



Testing geological models of evolution of the Isthmus of Panama in a phylogenetic framework

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The emergence and closure of the Isthmus of Panama had regional and global impacts that were rivalled by few other Cenozoic geological events. The closure of the Central American Seaway and the rise of the Isthmus had dramatic effects on climate and air and oceanic currents worldwide. Formation of the Isthmus also drove terrestrial biotic interchange, ending the isolation of South America by permitting the mixing of its biota with that of North and Central America. A dated phylogenetic tree of a well-sampled clade of palms in the tribe Trachycarpeae (*Copernicia*, *Pritchardia* and *Washingtonia*) was used to conduct biogeographical analyses. Examination of the timing of lineage dispersal from North into South America was performed and two contrasting temporal hypotheses of the Isthmus formation were tested: occurrence in the Pliocene (c. 5 Mya to the present) or in the Miocene (prior to c. 5 Mya). *Copernicia* is inferred to have dispersed through the Isthmus of Panama region into South America and subsequently into the Caribbean, where it underwent a rapid radiation. Consistent with a geologically older age for the Isthmus than previously understood, our results support recent geological and palaeobiological data that suggest an early Oligocene to early Miocene model of evolution of the Isthmus of Panama. © 2012 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2013, **171**, 287–300.

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INTRODUCTION

The formation of the Isthmus of Panama is considered by physical scientists as one of the most important geological events in Cenozoic history [last 60 million years (Mya); e.g. Graham, 2010]. The Isthmus is a narrow strip of land that separates the Caribbean Sea from the Pacific Ocean and links North and Central America with South America. The closure of the Central American Seaway (CAS) that separated North and South America stopped the westward palaeocurrent and all circulation between the Caribbean Sea and the Pacific Ocean (Collins, Budd & Coates, 1996; Newkirk & Martin, 2009), forcing Caribbean currents northeastward. The formation of the

Isthmus had an enormous impact on global climate and, although controversial (Klocker, Prange & Schulz, 2005; Molnar, 2008), the northeastern shift in Caribbean currents has been hypothesized to have played a fundamental role in the onset of Plio-Pleistocene glaciations (Haug & Tiedemann, 1998; Haug *et al.*, 2001; Bartoli *et al.*, 2005).

In addition to the climatic and oceanographic effects, the closure of the Isthmus of Panama is also considered to have been a defining event in the biogeography of the Americas (e.g. Gentry, 1982). New land connections between North and South America ended the ‘splendid isolation’ of South America (Simpson, 1980) and facilitated the ‘Great American Biotic Exchange’ (Stehli & Webb, 1985). The fossil record of mammal fauna supports few migrations across the Isthmus before the Late Pliocene and the

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Pleistocene (Simpson, 1980; Stehli & Webb, 1985; Graham, 1992; Burnham & Graham, 1999). For plants, a recent meta-analysis has shown older trans-CAS divergence times, implying a higher propensity for dispersal than animals throughout the geological period of Panamanian assembly (Cody *et al.*, 2010) and/or the presence of a dispersal corridor (approximating tectonic plates or stepping-stone islands between North and South America). The combined processes of plate disassembly and redistribution, together with phases of global warming and cooling, are thought to have afforded plants intermittent dispersal opportunities that could have contributed to the direction of angiosperm diversification (Morley, 2003). In particular, long-distance dispersal has been demonstrated to be the likely cause of many plant distributions, including those in the Neotropics (e.g. Dick, Abdul-Salim & Bermingham, 2003; Lavin *et al.*, 2004; Särkinen *et al.*, 2007).

Previous studies based on isotopic, geochemical and fossil faunal data from sedimentary strata across the Isthmus of Panama were inferred to indicate a Pliocene emergence and closure of the Isthmus [c. 3 million years ago (Mya); Keigwin, 1978, 1982; Duque-Caro, 1990; Coates *et al.*, 1992, 2004; Collins *et al.*, 1996; Kameo & Sato, 2000; Beu, 2001; Newkirk & Martin, 2009]. However, some of the evidence supporting this Pliocene evolution model has alternatively been interpreted to show no causal relationship with Isthmus closure because these studies relied on indirect evidence (geochemical, biological records) assumed to be correlated with a Pliocene Isthmus closure (e.g. Molnar, 2008). Indeed, previous results are in contrast with a recently proposed model of Isthmus formation based on new mapping, petrographical, geochronological, palaeomagnetic and thermochronological data, which infer that the Isthmus of Panama region comprised primarily uplifted terrestrial landscapes above sea level with some shallow sea incursions from the late Eocene (c. 40–34 Mya; Montes *et al.*, 2012a, b) until the early Miocene (c. 23–16 Mya; Farris *et al.*, 2011). This Isthmus chain implies that the likelihood of dispersal between North and South America increased with the initiation of collision between the easternmost tip of the Central American Arc and northwestern South America, and that emergence and closure of the Isthmus are much older than previously recognized (CAS closure at 15 Mya; Montes *et al.*, 2012a). This palaeogeographical configuration also greatly restricted the width of the CAS during the late Oligocene to early Miocene (200-km-wide sea gap at 25 Mya; Farris *et al.*, 2011; Montes *et al.*, 2012a).

The integration of phylogenetic, molecular dating and biogeographical methods can also be used to reconstruct the evolutionary history of the Isthmus of

Panama, particularly when examining groups that are keystone components of Neotropical forests (e.g. Pennington, Richardson & Lavin, 2006). Palms (Arecaceae) are among the most important and characteristic components of tropical forests, particularly in terms of species diversity and abundance of individuals (Kahn & de Granville, 1992; Phillips & Miller, 2002; Dransfield *et al.*, 2008; Eiserhardt *et al.*, 2011a). Over 90% of palm species diversity is restricted to tropical forests because of water- and energy-related variables (Bjorholm *et al.*, 2005; Kreft, Sommer & Barthlott, 2006; Eiserhardt *et al.*, 2011b) and because of fundamental anatomical constraints that inhibit palms from colonizing colder environments (Tomlinson, 2006). The rich fossil history of Arecaceae dates back to the Cretaceous, and a recent family-wide analysis of divergence times inferred that palms have diversified in the tropical rainforest biome since its mid-Cretaceous origin at northern latitudes (Couvreur, Forest & Baker, 2011). Furthermore, palms are present in the first record of Neotropical forests (late Palaeocene Cerrejón flora of Colombia; Gomez-Navarro *et al.*, 2009; Wing *et al.*, 2009). Taken together, palms are an excellent study system for understanding the evolutionary history of the Isthmus of Panama.

