UNIVERSIDADE FEDERAL DE MINAS GERAIS
INSTITUTO DE CIÊNCIAS BIOLÓGICAS
Departamento de Botânica
Programa de Pós-Graduação em Biologia Vegetal

INGRIDY OLIVEIRA MOURA

ACROSS AND WITHIN CONTINENTS DISPERSAL SHAPED THE BIOGEOGRAPHIC HISTORY IN THE FERN GENUS *AMAUROPELTA*

Dissertação apresentada ao Programa de Pós-Graduação em Biologia Vegetal do Departamento de Botânica do Instituto de Ciências Biológicas da Universidade Federal de Minas Gerais, como requisito parcial à obtenção do título de Mestre em Biologia Vegetal.

Área de Concentração: Morfologia, Sistemática e Diversidade Vegetal

BELO HORIZONTE – MG
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Orientador: Prof. Dr. Luiz Eduardo Vieira Del Bem
Universidade Federal de Minas Gerais

Coorientadora: Prof. Dra. Thaís Elias Almeida
Universidade Federal do Oeste do Pará

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FOLHA DE APROVAÇÃO

"Across and within continents dispersal shaped the biogeographic history in the fern genus *Amauropelta*"

Dissertação defendida por INGRIDY OLIVEIRA MOURA e aprovada, em 30 de agosto de 2021, pela banca examinadora constituída pelos professores:

Dr. Luiz Eduardo Vieira Del Bem (Universidade Federal de Minas Gerais)

Dr. Thiago José de Carvalho André (Universidade Federal do Oeste do Pará)

Dr. João Aguiar Nogueira Batista (Universidade Federal de Minas Gerais)

Dra. Thaís Elias Almeida (Universidade Federal do Oeste do Pará)

Belo Horizonte, 30 agosto de 2021.

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RESUMO

Thelypteridaceae é uma das maiores famílias de samambaias, com cerca de 1040 espécies, a maioria ocorrendo em regiões tropicais e subtropicais. Na família são reconhecidos 30 gêneros, dos quais, oito possuem espécies nativas na região Neotropical. *Amauropelta* é o maior gênero da família Thelypteridaceae com aproximadamente 215 espécies, das quais 200 ocorrem na região Neotropical e algumas na África, Madagascar, Ilhas do Oceano Índico, Ilhas do Pacífico e Sri Lanka. A monofilia de *Amauropelta* foi bem estabelecida em estudos filogenéticos anteriores, mas as relações entre grupos e espécies dentro do gênero ainda precisam ser compreendidas. Para preencher esta lacuna, expandimos a amostragem e, reconstruímos a história biogeográfica de *Amauropelta* à luz das estimativas de tempo de divergência. Nosso conjunto de dados compreendeu 64 espécies de *Amauropelta* e 11 grupos externos, com 104 novas sequências de seis regiões do genoma plastidial, resultando em uma matriz de dados combinada composta por 89 táxons terminais e 3013 pares de base. As inferências filogenéticas foram obtidas pelos métodos de máxima verossimilhança e inferência bayesiana. Os tempos de divergência foram estimados usando BEAST e as inferências biogeográficas foram realizadas usando BioGeoBEARS. Nossos resultados confirmam a monofilia de *Amauropelta*. *Amauropelta beddomei* e *A. glanduligera* da Ásia, assim como *A. nevadensis* e *A. noveboracensis* da América do Norte, antes vinculados à *Parathelypteris*, foram recuperados dentro de *Amauropelta*, corroborando estudos anteriores em Thelypteridaceae. Nossos resultados não suportam a classificação seccional de *Amauropelta* com base em caracteres morfológicos. Não encontramos nenhuma estruturação morfológica. Estruturações geográficas só foram registradas para os clados Ásia, África. América do Norte. Assumimos que a diversificação de *Amauropelta* começou por volta de 45,75 Mya de um ancestral asiático. Nós interpretamos a migração por dispersão de longa distância (LDD) da Ásia para a América como tendo ocorrido entre 45,75-41,86 Mya. Todos os clados dentro de *Amauropelta* divergiram em diferentes períodos ao longo do tempo, desde o Oligoceno (27,88 Mya) ao Quaternário (1,71 Mya). As espécies africanas provavelmente correspondem a duas linhagens distintas, originando-se de mais de um evento LDD, um que divergiu por volta de 18,93 Ma e uma linhagem mais jovem que divergiu por volta de 5,18 Mya. Apesar de LDD desempenhar um papel na história biogeográfica de *Amauropelta*, encontramos alta contribuição de especiação local (63,9% entre todos os eventos de especiação), enquanto expansões variadas representaram 27,2% e eventos fundadores 8,9% de todos os eventos de especiação. Nossos resultados revelam que as principais biorregiões de *Amauropelta* correspondem a quatro hotspots para samambaias nos neotrópicos, como os Andes Tropicais, América Central, Grandes Antilhas e Sudeste do Brasil.

Palavras-chaves: *Amauropelta,* samambaias, biogeografia histórica, dispersão à longa distância, Neotrópico, Thelypteridaceae.

ABSTRACT

Amauropelta is the richest genus in the fern family Thelypteridaceae with approximately 215 species, 200 of them occurring in the Neotropics, and some in Africa, Madagascar, Indian Ocean Islands, Pacific Islands, and Sri Lanka. The monophyly of *Amauropelta* was well established in previous phylogenetic studies, but the relationships between groups and species within the genus remain to be understood. To fill this gap, we expand the sampling, including 64 species of *Amauropelta*. We also reconstructed the biogeographical history of *Amauropelta* in the light of divergence time estimates. Our dataset comprises 64 species of *Amauropelta* and 11 outgroups, with 104 newly generated sequences from six plastid genome regions, resulting in a combined data matrix composed of 89 specimens and 3013 bp. The phylogenetic inferences were obtained through maximum likelihood and Bayesian inference methods. Divergence times were estimated using BEAST, and biogeographic inferences were performed using BioGeoBEARS. Our results confirm the monophyly of *Amauropelta*. *Amauropelta beddomei* and *A. glanduligera* from Asia, and *A. nevadensis* and *A. noveboracensis* from North America, placed before in *Parathelypteris*, were recovered inside *Amauropelta*, corroborating previous studies in Thelypteridaceae. Our results do not support the sectional classification of *Amauropelta* based on morphological characters. We found no morphological or geographical structuring in the lineages recovered in our results, except for Asia, North America, and Africa clades. We assume that the diversification of *Amauropelta* started around 45.75 Ma from an Asian ancestor. We interpreted the migration through long-distance dispersion (LDD) from Asia to America to have occurred between 45.75–41.86 Ma. All clades inside *Amauropelta* have diverged in different periods through time ranging from the Oligocene (27.88 Ma) to the Quaternary (1.71 Ma). African species probably correspond to two distinct lineages, originating from more than one LDD event, one that diverged at around 18.93 Ma and a younger lineage that diverged at around 5.18 Ma. Despite LDD playing a role in *Amauropelta* biogeographical history, we found high contribution from local speciation (63.9% among all speciation events), while ranging expansions accounted for 27.2% and founder events to 8.9% of all speciation events. Our results reveal that the main bioregions of *Amauropelta* match four hotspots for ferns in the neotropics such as Tropical Andes, Mesoamerica, Greater Antilles, and Southeastern Brazil.

Keywords: *Amauropelta,* ferns, historical biogeography, long-distance dispersal, Neotropics, Thelypteridaceae.

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SUMMARY

CAPÍTULO ÚNICO

Across and within continents dispersal shaped the biogeographic history in the fern genus *Amauropelta*.

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Across and within continents dispersal shaped the biogeographic history in the fern genus *Amauropelta*.

Ingridy Oliveira Moura[a], Alexandre Salino[a], Wenderson F. Rodrigues[b], Luiz-Eduardo Del-Bem[a,b], Thaís Elias Almeida[c]

[a] Programa de Pós-Graduação em Biologia Vegetal, Universidade Federal de Minas Gerais, Av. Pres. Antônio Carlos, 6627 - Pampulha, Belo Horizonte - MG, 31270-901, Brazil
[b] Programa de Pós-Graduação em Bioinformática, Universidade Federal de Minas Gerais, Av. Pres. Antônio Carlos, 6627 - Pampulha, Belo Horizonte - MG, 31270-901, Brazil.
[c] Herbário HSTM/Programa de Pós-Graduação em Biodiversidade, Universidade Federal do Oeste do Pará, Rua Vera Paz, sn, Santarém, PA 68040-255, Brazil

Highlights

- Within-area speciation and long-distance dispersal (LLD) are the major forces driving the biogeographic history of *Amauropelta*.
- Central America, Mexico, Greater Antilles, Andes and Northern South America are the main source and southeastern Bolivia and Paraguay, northern Argentina, southern and southeastern Brazil are the main sink for *Amauropelta*.
- We found strong asymmetry on dispersal between bioregions.
- Seven LDD dispersals to Eastern South America (five of them in the Miocene) emphasize the mountains in Southeastern Brazil may have acted as climatically refugia for lineages.

Abstract

Amauropelta is the richest genus in the fern family Thelypteridaceae with approximately 215 species, 200 of them occurring in the Neotropics, and some in Africa, Madagascar, Indian Ocean Islands, Pacific Islands, and Sri Lanka. The monophyly of *Amauropelta* was well established in previous phylogenetic studies, but the relationships between groups and species within the genus remain to be understood. To fill this gap, we expand the sampling, including 64 species of *Amauropelta*. We also reconstructed the biogeographical history of *Amauropelta* in the light of divergence time estimates. Our dataset comprises 64 species of *Amauropelta* and 11 outgroups, with 104 newly generated sequences from six plastid genome regions, resulting in a combined data matrix composed of 89 specimens and 3013 bp. The phylogenetic inferences were obtained through maximum likelihood and Bayesian inference methods. Divergence times were estimated using BEAST, and biogeographic inferences were performed using BioGeoBEARS. Our results confirm the monophyly of *Amauropelta*. *Amauropelta beddomei* and *A. glanduligera* from Asia, and *A. nevadensis* and *A. noveboracensis* from North America, placed before in *Parathelypteris*, were recovered inside *Amauropelta*, corroborating previous studies in Thelypteridaceae. Our results do not support the sectional classification of *Amauropelta* based on morphological characters. We found no morphological or geographical structuring in the lineages recovered in our results, except for Asia, North America, and Africa clades. We assume that the diversification of *Amauropelta* started around 45.75 Ma from an Asian ancestor. We interpreted the migration through long-distance dispersion (LDD) from Asia to America to have occurred between 45.75–41.86 Ma. All clades inside *Amauropelta* have diverged in different periods through time ranging from the Oligocene (27.88 Ma) to the Quaternary (1.71 Ma). African species probably correspond to two distinct lineages, originating from more than one LDD event, one that diverged at around 18.93 Ma and a younger lineage that diverged at around 5.18 Ma. Despite LDD playing a role in *Amauropelta* biogeographical history, we found high contribution from local speciation (63.9% among all speciation events), while ranging expansions accounted for 27.2% and founder events to 8.9% of all speciation events. Our results reveal that the main bioregions of *Amauropelta* match four hotspots for ferns in the neotropics such as Tropical Andes, Mesoamerica, Greater Antilles, and Southeastern Brazil.

Keywords: *Amauropelta,* ferns, historical biogeography, long-distance dispersal, Neotropics, Thelypteridaceae.

1. Introduction

Amauropelta Kunze is the richest genus in the fern family Thelypteridaceae Ching ex Pic.Serm. with approximately 215 species (PPG I, 2016), with 200 of them occurring in the Neotropics, nine in Africa, Madagascar and Indian Ocean Islands, three in the Pacific islands, and a single one in Sri Lanka. Besides the fact *Amauropelta* was described by Kunze in 1843, for over one and a half century, species belonging to the genus were treated under other genera such as *Lastrea* Bory, *Dryopteris* Adanson, and *Thelypteris* Schimidel. *Amauropelta* lacks a recent taxonomic revision. The broadest taxonomic treatments are the early contributions by Christensen (1907, 1913, 1920). Nonetheless, there are several regional taxonomic treatments such as seen in Mexico (Smith, 1981a; 1988), Antilles, Jamaica, and Puerto Rico (Proctor, 1977; 1985; 1989), Central America (Smith, 1995a), Guatemala (Smith, 1981b), Guianas (Smith, 1993), Venezuela (Vareschi, 1969; Smith, 1995b), Ecuador (Smith, 1983), Peru (Smith, 1992), Bolivia (Smith & Kessler, 2017), Brazil (Salino et al., 2020), Argentina (Ponce, 2016), and Uruguay (Legrand, 1952).

Despite all these works, many problems to delimit species and natural groups within the genus are common. Smith (1974) proposed a sectional classification of *Amauropelta* based on morphological characters that resulted in the recognition of nine sections. However, most sections were not recovered as monophyletic in molecular phylogenetic inferences done with a broad sampling of neotropical groups (Alvarez-fuentes, 2010; Almeida et al., 2016). Smith & Kessler (2017) pointed out that *Amauropelta* is a taxonomically difficult group, with insufficiente molecular sampling, especially throughout the American tropics. Difficulties in taxonomy and morphological definition of *Amauropelta* species were also highlighted by Almeida *et al.* (2016), suggesting that this could be due to a recent diversification of the group. They highlighted that the failure to accumulate divergent morphological features could be caused by hybridization or constraints in the assembly of morphological disparity.

Previous works using plastidial DNA recovered *Amauropelta* within a clade with the paleotropical genera *Parathelypteris* (H.Ito) Ching, *Coryphopteris* Holttum, and *Metathelypteris* (H.Ito) Ching (Smith and Cranfill, 2002; He and Zhang, 2012; Almeida *et al*., 2016), namely the Amauropeltoid clade. Although *Amauropelta* has been recognized as monophyletic by some works (Smith and Cranfill, 2002; Schuettpelz and Pryer, 2007; Alvarez-fuentes, 2010; Almeida et al., 2016), He and Zhang (2012) recovered it as paraphyletic. Their phylogenetic inference was based on the single locus *rbcL* of six species of *Amauropelta*. The authors, however, did not suggest any taxonomic changes in the genus.

