Heads. *Zool. Res. Divers. Conserv.* 2025, 2(4): 250−261
https://doi.org/10.24272/j.issn.2097-3772.2025.034
https://cstr.cn/32249.14.zrdc.2025.034

ZRDC | Zoological Research: Diversity and Conservation

Review Open Access

The incredible, enigmatic, fantastical distribution of iguanas, and the meaning of allopatry among high-level squamate clades

Michael Heads[1,*]

[1] *Buffalo Museum of Science*, 1020 *Humboldt Parkway*, *Buffalo*, *NY* 14211-1293, *USA*

ABSTRACT

Iguanas and their relatives comprise a group, Pleurodonta, that includes over 1 000 species. Nearly all are restricted to the Americas, but there are also species in Fiji and in Madagascar. Recent studies have discussed various dispersal theories for iguanas, but they have not considered a simple vicariance model. This proposes that a global ancestor differentiated, *in situ*, into Pleurodonta (mainly in the Americas) and their sister, Acrodonta (mainly in Africa, Asia, and Australia). The distribution of iguanas is often regarded as anomalous and puzzling. But its components, including trans-tropical Pacific connections, are quite normal and are repeated in different, unrelated groups of plants and animals. The pattern in iguanas is the result of a phylogenetic break in the south-west Pacific in a global ancestor, resulting in Pleurodonta and Acrodonta. This was followed by differentiation of their families and by large-scale extinction in the central Pacific. The extinction was caused by the cooling and subsidence of the seafloor by thousands of meters, during which large numbers of high, forested islands were reduced to low atolls and submerged seamounts.

Keywords: Biogeography; Dispersal; Metapopulation; Squamata; Tectonics; Vicariance

INTRODUCTION

Consider a clade endemic to areas A and B. It may have dispersed from one of the areas to the other. But it may also have evolved *in situ*, in both areas. The latter can occur if an ancestor present in A, B and a third area, C, differentiates, with one descendant evolving in A+B, and one in C. This concept, termed vicariance, was introduced to mainstream discussion in the 1970s and became popular, as it provides a simple explanation for allopatry. During vicariance, a widespread common ancestor differentiates *in situ*, and there is no dispersal. In contrast, what could be termed the "colonial" biogeography of nineteenth century Europe proposed that all distributions are brought about by dispersal outwards from an original center and colonization of new territory. In an influential passage, Darwin wrote:

"Undoubtedly there are many cases of extreme difficulty in understanding how the same species could possibly have migrated from some one point to the several distant and isolated points where now found. Nevertheless, the simplicity of the view that each species was first produced within a single region captivates the mind. He who rejects it, rejects the *vera causa* [true cause] of ordinary generation with subsequent migration, and calls in the agency of a miracle" (Darwin, 1859, p352).

This concept of "origin followed by migration" remained the standard explanation for allopatry over the next century. Ernst Mayr, a leading authority in 20th century biogeography, wrote: "Quite obviously, except for a few extreme [i.e. local] endemics, every species is a colonizer because it would not have the range it has, if it had not spread there by range expansion, by 'colonization', from some original place of origin." (Mayr, 1965, p203). Following the introduction of vicariance theory, Mayr (1982) responded critically. He wrote that some textbooks now showed "a widespread species cut in half by a geographical barrier", i.e. vicariance. However, he argued that "more detailed studies... suggest a different solution" (Mayr, 1982, p601), namely speciation by founder dispersal. Levin (2000) agreed; all new species, following their origin, expand "from narrow geographical centers…". In this way, colonial biogeography explained both distribution and speciation by dispersal and radiation from a center.

CHANCE DISPERSAL VS NORMAL DISPERSAL

In colonial biogeography, allopatry is explained by chance dispersal, a process also known as long-distance dispersal, jump dispersal, lineage dispersal, macroevolutionary dispersal, peripatric speciation, and budding speciation (Hackel & Sanmartin, 2021). Chance dispersal is a mode of

Received: 19 December 2025; Accepted: 13 January 2026; Online: 25 January 2026

*Corresponding author, E-mail: m.j.heads@gmail.com

speciation. It is not observed and is a theoretical, inferred process. It is thought to be extremely rare, often occurring only once in a group's history, which may have lasted for tens of millions of years. Chance dispersal is thought to take place, not by the group's usual, known means of dispersal, but by means that are "occasional" (Darwin, 1859) or "non-standard" (Higgins et al., 2003) and, therefore, difficult to investigate. Long-distance dispersal events are unique, random occurrences that can happen at any time, in any direction and over any distance, and are not related to any particular biological or geological factor.

In contrast with chance dispersal, normal dispersal is observed every day, as in the flight of birds or the invasion of weeds into newly cleared land. It does not lead to speciation. It occurs in all organisms and depends on the group's standard means of dispersal. Theories of chance dispersal are often controversial, but normal dispersal is accepted by all authors.

As Hackel & Sanmartin (2021) stressed, chance, or lineage, dispersal involves speciation and is not the same process as normal, observed dispersal. Normal dispersal also includes the process that paleontologists term "geodispersal" – the simultaneous range expansion of multiple clades and whole regional biotas caused by geological or climatic change (not chance). Rather than being a mode of allopatric speciation, the population mobilism involved in geodispersal will inhibit allopatric speciation.

How does observed dispersal in *individuals* relate to *clade* distribution? Every individual organism has dispersed to its present location. Because of this observation, it has been assumed that a clade must develop its range in the same way (Mayr, 1965, 1982). But in a vicariance event, the new distribution does not develop by physical movement, but by the cessation (or at least slowing) of dispersal and by evolution *in situ*.

THE PROBLEM OF THE FIJIAN IGUANAS

Members of the iguana family, Iguanidae, are widespread in the Americas, but there are also living populations in Fiji. The Fijian iguanas include the extant genus, *Brachylophus*, with four allopatric species in Fiji, and one extinct species in nearby Tonga (Fisher et al., 2017). Fiji also has another, distinctive fossil iguanid, *Lapitiguana* (Pleistocene) (Pregill & Worthy, 2003).

Brachylophus in Fiji occurs 8 500 km from its putative sister, *Dipsosaurus* of NW Mexico and SW United States. The usual explanation is that iguanas have rafted from America to Fiji, and this is often presented as an exemplary case of long-distance dispersal (Cogger, 1974; Gibbons, 1981; Zug, 1991; Keogh et al., 2008; Townsend et al., 2011; Scarpetta et al., 2025a). Scarpetta et al. (2025a) began by acknowledging the work of Mayr (1954) and others on the importance of long-distance, trans-oceanic dispersal and founder-event speciation. They described the rafting of iguanas to Fiji as "the greatest known long-distance oceanic dispersal event in the history of terrestrial vertebrates…". The distance would involve a journey time of around a year (Ali & Fritz, 2025) and mean that the inferred dispersal is "extraordinary" (Keogh et al., 2008), "puzzling" (Simões & Pyron, 2021), "enigmatic" and "incredible" (Scarpetta et al., 2025a). Instead, it is argued here that the distribution is completely normal, and that the "extraordinary" model was proposed only because a much simpler alternative was not considered.

DISTRIBUTION AND DIVERSITY IN IGUANIA, COMPRISING PLEURODONTA AND ACRODONTA

Brachylophus is a member of Iguanidae, which is itself part of the Pleurodonta. This large group (~1 000 species, 12 families) is found mainly in the New World and is sister to the mainly Old World Acrodonta (~800 species; Agamidae and Chamaeleonidae) (Figure 1A). The two make up the Iguania, a major group that includes about a quarter of all lizard species and forms one of 7 main clades of squamates (others include skinks, geckos and snakes).

Pleurodonta and Acrodonta are allopatric, except for minor overlap around their mutual boundary. In living groups, overlap is restricted to Madagascar, while fossils suggest additional marginal overlap in western Europe, the Gobi Desert, and the western US (Figure 1A).

The fossil record of Iguania, and difficulties with fossil identification

There are many interesting fossils of Iguania, but identifying them and placing them in a phylogeny is often difficult. Even with living material, morphological studies of squamates did not recognize many new groupings that have been proposed in molecular work and are now widely accepted. Examples include the trans-Atlantic lizard family Phyllodactylidae, the trans-Indian Ocean snake family Pseudaspididae (in southern Africa and SE Asia), and the trans-Bay of Bengal snake family Pareidae (O'Shea, 2021, 2023). Problems of identification based on morphology and traditional morphological homologies are multiplied when dealing with fossils, especially fragmentary and older material.

