The Chatham Islands (Rēkohu) biota as a fragment of East Gondwana biodiversity

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During my younger and more acquisitive days of insect collecting I sometimes found myself gazing wistfully at a red admiral butterfly (*Vanessa gonerilla*) as it rapidly swept by on a prevailing breeze, out of reach and too fast to catch. It seemed obvious to me that this was a fast moving species that could get around almost anywhere. This would seem to be corroborated by its widespread distribution across New Zealand (Gibbs 1980). But not quite everywhere. The species is noticeably absent from the Chatham Islands, where instead is found the closely related species (or subspecies) – the Chathams Island admiral, *V. ida* (Fig. 1).

The distributional difference between the two species raises some obvious questions. If the red admiral is so mobile, why is it absent from the Chathams? And if the Chathams are out of reach of the red admiral, how did the ancestor of the Chatham Islands admiral end up there? A further complication is the distribution of the closely related yellow admiral, *Vanessa itea*, widespread in both Australia and New Zealand but not the Chatham Islands. Perhaps one might argue (as so many have for various plants and animals) that the red admiral ancestor originally flew across the Tasman Sea to New Zealand from Australia. But there is no actual evidence for this. And if the yellow admiral can cross the Tasman, how did the red admiral ever achieve the geographic isolation necessary for divergence?
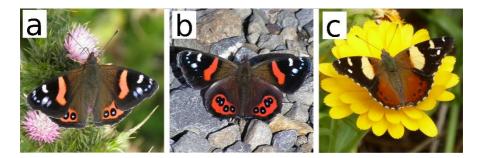
Fig 1. Australasian red admiral group: (a) *Vanessa ida,* Chatham Islands. Photo courtesy of Niklas Holmström, zealand2010.blogspot.com/2010/11/chatham-islands-on-12-16th.html, (b) *V. gonerilla,* mainland New Zealand. Photo by Tony Wills, Creative Commons Attribution-Share Alike 3.0 Unported, (c) *V. itea,* mainland New Zealand. Photo courtesy of Aalbert Rebergen inaturalist.org/observations/56491887.

The Australasian admirals are an example of the classic biogeographic contrast between ability of individuals to move about over great distances and the existence of allopatry (related taxa in different places). When attempts are made to explain allopatric distribution by accidents of movement (chance dispersal), one ends up in a quagmire of contradictions, because allopatry requires divergence in geographic isolation which cannot exist if a locality is permeable to movement or migration. One argument around this problem is to imagine that dispersal is a 'chance' process of exceptional events that almost always succeeds only once in each taxon by events or mechanisms sometimes characterized as mysterious, or even miraculous (Heads 2014a).

The co-existence of allopatry and mobility is not inconsistent if movement is not treated as a mechanism for differentiation or divergence. The movement of organisms (called ecological dispersal) is empirically observable and can explain the survival of species metapopulations and even range expansion, but it does not explain divergence which requires isolation. Conceptual integration of the two processes (ecological dispersal

and divergence) recognizes that dispersal maintains a biological continuity between populations while allopatric divergence occurs when that ecological continuity is disrupted by geological or climatic events that isolate populations from each other (a process known as vicariance). In a vicariance model the allopatric descendants have not individually moved or dispersed to their respective areas, but have diverged within the geographic range of the common ancestor. A vicariance approach does not reject dispersal (as erroneously claimed by some critics), but it does reject imaginary chance dispersal for explaining allopatric divergence.

The vicariance model provides a coherent explanation for the Australasian admiral butterflies. A widespread ancestral range encompassed what is now Australia, mainland New Zealand, and the Chatham Islands. With respect to phylogenetic sequence (Craw 1990), the first divergence separated *V. itea* of Australia and New Zealand, and this was followed by divergence between *V. gonerilla* of mainland New Zealand and *V. ida* Chatham lineages (Fig. 2). Ecological dispersal is responsible for establishing the ancestral range (Fig. 2a) within which each species then locally diverges (Figs 2b, c). The present geographic overlap between *V. itea* and *V. gonerilla* in mainland New Zealand is evidence of subsequent range expansion by *V. itea* (Fig. 2d; Craw 1990, Heads 2017).

