PNAS RESEARCH ARTICLE | EVOLUTION

Iguanas rafted more than 8,000 km from North America to Fiji

Simon G. Scarpetta[a,b,1], Robert N. Fisher[c], Benjamin R. Karin[b,d], Jone B. Niukula[e], Ammon Corl[b], Todd R. Jackman[f], and Jimmy A. McGuire[b]

Affiliations are included on p. 8.

Edited by Christopher Raxworthy, American Museum of Natural History, New York, NY; received November 7, 2023; accepted January 27, 2025 by Editorial Board Member David Jablonski

Founder-event speciation can occur when one or more organisms colonize a distant, unoccupied area via long-distance dispersal, leading to the evolution of a new species lineage. Species radiations established by long-distance, and especially transoceanic, dispersal can cause substantial shifts in regional biodiversity. Here, we investigate the occurrence and timing of the greatest known long-distance oceanic dispersal event in the history of terrestrial vertebrates—the rafting of iguanas from North America to Fiji. Iguanas are large-bodied herbivores that are well-known overwater dispersers, including species that colonized the Caribbean and the Galápagos islands. However, the origin of Fijian iguanas had not been comprehensively tested. We estimated the phylogenetic relationships and evolutionary timescale of the iguanid lizard radiation using genome-wide exons and ultraconserved elements (UCEs). Those data indicate that the closest living relative of extant Fijian iguanas is the North American desert iguana and that the two taxa likely diverged during the late Paleogene near or after the onset of volcanism that produced the Fijian archipelago. Biogeographic models estimate North America as the most probable ancestral range of Fijian iguanas. Our analyses support the hypothesis that iguanas reached Fiji via an extraordinary oceanic dispersal event from western North America, and which spanned a fifth of the earth's circumference (>8,000 km). Overwater rafting of iguanas from North America to Fiji strengthens the importance of founder-event speciation in the diversification of iguanids and elucidates the scope of long-distance dispersal across terrestrial vertebrates.

Fiji | dispersal | island biogeography | phylogenomics | lizards

Significance

Transoceanic dispersal to far-away islands is an important mechanism for the generation of new species lineages and biotas and has captivated scientists since at least the time of Darwin. Determining whether and how such events occur is challenging, particularly for hypothesized dispersals spanning thousands of kilometers. We addressed the enigmatic occurrence of Fijian iguanas via phylogenomic and biogeographic analyses, providing strong evidence that iguanas rafted >8,000 km from North America as early as the Paleogene. This represents the longest documented transoceanic dispersal in terrestrial vertebrates. Our findings elaborate on the importance of long-distance dispersal in the diversification of iguanids. Iguanid lizards display a propensity for overwater dispersal, which could stimulate further research into the predictability of these incredible biogeographic events.

Long-distance dispersal across oceanic barriers has long fascinated biologists because of the difficulty and apparent infrequency of such events and the potential of transoceanic dispersals to generate species and establish radiations of new floras and faunas (1–5). For many organisms, such as plants, insects, birds, and bats, aerial, or vector transport facilitates long-distance dispersal, potentially leading to founder-event speciation (1, 6). For larger terrestrial species, rafting on floating debris is the most viable transoceanic dispersal mechanism (1). Unsurprisingly, the occurrence and plausibility of oceanic rafting as a generator of species diversity have been vigorously debated, and extensive land-bridges, ancient vicariance, or past lineage extirpation are frequently posited as alternative hypotheses (7, 8). In some cases, biogeographic modeling of extant taxa and/or the fossil record has convincingly demonstrated vicariance or the occurrence of ghost lineages (9, 10). However, in other systems, especially those involving the colonization of oceanic islands, founder-event speciation via long-distance dispersal is often the favored hypothesis (2, 11). Oceanic islands have played a pivotal role in the development of biogeographic and evolutionary theory, harbor a high number of endemic species, and can have particularly diverse biotas of some taxa (12–15). Thus, it is important to better understand the processes that give rise to the unique biotas of oceanic islands.

The occurrence of extant (*Brachylophus*) and extinct (*Lapitiguana*) iguanas [Squamata, Iguanidae = Iguaninae *sensu* (16)] on the South Pacific islands of Fiji and Tonga is one of the most famous and remarkable potential cases of founder-event speciation via long-distance dispersal (8). Iguanas and chuckwallas compose 9 genera of large and generally herbivorous lizards that otherwise occur in North, Central, and South America, many Caribbean islands, and the Galápagos Islands (17, 18). *Brachylophus*, which contains 4 extant and 1 extinct species, is morphologically divergent from other iguanas and occurs extremely far from all of its extant relatives—the western coast of continental North America is >8,000 km away from Fiji, and there have been very few landmasses between the Americas and Fiji throughout the Cenozoic (19–22). Other extant members of the more inclusive lizard clade to which iguanas belong, Pleurodonta = Iguanidae *sensu* (16) (e.g., anoles, horned lizards, and relatives), are also largely restricted to the

Author contributions: S.G.S., R.N.F., B.R.K., J.B.N., A.C., and J.A.M. designed research; S.G.S., B.R.K., and A.C. performed research; S.G.S., B.R.K., A.C., and T.R.J. contributed new reagents/analytic tools; S.G.S., B.R.K., and A.C. analyzed data; and S.G.S., R.N.F., B.R.K., A.C., T.R.J., and J.A.M. wrote the paper.

The authors declare no competing interest.

This article is a PNAS Direct Submission. C.J.R. is a guest editor invited by the Editorial Board.

[1]To whom correspondence may be addressed. Email: sscarpetta@usfca.edu.

This article contains supporting information online at https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2318622122/-/DCSupplemental.

Published March 17, 2025.

western hemisphere (23). The anomalous occurrence of iguanas on Fiji and how they colonized this remote archipelago remains unresolved.

How could iguanas have reached the Fijian archipelago? One possibility is that they reached these islands in a single rafting event across the Pacific Ocean from the Americas (21, 24, 25). Alternatively, a hypothesized extinct lineage of iguanas may have arrived on the Fijian islands via steppingstone dispersal across Eurasia and/or the paleocontinent Gondwana and its constituent landmasses (8, 26, 27). While both models have been proposed, strong support for either hypothesis is lacking. In particular, the uncertain phylogenetic position and evolutionary timescale of *Brachylophus* with respect to other iguanids has prevented biogeographic hypothesis testing. Most analyses of multilocus Sanger-datasets or morphology placed *Brachylophus* as the sister lineage of all other iguanas except *Dipsosaurus*, the North American desert iguanas, and generally with low support (17, 21, 23, 28–31). Several other multilocus Sanger studies found a poorly supported sister taxon relationship between *Brachylophus* and *Dipsosaurus* (8, 32, 33). A recent phylogenomic analysis of hundreds of exons produced that sister–taxon relationship (34), but analyses of >1,000 ultraconserved elements (UCEs) placed *Brachylophus* as the earliest diverging iguanid genus (35, 36). Finally, timetrees disagree on whether the *Brachylophus* lineage first appeared during the Paleocene or early Eocene (~60 to 50 Ma) (8, 30), the middle Eocene ~43 Ma (37), or the latest Eocene to early Oligocene (~35 to 30 Ma) (28, 32).

A plausible theory for the origin of iguanas on Fiji must be compatible with the geologic history of the islands. Fiji arc magmatism initiated from subduction of the Pacific Plate under the Indo-Australian plate during the late Eocene c. 39 Ma (38, 39). Early subaerial (exposed to the air) volcanics on Fiji are evident from late Eocene and Oligocene exposures of the Yavuna and Wainimala groups on Viti Levu, and 34 Ma is the highest frequency zircon age of these early volcanics (38–42). Though the development of the volcanic arc is temporally well constrained to the end of the Paleogene, some studies had suggested that Cretaceous continental fragments compose the basement of the Fijian archipelago, similar to New Zealand and New Caledonia (38). Recent analysis of detrital zircons demonstrated a late Paleogene and solely intraoceanic arc setting, cementing the Cenozoic and oceanic origin of Fiji (38, 39).

Here, we investigate the phylogenetic relationships, divergence timing, and biogeography of iguanid lizards to determine the biogeographic origins of Fijian iguanas, using a sample of 14 extant species from eight of the nine recognized genera. We collected genome-wide sequence data from coding, noncoding, autosomal, and sex-linked loci [>4,000 loci, >2 million base pairs (bp)] with a sequence capture probe set that we developed for this study. We used species-tree and concatenated phylogenetic and divergence time analyses and statistical biogeography to evaluate the origins of Fijian iguanas. Our analyses strongly support the oceanic dispersal of *Brachylophus* from North America to Fiji, which is the greatest known oceanic dispersal event in the history of terrestrial vertebrates.

Results

Phylogenomics of Iguanids. We designed a sequence capture probe set to gather data from across the genome of lizards, with 1,628 autosomal loci and 2,813 exons from the X chromosome captured. The probe set contains both loci that we identified and loci used in other phylogenetic studies, including rapidly evolving long exon capture (RELEC) (43), anchored-hybrid enrichment (AHE) (44), UCEs (45), and Squamate Tree of Life (ToL) loci (46). RELEC markers are the centerpiece of our analyses because they are long exons with relatively fast evolutionary rates, which leads to more informative sites per locus and more accurate gene trees (43). RELEC markers are thus ideal for addressing difficult phylogenetic problems such as the position of *Brachylophus* and are better suited for multispecies coalescent (MSC) analyses in which gene tree accuracy is pivotal for topology estimation. Here, we present an expanded set of RELEC markers, adding 107 new loci to those from (43), for a total of 286 loci. In this study, the RELEC markers supported the same result as the other marker sets (see below) but provided the strongest bootstrap proportions (bs), posterior probabilities (pp), and gene concordance factors (gCF) across the iguanid tree and especially for the focal clade *Brachylophus–Dipsosaurus*. The RELEC loci also contain higher phylogenetic information content than the other marker sets (211 average informative sites per locus, <100 for other markers sets).

