

Going under down under? Lineage ages argue for extensive survival of the Oligocene marine transgression on Zealandia

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Funding information

Miss Hellaby Grassland Trust; Marsden
Fund; University of Otago

Abstract

Twenty-five years ago, it was suggested that current-day New Zealand, part of the largely sunken continent of Zealandia, could have been completely inundated during the Oligocene marine transgression (OMT) some 25–23 million years ago. Such an event would, of necessity, imply that all terrestrial, freshwater, and maybe coastal marine species must have dispersed there since. This idea has generated heated debate, on which geological, palaeontological and molecular data are being brought to bear. Here, we review the phylogeographic literature in the form of molecular estimates of divergence times between New Zealand lineages and their closest overseas sister groups. Using an event-based approach, we show that these divergence times follow approximately a smooth exponential over the last 50 Ma or more. Approximately 74 of these 248 lineages appear to have survived the OMT in situ; some of these major lineages comprise multiple additional lineages as a result of autochthonous speciation prior to the OMT. Non-volant terrestrial animals, freshwater animals and trees are particularly well represented in surviving lineages, whereas marine animals, herbs and shrubs tend to show more recent arrival times. There is no evidence for a deficit of pre-Oligocene lineages, nor an excess of ones arriving just afterwards. The pattern is one of geometric increase in new lineages with more recent time, reflecting a balance between immigration and extinction. Consequently, this large body of molecular data provides no evidence for complete inundation of New Zealand during the Oligocene. In conjunction with new geological and palaeontological findings, these data suggest that it is time to put the idea to rest.

KEYWORDS

biogeography, extinction, New Zealand, phylogeography, review

1 | INTRODUCTION

The colonization of islands through long-distance dispersal (LDD) has long been inferred from observation of the rapid establishment of biota on new volcanic islands (Gillespie et al., 2012), such as Krakatoa, where over 400 species established in the first decade after emergence (Emerson, 2002). Molecular analysis has been used to determine the origins of lineages on older, larger and more isolated volcanic archipelagos, notably the Galápagos (Torres-Carvajal,

Barnes, Pozo-Andrade, Tapia, & Nicholls, 2014), Hawaiian (Wagner & Funk, 1995) and Canary archipelagos (Juan, Emerson, Oromi, & Hewitt, 2000). By inference, one might expect the biota of a larger landmass such as New Zealand to have also been strongly influenced by LDD, especially given its relative proximity to Australia compared with smaller, more remote Pacific islands (MacArthur & Wilson, 1967). Although its biogeographers have long recognized many different sources and time depths for the origins of the biota (Fleming, 1979), New Zealand tends to have been characterized as a lost world

of archaic vicariant lineages, implicit in folk metaphors such as “Moa’s ark,” “life-raft” and “living fossil,” which have become a cultural icon for many (McGlone, 2005). This vision is further strengthened by evidence showing Zealandia to be a continental landmass, now largely submerged (Campbell & Mortimer, 2014), whose separation from Australia began some 82 Ma.

Over the last 25 years, however, molecular phylogenetic research has shown that many New Zealand radiations of plants (Perrie & Brownsey, 2007; Winkworth, Hennion, Prinzing, & Wagstaff, 2015; Winkworth, Wagstaff, Glenny, & Lockhart, 2002) and animals derive from more recent arrivals (De Queiroz, 2005; Wallis & Trewick, 2009), lending credence to the earlier provocative suggestion that New Zealand’s entire flora might derive from LDD (Pole, 1994). Key in this debate is the fact that during the Oligocene marine transgression (OMT) *ca.* 23 Ma, New Zealand was at least reduced to an archipelago of low-lying islands (Cooper, 1989). Some geologists have supported the more extreme position of complete inundation through further documentation of limestone deposits, and showing that what has been called a peneplain in lower South Island is in fact a wave-cut surface (Landis et al., 2008). The assumption of a continuous landmass has in some cases been based on the assumption of archaic elements in the flora and fauna, an argument that has been characterized as circular (Waters & Craw, 2006). If, indeed, no land remained, the entire terrestrial and freshwater flora and fauna, and maybe the coastal marine fauna, must have arrived since (Trewick, Paterson, & Campbell, 2007). More recently, other geologists have reported palaeogeographic evidence in support of continuous presence of land (Kamp, Tripathi, & Nelson, 2014; Mortimer & Strong, 2014; Strogon, Bland, Nicol, & King, 2014), and evidence for shorelines coinciding with the OMT maximum (Lee et al., 2014; Scott, Lee, Fordyce, & Palin, 2014), but the debate is far from resolved.

Fuel has been added to the fire as the vicariant origin of one classic archaic lineage after another has been seriously challenged (Biffin, Hill, & Lowe, 2010; Cook & Crisp, 2005; Knapp et al., 2005; Mitchell, Llamas, et al., 2014; Phillips, Gibb, Crimp, & Penny, 2010), leading to a rash of papers concerning “Goodbye Gondwana” (McGlone, 2005). An extensive review of New Zealand phylogeography suggested that the molecular data were inconsistent with archaic origins for most lineages, with the exception of tuatara, leiopelmatid frogs and wrens (Wallis & Trewick, 2009), paralleling findings for other regions of biogeographic significance (Stelbrink, Albrecht, Hall, & von Rintelen, 2012). However, it is easier to refute vicariance than it is to refute pre-Oligocene origins of today’s biota, because of the shallower time depth.

Uncertainty about rates of evolution and rate constancy in calibrating molecular clocks (Lanfear, Welch, & Bromham, 2010), choice of genes and models of molecular evolution (Hillis, Moritz, & Mable, 1996) and stochasticity in nucleotide substitution all impact on the ability to demonstrate dispersal versus vicariance (Crisp, Trewick, & Cook, 2011). Further complicating factors are lineage extinction and incomplete sampling. Whereas genetic divergence implying much less than 23 Ma between New Zealand (NZ) and, for example, an Australian lineage demonstrates post-OMT dispersal (though one

might argue about direction), a distance value of much more than 23 Ma is only *consistent with* surviving the OMT. The main reason for this imbalance is the possibility of extinction of a more closely related overseas lineage since the OMT. Wallis and Trewick (2009) stressed that although many lineages show post-OMT arrival, several are consistent with pre-OMT arrival. In the intervening decade, many more studies have been published on more species groups, with better data, reconstructions and dating; it is now appropriate to assess these data *en masse*.

The premise of our approach is that any one study is prone to error from the different sources mentioned above, but by considering a large number of studies together, one might be able to infer a general process from a general pattern. A classic early analysis of this sort (Sanmartín & Ronquist, 2004) did not consider dating, and there have been many studies since this, and other syntheses (Wallis & Trewick, 2009). There have been other compilations of splits between NZ and overseas lineages, but they have not resolved direction of dispersal, and concern plants alone (Perrie & Brownsey, 2007; Winkworth et al., 2015).

If most lineages arrived in NZ post-OMT, most genetic distances between NZ lineages and their overseas sister should indicate a time of <23 Ma. Given the supposed high dispersal rates to NZ, and the benefits that first arrivals accrue (Lack, 1947), across a large number of distance values, one would predict a pronounced spike in the distribution representing times of just under 23 Ma. Radiations should tend to date back to this point, but not precede it (Cooper & Cooper, 1995), except when there has been extinction of closer sister groups at source. In this paper, we test for this pattern by gathering 248 published dates for molecular divergences between NZ and overseas lineages, where there is good reason to believe that NZ was the recipient landmass. Additionally, we identify the continental origins of these lineages (Sanmartín & Ronquist, 2004) and quantify their provenance against time.

2 | MATERIALS AND METHODS

2.1 | Data collection

We compiled data on the estimated divergence dates of NZ taxa with their respective sister groups on another landmass, to produce a large data set of divergence times, representing either vicariance (>65 Ma), pre-Oligocene dispersal (65–23 Ma) or post-Oligocene arrival. This compilation was based upon (but not limited to) a search on the ISI Web of Science™ using the string: “phyloge*” and (dispers* or vicarian*) and Zealand.” This search yielded 561 papers on the molecular phylogenetics of plant and animal groups since 2009, up to 4 June 2018. Retrieved studies were excluded in the following cases: (a) the work focused on invasive species, corals or algae, (b) humans were the likely agents of introductions, (c) the study did not include molecular data, and (d) NZ was likely to be the source rather than the recipient. We examined all publications individually and recorded from all selected studies: (a) taxon information (NZ and overseas sister group), (b) markers used, (c) calibration details, (d) estimated divergence date of NZ

TABLE 1 Data set of published molecular clock estimates of divergence times between NZ lineages and their closest overseas relatives

| NZ taxon | Sister group split | Rank of split | Common name/ group | Genes | Calibration per Ma | Origin | AAR | Age | | | References |
|--|---|---------------|------------------------|--|--|---------|-----|--------|-------|--------|---------------------------------|
| | | | | | | | | Mean | Min | Max | |
| <i>Sphenodon</i> | Squamata | Order | Tuatara | RAG1 | 12 secondary | Archaic | n | 271.5 | 268 | 275 | Hugall et al. (2007) |
| <i>Craterostigmus crabilli</i> | <i>C. tasmanianus</i> | Species | Centipede | Review | Several | Archaic | n | 270 | 180 | 318 | Giribet and Boyer (2010) |
| Leiopelmatidae | Ascaphidae | Family | Frog | 95 nucl prot genes (+RAG1, CXCR4) | Fossils (20) | Archaic | y | 193.8 | 178.6 | 207 | Feng et al. (2017) |
| <i>Neopurcellia</i> , <i>Aoraki</i> , <i>Rakaia</i> | <i>Chileogovia</i> , <i>Purcellia</i> | Genus | Mite harvestman | cox1, 16S, 18S, 28S, H3 | Fossils (2) | Archaic | y | 142 | | | Giribet et al. (2012) |
| <i>Paralamyctes</i> sp. | <i>Paralamyctes</i> sp. | Species | Centipede | Review | Several | Archaic | n | 137 | | | Giribet and Boyer (2010) |
| <i>Paranephrops</i> | <i>Spinastacoides</i> , <i>Ombastacoides</i> | Genus | Crayfish | 16S, cox1, 18S, 28S | Fossils (6) | Archaic | n | 136 | 109 | 160 | Toon et al. (2010) |
| <i>Uropetala carovei</i> | <i>Phenes</i> , <i>Petalura</i> spp. | Genus | Petalurid dragonfly | cox1, cox2, cytb, 12S, 16S, 18S, 28S, H3 | Fossils (4) | Archaic | y | 127.4 | 80 | 175 | Ware et al. (2014) |
| <i>Lepidothamnus laxifolius</i> | <i>L. fonckii</i> | Species | Mountain rimu | rbcL | Fixed rate | Archaic | n | 109.3 | 70.1 | 148.5 | Wardle et al. (2001) |
| <i>Griselinia littoralis</i> , <i>G. lucida</i> | Apiaceae, Myodocarpaceae, Araliaceae, Pittosporaceae | Family | Broadleaf | rpl16 intron, trnD-trnY-trnE-trnT | Fossils (6) | Archaic | y | 103.06 | 90.2 | 115.84 | Nicolas and Plunkett (2014) |
| <i>Nesamblyops</i> | 16 genera | Genus | Carabid beetle | cox1, cox2, rrnL+trnL+nad1, SSU, LSU | Fossil + island emergence + fixed clock <i>Carabus</i> | Archaic | n | 100.4 | 70.4 | 134.5 | Andújar et al. (2016) |
| <i>Schistochila</i> (<i>Sciophilae</i>) <i>glaucescens</i> | 4 subgenera | Subgenus | Liverworts | rbcL, Rps4, trnL-F | Fossils (7) + plastid rate 0.05% | Archaic | y | 98.92 | | | Sun et al. (2014) |
| <i>Beaupreoidites</i> spp. (†) to 1 Ma | <i>Beauprea</i> | Genus | Proteaceae | matK, rbcL, trnL intron, trnL-trnF, atpB, atpB-rbcL, rpl16 intron, ITS | Fossil pollen | Archaic | n | 83 | 82.5 | 83.5 | He, Lamont, and Fogliani (2016) |
| <i>Calloria</i> , <i>Gyrothyris</i> , <i>Neothyris</i> , ' <i>Terebratella</i> ' sp. | Magellanic genera (4) | Genus | Long-looped brachiopod | cox1, SSU, LSU | Fossils (8) | Archaic | n | 82 | 48 | 120 | Cohen et al. (2011) |
| <i>Hemiandrus</i> spp. (6) | <i>Exogyrrilacris</i> , <i>Hypocophoides</i> , <i>Penalva</i> , genus B, H. sp. | Genus | Ground weta | cox1, 28S | 82 Ma plus relaxed cox1 insect rate 0.7%–1.2% | Archaic | n | 80 | | | Pratt et al. (2008) |

