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# Molecular phylogeny of the scincid lizards of New Caledonia and adjacent areas: Evidence for a single origin of the endemic skinks of Tasmantis

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## Abstract

We use ~1900 bp of mitochondrial (ND2) and nuclear (c-mos and Rag-1) DNA sequence data to recover phylogenetic relationships among 58 species and 26 genera of *Eugongylus* group scincid lizards from New Caledonia, Lord Howe Island, New Zealand, Australia and New Guinea. Taxon sampling for New Caledonian forms was nearly complete. We find that the endemic skink genera occurring on New Caledonia, New Zealand and Lord Howe Island, which make up the Gondwanan continental block Tasmantis, form a monophyletic group. Within this group New Zealand and New Zealand + Lord Howe Island form monophyletic clades. These clades are nested within the radiation of skinks in New Caledonia. All of the New Caledonian genera are monophyletic, except *Lioscincus*. The Australian and New Guinean species form a largely unresolved polytomy with the Tasmantis clade. New Caledonian representatives of the more widespread genera *Emoia* and *Cryptoblepharus* are more closely related to the non-Tasmantis taxa than to the endemic New Caledonian genera. Using ND2 sequences and the calibration estimated for the agamid *Laudakia*, we estimate that the diversification of the Tasmantis lineage began at least 12.7 million years ago. However, using combined ND2 and c-mos data and the calibration estimated for pygopod lizards suggests the lineage is 35.4–40.74 million years old. Our results support the hypothesis that skinks colonized Tasmantis by over-water dispersal initially to New Caledonia, then to Lord Howe Island, and finally to New Zealand.

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**Keywords:** Scincidae; Phylogeny; New Caledonia; Tasmantis; Lord Howe Island; New Zealand; Biogeography

## 1. Introduction

The French Pacific island territory of New Caledonia forms part of a large continental block, Tasmantis (Fig. 1), that detached from the eastern margin of Gondwanaland 80–90 MYA (Holloway, 1979; Kroenke, 1984; Kroenke, 1996; Otte and Rentz, 1985; Swenson et al., 2001). The other major emergent component of Tasmantis is New

Zealand, which is connected to New Caledonia via the submarine Norfolk Ridge, today emergent only at Norfolk Island. To the west, the Lord Howe Rise, including Lord Howe Island and its satellite islets, also constitutes part of Tasmantis. During portions of the Tertiary, emergent areas of the Norfolk Ridge and Lord Howe Rise were more extensive than today, but there is no consensus as to if or when direct land connections between New Caledonia and New Zealand existed (Swenson et al., 2001). If such linkages were once present, they were certainly sundered by the Oligocene Marine transgressions that inundated New Zealand during the Oligocene (Cooper and Millener, 1993) and may have submerged all or most of New Caledonia

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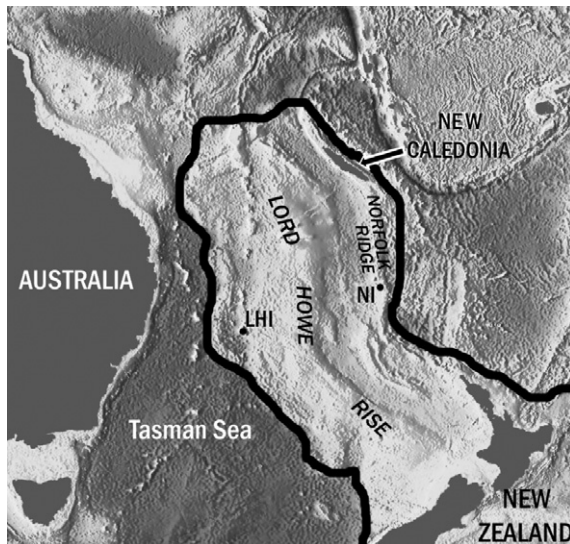


Fig. 1. Bathymetric map of the southwest Pacific Ocean showing areas discussed in this paper. LHI, Lord Howe Island; NI, Norfolk Island. Thick black line represents the approximate boundaries of the Tasmanian block. The southern limits of this block extend to the Auckland Islands and Campbell Island, while in the east they reach the Chatham Islands. Map modified from ETOPO2 2 min relief map, National Geophysical Data Center, National Oceanic and Atmospheric Administration, U.S. Department of Commerce.

(Cluzel et al., 2001; Murienne et al., 2005). Although some reconstructions suggest that New Caledonia may have been submerged for the first 30–50 Myr of its post-Gondwanan history (Hall, 1997), close links with New Zealand, whether direct or via island steppingstones, have long been supported by both geological data (Raven and Axelrod, 1972; Coleman, 1980; Stevens, 1980; Stevens, 1989) and biological distribution patterns (Penny, 1975; Winterbourn, 1980; Bauer, 1990; Swenson et al., 2001; Buckley et al., 2002).

Partly as the result of their long and complex geological and climatic histories and concomitant opportunities for cladogenesis and anagenesis, the terrestrial biota of the two largest components of Tasmantis, New Zealand and New Caledonia, exhibit high levels of species richness and endemism (Holloway, 1979; Daugherty et al., 1993; Chazeau, 1993). This is particularly true of New Caledonia, which has been identified as one of the world's hotspots of tropical biodiversity (Myers, 1988, 1990; Mittermeier et al., 1996; Lowry, 1998; Myers et al., 2000; Lowry et al., 2004). New Caledonia is especially significant as a center of floral endemism (Virot, 1956; Morat, 1993; Morat et al., 1986; Jaffré et al., 1998), and it supports a number of archaic forms, including *Amborella*, the sister group to all other flowering plants (Brown, 1999). Although less well studied than the flora, the terrestrial and freshwater fauna is also extremely rich and in some groups endemism reaches 100% (Chazeau, 1993; Platnick, 1993; Séret, 1997; Haase and Bouchet, 1998). In contrast, species diversity in the neighboring islands comprising the geologically younger and more heterogeneous Outer Melanesian Arc (extending from New Guinea east to the Tonga Trench and including the Admi-

rality, Bismarck, and Solomon Islands as well as Vanuatu, Fiji and Tonga) decreases rapidly from west to east and inter-island faunal similarity, especially at the generic level, is high (Polhemus, 1996; Bauer and Sadlier, 2000). Among vertebrates lizards constitute the most diverse and highly endemic component of the New Caledonian fauna (Bauer, 1989, 1999; Bauer and Sadlier, 2000), although all endemic taxa are representatives of either the gekkotan family Diplodactylidae or the scincid subfamily Lygosominae.

The earliest descriptions of New Caledonian scincids (Peters, 1869, 1879; Bavay, 1869; Günther, 1872, 1873; Bocage and Barboza, 1873) placed most species in the large and widespread genera *Eumeces*, *Lygosoma* and *Euprepes*, although several new genera were proposed for some New Caledonian species (the diminutive fossorial skinks *Anotis* Bavay, 1869 and *Nannoscincus* Günther, 1872; the large, keeled-scaled skinks *Tropidoscincus* Bocage and Barboza, 1873; and *Sauropsincus* Peters, 1879; and *Lioscincus* Bocage and Barboza, 1873). Boulenger (1887) relegated the majority of New Caledonian skinks to the cosmopolitan *Lygosoma* in *Catalogue of Lizards in the British Museum*, the first major treatise incorporating the New Caledonian lizard fauna. Likewise, the monograph of Roux (1913) dealing with the fauna of New Caledonia placed all 19 species and subspecies of skinks then recognized into *Lygosoma* (with the exception of the shore skink *Ablepharus boutoni*—now *Cryptoblepharus novocaledonicus*). Smith (1937) in reviewing the groups within *Lygosoma* basically retained this taxonomy, but explicitly recognized several infrageneric sections. Most New Caledonian taxa fell into his Section *Leiopisma*, although one (*deplanchei*) was placed in the Section *Sphenomorphus*, one (*cyanura*) was allocated to the genus *Emoia* and one (*garnieri*) to the subgenus *Riopa* (*Eugongylus*). Mittleman (1952) reallocated skink taxa at the generic level within the subfamily Lygosominae and recognized seven genera that included New Caledonian species (*Anotis*, *Cryptoblepharus*, *Emoia*, *Tachygyia*, *Lampropholis*, *Sphenomorphus* and *Leiopisma*), all of which also occurred extraliminally.

Greer (1970) provided the first modern review of the Scincidae, recognizing four subfamilies, one of which—the nearly cosmopolitan Lygosominae—included all of the New Caledonian skinks. Within the lygosomines, Greer (1974) subsequently reevaluated relationships among the extensive assemblage of species that made up the genus *Leiopisma* and its allies. His Group II included all of the New Caledonian taxa, which were placed among the genera *Leiopisma* (most species), *Anotis*, *Emoia*, *Cryptoblepharus*, and *Phoboscincus* (newly erected to accommodate the two largest species, *garnieri* and *bocourti*).

Greer (1974) regarded the Group II lygosomines, subsequently renamed the *Eugongylus* group (Greer, 1979), to have been derived from “a *Mabuya* stock,” based largely on shared primitive character states. Greer (1974) considered *Phoboscincus* to be closely allied to both *Eugongylus* (Halmahera through New Guinea to the Solomon Islands) and *Tachygyia* (Tonga). On the basis of distributional data,

he regarded *Tachygyia* and *Phoboscincus* to be independently derived from a *Eugongylus*-like ancestor. He also postulated the origin of *Cryptoblepharus* from *Emoia* and of *Emoia* from *Eugongylus* or a *Eugongylus*-like ancestor, although without specific mention of the New Caledonian members of the former two genera. Greer (1974) regarded *Anotis* as a specialized genus derived from *Leiolopisma* with three species (*gracilis*, *mariae*, *slevini*) from New Caledonia and two (*maccayi*, *graciloides*) from Australia, although he was unconvinced of its monophyly.

Böhme (1976) described the distinctive New Caledonian species *Eugongylus haraldmeieri*, which he regarded as intermediate between the giant Pacific Island skink genera *Phoboscincus* (New Caledonian) and *Tachygyia* (Tongan). On this basis he synonymized the two younger names with *Eugongylus*.

Sadlier (1986) comprehensively revised the New Caledonian scincids and accepted all of Greer's (1974) generic allocations outside of *Leiolopisma* proper, although *Anotis* spp. were transferred to *Nannoscincus* based on the preoccupation of the former name (Cogger, 1979; Czechura, 1981). Sadlier (1986) rejected Böhme's (1976) taxonomic conclusions regarding *Phoboscincus* and resurrected this genus, while establishing the monotypic *Geoscincus* to accommodate *Eugongylus haraldmeieri*. He also erected the monophyletic genera *Caledoniscincus*, *Marmorosphax* and *Sigaloseps*, and resurrected *Tropidoscincus* Bocage and Barboza, 1873 to accommodate most of the New Caledonian species formerly assigned to *Leiolopisma*, and described *Graciliscincus* for a distinctive newly discovered fossorial skink. Subsequently, the remaining morphologically primitive species that lack the apomorphies that would allow placement within any existing genus were transferred to the genus *Lioscincus* (type species *Lioscincus steindachneri* Bocage and Barboza, 1873) (Bauer and Sadlier, 1993), the only available generic name for any of the constituent species. However, the probable paraphyly or polyphyly of *Lioscincus* has been acknowledged (Bauer and Sadlier, 1993, 2000; Sadlier et al., 1998, 2004; Sadlier and Bauer, 1999b).

In the last decade extensive field work by the authors and their colleagues in New Caledonia has resulted in the discovery of numerous additional skink species, including highly apomorphic taxa that have been allocated to the new monotypic genera *Simiscincus* Sadlier and Bauer, 1997a; *Lacertoides* Sadlier et al., 1997 and *Kanakysaurus* Sadlier et al., 2004. Most recently, *Lygosoma euryotis* Werner, 1909 (initially placed in *Marmorosphax* by Sadlier, 1986) has been removed to a new genus, *Celatiscincus* Sadlier et al., 2006; which it shares with a newly recognized sister species. Thus, the present skink fauna of New Caledonia includes 49 species in 15 genera.

