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A dated phylogeny of the palm tribe Chamaedoreeae supports Eocene dispersal between Africa, North and South America

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Abstract

The palm tribe Chamaedoreeae reaches its higher diversity in Central America, however, its distribution ranges from the north eastern part of Mexico to Bolivia with a disjunction to the Mascarene Islands in the Indian Ocean. The disjunct distribution of Chamaedoreeae is generally considered a result of Gondwana vicariance and extinction from Africa and/or Madagascar. However, latitudinal migrations and their role in shaping the distribution of this tribe in the Americas have been largely overlooked. In this study we used seven plastid and two nuclear DNA regions to investigate the phylogenetic relationships and biogeography of the Chamaedoreeae. The resulting phylogeny fully resolved the generic relationships within the tribe. The exact area of origin of the tribe remains uncertain, but dating analyses indicated an initial diversification of the Chamaedoreeae during the Early Eocene, followed by long distance dispersion to the Mascarene Islands in the late Miocene. The radiation of *Hyophorbe* could have taking place on islands in the Indian Ocean now submerged, but its former presence in Africa or Madagascar cannot be ruled out. At least two independent migrations between North and South America predating the rise of the Panama isthmus need to be postulated to explain the distribution of Chamaedoreeae, one during the Middle Eocene and a second during the Miocene. Whereas the traditional interpretation of distribution of Chamaedoreeae species assumes a west Gondwana origin of the group, the findings presented in this paper make it equally possible to interpret the group as a primarily boreotropical element.

Keywords: Antilles; Arecaceae; Boreotropics; Caribbean geology; Central America; *Chamaedorea*; Dispersal; *Gaussia*; Gondwana break-up; *Hyophorbe*; Eocene land bridges; Latitudinal migrations; Mascarene Islands; Neotropics; Panama isthmus; *Synechanthus*; *Wendlandiella*; *ndhF*; *mat*K; *trn*L-*trn*F; *trn*D-*trn*T; *rps16* intron; PRK; RPB2

1. Introduction

Explaining disjunct distribution is an important aim of biogeography. Following the 1960s general acceptance of the theory of continental drift, vicariance became the predominant driver in historical biogeography. However, an increasing number of studies using dated phylogenies indicate that dispersal and not Gondwana vicariance often has been the driving force shaping the distribution of plant groups in the southern hemisphere (Davis et al., 2002; Muellner et al., 2006; Renner, 2004a; Sanmartín and Ronquist, 2004; Zerega et al., 2005), although Gondwana vicariance still holds in a number of cases (Sytsma et al., 2004). Proposed explanations for these findings include interplate dispersal routes across now submerged land bridges or island chains (Morley and Dick, 2003) or dispersal in sea water or on floating mats of vegetation following ocean currents and predominant wind directions (Renner, 2004a; Zhang et al., 2007). In the palm family, dated phylogenies of the Cocoseae (Gunn, 2004) and the Ceroxyloideae (Trénel et al., 2007) both indicate Eocene trans-oceanic dispersal between America and Africa. These results are also corroborated in a dated phylogeny of the palm subfamilies Ceroxyloideae and Arecoideae presented

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by Savolainen et al. (2006). The dismissal of the Gondwana vicariance hypothesis for these palm groups raises the question of whether Eocene interplate dispersal is a general explanation for amphi-continental disjunctions in the palm family and which dispersal routes are most likely to explain such events.

One of the most extreme examples of disjunct distribution within the palm family is presented by the tribe Chamaedoreeae consisting of four genera occurring in Central and South America and one endemic to the Mascarene Islands in the Indian Ocean. Included in the tribe is the largest Neotropical palm genus *Chamaedorea*, with 107 species ranging from Mexico to Bolivia (Govaerts et al., 2006). The genus has two pronounced centres of diversity in Central America, the fist in the southern part of Mexico and Guatemala, and the second in the mountains of Costa Rica and Panama (Hodel, 1992, 1999). The other Neotropical genera are less diverse and have more restricted ranges. *Gaussia* contains five species distributed in Mexico and the Caribbean region (Greater Antilles). *Synechanthus* includes two species ranging from Mexico to Ecuador along the Pacific Ocean. *Wendlandiella* with a single species is endemic to western Amazon region (Henderson et al., 1995). The last genus of the tribe, *Hyophorbe*, contains five species found on different islands of the Mascarene Archipelago (Uhl and Dransfield, 1987). All are listed as critically endangered, and one of them, *H. amaricaulis* is recognized as the most endangered plant species in the world, having only one remaining living individual in the wild (IUCN, 2006). *Hyophorbe* species are popular ornamental palms owing to their bottle shaped trunks and are widely cultivated in tropical gardens throughout of the world. Also *Gaussia* and *Chamaedorea* include popular ornamental palms. Species of the latter genus are also used for cutting leaves for floral arrangements and dietary uses, a practice which has led to a poor conservation status of some species.

Moore (1973a,b, 1978) suggested a West Gondwana origin of the Chamaedoreeae, with a subsequent extinction of the African members of the tribe, possible caused by climatic changes on the continent, and with an arrival to the Mascarene Islands either directly from Africa or via Madagascar. Bjorholm et al. (2006) proposed that initial diversification of the subfamily Arecoideae, to which Chamaedoreeae belongs, occurred in the Neotropics where the subfamily has a long history. New insight into the phylogeny of the palm family based on addition of the plastid region *ndhF* to the dataset of Asmussen et al. (2006) indeed indicates that Chamaedoreeae diverged early in the history of the arecoids (Conny Asmussen-Lange, unpublished data).

The radiation of *Hyophorbe* is assumed to have happened *in situ* on the Mascarene Islands (Savolainen et al., 2006). Strong evidence indicates that taxa, which colonize ocean archipelagos often speciate by adaptive radiation (Emerson, 2002; Francisco-Ortega et al., 1996; Gillespie, 2004). Our knowledge about the actual historical process of colonization in most archipelagos is, however, still sparse. In the case of the Mascarenes few studies exist. For reptiles such as geckos, tortoises, and skinks, a single colonization of the Mascarenes has been proposed, followed by an *in situ* radiation (Austin and Arnold, 2001; Austin et al., 2004). Australia and Madagascar have been proposed as the two areas of origin of reptile lineages represented in the Mascarenes. Whereas, long distance dispersal from Africa to the Mascarenes has been shown for the family Psiloxylaceae, part of the Myrtales (Sytsma et al., 2004).

Within the Neotropical Chamaedoreeae it is clear that latitudinal migrations must have occurred. Understanding ancient events of dispersal between North and South America is a complex issue that does not only involve the existence of possible bridges between the land masses but also the past climatic conditions of the region and its orogenic history. Palm groups occurring in Central America and the Caribbean have complex origins, with a mixture of boreotropical clades and Gondwana/south American groups (Bjorholm et al., 2006). A close relationship exists between certain Asian/Eurasian taxa and boreotropical clades present in Mexico, Central America, and the Caribbean, e.g., in Coryphoideae (e.g., Zona, 1990; Dransfield et al., 2005). Some Coryphoid lineages also managed to disperse into South America. Repeated migration between North and South America has likewise been proposed for subfamily Arecoideae, with events dating back to at least the early Tertiary (Bjorholm et al., 2006). To explain the ancient exchange of biota between North and South America it has been proposed that various land bridges existed for shorter or longer periods prior to the formation of the Panamanian isthmus ca. 3 My ago. These include a very old bridge in the Cretaceous-Palaeocene (Iturralde-Vincent and MacPhee, 1999); a more recent fragmented bridge involving the proto Antilles during the Middle Eocene (Graham, 2003; Pennington and Dick, 2004); and a brief connection involving the submerged Aves ridge in the Eocene–Oligocene boundary (Iturralde-Vincent and MacPhee, 1999).

The tribe Chamaedoreeae has been demonstrated convincingly to be monophyletic (Asmussen and Chase, 2001; Asmussen et al., 2006) but inter-generic relationships within the tribe remain incompletely understood. So does species level phylogeny within its major genera in spite of recent attempts at analysing this using plastid or nuclear DNA markers. Thomas et al. (2006) used two nuclear DNA regions (PRK and RPB2) to reconstruct the phylogenetic relationships within the largest genus *Chamaedorea*. They found that most the proposed *Chamaedorea* subgenera (Hodel, 1992) are non-monophyletic. This result has since been corroborated by plastid DNA data (*mat*K, *rps*16 intron, *trn*L-*trn*F, and *ndh*F; Cuenca and Asmussen-Lange, 2007). In both analyses, species groups not proposed by morphological studies have been identified. In addition, a few clades with well delimited geographic distributions have been recovered, e.g., the "South American"

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clade constituted by *C. linearis* and *C. fragrans* (Thomas et al., 2006). So far, no attempt to analyse the biogeography and diversification pattern of the tribe using molecular dating techniques has been undertaken.

