uhl, 1982). The extensive fossil record for palms, which dates back to the Turonian (89.0–93.5 Ma; Crié, 1892; Kvacek & Herman, 2004), has been highly influential in these respects. Three major biogeographical hypotheses have been erected for palms. First, the West Gondwana hypothesis was proposed by Moore (1973a) who regarded the distribution of the 'major groups of palms' (Moore, 1973b) in South America and Africa, specifically those he considered primitive, to be evidence for an origin of palms on the two continents while they were still in contact at the Jurassic/Cretaceous boundary. He proposed that palms then invaded Laurasia and dispersed westwards into North America and eastwards into Asia and Australasia. Austral routes via Antarctica were also thought by Moore (1973a) to have potentially played a role. Second, Uhl & Dransfield (1987) suggested that the abundance of apocarpous palms (bearing flowers with free carpels), presumed to be primitive within the family, in the Northern Hemisphere would support a hypothesis of a Laurasian origin. Third, Uhl & Dransfield (1987) also proposed an alternative in which the widespread distribution in Northern and Southern Hemispheres by the Eocene of fossil coryphoid palms, considered in their classification as the most primitive subfamily, was consistent with an origin at a time when Laurasia and Gondwana remained in contact in Pangea, followed by early diversification in each supercontinent.

In their analysis of palm evolutionary origins, Couvreur *et al.* (2011a) provided evidence that the extant lineages of

palms (i.e. the crown node) diversified initially in Laurasia towards the end of the Early Cretaceous around the Albian–Cenomanian boundary *c.* 100 Ma. This is congruent with the earliest unequivocal palm fossils, which are reported from the Cretaceous of Europe and North America (Dransfield *et al.*, 2008; Couvreur *et al.*, 2011a). The Northern Hemisphere mid-Cretaceous origin of palms post-dates the separation of most of the major component landmasses of Laurasia and Gondwana (Smith *et al.*, 1994), adding to the mounting evidence that dispersal, in contrast to Gondwanan vicariance (Moore, 1973a; Raven & Axelrod, 1974), is a major mechanism behind the pantropical distribution of certain tropical rain forest plant families (Kress & Specht, 2006; Muellner *et al.*, 2006; Bartish *et al.*, 2011; Buerki *et al.*, 2011; Couvreur *et al.*, 2011b). To date, formal biogeographical studies of palms have been undertaken only at the subfamily (Trénel *et al.*, 2007) or lower taxonomic levels (Gunn, 2004; Savolainen *et al.*, 2006; Cuenca *et al.*, 2008; Meerow *et al.*, 2009; Crisp *et al.*, 2010; Roncal *et al.*, 2010, 2011; Eiserhardt *et al.*, 2011b; Bacon *et al.*, 2012), providing limited insights into global biogeographical patterns of the family as whole. Thus, although the origins of the family are now better understood (Couvreur *et al.*, 2011a), the means by which palms achieved their present-day global distribution remain poorly explored.

Here, in two companion papers (see also Baker & Couvreur, 2012a), we build upon the study of Couvreur *et al.* (2011a) to provide an in-depth analysis of the spatial and temporal diversification of this archetypal tropical lineage. In this paper we provide the first detailed analysis of the historical biogeography of palms based on molecular dating and ancestral area reconstruction (AAR) methods as a foundation for regional biogeographical and diversification studies presented in the second paper (Baker & Couvreur, 2012a). We evaluate our results in the light of existing biogeographical literature and the fossil record to present a hypothesis for the evolution of palms in space and time.

MATERIALS AND METHODS

Dated molecular phylogeny of palms

We used the chronogram published by Couvreur *et al.* (2011a), which was based upon the complete genus-level supertree of palms of Baker *et al.* (2009) and calibrated with four fossils chosen following recent reviews of the fossil record across the family (Harley & Baker, 2001; Harley, 2006; Dransfield *et al.*, 2008). The stem node of palms was constrained by a uniform prior ranging from 110 to 120 Ma, which corresponds to the earliest reported monocot fossil (Friis *et al.*, 2004). The analysis was undertaken using a relaxed clock with uncorrelated rates as implemented in BEAST 1.5.3 (Drummond & Rambaut, 2007). Exponential prior distributions were used for each fossil calibration with the soft upper bound representing the possibility of older occurrences associated to each fossil (the mean of the exponential distribution). Choosing and quantifying prior

distributions (e.g. exponential, lognormal) is a difficult task and no clear cut solution exists. However, in the case of fossil evidence the exponential prior distribution is generally preferred because it assigns a minimum hard bound, implying that the node in question cannot be younger than the age of the fossil (Ho & Phillips, 2009). See Couvreur *et al.* (2011a) for full details on the molecular dating method, parameters used for the analysis and information about the fossils used.

