

ISSN 1759-0116 (Online)

ZooNova

Occasional Papers in Zoology

Number 33, Pages 1 – 18

**CAN GONDWANA VICARIANCE, RATHER THAN CENOZOIC CHANCE
DISPERSAL, BETTER EXPLAIN THE DISJUNCTION OF AMBULICINI
HAWKMOTHS BETWEEN MADAGASCAR AND NEW CALEDONIA?**

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Published on-line at <https://zoonova.afriherp.org>

Afriherp Communications, Greenford, United Kingdom

Date of publication: 18 June 2024

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Can Gondwana vicariance, rather than Cenozoic chance dispersal, better explain the disjunction of Ambulycini hawkmoths between Madagascar and New Caledonia?

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Abstract

The geographic disjunction between the hawkmoth genera *Compsulyx* in New Caledonia and *Batocnema* in East Africa-Madagascar is a biogeographic pattern shared with other plant and animal taxa, irrespective of their individual means of dispersal. The disjunction is almost identical to a sister species relationship in the plant genus *Acridocarpus* (Malpighiaceae), similar to *Cunonia* (Cunoniaceae) in New Caledonia and South Africa, and comparable to *Dietes* (Iridaceae) on Lord Howe Island and Madagascar/East Africa. These and other geographic disjunctions represent scattered elements of the numerous trans-Indian Ocean connections involving more widespread taxa, some with distributions that include the Pacific. The biogeographic patterns are consistent with Mesozoic tectonic events that disrupted the continuity of widespread ancestral distributions. The tectonic correlations are not in conflict with younger fossil or island calibrated molecular divergence ages that represent minimum estimates only. And they provide a potential falsification of centres of origin and chance dispersal models generated by ancestral-areas programmes.

Keywords: *Acridocarpus*, *Batocnema*, biogeography, Ceridoxylaceae, *Compsulyx*, *Cryptoblepharus*, *Dietes*, *Hyles*, Lepidoptera, *Lordhowea*, molecular clock, Sphingidae, tectonic correlation, tectonics

Introduction

Sister taxa descend from a common ancestor. When sister taxa are disjunct, the geographic break is often treated as a biogeographic problem. The further apart, the greater the perceived problem. The most common solution is to attribute the disjunctions to unobserved chance events, usually involving unique accidental dispersal of ancestors from one locality (the centre of origin) to another. Beginning with Darwin (1859), this perspective generated a paradox by attributing both geographic location and biological divergence to movement. Because isolation is necessary for divergence to take place, disjunct localities are supposed to be permeable to chance dispersal events while at the same time sufficiently impermeable to provide the isolation that makes divergence possible. This paradox becomes redundant when the movement of organisms is understood to be responsible for the ancestral range rather than biological divergence (Craw *et al.* 1999, Heads 2012).

Dispersal sustains the survival of species and is responsible for their distribution ranges as an observable ecological process that allows taxa to survive and persist through periods of ecological or geological instability. This metapopulation understanding of distribution explains how taxa may persist over tens of millions of years in geologically unstable regions. When there is sufficient ecological or geological upheaval, the ecological continuity of the ancestor's range may be disrupted and displaced, resulting in spatial isolation and local differentiation (vicariance) of descendent taxa within the ancestral range. This is a very different concept from mostly unique,

non-observable, 'chance dispersal' events invoked to explain allopatry or disjunct allopatric distributions of sister taxa in centre of origin-chance dispersal biogeography (Heads 2012, 2017; Parenti & Ebach 2013).

In this article we present some anomalies that arise from the assumption that chance dispersal is responsible for allopatric differentiation of the Ambulycini tribe of hawkmoths that includes sister taxa disjunct between Africa/Madagascar and New Caledonia. When viewed through the lens of chance dispersal, this distribution pattern makes no obvious geographic sense. When approached from the perspective of comparative spatial analysis of phylogeny and distribution, a different possibility becomes evident. Mapping the phylogeny and range of sister taxa allows evaluation of spatial correlations between taxa, and between taxa and Earth's tectonic structures as evidence of their having evolved together (see Craw *et al.* 1999, Heads 2012, 2014a, 2017 for global synthesis). We utilize this approach to evaluate the applicability of a Gondwana explanation for the Africa/Madagascar-New Caledonia disjunction in the Ambulycini hawkmoths.

Disjunctions in the Ambulycini hawkmoths

The idea that chance dispersal is the *si non qua* of trans-oceanic disjunctions was recently applied to a study of the Ambulycini hawkmoths of Madagascar, East Africa, and New Caledonia. Within this tribe, the genus *Compsulyx* is endemic to New Caledonia in the southwest Pacific (Fig. 1).



Fig. 1. *Compsulyx cochereaui* of New Caledonia. Left – adult, right – larva. Photos by Thierry Salesne.

The tribe Ambulycini is widespread in the Old and New Worlds, and yet notably absent from most of Africa (outside eastern Africa and Madagascar), northern Eurasia, North America mostly north of Mexico, New Zealand, and nearly all of Australia (Fig. 2). *Compsulyx* is located near the distributional boundary of the widespread east Asian genus *Ambulyx*, and it would be no surprise if they were sister taxa, but this is not the case.

Phylogenetic analysis by (Timmermans *et al.* 2019) identified the sister group of *Compsulyx* as the genus *Batocnema* of Madagascar and nearby central-eastern Africa. The two genera are together the sister group of *Protambulyx* in the New World. The next sister group is also a New World clade of three genera (*Orecta*, *Adhemarius*, *Trogolegnum*), followed by *Ambulyx*-*Amphyterus* of southern and eastern Asia as the basal clade (Fig. 2). Timmermans *et al.* (2019) found themselves perplexed over how to work out the labyrinthine sequence of chance dispersal. The distribution was assigned a centre of origin in tropical South-East Asia because this is where the smaller basal clades are located. There was no explanation as to why a 'centre of origin' is represented by where 'basal' taxa (usually smaller sister groups diverging near the base of the phylogeny) are found.

Having proposed a centre of origin, Timmermans *et al.* (2019) then found themselves 'unclear' as to whether there were two independent dispersal events to the New World, a single dispersal followed

by a return trip, or even a 'more complex scenario'. If this was not confusing enough, the biogeography was characterized as a highly enigmatic discrepancy.