Here we use plastid and nuclear DNA sequence data to reconstruct the phylogenetic relationships within Chamaedoreeae and to investigate divergence times within the tribe. The information is used to evaluate existing biogeographic hypotheses for the diversification of Chamaedoreeae regarding to (a) the disjunction between the Neotropics and the Indian Ocean, and possible migratory routs involved with the arrival of *Hyophorbe* to the Mascarene Islands, (b) the time and place of the radiation of extant *Hyophorbe* species, (c) latitudinal migration of the Neotropical members of Chamaedoreeae in relation to proposed land bridges between North and South America, and (d) the diversification of *Gaussia* in the Caribbean regions, particularly the relationship between Central American and Antillean species.

2. Materials and methods

2.1. Taxon sampling

For the phylogenetic analysis 40 species of tribe Chamaedoreeae were sampled (Appendix 1 in supplementary material), including all species of *Hyophorbe*, *Gaussia*, *Synechanthus,* and *Wendlandiella*, and 27 of the 107 species of *Chamaedorea* recognized by Govaerts et al. (2006). The latter included representatives of seven of Hodel's (1992, 1999) eight subgenera of *Chamaedorea*. In some few cases, problems with amplification of lack of plant material made it necessary to use more than a single accession for some species. Tribe Chamaedoreeae is nested convincingly within subfamily Arecoideae (Asmussen et al., 2006). Therefore, representatives of six other tribes of the Arecoideae were selected as outgroup (Appendix 1). The final taxon sample for phylogenetic analyses thus consisted of 46 species including six in the outgroup. That dataset will be referred to as M1 in the rest of this paper.

No reliable fossil record exists for tribe Chamaedoreeae. For dating analyses the M1 sample was therefore expanded to include a number of taxa belonging to related tribes within the Arecoideae, particularly the Cocoseae, where fossil records are more abundant and reliable. Dating methods are sensitive to uneven sampling across groups (Linder et al., 2005). We therefore reduced the number of *Chamaedorea* species in the dataset from 27 to 15, leaving only species where all the sequences were made from a single accession and taking care to include at least two species from each well supported clade. We also removed *H. amaricaulis* from the matrix because the RPB2 and half of the PRK sequence were unavailable for this taxon. The final taxon sample for dating analyses thus consisted of three species from subfamily Coryphoideae, *Nypa fruticans* from subfamily Nypoideae, six members of subfamily Ceroxyloideae, and 62 members of subfamily Arecoideae of which 27 were Chamaedoreeae. Representatives of all tribes in the Arecoideae were included. Among the non-chamaedoroid arecoid taxa there were one species from each of the four monogeneric tribes Oranieae, Sclerospermeae, Roystoneae, and Podococceae, three species from tribe Iriarteeae, 19 species from tribe Cocoseae representing all of its three subtribes, one species from each of the tribes Manicarieae, Geonomateae, Leopoldinieae, and Pelagodoxeae, and three species from tribe Areceae (Appendix 1 in the supplementary material). This dataset will be referred to as M2 in the rest of this paper.

2.2. DNA extraction, PCR amplification, and sequencing

We sequenced the plastid region *trn*L-*trn*F and two nuclear DNA regions: the one between the second and third intron of the phosporibulokinase gene (PRK) and the intron 23 of the second largest subunit of the RNA polymerase II (RPB2). In addition, sequences from four plastid DNA regions (*mat*K, *ndh*F, *trn*D-*trn*T, and *rps*16 intron) generated by Cuenca and Asmussen-Lange (2007) were included in the analysis. Total genomic DNA was extracted using either the DNeasy Plant Mini Kit (Qiagen, Crawley, West Sussex, UK) or a modification of the CTAB protocol of Doyle and Doyle (1987). The *trnL-trnF* region was amplified and sequenced following the protocol of Baker et al. (1999) and Asmussen et al. (2000). The PRK region was amplified using a two-step PCR procedure. In the first amplification, primers prk488f and prk1167r were used (Lewis and Doyle, 2002). The reaction was performed in 15 μl total volume using 13.5 μl of PCR ready mix (Ampliqon, Denmark), 2.0 mM $MgCl_2$, 5 pmol of each primer and approximately 25 ng of template DNA. The amplification conditions were: initial denaturalization at 94 °C for 5 min, 32 cycles of 1 min at 94 °C, 1 min at 55 °C, and 1 min at 72 °C, with a final extension step of 72 °C for 5 min. The result of this amplification was used as template for the second amplification. The second amplification was performed using the internal primers prk717f and prk969r (Lewis and Doyle, 2002) in a 50 μl total volume using 45 μl of PCR ready mix, 2.0 mM $MgCl_2$ (Ampliqon, Denmark), 10 pmol of each primer, and 2 μl of template. The PCR conditions were the same as in the first amplification and the reactions were carried out in an MJ Research thermocycler. The RPB2 region was amplified using the protocols of Thomas et al. (2006) and Loo et al. (2006).

2.3. Phylogenetic analyses of the tribe Chamaedoreeae

Consensus sequences from all taxa in the M1 sample were aligned visually in BioEdit 7.0.1 (Hall, 1999). Regions where the alignment could not be assessed unambiguously were excluded from the analysis, as suggested by Asmussen and Chase (2001) and Hahn (2002). Within PRK we excluded from the analyses a poly-A region at position 205–228 in the alignment and a poly-G region at position

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365–387, because both regions could not be aligned unambiguously. The same occurred with a poly-C region positioned from nucleotide 378–442 in the alignment of RPB2. In the plastid DNA regions we excluded a total of 127 characters, most of them belonging to the intergenic spacers heavily populated by indels and repetitive sequences.

The two nuclear DNA regions PRK and RPB2 were analysed separately. In addition a concatenated matrix including the five plastid regions (*trn*L-*trn*F, rps16, *ndh*F, *mat*K, and *trn*D-*trn*T) and the two nuclear DNA regions was constructed and analysed. To test for compatibility among DNA regions a partition homogeneity test (PHT) was performed in PAUP with heuristic search and 1000 replicates with 10 random stepwise addition sequences performed per replicate, saving maximum five trees per replicate. The PHT was performed for the combined plastid DNA data set tested against each of the nuclear DNA regions, and the two nuclear DNA regions were tested against each other. In all cases the PHT showed incongruence among datasets ($p < 0.05$). To explore the level of incongruence among different partitions we used instead Partition Bremer Support (PBS, Baker and DeSalle, 1997) as calculated in the program TreeRot V.2. (Sorenson, 1999) using a heuristic search with 100 replications, random stepwise addition to construct a starting tree for each replication, and saving maximum 500 trees in each replication. Decay indices (DI) for the combined tree were calculated by the same procedure.

Parsimony analyses were carried on in PAUP* version 4.0b10 (Swofford, 2002), excluding all parsimony-uninformative characters and with equal character weighting. An initial heuristic search was carried out doing 1000 replicates and holding maximum 10 trees per replicate. Random stepwise addition was used to get the starting trees. Branch swapping was performed using the tree-bisection-reconnection (TBR) algorithm with MulTrees in effect. Branches with maximum length equal to zero were collapsed. A second search was performed by TBR swapping the trees saved from the 1000 replicates in the first search. The trees in this second search were swapped until completion. Bootstrap values were calculated based on 1000 bootstrap replicates, using the same search strategy as in the heuristic search, but with only 10 random stepwise addition sequences performed per replicate.

Bayesian analysis was performed using MrBayes v. 3.1 (Huelsenbeck and Ronquist, 2003; Ronquist et al., 2005). The different models of DNA substitution were evaluated using ModelTest (Posada and Crandall, 1998). The GTR+G (General time reversible (Tavare, 1986) model+-gamma distribution) was used for all partitions, except RPB2 where the HKY+G model was selected. MrBayes was run with two simultaneous analyses with four parallel chains in each, sampling one tree for each 100 generations, starting with a random tree, and using the default priors, except for the temperature value that was set to 0.1. The program was run for 3 million generations at which point the standard deviation of split frequencies between the two simultaneous analyses was less than 0.005. Samples obtained prior to stabilization of the parameter estimates around a likelihood maximum were discarded (burn-in; 2500 samples).