In addition to recognizing *Amauropelta* as monophyletic, Almeida et al. (2016) retrieved that four species of *Parathelypteris* were related to the genus. In their inference, *Parathelypteris noveboracensis* and *P. nevadensis* restricted to North America formed a clade sister to the clade composed by the Asian species, *Parathelypteris nipponica* and *P. glanduligera*. These two clades together were recovered as sister to the other species of *Amauropelta*. Although Almeida et al. (2016) have included these four species within *Amauropelta*, Salino et al. (2015) proposed 186 new combinations for the core *Amauropelta* species alone, not including *Parathelypteris* species. The same result was retrieved by Fawcett et al. (in press), using an expanded nuclear genome dataset. In another work, Fawcett & Smith (in press) recovered the previously cited *Parathelypteris* species as embedded in *Amauropelta* and proposed new combinations.

Long-distance dispersal (LDD), vicariance, and extinction are the three main processes determining the biogeographic patterns of ferns and angiosperms across the globe. A single fertile fern individual can produce millions of spores, which can be dispersed thousands of kilometers by wind currents from low to high altitudes. These spores can be very resilient and survive extreme conditions such as low temperatures and high exposure to UV radiation (Kessler, 2010). The presence of *Amauropelta* species out of the Neotropics (center of diversity), including islands that were never connected to the mainland, such as Hawaii, implies a high capacity of LDD. On the other hand, regions with high richness such as the Andes (Colombia to Bolivia), Central America, Antilles, and Southern/Southeastern Brazil experience significant rates of endemic species.

Studies that integrate dated molecular phylogenies with biogeographic analyses have been very efficient in revealing the origins of different groups of ferns, and the role of dispersal and vicariance in the diversification and geographic distribution of ferns. Biogeographic histories were reconstructed for several fern families and genera, but a specific study for *Amauropelta* is still lacking. In the main studies that included all lineages of lycophytes and ferns, the sampling of *Amauropelta* species was very low (Schuettpelz & Pryer, 2009; Testo & Sundue, 2016), highlighting the need for more data collection.

In this study, we reconstructed the first dated molecular phylogeny for *Amauropelta* based on an expanded sampling, allowing us to infer the biogeographical history of the genus.

2. Materials and methods

2.1. Taxon Sampling

Our dataset comprises 64 species (68 specimens) of *Amauropelta* and eleven outgroup species (104 newly acquired sequences) (Table S1). Outgroups were selected representing the two subfamilies of Thelypteridaceae: Thelypteridoideae and Phegopteridoideae (Almeida et al., 2016; PPG I, 2016). In the Thelypteroidoideae, five genera were sampled: *Christella*, *Coryphopteris*, *Cyclosorus*, *Metathelypteris*, and *Thelypteris*. In the Phegopteroidoideae, three genera were sampled: *Macrothelypteris*, *Phegopteris,* and *Pseudophegopteris*. The samples were stored in silica gel and vouchers were incorporated at BHCB and HUA (acronyms according to Thiers, 2021). Vouchers and GenBank accessions are listed in Table S1 and the aligned data matrix was deposited in TreeBASE (link).

2.2. DNA extraction, amplification, and sequencing

Total genomic DNA was obtained from field-collected silica gel-dried tissue or fresh tissue. Extractions were made using Qiagen DNeasy Plant mini kit (QIAGEN Inc., Valencia, CA, USA) according to the manufacturer’s instructions. PCR was performed for six loci of the chloroplast genome: *rbc*L (*rbc*L gene); *rps*4–*trn*S (*rps*4 gene; *rps*4-*trn*S intergenic spacer); and *trn*L–*trn*F (*trn*L gene; *trn*L-*trn*F IGS; *trn*F gene). Amplifications were done in single reactions with primers ESRBCL1F and ESRBCL1361R (Korall et al., 2006) for *rbc*L, rps5F (Nadot et al., 1995) and trnSR (Smith and Cranfill, 2002) for *rps*4–*trn*S, and FERN1 and TRNTFF (Trewick et al., 2002) for *trn*L–*trn*F. PCR was done in 20 µL solutions, containing 1.0 µL of genomic DNA template, 2.0 µL of PCR buffer (Qiagen 10x PCR Buffer), 0.4 µL of dNTPs (10 mM), 0.3 µL (10 µM) of each primer, 1.0 µL of BSA (5 mg/mL), 0.12 U of Taq DNA polymerase (Qiagen, 5 U/µL) and 15.88 µL of ultrapure deionized water. Thermal cycling conditions were the same for all three regions: 5 min at 94°C, 35 cycles of 45 s at 94°C, 60 s at 53°C and 90 s at 72°C, followed by 5 min at 72°C. The amplicons were purified using EDTA 125 mM and absolute ethanol and resuspended in ultrapure deionized water. The samples were sequenced in both directions by Macrogen (Seoul, South Korea) using an ABI 3730xl DNA Analyzer.

2.3. Alignment

The electropherograms were edited using Geneious version R11 (http://www.geneious.com, (Kearse et al., 2012)). Consensus sequences were aligned with MUSCLE (Edgar, 2004), and the alignments were manually adjusted using MEGA X (Kumar et al., 2018).

2.4. Phylogenetic Inferences

Phylogenetic inferences were obtained by maximum likelihood (ML) and Bayesian inference (BI). To choose the right partitioning scheme and reduce false-positive ultrafast bootstrapping support (Hoang et al., 2018) (i.e. wrong branch receiving 100% support), the best partition schemes were selected by Partition Model (Chernomor et al., 2016) according to the principles of Gadagkar et al. (2005) (Table 1). Best substitution models for each partition were selected by ModelFinder (Kalyaanamoorthy et al., 2017) using the Bayesian Information Criterion (Schwarz, 1978) (Table 1). GenBank sequences of *Phegopteris decursive-pinnata* were used as outgroup for ML and BI analyses. We used IQTREE (Nguyen et al., 2015) to infer the maximum likelihood tree with branch support calculated by ultrafast bootstrap approximation with 1000 pseudoreplicates (Hoang et al., 2018) (Fig. S1). For BI, we performed a model-based Markov chain Montecarlo phylogenetic analysis using MrBayes v3.2.6 (Ronquist et al., 2012) through Cipres Science Gateway (Miller et al., 2010) with two independent runs with four chains performing 5×10^7 generations, sampling one tree every 1000 generations. We discarded 10% (5,000,000) of the first trees generated as burn-in and the remaining were used to assess topology and posterior probabilities (PP) in a majority-rule consensus (Fig. S2). The convergence of the runs was evaluated by checking the *ESS* (effective sample size) and *PSRF* (potential scale reduction factor) parameters (Ronquist et al., 2012) using Tracer v.1.7 (Rambaut et al., 2018). Results were summarized on a consensus tree (Fig. 1).

2.5. Divergence Times Estimations

Divergence times were estimated with the software BEAST 2.5 (Bouckaert et al., 2019) through the CIPRES Science Gateway (Miller et al., 2010). The matrix partitions and best substitution models for each partition were used as previously selected by ModelFinder. We used GTR for partition1 (rbcL + rps4 gene) and HKY for partition 2 (rps4 IGS + trnL-F). The trees and clock models were linked. In the absence of reliable fossils of *Amauropelta,* we used divergence dates estimates from Testo and Sundue (2016). Calibration nodes and ages were defined as follows: phegopteroid clade = 56.96 Mya; amauropeltoid clade = 52.62 Mya; cyclosoroid clade = 35.54 Mya. We used an uncorrelated log-normal relaxed clock, and the Yule Model tree prior, with the birth rate set for 1.0. Normal distribution was assigned for all calibrated nodes. All priors and parameters were set using BEAUti (Drummond et al., 2012). Two Markov chain Montecarlo runs were conducted using 10^9 generations with parameters sampled every 10,000 steps. We analyzed both independent runs to confirm the convergence and if ESSs were sufficient for all parameters using Tracer 1.7 (Rambaut et al., 2018). Trees were summarized and annotated with median ages estimates and 95% highest posterior density (HPD) using TreeAnnotator in BEAST2 (Bouckaert et al., 2019), discarding 10% of trees as burn-in. A maximum clade credibility tree was generated based on the remaining 9.001 trees (Fig. S3) and this topology was used in the subsequent biogeographical analyses.

2.6. Biogeographic Inferences

We downloaded and curated more than 24.000 occurrence records of *Amauropelta* from The Global Biodiversity Information Facility (GBIF, DOI: 10.15468/dl.fx84f4, DOI: 10.15468/dl.ph9xtn), SpeciesLink (https://splink.cria.org.br), and Reflora (http://reflora.jbrj.gov.br/reflora/herbarioVirtual/ConsultaPublicoHVUC/ConsultaPublicoHVUC.do) (Supp. Mat. 2). We checked the data for geographic and taxonomic errors, leaving only species represented in our phylogenetic hypothesis, resulting in a matrix with more than 9700 occurrence records (Supp. Mat. 2). We use it as an input for defining the bioregions through the web application Infomap bioregions (Edler et al., 2017) (Figure S4). We adapted the Infomap output, with ten defined bioregions: bioregion A (part of Bolivia +southeastern Paraguay+northern Argentina+southern and southeastern Brazil); bioregion B (Central America+Mexico); bioregion C (Africa + Madagascar); bioregion D (Pacific Islands), bioregion E (Greater Antilles); bioregion F (Western USA); bioregion G (Eastern USA); bioregion H (Lesser Antilles), bioregion I (Eastern Asia+Malesia); and bioregion J (Andes+Northern South America) (Fig. 2, Fig. S4). To infer the Biogeography history we used the R package BioGeoBEARS (Biogeography with Bayesian Evolutionary Analysis in R Scripts) (Matzke, 2013) in R version 4.1.0 through RStudio v. 1.4.1106 (R Core Team 2018). We tested three analyses implemented on BioGeoBEARS: DEC – dispersal-extinction-cladogenesis (Ree & Smith, 2008); DIVA - dispersal-vicariance analysis (Ronquist, 1997) referred to as DIVALIKE; and BayArea – Bayesian inference for discrete areas (Landis et al., 2013) referred to as BAYAREALIKE. Additionally, we performed more three analyses implementing the additional free parameter j (DEC+j, DIVALIKE+j, BAYAREALIKE+j), which takes into account events of colonization of a daughter lineage out of the ancestral range areas (Matzke, 2014). We then compared the six models tested using the Akaike information criterion (AIC) implemented in BioGeoBEARS and selected the best model. We also estimated the number and mode of biogeographical events implemented in BiogeoBEARS using Biogeographical Stochastic Mapping (BSM) (Dupin et al., 2016; Matzke, 2016) (Table 3; Fig. 4). Event frequencies were inferred based on the mean and standard deviation values from 100 BSMs.

3. Results

3.1. Phylogenetic Relationships

We obtained a combined data matrix including 89 specimens and 3,013 bp**.** In the base of the tree within the Amauropeltoid clade (Almeida et al., 2016) *Coryphopteris petelotii*, *C. japonica*, and *C. seemannii* formed a clade (PP=1.00; BS= 100%). *Metathelypteris hattorii* and *M. singalanensis* appeared as sister to *Amauropelta* (PP=0,97; BS=79%), which is recovered as monophyletic in both analyses (Fig. 1). The topologies inferred by the BI and ML analyses were similar, except for the position of the North American species, *Amauropelta nevadensis* and *A. noveboracensis*. Although they were recovered as a clade with high support in both analyses (PP=1.00; BS=100%), in the Bayesian inference they appeared sister of a clade (PP=1.00) formed by *A. glanduligera* and *A. beddomei* (PP=1.00; BS=100%), that is, in turn, sister of the remaining *Amauropelta* species (PP=1.00). In the ML inference, and also in the divergence time estimates and the subsequently biogeographical analyses, the Asia clade (*A. glanduligera*+*A. beddomei*) is sister to the North America clade (BS=100%), which is sister of the remaining species of the genus (BS=86%). Subsequently, *A. recumbens*, *A. thomsonii*, and *A. scalaris* formed a clade sister to the remaining species (PP=1.00; BS=97%). The Balbisii clade (PP=0.79; BS=88%) includes species with wide distribution like *A. opposita* and some endemics like *A. eriosorus and A. juergensii* from south and southeast Brazil. The endemic

Hawaiian species of the genus, *A. globulifera*, appeared as sister to the other species of *Amauropelta* (PP=0.81; BS=96%) (Fig. 1). In the Bayesian inference, *A. decurtata* is sister of the remaining species of *Amauropelta* (PP=0.97) (Fig. S2), although in ML it appears in a polytomy with the Firma clade and a big clade with the remainder of the species (Fig. S1). The Firma clade (PP=1.00; BS=99%) is composed of two sister species endemic to the Greater Antilles (Fig. 1). The Oligocarpa clade (PP=1.00, BS=99%) in both analyses is composed of the same species (*A. araucariensis, A. burkartii, A. raddii, A. retusa, A. amambayensis, A. soridepressa, A. regnelliana, A. patula, A. rivularioides*, *A. oligocarpa*, and *A. pilosula*) (Fig. 1; Fig. S1 & 3). In the ML tree, however, *A. pilosula* from Panama (Table S1) is in a polytomy with a subclade formed by *A. pilosula* from Ecuador plus all five specimens of *A. oligocarpa* and another subclade that includes the remaining species of the Oligocarpa clade (Fig. S1). In the BI tree, all specimens of *A. pilosula* and all *A. oligocarpa* specimens form a subclade (PP=0.56), sister of another subclade with the remaining species of the Oligocarpa clade (Fig. S2). *Amauropelta oppositiformis* appears sister to a clade (PP=1.00; BS=99%) formed by the other African species: *A. heteroptera, A. tomentosa, A. salazica, A. bergiana*, and *A. strigosa* and also of a clade (PP=0.98) with the remaining species of the genus. In ML, *A. oppositiformis* is in a polytomy (BS=99%) with the Africa clade and a clade composed of the remaining species of *Amauropelta.* In the next node, there is a clade (PP=0.98; BS=74%) including three remaining clades: the Heteroclita, the Germaniana, and the Steyermarkii clade (Fig. 1). These clades are in a polytomy in both ML and BI inferences, although in the BI, the Germaniana clade is recovered as sister of the Steyermarkii clade with very low support (PP=0.22) (Fig. 1; Fig. S1 & 3). The Heteroclita clade (PP=0.61; BS=79%) includes *A. longicaulis* (from the Andes), *A. atrovirens,* and *A. gracilis* (from Central America and Southern North America), *A. heteroclita* (from Greater and the Lesser Antilles) (Fig. 1). The Germaniana clade (PP=0.78; BS=71%) is composed of *A. germaniana, A. inabonensis,* and *A. linkiana* (Fig. 1). The Steyermarkii clade nest species endemic from the Andes: *A. brausei, A. corazonensis, A. euchlora, A. steyermarkii*, and *A. supina*; endemics from southern and southeastern Brazil: *A. saxicola* and *A. ptarmica*, and species more widely distributed like *A. rudis* (Fig. 1). Some species for which we included more than one specimen were not recovered as monophyletic lineages, such as *A. linkiana* and *A. rudis.*

3.2. Divergence Time Estimates

The origin of *Amauropelta* was marked by the separation between the clade composed by *Amauropelta*, *Coryphopteris*, and *Metathelypteris* at about 52.65 Mya (95% highest posterior density interval (HPD) 38.87–51.85 Mya) (Fig. S3). The first divergence within *Amauropelta* separating the Asia clade from the remaining living clades was estimated to have occurred around 45.75 Mya (95% HPD 38.87–51.85 Mya). The North America clade diverged from the rest of the lineage around 41.86 Mya (95% HPD 33.71–48.56 Mya), while the divergence of the Scalaris clade was estimated to have occurred at 37.24 Mya (95% HPD 29.18–44.66 Mya). The divergence of the Balbisii clade was estimated at 30.52 Mya (95% HPD 22.86–28.63 Mya) (Fig. S3). *Amauropelta globulifera* was estimated to have diverged around 28.26 Mya (95% HPD 20.19–35.94 Mya). We do not present the dates from the polytomy including *A. decurtata*, Firma clade and a clade with the remainder species of the genus, to accommodate the results recovered in both BI and ML. The Oligocarpa clade diverged around 24.58 Mya (95% HPD 16.99–30.55 Mya). The analysis recovered *A. oppositiformis* in a clade with the other African species even though in both ML and Bayesian, *A. oppositiformis* was not recovered in Africa clade (Fig. 3, S1). The Africa clade was estimated to have diverged around 21.17 Ma (95% HPD 14.42-28.19 Mya). The divergence of the clade encompassing the Heteroclita + Germaniana from the Steyermarkii clade was estimated to have occurred at 19.11 Ma (95% HPD 13.00–25.64 Mya). The divergence of the Heteroclita from the Germaniana clade was estimated to have occurred at 18.86 Mya (95% HPD 11.99–24.33 Mya) (Fig. S3).

