

Miocene skinks and geckos reveal long-term conservatism of New Zealand's lizard fauna

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The New Zealand (NZ) lizard fossil record is currently limited to late Quaternary remains of modern taxa. The St Bathans Fauna (early Miocene, southern South Island) extends this record to 19–16 million years ago (Myr ago). Skull and postcranial elements are similar to extant *Oligosoma* (Lygosominae) skinks and *Hoplodactylus* (Diplodactylinae) geckos. There is no evidence of other squamate groups. These fossils, along with coeval sphenodontines, demonstrate a long conservative history for the NZ lepidosaurian fauna, provide new molecular clock calibrations and contradict inferences of a very recent (less than 8 Myr ago) arrival of skinks in NZ.

Keywords: Reptilia; palaeontology; biogeography; Gondwana; Squamata; Miocene

1. INTRODUCTION

The Recent New Zealand (NZ) lizard fauna, like many insular terrestrial biotas, comprises endemic radiations of few lineages. There are only two groups: skinks (*Eugongylus* group Lygosominae) and geckos (Diplodactylinae). NZ skinks represent a single endemic radiation (Smith *et al.* 2007; Chapple *et al.* 2009), all recently placed in *Oligosoma* (Chapple *et al.* 2009; cf. Hardy 1977). NZ geckos are also monophyletic (Kluge 1967; Chambers *et al.* 2001), with *Hoplodactylus* being a primitive grade with respect to *Naultinus* (Chambers *et al.* 2001). There has been no direct evidence for the antiquity of this fauna, with fossils currently limited to the Quaternary (Worthy 1987, 1991). However, independent molecular dating suggested that NZ skinks diverged from their New Caledonian relatives as early as more than 20 Myr ago (Hickson *et al.* 2000) or as recently as 7.9 Myr ago (Smith *et al.* 2007). A more extensive

study by Chapple *et al.* (2009), calibrated using preliminary announcements of St Bathans lizards (e.g. Worthy *et al.* 2006), is not independent of the current study. Molecular dating acknowledged as coarse (Chambers *et al.* 2001) estimates that the most recent common ancestor of living NZ geckos existed 22.8 Myr ago. Other nodes were undated, but branch lengths in the published tree suggest that NZ geckos diverged from their sister clade (mainly New Caledonian) approximately 30 Myr ago.

The St Bathans Fauna (Bannockburn Formation, Manuhirikia Group, late Early Miocene, 19–16 Myr ago) provides the only information on NZ terrestrial vertebrates during the Tertiary (e.g. Worthy *et al.* 2007; Jones *et al.* 2009). Numerous specimens recovered help elucidate the history of NZ's distinctive lizard fauna and independently test molecular clock inferences.

2. MATERIAL AND METHODS

The general stratigraphy of St Bathans, and excavation methods, is described in Worthy *et al.* (2007). Appendix A in the electronic supplementary material lists precise site details and squamate specimens retrieved. Because material invariably was similar to extant NZ skinks and geckos, comparisons focused on these forms and extralimital taxa from Australasia and New Caledonia (appendix B, electronic supplementary material).

3. RESULTS

All diagnostic lizard material (table 1) was very similar to (if not indistinguishable from) corresponding elements from either NZ skinks or geckos, the only two indigenous lineages of squamates. They also differ greatly from coeval sphenodontines (Jones *et al.* 2009) in shape as well as size (e.g. fused frontals, pleurodontology, low blade-like neural spines and gracile limb elements). It is thus neither necessary nor parsimonious to assume that other groups are represented. Few traits consistently separate the highly diverse and globally widespread skinks and geckos (e.g. distinguishing limb features are elusive because both include limbless taxa). However, characters outlined below differ consistently between NZ skinks and geckos. Only diagnostic traits are noted, but for every element, the overall form is very similar to living NZ representatives of the relevant group. Abbreviations in parentheses refer to labels in figures 1 and 2.