Brachylophus and *Dipsosaurus* were inferred as sister taxa with very strong support values of 100 bs or ≥0.99 local pp in all concatenated and summary MSC analyses of the entire autosomal dataset (*SI Appendix*, Fig. S6) and the RELEC-only dataset, including outgroup sensitivity analyses (*SI Appendix*, Figs. S8–S9, S13, and S14). *Brachylophus* and *Dipsosaurus* were also sister taxa in all filtered X chromosome analyses (75 bs, 0.87 to 0.93 pp) and in AHE-only MSC analyses (0.67 to 0.80 pp). In a few analyses, *Dipsosaurus* was sister to all other iguanids, but these analyses generally had low support: the UCE ASTRAL-III analysis (0.6 pp), the ToL ASTRAL-Hyb analysis (0.63 pp), and the concatenated analyses of AHE (54 bs) and all X chromosome exons (96 bs). However, *Brachylophus* and *Dipsosaurus* were sister taxa in the other UCE and ToL analyses. Gene concordance factors favor a sister taxon relationship between *Brachylophus* and *Dipsosaurus* over alternative topologies (e.g., 35.7, 42.3, 39.6 gCF in analyses with all autosomal loci, RELEC-only, and filtered X chromosome datasets, respectively) (*SI Appendix*, Figs. S6 and S8–S10). Site concordance factors were more equivocal (e.g., 35 sCF in RELEC-only analysis), though previous phylogenomic studies suggested that aggregate site metrics probably do not provide dependable support in isolation from other measures for genome-scale datasets (34).

Divergence Times. The evolutionary timescale of iguanids was estimated on four reduced phylogenomic datasets: 1) 100 RELEC loci (280,661 bp), 2) 150 loci including 50 each of UCEs, AHE, and RELEC (247,093 bp), 3) 165 X chromosome exons (136,157 bp), and 4) 100 RELEC loci and 50 UCEs (321,074 bp) including five additional outgroups. Concatenated and full Bayesian MSC divergence time analyses of each of the first three datasets were performed in BEAST v2.7 (47) and StarBeast3 (48), respectively, with a set of fossil calibrations utilized for this study (*Methods* and *SI Appendix*). For the fourth dataset, only BEAST2 was used. We also performed total-evidence divergence dating under the fossilized birth–death (FBD) process in BEAST2 using the 150 locus AHE-RELEC-UCE dataset and a recently revised morphological matrix for iguanian lizards (29, 49, 50). StarBeast3 analyses with the RELEC and X chromosome exons found a *Brachylophus-Dipsosaurus* sister taxon relationship with pp > 0.95, as did those with the AHE-RELEC-UCE dataset though with lower support (pp = 0.73). All BEAST2 analyses found that sister taxon relationship with pp = 1 or 0.99. FBD analyses inferred the same relationships among extant species and placed the extinct iguanids *Armandisaurus* on the stem of *Dipsosaurus*, *Pumilia* on the stem of *Iguana*, and *Queironius* on the stem of the *Brachylophus–Dipsosaurus* clade (*SI Appendix*, Figs. S23 and S24).

Median divergence time estimates between *Brachylophus* and *Dipsosaurus* were near or under 34 Ma (Fig. 1). The 95% HPD

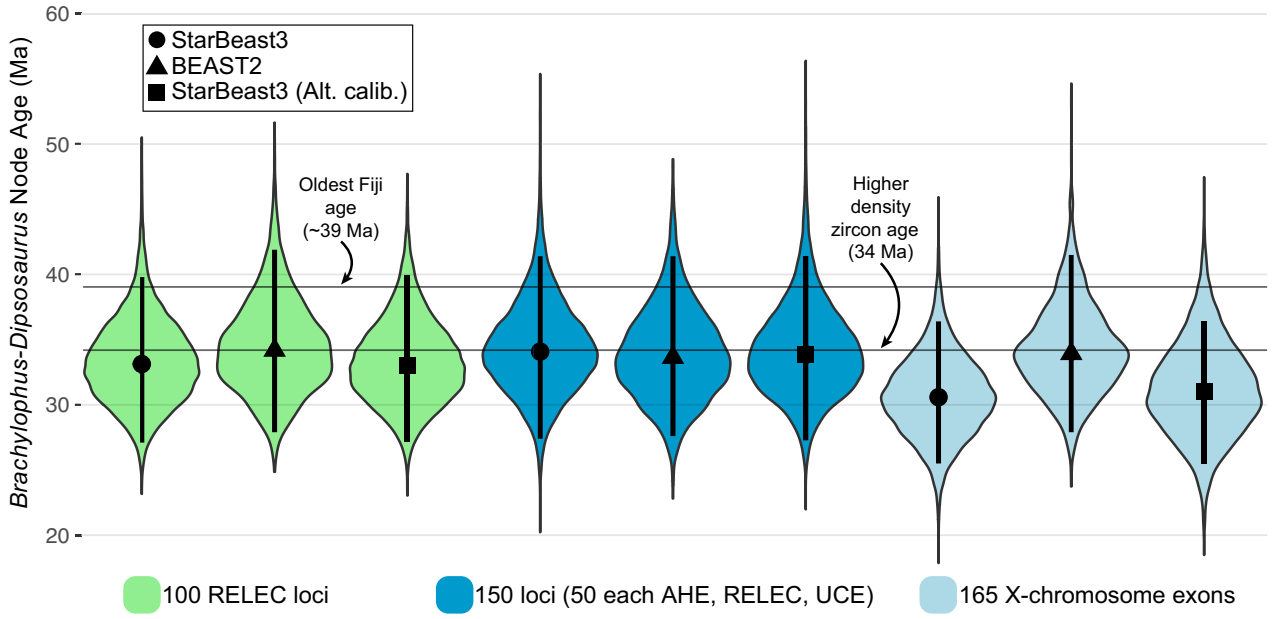

Fig. 1. Plot of the posterior age distribution of the *Brachylophus–Dipsosaurus* clade across divergence time analyses. The center symbol is the median divergence time from each analysis and the black bar is the 95% HPD interval.

intervals in the MSC and most concatenated analyses are near or postdate 40 Ma, but the HPD intervals approached 42 Ma in one analysis (Fig. 1). Median ages of the *Brachylophus* and *Dipsosaurus* split were higher in concatenated (up to 34.2 Ma) than in MSC analyses (33 to 31 Ma). Divergence estimates using the sex-linked exons were slightly younger (e.g., median of *Brachylophus* and *Dipsosaurus* split near 31 Ma in MSC analyses) than those using the autosomal exons and UCEs (e.g., median age ~33 Ma in MSC analyses) (Fig. 1). MSC analyses testing an alternative calibration (*Armandisaurus* anchoring *Brachylophus-Dipsosaurus* without fixing their monophyly) produced the same results as the analyses that used *Armandisaurus* as the offset for crown Iguanidae (Fig. 1). MSC analyses of the RELEC and X chromosome exons that tested the effect of outgroup inclusion on divergence times did not differ from those that included all outgroups (*SI Appendix*, Fig. S19). BEAST2 analysis with additional outgroups (*SI Appendix*, Fig. S25) and total-evidence FBD analyses using the 150-loci dataset (*SI Appendix*, Figs. S23 and S24) produced highly similar results to the other analyses.

Biogeography of Fijian Iguanas. Biogeographic analyses performed in BioGeoBEARS (51) reconstruct North America as the most probable ancestral range of the *Brachylophus–Dipsosaurus* clade (Fig. 2). Models that included the jump (long-distance) dispersal parameter were favored to heavily favored (summed AIC weight > 0.9; Δ AIC > 5 with two outgroups; Δ AIC >10 with nine outgroups; Table 1 and *SI Appendix*, Tables S6 and S7) across analyses of two different trees, presence or absence of outgroups, time-stratification or lack thereof, and inclusion of additional areas in the eastern hemisphere and Antarctica (see below). DEC+J was the best model according to the AIC and AICc tests for all analysis sets (Table 1 and *SI Appendix*, Tables S5–S10).

All analyses with additional areas favor long-distance dispersal from North America to Fiji over alternative hypotheses (Table 1 and *SI Appendix*, Figs. S35, S38, and S41 and Tables S8–S10). Those include dispersal of a stem lineage of *Brachylophus* to Fiji via Beringia, across Eurasia, through South America/Antarctica, and/or from Oceania (Fig. 3). North America was the most probable ancestral range for the *Brachylophus-Dipsosaurus* clade in all analyses that included extra areas (*SI Appendix*, Figs. S35–S43) and models with the jump (*j*) parameter were favored to heavily favored (summed AIC weight > 0.9; Δ AIC > 6 with two outgroups; Δ AIC > 10 with nine outgroups, see Table 1). For DEC+J analyses of the BEAST2 timetree with nine outgroups and in which each alternative hypothesis was tested via dispersal matrix constraints (*SI Appendix*, Figs. S44–S48), the unconstrained model of long-distance dispersal from North America to Fiji was strongly favored over all alternatives (AIC weight = 1; Δ AIC > 10; Table 2).

Discussion

Iguanas Rafted Across the Pacific from North America to Fiji. Here, we assessed whether Fijian iguanas (genus *Brachylophus*), which occur over 8,000 km away from their extant relatives in the Americas, rafted across the Pacific Ocean to Fiji. We collected a phylogenomic dataset composed of >4,000 loci and >2 million bp of sequence data to address the uncertain phylogenetic placement and origin time of *Brachylophus* and to provide phylogenetic trees for historical biogeographic analyses (21, 24, 25). Both concatenated and MSC phylogenetic analyses strongly support a sister–taxon relationship between *Brachylophus* and *Dipsosaurus*, the North American desert iguana. Timetrees generated with phylogenomic data and new fossil calibrations consistently place the age of the *Brachylophus* lineage during the late Paleogene (median age ~34 to 31 Ma) near or after the origin time of the Fijian islands, not tens of millions of years before as previously suggested (30, 34). Quantitative analyses of alternative biogeographic models in the context of our timetree estimates found that North America is the most probable ancestral range of total clade *Brachylophus* and that the occurrence of *Brachylophus* on Fiji is best explained by transoceanic dispersal from North America (Fig. 2). Those results correspond to the biogeography of extant species and also align with the known fossil record of iguanids (54–56).