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TABLE 1 (Continued)

| NZ taxon | Sister group split | Rank of split | Common name/ group | Genes | Calibration per Ma | Origin | AAR | Age | | | References |
|--|--|---------------|--------------------------|---|--|----------|-----|-------|-------|-------|---|
| | | | | | | | | Mean | Min | Max | |
| <i>Echydridella</i> spp. (3) | <i>Cucumerunio</i> , <i>Diplodon</i> , <i>Hyridella</i> , <i>Lortella</i> , <i>Velesunio</i> | Genus | Hyriid freshwater mussel | cox1, 28S | None | Archaic | n | 80 | | | Graf and Ó Foighil (2000), Marshall et al. (2014) |
| <i>Peripatoides</i> | <i>Tasmanipatus</i> | Genus | Velvet worm | cox1, 12S, 16S, 18S, 28S | Secondary calibration for stem age 382 Ma | Archaic | n | 77.7 | 55.4 | 103 | Murienne et al. (2014) |
| <i>Ooperipatellus</i> | <i>Ooperipatellus</i> | Species | Velvet worm | cox1, 12S, 16S, 18S, 28S | Secondary calibration for stem age 382 Ma | Archaic | n | 75.1 | 53.4 | 100.7 | Murienne et al. (2014) |
| <i>Acanthisitti</i> | Tyranni, Passeri | Suborder | Wren | 7 nuclear genes | Geological vicariance events + 3 fossils | Archaic | n | 72.84 | 59.02 | 85 | Ericson et al. (2014) |
| <i>Liboedrus plumosa</i> , <i>L. bidwillii</i> | <i>Actinostrobis</i> , <i>Austrocedrus</i> , <i>Callitris</i> + 4 other genera | Genus | Cupressaceae | matK, rbcL | Fossils (9) | Archaic | y | 70 | 63 | 97 | Crisp et al. (2011) |
| <i>Raukua anomalus</i> , <i>Schefflera digitata</i> | <i>R. spp.</i> (3), <i>Motherwellia</i> sp. <i>Caphalaralia</i> sp. | Species? | Araliaceae | atpB-rbcL, ndhF, psbA-trnH, rps16, trnL-F, rpl16, ITS | Fossils (3) | Archaic | y | 70 | 56 | 86 | Mitchell, Li, Brown, Schönberger, and Wen (2012) |
| <i>Nestor notabilis</i> | Psittacinae, Cacatuinae | Superfamily | Parrot | c-mos, RAG-1, Zenk | Fossils (2) non-parrots; <i>Cyanoramphus</i> NZ vs. <i>Eunymphicus</i> NC < 5 Ma | Archaic? | y | 58.6 | 44.9 | 72 | Schweizer, Seehausen, and Hertwig (2011) |
| <i>Paroichius aotearoae</i> , <i>P. araucanus</i> , <i>P. spinosus</i> | <i>Paroichius</i> 6 spp. | Species | Midge | cox1, 18S, 28S, CAD | Fossils (4) | Archaic? | n | 58 | | | Cranston et al. (2010) |
| <i>Microfrullania</i> | <i>Frullania</i> | Subgenus | Liverwort | trnG, trnL-F, ITS | Fixed rates for ITS and cpDNA | Archaic? | y | 55.2 | 36.1 | 78.2 | Carter et al. (2017) |
| Apterygiformes | Aepyornithiformes | Order | Kiwi | mtgenome; NGS nuclear | Fossils (7) | Mad? | n | 54.2 | 47.5 | 61.7 | Grealy et al. (2017) |
| <i>Novocrania huttoni</i> | <i>Novocrania</i> spp. | Species | Craniiform brachiopod | SSU, LSU, ITS2, 16S | Relative time: base set to 1.0 = 600 Ma | unknown | n | 54 | | | Cohen, Kaufuss, and Lüter (2014) |
| <i>Stictocladus pictus</i> | <i>S. sofour</i> group | Species | Midge | cox1, 28S, CAD | Fossils (2) + secondary calibration | Aus? | n | 53 | 36 | 71 | Krosch and Cranston (2013) |
| Dinornithiformes | Tinamiformes | Order | Moa | mtgenome; NGS nuclear | Fossils (7) | SAm? | n | 51.9 | 45.5 | 59.4 | Grealy et al. (2017) |

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TABLE 1 (Continued)

| NZ taxon | Sister group split | Rank of split | Common name/ group | Genes | Calibration per Ma | Origin | AAR | Age | | | References |
|--|--|---------------|-----------------------|---|---|----------|-----|-------|-------|-------|---|
| | | | | | | | | Mean | Min | Max | |
| <i>Hymenophyllum</i> | <i>Abrodictyum</i> , <i>Cephalomanes</i> | Genus | Fern | rbcl, Rbcl-AccD-AccD, rps4-trnS | 2 secondary: root and <i>Hymenophyllum</i> origin | Archaic? | y | 49.8 | 40.7 | 59.5 | Del Rio et al. (2017) |
| Griopterygidae (12 genera) | Aus & SAM gryopterygids | Genus | Gryopterygid stonefly | cox1, H3, 18S | Fossil + biogeographic calibrations | Aus/SAM | n | 48.2 | | | McCulloch et al. (2016) |
| <i>Pirara matakiri</i> | <i>Echinocladius martini</i> | Genus | Midge | cox1, 28S, CAD1, CAD3 | Fossils (2) | Aus? | n | 47.42 | 26.77 | 73.23 | Krosch et al. (2011) |
| <i>Stictocladius lacuniferus</i> | <i>S. multiserialis</i> group | Species | Midge | cox1, 28S, CAD | Fossils (2) + secondary calibration | Aus? | n | 47 | 31 | 64 | Krosch and Cranston (2013) |
| <i>Mystacina tuberculata</i> | 5 families | Family | Short-tailed bat | Nuclear genes (17) | Fossils (6) | SAM? | y | 46 | 41 | 51 | Teeling et al. (2005) |
| <i>Pseudowintera</i> | <i>Bubbia</i> , <i>Zygogynum</i> , <i>Bellium</i> , <i>Exospermum</i> | Genus | Winteraceae | trnL-F, ITS1-2 | Fossils (3) | Mad/NC | n | 45.18 | 34 | 57 | Thomas, Bruhl, Ford, and Weston (2014) |
| <i>Pseudoscione</i> | <i>Anzomyia pegasus</i> | Genus | Horse fly | cox1, cox2, 28S, AATS, Cad(1,3,4) | Fossil | Aus | n | 43.2 | 25 | 66 | Lessard, Cameron, Bayless, Wiegmann, and Yeates (2013) |
| <i>Hoplodactylus</i> , <i>Naultinus</i> | <i>Oedura</i> , <i>Strophurus</i> , <i>Diplodactylus</i> , <i>Rhynchoedura</i> | Genus | Gecko | ND2, 16S, RAG-1, PDC | Fossils (4) + emergence of NC + root constraint | Aus | n | 42.2 | 28.9 | 53.5 | Nielsen, Bauer, Jackman, Hitchmough, and Daugherty (2011) |
| <i>Naonella</i> , <i>Tonnoirocladius</i> , <i>Paulfreemanina</i> | <i>Echinocladius</i> sp. nov. | Genus | Midge | cox1, 28S, CAD1, CAD3 | Fossils (2) | SAM? | n | 41.84 | 22.7 | 65.93 | Krosch et al. (2011) |
| <i>Prumnopitys taxifolia</i> | <i>P. andina</i> | Species | Matai | rbcl | Fossils (47); 14 secondary | SAM | n | 41.8 | 22.1 | 58 | Winkworth et al. (2015) |
| <i>Limmophyes</i> sp.n. | <i>L. sp.</i> , <i>L. brachyarthra</i> | Species | Midge | cox1, 28S, CAD1, CAD3 | Fossils (2) | SAM? | n | 41.3 | 22.34 | 64.48 | Krosch et al. (2011) |
| <i>Micrelenchus</i> , <i>Cantharidus</i> | <i>Prothalotia</i> , <i>Roseaplagis</i> , <i>Oxystele</i> | Genus | Trochid gastropod | 16S, cox1, 12S, 28S; (only 16S used for dating) | Fossils (2) | Aus | n | 40.2 | 38.3 | 42.1 | Donald and Spencer (2016) |
| <i>Anzocladius kiwi</i> | <i>Ferringtonia patagonica</i> | Genus | Midge | cox1, 28S, CAD1, CAD3 | Fossils (2) | SAM? | n | 39.81 | 21.03 | 62.05 | Krosch et al. (2011) |

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TABLE 1 (Continued)

| NZ taxon | Sister group split | Rank of split | Common name/ group | Genes | Calibration per Ma | Origin | AAR | Age | | | References |
|--|---|---------------|-------------------------|---|--|------------------|-----|-------|-------|-------|---|
| | | | | | | | | Mean | Min | Max | |
| <i>Dicksonia</i> spp. (7) | <i>D. spp.</i> (21) | Species | Tree fern | trnL-trnF, trnG-trnR, rpl16, matK | Fossils (3) | Aus/Asia/ SAM | y | 39.8 | | | Noben et al. (2017) |
| <i>Coprosma</i> , <i>Nertera</i> | <i>Duringtonia</i> , <i>Leptostigma</i> , <i>Normandia</i> , <i>Opercularia</i> | Tribe | Rubiaceae | Rps16 Intron, tmQ-rps16, ITS, ETS, 5.8S | Fossil, root constraint, secondary calibration for ITS | Aus? | n | 39 | 30 | 47 | Cantley et al. (2016) |
| <i>Eukiefferiella brundini</i> , <i>E. insolida</i> | <i>E. insolida</i> | Species | Midge | cox1, 28S, CAD1, CAD3 | Fossils (2) | Aus? | n | 38.58 | 19.44 | 61.52 | Krosch et al. (2011) |
| <i>Manoao colensoi</i> | <i>Lagarostrobos franklinii</i> | Genus | Silver pine | rbcl | Fossils (47); 14 secondary | Tas | n | 38.2 | 20.1 | 55.9 | Winkworth et al. (2015) |
| <i>Cristaperla</i> , <i>Omanuperla</i> , <i>Spaniocercoides</i> | <i>Kimminisoperla</i> , <i>Neonemoura</i> , <i>Udamocercia</i> | Genus | Notonemourid stonefly | cox1, H3, 18S | Fossil + biogeographic calibrations | Aus/SAM | n | 38 | 18 | 48 | McCulloch et al. (2016) |
| <i>Austroperla cyrene</i> | <i>Klapopteryx</i> , <i>Austroperla</i> , <i>Tasmanoperla</i> | Genus | Austroperlid stonefly | cox1, H3, 18S | Fossil + biogeographic calibrations | Aus/SAM | n | 37 | 17 | 50 | McCulloch et al. (2016) |
| Tateidae (9 genera) | 8 tateid genera | Genus | Freshwater gastropod | 16S, cox1, 18S, 28S, H3 | 6 or single island emergence dates; cox1 rate | Aus | y | 36.89 | 29 | 46 | Zielske et al. (2017) |
| <i>Philesturnus carunculatus</i> | 5 genera | Genus | Saddleback (wattlebird) | 22 nuclear genes | 2 secondary calibrations (assumes wrens at 80 Ma) | NG | y | 36 | 26 | 46 | Aggerbeck, Fjeldså, Christidis, Fabre, and Jönsson (2014) |
| <i>Zelandochlus latipalpis</i> | <i>Parochlus araucanus</i> (not monophyletic) | Species | Midge | cox1, 18S, 28S, CAD | Fossils (4) | SAM | n | 35 | 24 | 50 | Cranston et al. (2010) |
| <i>Zelandobius</i> spp. | 5 genera | Genus | Antarctoperlin stonefly | cox1, H3, 18S | Fossil + biogeographic calibrations | SAM | n | 35 | 20 | 44 | McCulloch et al. (2016) |
| <i>Pseudopanax ferox</i> , <i>P. crassifolius</i> , <i>P. arboreus</i> | <i>Schefflera</i> , <i>Plerandra</i> , <i>Meryta</i> | Genus? | Araliaceae | atpB-rbcL, ndhF, psbA-trnH, rps16, trnL-F, rpl16, ITS | Fossils (3) | Asia | y | 34 | 23.5 | 45 | Mitchell et al. (2012) |
| <i>Acanthoxyla</i> , <i>Argosarchus</i> , <i>Astelaphasma</i> + 5 other genera | <i>Crispus</i> , <i>Labidiophasma</i> , Gen. nov. 3 | Genus | Stick insect | cox1, cox2, H3, 28S | Arthropod rate 1.15% | NC | y | 33.72 | 23.9 | 45.62 | Buckley et al. (2010) |

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TABLE 1 (Continued)

| NZ taxon | Sister group split | Rank of split | Common name/ group | Genes | Calibration per Ma | Origin | AAR | Age | | | References |
|--|--|---------------|---------------------------|---|---|-----------------|-----|-------|-------|-------|---------------------------|
| | | | | | | | | Mean | Min | Max | |
| <i>Mohoua</i> | All other corvids | Family | Yellowhead | 22 nuclear genes | 2 secondary calibrations (assumes wrens at 80 Ma) | NG | y | 32.6 | 23.8 | 41.6 | Aggerbeck et al. (2014) |
| <i>Spaniocerca zelandica</i> , <i>S. longicauda</i> | <i>Austrocercus</i> , <i>Austrocercoides</i> , <i>Austrocercella</i> | Genus | Notonemourid stonefly | cox1, H3, 18S | Fossil + biogeographic calibrations | Aus | n | 32 | 22 | 40 | McCulloch et al. (2016) |
| <i>Astelina</i> (<i>Tricella</i>), <i>A.</i> (<i>Collosperrum</i>), <i>A.</i> (<i>Astellopsis</i>) | <i>A. (Astelia)</i> spp. (5) | Subgenus | Asteliaceae | trnL, psbA-trnH, rps16, petL-psbE, NIA-i3 | Secondary + fossils | Aus | y | 31.6 | 24.1 | 44.9 | Birch and Keeley (2013) |
| <i>Notonemoura latipennis</i> , <i>N. hendersoni</i> | <i>N. maculata</i> | Species | Notonemourid stonefly | cox1, H3, 18S | Fossil + biogeographic calibrations | Aus | n | 31 | 19 | 38 | McCulloch et al. (2016) |
| <i>Fuchsia procumbens</i> , <i>F. excorticata</i> , <i>F. x</i> <i>colensoi</i> | <i>Fuchsia</i> spp. (15) | species | Onagraceae | trnL-trnF, rpl16, ITS | | S/CAm | n | 30 | | | Wallis and Trewick (2009) |
| <i>Spinotectarchus acornutus</i> | Gen. nov. 2 | Genus | Stick insect | cox1, cox2, H3, 28S | Arthropod rate 1.15% | NC | y | 29.9 | 19.79 | 41.16 | Buckley et al. (2010) |
| <i>Hylaues</i> (<i>Prosopistemon</i>) <i>matamoko</i> , <i>H. NZ</i> sp. 1 | 37 + species (4 subgenera) | Species | Colletid bee | cox1, 28S, EF-1a | Secondary calibration of the crown age of Hylaeinae | Aus | n | 29.5 | | | Kayaalp et al. (2013) |
| <i>Laurelia novae-zelandiae</i> | <i>L. sempervirens</i> | Species | Pukatea | rbcl | Fossils (47); 14 secondary | Aus/Ant/ SAm | n | 29.3 | 6.3 | 55.1 | Winkworth et al. (2015) |
| <i>Agathis australis</i> | <i>A. spp.</i> (9) | Species | Araucariaceae conifer | 11 cpDNA regions, ITS2 | Fossils (5) | Aus/Asia/NC | n | 29 | 12 | 55 | Kranitz et al. (2014) |
| <i>Placostylus ambagiosus</i> | <i>Placocharis strangei</i> , <i>Eumecostylus uliginosus</i> | Genus | Flax snail | cox1, H3, ITS2/28S | Fossils (3) | Melanesia | y | 28.9 | 18 | 42 | Breure and Romer (2012) |
| <i>Turnagra</i> (†) | <i>Vireo</i> | Family | Pipio | 7 nuclear genes | Geological vicariance events + 3 fossils | unknown | n | 28.67 | 20.43 | 36.85 | Ericson et al. (2014) |
| <i>Halticoperla tara</i> , <i>H. viridans</i> | <i>Neofulla</i> spp. | Genus | Notonemourid stonefly | cox1, H3, 18S | Fossil + biogeographic calibrations | SAm | n | 27 | 11 | 47 | McCulloch et al. (2016) |
| <i>Cominella</i> spp. (11) | <i>Josepha</i> | Subgenus | Buccinid whelk | 16S, cox1, 18S | Fossils (2) | unknown | y | 27 | >27.6 | >78 | Donald et al. (2015) |
| <i>Alseuosmia macrophylla</i> | <i>Wittsteinia</i> | Genus | Alseuosmiaceae | rbcl | Fossils (47); 14 secondary | Aus | n | 26.6 | 4.5 | 53.3 | Winkworth et al. (2015) |
| <i>Liothyrella neozelandica</i> | <i>L. uva</i> | Species | Long-looped brachiopod | cox1, SSU, LSU | Fossils (8) | Antarctica | n | 26 | 9 | 47 | Cohen et al. (2011) |