2.4. Construction of the phylogenetic trees used in the molecular dating

Consensus sequences for all taxa in the M2 taxon sample were aligned visually in BioEdit 7.0.1 (Hall, 1999). The same criteria were employed for exclusion of nucleotide characters as for the M1 matrix. This included several repetitive regions within PRK and RPB2 (188 bases) and 289 characters in the plastid dataset. For reasons given above a concatenated matrix including the five plastid DNA regions (*trn*L-*trn*F, *rps*16, *ndh*F, *mat*K, and *trn*D-*trn*T) and the two nuclear DNA regions (PRK and RPB2) was constructed without a previous PHT. We assume that simultaneous analyses based on different loci will detect the week signal in single datasets (Renner, 2004a). A maximum parsimony (MP) analysis of the concatenated matrix was performed following the same strategy described for the M1 sample. A likelihood ratio test of rate constancy was performed applying the evolutionary model and parameter estimates calculated by ModelTest using the Akaike information criterion for model choice. A strict molecular clock was rejected; therefore local clock methods allowing for varying substitution rates in different clades were employed. These included the Bayesian approach to divergence time estimation using the baseml of the PAML 3.14 packages (Yang, 1997) and multidivtime (Kishino et al., 2001; Thorne and Kishino, 2002; Thorne et al., 1998); and the non-parametric rate smoothing approach, penalized likelihood (PL; Sanderson, 1997), as implemented in the program r8s v. 1.7 (Sanderson, 2004).

Bayesian dating requires as input a fixed topology in addition to the nucleotide sequences of each partition. For the topology we used one tree selected at random from the most parsimonious trees obtained from the heuristic search of the M2 matrix. The parameters of the nucleotide substitution model in each dataset were estimated using baseml. To run baseml all characters with a gap or an ambiguity in at least half of the taxa in the analysis were excluded manually from the alignment, following Renner (2004a,b). This left a total of 6498 characters in the concatenated dataset. The programs paml2modelinf and estbranches, both part of multidivtime (Thorne and Kishino, 2002) were used to estimate the branch lengths for the rooted tree and the variance–covariance matrix for the datasets. This information is needed for multidivtime to calculate the node divergence time under the fixed topology. Multidivtime was run with the Markov chain set to 100,000 trees sampled each 10th generation and with a burn-in of 1000 trees. The *a priori* expected number of time units between tips and root was set to 1.7, where one time unit corresponds to 50 million years, and the standard deviation

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was set to 0.1. This estimate was based on the oldest unambiguously identified palm fossil (see root calibration). The *a priori* rate of evolution at the root node was set to 0.016 corresponding to the average of the distance among the root node and the tips divided by the number of time units (Renner 2004a, b). The *a priori* value of the Brownian motion parameter (nu), which determines the permitted rate change between ancestral and descendent nodes, was set to 0.7 following the recommendations in the program manual.

The topology input to r8s was the same as in the Bayesian analysis. Branch lengths were estimated by maximum likelihood using the model of DNA substitution for the concatenated dataset found by ModelTest (GTR+gamma distribution rate). *Nypa fruticans* was used only to root the tree during analysis and pruned in r8s. For the PL analysis the optimal smoothing parameter (λ) was selected using a cross validation procedure (Sanderson, 2002) with eight categories among a range from 1 to 1000 for λ. The cross validation analysis indicated a smoothing factor (λ) of 32 for the M2 matrix ($\chi^2 = 424.1$) This smoothing factor was used to calculate nodal ages in the penalized likelihood analysis. To calculate the substitution rates along the tree the Truncated-Newton algorithm (TN) was chosen. Confidence intervals were using a cut off value of four.

2.5. Fossil calibration points

As earlier stated no reliable fossils pertaining to the tribe Chamaedoreeae are known. Palm-leaves assigned to *Chamaedorea* (*C. danai* Berry), have been described from the Early Eocene in Florida (Berry, 1916), however, their identity needs to be confirmed (Uhl and Dransfield, 1987), therefore, this fossil was not used to calibrate our dating analyses. Several related tribes in the Arecoideae, however, have a fossil record providing potentially useful calibration points for phylogenetic dating.

2.5.1. Tribe Cocoseae

This tribe has one of the most complete fossil records within the palm family. A Cocoseae endocarp, *Cocos sahnii*, was reported from Kapurdi Rajasthan (Guleria et al., 1996; Kaul, 1951) in a formation dated to Lower Eocene (50–55 My; Rana et al., 2005). In addition, *Cocos intertrappeansis* (Patil and Uphadhye, 1984) and cf. *Cocos* (Sahni, 1946; Tripathi et al., 1999) have been found in Deccan Intertrappean beds. The age of these beds is not homogeneous, with deposits occurring from the Upper Cretaceous (140 My) to the Early Eocene (ca. 40 My). Dating of the fossils is therefore uncertain. The records do, however, confirm the presence of Cocoseae palms by the end of Eocene. We used this information to constrain the crown node of Cocoseae at minimum 50 My, a conservative estimate also used by Gunn (2004). The fossil record associated with subtribe Bactridinae includes two palm fruits from the Middle Oligocene in Puerto Rico, *Palmocarpon acrocomioides*, which has been compared with *Acrocomia crispa*, and *Bactris psuedocuesco* compared with extant *Bactris* species (Hollick, 1928). These fossils were used to calibrate the crown of subtribe Bactridinae at a minimal age of 30 My. Finally, the age of subtribe Attaleinae was constrained to a minimum age of 40 My, based on an endocarp described as *Attalea gunteri* from the Upper Eocene in Florida (Berry, 1929).

2.5.2. Socratea

Fossil flowers belonging to the genus *Socratea* (*S. brownii* Poinar) have been recorded from Mexican amber associated with marine formations from the Oligocene, with radiometric ages from 22.5 to 26 My. As the amber is secondarily deposited here (Poinar, 2002), the fossil must necessarily be older, but how much cannot be stated. Following this argument we imposed a minimal age constraint of 25 My for the node leading to *Socratea*.

2.5.3. Sclerosperma

Although fossilized pollen has often been dubiously associated with extant palm genera, the correspondence of some records with extant taxa can be unambiguously determined. Such is the case of the triporate pollen of *Sclerosperma* from the Miocene in Senegal (Médus, 1975). We used this fossil to constrain the node leading to *Sclerosperma* at a minimal age of 5 My.

2.5.4. Root node

The age of the root node was fixed in the PL analysis to 83.5 My following recent estimates provided by Gunn (2004) and Savolainen et al. (2006) based on the age of the oldest known palm fossil *Sabalites magothiensis* (Berry, 1905). In the case of the Bayesian dating, the *a priori* age of the root node was set to 85 million years (1.7 time units) with a standard deviation of 5 million years (0.1 time units).

3. Results

3.1. Analysis of plastid DNA sequences

The aligned matrix of *trnL-trnF* sequences consisted of 1043 characters, of which 29 (2.8%) were potentially parsimony informative. The heuristic search resulted in 12 MP trees (43 steps, CI = 0.79, RI = 0.93). The strict consensus tree (supplementary material) resolved *Hyophorbe* as non-monophyletic, whereas the tribe Chamaedoreeae and the other genera were monophyletic with bootstrap supports (BS) of 52% (Chamaedoreeae), 73% (*Gaussia*), 87% (*Chamaedorea*), and 92% (*Synechanthus*).

The combined matrix of cpDNA contained 5697 characters, of which 127 characters were excluded *a priori*, because homology could not been assessed unambiguously (see Cuenca and Asmussen-Lange, 2007). Of the remaining 5570 characters, 201 were potentially parsimony informative (3.6%). A total of 7301 trees were obtained after the two rounds in the heuristic search (341 steps, CI = 0.65,

RI = 0.88). The strict consensus tree recovered the tribe Chamaedoreeae (BS = 100%, DI = 20, Fig. 1) and each of the genera as monophyletic (BS = 100% in each case, DI ranged from nine steps in *Gaussia* to 17 steps in *Hyophorbe*). Two monophyletic groups were identified within Chamaedoreeae, one consisted of *Hyophorbe* and *Wendlandiella* (BS = 79%, DI = 2), and the other of *Chamaedorea, Synechanthus*, and *Gaussia* (BS = 68%, DI = 1); however, the relationship among these last three genera remains unresolved. Three lineages are recovered within *Chamaedorea*, the first including the clade formed by *C. linearis* and *C. fragrans* (BS = 100%, DI = 14), the second including all the species of subgenus *Eleutheropethalum* together with *C. elegans* (BS = 100%, DI = 10), and the third including all the remaining *Chamaedorea* species included in the analysis (BS = 53%, DI = 1).