Ancestral area reconstruction

To estimate ancestral areas, we used the maximum likelihood dispersal–extinction–cladogenesis (DEC) method (Ree *et al.*, 2005; Ree & Smith, 2008a) as implemented in the software LAGRANGE build 20091004 (Ree & Smith, 2008b). First, we defined seven geographical areas (Fig. 1; Couvreur *et al.*, 2011a) — A: South America, B: North America (including Central America and the Caribbean), C: Africa (including Arabia), D: Indian Ocean Islands, including Madagascar, E: India (including Sri Lanka), F: Eurasia (to Wallace’s Line, including Andaman and Nicobar islands) and G: the Pacific (including areas east of Wallace’s Line and Australia). Genera were assigned to one or more geographical areas based on extensive knowledge of palm genus distributions (Dransfield *et al.*, 2008). The widespread genus *Cocos*, the distribution of which has been substantially altered by humans, was assigned to area A, on account of it being nested among other South American genera (Meerow *et al.*, 2009). We conducted two separate LAGRANGE analyses, each incorporating a different model of dispersal probability between regions (see Appendix S1 in Supporting Information). The unconstrained (null) model (M_0) permitted an equal probability of dispersal between all areas at any time. In contrast, the constrained model (M_1) specified five discrete time frames within which dispersal probabilities between areas were scaled to reflect changing dispersal opportunities over time (very low or no dispersal = 0.01, low dispersal = 0.25, medium dispersal = 0.5, high dispersal = 0.75, areas adjacent or very close = 1; see Appendix S1 for full details of these models and justification of the values selected). Finally, because of the global scale of this analysis, we assumed that ancestral areas could not occur in more than two areas and constrained the analyses accordingly (Ree & Smith, 2008a). The best fitting results were chosen for interpretation by comparing the likelihoods at the root of each tree.

Biogeographical events within palms were inferred by comparing ancestral areas reconstructed by LAGRANGE at adjacent nodes (Ree & Smith, 2008a; Buerki *et al.*, 2011). Because relationships among species within genera were not reconstructed in the supertree of Baker *et al.* (2009), AARs could not be estimated within genera. As a result, only biogeographical events above the genus level were inferred. For example, the dispersal of *Raphia* from its inferred ancestral area (AC) to its present distribution (ABC) is not represented.

RESULTS

Dated molecular phylogeny of palms

Our results provide divergence estimates for all palm clades (Fig. 1, Table 1) and genera (Appendices S2 & S3). The raw dated tree file may be downloaded from the Dryad data repository (doi:10.5061/dryad.vb25b35j). Stem and crown node ages (with respective 95% highest probability densities, HPD) for all subfamilies, tribes and subtribes are given in Table 1. Ages for genera are provided in Appendix S3. The ages reported here are to be treated as minimum age estimations, as is usual when using fossil data to calibrate the tree. In this article, although we report the mean age estimates and their 95% confidence intervals, we restrict our interpretation to broad geologically defined time frames (e.g. Maastrichtian for an age estimate of 74 Ma). By doing so, our conclusions about the global biogeographical history of palms implicitly take into account that clade ages may be older. We also note that the ages obtained in the analyses fit well with the known fossil record of palms (Dransfield *et al.*, 2008; Couvreur *et al.*, 2011a), suggesting that greatly older ages are unlikely to be inferred.