Several previous studies hypothesized that iguanas colonized Fiji from southeast Asia and/or Gondwana (8, 26), which experienced final break-up of its constituent continental blocks during the early Cenozoic (57). These alternative scenarios entail an

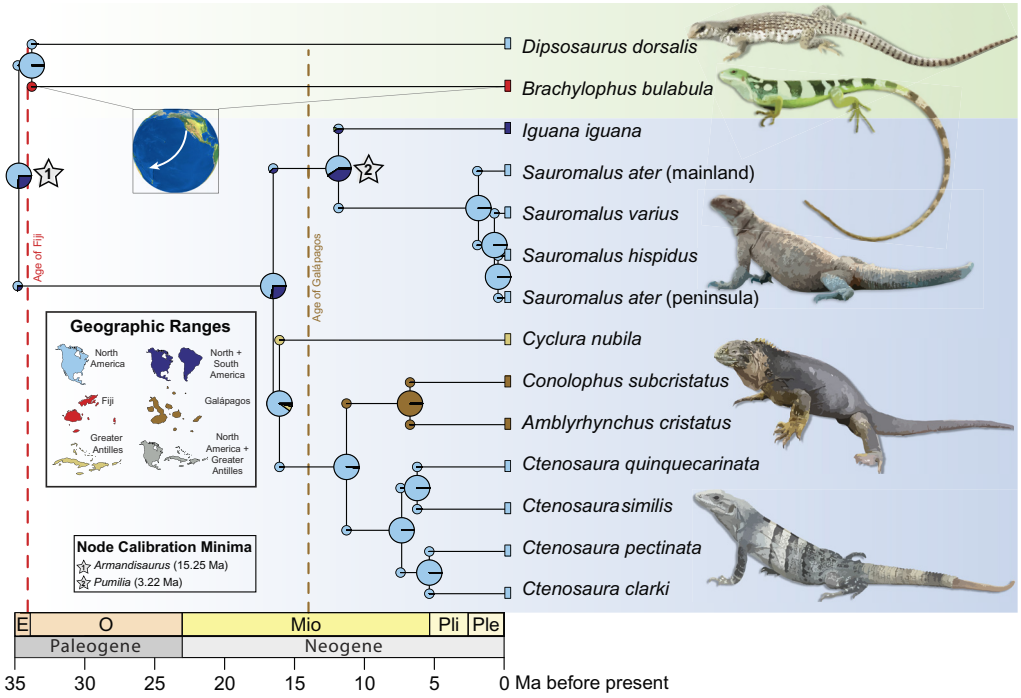

Fig. 2. Phylogenomic timetree of iguanas based on StarBeast3 analysis of 150 loci (50 AHE, UCE, RELEC) and three fossil calibrations (for brevity, only two calibrations labeled and outgroups removed), and time-stratified DEC+J analysis from BioGeoBEARS using areas allowed and manual dispersal matrices, and additional areas added to accommodate all alternative hypotheses for the origin of Fijian iguanas. Pie charts indicate the relative probability of the possible ancestral geographic ranges at nodes and at splits immediately after the corresponding cladogenetic event, and tip boxes indicate extant species ranges. Stars at nodes indicate fossil calibrations. The globe inset shows a representation of the transoceanic dispersal of iguanas from North America to Fiji that occurred at the divergence between *Dipsosaurus* and *Brachylophus* or along the *Brachylophus* branch.

ancient presence of iguanids on those landmasses and extinction later in the Cenozoic. The late Paleogene origin of the *Brachylophus*-*Dipsosaurus* clade precludes a Cretaceous or early Paleogene presence of that lineage in the eastern hemisphere. The fossil record provides additional context. Several Late Cretaceous fossils from east Asia are stem pleurodontan lizards, although a few studies inferred close relationships between some of those taxa and crown pleurodontans (49, 58, 59). However, there is no evidence linking any of those fossils to Iguanidae (*sensu stricto*) and little (60) if any evidence that pleurodontans in east Asia survived the K-PG mass extinction. Crown pleurodontans are known from the Paleogene of Europe, but those fossils are for the most part stem corytophanids (29, 61, 62) and do not inform on the origins of *Brachylophus*. In South America, there is an isolated and fragmentary vertebra from the Oligocene of Patagonia (c. 29 to 26 Ma) that was questionably referred to a non-*Dipsosaurus*

Table 1. Models, parameters, and AIC scores for time-stratified BioGeoBEARS analyses with areas-allowed and manual dispersal multipliers and incorporating four additional areas for east and west Eurasia, Antarctica, and Oceania

Model	LnL	n params	d	e	j	AIC	AIC_wt	Δ AIC	AICc	AICc_wt	Δ AICc
Model comparison of BioGeoBEARS analysis on StarBeast3 tree (2 outgroups, additional areas)											
DEC+J	−27.61	3	0.002	0.00	0.09	61.23	0.71	0.00	63.23	0.70	0.00
DIVALIKE+J	−29.05	3	0.003	0.00	0.11	64.10	0.17	2.87	66.10	0.17	2.87
BAYAREALIKE+J	−29.68	3	0.002	0.00	0.10	65.35	0.09	4.13	67.35	0.09	4.13
DEC	−32.29	2	0.014	0.01	0.00	68.58	0.02	7.35	69.50	0.03	6.28
DIVALIKE	−33.17	2	0.015	0.01	0.00	70.35	0.01	9.12	71.27	0.01	8.04
BAYAREALIKE	−33.95	2	0.015	0.02	0.00	71.89	0.00	10.67	72.82	0.01	9.59
Model comparison of BioGeoBEARS analysis on BEAST2 tree (9 outgroups, additional areas)											
DEC+J	−47.57	3	0.004	0.00	0.12	101.15	0.94	0.00	102.41	0.94	0.00
DIVALIKE+J	−50.43	3	0.006	0.00	0.13	106.85	0.05	5.70	108.11	0.05	5.70
BAYAREALIKE+J	−52.54	3	0.003	0.01	0.08	111.07	0.01	9.93	112.34	0.01	9.93
DEC	−55.66	2	0.010	0.00	0.00	115.33	0.00	14.18	115.93	0.00	13.52
BAYAREALIKE	−57.17	2	0.010	0.02	0.00	118.35	0.00	17.20	118.95	0.00	16.54
DIVALIKE	−58.70	2	0.015	0.01	0.00	121.40	0.00	20.26	122.00	0.00	19.59

The top values are for the analysis with two outgroups using the 150-locus StarBeast3 timetree, and those at the bottom are for the analysis with nine outgroups using the 100 RELEC 50 UCE BEAST2 timetree. The table is ordered by AIC weight.

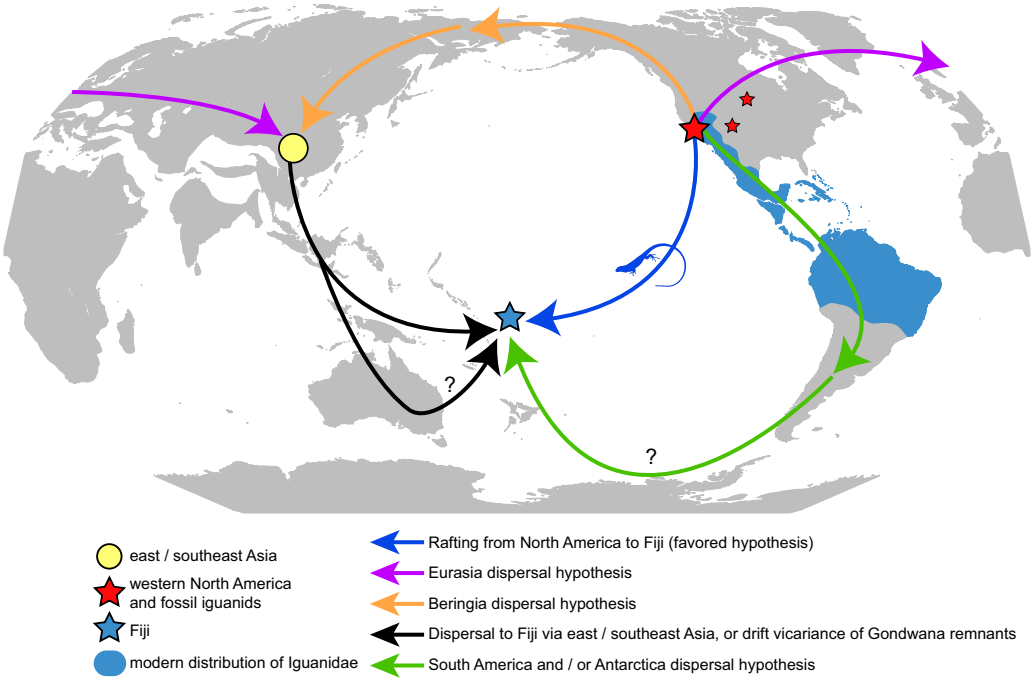

Fig. 3. Hypothesized biogeographic scenarios for the colonization of Fiji by *Brachylophus*, occurrences of fossil iguanids (i.e., *Pumilia*, *Armandisaurus*, and *Queironius*), and distribution of modern iguanids. The world map is set at 34 Ma on a Robinson projection. The paleogeographic map data were assembled using the R package *rgplates* using the plate model from Müller et al. (52, 53).

"derived iguanine" (63), though the fossil was not clearly differentiated from polychrotid, corytophanid, or teiid lizards. Fossils of total clade *Dipsosaurus* are known from the Miocene of New Mexico (c. 15 Ma) and possibly from as far east as Nebraska, from California during the Pliocene (c. 3 Ma), and a stem member of the *Brachylophus–Dipsosaurus* clade or a stem iguanid inhabited the Eocene of North Dakota near 35 Ma (49, 54–56) (*SI Appendix*, Fig. S19). Modern *Dipsosaurus* are found in northwestern Mexico, California, Arizona, Nevada, and Utah (18)—the total clade of *Dipsosaurus* is a North American group in both the extant and extinct biota.

Other biogeographic alternatives include late or post Paleogene dispersal of a stem lineage of *Brachylophus* to Fiji via Eurasia or through South America/Antarctica. Biogeographic models (Table 1 and *SI Appendix*, Figs. S35, S38, and S41) and environmental conditions during the late Paleogene favor dispersal from North America over southern or Eurasian routes (Fig. 3 and Table 2). Antarctic conditions likely became inhospitable to iguanids as the Cenozoic progressed due to the onset and continued development of ice sheets c. 34 Ma–present, and warmer, forested environments near or in the Arctic disappeared during the late Eocene (64, 65). The most viable time for both southern and likely Beringian/Eurasian dispersal was during early Eocene hothouse conditions (~56 to 47 Ma) when other iguanian lizards dispersed across the northern hemisphere (29), which precedes the oldest age of Fiji (39 Ma) and the origin of *Brachylophus* near 34 to 31 Ma. The other conceivable time for Beringian or Eurasian dispersal is during the warmer middle Miocene (66), when several frogs and lizards crossed Beringia into North America (67). That would require very recent extinctions of iguanids in Eurasia.

