


special issue:

Feathers to Fur

The ecological transformation of Aotearoa/New Zealand



The origin and history of New Zealand's terrestrial vertebrates

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Published on-line: 4 November 2009

Abstract: Since the 1980s, morphological and molecular research has resulted in significant advances in understanding the relationships and origins of the recent terrestrial vertebrate fauna in the New Zealand biogeographic region. This research has led to many taxonomic changes, with a significant increase in the number of bird and reptile species recognised. It has also resulted in the recognition of several more Holocene (<10 000 years ago) bird species extinctions. The conclusion that Holocene extinctions were primarily caused by human-hunting and predation by other introduced mammals (particularly rats and cats) has been supported by new data. Despite many local eradications of introduced pests, the number of introduced species has increased, with the establishment of five more foreign birds and (on Norfolk Island) the house gecko (*Hemidactylus frenatus*). Many new, significant New Zealand vertebrate fossils have been reported, including more dinosaurs from the Cretaceous, and the first Tertiary records of frogs, rhynchocephalids, lizards, crocodylians, bats and a terrestrial “Mesozoic ghost” mammal from the Early Miocene near St Bathans. For birds, the earliest known penguins in the world have been discovered, and there are intriguing Late Cretaceous – Early Paleocene remains still awaiting detailed description. Other significant Tertiary bird fossils reported include a rich avifauna from the Early Miocene St Bathans sites and a small terrestrial fauna from the Early Pleistocene near Marton. In line with the traditional theory, new research has supported the vicariant Gondwanan origin of some distinctive New Zealand terrestrial vertebrates, such as leiopelmatid frogs, tuatara and moa, and the immigration of many others, including New Zealand wattlebirds and piopio, during the Cenozoic. Extinctions caused by an asteroid impact and climate fluctuations probably explain the absence of many groups, such as crocodylians, dinosaurs, monotremes, palaelodids and swiftlets, from the modern fauna.

Keywords: dispersal; extinction; fossils; Gondwana; introduced species; taxonomy

Introduction

This article is an attempt to summarise recent major advances in our understanding of New Zealand's terrestrial vertebrate history. Firstly, it summarises new discoveries in the modern fauna, then explores origins and changes since the beginning of New Zealand as the continent Zealandia.

Major taxonomic changes in many modern vertebrate groups have occurred during the last 20 years and it is important to have a clear picture of this fauna in order to understand changes in the past. Without this knowledge, it is impossible to compare the living fauna with the fauna immediately before humans arrived or to examine changes much deeper in time. After summarising the modern and ancient faunas separately for amphibians, reptiles, birds and mammals, I examine the extinction event which began with the arrival of humans in the 1200s AD, then look at the debate over the origins of New Zealand's vertebrates.

One topical debate surrounds the effects on New Zealand's biota of the reduction in land area due to a major marine transgression—the so-called “Oligocene drowning”. Geological

theories have traditionally supported there being emergent land throughout the history of Zealandia (e.g. Fleming 1979: 46, 52; Pocknall 1982). However, recently this idea has been challenged, primarily on the basis of the lack of terrestrial Late Oligocene–Early Miocene rocks 25–22 million years ago (mya) and increasing evidence of dispersal of plant taxa to Zealandia (e.g. Pole 1994; Campbell & Landis 2001; Campbell & Hutching 2007; Campbell et al. 2008; Landis et al. 2008). If Zealandia had been completely immersed at this time, the entire modern flora and fauna must have arrived by dispersal in the subsequent 22 million years. Further research on the Early Miocene fauna, in combination with other biological data, suggests this is unlikely.

Methods

This article covers the history of New Zealand from when the continental fragment called Zealandia drifted away from Australis—the eastern remnant of the southern supercontinent Gondwana (see Gibbs 2006). The timing of this split has generally been thought to be about 85–80 mya in the Late

Cretaceous (e.g. Stevens 1989, 1991; Cooper & Millener 1993; Stevens et al. 1995; Cracraft 2001a; Gibbs 2006). However, this date has been challenged by new geological evidence that suggests possible on-going land links into the Early Eocene up to 52 mya (Gaina et al. 1998). While differences between these dates clearly have major biological implications, they do not confound the overall pattern of biological origins discussed here. “Gondwanan”, as defined here, means of vicariant origin, i.e. it refers to the direct ancestors of species being present in Zealandia due to rifting from the rest of Australis, rather than arriving later by dispersal.

New Zealand is defined here as a biogeographical region, including mainland New Zealand and all its inshore and offshore islands, as well as the Australian territories of Norfolk and Macquarie Islands, which have their closest terrestrial vertebrate links with the New Zealand fauna (e.g. Holdaway et al. 2001; Chapple et al. 2009). Terrestrial vertebrates dealt with here include all amphibian, reptile, bird and mammal species which breed naturally in the wild, but exclude marine reptiles and mammals. The sequence of bird orders follows Dickinson (2003) and the following orders are referred to as waterbirds: Hesperornithiformes, Anseriformes, Sphenisciformes, Procellariiformes, Podicipediformes, Phoenicopteriformes, Ciconiiformes, Pelecaniformes, Gruiformes and Charadriiformes. The taxonomic level used here for most comparisons is species. Numbers of subspecies and changes in higher taxonomic ranks, such as the placement of stitchbirds/hihi (*Notiomystis cincta*) in a new family (Driskell et al. 2007), are not discussed. “Recent advances” are those since about 1989 (when papers from the last New Zealand Ecological Society symposium on these topics were published (Rudge 1989)). Key comparisons are made with knowledge summarised by Holdaway (1989) on the impacts of humans on the Holocene fauna and with Stevens (1989) on the origins of the fauna. In addition, changes in the introduced fauna are summarised.

Advances in knowledge for each taxonomic group of animals (Amphibia, Reptilia, Aves and Mammalia) are discussed for: (1) the modern fauna, to see whether changes in numbers and interpretations have occurred; (2) the ancient fauna (prior to the relatively well-known modern fauna, i.e. pre-Late Pleistocene, before about 800 000 years ago) and its origins. Knowledge in many of these areas has expanded considerably since the 1980s, especially because of modern taxonomic tools, new fossil discoveries and molecular dating. Published molecular-based dates for the divergence of taxa may be artificially precise (e.g. Ho 2007; Pulquério & Nichols 2007; Ho et al. 2008) and the resulting biogeographical inferences made here should be treated cautiously (see Upchurch 2008).

Scientific names for taxa are only provided in the text if these are not explained in the tables and appendices.

Table 1. Geological timescale, based on Cooper (2004).

Era	Sub-era	Period	Epoch	Age (mya)
Cenozoic	Quaternary (<2.6 mya)		Holocene	<0.01
			Pleistocene	0.01-1.8
			Pliocene	1.8-5.3
	Tertiary	Neogene	Miocene	5.3-23.8
			Paleogene	
			Oligocene	23.8-33.7
	Eocene	33.7-55.5		
	Paleocene	55.5-65.0		
Mesozoic		Cretaceous		65.0-145.5

Results

Amphibians

The modern fauna

In the 1980s, six native frogs (Leiopelmatidae) were recognised, three of which were considered extinct. By 2009, seven species had been recognised, of which three were extinct (see Table 2). This change is due to the taxonomic splitting of the Maud Island frog (*Leiopelma pakeka*) from the existing Stephens Island species (*Leiopelma hamiltoni*) (see Appendix 1, although this split was questioned by Holyoake et al. (2001)), rather than the discovery of a new population. The number of introduced frog species established in the wild has remained at three during this period (see Table 2).

Table 2. Systematic list of the number of species in modern orders and genera of reptiles and amphibians recorded in New Zealand, including the Australian territory of Norfolk Island (1980s data: Meredith 1985; Gill 1986; Bauer & Russell 1988; Worthy 1987b, 2009 data: Worthy 1991; Gill & Whitaker 1996; Patterson 1997; Bell et al. 1998; Worthy & Holdaway 2002; Jewell & Leschen 2004; Cogger et al. 2006; Chapple & Patterson 2007; Smith et al. 2007; Bell & Patterson 2008; Chapple et al. 2008a, b, 2009; see Appendix 1). Given the concerns noted by Chapple & Hitchmough (2009), the taxonomy used by Jewell (2008) has not been followed here. *Christinus guentheri*, *Oligosoma lichenigera* and the newly established *Hemidactylus frenatus* are found only on Norfolk Island. The number of extinct species (in brackets) is a subset of the total to its left.

Abbreviations: no. = number; sp. = species. * = Introduced species.

Order	Genus	1980s no. sp. (no. extinct)	2009 no. sp. (no. extinct)
Anura	<i>Leiopelma</i>	6 (3)	7 (3)
	* <i>Litoria</i>	3 (0)	3 (0)
	Total	9 (3)	10 (3)
Rhynchocephalia	<i>Sphenodon</i>	1 (0)	2 (0)
	Total	1 (0)	2 (0)
Squamata	<i>Hoplodactylus</i>	9 (1)	11 (1)
	<i>Naultinus</i>	1 (0)	7 (0)
	* <i>Hemidactylus</i>	0 (0)	1 (0)
	<i>Phyllodactylus</i>	1 (0)	0 (0)
	<i>Christinus</i>	0 (0)	1 (0)
	<i>Leiolopisma</i>	16 (1)	0 (0)
	<i>Cyclodina</i>	6 (0)	0 (0)
	<i>Oligosoma</i>	0 (0)	35 (1)
	* <i>Lampropholis</i>	1 (0)	1 (0)
	Total	34 (2)	56 (2)
Overall total	44 (5)	68 (5)	

The ancient fauna

By the late 1980s, frog fossils were only known from Late Pleistocene–Holocene sites (Worthy 1987a, b), however, the Early Miocene freshwater St Bathans Fauna (within the period 19-16 mya) has now revealed the remains of three frog taxa: two leiopelmatids and a probable neobatrachian (Neobatrachia) (Worthy et al. 2009a; see Table 3). Amphibian (Stereospondyli) remains discovered in Triassic New Zealand rocks (Fordyce et al. 2003) pre-date the separation of Zealandia from Australis. Leiopelmatid frogs have long been considered to be a classic New Zealand example of vertebrates with a Gondwanan origin (e.g. Fleming 1979: 104; Robb 1980; Stevens 1980, 1989; Bell 1982; Scarlett & Molnar 1984) and new molecular (Roelants & Bossuyt 2005) and fossil (Worthy et al. 2009a) evidence supports the theory that they are “Mesozoic survivors” from Gondwana.

Table 3. Occurrence of fossil taxa in proto-New Zealand by geologic epoch and their relationship with the modern fauna. Abbreviations: O. = order; sO. = suborder; F. = family; SF. = superfamily; sF. = subfamily. Epochs: Ct = Cretaceous; Pc = Paleocene; Ec = Eocene; Og = Oligocene; Mi = Miocene; Pi = Pliocene; Ps = Pleistocene (<0.8 mya). A leading questionmark means epoch uncertain. "Closest relative" is nearest known relative in the modern native New Zealand fauna (only family level or below, otherwise *none*; if as in Taxa column then *same*). Reference numbers given at the end of this table.

