Marine introgressions and Andean uplift drives diversification in neotropical Monkey tree frogs (Anura, Phyllomedusinae)

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The species richness in Neotropics has been linked to environmental heterogeneity and a complex geological history. We evaluated which biogeographical processes were more associated with the diversification of Monkey tree frogs, an endemic clade from the Neotropics. We tested the hypothesis that the diversification of Phyllomedusinae occurred in a south-north direction in the Neotropics, and that marine introgressions and Andean uplift had a crucial role promoting their diversification. We used 13 molecular markers on a bayesian analysis to infer phylogenetic relationships among 57 species of Phyllomedusinae and to estimate their divergence times. We hypothesized the ancestral range based in 12 biogeographical units defined considering the distribution of the phyllomedusine species and potential biogeographical barriers. Ancestral range estimations were made by models implemented in BioGeoBEARS. We found that the Phyllomedusinae hypothetical ancestor range was probably widespread through the Neotropics, from Central America to Southern Atlantic Forest, at 38.6 Mya. Phyllomedusines' ancestors diverged mostly through vicariance during early stages of speciation, generally followed by jump-dispersals and speciation in sympatry. Dispersal among areas mostly occurred from Western Amazonia towards Northern Andes and the diagonal of dry landscapes, rejecting our south-north diversification hypothesis. Our results revealed a complex diversification of Monkey tree frogs, occurring simultaneously with the orogeny of Northern Andes and the South American marine introgressions in the last 30 million years.

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ABSTRACT

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found that the Phyllomedusinae hypothetical ancestor range was probably widespread through the Neotropics, from Central America to Southern Atlantic Forest, at 38.6 Mya. Phyllomedusines' ancestors diverged mostly through vicariance during early stages of speciation, generally followed by jump-dispersals and speciation in sympatry. Dispersal among areas mostly occurred from Western Amazonia towards Northern Andes and the diagonal of dry landscapes, rejecting our south-north diversification hypothesis. Our results revealed a complex diversification of Monkey tree frogs, occurring simultaneously with the orogeny of Northern Andes and the South American marine introgressions in the last 30 million years.

Keywords. Amphibia - Northern Andes - Biogeography - Neotropics - Paranaense sea - Pebas system

INTRODUCTION

Extending from the central portion of Mexico through the entire Central and South America (Morrone, 2014), the Neotropical region hosts the greatest biodiversity on Earth (Myers *et al.*, 2000; Antonelli & Sanmartín, 2011). The environmental heterogeneity in Neotropics, in association with its complex geological history from the early-Cenozoic, have driven patterns of species diversification, contributing to high levels of species richness and endemism for different taxa (Antonelli, 2016). Regarding the northern portion of South America, well-documented marine introgressions occurred from mid to the late-Cenozoic (~25–5 million years ago – Mya), the so-called Pebas and Acre systems (e.g., Hoorn *et al.*, 2010; Salas-Gismondi *et al.*, 2015). Probably related to global sea-level fluctuations (Hoorn, 1993), both flooding processes turned

the Western Amazonia into a lacustrine environment during the Miocene (23–7 mya; Hoorn *et al.*, 2010; Salas-Gismondi *et al.*, 2015), affecting Magdalena River delta, paleo-Orinoco, and proto-Amazonas River basins. Henceforth, Western Amazonia suffered drastic changes until the emergence of current fluvial systems, including flowing changes of its main rivers (Díaz de Gamero, 1996; Albert *et al.*, 2018). Moreover, some orogenic processes also promoted important changes into Neotropics, as the accelerated uplift of Eastern Cordillera of Andes during the Miocene (Hoorn, 1993; ~10–4 mya; Gregory-Wodzicki, 2000), that led to changes in the climatic and sedimentary sources for Western Amazonia (Insel *et al.*, 2010; Poulsen *et al.*, 2010; Hoorn *et al.*, 2017).

The entire uplift of Andes has been playing similar role for the southwestern part of Neotropics, since it started in the early-mid Cenozoic (Giambiagi *et al.*, 2016; Rodríguez Tribaldos *et al.*, 2017; Sundell *et al.*, 2019). The Andean orogeny, in addition to climatic factors throughout the entire Neogene and Quartenary (Garzione *et al.*, 2006; Hoorn *et al.*, 2020), has been responsible for the emergence of the South American diagonal of open/dry landscapes (DODL; Zanella, 2011; Azevedo *et al.*, 2020), especially during the Oligocene (~25 mya) and late Neogene (~5–3 mya). As DODL expanded, a single large forest block must have been splitted into Amazonian and Atlantic forests (Costa, 2003; Sobral-Souza *et al.*, 2015; Peres *et al.*, 2017), the last being southern confined by marine introgressions (Hernández *et al.*, 2005; Abello *et al.*, 2010).

Most studies examining the processes leading to biota diversification in the Neotropics focus on ecologically or geographically restricted groups (Smith *et al.*, 2014; Werneck *et al.*, 2015; e.g., Guarnizo *et al.*, 2016), in a local-scale approach. Studies focusing on widespread clades, on the other hand, could elucidate the role of multiple processes over space and deep

time, contributing to the macroevolutionary framework (e.g., Vicente *et al.*, 2017; Hamdan *et al.*, 2019; Prieto-Torres *et al.*, 2019; Pontes-Nogueira *et al.*, 2021), given the complex dynamic of biogeographical processes in the Neotropical region. Among anurans, this scenario fits well for Phyllomedusinae, a subfamily virtually occurring throughout the entire Neotropics. This charismatic group, commonly known as Monkey tree frogs, comprises 67 species (Frost, 2023), distributed from Argentina to Mexico (Duellman *et al.*, 2016; Frost, 2023).

Systematics of the subfamily seems to be well defined, regarding closely related frog groups. Except for phylogenetic analyses exclusively based on morphology (Haas, 2003; Wiens *et al.*, 2005), phyllomedusines are consistently recovered as monophyletic, and a sister taxon to Pelodryadinae from the Australo-Papuan region, both constituting subfamilies of Hylidae treefrogs (Wiens *et al.*, 2005; Frost *et al.*, 2006; Faivovich *et al.*, 2010; Pyron & Wiens, 2011; Duellman *et al.*, 2016; Jetz & Pyron, 2018; Dubois *et al.*, 2021). Phylogenetic relationships for some clades of Phyllomedusinae are also consistent in the most comprehensive phylogenetic approaches (Faivovich *et al.*, 2010; Pyron & Wiens, 2011). Some discussion occurs regarding the early branching events in the group, since molecular approaches on phyllomedusine's phylogeny show a low sampling for *Phrynomedusa* Miranda-Ribeiro, 1923, a rare genus only known from a few localities of the Serra do Mar and Serra da Mantiqueira on the South American Atlantic Forest (Baêta *et al.*, 2016). On the other hand, Pelodryadinae is widespread in Australia and Papua New Guinea (Frost, 2023). More speciose than Phyllomedusinae, the pelodryadine frog subfamily is a clade composed by 223 species, whose systematics is object of a long-term debate regarding its internal clades relationships (Dubois *et al.*, 2021; Frost, 2023).

Molecular estimates indicated that the split between phyllomedusines and pelodryadines occurred during the late Paleocene (~55 Ma), a time when both the Neotropics and Australo-

Papuan regions were connected to Antarctica via a land bridge (Duellman *et al.*, 2016; Van Den Ende *et al.*, 2017). Such estimates also suggest the Most Recent Common Ancestor (MRCA) of Phyllomedusinae emerging during the late Eocene, following the appearance of the MRCA of Pelodryadinae. Diversification within Phyllomedusinae started in the Oligocene (Duellman *et al.*, 2016; Jetz & Pyron, 2018) as South America began separating from Antarctica. Considering that some lineages diversified in South America after their ancestral lineages arrived via Antarctica (e.g., orchids, Givnish et al., 2016; sea spiders, Dietz et al., 2019; ungulate mammals, Reguero et al., 2014), it is plausible to hypothesize that the MRCA of all phyllomedusines also diversified in a south-north direction. Furthermore, certain speciation processes within phyllomedusines have tentatively been associated with the uplift of the Eastern Cordillera of the Andes (e.g., Duelman *et al.*, 2016; Ron *et al.*, 2013). However, the historical biogeography of this clade has not yet been explored in a statistical framework.

Herein, we combined sequences of multiple molecular markers of 53 species of Phyllomedusinae to produce a time-calibrated phylogeny. Then we reconstructed the subfamily diversification throughout Neotropical region, aiming to answer the following questions: (1) How were the hypothetical ancestors of Phyllomedusinae clade distributed along Neotropics? And (2) which biogeographical processes drove the current subfamily distribution? We tested the hypothesis that speciation in Phyllomedusinae occurred in a south-north direction in South America, and that diversification was associated to marine introgressions and Andean orogeny.

MATERIALS AND METHODS

Sequence data and phylogenetic analyses

We performed a phylogenetic inference using sequences retrieved from GenBank (Supplementary data S1). The molecular data available for the group warrants careful consideration. In the last decade, taxonomic reviews, phylogenies, and the description of new species based on molecular data have led to frequent species synonymy and the recognition of populations as new species within phylomedusines (e.g. Faivovich *et al.*, 2011; Baêta *et al.*, 2016; Castroviejo-Fisher *et al.*, 2017, Pereira *et al.*, 2018; Andrade *et al.*, 2020). However, GenBank curation has not been able to keep up to date with the taxonomy of the group. To avoid problems with misidentification and taxonomic inconsistencies, we took special care when selecting the sequences for Phyllomedusinae, considering the collection site of each accession number and cross-validating the species distribution following Frost (2023).

