

1 **There and back again: when and how the world's richest snake family**
2 **(Dipsadidae) dispersed and speciated across the Neotropical region**

3 **Running title:** Historical Biogeography of Neotropical snakes

4

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25 **ABSTRACT**

26 **Aim:** The widespread megadiverse Neotropical snake family Dipsadidae occurs
27 in a large range of diverse habitats. Thus it represents an excellent model to study the

28 diversification of Neotropical biota. Herein, by generating a time-calibrated
29 species-level phylogeny, we investigate the origin and historical biogeography of
30 Dipsadidae and test if its two main Neotropical subfamilies, Xenodontinae and
31 Dipsadinae, have different geographical origins.

32 **Location:** Neotropical region.

33 **Taxon:** Dipsadidae (Serpentes).

34 **Methods:** We generated a new Bayesian time-calibrated phylogeny including
35 sequences from six genes for 344 species, including 287 species of Dipsadidae. We
36 subsequently estimated ancestral areas of distribution by comparing models in
37 BioGeoBEARS: DEC (subset sympatry, narrow vicariance), DIVALIKE (narrow and
38 wide vicariance), BAYAREALIKE (no vicariance and widespread sympatry), also
39 testing jump dispersal.

40 **Results:** The best models show that Dipsadidae likely originated approximately
41 50 million years ago (mya) in Asia. Dispersal was a fundamental process in its
42 historical biogeography. The DEC model with jump dispersal indicated that this
43 family underwent a range extension from Asia and posterior vicariance of North and
44 Central America ancestors. Both Xenodontinae and Dipsadinae originated in Central
45 America and dispersed to South America during Middle Eocene, but did so to
46 different regions (cis and trans-Andean South America, respectively). Xenodontinae
47 entered cis-Andean South America around 39 mya and jump dispersed to the West
48 Indies around 33 mya, while Dipsadinae entered trans-Andean South America
49 multiple times 20 – 38 mya.

50 **Main conclusions:** Our results show that Dipsadidae has an Asian origin and that
51 the two main Neotropical subfamilies originated in Central America, later dispersing
52 to South America in different time periods. The current biogeographical patterns of
53 the family Dipsadidae, the most species-rich snake family in the world, have likely
54 been shaped by complex evolutionary and geological processes such as Eocene land
55 bridges, Andean uplift and the formation of the Panama isthmus.

56

57 **Keywords:** ancestral area, dispersal, diversification, historical biogeography,

58 Serpentes, vicariance

59

60 **Introduction**

61 The Neotropical realm is a climatically and geologically diverse
62 biogeographical region, encompassing a wide range of habitats, from the lush
63 rainforests of the Amazon and Central America to the snow-covered peaks of the
64 Andes. This diversity of habitats is the result of a rich and complex paleogeographical
65 history between and within two continental landmasses — Central and South
66 America — and the associated island systems (e.g., Galapagos, West Indies;
67 Clapperton, 1993; Pennington et al., 2004; Rull, 2011; Hughes, Pennington &
68 Antonelli, 2013). Even though major geological events such as the Gondwana
69 breakup and the formation of volcanic hotspots happened during the Mesozoic era
70 (Jokat, Boebel, König & Meyer, 2003; Wilf, Cúneo, Escapa, Pol & Woodburne,
71 2013), many geomorphological events relevant to modern-day Neotropical region
72 occurred in the Cenozoic. These include mountain uplift in Central America and the
73 Andes, the formation of the West Indies island system, a potential short-lived
74 land-bridge connecting South America to the West Indies (the Greater Antilles and
75 Aves Ridge, GAARlandia; Iturralde-Vinent & MacPhee, 1999; but see Ali & Hedges,
76 2021) and formation of the Isthmus of Panama, a contiguous landmass connecting
77 Central and South America whilst separating the Atlantic and Pacific oceans (Graham
78 2009; Hoorn et al. 2010).

79 These geomorphological events and their abiotic and biotic consequences
80 widely shaped the evolutionary history of the Neotropical biota, contributing for the
81 Neotropics to be today the world's most biodiverse region (Antonelli & Sanmartin
82 2011; Rull, 2011). Therefore, Neotropical faunal assemblages reflect several distinct
83 biogeographical histories. While some clades likely originated by mid-Cretaceous
84 vicariant event between South America and Africa (e.g., boid snakes: Noonan &
85 Chippindale, 2006; Iguanian and Scleroglossan lizards: Albino & Brizuela, 2014),
86 others later overwater dispersed from Africa (e.g., Epiplatine threadsnakes:
87 Adalsteinsson, Branch, Trape, Vitt & Hedges, 2009; Platyrrhine monkeys and
88 Caviomorph rodents: Defler 2019; South American Amphisbaenidae: Graboski,

89 Grazziotin, Mott & Rodrigues, 2022) or from Asia, via North America (viperid snakes:
90 Wüster, Peppin, Pook & Walker, 2008; turtles: Lichtig, Jasinski & Lucas, 2019).
91 Furthermore, the more recent Great American Biotic Interchange (GABI) promoted
92 dispersal and faunal admixture between Central and South American fauna — mainly
93 mammals and birds (Bacon et al., 2015; DeFler 2019; South American
94 Amphisbaenidae: Graboski et al., 2022) — despite some evidence of pre-GABI
95 dispersal (Heinicke, Duellman & Hedges, 2007; Agnolin, Chimento & Lucero, 2019).
96 Other groups, such as reptiles, are thought to have been less directly involved in
97 GABI, mostly diversifying in Central America with later dispersal to South America
98 with few groups doing the reverse path (Vanzolini & Heyer 1985).

99 Widely distributed taxa represent ideal models to study biogeographic
100 processes in the Neotropics (Colston et al., 2013; Torres-Carvajal, Echevarría, Lobos,
101 Venegas & Kok, 2019; Azevedo et al., 2020). Snakes are exceptionally diverse in the
102 Neotropical realm, where roughly one-third of all species occur (Guedes et al., 2017;
103 Roll et al., 2017; Nogueira et al., 2019). Dipsadidae (Bonaparte, 1838) is the richest
104 snake family in the Neotropics with over 700 known species, which are diverse in diet,
105 habitat use, and morphology (Cadle & Greene, 1993; Serrano et al., in prep.). This
106 high level of biological variation among dipsadids is reflected on the distributional
107 patterns and the phylogenetic relationships within the family, making it a promising
108 but scarcely explored model to evaluate biogeographic hypotheses of diversification
109 (Grazziotin et al. 2012, Zaher et al., 2019). It comprises four well-known groups: the
110 monophyletic and highly diverse subfamilies Dipsadinae and Xenodontinae, which
111 are widespread in the Neotropical realm (Cadle & Greene, 1993); plus two relict
112 groups, one distributed in North America that includes the subfamily Carphophiinae
113 and the genera *Heterodon* and *Farancia* (Pinou, Vicario, Marschner & Caccone,
114 2004), and another exclusively distributed in Asia composed of the genera
115 *Thermophis* and *Stichophanes* (Huang, Liu, Guo, Zhang, & Zhao; Grazziotin et al.,
116 2012; Zaher et al., 2019).

117 Despite the uncertainty around the family's geographical origin, hypotheses of
118 ancestral distribution have ranged from a Gondwanan distribution (Cadle, 1985), an

119 Asian origin followed by a dispersal from Asia via North America (Cadle, 1985) and
120 an African origin followed by a trans-Atlantic dispersal to South America (Cadle,
121 1984), possibly followed by a dispersal to North America (Duellman, 1979). Recent
122 phylogenetic studies have supported an Asian-North American dispersal event based
123 on the interpretation of the successive sister-group relationship between the Asian
124 genera *Thermophis* and *Stichophanes* and the clade composed by American dipsadids
125 (Grazziotin et al. 2012; Zaher et al., 2019). This Asian-North American dispersal
126 event has been supposed even before the studies positioning of *Thermophis* and
127 *Stichophanes* (Cadle, 1985), and it is frequently associated with the formation of the
128 Beringian Bridge during the Miocene, around 16–10 mya. The same hypothesis is
129 presented as the general biogeographical explanation for the presence of other snake
130 families, such as Colubridae and Natricidae in the New World (Vidal, Dewynter &
131 Gower, 2000; Pinou et al., 2004).

132 However, in recent studies, the estimated divergence between American and
133 Asian dipsadids is older than the Miocene. Zaher et al. (2018; 2019) estimated this
134 divergence between 22 mya and 27 mya, around the transition between the Oligocene
135 and Miocene. Other studies have suggested older dates, pointing to a divergence
136 between Asian and American dipsadids dated in the transition between the Eocene
137 and Oligocene (between 26 and 36 mya; Entiauspe-Neto, et al. *in press*). An
138 alternative hypothesis supporting pre-Miocene divergence times is related to
139 cladogenic events as the opening of the Greenland corridor approximately 48 mya.

140 Within the diversity of dipsadids, some studies restricted to small groups of
141 species (e.g., *Leptodeira*: Daza, Smith, Páez & Parkinson, 2009; Imantodini: Mulcahy,
142 2007; *Thermophis*: Huang et al., 2009) have only reconstructed recent
143 biogeographical patterns and attained some estimates of divergence times but
144 achieved inconclusive results regarding the ancestral range distribution and
145 biogeographic processes of the main groups. Since the classical studies of Cadle
146 (1984a, 1984b, 1984c), the evolutionary history of the two major dipsadid subfamilies
147 has been understood as reflecting independent origins and processes of diversification.
148 Following Cadle's hypothesis, Dipsadinae originated in Central America, where the

149 subfamily diversified and further dispersed to South America. Xenodontinae, on the
150 other hand, would have originated and diversified in South America, and from there,
151 dispersed to Central America. Although Duellman (1979) suggested a different
152 scenario—a common South American origin for Dipsadidae and further dispersal to
153 Central and North America — the hypothesis provided by Cadle was well accepted by
154 the herpetological community, and it has been supported by further studies (Cadle &
155 Greene, 1993; Vidal et al., 2000; Zaher et al., 2009; Hedges, Coulloux & Vidal, 2009;
156 Vidal et al., 2010; Graziotin et al., 2012; Zaher et al., 2018; Zaher et al., 2019).
157 Cadle also suggested that the divergence between both subfamilies had happened
158 during the late Palaeocene–Eocene separation of Central and South America, around
159 40–60 mya (Cadle, 1985). However, recent studies have estimated divergence times
160 between Dipsadinae and Xenodontinae varying around 19 mya and 24 mya, during
161 the Late Miocene (Zaher et al. 2018; 2019).

162 Zaher et al. (2019) also suggested that the sister group affinities retrieved
163 between Diaphorolepidini (an exclusive South American tribe) and the remaining
164 Dipsadinae, on the one hand, and Conophiini (an exclusive Central American tribe)
165 and the remaining Xenodontinae, on the other hand, points to a complex historical
166 scenario of origin and diversification of the two main Central- and South-American
167 dipsadid lineages than previously thought (Cadle, 1985; Cadle & Greene, 1993).
168 Therefore, both the family’s origin and its overall biogeographical history, such as
169 timing and route of dispersal between Central and South America, remains uncertain.

170 Historical biogeography (Posadas, Crisci & Katinas, 2006) is an essential tool
171 to understand the origin and composition of current Neotropical biotas such as snake
172 assemblages since biogeographical processes such as dispersal, vicariance, and
173 extinction strongly influence local and regional biodiversity through time (Ricklefs,
174 1987; Moritz, Patton, Schneider & Smith, 2000; Crisci, 2001). However,
175 comprehensive studies on Neotropical historical biogeography have been severely
176 hampered by the lack of detailed phylogenetic hypotheses and distributional data
177 (Bagley & Johnson, 2014) as well as analytical limitations (Landis, Matzke, Moore &
178 Huelsenbeck, 2013; Matzke, 2013). Despite information available on the distribution,

179 richness and phylogenetics of diverse groups such as snakes being increasingly
180 available (López-Aguirre, Hand, Laffan & Archer, 2018; Nogueira et al., 2019;
181 Azevedo et al., 2020), their historical biogeography is complex and still poorly
182 understood.

183 Here, we generate and use a comprehensive time-calibrated phylogeny and a
184 Bayesian estimation of the ancestral geographical ranges aiming to: (1) infer the most
185 likely distribution of ancestral lineages of Dipsadidae, (2) reconstruct the historical
186 biogeography of dipsadid snakes in the Neotropical region; and (3) complement the
187 current knowledge of paleogeographical scenarios related to the diversification and
188 current patterns of distribution of dipsadids in Central and South America.
189 Specifically, we tested the hypotheses that: i) Dipsadidae had an Asian origin with
190 dispersal via North America; and ii) Dipsadinae and Xenodontinae — the two
191 Neotropical subfamilies — have different geographical origins (Central and South
192 American, respectively).

193 **Materials and Methods**

194

195 *Phylogenetic tree*

196 We based our Bayesian phylogenetic analysis on the molecular dataset from
197 Zaher et al. (2018), the most complete and up-to-date available dataset considering the
198 diversity of Dipsadidae. The concatenated matrix included DNA sequences of six
199 genes (12S, 16S, cytb, bdnf, c-mos, and nt-3) for 344 species representing the families
200 Dipsadidae, Pseudoxenodontidae, Colubridae, Calamariidae, Sibynophiidae,
201 Grayiidae, Natricidae, Viperidae, Pareidae, and the superfamily Elapoidea. The boids
202 *Eryx conicus* and *Boa constrictor* were included to root the phylogenetic tree. The
203 dataset is largely biased towards Dipsadidae (287 species, 83.4% of species in the
204 phylogeny), with 283 New World species (84 genera), of which 10 (five genera)
205 belong to the subfamily Carphophiinae, 167 (54 genera) to Xenodontinae, and 106 (23
206 genera) to Dipsadinae. The Asian incertae sedis Dipsadidae genera *Thermophis* (three
207 species) and *Sticophanes* (one species) are also included in the molecular dataset to

208 allow the estimation of the origin and early evolution of South American dipsadids.
209 Overall, our sample of Dipsadidae represents nearly a third of all valid species for this
210 family (Uetz et al., 2020).