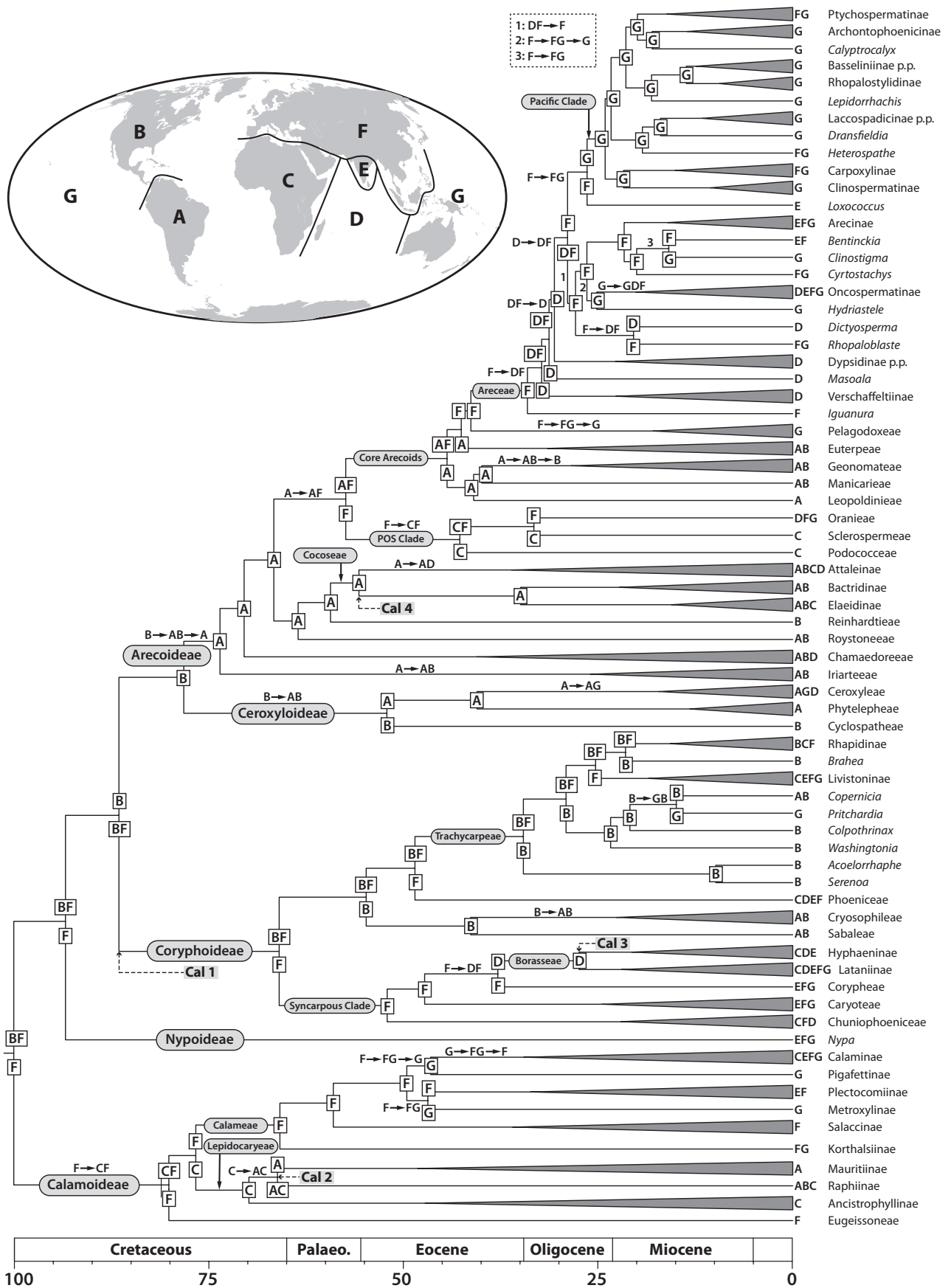
Ancestral area reconstruction

Overall, the two LAGRANGE analyses under different models of dispersal probability returned similar results. However, likelihood values indicated that M_1 was strongly favoured over M_0 ($\Delta\ln L = 53.3$) and thus we present the results based on model M_1 only. These results provide AARs for all nodes from the crown node of palms to the stem node of each genus (Fig. 1). The raw LAGRANGE output for M_1 may be downloaded from the Dryad data repository (doi:10.5061/dryad.vb25b35j). For 63% of the nodes, there was only one strongly supported AAR, providing a robust hypothesis of palm biogeography under the model used here. In the remaining cases alternative reconstructions were obtained within two log-likelihood units of the optimal reconstruction suggesting some degree of uncertainty. In those cases we represent the most likely AAR in Fig. 1. We acknowledge that the coding of genus-level terminals with their modern distributions is a potential source of bias in our analyses because the ancestral areas of the genera themselves are not taken into account, although the effect may be limited to shallower nodes (Couvreur *et al.*, 2011b).

DISCUSSION

Global biogeographical history of palms

Here, we provide for the first time a comprehensive, family-wide biogeographical analysis of palms based on molecular dating and AAR methods (Fig. 1). As stated by Couvreur *et al.* (2011a), the earliest divergence among extant lineages (i.e. the crown node of palms) is estimated to have occurred



in Laurasia (Eurasia and North America) at the end of the Early Cretaceous around the Albian–Cenomanian boundary (100 Ma; 95% HPD 92–108 Ma). This distribution corresponds to the ‘northern mid-latitude megathermal belt’ of Morley (2000, 2003), which is thought to be the putative ancestral area for several other pantropical megathermal clades such as Annonaceae (Couvreur *et al.*, 2011b), Menispermaceae (Wang *et al.*, 2012) and Zingiberales (Kress & Specht, 2006). Although influenced by the constraint of 110–120 Ma applied to the root node of palms (Couvreur *et al.*, 2011a), our estimate falls within the range reported for palms by previous authors (Bremer, 2000; Wikstrom *et al.*, 2001; Janssen & Bremer, 2004). These findings are consistent with the Laurasia hypothesis of Uhl & Dransfield (1987), although their rationale for the hypothesis, that the apocarpous flower indicates primitive lineages, is not supported by recent phylogenetic research (Rudall *et al.*, 2011). From their ancestral area in Laurasia, palms dispersed on a number of occasions into all major tropical regions, becoming important or even dominant elements of regional floras. Here, we use our results to interpret the biogeographical history of each of the five palm subfamilies. Taxonomic names follow the classification of Dransfield *et al.* (2008) and are indicated in Fig. 1.