Our analysis included 57 species of Phyllomedusinae in the ingroup, in addition to 20 Pelodryadinae and 18 Hylinae, both subfamilies composing the outgroup. Molecular sampling covered 85% of all known species of Phyllomedusinae, including all genera of the subfamily (Frost, 2023). Considering the data availability in GenBank, we included as much data as possible in our analysis, excluding only the sequences that showed no significant similarity due to the absence of query coverage (BLAST utility; Zhang *et al.*, 2000). Our analysis comprised all the species of *Callimedusa* Duellman, Marion, and Hedges, 2016 (6 spp.), *Cruziohyla* Faivovich, Haddad, Garcia, Frost, Campbell, and Wheeler, 2005 (3 spp.), *Hylomantis* (2 spp.), and *Pithecopus* Cope, 1866 (12 spp.), as well as a representative selection of *Agalychnis* (9 species sampled from 14 spp. described), *Phasmahyla* Cruz, 1991 (7 species sampled from 8 spp. described), *Phyllomedusa* Wagler, 1830 (15 species sampled from 16 spp. described), and *Phrynomedusa* (3 species sampled from 6 spp. described). We searched for 13 molecular

markers, both nuclear (CXCR4, POMC, RAG1, RHOD, SIAH, and Tyr) and mitochondrial genes (12S, tRNA-Val, 16S, tRNA-Leu, ND1, tRNA-Ile, and CytB) genes.

The amount of missing information ($\bar{x}$ = 33%, ranging from 6% to 92%; not accounting for gaps) does not seem alarming, considering that the two best-represented genes in our analyses (12S/16S) provided a strong backbone for placing most species, as stated by Pyron & Wiens (2011). In fact, 81% of the species had complete data for the 12S gene partition ($\bar{x}$ = 12% missing data), while the 16S partition was fully represented for 79% of the species ($\bar{x}$ = 9% missing data), and all species were represented in at least one of them. Previous studies in the literature have supported this sample design for conducting model-based phylogenetic analyses, both theoretically and empirically (e.g., Wiens, 2003; Driskell *et al.*, 2004; Thomson & Shaffer, 2010; Wiens & Morrill, 2011), yielding taxonomically highly congruent and well-supported results (for a detailed discussion, see Pyron & Wiens, 2011). We used *MAFFT* by EMBL-EBI web toolkit (Li *et al.*, 2015) for aligning our sequences. For nuclear markers, we employed the G-INS-i strategy, assuming global homology and aligning the entire region. For mitochondrial fragments, we used the E-INS-i algorithm, which is recommended for sequences with conserved domains and a high number of gaps. We concatenated all genes into a single matrix (7,290 bp, 95 terminals) using *SequenceMatrix* v.1.7 (Vaidya *et al.*, 2011; Supplementary data S2 and S3). To determine the appropriate nucleotide substitution models, we conducted a search using *PartitionFinder* (Lanfear *et al.*, 2017; 38 partitions; Supplementary data S1 and S2), under greedy algorithm.

For the phylogenetic analysis, we conducted a Bayesian inference concurrent with node dating using the software *BEAST* v2.7.4 (Bouckaert *et al.*, 2019). We performed two independent Markov chain Monte Carlo (MCMC) simulations with a chain length of 200,000,000 generations

and a pre-burn-in of 20% using the *CIPRES Science Gateway* (Miller *et al.*, 2010). We linked the partitions into one phylogenetic species tree and incorporated clock models specific to each gene. Due to the limited fossil record in Hylidae, we followed the approach of Hime *et al.* (2021) and calibrated our node dating using a fossil-calibrated phylogenomic tree. Specifically, we set a prior for the split between Phyllomedusinae and Pelodryadinae to the late Paleocene to early Eocene period, approximately 44.5 million years ago (95% HPD: 39.3–49.5 Mya). Unfortunately, both phyllomedusines and pelodryadines are underrepresented in Hime's study (n = 2 for both subfamilies). Given the low taxon-sampling represent a problem to the divergence time estimation (Soares & Schrago, 2012), we also incorporated molecular clock models based on substitution rates reported in the literature for a nuclear (POMC: 0.0043/site/Myr; de Magalhães et al., 2017) and a mitochondrial gene (CytB: 0.0161/site/Myr; Stöck et al., 2012). Thus, we performed our search using optimised relaxed clock models (Douglas *et al.*, 2021), with a substitution rate of 0.0161/site/Myr for CytB and 0.0043/site/Myr for POMC (Stöck *et al.*, 2012; Magalhães *et al.*, 2017). We estimated the mean clock rates for all the other partitions under weak priors (1/x distribution). We inferred the species tree using a Yule model prior, while keeping all other priors at their default values. We assessed the convergence of the MCMC chains by examining the estimated sample size (ESS > 200) and checking for model parameter stationarity using *TRACER* 1.7 (Rambaut *et al.*, 2018). We discarded the initial 25% of each chain as burn-in and summarized the output as a maximum clade credibility (MCC) tree using mean node heights in *TreeAnnotator* v.2.6.2 (Bouckaert *et al.*, 2014). We pruned the MCC tree using the *ape* R package (Paradis *et al.*, 2004), retaining only the species of Phyllomedusinae and Pelodryadinae for subsequent ancestral geographical range estimation.

187 **Geographical distribution data**

188 Our geographical dataset consists of georeferenced points obtained from the *Global*
189 *Biodiversity Information Facility* (GBIF, 2023; https://www.gbif.org/), which is the largest
190 online source of distributional records (Zizka *et al.*, 2020). The geographical points were
191 obtained using the R software (R Core Team, 2023) package *rgbif* (Chamberlain & Boettiger,
192 2017), and the records were later treated in the software to eliminate duplicates and remove
193 uncertain records.

194

195 **Study area and regionalization**

196 Multiple regionalization schemes have been proposed in the literature (e.g., Olson *et al.*,
197 2001; Morrone, 2006, 2014; Dinerstein *et al.*, 2017; Escalante, 2017). Our regionalization
198 scheme primarily relies on the terrestrial ecoregions of the world, which were defined based on
199 floristic maps and vegetational types (Olson *et al.*, 2001; Dinerstein *et al.*, 2017). Studies
200 focusing on neotropical species often involve a considerable number of biogeographical units
201 due to the landscape heterogeneity of the Neotropical region (see Carneiro *et al.*, 2018; Réjaud *et*
202 *al.*, 2020; Pontes-Nogueira *et al.*, 2021). Thereafter, we defined 12 biogeographical units (Fig.
203 1A) based on relevant landscape modifications that could have influenced Phyllomedusinae
204 diversification (Fig. 1B), such as the uplift of mountain ranges (e.g., Cordilleira of Andes),
205 riverine barriers (e.g., Amazonas and Madeira rivers) and phytophysiognomic differences (e.g.,
206 DODL). Given that the Neotropics were once connected to Oceania through an Antarctic land
207 bridge, we included the Australo-Papuan Pelodryadinae subfamily (the sister clade to the

Phyllomedusinae subfamily) sampled in our phylogeny for estimating the ancestral geographical range.

In order to refine the biogeographical results regarding the MRCA of Phyllomedusinae + Pelodryadinae, we also included Oceania in our regionalization scheme. Therefore, our regionalization scheme encompasses the following regions (Fig. 1A): Central America (A, being southern limited by Chocó Department and Pacific Coast of Colombia; its connectivity southwards having been enhanced over time due to the formation of Isthmus of Panama), Northern Andes (B, encompassing Western, Central and Eastern Cordilleras of Northern Andes; it becomes a geographical barrier through the Miocene, due to the acceleration on the uplift of Eastern Cordillera), Western (C), Eastern (D), and Southern Amazonia (E; limited by Amazonas and Madeira rivers; the three areas were differently affected by marine introgressions occurred along the Miocene), Caatinga (F; reducing connectivity between forested areas as the DODL expanded), Cerrado (G; reducing connectivity between forested areas as the DODL expanded), Northern (H), Central (I), and Southern Atlantic Forest (J; divided by Serra do Mar and Mantiqueira Mountain Ranges; the three areas being differently affected by the late uplift of both mountain ranges), Chaco/Pampas (K, encompassing Chaco, Pantanal, and the Uruguayan savanna, northern limited by Araucaria moist forests; reducing connectivity between forested areas as the DODL expanded), and Oceania (L, comprising the whole New Guinea island, the Wallacea region and Australia; continent with a complex history of connectivity with South America through Antarctica over geological time).

We used the R package *SpeciesGeoCoder* (Töpel *et al.*, 2017) to code the presence of all species in each biogeographical unit using a threshold of 5%. This means that for a species to be considered present in a unit, its distribution in that unit must be higher than 5% of all the

distributional records for that species. The result was later revised using Frost's (2023) description of the species distribution.

