

Article

Island-to-Island Vicariance, Founder-Events and within-Area Speciation: The Biogeographic History of the *Antillattus* Clade (Salticidae: Euophryini)

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Abstract: The Caribbean Archipelago is a biodiversity hotspot that plays a key role in developing our understanding of how dispersal ability affects species formation. In island systems, species with intermediate dispersal abilities tend to exhibit greater diversity, as may be the case for many of the salticid lineages of the insular Caribbean. Here, we use molecular phylogenetic analyses to infer patterns of relationships and biogeographic history of the Caribbean endemic *Antillattus* clade (*Antillattus*, *Truncattus*, and *Petemethis*). We test if the timing of origin of the *Antillattus* clade in the Greater Antilles is congruent with GAARlandia and infer patterns of diversification within the *Antillattus* clade among Cuba, Hispaniola, and Puerto Rico. Specifically, we evaluate the relative roles of dispersal over land connections, and overwater dispersal events in diversification within the Greater Antilles. Time tree analysis and model-based inference of ancestral ranges estimated the ancestor of the *Antillattus* clade to be c. 25 Mya, and the best model suggests dispersal via GAARlandia from northern South America to Hispaniola. Hispaniola seems to be the nucleus from which ancestral populations dispersed into Cuba and Puerto Rico via land connections prior to the opening of the Mona Passage and the Windward Passage. Divergences between taxa of the *Antillattus* clade from Cuban, Hispaniolan, and Puerto Rican populations appear to have originated by vicariance, founder-events and within-island speciation, while multiple dispersal events (founder-events) between Cuba and Hispaniola during the Middle Miocene and the Late Miocene best explain diversity patterns in the genera *Antillattus* and *Truncattus*.

Keywords: Caribbean biogeography; molecular dating; ancestral range analysis; endemics; founder-event; intermediate dispersal model



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1. Introduction

Since Darwin and Wallace, evolutionary biologists have been fascinated by the extraordinary diversity and richness of islands. Biogeography has been reinvigorated through the use of molecular methods to test divergence hypotheses [1–4] and matured through the successful reconciliation of theories that previously were treated as mutually exclusive: long-distance dispersal and vicariance. This progress has been aided by the growth of sophistication in testing long distance dispersal hypotheses—best supported when vicariance explanations are rejected by geological history (e.g., Matos-Maraví et al. [5])—and the development of models such as the intermediate dispersal hypothesis [6–13].

The Greater Antilles (Cuba, Hispaniola, Puerto Rico, and Jamaica) are one of the planet's recognized biodiversity hotspots [2,14]. The area is an excellent arena to test biogeographical hypotheses due to its complex geology (including, e.g., land bridge or Wallacean fragment islands, volcanic or Darwinian islands, and uplifted coral shelves), geography (including complex topography and diverse climates), and old age [2,11,15–27]. The uplift of the core Greater Antilles, arising from the earlier 'proto-Antilles ridge, began during the Middle Eocene (c. 48–37 Mya) and reached its maximum land area at the Eocene–Oligocene (c. 40–30 Mya) boundary [17,28–35]. Since that time, the Greater Antilles have remained above water with variation in island area and inter-island connections changing with sea level. For example, Hispaniola was physically connected to Puerto Rico and Cuba until the formation of the Mona Passage (late Oligocene to early Miocene, c. 30–23 Ma) and the Windward Passage (early-to-middle Miocene, c. 17–15 Ma), respectively [17,35–38].

The origin of the present-day terrestrial biota of the Greater Antilles has been hypothesized to extend back to the emergence of the proto-Antilles (c. 65 Mya), predicting the survival of relict lineages through periods of oceanic submergence of island fragments [28,32,39–41]. However, for most organisms, their origin more likely traces back to the permanent emergence of the Greater Antilles (c. 40 Mya) and could have involved both long-distance over-water dispersal events [42–44] (as occurred in *Solenodons* [45], Urocopid snails [46], Calliphoridae flies [47], and various spiders [26,48–52]) and vicariance. The oldest putative vicariance events are linked to the hypothesized existence of GAARlandia (GAAR = Greater Antilles Aves Ridge) a land bridge relatively briefly (c. 35 to 32 Mya) connecting the Greater Antilles and continental South America during the Eocene–Oligocene transition [32,33,44,53,54]. Though it remains under active debate [27], this hypothesis has received support in studies across a variety of taxa (e.g., freshwater fishes [55], lizards [16], bats [56], mammals [42,45], plants [57], and spiders [4,58]). However, a recent meta-analysis suggested that GAARlandia does not help explain the colonization of various land vertebrate lineages [27]. Regardless, both historical connections among islands leading to vicariant interchange of organisms, and long-distance dispersal are recognized as critically important components that must be considered together for a complete account of island biogeography [1,7–9,43,48,49,52,59].

In the last decades there has been a growing interest in studies on invertebrates [5,24,52,60–67] including arachnids [4,18,22,23,26,48–50,58,68]. These studies have found mixed support for vicariance [22,69,70] and dispersal [4,16,18,45,48,50,51]; often a combination of the two [5].

The geographic distribution of spiders in the euophryine *Antillattus* clade of the family Salticidae make them an interesting model for testing hypotheses of Caribbean dispersal corridors [68]. Salticids are a diverse, globally distributed group of spiders (c. 6392 total species) [71] known as “jumping spiders” due to their semi-hydraulic locomotion system [72–74]. Within Salticidae, euophryines are a relatively young group (c. 33–30 Mya) [69]. Phylogenetic reconstruction shows that much like other salticid lineages [75–77], New and Old-World euophryines are grouped into separate clades, indicating that most euophryine diversification occurred intra-continently [68]. In their landmark revisionary work on euophryines, Zhang and Maddison [68] highlighted the *Antillattus* clade as one of several salticid lineages that has diversified within the Caribbean. Members of the *Antillattus* clade (*Antillattus* Bryant [78], *Truncattus* Zhang and Maddison [79], and *Petemathis* Prószyński and Deeleman-Reinhold [68,80,81]) are small to medium-sized spiders of the Greater Antilles (Cuba, Hispaniola, and Puerto Rico) (Figures 1–3). During the morning, these spiders can be found in understory habitats and dense forests, and typically walk or jump between leaves, branches, and trunks. In the sunset and at night, they are found in their shelters, e.g., leaves, and under the bark).

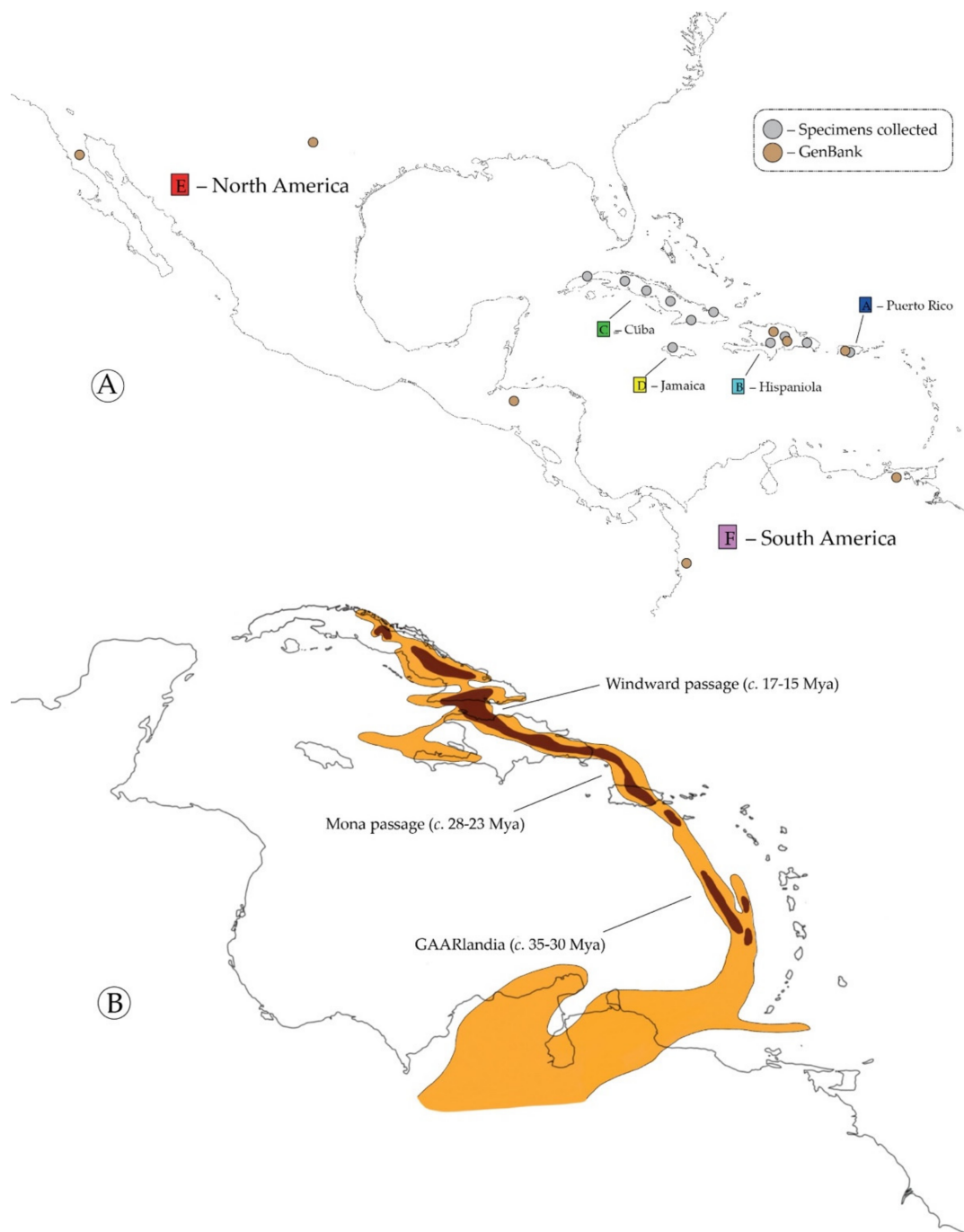


Figure 1. (A) Map of specimens collected for this work, including samples obtained from GenBank (Zhang and Maddison [69]). Area code used in the distribution ranges (A—Puerto Rico, B—Hispaniola, C—Cuba, D—Jamaica, E—North America, F—South America). (B) Schematic representations of the GAARlandia and Caribbean land areas available at certain time periods (Iturralde-Vinent [17], Iturralde-Vinent and MacPhee [32], MacPhee and Iturralde-Vinent [33]). Maps show simplified island positions in the respective time window used for the time-stratified analysis.