Within the palms, a monophyletic group of three closely related genera of the palm tribe Trachycarpeae, *Copernicia* Mart., *Pritchardia* Seem. & H.Wendl. and *Washingtonia* H.Wendl., are distributed on both sides of the Isthmus region in North and South America and comprise two explosive island radiations, one in the Caribbean (Cuba and Hispaniola) and the other in the Pacific (Hawaiian Islands; Fig. 1; Bacon, Baker & Simmons, 2012a; Bacon *et al.*, 2012b). A previous study has suggested that these genera originated from North America and that *Copernicia* lineages followed the Greater Antilles–Aves Ridge (GAARlandia) land bridge to disperse from the Caribbean to South America (Bacon *et al.*, 2012a). GAARlandia putatively comprised large, closely spaced islands or possibly a continuous peninsula that linked South America to the Greater Antillean Islands in the Eocene–Oligocene transition (35–33 Mya; Iturralde-Vinent & MacPhee, 1999; but see Ali, 2012; Bayona *et al.*, 2012). A GAARlandia dispersal route for *Copernicia* was proposed because the timing of dispersals predated a Pliocene Isthmus of Panama formation (Bacon *et al.*, 2012a), but the recently proposed geologically older model of Isthmus evolution merits examination as an alternative dispersal route.

Copernicia, *Pritchardia* and *Washingtonia* species occur in dry, open savannas, deserts and areas prone to seasonal flooding or, on Pacific islands, in wet windward or dry leeward forests (Dransfield *et al.*,

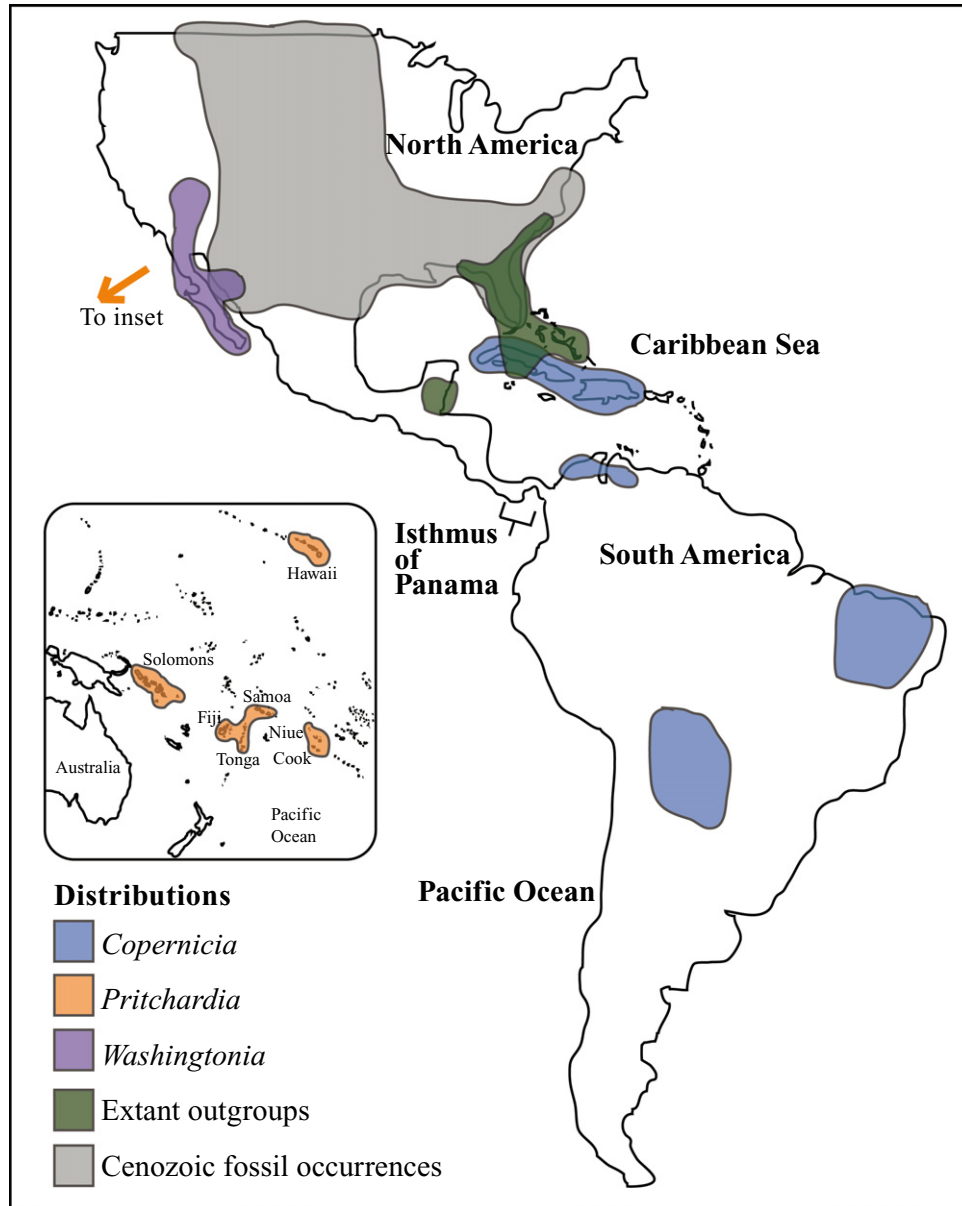


Figure 1. Map of the palm genera examined. *Copernicia* is distributed in Argentina, Brazil, Colombia, Cuba, Dominican Republic, Haiti, Paraguay and Venezuela. *Pritchardia* is distributed in the Cook, Fiji, Hawaiian, Niue, Samoa, Solomon and Tonga Islands. *Washingtonia* is distributed in the USA and Mexico. The Cenozoic fossil outgroups are based on *Sabalites* fossil occurrences, which were derived from Read & Hickey (1972), Weber (1978), Harley (2006) and Dransfield *et al.* (2008). Although the nomenclatural use of *Sabalites* does not unequivocally associate fossils with any extant genus (e.g. *Sabal*), it is a good hypothesis of the palaeodistribution of the lineages examined.

