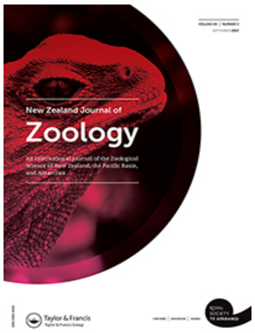

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REVIEW ARTICLE

Recent advances in avian palaeobiology in New Zealand with implications for understanding New Zealand's geological, climatic and evolutionary histories

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ABSTRACT
New Zealand, long recognised as a land where birds dominate the terrestrial vertebrate biota, lacked an informative fossil record for the non-marine pre-Pleistocene avifauna until the twenty-first century. Here we review recent research that alters the known diversity of the fossil Paleogene–Neogene birds and our understanding of the origin of New Zealand's recent or modern biota. Since 2010, there has been a 50% increase in the number of described fossil bird species (now 45) for the pre-Quaternary period. Many represent higher taxa that are new or listed for New Zealand for the first time, including 12 genera (35 total), nine family-level taxa (18 total), and seven ordinal taxa. We also review recent multidisciplinary research integrating DNA and morphological analyses affecting the taxonomic diversity of the Quaternary avifauna and present revised diversity metrics. The Holocene avifauna contained 217 indigenous breeding species (67% endemic) of which 54 (25%) are extinct.

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Fossil avifauna; Quaternary; review; St Bathans Fauna; Tertiary

Introduction

New Zealand is the emergent part of an India-sized continent (or sub-continent) once referred to as Tasmantis but now commonly termed Zealandia (Gibbs 2006; Grandcolas 2016; Mortimer et al. 2017), that stretches from New Caledonia in the north to the Chatham Islands in the east, south to the subantarctic Macquarie Island (Figure 1). Modern New Zealand comprises an archipelago of more than 254 islands larger than 8 ha and more than 400 less than 8 ha (Atkinson 1989; Worthy & Holdaway 2002) that total about 270,000 km^2; an area only about 3.5% the area of Australia. The two main islands, North Island (114,740 km^2) and South Island (151,120 km^2) account for most of this area, covering the latitudes between 34.4 and 46.6°S. At its closest point, New Zealand is 1635 km from mainland Australia (Cape Howe) and 1485 km from the southeasternmost point in Tasmania.

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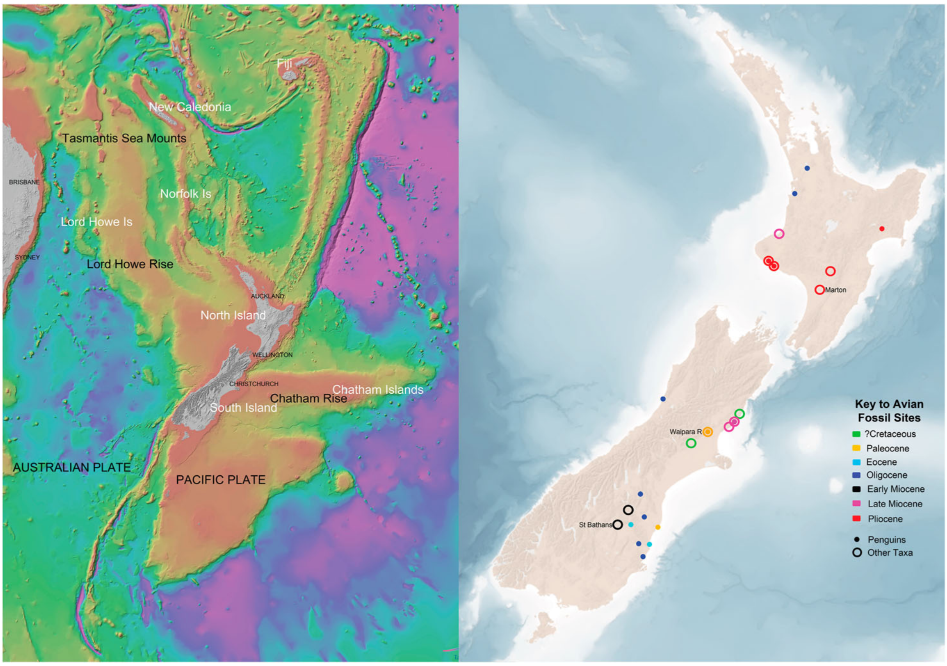

Figure 1. A, Hydrographical map of Zealandia showing extent of the submerged continent in relation to the deep oceanic basins; **B,** location of avian fossil sites that are older than the middle Pleistocene on the North and South Islands. We acknowledge the National Institute of Water and Atmospheric Research for the use of the background image in Figure 1A from Mitchell et al. (2012) that they provide with a BY-NN-NC-SA licence.

Zealandia began as part of Gondwana and began separating from Australia and Antarctica around 82 million years ago (Ma) by tectonic rifting in the south. This rifting progressively spread northwards with continental connections being severed perhaps by 60–55 Ma (Cooper & Millener 1993; Gaina et al. 1998; Sutherland 1999; Schellart et al. 2006). The distance of the emergent land from the Australian part of Gondwana increased until about 45 Ma, when the spreading centre migrated from the Tasman Sea to transect New Zealand, where it remains today. Thereafter, New Zealand has remained roughly the same distance from Australia. However, its connectivity with Australia has steadily been reduced as a consequence of various seamounts and islands along the Lord Howe Rise progressively sinking (McDougall & Duncan 1988; Quilty 1993; Meffre et al. 2006), such that now only Lord Howe and Norfolk Island separate Australia from New Zealand.

This geographical history, combined with our understanding of the evolutionary history of Australasian lineages (see below), sets temporal limits on when Gondwanan taxa could have joined the biota in proto-New Zealand. While the initial rifting of the Zealandia continental fragment commenced about 82 Ma, opportunity probably existed for many million years thereafter, for taxa to join the Zealandian terrestrial biota by overland dispersal, perhaps until about 55 Ma, as recently advocated for ancestral acanthisittids (Selvatti et al. 2015). These most likely will have included taxa from eastern Gondwana, before Australia became a separate continent. Thereafter, progressive subduction of the Lord Howe Rise meant that proto-New Zealand became the largest of a series of islands. The now drowned Tasmantis and Lord Howe Rise seamounts (Quilty 1993;

Meffre et al. 2006) when emergent could have potentially provided stepping stones for overwater dispersing taxa to New Zealand until the early Miocene, but after about 20 Ma the seamounts were submerged leaving New Zealand in its current very isolated situation. It is important to consider, however, that the source of such overwater dispersal probably included Antarctica, at least before the establishment of the circum-Antarctic current about 50 Ma and its subsequent cooling (Brown et al. 2006; Bijl et al. 2013; Wilf et al. 2013), which led to the establishment of the current prevailing westerly winds. Up until the late Eocene, Antarctica was a closer landmass than was Australia (Bijl et al. 2013) and can be assumed to have hosted a large terrestrial biota and so have been a faunal source for proto-New Zealand biota.

The fossil record has only recently begun to provide insights into how and when this terrestrial vertebrate fauna was assembled. As a result, answers to some of the following fundamental questions are now forthcoming. (1) Was New Zealand always a land of birds? (2) Has the present depauperate diversity of vertebrates always characterised the fauna? (3) Which components, if any, have a vicariant origin? And finally, (4) what was the impact of the Oligocene drowning event, which was recently proposed to have largely if not wholly inundated all land in New Zealand (Campbell & Hutching 2007; Landis et al. 2008)? To place these questions in context, a quick résumé of the New Zealand Recent avifauna, provided below, will show the extent of the problem.

The recent avifauna

New Zealand is well known as a land of birds (Oliver 1955; Worthy & Holdaway 2002; Ell 2016), but it is worth noting that the extant fauna is not a useful starting place from which to understand how New Zealand's avifauna was assembled. The extant birds are the survivors of a far more complex avifauna evolved over millennia that included many unique and highly specialised taxa. The evolution of the New Zealand avifauna was impacted catastrophically by the extinction of many taxa in the last 750 years following the arrival of humans (Wilmshurst et al. 2008, 2011). These extinctions occurred in a highly selective fashion, one strongly biased against flightless, terrestrial and highly derived forms. Hence, the remnant taxa are not representative of the avifauna that evolved in New Zealand and, like Holdaway et al. (2001), we treat the late Holocene fauna as our starting place. We, therefore, include all Holocene taxa that are now extinct as part of the fauna that defined New Zealand at the culmination of its evolution in isolation.

New Zealand has long intrigued evolutionary biologists because its native terrestrial vertebrate fauna was, and is, dominated by birds (Buller 1869; Hutton 1873; Oliver 1930, 1955; Fleming 1979). However, it displays a mix of traits, with high endemism at species and generic levels, yet low specific diversity (Bell 1991; Holdaway et al. 2001; Worthy & Holdaway 2002; King et al. 2009). This Holocene fauna was analysed by Holdaway et al. (2001), wherein one of the aims was to reveal many of the challenges then awaiting taxonomists. In doing so, Holdaway et al. revealed the disjunction between the then accepted nomenclature and taxonomy of New Zealand birds and the real diversity if all groups were treated in an equal way within a phylogenetic species concept. However, before any summary is made and subsequent comparisons can be drawn, as Holdaway et al.'s work further revealed, a fundamental decision has to be made at the outset: what is, or how does one define, the New Zealand avifauna? Holdaway et al. (2001) chose a biogeographical concept where New Zealand included North, South and Stewart islands and nearby smaller islands, plus outlying island groups from Norfolk Island in the northwest, the Kermadec group to the north, Chatham Islands to the east, and Bounty, Antipodes, Campbell, Auckland, Snares and Macquarie islands in the south, but they excluded islands south of Macquarie Island and the Ross Dependency. They then only included resident breeding taxa, or those that once were, and listed 245 species-level taxa of which 174 were endemic to the archipelago, in 110 genera, representing 46 families.