Within Iguania, pleurodont and acrodont dentition are features of Pleurodonta and Acrodonta, respectively, but both conditions also occur in other squamates, and identifying early fossil iguanians is challenging. For example, *Yaksha* (Burmese amber, Cretaceous) was originally identified as a stem chameleon, a member of Acrodonta. Daza et al. (2016) wrote that: "Twelve specimens… preserve fine details of soft tissue and osteology, and high-resolution x-ray computed tomography permits detailed comparisons to extant and extinct lizards. The extraordinary preservation allows several specimens to be confidently assigned to groups including stem Gekkota and stem Chamaeleonidae". Nevertheless, a subsequent study accepted that *Yaksha* is an amphibian (Daza et al., 2020). Likewise, *Gueragama* from Brazil was identified as a member of Acrodonta (Simões et al., 2015), but Evans (2022, p14) considered this "unlikely".

Most fossils currently identified as Pleurodonta and Acrodonta occur within the extant range of their group. There are also two assemblages of extralimital fossil Pleurodonta (Figure 1A). The first is a diverse, Cretaceous complex from the Gobi Desert (Gobiguania; Scarpetta, 2024). The second comprises *Geiseltaliellus* (Corytophanidae), *Cadurciguana*, *Pseudolacerta*, and *Bifurcodentodon* from western Europe, with the last genus "differing from all fossil and extant taxa of Pleurodonta by a unique and complex tooth morphology" (Čerňanský et al., 2022).

Acrodonta fossils outside the current range of the group include Cretaceous material from the Gobi (Scarpetta, 2024), slight extralimital extensions north in western Europe, and *Tinosaurus* from Wyoming (Eocene), as well as Europe and central, south and east Asia (Čerňanský, et al., 2022). *Tinosaurus* appears to be a widespread invasive. The

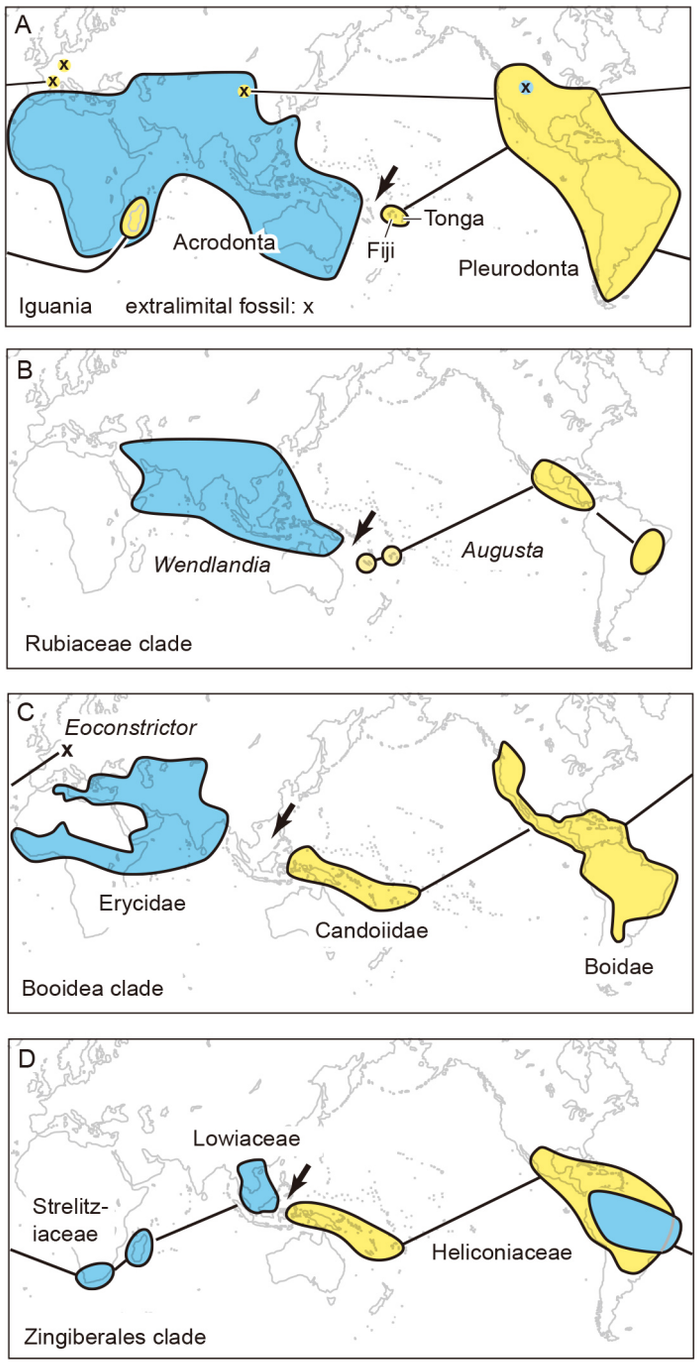

Figure 1 Distribution of some trans-Pacific groups and their sisters

Arrows indicate main breaks (nodes). A: Distribution of Iguania, comprising Pleurodonta and Acrodonta; B: Distribution of clade in Rubiaceae: *Augusta s.l.* (incl. *Lindenia*) sister to *Wendlandia (*incl. *Guihaiothamnus)* (Xie et al., 2014); C: Distribution of a clade in booid snakes. The fossil *Eoconstrictor* is allied with Boidae; D: Distribution of a clade in Zingiberales (monocots). Heliconiaceae have a trans-Pacific distribution and a strong concentration of species in Colombia (Mabberley, 2017).

localized, marginal overlap of Acrodonta and Pleurodonta in the north can be explained by secondary range expansion of a relatively small number of species by normal dispersal, following the differentiation of the two groups.

The evidence for trans-Pacific dispersal in iguanas: analyses of phylogeny in space and time

Scarpetta et al. (2025a) presented results from two sets of calculations supporting trans-Pacific dispersal in iguanas, namely, "biogeographic analyses that favor long-distance dispersal from North America over alternative hypotheses…" and "the late Paleogene divergence time between *Brachylophus* and *Dipsosaurus*". Ali & Fritz (2025) regarded these as "compelling", but a closer examination shows that both are problematic.

In their formal biogeographic analyses, Scarpetta et al. (2025a) proposed North America as the most probable ancestral range of Fijian iguanas. But the "ancestral area" algorithms that were used are flawed. In particular, they are heavily biased towards finding centers of origin in areas with basal paraphyletic grades (such as America for the iguanas), although a vicariance history without chance dispersal is much simpler (Heads et al., 2025). In contrast with the "ancestral

area" algorithms, the model used here assumes that allopatry indicates vicariance, and overlap indicates (normal) dispersal. There is no need to invoke long-distance dispersal as a mode of speciation.

The chronological analysis of Scarpetta et al. (2025a) calculated an Oligocene date for *Brachylophus*, but it was fossil-calibrated, and so the date is an estimate of minimum possible age only. Fossil-calibrated clade ages (minimums) are often treated, illogically, as maximums and then used to rule out vicariance (Heads, 2012a), for example, in the Madagascar Pleurodonta (Welt & Raxworthy, 2022). In a similar case from Acrodonta, Tolley & Townsend (2013) wrote that "Oceanic dispersal has emerged as an important factor contributing to biogeographic patterns in numerous taxa. Chameleons are a *clear example of* this, as they are primarily found in Africa and Madagascar, but the age of the family is post-Gondwanan break-up … ". Nevertheless, the family age was fossil-calibrated and provides a minimum estimate only, so it cannot be said to post-date Gondwana.

Problems with chance dispersal theory in iguanids and in general

In support of trans-Pacific dispersal in iguanas, Scarpetta et al. (2025a) cited many clades of terrestrial vertebrates that "have been demonstrated to cross oceanic barriers … including thousands of kilometers across the Atlantic or Indian oceans". But these events of lineage dispersal are theoretical only and have not been observed. In contrast, individuals in groups such as albatrosses are observed to cross the oceans, regularly. Despite this movement of individuals, each seabird *species* has its own discrete breeding range that is often quite localized. Thus, even in albatrosses, with their great powers of dispersal, differentiation can result if a breeding range is pulled apart, for example, by the opening of an ocean basin. One example is the pair *Diomedea sanfordi* and *Diomedea epomophora*, separated by the late Cretaceous Great South Basin in southern New Zealand. The differentiation has developed despite–not because of–the great means of dispersal in these birds.

As with the albatrosses, iguanas can be highly mobile, and the great swimming ability of the Galapagos species is well-known. *Iguana iguana* was introduced into the northern Lesser Antilles and has become invasive there. In one episode, animals were observed colonizing Anguilla on a floating mass of vegetation following a hurricane, perhaps from Montserrat or Guadeloupe, 250 km away (Censky et al., 1998). This demonstrated over-water rafting as a means of populating marine islands. But it does not demonstrate "chance" or "lineage dispersal", which is very rare (just once in 30 million years for the Fijian iguanas). Such rare events differ from the normal ecological processes which are observed every day, or at least every hurricane season, but do not lead to speciation. This would require a truly unusual event.

