

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

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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>Echyridella</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>Pruennopitrys 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>Hylaeus</i> (<i>Prosopistemon</i>) <i>matamoko</i> , <i>H. NZ</i> sp. 1 subgenera)	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>Coronanthra</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)

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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>Pittosporum</i>	<i>Pittosporum</i> spp.	Species		rpl16 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, bF17	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, rpl16, rbcL, ndhF, matK, atpB-rbcL, trnT-trnL, trnC-trnD, ITS, 26S		Afr	y	15.9			Linder, Rabosky, Antonelli, Wüest, and Ohlemüller (2014)

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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)

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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>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>Neocicindela</i> spp.	<i>Abroscelis and Macfarlandia</i>	Species	Tiger beetle	cox1, cyt b, 16S-tRNA ^{Leu} -nad1	Aus clade (<i>Rivacindela, Abroscelis, Macfarlandia, Neocicindela</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)

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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>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)

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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>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</i> spp. (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)
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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>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)

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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>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 raoultii</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)

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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>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>Ew. 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)

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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>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.</i> (11)	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.</i> (13)	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)

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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 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)

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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>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		Bestervan 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

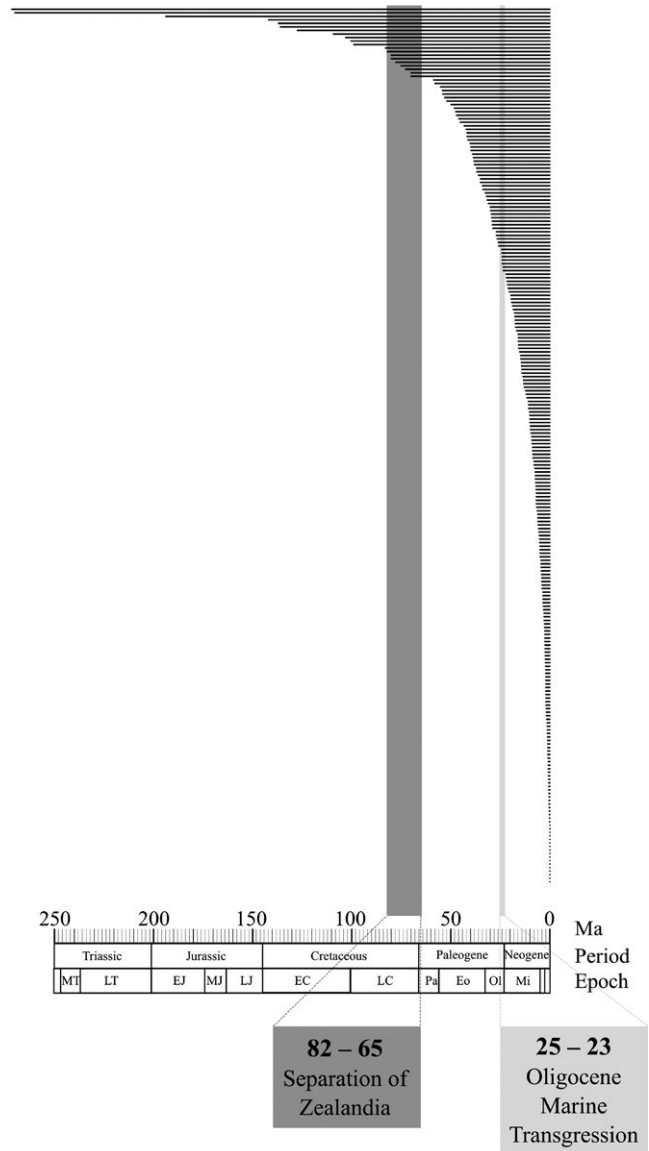


FIGURE 1 Univariate plot of ranked divergence times between NZ lineages and their closest overseas relatives (from Table 1). EC: Early Cretaceous; EJ: Early Jurassic; Eo: Eocene; LC: Lower Cretaceous; LJ: Lower Jurassic; LT: Lower Triassic; Mi: Miocene; MJ: Middle Jurassic; MT: Middle Triassic; Ol: Oligocene;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

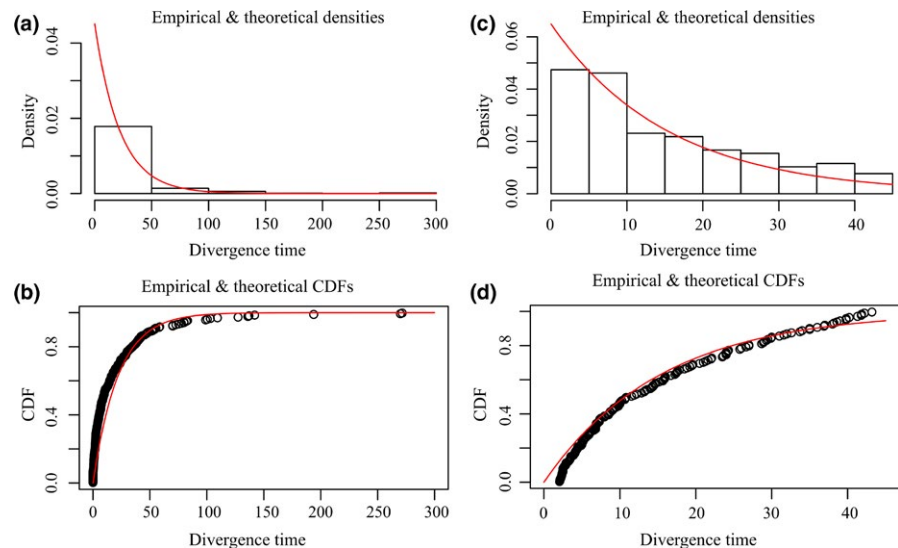


FIGURE 2 Fits of divergence times to an exponential distribution. (a,b) for the complete data set ($N = 248$); (c,d) for 43–3 Ma (OMT ± 20 Ma; $N = 137$). (a,c) empirical and theoretical densities; (b,d) empirical and theoretical cumulative distribution functions

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

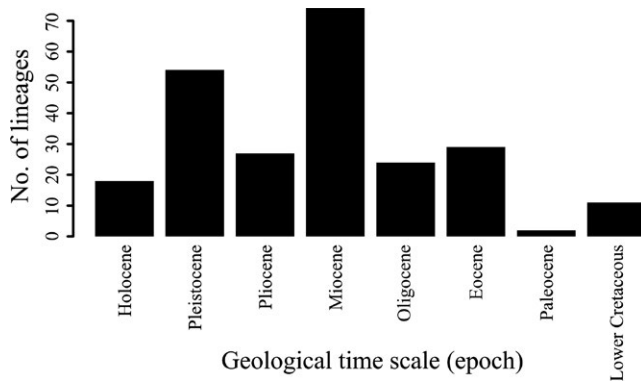


FIGURE 3 Histogram of divergence times grouped by epoch

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.

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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.

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