3.3. Biogeographical Analyses

According to the AIC, BAYAREALIKE+j was the best fitting model (LnL=−266.3; AIC=538.6), followed by BAYAREALIKE (LnL=−284.1; AIC=572.3) and DEC (LnL=−365.4 AIC=734.7) (Table 2). The model was inconclusive inferring the ancestral area for the amauropeltoid clade. Central America+Mexico, Greater Antilles, Eastern Asia+Malesia, and Andes+Northern South America (bioregions B, E, I, and J; Fig. 2–3) were suggested as possible ancestral areas. However, considering that the other amauropeltoid genera, *Coryphopteris* and *Metathelypteris*, are paleotropical, as is one of the clades in the first divergence inside *Amauropelta* (Asia Clade), we assume that the most likely hypothesis is for the last common ancestor of *Amauropelta* to have occurred in Asia. Inside *Amauropelta*, there are two distinct lineages, one formed by the Asian species (*A. beddomei* and *A. glanduligera*) restricted to Asia+Malesia, and another composed by the remaining species of the genus, geographically present in one or more of the remaining bioregions but not in bioregion I (Fig. 2–3). Using a security range of time, we interpreted the migration through long-distance dispersion (LDD) from Asia to America to have occurred between 45.75 and 41.86 Mya.

The majority of the backbone nodes in *Amauropelta* had their possible areas inconclusively recovered as Central America+Mexico (bioregion B), Greater Antilles (bioregion E), and Andes+Northern South America (bioregion J) (Fig. 3). Some LDD events could be observed from one of the previously listed areas, and the BSM results confirm they are probably the main source for all remaining bioregions, in terms of dispersal. Asymmetrically, together they are responsible for 63.4% (27.7) of the total (43.6) of dispersal events counts, while these three bioregions together respond for 23.6% of the recorded dispersal events (10.3) from the remaining areas. (Table 3; Fig. 4; Fig. 5). The main sink to where those dispersals have occurred is the region including part of Bolivia+southeastern Paraguay+northern Argentina+southern and southeastern Brazil (bioregion A) with 23.1% (10.1), while this region was listed as source for only 7.57% of the events (3.31) (Table 3; Fig. 4; Fig. 5). The second main sink is the Lesser Antilles (bioregion H) with 17.4% (7.61), while being the source of 6.91% of the events (3.02) (Table 3; Fig. 4). The Andes+Northern South America were also pointed as a sink, with 10.1% (4.43) while being the source 21.16% (9.31) among the total 43.68 recovered dispersal events.

The main LDD events observed occurred from Central America+Mexico (bioregion B), Greater Antilles (bioregion E), or Andes+Northern South America (bioregion J) to North America (bioregion F) ca. 41.86 Mya, Hawaii (bioregion D) around 28.26 Mya, Africa (bioregion C) approximately 18.93 Mya, and six times to the region including part of Bolivia+southeastern Paraguay+northern Argentina+southern and southeastern Brazil (bioregion A), estimated to have occurred at 25.21 Mya, 20.74 Mya, 18.45 Ma, 13.68 Mya, 11.72 Mya, and 5.4 Mya.

The total number of dispersal events (43.6) were divided in two categories: range expansion events and founder events (Table 3). Range expansions corresponded to 27.2% (32.9) of dispersal events, being more than three-fold more common than founder events with 8.89% (10.7) (Table 3). In both categories, the probable ancestral areas recovered were composed of Central America+Mexico (bioregion B), Greater Antilles (bioregion E), and Andes+Northern South America (bioregion J) as the main sources. Those bioregions are responsible for 59.15% (19.4) of range expansion dispersal events, and for 76.55% (8.2) of founder events (Fig. 4).

Sink bioregions differed regarding the two main categories of dispersal events (Fig. 4). Regarding range expansion, the main sink was the Greater Antilles (bioregion H), followed by the region formed by part of Bolivia+southeastern Paraguay+northern Argentina+southern and southeastern Brazil (bioregion A), with 21.74% (7.16) and 18.3% (6.0) of range expansion events, respectively. Among the founder events, the main sink was the region formed by part of Bolivia+southeastern Paraguay+northern Argentina+southern and southeastern Brazil (bioregion A) followed by the region composed by Asia+Malesia (bioregion I), with 37.86% (4.0) and 13.11% (1.4), respectively.

In addition to the total of 43.6 (36.11%) dispersal events, the BSM estimated 77.2 (63.89%) for within area speciation, totaling 120.9 diversification events in the biogeographical history of *Amauropelta*.

4. Discussion

We expanded the sampling in *Amauropelta* from 25 to 64 species compared to Almeida et al. (2016). The monophyly of *Amauropelta* (PP=1.00; BS=100%) was recovered and this result corroborates previous phylogenetic studies in Thelypteridaceae based on chloroplast DNA data (Smith and Cranfill, 2002; Almeida et al., 2016), and also an unpublished study based in nuclear genes (Fawcett et al., in press). *Amauropelta beddomei* and *A. glanduligera* from Asia, and *A. nevadensis* and *A. noveboracensis* from North America, placed before in *Parathelypteris*, were recovered inside *Amauropelta,* corroborating the results of Fawcett et al. (in press) and Fawcett and Smith (in press). There are no morphological or geographical patterns (except in the Asia, North America, and Africa clades) in the lineages recovered in our results.

Our results do not fit the sectional classification of *Amauropelta* based on morphological characters proposed by Smith (1974; Table 4). The nine sections were circumscribed by a combination of characters as rhizome habit, blade shape, trichomes, buds, indusia, aerophores, and scales (Smith, 1974). Some of these characters seem to be homoplastic, making it difficult to classify the *Amauropelta* species based just on macromorphology. Smith (1974) recognized there is no uniformity among some morphological characters. For example, in *A.* sect. *Adenophyllum*, the author stated that the rhizomes could vary from creeping to erect (Smith, 1974). The author recognized three different groups inside A. A. sect. *Adenophyllum* based on the rhizome and/or geographic distribution (Smith, 1974). Here, we sampled five species belonging to this section and they were recovered as belonging to different clades: *Amauropelta rivularioides* (Oligocarpa clade), *A. glandulosolanosa* (Balbisii clade), and *A. juergensii* (Balbisii clade) with long-creeping rhizomes, and *A. burkartii* (Oligocarpa clade) and *A. pilosula* (Oligocarpa clade) with erect rhizomes (Table S2).

The presence of uncinate trichomes was used as one of the diagnose characters for the *A.* sect. *Uncinella*. Through the evolution of *Amauropelta*, this feature seems to have appeared independently several times. Representatives of the A. A. sect. *Uncinella*, as *A. amambayensis*, *A. recumbens*, and *A. saxicola*, belongs to three different clades: Oligocarpa, Scalaris, and Steyermarkii clade, respectively (Fig. 1; Table S2). Another example of morphological convergence is the two bipinnate-pinnatifid species *A. patula* and *A. pteroidea.* Smith (1974) classified both species in *A.* sect. *Lepidoneuron* and cited this characteristic as a trend in this section. However, in our analyses they were not recovered as closely related, instead belonging to different clades. *A. patula* was recovered in the Oligocarpa clade and *A. pteroidea* in the Steyermarkii clade, showing that frond dissection is likely convergent (Fig. 1; Table S2).

In the Steyermarkii clade, only *Amauropelta saxicola* and *A. ptarmica* are endemic from the region composed by part of Bolivia+southeastern Paraguay+northern Argentina+southern and southeastern Brazil (bioregion A). These species are strongly misidentified because they share the same ecological niche and some morphological characters. Both are usually found in mountainous regions on rocks along the streams. According to our divergence time inference (Fig. S3), they have diverged less than 1.5 Mya, but it is unclear if they are truly distinct species. They are differentiated by the presence of indusia and setiform trichomes in *A. ptarmica* while in *A. saxicola* the indusia are absent and the trichomes are uncinate. We assume that there are no functional differences between setiform and uncinate trichomes and in this particular case, they are in fact very similar except for a fold at the tip of the uncinate trichomes. Many species in *Amauropelta* could present or not indusia without probably affecting their reproducibility. The morphological differences between them could be due to phenotypic plasticity or they can correspond to populations of the same species under selective pressures in an incipient speciation process.

Smith (1974) classified *A. bergiana* as belonging to the A. sect. *Uncinella*. The other African species were not cited in that classification, but using his key to the sections, *A. oppositiformis* belongs to A. sect. *Amauropelta* and *A. tomentosa*, *A. salazica*, *A. strigosa*, and *A. heteroptera* did not fit in any of the sections. We recovered that part of the African species form a clade (Fig. 2) but according to Smith (1974) they would belong to different sections (Table S2). According to our results, it is likely that none of the nine sections defined using morphological characters (Smith, 1974) are natural, with most species inside any section belonging to at least two different clades (Table S2).

All clades recovered and described here presented high support values in both ML and BI analyses (Fig. 1). Some supposedly conspecific specimens from different regions were nested in distinct natural groups, such as *A. rudis* and *A. linkiana*. *Amauropelta rudis* from Colombia was placed into the Balbisii clade while the specimens from Panama and Cuba were placed in the Steyermarkii clade. *Amauropelta linkiana* from the Dominican Republican is nested in the Germaniana clade while the specimen from Panama was recovered in the Steyermarkii clade. Those conflicted positionings could be explained by misidentified specimens from sequences acquired from Genbank (Table S1). Another possible explanation is that these non-monophyletic species are ill-circumscribed, and/or that the observed relationships reflect hybridization or introgression processes. The reticulation process was also documented within other genera of Thelypteridaceae (Bloesch *et al*., in prep). The other two species commonly misidentified are *Amauropelta oligocarpa* and *A. raddii*, due to their morphological similarity. Smith (1974) classified them together in *A.* sect. *Uncinella* (Table S2) but we recovered that each species is placed in different lineages within the Oligocarpa clade (Fig. 1). The specimens of the widely distributed *Amauropelta oligocarpa* (Bioregions A+B+E+H+J) are sister of *A. pilosula* (Bioregions B+E+J) that have diverged at around 16.71 Mya. *Amauropelta raddii* and its sister species have diverged at around 9.92 Ma and are endemic to the region including part of Bolivia+southeastern Paraguay+northern Argentina+southern and southeastern Brazil (with the exception of *A. rivularioides* that occurs also in Andes+Northern South America) (Fig. S3). Maybe the morphological characteristics shared between *A. oligocarpa* and *A. raddii* were present in the ancestral of the Oligocarpa clade and were kept in these species and lost in the remaining species of the clade or it might be another example of morphological convergence within the genus.

All clades inside *Amauropelta* have diverged in different periods through the Oligocene to the Quaternary (Fig. S3). The oldest is the Balbisii clade that diverged in the Late Oligocene at around 27.88 Mya. Even though the Balbisii clade diverged early in the history of the genus, some of its species are very recent. The clade composed of *A. tamandarei*, *A. eriosorus*, and *A. juergensii*, all endemic to the region composed of part of Bolivia+southeastern Paraguay+northern Argentina+southern and southeastern Brazil (bioregion A), have emerged at around 3.06 Mya (Fig. S3). The ancestral area inferred for these species was inconclusive, indicated as either Greater Antilles (bioregion E) or Andes+Northern South America (bioregion J). Although we do not know for sure their ancestral area, we can say that this is a long-distance dispersal event from bioregion E or bioregion J to bioregion A. This hypothesis is supported by the high percentage of fern species (approximately 20%) shared between Greater Antilles (Bioregion E) and southeastern Brazil (part of Bioregion A), and the ca. 18% of fern species are shared between the Andes and southeastern Brazil (Suissa and Sundue, 2020). We have recovered another six LDD events to bioregion A in our analysis (Fig. 2), indicating a strong migration direction in the lineage eastern and southeastern wards

In both ML and BI, the african *A. oppositiformis* was placed with high support outside of the Africa clade, as sister of the remaining species of *Amauropelta* (Fig. 1), a result in conflict with what was recovered in the divergence time estimate tree, where all African species formed a clade. Within that clade, two distinct lineages were recovered: *A. oppositiformis* that have diverged at around 18.93 Mya, sister to a younger lineage diverged ca. 5.18 Mya, named here Africa clade to account for the incongruence among the analyses (Fig. 1). The hypothesis that African *Amauropelta* does not form a monophyletic group (Fig. S1; Fig. S2 our ML and BI) is also supported by the topology recovered by Fawcett *et al.* (in press), indicating that they probably originated from more than one across-continents LDD events.

