

Towards an Understanding of Marsupial Interchange between Australia and New Guinea

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ABSTRACT. A review of the geology, palaeontology, genetic, and morphology studies indicates that during the mid-Miocene to Pliocene, New Guinea consisted of four island Blocks (Vogelkop, Maokop, Central, and Southeastern). The initial dispersal of marsupials from Australia was into the Vogelkop Block. The ancestors of at least six genera (*Dactylonax*, *Microperorytes*, *Myoictis Pseudochirops*, *Spilocuscus*, *Tous*) and three species (*Dendrolagus inustus*, *Dendrolagus ursinus*, *Dorcopsis muelleri*) of endemic New Guinean marsupials are likely to have reached New Guinea via this route. The *Dendrolagus dorianus* complex and two marsupial genera (*Dactylopsila* and *Phalanger*) may have reached New Guinea via the Maokop Block, with *Thylogale* arriving either via the Maokop or Southeastern Block. Four species, or species complexes, of marsupials in the genera *Dendrolagus*, *Dorcopsis*, *Murexia*, and *Peroryctes* may have arrived via the Southeastern Block. The Central Block lacks evidence of Tertiary marsupial transfers from Australia, and may not have been connected with Australia prior to its incorporation into New Guinea. Two possum taxa (*Tous ayamaruensis* and *Dactylonax kambuayai*), which occur in the Vogelkop lowlands, are hypothesized to have been restricted from expansion into the slopes of the Central Cordillera by a combination of tectonics and ecological barriers. A further two species pairs/triplets (*Dactylonax palpator/ernstmayri*, *Pseudochirops albertisii/coronatus/cupreus*) provide evidence of a highly unusual pattern of dispersal within New Guinea, whereby the high-elevation members of each pair have dispersed and speciated, while the mid-elevation members have not. Finally, marsupial distributions indicate that in the early Pleistocene a contiguous mountain range, named here the Northern Cordillera, extended from Vogelkop to the Torricelli Mountains.

Introduction

Australasian marsupials

Marsupials constitute a moderately diverse group of mammals with limited over-water dispersal ability. The Australasian genera *Phalanger* and *Spilocuscus* of the family Phalangeridae and bandicoots of the family Peroryctidae have dispersed over water to non-landbridge islands where they are represented by distinctive insular taxa (Flannery, 1995a; Helgen & Flannery, 2004). Many other insular populations of these and other marsupials are now known

to have originated as prehistoric and historic human introductions (e.g., Flannery & White, 1991; Williams, 1999). The vast majority of Australasian marsupials occur on continental landmasses, or islands of continental origin. Many Melanesian, and a few Australian, taxa are limited to higher elevations, and some clades have unusual distributions that hint to their zoogeographic histories. All of these factors make the marsupials an ideal group with which to investigate faunal interchange between Australia and New Guinea.

It has long been accepted that the marsupial fauna of New Guinea originated from Australia (Schodde & Calaby, 1972;

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Flannery, 1995b). However, the number of dispersal events, and which paleo-islands received which faunal elements, remain highly contested. The history of marsupials in Australia offers some constraints on the timing of dispersals to proto-New Guinea. Marsupials arrived in Australia from South America, via Antarctica, *ca.* 54 mya (Godthelp *et al.*, 1992). There is a 29 million year-long gap in their fossil record in Australia between around 54 and 25 mya (Megirian *et al.*, 2010). When the fossil record resumes in the late Oligocene, many of the extant families (as well as those that became extinct in the late Pleistocene) are represented. Several lines of evidence, including the fossil record and phylogenetic studies, suggest that most if not all marsupial migrations from Australia to New Guinea occurred between the late Miocene and the Pleistocene.

Only the later Pleistocene migrations of marsupials are well understood. These interchanges occurred during periods of low sea level when a broad land-bridge opened between Australia and New Guinea. It is likely that savannah woodland dominated the land-bridge, but some gallery forest must also have been present (Schodde & Calaby, 1972). *Notamacropus agilis*, *Thylogale stigmatica*, *Lagorchestes conspicillatus*, *Sminthopsis virginiae* and possibly other marsupial taxa migrated from Australia to New Guinea at this time, while *Echymipera rufescens*, *Spilocuscus maculatus*, *Phalanger mimicus*, and possibly other marsupials, dispersed from New Guinea into northern Australia (penetrating no further south than northern Cape York (Baker & Gynther, 2023).

The precise location, nature and duration of earlier land-bridges between Australia and the paleo-islands that would make up New Guinea remain unknown. But the fact that numerous extant Australian marsupial families, including Myrmecobiidae, Notoryctidae, Chaeropodidae, Thylacomyidae, Phascolarctidae, Vombatidae, Tarsipedidae, Hypsiprymnodontidae, and Potoroidae, are absent from New Guinea, indicates either that severe filtering mechanisms existed, or that extensive extinctions have occurred in New Guinea over the Neogene.

Two pioneering works have inspired our approach to unravelling the zoogeographic history of Melanesian marsupials. The first is Ziegler's (1977) synthesis of the zoogeography of lowland Melanesian marsupials, in which he introduced the concept that the distributions of some taxa might reflect their original dispersion pathways into New Guinea millions of years earlier. Ziegler's argument implies that, despite a lack of ecological competitors, and the historic presence of contiguous rainforest, some marsupial range expansions have been extremely slow. We think it possible that geologically recent tectonic changes, along with the existence of hard to discern zones of unsuitable habitat, may help explain this slow rate of dispersal. The second influence is Aplin's (1998) overview of the vertebrate zoogeography of Vogelkop. Aplin was the first researcher to identify the primacy of Vogelkop as 'a possible major focus of vertebrate speciation during the late Tertiary' (Aplin, 1998: 805). Both recent tectonic shifts and ecological barriers are likely to have been particularly impactful on Vogelkop. The region is geologically complex, leading to edaphic influence on vegetation over short distances, and there is evidence in the mammal distributions we discuss, of marked tectonic changes that have, in the geologically recent past, connected Vogelkop to various regions of New Guinea, as well as severing other connections (Aplin, 1998).

