Miocene mammal reveals a Mesozoic ghost lineage on insular New Zealand, southwest Pacific

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New Zealand (NZ) has long been upheld as the archetypical example of a land where the biota evolved without nonvolant terrestrial mammals. Their absence before human arrival is mysterious, because NZ was still attached to East Antarctica in the Early Cretaceous when a variety of terrestrial mammals occupied the adjacent Australian portion of Gondwana. Here we report discovery of a nonvolant mammal from Miocene (19–16 Ma) sediments of the Manuherikia Group near St Bathans (SB) in Central Otago, South Island, NZ. A partial relatively plesiomorphic femur and two autapomorphically specialized partial mandibles represent at least one mouse-sized mammal of unknown relationships. The material implies the existence of one or more ghost lineages, at least one of which (based on the relatively plesiomorphic partial femur) spanned the Middle Miocene to at least the Early Cretaceous, probably before the time of divergence of marsupials and placentals >125 Ma. Its presence in NZ in the Middle Miocene and apparent absence from Australia and other adjacent landmasses at this time appear to reflect a Gondwanan vicariant event and imply persistence of emergent land during the Oligocene marine transgression of NZ. Nonvolant terrestrial mammals disappeared from NZ some time since the Middle Miocene, possibly because of late Neogene climatic cooling.

Gondwana | Miocene | nontherian mammal | vicariant event

New Zealand (NZ), the emergent part of a continental fragment ≈1,400 km east of Australia, is a land of birds, where the only known terrestrial mammals in the Recent fauna are three species of bats (1) whose ancestors may have dispersed from Australia sometime in the mid to late Cenozoic (2). Lack of evidence for nonflying mammals before the arrival of humans has been enigmatic, because NZ was still attached to East Antarctica in the Early Cretaceous, a time when a variety of terrestrial mammals occupied the adjacent Australian portion of Gondwana (3, 4). NZ separated from Gondwana ≈82 Ma (5, 6), and much of its endemic biota (e.g., southern beeches, onychophorans, leiopelmatid frogs, tuatara, and acanthisittid wrens) is generally thought to reflect this last continental attachment (1, 5). Such a view assumes that land was continuously present during the Tertiary, but that eustatic submergence of most of NZ in the Oligocene (30–25 Ma) reduced the land area of this archipelago to ≈20% of current size (5, 7) and may have led to the extinction of some Gondwanan groups (7, 8). In contrast to the prevailing view that some land and hence biota existed throughout the Tertiary, some geologists and biogeographers have recently argued that during the Oligocene transgression, there was possibly no emergent land (9), and the entire modern biota of NZ may be the result of dispersal from nearby landmasses (e.g., refs. 10–12).

The NZ terrestrial fossil faunal record has been silent in this regard; although NZ has a rich late Quaternary terrestrial fossil vertebrate record, it has one of the world's poorest preQuaternary records. Except for fragmentary Late Cretaceous (80–71 Ma) dinosaur material (13) and isolated moa bones from marine sediments up to 2.5 Ma (1, 14), the terrestrial record older than 1 Ma is extremely limited. Until now, there has been no direct evidence for the pre-Pleistocene presence in NZ of any of its endemic vertebrate lineages, particularly any group of terrestrial nonvolant mammals, let alone the latter's survival into the Miocene.

In 1978, a previously unknown fauna was discovered near SB, Central Otago, South Island, NZ, in the Early Miocene sediments of the Manuherikia Group, containing, anatids and fish (8, 15). Recent excavations from three locations in the SB district have recovered a sphenodontid, a crocodilian, geckos, skinks, bats, a minimum of 24 avian taxa (16, 17), and a terrestrial mammal described below.

An Early to earliest Middle Miocene age (19–16 Ma) for sediments in the Manuherikia River section has been determined by comprehensive palynology studies, placing the vertebrates within the Casuarinaceae biozone of the regional palynostratigraphic scheme (18–20). Globally, this was a period of habitat change where warm perpetually wet forests became drier and cooler, with more seasonal definition (21). Lake Manuherikia was surrounded by an extensive fluvial plain with grasslands, herbfields, and peat-forming swamp-woodland, with relatively dry Casuarinaceae woodland nearby (18, 22).

