Article

Phylogeography and taxonomic revision of the New Zealand cryptic skink (*Oligosoma inconspicuum*; Reptilia: Scincidae) species complex

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Abstract

The New Zealand skink fauna is highly diverse and contains numerous cryptic, undescribed or hitherto undiscovered species. We completed a taxonomic revision of the cryptic skink (*Oligosoma inconspicuum*) species complex using molecular (550 bp of the ND2 mitochondrial gene) and morphological analyses. Four new species are described, with each diagnosable by a range of morphological characters and genetic differentiation from several closely related species: *O. inconspicuum* (sensu stricto), *O. notosaurus*, *O. maccanni*, *O. stenotis* and *O. grande*. *Oligosoma tekakahu* **sp. nov.** is restricted to Chalky Island in Fiordland, and is most closely related to *O. inconspicuum* and *O. notosaurus*. The other three new species are restricted to particular mountainous regions in central and western Otago (*O. burganae* **sp. nov.**, Lammermoor and Rock and Pillar Ranges; *O. toka* **sp. nov.**, Nevis Valley; *O. repens* **sp. nov.**, Eyre Mountains) and are most closely related to *O. stenotis* and *O. grande*. We also re-described *O. inconspicuum*. Two proposed new taxa, the 'Big Bay' skink and 'Mahogany' skink, were found to represent Westland/Fiordland populations of *O. inconspicuum* rather than distinct taxa. We discuss the evolutionary and phylogeographic implications of cryptic and 'anti-cryptic' species within the *O. inconspicuum* species complex, and suggest that morphologically aberrant populations are the result of local adaptation to novel selective regimes.

Key words: cryptic species, Fiordland, Miocene, mitochondrial DNA, molecular clock, morphology, ND2, Otago, Pliocene tectonism, Southland, Stewart Island

Introduction

The study of cryptic species is important within the field of evolutionary biology, because they have the potential to increase our understanding of fundamental concepts such as the nature of species and the mechanisms of speciation. For example, the existence of cryptic species led Ernst Mayr to question the definition of species based on morphological distinctiveness and to develop the biological species concept, which instead defines species based on their reproductive isolation (Mayr 1942). Likewise, Mayr's observations on morphologically aberrant populations (which could be thought of as the logical opposite of cryptic species) produced fundamental debate about the roles of drift and selection on speciation and led Mayr to develop the hypothesis of founder-effect speciation (Mayr 1942, 1954; reviewed in Coyne & Orr 2004). The rapid increase in molecular phylogenetic studies since the introduction of the polymerase chain reaction (PCR) has led to renewed interest in cryptic species (Bickford *et al*. 2007). However, despite the rapidly increasing number of cryptic species being discovered using molecular methods, our understanding of the processes that underlie cryptic speciation is poor (reviewed in Bickford *et al*. 2007). There has been a recent call not only for continued 'tallying' of cryptic species but also for scientific inquiry into the conditions which cause cryptic species to arise (Saez & Lozano 2005).

The New Zealand skink fauna provides a diverse set of potentially informative cases of cryptic species. Despite the New Zealand archipelago's temperate latitude and small land area of just 270,000 m^2, there are currently 33 described species in a single genus, *Oligosoma* (Chapple *et al*. 2009). For comparison, Australia, an acknowledged centre of skink diversity, is nearly 30 times as large, but has only 12 times as many described skink species (Wilson & Swan 2008). It is believed that numerous species of New Zealand skinks remain undescribed (10–15+ species; Chapple *et al*. 2009), due largely to the high incidence of cryptic species, as well as a steadily increasing number of morphologically unusual skinks of uncertain taxonomic affinity being discovered in isolated and mountainous regions of the archipelago (Jewell & Tocher 2005; Jewell 2007, 2008; but see Chapple & Hitchmough 2009).

The cryptic skink, *Oligosoma inconspicuum* (Patterson & Daugherty), is so named due to its morphological similarity to several closely-related species and cryptic behaviour (Patterson & Daugherty 1990). *Oligosoma inconspicuum* is a small skink with a maximum snout-vent length (SVL) of 70 mm (Patterson & Daugherty 1990). Its dorsal colour and pattern is highly variable, ranging from a reddish brown with a vertebral stripe to jet black with no median stripe, while the ventral surface is usually yellow (Patterson & Daugherty 1990). *Oligosoma inconspicuum* was originally discovered using morphological analyses of scale counts and body measurements, and subsequently allozymes, to identify it within a complex of small brown skinks (recognised at the time as *Leiolopisma nigriplantare maccanni*, the New Zealand common skink species complex). Taxonomic work on the *L. nigriplantare maccanni* complex during the 1990's (Daugherty *et al*. 1990; Patterson & Daugherty 1990, 1994; Patterson 1997) resulted in the recognition and description of 7 species: *O. inconspicuum*, *O. maccanni* (Patterson & Daugherty) (McCann's skink), *O. polychroma* (Patterson & Daugherty) (common skink), *O. microlepis* Patterson & Daugherty (small-scaled skink), *O. notosaurus* (Patterson & Daugherty) (southern skink), *O. stenotis* (Patterson & Daugherty) (small-eared skink), and *O. longipes* Patterson (long-toed skink) (In 1995, Patterson & Daugherty resurrected *Oligosoma* to accommodate all New Zealand *Leiolopisma* species, and Chapple *et al*. 2009 expanded the definition of *Oligosoma* to include all native skink species in New Zealand). *Oligosoma inconspicuum* could only be differentiated morphologically from other species within the former common skink species complex by using multivariate analysis of morphological characters, and it exhibits substantial morphological overlap with *O. notosaurus*, *O. polychroma* and *O. maccanni* (Daugherty *et al*. 1990; Patterson & Daugherty 1990). However, the concept of *O. inconspicuum* at that time included the species that we describe here as *O. burganae* **sp. nov.** and *O. toka* **sp. nov.**.

Oligosoma inconspicuum is found in the southern-most regions of New Zealand (Figure 1). Despite the cold southern climate, at least a dozen other skink species can also be found in these regions (Gill & Whitaker 2001). *Oligosoma inconspicuum* occurs in Otago and Southland (Patterson & Daugherty 1990), and on islands in the northern Foveaux Strait (Whitaker *et al*. 2002) (Figure 1). It is sympatric with *O. maccanni* and *O. polychroma*, and morphologically difficult to distinguish from either species (Whitaker *et al* 2002). *Oligosoma inconspicuum* is found from sea-level up to 1700 m, and prefers damp, herb or shrubland habitat over tussock and other grassland (Patterson & Daugherty 1990; Gill & Whitaker 2001; Whitaker *et al*. 2002). Although sometimes found in grassland (Whitaker *et al*. 2002), it avoids the rocky outcrops favoured by several other species in the region (e.g. the grand skink, *O. grande* (Gray), and the Otago skink, *O. otagense* (Hardy)) (Patterson 1984).
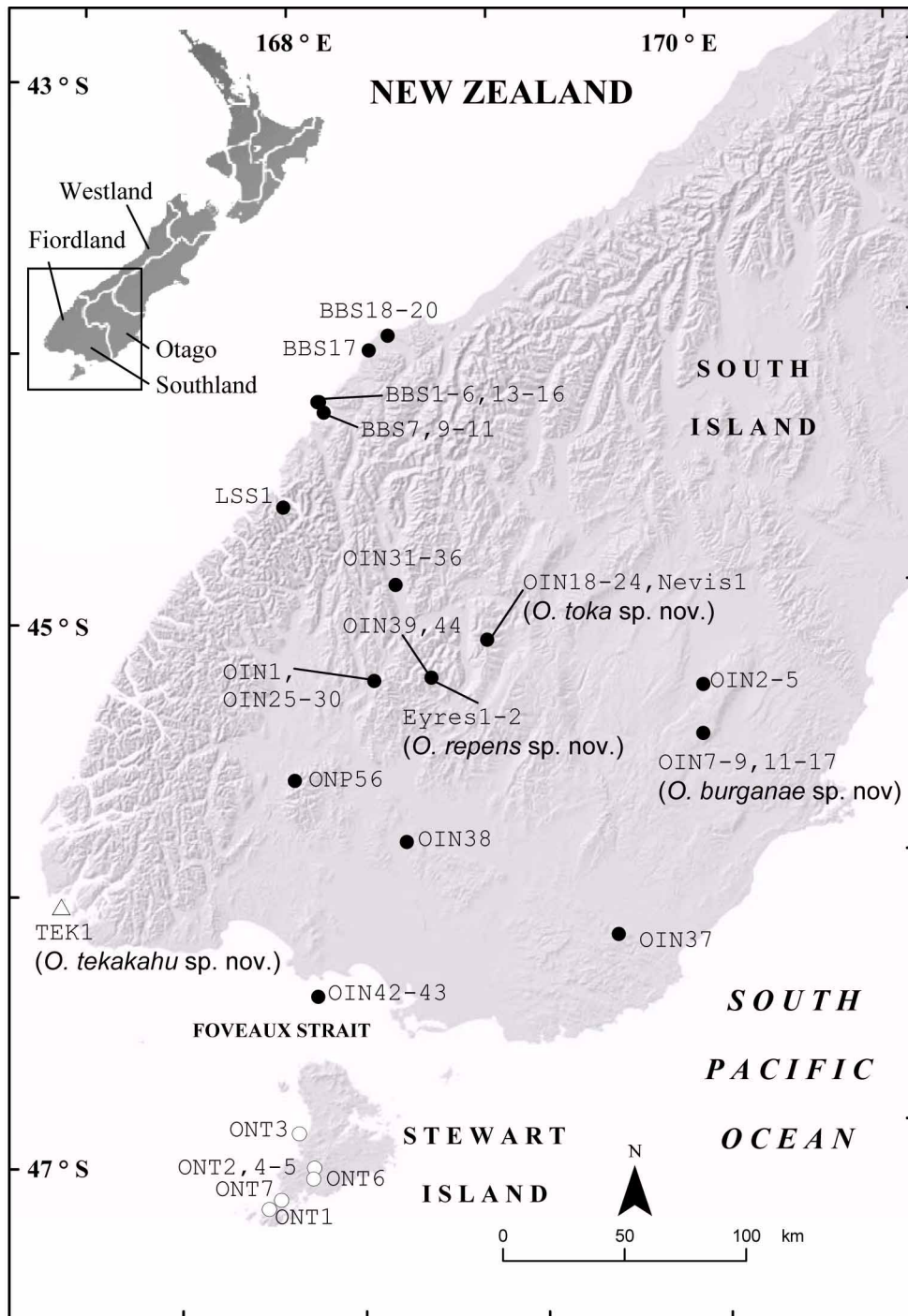
FIGURE 1. Map showing the sampling localities for the *Oligosoma inconspicuum* species complex samples listed in Table 1 (*O. inconspicuum*, solid black dots; *O. notosaurus*, white dots; 'Te Kakahu' skink [*O. tekakahu* **sp. nov.**], white triangles). The geographical distribution of the new taxa (*O. burganae* **sp. nov.**, *O. repens* **sp. nov.**, *O. toka* **sp. nov.**) identified in Figure 2 is shown. Inset: Sampling region, with New Zealand geographic region names used in the text.

The regions of New Zealand in which the species is found are, like the rest of the South Island, geologically unstable and topographically young. The rugged terrain of the island dates back no further than the Pliocene (Gage 1980; Landis *et al*. 2008; Wallis & Trewick 2009), and in Otago, some mountain ranges were formed as recently as the Pleistocene (Jackson *et al*. 1996). The Southern Alps, which bisect the South Island south-west to north-east and, rising to over 3000 m, form the South Island's principal biogeographic barrier, were created by Pliocene uplift which is still continuing (Gage 1980; Lee *et al*. 2001; Wallis & Trewick 2009). Prior to this, throughout the Miocene, the island was an eroded peneplain (Cooper & Millener 1993; Cooper & Cooper 1995). The coastlines of the

South Island have also changed radically throughout this time, due to the tectonism as well as rising and falling sea levels (Newnham *et al*. 1999). Thus, for example, many modern-day offshore islands within the New Zealand archipelago have been repeatedly joined to and separated from the mainland. Changing topography and coastlines are both likely to have implications for the genetic patterns within *O. inconspicuum*.

Over the past decade there have been suggestions that *O. inconspicuum* could contain one or more cryptic species, since different forms of the species have been observed occurring sympatrically or allopatrically on certain mountain ranges in Otago (Jewell 2006, 2008). *Oligosoma inconspicuum* is also thought to harbour 'anti-cryptic' species, a term recently coined to describe the situation in which rapid morphological divergence occurs without substantial genetic change or speciation (Bickford *et al*. 2007). In this respect, several morphologically unusual individuals or populations have been discovered in recent years, which are thought to have close affinities with *O. inconspciuum*: the 'Te Kahahu' skink, the 'Big Bay' skink, the 'Okuru' skink, and the 'mahogany' skink (Jewell 2008). The 'Te Kakahu' skink occurs only on Chalky (Te Kakahu) Island off southern Fiordland (Hitchmough *et al*. 2007; Jewell 2008; Figure 1). The 'Big Bay' skink occurs in large populations in Big Bay, Barn Bay and on the Cascade Plateau in southern Westland (Miller 1999; Tocher 1999; Jewell 2008; Figure 1). The 'mahogany' skink (Jewell 2008), is known from several specimens and a single tissue sample (Table 1), and was found in the Sinbad Valley near Milford Sound (see Bell & Patterson 2008 for a detailed site description) (Figure 1). Each taxon has been proposed to represent a new species (Jewell 2008), but no genetic analysis has been conducted, except for the 'Big Bay' skink, where mitochondrial and nuclear DNA sequence data indicates that it is conspecific with *O. inconspicuum* (Chapple *et al*. 2009). *Oligosoma inconspicuum* is most closely related to *O. notosaurus* and *O. maccanni* (Chapple *et al*. 2009), and collectively *O. inconspicuum*, *O. notosaurus* and the proposed new taxa are referred to as the *O. inconspicuum* species complex.

What processes could underlie the presence of both cryptic and anti-cryptic lineages within the *O. inconspicuum* species complex? Here we use a combination of mitochondrial DNA sequence data (ND2) and morphological analyses to resolve the numerous taxonomic issues within the *O. inconspicuum* species complex, and describe new species where appropriate. We then examine the phylogeographic pattern within the complex, to elucidate the different biogeographic processes which underlie these contrasting (cryptic and anti-cryptic) patterns within *O. inconspicuum*.

Material and methods

Molecular analyses. Samples were obtained from the National Frozen Tissue Collection (NFTC; Victoria University of Wellington, New Zealand) and from ethanol-preserved museum species from Te Papa (National Museum of New Zealand, Wellington), for sites covering the entire known range of *O. inconspicuum* and *O. notosaurus* (Figure 1, Table 1). Our samples incorporated most of the specimens examined in the descriptions of *O. inconspicuum* and *O. notosaurus* (Patterson & Daugherty 1990), including samples collected at the same locality (Tree Island in Lake Wakatipu) as the holotype for *O. inconspicuum* (Table 1). We obtained all of the tissue samples that are available for the 'Big Bay' skink, 'Te Kakahu' skink, and the 'mahogany' skink (Table 1). However, we were unable to obtain a tissue sample for the 'Okuru' skink. The *O. inconspicuum* species complex is most closely related to *O. maccanni* (Chapple *et al*. 2009), therefore we included two *O. maccanni* samples (EF081195, EF447117). We also included samples from *O. stenotis* (EU567718, EU567719) and *O. grande* (EU567720, EU567721), which represent a well-supported lineage within the New Zealand skink radiation (Chapple *et al*. 2009), as they are the most closely-related to the divergent new taxa identified in this study. Two endemic New Caledonian skink species, *Nannoscincus mariei* Bavay (earless dwarf skink; EU423132) and *Marmorosphax tricolor* Bavay (marble-throated skink; EU423133), were chosen as outgroups based on the broader phylogenetic study of New Zealand skinks (Chapple *et al*. 2009).

We extracted total genomic DNA using a modified phenol and chloroform protocol (Sambrook *et al*. 1989) followed by ethanol precipitation. We used PCR with the primers L4437 (5'-AAGCTTTCGGGCCCATACC-3'; Macey *et al*. 1997) and ND2r102 (5'- CAGCCTAGGTGGGCGATTG-3'; Sadlier *et al*. 2004) to amplify a 600-bp fragment of the ND2 mitochondrial gene. We targeted this region because our previous studies have shown it to be phylogenetically informative at both the intra- and inter-specific level among New Zealand skinks (Greaves *et al*. 2007, 2008; Chapple & Patterson 2007; Hare *et al*. 2008; Liggins *et al*. 2008a,b; O'Neill *et al*. 2008; Chapple *et al*. 2008a,b,c; Miller *et al*. 2009). PCR and sequencing were conducted as outlined in Greaves *et al*. (2007).

TABLE 1. Locality information and GenBank accession numbers for samples used in the molecular analyses. Samples with CD or FT codes were obtained from the National Frozen Tissue Collection (NFTC) housed at Victoria University of Wellington, New Zealand. Samples with RE codes were obtained from ethanol preserved specimens housed at Te Papa. National Museum of New Zealand, Wellington (S codes refer to specimens from the former Ecology Division collection, now housed at Te Papa).

