Phylogeny and Historical Biogeography of the Neotropical Palm Tribe Euterpeae (Arecaceae)

by

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Abstract

Tribe Euterpeae is a group of Neotropical palms that comprises 33 species in 5 genera distributed from Central America to Southeastern Brazil and Bolivia, including the Caribbean islands. Some species are important elements of Amazonian forests since they can be among the 10 most abundant trees. Some members of this tribe are economically important for their oil production and edible palm heart. In this study I aimed to clarify the intergeneric and interspecific relationships within Euterpeae and estimate the time and place of origin of its taxa. I also tested for changes in inflorescence types in the tribe. I reconstructed a phylogenetic tree with maximum likelihood and a dated Bayesian phylogenetic tree using one plastid (*trnD-trnT*) and four low-copy nuclear DNA regions (CISP4, WRKY6, RPB2, and PHYB). I used five fossil and two secondary calibration points to estimate divergence times. I amplified sequences from 27 Euterpeae species including 7 infra-specific taxa and 41 outgroup taxa. The tribe and each genus were monophyletic with high support. *Hyospathe* was sister to the rest of the genera. *Euterpe* was sister to *Neonicholsonia* and *Prestoea* was sister to *Oenocarpus*. The ancestral inflorescence type of Euterpeae is likely one with rachillae all around the main axis from which the hippuriform (horsetail shape) inflorescence of *Oenocarpus* originated. Some widely distributed species with infra-specific taxa (*Euterpe precatoria*, *Prestoea acuminata* and *Hyospathe elegans*) were not monophyletic, which invites a revision of these species circumscriptions. The

Euterpeae diverged from its sister clade Areceae at around 46 million years ago (Mya), while the crown age of the Euterpeae was estimated at around 40 Mya. Although Euterpeae's origin occurred in the Eocene most of the extant genera had crown ages after the middle Miocene (<17 Mya) with some species originating later during the Pliocene to Pleistocene. This work represents the most complete molecular phylogeny of the group, and inclusion of the few missing narrow endemic taxa will provide a more complete understanding of the interspecific relationships of the tribe.

To my parents Fritz Pichardo Cornelio and Matilde Marcano Martínez

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Co-Authorship Statement

Prof. Julissa Roncal (JR) designed the study. Laboratory work was conducted by myself with the help of Nicolle MacDonald and MUCEP students. I performed the data analyses with suggestions from JR and the help of María E. Nieto-Blazquez. I wrote the manuscript with insight from JR. I aim to publish the results from this study as an article in a journal related to molecular phylogenetics and biogeography studies.

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List of Abbreviations

AIC	Akaike information criterion
BI	Bayesian inference
BS	Maximum likelihood bootstrap values
GAARlandia	Greater Antilles/Aves Ridge
GTR	General time reversible model
HPD	Highest posterior densities
MCMC	Markov chain Monte Carlo
ML	Maximum likelihood
Mya	Millions of years ago
pp	Bayesian posterior probabilities

1. Introduction

1.1 Systematics and biogeography of Arecaceae

The palm family (Arecaceae) is a morphologically distinctive plant family, nested within the clade of the commelinoid monocotyledons (Chase et al., 2006), a clade formed by the orders Arecales, Poales, Commelinales and Zingiberales sensu Soltis et al. (2005) (Chase et al., 2016). The palm family is very diverse in morphology and ecology (Dransfield et al., 2008), comprising 2,585 species in 188 genera (Govaerts et al., 2015). The group exhibits a great variety of growth patterns, leaves and inflorescence morphology. Palms are usually recognized by a solitary stem or cluster of stems bearing a crown of leaves. The growth habit can be erect or prostrate, with a solitary stem, with or without branching, or with clustered stems with branching at the basal nodes (Dransfield et al., 2008). Size also varies in the family, with height of different species ranging from < 1 m to 60 m. Two basic leaf types can be found in palms: pinnate and palmate. Pinnate leaves are the most common type (Dransfield et al., 2008); they have a feather-like appearance and a blade consisting of many leaflets or pinnae. In contrast, palmate leaves have a fan-like appearance. The most common variation of fan-shape leaves are costapalmate leaves, in which the axis of the leaf extend into the blade. Costapalmate leaves are distinctive of most species in the

subfamily Coryphoideae (Dransfield et al., 2008). Palms grow in several tropical and subtropical biomes, such as tropical rain forests, montane forests, deserts, inundated forests or riverine forests (Dransfield et al., 2008). With a rich history of systematic studies dating back several decades (e.g. Dransfield et al., 2008; Uhl and Dransfield, 1987), and a rich fossil record (Harley, 2006), palms are an excellent group to study diversification times and the biogeographic history of the (sub)tropics.

The Arecaceae are key members of many tropical rainforest formations. Couvreur and Baker (2013) proposed palms as a model group to infer the origin and the evolution of biodiversity patterns of tropical formations, because of the family's great diversity in tropical areas and the availability of many studies on taxonomy, distribution, and phylogenetic relationships. Palm phylogenetics have evolved quickly since 1990, with 46 phylogenetic studies at different taxonomic levels up to 2008 (Dransfield et al., 2008), and 28 further studies up to 2016 (Baker and Dransfield, 2016).

The Arecaceae comprises five subfamilies—Calamoideae, Nypoideae, Coryphoideae, Arecoideae, Ceroxyloideae—of which the Arecoideae is the largest and most diverse (Asmussen et al., 2006; Dransfield et al., 2005). Dransfield et al. (2008) recognize 13 tribes in the Arecoideae. One distinctive characteristic of the Arecoideae is that the flowers are grouped in triads (a group of two lateral staminate and a central pistillate flower) and have commonly pinnate leaves (Dransfield et al., 2008). Recent studies support the Arecoideae as a monophyletic group (Baker et al., 2011, 2009; Comer et al., 2015); however the phylogenetic relationships among tribes in the Arecoideae are not completely resolved (Comer et al., 2015; Couvreur et al., 2011; Dransfield et al., 2008). Phylogenetic studies have been conducted for other subfamilies like Calamoideae (Baker et al., 2000a,b) and Ceroxyloideae (Trénel et al., 2007).

The family Arecaceae as a whole is hypothesized to have originated and diversified in the early Cretaceous, and all higher taxa of the family diversified before the end of this period (ca. 100 million years ago (Mya)) (Baker and Couvreur, 2013; Bremer, 2000; Couvreur et al., 2011; Janssen and Bremer, 2004). Several studies support Laurasia as the ancestral area for the diversification of the family (Baker and Couvreur, 2013; Couvreur et al., 2011). The diversification of the family occurred after the rupture of Gondwana and Laurasia, thus dispersal events likely played a key role in the evolution and diversification of palms (Baker and Couvreur, 2013).

While subfamilies Calamoideae, Nypoideae and Coryphoideae have a Laurasia/Eurasia origins, Arecoideae and Ceroxyloideae diverged from Coryphoideae in North America with subsequent dispersal to South America (Baker and Couvreur, 2013). The stem lineage of Arecoideae became extinct in North America before its diversification at the crown age. This supports the view of the South American origin of Arecoideae (Baker and Couvreur, 2013; Dransfield et al., 2008).

1.2 Economic importance of the palm family

Some palm species are important in the world economy, e.g. the coconut (*Cocos nucifera* L.), which has high worldwide production of oil and seed (Johnson, 1998; Vollmann and Rajcan, 2010). For example, worldwide coconut production in 2014 was calculated to be around 60 million tonnes and an area of around 20 million hectares was dedicated to coconut cultivation (FAO, 2017). The African oil palm (*Elaeis guinensis* Jacq.) has been widely cultivated to extract oil as food source and for the production of biodiesel (Johnson, 1998; Vollmann and Rajcan, 2010). Rattan palms

(*Calamus* spp., *Daemonorops* spp.) constitute the most commonly used palms in Asia for the furniture industry, and secondarily for the creation of woven products like baskets, bags, and fish traps (Johnson, 1998). Date palm fruit (*Phoenix dactylifera* L.) is also a valuable economic resource. In 2014, around 7.6 million tonnes of dates were harvested worldwide and an area of around 1 million hectares was used in the cultivation of date palm (FAO, 2017).

Many species of palms are also of great value at smaller scale at local markets or domestic use where these species occur. Most of the uses revolve around food (e.g. fruit, beverage, oils), as raw materials to make tools and utensils (e.g. domestic tools, labor tools, rope), in construction (e.g. thatch, house building, bridges), and as animal food, and they also have medicinal value (Balick, 1986; Macía et al., 2011; Moraes et al., 2017). In western Brazil the inhabitants use *Acrocomia aculeata* (Jacq.) Lodd. ex Mart. fruit as a source of food, and *Mauritia flexuosa* L.f. to create many household utensils (Martins et al., 2014). Leaves of the latter species and of *Attalea compta* Mart. are used for thatching (Martins et al., 2014). Different palm organs have medicinal properties, and some have been tested pharmacologically. For example, *Euterpe precatoria* Mart. roots are used to treat malaria as root extracts have antiplasmodial activity (Sosnowska and Balslev, 2009). Roots of *Acrocomia aculeata* contain hypoglycemic compounds, which accounts for the traditional use of these roots to treat diabetes (Sosnowska and Balslev, 2009).

1.3 Geological events in the Neotropics and their relationships with the evolution of palms

The Neotropics have a complex geological history that has shaped the distribution of species through geological time and enabled or hindered diversification of plant lineages (e.g. Cuenca et al., 2008; Eiserhardt et al., 2011; Roncal et al., 2013). Main geological events included: the Andean Cordillera uplift from the Oligocene to the Pleistocene (Gregory-Wodzicki, 2000; Hoorn et al., 1995); the formation of an aquatic system called Pebas (ca. 23–8 Mya) (Wesselingh and Salo, 2006); the formation of land bridges between South and North America in different time periods, like the proto-Antillean Bridge (ca. 50 Mya) (Graham, 2003), the Greater Antilles/Aves Ridge (GAARlandia) (35–33 Mya) (Iturralde-Vinent and MacPhee, 1999), and the closure of the Panamanian Isthmus (ca. 15 Mya) (Montes et al., 2015).

The Andean uplift has played a role in the diversification of several palm groups. For some groups it has been suggested that the emerging Andes acted as a barrier, thus diversification could have happened by interrupting gene flow between ancestral populations. This is the case of diversification within the palm tribe Phytelepheae (Trénel et al., 2007), and the split of *Parajubaea* and *Allagoptera* (Meerow et al., 2015). For other groups the raising Andes could have provided new habitat types, promoting divergence in different niches. This scenario has been proposed for the palm genus *Ceroxylon* (Sanín et al., 2016; Trénel et al., 2008) and *Aiphanes* (Eiserhardt et al., 2011). It has also been proposed that different geological activities of tectonic uplift in the Fitzcarrald arch versus subsidence in the northern Amazonian foreland basin and their

different associated climatic regimes could have promoted divergence of *Astrocaryum* section *Huicungo* in Western Amazonia (Jiménez-Vásquez et al., 2017; Roncal et al., 2015). The appearance of dry formations in South America created new habitats for plant colonization, e.g. for *Attalea* (Freitas et al., 2016). In contrast, the formation of the aquatic Pebas system could have hindered plant species diversification, especially for Western Amazonia clades, by restricting colonization of flooded areas. For example, much of the species diversification within *Astrocaryum* in western Amazonia occurred after the drainage of the Pebas system (Roncal et al., 2013).

Palms have a good ability for transoceanic dispersal (Bacon et al., 2012; Cuenca et al., 2008; Meerow et al., 2015; Trénel et al., 2007), but land bridges between South and North America could also have played a role in species dispersal. The timing and method of dispersal among North, Central and South America, and the Caribbean, vary by group.

The proto-Antilles (ca. 50 Mya) has been proposed to be an old land bridge connecting North and South America by means of emerged island fragments (Graham, 2003). Cuenca et al. (2008) suggested that an early split in the Neotropical Chamaedoreae (ca. 45 Mya) which denoted a clade dispersal between North and South America, could be explained by the presence of the proto-Antilles.

Divergence in some palm groups coincided with the existence of GAARLandia, suggesting that some palm ancestors used this land bridge to disperse to the Caribbean or between Central and South America. Some examples of palm that could have used GAARLandia as a colonization route are *Hexopetion/Astrocaryum* clade (Roncal et al., 2013), subtribe Bactridiinae (Meerow et al., 2015), and the genus *Copernicia* (Bacon et al., 2012). In contrast, the current distribution of some clades in the Caribbean

cannot be explained by GAARlandia, based on divergence times occurring much later than when GAARlandia was present. For example, *Calyptronoma-Calyptrogyne* clade (Roncal et al., 2010) and *Attalea crassipatha* (Meerow et al., 2015) diverged after the existence of the GAARLandia land-bridge.

In recent years it has been proposed, based on new geological evidence, that the closure of the Panama Isthmus happened earlier (ca. 15 vs. 3.5 Mya) and in a more complex way than believed previously (Coates et al., 1992; Montes et al., 2015). This change in viewpoint has prompted reviews of the diversification history of North and South America biota. Bacon et al. (2015) evaluated the timing of biotic interchange between North and South America using published molecular and fossil data. They found that dispersal waves coincided with the evidence of an older closure of the Panama Isthmus, with significant dispersal waves of terrestrial organisms as early as 20 Mya.

1.4 Tribe Euterpeae

1.4.1 Taxonomic circumscription and phylogeny

Euterpeae is in the palm subfamily Arecoideae. The tribe comprises 33 species in five genera: *Euterpe* Mart. (7 species), *Hyospathe* Mart. (5 species), *Neonicholsonia* Dammer (1 species), *Oenocarpus* Mart. (10 species), and *Prestoea* Hook.f. (10 species) (Govaerts et al., 2015). Table 1 describes the current geographic distribution of genera in Euterpeae and the synapomorphies or character combinations useful to identify them. A sixth genus, *Jessenia* H. Karst., is monotypic and taxonomically controversial.

Jessenia was separated from *Oenocarpus* based on flowers with 9-20 stamens in contrast to six in *Oenocarpus*, presence of a ruminate endocarp instead of homogeneous, having bifid eophyls instead of 4-blade eophyls, presence of sicklelike trichomes on the abaxial side of the pinnae and different patterns of flavonoid components (Balick, 1986; Bernal et al., 1991; Burret, 1928). Moreover, the taxonomic recognition and rank of *Prestoea* and *Euterpe* have been controversial. Some authors have included in *Euterpe* the species now recognized as belonging to *Prestoea* (Table 2).

Euterpeae is restricted to the Neotropics, and is distributed from Central America to Southeastern Brazil and Bolivia, including the Caribbean islands (Table 1). Species grow in a wide elevation range, from sea level to 2,500 m of elevation, and are found in diverse habitats such as swamps, white sands and other terrestrial habitats, along river margins, and floodplain forests (Dransfield et al., 2008).

The Euterpeae was first classified as a subtribe within the Areceae (Dransfield and Uhl, 1986). Subsequently, based on molecular phylogenetic studies, it was elevated to the rank of tribe together with other previously recognized subtribes of Areceae (Dransfield et al., 2005). Henderson (1999) identified four synapomorphies for the tribe: 1) presence of an ocrea, 2) inflorescences branched to one order or spicate, 3) purple-black fruit, and 4) a crustaceous endocarp. There is also a tendency for rachillae to be absent in the adaxial side of the main inflorescence axis in some species of *Euterpe* (e.g. *Euterpe broadwayi*), a tendency that is developed further in *Oenocarpus*, in which the inflorescence is hippuriform (i.e. has the shape of a horsetail) (Henderson and Galeano, 1996). See section 1.4.3 for a description of different inflorescence types in Euterpeae. Other features of the tribe include fruits with stigmatic remains and a smooth epicarp (Dransfield et al., 2008). Figure 1 gives an overview of growth form

Table 1: Currently recognized genera of Euterpeae according to Henderson (1999), and morphological characters and synapomorphies used for genus delimitation. Taxa in Euterpeae have a widespread distribution in the Neotropics.

