

‘Moa’s Ark’ or ‘Goodbye Gondwana’: is the origin of New Zealand’s terrestrial invertebrate fauna ancient, recent, or both?

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Abstract. Evaluating the hypothesis of New Zealand’s total submersion during the Oligocene requires the strictest tests, including sound phylogenetic data and dating of phylogenies. Although New Zealand has been traditionally considered to host ancient biota that originated by vicariance after it separated from Australia ~80 Mya, the ancient origins of its biota have been recently questioned, with some authors even suggesting that all current land organisms had to arrive to the islands after it re-emerged from the ocean 22 million years ago. Here we examine examples of short-range endemic soil-dwelling invertebrates and find compelling evidence that at least some of them are the result of old lineages that diversified in New Zealand before the hypothesised submersion event 22 million year ago. We conclude that New Zealand indeed has old lineages as well as recently diversified lineages and compare this situation with that of other more stable areas of the Neotropics.

Introduction

New Zealand is, without doubt, one of the most fascinating archipelagos in the world. Its geology and probably parts of its biota reflect a dynamic history of ancient Gondwanan origin, long-term isolation from other continental landmasses, marine inundation during the Oligocene, glaciation during the Pleistocene, and evolutionary radiations that have produced a spectacular proportion of endemic species (Gibbs 2006). New Zealand has received considerable attention from biogeographers, beginning with Ernst Dieffenbach, a German naturalist who lived there from 1839–1841 and corresponded with Charles Darwin about the biogeographical affinities of the islands’ birds. Researchers have focused on New Zealand’s biogeography with particular vigour over the past two decades as molecular systematics has provided new tools with which to approach evolutionary questions. Molecular systematists and biogeographers have addressed topics such as the number and location of Pleistocene refugia (e.g. Marske *et al.* 2009; Buckley *et al.* 2010), the Alpine Fault Hypothesis (e.g. Heads and Craw 2004) and, most contentiously, a vicariance- v. dispersal-based origin of New Zealand’s terrestrial biota (e.g. Trewick *et al.* 2007; Phillips *et al.* 2010).

Although researchers have long recognised that land area was drastically reduced (i.e. to less than 15% of its current size) during the marine incursions of the Oligocene (e.g. Cooper and Cooper 1995), more recently Waters and Craw (2006) suggested that there is no strong evidence for continuously emergent land through the period (see also Landis *et al.* 2008). Trewick *et al.*

(2007) and Wallis and Trewick (2009) asserted that the preponderance of biogeographical evidence favours a scenario of complete submergence during the Oligocene, and some authors have suggested that the entire terrestrial biota arrived via dispersal during the last 22 million years (Landis *et al.* 2008).

Even if a large fraction of the terrestrial biota presently inhabiting New Zealand arrived via dispersal, there is compelling evidence for an archaic Gondwanan origin for some of New Zealand’s invertebrates – i.e. lineages that have been continuously present in New Zealand since its connection to other Gondwanan landmasses. Here, we review the debate and make our case for the importance of vicariance in the establishment of at least some of this unique fauna.

Moa’s Ark and Goodbye Gondwana

New Zealand originated as part of the former supercontinent Gondwana, which formed the southern portion of Pangaea during the Triassic. Gondwana broke into fragments starting ~165–160 Mya when the continental block formed by Madagascar and India began to rift from both Australia and Africa; 135–130 Mya the South Atlantic Ocean opened at the far southern tip of Africa and South America. It was not until 165–110 Mya that Africa and Antarctica finally separated. Approximately 88–84 Mya India and Madagascar rifted from one another, with India eventually colliding with Asia around 50 Ma. New Zealand, South America and Australia were originally connected across Antarctica; 80 Mya New Zealand began to drift away from West Antarctica, opening the Tasman

Sea. Final terrestrial connections between New Zealand and Australia were broken by 60 Mya, although Australia and South America remained in contact across Antarctica until at least the early Eocene. At this time Antarctica had a temperate climate and was home to *Nothofagus* forests, but by 46 Mya cold conditions were severe enough that overland dispersal by temperate-adapted organisms would have been impaired (e.g. Scotese *et al.* 1988; reviewed in Sanmartín 2002). Southern South America and Antarctica still remained in contact through the Antarctic Peninsula until the opening of the Drake Passage at the Eocene–Oligocene boundary (30–28 Mya). This led to the establishment of the Antarctic Circumpolar Current and the onset of the first Antarctic glaciation (reviewed in Sanmartín 2002; Sanmartín and Ronquist 2004), which has influenced the New Zealand biota to certain extent.