Data bearing on entry points of the New Guinean marsupial radiations

Four sources of information are potentially useful in determining the initial entry points of New Guinean marsupial lineages including: (1) geological evidence, (2) the fossil record, (3) molecular studies, and (4) cladistic assessment of morphological evolution. All four data sets are frustratingly incomplete. For example, while the tectonic evolution of New Guinea is well understood in broad terms, precise details, including the timing of emergence of land bridges and island landmasses, and the coalescence of island landmasses into the single island that is New Guinea, remain unclear (Baldwin *et al.*, 2012). The incomplete fossil record is likewise vexing: the two areas with the highest endemism of marsupials, Vogelkop and southeastern New Guinea, entirely lack a fossil record, while the fossil record elsewhere in New Guinea is severely biased towards larger, now extinct megafauna. Molecular phylogenies are highly useful in determining dispersal events, but in this case a lack of molecular data for key marsupial taxa severely limits its use. Morphological comparisons offer some island-wide comparisons, but even here, detailed analysis is severely limited.

Tectonic evolution of the New Guinean region

New Guinea and surrounding regions are arguably one of the most tectonically complex areas on Earth (Baldwin *et al.*, 2012). On the basis of what is known of its geology, tectonic history and marsupial faunas, we divided New Guinea into four principal 'blocks', which appear to have been islands prior to their incorporation into New Guinea. These four blocks are: (1) the Vogelkop area and its associated 'Northern Cordillera' (newly defined here), (2) the Maokop Block (from the Wissel Lakes to the Hak-Om Divide), (3) the Central Block (from the Hak-Om Divide to the Wau area), and (4) the Southeastern Peninsula.

The Vogelkop Block consists of several continental terranes that collectively comprise the northernmost region of the Australian continental plate. Most of the terranes are composed of deformed Silurian-Devonian marine sediments that are intruded by Permian-Triassic granitoids (Pieters *et al.*, 1983). These continental terranes are fault-bounded by allochthonous blocks of Early Tertiary, oceanic island arc affinity. These oceanic island arc rocks also underlie some zoogeographically important regions—including Yapen, the Wondiwoi Mountains and the Weyland Range. Rocks of oceanic island arc origin also comprise the Foja, Cyclops, and Bewani-Torricelli Mountain Ranges (which, with Yapen, comprise the Northern Cordillera).

The Vogelkop Block is actively deforming via anticlockwise rotation and subparallel sinistral strike-slip faulting at a rate of *ca.* 8 cm/year relative to the rest of the Australian plate (Pigram & Symonds, 1991; Stevens *et al.*, 2002; Bailly *et al.*, 2009). Since *ca.* 6 mya, this process has shifted the Vogelkop Block through 30–40° of anticlockwise rotation and formed the Cenderawasih Rift (Charlton, 2000).

The collision between the Australian Plate and the Melanesian arc is oblique, resulting in diachronous collisional mountain building. The collision, and thus mountain building, began in the west and has moved eastward (Cloos *et al.*, 2005). As a result, the eastern fold-and-thrust belt (part of our Southeastern Block) is now at

the same stage of development as the Maokop Block was at ~4 mya (Baldwin *et al.*, 2012). After the Vogelkop Block, the oldest portion of the New Guinean Central Cordillera is the Maokop Block (Fig. 1.) It is also the highest part of the Central Cordillera, Puncak Jaya reaching 4,884 m above sea level (asl). Mountains have existed in the region of the Maokop Block since *ca.* 12 mya (Cloos *et al.*, 2005). Thick basement sediments indicate that by 8 mya, elevations of up to 2 km asl had been reached, and by 6 mya, elevations of *ca.* 4 km asl existed (Cloos *et al.*, 2005).

The elevation of the Central Block (that part of the Central Cordillera lying between the Hak-Om Divide and the Wau area), is more recent than that of the Maokop, but older than that of the Southeastern Block. The Porgera Intrusive Complex was emplaced in the late Miocene, suggesting that orogenic activity was underway by that time (Baldwin *et al.*, 2012). Uplift of the Southeastern Block is even more recent. The Mt Dayman-Suckling Range (the highest point of the Southeastern Block) appears to have been uplifted during the early-mid Pliocene, between *ca.* 4.6–3.4 mya (Österle, 2019).

The New Guinean fossil record

New Guinea's marsupial fossil record consists of a single possible late Miocene find (Menzies *et al.*, 2008), a single modestly diverse late Pliocene fauna (Hoch & Holm, 1986; Plane, 1967), and a scatter of Pleistocene sites (Flannery, 1994; Menzies & Ballard, 1994; Jackson *et al.*, 2024).

The Miocene fossil record of New Guinea consists of a single, doubtfully dated dentary fragment of a diprotodontid from Yonki, Eastern Highlands Province (Central Block). K/Ar dating of minerals in the breccia adhering to the dentary indicate an age of 13.2 mya. The dentary may well be younger, but volcanic activity in the region ceased around 7.4 mya, providing a tentative youngest date. The dentary is similar in morphology and size to the Plio-Pleistocene New

Guinean taxon *Nototherium watutensis* Anderson, 1937, the phylogenetic affinity of which is disputed. Menzies *et al.* (2008) place it in *Kolopsis* (Zygomaturinae), while Mackness (2012) and Jackson *et al.* (2024) retains it in *Nototherium* (Diprotodontinae).