The genera *Celatiscincus*, *Geoscincus*, *Graciliscincus*, *Kanakysaurus*, *Lacertoides*, *Lioscincus*, *Marmorosphax*, *Nannoscincus*, *Phoboscincus*, *Sigaloseps*, *Simiscincus*, and *Tropidoscincus* are strictly endemic to New Caledonia, chiefly on the Grande Terre, but also on the neighboring

Loyalty Islands, Isle of Pines and smaller satellite islands. Note that *Nannoscincus* has only recently been restricted to the New Caledonian species, and the Australian species *Saiphos maccayi* Lucas & Frost, 1894 (formerly regarded as part of *Nannoscincus*) is now assigned to the genus *Anepischetosia* (Sadlier et al., 2006). *Caledoniscincus* is nearly endemic, with a single species, (*C. atropunctatus*), extending northeastwards to the southern islands of Vanuatu (Medway and Marshall, 1975; Bauer and Sadlier, 2000). *Cryptoblepharus novocaledonicus* is a putatively endemic species that is representative of a relatively speciose genus occurring elsewhere in Australia and on numerous islands in the Pacific and Indian Oceans. Finally, *Emoia* is a southeast Asian and Pacific genus with one widespread species (*E. cyanura*) and one endemic species (*E. loyaltiensis*) in the Loyalty Islands.

Recently, molecular approaches have been widely applied to problems of lygosomine relationships, however, most of these broader analyses have not included even a single member of the New Caledonian *Eugongylus* group taxa (Honda et al., 1999, 2000, 2003; Whiting et al., 2003; Brandley et al., 2005) and the only published molecular phylogeny using New Caledonian taxa employed only six taxa (Sadlier et al., 2004). Although alternative higher order relationships among skinks as a whole have been proposed (e.g., Whiting et al., 2003; Brandley et al., 2005) and the monophyly of the Lygosominae has been called into question, there is strong support for the monophyly of the *Eugongylus* group and for all lygosomines exclusive of the *Sphenomorphus* group (Honda et al., 2000, 2003; Whiting et al., 2003).

The monophyly of the *Eugongylus* group has been corroborated by a variety of studies (Donnellan, 1985; Greer, 1989, 1990; Hutchinson, 1993; Hutchinson and Donnellan, 1993; Hutchinson et al., 1990; Honda et al., 2000, 2003; Smith, 2001), although relationships within the group remain contentious. To date, however, limited morphological, immunological and molecular sequence approaches have failed to clarify relationships within New Caledonia, or between New Caledonia and other neighboring radiations. Hutchinson et al. (1990), based on unpublished data from micro-complement fixation, implied that New Caledonian members of the *Eugongylus* group were not particularly closely related to their New Zealand or Australian counterparts, although all formed part of a monophyletic *Eugongylus* group radiation in the Australian region. Both Hardy (1977) and Hickson et al. (2000) postulated that the New Caledonian skinks were perhaps the closest relatives of those on New Zealand, but they lacked comparative material to test this hypothesis.

A number of largely phenetic working hypotheses regarding New Caledonian skinks have been proposed. These include the close relationship of *Phoboscincus* and *Geoscincus* (Böhme, 1976; Börner, 1980), *Graciliscincus* to *Simiscincus* (Sadlier and Bauer, 1997b), and *Tropidoscincus* and *Lacertoides* to *Lioscincus maruia* and *L. tillieri* (Sadlier et al., 1997; Sadlier and Bauer, 1999b). Böhme (1979) also



remarked on the clear similarity of *Leiopisma greeri* to *L. nigrofasciatus* and their affinity has been accepted by subsequent authors (Sadlier, 1986; Bauer and Sadlier, 2000).

Relationships among some species of *Caledoniscincus* have been investigated using allozymes (Sadlier et al., 1999) and a revision of *Emoia* (Brown, 1991) suggests that the two New Caledonian species are not especially closely related to one another. Sadlier (1990; Sadlier et al., 2002) recognized the New Caledonian members of *Nannoscincus* as a monophyletic group, identifying two species groups on the basis of morphological data. Most recently, Sadlier et al. (2004) described *Lioscincus vivae* and presented both morphological and molecular evidence for its close relationship to *L. steindachneri*. Although monophyletic subunits of the New Caledonian skink fauna can be readily identified on the basis of derived features of scalation, osteology and soft anatomy, such data sets have proved ineffective at elucidating patterns of relationship among these highly distinctive clades.

In this study, we use mitochondrial and nuclear DNA sequence data to address the following questions: (1) do the scincid lizards of New Caledonia belong to a single monophyletic clade and, if so, what is the relationship between this clade and skinks in other Tasmantis landmasses? (2) are the New Caledonian skink genera as currently constituted monophyletic? and (3) how are genera within New Caledonia related?

## 2. Materials and methods

### 2.1. Taxon sampling

Sequences were obtained from representatives of all recognized species of New Caledonian scincid lizards except *Geoscincus haraldmeieri*, *Phoboscincus bocourti*, *Lioscincus greeri* and *Nannoscincus exos* (Table 1). *Nannoscincus exos* is a recently described form (Bauer and Sadlier, 2000; Sadlier et al., 2002) known from only a few specimens; *L. greeri* also remains known from only a few specimens and the remaining two taxa are known only from the types (although *P. bocourti* has recently been rediscovered on Ile Brosse, off of the Isle of Pines (Ineich, 2004)). Attempts to obtain sequence from the ethanol-preserved types of *G. haraldmeieri* and *L. greeri* were unsuccessful. Where possible we sampled two localities for each species. For widespread species, localities were chosen to represent as much of the species range as possible (Fig. 2).

Representative taxa from non-New Caledonian lineages were chosen from extralimital members of the *Eugongylus* group; and from other lineages of lygosomine skinks. Within the *Eugongylus* group we sampled several skinks from other components of Tasmantis: “*Oligosoma*” *lichenigera* from Lord Howe Island and three species of *Oligosoma* and one *Cyclodina* from New Zealand (c-mos and Rag-1 sequences for Lord Howe Island and New Zealand taxa are from Smith, 2001). The Australian genera *Catula*, *Morethia*, *Menetia*, *Pseudemoia*, *Saproscincus*, *Lygisaurus*,

*Lampropholis*, and *Niveoscincus* (one species each) were also sampled. Remaining *Eugongylus* group taxa included in the analysis were *Leiopisma telfairii* from Round Island, Mauritius and New Guinean representatives of *Eugongylus* and *Emoia*. Outgroup taxa included *Sphenomorphus*, *Eutropis* (*Mabuya*), *Apteryogodon*, *Panaspis*, *Tropidophorus* and *Tiliqua*.

Tissue samples for New Caledonian taxa were obtained chiefly from our own field work and corresponding specimens have been deposited in the collections of the Australian Museum, Sydney (AMS) and California Academy of Sciences, San Francisco (CAS). Additional samples were obtained from Christopher C. Austin, Louisiana State University (CCA), Charles H. Daugherty, National Frozen Tissue Collection (NFTC) housed at Victoria University of Wellington, New Zealand (CD and FT), and the Zoologisches Forschungsinstitut und Museum A. Koenig, Bonn, Germany (ZFMK).

### 2.2. DNA extraction, PCR amplification, and sequencing

We included DNA sequence data from one mitochondrial and two nuclear genes, including the mitochondrial NADH dehydrogenase subunit 2 (ND2; 514 bp); and nuclear recombination activating gene 1 (Rag-1; 830 bp) and oocyte maturation factor (c-mos; 549 bp). DNA was extracted from liver tissue that had been frozen or stored in 95% ethanol using the DNeasy kit (Qiagen). PCR was conducted using Eppendorf mastertaq. ND2 was amplified and sequenced using primers L4437b (Macey et al., 1997) and ND2r102 (Sadlier et al., 2004). Rag-1 primers were R13 from Groth and Barrowclough (1999) and an additional reverse primer G425 (primer sequence—5'-AAA GCA AGG ATA GCG ACA AGA G-3'; Smith, 2001). C-mos was amplified using G303 (primer sequence—5'-ATT ATG CCA TCM CCT MTT CC-3'; Saint) and G74 (Saint et al., 1998). Amplification conditions were: initial denaturation at 94 °C for 2 min, denaturation at 94 °C for 45 s, annealing at 52 °C for 45 s, and extension at 72 °C for 1 min, for 34 cycles. Negative controls were run for all amplifications. Amplified products were purified using GFX PCR purification columns (Amersham Biosciences). Both strands of each PCR product were purified and sequenced using an ABI 373 or 3700 automated sequencer. GenBank accession numbers, are provided in Table 1.

### 2.3. Phylogenetic analyses

Alignment of sequences was performed using Clustal X.1.81 (Thompson et al., 1997) with default parameters (gap opening = 15; gap extension = 6.666; delay divergent sequences = 30%; transition:transversion = 50%), with adjustments by eye using Se-Al v1.0 (Rambaut, 1995). A few taxa lacked data for one or more genes (Table 1), however recent simulations (Wiens, 2003; Phillippe et al., 2004) and analyses of empirical data sets (Phillippe et al., 2004; Driskell et al., 2004; Wiens et al., 2005) suggest that