Figure 2. A–F *gracilis* group. (A,B) *Antillattus cambridgei*, male and female habitus. (C,D) *Antillattus gracilis*, male and female habitus. (E,F) *Antillattus placidus*, male and female habitus. Images by Wayne Maddison, released under a Creative Commons Attribution (CC–BY) 3.0 license.

The *Antillattus* clade is relatively late-diverging with an estimated origin in the Caribbean by dispersal in the Miocene [c. 22.34–19.74 Mya], a scenario that implies ancestors dispersed over the Greater Antilles via land connections prior to the opening of the Mona Passage and the Windward Passage [68]. Members of the *Antillattus* clade appear to have relatively low dispersal potential based on their biology and absence from Jamaica and the isolated volcanic islands of the Lesser Antilles—none of which formed a part of the hypothetical GAARlandia land bridge (Cuba, Hispaniola, Puerto Rico). We predict that the Mona Passage and Windward Passage may have been integral to the dispersal of the *Antillattus* clade among the Greater Antilles. Here, we evaluate the non-GAARlandia (over-water dispersal) and GAARlandia hypotheses to infer the timing and ancestral colonization route of Caribbean euophryines; analyze the relationship of the *Antillattus* clade to other Greater Antilles euophryines (*Popcornella*, *Corticattus*, and the *Agobardus* clade); and infer

the details of diversification within the *Antillattus* clade. We use time-calibrated phylogenies to see if divergence times of taxa on Cuba, Hispaniola, and Puerto Rico correspond to estimated dates of the land connections (Mona Passage and Windward Passage), or if they are better explained by overwater dispersal. Finally, we apply biogeographical stochastic mapping (BSM) to estimate how the frequency of dispersal and vicariance events of the clade resulted in the present-day distribution and diversity.



Figure 3. A–F *darlingtoni* group. (A,B) *Antillattus applanatus*, male and female habitus. (C,D) *Antillattus darlingtoni*, male and female habitus. (E,F) *Antillattus maxillosus*, male and female habitus. Images by Wayne Maddison, released under a Creative Commons Attribution (CC–BY) 3.0 license.

2. Materials and Methods

Study Group and Taxon Sample

Antillattus clade intergeneric relationships and their outgroup structure are poorly known (see Zhang and Maddison [81]), while the broader phylogenetic placement of the *Antillattus* clade is better established (see Zhang and Maddison [68,81]). The *Antillattus*

clade was instated as a clade separate from the insular Caribbean *Anasaitis-Corythalia* clade and closely related to the genera *Popcornella*, *Corticattus* and the *Agobardus* clade based on molecular and morphological studies (Zhang and Maddison [68]). These studies also resulted in the transfer of insular Caribbean species of *Pensacola* and *Cobanus*, and some species of *Agobardus* from Cuba, to the genus *Antillattus* (Zhang and Maddison [68]). Here, for phylogenetic inference, we included as outgroups the continental *Pensacola-Mexigonus* clade, and *Sidusa* clade, the Greater Antilles genera *Popcornella*, *Corticattus*, and the *Agobardus* clade (*Agobardus*, *Compsodecta* and *Bythocrotus*).

The *Antillattus* clade is currently composed of twenty-three species distributed as follows: ten species of *Antillattus* from Hispaniola and three species from Cuba, five species of *Truncattus* from Hispaniola, and five species of *Petemathis* from Puerto Rico. Here, we include a total of thirty-two taxa collected using beating and visual search methods in Cuba, Puerto Rico, and Hispaniola (Figures 1 and 4, Table 1). Material collected was fixed in the field in 95% ethanol. Caribbean voucher specimens will be deposited in the Smithsonian Institute, Washington DC. We collect and identify just over 60% of the known species for the *Antillattus* clade (nine *Antillattus*, three *Petemathis*, and three *Truncattus*), while the remaining sampled taxa could not be attributed to known species (Figures 2 and 3, Table 1).

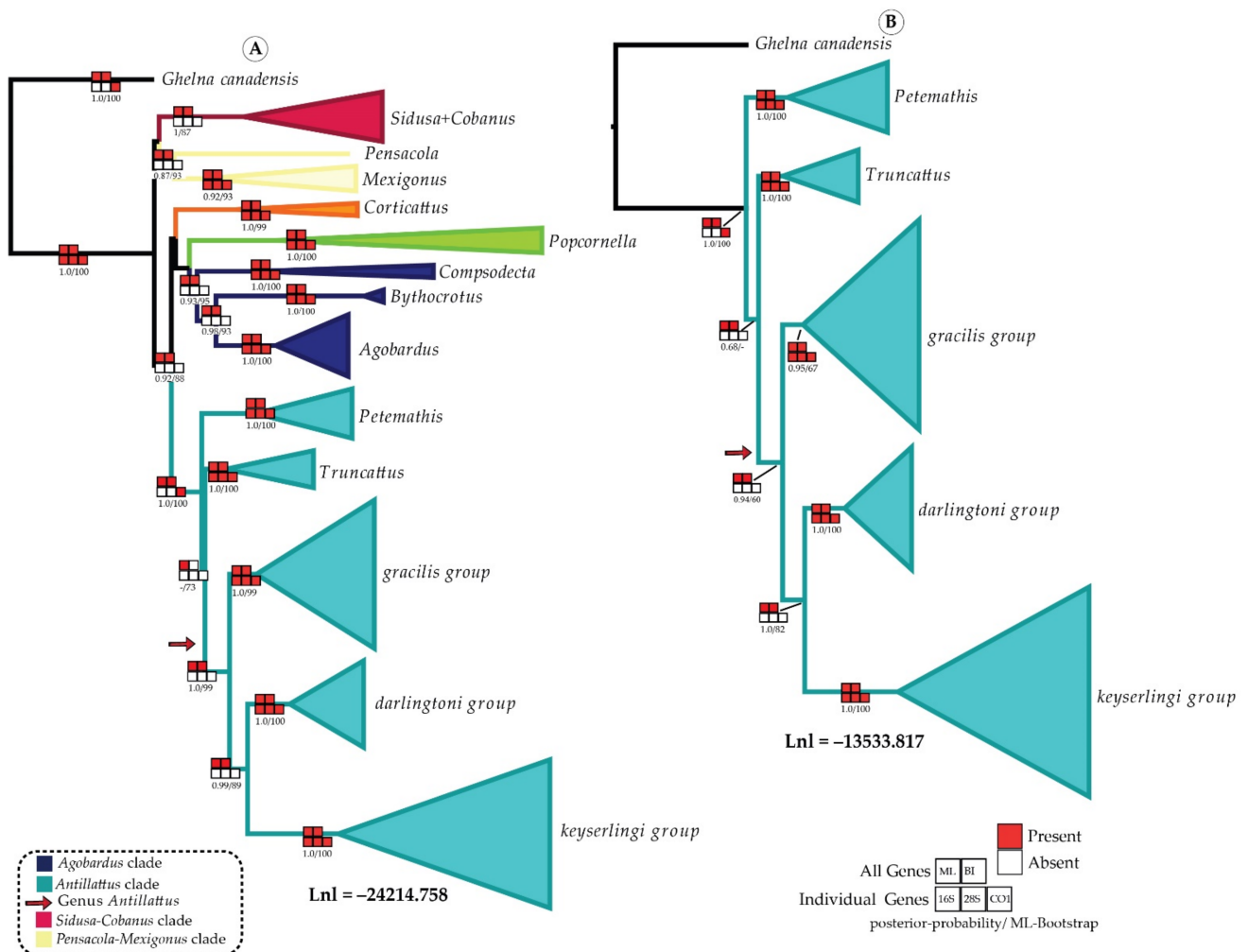


Figure 4. Summary of (A) ML (Lnl = -24,214.785) and BI (Harmonic-means -24,208.96) with outgroups and (B) ML (Lnl = -13,533.817) and BI (Harmonic-means = -13,597.32) without outgroups, based on analyses on the molecular datasets (28S, 16S-ND1 and CO1). Individual Gene refers to support for a clade in the ML tree of individual genes.

Table 1. Taxon sample with specific collection information and Genbank accession numbers of the previous published sequence. Checkmark (✓) refers sequence obtained from this study.