Ancestral geographical range estimation

Ancestral range estimation is performed based on the current distribution of sampled species and their phylogenetic relationships (Sanmartín, 2016). Several models for ancestral range estimation have been proposed in the literature, with the Dispersal-Vicariance Analysis (DIVA; Ronquist, 1997), the Dispersal-Extinction-Cladogenesis (DEC; Ree *et al.*, 2005; Ree & Smith, 2008), and the BayArea model (Landis *et al.*, 2013) being the most widely employed. These models have been incorporated into the *BioGeoBEARS* R package (Matzke, 2013, 2014) which provides a unified Maximum Likelihood (ML) environment for biogeographical analysis. This allows for the use of parameters that control biogeographical processes and model testing, eliminating the need for arbitrary model selection. In our study, we implemented eight models in *BioGeoBEARS*, all of them being variations of DEC and DIVALIKE (the ML version of the original DIVA included in *BioGeoBEARS*). We chose not to use BAYAREALIKE (the ML version of the original BayArea included in *BioGeoBEARS*) because it does not consider vicariance in its estimation (Matzke, 2013). Some models considered time-stratified dispersal matrices (TS), which are multipliers based on the landscape evolution of the study region (see Fig. 1C, and Supplementary data S4 and Table S4.1 for details). The values in the TS matrices restrict the probabilities of dispersal between geographical units, ranging from 0 (when a geographical barrier completely prevents dispersal) to 1 (when there are no dispersal limitations between units). To weigh the relative significance of the TS matrices, we also included the free parameter *w*, which acts as an exponent on the matrices (see Dupin *et al.*, 2017). Additionally, to

account for the colonization of novel biogeographical areas at the time of cladogenesis (Matzke, 2014, 2022; Klaus & Matzke, 2020), we included the parameter *j*. We set the maximum range size to 5, which corresponds to the number of areas occupied by the most widespread species in our clade. We compared all the models using AIC (Akaike Information Criterion) and calculated Akaike weights (Akaike, 1974; Burnham & Anderson, 2004; Wagenmakers & Farrell, 2004).

RESULTS

Phylogeny and divergence time estimation

Bayesian inference recovered all the genera in our sample with high posterior probabilities (PP = 1.00 for all genera; Fig. 2), both in Phyllomedusinae and Pelodryadinae. We recovered *Cruziohyla* as the sister clade to the other Phyllomedusinae genera (PP = 1.00; Fig. 2), with the MRCA of the genus dating from 16.2 Mya (HPD 95%: 4.4–30.6 Mya). *Phrynomedusa*, the next diverging lineage (PP = 0.59; Fig. 2), exhibited an MRCA that diversified from 17.8 Mya (HPD 95%: 8.0–28.7 Mya). We found *Agalychnis* Cope, 1864 as the sister to *Hylomantis* Peters, 1873 (PP = 1.00; Fig. 2), a clade age estimated to be 29.8 Mya (HPD 95%: 24.3–35.7 Mya). Regarding the core of Phyllomedusinae (i.e., MRCA of *Callimedusa*, *Phasmahyla*, *Phyllomedusa*, and *Pithecopus*; PP = 1.00; Fig. 2), a clade mainly diversified in forested areas, our estimation suggests an age of 32.4 Mya (HPD 95%: 27.1–38.0 Mya). We recovered *Phasmahyla* as sister group to the other three genera, being the MRCA of the clade *Phyllomedusa* (*Callimedusa* + *Pithecopus*) (PP = 1.00; Fig. 2) estimated to be 27.1 Mya (HPD 95%: 22.5–32.0 Mya).

Ancestral geographical range estimation

The best-fitted model in our analysis was DECTS+*j* (Table 1; AIC = 406.9; AICw ~ 1.00), incorporating landscape evolution in the Neotropics and jump dispersal processes (Fig. 3; see Supplementary data S5 for details). We found the divergence of Phyllomedusinae + Pelodryadinae (52.4 Mya; HPD 95%: 46.6–58.6 Mya) occurred through vicariance, with the MRCA of Pelodryadinae subsequently dispersing through Oceania (unit L; Figs. 3, 4a; Supplementary data S5). Meanwhile, the MRCA of Phyllomedusinae exhibited a wide distribution across the Neotropics, encompassing units ABHI (Figs. 3, 4a).

The earliest diversification event within the clade occurred when sympatric populations of the MRCA gave rise to *Cruziohyla* in Central America (unit A, 38.6 Mya; HPD 95%: 32.7–45.0 Mya). Subsequently, a vicariant event isolated populations in the Central Atlantic Forest at 36.9 Mya (HPD 95%: 31.3–43.0 Mya), leading to the origin of the *Phrynomedusa* genus (unit I; Figs. 3, 4b; Supplementary data S5). Within the ABH range, ancestral populations underwent another vicariant process at 29.8 Mya (HPD 95%: 24.3–35.7 Mya; Figs. 4c), resulting in the emergence of *Hylomantis* in the Northern Atlantic Forest (unit H) with species diversifying in sympatry, and *Agalychnis* in Central America and the Northern Andes (units AB). The MRCA of *Agalychnis* underwent an early vicariant process (27.4 Mya; HPD 95%: 21.9–33.1 Mya; Fig. 4d), resulting in the divergence of the Andean species *A. hulli* Duellman and Mendelson, 1995 (unit B) from other species (unit A). Subsequently, the Central American species of *Agalychnis* began to diversify primarily in sympatry in the last 24 million years.

Table 1. AIC comparisons of the Ancestral range estimation models.

Models	LnL*	n*	*d**	*e**	*j**	*w**	AIC	AIC weights

DECTS+*j***	**-200.5**	**3**	**0.0072**	**<0.001**	**0.051**	**1**	**406.9**	**~1**
DECTS	-208	2	0.0086	<0.001	0	1	420	0.0015
DIVALIKETS+*j*	-210.7	3	0.0079	<0.001	0.052	1	427.3	<0.001
DECTS+*j*+*w*	-215.7	4	0.004	<0.001	0.017	0.0067	439.4	<0.001
DIVALIKETS	-218.4	2	0.011	<0.001	0	1	440.7	<0.001
DECTS+*w*	-220.6	3	0.0048	<0.001	0	0.0031	447.2	<0.001
DIVALIKETS+*j*+*w*	-225.6	4	0.0048	<0.001	0.018	0.0049	459.3	<0.001
DIVALIKETS+*w*	-230	3	0.0068	<0.001	0	0.083	466.1	<0.001
DEC+*j*	-236.9	3	0.0025	<0.001	0.0087	1	479.9	<0.001
DEC	-240.3	2	0.0029	<0.001	0	1	484.7	<0.001
DIVALIKE+*j*	-244.4	3	0.0028	<0.001	0.012	1	494.8	<0.001
DIVALIKE	-250.3	2	0.0037	<0.001	0	1	504.7	<0.001

*LnL = log-likelihood of the model. n = number of free parameters in the model (that being *d*, *e*, *j* and *w*); *d* = rate of range expansion (i.e. anagenetic dispersal); *e* = rate of range contraction (i.e. extinction); *j* = jump dispersal process; and *w* = dispersal multiplier parameter (for TS models).

**DECTS+j is shown in bold and represents the best model under AIC and AIC weights.

On the other hand, the MRCA of *Phasmahyla* + (*Phyllomedusa* (*Callimedusa* + *Pithecopus*)) colonised the Central Atlantic Forest (unit I; 32.4 Mya; HPD 95%: 27.1–38.0; Fig. 4b) through a jump dispersal event from the ancestral range ABH. Sympatric populations in the Central Atlantic Forest gave rise to the genus *Phasmahyla* (unit I). This genus displayed two distinct clades: one diversified through jump dispersal to the Northern Atlantic Forest and Cerrado (units G and H) in the past 7 Mya, while the other clade began diversifying through dispersal within the Central Atlantic Forest (unit I) and subsequent jump dispersal to the Northern Atlantic Forest approximately 5 Mya. Additionally, ancestral populations from the Central Atlantic Forest (unit I) underwent jump dispersal to Western Amazonia (unit C) at 27.1

311 Mya (HPD 95%: 22.5–32.0 Mya; Fig. 4b), leading to the MRCA of (*Phyllomedusa* (*Callimedusa*
312 + *Pithecopus*)) in sympatry.

313 We identified at least three major diversification patterns within the *Phyllomedusa* genus
314 (Fig. 3). Firstly, the clade comprising *Ph. vaillanti* Boulenger, 1882 and *Ph. bicolor* Boddaert,
315 1772 originated at 13.2 Mya (HPD 95%: 8.4–18.1 Mya) through sympatric speciation within
316 Western Amazonia, followed by subsequent dispersal throughout Amazonia and the Northern
317 Andes. Secondly, the *Ph. tarsius* Cope, 1868 group experienced jump dispersal events, initially
318 colonizing the Northern Andes at 6.1 Mya (HPD 95%: 2.7–9.9 Mya) and later moving to Eastern
319 Amazonia from 4.5 Mya (HPD 95%: 1.8–7.7 Mya). Species within this group then dispersed to
320 Southern Amazonia (*Ph. camba* De la Riva, 1999; units CE) and the Northern Andes (*Ph.*
321 *tarsius*; units BCD). Thirdly, the *Ph. burmeisteri* Boulenger, 1882 group underwent jump
322 dispersal events, colonizing Chaco (unit K), followed by subsequent dispersal to the Northern
323 Atlantic Forest (unit H) and Southern Atlantic Forest (unit J) between 16.2 (HPD 95%: 12.0–
324 20.7 Mya; Fig. 4e) to 7.6 (HPD 95%: 5.3–10.1 Mya; Fig. 4e) million years ago. Species from
325 this group further dispersed to Chaco (*Ph. iheringii* Boulenger, 1885; units JK), Caatinga (*Ph.*
326 *bahiana* Lutz, 1925; units FH), Central Atlantic Forest (*Ph. tetraploidea* Pombal and Haddad,
327 1992 and *Ph. distincta* Lutz, 1950; units IJ), Central America (*Ph. venusta* Duellman and Trueb,
328 1967; units AB), and Cerrado (*Ph. burmeisteri*; units GHIJ) within the last 2 million years.