Class and Order	Taxa	Epoch (time periods)		Closest relative (Reference)
Class Amphibia, O. Anura				
sO. Archaeobatrachia	? <i>Leiopelma</i> sp.		Mi	same (1)
?sO. Neobatrachia			Mi	none (1)
Class Reptilia				
O. Chelonia	? <i>Glyptops</i> sp.	Ct		none (2, 3)
O. Rhynchocephalia	? <i>Sphenodon</i>		Mi	same (1, 4)
O. Squamata	? <i>Hoplodactylus</i> sp.		Mi	same (1, 5)
	? <i>Oligosoma</i> sp.		Mi	same (1, 5)
O. Crocodylia			Mi	none (1, 6, 7)
O. Pterosauria	?F. Anhangueridae	Ct		none (8, 9, 10)
O. Saurischia				
sO. Sauropodomorpha	?sF. Titanosauroidea	Ct		none (9, 11)
sO. Theropoda		Ct		none (9, 12, 13, 14)
O. Ornithischia				
sO. Ankylosauria	?F. Nodosauridae	Ct		none (9)
sO. Ornithopoda	?F. Dryosauridae	Ct		none (9, 15, 16)
Class Aves				
O. ?Hesperornithiformes		Ct		none (17)
O. Dinornithiformes			Mi	O. Dinornithiformes (18)
	<i>Anomalopteryx didiformis</i>		?Pi Ps	same (19, 20)
	<i>Euryapteryx curtus</i>		Pi Ps	same (19, 21)
	<i>Dinornis novaezealandiae</i>		?Pi Ps	same (19)
O. Apterygiformes			Ps	<i>Apteryx</i> spp. (22)
O. Anseriformes	sF. Anserinae		Mi	same (23)
	<i>Cnemiornis gracilis</i>		Ps	same (19)
	<i>Manuherikia lacustrina</i>		Mi	sF. Oxyurinae (18, 24)
	<i>Manuherikia minuta</i>		Mi	sF. Oxyurinae (18, 24)
	<i>Manuherikia douglasi</i>		Mi	sF. Oxyurinae (23, 24)
	<i>Dunstanetta johnstoneorum</i>		Mi	sF. Oxyurinae (18, 24)
	<i>Miotadorna sanctibathansi</i>		Mi	sF. Tadorninae (18, 24)
	<i>Matanas enrighti</i>		Mi	? <i>Chenonetta finschi</i> (18)
O. Sphenisciformes	<i>Waimanu manneringi</i>	Pc		F. Spheniscidae (25)
	<i>Waimanu tuatahi</i>	Pc		F. Spheniscidae (25)
	<i>Palaeudyptes antarcticus</i>		?Ec?Og?Mi	F. Spheniscidae (26)
	<i>Palaeudyptes marplei</i>		?Ec?Og?Mi	F. Spheniscidae (26)
	<i>Pachydyptes ponderosus</i>		Ec	F. Spheniscidae (26)
	<i>Platydyptes novaezealandiae</i>		Og ?Mi	F. Spheniscidae (26)
	<i>Platydyptes amiesi</i>		Og ?Mi	F. Spheniscidae (26)
	<i>Platydyptes marplei</i>		Og ?Mi	F. Spheniscidae (26)
	<i>Archaeospheniscus lowei</i>		Og	F. Spheniscidae (26)
	<i>Archaeospheniscus lopdelli</i>		Og	F. Spheniscidae (26)
	<i>Duntroonornis parvus</i>		Og	F. Spheniscidae (26)
	<i>Korora oliveri</i>		Mi	F. Spheniscidae (26)
	<i>Marplesornis novaezealandiae</i>		?Mi ?Pi	F. Spheniscidae (26)
	<i>Tereingaornis moisleyi</i>		Pi	F. Spheniscidae (26)
	<i>Aptenodytes ridgeni</i>		?Mi ?Pi	<i>Aptenodytes</i> spp. (26)
	<i>Megadyptes antipodes</i>		?Ps	<i>Megadyptes</i> spp. (27)
	<i>Pygoscelis tyreei</i>		?Mi ?Pi	<i>Pygoscelis</i> spp. (26)
	<i>Eudyptula minor</i>		?Pi ?Ps	same (28)
O. Procellariiformes	<i>Puffinus</i> sp.		Pi	same (29)
	<i>Pelecanoides miokuaka</i>		Mi	<i>Pelecanoides</i> spp. (18, 30)
O. Phoenicopteriformes	<i>Palaelodus</i> sp.		Mi	none (1)
O. Ciconiiformes	F. Ardeidae		Mi	same (1)
O. Pelecaniformes	<i>Pelagornis miocaenus</i>		Mi	none (26)
	<i>Neodontornis stirtoni</i>		?Mi ?Pi	none (26, 31)
O. Accipitriformes	F. Accipitridae		Mi	same (1, 18)
O. Gruiformes	?F. Aptornithidae		Mi	same (18)
	F. Rallidae		Mi	same (18)
	<i>Pleistorallus flemingi</i>			F. Rallidae (20)
	? <i>Gallirallus</i> sp.			? <i>Gallirallus</i> spp. (20)
O. Charadriiformes	?F. Charadriidae		Mi	same (18)
	?F. Scolopacidae		Mi	same (18)
	?F. Laridae		Mi	same (18)
O. Columbiformes	<i>Rupephaps taketake</i>		Mi	<i>Hemiphaga</i> spp. (1, 18, 32)
O. Psittaciformes	F. Psittacidae		Mi	same (18)
O. Aegotheliformes	<i>Aegotheles</i> sp.		Mi	<i>A. novaezealandiae</i> (18)

Table 3 continued

Class and Order	Taxa	Epoch (time periods)	Closest relative (Reference)
O. Passeriformes	<i>Collocalia</i> sp.	Mi	none (18)
	F. Acanthisittidae	Mi	<i>Acanthisitta chloris</i> (1, 33)
	F. Cracticidae	Mi	none (18)
Class Mammalia			
O. Chiroptera	SF. Noctilionoidea, F. Mystacinidae	Mi	same (7)
	SF. ?Noctilionoidea (not F. Mystacinidae)	Mi	none (1)
	SF. Vespertilionoidea, F. Vespertilionidae	Mi	F. Vespertilionidae (7)
?O. "Mesozoic ghost"		Mi	none (1, 34)

References: 1, Worthy et al. 2009a. 2, McKee & Wiffen 1989. 3, Wiffen 1996. 4, Jones et al. 2009. 5, Lee et al. in press. 6, Molnar & Pole 1997. 7, Worthy et al. 2006a. 8, Wiffen & Molnar 1988. 9, Molnar & Wiffen 1994. 10, Jones 2005. 11, Molnar & Wiffen 2007. 12, Molnar 1981. 13, Scarlett & Molnar 1984. 14, Stilwell et al. 2006. 15, Wiffen & Molnar 1989. 16, Long 1998. 17, Fordyce 1991: 1233. 18, Worthy et al. 2007. 19, Worthy et al. 1991. 20, Worthy 1997. 21, Tennyson & Martinson 2007. 22, Worthy & Holdaway 2002. 23, Worthy et al. 2008. 24, Worthy & Lee 2008. 25, Slack et al. 2006. 26, Checklist Committee 1990. 27, Fleming 1979: 75. 28, Simpson 1975. 29, McKee 1994. 30, Scofield et al. 2006. 31, Matsuoka et al. 2003. 32, Worthy et al. 2009b. 33, Worthy et al. in press. 34, Worthy et al. 2006b.

Reptiles

The modern fauna

In the 1980s, 34 native reptiles were recognised, two of which were considered extinct; by 2009, 56 species had been recognised, of which two were extinct (see Table 2). Many of these changes are due to taxonomic splitting of populations out of existing species and the resurrection of previously used names, rather than discovery of new populations of unknown animals (see Appendix 1). The attribution of New Zealand as the collection locality of the giant kawekawau gecko (*Hoplodactylus delcourti*) (Bauer & Russell 1988) has been questioned (Worthy & Holdaway 2002: 463–464), but this species is retained in the New Zealand faunal list pending further information. One new description was based on the discovery of the extinct Northland skink (*Oligosoma northlandi*) (Worthy 1991), but another supposedly extinct species (*Oligosoma gracilicorpus*) is now considered conspecific with a living species (Chapple et al. 2009). Late Pleistocene–Holocene lizard remains are common, but little work has been done on their identification (Worthy 1991), so more extinct species can be expected. Hitchmough et al. (2007, 2009), Bell & Patterson (2008), Hare et al. (2008), Jewell (2008), Chapple et al. (2009) and King et al. (2009) all indicate that many more living, undescribed skinks and geckos (both Squamata) await formal naming. The latest research suggests that all skinks in the New Zealand biogeographic region should be in a single genus, *Oligosoma* (Chapple et al. 2009). Jewell (2008) and Chapple & Hitchmough (2009) have suggested that the gecko genera need revision also. The number of introduced species established in the wild has increased from one to two since the 1980s, with the establishment of the house gecko (*Hemidactylus frenatus*) on Norfolk Island (see Table 2).

The ancient fauna

Fossils

New Zealand's first dinosaur finds were reported in the 1980s (from the Late Cretaceous (73 mya) site in the Mangahouanga Valley, Hawkes Bay); a probable small theropod (Saurischia, Theropoda) (Molnar 1981; Scarlett & Molnar 1984) and a dryosauroid (Ornithischia, Ornithopoda) (Wiffen & Molnar 1989). New Zealand's first pterosaur (Pterosauria: Wiffen & Molnar 1988) and a possible freshwater turtle (McKee & Wiffen

1989; Wiffen 1996) were reported from the same locality. At that time, no other pre-Late Pleistocene New Zealand terrestrial reptile remains were known, although it was presumed that ancestral tuatara (*Sphenodon* spp., Rhynchocephalia) must have been present on Zealandia since the Cretaceous (e.g. Fleming 1979: 43; Stevens 1980, 1989; Scarlett & Molnar 1984). The fossil record of terrestrial reptiles (excluding pre-80 mya remains, e.g. Molnar et al. 1998) has since been radically expanded, with the discovery and description of much new material. Remains similar to tuatara have been found in the Early Miocene (Jones et al. 2009). Several new dinosaurs were reported from the Late Cretaceous, including a probable titanosaurian sauropod (Saurischia, Sauropodomorpha), a probable nodosaur (Ornithischia, Ankylosauria) and other theropods from the Mangahouanga Valley site (Molnar & Wiffen 1994, 2007; Judd 2008). A second pterosaur bone (Pterodactyloidea, ?Anhangueridae) from the Mangahouanga Valley (Molnar & Wiffen 1994) and a probable pterosaur bone from near Kaikoura (Jones 2005) were reported. A dinosaur deposit, containing a range of theropod bones, has been discovered on the Chatham Islands and has been dated at about 65 mya (Stilwell et al. 2006; Stilwell 2007), but this age is disputed by Campbell & Hutching (2007) who consider these bones to be pre-Zealandian at 100–90 mya but reworked into an Early Paleocene deposit. Rhynchocephalid, gecko (?*Hoplodactylus* sp.) and skink (?*Oligosoma* sp.) fossils have been found in the Early Miocene St Bathans Fauna (Worthy et al. 2009a; Lee et al. in press). In addition, the St Bathans Fauna has revealed New Zealand's first crocodylian (Crocodylia) (Molnar & Pole 1997; Worthy et al. 2006a, 2009a).