Species	Voucher	Locality	CO1	16S-ND1	28S
<i>Agobardus anormalis montanus</i>	JXZ357	DOMINICAN REPUBLIC: Pedernales, (N18.128, W71.558)	KC615636	KC615802	KC615376
<i>Agobardus bahoruco</i>	JXZ324	DOMINICAN REPUBLIC: Pedernales, (N18.128, W71.558)		KC615844	KC615417
<i>Agobardus cf. brevitarsus</i>	JXZ311	DOMINICAN REPUBLIC: Pedernales, (N18.128, W71.558)	KC615637	KC615803	KC615637
<i>Agobardus cordiformis</i>	JXZ358	DOMINICAN REPUBLIC: Pedernales, (N17.965, W71.635)	KC615634	KC615800	KC615374
<i>Agobardus gramineus</i>	JXZ314	DOMINICAN REPUBLIC: Pedernales, (N17.965, W71.635)	KC615635	KC615801	KC615375
<i>Agobardus oviedo</i>	JXZ312	DOMINICAN REPUBLIC: Pedernales, (N17.802, W71.349)	KC615638	KC615804	KC615378
<i>Antillattus</i> [Cuba1]	CU787945 CU00107A	CUBA: Granma, Bartolomé Maso, (N20.009, W76.894)	✓	✓	✓
<i>Antillattus</i> [Cuba2]	CU00025A CU00086A CU00090A CU00004A CU00016A	CUBA: Granma, Bartolomé Maso, (N20.013, W76.834)	✓	✓	
<i>Antillattus</i> [Cuba3]	CU787957 CU03506A	CUBA: Pinar del Rio, Viñales, (N22.657, W83.701)	✓		
<i>Antillattus</i> [Cuba4]	CU00100A CU03361A CU03317A	CUBA: Guantánamo, Baracoa, (N20.331, W74.569)	✓		
<i>Antillattus</i> [Cuba4]	CU03121A	CUBA: Guantánamo, Nibujón, (N20.052, W76.502)	✓		
<i>Antillattus cambridgei</i>	JXZ321	DOMINICAN REPUBLIC: La Vega, (N19.033, W70.543)	KC615646	KC615818	KC615392
<i>Antillattus cambridgei</i>	DR784676 DR785410 DR785798 DR782454	DOMINICAN REPUBLIC: La Alta Gracia, (N19.067, W69.463)	✓	✓	
<i>Antillattus cambridgei</i>	DR785494 DR782541	DOMINICAN REPUBLIC: La Alta Gracia, (N19.893, W71.653)	✓	✓	
<i>Antillattus cambridgei</i>	DR782541 DR785783 DR785508	DOMINICAN REPUBLIC: La Alta Gracia, (N19.355, W070.111)	✓	✓	
<i>Antillattus cambridgei</i>	DR782598	DOMINICAN REPUBLIC: La Alta Gracia, (19.355N, W70.111)	✓	✓	✓

Table 1. Cont.

Species	Voucher	Locality	CO1	16S-ND1	28S
<i>Antillattus cambridgei</i>	DR784852 DR785098 DR785696 DR785438 DR787296	DOMINICAN REPUBLIC: La Alta Gracia, (19.067, W69.463)	✓	✓	
<i>Antillattus cambridgei</i>	DR787296 DR787293 DR787254 DR787223	DOMINICAN REPUBLIC: La Vega, (N19.036, W70.543)	✓	✓	
<i>Antillattus cambridgei</i>	DR787328 DR787252 DR787285 DR787207 DR787327 DR787319 DR787324	DOMINICAN REPUBLIC: Santo Domingo, (19.051 N, W70.888)	✓	✓	
<i>Antillattus cambridgei</i>	DR787105	DOMINICAN REPUBLIC: San Juan, (N19.175, W71.049)	✓	✓	
<i>Antillattus cf. applanatus</i>	JXZ336	DOMINICAN REPUBLIC: Barahona, Cachote (N18.101, W71.194)	KC615699	KC615911	KC615699
<i>Antillattus cubensis</i>	CU003076 CU002975 CU003097 CU003360 CU002456 CU003486 CU02560A CU02975A CU03033A CU03076A CU03097A CU03360A	CUBA: Cienfuegos, Soledad, (N22.124, W80.325)	✓		
<i>Antillattus cubensis</i>	CU03417A CU03488A	CUBA: Santiago de Cuba, San Luis, (N20.179, W75.783)	✓		
<i>Antillattus cubensis</i>	CU3075A	CUBA: Santiago de Cuba, (N20.010, W76.037)	✓		
<i>Antillattus cubensis</i>	CU02583A	CUBA: Guantánamo, Baracoa, (N20.331, W74.569)	✓		
<i>Antillattus cubensis</i>	CU787598 CU783280 CU787621 CU787283 CU787277	CUBA: Granma, Bartolomé Maso, (N20.009, W76.894)	✓		
<i>Antillattus darlingtoni</i>	JXZ341	DOMINICAN REPUBLIC: La Vega, Ébano Verde, (N19.033, W70.543)	KC615762	KC616005	KC615583
<i>Antillattus darlingtoni</i>	DR787120	DOMINICAN REPUBLIC: San Juan, Pico Duarte	✓	✓	

Table 1. Cont.

Species	Voucher	Locality	CO1	16S-ND1	28S
<i>Antillattus darlingtoni</i>	DR786937 DR784873	DOMINICAN REPUBLIC: Valle nuevo	✓	✓	
<i>Antillattus darlingtoni</i>	DR784828 DR784873	DOMINICAN REPUBLIC: La Vega, Ébano Verde, (N19.026, W19.0264)	✓	✓	
<i>Antillattus gracilis</i>	JXZ320	DOMINICAN REPUBLIC: La Vega, P.N.Armando Bermúdez, (N19.06, W70.86)		KC615817	KC615391
<i>Antillattus gracilis</i>	DR782845 DR787278	DOMINICAN REPUBLIC: Santo Domingo, Los Tablones (N19.051, W70.888)	✓	✓	
<i>Antillattus keyserlingi</i>	CU03135A	CUBA: Holguin, Frank Pais, (N20.529N, N75.768)	✓		
<i>Antillattus keyserlingi</i>	CU02571A	CUBA: Santiago de Cuba, Gran Piedra, (N20.011, W75.623)	✓		
<i>Antillattus keyserlingi</i>	CU787312	CUBA: Guantánamo, Baracoa, (20.331N, W74.569)	✓		
<i>Antillattus keyserlingi</i>	CU00081A CU00088A CU02951A CU02985A CU03043A CU782822 CU783187 CU783232 CU783245 CU783281 CU783404 CU783425 CU787302 CU787433 CU787625	CUBA: Granma, Bartolomé Maso, (N20.052, W76.502)	✓	✓	✓
<i>Antillattus keyserlingi</i>	CU02467A CU03538A CU03395A	CUBA: Holguin, Frank Pais, (N20.529, W75.768)	✓	✓	✓
<i>Antillattus keyserlingi</i>	CU03036A CU03274A	CUBA: Granma, Bartolomé Maso, (N20.015–W76.839)	✓		
<i>Antillattus maxillosus</i>	JXZ335	DOMINICAN REPUBLIC: La Vega, road Constanza to Ocoa, Valle Nuevo (N18.700, W70.606)	KC615708	KC615935	KC615510
<i>Antillattus maxillosus</i>	DR786952 DR786992 DR786981	DOMINICAN REPUBLIC: Valle nuevo, Villa Pajón (N18.82208, W070.6838)	✓	✓	
<i>Antillattus</i> [Cuba5]	CU03373A CU03396A CU03539A CU03534A	CUBA: Pinar del Rio, Viñales, (N22.653, W83.699)	✓		
<i>Antillattus placidus</i>	DR787249	DOMINICAN REPUBLIC: La Vega, Jarabacoa, (N19.036, W70.543)	✓	✓	

Table 1. Cont.

Species	Voucher	Locality	CO1	16S-ND1	28S
<i>Antillattus placidus</i>	DR782502 DR785683 DR785081	DOMINICAN REPUBLIC: La Alta Gracia, Yuma, (N19.355, W70.111)	✓	✓	
<i>Antillattus scutiformis</i>	JXZ326	DOMINICAN REPUBLIC: La Vega, road Constanza to Ocoa, Valle Nuevo (N18.848, W70.720)		KC615860	KC615433
<i>Bythocrotus cf. crypticus</i>	JXZ323	DOMINICAN REPUBLIC: El Seibo, Pedro Sanchez, (N18.86, W69.11)	KC615661	KC615839	KC615412
<i>Bythocrotus crypticus</i>	JXZ322	DOMINICAN REPUBLIC: Barahona, (N18.424, W71.112)	KC615660	KC615838	KC615411
<i>Cobanus cambridgei</i>	JXZ122	COSTA RICA: Prov. San José, (N9.65, W83.97)		KC615872	KC615445
<i>Cobanus extensus</i>	JXZ122	ECUADOR: Pichincha, near El Cisne, (N0.1493, W79.0317)		KC615872	KC615445
<i>Cobanus mandibularis</i>	JXZ245	PANAMA: Panamá: Gamboa, Pipeline Road, (N9.15840, W79.74252)		KC615876	KC615449
<i>Cobanus unicolor</i>	JXZ244	PANAMA: Chiriqui: Fortuna, Quebrada Samudio, (N8.73464, W82.24839)		KC615878	KC615451
<i>Compsodecta festiva</i>	JAM4122A	JAMAICA: Portland, Millbank, (N18.013, W76.379)	✓		
<i>Compsodecta haytiensis</i>	JXZ325	DOMINICAN REPUBLIC: Barahona, Highway 44 south of Barahona (N18.138, W71.070)	KC615671	KC615859	KC615432
<i>Compsodecta peckhami</i>	JXZ327	DOMINICAN REPUBLIC: Pedernales, Rio Mulito (N18.155, W71.758)		KC615884	KC615457
<i>Corticattus guajataca</i>	JXZ305	PUERTO RICO: Isabela: Bosque de Guajataca (N18.421, W66.966)	KC615715	KC615945	KC615521
<i>Corticattus latus</i>	JXZ337	DOMINICAN REPUBLIC: Pedernales: Laguna de Oviedo (N17.802 W71.349)	KC615698	KC615908	KC615483
<i>Mexigonus arizonensis</i>	JXZ163	USA: Arizona: Yavapai Co., Iron Springs (N34.58476, W112.57071)	KC615747	KC615988	KC615564
<i>Mexigonus cf. minuta</i>	d117	ECUADOR: Pichincha: Quito	✓	✓	✓
<i>Mexigonus morosus</i>	JXZ362	USA: California: San Mate Co.,(N37.434, W122.311)		KC615990	KC615566

Table 1. Cont.