(Continues)

TABLE 1 (Continued)

| NZ taxon | Sister group split | Rank of split | Common name/ group | Genes | Calibration per Ma | Origin | AAR | Age | | | References |
|--|---|---------------|-----------------------|--|---|--------------|-----|-------|------|-------|---|
| | | | | | | | | Mean | Min | Max | |
| <i>Roseaplagis</i> | <i>Prothalotia</i> | Genus | Trochid gastropod | 16S, cox1, 12S, 28S; (only 16S used for dating) | Fossils (2) | Aus | n | 25.8 | 16.2 | 34.9 | Donald and Spencer (2016) |
| <i>Trichomanes colensoi</i> | <i>T. hymenophylloides</i> | Species | Fern | rbcl | Fossils (47); 14 secondary | SAm | n | 24.2 | 11.8 | 35 | Winkworth et al. (2015) |
| <i>Neochanna</i> spp. (5) | <i>N. cleaveri</i> , <i>Galaxias zebratus</i> | Species | Mudfish | cytb, 16S, RAG-1, S7 + morphology | Biogeographic constraints (9) | Aus? | y | 24 | 18 | 31 | Burridge et al. (2012) |
| 25 <i>Galaxias</i> + <i>Nesogalaxias</i> spp. | <i>G. truttaceus</i> , <i>G. auratus</i> , <i>G. tanycephalus</i> | Species | Galaxiid fish | cytb, 16S, RAG-1, S7 + morphology | Biogeographic constraints (9) | Aus | y | 24 | 13 | 31 | Burridge et al. (2012) |
| <i>Hemiphaga novaezelandiae</i> | <i>Gymnophaps</i> , <i>Lopholaimus</i> | Genus | Pigeon | 12S, cox3, ND2, cytb, cox1, Rag-1, IRBP, FIB7 | | Aus | y | 24 | 19.2 | 29.6 | Wallis and Trewick (2009) |
| <i>Lophomyrtus</i> , <i>Neomyrtus</i> | <i>Myrteola nummularia</i> | Genus | Myrtaceae | MatK, ndhF, ITS | Fossils (12) | SAm | y | 23.62 | 23 | 25.5 | Thornhill, Ho, K  lheim, and Crisp (2015) |
| <i>Aphis</i> spp. (3), <i>Paradoxaphis</i> spp. (2) | <i>A. spp. (4)</i> , <i>Toxoptera citricida</i> | Species | Aphid | cox2, tRNA ^{Leu} ; EF1a | Fossil | Aus/Asia | n | 23.5 | 16 | 29 | Wallis and Trewick (2009) |
| <i>Lyallia kerguelensis</i> , <i>Hectorella caespitosa</i> | <i>Claytonia?</i> | Genus | Portulacaceae | rbcl, trnK-matK | Fixed rates for rbcl & matK | Subantarctic | n | 22.1 | 11.4 | 29.9 | Wallis and Trewick (2009) |
| <i>Rhabdothermus solandri</i> | <i>Coronanthus</i> spp. (7) | Genus | Gesneriaceae shrub | ITS (ITS1, ITS2, 5.8S), trnL-TrnF, psbA-TrnK | 1 geological + minimum root age | NC | y | 22 | 18 | 29.5 | Woo, Funke, Smith, Lockhart, and Garnock-Jones (2011) |
| <i>Hymenosoma depressum</i> | <i>Hymenosoma</i> spp.? | Species? | Crab | cox1, 12S, 16S, ANT, 18S | Fossils (2) and secondary calibration | Aus | n | 21.6 | | | Teske et al. (2009) |
| <i>Podocarpus totara</i> | <i>P. nubigenus</i> | Species | Totara | rbcl | Fossils (47); 14 secondary | SAm | n | 21.3 | 4.4 | 39.2 | Winkworth et al. (2015) |
| <i>Elaeocarpus hookerianus</i> | <i>E. arnhemicus</i> , <i>E. bancroftii</i> | Species | Pokaka | trnL/trnF, ITS | Fossil + secondary | Aus | n | 21 | | | Wallis and Trewick (2009) |
| <i>Deinacrida</i> spp. (2), <i>Hemideina</i> spp. (2) | genus <i>A. Gryllotaurus</i> , <i>Anostostoma</i> | Genus | Tree/giant weta | cox1, 28S | 82 Ma plus relaxed cox1 insect rate 0.7%–1.2% | Aus | n | 20.5 | 3 | 38 | Pratt et al. (2008) |
| <i>Aristotelia serrata</i> | <i>A. australasica</i> | Species | Mako/wineberry | rbcl | Fossils (47); 14 secondary | Aus | n | 19.62 | 2.16 | 44.15 | Winkworth et al. (2015) |
| <i>Cantuarina dendyi</i> , <i>C. johnsi</i> , <i>C. stewarti</i> | <i>Misgolas</i> , <i>Blakistonina</i> | Genus | Trapdoor spider | NGS + cox1, cytb, 5.8S, 18S, 28S, ITS1-2, H3 | Fossils and rate calibrated | Aus | y | 19.5 | 15 | 24 | Rix et al. (2017) |

(Continues)

TABLE 1 (Continued)

| NZ taxon | Sister group split | Rank of split | Common name/ group | Genes | Calibration per Ma | Origin | AAR | Age | | | References |
|---|--|---------------|---------------------------|---|---|-----------------|-----|-------|------|-------|--|
| | | | | | | | | Mean | Min | Max | |
| <i>Pittosporum</i> | <i>Pittosporum</i> spp. | Species | | rp116 intron, trnD-trnY-trnE-trnT | Fossils (6) | Aus | y | 19.2 | | | Nicolas and Plunkett (2014) |
| <i>Toronia toru</i> | <i>Persoonia</i> | Genus | Toru/toro | rbcl | Fossils (47); 14 secondary | Aus | n | 18.85 | 2.85 | 42.17 | Winkworth et al. (2015) |
| <i>Muehlenbeckia astonii</i> | <i>M. spp. (6)</i> | Species | Polygonaceae buckwheat | matK, ndhF, trnL-trnF, ITS | fossils (7) + root constraint | Aus? | n | 18.5 | 12.7 | 27.5 | Schuster, Setaro, and Kron (2013) |
| <i>Oligosoma</i> | <i>O. lichenigera</i> | Genus | skink | cytb, ND2, ND4, 12S, 16S, Rag-1 | | NC/ LordHowe | n | 18.34 | 16 | 22.6 | Chapple et al. (2009) |
| <i>Retropinna retropinna</i> , <i>Stokellia anisodon</i> | <i>R. tasmanica</i> , <i>R. semoni</i> | Species | Smelt | 16S | Fish 16S rate 0.23% | Aus | n | 17.82 | | | Wallis and Trewick (2009) |
| <i>Paracalliope fluviatilis</i> | <i>Eusirus perdentatus</i> | Genus | Freshwater amphipod | cox1 | Fixed rate for cox1 1.4%–2.6% | Aus | n | 17.6 | | | Sutherland, Hogg, and Waas (2010) |
| <i>Thinornis novaeseelandiae</i> , <i>Elseya melanops</i> | <i>T. rubricollis</i> | Species | Dotterel | cytb, CR, 12S, bFI7 | Secondary calibration MRCA of all Charadriidae except <i>Pluvialis</i> | Aus? | n | 17.5 | 12 | 23.4 | Barth, Matschner, and Robertson (2013) |
| <i>Hoheria</i> (7 spp.) | <i>Lawrencia</i> spp. (4) | Genus | Malvaceae tree mallow | 5'trnK/matK, ITS | Fossil, 1 secondary calibration, 1 geological calibration | Aus | y | 17.4 | 8 | 23 | Wagstaff and Tate (2011) |
| <i>Hedycarya arborea</i> | <i>Kibaraopsis caledonica</i> | Species | Monimiaceae pigeonwood | trnL-trnF, rbcl, 5.8S, ITS1-2 | Fossils (2) | NC | y | 17.24 | | | Renner, Strijk, Strasberg, and Thébaud (2010) |
| <i>Wurmbea novae-zelandiae</i> | <i>W. biglandulosa</i> | Species | Liliales | 75 plastid genes; timing: matK, rbcl | Fossils (17) | Aus | y | 16.7 | | | Givnish et al. (2016) |
| <i>Stenoperla helsoni</i> | <i>Neuroperlopsis</i> , <i>Neuroperla</i> | Genus | Eutheniid stonefly | cox1, H3, 18S | Fossil + biogeographic calibrations | SAm | n | 16 | 11 | 20 | McCulloch et al. (2016) |
| <i>Chionochloa</i> | 13 genera | Genus | Poaceae grass | trnL-trnF, rp116, rbcl, ndhF, matK, atpB-rbcl, trnT-trnL, trnC-trnD, ITS, 26S | | Afr | y | 15.9 | | | Linder, Rabosky, Antonelli, Wüest, and Ohlemüller (2014) |

(Continues)

TABLE 1 (Continued)

| NZ taxon | Sister group split | Rank of split | Common name/ group | Genes | Calibration per Ma | Origin | Age | | | | References |
|---|---|---------------|---------------------------|---|--|---------|-----|-------|------|-------|--|
| | | | | | | | AAR | Mean | Min | Max | |
| <i>Leptospermum scoparium</i> | <i>L. trinervium</i> | Species | Myrtaceae | MatK, ndhF, ITS | Fossils (12) | Aus | y | 15.9 | 6.7 | 26.8 | Thornhill et al. (2015) |
| <i>Drosera stenopetala</i> | <i>D. uniflora</i> | Species | Sundew | rbcl | Fossils (47); 14 secondary | SAm | n | 15.72 | 2.86 | 30.81 | Winkworth et al. (2015) |
| <i>Nothofagus menziesii</i> | <i>N. cunninghamii</i> | Species | Silver beech | rbcl | Fossils (47); 14 secondary | Aus | n | 15.66 | 3.75 | 30.22 | Winkworth et al. (2015) |
| <i>Diloma</i> | <i>Austrocochlea</i> spp. (5) | Genus | Trochid gastropod | 16S, cox1, actin | Two marine gastropod rates 0.7% and 2.4% | Aus | n | 15.15 | 6.6 | 23.7 | Donald et al. (2005) |
| <i>Notogrammitis</i> spp. (5) | <i>Grammitis</i> | Genus | Polypodiaceae fern | atpβ, rbcl, trnL-trnF, rps4-trnS, trnG-trnR | 4 secondary | NC | y | 14.7 | 8.6 | 21 | Sundue et al. (2014) |
| <i>Muehlenbeckia complexa</i> , <i>M. axillaris</i> , <i>M. ephedroides</i> | <i>M. adpressa</i> | Species | Polygonaceae buckwheat | matK, ndhF, trnL-trnF, ITS | Fossils (7) + root constraint | Aus? | n | 14.6 | 7.1 | 24.1 | Schuster et al. (2013) |
| <i>Syzygium maire</i> | <i>S. claviflorum</i> , <i>S. canicortex</i> , <i>S. apodophyllum</i> | Species | Myrtaceae | MatK, ndhF, ITS | Fossils (12) | Aus | y | 14.4 | 9.2 | 20.3 | Thornhill et al. (2015) |
| <i>Ophiopteris antipodum</i> | <i>Ophiopteris papillosa</i> | Species | Brittle star | cox1, ITS2, 28S, microsatellite (6) | Fixed rate: cox1, 2.48%; 28S, 0.031%; ITS, 1.5% per lineage | NAm | n | 14.36 | 8 | 22 | Naughton, O'Hara, Appleton, and Cisternas (2014) |
| <i>Myriophyllum robustum</i> , <i>M. triphyllum</i> | <i>M. decussatum</i> | species | watermilfoil | ITS, matK, trnK'5 and trnK 3'introns | Fossils (2) | Aus | y | 14.2 | | | Chen et al. (2014) |
| <i>Cellana ornata</i> | <i>Cellana</i> spp. (15) | Species | Nacellid limpet | 12S, 16S | secondary split with <i>Nacella</i> ; redated from González-Wevar, Nakano, Cañete, and Poulin (2010) | SAm/Ant | n | 14 | 12.2 | 15.8 | Wallis and Trewick (2009) |
| <i>Phyllachne rubra</i> | <i>P. uliginosa</i> | Species | Cushion plant | rbcl | Fossils (47); 14 secondary | Aus/SAm | n | 13.54 | 2.06 | 28.2 | Winkworth et al. (2015) |
| <i>Charadrius obscurus</i> , <i>C. binctus</i> , <i>Anarhynchus frontalis</i> | 12 <i>Charadrius</i> spp. | Species | Dotterel, wrybill, plover | cytb, CR, 12S, bF17 | Secondary calibration MRCA of all Charadriidae except <i>Pluvialis</i> | Aus? | n | 13.3 | 9.6 | 16.9 | Barth et al. (2013) |