The combination of evidence supporting oceanic rafting from North America to Fiji is 1) phylogenomic analyses that support a sister taxon relationship between *Brachylophus* and *Dipsosaurus*, 2) the distribution of fossil iguanids, extant *Dipsosaurus*, and most other extant iguanids in North America, 3) statistical biogeographic analyses that favor long-distance dispersal from North America over alternative hypotheses, including dispersal via Eurasia, South America, Antarctica, and/or Oceania, and 4) the

Table 2. Model comparison of DEC + J analyses of the 100 RELEC 50 UCE BEAST2 timetree and nine outgroups, with areas-allowed and manual dispersal multipliers, and incorporating 4 additional areas for east and west Eurasia, Antarctica, and Oceania

Route constraint of DEC+J on BEAST2 tree (9 outgroups, additional areas; K = 3)	LnL	AIC	AIC_wt	Δ AIC	AICc	AICc_wt	Δ AICc
Unconstrained, long-distance dispersal from North America	−47.57	101.15	1.00	0.00	103.15	1.00	0.00
Southern dispersal, jump from North America to Antarctica allowed	−58.48	122.97	0.00	21.82	124.97	0.00	21.82
Southern dispersal forced through South America	−60.50	127.01	0.00	25.86	129.01	0.00	25.86
Trans-Beringian dispersal	−53.92	113.85	0.00	12.70	115.85	0.00	12.70
Cross-Laurasian dispersal	−56.24	118.49	0.00	17.34	120.49	0.00	17.34
Fixed origin of *Brachylophus-Dipsosaurus* in east Asia	−62.40	130.81	0.00	29.66	132.81	0.00	29.66

Analyses are constrained to each alternative hypothesis for the origin of Fijian iguanas and AIC scores are compared to the best model, the unconstrained analysis that inferred long-distance dispersal from North America to Fiji.

late Paleogene divergence time between *Brachylophus* and *Dipsosaurus*. Alternative hypotheses require large range expansions and subsequent and relatively recent extinction of the *Brachylophus* lineage in continental Eurasia, mainland and island southeast Asia, or South America/Antarctica, long overland dispersals, and multiple smaller but still substantial overwater dispersal events (e.g., South America to Antarctica to Fiji; rafting through southeast Asia) (Fig. 3 and *SI Appendix*, Table S11). Paleogene or potentially Miocene fossils referable to the stem of *Brachylophus*+*Dipsosaurus* or of either genus in Asia, Europe, and South America/Antarctica would provide the best evidence in support of alternative hypotheses. Available data from the extant biota and the fossil and geologic records indicate that alternative hypotheses are unlikely to be viable and that a direct dispersal from North America is the best explanation for the occurrence of iguanas on Fiji.

Logistics of Dispersal. Given a dispersal from North America, where precisely did Fijian iguanas raft from and how did they survive the journey? *Dipsosaurus* is presently restricted to highly arid deserts of the western USA and northern Mexico (68). Fossil *Dipsosaurus* and stem representatives are known from within or close to the range of the genus in the western United States and Mexico (49, 54, 55). Although significant cooling and aridification occurred at the Eocene–Oligocene transition, the deserts inhabited by modern *Dipsosaurus* did not appear until the late Neogene (69, 70), and so the habitat of the *Brachylophus*–*Dipsosaurus* common ancestor may have been comparatively mesic. It is possible that iguanas dispersed to Fiji from within or from near the extant range of *Dipsosaurus*; Fiji and continental North America are unlikely to have been substantially further apart (or closer together) during the late Paleogene than they are today (71–73). Paleocurrent evidence provides auxiliary support for the North American origin of Fijian iguanas. A dispersal route from coastal Mexico to the South Pacific is plausible based on episodic availability of floating debris (74), and modeling efforts indicate an equator-directed current along the western coast of North America and a southern equatorial current that moved water westward across the Pacific during the Eocene-Oligocene transition, providing a potential dispersal path (75, 76). Previous estimates of the America-Fiji voyage range from 4 to 12 mo (8, 25, 77), but recent simulations of oceanic drift of domesticated sweet potato from South America to Polynesia indicate a dispersal time as low as 80 to 120 d (78). Herbivorous iguanids forgo food for months at a time during brumation, and extant *Dipsosaurus* brumate from October–March. However, floating vegetation mats are a known substrate for oceanic dispersal (79), so iguanas rafting from North America to Fiji could have had a food source during their journey. Additionally, some iguanas have other traits that may augment their capacity to survive overwater dispersal, including resistance to heat and dehydration. For example, *Dipsosaurus* have the highest voluntary thermal maximum temperature among lizards and largely inhabit areas without permanent freshwater (80, 81).

Considerations for Rafting from North America. Although our analyses indicate that Fijian iguanas originated in and rafted from North America, there are a few additional considerations. First, it is possible that the split between *Dipsosaurus* and *Brachylophus* occurred in North America and that the iguanid disperser to Fiji was an extinct lineage on the *Brachylophus* branch rather than the *Dipsosaurus*–*Brachylophus* common ancestor. Second, it cannot be entirely excluded that the ancestor of *Brachylophus* arrived on Fiji via island-hopping through the Pacific, potentially across transient volcanic islands that left no record of dispersal. We note that there is no Pacific fossil record of iguanas outside Fiji and Tonga (82) and stepping-stone dispersal would likely require iguanas to colonize many Pacific islands on which they are now extinct. Finally, it has yet to be shown that the extinct Fijian iguana *Lapitiguana* is the sister lineage of *Brachylophus*. Fossils of *Lapitiguana* lack apomorphies of iguanin iguanas but also lack key features of extant *Brachylophus* (82). Thus, the possibility of multiple dispersals of iguanas from North America also cannot be entirely excluded. The fossil record has a strong and perhaps singular potential to further illuminate the origin of Fijian iguanas.

Scope and Predictability of Transoceanic Dispersal in Terrestrial Vertebrates. Long-distance dispersal via oceanic rafting is recognized as an important mechanism for biological diversification (83, 84), and the capacity of terrestrial vertebrates to cross oceans and found new species lineages and even adaptive radiations is well established (1). Terrestrial vertebrates with diverse organismal traits, including primates (85, 86), rodents (87) geckos (88), skinks (11, 89), amphisbaenians (90), and even frogs (91, 92) have been demonstrated to cross oceanic barriers (Fig. 4*B*), including thousands of kilometers across the Atlantic or Indian oceans. Among vertebrates, lizards are especially well-known overwater dispersers, especially pleurodontans such as iguanids and the Malagasy oplurids (11, 36, 79, 88). Several iguanid lineages have notably colonized oceanic islands, including the ancestors of marine and land iguanas in the Galápagos and rock iguanas in the Caribbean (32, 93). In 1995, a vegetation mat with at least 15 individual green iguanas (*Iguana iguana*) that likely originated on the islands of Guadeloupe was observed making landfall on Anguilla, an island 300 km away that was already inhabited by a different species of iguana, *I. delicatissima* (79). This resulted in the successful colonization of Anguilla by *I. iguana* and subsequent hybridization with the critically endangered *I. delicatissima* (94). The direct observation of *I. iguana* colonizing Anguilla demonstrated in real time the viability of long-distance, overwater rafting as a mechanism for populating marine islands.

No other nonvolant vertebrate, including oplurids or any other lizard (Fig. 4*B*), is known to have crossed distances as long as the ancestors of Fijian iguanas, which rafted over 8,000 km across the Pacific Ocean—a journey otherwise reserved for marine organisms, birds, plants, or terrestrial invertebrates (1, 97). More generally, iguanids are an exemplar radiation in which rafting dispersal and founder-event speciation appear to occur with unusual frequency. Of the 45 extant species of iguanids, only 11 do not occur on islands and 28 are island endemics (Fig. 4*A*). For many if not most of the islands on which iguanids occur, land bridges mediated by eustatic sea-level changes were a highly unlikely dispersal mechanism (98), leaving rafting as the only viable dispersal hypothesis. Iguanids—animals that are large, herbivorous, and resistant to both heat and starvation—clearly are successful at dispersing to and propagating on islands, and have on several occasions colonized islands that are very far from the mainland (Fig. 4*A*). In fact, the longest distance dispersal events among iguanas (to the Galápagos and to Fiji) each resulted in radiations of multiple species, potentially a reflection of the unoccupied niche space available to those lineages upon arrival (99). We emphasize that even within a dispersal-prone lineage such as Iguanidae, the length of the transoceanic voyage made by the ancestors of Fijian iguanas is an incredible outlier by an order of magnitude. Our results and the entire iguanid radiation support the strengthening paradigm of trait-enhanced long-distance dispersal (11, 100). Iguanidae should provide a fruitful system for future research investigating a broader framework for understanding and predicting these remarkable dispersal events.