Species	Locality	No. Samples	Tissue Codes	Museum Codes	GenBank Accession No.
Oligosoma inconspicuum	Gorge Burn, Eyre Mountains, Southland	7	OIN1; OIN25-30	CD1101; CD1100-CD1105, CD1124	EU567708; EU728632-EU728637
O. inconspicuum	Eyre Mountains, Southland	1	OIN44	field collected	HQ113370
O. inconspicuum	Macraes Flat, Otago	4	OIN2-5	CD421, 2 field collected, CD423	EU567709, EU728612-EU728614
O. inconspicuum	Tree Island, Lake Wakatipu, Otago	6	OIN31-36	CD1905-CD1908, FT2063-FT2064	EU728638-EU728643
O. inconspicuum	Catlins, Department of Conservation Red Tussock Reserve, Southland	1	OIN37	FT3633	EU728644
O. inconspicuum	Dipton, Southland	1	OIN38	RE001889	EU728645
O. inconspicuum	Eyre Mountains, Southland	1	OIN39	RE002122	EU728646
O. inconspicuum	Centre Island, Foveaux Strait	2	OIN42-43	RE004878 (S1241), RE004879 (S1242)	EU728647-EU728648
O. inconspicuum	Tower Peak, Takitimu Range, Southland	1	ONP56	FT2924	EU728649
O. inconspicuum 'Big Bay'	Awarua Point, Big Bay, Westland	7	BBS1; BBS3-4; BBS13-16	FT3783; FT3784-FT3785; FT3031-FT3034	EU567705; EU728596-EU728597; EU728607 EU728604-
O. inconspicuum 'Big Bay'	Mouth of Mackenzie River, Big Bay, Westland	3	BBS2; BBS5-6	FT3786; FT3787-FT3788	EU567706; EU728598-EU728599
O. inconspicuum 'Big Bay'	Mid-point Mackenzie River, Big Bay, Westland	2	BBS7; BBS9	FT3789, FT3791	EU728600-EU728601
O. inconspicuum 'Big Bay'	Big Bay, Westland	2	BBS10-11	FT3792-FT3793	EU728602-EU728603
O. inconspicuum 'Big Bay'	Barn Bay, Westland	1	BBS17	FT3813	EU567707
O. inconspicuum 'Big Bay'	Cascade Plateau, Westland	3	BBS18-20	FT7652-FT7654	EU728608- EU728610
O. inconspicuum 'Mahogany'	Sinbad Gully, Llawrenny Peaks, Fiordland	1	LSS1	FT7739	EU728611
O. inconspicuum (**O. burganae sp. nov.**)	Rock & Pillar Range, Burgan Stream Hut, Otago	10	OIN7-9; OIN11-17	CD766-CD768; CD770-CD776	EU728615-EU728617; EU728618-EU728624
O. inconspicuum (**O. toka sp. nov.**)	Nevis Range, Central Otago	8	OIN18-24, Nevis1	CD935-941, field collected	EU728625-EU728631, HQ113373
O. inconspicuum (**O. repens sp. nov.**)	Eyre Mountains, Southland	2	Eyres1, Eyres2	field collected	HQ113371-HQ113372
Oligosoma 'Te Kakahu' (**O. tekakahu sp. nov.**)	'Blowout', Chalky Island, Fiordland	1	TEK1	FT7650	EU728655
Oligosoma notosaurus	Magog, Stewart Island	1	ONT1	FT575	EU567710
O. notosaurus	Arena Ridge, Stewart Island	3	ONT2, ONT4-5	CD1089-CD1091	EU567711, EU728651-EU728652
O. notosaurus	Mason Bay, Stewart Island	1	ONT3	CD500	EU728650
O. notosaurus	Kakapo Study Site, Stewart Island	1	ONT6	CD1125	EU728653
O. notosaurus	Jacksons River, Stewart Island	1	ONT7	RE001888	EU728654

Sequence data were edited manually using CONTIG EXPRESS in VECTOR NTI ADVANCE 9.1.0 (Invitrogen, Carlsbad CA, USA) or GENEIOUS Pro 4.8 (Drummond *et al.* 2010), and trimmed to 550bp. The dataset was then aligned using CLUSTALX (Thompson *et al.* 1997) executed in MEGA 4 (Tamura *et al.* 2007). We translated all sequences to confirm that none contained premature stop codons. Sequence data were submitted to GenBank under the accession numbers provided in Table 1. We constructed a TrN neighbour-joining distance phylogram with 1000 bootstraps in MEGA. We considered branches supported by bootstrap values of 70% or greater (Hillis & Bull 1993) to be supported by our data.

To estimate the time since the divergence of lineages within the *O. inconspicuum* species complex, we calibrated the evolutionary rate of ND2 by re-analysing data from Macey *et al.* (1998) for the agamid genus *Laudakia*. Macey *et al.* (1998) calibrated this rate by geological dating of tectonic events on the Iranian Plateau. Their rate (~ 1.2–1.4% per myr) has been demonstrated to be consistent across several vertebrate groups (fish, amphibians, reptiles; reviewed in Weisrock *et al.* 2001). Specifically, we re-calculated the evolutionary rate for *Laudakia* using only the 550bp fragment of ND2 used in the present study (e.g. Smith *et al.* 2007). We calculated average between-group nucleotide differences (uncorrected) across each of the calibrated nodes from Macey *et al.* (1998) (1.5, 2.5 and 3.5 mya), plotted them against time and used the slope of the linear regression to calculate a rate of evolution for our 550bp fragment of ND2. This resulted in a divergence rate of 1.4% per myr (0.7% evolution per lineage, per myr) and is slightly faster than the rate of 1.3% per myr found by Macey *et al.* (1998) for their longer fragment of ND2.

Morphological analyses. We conducted morphological analyses on all taxa within the *O. inconspicuum* species group (*O. inconspicuum*, *O. notosaurus*, 'Te Kahahu' skink, 'Big Bay' skink, and the 'mahogany' skink), except for the 'Okuru' skink. Our analyses built upon the morphological measurements for *O. inconspicuum* and *O. notosaurus* published previously in Patterson & Daugherty (1990). Additional morphological comparisons were made with *O. maccanni* (41 specimens) and *O. polychroma* (72 specimens) (data for both species was obtained from Patterson & Daugherty 1990). The majority of specimens examined were obtained from Te Papa Tongarewa, National Museum of New Zealand (RE codes). Several additional specimens (including some holotypes) were collected using the methods outlined in Bell & Patterson (2008), and were lodged at Te Papa.

Descriptions of morphology follow the techniques described in Patterson & Daugherty (1990) and Chapple *et al.* (2008a). Midbody scale rows were counted at the midpoint between the fore- and hind legs. Ventral scales were counted in a line from the mental scale to the vent (including the mental and one preanal scale). The subdigital lamellae were counted on the fourth hind toe of the right foot. The number of selected head scales were counted and their arrangement described as outlined in Patterson & Daugherty (1990). Ten measurements (mm) were made on all specimens: i) axilla to groin (AG), ii) snout to axilla (SF), iii) snout to ear (SE), iv) ear to axilla (EF), head length (HL) from the posterior part of the interparietal to the tip of the snout, v) head width (HW) between the lateral edges of the left and right parietals, vi) intact tail length (TL), vii) fourth hind toe length from base of toe to tip excluding nail (FTL), viii) snout-vent length (SVL), ix) hindlimb length (HLL), measured from groin to tip of fourth toe including nail, and x) forelimb length (FLL), measured from forelimb insertion to tip of fourth finger, including nail (Patterson & Daugherty 1990, 1994; Chapple *et al.* 2008a). Numbers are provided where specimens had missing toes. Colour descriptions are based on the NBS/IBCC colour system (Mundle 1995; see http://www.anthus.com/Colors/NBS.html).

Results

Molecular analyses

The final dataset contained sequences from 71 individuals in the *O. inconspicuum* species complex, along with sequences from three closely-related species (*O. maccanni*, *O. stenotis*, *O. grande*) and two outgroup species. The final alignment comprised 550 characters from the ND2 mitochondrial gene, of which 228 (41%) were variable and 194 (35%) were parsimony-informative. For the ingroup only, the alignment contained 166 (30%) variable characters, of which 150 (27%) were parsimony-informative. Base frequencies were unequal (A = 0.316, T = 0.241, C = 0.306, G = 0.137). A χ^2 test confirmed the homogeneity of base frequencies among sequences (df = 234, P = 1.0). All sequences were full-length, except that for one sample (OIN38) only 522bp of sequence data was obtained due to the poor quality of the DNA template.

Our molecular analyses indicate that the *O. inconspicuum* species complex comprises six distinct species (Figure 1). The new species are diagnosable under both the phylogenetic and morphological species concepts. The first well-supported taxon (90 bootstrap [BS]) encompasses the type locality for *O. inconspicuum* (OIN31-36: Tree Island, Lake Wakatipu) and therefore represents *O. inconspicuum* sensu stricto (Figure 2). It occurs throughout the southern South Island with phylogeographic structure evident among Westland/Fiordland, western Otago/Southland (including Foveaux Strait), and eastern Otago/Southland (Figures 1 and 2). Two proposed new species, tentatively referred to as the 'Big Bay' skink and 'mahogany' skink, were not found to be distinct species (indeed, the 'mahogany' skink was nested within a clade containing the 'Big Bay' skink samples). Instead, they represent populations of *O. inconspicuum* (sensu stricto) in Westland and Fiordland, a range extension for the species (Figures 1 and 2).

The second well-supported taxon (91 BS) represents *O. notosaurus* and is restricted to Stewart Island (Figures 1 and 2). The third taxon is the 'Te Kakahu' skink, described here as *O. tekakahu* **sp. nov.** (Figures 1 and 2). At present, this species is only known from Chalky (Te Kakahu) Island in Fiordland (Figure 1). The remaining three well-supported taxa are genetically divergent (~15%) from *O. inconspicuum* (sensu stricto) (Table 2) and each have restricted distributions within particular mountain ranges in central Otago (Figure 1). The fourth taxon (99 BS) is restricted to subalpine regions of the Lammermoor and Rock and Pillar Ranges of central Otago (Figures 1 and 2), and is described here as *O. burganae* **sp. nov.** (the Burgan skink). The fifth taxon (99 BS) occurs in the Eyre Mountains of western Otago and exhibits substantial genetic divergence (15.7%) from the *O. inconspicuum* (sensu stricto) (e.g. OIN1, 25-30, 44) that occur sympatrically in this region (Figures 1 and 2). It is described here as *O. repens* **sp. nov.**, the Eyres skink. The final taxon (99 BS) is restricted to the Nevis Valley of central Otago (Figures 1 and 2), and is described here as *O. toka* **sp. nov.** (the Nevis skink).

There is substantial variation in the level of genetic divergence among the six species (Table 2). Divergences among *O. inconspicuum* (sensu stricto), *O. notosaurus* and *O. tekakahu* **sp. nov.** are relatively low (4.6–8.1%) compared to that evident between these three species and the three new range-restricted species (*O. burganae* **sp. nov.**, *O. repens* **sp. nov.**, *O. toka* **sp. nov.**) in central and western Otago (14.8–16.3%; Table 2). Intermediate levels of genetic divergence (9.1–10.7%) are present among the three new species in Otago (Table 2). The three new species from Otago are most closely related to two species (*O. grande*: Otago, *O. stenotis*: Stewart Island endemic) that also occur in the southernmost regions of New Zealand (Figures 1 and 2; Table 2).

TABLE 2. Mean uncorrected ND2 genetic distances among the species within the *Oligosoma inconspicuum* species complex. Comparison is also made to the species (i.e. *O. maccanni*, *O. stenotis*, *O. grande*) that are most closely related to the *O. inconspicuum* species complex.

|	*O. inconspicuum*	*O. notosaurus*	*O. tekakahu*	*O. burganae*	*O. repens*	*O. toka*	*O. maccanni*	*O. stenotis*	*O. grande*
O. inconspicuum	-								
O. notosaurus	0.046	-							
O. tekakahu	0.081	0.058	-						
O. burganae	0.158	0.154	0.154	-					
O. repens	0.153	0.148	0.163	0.107	-				
O. toka	0.152	0.155	0.157	0.104	0.091	-			
O. maccanni	0.152	0.147	0.148	0.129	0.124	0.116			
O. stenotis	0.150	0.147	0.151	0.110	0.106	0.117	0.108	-	
O. grande	0.151	0.149	0.167	0.123	0.102	0.103	0.127	0.115	-
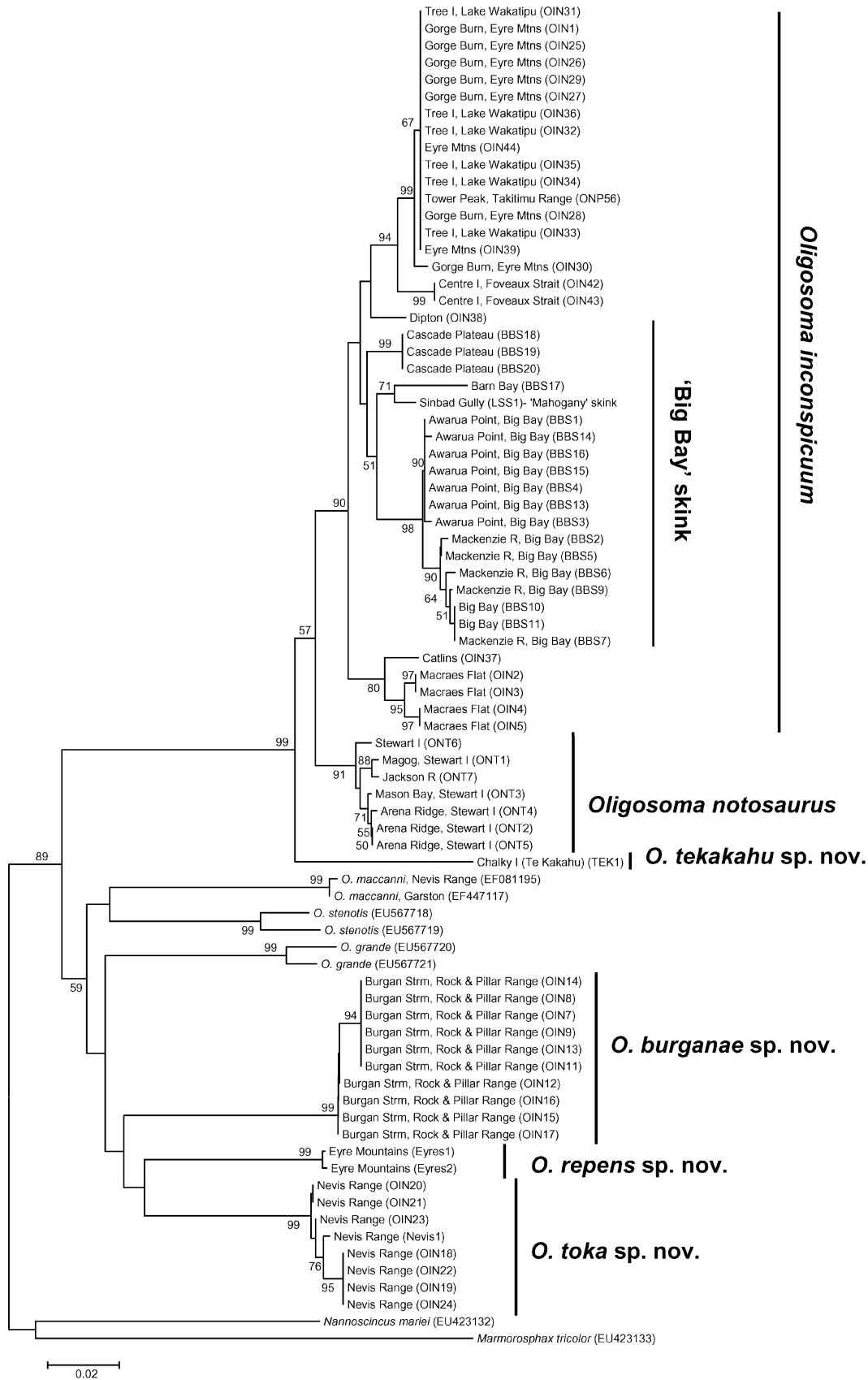
FIGURE 2. Neighbour-joining phylogram for the *Oligosoma inconspicuum* species complex based on 550 bp of the ND2 mitochondrial gene. Bootstrap values (1000 replicates) are shown. Where no support value is shown, the node is unsupported (i.e. it is less than 70% bootstrap). Six taxa within the *O. inconspciuum* species complex are identified.

Species descriptions

Genus *Oligosoma* Girard, 1857

Oligosoma inconspicuum (Patterson & Daugherty, 1990)
Figure 3

Oligosoma inconspicuum Chapple *et al*. 2009: 485
Oligosoma inconspicuum Jewell 2008: 88
Oligosoma sp. 'mahogany skink' Bell & Patterson 2008: 65
Oligosoma sp. 'mahogany skink' Bell *et al.* 2008: 12
Oligosoma sp. 7 (Big Bay skink) Jewell 2008: 90
Oligosoma sp. 8 (mahogany skink) Jewell 2008: 91
Oligosoma inconspicuum Gill & Whitaker 2001: 72
Leiolopisma inconspicuum Patterson & Daugherty 1990: 66

Holotype. Tree Island, Lake Wakatipu (44º 55'S, 168º 25'E), RE002079, adult male (coll. C. Daugherty & R. Marquand, November 1988).