211 To determine the optimal partitioning scheme and nucleotide substitution
212 models of DNA, we used PartitionFinder v2.1.1 (Lanfear, Calcott, Ho & Guindon.,
213 2012). We previously partitioned our concatenated matrix based on gene fragments
214 and we tested all models implemented in MrBayes 3.1.2 (Ronquist & Huelsenbeck,
215 2003) through Bayesian Information Criterion (BIC), while using the ‘greedy’
216 algorithm (Lanfear, 2012).

217 Although Zaher et al. (2018) have phylogenetically analyzed the same matrix
218 using Maximum Likelihood (ML), they only estimated divergence times based on a
219 considerably reduced matrix (with 67 terminals), focusing on the evolution of
220 Pseudalsophis in the Galápagos Archipelago. Here, we greatly extended their analysis
221 by performing a time-calibrated Bayesian inference in MrBayes 3.1.2 using the
222 complete matrix with 344 terminals, aiming to estimate divergence time within the
223 whole diversity of Dipsadidae. We defined a set of topological constraints based on
224 the ML topology presented by Zaher et al. (2018) to reduce the tree space and
225 decrease the running time of our analysis. The set of topological constraints is listed
226 in the nexus file (available at figshare [figshare address]). Node calibration points
227 were defined based on the fossil record and we used similar ages and fossil
228 interpretations as described by Zaher et al. (2018) and Zaher et al. (2019). The list of
229 calibration points and their respective references are available in the Supp. Mat. S1).

230 We set the branch length prior as a birth-death clock model (Yang and
231 Rannala, 1997), with speciation and extinction probabilities set to exponential
232 ($\lambda = 10$) and beta ($\alpha = 1$ and $\beta = 1$) distributions, respectively. We
233 divided the total number of terminals in our molecular matrix by the approximate total
234 number of extant alethinophidians (Uetz et al., 2020) and we set the sample
235 probability to 0.109. For the model of variation of the clock rate across lineages, we
236 used the independent gamma rates (IGR) model (Ronquist et al. 2012) with the
237 parameter IGRvar — the amount of rate variance across branches — set to the

238 exponential ($\lambda = 10$). To set the clock rate, we followed Pyron (2017), and we
239 used a log normal distribution with a mean corresponding to the log of the average
240 number of substitutions per site from root to tips estimated from the tree provided by
241 Zaher et al. (2018), divided by the mean root age (-3.295561). The standard deviation
242 for the log normal distribution was set as the exponent of the mean (1.037742).

243 We implemented this analysis in two independent runs with eight Markov
244 Chains Monte Carlo (MCMC, one cold and seven incrementally heated) and 50
245 million generations. To generate the 50% majority rule consensus tree, a conservative
246 burn-in of 25% was applied after checking the log-likelihood scores and the
247 split-frequencies of the runs, and all sampled trees prior to reaching these generations
248 were discarded.

249 Clades with support values ≥ 0.85 were considered well-supported. We
250 combined the resulting trees from the two runs using the `sumt` command in MrBayes,
251 and eventual polytomies were randomly solved by adding small branch-lengths
252 (0.0001) using functions from the ‘ape’ package (Paradis & Schliep, 2019) in R 3.5.2
253 (R Core Team, 2019). The complete time-calibrated Bayesian tree was pruned to
254 Dipsadidae and its closest sister group to implement further historical biogeographical
255 analysis.

256 *Biogeographical analysis and ancestral range estimation*

257 Several methods have been used to define biogeographical units (Ferrari, 2017),
258 varying from areas of endemism (Morrone, 1994; Linder, 2001), biotic elements
259 (Hausdorf & Hennig, 2003), bioregions (Edler, Guedes, Zizka, Rosvall & Antonelli,
260 2017), tectonic plates (Sanmartín & Ronquist, 2004) and zoogeographic realms (Holt
261 et al., 2013), among others. All of them present strengths and weakness (Ferrari 2017),
262 but regarding the scope of our study, and the geographical and phylogenetic pattern of
263 Dipsadidae, we based our units combining a modified version of zoogeographic
264 realms (Holt et al. 2013) with areas of endemism (Morrone, 2010; Morrone et al.,
265 2014). We used the ‘Mexican transition zone’ as the limit between North and Central
266 America since it separates the Nearctic and Neotropical regions (Morrone, 2010;

267 Morrone, Escalante & Rodriguez-Tapia, 2017), and northern Nicaragua as the limit to
268 Central America because it represents the austral border of the Mesoamerican
269 Dominion (Morrone et al., 2014) and its southern portion (Panama, Costa Rica and
270 southern Nicaragua) is much younger than its northern portion due to their different
271 geological histories (Bacon et al., 2015; O’Dea et al., 2016). Since we aimed to
272 understand only major biotic exchanges between insular and continental landmasses,
273 the West Indies were treated as a single area to decrease the number of
274 biogeographical units and consequently the models’ running time. These
275 biogeographic units are congruent with several main geographic/phylogenetic groups
276 of Dipsadidae included in our analysis (Asian dipsadids: *Thermophis* and
277 *Stichophanes*; North American dipsadids: Carphophiinae, Heterodon and Farancia;
278 Central American dipsadids: most of the Dipsadinae; cis-Andean South American
279 dipsadids: most of the Xenodontinae; trans-Andean South American dipsadids: rare
280 radiations present in both subfamilies, Xenodontinae and Dipsadinae; and West
281 Indian dipsadids: mainly the tribe Alsophiini).

282 We considered six biogeographical units (Fig. 1a), assigning each species
283 distribution to one or more than one of them: (A) Asia, (B) North America (American
284 continent north of the Trans-Mexican Volcanic Belt), (C) Central America (from the
285 Trans-Mexican Volcanic Belt to northern Nicaragua), (D) the West Indies, (E)
286 Trans-Andean South America (from western slopes of the Andes to the Pacific Ocean
287 shores) and (F) cis-Andean South America (from eastern slopes of the Andes to the
288 Atlantic Ocean shores). We constrained the maximum number of occupied units to
289 three, since none of the extant species occurs in more than three areas.

290 We estimated the ancestral ranges for Dipsadidae using the *BioGeoBEARS*
291 package (Matzke, 2013) in R 3.5.2 (R Core Team, 2019), using variations of the
292 likelihood models DEC (Dispersal-Extinction-Cladogenesis; Ree & Smith, 2008),
293 DIVA-like (Dispersal-Vicariance Analysis; Ronquist, 1997) and BayArea-like
294 (Bayesian Inference of Historical Biogeography for Discrete Areas; Landis et al.,
295 2013). The DEC (Dispersal-Extinction Cladogenesis — Ree & Smith, 2008; Matzke,
296 2013) model assumes that derived lineages following cladogenesis can only inherit a

297 single range area, which is a subset of their ancestor's range; DIVAlIke (Ronquist &
298 Sanmartin, 2011) which allows vicariant events, but does not allow for
299 sympatric-subset speciation by derived lineages. BAYAREAlIke (Landis et al., 2013),
300 on the other hand, assumes that no range evolution occurs at cladogenesis, and
301 derived lineages inherit the same range of the ancestral state, making it a heavily
302 dispersalist model.

303 Although we tested all models implemented in *BioGeoBEARS*, we
304 acknowledge that statistical comparison among models without incorporating
305 subjective biological knowledge can favour models that, despite increasing the data
306 likelihood, do not necessarily incorporate the most probable historical scenario
307 (Sanmartín, 2021). We assume that for an old (probably more than 40 my old) wide
308 dispersed taxa (four continents) like Dipsadidae, evolution by vicariance needs to be
309 considered in biogeographical models, even if it occurs at a low rate. Therefore, we
310 maintained BAYAREAlIke models in our analysis only to test the relative importance
311 of scenarios mainly driven by dispersal (see results below), but we base our main
312 discussion on the best models that allow vicariant processes.

313 We furthermore compared the above models with the added +j parameter,
314 which allows founder-event speciation and was added due to its potential importance
315 in reconstructing insular historical biogeography (Klaus and Matzke; 2020; Matzke,
316 2022; but see Ree and Sanmartín; 2018). To each model we also added a
317 time-stratified matrix with dispersal probabilities (Supp. Mat. 2) between pairs of
318 areas specified based on geological events occurring in each period (Fig. 1b), varying
319 between 0.1 (unlikely), 0.5 (probable) and 1 (likely). For this matrix we considered
320 potentially relevant events (Figure 1b) at 46 mya [million years ago] (origin of the
321 clade), 35 mya (potential uplift of GAARlandia or stepping stone islands;
322 Iturralde-Vinent & MacPhee, 1999), 30 mya (disappearance of GAARlandia or
323 stepping stone islands; Iturralde-Vinent & MacPhee, 1999), 25 mya (approximation of
324 the Central American and South American tectonic plates; Montes et al., 2012) and 15
325 mya (complete formation of the Panama Isthmus; Bacon et al., 2015 but see O'Dea et
326 al., 2016). All models were implemented in the Maximum Likelihood framework of

327 BioGeoBEARS, (Matzke, 2013). In total, we implemented six Maximum Likelihood
328 models which were compared via Akaike information Criterion – AIC (Akaike, 1974;
329 Wang, 2006).

330 **Results**

331 *Phylogeny and divergence time estimation*

332 Our phylogeny (Fig. 2) suggests a crown age of Colubroidea of 56.6 my
333 (49.2-63.7 my 95% HPD), with the main split between Dipsadidae — strongly
334 supported as monophyletic — and the remaining Colubroidea occurring in mid
335 Eocene approximately 49.1 mya (44.1-55.4 mya 95% HPD) (available at
336 10.6084/m9.figshare.22634854). The split between Asian and American Dipsadidae
337 occurred at 44.9 mya (40.1-50.2 mya 95% HPD), with the more species-rich
338 Neotropical Dipsadidae splitting from the North American relictual clade at 43.1 mya
339 (38.2 -47.3 mya 95% HPD). Both Xenodontinae and Dipsadinae were strongly
340 recovered as monophyletic, while Carphophiinae was recovered as non-monophyletic.
341 While most clades within Xenodontinae were well resolved (bar the *Erythrolamprus*
342 and *Helicops* genera and the Tachymenini tribe, for instance), several clades within
343 Dipsadinae showed low to moderate support with the most noticeable being the
344 Dipsadini tribe and the *Atractus* + *Geophis* clade.

345

346 *Ancestral range estimation*

347 The best fitted model was BAYAREALIKE +j (AICc = 619.9), followed by DEC
348 +j (AICc = 647.2). This highlights the importance of dispersal for this snake clade,
349 especially since the founder-event parameter was present in the three best models
350 (Table 1). It also highlights that the anagenetic processes and range heritage were
351 more important in the evolution of the dipsadids than the cladogenetic processes.
352 However, as stated before, since BAYAREALIKE does not consider vicariant
353 processes, we illustrate the historical biogeography of Dipsadidae with DEC +j. The
354 most recent ancestor of Dipsadidae likely occurred in Asia, splitting from its sister
355 group (the family Pseudoxenodontidae) during the Early Eocene. The clade's

356 extension of distribution to the New World (current North America and Central
357 America) was then followed by a vicariant event between the Asian dipsadids and the
358 American clade around 44.6 mya (40.1 – 50.2 mya 95% HPD) (Fig. 3). In the Mid
359 Eocene, around 42.8 mya (37.6 – 48.6 mya 95% HPD), there was another vicariant
360 event splitting the Carphophiinae subfamily in North America and the ancestor of the
361 speciose Neotropical dipsadids in Central America. From then, around 42 mya, the
362 two current major Neotropical subfamilies underwent distinct biogeographical
363 processes. For Xenodontinae, a small lineage remained in Central America
364 (Conophini), while the ancestor of the subfamily dispersed into cis-Andean South
365 America via jump dispersal. The ancestor lineage of Dipsadinae remained in Central
366 America, with a further jump dispersal by the ancestor of the small lineage
367 Diaphorolepidini to trans-Andean South America around the Eocene - Oligocene
368 transition. Thereafter, Xenodontinae mainly maintained a cis-Andean distribution,
369 except for the Alsophini clade, which underwent a major jump dispersal event to the
370 West Indies during the early Oligocene, around 33.0 mya. The subfamily Dipsadinae,
371 on the other hand, underwent many relevant biogeographical changes, especially since
372 30.7 mya, where the *Hypsiglena* + *Pseudoleptodeira* clade majorly reverted its
373 distribution to North America. Compared to Xenodontinae, the occupation of South
374 America by previously Central American dipsadines occurred much later, during the
375 Oligo-Miocene transition, and by several jump dispersal events: at around 25.4 mya
376 for the tribe Dipsadini and at around 22.3 mya for the genus *Atractus*. Overall, range
377 extensions (e.g., range extension of a trans-Andean species to Central America)
378 occurred at more recent times during Late Miocene and mainly within the subfamily
379 Dipsadinae. Major events are summarized in Fig. 4.

