

A sphenodontine (Rhynchocephalia) from the Miocene of New Zealand and palaeobiogeography of the tuatara (*Sphenodon*)

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Jaws and dentition closely resembling those of the extant tuatara (*Sphenodon*) are described from the Manuherikia Group (Early Miocene; 19–16 million years ago, Mya) of Central Otago, New Zealand. This material is significant in bridging a gap of nearly 70 million years in the rhynchocephalian fossil record between the Late Pleistocene of New Zealand and the Late Cretaceous of Argentina. It provides the first pre-Pleistocene record of Rhynchocephalia in New Zealand, a finding consistent with the view that the ancestors of *Sphenodon* have been on the landmass since it separated from the rest of Gondwana 82–60 Mya. However, if New Zealand was completely submerged near the Oligo-Miocene boundary (25–22 Mya), as recently suggested, an ancestral sphenodontine would need to have colonized the re-emergent landmass *via* ocean rafting from a currently unrecorded and now extinct Miocene population. Although an Early Miocene record does not preclude that possibility, it substantially reduces the temporal window of opportunity. Irrespective of pre-Miocene biogeographic history, this material also provides the first direct evidence that the ancestors of the tuatara, an animal often perceived as unsophisticated, survived in New Zealand despite substantial local climatic and environmental changes.

Keywords: biogeography; fossil; Gondwana; Miocene; Rhynchocephalia; Sphenodontinae

1. INTRODUCTION

The New Zealand tuatara (*Sphenodon*) is the only living member of the Rhynchocephalia (*sensu* Gauthier *et al.* 1988), the sister taxon to the Squamata (snakes, amphisbaenians and lizards). *Sphenodon* is often mistakenly described as a ‘living fossil’ (e.g. Robb 1977). However, fossil rhynchocephalians were surprisingly diverse in their morphology, diet and lifestyle (e.g. Reynoso 2000; Jones 2006*a,b*, 2008), and many features of the living genus, previously thought primitive, are now known to be derived (e.g. Gans 1983; Whiteside 1986; Evans 2003; Jones 2008). Furthermore, although squamates and rhynchocephalians separated 240–250 Mya, the latter are the more common in early Mesozoic assemblages and are found worldwide (figure 1), including England and Wales where their fossil remains occur in substantial quantities (e.g. Fraser 1988). However, the geographical range of rhynchocephalians seems to contract after the Early Jurassic, first in Laurasia and later in Gondwana (Evans *et al.* 2001, Apesteguía & Novas 2003; Apesteguía 2005*a*; Jones 2006*c*), possibly as the result of the competition with derived lizards (Saint-Girons 1985; Milner *et al.* 2000) and/or mammals (Gorniak *et al.* 1982; Whiteside 1986; Jones 2006*b*).

In marked contrast to its Early Mesozoic relatives, *Sphenodon* is restricted to approximately 35 islands off the coast of New Zealand (MacAvoy *et al.* 2007), mainland populations having become extinct with the arrival of humans (and associated animals, such as rats) *ca* 750 years ago (Towns & Daugherty 1994, Higham *et al.* 1999). *Sphenodon* bones are known from several Holocene localities (e.g. Crook 1975, Worthy & Holdaway 1996) but the oldest known rhynchocephalian material from New Zealand is currently Late Pleistocene in age, between 27 000 and 34 000 years old (Worthy & Grant-Mackie 2003). Previous reports of Miocene *Sphenodon* material (e.g. Crook 1975, p. 338; Rich 1975, p. 50; Robb 1977, p. 4) were based on a misidentified Holocene prey accumulation of the laughing owl *Sceloglaux albifacies* (Worthy & Holdaway 1996). Outside New Zealand, apart from a problematic lepidosaur specimen from the Palaeocene of Morocco (Augé & Rage 2006), the next most recent records of rhynchocephalians are from the Late Cretaceous Allen (Martinelli & Forasiepi 2004; Apesteguía & Rougier 2007) and Los Alamos formations (Apesteguía 2005*b*) of Argentina (*ca* 70 Mya).