Paratypes (5 specimens). Tree Island, Lake Wakatipu (44º 55'S, 168º 25'E), 4 specimens (RE006135 [CD1905], female; RE006402 [CD1906], male; RE006136 [CD1907], male; RE006137 [CD1908], female) (coll. I. Southey, March 1986); Tree Island, Lake Wakatipu (44º 55'S, 168º 25'E), RE006169 [FT2063], female (coll. unknown, December 1988)

Other specimens examined (29 specimens). Gorge Burn, Eyre Mountains (44º 18'S, 168º 15'E), 5 specimens (RE006127 [CD1101], male; RE006128 [CD1102], female; RE006129 [CD1103], female; RE006013 [CD1104], male; RE006131 [CD1124], sex unknown) (coll. G. Patterson, March 1985); Eyre Mountains (grid reference unknown), RE002122, female (coll. I. Southey, April 1986); Macraes Flat (45º 23'S, 170º 26'E), 2 specimens (RE006141 [CD421], male; RE006142 [CD423], subadult) (coll. C. Daugherty, December 1983); McKenzie Creek, Big Bay, South Westland (44º 22'S, 168º 02'E), 4 specimens (RE005382 [FT3788], female; RE005383 [FT3789], female; RE005386 [FT3792], female; RE005387 [FT3793], female) (coll. R. van Mierlo & P. van Klink, January 1998); Barn Bay, Westland (44º 04'S, 168º 18'E), RE005507 [FT3813], male (coll. R. van Mierlo & P. van Klink, January 1998); Awarua Point, Big Bay, Westland (44º 16'S, 168º 03'E), 4 specimens (RE005434 [FT3031], female; RE005435 [FT3032], male; RE005436 [FT3033], male; RE005437 [FT3034], male) (coll. I. Southey, September 1992); Awarua Point, Big Bay, Westland (44º 16'S, 168º 03'E), 6 specimens (RE005377 [FT3783], subadult; RE005378 [FT3784], male; RE005371 [FT3785], subadult; RE005380 [FT3786], male; RE005381 [FT3787], female; RE005385 [FT3791], juvenile) (coll. M. Tocher, January 1998); Te Anau township (45º 26'S, 167º 43'E), RE002393, female (coll. G Patterson, February 1985); Tower Peak, Cameron Mountains (46º 01'S, 167º 02'E), RE005497 [FT2924], subadult (coll. G. Gibbs, January 1991); Dipton, Southland (45º 87'S, 168º 23'E), RE001889, female (coll. M. Smith, November 1977); Catlins, Department of Conservation Red Tussock Reserve (45º 36'S, 167º 14'E), RE006529 [FT3633], male (coll. M. Tocher, January 1997); Sinbad Gully, Llawrenny Peaks, Fiordland (44º 38'S, 167º 48'E), RE006880, male (coll. T. Bell February 2008); Mt Nicholas Road, Eyre Mountains (45º 15'S, 168º 18'E), 4 specimens (RE007284, female; RE007288, female; RE007293, female; RE007298, female) (coll. J. Reardon, January 2010).

Diagnosis. *Oligosoma inconspicuum* can be distinguished from other related *Oligosoma* species through a combination of characters (Figure 4; Wessa 2011). Compared to *O. maccanni, O. inconspicuum* has a glossy appearance, with brown predominating whereas *O. maccanni* has a greyer ground colour. *Oligosoma maccanni* has a pale grey ventral colour rather than the yellow or bronze ventral colour seen in *O. inconspicuum.* The ear opening in *O. maccanni* often has large projecting scales on the interior margin, whereas these are often minimal or lacking altogether in *O. inconspicuum.* Longitudinal striping is more pronounced in sympatric populations of *O. polychroma,* which almost always have a pale stripe on the outside of the forelimbs. The ear opening in *O. polychroma* often has prominent projecting scales on the interior margin. There are statistical differences between *O. inconspicuum* and *O. burganae* **sp. nov.** (AG/SF, HL/HW, SE/EF, SVL/HL, SVL/FLL), *O. notosaurus* (SVL/HL, ventral scales), and *O. toka* sp. nov (SVL/FLL, SVL/HLL ventral scales) (see Figure 4). Unlike *O. repens* **sp. nov.** and *O. toka* **sp. nov.** which have three supraoculars all *O. inconspicuum* have four supraoculars. Most *O. burganae* **sp. nov.** have only three supraoculars. *Oligosoma repens* **sp. nov.** has a more elongate appearance than *O. inconspicuum* (e.g. TL/SVL of 1.28 and 1.16, respectively). The number of subdigital lamellae (17–23) is greater in *O. inconspicuum* compared to *O. tekakahu* **sp. nov.** (16).

Description of Holotype: Body elongate, oval in cross-section; limbs moderately well-developed, pentadactyl. Lower eyelid with a transparent palpebral disc, bordered on sides and below by small, oblong granules. Nostril centred just below middle of nasal, pointing up and back, not touching bottom edge of nasal. Supranasals absent. Rostral broader than deep. Frontonasal broader than long, separated from frontal by scale between prefrontals. Frontal longer than broad, shorter than frontoparietal and interparietal together, in contact with 2 anteriormost supraoculars. Supraoculars 4, the second is the largest. Frontoparietals distinct, larger than interparietal. A pair of parietals meeting behind interparietal and bordered posteriorly by a pair each of nuchals and temporals, also in contact with interparietal, frontoparietal, third/fourth supraocular and 2 postoculars. Loreals 2, anterior one the larger; anterior loreal in contact with first supralabial, posterior loreal, prefrontal, frontonasal and nasal; posterior loreal in contact with second supralabial, first subocular, upper and lower preocular, prefrontal and anterior loreal. Supralabials 7, the sixth is the largest. Infralabials 7, several of them equal in size; fifth supralabial below centre of eye. Mental broader but shallower than rostral. Suboculars 3 and 4 separated by fifth supralabial. Postmental larger than mental. Chinshields 3 pairs. One primary temporal. Dorsal scales largest, weakly striate. Ventral scales smooth. Subdigital lamellae smooth. Ear opening round, moderately large, with one projecting granule on anterior margin. Forelimbs shorter than hindlimbs. Adpressed limbs not meeting in adult. Digits moderately long, cylindrical. Third front digit shorter than the fourth.


FIGURE 3. Holotype of *Oligosoma inconspicuum* (RE002079), Tree Island, Lake Wakatipu.

Measurements (in mm; holotype with the variation shown in the paratypes/specimens examined in parentheses). SVL 61.5 (mean 54.7, range 24.0–74.4), HL 8.5 (mean 7.8, range 5.2–9.7), HW 6.2 (mean 5.4, range 3.2–6.7), AG 32.1 (mean 28.9, range 10.5–44.9), SF 22.2 (mean 20.1, range 11.0–25.4), SE 10.7 (mean 9.4, 5.7–11.8), EF 11.2 (mean 10.6, range 5.1–14.5), HLL 21.5 (mean 19.1, 11.5–23.7), FLL 15.5 (mean 13.5, 8–16.0) and TL unknown (not intact) (mean 64.4, range 41.0–82.0; N = 14).

Variation (holotype with the variation shown in the paratypes/specimens examined in parentheses). Upper ciliaries 7 (mean 7, range 6-9); lower ciliaries 10 (mean 10, range 9–13); nuchals 2 pair (mean 3 pairs, range 1–4 pairs); midbody scale rows 28 (mean 29, range 27–32); ventral scale rows 74 (mean 74, range 67–86); subdigital lamellae 22 (mean 20, range 17–23); supraciliaries 5[right]/6[left] (mean 5, range 5–6); suboculars 6 (mean 7, range 4–8). Frontonasal not usually separated from frontal by prefrontals meeting in midline. Anterior loreal always in contact with first and second supralabial, posterior loreal usually in contact with second supralabial only. Supralabials 7 (usual) or 8, the sixth or seventh the largest. Infralabials 5, 6 (usual), or 7. Third front digit as long as or shorter than the fourth. Maximum SVL 74.4 mm. Fourteen specimens had intact tails (TL/SVL = 1.16). Ratios for morphological measurements ($\pm$ SD): AG/SF: 1.42 ± 0.18; SE/EF: 0.91 ± 0.10; HL/HW: 1.45 ± 0.10.
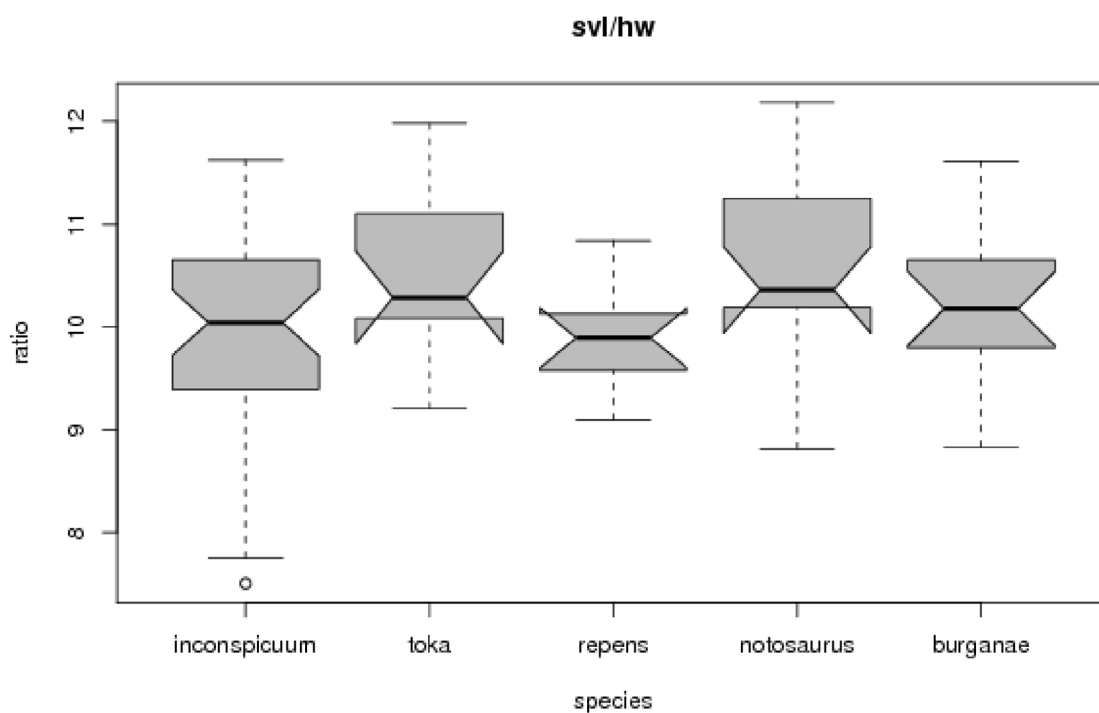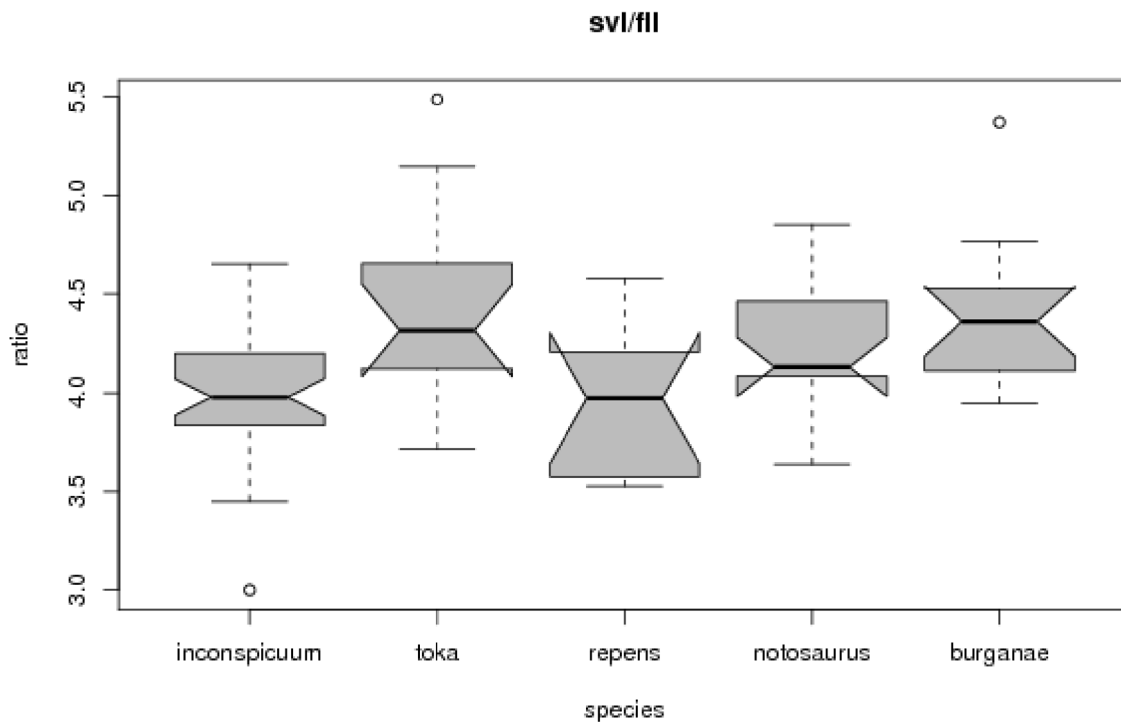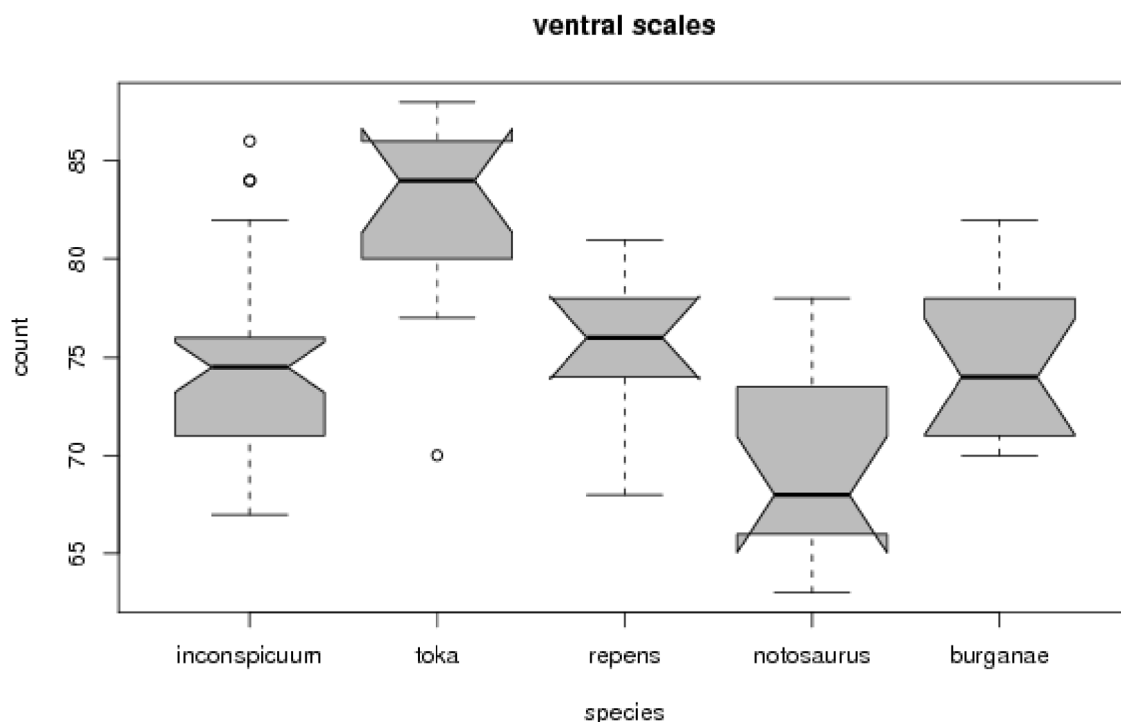
a)
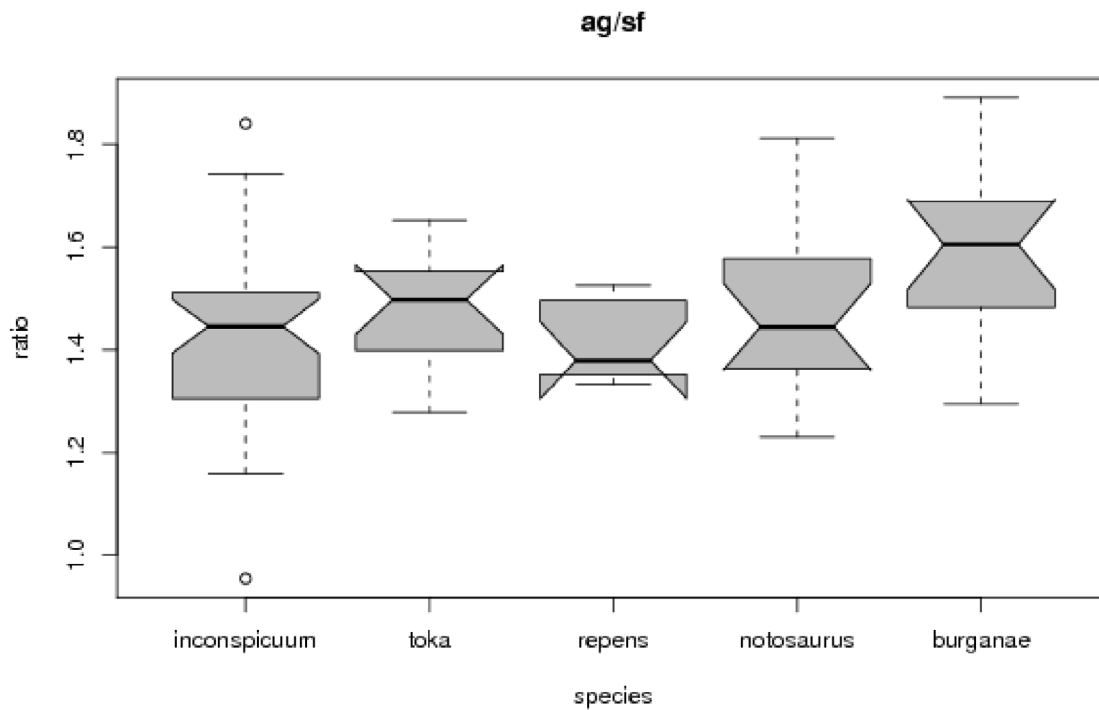
b)