Calamoideae

Subfamily Calamoideae diverged from other palms at the crown node of the family in Eurasia, expanding into Africa prior to its crown node divergence (80 Ma; 95% HPD 70–90), somewhat earlier than proposed by Wikstrom *et al.* (2001; 63–73 Ma). Together, these dates and AARs are inconsistent with the hypothesis of Baker & Dransfield (2000), which invokes an early history in Gondwana and vicariance related to Gondwanan break-up *c.* 130 Ma. This hypothesis was based primarily on fossil evidence in the pre-collision Cenozoic of India for *Eugeissona* (Morley, 1998), the sister group of all remaining Calamoideae, which was interpreted as evidence for a vicariance driven by Gondwanan break-up. In this study, tribe Eugeissonae is inferred to have diverged from the remaining Calamoideae at the crown node of Calamoideae in Eurasia, which is more compatible with the current distribution of the group (Malay Peninsula and Borneo). Although the putative existence of *Eugeissona* from the Middle Eocene onwards of India is not accounted

for in our DEC model, these fossil records may be explained as immigrants from Asia (Morley, 2000) that have subsequently gone extinct.

In the Campanian (77 Ma; 95% HPD 69–86), tribes Calameae and Lepidocaryeae diverged from each other, the former in Eurasia and the latter in Africa. The shared stem lineage of Mauritiinae and Raphiinae (Lepidocaryeae) expanded into South America around the end of the Cretaceous between 66 (95% HPD 65–69; calibration point) and 69 Ma (95% HPD 65–76), an event supported by the fossil record, which includes pollen evidence (attributed to Mauritiinae) in both South America and Africa from the Late Cretaceous and early Cenozoic (Rull, 1998; Pan *et al.*, 2006). The American–African distribution patterns in the Lepidocaryeae have been attributed to the break-up of the two continents in the mid-Cretaceous (Baker & Dransfield, 2000), but our findings are more consistent with an alternative hypothesis of dispersal along island chains in the Late Cretaceous (Pennington & Dick, 2004), the Mauritiinae later becoming isolated in South America.

Early divergences within the Calameae were inferred to have occurred in Eurasia, as suggested by Dransfield *et al.* (2008) and the abundant fossil record for the group in the Northern Hemisphere (Harley, 2006; Dransfield *et al.*, 2008). Dispersals eastwards into the Pacific region east of Wallace’s Line took place on multiple occasions from as early as 50 Ma onwards (95% HPD 46–71), or potentially even earlier (see Korthalsiinae). A complex pattern of westwards expansion into the Pacific and extinction in Eurasia, followed by eastwards expansion into Eurasia and extinction in the Pacific is inferred for the lineages leading to the Calamineae, although other reconstructions of similar likelihood were obtained. **Many of the migrations across Wallace’s Line inferred here pre-date the Miocene**, contradicting in part the established link between the geological evolution of Malesia (Hall, 2009) and biogeographical patterns in Calameae (Dransfield, 1981, 1987; Dransfield *et al.*, 2008). **Eocene fossil pollen records in Australia (Truswell *et al.*, 1987) and Sulawesi (Morley, 1998) are consistent with our conclusion that the Calameae had achieved a wide distribution including the Pacific before the Miocene (Baker & Couvreur, 2012b).** However, it is likely that migrations across Wallace’s Line also took place afterwards, for example in *Calamus* and *Daemonorops*.

Figure 1 Spatial and temporal dimensions of palm evolution. Chronogram for the palm family, summarized where possible to the tribal and subtribal level (see also Table 1, Appendices S2 & S3, and tree file at the Dryad data repository, doi:10.5061/dryad.vb25b35j). For taxonomy see Dransfield *et al.* (2008). Calibration points are marked in grey boxes – Cal 1: *Sabalites carolinensis* (Berry, 1914), Cal 2: *Mauritidites* (Schrank, 1994), Cal 3: *Hyphaene kapelmanii* (Pan *et al.*, 2006), Cal 4: fossil Attaleinae (Gomez-Navarro *et al.*, 2009). The most likely ancestral areas determined with LAGRANGE under model M₁ (Couvreur *et al.*, 2011a) are given in boxes at each node. For alternative reconstructions within two log-likelihood units see raw LAGRANGE output at Dryad data repository, doi:10.5061/dryad.vb25b35j. The inset map illustrates geographical areas defined for this study – A: South America, B: North America (including Central America and the Caribbean), C: Africa (including Arabia), D: Indian Ocean Islands (including Madagascar) E: India (including Sri Lanka), F: Eurasia (to Wallace’s Line, including Andaman and Nicobar islands) and G: the Pacific (including areas east of Wallace’s Line and Australia). Inferred range expansion events are marked where appropriate on internal branches. Due to the lack of phylogenetic resolution and ancestral area reconstructions within genera, range expansion inferences are not made on terminal (i.e. genus-level) branches.