(Continues)

TABLE 1 (Continued)

| NZ taxon | Sister group split | Rank of split | Common name/ group | Genes | Calibration per Ma | Origin | AAR | Age | | | References |
|---|---|---------------|----------------------------------|--|---|----------|-----|-------|------|-------|---|
| | | | | | | | | Mean | Min | Max | |
| <i>Carmichaelia, Cilianthus</i> | <i>Swainsona</i> spp. (12), <i>Montigena novae-zelandiae</i> | Genus | Broom, kakabeak | ITS | ITS rate 0.215% | Aus | n | 13.2 | | | Wallis and Trewick (2009) |
| <i>Perna canaliculus</i> | <i>P. perna</i> | Species | Green shell mussel | cox1, ITS2 | Two marine gastropod rates 0.7% and 2.4% | Atlantic | y | 12.85 | 5.8 | 19.9 | Wallis and Trewick (2009) |
| <i>Pachyrhamma, Pallidoplectrum, Talitropsis, Pleioplectron</i> | <i>Novotetrix, Macropathinae, Micropathus</i> | Genus | Cave weta | 12S, 16S, 28S | insect rates by gene | Aus/Afr | n | 12.2 | 8.6 | 16.5 | Beasley-Hall, Tierney, Weinstein, and Austin (2018) |
| <i>Nothofagus fusca</i> | <i>N. gunnii</i> | Species | Red beech | rbcl | Fossils (47); 14 secondary | Aus | n | 11.89 | 1.61 | 25.51 | Winkworth et al. (2015) |
| <i>Leptinella</i> | <i>L. wilhelminensis, L. altilittoralis, L. filicula, Cotula alpina</i> | Species | Compositae | psbA-trnH, trnC-petN, ITS | Secondary calibration, outgroup fossil, emergence of Chathams | Aus/NG | n | 11.53 | | | Himmelreich, Breittwieser, and Oberprieler (2012) |
| <i>Neocincindela</i> spp. | <i>Abroscelis and Macfarlandia</i> | Species | Tiger beetle | cox1, cyt b, 16S-tRNA ^{Leu} -nad1 | Aus clade (<i>Rivacindela, Abroscelis, Macfarlandia, Neocincindela</i>) = 12.4 Ma | Aus | n | 10.82 | 8.38 | 13.31 | Pons et al. (2011) |
| <i>Petroica traversi, P. macrocephala, P. australis</i> | <i>P. multicolor</i> | Species | Robin, tomtit | cytb, CR | Avian cytb rate 0.7%–1.7% | Aus/Pac | n | 10.7 | 6.2 | 15.1 | Wallis and Trewick (2009) |
| <i>Austrolittorina antipodum, A. cincta</i> | <i>A. unifasciata</i> | Species | Winkle | cox1 | Panama rates | Aus | n | 10.65 | 6.88 | 23.57 | Wallis and Trewick (2009) |
| <i>Diadema palmeri</i> | <i>D. spp. (5)</i> | Species | Sea urchin | cox1, tRNA ^{Lys} -A6, A8 | Panama urchin rate 1.6%–2.6% | Indo/Pac | n | 10.25 | 6.5 | 14 | Wallis and Trewick (2009) |
| <i>Azorella (=Schizeilema) nitens</i> | <i>A. fuegiana</i> | Species | Apiaceae | rbcl | Fossils (47); 14 secondary | SAm | n | 10.09 | 1.32 | 21.83 | Winkworth et al. (2015) |
| <i>Amphipsalta, Notopsalta</i> | <i>Cicadetta celis, C. puer</i> | Genus | Cicada | cox1, cox2, 12S, 16S, EF1a | | Aus | n | 10 | | | Wallis and Trewick (2009) |
| <i>Kikihia, Maoricicada, Rhodopsalta</i> | <i>Pauropsalta johanae, Myersalta depicta</i> | Genus | Cicada | cox1, cox2, 12S, 16S, EF1a | | NC | n | 10 | | | Wallis and Trewick (2009) |
| <i>Isotoma rivalis</i> (syn <i>L. ionantha</i>) | <i>I. fluviatilis</i> | Species | Campanulaceae (<i>Lobelia</i>) | rbcl | Fossils (47); 14 secondary | Aus | n | 9.84 | 0.52 | 24.98 | Winkworth et al. (2015) |

(Continues)

TABLE 1 (Continued)

| NZ taxon | Sister group split | Rank of split | Common name/ group | Genes | Calibration per Ma | Origin | AAR | Age | | | References |
|--|------------------------------|---------------|-----------------------|--|---|--------------|-----|------|------|-------|--|
| | | | | | | | | Mean | Min | Max | |
| <i>Montigena novae-zelandiae</i> | <i>Swainsona galegifolia</i> | Genus | Scree pea | ITS | ITS rate 0.215% | Aus | n | 9.8 | | | Wallis and Trewick (2009) |
| <i>Diaphorapteryx hawkinsi</i> (†) | <i>Habroptila wallacii</i> | Genus | Rail | cytb, cox1, 16S, FGB-7, RAG-1 | Fossil | SEAsia | n | 9.5 | | | García-R, Gibb, and Trewick (2014) |
| <i>Kunzea ericoides</i> | <i>K. capita</i> | Species | Myrtaceae | MatK, ndhF, ITS | Fossils (12) | Aus | y | 9.2 | 2.5 | 18.7 | Thornhill et al. (2015) |
| <i>Lilaeopsis ruthiana, novae-zelandiae</i> 1,2 | <i>Lilaeopsis</i> spp. (9) | Species | Apiaceae | ITS | Fossils (2) | SAm | y | 9.1 | | | Spalik et al. (2010) |
| <i>Sophora microphylla, S. tetraptera</i> | <i>S. howinsula</i> | Species | Kowhai | atpB-rbcL | Fossil | Lord Howe? | n | 9 | | | Hurr, Lockhart, Heenan, and Penny (1999) |
| <i>Paracorphium excavatum, P. lucasi</i> | <i>P. brisbanensis</i> | Species | Estuarine amphipod | cox1 | Fixed rate for cox1 1.4%–2.3% | Aus | n | 8.73 | 6.61 | 10.85 | Knox, Hogg, and Pilditch (2011) |
| <i>Ranunculus lyallii, R. verticillatus, R. insignis, R. pinguis, R. viridis</i> | <i>R. spp.</i> (15) | Species | Buttercup | psbJ-petA, matK-trnK, nrITS | Fossil, molecular and ecological information, NZ crown group | unknown | n | 8.7 | 4.9 | 12.5 | Lehnebach, Winkworth, Becker, Lockhart, and Hennion (2017) |
| <i>Gunnera dentata</i> | <i>G. cordifolia</i> | Species | Gunneraceae | rbcl | Fossils (47); 14 secondary | Aus | n | 8.55 | 0.37 | 23.65 | Winkworth et al. (2015) |
| <i>Cellana flava, C. radians</i> | <i>Cellana</i> spp. (7) | Species | Nacellid limpet | cox1, cytb | Fossils (3) | Asia/Pac/Aus | n | 8.5 | | | González-Wevar et al. (2010) |
| <i>Cyanoramphus auriceps, C. novaezelandiae</i> | <i>Eunymphicus cornutus</i> | Genus | Parrot | ND2, cytb, c-mos, RAG-1, Zenk | Secondary calibration using well-accepted fossils outside parrots | NC | y | 7.97 | 4.62 | 11.42 | Schweizer, Güntert, and Hertwig (2012) |
| <i>Myosotis</i> spp. (5) | <i>M. spp.</i> (10) | Species | Forget-me-not | matK, ndhF, trnK-psbA, ITS | Fossils and secondary | Eur | n | 7.95 | 1.2 | 14.7 | Wallis and Trewick (2009) |
| <i>Pachycladon</i> spp. (9), <i>Menkea</i> | 10 genera | Genus | Microlepid crucifer | CHS, A-PHYA, nadhF (nadhF only for dating) | 2 secondary | Aus | n | 7.52 | 5.04 | 10.17 | Mandáková et al. (2017) |

(Continues)

TABLE 1 (Continued)

| NZ taxon | Sister group split | Rank of split | Common name/ group | Genes | Calibration per Ma | Origin | AAR | Age | | | References |
|--|---|---------------|-----------------------|---|---|--------------|-----|------|------|-------|------------------------------|
| | | | | | | | | Mean | Min | Max | |
| <i>Hectorella caespitosa</i> | <i>Lyellia</i> | Family | Cushion plant | rbcl | Fossils (47); 14 secondary | Subantarctic | n | 7.36 | 0.47 | 19.35 | Winkworth et al. (2015) |
| <i>Plagianthus regius</i> , <i>P. divaricatus</i> | <i>Asterotrichion discolor</i> , <i>Gynatrix pulchella</i> | Genus | Malvaceae tree mallow | 5'trnK/matK, ITS | Fossil, 1 secondary calibration, 1 geological calibration | Aus | y | 7.3 | 4 | 14 | Wagstaff and Tate (2011) |
| <i>Gallirallus australis</i> | 13 species | Species | Weka | cytb, cox1, 16S, FGB-7, RAG-1 | Fossil | Aus/Pac | n | 7.3 | | | Garcia-R et al. (2014) |
| <i>Asplenium flabellifolium</i> | <i>A. flabellifolium</i> | Subspecies | Necklace fern | rbcl | Fossils (47); 14 secondary | Aus | n | 7.14 | 0.47 | 16.85 | Winkworth et al. (2015) |
| <i>Austroderia</i> | <i>Notochloe</i> , <i>Plinthanthesis</i> | Genus | Poaceae grass | trnL-trnF, rpl16, rbcl, ndhF, matK, atpB-rbcl, trnT-trnL, trnC-trnD, ITS, 26S | Review | Aus | y | 6.9 | | | Linder et al. (2014) |
| <i>Scutus breviculus</i> | <i>S. antipodes</i> | Species | Sea slug | cox1 | Panama rates | Aus | n | 6.9 | 4.46 | 15.29 | Wallis and Trewick (2009) |
| <i>Polystichum vestitum</i> | <i>P. proliferum</i> | Species | Prickly shield fern | rbcl | Fossils (47); 14 secondary | Aus | n | 6.8 | 0.2 | 17.9 | Winkworth et al. (2015) |
| <i>Myriophyllum votschi</i> | <i>M. lophatum</i> | Species | Watermilfoil | ITS, matK, trnK'5 and trnK 3'introns | Fossils (2) | Aus | y | 6.8 | 3.9 | 9.7 | Chen et al. (2014) |
| <i>Gonocarpus acanthocarpus</i> | <i>G. leptothecus</i> | Species | Watermilfoil | ITS, matK, trnK'5 and trnK 3'introns | Fossils (2) | Aus | y | 6.8 | | | Chen et al. (2014) |
| <i>Dracophyllum</i> (19 spp.) | <i>D. spp.</i> (9), <i>Richea spp.</i> (4) | Species | Ericaceae | rbcl, matK | Fossils (4) + emergence of Lord Howe | Aus | n | 6.8 | 2.6 | 11.2 | Wagstaff et al. (2010) |
| <i>Pennantia corymbosa</i> | <i>P. cunninghamii</i> | Species | Kaikōmako | rpl16 intron, trnD-trnY-trnE-trnT | Fossils (6) | Aus | y | 6.6 | | | Nicolas and Plunkett (2014) |
| <i>Nothoceros giganteus</i> | <i>N. endiviifolius</i> | Species | Hornwort | rbcl, trnL-F, rps4-trnS, matK, nad5-nad4, 5.8S, ITS2 | Relaxed clock rate used | SAm | n | 6.3 | 1.2 | 13.4 | Villarreal and Renner (2014) |
| <i>Lasaea</i> | <i>Lasaea</i> | Species | Clam | cox3 | | Saf | n | 6 | | | Wallis and Trewick (2009) |
| <i>Galaxias brevipinnis</i> | 11 <i>Galaxias</i> + <i>Nesogalaxias</i> spp. | Species | Koaro | cytb, 16S, RAG-1, S7 + morphology | Biogeographic constraints (9) | Aus | y | 6 | 4 | 8 | Burridge et al. (2012) |
| <i>Rytidosperma</i> | <i>Notodanthonia</i> | Genus | Poaceae grass | rbcl | Fossils (47); 14 secondary | Aus | n | 5.95 | 0.99 | 12.49 | Winkworth et al. (2015) |
| (Continues) | | | | | | | | | | | |

(Continues)