Geological events spatially correlated with divergence of the Australasian admirals include formation of the southern Tasman Sea at about 80 Ma, and submergence of the Chatham Rise (other than emergent volcanic islands) by about 65 Ma. This tectonic correlation supports the existence of these butterfly lineages at the end of the Mesozoic as part of New Zealand's original 'Gondwana' biodiversity. This model cannot be contradicted by more recent molecular divergence dates based on fossil calibrations (as many authors argue) because the date of the oldest fossil only gives a minimum age for the group. Any molecular extrapolations from this are therefore minimum ages only, and do not represent empirical evidence of phylogenetic age (Heads 2017, 2019).
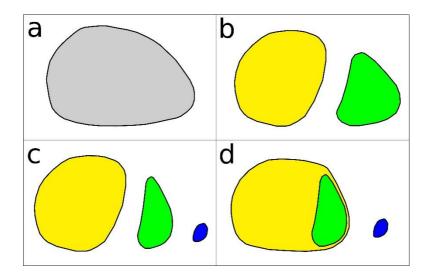
Fig. 2. Generalized vicariance model for the origin of the Australasian admiral butterflies: (a) ancestral distribution range in Australia, New Zealand mainland and the Chathams. (b) differentiation of *Vanessa itea* (yellow shading), and common ancestor of the New Zealand species (green shading), (c) allopatric differentiation of *V. gonerilla* (green shading) and *V. ida* (blue shading), (d) subsequent range expansion by *V. itea* resulting in geographic overlap with *V. gonerilla* in mainland New Zealand.

The admiral butterfly example demonstrates a biogeographic pattern that is consistent with the Chatham Islands being part of the ancestral range of this butterfly group at the end of the Mesozoic, implying that the local species has persisted at these islands for at least 65 million years. Patrick and Patrick (2012) similarly concluded that the origin of *V. ida* was the result of major geographic changes along the Chatham Rise rather than by overseas chance dispersal. This evolutionary history has been recognized by only a few scholars (e.g. Mahlfeld 2008 for land snails), but the phylogenetic and geographic relationships are consistent with the Chatham

Islands' biota having originated locally and persisted in the region from Mesozoic time (Heads 2017).

During the Mesozoic, the Chatham Rise was aligned with the east coast of the North Island along the eastern margin of Gondwana, and later of Zealandia after this continental block had separated from Antarctica and Australia (Fig. 3a). About 100 Ma the Hikurangi Plateau collided with the Chatham Rise. This plateau is a fragment of the super-Plateau Ontong Java Nui that formed in the central Pacific about 125 Ma and is estimated to have been the size of Australia (Chandler *et al.* 2012). The plateau initially subducted beneath Gondwana until the subduction zone became choked and subduction stopped. This collision coincides with the formation of a new tectonic fault zone or rift that was the precursor of the Alpine fault (Fig.3a). By 45 Ma there was sinistral movement (left direction on the opposite side when facing the fault) along this fault, but this was later reversed by dextral movement in the modern Alpine Fault about 23 Ma resulting in an anticlockwise and southward translocation of the western South Island (van der Meer *et al*. 2017, Mortimer 2018, Lamb & Mortimer 2020, Riefstahl *et al.* 2020). The former Pacific coast of Zelandia became a triangular indentation now occupied by the remains of the Hikurangi Plateau; the Chatham Rise and North Island are positioned on the southern and northern margins of the plateau respectively (Fig. 3b).