Species	Voucher	Locality	CO1	16S-ND1	28S
<i>Pensacola signata</i>	JXZ371	GUATEMALA: Depto. Petén, Reserva Natural Ixpanpajul		KC616006	KC615584
<i>Petemathis portoricensis</i>	PR782206	PUERTO RICO: Villalba: Toro negro, El Bolo Trail (N18.1777401, W66.488319)	✓	✓	
<i>Petemathis portoricensis</i> [Adjuntas]	JXZ306	PUERTO RICO: Adjuntas, HWY143 to Cerro Punta (N18.167, W66.576)	KC615716	KC615946	KC615522
<i>Petemathis portoricensis</i> [Maricao]	JXZ303	PUERTO RICO: Maricao, Bosque de Maricao (N18.150, W66.994)	KC615711	KC615940	KC615515
<i>Petemathis tetuani</i>	JXZ303	PUERTO RICO: Maricao, Bosque de Maricao (N18.150, W66.994)	KC615711	KC615940	KC615515
<i>Petemathis tetuani</i>	PR782277	PUERTO RICO: Villalba: Toro negro, El Bolo Trail, (N18.177, W66.488)	✓	✓	
<i>Petemathis tetuani</i>	PR392859	PUERTO RICO: Río Grande, El Yunque, Mt. Britton, (N18.2957, W65.7906)	✓	✓	
<i>Popcornella furcata</i>	JXZ334	DOMINICAN REPUBLIC: La Vega, Reserva Científica Ébano Verde, (N19.04, W70.518)	KC615714	KC615944	KC615520
<i>Popcornella spiniformis</i>	JXZ339	DOMINICAN REPUBLIC: Barahona, Cachote (N18.098, W71.187)		KC615914	KC615489
<i>Popcornella yunque</i>	JXZ309	PUERTO RICO: Río Grande, El Yunque Nat. Forest, (N18.3174, W65.8314)		KC615937	KC615512
<i>Sidusa</i> [French guiana1]	JXZ128	FRENCH GUIANA: Commune Règina, les Nourages Field Station (N4.069, W52.669)	KC615770	KC616015	KC615593
<i>Sidusa</i> [French guiana2]	JXZ100	FRENCH GUIANA: Commune Règina, les Nourages Field Station, (N4.069, W52.669)	KC615679	KC615871	KC615444
<i>Truncattus</i> [Cuba1]	CU3492A	CUBA: Granma, Bartolomé Maso, National Park Pico Turquino (N 20.0526, W76.502)	✓		
<i>Truncattus</i> [Cuba2]	CU787947 CU03405A	CUBA: Granma, Bartolomé Maso, National Park Pico Turquino (N20.0526, W76.5029)	✓	✓	✓

Table 1. Cont.

Species	Voucher	Locality	CO1	16S-ND1	28S
<i>Truncattus</i> [Cuba3]	CU787949 CU00083A CU03065A	CUBA: Granma, Bartolomé Maso, National Park Pico Turquino (N20.0526, W76.5029)	✓		
<i>Truncattus</i> [Cuba4]	CU00014A	CUBA: Granma, Bartolomé Maso, National Park Pico Turquino (N20.052, W76.502)	✓		
<i>Truncattus</i> [Dominican Republic1]	DR787029	DOMINICAN REPUBLIC: Valle nuevo, Villa Pajón, (N18.82208, W070.6838)	✓		
<i>Truncattus cachotensis</i>	JXZ338	DOMINICAN REPUBLIC: Barahona, Cachote, (N18.101, W71.194)	KC615701	KC615913	KC615488
<i>Truncattus dominicanus</i>	JXZ340	DOMINICAN REPUBLIC: La Vega, P.N.Armando Bermúdez,(N19.06, W70.86)	KC615703	KC615920	KC615495
<i>Truncattus dominicanus</i>	DR787325	DOMINICAN REPUBLIC: San Juan, Los tablones,(N19.0511, W70.888)	✓	✓	
<i>Truncattus flavus</i>	JXZ332	DOMINICAN REPUBLIC: La Vega, P.N.Armando Bermúdez, (N19.06, W70.86)	KC615707	KC615933	KC615508
Outgroups					
<i>Agobardus anormalis montanus</i>	JXZ357	DOMINICAN REPUBLIC: Pedernales, (N18.128, W71.558)	KC615636	KC615802	KC615376
<i>Agobardus bahoruco</i>	JXZ324	DOMINICAN REPUBLIC: Pedernales, (N18.128, W71.558)		KC615844	KC615417
<i>Agobardus cf. brevitarsus</i>	JXZ311	DOMINICAN REPUBLIC: Pedernales, (N18.128, W71.558)	KC615637	KC615803	KC615637
<i>Agobardus cordiformis</i>	JXZ358	DOMINICAN REPUBLIC: Pedernales, (N17.965, W71.635)	KC615634	KC615800	KC615374
<i>Agobardus gramineus</i>	JXZ314	DOMINICAN REPUBLIC: Pedernales, (N17.965, W71.635)	KC615635	KC615801	KC615375
<i>Agobardus oviedo</i>	JXZ312	DOMINICAN REPUBLIC: Pedernales, (N17.802, W71.349)	KC615638	KC615804	KC615378
<i>Bythocrotus cf. crypticus</i>	JXZ323	DOMINICAN REPUBLIC: El Seibo, Pedro Sanchez, (N18.86, W69.11)	KC615661	KC615839	KC615412
<i>Bythocrotus crypticus</i>	JXZ322	DOMINICAN REPUBLIC: Barahona, (N18.424, W71.112)	KC615660	KC615838	KC615411

Table 1. Cont.

Species	Voucher	Locality	CO1	16S-ND1	28S
<i>Cobanus cambridgei</i>	JXZ122	COSTA RICA: Prov. San José, (N9.65, W83.97)		KC615872	KC615445
<i>Cobanus extensus</i>	JXZ122	ECUADOR: Pichincha, near El Cisne, (N0.1493, W79.0317)		KC615872	KC615445
<i>Cobanus mandibularis</i>	JXZ245	PANAMA: Panamá: Gamboa, Pipeline Road, (N9.15840, W79.74252)		KC615876	KC615449
<i>Cobanus unicolor</i>	JXZ244	PANAMA: Chiriqui: Fortuna, Quebrada Samudio, (N8.73464, W82.24839)		KC615878	KC615451
<i>Compsodecta festiva</i>	JAM4122A	JAMAICA: Portland, Millbank, (N18.013, W76.379)	✓		
<i>Compsodecta haytiensis</i>	JXZ325	DOMINICAN REPUBLIC: Barahona, Highway 44 south of Barahona (N18.138, W71.070)	KC615671	KC615859	KC615432
<i>Compsodecta peckhami</i>	JXZ327	DOMINICAN REPUBLIC: Pedernales, Rio Mulito (N18.155, W71.758)		KC615884	KC615457
<i>Corticattus guajataca</i>	JXZ305	PUERTO RICO: Isabela: Bosque de Guajataca (N18.421, W66.966)	KC615715	KC615945	KC615521
<i>Corticattus latus</i>	JXZ337	DOMINICAN REPUBLIC: Pedernales: Laguna de Oviedo (N17.802, W71.349)	KC615698	KC615908	KC615483
<i>Mexigonus arizonensis</i>	JXZ163	USA: Arizona: Yavapai Co., Iron Springs (N34.58476, W112.57071)	KC615747	KC615988	KC615564
<i>Mexigonus cf. minuta</i>	d117	ECUADOR: Pichincha: Quito	KC615748	KC615989	KC615565
<i>Mexigonus morosus</i>	JXZ362	USA: California: San Mateo Co., (N37.434, W122.311)		KC615990	KC615566
<i>Pensacola signata</i>	JXZ371	GUATEMALA: Depto. Petén, Reserva Natural Ixpanpajul		KC616006	KC615584
<i>Popcornella furcata</i>	JXZ334	DOMINICAN REPUBLIC: La Vega, Reserva Científica Ébano Verde, (N19.04, W70.518)	KC615714	KC615944	KC615520
<i>Popcornella spiniformis</i>	JXZ339	DOMINICAN REPUBLIC: Barahona, Cachote (N18.098, W71.187)		KC615914	KC615489
<i>Popcornella yunque</i>	JXZ309	PUERTO RICO: Río Grande, El Yunque Nat. Forest, (N18.3174, W65.8314)		KC615937	KC615512

Table 1. Cont.