Several "textbook examples" of dispersal to the Galápagos Archipelago–iguanids, giant tortoises, phyllodactylid geckos, and colubrid snakes–have been cited as cases of trans-oceanic dispersal (Ali & Fritz, 2025). But this overlooks the discovery that the Galápagos hotspot has been creating islands for much longer than was thought (since Early Cretaceous). It also neglects an alternative, metapopulation-vicariance model for the Galápagos biota that was proposed in light of this (Heads & Grehan, 2021). Evidence from the Galápagos biota as a whole indicates that the endemics, including the squamates, evolved there from earlier, generalised ancestors, as long-lived metapopulations surviving at a long-lived center of volcanism.

In many groups, the normal, observed means of dispersal conflict with the proposed "chance dispersal" events, as the former are either not effective enough or too effective. The epic voyage of the iguanas from America to Fiji is often acknowledged as enigmatic, puzzling or even incredible, as its magnitude seems incompatible with the group's usual behavior. Iguanas may raft for 250 km in the Caribbean, but this does not mean they can raft 8 500 km across the Pacific. While some trans-Pacific squamates, such as iguanids, show at least some effective dispersal in maritime settings, others do not. The blind skinks, Dibamidae, have a trans-Pacific distribution, occurring from Southeast Asia to New Guinea (fossil in Mongolia) and in Mexico. Townsend et al. (2011) concluded that the group is "a striking example of a long-distance dispersal event in a taxon that otherwise appears to have exceptionally low vagility". The animals are blind, limbless and burrow in soil, and the species are highly localized microendemics.

The standard theory that iguanas were able to disperse westward for thousands of kilometers across the Pacific raises the question: why did they not disperse west of Fiji? Likewise, why are there no Acrodonta east of the Solomon Islands, although they are present on Madagascar and hundreds of other islands around the Indian Ocean? In dispersal theory, these are two separate questions, with Pleurodonta and Acrodonta each having their own center of origin. But in vicariance theory the answer to both questions is the same. The node in Iguania between the Solomon Islands (with Acrodonta) and Fiji (with Pleurodonta) is one part of the global break in a common ancestor, and others are located between America and Africa, and around Madagascar. All these are areas of large-scale deformation in the Earth's crust.

The origin of Acrodonta and Pleurodonta by vicariance rather than radiation

The main issue in the biogeography of Iguania lies in explaining the overall global allopatry of the group's two components, Acrodonta and Pleurodonta, living and fossil. A dispersal model explains allopatry by unique journeys or jumps by a few colonists into new territory. The colonists evolve into a new group which disperses outwards, eventually meeting the ancestor and establishing allopatry.

In contrast, a vicariance model explains allopatry by phylogenetic breaks in a global ancestor. The origin of northern hemisphere and southern hemisphere sister groups by vicariance in a global ancestor is acknowledged in groups such as the cypresses, with subfamily Cupressoideae in the north and its sister Callitroideae in the south (Mao et al., 2012). Similar vicariance in a global ancestor could produce Pleurodonta, mainly in the Americas, and Acrodonta, mainly in Africa-Eurasia. In contrast, Iguania as a whole (Acrodonta+Pleurodonta) are widespread globally, and their sister, Anguimorpha, is too. In this case, the overlap is almost complete, and it probably indicates large-scale dispersal in one or both groups (sympatric differentiation is less likely).

It has been suggested that Acrodonta and Pleurodonta evolved by radiation, with each group having spread out from its own, localized center of origin (Blankers et al., 2013). But centers of origin and radiations are unnecessary if both groups originated by vicariance. In a vicariance model, a lineage of

generalized Iguania lizards in the Fiji region evolved there into pre- and then proto-Pleurodonta, then into generalized iguanids and finally *Brachylophus* and the fossil *Lapitiguana*. There is no need for fully-fledged Pleurodonta, let alone iguanids or *Brachylophus*, to have migrated to the region from anywhere else.

In a vicariance model, the phylogenetic-biogeographic break between Pleurodonta in Fiji and Acrodonta in the Solomon Islands is the key to explaining the family distribution boundaries. In this model, the Pleurodonta and Acrodonta boundary is much older than the particular taxa that now define it, namely *Brachylophus* in Fiji and *Hypsilurus* in the Solomon Islands, and it is also much older than the current islands in these archipelagoes.

AMERICA – FIJI CONNECTIONS: A STANDARD PATTERN

Scarpetta et al. (2025a) wrote that the occurrence of iguanas on Fiji is "anomalous", but disjunct Fiji – America connections are well-documented in other groups, including seven mapped in Figures 1, 2.

The trans-Pacific groups show major breaks (arrows in the figures) with sisters to the west of Fiji. Scarpetta et al. (2025a) also suggested that the America–Fiji connection in iguanas is unique among terrestrial vertebrates. However, even in squamates there is another example matching the iguanids. The boas (Boidae), an American group of terrestrial snakes, are sister to Candoiidae, distributed from the Moluccas to Fiji and Samoa (Figure 1C; Burbrink et al., 2020; Palci et al., 2024).

The pantropical mangrove *Rhizophora* (Rhizophoraceae) (Figure 2A) comprises one trans-Pacific and trans-Atlantic clade, and another based around the Indian Ocean (Takayama, 2021). Overlap of the clades, suggesting local range expansion in one or both, is restricted to New Caledonia and Fiji. Likewise, in a clade of the mahogany family, Meliaceae, the trans-Pacific component and its SE Asian sister overlap only in New Caledonia, Vanuatu and Fiji (Figure 2B).

The only lianes in the family Violaceae form a well supported, trans-Pacific clade (bright yellow in Figure 2C) that forms part of a broader trans-Pacific group (pale yellow in Figure 2C) (Wahlert et al., 2014). Its sister group is not resolved, but it is likely to include *Pigea* ("*Hybanthus enneaspermus* group").

In the fan palm tribe Trachycarpeae (Arecaceae), *Pritchardia* of the central Pacific is sister to a tropical America pair (Figure 2D). This trans-Pacific clade is sister to the rest of the tribe, concentrated along the old Tethyan basins.The two overlap only in the Caribbean region. *Pritchardia* differs from the others groups in Figures 1, 2, as its members, which can survive the harsh ecology of small limestone islets, are in Fiji but have also persisted in the central Pacific, on the Cook, Society and Hawaiian islands.

Other trans-tropical disjunctions between Fiji and South America are seen in the spider *Masteria* (Heads, 2014) and the tree *Retrophyllum* (Podocarpacea) (Heads, 2014). In another example, a group of Proteaceae present in New Caledonia (*Kermadecia* and *Sleumerodendron*), Vanuatu and Fiji (*Turrillia*) is sister to *Euplassa* of tropical South America (Pillon et al., 2023).

Age of trans-Pacific groups

Molecular clock studies would probably show that the America–Fiji disjunctions shown in Figures 1, 2 have different ages in the different groups. In fact, the component clades in all biogeographic patterns show a range of dates that form a curve, and in well-studied areas with hundreds of dated clades, such as New Zealand, the curve becomes "surprisingly smooth" (McCulloch & Waters, 2019). This means that either vicariance never occurs, or that the clock ages are wrong (at least if they treated as actual clades ages rather than estimates of minimum age). All authors now accept that vicariance occurs, at least sometimes, and so the second option appears more reasonable. It is also consistent with Klopfstein's (2021) critique of molecular clock studies:

"Until such a time when alternative approaches to dating become fully fledged …, I suggest shifting the objective of node dating to those aspects of the approach that can be scientifically justified: minimum ages of particular nodes as based on the fossil record. While we lose some of the explanatory power of traditionally dated trees, I would argue that this is an acceptable price to pay for increased scientific rigour."

TERRESTRIAL GROUPS IN OCEANIC SETTINGS SURVIVE AS DYNAMIC METAPOPULATIONS AT CENTERS OF TECTONISM AND VOLCANISM

Ali & Fritz (2025) discussed the Fiji iguanas and argued that oceanic islands in general "have never had terrestrial connections with the continents, hence their land-bound biotic components had to disperse over water to reach them". Likewise, Welt & Raxworthy (2022) proposed that the ability of iguanas to survive long journeys overwater "is demonstrated by … their distribution on many isolated volcanic islands … ". Iguanas on young volcanic islands, or young volcanic strata in general, must have colonized from somewhere. But exactly where they have dispersed from is problematic. A metapopulation vicariance model proposes that new volcanic islands are colonized from former islands nearby. Island populations do not necessarily result from long journeys if there were other former islands in the region, and this is almost inevitable at the subduction zones, divergent margins, hotspots, lithospheric cracks, hotlines, and larger regions of thermal-isotopic anomalies where most oceanic islands are produced. Metapopulation survival at these sites requires normal, observed overwater dispersal of, say, tens of kilometers, not thousands, and as long as new islands are produced, an oceanic metapopulation can survive *in situ* indefinitely.