The only Pliocene marsupial fossil localities in New Guinea occur in the Otibanda Formation, located on the eastern margin of the Central Block. K/Ar dating of pyroclastic rock close to the Watut 3 locality returned an age of 2.9 ± 0.4 mya (late Pliocene) (Hoch & Holm, 1986). Three diprotodontid taxa are recorded from the Otibanda Formation. *Nototherium watutense* is the largest marsupial known from New Guinea. It has also been tentatively recorded from the late Miocene, as well as undated sediments near Nimboran, Jayapura area, Indonesia (Hardjasmita, 1985). *Kolopsis rotundus* and *Kolopsoidea cultridens* are both zygomaturine diprotodontids (Long *et al.*, 2002). Species of *Kolopsis* occur in late Miocene deposits in central and southern Australia, while *Kolopsoidea* is a New Guinean endemic. Only three extant marsupial lineages, Dorcopsini and Dendrolagini (both Macropodidae), and Dasyuridae, are represented in the Otibanda fauna. The macropodid lineages have complex and disputed taxonomic histories. Kerr and Prideaux (2024) allocate '*Protemnodon*' *buloloensis* to *Dorcopsoides*, as well as placing *Watutia novaeguineae* in Dorcopsini. Regardless of their higher-level classification, neither of these taxa appear to be ancestral to any of the extant New Guinean dorcopsins. *Bohra planei* from the Otibanda Formation is the oldest dendrolagin from New Guinea. It is likewise unlikely to be ancestral to any extant Melanesian dendrolagins (Prideaux & Warburton, 2023). The dasyurid is represented by a dentary fragment with an m2 which was assigned to the New Guinean endemic genus *Myoictis* by Archer (1982).

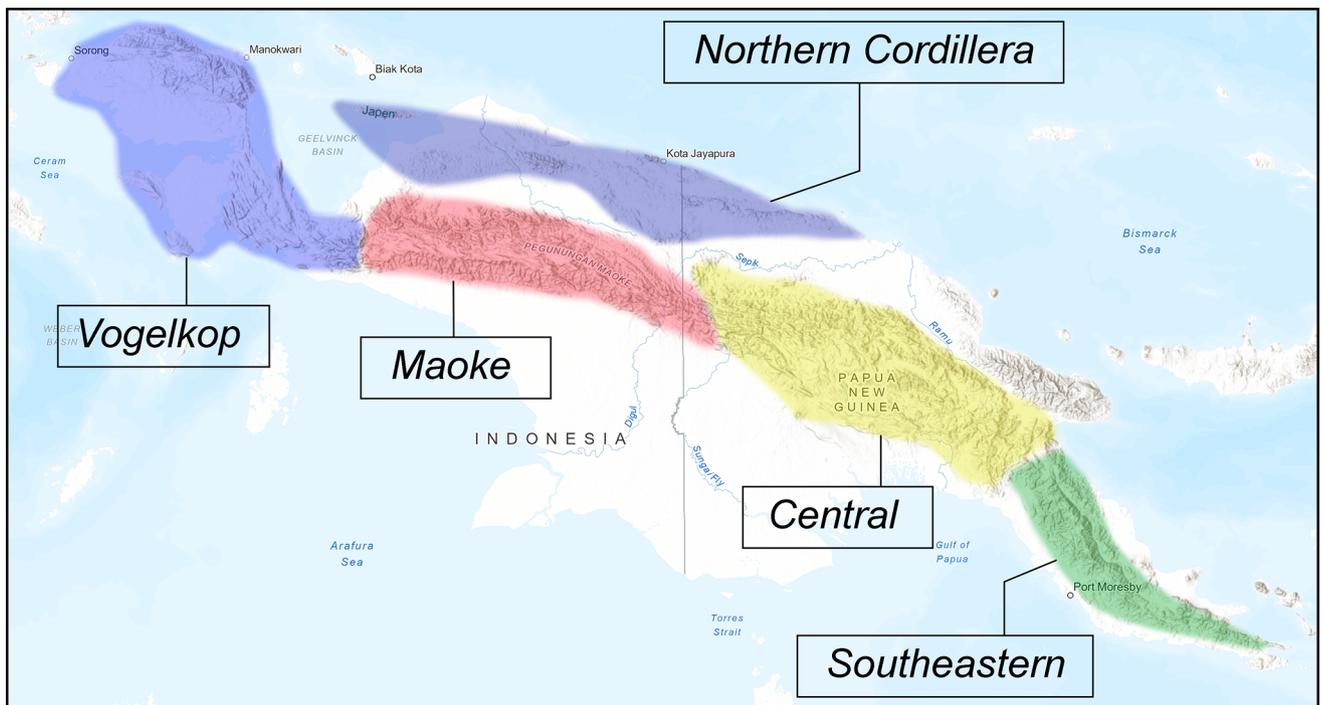


Figure 1. Map of the island of New Guinea, showing the Vogelkop Block and Northern Cordillera (purple), the Maokop Block (pink), Central Block (yellow) and Southeastern Block (green).

Species of *Kolopsis* and *Dorcopsoides* are known only from the late Miocene of Australia and the mid-Pliocene of New Guinea. This strongly suggests a late Miocene migration from Australia into New Guinea, and that by the mid-Pliocene, at the latest, members of these two genera had reached the Central Block, by which time they were extinct in Australia.