FIGURE 4 a–b. Notched boxplots comparing the morphological characteristics of the species in the *Oligosoma inconspicuum* species group (*O. inconspicuum* sensu stricto, *O. toka* **sp. nov.**, *O. repens* **sp. nov.**, *O. notosaurus*, *O. burganae* **sp. nov.**): **a)** axilla-groin(AG)/snout-forelimb (SF), **b)** snout-vent length (SVL)/head width (HW). *Oligosoma tekakahu* **sp. nov.** was not included in the analysis as only one specimen was available. If there is no overlap between two medians, then the medians are significantly different at a 95% confidence level.
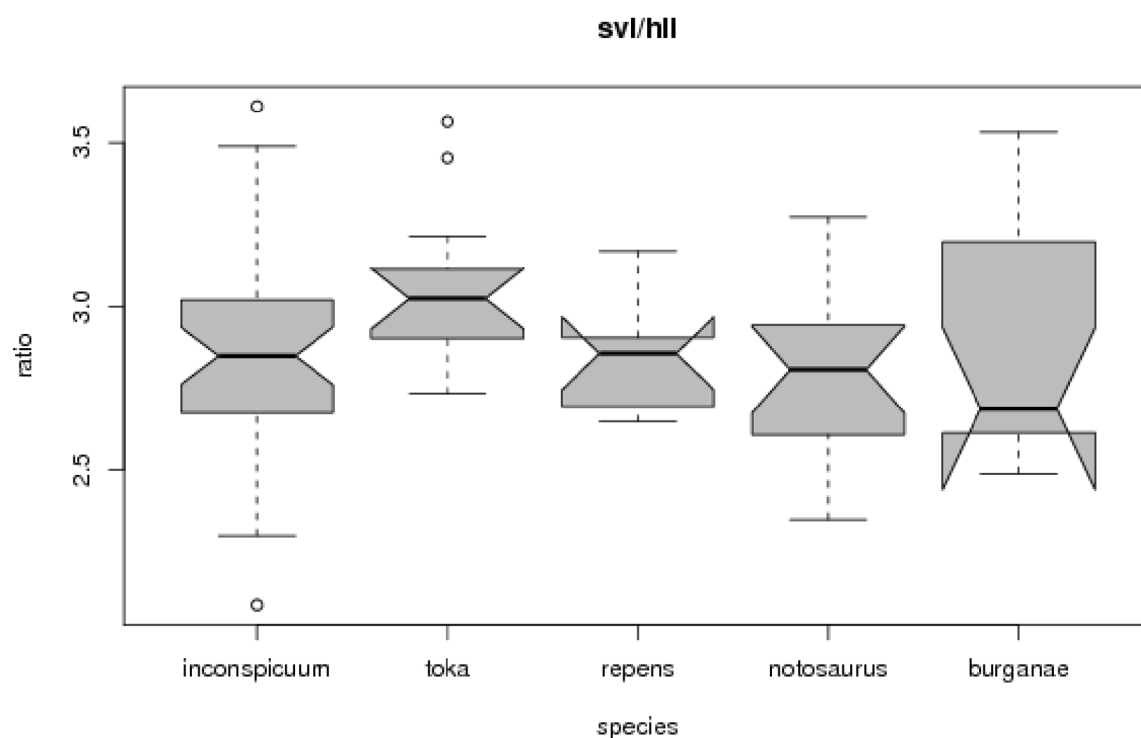
c)

d)

FIGURE 4 c–d. Notched boxplots comparing the morphological characteristics of the species in the *Oligosoma inconspicuum* species group (*O. inconspicuum* sensu stricto, *O. toka* **sp. nov.**, *O. repens* **sp. nov.**, *O. notosaurus*, *O. burganae* **sp. nov.**): **c)** snout-vent length (SVL)/forelimb length (FLL), **d)** ventral scales, **e)** snout-vent length (SVL)/hind limb length (HLL). *Oligosoma tekakahu* **sp. nov.** was not included in the analysis as only one specimen was available. If there is no overlap between two medians, then the medians are significantly different at a 95% confidence level.

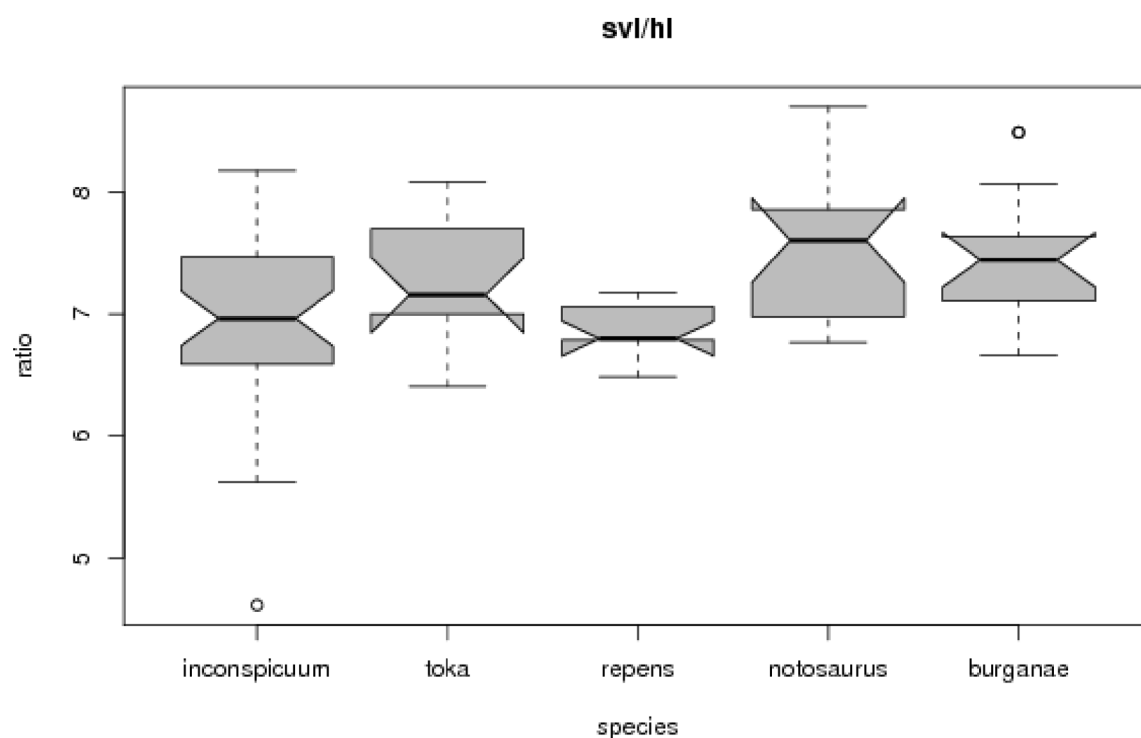CHAPPLE *ET AL.*
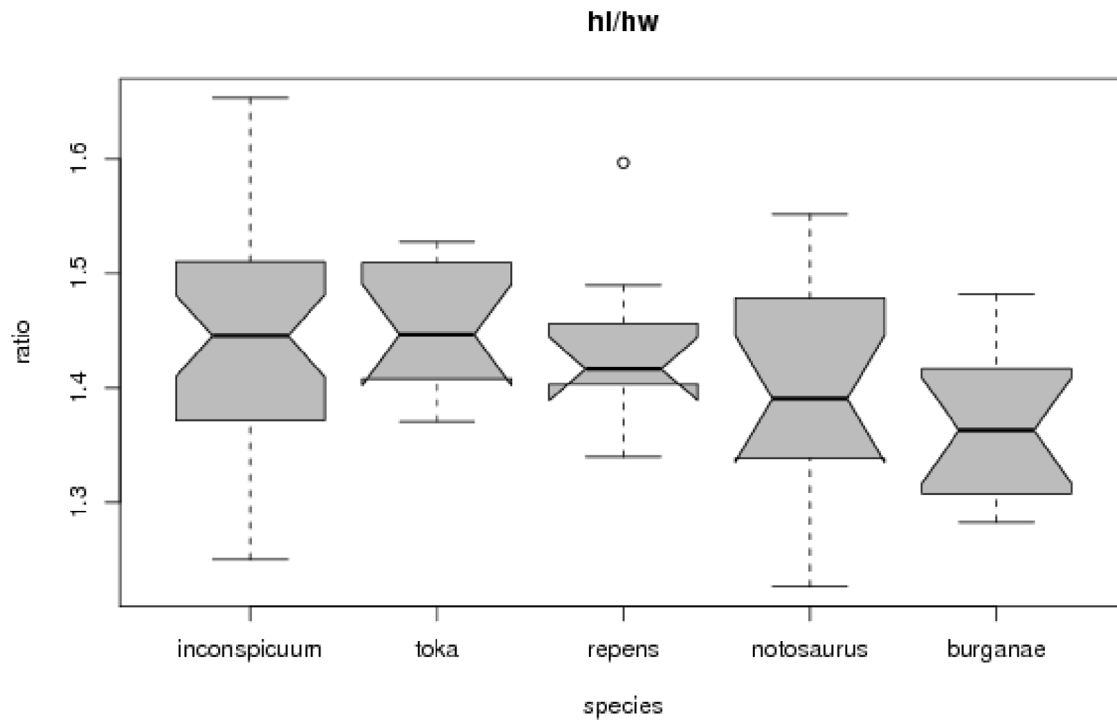
e)

f)

FIGURE 4 e–f. Notched boxplots comparing the morphological characteristics of the species in the *Oligosoma inconspicuum* species group (*O. inconspicuum* sensu stricto, *O. toka* **sp. nov.**, *O. repens* **sp. nov.**, *O. notosaurus*, *O. burganae* **sp. nov.**): **e)** snout-vent length (SVL)/hind limb length (HLL), **f)** snout-vent length (SVL)/head length (HL). *Oligosoma tekakahu* **sp. nov.** was not included in the analysis as only one specimen was available. If there is no overlap between two medians, then the medians are significantly different at a 95% confidence level.

g)
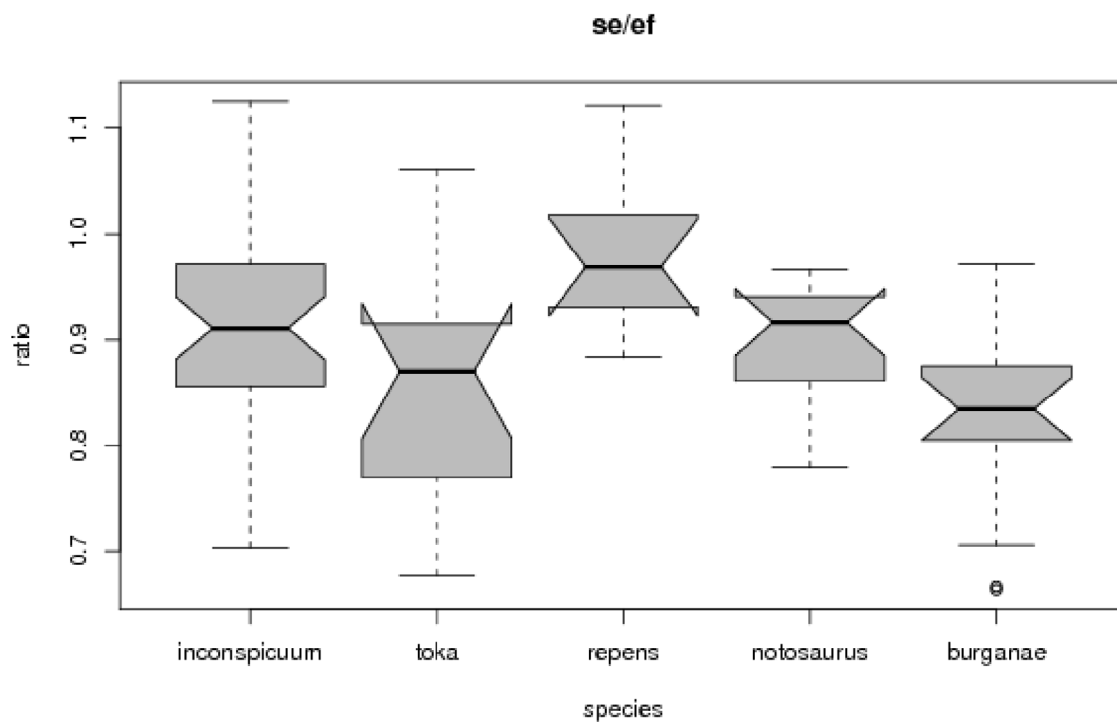

hl/hw

h)

se/ef

FIGURE 4 g–h. Notched boxplots comparing the morphological characteristics of the species in the *Oligosoma inconspicuum* species group (*O. inconspicuum* sensu stricto, *O. toka* **sp. nov.**, *O. repens* **sp. nov.**, *O. notosaurus*, *O. burganae* **sp. nov.**): **g)** head length (HL)/head width (HW), and h) snout-ear (SE)/ear-forelimb (EF). *Oligosoma tekakahu* **sp. nov.** was not included in the analysis as only one specimen was available. If there is no overlap between two medians, then the medians are significantly different at a 95% confidence level.
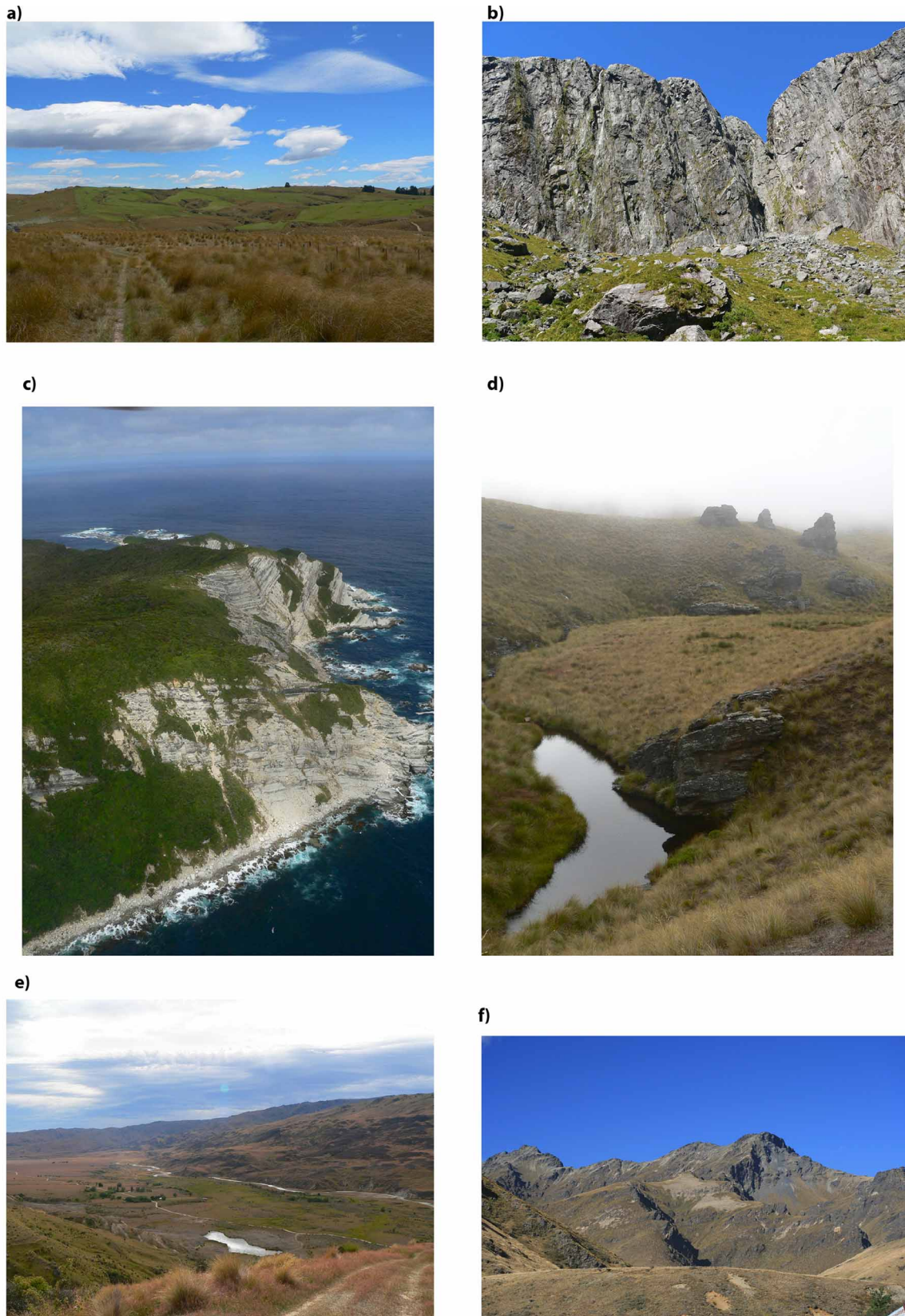
FIGURE 5. Representative habitats of the members of the *Oligosoma inconspicuum* species complex. **a)** *O. inconspicuum*, Macraes Flat, Otago. **b)** *O. inconspicuum* (mahogany form), Sinbad Valley, Fiordland. **c)** *O. tekakahu* **sp. nov.**, Chalky Island, Fiordland. **d)** *O. burganae* **sp. nov.**, Rock and Pillars Range, central Otago. **e)** *O. toka* **sp. nov.** and *O. inconspicuum*, Nevis Valley, central Otago. **f)** *O. repens* **sp. nov.** and *O. inconspicuum*, Eyre Mountains, central Otago.