The result from 100 BSMs recovered the bioregions B+E+J as the more frequent sources, and bioregion A as the principal sink among the total dispersal events (range expansion and founder events) (Fig. 4; Fig. 5). These bioregions (A, B, E, and J) correspond in part to four (out of the six) hotspots of fern diversity in the Neotropics, indicated by Suissa & Sundue (2020): Tropical Andes (part of bioregion J), Greater Antilles (Bioregion E), and Mesoamerica (part of bioregion B) are the regions with highest levels of endemism, followed by Southeastern Brazil (part of bioregion A) (Suissa and Sundue, 2020). The Andes cycles of uplift have led to the emergence of new habitats as well as in the young mountain ranges in the Greater Antilles (bioregion E), and Mesoamerica (part of bioregion B) (Dengo et al., 1970; Khudoley and Meyerhoff, 1971; Gregory-Woodicki, 2000; Garzione et al., 2008; Janzen, 2018). The association of climatic and seasonal conditions within tropical mountains could lead to decreased gene flow, dispersal and range sizes of the populations and favoring ecological speciation (Haufler et al., 2000). That could explain the high value of within-area speciation in *Amauropelta* (63.9% of the speciation events), recovered as the major force driving the evolution and biogeographical history of *Amauropelta* (Table 3).

A strong positive relationship between niche heterogeneity and speciation rates was found by Suissa and Sundue (2020) in all neotropical hotspots, with the exception of Southeastern Brazil (part of bioregion A). Different from the other hotspots, the distribution pattern of fern species in that region was found to be shaped by a combination of migration and the presence of relictual endemic species (Suissa and Sundue, 2020). We recovered seven LDD events to the region composed of part of Bolivia+southeastern Paraguay+northern Argentina+southern and southeastern Brazil (bioregion A) (Fig. 2). Five of those LDD events happened during the Miocene (23.03-5.33 Mya), concomitantly with periods of cycles of climatic drying and cooling, when the mountains in Southeastern Brazil may have acted as climatically refugia for lineages, as suggested in studies with other vascular plants such as Gesneriaceae (Suissa and Sundue, 2020; Perret et al., 2013). In fact, three among those LDD events gave rise to endemic lineages of *Amauropelta* in bioregion A (Fig. 3).

Dispersal (range expansion and founder events) is responsible for 36.1% of the speciation events in *Amauropelta* (Table 3). Beyond the within-continent LDD described previously, the high dispersal capacity of *Amauropelta* can be further exemplified by the across-continent LDD. The colonization of oceanic volcanic islands like Hawaii, which have never been connected to the mainland, and also the colonization of other continents, such as Africa, are good examples. However, range expansion events were three times more frequent than founder events, corroborating that LDD, despite being rarer (Kessler, 2010), was decisive for the evolution and diversification, and further establishment of biogeographic patterns in *Amauropelta*.

Dispersal events play a fundamental role in defining the distribution patterns of species in the Southern Hemisphere (Sanmartín et al., 2007). We observed asymmetry on dispersal movements in *Amauropelta* (Fig. 4; Fig. 5), a similar trend that was registered for different groups of plants in geographically distinct areas (Sanmartín et al., 2007; Sniderman and Jordan, 2011; Richardson et al., 2012; Crayn et al., 2015). Dispersion events from the Andes (bioregion J) to the region including part of Bolivia+southeastern Paraguay+northern Argentina+southern and southeastern Brazil (bioregion A) are more than twice more frequent than the opposite. The dispersion rates from the region including part of Bolivia+southeastern Paraguay+northern Argentina+southern and southeastern Brazil (bioregion A) to the Greater Antilles (Bioregion E) are ten times less frequent than the opposite flow (Fig. 4; Fig. 5). Other examples of asymmetric dispersal were observed and described in the results (Fig. 4). Despite the high dispersal capacity of *Amauropelta* spores, the establishment of lineages in certain regions are more related to factors such as competition, availability of niches, altitude, and temperature, than to the ability of the spores to reach such locations. This might help explain patterns of asymmetrical dispersal, because even if spores are exchanged equally between two locations, the ability of such spores to thrive might be different depending on which is the source and the sink. Not much is known about mechanisms involved in the dispersal processes of plants, making it difficult to establish a simple causal explanation between dispersal movements and the biogeographic history of a group. (Sanmartín et al., 2007).

5. Conclusion

Our results indicate that *Amauropelta* is monophyletic, in accordance with some of previous literature (Smith and Cranfill, 2002; Schuettpelz and Pryer, 2007; Alvarez-fuentes, 2010; Almeida et al., 2016), and likely originated in Asia. The genus migrated to the neotropics, where it led to the emergence of a center of diversification, in the Middle Eocene (time frame here). The diversification of *Amauropelta* likely happened through the Oligocene to the Quaternary. We did not find any support for morphological or geographical structuring in the recovered clades, suggesting that morphological traits might have evolved or been lost multiple times independently. LDD within or between continents was determinant to shape the distribution pattern and evolutionary history of the genus, with within-area speciation being the major evolutionary mechanism driving the diversification and biogeographical history of *Amauropelta*.

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Table 1

Number of taxa, alignment length, number of informative and invariant sites, and nucleotide substitution models selected for each partition used in this study.

Partition	Nº of taxa	Length	Informative sites	Invariant sites	Selected model-Bayesian Inference	Selected model-Maximum Likelihood
rbcL+rps4 gene	88	1763	188	1376	K80+I+G	K2P+I+G4
rps4 IGS+trnL-trnF intron and IGS	87	1250	404	633	HKY+F+G4	HKY+F+G4
Combined	89	3013	592	2009	-	-

Table 2

Comparative statistics among biogeographic models tested. LnL = log-likelihood; d = dispersal rate; e = extinction rate; j = founder-event speciation, AIC = Akaike Information Criterion; DEC = Dispersal Extinction Cladogenesis model; DIVALIKE = BioGeoBEARS implementation of the DIVA model; BAYAREALIKE = BioGeoBEARS implementation of the BayArea model.

Model	Nº Free Parameters	LnL	d	e	j	AIC
DEC	2	-365.35	0.0064	1.00e−12	0	734.84
DEC+J	3	-364.88	0.0063	1.00e−12	0.0046	736.06
DIVALIKE	2	-377.35	0.0073	1.00e−12	0	758.85
DIVALIKE+J	3	-377.32	0.0073	1.00e−12	0.0008	760.93
BAYAREALIKE	2	-284.13	0.0019	0.02	0	572.40
BAYAREALIKE+J	3	-266.29	0.0013	0.01	0.0095	538.87

Table 3

Summary of biogeographical stochastic mapping counts for *Amauropelta* using the BAYAREALIKE+j model. Mean numbers for the different types of events estimated are shown here along with standard deviations in parenthesis.

Mode	Type	Mean (SD)	%
Within-area speciation	Speciation	77.25 (1.45)	63.89
Dispersal	Founder events	10.75 (1.45)	8.89
	Range expansions	32.93 (4.59)	27.23
Total		120.9 (4.59)	100

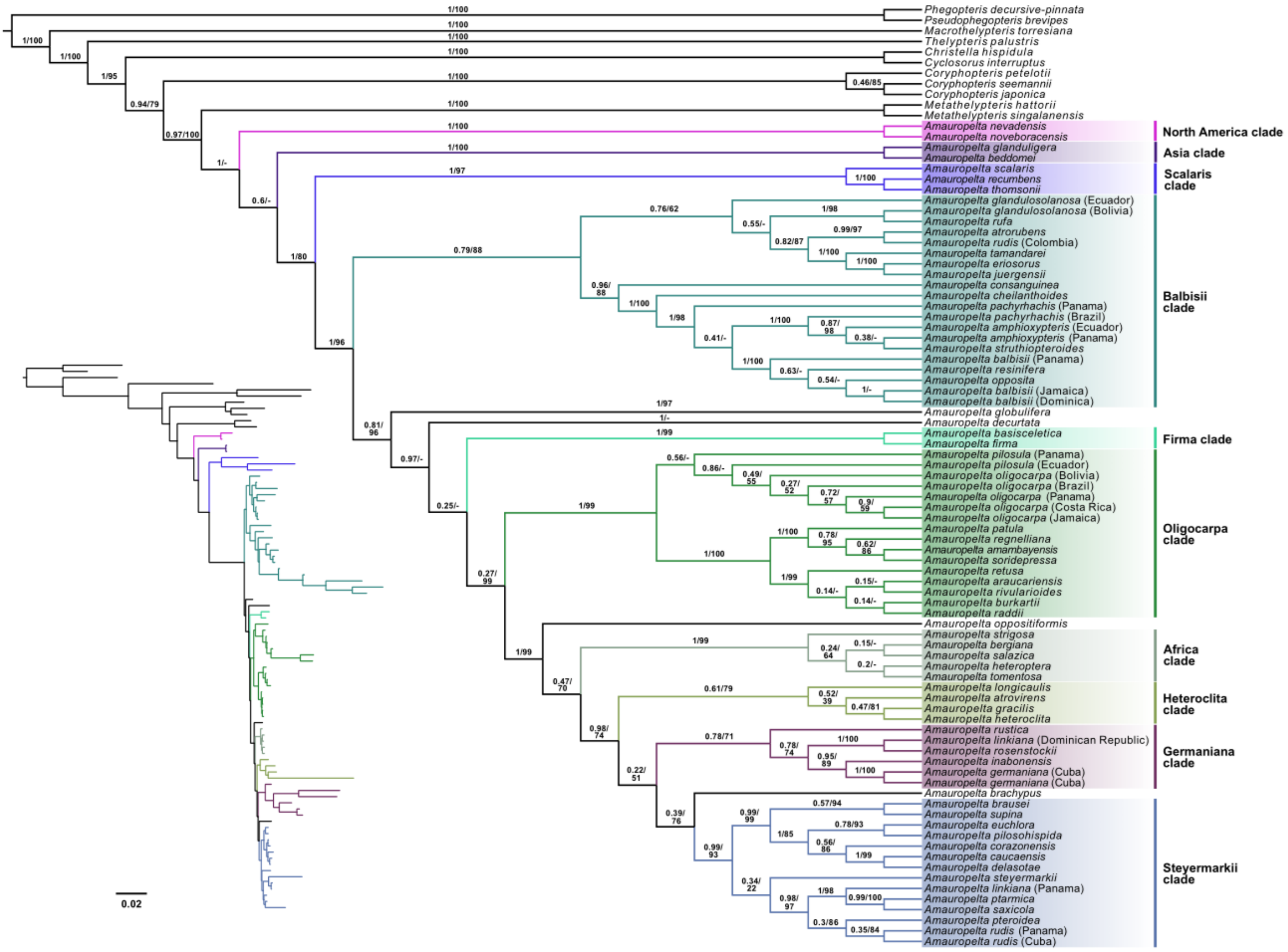


Fig. 1. Majority-rule consensus cladogram and phylogram from Bayesian Inference based on the combined dataset using *rbc*L, *rps*4-trnS, and *trn*L-*trn*F sequences. Values above branches represent Bayesian posterior probabilities and ultrafast bootstrap from the Maximum Likelihood analysis, respectively. Clades recovered in both Bayesian and Maximum Likelihood analysis were nominated and colored in the right side of the tree. The phylogram (lower-left) shows the genetic distances between the terminals.

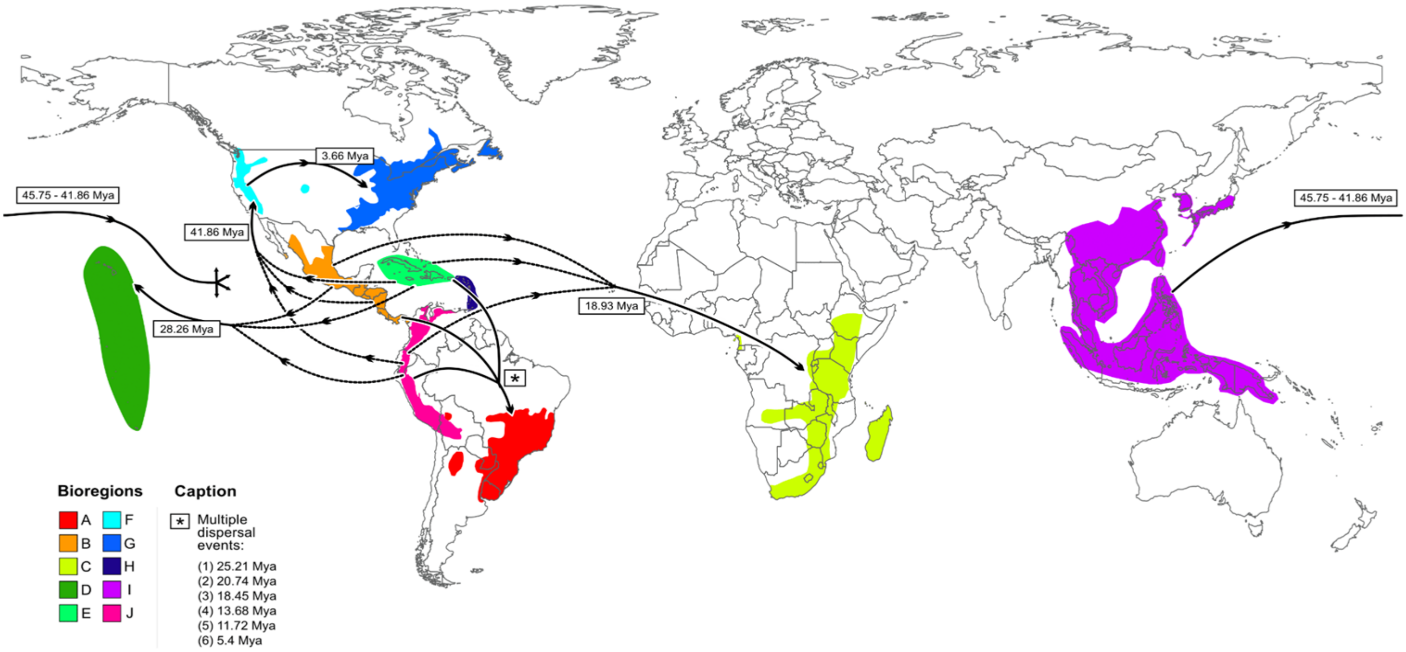


Fig. 2. Long-distance dispersal events inferred in the biogeographical history of *Amauropelta*. The dotted lines indicate undefined origin, while solid lines indicate high confidence of origin and/or destination. The color scheme reflects the different bioregions. The multiple headed arrow between Asia and the Americas represents the geographical uncertainty of initial colonization in the Americas.

