

Molecular Phylogenetic Studies of Caribbean Palms (Arecaceae) and Their Relationships to Biogeography and Conservation

Julissa Roncal^{1,4} · Scott Zona² · Carl E. Lewis^{2,3}

¹ Department of Biological Sciences, University of Aarhus, Ny Munkegade 1540, DK-8000, Aarhus C, Denmark

² Department of Biological Sciences, Florida International University, 11200 SW 8th St., Miami, FL 33199, USA

³ Center for Tropical Plant Conservation, Fairchild Tropical Botanic Garden, 11935 Old Cutler Road, Coral Gables, FL 33156, USA

⁴ Author for Correspondence; e-mail: julissa.roncal@biology.au.dk

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Abstract The Caribbean Islands are one of the world's 34 biodiversity hotspots, remarkable for its biological richness and the high level of threat to its flora and fauna. The palms (family Arecaceae) are well represented in the West Indies, with 21 genera (three endemic) and 135 species (121 endemic). We provide an overview of phylogenetic knowledge of West Indian Palms, including their relationships within a plastid DNA-based phylogeny of the Arecaceae. We present new data used to reconstruct the phylogeny of tribe Cryosophileae, including four genera found in the West Indies, based on partial sequences of the low-copy nuclear genes encoding phosphoribulokinase (PRK) and subunit 2 of RNA polymerase II (RPB2). Recently published phylogenetic studies of tribe Cocoseae, based on PRK sequences, and tribes Cyclospatheae and Geonomateae, based on PRK and RPB2 sequences, also provide information on the phylogenetic relationships of West Indian palms. Results of these analyses show many independent origins of the West Indian Palm flora. These phylogenetic studies reflect the complex evolutionary history of the West Indies and no single biogeographical pattern emerges for these palms. The present day distributions of West Indian palms suggest complicated evolutionary interchange among islands, as well as between the West Indies and surrounding continents. We identified six palm lineages that deserve conservation priority. Species-level phylogenies are needed for *Copernicia*, *Sabal*, and *Roystonea* before we can build a more complete understanding of the origin and diversification of West Indian palms.

Resumen Las Islas del Caribe constituyen uno de los 34 “hotspots” de biodiversidad del mundo, notables por su riqueza biológica y el alto grado de amenaza de su flora y fauna. La familia Arecaceae esta bien representada en Las Antillas con 21 géneros (tres endémicos) y 135 especies (121 endémicas). Presentamos una síntesis del conocimiento filogenético de las palmas de Las Antillas incluyendo su posición dentro de la filogenia de la familia Arecaceae basada en ADN cloroplástico. Construimos una nueva filogenia para la tribu Cryosophileae,

la cual incluye cuatro géneros de Las Antillas, basada en secuencias parciales de los genes nucleares de copia baja fosforibulokinasa (PRK) y la ARN polimerasa II (RPB2). Los estudios filogenéticos publicados de la tribu Cocoseae basada en secuencias de PRK, y de las tribus Cyclospatheae y Geonomateae basadas en secuencias de PRK y RPB2, también proveen información sobre las relaciones filogenéticas de las palmas de Las Antillas. Estos resultados indican el origen evolutivo múltiple de estas palmas. Los estudios filogenéticos reflejan la compleja historia evolutiva de Las Antillas y no existe un único patrón biogeográfico para las palmas de esta región. Las distribuciones actuales de las palmas de Las Antillas sugieren un complejo intercambio entre islas, así como estre islas y las masas continentales vecinas. Identificamos seis linajes de palmas que merecen prioridad de conservación. Se necesitan estudios filogenéticos para los géneros *Copernicia*, *Sabal*, y *Roystonea* con el fin de mejorar nuestro entendimiento sobre el origen y diversificación de las palmas de Las Antillas.

Keywords Molecular Phylogenetic Studies · Caribbean Palms (Arecaceae) · Biogeography · Conservation · Low-copy Nuclear DNA

Introduction

Palms are symbols of tropical forest landscapes, and their usefulness, especially for human inhabitants of the tropics, has been documented for over 100 years (e.g. Wallace, 1853; Levi-Strauss, 1952; Dugand, 1972; Balick & Deck, 1990; Byg & Balslev, 2006). The economic importance of palms is comparable only to the that of grasses and legumes, as they provide sources of food, starch, salt, wax, fiber, oil, thatch, construction material, and medicine (e.g. Kahn & de Granville, 1992; Borchsenius et al., 1998; Vormisto, 2002). The importance and usefulness of palms to the Caribbean people have been noted since Europeans first came to the region (Columbus, 2001) and continue to this day (Read, 1988; Horst, 1997). In addition many Caribbean palms such as *Roystonea* and *Coccothrinax* have ornamental importance.

The fossil record of palms begins in the mid Late Cretaceous (Muller, 1981; Uhl & Dransfield, 1987; Harley, 2006). This long history has allowed them to diversify into hundreds of species and occupy almost every habitat in the tropics and subtropics (Henderson et al., 1995). Approximately 75% of the palms are restricted to tropical rain forests, where they are often abundant in the canopy and understory (Uhl & Dransfield, 1987; Kahn & de Granville, 1992; Terborgh et al., 1996; Borchsenius et al., 1998; Svenning, 2001). Not only are palms structurally significant in tropical forests, they are also major components in the diet of the invertebrate and vertebrate fauna, and some species are even considered to be “keystone” (Uhl & Dransfield, 1987; Peres, 1994; Svenning, 2001; Brightsmith, 2005).

The Caribbean Basin comprises three archipelagos and the neighboring continental areas along the Gulf of Mexico, Central America and Northern South America. The three Caribbean archipelagos are: the Greater Antilles, the Lesser Antilles and the Bahamas, which collectively are also known as the Caribbean Islands or the West Indies. Plant diversity of the West Indies consists of approximately 12,000

vascular species (in about 200 families), of which over 50% are endemic to the region (Myers et al., 2000; Santiago-Valentin & Olmstead, 2004; Smith et al., 2004). These endemic species make the Caribbean a biodiversity hotspot (Smith et al., 2004) as they represent 2% of the total number of vascular plants on Earth (Myers et al., 2000).

The two largest islands, Cuba and Hispaniola, contain the highest number of endemics at the specific and generic-levels (Gentry, 1982). Jamaica and Puerto Rico contain less diversity, and endemism on those islands is primarily at the species level (Santiago-Valentin & Olmstead, 2004). This pattern is exemplified in palms in that Cuba and Hispaniola have endemic palm genera while Jamaica and Puerto Rico have endemic species but no endemic genera.

Three main hypotheses explain the high species diversity in the West Indies. The first is the geographical proximity of the West Indies to the continental Neotropics rich in species diversity. The second is the presence of a mosaic of habitats that result from a wide range of altitudes, precipitation regimes, temperatures and geology. Third, some parts of the Greater Antilles date from approximately 70 to 100 Mya (Donovan & Jackson, 1994), a long time for species to originate and accumulate (Santiago-Valentin & Olmstead, 2004).

Most of our knowledge on the evolution and biogeography of the Caribbean biota comes primarily from zoological studies (e.g. Bermingham, 1994; Schubart et al., 1998; Hedges, 2006). There is however, an increasing interest in the application of plant phylogenetics to complement our understanding of the biogeography of this region (e.g. McDowell & Bremer, 1998; Graham, 2003; Fritsch & McDowell, 2003; Santiago-Valentin & Olmstead, 2004; Francisco-Ortega et al., 2007).

Here, we review the diversity and distribution of palms from the islands of the West Indies, recent molecular phylogenetic studies that include these palms, and provide some notes on the conservation and biogeography of these taxa. We do not include the islands of Trinidad and Tobago since floristically they are more similar to South America than to the West Indies and because they do not belong to the Caribbean Island Biodiversity hotspot. Nomenclature follows Govaerts & Dransfield (2005) for species and Dransfield et al. (2005) for genera, tribes and subfamilies.

Diversity and Distribution of Palms in the West Indies

Palms are a diverse group in the West Indies represented by quintessentially Caribbean genera like *Copernicia* and mainland South America genera like *Bactris*. Three of the five subfamilies recognized in the new classification of the Arecaceae (Dransfield et al., 2005; Asmussen et al., 2006) have indigenous species in the West Indies (Table 1). There are 135 species in 21 genera of palms in the West Indies, of which 121 are strictly endemic (Zona et al., 2007).