Nearly a decade later, some of the taxonomic issues had been addressed, and the New Zealand Checklist (Gill et al. 2010) followed the same biogeographical definition as Holdaway et al. (2001) and listed 435 species from New Zealand, including vagrants, Pleistocene–Holocene and introduced taxa; see also Tennyson (2010) following the same geographic definition of New Zealand for a review to that time. Restricting this appraisal to indigenous taxa, i.e. naturally occurring and breeding in New Zealand and its nearby archipelagos before 1860 (so excluding more recent colonists, vagrants, migrants and taxa from Macquarie Island, Norfolk Island and Antarctica), results in 214 indigenous breeding species, of which 144 (67%) were/are endemic, in 46 families (10 endemic) and 107 genera (32% endemic). These species included 126 (59%) land and freshwater taxa and 54 (25%) that are extinct. New Zealand's avifauna is therefore diverse at the family level, but has low species diversity within genera or families, especially within terrestrial and freshwater taxa. For example, the most diverse passerine family in New Zealand is Acanthisittidae, having five genera but just seven species. This contrasts markedly with Australian radiations, for example the honeyeaters (Meliphagidae) have 74 species in 26 genera (Christidis & Boles 2008), whereas New Zealand has just three species in this family. This does beg the question whether there was ever a time in which species-level diversity was higher and whether previous extinction events have gone unnoticed.

This avian diversity contrasts markedly with other groups of vertebrates in the Holocene fauna (Tennyson 2010). Non-marine mammals were/are represented by three species of bats in just two genera (*Mystacina*, *Chalinolobus*). Frogs are represented by just one family (Leiopelmatidae), formerly with six species (three now extinct) (King et al. 2009). Similarly, squamates are depauperate at higher taxonomic levels, with only Eugongylinae skinks (Scincidae: *Oligosoma*) and geckos (Diplodactylidae: seven genera) represented, but these families have only recently been recognised as the most diverse vertebrate families in New Zealand with 40 skink (1 extinct; plus 22 undescribed) and 19 gecko (1 extinct; plus 24 undescribed) species (Hitchmough et al. 2016). There is only one other reptile, the Tuatara (Sphenodontidae: *Sphenodon punctatus*), which like the leiopelmatid frogs has high evolutionary significance as the last of its kind with roots deep in the Mesozoic.

It is well known that New Zealand's Quaternary fossil record (Holocene, 10,000–0 years ago and Pleistocene, 2.56 Ma to 10,000 years ago) is exceptionally rich for terrestrial vertebrates and birds (e.g. Fordyce 1991; Millener 1991; Worthy & Holdaway 2002; Tennyson 2010), but in reality this record is largely restricted to the most recent 50,000 years. Fossil sites dating from this interval, which samples the last glacial period and the Holocene, are abundant in coastal dunes, caves and swamps, and less so in lacustrine deposits. Probably because of the lack of small scavenging mammals, these deposits are rich on a global scale, with very large numbers of fossils, whose representation of the original biocoenosis is often limited only by physical taphonomic factors such as erosion by water (Worthy & Holdaway 2002). Hence the composition of avifaunas, at least on land, is largely unknown for the early to mid-Pleistocene and all older periods. In contrast, the marine vertebrate fossil record is very good throughout most of the Cenozoic (the last 65 Ma), as a more or less continuous series of shallow-water deposits represent the entire interval (Fleming 1979; Fordyce 1991; Crampton et al. 2006; King et al. 2009).

Concordant with our starting point that the modern fauna is that which was existing in the late Holocene, here we distinguish the fossil record older than 0.8 Ma from the late Pleistocene–Holocene fauna. This is based on the observation that although the known late Pleistocene fauna does not differ in any way from the Holocene fauna in terms of species content, the 1 Ma Marton fauna (Worthy 1997) has several taxa not seen in the more recent faunas. In the following text, we follow the convention that species authorities are not given for living and historically known Recent birds, as these are readily available in checklists, e.g. Gill et al. (2010), but all taxa known only as fossils have species authorities at first mention.

Recent changes in the knowledge of the diversity of New Zealand's fossil avifauna are the focus of this review and will be addressed in two sections. We take the inventory in the 2010 New Zealand Checklist (Gill et al. 2010) as our starting point and consider discoveries that have modified the information therein. First, we will focus on the fossil record older than 0.8 Ma, considering the oldest faunas first, starting with the Paleogene. Second, the discoveries affecting knowledge of the late Holocene biota will also be reviewed to enable more pertinent comparisons of the fossil and Holocene or modern biotas. These data, detailed below, are summarised in Table 1 and reveal that since 2010 there has been a 50% increase in the number of species described. It is the purpose of this review to outline how these discoveries affect the interpretation of the diversity, composition and assembly of the New Zealand avifauna. For the reader's convenience, we present the relationships of family-level taxa occurring in New Zealand in Figure 2 with an indication of fossil and current diversity.

Discoveries of fossil birds from New Zealand since 2010

Paleocene

To date, Paleocene sediments in New Zealand have only yielded marine taxa. The Waipara Greensands of Paleocene (61.6–60.5 Ma) age, North Canterbury, have revealed two species of the important stem-penguin *Waimanu* (Sphenisciformes) (Slack et al. 2006), which securely anchors the evolutionary origin of penguins in the Paleocene. Most recently, a new stem penguin has been described from the Waipara Greensands (Mayr et al. 2017) that shows ancestral penguins of very large size and comparatively modern morphology coexisted with *Waimanu*, thereby potentially suggesting penguins diverged from their sister taxon (Procellariiformes) in the Cretaceous. Ongoing collection has revealed several more specimens of these taxa and some of hitherto undescribed penguin-like taxa. Such discoveries are also augmented by Paleocene penguins from the Chatham Islands, which have been noted (Mayr 2009) but have not yet been described.

Table 1. Fossil avian taxa above the species-level that pre-date the mid-Quaternary record of New Zealand with number of species known in 2010 and at present. Taxa shaded are new or newly represented in the New Zealand pre-Quaternary record, reflecting a 50% increase in species-level taxa since 2010.

Order	Family	Genus	2010	now
Apterygiformes	Apterygidae	*Proapteryx*	0	1
Anseriformes	Anatidae	*Manuherikia*	3	3
		Dunstanetta	1	1
		Matanas	1	1
		Miotadorna	1	1
Procellariiformes	Pelecanoididae	*Pelecanoides*	1	1
Ardeiformes	Ardeidae	*Matuku*	0	1
		Pikaihao	0	1
Sphenisciformes	Spheniscidae	*Waimanu*	2	2
		Gen. nov. (*Waipara*)	0	1
		Palaeeudyptes	2	2
		Pachydyptes	1	1
		Kairuku	0	2
		Kaiika	0	1
		Platydyptes	3	3
		Archaeospheniscus	2	2
		Duntroonornis	1	1
		Korora	1	1
		Marplesornis	1	1
		Aptenodytes	1	1
		Pygoscelis	1	1
		Tereingaornis	1	1
Phaethontiformes	Family indet.	Genus indet.	0	1
Phoenicopteriformes	Palaelodidae	*Palaelodus*	0	1
Gruiformes	Rallidae	*Pleistorallus*	1	1
	Aptornithidae	*Aptornis*	0	1
Columbiformes	Columbidae	*Rupephaps*	1	1
Apodiformes	Aegothelidae	*Aegotheles*	1	1
	Apodidae	*Collocalia*	1	1
Charadriiformes	Scolopaci: fam. indet.	*Hakawai*	0	1
	Chionoidea: fam. indet.	*Neilus*	0	1
Psittaciformes	Nestoridae	*Nelepsittacus*	0	3
Passeriformes	Acanthisittidae	*Kuiornis*	0	1
Order Indet.	Pelagornithidae	*Pelagornis*	2	2
	Family indet.	*Manu*	1	1
	Family indet.	*Australornis*	0	1
Total			30	46

The most exciting development in the exploration of the Waipara Greensands is the discovery of taxa other than stem penguins. These to date include two volant seabirds: *Australornis lovei* Mayr and Scofield, 2014, a large bird of unknown affinity (Mayr & Scofield 2014) and an unnamed species considered to represent a phaethontiform tropicbird (Mayr & Scofield 2016). These discoveries herald the possibility of other, perhaps non-aquatic, taxa being recovered. The potential also exists elsewhere in New Zealand for similarly old fossils as shown by the report of a worn left tarsometatarsus discovered in a late Cretaceous–early Paleocene section near Woodstock in the Waimakariri River gorge (Ksepka & Cracraft 2008). This fossil does not differ notably from tarsometatarsi of procellariid seabirds (Procellariiformes). The presence of procellariiforms during this time should be expected, as indicated by their sister-taxon relationship to Sphenisciformes (Jarvis et al. 2014), whose presence at this time is indicated by *Waimanu*.