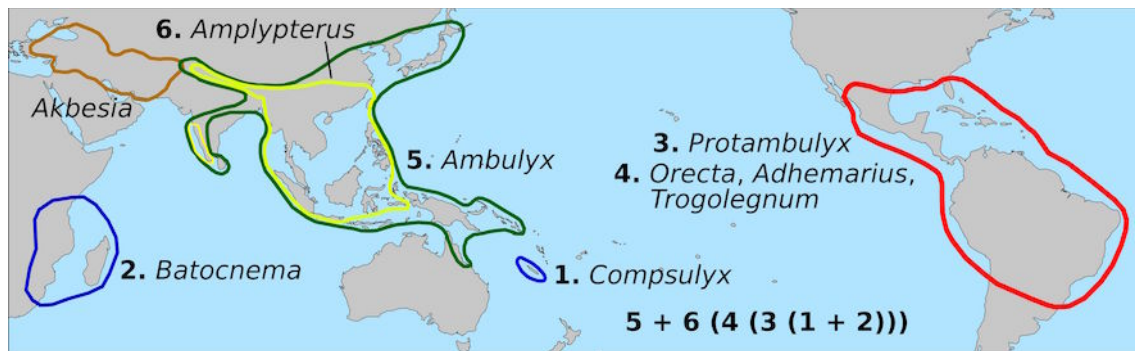


Fig. 2. Distribution of Ambulycini hawkmoths. Continental distributions from <https://sphingidae.myspecies.info> and *Akbesia* from https://tpittaway.tripod.com/sphinx/a_dav.htm. Phylogeny from Timmermans *et al.* (2019, not including *Akbesia*).

Hawkmoths are characterised as strong fliers (Kawahara & Barber 2015). Some species have 'exceptionally' large ranges and many are regarded as likely to be extraordinarily good dispersers (Beck *et al.* 2006, Timmermans *et al.* 2019). From this perspective, hawkmoths should be able to cross oceans, especially if assisted by favourable winds (Hundsdoerfer *et al.* 2009). While this ability may explain how some species have attained widespread oceanic ranges (Moulds *et al.* 2020), even global, distributions (including widely scattered 'vagrants'), "...it does not explain disjunct distributions such as observed with the Ambulycini, absence of the group from areas with putatively suitable habitats (e.g. much of Australia and Africa), and more generally, explain the absence of endemic sphingids from New Zealand. Timmermans *et al.* (2019) drew attention to the rarity of long distance disjunctions in Lepidoptera, but without documentation or explaining their significance for understanding the biogeography of the Ambulycini. While rarity is relative, there are examples of various Lepidoptera clades that have trans-oceanic disjunctions, some reaching 18,000 km (Table 1). Within the Ambulycini, the 2,000 km disjunction within the *Compsulyx*-*Batocnema* clade is far less than the ~10,000 km disjunction between this clade and its sister group, *Protambulyx*, in the New World.

An alternative possibility for the *Compsulyx*-*Batocnema* disjunction is vicariance. In broad terms, vicariance is a concept of allopatric divergence within the distribution range of a common ancestor where ecological dispersal (as an observable process) is responsible for the origin of the ancestral range. Local isolation within that range (vicariance) may result in subsequent allopatric divergence. Disruptive geological or tectonic processes can result in geographically disjunct sister taxa across wide regions now occupied by oceans or seas (Craw *et al.* 1999, Heads 2012).

Considered in the context of comparative biogeography, a vicariance explanation for an individual taxon may be corroborated or rejected. The potential value of comparison was alluded to by Timmermans *et al.* (2019) who briefly noted that the hawkmoths *Hyles biguttata* in Madagascar/Réunion Island and *H. livornicoides* in Australia appeared to represent a similar pattern to that in the Ambulycini. The unsettled state of *Hyles* systematics precluded further analysis (Hundsdoerfer *et al.* 2017, Hundsdoerfer & Kitching 2020), but the point was made - what does it mean for biogeography if there should be one or more similar disjunctions between Africa-Madagascar and New Caledonia? And if such disjunctions occur, how may they be integrated into the biogeography of the Indian Ocean in general?

Table 1. Examples of trans-oceanic disjunctions in Lepidoptera taxa (minimum distance). Measurements approximate, derived from GoogleEarth.

Taxon	Disjunction	Distance (km)	Literature source
<i>Batocnema-Compsulyx</i>	Madagascar-New Caledonia	2000	Timmermans <i>et al.</i> (2019)
<i>Compuly-Protambulyx</i>	New Caledonia-S. America	12000	Timmermans <i>et al.</i> (2019)
Paleosetidae	Taiwan-Colombia	16400	Kristensen & Nielsen (1994)
Arrhenophanidae	Australia-northern S. America	14500	Davis (2003)
South East Asia Triodini- <i>Parades/Euryades</i>	Solomons-northern S. America	13000	Grehan (2019)
<i>Pharmacophagus</i> -South East Asia Triodini	Madagascar-India	3800	Grehan (2019)
Dudgeonea (Dudgeonidae)	Madagascar-Himalayas	5800	Schulze & Fiedler (1996)
Dismorphiinae (Pieridae)	Japan-Central America	10700	Braby <i>et al.</i> (2006); Llorente-Bousquets & Castro-Gerardino (2018)
Castniidae	Australia-South America	13000	Vinciguerra (2008); González <i>et al.</i> (2019)
Euptychiina (Nymphalidae)	N America-China		Peña <i>et al.</i> (2010)
Neopseustidae	Chile-Taiwan	18000	Davis (1975)
<i>Parnara</i> (Hesperiidae)	Madagascar-Sumatra	5500	Williams (2020); Huang <i>et al.</i> (2019); Chiba & Eliot (1991).
Callidulidae	Madagascar-India	3800	Minet (1989)
Coenonymphina subclade (Nymphalidae)	Australia-Colombia	13000	Heads <i>et al.</i> (2023)
<i>Xanadoses-Scyrotis/Ptisanora</i> (Cecidosidae)	New Zealand-South Africa	10000	Hoare & Dugdale (2003)
Orthomecyna- Miyakea (Pyrilidae)	China-Hawaii	8000	Léger <i>et al.</i> (2019)
Palaephatidae	New Zealand-Chile	8000	Davis (1986)
<i>Actinote-Telchinia</i> (Nymphalidae)	South America-Africa	3000	Williams & Henning (2023)
<i>Vanessa tameamea - Vanessa atalanta</i> (Nymphalidae)	Hawaii-North America	3600	Wahlberg & Rubinoff (2011)
<i>Imma</i> (Immidae)	South America-Africa	3000	Heppner (1982)
<i>Siga-Eporidia</i> (Crambidae)	South America-Africa	3000	Mally <i>et al.</i> (2019)