329 The MRCA of *Pithecopus* and *Callimedusa* remained in Western Amazonia (unit C) at
330 23.6 Mya (HPD 95%: 19.1–28.2 Mya). Both genera exhibited distinct patterns of diversification.
331 *Pithecopus* displayed a colonization pattern in the Cerrado region (unit G) through two separate
332 jump dispersal events. The first jump dispersal to the Cerrado occurred at 15.7 Mya (HPD 95%:
333 12.2–19.3 Mya; Fig. 4f), leading to a clade that diversified through sympatric speciation in

Cerrado and additional jump dispersals to the Atlantic Forest. The second jump dispersal to the Cerrado took place around 14.2 Mya (HPD 95%: 10.9–17.8 Mya; Fig. 4f), resulting in a clade primarily diversifying through sympatric speciation in Cerrado and range expansions (i.e., anagenetic dispersals) to the Atlantic Forest and Chaco. Additionally, *Pi. hypochondrialis* Daudin, 1800 reached the Northern Andes and Eastern/Southern Amazonia. However, *Pi. gonzagai* Andrade, Haga, Ferreira, Recco-Pimentel, Toledo, and Bruschi, 2020, a species within this clade, originated from a jump dispersal event from the Cerrado to the Northern Atlantic Forest and Caatinga at 5.3 Mya (HPD 95%: 1.6–9.1 Mya). On the other hand, the *Callimedusa* genus had an early sympatric speciation that gave rise to *C. tomopterna* Cope, 1868. This species expanded its range through the entire Amazonia region (units CDE) at 18.6 Mya (HPD 95%: 13.4–24.0 Mya) and colonised the Northern Andes (unit B). Subsequently, another sympatric speciation occurred within Western Amazonia around 14.2 Mya (HPD 95%: 8.2–20.3 Mya; Fig. 4f). This cladogenesis resulted in the origin of *C. atelopoides* Duellman, Cadle, and Cannatella, 1988 and the MRCA of the other *Callimedusa* species, who reached the Northern Andes by jump dispersal, afterward diversifying in sympatry since 10.4 Mya (HPD 95%: 5.1–15.8 Mya; Fig. 4f).

DISCUSSION

In the present study, we provided a detailed analysis of the diversification and colonisation history of Monkey tree frogs across the Neotropics. By sampling 85% of the formally described phyllomedusine species, using mitochondrial and nuclear markers, our results represent a robust framework to discuss the processes concerning the biogeographical history of the group. Regarding the phylogenetic relationships among phyllomedusine genera, our topology is mostly congruent with previous studies in literature based on molecular data (e.g., Faivovich *et*

357 *al.*, 2005; 2010; Pyron & Wiens, 2011; Rivera-Correa *et al.*, 2013; Duellman *et al.*, 2016; Jetz &
358 Pyron, 2018). Furthermore, our results on node dating and ancestral geographical range
359 estimation indicates the diversification of phyllomedusines was markedly influenced by
360 environmental changes resulting from the Miocene marine introgressions and Andean orogeny.
361 In detail, most lineages in Phyllomedusinae diversified in a dynamic scenario that occurred in
362 Western Amazonia, which was limited by the Pebas System and the Paranaense sea
363 (north/westward and southward, respectively) during the Miocene.

364 The most evident divergence recovered in phylogenetic inference was the relative
365 position of *Cruziohyla* and *Phrynomedusa* genera. Previous studies usually recover
366 *Phrynomedusa* as the first branching lineage in Phyllomedusinae (Faivovich *et al.*, 2005; 2010;
367 Pyron & Wiens, 2011) or composing a clade *Cruziohyla* + *Phrynomedusa* (Duellman *et al.*,
368 2016; Jetz & Pyron, 2018). Since the split between the lineage that will give rise to *Cruziohyla*
369 and the other phylomedusines occurred at 38.6 Mya (HPD 95%: 32.7–45.0 Mya), our results
370 imply a first conquest of the northern Neotropics between the late Eocene and middle Oligocene.
371 At the genus level, the topology we found for *Phasmahyla* deviates from the previous studies,
372 but none of them coincide (Faivovich *et al.*, 2005; 2010; Pyron & Wiens, 2011; Duellman *et al.*,
373 2016; Jetz & Pyron, 2018; Pereira *et al.*, 2018), and therefore the phylogeny of the genus remains
374 under debate. Also, some inconsistences regarding *Phasmahyla* argue for a careful taxonomic
375 review. *Phasmahyla cruzi* Carvalho-e-Silva, Silva, and Carvalho-e-Silva, 2009, for instance, is
376 assumed to be known only from its type locality (Rio das Pedras Reserve, Municipality of
377 Mangaritiba, state of Rio de Janeiro, Brazil; Frost, 2023). However, there are no molecular data
378 on Genbank from this population, and the species was represented by a specimen assigned to
379 other locality (Picinguaba, municipality of Ubatuba, state of São Paulo, Brazil; Pyron & Wiens,

2011; Faivovich *et al.*, 2005; 2010; Duellman *et al.*, 2016; Jetz & Pyron, 2018; Pereira *et al.*, 2018; present study, Supplementary data S1). We found other occasional divergences regarding the relative position of some species in *Pithecopus* and *Phyllomedusa*, compared to other studies (Faivovich et al., 2010; Pyron & Wiens, 2011; Duellman *et al.*, 2016; Jetz & Pyron, 2018; Pereira *et al.*, 2018).

Much of the current information provided on the node dating of phylomedusine' frogs come from studies focusing on large-scale approaches, but with a low representativeness for the clade. Phylogenomic studies using similar sets of fossil calibrations point to a split between Phyllomedusinae and Pelodryadinae occurring at 47.4 Mya (Feng et al., 2017) or 44.5 Mya (Hime et al., 2020; Portik et al., 2023), implying in an early diversification of phyllomedusines at 24.5 Mya (CI 95%: 20.0–29.7 Mya; Feng et al., 2017), 23.2 Mya (HPD 95%: 18.4–28.1 Mya; Hime et al., 2020) or 27.5 Mya (HPD 95%: 24.0–35.8 Mya; Portik et al., 2023). The divergence time estimation of the clade may be taken carefully, given the low representativeness of phyllomedusines in some of these previous works (Feng et al., 2017; Hime et al., 2020) and the recognised impact of taxon-sampling on time estimations under bayesian frameworks (Soares & Schrago, 2012; Matschiner, 2019; Luo et al., 2023). Our results set both the split phyllomedusine-pelodryadine and the early onset of diversification in Phyllomedusidae to the past, occurring at 52.4 Mya (HPD 95%: 46.6–58.6 Mya) and 38.6 Mya (HPD 95%: 32.7–45.0 Mya), respectively. In other words, our findings assign the phyllomedusines the status of a clade that dates from the late-Eocene/early-Oligocene rather than the late-Oligocene. Similar results were obtained previously by a maximum likelihood approach performed using an extensive sampling of the subfamily (Duellman et al., 2016), suggesting the split phyllomedusine-

pelodryadine to be 61.8 Mya (HPD 95%: 57.5–66.1 Mya) and the Phyllomedusinae dated to 33.3 Mya (HPD 95%: 29.0–37.6 Mya).

The split we found for the MRCA of Phyllomedusinae + Pelodryadinae occurred by vicariance (Figures 3 and 4A; Supplementary data S5). At the early Eocene, our results suggest that the MRCA of Phyllomedusinae + Pelodryadinae was widely distributed throughout South America, Oceania, and, therefore, Antarctica (Fig. 4A). The diversification between the two subfamilies during the passage from late-Eocene to early-Oligocene occurred concurrently to the convoluted process of separation between the three continents, as proposed by Duellman et al. (2016). Hence, the vicariance associated was probably caused by landmasses movement, promoting the initial divergence of pelodryadines and phyllomedusines. Moreover, our results emphasize much of the early diversification of the Phyllomedusinae was influenced by vicariances from this widespread Neotropical ancestor (e.g., MRCA of the clade *Hylomantis* + *Agalychnis*, diversification of *Phrynomedusa* and *Agalychnis* genera; Figure 3 and 4B-D). Hence, our results reject the "south-north" diversification hypothesis of the Phyllomedusinae subfamily, as the diversification within the group occurred from Western Amazonia towards Northern Andes and the diagonal of dry landscapes. Our findings show a different scenario from Duellman et al. (2016) proposal, where the authors argued the split between the two subfamilies may took place within the Neotropics, with "protopelodryadines" dispersing to Australia afterward. Since our sampling focused in Phyllomedusinae, it is difficult to extend the discussion to the context of the whole Hylidae family. We encourage future biogeographical studies to examine the question in more detail.