2008) and are dispersed by small mammals and birds (Henderson, 2002). Most wrens are insectivorous, but the largest species (*Campylorhynchus griseus*) nests and forages preferentially on *Copernicia tectorum* Mart. and, although it has been shown to disperse *Copernicia* seeds (Rabenold, 1990), dispersal does not occur over long distances because of their nonmigratory nature. *Washingtonia* spp. are also dispersed by

nonmigratory birds (Bullock, 1980) and by coyotes (Cornett, 1985). In contrast, *Pritchardia* spp. disperse across long distances along avian migratory routes of various plovers (*Pluvialis* spp.) (e.g. Hodel, 2007). These differences in dispersal capabilities, together with the phylogenetic relationships among genera, can be used to test the temporal biogeographical history of the clade in the Neotropics.

In this study, we investigate the origin and diversification of *Copernicia*, *Pritchardia* and *Washingtonia* palms in space and time by estimating speciation events under different biogeographical models. We explore the biogeographical history of *Copernicia* and the evolution of the Isthmus of Panama by testing whether the timing of lineage dispersal occurred in the Pliocene (5.25 Mya to the present; H₁ *sensu* Keigwin, 1978) or whether it occurred in the Miocene (before 5.25 Mya; H₂ *sensu* Montes *et al.*, 2012a). Elucidation of the timing of formation of the Isthmus has major implications for the timing of biotic interchange between North and South America, and hence for the elucidation of the diversification history of *Copernicia*, *Pritchardia* and *Washingtonia*.

MATERIAL AND METHODS

PHYLOGENETIC ANALYSES AND ESTIMATION OF DIVERGENCE TIMES

Species of *Copernicia*, *Pritchardia* and *Washingtonia* and three outgroups representing other tribes of Coryphoideae [Fig. 1; *Cryosophila stauracantha* (Heynh.) R.J.Evans, *Phoenix roebelenii* O'Brian and *Sabal palmetto* (Walter) Lodd. ex Schult. & Schult.f.] were sequenced for three plastid and three nuclear genes (Bacon *et al.*, 2012a, b). Eighty per cent of species were sampled, including 13 of the 22 species of *Copernicia*, one of the two *Washingtonia* species and all 26 currently recognized species of *Pritchardia* (Hodel, 2007; Bacon *et al.*, 2012b). Forty-three terminals were included in the simultaneous analysis (Kluge, 1989; Nixon & Carpenter, 1996). Preliminary nucleotide alignments were obtained independently for each of the six loci using default parameters in MUSCLE v3.6 (Edgar, 2004) and manually adjusted in MacClade v4.03 (Maddison & Maddison, 2001) following Simmons (2004). Maximum parsimony (MP) tree searches were conducted using 1000 random addition tree bisection–reconnection (TBR) searches in PAUP* v4.0b10 (Swofford, 2001) with a maximum of ten trees held per replicate. Parsimony jackknife (JK) analyses (Farris *et al.*, 1996) were conducted using PAUP* and 1000 replicates were performed with 100 random addition TBR searches per replicate.

jModeltest v0.1.1 (Posada, 2008) was used to select the best-fit model of sequence evolution for each data matrix using the Akaike Information Criterion (Akaike, 1974) without considering invariant-site models, following Yang (2006). The data were partitioned by locus to allow for variation in substitution models and the analysis was run using the GTR + Γ model of nucleotide substitution with four rate categories. Three iterations of Markov chain Monte Carlo (MCMC) analysis were conducted with 50

million generations sampled every 1000th generation to estimate the Bayesian topology in BEAST v1.6.2 (Drummond *et al.*, 2006; Drummond & Rambaut, 2007). We estimated the divergence times using an uncorrelated log-normal molecular clock model and the Yule pure birth speciation model. We do not know of any unambiguously identified fossils in *Copernicia*, *Pritchardia* or *Washingtonia*, and we therefore used two secondary calibration points obtained from a family-level analysis based on four primary fossil calibrations (Couvreur *et al.*, 2011). Normally distributed priors have been shown to be most appropriate for modelling secondary calibrations because they reflect the uncertainty in age estimates (Ho, 2007; Ho & Phillips, 2009). Normal distributions for both the stem and crown nodes of Trachycarpeae were estimated and the bounds on the prior reflect the 95% credible interval of the constraints. The mean ages were 54 and 34 Mya, respectively, *sensu* Couvreur *et al.* (2011), and the standard deviations were set to 6 and 5 Mya, respectively, to capture the variation estimated around the mean (71–38 and 47–23 Mya, respectively, for the stem and crown nodes). The performance of the separate analyses (convergence of parameters, effective sample sizes) was assessed in AWTY (Wilgenbusch, Warren & Swofford, 2004; Nylander *et al.*, 2008) and in Tracer v1.5 (Drummond & Rambaut, 2007).

ANCESTRAL RANGE RECONSTRUCTION

A presence–absence matrix was built representing the distribution of species (Fig. 1) in nine non-overlapping areas that reflect the distributions and endemism of genera, while at the same time minimizing the total number of areas (Sanmartín & Ronquist, 2004): SU (southern USA: Arizona, California, Florida, Georgia, North and South Carolina); CM (Central America and Mexico); NW (northwestern South America: Colombia and Venezuela); SC (south-central South America: Argentina and Brazil); HA (Hispaniola: Dominican Republic and Haiti); CU (Cuba); SP (south Pacific Islands: Cook, Fiji, Niue, Samoa, Solomon and Tonga); HI (Hawaiian Islands); and AS (Asia: China to Vietnam). Each species was assigned to one or more of the areas on the basis of its known current distribution (Henderson, Galeano & Bernal, 1995; Hodel, 2007).