3.2. Analysis of PRK

PRK sequences ranged from 531 base pairs in *Gaussia maya* to 638 base pairs in *Manicaria saccifera*. The aligned matrix consisted of 706 characters of which 47 characters

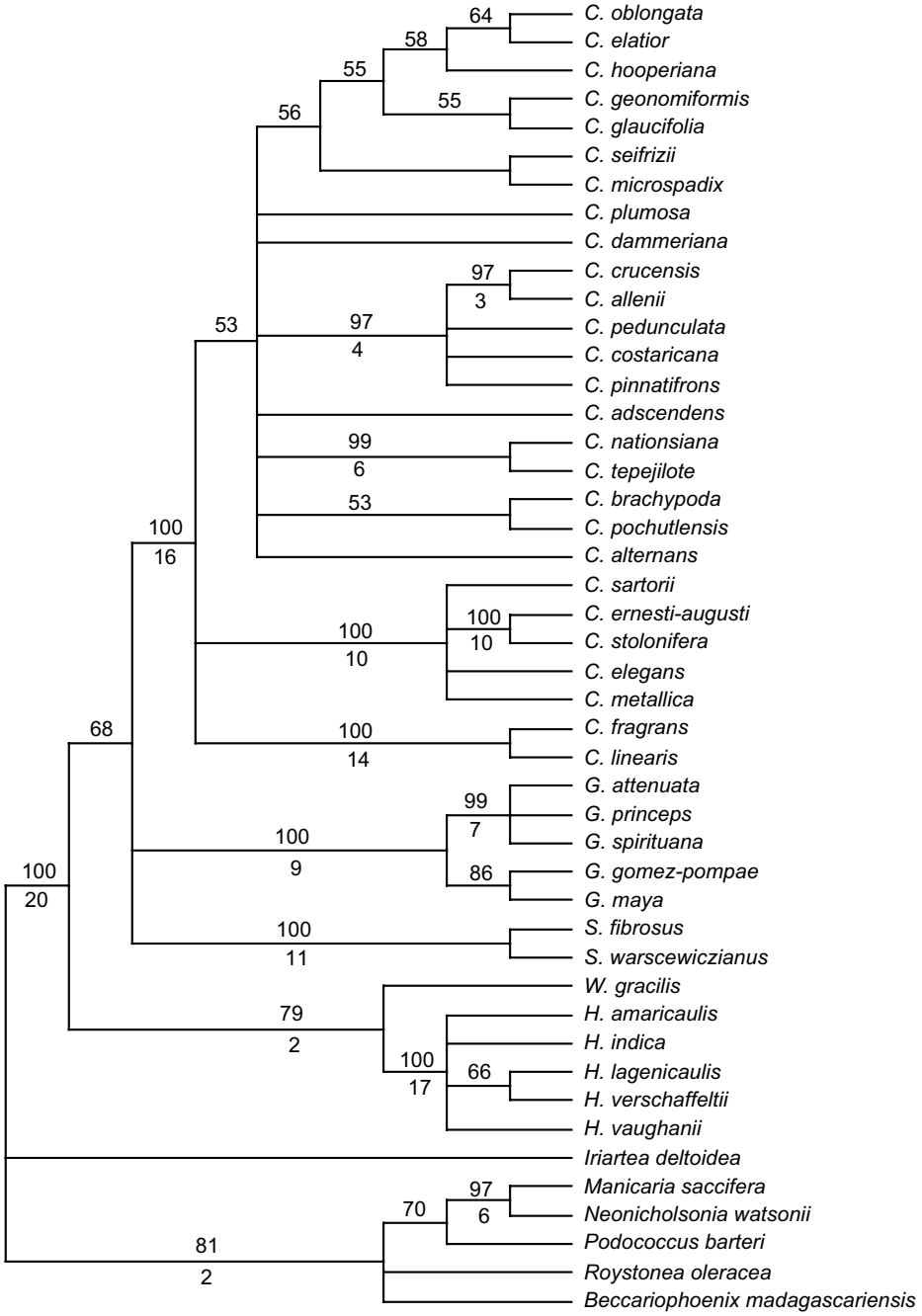

Fig. 1. Strict consensus tree of the 7301 most parsimonious trees resulting from a combined analysis of five plastid regions (*mat*K, *rps*16 intron, *trn*D-*trn*T, *ndh*F, and *trn*L-*trn*F; 5570 included characters, 201 potentially informative characters, length = 341 steps, CI = 0.65, RI = 0.88). BS values are shown above the branches and DI values different than one are shown below the branches.

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were excluded from analysis due to difficulties in assessing homology in alignment. Of the remaining 659 characters, 140 (21.2%) were potentially parsimony informative. The MP analysis of PRK sequences resulted in 30 MP trees (length = 245 steps, CI = 0.75, RI = 0.92). The strict consensus tree recovered Chamaedoreeae, *Hyophorbe*, *Gaussia*, and *Chamaedorea* as monophyletic (Fig. 2A). The relationships among genera were resolved with *Hyophorbe* as sister to the other four Chamaedoreeae genera (BS = 100%, DI = 6). *Wendlandiella* was placed as sister to the remaining three genera from the Americas (BS = 83) which were resolved with *Synechanthus* as sister to *Gaussia* and *Chama-*

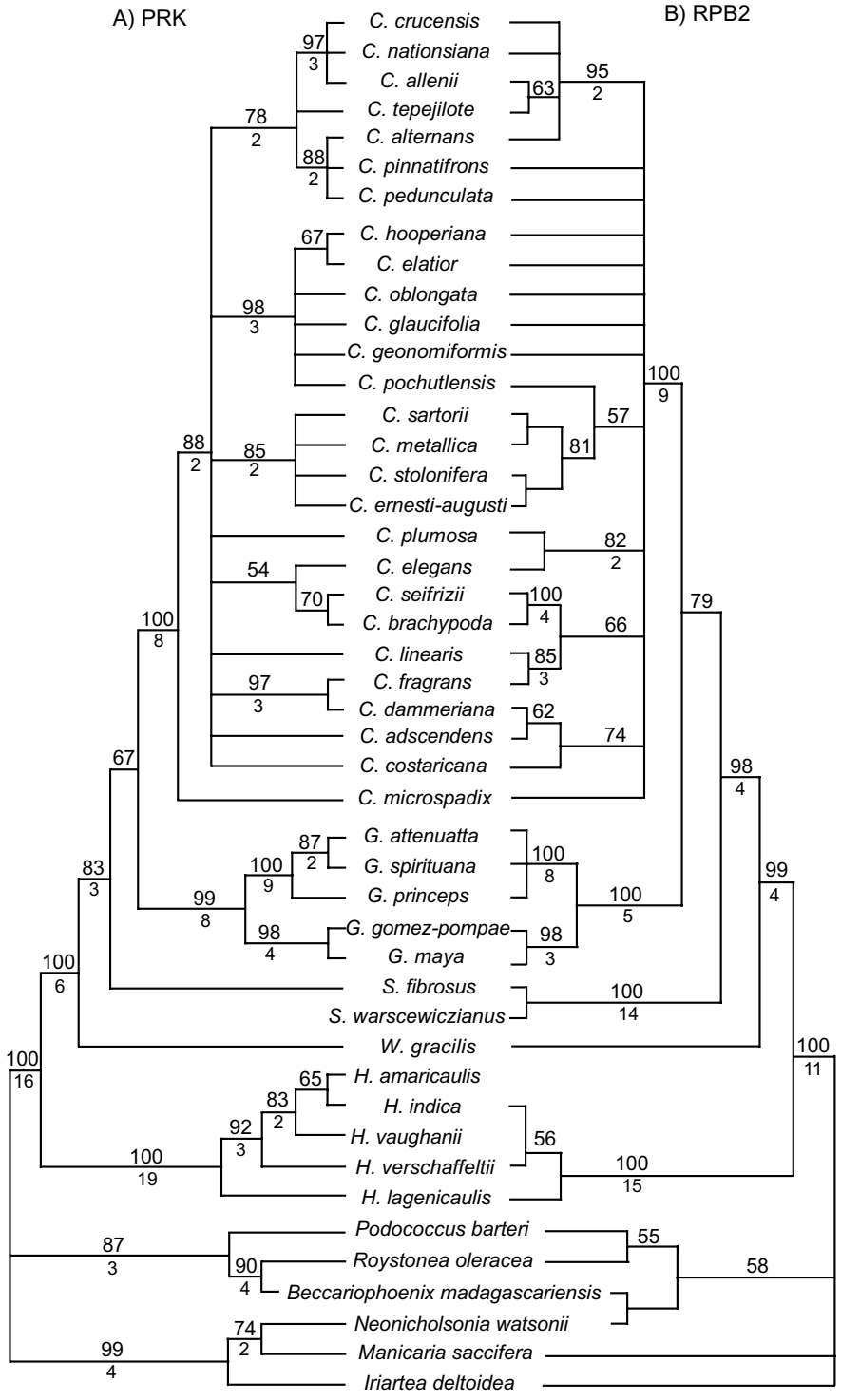

Fig. 2. (A) Strict consensus tree of the 30 most parsimonious trees resulting from an analysis of the nuclear region PRK (659 bases, 140 potentially informative characters, length = 245 steps, CI = 0.75, RI = 0.92). (B) Strict consensus tree of the eight most parsimonious trees resulting from an analysis of the nuclear region RPB2 (927 bases, 141 potentially informative characters, length = 268 steps, CI = 0.69, RI = 0.83). BS values are shown above the branches and DI values different than one below the branches.