Species	Voucher	Locality	CO1	16S-ND1	28S
<i>Sidusa</i> [French guiana1]	JXZ128	FRENCH GUIANA: Commune Règina, les Nourages Field Station (N4.069, W52.669)	KC615770	KC616015	KC615593
<i>Sidusa</i> [French guiana2]	JXZ100	FRENCH GUIANA: Commune Règina, les Nourages Field Station, (N4.069, W52.669)	KC615679	KC615871	KC615444
<i>Ghelna canadensis</i>	d005	USA: North Carolina (N35.704, W82.373)	EF201651	JQ312080	KT462689

3. DNA Extraction, Amplification and Sequencing

DNA was isolated with a Qiagen DNeasy Tissue Kit (Qiagen, Valencia, CA, USA). We sequenced fragments of CO1, 16S-ND1, and 28S. We amplified CO1 using the LCO1490 (GGTCAACAAATCATAAAGATATTGG) [82] and C1-N-2776 (GGATAATCAGAATATCGTC-GAGG) [83] primers. The fragment of 16S-ND1 ribosomal RNA was amplified with the primers 16SA/12261 (CGCCTGTTTACCAAAAACAT) [82] and 16SB (CCGGTTTGAACCTCA-GATC) [83]. The 28S ribosomal RNA fragment was amplified with the 28SO (TCGGAAG-GAACCAGCTACTA) and 28SC (GAAACTGCTCAAAGGTAAACGG) primers. For CO1, 16S-ND1, and 28S, the polymerase chain reactions (PCR) were performed with an initial denaturation at 94 °C for 2 min, followed by 40 cycles of denaturation at 94 °C for 25 s, annealing at 50 °C (first round)/44.5 °C (second round) for 25 s and extension at 65 °C for 2 min (first round)/1 min (second round); with a final extension at 72 °C for 10 min. We sequenced amplified fragments in both directions using Sanger sequencing at GENEWIZ's New Jersey facility. The forward and reverse reads were interpreted with Phred and Phrap [84,85] via Chromaseq v. 1.31 [86] in Mesquite v. 3.6 [87] using default parameters.

3.1. Phylogenetic Inference

We aligned sequences in MAFFT [88] using L-INS-I with a parameter 1PAM/k = 200, and a Gap opening penalty of 1.53. Gaps were treated as missing characters. The data resulting from the alignments were manually reviewed in Mesquite 3.6 (Maddison and Maddison [87]) with reference to the translation of amino acids using the “Color Nucleotide by Amino Acid” option. The dataset was partitioned by gene (and in the case of CO1 by codon), and the appropriate substitution model for each partition was selected with jModeltest 2.1.10 [89] using the Akaike information criterion [90] to select among the 24 models that can be implemented in MrBayes (Supplementary Table S1).

Maximum likelihood analyses were conducted in IQ-TREE v.2.0 [91]. ModelFinder [92], as implemented in IQ-TREE v.2.0 [91], was used to select the optimal partition scheme and substitution models for the molecular characters (iqtree-s dataMatrix.nex—runs 1000-m TESTMERGEONLY-spp setsBlock.nex-pre iqtreeAnalysis-nt AUTO). Finally, we used the CIPRES online portal [93,94] to run a Bayesian analysis with MrBayes v. 3.2.6 [95,96]. We ran the Markov chain Monte Carlo (MCMC) with four chains for 25,000,000 generations, sampling every 1000 generations, with a sampling frequency of 100 and a burn-in of 25%. The results were examined in Tracer v.1.7 [97] to verify proper mixing of chains, that stationarity had been reached, and to determine adequate burn-in. All resulting trees were interpreted in FIGTREE v.1.4.2 and edited in Adobe Illustrator CS6.

3.2. Time Calibration and Divergence Estimation

For the divergence time estimation analysis, the monophyly of *darlingtoni* group was constrained based on the results of the Bayesian and ML analyses. Node ages were estimated using a Bayesian, multi-gene approach in BEAST 1.10.4 [98] using a two-tier

approach: (1) including outgroups, (2) excluding outgroups. Here, for the divergence estimation, we included as outgroups the South American representatives of *Pensacola-Mexigonus* clade (*Mexigonus* cf. *minuta*, *M. arizonensis*), and *Sidusa* clade and the Greater Antilles *Agobardus* clade (*Agobardus*, *Compsodecta* and *Bythocrotus*).

The dating analyses were run under a lognormal relaxed clock model [99] with a CO1 substitution rate parameter (ucl.d.mean) as a normal prior (mean = 0.0112 and s.d. = 0.001) [100] and an estimated substitution rate parameter for 28S and 16S-ND1. The lognormal relaxed clock model was selected between alternative clock models (non-clock, strict clock, relaxed clock) using a stepping-stone method [101] of Bayes Factors in MrBayes 3.2.7a [96,102]. The analysis ran for 20,000,000 generations with a birth-death process [103] under a GTR + G+I model, with default options for all other prior and operator settings. The birth-death model was used for the tree prior because it can simulate speciation and extinction rates over time; thus, at any point in time, every lineage can undergo speciation at rate λ or go extinct at rate μ [104].

We used a combination of calibrations with fossils and calibrations based on the results of Zhang and Maddison [68]. Our fossil calibration point is based on the Dominican amber genus *Pensacolatus* (type species *Pensacolatus coxalis* Wunderlich, 1988 [105]) (see Penney, [106]). Wunderlich [105] described *Pensacolatus* based on a Dominican amber fossil (20–15 Mya) and discusses similarity with the species described by Bryant [79] as *Pensacola* (Peckham and Peckham [107]). We confidently place *Pensacolatus coxalis* within the *Antillattus darlingtoni* group after thorough review of the original description of *P. coxalis* and comparison of morphological details with those compiled for taxa in this lineage in Zhang and Maddison [81]. Key characteristics in this assessment include one retromarginal tooth, post-epigastrium without a visible pre-spiracular bump, endite with an anterolateral cusp, palp with a proximal tegular lobe, and ventral tibial apophysis. Therefore, we use this fossil to calibrate the MRCA (Most Recent Common Ancestor) of the *darlingtoni* group (logNormal Prior [tmrca, mu = 0.01, sigma = 1.0, offset = 16]) (see [68,105]). Our second calibration is MRCA of *Antillattus* clade secondarily based on dating inferences within this lineage from Zhang [108] [tmrca, normalPrior mean = 27.24 stdev = 5.0]. The convergence of parameters was examined in Tracer 1.7 [97] to determine burn-in and to check for stationarity. The maximum clade credibility tree was produced in TreeAnnotator v1.10.4, with 25% burn-in.

4. Biogeographical Estimation

For ancestral range estimation of the *Antillattus* clade, we used the tree of the divergence dating analysis resulting from the first tier approach (analysis with outgroups). We coded the Caribbean islands in their past shape, considering their historical composition of multiple paleo-islands [32]. The distribution ranges were divided into the following areas: A—Puerto Rico, B—Hispaniola, C—Cuba, D—Jamaica, E—North America, F—South America (Figure 1). We carried out the ancestral range estimation in the R package BioGeoBEARS v. 1.1.1 [109,110] to test different time periods and infer which are more likely with base of the model's configuration. This package tests three models in a maximum likelihood framework with various parameters that can be altered to test specific scenarios: a DEC model [110,111], a DIVALIKE model (likelihood version of the DIVA model [111,112]) and a BAYAREALIKE model (likelihood version of the BayArea model [113]). Moreover, each model is available in its original version and with an additional parameter +j (i.e., peripatric speciation) representing jump dispersal, or a founder event, which is speciation following long-distance dispersal [111].

To estimate the ancestral range distribution for *Antillattus* clade and outgroups, we conducted time-stratified analyses testing (1) non-GAARlandia (overwater dispersal), and (2) GAARlandia as the *Antillattus* clade ancestor colonization route using a set of 36 models that varied in the parameters [e—the rate of range contraction, d—the base rate of range expansion, and j—the weight of founder-event speciation at cladogenesis] and in the configuration of dispersal multiplier matrices used [109]. To estimate the ancestral

range distribution among *Antillattus* clade without outgroups, we conducted time-stratified analyses testing (1) overwater dispersal, and (2) land connections prior to the opening of the Mona Passage and the Windward Passage using a set of 72 models that varied in the parameters and in the configuration of dispersal multiplier matrices used [109]. In both approaches, we tested three dispersal probability hypotheses: (a) the dispersal probability decreases with distance, (b) dispersal probability is independent of distance, and (c) the probability of overwater dispersal is essentially zero (Table 2) (see Crews and Esposito [52]). Dispersal probabilities were set as follows: they were set to 0.8 when two areas were adjacent, to 0.5 when two areas were weakly separated by a geographical barrier, to 0.2 when two areas were separated by water over a distance less than 200 km, to 0.05 for connection by island chain (e.g., Lesser Antilles) or intermediate island (e.g., Hispaniola between Cuba and Puerto Rico), to 0.001 for long-distance dispersal (areas separated by more than 200 km from sea), and to 0.0000001 when dispersal was not possible by the lack area availability (we followed the BioGeoBEARS manual in setting extremely low rather than zero probabilities). Time periods were defined as follows to reflect the paleogeography of the area in each period [5,17,24]: (1) 23–15 Mya: Windward Passage, (2) 30–23 Mya: Mona Passage, (6) 32–35: GAARlandia hypothesis [32,33].

Table 2. Biogeographic specific scenarios analyzed in BioGeoBEARS for (a) *Antillattus* clade and outgroups and (b) *Antillattus* clade without outgroups. Each dispersal or vicariance scenario was tested using the six models available in BioGeoBEARS (DEC, DEC+J, DIVALIKE, DIVALIKE+J, BAYAREALIKE, BAYAREALIKE+J). Abbreviations: MO, Mona passage; WI, Windward passage.

(1) Non-GAARlandia/(2) GAARlandia			
	A: Dispersal probability decreases as distance increases	B: Distance does not affect dispersal probability	C: Probability of overwater dispersal is very low
(A) GA1	A1a/A2a	A1b/A2b	A1c/A2c
(1) Non-land connections/(2) Land connections			
	A: Dispersal probability decreases as distance increases	B: Distance does not affect dispersal probability	C: Probability of overwater dispersal is very low
(A) MO	A1a/A2a	A1b/A2b	A1c/A2c
(B) MO+WI	B1a/B2a	B1b/B2b	B1c/B2c

The +j parameter represents an approximation to model dispersal-dominated systems [109,114]; however, the validity of comparing models with and without +j parameter is controversial [115,116]. To conservatively address these issues [108,114–116], we use the best-fitting basic model and the best fitting model with +j parameter to discuss the ancestral range estimation, to estimate the number of lineages through time by area, and the number and type of biogeographical events [extinction, speciation (sympatric–subset speciation, within–area speciation, founder–event speciation), vicariance and dispersal events (anagenetic dispersal, range–expansion dispersal)]. Both the basic model with +j parameter were compared using likelihood values and the Akaike information criterion corrected for small sample sizes (AICc) [117]. Finally, to estimate the number of lineages through time, and the number and type of biogeographical events, we used the best model resulted in the analysis of *Antillattus* clade without outgroups. We ran biogeographical stochastic mapping (BSM) using the maximum clade credibility (MCC) tree [118,119]. Event frequencies were estimated by taking the mean and standard deviation of event counts from 100 BSMs.