Our results on the DECTS+*j* model suggest that Western Amazonia (unit C) acted as a species pump for *Phyllomedusa*, *Pithecopus* and *Callimedusa* genera. This area is frequently

recovered for ancestral ranges in several animal groups (e.g., lizards, Prates *et al.*, 2017; snakes, Dal Vechio *et al.*, 2018; Pontes-Nogueira *et al.*, 2021). Western Amazonia was recovered as the ancestral area for the clade *Phyllomedusa* (*Callimedusa* + *Pithecopus*) after a jump dispersal in the split between *Phasmahyla* and the clade *Phyllomedusa* (*Callimedusa* + *Pithecopus*). This scenario took place from the early to the middle Miocene, concomitantly to the occurrence of lacustrine conditions due to the Pebas system (Hoorn *et al.*, 2010, 2017; Jaramillo *et al.*, 2010; Figs. 4e, 4f), and virtually affecting the entire Western Amazonia. Previous studies also emphasise the influence of Pebas system over the biogeography of neotropical anuran fauna, driving their evolutionary history in different ways (Carvalho, 1954; Zimmermann and Zimmermann, 1988; Fouquet *et al.*, 2012; 2021a; 2022; Réjaud *et al.*, 2020). The absence of an overall pattern in Anura seems to be related to the diversity of natural history traits. Hence, Pebas system turned Western Amazonia an unsuitable environment for ground-dweller frogs, negatively affecting the diversification of terrestrial (Phyzelaphryninae and *Allobates* Zimmermann and Zimmermann, 1988; Fouquet *et al.*, 2012; Réjaud *et al.*, 2020) and burrowing (*Synapturanus* Carvalho, 1954; Fouquet *et al.*, 2021a) clades. On the other hand, the marine incursion was crucial for the origin and diversification of aquatic clades (*Pipa* Linnaeus, 1758; Fouquet *et al.*, 2022). Here, we found evidence of Pebas system promoting the diversification of arboreal anurans, given that the most speciose clade in Phyllomedusinae had origin and diversification in this area. This is an important finding, since other studies regarding arboreal frogs have shown diversification after the regression of the Pebas system (e.g., *Boana albopunctata* Spix, 1824 species group; Fouquet *et al.*, 2021b). As far as we know, our present study is the most comprehensive framework on this issue.

From Western Amazonia, we found that phyllomedusines conquered the central and southern regions of the Neotropics in the last 16 million years (Figs. 4E and 4F), encompassing the genera *Pithecopus* and *Phyllomedusa*. *Pithecopus* lineages jump-dispersed from Western Amazonia twice during the middle Miocene, occupying areas that would later become the diagonal of open/dry landscapes (DODL). We observed a similar pattern in the most speciose clade in *Phyllomedusa*, encompassing the *Ph. burmeisteri* group (sensu Faivovich *et al.*, 2010): *Ph. boliviana* Boulenger, 1902, *Ph. sauvagii* Boulenger, 1882, and *Ph. venusta* Duellman and Trueb, 1967. Both cases exemplify a “north-southern" biogeographical colonisation of the Neotropics, far mentioned on literature for several groups (snakes, Wüster *et al.*, 2002; Hamdan *et al.*, 2019; termites, Carrijo *et al.*, 2020), including frogs (e.g., Fouquet *et al.*, 2012, 2014). This further contradicts the hypothesis of a “south-north” diversification pattern for this subfamily.

By occurring during the middle Miocene, these biogeographical processes are concurrent to the transition from Pebas into the Acre system, taking place in an Amazonian wetland. Firstly, all those lineages left Western Amazonia coincidently with a period of recurring marine incursions of the Paranaense sea (Hernández *et al.*, 2005), that may have limited the Amazonia region southward (Figs. 4E and F). These findings suggest a progressive isolation of the core Phyllomedusinae in northern South America, agreeing with previous studies regarding the influence of Paranaense sea in biogeographical history of herpetofauna (e.g., Magalhães, 2012; Seger *et al.*, 2021). The subsequent regression of the Paranaense sea could have facilitated the colonisation of southern areas, helping to explain the diversification pattern we found. Secondly, the subsequent colonisation of South American Atlantic Forest by some of these Miocene lineages of Phyllomedusinae is congruent with the very early opening of DODL, and the late orogeny of the Serra do Mar Mountain Range. This pattern represents a jump dispersal response

to the retraction of forested areas in due to the environmental changes drove by the opening of DODL, commonly found in other anuran groups (e.g., Pirani *et al.*, 2020; Carvalho *et al.*, 2021). The whole biogeographical process also shed light on our findings about the diversification of *Phasmahyla* genus, that remained isolated in South American Atlantic Forest in the last 10 million years.

Also, we found that several phyllomedusine' lineages diversified along the Miocene from Western Amazonia to northward (Figs. 3 and 4F), through the Andes and Central America. The biogeographical history of these species suggests a colonisation of Amazonia and Northern Andes, occupying the forested lowlands from the Miocene to the Pleistocene. During a period of drastic changes in local drainage patterns due to the transition from Pebas into the Acre system (Hoorn *et al.*, 2010), we found the *Phyllomedusa* genus has been particularly successful colonising the entire Amazonian region. Together, these results seem to reinforce the idea that phyllomedusine frogs were able to survive in the lacustrine environment resulting from changes in the Amazonian drainage pattern when compared to other frog groups. Previous studies have already suggested the isolation and geographic expansion in other arboreal frogs may have been affected by the Miocene marine introgressions, depending on their capacity to exploit wetland environments for reproduction (e.g., Ortiz *et al.*, 2023).

Following this northward diversification (Fig. 4F), we found some aspects of the historical biogeography of phyllomedusines as closely related to the uplift of the Northern Andes. Populations of the MRCA of *Callimedusa* in Western Amazonia experienced an early divergence within this region, giving rise to *Callimedusa tomopterna* (Fig. 3). Subsequently, populations from the MRCA of other *Callimedusa* species jump-dispersed to the Northern Andes, where mountain uplifts potentially facilitated sympatric speciation during the mid-

493 Miocene (Fig. 4F). The diversification of *Pithecopus* in the Cerrado can also be directly
494 attributed to the Andes uplift. Although the MRCA of *Pithecopus* primarily were in Western
495 Amazonia, ancestral populations reached the Cerrado by two separate jump dispersal events (Fig.
496 3). Divergences coincided with the final opening of the DODL, where the late Andean uplift
497 contributed to the uplift and dryness of the Brazilian Plateau and the subsidence of the Chaco
498 region (Figs. 4E and 4F; Zanella, 2011; see also Silva, 1995; Pontes-Nogueira et al., 2022). Once
499 ancestral lineages of *Pithecopus* colonised the Cerrado, they diversified in sympatry alongside
500 the changing landscape of this region (Fig. 3). Thus, the uplift of the Andes probably played a
501 main role in cladogenetic processes in phyllomedusine lineages during mountain uplift events, as
502 well as in areas that suffered landscape changes influenced by the elevation of the mountain
503 range.

504 The diversification of the *Agalychnis* and *Cruziohyla* genera during their conquest of
505 Central America is intriguing. In *Agalychnis*, the colonisation of the Central America by the
506 ancestors of the Phyllomedusinae frogs before Miocene precedes the formation of the Isthmus of
507 Panama, proposed to occur in the Plio-Pleistocene (~3 mya; Fig. 3; Haug & Tiedemann, 1998;
508 O'Dea *et al.*, 2016). Bacon *et al*. (2015) demonstrated two significant waves of dispersal
509 between South and North America at around 20 and 5 Mya, also preceding the recent formation
510 hypothesis times. At a first glance, our results for *Cruziohyla* are in accordance with the first
511 wave of dispersal, as the MRCA of *Cruziohyla* is synchronous to the very early formation of
512 Isthmus of Panama and early uplift of the Eastern Cordillera of Northern Andes (Gregory-
513 Wodzicki, 2000). Recent biological (Bacon *et al.*, 2013, 2015; Bloch *et al.*, 2016) and geological
514 (Farris *et al.*, 2011; Montes *et al.*, 2012, 2015; Jaramillo *et al.*, 2017) findings suggest an older
515 formation for the Isthmus of Panama (early-mid Miocene), despite the discussion in literature

(e.g., O'Dea *et al.*, 2016). However, any statement in this sense is imprecise, as the biogeographical process associated with the early conquest of Central America during the split between phyllomedusines and pelodryadines is not known. It is thought that range expansion (i.e., anagenetic dispersal) is more plausible to occur by land (for land animals) and that jump dispersals are predominantly associated with geographical barriers (see Matzke, 2014 for more information), Therefore, further studies considering the whole Hylidae family may address this issue more precisely. The biogeography of the Neotropics is surely intriguing and intricate, and the history of the monkey tree frogs described here comes to add even more a level of certainty to this statement.

CONCLUSIONS

We found that the biogeographical history of Phyllomedusinae started with a vicariance splitting the Neotropical region, Oceania, and Antarctica. Indeed, vicariance was a common biogeographical process at the early diversification of phyllomedusines, while jump dispersals must have been responsible for the majority of colonizations in the group since the Miocene. Western Amazonia seems to have figured as a species pump for most of the monkey tree frogs, with species colonising the area and diversifying sympatrically even during the highly unstable environment of the Miocene. Also, the orogeny of Northern Andes could have played an important role in species diversification, promoting sympatric speciation both through the uplift of mountains and in areas with drastic landscape changes provoked by the elevation of the Andean Mountain range. Our results also reject the hypothesis of a "south-north" diversification for the group. In brief, we successfully encompassed most of the historical biogeography of this

speciose group, enabling a highly detailed description of the diversification of a charismatic frog subfamily.