Genera	**No. Species**	**Distinguishing morphological characters**[a]	**Distribution**[b]
Hyospathe	6	Falcate pinna shape. Pedicellate staminate flowers. Basal and rounded fruit hilum	Costa Rica to Peru
Prestoea	10	Small fibrous ocrea. Leaf hypodermis present. Globose fruits. Subapical to lateral stigmatic fruit residue. A basal sclerified layer of fruit endocarp is present	West Indies, from Nicaragua southward in Central America, and into Brazil, Peru and Bolivia
Oenocarpus	9	Elongate more or less solid and persistent ocrea. Pinnae waxy gray abaxially. Strongly pendulous rachillae. Large embryo. Rachillae confined to the lateral and abaxial surfaces of the rachis. Flower triads sightly sunken in the rachillae. Lateral and elongate fruit hilum	from Costa Rica and Panama to the Amazon and Orinoco Valleys in Colombia, Ecuador, Venezuela, Guyana, Surinam, French Guiana, Brazil, Peru and Bolivia
Euterpe	7	Strongly pendulous pinnae, leaves with raised and twisted petiole scales. Linear pinna shape. Subapical to lateral stigmatic fruit residue	from the Lesser Antilles and Central America south through Brazil to Peru and Bolivia
Neonicholsonia	1	Persistent leaf sheaths. Persistent peduncular bract. Staminate flowers with sepals half as long as the petals	Panama and Nicaragua

[a]Henderson (1999), [b]Dransfield et al. (2008)

and general appearance of taxa in Euterpeae.

There are many studies on the taxonomy and systematics of this tribe, including monographs and taxonomic reviews, e.g.: *Oenocarpus* (Balick, 1986; Bernal et al., 1991; Burret, 1928), *Euterpe* (Burret, 1929; Henderson and Galeano, 1996), *Prestoea* (Henderson and Galeano, 1996), *Neonicholsonia* (Henderson and Galeano, 1996), and *Hyospathe* (Henderson, 2004; Skov and Balslev, 1989).

Table 2: Controversy on the taxonomic recognition of two pairs of Euterpeae genera. * indicates the recognized genus when combined.

Euterpe* and ***Prestoea***		***Oenocarpus**** and ***Jessenia***	
Separate	**Combined**	**Separate**	**Combined**
Moore (1963)	Martius (1823)	Burret (1928)	Martius (1823)
Uhl and Dransfield (1987)	Burret (1929)	MacBride (1960)	Wessels Boer (1965)
Henderson and de Nevers (1988)	MacBride (1960)	Balick (1986)	Bernal et al. (1991)
Henderson (1995)	Wessels Boer (1965)	Uhl and Dransfield (1987)	Henderson (1995)
Henderson and Galeano (1996)			Henderson (1999)
Dransfield et al. (2008)			Dransfield et al. (2008)

Based on a morphological phylogenetic analysis, Henderson (1999) proposed that *Prestoea* and *Oenocarpus* are sister taxa. On this basis, he suggested (Henderson, 1999) that *Prestoea* and *Euterpe* should be treated as separate genera, whereas some earlier workers placed them in the same genus (Burret, 1929; MacBride, 1960; Wessels Boer, 1965). Henderson (1999) also suggested that species in the genera *Oenocarpus* and *Jessenia* should be placed in a single genus, because *J. bataua* was nested within a clade of *Oenocarpus*. Henderson's (1999) work is the most comprehensive phylogenetic analysis of the group to date, but many species relationships in *Prestoea* and in *Oenocarpus* remain unresolved. In addition, Henderson (1999) evaluated this 54 anatomical characters with a maximum parsimony approach and with no measurement of branch support; thus the strength and reliability of the relationships he recovered

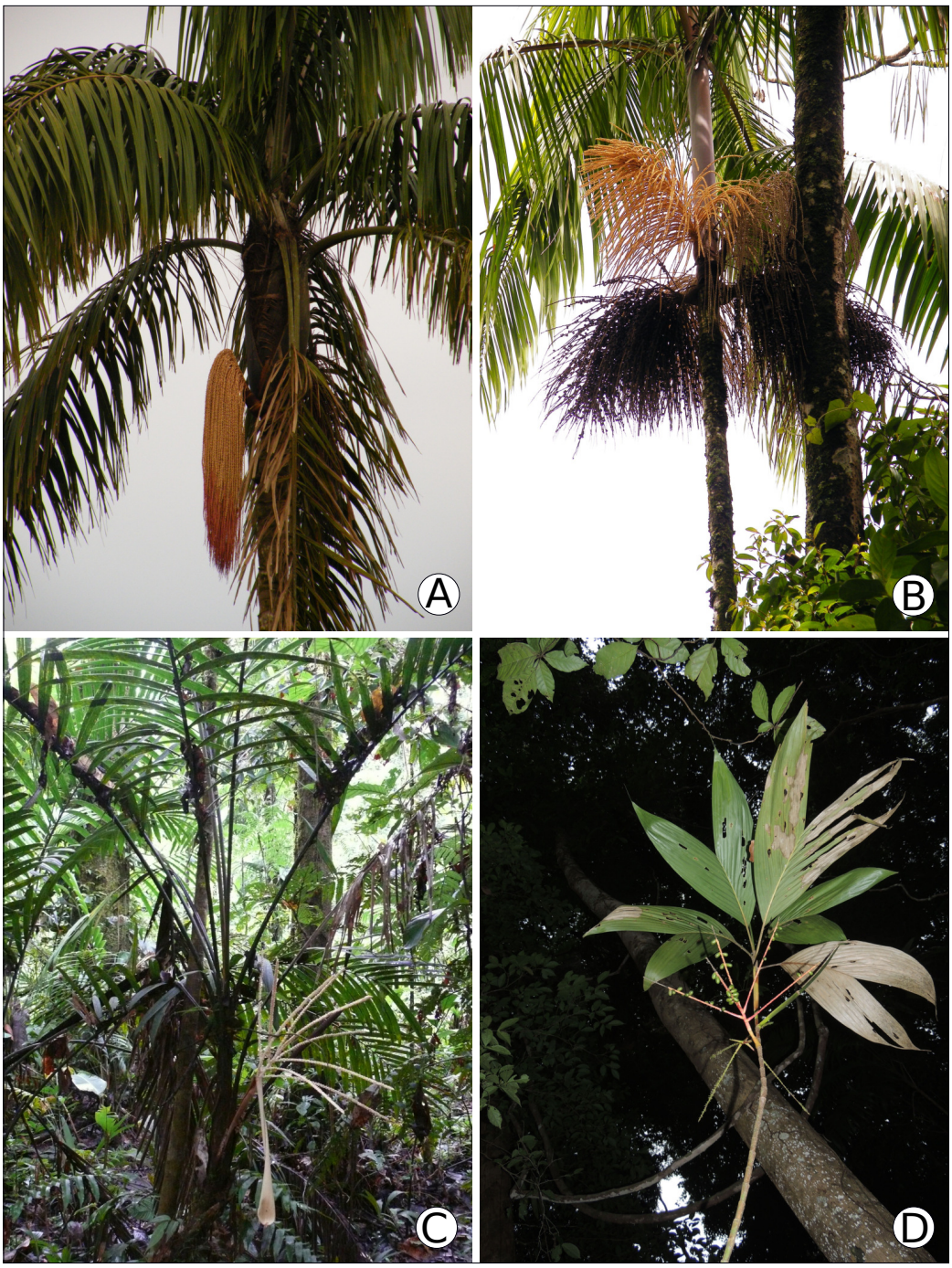

Figure 1: Growth form in Euterpeae. Tall slender palms: (A) *Oenocarpus bacaba*, (B) *Euterpe precatoria* var. *longivaginata*. Small forest understory palms: (C) *Prestoea schultzeana*, (D) *Hyospathe elegans* subsp. *tacarcunensis*. (Photos: Rodrigo Bernal)

cannot be judged by other workers.

Montúfar and Pintaud (2008) further tested if *Oenocarpus* and *Jessenia* should be considered as a single genus. They used plastid DNA to reconstruct a phylogeny for 12 of the 33 species in all five genera of Euterpeae. Relationships among genera were not recovered except for the sister relationship between *Euterpe* and *Oenocarpus* with low bootstrap support (BS) of 65%. The monophyly of the tribe was also supported only weakly (BS = 59%) (Montúfar and Pintaud, 2008). Recognition of *Jessenia* as a genus was rejected due to the lack of support in the phylogenetic tree; *Oenocarpus* and *Jessenia* formed a low-supported monophyletic group.

Monophyly of the Euterpeae is supported by several phylogenetic studies, although most studies included only a few taxa (Asmussen et al., 2006; Henderson, 1999). Euterpeae has been recovered in a group called the Core Arecoids formed by tribes Areceae, Euterpeae, Geonomateae, Leopoldinieae, Manicarieae, and Pelagodoxeae (Asmussen et al., 2006; Dransfield et al., 2005). Although the core arecoids clade has been recovered consistently in different studies, relationships among tribes remain only partially resolved (Baker et al., 2011; Barrett et al., 2016; Comer et al., 2016). Sister relationships (most poorly supported) of the Euterpeae with Areceae, Geonomateae and Pelagodoxeae have been proposed (Asmussen and Chase, 2001; Asmussen et al., 2006; Hahn, 2002; Loo et al., 2006). However, a sister-group relationship between Areceae and Euterpeae has been proposed recently with very high support (96 and 100 % bootstrap values), based on the analysis of 114 chloroplast genes and 168 nuclear genes, obtained with next-generation sequencing (Comer et al., 2015, 2016).

1.4.2 Ecological and economic importance of tribe Euterpeae

Members of the Euterpeae are important structural components of Amazonian rain forests. Some species of the tribe, like *Euterpe precatoria*, *Euterpe oleracea* Mart., and *Oenocarpus bataua* Mart., are among the 10 most abundant tree species in Amazonia (ter Steege et al., 2013). The Euterpeae also is economically important for local industry and indigenous communities (Balick, 1986). The oil-rich fruit mesocarp of several *Oenocarpus* species is used for high-quality oil similar to olive oil, and to produce a nutritious beverage (Balick, 1986; Montúfar et al., 2010). The economic potential of *Oenocarpus* is promising and awaits industrialization. Other uses of *Oenocarpus* species by local communities include the production of baskets, and the manufacture of walls for houses and roof thatching; the spines are used to make blowdarts (Balick, 1986). The primary meristem (palm heart) of *Euterpe* species like *E. oleracea* is a valuable economic resource for Amazonian communities (Johnson, 1998), and the fruit is a good source of nutrition (Wycoff et al., 2015).

Cultivation popularity of some species might create conservation problems for some rarer endemics. Such was the case with cultivation of *Euterpe oleracea* in the Atlantic rainforest of Brazil, where natural populations of the restricted species occur. This could lead to hybridization of the two species and decrease of *Euterpe edulis* populations (Tiberio et al., 2016).

1.4.3 Euterpeae inflorescence and pollination system

Four inflorescence types occur in tribe Euterpeae (see Figure 2). The most common inflorescence type is that with rachillae (i.e. inflorescence branches) growing all around

the main axis of the inflorescence (Henderson and Galeano, 1996). This type is found in *Prestoea*, *Hyospathe*, and some species of *Euterpe*. A variation of this inflorescence type is found in some species of *Euterpe*, where a partial loss of rachillae in the adaxial surface of the main axis occurs (Henderson and Galeano, 1996). A third type is found in *Oenocarpus* with long and pendulous rachillae, and with no rachillae in the adaxial surface of the main axis (hippuriform inflorescence) (Balick, 1986; Henderson and Galeano, 1996). The last type is the long unbranched (spicate) inflorescence of *Neonicholsonia* (Henderson and Galeano, 1996). Balick (1986) proposed that the inflorescence of *Oenocarpus* is derived from an inflorescence with rachillae all around the main axis as most species in *Euterpe*, through the loss of the adaxial rachillae. His hypothesis was based on the observation of triangular bracts on the place where aborted rachillae would occur. No study has evaluated the shifts of these inflorescence types.

Insects are the most common pollination vector in palms (Henderson, 2002, 1986), especially species in the orders Coleoptera, Hymenoptera, and Diptera. Some Euterpeae species may be specialized for pollination by specific insect taxa but pollination in others is effected by diverse insects (Listabarth, 2001). In Euterpeae, the three insect groups mentioned above act as pollinators. *Euterpe* is generally pollinated by several beetle families (e.g. Curculionidae, Chrysomelidae and Staphylinidae) and bees of the family Halictidae (Küchmeister et al., 1997). *Prestoea* is pollinated by bees in the families Halictidae and Apidae, and small flies of several families (Ervik and Bernal, 1996; Ervik and Feil, 1997). *Hyospathe* is possibly pollinated by a range of families of bees and flies (Listabarth, 2001), *Oenocarpus* is pollinated almost exclusively by Curculionidae (Núñez-Avellaneda and Rojas-Robles, 2008; Núñez-Avellaneda et al.,

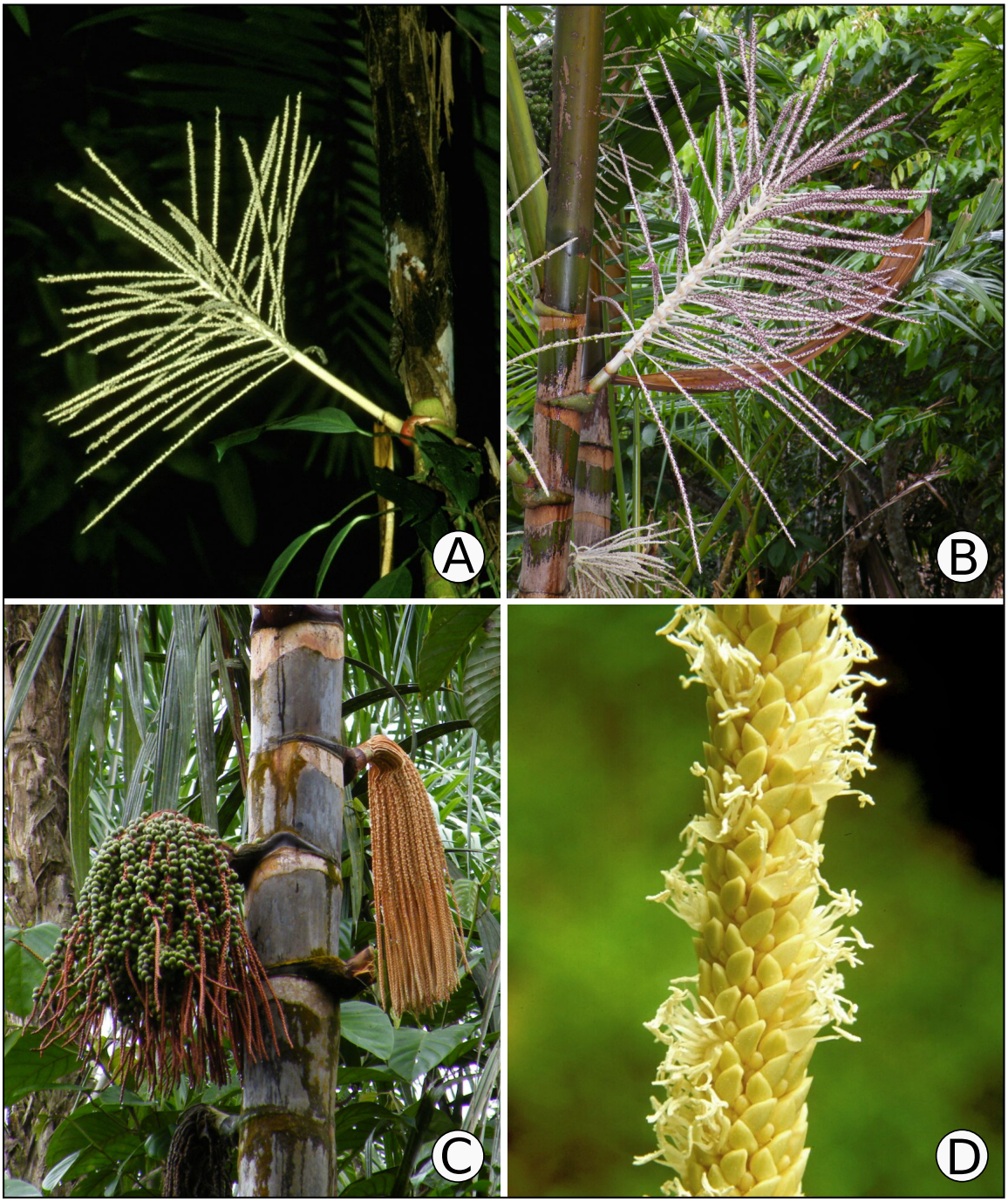

Figure 2: Euterpeae inflorescence types: (B) *Prestoea decurrens* with rachillae all around the main axis, (C) *Euterpe oleracea* with partial loss of adaxial rachillae, (D) *Oenocarpus balickii* showing complete loss of adaxial rachillae (hippuriform), (E) *Neonicholsonia watsonii* with a non-branching inflorescence (spicate). (Photos: Rodrigo Bernal).

