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BIOGEOGRAPHICAL ORIGIN OF CARIBBEAN PALMS

Did palms colonize the Caribbean through
GAARlandia?



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Photo of Sabal domingensis taken by Tobias Lindberg

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Abstract

The biogeography of the Caribbean islands is an ongoing mystery, with many possible explanations to how biota colonized the region. One hypothesis is the Greater Antilles and Aves Ridge (GAARlandia), which acted as a landbridge and connected the Caribbean and South America 35-32 million years ago. The palm family is an excellent taxonomic group to examine this and other hypotheses since palms are well established in the region and have a rich evolutionary history. A dated phylogenetic tree of all palms with distribution records for all species mapped on the tree was used to explore the hypotheses. Ancestral state reconstruction was performed for the phylogeny under different models. The statistically best fitting model was selected by comparing the AIC values for the models. Colonization by most Caribbean palms occurred either in a different time period from when GAARlandia existed or originated from regions that are not indicative of GAARlandia. However, one genus of Caribbean palms, *Acrocomia*, supports the existence of GAARlandia. The existence of GAARlandia can not be proven by *Acrocomia* alone. More biota in the Caribbean need to be analyzed in order to determine the existence of GAARlandia. Our mixed findings can at least provide a clue to the complex biogeographical history of the Caribbean and reflect the importance of conservation in the Caribbean Biodiversity Hotspot.

Keywords: Arecaceae, historical biogeography, Caribbean biodiversity, GAARlandia

Sammanfattning

De Karibiska öarnas biogeografi är fortfarande ett mysterium, med många möjliga förklaringar på hur organismer koloniserade regionen. En hypotes är den så kallade Greater Antilles and Aves Ridge (GAARlandia), som bygger på att en landbrygga mellan de Karibiska öarna och Sydamerika existerade 35-32 miljoner år sedan. Palmer är en utmärkt taxonomisk grupp att undersöka hypotesen eftersom gruppen är väl etablerad i regionen och har en lång evolutionär historia. Hypotesen analyserades med ett daterat fylogenetiskt träd för alla palmer tillsammans med utbredningsinformation för alla arter i trädet. Ancestral state reconstruction genomfördes på det fylogenetiska trädet under olika modeller. Den statistiskt bäst lämpade modellen utsågs genom att jämföra modellernas AIC-värden. Majoriteten av de Karibiska palmerna koloniserade regionen antingen i en annan tidpunkt än GAARlandias tidsintervall eller hade ursprung från områden som inte indikerar GAARlandia. Däremot var det ett släkte av palmer som indikerar GAARlandia, *Acrocomia*. Existensen av GAARlandia kan dock inte bevisas av endast *Acrocomia*, eftersom fler grupper av organismer behöver analyseras för att bedöma om GAARlandia existerade eller inte. De varierande resultaten kan åtminstone förse med en ledtråd till Karibiens komplexa biogeografiska historia och reflekterar samtidigt varför det är viktigt att bevara den Karibiska Biodiversitet Hotspot.

Nyckelord: Arecaceae, historisk biogeografi, Karibisk biodiversitet, GAARlandia

1. Introduction

Biodiversity hotspots are defined as regions that harbor significant concentrations of species that are endemic and that are facing significant loss of habitat (Myers et al. 2000). The Caribbean islands are one of the global biodiversity hotspots. The number of plant species that occur in the Caribbean is approximately 12 000, with 7 000 of those being endemic species (Myers et al. 2000). The endemic plant taxa of the Caribbean colonized the different islands from different biogeographical regions, particularly Central, North, and South America (Nieto-Blázquez et al. 2017).

There are four main hypotheses to explain the colonization and distribution of the Caribbean biota. The first hypothesis is that colonization and distribution of the Caribbean biota could be explained by dispersal overwater. This is based on the possibility of dispersal through or over the water and/or by using islands as stepping stones to arrive on different Caribbean islands (Cuenca et al., 2008). The closure of the Panama seaway changed the ocean currents, with currents heading from northeastern South America to the Caribbean islands enabling dispersal of biota from South America (Sarnthein et al., 2009; Roncal et al., 2020). This can be explained by sediment from Panamanian rivers being transported and deposited in the shallow seas of northern South America 13 to 15 million years ago (Montes et al., 2015). Following this hypothesis, we predict to find clades that are more closely related to clades that are isolated from the Caribbean islands by water.

A second hypothesis to explain the distribution of the Caribbean biota is in situ speciation, where the monophyly of endemic species acts as a strong indicator for speciation in an archipelago or on individual island settings (Warren et al., 2015). An example of this is the speciation of diving beetles in New Guinea, where species of New Guinean *Papuadytes* form a monophyletic group (Balke et al., 2007). Following this hypothesis, we predict to find monophyletic clades of species on each island. Ancestral areas in this particular hypothesis are not informative per se, since they do not indicate the origin of the biota. This hypothesis is not necessarily mutually exclusive with other hypotheses, because in situ speciation could have occurred after dispersal to the Caribbean through for example GAARlandia.

A third hypothesis is late Cretaceous vicariance to explain colonization on the Caribbean islands. Here, an overland rupture occurred on the proto-Antilles land mass between 70 to 80 million years ago, which is resulted by a eastward migration of the land mass on the Caribbean plate itself (Roncal et al., 2020). Ancient biota got carried with the land mass which resulted in allopatric speciation after the fragmentation of the archipelago (Roncal et al., 2020). With this hypothesis the ancestral area is not informative either. Rather we expect to find old and isolated clades of palms where the last common ancestor of Caribbean and non-Caribbean palms existed before the Caribbean plate became isolated.

And lastly, a land bridge is hypothesized to have connected the Caribbean islands and South America at the Eocene-Oligocene boundary (c. 34 Ma; Iturralde-Vincent & McPhee 1999). The Greater Antilles and Aves Ridge (GAARlandia) is highly debated, where some have shown it to lack geological evidence (Ali & Hedges 2021), while others have identified supporting

information (Iturralde-Vincent & McPhee 2023). The new evidence is derived from recent geological, seismic, and paleontological data from northern South America and eastern Caribbean islands. It suggests that the upper parts of the Aves Ridge were above sea level between the middle Eocene to the early Miocene, especially in the transition between the Eocene and Oligocene 35 to 32 million years ago (Iturralde-Vincent & McPhee 2023). A hypothesis can be tested using a geogenomic approaches, where historical biogeography can inform on the impact of geological processes on biotic patterns (Baker et al. 2014). Following this hypothesis, we expect lineages to have ancestral areas in South America, with colonization to the Caribbean, ca. 34 Million years ago when GAARlandia is hypothesized to have been present.