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edorea with BS = 67%. Within the genus *Chamaedorea*, subgenus *Eleutheropethalum* was recovered as monophyletic (BS = 85%, DI = 2). Subgenus *Stephanostachys* was paraphyletic with *C. pedunculata* and *C. pinnatifrons* while subgenera *Chamaedorea* and *Chamaedoropsis* were both polyphyletic.

3.3. Analysis of RPB2

The RPB2 sequences ranged from 666 base pairs in *Roystonea oleracea* to 823 base pairs in *Gaussia princeps*. The aligned matrix consisted of 992 characters of which 65 were excluded from analysis due to difficulties in assessing homology. Of the remaining 927 characters, 141 (15.2%) were potentially parsimony informative. Analysis of RPB2 sequences resulted in eight MP trees (length = 268 steps, CI = 0.69, RI = 0.83). The tribe Chamaedoreeae and all its genera were resolved as monophyletic with a similar topology as in the PRK analysis but with slightly higher BS support (Fig. 2B). *Chamaedorea* subgenera *Eleutheropethalum* and *Stephanostachys* were both recovered as monophyletic with BS = 81% and 95%, respectively.

3.4. Combined analysis of plastid and nuclear sequences

The combined matrix of plastid and nuclear DNA sequences included 7395 characters, of which 239 were excluded *a priori*. Of the remaining 756 characters, 482 were parsimony informative. The MP analysis (Fig. 3) resulted in 85 trees (length = 906 steps, CI = 0.65, RI = 0.86). The topology of the Bayesian 50% majority rule consensus tree was identical to that of the MP analysis, except for the node (*C. seifrizii*, *C. brachypoda*), (*C. linearis*, *C. fragrans*), which was collapsed in the Bayesian tree. In both analyses all genera were recovered as monophyletic with high support (BS = 100%, PP = 1.0). *Hyophorbe* was placed as sister to the remaining members of the tribe (BS = 98%, DI = 9, PP = 1). The relationships within *Hyophorbe* were fully resolved with BS support of 80–94% at internal nodes. *Wendlandiella* was recovered as sister to the other three genera from the Americas (BS = 99%, DI = 9, PP = 1.0). *Synechanthus* was resolved as sister to a (*Gaussia, Chamaedorea*) clade with moderate support (BS = 72%, DI = 2, PP = 0.57).

Within *Chamaedorea* a limited number of species groups were recovered with high BS support, but the relationships among these groups were mostly unresolved. *Chamaedorea microspadix* was placed as sister to the remaining *Chamaedorea* species (BS = 65%, DI = 1, PP = 0.71). Subgenus *Stephanostachys* was recovered as paraphyletic. *Chamaedorea elegans* was firmly placed as sister to subgenus *Eleutheropethalum* (BS = 98%, DI = 10, PP = 1). Otherwise clades did not correspond to the subgenera previously defined in the genus.

Although the PHT showed incongruence among all partitions, the Partition Bremer support indicated only few nodes with a high level of incongruence. At the generic level, the placement of *Gaussia* as sister to *Chamaedorea* had low support by nuclear regions (PBS = 1 + 1) and it is slightly rejected by plastid data (PBS = −1). The position of *Wendlandiella* is strongly supported by nuclear data (PBS = 6 + 5) but slightly rejected by plastid data (PBS = −2). Otherwise incongruence related mostly to internal nodes in the genus *Chamaedorea*, most notably the clade formed by subgenus *Stephanostachys* together with *C. pinnatifrons, C. costaricana*, and *C. pedunculata*, where nuclear data support the clade with a PBS of 3.5 + 2.8 while plastid data reject it with a PBS of −5.3.

3.5. Divergence time analysis

The combined M2 matrix of seven DNA regions (*mat*K, *ndh*F, *trn*D-*trn*T, *rps*16 intron, *trn*L-*trn*F, PRK, and RPB2) included 8480 characters, of which 477 were excluded *a priori*. Of the remaining 8003 characters, 887 (11.1%) were potentially parsimony informative. The MP analysis recovered 192 most parsimonious trees (length = 2,400 steps, CI = 0.523, RI = 0.790). The relationships among members of Chamaedoreeae were the same in the analysis of the M1 and M2 matrices.

Penalized likelihood analysis of the M2 matrix estimated the stem of Chamaedoreeae to 71.9 My, whereas the crown node of tribe Chamaedoreeae was estimated to 53.2 My. The crown age for each genus was estimated to 20.1 My for *Chamaedorea*, 19.3 My for *Synechanthus*, 17.9 My for *Gaussia*, and 11.7 My for *Hyophorbe* (Table 1, Figs. 4 and 5). Analyses performed on the complete data matrix (reversing the exclusion of 12 *Chamaedorea* species to improve the balance of the taxon sample; results not shown) gave an identical value of the smoothing factor ($\lambda = 32$) and divergence time estimates for members of Chamaedoreeae varied between 0.5 and 1.7 My from the results obtained using the M2 matrix.

The Bayesian dating analysis, where the age of the root was freely estimated rather than fixed, in general resulted in older divergence time estimates than PL for all nodes. The age of the crown of subfamily Arecoideae was estimated to be 81.4 ± 4.8 My. The stem node of Chamaedoreeae was estimated to be 79.5 My old and the crown node 50 My. The crown nodes of the Chamaedoreeae genera were estimated to 21.2 My for *Chamaedorea*, 19.5 My for *Synechanthus*, 20.8 My for *Gaussia*, and 14.0 My for *Hyophorbe* (Table 1, Fig. 5). The age estimates for the deeper nodes in the phylogeny were slightly younger when all taxa were included, while those of the more recent nodes in general were slightly older (around 1 My older).

4. Discussion

4.1. Phylogenetic relationships of the tribe Chamaedoreeae

The present study is the first to provide a full resolution of the generic relationships among members of Chamaedoreeae based on molecular data. Analyses based in plas-