The long-term survival of many groups of terrestrial metapopulations in volcanic island systems explains the fact that many island endemics are older than their island (Heads, 2018). In contrast, a "colonist" model proposes that archipelago organisms cannot survive *in situ* as a metapopulation by dispersing tens of kilometers over water, but that they can disperse over water for 1 000s km to reach the archipelago in the first place, and this is not a convincing argument.

The presence of Pleurodonta in Madagascar (Figure 1A) has been explained by overwater dispersal from South America to Madagascar (~5 000 km), because of the lack of "continuous subaerial connection" (Welt & Raxworthy, 2022). But continuous land connection is not necessary for oceanic metapopulation survival and vicariance in many terrestrial species. Continuous land would be needed only for organisms which cannot undergo even small-scale dispersal across

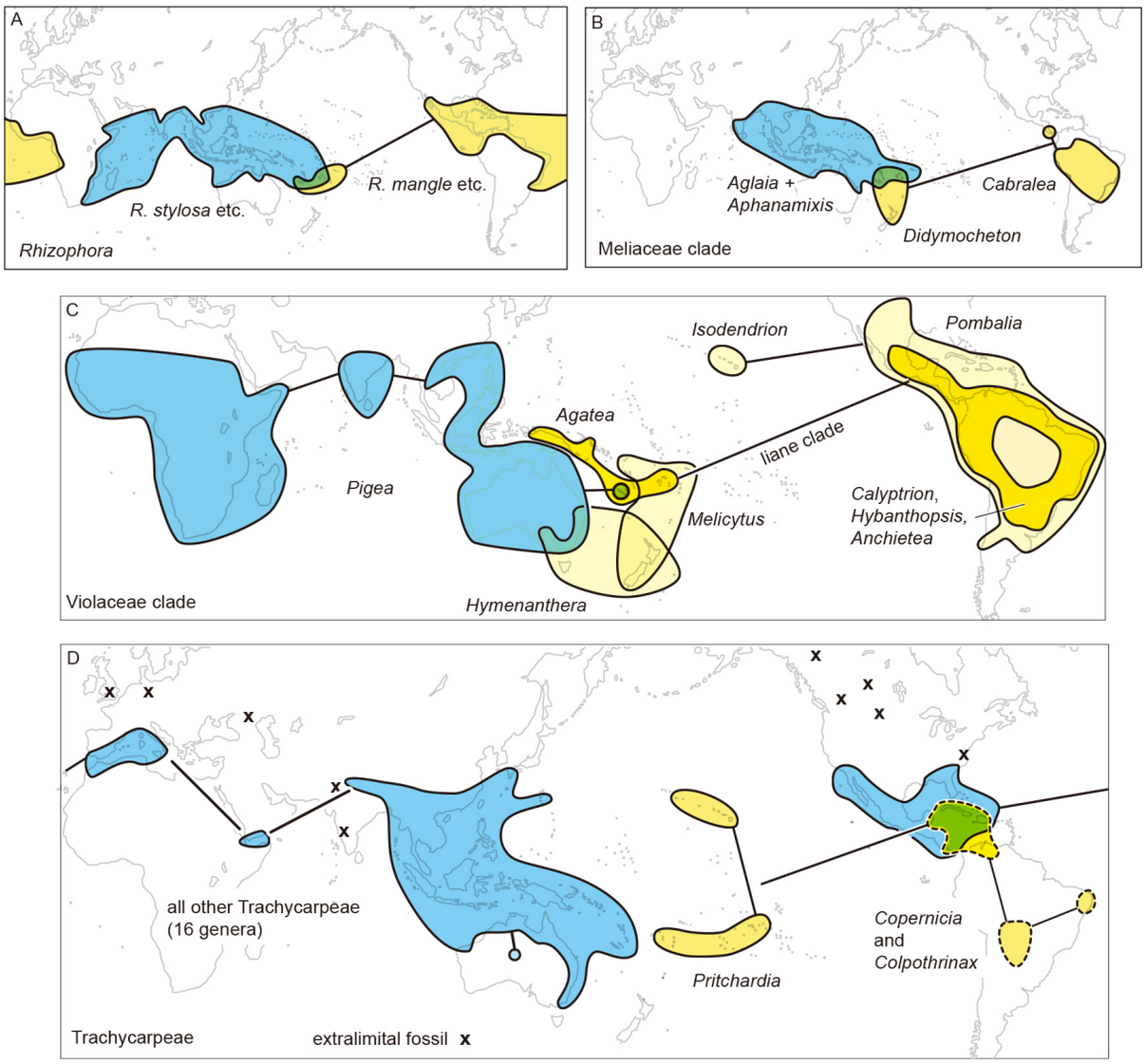

Figure 2 Distribution of some trans-Pacific clades and their sisters

A: Distribution of *Rhizophora* (Rhizophoraceae) and its two main clades (Takayama et al., 2021); B: Distribution of the lianescent clade of Violaceae (*Agatea*, *Anchietea*, *Calyptrion* (formerly *Corynostylis*) and *Hybanthopsis*) (bright yellow), their immediate relatives (pale yellow), and the possible sister of this trans-Pacific group, *Pigea* (blue) (Wahlert et al., 2014; Heads, 2014); C: Distribution of a clade in Meliaceae (Heads, 2019); D: Distribution of Trachycarpeae (Arecaceae). *Pritchardia*, *Copernicia* and *Colpothrinax* (yellow) form a clade that is sister to the remaining 18 genera (blue) (Yao et al., 2023).

water to new islands as they appear.

Likewise, the colonial model for iguanas proposes that *either* there was continuous land between Fiji and America, *or* an 8 000 km long-distance dispersal event took place (Ali & Fritz, 2025). But this overlooks the large-scale volcanism that has occurred through the South Pacific since the Mesozoic (allowing metapopulation survival) and ocean floor subsidence in the central Pacific (causing metapopulation extinction).

Modern geologists do not accept former continental crust in the Pacific, but metapopulations can survive in regions of oceanic volcanism on volcanic islands in the same way they survive in dynamic habitat islands on continents. In a vicariance model, ephemeral volcanic islands act as habitat allowing regional survival of metapopulations, not as "stepping-stones" facilitating directional migration across an ocean.

Scarpetta et al. (2025a) wrote that: "A plausible theory for the origin of iguanas on Fiji must be compatible with the geologic history of the islands. Fiji arc magmatism was initiated by subduction of the Pacific Plate under the Indo-Australian plate during the late Eocene c. 39 Ma." But this focus on the *current* islands neglects volcanism in the region before modern Fiji existed – subduction of the Pacific plate (and volcanism) in the region did not begin at 39 Ma. One model proposed that subduction along the New Guinea – New Caledonia subduction zone began between 90 and 60 Ma (van de Lagemaat & van Hosbergen, 2024).

Metapopulations of terrestrial organisms in volcanic archipelagos colonize new volcanics from older ones. For this reason, the age of the current Fiji Islands is not directly relevant to the history of their endemics. In the same way, a regional endemic that survives as a metapopulation inhabiting ephemeral puddles is much older than any of the individual puddles. The iguanas' rafting and swimming ability is part of a suite of features that enables their survival as a dynamic metapopulation in a region of volcanism and rifting. In the

Pacific and in other areas of oceanic volcanism, many terrestrial organisms have survived for tens of millions of years with no need for continental crust or continuous land.

GENERATION OF OLD ENDEMICS ON YOUNG ISLANDS BY METAPOPULATION VICARIANCE

It is often assumed that the main cause of vicariance is continental breakup by seafloor spreading. But many other tectonic and geomorphological processes, at different scales, can cause vicariance. Far from the continents, in the oceans, widespread terrestrial and reef metapopulations can undergo vicariance if they are separated, for example by rifting of island arcs or subsidence of archipelagos. For example, the Solomon Islands, Vanuatu, Fiji and Tonga are sections of an active arc that has been pulled apart by Cenozoic rifting, and the region provides classic examples of metapopulation vicariance (Heads, 2018). The fracturing of the island arc provides a modern analogue of the original Pleurodonta *vs* Acrodonta break, which occurred in the same region but much earlier (both groups have Cretaceous fossils).