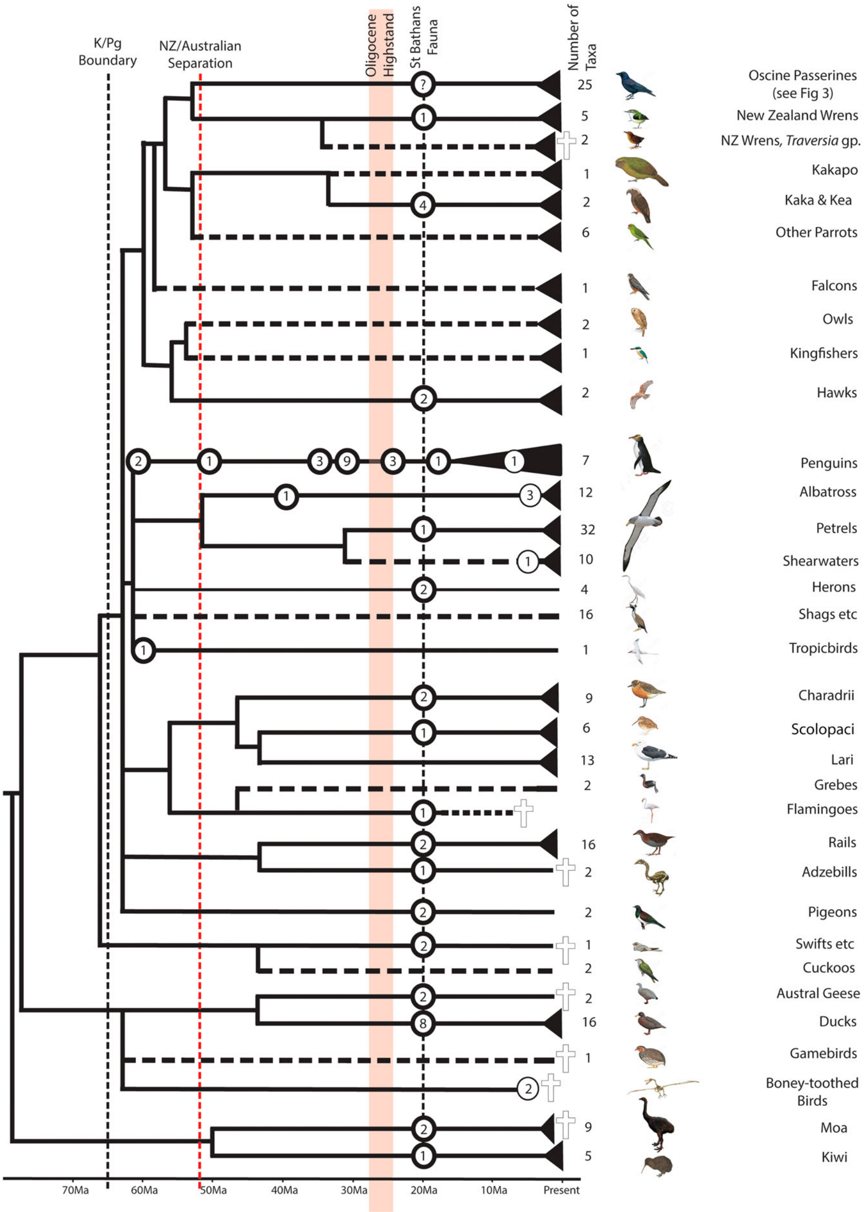

Figure 2. An indicative phylogeny showing the major clades of birds known from the fossil and extant records of New Zealand within the constraints of the avian relationships found by Prum et al. (2015) with uncertain relationships left unresolved. The nodes are calibrated using the age estimates of Prum et al. (2015). The time of deposition of the St Bathans Fauna and the major events of the Oligocene marine highstand and the K-Pg boundary are shown relative to the clades. No attempt is made to capture the age of the crown group radiation of each of these groups. Dotted lines show a lineage where the presence in New Zealand was not confirmed until its late Holocene appearance, so for example, molecular data support the ancient divergence of Galliformes, but no fossils of it or its lineage are known from New Zealand until the late Pleistocene. Numbers in circles are counts of fossil species-level taxa, some undescribed, (based on published data only) and, at terminals, are numbers of late Holocene species known from New Zealand. Crosses indicate extinction. Images from de Hoyo et al. (2003) used with permission.

Eocene

There is a gap in the avian fossil record from the early Paleocene to the early Eocene. The next oldest penguin known from New Zealand is the giant *Kaiika maxwelli* Fordyce and Thomas, 2011, which was described from a single femur from the early Eocene (55.5–49.5 Ma) (Fordyce & Thomas 2011). There is then another considerable gap of c. 10 Ma in the fossil record to when *Palaeeudyptes marplesi* Brodkorb, 1963 and *Pachydyptes ponderosus* Oliver, 1930 are known from late Eocene rocks 36–34 Ma (Gill et al. 2010). These species are stem Spheniscidae, or outside the crown group of this family.

Oligocene

The Oligocene marks the time of greatest diversity in fossil penguins in New Zealand, with eight species listed by Gill et al. (2010), all stem taxa within Spheniscidae. This diversity was added to in 2012 when several spectacular fossils from the late Oligocene Kokoamu Greensand were described in the new genus *Kairuku*, with two new species *Kairuku waitaki* Ksepka, Fordyce, Ando and Jones, 2012 and *Kairuku grebneffi* Ksepka, Fordyce, Ando and Jones, 2012, erected. These taxa are apparently most closely related to species of *Palaeeudyptes*, which however are known from much less complete material, precluding their phylogenetic resolution relative to morphologically similar taxa (Ksepka et al. 2012). Further discoveries will be needed to resolve the problem. Meanwhile, an as yet unnamed species referred to *Kairuku* was identified from a specimen collected years ago from Glen Murray in the North Island (Thomas & Ksepka 2016), making it the first record of the genus for the North Island. Other recent North Island material, including the relatively complete 'Kawhia penguin' (http://www.stuff.co.nz/waikato-times/news/69218680/kawhia-giant-penguin-brought-to-virtual-life) remains undescribed.

Miocene

The New Zealand fossil record includes two pelagornithid taxa *Pelagornis miocaenus* Lartet, 1857 and *Pseudodontornis stirtoni* Howard and Warter, 1969. This latter taxon was listed in *Neodontornis* in Gill et al. (2010), but Mayr and Rubilar-Rogers (2010) transferred this species to *Pelagornis*, which position we follow here.

The St Bathans Fauna provides virtually the only insight into terrestrial vertebrates living in New Zealand between 65 Ma and 4 Ma (Worthy et al. 2007). The St Bathans Fauna is derived from the lower parts of the Bannockburn Formation, the lacustrine unit of the Manuherikia Group sediments. The sediments outcrop over a wide area of Otago in the South Island from the Waitaki River in the North to Cromwell in the south-west, but generally as small exposures separated by several upthrust mountain ranges and often buried by overlying sediments. The Bannockburn Formation sediments are not well dated, but based on pollen assemblages, they are considered to be upper early Miocene (19–16 Ma; local stage Altonian) in age, and were deposited near a river delta on one side of palaeo-lake Manuherikia that extended over some 5600 km^2 (Douglas 1986; Mildenhall 1989; Mildenhall & Pocknall 1989; Pole & Douglas 1998; Pole et al. 2003). Vertebrate fossils were first discovered in these deposits in the early 1980s (Douglas et al. 1981), but it was not until 2001 that excavations specifically targeting the vertebrates began, and in 2007, the first analysis was published (Worthy et al. 2007). The fauna contains a diverse range of invertebrates and vertebrates including molluscs (Marshall 2011; Marshall & Worthy 2017), fish (Schwarzhans et al. 2012), frogs (Worthy et al. 2013a), reptiles (Jones et al. 2009; Lee et al. 2009; Worthy et al. 2011a) and mammals, including both bats (three mystacinids and several undescribed taxa) and undescribed terrestrial mammals (Worthy et al. 2006; Hand et al. 2013, 2015), but here we focus on the minimally 40 species of birds represented in this fauna (Table 2).

Dinornithiformes (moa). To date, only indeterminate bone fragments and eggshell inseparable from those of moa represent this order in the St Bathans Fauna (Tennyson et al. 2010). The eggshell includes two kinds, as shown by the thickness and structure of the fragments. A common shell type has thickness of 0.58–1.19 mm, mean = 0.94 mm, *n* = 154, similar to that of *Anomalopteryx didiformis* (Owen, 1844), and so is from a 40–60 kg bird; a second type is

Table 2. A summary of the St Bathans Fauna from the late early Miocene listing described species and or genera (shaded) and others known but not yet described to indicate the overall composition of the avifauna.

Family	Genus	Species
Dinornithiformes	Genus indet.	Sp. indet. ×2 (eggshell)
Apterygiformes	*Proapteryx*	*P. micromeros*
Pelecanoididae	*Pelecanoides*	*P. miokuaka*
Anatidae	*Manuherikia*	*M. lacustrina*
		M. minuta
		M. douglasi
		sp. nov. 1
	Miotadorna	*M. sanctibathansi*
	Dunstanetta	*D. johnstoneorum*
	Matanas	*M. enrighti*
Anserinae	cf *Cereopsis*	sp. nov. 1
		sp. indet.
Palaelodidae	*Palaelodus*	*P. aotearoa*
Accipitridae	Eagle: genus indet.	sp. nov. 1
	Kite: genus indet.	sp. nov. 2
Ardeidae	*Matuku*	*M. otagense*
	Pikaihao	*P. bartlei*
?Aptornithidae	*?Aptornis*	*?A. proasciarostratus*
Rallidae ‘rail’	Genus indet.	sp. nov.1
		sp. nov.2
Charadriiformes		
Lari	Genus indet.	sp. nov. 1
		sp. nov. 2
Scolopaci	*Hakawai*	*H. melvillei*
Charadrii	*Neilus*	*N. sansomae*
		sp. nov. 1
		sp. nov. 2
Columbidae	*Rupephaps*	*R. taketake*
	Genus indet.	sp. nov. 1
Strigopidae	*Nelepsittacus*	*N. minimus*
		N. donmertoni
		N. daphneleeae
	Genus indet.	sp. nov. 1
Aegothelidae	*Aegotheles*	sp. nov. 1
Apodidae	*Collocalia*	sp. nov. 1
Aves fam. nov.	Genus indet.	sp. nov. 1
Passeriformes	*Kuiornis*	*K. indicator*
	Cracticidae: Genus indet.	sp. nov. 1
	Genus indet.	spp. nov. 2–5

1.68 mm thick with a different structure and indicates a bird that was probably twice as large. Some bone fragments are very similar to bones of the moa *Megalapteryx didinus* (Owen, 1883) and so are probably from the small taxon.