Table 1  
Specimens sampled for this study

Taxon	Specimen	Locality	GenBank Accession Nos.		
<i>Eugongylus</i> group			ND2	Rag-1	C-mos
New Caledonia					
<i>Caledoniscincus aquilonius</i>	AMS R161247	(5) Dôme de Tiébaghi	DQ675194	DQ675274	DQ675399
<i>Caledoniscincus atropunctatus</i>	CAS231910	(21) NW of Moindou	DQ675195	DQ675275	DQ675400
<i>Caledoniscincus atropunctatus</i>	AMS R161083	(2) Île Art, Îles Belep	DQ675196	DQ675276	DQ675401
<i>Caledoniscincus auratus</i>	AMS R157911	(11) Tia	DQ675197	DQ675277	DQ675402
<i>Caledoniscincus austrocaledonicus</i>	AMS R1161186	(16) Creek Hervouët	DQ675198	DQ675278	DQ675403
<i>Caledoniscincus austrocaledonicus</i>	CAS231888	(32) Île des Pins	DQ675199	DQ675279	DQ675404
<i>Caledoniscincus chazeau</i>	AMS R138515	(6) Koulnoué	DQ675272	—	—
<i>Caledoniscincus festivus</i>	AMS R161882	(28) Monts Kwa Ne Mwa	DQ675200	DQ675280	DQ675405
<i>Caledoniscincus haplorhinus</i>	EBU15039	(3) Maa Bwén, Île Baaba	DQ675201	DQ675281	DQ675406
<i>Caledoniscincus orestes</i>	AMS R149926	(18) Néoua area, Mé Adéo	DQ675202	DQ675282	DQ675407
<i>Caledoniscincus renevieri</i>	AMS R165851	(14) Mt. Aoupinié	DQ675268	DQ675348	—
<i>Caledoniscincus terma</i>	CAS198680	(4) Mt. Mandjélia	DQ675271	—	—
<i>Celatiscincus euryotis</i>	AMS R138574	(32) Île des Pins	DQ675204	DQ675284	DQ675409
<i>Celatiscincus similis</i>	AMS R153504	(8) Tsiba	DQ675203	DQ675283	DQ675408
<i>Cryptoblepharus novocaledonicus</i>	AMS R165930	(32) Île des Pins	DQ675205	DQ675285	DQ675410
<i>Emoia cyanura</i>	AMS R163421	(33) Maré, Îles Loyauté	DQ675263	DQ675343	—
<i>Emoia loyaltiensis</i>	AMS R163417	(33) Maré, Îles Loyauté	DQ675206	DQ675286	DQ675411
<i>Graciliscincus shonae</i>	AMS R147856	(27) Mt. Koghis	DQ675254	DQ675334	DQ675391
<i>Graciliscinus shonae</i>	AMS R165813	(25) Mt. Ouin	DQ675207	DQ675287	DQ675412
<i>Kanakysaurus viviparus</i>	AMS R161232	(5) Dôme de Tiébaghi	DQ675208	DQ675288	DQ675413
<i>Kanakysaurus viviparus</i>	AMS R161299	(1) Île Pott, Îles Belep	DQ675209	DQ675289	DQ675349
<i>Lacertoides pardalis</i>	CAS 205483	(31) Kwa Née	DQ675210	DQ675290	DQ675350
<i>Lacertoides pardalis</i>	AMS R148051	(31) Kwa Née	DQ675211	DQ675291	DQ675351
<i>Lioscincus maruia</i>	AMS R163164	(11) Plateau de Tia	DQ675213	DQ675293	DQ675353
<i>Lioscincus maruia</i>	AMS R149897	(18) Mé Adéo	DQ675214	DQ675294	DQ675354
<i>Lioscincus nigrofasciolatus</i>	AMS R149334	(7) Mt. Panié	DQ675215	DQ675295	DQ675355
<i>Lioscincus nigrofasciolatus</i>	AMS R138624	(32) Île des Pins	DQ675216	DQ675296	DQ675356
<i>Lioscincus novocaledonicus</i>	AMS R166364	(19) Bourail	DQ675251	DQ675331	—
<i>Lioscincus novocaledonicus</i>	AMS R166367	(19) Bourail	DQ675252	DQ675332	—
<i>Lioscincus steindachneri</i>	AMS R149418	(14) Mt. Aoupinié	DQ675217	DQ675297	DQ675357
<i>Lioscincus steindachneri</i>	AMS R149890	(18) Mé Adéo	DQ675218	DQ675298	DQ675358
<i>Lioscincus tillieri</i>	AMS R148013	(26) Mt. Mou	DQ675219	DQ675299	DQ675359
<i>Lioscincus tillieri</i>	AMS R148037	(24) Mt. Vulcain	DQ675220	DQ675300	DQ675360
<i>Lioscincus viviae</i>	CAS 226163	(12) Kopéto	DQ675221	DQ675301	DQ675361
<i>Marmorosphax montana</i>	AMS R165922	(25) Mt. Ouin	DQ675226	DQ675306	DQ675366
<i>Marmorosphax montana</i>	AMS R165802	(25) Mt. Ouin	DQ675255	DQ675335	DQ675392
<i>Marmorosphax</i> sp. nov. 1	AMS R165973	(9) Mt. Taom	DQ675224	DQ675304	DQ675364
<i>Marmorosphax</i> sp. nov. 2	AMS R163197	(15) Boulinda	DQ675225	DQ675305	DQ675365
<i>Marmorosphax tricolor</i>	CAS 214451	(27) Mt. Koghis	DQ675227	DQ675307	DQ675367
<i>Marmorosphax tricolor</i>	AMS R163178	(15) Boulinda	DQ675223	DQ675303	DQ675363
<i>Nannoscincus garrulus</i>	AMS R163453	(23) Pic Ningua	DQ675261	DQ675341	—
<i>Nannoscincus garrulus</i>	CAS 226166	(23) Pic Ningua	DQ675262	DQ675342	—
<i>Nannoscincus gracilis</i>	AMS R144351	(22) Sarraméa	DQ675229	DQ675309	DQ675369
<i>Nannoscincus gracilis</i>	AMS R149892	(18) Mé Adéo	DQ675233	DQ675313	DQ675373
<i>Nannoscincus greeri</i>	CAS 231942	(10) Nèmèrétina	DQ675230	DQ675310	DQ675370
<i>Nannoscincus hanchisteus</i>	AMS R149355	(17) Pindaï	DQ675270	—	—
<i>Nannoscincus humectus</i>	AMS R149498	(13) Forêt Plate	DQ675269	—	—
<i>Nannoscincus mariei</i>	AMS R135111	(27) Mt. Koghis	DQ675231	DQ675311	DQ675371
<i>Nannoscincus mariei</i>	AMS R146484	(26) Mt. Mou	DQ675232	DQ675312	DQ675372
<i>Nannoscincus sleveni</i>	AMS R147879	(20) Plateau de Dogny	DQ675256	DQ675336	—
<i>Phoboscincus garnieri</i>	AMS R146293	(32) Île des Pins	DQ675236	DQ675316	DQ675376
<i>Phoboscincus garnieri</i>	AMS R151964	(29) Mt. Dore	DQ675237	DQ675317	DQ675377
<i>Sigaloseps deplanchei</i>	AMS R148065	(30) Plaine des Lacs	DQ675238	DQ675318	DQ675378
<i>Sigaloseps ruficauda</i>	AMS R146482	(26) Mt. Mou	DQ675239	DQ675319	DQ675379
<i>Simiscincus aurantiacus</i>	AMS R144356	(27) Mt. Koghis	DQ675250	DQ675330	DQ675389
<i>Tropidoscincus aubrianus</i>	CAS 198661	(32) Île des Pins	DQ675260	DQ675340	—
<i>Tropidoscincus boreus</i>	AMS R163185	(15) Boulinda	DQ675241	DQ675321	DQ675381
<i>Tropidoscincus variabilis</i>	AMS R161879	(28) Monts Kwa Ne Mwa	DQ675242	DQ675322	DQ675382
<i>Tropidoscincus variabilis</i>	AMS R150734	(29) Mt. Ouin	DQ675243	DQ675323	DQ675383
New genus	AMS R161182	(9) Mt. Taom	DQ675193	DQ675273	DQ675398

(continued on next page)

Table 1 (continued)

Taxon	Specimen	Locality	GenBank Accession Nos.		
<i>Eugongylus</i> group			ND2	Rag-1	C-mos
Australia					
<i>Catula zia</i>	AMS R151812	Border Ranges N.P., NSW	DQ675264	DQ675344	—
<i>Lampropholis guichenoti</i>	AMS R145994	Near Penrith, NSW	DQ675212	DQ675292	DQ675352
<i>Lygisaurus foliorum</i>	AMS R151327	Lake Burragarang area, NSW	DQ675222	DQ675302	DQ675362
<i>Menetia greyii</i>	AMS R151714	Sturt National Park, NSW	DQ675266	DQ675346	—
<i>Morethia adelaidensis</i>	AMS R155359	Sturt National Park, NSW	DQ675228	DQ675308	DQ675368
<i>Niveoscincus pretiosus</i>	AMS R133014	Chappell Island, TAS	DQ675234	DQ675314	DQ675374
<i>Pseudemoia pagenstecheri</i>	AMS R148177	Riamukka State Forest, NSW	DQ675267	DQ675347	—
<i>Saproscincus rosei</i>	AMS R152292	vic. Barrington House, NSW	DQ675248	DQ675328	—
New Zealand					
<i>Cyclodina aenea</i>	FT5253	Pukerua Bay	DQ675244	DQ675324 <sup>a</sup>	DQ675384 <sup>a</sup>
<i>Oligosoma microlepis</i>	CD1299	Taihape	DQ675235	DQ675315 <sup>a</sup>	DQ675375 <sup>a</sup>
<i>Oligosoma smithi</i>	FT193	Ocean Beach, Whangarei	DQ675246	DQ675326 <sup>a</sup>	DQ675386 <sup>a</sup>
<i>Oligosoma suteri</i>	FT148	Green Island, Mercury Islands	DQ675247	DQ675327 <sup>a</sup>	DQ675387 <sup>a</sup>
Lord Howe/Norfolk Island groups					
<i>Oligosoma lichenigera</i>	AMS R 93465	Balls Pyramid, Lord Howe Island	DQ675245	DQ675325 <sup>a</sup>	DQ675385 <sup>a</sup>
Papua New Guinea					
<i>Eugongylus rufescens</i>	AMS R122480	Bobole SHP, Papua New Guinea	DQ675253	DQ675333	DQ675390
Round Island, Mauritius					
<i>Leiopisma telfairii</i>	no number	Round Island, Mauritius	DQ675259	—	DQ675396
<b>Outgroups</b>					
<i>Apterygodon vittatum</i>	CCA7218	Borneo, Sarawak, Kuching, Malaysia	—	DQ675338	DQ675393
<i>Lygosoma punctata</i>	AMB no number	Vellore, India	DQ675265	DQ675345	—
<i>Eutropis multicarinata</i>	CCA1255	Mindanao Island, Davo City, Malagos Eagle Camp, Philippines	—	DQ675339	DQ675394
<i>Panaspis africana</i>	CAS 218730	Java, São Tomé et Príncipe	DQ675257	DQ675337	—
<i>Sphenomorphus fasciatus</i>	CCA1251	Mindanao Island, Davo City, Malagos Eagle Camp, Philippines	DQ675240	DQ675320	DQ675380
<i>Sphenomorphus jobiense</i>	THNM 51276	Morobe Province, Bakia Village No. 1, 11 km SE, Garaina, Garaina Valley, Papua New Guinea	DQ675258	—	DQ675395
<i>Tiliqua scincoides</i>	AMS R154684	Yathong Nature Reserve	DQ675249	DQ675329	DQ675388
<i>Tropidophorus brookei</i>	AMB no number	Sarawak, Borneo, Malaysia	DQ675192	—	DQ675397

Parenthetical numbers in locality column correspond to localities plotted on Fig. 2.

<sup>a</sup> Data from Smith, 2001. Collection abbreviations are as follows: AMS, Australian Museum, Sydney; CAS, California Academy of Sciences, San Francisco; CCA, Christopher C. Austin, Louisiana State University; CD and FT, Charles H. Daugherty, Victoria University of Wellington, New Zealand (CD and FT); ZFMK, Zoologisches Forschungsinstitut und Museum A. Koenig, Bonn, Germany.

incomplete taxa can be accurately placed in phylogenetic analyses if the overall number of characters is high.

Data were analyzed using maximum parsimony and Bayesian methods. Each gene was initially analyzed separately to look for incongruence. Maximum parsimony analyses were implemented in PAUP\* 4.0b10 (Swofford, 2002), using an heuristic search with tree-bisection–reconnection (TBR) branch swapping and 1000 random taxon-addition–sequence replicates per search. Support for clades was evaluated using non-parametric bootstrapping (Felsenstein, 1985). Bootstrap analyses used 500 pseudoreplicates each with TBR branch swapping and 10 random addition sequence replicates per bootstrap pseudoreplicate. Bayesian analyses were implemented using MrBayes version 3.1.2 (Huelsenbeck and Ronquist, 2001). We used hierarchical likelihood-ratio tests (implemented in MrModeltest version 2.0; Nylander, 2004) to find the most appropriate model of sequence evolution for each gene. We investigated two par-

tioning strategies for Bayesian analysis of this data. First, we used a single partition for each gene; second, we used three partitions for each gene representing first, second and third codon positions. In each case we used the model suggested by MrModeltest for all partitions within a gene. We used comparison of Bayes factors (Nylander et al., 2004) to determine which of these sampling strategies performs better (see Brandley et al., 2005; Wiens et al., 2005). Our analyses suggest that the best overall modeling and partitioning strategy for the combined molecular data uses the GTR+I+ $\Gamma$  model for each codon position in ND2, and HKY+ $\Gamma$  for each codon position in Rag-1 and HKY+I for each codon position in c-mos. We ran four replicate searches with  $5.0 \times 10^6$  generations each, sampling every 1000 generations. Each analysis used four chains and default priors. Standard deviations of split frequencies and plots of log-likelihoods over time were examined for stationarity. All analyses appeared to reach stationarity before

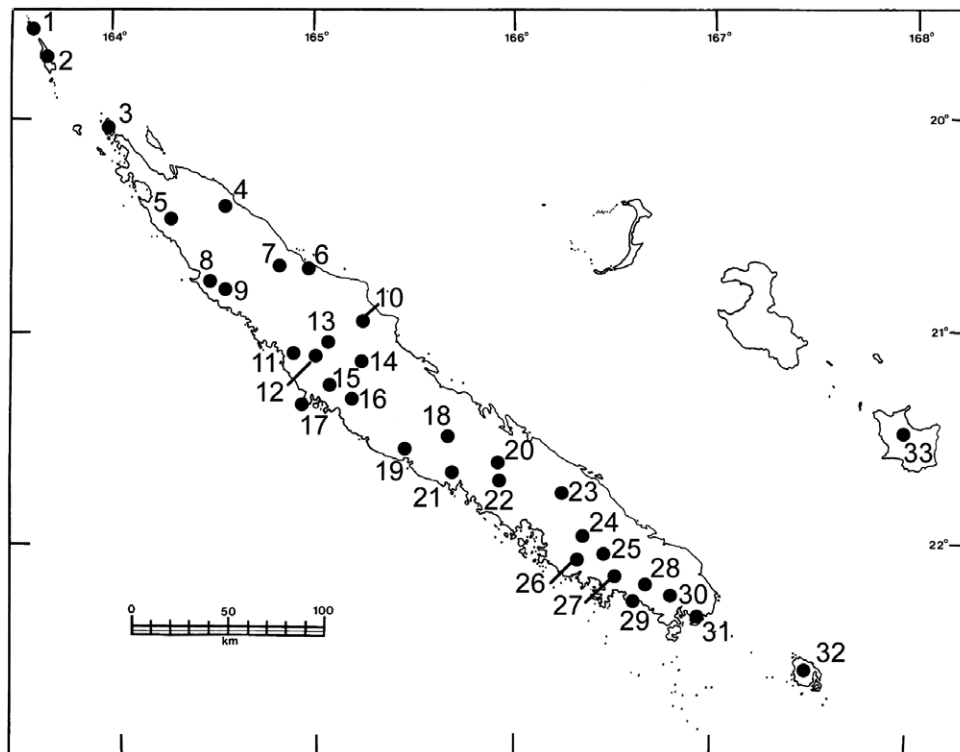


Fig. 2. Map of New Caledonia showing the collection localities of the skinks sampled. Numbered localities correspond to those listed in locality column of Table 1.