The potential mechanisms of colonization and dispersal in Caribbean palms do not need to be mutually exclusive. A combination of different colonization methods under multiple colonization events may explain Caribbean colonization by palms. For example, dispersal may have both occurred over water and over the proposed GAARlandia landmass.

In this thesis I will infer the ancestral origin of all palm species of the Caribbean based on the four main hypotheses of dispersal and the timing of those colonization events. This results in the ability to determine the GAARlandia hypothesis. One plant family that is characteristic of tropical environments and is well-represented in the Caribbean is the palm family, Arecaceae (Roncal et al., 2020). I will use palms to test amongst the four hypotheses outlined above and infer the biogeographic history of Caribbean palms.

Previous work has determined that the ancestral origin of most endemic palm species was mainly Central American (Roncal et al. 2020). In the subfamily Coryphoideae, dispersal to the Caribbean was primarily overwater and to a smaller extent, through the GAARlandia landbridge that connected the mainland with the Caribbean (Cano et al., 2018). One other possible source of palm taxa is the southern part of the current day United States of America, which is the source of Caribbean species of *Copernicia* (Bacon et al., 2013). These taxa first dispersed to Northwestern South America through the biotic interchange caused by the formation of the Panama isthmus (between 16.3-31 million years ago), where dispersal to the Caribbean occurred between 5.5-16.3 million years ago (Bacon et al., 2013). It is also possible that some palm species have ancestors that originated in the Antilles, which is the case for *Thrinax* and *Zombia*, where the estimated divergence of the taxa happened during the Neogene (Nieto-Blázquez et al., 2017). *Thrinax* and *Zombia* did however also have ancestors originating from North America, which explain the origin of the Antillean ancestors (Nieto-Blázquez et al., 2017).

My thesis will go beyond previous works by examining the ancestral origin of all palm species of the Caribbean as well as the timing of those colonization events in a biogeographical approach. I will use a comprehensive species-level dated molecular phylogeny and explicit biogeographic models to infer ancestral area. This work is important to understand the evolution of the Caribbean biodiversity hotspot and one of its most characteristic groups: the palms.

Aims

The aim of this study is to determine the ancestral origin and the timing of colonization of Caribbean palms and to determine the possibility of colonization to the Caribbean through GAARlandia.

Hypothesis

The hypothesis of this study is that the first taxa of palms colonized the Caribbean islands approximately 30 million years ago through GAARlandia. The hypothesized colonization timing for the first taxa of Caribbean palms is at 32 million years ago, because there are several independent colonization events that occurred around that time. This is also the time when the GAARlandia land bridge is estimated to have existed.

2. Methods

For the biogeographical analyses I used the molecular phylogeny of all palms (Hill et al. 2023). The phylogeny is dated to absolute time using fossil constraints and morphology (e.g. Drummond and Rambaut 2007). To determine the ancestral origins of Caribbean palms, I began by defining the possible biogeographical regions of origin for all palms. The regions of North America, Central America, South America and non-American regions were used in the ancestral area reconstruction. North America is assigned to species that occur in continental United States and Northern Mexico. Central America is assigned to species that occur from Southern Mexico (Mexico Gulf, Mexico Southeast and Mexico Southwest in Palmweb and Plants of the world online) in the north to Panama in the south (Palmweb., 2024; Plants of the world online., 2024). South America is defined for species that occur on the mainland and in the islands of the Venezuelan Antilles and Trinidad and Tobago. Species that occur in other areas were classified as other. Species are only assigned to areas where a species is native, which means that introduced and invasive occurrences caused by humans were not included. After assigning each species in the phylogeny to one or more biogeographical areas, a historical biogeographical analysis was performed in R (version 4.3.2) using the BioGeoBEARS package (Matzke 2013). Both a constrained and an unconstrained biogeographical analysis was done. These analyses were done with the DIVA (dispersal vicariance analysis) model (Ronqvist 1997), the DEC (dispersal extinction cladogenesis) model (Ree & Smith 2008), and the BAYAREA model (Lantis et al., 2013). Models were compared by comparing the values of Akaike Information Criterion (AIC) for the different models. The best model was used to test the hypotheses regarding the ancestral origin of Caribbean palms and when the palms colonized the region. The results were tested by comparing the results of a dispersal matrix based on the biogeography from 100 million years ago to present (Which is based on data from Wen et al., 2016) and the results of an unconstrained matrix.

The number of observed dispersal and local extinctions events on the ancestral state reconstruction was counted and compared based on the origin of dispersal. Dispersal events are defined in this thesis as when any species of palms colonized a new region (i.e North America, Central America, Caribbean, South America or other regions). However, dispersal events are only valid if a species colonizes a new region that has not been colonized by the species or its ancestors before. This means that speciation from vicariance events are not defined as dispersal events (for example if an ancestor in the regions A and B speciates with species A in area A and species B in area B).



Figure 1: the definition of Central America in this thesis, where the green represents the distribution of *Bactris major* (Source: Plants Of The World Online), which is in the mentioned Central American region.

3. Results

3.1 Ancestral state reconstruction

Sabal and Cryosophileae

Five species of *Sabal* have colonized the Caribbean: *S. yapa*, *S. domingensis*, *S. palmetto*, *S. maritima*, and *S. causiarum*, through 4 colonization events. 3 of these events had their origin in North America (*S.domingensis*, *S.palmetto* and the ancestor to *S.maritima* and *S.causiarum*) and one from Central America (*S.yapa*). Dispersal overwater from North America and Central America is the most likely explanation for *Sabal*. 3 genera (*Coccothrinax*, *Hemithrinax* and *Thrinax*) and 2 monotypic genera (*Leucothrinax morrisii* and *Zombia antillarum*) of Cryosophileae have colonized the Caribbean from a single colonization event, originating from Central America. However, *Coccothrinax readii* dispersed back to Central America.

Copernicia

All species except *C.alba*, *C.prunifera* and *C.tectorum* colonized the Caribbean from a single colonization event that originated outside of North America, Central America and South America.