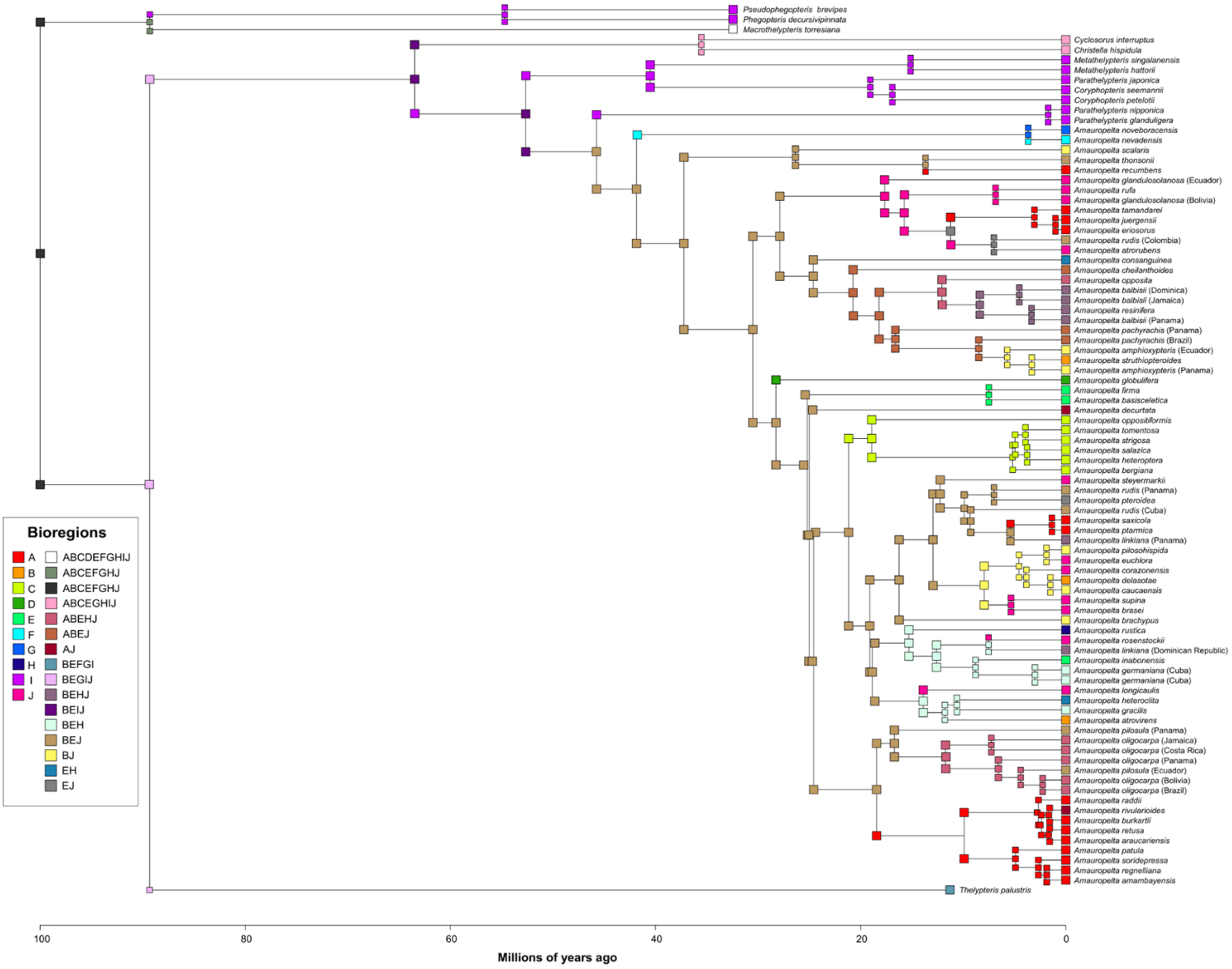
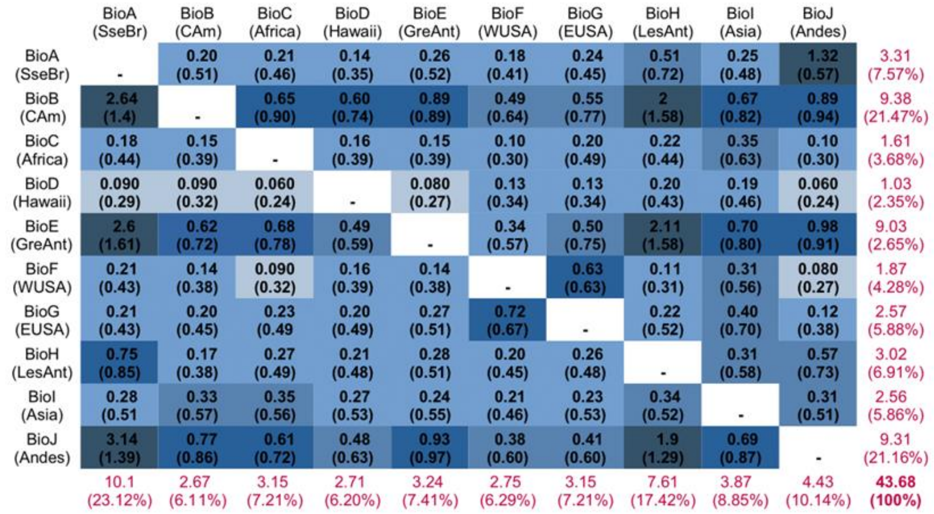


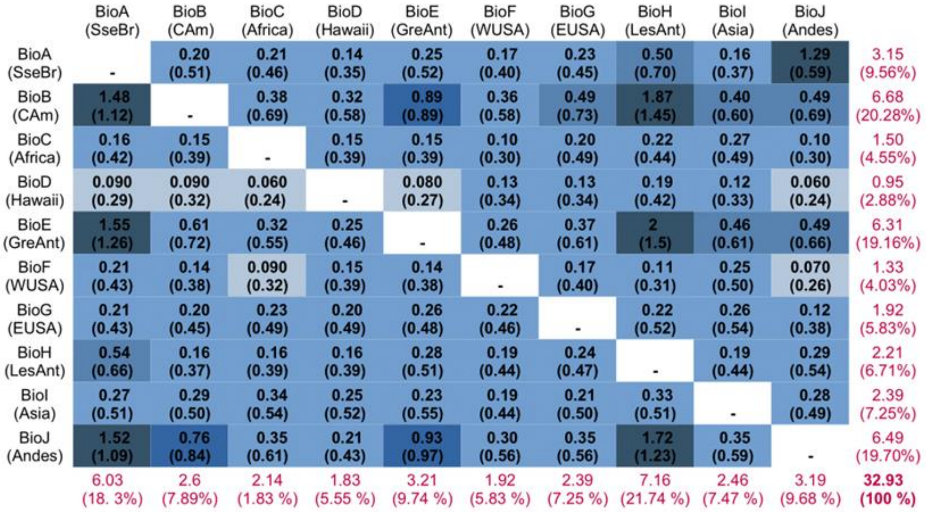
Fig. 3. Divergence time estimation tree resulting from the BEAST analysis, and ancestral areas estimated by BioGeoBEARS for the genus *Amauropelta*. Bioregion color scheme is the same as in Fig. 2.

(A) Summary of dispersal events counts (and standard deviations)



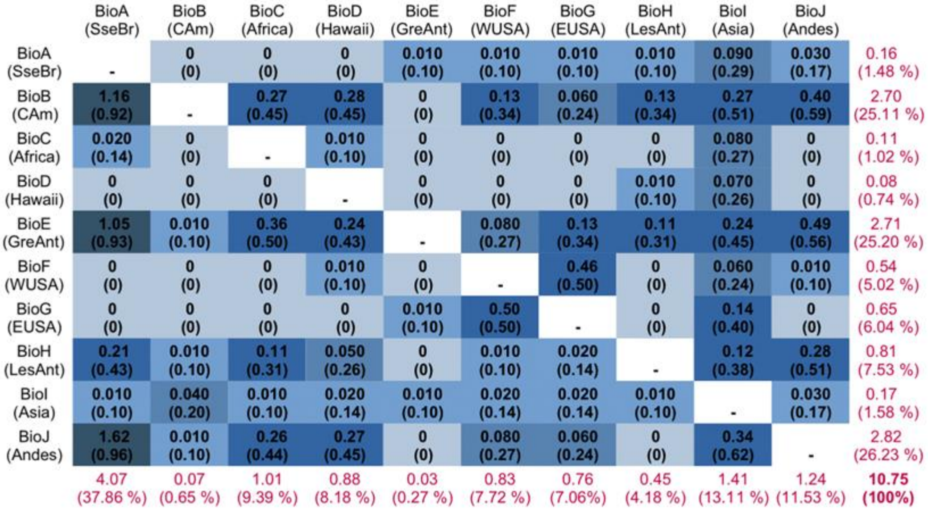
	BioA (SseBr)	BioB (CAm)	BioC (Africa)	BioD (Hawaii)	BioE (GreAnt)	BioF (WUSA)	BioG (EUSA)	BioH (LesAnt)	BioI (Asia)	BioJ (Andes)	
BioA (SseBr)	-	0.20 (0.51)	0.21 (0.46)	0.14 (0.35)	0.26 (0.52)	0.18 (0.41)	0.24 (0.45)	0.51 (0.72)	0.25 (0.48)	1.32 (0.57)	3.31 (7.57%)
BioB (CAm)	2.64 (1.4)	-	0.65 (0.90)	0.60 (0.74)	0.89 (0.89)	0.49 (0.64)	0.55 (0.77)	2 (1.58)	0.67 (0.82)	0.89 (0.94)	9.38 (21.47%)
BioC (Africa)	0.18 (0.44)	0.15 (0.39)	-	0.16 (0.39)	0.15 (0.39)	0.10 (0.30)	0.20 (0.49)	0.22 (0.44)	0.35 (0.63)	0.10 (0.30)	1.61 (3.68%)
BioD (Hawaii)	0.090 (0.29)	0.090 (0.32)	0.060 (0.24)	-	0.080 (0.27)	0.13 (0.34)	0.13 (0.34)	0.20 (0.43)	0.19 (0.46)	0.060 (0.24)	1.03 (2.35%)
BioE (GreAnt)	2.6 (1.61)	0.62 (0.72)	0.68 (0.78)	0.49 (0.59)	-	0.34 (0.57)	0.50 (0.75)	2.11 (1.58)	0.70 (0.80)	0.98 (0.91)	9.03 (2.65%)
BioF (WUSA)	0.21 (0.43)	0.14 (0.38)	0.090 (0.32)	0.16 (0.39)	0.14 (0.38)	-	0.63 (0.63)	0.11 (0.31)	0.31 (0.56)	0.080 (0.27)	1.87 (4.28%)
BioG (EUSA)	0.21 (0.43)	0.20 (0.45)	0.23 (0.49	0.20 (0.49)	0.27 (0.51)	0.72 (0.67)	-	0.22 (0.52)	0.40 (0.70)	0.12 (0.38)	2.57 (5.88%)
BioH (LesAnt)	0.75 (0.85)	0.17 (0.38)	0.27 (0.49)	0.21 (0.48)	0.28 (0.51)	0.20 (0.45)	0.26 (0.48)	-	0.31 (0.58)	0.57 (0.73)	3.02 (6.91%)
BioI (Asia)	0.28 (0.51	0.33 (0.57)	0.35 (0.56)	0.27 (0.53)	0.24 (0.55)	0.21 (0.46)	0.23 (0.53)	0.34 (0.52)	-	0.31 (0.51)	2.56 (5.86%)
BioJ (Andes)	3.14 (1.39)	0.77 (0.86)	0.61 (0.72)	0.48 (0.63)	0.93 (0.97)	0.38 (0.60)	0.41 (0.60)	1.9 (1.29)	0.69 (0.87)	-	9.31 (21.16%)
	10.1 (23.12%)	2.67 (6.11%)	3.15 (7.21%)	2.71 (6.20%)	3.24 (7.41%)	2.75 (6.29%)	3.15 (7.21%)	7.61 (17.42%)	3.87 (8.85%)	4.43 (10.14%)	**43.68 (100%)**

(B) Range expansion event counts (and standard deviations)



	BioA (SseBr)	BioB (CAm)	BioC (Africa)	BioD (Hawaii)	BioE (GreAnt)	BioF (WUSA)	BioG (EUSA)	BioH (LesAnt)	BioI (Asia)	BioJ (Andes)	
BioA (SseBr)	-	0.20 (0.51)	0.21 (0.46)	0.14 (0.35)	0.25 (0.52)	0.17 (0.40)	0.23 (0.45)	0.50 (0.70)	0.16 (0.37)	1.29 (0.59)	3.15 (9.56%)
BioB (CAm)	1.48 (1.12)	-	0.38 (0.69)	0.32 (0.58)	0.89 (0.89)	0.36 (0.58)	0.49 (0.73)	1.87 (1.45)	0.40 (0.60)	0.49 (0.69)	6.68 (20.28%)
BioC (Africa)	0.16 (0.42)	0.15 (0.39)	-	0.15 (0.39)	0.15 (0.39)	0.10 (0.30)	0.20 (0.49)	0.22 (0.44)	0.27 (0.49)	0.10 (0.30)	1.50 (4.55%)
BioD (Hawaii)	0.090 (0.29)	0.090 (0.32)	0.060 (0.24)	-	0.080 (0.27)	0.13 (0.34)	0.13 (0.34)	0.19 (0.42)	0.12 (0.33)	0.060 (0.24)	0.95 (2.88%)
BioE (GreAnt)	1.55 (1.26)	0.61 (0.72)	0.32 (0.55)	0.25 (0.46)	-	0.26 (0.48)	0.37 (0.61)	2 (1.5)	0.46 (0.61)	0.49 (0.66)	6.31 (19.16%)
BioF (WUSA)	0.21 (0.43)	0.14 (0.38)	0.090 (0.32)	0.15 (0.39)	0.14 (0.38)	-	0.17 (0.40)	0.11 (0.31)	0.25 (0.50)	0.070 (0.26)	1.33 (4.03%)
BioG (EUSA)	0.21 (0.43)	0.20 (0.45)	0.23 (0.49)	0.20 (0.49)	0.26 (0.48)	0.22 (0.46)	-	0.22 (0.52)	0.26 (0.54)	0.12 (0.38)	1.92 (5.83%)
BioH (LesAnt)	0.54 (0.66)	0.16 (0.37)	0.16 (0.39)	0.16 (0.39)	0.28 (0.51)	0.19 (0.44)	0.24 (0.47)	-	0.19 (0.44)	0.29 (0.54)	2.21 (6.71%)
BioI (Asia)	0.27 (0.51)	0.29 (0.50)	0.34 (0.54)	0.25 (0.52)	0.23 (0.55)	0.19 (0.44)	0.21 (0.50)	0.33 (0.51)	-	0.28 (0.49)	2.39 (7.25%)
BioJ (Andes)	1.52 (1.09)	0.76 (0.84)	0.35 (0.61)	0.21 (0.43)	0.93 (0.97)	0.30 (0.56)	0.35 (0.56)	1.72 (1.23)	0.35 (0.59)	-	6.49 (19.70%)
	6.03 (18. 3%)	2.6 (7.89%)	2.14 (1.83 %)	1.83 (5.55 %)	3.21 (9.74 %)	1.92 (5.83 %)	2.39 (7.25 %)	7.16 (21.74 %)	2.46 (7.47 %)	3.19 (9.68 %)	**32.93 (100 %)**