Table 1 Estimated divergence times at the subfamily, tribe and subtribe levels for palms. Stem and crown node estimates with 95% highest probability density (HPD) values. Bold lines represent calibration points.

	Stem (Ma)	HPD upper (Ma)	HPD lower (Ma)	Crown (Ma)	HPD upper (Ma)	HPD lower (Ma)
ARECACEAE	117.86	113.83	120.00	100.14	92.02	108.78
CALAMOIDEAE	100.14	92.02	108.78	80.21	70.29	99.30
Eugeissoneae	80.21	70.29	99.30	–	–	–
Lepidocaryeae	76.74	68.58	85.72	69.92	65.36	76.10
Ancistrophyllinae	69.92	65.36	76.10	47.27	28.9	64.37
Raphiinae	66.24	65.68	71.00	–	–	–
Mauritiinae	66.24	65.68	71.00	48.23	29.51	63.20
Calameae	76.74	68.58	85.72	65.93	53.14	78.55
Korthalsiinae	65.93	53.14	78.55	–	–	–
Salaccinae	59.07	45.82	71.43	36.02	19.47	54.93
Metroxylinae	46.91	33.72	59.97	–	–	–
Pigafettinae	46.56	33.47	58.92	–	–	–
Plectocomiinae	46.91	33.72	59.97	33.72	19.46	47.83
Calaminae	46.56	33.47	58.92	34.58	22.92	46.94
NYPOIDEAE	93.5	87.52	100.67	–	–	–
CORYPHOIDEAE	86.62	85.8	88.25	66.02	51.36	80.08
Sabaleae	41.41	23.07	58.81	–	–	–
Cryosophileae	41.41	23.07	58.81	22.68	13.28	32.70
Phoeniceae	48.57	33.01	65.43	–	–	–
Trachycarpeae	48.57	33.01	65.43	34.63	22.98	47.15
Rhapidiinae	21.50	13.39	30.88	15.78	8.61	23.08
Livistoninae	25.35	16.78	35.12	18.55	10.28	27.50
Chuniophoeniceae	52.14	39.86	65.65	22.07	9.15	36.74
Caryoteae	47.32	35.18	59.78	24.53	12.18	38.20
Corypheae	37.92	29.35	47.91	–	–	–
Borasseae	37.92	29.35	47.91	27.47	27.00	28.42
Hyphaeninae	27.47	27.00	28.42	20.69	13.63	26.78
Lataniinae	27.47	27.00	28.42	22.03	13.8	27.86
CEROXYLOIDEAE	78.29	70.68	85.27	52.17	29.99	74.23
Cyclospatheae	52.17	29.99	74.23	–	–	–
Ceroxyleae	40.59	21.10	63.43	17.23	7.13	29.20
Phytelepheae	40.59	21.10	63.43	13.24	14.32	24.23
ARECOIDEAE	78.29	70.68	85.27	73.63	66.18	81.37
Irarteeae	73.63	66.18	81.37	26.84	12.37	43.95
Chamaedoreae	70.53	63.35	78.27	40.63	23.83	56.69
Podococceae	42.80	24.23	61.04	–	–	–
Oranieae	33.26	14.99	51.77	–	–	–
Sclerospermeae	33.26	14.99	51.77	–	–	–
Roystoneae	63.59	58.10	70.05	–	–	–
Reinhardtiae	59.43	55.68	64.04	–	–	–
Cocoseae	59.43	55.68	64.04	55.77	54.80	57.68
Attaleinae	55.77	54.80	57.68	36.17	23.29	49.78
Bactridinae	34.99	19.96	50.60	22.30	11.99	34.20
Elaeidinae	34.99	19.96	50.60	15.61	3.85	30.32
Manicariae	39.98	28.70	52.70	–	–	–
Euterpeae	42.62	32.98	52.89	31.54	16.37	45.07
Geonomateae	39.98	28.70	52.70	28.52	16.99	40.07
Leopoldiniaee	41.02	30.09	53.90	–	–	–
Pelagodoxeae	41.38	32.45	51.88	17.98	5.54	31.47
Areceae	41.38	32.45	51.88	34.11	25.95	42.42
Archontophoenicinae	18.08	12.71	23.52	13.58	8.37	19.31
Arecinae	21.68	14.86	28.65	16.10	9.23	23.33
Basseliniinae	21.45	16.44	27.12	18.16	11.30	24.89
Carpoxylinae	21.75	15.10	28.71	15.12	7.86	22.62
Clinospermatinae	21.75	15.10	28.71	10.61	2.67	19.74
Dypsidinae (paraphyletic)	–	–	–	–	–	–
Laccospadicinae (paraphyletic)	–	–	–	–	–	–
Oncospermatinae	25.20	18.28	32.45	20.17	12.05	27.75