Coryphoideae

Eighty-one species in eight of the 44 genera of Coryphoideae are found in the West Indies (Table 1). Five species of *Sabal* [*S. causiarum* (O.F. Cook) Becc., *S. domingensis* Becc., *S. maritima* (Kunth) Burret, *S. palmetto* (Walter) Lodd. ex Schult. and Schult.f., *S. yapa* C. Wright ex Becc.] are distributed from the Bahamas

Table 1 Diversity and Distribution of West Indian Palm Flora

Subfamily–Tribe–Genus	Spp.	Distribution
CORYPHOIDEAE Burnett		
Sabaleae Mart ex. Dumort		
<i>Sabal</i> Adans.	5/16	Bah, Cub, His, Jam, PR
Cryosophileae J. Dransf, N. Uhl, C.A smussen, W. Baker, M. Harley and C. Lewis		
<i>Zombia</i> L.H. Bailey	1/1	His
<i>Coccothrinax</i> Sarg.	48/50	Bah, Cub, His, Jam, LA, PR
<i>Hemithrinax</i> Hook.f. in G. Bentham and J.D. Hooker	3/3	Cub
<i>Thrinax</i> L.f. ex Sw.	4/4	Bah, Cub, His, Jam, LA, PR
Trachycarpeae J. Dransf, N. Uhl, C. Asmussen, W. Baker, M. Harley and C. Lewis		
<i>Acoelorrhaphe</i> H. Wendl.	1/1	Bah, Cub
<i>Colpothrinax</i> Griseb. and H. Wendl.	1/3	Cub
<i>Copernicia</i> Mart. ex Endl.	18/21	Cub, His
CEROXYLOIDEAE Drude		
Cyclospatheae O.F. Cook		
<i>Pseudophoenix</i> H. Wendl. ex Sarg.	4/4	Bah, Cub, His, PR, LA
ARECOIDEAE Burnett		
Chamaedoreae Drude		
<i>Gaussia</i> H. Wendl.	3/5	Cub, His, PR
Roystoneae J. Dransf, N. Uhl, C. Asmussen, W. Baker, M. Harley and C. Lewis		
<i>Roystonea</i> O.F. Cook	9/10	Bah, Cub, His, Jam, PR, LA
Reinhardtiae J. Dransf, N. Uhl, C. Asmussen, W. Baker, M. Harley and C. Lewis		
<i>Reinhardtia</i> Liebm.	1/6	His
Cocoseae Mart.		
<i>Acrocomia</i> Mart.	2/3	Cub, His, Jam, PR, LA
<i>Aiphanes</i> Willd.	1/23	His, PR, LA
<i>Bactris</i> Jacq. Ex Scop.	3/76	Cub, His, Jam
<i>Desmoncus</i> Mart.	1/12	LA
<i>Attalea</i> Kunth in F.W.H. von Humboldt, A.J.A. Bonpland and C.S. Kunth	1/69	His
<i>Syagrus</i> Mart.	1/31	LA
Geonomeae Lueres		
<i>Geonoma</i> Willd.	2/59	His, LA
<i>Calyptronoma</i> Griseb.	3/3	Cub, His, Jam, PR
Euterpeae J. Dransf, N. Uhl, C. Asmussen, W. Baker, M. Harley and C. Lewis		
<i>Euterpe</i> Mart.	1/7	LA
<i>Prestoea</i> Hook.f. in G. Bentham and J.D. Hooker	1/10	Cub, His, PR, LA

For each genus, the taxonomic placement within the Arecaceae, the number of species in the West Indies/ total species number in the genus, and its geographical distribution are indicated. Island or archipelago abbreviations are as follows: *Bah* Bahamas, *Cub* Cuba, *His* Hispaniola, *Jam* Jamaica, *PR* Puerto Rico, and *LA* Lesser Antilles

to the Greater Antilles, growing in such diverse habitats as marshes, sandy coastal plains, tidal flats, seasonally inundated savannas, disturbed areas and pastures (Zona, 1990; Henderson et al., 1995).

The monotypic genus *Zombia* [*Z. antillarum* (Desc.) L.H. Bailey] is endemic to Hispaniola where it grows on low elevation seasonally dry forest, often over serpentine soil (Henderson et al., 1995). With its forty eight species, *Coccothrinax* is

the most diverse and widely distributed genus in the Caribbean, occurring in all three archipelagos, as well as areas bordering the Caribbean Basin. Its species grow on dunes, open woods, sandy soils overlying limestone, pinelands, limestone and serpentine soils, coastal or scrub woodland, seasonally flooded savannas, from sea level to 500 m elevation (León, 1939; Read, 1979; Borhidi & Muñoz, 1983; Henderson et al., 1995). *Hemithrinax* is endemic to Cuba and its three species [*H. compacta* (Griseb. and H. Wendl.) Hook.f. in G. Bentham and J.D. Hooker, *H. ekmaniana* (Burret) Borhidi and O. Muniz, and *H. rivularis* León] are confined to limestone cliffs, wet savannas, and serpentine soils (Borhidi & Muñoz, 1985). *Thrinax* contains four species, two of which are restricted to Jamaica [*T. excelsa* Lodd ex Mart., *T. parviflora* Sw.]. *Thrinax morrisii* H. Wendl., is more widely distributed occurring from the Florida Keys to the Bahamas, Cuba, Puerto Rico and western Lesser Antilles. *Thrinax radiata* Lodd ex Schult. and Schult.f. inhabits the northwestern Caribbean, from south Florida to Hispaniola, including coastal regions of northern Central America (Read, 1975; Henderson et al., 1995).

Acoelorrhaphe is a monotypic genus [*A. wrightii* (Griseb. & H. Wendl.) H. Wendl. ex Becc.] of Cuba and the Bahamas, but it is not endemic to the West Indies since it is also distributed in south Florida, and the Atlantic coast of Central America and the Colombian island of Providencia (Bailey, 1940; Galeano-Garcés, 1986; Henderson et al., 1995). One species of *Colpotherinax* [*C. wrightii* Griseb. and H. Wendl. ex Siebert and Voss] is restricted to Cuba, growing in seasonally flooded savannas and grasslands on white sand (Evans, 2001). The last genus in the Coryphoideae, *Copernicia*, contains 16 species restricted to Cuban savannas and woodlands, and two species endemic to Hispaniola (Dahlgren & Glassman, 1963; Moya et al., 1989; Henderson et al., 1995).

Ceroxyloideae

Only one of the eight genera of Ceroxyloideae occurs in the West Indies. *Pseudophoenix* has four species of which three are endemic to dry, open hillsides and lowlands of Hispaniola, whereas *P. sargentii* H. Wendl. ex Sarg. is more widely distributed from the Florida Keys, the Bahamas, Cuba, Hispaniola, and Dominica, to Mexico and Belize. It grows near the sea on sandy or limestone soils (Read, 1969; Henderson et al., 1995; Zona, 2002).

Arecoideae

Of the 113 genera in this subfamily, only 13 occur in the West Indies. *Gaussia* has three species [*G. attenuata* (O.F. Cook) Becc., *G. princeps* H. Wendl., *G. spiritwana* Moya and Leiva] distributed in Cuba, Hispaniola, and Puerto Rico, on well-drained limestone hills or mogotes (Quero & Read, 1986; Moya et al., 1991). Nine out of ten *Roystonea* species are present in the West Indies, usually on low-lying, inundated areas or disturbed habitats (Henderson et al., 1995; Zona, 1996). *Reinhardtia paiewonskiana* Read, Zanoni and M.M. Mejía is endemic to the Dominican Republic, where it inhabits slopes of premontane rainforests (Read et al., 1987).

Four genera of subtribe Bactridinae of tribe Cocoseae are represented in the Caribbean Islands: *Acrocomia*, *Aiphanes*, *Bactris* and *Desmoncus*. *Acrocomia*

aculeata (Jacq.) Lodd. ex Mart. is widely distributed in open savannas, woodlands, and disturbed areas of the Greater and Lesser Antilles (Henderson et al., 1995). *Acrocomia crispa* (Kunth) (formerly called *Gastrococos crispa*) endemic to Cuba growing on calcareous soils. A single species in *Aiphanes* [*A. minima* (Gaertn.) Burret] grows on limestone hills and in the understory of seasonal or humid forests, from the Dominican Republic to the Lesser Antilles (Borchsenius & Bernal, 1996). The Antillean species of *Bactris* are known from Cuba [*B. cubensis* Burret], Hispaniola [*B. plumeriana* Mart.], and Jamaica [*B. jamaicana* L.H. Bailey]. These species are mostly found in lowland to mid-elevation humid forests on limestone or serpentine soils (Salzman & Judd, 1995). *Desmoncus polyacanthos* Mart. reaches St. Vincent Island at the northernmost limit of its range, growing on river banks, open areas, forest margins and coastal zones (Henderson et al., 1995).