(a) *Scincidae*

The elements are of moderate size, typically intermediate between the living *Oligosoma zelandicum* and *Oligosoma infrapunctatum* (60–90 mm snout-vent length (SVL); Gill & Whitaker 1996). The cryptozoic *Cyclodina* is nested within, and now synonymized with, the surface-active *Oligosoma* (Chapple *et al.* 2009). The frontal, compound and sacralis show similarities to taxa examined (appendix B, electronic supplementary material) with the depressed '*Oligosoma* morphotype' rather than the cylindrical '*Cyclodina* morphotype'. The remaining elements could be from either morphotype.

(i) *Frontal* (figure 1a,b)

Identifiable as Scincidae by adpressed cephalic osteoderms (Scincoidea apomorphy: Estes *et al.* 1988) and shallow crista cranii (cc; subolfactory processes) that do not meet ventrally (figure 1b). The long prefrontal facet

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsbl.2009.0440> or via <http://rsbl.royalsocietypublishing.org>.

Table 1. Squamate elements from St Bathans referable to either Scincidae or Gekkota.

taxon and element	museum of NZ number (right/left element)	details
Scincidae		
frontal	S42688, S44217, S51260	posterior and interorbital region
maxilla	S42620 ^(R) , S43074 ^(R) , S44218 ^(R) , S50707 ^(L)	central portion
compound mandibular element	S42689 ^(R)	largely complete, missing part of the retroarticular process and the anterior tip
vertebrae	S42618, S42728, S44001, S44302, S44216, S50022, S50024, S50388, S50819, S50943, S51262, S50708	all isolated dorsals except: 42618 (2 elements), 44216 (3 elements), 51262 (3 elements), 50708 (isolated dorsal and two sacrals missing distal ends of all sacral ribs)
humerus	S44002 ^(R) , S50938 ^(R)	distal portion with attached epiphysis
femur	S50945 ^(R) , S50810 ^(R)	50945 is a proximal end, including capitellum; 50810 is almost complete, lacking capitellum and distal epiphysis
Gekkota		
frontal	S43124	most of posterior portion
pterygoid	S44154 ^(L)	central portion
maxilla	S51004 ^(L) , S44152 ^(R)	central portion
dentary	S42296 ^(L) , S51324 ^(L)	42296 central portion, 51324 anterior portion
compound mandibular element	S42341 ^(L) , S42342 ^(L) , S42577 ^(L) , S42731 ^(L) , S44003 ^(R) , S44153 ^(L) , S44338 ^(R)	posterior portion
vertebrae	S42343, S42616, S42687, S42730, S43125, S51269	all are dorsals except for 51269, which appears to be caudal based on transverse processes in the middle region (broken), and an articulatory surface for the chevron
humerus	S44072 ^(L)	proximal portion (with attached epiphysis) and most of shaft
femur	S50709 ^(R)	distal portion (with attached epiphysis) and part of shaft

(pf) indicates the prefrontal extended posteriorly past the centre of the orbit, a trait found in living NZ skinks, but absent in extralimital taxa examined. Finally, the cristae cranii are very shallow and attenuate posteriorly, as in the *Oligosoma* morphotype but unlike the more prominent structures in the *Cyclodina* morphotype.

(ii) *Maxilla* (figure 1c,d)

Identifiable as Scincidae by the anterior position of the internal (superior alveolar) foramen (saf) for the maxillary nerve and artery and the absence of lateral maxillary foramina on the posterior margin. There are approximately 14 alveoli in the best-preserved element. Teeth are peg-shaped and not recurved. Five closely spaced external foramina (ef) are present anteriorly (others probably present on the missing end).

(iii) *Compound element* (figure 1e,f)

Identifiable as Scincidae by a wide flaring retroarticular process (rp), and an articular surface (as) that is more horizontally than vertically orientated. The retroarticular process is distinctly angled medially (Scincoidea apomorphy: Estes *et al.* 1988), more than in the *Cyclodina* morphotype and resembling the *Oligosoma* morphotype.

(iv) *Vertebra* (figure 1i,j)

Identifiable as Scincidae by procoelous articulations. In the sacrals (figure 1g,h), the first rib (s1) is more

gracile than the second (s2), as in the *Oligosoma* morphotype but unlike the *Cyclodina* morphotype.