$1.0 \times 10^6$  generations, so the first 1000 trees were discarded as burn-in. Our alignments and treefiles have been submitted to TreeBase as study number S1702 and matrix accession numbers M3075–3077.

#### 2.4. Molecular clock considerations and hypothesis testing

We estimated the age of the New Caledonian radiation using two different molecular clock calibrations. We used Macey et al.'s (1998) calibration for ND2 calculated from the agamid *Laudakia*, and Jennings et al.'s. (2003) calibration for combined ND2 and c-mos calculated from the pygopod *Pygopus*. We then used these estimates of the rate to calculate the age of divergence between selected lineages whose sister group relationships were well supported by both Bayesian and maximum parsimony analyses (see Section 3).

To estimate the age of the New Caledonian radiation using the calibration points for ND2 for the agamid lizard genus *Laudakia* (Macey et al., 1998), we reanalysed the *Laudakia* data using the 514 bp fragment of ND2 that we used for our phylogenetic analysis. We estimated the average pairwise GTR distance between pairs of taxa at the nodes for which Macey et al. (1998) gave dates (1.5, 2.5, 3.5 and 9 Myr old). We regressed the ages of these 4 nodes against the pairwise GTR distance; the slope of this regression is the rate of sequence evolution.

To estimate the age of the New Caledonian radiation using the calibration point for ND2 and c-mos for the pygopod lizard genus *Pygopus* (Jennings et al., 2003), we

used 844 bp of sequence for which we have both *Pygopus* and skink sequences. Using this data we calculated the GTR distance between *P. orientalis* and *P. lepidopodus*, and between *P. orientalis* and *P. nigriceps*. We then calculated the rate of sequence evolution when this node is 20 million years-old, and 23 million years-old (Jennings et al., 2003).

We tested whether our data can statistically reject alternative trees in which the New Caledonia and New Zealand taxa form reciprocally monophyletic clades. We tested alternative trees under maximum parsimony using the Templeton test (Templeton, 1983). Alternative trees are statistically rejected using Bayesian criteria if they do not occur in the 95% CI set of trees.

### 3. Results

Analyses of the three genes combined included a total of 1893 nucleotides, of which 961 were variable and 647 were parsimony informative. Analysing genes separately did not reveal any strongly supported incongruence so we discuss the results of analysis of the three genes combined. The Bayesian and maximum parsimony topologies were generally similar and all nodes strongly supported by maximum parsimony bootstrapping were also supported by high Bayesian posterior probabilities ( $P_p$ ) (Fig. 3).

Relationships among the non-lygosomine outgroup taxa are well supported ( $P_p \geq 0.99$ ). The two *Sphenomorphus* included in the analysis, *S. fasciatus* and *S. jobiense*, do not form a monophyletic group, nor do the *Mabuya* group taxa *Apterygodon vittatum* and *Eutropis multicarinata*.



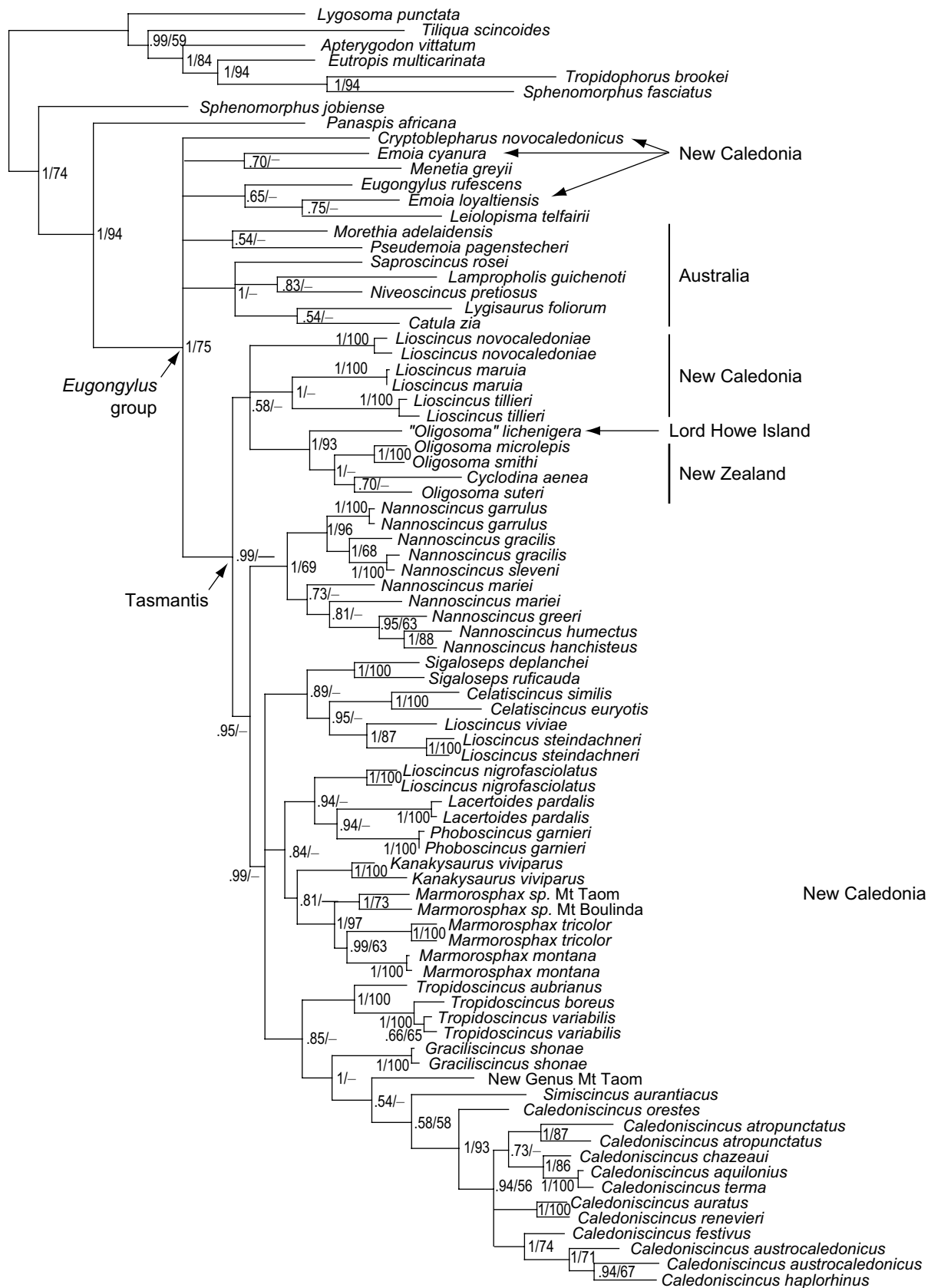


Fig. 3. Phylogeny based on combined, partitioned Bayesian analysis of one mitochondrial and two nuclear genes. Support values are shown as Bayesian posterior probability/bootstrapping support values. Support less than  $P_p$  0.50 or bootstrap 50% are not shown.

There is strong support ( $P_p = 1.0$ ) for both the *Eugongylus* group + *Panaspis*, and the *Eugongylus* group proper. Within the *Eugongylus* group there is a polytomy between the endemic Tasmantis genera and a series of clades including all remaining taxa, including the two New Caledonian area *Emoia* and *Cryptoblepharus novocaledonicus* as well as *Leiopisma telfairii* and all Australian and New Guinea taxa sampled. There is strong support ( $P_p = 1.0$ ) for the clade including the Australian genera *Saproscincus*, *Lygisaurus*, *Catula*, *Lampropholis*, and *Niveoscincus*. Although branch length is short, there is strong support ( $P_p = 0.99$ ) for a large clade corresponding to the endemic Tasmantis genera of the *Eugongylus* group. The New Zealand skinks *Oligosoma* + *Cyclodina* form a monophyletic group embedded within the New Caledonian radiation, with the Lord Howe/Philip Island (a satellite of Norfolk Island) “*Oligosoma*” *lichenigera* well supported as its immediate sister group. The one species of *Cyclodina* included renders *Oligosoma* paraphyletic. The New Caledonian *Lioscincus novocaledonicus* and the well-supported species pair (*L. maruia* + *L. tillieri*) form a polytomy with the New Zealand and Lord Howe/Phillip Island species, but there is no significant support for the larger clade incorporating all three of these lineages and we cannot reject the hypothesis that the New Zealand/Lord Howe clade is the sister group of a monophyletic New Caledonian lineage (309 trees with this topology are found in the 7596 trees in the 95% confidence interval from our Bayesian analysis and  $P \geq 0.9219$  using maximum parsimony).

All remaining New Caledonian skinks are members of a clade within which all constituent genera except *Lioscincus*, and all species except *Caledoniscincus austrocaledonicus*, *Nannoscincus mariei* and *N. gracilis* have strong support. *Nannoscincus* is the sister group to all New Caledonian genera in this clade. The remaining taxa constitute a number of discrete subclades as follows: *Lioscincus vivae* + *L. steindachneri* together are the sister group to *Celatiscincus*; together these are the sister group of *Sigaloseps*. A second clade has the pattern ((*Marmorosphax* + *Kanakysaurus*) (*Lioscincus nigrofasciolatus* (*Lacertoides* + *Phoboscincus*))). *Tropidoscincus* is the sister group to a trichotomy consisting of *Graciliscincus*, *Simiscincus* + *Caledoniscincus*, and an undescribed species from Mt. Taom representing a new genus. However, support for intergeneric relationships within this clade, and particularly for the placement of *Simiscincus* and the new genus is lacking.

Our reanalysis of 514 bp of *Laudakia* data using a GTR model of sequence evolution resulted in an estimate of the rate of sequence evolution for this section of ND2 of 1% per lineage per million years. This is higher than the 0.65% rate estimated by uncorrected distance for the ~1700 bp of mitochondrial sequence used by Macey et al. (1998). Using this rate, the age of the split between the New Caledonia + New Zealand lineage and the Australian/New Guinea species is at least 12.7 Myr. The split between “*Oligosoma*” *lichenigera* and *Oligosoma*/*Cyclodina* is 7.9 Myr.

The ages of these nodes recovered using Jennings et al. (2003)’s calibration for pygopods is much older. The rate of molecular evolution for ND2 + c-mos is 0.49–0.57% per lineage per million years (using node ages of 23 and 20 millions years). Using this rate, the age of the split between the New Caledonia + New Zealand lineage and the Australian/New Guinea species is approximately 35.4–40.7 Myr. The split between “*Oligosoma*” *lichenigera* and *Oligosoma*/*Cyclodina* is 19.9–22.9 Myr.

## 4. Discussion

### 4.1. *Eugongylus* group phylogeny

Our results corroborate the monophyly of the *Eugongylus* group lygosomines (sensu Greer, 1979) as a whole and are thus consistent with all previous studies (Donnellan, 1985; Greer, 1989, 1990; Hutchinson, 1993; Hutchinson and Donnellan, 1993; Hutchinson et al., 1990; Honda et al., 2000, 2003; Smith, 2001; Reeder, 2003; Austin and Arnold, 2006). Greer (1979) demonstrated that the Mascarene species *Leiopisma telfairii* shares a number of diagnostic features with taxa in the *Eugongylus* group (alpha palate with posteromedial processes on trailing edges of palatines, 11 premaxillary teeth, 28 presacral vertebrae), but excluded it from membership as at least some individuals retain pterygoid teeth (Arnold, 1980). However, our data suggest that *Leiopisma* is, indeed, a member of the *Eugongylus* clade. The sister group relationship between *Leiopisma* and some *Emoia* was also recovered with low support by Austin and Arnold (2006), although the weakly supported relationship between this clade and *Eugongylus* was not recovered in their analysis. We also found support for the relatively close relationship of the African *Panaspis* to the *Eugongylus* group, as previously proposed by Greer (1979) and Smith (2001). Greer (1974) suggested that the beta palate morphology had been independently derived from the alpha palate in two different lineages, a sub-Saharan African one including *Panaspis*, and an Australo-Papuan one including *Lampropholis* and its relatives. Greer (1979) subsequently favored a monophyletic group of beta palate skinks, his *Lampropholis* subgroup, but our limited data support his earlier interpretation.