New Zealand has long been considered to host a large number of lineages of Gondwanan origin, an idea captured by the phrase ‘Moa’s Ark’, the title of a popular documentary on the country’s natural history (Bellamy *et al.* 1990). The ‘Moa’s Ark’ paradigm is based on charismatic examples of supposed vicariance in ratite birds, chironomid midges, and the Southern beech, or on the presence of ancient relicts such as the tuatara and leiopelmatid frogs, with no close extant relatives outside of New Zealand (Trewick *et al.* 2007). However, recent reinterpretations of New Zealand’s geology and its fauna have led to very different conclusions, framed as the ‘Goodbye Gondwana’ paradigm (McGlone 2005), which questions the antiquity of the land surface and thus of its terrestrial biota, and postulates that virtually every terrestrial group has reached New Zealand through fortuitous over-water dispersal during the past 22 million years (Landis *et al.* 2008), with subsequent diversification (Waters and Craw 2006; Trewick *et al.* 2007; Goldberg *et al.* 2008).

Support for the ‘Goodbye Gondwana’ paradigm comes from different sources of evidence, including the fossil record (e.g. Pole 2001), but chiefly from molecular systematics and estimation of divergence times that for example provides evidence for trans-oceanic dispersal of the Southern beech (e.g. Cook and Crisp 2005b; Knapp *et al.* 2005), formerly the textbook example of a classic Gondwanan taxon (e.g. Swenson *et al.* 2001). More surprisingly, the monophyly of the flightless ratite birds (the moas, kiwis and their relatives, the emus, rheas, cassowaries and ostriches) has recently been questioned through a new analysis of mitochondrial genomic data, including New Zealand’s now-extinct moas, whose DNA was sequenced from exceptionally well-preserved bones in museum collections (Phillips *et al.* 2010). This analysis identified tinamous, which can fly and have not traditionally been included within the ratites, as the sister group to the flightless moas. If the most recent common ancestor of moas and tinamous could fly, it may no longer be necessary to invoke Gondwanan vicariance to explain their arrival on New Zealand – although the fact that an animal’s ancestor had the ability to fly does not necessarily indicate that vicariance has not played a role in shaping current distributions, as shown for example in forest dwelling birds (Weir *et al.* 2009).

More broadly, a recent compilation of molecular phylogenetic analyses of ~100 plant and animal groups suggests that only 10% of these are even plausibly of archaic origin predating the

vicariant split of Zealandia from Gondwana (Wallis and Trewick 2009). They summarise current opinion on the extent of the Oligocene drowning episode thusly: ‘If further paleontological data reveal evidence of uninterrupted fossil records through the Oligocene, complete inundation is made less likely (Winkworth *et al.* 1999; Lee *et al.* 2009). Notwithstanding these gaps in our knowledge, many commentators have already debunked the concept of NZ as a Gondwanan relictual ark (McGlone 2005; Waters & Craw 2006; Trewick *et al.* 2007; Landis *et al.* 2008)’ (Wallis and Trewick 2009: p. 3565). The same authors do concede (p. 3565) that ‘[m]ore work on arthropods is needed; they are likely to include recent and ancient dispersers as well as Gondwanan relicts (Gressitt 1961, 1970; Boyer & Giribet 2007)’. In another paper Goldberg *et al.* (2008) review the molecular evidence for several New Zealand terrestrial animals, concluding that the New Zealand biota is ‘in most respects, more like that of an oceanic archipelago than a continent’ (p. 3319). Few have questioned this new trend in interpretation of New Zealand biogeography (Knapp *et al.* 2007; Edgecombe and Giribet 2008; Boyer and Giribet 2009; Allwood *et al.* 2010).