5. Results

Phylogeny and Divergence Time

The combined molecular dataset consisted of 3071 sites (27,369 internal gaps), the best BI tree has a harmonic-means = -24208.96 , and the best ML tree has an $\ln L = -24,214.758$ (Figure 4). The *Antillattus* clade is supported as monophyletic (ML, bootstrap = 100%). The phylogeny suggests that the *Antillattus* clade is sister to other Caribbean (e.g., *Agobardus* clade) (ML, bootstrap = 88%) and continental clades (e.g., *Mexigonus-Pensacola* clade). The relationships among the three genera in the *Antillattus* clade are not well resolved. The genus *Petemathis* is resolved as sister to *Truncattus* + *Antillattus* with low support (bootstrap = 73%, pp = 0). A second analysis without outgroups (Figure 4, $\ln L = -13,533.817$, Harmonic-means = $-13,597.32$) support *Petemathis* as sister to *Truncattus* + *Antillattus* (ML, bootstrap = 100%, BI, pp = 1.0), while *Truncattus* is poorly resolved as sister to *Antillattus* (ML, bootstrap = 0%, BI, pp = 0.68). In both analyses, the genus *Antillattus* is monophyletic, however, the relationships within the genus are not well resolved. The representatives of the genus *Antillattus* were divided into three groups of species that we refer to as the *darlingtoni*, *keyserlingi*, and *gracilis* groups, with *gracilis* sister to the other two. The phylogeny recovered the genus *Petemathis*, the *darlingtoni* group, and the *keyserlingi* group as single-island endemic lineages. The *gracilis* group and *Truncattus* are found both on Hispaniola and Cuba.

In both BEAST analyses (including outgroups and excluding outgroups), the posterior probability values from our BEAST analyses are higher than those in the MrBayes analysis (Figures 4 and S1). For example, the genus *Truncattus* is recovered as sister group of the genus *Antillattus* with better support values (pp = 0.91). The chronogram of the *Antillattus* clade based on the birth–death process derived chronogram with a relaxed clock model (Figure 5), indicates that the MRCA of the *Antillattus* clade diverged during the Oligocene (c. 25 ± 3 Mya), and most of the subsequent divergences happened in the Miocene to present (c. present–21 Mya). The lineage leading to *Petemathis* diverged during the late Oligocene (c. 25 ± 3 Mya). The divergence of the lineages leading to *Truncattus*, and the genus *Antillattus* were dated to the early Miocene (c. 21 ± 3 Mya and c. 19 ± 2 Mya respectively). Finally, the lineages leading to the *gracilis*, *keyserlingi*, and *darlingtoni* groups were dated to the early Miocene (c. 19 ± 2 Mya and c. 17 ± 2 Mya, respectively).

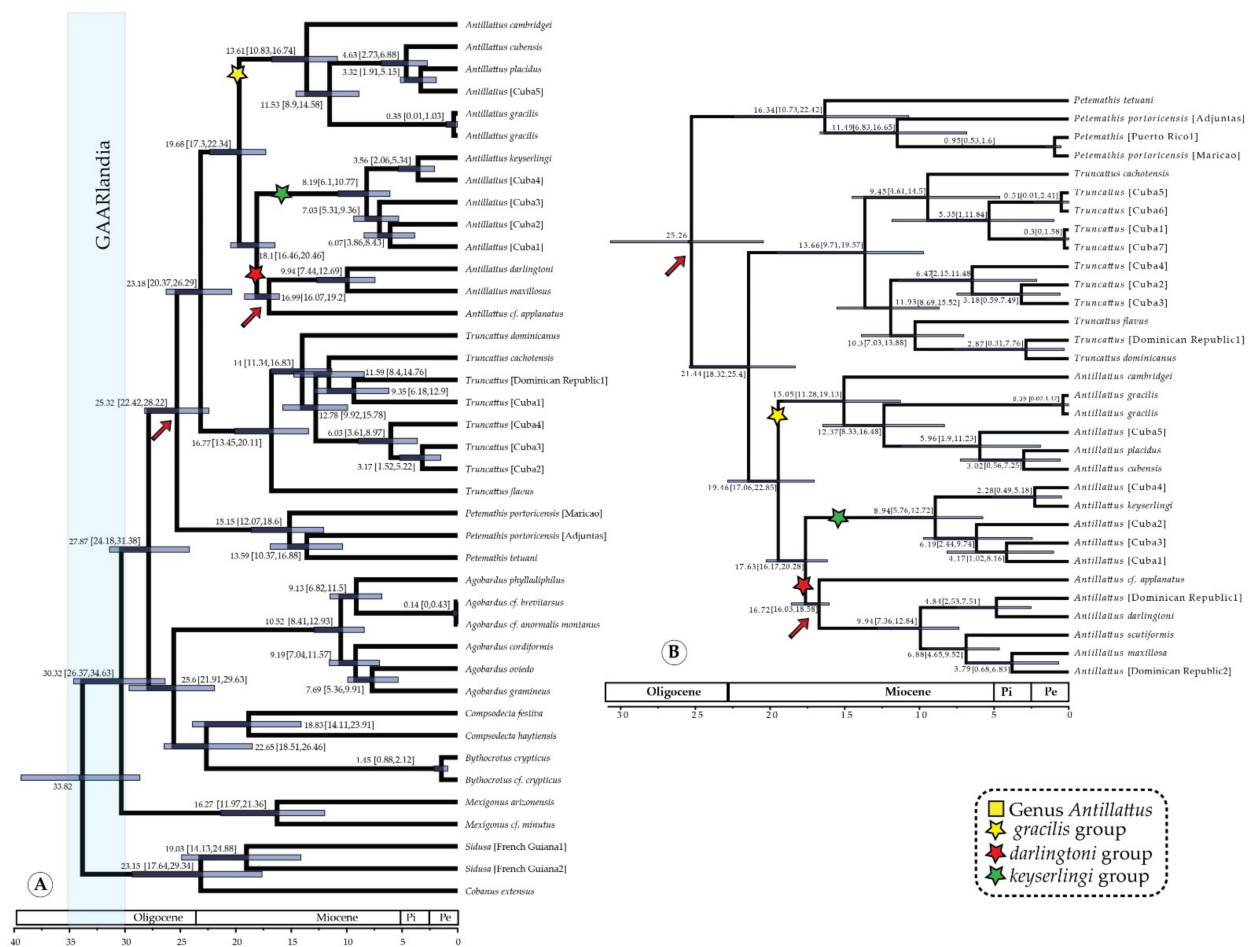


Figure 5. Beast divergence time estimations of all genes (CO1, 16S-ND1, 28S) using a Bayesian relaxed molecular clock (A) with outgroups and (B) without outgroups. The scale is in millions of years. Bars show 95% HPD [highest posterior density]. Stars indicate species groups within the genus *Antillattus* (blue star *gracilis* group, red star *darlingtoni* group, and green star *keyserlingi* group). Arrows indicate calibrated nodes.

6. Model Selection and Ancestral Range Estimation

The A2a DEC+J model (log likelihood: LnL = -33.87; parameter estimates: d = 0; e = 0; j = 0.22) and the A2a DEC model (log likelihood: LnL = -43.84; parameter estimates: d = 0.022; e = 0; j = 0) (Table 3, Supplementary Data S3) are consistent with the GAARlandia, and dispersal probability decreasing with distance. Both the basic and +j models resolve the most probable ancestral area for the extant species of the *Antillattus* clade is Northern South America and Hispaniola. The estimation of ancestral ranges among *Antillattus* clade, show that the favored model was the B2a DIVALIKE +j model (log likelihood: LnL = -17.6; parameter estimates: d = 0; e = 0; j = 0.29), while the best model within the basic models was the B2a DIVALIKE model (log likelihood: LnL = -25.01; parameter estimates: d = 0.048; e = 0; j = 0) (Table 3, Supplementary Data S3). Both models are consistent with the land connections prior to the Mona Passage and the Windward Passage hypothesis, and dispersal probability decreasing with the distance. Both the basic and +j models show again Hispaniola as a probable ancestral area (Figure 6).

Table 3. BioGeoBEARS' relative model probabilities for non-time-stratified analyses and time-stratified analyses corresponding to the most likelihood specific scenario A2a of the 12 specific scenarios tested for the non-GAARlandia and GAARInadia hypotheses, and B2a of the 12 specific scenarios tested for the overwater dispersal and land connections prior to the Mona Passage and the Windward Passage hypotheses. The best performing model is marked with an asterisk for groups of analyses. LnL = log likelihood; n par = number of parameters in the analysis; d, e, j = parameters of the model (d = dispersal, e = extinction, j = founder event); AIC = Aikake information criterion; AICc = size-corrected AIC. * = Best-performing model for each groups of analyses.