Table 1 Continued

	Stem (Ma)	HPD upper (Ma)	HPD lower (Ma)	Crown (Ma)	HPD upper (Ma)	HPD lower (Ma)
Ptychospermatinae	19.97	14.83	25.11	16.20	11.53	21.30
Rhopalostylidinae (nested)	13.68	7.83	20.24	9.43	2.91	16.29
Verschaffeltiinae	32.28	25.23	40.42	22.75	12.65	32.73

Nypoideae

The ancestral area of Nypoideae, which diverged from other palms at 94 Ma (95% HPD 88–101), is unequivocally reconstructed as Eurasia. *Nypa* appears in the fossil record almost simultaneously in the Maastrichtian of South America, Africa, India and Malesia (Gee, 1990; Dransfield *et al.*, 2008). The outstanding fossil record for *Nypa* indicates that the lineage was widely distributed in the tropics and subtropics by the climatic optimum of the Early Eocene, and has contracted to its modern distribution (Sri Lanka to the Solomon Islands) since that time. The AAR and divergence time estimate imply early range expansions from a Eurasian origin, perhaps facilitated by the mangrove habit and floating seeds, which are characteristic of modern *Nypa*. However, the AAR does not take the palaeodistribution into account, which may have biased the result.

Coryphoideae

Subfamily Coryphoideae is inferred to have originated in Laurasia, the timing of which (87 Ma; 95% HPD 86–88) is influenced by the constraint of a fossil calibration point. Nevertheless, this corresponds closely with the hypotheses based on the fossil record for coryphoids that suggest that the group originated in the Northern Hemisphere in the Late Cretaceous and diversified in boreotropical regions through the Cenozoic (Bjorholm *et al.*, 2006; Dransfield *et al.*, 2008), contradicting an earlier hypothesis of coryphoid origins in Gondwana (Moore, 1973a).

The syncarpous clade (comprising Borasseae, Caryoteae, Chuniophoeniceae and Corypheae) diverged from all remaining coryphoids in Eurasia at the end of the Cretaceous (66 Ma; 95% HPD 51–80). Following a range expansion into the Indian Ocean in the stem lineage of tribes Borasseae and Corypheae, the former diverged in the Indian Ocean at 38 Ma (95% HPD 29–48). Its two subtribes (Hyphaeninae, Lataniinae) are also inferred to have originated in the Indian Ocean, subsequently expanding into Africa and India and, in Lataniinae, into Eurasia and the Pacific, too. These results are broadly consistent with the hypothesis of Dransfield *et al.* (2008) that the group is derived from within a Laurasian group (the syncarpous clade), but underwent its early diversification in a Gondwanan area. They contradict the hypothesis that the group's history dates back to the break-up of Gondwana (Uhl & Dransfield, 1987). The Borasseae produce some of the largest fruit in the plant kingdom, notably the double coconut (*Lodoicea maldivica*), the largest seed in the

world, and viable seeds appear not to float. Despite their apparently ineffective dispersal mechanisms, long-distance oceanic dispersal appears to have played a key role in this group (Dransfield *et al.*, 2008).

The Caryoteae and Chuniophoeniceae diversified initially in Eurasia around the Miocene–Oligocene boundary. Our results support previous hypotheses that the Caryoteae migrated eastwards across Wallace's Line during the Miocene evolution of Malesia (Dransfield, 1987; Hahn & Sytsma, 1999; Dransfield *et al.*, 2008; Baker & Couvreur, 2012b) as well as dispersing into India. The Chuniophoeniceae has since achieved a widely disjunct distribution in Indochina, Peninsular Thailand, the Middle East and, by long-distance dispersal, Madagascar and has also undergone substantial ecological niche differentiation to occupy rainforest, seasonal and desert environments, despite comprising only four genera and six species.

Around 55 Ma (95% HPD 39–72), the stem lineage of the New World thatch palm clade (comprising Sabaleae and Cryosophileae) diverged in North America, confirming the hypothesis of Dransfield *et al.* (2008) that the two tribes have Laurasian origins. Some leaf fossils linked to *Sabal* (typically as *Sabalites*) pre-date these estimates (e.g. Berry, 1914), although these cannot be confidently assigned to modern genera (Dransfield *et al.*, 2008). The two tribes diverged at 41 Ma (95% HPD 23–59), expanding into South America after this time. The extant lineages of Cryosophileae began to radiate from 23 Ma (95% HPD 13–33), undergoing a putative adaptive radiation in the Caribbean (Dransfield *et al.*, 2008; Roncal *et al.*, 2008) from 21 Ma (95% HPD 12–30) onwards.