Interestingly, a similar argument has emerged for New Caledonia (Murienne *et al.* 2005; Grandcolas *et al.* 2008), also considered part of Zealandia, although in this case there is significant geological evidence supporting the total submergence of New Caledonia under the adjacent oceanic plate, followed by ophiolitic obduction in the Eocene. By contrast, the evidence of complete submersion for New Zealand is not as strong. Murienne (2009) recently summarised the three existing models for New Caledonia, also applicable to New Zealand. The ‘museum model’ implies that the island has acted as a museum and the origin and diversification of the New Caledonia lineages precedes a supposed drowning event. The two other models suppose that the diversification initiates after the land re-emerged; one with a series of ‘mountain refugia, island refugia and long-distance dispersal’ and another without refugia and explaining all the current diversity by long-distance dispersal. The author concluded that the three models might render identical phylogenetic patterns, making these models difficult to choose from, but molecular dating could at least discern between the first and last models. An additional model: a cryptic mass extinction, leaving a phylogenetic pattern indistinguishable from that of an evolutionary radiation, has been recently proposed as an alternative (Crisp and Cook 2009).

Dispersal hypotheses are difficult, if not impossible, to falsify, but easy to corroborate with a phylogenetic pattern that results in paraphyly of the source group (Edgecombe and Giribet 2008) (see Fig. 1). Hence, if one postulates that an endemic clade from New Zealand has originated in Australia, it should render its Australian counterparts paraphyletic, with the New Zealand lineage nested within (but see Cook and Crisp 2005a for a different interpretation). But more relevant, perhaps, is the recent use of molecular dating in phylogenetic analyses. Given enough data and even considering broad errors in dating techniques, it is now feasible to distinguish whether a lineage has originated before or after a postulated geological event. In the context of New Zealand, 22 Mya is the age that would distinguish the competing ‘Moa’s Ark’ and ‘Goodbye Gondwana’ scenarios. Therefore, in this article we revisit some cases of our ‘favourite’

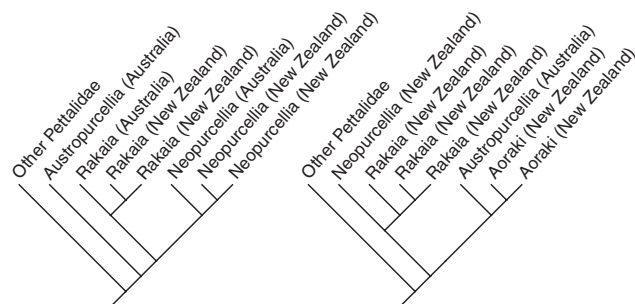


Fig. 1. Two alternative possible resolutions of the trans-Tasman pettalid genera. (Left) Initial model of two trans-Tasman genera and one Australian genus rendering Australia paraphyletic. This was the taxonomic hypothesis available before the studies of Boyer and Giribet (2007). (Right) Current phylogenetic hypothesis where each genus occurring is restricted to a single landmass.

organisms, arthropods and other related terrestrial invertebrates, to test the 22 Mya barrier. We are not arguing that Gondwanan vicariance is the mechanism explaining all or even the majority of the New Zealand biota. Rather, we are interested in identifying cases that firmly establish that New Zealand has acted, even if in few instances, as a biodiversity ark for Gondwanan taxa, and that some of them may even be considered relictual (e.g. *Craterostigmomorpha*, *Sphenodontida*).

Examples of supposed Gondwanan relicts in New Zealand

Many groups of terrestrial New Zealand animals show Gondwanan distributions, as summarised in previous reviews (e.g. Sanmartín and Ronquist 2004; Trewick *et al.* 2007; Goldberg *et al.* 2008), but a Gondwanan distribution is not sufficient for accepting a hypothesis of vicariance for New Zealand's fauna (Trewick *et al.* 2007). Here, we focus on four groups of terrestrial invertebrates that plausibly arrived in New Zealand before the 22 Mya Oligocene drowning barrier: mite harvestmen, *Craterostigma* centipedes, stone centipedes, and peripatus or velvet worms.

The reasons for choosing these examples are the existence of (1) resolved phylogenies and (2) molecular dating. These are also taxa that fall in the category of short-range endemics, characterised by Harvey (2002) as taxa that lack active dispersal mechanisms and rely on permanently moist micro-habitats, features that may preclude them from trans-oceanic dispersal. These characteristics may make the selected examples useful candidates for biogeographic study.