Here, we describe the first unambiguous pre-Pleistocene and post-Mesozoic rhynchocephalian material from the Miocene of New Zealand. This makes a significant addition to both the poorly known fossil record of New Zealand and the scant post-Mesozoic history of Rhynchocephalia. It also impacts on an ongoing debate as to the history of

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Figure 1. Rhynchocephalian localities. (a) Global map showing fossil localities (see the electronic supplementary material). (b) New Zealand, redrawn from Hay *et al.* (2003). Triangles, Triassic; squares, Jurassic; filled circles, Cretaceous; diamonds, Palaeocene?; asterisk, Miocene; pluses, Pleistocene; open circles, Holocene; down triangles, extant populations. Scale bar, 200 km. 175×73 mm (600×600 dpi).

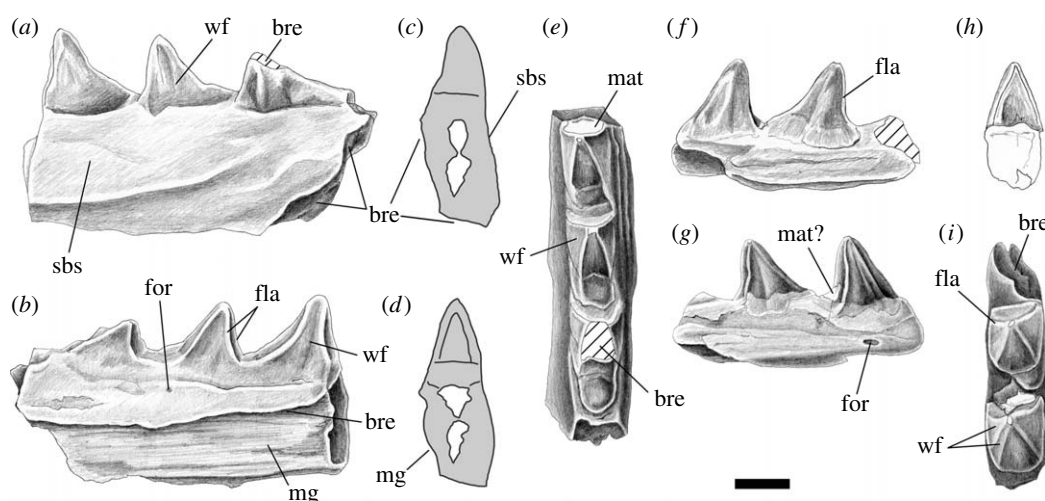


Figure 2. Partial sphenodontine dentaries from the Miocene Bannockburn Formation of New Zealand. (a,e) Specimen NMNZ S42282 and (f,i) specimen NMNZ S43075; (a,f) labial views, (b,g) lingual views, (c,h) anterior views, (d) posterior view, and (e,i) apical views. bre, breakage; fla, flange; for, foramen; mat, matrix; mg, meckelian groove; sbs, secondary bone skirt; wf, wear facet. Scale bar, 1 mm. 175×82 mm (600×600 dpi).

New Zealand’s unique fauna and flora. It has recently been proposed that New Zealand was totally submerged sometime around the Oligocene–Miocene boundary (25–22 Mya), requiring that New Zealand’s entire fauna, previously considered partially vicariant and archaic, is actually secondary (e.g. Campbell & Landis 2001; Waters & Craw 2006; Trewick *et al.* 2007; Campbell & Hutching 2008; Landis *et al.* 2008). An Early Miocene rhynchocephalian clearly has implications for this hypothesis.

2. SYSTEMATIC PALAEONTOLOGY

Rhynchocephalia Günther (1867) *sensu* Gauthier *et al.* (1988).

Sphenodontinae Cope (1871) *sensu* Reynoso (1996) cf. *Sphenodon* sp.

(a) Material

Three partial dentaries: a right bearing two posterior teeth (NMNZ S43075); a left bearing three posterior teeth (NMNZ S42282); and a left bearing five anterior teeth (NMNZ S50860) (figures 2 and 3).