Origins

The tuatara had long been considered another classic Gondwanan "Mesozoic survivor" and this view held during the 1980s (Fleming 1979: 104; Stevens 1980, 1989). However, accounting for the absence of snakes (Squamata) and other terrestrial reptiles from New Zealand required "special explanations", because they should have been present given the timing of the break-up of Gondwana (Fleming 1975: 18, 1979: 35, 42–43). Fleming (1979: 43) surmised that such animals may have become extinct since Zealandia separated from Gondwana. The tuatara's origin as a Gondwanan relict has now been supported by the Early Miocene fossil discoveries

(Jones et al. 2009) and new molecular finds which suggest its ancestors diverged from other reptiles 230-285 mya (Rest et al. 2003). Extinction as an explanation for the absence of other reptile groups in New Zealand now seems likely, given the loss of many taxa from the Zealandian fauna since the end of the Cretaceous, including possible freshwater turtles, crocodylians, pterosaurs and dinosaurs (McKee & Wiffen 1989; Molnar & Wiffen 1994; Worthy et al. 2006b). Snakes are considered to have been present in Australia by the Late Cretaceous (Scanlon 2006), so probably reached Zealandia before it separated from the rest of Australis (contra Fleming 1974, 1975: 24, 1982: 22; Bull & Whitaker 1975: 238; Stevens 1980: 262, 1991).

The origin of New Zealand's skinks and geckos was still under debate in the 1980s – some considered them to have Gondwanan origins (e.g. King 1987; Stevens 1989), while others believed they arrived via dispersal during the Tertiary (e.g. Towns 1974; Bull & Whitaker 1975: 238-239; Hardy 1977; Robb 1980). New molecular research suggests that New Zealand geckos probably have a Gondwanan origin, but the current diversity dates to after the Oligocene marine transgression (Chambers et al. 2001; Hitchmough et al. 2009). There is still no evidence to show that New Zealand skinks arrived vicariantly from Gondwana. Based on molecular work, Hickson & Slack (1998), Hickson et al. (2000) and Chapple et al. (2009) suggested that ancestral skinks arrived in Zealandia between the Late Eocene and the Late Oligocene, and that the diversity seen in the modern New Zealand fauna originated in the Oligocene and/or Miocene. A Miocene origin of some skink species was also supported by the findings of Chapple

et al. (2008a) and Liggins et al. (2008). Smith et al. (2007) concluded that the ancestors of all modern skinks in the New Zealand region date to less than 7 mya (Late Miocene). Daugherty et al. (1990), Greaves et al. (2007), Chapple et al. (2009) and King et al. (2009) considered it unlikely that New Zealand's skink fauna could be as young as 7 million years and such a young date would be discredited if the Early Miocene fossils are *Oligosoma* species (Worthy et al. 2009a; Lee et al. in press). Several skink species, such as the small-scaled skink (*Oligosoma microlepis*), are considered to have originated during the Pliocene (1.8-5.3 mya) (Greaves et al. 2008; Hare et al. 2008; Chapple et al. 2009).

Overall, recent discoveries in the reptile fauna have strengthened the links to Gondwana and suggest that many New Zealand taxa have origins deeper in time than previously realised.

Birds

The modern fauna

In the 1980s, 206 native breeding New Zealand bird species were recognised; of these, 51 (25%) were considered recently extinct and eight were recently established breeding colonists (see Table 4). In 2009, 242 native breeding bird species had been recognised; of these, 59 (24%) were considered recently extinct and 16 were recently established breeding colonists (see Table 4). In addition, in the 1980s, 36 bird species had been established through human introductions; a figure which had risen to 38 by 2001 (see Table 5).

These significant changes in species numbers since the

Table 4. Systematic list of orders and genera of modern native birds breeding in New Zealand, including the Australian territories of Norfolk and Macquarie Islands (1980s data: Checklist Committee 1970, 1980; Olson 1977; Schodde et al. 1983; Brothers 1984; Meredith 1985; Holdaway 1989. 2009 data: Holdaway et al. 2001 with modifications from Bourne 1989; McCracken & Sheldon 1998; Baker et al. 2007; Tennyson & Martinson 2007; Steinheimer et al. 2008 and Boessenkool et al. 2009). *Pterodroma solandri*, *Accipiter fasciatus*, *Hemiphaga spadicea*, *Gallinula norfolciensis*, *Nestor productus*, *Cyanoramphus cookii*, *Lalage leucopyga*, *Turdus poliocephalus*, *Pachycephala xanthoprocta*, *Gerygone modesta*, *Petroica multicolor*, *Zosterops albogularis*, *Zosterops tenuirostris* and *Aplonis fusca* are/were only found on Norfolk Island. *Aptenodytes patagonicus*, *Pygoscelis papua*, *Eudyptes schlegeli*, *Diomedea exulans*, *Macronectes giganteus*, *Halobaena caerulea*, *Oceanites oceanicus*, *Leucocarbo purpurascens* and *Gallirallus macquariensis* are/were only found on Macquarie Island. Numbers in brackets show recent colonists. Abbreviations: No. = number; sp. = species. * = species transferred to another genus.

Order	Genus	No. sp. 1980s	No. extinct 1980s	No. sp. 2009	No. extinct 2009
Dinornithiformes	<i>Anomalopteryx</i>	1	1	1	1
	<i>Megalopteryx</i>	1	1	1	1
	<i>Pachyornis</i>	3	3	3	3
	<i>Emeus</i>	1	1	1	1
	<i>Euryapteryx</i>	2	2	1	1
	<i>Dinornis</i>	3	3	2	2
	Total	11	11	9	9
Apterygiformes	<i>Apteryx</i>	3	0	5	0
	Total	3	0	5	0
Galliformes	<i>Megapodiidae</i>	0	0	1	1
	<i>Coturnix</i>	1	1	1	1
	Total	1	1	2	2
Anseriformes	<i>Cygnus</i>	1	1	1	0
	<i>Cnemiornis</i>	2	2	2	2
	<i>Pachyanas</i>	1	1	1	1
	<i>Euryanas</i>	1	1	0*	0
	<i>Chenonetta</i>	0	0	1	1
	<i>Malacorhynchus</i>	1	1	1	1
	<i>Biziura</i>	1	1	1	1
	<i>Oxyura</i>	1	1	1	1
	<i>Tadorna</i>	1	0	1	0
<i>Anas</i>	4	0	6	0	

Table 4 continued

Order	Genus	No. sp. 1980s	No. extinct 1980s	No. sp. 2009	No. extinct 2009
	<i>Hymenolaimus</i>	1	0	1	0
	<i>Aythya</i>	1	0	1	0
	<i>Mergus</i>	1	1	1	1
	Total	16	9	18	8
Sphenisciformes	<i>Aptenodytes</i>	1	0	1	0
	<i>Megadyptes</i>	1	0	2	1
	<i>Pygoscelis</i>	1	0	1	0
	<i>Eudyptula</i>	1	0	1	0
	<i>Eudyptes</i>	4	0	5	0
	Total	8	0	10	1
Procellariiformes	<i>Diomedea</i>	6	0	4*	0
	<i>Thalassarche</i>	0	0	7(1)	0
	<i>Phoebastria</i>	1	0	1	0
	<i>Macronectes</i>	2	0	2	0
	<i>Daption</i>	1	0	1	0
	<i>Pterodroma</i>	12	0	12(1)	0
	<i>Halobaena</i>	1	0	1	0
	<i>Pachyptila</i>	4	0	4	0
	<i>Procellaria</i>	4	0	4	0
	<i>Puffinus</i>	7	0	9	1
	<i>Oceanites</i>	0	0	1	0
	<i>Pealeornis</i>	0	0	1	0
	<i>Garrodia</i>	1	0	1	0
	<i>Pelagodroma</i>	1	0	1	0
	<i>Fregatta</i>	2	0	2	0
	<i>Pelecanoides</i>	2	0	2	0
	Total	44	0	53(2)	1
Podicipediformes	<i>Podiceps</i>	2	0	1*	0
	<i>Poliiocephalus</i>	0	0	1	0
	<i>Tachybaptus</i>	0	0	1(1)	0
	Total	2	0	3(1)	0
Ciconiiformes	<i>Ardea</i>	1(1)	0	1*	0
	<i>Egretta</i>	2	0	2(1)*	0
	<i>Botaurus</i>	1	0	1(1)	0
	<i>Ixobrychus</i>	1	1	1	1
	<i>Platalea</i>	1(1)	0	1(1)	0
	Total	6(2)	1	6(3)	1
Pelecaniformes	<i>Phaethon</i>	1	0	1	0
	<i>Pelecanus</i>	1	1	0	0
	<i>Sula</i>	1	0	1	0
	<i>Morus</i>	1	0	1	0
	<i>Phalacrocorax</i>	4	0	4(1)	0
	<i>Leucocarbo</i>	3	0	6	0
	<i>Stictocarbo</i>	1	0	2	0
	Total	12	1	15(1)	0
Falconiformes	<i>Circus</i>	3	2	2(1)	1
	<i>Harpagornis</i>	1	1	1	1
	<i>Haliaeetus</i>	1	1	0	0
	<i>Falco</i>	2(1)	0	2(1)	0
	<i>Accipiter</i>	1	1	1	1
	Total	8(1)	5	6(2)	3
Gruiformes	<i>Aptornis</i>	1	1	2	2
	<i>Rallus</i>	3	1	0*	0
	<i>Dryolimnas</i>	0	0	1	0
	<i>Cabalus</i>	0	0	1	1
	<i>Gallirallus</i>	2	1	4	2
	<i>Capellirallus</i>	1	1	1	1
	<i>Diaphorapteryx</i>	1	1	1	1
	<i>Gallinula</i>	1	1	1	1
	<i>Porzana</i>	2	0	2	0
	<i>Porphyrio</i>	2	0	3(1)	1
	<i>Fulica</i>	2(1)	1	3(1)	2
	Total	15(1)	7	19(2)	11
Charadriiformes	<i>Haematopus</i>	3	0	3	0
	<i>Vanellus</i>	1(1)	0	1(1)	0
	<i>Charadrius</i>	3(1)	0	3(1)	0