2015), and therefore has the most specialized pollination system. These beetles have an intricate relationship with *Oenocarpus* inflorescences, which they use for oviposition (Núñez-Avellaneda and Rojas-Robles, 2008; Núñez-Avellaneda et al., 2015).

1.4.4 Euterpeae divergence times and biogeography

Only one family-level phylogenetic study has previously estimated the divergence time of the Euterpeae and its area of origin. Baker and Couvreur (2013) proposed that Euterpeae originated from a branch of the Arecoideae in South America with a mean stem age of 42.62 Mya, and a mean crown age of 31.54 Mya, whereas its sister tribe, the Areceae (Comer et al., 2015), diverged in Eurasia later (mean crown age of 34.11 Mya), greatly diversifying in the Indo-Pacific (Baker and Couvreur, 2013). Baker and Couvreur (2013) estimated the divergence time of Euterpeae, but their study focused on the family level, and only included one species per genus. It has been suggested that under-sampling the clade of interest can lead to underestimating the divergence ages within that clade (Schulte, 2013).

1.5 Objectives

My thesis had three main objectives:

1. Reconstruct a species-level dated phylogenetic tree of the Euterpeae using nuclear and chloroplast DNA sequences, to shed light on the taxonomic debate surrounding *Jessenia* and *Oenocarpus* and will test whether a DNA-based tree supports the morphology-based tree of the tribe (Henderson, 1999).

2. Test Balick's (1986) hypothesis on the evolution of *Oenocarpus* inflorescence by evaluating the evolution of inflorescence types in tribe Euterpeae.

3. Provide insight on the historical biogeography of tribe Euterpeae, estimating its ancestral distribution area, possible colonization events, and identifying geological events that may have influenced the diversification and distribution of the tribe.

2. Materials and methods

2.1 Taxon sampling

I sampled 33 accessions from 27 of the 33 accepted species in Euterpeae including seven infra-specific taxa, thus achieving 81.8% taxon sampling. The total number sampled species represent five of the seven species in *Euterpe*, all six species in *Hyospathe*, eight of the 10 species in *Prestoea*, seven of the nine species in *Oenocarpus*, and the monotypic genus *Neonicholsonia* (Govaerts et al., 2015; Henderson, 2004). Most of the missing taxa are narrow endemics: *E. luminosa* A.J.Hend., Galeano & Meza, found in a small high-elevation area in Peru (Henderson et al., 1991); *P. pubigera* (Griseb. & H.Wendl.) Hook.f., found in steep slopes of cloud forests in the Península de Paria of Sucre in Venezuela (Henderson and Galeano, 1996); *O. circumtextus* Mart., known only from the Cerro La Pedrera in Colombia and a small area across the Caquetá river (Bernal et al., 1991); *O. makeru* R.Bernal, Galeano & A.J.Hend., found in a small forested area along the Caquetá river in Colombia (Bernal et al., 1991); *P. simplicifolia* Galeano-Garcés, distributed in the western slope of the Cordillera Occidental in Colombia (Henderson and Galeano, 1996); and *E. longibracteata* Barb.Rodr., from which DNA of good quality could not be extracted.

No reliable fossils of Euterpeae are available that could be used for tree calibration,

so I used a wide taxon sampling for the outgroup that included 41 species. The outgroup was selected from all major tribes in Arecoideae, but also from Ceroxyloideae and Coryphoideae. Silica-gel dried leaves were obtained from the Quindio Botanical Garden, Fairchild Tropical Botanic Garden, Montgomery Botanical Center, fieldwork, and donations from palm specialists. I followed the classification of Henderson (2004) for the genus *Hyospathe*, otherwise I used accepted names as compiled in Govaerts et al. (2015). The complete list of DNA samples, and herbarium voucher information, are reported in Table 3.

Table 3: Samples used for the dated molecular phylogeny of tribe Euterpeae. The X below each marker name represents new sequences generated in this study. 73 sequences were obtained from GenBank with NCBI accession and herbarium numbers indicated.

Taxon name	**Voucher/ Accession number**	**WRKY6**	**CISP4**	**RPB2**	**TrnD-trnF**	**PHYB**
Acrocomia crispa	2004-0120B (FTG)	KM050896.1 Harris 014 (FTG)		X		
Aiphanes minima	2006-0935C (FTG)	KM050899.1 Harris 012 (FTG)	JQ822037.1 S.Zona 873 (FTG)	X	DQ159253.1, Zona 873	JQ822075.1, S. Zona 873 (FTG)
Allagoptera leucocalyx	76237A (FTG)	FJ957071.1, Zardini 54930 (FTG)	X	X	X	
Astrocaryum murumuru		KM050907.1, Harris 002 (FTG)	JQ822020.1, A. Perez 718 (CAY)	HQ265637.1, Perez 718 (CAY)	EU004228.1, JCP 311	JF422046.1, Perez 718 (CAY)
Attalea crassispatha	2000845 A (FTG)	FJ957078.1, Noblick 5516 (FTG)	KR559531.1	X	DQ159254.1, FTG 91 411A	KR559516.1, Henderson 806 (NY)

Taxon name	**Voucher/ Accession number**	**WRKY6**	**CISP4**	**RPB2**	**TrnD-trnF**	**PHYB**
Bactris major	58552 A (FTG)	FJ957092.1, Noblick 4942 (FTG)	X	HQ265652.1, H. Balslev 6737 (AAU)	DQ159244.1, FTG 57 819B	
Butia paraguayensis	2012-0012A (FTG)	FJ957102.1, Noblick 5285 (FTG)	X		X	X
Calyptrogyne ghiesbreghtiana	2002-0662 A (FTG)	X	JQ417557.1, Knudsen & Asmussen 627 (AAU)	X	X	X
Calyptronoma rivalis	F.J. Pichardo 15-002 (USD)	X	X	X	X	X
Carpentaria acuminata	2006-0780C (FTG)	X	X	AJ830196.1	X	
Carpoxylon macrospermum	961551P (FTG)	X	X	AJ830055.1	X	
Ceroxylon echinulatum	J. Roncal 515 (AMAZ)		X	EF128426.1, Borchsenius 639 (AAU)	EF128351.1, Borchsenius 625 (AAU)	X

Taxon name	**Voucher/ Accession number**	**WRKY6**	**CISP4**	**RPB2**	**TrnD-trnF**	**PHYB**
Chamaedorea schippii	2004-0341J (FTG)	X	X	DQ177752.1, Hodel 1132 (BH)	X	
Chelyocarpus ulei	J.Roncal 525 (AMAZ)	X	X	EU215491.1, J.Roncal 084 (FTG)	X	X
Cocos nucifera	2011-0236 (FTG)	FJ957109.1, Meerow 3206 (NA)	X	EF491150.1, 1968-4480 (K)	DQ227240.1, 1968-4480 (K)	JQ822083.1, Kew 1968-4480
Dictyocaryum lamarckianum	J.Roncal 518 (AMAZ)	X	KF776077.1, H. Balslev 8319 (AAU)	KF775749.1, H. Balslev 8319 (AAU)	KF775697.1, R. Bernal 4757 (COL)	X
Dictyosperma album	2011-0721 (FTG)	X	X	AJ830064.1	X	
Dypsis lutescens	P. 3072 A (FTG)	X	X	AJ830078.1	X	
Euterpe broadwayi	L. Noblick 5506B: 20070296 (MBC)	X	X	X	X	X
Euterpe catinga var. *catinga*	829 (Quindío Bot. Gard.)	X	X		X	X

Taxon name	**Voucher/ Accession number**	**WRKY6**	**CISP4**	**RPB2**	**TrnD-trnF**	**PHYB**
Euterpe edulis	2011-0603C (FTG)	X	X		X	X
Euterpe oleracea	G.Galeano 8180 (AAU)	X	X		X	X
Euterpe precatoria	L.Noblick 5478: 20070239A (MBC)	X	X		X	X
Euterpe precatoria var. *longivaginata*	H. Balslev 8330 (AAU)	X	X		X	
Gastrococos crispa			JQ417542.1, J. Roncal 79 (FTG)		HQ265714.1, J. Roncal 79 (FTG)	JF422042.1, Roncal 79 (FTG)
Gaussia attenuata	941269K (FTG)	X	X	EF491138.1, A. Cuenca AC14 (FTG)	DQ227205.1, A. Cuenca AC14 (FTG)	X
Geonoma frontinensis	1187 (Quindío Bot. Gard.)	X	JQ417587.1, Daly 6057 (NY)	JQ417507.1, Daly 6057 (NY)	X	X

Taxon name	**Voucher/ Accession number**	**WRKY6**	**CISP4**	**RPB2**	**TrnD-trnF**	**PHYB**
Howea forsteriana	93271F (FTG)	X	X	X	X	X
Hyophorbe lagenicaulis	2003-1162E (FTG)	X	X	AJ830168.1	DQ227192.1, A. Cuenca AC1 (FTG)	X
Hyospathe elegans subsp. *elegans* 2	H. Balslev 7574 (AAU)	X	X	X	X	X
Hyospathe elegans subsp. *elegans*	1077 (Quindío Bot. Gard.)	X	X	X	X	X
Hyospathe frontinensis	s.n. (COL)	X	X	X	X	X
Hyospathe macrorhachis	H.Balslev 6421 (AAU)	X	X	X	X	X
Hyospathe peruviana	s.n. (IRD)	X	X	X	X	X
Hyospathe pittieri	G.Galeano 8821 (COL)	X	X	X	X	X

Taxon name	Voucher/ Accession number	WRKY6	CISP4	RPB2	TrnD-trnF	PHYB
Hyospathe wendlandiana	R.Bernal 4744 (COL)	X	X	X	X	X
Iriartea deltoidea	J.Roncal 138 (FTG)	X	KF776080.1, H.Balslev 8081 (AAU)	KF775758.1, H.Balslev 8081 (AAU)	KF775742.1, H.Balslev 8081 (AAU)	
Iriartella stenocarpa			KF776086.1, H.Balslev 7593 (AAU)	KJ540557.1, H.Balslev 7794 (AAU)	KJ540548.1, H. Balslev 7688 (AAU)	
Manicaria saccifera	L.Noblick 5524D: 2009-0226A (MBC)	X	JQ417544.1, 93495A (FTG)	AY543103.1, Henderson sn.	DQ227241.1, Lewis 03-010 (FTG)	X
Mauritia flexuosa	L.Noblick 5470: 2007-0231C (MBC)			X	X	X
Neonicholsonia watsonii	2688A (FTG)	X	X	X	X	X
Oenocarpus bacaba	1053 (Quindío Bot. Gard.)	X	X	X	X	X
Oenocarpus balickii	G.Galeano 8558 N.1 (COL)	X	X	X	X	X

Taxon name	**Voucher/ Accession number**	**WRKY6**	**CISP4**	**RPB2**	**TrnD-trnF**	**PHYB**
Oenocarpus bataua var. *bataua* 2	G.Galeano 8137 (COL)	X	X	X	X	X
Oenocarpus bataua var. *bataua*	H.Balslev 7811 (AAU)	X	X	X	X	
Oenocarpus distichus	88579 (FTG)	X	X	X	X	X
Oenocarpus mapora	H.Balslev 6736 (AAU)	X	X	X	X	X
Oenocarpus minor	R.Bernal 4810 (COL)	X	X	X	X	X
Oenocarpus simplex	Tuberquia 447 (NY)	X	X	X	X	X
Oncosperma tigillarium	6472D (FTG)	X	X	X	X	X
Orania palindan	85370A (FTG)		X		X	X
Pelagodoxa henryana	2002-0212A (FTG)	X	X	AJ830135.1	EU004861.1, 1988-2935 (K)	

Taxon name	**Voucher/ Accession number**	**WRKY6**	**CISP4**	**RPB2**	**TrnD-trnF**	**PHYB**
Phoenix canariensis	Carlo Morici CMRO.3: 9716J (MBC)		X	X	EU004212.1, JCP 590 (P)	X
Pholidostachys pulchra	88508D (FTG)	X	JQ417643.1, J.Roncal 26 (FTG)	AJ830211.1	X	
Phytelephas macrocarpa	J.Roncal 527 (AMAZ)	X	X	AJ830179.1	EF128325.1, Ely 9 (K)	X
Prestoea acuminata var. *dasystachys*	R.Bernal 4832 (COL)	X	X	X	X	
Prestoea acuminata var. *montana* 2	L.Noblick 5615A (MBC): 20120429 (MBC)	X	X	X	X	X
Prestoea acuminata var. *montana*	F.Pichardo 15-001 (USD)	X	X	X	X	X
Prestoea carderi	1186 (Quindío Bot. Gard.)	X	X	X	X	

Taxon name	**Voucher/ Accession number**	**WRKY6**	**CISP4**	**RPB2**	**TrnD-trnF**	**PHYB**
Prestoea decurrens	G.Galeano 8107 (COL)	X	X	X	X	
Prestoea ensiformis	R.Bernal 4792 (COL)	X	X	X	X	X
Prestoea longipetiolata var. *cuatrecasasii*	R.Bernal 4822 (COL)	X	X	X	X	
Prestoea pubens var. *semispicata*	J.Roncal 390 (AAU)	X		X	X	
Prestoea pubens var. *semispicata* 2	Henderson 3031 (NY)	X	X	X	X	X
Prestoea schultzeana	R.Bernal 4801 (COL)	X	X	X	X	X
Prestoea tenuiramosa	R.Keller 4181 (G)	X			X	X
Pseudophoenix vinifera	W.Hahn 7732: 96348G (MBC)	X	X	AJ830181.1	DQ227238.1, Baker 1002 (FTG)	

Taxon name	**Voucher/ Accession number**	**WRKY6**	**CISP4**	**RPB2**	**TrnD-trnF**	**PHYB**
Ptychosperma macarthurii	94305F (FTG)	X	X	AJ830201.1	X	
Ravenea hildebrandtii	DeArmand Hull s.n/931108D (MBC)	X	X	EF128411.1, Chase 18145 (K)	EF128335.1, Chase 18145 (K)	X
Roystonea borinquena	A. Calonje PR03(1): 2003-0260B (MBC)	X	X	X	X	X
Sabal causiarum	A. Calonje PR06(1): 2003-0264B (MBC)	X			X	X
Socratea exorrhiza			KF776040.1, CDB1 (COL)	KF775753.1, H.Balslev 6739 (AAU)	KF775745.1, H.Balslev 7905 (AAU)	
Welfia alfredii	J.Roncal 507 (USM)	X	X	X	X	X
Wendlandiella gracilis	77248B (FTG)	X	X	AJ830167.1	DQ227221.1, A.Cuenca AC32 (FTG)	X

Taxon name	**Voucher/ Accession number**	**WRKY6**	**CISP4**	**RPB2**	**TrnD-trnF**	**PHYB**
Wettinia augusta			KF776058.1, H.Balslev 7696 (AAU)	KF775778.1, H.Balslev 8031 (AAU)	KF775718.1, H.Balslev 8031 (AAU)	

2.2 DNA extraction, amplification, sequencing and alignment

I selected one chloroplast and four low-copy nuclear DNA regions to reconstruct the phylogenetic tree: a chloroplast intergenic-spacer (*trnT-trnD*; Demesure et al., 1995), intron 4 of RNA polymerase II subunit 2 (RPB2; Thomas et al., 2006), a region amplified by the conserved intron-scanning primer set number 4 (CISP4; Bacon et al., 2008), partial exon 1 of phytochrome B (PHYB; Ludeña et al., 2011), and WRKY transcription factor 6 (WRKY6; Meerow et al., 2009). The list of primers used can be found in Table A.1

Chloroplast DNA in palms tends to be highly conserved (Barrett et al., 2016; Wilson et al., 1990); Domenech et al. (2014) emphasized that nuclear DNA gives best resolution to the nodes in a phylogenetic tree. I therefore did not sequence more chloroplast regions.