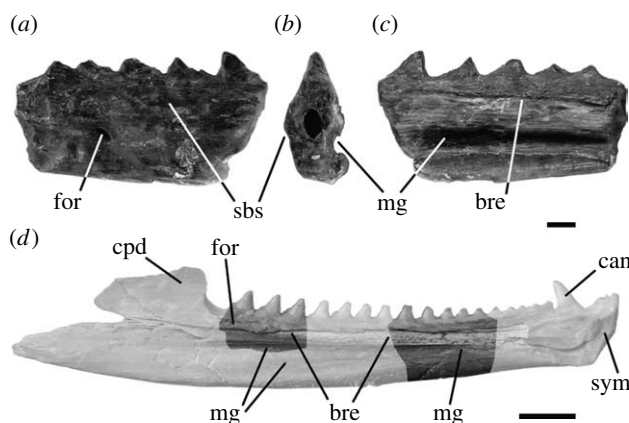


Figure 3. Dentaries. Specimen NMNZ S50860 in (a) labial, (b) posterior and (c) lingual view. (d) A Holocene *Sphenodon* left dentary (CMC Rep35 from Marfell’s Beach, Lake Grassmere, Marlborough, northern South Island) in lingual view indicating the parts of the dentary preserved by NMNZ S42282 and NMNZ S50860. bre, breakage; can, caniniform; cpd, coronoid process of the dentary; mg, Meckelian groove; sym, symphysis. Scale bar (a–c), 1 mm; scale bar (d), 5 mm. 83×57 mm (600×600 dpi).

(b) Locality

St Bathans, Central Otago, South Island, NZ; Bannockburn Formation of the Manuherikia Group, Early Miocene, 19–16 Mya, St Bathans Fauna (Worthy *et al.* 2006, 2007; see the electronic supplementary material).

(c) Palaeoenvironment

Sediments from the palaeo-Lake Manuherikia (more than 5600 km²) have yielded a diverse array of invertebrates, fishes, geckos, skinks, birds, a crocodylian, bats and an archaic terrestrial mammal (Molnar & Pole 1997; Worthy *et al.* 2002, 2006, 2007; Pole *et al.* 2003; Gibbs 2006; Worthy & Lee 2008). The climate was warm temperate and there was a wide range of vegetation including eucalypts, casuarinas, podocarps and palms (Pole *et al.* 2003; Pole 2008).

(d) Description

Although incomplete, the dentaries are well preserved. The teeth are acrodont (fused to the crest of the jawbone) and pyramidal with an anteriorly positioned apex (figure 2*a,b,f,g*). The anterior surface of each tooth is concave and bordered by weak anterolingual and anterolabial flanges (figure 2*e,i*), and the labial and lingual surfaces of all teeth are slightly worn (figure 2*e,i*). The bases of the teeth in NMNZ S42282 decrease in mesiodistal length from the posterior end (figure 2*a,e*).

The labial surface of NMNZ S42282 shows the posterior end of a secondary bone 'skirt' below the tooth row (figure 2*a*) whereas NMNZ S50860 shows the anterior end (figure 3). The lingual surfaces of NMNZ S42282 and NMNZ S50860 preserve part of the meckelian groove but the anterodorsal margin is broken away as is common in Holocene material (figures 2*b,c* and 3). The surface texture of the groove consists of very subtle longitudinal ridges (figure 2*b*). A small foramen is present (NMNZ S43075 and NMNZ S42282) on the lingual surface just ventral to the most posteriorly preserved tooth (figure 2*b,g*), and anteriorly on the lateral surface below the skirt of secondary bone in specimen NMNZ S50860. These probably correspond to similarly located nutrient foramina found in *Sphenodon* (e.g. specimens LDUCZ ×723, ×804).

3. PHYLOGENETIC AFFINITY

The Manuherikia jaws reveal two diagnostic features of rhynchocephalians: acrodont teeth and an enlarged palatine tooth row near parallel to the maxillary row as inferred by the characteristic pattern of lingual wear on the dentary teeth (Reynoso 1996; Evans 2003). In addition, a secondary bone skirt is a character of derived rhynchocephalians, such as *Clevosaurus* and *Sphenodon* (Fraser 1988; Jones 2006*a,c*). The dentary teeth are unlike those of 'basal taxa', clevososaurs, pleurososaurs, saphesosaurs or eilenodontines; instead, they closely resemble those of *Sphenodon* (Robinson 1976; Gorniak *et al.* 1982; Jones 2006*a,b*) and of Mesozoic fossils, such as *Cynosphenodon* (Middle Jurassic of Mexico), that are allied with *Sphenodon* in Sphenodontinae (*sensu* Reynoso 1996). As well as characteristic pyramidal dentary teeth, sphenodontines are grouped by the possession of one or more caniniform teeth and smooth dental enamel (Reynoso 1996). The Miocene material is too incomplete to record the presence of a caniniform but the preserved enamel is smooth.