The stratigraphic record is often ambiguous or lacking information relevant to biogeographic questions, especially when much of the landscape is submerged and difficult to access, as is the case for most of the Chatham Rise. Uplift and emergence of the modern Chatham Islands is usually presented as being less than 5 m.y. old, and while some molecular studies have assumed this to be the oldest possible age for Chatham Island organisms, other molecular studies have predicted divergence ages older than the current islands (Heads 2011). These older dates are not surprising if there were earlier islands already present at or near the modern Chathams. From the limited volcanic deposits on the current islands there is evidence of widespread eruptions at 63-55 Ma, 42-34 Ma, 6 Ma, and 5-3 Ma (Campbell 2008, Campbell *et al*. 2008). Remnants of other former volcanic islands may be present, but eroded, buried, or submerged beneath
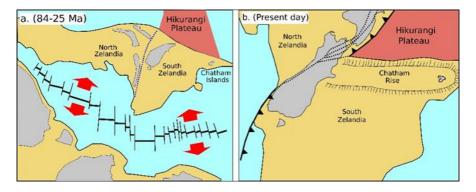
Fig 3. Position of the Hikurangi Plateau and the eastern margin of Zealandia in (a) the Late Cretaceous – early Cenozoic and (b) the present day. Red arrows – direction of seafloor spreading between Zealandia and Antarctica and Australia; dotted line in 'a' – approximate position of pre-Alpine Fault; dotted line in 'b' – present day faults; toothed line – subduction zones with barbs on the overriding plate. Chatham Rise outline generalized. Modified from van der Meer (2020: fig. 1).

the sea. Many submarine volcanoes occur around the southern rim of the Chatham Rise and near the Chatham Islands (Rowden *et al.* 2005, Timm *et al.* 2014).

At the western end of the Chatham Rise there are numerous submerged volcanic cones, some up to 2 km in diameter. Most have a horizontal surface indicating that they were subject to sea level erosion (Collins *et al.* 2011). In addition to volcanic islands, faulting may also contribute to subaerial emergence of the Chatham Rise, and major faults occur on the Chatham Islands. Marine sediments at the highest point on the Chatham Islands may not indicate submersion of the entire island if, as the evidence suggests, there was differential uplift and subsidence on multiple faults (see Heads 2015, 2017 for further details).

The available volcanic evidence indicates sustained activity and volcanic islands at or near the present-day Chatham Islands throughout the

Cenozoic (Fig. 4). A continuous series of islands over time would allow animal and plant taxa to survive on the Chatham Rise from Mesozoic time to the present.
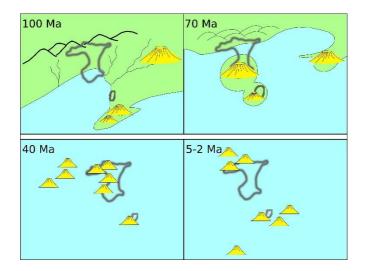

Fig. 4. Minimal snapshots over time showing the presence of subaerial volcanic islands on or near the modern Chatham Islands (outlined in pale grey) from the time of East Gondwana (100 Ma) and early Zelandia (70 Ma) to the present. Green shading – terrestrial surface along Chatham Rise. Modified from Campbell (2008).

Geological evidence for island persistence at or near the Chathams from Mesozoic time to the present means that there is no need for the Chathams biota to have arrived from somewhere else, and it also explains otherwise anomalous biogeographic relationships involving the Chatham Islands (Heads 2017). For example, the two extinct species of flightless Chatham Islands rail, *Gallirallus modestus* and *G. dieffenbachii*, are not most closely related to rails on mainland New Zealand, as might be expected if

they were just recent strays that colonized the islands. Instead, they are part of a widespread group whose range includes South East Asia, and in which the first divergences separated *G. modestus* and then *G. dieffenbachii* from all other members of the clade (Garcia-R e*t al.* 2015). A vicariance origin for this group involves a widespread ancestral range between Okinawa and the Chatham Islands that locally diverged into its component species, with the earliest events separating the Chatham Islands lineages from the rest (Fig 5).
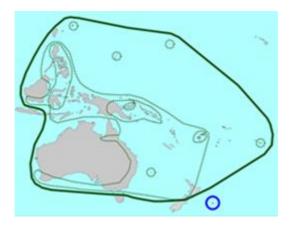

Fig 5. Distribution of rail clades. Blue outline - two basal lineages *Gallirallus modestus* and *G. dieffenbachii*, at the Chatham Islands; green outline – widespread clade; dotted lines – individual species with *G. philippensis* widespread between New Zealand, Australia, and southeastern Asia. Distribution data from Garcia-R e*t al.* (2015).

