Ancient Mesozoic roots of New Zealand's ringlet butterflies (Lepidoptera: Satyrinae).

John R. Grehan

Research Associate, McGuire Center for Lepidoptera and Biodiversity, Florida, USA. calabar.john@gmail.com

Among the more obscure and rarely seen butterflies is the forest ringlet (*Dodonidia helmsi*). I never saw more than one individual at a time during my various forest excursions, until a visit to the Wi Tako Ngatata Scenic Reserve of Upper Hutt. As usual, I saw nothing of the butterfly even though I had previously reared an adult from a pupa collected at the reserve (Fig. 1). But at this time I happened to glance up at the beech forest canopy above. To my surprise, there was a cloud of about 20 forest ringlets flitting back and forth, just under the canopy. Perhaps this was a mating lek, but I did not think any more about it at the time, even though it was a rather astonishing sight. Not until decades later were these butterflies to again come to my attention in a biogeographic study of the New Zealand ringlet butterflies and their overseas relatives.

The forest ringlet is one of four butterfly genera endemic to New Zealand that together comprise a monophyletic group, the other three genera being *Erebiola* (Butler's ringlet), *Argyrophenga* (four species of tussock butterflies), and *Percnodaimon* (black mountain ringlet). The next most closely related group is made up of eight genera in Australia and New Guinea. This phylogenetic connection across the Tasman Sea presents two options for understanding the historical origin of the New Zealand ringlets – either they are the result of vicariance during the separation of the Zealandia continent from the rest of east Gondwana, or the ancestor of the New Zealand butterflies drifted across the Tasman Sea (a commonly invoked scenario based on the predominantly westerly winds and storms). These possibilities can be evaluated through biogeographic methods that examine the spatial relationships between phylogenetic breaks, or divergences, and the earth's tectonic structure. A recent study analysis by Heads, Grehan, Patrick, and Nielsen (2023) presents new evidence in support of a vicariance origin for the New Zealand ringlets in early Cretaceous time.

Figure 1. Forest ringlet (*Dodonidia helmsi*), reared from Wi Tako Ngatata Scenic Reserve, Upper Hutt

Evolution of the New Zealand ringlets involves a primary divergence between the forest ringlet (*Dodonidia*) and the other three genera (*Erebiola*: Butler's Ringlet, *Argyrophenga*: the tussock butterflies, and *Percnodaimon*: Black Mountain Ringlet). Ringlet butterflies are active fliers. One might expect their species to occur wherever suitable habitat is present. This is not the case. While many species are widespread, they are not everywhere, and they do not always overlap with each other. The only ringlet species in the

North Island is the forest ringlet, which is also found in the northern South Island. The other three genera are restricted to the South Island (Fig. 2). This distribution pattern is predominantly allopatric, where geographic overlap is restricted to parts of the northern South Island, and, perhaps, the Humboldt Mts (an isolated historical record by George Vernon Hudson of *Dodonidia* that needs to be corroborated). This high level of allopatry is consistent with both groups originating by vicariance from a widespread ancestor, followed by range expansion of one or other group through local dispersal resulting in the present day overlap in the northern South Island.

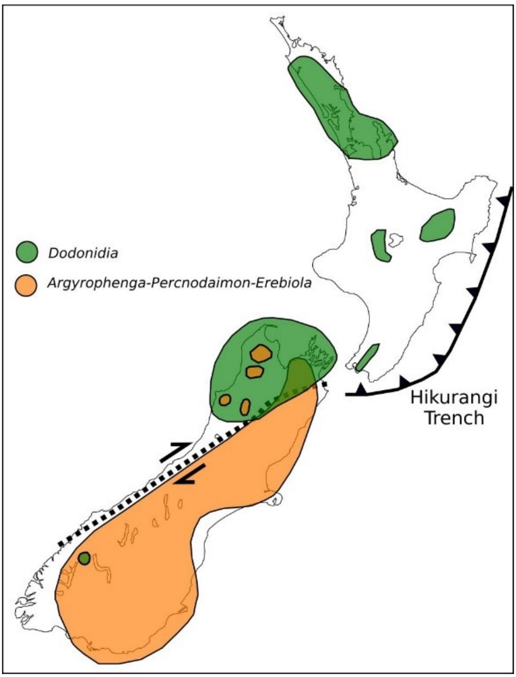

Figure 2. Distribution and tectonics for the New Zealand ringlet butterfly genus *Dodonidia* and its sister group (*Argyrophenga*+*Percnodaimon*+*Erebiola*). Dashed line – Alpine fault. Southern *Dodonidia* locality from historical record. From Heads *et al.* (2023).