Phoeniceae diverged from Trachycarpeae around 49 Ma (95% HPD 33–65) in Eurasia, expanding subsequently into Africa, the Indian Ocean and India. The ancestral area of Trachycarpeae is inferred to be Laurasia, but following its crown node radiation (35 Ma; 95% HPD 23–47), several lineages diverged independently in North America at various times. The ancestral area of subtribe Livistoninae and all of its internal nodes is inferred unequivocally to be Eurasia. Expansions into other regions (Africa, India and the Pacific) occurred independently in all lineages of Livistoninae (except for *Johannesteijsmannia*) following its crown node radiation at 19 Ma (95% HPD 10–28). A widespread Laurasian ancestral area is inferred for subtribe Rhapidinae, which diverged 22 Ma (95% HPD 13–31). Our findings support a previous hypothesis that the Trachycarpeae has Laurasian origins (Dransfield *et al.*, 2008) and are consistent in many respects with those of Bacon *et al.* (2012) who, using similar methods

but different data, inferred that much of the history of the tribe can be linked to the widespread occurrence of boreotropical forests in the Northern Hemisphere in the Eocene and Oligocene, and dispersal opportunities afforded by the North Atlantic and Bering land bridges or their remnants. Our results also support the hypotheses that the tribe dispersed eastwards across Wallace's Line into the Pacific on multiple occasions within Livistoninae (Crisp *et al.*, 2010; Bacon *et al.*, 2012; Baker & Couvreur, 2012b) and also entered the Pacific by westward migration from North America in the case of *Pritchardia* (Bacon *et al.*, 2012).

Ceroxyloideae

The Arecoideae/Ceroxyloideae clade diverged from the Coryphoideae in North America at 87 Ma (95% HPD 86–88; calibration point). Subfamilies Arecoideae and Ceroxyloideae subsequently diverged from each other in this region at 78 Ma (95% HPD 71–85). Following expansion of the Ceroxyloideae stem lineage into South America, tribe Cyclospatheae diverged in North America and the remainder in South America (52 Ma; 95% HPD 30–74). These ages are similar to those obtained by Savolainen *et al.* (2006) and, with the AARs, are consistent with the hypothesis of Dransfield *et al.* (2008) that a vicariance occurred at the base of the subfamily that may have been caused by the breaking of a land bridge between North and South America in the early Cenozoic (Morley, 2000, 2003). Tribes Ceroxyleae and Phytelpeheae diverged in South America at 41 Ma (95% HPD 21–63), with the Ceroxyleae expanding into the Pacific between 41 Ma (95% HPD 21–63) and 17 Ma (95% HPD 7–29) and dispersing into the Indian Ocean Islands from 13 Ma (95% HPD 4–25). Our results are similar to previous age estimates for these groups (Savolainen *et al.*, 2006; Trénel *et al.*, 2007) and support the assertions of Trénel *et al.* (2007) that the disjunct Southern Hemisphere distribution of tribe Ceroxyleae is best explained by dispersal during the mid-Cenozoic, rather than by Gondwanan vicariance (Dransfield *et al.*, 1985; Uhl & Dransfield, 1987). Moreover, the diversification of tribe Phytelpeheae is better accounted for by the Neogene uplift of the Andes (Barfod *et al.*, 2010) than by Pleistocene refugia (Moore, 1973a).

Arecoideae

The most likely area reconstructions suggest that the stem lineage of subfamily Arecoideae expanded into South America, becoming extinct in North America prior to the clade's crown node divergence in South America at 74 Ma (95% HPD 66–81), confirming the traditional view that the subfamily has South American origins (Moore, 1973a; Uhl & Dransfield, 1987; Bjorholm *et al.*, 2006; Dransfield *et al.*, 2008). Many early divergence events in Arecoideae are inferred to have taken place in South America. Our reconstruction indicates that tribes Iriarteae, Chamaedoreae (71 Ma; 95% HPD 63–78), Roystoneae (64 Ma; 95% HPD

58–70), Reinhardtiae and Cocoseae (59 Ma; 95% HPD 56–64) all diverged initially in South America. Following a crown node diversification in South America at 41 Ma (95% HPD 24–57), the Chamaedoreae expanded into the Indian Ocean islands by 31 Ma (95% HPD 13–50) and thereafter into North America. The conclusion of Cuenca *et al.* (2008) that the disjunct distribution of Chamaedoreae between the Americas and the Mascarenes was achieved by mid-Cenozoic dispersal is supported, as opposed to earlier hypotheses of Gondwanan vicariance (Moore, 1973a; Uhl & Dransfield, 1987), although extinction in Africa and/or Madagascar, as proposed by Moore (1973a), cannot be ruled out.