Colpothrinax, *Acoelorrhaphe wrightii* and *Pseudophoenix*

The only Caribbean species of *Colpothrinax* is *C. wrightii*, while *Acoelorrhaphe wrightii* and all species of *Pseudophoenix* are native to the Caribbean. Three colonization events (*C.wrightii*, *Acoelorrhaphe wrightii* and *Pseudophoenix* respectively) occurred, *C. wrightii* from Central America, *Acoelorrhaphe wrightii* from North America or Central America and *Pseudophoenix* from outside of North, Central and South America.

Gaussia

Three species of *Gaussia* are Caribbean (*G. attenuata*, *G. princeps* and *G. spirituana*), which originated from a single colonization event from Central America.

Roystonea, Reinhardtia paiewonskiana and Attalea crassispata

All species of *Roystonea* except for *R. dunlapiana*, *Reinhardtia paiewonskiana* and *Attalea crassispata* are species in the Caribbean, with three colonization events for these genera. *Roystonea* colonized from outside of North, Central and South America, *R. paiewonskiana* from Central America and *A. crassispata* from South America. There was also an extinction event or dispersal back to Central America in the species *R. dunlapiana*.

Syagrus amara

S. amara is the only *Syagrus* species that is found in the Caribbean. It dispersed to the Caribbean from South America by a single colonization event.

Bactris

Three species of *Bactris* are present in the Caribbean, *B. cubensis*, *B. jamaicana* and *B. plumeriana*. *Bactris jamaicana* and the ancestor of *B. cubensis* and *B. plumeriana* colonized the Caribbean from South America in two independent colonization events.

Desmoncus polyacanthos, Aiphanes and Acrocomia

D. polyacanthos, *Aiphanes acanthophylla*, *A. minima*, *Acrocomia aculeata*, *A. crispa* and *A. media* are species that are found in the Caribbean. Three separate colonization events (*D. polyacanthos*, the ancestor to the Caribbean species of *Aiphanes* and the ancestor to the Caribbean species of *Acrocomia* respectively) occurred from South America.

Calyptronoma and Geonoma

All species of *Calyptronoma* and *Geonoma pinnatifrons* are found in the Caribbean. Two colonization events (The ancestor to *Calyptronoma* species and *G. pinnatifrons*) occurred separately from South America.

Euterpe broadwayi and Prestoea acuminata

E. broadwayi and *P. acuminata* are the only Caribbean species of their respective genera. These two species colonized the Caribbean through two separate events from South America.

Dispersal region of origin

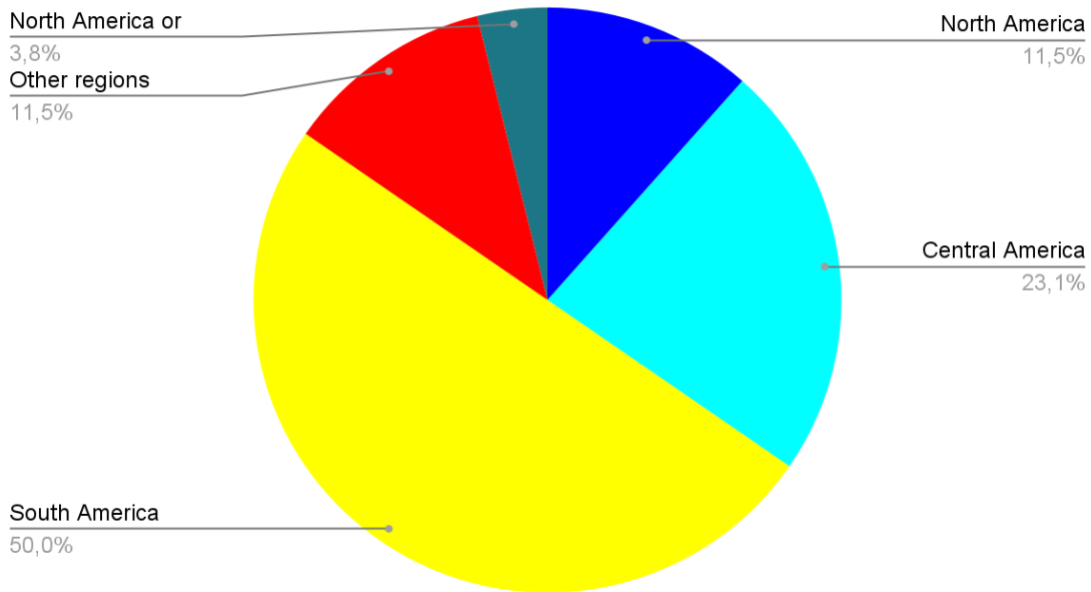


Figure 4: Pie-chart of the proportion of the origins of the colonization events.

Table 2: Approximate colonization timing for Caribbean palms and region of origin. Table continues to page 11.

Genera and species	Colonization time (million years ago)	minimum colonization time (million years ago)	Maximum colonization time (million years ago)	Region of origin
<i>Sabal yapa</i>	15.49	0.00	30.98	Central America
<i>Sabal domingensis</i>	23.23			North America
<i>Sabal palmetto</i>	6.76			North America
<i>Sabal maritima and S.causiarum</i>	10.51	8.05	12.96	North America
<i>Cryosophileae (except Thrinax)</i>	17.91	13.79	22.02	Central America
<i>Thrinax</i>	13.96	5.90	22.02	Central America
<i>Copernicia</i>	23.89	20.77	27.00	Other regions

<i>Colpotherinax wrightii</i>	12.66	7.97	17.35	Central America
<i>Acoelorrhaphe wrightii</i>	10.29			North America and Central America
<i>Pseudophoenix</i>	41.626	16.75	66.50	Other regions
<i>Gaussia</i>	22.54	12.86	32.21	Central America
<i>Roystonea</i>	48.46	31.80	65.11	Other regions
<i>Reinhardtia paiewonskiana</i>	14.23	0.00	28.46	Central America
<i>Attalea crassispatha</i>	8.76	7.41	10.11	South America
<i>Syagrus amara</i>	11.37			South America
<i>Bactris jamaicana</i>	9.09	4.39	13.79	South America
<i>Bactris plumeriana and B.cubensis</i>	8.64	3.56	13.71	South America
<i>Desmoncus polyacanthos</i>	5.39	0.00	10.77	South America
<i>Aiphanes acanthophylla and A.minima</i>	4.64			South America
<i>Acrocomia crispa</i>	25.23	18.30	32.15	South America
<i>Acrocomia media</i>	22.99	13.82	32.15	South America
<i>Acrocomia aculeata</i>	22.95	13.74	32.15	South America
<i>Calyptronoma</i>	14.38	8.60	20.16	South America
<i>Geonoma pinnatifrons</i>	0.92	0.00	1.84	South America