Colouration: Although colouration in the species is extremely variable, brown is the predominant colour. Dorsal surface light brown or tan to dark brown, with irregular flecks. Mid-dorsal stripe where present not usually continuous, and margins not straight. Often a pale dorsolateral stripe extending from near tip of snout to base of tail, becoming indistinct thereafter. Brown lateral stripe two or more scale rows wide, notched on upper and lower edges, running from tip of snout through eye towards tip of tail. May contain flecks of dark and light brown. Soles of feet brown/black. Belly yellow, bronze (in Big Bay animals, Tocher 1999), or deep yellow (in the 'mahogany' form), often unmarked. Outer surface of forelimbs brown, speckled with light and dark. Chin and neck may be pale, usually speckled with black, or uniformly black. There do not appear to be sexually dimorphic colour patterns. Juvenile colouration similar to adult.

Etymology. From *inconspicuum* (Latin, neuter)—not readily visible, referring both to the difficulty in distinguishing this taxon from other similar sympatric species, and the cryptic behaviour of this species in its natural environment. The common name is the cryptic skink.

Habitat and life history. This species is found throughout the lower South Island, as far north as central Otago (Figure 5a,b). This species has been recorded throughout the lower South Island and central Otago in the following Ecological Regions and Districts (McEwen 1987; regions are in capitals, districts in lower case): ASPIRING 51.07 Dart; WAITAKI 64.02 St Mary, 64.04 St Bathans; LAKES 66.03 Richardson, 66.05 Remarkables; CENTRAL OTAGO 67.01 Lindis, 67.03 Dunstan, 67.04 Maniototo, 67.05 Old Man; LAMMERLAW 68.01 Macraes, CATLINS 70.01 Waipahi; OLIVINE 71.01 Cascade, 71.02 Pyke; FIORD 72.01 Darran; MAVORA 73.02 Eyre, 73.03 Upukerora; WAIKAIA 74.01 Nokomai; GORE 75.01 Gore; SOUTHLAND HILLS 76.01 Takitimu, 76.02 Taringatura, 76.03 Hokonui; TE WAE WAE 77.03 Longwood; MAKAREWA 78.01 Southland Plains, 78.02 Waituna. Similarly, environmental classifications range from (to Level II only): K3; L1, L3, L4; M1; N3, N4, N5, N6; O1; P5; Q1, Q2, Q3, Q4; R1, R2; and S2 (Leathwick *et al.* 2003). Consequently this species tolerates an extremely wide range of environmental conditions from coastal to montane environments in both cold or cool, wet climates and cool but dry climates with low to moderate radiation (McEwen 1987, Leathwick *et al.* 2003).

It has a distinct microhabitat preference for herbs and shrubs over tussocks and rocks, and tends to tolerate quite damp environments such as Sinbad Gully in Fiordland and Big Bay on the West Coast. Adults usually give birth in February-March, with number of offspring ranging from one to three. Diet consists of fruit and insects (Patterson and Daugherty 1990; Tocher 1999).

Conservation status. *Oligosoma inconspicuum* is currently considered Not Threatened (Partial Decline) in the New Zealand Department of Conservation's national threat classification lists (Hitchmough *et al.* 2010).

Oligosoma tekakahu sp. nov.
Figure 6

Oligosoma inconspicuum 'Te Kakahu' Chapple *et al.* 2009: 485
Oligosoma sp. 6 (Te Kakahu skink) Jewell 2008: 89

Holotype. Chalky Island (Te Kakahu), Fiordland (46º 03'S, 166º 31'E), RE006879, adult male (coll. T. Bell, January 2008).

Live animals examined. Chalky Island, Fiordland (46º 03'S, 166º 31'E), 16 animals (7 adult males, 6 adult females, 3 subadults) (data collected by T. Bell, January 2008).

Diagnosis. *Oligosoma tekakahu* can be distinguished from other related *Oligosoma* species through a combination of characters (Figure 4). Compared to *O. maccanni, O. tekakahu* has a glossy appearance, with brown predominating whereas *O. maccanni* has a greyer ground colour. The ear opening in *O. maccanni* often has large projecting scales on the interior margin, whereas these are minimal in *O. tekakahu.* The number of subdigital lamellae in *O. maccanni* (19–28) does not overlap with *O. tekakahu* (16). Longitudinal striping is more pronounced in adjacent populations of *O. polychroma,* which almost always have a pale stripe on the outside of the forelimbs and a prominent mid-dorsal stripe which *O. tekakahu* lacks. The ear opening in *O. polychroma* often has prominent projecting scales on the interior margin. The number of subdigital lamellae in *O. tekakahu* (16) is less than in any other member of the *O. inconspicuum* species complex. The number of ventral scales in *O. tekakahu* (68) is fewer than *O. toka* **sp. nov.** (70–88). *Oligosoma tekakahu* has a larger head relative to SVL than any other member of the *O. inconspicuum* species complex (its head length, 9.8 mm, was longer than any other specimen measured in the study).

Description of holotype. Body elongate, oval in cross-section; limbs moderately well-developed, pentadactyl. Lower eyelid with a transparent palpebral disc, bordered on sides and below by small, oblong granules. Nostril centred just below middle of nasal, pointing up and back, not touching bottom edge of nasal. Supranasals absent. Rostral broader than deep. Frontonasal broader than long, not separated from frontal by prefrontals meeting in midline. Frontal longer than broad, shorter than frontoparietal and interparietal together, in contact with 2 anteriormost supraoculars. Supraoculars 3[left]/4[right], the second is the largest. Frontoparietals distinct, larger than interparietal. A pair of parietals meeting behind interparietal and bordered posteriorly by a pair each of nuchals and temporals, also in contact with interparietal, frontoparietal, third/fourth supraocular and 2 postoculars. Loreals 2, anterior one the larger; anterior loreal in contact with first supralabial, posterior loreal, prefrontal, frontonasal and nasal; posterior loreal in contact with second supralabial, first subocular, upper and lower preocular, prefrontal and anterior loreal. Supralabials 7, the sixth is the largest. Infralabials 6, several of them equal in size; fifth supralabial below centre of eye. Mental broader but shallower than rostral. Suboculars 3 and 4 separated by fifth supralabial. Postmental larger than mental. Chinshields 3 pairs. One primary temporal. Dorsal scales largest, weakly striate. Ventral scales smooth. Subdigital lamellae smooth. Ear opening round, small with no projecting granules. Forelimbs shorter than hindlimbs. Adpressed limbs not meeting in adult. Digits moderately long, sub-cylindrical. Third front digit shorter than the fourth.

Measurements (in mm; holotype only). SVL 67.2; HL 9.8; HW 6.8; AG 35.6; SF 24.0; SE 11.3; EF 13.0. TL unknown (not intact). Ratios for morphological measurements: AG/SF 1.48; SE/EF 0.87; HL/HW 1.44 (in mm; live animals): The mean SVL size (from 14 live animals) was 64.08 mm (range 50–79 mm), and the mean mass was 5.6 g (range 1.6–10 g).

Holotype scale counts. Upper ciliaries 7; lower ciliaries 9; nuchals 3 pairs; midbody scale rows 30; ventral scale rows 73; subdigital lamellae 17; supraciliaries 5; suboculars 6. One primary temporal. Third front digit as long as the fourth.

Colouration. Dorsal surface light olive to chestnut brown, often with highly irregular random dark flecks. A broken dorsolateral line formed by a single row of triangular-shaped dark or black flecks runs from the posterior margin of the eye to the base of the tail. This row is bordered by a pale dorsolateral band approximately a half scale row wide above, and by a broad dark brown lateral band, below, which commences from the posterior of eye, passing above limb insertions and concluding near tail base. A pale grey lateroventral band similarly runs from the lower jaw to the tail base. The edges between the lateral band and lateroventral band is variable in markings in individuals, from scattered black and white flecks running across the body mid-laterally, to a rudimentary but broken black above/white below mid-lateral stripes. Ventral surface entirely yellow, or sometimes with pale grey chins. Ventral surface plain without speckling or other markings. Outer surface of forelimbs strong yellowish brown with darker and lighter specks. Juvenile colouration is unknown, but likely to be similar to adults.

Etymology. From Te Kakahu, the Maori name for the type locality (= Chalky Island). The common name is the Te Kakahu skink.

Habitat and life history. *Oligosoma tekakahu* is currently known only to occupy open coastal herbfield and prostrate shrubs growing on chalk chip strata at one location on northwestern Chalky Island (Loh 2003; this study; Figure 5c). Chalky Island is located in the southern part of the FIORD 72.04 Preservation Ecological District (McEwen 1987), a region which consists of non-glaciated coastal plateaus in the south west (100–500 m asl). Preservation ED is cool, often cloudy and windy, with high annual rainfall (3200–8000 mm), typical of Environment O5 (Leathwick *et al.* 2003). At Chalky Island, these skinks occur in generally high densities at the type location with over fifty skinks encountered in a small area of 50 x 50 m over two days (this study). The type location is at an altitude of 134–142 m, at the head of chalk cliffs. The flora around the type location consists of windswept grasses and complex prostrate shrubs including *Olearia avicennifolia*, *O. oporina, Coprosma* spp., *Metrosideros umbellata, Phormium cookianum*, *Coriaria arborea*, *Helischrysum*, *Poa colensoi*, *Haloragis erectus*, *Griselina littoralis*, *Hebe elliptica*, *Pimelia lyallii*, and *Chionochloa conspicua* (Loh 2003). The skink is currently known to be associated with *Olearia avicennifolia*, *O. oporina*, the grasses *Carex s*pp. and *Rytidosperma* spp. (this study). Although the extent of habitat similar to the type location is remarkably small on the entire island, *O. tekakahu* are also likely to also occupy the largely inaccessible coastal vegetation and prostate scrub vegetation along the entire coastline of Chalky Island. Skinks have also adapted to open areas created within the scrub by the cutting of tracks leading to and away from the type location, an observation also recorded by Loh (2003).
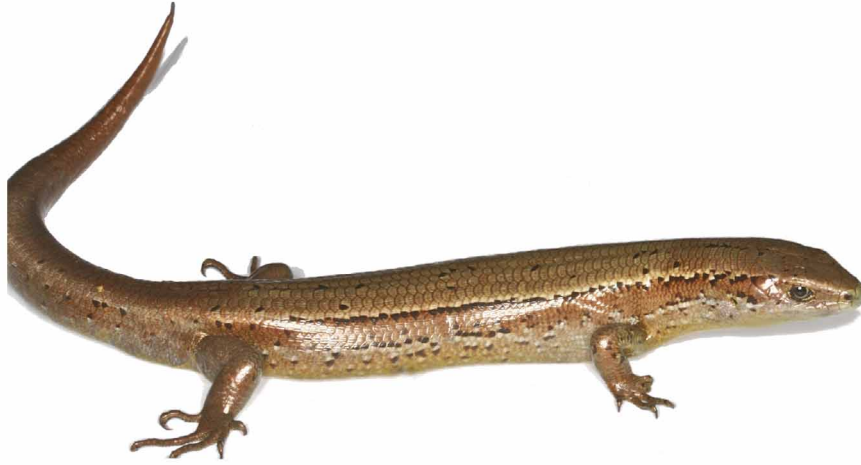
FIGURE 6. a) Holotype of *O. tekakahu* (RE006879), Chalky Island. **b)** Lateral view of the head of the *O. tekakahu* holotype (RE006879). **c)** Live specimen of *O. tekakahu* at the type locality (Chalky Island).

Oligosoma tekakahu is a diurnal, terrestrial species, and strongly heliothermic with avid sun-basking behaviour even during windy conditions by utilising sheltered micro-sites (Loh 2003, TPB, pers. obs.). The following observations on Te Kakahu skinks were made by TPB. The skinks will bask readily on chalk flakes in air temperatures up to 23.8 °C, above which they retreat to bask partially shaded within vegetation. Basking extends to as late as 8 pm in the mid-summer. *Oligosoma tekakahu* appear to have small home ranges and do not appear to defend territories, often basking in close proximity to other skinks. Skinks generally forage or bask in close proximity to cover or vegetation, but will cross quickly between habitat patches over chalk. The sex ratio of captured skinks was almost equal (8 males:6 females). Almost all adult female skinks were heavily gravid by January, and three neonates were sighted, suggesting the possibility of an unusually early season parturition period in late January. The smallest reproductively mature individual was a 61 mm SVL gravid female. These skinks flick their tongues relatively frequently as they move. Their tongues were noted to be relatively long and coloured bluish-grey. The incidence of regenerated tails or body scarring evident in the sample (N = 15) was generally high (53%). The New Zealand falcon (*Falco novaezeelandiae*) is likely to be a predator and was recorded daily at the type location during the field work for this study (TPB, pers. obs.). There are no other known sympatric species of lizard on Chalky Island.

Conservation status. The Te Kakahu skink is currently considered Nationally Critical (criterion A. Naturally or unnaturally very small natural population; with qualifiers Conservation Dependent, Data Poor, and One Location) in the New Zealand Department of Conservation's national threat classification list (Hitchmough *et al.* 2010). These skinks appear to be very locally abundant, and may yet be found in new locations on Chalky Island and nearby islands such as the Passage and Coal Islands. Protection is provided by the status of a mammalian predator-free offshore island within a national park, and along with ongoing monitoring for invasive mammal incursions by the New Zealand Department of Conservation. Potential future threats appear to be the invasive mammal pests (e.g. rats, *Rattus* spp., and stoats, *Mustela erminea*) which are present on the adjacent mainland. These skinks exhibit highly naive behaviour to potentially novel predators, and would likely suffer severe losses as a result of invasion of rats or stoats. Stoats were present until 1999 on Te Kakahu Island and the population is likely to be in the process of recovery from their impacts.

Oligosoma burganae **sp. nov.**
Figure 7

Leiolopisma inconspicuum Patterson & Daugherty 1990: 66
Leiolopisma nigriplantare maccanni Patterson 1984

Holotype. Burgan Stream, Rock and Pillar Range (45º 35'S, 169º 56'E), RE002390/1, adult female (coll. G. Patterson, 1982).

Paratypes (13 specimens). Burgan Stream, Rock and Pillar Range (45º 35'S, 169º 56'E), 12 specimens (RE006149 [CD765], male; RE006150 [CD766], female; RE006151 [CD767], male; RE006152 [CD768], female; RE006153 [CD769], female; RE006154 [CD770], male; RE006155 [CD771], male; RE006156 [CD772], female; RE006157 [CD773], female; RE006159 [CD774], female; RE006160 [CD775], male; RE006161 [CD776], female) (coll. G. Patterson, April 1984); Burgan Stream, Rock and Pillar Range (45º 35'S, 169º 56'E), RE002391/1, female (coll. G. Patterson, November 1981).