Apterygiformes (kiwi). One of the most striking discoveries since 2010 is that of a small kiwi (Apterygidae) in the St Bathans Fauna, *Proapteryx micromeros* Worthy TH, Worthy JP, Tennyson, Salisbury, Hand and Scofield, 2013. It was a tiny bird, about a third the size of the Little-spotted Kiwi (*Apteryx oweni*) and is rare, with just a femur and a quadrate known to date (Worthy et al. 2013b). Given its very small size, the authors speculated that this, the oldest member of the kiwi lineage, could have been volant and if indeed a representative of ancestral kiwi, it showed that Gould's hypothesis (Gould 1986, 1991) that the kiwi ancestor was a moa-sized taxon that had dwarfed over time was wrong. The contention that kiwi and moa are sister taxa, as was long thought, is now thoroughly debunked, with moa known to be the sister group of tinamous (Tinamidae) (Phillips et al. 2010) and kiwi the sister group to elephant birds (Aepyornithidae) (Mitchell et al. 2014a). These relationships are based on abundant molecular data and indicate that the ancestors of both moa and kiwi must have flown to New Zealand and subsequently become flightless, so *Proapteryx* may well be such a volant ancestor of kiwi.

Anseriformes (waterfowl). By 2010, it was already demonstrated that anseriforms dominated the St Bathans Fauna in both numbers of fossils and in diversity of represented species (Worthy et al. 2007, 2008). Now, minimally nine species are known, making it the richest fossil waterfowl fauna globally. Perhaps only one genus and none of the species are shared with Australia, and more than 4000 specimens are now known (THW unpubl. data). They represent several subfamilies and genera as follows:

Anserinae (geese). A few bones have been referred to the extant genus *Cereopsis* (Cape Barren Goose) and were inferred to represent the ancestor of the species of *Cnemiornis* known from late Pleistocene–Holocene faunas (Worthy et al. 2008). As yet, material considered adequate to erect a species has not been identified. A second possible anserine was also noted by Worthy et al. (2008) based on coracoids. It is notable that the Australian *Cereopsis* is the sister taxon of *Coscoroba* from South America, and together they form a sister-group clade to Northern Hemisphere anserines (Gonzalez et al. 2009) revealing a hemispheric separation in anserine evolution.

Erismaturinae (= Oxyurinae stiff-tailed ducks). Several species attributed to Oxyurinae dominate the fauna in terms of both diversity and abundance as fossils. These are *Manuherikia lacustrina* Worthy, Tennyson, Jones, McNamara, and Douglas, 2007, *Manuherikia minuta* Worthy, Tennyson, Jones, McNamara, and Douglas, 2007, *Manuherikia douglasi* Worthy, Tennyson, Hand, and Scofield, 2008 and *Dunstanetta johnstoneorum* Worthy, Tennyson, Jones, McNamara, and Douglas, 2007, see Worthy et al. (2007, 2008) and Worthy and Lee (2008). More recent excavations have revealed a further undescribed species of *Manuherikia* which replaces *Manuherikia lacustrina* higher in the stratigraphic section (THW unpubl. data).

Tadorninae (shelducks). Only one species of shelduck, *Miotadorna sanctibathansi* Worthy, Tennyson, Jones, McNamara, and Douglas, 2007, has so far been described from the St Bathans Fauna. It was larger than the Chestnut-breasted Shelduck (*Tadorna tadornoides*) and is a relatively common species in the fauna.

Anatinae (dabbling ducks). Only one species of the more derived (among anatids) subfamily Anatinae has so far been identified. To date, this species, *Matanas enrighti* Worthy, Tennyson, Jones, McNamara, and Douglas, 2007, remains poorly known with only a few specimens attributed to it.

Procellariiformes: Pelecanoididae(diving petrel). A diving petrel was reported by Worthy et al. (2007) based on a distal humerus. Since then, another specimen of a humerus has been discovered but the taxon remains rare. This is the oldest record of *Pelecanoides* globally. The next youngest fossil is an ulna from the Double Corner Shell Beds (Waiauan; mid-Miocene) of North Canterbury, New Zealand (Scofield et al. 2006).

Ardeiformes: Ardeidae (herons). The St Bathans Fauna has recently revealed the first fossil herons from Australasia. *Matuku otagense* Scofield, Worthy, and Tennyson, 2010, based on a few bones, is a basal heron (Scofield et al. 2010), and is about the size of a White-faced Heron (*Ardea novaehollandiae*). *Pikaihao bartlei* Worthy TH, Worthy JP, Tennyson, and Scofield, 2013 is the oldest bittern globally (Worthy et al. 2013c) and is a bit larger than a Little Bittern (*Ixobrychus* sp.). It is known by just two specimens including a complete tarsometatarsus.

Phoenicopteriformes: Palaelodidae (palaelodids). Flamingos are represented by two families in the fossil record, the extant Phoenicopteridae and the extinct Palaelodidae, that had a global distribution including Australia (Baird & Vickers-Rich 1998) as reviewed in Worthy et al. (2010b). A handful of fossils named *Palaelodus aotearoa* Worthy, Tennyson, Archer, and Scofield, 2010 show that a palaelodid about the size of the Australian *Palaelodus wilsoni* Baird and Vickers-Rich, 1998 was a member of the St Bathans Fauna (Worthy et al. 2010b). No evidence of phoenicopterids has been found, which is surprising given their presence in Australia with several species from the late Oligocene to the late Pleistocene (Miller 1963; Rich et al. 1987).

Accipitriformes (eagles and hawks). Two accipitrids are known from the St Bathans Fauna. One is an eagle about the size of a small Wedge-tailed Eagle (*Aquila audax*), see Worthy et al. (2007) and the other a smaller hawk-sized species. Both are rare in the fauna and await taxonomic description.

Gruiformes: Aptornithidae (adzebills). Soon after its discovery, the endemic family Aptornithidae was recognised as having gruiform affinities (Owen 1871, 1872; Fürbringer 1888; Beddard 1898; Lowe 1926). Its relationship to other members of the gruiform clade, however, have long remained enigmatic, being variously thought to be related to trumpeters (*Psophia* spp.) of South America (Parker 1866), or the Kagu (*Rhynochetos jubatus*) of New Caledonia (Cracraft 1982; Olson 1985; Livezey 1998; Livezey & Zusi 2007), or to some basal gruiform (Fürbringer 1888; Beddard 1898; Lowe 1926). A galloanseriform relationship has also been suggested (Weber & Hesse 1995). The discovery of *?Aptornis proasciarostratus* Worthy, Tennyson, and Scofield, 2011 shows that the lineage has been in New Zealand since at least the early Miocene (Worthy et al. 2011b). It was then already a large species, but the recognised elements (vertebrae and femur) are insufficient to show whether it was then a flightless taxon.

Rallidae (rails). Two species of rails were noted in the St Bathans Fauna by Worthy et al. (2007), one of which may have been flightless. Despite fossils of this group being abundant in the fauna, with about 800 fossils known, the species remain undescribed, although work in progress confirms that only two species are represented (EK Mather and THW unpubl. data).

Charadriiformes (waders). When the St Bathans Fauna was originally described a variety of waders was noted (Worthy et al. 2007) with a few fossils tentatively attributed to Laridae (gulls and kin) and others that indicated two small waders. Research to identify the relationships of these fossil waders has begun with two papers recently published. A small species described as *Hakawai melvillei* De Pietri, Scofield, Tennyson, Hand, and Worthy, 2016 was found to be a member of the suborder Scolopaci and a representative of the clade that comprises the South American seedsnipes (Thinocoridae) and the Australian Plains-wanderer (Pedionomidae) (De Pietri et al. 2016a). It is therefore evidence of a uniquely Southern Hemisphere radiation. The presence of bones attributable to chicks further revealed that *Hakawai melvillei* had a breeding population in New Zealand, and was not a trans-equatorial migrant. The second St Bathans wader to be described was found to be a member of Chionoidea, a clade that includes the Magellanic Plover (Pluvianellidae) and sheathbills (Chionidae). Named as *Neilus sansomae* De Pietri, Scofield, Hand, Tennyson, and Worthy, 2016, this chionoid was apparently a rare member of the fauna (De Pietri et al. 2016b), but its importance lies chiefly in its identity as another endemic member of a Southern Hemisphere group present in the Australasian Region during the early Miocene.

Research assessing the affinities of the remaining wader taxa is underway, but they are known to include the aforementioned gull-like bird, at least one other Lari, and at least two members of Charadrii. These first data, the two described taxa and the presence of three more, already suggest that this early Miocene wader fauna from New Zealand had little affinity with those of equivalent age from the Northern Hemisphere. Moreover, they reveal an interesting trend that once research addresses a group in detail, initial estimates of diversity are found to be conservative.

Columbiformes (pigeons). The St Bathans Fauna has revealed sparse remains of two species of pigeons. Worthy et al. (2009) described *Rupephaps taketake* Worthy TH, Hand, Worthy JP, Tennyson, and Scofield, 2009 based on a coracoid of similar size to that of the New Zealand Pigeon (*Hemiphaga novaeseelandiae*). This fossil taxon was hypothesised to be a ptilinopine fruit pigeon closely related to *Hemiphaga novaeseelandiae* and the Topknot Pigeon (*Lopholaimus antarcticus*); hence, *Rupephaps* is likely to be either an early member of the *Hemiphaga* lineage or the sister taxon to a clade that includes *Hemiphaga* and *Lopholaimus*. Rare fossils of a smaller unnamed pigeon, similar in size to the Wompoo Fruit-dove (*Ptilinopus magnificus*), occur in the St Bathans Fauna, but it remains unnamed.