Table 4 continued

Order	Genus	No. sp. 1980s	No. extinct 1980s	No. sp. 2009	No. extinct 2009
	<i>Thinornis</i>	1	0	1	0
	<i>Anarhynchus</i>	1	0	1	0
	<i>Coenocorypha</i>	2	1	6	3
	<i>Himantopus</i>	2	0	2(1)	0
	<i>Stercorarius</i>	1	0	1	0
	<i>Larus</i>	3	0	3	0
	<i>Sterna</i>	6	0	6	0
	<i>Anous</i>	2	0	2	0
	<i>Gygis</i>	1	0	1	0
	<i>Procelsterna</i>	1	0	1	0
	Total	27(2)	1	31(3)	3
Columbiformes	<i>Hemiphaga</i>	1	0	3	1
	<i>Gallicolumba</i>	1	1	1	1
	Total	2	1	4	2
Psittaciformes	<i>Strigops</i>	1	0	1	0
	<i>Nestor</i>	3	1	3	1
	<i>Cyanoramphus</i>	4	0	6	0
	Total	8	1	10	1
Cuculiformes	<i>Chrysococcyx</i>	1	0	1	0
	<i>Eudynamis</i>	1	0	1	0
	Total	2	0	2	0
Strigiformes	<i>Ninox</i>	2	0	1	0
	<i>Sceloglaux</i>	1	1	1	1
	Total	3	1	2	1
Caprimulgiformes	<i>Megaegotheles</i>	1	1	0*	0
	<i>Aegotheles</i>	0	0	1	1
	Total	1	1	1	1
Coraciiformes	<i>Halcyon</i>	1	0	0*	0
	<i>Todiramphus</i>	0	0	1	0
	Total	1	0	1	0
Passeriformes	<i>Acanthisitta</i>	1	0	1	0
	<i>Xenicus</i>	2	1	2	1
	<i>Traversia</i>	1	1	1	1
	<i>Pachyplichas</i>	2	2	1	1
	Acanthisittidae N. gen. 1	1	1	0*	0
	<i>Dendroscansor</i>	0	0	1	1
	<i>Notiomystis</i>	1	0	1	0
	<i>Anthornis</i>	1	0	2	1
	<i>Prothemadera</i>	1	0	1	0
	<i>Hirundo</i>	1(1)	0	1(1)	0
	<i>Lalage</i>	1	1	1	1
	<i>Anthus</i>	1	0	1	0
	<i>Bowdleria</i>	1	0	3	1
	<i>Finschia</i>	1	0	0*	0
	<i>Mohoua</i>	2	0	3	0
	<i>Gerygone</i>	2	0	3	0
	<i>Rhipidura</i>	1	0	1	0
	<i>Petroica</i>	4	0	7	0
	<i>Pachycephala</i>	1	0	1	0
	<i>Turdus</i>	1	0	1	1
	<i>Zosterops</i>	3(1)	0	3(1)	0
	<i>Aplonis</i>	1	1	1	1
	<i>Philesturnus</i>	1	0	2	0
	<i>Heteralocha</i>	1	1	1	1
	<i>Callaeas</i>	1	0	2	1
	<i>Turnagra</i>	2	2	2	2
	<i>Corvus</i>	1	1	2	2
	Total	36(2)	11	45(2)	15
Overall Total		206(8)	51	242(16)	59

Table 5. Systematic list of orders and genera of introduced birds breeding in New Zealand, including the Australian territories of Norfolk and Macquarie Islands (data from Checklist Committee 1970, 1980, 1990; Schodde et al. 1983; Holdaway et al. 2001; see Appendix 2). *Chalcophaps indica* is only found on Norfolk Island. * = species transferred to another genus.

Order	Genera, giving numbers of species (1980s, 2001)	Totals 1980s, 2001
Galliformes	<i>Gallus</i> (1, 1), <i>Alectoris</i> (1, 2), <i>Perdix</i> (1, 0), <i>Synoicus</i> (1, 1), <i>Colinus</i> (1, 0), <i>Lophortyx</i> (1, 0*), <i>Callipepla</i> (0, 1), <i>Phasianus</i> (1, 1), <i>Pavo</i> (1, 1), <i>Meleagris</i> (0, 1), <i>Numida</i> (0, 1)	8, 9
Anseriformes	<i>Cygnus</i> (2, 1), <i>Branta</i> (1, 1), <i>Anser</i> (0, 1), <i>Anas</i> (1, 1)	4, 4
Columbiformes	<i>Columba</i> (1, 1), <i>Streptopelia</i> (2, 2), <i>Chalcophaps</i> (1, 1)	4, 4
Psittaciformes	<i>Cacatua</i> (1, 2), <i>Platycercus</i> (2, 2)	3, 4
Strigiformes	<i>Athene</i> (1, 1)	1, 1
Coraciiformes	<i>Dacelo</i> (1, 1)	1, 1
Passeriformes	<i>Alauda</i> (1, 1), <i>Prunella</i> (1, 1), <i>Turdus</i> (2, 2), <i>Emberiza</i> (2, 2), <i>Fringilla</i> (1, 1), <i>Carduelis</i> (3, 3), <i>Passer</i> (1, 1), <i>Sturnus</i> (1, 1), <i>Acridotheres</i> (1, 1), <i>Gymnorhina</i> (1, 1), <i>Corvus</i> (1, 1)	15, 15
Overall Total		36, 38

1980s are explained by ten developments (see Appendix 2). By far the most significant change has been the shuffling of taxonomic status, including elevation of 34 subspecies to full species status, reduction of 10 species to junior synonyms of valid species and acceptance of five species previously described (but not accepted in the 1980s) as valid species. Only five new bird species were formally described during this period (1991 long-billed wren, 1994 Scarlett's shearwater, 2003 Okarito brown kiwi, 2005 New Zealand stiff-tailed duck, 2009 Waitaha penguin – all but the kiwi are extinct), but two of these were already noted as undescribed species in 1980s lists. The status of two species was revised in light of fossil analyses – the black swan (formerly considered to be introduced by humans) and Kermadec megapode are now considered to be part of New Zealand's original avifauna. Another species (New Zealand storm petrel) was accepted as valid by Holdaway et al. (2001) but considered extinct, then rediscovered alive in 2003 (Flood 2003; Stephenson 2004).

Another important development in understanding the history of the avifauna has been a doubling (from 8 to 16) in the number of species now considered to have colonised New Zealand independently since humans colonised New Zealand. Also bird species introduced by humans continue to colonise New Zealand (feral goose, red-legged partridge, turkey, tufted guinea fowl and galah), although some of these may have had undocumented feral populations in the 1980s. The establishment of such species may be transient, as shown by the confirmed extinction of two other introduced species (grey partridge and bobwhite quail) during the same period. One seabird species (Wilson's storm petrel) was discovered breeding in the New Zealand region (at the Macquarie Island group).

The number of bird species currently considered extinct

has risen from 51 to 59 (see Table 4). This change largely results from recognition of already extinct subspecies as full species (Dieffenbach's rail, Macquarie Island rail, moho/North Island takahe *Porphyrio mantelli*, South Island snipe, North Island snipe, Norfolk Island pigeon, Chatham Island fernbird, Chatham Island bellbird, South Island kokako *Callaeas cinerea*), accepting extinct species that were previously considered invalid (Mantell's moa, South Island giant moa, Kermadec megapode, South Island adzebill, New Zealand coot, New Zealand raven) and from descriptions of species already extinct (Waitaha penguin, Scarlett's shearwater). Only one species (Norfolk Island's grey-headed blackbird *Turdus poliocephalus*) is accepted, since the 1980s, as having become extinct. At the same time, ten taxa previously considered to be extinct species are no longer considered valid (Mappin's moa, stout-legged moa *Euryapteryx geranoides*, slender bush moa, giant moa *Dinornis giganteus*, New Zealand swan, New Zealand pelican, New Zealand hawk, southern sea eagle, weka *Gallirallus minor*, North Island stout-legged wren). However, there is evidence that several more undescribed bird species that became extinct in the Holocene await description (Holdaway et al. 2001).

The ancient fauna

Fossils

While the Late Pleistocene–Holocene fossil record of birds in New Zealand is unrivalled worldwide (Worthy & Holdaway 2002), the pre-Late Pleistocene fossil record was until recently poor, apart from marine birds, notably 16 species of penguin (Simpson 1975; Fleming 1979: 75; Checklist Committee 1990). In the 1980s, only one bird bone (a tarsometatarsus from Canterbury) of possible Cretaceous age, and a few

Table 6. Systematic list of orders and genera of modern native mammals in New Zealand, including the Australian territory of Norfolk Island (Meredith 1985; Tidemann 1986; King 1990, 2005; Anon 2007; Hoyer et al. 2008). In the New Zealand biogeographic region, *Chalinolobus gouldii* is found only on Norfolk Island, where it may now be extinct (Tidemann 1986; Anon 2007). *Mormopterus norfolkensis* was thought to have occurred on Norfolk Island, but this locality record of this east coast Australian species appears to be an error (Hoyer et al. 2008).

Order	Genus	No. species 1980s	No. extinct 1980s	No. species 2009	No. extinct 2009
Chiroptera	<i>Mormopterus</i>	1	?1	0	0
	<i>Chalinolobus</i>	2	?1	2	?1
	<i>Mystacina</i>	2	1	2	1
Total		5	1-3	4	1-2

Table 7. Systematic list of taxa of introduced mammals in New Zealand, including the Australian territories of Norfolk and Macquarie Islands (Schodde et al. 1983; Meredith 1985; King 1990, 2005; Copson & Whinam 1998; Tennyson & Martinson 2007). All the same species were present in the 1980s and in 2009.

Taxa	Genera, and numbers of species	Totals
Infraclass Marsupialia	<i>Macropus</i> 3, <i>Petrogale</i> 1, <i>Wallabia</i> 1, <i>Trichosurus</i> 1	6
Order Insectivora	<i>Erinaceus</i> 1	1
Order Lagomorpha	<i>Oryctolagus</i> 1, <i>Lepus</i> 1	2
Order Rodentia	<i>Rattus</i> 3, <i>Mus</i> 1	4
Order Carnivora	<i>Mustela</i> 3, <i>Felis</i> 1	4
Order Perissodactyla	<i>Equus</i> 1	1
Order Artiodactyla	<i>Sus</i> 1, <i>Bos</i> 1, <i>Rupicapra</i> 1, <i>Hemitragus</i> 1, <i>Capra</i> 1, <i>Ovis</i> 1, <i>Cervus</i> 4, <i>Dama</i> 1, <i>Odocoileus</i> 1, <i>Alces</i> 1	13
Overall Total		31

fragmentary bones of Paleocene age from Moeraki, were known (Fleming 1979: 40; see Fordyce 1991: 1233). A toe bone from Cretaceous rock may be from either a bird or a dinosaur (Scarlett & Molnar 1984). Most fossil penguins known from New Zealand were Oligocene in age (Fleming 1979: 53; Checklist Committee 1990), with the earliest from the Late Eocene (Fleming 1979: 49). A possible albatross from Oligocene rocks (Fleming 1979: 53) was later regarded as indeterminable to family (Olson 1985). At least two forms of waterfowl (?Anatidae) and eggshell were discovered in the Early Miocene deposits near St Bathans between 1978 and 1981 (Douglas et al. 1981; Fordyce 1991). Possible “kiwi” (Apterygiformes) footprints were reported from the uppermost Miocene and some moa (Dinornithiformes) bones were considered to be possibly of this age also (Fleming 1979: 64–66). From the Late Pliocene at Motunau, a bony-toothed pelican (Pelecaniformes) and three fossil penguin species (Spheniscidae) were known (Fleming 1979: 69). Other bony-toothed pelican remains were found at Motunau, near the Waipara river mouth (early Late Miocene) and in Pliocene sediments of Taranaki (Fordyce 1991: 1235–1236). There is a possible record of a little penguin (*Eudyptula minor*) from the Late Pliocene (Simpson 1975) and a yellow-eyed penguin (*Megadyptes antipodes*) bone from the Pleistocene (Okehuan, 1.19–0.45 mya) (Fleming 1979: 75). The extinct North Island goose (*Cnemiornis gracilis*) was known from Early Pleistocene sediments (Worthy et al. 1991).