(C) Founder event counts (and standard deviations)



	BioA (SseBr)	BioB (CAm)	BioC (Africa)	BioD (Hawaii)	BioE (GreAnt)	BioF (WUSA)	BioG (EUSA)	BioH (LesAnt)	BioI (Asia)	BioJ (Andes)	
BioA (SseBr)	-	0 (0)	0 (0)	0 (0)	0.010 (0.10)	0.010 (0.10)	0.010 (0.10)	0.010 (0.10)	0.090 (0.29)	0.030 (0.17)	0.16 (1.48 %)
BioB (CAm)	1.16 (0.92)	-	0.27 (0.45)	0.28 (0.45)	0 (0)	0.13 (0.34)	0.060 (0.24)	0.13 (0.34)	0.27 (0.51)	0.40 (0.59)	2.70 (25.11 %)
BioC (Africa)	0.020 (0.14)	0 (0)	-	0.010 (0.10)	0 (0)	0 (0)	0 (0)	0 (0)	0.080 (0.27)	0 (0)	0.11 (1.02 %)
BioD (Hawaii)	0 (0)	0 (0)	0 (0)	-	0 (0)	0 (0)	0 (0)	0.010 (0.10)	0.070 (0.26)	0 (0)	0.08 (0.74 %)
BioE (GreAnt)	1.05 (0.93)	0.010 (0.10)	0.36 (0.50)	0.24 (0.43)	-	0.080 (0.27)	0.13 (0.34)	0.11 (0.31)	0.24 (0.45)	0.49 (0.56)	2.71 (25.20 %)
BioF (WUSA)	0 (0)	0 (0)	0 (0)	0.010 (0.10)	0 (0)	-	0.46 (0.50)	0 (0)	0.060 (0.24)	0.010 (0.10)	0.54 (5.02 %)
BioG (EUSA)	0 (0)	0 (0)	0 (0)	0 (0)	0.010 (0.10)	0.50 (0.50)	-	0 (0)	0.14 (0.40)	0 (0)	0.65 (6.04 %)
BioH (LesAnt)	0.21 (0.43)	0.010 (0.10)	0.11 (0.31)	0.050 (0.26)	0 (0)	0.010 (0.10)	0.020 (0.14)	-	0.12 (0.38)	0.28 (0.51)	0.81 (7.53 %)
BioI (Asia)	0.010 (0.10)	0.040 (0.20)	0.010 (0.10)	0.020 (0.14)	0.010 (0.10)	0.020 (0.14)	0.020 (0.14)	0.010 (0.10)	-	0.030 (0.17)	0.17 (1.58 %)
BioJ (Andes)	1.62 (0.96)	0.010 (0.10)	0.26 (0.44)	0.27 (0.45)	0 (0)	0.080 (0.27)	0.060 (0.24)	0 (0)	0.34 (0.62)	-	2.82 (26.23 %)
	4.07 (37.86 %)	0.07 (0.65 %)	1.01 (9.39 %)	0.88 (8.18 %)	0.03 (0.27 %)	0.83 (7.72 %)	0.76 (7.06%)	0.45 (4.18 %)	1.41 (13.11 %)	1.24 (11.53 %)	**10.75 (100%)**

Fig. 4. Number of dispersal events estimated in the evolutionary history of *Amauropelta* (Thelypteridaceae). Data integrates 100 biogeographical stochastic mapping (BSM). Standard deviations are presented in parentheses. A. Summary of the total events (range expansion and founder event). B. Summary of the range expansion counts. C. Summary of the founder counts. The darker the color, the more common the event. The rows represent ancestral states (source area) and columns represent descendant states (sink area). Red values to the right and below table represent sum and percentages of events for each area, either as source (the rows) or sink (the columns). Area names in rows and columns are abbreviated as follows: bioregion A - part of Bolivia+southeastern Paraguay+northern Argentina+southern and southeastern Brazil (BioA-SseBr), bioregion B - Central America+Mexico (BioB-CAm), bioregion C -Africa + Madagascar(BioC- Africa), bioregion D - Pacific Islands (BioD- Hawaii), bioregion E - Greater Antilles (BioE- GrAnti), bioregion F - West of USA (BioF- WUSA), bioregion G - East of USA (BioG- EUSA), bioregion H - Lesser Antilles (BioH- LesAn), bioregion I - Eastern Asia+Malesia (BioI- Asia), bioregion J – Andes+Northern America (BioJ- Asia).

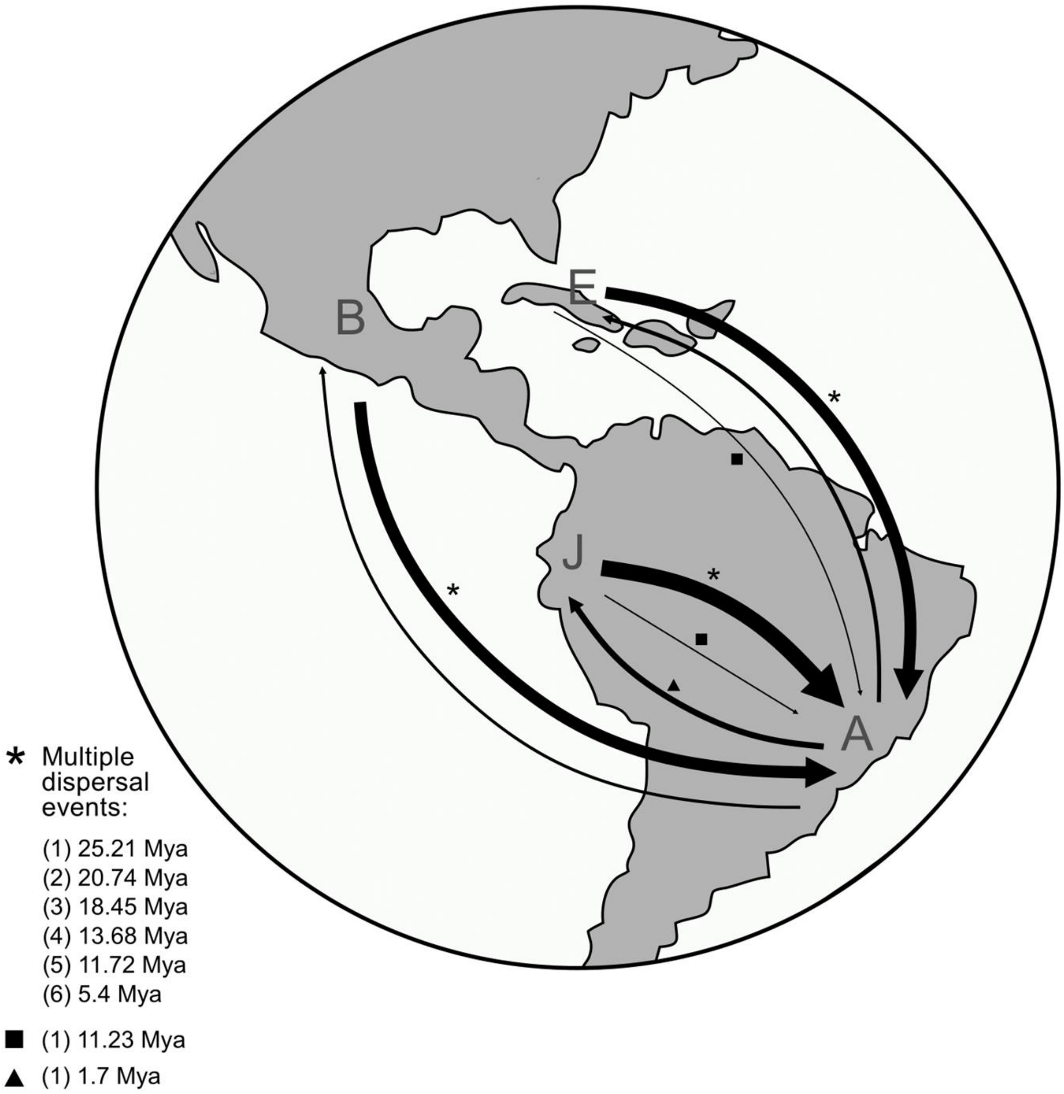


Fig. 5. Map of Neotropical region showing the asymmetrical dispersal movements between the main sources and the main sink. The bioregions are indicated by the letters. The arrow thickness corresponds approximately to the frequency of the dispersal events.

Supplementary Material 1

Table S1

Collection information for voucher specimens of sequences generated in this study and GenBank accession numbers. * Indicates sequences from previously published works and available at GenBank. - sequence not available.

Taxon	**Voucher**	***rbcL***	***rps4-trnS***	***trnL-trnF***
Amauropelta amambayensis (Christ) Salino & A.R.Sm.	Brazil, Almeida 2384 (BHCB)		KT805073*	KT804997*
Amauropelta amphioxypteris (Sodiro) Salino & T.E.Almeida	Panama, Salino 15381 (BHCB)		-	
Amauropelta amphioxypteris (Sodiro) Salino & T.E.Almeida	Ecuador, Alvarez-Fuentes et al. 608 (MSC)	-	MG818257*	MG818278*
Amauropelta araucariensis (Ponce) Salino & T.E.Almeida	Brazil, Salino 14805 (BHCB)			
Amauropelta atrorubens (Mett. ex Kuhn) Salino & T.E.Almeida	Bolivia, Almeida 3131 (BHCB)			
Amauropelta atrovirens (C.Chr.) Salino & T.E.Almeida	Panama, Salino 15366 (BHCB)			
Amauropelta balbisii (Spreng.) A.R.Sm.	Panama, Salino 15376 (BHCB)			-
Amauropelta balbisii (Spreng.) A.R.Sm.	Jamaica, Alvarez-Fuentes et al. 527 (MSC)	-	MG818259*	MG818280*
Amauropelta balbisii var. longipilosa (C.Chr.) C. Sánchez, Álvarez, O. & Caluff	Dominica, O. Alvarez & Caluff, Hill 25604 (US)	-	MG818258*	MG818279*
Amauropelta basisceletica (C.Sánchez, Caluff & Álvarez, O.) Salino & T.E.Almeida	Cuba, Sánchez et al. 82028 (MSC)	-	MG818249*	MG818272*
Amauropelta beddomei (Baker) Y.H. Ching	China, Zhang 5449 (PE)	JN572357*	JN572195*	-

Amauropelta bergiana (Schltdl.) Holttum	Reúnion, E. Grangaud & P. Acock s.n. (BM, REU)	KF992414*	KT805074*	KT804998*
Amauropelta brachypus (Sodiro) Salino & T.E.Almeida	Panama, Salino 15377 (BHCB)			
Amauropelta brausei (Hieron.) A.R.Sm.	Bolivia, Almeida 3075 (BHCB)		-	
Amauropelta burkartii (Abbiatti) Salino & T.E.Almeida	Brazil, Salino 14781 (BHCB)		KT805075*	KT804999*
Amauropelta caucaensis (Hieron.) A.R.Sm.	Panama, Salino 15451 (BHCB)			
Amauropelta cheilanthoides (Kunze) Á.Löve & D.Löve	Panama, Salino 15426 (BHCB)			
Amauropelta consanguinea (Fée) Salino & T.E.Almeida	Dominica, Hill 25724 (US)	-	MG818260*	MG818281*
Amauropelta corazonensis (Baker) Salino & T.E.Almeida	Panama, Salino 15460 (BHCB)			
Amauropelta decurtata (Kunze) Salino & T.E.Almeida	Brazil, Salino 14751 (BHCB)		KT805077*	KT805001*
Amauropelta delasotae (A.R.Sm. & Lellinger) Salino & T.E.Almeida	Panama, Salino 15452 (BHCB)			
Amauropelta eriosorus (Fée) Salino & T.E.Almeida	Brazil, Almeida 1535 (BHCB)		KT805078*	KT805002*
Amauropelta euchlora (Sodiro) A.R.Sm.	Bolivia, Almeida 311 (BHCB)			
Amauropelta firma (Baker ex Jenman) Salino & T.E.Almeida	Jamaica, Alvarez-Fuentes et al. 556 (MSC)	-	MG818251*	-
Amauropelta germaniana (Fée) Salino & T.E.Almeida	Cuba, Sánchez et al. 82080 (MSC)	-	MG818261*	MG818282*
Amauropelta germaniana (Fée) Salino & T.E.Almeida	Cuba, Sánchez et al. s.n. (MSC)	-	MG818262*	MG818283*