Thylacinus (Thylacinidae) is known from late Pleistocene-Holocene archaeological deposits from ‘the Eastern Highlands’, Central Block (Van Deusen, 1963). *Thylacinus* is not known from extensive Pleistocene/Holocene deposits representing subalpine and alpine habitats in the Maokop Block (Hope, 1981; Flannery, 1992, 1999). High elevation, subalpine areas of the Maokop Block offer the most extensive areas of suitable habitat for *Thylacinus* in all of New Guinea, so the absence of the genus there likely indicates that a barrier for *Thylacinus* existed between the Maokop and Central Blocks. Four genera of diprotodontids (*Hulitherium*, *Maokopia*, *Nototherium*, and an unnamed genus) are known from the Pleistocene of New Guinea. *Hulitherium tomasettii* is known from five occurrences, two in the Telefomin area (Maokop Block) and one each in the Hela, Chimbu, and Enga areas (Central Block) (Menzies & Ballard, 1994; Prideaux *et al.*, 2022). *Maokopia* is known from three occurrences (two in the Maokop Block and one from the Central Block (Flannery, 1994; Menzies & Ballard, 1994). An undescribed genus of diprotodontid is known from a single specimen from Mt Kare, Central Block (Menzies & Ballard, 1994). Two genera of extinct macropodines are known from the Pleistocene of New Guinea: *Protemnodon* and *Nombe*. Kerr & Prideaux (2022) reassigned *Protemnodon nombe* to the new genus *Nombe*. The genus *Nombe* is known from a single occurrence in the Central Block (Flannery *et al.*, 1983). *Protemnodon* is represented by two (*P. tumbuna* and *P. sp.*) or possibly three species. Kerr *et al.* (2024) synonymized *Protemnodon hopei* with *P. tumbuna*. If this synonymy is accepted, *P. tumbuna* is known from three occurrences, one in the Maokop Block and two in the Central Block (Flannery, 1994; Menzies & Ballard, 1994). An unnamed species of *Protemnodon* is known from the North Coast Ranges (Koungoulos *et al.*, 2024).

It seems likely that, other things being equal, larger-bodied marsupials should be able to disperse more readily than smaller-bodied forms, leading to less geographic diversification. Conversely, taxonomic lumping may occur in classifying partial fossil remains. The fact that *Hulitherium*, *Maokopia*, and *Protemnodon* are known from multiple occurrences suggests that, at the generic level at least, the Pleistocene megafauna of New Guinea may be relatively completely known (Flannery, 1994; Menzies & Ballard, 1994).

Overall, the fossil record of marsupials in New Guinea is so patchy as to be only marginally useful in investigating the origins of the extant New Guinean marsupial fauna. It is, however, informative in that it supports the hypothesis, as evidenced by the extant fauna, that either a severe filter existed between Australia and New Guinea, or that large-scale extinction has occurred in New Guinea. This is because only two or three extinct Pleistocene megafaunal subfamilies are represented: Macropodinae and Zygomaturinae/Nototheriinae. The following families and subfamilies are notable for their absence from the New Guinean fossil record: Ektopodontidae, Thylacoleonidae, Diprotodontinae, Vombatidae, Phascolarctidae, Propleopinae, and Sthenurinae. Most are abundant and widespread in the late Cenozoic fossil record of Australia.

Molecular studies

Aplin *et al.* (1993) is the earliest molecular study that attempts to elucidate faunal exchange between Australia and New Guinea using divergence times as a guide. It posits major episodes of dispersal of ancestral peroryctids, phalangerids and acrobatids to New Guinea in the early Miocene (*ca.* 20 mya); of some pseudocheirids, petaurids, macropodids and dasyurids in the late Miocene (*ca.* 10–12 mya); and of pseudocheirids, ancestral *Dendrolagus* and *Myoictis* between 4.7–2.7 mya. Diversification within some or all of these clades may, however, have occurred within Australia prior to dispersal to New Guinea.

In the last few decades improvements to molecular genetic techniques and advances in methods of phylogenetic analysis have resulted in a much more comprehensive, robust and detailed understanding of marsupial evolution (Meredith *et al.*, 2009a, 2009b; Mitchell *et al.*, 2014; Duchene *et al.*, 2018). The ancestor of extant Australidelphian marsupials appears to have originated in the Paleocene (66–56 mya), with the diversification of most extant families occurring in the late Eocene and early Oligocene (Duchene *et al.*, 2018). The divergence of many endemic (or near endemic) extant New Guinean genera (*Echymipera*, *Peroryctes*, *Microperoryctes*, *Murexia*, *Phascolosorex*, *Neophascogale*, *Myoictis*, *Spilocuscus*, *Phalanger*, *Dactylopsila*) dates from the mid-late Miocene, except for *Distoechurus* whose divergence from *Acrobates* occurred in the Oligocene (Westerman *et al.*, 2012; Mitchell *et al.*, 2014; Westerman *et al.*, 2016; Kealy *et al.*, 2020). How the extinction of these or related lineages in an increasingly arid Australia impacts these estimates remains unclear.

The divergences of genera with endemic species in both New Guinea and Australia show a more complex pattern, but divergences within genera typically commence in the late Miocene, with the basal lineages often present in Australia (e.g., *Pseudocheirops*, *Pseudocheirus*, *Dendrolagus*, *Dasyurus*, *Thylogale*), or known to have occurred in Australia from fossil evidence (e.g., *Dorcopsis*, *Distoechurus*) (Macqueen *et al.*, 2010; Meredith *et al.*, 2010; Westerman *et al.*, 2016; Eldridge *et al.*, 2018, 2026a). The endemic New Guinean species mostly appear as the result of secondary radiations and date from the late Miocene (e.g., *Pseudocheirops*) through to the Plio-Pleistocene (e.g., *Dendrolagus*, *Petaurus*, *Thylogale*) (Macqueen *et al.*, 2010; Meredith *et al.*, 2010; Eldridge *et al.*, 2018). Regrettably, key Vogelkop endemics remain unsampled in these genetic studies, including *Phascolosorex doriae*, *Microperoryctes murinus/aplini*, *Dactylonax kambuayai/palpator*, *Pseudocheirus schlegeli* and *Pseudocheirops coronatus*, limiting our ability to test our Vogelkop Block origin hypothesis using genetic data.