Attalea crassispatha (Mart.) Burret is a rare and endemic palm from the southwestern peninsula of Haiti that grows on slopes of limestone soil and disturbed areas (Henderson & Balick, 1991; Henderson et al., 1995). All other 68 *Attalea* species are confined to Mexico and Central and South America. *Syagrus* is another South American genus, with one species [*S. amara* (Jacq.) Mart.] endemic to central volcanic isles of the Lesser Antilles in dry coastal forests (Glassman, 1987; Henderson et al., 1995).

Within the Geonomateae, two genera, *Geonoma* and *Calyptronoma*, are present in the West Indies. *Geonoma* is the largest genus in the tribe and contains only two species, *G. interrupta* (Ruiz and Pavon) Mart. and *G. undata* Klotzsch, growing on lowland and high elevation forests, respectively, of Haiti and the Lesser Antilles (Henderson et al., 1995). *Calyptronoma*, a genus of three species [*C. plumeriana* (Mart.) Lourteig, *C. rivalis* (O.F. Cook) L.H. Bailey, *C. occidentalis* (Sw.) H.E. Moore], is endemic to the Greater Antilles usually found on wet habitats near stream banks (Zona, 1995).

Finally, two species in two genera of the Euterpeae occur in the West Indies. *Euterpe broadwayi* Becc. ex Broadway inhabits steep river valleys or exposed forested mountain ridges of the Lesser Antilles and *Prestoea acuminata* (Willd.) H. E. Moore more widely distributed in the Greater and Lesser Antilles on mountain slopes (Henderson & Galeano, 1996).

Phylogenetic Position of West Indian Palms at the Family and Subfamily Levels

The palm family (Arecaceae or Palmae) forms a monophyletic group within the Monocotyledones in all molecular and morphological phylogenetic studies (e.g. Uhl et al., 1995; Baker et al., 1999; Hahn, 1999; Chase et al., 2000; Asmussen & Chase, 2001; Lewis & Doyle, 2001; Asmussen et al., 2006). The most recent and comprehensive molecular phylogenetic reconstruction of palms is based on plastid DNA regions of *matK*, *trnL-trnF*, *rps16* intron and *rbcL* (Asmussen et al., 2006). On the basis of this hypothesis, Asmussen et al., (2006) provided a justification for a formal reclassification of the Arecaceae. West Indian palms fall within the new circumscriptions of the monophyletic subfamilies Ceroxyloideae, Coryphoideae, and Arecoideae (Fig. 1). They also form part of different clades within this most recent family-level phylogenetic tree, suggesting that West Indian palms do not represent a single evolutionary event (Fig. 1).

The position of Coryphoideae as sister to all palms except the Calamoideae and *Nypa* was shown by Asmussen et al. (2006) and Hahn (2002). The phylogenetic analysis of Asmussen et al. (2006) included all 44 genera in the Coryphoideae and recovered three main clades within this subfamily. West Indian palms are present in two of them; the first is sister to the other two clades and includes the New World tribes Sabaleae and Cryosophileae. The second clade groups members of tribes Phoeniceae and Trachycarpeae, the three West Indian genera within the latter did not form a clade.

Moore's (1973) Arecoid line of palms corresponds to a clade comprising subfamilies Ceroxyloideae and Arecoideae in Asmussen et al. (2006). The Caribbean genus *Pseudophoenix* belongs to the monogeneric tribe Cyclospatheae within subfamily Ceroxyloideae and has been recognized as an isolated member in the palm family, with no close relationships to any other Ceroxyloideae (Baker et al.,

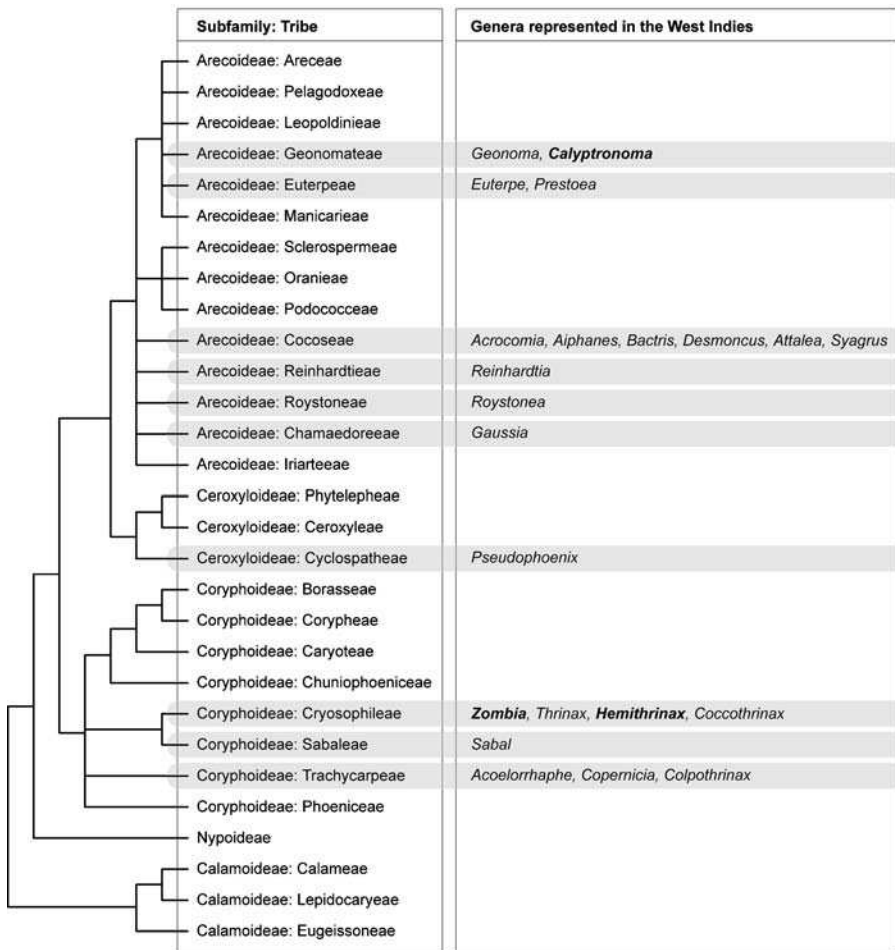


Fig. 1 Schematic representation of the phylogenetic position of West Indian palm genera at the family, subfamily, and tribal levels. Endemic genera are shown in **bold type** [adapted from Asmussen et al. (2006)]

1999; Asmussen et al., 2000; Zona, 2002). This genus was recovered as sister to the other 7 genera of Ceroxyloideae in Asmussen et al. (2006). In another phylogenetic reconstruction of 45 palm species using exon regions of the malate synthase nuclear gene, *Pseudophoenix sargentii* appeared as sister to all the palms except *Nypa*. This position however was supported by a bootstrap value of less than 50% (Lewis & Doyle, 2001).

Asmussen et al. (2006) sampled 96 out of 113 genera of subfamily Arecoideae. Tribe Iriarteeae was resolved as sister to a clade consisting of the remaining members of the subfamily (Asmussen et al., 2006). The base of this latter clade was highly unresolved and included the West Indian genera *Roystonea* and *Reinhardtia*. Two tribes within the Arecoideae (with West Indian genera in parentheses) were recovered as monophyletic: tribe Chamaedoreae (*Gaussia*) and tribe Euterpeae (*Prestoea* and *Euterpe*). Tribe Cocoseae was resolved as paraphyletic as a result of what appears to be a spurious resolution of the Malagasy genus *Bismarkia*. However, its subtribe Elaeidinae was included in a clade with subtribe Bactridinae (*Acrocomia*, *Aiphanes*, *Bactris* and *Desmoncus*). *Syagrus* and *Attalea* formed part of another clade that grouped all members of subtribe Attaleinae except *Beccariophoenix*. The Geonomateae was not monophyletic but *Geonoma*, *Calyptronoma*, *Calyptrogyne* and *Asterogyne* formed a clade.