To reconstruct the historical biogeography of lineages and, in particular, to examine whether *Copernicia* lineages followed a Central American (Isthmus of Panama) or Caribbean (GAARlandia) dispersal route into South America, we analysed an unconstrained matrix in which dispersal among all regions was equally probable using two methods: the Bayesian statistical dispersal–vicariance analysis, as imple-

mented in Reconstruct Ancestral State in Phylogenies (RASP in S-DIVA; Yu, Harris & He, 2010), and the dispersal–extinction–cladogenesis likelihood model (DEC), as implemented in Lagrange (build 20110117; Ree *et al.*, 2005; Ree & Smith, 2008). To take into account the influence of phylogenetic uncertainty on biogeographical inference, unconstrained ancestral areas were optimized across a random sample of 1000 post-burn-in Bayesian trees from the dating analysis in RASP. Relative frequencies of ancestral areas for each node of the BEAST tree were computed by counting all trees with a certain area uniquely assigned to the node. Results that included the proportion of ambiguous reconstructions (< 6% relative probability) across the random sample were then translated into pie charts by importing the estimated relative frequencies from the RASP ‘node view’ into Excel.

We also used the ultrametric tree generated by BEAST to infer ancestral distributions with DEC default parameters employing an unconstrained dispersal matrix, and compared it with two constrained matrices, to test between alternative models on the formation of the Isthmus of Panama. The constrained matrices corresponded to Pliocene or Miocene palm dispersal and were based on the fact that dispersal probability increases as distance between areas decreases (isolation by distance; e.g. MacArthur & Wilson, 1967). Furthermore, the constraints restricted dispersal between North and South America and the Caribbean and Pacific basins, leaving the Asian and south-central South American biogeographical regions unconstrained. Constraints were defined by the mean of the age ranges of the two hypotheses: 5.25 Mya for the H_1 Pliocene model (mean of 7.0 and 3.5 Mya) and 21.5 Mya for the Miocene H_2 model [mean of 35 and 8 Mya; timing of the 200-km CAS gap *sensu* Farris *et al.* (2011) and Montes *et al.* (2012a)]. Differences between models were assessed by direct comparison of their respective log-likelihoods using the conventional cut-off value of two log-likelihood units following Ree *et al.* (2005). Palms do not require strict over-land dispersal or, in this case, completion of the Panamanian land bridge, but because of the dispersal capabilities of *Copernicia*, long-distance over-water events are unlikely. We therefore formed discrete hypotheses to allow for comparison and to emphasize two distinct temporal scenarios of isthmian evolution.

Two iterations of hypothesis testing using biogeographical constraints were performed. In the ‘strict’ analysis, the H_1 matrix was constrained to only allow dispersal of palms from North America (SU and CM) across the Isthmus to South America (NW) from 7 to 0 Mya and through the CAS either to the Pacific (SP and HI) or Caribbean basins (CU and HA) from 20.00

to 5.25 Mya. We compared the likelihoods for H_1 with H_2 , where the matrix was constrained to only allow dispersal across the Isthmus between 35 and 8 Mya and through the CAS from 50 to 21.5 Mya. In the ‘relaxed’ analysis, the H_1 matrix allowed for low dispersal (0.25) into South America from 20.00 to 5.25 Mya and the H_2 matrix allowed a medium rate of dispersal (0.5) into South America from 7 to 0 Mya.

RESULTS

PHYLOGENETIC RELATIONSHIPS

Phylogenetic analyses of 6843 bp of nuclear and plastid data using parsimony and Bayesian methods were consistent with the maximum likelihood topology, but differed from the Bayesian topology, presented in Bacon *et al.* (2012a; figs 2, 4 versus fig. 5) with respect to the placement of *Washingtonia*. Eleven nodes had relatively poor support values, but they corresponded to lineages within recent and rapid island radiations (Supporting Information, Fig. S1). Each genus was highly supported [posterior probability (PP) = 1; JK = 100%] as monophyletic, as were major clades within genera, such as South American *Copernicia*, south-central South American *Copernicia*, Hispaniolan *Copernicia*, Cuban *Copernicia*, south Pacific *Pritchardia* and Hawaiian *Pritchardia*. Many of the *Pritchardia* clades endemic to particular Hawaiian Islands were also resolved as highly supported monophyletic biogeographical groups (PP = 1 for Kaua’i, Maui Nui and Hawaiian clades; Fig. 2).

TEMPORAL RANGE EVOLUTION ACROSS THE ISTHMUS OF PANAMA

Each of the three iterations of 50 million generations resulted in high effective sample sizes (ESSs) (> 500) and convergence of parameters (‘Compare’ function in AWTY), and 10% of the sampled trees were subsequently treated as burn-in and removed. For all four data partitions (plastid, CISP4, CISP5, RPB2), the rate of covariance was centred on zero, which can be interpreted as a lack of evidence for rate autocorrelation among lineages (Drummond & Rambaut, 2007). The estimated ages of the major clades are given in Table 1.

The estimation of ancestral ranges was consistent between likelihood (DEC) and Bayesian (RASP) unconstrained inferences. Relative frequencies from the RASP analysis across the sample of posterior trees (Fig. 2) reconstructed the ancestral area of *Copernicia*, *Pritchardia* and *Washingtonia* as primarily distributed in the southern USA, but a few topologies supported a Central America + Mexico ancestral area or a combination of the two regions. The ancestral area of the *Copernicia* and *Pritchardia* clade was