380

381 **Discussion**

382 Overall, we reconstruct the complex biogeographical history of the
383 family Dipsadidae, the most species rich clade of Neotropical snakes and an important
384 component of Neotropical biodiversity. Our results show that Dipsadidae has an

385 Asian origin, corroborating our first hypothesis, and that the two main Neotropical
386 subfamilies likely originated in Central America, contrary to our second hypothesis.

387

388 *Origin of New world dipsadids*

389 Our findings strongly corroborate an Asian origin for dipsadids, as previously
390 suggested (Cadle, 1984c; Grazziotin et al., 2012; Zaher et al., 2019), and thus
391 challenge studies that suggested that the Dipsadidae could have an African or
392 Gondwanan origin (Cadle, 1985) or that Dipsadidae could have dispersed from South
393 America to North America during its early diversification (Duellman, 1979). This
394 origin is also consistent with the current distribution of its closest clades, including the
395 Asian Pseudoxenodontidae and Natricidae. In spite of being almost globally
396 widespread (i.e. occurring in the Palearctic, Nearctic and Afrotropical regions),
397 Natricidae is mostly absent from the Neotropical region and its ancestral distribution
398 is Asian (Deepak et al., 2022). This validates our first hypothesis of an Asian origin
399 for the Dipsadidae and subsequent dispersal to North America, possibly via the
400 Beringia Land Bridge. This land bridge is estimated to have connected the Palearctic
401 and Nearctic realms during the Eocene (33-55 mya; Wolfe, 1975; Baskin & Baskin,
402 2016), being covered by warmer boreotropical forests which would have been suitable
403 for ectotherms (Sanmartín, Enghoff & Ronquist, 2001; Townsend, Leavitt & Reeder,
404 2011; Baskin & Baskin, 2016; Graham, 2018). This dispersal pattern is coeval with
405 other squamate taxa (Dibamid lizards: Townsend et al., 2011) and similar, albeit
406 earlier than, coral snakes (Kelly, Barker, Villet & Broadley, 2009), lampropeltine rat
407 snakes (Burbrink, Chen, Myers, Brandley & Pyron, 2012) and crotaline vipers
408 (Wüster et al., 2008; Alencar et al., 2016). Alternatively, Dipsadidae could have
409 reached North America from Asia via North Atlantic Land Bridges, especially the
410 Thulean bridge, which were also present at the time of their origin (Tiffney, 1985;
411 Jian et al., 2019). The Thulean land bridge connected southern Europe to Greenland,
412 which in turn was connected to eastern North America and was available throughout
413 the Early Tertiary until its submersion approximately 50 mya (Tiffney, 1985; Jian et
414 al., 2019). Both plants and vertebrates have been suggested to have migrated via

415 climatically suitable forest-covered North Atlantic Land Bridges (Sanmartín et al.,
416 2001; Jian et al., 2019). However, dispersal via the Thulean bridge would imply that
417 Dipsadidae once occupied and then went extinct in most of the Eurasian continent.
418 While fossils associated with Dipsadidae (Paleoheterodon and Heterodon) have been
419 described from southern Europe and North America, these are dated to Miocene/early
420 Pliocene and could likely be a posterior incursion of North American fauna into
421 Europe via the North Atlantic Greenland-Faroes bridge. Therefore, while both
422 dispersal routes are possible, it likely that the geographically closer Beringia bridge
423 likely provided a more suitable intercontinental dispersal route, as also suggested for
424 other reptiles (e.g., Chen et al., 2013; Townsend et al., 2011).

425

426 *The distinct processes shaping the diversity of dipsadines and xenodontines*

427 We show that the main cladogenetic event originating both Neotropical
428 subfamilies of Dipsadidae (Dipsadinae and Xenodontinae) must have occurred in
429 Central America, prior to their dispersal to South America, as hypothesized for
430 different clades of the Neotropical herpetofauna (Vanzolini & Heyer, 1985). Thus, our
431 results rejected the hypothesis of different geographical origins for Dipsadinae and
432 Xenodontinae as suggested by Cadle & Greene (1993).

433 The DEC + j model shows that Dipsadidae has dispersed to South America
434 several times during its diversification. Both subfamilies originated and begun to
435 diversify in the Middle Eocene, when a major increase in temperature - the Middle
436 Eocene Climatic Optimum or MECO - took place, which has been shown to have
437 increase the diversity of plants and mammals (Woodburne et al., 2014; Fernandez,
438 Santamarina, Palazzesi, Tellería, & Barreda, 2021). Numerous other significant
439 intercontinental faunal dispersals have been documented for this period for many
440 vertebrates (Beard, Qi, Dawson, Wang & Li, 1994; Chaimanee et al., 2012).
441 Furthermore, both Neotropical subfamilies, despite first entering South America
442 quasi-simultaneously around 40 mya, have different biogeographical histories, despite
443 the common biogeographical origin. Xenodontinae likely incurred in a single
444 colonization through jump dispersal to South America by a Central American

445 ancestor in the Middle Eocene (~ 39 mya), that was followed by quasi-isolation of the
446 group in the region (Simpson, 1980; Cadle 1985). The exceptions to this isolation are
447 dispersing species that returned to Central America and/or some lineages that
448 dispersed to the West Indies, including the jump dispersal by the Alsophini clade (Fig
449 3). The presence of Dipsadinae in South America is also explained by jump dispersal
450 to South America from a Central American ancestors, although through multiple
451 events (at least five) occurred in the Middle Eocene (Diaphorolepidini), Early Miocene
452 (South American species of goo-eaters), and in the Middle (South American species
453 of *Imantodes*) and Late Miocene (South American species of *Leptodeira*). The time of
454 the first dispersal event of dipsadines (~ 38 mya) coincides with that estimated for
455 Xenodontinae (Fig 3), although the time frame of these dispersal events from Central
456 to South America indicated by our results is not congruent with paleogeographical
457 reconstructions of a contiguous connection of the two continents, which suggested a
458 large seaway separating the two landmasses (Montes et al., 2012, but see Coates &
459 Stallard, 2016). Although this seaway likely represented a major obstacle to biotic
460 interchange, the migration rate between the two continental masses has already been
461 shown to have significantly increased around 41 mya (Bacon et al., 2015).
462 Long-distance rafting and over-water dispersal from continental landmasses could
463 explain such dispersal events (O’Dea et al., 2016), especially stepping-stone dispersal
464 via islands in the present-day Caribbean Sea, as suggested for other species (ants:
465 Archibald, Cover & Moreau, 2006; butterflies: Condamine, Silva-Brandão, Kergoat &
466 Sperling, 2012; carnivorous plants: Ellison et al., 2012). Even though most islands of
467 the West Indies were not above sea level before about 40 mya for Greater Antilles and
468 15 mya for Lesser Antilles (MacPhee & Iturralde-Vinent, 1994; Iturralde-Vinent
469 2006), it is still possible that other existing island chains facilitated dispersal
470 (Iturralde-Vinent & MacPhee 1999). For instance, as it moved eastward, the
471 Caribbean plate’s leading edge might have provided an island corridor — the
472 proto-Greater Antilles — which allowed for dispersal (albeit probably limited)
473 between Central America and South America during the Middle Eocene,
474 approximately since 49-45 mya (Iturralde-Vinent and MacPhee 1999; Ali, 2012;

475 Roncal, Nieto-Blázquez, Cardona & Bacon, 2020). Additionally, other proposed
476 paleogeographical scenarios such as ‘GrANoLA’ — a Greater Antilles-Northern
477 Lesser Antilles intra-oceanic subaerial connection (Philippon et al., 2020) — might
478 also have played a role in the dispersal of dipsadid snakes from Central to South
479 America, via continental islands (Cornee et al., 2021). Despite these ephemeral
480 landmasses not being present in our analyses due to their disappearance
481 (Iturralde-Vinent & MacPhee, 1999) and consequent lack of dipsadid records, jump
482 dispersal likely played a role in the biogeographical history of this group, as supported
483 by the +j (founder event) parameter in the best models.

484 Most lineages from the subfamily Xenodontinae diversified outside Central
485 America and in the last million years in cis-Andean South America. One example is
486 the tribe Alsophiini (Xenodontinae) which dispersed to and subsequently diversified
487 in the West Indies during the Eocene-Oligocene transition (ca. 34 mya), which
488 confirms that most of this insular extant fauna has a South American origin (Agnolin,
489 Chimento & Lucero, 2019; Crews & Esposito, 2020), as previously suggested for
490 Alsophiini (Hedges et al., 2009). This pattern and time frame are perfectly congruent
491 with the GAARlandia scenario (Iturralde-Vinent & MacPhee, 1999). While the
492 existence of GAARlandia has been increasingly questioned due to conflicting
493 geological and paleo-oceanographic data (Ali, 2012; Ali & Hedges, 2021), several
494 taxa with different dispersal abilities have been shown to have dispersed to the West
495 Indies during this period such as giant sloths (Delsuc et al., 2019), arthropods (Crews
496 & Esposito, 2020), freshwater fishes (Říčan, Piálek, Zardoya, Doadrio & Zrzavý,
497 2013), and amphisbaenids (Graboski et al., 2022). However, despite the congruent
498 temporal window, it is still possible that West Indian xenodontines were the result of
499 successive dispersal across the non-contiguous Aves Ridge, as suggested by the jump
500 dispersal model and other taxa with similar patterns (Crews & Esposito, 2020, but see
501 Ali & Hedges, 2021). Over-water dispersal seems to also be the process responsible
502 for the more recent (~ 10 mya) dispersal of *Erythrolamprus juliae* and *E. cursor* into
503 the Lesser Antilles, since these islands are younger than 15 mya (Iturralde-Vinent,

504 2006), and thus long after GAARlandia had emerged and disappeared, as also shown
505 for *Corallus* boids (Henderson & Hedges, 1995).

506 The timing of a contiguous land bridge, the Panama isthmus, between Central
507 America and South America has been a hot debate topic among geologists, ecologists
508 and biogeographers, with recent studies providing evidence that it likely occurred
509 before the Late Miocene (~ 10 mya) — much earlier than previously thought (~ 3.5
510 mya; see Bacon et al., 2015; Buchs et al., 2019). While dipsadids entered South
511 America before the earliest estimates of the formation of the Panama isthmus, there is
512 evidence of recent expansion to and from Central America, coincident with other two
513 significant increases in migration rate (Bacon et al., 2015). This expansion occurred
514 mainly for dipsadines between 12 and 9 mya, with several genera (e.g., *Sibon* and
515 *Imantodes*) reaching trans-Andean South America. This is also true for some species
516 of Xenodontinae (e.g., *Oxyrhopus*, *Pseudoboa* and *Erythrolamprus* genera) which
517 underwent the inverse path more recently — expanding from the cis-Andean region to
518 the trans-Andean region and Central America. However, all these xenodontines are
519 also broadly distributed in South America, and their presence in Central America
520 represents the extreme north of their distributions. Besides Conophiini there is no
521 species of Xenodontinae that is exclusive to Central America. Further studies might
522 focus on the processes behind this pattern, especially if differences in phylogenetic
523 niche conservatism for habitat or other ecological aspects might have played a role in
524 this extension, as some species have marked habitat-associated distributions (Serrano,
525 Vieira-Alencar, Díaz-Ricaurte & Nogueira, 2020; Serrano et al., 2023).

526 Regarding the Early Miocene of dipsadines from Central America into South
527 America, different processes may be involved, as show for two closely related clades
528 in close temporal proximity: representants of the tribe Dipsadini between 20-25, and
529 the speciose genera *Geophis* and *Atractus* at around 22 mya. The ancestor of both
530 theses clades was Central American, but our results suggest that the ancestor of
531 Dipsadini first extended its distribution to South America and later underwent
532 vicariance, while *Atractus* most likely jump dispersed. Even though there was no
533 contiguous landmass connecting the two continents at that time, other proposed

534 hypotheses might explain how these two clades entered present-day trans-Andean
535 South America: stepping-stone dispersal by volcanic island chains and/or over-water
536 dispersal, both facilitated by the collision of the Choco block with the South
537 American continent (North Andean block; Bacon et al., 2015; Buchs et al., 2019) in
538 the Early Miocene, at around 25-23 mya, corroborated by thermochronology and
539 changes in geochemical profiles (Farris et al., 2011). Furthermore, this aligns with
540 another significant increase in migration rates between the two continents (Bacon et
541 al., 2015). While the exact timing for a contiguous terrestrial connection between
542 Central America and South America is disputed (O’Dea et al., 2016, but see Jaramillo
543 et al., 2017; Molnar, 2017), the formation of a land bridge is a complex and gradual
544 process which might have allowed for over-water or stepping-stone dispersal into
545 present-day trans-Andean South America over time, as suggested for other taxa
546 (O’Dea et al., 2016), including dipsadid snakes of the genera *Imantodes* and
547 *Leptodeira* (Daza et al., 2009; Costa et al., 2022).