Since the 1980s, some very important bird fossils have been reported, including the first significant terrestrial Tertiary avifauna from New Zealand. A Late Cretaceous partial femur of a diving *Baptornis*-like bird (?Hesperornithiformes) has been identified from near Cheviot, Canterbury (Fordyce 1991: 1233) and at least two forms of bird have been found near the Cretaceous–Paleogene boundary at the Chatham Islands (Consoli & Stilwell 2007; Stilwell 2007; Judd 2008). The tarsometatarsus from Canterbury (see Fordyce 1991: 1233) has been more fully described and dated. It represents a modern water bird (Neornithes) from the Cretaceous–Paleogene boundary (Ksepka & Cracraft 2008). In the Paleocene, aside from fragmentary bones from Moeraki, two well-preserved 61–62 million year old penguin species from Canterbury have been described (Slack et al. 2006). From Late Oligocene–Early Miocene marine limestones, further penguin material has been studied (but not taxonomically described), and two unstudied non-penguin bones have been found (Fordyce & Jones 1990; Fordyce 1991: 1234). The age of the bony-toothed pelican and penguins from Motunau has been questioned – this site may be considerably older, possibly Early Miocene (Fordyce

1991). In 2001, extensive investigation of the Early Miocene St Bathans sites began and this work has now produced a diverse avifauna of at least 31 bird species (Worthy et al. 2007, 2008, 2009a). Scofield et al. (2006) reported the remains of a diving petrel (*Pelecanoides* sp.) from a Mid-Miocene site in Canterbury. Fordyce (1991: 1234) reported fragmentary Mid–Late Miocene bird remains from freshwater limestone in the Waitaki Valley. Eagle et al. (2005) reported a penguin and pigeon (cf. *Hemiphaga*) bone from the Pliocene of the Chatham Islands, but the age of the pigeon fossil is questionable because its preservation differs from that of the penguin bone. Although it was supposedly in a marine deposit, Holocene terrestrial material of a similar taxon is common near this site (A. Tennyson, pers. obs. 1997). McKee (1994) and D. Allen (A. Tennyson, pers. obs. 2009) have found further marine bird remains in the Pliocene rocks of Taranaki, including a shearwater (*Puffinus* sp.). Moa remains, once considered possibly to be of Miocene age (Fleming 1979: 64–66), were found to be no more than 2.5 million years old (i.e. Pliocene; Worthy et al. 1991). A one million year old site near Marton has produced a small fauna including moa remains, rails (Rallidae, including Fleming’s rail *Pleistorallus flemingi*) and a kiwi (Worthy 1997; Worthy & Holdaway 2002: 8).

Origins

Although the time and means of origin of New Zealand’s land birds has long been debated, ratites (Paleognathae), including moa and kiwi, have usually been considered iconic “Mesozoic survivors” from Gondwana (e.g. Cracraft 1974; Fleming 1974, 1975: 24, 1979: 42, 104; Stevens 1980; Stevens et al. 1988: 39). However, by the 1980s, the Gondwanan status of the kiwi was being questioned (see Stevens 1989, 1991; Pole 1994). Many other distinctive bird taxa (those endemic to New Zealand at generic level or higher) were assumed to have had a long history but were still considered to have dispersed here during the Tertiary (e.g. Falla 1953; Fleming 1962, 1974, 1979: 47, 69, 1982: 22–23; Sibley & Ahlquist 1987; Holdaway 1988; Stevens 1989). However, some researchers thought that some of these taxa, particularly the New Zealand wrens (Acanthisittidae) and New Zealand wattlebirds (Callaeidae), had a Gondwanan origin (see Stevens 1980, 1989; Sibley et al. 1982; Gibbs 2006: 88; Murphy et al. 2006 and Shepherd & Lambert 2007). Most other less distinctive terrestrial bird taxa (those distinct from foreign taxa only at species level or less) were presumed to have arrived by over-water dispersal since the Pliocene (Fleming 1962, 1974; Holdaway 1988). Worldwide, most modern New Zealand bird orders were known to have evolved by the Early Tertiary (Olson 1985), but, apart

from penguins in the Eocene, and waterfowl and bony-toothed pelicans (and possibly moa and kiwi) in the Miocene, the pre-Late Pleistocene New Zealand fossil record of other groups gave no clues as to when they arrived. Waterbird genera, such as many of the petrels (Procellariiformes), were postulated to have evolved between the Eocene and Pliocene (Imber 1985), with modern species, such as the prions (*Pachyptila* spp.), first appearing in the Pliocene–Pleistocene (Fleming 1941). However, when these taxa first reached Zealandia was unknown.

Recent fossil and molecular research has markedly added to our knowledge of the origins and history of New Zealand's birds, but the overall conclusions remain the same – a few arrived overland from Gondwana, whereas most dispersed here later, often from Australia. Increasing evidence indicates that most modern bird groups evolved in the Cretaceous (e.g. van Tuinen & Hedges 2001; Crowe et al. 2006; Baker et al. 2007; Fain et al. 2007; Pereira et al. 2007). This is earlier than previously believed, but the fossil record of modern birds from this time is virtually non-existent worldwide.

New molecular work suggests that ratites may not be the classic example of Gondwanan vicariant dispersal because there is increasing evidence that flightlessness evolved several times in this group (Harshman et al. 2008). However, molecular findings still support a Late Cretaceous origin of moa in New Zealand (Cooper et al. 2001). Early Miocene eggshell at St Bathans is now the oldest fossil record of moa (Worthy et al. 2007). In contrast with moa, kiwi ancestors may not have arrived until later – possibly by dispersal 72–50 mya (Stevens 1991; Cooper et al. 1992, 2001; Pole 1994; van Tuinen & Hedges 2001; but see Bourdon et al. 2009). New Zealand wrens appear to be of Gondwanan origin (Cracraft 2001a, b; Ericson et al. 2002). Molecular and fossil research indicates that the modern wren radiation dates from at least the Late Oligocene–Early Miocene (Cooper & Cooper 1995; Worthy et al. 2009a, in press). Another group with a likely Gondwanan origin are New Zealand's large parrots (*Strigops habroptilus* and *Nestor* spp.) (Cooper & Penny 1997; Tavares et al. 2006; Wright et al. 2008; contra Fleming 1974, 1982: 23; Stevens et al. 1988, 1995; Stevens 1991). Possible fossils of these parrots have now been found in the Early Miocene of New Zealand (Worthy et al. 2007).

The closest relatives of a fossil pigeon (Columbidae) and owlet-nightjar (*Aegotheles* sp.) from the Early Miocene appear to be the New Zealand pigeon (*Hemiphaga novaeseelandiae*) and the recently extinct owlet-nightjar (Worthy et al. 2007, 2009a, b), suggesting an early arrival of these birds' ancestors in Zealandia. Molecular research indicates that the New Zealand pigeon diverged from its nearest relatives 24.2 mya (Pereira et al. 2007), backing Fleming's (1982: 23) earlier theory. Molecular results have supported previous suggestions that the ancestors of many unusual New Zealand land bird groups arrived here fairly early in the Tertiary, e.g. New Zealand wattlebirds (39–34 mya), stitchbirds/hihi (33.8 mya), Mohouinae (30–29 mya), piopio (*Turnagra* spp.) (27 mya) and tui/bellbirds (*Prothemadera novaeseelandiae*, *Anthornis* spp.) (23.8 mya) in the Eocene–Oligocene (Sibley & Ahlquist 1987; Christidis et al. 1996; Driskell et al. 2007; Shepherd & Lambert 2007). This is earlier than previously thought for stitchbirds/hihi and tui/bellbirds (e.g. Holdaway 1995) but some authors (e.g. Stevens 1991; Stevens et al. 1995: 60) considered wattlebirds and piopio to be older than they are. Another example of previous over-estimation of the age of a taxon is Haast's eagle (*Harpagornis moorei*) – its ancestors seem to have arrived only in the Pleistocene about 1 mya (Bunce et al.

2005; Bunce & Holdaway 2006), whereas Fleming (1962, 1974) considered the ancestors of many taxa endemic at generic level to have arrived as early as the Miocene or before. However, accipitriforms (kites, eagles, hawks) were already present in Zealandia in the Early Miocene (Worthy et al. 2007, 2009a). Swiftlets (Aegotheliformes, Apodidae) and cracticid songbirds (Cracticidae) were in the Early Miocene St Bathans Fauna, but are not part of the modern native fauna (Worthy et al. 2007). Molecular results support a Pliocene–Pleistocene origin for New Zealand robins and tomtits (*Petroica* spp.) (Miller & Lambert 2006), in agreement with Fleming's (1974) earlier theory. The very recent (Pleistocene–Holocene) arrival of many other land bird species has gained support from the Late Pleistocene–Holocene fossil record (see Holdaway et al. 2001 and Table 4) and molecular research, e.g. on *Cyanoramphus* parakeets (see Gibbs 2006: 117; contra Fleming 1982: 23) and the Norfolk Island grey-headed blackbird (Nylander et al. 2008).

For waterbirds, the *Baptornis*-like femur (Fordyce 1991: 1233) (discussed earlier) suggests that Zealandia held part of a worldwide radiation of the toothed Cretaceous Hesperornithiformes. Anseriformes (geese and ducks) are represented by eight taxa in the Early Miocene – globally the richest Miocene fauna known (Worthy et al. 2008) – but ancestors of modern ducks are thought to have arrived in Zealandia at widely varying times, e.g. New Zealand geese (*Cnemiornis*) in the Early Miocene or before (Worthy et al. 2008) and Finsch's duck only in the Late Pleistocene (Worthy & Olson 2002). The new penguin fossils, in combination with molecular findings, indicate a Mesozoic origin for this group (Slack et al. 2006) and suggest their presence in Zealandia in the Late Cretaceous. However, although the lineage of penguins may have extended back into the Cretaceous, the modern radiation of this group may be no older than about 12 million years (Slack et al. 2006; Clarke et al. 2007), so modern penguins may not have been in Zealandia before the Miocene (Goldberg et al. 2008). Petrels are now confirmed from the Early Miocene of Zealandia and represent the earliest record of the diving petrels (Pelecanoididae) worldwide (Worthy et al. 2007). Molecular evidence suggests that several modern petrel genera, and even some species, arose during the Miocene (Viot et al. 1993). However, many modern species, including prions, arose later, during the Pliocene–Pleistocene (Viot et al. 1993; Techow et al. 2009), supporting Fleming's (1941) earlier hypothesis. The now globally extinct flamingo-like palaeodids (Palaeodidae) were in the Early Miocene St Bathans Fauna (Worthy et al. 2009a).