<i>Prestoea acuminata</i>	4.105	0.00	8.21	South America
<i>Euterpe Broadwayi</i>	2.68			South America

4. Discussion

4.1 Analysis of the results

The AIC-values for the six types of biogeographical models indicates that the DEC+J model is the best fitting model, since it had the lowest AIC-value. The resulting colonization events under the DEC+J model suggests that the majority of Caribbean palm species dispersed overwater from nearby regions or over long distances. In situ speciation is also suggested for some palm genera, such as *Coccothrinax spp.* and *Copernicia spp.* One genus of palm, *Acrocomia*, does show signs that are indicative for the existence of the GAARlandia land bridge, since the ancestor of all *Acrocomia* species existed in the timespan of GAARlandia. The ancestor is estimated to have lived in South America, where the ancestors to Caribbean species slowly began to colonize the Caribbean, which might indicate that a vicariance event occurred as a consequence of the disappearance of the GAARlandia landbridge. This is also supported by the existence of South American species in the genus. However, it is also possible that *A. aculeata* dispersed to the Caribbean by humans (Lima et al., 2018). But this is unlikely for *A. crispa* and *A. media*, since those species are endemic to the Caribbean region.

4.2. Limitations of historical biogeography

Reconstruction of ancestral states for species using phylogenies and geographic data is a useful tool for estimating the origin of clades in various types of lifeforms. However, ancestral state reconstruction cannot guarantee a completely accurate and unbiased reconstruction of the evolutionary and biogeographical history of a phylogeny (Ekman et al., 2008).

For example, the gymnosperm *Ginkgo biloba* is only naturally found in Eastern Asia in recent time, while fossils of the order Ginkgoales have been found in other regions of the world as well (Zhou 2009). This makes ancestral state reconstruction estimate an origin in Eastern Asia, despite the fossil record.

4.3. Dispersal by animals to the Caribbean

There are also some other types of dispersal to the Caribbean that might contribute to the palm diversity in the Caribbean. One hypothesis that is possible is dispersal by frugivorous animals. Some examples of suitable animal groups are birds, bats and other species of mammals (Zona & Henderson 1989). The ability of flight in bats and birds makes it possible for dispersal overwater to islands and dispersal on land by terrestrial mammals when the GAARlandia landbridge was present.

4.4. Limitations and suggestion for further research

The first limitation for this study were the constrained results, since the likelihood and AIC-values were non-consistent for the constrained results compared to the unconstrained results and were thereby excluded. The existence of GAARlandia cannot however be proven entirely by the

colonization of *Acrocomia* in the Caribbean and further ancestral state reconstructions of Caribbean biota are required in order to prove the existence of the GAARlandia landbridge. Further data of the Fossil record of Caribbean and South American palms are also vital in order to generate a proper biogeographical history of Caribbean palms. The extinction event or dispersal from the Caribbean for *Coccothrinax readii* and *Roystonea dunlapiana* is an interesting observation. This observation could be a potential basis for future studies, since both of these are found in Central America. The uncertainty of the ancestral origin of *Acoelorrhaphe wrightii* is also a potential basis for future studies, since that species might be two separate species because of the ancestral origin being both North American and Central American. Further studies of the biogeographical history of the Caribbean biota are however dependent on the conservation of Caribbean biota and habitats, since the Caribbean forests are threatened by the highest rate of deforestation amongst hotspots of 13 tropical forest regions (Brooks et al., 2002) and by the rising sea level (Bellard et al., 2014).

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7. Appendix

Legend for the abbreviations and colouration of the geographical regions

A = North America
B = Central America
C = Caribbean
D = South America
E = Other regions
AB = A+B
AC = A+C
BC = B+C
BD = B+D
CD = C+D
ABC = A+B+C
ACD = A+C+D
ABD = A+B+D
BCD = B+C+D
ABCD = A+B+C+D