548 The collision of the Choco and North Andean blocks in Early Miocene allowed
549 for biotic dispersal between the two continental masses, and also triggered important
550 geological changes in South America: increased Andean orogenesis and propagation
551 of the Llanos basin (Farris et al., 2011; Mora et al., 2020). While exhumation of the
552 Andean metamorphic rocks had likely began in the Late Cretaceous (before the
553 Andean orogenesis, around ~ 100 mya; Avellaneda-Jiménez et al., 2020), the uplift of
554 its northernmost portions (e.g., the Central and Western Cordilleras) significantly
555 accelerated in the Miocene, around 23 mya (Hoorn et al. 2010; Chen, Wu & Suppe,
556 2019). As a consequence, diversification increased for several plant and animal taxa
557 and the Dipsadinae were no exception. Our results show that the early diversifications
558 of the tribe Dipsadini and the genus *Atractus* in South America are congruent with
559 peak uplifts in early Miocene (~23 mya), similarly to Aromabatidae frogs (Boschman
560 & Condamine, 2021) and clearwing butterflies (Elias et al., 2009), even though a
561 large portion of the Andes was at half its present elevation (Gregory-Wodzicki, 2000).
562 An increasing geographical and genetic isolation likely occurred for species with
563 cross-Andean distributions imposed by Andean uplift that subsequently led to a

564 pattern of coeval cis-Andean/trans-Andean vicariant events in Dipsadidae – within the
565 *Atractus* genus at 11 mya, as previously suggested (Passos, Lynch & Fernandes,
566 2008) – and in Xenodontinae, in the *Siphlophis* genus (~ 8 mya), as well as for
567 Neotropical pitvipers (Pontes-Nogueira, Martins, Alencar & Sawaya, 2021). The
568 Andean uplift may have indirectly contributed to speciation by altering climate and
569 environment in pan-Amazonia (Hoorn et al., 2010), as such events have been shown
570 to be strong drivers of diversification in the region (Pinto-Ledezma, Simon,
571 Diniz-Filho & Villalobos, 2017; Rangel et al. 2018; Vasconcelos et al., 2020),
572 especially for ectotherms (Santos, Coloma & Summers, 2009; Esquerré, Brennan,
573 Catullo, Torres-Pérez & Keogh, 2019; Meseguer et al., 2021). Further intense pulses
574 of Andean Mountain building in middle Miocene (~12 mya) and early Pliocene (~4.5
575 Ma) coincide with potential cis-Andean/trans-Andean dispersal in xenodontine clades
576 (the tribes Pseudoboini and Tachymenini, and in the genus *Erythrolamprus*) as well as
577 increased speciation in *Atractus*. These direct and indirect effects of mountain uplift
578 corroborate the role of the Andes as a “species pump”, increasing species
579 diversification into surrounding environments such as the Amazon and the Choco
580 (Rangel et al., 2018, Rahbek et al., 2019).

581 However, some trans/cis Andean biogeographical patterns within Xenodontinae
582 seem to have been only indirectly impacted by the uplift of the Andes. The ancestral
583 of the genus *Pseudalsophis* jump-dispersed to trans-Andean region—and after to the
584 Galapagos Archipelago (Zaher et al., 2018)—around 34 mya, long before the first
585 stages of the Andean uplift. Similarly, *Saphenophis* and the recently described
586 trans-Andean genus *Incaspis* (not sampled in our analysis) have been recovered as
587 independent and old lineages (tribes Saphenophiini and Incaspidini). The latter is
588 strongly recovered as sister to the cis-Andean tribes Tropicodryadini and
589 Philodryadini (Arredondo et al., 2020), likely suggesting other dispersal events
590 between both regions in the early Oligocene, before the mountain uplift.

591 Our results show that current biogeographical patterns of the family Dipsadidae,
592 the most species rich snake clade in the Neotropical region, have been shaped by
593 complex evolutionary and geological processes. Our reconstructed model recovered

594 an Asian origin for the Dipsadidae family and potential significant paleogeographical
595 events such as Eocene land bridges, Andean uplift and the formation of the Panama
596 isthmus. While both dipsadines and xenodontines originated in Central America, they
597 showed different evolutionary and biogeographical trajectories since they have
598 dispersed into South America at different time periods and in two different regions:
599 trans-Andean and cis-Andean South America. This is likely responsible for not only
600 their present distribution, co-occurrence and regionalization patterns but also for
601 relevant differences in their ecology and richness, which may help to explain why
602 both these two Neotropical subfamilies are much richer than their Asian and North
603 American counterparts (Cadle & Greene, 1983; Serrano et al., in prep). Additionally,
604 our results provide a refinement on the understanding of the historical biogeography
605 of the Neotropical region and how important events have shaped its biota.

606

607 **CONFLICT OF INTEREST**

608 The authors declare no conflict of interest.

609

610 **TABLES**

611

612 **Table 1** - The best-fitted models of ancestral range estimation of Dipsadidae with
613 BioGeoBEARS, all including a transition matrix. Model comparison based on
614 log-likelihood (LnL), the corrected Akaike information criterion; n, number of
615 parameters; d, rate of dispersal; e, rate of extinction; j, relative probability of
616 founder-event speciation. The best model is shown in bold.

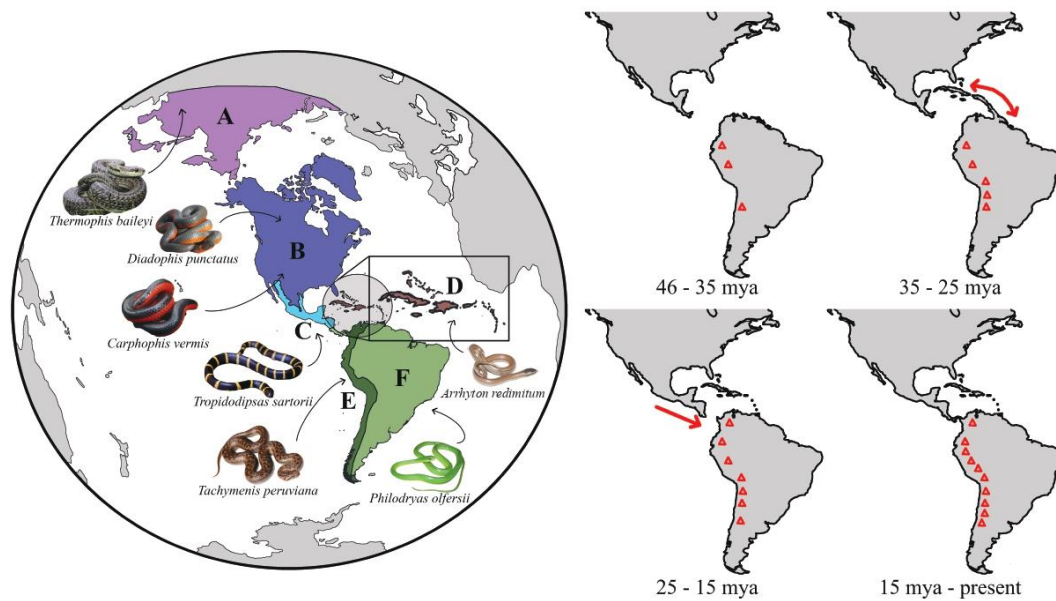
617

Model	LnL	n	d	e	j	AICc
BAYAREALIKE +j	-306.9	3	0.0035	0.0003	0.039	619.9
DEC +j	-320.6	3	0.0055	1.00E-12	0.03	647.2
DIVALIKE +j	-332.6	3	0.006	1.00E-12	0.033	671.3
DEC	-340.6	2	0.0079	1.00E-12	0	685.3
DIVALIKE	-350.2	2	0.0095	1.00E-12	0	704.4
BAYAREALIKE	-370.6	2	0.0046	0.016	0	745.2

618

619 **FIGURES**

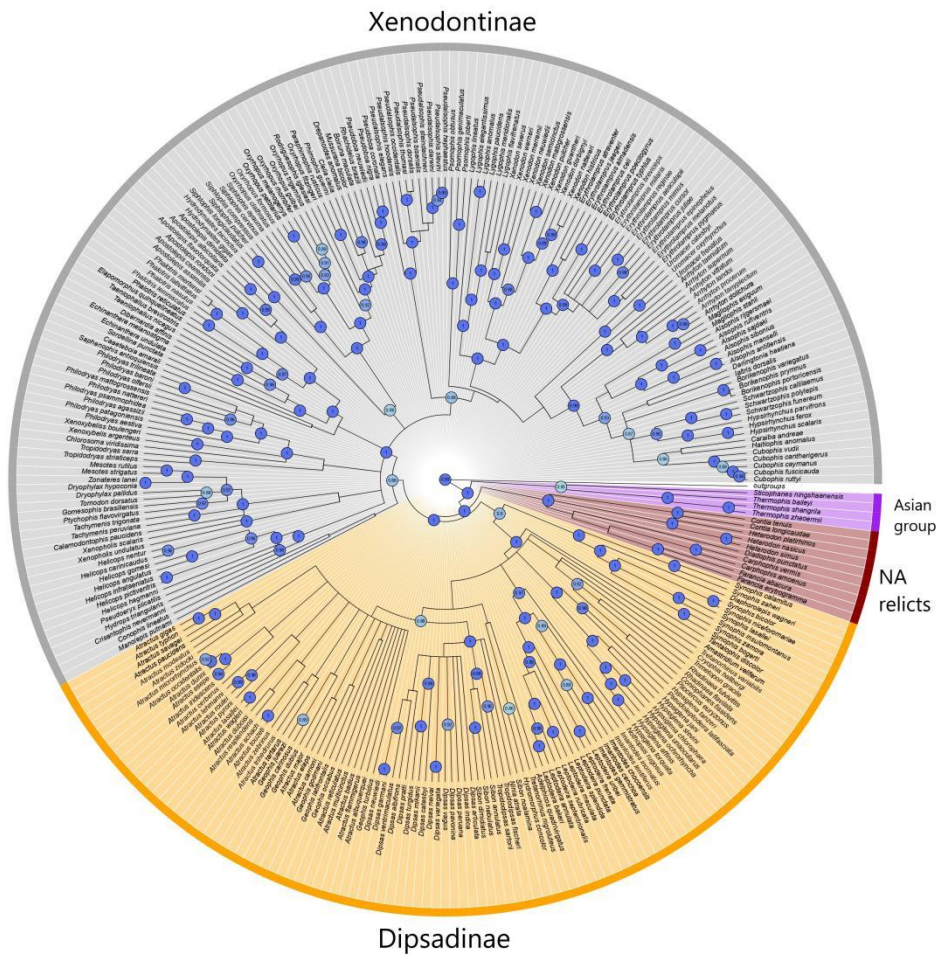
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621

622 **Figure 1** - a) Biogeographical units considered in this study and their representative
623 species; A - Asia, B - North America, C - Central America, D - West Indies, E -
624 trans-Andean South America and F - cis-Andean South America. b) Relevant
625 geomorphological events in the Neotropical region since the Eocene Epoch (56 to
626 33.9 million years ago - mya). Red arrows represent land connections and red
627 triangles represent increasing elevation in the Andes.

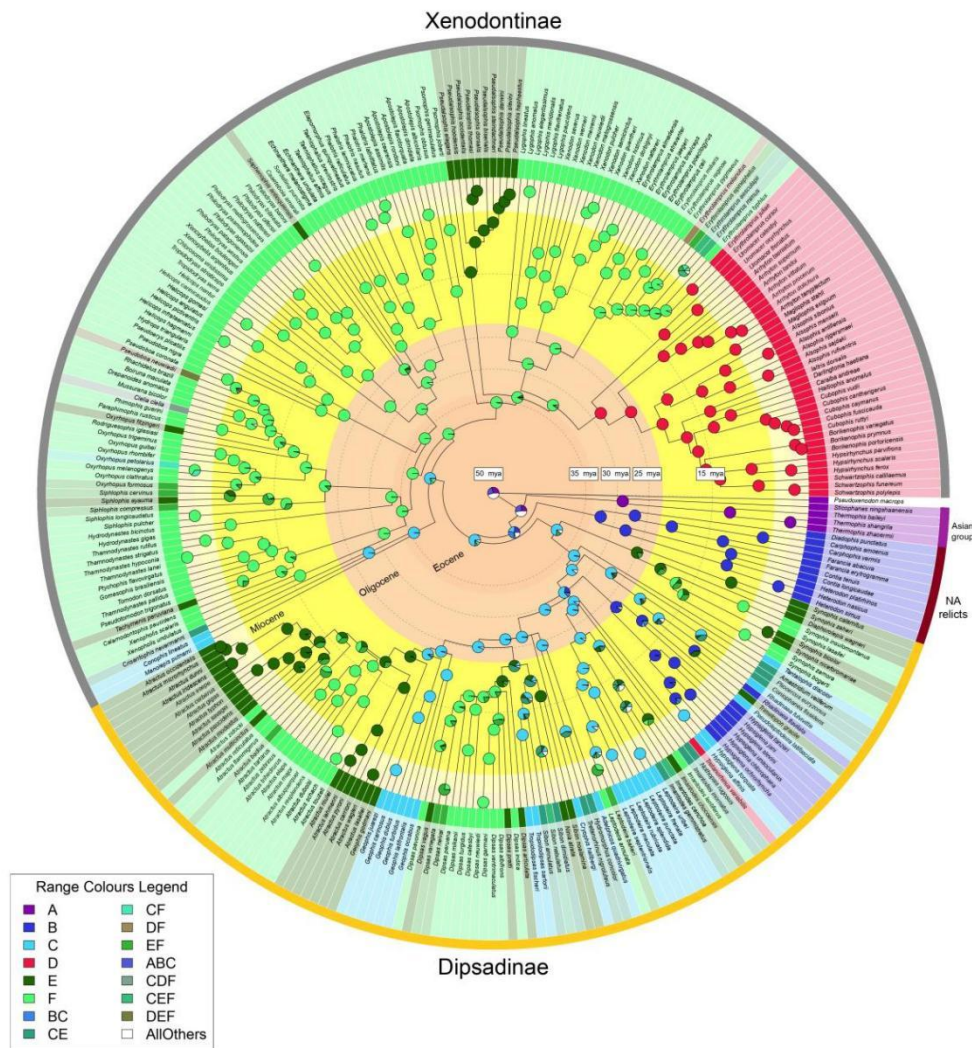
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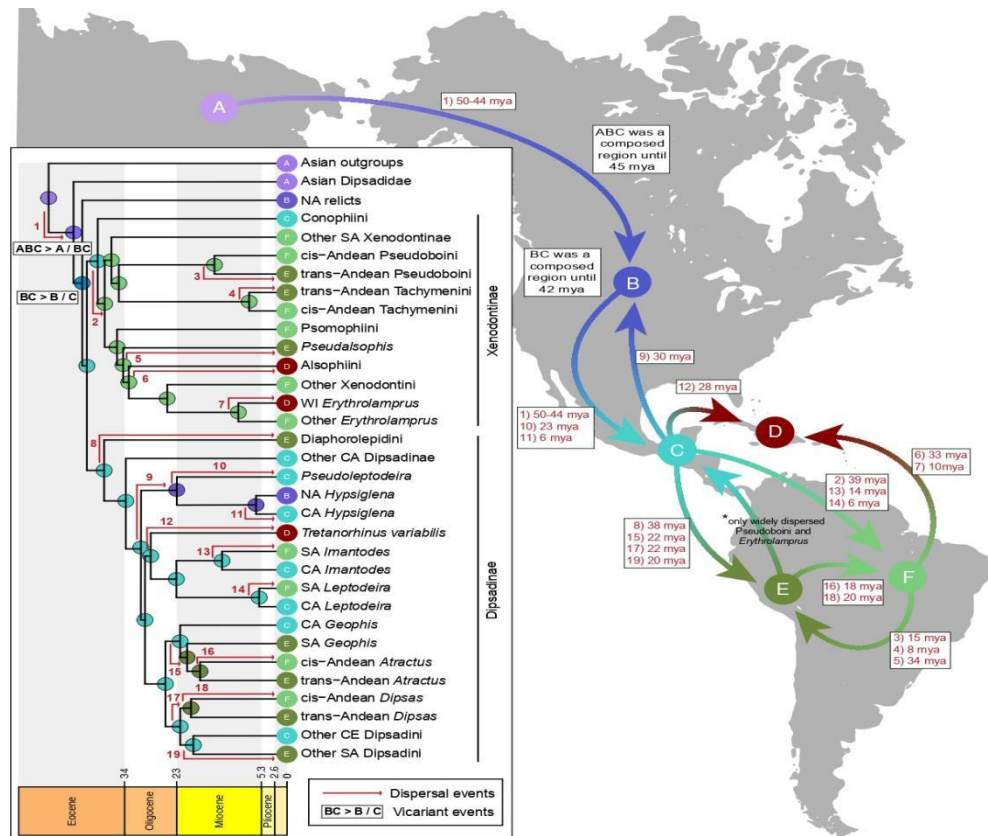
630 **Figure 2** - Time-calibrated Bayesian consensus phylogeny of Dipsadidae, with major
631 groups represented: Xenodontinae (grey), Dipsadinae (orange), Carphophiinae (North
632 American relicts, dark red) and Asian dipsadids (purple). Blue circles indicate
633 statistical support for nodes > 85%