West Indian Palm Phylogenies Based on Low-Copy Nuclear Genes

Well-characterized plastid (cp) and nuclear ribosomal (nr) DNA loci have been popular in addressing several evolutionary biology questions in plants. The generation of DNA sequences from regions such as *matK*, *trnL-trnF*, *psbA-trnH*, ITS, among others, can be relatively easily accomplished because universal primers are available. These regions, however, are not adequate for all plant families at every taxonomic level. In palms, in spite of the high resolution and support achieved at the family-level cpDNA phylogeny (Asmussen et al., 2006), the cp *trnL-trnF* intergenic spacer and the *rps16* intron provided limited informative characters for species and inter-generic relationships (Asmussen, 1999a; Baker et al., 1999, 2000a). Furthermore, studies on the palm subfamily Calamoideae using the internal (ITS) and external (ETS) transcribed spacer regions of 18S-26S nrDNA and the nontranscribed spacer of the 5S nrDNA, suggested the limited value of these two nuclear regions in palm phylogenetics because of a lack of homogeneity among repeats within genomes (Baker et al., 2000a, b).

The slower evolutionary rate of cpDNA in palms compared to that of other plant families (Wilson et al., 1990; Gaut et al., 1992; Hahn, 1999; Lewis et al., 2000), the incomplete concerted evolution of nrDNA in palms, and the requirement of additional phylogenetic markers to provide independent estimates of a species phylogeny led to the exploration of low-copy nuclear markers in palm phylogenetics. Low-copy nuclear genes are promising sources of phylogenetically useful characters since they evolve up to five times faster than the plastid genome, they show bi-parental inheritance, can produce datasets from unlinked loci, and can resolve recently and rapidly diversifying lineages (Sang, 2002; Mort & Crawford, 2004; Small et al., 2004; Norup et al., 2006). Despite the problems associated with

the use of low-copy nuclear sequences (e.g. paralogy, concerted evolution, intragenic polymorphism), these regions have been successfully used in resolving palm phylogenetic relationships especially at lower taxonomic levels (Lewis & Doyle, 2001, 2002; Gunn, 2004; Bayton, 2005; Roncal et al., 2005a; Thomas et al., 2006; Loo et al., 2006; Norup et al., 2006; Trénel et al., 2007).

Two low-copy nuclear DNA regions have been particularly successful: Intron 4 of phosphoribulokinase (PRK), a regulatory enzyme of the Calvin cycle for carbon dioxide assimilation, and intron 23 of RNA polymerase II subunit 2 (RPB2), an enzyme complex responsible for DNA transcription of protein-coding genes in all eukaryotes. In a study of the palm genus *Hyophorbe*, Lewis and Martinez (2000) found two PRK paralogues, one of which was informative and consequently used in palm phylogenies across a wide range of taxonomic levels. Partial PRK sequences rendered well resolved phylogenies for subfamily Ceroxyloideae (Trénel et al., 2007), tribes Areceae, Boraseae, Cocoeae, and Geonomateae (Lewis & Doyle, 2002; Gunn, 2004; Bayton, 2005; Roncal et al., 2005a; Norup et al., 2006), subtribe Arcinae (Loo et al., 2006), and in the genus *Chamaedorea* (Thomas et al., 2006). Gunn (2004) and Loo et al. (2006) sequenced three to five or more clones within species to assess for gene heterogeneity. All the PRK clones within a species were resolved as monophyletic, suggesting that although different copies of the target sequence may occur within a species, they seem to represent recent paralogues or alleles. In addition, Thomas et al. (2006) found in five *Chamaedorea* species a third PRK paralogue, which they identified as potentially useful for phylogenetic analysis. These findings should serve as a warning to the discovery of gene duplications, which if uncritically used can lead to incorrect phylogenetic reconstructions. To our knowledge, PRK has not been used in other plant families.

The use of RPB2 gene, on the other hand, was first explored in a broad angiosperm study (Denton et al., 1998) and later used for several seed plants (Popp & Oxelman, 2001; Nickerson & Drouin, 2004; Oxelman et al., 2004; Pfeil et al., 2004). These studies found RPB2 to be phylogenetically informative but also found evidence of two or even more paralogues. To date, no RPB2 paralogues have been identified in palms (Roncal et al., 2005a; Thomas et al., 2006; Loo et al., 2006; Norup et al., 2006; Trénel et al., 2007); however, multiple versions of this sequence may yet be discovered given the evolutionary history of this region in other plant families. PRK and RPB2 sequences were used as molecular markers in the following palm phylogenies.

Cryosophileae

Here we present unpublished data from partial PRK and RPB2 sequences which we used to reconstruct a phylogeny of tribe Cryosophileae that included species-level sampling of West Indian taxa (Table 2, Fig. 2). We sampled nine species of *Coccothrinax*, all four species of *Thrinax*, all three species of *Hemithrinax*, and the monotypic genus *Zombia*. The Central and South American species *Chelyocarpus ulei* Dammer, *Cryosophila stauracantha* (Heynh.) R.J. Evans, *Itaya amicorum* H.E. Moore, and *Schippia concolor* Burret were also included. Six outgroup taxa were selected from tribes Sabaleae and Trachycarpeae (Table 2, Fig. 2).

Amplification, bacterial cloning, and sequencing protocols followed Roncal et al., 2005a. The PRK sequences ranged in length from 532 bp in *Schippia concolor* to

689 bp in *Coccothrinax argentea* (Lodd. ex Schult. and Schult.f.) Sarg. ex Becc. and had uncorrected pairwise distances ranging from 0.003 to 0.104 (avg.=0.048). The RBP2 sequences had lengths of 763 bp in *Rhapidophyllum hystrix* (Fraser ex Thouin) H. Wendl. and Drude to 1,072 bp in *Coccothrinax crinita* (Griseb. and H.

Table 2 Voucher Information and GenBank Accession Numbers for the Taxa Sampled in the Phylogenetic Analysis of Tribe Cryosophileae

Taxon	Voucher	PRK GenBank accession	RBP2 GenBank accession
<i>Acoelorrhaphe wrightii</i> (Griseb. and H. Wendl.) H. Wendl. ex Becc.	W. M. Houghton 1056 (FTG)	EU215477	EU215508
<i>Chelyocarpus ulei</i> Dammer	J. Roncal 84 (FTG)	EU215461	EU215491
<i>Coccothrinax argentea</i> (Lodd. ex Schult. and Schult. f.) Sarg. ex Becc.	S. Zona 1043 (FTG)	EU215476	EU215507
<i>Coccothrinax barbadensis</i> (Lodd. Ex Mart.) Becc.	S. Kiem 221 (FTG)	EU215472	EU215503
<i>Coccothrinax borhidiana</i> O. Muñiz	S. Zona 908 (FTG)	EU215479	EU215510
<i>Coccothrinax crinita</i> ssp. <i>brevicrinis</i> Borhidi and O. Muñiz	D. Bogler 1265 (FTG)	EU215473	EU215504
<i>Coccothrinax crinita</i> (Griseb. and H. Wendl. ex C.H. Wright) Becc. ssp. <i>crinita</i>	P. R. Fantz 3209 (FTG)	EU215475	EU215506
<i>Coccothrinax inaguensis</i> Read	D. Bogler 1266 (FTG)	EU215471	EU215502
<i>Coccothrinax miraguama</i> (Kunth) Becc. ssp. <i>miraguama</i>	D. Bogler 1269 (FTG)	EU215470	EU215501
<i>Coccothrinax salvatoris</i> León	D. Bogler 1273 (FTG)	EU215469	EU215500
<i>Coccothrinax spissa</i> L. H. Bailey	D. Bogler 1275 (FTG)	EU215474	EU215505
<i>Colpotherinx wrightii</i> Griseb. and H. Wendl. ex Voss	D. Bogler 1278 (FTG)		EU215499
<i>Copernicia prunifera</i> (Mill.) H.E. Moore	D. Bogler 1287 (FTG)	EU215482	EU215513
<i>Cryosophila stauracantha</i> (Heynh.) R.J. Evans	S. Zona 866 (FTG)	EU215462	EU215492
<i>Itaya amicum</i> H.E. Moore	W. J. Baker 990 (FTG)	EU215456	EU215485
<i>Rhapidophyllum hystrix</i> (Fraser ex Thouin) H. Wendl. and Drude	S. Zona 900 (FTG)	EU215458	EU215488
<i>Sabal bermudana</i> L. H. Bailey	J. Roncal 070 (FTG)	EU215481	EU215512
<i>Schippia concolor</i> Burret	D. Bogler 1311 (FTG)	EU215457	EU215486
<i>Serenoa repens</i> (W. Bartram) Small	J. Roncal 54 (FTG)	EU215464	EU215494
<i>Thrinax compacta</i> (Griseb. and H. Wendl.) M. Gómez	C. Lewis 02–072 (HAJB)	EU215468	EU215498
<i>Hemithrinax ekmaniana</i> Burret	C. Lewis 02–065 (FTG)	EU215478	EU215509
<i>Thrinax excelsa</i> Lodd. ex Mart.	S. Zona 1114 (FTG)		EU215487
<i>Thrinax excelsa</i> Lodd. ex Mart.	J. Roncal 39 (FTG)	EU215459	EU215489
<i>Thrinax morrisii</i> H. Wendl.	J. Roncal 43 (FTG)	EU215463	EU215493
<i>Thrinax morrisii</i> H. Wendl.	J. Roncal 37 (FTG)	EU215483	EU215514
<i>Thrinax parviflora</i> Sw. ssp. <i>parviflora</i>	J. Roncal 78 (FTG)	EU215466	EU215496