Comparative evidence

The disjunct pattern of Ambulycini and *Hyles* is indeed far from exceptional. An almost identical distribution is found in the plant genus *Acridocarpus* (Malpighiaceae), with sister species present in New Caledonia and Madagascar/Mauritius (Fig. 3). A tectonic mechanism for this disjunction was precluded by Davis *et al.* (2002a) who converted a minimum fossil calibrated age of 63 Ma to justify chance dispersal from Africa to Madagascar, then across the Indian Ocean to New Caledonia ~15-8 mya (Davis *et al.* 2002b, Guesdon *et al.* 2019, da Costa Santos *et al.* 2023). As with the hawkmoth study, the centre of origin and chance dispersal brought little clarity, only a 'perplexing' biogeographic questions about 'discordant' elements (meaning the relationships do not make any sense to the authors).

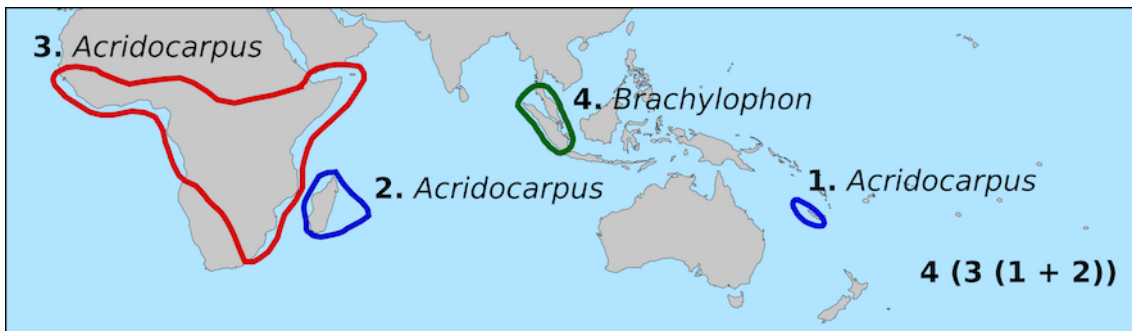


Fig. 3. Distribution and phylogeny of *Acridocarpus* and its sister genus *Brachylophon*. From Davis *et al.* (2002b, 2010).

A vicariance origin for *Acridocarpus* and its sister group *Brachylophon* is consistent with allopatry of the four principal clades, and does not require speculations on unobserved chance dispersal events (Heads 2014a). An initial divergence occurred between *Brachylophon* and the ancestor of *Acridocarpus*. Within *Acridocarpus*, the African clade (clade 3) separated from the common ancestor of the Madagascar/Mauritius and New Caledonia species. The only evidence of geographic dispersal is the distributional overlap of two subclades (not shown here) within the African range. The phylogenetic break between the African and New Caledonia/Madagascar clades is at the Mozambique Channel, which has a tectonic age of about 145 Ma (Phethean *et al.* 2016, Dasgupta & Mukherjee 2017).

A mainland African connection to New Caledonia is seen in the genus *Cunonia* (Cunoniaceae) present in New Caledonia and the Western Cape region of South Africa only (Fig. 4). The immediate sister group of *Cunonia* is the New Caledonian endemic genus *Pancheria* (clade 2), followed by a widespread clade (clade 3 + 4) extending between the western Pacific and Madagascar, overlapping with *Cunonia* only at New Caledonia. These taxa are collectively the sister group to *Weinmannia* section *Weinmannia* (clade 5) in the New World and the Indian Ocean islands of Mauritius. The 'basal' sistergroup of all these clades is *Vesselowskya* of central-eastern Australia.

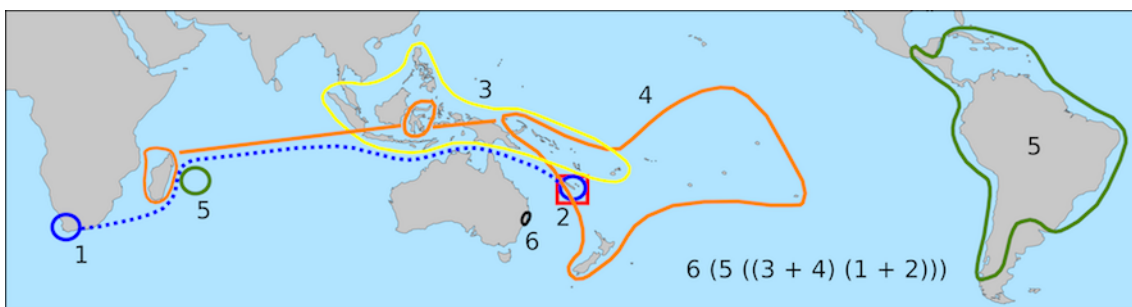


Fig. 4. Distribution of tribe Cunoniaceae (Cunoniaceae). Clades: 1 – *Cunonia*, 2 – *Pancheria*, 3 – *Weinmannia* sections *Inspersae* *Spicatae*, *Leiospermum*, 4 – *Pterophylla* section *Fasciculatae*, 5 – *Weinmannia* section *Weinmannia*, 6 – *Vesselowskya*. Distribution from Heads (2010), phylogeny from Pillon *et al.* (2021).

Pillon *et al.* (2021) attributed the distribution of Cunoniaceae to chance dispersal from a centre of origin in Australia/New Guinea/New Caledonia derived from ancestral area analysis. As noted by Heads (2012), this would require a convoluted series of improbable 10,000-km-long dispersal events. The New World-Mauritius disjunction (clade 5) was characterized by Pillon *et al.* (2021) as perhaps one of the most intriguing dispersal events known, but did not explain why. That this 'intriguing' relationship also occurs in the palm tribe Chamaedoreae was considered noteworthy, but elicited no further insight. And the sister species of *Dietes* in eastern Africa and Lord Howe Island east of Australia was also considered worthy of mention, but again without additional clarity. A centre of origin was found for the Cunoniaceae because the idea was built into the ancestral area analysis (e.g. BioGeoBears). The centre of origin and chance dispersal model failed to provide any

coherent insight into why the the principle clades Cunonieae (1+2, 3+4, 5, 6) are globally allopatric, other than at New Caledonia. In contrast to the lack of biogeographic clarity based on improbable chance events, a vicariance differentiation sequence for the Cunonieae is uncomplicated. The ancestral Cunonieae has differentiated around two principle evolutionary centres (or nodes): the southwestern Pacific, and southwestern Indian Ocean, resulting in a phylogeny that gives the appearance of repeated long-distance dispersal jumps (Heads 2012).