Diagnosis. *Oligosoma burganae* can be distinguished from other related *Oligosoma* species through a combination of characters (Figure 4). Compared to *O. maccanni, O. burganae* has a glossy appearance, with brown predominating whereas *O. maccanni* has a greyer ground colour. *Oligosoma maccanni* has a pale grey ventral colour rather than the yellow/grey ventral colour seen in *O. burganae*. The ear opening in *O. maccanni* often has large projecting scales on the interior margin, whereas these are often minimal or lacking altogether in *O. burganae*. Longitudinal striping is more pronounced in sympatric populations of *O. polychroma,* which almost always have a pale dorsal stripe on the outside of the forelimbs. The ear opening in *O. polychroma* often has prominent projecting scales on the interior margin. There are statistical differences between *O. burganae* and *O. inconspicuum* (AG/SF, HL/HW, SE/EF, SVL/HL, SVL/FLL), *O. toka* **sp. nov.** (SVL/HLL, ventral scales), *O. notosaurus* (ventral scales), and *O. repens* **sp. nov.** (SVL/HL, SVL/FL, AG/SF) (Figure 4). All *O. inconspicuum* have four supraoculars whereas most *O. burganae* have only three supraoculars. *Oligosoma repens* **sp. nov.** has a more elongate appear-

ance than *O. burganae* (TL/SVL of 1.1 and 1.28, respectively). The number of subdigital lamellae (18–23) is greater than in *O. tekakahu* (16). The head of *O. burganae* is noticeably blunter and deeper than *O. repens* **sp. nov.** and *O. toka* **sp. nov.** (Figures 4, 7–9).

Description of holotype. Body elongate, oval in cross-section; limbs moderately well-developed, pentadactyl. Lower eyelid with a transparent palpebral disc, bordered on sides and below by small, oblong granules. Nostril centred just below middle of nasal, pointing up and back, not touching bottom edge of nasal. Supranasals absent. Rostral broader than deep. Frontonasal broader than long, not separated from frontal by prefrontals meeting in midline. Frontal longer than broad, shorter than frontoparietal and interparietal together, in contact with 2 anteriormost supraoculars. Supraoculars 3, the second is the largest. Frontoparietals distinct, larger than interparietal. A pair of parietals meeting behind interparietal and bordered posteriorly by a pair each of nuchals and temporals, also in contact with interparietal, frontoparietal, third supraocular and 2 postoculars. Loreals 2, anterior one the larger; anterior loreal in contact with first supralabial, posterior loreal, prefrontal, frontonasal and nasal; posterior loreal in contact with second supralabial, first subocular, upper and lower preocular, prefrontal and anterior loreal. Supralabials 7, the sixth is the largest. Infralabials 6, several of them equal in size; fifth supralabial below centre of eye. Mental broader but shallower than rostral. Suboculars 3 and 4 separated by fifth supralabial. Postmental larger than mental. Chinshields 3 pairs. One primary temporal. Dorsal scales similar in size to ventral scales, weakly striate. Ventral scales smooth. Subdigital lamellae smooth. Ear opening round, small with no projecting granules. Forelimbs shorter than hindlimbs. Adpressed limbs not meeting in adult. Digits moderately long, sub-cylindrical. Third front digit shorter than the fourth.

Measurements (in mm; holotype with the variation shown in the type series in parentheses). SVL 58.9 (mean 55.0, range 46.8–67.1), HL 8.0 (mean 7.3, range 6.6–9.0), HW 5.4 (mean 5.4, range 4.8–6.3), AG 34.3 (mean 31.8, range 25.2–42.0), SF 20.3 (mean 20.0, range 16.8–23.2), SE 10.0 (mean 8.8, 7.2–10.6), EF 10.3 (mean 10.9, range 8.3–12.9), and TL 56.2.

Variation (holotype with the variation shown in the type series in parentheses). Upper ciliaries 7 (mean 6, range 5–8); lower ciliaries 10 (mean 9, range 7–10); nuchals 3 pairs (mean 2 pairs, range 0–3 pairs); midbody scale rows 32 (mean 31, range 30–34); ventral scale rows 76 (mean 75, range 70–82); subdigital lamellae 20 (mean 20, range 18–23); supraciliaries 5 (mean 6, range 4–6); suboculars 7 (mean 6, range 6–7). Frontonasal never separated from frontal by prefrontals meeting in midline. Anterior loreal in contact with first or second supralabial. Supralabials 7 (usual) or 8, the sixth or seventh are the largest. Infralabials 6 (usual) or 7. Third front digit as long as (usual) or shorter than the fourth. Maximum SVL 66.2 mm (shrinkage about 5% based on original records). One specimen had an intact tail (TL/SVL = 1.00). Ratios for morphological measurements ($\pm$ SD): AG/SF 1.60 ± 0.17; SE/EF 0.82 ± 0.09; HL/HW 1.37 ± 0.07. The maximum SVL observed was 65 mm for males and 70 mm for females. Intact TL/SVL = 1.1 (N=18) (Patterson 1985).

Colouration. Dorsal surface moderate olive to dark olive brown, occasionally black, with irregular flecks. A median dorsal dark grayish brown longitudinal stripe, 2 half-scale rows wide, well or partially developed, commencing behind the head and passing back to the base of the tail. A light brown dorsal band 2 half-scale rows wide with light flecks. Another broken dark brown band, 1 half- to 2 half-scale rows wide, shading on to a pale dorsolateral band 1 half- to 2 half-scale rows wide. A pale dorsolateral band, extending from posterior margin of eye to first one-third of tail. This stripe bordered laterally by a dark brown band usually with notched edges above and below. A broad dark reddish brown lateral band 1.5 to 2.5 scale rows wide, originating at tip of snout, passing through the eye and ending near tip of tail, bordered laterally by a very dark brown broken band and with pale scales extending into it from above and below; sometimes flecked with white. Below this an indistinct pale stripe passes from beneath the anterior border of the eye through the ear, above the limbs to the tail. This stripe is irregularly defined below by brown scales which merge gradually with the yellowish grey ventral colouration. Ventral surface usually speckled with black spots on chin and throat. Outer surface of forelimbs is dark brown with black and white specks. Juvenile colouration similar to adult, but generally lighter. Ear opening round, small, with no projecting granules on anterior margin. There do not appear to be sexually dimorphic colour patterns.

Etymology. Refers to the Burgan Stream area, the type locality for the species. The common name is the Burgan skink.

Habitat and life history. *Oligosoma burganae* appears to be confined to the Rock and Pillar Ranges (Figure 5d) and Lammermoor Ranges (CENTRAL OTAGO: 67.07 Rock and Pillar and LAMMERLAW: 68.02 Waipori; McEwen 1987) of central Otago, and only occurs above 900 m (i.e. a subalpine species). The Rock and Pillar ED
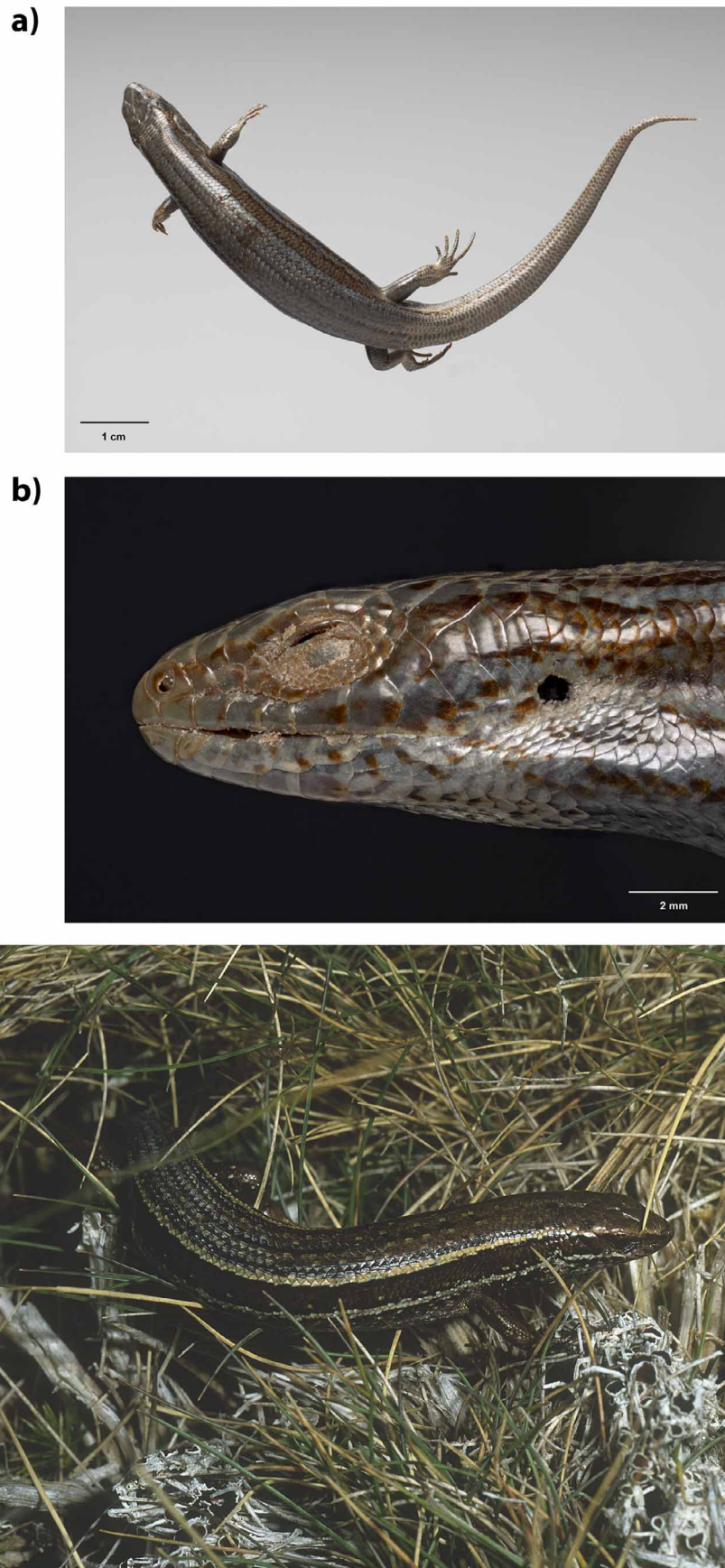
FIGURE 7. a) Holotype of *O. burganae* (RE002390/1), Rock and Pillar Range. **b)** Lateral view of the head of the *O. burganae* holotype (RE002390/1). **c)** Live specimen of *O. burganae* (photo: J. Reardon).

consists of sub-continental schist block mountains rising steeply from an altitude of 400–1450 m, with annual rainfall from 500–1700 mm and snow to 1000 m during winter. This area is classified as Environment Q3 (Leathwick *et al.* 2003). The predominant vegetation of the area is montane short and tall *Chionochloa* tussockland, with some scrub, particularly *Coprosma* and *Olearia* spp. The Waipori ED consists of peaty uplands of the Lammermoor and Lammerlaw Plataeu (up to 1200m asl), which experience cool, dry or moist subcontintental conditions (annual rainfall 500–1200 mm), with snow down to 900m during winter. Predominant vegetation is similar to the Rock and Pillar Ranges, but with pastoral development for sheep and cattle up to 600 m.

The biology, ecology and life-history of *O. burganae* have been documented previously in Patterson (1985, 1992). The species becomes sexually mature at 49 mm SVL, and has a maximum litter size of six. Parturition occurs in late January or early February. Some sperm was present in the epididymis from October to March, with a large increase of sperm in January. The average home range size for *O. burganae* was 13.4 m^2. Specific site defence was noted on several occasions, usually towards other skink species. The preferred microhabitat appeared to be herbs and shrubs rather than rocks and grasses. This microhabitat preference appeared to be the main reason why this species was able to coexist with other similarly-sized skink species (*O. polychroma* and *O. maccanni*) throughout its range. Like most *Oligosoma*, *O. burganae* is a diurnal heliotherm. Its diet consists of a range of invertebrates, particularly spiders, and berries from several shrub species such as snowberry (*Gaultheria depressa*). The climate throughout the species' range is harsh, where snow may occur at any time of the year. Abdominal fat bodies were noted in many specimens, which increased in size during the summer months, and probably aided the skinks in hibernation during winter. Tails, likewise, were relatively emaciated after the skinks emerged from hibernation in the spring, and became plumper over summer as the skinks increased their fat reserves. A population census from 24 January to 20 February 1983 gave a mean density of one animal per 27 m^2 in the type locality. The survival of *O. burganae* after a controlled burn-off of an area of tussock grassland was noted by Patterson (1984).

Conservation status. *Oligosoma burganae* is currently considered At Risk: Declining (B, large population and low to moderate ongoing or predicted decline; with qualifiers Data Poor, and Range Restricted) in the New Zealand Department of Conservation's national threat classification lists (Hitchmough *et al.* 2010). A recent assessment of the Burgan skink population (this study) suggests that there has been a serious population decline in the species since 1985 (Patterson 1985). Thus, research is needed to identify the current population status and trend, establish the species' known range, and identify potential threats.

Oligosoma toka sp. nov.
Figure 8

Oligosoma inconspicuum Jewell 2008: 88
Leiolopisma inconspicuum Patterson & Daugherty 1990: 66

Holotype. Schoolhouse Flat, Nevis Valley, (45º 11'S, 168º 59'E), RE007278, adult male (coll. T. Bell, 2009).

Paratypes (12 specimens). Nevis Range F42 5551813.9 2183702.9 (45º 10'S, 168º 52'E), 7 specimens (RE006165 [CD938], female; RE006166 [CD939], male; RE006163 [CD936], female; RE006164 [CD937], female; RE006167 [CD940], male; RE006168 [CD941], female; RE006162 [CD935], female) (coll. A.H. Whitaker, March 1986); Schoolhouse Flat, Nevis Valley, (45º 11'S, 168º 59'E), 5 specimens (RE007281, female; RE007286, female; RE007289, female; RE007290, male; RE007297, male) (coll. J. Reardon January 2010).

Live animals examined. Schoolhouse Flat, Nevis Valley (45º 11'S, 168º 59'E), 13 specimens (5 adult males, 5 adult females, 3 juveniles) (data collected by T. Bell, 2009).

Diagnosis. *Oligosoma toka* can be distinguished from other related *Oligosoma* species through a combination of characters (Figure 4). Compared to *O. maccanni, O. toka* has a glossy appearance, with brown predominating whereas *O. maccanni* has a greyer ground colour. *Oligosoma maccanni* has a pale grey ventral colour rather than the yellow ventral colour seen in *O. toka.* The ear opening in *O. maccanni* often has large projecting scales on the interior margin, whereas these are often minimal or lacking altogether in *O. toka. Oligosoma maccanni* has four supraocular scales compared with three in *O. toka*, an unusually low number for New Zealand skinks. Sympatric *O. polychroma* have very similar colour patterns, but can be distinguished by a pale dorsal stripe on the outside of the forelimbs, and a greyish-brown ventral colouration. The ear opening in *O. polychroma* often has prominent project-

ing scales on the interior margin. There are statistical differences between *O. toka* and *O. repens* **sp. nov.** (SVL/HL, SVL/HLL, ventral scales, SE/EF), *O. burganae* (SVL/HLL, ventral scales), *O. inconspicuum* (SVL/FL, SVL/HLL, ventral scales), and O. *notosaurus* (ventral scales) (Figure 4). All *O. toka* have three supraoculars whereas all *O. inconspicuum* and *O. notosaurus* have four. The number of ventral scales in *O. tekakahu* (68) is fewer than *O. toka* (70–88), and the number of subdigital lamellae (16) is fewer than *O. toka* (17–23). The dorsal surface of the head is usually more strongly marked than in *O. repens* **sp. nov.**, and the mid-dorsal and dorsolateral stripes in *O. toka* are more prominent than in *O. repens* **sp. nov.**.

Description of Holotype. Body elongate, oval in cross-section; limbs moderately well-developed, pentadactyl. Lower eyelid with a transparent palpebral disc, bordered on sides and below by small, oblong granules. Nostril centred just below middle of nasal, pointing up and back, not touching bottom edge of nasal. Supranasals absent. Rostral broader than deep. Frontonasal broader than long, not separated from frontal by prefrontals meeting in midline. Frontal longer than broad, shorter than frontoparietal and interparietal together, in contact with 2 anteriormost supraoculars. Supraoculars 3, the second is the largest. Frontoparietals distinct, larger than interparietal. A pair of parietals meeting behind interparietal and bordered posteriorly by a pair each of nuchals and temporals, also in contact with interparietal, frontoparietal, third supraocular and 2 postoculars. Loreals 2, similar size; anterior loreal in contact with first and second supralabial, posterior loreal, prefrontal, frontonasal and nasal; posterior loreal in contact with second supralabial, first subocular, upper and lower preocular, prefrontal and anterior loreal. Supralabials 8[left]/7[right], the sixth and seventh are the equal largest. Infralabials 6, several of them equal in size; sixth[left]/ fifth[right] supralabial below centre of eye. Mental broader but shallower than rostral. Suboculars 3 and 4 separated by sixth[left]/fifth[right] supralabial. Chinshields 3 pairs. One primary temporal, similar size to lower secondary temporal. Dorsal scales similar in size to ventral scales, weakly striate. Ventral scales smooth. Subdigital lamellae smooth. Ear opening round, small with insignificant projecting granules. Forelimbs shorter than hindlimbs. Adpressed limbs not meeting in adult. Digits moderately long, sub-cylindrical. Third front digit shorter than the fourth.