Table 2 (continued)

Taxon	Voucher	PRK GenBank accession	RPB2 GenBank accession
<i>Thrinax radiata</i> Lodd. ex Schult. and Schult. f.	J. Roncal 40 (FTG)	EU215460	EU215490
<i>Thrinax radiata</i> Lodd. ex Schult. and Schult. f.	J. Roncal 42 (FTG)	EU215465	EU215495
<i>Hemithrinax rivularis</i> León	S. Zona 839 (FTG)	EU215480	EU215511
<i>Zombia antillarum</i> (Desc.) L. H. Bailey	B. Wood s.n. (FTG)	EU215467	EU215497
<i>Zombia antillarum</i> (Desc.) L. H. Bailey	R. Sanders 1763 (FTG)	EU215484	EU215515

Wendl. ex C.H. Wright) Becc. and had uncorrected pairwise distances ranging from 0.001 to 0.130 (avg.=0.055).

The aligned PRK matrix of 752 bp with nine indels was combined with the aligned RPB2 matrix of 1,337 bp with 16 indels for a total data set of 2,089 aligned bases. Parsimony analysis using NONA (Heuristic search with 1,000 random-addition replicates, TBR branch swapping holding ten trees per replicate, followed by TBR branch swapping on all trees resulting from the 1000 random-addition

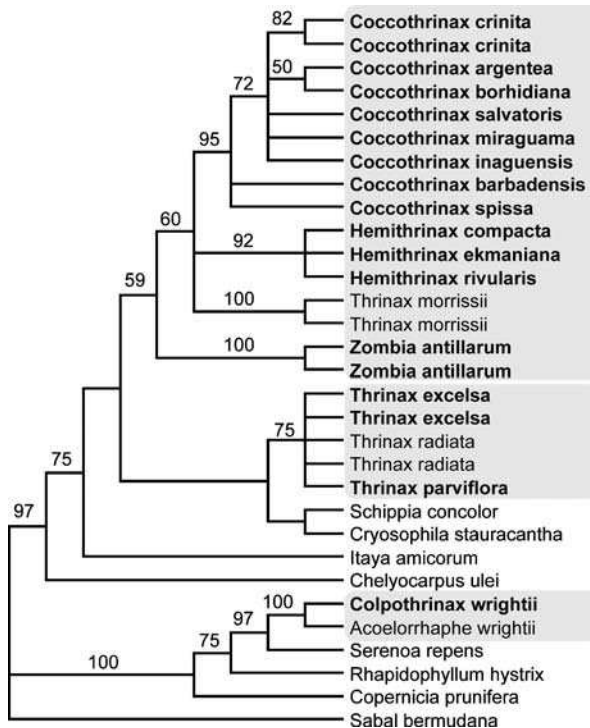


Fig. 2 Strict consensus of 12 trees for tribe Cryosophileae based on sequences of the nuclear genes PRK and RPB2. Numbers above the branches are bootstrap values. Species represented in the West Indies are shaded, and West Indian endemics are shown in bold type

replicates) yielded twelve equally parsimonious trees with a length of 849, a CI of 0.83 and an RI of 0.81. Strict consensus bootstrap frequencies were calculated using NONA, with 1,000 bootstrap replicates, each consisting of 100 random-addition heuristic search replicates holding ten shortest trees per replicate.

The resulting strict consensus tree indicated a monophyletic Cryosophileae (97% bootstrap support), a monophyletic *Coccothrinax* (95% bootstrap), a monophyletic *Hemithrinax* (92% bootstrap) and a polyphyletic *Thrinax*. The clade of *Thrinax radiata*, *T. excelsa*, and *T. parviflora* was resolved as monophyletic with 75% bootstrap support, but *T. morrisii* was placed in a clade with *Hemithrinax* and *Coccothrinax* with 60% bootstrap support (Fig. 2).

Cyclospatheae

The Ceroxyloideae is a small but morphologically and biogeographically heterogeneous palm subfamily that includes three tribes: a Gondwanan disjunction tribe (Ceroxyleae), an amphi-Andean tribe (Phytelepheae) and a Caribbean tribe (Cyclospatheae). Here we review the results of Trénel et al. (2007) of a molecular phylogenetic analysis for subfamily Ceroxyloideae, focusing on tribe Cyclospatheae. Trénel et al. (2007) combined three plastid and two low-copy nuclear DNA regions in their analysis and reported that subfamily Ceroxyloideae and its three tribes were monophyletic, all with 100% bootstrap support (Fig. 3). This study had an extensive subfamily sampling that included 85% of its accepted species in all eight genera, and sequenced more than 5.5 kb of the genes *matK*, *ndhF*, *trnD-trnT*, PRK intron 4, and RPB2 intron 23 (Trénel et al., 2007). The increased taxonomic sampling in this study compared to the one in Asmussen et al. (2006) resulted in an increased resolution and bootstrap support for the subfamily (from 63% to 100% bootstrap) and in clades recovered.

Heuristic maximum parsimony search of the combined DNA sequences revealed the relationships among the Cyclospatheae, with the clade of *Pseudophoenix ekmanii* Burret and *P. lediniana* Read recovered as sister to the clade of *P. sargentii* and *P. vinifera* (Mart.) Becc. (Fig. 3). However, clades were weakly supported (66–78% bootstraps) and cpDNA phylogenetic signal appeared to be in conflict with that of nDNA for the sister relationship of *P. sargentii* and *P. vinifera* (Fig. 3; Trénel et al., 2007). This five-gene dataset was also used to estimate divergence times for the Cyclospatheae based on penalized likelihood and Bayesian dating methods, making this study one of the few to use time estimates on biogeographical analysis of West Indian plant genera (Francisco-Ortega et al., 2007). Lineage age estimates ranged from 2–7 Mya indicating a recent radiation of the tribe in the Pliocene just after the modern geography of the Caribbean was established (Graham, 2003; Trénel et al., 2007).

Cocoseae

We review and discuss the phylogenetic relationships of Caribbean taxa within tribe Cocoseae published in Gunn (2004). The author performed a generic-level phylogenetic analysis for the Cocoseae based on nDNA sequences of the PRK gene including 34 taxa from all 20 genera recognized in the five subtribes. Maximum parsimony, maximum likelihood and Bayesian analyses revealed the

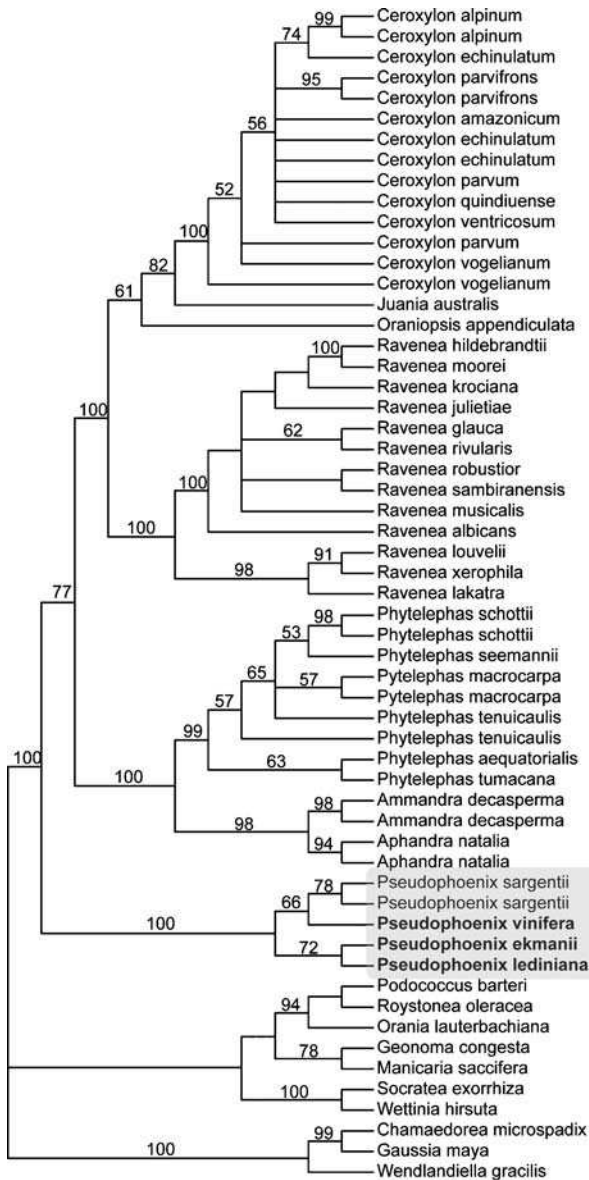


Fig. 3 Strict consensus of 5471 most parsimonious trees for subfamily Ceroxyloideae based on combined analysis of plastid *matK*, *ndhF*, and *trnD-trnT* sequences and nuclear PRK and RPB2 sequences. Numbers above branches are bootstrap values. Species represented in the West Indies are shaded, and West Indian endemics are shown in **bold type** [adapted from Trénel et al. (2007)]