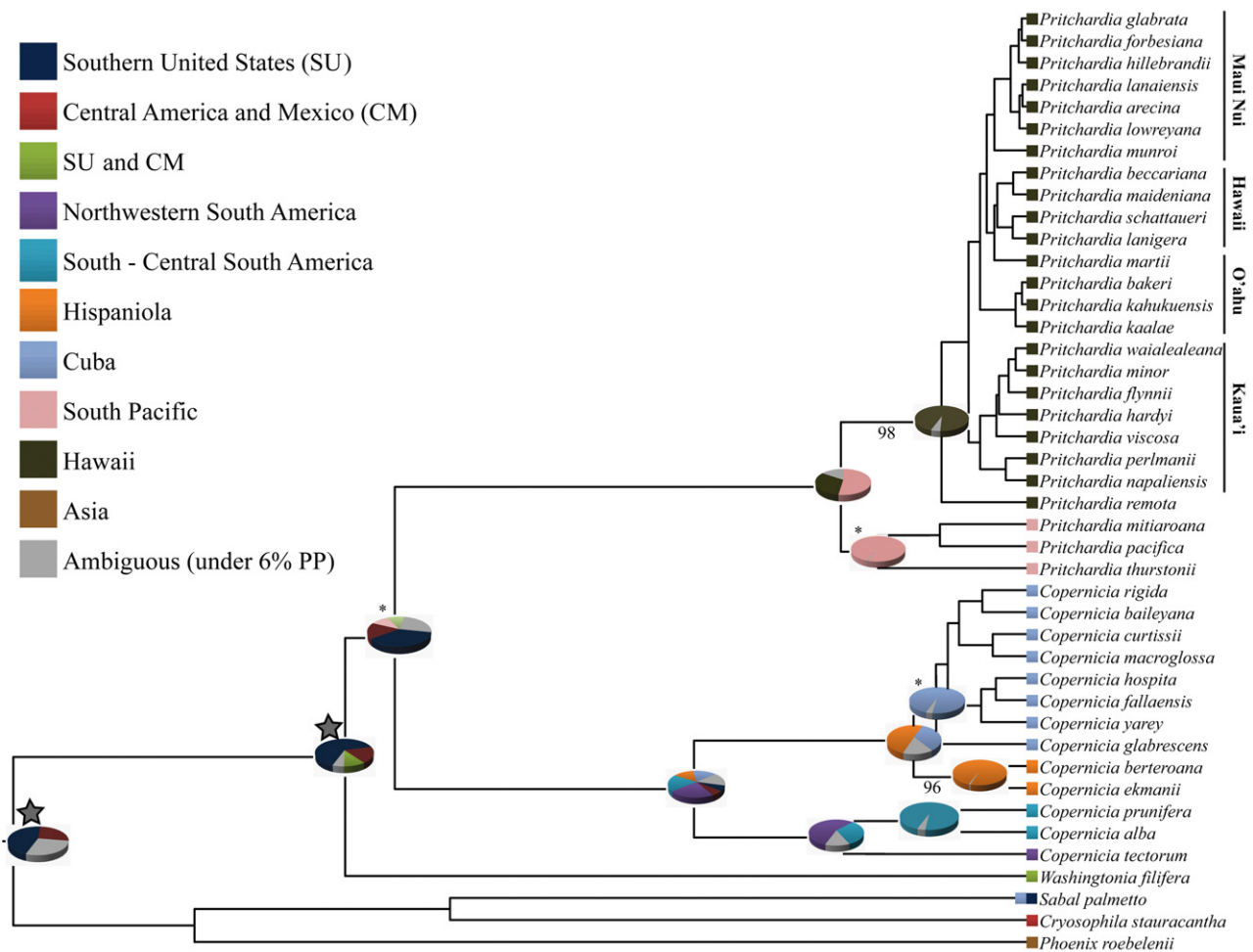


Figure 2. Bayesian topology derived from three iterations of a 50-million-generation Markov chain Monte Carlo (MCMC) search. Branch support values for the nodes of interest were all resolved with a Bayesian posterior probability (PP) of 1.0. Nodes of interest that were resolved with less than 100% jackknife (JK) on the maximum parsimony (MP) strict consensus tree are beneath the respective branches, and * indicates relationships that were not present in the strict consensus. Pie charts of the relative frequencies of ancestral ranges at the nodes of interest are derived from 1000 posterior trees in Reconstruct Ancestral State in Phylogenies (RASP) and the grey stars indicate the two calibration points.

inferred in the southern USA. The area reconstruction suggests that *Copernicia* subsequently dispersed across the Isthmus of Panama region into northwestern South America, with lineages reaching the Caribbean only after the colonization of South America.

Comparison of H_1 and H_2 across the two iterations of DEC constrained analyses resulted in four biogeographical scenarios that were within two log-likelihood units of one another (Table 2). The best estimate from the comparison of log-likelihood values was that of a relaxed constraint on a Miocene (H_2) colonization of South America across the Isthmus of Panama. This scenario was 0.35 log-likelihood units lower than the unconstrained and 0.22 units lower than the relaxed H_1 results. Range evolution inferences under the relaxed H_2 constraint exhibited less

uncertainty in range reconstructions than did the strict or unconstrained models, showing that the relaxed model fit the data better.

The likelihood-based and Bayesian biogeographical reconstructions are highly congruent and allow for a most likely hypothesis of lineage diversification and range evolution in *Copernicia*, *Pritchardia* and *Washingtonia* (Fig. 3): the ancestral area of the three palm genera was located in the southern USA (SU) around 33.5 Mya with subsequent divergence of *Copernicia* and *Pritchardia* lineages also occurring in SU around 31 Mya. *Copernicia* dispersed into northwestern South America between 31 and 16.3 Mya, and then to the Caribbean islands between 16.3 and 5.5 Mya, whereas *Pritchardia* dispersed to the Pacific islands between 31 and 9.1 Mya (Table 1), with both genera

Table 1. Crown and stem node mean and highest posterior density estimations in millions of years ago (Mya) for clades of interest based on two calibration points

| Clade | Stem | | | Crown | | |
|--|-------|-------|-------|-------|-------|-------|
| | Mean | Upper | Lower | Mean | Upper | Lower |
| <i>Pritchardia</i> | 31.04 | 38.98 | 23.13 | 9.12 | 13.26 | 5.30 |
| South Pacific <i>Pritchardia</i> | 9.12 | 13.26 | 5.30 | 7.34 | 11.02 | 4.12 |
| Hawaiian Islands <i>Pritchardia</i> | 9.12 | 13.26 | 5.30 | 4.17 | 6.35 | 2.19 |
| Kaua'i <i>Pritchardia</i> | 2.84 | 4.28 | 1.55 | 2.28 | 3.62 | 1.09 |
| Maui Nui <i>Pritchardia</i> | * | * | * | 1.57 | 2.63 | 0.66 |
| Hawai'i <i>Pritchardia</i> | * | * | * | 1.43 | 2.44 | 0.55 |
| <i>Copernicia</i> | 31.04 | 38.98 | 23.13 | 16.34 | 22.11 | 10.65 |
| Central-east South America <i>Copernicia</i> | 9.66 | 14.17 | 5.53 | 4.99 | 8.02 | 2.36 |
| Hispaniola <i>Copernicia</i> | 5.55 | 8.26 | 3.07 | 2.33 | 4.23 | 0.73 |
| Cuban <i>Copernicia</i> | 5.55 | 8.26 | 3.07 | 4.45 | 6.68 | 2.49 |
| <i>Copernicia</i> + <i>Pritchardia</i> | 33.49 | 41.65 | 25.54 | 31.04 | 38.98 | 23.13 |
| <i>Copernicia</i> + <i>Pritchardia</i> + <i>Washingtonia</i> | 49.80 | 60.50 | 39.28 | 33.49 | 41.65 | 25.54 |

*Nodes supported by posterior probabilities lower than 0.50.

subsequently undergoing rapid radiations in Cuba (17 species at 4.45 Mya; Table 1) and the Hawaiian Islands (23 species at 4.17 Mya), respectively.