634



635

636 **Figure 3** - Ancestral area estimations from the DEC+j model implemented in
 637 BIOGEOBEARS. The most probable ancestral areas are mapped by pie charts at each
 638 node and the actual occurrence of each specie is colour coded next to the species
 639 name (see legend). Orange and yellow-ish circles inside the phylogeny indicate
 640 geological epochs (Miocene, Oligocene and Eocene are named). Dashed circles
 641 represent the time divisions present on the time-stratified matrix, with time in millions
 642 of years ago (mya) indicated at the white boxes.



643

644 **Fig. 4** - Summary of major biogeographical events of Dipsadidae. The purple circle
 645 represents the likely origin of the family, while arrows represent dispersal within the
 646 family at different time periods between regions. Inset: summarized phylogeny for
 647 representative taxa with numbered relevant dispersal and vicariant events.

648

649 REFERENCES

- 650 Adalsteinsson, S. A., Branch, W. R., Trape, S., Vitt, L. J., & Hedges, S. B. (2009).
 651 Molecular phylogeny, classification, and biogeography of snakes of the Family
 652 Leptotyphlopidae (Reptilia, Squamata). *Zootaxa*, 2244(1), 1-50.
- 653 Agnolin, F. L., Chimento, N. R., & Lucero, S. O. (2019). Pre-GABI biotic
 654 connections between the Americas: an alternative model to explain the
 655 “less-splendid isolation” of South America. *Revista Geológica de América*
 656 *Central*, 61, 91-106.

- 657 Akaike, H. (1974). A New Look at the Statistical Model Identification. *IEEE*
658 *Transactions on Automatic Control*, 19(6), 716-723.
- 659 Albino, A. M., & Brizuela, S. (2014). An overview of the South American fossil
660 squamates. *The Anatomical Record*, 297(3), 349-368.
- 661 Alencar, L. R., Quental, T. B., Graziotin, F. G., Alfaro, M. L., Martins, M., Venzon,
662 M., & Zaher, H. (2016). Diversification in vipers: Phylogenetic relationships,
663 time of divergence and shifts in speciation rates. *Molecular Phylogenetics and*
664 *Evolution*, 105, 50-62.
- 665 Ali, J. R. (2012). Colonizing the Caribbean: is the GAARlandia land - bridge
666 hypothesis gaining a foothold?. *Journal of Biogeography*, 39(3), 431-433.
- 667 Ali, J. R. & Hedges, S. B. (2021). Colonizing the Caribbean: New geological data and
668 an updated land-vertebrate colonization record challenge the GAARlandia land-
669 bridge hypothesis. *Journal of Biogeography*, 48(11), 2699-2707.
- 670 Antonelli, A., & Sanmartín, I. (2011). Why are there so many plant species in the
671 Neotropics?. *Taxon*, 60(2), 403-414.
- 672 Archibald, S. B., Cover, S. P., & Moreau, C. S. (2006). Bulldog ants of the Eocene
673 Okanagan Highlands and history of the subfamily (Hymenoptera: Formicidae:
674 Myrmeciinae). *Annals of the Entomological Society of America*, 99(3), 487-523.
- 675 Avellaneda-Jiménez, D. S., Cardona, A., Valencia, V., Barbosa, J. S., Jaramillo, J. S.,
676 Monsalve, G., & Ramírez-Hoyos, L. (2020). Erosion and regional exhumation
677 of an Early Cretaceous subduction/accretion complex in the Northern Andes.
678 *International Geology Review*, 62(2), 186-209.
- 679 Azevedo, J. A., Guedes, T. B., Nogueira, C. D. C., Passos, P., Sawaya, R. J., Prudente,
680 A. L., ... Antonelli, A. (2020). Museums and cradles of diversity are
681 geographically coincident for narrowly distributed Neotropical snakes.
682 *Ecography*, 43(2), 328-339.
- 683 Bacon, C. D., Silvestro, D., Jaramillo, C., Smith, B. T., Chakrabarty, P., & Antonelli,
684 A. (2015). Biological evidence supports an early and complex emergence of the
685 Isthmus of Panama. *Proceedings of the National Academy of Sciences*, 112(19),
686 6110-6115.

- 687 Bagley, J. C., & Johnson, J. B. (2014). Phylogeography and biogeography of the
688 lower Central American Neotropics: diversification between two continents and
689 between two seas. *Biological Reviews*, *89*(4), 767-790.
- 690 Baskin, J. M., & Baskin, C. C. (2016). Origins and Relationships of the Mixed
691 Mesophytic Forest of Oregon–Idaho, China, and Kentucky: Review and
692 Synthesis 1. *Annals of the Missouri Botanical Garden*, *101*(3), 525-552.
- 693 Beard, K. C., Qi, T., Dawson, M. R., Wang, B., & Li, C. (1994). A diverse new
694 primate fauna from middle Eocene fissure-fillings in southeastern China. *Nature*,
695 *368*(6472), 604-609.
- 696 Boschman, L. M., & Condamine, F. L. (2022). Mountain radiations are not only rapid
697 and recent: Ancient diversification of South American frog and lizard families
698 related to Paleogene Andean orogeny and Cenozoic climate variations. *Global
699 and Planetary Change*, *208*, 103704.
- 700 Buchs, D. M., Irving, D., Coombs, H., Miranda, R., Wang, J., Coronado, M., ...
701 Redwood, S. D. (2019). Volcanic contribution to emergence of Central Panama
702 in the Early Miocene. *Scientific Reports*, *9*(1), 1-16.
- 703 Burbrink, F. T., & Lawson, R. (2007). How and when did Old World ratsnakes
704 disperse into the New World?. *Molecular Phylogenetics and Evolution*, *43*(1),
705 173-189.
- 706 Burbrink, F. T., Chen, X., Myers, E. A., Brandley, M. C., & Pyron, R. A. (2012).
707 Evidence for determinism in species diversification and contingency in
708 phenotypic evolution during adaptive radiation. *Proceedings of the Royal
709 Society B: Biological Sciences*, *279*(1748), 4817-4826.
- 710 Cadle, J. E. (1984). Molecular systematics of Neotropical xenodontine snakes. III.
711 Overview of xenodontine phylogeny and the history of New World snakes.
712 *Copeia*, 641-652.
- 713 Cadle, J. E. (1985). The Neotropical colubrid snake fauna: Lineage components and
714 biogeography. *Systematic Zoology*, *34*(1):1–20
- 715 Cadle, J. E., & Greene, H. W. (1993). Phylogenetic patterns, biogeography, and the
716 ecological structure of Neotropical snake assemblages. Species diversity in

- 717 ecological communities: historical and geographical perspectives. University of
718 Chicago Press, Chicago, 281-293.
- 719 Chaimanee, Y., Chavasseau, O., Beard, K. C., Kyaw, A. A., Soe, A. N., Sein, C., ...
720 Jaeger, J. J. (2012). Late Middle Eocene primate from Myanmar and the initial
721 anthropoid colonization of Africa. *Proceedings of the National Academy of*
722 *Sciences*, 109(26), 10293-10297.
- 723 Chen, X., Huang, S., Guo, P., Colli, G. R., de Oca, A. N. M., Vitt, L. J., ... Burbrink, F.
724 T. (2013). Understanding the formation of ancient intertropical disjunct
725 distributions using Asian and Neotropical hinged-teeth snakes (*Sibynophis* and
726 *Scaphiodontophis*: Serpentes: Colubridae). *Molecular Phylogenetics and*
727 *Evolution*, 66(1), 254-261.
- 728 Chen, Y.-W., Wu, J. & Suppe, J. (2019). Southward propagation of Nazca subduction
729 along the Andes. *Nature*, 565, 441-447.
- 730 Clapperton CM (1993) Quaternary Geology and Geomorphology of South America.
731 Elsevier, New York
- 732 Coates, A. G., & Stallard, R. F. (2016). Comments to Middle Miocene closure of the
733 Central American Seaway. *Science*, 348(6231).
- 734 Colston, T. J., Graziotin, F. G., Shepard, D. B., Vitt, L. J., Colli, G. R., Henderson, R.
735 W., ... Burbrink, F. T. (2013). Molecular systematics and historical
736 biogeography of tree boas (*Corallus* spp.). *Molecular Phylogenetics and*
737 *Evolution*, 66(3), 953-959.
- 738 Condamine, F. L., Silva-Brandão, K. L., Kergoat, G. J., & Sperling, F. A. (2012).
739 Biogeographic and diversification patterns of Neotropical Trodini butterflies
740 (Papilionidae) support a museum model of diversity dynamics for Amazonia.
741 *BMC Evolutionary Biology*, 12(1), 1-17.
- 742 Cornee, J. J., Münch, P., Philippon, M., Boudagher-Fadel, M., Quillévéré, F.,
743 Melinte-Dobrinescu, M., ... Marivaux, L. (2021). Lost islands in the northern
744 Lesser Antilles: possible milestones in the Cenozoic dispersal of terrestrial
745 organisms between South-America and the Greater Antilles. *Earth-Science*
746 *Reviews*, 217:103617.

- 747 Costa, J.C., Graboski, R., Grazziotin, F.G., Zaher, H., Rodrigues, M.T. & Prudente,
748 A.L.D.C. (2022). Reassessing the systematics of *Leptodeira* (Serpentes,
749 Dipsadidae) with emphasis in the South American species. *Zoologica Scripta*,
750 51(5), 614-615.
- 751 Crews, S. C., & Esposito, L. A. (2020). Towards a synthesis of the Caribbean
752 biogeography of terrestrial arthropods. *BMC Evolutionary Biology*, 20(1), 1-27.
- 753 Crisci, J. V. (2001). The voice of historical biogeography. *Journal of Biogeography*,
754 28(2), 157-168.
- 755 Daza, J. M., Smith, E. N., Páez, V. P., & Parkinson, C. L. (2009). Complex evolution
756 in the Neotropics: The origin and diversification of the widespread genus
757 *Leptodeira* (Serpentes: Colubridae). *Molecular Phylogenetics and Evolution*,
758 53(3), 653-667.
- 759 Deepak, V., Cooper, N., Poyarkov, N. A., Kraus, F., Burin, G., Das, A., ... Gower, D.
760 J. (2022). Multilocus phylogeny, natural history traits and classification of
761 natricine snakes (Serpentes: Natricinae). *Zoological Journal of the Linnean*
762 *Society*, 195(1), 279-298.
- 763 Deffler T. (2019) History of terrestrial mammals in South America: how South
764 American mammalian fauna changed from the mesozoic to recent times.
765 Springer Nature Switzerland Ag. 1st ed. Basel: Springer Nature Switzerland Ag.
- 766 Delsuc, F., Kuch, M., Gibb, G. C., Karpinski, E., Hackenberger, D., Szpak, P., ...
767 Poinar, H. N. (2019). Ancient mitogenomes reveal the evolutionary history and
768 biogeography of sloths. *Current Biology*, 29(12), 2031-2042.
- 769 Hausdorf, B., & Hennig, C. (2003). Biotic element analysis in biogeography.
770 *Systematic Biology*, 52(5), 717-723.
- 771 Holt, B. G., Lessard, J. P., Borregaard, M. K., Fritz, S. A., Araújo, M. B., Dimitrov,
772 D., ... & Rahbek, C. (2013). An update of Wallace's zoogeographic regions of
773 the world. *Science*, 339(6115), 74-78.
- 774 Edler, D., Guedes, T., Zizka, A., Rosvall, M., & Antonelli, A. (2017). Infomap
775 bioregions: interactive mapping of biogeographical regions from species
776 distributions. *Systematic Biology*, 66(2), 197-204.