(v) *Humerus* (figure 1k,l)

Identifiable as Scincidae by the large ulna condyle (uc) and the absence of a notch on the preaxial distal corner (pd).

(vi) *Femur* (figure 1m,n)

Identifiable as Scincidae by the trochanter major (tm), which tapers gradually in height distally.

(b) *Gekkota*

Elements recovered are mostly from large geckos intermediate in size between *Hoplodactylus maculatus* and *Hoplodactylus duvaucelii* (100–140 mm SVL; Gill & Whitaker 1996). Two forms, differing in adult size, are represented (see Compound). Taxa can be assigned to Gekkonidae *sensu lato* based on the presence of apomorphies with Gekkota (Gekkonidae+Pygopodidae) but the absence of apomorphies of Pygopodidae (e.g. limb reduction). The frontal shows similarities to *Hoplodactylus* rather than *Naultinus*.

(i) *Frontal* (figure 2a,b)

Identifiable as Gekkonidae by the absence of adpressed cephalic osteoderms, and deep, ventrally fused cc, a Gekkota apomorphy (Estes *et al.* 1988; Evans 2008).

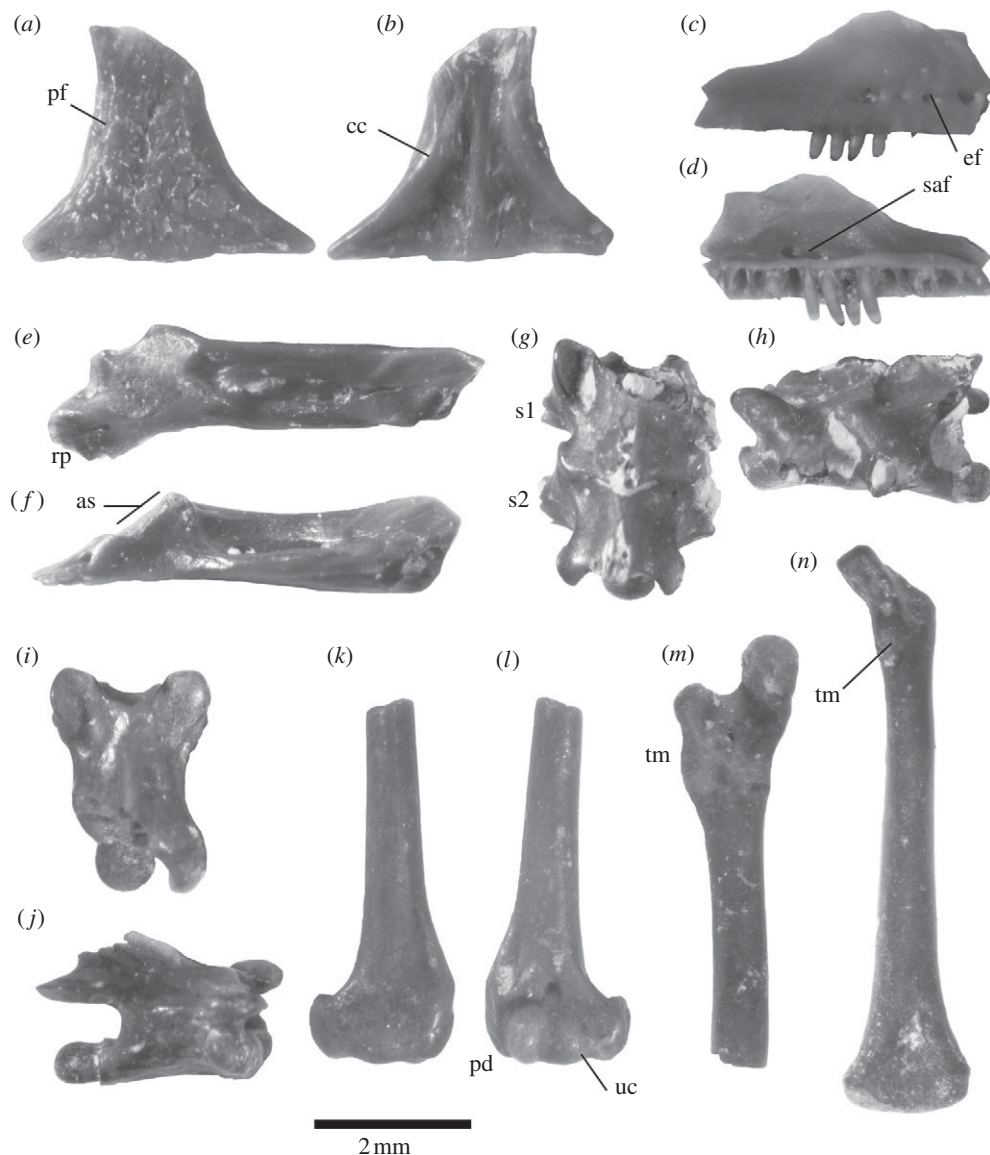


Figure 1. Scincid material; for colour version, see appendix C in the electronic supplementary material. (a) Dorsal and (b) ventral view of frontal NMNZ S42688. (c) Lateral and (d) medial view of right maxilla 44218. (e) Dorsal and (f) medial view of right compound lower jaw element 42689. (g) Dorsal and (h) left lateral view of sacral vertebrae 50708. (i) Dorsal and (j) right lateral view of dorsal vertebra 50708. (k) Dorsal and (l) ventral view of distal end of right humerus 44002. (m) Postaxial (posterior) and (n) ventral view of right femur 50945 and 50810, respectively. Abbreviations in main text and table 1.