Mite harvestmen: Pettalidae (Fig. 2a–d)

Mite harvestmen (Arachnida, Opiliones, Cyphophthalmi), and the family Pettalidae in particular, have played a role in the study of Gondwanan and New Zealand biogeography. The family has a typical temperate Gondwanan distribution, with species in Chile, South Africa, Madagascar, Sri Lanka, Australia and New Zealand (but not in New Caledonia, which hosts a member of a tropical Gondwanan clade, the family Troglosironidae) (Boyer *et al.* 2007b; Boyer and Giribet 2007). Originally, New Zealand's mite harvestmen were described in two genera, *Rakaia* and

Neopurcellia, each of which also included species in Queensland, Australia, implying a shared evolutionary history spanning the Tasman Sea (Fig. 1). However, recent taxonomic revision by Boyer and Giribet (2007), based on a combined analysis of morphological and molecular data, refutes that hypothesis. The mite harvestmen of Queensland were found to be monophyletic and are now grouped in a single genus (*Austropurcellia*) with no New Zealand representatives. The New Zealand species are grouped into three genera: *Aoraki* (Fig. 2a) in the North and South islands, *Rakaia* (Fig. 2c, d) in the North, South and Stewart islands, and *Neopurcellia* (Fig. 2b) in the south-west coast of the South Island (Boyer and Giribet 2007, 2009). The natural history of these slow-moving leaf-litter dwellers suggests extremely poor dispersal capabilities, with species ranges typically measuring 100 km in diameter or less. Population genetic data generated from New Zealand's only 'widespread' mite harvestman, found throughout the north-west quadrant of the South Island, indicate deep structure associated with geography, corroborating this point of view (Boyer *et al.* 2007a).

Pettalids have been a centre of discussion on the age of New Zealand's terrestrial fauna. For example, Boyer and Giribet (2009: 1095) state that: 'If New Zealand has indeed been submerged, and the terrestrial biota of the archipelago has arrived solely through transoceanic dispersal, we would expect to see close relationships between the pettalid fauna of New Zealand and species from other nearby land masses.' However, Goldberg *et al.* (2008: 3323) postulate that: 'the levels of molecular divergence among the pettalid lineages are too low to be consistent with an ancient origin, unless there has been a very substantial taxon specific change in mutation rate. Diversity and spatial structuring on South Island mountains that are ca. 5 Ma old suggest an arrival within the past few million years.' This latter statement is interesting, as no dating had been performed in the analyses of Boyer and Giribet (2007, 2009). A more recent article on broader Opiliones phylogeny incorporated samples of the three New Zealand pettalid genera and the two Australian genera, and used a parametric rate-smoothing approach to estimate the origin of *Aoraki* at 55 Mya (± 21), *Rakaia* at 118 Mya (± 22), a divergence between *Neopurcellia* and *Rakaia* at 150 Mya (± 25), and a divergence of *Austropurcellia* and *Aoraki* at 167 Mya (± 27) (Giribet *et al.* in press). All these ages are much older than 22 Mya, contradicting the suggestion by Goldberg *et al.* (2008) that the New Zealand pettalids arrived within the past 5 million years.

Centipedes: *Craterostigma* (Fig. 2e)

Centipedes are ubiquitous terrestrial predators currently classified in five extant orders (Edgecombe and Giribet 2007). One of these orders, *Craterostigmomorpha*, remained monotypic until the recent formal description of a second species from New Zealand (Edgecombe and Giribet 2008), although the presence of *Craterostigma* in New Zealand had been known for quite some time (Archey 1917; R. E. Crabill, Jr, pers. comm. in Lewis 1981) considered at least two species to be distinguishable within *Craterostigma* based on morphology, but his arguments in favour of the distinctness of a New Zealand