Other Early Miocene waterbird fossils show that herons (Ardeidae), rails (Rallidae), gulls and waders (Charadriiformes) were present in Zealandia at least by 16 mya (Worthy et al. 2007, 2009a), but, because of the great dispersal abilities of waterbirds, it is difficult to deduce the arrival times of the direct ancestors of modern taxa from these records. It has been suggested that the predatory adzebills (*Aptornis* spp.) have a Gondwanan origin (Cracraft 2001a, b) and possible fossils of this group have now been found in the Early Miocene of New Zealand (Worthy et al. 2007). Flightless modern New Zealand rails, such as moho, takahe and weka (*Gallirallus australis*), are presumed to have evolved from flying ancestors dispersing to Zealandia in, at most, only the past few million years (e.g. Fleming 1974; Trewick 1997; Worthy & Wragg 2003; and see Gibbs 2006: 47, 115–116), so it is interesting to note that a similar process has been occurring with Zealandian rails much deeper in time (Worthy et al. 2007). Molecular findings indicate Oligocene or Miocene origins of many genera of

tern (Sterninae) and noddy (Megalopterinae) (Bridge et al. 2005; Baker et al. 2007), with New Zealand's endemic black-fronted (*Sterna albostrata*) and white-fronted (*Sterna striata*) terns thought to have originated in the Miocene (Bridge et al. 2005). In contrast, Fleming (1974) theorised that black-fronted terns evolved only 20 000 years ago. On the other hand, molecular results suggest that modern gull (Laridae) and skua (Stercorariidae) species arose mainly during the last 1 million years (Viot et al. 1993; Crochet et al. 2000), although modern gull and skua genera may extend back into the Miocene or even the Oligocene (Baker et al. 2007). Endemic New Zealand wading bird genera (the plovers *Thinornis* and *Anarhynchus*) and snipe (*Coenocorypha* spp.) (whose surviving populations are confined to New Zealand) appear to have a history extending back into the Eocene or Oligocene (Baker et al. 2007), so may be long-standing members of Zealandia's avifauna. However, some wading bird species splits appear to be very recent, e.g. the ancestors of Finsch's (*Haematopus finschi*) and variable oystercatchers (*Haematopus unicolor*) separated only 15–13 000 years ago (Banks & Paterson 2007).

Mammals

The modern fauna

In the 1980s, five species of bats (two extant: lesser short-tailed bat *Mystacina tuberculata*, New Zealand long-tailed bat *Chalinolobus tuberculatus*; and three probably extinct: east-coast free-tailed bat *Mormopterus norfolkensis* and Gould's wattled bat *Chalinolobus gouldii* (both only on Norfolk Island) and greater short-tailed bat *Mystacina robusta*) and 31 introduced species of mammal were recognised in the New Zealand fauna (see Tables 6 & 7). By 2009, no further mammal species had been described and no further species had established or become extinct. The current status of the two bat species on Norfolk Island remains unclear, but it appears that the east-coast free-tailed bat may never have occurred there (Hoye et al. 2008).

The ancient fauna

Late-Pleistocene–Holocene bat fossils are common in some parts of New Zealand (Worthy & Holdaway 2002), but in the 1980s, no older mammal remains were known. Again, the Early Miocene St Bathans Fauna has now revealed four (as yet undescribed) bat taxa and, most remarkably, a mouse-sized ground-dwelling “Mesozoic ghost” mammal with no close affinities to any living groups (Worthy et al. 2006a, b, 2009a).

In the 1980s, the absence of marsupials (Marsupialia) and monotremes (Monotremata) from New Zealand required “special explanations” (Fleming 1975: 18, 24, 1979: 35, 42–43). Possible explanations included inhospitable climate preventing colonisation, extinction after their arrival, or dispersal of marsupials to proto-Australia after Zealandia had separated from it (Fleming 1975: 24, 1979: 43; Stevens 1980, 1989; Stevens et al. 1988: 44). Fossil finds have shown that monotremes were certainly present in proto-Australia in the Early Cretaceous (*Steropodon galmani*, *Teinolophos trusleri*) and probably several other taxa: Archer et al. 1985; Rich et al. 2001; Musser 2003, 2006; Pridmore et al. 2005). This supports Fleming's (1979) theory that monotremes were present in Zealandia when it split from Australis (contra Bull & Whitaker 1975: 267; Fleming 1975: 15; Stevens et al. 1995: 44). Marsupials first appear in the Australian fossil record at 55 mya (Archer et al. 1993; Beck et al. 2008), although they

may have been present 70 mya (Archer et al. 1993; Woodburne & Case 1996; Wroe & Archer 2006; Archer & Hand 2006; Goin et al. 2006; Beck et al. 2008). If the final separation of Zealandia occurred as late as 52 mya (Gaina et al. 1998), then marsupials should have reached Zealandia also.

Although fossils of the third group of living mammals (placentals) have been claimed from the Cretaceous (*Ausktribosphenos nyktos*, *Bishops whitmorei*) and Eocene (*Tingamarra porterorum*) of Australia (Godthelp et al. 1992; Rich et al. 1997, 1999, 2001), these identifications are contentious (Woodburne & Case 1996; Kielan-Jaworowska et al. 1998; Luo et al. 2001, 2002; Musser 2003, 2006; Wroe & Archer 2006). What is clear is that there was a considerable diversity of mammals (monotremes, multituberculates (*Corriebaatar marywaltersae*, Multituberculata) and the enigmatic forms: *Kollikodon ritchiei*, *Ausktribosphenos nyktos*, *Bishops whitmorei* and *Kryoryctes cadburyi*) living in proto-Australia during the Early Cretaceous (Musser 2003; Rich & Vickers-Rich 2004; Pridmore et al. 2005; Rich et al. 2009) and that many forms were present early enough to have reached Zealandia (contra Fleming 1982: 22). The ground-dwelling mammal from the Early Miocene of New Zealand is, surprisingly, neither a monotreme nor apparently similar to the other Cretaceous mammals found so far as fossils in Australia (Worthy et al. 2006b). Without any close relatives, it seems highly likely that this mammal was a “Mesozoic survivor” dating from Zealandia's connection with Gondwana – its ancestors are thought to have diverged from their nearest relatives more than 125 mya (Worthy et al. 2006b).

In contrast, all of New Zealand's bats, including the distinctive mystacinids, have been considered to be Tertiary colonists (Fleming 1979: 104; Stevens 1989, 1991). Bats (Chiroptera) are thought to have evolved near the beginning of the Paleocene about 65 mya and possibly earlier (Eick et al. 2005). Although ancestral mystacinids may have diverged from other bats as long ago as 51 mya in the Early Eocene (Teeling et al. 2005; Miller-Butterworth et al. 2007), an Oligocene arrival in Zealandia is postulated (Hand 2006). Ancestors of the New Zealand long-tailed bat are thought to have arrived in the Early Pleistocene (King 2005). The initial Miocene bat fossil discoveries represent at least the Mystacinidae and Vespertilionidae (but not *Chalinolobus*) and another related to the Noctilionoidea (previously this material was considered to be close to the Archaeonycteridae); these make it clear that New Zealand's modern bat fauna is depauperate compared with the early Neogene fauna (Worthy et al. 2006a, 2009a; King et al. 2009).

Discussion

The modern fauna

Since the 1980s, several more terrestrial vertebrate taxa (including frogs, reptiles and birds) have been recognised in the modern New Zealand fauna. Most of this increase in number is due to the taxonomic splitting of known species and the elevation of subspecies to full species, rather than the discovery of new populations of unknown animals. This “taxonomic inflation” (Isaac et al. 2004) is a reflection of the worldwide shift away from the Biological Species Concept to the Phylogenetic Species Concept.

“Taxonomic inflation” is also reflected in the increased number of species considered extinct in human times. In fact, no new amphibian, reptile or mammal extinctions are confirmed

for the last 20 years (although Norfolk Island's Gould's wattled bat may have become extinct during this period). The percentage of extinct bird species remains at about a quarter of the native avifauna, with only one further species in the region accepted as extinct (Norfolk Island's grey-headed blackbird, last confirmed in 1975). This suggests that conservation measures may finally have slowed the high recent rate of extinctions (Tennyson & Martinson 2007). However, many species remain seriously endangered and survive only as relict populations (Hitchmough et al. 2007) – most notably Norfolk Island's white-breasted white-eye (*Zosterops albogularis*), which may already be extinct (Tennyson & Martinson 2007).

The causes of recent vertebrate extinctions proposed by Holdaway in 1989 (habitat loss, human-hunting, predation by introduced animals and competition for food) have been refined. The role of predation is now seen as even more important (see also Innes et al. 2010). In agreement with Holdaway (1989), all Holocene extinctions are thought to have occurred after human colonisation and none is due to climate change. Human-hunting contributed to most bird extinctions, followed by (in decreasing order), predation by Pacific rats (*Rattus exulans*), cats (*Felis catus*), ship rats (*Rattus rattus*), Norway rats (*R. norvegicus*) and a range of other introduced taxa, as well as loss of prey for raptors (Tennyson & Martinson 2007). The extinction of native frog, lizard and bat species is still blamed primarily on rat predation (especially Pacific rats) (Worthy 1987a; Holdaway 1989; Worthy & Holdaway 2002). Today, there are some differences in views of the mechanisms of extinction compared with the 1980s, e.g. Polynesian dogs (*Canis familiaris*) are no longer thought to be important predators because they rarely ventured far from Polynesian camps; and habitat loss and competition for food appear to have been less important in causing extinctions than once thought (Tennyson & Martinson 2007; Sax & Gaines 2008).

Other notable discoveries since the 1980s include the rediscovery of one bird previously thought extinct (the New Zealand storm petrel), as well as the addition of one seabird species to the native breeding fauna (found at the Macquarie Island group). These findings indicate there are still major knowledge gaps in our understanding of seabird distribution. New information has shown that eight more bird taxa than previously realised are immigrants to the New Zealand region since human colonisation, which demonstrates that faunal change due to human modifications has been even greater than previously realised. Should these "native invaders" (Tennyson & Martinson 2007: 14) be given a lower level of legal protection than other native species, so they can be more actively managed when they have negative ecological impacts? The number of introduced vertebrate species established in the wild has increased. It is worrying to note that five more bird species and one gecko have become established. Offsetting this concern is the fact that two previously established introduced birds have now died out (without management) in the wild. This shows that some establishments are temporary. Although many vertebrate pests have been eradicated from conservation areas (e.g. 184 populations of alien mammals cleared from islands; Parkes & Murphy 2003; Towns & Broome 2003; Bellingham et al. 2010) and numerous species are kept out of New Zealand using biosecurity laws, it is notable that no introduced species have been eradicated from New Zealand since the 1980s and that several new foreign species (mainly birds) have established wild populations. Potential conservation impacts of all these newly established foreign species appear not to have been considered seriously.