Apodiformes: Aegothelidae (owlet-nightjars). Worthy et al. (2007) reported a proximal tarsometatarsus of a species of owlet-nightjar *Aegotheles* sp. that was of similar size to the extinct New Zealand Owlet-nightjar (*Aegotheles novaezealandiae* Scarlett, 1968). To date this remains the only specimen referred to this taxon.

Apodidae (swiftlets). Worthy et al. (2007) also reported a single ulna of a species of the swiftlet genus *Collocalia*, and this specimen also remains unique. This genus is known from at least two species from deposits at Riversleigh World Heritage Area, northwest Queensland (Boles 2001). However, ulnae of the Australian fossil taxa are not yet known, so direct comparisons with the St Bathans fossil are currently not possible.

Psittaciformes: Strigopoidea, Nestoridae (New Zealand parrots). Worthy et al. (2007) reported unidentified parrots in the St Bathans Fauna, but with the recovery of more specimens including near complete elements, especially of tarsometatarsi, three species were described and another larger one was noted based on more fragmentary material (Worthy et al. 2011c). These taxa were placed in *Nelepsittacus* in Nestorinae, now Nestoridae (Joseph et al. 2012) and ranged in size from that of a *Cyanoramphus* species to one (unnamed) as large as the extant Kea (*Nestor notabilis*). To date no evidence for an ancestral Kakapo (*Strigops habroptilus*) has been found, although the referral of these specimens to Nestoridae suggests that Strigopidae was likely to be present in New Zealand then.

Passeriformes (songbirds). To date the passeriform fossils from St Bathans have received little attention. Worthy et al. (2007) reported the presence of a cracticid about the size of an Australian Magpie *Cracticus tibicen* based on a scapula and a further 10 bones representing birds the size of Saddleback or Tui. Since then a species of acanthisittid similar in size to the Rifleman (*Acanthisitta chloris*) was described and named *Kuiornis indicator* Worthy TH, Hand, Nguyen, Tennyson, Worthy JP, Scofield, Boles, and Archer, 2010 based on four bones (Worthy et al. 2010a). The accompanying phylogenetic analysis suggested that *Kuiornis indicator* was the sister taxon to *Acanthisitta chloris* and together were the most deeply nested taxa in the family. Continued collection of fossil sediments and subsequent sorting has seen the sample of passerine fossils expand considerably and now several taxa await description (THW unpubl. data).

Pliocene

In the 1980s, a new avian marine fossil fauna from the Pliocene of the southern North Island came to the attention of science. Ron Scarlett, osteologist at Canterbury Museum, Christchurch, New Zealand, published on a partial skeleton of a penguin from the Te Reinga Falls near Wairoa on the North Island's east coast that he named *Tereingaornis moisleyi* Scarlett, 1983. Subsequently, the private collector Joseph McKee published on several bones that he referred to the same taxa from concretions found near Hawera on the southern coast of Taranaki (Figure 1). The fossiliferous concretions of the southern Taranaki coast are primarily from the mid-Pliocene (c. 3.4–3.0 Ma) Tangahoe Formation (Naish et al. 2005). McKee had previously published on his findings of a small, unnamed, bony-toothed bird (Pelagornithidae) from the same locality (McKee 1985). Throughout the late 1980s and 1990s, McKee published references to further pelagornithid, procellariid and penguin material collected from the southern Taranaki coast and the Hawkes Bay (i.e. McKee 1987, 1989, 1999), but none of this material has been formally described, nor placed in a public repository.

In 2010, the cranium of a shearwater (*Puffinus*) similar in size to the extant tropical *Puffinus pacificus*, was described from a third mid-Pliocene marine site in the hills behind Taihape (Henderson & Gill 2010). Following on from McKee's unsubstantiated reports, a generation of amateur collectors including Dave Allen and Alastair Johnson have been collecting from these sites, with bones of *Diomedea* and *Thalassarche* albatrosses, *Procellaria* and *Macronectes* petrels, at least two species of penguins, and pelagornithids being collected (Allen & Scofield 2014). Work is currently underway to describe this fauna, but early indications are that it is unusual in having both tropical and sub-Antarctic elements and taxa that are very similar (or indeed identical, i.e. *Procellaria*) to extant taxa and others that represent extinctions at the family level (i.e. Pelagornithidae).

Quaternary

The 1 Ma Marton fauna was reported in 1997 with the description of *Pleistorallus flemingi* Worthy, 1997 and associated fossils by Worthy (1997). However, while it contains moa found in the late Pleistocene, including *Anomalopteryx didiformis* and *Dinornis* sp., other taxa, such as an undescribed duck and an undescribed kiwi (Worthy 1997; Holdaway et al. 2001; Worthy & Holdaway 2002, p. 8), indicate that this fauna deserves much more attention. Minimally, these taxa attest to considerable faunal turnover in the last one million years.

Extinct late Pleistocene–Holocene taxa: DNA and morphology

Although very well known, the late Pleistocene–Holocene fossil avifaunas are still attracting attention. There has been a strong trend towards multidisciplinary studies combining morphological and molecular analyses and these have revealed a string of major insights into some of the extinct birds of New Zealand.

Dinornithiformes (moa). Multiple research labs in Australia and New Zealand continue to investigate various aspects of moa biology using DNA. Here we do not consider the many studies on diet and other aspects of biology, rather we restrict ourselves to those studies that have been most significant for understanding relationships within moa and between them and other palaeognathous birds. The first that affected the treatment given by the 2010 Checklist was that of Bunce et al. (2009) that erected the family Megalapterygidae for *Megalapteryx didinus*, and showed that only one species of *Euryapteryx*, *Euryapteryx curtus* (Owen, 1846), could be maintained. Shortly after this, Phillips et al. (2010) showed that tinamous made ratites paraphyletic and that therefore flightlessness had evolved multiple times in the group. More recently, the paper by Mitchell et al.

(2014a) on phylogenetic relationships of ratites discovered a kiwi–elephant bird clade (originating at 50 Ma) and confirmed the moa–tinamou clade, first proposed by Phillips et al. (2010), with a divergence date of c. 58 Ma, so attesting to multiple parallel occurrences of loss of flight in ratite history.

Most recently, Yonezawa et al. (2016) recovered considerable nuclear data for *Aepyornis maximus* Geoffroy Saint-Hilaire, 1851 and *Mullerornis* sp. and near complete mitochondrial genomes (15 381 base pairs), and with this analysed the phylogenetic relationships of palaeognaths with a supermatrix approach. Although with slightly older ages, these authors confirmed the kiwi–elephant bird clade (mean c. 62 Ma) and the moa–tinamou clade (mean c. 63 Ma). Of immediate interest here, is the observation that Yonezawa et al. (2016) included five moa and found a novel relationship with *Dinornis giganteus* (GenBank Accession no. AY016013, which derives from the specimen Museum of New Zealand MNZ S34094, from Hodge Creek, in South Island, so is therefore *Dinornis robustus* Owen, 1846 in current nomenclature) and *Megalapteryx didinus* being recovered as sister taxa with a divergence age of 9.38 Ma. This is the only difference in moa relationships found by Yonezawa et al. (2016) compared with the earlier analyses of Bunce et al. (2009) and Mitchell et al. (2014a). However, unexplored effects of data disparity may be driving this pairing, as *Dinornis* was represented by a mitochondrial genome but no nuclear data, whereas *Megalapteryx didinus*, although with fewer base pairs of data, was represented by several nuclear genes. This clade was the sister group to the emeid trio of *Anomalopteryx didiformis* + (*Emeus crassus* + *Pachyornis australis*) with a divergence age between them of 12.69 Ma. Among the emeids, the split between *Emeus crassus* (Owen, 1846) and *Pachyornis australis* Oliver, 1949 was 6.1 Ma and between these and *Anomalopteryx didiformis* 6.67 Ma. These dates are somewhat older than those favoured by Bunce et al. (2009) and Mitchell et al. (2014a) (basal moa split at 5.27 and 7.7 Ma, respectively). If this trend towards older divergences within moa more correctly reflects evolution within the group, then the major splits all occurred before the Pliocene. The initial diversification at 12.69 Ma is concordant with, and may have been driven by, the marked (c. 7°C) temperature drop of the middle Miocene transition (Flower & Kennett 1994; Shevenell et al. 2004). The thick sequences of well-rounded fluvial gravels deposited by major braided river systems that comprise the Dunstan Formation attest to the presence of a range of considerable size in the headwaters of palaeo-lake Manuherikia in the late early Miocene (Douglas 1986). Already existing as high land, these ranges were further developed in the early Miocene by folding and faulting associated with the inception of the Alpine Fault about 23 Ma (Douglas 1986; Youngson & Craw 1996). The 7°C temperature drop reflecting global cooling during the middle Miocene transition would have been associated with major changes in the altitudinal zonation of floral communities, e.g. the tree line would be lowered by about 700 m, and so this middle Miocene transition will have been associated with major habitat diversification. The later diversification events in moa were perhaps driven by the intensification of the Kaikoura Orogeny in the late Miocene and establishment of rain shadow zones and greater diversification of floral communities including subalpine habitats. The earlier diversification for moa proposed by Yonezawa et al. (2016) better fits the fossil record than late diversification scenarios (Bunce et al. 2009; Mitchell et al. 2014a) given the observation that there were two large and flightless moa taxa present in the early Miocene and probably two modern species were present in the 1 Ma Marton fauna.