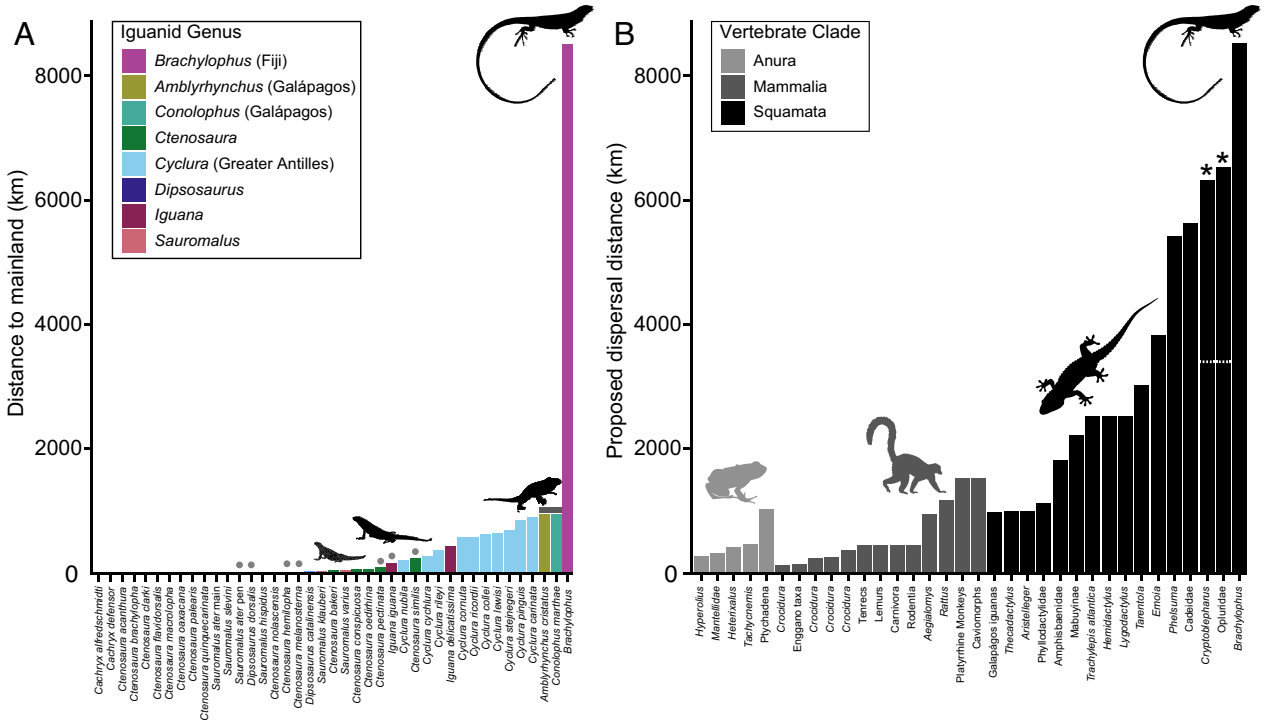

Fig. 4. (*A*) Distances between island and mainland for extant iguanid lizards and (*B*) distances for other proposed long-distance, overwater dispersal events in terrestrial vertebrates. For the iguanids, a minimum distance was taken for each species between the mainland and the closest island inhabited by each taxon to the mainland using GoogleEarth (19). Species occurrence data were taken from ref. 18. Species that are not found on islands are at 0, and those that are found on both island and mainland are marked with a gray circle next to the distance bar. A dark gray line across the upper ends of adjacent bars mark taxa that (almost certainly) resulted from a single dispersal event. Bars are color coded by genus and the legend also lists the relevant island(s) for exclusively island radiations. For other vertebrate dispersal events, distances were taken from refs. 11, 36, 88–91, 95, 96 and/or measured during the relevant time period using GPlates (52). Asterisks above bars indicate the longest possible dispersal distances, and white dashes on the same bars indicate maximum distances given a steppingstone model.

Methods

Taxon Selection for Sequence Capture. We acquired samples for every iguanid genus except for *Cachryx*. Multiple species were included for *Sauromalus* and *Ctenosaura,* and individual species were included for *Brachylophus*, *Iguana*, *Dipsosaurus*, *Conolophus*, and *Amblyrhynchus*. For outgroups, we included *Phrynosoma blainvilli* and *Sceloporus occidentalis* (Phrynosomatidae), *Oplurus cyclurus* (Opluridae), and *Diplolaemus leopardinus* (Leiosauridae), which were chosen to bracket pleurodontan diversity. Phrynosomatidae is frequently inferred to be the sister taxon of all other pleurodontans, and Iguanidae is usually found to be sister to the remaining clades (34, 35). We also performed outgroup sensitivity analyses with the RELEC-only dataset that included additional pleurodontan outgroups (*Anolis sagrei*, *Crotaphytus collaris*, *Basiliscus vittatus*, *Leiocephalus barahonensis*, and *Enyalioides palpebralis*).

Probe Design. We used target sequence capture to generate genome-wide molecular data using a custom probe set designed for this and related research projects. We selected 1,000 UCEs (45) with high phylogenetic utility from the UCEs used in a recent phylogenomic study of pleurodontan iguanians (36) using the R (101) package *genesortr* (102), excluding Robinson–Foulds (RF) distance to their species tree as a locus-ordering criterion. To those UCEs, we added 500 bp of *Anolis carolinensis* flanking sequence on each end of the UCE core region using phyluce v1.7.1 (103). The probe set also leverages the 179 RELEC loci developed by Karin et al. (43) along with an additional 107 RELEC loci developed with a similar methodology to ref. 43 for this and other phylogenomic studies. We found this expanded set by conducting searches with tBLASTn utilizing all 931 human exons greater than 1,899 bp (633 amino acids) against available squamate genomes on GenBank and individually confirmed they met the following criteria. We retained markers in which the resulting hits were (1) single-copy and retained as a single exon at sufficient length (1,500 bp) across squamates, (2) more rapidly evolving than RAG1, and (3) produced relatively accurate gene trees that displayed well-supported relationships (e.g., monophyletic Serpentes). Finally, to the autosomal dataset, we added 316 AHE loci (44) and 38 ToL loci (46). The ToL loci were taken from the Squamate Conserved Loci (SqCL) probe set and blasted to the AnoCar 2.0 genome assembly, from which the full-length exon was extracted (104, 105). The AHE loci were taken directly from the SqCL probe set (105). Additionally, loci on the sex chromosome may have high utility for phylogenetic reconstruction (106) so we targeted 3,625 exons comprising the longest transcripts of all 328 X chromosome genes annotated from the *Sceloporus undulatus* genome assembly (SceUnd_v.1.1, NC_056531) (107). Short exons were padded with flanking genomic sequence to reach the 200 bp probe size, and neighboring exons within 400 bp of each other were joined into a single target region tiled with probes, resulting in 2,836 target sequences. These target sequences were supplemented with targets for other projects and sent to Arbor Biosciences to design a custom sequence capture kit.

Lab Work and Sequencing. A detailed protocol is available in *SI Appendix*. In brief, we used an Omega MagBind® Bead kit to extract genomic DNA from tissue samples. A QSonica sonicator was used to fragment 1 μg of DNA, which was then size selected to 300 to 500 bp. Libraries were constructed using a Kapa Hyper Prep Kit. Library concentrations were assessed using a Qubit Fluorometer or the Biotium Plate Reader. Sequence capture was performed using the custom MyBaits kit from Arbor. Sequencing was performed on a Novaseq 6000 platform using half a lane with an S4 flowcell at the UC Berkeley Vincent J. Coates Genomics Sequencing Lab.

Bioinformatics. We used HTStream v 1.3.3 (108) to 1) remove phiX sequences, PCR duplicates, and adapter sequences, 2) merge overlapping reads, 3) remove low quality bases with a window size of 10 bp and a quality threshold of 20, 4) trim off sequences containing N characters, and 5) exclude reads smaller than 20 bp. We mapped the cleaned reads to our target loci with BWA-MEM 0.7.17-r1188 (109). The bam files of mapped reads were merged, sorted, and indexed with Samtools (110), read groups were added with Picard v. 2.23.4 (111), and reads surrounding indels were realigned with GATK v3.6 (112). For each locus, a consensus sequence in Fasta format was generated using ANGSD v. 0.933-79-gda26ba4 (113) with a minimum depth of 3, a maximum depth of 10000, a minimum base quality of 20,

and a minimum mapping quality of 30. Quality control was conducted with FastQC v 0.11.8 (114), Qualimap v.2.2.1 (115), and MultiQC version 1.1 (116). Average coverage across all individuals in the study was 74X (range 22X to 128X). Coverage data are provided in *SI Appendix*, Table S3 and Figs. S1 and S2. Coverage data for the additional outgroups are in *SI Appendix*, Fig. S3.

There was some overlap between datasets, so to avoid overweighting individual loci in analyses that included all marker sets, we retained only one copy of each locus using the ordering scheme (RELEC, ToL, AHE, UCE). We captured 315 AHE loci, 38 Squamate ToL loci, 283 RELEC loci, and 992 UCEs drawn from across the genome, as well as 2,813 exons from the X chromosome. To expand our taxonomic sampling, published UCE sequences were acquired for *Ctenosaura quinquecarinata* and *Cyclura nubila* (36), and AHE sequences were obtained for *Brachylophus* cf. *bulabula* [our identification of the sample from (34)]. Sequences were downloaded from the original publications and aligned to the existing alignments with *mafft* (117) using global pair alignment with a maximum of 1,000 iterations. Complete alignments were trimmed using *trimal* (118) in *phyluce* v1.7.2 using default settings.

Phylogenomics and Divergence Time Analysis. Phylogenetic inference was performed with concatenated maximum likelihood (IQTREE2) (119) and the summary MSC methods ASTRAL III (120) and ASTRAL-Hybrid (121), a weighted method that automatically reduces the topological impact of poorly supported quartets and/or long branch lengths. Analyses were performed on the entire autosomal dataset (1,734,499 bp) and each marker set (RELEC, AHE, UCE, and ToL loci). We also performed concatenated analysis of all X chromosome exons (609,725 bp) and concatenated and summary MSC analyses of a filtered X chromosome dataset of 165 exons (see below). A GTR+G site model was applied across the entire alignment for concatenated maximum-likelihood analyses and with 1,000 bootstrap replicates. Gene trees for summary MSC methods were estimated in RAxML v8 (122) using a GTRCAT model and 100 bootstrap replicates.

Datasets were reduced for computational tractability in Bayesian divergence time analyses using the R package *genesortr*, which performs multivariate subsampling to recover phylogenetically useful loci from phylogenomic data (102). We reduced the RELEC data to 100 loci, including RF distance to the ASTRAL-Hyb species tree as a criterion but collapsing the *Brachylophus–Dipsosaurus* clade to avoid biasing locus selection toward that relationship. We iterated the same procedure for 50 loci each of RELEC, UCE, and AHE and again for 100 RELEC and 50 UCE alignments that included the expanded outgroup set. The X chromosome data were filtered using *phyluce* (103), retaining alignments that were at least 75% complete per locus and that were each >500 bp.