division of the Cocoseae into two main clades, the spiny and non-spiny (Fig. 4). Within the spiny clade, *Aiphanes* formed a monophyletic group (100% bootstrap), with the West Indian *Aiphanes minima* as sister to the other two congeneric species sampled (*A. aculeata* and *A. caryotifolia*). *Acrocomia* was paraphyletic with *Gastrococos crispera* and *Acrocomia aculeata*, forming a clade supported by 83%

bootstrap and differing by only two base pair positions (Gunn, 2004; Fig. 4). These two taxa are vegetatively similar differing primarily in floral arrangement, morphology, and pollen size (Gunn, 2004). These phylogenetic results changed the status of the Caribbean Island endemic genus *Gastrococos* to be part of the more widely distributed *Acrocomia*, this latter was first proposed by von Martius (1824)

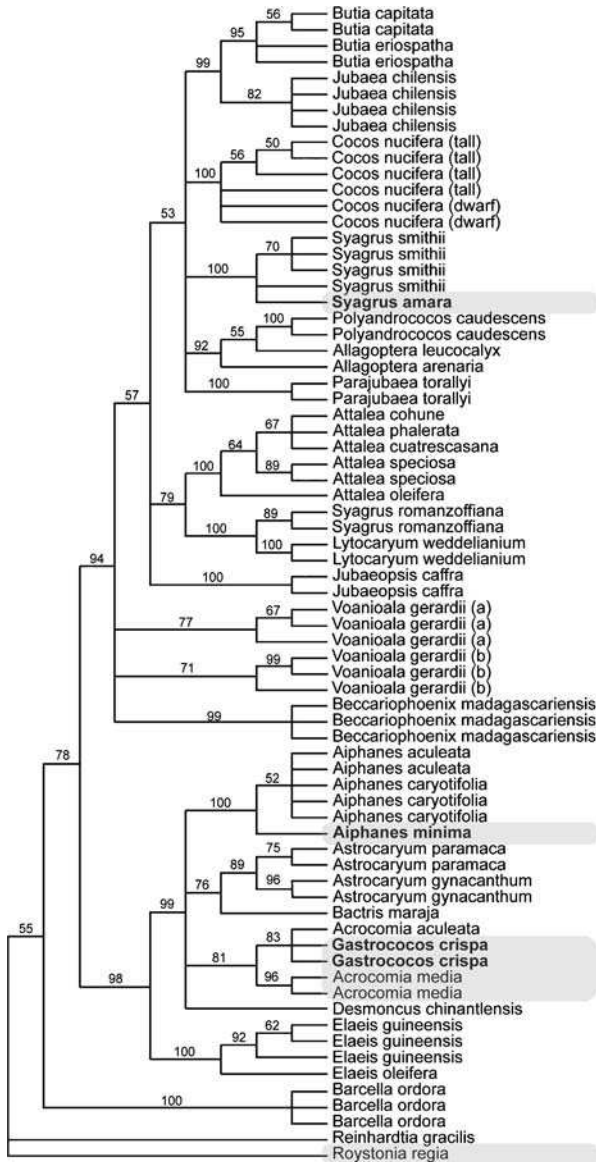


Fig. 4 Strict consensus of 14,071 trees for tribe Cocoseae based on sequences from the nuclear PRK gene. Numbers above branches are bootstrap values. Species represented in the West Indies are shaded, and West Indian endemics are shown in bold type [adapted from Gunn (2004)]

who described a single species from the West Indies (*A. aculeata*). Furthermore, based on morphological characters, Beccari (1912) had previously recognized *Acrocomia crispa* on his treatment to the palms indigenous to Cuba. Gunn's (2004) work also showed that *A. aculeata* was non-monophyletic thus a revision of the species delimitation is needed.

Syagrus is a large genus of 30 species within the non-spiny clade of Cocoseae, and appeared polyphyletic in the PRK tree with the Lesser Antillean endemic *S. amara* and the South American *S. smithii* forming a clade (100% bootstrap) in the Cocos alliance (Gunn, 2004; Fig. 4). These two species share some fruit morphological characters such as the ridged endocarp with basal pores and the ruminant endosperm (Gunn, 2004). The PRK phylogenetic study did not include the Caribbean taxa of *Bactris*, *Desmoncus* and *Attalea*, thus their position within the Cocoseae awaits further investigation.

Geonomeae

We finally review the phylogenetic results in Roncal et al. (2005a, b) for Caribbean taxa of the Geonomeae. The Geonomeae resolves as monophyletic in some higher-level molecular phylogenetic studies of palms (Asmussen et al., 2000; Asmussen & Chase, 2001; Hahn, 2002). Its monophyly was revealed for the first time in a phylogenetic analysis based on sequences of the cpDNA *rps16* intron (Asmussen, 1999a), jackknife support however was only of 57%. In the PRK and RPB2 phylogenetic analysis, the tribe was resolved as monophyletic with strong bootstrap support in both separate (99% and 100% bootstrap) and combined analyses (100% bootstrap; Roncal et al., 2005a; Fig. 5). This molecular phylogeny sampled 30 species in all 6 genera of the Geonomeae. The largest genus in the tribe, *Geonoma*, was recovered monophyletic, supporting a previous hypothesis based on the cpDNA *rpl16* intron of five *Geonoma* species (Asmussen, 1999b). The two West Indian species of *Geonoma* did not form a clade. *Geonoma undata* formed part of a clade of high elevation palms distributed through the Andes and Central American mountains, and *G. interrupta* appeared as sister to all taxa of one of the two main clades in *Geonoma* except *Geonoma deversa* (Poit.) Kunth (Roncal et al., 2005a; Fig. 5).

The taxonomic rank of the Greater Antillean endemic *Calyptronoma* has been controversial for over a century. Among the studies and/or treatments that recognize *Calyptronoma* as a genus are those of Grisebach, 1864; Drude, 1889; Bailey, 1938; Hawkes, 1949; Moore, 1973; Uhl & Dransfield, 1987; de Nevers, 1995; Zona, 1995; and Govaerts & Dransfield, 2005. Others place *Calyptronoma* as a subgenus of *Calyptrogyne* (Hooker, 1883; Beccari, 1912; Burret, 1930; León, 1944; Wessels Boer, 1968; and Glassman, 1972) based on the floral characters shared between the two such as the basally connate corolla in pistillate flowers and the circumscissile cap that falls at anthesis.