More similar to *Hoplodactylus* than to *Nautinus* in possessing long, delicate posterolateral processes (pp), with the caveat that this trait is highly variable across Gekkota.

(ii) *Pterygoid* (figure 2c,d)

Identifiable as Gekkonidae by a narrow, rod-like posterior ramus (pr) and a concave margin bordering a large interpterygoid vacuity (iv).

(iii) *Maxilla* (figure 2e,f)

Identifiable as Gekkonidae by the posterior position of the internal (superior alveolar) foramen (saf) for the maxillary nerve and artery.

(iv) *Dentary* (figure 2g,h)

Identifiable as gekkonidae by the sublingual shelf (ss), which is straight rather than dorsally concave in medial/lingual view.

(v) *Compound* (figure 2i,j)

Identifiable as Gekkonidae by a narrow retroarticular process (rp), resulting in a 'lateral notch' (Evans 2008) where it joins the wider, main portion of the lower jaw (Gekkota apomorphy: Estes *et al.* 1988), and an articular surface (as) that is more vertically than horizontally oriented. The adductor fossa bears a large ossified posterior shelf (ps), a distinctive trait found in some NZ geckos (e.g. *H. duvaucelii* and *Nautinus elegans*) but poorly developed or absent in extralimital taxa examined. One specimen (NMNZ S44338) is presumably adult with no trace of the surangular-articular suture; this represents a moderate-sized gecko approximately 20 per cent larger than living *H. maculatus*. Three specimens (42342, 44003 and 44153) are markedly larger than 44338 yet retain this suture, suggesting that they are immature individuals of a larger taxon that, when fully grown, was at least as large as living *H. duvaucelii*.