We performed full MSC analyses in StarBeast3 (48) on the reduced 165 X chromosome exons, 150 autosomal loci, and 100 RELEC loci datasets. We used the HKY+G model with four gamma parameters to model site variation, a relaxed clock model, and a Yule tree model, which were unlinked across all loci in the analyses of autosomal data. For the X chromosome data, the ploidy was set at 1.5. Some of the filtered X chromosome exons were from the same gene, so for those analyses, we linked the tree and clock models of those exons. Iguana relationships were fixed to the ASTRAL-Hyb tree except for the relationships of *Brachylophus* and *Dipsosaurus* to each other and to the rest of Iguanidae. MSC analyses were run for 4×10^8 generations for the 150 locus dataset, 3×10^8 for the 100 exon RELEC dataset, and 2×10^8 for the 165 exon X chromosome dataset. We also performed analyses testing the impact of an alternative calibration strategy (Fig. 1) and the impact of removing outgroups. Concatenated divergence time analyses were performed in BEAST2 for all datasets using the optimized relaxed clock model (123). Clock models and trees were linked across all partitions, the site model was HKY+G with four gamma parameters, and analyses were run for 5×10^7 generations for most analyses and 6×10^7 generations for the 100 RELEC, 50 UCE dataset. Adequate MCMC sampling was assessed with ESS > 200 in Tracer 1.7 (124). The rationale for the node calibrations used in these analyses is in *SI Appendix*, with the calibrations given in Table 3. Total-evidence analyses used the FBD tree prior, separate molecular and morphological clocks, the morphological data from (49), and fossil dates set at their minimum age (*SI Appendix*). Otherwise, FBD analyses used the same site models as node-calibrated analyses and were also run for 5×10^7 generations.

Table 3. Summary of fossil calibration parameters for node-calibrated divergence time analysis

Node calibrated	Extinct taxon anchoring offset	Offset (Ma)	Mean (ma)	Std. Dev
Pleurodonta	*Geiseltaliellus* (61)	56	19	0.52
Iguanidae	*Armandisaurus* (54)	15.25	19.95	0.38
(*Brachylophus-Dipsosaurus*) (alternative calibration)	*Armandisaurus* (54)	15.25	18	0.37
(*Sauromalus*, *Iguana*)	*Pumilia* (55)	3.22	8.5	0.5

Biogeographic Analysis. Statistical biogeographic analysis was performed in the R package BioGeoBEARS (51). Time-stratified models were used that included areas allowed and manual dispersal modifier parameters, and we tested the DEC, DIVA-like, and BAYAREA-like models with and without the *j* (founder-event speciation) parameter (2). We tested models that were not time-stratified and that did not have a manual dispersal multiplier. We also performed analyses that included no outgroups, two outgroups, or nine outgroups. For most analyses, we used the 150-locus StarBeast3 tree, and for the analyses using additional outgroups, we used the 100 RELEC 50 UCE BEAST2 tree. We performed an additional set of analyses for both trees that included areas for western and eastern Eurasia, Antarctica, and Oceania (i.e., eastward dispersal through Australia, New Guinea, New Zealand, and/or adjacent islands to Fiji) to quantitatively test all alternatives to long-distance dispersal from North America. Finally, we performed DEC+J analyses on the 100 RELEC 50 UCE BEAST2 tree and with all outgroups, in which manual dispersal matrices were modified such that dispersal to Fiji was constrained to each alternative hypothesis in Fig. 3. For any analysis that included all outgroups, *Basiliscus vittatus* and *Anolis sagrei* were coded for the range of their entire family-level clade to avoid overweighting the individual ranges of those species. When relevant, the *Brachylophus* cf. *bulabula* branch was collapsed for biogeographic analysis. Model support was compared via AIC and AICc.

Data, Materials, and Software Availability. 1) Short Read Sequence Data; 2) Multiple sequence alignments (fasta), biogeographic analysis files (.R, .txt), species-tree and divergence time analysis files (.xml), and resulting treefiles (.tre). Data have been deposited in 1) SRA (NCBI) (125); 2) Dryad (126). Short reads are on SRA, under the BioProject ID PRJNA1217946 at https://www.ncbi.nlm.nih.gov/sra/PRJNA1217946; 2) All other files are accessioned on Dryad at https://doi.org/10.5061/dryad.4tmpg4fjr.

ACKNOWLEDGMENTS. This work was funded by an NSF postdoctoral research fellowship to SGS (DBI # 2109461). We thank Lydia Smith and Michelle Davila of the Evolutionary Genetics Lab at UC Berkeley for lab work assistance. Sequencing was performed by QB3 Genomics (UC Berkeley, Berkeley, CA, RRID:SCR_022170). We also thank the collections and staff of MSB, MVZ, ROM, YPM, FLMNH, LSUMZ, and MCZ for tissue loans. Research in Fiji was funded through the International Iguana Foundation. The Department of Environment and Ministry of Education in Fiji provided research permits and CITES export permits for the Fijian iguana sample. The McGuire lab at UC Berkeley provided feedback on earlier drafts of the paper. We thank Kevin de Queiroz and four anonymous reviewers, the editor, and the editorial board member for providing critical and thoughtful feedback that greatly improved the manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government.

Author affiliations: [a]Department of Environmental Science, University of San Francisco, CA 94117; [b]Museum of Vertebrate Zoology, Department of Integrative Biology, University of California, Berkeley, CA 94720; [c]U.S. Geological Survey, Western Ecological Research Center, San Diego, CA 92101; [d]Department of Environmental Science, Policy, and Management, University of California, Berkeley, CA 94720; [e]NatureFiji-MareqetiViti, Suva, Fiji; and [f]Department of Biology and Center for Biodiversity and Ecosystem Stewardship, Villanova University, Villanova, PA 93106