Time-Constrained/GAARlandia (A2a)							
	LnL	n par	d	e	j	AIC	AICc
DEC	−43.84 *	2	0.021	<0.0001	0	91.69	92.01
DEC +J	−33.87 *	3	<0.0001	<0.0001	0.22	73.73	74.4
DIVALIKE	−47.05	2	0.035	<0.0001	0	98.1	98.43
DIVALIKE +J	−36	3	0.005	<0.0001	0.22	77.99	78.66
BAYAREALIKE	−60.83	2	0.021	0.031	0	125.7	126
BAYAREALIKE +J	−36.73	3	0.0038	<0.0001	0.21	79.45	80.12
Time-constrained/land connections prior to the Mona Passage and the Windward Passage (B2a)							
DEC	−25.1	2	0.033	<0.0001	0	54.19	54.61
DEC +J	−18.09	3	<0.0001	<0.0001	0.31	42.18	43.04
DIVALIKE	−25.01 *	2	0.048	<0.0001	0	54.01	54.43
DIVALIKE +J	−17.62 *	3	<0.0001	<0.0001	0.29	41.25	42.1
BAYAREALIKE	−34.22	2	<0.0001	0.041	0	72.44	72.86
BAYAREALIKE +J	−18.8	3	<0.0001	<0.0001	0.27	43.61	44.46

Estimation of Biogeographical Events

The DIVALIKE and DIVALIKE +j BioGeoBEARS stochastic map (BSM) based on 100 stochastic historical maps revealed that most probabilistic biogeographical events comprise within-area speciation (between 65 and 76% of probabilistic events in stochastic runs), founder-event (21%), range-expansion dispersal (15%), and vicariance (between 18 and 3%) (Table 4, Figure 6). The high number of within-area speciation probabilistic events in Hispaniola (between 43 and 48% of the total of the DIVALIKE and DIVALIKE +j within-area speciation probabilistic events), Cuba (between 40 and 44%), and Puerto Rico (between 12 and 13%) could be closely related to species richness. Most of the probabilistic estimated vicariance events among Cuba, Puerto Rico, and Hispaniola involved Hispaniola–Cuba (between 84 and 27% of the DIVALIKE and DIVALIKE +j vicariance probabilistic events), Hispaniola–Cuba–Puerto Rico (between 2 and 16%), Cuba–Puerto Rico (between 2 and 32%), and Hispaniola–Puerto Rico (between 1 and 26%).

Dispersal events are represented by range-expansions and founder-events (Table 4). Focusing on the range-expansion between Puerto Rico, Cuba, and Hispaniola, we found that the movement patterns varied enormously between areas and were highest among groups that have their ancestral range in Hispaniola (73% of the range-expansion probabilistic events and 45% of the founder-events probabilistic events). Range-expansion events only involved movements from Hispaniola–Cuba (73% of the range-expansion probabilistic events), and from Hispaniola–Puerto Rico (27%), while the range-expansion from Puerto Rico to Cuba and Hispaniola, and Cuba and Hispaniola to Puerto Rico were improbable (0% of simulations) (Supplementary Data S4). In contrast to the range-expansion events, founder-event speciation occurred in lineages that have their ancestral range in Cuba (51%), and the highest number of founder-event speciation involved movements from Cuba to Hispaniola (49% of the founder-event probabilistic events) and Hispaniola to

Cuba (45%), with other events playing little or no role (less 2%). Finally, the number of lineages estimated through time by zone showed the occurrence of a greater number of events [within-area speciation, dispersions, and vicariances] representing movement from Hispaniola (Figure 7).

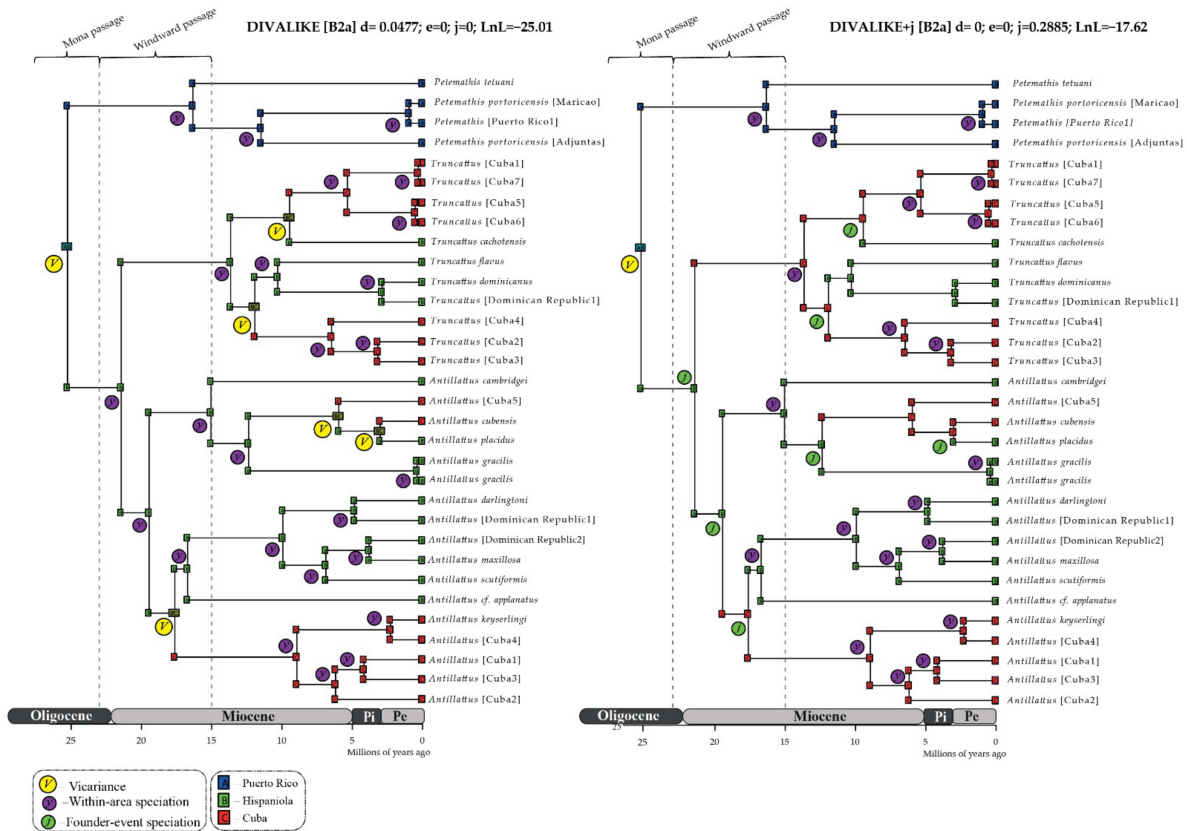


Figure 6. BioGeoBEARS phylograms corresponding to the time-stratified DIVALIKE and DIVALIKE+J B2a model (Table 1). The trees show the most probable geographic range pre- and post-split. The scale is in millions of years.

Table 4. Summary count of time-constrained Biogeographic Stochastic Mappings. DIVALIKE and DIVALIKE +j. Abbreviations: j, jump dispersal or founder-event speciation; a, range-switching dispersal; d, range-expansion dispersal; e, extinction; s, sympatric-subset speciation; v, vicariance; y, within-area speciation; $\check{Y}d$, allopatric dispersal; Ad, anagenetic dispersal; $\check{Y}a$: allopatric anagenetic; $\check{Y}c$: allopatric cladogenetic; sums, adds up all of the events across the stochastic maps.

DIVALIKE												
	j	a	d	e	s	v	y	$\check{Y}d$	Ad	$\check{Y}a$	$\check{Y}c$	Total events
means	0	0	5.5	0	0	6.61	24.39	5.5	5.5	5.5	31	36.5
stdevs	0	0	0.64	0	0	0.67	0.67	0.64	0.64	0.64	0	0.64
sums	0	0	550	0	0	661	2439	550	550	550	3100	3650
DIVALIKE+j												
	j	a	d	e	s	v	y	$\check{Y}d$	Ad	$\check{Y}a$	$\check{Y}c$	Total events
means	6.63	0	0	0	0	0.82	23.55	6.63	0	0	31	31
stdevs	1.04	0	0	0	0	0.64	0.94	1.04	0	0	0	0
sums	663	0	0	0	0	82	2355	663	0	0	3100	3100