As noted by Pillon *et al.* (2021), the genus *Dietes* includes a sister species relationship between Lord Howe Island, and East Africa (Fig. 5). The next sister group is a clade of three genera (*Bobartia*, *Ferraria*, and *Moraea*) distributed across much of sub-Saharan Africa, the Mediterranean and central Asia. Goldblatt (1981) regarded this to be one of the “puzzles” of plant geography. Downing *et al.* (2020) thought the Lord Howe Island species to be a “biogeographical enigma” for which long distance (chance) dispersal was the only 'reasonable' explanation. Presumably the same 'reasonable' explanation would be required for the daisy *Lordhowea* (Asteraceae) of Lord Howe Island/eastern Australia that is disjunct from its South African sister group *Phaneroglossa* (cf. Heads 2014a, Schmidt-Lebuhn *et al.* 2020).

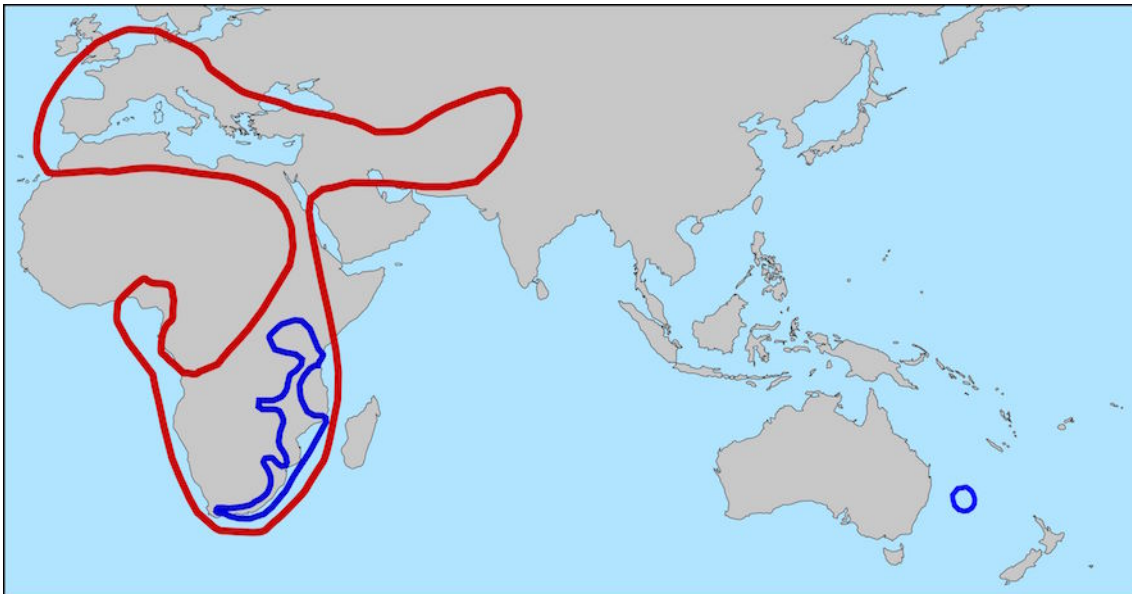


Fig. 5. Distribution of *Dietes* (blue outline) and its sister group (red outline) comprising *Bobartia*, *Ferraria*, *Moraea*. Distribution of *Dietes* from Goldblatt (1981), sister group generalized from description in Goldblatt *et al.* (2008) and GBIF.

Goldblatt *et al.* (2008) proposed an Antarctic-Australasia centre of origin for Iridaceae based on the presence of basal clades in Australasia. As with previous examples, no evidence was offered for correlating basal clade location with a centre of origin. The estimated age of *Dietes* was given as ~45 Ma, but this fossil calibrated estimate is a minimum age only. The geological age of Lord Howe Island is about 9 Ma, whereas *Dietes* could have persisted in the region for tens of millions of years, as a metapopulation occupying former islands in the region from Mesozoic time (cf. Heads 2014a). Disjunctions between the western Pacific and Africa/Madagascar are not confined to small islands. In the tribe Ceroyaleae, the palm genus *Oraniopsis* occupies a small, 'island-like' area of continental Australia (Fig. 6). It is geographically disjunct from *Ravenea* in Madagascar, but the immediate sister group is *Ceroxylon* of the northern Andes and *Juania* of the Juan Fernandez islands (Trénel *et al.* 2007). These genera together form the sister group of *Ravenea* in Madagascar and Comoros. Further basal lineages are located in the Caribbean and South America (Fig. 6).



Fig. 6. Distribution and phylogenetic sequence of Ceroxyleae palms (from Trénel *et al.* 2007).

For the Ceroxylaceae, Trénel *et al.* (2007) explicitly agreed with Heads (2005) that fossil calibrated nodes must always be recognized as minimum ages, and then rejected this reality because a Gondwana tectonic calibration would render an age of 245-172 Ma for the Ceroxylaceae. But this objection only applies if the molecular clock rate is constant throughout the existence of a taxon. The basal phylogenetic break in the Ceroxyleae is located between the Yucatan-Antillean arc (*Pseudophoenix*) and northern South America. This phylogenetic break corresponds to the Late Cretaceous insertion of the Greater Antillean arc between North and South America (Barrera-Lopez *et al.* 2022). The western boundary of Ceroxyleae corresponds to the 145 Ma age separation of Madagascar through opening of the Mozambique channel. These tectonically correlated ages are not precluded by fossil calibrated divergence estimates because they represent minimum clade ages only.