TABLE 1 (Continued)

| NZ taxon | Sister group split | Rank of split | Common name/ group | Genes | Calibration per Ma | Origin | AAR | Age | | | References |
|---|---|---------------|-----------------------------|-----------------------------------|--|----------|-----|------|------|-------|---|
| | | | | | | | | Mean | Min | Max | |
| <i>Knightia excelsa</i> | <i>Hollandaea</i> | Genus | Rewarewa | rbcl | Fossils (47); 14 secondary | Aus | n | 5.8 | 0 | 16.2 | Winkworth et al. (2015) |
| <i>Asplenium flaccidum</i> | <i>A. difforme</i> | Species | Aspleniaceae fern | rbcl | | NorfolkI | n | 5.6 | 3.4 | 7.8 | Perrie and Brownsey (2007) |
| <i>Oreostylidium (=Stylidium) subulatum</i> | <i>Stylidium</i> | Genus | Cushion plant | rbcl | Fossils (47); 14 secondary | Aus | n | 5.48 | 0.25 | 13.92 | Winkworth et al. (2015) |
| <i>Diaea ambara</i> | <i>D. sp.</i> | Species | Thomisid spider | cox1, ND1, 28S, H3 | Arthropod rate of 2.3% | Aus | n | 5.3 | | | Sirvid, Moore, Chambers, and Prendergast (2013) |
| <i>Sidymella angularis</i> | <i>S. longipes</i> | Species | Thomisid spider | cox1, ND1, 28S, H3 | Arthropod rate of 2.3% | Aus | n | 5.2 | | | Sirvid et al. (2013) |
| <i>Tetrachondra hamiltonii</i> | <i>T. patagonica</i> | Species | Tetrachondraceae | rbcl | Fossils (47); 14 secondary | SAm | n | 5.16 | 0.15 | 13.64 | Winkworth et al. (2015) |
| <i>Ourisia</i> spp. (12) | <i>O. spp. (11)</i> | Species | Plantaginaceae | matK, rps16, ITS, ETS | | SAm | n | 5 | | | Wallis and Trewick (2009) |
| <i>Anoteropsis</i> | <i>Artoria</i> | Genus | Wolf spider | cox1, ND1 | Alpine uplift | Aus | n | 5 | | | Wallis and Trewick (2009) |
| <i>Galaxias maculatus</i> | <i>G. maculatus</i> , <i>G. rostratus</i> | Subspecies? | Inanga | cytb, 16S, RAG-1, S7 + morphology | Biogeographic constraints (9) | Aus | y | 5 | 3 | 7 | Burridge et al. (2012) |
| <i>Corynocarpus laevigatus</i> | <i>C. dissimilis</i> | Species | Karaka tree | ITS, WAXY | ITS in 18 woody plants 0.215% | NC | n | 4.9 | 1.6 | 8.9 | Atherton et al. (2015) |
| <i>Psychrophila (=Caltha) novae-zelandiae</i> | <i>P. appendiculata</i> | Species | Marsh marigold | rbcl | Fossils (47); 14 secondary | SAm | y | 4.47 | 0.13 | 11.73 | Winkworth et al. (2015) |
| <i>Scleranthus biflorus</i> , <i>S. brockiei</i> , <i>S. uniflorus</i> | <i>S. pungens</i> , <i>S. minusculus</i> , <i>S. fasciculatus</i> , <i>S. singuliflorus</i> | Species | Caryophyllaceae | ITS | Fossil | Aus | n | 4.45 | 1.2 | 7.7 | Wallis and Trewick (2009) |
| <i>Chaerophyllum</i> spp. (4) | <i>Chaerophyllum</i> spp. (4) | Species | Apiaceae | atpB-rbcl, trnS-trnG, ITS | Fossils (2) | NG | y | 4.4 | | | Spalik et al. (2010) |
| <i>Wahlenbergia</i> (10 rhizomatous spp.) | <i>Wahlenbergia</i> spp. (14) | Species | Harebell | ITS, trnL-F | Fossils (2) + secondary calibration for root | Aus | y | 4.3 | | | Prebble et al. (2011) |
| <i>Abrotanella</i> spp. (10) | <i>A. forsteroides</i> , <i>A.</i> | Species | Asteraceae | trnK/matK, ITS | Fossil | SAm/Aus | n | 4.2 | | | Wallis and Trewick (2009) |
| <i>Phyllocladus alpinus</i> | <i>P. asplenifolius</i> | Species | Mountain toatoa/celery pine | rbcl | Fossils (47); 14 secondary | Tas | n | 4.1 | 0.04 | 12.43 | Winkworth et al. (2015) |

(Continues)

TABLE 1 (Continued)

| NZ taxon | Sister group split | Rank of split | Common name/ group | Genes | Calibration per Ma | Origin | AAR | Age | | | References |
|--|--|---------------|--------------------------|--|---------------------------------------|----------|-----|------|---------|-------|---|
| | | | | | | | | Mean | Min | Max | |
| <i>Jovellana sinclairii</i> , <i>J. repens</i> | <i>J. violacea</i> , <i>J. punctata</i> | Species | Calceolariaceae | matK, rbcL, atpB-rbcL, rps16, trnL-F, AP3, Gcyc, UFO, ITS | Fossils (11) | SAm | n | 4.1 | 0.4–7.1 | | Nylinder, Swenson, Persson, Janssens, and Oxelman (2012) |
| <i>Ascarina lucida</i> | <i>A. swamyana</i> , <i>A. polystachya</i> | Species | Chloranthaceae | rbcL, rpl20-rps12, trnL, trnL-F | Fossils; 2 alternatives | Pacific | n | 3.96 | 2.64 | 5.27 | Wallis and Trewick (2009) |
| <i>Hebe</i> spp. (4), <i>Parahebe</i> , <i>Heliophebe raoulii</i> , <i>Chionohebe densifolia</i> | <i>Derwentia nivea</i> , <i>Veronica</i> spp. (4), <i>H. formosa</i> | Species | Scrophulariaceae | rbcL, ITS | Fossil | Aus | n | 3.9 | | | Wallis and Trewick (2009) |
| <i>Cheilanthes distans</i> | <i>C. distans</i> | Subspecies | Bristly cloak fern | rbcL | Fossils (47); 14 secondary | Aus | n | 3.53 | 0.02 | 10.57 | Winkworth et al. (2015) |
| <i>Wiseana</i> , <i>Dumbletonius</i> , <i>Dioxycanus</i> , <i>Heloxycanus</i> , <i>Cladoxycanus</i> | <i>Oxycanus</i> spp. (3), <i>Jeana robiginosa</i> | Genus | Hepialid moth | cox1, cox2 | Arthropod rate of 2%–2.3% | Aus | n | 3.5 | 3 | 4 | Wallis and Trewick (2009) |
| <i>Amaurobioides pleta</i> , <i>A. pallida</i> , <i>A. maritima</i> | <i>A. isolata</i> | Species | Spider | cox1, 16S, H3-a, 28S | Fossils (2) anyphaenids | Aus | y | 3.47 | | | Ceccarelli et al. (2016) |
| <i>Apium prostratum</i> <i>filiforme</i> | <i>A. panul</i> , <i>A. australe</i> , <i>A. chilense</i> | Species | Apiaceae | ITS | Fossils (2) | SAm | y | 3.4 | | | Spalik et al. (2010) |
| <i>Empodisma minus</i> | <i>E. minus</i> | Subspecies | Wire rush | rbcL | Fossils (47); 14 secondary | Aus | n | 3.29 | 0.03 | 9.38 | Winkworth et al. (2015) |
| <i>Rytidosperma thomsonii</i> | <i>R. pumilum</i> | Species | Poaceae grass | rbcL | Fossils (47); 14 secondary | Aus | n | 3.15 | 0 | 11.28 | Winkworth et al. (2015) |
| <i>Luzuriaga parviflora</i> | <i>L. marginata</i> | Species | Alstroemeriaceae lily | ndhF, matK, rbcL, matR, ITS | Fossils (3) + 1 secondary for root | SAm | y | 2.9 | 0.4 | 6.1 | Chacón, Camargo de Assis, Meerow, and Renner (2012) |
| <i>Geranium solanderi</i> , <i>G. homeanum</i> | <i>G. carolinianum</i> , <i>G. sessiliflorum</i> | Species | Cranesbill | rbcL, TrnL-trnF, ITS | 2 secondary | Americas | y | 2.9 | | | Marcussen and Meseguer (2017) |

(Continues)

TABLE 1 (Continued)

| NZ taxon | Sister group split | Rank of split | Common name/ group | Genes | Calibration per Ma | Origin | AAR | Age | | | References |
|---|---|---------------|-------------------------|---|---|--------------|-----|------|------|------|---|
| | | | | | | | | Mean | Min | Max | |
| <i>Anas</i> spp (4) | <i>A. bernieri</i> | Species | Teal | Complete mtDNA (excl CR) | Fossil <i>A. sporata</i> : middle-Miocene (outgroup to extant <i>Anas</i>) | Madagascar? | n | 2.85 | 1.78 | 3.95 | Mitchell, Wood, Scofield, Llamas, and Cooper (2014) |
| <i>Sporadanthus ferrugineus</i> | <i>S. gracilis</i> | Species | Bamboo rush | rbcl | Fossils (47); 14 secondary | Aus | n | 2.68 | 0 | 9.72 | Winkworth et al. (2015) |
| <i>Astelia linearis</i> , <i>A. subulata</i> | <i>A. alpina</i> | Species | Asteliaceae | trnL, psbA-trnH, rps16, petL-psbE, NIA-i3 | Secondary + fossils | Aus | y | 2.6 | | | Birch and Keeley (2013) |
| <i>Pseudognaphalium luteoalbum</i> | <i>Anaphalis javanica</i> , <i>A. triplinervis</i> | Genus | Asteraceae | ITS | | Asia | y | 2.5 | | | Wallis and Trewick (2009) |
| <i>Ewartia</i> , <i>Rouilia</i> , <i>Helichrysum</i> , <i>Leucogenes</i> , <i>Rachelia</i> , <i>Anaphaliodes</i> | <i>A. mariae</i> , <i>Eu. spp.</i> (4), <i>Pterygopappus</i> + 3 other genera | Species | Asteraceae | ITS | | Aus | y | 2.5 | | | Wallis and Trewick (2009) |
| <i>Euchiton</i> spp. (6) | <i>Craspaedia</i> , <i>Pycnosorus globosus</i> , <i>Eu. spp.</i> (2), <i>Ewartia</i> | Species | Asteraceae | ITS | | Aus | y | 2.5 | | | Wallis and Trewick (2009) |
| <i>Ozothamnus leptophyllus</i> | <i>Craspaedia</i> spp. (3), <i>Pycnosorus globosus</i> | Genus | Asteraceae | ITS | | Aus | y | 2.5 | | | Wallis and Trewick (2009) |
| <i>Lycopodiella</i> sp. | <i>Lycopodiella</i> sp. | Subspecies | Little wolf's foot fern | rbcl | | Aus | n | 2.4 | 0.8 | 4 | Perrie and Brownsey (2007) |
| <i>Amaurobioides maritima</i> | <i>A. n. sp.</i> | Species | Spray zone spider | ITS1, ND1 | Spider rate for ND1 2.3% | Aus (Tas) | n | 2.37 | | | Opell, Helweg, and Kiser (2016) |
| <i>Porphyrio hochstetteri</i> | Widespread purple swamphen | Species | Takahe, South Island | CR, cytb, 12S, 16S, BFG-7, RAG1 | Calibration on basal split | Aus/Asia/Af? | n | 2.35 | 1 | 7.5 | Garcia-R and Trewick (2015) |
| <i>Ranunculus amphitrichus</i> , <i>R. glabrifolius</i> | <i>R. acaulis</i> , <i>R. papulentus</i> | Species | Buttercup | psbJ-petA, matK-trnK, nrITS | Fossil, molecular and ecological information, NZ crown group | Aus/SubAnt | n | 2.3 | | | Lehnebach et al. (2017) |
| <i>Craspaedia</i> spp. (13) | <i>C. spp.</i> (6) | Species | Asteraceae | psbA-trnH, ITS, ETS | | Aus | y | 2.25 | 1.5 | 3 | Wallis and Trewick (2009) |

(Continues)

TABLE 1 (Continued)

| NZ taxon | Sister group split | Rank of split | Common name/ group | Genes | Calibration per Ma | Origin | AAR | Age | | | References |
|---|---|---------------|-------------------------|---|----------------------------|--------------|-----|------|------|------|---|
| | | | | | | | | Mean | Min | Max | |
| <i>Rytidosperma exiguum</i> | <i>R. vickeryae</i> | Species | Poaceae grass | trnL-trnF, rpl16, rbcL, ndhF, matK, atpB-rbcL, trnT-trnL, trnC-trnD, ITS, 26S | | Aus | y | 2.2 | | | Linder et al. (2014) |
| <i>Leptocophylla robusta</i> , <i>L. juniperina juniperina</i> | <i>L. divaricata</i> | Species | Ericaceae | rbcL, matK, atpB-rbcL | Fossils (2) vs. secondary | Tas | n | 2.11 | 0.87 | 3.81 | Puente-Leièvre et al. (2013) |
| <i>Cyathea cunninghamii</i> | <i>C. cunninghamii</i> | Subspecies | Tree fern | rbcL | Fossils (47); 14 secondary | Aus | n | 2.09 | 0 | 7.34 | Winkworth et al. (2015) |
| <i>Gentianella astonii</i> , <i>G. bellidifolia</i> , <i>G. saxosa</i> , <i>G. patula</i> | <i>G. spp. (11)</i> | Species | Gentian | matK, ITS | NAm split and fossil | SAm | n | 2.05 | 0.8 | 3.8 | Wallis and Trewick (2009) |
| <i>Gleichenia dicarpa</i> | <i>G. alpina</i> | Species | Alpine coral fern | rbcL | Fossils (47); 14 secondary | Aus | n | 2 | 0 | 6.8 | Winkworth et al. (2015) |
| <i>Haloragis erecta</i> | <i>H. serra</i> , <i>H. aspersa</i> | species | watermilfoil | ITS, matK, trnK'5 and trnK 3'introns | fossils (2) | Aus | y | 2 | | | Chen et al. (2014) |
| <i>Plantago lanigera</i> , <i>P. obconica</i> , <i>P. aucklandica</i> | <i>Plantago spp. (13)</i> | Species | Plantaginaceae plantain | coxI, ndhF-rpl32, ITS | 2 secondary calibrations | Aus | y | 2 | 0.94 | 2.29 | Tay, Meudt, Garnock-Jones, and Ritchie (2010) |
| <i>Latrodectus katipo</i> , <i>L. atritus</i> | <i>L. hasseltii</i> | Species | Katipo | cox1, ND1 | Insect rate for mtDNA | Aus | n | 2 | | | Wallis and Trewick (2009) |
| <i>Cephalorhynchus hectori</i> | <i>C. commersoni</i> , <i>C. eutropa</i> | Species | Hector's dolphin | CR | | Saf | n | 2 | | | Wallis and Trewick (2009) |
| <i>Cyathea dealbata</i> | <i>C. australis</i> | Species | Tree fern | rbcL | Fossils (47); 14 secondary | Aus | n | 1.97 | 0 | 6.94 | Winkworth et al. (2015) |
| <i>Zostera novazelandica</i> | <i>Z. muelleri</i> | Species | Sea grass | rbcL | Fossils (47); 14 secondary | Aus | n | 1.97 | 0 | 6.81 | Winkworth et al. (2015) |
| <i>Olearia chathamica</i> | <i>Pleurophyllum criniferum</i> | Genus | Asteraceae | rbcL | Fossils (47); 14 secondary | Subantarctic | y | 1.95 | 0 | 6.96 | Winkworth et al. (2015) |
| <i>Apium prostratum</i> 4, 5 | <i>A. insulare</i> | Species | Apiaceae | ITS | Fossils (2) | SAm/Aus | y | 1.9 | | | Spalik et al. (2010) |
| <i>Acrothamnus colensoi</i> | <i>A. suaveolens</i> | Species | Ericaceae | rbcL, matK, atpB-rbcL | Fossils (2) vs. secondary | Aus/NG | n | 1.78 | 0.31 | 3.84 | Puente-Leièvre et al. (2013) |