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983 **DATA AVAILABILITY STATEMENTS**

Supplementary data is available at Figshare, under the following DOI: https://doi.org/10.6084/m9.figshare.24282592.v1. The third-party data used in this study is available at GBIF under the following URL: https://www.gbif.org/species/4817115.

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Figure 1

A, Map of biogeographical areas in Neotropical region;

B, Map of biogeographical areas in Oceania. The areas are: Central America (A), Northern Andes (B), Western Amazonia (C), Eastern Amazonia (D), Southern Amazonia (E), Caatinga (F), Cerrado (G), Northern Atlantic Forest (H), Central Atlantic Forest (I), Southern Atlantic Forest (J), Chaco/Pampas (K), and Oceania (L); C, The summary of events acting as potential geographical barriers. We have used double arrows to specify instances where dispersal probabilities between the areas denoted were the only ones being affected; in contrast, we used commas to specify the cases where any dispersal through those areas had their probability decreased. Time stratification was applied to address landscape dynamics to our analysis, being indicated by the gray-white transition in geological time scale. In Neotropics, the complex Amazonas/Madeira was denoted as a geographical barrier to dispersal between Amazonian areas since late-Miocene; previously, Pebas and Acre systems were actuating on the same region along the entire Miocene. Moreover, Paranaense sea was another marine introgression occurring in Neotropics along the Miocene. The increase in connectivity between North and South America since the mid-Miocene, due to the formation of Panamá Isthmus bring another example of a geographical barrier “softened” through time. On the other hand, the uplift rates of Northern Andes and Serra do Mar and Mantiqueira Mountain Ranges had increased since mid-Miocene, becoming a harsher barrier. This is also the case of DODL, that reduced connectivity between Amazonian and Atlantic forested areas by the expansion of aridity since the very late-Miocene. In Oceania, the connectivity between Australia and both New Guinea and Zealand has also varied over the time. Furthermore, deserts had firstly isolated Western Mesic Biome, subsequently expanding to the East since Oligocene and affecting dispersals to the Eastern Mesic Biome. See Supplementary data S4 and Tables S4.1 and S4.2 for details.

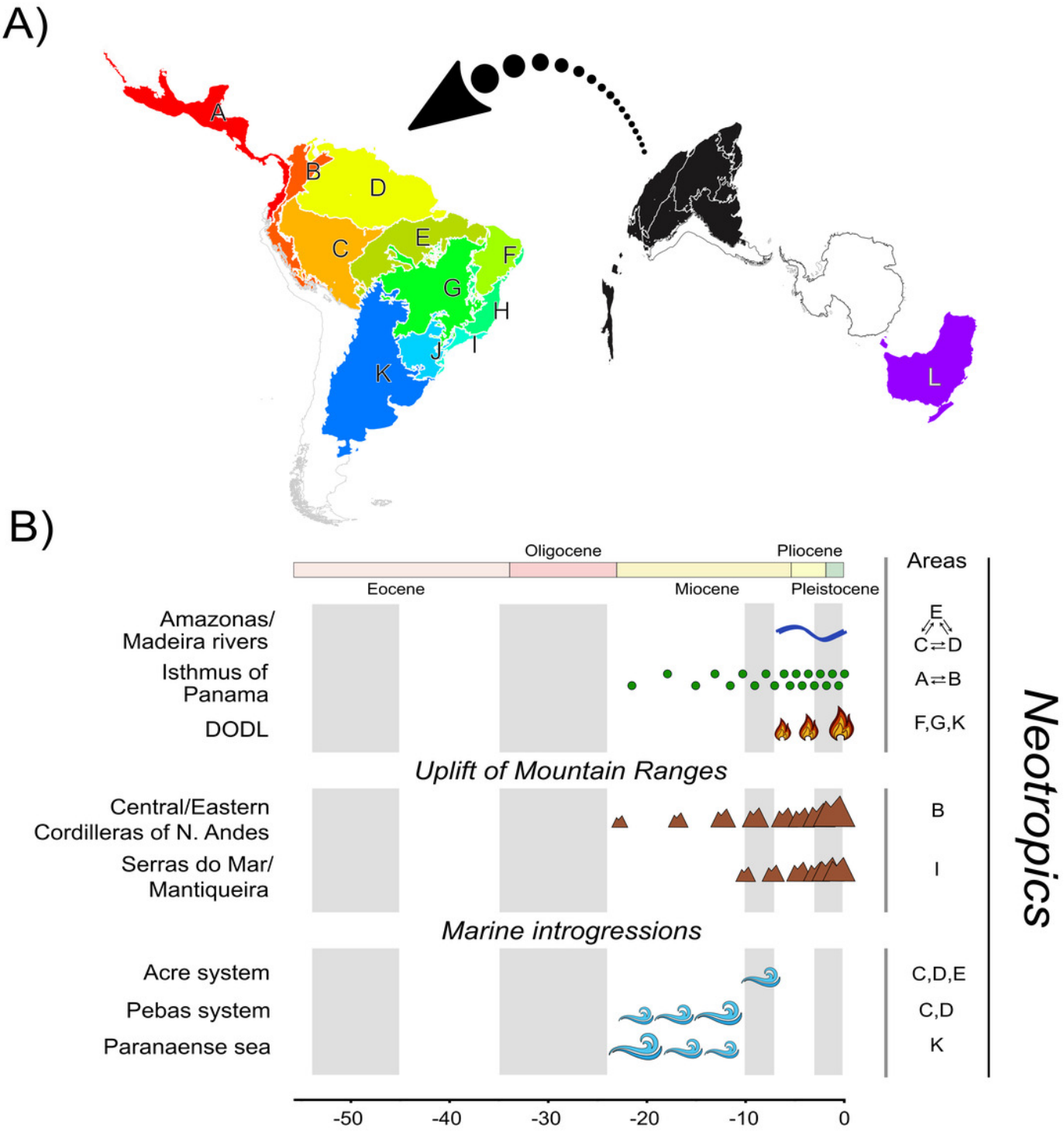
A)
A
B
C
D
E
F
G
H
I
J
K
L
B)
Oligocene
Pliocene
Areas
Eocene
Miocene
Pleistocene
Amazonas/
Madeira rivers
E
C⇄D
Isthmus of
Panama
A⇄B
DODL
F,G,K
Uplift of Mountain Ranges
Central/Eastern
Cordilleras of N. Andes
B
Serras do Mar/
Mantiqueira
I
Marine introgressions
Acre system
C,D,E
Pebas system
C,D
Paranaense sea
K
Neotropics
-50
-40
-30
-20
-10
0

Figure 2

Bayesian dated phylogenetic tree of Phyllomedusidae, based on 13 mitochondrial and nuclear concatenated loci (7,290 bp, 95 terminals).

Horizontal green bars represent the 95% HPD (height posterior density) intervals for the divergence date estimates. Black asterisks indicate clades where the value of posterior probability (pp) is lower than 0.9. See Supplementary data S1 for details about partitioning and the models of nucleotide substitution.