Morphological evolution

Detailed morphological studies of a few lineages have proved to be useful in discerning phylogenetic divergences. The genus *Dactylonax* is known from three extant taxa, two of which are restricted to Vogelkop. The morphologically most plesiomorphic is *D. kambuayai*, a diminutive species that is restricted to Vogelkop lowlands but may also be present in mid-Pleistocene fossils from central Queensland (Hocknull *et al.*, 2007; Flannery *et al.*, 2026a). It lacks many of the auditory and digital specializations present

in other members of the genus, which facilitate feeding on wood-boring insect larva. *Dactylonax palpator* is a large species restricted to forests above 1,300 m asl in the Arfak Mountains of Vogelkop, while *D. ernstmayri* is widely distributed at elevations above 800 m asl from the Weyland Range to southeast Papua. It is clearly closely related to *D. palpator*, but is even more specialized in its digital and auditory adaptations (Flannery *et al.*, 2026a). *Pseudochirops* is represented in New Guinea by four species, three of which (*P. albertisii*, *P. coronatus*, and *P. cupreus*) are morphologically and ecologically similar and presumably form a clade. *Pseudochirops albertisii* is distributed at mid to high elevations, though with occasional records as low as 300 m (Helgen, 2007) on Vogelkop, Yapen, the North Coast Ranges, and the Weyland Range. It is the most plesiomorphic member of the group, having a relatively elongated skull and unspecialized tail. *Pseudochirops coronatus* is restricted to primary forest above 1,300 m in the Arfak Mountains (Vogelkop), while its putative sister taxon, *P. cupreus*, is widespread above 1,700 m asl on the Central Cordillera from the Weyland Range to the southeast (Flannery, 1995b). Four of the five members of the genus *Spilocuscus* occur on Vogelkop or nearby islands, providing some evidence of a Vogelkop Block point of origination, while the highly morphologically divergent *Microperoryctes aplini*, a Vogelkop endemic, indicates a long history, if not a point of origination, for New Guinean members of the genus.

Taxa with a putative Vogelkop Block entry point

Dactylonax. A recent revision of the genus *Dactylonax* (Flannery *et al.*, 2026a) based on morphological analysis and molecular data, gives us a high degree of confidence that *Dactylonax* originated in Australia, and spread throughout New Guinea from the Vogelkop lowlands. The most plesiomorphic member of the genus, *D. kambuayai*, is restricted to Vogelkop at elevations below 867 m asl. *Dactylonax palpator*, which is restricted to elevations above around 1,300 m asl, is derived from a *D. kambuayai*-like ancestor, while *D. ernstmayri*, which is widespread above 800 m asl on the Central Cordillera and Huon Peninsula, is derived from a *D. palpator*-like ancestor.

Tous. *Tous ayamaruensis* is primarily known from subfossils, but has recently been reported as a living animal (Flannery *et al.*, 2026b). It is distributed in Vogelkop, and the Wutung area (part of the PNG North Coast Ranges, fossil only) and possibly the Torricelli Mts (Flannery *et al.*, 2026b). It is known only from elevations below 400 m asl and is entirely absent from the New Guinean Central Cordillera.

Dendrolagus. *Dendrolagus inustus* is the only member of the long-footed group of tree-kangaroos occurring in New Guinea and is the sister taxon to all other New Guinean tree-kangaroos (Eldridge *et al.*, 2018). It is restricted to lowlands below 1,400 m asl (Flannery, 1995b), and is present in all of the fragments of the putative Northern Cordillera, yet is entirely absent from the Central Cordillera.

Dendrolagus ursinus is endemic to Vogelkop where it occurs at all elevations, and is sympatric with *D. pulcherrimus* and *D. inustus*. It is a member of the short-footed group, but is probably deeply divergent from the other clades.

Pseudochirops. *Pseudochirops albertisii* is present on all the major fragments of the putative Northern Cordillera

(including Vogelkop), where it commonly occurs at elevations above 1,000 m asl, with occasional records from as low as 300 m asl. It can persist in disturbed forest.

Microperoryctes. The genus includes the tiny *M. aplini* (Vogelkop) and *M. murinus* (Weyland Range). No genetic data has been published pertaining to these morphologically divergent taxa, which are similar in body size to mid-late Miocene bandicoots. Vogelkop is also the type locality for *M. longicaudata*, Vogelkop populations of which are unsampled genetically.

Spilocuscus. Four of the five known species of *Spilocuscus* occur on Vogelkop or on nearby islands, suggesting that the Vogelkop Block was the centre of radiation for the genus (Flannery, 1995a, b).

Dorcopsis. Eldridge *et al.* (2026b) reveal deeply divergent lineages within *Dorcopsis*, which is paraphyletic with regard to *Dorcopsulus*. The western species *Dorcopsis muelleri* and *D. hageni* split from the eastern *D. luctuosa* in the late Miocene (6.57 mya), while *Dorcopsulus* split from within *Dorcopsis* in the latest Miocene (5.71 mya). It is likely that the western *Dorcopsis* species arrived via a Vogelkop Block Route, while the eastern *Dorcopsis* species arrived via a Southeastern Block route. As fossils of *Dorcopsulus* sized dorcopsins are known from a 4.46 mya site in Australia, they are likely to have independently dispersed, making it likely that there were multiple independent dispersal events of dorcopsins from Australia. Vogelkop is the only region on New Guinea where two taxa of diminutive montane species (previously *Dorcopsulus*) co-occur (Aplin *et al.*, 1999). All occurrences in Vogelkop are subfossil. More sampling of the modern fauna is required.

Myoictis. The Vogelkop taxon *M. melas* is basal (Phillips *et al.*, 2022). The closest relatives to *Myoictis* are all Australian and have predominantly western or northwestern Australian distributions (*Dasyuroides*, *Parantechinus*, *Dasykaluta*, *Dasyercus*), tentatively suggesting a western (Vogelkop Block) entry for the genus.