Total genomic DNA was extracted from silica-gel dried leaves and herbarium specimens using the Qiagen DNeasy Plant Mini Kit (Germany). The DNA extraction protocol was modified in order to increase DNA yield from fibrous palm leaves. Changes in the procedure were as follows: I used 45 mg of dried leaf material, 600 µL of Buffer AP1, an incubation period of 15 minutes at 65℃ after the addition of Buffer AP1, 195 µL of Buffer P3, DNA was eluted in 50 µL of Buffer AE, and an incubation period of 10 minutes at room temperature before the final centrifugation step. I used polymerase chain reaction (PCR) to amplify the selected DNA regions using the Qiagen Top Taq Master Mix Kit (Germany). A 25 µL solution was prepared with 8.5 µL of RNA-free

H_2O, 12.5 µL of the TopTaq Master Mix 2x, 1 µL of forward and reverse primer at a concentration of 10 µM and 2 µL of the total DNA extraction at 30 ng/µL or less. When the procedure with the Qiagen Top Taq Master Mix Kit was not successful I tried the Epicentre Failsafe PCR Premix Kit (Madison, WI, USA). I prepared a 25 µL solution with 9.45 µL of RNA-free H_2O, 12.5 µL of Failsafe Buffer E 2x, 0.4 µL of forward and reverse primer at a concentration of 25 µM, 0.25 µL of the enzyme mix and 2 µL of the total DNA extraction at 30 ng/µL. I used the PCR conditions as in the publications for each primer pair, and specific annealing temperatures can be seen in Table 4.

Table 4: DNA marker length, annealing temperature and nucleotide substitution model used in the phylogenetic analysis of tribe Euterpeae (Arecaceae).

DNA markers	**Product length in bp**	**Annealing temperature °C**
CISP4	625–920	55
RPB2	410–885	55
WRKY6	597–1180	58
PHYB	515-862	64
trnD-trnT	718–855	54

I could not obtain RPB2 products for most *Euterpe* species. Only *Euterpe broadwayi* Becc. ex Broadway was successfully amplified when I performed a two-step nested PCR. In the first step, I used primers RPB2-P10F (Denton et al., 1998) and RPB2-M11R (Roncal et al., 2005) with the Epicentre Failsafe Kit (Madison, WI, USA). In the second step the PCR was run using primers RPB2-F and RPB2-R (Thomas et al., 2006) and the first PCR products as the DNA template.

PCR products were purified using the Qiagen QIAquick Plant Purification Kit

(Germany) before being sent for Sanger sequencing to Eurofins genomics (Germany, https://www.eurofinsgenomics.eu/). The resulting chromatograms were observed in Geneious v. 7.1.8 (www.geneious.com, Kearse et al., 2012) to assemble forward and reverse sequences into contigs. IUPAC codes were used to treat heterozygotes. Sequences for each molecular marker were aligned individually with MAFFT v. 7.271 (Katoh and Standley, 2013) using the method L-INS-i for WRKY6, CISP4, PHYB, and *trnD-trnT*; and E-INS-i for RPB2, which helped to align difficult regions in RPB2. Alignments were manually refined. The total concatenated DNA matrix consisted of 4,593 bp and 4% missing data.

2.3 Phylogenetic reconstruction

I used two model-based methods to reconstruct the phylogenetic tree of tribe Euterpeae. A Bayesian inference (BI) analysis was carried out in BEAST v. 2.4.4 (Bouckaert et al., 2014) and a maximum likelihood (ML) analysis was conducted in RaxML v. 8.2.4. (Stamatakis, 2014).

RaxML was run using the concatenation of four markers (WRKY6, CISP4, RPB2 and *trnD-trnT*—PHYB was excluded see results section 3.1) with the general time reversible nucleotide substitution model and with the gamma parameter (GTR+GAMMA). GTR is the only nucleotide substitution model available in RaxML. The concatenated alignment was partitioned within RaxML to allow parameters to be estimated individually for each marker. A single best scoring ML tree was selected. I performed 1,000 bootstrap replicates using the rapid bootstrapping algorithm to assess branch support.

BEAST was used to reconstruct a phylogenetic tree and to estimate divergence times within Euterpeae. The analysis in BEAST was conducted using one partition for each of the four markers (WRKY6, RPB2, CISP4, *trnD-trnT*). The best nucleotide substitution model was selected for each marker using the Bayesian information criterion in Jmodeltest2 (Darriba et al., 2012) as implemented in the CIPRES portal (Miller and Pfeiffer, 2010). I selected the best scoring model, which parameters were also natively implemented in BEAUTi (HYK+G+I for *trnD-trnT* and HYK+G for the rest) (Bouckaert et al., 2014). A relaxed log normal molecular clock model was used with the Yule pure birth speciation tree model without specifying a starting tree. I used two runs of a Markov chain Monte Carlo (MCMC) chain length of 30 million generations storing every 3,000 trees and a pre-burnin of 100,000 generations. Tree and log files were combined with Log Combiner v. 2.4.4 (Bouckaert et al., 2014), and a maximum clade credibility tree was obtained from 15,002 trees after a burnin of 25% of the trees with Tree Annotator v. 2.4.4 (Bouckaert et al., 2014). I verified that the MCMC run had reached convergence using the program Tracer v1.6 (Rambaut et al., 2014) and by ensuring that the effective sample sizes exceeded 200. I visualized ML and BI trees using the program FigTree v. 1.4.2 (http://tree.bio.ed.ac.uk/software/figtree/).

I set up monophyly priors for subfamily Coryphoideae and for the clade Ceroxyloideae+Arecoideae. The monophyly of these groups is well supported (Asmussen et al., 2006; Baker et al., 2009; Dransfield et al., 2005; Faurby et al., 2016).

2.4 Divergence time estimation

To calibrate the resulting phylogenetic tree I selected seven calibration points. Five of these were fossils carefully selected according to the five criteria proposed as best practices for justifying fossil calibrations (Parham et al., 2012). In addition, I used two secondary calibration points obtained from the literature.

Chief among the fossil selection criteria is the reliability of the taxonomic identity. Although the palm family has a rich fossil record, there is no reliable fossil that could be identified to belong to Euterpeae. The fossil *Palmaepites eocenica* was first assigned a relationship with *Jessenia* (*Oenocarpus*) or *Juania*. However, Harley (2006), in a review of palm fossils, found the association with either genus was unfounded. Poinar (2002) mentioned a flower fossil found in Mexican amber with a resemblance to the genus *Neonicholsonia*, but could not place this fossil in any extant genus with certainty. Hoorn (1994, 1993) described pollen fossils that resemble *Euterpe* (*Psilamonocolpites amazonicus*) and others having an affinity to the palm family (*P. nanus*). In a recent publication, affinities of these fossils were changed to *Geonoma/Euterpe*, and *Euterpe*, respectively (Salamanca Villegas et al., 2016). Therefore, I decided not to include these fossils for calibration, given the confusing history of their affinity with *Euterpe*.

Because of the lack of reliable fossils within the study group, I searched for fossils in other tribes of Arecoideae. The fossil record of Cocoseae is abundant and reliable; thus two fossils were used to calibrate nodes in Cocoseae: (1) *Bactris pseudocuesco* from the Middle Oligocene of Puerto Rico (Collazo Shale Formation) was used to calibrate the crown node of subtribe Bactridiinae (Hollick (1928) noted that the fossilized fruits of this sample resembled those of the extant *Bactris cuesco*); and (2) a calibration

point for the stem node of Attaleinae was based on the fossilized fruit of *Tripylocarpa aestuaria* from the late Danian of Argentina (Salamanca Formation; this fossilized fruit shows mesocarp with furrows or striations and three distinctive longitudinal markings running from apex to base of the epicarp, similar to Attaleinae (Futey et al., 2012)); and (3) fossil flowers of *Socratea brownii* from the Late Oligocene of Mexico (Quinta Formation) were used to calibrate the stem node of *Socratea* (the fossil is composed of staminate flowers preserved in amber with morphological characters and stamen number similar to *Socratea* (Poinar, 2002)). Outside Arecoideae I selected two fossils as representatives of subfamilies Ceroxyloideae and Coryphoideae : (4) *Echimonoporopollis grandiporus* pollen fossil from Lower to Middle Eocene of India (Neyveli Formation, Saxena et al., 1992) was used to calibrate the stem node of *Ravenea*, based on Harley's (2006) finding of a resemblance with *Ravenea* in subfamily Ceroxyloideae; and (5) the stem of Coryphoideae was calibrated based on the fossil *Sabalites carolinensis* from the late Coniacian to early Santonian of the United States of America (this fossil consists of impressions of a fan palm with very flabellate leaves and numerous rays that resemble those of subfamily Coryphoideae (Berry, 1914); this fossil served also to calibrate the root of the tree). The two secondary calibration points were: (6) the crown age of tribe Geonomateae as estimated in Roncal et al. (2010); and (7) the crown age of tribe Chamaedoreeae based on the work of Cuenca et al. (2008). Table 5 shows the settings used in BEAST for all of the above calibrations. I used an exponential distribution for the fossil calibrations and normal distributions for the secondary calibrations, following the recommendations of Ho and Phillips (2009).

Table 5: Fossil and secondary calibration points in the dated molecular phylogenetic tree of tribe Euterpeae and their parameter settings in BEAUTi v. 2.4.4.

Number	Fossil name	Calibrated node	Hard lower bound (Mya)	Soft upper bound 95% (Mya)	Exponential mean (uncertainty)
I	*Sabalites carolinensis*	stem of Coryphoideae	84.0	90.0	2.0
II	*Echimonoporopollis grandiporus*	stem of *Ravenea*	41.2	65.2	8.0
III	*Socratea brownii*	stem of *Socratea*	22.5	31.5	3.0
IV	*Tripylocarpa aestuaria*	stem of Attaleinae	61.9	64.9	1.0
V	*Bactris pseudocuesco*	crown of Bactridiinae	26.0	33.5	2.5
	Secondary calibrations		**Mean**	**Standard deviation**	
VI	Geonomateae	crown of Geonomateae	30.7	4.0	
VII	Chamadoreeae	crown of Chamaedoreeae	50	4.5	

Mya = million years ago

2.5 Ancestral character state reconstruction of the inflorescence type in Euterpeae

I reconstructed the evolution of the inflorescence branching pattern in Euterpeae using a maximum likelihood approach with the function 'ace' of the 'ape' package in R (Paradis et al., 2004). I used a trimmed version of the Bayesian dated phylogenetic tree of BEAST for this analysis, excluding all taxa outside tribes Euterpeae and Areceae (the sister tribe, see results section 3.1). I assigned the following character states for taxon based on the literature (Balick, 1986; Bernal et al., 1991; Dransfield et al., 2008; Henderson, 2004; Henderson and Galeano, 1996): (1) inflorescence with rachillae all around the main axis; (2) inflorescence with a partial loss of adaxial rachillae; (3) inflorescence with a complete loss of adaxial rachillae (hippuriform); and (4) unbranched inflorescence (spicate). Data were tested under three different predefined character state transition rates models under the function 'ace': (1) ER (equal rates model); (2) SYM (symmetrical rates model); and (3) ARD (all rates different model). The likelihood value for each model was compared between each other and a likelihood ratio test was performed to test whether an increment in the likelihood for the model with the highest likelihood is significant.

2.6 Ancestral biogeographical range estimation

I defined seven biogeographical areas based on geomorphological barriers in the Neotropics, its geological history, and the current distribution of Euterpeae and Areceae.

These were: (A) Central America and Chocó; (B) Caribbean; (C) Andes (comprising northern and central Andes); (D) Amazonia; (E) Guiana Shield; (F) Brazilian Atlantic Forest; and (G) Indo-Pacific Region. Polygons for areas in Central and South America were designed using The Nature Conservancy (TNC) terrestrial ecoregions of the world (The Nature Conservancy, 2009). I coded a distribution matrix in presence-absence format for each taxon on each of the seven biogeographic areas based on data available at The Global Biodiversity Facility (GBIF, http://gbif.org) from preserved specimens or human observations, expert maps, and species identification guides (Borchsenius et al., 1998; Galeano and Bernal, 2010; Henderson, 2004; Henderson and Galeano, 1996; Henderson et al., 1997; Lorenzi et al., 2010). When a taxon had only a few (2–3) occurrences within a given biogeographical area, this 'rare' area was coded as absent if the taxon had many other occurrences in other biogeographical area(s). Thus, I coded as present only biogeographical areas in which a taxon was common and discarded those where the taxon was rare in order to more narrowly infer ancestral areas and biogeographical movements (Table 6)

To test the geographical pattern of diversification history in the Euterpeae, I performed a biogeographical range evolution analysis using maximum likelihood in the R package 'BioGeoBears' v. 0.2.1 (Matzke, 2013). I used a trimmed version of the dated Bayesian phylogenetic tree to include only tribes Euterpeae and Areceae. BioGeoBears implements commonly used models of range evolution such as dispersal, extinction, cladogenesis (DEC), BAYAREALIKE, and DIVALIKE (Ree and Smith, 2008). It also implements a jump parameter +J, which adds a founder-event parameter to the models (Martins et al., 2014). The analysis was run under the DEC, BAYAREALIKE and DIVALIKE models with and without the +J parameter.

Table 6: Occurrence table of taxa in Euterpeae by geographic area. A=Central America and Chocó, B=Caribbean, C=Andes, D=Amazonia, E=Guiana Shield, F=Atlantic Forest, G=Indo-Pacific.

Taxa	**A**	**B**	**C**	**D**	**E**	**F**	**G**
Euterpe broadwayi	0	1	0	0	0	0	0
Euterpe catinga	0	0	1	1	1	0	0
Euterpe edulis	0	0	0	0	0	1	0
Euterpe oleracea	1	0	0	1	1	0	0
Euterpe precatoria	1	0	1	1	1	0	0
Euterpe precatoria var. *longivaginata*	1	0	1	1	0	0	0
Hyospathe elegans subsp. *elegans*	0	0	1	1	1	0	0
Hyospathe frontinensis	0	0	1	0	0	0	0
Hyospathe macrorhachis	0	0	1	0	0	0	0
Hyospathe peruviana	0	0	1	0	0	0	0
Hyospathe pittieri	0	0	1	0	0	0	0
Hyospathe wendlandiana	0	0	1	0	0	0	0
Neonicholsonia watsonii	1	0	0	0	0	0	0
Oenocarpus bacaba	0	0	0	1	1	0	0
Oenocarpus balickii	0	0	0	1	0	0	0
Oenocarpus bataua var. *bataua*	1	0	0	1	1	0	0
Oenocarpus distichus	0	0	0	1	0	0	0
Oenocarpus mapora	1	0	1	1	0	0	0
Oenocarpus minor	1	0	1	1	0	0	0
Oenocarpus simplex	0	0	0	1	0	0	0
Prestoea acuminata var. *dasystachys*	0	0	1	0	0	0	0
Prestoea acuminata var. *montana*	0	1	0	0	0	0	0
Prestoea carderi	0	0	1	0	0	0	0
Prestoea decurrens	1	0	0	0	0	0	0
Prestoea ensiformis	1	0	1	0	0	0	0
Prestoea longipetiolata var. *cuatrecasasii*	0	0	1	0	0	0	0
Prestoea pubens var. *semispicata*	1	0	0	0	0	0	0
Prestoea schultzeana	1	0	0	1	0	0	0
Prestoea tenuiramosa	0	0	0	0	1	0	0
Carpentaria acuminata	0	0	0	0	0	0	1
Carpoxylon macrospermum	0	0	0	0	0	0	1
Dictyosperma album	0	0	0	0	0	0	1
Dypsis lutescens	0	0	0	0	0	0	1
Howea forsteriana	0	0	0	0	0	0	1
Oncosperma tigillarium	0	0	0	0	0	0	1
Ptychosperma macarthurii	0	0	0	0	0	0	1

I tested three biogeographic models, which enforce constraints in terms of dispersal probabilities throughout different time periods. The first was a 'null' model with equal probability of dispersal among all biogeographic areas through time. Thus, no penalty was imposed for dispersal from any one area to another at any given time. For the second and third model a dispersal cost matrix was created for each time period to reflect the easiness of dispersal from one area to the other taking into account the geomorphological history of the Neotropics in the last 47 million years. The best biogeographical and range evolution model was selected based on the Akaike information criterion (AIC). Eighteen models were compared.