DISCUSSION

Robust molecular age estimates and biogeographical analysis of *Copernicia*, *Pritchardia* and *Washingtonia* were used to examine the likely dispersal route of *Copernicia* from North to South America and, subsequently, to infer the timing of palm dispersal and diversification across the Panamanian Isthmus and to the Caribbean and Pacific oceanic basins. Divergence time estimations are consistent with a general pattern of angiosperm colonization of Hawaiian Islands occurring at approximately 5 Mya (~4 Mya in *Pritchardia*, Table 1; e.g. Baldwin & Sanderson, 1998; Frajman, Eggens & Oxelman, 2009; Bacon *et al.*, 2012a), which has been attributed to the emergence of the extant volcanic islands, and also with the timing of the formation of the distinct components of Cuba into a single island terrain (Pliocene Cuban *Copernicia* radiation; Iturralde-Vinent & MacPhee, 1999; Graham, 2003; MacPhee, Iturralde-Vinent & Gaffney, 2003). Our results support a *Copernicia* dispersal event from North America via the Isthmus of Panama region into South America. Our results are also consistent with an early Oligocene to early Miocene formation of the Isthmus, which is older than traditionally understood and is further supported by recent geological and palaeobiological data in the proposal of a revised tectonic model of evolution of the Isthmus of Panama.

TESTING ALTERNATIVE HYPOTHESES ON THE FORMATION OF THE ISTHMUS OF PANAMA IN TRACHYCARPEAE PALMS

After identifying a *Copernicia* dispersal route through the Isthmus of Panama region, we used a likelihood approach to test two alternative hypotheses. The first hypothesis (H_1) was consistent with previous studies showing Pliocene dispersal across the Isthmus (here defined as a mean age of 5.25 Mya; but see Cody *et al.*, 2010). The second hypothesis (H_2) tested a revised tectonic model of Isthmus evolution proposed by Farris *et al.* (2011) and Montes *et al.* (2012a, b), where land emergence and subsequent formation of the Isthmus of Panama allowed for earlier biotic exchange (late Oligocene to early Miocene; here defined as a mean age of 21.5 Mya).

The phylogenetic analysis suggests a biogeographical disjunction between the Caribbean and Pacific basins. Sister groups that are disjunct between the Caribbean and Pacific are apparently rare and have been correlated with the formation of the Isthmus (Namoff *et al.*, 2010), including the effects on global climate and air and oceanic currents. In angiosperms, this disjunction is exemplified in *Darwiniothamnus* Harling and *Erigeron* L. (Andrus *et al.*, 2009), *Jacquemontia* Choisy (Namoff *et al.*, 2010), *Fitchia* Hook.f, *Oparanthus* Sherff, *Narvalina* Cass. and *Selleophytum* Urb. (Mort *et al.*, 2008), *Siemensia* Urb. (Motley, Wurdack & Delprete, 2005), and as found here in *Copernicia* and *Pritchardia*. These genera of Trachycarpeae originated in North America between 41 and 25 Mya (Table 1) and lineages dispersed both across the Isthmus of Panama and to Pacific islands.

Table 2. Constraints implemented in dispersal–extinction–cladogenesis likelihood model (DEC) analyses to test between the alternative models of Isthmus of Panama formation

| | H₁ | | | | | H₂ | | | | |
|----------------|----------------------|-----|-------|-----|-----|----------------------|------|-------|------|------|
| | NW | SP | HI | HA | CU | NW | SP | HI | HA | CU |
| Strict | | | | | | | | | | |
| 0–5.25 Mya | | | | | | | | | | |
| SU | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| CM | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 5.25–21.5 Mya | | | | | | | | | | |
| SU | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 |
| CM | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 |
| 21.5–50 Mya | | | | | | | | | | |
| SU | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 |
| CM | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 |
| –ln L | | | 42.76 | | | | | 42.47 | | |
| Relaxed | | | | | | | | | | |
| 0–5.25 Mya | | | | | | | | | | |
| SU | 1 | 0 | 0 | 0 | 0 | 0.5 | 0 | 0 | 0 | 0 |
| CM | 1 | 0 | 0 | 0 | 0 | 0.5 | 0 | 0 | 0 | 0 |
| 5.25–21.5 Mya | | | | | | | | | | |
| SU | 0.25 | 1 | 1 | 1 | 1 | 1 | 0.25 | 0.25 | 0.25 | 0.25 |
| CM | 0.25 | 1 | 1 | 1 | 1 | 1 | 0.25 | 0.25 | 0.25 | 0.25 |
| 21.5–50 Mya | | | | | | | | | | |
| SU | 0 | 0.5 | 0.5 | 0.5 | 0.5 | 0 | 1 | 1 | 1 | 1 |
| CM | 0 | 0.5 | 0.5 | 0.5 | 0.5 | 0 | 1 | 1 | 1 | 1 |
| –ln L | | | 42.54 | | | | | 42.32 | | |

All other biogeographical regions not listed in the constraint matrix below were left unconstrained with a dispersal capability of ‘1’. The strict analysis reduced dispersal to zero and prohibited movement between two areas during particular time periods, whereas the relaxed analysis reduced dispersal to 0.25 and 0.5 to allow for lower levels of dispersal. Constrained biogeographical areas are abbreviated as southern USA (SU), Central America and Mexico (CM), northwestern South America (NW), south Pacific Islands (SP), Hawaiian Islands (HI), Hispaniola (HA) and Cuba (CU). The three time periods constrained in Lagrange were 5.25 Mya (mean of 7–3.5 Mya *sensu* Keigwin, 1978), 21.5 Mya (mean of 35–8 Mya *sensu* Montes *et al.*, 2012a) and 50 Mya (the stem node of the phylogeny estimated). Global maximum likelihood values at the root nodes (as measured by $-\ln L$) are used to test amongst the two constrained and unconstrained ($-\ln L$ of 42.67) likelihood analyses.