A vicariance origin for the two ringlet groups is indicated by the spatial correlation between the phylogenetic and geographic break between the two clades that coincides with the Alpine fault and Hikurangi Trench. This biogeographic-tectonic correlation supports an original allopatric divergence of the two ringlet groups either side of this fault system, followed by range expansion in the region that is now northwestern South Island. The Alpine fault zone has a long geological history. Before the current 480 km of dextral movement (opposite side moving right when facing the fault) beginning about 23 Ma, there was a proto-Alpine fault system that began with a sinistral strike slip (opposite direction moving left) between 100-80 Ma which was associated with rifting between East and West Antarctica (Fig. 3). This spatial correlation supports differentiation of the forest ringlet and its South Island sister group by about 80 Ma and precludes support for unnecessary theories of recent dispersal across the Tasman Sea after its formation between 80 and 55 Ma.

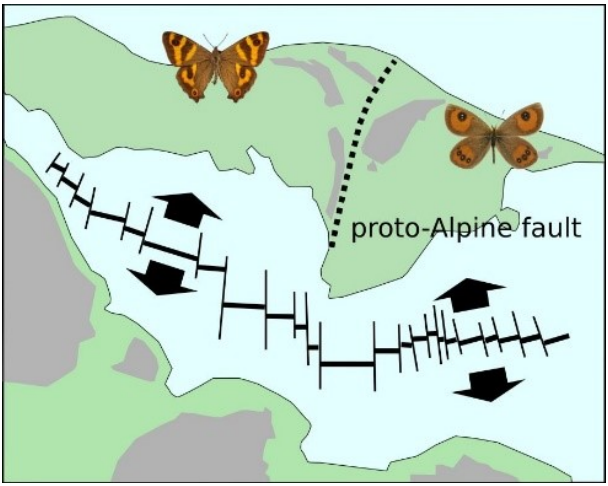

Figure 3. Divergence between *Dodonidia* and its sister group (illustrated here by *Argyrophenga antipodum*) across the proto-Alpine fault.

Further tectonic evidence of an early origin for the New Zealand ringlets is indicated by the southern distributional limits of the South Island group in the Fiordland region. *Percnodaimon* is not throughout the region, but reported from the eastern mountain belt only. The distribution of *Argyrophenga* has a similar western limit, while *Erebiola* reaches only the northern margin of Fiordland (Fig. 4). These genera are absent in western Fiordland and Stewart Island, despite extensive areas of apparently suitable habitat in both. And the group has not been recorded from the small areas of natural grassland on the West Coast (west of the Alpine fault). In the North Island, *Dodonidia* is notably absent from Taranaki region. These absences suggest that the distribution reflects historical factors, rather than present environment and ecology.

Outside Nelson and northern Westland, the western limit of the New Zealand ringlets coincides closely with the main tectonic boundary in New Zealand that separates the geological Western Province (most of Stewart Island, western Fiordland, West Coast, and western Taranaki) from the Eastern Province (eastern Fiordland, rest of Otago, etc.) (see Heads, 2017). Along the geological boundary is the Median Batholith, a belt of volcanic eruption between Antarctica and New Guinea that was active about 130 Ma, well before formation of the Tasman Sea. This magmatic activity would have had a profound impact on biological communities, and it coincides spatially with the otherwise anomalous south-western limit of the New Zealand ringlet butterflies.