The PRK and RPB2 phylogenetic analysis rendered *Calyptronoma* paraphyletic since the two *Calyptrogyne* species formed a 100% supported clade embedded within *Calyptronoma* (Fig. 5; Roncal et al., 2005a). In addition, both genera formed a well supported clade (100% bootstrap) corroborating the results obtained earlier with the *rps16* phylogeny (Asmussen, 1999a). These clades were recovered in

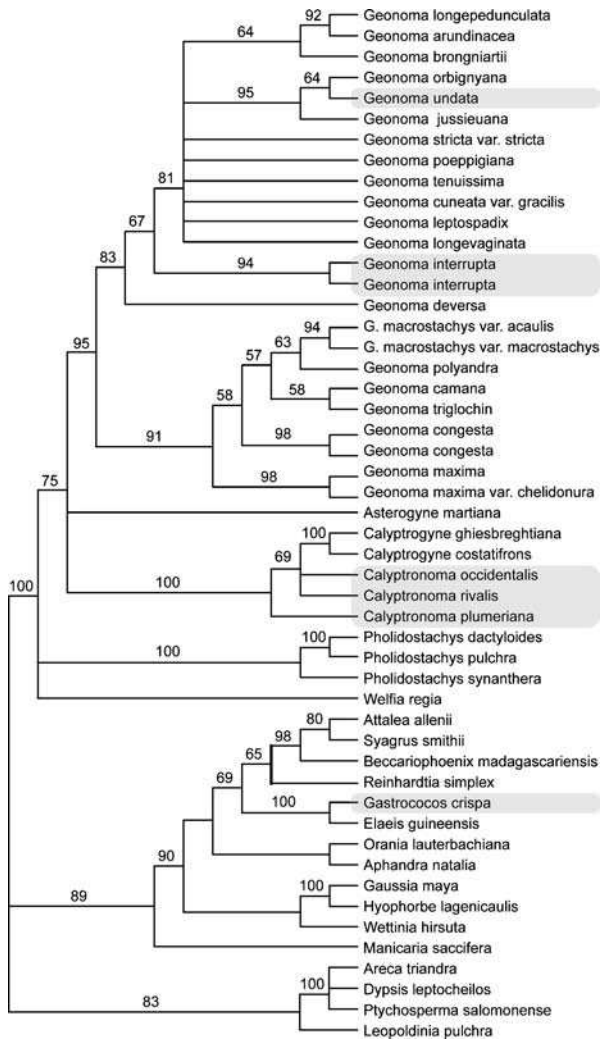


Fig. 5 Strict consensus of 17,347 most parsimonious trees for tribe Geonomateae based on combined analysis of PRK and RPB2 sequence data. Numbers above branches are bootstrap values. Species represented in the West Indies are shaded [adapted from Roncal et al. (2005a)]

phylogenetic analyses of both nuclear DNA regions separately as well as in combination (Roncal et al., 2005a). A new taxonomic combination resulted from this study (Roncal et al., 2005b). Since this low-copy nuclear DNA phylogeny sampled only two out of 21 species of *Calyptrogynne* (Henderson, 2005), increasing the taxonomic sampling will provide a better test for these results, including the combined analysis of low-copy nuclear DNA sequences with morphological characters (F. Borchsenius, unpubl. data), and sequences from the plastid regions *trnL-trnF*, *rps16*, *rpl16*, *rbcL*, *matK*, and the nuclear ribosomal 5S region (C. Asmussen, unpubl. data).

Biogeographical Patterns of West Indian Palms

The palms of the West Indies evolved in an area where plate tectonic movements, sea-level changes, volcanism, climate changes, and the collision of an asteroid 65 Mya have all left a marked environmental signature (Graham, 2003; Santiago-Valentín & Olmstead, 2004; Francisco-Ortega et al., 2007). Phylogenetic studies of West Indian palms reflect this complex environmental history. As the West Indian palms are not the product of a single radiation (Fig. 1), each clade of West Indian palms tells a unique story. The present day distributions of West Indian palms suggest complicated evolutionary interchange among islands, as well as between the West Indies and surrounding continents. No single biogeographical picture emerges.

There are several patterns of shared genera between the continental mainland and the islands. The West Indian species of *Aiphanes*, *Desmoncus*, *Euterpe*, *Geonoma*, *Prestoea*, and *Syagrus* are part of species-rich genera that are widespread in South America (Henderson et al., 1995). *Colpothrinax* and *Reinhardtia* have phylogenetic ties to Meso-America, where these genera are widespread. West Indian *Sabal* species are related to North American and Mexican species (Zona, 1990). *Acrocomia*, *Attalea* and *Bactris* are widely distributed in Mexico, Central America and South America, so the patterns of relationship between island and continental species are difficult to discern.

Species from different subfamilies are shared between the continental mainland and the islands: *Acoelorrhaphe wrightii* (Mexico, Central America, Florida, Cuba, Bahamas), *Acrocomia aculeata* (Mexico, Central and South America, Greater and Lesser Antilles) *Coccothrinax argentata* (Florida, Bahamas), *Desmoncus polyacanthos* (South America, Lesser Antilles), *Geonoma interrupta* (Central and South America, Hispaniola, Lesser Antilles), *Geonoma undata* (Central and South America, Lesser Antilles), *Roystonea regia* (Mexico, Florida, Bahamas, Cuba, Cayman Islands), *R. oleracea* (South America, Lesser Antilles), *Prestoea acuminata* (Central and South America, Cuba, Hispaniola, Puerto Rico, Lesser Antilles), *Pseudophoenix sargentii* (Florida, Mexico, Cuba, Bahamas, Hispaniola, Puerto Rico, Lesser Antilles), *Sabal palmetto* (Florida, Cuba, Bahamas), *S. yapa* (Mexico, Cuba), *Thrinax morisii* (Florida, Bahamas, Cuba, Puerto Rico), and *T. radiata* (Mexico, Florida, Cuba, Jamaica, Hispaniola). Not unexpectedly, islands that are geographically close to the mainland are more likely to share mainland species.

Among the islands of the West Indies, many palm genera are shared (Table 1). *Acrocomia*, *Calyptronoma*, *Coccothrinax*, *Roystonea*, *Sabal*, and *Thrinax* occur throughout the Greater Antilles. Only a few palm species occur in more than one island. In addition to many of the species listed in the preceding paragraph, the following species occur on more than one island or island group: *Aiphanes minima* (Hispaniola, Puerto Rico, Lesser Antilles), *Calyptronoma plumeriana* (Cuba, Hispaniola), *C. rivalis* (Hispaniola, Puerto Rico), *Coccothrinax barbadensis* (Puerto Rico, Lesser Antilles), *Gaussia attenuata* (Hispaniola, Puerto Rico), *Roystonea borinquena* (Hispaniola, Puerto Rico) *Sabal causiarum* (Hispaniola, Puerto Rico), *S. domingensis* (Cuba, Hispaniola), and *S. maritima* (Cuba, Jamaica). Again, the only pattern that emerges is that geographically close islands are more likely to share species than geographically distant islands.

The case of *Acrocomia aculeata* is noteworthy, as this species is the most widespread palm in the West Indies, absent from only the Bahamas; however,

taxonomic confusion may be obscuring biogeographical patterns. [Gunn \(2004\)](#) analyzed two samples of *A. aculeata*: one from Brazil and one (as *A. media* O.F. Cook) from Puerto Rico. These samples did not resolve as sister taxa in her analyses (Fig. 4). *Acrocomia aculeata* (Brazil) and *A. (Gastrococos) crispa* formed a well-supported clade that was sister to *A. aculeata* (Puerto Rico). Gunn's findings suggest that additional sampling from the entire range of *A. aculeata* may reveal unrecognized genetic diversity within this single taxon.

Palms have a long history in the West Indies, although the fossil flora shows similarities and dissimilarities with the modern palm flora, with no clear biogeographical patterns emerging. Palm fossils in amber attest to the presence of both Coryphoideae and Arecoideae in Hispaniola between 15–45 Mya (Miocene to Eocene) ([Poinar, 2002a, b](#)). [Poinar \(2002a\)](#) described *Trithrinax dominicana* Poinar (Coryphoideae: Cryosophileae), but extant species of *Trithrinax* are confined to South America ([Uhl & Dransfield, 1987](#)). Another fossil of staminate flowers was referred to a new genus of Coryphoideae: Trachycarpeae, *Palaeoraphe* Poinar ([2002b](#)). [Poinar \(2002b\)](#) and [Poinar & Santiago-Blay \(1997\)](#) described fossils in amber of *Roystonea* flowers and of a palm bug belonging to Thaumastocoridae: Xylastodorinae, whose closest extant relative feeds on *Roystonea* leaves. These fossils preserved in amber provide detailed evidence of palm diversity in the West Indies, but there are not enough fossils in amber to provide a clear, island-by-island picture of the early palm flora.

As our phylogenetic analysis of the Cryosophileae and Trachycarpeae shows both tribes are represented in the West Indies, but both have representatives on the continental mainland as well (Fig. 2). In the analysis of both tribes, the island taxa occur in terminal positions on the cladogram, which is compatible with the hypothesis of island radiation from a continental ancestor. The cladistic analysis of the Ceroxyloideae (Fig. 3) places Cyclospatheae, which is primarily an island group, sister to the remaining Ceroxyloideae. This pattern is equivocal in resolving the origin—either continental or island—of the group.

The analyses of the Cocoseae (Fig. 4) and Geonomateae (Fig. 5) suggest multiple introductions of lineages from both tribes into the West Indies from continental sources; however, a scenario in which island taxa gave rise to continental species is entirely plausible and not inconsistent with some of the observed patterns in Figs. 4 and 5 (e.g., *Calyptronoma* from the islands and *Calyptrogyne* from the mainland or *Syagrus amara* from the Lesser Antilles and *Syagrus* spp. from South America).