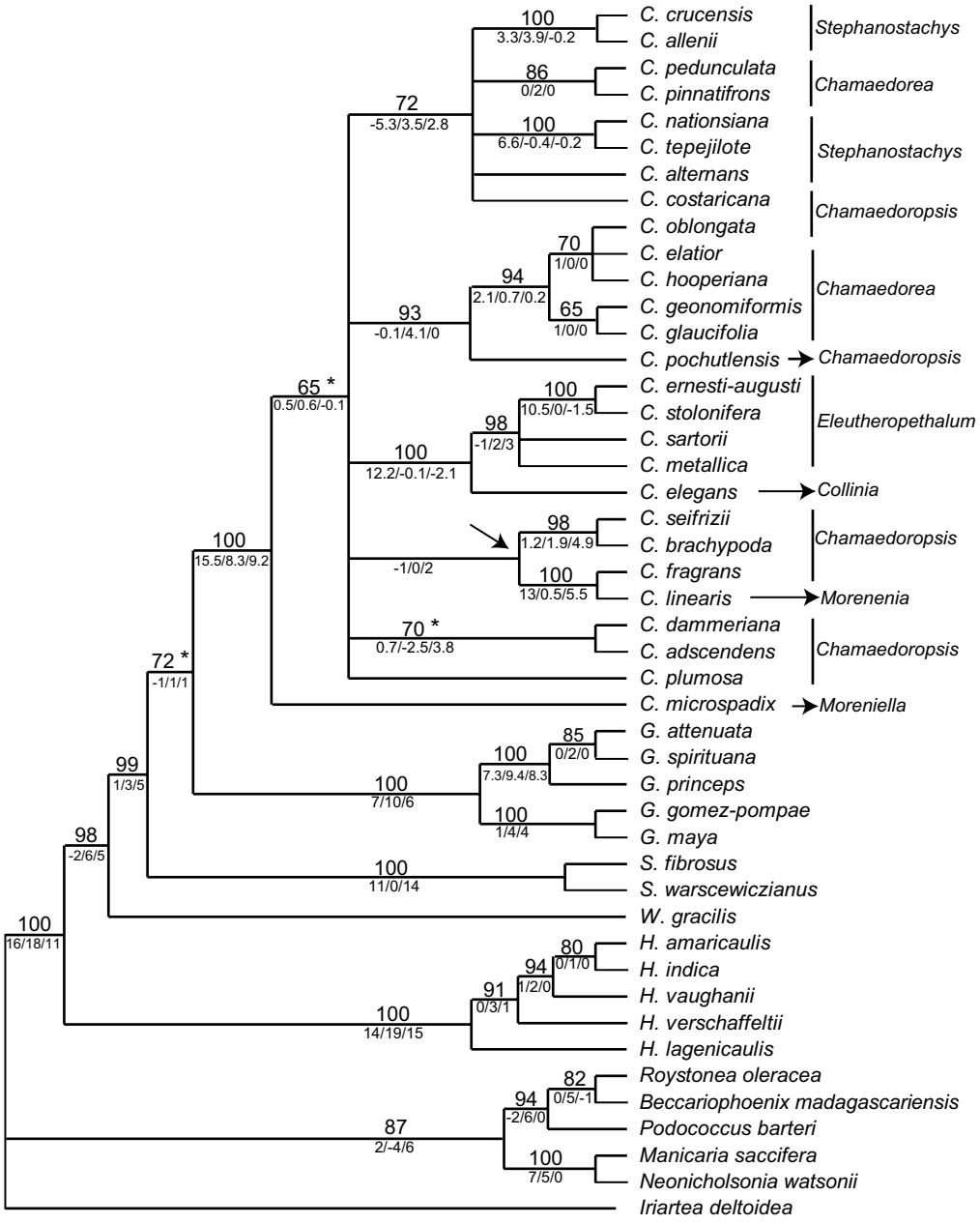

Fig. 3. Strict consensus tree of the 85 equally most parsimonious trees resulting from a combined analysis of two nuclear (PRK and RPB2) and five plastid (*mat*K, *ndh*F, *trn*L-*trn*F, *rps*16 intron, *trn*D-*trn*T) DNA regions (7156 bases, 482 informative characters, length = 906 steps, CI = 0.65, RI = 0.86). BS values are shown above the branches. Nodes with posterior probabilities (PP) smaller than 0.95 are indicated with an asterisk. PBS values are indicated above the branches in the following order: plastid/PRK/RPB2. Hodel's (1992) subgeneric classification of *Chamaedorea* is indicated at the right. The arrow indicates the node that is collapsed in the Bayesian 50% majority rule consensus tree.

tid DNA sequences (Cuenca and Asmussen-Lange, 2007; the present paper) recovered *Hyophorbe* and *Wendlandiella* as sister genera, with moderate support (Fig. 1). Analyses based on nuclear DNA sequences placed *Hyophorbe* as sister of the remaining chamaedoroid genera, and *Wendlandiella* as sister to the other American genera within the tribe (Fig. 2; Thomas et al., 2006). This same topology is obtained when plastid and nuclear DNA data are combined (Fig. 3). On the combined analysis both, *Hyophorbe* as sister to the remaining genera of Chamaedoreeae (BS = 98%) and *Wendlandiella* as sister to the remaining American genera, are recovered with high bootstrap support (98% and 99%, respectively, Fig. 3). We therefore consider the position of these genera fully resolved. The relationships among *Gaussia*, *Synechanthus*, and *Chamaedorea* are more problematic. The two studies cited above recovered either a polytomy among the three genera or placed *Gaussia* as sister to *Synechanthus* with low support. Our findings indicate that *Gaussia* and *Chamaedorea* are sister genera (Fig. 3) with moderate bootstrap support in the combined analysis of all data sets (BS = 72%). The association between *Chamaedorea* and *Gaussia* is striking,

Table 1
Ages in million years estimated for members of Chamaedoreeae based on a combined analysis of two nuclear DNA regions (PRK and RPB2) and five plastid DNA regions (*mat*K, *ndh*F, *rps*16 intron, *trn*L-*trn*F, and *trn*D-*trn*T) and two dating methods implemented

	PL analysis	Bayesian dating
Chamaedoreeae (stem)	71.9 (64.6–74.4)	79.5 (70.4–89.2)
Chamaedoreeae	53.2 (38.7–54.3)	50.0 (39.9–60.0)
Hyophorbe	11.7 (5.6–15.4)	14.0 (7.5–23.5)
Wendlandiella (stem)	45.7 (32.5–49.6)	44.0 (34.1–54.5)
Synechanthus	19.3 (11.7–23.7)	19.5 (12.2–28.8)
Gaussia	17.9 (10.2–22.6)	20.8 (12.7–30.4)
Chamaedorea	20.1 (12.7–24.9)	21.2 (13.9–30.1)

The ages correspond to the crown group of each clade, except were it is indicated otherwise. Confidence intervals obtained from the Penalized likelihood analysis, as well 95% probability intervals from the Bayesian analysis are indicated for each node.

since the two genera seem very different in their habitat, size, leaf, and root morphology, and reproductive system. A similar result, however, is obtained when plastid and morphological data are combined (Argelia Cuenca, unpublished data).

This study also provides full resolution at species level in *Hyophorbe* and *Gaussia*. We recovered *Hyophorbe lagenicaulis,* endemic to Mauritius, as sister to all other *Hyophorbe* species, followed by *H. verschaffeltii* from Rodriges Island sister to the remaining three species. This result disagrees slightly with the monographic work of *Hyophorbe* by Moore (1978) who considered *H. verschaffeltii* to be the species with most ancestral character states. In our phylogeny *Hyophorbe indica*, an endemic to the youngest of the Mascarene Islands, Reunion, is embedded in a clade formed by two species occurring on Mauritius (*H. amaricaulis* and *H. vaughanii*), perhaps reflecting a recent migration from that island. For *Gaussia* the findings presented here correspond to those of previous studies (Cuenca and Asmussen-Lange, 2007). The genus consists of two highly supported clades, corresponding to the two-continental species *G. maya* and *G. gomez-pompae*, once placed in the genus *Opsiandra*, and the three Caribbean species, respectively. *Opsiandra* and *Gaussia* were united by Quero and Read (1986) as they found fruit size and shape to be the single consistent morphological difference between the two species groups. Although our results suggest that the continental and Caribbean species form two independent lineages, the weak morphological differentiation does not justify their separation into distinct genera.

Our study does not support the subgeneric division of *Chamaedorea* proposed by Hodel (1992) based on flower and inflorescence morphology. A few of Hodel's subgenera, however, appear to constitute natural entities. Subgenus *Eleutheropethalum* is supported as monophyletic with 98% BS support. Subgenus *Stephanostachys* was recovered as paraphyletic with *C. pinnatifrons*, *C. pedunculata*, and *C. costaricana*, which is consistent with plastid DNA sequences, but not with nuclear data, which recovered *Stephanostachys* as monophyletic (see Thomas et al., 2006). *Chamaedorea microspadix* from subgenus *Morenielle* is placed as sister to the remaining *Chamaedorea* species with low support (BS = 65%, PP = 0.71), a result also obtained by Thomas et al. (2006). Otherwise resolution within *Chamaedorea* was low. A polytomy of five clades was recovered (Fig. 3), two of which were well supported. The two South American species *C. linearis* and *C. fragrans* were recovered as sisters, a result which is consistent with previous phylogenetic analyses (Cuenca and Asmussen-Lange, 2007; Thomas et al., 2006).

4.2. Biogeography of Chamaedoreeae

The results of our analyses placed the stem of the Chamaedoreeae at the end of the Cretaceous, from the Campanian to the Maastritchian (70–85 My old; Table 1. Figs. 4 and 5), whereas its crown group was placed in the Lower Eocene (50 My, Table 1, Figs. 4 and 5). To explain the current distribution of the Chamaedoreeae, a West Gondwanan origin for the tribe has been suggested, with subsequent diversification following the Gondwana break-up and extinction of species in the bridging places such as Africa (Moore, 1973a,b, 1978; Uhl and Dransfield, 1987). The separation of the African and South American plates occurred by the end of the Albian (96 My), but it is known that plant dispersals were frequent across the newly formed Atlantic until the early Tertiary, possibly through a series of islands that remained emergent throughout this period (Morley, 2000). As expected, the basal diversification of the tribe (node A, Fig. 5) is clearly too young (40–60 My, Table 1) to be caused by the Gondwana break-up. A number of interplate dispersal routes for megathermal angiosperms, however, have been proposed to exist during the early tertiary (Palaeocene–Eocene), facilitated by the combination of warm climates and relative proximity of the major continents (Morley, 2003; Muellner et al, 2006; Pennington and Dick, 2004). These include (1) a trans-oceanic dispersal route either along the mid-oceanic Rio Grande ridge, which could have been above sea level until the Oligocene (Morley, 2000), or along the more southern Walvis ridge and (2) a Boreotropical dispersal route across a North Atlantic land bridge connecting Europe and North America, as suggested for, e.g., Malphigiaceae (Davis et al., 2002). Both of these passageways could in principle have facilitated exchange of ancestral Chamaedoreeae between the Old and the New World within the time-frame indicated by our dating estimates for the basal split in the tribe. These findings do not contradict the hypothesis stated by Moore (1978) that *Hyophorbe* is a lineage with a long evolutionary history whose ancestors possibly migrated to the Mascarene Islands from Africa or Madagascar, where they are now extinct. There is, however, no evidence for the presence of *Hyophorbe* or any other member of the Chamaedoreeae in Africa.