Taxa with a putative Maokop Block entry point

Dendrolagus dorianus group. The morphologically most divergent member of the group is *D. mbaiso*, which is endemic to high elevations on the Maokop Block (Eldridge *et al.*, 2026; Flannery *et al.*, 1995).

Dactylopsila megalura is morphologically plesiomorphic, having cranial proportions more similar to basal petaurids than to other members of the genus *Dactylopsila*. It is restricted to a narrow elevational range centred on 1,400 m asl in the Maokop Block (Flannery, 1995b).

Phalanger. The most basal New Guinean member of the group is *Phalanger matanim* (Colgan *et al.*, 1993), which is restricted to mid-elevations (1,400–2,300 m asl) in the Telefomin region of the Maokop Block (Flannery, 1987).

Thylogale. There have been multiple entries from Australia (*T. stigmatica* is likely to be a Pleistocene arrival via the Torres landbridge) The most morphologically distinctive, and possibly the most plesiomorphic of the New Guinean taxa, is *T. christenseni*, which is known only from subfossils from high elevations on the Maokop Block (Hope, 1981). The genus is absent from the Vogelkop Block, but is diverse in eastern New Guinea (where *T. browni*, *T. brunii* and *T. calabyi* occur). A Maokop or Southeastern Block entry, or both, seem possible.

Taxa with a putative Southeastern Block entry point

The *Dendrolagus goodfellowi* complex. This complex includes *D. goodfellowi* (the basal member, inhabits the Southeastern Peninsula, westwards to near Wau), *D. buergeri* (between the Wau area and Mt Bubiari, Sundaun Province), *D. spadix* (low elevations between Lake Murray and the Gulf of Papua), *D. matschiei* (the Huon Peninsula), and *D. pulcherrimus* (Northern Cordillera) (Eldridge *et al.*, 2024). Its most divergent lineages are in the east, with a single lineage reaching Vogelkop. It is possibly absent from the Maokop Block (Eldridge *et al.*, 2024).

Microperoryctes. *Microperoryctes papuensis* is restricted to mid-montane elevations of the Southeastern Block, where it co-occurs with *Microperoryctes ornatus* (Flannery, 1995b). Alternatively, the endemic *M. papuensis* may have evolved more recently from a *M. ornatus*-like ancestor.

Peroryctes. *Peroryctes broadbenti* is restricted to lowlands of southeastern New Guinea and a narrow zone across southeast Papua New Guinea, extending in a latitudinally narrow band along the southern lowlands, west to the Aru Islands. *Peroryctes raffrayanus* is widespread at mid elevations across the Central Cordillera west to Vogelkop. A third species is known from the Maokop Block (Travouillon *et al.*, 2026). The predominantly southeastern distribution of *P. broadbenti* may be evidence of a southwest Papuan origin.

Murexia. *Murexia rothschildi* is endemic to the eastern parts of the of the Southeastern Peninsula, east of the Aroa River (Flannery, 1995b). It is highly divergent within *Murexia sensu lato*, and has no obvious ecological vicars in the rest of New Guinea.

Dorcopsis. The eastern *Dorcopsis* species *D. luctuosa* and possibly *D. phyllis*, are deeply divergent within *Dorcopsis* (Eldridge *et al.*, 2026). Their late Miocene divergence from other *Dorcopsis* and eastern distribution suggest an independent migration to New Guinea via the Southeastern Block.

It is currently not possible to speculate meaningfully about the entry route of *Distoechurus*, *Cercartetus*, and *Pseudochirulus*, all of which have species that are widespread throughout lowland New Guinea. *Cercartetus caudatus*, *Dactylopsila trivirgata*, and *Petaurus breviceps* (*sensu lato*), occur in both Australia and New Guinea. Colgan and Flannery (1992) and Malekian *et al.* (2010) found considerable genetic diversity in *P. breviceps* (*sensu lato*) in New Guinea, suggesting an older migration for this genus. The genus *Echymipera* remains problematic. It has high diversity in southern New Guinea (where *E. kalubu*, *E. rufescens* and *E. echinista* are present), but the most divergent member of the genus (*E. clara*) is restricted to the northern lowlands, where it co-occurs broadly with *E. kalubu* and *E. rufescens*. More genetic analysis is required if zoogeographic patterns within these lineages are to be understood.

The marsupial assemblages of the four tectonic blocks

The Vogelkop Block and 'Northern Cordillera'. This region is unique in New Guinea in having a highly endemic element in its lowland marsupial fauna, *Dactylonax kambuayai* (Vogelkop only) and *Tous ayamaruensis* (Vogelkop and North Coast Ranges) being entirely restricted to lowland rainforests.

Lowland rainforest is (or was prior to logging over recent decades) contiguous from Vogelkop to the southeastern tip of New Guinea. Yet no ecologically similar taxa occur in the lowlands elsewhere on New Guinea, so their absence from the rest of New Guinea cannot be explained, at least at a gross level, by habitat discontinuity or competitive exclusion.

A number of endemics occur in high-elevation forests on Vogelkop (maximum elevation 2,955 m asl), including *Microperoryctes aplini*, *Pseudochirops coronatus*, *Pseudochirulus schlegeli* and *Dactylonax palpator*. Two other endemics, *Dendrolagus ursinus* and the monotreme *Zaglossus bruijnii* occur at all elevations through Vogelkop. A number of other species otherwise known only from Vogelkop (*Dendrolagus inustus*, *D. pulcherrimus*, *Pseudochirops albertisii* and *Tous ayamaruensis*), occur on at least one of a series of isolated ranges across the north of New Guinea, including on Yapen (max. elevation 1,496 m asl) and the Foja Mountains (max. elevation 2,193 m asl) in Indonesia, and the Torricelli Range in Papua New Guinea (max. elevation 1,650 m asl). The distribution of these marsupial clades suggests that in the past a continuous mountain range once extended eastwards from Vogelkop. We refer to this paleo mountain range as the Northern Cordillera, as it paralleled the New Guinean Central Cordillera over its western half.

