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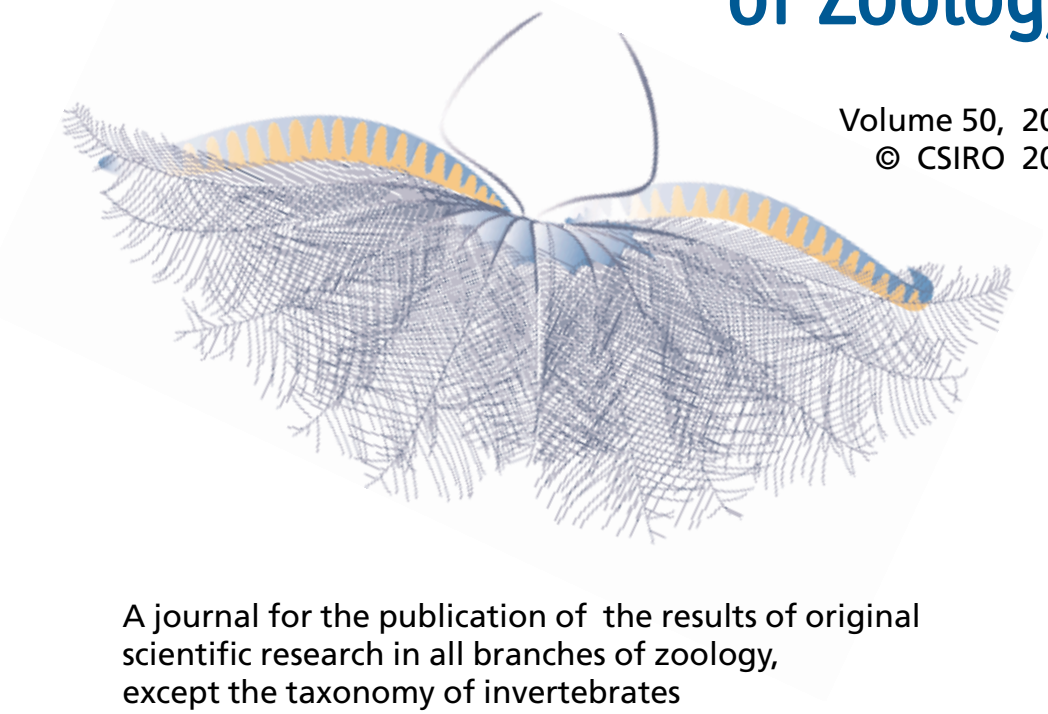

Volume 50, 2002

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Australian Journal of Zoology, 2002, **50**, 439–459

Systematics of the *Egernia whitii* species group (Lacertilia: Scincidae) in south-eastern Australia

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Abstract

Allozyme electrophoresis was used to assess the taxonomic significance of colour pattern variation within and between populations of the *Egernia whitii* species group from 41 locations in south-eastern Australia. Analysis of the products of 39 presumed loci revealed that a minimum of three species are present in southern New South Wales among populations previously referred to *Egernia whitii*. Fixed allelic differences were maintained where pairs of species were sympatric. One of these three species is wide-ranging and is the one to which the name *E. whitii* is properly applied. The other two are more restricted ecologically and geographically and are described here as new. The three species are genetically and morphologically distinct from the other three eastern Australian members of the species group, *E. margaretae*, *E. modesta*, and *E. multiscutata*. Genetic data and a review of the morphological evidence provide no support for the recognition of subspecies within either *E. whitii* (*sensu stricto*) or *E. multiscutata*.

Introduction

Recent studies of biochemical genetic variation among Australian reptiles assayed by allozyme electrophoresis have revealed the presence of cryptic species among several genera of skinks in south-eastern Australia, e.g. *Pseudemoia* (Donnellan and Hutchinson 1990; Hutchinson and Donnellan 1992), *Niveoscincus* (Hutchinson and Schwaner 1991) and *Saproscincus* (Sadlier *et al.* 1993). It might be expected that the diversity of the vertebrate fauna of this area of Australia would be well documented. However, some other reptile and frog 'species' from south-eastern Australia show characteristics that suggest that they are also composite (e.g. Donnellan *et al.* 1999; Smith *et al.* 1999; Mahony *et al.* 2001). An example is the complex of species Storr (1968) termed the *Egernia whitii* 'superspecies', a sibling species complex he identified within the larger *Egernia whitii* species group, which presently comprises, in south-eastern Australia, *E. margaretae*, *E. modesta*, *E. multiscutata* and *E. whitii* (Storr 1968, 1978; Horton 1972).