The ancient fauna

Recent fossil discoveries have added significantly to our understanding of the terrestrial vertebrate history of New Zealand. Zealandia's Late Cretaceous dinosaur fauna is now known to be quite diverse, with both of the two dinosaur orders and all the main groups represented (Molnar & Wiffen 1994). The fossil record of birds has been radically expanded, with further Cretaceous, Paleocene, Oligocene, Miocene, Pliocene and Early Pleistocene material reported. Of special note is the discovery of the world's most ancient penguins. The rich Early Miocene St Bathans Fauna has revealed the first frog, rhynchocephalid, gecko, skink, crocodylian and bat fossils for the Tertiary of Zealandia (Molnar & Pole 1997; Worthy et al. 2009a; Lee et al. in press). It has also produced a diverse avifauna (Worthy et al. 2007, 2008, 2009a), but most remarkable is the discovery here of a mouse-sized ground-dwelling mammal with no close affinities to any living groups (Worthy et al. 2006b), proving that land mammals did inhabit Zealandia. The only plausible explanation for their origin is that mammals were present in Zealandia as it split from Australis, and they then survived until at least the Early Miocene. This mammal joins other Miocene elements of the fauna (?neobatrachian frogs, crocodylians, palaelodids, swiftlets, cracticid songbirds and a ?noctilionoid bat) that are not represented in the modern New Zealand fauna. Despite these exciting fossil discoveries, many specimens remain to be studied in detail and most time periods in Zealandia's terrestrial vertebrate history still have a poor fossil record (see Table 3).

The origins of the modern New Zealand vertebrate fauna suggested by Fleming (1979) and Stevens (1980, 1989) have been largely supported by recent work. New research supports classic vertebrate examples – leiopelmatid frogs, tuatara and moa – as being of Gondwanan origin. Additionally, geckos, New Zealand's large parrots, New Zealand wrens and the Miocene land mammal (and possibly adzebills) can be added to these examples. However, the iconic kiwi may not in fact be Gondwanan in origin. Nevertheless, overall recent discoveries have strengthened the links to Gondwana and suggest that many New Zealand taxa have origins deeper in time than previously realised (contra Goldberg et al. 2008). The timing of the separation of Zealandia from the rest of Gondwana suggests that other vertebrate groups, such as monotremes and other ancient forms of mammal, and probably snakes, were also present, but did not survive until the present day. Extinction as an explanation for the absence of such groups is backed up by evidence of extinction of several other groups (?neobatrachian frogs, ?freshwater turtles, crocodylians, pterosaurs, dinosaurs, ?hesperornithids, bony-toothed pelicans, palaelodids, swiftlets, cracticid songbirds, a ?noctilionoid bat and the Miocene land mammal) on proto-New Zealand.

Other than vertebrates, notable Gondwanan elements in the biota are thought to include some plants and many invertebrates, e.g. kauri (*Agathis australis*), Petalidae harvestmen, Micropterigidae moths, weta (Orthoptera), freshwater crayfish (*Paranephrops* spp.) and bivalves (Hyriidae), and many other freshwater species (Stevens et al. 1995; Graf & Foighil 2000; Stöckler et al. 2002; Gibbs 2006; Knapp et al. 2007; Boyer & Giribet 2009; McDowall 2010).

Overall though, and as was traditionally held, new research has supported theories that a majority of terrestrial vertebrates (e.g. skinks, most birds and bats) reached Zealandia by dispersal since its separation from Australis.

The debate about Gondwanan versus dispersal origins is confounded somewhat by on-going uncertainty about the timing

of the complete separation of Zealandia from Australis. The widely used date of about 85–80 million years for the separation (e.g. Stevens 1989, 1991; Cooper & Millener 1993; Stevens et al. 1995; Cracraft 2001a; Gibbs 2006) has been challenged by new evidence. A possible land bridge connection between Zealandia and part of Australis (Queensland today) until the Early Eocene (Gaina et al. 1998) and other possible land bridges or emergent land north of proto-New Zealand even later than this (e.g. Herzer 1998; Lee et al. 2001; Meffre et al. 2006; Schellart et al. 2006; Ladiges & Cantrill 2007; Herzer et al. 2009) may have allowed terrestrial taxa, e.g. flightless kiwi ancestors, to reach proto-New Zealand overland much later than recently contemplated. A land connection between the landmass of Zealandia and proto-Queensland during the Late Cretaceous would explain the close relationship between the dinosaur faunas of these regions (Molnar & Wiffen 1994). It may also mean that, although pterosaurs and dinosaurs lived on Australis, they were extinct by the time of Zealandia's complete separation, so were not an insular fauna (contra Molnar & Wiffen 1994; Wiffen 1996; King et al. 2009). Such a land connection would have allowed dinosaurs to migrate to warmer areas during seasonally harsh conditions and could explain their apparently anomalous presence at such high latitudes (Molnar & Wiffen 1994; Wiffen 1996; Long 1998; King et al. 2009).

What happened to lineages of terrestrial vertebrates that were part of Zealandia's fauna, but left no modern descendants? Pterosaurs and dinosaurs were part of a worldwide extinction at the end of the Cretaceous 65 mya due to an asteroid impact (Alvarez et al. 1980; Hildebrand et al. 1991) and it is certain there were other extinction events in Zealandia's history. Some dramatic global climate changes have occurred during the last 50 million years and temperature drops appear to have had a considerable impact on southern biotas (e.g. Hornibrook 1992; Zachos et al. 2001). The Oligocene marine transgression markedly reduced the land area of Zealandia and may have been a cause of disruption to the vertebrate fauna (Cooper & Cooper 1995). Stevens (1989) speculated that Zealandian monotremes could have been a casualty of any of these environmental changes.

Many modern New Zealand terrestrial animal lineages may have gone through a genetic bottleneck as a result of the Oligocene marine transgression (Cooper & Cooper 1995; Baker 2007). It has been theorised that this transgression caused extinctions, then an expansion of habitat for taxa to spread and evolve into (Cooper & Cooper 1995). While no vertebrate fossils conclusively prove continuous land since Zealandia separated from Australis, they do supply evidence that a diverse range of taxa survived in Zealandia through the Oligocene. The rich Early Miocene terrestrial fossil fauna occurs perhaps as little as 3 million years after Zealandia was, according to some authors, completely inundated 25–22 mya (Campbell & Landis 2001; Campbell & Hutching 2007; Campbell et al. 2008; Landis et al. 2008). Several of the groups often considered to be Gondwanan have been found in this fauna indicating that they also would have had only a few million years to disperse to Zealandia if it had been completely submerged at the Oligocene–Miocene boundary. A more plausible scenario is that some land remained during this time and supported populations of these taxa. Molecular studies of several modern New Zealand vertebrates not thought to be of Gondwanan origin also indicate that they originated before the time of the maximum Oligocene transgression (e.g. *Anarhynchus* plovers in the Middle Eocene, Baker et al. 2007;

New Zealand wattlebirds in the Mid to Late Eocene, Shepherd & Lambert 2007; stitchbirds/hihi near the Eocene–Oligocene boundary, Driskell et al. 2007; Mohouinae in the Early Oligocene, Sibley & Ahlquist 1987; *Thinornis* plovers, snipe and piopio in the middle Oligocene, Christidis et al. 1996; Baker et al. 2007). In addition, the terrestrial plant fossil record spans the entire Oligocene (and, in fact, the entire Cenozoic history of Zealandia) and the Oligocene marine transgression does not even appear to have been a time of significant floral extinctions (Lee et al. 2001; contra Cooper & Millener 1993 and Goldberg et al. 2008). Moreover, rather than a time of extinctions, the Oligocene may have been a key period for allopatric speciation among New Zealand's *Oligosoma* skinks (Hickson et al. 2000). The biological evidence does not support the theory that Zealandia was completely submerged during the Late Oligocene–Early Miocene.

The two most probable causes of vertebrate extinctions between the Early Miocene and the time that humans arrived in New Zealand are the Middle Miocene climatic transition (abrupt cooling about 14 mya; Shevenell et al. 2004; Lewis et al. 2008) and the repeated climate fluctuations of the Late Pliocene–Pleistocene, since about 3 mya (Stevens 1980; Hornibrook 1992; Cooper & Millener 1993). There have been many climate-related extinctions in the flora of Zealandia since the Early Miocene (Mildenhall & Pocknall 1989; Pole 1994; Lee et al. 2001) but almost nothing is known about the effect of such events on Zealandia's vertebrate fauna because there are so few fossils known from this period. Fleming's (1962, 1974) suggestion that a "very large number of Tertiary [bird] colonists must have failed to survive till post-Pleistocene time" is supported by analysing the Early Miocene fauna from St Bathans. This fauna includes many genera and species not found in the modern fauna (Worthy et al. 2007). Overall however, the St Bathans avifauna bears a striking resemblance to the modern fauna at the family level, with the exception of the palaelodid, swiftlet and cracticid songbird – extinction of swiftlets is not unexpected given their tropical habitat preference and the much warmer climate in proto-New Zealand at the time (Worthy et al. 2007). Cooling climate is also the best explanation for the loss of ?neobatrachian frogs, crocodylians, cracticid songbirds, a ?noctilionoid bat and the Miocene land mammal from the fauna. Palaelodids became globally extinct in the Pleistocene and Baird & Vickers-Rich (1998) suggested that in Australia this was due to Late Pleistocene aridity. A similar reason may well explain their loss from New Zealand. Bony-toothed pelicans became globally extinct by the Pliocene (Olson 1985), for unknown reasons.

Clearly, some vertebrate groups left no descendants in New Zealand's modern fauna – but which other taxa became extinct and which left descendants? No modern species have a clear fossil record before the Pliocene (see Table 3). It seems that many vertebrate groups experienced a complex history on Zealandia, with extinctions and re-invasions through time. Examples of such a faunal change-over probably include oxyurine ducks, tadornine shelducks, diving petrels, penguins, rallid rails and vespertilionid bats. Zealandian fossils of these groups from the Early Pleistocene or before may not be direct ancestors of similar taxa in the modern fauna (see Worthy 1997; Worthy et al. 2006a, 2007; Worthy & Pledge 2007; Goldberg et al. 2008; Worthy & Lee 2008; and Table 3). Fossils may not necessarily identify the origins of related modern taxa nor indicate a continuous presence of such a group through to recent times. Further investigations and fossil discoveries are required to explain the origin and history of many of New Zealand's vertebrates.

Acknowledgements

Thanks to Tony Whitaker and Rod Hitchmough for advice on lizard taxonomy; Anne Musser for help with mammal history; Trevor Worthy, Sue Hand and Paul Scofield for providing valuable references and discussion; Te Papa staff: Jean-Claude Stahl for providing some biogeographic references, Jane Cherry for providing numerous bibliographic references; the many researchers whose work is summarised here; Dave Kelly and two anonymous referees for helpful comments on the manuscript; and the Department of Conservation and Landcare Research for sponsoring the publication of this special journal issue.