Measurements (in mm; holotype with the variation shown in the type series in parentheses). SVL 71.1 (mean 59.8, range 45.1–66.2), HL 8.8 (mean 8.2, range 6.9–9.0), HW 6.4 (mean 5.7, range 4.8–6.5), AG 40.5 (mean 32.0, range 24.1–40.5), SF 24.5 (mean 21.7, range 17.0–24.5), SE 12.2 (mean 10.0, range 8.7–12.2), EF 12.6 (mean 11.7, range 8.3–13.8), and TL 58.5 (mean 58.5, range 53.5–66.0, N=3).

Variation (holotype with the variation shown in the type series in parentheses). Upper ciliaries 7 (mean 6, range 5–7); lower ciliaries 8 (mean 8, range 7–9); nuchals 4 pairs (mean 3 pairs, range 2–4 pairs); midbody scale rows 32 (mean 32, range 30–34); ventral scale rows 80 (mean 82, range 70–88); subdigital lamellae 21 (mean 21, range 17–23); supraciliaries 5 (mean 5, range 5–7); suboculars 7 (mean 6, range 4–7). Frontonasal seldom separated from frontal by prefrontals meeting in midline. Anterior loreal in contact with first or second supralabial. Secondary loreal usually in contact with secondary supralabial only. Supralabials 6, 7 (usual) or 8, the fifth, sixth or seventh are the largest. Infralabials 5, 6 (usual) or 7. Third front digit as long as (usual) or shorter than the fourth. Maximum SVL 71.1 mm. Three specimens had an intact tail (TL/SVL = 1.16). Ratios for morphological measurements (± SD): AG/SF 1.47 ± 0.12; SE/EF 0.86 ± 0.11; HL/HW 1.45 ± 0.06.

Colouration. Dorsal surface light to dark yellowish brown, often with irregular flecks. A median dorsal dark yellowish brown longitudinal stripe, 2 half-scale rows wide, well developed, commencing behind the head and passing back to the base of the tail, becoming indistinct thereafter. A light to grayish yellowish brown dorsal band 2 half-scale rows wide sometimes with light and dark flecks. This band is often bounded on both sides by a pale stripe less than one scale wide. Another dark yellowish brown band 1 to 2 half-scale rows wide, shading onto a prominent pale dorsolateral band 2 half-scale rows wide. This pale band extends from above posterior margin of eye to base of tail, or further along tail. A broad strong yellowish brown lateral band 1 to 2 scale rows wide, originating near tip of snout, passing through eye and ending at base or further along tail, bordered laterally by two dark yellowish brown bands, and often with pale scales extending into it from above and below; sometimes flecked with white. Below this an indistinct pale stripe passes from beneath the posterior border of the eye above the ear and limb insertions to the tail. This stripe is irregularly defined below by brown scales which merge gradually with the yellow ventral colouration. Yellow colouration extends along first third of tail. Ventral surface usually lightly speckled with black spots on chin and throat, which are white. Outer surface of forelimbs is dark brown with black and white specks. Juvenile colouration similar to adult, but generally lighter and lacking distinct mid-dorsal stripe. There do not appear to be sexually dimorphic colour patterns.
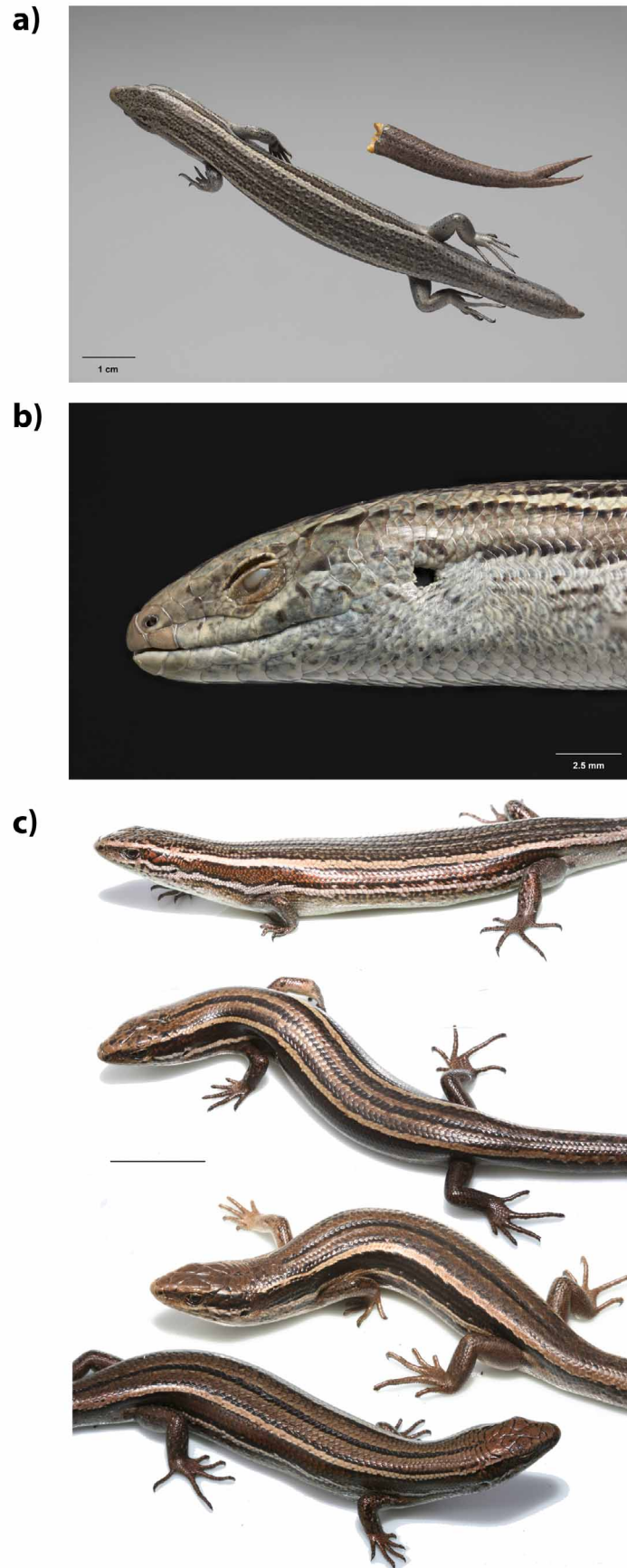
FIGURE 8. a) Holotype of *O. toka* (RE007278), Schoolhouse Flat, Nevis Valley. **b)** Lateral view of the head of the *O. toka* holotype (RE007278). **c)** Live specimens of *O. toka* from the type locality.

Etymology. From 'toka', the Maori word for rock or boulder. Refers to the rocky habitat on which this species occurs in the Nevis Valley. The common name is the Nevis skink.

Habitat and life history. *Oligosoma toka* appears to be confined to Nevis Valley (WAIKAIA 74.01 Nokomai Ecological District; McEwen 1987) of central Otago (Figure 5e). The area where *O. toka* has been recorded so far is classified as Environments N3, N4 and Q3 (Leathwick *et al.* 2003). The Nokomai ED consists of broad plateaus and hills of a lower altitude (> 600 m to 1500 m asl) than the Eyres ED. The geological composition is complex, but usually consists of schist and greywacke rock formations. The climate is cool, with annual rainfall typically around 800–1200 m. It is unclear how far south the Nevis skink population extends to, but it is likely to be the entire valley and adjacent areas. The predominant ecology consists of exotic pasture for sheep and cattle grazing, with lowland tussockland in the foothills, and red or subalpine tall tussockland at higher elevations. *Oligosoma toka* are extremely abundant around rock piles (old gold tailings) along the eastern side of the Nevis River, but not as abundant elsewhere where cover is scarce on the open Nevis Valley flats. However, they do occur widely in the area, on the river flats, around the foothills and up to the Nevis Crossing. The artificial rock piles are likely to be important refugia for the population in the Nevis Valley, and *O. toka* is the most abundant species in the valley, especially adjacent to the Nevis River (T. Jewell, pers. obs.). However, high abundance at certain localities (e.g. 5–7 skinks per 10 m^2 in artificial and natural rock formations; T. Jewell, unpublished data) does not necessarily imply overall species security, given the apparent restricted range of the species. Important vegetation for *O. toka* include tussocks and rank grasses (native, exotic), *Coprosma*, *Discaria Muehlenbeckia*, *Melicytus* and *Rubus* spp. In the wider Nevis Valley, *O. toka* is sympatric with *O. inconspicuum*, *O. polychroma*, *O. maccanni*, *Hoplodactylus* sp. 'Cromwell', and *Hoplodactylus* sp. 'Otago large' (T. Jewell, pers. obs.; this study). It is possible that *O. toka* might also be present in the adjacent Hector and Garvie Mountains (T. Jewell, pers. comm.).

Conservation status. Little is known about the range, abundance and population viability of *O. toka*. It is currently considered Data Deficient in the New Zealand Department of Conservation's national threat classification lists (Hitchmough *et al.* 2010). Resolution of this species' conservation status may be urgent (Townsend *et al.* 2008).

Oligosoma repens **sp. nov.**
Figure 9

Oligosoma inconspicuum Jewell 2008: 88

Holotype. Mt Nicholas Road, Eyre Mountains, (45º 15'S, 168º 18'E), RE007279, adult male (coll. T. Bell, 2009).

Paratypes (8 specimens). Cascade Creek, Eyre Mountains (45º 13'S, 168º 26'E), 5 specimens (RE007282, female; RE007285, male; RE007287, male; RE007292, female; RE007294, male) (coll. J. Reardon, January 2010); Lower Nevis Valley (45º 10'S, 168º 57'E), 3 specimens (RE007291, male; RE007295, male; RE007296, male) (coll. B. Barratt, December 2009–January 2010).

Diagnosis. *Oligosoma repens* can be distinguished from other related *Oligosoma* species through a combination of characters (Figure 4). Compared to *O. maccanni, O. repens* has a glossy appearance, with brown predominating whereas *O. maccanni* has a greyer ground colour. *Oligosoma maccanni* has a pale grey ventral colour rather than the bright yellow ventral colour in *O. repens*. The ear opening in *O. maccanni* often has large projecting scales on the interior margin, whereas these are often minimal or lacking altogether in *O. repens*. *Oligosoma maccanni* has four supraocular scales compared with three in *O. repens*. *Oligosoma polychroma* from nearby areas have very similar colour patterns to *O. repens*, but can be distinguished by a pale dorsal stripe on the outside of the forelimbs, and a greyish-brown ventral colouration. The ear opening in *O. polychroma* often has prominent projecting scales on the interior margin. There are statistical differences between *O. repens* and *O. toka* (SVL/HL, SVL/HLL, ventral scales), *O. burganae* (AG/SF, SE/EF, HL/HW, SVL/HL), and O. *notosaurus* (SVL/HL, ventral scales) (Figure 4). All *O. repens* have three supraoculars whereas all *O. inconspicuum* and *O. notosaurus* have four. The number of subdigital lamellae in *O. tekakahu* (16) is fewer than *O. repens* (19–23). The dorsal surface of the head is usually unmarked in *O. repens*, in contrast with *O. toka* and *O. notosaurus* in particular. The species is more gracile than the other members of the species complex.
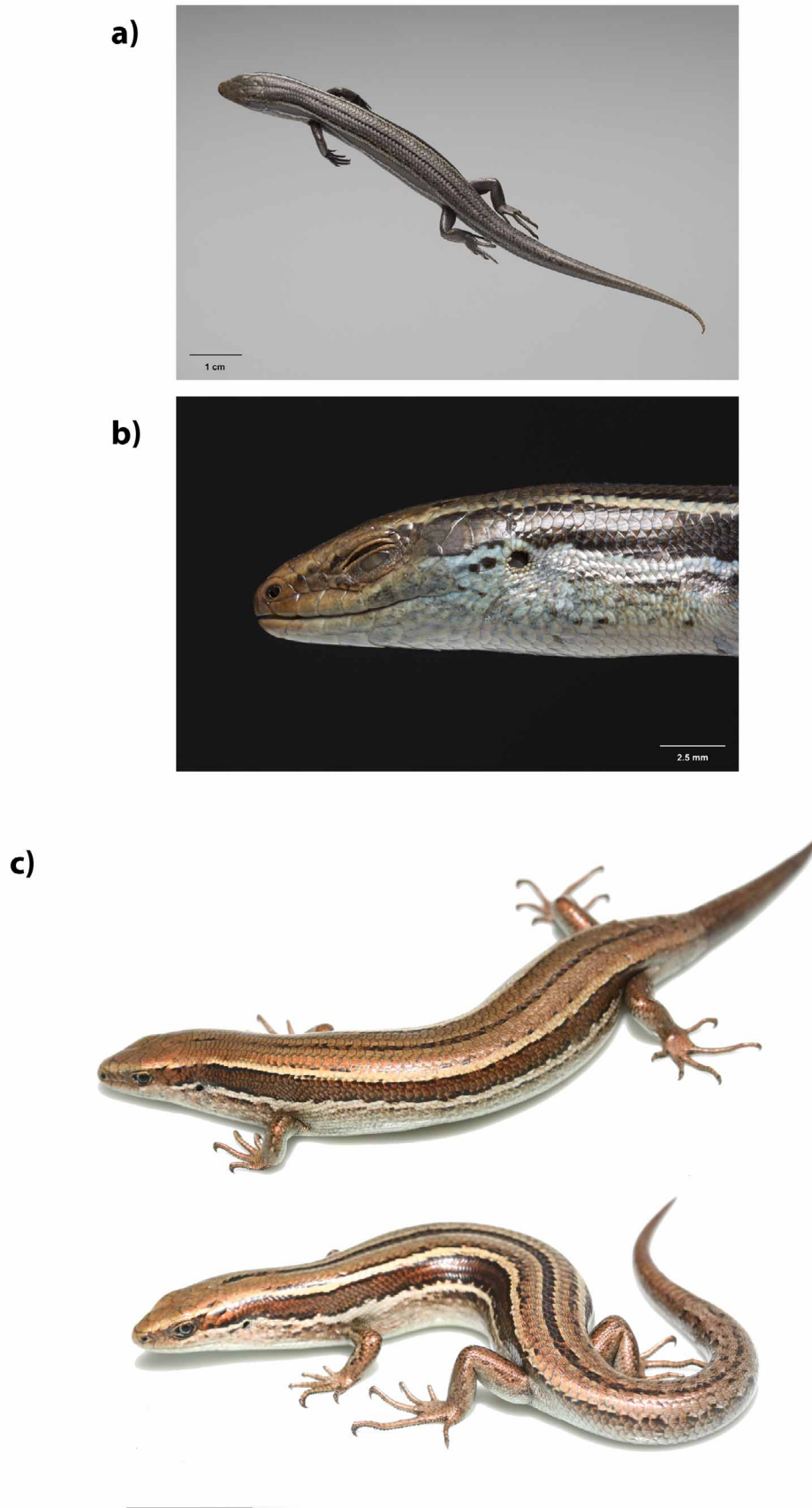
FIGURE 9. **a)** Holotype of *O. repens* (RE007279), Mt Nicholas Road, Eyre Mountains. **b)** Lateral view of the head of the *O. repens* holotype (RE007279). **c)** Live specimens of *O. repens* from the type locality.

Description of holotype. Body elongate, oval in cross-section; limbs moderately well-developed, pentadactyl. Lower eyelid with a transparent palpebral disc, bordered on sides and below by small, oblong granules. Nostril centred just below middle of nasal, pointing up and back, not touching bottom edge of nasal. Supranasals absent. Rostral broader than deep. Frontonasal broader than long, separated from frontal by prefrontals meeting in midline. Frontal longer than broad, shorter than frontoparietal and interparietal together, in contact with 2 anteriormost supraoculars. Supraoculars 3, the second is the largest. Frontoparietals distinct, larger than interparietal. A pair of parietals meeting behind interparietal and bordered posteriorly by a pair each of nuchals and temporals, also in contact with interparietal, frontoparietal, third supraocular and 2 postoculars. Loreals 2, similar size; anterior loreal in contact with first and second supralabial, posterior loreal, prefrontal, frontonasal and nasal; posterior loreal in contact with second and third supralabial, first subocular, upper and lower preocular, prefrontal and anterior loreal. Supralabials 7, the sixth and seventh are the equal largest. Infralabials 6, several of them equal in size; fifth supralabial below centre of eye. Mental broader but shallower than rostral. Suboculars separated by fifth supralabial. Chinshields 3 pairs. One primary temporal, approximately half the size of lower secondary temporal. Dorsal scales similar in size to ventral scales, weakly striate. Ventral scales smooth. Subdigital lamellae smooth. Ear opening round, small with insignificant projecting granules. Forelimbs shorter than hindlimbs. Adpressed limbs not meeting in adult. Digits long, sub-cylindrical. Third front digit shorter than the fourth.