(Continues)

TABLE 1 (Continued)

| NZ taxon | Sister group split | Rank of split | Common name/ group | Genes | Calibration per Ma | Origin | AAR | Age | | | References |
|---|--|---------------|-------------------------|---|--|------------------|-----|------|------|--------------|-----------------------------------|
| | | | | | | | | Mean | Min | Max | |
| <i>Dicksonia fibrosa</i> | <i>D. antarctica</i> , <i>D. timorensis</i> | Species | Tree fern | trnL-trnF, trnG-trnR, rpl16, matK | Fossils (3) | Aus/Asia/ SAM | y | 1.7 | | | Noben et al. (2017) |
| <i>Ranunculus multiscapus</i> , <i>R. subscapus</i> | <i>R. muelleri</i> | Species | Buttercup | psbJ-petA, matK-trnK, nrITS | Fossil, molecular and ecological information, NZ crown group | Aus/SubAnt | n | 1.7 | 0.5 | 3 | Lehnebach et al. (2017) |
| <i>Porphyrio mantelli</i> | widespread purple swampen | Species | Takahe, North Island | CR, cytb, 12S, 16S, BFG-7, RAG1 | Calibration on basal split | Aus/Asia? | n | 1.5 | 0.5 | 3.3- 16.1 | García-R and Trewick (2015) |
| <i>Leucopogon fasciculatus</i> | <i>L. lanceolatus</i> | Species | Ericaceae | rbCL, matK, atpb-rbCL | Fossils (2) vs. secondary | Aus | n | 1.33 | 0.25 | 3.09 | Puente-Lelièvre et al. (2013) |
| <i>Hieraetetus moorei</i> | <i>H. morphnoides</i> , <i>H. pennatus</i> | species | Haast eagle | cytb, ND2 | Avian cytb rate 0.7%–1.7% | Aus | n | 1.25 | 0.7 | 1.8 | Wallis and Trewick (2009) |
| <i>Notodanthonia gracilis</i> | <i>N. gracilis</i> | Subspecies | Poaceae grass | rbCL | Fossils (47); 14 secondary | Aus | n | 1.2 | 0 | 3.9 | Winkworth et al. (2015) |
| <i>Wahlenbergia</i> (5 radiate spp.) | <i>W. gracilis</i> | Species | Harebell | ITS, trnL-F | Fossils (2) + secondary calibration for root | Aus | y | 1.2 | | | Prebble et al. (2011) |
| <i>Plantago spathulata</i> , <i>P. sp. "Sylvester"</i> , <i>P. raoulii</i> , <i>P. triantha</i> | | Species | Plantain | coxL, ndhF-rpl32, ITS | 2 secondary calibrations | Aus | y | 1.01 | 0.5 | 1.52 | Tay et al. (2010) |
| <i>Ripogonum scandens</i> | <i>R. album?</i> | Species | Liliales | 75 plastid genes; timing: matK, rbCL | Fossils (17) | Aus | y | 1 | | | Givnish et al. (2016) |
| <i>Weinmannia racemosa</i> , <i>W. silvicola</i> | <i>W. raatensis</i> , <i>W. samoensis</i> | Species | Cunoniaceae | trnL-F, ITS1-2 | | NC/Pac | n | 1 | | | Wallis and Trewick (2009) |
| <i>Plantago triandra</i> , <i>P. unibracteata</i> | <i>P. muelleri</i> | Species | Plantain | coxL, ndhF-rpl32, ITS | 2 secondary calibrations | Aus | y | 1 | 0.94 | 2.29 | Tay et al. (2010) |
| <i>Himantopus novaezelandiae</i> | <i>H. leucocephalus</i> | Subspecies | Kaki | CR, cytb | | Aus | n | 1 | | | Wallis and Trewick (2009) |
| <i>Cosciniasterias muricata</i> | <i>C. muricata</i> | Subspecies | Seastar | cox1, CR, ITS2 | Panama echinoid rate | Aus | n | 0.95 | 0.6 | 1.3 | Wallis and Trewick (2009) |
| <i>Lewinia muelleri</i> | <i>Lewinia pectoralis</i> | Species | Rail | cytb, cox1, 16S, FGB-7, RAG-1 | Fossil | Aus/SEAsia | n | 0.9 | | | García-R et al. (2014) |
| <i>Utricularia novae-zelandiae</i> | <i>U. dichotoma</i> , <i>U. monanthos</i> | Species | Lentibulariaceae | rps16, trnL-trnF, trnD-trnT | 2 secondary | Aus | y | 0.74 | | | Jobson, Baleeiro, and Reut (2017) |
| <i>Clarkoma bollonsi</i> | <i>Clarkoma bollonsi</i> | Subspecies | Brittle star | cox1, ITS2, 28S, microsatellite (6) | Fixed rate: cox1, 2.48%; 28S, 0.031%; ITS, 1.5% per lineage | WAus | n | 0.71 | | | Naughton et al. (2014) |

(Continues)

TABLE 1 (Continued)

| NZ taxon | Sister group split | Rank of split | Common name/ group | Genes | Calibration per Ma | Origin | AAR | Age | | | References |
|--|--|---------------|--------------------------|---|--|--------------|-----|------|------|------|--|
| | | | | | | | | Mean | Min | Max | |
| <i>Lepidium sisymbrioides</i> , <i>L. naufrogorum</i> | <i>L. spp. (7)</i> | Species | Pepperweed | ITS, trnT-L, trnL intron, trnL-F | Fossil | Aus | n | 0.7 | 0.7 | 1.3 | Wallis and Trewick (2009) |
| <i>Sicyos mawhai</i> | <i>S. australis</i> , <i>S. undara</i> | Species | Cucurbitaceae | trnL, trnL-trnF, rpl20-rps12, trnS-trnG, psbA-trnH, rbcL, ITS | Fossil + secondary calibration for root | Aus | y | 0.7 | 0.1 | 1.6 | Sebastian, Schaefer, Lira, Telford, and Renner (2012) |
| <i>Montitega dealbata</i> | <i>M. dealbata</i> | Subspecies | Ericaceae | rbcL, matK, atpb-rbcL | Fossils (2) vs. secondary | Tas | n | 0.68 | 0.01 | 2.31 | Puente-Lelièvre et al. (2013) |
| <i>Deparia tenuifolia</i> | <i>D. petersenii</i> | Species | Athyriaceae fern | rps16-matK, trnL-L-F, matK, rbcL | Secondary calibrations | Asia/Pac/Aus | y | 0.61 | 0.02 | 1.65 | Kuo et al. (2016) |
| <i>Leucopogon xerampelinus</i> | <i>L. parviflorus</i> | Species | Ericaceae | rbcL, matK, atpb-rbcL | Fossils (2) vs. secondary | Aus | n | 0.6 | 0.07 | 1.54 | Puente-Lelièvre et al. (2013) |
| <i>Stigmatopora nigra</i> | <i>S. nigra</i> | Subspecies | Pipefish | 16S, CR, CK int6, a-Tropomyosin int5 | Fixed rate for CR 1.9% | Aus | y | 0.56 | 0.2 | 1.5 | Dawson (2012) |
| <i>Lepidium banksii</i> , <i>L. oleraceum</i> , <i>L. flexicaule</i> | <i>L. spp. (4)</i> | Species | Pepperweed | ITS, trnT-L, trnL intron, trnL-F | Fossil | Aus | n | 0.55 | 0.3 | 0.55 | Wallis and Trewick (2009) |
| <i>Trithuria inconspua</i> | <i>T. filamentosa</i> | Species | Hydatellaceae aquatic | 13 plastid genes; 4 plastid + ITS for dating | Fossils (8) secondary calibration | Aus | y | 0.51 | 0 | 1.12 | Iles et al. (2014) |
| <i>Apodactylus arctidens</i> | <i>A. arctidens</i> | Subspecies | Marblefish | cox1, cytb | Fixed rate | Aus | n | 0.5 | | | Burridge (2000) |
| <i>Nemadactylus douglasii</i> | <i>N. douglasii</i> | Subspecies | Porae | cox1, cytb | Fixed rate | Aus | n | 0.5 | | | Burridge (2000) |
| <i>Stigmatopora macropterygia</i> | <i>S. argus</i> | Species | Pipefish | 16S, CR, CK int6, a-Tropomyosin int5 | Fixed rate for CR 1.9% | Aus | y | 0.47 | 0.12 | 1.18 | Dawson (2012) |
| <i>Amaurobioides pleta</i> | <i>A. isolata</i> | Species | Spray zone spider | ITS1, ND1 | Spider rate for ND1 2.3% | Aus (SA) | n | 0.38 | | | Opell et al. (2016) |
| <i>Leucopogon fraseri</i> | <i>L. fraseri</i> | Subspecies | Ericaceae | rbcL, matK, atpb-rbcL | Fossils (2) vs. secondary | Tas | n | 0.27 | 0 | 1.1 | Puente-Lelièvre et al. (2013) |
| <i>Himantopus leucocephalus</i> | <i>H. leucocephalus</i> | Subspecies | Poaka | CR, cytb | | Aus | n | 0.2 | | | Wallis and Trewick (2009) |
| <i>Zosterops lateralis</i> | <i>Z. lateralis</i> | Subspecies | White eye | ND2-3, TGFB2 | | Aus | n | 0.2 | | | Wallis and Trewick (2009) |
| <i>Pentachondra pumila</i> | <i>P. pumila</i> | Subspecies | Ericaceae | rbcL, matK, atpb-rbcL | Fossils (2) vs. secondary | Aus | n | 0.11 | 0 | 0.42 | Puente-Lelièvre et al. (2013) |
| <i>Pyrrhobryum mnioides</i> | | Species | Moss | atpB-rbcL, trnL, rps4 | | Aus | n | 0 | | | Wallis and Trewick (2009) |

(Continues)

TABLE 1 (Continued)

| NZ taxon | Sister group split | Rank of split | Common name/ group | Genes | Calibration per Ma | Origin | Age | | | References |
|----------------------------------|--------------------------|---------------|-----------------------|--------------------------------------|--------------------|--------------|-----|------|-----|-----------------------------------|
| | | | | | | | AAR | Mean | Min | Max |
| <i>Gonocarpus montanus</i> | <i>G. montanus</i> | Species | Watermilfoil | ITS, matK, trnK'5 and trnK 3'introns | Fossils (2) | Aus | y | 0 | | Chen et al. (2014) |
| <i>Gonocarpus micranthus</i> | <i>G. micranthus</i> | Species | Watermilfoil | ITS, matK, trnK'5 and trnK 3'introns | Fossils (2) | Aus | y | 0 | | Chen et al. (2014) |
| <i>Myriophyllum pedunculatum</i> | <i>M. pedunculatum</i> | Species | Watermilfoil | ITS, matK, trnK'5 and trnK 3'introns | Fossils (2) | Aus | y | 0 | | Chen et al. (2014) |
| <i>Nerita atramentosa</i> | <i>N. atramentosa</i> | Suspecies | Neritid gastropod | cox1 | | Aus | n | 0 | | Wallis and Trewick (2009) |
| <i>Jasus edwardsii</i> | <i>J. edwardsii</i> | Subspecies | Southern rock lobster | mtDNA | | Aus | n | 0 | | Ward and Elliot (2001) |
| <i>Galeorhinus galeus</i> | <i>G. galeus</i> | Subspecies | Tope shark | ND2 | | Aus | n | 0 | | Beste-van der Merwe et al. (2017) |
| <i>Nemadactylus macropterus</i> | <i>N. macropterus</i> | Subspecies | Tarakihi | mtDNA | | Aus | n | 0 | | Ward and Elliot (2001) |
| <i>Rexea solandri</i> | <i>R. solandri</i> | Subspecies | Gemfish | mtDNA | | Aus | n | 0 | | Ward and Elliot (2001) |
| <i>Macruronus novaezelandiae</i> | <i>M. novaezelandiae</i> | Subspecies | Blue grenadier | mtDNA | | Aus | n | 0 | | Ward and Elliot (2001) |
| <i>Hoplostethus atlanticus</i> | <i>H. atlanticus</i> | Subspecies | Orange roughy | mtDNA | | Aus | n | 0 | | Ward and Elliot (2001) |
| <i>Neocyttus rhomboidalis</i> | <i>N. rhomboidalis</i> | Subspecies | Spikey oreo | mtDNA | | Aus | n | 0 | | Ward and Elliot (2001) |
| <i>Pseudocyttus maculatus</i> | <i>P. maculatus</i> | Subspecies | Smooth oreo | mtDNA | | Aus | n | 0 | | Ward and Elliot (2001) |
| <i>Alloctytus niger</i> | <i>A. niger</i> | Subspecies | Black oreo | mtDNA | | Aus | n | 0 | | Ward and Elliot (2001) |
| <i>Megadyptes antipodes</i> | <i>M. antipodes</i> | Species | Yellow-eyed penguin | CR | | Subantarctic | n | 0 | | Boessenkool et al. (2009) |
| <i>Eudyptula novaezelandiae</i> | <i>E. novaezelandiae</i> | Species | Little (blue) penguin | CR | | Aus | n | 0 | | Grosser et al. (2015) |
| <i>Tursiops truncatus</i> | <i>T. truncatus</i> | Subspecies | Bottlenose dolphin | CR | | Worldwide | n | 0 | | Wallis and Trewick (2009) |

Note. Shown are NZ taxon name(s), sister group, rank of split, common name, markers used, calibration used, area of origin of NZ clade, whether ancestral area reconstruction (AAR) was used, molecular dating of split (or mean), reference. †=extinct.

taxon from its non-NZ sister taxon (and confidence intervals where given), (e) likely ancestral area, and (f) whether any sort of ancestral area reconstruction (AAR) was carried out. If there were no AAR, direction was inferred from a combination of factors including author preferences, fossil evidence, geological reconstructions, distribution of progressively deeper lineages in the group, physical means of dispersal (wind, currents) and life history information. If, after consideration of all of these aspects, there was no clear preference for direction of dispersal, that particular split was not included.