Indian Ocean disjunctions are so numerous as to be almost beyond count (Croizat 1958, 1968, Craw *et al.* 1999, Heads 2010, 2014a, Parenti & Ebach 2013). The *Compsulyx-Batocnema* disjunction only stands out because New Caledonia is a small area that is geographically isolated from the Indian Ocean by continental Australia. The spatial relationships and distributional boundaries represented by the New Caledonia, Lord Howe Island, and Queensland disjunctions are repeated with more widely distributed taxa such as the *Hybanthus* group of violets (Violaceae) with a clade distributed in Africa, India, southeastern Asia, Australia, and New Caledonia (Fig. 7). This clade (clade 1) is allopatric to its sister group other than New Caledonia (cf. Cunonieae in Fig. 4), and central-eastern Australia, and yet the sister group is widespread across other regions of the West Pacific, Hawaii, and the New World. The Australian overlap corresponds to a major biogeographic boundary and centre of diversity known as the MacPherson/Macleay overlap, (Heads 2014a, Grehan & Mielke 2018, Heads *et al.* 2023). This node is located at the Clarence Moreton Basin that formed by Late Triassic to Early Cretaceous time. Closure of this basin could have been responsible for the local overlap between clades 1 and 2 by normal ecological dispersal.

A similar distribution range and pattern of allopatry occurs in the lizard genus *Cryptoblepharus* (Fig. 8). An East Africa/Madagascar/Mauritius and Australia/southeastern Asia/New Caledonia clade is allopatric to a trans-Pacific clade with the boundary occurring between Fiji, Solomon Islands, and Micronesia (Grehan 2021). There is no dispersal 'barrier' at the phylogenetic break between the two clades. Rather, the break occurs at the boundary of Indian Ocean and Pacific tectonic basins.

Tectonic details

Centre of origin and chance dispersal approaches overlook details of distribution that are tectonically pertinent. The hawkmoth sister group of the *Compsulyx-Batocnema* clade is not to be found in the nearby Asian clades, but across the Pacific in the New World (*Protambulyx*). The next sister group is another New World clade before the initial divergence of the East Asian clade (5 + 6). No wonder Timmermans *et al.* (2019) found themselves confronted with 'complex scenarios' for chance dispersal. In a vicariance context, the phylogeny represents sequences of local differentiation that are now disjunct across the Pacific basin.

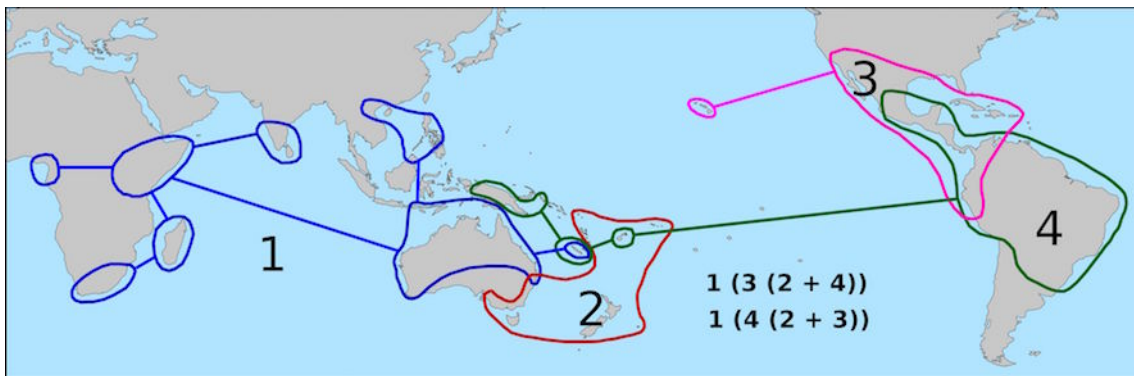


Fig. 7. Distribution of principal lineages of the '*Hybanthus*' (Violaceae) group. The Indian Ocean clade (1) is represented in New Caledonia and is the sister group of a trans-Pacific group (2, 3, 4) with two potential alternative relationships for clade 2. Simplified from Heads (2010: fig. 13).

The Pacific region includes endemic groups, allopatric distributions, allopatric mainland sister groups, and trans-Pacific disjunctions (Heads 2012, 2014a, Heads & Grehan 2021). These biogeographic features are consistent with widespread ancestral ranges fragmented by Pacific plate expansion. Convergence of Indian and Pacific Ocean taxa is often found between Southeast Asia and Australasia, a region well known for a melding of island arcs, continental fragments, and large, igneous plateaus with sub-aerial islands (Heads 2012). Within this region of convergence, *Hybanthus* of New Caledonia marks the intersection between an Indian Ocean clade (clade 1) with a trans-Pacific clade (clade 4). Clade 4 also occurs in Fiji and New Guinea which are located along a former subduction zone (Vitiiaz Arc). Between Fiji and New Guinea, some islands were displaced south by expansion of the North Fiji Basin ~10 Ma (Fig. 9). One result was for a portion of the Pacific clade along the Vitiiaz arc being brought into contact with the Indian Ocean clade in New Caledonia. This geographic and tectonic relationship with the Vitiiaz Arc is seen in various other western Pacific taxa (Heads 2014a, 2023, Grehan & Mielke 2020, Ferguson *et al.* 2023), and cannot be scientifically dismissed as uninformative 'chance'.

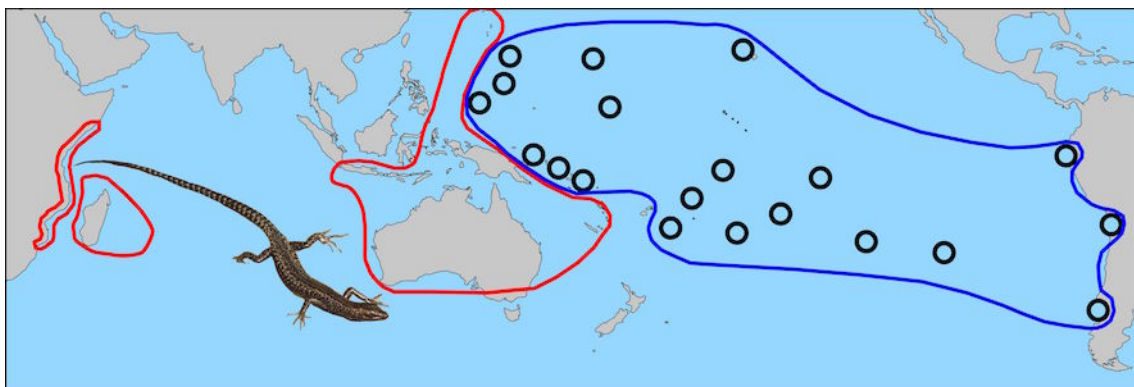


Fig. 8 Distribution of *Cryptoblepharus* lizards (Scincidae). Clades indicated by red and blue outlines. See Grehan (2021) for details.