The biogeographical disjunction between *Copernicia* and *Pritchardia* evolved between 31 and 9.1 Mya and implies long-distance dispersal of *Pritchardia* by migratory birds from North America to the Hawaiian Islands and therefore may be unrelated to Isthmus formation, but this temporal framework corresponds to increased constriction of the CAS as inferred from geological and palaeobiological data (early Oligocene to early Miocene; Montes *et al.*, 2012b). CAS closure not only rerouted air and west to east oceanic currents (Collins *et al.*, 1996), but potentially avian migratory (and palm dispersal) routes by forming emergent terrestrial proto-isthmus breeding and feeding grounds that mitigated against further dispersal.

Our results from divergence time and ancestral range reconstructions are consistent with an early

Oligocene to early Miocene model of evolution for the Isthmus of Panama. In this model, dispersal between North and South America (Table 2) occurred between 31 and 16.3 Mya. Considering these scenarios in relation to current species richness, it is striking that the North American ancestor lineage apparently did not diversify in a continental setting. Two *Washingtonia* spp. and three non-Caribbean *Copernicia* spp. gave rise to much more diverse island lineages: 19 Caribbean island *Copernicia* spp. and 26 South Pacific island *Pritchardia* spp. The lack of continental diversification is interesting given that there was no dispersal barrier into newly available South American niches, as seen by *Copernicia* lineages that apparently failed to diversify after colonizing northwestern South America by at least 16 Mya, unlike other angiosperms [e.g. *Guatteria* Ruiz & Pav. (Erkens

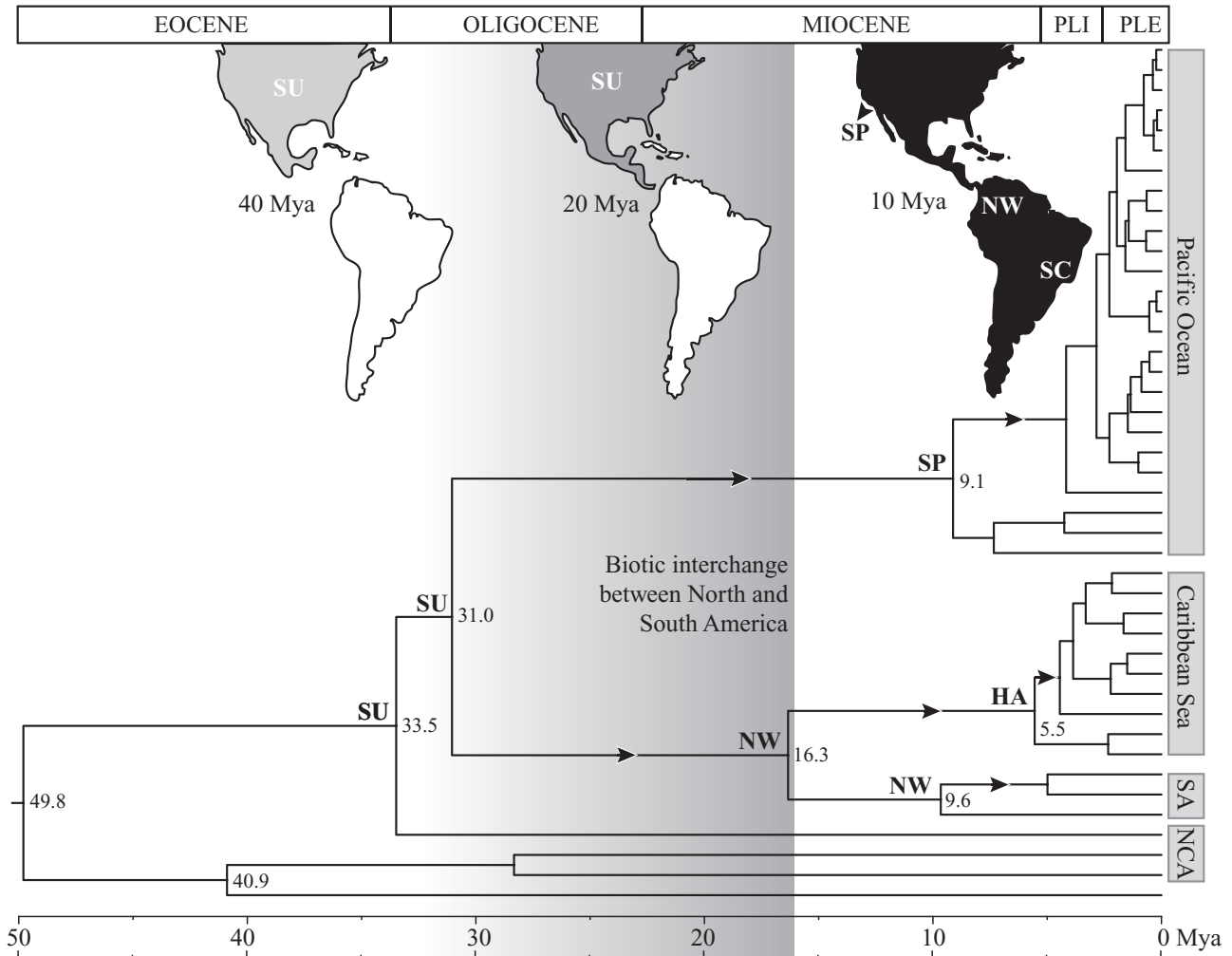


Figure 3. The most likely hypothesis of biogeographical events and diversification of Caribbean, Pacific, South American (SA) and North and Central American (NCA) lineages. Ancestral nodes are plotted against hypothetical palaeomaps of the Isthmus of Panama, where the shading darkens with the probability of biotic exchange between North and South America. Inferred dispersal events (arrows) and most likely ancestral areas are also indicated at the nodes of interest. HA, Hispaniola; NW, northwestern South America; PLE, Pleistocene; PLI, Pliocene; SC, south-central South America; SP, south Pacific; SU, southern USA. The grey gradient indicates the timing of palm dispersal across the Isthmus of Panama.

et al., 2007); *Inga* Mill. (Richardson *et al.*, 2001)] or other groups [e.g. tanager birds (Weir, Bermingham & Schluter, 2009); North American mammals (Kirby, Jones & MacFadden, 2008)].