We used the earlier stem sister split rather the later crown group radiation time presented by some authors (Prebble, Cupido, Meudt, & Garnock-Jones, 2011), though in practice, this almost never made a difference to inference of pre- versus post-OMT status. We exclude dispersive lineages that are likely to be human-mediated (e.g., Kayaalp, Schwarz, & Stevens, 2013). Where multiple analyses were presented, we used the one that was better supported or given primacy by the authors; in occasional cases where necessary, our preferences were as follows: Bayesian > maximum likelihood > maximum parsimony. Where multiple calibrations were used, we used the one favoured by authors, or a mean estimate where necessary. Whenever there was more than one paper on a particular species or species group, we preferred the one with the most extensive data or more reliable ancestral area determination, usually the most recent. Data were supplemented by Table 1 of Wallis and Trewick (2009), and estimates of molecular disjunctions times from a recent synthesis and re-analysis of published data (Winkworth et al., 2015), unless superseded by newer studies.

To assess the two hypotheses of complete submergence versus continuous emergent land, we fitted an exponential distribution to divergence times, as well as to a subset of data centred around the OMT (43–3 Ma). Complete submergence would result in an excess of times after the OMT (and a deficit before), resulting in a poor fit around this period. In contrast, a continuous landmass through the OMT would predict a continuous, smooth, geometric accumulation of new lineages through time, through the OMT into more recent time. Analyses were performed in R (R Core Team 2017), using the “fitdist” function of the R package “fitdistrplus” (Delignette-Muller, Pouillot, Denis, & Dutang, 2014) for fitting univariate distributions to non-censored data and goodness-of-fit statistics.

3 | RESULTS AND DISCUSSION

Building upon the database of Wallis and Trewick (2009), we found ~95 new papers giving dates for a total of 248 splits involving NZ lineages of plants and animals (Table 1). We ranked these from most archaic to most recent and plotted the divergence times as a univariate to show the relationship between ages of lineages and how commonly they occurred (Figure 1).

3.1 | Archaic lineages

Strikingly, this compilation reveals ~25 different lineages whose taxonomic distinctiveness and/or fossil record is matched by high

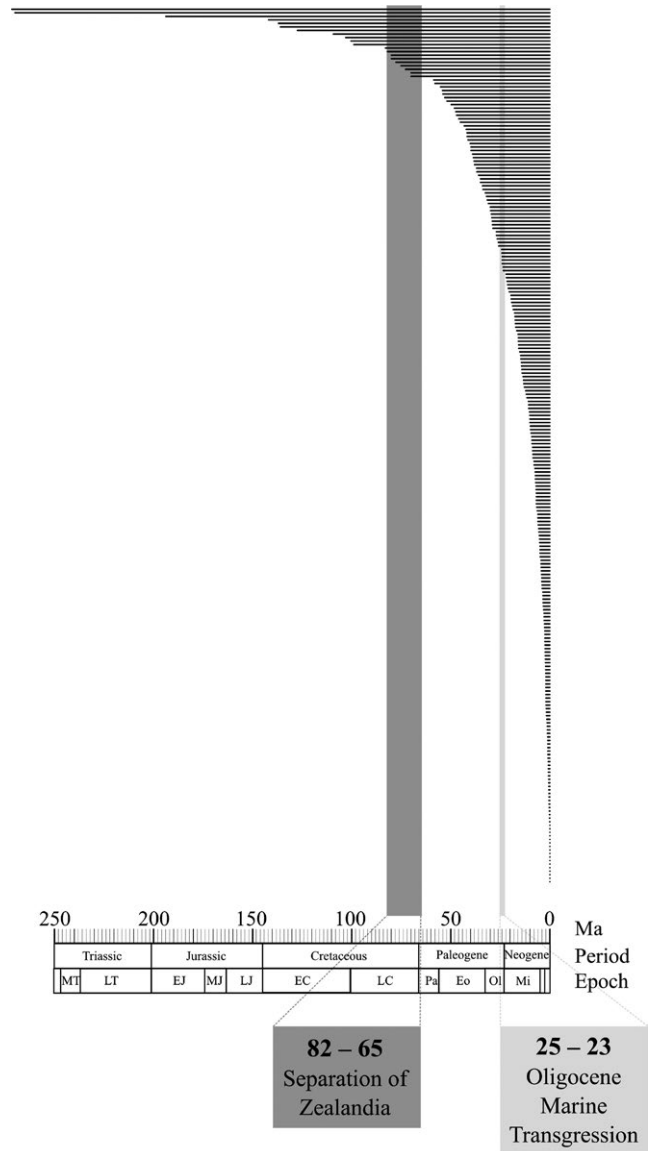


FIGURE 1 Univariate plot of ranked divergence times between NZ lineages and their closest overseas relatives (from Table 1). EC: Early Cretaceous; EJ: Early Jurassic; Eo: Eocene; LC: Lower Cretaceous; LJ: Lower Jurassic; LT: Lower Triassic; Mi: Miocene; MJ: Middle Jurassic; MT: Middle Triassic; Ol: Oligocene; Pa: Palaeocene

differentiation at the molecular level consistent with archaic Gondwanan origins, including tuatara (Hugall, Foster, & Lee, 2007), frogs (Feng et al., 2017), wrens (Ericson, Klopstein, Irestedt, Nguyen, & Nylander, 2014), crayfish (Toon et al., 2010), centipedes (Giribet & Boyer, 2010), ground weta (Pratt, Morgan-Richards, & Trewick, 2008), dragonflies (Ware et al., 2014), beetles (Andújar et al., 2016), peripatus (Murienne, Daniels, Buckley, Mayer, & Giribet, 2014), freshwater mussels (Graf & Ó Foighil, 2000; Marshall, Fenwick, & Ritchie, 2014), brachiopods (Cohen et al., 2011), cypress (Crisp et al., 2011), *Griselinia* (Nicolas & Plunkett, 2014), mountain rimu (Wardle, Ezcurra, Ramírez, & Wagstaff, 2001) and liverworts (Sun, He, & Glenny, 2014). In mite harvestmen alone (Giribet et al., 2012), some ten lineages across three extant NZ genera are sufficiently divergent to be vicariant at >65 Ma. The picture is complicated by

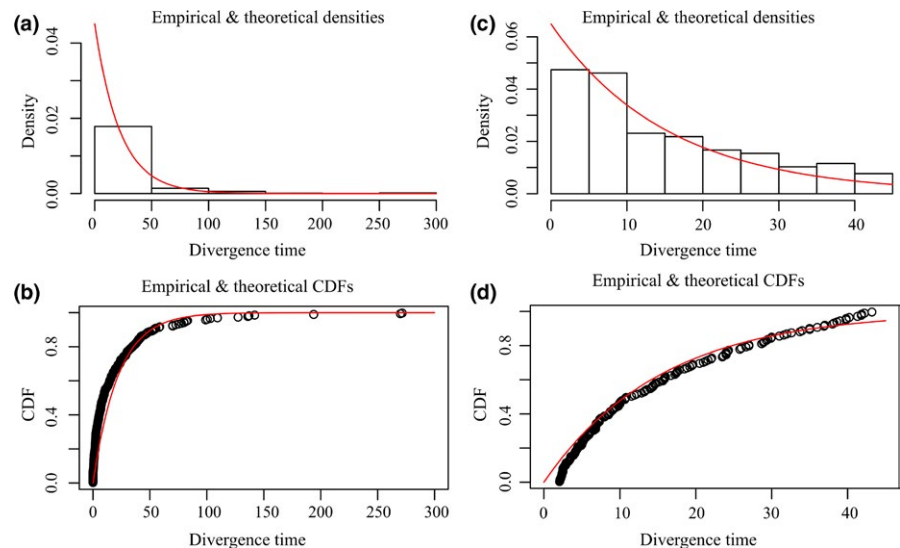


FIGURE 2 Fits of divergence times to an exponential distribution. (a,b) for the complete data set ($N = 248$); (c,d) for 43–3 Ma (OMT ± 20 Ma; $N = 137$). (a,c) empirical and theoretical densities; (b,d) empirical and theoretical cumulative distribution functions

TABLE 2 Details of divergence times binned into some major taxonomic and ecological groups

| Group | Lineages | | | Ages; Ma | | |
|---------------------------|----------|----------|-----|----------|--------|------|
| | N | Post-OMT | % | Range | Median | Mean |
| Reptiles and amphibians | 4 | 1 | 25 | 18–272 | 118 | 131 |
| Birds | 22 | 14 | 64 | 0.2–73 | 10.1 | 19.8 |
| Freshwater invertebrates | 5 | 1 | 20 | 18–80 | 36.9 | 59.9 |
| Terrestrial invertebrates | 44 | 15 | 34 | 0.4–270 | 34.4 | 44.2 |
| Marine invertebrates | 21 | 15 | 71 | 0–40 | 12.9 | 18.4 |
| Freshwater fishes | 5 | 3 | 60 | 5–24 | 17.8 | 15.4 |
| Marine vertebrates | 16 | 16 | 100 | 0–2 | 0 | 0.3 |
| Trees | 35 | 21 | 60 | 1–109 | 19.2 | 28.5 |
| Ferns | 14 | 11 | 79 | 0.6–50 | 4.6 | 11.6 |
| Herbs, vines, shrubs | 77 | 75 | 97 | 0–31.6 | 3.2 | 6 |

Note. Shown for each group are number of comparisons (N), number of post-OMT splits; % of that group represented in post-OMT divergences, range of ages, median age and mean age of divergences.

uncertainty over when links with Australia were finally severed. Recent reconstructions (Schellart, Lister, & Toy, 2006) suggest an end to seafloor spreading, and hence complete separation, at 55–52 Ma (Ho et al., 2015). The size of the gap, however, crucially depends on the progressive subsidence and submergence of Zealandia through thinning of the continental crust (Neall & Trewick, 2008). There could also have been island chain links. Notwithstanding these examples and uncertainty over timing, the large majority (~90%) of extant lineages appear to have dispersed to NZ post-Gondwanan break-up (Figure 1).

3.2 | The shape of arrival times in NZ

Looking specifically at the univariate distribution of estimated divergence times with respect to our original question, the overwhelming picture is one of a smooth decay curve with time (Figure 1); that

is, the number of extant lineages falls off ever more slowly with increasing geological age of origin (or increases exponentially in more recent time). This pattern is continuous through the Oligocene; that is, there is no evidence for a spike of arrivals after the OMT, or deficit before it, as would be expected if the land forming current-day New Zealand was completely inundated. We tested the entire set of 248 divergence times for goodness of fit to an exponential distribution (Figure 2a–b). The cumulative distribution function (CDF) plot (Figure 2b) of empirical versus theoretical distribution is very close, with the actual data falling off slightly more steeply over 0–30 Ma before joining the theoretical line. The Q–Q plot (Figure S1a), representing empirical quantiles against theoretical quantiles (emphasizing any lack of fit at tails), gives a very close fit until just past 50 Ma, when there starts to be an excess of older divergences. This feature is evident from a slight inflection at this point in the univariate

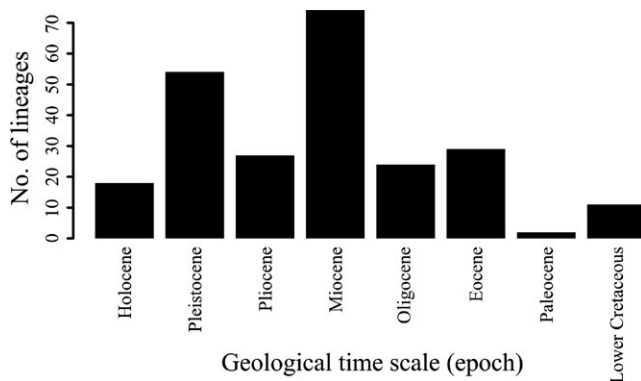


FIGURE 3 Histogram of divergence times grouped by epoch

plot (Figure 1). The P–P plot (Figure S1b), representing the empirical distribution function evaluated at each data point against the fitted distribution function (emphasizing any lack of fit at the centre of the distribution), like the CDF plot, shows an almost immediate departure from the theoretical in the form of a smooth curve, later joining the theoretical. We repeated these analyses for 137 values 20 Ma either side of the OMT (3–43 Ma) for several reasons. First, the number of zero (or near zero) values is essentially unbounded and hard to quantify. Any taxon shared between Australia and New Zealand could be included; for example, we included several marine species from one paper based on RFLPs (Ward & Elliot, 2001). In some cases, comparative data were not presented in a form that we could use (Burnard, Shepherd, Perrie, & Munkacs, 2016). These zeroes are not meaningful to our question and could be skewing the distribution. Second, there is probably a bias (over-representation) of potentially archaic lineage splits in the literature, since these make attractive topics for research being the obvious ones to assess first. Finally, and most importantly, we are specifically interested in the region either side of the OMT and simply require enough points in this region to generate a meaningful distribution. Fits of divergence times to an exponential distribution for the region around the OMT show an even better fit (Figure 2c–d). As before, the Q–Q plot (Figure S1c) starts to deviate only at the higher end. The P–P plot (Figure S1d), which specifically tests lack of fit in the very region in which we are interested, is now very close, departing only slightly at each end of the distribution. Key in all of these analyses is the obvious smoothness of the transition from pre-OMT to post-OMT.