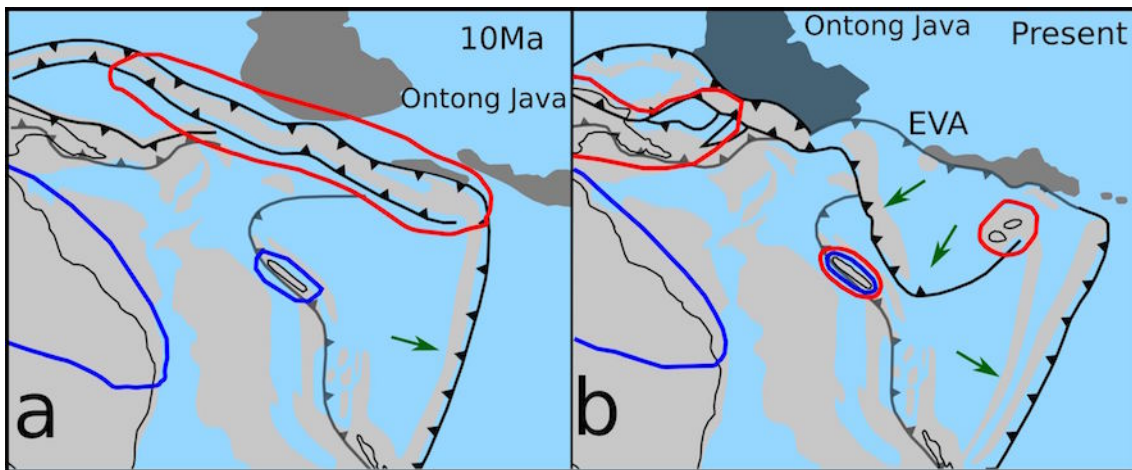


Fig. 9. Conceptual model of how the trans-Pacific *Hybanthus* clade (red outline) originally ranging along the Vitiiaz Arc (a) is partially displaced south by expansion of the North Fiji basin (b), resulting in overlap with the Indian Ocean clade (blue line) in New Caledonia. Green arrows - direction of plate movement. EVA = extinct Vitiiaz arc. Dark grey shading – magmatic plateaus. Tectonic model modified from Heads (2014a).

By the late Cretaceous time, ~77 Ma, terrestrial environments on or around what is now New Caledonia were geographically isolated from the rest of East Gondwana by extensive marine incursion (Strogen *et al.* 2024). Some biogeographers have proposed complete submergence of New Caledonia prior to 37 Ma, and that its biota must be of recent origin, but there is no single marine stratum across all, or even most of the island. Even if large portions of New Caledonia were submerged at any one time, there is no geological evidence to exclude the continuous presence of small islands in this region. New Caledonia is surrounded by submerged islands, including flat-topped seamounts representing former islands eroded by wave action to sea level before subsiding below sea level (Heads 2010, 2023). In this geological context, the Ambulycini hawkmoths and other taxa could survive from Mesozoic time as metapopulations by sequentially colonizing multiple islands, especially those that would have existed along the New Caledonia subduction zone.

The presence of *Cryptoblepharus*, *Cunonieae*, and *Acridocarpus* on Mauritius might be regarded as recent arrivals from other regions as the island is geologically young at ~9-8 Ma (Paul *et al.* 2007, Ashwal *et al.* 2017). However, as with New Caledonia, the inhabitants of the Mauritius could represent long-term metapopulation persistence from Mesozoic time. The Mauritius is part of a hotspot track extending between Réunion and the Deccan Large Igneous Province of India that formed ~65 Ma. Mauritius is underlain by a continental fragment that Ashwal *et al.* (2017) argued was originally wedged between Madagascar and India until 90-85 Ma (Fig. 10a) when the Marion Plume (now represented by Réunion island) covered much of Madagascar with flood basalts. This region broke apart and the fragments were tectonically displaced to their current positions (Fig. 10b).

Volcanic activity along the hotspot track from 90 Ma to the present would result in a series of sequential islands at or near Mauritius that could support metapopulations of Mesozoic biota long after continental displacement (see Heads & Grehan 2021 for the Galapagos as a comparable example). Even classically 'oceanic' islands such as Hawaii can support ancient life surviving within the Pacific on a multitude of former islands now evident as submerged seamounts in the Hawaiian region (Heads 2012: fig. 7-2). These metapopulations were part of ancestral ranges sometimes extending across both the Pacific and Indian ocean regions (such as (*Hybanthus* and *Cryptoblepharus*). The ancestral ranges (established by normal ecological dispersal) were subsequently displaced or disrupted by tectonic extension (seafloor spreading) and convergence (at subduction zones).

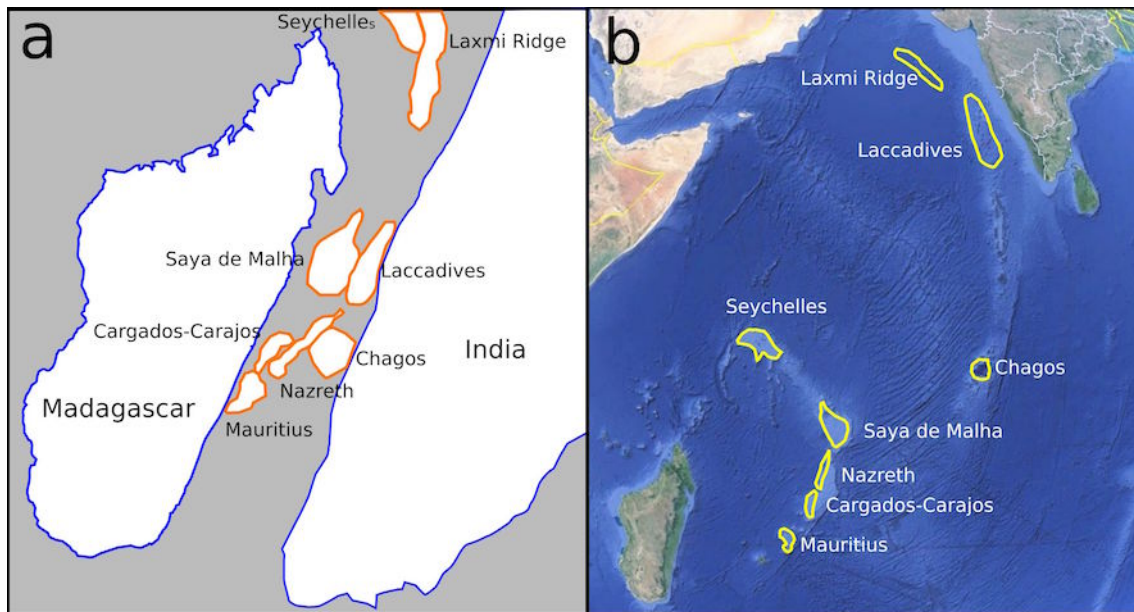


Fig. 10. Conceptual model for the location of East Indian Ocean islands and seamounts (orange outline) between Madagascar and India at 90 Ma (a) and their current location resulting from tectonic displacement (b). Modified from Ashwal *et al.* (2017).