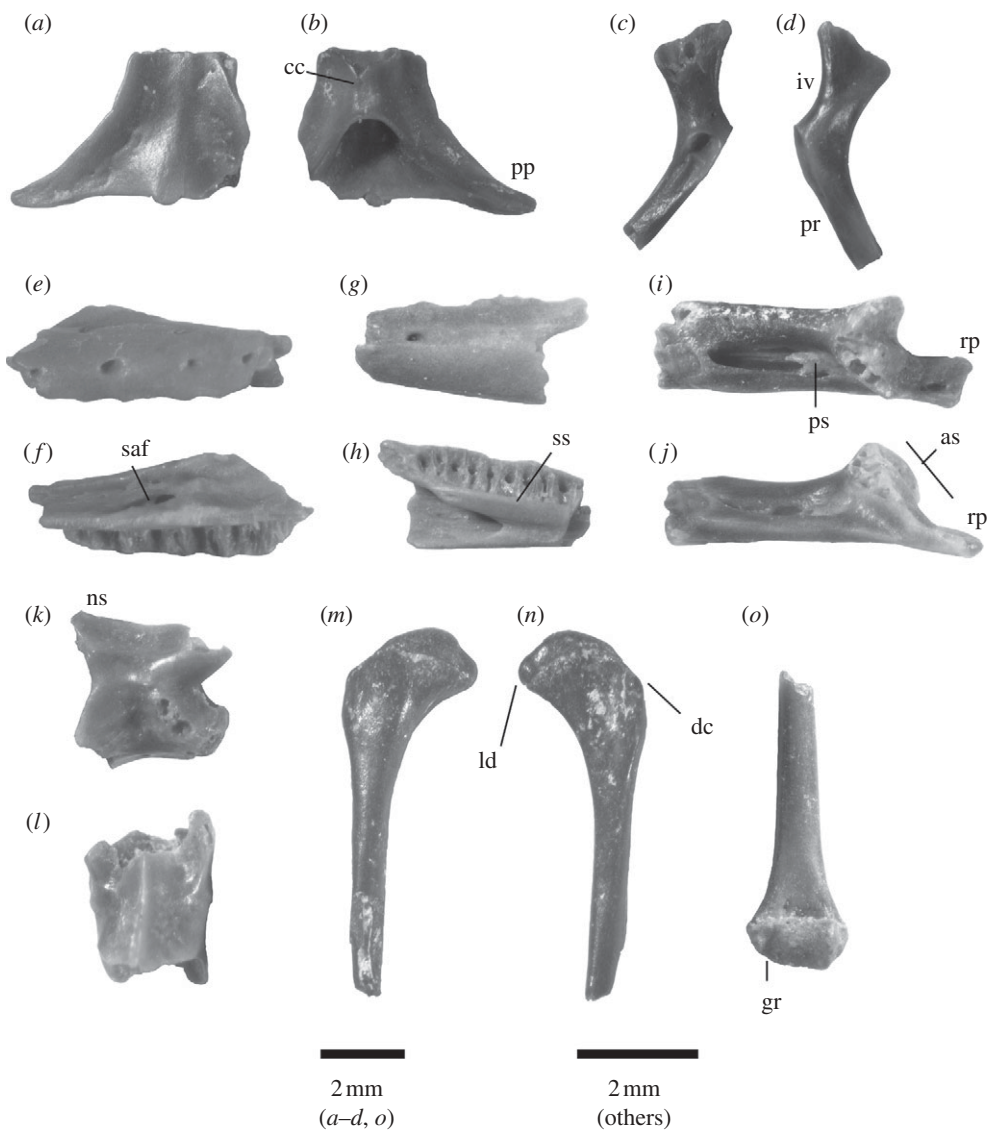


Figure 2. Gekkotan material; for colour version, see appendix C in the electronic supplementary material. (a) Dorsal and (b) ventral view of frontal NMNZ S43124. (c) Lateral and (d) medial view of right left pterygoid 44154. (e) Lateral and (f) medial view of left maxilla 51004. (g) Lateral and (h) medial view of left dentary 42296. (i) Dorsal and (j) medial view of right compound bone of lower jaw 44338. (k) Right lateral and (l) dorsal view of dorsal vertebra 42730. (m) Dorsal and (n) ventral view of proximal portion of left humerus 44072. (o) Ventral view of distal end of right femur 50709. Abbreviations in main text and table 1.

(vi) *Vertebrae* (figure 2*k,l*)

Identifiable as Gekkonidae based on amphicoelous articulations, an apomorphic reversal in squamates widespread in Gekkota (Estes *et al.* 1988).