species were never published, and only recently some minor morphological differences between these two species have been proposed (Prunescu and Prunescu 2006; Edgecombe and Giribet 2008). Edgecombe and Giribet (2008) focused on genetic distances within and among the two species to postulate an ancient split of these two lineages, despite the minimal morphological variation between the two, and Giribet *et al.* (2009) further tested the reciprocal monophyly of the species. However, the lack of *Craterostigmus* fossils prevented the authors from calibrating this molecular tree (Edgecombe and Giribet 2008). In a more recent analysis of the whole centipede order, Muriénne, Edgecombe and Giribet (unpubl. data) used several calibrations in the centipede tree to conclude that the two species of *Craterostigmus* diverged from each other 270 Mya (s.d. = 26.30, min = 179.75, max = 317.79), at least by the Jurassic. Certainly the ages for *Craterostigmus* divergences, even if perhaps inflated owing to methodological issues (see Muriénne, Edgecombe and Giribet, unpubl. data), contradict the possibility of *C. crabilli* being a geologically young introduction to New Zealand, as postulated by some.

Stone centipedes: *Paralamyctes* (Fig. 2f)

Other centipede groups that have been proposed to show Gondwanan patterns involving New Zealand are found in the lithobiomorph family Henicopidae (Edgecombe *et al.* 2002; Edgecombe and Giribet 2003). Among henicopids, the best-studied genus is *Paralamyctes*, found in Chile, South Africa, Madagascar, India, Australia (including Tasmania) and New Zealand (Giribet and Edgecombe 2006), a distribution paralleling those of Pettalidae and Peripatopsidae (see below). However, in these other groups, none or just a few genera have a vicariant distribution across multiple land masses, whereas *Paralamyctes* is widespread and distributed across the former temperate Gondwana, suggesting either an ancient age for the genus or a much higher dispersal capability than the one observed in the groups discussed above. No *Paralamyctes* fossil is known for calibrating the trees; however, the recent dating of a densely sampled centipede tree (Muriénne, Edgecombe and Giribet, unpubl. data) suggests that divergences within the eight sampled species in the genus range between 137 and 253 Mya, hence suggesting that the multiple trans-Tasman clades are a result of old vicariant events, and not due to recent dispersal.

Velvet worms or 'Peripatus': the family Peripatopsidae (Fig. 2g, h)

Onychophorans famously require very specific environmental conditions to avoid desiccation. Of the two extant families, Peripatopsidae has a temperate Gondwanan distribution

paralleling those of Pettalidae and *Paralamyctes* with some minor differences. Members of Peripatopsidae are known from Chile, South Africa, Australia (including Tasmania), New Guinea, and New Zealand (Reid 1996; Mayer 2007) (pettalids are also known from Sri Lanka and Madagascar, but they are not known from Tasmania or New Guinea; *Paralamyctes* is missing from New Guinea but present in the Indian subcontinent). The New Zealand Onychophora has been studied in detail (Gleeson 1996; Trewick 1998, 1999, 2000; Allwood *et al.* 2010). Two independent genera are recognised in New Zealand, *Peripatoides* and *Ooperipatellus*, both of which find their sister clade in Tasmania (*Ooperipatellus* is a trans-Tasman genus), or Tasmania and/or mainland Australia (*Peripatoides*) (Gleeson *et al.* 1998; Allwood *et al.* 2010). The presence of deep genetic structure within *Peripatoides* has been interpreted to indicate an ancient origin with local survival of populations through climate cycles (Goldberg *et al.* 2008). Allwood *et al.* (2010) estimated divergence times of the New Zealand clades, suggesting that the New Zealand and Australian genera probably diversified during the Cretaceous, but all of the New Zealand *Ooperipatellus* divergences had a large error and overlapped both with the Oligocene Drowning and the rifting of New Zealand from Australia. However, the diversification of *Peripatoides* pre-dated the peak of the Oligocene Drowning (Allwood *et al.* 2010).

Conclusions

Evaluating the hypothesis of New Zealand's total submersion during the Oligocene requires the strictest tests, nowadays perhaps satisfactorily addressed only by rigorous phylogenetic analysis (the phylogenetic pattern must be congruent with the hypothesis tested; e.g. recent dispersal likely results in paraphyly of the source landmass) and dating of the phylogenies examined. The era of invoking vicariance without phylogenetic analysis has long passed and, likewise, phylogenetic dating must be incorporated to discern between contrasting hypotheses. The four cases discussed above suggest, to us, a pattern that contradicts the recent idea of total submersion of New Zealand. This is evidenced both by the reciprocal monophyly of the New Zealand clades and their sister taxa in the case of Pettalidae, and by the dating of the cladogenetic events that led to the current diversity. Such dating indicates an origin much older than the proposed episode of total submersion. The case of the onychophoran clades is more contentious, as molecular dating results remain ambiguous.