Allopatric sister taxa disjunct across the Indian Ocean may be the result of single fragmentation event, but a more complex history is indicated by the distribution of *Cunoniae* where there is a 'layering' of parallel arcs across the Indian Ocean and Western Pacific (Heads 2012). A northern arc comprises clades 3 and 4 between Madagascar and the western-central Pacific. Next is the *Cononia* clade (1 + 2) of southern Africa and New Caledonia, followed by clade 5 of the New World and Mauritius, and lastly clade 6 of the Macleay-McPherson Overlap (Fig. 4). Parallel arcs are found in many taxa, and cannot be coherently explained by appealing to chance dispersal, or to a single fragmentation model (Heads 2012). The *Cunoniae* pattern conforms to a process of sandwiching different clades together by displacement of Gondwana terranes moving north across the Tethys Ocean and accreting to southern Laurasia (Fig. 11).

Absence of Indian Ocean taxa from Australia may be the result of extinction, and this is sometimes evident by the presence of fossil relatives such as '*Weinmannia*' in Australia where this genus is now absent. But it is also possible for some African-western Pacific taxa to have 'bypassed' most or all of Australia as suggested for *Acridocarpus* by Heads (2014a). This could occur with ancestral ranges that extended across East Antarctica, resulting in a fragmented range for the Indian Ocean Ambulycini hawkmoths that does not include Australia (Fig. 12). This model is not the centre of origin-chance dispersal theory that treats Antarctica as a chance dispersal land-bridge. Instead, it recognizes the continent was host to an ancestral biota with widespread distributions over parts of southern Gondwana.

Vicariance or centres of origin and chance dispersal?

Acceptance of centre of origin-chance dispersal biogeography in many Lepidoptera studies is not proof of its ability to provide coherent and consistent reconstructions. For the examples discussed here, there is a smorgasbord of 'unclear' and 'complex scenarios', 'enigmas', 'discordant elements', and 'discrepancies'. The biogeographer is left with 'perplexing' questions and 'puzzles'. Ancestral areas analysis provides the appearance of authenticity by obscuring or ignoring the fact that paraphyletic area relationships that generate sequential dispersal can also be the result of sequential vicariance (Heads *et al.* 2023). Phylogeny is not biogeography, even if Lepidoptera studies continue to assume otherwise (e.g. Taberer 2023).

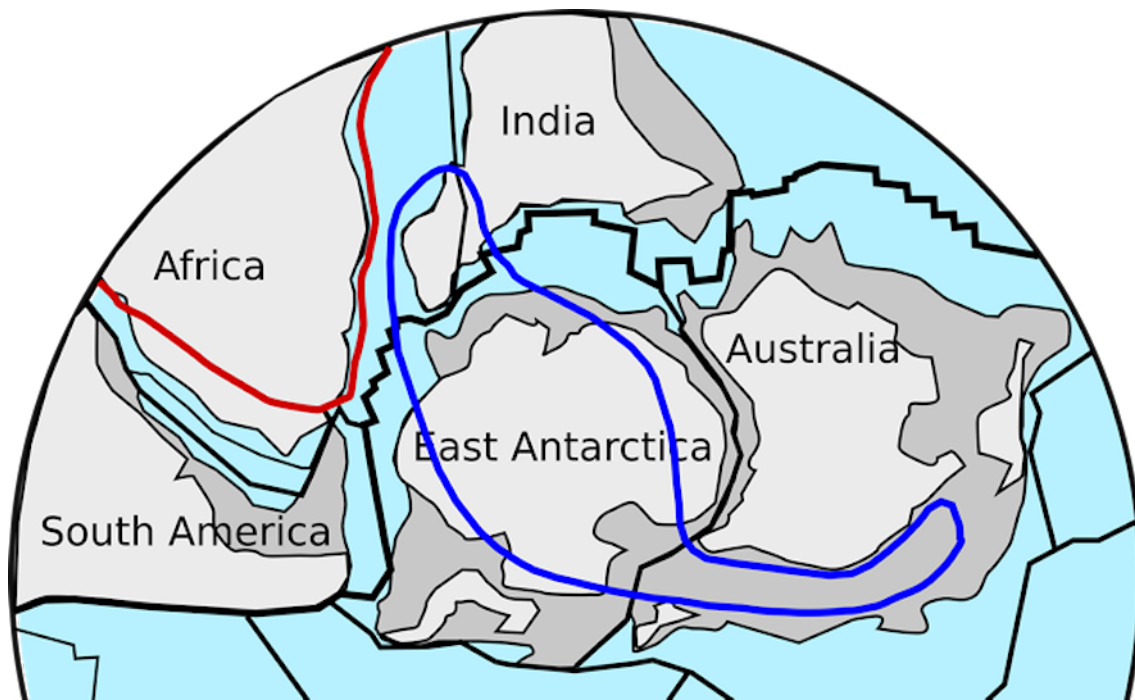


Fig 11. Generalized conceptual map of tectonic displacement along northeastern Gondwana showing separation and northern movement of portions of Southeast Asia ~130 Ma. Modified from Van de Lagemaat *et al.* (2024).

There is no empirical evidence for identifying a centre of origin where the basal sister group is found, either for Ambulycini hawkmoths or any of the other taxa presented here. This is only one of 13 (sometimes contradictory) arbitrary criteria that have been invented for identifying an imagined centre of origin. According to Cain (1943), the assumptions involved have, in many instances, “so thoroughly permeated the science of [bio]geography and have so long been a part of its warp and woof that students in the field can only with difficulty distinguish fact from fiction.”