Measurements (in mm; holotype with the variation shown in the type series in parentheses). SVL 56.4 (mean 55.1, range 47.6–61.8), HL 8.0 (mean 8.0, range 7.0–9.1), HW 5.7 (mean 5.6, range 4.7–6.0), AG 28.7 (mean 28.8, range 23.6–33.8), SF 20.8 (mean 20.3, range 17.6–22.6), SE 10.5 (mean 10.1, range 9.0–11.3), EF 10.0 (mean 10.4, range 9.1–12.0), and TL unknown (mean 66.5, range 65.0–67.9, N=2).

Variation (holotype with the variation shown in the type series in parentheses). Upper ciliaries 6 (mean 7, range 5–7); lower ciliaries 10 (mean 9, range 7–10); nuchals 0 pairs (mean 2 pairs, range 0–3 pairs); midbody scale rows 32 (mean 32, range 30–34); ventral scale rows 77 (mean 76, range 68–81); subdigital lamellae 22 (mean 21, range 19–23); supraciliaries 6 (mean 6, range 6–7); suboculars 7 (mean 7, range 6–9). Frontonasal seldom separated from frontal by prefrontals meeting in midline. Anterior loreal in contact with first or second supralabial. Secondary loreal usually in contact with secondary and third supralabial. Supralabials 7, the fifth or sixth are the largest. Infralabials 5 or 6 (usual). Third front digit shorter (usual) or as long as the fourth. Maximum SVL 61.8 mm. Two specimens had intact tails (TL/SVL = 1.28). Ratios for morphological measurements (± SD): AG/SF 1.42 ± 0.07; SE/EF 0.98 ± 0.07; HL/HW 1.43 ± 0.07.

Colouration. Dorsal surface yellowish brown often with a median dorsal very dark brown longitudinal stripe, 2 half-scale rows wide, well or partially developed, commencing behind the head and passing back to the base of the tail. A yellowish brown dorsal band 2 half-scale to 1.5 scale rows wide sometimes with light flecks. Another broken dark brown band, 1 half- to 2 half-scale rows wide, shading on to a pale dorsolateral band 1 half- to 2 half-scale rows wide. This pale dorsolateral band, extending from above and behind posterior margin of eye to base of tail. This stripe bordered laterally by a strong yellowish brown band 1–2 scale rows wide, originating behind nostril, passing through eye and ending past base of tail, bordered laterally by a dark yellowish brown band. The strong yellowish band sometimes flecked with white and dark brown. Below this an indistinct pale stripe passes from beneath the posterior border of the eye through the ear, above the limbs to the base of the tail. This stripe is irregularly defined below by brown scales which merge gradually with the yellow ventral colouration. Ventral surface may be lightly speckled with black spots on chin and throat, which are white. Outer surface of forelimbs is dark brown with black and white specks. Juvenile colouration similar to adult, but generally lighter. There do not appear to be sexually dimorphic colour patterns. Dorsal surface of head normally unmarked.

Etymology. From 'repens' (Latin, neuter) = unexpected. Refers to the unexpected discovery of a genetically divergent new species in the Eyre Mountains that occurs sympatrically with *O. inconspicuum* (sensu stricto). The common name is the Eyres skink.

Habitat and life history. The extent of its distribution is unknown, but *Oligosoma repens* appears to be confined to the Eyre Mountains and also the Hector Mountains (MAVORA 73.02 Eyre; WAIKAIA 74.01 Nokomai; McEwen 1987) of western Otago (Figure 5f). Environmental classifications for the Eyres are O1 and Q1 and, for the Hector Mountains, Q1 and Q2 (Leathwick *et al.* 2003). *Oligosoma repens* appears to be abundant around rock piles and screes along the Eyre Mountains foothills (~700 m asl, and likely higher), but less abundant elsewhere where cover is scarce on the open Eyre valley flats, except where screes occur. The Eyre Ecological District consists of highly dissected, steep and eroding schist or greywacke mountains with narrow valley floors (ranging from

600–2025 m asl) (McEwen 1987). The climate of the Eyres ED is cool and moderately wet (annual rainfall 800–1200 mm); snow may accumulate above 1000 m asl during winter. Much of the Eyres ED was once beech forest, but have been converted to a mixture of exotic pastoral grasslands and native fescue, red or snow tussockland (McEwen 1987). The skink is sympatric with *O. inconspicuum*, *O. maccanni*, and the gecko *Hoplodacylus* sp. 'Otago Large', another undescribed taxon within the *H. maculatus* species-complex. *Oligosoma chloronoton* may also be a sympatric species (McEwen 1987), as well as *O. polychroma*.

Conservation status. Little is known about the range, abundance and population viability of *O. repens*. It is currently considered Not Threatened (Range Restricted) in the New Zealand Department of Conservation's national threat classification lists (Hitchmough *et al.* 2010). Further research will be required to assess the conservation status of *O. repens*.

Oligosoma notosaurus (Patterson & Daugherty, 1990)

A full description of *O. notosaurus* is contained in Patterson & Daugherty (1990). For the current study we re-examined all of the specimens included in the original description apart from the holotype, which has been lost from the Te Papa collection.

Discussion

Our taxonomic revision has demonstrated, using molecular and morphological analyses, that the *O. inconspicuum* species complex comprises six distinct species and is paraphyletic. While the presence of several undescribed species within the *O. inconspicuum* species complex had been anticipated (e.g. Miller 1999; Tocher 1999; Jewell 2006, 2008; Hitchmough *et al.* 2007; Chapple *et al.* 2009), several of our results were surprising. Two of the three proposed new species (i.e. the 'Big Bay' skink and 'mahogany' skink) were not found to be distinct species, but instead represented geographically disjunct populations of the widespread *O. inconspicuum* sensu stricto. The third proposed new species (i.e. the 'Te Kakahu' skink) was confirmed as a distinct species (*O. tekakahu*) and was found to be most closely related (5.8–8.1% genetic divergence) to *O. inconspicuum* and *O. notosaurus*. Chapple *et al.* (2009) demonstrated that the divergence between *O. inconspicuum* and *O. notosaurus* had occurred more recently compared to most other speciation events within the New Zealand skink radiation. However, the distinct species status of *O. inconspicuum* and *O. notosaurus* is supported by the considerable genetic divergence between these taxa (4.6%), and the fact that *O. notosaurus* is not most closely related to the *O. inconspicuum* populations that occur on the islands in Foveaux Strait (Figures 1 and 2).

In contrast, the other three new species (*O. burganae*, *O. toka*, *O. repens*) were deeply divergent 'cryptic' taxa (14.8–16.3%) with restricted distributions in the mountainous regions of central Otago. These three species were found to be more closely related to *O. stenotis* and *O. grande* than to the taxon (*O. inconspicuum*) that they were previously assigned. This represents a particularly surprising result as *O. inconspicuum* and its most closely related species (i.e. members of the former common skink, *Leiolopisma nigriplantare maccanni*, species complex) have been the subject of considerable taxonomic study over the past two decades (Daugherty *et al.* 1990; Patterson & Daugherty 1990, 1994; Patterson 1997). Neither the allozyme work, nor the discriminate function analyses using morphological traits, had previously detected these deeply divergent lineages (Daugherty *et al.* 1990; Patterson & Daugherty 1990). The cryptic nature of these taxa is highlighted by the fact that specimens from two lineages (i.e. *O. burganae*, *O. toka*) were examined in the original description of *O. inconspicuum* (Patterson & Daugherty 1990). Indeed, the majority of tissue samples used in this study were obtained from specimens examined in the original description (Table 1; Patterson & Daugherty 1990).

Our study therefore suggests that there are further cryptic, undescribed or as yet undiscovered members of the *O. inconspicuum* species complex present in the southern South Island of New Zealand. The phylogenetic affinities of the 'Okuru' skink are unknown, and since the only known specimen had keeled scales similar to that found in *O. stenotis* (Jewell 2008), future work on this taxon may indicate that it also represents a new species.

Intriguingly, several members of the *O. inconspicuum* species complex occur in sympatry in certain regions of the South Island. *Oligosoma repens* occurs sympatrically with *O. inconspicuum* in at least one locality in the Eyre

Mountains, with substantial genetic divergence (15.7%) between the two species at this location. Similarly, *O. inconspicuum* occurs in sympatry with *O. toka* in the Nevis Valley, the type locality for the latter species (our observations). In contrast, *O. burganae* does not occur in sympatry with any other members of the species complex, but occurs within a few kilometres of an *O. inconspicuum* population at Macraes Flat (Patterson & Daugherty 1990). However, it does occur together with *O. maccanni* and *O. polychroma* in the Rock and Pillars and Lammermoor Ranges (Patterson 1984; Patterson & Daugherty 1990). In addition, *O. repens* also occurs in sympatry with *O. maccanni* at several locations (our observations). *Oligosoma tekakahu* is the only skink species present on Chalky Island in Fiordland, while *O. notosaurus* occurs sympatrically with *O. stenotis* and *O. polychroma* on Stewart Island (Gill & Whitaker 2001; Jewell 2008).

The genetic divergence between the lineage comprising *O. inconspicuum*, *O. notosaurus* and *O. tekakahu* and the lineage containing *O. burganae*, *O. repens* and *O. toka* was 14.8–16.3%. Given a rate of molecular evolution of approximately 1.4% per myr, these two lineages are estimated to have diverged during the mid-late Miocene (~10 mya). This corresponds to a period in New Zealand's history of rapid change, as the climate cooled and dried, and increases in land area occurred, due to land uplift and falling sea levels (Lee *et al*. 2001). New habitat formed as sub-tropical rainforest fragmented and gave way to expanding herb land (Pole *et al*. 2003), and the newly-activated Alpine Fault began to form high, rugged hills on what had previously been an eroded peneplain (Cooper & Millener 1993; Cooper & Cooper 1995; Lee *et al*. 2001). Novel habitats and range fragmentation during the Miocene have been implicated in the speciation of other New Zealand endemic taxa. In particular, deeper divergences among species of giant weta (genus *Deinacrida*), which includes both alpine and lowland species, have been dated to the Miocene (Trewick & Morgan-Richards 2005), as has the radiation of alpine cicadas (genus *Maoricicada*; Buckley & Simon 2007).

In *O. inconspicuum*, the genetic distance between the populations in central Otago/Southland and eastern Otago/Southland is 3.8%, which suggests divergence during the Pliocene (~2.7 mya). Pliocene-age, east-west phylogeographic splits across the Otago region have also been observed in the grand skink, *O. grande* (Berry & Gleeson 2005), and in McCann's skink, *O. maccanni* (O'Neill *et al*. 2008). This phylogeographic break may be associated with habitat partitioning either side of the Nevis-Cardrona fault system, which is marked by the Cardrona and Nevis rivers. The fault marks the boundary between the high relief, mountainous habitat found in the west, and the undulating grassland habitat found on the lower mountains, hills and wide basins that characterise central and eastern Otago (Waters *et al*. 2001).

Oligosoma notosaurus, which is endemic to Stewart Island, is separated from the South Island populations of *O. inconspicuum* by Foveaux Strait. Genetic divergence between these two species is 4.6%, which places the split at 3.3 mya. This is surprising since Foveaux Strait is narrow and relatively shallow. The strait is bridged during glacial periods, most recently ~11,500 years ago when Stewart Island was joined to Southland by a broad coastal plain (McGlone & Wilson 1996). Evidence for recent (i.e. Pleistocene) geneflow across Foveaux Strait in skinks is equivocal. In a study of the green skink, *O. chloronoton* (Hardy), the minimum distance across Foveaux Strait was similar, at 5.1% (Greaves *et al*. 2007). However, the common skink, *O. polychroma*, shows very little structure across this waterway (Liggins *et al*. 2008b). This implies that glacial land bridges provided suitable habitat for the migration or range expansion of some, but not all, species of skink.

In contrast, the genetic distance among the new range-restricted species from central and western Otago (*O. burganae*, *O. repens* and *O. toka*) is 9.1–10.7%. These three species therefore diverged much earlier than *O. inconspicuum*, *O. notosaurus*, and *O. tekakahu*, possibly in the Miocene (6.5–7.6 mya) before the landscape of Otago became mountainous. Climate change and habitat fragmentation during the Miocene may therefore underlie divergence in these three species (e.g. Lee *et al*. 2001).

Our study shows that the *O. inconspicuum* species complex contains both cryptic and 'anti-cryptic' taxa (Figure 10), and raises the question of why both occur within a single complex. The anti-cryptic forms (i.e. 'Big Bay' skink, 'mahogany' skink) occur in regions of the South Island that are completely isolated, either in valleys on steep-sided mountains, or in bays surrounded by such mountains. In contrast, *O. inconspicuum* (sensu stricto) occurs across a much broader range, and three of the new species (*O. burganae*, *O. repens* and *O. toka*) occur in the mountainous regions of central and western Otago, sometimes in sympatry with *O. inconspicuum*. This is an example of a geographic pattern noted by Mayr (1942); he observed that peripheral, isolated populations are often morphologically 'aberrant', while populations in the interior of a species range show very little morphological variation. Mayr (1954) reasoned that rapid genetic drift in small, isolated populations, was the main evolutionary

force causing the morphological divergence (and ultimately, speciation) of these peripheral populations. However, the idea that drift rather than selection drives this geographical pattern has proven controversial (reviewed in Coyne & Orr 2004). There is little empirical evidence that genetic drift has a major role in morphological evolution (Coyne *et al*. 1997) but much demonstrating rapid morphological change in small, isolated populations subjected to novel selection (reviewed in Turelli *et al*. 2001). Thus, the unusual anti-cryptic forms in the *O. inconspicuum* species complex are likely to represent local adaptation to the unusual environmental conditions in which these skinks are found.
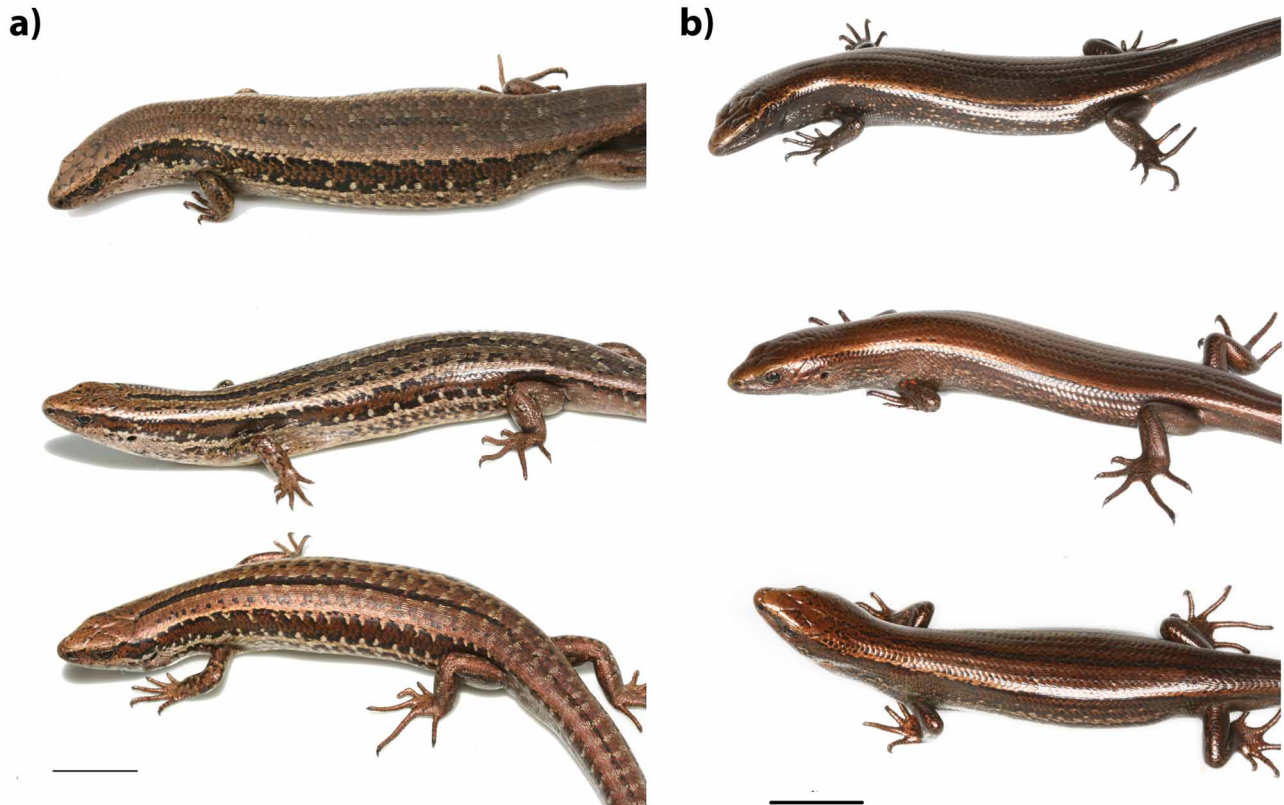
FIGURE 10. Comparison of **a)** the typical form of *Oligosoma inconspicuum* (top: Macraes Flat, Otago; middle and bottom: Eyre Mountains, central Otago), and **b)** the 'mahogany' form of *O. inconspicuum* (Sinbad Valley, Fiordland). The 'mahogany' form is distinguished by extremely elongated toes, flattened head and deep yellow belly colouration.

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