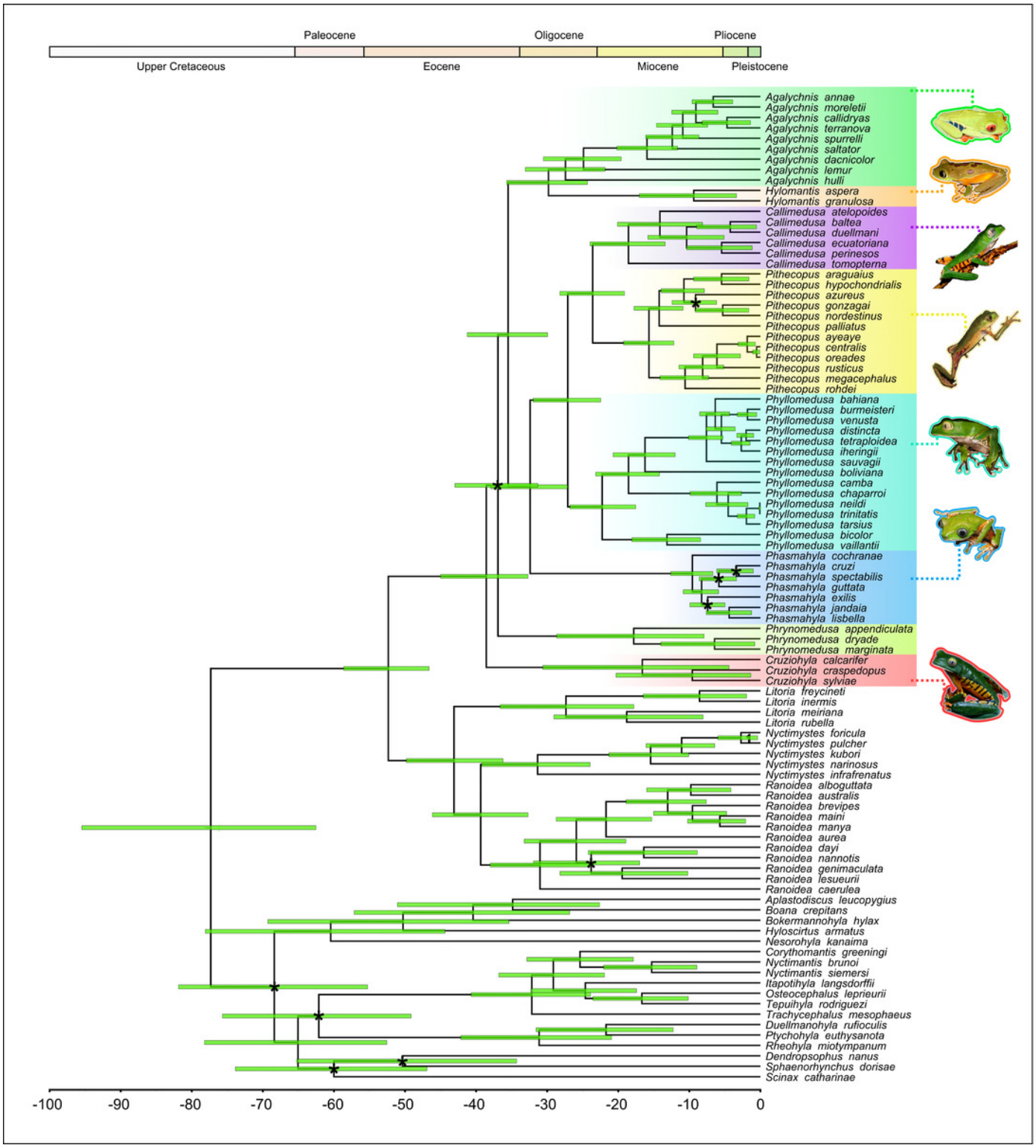
Paleocene
Oligocene
Pliocene
Upper Cretaceous
Eocene
Miocene
Pleistocene
Agalychnis annae
Agalychnis moreletii
Agalychnis callidryas
Agalychnis terranova
Agalychnis spurrelli
Agalychnis saltator
Agalychnis dacnicolor
Agalychnis lemur
Agalychnis hulli
Hylomantis aspera
Hylomantis granulosa
Callimedusa atelopoides
Callimedusa baltea
Callimedusa duellmani
Callimedusa ecuatoriana
Callimedusa perinesos
Callimedusa tomopterna
Pithecopus araguaius
Pithecopus hypochondrialis
Pithecopus azureus
Pithecopus gonzagai
Pithecopus nordestinus
Pithecopus palliatus
Pithecopus ayeaye
Pithecopus centralis
Pithecopus oreades
Pithecopus rusticus
Pithecopus megacephalus
Pithecopus rohdei
Phyllomedusa bahiana
Phyllomedusa burmeisteri
Phyllomedusa venusta
Phyllomedusa distincta
Phyllomedusa tetraploidea
Phyllomedusa iheringii
Phyllomedusa sauvagii
Phyllomedusa boliviana
Phyllomedusa camba
Phyllomedusa chaparroi
Phyllomedusa neildi
Phyllomedusa trinitatis
Phyllomedusa tarsius
Phyllomedusa bicolor
Phyllomedusa vaillantii
Phasmahyla cochranae
Phasmahyla cruzi
Phasmahyla spectabilis
Phasmahyla guttata
Phasmahyla exilis
Phasmahyla jandaia
Phasmahyla lisbella
Phrynomedusa appendiculata
Phrynomedusa dryade
Phrynomedusa marginata
Cruziohyla calcarifer
Cruziohyla craspedopus
Cruziohyla sylviae
Litoria freycineti
Litoria inermis
Litoria meiriana
Litoria rubella
Nyctimystes foricula
Nyctimystes pulcher
Nyctimystes kubori
Nyctimystes narinosus
Nyctimystes infrafrenatus
Ranoidea alboguttata
Ranoidea australis
Ranoidea brevipes
Ranoidea maini
Ranoidea manya
Ranoidea aurea
Ranoidea dayi
Ranoidea nannotis
Ranoidea genimaculata
Ranoidea lesueurii
Ranoidea caerulea
Aplastodiscus leucopygius
Boana crepitans
Bokermannohyla hylax
Hyloscirtus armatus
Nesorohyla kanaima
Corythomantis greeningi
Nyctimantis brunoi
Nyctimantis siemersi
Itapotihyla langsdorffii
Osteocephalus leprieurii
Tepuihyla rodriguezi
Trachycephalus mesophaeus
Duellmanohyla rufioculis
Ptychohyla euthysanota
Rheohyla miotympanum
Dendropsophus nanus
Sphaenorhynchus dorisae
Scinax catharinae
-100
-90
-80
-70
-60
-50
-40
-30
-20
-10
0

Figure 3

Ancestral range estimations from DECTS + *j* model implemented in BioGeoBEARS.

Colored boxes with letters represent the most probable range estimated by the model (boxes for nodes in the last 20 million years are not shown for better visualization of these nodes). Ancestral area estimations at nodes represent areas before an inferred instantaneous speciation event; colored rectangles at the tips with letters indicate the current distribution of extant species. Pie charts on nodes represent probabilities of ranges. Only the four most probable states at each node are shown for better visualization, and blank spaces represents all other probabilities (see Supplementary data S5 for more information).

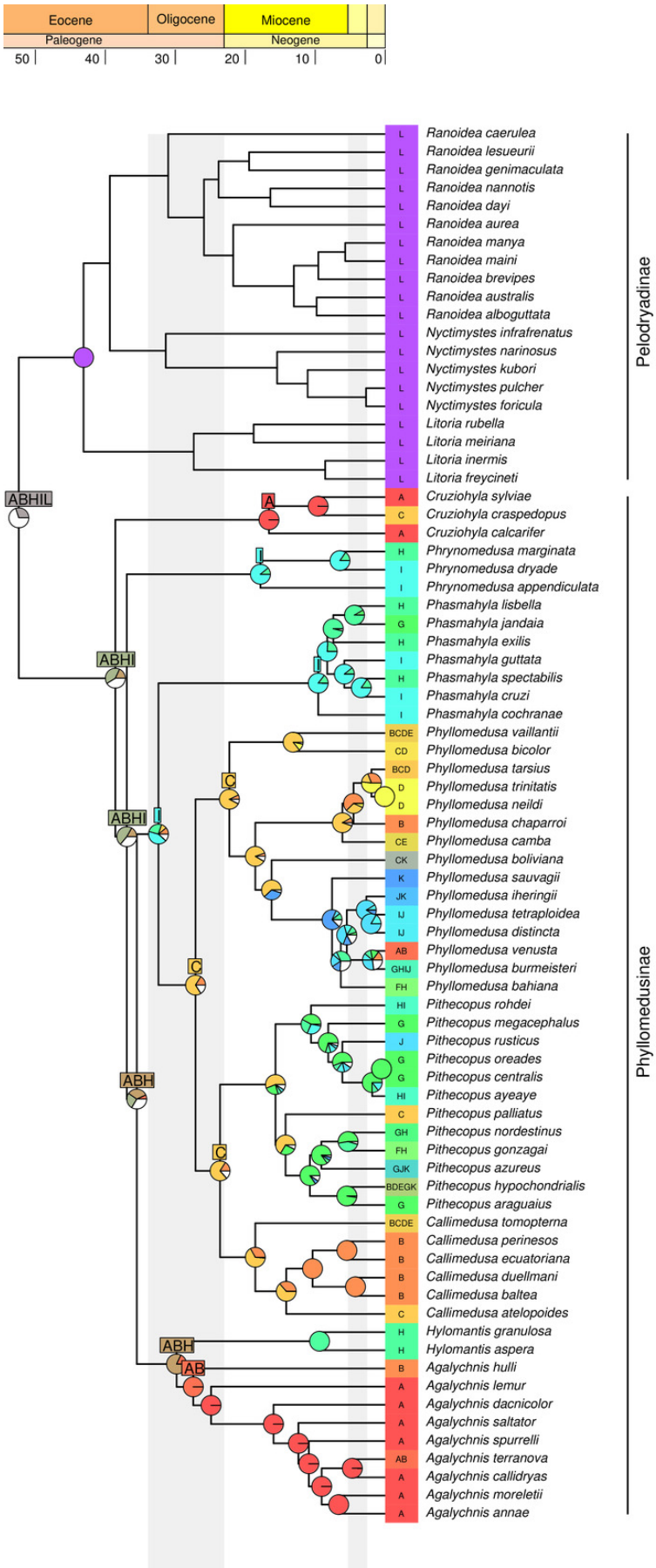
Eocene
Oligocene
Miocene
Paleogene
Neogene
50
40
30
20
10
0
Ranoidea caerulea
Ranoidea lesueurii
Ranoidea genimaculata
Ranoidea nannotis
Ranoidea dayi
Ranoidea aurea
Ranoidea manya
Ranoidea maini
Ranoidea brevipes
Ranoidea australis
Ranoidea alboguttata
Nyctimystes infrafrenatus
Nyctimystes narinosus
Nyctimystes kubori
Nyctimystes pulcher
Nyctimystes foricula
Litoria rubella
Litoria meiriana
Litoria inermis
Litoria freycineti
Cruziohyla sylviae
Cruziohyla craspedopus
Cruziohyla calcarifer
Phrynomedusa marginata
Phrynomedusa dryade
Phrynomedusa appendiculata
Phasmahyla lisbella
Phasmahyla jandaia
Phasmahyla exilis
Phasmahyla guttata
Phasmahyla spectabilis
Phasmahyla cruzi
Phasmahyla cochranae
Phyllomedusa vaillantii
Phyllomedusa bicolor
Phyllomedusa tarsius
Phyllomedusa trinitatis
Phyllomedusa neildi
Phyllomedusa chaparroi
Phyllomedusa camba
Phyllomedusa boliviana
Phyllomedusa sauvagii
Phyllomedusa iheringii
Phyllomedusa tetraploidea
Phyllomedusa distincta
Phyllomedusa venusta
Phyllomedusa burmeisteri
Phyllomedusa bahiana
Pithecopus rohdei
Pithecopus megacephalus
Pithecopus rusticus
Pithecopus oreades
Pithecopus centralis
Pithecopus ayeaye
Pithecopus palliatus
Pithecopus nordestinus
Pithecopus gonzagai
Pithecopus azureus
Pithecopus hypochondrialis
Pithecopus araguaius
Callimedusa tomopterna
Callimedusa perinesos
Callimedusa ecuatoriana
Callimedusa duellmani
Callimedusa baltea
Callimedusa atelopoides
Hylomantis granulosa
Hylomantis aspera
Agalychnis hulli
Agalychnis lemur
Agalychnis dacnicolor
Agalychnis saltator
Agalychnis spurrelli
Agalychnis terranova
Agalychnis callidryas
Agalychnis moreletii
Agalychnis annae
ABHIL
ABHI
ABHI
ABH
ABH
AB
Pelodryadinae
Phyllomedusinae