Amauropelta glanduligera (Kunze) Y.H. Ching	China.Zhang, 4419 (PE)	JN572356*	JN572194*	-
Amauropelta glandulosolanosa (C.Chr.) Salino & T.E.Almeida	Bolivia, Almeida 3103 (BHCB)			
Amauropelta glandulosolanosa (C.Chr.) Salino & T.E.Almeida	Ecuador, Alvarez-Fuentes et al. 589 (MSC)	-	MG818250*	MG818273*
Amauropelta globulifera Holttum	Hawaii, Game s.n. (UC)	EF463287*	KT805079*	KT805003*
Amauropelta gracilis (Heward) A.R.Sm.	Jamaica, Alvarez-Fuentes et al. 548 (MSC)	-	MG818248*	MG818271*
Amauropelta heteroclita (Desv.) Pic.Serm.	Jamaica, Alvarez-Fuentes et al. 550 (MSC)	-	MG818255*	MG818276*
Amauropelta heteroptera (Desv.) Holttum	Reúnion, E. Grangaud & P. Acock s.n. (BM, REU)	KF992415*	KT805080*	KT805004*
Amauropelta inabonensis (Proctor) Salino & T.E.Almeida	Puerto Rico, Axelrod & Chavez 4312 (US)	-	MG818263*	MG818284*
Amauropelta juergensii (Rosenst.) Salino & T.E.Almeida	Brazil, Salino 14753 (BHCB)		KT805081*	KT805005*
Amauropelta linkiana (C. Presl) Pic.Serm.	Panama, Salino 15399 (BHCB)			
Amauropelta linkiana (C. Presl) Pic.Serm.	Dominican Republic, Mickel 9088 (NY)	-	MG818264*	MG818285*
Amauropelta longicaulis (Baker) Salino & T.E.Almeida	Colombia, I. Moura 137 (BHCB, HUA)		-	
Amauropelta nevadensis (Baker) S.E.Fawcett & A.R.Sm. comb. nov. ined.	USA, U.C. Bot. Gard. 60.0707 (JEPS)	-	AF425178*	AF425138*
Amauropelta noveboracensis (L.) S.E.Fawcett & A.R.Sm. comb. nov. ined.	USA, Zhang 3798 (PE)	JN572358*	JN572196*	-
Amauropelta oligocarpa (Humb. & Bonpl. ex Willd.) Pic.Serm.	Brazil, Salino 14817 (BHCB)		KT805082*	KT805006*

Amauropelta oligocarpa (Humb. & Bonpl. ex Willd.) Pic.Serm.	Bolivia, Almeida 3087 (BHCB)			
Amauropelta oligocarpa (Humb. & Bonpl. ex Willd.) Pic.Serm.	Panama, Salino 15394 (BHCB)			
Amauropelta oligocarpa (Humb. & Bonpl. ex Willd.) Pic.Serm.	Costa Rica, U.C. Bot. Gard. 57.0002 (UC)	-	AF425162*	AF425125*
Amauropelta oligocarpa (Humb. & Bonpl. ex Willd.) Pic.Serm.	Jamaica, Alvarez-Fuentes et al. 532 (MSC)	-	MG818252*	MG818274*
Amauropelta opposita (Vahl) Pic.Serm.	Trinidad, Knobloch s.n. (MSC)	-	MG818265*	MG818286*
Amauropelta oppositiformis (C.Chr.) Holttum	Comoros, Kluge 7746 (GOET)	KF992416*	KT805083*	KT805007*
Amauropelta pachyrhachis (Kunze ex Mett.) Salino & T.E.Almeida	Brazil, Almeida 1802 (BHCB)		-	KT805008*
Amauropelta pachyrhachis (Kunze ex Mett.) Salino & T.E.Almeida	Panama, Salino 15400 (BHCB)			
Amauropelta patula (Fée) Salino & T.E.Almeida	Brazil, Almeida 1631 (BHCB)		KT805084*	KT805009*
Amauropelta pilosohispida (Hook.) A.R.Sm.	Bolivia, Almeida 3117 (BHCB)			
Amauropelta pilosula (Klotzsch & H. Karst. ex Mett.) Á. Löve & D. Löve	Panama, Salino 15458 (BHCB)			
Amauropelta pilosula (Klotzsch & H. Karst. ex Mett.) Á.Löve & D.Löve	Ecuador, Alvarez-Fuentes et al. 570 (MSC)	-	MG818269*	MG818290*
Amauropelta ptarmica (Kunze ex Mett.) Pic.Serm.	Brazil, Salino 14709 (BHCB)			
Amauropelta pteroidea (Klotzsch) A.R.Sm.	Colombia, Salino 16184 (HUA ???)		-	
Amauropelta raddii (Rosenst.) Salino & T.E.Almeida	Brazil, Almeida 2373 (BHCB)		KT805086*	KT805011*

Amauropelta recumbens (Rosenst.) Salino & T.E.Almeida	Brazil, Lautert 236 (BHCB)	-		
Amauropelta regnelliana (C.Chr.) Salino & T.E.Almeida	Brazil, Almeida 1588 (BHCB)	-	KT805087*	KT805012*
Amauropelta resinifera (Desv.) Pic.Serm.	Jamaica, Alvarez-Fuentes et al. 502 (MSC)	-	MG818247*	-
Amauropelta retusa (Sw.) Pic.Serm.	Brazil, Salino 14778 (BHCB)		KT805088*	KT805013*
Amauropelta rivularioides (Fée) Salino & T.E.Almeida	Brazil, Almeida 2377 (BHCB)		KT805089*	KT805014*
Amauropelta rosenstockii (C.Chr.) Salino & T.E.Almeida	Ecuador, Alvarez-Fuentes et al. 583 (MSC)	-	MG818266*	MG818287*
Amauropelta rudis (Kunze) Pic.Serm.	Panama, Salino 15444 (BHCB)			
Amauropelta rudis (Kunze) Pic.Serm.	Colombia, Salino 16071 (HUA ???)			
Amauropelta rudis (Kunze) Pic.Serm.	Cuba, Sánchez et al. 82081 (MSC)	-	MG818254*	MG818275*
Amauropelta rufa (Poir.) Salino & T.E.Almeida	Ecuador, Alvarez-Fuentes et al. 584 (MSC)	-	MG818267*	MG818288*
Amauropelta rustica (Fée) Salino & T.E.Almeida	Dominica, Hill 24639 (US)	-	MG818268*	MG818289*
Amauropelta salazica (Holttum) Holttum	Réunion, S. Hennequin 2009-R112 (BM, REU)	KF992417*	KT805090*	KT805015*
Amauropelta saxicola (Sw.) Salino & T.E.Almeida	Brazil, Almeida 2382 (BHCB)		KT805091*	KT805016*
Amauropelta scalaris (Christ) Á.Löve & D.Löve	Panama, Salino 15378 (BHCB)			
Amauropelta soridepressa (Salino & V.A.O. Dittrich) Salino & T.E.Almeida	Brazil, Almeida 3263 (BHCB)			

Amauropelta steyermarkii (A.R.Sm.) Salino & T.E.Almeida	Bolivia, Almeida 3097 (BHCB)		-	
Amauropelta strigosa (Willd.) Holttum	Réunion, E. Grangaud & P. Acock s.n. (BM,REU)	KF992418*	-	-
Amauropelta struthiopteroides (C.Chr.) Salino & T.E.Almeida	Panama, Salino 15383 (BHCB)			
Amauropelta supina (Sodiro) Salino & T.E.Almeida	Bolivia, Almeida 3085 (BHCB)			
Amauropelta tamandarei (Rosenst.) Salino & T.E.Almeida	Giacomin 1371			
Amauropelta thomsonii (Jenman) Pic.Serm.	Panama, Salino 15445 (BHCB)			
Amauropelta tomentosa (Thouars) Holttum	Mauritius, E. Grangaud s.n. (BM, REU)	KF992419*	KT805092*	KT805017*
Christella hispidula (Decne.) Holttum	Brazil, Almeida 1984 (BHCB)			
Coryphopteris japonica (Baker) L.J.He & X.C.Zhang	Korea, Zhang 3605 (PE)	JN572335*	JN572174*	JN572253*
Coryphopteris petelotii (Ching) Holttum	China, Zhang 6009 (PE)	JN572337*	JN572176*	JN572255*
Coryphopteris seemannii Holttum	Fiji, Game 95/147B (UC)	EF463300*	AH011224*	AF427096*
Cyclosorus interruptus (Willd.) H.Itô	Reúnion, S. Hennequin 2009-R65 (BM, REU)	KF992466*	KT805100*	KT805026*
Macrothelypteris torresiana (Gaudich.) Ching	China, Zhang 4087 (PE)	JN572346*	JN572184*	JN572265*
Metathelypteris hattorii (H. Itô) Ching	China, Liu 2022891 (PE)	JN572353*	JN572191*	JN572271*
Metathelypteris singalanensis (Baker) Ching	China, Zhang 4195 (PE)	JN572354*	JN572192*	JN572272*
Phegopteris decursive-pinnata	South Korea, Zhang 3559 (PE)	JN572360*	JN572198*	JN572275*

(H.C. Hall) Fée				
Pseudophegopteris brevipes Ching & S.K.Wu	China, Zhang & Wang 5084 (PE)	-	JN572221*	HQ890420*
Thelypteris palustris Schott	South Korea, Zhang 2389 (PE)	JN572401*	JN572231*	JN572313*

Table S2

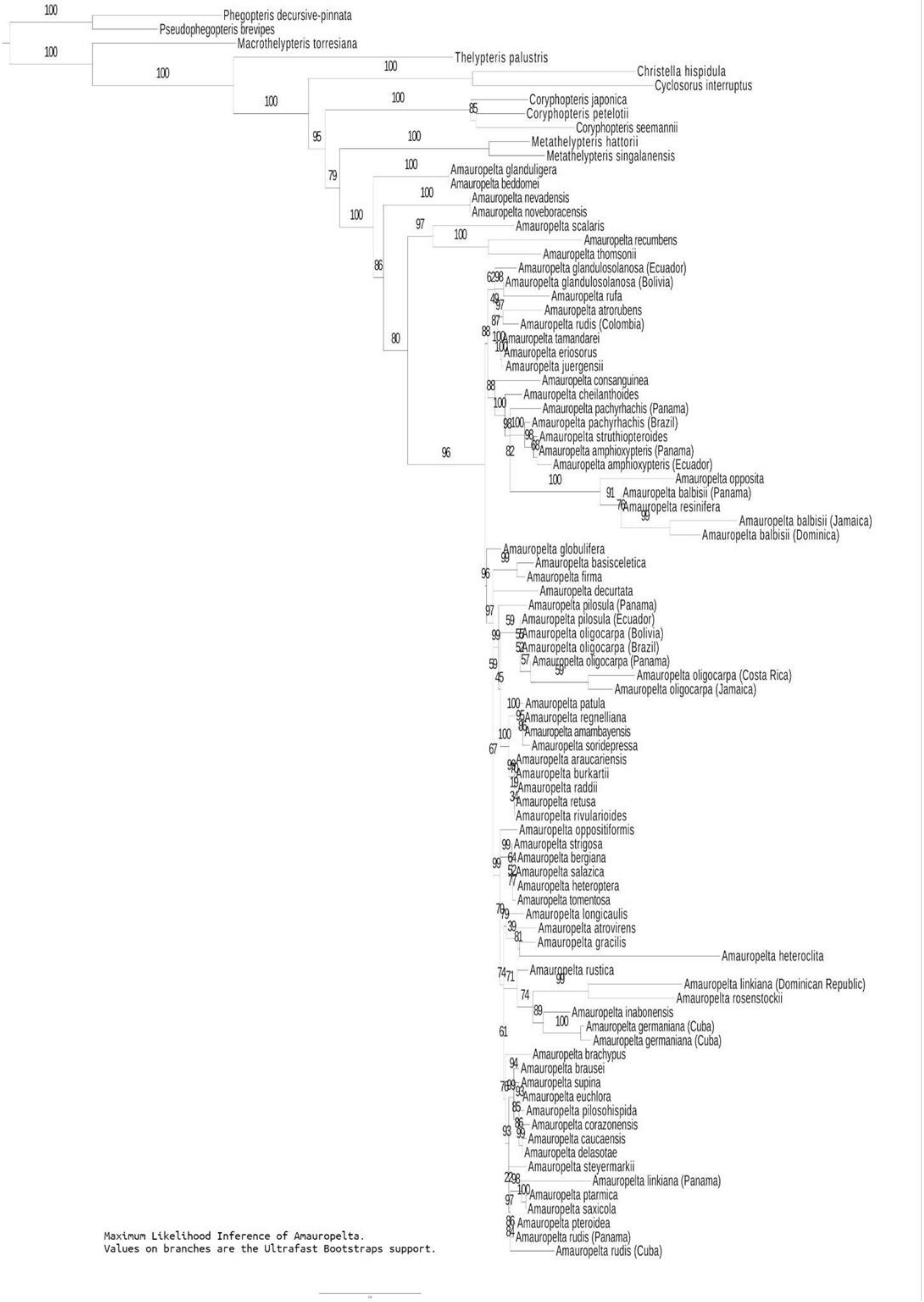
Comparative table between the recovered clades in this work and sections defined by Smith (1974).

Species	**Clade (this work)**	**Secion (Smith, 1974)**
Amauropelta bergiana (Schltdl.) Holttum	Africa	*Uncinella*
Amauropelta heteroptera (Desv.) Holttum	Africa	*Incertae sedis*
Amauropelta salazica (Holttum) Holttum	Africa	*Incertae sedis*
Amauropelta strigosa (Willd.) Holttum	Africa	*Incertae sedis*
Amauropelta tomentosa (Thouars) Holttum	Africa	*Incertae sedis*
Amauropelta amphioxypteris (Sodiro) Salino & T.E.Almeida	Balbisii	*Amauropelta*
Amauropelta atrorubens (Mett. ex Kuhn) Salino & T.E.Almeida	Balbisii	*Uncinella*
Amauropelta balbisii (Spreng.) A.R.Sm.	Balbisii	*Amauropelta*
Amauropelta cheilanthoides (Kunze) Á.Löve & D.Löve	Balbisii	*Blennocaulon*
Amauropelta consanguinea (Fée) Salino & T.E.Almeida	Balbisii	*Amauropelta*
Amauropelta eriosorus (Fée) Salino & T.E.Almeida	Balbisii	*Incertae sedis*
Amauropelta glandulosolanosa (C.Chr.) Salino & T.E.Almeida	Balbisii	*Adenophyllum*