For the second model ('complex biogeographic model 1'), I constrained the dispersal probability among biogeographical areas during four time periods. Throughout the first period (0–10 Mya), the Andes achieved their maximum elevation and thus could have acted as a dispersal barrier (Gregory-Wodzicki, 2000). The second time period (10–15 Mya) was characterized by the closure of the Panamanian Isthmus, and the Andes had already risen up to approximately half of their current elevation (Gregory-Wodzicki, 2000; Montes et al., 2015). During the third time period (15–20 Mya), the Panama Isthmus was open diminishing the potential of crossing between Central and South America; the Andes also achieved around half their current elevation (Gregory-Wodzicki, 2000; Montes et al., 2015). In the course of the fourth time period (20–47 Mya), the central and northern Andes did not have an elevation that would impede movement of taxa across or into these lands (Gregory-Wodzicki, 2000), and there was no landmass uniting Central and South America (Montes et al., 2015).

For the third biogeographic model ('complex biogeographic model 2') I used a six-time partition. I used the same time periods as in the complex biogeographic

model 1 and included a new time period (33–35 Mya), when a land bridge called GAARlandia is hypothesized to have existed (Iturralde-Vinent and MacPhee, 1999) that would have facilitated the movement of taxa between Central and South America.

Values in the dispersal cost matrix (Table 7) followed the criteria of Roncal et al. (2013). Dispersal values closer to 0 represent a greater dispersal penalty, and a value of 1 was assigned to adjacent areas with no dispersal barriers (e.g. mountains, water). I imposed a dispersal value of 0.5 to non-adjacent areas separated by two steps and no other dispersal constraints, or to dispersal from the Andes to adjacent areas or vice-versa, between 10–20 Mya (when the Andes were at half their current elevation). A value of 0.33 was attributed to dispersal from non-adjacent areas separated by three or more steps and no other dispersal constraint. A dispersal constraint of 0.33 was also assigned for the dispersal between the Andes and adjacent areas between 0–10 Mya (Andean at current elevation), or the dispersal across the Andes between 10–20 Mya. A value of 0.1 was imposed for areas that lacked land connectivity— taxa must have therefore dispersed across the water; and for the dispersal across the fully formed Andes between 0–10 Mya. At last, I imposed a value of 0.01 for the dispersal to or from the Indo-Pacific Region.

Table 7: Dispersal cost matrices for biogeographical analysis of tribe Euterpeae. A=Central America and Chocó, B=Caribbean, C=Andes, D=Amazonia, E=Guiana Shield, F=Atlantic Forest, G=Indo-Pacific.

Complex model 1

0–10 Mya

	A	B	C	D	E	F	G
A	0	0.1	0.33	0.1	0.1	0.1	0.01
B	0.1	0	0.1	0.1	0.1	0.1	0.01
C	0.33	0.1	0	0.33	0.1	0.1	0.01
D	0.1	0.1	0.33	0	1	0.5	0.01
E	0.1	0.1	0.1	1	0	0.33	0.01
F	0.1	0.1	0.1	0.5	0.33	0	0.01
G	0.01	0.01	0.01	0.01	0.01	0.01	0

10–15 Mya

	A	B	C	D	E	F	G
A	0	0.1	0.5	0.33	0.33	0.33	0.01
B	0.1	0	0.1	0.1	0.1	0.1	0.01
C	0.5	0.1	0	0.5	0.33	0.33	0.01
D	0.33	0.1	0.5	0	1	0.5	0.01
E	0.33	0.1	0.33	1	0	0.33	0.01
F	0.33	0.1	0.33	0.5	0.33	0	0.01
G	0.01	0.01	0.01	0.01	0.01	0.01	0

15–20 Mya

	A	B	C	D	E	F	G
A	0	0.1	0.1	0.1	0.1	0.1	0.01
B	0.1	0	0.1	0.1	0.1	0.1	0.01
C	0.1	0.1	0	0.5	0.33	0.33	0.01
D	0.1	0.1	0.5	0	1	0.5	0.01
E	0.1	0.1	0.33	1	0	0.33	0.01
F	0.1	0.1	0.33	0.5	0.33	0	0.01
G	0.01	0.01	0.01	0.01	0.01	0.01	0

20–47 Mya

	A	B	C	D	E	F	G
A	0	0.1	0.1	0.1	0.1	0.1	0.01
B	0.1	0	0.1	0.1	0.1	0.1	0.01
C	0.1	0.1	0	1	0.5	0.33	0.01
D	0.1	0.1	1	0	1	0.5	0.01
E	0.1	0.1	0.5	1	0	0.33	0.01
F	0.1	0.1	0.33	0.5	0.33	0	0.01

G	0.01	0.01	0.01	0.01	0.01	0.01	0

Complex model 2 (0–20 Mya time frame equal to complex model 1)

20–33 Mya

	A	B	C	D	E	F	G
A	0	0.1	0.1	0.1	0.1	0.1	0.01
B	0.1	0	0.1	0.1	0.1	0.1	0.01
C	0.1	0.1	0	1	0.5	0.33	0.01
D	0.1	0.1	1	0	1	0.5	0.01
E	0.1	0.1	0.5	1	0	0.33	0.01
F	0.1	0.1	0.33	0.5	0.33	0	0.01
G	0.01	0.01	0.01	0.01	0.01	0.01	0

33–35 Mya

	A	B	C	D	E	F	G
A	0	1	0.33	0.33	0.5	0.1	0.01
B	1	0	0.5	0.5	1	0.33	0.01
C	0.33	0.5	0	1	0.5	0.33	0.01
D	0.33	0.5	1	0	1	0.5	0.01
E	0.5	1	0.5	1	0	0.33	0.01
F	0.1	0.33	0.33	0.5	0.33	0	0.01
G	0.01	0.01	0.01	0.01	0.01	0.01	0

35–47 Mya

	A	B	C	D	E	F	G
A	0	0.1	0.1	0.1	0.1	0.1	0.01
B	0.1	0	0.1	0.1	0.1	0.1	0.01
C	0.1	0.1	0	1	0.5	0.33	0.01
D	0.1	0.1	1	0	1	0.5	0.01
E	0.1	0.1	0.5	1	0	0.33	0.01
F	0.1	0.1	0.33	0.5	0.33	0	0.01
G	0.01	0.01	0.01	0.01	0.01	0.01	0

Mya = million years ago

3. Results

3.1 Phylogenetic relationships within Euterpeae

PHYB was removed from the concatenated phylogenetic analysis due to a very strong discrepancy in the phylogenetic signal with other DNA markers. The PHYB gene tree rendered the genus *Hyospathe* and some taxa of *Prestoea* forming a strongly supported clade with the Geonomateae (Figure A.1). This could be due to incomplete linage sorting where these Euterpeae taxa share some ancestral alleles with the Geonomateae at the PHYB locus, or due to hybridization. Visual inspection of the four gene trees showed no phylogenetic conflict among them, thus I concatenated them for the final analysis. The Bayesian analysis yielded high effective sample sizes (>200) and consistent results between the two MCMC chain iterations. The MCMC runs reached convergence as observed in Tracer v. 1.6 (Rambaut et al., 2014). Both BI and ML concatenated analyses recovered congruent topologies within Euterpeae and the outgroup. The Euterpeae was monophyletic with high support (0.97 posterior probability (pp), 100% BS) and was sister to the Areceae with high support (0.98 pp, 96% BS, Figure 3).

All genera within Euterpeae were monophyletic with high support, and all inter-generic relationships were recovered with high support too (Figure 3). The genus

Hyospathe was sister to all other genera (0.97 pp, 100% BS). *Oenocarpus* was sister to *Prestoea* with high support in the Bayesian tree (0.97 pp) and with moderate support in the ML tree (73% BS). *Euterpe* was sister to the monotypic genus *Neonicholsonia* (1.0 pp, 100% BS). The clade *Euterpe* + *Neonicholsonia* was sister to the clade *Oenocarpus* + *Prestoea* (0.97 pp, 100% BS, Figure 3).

Most of the interspecific relationships were resolved with fairly good resolution (>0.95 pp, >90% BS), especially for *Hyospathe*, *Euterpe*, and most of the clades in *Prestoea*. I also found that some widespread species were para- or polyphyletic. This was the case, for example, for *Prestoea acuminata* (Willd.) H.E.Moore, *Euterpe precatoria* and *Hyospathe elegans* Mart. All interspecific relationships within *Hyospathe* were well supported except for the relationship between *H. macrorhachis* Burret and *H. peruviana* A.J.Hend. (0.82 pp, 58% BS). Two main clades were recovered. One grouped *H. elegans* subsp. *elegans* 2, *H. macrorhachis*, and *P. peruviana*. The other grouped *H. elegans* subsp. *elegans* 1, *H. frontinensis* A.J.Hend., *H. wendlandiana* Dammer ex Burret, and *H. pittieri* Burret.

All relationships within *Euterpe* were well supported (> 0.98 pp, > 93% BS). I found *E. oleracea*, distributed near the coast and rivers in Northern South America and Central America, as sister to all other species in my sampling.

Within *Prestoea*, the analyses recovered two main clades. One consisted of five species distributed in montane or premontane habitats (350 to 2000 m of elevation), and the second consisted of three species distributed in lowland tropical rainforests to premontane habitats (from 0 up to 900 m of elevation). The BI analysis rendered a slightly different topology than the ML analysis for some relationships within *Prestoea*, but the discrepancy was not strong (pp values < 0.55, BS < 46%). For example, the

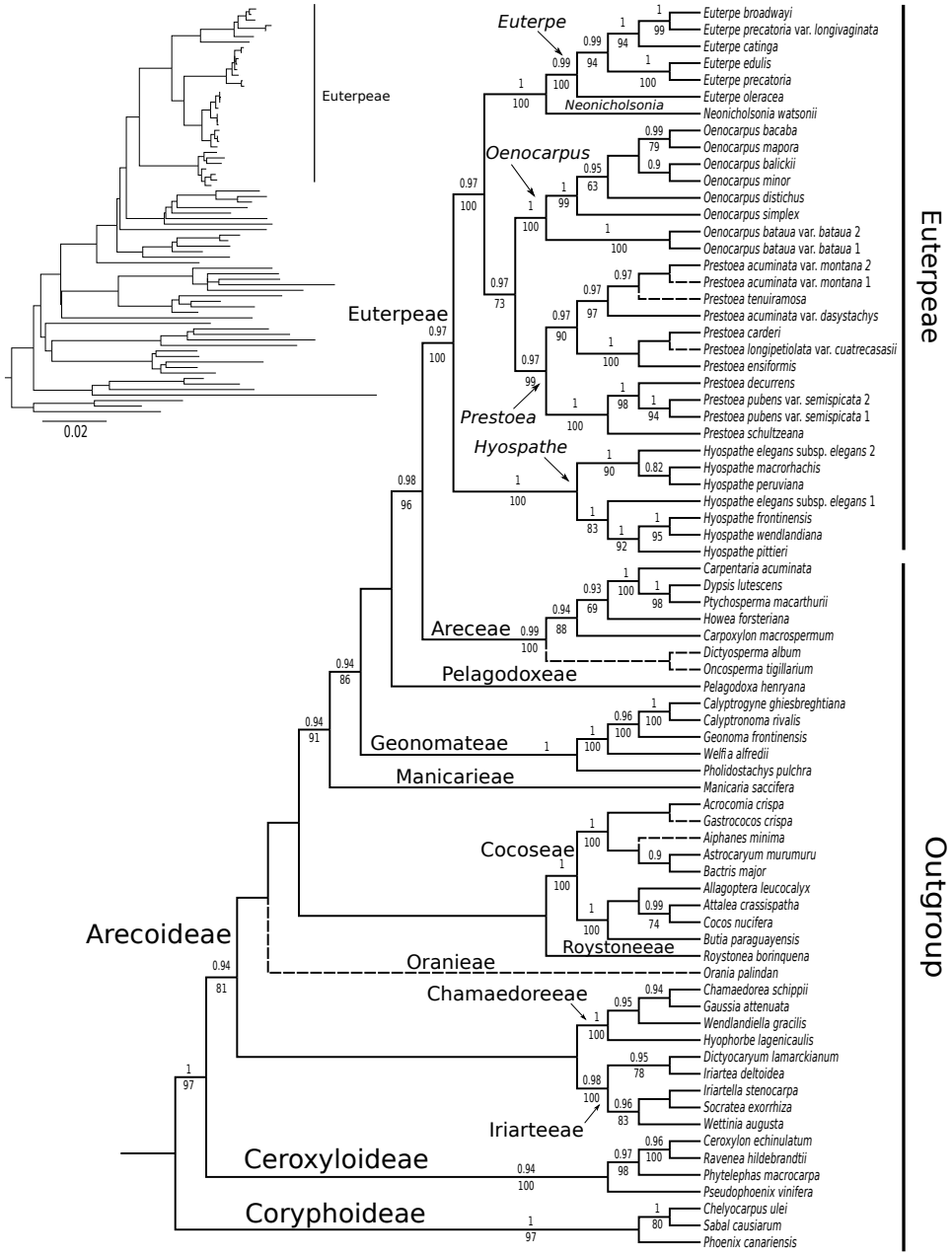

Figure 3: Bayesian maximum clade credibility tree of Euterpeae and outgroup resulting from the combined analysis of three nuclear and one chloroplast DNA markers. Values above the branches are the Bayesian posterior probabilities (pp) > 0.8, and values below the branches the maximum likelihood bootstrap values (BS) > 60. Dashed lines depict relationships that were not recovered in the maximum likelihood tree. Inset is the maximum likelihood phylogram showing branch lengths.

weak relationship of *P. carderi* (Hook.f.) Burret and *P. longipetiolata var. cautrecasasii* (H.E.Moore) A.J.Hend. & Galeano (0.5 pp) was not obtained in the ML analysis, where *P. longipetiolata var. cuatrecasassi* formed a group with *P. ensiformis* (Ruiz & Pav.) H.E.Moore with moderate support (87% BS).

For *Oenocarpus*, my results showed that the widely distributed *O. bataua* was sister to all other *Oenocarpus* species sampled. BI support values for clades within *Oenocarpus* were in some cases higher than the ML bootstrap support. For example, the clade formed by *O. distichus* Mart. + *O. minor* Mart. + *O. balickii* F.Kahn + *O mapora* H.Karst. + *O. bacaba* Mart. had a pp of 0.95 and a BS of 63%.

3.2 Divergence times

Differences between mean and median node ages differed little (Table 8). Therefore, I refer to mean node ages for divergence times hereafter. Based on the analysis in BEAST the mean crown age for Euterpeae was 40.57 Mya (95% HPD 35.23–49.36), and the mean stem age was 46.62 Mya (95% HPD 39.11–56.02).

Euterpeae diverged from Areceae during the Eocene but cladogenesis within the extant genera of Euterpeae began after the Middle Miocene, beginning around 15 Mya and extending into the Pliocene and Pleistocene. The monotypic *Neonicholsonia* diverged first at around 20 Mya. *Hyospathe*, *Prestoea*, and *Euterpe* had concurrent crown ages around 10 Mya. In the genus *Hyospathe* I found a very long time span between the stem age at 40.57 Mya, and the mean crown age at 10.21 Mya. Divergence times of lowland and montane *Prestoea* clades were estimated at around 4 and 6 Mya, respectively. *Oenocarpus* had the most recent crown age among all Euterpeae

genera at around 7 Mya. Figure 4 and Table 8 show the dated phylogenetic tree of the Euterpeae with divergence times for 30 nodes of interest including those for all genera and their confidence intervals (95% HPD).

Table 8: Divergence times and ancestral area probabilities for selected nodes (see. Figure 4). 95% HPD=95% highest posterior density. Biogeographic areas: A=Central America and Chocó, B=Caribbean, C=Andes, D=Amazonia, E=Guiana Shield, F=Atlantic Forest, G=Indo-Pacific. Only ancestral biogeographic ranges with a probability > 0.10 are shown, except in node 18 where all probabilities were below the threshold.