The nature of the connection between Vogelkop and the Northern Cordillera remains obscure. We have not marked it in Figure 1 because two distinct possibilities exist. One is that the connection lay between the Weyland Range (which is of oceanic arc origin) and the Van Rees/Foja Mountains. The second is that it ran between the Arfak Mountains and Yapen. The Weyland Range is crucial to this problem. It shares *Pseudochirops albertisii* and *Microperoryctes murinus* (possible sister taxon to *M. aplini*) with Vogelkop, suggesting a past connection. Some Weyland taxa are also shared with the Maokop Block (e.g., *Pseudochirops cupreus*, see Flannery, 1995b). No mammal collecting has been done in the Weylands for nearly a century, making it a priority for future research.

The high elevation Vogelkop endemics *Dactylonax palpator* and *Pseudochirops coronatus* are absent from high elevation forests on Yapen, the Fojas and the Torricelli Mountains, suggesting that the Northern Cordillera was bisected by low points which, judging by the distribution of *P. albertisii*, were no lower than 300 m asl. Treeline depression due to glacial cycles, or the Massenerhebung effect, however, may have lowered past vegetational zonation, so these hypothetical breaks in the Northern Cordillera may have been at somewhat lower elevations. Other barriers to the dispersal of marsupials also clearly existed between Vogelkop and the Northern Cordillera, because several Vogelkop taxa that might be expected to occur on the remnants of the Northern Cordillera are absent in both the modern fauna and archaeological record, notably *Dactylonax kambuayai* and *Dendrolagus ursinus*, both of which are widespread and reported from the Vogelkop lowlands.

The majority of the marsupials that occur on both Vogelkop and the Northern Cordillera have a putative Vogelkop Block entry point. The exception is *D. pulcherrimus*, which occurs on Vogelkop, Foja and Torricelli Mts above 700 m asl. It is a member of the *D. goodfellowi* complex, which appears to have entered New Guinea from Australia via the Southeastern Block, migrating thence into the Northern Cordillera and Vogelkop Block. Two marsu-

pials are endemic to the Northern Cordillera: *Dendrolagus scottae*, which is a relatively recently derived member of the *D. dorianus* group (Eldridge *et al.*, 2018), and which occurs only on the Torricelli Mountains and the Menawa Range, and *Petaurus abidi*, the only marsupial endemic to the Torricelli Mountains. It is deeply divergent from other New Guinean *Petaurus* (Malekian *et al.*, 2010) and may have arrived via overwater dispersal while the Torricelli Mountains were islands.

Maokop Block. The Maokop Block appears to have received a basal dactylopsilinae (*Dactylopsila megalura*) and possibly species of *Thylogale* from Australia. *Dactylopsila megalura* remains restricted to mid-elevation forests of the Maokop Block. Species of *Thylogale* are absent from Vogelkop, but spread to the Central and Southeastern Blocks, suggesting to us that the Maokop Block joined the Central and possibly Southeastern Blocks prior to connection with the Vogelkop Block. Additionally, the Maokop Block may have been the point of origin of *Phalanger*, which may have spread from there into the Central and Southeastern Blocks. The only montane phalanger to have reached Vogelkop is *Phalanger vestitus*. It occurs at lower elevations than the other montane phalangers, and may have reached Vogelkop at the same time that the murid genera *Mallomys* and *Hyomys* did.

Central Block. The Central Ranges comprise an extensive region including high peaks such as Mt Wilhelm (4,509 m asl). Remarkably, in our analysis, no extant marsupial lineage has a putative origin in the Central Block, suggesting that it may have lacked connections with Australia prior to its docking with the Maokop and Southeastern Blocks. One Holocene extinct taxon, however, may have originated in this region. A species of *Thylacinus* is known from Pleistocene fossils in the Central Ranges. Its systematic status remains uncertain (TF *pers. obs.*). It may be a distinct species which is descended from Pliocene immigrants, or a population of *T. cynocephalus* resulting from Pleistocene immigration from Australia.

Southeastern Block. The Southeastern Block has a scatter of endemic marsupials that indicate a past connection with Australia. It is difficult to date these dispersal events, but the presence of the near-endemic murid genus *Chiruromys* on the Southeastern Block suggests that its marsupial fauna may post-date the arrival of murids in Australia. It is possible that the genus *Peroryctes* arrived in New Guinea at this time, along with *Murexia rothschildi* and the ancestor of the *Dendrolagus goodfellowi* complex. If so, *Peroryctes raffrayanus* spread throughout New Guinea, while its sister taxon *P. broadbenti* remained restricted to the southeast and south. *Murexia rothschildi* remains restricted to the southeast, while the *D. goodfellowi* group has its basal member (*D. g. goodfellowi*) almost entirely restricted to the southeastern block.

Discussion

Baldwin *et al.* (2012) listed a number of regionally significant unanswered questions about the tectonic evolution of the New Guinea region which zoogeographic analysis may help answer. The questions included: (1) how many island arcs existed north of the Australian plate during the Cenozoic, (2) how did they form, (3) what was their polarity, (4) what

was their accretion history, and (5) how are tectonic events in the New Guinea region linked in space and time? Our analysis of marsupial distributions helps shed some light on questions 1 and 4.

In regard to Q1, distributional patterns among New Guinean marsupials are consistent with geological analysis and results in the division of the New Guinean Cordillera into four major 'Blocks' (Vogelkop, Maokop, Central, and Southeastern). These Blocks appear to have originated as islands, each of which has a unique history of connection with the Australian landmass.