Another example of a 'basal' phylogenetic group in the Chathams and absent from mainland New Zealand occurs in the dipteran genus *Fannia*. The Chatham Island endemic, *Fannia mangarensis,* is the sister group of 16 other species in which the two basal species are *F. laqueorum* in Snares Island and *F. anthracinalis* in the Auckland, Campbell, Chatham, and Three Kings islands. All the other species are in Australia and South

America (Domínguez & Pont 2014). In this biogeographic pattern the Chathams species is part of a basal group that extends around mainland New Zealand, a pattern exemplified by the range of *F. anthracinalis* (Fig. 6). The distribution pattern is consistent with a vicariance origin involving a geographic sector or area that is now represented by 'off shore' islands and a broader region that now spans the south Pacific (Heads 2017). Speculations of chance dispersal do not make coherent sense of the geography or the standard characteristics of this pattern which is shared by many other taxa, including the trans-Pacific relationship. And it is not necessary to postulate chance dispersal anyway.
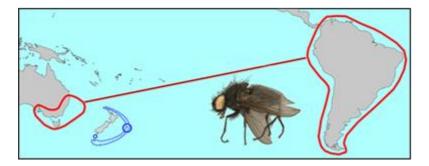

Fig 6. Distribution of a Chatham Islands *Fannia* flies with basal groups in the Chathams and other offshore islands around New Zealand (blue outline connected by dotted lines), and a trans-Pacific group (red outline).

While the modern Chatham Islands is a geographic outlier, this cannot be said of its biodiversity. The foregoing examples illustrate how the Chatham Islands is an integral component of both regional and global biodiversity. The origin of Chatham Island butterflies and rails is closely involved with the biogeography of southeastern Asia and western Pacific, but the *Fannia* flies illustrate another major global biogeographic pattern where New Zealand affinities span the Pacific Ocean (Craw *et al.* 1999, Heads 2014b, 2017). The Chatham Islands biota is also an integral part of

mainland New Zealand biodiversity, as illustrated by connections between the islands and the Alpine Fault. For example, the beetle *Pristoderus bakewelli* includes a clade on the Chatham Islands and Southland-Otago east of the Alpine Fault, while its sister clade is disjunct to the north and west of the Alpine Fault (Fig. 7a). That this is not a freak of nature is attested to by a similar pattern found in the plant genus *Libertia* (Fig. 7b). The Alpine Fault correlation shows how an originally contiguous distribution between the mainland and the Chatham Islands has been displaced by lateral fault movement beginning about 23 Ma (Fig. 7c). A similar tectonic impact has been identified for at least 225 other animal and plant taxa (Heads & Craw 2004, Heads 2017).
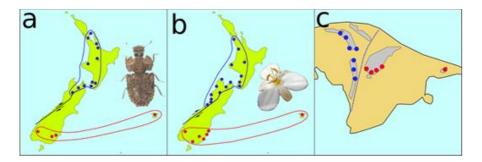

Fig 7. Biogeographic relationships between the Chatham Islands and the Alpine Fault: (a) Sister clades in *Pristoderus bakewelli* (Coleoptera: Zopheridae) (Heads 2017: fig. 9.7), (b) Sister species of *Libertia* (Angiosperms: Iridaceae) (Heads 2017: fig. 9.6), (c) positional relationships before Alpine Fault movement for *Pristoderus*.