Results

Palaeontology: First Nonvolant Terrestrial Mammal from NZ. At least one species of nonflying terrestrial mammal is represented by three specimens from the HH1a site, two almost-identical mandibular fragments and one femoral fragment. Because all three could represent the same mouse-sized animal and are the first remains of a terrestrial mammal known from NZ, we have tentatively presumed they represent a single phylogenetically enigmatic taxon. An alternative hypothesis would be that the femoral fragment represents a relatively archaic mammal, whereas the mandibles represent a second relatively more derived mammal. Discovery of further material will be required before these alternative hypotheses can be adequately tested. In the meantime, we provide here a description and comparison of all of the terrestrial mammal material discovered to date.

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Abbreviations: NZ, New Zealand; SB, St Bathans.

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EVOLUTION

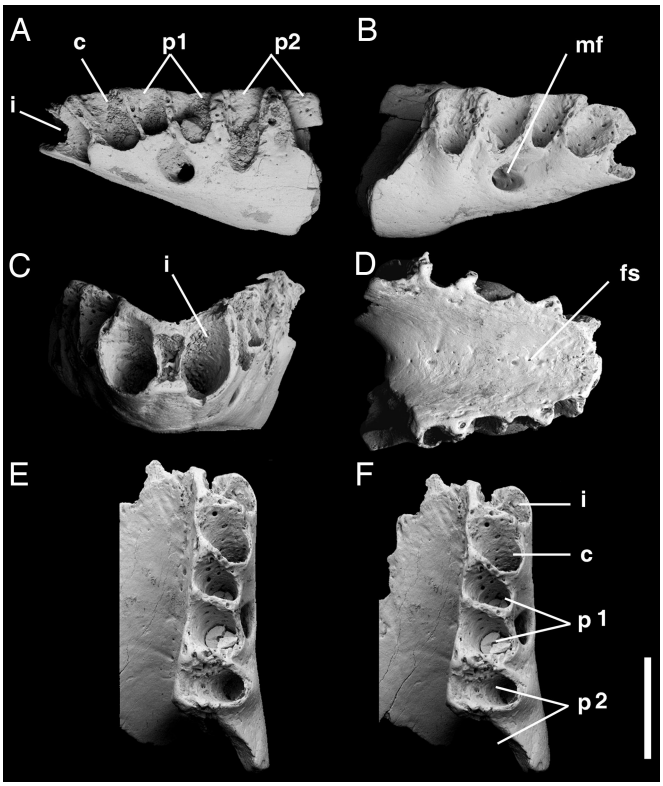

Fig. 1. First pre-Pleistocene mammal from NZ. MNZ S.40958, edentulous mandibular fragment. (*A*) Left lateral view. (*B*) Right lateral view. (*C*) Anterior view. (*D*) Dorsal view. (*E* and *F*) Stereopair occlusal view. fs, fused symphysis; i, c, p1, and p2, alveoli for incisor, canine, and two premolars (the homology of premolars is uncertain); mf, mental foramen; MNZ S, prefix for catalog numbers of the Vertebrate Fossil Collection, Museum of New Zealand Te Papa Tongarewa, Wellington. (Scale bar, 2 mm.)