Node numbers	**Mean node ages**	**Median node ages**	**95% HPD**	**Ancestral biogegraphic range probabilities**
1	40.57	40.42	32.23–49.36	A:0.16; ACDE:0.12
2	10.21	9.58	4.82–17.6	CDE:0.25; CDEF:0.21; ACDE:0.16; C:0.12
3	6.63	6.24	2.86–11.34	C:0.40; CDE:0.22; CD:0.11
4	7.35	7.06	3.43–12.08	C:0.45; CDE:0.18; CD:0.10
5	29.89	29.31	21.72–36.97	A:0.62
6	22.74	22.08	14.83–30.72	A:0.64
7	10.52	9.39	5.46–14.73	A:0.32; :AC:0.19; ABCE:0.16
8	4.19	4.01	1.53–7.77	A:0.81; AD:0.18
9	5.78	4.61	2.05–7.9	AC:0.25; ABCE:0.21; BCE:0.14; C:0.10
10	3.27	2.12	0.69–4.06	BCE:0.64; BC:0.17; CE:0.13
11	1.79	0.65	0.06–1.72	BE:0.95
12	7.32	7.15	3.66–13.11	AD:0.25; ADE:0.24; D:0.23; DE:0.15
13	1.28	1.06	0.07–2.71	ADE: 0.74; DE:0.11
14	4.11	3.95	1.67–7.3	D:0.90
15	0.74	0.65	0.04–1.61	D:0.31; ACD:0.19; CD:0.18; DE:0.15
16	19.93	20.03	13.75–28.64	A:0.69
17	10.42	10.34	6.02–15.82	A:0.14; ACDE:0.13

Node numbers	Mean node ages	Median node ages	95% HPD	Ancestral biogegraphic range probabilities
18	8.43	8.37	4.68–13.18	A:0.084; ACDF:0.072; ABCD:0.064
19	1.47	1.3	0.02–3.08	ACDF:0.27; ADEF:0.25; CDEF:0.23; ACEF:0.15
20	4.33	4.21	1.72–7.65	ABCD:0.25
21	46.62	46.59	39.11–56.02	AG:0.19
22	33.46	34.06	25.39–43.39	G:0.99
23	32.62	33.22	25.82–40.06	N/A
24	62.67	62.41	61.9–64.17	N/A
25	30.98	30.41	26–37.44	N/A
26	28.84	28.64	17.85–42.23	N/A
27	48.43	48.74	41.17–56.54	N/A
28	30	29.17	23.8–36.61	N/A
29	69.51	69.18	59.71–78.99	N/A
30	60.69	61.86	37.19–83.16	N/A

3.3 Ancestral character state reconstruction of the inflorescence type in Euterpeae

Although the log likelihood values for the parameter-rich character-state transition models SYM (-20.329) and ARD (-16.156) were higher than that of ER (-22.778), a likelihood ratio test showed that the increase in likelihood with the additional parameters of SYM and ARD was not significant ($p > 0.05$). This suggested that the models did not differ, so I chose the simplest ER model to conduct the inflorescence ancestral character-state reconstruction.

My analysis suggested that the ancestral character state for inflorescence branching pattern in Euterpeae was an inflorescence with rachillae distributed all around the main axis (Figure 5). From this ancestral state, I observed numerous shifts to different

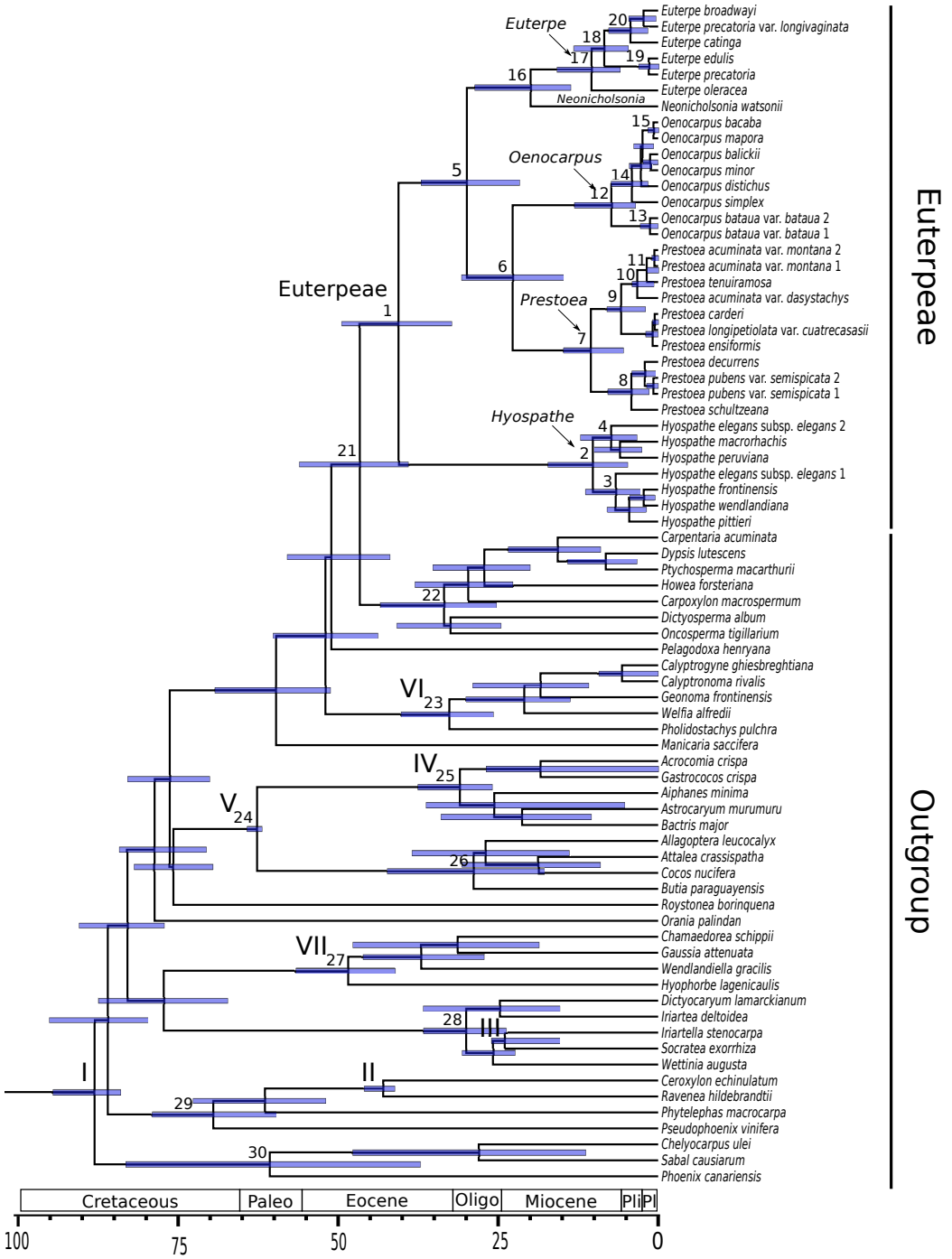

Figure 4: Chronogram of Euterpeae and outgroup based on the Bayesian dating analysis in BEAST using three nuclear and one chloroplast DNA markers. Blue bars represent the 95% highest posterior densities. Roman numbers represent calibration points (see Table 5). Arabic numbers represent nodes of interest (see Table 8). Paleo=Paleocene, Oligo=Oligocene, Pli=Pliocene, Pl=Pleistocene.

inflorescence types. One shift was a complete loss of adaxial rachillae (hippuriform inflorescence); this was seen in *Oenocarpus*. The analysis recovered two shifts to an inflorescence with partial loss of adaxial rachillae, one in the Caribbean endemic *Euterpe broadwayi*, and the second in *E. oleracea*. Two shifts to a spicate (unbranched) inflorescence type were recovered: one in *Neonicholsonia* and the other in *Oenocarpus simplex*. The latter, however, occurred from the hippuriform inflorescence type not from the ancestral state of rachillae around the main axis.

3.4 Ancestral biogeographical range estimation

The AIC showed that the model that best explains the data was the DEC model under the 'complex biogeographical model 1' with the four time periods.

The biogeographic analysis showed that Central America plus Chocó was the most likely inherited ancestral range for the Euterpeae, although there was much uncertainty in this reconstruction (Figure 6, Table 8). Table 8 shows the probabilities for each of the ancestral areas recovered at nodes of interest.

Considering only the ancestral area that received the highest probability at each node, at most four independent colonization events from Central to South America were recovered. The first was by the ancestor of *Hyospathe* between 40 to 10 Mya to a wide area in Amazonia, the Andes, and the Guiana Shield. Subsequently, diversification in the Andes was evidenced in *Hyospathe* with most divergence occurring in the last 8 million years. The second event was by the ancestor of *Oenocarpus* between 23 to 7 Mya, expanding from Central America to Amazonia. I observed diversification in Amazonia by many *Oenocarpus* extant species starting at ca. 4 Mya, and a

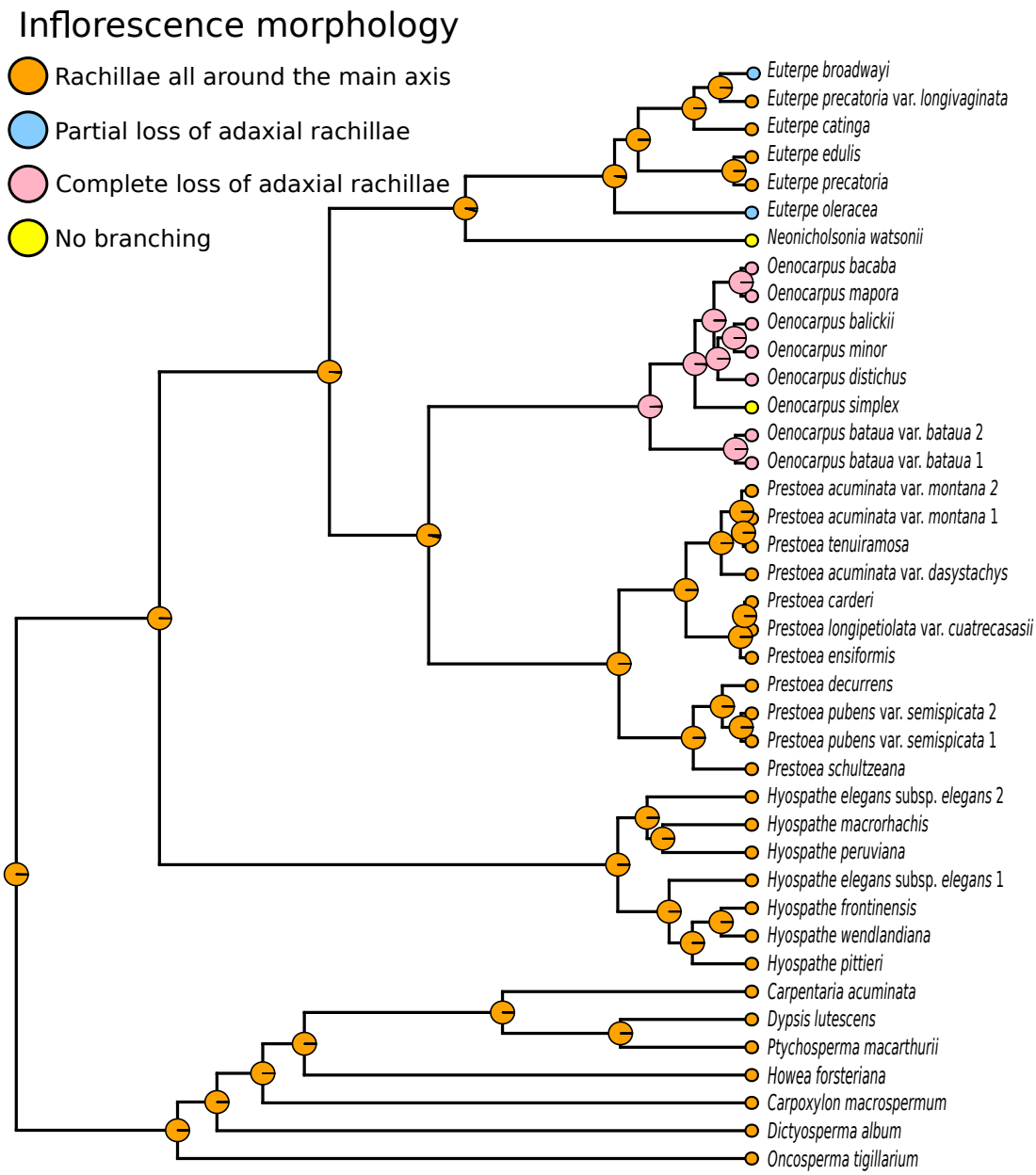

Figure 5: Inflorescence trait evolution in Euterpeae, where pie charts show the probability of each character state at ancestral nodes.

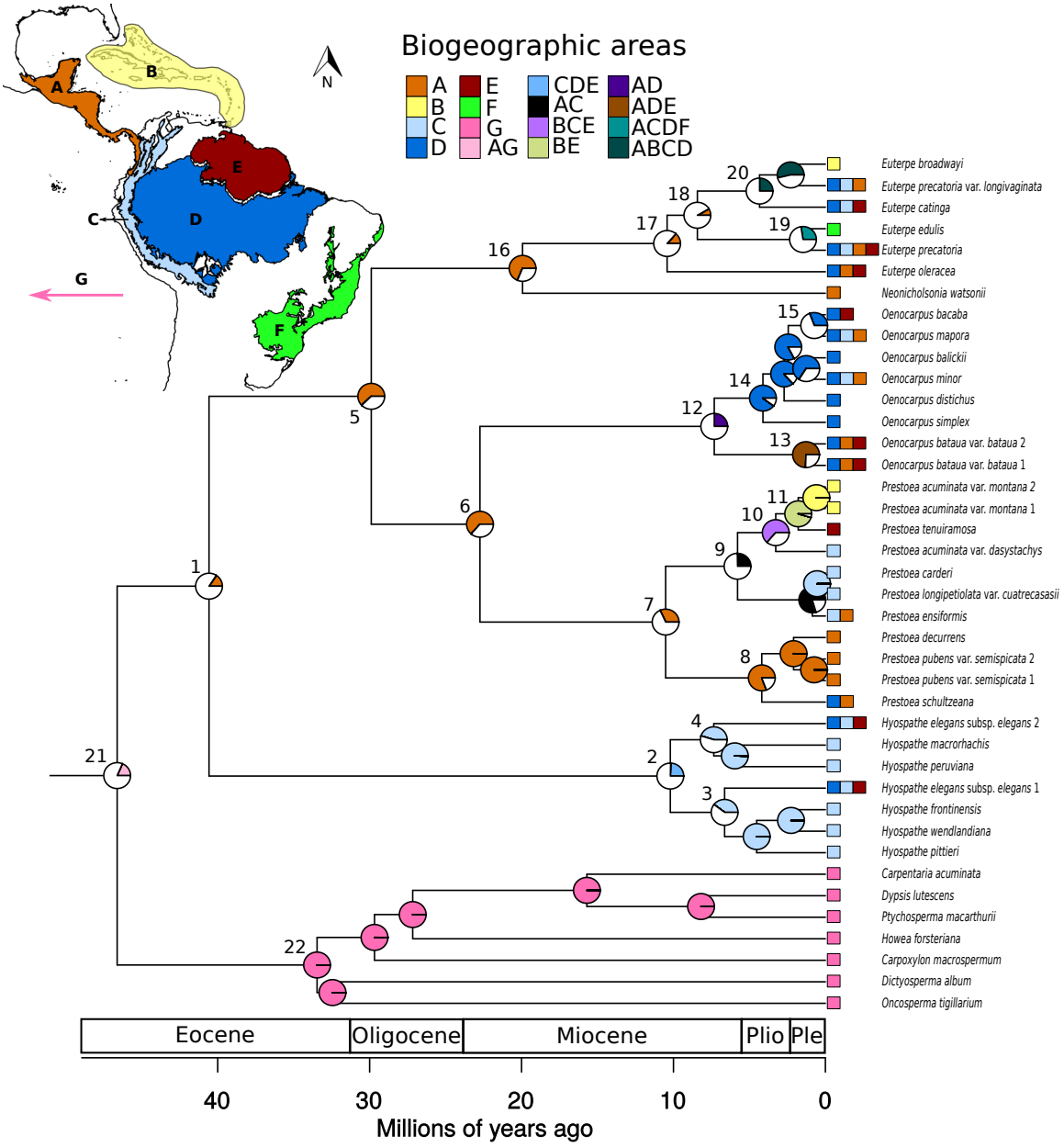

Figure 6: Ancestral area estimation of the Euterpeae. The colored section of the pies show the most probable distribution for the ancestor at each node and the white section represents the rest of the combined probabilities for each node (see Table 8 for numbered nodes of interest). Colored squares at the tips indicate the current distribution of each taxon. Areas: A=Central America and Chocó, B=Caribbean, C=Andes, D=Amazonia, E=Guiana Shield, F=Atlantic Forest, G=Indo-Pacific. Plio=Pliocence, Ple=Pleistocene. Areas designed using TNC terrestrial ecoregions of the world (The Nature Conservancy, 2009).

final expansion of this genus to the Guiana Shield between 7 to 1 Mya. The third colonization event to South America, and more specifically to the Andes, was found in the ancestor of the montane *Prestoea* clade at around 11 to 6 Mya. A subsequent expansion occurred into the Guiana Shield and the Caribbean at ca. 3 Mya by the ancestor of the clade that includes the widespread species *P. acuminata*. Divergence of the Caribbean endemic *P. acuminata* var. *montana* occurred at around 2 Mya (95% HPD 0.06–1.72). Lastly, colonization to South America (broadly Andes, Amazonia, and Guiana Shield) occurred in a lineage within *Euterpe*. However, the age of this event is difficult to determine because of the high uncertainty in the ancestral area estimated for the crown node of *Euterpe* and its inner nodes. Thus, this event could have taken place between 20 to 4 Mya. Divergence of the Caribbean species *E. broadwayi* happened later at ca. 2.3 Mya (95% HPD 0.39–4.56). *Neonicholsonia* evolved in Central America and did not migrate to South America.