In regard to Q4, judging from its high level of endemism and the phylogenetic histories of its lineages, the Vogelkop Block received the earliest migration of marsupial from Australia. Judging from the lack of an endemic murid radiation on Vogelkop, this occurred prior to the arrival of murids in New Guinea, which occurred at some time between the late Miocene and the mid-Pliocene (Roycroft *et al.*, 2022). Prior to the arrival of murids on Vogelkop, a migration of marsupials to the Maokop Block occurred, but it was a highly unusual one that favoured the dispersal of high elevation taxa, over those living at lower altitudes. Among the genera that dispersed were *Dactylonax* and *Pseudochirops*, which gave rise to Vogelkop and Central Cordilleran species pairs (*D. palpator/ernstmayeri*, *P. coronatus/cupreus*). A subsequent dispersal event involved the spread of *Pseudochirops albertisii* and *Dendrolagus inustus* from the Vogelkop Block to the North Coast Ranges of Papua New Guinea. This event involved the orogeny of the Northern Cordillera, which must have connected the Vogelkop, Yapen, the Foja Mountains and the North Coast Ranges into a continuous mountain range. This event was so recent that although some variation in average body size exists between some isolated populations, speciation has not yet been demonstrated among the now isolated populations of these marsupial species.

The genus *Myoictis* offers an intriguing hint to the timing of New Guinea's accretionary history. Its putative point of origin is in Vogelkop and it is known as a 2.9 mya fossil from the Otibanda Formation, on the eastern margin of the Central Block. This suggests that the Vogelkop, Maokop, and Central blocks had established subaerial contact by the late Pliocene.

Temporal constraints. The sequence of dispersal events between Australia and New Guinea, and within New Guinea, as we reconstruct them, are constrained by a number of factors. Molecular studies indicate that the invasion of most if not all marsupial lineages must postdate the mid-Miocene. Two Australasian-wide dispersal events provide the opportunity to constrain the dating of these dispersals. The first is the arrival of hydromyine murids into Australia-New Guinea. Molecular studies date the divergence of Australia/New Guinea hydromyine lineages to the late Miocene (Roycroft *et al.*, 2020, 2022). However, molecular divergence times do not offer unequivocal evidence of entry times of hydromyines into Australo/New Guinea because the lineages may have begun to differentiate prior to their arrival in Sahul, for example in Maluku, Sulawesi, or even further west. The earliest fossils of hydromyine rodents in Australia/New Guinea are from Wellington Caves, NSW and date to the lower Pliocene. The fact that only a single species of hydromyine is represented by dozens of fossils suggests that the site dates close to the time of arrival of hydromyines in Australia (Dawson *et al.*, 1999).

The fact that Vogelkop does not have a radiation of highly endemic hydromyine murids suggests that it received its earliest marsupial migrants prior to the arrival of hydromyines. It is possible that a diverse fauna of marsupials on Vogelkop may have limited opportunities for hydromyine diversification. The Central Cordillera is home to a broad variety of hydromyines, including species of *Anisomys*, *Hyomys*, *Macruromys*, and *Mallomys*. One species each of the genera *Hyomys* and *Mallomys* occurs on Vogelkop, but the Vogelkop populations are only weakly differentiated from their Central Cordilleran relatives, suggesting that the Vogelkop populations result from a Pleistocene dispersal. The North Coast Ranges of PNG, that once comprised the Northern Cordillera, entirely lack these genera. Indeed, thus far the only endemic murids documented from the 'Northern Cordillera' are *Parahydromys rufilatus* and the poorly known *Hydromys zieglerti*. From this we infer that the Northern Cordillera had subsided prior to the arrival of *Hyomys* and *Mallomys* into the Vogelkop.

The second temporal constraint concerns the arrival of *Rattus* in Australia/New Guinea in the early Pleistocene. A few species of *Rattus* (notably *R. praetor*) occur in the lowlands of New Guinea, and a larger number (e.g., *R. niobe*, *R. verecundus*) occur above 1,000 m asl. While *R. niobe* occurs on the Vogelkop, the montane *Rattus* group is entirely absent from the Northern Cordillera. Intriguingly, *Rattus steini* is also absent on the Vogelkop, where it is replaced by *Rattus praetor*. This suggests that the arrival of *Rattus* on the Vogelkop postdates the severance of the contact between the Vogelkop and the Northern Cordillera. Our provisional chronology for mammalian arrivals into New Guinea is as follows:

Vogelkop/ Northern Cordillera. Arrival of *Rattus niobe*, *Phalanger vestitus*, *Hyomys*, *Mallomys* in Vogelkop (**Pleistocene**). Dispersal of *Dendrolagus inustus/Pseudochirops albertisii* to the Northern Cordillera (**Mid Pliocene**). Dispersal of *Dactylonax/Pseudochirops* to the Maokop Block (**Early-Mid Pliocene**). Initial dispersal of marsupials from Australia to Vogelkop (**Mid-Miocene-mid Pliocene**).

Maokop Block. Diversification of New Guinea *Phalanger* species (**Miocene-Pleistocene**). Arrival of *Dactylopsila/Thylogale* (**Pliocene**).

Southeastern Block. Arrival of ancestral *Dendrolagus goodfellowi*, *Murexia rothschildi*, *Peroryctes*, from Australia (**Pliocene**).

Envoi. We consider this work a preliminary assessment. Several important tests of our hypothesis could be made with further fieldwork, the most important of which involve genetic assessment of the numerous Vogelkop endemics whose genetics remain unknown. Species of *Dactylonax*, *Pseudochirops*, *Phascolosorex*, and *Microperoryctes* should be priorities here. Equally urgent is the search for a Tertiary fossil record from the Vogelkop and Southeastern Blocks, especially for small to medium sized marsupials, for it is only the fossil record that can offer unequivocal evidence of the timing of past migrations.

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