Taken together, these analyses show mathematically that there is no evidence for any spike of arrivals after the OMT or indeed any sort of irregularity for a period of 40 Ma encompassing the OMT. We can go further and say that the approximate fit to an exponential distribution suggests a deterministic process of an equilibrium model of continuous loss of lineages by extinction through time, balanced by continual immigration (MacArthur & Wilson, 1967). This is perhaps a surprising result, as one might have expected a detectable loss of lineages by reduced land area *alone* over the duration of the OMT. The result, therefore, provides circumstantial biological evidence for a rather considerable landmass through the OMT, in keeping with recent geophysical reconstructions (Kamp et al., 2014; Strogon et al.,

2014). The fit to an equilibrium model could also be seen as surprising for an old, remote and large landmass; that is, most lineages in NZ are well into the late colonization phase, having undergone considerable adaptation and adaptive radiation, yet the landmass is still recruiting new lineages.

3.3 | Lineages surviving through the Oligocene marine transgression

Approximately 74 major lineages show divergence times before 23 Ma, suggesting that they survived the OMT *in situ*. Some lineages are particularly informative with respect to the central thesis of this paper. In mite harvestmen once again, at least 26 lineages (enlarged in number by *in situ* speciation) are claimed to have survived through the OMT: *Rakaia* [16], *Aoraki* [9] and *Neopurcellia* [1] (Giribet et al., 2012). For *Hymenophyllum* ferns (Del Rio et al., 2017) and *Schistochila* liverworts (Sun et al., 2014), slowly evolving cpDNA suggests that at least 13 and 9–10 lineages, respectively, survived the NZ OMT. Two lineages of ground weta, tusked weta and possibly tree/giant weta, appear to have survived *in situ* (Pratt et al., 2008; Trewick & Morgan-Richards, 2005). Stoneflies and midges, too, provide extensive evidence for many surviving pre-OMT NZ lineages (Cranston, Hardy, Morse, Puslednik, & McCluen, 2010; Krosch, Baker, Mather, & Cranston, 2011; McCulloch, Wallis, & Waters, 2016), although are probably not archaic. In these two flighted insect groups, there may be some ambiguity with respect to direction of dispersal involving NZ and South America, but the timing of NZ lineages is always pre-OMT, implying widespread continuous existence in NZ through this period.

3.4 | Lineages arriving post-Oligocene marine transgression

Groups that show no evidence of pre-OMT existence in NZ, followed by extensive NZ radiations soon after, are more indicative of post-OMT arrival, for example, *Oligosoma* skinks (Chapple, Ritchie, & Daugherty, 2009) and some lineages of galaxiid fishes (Burridge, McDowall, Craw, Wilson, & Waters, 2012). However, it is dangerous to make inferences from species numbers and crown ages alone in this way; extinction of lineages originating prior to the OMT can cause the root to shift and make it appear that there is a sharp upturn in speciation subsequently (Sharma & Wheeler, 2013). So just as the extinction of overseas sister lineages can push back stem divergence times, the winnowing of crown lineages can push the root of the crown group forward, leading to inference of more recent radiation.

Summarizing across the broad taxonomic and ecological distribution of lineages of species with post-OMT divergences (Table 2), a signal of either over- or under-representation is discernible for many groups. Post-OMT arriving lineages include all marine vertebrates, 97% of all herbs and shrubs (excludes liverworts, hornworts, mosses, ferns), 79% of ferns, 71% of marine invertebrates and 64% of birds (excludes penguins). In contrast, 34% of terrestrial invertebrate, 25% of reptile and amphibian and 20% of freshwater invertebrate

lineages are found in this group. In contrast to other plants, only 60% of tree lineages arrive post-OMT.

3.5 | Source–sink scenarios and estimation of NZ lineage age

Even with AAR, it is often difficult to assign ancestral area with confidence, unless there is a large number of taxa and little evidence for overseas dispersal, such as in phasmids (Buckley, Attanayake, Nylander, & Bradler, 2010). The styphelioid Ericaceae have over 300 representatives in Australia and only 10 in NZ, 3–4 of which are also in Australia. Through frugivory and west-wind drift, it is preferable to assume that each NZ lineage results from a separate independent dispersal event (Puente-Lelièvre, Harrington, Brown, Kuzmina, & Crayn, 2013), rather than having existed in NZ throughout the OMT, before undergoing several countercurrent dispersal events back to Australia, in the absence of fossil confirmation. The fern genus *Dicksonia*, however, could be archaic in NZ, though a two-dispersal scenario is preferred (Noben et al., 2017). The plant genus *Coprosma* splits from its sister genus (*Nertera*) at about 25 Ma and radiates extensively subsequent to evolving woodiness and dioecy after 15 Ma (Cantley, Markey, Swenson, & Keeley, 2016). We have included the *Coprosma*–*Nertera* lineage as having pre-OMT NZ roots, but as 30 later dispersal events around the Pacific are inferred for *Coprosma*, we cannot have much confidence that the lineage was specifically located in NZ through the OMT. As with *Coprosma*, the choice of stem over crown age implies that NZ tateid gastropods survived the OMT in situ (Zielske, Ponder, & Haase, 2017). *Griselinia* could well have dispersed to NZ from Australia in the Miocene, but in the absence of more taxa to break the long edge, or more fossil information, it is a moot point (Nicolas & Plunkett, 2014).

In general, we have sought to err on the side of inclusivity, though improved sampling and analyses may change dates or ancestral areas in some cases, but that has always been the case in biogeography. Although we have followed authors preferred scenarios, occasional authors mention the NZ OMT as at least part of the reason to prefer a more recent Australian origin in the face of a deeper split (Nicolas & Plunkett, 2014). AAR is still in its infancy and future methods should seek to incorporate biological (e.g., dispersal capabilities, habitat requirements) and physical phenomena (e.g., paleogeology, paleoclimate, winds, currents) as recommended recently (Sukumaran & Knowles, 2018).

Any single analysis is open to substantial error when the direction of dispersal is ambiguous. When a paper either tacitly assumes dispersal from Australia to NZ in an easterly direction via west-wind drift, or AAR marginally supports it, a dating for arrival from Australia is invalidated if in fact dispersal was in the opposite direction. There is some support for countercurrent drift, or at least dispersal from NZ to Australia by some route (Donald, Kennedy, & Spencer, 2005; Donald, Winter, Ashcroft, & Spencer, 2015; Sanmartin & Ronquist, 2004; Swenson & Bremer, 1997), and if this turns out to be widely applicable, many published estimates of arrival times could be

underestimates. Importantly, this would push back the ages of lineages further, increasing the number apparently surviving the OMT. Some papers infer countercurrent drift, leaving no estimate of origin of the group in NZ. In the case of *Cominella* and related genera of whelks, for example, AAR narrowly preferred countercurrent dispersal, suggesting that the assemblage had been in NZ for >27.6–78 Ma (Donald et al., 2015). If dispersal had been assumed to be in the more usual easterly direction, two dispersal events (14.5–40.9 and 18.5–54.6 Ma) would be indicated. Given the (inferred) missing outgroup, ambiguity and wide error on dating, it is difficult to know how to proceed with such studies. In this case, NZ fossil *Cominella* are known from 27 Ma, so this date is included so as not to bias omission of surviving pre-OMT lineages (even if two more recent dispersal events from Australia were inferred, they are close to or pre-OMT anyway).

On balance, though, data strongly suggest that easterly drift is much more common. For example, only 8% of pollen or spore-forming plants have a fossil record in NZ earlier than that of south-eastern Australia (Macphail, 1997). In some groups (e.g., *Lagenophora* asters), AAR was so ambivalent about ancestral areas that we did not use them. In others, AAR gives a preference, but it may not have much foundation: NZ *Libocedrus* could have South American or New Caledonian origins, but species distribution implies continuous existence in NZ (Crisp et al., 2011). In general terms, we believe that our approach in synthesizing a large number of analyses largely overcomes the ambiguities of any single study.

3.6 | The changing face of Zealandia

To highlight the relevant importance of geological epochs, we binned divergence times and plotted them against geological time (Figure 3). As our distribution (Figure 1) and analysis show an ever-increasing likelihood of finding recently arrived lineages, differences in frequency of arrivals among epochs reflect recency and duration of epoch. Hence, the relatively long and recent Miocene is a major period for arrival of currently extant lineages in NZ. This epoch was warm and stable, with steadily increasing land area, but without much topography (Wallis, Waters, Upton, & Craw, 2016), housing a recognizably modern flora and fauna.

To show any general qualitative taxonomic patterns, we tabulate median divergence times across some major groups (Table 2). The (four) reptiles and amphibians have the deepest divergences (median; 118 Ma), with freshwater (36.9 Ma) and terrestrial invertebrates (34.4 Ma) next, both deeper than marine invertebrates (12.9 Ma), reflecting perhaps the high larval dispersal capabilities of many marine invertebrates. Marine vertebrates, however, have much more recent origins (0 Ma), suggesting high adult motility in these larger species. As with the invertebrates, freshwater fishes have much deeper overseas affiliations (17.8 Ma) than marine vertebrates, in keeping with the fact that freshwater habitats on different continents are more obviously disjunct than marine habitats. Ferns (4.6 Ma) show similar depths to other herbs (3.2 Ma), despite their renowned colonization ability, with birds (excluding penguins) much deeper (10.1 Ma), and trees (19.2) deeper again. Note that these patterns are completely

counter to what would be predicted under extensive submergence, where marine species might be more likely to survive in shallow sea, yet elements of the terrestrial fauna would go extinct, necessitating subsequent re-colonization from elsewhere.

Australia dominates the likely source of lineages across the entire set of data (Table 1), but less so for older divergences. For example, from 0 to 3 Ma, Australia makes up 83% of inferred source lineages, with no other single region reaching 5%. For the period 3–23 Ma, Australia's contribution is 61%, South America 15% and New Caledonia (part of Zealandia) 7%. From 23 to 60 Ma, Australia's contribution is only 48%, South America 30% and New Caledonia 7%. Australia would seem to dominate as a recent source of lineages because of its proximity. As we go back in time, links to South America are much stronger, probably because of higher connectivity through a warmer Antarctica and Subantarctic region, making it a major source before the southern circulation established (Winkworth et al., 2015). The dearth of South African links is informative, while not surprising. Africa was not connected through stepping-stone dispersal along the edge of a warmer Antarctica because of its greater distance north, and it has a warmer-adapted flora and fauna.

The extensive group of lineages whose divergence times are consistent with surviving the OMT in situ, permits some speculation about the likely landscape and ecology of New Zealand prior to the OMT. The many trees, ferns and liverworts are consistent with lowland forest, supported by recent description of late Oligocene fossils derived from coastal forest at Cosy Dell (Conran et al., 2014). Such habitat could support birds, reptiles, frogs, peripatus, as well as the many insect lineages identified. To these could be added extinct Miocene lineages, including perhaps crocodylians and terrestrial mammals (Worthy et al., 2006), the picture is one of a diverse ecosystem. Components of an expected coastal habitat are there with marine molluscs and brachiopods, in keeping with the diverse rocky shore and shallow water fossil assemblage of the period (Buckeridge, Lee, & Robinson, 2014; Conran et al., 2014; Lee et al., 2014; Scott et al., 2014). As expected, montane and alpine groups, now well represented in NZ, are conspicuous by their absence, consistent with late Miocene or Pliocene origins of the current Southern Alps (Heenan & McGlone, 2013). All herbs, vines and shrubs (excluding liverworts, *Astelia* and *Alseuosmia*) are later arrivals on the scene too, consistent with either domination of the lowlands by forest and little open habitat, or more lineage turnover in these groups.

Definitive evidence of continuous existence prior to, during and after the OMT could best be derived from the fossil record and dating techniques. The fossil record, however, is never "complete," with respect to either taxonomy or time. Earliest records may have long been lost with older sediments, and fragmentary records could imply repeated colonization rather than an incomplete record (Pole, 2001). Material such as pollen grains can get recycled between sediments (Mildenhall, Mortimer, Bassett, & Kennedy, 2014). Even with a good fossil record, it may not be easy to attribute fossils to lineages at >23 Ma, as evidenced by argument about affinities of much more recent and extensive hominid fossils. Palaeontologists are making good headway in finding material offering transects across the OMT

(Conran et al., 2014; Lee et al., 2014; Worthy, De Pietri, & Scofield, 2017), though it might still be difficult to distinguish continuity from repetitive colonization (e.g., windborne or marine), and light material such as pollen grains may be carried from some distance away. Taken together with more recent geological and palaeontological data consistent with continuous landmass, it is our view that complete inundation should remain an unsubstantiated concept inferior to the long-held view that at least some of our flora and fauna survived the OMT and in some cases appear to be archaic (Jolivet & Verma, 2010). Our data go further to suggest that the OMT may have had a relatively mild extinction impact on the flora and fauna of New Zealand, leaving no discernible signature in an apparent equilibrium pattern of colonization of lineages to New Zealand across the OMT boundary.

ACKNOWLEDGEMENTS

Research in GPW's laboratory has received funding from the Marsden Fund, Miss Hellaby Grassland Trust and University of Otago over the last three decades. GPW acknowledges the kind hospitality of Brent Emerson (INRA CSIC Tenerife) while on study leave. Brent Emerson and three anonymous reviewers also made extensive suggestions that greatly improved the manuscript.

AUTHOR CONTRIBUTION

FJ sourced new publications for Table 1, performed analyses in R and produced the Figures. GPW conceived the paper, assembled Tables, directed analyses and wrote the paper, to which FJ made edits.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Wallis GP, Jorge F. Going under down under? Lineage ages argue for extensive survival of the Oligocene marine transgression on Zealandia. *Mol Ecol*. 2018;27:4368–4396. <https://doi.org/10.1111/mec.14875>