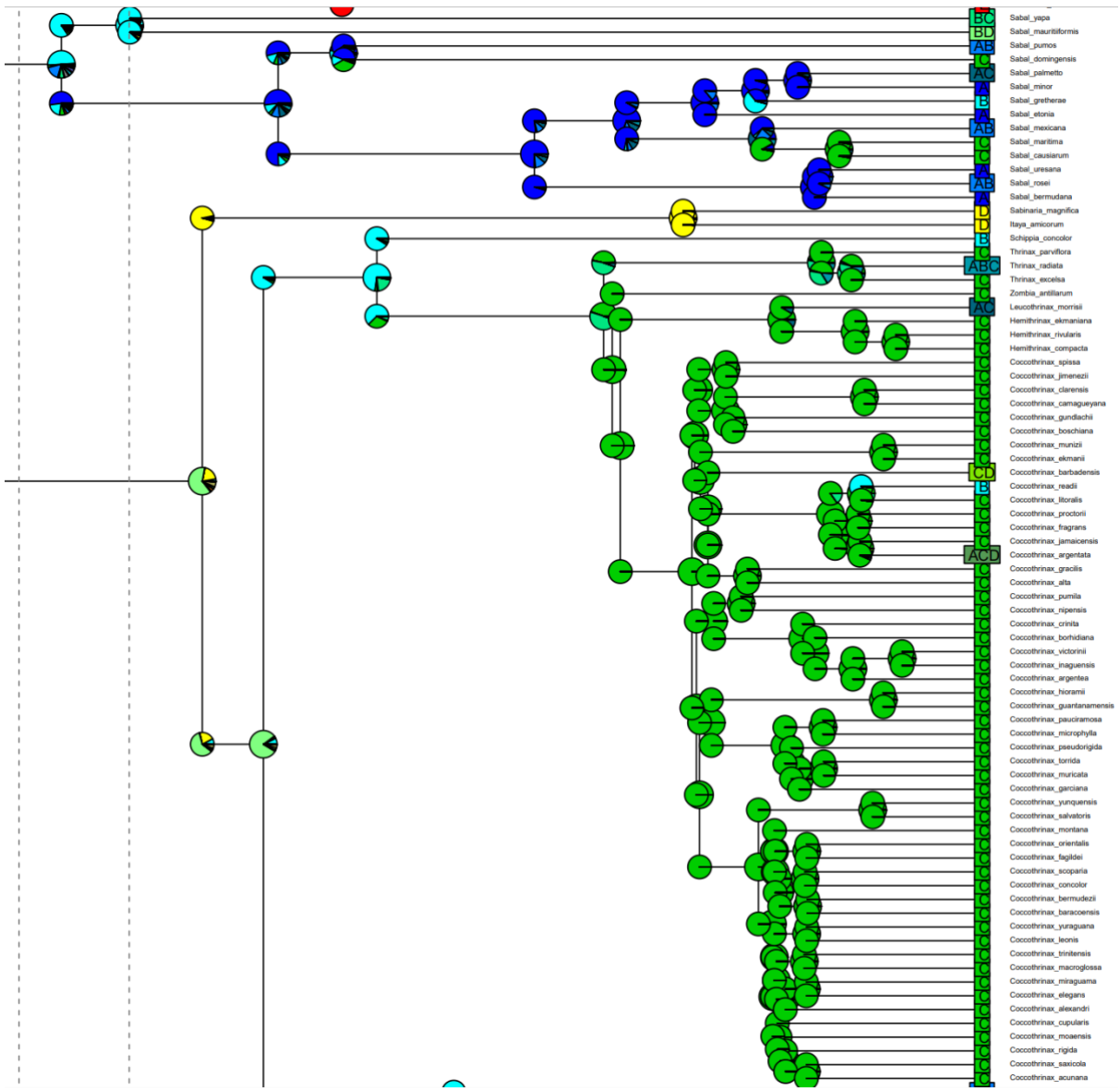


Figure 4: Ancestral state reconstruction for *Sabal* and *Cryosophileae*

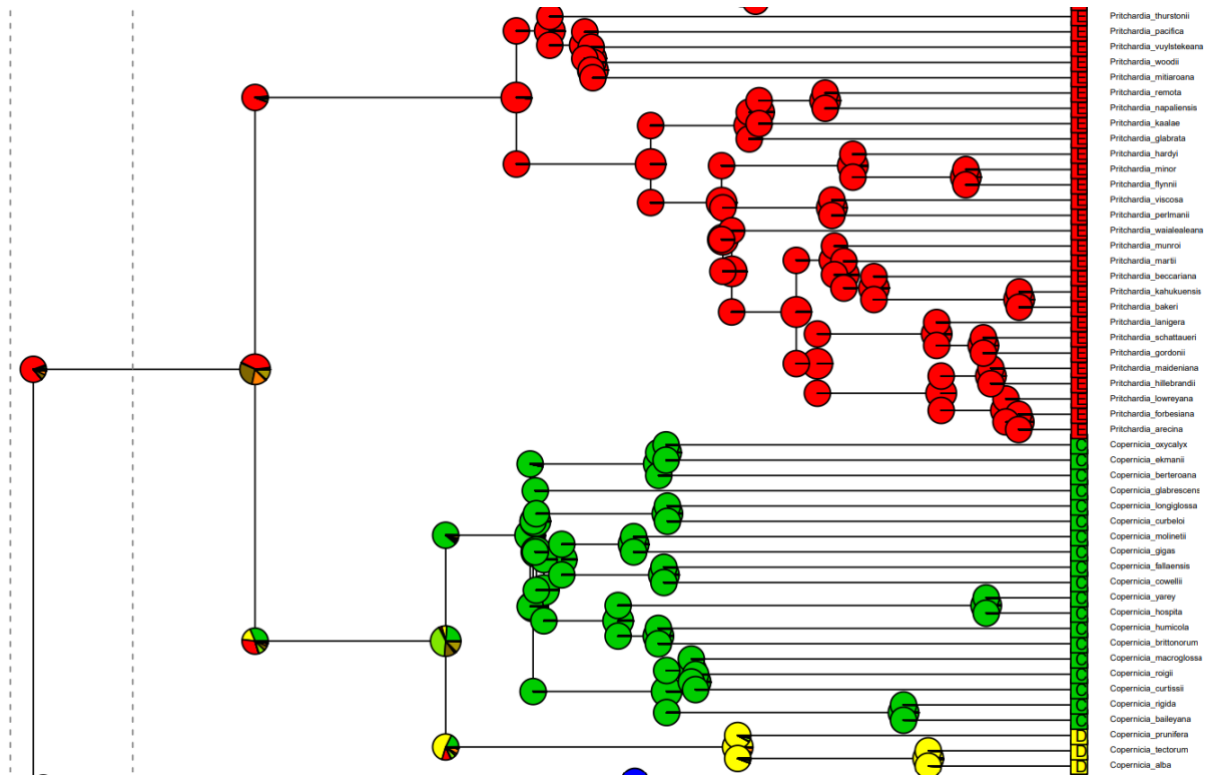


Figure 5: Ancestral state reconstruction for *Copernicia*.



Figure 6: Ancestral state reconstruction for *Colpothrinax wrightii*, *Acoelorrhaphe wrightii* and *Pseudophoenix*.

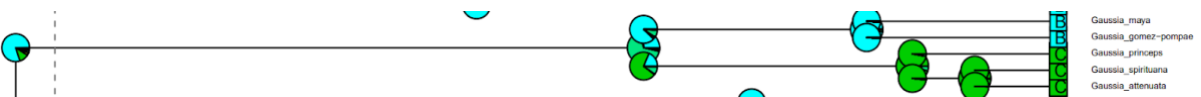


Figure 7: Ancestral state reconstruction for *Gaussia attenuata*, *G. princeps* and *G. spirituana*