Trans-Atlantic dispersal between Africa and South America is well in line with the Amazon distribution of *Wendlandiella*. Under such a scenario there would have

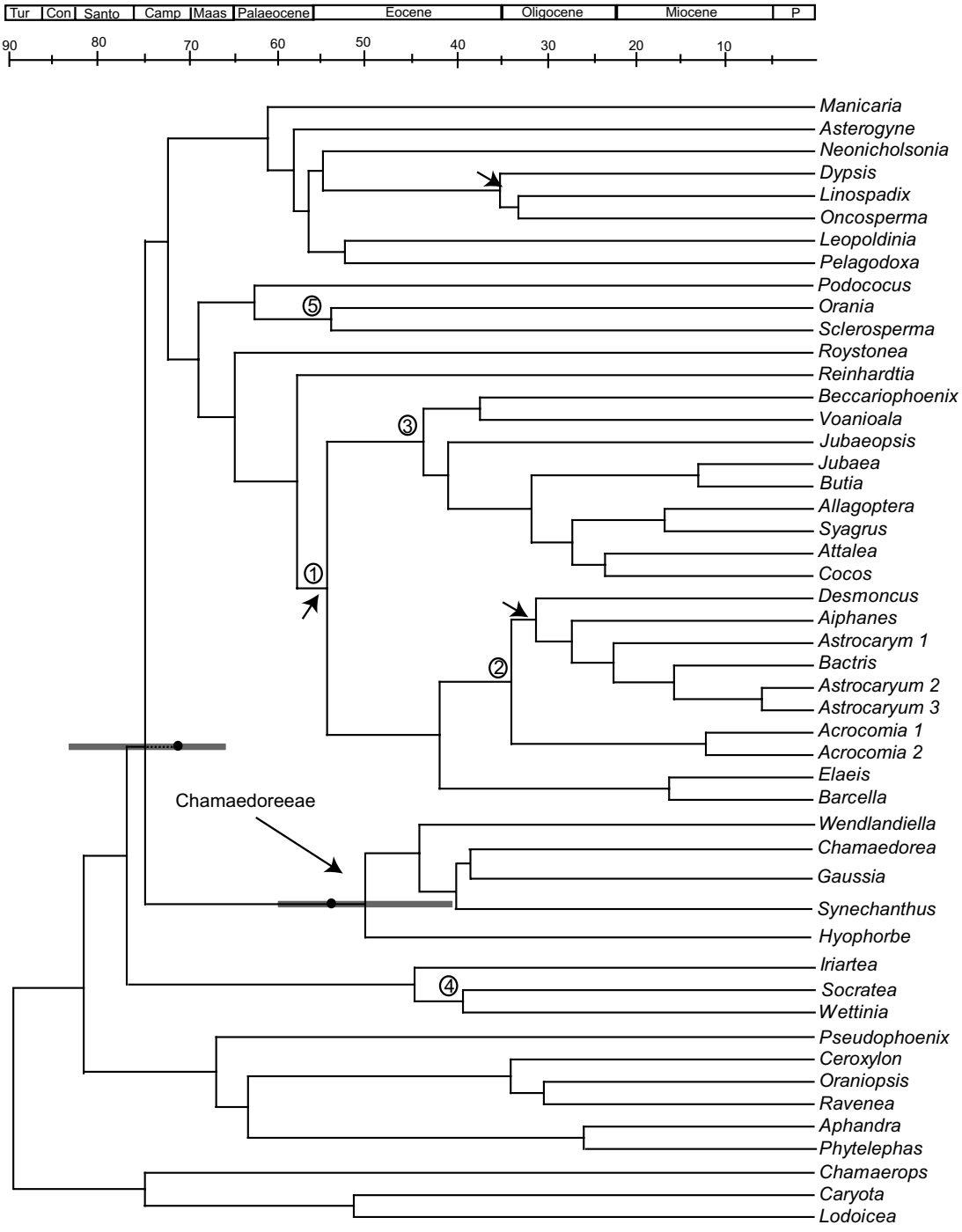

Fig. 4. Cronogram resulting from the dating analysis of the extended matrix (M2) indicating calibration nodes. The 95% probability interval obtained in multidivtime for the stem and crown nodes of Chamaedoreeae are given in grey. The full circles indicate the age estimated using penalized likelihood for each node. The small arrows indicate nodes collapsed in the strict consensus tree from the parsimony analysis. The species of Chamaedoreeae have been removed in order to gain clarity in the figure. The ruler at the top of the figure indicate ages in My and the geological timescale.

been an ancestral distribution of the American Chamaedoreeae in South America, followed by an early dispersal to North America of the ancestor of the *Synechanthus–Gaussia–Chamaedorea* clade. Independent redispersals from North to South would then have occurred in *Synechanthus warscewiczianus* and at least two subclades of *Chamaedorea* (*C. linearis–C. fragrans* clade; *C. pinnatifrons*; the latter not included in our taxon sample but shown by Thomas et al. (2006) and Cuenca and Asmussen-Lange (2007) to belong to a clade different from the first two species). Alternatively, a Boreotropical dispersal route would assume a north hemispherical ancestral distribution of the American Chamaedoreeae with an early migration of the ancestor of *Wendlandiella* into South America. Again independent redispersals of *Synechanthus* and *Chamaedorea* species to South America would be

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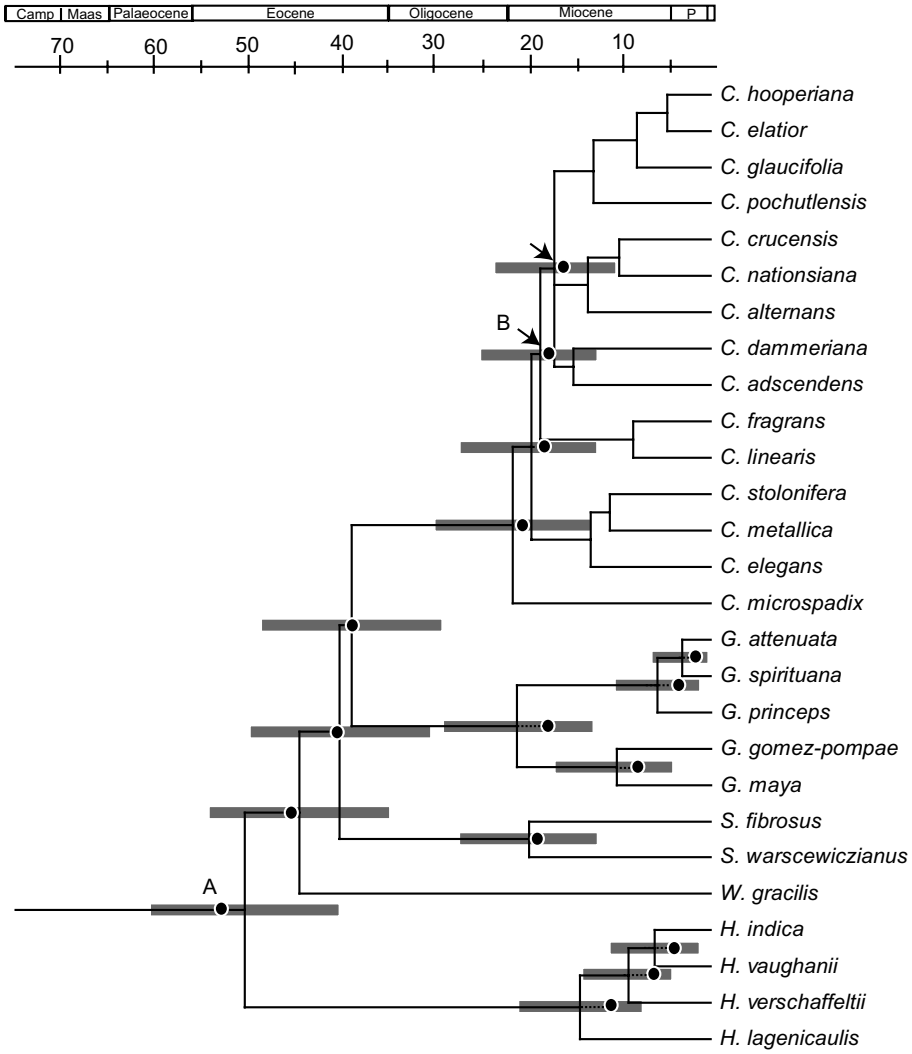

Fig. 5. Cronogram for members of the tribe Chamaedoreeae. Relevant nodes with their 95% probability interval obtained in multidivtime in grey. The full circles indicate the age estimated using PL for each node. The small arrows indicate nodes collapsed in the consensus tree from the parsimony analysis. The ruler at the top of the figure indicate ages in My and the geological timescale. Node A indicates the separation of *Hyophorbe* from the American genera. Node B indicates the separation of the South American species of *Chamaedorea* from their Central American relatives.

required. The two solutions are equally parsimonious when Chamaedoreeae is regarded in isolation, but assuming a Gondwana origin of the entire Arecoideae subfamily, as suggested by Moore (1973b), and a sub basal position of Chamaedoreeae within this subfamily, the former solution may seem more likely. An alternative hypothesis includes dispersal through Antarctica into southern Africa; however, this seems improbable in view of the ancient split between Africa and Australasia (Davis et al., 2002; Morley, 2000). No matter which scenario is favoured an early arrival and radiation of Chamaedoreeae in North America is strongly indicated by our results.