Brachylophus of Fiji and its sister *Dipsosaurus* of SW USA and northern Mexico differ greatly from their sister, which comprises all other Iguanidae (Scarpetta et al., 2025a), and many other island squamates are also phylogenetically distinctive. For example, the Bolyeridae of Round Island off Mauritius are sister to all other Pythonoidea, a worldwide clade of 13 families; Cyclocoridae of the Philippines are sister to all other Elapoidea, a worldwide clade of seven families (Weinell et al., 2024); Leiocephalidae of the Greater and Lesser Antilles are sister to all other Pleurodonta, widespread in the Americas (Figure 1A). In a dispersal model, these groups present the same problems as Fijian iguanas: where was their center of origin, and which route did they use to colonise their islands? A metapopulation-vicariance model is much simpler: the island endemics evolved in their respective regions.

Fiji – Solomon Islands as both a main break zone and a center of endemism

In a metapopulation-vicariance model, the problem is not to explain how iguanids got from America to Fiji, but why the main phylogenetic break in Iguania is located in the region currently occupied by Fiji and the Solomon Islands. Deformation at the Pacific–Australia plate margin could provide a mechanism. Other global groups with their primary phylogenetic break at the Solomon Islands include the butterfly clade Coenonymphina (Heads et al., 2023).

The break between iguanids in Fiji and their sister group, agamids, in Papua New Guinea, Eastern Australia, Solomon Islands etc. is also seen in many other family-level groups. These include the plant family Degeneriaceae of Fiji and its sister, Himantandraceae of Papua New Guinea and eastern Australia. Recent estimates for the age of the break between the two are all 80 Ma (Late Cretaceous) or older (Stevens, 2025).

As is often the case, the Fiji–Solomon Islands break-zone is also an important center of endemism. The burrowing snake *Ogmodon* (Elapidae) of Fiji forms a clade with *Loveridgelaps* and *Salomonelaps* of the Solomon Islands (but not Bougainville; the unsequenced *Parapistocalamus* from Bougainville may also belong here). This Fiji–Solomons clade is sister to the rest of the Hydrophiinae (except *Laticauda*), a diverse group that ranges from East Africa to Asia, the Pacific and western parts of the Americas (Strickland er al., 2016).

EXTINCTION IN THE CENTRAL PACIFIC WITH COOLING AND SUBSIDENCE OF THE PACIFIC PLATE

A vicariance model for the Fijian iguanas requires two key steps. In the first, Pleurodonta, now found through the Pacific basin and the Americas, differentiated from Acrodonta, found through Africa and Asia, at a break lying, in part, between the Fiji (Asia) and Solomon Islands (Pacific) regions. Intraplate volcanism producing high islands has been widespread on the Pacific plate, especially in a large, central region (the South Pacific Isotopic and Thermal Anomaly) ever since the Cretaceous (Koppers et al., 2003; Zhao et al., 2022). This volcanism has allowed metapopulations to persist by constant invasion of new islands from older ones in the vicinity.

In the second step of the vicariance history, massive extinction of central Pacific populations of Pleurodonta took place with large-scale subsidence of the seafloor. This led to the phylogenetic break between *Brachylophus* of Fiji and *Dipsosaurus* of North America.

Scarpetta et al. (2025a) inferred direct dispersal of Fiji iguanas from America, as “there have been very few landmasses between the Americas and Fiji throughout the Cenozoic … ”. Yet there are currently many islands between America and Fiji, and this was also the case throughout the Cenozoic. For example, the Line Islands chain, ~4 500 km long including seamounts, lies mid-way between America and Fiji. It originally comprised high, volcanic islands erupted at 88 —50 Ma (Pockalny et al., 2021), but these are now represented above water only by low, flat coral islands and atolls.

The idea that atolls represent former, sunken high islands (Darwin, 1842) is now widely accepted, and the thousands of atolls in the Pacific indicate a very different former geography. Note that small islets 100 m across can host considerable biodiversity, but the history of most such islands over the last 100 Ma will never be known. There are many difficulties in reconstructing the detailed paleogeography of individual islands, as in the debate about whether or not the Hawaiian islands were ever completely submerged (Heads, 2012b). But, in contrast, there is now a great deal of information on the tectonics and volcanism of the Pacific, and this can be integrated with the biogeographic data to give a coherent geological and phylogenetic history of the iguanids. Similar biogeographic models, based on tectonics and volcanism rather than stratigraphy and paleogeography, have been presented for the Galápagos and Juan Fernández islands (Heads & Grehan, 2021; Heads & Saldivia, 2024).

The Pacific plate is formed at a spreading ridge, the East Pacific Rise, and moves west, while its conjugate plates at the ridge move east. As new sea floor drifts away from the ridge producing it, over tens of millions of years it cools, increasing its density, and subsides by large amounts (van der Pluijm & Marshak, 2004). Cooling of the oceanic lithosphere is the main factor controlling global seafloor depth (Stein et al., 1992, Huppert et al., 2020), and the Pacific seafloor has sunk by 1 000s m, following a standard temperature-depth relationship (Zhong et al., 2007). As the seafloor subsided, the many high islands on the plate subsided with it, and many are now represented only by atolls, reefs or submerged seamounts. Many others have been destroyed completely by subduction at the Pacific margins.

In addition to the former high volcanic islands, continent-

sized large igneous plateaux (Ontong Java Plateau and others) were emplaced in the Cretaceous in the central Pacific Cook Islands region. Parts of these were formerly subaerial, and they include fossil wood (Heads, 2012b, 2014; Buchs et al., 2018; Hochmuth et al., 2019), but they are now almost completely submerged.

Dispersal models for island biotas often do not acknowledge the massive subsidence in the Pacific basin (Cantley et al., 2016) or even reject it (O'Grady et al., 2012). Nevertheless, it is a likely cause of breaks in the terrestrial and reef metapopulations present on the islands (Heads, 2018). With subsidence, high, forested islands have become atolls with dry, sandy, saline soil and depauperate vegetation, and on the atoll Eniwetok there are fossils of landsnails that are known, living, only in montane cloud-forest (Solem, 1983).

Iguanids are represented in Fiji by the extant *Brachylophus* and the extinct *Lapitiguana* (Quaternary). *Lapitiguana* is distinctive and more than twice as long as *Brachylophus*; there is no evidence that the two are sisters (Pregill & Worthy, 2003). This is consistent with the idea that the Fijian iguanas, living and fossil, are a relic of a more diverse iguanian complex that was almost entirely extirpated through the central Pacific region by seafloor subsidence and island submergence.

ALLOPATRY IS WIDESPREAD IN HIGH-LEVEL SQUAMATE CLADES

The allopatry between Pleurodonta and Acrodonta is not absolute, as there is some marginal overlap. But the overall pattern is clear: the geographic concentrations of diversity in each of the two clades, living and fossil, are allopatric. In fact, this is a standard pattern. 31 high-level clades in squamates (families and subfamilies), 18 in lizards and 13 in snakes, also show allopatry. These are listed with their distributions in the online Appendix, and examples are mapped in Figures 3, 4. The process of metapopulation vicariance that explains Iguanidae also explains these other examples.

Most of the allopatry in the high-level squamate clades has been attributed to trans-oceanic chance dispersal, but a general vicariance explanation for allopatry results in a much simpler model for squamates overall. Extant Iguania – Pleurodonta and Acrodonta – are easily derived by vicariance within a global ancestor, and make up one of the seven clades of squamates. Vicariance in a small number of widespread, global ancestors – one for Elapidae (Figure 4B), one for Viperidae (Figure 4A) and so on – could produce all the extant squamates.

DISCUSSION

The dispersal model of biogeography rests on two main assumptions. The first is that basal grades occupy centers of origin; the second is that fossil-calibrated clocks give valid estimates of maximum clade age. Both of these are flawed. If the assumptions are accepted, every America–Fiji clade will require its own separate dispersal event, at a different time from others and unrelated to any environmental factor. If, instead, the assumptions are rejected, a coherent explanation is possible for the repetition of the America–Fiji connection in terms of geological change that has affected multiple components of communities in the region (Figure 1, 2).

Statistical outliers, extremely rare events, do occur in biogeography, but their importance in establishing main patterns is debatable. In colonial biogeography, rare (or unique) dispersal events, statistical outliers, determine the course of evolution. (If dispersal continued after the initial event, as with normal dispersal, differentiation would not take place). In contrast, a vicariance model explains evolution in terms of normal biological and geological processes that are observed every day. Normal dispersal is a key factor enabling survival, while geological and climatic changes have affected whole communities and led to differentiation and extinction. Uniquely, chance dispersal events explain idiosyncratic distributions, but not the main biogeographic patterns and features of patterns that are repeated in multiple, unrelated groups. Their repetition indicates that community-wide processes, such as vicariance and geodispersal, are responsible (see "Chance dispersal vs normal dispersal", above).