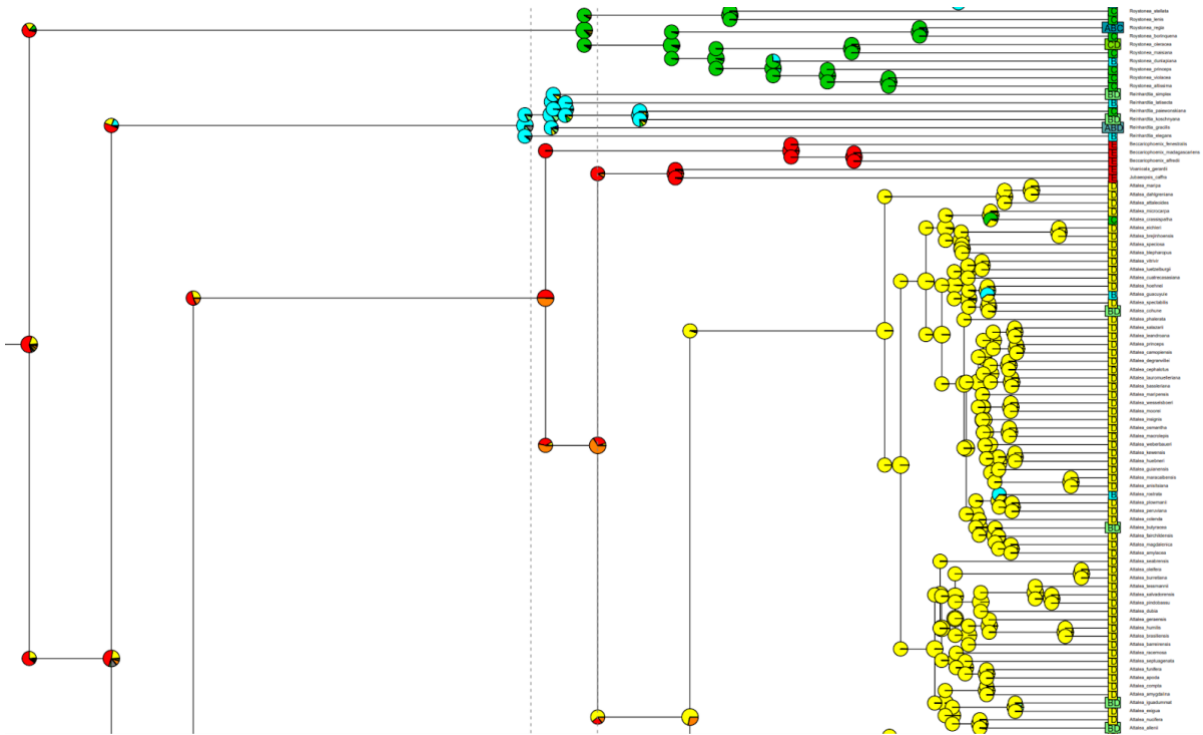


Figure 8: Ancestral state reconstruction for *Roystonea*, *Reinhardtia paiewonskiana* and *Attalea crassispatha*