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Appendix 1. Explanations for the changed taxonomic status of amphibian and reptile species between the 1980s and 2009 (see Table 2).

Part 1. Species that have been named since 1989

Leiopelma pakeka Bell, Daugherty & Hay 1998; *Hoplodactylus cryptozoicus* Jewell & Leschen 2004; *Oligosoma inconspicuum* Patterson & Daugherty 1990; *Oligosoma polychroma* Patterson & Daugherty 1990; *Oligosoma microlepis* Patterson & Daugherty 1990; *Oligosoma notosaurus* Patterson & Daugherty 1990; *Oligosoma stenotis* Patterson & Daugherty 1994; *Oligosoma longipes* Patterson 1997; *Oligosoma taumakae* Chapple & Patterson 2007; *Oligosoma pikitanga* Bell & Patterson 2008; *Oligosoma northlandi* (Worthy 1991) (extinct); *Oligosoma townsi* (Chapple et al. 2008a); *Oligosoma hardyi* (Chapple et al. 2008b); *Oligosoma levidensa* (Chapple et al. 2008b).

Part 2. Species accepted in 2009 that were already named, but not accepted, in 1989

(see Gill & Whitaker 1996)

Sphenodon guntheri Buller 1877; *Hoplodactylus nebulosus* (McCann 1955); *Naultinus gemmeus* (McCann 1955); *Naultinus grayii* Bell 1843; *Naultinus manukanus* (McCann 1955); *Naultinus rudis* (Fischer 1882); *Naultinus stellatus* Hutton 1872; *Naultinus tuberculatus* (McCann 1955); *Oligosoma chloronoton* (Hardy 1977); *Oligosoma maccanni* (Hardy 1977).

Part 3. Species accepted in 1989, but not accepted in 2009

(see Gill 1986; Chapple et al. 2009)

Oligosoma gracilicorpus (Hardy 1997)

Part 4. Generic changes between 1989 and 2009

The Norfolk Island gecko *Phyllodactylus* became *Christinus* (see Cogger et al. 2006). All *Leiopelma* (in New Zealand) and *Cyclodina* skinks became *Oligosoma* (Patterson & Daugherty 1995; Cogger et al. 2006; Chapple et al. 2009).

Appendix 2. Explanations for the changed taxonomic status of bird species between the 1980s and 2009 (see Tables 4 & 5)

Part 1. Changes that have affected the numbers of species within orders

1) 34 subspecies have been elevated to full species status:

North Island brown kiwi (*Apteryx mantelli*), Auckland Island teal (*Anas aucklandica*), Campbell Island teal (*Anas nesiotis*), northern royal albatross (*Diomedea sanfordi*), antipodean albatross (*Diomedea antipodensis*), Chatham Island albatross (*Thalassarche eremita*), Campbell Island albatross (*Thalassarche impavida*), Salvin's albatross (*Thalassarche salvini*), subantarctic little shearwater (*Puffinus elegans*), Chatham Island shag (*Leucocarbo onslowi*), Bounty Island shag (*Leucocarbo ranfurlyi*), Auckland Island shag (*Leucocarbo colensoi*), Pitt Island shag (*Stictocarbo featherstoni*), Dieffenbach's rail (*Gallirallus dieffenbachii*), Macquarie Island rail (*Gallirallus macquariensis*), takahe (*Porphyrio hochstetteri*), New Zealand coot (*Fulica prisca*), North Island snipe (*Coenocorypha barrierensis*), South Island snipe (*Coenocorypha iredalei*), Chatham Island snipe (*Coenocorypha pusilla*), Snares Island snipe (*Coenocorypha huegeli*), Norfolk Island pigeon (*Hemiphaga spadicea*), Chatham Island pigeon (*Hemiphaga chathamensis*), Norfolk Island green parrot (*Cyanoramphus cookii*), Forbes' parakeet (*Cyanoramphus forbesi*), Chatham Island fernbird (*Bowdleria rufescens*), Snares Island fernbird (*Bowdleria caudata*), Norfolk Island gerygone (*Gerygone modesta*), North Island tomtit (*Petroica toitoi*), Snares Island tomtit (*Petroica dannefaerdi*), North Island robin (*Petroica longipes*), Chatham Island bellbird (*Anthornis melanocephala*), North Island kokako (*Callaeas wilsoni*), North Island saddleback (*Philesturnus rufusater*) (Holdaway et al. 2001; for *Apteryx mantelli* see Tennyson et al. 2003, for *Diomedea antipodensis* see BirdLife International 2000, and for *Gerygone modesta* see Christidis & Boles 1994).

2) Ten species have been relegated into junior synonymy with other species (senior synonyms are given in square brackets): Mappin's moa *Pachyornis mappini* [Mantell's moa *Pachyornis geranoides*] (Worthy 2005a), stout-legged moa *Eurapteryx geranoides* [stout-legged moa *Eurapteryx curtus*] (Tennyson & Martinson 2007), slender bush moa *Dinornis struthoides* [North Island giant moa *Dinornis novaezealandiae*], giant moa *Dinornis giganteus* [North Island giant moa *Dinornis novaezealandiae*] (Bunce et al. 2003), New Zealand pelican *Pelecanus conspicillatus novaezealandiae* [Australian pelican *Pelecanus conspicillatus*, which occurred in New Zealand only as a vagrant] (Worthy 1998; Gill & Tennyson 2002; Scofield et al. 2003), New Zealand hawk *Circus eylesi* [Forbes' harrier *Circus teauteensis*] (Tennyson & Martinson 2007), southern sea eagle *Haliaeetus australis* [a non-New Zealand eagle of uncertain species] (Holdaway et al. 2001; Worthy & Holdaway 2002), weka *Gallirallus minor* [weka *Gallirallus australis*] (Holdaway & Worthy 1997), Norfolk Island boobook *Ninox undulata* [*Ninox novaeseelandiae undulata*] (Holdaway et al.

2001), North Island stout-legged wren *Pachyplichas jagmi* [South Island stout-legged wren *Pachyplichas yaldwyni*] (Holdaway et al. 2001; Worthy & Holdaway 2002).

3) Seven further species have been recognised as post-human settlement immigrants: black-browed albatross (*Thalassarche melanophris*), soft-plumaged petrel (*Pterodroma mollis*), Australasian bittern (*Botaurus poiciloptilus*), little black shag (*Phalacrocorax sulcirostris*), Australasian harrier (*Circus approximans*), pukeko (*Porphyrio melanotus*), pied stilt (*Himantopus leucocephalus*) (Holdaway et al. 2001).

4) Five species previously described, but regarded as junior synonyms of other species, are now regarded as valid species: Mantell's moa (*Pachyornis geranoides*) (Worthy 2005a), South Island giant moa (*Dinornis robustus*) (Bunce et al. 2003), Forbes' harrier (*Circus teauteensis*) (Tennyson & Martinson 2007), South Island adzebill (*Aptornis defosser*) (Checklist Committee 1990), New Zealand raven (*Corvus antipodum*) (Gill 2003).

5) Five foreign species introduced by humans have become established breeders in the wild in New Zealand: the red-legged partridge (*Alectoris rufa*) was introduced in the 1980s; turkeys (*Meleagris gallopavo*), tufted guineafowl (*Numida meleagris*), feral geese (*Anser anser*) and galahs (*Cacatua roseicapilla*) are now regarded as established breeders (Checklist Committee 1990; Holdaway et al. 2001). However, the establishment of some of these species may be fleeting, as two other introduced species (grey partridge *Perdix perdix* and bobwhite quail *Colinus virginianus*) have been removed from the list of established breeders during the same period (Holdaway et al. 2001) and red-vented bulbuls (*Pycnonotus cafer*) do not appear to have established in New Zealand recently (Robertson et al. 2007; contra Holdaway et al. 2001).

6) Three species not in 1980s lists are newly described: Okarito brown kiwi (*Apteryx rowi*) (Tennyson et al. 2003), Waitaha penguin (*Megadyptes waitaha*) (Boessenkool et al. 2009) and Scarlett's shearwater (*Puffinus spelaeus*) (Holdaway & Worthy 1994).

7) The Kermadec megapode (*Megapodius* species unknown) is a unique case. Its existence was in doubt in the 1980s, but new evidence corroborates nineteenth century eye-witness accounts (Holdaway et al. 2001).

8) The black swan (*Cygnus atratus*) is a unique case. Although many were introduced to New Zealand, it is now regarded as a native species because it has a fossil record (formerly regarded as the New Zealand swan *Cygnus sumnerensis*) and continues to colonise naturally from Australia (Holdaway et al. 2001).

9) Discovery of a breeding population of one species in the New Zealand region: Wilson's storm petrel (*Oceanites oceanicus*) breeds on Bishop Island, south of Macquarie Island (Garnett & Crowley 2002).

10) Rediscovery of one living species (the New Zealand storm petrel *Pealeornis maorianus*) that was not considered a valid species in the 1980s (Holdaway et al. 2001; Flood 2003; Stephenson 2004).

Part 2. Generic and species status changes that have not affected the numbers of species within orders

1) 14 species placed in different genera (the 1980s name is given in square brackets): Californian quail (*Callipepla californica*)

[*Lophortyx californica*], Finsch's duck (*Chenonetta finschi*) [*Euryanas finschi*], Buller's albatross (*Thalassarche bulleri*) [*Diomedea bulleri*], white-capped albatross (*Thalassarche cauta*) [*Diomedea cauta*], grey-headed albatross (*Thalassarche chrysostoma*) [*Diomedea chrysostoma*], New Zealand dabchick (*Poliiocephalus rufopectus*) [*Podiceps rufopectus*], white heron (*Ardea alba*) [*Egretta alba*], white-faced heron (*Egretta novaehollandiae*) [*Ardea novaehollandiae*], banded rail (*Gallirallus philippensis*) [*Rallus philippensis*], Auckland Island rail (*Dryolimnas muelleri*) [*Rallus pectoralis muelleri*], Hutton's rail (*Cabalus modestus*) [*Rallus modestus*], New Zealand owllet-nightjar (*Aegotheles novaeseelandiae*) [*Megaegotheles novaeseelandiae*], sacred kingfisher (*Todiramphus sanctus*) [*Halcyon sancta*], brown creeper (*Mohoua novaeseelandiae*) [*Finschia novaeseelandiae*].

2) The specific name of four species changed within a genus (the 1980s name is given in square brackets): New Zealand stiff-tailed duck *Oxyura vantetsi* new species (Worthy 2005b) [*Oxyura australis* (Holdaway 1989; Checklist Committee 1990)]; Australasian bittern *Botaurus poiciloptilus* (Checklist Committee 1990) [*Botaurus stellaris poiciloptilus* (Checklist Committee 1970)]; Macquarie Island shag *Leucocarbo purpurascens* (Holdaway et al. 2001) [*Leucocarbo albiventer purpurascens* (Checklist Committee 1970)]; long-billed wren *Dendroscansor decurvirostris* new species (Millener & Worthy 1991) [*Acanthisittidae* N. gen. 1 (Holdaway 1989)].