4. Discussion

4.1 Phylogenetic analysis

I found strong support for the sister relationship between the Euterpeae and Areceae. This relationship was recovered previously by Comer et al. (2015) and Comer et al. (2016), which were the first studies to obtain a strong support for the sister group of Euterpeae. The intergeneric relationships found in this study differ from other phylogenetic reconstructions that include all genera of Euterpeae (Baker et al., 2009; Faurby et al., 2016; Henderson, 1999; Montúfar and Pintaud, 2008). A new sister relationship between *Euterpe* and *Neonicholsonia* was recovered in my study, which was not recovered in any previous work. This strong sister relationship (1pp, 100% BS) was unexpected given that there are no morphological synapomorphies that support this relationship; thus inviting further morphological research to identify possible synapomorphies between these two genera.

Some previously proposed clades, however, were supported in my study. For example, as in Henderson (1999), I recovered a sister relationship between *Prestoea* and *Oenocarpus*, and as in Baker et al. (2009) and Faurby et al. (2016), I recovered *Hyospathe* as sister to all other genera. The sister relationship between *Prestoea* and *Oenocarpus* was supported in Henderson (1999), based on morphological characters

like transverse veins forming a continuous pattern between longitudinal veins, free sepals on the staminate (male) flowers, fruit mesocarp with a distinctive layer of sub-epidermal sclerosomes, and a distinctive layer of flattened, closely spaced fibers forming a "stockade" around the fruit endocarp. That *Hyospathe* forms a lineage sister to all other genera could be expected because this genus has some flower characters that are considered distinctive and unusual in the whole palm family, e.g. the difference in length of antesepalous and antepetalous stamens, and the adnation of the antepetalous filaments to the pistillode (Uhl and Dransfield, 1987). The intergeneric relationships recovered in the present paper support the recognition of *Euterpe* and *Prestoea* as different genera. These two genera were thought to be closely related based on overlapping morphological characters (e.g. similar fruits with lateral stigmatic remains; Henderson, 1995; Henderson et al., 1997). In early work, such similarities led to many species of *Prestoea* to be classified as *Euterpe* (e.g. *Prestoea acuminata*; Burret, 1929).

Some interspecific clades I recovered in my study were concordant with those in Henderson (1999). In *Euterpe*, the clade formed by *E. catinga*, *E. broadwayi* and *E. precatoria* (1 pp, 94% BS) appeared in Henderson's (1999) phylogeny with apically hairy sepals on pistillate (female) flowers as a synapomorphy. In *Prestoea*, the clade of *P. pubens*, *P. decurrens*, and *P. schultzeana* (1 pp, 100% BS) was supported in Henderson's (1999) phylogenetic tree based on the presence of abaxially pilose petals on staminate flowers, filaments adnate to petals (epipetalous), and apically rounded, abaxially pilose sepals on pistillate flowers.

Within *Oenocarpus* a clade that includes the species of the subgenus *Oenocarpus* (*O. bacaba*, *O. mapora*, *O. balickii*, *O. minor*, *O.distichus*) (Balick, 1986; Bernal et al.,

1991) had good support in our Bayesian analysis (0.95 pp) but had low support in the maximum likelihood analysis (63% BS). This clade was supported in Henderson's (1999) study based on the presence of pinnae in strongly clustered arrangement. *O. simplex* of subgenus *Oenocarpopsis* (Bernal et al., 1991) was sister to this clade. *O. circumtextus*, the only other species in subgenus *Oenocarpopsis*, was not included in my analysis. Balick (1986) proposed a close relationship between *O. bacaba* and *O. distichus* based on the high percentage of shared flavonoids (82%), but our results do not support this close relationship: *O.bacaba* formed a clade with *O. mapora* (0.99 pp, 79% BS). Our results recovered *O. bataua* as sister to the rest of the genus. This arrangement differs from Henderson's (1999) phylogenetic tree, in which *O. bataua* formed a clade with *O. simplex* and *O. circumtextus*. The relationship found in Henderson (1999) supported the merging of *Jessenia* within *Oenocarpus* (Balick, 1986; Bernal et al., 1991; Henderson, 1999). In my phylogenetic tree, *O. bataua* was sister to all other species of *Oenocarpus*, neither supporting nor rejecting the recognition of *Jessenia* as a different genus.

A similar case to that of *Jessenia* can be found in *Hexopetion*. This genus was revalidated and separated from *Astrocaryum* by Pintaud et al. (2008) based on morphological and anatomical characters. In subsequent studies *Hexopetion* was recovered as sister to *Astrocaryum* Eiserhardt et al. (2011); Roncal et al. (2013). Therefore, the phylogenetic relationship between both genera does not clarify the taxonomic rank for the *Hexopetion* clade.

Nonetheless, the discovery of *Oenocarpus* species that share some of the unique characters of *Jessenia*, like the ruminate endosperm (in *O. makeru*) and bifid eophyls (in *O. simplex*) weaken the argument for the recognition of *Jessenia* as a different

genus (Bernal et al., 1991). Henderson (1995) commented that *O. makeru* could be a hybrid between *O. bataua* and *O. minor*. Hybridization in the genus is known, *O. x andersonii* has been described as a hybrid species (Balick, 1991). Further information on genome size/chromosome number could perhaps help to detect and confirm cases of hybridization in Euterpeae. Hybridization has been reported also in other genera of palms, including *Syagrus* (Meerow et al., 2015) and *Orbignya* (Balick et al., 1987).

I found the widespread species *H. elegans* and *E. precatoria* to be polyphyletic and *P. acuminata* was recovered as paraphyletic. This suggests that further field and laboratory research is needed to resolve the full evolutionary history and phylogenetic relationships in the Euterpeae. Additionally, future research could use modern methods of species delimitation based on coalescence theory and taking into account gene flow (Jackson et al., 2017; Yang and Rannala, 2014) to unveil new species within these non-monophyletic currently recognized widespread taxa. Phylogenies have been useful to identify taxonomic classification problems at different taxonomic levels—species in *Attalea* (Freitas et al., 2016), subgenera in *Chamaedorea* (Cuenca et al., 2008), and the genus *Calyptrogyne* nested within *Calyptronoma* in the tribe Geonomateae (Roncal et al., 2012, 2005).

4.2 Evolution of Euterpeae inflorescence

The results show that an inflorescence with rachillae all around the main axis is the most likely ancestral character state in Euterpeae. This inflorescence type is also the most common within the tribe, and is present in all species in *Prestoea* and *Hyospathe* and some species of *Euterpe* (Henderson, 2002; Henderson and Galeano, 1996). This

interpretation is in line with the hypothesis proposed by Balick (1986) on the ancestral inflorescence of *Oenocarpus*. Balick (1986) put forward his hypothesis based on the presence of triangular bracts on the adaxial side of the rachis in *Oenocarpus*, suggesting the loss of adaxial rachillae. Henderson and Galeano (1996) also noted that some species of *Euterpe* have triangular bracts, as in *Oenocarpus*, which I view as having a partial loss of adaxial rachillae. My study suggests that the shift to a partial loss of adaxial rachillae did not happen in a single evolutionary event within *Euterpe*, as both species treated in this study that have this inflorescence type (*E. broadwayi* and *E. oleracea*) were recovered in different lineages. Because *E. luminosa* and *E. longebracteata*, also presenting a partial loss of rachillae, were not included in this study, the total number of shifts in inflorescence types in *Euterpe* could not be determined.

Pollinators can play important roles in promoting rapid morphological evolution of inflorescences (Henderson, 1986). Coleopterans, hymenopterans, and dipterans are the most important pollinating insect groups for palms (Henderson, 2002, 1986); all pollinate species of Euterpeae. Genera in which the inflorescence has rachillae all around the rachis are mainly pollinated by flies or bees (*Hyospathe*, *Prestoea*, *Euterpe*) (Ervik and Bernal, 1996; Ervik and Feil, 1997; Küchmeister et al., 1997; Listabarth, 2001). Genera with loss of rachillae on the adaxial side are mainly or partially pollinated by coleopterans (*Oenocarpus*, some species in *Euterpe*) (Küchmeister et al., 1997; Núñez-Avellaneda and Rojas-Robles, 2008; Núñez-Avellaneda et al., 2015). Another way to look at pollination patterns in Euterpeae is based on elongation of the inflorescence. Henderson (2002) classified the palm inflorescence as condensed or elongated, based on the length of the peduncle and rachis, and on the branching order of the rachillae. Henderson (2002) showed that condensed inflorescences, like in

Oenocarpus, are more likely to be pollinated by coleopterans and elongate ones, like in *Prestoea*, more likely to be pollinated by hymenopterans or dipterans. Henderson (2002) considered *Euterpe* as intermediate, with a short peduncle and relatively long rachis, and has pollination by hymenopterans and coleopterans (Küchmeister et al., 1997). This same pattern also occurs in other palms. *Attalea allenii* H.E.Moore and *Wettinia quinaria* O.F.Cook & Doyle, both have condensed inflorescences (Henderson, 2002) and are pollinated mainly by *Mystrops* beetles (Núñez-Avellaneda et al., 2005). In contrast, *Licuala* species with an elongated inflorescence (Henderson, 2002) are pollinated by calliphorid and tachinid flies, halictid bees, and eumenid wasps (Barfod et al., 2003). The evolutionary advantage for condensed inflorescences for pollination by coleopterans is unknown. However, condensed inflorescences might be a way to optimize pollination by allowing several flowers to be pollinated during a single visit.

Coleopterans pollinating palm inflorescences tend to have an intricate relationship with the palm, not limited to feeding but also for oviposition (Ervik and Barfod, 1999; Núñez-Avellaneda et al., 2015, 2005). It has been suggested that beetle-pollinated palms increase the inflorescence temperature during anthesis as a reward for beetles, providing heat energy and promoting the maturation of the larvae oviposited (Ervik and Barfod, 1999; Núñez-Avellaneda and Rojas-Robles, 2008; Núñez-Avellaneda et al., 2015). This close interaction between beetles and the palms they pollinate could suggest a specialization in this plant-pollinator relationship. This does not fully explain, however, the complete or partial loss of the adaxial rachillae in *Oenocarpus* and *Euterpe*.

Another hypothesis is that the loss of adaxial rachillae is related to the size and amount of the fruits in the inflorescence. Balick (1986) suggested that the shape of

the *Oenocarpus* inflorescence, the loss of the rachillae and having pendulous rachillae could allow inflorescences to bear a big amount of weight from the combined fruit mass. *Oenocarpus bataua* inflorescences are reported to weight as much as 15–20 Kg (Balick, 1986). Balick (1986) argued that adaxial rachillae would need to be stiffer than lateral and abaxial rachillae in order to carry a larger amount of fruits. Yet another hypothesis to explain the transitions between inflorescence form is that of developmental constraints. The reason why adaxial rachillae have been lost in some clades in Euterpeae is an open question for future research.

4.3 Divergence times and historical biogeography

Divergence dates estimated in this study agree with a broad study that included all genera of palms. I recovered a mean crown node age for the Euterpeae that was older than that recovered by Couvreur and Baker (2013) but the values fall within the 95% HPD of each other (Table 9). This difference might be due to the different number of taxa included in the studies. Couvreur and Baker (2013) conducted a broader-scale study that included only one species per genus in the Euterpeae. Similarly, the mean node age and the 95% HPD for the crown of tribe Areceae, Euterpeae's sister clade, is very similar to that recovered by Couvreur and Baker (2013) (Table 9). Mean crown ages for related tribes like Geonomateae, Cocoseae, and Chamaedoreeae, agree closely with studies specifically treating these groups in Roncal et al. (2010), Meerow et al. (2015) and Cuenca et al. (2008), respectively (Table 9).

I concluded that most divergence of the extant genera of Euterpeae occurred after the Middle Miocene, with many species-level divergence events happening in the last

Table 9: Comparison of divergence times for subfamilies in Arecaceae and major tribes in Arecoideae. HPD = Highest posterior density

		Crown age		Stem age	
Taxa	**Source**	Mean	95% HPD	Mean	95% HPD
Euterpeae	(Baker and Couvreur, 2013)	31.54	16.37–45.07	42.62	32.98–52.89
	Current study	40.57	32.23–49.36	46.62	39.11–56.02
Areceae	(Baker and Couvreur, 2013)	4.11	25.95–42.42	41.38	32.45–51.88
	Current study	33.46	25.39–43.39	46.62	39.11–56.02
Geonomateae	(Baker and Couvreur, 2013)	28.52	16.99–40.07	39.98	28.70–52.70
	(Roncal et al., 2010)	31.00	21.20–33.50	43.00	35.90–49.60
	Current study	32.62	25.82–40.06	51.99	43.84–60.17
Cocoseae	(Baker and Couvreur, 2013)	55.77	54.80–57.68	59.43	55.68–64.04
	(Meerow et al., 2015)	63.81	62.00–68.22	66.26	62.00–70.60
	Current study	62.67	61.90–64.17	75.74	69.58–81.78
Chamaedoreeae	(Baker and Couvreur, 2013)	40.63	23.83–56.69	70.53	63.35–78.27
	(Cuenca et al., 2008)	50.00	39.90–60.00	79.50	70.40–89.20
	Current study	48.43	41.17–56.54	77.25	67.39–87.43
Iriarteeae	(Baker and Couvreur, 2013)	26.84	12.37–43.95	73.63	66.18–81.37
	Current study	30.00	23.80–36.61	77.25	67.39–87.43
Arecoideae	(Baker and Couvreur, 2013)	73.63	66.18–81.37	78.29	70.68–85.27
	Current study	82.92	77.29–90.44	86.00	79.77–95.11
Ceroxyloideae	(Baker and Couvreur, 2013)	52.17	29.99–74.23	78.29	70.68–85.27
	Current study	69.51	59.71–78.99	86.00	79.77–95.11
Coryphoideae	(Baker and Couvreur, 2013)	66.02	51.36–80.08	86.62	85.80–88.25
	Current study	60.69	37.19–83.16	88.06	84.00–94.43

10 million years. This is a common time frame for divergence events of South American biota, including amphibians, mammals, birds, insects, and plants (Hoorn et al., 2010; Turchetto-Zolet et al., 2013).

The appearance of the dry vegetation formations of the Chaco, Cerrado, and Caatinga are suggested to have promoted plant diversification by creating new habitat types (Freitas et al., 2016). Some studies have estimated the time of appearance of these dry formations based on divergence times of lineages occurring in those areas (e.g. *Mimosa*, *Andira*, *Lupinus*, and Microlicieae (Simon et al., 2009); Attaleinae: Arecaceae (Bacon et al., 2017; Freitas et al., 2016)). These studies suggest that formations

like the Cerrado most likely started to appear in the last 10 million years. For the Euterpeae, this dry forest belt could have promoted a vicariant split of *Euterpe edulis* from its widespread ancestor in southern Amazonia by isolating it in the Atlantic rain forest. The estimated divergence time of *E. edulis* (ca. 1.5 Mya) agrees with the period of the aforementioned appearance of dry formations in South America.