The endemism and phylogenetic relationships of living Chatham Islands taxa, the molecular dates for clades that are older than the modern islands, and the geological evidence for continuous land in the area, all support the idea that the Chatham Islands biota is derived from widespread ancestors rather than stray derivatives from mainland New Zealand (Heads 2014a). The biogeographic patterns and their tectonic correlations demonstrate that

it is still possible to trace the geographic outlines of East Gondwana biodiversity back 100 million years, despite all the geological, geographic, and ecological upheavals over the period. A Gondwana timeline for Chatham Islands biodiversity is incredible only if one fails to recognize that organisms *are* dispersable and able to suvive and persist within geographically and geologically unstable environments over long geological periods. The Chatham Islands represent a classic example of species survival by dispersal and colonization of newer islands as the islands emerge from the sea, either through volcanic activity or tectonic uplift (as seen on the present day Chatham Islands and other oceanic islands such as the Canaries; Grehan 2017). Long term survival by sequential transfer of organisms from older to newer islands has been recognized for decades, even in traditional biogeography (Axelrod 1972). It is one of the principal lessons of evolutionary biology.

The Chatham Islands are biogeographically an integral part of the biodiversity of the rest of New Zealand (Craw 1988; Heads 1990). This geographic and phylogenetic structure means that biodiversity is not reducible to a collation of organisms, species, higher taxa or other biological units – the natural structure of biodiversity is all about relationships and connections, not isolation and uniqueness (Heads 2017). Efforts to divide up biodiversity into containers, such as 'natural' areas in conservation science, reflects a Euro-centric practice of creating boundaries that goes back to Imperial Roman times (Craw 1993). But biodiversity has no dividing lines. All places and taxa are evolutionarily connected, and in this respect the biogeographic approach (as outlined here) does not conflict with traditional Maori perspectives that also emphasize the interrelationships between places, but contrasts with government biodiversity methods that have failed to recognize the interconnected structure of New Zealand's biodiversity for over three decades (Grehan 2020).

This vicariance approach for the Chatham Islands integrates dispersal as an ecological process of range establishment, maintenance, and expansion of ancestral distributions that included the region now occupied by the present day islands. Subsequent disruption of that former continuity by

sinking of the Chatham Rise resulted in the geographic isolation of populations that survived on a series of volcanic islands, and possibly occasional subaerial emergence through tectonic faults. This reconstruction is compatible with, and incorporates, recent findings from research fields as varied as molecular phylogeny, molecular divergence, computational biology, and geophysics.

Perhaps the greatest potential of biogeographic mapping for advancing evolutionary biology is that it remains the great equalizer: it is a science accessible to anyone – amateur or professional – and does not require specialist skills in some arcane technique such as molecular algorithms or phylogenetic construction. Anyone can directly map the results of systematic and taxonomic studies to identify their geographic structures and tectonic relationships. Sometimes the best things in science are indeed the simplest.

References

Axelrod DI. 1972. Ocean-floor spreading in relation to ecosystematic problems. *University of Arkansas Museum Occasional Paper* 4: 15–68.

Campbell HJ. 2008. Geology. In: Miskelly, C. ed. *Chatham Islands: Heritage and Conservation*. Christchurch. Canterbury University Press. pp. 35–53.

Campbell HJ, Adams CJ, Mortimer N. 2008. Exploring the Australian geological heritage of Zealandia and New Zealand. *Proceedings of the Royal Society of Victoria* 120: 38–47.

Chandler MT, Wessel P, Taylor B, Seton M, Kim S-S, Hyeong K 2012. Reconstructing Ontong Java Nui: Implications for Pacific absolute plate motion, hotspot drift and true polar wander. *Earth and Planetary Science Letters* 331-332: 140–151.

Collins JA, Molnar P, Sheehan AF. 2011. Multibeam bathymetric surveys of submarine volcanoes and mega-pockmarks on the Chatham Rise, New Zealand. *New Zealand Journal of Geology and Geophysics* 54: 329–339.

Craw RC. 1993. Reciprocal traces: from Motherland to (M)otherlands. In: *The Body of the Land*. Dunedin, South Island Art Projects 1993. pp. 15–20.