A REVISED MODEL OF EVOLUTION OF THE ISTHMUS OF PANAMA: ISSUES AND FUTURE PROSPECTS

Despite the caveats involved in studies employing secondary calibration and a lack of biogeographical algorithms that take into account rate differences amongst regions in speciation, extinction or range evolution (Goldberg, Lancaster & Ree, 2011), our inferences from phylogenetic, divergence time and biogeographical analyses are consistent with an early

Oligocene to early Miocene evolution of the Isthmus of Panama, as suggested previously by Farris *et al.* (2011). We did not find support for Eocene evolution as proposed by Montes *et al.* (2012a, b), in these palm lineages, perhaps because estimates based on fossil data can only provide minimum ages (e.g. Ho, 2007). Our data on *Copernicia* and *Pritchardia* support a divergence between the two clades showing east–west (31–9.1 Mya) and north–south (31–16 Mya) disjunctions, consistent with the idea of an earlier formation of the Isthmus of Panama.

These results together with a geologically older formation of the Isthmus of Panama are consistent with other studies on Neotropical palms (Cuenca, Asmussen-Lange & Borchsenius, 2008; Roncal *et al.*,

2010, 2011, 2012; Bacon *et al.*, 2012a), where dispersal events from North to South America predate a Pliocene model of Isthmus of Panama formation. Excluding studies that used the Isthmus as a calibration point, which cannot test for the effects of closure, other phylogenetic studies are consistent with a model of Isthmus formation that is older than the Pliocene [e.g. other angiosperms (Cody *et al.*, 2010), freshwater fish (Bermingham & Martin, 1998) and salt-water-intolerant frogs (Weight *et al.*, 2005; Pinto-Sánchez *et al.*, 2012)].

Support for an older early Oligocene to early Miocene model of Isthmus of Panama formation also derives from the palaeobiological record. Land mammal fossil occurrences have been shown to require a continuous land connection of Panama with North America by the early Miocene (Whitmore & Stewart, 1965; Kirby & MacFadden, 2005; Kirby *et al.*, 2008). Fossil benthic foraminifera also indicate an effective biogeographical barrier between Caribbean and Pacific surface water in the middle to late Miocene (Collins *et al.*, 1996). Furthermore, regional palaeogeographical reconstructions account for a narrow gap, or the complete absence of a gap, between Central America and northwest South America in the Neogene (Wadge & Burke, 1983; Pindell & Kennan, 2009). Despite this evidence, other data remain to be explained, such as the dramatically low mitochondrial rate of mutation required to explain marine geminate sister species formed by a much older Isthmus of Panama vicariant event (e.g. Lessios, 2008). To this end, more dated phylogenetic analysis of Neotropical groups and refined meta-analyses examining biotic interchange in both marine and terrestrial organisms are needed (C. D. Bacon, C. Jaramillo & A. Antonelli, unpubl. data, but see Lessios, 2008; Weir *et al.*, 2009; Cody *et al.*, 2010; Smith & Klicka, 2010).

The implications of a geologically older model of the emergence and formation of the Isthmus of Panama are wide ranging and include biological, climatic, oceanic and tectonic factors. Biologically, an early Oligocene to early Miocene (31–16.3 Mya) land connection between Central America and South America through the Isthmus of Panama implies that the lack of interchange in land mammals across the Isthmus until the late Pliocene–early Pleistocene may have been the result of a wet and hot climate in northern South America that stalled mammal dispersal until the formation of northern ice sheets and the evolution of savanna-like environments in Panama and northern South America (Molnar, 2008; Montes *et al.*, 2012a). In contrast, if a phylogenetic niche conservatism hypothesis is asserted, the dispersal of dry-adapted *Copernicia* palms that are resistant to intermittent flooding may indicate the presence of

savanna-type ecosystems at least in the Miocene, but further studies of biotic interchange among characteristic savanna species are needed to shed further light on the palaeoenvironment in the region.

An early Oligocene to early Miocene Isthmus formation and land connection between Central and South America are also significant in the context of mountain building in the Andes. From the central (Oncken *et al.*, 2006) to the northern (Mora *et al.*, 2010) Andes, it has been suggested that deformation reached most of the present-day extension of the modern Andes in the late Oligocene to early Miocene. Farris *et al.* (2011) suggested the late Oligocene to early Miocene to be an important episode of deformation in Panama. It appears likely that the faster westward South American drift, which is thought to be responsible for orogenesis in the Andes (Silver, Russo & Lithgow-Bertelloni, 1998; Oncken *et al.*, 2006; Mora *et al.*, 2010; Husson, Conrad & Faccenna, 2012), also influenced the late Oligocene to early Miocene closure of the CAS. Our data are robust to these suggestions because the age for Isthmus formation is coeval with important processes in the Andes. The refined inference of the formation of the Isthmus of Panama also has implications for the understanding of Andean biogeography. Previous studies of Andean lineages lacked unique and testable predictions that facilitated such investigations (e.g. Brumfield & Capparella, 1996) because events and processes causing Andean biogeographical and temporal patterns were thought to occur at overlapping time intervals (Pleistocene climatic shifts, uplift of the eastern cordillera of the northern Andes and the completion of the Isthmus of Panama; Pennington & Dick, 2010). Our results, together with the new tectonic model of evolution in the Isthmus of Panama proposed by Farris *et al.* (2011) and Montes *et al.* (2012a, b), allow for the disentanglement of the effects of the Isthmus closure and Pleistocene glacial cycles.

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SUPPORTING INFORMATION

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

Figure S1. Chronogram from BEAST analysis with all posterior probability (PP) support values shown for nodes under PP = 1.0.