The Manuherikia specimens fall within the range of morphological variation exhibited by modern *Sphenodon*, but cannot be referred to it with confidence because our knowledge of other sphenodontines is so limited. Sphenodontines are now known from several localities worldwide but the material consists almost exclusively of partial jaws (e.g. Reynoso 1996). Interrelationships between representative taxa are poorly understood because comparisons are generally limited to caniniform number and minor differences in tooth morphology. Furthermore, some taxa cannot be directly compared with each other because they are each represented by different elements (see the electronic supplementary material). Moreover, characters currently used to distinguish sphenodontines from one another may not be reliable in small sample sizes because of the way rhynchocephalian teeth grow and are worn (Robinson 1976). For example, spacing of the dentary tooth cusps is considered smaller in *Cynosphenodon*, *Sphenovipera* and *Theretairus* than in *Sphenodon* (Reynoso 1996, 2005), but this feature is highly variable in the latter taxon (see the electronic supplementary material). We therefore refer the material to Sphenodontinae but not necessarily *Sphenodon*.

4. FOSSIL RECORD AND BIOGEOGRAPHY

This material helps to bridge a gap in the rhynchocephalian fossil record of nearly 70 Mya between the Late Pleistocene (Worthy & Grant-Mackie 2003) and the Late Cretaceous (Apesteguía & Novas 2003; Martinelli & Forasiepi 2004; Apesteguía 2005*a,b*). It also represents the first direct evidence that a rhynchocephalian was present on New Zealand prior to the Pleistocene. This is significant because it suggests that the ancestors of *Sphenodon*, an animal often considered to be primitive and unspecialized (e.g. Robb 1977; Dawbin 1982), survived in New Zealand despite substantial changes in climate and environment. These include not only a global temperature drop of approximately 8°C after the Mid-Miocene optimum, but also, more locally, mountain building, Pleistocene glacial–interglacial oscillations, floral overturn and faunal changes (Cooper & Millener 1993; Pole 1994; Cooper & Cooper 1995; Worthy *et al.* 2006; Pole 2008). This does not necessarily dispute recent suggestions that the living *Sphenodon* will be threatened by global warming because today's populations are geographically restricted and less extensive (Nelson *et al.* 2004; Mitchell *et al.* 2008).

The pre-Miocene history of rhynchocephalians on New Zealand remains unknown, as does the more general post-Mesozoic history of rhynchocephalians globally. The terrestrial Mesozoic fossil record of New Zealand vertebrates is limited to the non-avian dinosaurs and pterosaurs of the Late Cretaceous (75–80 Mya) Maungataniwha Sandstone (e.g. Molnar & Wiffen 1994; Molnar *et al.* 1996, 1998). However, most workers have inferred that rhynchocephalians ancestral to the modern *Sphenodon* were present on New Zealand when it separated from Antarctica and the rest of Gondwana 82–60 Mya (e.g. Fleming 1975; Robb 1977; Dawbin 1982; Cooper & Millener 1993; Cooper & Cooper 1995; Evans *et al.* 2001; Hay *et al.* 2003; Apesteguía 2005*a,b*; Gibbs 2006). At that time, the climate of Antarctica was warm to cool temperate (Dingle & Lavelle 1998).

Between the Late Oligocene and earliest Miocene (35–22 Mya) a eustatic sea-level rise submerged much of Zealandia (New Zealand and associated continental crust; Luyendyk 1995) and this may have caused the genetic bottleneck found in birds, skinks and flightless Orthoptera (Daugherty *et al.* 1993; Cooper & Cooper 1995; Trewick & Morgan-Richards 2005). Genetic divergence of living *Sphenodon* populations occurred fairly recently, perhaps related to climate change in the Pleistocene (Hay *et al.* 2003), and this unfortunately masks any evidence for or against an ‘Oligocene bottleneck’ in the genus.