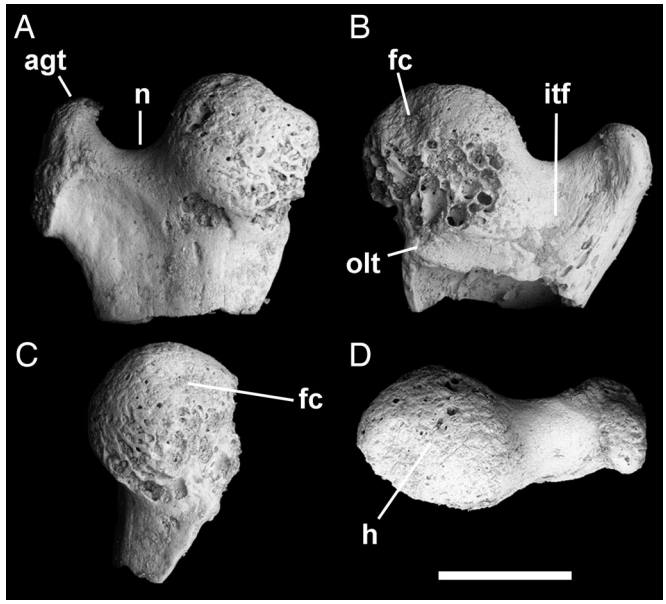

Fig. 2. First pre-Pleistocene mammal from NZ. MNZ S.42214, proximal section of a right femur. (*A*) Dorsal view. (*B*) Ventral view. (*C*) Medial view. (*D*) Proximal view. agt, apex of greater trochanter; fc, fovea capita for acetabular ligament; h, head; itf, intertrochanteric fossa; n, notch between greater trochanter and head; olt, origin of lesser trochanter. (Scale bar, 2 mm.)

Mandibles. MNZ S.40958 (Fig. 1) is an edentulous mandibular fragment consisting of fused left and right anterior ends of the dentaries with six alveoli preserved on the left side and five on the right. MNZ S.41866 is a second smaller nearly identical edentulous mandibular fragment preserving the same but fewer features, reflecting its more incomplete nature. Key features include the long fused symphysis; evidently procumbent medial incisor; and five additional alveoli that suggest a dental formula of one incisor, one canine, and two double-rooted premolars [see supporting information (SI)].

Femur. MNZ S.42214 (Fig. 2) is the proximal end of a right femur. It preserves the head, greater trochanter, and proximal edge of the crest that led to the lesser trochanter. Some muscle scars are also preserved. Key features include the round head, which sits on a very short poorly defined neck, the latter being less well defined than it is in monotremes; the surface bone is dense and preserves sharply defined features indicating it is adult; there are no indications of fused epiphyses (see SI), and the specimen has a distinct fovea for the acetabular ligament on the head (in therians, the fovea is on the epiphysis); the head and neck are orientated slightly dorsomedially with respect to the long axis of the femoral shaft; the greater trochanter projects laterally with little dorsal expansion; a marked trough separates the head and neck from the greater trochanter; ventrally a shallow intertrochanteric fossa is present (no digital or obturator fossa); and the lesser trochanter appears to have been on the postero- or ventromedial side of the shaft (see SI).

The orientation of the femur with respect to the body cannot be determined with confidence, in part because of uncertainty about the orientation of the glenoid fossa of the pelvis. That the fovea capita is positioned near the top of the head, which lacked a well developed neck, suggests the animal had an abducted or somewhat sprawling femoral posture. But, if we are correct in interpreting that the femoral head projects slightly dorsomedially with respect to the shaft of the femur, and that the lesser trochanter had its origin ventrally, then the femur did not project out to the side in the extreme abducted posture of monotremes.

Comparisons: Evidence for an Archaic Mammalian Lineage. For reasons noted below, we have made the assumption on the basis of parsimony that the mandibular and femoral remains represent a single taxon. Because these comparisons involve all of the material, if our single-species assumption is subsequently falsified, comparisons presented below will still stand. In terms of which specific groups of mammals would be most appropriately compared with the SB taxon, whether the SB mammal occurs in NZ as the result of a vicariant event relating to the 82-Ma separation of NZ from Antarctica or as the result of a dispersal event occurring subsequent to that time, the nearest large land masses likely to provide an ancestral source for the SB mammal are Australia and East Antarctica. Australia has hosted evolutionary radiations of monotremes, ausktribosphenids, marsupials, bats, and other tribosphenidan groups (see also SI) (3, 23–26). Although no fossil mammals have yet been found in East Antarctica, because monotremes, marsupials, and placentals are also known to have been in South America (and some in West Antarctica) while that continent was still joined to Antarctica, detailed comparison with these mammal groups in particular is warranted (3, 4, 23, 27).