Our sampling of Australian taxa is insufficient to draw any broad conclusions, but our results are largely consistent with those of previous authors. Greer (1979) placed *Eugongylus* group skinks into two subgroups, the *Eugongylus* and *Lampropholis* subgroups based chiefly on palatal morphology and later (Greer, 1989) diagnosed the *Pseudemoia* group (including the *Lampropholis* subgroup) on the basis of the derived presence of a fused atlantal arch. Hutchinson et al. (1990), proposed a number of new genera for the Australian *Eugongylus* group members based chiefly on immunological (MCF) data. Their allocation of taxa resulted in species with both distinct and fused atlantal arches in a redefined genus *Pseudemoia*, and as such is clearly at odds with Greer’s concept of the *Pseudemoia*

group. Our data does not support the higher order relationships of Hutchinson et al. (1990), nor does it support Greer's (1989) *Pseudemoia* group in its entirety, as the Australian and New Caledonian members are not parts of the same monophyletic group. This would indicate that fusion of the atlantal arches of the first cervical vertebrae has evolved on at least two occasions within skinks. Our data does support the monophyly of the Australian members of Greer's (1979) *Lampropholis* subgroup (here represented by *Saproscincus*, *Lygisaurus*, *Catula*, *Niveoscincus* and *Lampropholis*; Fig. 3), and it appears that the beta palate of the *Lampropholis* subgroup has evolved within a more extensive alpha palate lineage, rendering the alpha palate group paraphyletic. However, because relationships between the *Lampropholis* clade and others within the *Eugongylus* group are poorly supported, we cannot reject the alternative hypothesis that Greer's (1979) *Eugongylus* subgroup is monophyletic.

#### 4.2. *Tasmantis* skinks

In our analysis, the species belonging to the widespread Pacific region genera *Cryptoblepharus* (*novocaledonicus*) and *Emoia* (*cyanura* and *loyaltiensis*) are the only members of the New Caledonian skink fauna that do not form part of a monophyletic group also including the New Zealand skinks and "*Oligosoma*" *lichenigera* from the Lord Howe and Norfolk Island groups. The two New Caledonian species of *Emoia* (*cyanura* and *loyaltiensis*) do not occur on the New Caledonian mainland (Grande Terre), but are restricted to the neighboring Loyalty Islands. These two species belong to different lineages; *E. loyaltiensis* is a member of the *samoensis* group sensu Brown (1991) and weakly groups with *Leiopisma telfairii* and *Eugongylus rufescens* in our analysis, whereas *E. cyanura* was weakly supported as the sister species to *Menetia greyii* among the taxa sampled. These results are consistent with Smith's (2001) suggestion that *Emoia* is non-monophyletic. The New Caledonian *Cryptoblepharus* (*novocaledonicus*) is widespread on the Grande Terre and on satellite islands where it occupies low elevation sites, chiefly in or near the high tide zone (Bauer and Sadlier, 1994; Bauer and Sadlier, 2000; Sadlier and Bauer, 1997a). It did not show close relationships to *Emoia*, *Morethia*, or *Menetia*, all of which have been proposed at different times as sharing affinities with *Cryptoblepharus* (Greer, 1974, 1980, 1989).

All remaining *Eugongylus* group taxa are part of a well supported clade representing the lineages of the Tasmantis islands: New Caledonia, Lord Howe, Norfolk Island and New Zealand. Within this group, the New Zealand skinks form a strongly supported clade. But within New Zealand *Oligosoma* is paraphyletic, with *Cyclodina aenea* embedded within it. Generic placement of the New Zealand skinks has had a history of progressive sub-division, somewhat contemporary with the dismantling of the New Caledonian and Australian *Leiopisma* species. Greer (1974, 1979) included all New Zealand skinks in *Leiopisma*. Hardy (1977) rec-

ognized those species with scaly or opaque lower eyelids as *Cyclodina*, and Patterson and Daugherty (1995) resurrected *Oligosoma* for the remaining New Zealand species of "*Leiopisma*" (contra Cogger, 1992 who placed these species in *Pseudemoia*). Although the monophyly of New Zealand skinks has been implied (Hutchinson et al., 1990), Hickson et al. (2000) were unable to demonstrate this using their data from 12S rRNA. Our results corroborate earlier findings that the New Zealand skinks are monophyletic (Smith, 2001), that *Oligosoma smithi* and *O. microlepis* are closely related, and that *Cyclodina* renders *Oligosoma* paraphyletic (Hickson et al., 2000; Smith, 2001). Even the most comprehensive phylogeny of New Zealand skinks to date (Smith, 2001) has only sampled about half of the recognized species, and all attempts have had poor support for at least parts of their resultant trees. *Oligosoma* is noted for its cryptic species (Patterson and Daugherty, 1990; Daugherty et al., 1990) and at least 22–23 *Oligosoma* and 7–8 species (some undescribed) of *Cyclodina* are currently recognized (Daugherty et al., 1994; Berry et al., 2003). Any conclusions regarding the phylogeny of New Zealand skinks will require more extensive taxon sampling and perhaps a broader range of genetic markers.

Our results support those of Smith (2001) with respect to the placement of "*Oligosoma*" *lichenigera*, which inhabits Philip Island and the Lord Howe group, as the sister group to the New Zealand skink clade. This isolated species had previously been hypothesized to be closely related to *Oligosoma suteri* (Townes, 1974), to be relatively "basal in the lineage of *Leiopisma* type skinks" (Hardy, 1977), or to be a member of *Cyclodina* (Cogger, 1986; Greer, 1989; Hickson et al., 1992). We were not able to include in our study another enigmatic Pacific species, *Leiopisma alazon* from Fiji, which has previously been conjectured to be related to the New Zealand skinks (Zug, 1985; Hutchinson et al., 1990).

#### 4.3. Endemic New Caledonian skink genera

Our analysis suggests that the New Zealand skinks + "*Oligosoma*" *lichenigera* render the New Caledonian clade paraphyletic. However, we cannot statistically reject the hypothesis of New Caledonian monophyly. There is strong support for the monophyly of each of the endemic New Caledonian genera sampled except *Lioscincus*. The polyphyly of this genus was suspected by Hutchinson et al. (1990) and acknowledged by Bauer and Sadlier (1993, 2000). *Lioscincus steindachneri* (type species) and *L. vivae* form a well supported clade nested deep inside the main New Caledonian lineage. *Lioscincus nigrofasciolatus* clusters not with these taxa, but with a clade including the monotypic *Lacertoides* + *Phoboscincus garnieri*. Although not included in our analysis, *Lioscincus greeri*, is almost certainly the sister group to *L. nigrofasciolatus* based on morphological similarities (Böhme, 1979; Sadlier, 1986; Bauer and Sadlier, 2000). The remaining species of *Lioscincus* form two lineages *L. tillieri* + *L. maruia* and the distinctive

*L. novocaledonicus* which, with the New Zealand taxa, form a polytomy, but this larger clade receives no support. It is clear that at least two new genera need to be erected in order to accommodate those species not part of the monophyletic group that includes the type species of *Lioscincus*, *L. steindachneri*. However, this will require detailed diagnoses based on morphological data and will be dealt with in a subsequent publication.

Within the main New Caledonian clade, the diminutive fossorial skinks of the genus *Nannoscincus* are the sister to remaining taxa. The monophyly of the New Caledonian *Nannoscincus* was previously demonstrated by Sadlier (1990). Sadlier et al. (2002) identified two lineages within the genus, the *gracilis* group and the *mariei* group, the latter with the loss of the left oviduct in females. In our analysis, the *gracilis* group is well supported, but the *mariei* group is not (see also Sadlier et al., 2004), and the namesake species in both groups are themselves non-monophyletic. Several new species have recently been described within the genus (Sadlier et al., 2004, 2006) and a species level revision is in progress.

*Sigaloseps*, with two recognized species is weakly supported as the sister group to *Celatiscincus* + *Lioscincus* sensu stricto. *Celatiscincus* (type species *Lygosoma euryotis*, Werner) was previously placed in *Marmorosphax* (Sadlier, 1986), but later removed from this genus and left incertae sedis by Bauer and Sadlier (2000). Sadlier et al. (2006) erected a new genus for the one known species and described a second, cryptic form, *C. similis*, from the northern Grande Terre. *Celatiscincus* and *Lioscincus* have not previously been hypothesized to be closely related, however, all constituent taxa are chiefly mesic-adapted forest species. Both species of *Sigaloseps* are restricted to the extensive southern ultramafic block in New Caledonia (Bauer and Sadlier, 2000). *Sigaloseps deplanchei* is widespread in southern New Caledonia, whereas *S. ruficauda* is restricted to the summit areas of Mt. Ouin and Mt. Mou. The former species is currently under investigation in a fine scaled analysis to determine if it may be a composite of several cryptic species.

*Lioscincus nigrofasciolatus* is the sister to *Lacertoides* + *Phoboscincus garnieri*. Although these are all large, strongly-limbed, long-tailed species, they have not previously been suggested as allies. Indeed, Sadlier and Bauer (1999b) suggested that *L. tillieri* and *Tropidoscincus* might be allied to *Lacertoides*, based chiefly on their shared possession of exceedingly long tails. *Phoboscincus bocourti* has recently been rediscovered after more than a century (Ineich, 2004) and it will be intriguing to place it in its phylogenetic context as there is some morphological evidence that it may not be congeneric with *P. garnieri*.

*Marmorosphax* and *Kanakysaurus* are sister taxa, with weak support. The two genera are similar in appearance and both are viviparous, a feature otherwise found in New Caledonia only in *Lioscincus tillieri* (Sadlier et al., 2004). *Marmorosphax* is a monophyletic clade that includes one widespread member, *M. tricolor*, and several new taxa from

isolated ultramafic peaks in the northwest of the island (Sadlier et al., in press), and the southern ultramafic endemic, *M. montana*.

*Tropidoscincus* are large, terrestrial skinks with long limbs and tails and have previously been interpreted as potentially allied to *Lacertoides* and *Lioscincus tillieri* (Sadlier and Bauer, 1999b) in sharing exceptionally long tails. The most distinctive member of the genus, *T. aubrianus*, is the sister to the other two species. Extensive sampling within *T. boreas* and *T. variabilis*, suggests that the latter may be paraphyletic, but this requires further investigation. *Tropidoscincus* is the sister group to the most surprising clade of New Caledonian skinks. This includes the monotypic *Graciliscincus* and *Simiscincus*, a new genus (to be described elsewhere) and *Caledoniscincus*, the most widespread and speciose genus in New Caledonia. The former two genera are fossorial and restricted to the southern portion of New Caledonia and the third is known only from a single ultramafic peak in the northwest of the island, whereas the latter is terrestrial, heliophilic, and occurs throughout New Caledonia, its offshore islands (Bauer et al., 1992; Bauer and Sadlier, 1994; Sadlier and Bauer, 1997a) and southern Vanuatu (Medway and Marshall, 1975), from the intertidal zone (Bauer and DeVaney, 1987) to elevations of over 1000 m. Relationships among these genera are poorly resolved, but the diverse *Caledoniscincus* is strongly supported as monophyletic. Although there are areas of conflict, our data are consistent with the sister-group pairing *C. auratus*–*C. renevieri* retrieved using allozyme data (Sadlier et al., 1999). A more extensive analysis of this genus (Sadlier, Smith, Bauer, in prep.) reveals that some morphological species include cryptic forms and that species boundaries within *Caledoniscincus* need to be reevaluated.

The only genus not included in the analysis was *Geoscincus*, known only from the two types of *G. haraldmeieri*. Although Böhme (1976) and Börner (1980) suggested that this species was related to *Phoboscincus*, there is no objective basis for this, and its affinities remain uncertain.

#### 4.4. Biogeographic history of the Tasmantis skinks

Evidence for biotic relationships of vicariant origin between Australia on one hand and New Caledonia + New Zealand on the other are supported by a variety of taxa (Cracraft, 1980). Dating of the trans-Tasman split between Australian and New Caledonian diplodactylid geckos is supportive of a Gondwanan origin for this group (King, 1987; Bauer, 1990), although the modern New Caledonian radiation of geckos probably dates only from the Oligocene (Jackman, 2005), perhaps reflecting a major faunal turnover associated with ultramafic overthrusting during this period (Cluzel et al., 2001; Bauer et al., 2006).

Although Adler et al. (1995) suggested that the New Caledonian skink fauna might be a relict of ancient Gondwanan connections, Sadlier (1986) and Bauer and Sadlier (1993, 2000) proposed over-water dispersal for the



colonization of the region, but considered that the extreme morphological diversity amongst the endemic genera argued against a Pliocene origin, as had been assumed by many herpetologists for the endemic skinks of New Zealand (see below).