Elevational changes in the Andes have been suggested to be responsible for diversification by creating new habitat types for palms and other plant taxa: *Ceroxylon* (Sanín et al., 2016; Trénel et al., 2008), *Aiphanes* (Eiserhardt et al., 2011), *Jaborosa* (Chiarini et al., 2016), *Lupinus* (Drummond et al., 2012), and Lobelioideae (Lagomarsino et al., 2016). Most divergence events within *Hyospathe*, a mostly Andean distributed genus, and within *Prestoea* occurred in the last 10 million years. This period is characterized by an accelerated uplift of the northern Andes (Gregory-Wodzicki, 2000). Therefore, the final period of Andean uplift could have played a role in the diversification of *Hyospathe*, and the Andean *Prestoea* clade.

Amazonia was recovered as an important area for the diversification of *Oenocarpus*. I estimated that a clade with an exclusively Amazonian ancestor diversified in the last 4 million years. The time of formation of the transcontinental Amazon River is controversial, and many divergent times estimates have been proposed for the events leading to the connection of the Amazonian riparian system to the Atlantic Ocean and the Andes. Diverse studies in different disciplines have estimated that these events occurred from the late Miocene to the Pliocene and Pleistocene, based on analysis of marine or terrestrial sediments, palynology, and geochemistry (Campbell et al., 2006; Hoorn et al., 2017; van Soelen et al., 2017). Diversification of the Amazonian clade in *Oenocarpus* falls within the range of the younger estimates for the Amazon River age.

Therefore, I conclude that Amazonian *Oenocarpus* species evolved after all marine incursions and the Lake Pebas had receded (Hoorn et al., 2010), and the Amazon River had already achieved its current easterly flow. The new habitats available in the Amazon basin could have contributed to the diversification of *Oenocarpus*.

My results show that the most probable ancestral area for the Euterpeae is Central America and Chocó. Although this is the best estimation, the probability supporting this hypothesis is low (16%). The second most probable ancestral area is broad and includes all areas in northern South America and Central America and Chocó (ACDE=12%). Subsequent nodes in the lineage leading to all genera except *Hyospathe* (nodes 5, 6, 16) show Central America as the most probable ancestral range with higher confidence ($\geq$ 62%), with subsequent colonization events of South America. A widespread Euterpeae ancestor in both Central and South America would suggest an early extinction in South America with three later recolonization events to South America; a Central American origin would suggest four independent colonization events of South America.

The evolution of the palm family followed a North-to South-America migration (Couvreur and Baker, 2013), a trend that is shown in my results. However, Couvreur and Baker (2013) suggested that the lineage leading to Euterpeae and its ancestor was distributed only in South America, and subsequently expanded to Central America. In this latter scenario, however, remains difficult to explain the possibility of extinction of most Euterpeae clades in South America (as shown by many of the internal node ancestral reconstructions) and recolonization by the ancestor of extant genera.

Independently of the ancestral range of the crown of Euterpeae, at least three colonization or recolonization events to South America happened within the Euterpeae.

One concerns *Oenocarpus* reaching the Amazon region, another is the montane clade of *Prestoea*, and the last in the genus *Euterpe*. Within *Euterpe* the age of the ancestral lineage that experienced the colonization is difficult to interpret due to the uncertainty of the ancestral range reconstruction for nodes within the genus. The most likely distribution of the ancestor of *Hyospathe* is South America (Amazonia, Guiana Shield and Andes). Depending on how the distribution of the ancestor the Euterpeae is interpreted, the range of the ancestor of *Hyospathe* can be considered to represent migration to South America with extinction in Central America, or an extinction in Central America. Nevertheless, further diversification of *Hyospathe* occurred in the Andes.

My results reveal two recent expansions of Euterpeae to the Caribbean: *Euterpe broadwayi* and *Prestoea acuminata var. montana*. These events happened long after the existence of the proposed GAARlandia land-bridge, therefore could have only happened by over-water dispersal.

The Areceae, the sister clade to Euterpeae, does not have representatives in the Neotropics, and it is restricted to the Indo-Pacific region. Because of the scale of my study, no inference can be drawn for the split of Euterpeae and Areceae, and thus no inference on the direction of migration was obtained. Nonetheless, Couvreur and Baker (2013) proposed a long-distance dispersal event of the ancestor of Areceae from South America to the Indo-Pacific region.

The present work constitutes a first approach to understand the biogeographic history of the taxa within the Euterpeae. The ancestral geographic range for the ancestor of Euterpeae remains unresolved due to the uncertainty of certain nodes, especially, the crown node of Euterpeae and clades within the genus *Euterpe*. Further

research should include a finer-scale phylogeographic study, and analyses to resolve the paraphyletic *Prestoea acuminata*, and the polyphyletic *Hyospathe elegans* and *Euterpe precatoria*.

5. Conclusions and future research directions

I resolved all intergeneric relationships in the Euterpeae and obtained a good resolution of interspecific relationships. The widespread species *Euterpe precatoria* and *Hyospathe elegans* were found to be polyphyletic and *Prestoea acuminata var. montana* paraphyletic. Therefore, population scale studies, with samples from all their distribution range, are needed to address species delimitation of widespread species in Euterpeae.

Furthermore, the use of more markers obtained with techniques such as next generation sequencing could help to further resolve species relationships in *Oenocarpus*. Some clade concordance was found with previous phylogenetic studies, notably with the morphology-based phylogenetic tree of Henderson (1999). One example is the sister relationship of *Oenocarpus* and *Prestoea*, further supporting the taxonomic separation of *Prestoea* and *Euterpe*. *Oenocarpus bataua*, previously *Jessenia bataua*, was recovered as sister to the rest of members of the genus, which neither supports nor rejects the recognition of the genus *Jessenia*. Nonetheless, I suggest that the species previously described in *Jessenia* remain in *Oenocarpus*, since I find further taxonomic splitting unnecessary when there is no decisive evidence at hand. In this case, the long branch in the phylogram that subtends all species in *Oenocarpus* does not support

the recognition of *Jessenia*.

I inferred that the most likely ancestral state of the inflorescence of Euterpeae is one with rachillae all around the main axis; the hippuriform inflorescence of *Oenocarpus* represents a shift from this ancestral state. Further research is needed to understand the mechanism by which the loss of adaxial rachillae happened, and to understand its adaptive significance or evolutionary value with respect to pollination. The Euterpeae most likely originated during the Eocene, with most extant genera diverging early after the Middle Miocene around 15 Mya, and extending into the Pliocene and Pleistocene, especially in *Prestoea* and *Oenocarpus*. My results recovered Central America plus Chocó as the most likely ancestral area of Euterpeae, yet there is very high uncertainty for this reconstruction and it should be accepted with caution. Regardless of the area of origin for Euterpeae, subsequent inner nodes suggest at least three colonization or recolonization events to South America from Central America and Chocó, and that coincided with the geological history events of the Neotropics.

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A. Appendix

Table A.1: List of primers used in this study and their original publications.

Primer Name	Sequences (5'-3')	Publication
CISP4 F (ORSC2_007)	GGAGATCAACGTCTTCTTGT	Bacon et al. (2008)
CISP4 R (ORSC2_007)	GCATACTCAGGAGCACAATA	Bacon et al. (2008)
PHYB F (PhyBact-F)	CGCTCCCTGGCGGTGACATC	Ludeña et al. (2011)
PHYB R (PHYBact-R)	CCTCCGGGTGATGCTTCGCA	Ludeña et al. (2011)
RPB2 F	GAGCACTTGCCTTTAGAGTTC	Thomas et al. (2006)
RPB2 R	GGACTATAAGCTTCCATGACCTC	Thomas et al. (2006)
RPB2-P10F	CARGARGATATGCCATGGAC	Denton et al. (1998)
RPB2-M11R	CCACGCATCTGATATCCAC	Roncal et al. (2005)
trnD-trnT F	ACCAATTGAACTACAATCCC	Demesure et al. (1995)
trnD-trnT R	CTACCACTGAGTTAAAAGGG	Demesure et al. (1995)
WRKY6 F	CCAAACCCAAGGTAGGTTTCAGC	Meerow et al. (2009)
WRKY6 R	CCTAACAGGGCACCCAGCATT	Meerow et al. (2009)

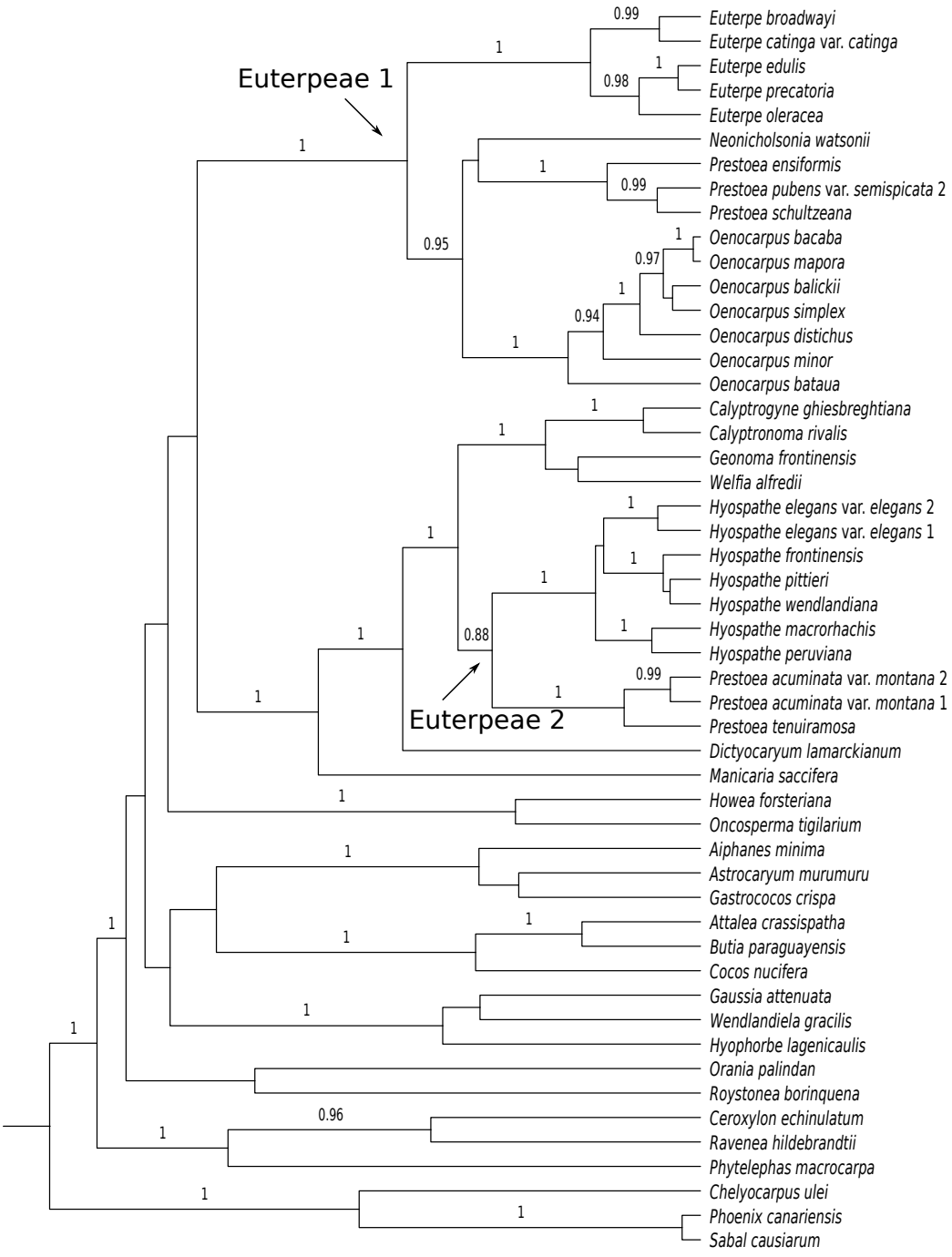

Figure A.1: Bayesian maximum credibility tree of tribe Euterpeae using the low-copy nuclear gene PHYB. Number above the branches represent bayesian posterior probabilities > 0.80.

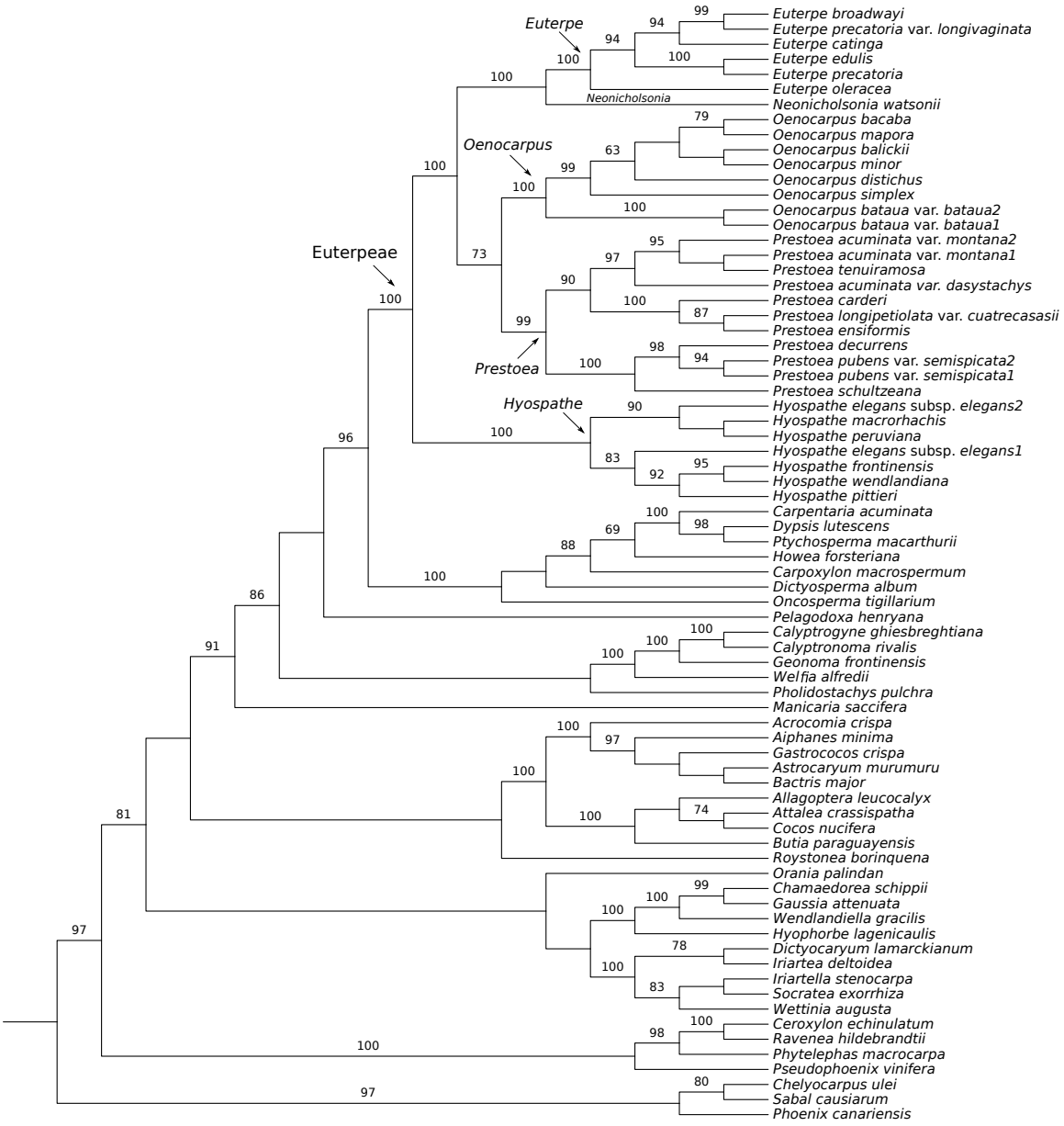

Figure A.2: Best-scoring ML tree for tribe Euterpeae using three nuclear markers and one chloroplast intergenic spacer (see methods section 2.2). Number above the branches represent ML bootstrap values > 60.