1. R. G. Gillespie *et al.*, Long-distance dispersal: A framework for hypothesis testing. *Trends Ecol. Evol.* **27**, 47–56 (2012).
2. N. J. Matzke, Model selection in historical biogeography reveals that founder-event speciation is a crucial process in island clades. *Syst. Biol.* **63**, 951–970 (2014).
3. A. R. Templeton, The reality and importance of founder speciation in evolution. *BioEssays* **30**, 470–479 (2008).
4. E. Mayr, "Change of genetic environment and evolution" in *Evolution as a Process*, J. Huxley, E. B. Ford, Eds. (Allen and Unwin, 1954), pp. 157–180.
5. Z. Lindo, Transoceanic dispersal of terrestrial species by debris rafting. *Ecography* **43**, 1364–1372 (2020).
6. C. Darwin, *On the Origin of Species by Means of Natural Selection* (J. Murray, London, 1859).
7. R. D. E. MacPhee, M. Iturralde-Vinent, First tertiary land mammal from greater Antilles: An early miocene sloth (Xenarthra, Megalonychidae) from Cuba. *Am. Mus. Novit.* **3094**, 1–13 (1994).
8. B. P. Noonan, J. W. Sites Jr., Tracing the origins of iguanid lizards and boine snakes of the Pacific. *Am. Nat.* **175**, 61–72 (2010).
9. Y.-J. Feng *et al.*, Phylogenomics reveals rapid, simultaneous diversification of three major clades of Gondwanan frogs at the Cretaceous-Paleogene boundary. *Proc. Natl. Acad. Sci. U.S.A.* **114** (2017).
10. K. Roelants, F. Bossuyt, Archaeobatrachian paraphyly and Pangaean diversification of crown-group frogs. *Syst. Biol.* **54**, 111–126 (2005).
11. M. P. K. Blom *et al.*, Habitat preference modulates trans-oceanic dispersal in a terrestrial vertebrate. *Proc. R. Soc. B Biol. Sci.* **286**, 20182575 (2019).
12. K. A. Jønsson, B. G. Holt, Islands contribute disproportionately high amounts of evolutionary diversity in passerine birds. *Nat. Commun.* **6**, 8538 (2015).
13. G. Kier *et al.*, A global assessment of endemism and species richness across island and mainland regions. *Proc. Natl. Acad. Sci. U.S.A.* **106**, 9322–9327 (2009).
14. H. Kreft, W. Jetz, J. Mutke, G. Kier, W. Barthlott, Global diversity of island floras from a macroecological perspective. *Ecol. Lett.* **11**, 116–127 (2008).
15. C. Leclerc, F. Courchamp, C. Bellard, Insular threat associations within taxa worldwide. *Sci. Rep.* **8**, 6393 (2018).
16. J. A. Schulte, J. P. Valladares, A. Larson, Phylogenetic relationships within Iguanidae inferred using molecular and morphological data and a phylogenetic taxonomy of iguanian lizards. *Herpetologica* **59**, 399–419 (2003).
17. K. de Queiroz, "Phylogenetic systematics of iguanine lizards: A comparative osteological study" in *Univ. Calif. Publ. Zool.* (University of California Press, Berkeley, 1987) vol. **118**.
18. L. J. Buckley *et al.* "A checklist of the iguanas of the world (Iguanidae; Iguaninae)" in *Iguanas: Biology, Systematics, and Conservation*, J.B. Iverson, T.D. Grant, C.R. Knapp, S.A. Pasachnik, Eds. (Herpetological Conservation and Biology, 2016), vol. **11**, pp. 4–46.
19. Google Earth Pro, Google Earth (Version 7.3.6.9750). Google. https://www.google.com/earth/. Accessed 19 September 2023.
20. V. E. Neall, S. A. Trewick, The age and origin of the Pacific Islands: A geological overview. *Philos. Trans. R. Soc. B Biol. Sci.* **363**, 3293–3308 (2008).
21. J. S. Keogh, D. L. Edwards, R. N. Fisher, P. S. Harlow, Molecular and morphological analysis of the critically endangered Fijian iguanas reveals cryptic diversity and a complex biogeographic history. *Philos. Trans. R. Soc. B Biol. Sci.* **363**, 3413–3426 (2008).
22. R. N. Fisher, J. Niukula, D. Watling, P. S. Harlow, A new species of iguana *Brachylophus* Cuvier 1829 (Sauria: Iguania: Iguanidae) from Gau Island, Fiji Islands. *Zootaxa* **4273**, 407 (2017).
23. T. M. Townsend *et al.*, Phylogeny of iguanian lizards inferred from 29 nuclear loci, and a comparison of concatenated and species-tree approaches for an ancient, rapid radiation. *Mol. Phylogenet. Evol.* **61**, 363–380 (2011).
24. H. Cogger, Voyage of the banded iguana. *Aust. Nat. Hist.* **18**, 144–149 (1974).
25. J. R. H. Gibbons, The biogeography of *Brachylophus* (Iguanidae) including the description of a new species, *B. vitiensis,* from Fiji. *J. Herpetol.* **15**, 255 (1981).
26. D. McCarthy, The trans-Pacific zipper effect: Disjunct sister taxa and matching geological outlines that link the Pacific margins. *J. Biogeogr.* **30**, 1545–1561 (2003).
27. T. H. Worthy, The fossil megapodes (Aves: Megapodiidae) of Fiji with descriptions of a new genus and two new species. *J. R. Soc. N.Z.* **30**, 337–364 (2000).
28. C. L. Malone, V. H. Reynoso, L. Buckley, Never judge an iguana by its spines: Systematics of the Yucatan spiny tailed iguana, *Ctenosaura defensor* (Cope, 1866). *Mol. Phylogenet. Evol.* **115**, 27–39 (2017).
29. K. T. Smith, Eocene lizards of the clade *Geiseltaliellus* from Messel and Geiseltal, Germany, and the early radiation of Iguanidae (Reptilia: Squamata). *Bull. Peabody Mus. Nat. Hist.* **50**, 219–306 (2009).
30. Y. Zheng, J. J. Wiens, Combining phylogenomic and supermatrix approaches, and a time-calibrated phylogeny for squamate reptiles (lizards and snakes) based on 52 genes and 4162 species. *Mol. Phylogenet. Evol.* **94**, 537–547 (2016).
31. K. Rassmann, Evolutionary age of the Galápagos iguanas predates the age of the present Galápagos Islands. *Mol. Phylogenet. Evol.* **7**, 158–172 (1997).
32. A. MacLeod *et al.*, Hybridization masks speciation in the evolutionary history of the Galápagos marine iguana. *Proc. R. Soc. B Biol. Sci.* **282**, 20150425 (2015).
33. R. Pyron, F. T. Burbrink, J. J. Wiens, A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. *BMC Evol. Biol.* **13**, 93 (2013).
34. F. T. Burbrink *et al.*, Interrogating genomic-scale data for Squamata (lizards, snakes, and amphisbaenians) shows no support for key traditional morphological relationships. *Syst. Biol.* **69**, 502–520 (2020).
35. J. W. Streicher, J. A. Schulte, J. J. Wiens, How should genes and taxa be sampled for phylogenomic analyses with missing data? An empirical study in iguanian lizards *Syst. Biol.* **65**, 128–145 (2016).
36. R. S. Welt, C. J. Raxworthy, Dispersal, not vicariance, explains the biogeographic origin of iguanas on Madagascar. *Mol. Phylogenet. Evol.* **167**, 107345 (2022).
37. P. O. Title *et al.*, The macroevolutionary singularity of snakes. *Science* **383**, 918–923 (2024).
38. D. Cluzel, S. Meffre, In search of Gondwana heritage in the Outer Melanesian Arc: No pre-upper Eocene detrital zircons in Viti Levu river sands (Fiji Islands). *Aust. J. Earth Sci.* **66**, 265–277 (2019).
39. R. Clarke, D. Smith, J. Naden, Source controls on mineralisation: Regional geology and magmatic evolution of Fiji. *Lithos* **432–433**, 106897 (2022).
40. P. Rodda, Outline of the geology of Viti Levu. *N. Z. J. Geol. Geophys.* **10**, 1260–1273 (1967).
41. B. Hathway, Sedimentation and volcanism in an Oligocene-Miocene intra-oceanic arc and fore-arc, southwestern Viti Levu, Fiji. *J. Geol. Soc.* **151**, 499–514 (1994).
42. E. Todd, J. B. Gill, J. A. Pearce, A variably enriched mantle wedge and contrasting melt types during arc stages following subduction initiation in Fiji and Tonga, southwest Pacific. *Earth Planet. Sci. Lett.* **335–336**, 180–194 (2012).
43. B. R. Karin, T. Gamble, T. R. Jackman, Optimizing phylogenomics with rapidly evolving long exons: Comparison with anchored hybrid enrichment and ultraconserved elements. *Mol. Biol. Evol.* **37**, 904–922 (2020).
44. A. R. Lemmon, S. A. Emme, E. M. Lemmon, Anchored hybrid enrichment for massively high-throughput phylogenomics. *Syst. Biol.* **61**, 727–744 (2012).
45. B. C. Faircloth *et al.*, Ultraconserved elements anchor thousands of genetic markers spanning multiple evolutionary timescales. *Syst. Biol.* **61**, 717–726 (2012).
46. J. J. Wiens *et al.*, Resolving the phylogeny of lizards and snakes (Squamata) with extensive sampling of genes and species. *Biol. Lett.* **8**, 1043–1046 (2012).
47. R. Bouckaert *et al.*, BEAST 2.5: An advanced software platform for Bayesian evolutionary analysis. *PLOS Comput. Biol.* **15**, e1006650 (2019).
48. J. Douglas, C. L. Jiménez-Silva, R. Bouckaert, StarBeast3: Adaptive Parallelized bayesian inference under the multispecies coalescent. *Syst. Biol.* **71**, 901–916 (2022).
49. S. G. Scarpetta, A Palaeogene stem crotaphytid (*Aciprion formosum*) and the phylogenetic affinities of early fossil pleurodontan iguanians. *R. Soc. Open Sci.* **11**, 221139 (2024).
50. C. Zhang, T. Stadler, S. Klopfstein, T. A. Heath, F. Ronquist, Total-evidence dating under the fossilized birth–death process. *Syst. Biol.* **65**, 228–249 (2016).
51. N. J. Matzke, BioGeoBEARS: BioGeography with Bayesian (and Likelihood) evolutionary analysis in R Scripts R package. version 0.2.1 (2013).
52. R. D. Müller *et al.*, GPlates: Building a virtual earth through deep time. *Geochem. Geophys. Geosystems* **19**, 2243–2261 (2018).
53. R. D. Müller *et al.*, A global plate model including lithospheric deformation along major rifts and orogens since the triassic. *Tectonics* **38**, 1884–1907 (2019).
54. M. Norell, K. de Queiroz, The earliest iguanine lizard (Reptilia; Squamata) and its bearing on iguanine phylogeny. *Am. Mus. Novit.* **2997**, 1–16 (1991).
55. M. A. Norell, Late Cenozoic lizards of the Anza Borrego Desert, California. *Contrib. Sci. Nat. Hist. Mus. Los Angeles Cty.* **414**, 1–31 (1989).
56. K. T. Smith, The evolution of mid-latitude faunas during the Eocene: Late Eocene lizards of the Medicine Pole Hills reconsidered. *Bull. Peabody Mus. Nat. Hist.* **52**, 3–105 (2011).
57. M. Seton *et al.*, Global continental and ocean basin reconstructions since 200Ma. *Earth-Sci. Rev.* **113**, 212–270 (2012).
58. J. D. Daza, V. Abdala, J. S. Arias, D. García-López, P. Ortiz, Cladistic analysis of Iguania and a fossil lizard from the late Pliocene of northwestern Argentina. *J. Herpetol.* **46**, 104–119 (2012).
59. T. R. Simões *et al.*, The origin of squamates revealed by a Middle Triassic lizard from the Italian Alps. *Nature* **557**, 706–709 (2018).
60. V. R. Alifanov, Lizards of the family Arretosauridae Gilmore, 1943 (Iguanomorpha, Iguania) from the Paleogene of Mongolia. *Paleontol. J.* **46**, 412–420 (2012).
61. A. Čerňanský, R. Smith, T. Smith, A. Folie, Iguanian lizards (Acrodonta and Pleurodonta) from the earliest Eocene (MP 7) of Dormaal, Belgium: The first stages of these iconic reptiles in Europe. *J. Vertebr. Paleontol.* **42**, e2184696 (2023).
62. M. Augé, Past and present distribution of iguanid lizards. *Arquivos Mus. Nac. Rio Jan.* **65**, 403–416 (2007).
63. A. M. Albino, S. Brizuela, First record of squamate reptiles from the Oligocene of South America. *Alcheringa Australas. J. Palaeontol.* **38**, 412–421 (2014).
64. T. Westerhold *et al.*, An astronomically dated record of Earth's climate and its predictability over the last 66 million years. *Science* **369**, 1383–1387 (2020).
65. J. J. Eberle, D. R. Greenwood, Life at the top of the greenhouse Eocene world–a review of the Eocene flora and vertebrate fauna from Canada's High Arctic. *Geol. Soc. Am. Bull.* **124**, 3–23 (2012).
66. M. Steinthorsdottir *et al.*, The Miocene: The future of the past. *Paleoceanogr. Paleoclimatol.* **36**, e2020PA004037 (2021).
67. J. R. Macey *et al.*, Assembly of the eastern North American herpetofauna: New evidence from lizards and frogs. *Biol. Lett.* **2**, 388–392 (2006).
68. R. C. Stebbins, *Western Reptiles and Amphibians* (Houghton Mifflin Company Boston, MA, 2003).
69. M. Fan, S. A. Ayyash, A. Tripati, B. H. Passey, E. M. Griffith, Terrestrial cooling and changes in hydroclimate in the continental interior of the United States across the Eocene–Oligocene boundary. *GSA Bull.* **130**, 1073–1084 (2018).
70. D. I. Axelrod, Evolution of desert vegetation in western North America. *Contrib. Palaeontol. Carnegie Inst. Wash.* **590**, 215–306 (1950).
71. N. Mortimer *et al.*, Eocene and Oligocene basins and ridges of the Coral Sea-New Caledonia region: Tectonic link between Melanesia, Fiji, and Zealandia. *Tectonics* **33**, 1386–1407 (2014).
72. S. Meffre *et al.*, Basalts erupted along the Tongan fore arc during subduction initiation: Evidence from geochronology of dredged rocks from the Tonga fore arc and trench. *Geochem. Geophys. Geosystems* **13**, 1–17 (2012).
73. R. C. Blakey, W. D. Ranney, *Ancient Landscapes of Western North America: A Geologic History with Paleogeographic Maps* (Springer International Publishing, Cham, Switzerland, 2018).
74. M. Thiel, P. Haye, "The ecology of rafting in the marine environment-III. Biogeographical and evolutionary consequences" in *Oceanogr. Mar. Biol.: Annu. Rev.*, R. N. Gibson, R. J. A. Atkinson, J. D. M. Gordon, Eds. (Taylor and Francis, Boca Raton, 2006), pp. 323–429.
75. F. Hodel *et al.*, Eocene-Oligocene southwest Pacific Ocean paleoceanography new insights from foraminifera chemistry (DSDP site 277, Campbell Plateau). *Front. Earth Sci.* **10**, 998237 (2022).
76. E. O. Straume, A. Nummelin, C. Gaina, K. H. Nisancioglu, Climate transition at the Eocene-Oligocene influenced by bathymetric changes to the Atlantic-Arctic oceanic gateways. *Proc. Natl. Acad. Sci. U.S.A.* **119**, e2115346119 (2022).
77. J. R. Gibbons, "The biogeography and evolution of Pacific island reptiles and amphibians" in *Biology of Australasian Frogs and Reptiles*, G. Grigg, R. Shine, H. Ehmann, Eds. (Surrey Beatty & Sons Pty Ltd, Sydney, 1985), pp 125–142.
78. J. Temmen, A. Montenegro, S. Juras, J. S. Field, J. DeGrand, Floating the sweet potato to Polynesia: Considering the feasibility of oceanic drift for the prehistoric introduction of the sweet potato (*Ipomoea batatas*) to Pacific Islands. *Quat. Sci. Rev.* **295**, 107709 (2022).
79. E. J. Censky, K. Hodge, J. Dudley, Over-water dispersal of lizards due to hurricanes. *Nature* **395**, 553–554 (1998).
80. K. S. Norris, The ecology of the desert iguana *Dipsosaurus dorsalis*. *Ecology* **34**, 265–287 (1953).
81. B. H. Brattstrom, Body temperatures of reptiles. *Am. Midl. Nat.* **73**, 376–422 (1965).
82. G. Pregill, T. Worthy, A new iguanid lizard (Squamata, Iguanidae) from the Late Quaternary of Fiji, southwest Pacific. *Herpetologica* **59**, 57–67 (2003).
83. R. H. Cowie, B. S. Holland, Dispersal is fundamental to biogeography and the evolution of biodiversity on oceanic islands. *J. Biogeogr.* **33**, 193–198 (2006).