Chance dispersal explanations are given the appearance of credibility where molecular divergence estimates represent a transmogrification of minimum ages into estimates that are represented as actual (often as a mean value with a probability range) or maximal ages. This conversion involves transmogrification because it involves changing one thing (a minimum age) into something else (actual or maximum age). Transmogrification is necessary because fossil or island calibrated ages can only be minimum estimates since fossil or island ages provide only minimum ages. Fossil ages give the age of the oldest fossil, not necessarily the oldest age of the taxon, and island ages may represent an underestimate due to covering of older strata, or the taxon may originate on an older former island in the vicinity. Under these empirical circumstances, statistical constraints used in many studies cannot empirically constrain the upper age limit of a taxon (Heads 2005, 2012, 2014a,b, 2017; Nelson & Ladiges 2009; Parenti & Ebach, 2013; Parenti 2017; Heads & Grehan 2021; Heads *et al.* 2023; Mahlfeld & Parenti 2023). Calibrations using multiple biogeographic events provide an independent estimation of actual (rather than minimum) phylogenetic age to those based solely on fossil or fossil calibrated extrapolations (see Heads 2012, Heads *et al.* 2023 for *Coenonymphina* butterflies). Arguments that molecular clock extrapolations of tectonic correlations may render impossibly old estimates for higher taxa are not sustainable because a universal linear relationship between molecular divergence and time is not to be expected, even by molecular clock theorists (e.g. Bromham & Penny 2003). And rate changes may occur both at phylogenetic nodes and along branches (Bromham 2017). At best, the molecular clock may be considered as extremely relaxed and very local so that upper age limits cannot be imposed from fossil or island age calibrations (Heads 2012). Bromham (2006) doubted whether molecular clocks could ever be trusted at all. The phylogenetic and geographic approach outlined here (panbiogeography) utilizes the results of molecular studies with the caveat that calibrations render minimum ages only (as

sometimes admitted, even if inconsistently, by molecular biogeographers), and that ancestral area analysis may generate artificial vicariance or chance dispersal events.



Fig. 12. Conceptual illustration of widespread ancestral range (blue outline) of taxa such as *Acridocarpus* and *Ambulycini* hawkmoths connecting Madagascar and New Caledonia via East Antarctica. Australia may be marginally occupied or bypassed. Model modified from Heads (2014a).

Reliance on fossil or island calibrated molecular clocks has widely led to a premature erasing of vicariance-based explanations rather than encouraging investigations into why molecular clock dated phylogeny conflicts with vicariance analysis (Marinov 2015, Mahlfeld & Parenti 2023). Centre of origin-chance dispersal molecular studies cannot provide coherence in biogeography because everything is reduced to 'chance' (Heads 2014b). Because everything is chance, the actual geography of clades is not seen as informative, other than as a few artificial area units plugged into vicariance-dispersal programs. It is as if the real geography of distribution is the enemy of biogeography. And centre of origin-chance dispersal biogeography requires little effort. There is no need to understand geology and tectonics, or understand how any one taxon distribution may be related to any other in general (Heads 2014b). The assumption of long-distance dispersal was described by Cain (1944: 305-306) as a careless and easy way out of a difficult problem and it leads to fanciful and even ridiculous conclusions. Crisp *et al.* (1999) considered some Indian Ocean disjunctions, including *Cunonia*, and *Dietes*, to be rather bizarre and unique inexplicable events. And yet decades earlier, Good (1950) realized that the New Caledonia-Madagascar relationship required explanations better than chance or coincidence alone. Very soon after, Croizat (1952) gave

substance to this assertion by showing how the biogeography of New Caledonia was integrated with the global phylogenetic and geographic structure of life.

The idea that trans-oceanic chance dispersal is plausible for disjunct hawkmoths appears to be exemplified by long-distance migratory species and other species with very wide distribution ranges. But this conflation of flight ability and the origin of disjunct allopatry is ecologically problematic. Hawkmoths are similar to hummingbirds in that they are both extremely agile, swift fliers and hover over flowers to feed. The morphology of adult hawkmoths is reminiscent of a fighter jet, with a low surface area to weight ratio that lends itself to speed and agility. This in turn means the moths have high metabolic requirements and must feed very regularly. Migratory species may cover very long distances, but they need to feed regularly enough by recognizing multiple flower sources as a consequence of meeting their energy demands (Stöck & Kelber 2019). These energetic and ecological requirements are not conducive to trans-Indian Ocean dispersal events.

The Madagascar-New Caledonia disjunction of the Ambulycini hawkmoths is fully consistent with allopatric divergence within the range of a widespread ancestor. This is falsified neither by calibrated divergence estimates that represent minimum ages of taxa, nor by ancestral areas analysis that rely on non-empirical chance dispersal between non-empirically existent biogeographic areas. The fact that Ambulycini biogeography is consistent with the biogeography of plant and animal life in general is empirical evidence that the geographic and phylogenetic origin of this hawkmoth group is not an accident of chance. Rather, it is an integral part of the global structure of biodiversity biodiversity (cf. Grehan 2021). There is no evidence that *Compsulyx* ever left Madagascar to fly to New Caledonia. For these moths, a biogeographic explanation of Earth and Life evolving together is a more compatible explanation for their current distribution given their biogeographic context and energetically expensive ecology, rather than an implausible chance dispersal event over vast areas of ocean in the absence of food resources.

Acknowledgments

We are grateful to Ulf Buchsbaum (Zoologische Staatssammlung München, Germany), Jorge Gonzalez (University of Florida, Gainesville, Florida, USA), Ian Kitching (Natural History Museum, London, UK), Théo Léger (Museum fuer Naturkunde Berlin, Germany), Greg Pohl (Natural Resources Canada, Edmonton, Alberta, Canada), Rodolphe Rougerie (Muséum National d'Histoire Naturelle, Paris, France), and Thierry Salesne (New Caledonia) for information during development of this article. We thank Jeremy Holloway (Natural History Museum, London, UK), Lynne Parenti (National Museum of Natural History, Washington DC, USA), Karin Mahlfeld and Frank Climo (Openlabnz, Wellington, New Zealand), and two anonymous reviewers for feedback.

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Submitted: 27 April 2024

Accepted for Publication: 13 June 2024