Figure 4

Summary of the recovered biogeographical processes using arrows, following our time stratification (from the oldest to the newest).

A, a vicariant event at the split between Pelodryadinae + Phyllomedusinae, isolating both subfamilies from a wide-distributed MRCA; B, a vicariant event originating the *Phrynomedusa* genus by the isolation of populations in the Central Atlantic Forest, the same biogeographical unit from where jump-dispersed the populations who conquest the Western Amazonia and lead to the MRCA of (*Phyllomedusa* (*Callimedusa* + *Pithecopus*)) at 32.4 Mya; C, a vicariant event, resulting in the emergence of *Hylomantis* and *Agalychnis* genera from a wide-distributed MRCA; D, another vicariant event at the early diversification of *Agalychnis* genus, at the divergence of the Andean species *A. hulli*; E, north-south pattern of diversification of *P. burmeisteri* group, whose MRCA jump dispersed from Western Amazonia giving rise to a diversification along Chaco and, subsequently, Atlantic Forest' units during the early opening of DODL; F, the divergent patterns of diversification in *Pithecopus* (north-south, colonizing the Cerrado by jump dispersal in two waves) and *Callimedusa* (south-north, colonizing the Northern Andes by range expansion) genera, both taking place in Miocene concurrently to the Pebas system. See Fig. 3 for info about the units' colors and letters.

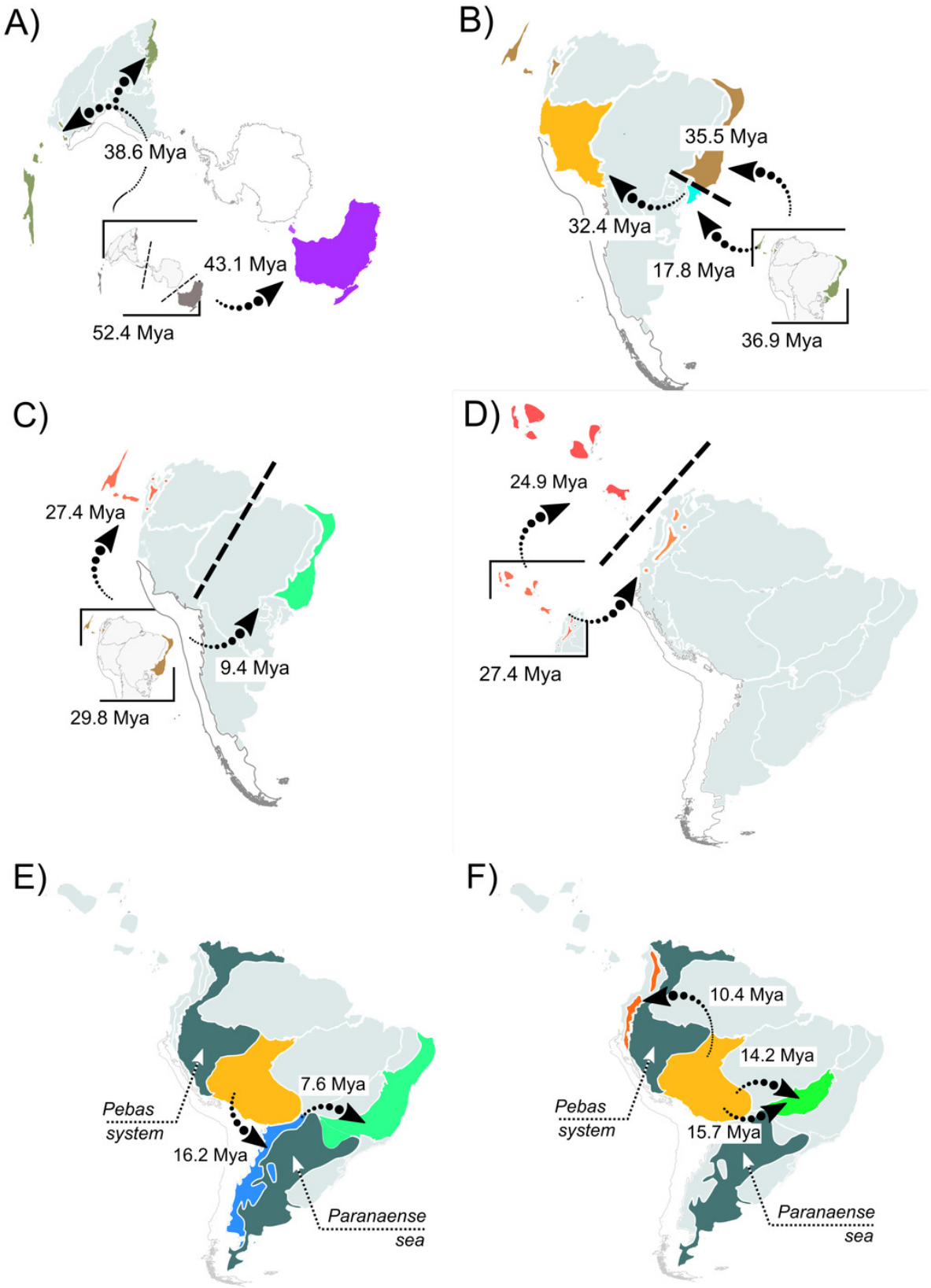
A)
38.6 Mya
43.1 Mya
52.4 Mya
B)
35.5 Mya
32.4 Mya
17.8 Mya
36.9 Mya
C)
27.4 Mya
9.4 Mya
29.8 Mya
D)
24.9 Mya
27.4 Mya
E)
7.6 Mya
Pebas system
16.2 Mya
Paranaense sea
F)
10.4 Mya
14.2 Mya
Pebas system
15.7 Mya
Paranaense sea

Table 1(on next page)

AIC comparisons of the Ancestral range estimation models.

LnL = log-likelihood of the model. n = number of free parameters in the model (that being d, e, j and w); d = rate of range expansion (i.e. anagenetic dispersal); e = rate of range contraction (i.e. extinction); j = jump dispersal process; and w = dispersal multiplier parameter (for TS models). DECTS+j is shown in bold and represents the best model under AIC and AIC weights.

Table 1. AIC comparisons of the Ancestral range estimation models. LnL = log-likelihood of the model. n = number of free parameters in the model (that being d, e, j and w); d = rate of range expansion (i.e. anagenetic dispersal); e = rate of range contraction (i.e. extinction); j = jump dispersal process; and w = dispersal multiplier parameter (for TS models). DECTS+j is shown in bold and represents the best model under AIC and AIC weights.

Models	LnL	n	*d*	*e*	*j*	*w*	AIC	AIC weights
DECTS+*j*	**-200.5**	**3**	**0.0072**	**<0.001**	**0.051**	**1**	**406.9**	**~1**
DECTS	-208	2	0.0086	<0.001	0	1	420	0.0015
DIVALIKETS+*j*	-210.7	3	0.0079	<0.001	0.052	1	427.3	<0.001
DECTS+*j*+*w*	-215.7	4	0.004	<0.001	0.017	0.0067	439.4	<0.001
DIVALIKETS	-218.4	2	0.011	<0.001	0	1	440.7	<0.001
DECTS+*w*	-220.6	3	0.0048	<0.001	0	0.0031	447.2	<0.001
DIVALIKETS+*j*+*w*	-225.6	4	0.0048	<0.001	0.018	0.0049	459.3	<0.001
DIVALIKETS+*w*	-230	3	0.0068	<0.001	0	0.083	466.1	<0.001
DEC+*j*	-236.9	3	0.0025	<0.001	0.0087	1	479.9	<0.001
DEC	-240.3	2	0.0029	<0.001	0	1	484.7	<0.001
DIVALIKE+*j*	-244.4	3	0.0028	<0.001	0.012	1	494.8	<0.001
DIVALIKE	-250.3	2	0.0037	<0.001	0	1	504.7	<0.001