- 777 Elias, M. J. B. P., Joron, M., Willmott, K., Silva - Brandão, K. L., Kaiser, V., Arias,
778 C. F., ... Jiggins, C. D. (2009). Out of the Andes: patterns of diversification in
779 clearwing butterflies. *Molecular Ecology*, 18(8), 1716-1729.
- 780 Ellison, A. M., Butler, E. D., Hicks, E. J., Naczi, R. F., Calie, P. J., Bell, C. D., ...
781 Davis, C. C. (2012). Phylogeny and biogeography of the carnivorous plant
782 family Sarraceniaceae. *PLoS One*, 7(6), e39291.
- 783 Esquerré, D., Brennan, I. G., Catullo, R. A., Torres-Pérez, F., & Keogh, J. S. (2019).
784 How mountains shape biodiversity: The role of the Andes in biogeography,
785 diversification, and reproductive biology in South America's most species - rich
786 lizard radiation (Squamata: Liolaemidae). *Evolution*, 73(2), 214-230.
- 787 Duellman, W. E. (1979). The South American herpetofauna: its origin, evolution, and
788 dispersal (Vol. 7). Lawrence, KS: Museum of Natural History, University of
789 Kansas.
- 790 Farris, D. W., Jaramillo, C., Bayona, G., Restrepo-Moreno, S. A., Montes, C.,
791 Cardona, A., ... Valencia, V. (2011). Fracturing of the Panamanian Isthmus
792 during initial collision with South America. *Geology*, 39(11), 1007-1010.
- 793 Fernandez, D. A., Santamarina, P. E., Palazzesi, L., Tellería, M. C., & Barreda, V. D.
794 (2021). Incursion of tropically-distributed plant taxa into high latitudes during
795 the middle Eocene warming event: Evidence from the Rio Turbio Fm, Santa
796 Cruz, Argentina. *Review of Palaeobotany and Palynology*, 295, 104510.
- 797 Ferrari, A. (2018). Biogeographical units matter. *Australian Systematic Botany*, 30(6),
798 391-402.
- 799 Graboski, R., Grazziotin, F. G., Mott, T., & Rodrigues, M. T. (2022). The
800 phylogenetic position of Ridley's worm lizard reveals the complex
801 biogeographic history of New World insular amphisbaenids. *Molecular*
802 *Phylogenetics and Evolution*, 173:107518.
- 803 Graham, A. (2009). The Andes: a geological overview from a biological perspective.
804 *Annals of the Missouri Botanical Garden*, 96(3), 371-385.

- 805 Graham, A. (2018). The role of land bridges, ancient environments, and migrations in
806 the assembly of the North American flora. *Journal of Systematics and Evolution*,
807 56(5), 405-429.
- 808 Grazziotin, F. G., Zaher, H., Murphy, R. W., Scrocchi, G., Benavides, M. A., Zhang,
809 Y. P., ... Bonatto, S. L. (2012). Molecular phylogeny of the new world
810 Dipsadidae (Serpentes: Colubroidea): a reappraisal. *Cladistics*, 28(5), 437-459.
- 811 Gregory-Wodzicki, K. M. (2000). Uplift history of the Central and Northern Andes: a
812 review. *Geological Society of America Bulletin*, 112(7), 1091-1105.
- 813 Guedes, T. B., Sawaya, R. J., Zizka, A., Laffan, S., Faurby, S., Pyron, R. A., ...
814 Antonelli, A. (2018). Patterns, biases and prospects in the distribution and
815 diversity of Neotropical snakes. *Global Ecology and Biogeography*, 27(1),
816 14-21.
- 817 Hedges, S. B., Couloux, A., & Vidal, N. (2009). Molecular phylogeny, classification,
818 and biogeography of West Indian racer snakes of the Tribe Alsophiini
819 (Squamata, Dipsadidae, Xenodontinae). *Zootaxa*, 2067(1), 1-28.
- 820 Heinicke, M. P., Duellman, W. E., & Hedges, S. B. (2007). Major Caribbean and
821 Central American frog faunas originated by ancient oceanic dispersal.
822 *Proceedings of the National Academy of Sciences*, 104(24), 10092-10097.
- 823 Henderson, R. W., & Hedges, S. B. (1995). Origin of West Indian populations of the
824 geographically widespread boa *Corallus enydris* inferred from mitochondrial
825 DNA sequences. *Molecular Phylogenetics and Evolution*, 4(1), 88-92.
- 826 Huang, S., Liu, S. Y., Guo, P., Zhang, Y. P., & Zhao, E. M. (2009). What are the
827 closest relatives of the hot-spring snakes (Colubridae, *Thermophis*), the relict
828 species endemic to the Tibetan Plateau?. *Molecular Phylogenetics and*
829 *Evolution*, 51(3), 438-446.
- 830 Hughes, C. E., Pennington, R. T., & Antonelli, A. (2013). Neotropical plant evolution:
831 assembling the big picture. *Botanical Journal of the Linnean Society*, 171(1),
832 1-18.

- 833 Hoorn, C., Wesselingh, F. P., Ter Steege, H., Bermudez, M. A., Mora, A., Sevink,
834 J., ... Antonelli, A. (2010). Amazonia through time: Andean uplift, climate
835 change, landscape evolution, and biodiversity. *Science*, 330(6006), 927-931.
- 836 Iturralde-Vinent, M. A. (2006). Meso-Cenozoic Caribbean paleogeography:
837 implications for the historical biogeography of the region. *International*
838 *Geology Review*, 48(9), 791-827.
- 839 Iturralde-Vinent, M., & MacPhee, R. D. (1999). Paleogeography of the Caribbean
840 region: implications for Cenozoic biogeography. *Bulletin of the American*
841 *Museum of Natural History*, 238: 1-95.
- 842 Jaramillo, C., Montes, C., Cardona, A., Silvestro, D., Antonelli, A., & Bacon, C. D.
843 (2017). Comment (1) on “Formation of the Isthmus of Panama” by O’Dea et al.
844 *Science Advances*, 3(6), e1602321.
- 845 Jiang, Y., Gao, M., Meng, Y., Wen, J., Ge, X. J., & Nie, Z. L. (2019). The importance
846 of the North Atlantic land bridges and eastern Asia in the post-Boreotropical
847 biogeography of the Northern Hemisphere as revealed from the poison ivy
848 genus (*Toxicodendron*, Anacardiaceae). *Molecular Phylogenetics and Evolution*,
849 139, 106561.
- 850 Jokat, W., Boebel, T., König, M., & Meyer, U. (2003). Timing and geometry of early
851 Gondwana breakup. *Journal of Geophysical Research: Solid Earth*, 108(B9).
- 852 Kelly, C. M., Barker, N. P., Villet, M. H., & Broadley, D. G. (2009). Phylogeny,
853 biogeography and classification of the snake superfamily Elapoidea: a rapid
854 radiation in the late Eocene. *Cladistics*, 25(1), 38-63.
- 855 Klaus, K. V., & Matzke, N. J. (2020). Statistical comparison of trait-dependent
856 biogeographical models indicates that Podocarpaceae dispersal is influenced by
857 both seed cone traits and geographical distance. *Systematic Biology*, 69(1),
858 61-75.
- 859 Landis, M. J., Matzke, N. J., Moore, B. R., & Huelsenbeck, J. P. (2013). Bayesian
860 analysis of biogeography when the number of areas is large. *Systematic Biology*,
861 62(6), 789-804.

- 862 Lanfear, R., Calcott, B., Ho, S. Y., & Guindon, S. (2012). PartitionFinder: combined
863 selection of partitioning schemes and substitution models for phylogenetic
864 analyses. *Molecular Biology and Evolution*, 29(6), 1695-1701.
- 865 Lichtig, A. J., Jasinski, S. E., & Lucas, S. G. (2019). Eocene North American
866 Testudinidae and Geoemydidae (Reptilia, Testudines): A re-evaluation of their
867 alpha taxonomy, ecology, and origin. In *Multidisciplinary Digital Publishing
868 Institute Proceedings* (Vol. 24, No. 1, p. 24).
- 869 Linder, H. P. (2001). On areas of endemism, with an example from the African
870 Restionaceae. *Systematic Biology*, 50(6), 892-912.
- 871 López-Aguirre, C., Hand, S. J., Laffan, S. W., & Archer, M. (2018). Phylogenetic
872 diversity, types of endemism and the evolutionary history of New World bats.
873 *Ecography*, 41(12), 1955-1966.
- 874 MacPhee, R. D. E., & Iturralde-Vinent, M. (1994). First Tertiary land mammal from
875 Greater Antilles: An Early Miocene sloth (Xenarthra, Megalonychidae) from
876 Cuba. *American Museum of Natural History Novitates*, 3094:1–13
- 877 Matzke, N. J. (2013). Probabilistic historical biogeography: new models for
878 founder-event speciation, imperfect detection, and fossils allow improved
879 accuracy and model-testing. *Frontiers of Biogeography*, 5(4), 242-248
- 880 Matzke, N. J. (2014). Model selection in historical biogeography reveals that
881 founder-event speciation is a crucial process in island clades. *Systematic
882 Biology*, 63(6), 951-970.
- 883 Matzke, N. J. (2022). Statistical comparison of DEC and DEC+J is identical to
884 comparison of two ClaSSE submodels, and is therefore valid. *Journal of
885 Biogeography*, 49(10), 1805-1824
- 886 Meseguer, A. S., Michel, A., Fabre, P. H., Pérez-Escobar, O. A., Chomicki, G., Riina,
887 R., ... Condamine, F. L. (2021). The origin and drivers of Neotropical plant and
888 tetrapod diversification. bioRxiv. <https://doi.org/10.1101/2021.02.24.432517>
- 889 Molnar, P. (2017). Comment (2) on “Formation of the Isthmus of Panama” by O’Dea
890 et al. *Science Advances*, 3(6), e1602320.

- 891 Montes, C., Cardona, A., McFadden, R., Morón, S. E., Silva, C. A., trepo-Moreno,
892 S., ... Flo, J. A. (2012). Evidence for middle Eocene and younger land
893 emergence in central Panama: Implications for Isthmus closure. *Geological*
894 *Society of America Bulletin*, 124(5-6), 780-799.
- 895 Mora, A., Villagómez, D., Parra, M., Caballero, V. M., Spikings, R., Horton, B. K., ...
896 Arias–Martínez, J. P. (2020). Late Cretaceous to Cenozoic uplift of the northern
897 Andes: Paleogeographic implications. *The Geology of Colombia*, 3, 89-121.
- 898 Moritz, C., Patton, J. L., Schneider, C. J., & Smith, T. B. (2000). Diversification of
899 rainforest faunas: an integrated molecular approach. *Annual Review of Ecology*
900 *and Systematics*, 31(1), 533-563.
- 901 Morrone, J. J. (1994). On the identification of areas of endemism. *Systematic Biology*,
902 43(3), 438-441.
- 903 Morrone, J. J. (2010). Fundamental biogeographic patterns across the Mexican
904 Transition Zone: an evolutionary approach. *Ecography*, 33(2), 355-361.
- 905 Morrone, J. J. (2014). Cladistic biogeography of the Neotropical region: identifying
906 the main events in the diversification of the terrestrial biota. *Cladistics*, 30(2),
907 202-214.
- 908 Morrone, J. J., Escalante, T., & Rodriguez-Tapia, G. (2017). Mexican biogeographic
909 provinces: Map and shapefiles. *Zootaxa*, 4277(2), 277-279.
- 910 Mulcahy, D. G. (2007). Molecular systematics of neotropical cat-eyed snakes: a test
911 of the monophyly of Leptodeirini (Colubridae: Dipsadinae) with implications
912 for character evolution and biogeography. *Biological Journal of the Linnean*
913 *Society*, 92(3), 483-500.
- 914 Nogueira, C. C., Argôlo, A. J., Arzamendia, V., Azevedo, J. A., Barbo, F. E., Bérnils,
915 R. S., ... Martins, M. (2019). Atlas of Brazilian snakes: verified point-locality
916 maps to mitigate the Wallacean shortfall in a megadiverse snake fauna. *South*
917 *American Journal of Herpetology*, 14(sp1), 1-274.
- 918 Noonan, B. P., & Chippindale, P. T. (2006). Dispersal and vicariance: the complex
919 evolutionary history of boid snakes. *Molecular Phylogenetics and Evolution*,
920 40(2), 347-358.