Within Cocoseae, the stem node divergences of the Attaleinae (56 Ma; 95% HPD 55–58; calibration point), Bactridinae and Elaeidinae (35 Ma; 95% HPD 20–51) occurred in South America. Subtribe Attaleinae expanded into the Indian Ocean Islands by its crown node age of 36 Ma (95% HPD 23–50) and into Africa after 29 Ma (95% HPD 18–41). Within Bactridinae, expansion into North America occurred after 22 Ma (95% HPD 12–34). The Elaeidinae expanded into North America and Africa after 16 Ma (95% HPD 4–30). Despite some variation in topologies and divergence time estimates, the findings of previous studies (Gunn, 2004; Meerow *et al.*, 2009) are largely borne out by our results, and suggest that the earliest divergences in the Cocoseae took place during the Palaeocene and Early Eocene at least initially in South America. While the age estimates of Eiserhardt *et al.* (2011b) are somewhat older, their results are also compatible with this scenario. Our results contradict suggestions that the group's distribution reflects the break-up of Gondwana (Uhl & Dransfield, 1987; Hahn, 2002). However, we recognize that our AAR does not take into account the full palaeodistribution of Cocoseae. For example, fossils attributed to Cocoseae are known from the Pacific region (e.g. New Zealand) from as far back as the Eocene (Gunn, 2004) and a cocosoid palm has been recorded from Easter Island from as little as 800 years ago (Dransfield *et al.*, 1984).

The first expansion of Arecoideae into Eurasia from South America occurs in the stem lineage shared by the Podococceae–Oranieae–Sclerospermeae (POS) clade and the core arecoid clade (Areceae, Euterpeae, Geonomateae, Leopoldinieae, Manicarieae, Pelagodoxeae) between 67 Ma (95% HPD 60–73) and 57 Ma (95% HPD 45–69). At this latter date, the POS clade diverged from the core arecoid clade in Eurasia, expanding into Africa before 43 Ma (95% HPD 24–61). Tribes Oranieae and Sclerospermeae diverged in Eurasia and Africa respectively at 33 Ma (95% HPD 15–52), Oranieae later dispersing into the Indian Ocean Islands and the Pacific. Following the crown node of the core arecoids at 44 Ma (95% HPD 35–55), tribes Euterpeae (43 Ma; 95% HPD 33–53), Leopoldinieae (41 Ma; 95% HPD 30–54), Geonomateae and Manicarieae (40 Ma; 95% HPD 29–53) all diverged in South America, all but Leopoldinieae later expanding into North America. Our divergence time estimates for Geonomateae closely match those obtained by Roncal *et al.* (2010).

Tribe Areceae and its sister tribe Pelagodoxeae diverged in Eurasia at 41 Ma (95% HPD 32–52). Pelagodoxeae subsequently expanded into the Pacific and became extinct in Eurasia by 18 Ma (95% HPD 6–31). The crown node radiation of Areceae (Baker & Couvreur, 2012a), a major clade with a wide Indo-Pacific distribution, commenced at 34 Ma (95% HPD 26–42) in Eurasia, corresponding closely to the finding of Savolainen *et al.* (2006). The early diversification history of the tribe is characterized by expansion into the Indian Ocean and divergence of a number of lineages in this region (e.g. Dypsidinae, Verschaffeltiinae). From 29 Ma (95% HPD 22–36), numerous independent expansions into the Pacific from Eurasia are inferred. Notable among these is the dispersal that founded the Pacific clade of Areceae (Norup *et al.*, 2006) by 26 Ma (95% HPD 20–32), a major radiation of several subtribes (e.g. Archontophoenicinae, Clinospermatinae, Basseliniinae, Ptychospermatinae) within the tribe. Within the Pacific clade, westwards dispersals across Wallace's Line become frequent from 19 Ma (95% HPD 13–26), such as *Adonidia* in the Ptychospermatinae (Zona *et al.*, 2011). The very wide distribution of tribe Areceae across numerous archipelagos indicates that long-distance dispersal over oceans has played a key role in its biogeographical history (Dransfield *et al.*, 2008; Baker & Couvreur, 2012b). Despite its size and diversity, the Areceae has no biogeographical history in either Africa or the Americas.

CONCLUSIONS

Our biogeographical analyses provide evidence that the earliest divergences among the extant lineages of palms occurred in Laurasia, as suggested by Uhl & Dransfield (Uhl & Dransfield, 1987), in the middle Cretaceous. Hypotheses of palm origins in Gondwana (Moore, 1973a; Baker & Dransfield, 2000) or Pangaea (Uhl & Dransfield, 1987) were not supported. Before the end of the Cretaceous, the family migrated out of Laurasia into Africa and South America, and thereafter, through the Cenozoic, into all tropical and subtropical regions of the world. Although palms are known to be relatively strongly dispersal limited (Kissling *et al.*, 2012b), they have achieved a pan-tropical/subtropical distribution. Long-distance oceanic dispersal must be invoked to explain many of the biogeographical patterns in the family. Further studies of these lineage dispersals and the traits associated with them may serve to shed further light on the processes by which these distributions were achieved.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Supplementary methods – dispersal probability models for ancestral area reconstructions.

Appendix S2 Complete genus-level chronogram for the palm family.

Appendix S3 Stem node ages and diversification rates estimated for palm genera.

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BIOSKETCHES

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