Ausktribosphenida. Ausktribosphenids have a long, unfused, transversely narrow symphysis unlike that of the SB mandibles (4, 23). Alveoli for the anterior cheekteeth are narrow and elongate rather than round, with long spaces of nondentigenous areas between the premolars. Postcranials of ausktribosphenids are unknown.

Monotremata. All known monotremes have unfused jaws, no canines, epiphyses on the long bones, and they lack a fovea capita

on the femoral head. In these features, they differ markedly from the SB mammal. None of the extinct monotremes, including the exceptionally preserved *Obdurodon dicksoni* (28), is represented by a complete anterior part of the dentary or the proximal end of a femur. However, the SB femur is further unlike those of living monotremes in having a more oval crosssection of the shaft at the level of the top of the lesser trochanter rather than a broad (relatively plesiomorphic) and compressed crosssection. The remnant of the crest leading to the missing lesser trochanter suggests this process was more reduced and ventrally shifted than in living monotremes.

Marsupialia and Placentalia. On the SB mandibles, the position of the mental foramen beneath the alveoli is further forward than in most marsupials, in which it is normally below or near m1. Fusion of the symphysis is absent in archaic marsupial groups (25), although it occurs in some derived Cenozoic groups (e.g., vombatids and sthenurine macropodids) and in some derived placentals (e.g., some primates). The length and transversely flattened shape of the symphysis are also unlike the condition in plesiomorphic marsupials or placentals. The apparent reduced number of incisors in each dentary is unlike any Mesozoic marsupial group in which at least three small incisors are present. However, certain derived marsupials (e.g., diprotodontians) have a reduced lower incisor number and a procumbent hypertrophied i1, which may be similar to (preservation is not adequate to be certain) the SB mammal. The femur is unlike that of any marsupial in its very short neck below the head and in the presence of a shallow ventral intertrochanteric fossa rather than a deep digital fossa.

The mandibular fragments and proximal end of the femur do not resemble those of any group of placentals. Closer comparison with bats in particular, which are an existing group in NZ and good intercontinental dispersers, reveals none of the chiropteran synapomorphies such as a chin process. Undoubted mystacinids, a group of Gondwanan bats that characterize the modern NZ biota, are, however, represented by other SB postcranial elements.

Other Mesozoic Mammaliaforms and Cynodonts. The SB mammal was compared with other Mesozoic mammaliaform groups and cynodonts represented by dentaries and/or femora (see SI), including *Oligokyphus*, eutriconodontans (*Jeholodens*), morganucodontans, multituberculates, spalacotheroid symmetrodonts (*Zhangheotherium*), vincelestids (*Vincelestes*), docodonts (*Haldanodon*), and early placentals (*Eomaia*). None shares the unique combination of distinctive mandibular and femoral derived features.

In the SB mammal, presence of a trochantal notch and the absence of a ridge on the trochanter indicate it is more derived than all cynodonts except tritylodontids; absence of a ridge between the head and greater trochanter suggests it is more derived than tritylodontids and morganucodontans; a marked fovea capita indicates it is at least as derived as morganucodontans, although eutriconodontans (*Jeholodens* and *Gobiconodon*), docodonts (*Haldanodon*), and monotremes lack a fovea; lateral orientation of the greater trochanter (as opposed to dorsal) is like morganucodontans, *Haldanodon* (29) and *Ornithorhynchus* and differs markedly from the dorsal orientation of multituberculates and most trechnotheres sensu Luo *et al.* (26, 30); absence of several apomorphic states (a well developed digital fossa, a well developed neck for the head, dorsal orientation of greater trochanter, and apparent lack of epiphyses) excludes it from membership in crown groups of mammals more derived than *Gobiconodon* and *Jeholodons*. A notable exception is the specialized spalacotheriid symmetrodont *Akidolestes* (a trechnothere) in which the proximal femur had a similar structure to those of morganucodontans with a short neck and shallow ventral intertrochanterial fossa (presence of a fovea was not mentioned), features related to locomotion and a sprawling posture shared with monotremes (31); however, the mandibular fragments of the SB mammal exhibit no affinities with *Akidolestes*.