In addition to the further testing of candidate groups such as velvet worms, there may be many other examples to be studied, such as the harvestmen (Arachnida, Opiliones) of the family Monoscutidae (Fig. 2i), restricted to Australia, Tasmania,

Fig. 2. (a) *Aoraki longitarsa* from Governor's Bush, Aoraki – Mount Cook National Park, South Island, photographed January 14th, 2006. (b) *Neopurcellia salmoni* from Roaring Billy Falls, Te Wahipoumanu, Westland, South Island, photographed February 15th, 2008. (c) *Rakaia pauli* from Kelcey's Bush, Waimate, South Island, photographed February 18th, 2008. (d) *Rakaia stewartiensis* from Fern Gully, Oban, Stewart Island, photographed February 17th, 2008. (e) *Craterostigmus crabilli* from Flora Camp, Kahurangi National Park, Arthur Range, South Island, photographed February 10th, 2008. (f) *Paralamyctes rahuensis* from Rahu Scenic Reserve, near Springs Junction, South Island, photographed January 31st, 2003. (g) *Peripatoides aurorbis* from Otari – Wilton's Bush, Wellington, North Island, photographed February 8th, 2008. (h) *Peripatoides cf. novaezealandiae* from Panekiri Bluffs, Te Urewera National Park, North Island, photographed January 22nd, 2003. (i) Monoscutid species (Opiliones, Eupnoi, Monoscutidae) from Inland Pack Track, Woodpecker Bay, South Island, photographed February 12th, 2008. (j) *Hendea* sp. (Opiliones, Laniatores, Triaenonychidae) from Nature Walk, Brunner Peninsula, Lake Rotoiti, Nelson Lakes National Park, South Island, photographed 11 February 2008. All photographs by G. Giribet.

and New Zealand (including the subantarctic islands) (Cokendolpher and Taylor: 118–121, in Pinto-da-Rocha and Giribet 2007; Taylor and Hunt 2009); the harvestman families Triaenonychidae (Fig. 2j) and Caddidae, with lineages well represented in New Zealand (Forster 1947, 1954, 1962, 1963; Giribet and Kury 2007); and the New Zealand endemic springtail genus *Holacanthella* (Hexapoda, Collembola, Neanuridae) with close relatives in Australia, New Caledonia, India and nearby non-Gondwanan landmasses (Stevens *et al.* 2007). Sound phylogenetic relationships need to be obtained before being able to add these taxa to the list of possible relictual candidates of ‘Moa’s Ark’. Certain families of Acari and Pseudoscorpiones have also been proposed for biogeographic studies of Gondwanan patterns (Harvey 1996a, b), but a recent phylogenetic analysis of pseudoscorpions yielded little broad biogeographic structure (Murienne *et al.* 2008), perhaps owing to the presence of phoresy in many pseudoscorpion species. Minute soil-dwelling spiders (e.g. Micropholcommatidae: Rix *et al.* 2008; Rix and Harvey 2010) and certain trap-door spiders (Mygalomorphae) (Forster and Wilton 1968; Griswold and Ledford 2001) could be excellent candidates for more detailed biogeographic research.

Although many, or even the overwhelming majority, of the terrestrial animal lineages represented in New Zealand today might have arrived via dispersal following submergence of land during the Oligocene, or at least show patterns of recent diversification (e.g. Brown *et al.* 1999; Buckley and Simon 2007), the cases reviewed here indicate that, for at least a few groups, vicariance is still a plausible biogeographical scenario. In fact, the combination of a few ancient divergences with more recent diversifications is not very different from the model proposed for the leaf beetle diversity of the Neotropics (McKenna and Farrell 2006), a combination of ‘evolutionary cradles’ and ‘museums of diversity’. Having an unbalanced mix of old species-poor lineages and a larger proportion of recent radiations may actually be expected even in stable parts of our planet. It is not yet time to bid New Zealand’s Gondwanan heritage goodbye.

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