In their study of biogeography in the Fiji iguanas, Scarpetta et al. (2025a) aimed to test all alternatives to long-distance dispersal from North America. But the alternatives that they considered did not include the simplest – a vicariance model, in which iguanas "reached" the SW Pacific by evolving there, not by migrating. Ali & Fritz (2025) described the iguanas' proposed trip from America to Fiji as "… Incredible, yes, but to quote Sir Arthur Conan Doyle through his creation Sherlock Holmes '…when you have eliminated the impossible, whatever remains, however improbable, must be the truth'". But neither these authors nor Scarpetta et al. (2025a) considered a vicariance model, and so they did not eliminate it as impossible.

Vicariance models have already been proposed for the higher-level clades in Acrodonta (Okajima & Kumazawa, 2009) and for the main clades in the largest family, Agamidae Macey et al., 2000. This vicariance proposed for evolution *within* Acrodonta fits neatly with a vicariance origin of both Acrodonta itself and Pleurodonta.

CONCLUSIONS

Dispersal and extinction take place everywhere, all the time. But this does not justify basing explanations of distribution patterns on these two processes alone. All groups disperse, and a group's normal means of dispersal are a critical component of its means of survival. In addition, a clade can establish in a new area through range expansion by dispersal. But clades, unlike individuals, can also establish in an area by *evolving* there, by vicariance and without any physical movement.

Molecular phylogenies are invaluable for biogeography and have solved many problems. In contrast, current methods for estimating the age and ancestral distributions of clades are unreliable. Using these same methods, Scarpetta et al. (2025a) concluded that Fiji iguanas dispersed from elsewhere. But they did not consider a vicariance model, in which the iguanas colonized Fiji using their normal, observed means of dispersal, and arrived from other, former islands in the region that are now submerged or subducted. In a vicariance model, iguanids did not arrive in Fiji from America by walking, swimming, or rafting on vegetation or drifting plates. Generalized Iguania already occupied the south-west Pacific before Pleurodonta, let alone iguanids, were distinct.

If the focus of biogeographic studies in squamates and other groups shifted from speculations about centers of origin and dispersal, to study of the actual break zones (nodes) in groups, critical questions could be answered. Questions about

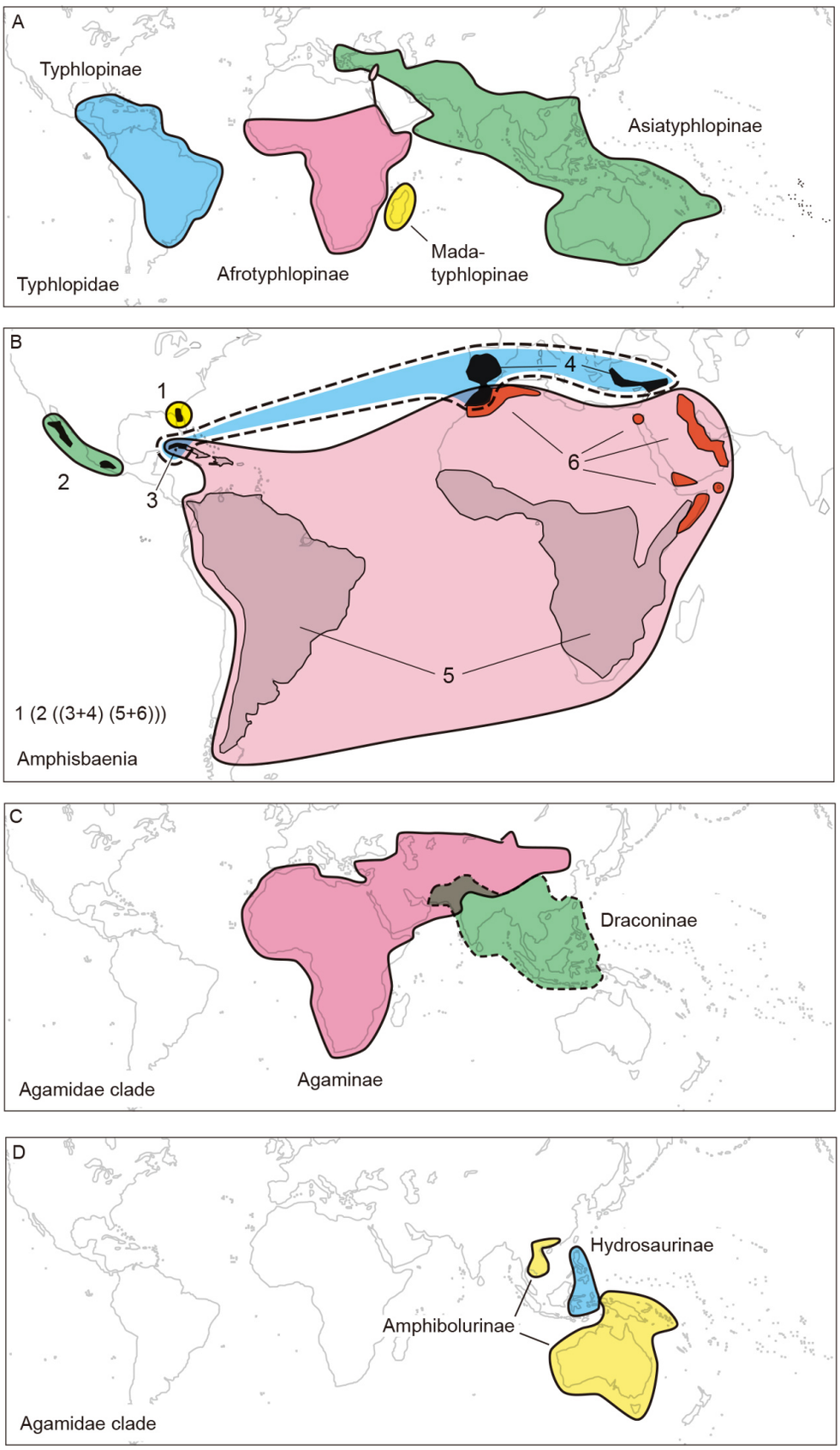

Figure 3 Distribution of some high-level clades of squamates

A: Distribution of Typhlopidae and its four subfamilies (Miralles et al., 2018); B: Distribution of Amphisbaenia (Squamata). 1=Rhineuridae, 2=Bipedididae, 3=Cadeidae, 4=Blanidae, 5=Amphisbaenidae, 6=Trogonophidae. (Phylogeny from Zheng & Wiens, 2016); C: Distribution of a clade in Agamidae (O'Shea, 2021); D: Distribution of a clade in Agamidae, sister to the clade in Figure 3C (O'Shea, 2021). An alternative phylogenetic arrangement for the groups in Figure 3C, D is: (Hydrosaurinae (Amphibolurinae (Agaminae+Draconinae))) (Scarpetta et al., 2025b).

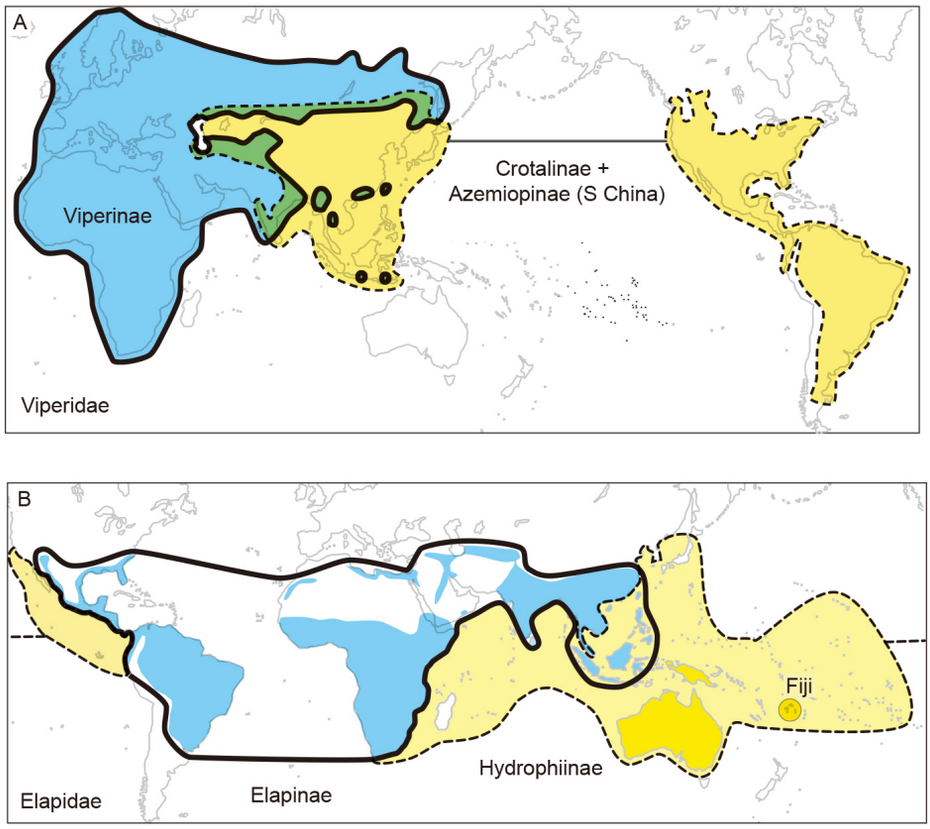

Figure 4 Distribution of two snake families

A: Distribution of Viperidae (O'Shea, 2023); B: Distribution of Elapidae. Elapinae are all terrestrial. Hydrophiinae include the sea-snakes (pale yellow) and many terrestrial species (dark yellow), the latter restricted to Australia, New Guinea and Fiji (O'Shea, 2023; iucnredlist.org).