Other extinct birds. A series of papers have investigated extinct taxa from the Chatham Islands that have long been considered distinct (e.g. Millener 1999; Holdaway et al. 2001), albeit often undescribed. The Chatham Islands Kaka (*Nestor chathamensis* Wood, Mitchell, Scofield, and Tennyson, 2014) was described by Wood et al. (2014), the Chatham Islands Merganser (*Mergus milleneri* Williams and Tennyson, 2014) by Williams et al. (2014), and a petrel *Pterodroma imberi* Tennyson, Cooper, and Shepherd, 2015. In the latter case, DNA was extracted through the novel approach of soaking DNA from the bones (Tennyson et al. 2015).

A series of investigations of already known taxa has led to revisions of their affinities. The Chatham Island Duck *Pachyanas chathamica* Oliver, 1955 has been shown to be a teal, and the species was transferred to *Anas* by Mitchell et al. (2014b). Skeletal analyses of this taxon have shown that it was flightless and that it had pronounced carpal knobs in males indicating long-term pair bonds and vigorous defence of territories (Williams 2015a, 2015b).

Some extinct Holocene taxa from the North and South islands have also received attention. A combined DNA and morphological analysis has shown that the aberrant flightless acanthisittid wrens in *Pachyplichas* are the sister taxon of Rock Wren *Xenicus gilviventris*, and as a consequence, the genus was synonomised with *Xenicus* by Mitchell et al. (2016). Similarly, the well-known Laughing Owl *Sceloglaux albifacies* (G.R. Gray, 1844) was shown to be an aberrant terrestrially adapted member of *Ninox* by Wood et al. (2016). Recently, mitochondrial genome sequences were assembled for the extinct New Zealand crows and analysed with data from a wide range of other *Corvus* species (Scofield et al. 2017). This paper concluded that the New Zealand taxa diverged from the Australian clade in the early Pleistocene about 1.73 Ma (1.14–2.41 Ma 95% highest posterior density) and the Chatham and New Zealand populations barely differed, both genetically and morphologically, prompting these authors to subsume *Corvus antipodum* (Forbes, 1893) as a subspecies of *Corvus moriorum* Forbes, 1892, so recognising only one species in New Zealand. Lastly, the distinctiveness of *Puffinus spelaeus* Holdaway and Worthy, 1994 was verified by analysis of the mitochondrial DNA cytochrome *b* locus from several specimens from the type locality (Tennyson & Shepherd 2017). The sister taxon of Scarlett's Shearwater was determined to be Fluttering Shearwater *Puffinus gavia*, with their divergence estimated to be about 630,000 years ago. However, the type locality of *Puffinus spelaeus* is at the southern end of the range of this taxon, and potential variation in successively more northern extinct colonies at the Heaphy River Mouth and near Paturau remain to be investigated.

Fine-tuning knowledge of relationships within the extant avifauna

A series of studies in the last few years has resulted in a refined understanding of several extant birds from New Zealand. Those that impact on nomenclature and determination of modern biodiversity are listed briefly here so that the modern context for the fossil diversity can be appreciated.

Following a series of papers showing that Little Penguins in Otago were genetically dissimilar to those in the rest of New Zealand and perhaps the same as those in Australia, the Australian Little Penguin was elevated to species status by Grosser et al. (2015) with the Otago birds recognised as an extralimital population, so that two species of *Eudyptula* are now recognised in New Zealand. The New Zealand Grey-faced Petrel, long considered a subspecies of Great-winged Petrel (*Pterodroma macroptera*), was recognised in a study based also on molecular and morphological data (Wood et al. 2017) to be a distinct species, *Pterodroma gouldi*, that is more closely related to the White-headed Petrel (*Pterodroma lessonii*), thereby adding an endemic species to the New Zealand list. The New Zealand Storm Petrel has been returned from the oblivion of extinction since 2003 (Saville et al. 2003; Stephenson et al. 2008) and the species placed in *Fregetta* as *Fregetta maoriana*, see Robertson et al. (2011), so losing an endemic genus from the New Zealand list.

Cormorants have attracted a considerable amount of attention. Following global acceptance of its distinctiveness, the Little Cormorant (Little Pied Shag in New Zealand parlance) is now listed as *Microcarbo melanoleucos*, so adding a genus to the New Zealand list. A series of papers looking at the relationships of *Leucocarbo* shags in southern New Zealand culminated in the Foveaux Shag (*Leucocarbo stewarti*) being raised to a full species, distinct from the Otago Shag (*Leucocarbo chalconotus*), see Rawlence et al. (2016), and references therein. Related research continues on other members of the New Zealand *Leucocarbo* and *Stictocarbo* radiations, assessing the distinctiveness of fossils and extant populations in the North Island.

Haast's Eagle, retained in *Aquila* while the taxonomy and nomenclature of booted eagles was resolved, now must be transferred to *Hieraaetus* as a giant member of the Little and Booted Eagle clade (Bunce et al. 2005; Lerner et al. 2017). Following Dickinson and Remsen (2013), the genus *Gallirallus* is restricted to Weka (*Gallirallus australis*) of New Zealand, and the New Caledonian Rail (*Gallirallus lafresnayanus*) and the Buff-banded Rail (*Gallirallus philippensis*) are placed in *Hypotaenidia* with the bar-winged rails. We retain *Cabalus*, *Diaphorapteryx* and *Capellirallus* as monotypic genera for these extinct long-billed species, as the hypothesis of relationships shown in Garcia-R et al. (2014) appear preliminary and the sequenced genes are contradictory. *Gallinula hodgenorum* (Scarlett, 1955) is transferred to *Tribonyx*, following the re-recognition of this genus (Dickinson & Remsen 2013; Sangster et al. 2015).

Ongoing research on the phylogenetic relationships of passerines has meant several significant changes for New Zealand taxa. The piopios (*Turnagra* spp.) have been shown to be orioles and have therefore been transferred to Oriolidae (Johansson et al. 2011; Zuccon and Ericson 2012). The three species of *Mohoua* have been identified as a distinct New Zealand family Mohouidae (Jønsson et al. 2011; Zuccon & Ericson 2012; Aidala et al. 2013; Aggerbeck et al. 2014; Gibb et al. 2015) that Aggerbeck et al. (2014) and Jønsson et al. (2016) found strong support for being the sister taxon of remaining Corvida.

Discussion

Vicariance versus dispersal

An understanding of the taxonomic composition of the St Bathans Fauna, conservatively dated at 19–16 Ma, but probably from the older part of this range, is crucial to the debate on the origin of the New Zealand avifauna. The St Bathans Fauna has provided important information relevant to assessing what faunal components might be of vicariant origin. In addition, it has helped constrain the timing of colonisation of New Zealand via overwater dispersal and extinction events that subsequently modified the original fauna. It includes all of the iconic New Zealand endemic taxa long assumed to be either of vicariant or ancient dispersal origin, such as the leiopelmatid frogs, sphenodontid reptiles, and among birds the dinornithiforms, apterygiforms and acanthisittids (e.g. Fleming 1979; Gibbs 2006), conclusively showing that no such taxa dispersed to New Zealand in (minimally) the last 16 Ma. Furthermore, it is notable that the entire avifauna had high endemicity at all taxon levels. For example, described taxa include no species and only three genera (*Palaelodus*, *Pelecanoides*, *Collocalia*) shared with Australia, and waterfowl, well known from thousands of specimens, are all of species endemic at the genus level. In addition, several genera are speciose, e.g. *Manuherikia* and *Nelepsittacus*. These observations have relevance to the Oligocene drowning debate.

Oligocene drowning debate

The degree to which Zealandia was submerged during the Oligocene marine highstand has fundamental implications for the origins of the present New Zealand terrestrial fauna. If it had been wholly drowned, then all modern taxa had to arrive by over-water dispersal across the same width of oceans as now exists about New Zealand. The hypothesis that Zealandia was entirely submerged during the late Oligocene–earliest Miocene (25–22 Ma) marine highstand was based on three lines of evidence: (1) a widespread erosion surface, associated with (2) the presence of widespread Oligocene limestone, and (3) the absence of terrestrial fossil deposits of late Oligocene age (Waters & Craw 2006; Campbell & Hutching 2007; Trewick et al. 2007; Landis et al. 2008; Wallis & Trewick 2009). This hypothesis has been hotly debated (e.g. Knapp et al. 2007; Lee et al. 2007; Goldberg et al. 2008; Boyer & Giribet 2009; Giribet & Boyer 2010; Worthy et al. 2010a), but the opinion that some part of Zealandia that went on to become New Zealand remained emergent during the late Oligocene highstand now has strong support from geological evidence (e.g. Kamp et al. 2014; Mortimer & Strong 2014; Strogen et al. 2014).

Biotic evidence, including both floristic (e.g. Knapp et al. 2007; Lee et al. 2007 (but see Biffen et al. 2010); Lee et al. 2012, 2014; Conran et al. 2013, 2014; Sun et al. 2014) and faunistic data, including invertebrates notably from freshwater (e.g. Graf & Ó Foighil 2000; Apte et al. 2007; Toon et al. 2010; Marshall 2011; Krosch & Cranston 2013) and from soil or litter habitats (e.g. Boyer & Giribet 2007, 2009; Pratt et al. 2008; Wesenera & Vanden Spiegel 2009; Allwood et al. 2010; Buckley et al. 2011) also supports the survival of a terrestrial and freshwater biota through the marine highstand. Soil or litter-dwelling invertebrates have the greatest power to reveal a long geological history of continuous terrestrial environments, because they require relatively small areas of habitat compared with vertebrates. Such habitats are more likely to be found on the relatively small islands persisting during the marine highstand. Nevertheless, several extant vertebrate lineages such as leiopelmatid frogs, wherein the divergence of the two extant clades (using *Leiopelma archeyi* and *Leiopelma hochstetteri*) dates to about 50 and 40 Ma (Roelants et al. 2007) or > 65 Ma (Carr et al. 2015), tuatara, acanthisittid wrens, ratites and flightless terrestrial fossil mammals other than bats indicate that vertebrates also survived the highstand (Worthy et al. 2006, 2013a; Jones et al. 2009; Mitchell et al. 2014a, 2016).