Amauropelta juergensii (Rosenst.) Salino & T.E.Almeida	Balbisii	*Adenophyllum*
Amauropelta opposita (Vahl) Pic.Serm.	Balbisii	*Amauropelta*
Amauropelta pachyrhachis (Kunze ex Mett.) Salino & T.E.Almeida	Balbisii	*Pachyrachis*
Amauropelta resinifera (Desv.) Pic.Serm.	Balbisii	*Amauropelta*
Amauropelta rudis (Kunze) Pic.Serm. (pro parte)	Balbisii	*Lepidoneuron*
Amauropelta rufa (Poir.) Salino & T.E.Almeida	Balbisii	*Incertae sedis*
Amauropelta struthiopteroides (C.Chr.) Salino & T.E.Almeida	Balbisii	*Amauropelta*
Amauropelta tamandarei (Rosenst.) Salino & T.E.Almeida	Balbisii	*Incertae sedis*
Amauropelta basisceletica (C.Sánchez, Caluff & Álvarez) Salino & T.E.Almeida	Firma	*Amauropelta*
Amauropelta firma (Baker ex Jenman) Salino & T.E.Almeida	Firma	*Amauropelta*
Amauropelta germaniana (Fée) Salino & T.E.Almeida	Germaniana	*Uncinella*
Amauropelta inabonensis (Proctor) Salino & T.E.Almeida	Germaniana	*Uncinella*
Amauropelta linkiana (C. Presl) Pic.Serm.	Germaniana	*Uncinella*
Amauropelta rosenstockii (C.Chr.) Salino & T.E.Almeida	Germaniana	*Lepidoneuron*
Amauropelta rustica (Fée) Salino & T.E.Almeida	Germaniana	*Uncinella*
Amauropelta atrovirens (C.Chr.) Salino & T.E.Almeida	Heteroclita	*Uncinella*
Amauropelta gracilis (Heward) A.R.Sm.	Heteroclita	*Uncinella*
Amauropelta heteroclita (Desv.) Pic.Serm.	Heteroclita	*Uncinella*
Amauropelta longicaulis (Baker) Salino & T.E.Almeida	Heteroclita	*Amauropelta*
Amauropelta amambayensis (Christ) Salino & A.R.Sm.	Oligocarpa	*Uncinella*
Amauropelta araucariensis (Ponce) Salino & T.E.Almeida	Oligocarpa	*Blennocaulon*
Amauropelta burkartii (Abbiatti) Salino & T.E.Almeida	Oligocarpa	*Adenophyllum*
Amauropelta oligocarpa (Humb. & Bonpl. ex Willd.) Pic.Serm.	Oligocarpa	*Uncinella*

Amauropelta patula (Fée) Salino & T.E.Almeida	Oligocarpa	*Lepidoneuron*
Amauropelta pilosula (Klotzsch & H.Karst. ex Mett.) Á.Löve & D.Löve	Oligocarpa	*Adenophyllum*
Amauropelta raddii (Rosenst.) Salino & T.E.Almeida	Oligocarpa	*Uncinella*
Amauropelta regnelliana (C.Chr.) Salino & T.E.Almeida	Oligocarpa	*Uncinella*
Amauropelta retusa (Sw.) Pic.Serm.	Oligocarpa	*Uncinella*
Amauropelta rivularioides (Fée) Salino & T.E.Almeida	Oligocarpa	*Adenophyllum*
Amauropelta soridepressa (Salino & V.A.O. Dittrich) Salino & T.E.Almeida	Oligocarpa	*Apelta*
Amauropelta recumbens (Rosenst.) Salino & T.E.Almeida	Scalaris	*Uncinella*
Amauropelta scalaris (Christ) Á.Löve & D.Löve	Scalaris	*Uncinella*
Amauropelta thomsonii (Jenman) Pic.Serm.	Scalaris	*Phacelothrix*
Amauropelta brausei (Hieron.) A.R.Sm.	Steyermarkii	*Lepidoneuron*
Amauropelta caucaensis (Hieron.) A.R.Sm.	Steyermarkii	*Lepidoneuron*
Amauropelta corazonensis (Baker) Salino & T.E.Almeida	Steyermarkii	*Lepidoneuron*
Amauropelta delasotae (A.R.Sm. & Lellinger) Salino & T.E.Almeida	Steyermarkii	*Lepidoneuron*
Amauropelta euchlora (Sodiro) A.R.Sm.	Steyermarkii	*Lepidoneuron*
Amauropelta pilosohispida (Hook.) A.R.Sm.	Steyermarkii	*Lepidoneuron*
Amauropelta ptarmica (Kunze ex Mett.) Pic.Serm.	Steyermarkii	*Uncinella*
Amauropelta pteroidea (Klotzsch) A.R.Sm.	Steyermarkii	*Lepidoneuron*
Amauropelta rudis (Kunze) Pic.Serm. (pro part)	Steyermarkii	*Lepidoneuron*
Amauropelta saxicola (Sw.) Salino & T.E.Almeida	Steyermarkii	*Uncinella*
Amauropelta steyermarkii (A.R.Sm.) Salino & T.E.Almeida	Steyermarkii	*Incertae sedis*
Amauropelta supina (Sodiro) Salino & T.E.Almeida	Steyermarkii	*Blennocaulon*

Amauropelta brachypus (Sodiro) Salino & T.E.Almeida	-	*Uncinella*
Amauropelta decurtata (Kunze) Salino & T.E.Almeida	-	*Blennocaulon*
Amauropelta globulifera Holttum	-	*Amauropelta*
Amauropelta oppositiformis (C.Chr.) Holttum	-	*Amauropelta*
Amauropelta beddomei (Baker) Y.H.Ching	Asia clade	-
Amauropelta glanduligera (Kunze) Y.H.Ching	Asia clade	-
Amauropelta nevadensis (Baker) S.E.Fawcett & A.R.Sm. comb. nov. ined.	North America	-
Amauropelta noveboracensis (L.) S.E.Fawcett & A.R.Sm. comb. nov. ined.	North America	-



Maximum Likelihood Inference of Amauropelta.
Values on branches are the Ultrafast Bootstraps support.

Fig. S1 - Maximum likelihood inference based on the combined dataset using *rbc*L, *rps*4-trn*S*, and *trn*L-*trn*F sequences of *Amauropelta.* Values on branches are the Ultrafast Bootstraps supports.

Fig. S2 - Bayesian inference based on the combined dataset using *rbc*L, *rps*4-trn*S*, and *trn*L-*trn*F sequences of *Amauropelta.* Values on branches are the posterior probabilities.

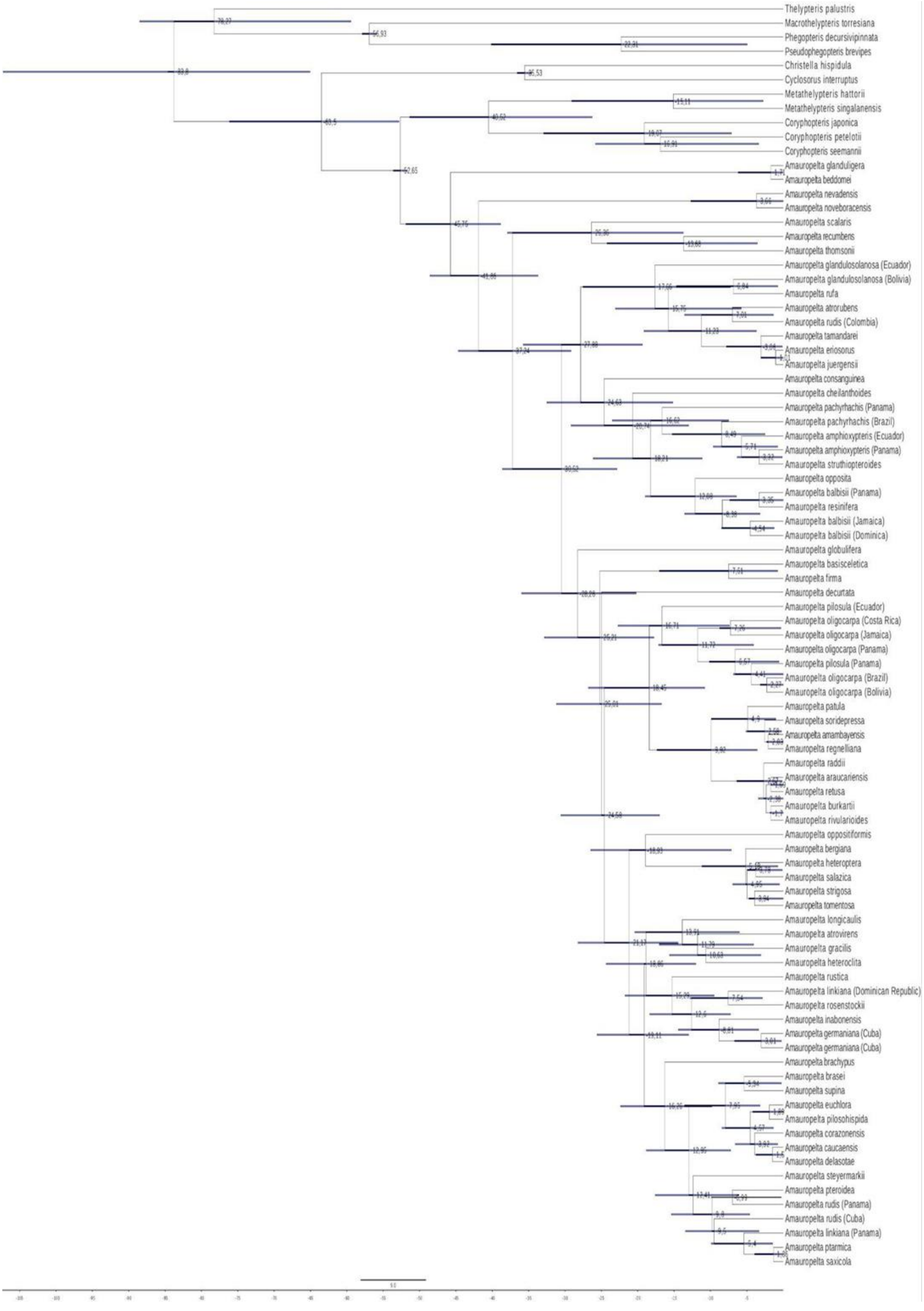


Fig. S3 - Maximum credibility tree based on the combined dataset using *rbc*L, *rps4*-trn*S*, and *trn*L-*trn*F sequences of *Amauropelta.* Horizontal blue bars correspond to 95% HPD intervals of the median ages. Dates are given in million years (Mya).

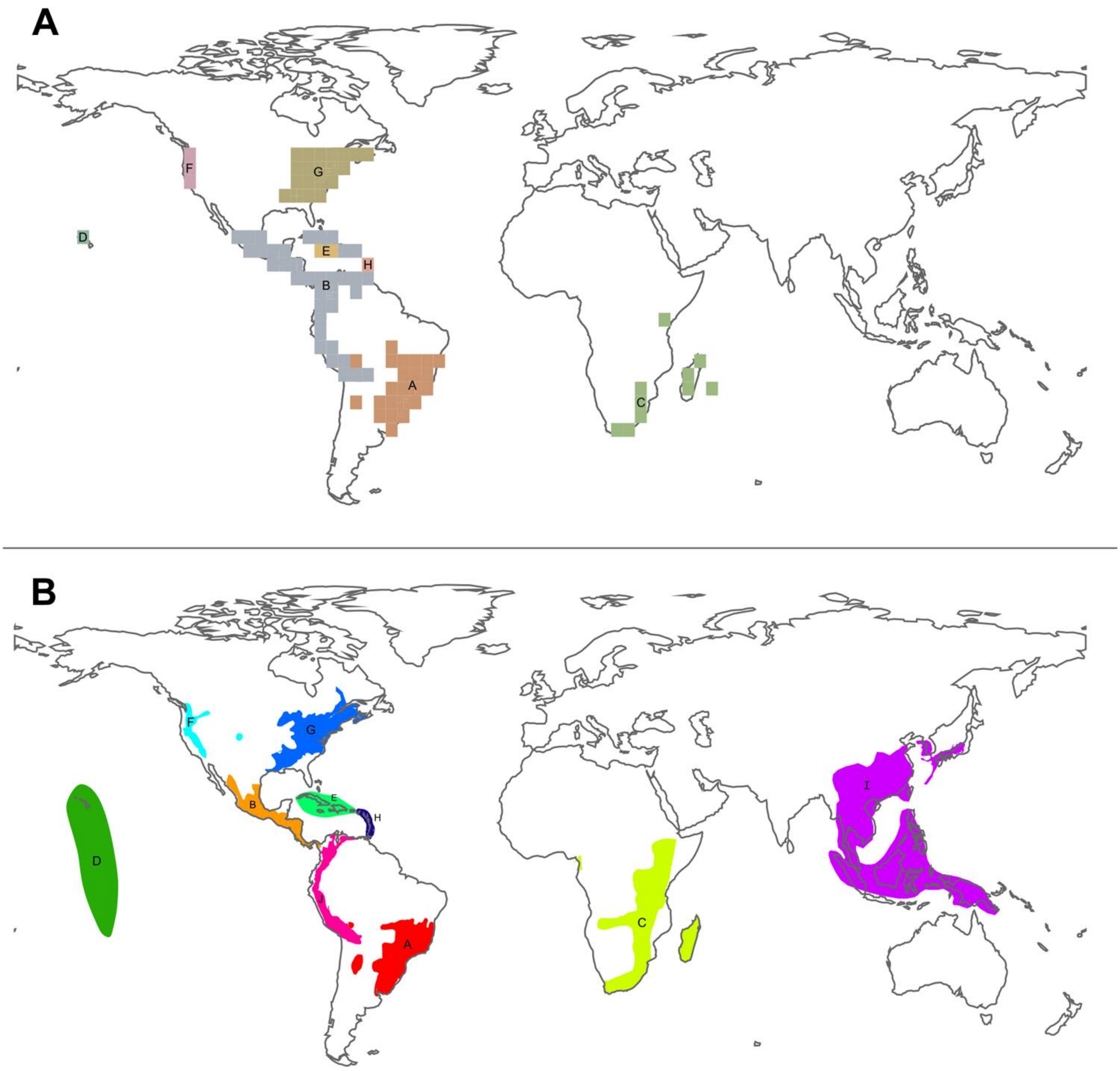


Fig. S4 - Comparision between the definition of areas by the Infomap Bioregions and our definition. A- Infomap Bioregions is indicated by the colour and letter within it Bioregions, as follow: brown+A (bioregion A); grey+B (bioregion B); light green+C (bioregion C); dark green+D (bioregion D); beige+E (bioregion E); khaki+G (bioregion G). B- Our definition of bioregions is indicated by the colour and letter within it Bioregions, as follow: red+A (bioregion A - part of Bolivia+southeastern Paraguay+northern Argentina+southern and southeastern Brazil); orange+B (bioregion B-Central America+Mexico); yellow +C (bioregion C-Africa + Madagascar); dark green colour+D (bioregion D-Pacific Islands); light green+E (bioregion E-Greater Antilles); light blue colour+F (bioregion F-West of USA); dark blue+G (bioregion G-East of USA); dark purple+H (bioregion H-Lesser Antilles); light purple+I (bioregion I-Eastern Asia+Malesia); pink+J (bioregion J-Andes+Northern America).