the nodes include their general location and precise, their small-scale structure (usually requiring field observations and mapping), their repetition in other groups of plants and animals, and their spatial coincidence with past geological and climatic events. Dispersal theorists have misinterpreted the significance of the Fijian iguanas, as they have not considered the global phylogenetic breaks around Fiji and the Solomon Islands. They have assumed that these islands are simply remote outposts whose biota must have been supplied from continental centers of origin.

The study by Scarpetta et al. (2025a) supported the traditional view that *Brachylophus* and *Dipsosaurus* are sisters, and that *Brachylophus* dispersed to Fiji from America. Yet despite this lack of novelty, the paper was widely reported in journals such as *Nature* (Anonymous, 2025) and *Trends in Ecology and Evolution* (Ali & Fritz, 2025), with the latter describing it as a "major advance" and a "revelation". Earlier reports of iguanids rafting on masses of vegetation in the Caribbean were also publicised in *Nature* (Censky et al., 1998; Lawrence, 1998). For these authors, the almost miraculous nature of the long-distance dispersal in Fiji iguanids, and the great authority of Darwin and Mayr, together prove that chance dispersal exists and is crucial for evolution.

Ali & Fritz (2025) described the trans-Pacific disjunction and inferred dispersal of the Fiji iguanas as "remarkable", "one of the wonders … of Natural History", and "fantastical". Other authors have regarded the pattern as incredible, extraordinary, anomalous, puzzling and enigmatic. In fact, the distribution is none of these things, and in the context of other America–Fiji groups, as well as the Pleurodonta-Acrodonta allopatry, it is seen to be quite ordinary.

SUPPLEMENTARY DATA

Supplementary data to this article can be found online.

COMPETING INTERESTS

The author declare that he has no competing interests.

ACKNOWLEDGMENTS

I'm grateful to John Grehan, Karin Mahlfeld, Milen Marinov, Duncan Nicol and Patricio Saldivia for very useful comments and help obtaining literature.

REFERENCES

Ali JR, Fritz U. 2025. New twist to a fantastical distribution: Fiji–Tonga iguanas. *Trends in Ecology and Evolution*, **40**: P536–538

Anonymous. 2025. Iguanas reached Fiji by floating 8, 000 kilometres across the sea. *Nature*, **639**: 841.

Blankers T, Townsend TM, Pepe K, Reeder TW, Wiens JJ. 2013. Contrasting global-scale evolutionary radiations: phylogeny, diversification, and morphological evolution in the major clades of iguanian lizards. *Biological Journal of the Linnean Society*, **108**: 127–143.

Buchs DM, Kerr AC, Brims JC, Zapata-Villada JP, Correa-Restrepo T, Rodríguez G. 2018. Evidence for subaerial development of the Caribbean oceanic plateau in the Late Cretaceous and palaeo-environmental implications. *Earth andPlanetary Science Letters*, **499**: 62–73.

Burbrink FT, Grazziotin FG, Pyron A, et al. 2020. Interrogating genomic-scale data for Squamata (lizards, snakes, and amphisbaenians) shows no support for key traditional morphological relationships. *Systematic Biology*, **69**: 502–520.

Cantley JT, Markey AS, Swenson NG, Keeley SC. 2016. Biogeography and evolutionary diversification in one of the most widely distributed and species rich genera of the Pacific. *AoB Plants*, **8**: plw043.