Although it is now beyond debate that some land was present during the marine highstand towards the end of the Oligocene, land area was clearly markedly reduced and this would have limited the diversity of animals surviving in terrestrial environments. As just reviewed above, it is therefore likely to be no coincidence that most evidence for lineages predating the highstand come from invertebrates that require small areas of habitat such as soil and litter dwellers. Larger vertebrate taxa, require much larger areas of habitat and so this period would have been a major evolutionary bottleneck for terrestrial vertebrates (Cooper & Cooper 1995), through which predictably few lineages would have passed. There is, however, some evidence for vertebrate lineages passing through this bottleneck.

Several avian lineages represented in the St Bathans Fauna are endemic to New Zealand and deeply divergent from their closest extant relatives. Foremost of these are the palaeognaths moa (Dinornithiformes) and kiwi (Apterygiformes). These have long been assumed to have a vicariant origin (Hutton 1873; Cracraft 1974a, 1974b; Fleming 1979; Gibbs 2006) but molecular evidence now strongly supports that volant ancestors of both dispersed to New Zealand in the late Paleocene or Eocene (Phillips et al. 2010; Mitchell et al. 2014a). Mitchell et al. (2014a) estimated that moa diverged from tinamous about 58 Ma, and kiwi from elephant birds about 50 Ma, although the crown group radiations of both were considerably more recent, about 8 Ma for moa, and 8.6 Ma for kiwi (see Figure 2). In this context, the presence of both lineages in the St Bathans Fauna 19–16 Ma, and with moa being large and flightless already, strongly suggests that these lineages have had a long history in New Zealand, possibly dating to their separation from tinamous and elephant bird lineages, respectively.

The second group of birds relevant to the Oligocene drowning issue is the acanthisittid wrens (Figure 2), which are important as the sister group of all other passeriforms (Selvatti et al. 2015). A recent and comprehensive molecular analysis of this group showed that at least two lineages of this group (*Dendroscansor* was not analysed) survived the Oligocene marine highstand with the basal split of Lyall's Wren (*Traversia lyalli*) from remaining acanthisittids dating to the early Oligocene (Mitchell et al. 2016). The St Bathans Fauna includes *Kuiornis indicator*, a tiny acanthisittid, which was recovered as the sister taxon to *Acanthisitta* by Worthy et al. (2010a) and Mitchell et al. (2016), and is fossil evidence for one of these two modern lineages.

Mitchell et al. (2016) also included several psittaciforms in their analyses of acanthisittids and this revealed that Kea (*Nestor notabilis*) and Kakapo (*Strigops habroptilus*) also diverged in the earliest Oligocene, showing that the two main lineages of Strigopoidea also both survived the marine highstand. To date the St Bathans Fauna has only revealed evidence for Nestoridae, with three species of *Nelepsittacus* described (Worthy et al. 2011c).

In summary, both the fossil evidence and the molecular data are in agreement that a diverse component of the New Zealand avifauna and other vertebrates survived the marine highstand on proto-New Zealand. The alternative, required by the complete drowning hypothesis, is that a large number of lineages, including all the iconic endemic taxa, dispersed to New Zealand in the short geological interval after the marine highstand, perhaps a period as short as 3 Ma, and that none of these iconic taxa arrived thereafter. Moreover, for this unparsimonious hypothesis to be tenable, each of the ancestors of these endemic lineages had to become extinct in their source regions leaving no trace of a former presence.

Miocene dispersal to and colonisation of New Zealand

Among other vertebrates it is long known that squamate lizards must have dispersed to New Zealand. The radiation of diplodactylid geckoes in New Zealand is thought to predate the Oligocene highstand and reflect a single colonisation event (Nielsen et al. 2011). Similarly, that of skinks is now also considered to be the result of a single colonisation, but after the highstand in the early Miocene (Chapple et al. 2009).

Birds can fly, so intuitively, one would expect over-water dispersals resulting in colonisations to be more numerous. They are, but not greatly so, and only pigeons in the St Bathans Fauna are necessarily present following colonisation in the early Miocene, although it is likely some as yet undescribed passerines may fit in this category.

The St Bathans Fauna includes two species of pigeons, one of which is *Rupephaps taketake*, a fruit pigeon considered to be more similar to the New Zealand Pigeon (*Hemiphaga novaeseelandiae*) than to the Topknot Pigeon (*Lopholaimus antarcticus*) within the fruit pigeons (Worthy et al. 2009). The extant New Zealand *Hemiphaga* lineage is the sister group of the Australasian *Lopholaimus–Gymnophaps* clade, and their divergence was estimated at about 24 Ma (Pereira et al. 2007). A recent analysis of complete mitochondrial genomes suggests a much more recent diversification of columbiforms with the divergence of *Hemiphaga* and *Otidiphaps* estimated at about 20 Ma (Soares et al. 2016). The same split in Pereira et al. (2007) was dated about 46 Ma, which would necessarily make the *Hemiphaga–Lopholaimus* node about 15 Ma. Unfortunately, Soares et al. (2016) overlooked relevant fossils (Worthy et al. 2009; Worthy 2012), claiming that no fossils were known. Instead, they used the divergence between Columbiformes and Pterocliformes of 55 ± 15 Ma, a number apparently derived from Prum et al. (2015), as Jarvis et al. (2014), whom Soares et al. (2016) also attributed this date to, actually had a date of c. 65 Ma for this split. We assume that use of 65 Ma as found by Jarvis et al. would have resulted in the origin of crown columbiforms being some 10 Ma older, at about 35 Ma. This would better fit the columbid fossil record, as the 26–24 Ma phabine pigeon *Primophaps schoddei* Worthy, 2012 from Australia, overlooked by Soares et al. (2016), reveals that both fruit pigeons and phabines must have diverged earlier than this time (Worthy 2012). Similarly, the presence of *Rupephaps* in the St Bathans Fauna (Worthy et al. 2009) suggests that the *Hemiphaga–Otidiphaps* divergence has to be older than 20 Ma to accommodate the divergences among fruit pigeons and related taxa that precede the *Hemiphaga–Lopholaimus* split (Pereira et al. 2007). Nevertheless, the *Hemiphaga* lineage is probably the result of an early Miocene colonisation of Zealandia.

The majority of the St Bathans fossil passerines have yet to be analysed as to their identity and relationships. However, some predictions as to likely contenders can be made as a result of molecular analyses. These show that all the families of passerines endemic to New Zealand other than Acanthisittidae appear to minimally have an early Miocene divergence from Australian taxa, indicating a more recent colonisation. The callaeids (*Callaeas*, *Philesturnus* and *Heteralocha*) diverged from most Core Passerides about 23 Ma, *Mohoua* and *Turnagra*—the latter is the sister group to orioles (Johansson et al. 2011; Zuccon and Ericson 2012)—diverged from Australian Corvides about 20–18 Ma (Johansson et al. 2011; Moyle et al. 2016), although somewhat older estimates (40–30 Ma) were generated by Aggerbeck et al. (2014) and Gibb et al. (2015). Stitchbirds (Notiomystidae) are sister