- 921 O'Dea, A., Lessios, H. A., Coates, A. G., Eytan, R. I., trepo-Moreno, S. A., Cione, A.
922 L., ... Jackson, J. B. (2016). Formation of the Isthmus of Panama. *Science*
923 *Advances*, 2(8), e1600883.
- 924 Paradis, E., & Schliep, K. (2019). ape 5.0: an environment for modern phylogenetics
925 and evolutionary analyses in R. *Bioinformatics*, 35(3), 526-528.
- 926 Passos, P., Lynch, J. D., & Fernandes, R. (2008). Taxonomic status of *Atractus*
927 *sanctaemartae* and *Atractus nebularis*, and description of a new *Atractus* from
928 the Atlantic coast of Colombia. *The Herpetological Journal*, 18(4), 175-186.
- 929 Philippon, M., Cornée, J-J., Münch, P., van Hinsbergen, D. J. J., BouDagher-Fadel,
930 M., Gailler, L., ... Antoine, P. (2020). *PLoS One*, 15(10):e0241000.
- 931 Pinto-Ledezma, J. N., Simon, L. M., Diniz-Filho, J. A. F., & Villalobos, F. (2017).
932 The geographical diversification of Furnariides: the role of forest versus open
933 habitats in driving species richness gradients. *Journal of Biogeography*, 44(8),
934 1683-1693.
- 935 Pennington, R. T., & Dick, C. W. (2004). The role of immigrants in the assembly of
936 the South American rainforest tree flora. *Philosophical Transactions of the*
937 *Royal Society of London. Series B: Biological Sciences*, 359(1450), 1611-1622.
- 938 Pennington, R. T., Lavin, M., Prado, D. E., Pendry, C. A., Pell, S. K., & Butterworth,
939 C. A. (2004). Historical climate change and speciation: neotropical seasonally
940 dry forest plants show patterns of both Tertiary and Quaternary diversification.
941 *Philosophical Transactions of the Royal Society of London. Series B: Biological*
942 *Sciences*, 359(1443), 515-538.
- 943 Pinou, T., Vicario, S., Marschner, M., & Caccone, A. (2004). Relict snakes of North
944 America and their relationships within Caenophidia, using likelihood-based
945 Bayesian methods on mitochondrial sequences. *Molecular Phylogenetics and*
946 *Evolution*, 32(2), 563-574.
- 947 Pontes-Nogueira, M., Martins, M., Alencar, L. R., & Sawaya, R. J. (2021). The role of
948 vicariance and dispersal on the temporal range dynamics of forest vipers in the
949 Neotropical region. *PloS One*, 16(9), e0257519.

- 950 Posadas, P., Crisci, J. V., & Katinas, L. (2006). Historical biogeography: a review of
951 its basic concepts and critical issues. *Journal of Arid Environments*, 66(3),
952 389-403.
- 953 Pyron, R. A. (2017). Novel approaches for phylogenetic inference from
954 morphological data and total-evidence dating in squamate reptiles (lizards,
955 snakes, and amphisbaenians). *Systematic Biology*, 66(1), 38-56.
- 956 R Core Team (2019). R: a language and environment for statistical computing.
957 Version version 3.5. 2. R Foundation for Statistical Computing, Vienna,
958 Austria.
- 959 Rahbek, C., Borregaard, M.K., Antonelli, A., Colwell, R.K., Holt, B.G.,
960 Noguez-Bravo, D. ... Fjeldså, J. (2019). Building mountain biodiversity:
961 Geological and evolutionary processes. *Science*, 365, 1114–1119.
- 962 Rangel, T.F., Edwards, N.R., Holden, P.B., Diniz-Filho, J.A.F., Gosling, W.D.,
963 Coelho, M.T.P., ... Colwell, R. K. (2018). Modeling the ecology and evolution
964 of biodiversity: biogeographical cradles, museums, and graves. *Science*, 361,
965 eaar5452.
- 966 Ree, R. H., & Smith, S. A. (2008). Maximum Likelihood Inference of Geographic
967 Range Evolution by Dispersal, Local Extinction, and Cladogenesis. *Systematic
968 Biology*, 57(1), 4-14.
- 969 Ree, R. H., & Sanmartín, I. (2018). Conceptual and statistical problems with the
970 DEC+ J model of founder - event speciation and its comparison with DEC via
971 model selection. *Journal of Biogeography*, 45(4), 741-749.
- 972 Řičan, O., Piálek, L., Zardoya, R., Doadrio, I., & Zrzavý, J. (2013). Biogeography of
973 the Mesoamerican Cichlidae (Teleostei: Heroini): colonization through the
974 GAARlandia land bridge and early diversification. *Journal of Biogeography*,
975 40(3), 579-593.
- 976 Ricklefs, R. E. (1987). Community diversity: relative roles of local and regional
977 processes. *Science*, 235(4785), 167-171.

- 978 Roll, U., Feldman, A., Novosolov, M., Allison, A., Bauer, A. M., Bernard, R., ...
979 Meiri, S. (2017). The global distribution of tetrapods reveals a need for targeted
980 reptile conservation. *Nature Ecology & Evolution*, *1*(11), 1677-1682.
- 981 Roncal, J., Nieto-Blázquez, M. E., Cardona, A., & Bacon, C. D. (2020). Historical
982 biogeography of caribbean plants revises regional paleogeography. In
983 Neotropical diversification: Patterns and processes (pp. 521-546). Springer,
984 Cham.
- 985 Ronquist, F. (1997). Dispersal-Vicariance Analysis: A New Approach to the
986 Quantification of Historical Biogeography. *Systematic Biology*, *46*(1), 195-203.
- 987 Ronquist, F., & Huelsenbeck, J. P. (2003). MrBayes 3: Bayesian phylogenetic
988 inference under mixed models. *Bioinformatics*, *19*(12), 1572-1574.
- 989 Ronquist, F., Teslenko, M., Van Der Mark, P., Ay, D. L., Darling, A., Höhna, S., ...
990 Huelsenbeck, J. P. (2012). MrBayes 3.2: efficient Bayesian phylogenetic
991 inference and model choice across a large model space. *Systematic Biology*,
992 *61*(3), 539-542.
- 993 Rull, V. (2011). Neotropical biodiversity: timing and potential drivers. *Trends in*
994 *Ecology & Evolution*, *26*(10), 508-513.
- 995 Sanmartín, I., Enghoff, H., & Ronquist, F. (2001). Patterns of animal dispersal,
996 vicariance and diversification in the Holarctic. *Biological Journal of the*
997 *Linnean Society*, *73*(4), 345-390.
- 998 Sanmartín I., & Ronquist, F. (2004). Southern hemisphere biogeography inferred by
999 event-based models: plant versus animal patterns. *Systematic Biology*, *53*(2),
1000 216–243.
- 1001 Santos, J. C., Coloma, L. A. & Summers, K. (2009). Amazonian amphibian diversity
1002 is primarily derived from late Miocene Andean lineages. *PLoS Biology*, *7*,
1003 e1000056.
- 1004 Serrano, F. A. C., dos Santos Vieira-Alencar, J. P., Díaz-Ricaurte, J. C., & de Campos
1005 Nogueira, C. (2020). Mapping local and regional distribution of *Lygophis*

- 1006 *paucidens* Hoge, 1952 (Serpentes, Dipsadidae), an elusive snake from the sandy
1007 savannas of Brazil and Paraguay. *Check List*, 16(1), 75-81.
- 1008 Serrano, F. C., dos Santos Vieira-Alencar, J. P., Díaz-Ricaurte, J. C., Valdujo, P. H.,
1009 Martins, M., & de Campos Nogueira, C. (2023). The Wallacean Shortfall and
1010 the role of historical distribution records in the conservation assessment of an
1011 elusive Neotropical snake in a threatened landscape. *Journal for Nature
1012 Conservation*, 72, 126350.
- 1013 Simpson, G. G. (1980). *Splendid Isolation. The Curious History of South American
1014 Mammals.* - Yale University Press, New Haven, Connecticut
- 1015 Tiffney, B. H. (1985). The Eocene North Atlantic land bridge: its importance in
1016 Tertiary and modern phytogeography of the Northern Hemisphere. *Journal of
1017 the Arnold Arboretum*, 66(2), 243-273.
- 1018 Torres-Carvajal, O., Echevarría, L. Y., Lobos, S. E., Venegas, P. J., & Kok, P. J.
1019 (2019). Phylogeny, diversity and biogeography of Neotropical sipo snakes
1020 (Serpentes: Colubrinae: *Chironius*). *Molecular Phylogenetics and Evolution*,
1021 130, 315-329.
- 1022 Townsend, T. M., Leavitt, D. H., & Reeder, T. W. (2011). Intercontinental dispersal
1023 by a microendemic burrowing reptile (Dibamidae). *Proceedings of the Royal
1024 Society B: Biological Sciences*, 278(1718), 2568-2574.
- 1025 Uetz, P., Freed, P., Aguilar, R. & Hošek, J. (eds.) (2020) The Reptile Database,
1026 <http://www.reptile-database.org>, accessed 20 January 2020
- 1027 Vanzolini, P. E., & Heyer, W. R. (1985). The American herpetofauna and the
1028 interchange. In *The great American biotic interchange* (pp. 475-487). Springer,
1029 Boston, MA.
- 1030 Wolfe, J. A. (1975) Some aspects of plant geography of the Northern Hemisphere
1031 during the Late Cretaceous and Tertiary. *Annals of the Missouri Botanical
1032 Garden*, 62, 264–279. (doi:10.2307/2395198)
- 1033 Vasconcelos, T. N. C., Alcantara, S., Andrino, C. O., Forest, F., Reginato, M., Simon,
1034 M. F. & Pirani, J. R. (2020). Fast diversification through a mosaic of
1035 evolutionary histories characterizes the endemic flora of ancient Neotropical

- 1036 mountains. *Proceedings of the Royal Society B: Biological Sciences*, 287,
1037 20192933.
- 1038 Vidal, N., Dewynter, M., & Gower, D. J. (2010). Dissecting the major American
1039 snake radiation: a molecular phylogeny of the Dipsadidae Bonaparte (Serpentes,
1040 Caenophidia). *Comptes Rendus Biologies*, 333(1), 48-55.
- 1041 Wang, Y., & Liu, Q. (2006). Comparison of Akaike information criterion (AIC) and
1042 Bayesian information criterion (BIC) in selection of stock–recruitment
1043 relationships. *Fisheries Research*, 77(2), 220-225.
- 1044 Wilf, P., Cúneo, N. R., Escapa, I. H., Pol, D., & Woodburne, M. O. (2013). Splendid
1045 and seldom isolated: the paleobiogeography of Patagonia. *Annual Review of*
1046 *Earth and Planetary Sciences*, 41, 561-603.
- 1047 Woodburne, M. O., Goin, F. J., Bond, M., Carlini, A. A., Gelfo, J. N., López, G. M., ...
1048 Zimicz, A. N. (2014). Paleogene land mammal faunas of South America; a
1049 response to global climatic changes and indigenous floral diversity. *Journal of*
1050 *Mammalian Evolution*, 21(1), 1-73.
- 1051 Wüster, W., Peppin, L., Pook, C. E., & Walker, D. E. (2008). A nesting of vipers:
1052 phylogeny and historical biogeography of the Viperidae (Squamata: Serpentes).
1053 *Molecular Phylogenetics and Evolution*, 49(2), 445-459.
- 1054 Yang, Z., & Rannala, B. (1997). Bayesian phylogenetic inference using DNA
1055 sequences: a Markov Chain Monte Carlo method. *Molecular Biology and*
1056 *Evolution*, 14(7), 717-724.
- 1057 Zaher, H., Yáñez-Muñoz, M. H., Rodrigues, M. T., Graboski, R., Machado, F. A.,
1058 Altamirano-Benavides, M., ... Grazziotin, F. G. (2018). Origin and hidden
1059 diversity within the poorly known Galápagos snake radiation (Serpentes:
1060 Dipsadidae). *Systematics and Biodiversity*, 16(7), 614-642.
- 1061 Zaher, H., Murphy, R. W., Arredondo, J. C., Graboski, R., Machado-Filho, P. R.,
1062 Mahlow, K., ... Grazziotin, F. G. (2019). Large-scale molecular phylogeny,
1063 morphology, divergence-time estimation, and the fossil record of advanced
1064 caenophidian snakes (Squamata: Serpentes). *PloS One*, 14(5), e0216148.
- 1065