Censky EJ, Hodge K, Dudley J. 1998. Over-water dispersal of lizards due to

hurricanes. *Nature*, **395**: 556–556.
Čerňanský A, Smith R, Smith T, et al. 2022. Iguanian lizards (Acrodonta and Pleurodonta) from the earliest Eocene (MP 7) of Dormaal, Belgium: the first stages of these iconic reptiles in Europe. *Journal of Vertebrate Paleontology*, **42**: e2184696.
Cogger HG. 1974. Voyage of the banded iguana. *Australian Natural History*, **18**: 144–149.
Darwin C. 1842. *The structure and distribution of coral reefs*. 1st ed. London: Smith, Elder & Co.
Darwin C. 1859. On the origin of species. 1st ed. John Murray, London.
Daza JD, Stanley EL, Bolet A, et al. 2020. Enigmatic amphibians in mid-Cretaceous amber were chameleon-like ballistic feeders. *Science*, **370**: 687–691.
Daza JD, Stanley EL, Wagner P, et al. 2016. Mid-Cretaceous amber fossils illuminate the past diversity of tropical lizards. *Science Advances*, **2**: e1501080.
Evans SE. 2022. The origin and early diversification of squamates. In: Gower DJ, Zaher H (Eds.), *The origin and early evolutionary history of snakes*. Cambridge University Press, Cambridge U. K. , pp. 7–25.
Fisher RN, Niukula J, Watling D, et al. 2017. A new species of iguana *Brachylophus* Cuvier 1829 (Sauria: Iguania: Iguanidae) from Gau Island, Fiji Islands. *Zootaxa*, **4273**: 407–422.
Gibbons JR. 1981. The biogeography of *Brachylophus* (Iguanidae) including the description of a new species, *B. vitiensis*, from Fiji. *Journal of Herpetology*, **15**: 255–273.
Hackel J, Sanmartín I. 2021. Modelling the tempo and mode of lineage dispersal. *Trends in Ecology and Evolution*, **36**: 1102–1112.
Heads M. 2012a. Bayesian transmogrification of clade divergence dates: a critique. *Journal of Biogeography*, **39**: 1749–1756.
Heads, M. 2012b. *Molecular panbiogeography of the tropics*. University of California Press, Berkeley, California.
Heads M. 2014. *Biogeography of Australasia: A molecular analysis*. Cambridge University Press, Cambridge U. K.
Heads M. 2018. Metapopulation vicariance explains old endemics on young volcanic islands. *Cladistics*, **34**: 292–312.
Heads M. 2019. Biogeography and ecology in a pantropical family, the Meliaceae. *Gardens' Bulletin, Singapore*, **71**(Suppl.2): 335–461.
Heads M, Grehan JR. 2021. The Galápagos Islands: biogeographic patterns and geology. *Biological Reviews*, **96**: 1160–1185.
Heads M, Grehan JR, Nielsen J, et al. 2023. Biogeographic-tectonic calibrations of 14 nodes in a butterfly timetree. *Cladistics*, **39**: 293–336.
Heads M, Nicol DA, Saldivia P. 2025. Ancestral-area algorithms are unreliable. *Biological Reviews*. https://doi.org/10.1111/brv.70092
Heads M, Saldivia P. 2024. The challenging biogeography of the Juan Fernández Islands and the central Chilean Coast Range explained by a new model of East Pacific tectonics. *Biological Reviews*, **99**: 2274–2303.
Higgins SI, Nathan R, Cain ML. 2003. Are long‐distance dispersal events in plants usually caused by nonstandard means of dispersal. *Ecology*, **84**: 1945–1956.
Hochmuth K, Gohl K, Uenzelmann-Neben G, Werner R. 2019. Multiphase magmatic and tectonic evolution of a large igneous plateau: evidence from the crustal structure of the Manihiki Plateau, western Pacific. *Tectonophysics*, **750**: 434–457.
Huppert KL, Perron JT, Royden LH. 2020. Hotspot swells and the lifespan of volcanic ocean islands. *Science Advances*, **6**(1): eaaw6906.
Keogh JS, Edwards DL, Fisher RN, Harlow PS. 2008. Molecular and morphological analysis of the critically endangered Fijian iguanas reveals cryptic diversity and a complex biogeographic history. *Philosophical Transactions of the Royal Society B: Biological Sciences* **363**: 3413-3426.
Klopfstein S. 2021. The age of insects and the revival of the minimum age tree. *Austral Entomology*, **60**: 138–146.
Koppers AAP, Staudigel H, Pringle MS, Wijbrans JR. 2003. Short-lived and discontinuous intraplate volcanism in the South Pacific: Hot spots or extensional volcanism? *Geochemistry Geophysics Geosystems*, **4**: 1089. doi:10.1029/2003GC000533
Lawrence E. 1998. Iguanas ride the waves. *Nature*. https://doi.org/10.1038/news981015-3
Levin DA. 2000. *The origin, expansion, and demise of plant species*. Oxford University Press, New York.
Mabberley DJ. 2017. *Mabberley's plant-book: A portable dictionary of plants*, 4th edition. Cambridge University Press, Cambridge, UK.
Macey JR, Schulte JA, Larson A, et al. 2000. Evaluating trans-Tethys migration: an example using acrodont lizard phylogenetics. *Systematic Biology*, **49**: 233–256.
Mao K, Milne RI, Zhang L, et al. 2012. The distribution of living Cupressaceae reflects the breakup of Pangea. *Proceedings of the National Academy of Sciences of the United States of America*, **109**: 7793–7798.
Mayr E. 1954. Change of genetic environment and evolution. In: Huxley J, Ford EB (Eds.), *Evolution as a process*. Allen and Unwin, London, pp. 157–180.
Mayr E. 1965. Summary. In: Baker HG, Stebbins GL (Eds.), *The genetics of colonizing species*. Academic Press, New York, pp. 553–562.
Mayr E. 1982. *The growth of biological thought: diversity, evolution, and inheritance*. Harvard University Press, Cambridge, MA.
McCulloch GA, Waters JM. 2019. Phylogenetic divergence of island biotas: Molecular dates, extinction, and 'relict' lineages. *Molecular Ecology*, **28**: 4354–4362.
Miralles A, Marin J, Markus D, Herrel A, Hedges SB, Vidal N. 2018. Molecular evidence for the paraphyly of Scolecophidia and its evolutionary implications. *Journal of Evolutionary Biology*, **31**: 1782–1793.
O'Grady PM, Bennett GM, Funk VA, Altheide TK. 2012. Retrograde biogeography. *Taxon*, **61**: 702–705.
Okajima Y, Kumazawa Y. 2009. Mitogenomic perspectives into iguanid phylogeny and biogeography: Gondwanan vicariance for the origin of Madagascan oplurines. *Gene*, **441**: 28–35.
O'Shea M. 2021. *Lizards of the world: A guide to every family*. Princeton University Press, Princeton, NJ.
O'Shea M. 2023. *Snakes of the world: A guide to every family*. Princeton University Press, Princeton, NJ.
Palci A, Onary S, Lee MS, et al. 2024. A new booid snake from the Eocene (Lutetian) Konservat-Lagerstätte of Geiseltal, Germany, and a new phylogenetic analysis of Booidea. *Zoological Journal of the Linnean Society*, **202**: zlad179.
Pillon Y, Gotty K, Hopkins HCF. 2023. Expanded generic concepts for *Kermadecia* and *Persoonia*, Proteaceae of New Caledonia and neighboring islands. *Botany Letters*, **170**: 488–505.
Pockalny R, Barth G, Eakins B, Kelley KA, Wertman C. 2021. Multiple melt source origin of the Line Islands (Pacific Ocean): *Geology*, **49**: 1358–1362
Pregill G, Worthy T. 2003. A new iguanid lizard (Squamata, Iguanidae) from the Late Quaternary of Fiji, southwest Pacific. *Herpetologica*, **59**: 57–67.
Scarpetta SG. 2024. A Palaeogene stem crotaphytid (*Aciprion formosum*) and the phylogenetic affinities of early fossil pleurodontan iguanians. *Royal Society Open Science*, **11**: 221139.
Scarpetta SG, Fisher RN, Karin BR, et al. 2025a. Iguanas rafted more than 8, 000 km from North America to Fiji. *Proceedings of the National Academy of Sciences of the United States of America*, **122**: e2318622122.
Scarpetta SG, Karin BR, Corl A, McGuire JA. 2025b. The evolutionary history of dragon lizards (Squamata: Agamidae) revealed by phylogenomics. *Systematic Biology*, syaf088, https://doi.org/10.1093/sysbio/syaf088
Simões TR, Pyron RA. 2021. The squamate tree of life. *Bulletin of the Museum of Comparative Zoology*, **163**: 47–95.

Simões TR, Wilner E, Caldwell MW, et al. 2015. A stem acrodontan lizard in the Cretaceous of Brazil revises early lizard evolution in Gondwana. *Nature Communications*, **6**: 8149.

Solem, A. , 1983. *Endodontoid land snails from Pacific islands (Mollusca: Pulmonata: Sigmurethra), Part II: Families Punctidae and Charopidae, zoogeography*. Field Museum of Natural History, Chicago, IL.

Stein CA, Stein S. 1992. A model for the global variation in oceanic depth and heat flow with lithospheric age. *Nature*, **359**: 123–129

Stevens PF. 2025. Angiosperm Phylogeny Website. https://www.mobot.org/mobot/research/apweb/welcome.html

Strickland JL, Carter S, Kraus F, et al. 2016. Snake evolution in Melanesia: origin of the Hydrophiinae (Serpentes, Elapidae), and the evolutionary history of the enigmatic New Guinean elapid *Toxicocalamus. Zoological Journal of the Linnean Society*, **178**: 663–678.

Takayama K, Tateishi Y, Kajita T. 2021. Global phylogeography of a pantropical mangrove genus *Rhizophora. Scientific Reports*, **11**: p. 7228.

Tolley KA, Townsend TM, Vences M. 2013. Large-scale phylogeny of chameleons suggests African origins and Eocene diversification. *Proceedings of the Royal Society B: Biological Sciences*, **280**: 20130184.

Townsend TM, Leavitt DH, Reeder TW. 2011. Intercontinental dispersal by a microendemic burrowing reptile (Dibamidae). *Proceedings of the Royal Society B: Biological Science*. **278**: 2568–2574.

van de Lagemaat SH, van Hinsbergen DJ. 2024. Plate tectonic cross-roads: Reconstructing the Panthalassa-Neotethys Junction Region from Philippine Sea Plate and Australasian oceans and orogens. *Gondwana Research*, **126**: 129–201.

van der Pluijm BA, Marshak M. 2004. *Earth structure: an introduction to structural geology and tectonics*. 2nd edn. Norton, New York.

Wahlert GA, Marcussen T, de Paula-Souza J, et al. 2014. A phylogeny of the Violaceae (Malpighiales) inferred from plastid DNA sequences: implications for generic diversity and intrafamilial classification. *Systematic Botany*, **39**: 239–252.

Weinell JL, Burbrink FT, Das S, Brown RM. 2024. Novel phylogenomic inference and 'Out of Asia' biogeography of cobras, coral snakes and their allies. *Royal Society Open Science*, **11**: 240064.

Welt RS, Raxworthy CJ. 2022. Dispersal, not vicariance, explains the biogeographic origin of iguanas on Madagascar. *Molecular Phylogenetics and Evolution*, **167**: 107345.

Xie P, Tu T, Razafimandimbison SG, Zhu C, et al. 2014. Phylogenetic position of *Guihaiothamnus* (Rubiaceae): Its evolutionary and ecological implications. *Molecular Phylogenetics and Evolution*, **78**: 375–385.

Yao, G., Zhang, Y. Q., Barrett, C., et al. 2023. A plastid phylogenomic framework for the palm family (Arecaceae). *BMC Biology*, **21**: 50.

Zhao Y, Riel B, Foulger G, Ding W. 2022. How strongly do plumes influence Pacific seamount distribution. *Earth and Planetary Science Letters*, **595**: 117786.

Zheng Y, Wiens JJ. 2016. Combining phylogenomic and supermatrix approaches, and a time-calibrated phylogeny for squamate reptiles (lizards and snakes) based on 52 genes and 4162 species. *Molecular Phylogenetics and Evolution*, **94**: 537–547.

Zhong S, Ritzwoller M, Shapiro N, et al. 2007. Bathymetry of the Pacific plate and its implications for thermal evolution of lithosphere and mantle dynamics. *Journal of Geophysical Research*, **112**: B06412.

Zug GR. 1991. Lizards of Fiji: Natural history and systematics. *Bishop Museum Bulletin in Zoology*, **2**: 1–136.