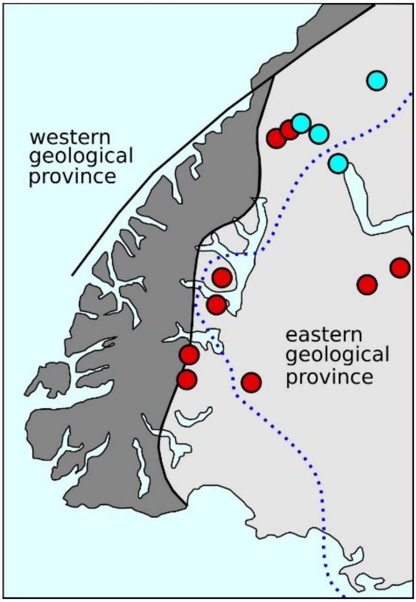

Figure 4. Geological provinces in southwesternNew Zealand and distribution limits of New Zealand ringlets: *Percnodaimon* (red dots), *Erebiola* (blue dots), *Argyrophenga* (dashed blue line). Modified from Heads et al. (2023).

The Median Batholith is part of a belt of magmatic eruption extending between Antarctica, New Zealand, Australia (as the Whitsunday Volcanic Province). This immense zone of volcanic activity would have severely disrupted the distributional continuity of many animal and plant taxa in the region. As these populations became geographically isolated from each other, some would have undergone divergence either side of the volcanic belt. This process would explain patterns of absence of the New Zealand ringlets west of the Median Batholith while its Australian sister group is present (Fig. 5). In summary, biogeographic-tectonic correlation supports an ancient (at least 80 Ma) presence of the two primary New Zealand ringlet clades in the region that is now New Zealand. The ancestor of the New Zealand ringlets and the Australian sister group had a widespread distribution along eastern Gondwana. This ancestor differentiated into the 'Australian-New Guinea" and 'New Zealand' clades through geologically mediated isolation resulting from a massive belt of magmatic eruption about 130 Ma (Heads et al. 2023).

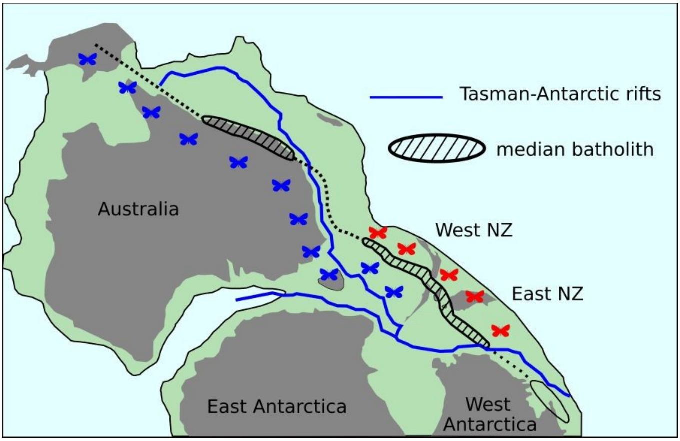

Figure 5. Reconstruction of the southwest Pacific at 115 Ma (mid-Cretaceous), and divergence of the Australian-New Guinea clade (blue shaded) and New Zealand (red shaded) ringlets to the east and west of the Median Batholith magmatic zone. Modified from Heads *et al.* (2023).

Returning to my observation of the swarming or lekking behaviour of forest ringlets at the Wi Tako Ngatata Scenic Reserve. The biogeographic evidence indicates that this flight behaviour under the beech canopy cannot be treated as an evolutionarily recent development in New Zealand, but one that would have been observable at the original divergence of *Dodonidia* in early Cretaceous time. The intriguing report of this species in the Humboldt Mountains may well represent a later southward dislocation of a forest ringlet population by movement of the Alpine fault. Verification of this locality should be a high priority for butterfly conservation enthusiasts.

Nothing in the evolutionary reconstruction presented here for the New Zealand ringlets is contradicted by any other scientific evidence. The Mesozoic origin is concordant with all current molecular divergence ages calibrated by fossil or island ages as these can generate minimum ages only, and do not impose any empirical upper limits on phylogenetic age (Heads 2019, Heads et al. 2023). As shown for the New Zealand red admirals (see earlier review in *The Wētā*, Grehan 2021), biogeographic evidence supports the existence of a 'modern' butterfly fauna that was already present in 'New Zealand' when it was first geologically isolated from what is now Australia. There is no need to speculate of any miraculous flights over the Tasman to understand the presence of these animals, or perhaps any of the other endemic animal and plant life that makes up New Zealand's natural heritage (Heads 2014, 2017).

References

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