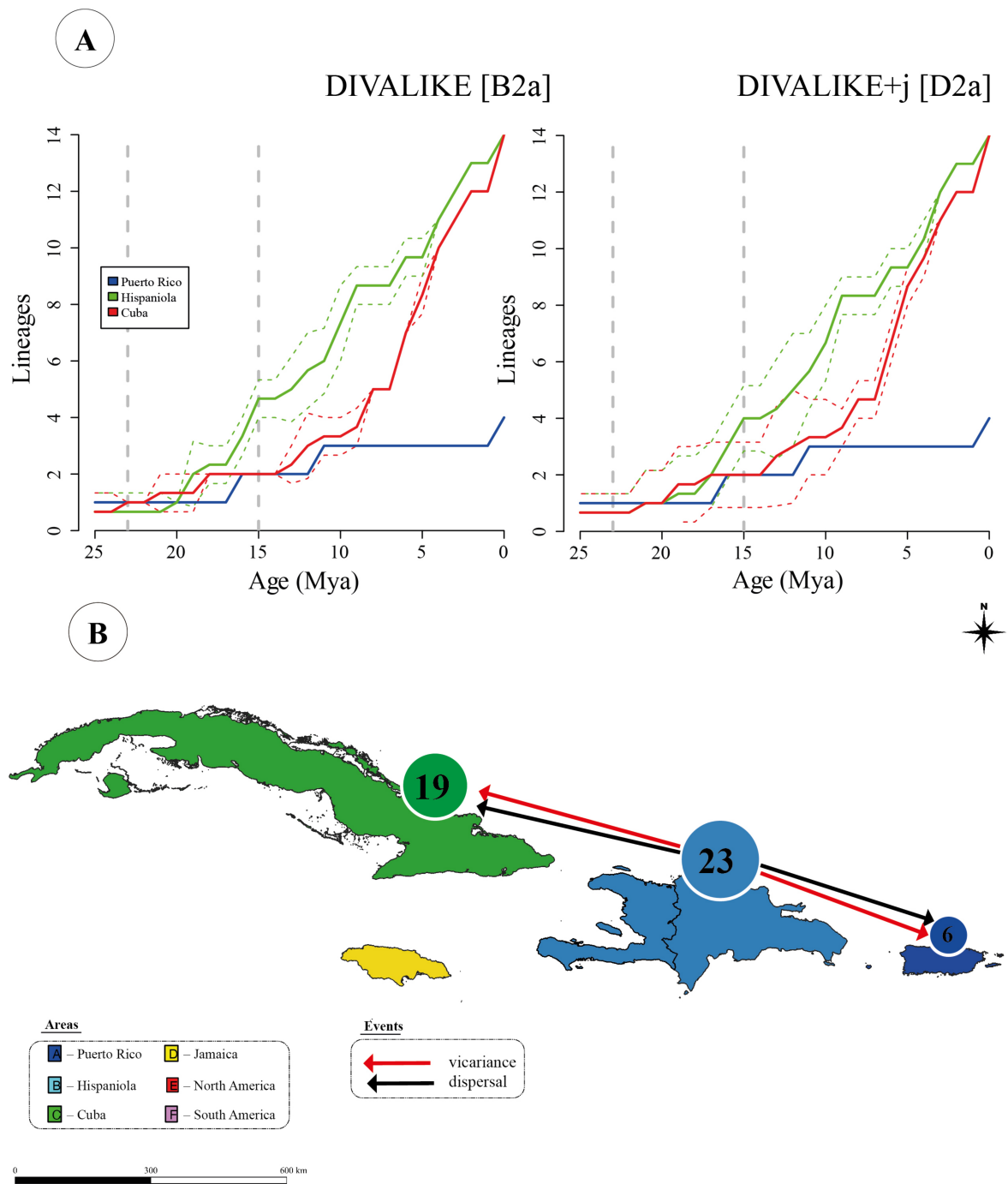


Figure 7. (A) Number of lineages occupying each area through time estimates under DIIVALIKE and DIIVALIKE +j and (B) the ancestral range. (A) Colored solid lines are the average of 100 biogeographic stochastic maps. Colored dashed lines are the 95% confidence interval. Gray dashed vertical line indicates the boundary between time slices in the time-stratified analysis. (B) Black arrows represent all dispersal events between areas. Red arrows represent a vicariance event between areas. Numbered circles indicate the inferred number of within-area speciation in each of the areas.

7. Discussion

7.1. Ancestral Range of the *Antillattus* Clade and GAARlandia

Our expanded Caribbean sampling within the *Antillattus* clade provides a more thorough analysis of diversification within the Caribbean and an opportunity to reassess its biogeographic origins. Our data suggest that the ancestor of the *Antillattus* clade

colonized the Greater Antilles once from South America within a time frame consistent with GAARlandia; however, our continental outgroup taxon sampling limits confidence in inference of the source [32,33] (Figure 4). The estimated time of divergence of the *Antillattus* clade (25 ± 3 Mya) is consistent with dates inferred by Zhang and Maddison [68]. Neither the colonization of the Caribbean by *Antillattus* clade ancestors, nor the diversification of the group can in any way be linked to the colonization of the proto-Antillean volcanic arc in the Late Cretaceous (c. 65.5 Mya) [39,40].

7.2. Inter-Island Biogeographical History

The phylogenetic structure within the Greater Antilles reflects patterns consistent with historical island connectivity and breakup. Our estimation of the biogeographic history identified speciation within the Caribbean as the driving force of diversification (Table 4), consistent with the high levels of endemism in these spiders. For example, the species of the *darlingtoni* group are restricted to Hispaniola suggesting diversification exclusively within the island, while members of the genus *Truncattus* and the *gracilis* group are present in Cuba and Hispaniola, suggesting diversification both within and between these islands (Supplemental Data S4 and S5). The estimated divergence between Hispaniolan and Puerto Rican clades is c. 25.16 Mya consistent with the approximate timing of separation of these islands (c. 23–30 Mya). Similarly, Hispaniolan and Cuban clades split around 17–22 Mya coinciding with the geological separation of these islands. Hence, vicariance hypotheses can readily explain the distribution of major clades among islands. Similarly, the Puerto Rican genus *Petemathis* branched off from a Hispaniola lineage at c. 25 ± 3 Mya prior to the estimated timeframe of the Hispaniola and Puerto Rico split (20–30 Mya). While *Petemathis* only began to diversify later to around c. 16.34 ± 6 Mya the split between Hispaniola and Puerto Rican lineages is easily explained by paleogeographical models and no long-distance dispersal is implied. Similarly, the *keyserlingi* and *darlingtoni* groups branched off from a Hispaniola lineage at c. 17.63 ± 2 Mya. The *keyserlingi* group only begins diversifying much later (c. 8.94 ± 3 Mya) and is restricted to Cuba. Of course, we cannot rule out earlier diversification of the group followed by extinction of early branches without much more detailed fossil record than is currently available. The *darlingtoni* group quickly diversified (c. 16.7 ± 1 Mya), presumably facilitating their colonization of Cuba before Hispaniola and Cuba split (c. 14–17 Mya).

On the other hand, the BSM analyses imply that dispersal between Hispaniola and Cuba continued happening after the geological separation of these islands suggesting that overwater dispersal also played an important role in shaping the current distribution and diversity of the lineage (Figure 6, Supplementary Data S4). As in other groups of spiders, overwater dispersal is common in at least some lineages (e.g., Čandek et al. [50]; Crews and Esposito [52], Agnarsson et al. [46], Shapiro et al. [120], and can explain non-vicariant movement among Caribbean islands. Long-distance dispersal followed by range-expansion seems important in *Truncattus* (c. 13.66 ± 5 Mya) and the *gracilis* group (c. 15.5 ± 4 Mya). Similar studies show the occurrence of overwater dispersal/colonization events (e.g., founder-events and range-expansions) as the best explanation of among island movement after Hispaniola–Cuba split (butterflies *Calisto*: Matos–Maraví et al. [5]; aquatic beetles *Phaenonotum*: Deler–Hernández et al. [24]; weevils *Exophthalmus*: Zhang et al. [67]; mastiff bats *Molossus*: Loureiro et al. [121]).

7.3. From Hispaniola to Cuba and Puerto Rico

Our study indicates Hispaniola as a potential source for subsequent radiations throughout the Greater Antilles, with multiple exchanges between Hispaniola and Cuba (Figures 6 and 7, Supplementary Data S4 and S5). Other studies also support Hispaniola as a point of dispersal to other Antillean islands [122,123]. Fabre et al. [124] found evidence in Caribbean Capromyidae (hutias) supporting Hispaniola as a potential source of colonization to other Greater Antilles islands and the Bahamas. In their study, they suggest either (i) a vicariant event between eastern (Hispaniola) and western (Bahamas, Cuba, Jamaica) hutias or (ii)

stepping-stone colonization from east to west. Čandek et al., [50] found that in *Cyrtognata* spiders dispersal from Hispaniola explains their colonization of the rest of the Caribbean Archipelago. The BioGeoBEARS ancestral range estimation of the GAARlandia DEC+j model for *Deinopis* (see, Chamberland et al., [4]) also supports the hypothesis that Hispaniola plays a pivotal role in Caribbean dispersal. McHugh et al. [48] and Shapiro et al. [120] provide evidence that Caribbean *Micrathena* are not monophyletic and likely colonized the region multiple times, with evidence of interchanges between Cuba, Hispaniola and Puerto Rico. In the case of the origin of the *Antillattus* clade, the exact role of Hispaniola is less clear; however, the available evidence indicates that it may be the area of the Caribbean first colonized by the ancestor of the clade. Further studies of Caribbean biota will further clarify the role of Hispaniola in the overall biogeographical complexity of the Greater Antilles.

8. Conclusions

Our study sheds new light on the biogeography of the *Antillattus* clade and their Caribbean radiation. The phylogenetic and biogeographical evidence presented in this study fits the Caribbean palaeogeographical model of colonization and suggests a complex interplay of vicariance and overwater dispersal driven diversification in shaping the biota of this biodiversity hotspot. The ancestor of the *Antillattus* clade appears to have colonized the Greater Antilles (Puerto Rico, Hispaniola, and Cuba) during the timespan of GAARlandia and land connections prior to the Mona Passage and the Windward Passage. Our results suggest that the evolution of the *Antillattus* clade included both vicariant processes and long-distance dispersal with the majority of diversification attributed to within island speciation. Finally, among other insights, we have uncovered the importance of Hispaniola in the *Antillattus* clade colonization of the Caribbean, thereby providing further evidence that islands can function as key diversification hubs for archipelagos.

Supplementary Materials: The following are available online at <https://www.mdpi.com/article/10.3390/d14030224/s1>, <https://drive.google.com/drive/folders/1HotuTFZ1UVIsRbIDCfOK5Xk4GmNr-jqg?usp=sharing> (Accessed on 10 November 2021). Table S1: Substitution models selected by jModelTest and ModelFinder for each individual gene region and partition. Dataset including outgroups and excluding outgroups. Data S1: DNA analysis for dataset including outgroups and excluding outgroups. Data S2: Beast divergence time estimations (including outgroups and excluding outgroups) of all genes (CO1, 16S-ND1, 28S) using a Bayesian relaxed molecular clock. Data S3: BioGeoBEARS *Antillattus* clade (including outgroups and excluding outgroups). Data S4: B2a model (stochastic mapping (BSM)). Data S5: B2a model (number of lineages through time).

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