Although our data do support the monophyly of the endemic skinks of the Tasmantis block, they do not imply Gondwanan relationships or a vicariant origin of the regional scincid fauna. Our two methods of age estimation differ significantly from one another, yielding a range of possible divergences of the Tasmantis lineage from other *Eugongylus* group skinks from 12.7 to 40.7 Myr. If the true age of this split is closer to the upper limit it would be consistent with the estimate of Hickson et al. (2000) of at least 23 Myr for the age of *Oligosoma*, whereas the lower estimate is compatible with the estimate of a maximum of 17 Myr since the divergence of *Leiopisma* from the rest of the *Eugongylus* group (Austin and Arnold, 2006). Both of these estimates are based on 12S sequences. However, the estimate of the age of *Oligosoma* is calibrated using bovids and ratites aged between 28 and 19 Myr, and the *Leiopisma* date is based on a calibration point in the scincine genus *Chalcides* at 1 Myr. We believe that a younger date is more likely correct based on two main lines of evidence. First, a recent chronogram of squamate reptiles (Wiens et al., 2006) suggests that the 20–23 Myr date for *Pygopus* (Jennings et al., 2003) used as a calibration point to estimate rates of sequence evolution may be overestimated by a factor of 2. Second, older dates imply overwater colonization during periods of minimal emergent land in the southwest Pacific and also imply the divergence of *Oligosoma lichenigera* from New Zealand skinks long before the emergence of Lord Howe Island (see below). Consequently, we base our biogeographic hypotheses on a Miocene origin of the Tasmantis group of skinks.

Our data strongly support the hypothesis that New Caledonia was colonized, probably only once, by *Eugongylus* group skinks during the Middle Miocene. This was a period of uplift and marine regression in New Caledonia which followed a period of Oligocene marine transgressions, which reduced neighboring New Zealand to an area of about 18% of its current aerial land mass (Cooper and Millener, 1993) and may have submerged the majority of New Caledonia (Muriene et al., 2005).

A lack of resolution at the base of the *Eugongylus* group phylogeny precludes identification of a probable source of this colonization. However, emergent seamounts along the Norfolk Ridge may have provided an ephemeral link between portions of the Outer Melanesian Arc and New Caledonia during parts of the Miocene (Holloway, 1979; Herzer et al., 1997; Waters et al., 2000; Swenson et al., 2001) and the Queensland Rise, roughly in the middle of the Coral Sea, may have offered stepping stones from Australia during periods of lowered sea levels (Raven and Axelrod, 1972).

In contrast to earlier interpretations of the New Caledonian fauna (e.g., Diamond, 1984), there now exists clear evi-

dence that New Caledonia has been the site of numerous in situ radiations of vertebrate taxa (Bauer, 1989; Bauer and Sadlier, 1993, 2000; Adler et al., 1995). Indeed, animals and plants of many groups exhibit significant radiations within New Caledonia (e.g., Haase and Bouchet, 1998; Eibl et al., 2001). Our data suggest that the modern generic diversity of New Caledonian skinks was established shortly after the colonization of the island, and the lack of support for most patterns of intergeneric relationships may be a reflection of a relatively explosive radiation of adaptive types. Speciation within the endemic genera has probably been influenced by significant climatic and vegetational changes that characterized major portions of the later Tertiary (Lowry, 1998; Lee et al., 2001), but specific candidate cladogenetic events remain elusive. In most instances, however, there is no evidence of adaptive intrageneric radiations with significant anagenetic change. Rather, speciation appears to have been the result of fragmentation, yielding morphologically and ecologically similar congeners in allopatry.

Our data also strongly suggest a monophyletic origin (based on our limited sampling) of the New Zealand plus Lord Howe/Norfolk Island *Eugongylus* group skinks, probably from New Caledonia (although a sister group relationship to the New Caledonian clade cannot be rejected). Caughley (1964) proposed two invasions of New Zealand from Australia, and Whitaker (1968) proposed three, while Towns (1974) suggested that New Caledonia might have been a source area for the New Zealand fauna. Hardy (1977) also proposed multiple invasions of New Zealand from New Caledonia, but also believed that at least some *Leiopisma* (now *Oligosoma*) in New Zealand had arrived overwater from Australia. He also proposed the independent derivation of *O. lichenigera* from eastern Australia. Our data contradict this scenario and confirm that this lineage is considerably older than Hardy (1977) had supposed. Based on our lower age estimates the split between “*Oligosoma*” *lichenigera* and the endemic New Zealand clade took place approximately 7.9 Myr. This corresponds well to the 7 Myr estimate for the age of Lord Howe Island (McDougall et al., 1981; Pickard, 1983). The younger (2.3–3.0 Myr) age of Norfolk Island (Jones and McDougall, 1973; Otte and Rentz, 1985) suggests that colonization was by way of Lord Howe, although our sampling did not permit us to test this.

Earlier estimates placed the origin of the New Zealand skinks in the Pliocene (Robb, 1973; Towns, 1974; Bull and Whitaker, 1975; Hardy, 1977). More recent allozyme (Towns et al., 1985; Daugherty et al., 1990) and mtDNA sequence-based studies (Hickson et al., 2000) have estimated the age of the New Zealand skink fauna to be 20 Myr or more. If our preferred (younger) age estimate is correct, it suggests that the New Zealand *Oligosomal/Cyclodina* clade is less than 7 Myr old. This is far younger than the estimate of Hickson et al. (2000), but consistent with estimates for the diversification of a variety of other elements of the New Zealand biota (Chambers et al., 2001; Trewick and Wallis, 2001; Trewick and Morgan-Richards, 2005).

Although our sampling is insufficient to suggest either a source or the timing of the colonization of the New Caledonian region by *Emoia loyaltiensis*, *E. cyanura*, or *Cryptoblepharus novocaledonicus*, it is likely that these events were very recent. *Emoia cyanura* is widespread in the tropical Pacific (Brown, 1991) and *C. novocaledonicus* exhibits almost no genetic variability across its range in New Caledonia (Smith et al., unpublished) and is very similar to congeneric populations elsewhere, particularly in Vanuatu (G. Zug, pers. commun.). Further, both species of *Emoia* are limited in their New Caledonian distribution to the Loyalty Islands, which have been emergent only since the Pleistocene (Paris, 1981).

As no modern geological reconstructions of the late Tertiary history of the southwest Pacific support the existence of direct land connections among the components of the Tasmanian block, or between this unit and either Australia or elements of the Outer Melanesian Arc islands, we are able to reject vicariant hypotheses regarding the origin of the skinks of the region. Each island group was colonized over water, almost certainly in the order New Caledonia—Lord Howe Island—New Zealand, with a subsequent colonization of Norfolk Island from Lord Howe in the last 3 Myr. Deeper sampling of the Australian, New Guinean and other Melanesian *Eugongylus* group lineages may eventually clarify the probable source area for this diverse clade of skinks and finer scaled sampling within New Caledonia and especially New Zealand may shed light on patterns of “continental” speciation and radiation in these islands.

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## References

- Adler, G.H., Austin, C.C., Dudley, R., 1995. Dispersal and speciation of skinks among archipelagos in the tropical Pacific Ocean. *Evol. Ecol.* 9, 529–541.
- Arnold, E.N., 1980. Recently extinct reptile populations from Mauritius and Reunion, Indian Ocean. *J. Zool., London* 191, 33–47.
- Austin, J.J., Arnold, E.N., 2006. Using ancient and recent DNA to explore relationships of extinct and endangered *Leiopisma* skinks (Reptilia: Scincidae) in the Mascarene islands. *Mol. Phylogenet. Evol.* 39, 503–511.
- Bauer, A.M., 1989. Reptiles and the biogeographic interpretation of New Caledonia. *Tuatara* 30, 39–50.
- Bauer, A.M., 1990. Phylogenetic systematics and biogeography of the Carphodactylini (Reptilia: Gekkonidae). *Bonn. Zool. Monogr.* 30, 1–220.
- Bauer, A.M., 1999. The terrestrial reptiles of New Caledonia: the origin and evolution of a highly endemic herpetofauna. In: Ota, H. (Ed.), *Tropical Island Herpetofauna: Origin, Current Diversity, and Conservation*. Elsevier, Amsterdam, pp. 3–25.
- Bauer, A.M., DeVaney, K.D., 1987. Aspects of diet and habitat use in some New Caledonian lizards. *Amphibia-Reptilia* 8, 349–364.
- Bauer, A.M., Sadlier, R.A., 1993. Systematics, biogeography and conservation of the lizards of New Caledonia. *Biodiv. Lett.* 1, 107–122.
- Bauer, A.M., Sadlier, R.A., 1994. The terrestrial herpetofauna of the Ile des Pins, New Caledonia. *Pacific Sci.* 48, 353–366.
- Bauer, A.M., Sadlier, R.A., 2000. The Herpetofauna of New Caledonia. Society for the Study of Amphibians and Reptiles, Ithaca.
- Bauer, A.M., Renevier, A., Sadlier, R.A., 1992. *Caledoniscincus austrocaledonicum* (Reptilia: Scincidae) from Ile Surprise, d'Entrecasteaux Reefs, New Caledonia. *Pacific Sci.* 46, 86–89.
- Bauer, A.M., Jackman, T., Sadlier, R.A., Whitaker, A.H., 2006. A revision of the *Bavayia validiclavus* group (Squamata: Gekkota: Diplodactylidae), a clade of New Caledonian geckos exhibiting microendemism. *Proc. California Acad. Sci.* 57, 503–547.
- Bavay, A., 1869. Catalogue des reptiles de la Nouvelle-Calédonie et description d'espèces nouvelles. *Mém. Soc. Linn. Normandie* 15, 1–37.
- Berry, O., Gleeson, D.M., Sarre, S.D., 2003. Microsatellite DNA markers for New Zealand skinks. *Conserv. Genet.* 4, 411–414.
- Bocage, J.V., Barboza, du., 1873. Sur quelques sauriens nouveaux de la Nouvelle Calédonie et de l'Australie. *J. Sci. Math. Phys. Nat. Lisboa* 4, 228–232.
- Böhme, W., 1976. Über die Gattung *Eugongylus* Fitzinger, mit Beschreibung einer neuer Art (Reptilia: Scincidae). *Bonn. Zool. Beitr.* 27, 245–251.
- Böhme, W., 1979. Eine neue Art der Gattung *Leiopisma* Duméril et Bibron, 1839 aus Neukaledonien (Reptilia: Sauria: Scincidae). *Salamandra* 15, 140–145.
- Börner, A.-R., 1980. Über neukaledonische Skinke des *Leiopisma austrocaledonicum*—Komplexes. *Misc. Art. Saurol.* 5, 1–15.
- Boulenger, G.A., 1887. Catalogue of the Lizards in the British Museum (Natural History), Second Edition. Vol. 3. Lacertidae, Gerrhosauridae, Scincidae, Anelytropidae, Dibamidae, Chamaeleonidae. British Museum (Natural History), London.
- Brandley, M.C., Schmitz, A., Reeder, T.W., 2005. Partitioned Bayesian analysis, partition choice, and the phylogenetic relationships of scincid lizards. *Syst. Biol.* 54, 373–390.
- Brown, W.C., 1991. Lizards of the genus *Emoia* (Scincidae) with observations on their evolution and biogeography. *Mem. Calif. Acad. Sci.* 15, vi + 94.
- Brown, K.S., 1999. Deep Green rewrites evolutionary history of plants. *Science* 285, 990–991.
- Buckley, T.R., Arensburger, P., Simon, C., Chambers, G.K., 2002. Combined data, Bayesian phylogenetics, and the origin of the New Zealand cicada genera. *Syst. Biol.* 51, 4–18.
- Bull, P.C., Whitaker, A.H., 1975. The amphibians, reptiles, birds and mammals. In: Kuschel, G. (Ed.), *Biogeography and Ecology in New Zealand*. Dr. W. Junk, The Hague, pp. 231–276.
- Caughley, G., 1964. Does the New Zealand vertebrate fauna conform to zoogeographic principles? *Tuatara* 12, 49–58.
- Chambers, G.K., boon, W.M., Buckley, T.R., Hitchmough, R.A., 2001. Using molecular methods to understand the Gondwanan affinities of the New Zealand biota: three case studies. *Austral. J. Bot.* 49, 377–387.