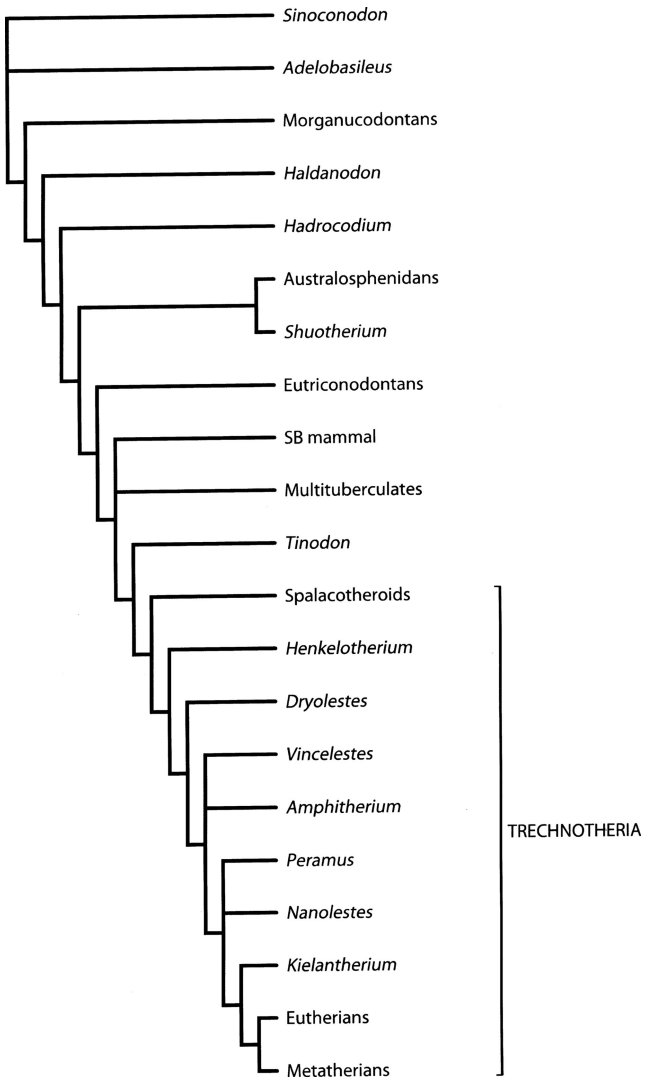

Fig. 3. Position of the SB mammal in the phylogeny of mammaliaforms based on the strict consensus of 192 equally parsimonious trees from a matrix of 75 taxa and 414 morphological characters (ref. 31; see also SI supporting information). Treelength, 1,826; consistency index, 0.404; retention index, 0.793. Nonmammalian outgroups are not shown. Morganucodontans, australosphenidans, eutriconodontans, multituberculates, spalacotheroids, eutherians, and metatherians all comprise multiple taxa that have been collapsed to single terminals (see SI supporting information). Trechnotheria (including therians and closely related groups) is indicated.

Phylogenetic Position Within Mammaliaforms. The comparisons above suggest that the SB material, presumed here to represent a single taxon, is from a basal mammal probably more derived than morganucodontans and more primitive than multituberculates and trechnotheres and which is not a monotreme or an eutriconodontan, accepting the phylogenetic systematics of Luo *et al.* (ref. 26, Fig. 1). A strict consensus of 192 equally parsimonious trees from a matrix of 75 mammaliform taxa and 414 morphological characters (see *Materials and Methods*) places the SB mammal in an unresolved trichotomy with multituberculates and (trechnotherians + *Tinodon*), with monotremes and other australosphenidans outside this clade (Fig. 3); this suggests that the SB taxon is a member of the mammalian crown group but a distinct lineage separate from both monotremes and therians.

However, alternative positions for the SB mammal, including within Monotremata and within Theria cannot be statistically rejected (see SI).