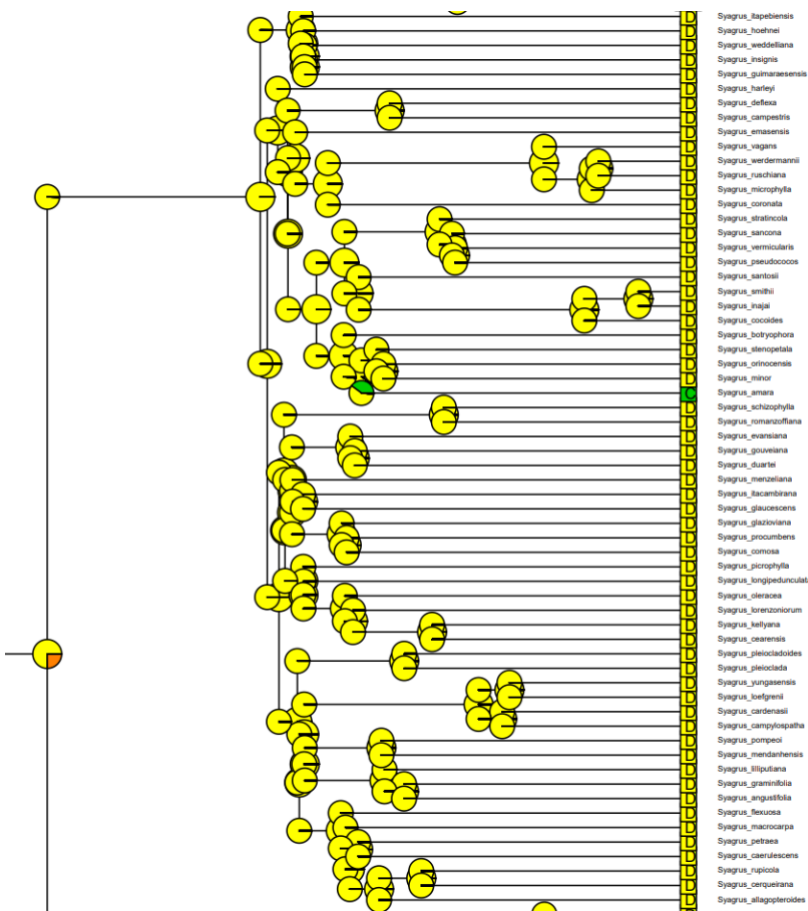


Figure 9: Ancestral state reconstruction for *Syagrus amara*

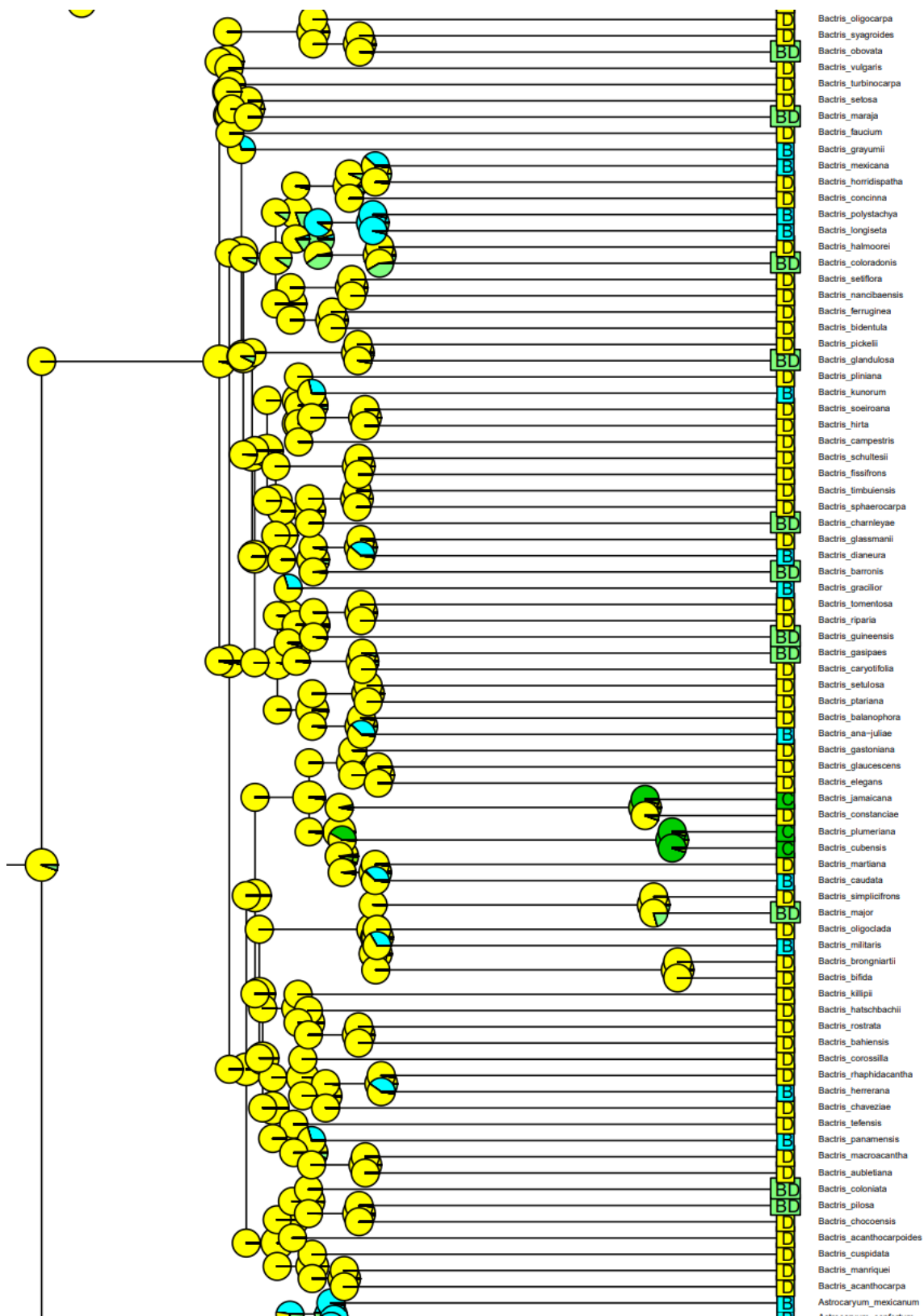


Figure 10: Ancestral state reconstruction for *Bactris cubensis*, *B. jamaicana* and *B. plumeriana*

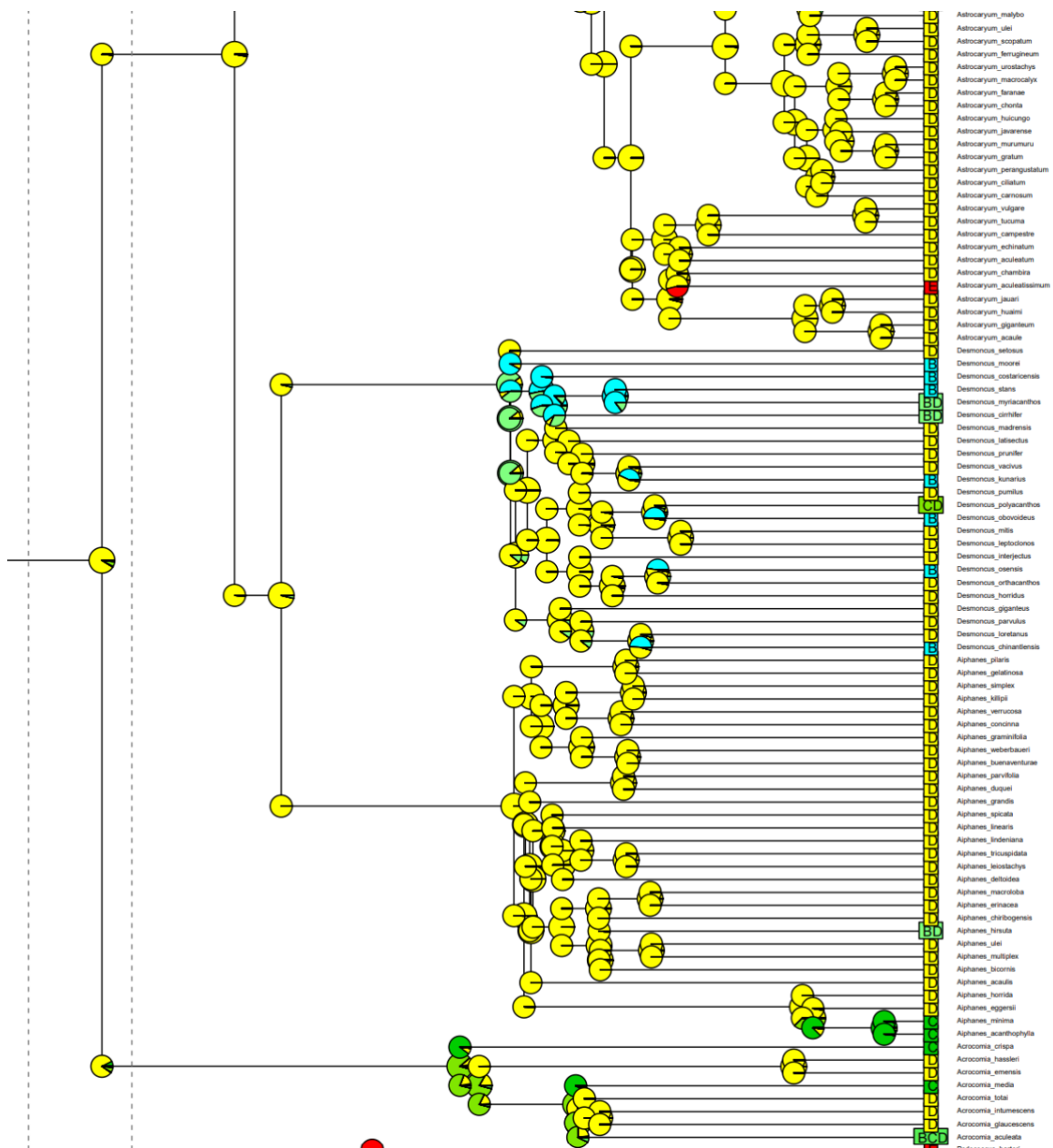


Figure 11: Ancestral state reconstruction for *Desmoncus polyacanthos*, *Aiphanes acanthophylla*, *A. minima*, *Acrocomia crispa*, *A. media* and *A. aculeata*