- Chazeau, J., 1993. Research on New Caledonian terrestrial fauna: achievements and prospects. *Biodiv. Lett.* 1, 123–129.
- Cluzel, D., Aitchison, J.C., Picard, C., 2001. Tectonic accretion and underplating of mafic terranes in the Late Eocene intraoceanic fore-arc of New Caledonia (Southwest Pacific): geodynamic implications. *Tectonophysics* 340, 23–59.
- Cogger, H.G., 1979. *Reptiles and Amphibians of Australia*, 2nd ed. Reed, Sydney.
- Cogger, H.G., 1986. *Reptiles and Amphibians of Australia*, fourth ed. Reed, Sydney.
- Cogger, H.G., 1992. *Reptiles and Amphibians of Australia*, 5th ed. Reed Books, Chatswood, NSW.
- Coleman, P.J., 1980. Plate tectonics background to biogeographic development in the southwest Pacific over the last 100 million years. *Paleogeogr., Paleoclimatol., Paleoecol.* 31, 105–121.
- Cooper, R.A., Millener, P.R., 1993. The New Zealand biota: historical background and new research. *Trends Ecol. Evol.* 8, 429–433.
- Cracraft, J., 1980. Biogeographic patterns of terrestrial vertebrates in the southwest Pacific. *Paleogeogr., Paleoclimatol., Paleoecol.* 31, 353–369.
- Czechura, G.V., 1981. The rare scincid lizard, *Nannoscincus graciloides*: a reappraisal. *J. Herpetol.* 15, 315–320.
- Daugherty, C.H., Patterson, G.B., Thorn, C.J., French, D.C., 1990. Differentiation of the members of the New Zealand *Leiopisma nigriplantare* species complex (Lacertilia: Scincidae). *Herpetol. Monogr.* 4, 61–76.
- Daugherty, C.H., Gibbs, G.W., Hitchmough, R.A., 1993. Mega-island or micro-continent? New Zealand and its fauna. *Trends Ecol. Evol.* 8, 437–442.
- Daugherty, C.H., Patterson, G.B., Hitchmough, R.A., 1994. Taxonomic and conservation review of the New Zealand herpetofauna. *N. Zealand J. Zool.* 21, 317–323.
- Diamond, J., 1984. Biogeographic mosaics in the Pacific. In: Radvosky, F.J., Raven, P.H., Sohmer, S.H. (Eds.), *Biogeography of the Tropical Pacific*. Bishop Museum Special Publication, 72, pp. 1–14.
- Donnellan, S.C., 1985. The evolution of sex chromosomes in scincid lizards. Ph.D. dissertation, Macquarie University.
- Driskell, A.C., Ané, C., Burleigh, J.G., McMahon, M.M., O'Meara, B.C., Sanderson, M.J., 2004. Prospects for building the Tree of Life from large sequence databases. *Science* 306, 1172–1174.
- Eibl, J.M., Plunkett, G.M., Lowry, P.P., II, 2001. Evolution of *Polyscias* sect. *Tieghemopanax* (Araliaceae) based on nuclear and chloroplast DNA sequence data. *Adansonia*, sér. 3 23, 23–48.
- Felsenstein, J., 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39, 783–791.
- Greer, A.E., 1970. A subfamilial classification of scincid lizards. *Bul. Mus. Comp. Zool.* 139, 151–184.
- Greer, A.E., 1974. The generic relationships of the scincid lizard genus *Leiopisma* and its relatives. *Austral. Jour. Zool. Suppl. Ser.* 31, 1–67.
- Greer, A.E., 1979. A phylogenetic subdivision of Australian skinks. *Rec. Austral. Mus.* 32, 339–371.
- Greer, A.E., 1980. A new species of *Morethia* (Lacertilia: Scincidae) from Northern Australia, with comments on the biology and relationships of the genus. *Rec. Austral. Mus.* 33, 89–122.
- Greer, A.E., 1989. *The Biology and Evolution of Australian Lizards*. Surrey Beatty and Sons Pty., Ltd., Chipping Norton, NSW.
- Greer, A.E., 1990. Overlap pattern in the preanal scale row: an important systematic character in skinks. *J. Herpetol.* 24, 328–330.
- Groth, J.G., Barrowclough, G.F., 1999. Basal divergences in birds and the phylogenetic utility of the nuclear RAG-1 gene. *Mol. Phylogenet. Evol.* 12, 115–123.
- Günther, A., 1872. On some new species of reptiles and fishes collected by J. Brenchley. *Esq. Ann. Mag. Natur. Hist.* (41), 418–420.
- Günther, A., 1873. Reptiles. In: Brenchly, J.L. (Ed.), *Jottings During the Cruise of H.M.S. Curacoa Among the South Sea Islands in 1865*. Longmans, Green and Co., Germany, pp. 396–407.
- Haase, M., Bouchet, P., 1998. Radiation of crenobiontic gastropods on an ancient continental island: the *Hemistomia*-clade in New Caledonia (Gastropoda: Hydrobiidae). *Hydrobiologia* 367, 43–129.
- Hall, R., 1997. Cenozoic tectonics of SE Asia and Australasia. In: Howes, J.V.C., Noble, R.A. (Eds.), *Proceedings IPA Petroleum Systems of SE Asia and Australasia Conference*. Jakarta, pp. 47–62.
- Hardy, G.S., 1977. The New Zealand Scincidae (Reptilia: Lacertilia): a taxonomic and zoogeographic study. *New Zealand J. Zool.* 4, 221–325.
- Herzer, R.H., Chaproniere, G.C.H., Edwards, A.R., Hollis, C.J., Pelletier, B., Raine, J.I., Scott, G.H., Stagpoole, V., Strong, C.P., Symonds, P., Wilson, J.G., Zhu, H., 1997. Seismic stratigraphy and structural history of the Reinga Basin and its margins, southern Norfolk Ridge System. *New Zealand J. Geol. Geophys.* 40, 425–451.
- Hickson, R.E., Penny, D., Scott, D.B., 1992. Molecular systematics and evolution in New Zealand: applications to cryptic skink species. *New Zealand J. Zool.* 19, 33–44.
- Hickson, R.E., Slack, K.E., Lockhart, P., 2000. Phylogeny recapitulates geography, or why New Zealand has so many species of skinks. *Biol. J. Linn. Soc.* 70, 415–433.
- Holloway, J.D., 1979. *A Survey of the Lepidoptera, Biogeography and Ecology of New Caledonia*. Dr. W. Junk, The Hague.
- Honda, M., Ota, H., Kobayashi, M., Hikida, T., 1999. Phylogenetic relationships of Australian skinks of the *Mabuya* group (Reptilia: Scincidae) inferred from mitochondrial DNA sequences. *Genes Genet. Syst.* 74, 135–139.
- Honda, M., Ota, H., Kobayashi, M., Nabhitabhata, J., Yong, H.-S., Hikida, T., 2000. Phylogenetic relationships, character evolution, and biogeography of the subfamily Lygosominae (Reptilia: Scincidae) inferred from mitochondrial DNA sequences. *Molec. Phylogenet. Evol.* 15, 452–461.
- Honda, M., Ota, H., Köhler, G., Ineich, I., Chirio, L., Chen, S.-L., Hikida, T., 2003. Phylogeny of the lizard subfamily Lygosominae (Reptilia: Scincidae), with special reference to the origin of the New World taxa. *Genes Genet. Syst.* 78, 71–80.
- Huelsenbeck, J.P., Ronquist, F., 2001. MrBayes: Bayesian inference of phylogeny. *Bioinformatics* 17, 754–755.
- Hutchinson, M.N., 1993. Family Scincidae. In: Glasby, C.J., Ross, G.J.B., Beesley, P.L. (Eds.), *Fauna of Australia*, vol. 2A. Amphibia and Reptilia. Australian Government Printing Service, Canberra, pp. 261–279.
- Hutchinson, M.N., Donnellan, S.C., 1993. Biogeography and phylogeny of the Squamata. In: Glasby, C.J., Ross, G.J.B., Beesley, P.L. (Eds.), *Fauna of Australia* vol. 2A. Amphibia and Reptilia. Australian Government Publishing Service, Canberra, pp. 210–220.
- Hutchinson, M.N., Donnellan, S.C., Baverstock, P.R., Krieg, M., Simms, S., Burgin, S., 1990. Immunological relationships and generic revision of the Australian lizards assigned to the genus *Leiopisma* (Scincidae: Lygosominae). *Austral. J. Zool.* 38, 535–554.
- Ineich, I., 2004. Le squinque terrifiant de Bocourt retrouvé en Nouvelle-Calédonie. Press release, Muséum national d'histoire naturelle, Paris, 3 Mars 2004.
- Jackman, T., 2005. Tempo and mode of diversification of endemic New Caledonian lizards. Abstracts, 2005 Joint Meeting of Ichthyologists and Herpetologists, Tampa, Florida, 243.
- Jaffré, T., Bouchet, P., Veillon, J.-M., 1998. Threatened plants of New Caledonia: is the system of protected areas adequate? *Biodiv. Conserv.* 7, 109–135.
- Jones, J.G., McDougall, J., 1973. Geological history of Norfolk and Philip Islands, southwest Pacific Ocean. *J. Geol. Soc. Austral.* 20, 239–257.
- King, M., 1987. Origin of the Gekkonidae: chromosomal and albumin evolution suggests Gondwanaland. *Search* 18, 252–254.
- Kroenke, L.W., 1984. Cenozoic tectonic development of the southwest Pacific. United Nations Economic and Social Commission, Committee for Coordination of Joint Prospecting for Mineral Resources in the South Pacific Offshore Area. *Tech. Bull.* 6, 1–122.
- Kroenke, L.W., 1996. Plate tectonic development of the western and southwestern Pacific: Mesozoic to the present. In: Keast, A., Miller, S.E. (Eds.), *The Origin and Evolution of Pacific Island Biotas*. In: New Guinea to Eastern Polynesia: Patterns and Processes SPB Academic Publishing, Amsterdam, pp. 19–34.
- Lee, D.E., Lee, W.G., Mortimer, N., 2001. Where and why have all the flowers gone? Depletion and turnover in the New Zealand Cenozoic