Craw RC. 1988. Continuing the synthesis between panbiogeography, phylogenetic systematics and geology as illustrated by empirical studies on the biogeography of New Zealand and the Chatham Islands. *Systematic Biology* 37: 291–310.

Craw RC. 1990. New Zealand biogeography: a panbiogeographic approach. *New Zealand Journal of Zoology* 14: 527–547.

Craw RC, Grehan JR, Heads MJ. 1999. *Panbiogeography: Tracking the History of Life*. New York, Oxford University Press.

Dominguez MC, Pont AC. 2014. Fanniidae (Insecta Diptera). *Fauna of New Zealand* 71: 1-91.

Garcia-R JC, Elliott G, Walker K, Castro I, Trewick SA. 2015. Trans-equatorial range of a land bird lineage (Aves: Rallidae) from tropical forests to subantarctic grasslands. *Journal of Avian Biology* 46: 001–008.

Gibbs GW. 1980 *New Zealand Butterflies: Identification and Natural History.* Auckland, Collins.

Grehan JR. 2017. Biogeographic relationships between Macaronesia and the Americas. *Australian Systematic Botany* 29: 447–472.

Grehan JR. 2020. Conserving biodiversity as well as species. *Newsletter of the Otago Botanical Society* 90: 14–18.

Heads M. 1990. Integrating earth and life sciences in New Zealand natural history: the parallel arcs model. *New Zealand Journal of Zoology* 14: 549–585.

Heads M. 2011. Old taxa on young islands: A critique of the use of island age to date island-endemic clades and calibrate phylogenies. *Systematic Biology* 60: 1–15.

Heads M. 2014a. Biogeography by revelation: investigating a world shaped by miracles. *Australian Systematic Botany* 27, 282–304.

Heads M. 2014b. *Biogeography of Australasia: A Molecular Analysis.* Cambridge, Cambridge University Press.

Heads M. 2015. Biogeography by revelation: investigating a world shaped by miracles.*Australian Systematic Botany* 27: 282–304.

Heads, M. 2017. *Biogeography and Evolution in New Zealand*. Boca Raton, CRC Press. 636 pp.

Heads M. 2019. Recent advances in New Caledonian biogeography. *Biological Reviews* 94: 957-980

Heads MJ, Craw RC. 2004. The Alpine fault biogeographic hypothesis revisited. *Cladistics* 20: 184–190.

Lamb S, Mortimer N. 2020. Taking time to twist a continent—Multistage origin of the New Zealand orocline. *Geology* :49: 1–5.

Mortimer N. 2018. Evidence for a pre-Eocene proto-Alpine Fault through Zealandia. *New Zealand Journal of Geology and Geophysics* 61: 251–259.

Patrick BH. Patrick H. 2012 Butterflies of the South Pacific. Dunedin, Otago University Press.

Mahlfeld K. 2008. Land Snails. In: Miskelly, C. ed. *Chatham Islands: Heritage and Conservation*. Christchurch. Canterbury University Press. P. 124.

Riefstahl F, Gohl K, Davy B, Barrett R. 2020. Extent and Cessation of the Mid-Cretaceous Hikurangi Plateau Underthrusting: Impact on Global Plate Tectonics and the Submarine Chatham Rise. *Journal of Geophysical Research: Solid Earth* 125: 1–22.

Rowden AA, Clark MR, Wright IC. 2005. Physical characterisation and a biologically focused classification of "seamounts" in the New Zealand region. *New Zealand Journal of Marine and Freshwater Research* 39: 1039–1059.

Timm C, Hoernle K, Werner R, Hauff F, van den Bogaard P, White J, Mortimer N, Garbe-Schönberg D. 2014. Temporal and geochemical evolution of the Cenozoic intraplate volcanism of Zealandia. *Earth Science Reviews* 98: 38–64.

van der Meer, QHA, Waight TE, Scott JM, Munker C. 2017. Variable sources for Cretaceous to recent HIMU and HIMU-like intraplate magmatism in New Zealand. *Earth and Planetary Science Letters* 469: 27–41.