An absence of Oligocene terrestrial sediments has prompted the suggestion that Zealandia was ‘totally’ submerged during the Waitakian Stage 25–22 Mya (Campbell & Landis 2001; Trewick *et al.* 2007; Campbell & Hutching 2008; Landis *et al.* 2008). If correct, this would require rhynchocephalians (and other taxa recorded from the Manuherikia Group) to have colonized New Zealand shortly after its re-emergence (Trewick *et al.* 2007). There is evidence that much of the New Zealand biota arrived post-Oligocene (including many plants; Pole 1994; Waters & Craw 2006). However, the biota of Madagascar has also undergone radical changes since the Mesozoic, and yet its complete submergence has never been required as an explanation (Krause *et al.* 1997). The age of the fossil material described here is compatible with both the ancient vicariance hypothesis and the post-Oligocene transoceanic dispersal hypothesis, but it does reduce the time available for a transoceanic dispersal from up to 25 Ma to perhaps as little as 3 Ma.

Waters & Craw (2006) stated that *Sphenodon* is ‘uninformative with regards to New Zealand’s geological history’. They seem to accept *a priori* (without any reference to *Sphenodon* biology or a single citation on the rhynchocephalian fossil record) that a transoceanic dispersal was possible, and that a population of *Sphenodon*-like rhynchocephalians existed outside New Zealand until after the Oligocene. Oceanic dispersal of squamates probably occurred more frequently than previously appreciated (e.g. Carranza *et al.* 2000; Calsbeek & Smith 2003; De Queiroz 2005; Vidal *et al.* 2008), but the transoceanic capabilities of modern *Sphenodon* are questionable. It can swim, but only short distances (Newman 1878; C. H. Daugherty 2008, personal communication). It is able to survive without food for several months (Buller 1879), but dehydration would be a serious problem for a journey of several thousand kilometres (or several weeks) because *Sphenodon* demonstrates high rates of cutaneous water loss relative to its body mass (Cree & Daugherty 1991; A. Cree 2008, personal communication; C. H. Daugherty 2008, personal communication).

There is currently no evidence of a post-Oligocene source population outside New Zealand. Sanmartín & Ronquist (2004) showed that transoceanic dispersals to New Zealand are most likely to have come from the west but no rhynchocephalians have yet been recovered from the otherwise productive Oligo-Miocene sites at Riversleigh (over 200 localities) or in the Eyre Basin of Australia (Evans *et al.* 2001; Brace 2003; M. N. Hutchinson 2008, personal communication). A possible record from the Palaeocene of Morocco (Augé & Rage 2006) is based on an indeterminate partial dentary bearing a single tooth (not impossibly an acrodont squamate). Post-Mesozoic populations of rhynchocephalians may have persisted in

South America for some time (Apesteguía 2005a), but there is currently no direct evidence of this. The record of Antarctica remains poorly known in general. Absence of evidence is not evidence of absence (Sagan 1996, p. 213), but this also applies to the absence in New Zealand of Cretaceous–Palaeogene rhynchocephalian fossil remains and of Oligocene terrestrial sediments. The sediments may have been eroded away in the 25 million years since their deposition, and known New Zealand Mesozoic localities (comprising shallow marine sediments with transported terrestrial components) have a low preservation potential for small animals; even the recovered pterosaur bone is fairly large (Molnar & Wiffen 1994). We urge further surveying and use of sieving techniques (e.g. Ward 1984).

It currently seems more likely that some local land surface persisted during the Oligocene and allowed the ancestors of *Sphenodon*, leiopelmatid frogs, *Agathis* (the kauri tree), certain birds, an archaic mammal, *Hyridella* (freshwater mussels) and numerous other invertebrates to survive the transgression (Graf & Foighil 2000; Gibbs 2006; Worthy *et al.* 2006; Knapp *et al.* 2007; Lee *et al.* 2007). The extent of the emergent land surface is open to speculation. Landis *et al.* (2008) have argued that it was much less than approximately 40 000 km² (15% of the present-day land area), as estimated by Cooper & Cooper (1995), with no certainty that any land remained above water. However, even if Zealandia was reduced to only 1 per cent of today’s surface area it would still represent over 2500 km², well over 1000 times the surface area of Stephen’s Island (1.5 km²), where over 30 000 *Sphenodon* currently live (MacAvoy *et al.* 2007).

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