- angiosperm flora in relation to palaeogeography and climate. *Austral. J. Bot.* 49, 341–356.
- Lowry, P.P. II., 1998. Diversity, endemism, and extinction in the flora of New Caledonia: a review. In: Peng, C.I., Lowry, P.P., II (Eds.), *Rare, Threatened, and Endangered Floras of Asia and the Pacific Rim*. Institute of Botany, Academia Sinica Monograph Series No. 16. Taipei, pp. 181–206.
- Lowry, P.P. II., Munzinger, J., Bouchet, P., Géraux, H., Bauer, A.M., Langrand, O., Mittermeier, R.A., 2004. New Caledonia. In: Mittermeier, R.A., Gil, P.R., Hoffmann, M., Pilgrim, J., Brooks, T., Mittermeier, C.G., Lamoreux, J., Da Fonseca, G.A.B. (Eds.), *Hotspots Revisited*. CEMEX, Mexico City, pp. 192–197.
- Macey, J.R., Larson, A., Ananjeva, N.B., Papenfuss, T.J., 1997. Evolutionary shifts in three major structural features of the mitochondrial genome among iguanian lizards. *J. Mol. Evol.* 44, 660–674.
- Macey, J.R., Schulte II, J.A., Ananjeva, N.B., Larson, A., Rastegar-Pouyani, N., Shammakov, S.M., Papenfuss, T.J., 1998. Phylogenetic relationships among agamid lizards of the *Laudakia caucasia* species group: testing hypotheses of biogeographic fragmentation and an area cladogram for the Iranian Plateau. *Mol. Phylogenet. Evol.* 10, 118–131.
- McDougall, I., Embleton, B.J.J., Stone, D.S., 1981. Origin and evolution of Lord Howe Island—South-west Pacific Ocean. *J. Geol. Soc. Austral.* 28, 156–176.
- Medway, Lord., Marshall, A.G., 1975. Terrestrial vertebrates of the New Hebrides: origin and distribution. *Phil. Trans. Roy. Soc. London* 272, 423–465.
- Mittermeier, R.A., Werner, T.B., Lees, A., 1996. New Caledonia—a conservation imperative for an ancient land. *Oryx* 30, 104–112.
- Mittleman, M.B., 1952. A generic synopsis of the lizards of the subfamily Lygosominae. *Smithsonian Misc. Coll.* 117 (17), 1–35.
- Morat, P., 1993. Our knowledge of the flora of New Caledonia: endemism and diversity in relation to vegetation types and substrates. *Biodiv. Lett.* 1, 72–81.
- Morat, P., Jaffré, T., Veillon, J.-M., MacKee, H.S., 1986. Affinités floristiques et considérations sur l'origine des maquis miniers de la Nouvelle-Calédonie. *Bull. Mus. Natl. Hist. Nat., Paris*, 4<sup>e</sup>, 8, sect. B, Adansonia n° 2, 133–182.
- Murienne, J., Grandcolas, P., Piulachs, M.D., Bellés, X., D'Haese, C., Legendre, F., Pellens, R., Guilbert, E., 2005. Evolution on a shaky piece of Gondwana: is local endemism recent in New Caledonia? *Cladistics* 21, 2–7.
- Myers, N., 1988. Threatened biotas: “hot spots” in tropical forests. *The Environmentalist* 8, 187–208.
- Myers, N., 1990. The biodiversity challenge: expand hot-spot analysis. *The Environmentalist* 10, 243–256.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. *Nature* 403, 853–858.
- Nylander, J.A. 2004. MrModelTest. 2.0. Distributed by the author. Evolutionary Biology Centre, Uppsala University, Uppsala.
- Nylander, J.A.A., Ronquist, F., Huelsenbeck, J.P., Nieves-Aldrey, J.L., 2004. Bayesian phylogenetic analysis of combined data. *Syst. Biol.* 53, 47–67.
- Otte, D., Rentz, D.C.F., 1985. The crickets of Lord Howe and Norfolk Islands (Orthoptera, Gryllidae). *Proc. Acad. Nat. Sci. Philadelphia* 137, 79–101.
- Paris, J.P., 1981. Géologie de la Nouvelle-Calédonie. *Mém. Bur. Rech. Géol. Minières* 113, 1–278. 2 maps.
- Patterson, G.B., Daugherty, C.H., 1990. Four new species and one new subspecies of skinks, genus *Leiopisma* (Reptilia: Lacertilia: Scincidae) from New Zealand. *J. Roy. Soc. New Zealand* 20, 65–84.
- Patterson, G.B., Daugherty, C.H., 1995. Reinstatement of the genus *Oligosoma* (Reptilia: Lacertilia: Scincidae). *J. Roy. Soc. New Zealand* 25, 327–331.
- Penny, N.D., 1975. Evolution of extant Mecoptera. *J. Kansas Entomol. Soc.* 40, 331–350.
- Peters, W., 1869. Über neue Gattungen und neue oder weniger bekannte Arten von Amphibien Monatsber. Königl. Preuss. Akad. Wiss., Berlin. pp. 432–445, 1 pl.
- Peters, W., 1879. Über *Sauropsincus*, eine neue Gattung von Scincoiden, aus Neu-Caledonien. *Sber. Ges. Naturf. Freunde Berlin* 1879, 149–150.
- Phillipe, H., Snell, E.A., Baptiste, E., Lopez, P., Holland, P.W.H., Casane, D., 2004. Phylogenomics of eukaryotes: impact of missing data on large alignments. *Mol. Biol. Evol.* 21, 1740–1752.
- Pickard, J., 1983. Vegetation of Lord Howe Island. *Cunninghamia* 1, 133–266.
- Platnick, N.I., 1993. The araneomorph spider fauna of New Caledonia. *Biodiv. Lett.* 1, 102–106.
- Polhemus, D.A., 1996. Island arcs and their influence on Indo-Pacific biogeography. In: Keast, A., Miller, S.E. (Eds.), *The origin and evolution of pacific island biotas, New Guinea to Eastern Polynesia: Patterns and Processes*. SPB Academic Publishing, Amsterdam, pp. 51–66.
- Rambaut, A., 1995. Se-AI. Sequence Alignment Editor, Evolutionary Biology Group. University of Oxford, Oxford.
- Raven, P.H., Axelrod, D.I., 1972. Plate tectonics and Australasian paleobiogeography. *Science* 176, 1379–1386.
- Reeder, T.W., 2003. A phylogeny of the Australian *Sphenomorphus* group (Scincidae: Squamata) and the phylogenetic placement of the crocodile skinks (*Tribolonotus*): Bayesian approaches to assessing congruence and obtaining confidence in maximum likelihood inferred relationships. *Mol. Phylogenet. Evol.* 27, 384–397.
- Robb, J., 1973. Reptiles and amphibians. In: Williams, G.R. (Ed.), *The Natural History of New Zealand: An Ecological Survey*. Reed, Wellington, pp. 285–303.
- Roux, J., 1913. Les reptiles de la Nouvelle-Calédonie et des Îles Loyalty. In: Sarasin, F., Roux, J. (Eds.), *Nova Caledonia, Zoologie*, vol. 1(2). C.W. Kreidels Verlag, Wiesbaden, pp. 79–160.
- Sadler, R.A., 1986. A review of the scincid lizards of New Caledonia. *Rec. Austral. Mus.* 39, 1–66.
- Sadler, R.A., 1990. The scincid lizard genus *Nannoscincus* Günther: a revaluation. *Mem. Qld. Mus.* 29, 487–494.
- Sadler, R.A., Bauer, A.M., 1997a. The terrestrial herpetofauna of the Loyalty Islands. *Pacific Sci.* 51, 76–90.
- Sadler, R.A., Bauer, A.M., 1997b. A new genus and species of lizard (Reptilia: Scincidae) from New Caledonia, southwest Pacific. *Pacific Sci.* 51, 91–96.
- Sadler, R.A., Bauer, A.M., 1999b. The scincid lizard *Lioscincus tillieri* from New Caledonia in the southwest Pacific: new information on the species biology, distribution, and morphology. *Rec. Austral. Mus.* 51, 93–98.
- Sadler, R.A., Shea, G.M., Bauer, A.M., 1997. A new genus and species of lizard (Squamata, Scincidae) from New Caledonia, southwest Pacific. *Zool. Neocaledonia* 4. *Mém. Mus. Natl. Hist. Nat.* 171, 379–385.
- Sadler, R.A., Whitaker, A.H., Bauer, A.M., 1998. *Lioscincus maruia*, a new species of Lizard (Reptilia: Scincidae) from New Caledonia. *Southwest Pacific. Pacific Sci.* 52, 334–341.
- Sadler, R.A., Bauer, A.M., Colgan, D.J., 1999. The scincid lizard genus *Caledoniscincus* (Reptilia: Scincidae) from New Caledonia in the southwest Pacific: a review of *Caledoniscincus austrocaledonicus* (Bavay) and description of six new species from Province Nord. *Rec. Austral. Mus.* 51, 57–82.
- Sadler, R.A., Bauer, A.M., Whitaker, A.H., 2002. The scincid lizard genus *Nannoscincus* Günther from New Caledonia in the southwest Pacific: a review of the morphology and distribution of species in the *Nannoscincus mariei* species group, including the description of three new species from Province Nord. *Zool. Neocaledonia* 5. *Mem. Mus. Natl. Hist. Nat.* 187, 269–276.
- Sadler, R.A., Bauer, A.M., Whitaker, A.H., Smith, S.A., 2004. Two new scincid lizards (Squamata: Scincidae) from the Massif de Kopéto, northwestern New Caledonia. *Proc. Calif. Acad. Sci.* 55, 208–221.
- Sadler, R.A., Smith, S.A., Bauer, A.M., Whitaker, A.H., 2004. A new genus and species of live-bearing scincid lizard (Reptilia: Scincidae) from New Caledonia. *J. Herpetol.* 38, 320–330.
- Sadler, R.A., Bauer, A.M., Smith, S.A., 2006. A new species of *Nannoscincus* Günther (Squamata: Scincidae) from high elevation forest in southern New Caledonia. *Rec. Austral. Mus.* 58, 29–36.
- Sadler, R.A., Smith, S.A., Bauer, A.M., 2006. A new genus for the New Caledonian scincid lizard *Lygosoma euryotis* Werner 1909, and the description of a new species. *Rec. Austral. Mus.* 58, 19–28.



- Séret, B., 1997. Les poissons d'eau douce de Nouvelle-Calédonie: implications biogéographiques de récentes découvertes. *Mém. Mus. Natl. Hist. Nat.*, Paris 171, 369–378.
- Smith, M.A., 1937. A review of the genus *Lygosoma* (Scincidae: Reptilia) and its allies. *Rec. Indian Mus.* 39, 213–234.
- Smith, S.A., 2001. A molecular phylogenetic study of the *Eugongylus* group of skinks. Ph.D. dissertation, University of Adelaide, Adelaide, Australia.
- Stevens, G.R., 1980. New Zealand Adrift: The Theory of Continental Drift in a New Zealand Setting. A.H. & A.H. Reed, Wellington.
- Stevens, G.R., 1989. The nature and timing of biotic links between New Zealand and Australia in Mesozoic and early Cenozoic times. In: Crame, J.A. (Ed.), *Origins and Evolution of the Antarctic Biota*. Geological Society Special Publication 47. Geological Society, London, pp. 141–166.
- Swenson, U., Backland, A., McLoughlin, S., Hill, R.S., 2001. *Nothofagus* biogeography revisited with special emphasis on the enigmatic distribution of subgenus *Brassospora* in New Caledonia. *Cladistics* 17, 28–47.
- Swofford, D.L., 2002. *PAUP\*: Phylogenetic Analysis Using Parsimony* (\* and other methods). Sinauer Associates, Sunderland, MA.
- Templeton, A., 1983. Phylogenetic inference from restriction endonuclease cleavage site maps with particular reference to the evolution of humans and the apes. *Evolution* 37, 221–224.
- Thompson, J.D., Gibson, T.J., Plewniak, F., Jeanmougin, F., Higgins, D.G., 1997. The ClustalX windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nuc. Acids Res.* 24, 4876–4882.
- Towns, D.R., 1974. Zoogeography of the New Zealand Scincidae. *J. Roy. Soc. New Zealand* 4, 217–226.
- Towns, D.R., Daugherty, C.H., Newman, D.G., 1985. An overview of the ecological biogeography of the New Zealand lizards (Gekkonidae, Scincidae). In: Grigg, G., Shine, R., Ehmann, H. (Eds.), *The Biology of Australasian Frogs and Reptiles*. Surrey Beatty and Sons Pty., Ltd., Chipping Norton, NSW, pp. 107–115.
- Trewick, S.A., Morgan-Richards, M., 2005. After the deluge: mitochondrial DNA indicates Miocene radiation and Pliocene adaptation of tree and giant weta (Orthoptera: Anostomatidae). *J. Biogeogr.* 32, 295–309.
- Trewick, S.A., Wallis, G.P., 2001. Bridging the “beech-gap”: New Zealand invertebrate phylogeography implicates Pleistocene glaciation and Pliocene isolation. *Evolution* 55, 2170–2180.
- Viot, R., 1956. La végétation canaque. *Mém. Mus. Natl. Hist. Nat. n.s.*, B 7, 1–398.
- Waters, J.M., López, J.A., Wallis, G.P., 2000. Molecular phylogenetics and biogeography of galaxiid fishes (Osteichthyes: Galaxiidae): dispersal, vicariance, and the position of *Lepidogalaxias salamandroides*. *Syst. Biol.* 49, 777–795.
- Whitaker, A.H., 1968. *Leiopisma suteri* (Boulenger): an oviparous skink in New Zealand. *N. Zealand J. Sci.* 11, 425–432.
- Whiting, A.S., Bauer, A.M., Sites Jr., J.W., 2003. Phylogenetic relationships and limb loss in sub-Saharan African scincine lizards (Squamata: Scincidae). *Mol. Phylogen. Evol.* 29, 582–598.
- Wiens, J.J., 2003. Missing data, incomplete taxa, and phylogenetic accuracy. *Syst. Biol.* 52, 528–538.
- Wiens, J.J., Fetzner, J.W., Parkinson, C.L., Reeder, T.W., 2005. Hylid frog phylogeny and sampling strategies for speciose clades. *Syst. Biol.* 54, 719–748.
- Wiens, J.J., Brandley, M.C., Reeder, T.W., 2006. Why does a trait evolve multiple times within a clade? Repeated evolution of snakelike body form in squamate reptiles. *Evolution* 60, 123–142.
- Winterbourn, M.J., 1980. The freshwater insects of Australia and their affinities. *Paleogeogr., Paleoclimatol., Paleoecol.* 31, 235–249.
- Zug, G.R., 1985. A new skink (Reptilia: Sauria: *Leiopisma*) from Fiji. *Proc. Biol. Soc. Washington* 98, 221–231.