4.3. *Hyophorbe*

The Mascarene Islands are a group of volcanic islands of recent geological formation located 700–1400 km east from Madagascar. The age of Mauritius, the oldest of the Mascarene Islands, has been estimated to ca. 7.5 million years (McDougall and Chamalaun, 1969), however, it has been suggested that Rodrigues Island could be at least as old as Mauritius, with an age between 8 and 10 million years (Austin et al., 2004). Reunion, the third of the Mascarene Islands, is younger, formed around 3 My ago. If *Hyophorbe* arose in the Mascarenes, then the crown group of this genus should be younger than the archipelago. Bayesian analysis indicate an age of 14 My (95% = 7.5–23.5 My) for the crown group of *Hyophorbe* while PL suggest an age of 11.7 My (5.6–15.4 My; Table 1). Both estimates are older than the Mascarenes although the lower 95% confidence interval boundary just falls within the assumed age of the islands. If *Hyophorbe* is older than the Mascarenes then it could be explained by at least two non-exclusive scenarios. The first one involves independent migration of the ancestor of *H. lagenicaulis* to Mauritius followed by dispersal of the ancestor of the

remaining *Hyophorbe* species to Rodrigues. The second assumes the occurrence of the ancestral population of *Hyophorbe* on islands that are currently submerged. The Reunión hotspot, which created the Mascarene Islands 8 My ago, started its activity around 65 My and there is some evidence that the Mascarene plateau once formed an archipelago much bigger than the Mascarenes today. Most of these islands are now placed 10–40 m below sea level, and only small islets remain emerged (Austin et al., 2004; Turner and Klaus, 2005). It has been proposed that these now submerged islands have played an important role in the colonization of the Mascarenes, constituting places where old groups that are now endemics to these islands could have occurred (see for example the case of the *Phelsuma* gekos, Austin et al., 2004; and the dodo, Shapiro et al., 2002). These observations stress the potential risk of using the age of volcanic islands for phylogenetic dating.

4.4. Connections between North and South America

As earlier stated, our analyses indicate that the first diversification of the Neotropical Chamaedoreeae members occurred with the separation of the lineage leading to *Wendlandiella* from that leading to *Synechanthus*, *Gaussia*, and *Chamaedorea* (Fig. 5). *Wendlandiella* is a monotypic genus distributed in the western Amazon region, whereas *Chamaedorea* and *Synechanthus* occur in both North America and western South America. *Gaussia* is exclusively North American. The basal diversification of the Neotropical genera corresponds in time to the Eocene, around 45 My ago (Figs. 4 and 5). This is consistent with the hypothesis of a pathway connecting South and North America when the proto Antilles collided with the Bahamas plate, and with the principal emergence of the islands in the Middle Eocene. This hypothesis suggested that the recently emerged Antilles could form a fragmented migratory pathway between both land masses around 50 My ago (Graham, 2003; Morley, 2003; Pennington and Dick, 2004). Otherwise the observed pattern of cladogenesis showed at least two subsequent interplate migrations. These include (1) a dispersal of *Synechanthus warscewiczianus* to the Choco region and western Ecuador and (2) migration of the (*Chamaedorea linearis*, *C. fragrans*) clade to western South America. With exception of *C. pauciflora*, also part of the (*C. linearis*, *C. fragrans*) clade (Thomas et al., 2006), the phylogenetic position of the other *Chamaedorea* species endemics to South American is not known at present. While interplate dispersal of *Synechanthus* could have been a recent event, the *Chamaedorea* species endemic to South America form a clade that is clearly too young (18.3 My, 95% interval = 12–26 My) to be explained by a migration through the Middle Eocene bridge (ca. 50 My ago) or by the Aves ridge bridge (ca. 35–33 My ago). *Chamaedorea* is too old to have used the Panamanian isthmus (ca. 3 My). This result mirrors those of several other studies indicating that a significant dispersal took place between Mesoamerica and South America prior to the closure of the Isthmus of Panama. Examples are Neotropical trees (Cavers et al., 2003), Valerianaceae plants (Bell and Donoghue, 2005), hummingbirds (García-Moreno et al., 2006), frogs (Crawford, 2003), reptiles (Savage, 1982), artropods (Zeh et al., 2003), and primary (Bermingham and Martin, 1998) and secondary (Concheiro-Pérez et al., 2007) fresh water fishes. Since these migrations in many cases involve groups that are not able to tolerate salt water, a dry-land connection between the continents during the Miocene has been inferred (Bermingham and Martin, 1998; Zeh et al., 2003; Concheiro-Pérez et al., 2007). Our results point in the same direction, even though no geological evidence for a connection has been produced so far. In addition, recent independent dispersals must have occurred in species such as *C. pinnatifrons*, the distribution of which includes both sides of the Panama isthmus (Fig. 3).

4.5. Diversification of Gaussia in the Caribbean

The colonization of the Greater Antilles from the central America by *Gaussia* is marked by the divergence of the clade formed by *G. princeps, G. attenuata*, and *G. spirituana* from the continental species ca. 20 My ago (Fig. 5). A physical connection between Cuba and the Yucatan Peninsula during the Early Eocene has been proposed (Graham, 2003), however, this event is clearly too old to explain the presence of *Gaussia* in the Greater Antilles. In the same way, the separations of Cuba from Hispaniola and of Hispaniola and Puerto Rico in the Early to Middle Miocene are also too old to explain the cladogenesis events among *Gaussia* species. Instead, the phylogenetic relationships among the three members of *Gaussia* occurring in the Greater Antilles could be explained by a migration via stepping stone, from the Eastern part of Cuba (Pinar del Rio, *G. princeps*) to the central part of the island (*G. spirituana*, Sierra de Jatibonico) and from there to Puerto Rico and possibly Hispaniola (*G. attenuata*).

4.6. Conclusion

The present study provides resolution of the phylogenetic relationships among the genera of tribe Chamaedoreeae, albeit with low support for the sister relationship between *Gaussia* and *Chamaedorea*. The disjunction between the ancestor of *Hyophorbe* and the ancestor of the Neotropical genera of the tribe is found to be too young to be caused by a Gondwanan vicariance followed by displacement of *Hyophorbe* to the Mascarenes. Inter plate dispersal during the Late Eocene is needed to explain the presence of *Hyophorbe* in the Mascarene Islands. Evidence for Eocene inter-continental dispersal in Chamaedoreeae match the findings in other recent studies of the palm family, e.g., within the Cocoseae (Gunn, 2004) and the Ceroxyleae (Trénel et al., 2007). The estimated age for the crown node of *Hyphorbe* in combination with data on the geology of the Mascarene Islands suggest that the radiation of *Hyophorbe* may have taken place on

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islands in the Indic Ocean now submerged predating the creation of the present day Mascarene archipelago.

Latitudinal migration has played an important role shaping the diversity and biogeography of the American Chamaedoreeae, as for several other plant and animal groups. At least two independent dispersals between North and South America predating the closure of the Isthmus of Panama are needed to explain the current distribution of the tribe: one during the Middle Eocene and the other in the Miocene. Species such as *Synechanthus warscewiczianus* and *Chamaedorea pinnatifrons* could have reached South America after the isthmus was formed. To explain the presence of *Gaussia* in the Caribbean Islands, we suggest a west–east stepping stone/sweepstake dispersal process starting in the Central America and ending in Puerto Rico. While the traditional interpretation of the Chamaedoreeae assumes a west Gondwana origin with subsequent dispersal to North America, our results make it equally possible to interpret the group as a primarily boreotropical element. Under this scenario, the present day distribution of Chamaedoreeae may reflect a retraction following the demise of the boretropical palaeobiome resulting from Mid-Tertiary global cooling. A strong northern bias in the biogeography of the *Synechanthus–Gaussia–Chamaedorea* assemblage, together with a possible leaf macrofossil (*C. danai*) indicating an even more northerly distribution of chamaedoroid palms in the Eocene, is compatible with such interpretation.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ympev.2007.10.010.

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