To reiterate, both present and past patterns of biogeography point to a complex evolutionary history involving extinction, migration, and diversification. No single pattern predominates. In some cases, additional molecular genetic data may yield information regarding the timing of origin or direction of migration of palms in the West Indies, but our current understanding of palm biogeography in the West Indies is incomplete.

Future Research Directions for West Indian Genera in Need of Phylogenetic Studies

Molecular phylogenetic studies of West Indian palms have revealed interesting results especially regarding genera circumscriptions and nomenclatural changes.

There are, however, several other West Indian genera and species for which evolutionary relationships are yet unknown and from which biogeographical hypotheses will greatly benefit if they exist. The cpDNA phylogeny of Asmussen et al. (2006) recovered the monogeneric tribe Sabaleae as sister to tribe Cryosophileae. A species-level phylogenetic analysis for *Sabal* that will untangle relationships among the five Caribbean taxa and the continental species is needed. Given that the majority of *Sabal* species occur in Mesoamerica, a molecular phylogenetic study may provide information on the colonization direction between the West Indies and the mainland. A molecular phylogeny for tribe Trachycarpeae is also needed since the strict consensus tree of Asmussen et al. (2006) only recovered six clades within this tribe supported by bootstrap values greater than 50%. Cladistic relationships among the 21 *Copernicia* species may provide insight on the adaptive radiation within the West Indies and results can be compared with those obtained from *Coccothrinax*, the most species-rich Caribbean palm genus.

To our knowledge there are no molecular phylogenetic studies on *Roystonea*, and the three insular species of *Gaussia* formed a clade on a cpDNA phylogenetic reconstruction (Cuenca & Asmussen-Lange, 2007). There is thus a need for future phylogenetic studies based on nuclear DNA regions. A molecular phylogenetic approach can also test Moore's (1957) ideas on the linear series of size reduction in *Reinhardtia*, and Henderson's (2002) hypothesis that speciation in this genus has taken place from north to south and from high to low elevation. Henderson's (2002) phylogenetic study based on morphological characters resolved the Hispaniolan species of *Reinhardtia* [*R. paiewonskiana*] as sister to the other five species in this genus.

Two earlier cladistic analyses of the genus *Bactris* based on morphological and anatomical evidence recovered a non-ocreate clade comprised by the Antillean and *Guilielma* species of *Bactris* (Sanders, 1991; Salzman & Judd, 1995). Several synapomorphies supported the monophyly of the Antillean clade and within this group *B. cubensis* appeared sister to a clade of *B. jamaicana* and *B. plumeriana* (Sanders, 1991; Salzman & Judd, 1995). New molecular systematic studies may further test the phylogenetic and biogeographic hypotheses of Salzman & Judd (1995), based on Caribbean plate-tectonic history, for the Antillean species of *Bactris*. Also, as mentioned before the positions of the West Indian representatives of *Desmoncus* and *Attalea* have not been analyzed using molecular markers.

A phylogenetic study of tribe Euterpeae (as Euterpeinae) based on 54 morphological and anatomical characters yielded one most parsimonious tree and recovered *Euterpe* and *Prestoea* as two monophyletic genera (Henderson, 1999). In this analysis, the West Indian *E. broadwayi* was sister to the Central and South American *E. precatorea* in the most derived clade of the genus. Relationships among *Prestoea* species were mostly unresolved but the Caribbean *P. acuminata* appeared sister to all other *Prestoea* species except *P. pubigera* (Henderson, 1999). Low-copy nuclear genes may therefore provide independent informative characters to confirm or further resolve these relationships.

In recent years, new avenues for isolation, characterization and use of nuclear DNA loci have emerged and these are reviewed in Schlüter et al. (2005) and in Hughes et al. (2006). Methods that screen multiple low-copy nuclear loci to assess levels of variation prior to generating full trees have been successful (Syring et al., 2005). In the so called Comparative Anchor Tagged Sequence-based approach,

genomic sequences from the target group are compared to identify conserved anchor tag sequences and subsequently design primer pairs (i.e. Syring et al., 2005). In the Sequence Characterize Amplified Region-based approach, RAPD-generated DNA fragments from the target group are sequenced and screened for variation before primer design (i.e. Bailey et al., 2004). Regardless the approach used the solution for low-level phylogenies seem to be lineage specific, enhancing the importance of a priori screening for candidate loci.

Conservation of West Indian Palms

The most recent review and assessment of the conservation status of West Indian palms (Zona et al., 2007) used the IUCN Red List Categories and Criteria version 3.1 (IUCN, 2001) with sources of data from current literature and field observations since 1985. This assessment recognized one species as extinct (*Roystonea stellata* León), 11 species as critically endangered, 19 as endangered, 21 as vulnerable, 57 of least concern, and 25 as data deficient (Zona et al., 2007). Land clearing for agriculture and construction, overexploitation, anthropogenic fires, habitat degradation, livestock, invasive exotic plants, and introduced pathogens and pests, are the major threats against the conservation of these taxa (Zona et al., 2007).

From the molecular and morphological phylogenetic studies reviewed here we can identify four small lineages of taxa distributed only in the West Indian islands. The Antillean *Bactris* clade (three spp.), an insular *Gaussia* clade (three spp., of which *G. spirituana* is listed as Endangered), the *Hemithrinax* clade (one sp. Vulnerable and two spp. Endangered), and a *Zombia* clade (one sp. listed Vulnerable). Two other lineages include taxa distributed mainly in the islands but reaching also the bordering areas of the continental Caribbean Basin, viz. the *Coccothrinax* clade (with eight spp. sampled in the nDNA analysis, of which *C. crinita* and *C. borhidiana* are Critically Endangered) and the *Pseudophoenix* clade (with four species of which *P. lediniana* is Critically Endangered). These West Indian palm clades thus follow the pattern detected in other plant families of this and other archipelagos where endemic taxa group together forming monophyletic groups (Francisco-Ortega et al., 2007). These lineages should therefore receive high conservation priority within the Caribbean Islands biodiversity hotspot.

Conclusions

Plant diversity in the West Indies is reflected in the diversity and distribution of its palms. A total of 135 Caribbean palm species in 21 genera are found growing in diverse habitats over limestone and serpentine soils. Three genera (*Zombia*, *Hemithrinax* and *Calyptronoma*) and 121 species are endemic to the West Indies. West Indian palms fall within the new circumscriptions of the monophyletic subfamilies Ceroxyloideae, Coryphoideae, and Arecoideae in the most recent and comprehensive family-level phylogeny based on four plastid DNA sequences.

Given the limited phylogenetic value of plastid and nrDNA for inferences at low taxonomic levels in palms, the exploration and successful utilization of low-copy nuclear genes revealed the relationships presented here for the Cryosophileae, the Cyclospatheae, the Cocoseae, and the Geonomateae. Our analysis of the Cryosophileae revealed that the Caribbean genera *Coccothrinax* and *Hemithrinax* are monophyletic, but the genus *Thrinax* is polyphyletic. Tribe Cyclospatheae was monophyletic and had a clade of *Pseudophoenix ekmanianii* and *P. lediniana* sister to a clade of *P. sargentii* and *P. vinifera*. The phylogeny of the Cocoseae rendered *Acrocomia* paraphyletic, with *Gastrococos crispa* nested within *Acrocomia*. As a consequence, the Caribbean endemic genus *Gastrococos* is now regarded as part of the widespread genus *Acrocomia*. The phylogenetic reconstruction of tribe Geonomateae rendered *Calyptronoma* paraphyletic, with *Calyptrogyne* nested within *Calyptronoma*.

Current distributions and phylogenetic studies of West Indian palms support the complex biogeography of the region. The two main patterns of colonization, dispersal or vicariance, are equally plausible and we can not discern the origin of some West Indian species in relation to their continental congeners. Certain West Indian genera (i.e. *Syagrus*, *Euterpe*, *Geonoma*, *Aiphanes*, *Attalea*) are species-rich in the adjacent continental land and may thus have their origin in these areas. *Coccothrinax* and *Copernicia* represent examples of adaptive radiations in the West Indies.

Several West Indian genera are on a waiting list for phylogeny reconstruction. These include *Sabal*, genera of tribe Trachycarpeae, and *Roystonea*. Several other genera primarily distributed in the mainland but with West Indian representatives (i.e. *Bactris*, *Euterpe*, *Prestoea*, *Reinhardtia*, *Desmoncus*, *Attalea*) need a molecular phylogenetic analysis to test earlier hypotheses or formulate new ones about their relationships with continental congeners.

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