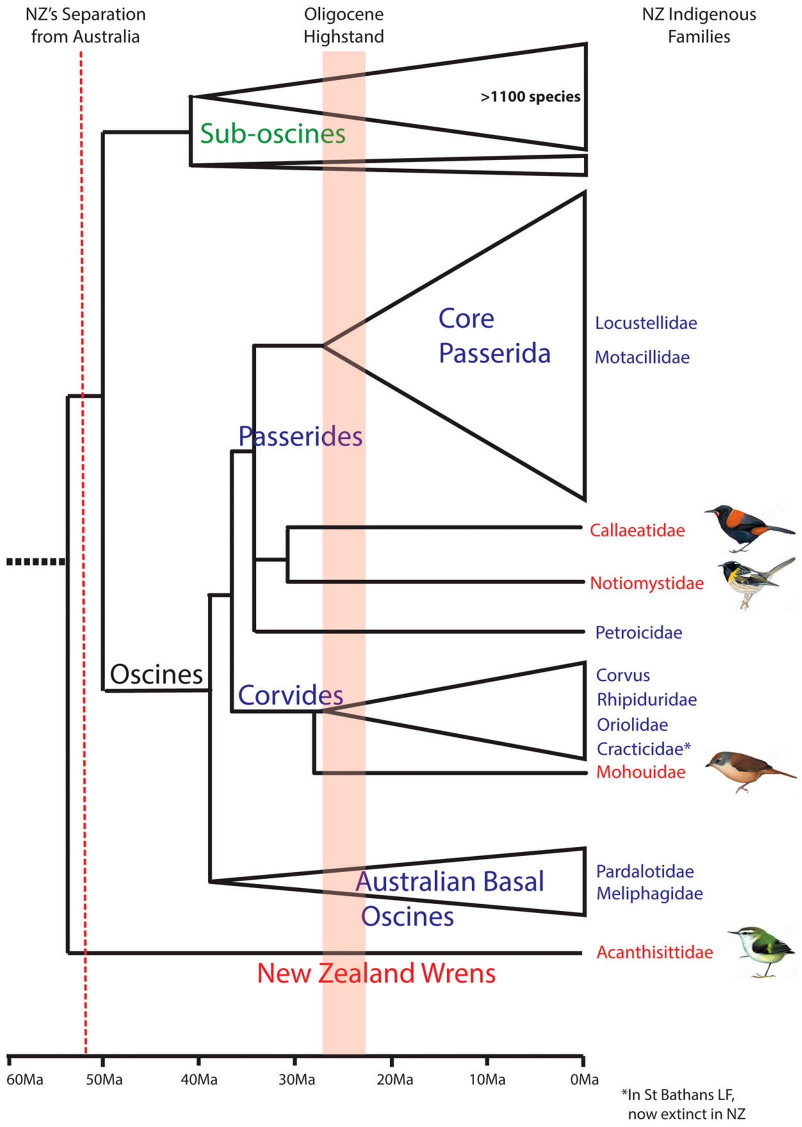

Figure 3. An indicative phylogeny showing the major clades of Passerine songbirds and the indigenous families of Passerine songbirds known from the fossil and extant records of New Zealand within the constraints of the avian relationships found by Selvatti et al. (2015) and Moyle et al. (2016), with uncertain relationships left unresolved. The nodes are calibrated using the ages found by Moyle et al. (2016) with reference to Prum et al. (2015). The Oligocene marine highstand and the latest date of New Zealand's separation from Australia are shown relative to the clades. Taxa in red font are endemic to New Zealand. Images from de Hoyo et al. (2003) are used with permission.

group to callaeids (Driskell et al. 2007; Gibb et al. 2015), so are similarly old. These data suggest that all these lineages might be found among the St Bathans passerines when this group is analysed (Figure 3).

The New Zealand avifauna after the early Miocene

The St Bathans Fauna has multiple elements indicating a warmer climate than today. These included crocodilians, terrestrial tortoises and swiftlets. The associated flora had many subtropical taxa, e.g. cycads, eucalypts, diverse Proteaceae, Casuarinaceae, Arecaceae palms, minimally 22 taxa of Lauraceae, in addition to a diverse range of podocarps and *Nothofagus* taxa (e.g. Mildenhall 1989; Mildenhall & Pocknall 1989; Pole 1993, 1997, 1998, 2007a, 2007b; Pole et al. 2003). The flora has been interpreted to reflect a warm-temperate to marginally subtropical climate with mean annual temperatures of 16.5°C–20°C and high (1500–2500 mm) annual precipitation (Reichgelt et al. 2015), and it maintained the high diversity seen in earlier late Oligocene–early Miocene sites (Lee et al. 2012).

Sometime between the deposition of the St Bathans Fauna and the late Quaternary, New Zealand lost its subtropical animals (crocodilians, terrestrial tortoises, swiftlets, palaelodids) and also probably lost considerable diversity within some groups such as columbids and psittaciforms. In the same interval, it lost most of the warmth loving plants such as the Arecaceae, Casuarinaceae, all eucalypts, and most of the Proteaceae and Lauraceae (Lee et al. 2012). This loss of floral diversity, e.g. considering the loss of some 20 species of laurels alone, leaving just three tree species (*Litsea calicaris*, *Beilschmiedia tawa*, *Beilschmiedia tarairi*) in the flora, had an obvious impact on the potential feeding niches of fruit-eating birds, such as pigeons.

The reason for this loss of warmth-loving biota probably lies in the marked climatic cooling during the period 14.2 to 13.8 Ma following the Middle Miocene Optimum, which may have seen mean annual temperatures as much as 7°C cooler (Flower & Kennett 1994; Shevenell et al. 2004). The emergent parts of New Zealand have remained essentially where they now are for the last 25 Ma at least and were at 44°S–49°S during the early Miocene (Reichgelt et al. 2015). This temperature decline was related to enhanced glaciation on Antarctica and not to any latitudinal displacement of New Zealand. The floral and faunal effects of the middle Miocene temperature drop were further exacerbated by the Pleistocene glacial–interglacial oscillations that culminated in a further c. 6°C drop in the last glacial period, which saw most of New Zealand at latitudes greater than 38°S bereft of forest cover (e.g. Newnham et al. 2013).

Although this general climatic deterioration resulted in reduced floral diversity and loss of several major clades of warmth-loving animals, the associated biotic perturbations created new niches. And so, the stretch comprising the later Pliocene and early Pleistocene is a period where many lineages of birds made their first appearance in New Zealand. Such inference is based wholly on molecular data at present but new arrivals included the *Hieraaetus* eagles that became Haast's Eagle, swamphens than gave rise to takahe *Porphyrio hochstetteri* and *Porphyrio mantelli*, the crows *Corvus* species, and *Ninox* that became the large Laughing Owl (*Ninox albifacies*). Divergence estimates for most New Zealand waterfowl from their Australian congeners are not yet available, but the recent and rapid morphological changes associated with reduced flight ability for Finsch's Duck (*Chenonetta finschi*), see Worthy (1988, 1997), clearly suggest the recent arrival of this taxon. Undoubtedly, many of the passerines that differ little from Australian congeners will be shown to have similar recent divergence ages, e.g. species of *Petroica*, *Rhipidura* and *Gerygone*, as long inferred, e.g. by Fleming (1979).

A few taxa remain enigmatic as to their affinities or origins. *Aptornis* is foremost among these, but work in progress will shortly reveal its affinities in detail. Other groups for which the affinities of the New Zealand taxa are unclear, include the long-legged *Fulica* coots, the mergansers, the New Zealand Scaup (*Aythya novaeseelandiae*) and rails such as the species of *Capellirallus*, *Cabalus* and *Diaphorapteryx*. At deeper levels, the real affinities of the endemic Australasian anatids within Anatidae remain essentially ignored in this modern genomic world—their relationships are crucial to understanding global anatid evolution. Within this group, the divergence of cereopsine geese within Australasia and from Northern Hemisphere anserines is similarly of great interest and key to this problem. The St Bathans fossils show this event was during or before the early Miocene. Some work on avian fossils shows that this southern–northern dichotomy has ancient roots, e.g. among waders (De Pietri et al. 2016a, 2016b) and waterfowl (De Pietri et al. 2016c) and it seems likely that as austral faunas are better revealed this dichotomy will only strengthen.

Conclusion

The period of about 7 years since the 2010 New Zealand Checklist (Gill et al. 2010) was published has seen an unprecedented increase in the rate of discovery and advances in understanding of the fossil record for New Zealand birds. There has been a 50% increase in the diversity of pre-Quaternary species-level taxa described. These discoveries have not been limited to one period or fauna, but span the entire Cenozoic. Foremost of these have been taxa from the early Miocene St Bathans Fauna, but we hypothesise that this is only the tip of the iceberg. As Table 2 shows, only about half the known taxa in the St Bathans Fauna have been described and work addressing the remaining taxa is ongoing, and multiple new species are likely to be described in the next 5 years. This new fossil diversity is not restricted to the early Miocene—ongoing work will lead to the description of several new Paleogene taxa in the near future and many Pliocene taxa await description as well. Truly, this is an age of discovery for the fossil record of birds in New Zealand.

Furthermore, whereas New Zealand is well known as having one of the most completely known late Quaternary avifaunas (e.g. Worthy & Holdaway 2002), ongoing studies re-examining taxa via analyses of DNA continue to refine our understanding of those taxa (*Sceloglaux*, *Pachyanas*, *Pachyplichas*), in some cases finding hidden diversity (*Leucocarbo*), yet in others revealing over-splitting (*Corvus*). These tweaks to the diversity of the original ‘Holocene’ fauna have not greatly altered the main trends that of the 105

Table 3. Summary of key metrics of the Late Holocene New Zealand avifauna, including those now extinct, as it was known in 2010 versus at present in 2017.

	2010	2017
Indigenous species breeding in New Zealand region	214	217
Endemic genera (% of genera)	34 (32%)	27 (30.5%)
Endemic species	144	145
Endemic species as % breeding taxa	67.3%	66.8%
Extinct species	54	58
Extinct species as % breeding taxa	25.2%	24.9%

genera, 30.5% were endemic, 67% of 217 indigenous breeding species were endemic, of which 54 (25%) are extinct and 126 (58%) were land and freshwater taxa. Several Holocene taxa await description, e.g. penguins and a shelduck from the Chatham Islands, but these will not alter the main patterns shown here (Table 3).

We are now in a position to use the fossil record to address the questions raised at the outset of this review. It is clear, that at least from the early Miocene onwards, New Zealand has been a land dominated numerically by birds. We now understand that the limited diversity of the Recent fauna, is due to extinction winnowing the diversity of the early Miocene fauna. As yet, we only have a limited knowledge of the extent of the diversity lost, but minimally, several warmth-loving taxa have disappeared. That former diversity was supported by higher temperatures and far more diverse early Miocene floral communities that potentially created far greater niche variety. It is further clear that one or two lineages of modern birds, e.g. the acanthisittids, may have had a vicariant origin in New Zealand along with leiopelmatid frogs and sphenodontids, but the majority arrived by dispersal during the Paleogene and survived the marine highstand of the latest Oligocene. These likely included ancestral forms of the moa and kiwi lineages. So lastly, in answer to what was the impact of the Oligocene drowning, we do not know, as New Zealand crucially lacks terrestrial avifaunas of pre-drowning age. Multiple taxa however, passed through the event in New Zealand, including acanthisittid wrens and strigopoid parrots. Undoubtedly lineage diversification underwent some bottlenecks (Cooper & Cooper 1995), and a foremost contender for such must be the moas (Dinornithiformes), as unlike acanthisittids and strigopoids, molecular evidence only supports one lineage in the late Miocene before the diversification of the crown group.

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