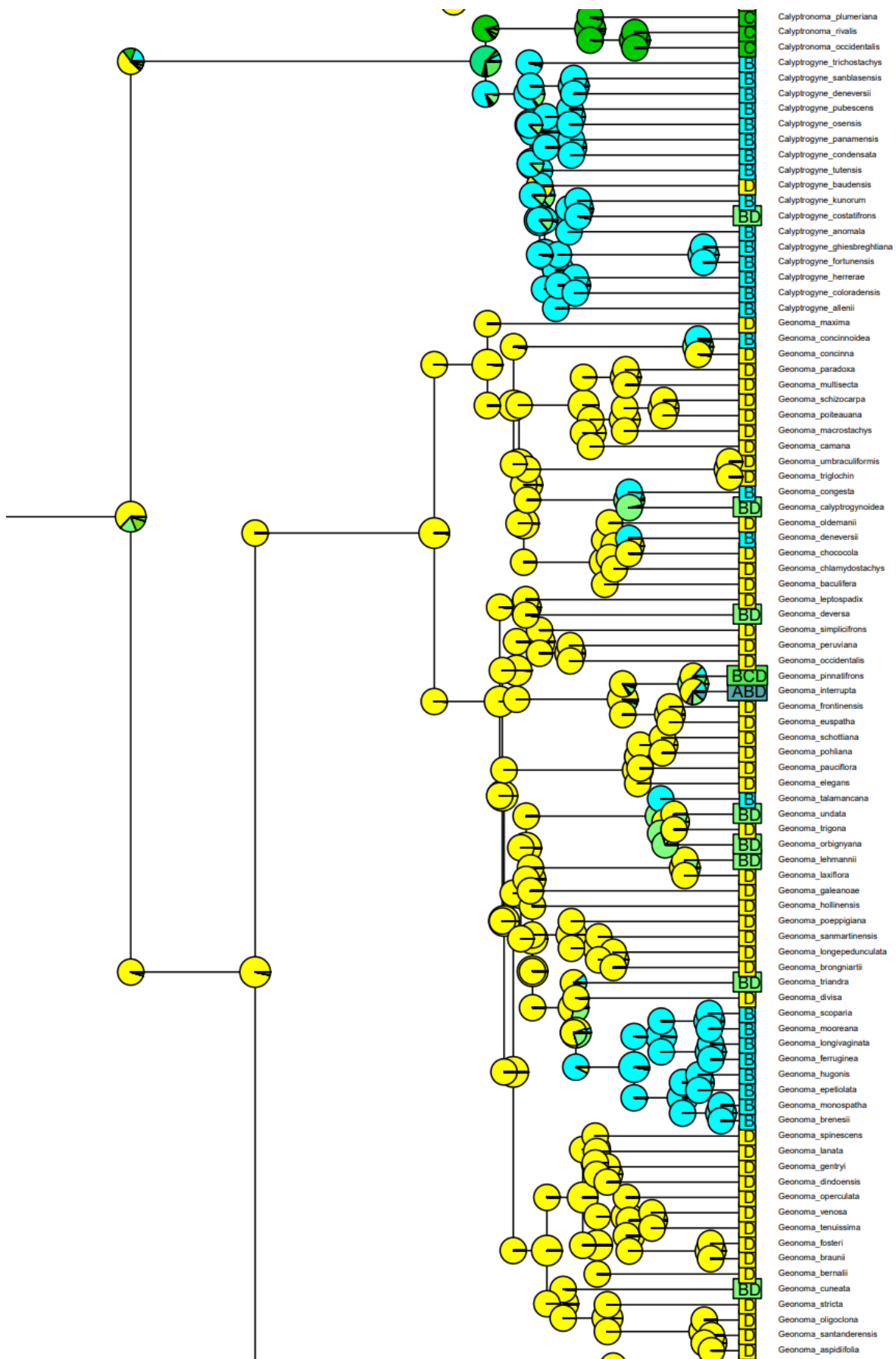


Figure 12: Ancestral state reconstruction for *Calyptronoma* and *Geonoma pinnatifrons*

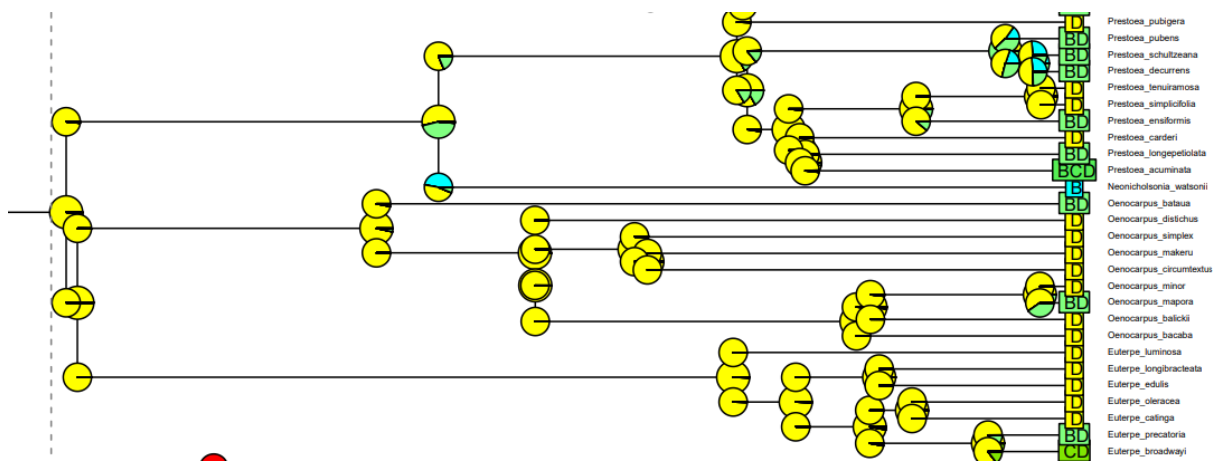


Figure 13: Ancestral state reconstruction for *Prestoea acuminata* and *Euterpe broadwayi*