1066 **DATA AVAILABILITY**

1067 Data are available from Figshare: to be added

1068

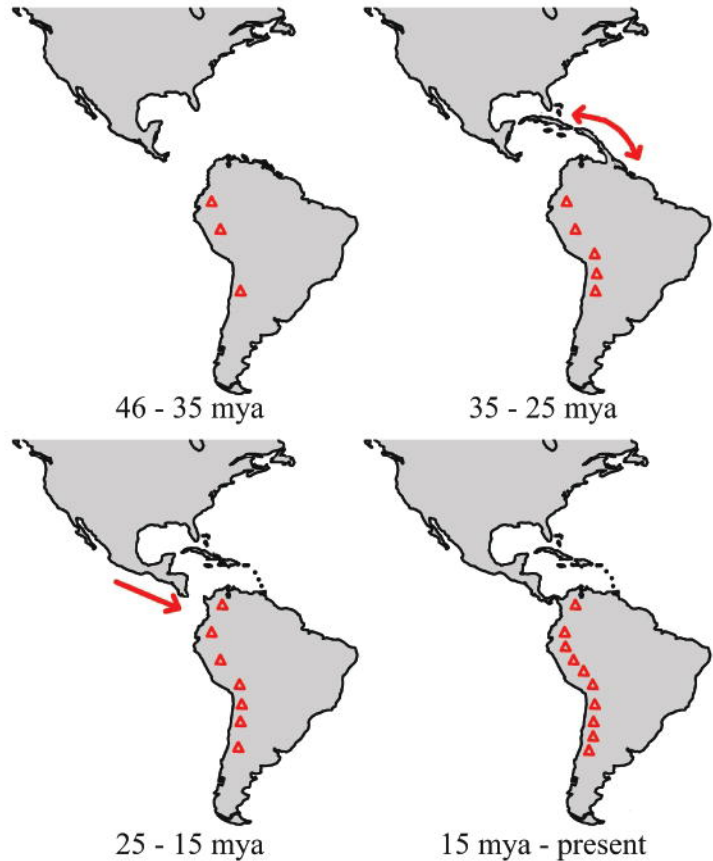
1069 **BIOSKETCH**

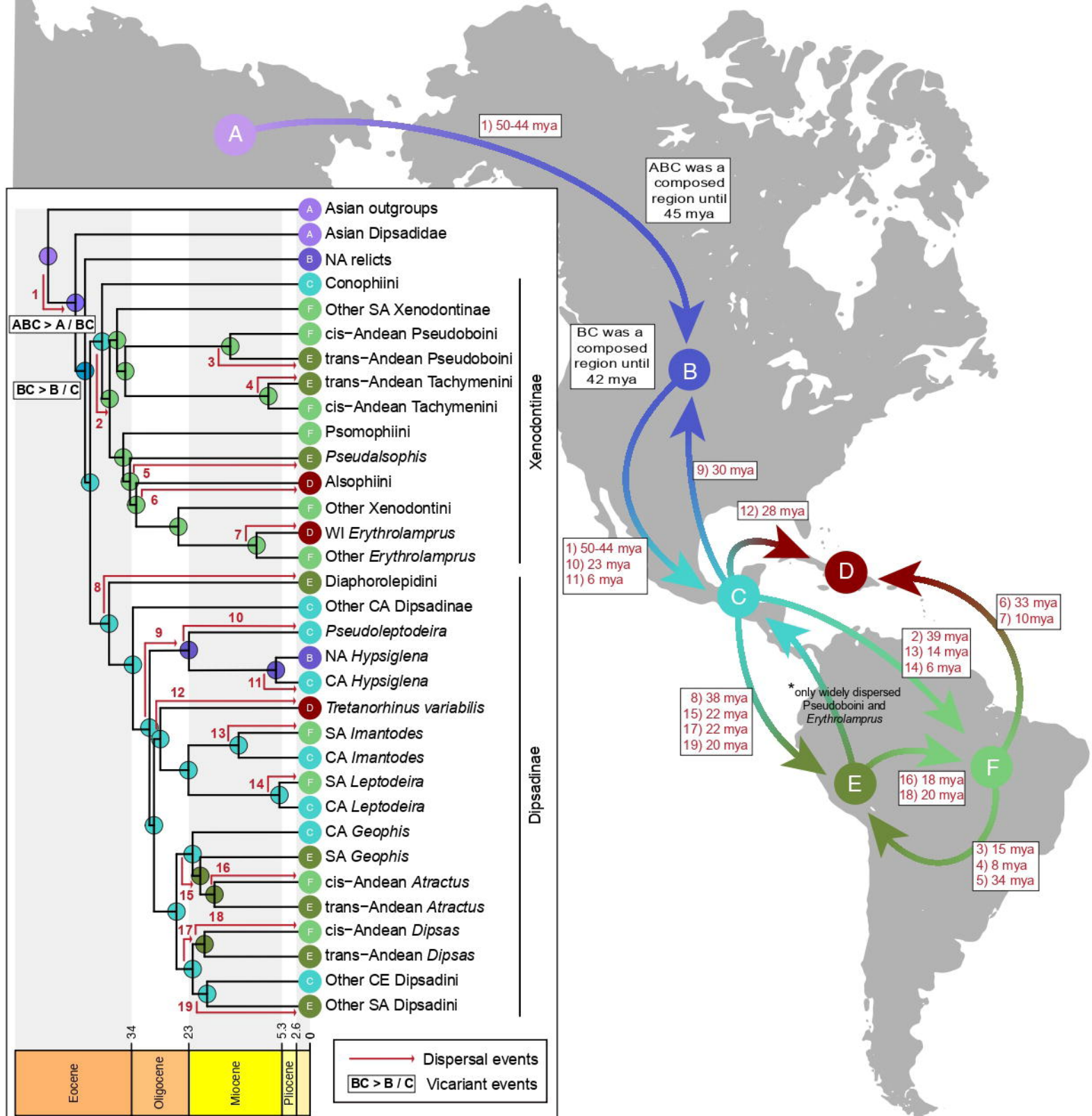
1070 **Filipe C. Serrano** is an ecologist interested in the spatial distribution of
1071 evolutionary processes, with a focus on herpetofauna. His current research topics
1072 include investigating how distribution at different scales may be used to infer
1073 ecological relationships and conservation status. This article represents the first
1074 chapter of his doctoral project “Phylogenetic diversity, endemism and conservation of
1075 cis-andean Dipsadid snakes” at the University of São Paulo (Brazil).

1076

1077 **AUTHOR CONTRIBUTIONS:** FCS, MPN and FG conceived and designed the
1078 study. FCS, MPN and FG analysed the data. FCS wrote the paper. MPN, FG, CN,
1079 RJS and LRVA contributed critically to the drafts and all authors gave final approval
1080 for publication of the paper. This research has not previously been presented
1081 elsewhere.

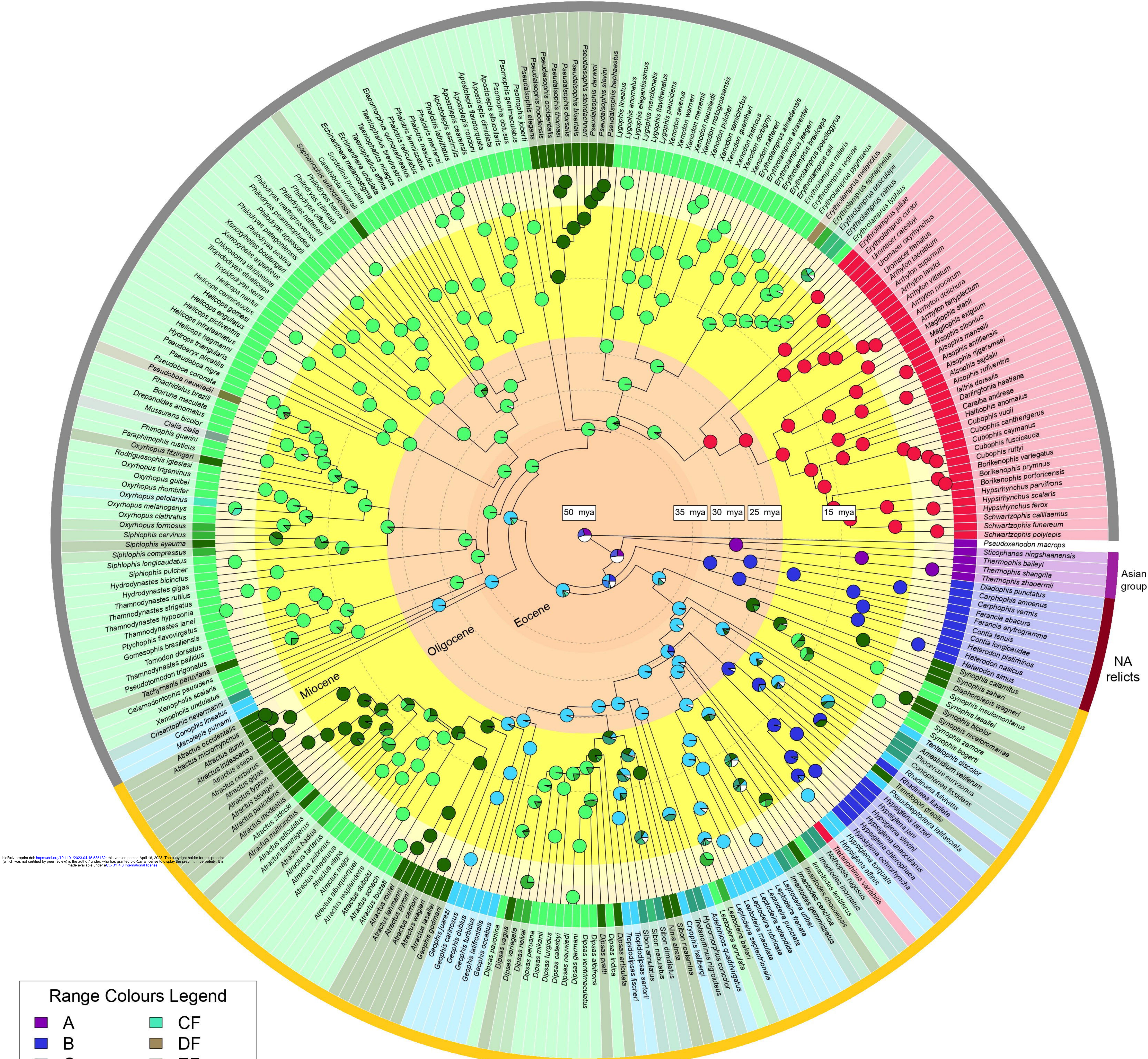
1082





Xenodontinae

Dipsadinae

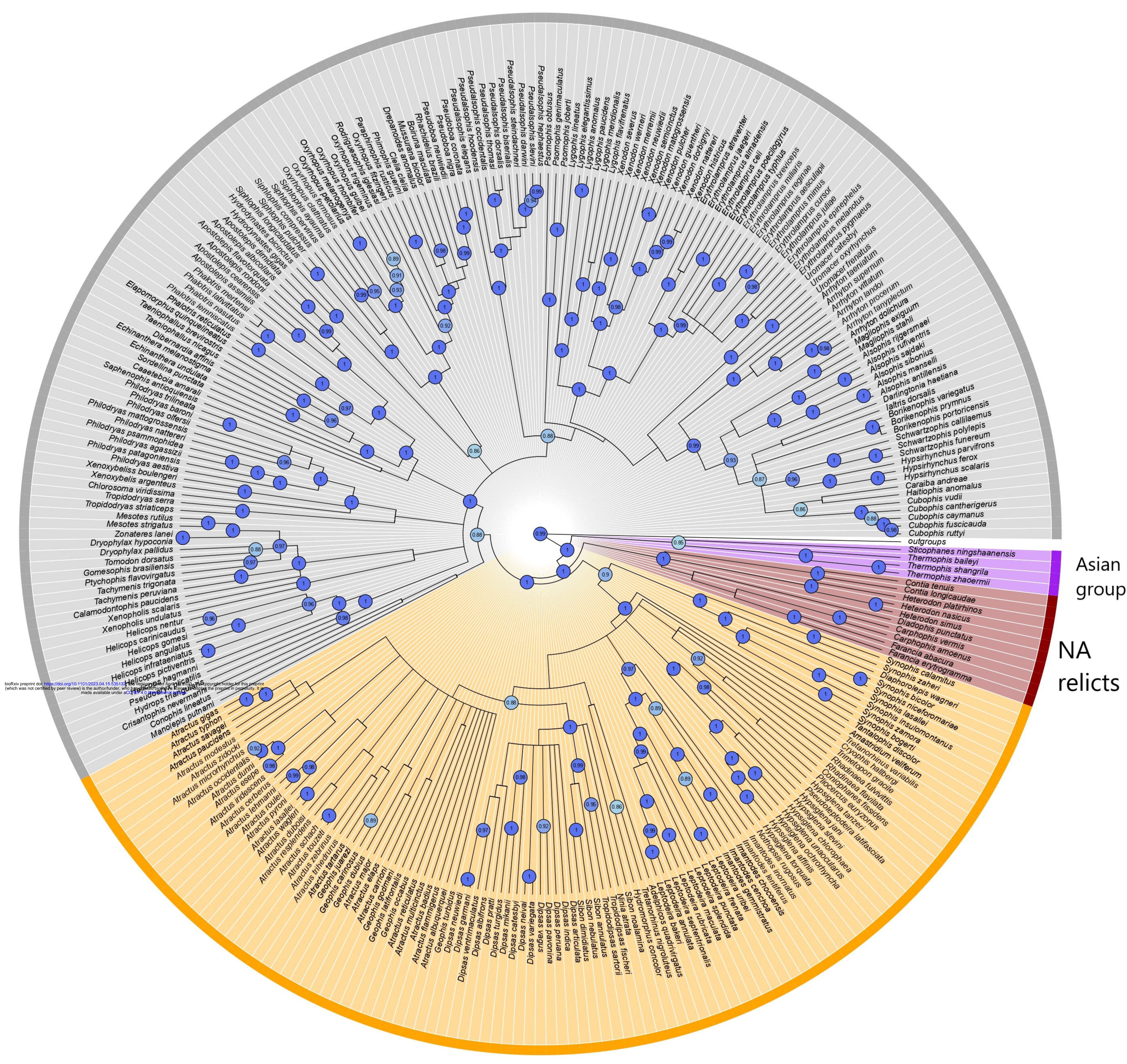


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Range Colours Legend

- | | |
|--|--|
| ■ A | ■ CF |
| ■ B | ■ DF |
| ■ C | ■ EF |
| ■ D | ■ ABC |
| ■ E | ■ CDF |
| ■ F | ■ CEF |
| ■ BC | ■ DEF |
| ■ CE | □ AllOthers |

Xenodontinae



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Dipsadinae