Discussion

The Manuherikia Group sediments provide the first terrestrial vertebrate fauna of Tertiary age for NZ. Although the palynological dating is imprecise at 19–16 Ma, it is based on floras from sediments bounding the beds containing the mammal fossils. We consider that there is no possibility that the vertebrate fossils come from unrecognized significantly older deposits. The Manuherikia sediments extend as the fluvial Dunstan Formation many tens of meters below the Bannockburn Formation and were deposited on unfossiliferous schist. The mammal bones derive from a well differentiated sand layer within the Bannockburn Formation. The associated diverse fossil avifauna is typical of global Miocene faunas (16) and reworking, transport, and inclusion of three small fragile mammal fossils a significant distance from an unknown source is most improbable.

The SB fauna also provides the first look at the mammals and other vertebrates living in NZ subsequent to the maximum Oligocene submergence ca. 30–25 Ma, hypothesized to have been a bottleneck to species diversity based on DNA divergence dates for various taxa (7). Our results suggest that previously undetected higher-order taxa, including at least one group of terrestrial mammals, survived in NZ after separation from Gondwana 82 Ma, and that there have been considerable changes to NZ's vertebrate community since the late Early Miocene. It is theoretically possible that this SB mammal was natatorial and dispersed or rafted across the open ocean from Australia to NZ sometime after the Oligocene, subsequently going extinct in Australia, but three factors make this seem improbable. First, the preserved portion of the femur is rather conventionally shaped with little if anything to suggest that its owner would have been a good swimmer (and certainly nothing to suggest it was a good flyer). Second, despite discovery of many early Tertiary mammals from Murgon, southeastern Queensland (32), and highly diverse mammals from the Oligocene to Pliocene of central Australia and Riversleigh (33), nothing like the SB remains have been recovered from these richly fossiliferous Australian deposits. Third, NZ was >1,000 km distant from Australia, Antarctica, and South America by 65 Ma, further reducing the probability that a terrestrial group of mammals, otherwise unknown from any of the closest land masses, dispersed sometime in the Cenozoic to NZ.

We conclude that at least one previously unknown group of terrestrial mammals of uncertain affinities inhabited NZ between the Late Cretaceous and Early Miocene. This small mammal implies a long-surviving ghost lineage on the NZ archipelago and is thus a Mesozoic survivor, as are leiopelmatid frogs, tuatara, and acanthisittid wrens, archaic groups that persist in the Recent NZ fauna. The presence of this archaic mammalian lineage in the NZ fossil record and its absence from the fossil record of Australia and other adjacent landmasses suggest it represents a Gondwanan vicar and imply that at least some land remained emergent during the Oligocene drowning of NZ. Continued excavation of the SB deposits will provide additional independent evidence about the pre-Pleistocene history of NZ's terrestrial vertebrates that will further test competing biogeographic hypotheses about the origins of its biota (10).

Finally, the SB mammal indicates that evolution of the biota in the "land of birds" may have been only in the absence of land mammals for the last few million years, not the 82 Ma commonly presumed. Reasons for its Neogene extinction may be related to the severe and widespread climate deterioration that began in the southwest Pacific in the Middle Miocene (21, 34).

Materials and Methods

Stratigraphy. The SB vertebrate remains were recovered from near-shore freshwater lake sediments (Bannockburn Formation) deposited in Miocene Lake Manuherikia, which extended >5,600 square kilometers (22). Slight abrasion suggests the bones have been transported by water. The mammal bones derive from Bed HH1a, a sand layer bound by clay layers, in the Manuherikia River section, 6.88–7.0 m above the base of the Bannockburn Formation, allocated H41/f88 in the archival Fossil Record File of the Geological Society of NZ.

Phylogenetic Analysis. To formally assess the phylogenetic affinities of the SB mammal, we added it to a large morphological character matrix recently used to investigate mammaliaform relationships (31). We also included an additional character ("form of ventral intertrochanteric area"), resulting in a matrix of 414 characters (of which 13 could be scored in the SB mammal) for 75 taxa. One thousand heuristic replicates were carried out, saving 10 trees per replicate, followed by a second heuristic search within the trees saved from the first stage, by using PAUP (version 4.0b1.0; SI), with all characters unordered.

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