(vii) *Humerus* (figure 2*m,n*)

Identifiable as Gekkonidae based on the indistinct deltopectoral crest (dc) and flange for the latissimus dorsi (ld); in NZ scincids, these are clearly off-set (via a concavity) from the proximal articulation.

(viii) *Femur* (figure 2*o*)

Identifiable as Gekkonidae by the groove (gr) on the preaxial region of the distal articular surface.

4. DISCUSSION

The first pre-Pleistocene fossil record of squamates in NZ fills a major gap in the regional fossil record. The fossils are most parsimoniously interpreted as related

to living lineages: they are extremely similar to, and share some putative-derived characters with, extant NZ diplodactyline geckos or lygosomine skinks. Early Miocene presence of both living lineages of NZ lizards, as well as sphenodontines (Jones *et al.* 2009), and apparent absence of all other lepidosaur groups indicate long-term conservatism of the NZ reptile fauna. Since then, there have been no new colonizing lineages and limited phenotypic divergence within each lineage; a situation contrasting greatly with the nearest continental fauna, Australia (e.g. Greer 1989). The squamate fossils cannot refute or confirm the debated Oligo-Miocene submergence of NZ (Landis *et al.* 2008), but the presence of many vertebrate lineages soon afterwards (e.g. see Worthy *et al.* 2006; Jones *et al.* 2009) suggests either continuous persistence of land or subsequent rapid colonization.

The lizard fossils reveal that NZ was occupied 19–16 Myr ago by at least one skink taxon resembling extant species with the *Oligosoma* morphotype and two

gecko taxa resembling extant *Hoplodactylus* species. Both these morphotypes represent primitive grades in their respective NZ lineages (Chambers *et al.* 2001; Smith *et al.* 2007; Chapple *et al.* 2009), and it might be expected that early fossils would be attributable to these taxa. The fossils are too fragmentary to exhibit diagnostic differences from extant species of *Oligosoma* and *Hoplodactylus* and thus cannot be named. The lack of evidence for derived skinks (*Cyclodina* morphotype) and derived geckos (*Naultinus*) despite numerous fossils is consistent with these taxa having a later (post early Miocene) origin, although support consisting of absence of fossils must be acknowledged as weak.

These fossils are also important given the rarity of robust fossil calibration points within modern scincids and gekkotans for molecular clock analyses (e.g. Skinner *et al.* 2008). They provide the first minimum age constraints for the divergence of the endemic NZ scincid and gekkotan clades from their extralimital sister groups (Chapple *et al.* 2009). Molecular divergence dating using other calibration points has thus far yielded highly disparate dates for the age of NZ skinks, suggesting that they diverged from New Caledonian relatives 20 Myr ago (Hickson *et al.* 2000) or either 22.9–19.9 or 7.9 Myr ago, depending on calibrations and genes employed (Smith *et al.* 2007). For geckos, the only study suggests NZ geckos diverged from (primarily) New Caledonian relatives about 30 Myr ago (Chambers *et al.* 2001; see §1). The fossils described here demonstrate that both endemic NZ lizard lineages were already present 16 Myr ago and thus refute the younger molecular estimates for skinks. Deep phylogeographic divergences found within NZ skink species complexes also suggest early origins (Greaves *et al.* 2007; Chapple *et al.* 2009). Further, the 7.9 Myr date was inferred by applying mtDNA substitution rates for agamids to skinks. Because agamids have approximately twice the rate of mtDNA evolution of skinks (e.g. Kumazawa 2007), this extrapolation would underestimate (by half) divergence dates within skinks. Thus, the deeper molecular estimates for NZ skink origins (more than 20 Myr ago: Hickson *et al.* 2000; Chapple *et al.* 2009) are best supported by the fossil record, phylogeography and methodological considerations.

We thank Ann and Euan Johnstone and Jack Enright for site access, numerous field volunteers (appendix A, electronic supplementary material) and Michael Caldwell and two anonymous referees for helpful comments. Supported by Australian Research Council Grant DP0770660 and UNSW Strategic Initiative Funding Scheme to S. Hand, M.A. and T.H.W.

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