84. A. de Queiroz, The resurrection of oceanic dispersal in historical biogeography. *Trends Ecol. Evol.* **20**, 68–73 (2005).
85. J. R. Ali, M. Huber, Mammalian biodiversity on Madagascar controlled by ocean currents. *Nature* **463**, 653–656 (2010).
86. Y. Chaimanee *et al.*, Late middle Eocene primate from Myanmar and the initial anthropoid colonization of Africa. *Proc. Natl. Acad. Sci. U.S.A.* **109**, 10293–10297 (2012).
87. D. L. Rowe, K. A. Dunn, R. M. Adkins, R. L. Honeycutt, Molecular clocks keep dispersal hypotheses afloat: Evidence for trans-Atlantic rafting by rodents. *J. Biogeogr.* **37**, 305–324 (2010).
88. T. Gamble *et al.*, Coming to America: Multiple origins of New World geckos. *J. Evol. Biol.* **24**, 231–244 (2011).
89. S. Carranza, E. N. Arnold, Investigating the origin of transoceanic distributions: Mtdna shows *Mabuya* lizards (Reptilia, Scincidae) crossed the Atlantic twice. *Syst. Biodivers.* **1**, 275–282 (2003).
90. N. Vidal, A. Azvolinsky, C. Cruaud, S. B. Hedges, Origin of tropical American burrowing reptiles by transatlantic rafting. *Biol. Lett.* **4**, 115–118 (2008).
91. R. C. Bell *et al.*, Overseas dispersal of *Hyperolius* reed frogs from Central Africa to the oceanic islands of São Tomé and Príncipe. *J. Biogeogr.* **42**, 65–75 (2015).
92. R. A. Pyron, Biogeographic analysis reveals ancient continental vicariance and recent oceanic dispersal in amphibians. *Syst. Biol.* **63**, 779–797 (2014).
93. R. G. Reynolds *et al.*, Phylogenomics and historical biogeography of West Indian rock iguanas (genus *Cyclura*). *Mol. Phylogenet. Evol.* **174**, 107548 (2022).
94. K. C. Pounder *et al.*, Testing for hybridisation of the critically endangered *Iguana delicatissima* on Anguilla to inform conservation efforts. *Conserv. Genet.* **21**, 405–420 (2020).
95. J. R. Ali, M. Vences, Mammals and long-distance over-water colonization: The case for rafting dispersal; the case against phantom causeways. *J. Biogeogr.* **46**, 2632–2636 (2019).
96. B. R. Karin, M. Metallinou, J. L. Weinell, T. R. Jackman, A. M. Bauer, Resolving the higher-order phylogenetic relationships of the circumtropical *Mabuya* group (Squamata: Scincidae): An out-of-Asia diversification. *Mol. Phylogenet. Evol.* **102**, 220–232 (2016).
97. J. T. Carlton *et al.*, Tsunami-driven rafting: Transoceanic species dispersal and implications for marine biogeography. *Science* **357**, 1402–1406 (2017).
98. J. R. Ali, S. B. Hedges, Colonizing the Caribbean: New geological data and an updated land-vertebrate colonization record challenge the GAARlandia land-bridge hypothesis. *J. Biogeogr.* **48**, 2699–2707 (2021).
99. R. G. Gillespie, G. K. Roderick, Arthropods on islands: Colonization, speciation, and conservation. *Annu. Rev. Entomol.* **47**, 595–632 (2002).
100. K. V. Klaus, N. J. Matzke, Statistical comparison of trait-dependent biogeographical models indicates that Podocarpaceae dispersal is influenced by both seed cone traits and geographical distance. *Syst. Biol.* **69**, 61–75 (2020).
101. R Core Team, *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, 2023).
102. N. Mongiardino Koch, Phylogenomic subsampling and the search for phylogenetically reliable loci. *Mol. Biol. Evol.* **38**, 4025–4038 (2021).
103. B. C. Faircloth, PHYLUCE is a software package for the analysis of conserved genomic loci. *Bioinformatics* **32**, 786–788 (2016).
104. J. Alföldi *et al.*, The genome of the green anole lizard and a comparative analysis with birds and mammals. *Nature* **477**, 587–591 (2011).
105. S. Singhal, M. Grundler, G. Colli, D. L. Rabosky, Squamate conserved loci (Sq CL): A unified set of conserved loci for phylogenomics and population genetics of squamate reptiles. *Mol. Ecol. Resour.* **17**, e12–e24 (2017).
106. A. Corl, H. Ellegren, Sampling strategies for species trees: The effects on phylogenetic inference of the number of genes, number of individuals, and whether loci are mitochondrial, sex-linked, or autosomal. *Mol. Phylogenet. Evol.* **67**, 358–366 (2013).
107. A. K. Westfall *et al.*, A chromosome-level genome assembly for the Eastern Fence Lizard (*Sceloporus undulatus*), a reptile model for physiological and evolutionary ecology. *GigaScience* **10**, 1–17 (2021).
108. K. R. Petersen, D. A. Streett, A. T. Gerritsen, S. S. Hunter, M. L. Settles, "Super deduper, fast PCR duplicate detection in fastq files" in *Proceedings of the 6th ACM Conference on Bioinformatics, Computational Biology and Health Informatics* (2015), pp. 491–492.
109. H. Li, R. Durbin, Fast and accurate short read alignment with Burrows-Wheeler transform. *Bioinformatics* **25**, 1754–1760 (2009).
110. P. Danecek *et al.*, Twelve years of SAMtools and BCFtools. *GigaScience* **10**, giab008 (2021).
111. Broad Institute, Picard toolkit, GitHub repository. (2019), https://broadinstitute.github.io/picard/.
112. A. McKenna *et al.*, The genome analysis toolkit: A MapReduce framework for analyzing next-generation DNA sequencing data. *Genome Res.* **20**, 1297–1303 (2010).
113. T. S. Korneliussen, A. Albrechtsen, R. Nielsen, ANGSD: Analysis of next generation sequencing data. *BMC Bioinformatics* **15**, 356 (2014).
114. S. Andrews, FastQC: A quality control tool for high throughput sequence data. http://www.bioinformatics.babraham.ac.uk/projects/fastqc/. Accessed 19 December 2022.
115. K. Okonechnikov, A. Conesa, F. García-Alcalde, Qualimap 2: Advanced multi-sample quality control for high-throughput sequencing data. *Bioinformatics* **32**, 292–294 (2016).
116. P. Ewels, M. Magnusson, S. Lundin, M. Käller, MultiQC: Summarize analysis results for multiple tools and samples in a single report. *Bioinformatics* **32**, 3047–3048 (2016).
117. K. Katoh, D. M. Standley, MAFFT multiple sequence alignment software Version 7: Improvements in performance and usability. *Mol. Biol. Evol.* **30**, 772–780 (2013).
118. S. Capella-Gutiérrez, J. M. Silla-Martínez, T. Gabaldón, trimAl: A tool for automated alignment trimming in large-scale phylogenetic analyses. *Bioinformatics* **25**, 1972–1973 (2009).
119. B. Q. Minh *et al.*, IQ-TREE 2: New models and efficient methods for phylogenetic inference in the genomic era. *Mol. Biol. Evol.* **37**, 1530–1534 (2020).
120. C. Zhang, M. Rabiee, E. Sayyari, S. Mirarab, ASTRAL-III: Polynomial time species tree reconstruction from partially resolved gene trees. *BMC Bioinformatics* **19**, 153 (2018).
121. C. Zhang, S. Mirarab, Weighting by gene tree uncertainty improves accuracy of quartet-based species trees. *Mol. Biol. Evol.* **39**, msac215 (2022).
122. A. Stamatakis, RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* **30**, 1312–1313 (2014).
123. J. Douglas, R. Zhang, R. Bouckaert, Adaptive dating and fast proposals: Revisiting the phylogenetic relaxed clock model. *PLOS Comput. Biol.* **17**, e1008322 (2021).
124. A. Rambaut, A. J. Drummond, D. Xie, G. Baele, M. A. Suchard, Posterior summarization in Bayesian phylogenetics using Tracer 1.7. *Syst. Biol.* **67**, 901–904 (2018).
125. S. G. Scarpetta *et al.*, BioProject ID PRJNA1217946. Sequence Read Archive. https://www.ncbi.nlm.nih.gov/sra/PRJNA1217946. Deposited 28 February 2025.
126. S. G. Scarpetta *et al.*, Iguanas rafted more than 8,000 km from North America to Fiji (Supporting Information). Dryad. https://doi.org/10.5061/dryad.4tmpg4fjr. Deposited 26 February 2025.