All of these species show both local and regional variation in colour patterns, notably involving polymorphism in back pattern where individuals may have either patterned or plain dorsal colour patterns (see Fig. 2). In some species, for example *E. multiscutata* and *E. whitii*, 'patterned' individuals are more common than 'plain', while in *E. margaretae* and *E. modesta*, the patterned morph is rare. In *E. whitii* the frequency of the plain morph varies geographically (Storr 1968); in some areas, such as on Kangaroo Island, South Australia, there is a high frequency of plain individuals, while in others, notably Tasmania, plain individuals have not been recorded. Milton *et al.* (1983), utilising allozyme electrophoresis, have shown the genetic distinctness, in sympatry, of *E. whitii* and *E. modesta*, which share the plain colour morph. Milton (1990) showed that the two colour-pattern morphs present in populations of *E. whitii* interbreed in three locations in northern New South Wales and southern Queensland, but suggested that they do not interbreed at random.

 10.1071/ZO01065 0004-959X/02/050439

Variation within the species in the complex has led to the recognition of subspecies in *E. whitii*, *E. margaretae* and *E. multiscutata* (Storr 1968, 1978; Cogger 2000). The genetic distinctiveness of these named subpopulations has not been examined. In addition, variation in *E. whitii* in southern New South Wales (Wilson and Knowles 1988; Green and Osborne 1994) and elsewhere (Storr 1968; Chesterfield *et al.* 1983) is greater than generally recognised, and the presence of atypically patterned individuals of uncertain taxonomic status suggests that further examination of genetic variation across the species' range is warranted.

In the present study we analysed genetic variation, as measured by allozyme electrophoresis, among and within taxa of the *Egernia whitii* species group in south-eastern Australia and Tasmania, with particular emphasis on *E. whitii*. Following the delimitation of genetic groups, we determined that the genetic variation is concordant with consistent differences in external appearance and ecology. The study demonstrates the presence of three species within '*E. whitii*' in south-eastern New South Wales, with all three species co-existing on the Ramshead Range, Kosciuszko National Park.

Materials and Methods

We collected 112 specimens of the *Egernia whitii* species group from 46 localities in south-eastern Australia (Fig. 1 and Appendix). We sampled all named forms, any morphological variants not already reported in the literature, and from disjunct areas of the species group's distribution. Museum registration numbers and collection details of specimens are listed in the Appendix. Livers were dissected from fresh specimens and stored at –80°C.

Homogenates of liver were electrophoresed on sheets of cellulose acetate (Cellogel: Chemetron) as described by Richardson *et al.* (1986), and were assayed for 32 enzymes encoded by 39 presumptive loci. The enzymes stained, abbreviations and E.C. numbers (Murphy *et al.* 1996) are: aspartate aminotransferase (AAT, E.C. 2.6.1.1), aconitate hydratase (ACOH, E.C. 4.2.1.3), alcohol dehydrogenase (ADH, E.C. 1.1.1.1), carbonate dehydratase (CA, EC 4.2.1.1), leucine aminopeptidase (CAP, E.C. 3.4.11.1), diaphorase (DIA, EC 1.6.99.?), enolase (ENO, E.C. 4.2.1.11), fructose-diphosphatase (FBP, E.C. 3.1.3.11), fumarate hydratase (FUMH, E.C.4.2.1.2), glyceraldehyde-phosphate dehydrogenase (GAPDH, E.C. 1.2.1.2), guanine deaminase (GDA, EC 3.5.4.3), glycerol-3-phosphate dehydrogenase (G3PDH, E.C. 1.1.1.8), glucose-phosphate isomerase (GPI, E.C. 5.3.1.9), glutamate dehydrogenase (GTDH, E.C. 1.4.1.3), L-iditol dehydrogenase (IDDH, E.C. 1.1.1.14), isocitrate dehydrogenase (IDH, E.C. 1.1.1.42), lactate dehydrogenase (LDH, E.C. 1.1.1.27), lactoyl-glutathione lyase (LGL, E.C. 4.4.1.5), malate dehydrogenase (MDH, E.C. 1.1.1.37), 'malic' enzyme (MDHP, EC 1.1.1.40), mannose-phosphate isomerase (MPI, E.C. 5.3.1.8), purine-nucleoside phosphorylase (NP, EC 2.4.2.1), peptidases (PEP, E.C. 3.4.11.? or 3.4.13.?), phosphoglycerate mutase (PGAM, EC 5.4.2.1), 6-phosphogluconate dehydrogenase (PGDH, E.C. 1.1.1.44), phosphoglycerate kinase (PGK, E.C. 2.7.2.3), phosphoglucomutase (PGM, E.C. 2.7.5.1), superoxide dismutase (SOD, E.C. 1.15.1.1), and triose-phosphate isomerase (TPI, E.C. 5.3.1.1). Electromorphs were identified by comparison with samples that were repeatedly included on each gel (internal controls) and through critical side-by-side comparisons (line-ups; see Richardson *et al.* 1986). Of 112 specimens collected, 107 were scored for all the loci examined; the remaining five individuals of *E. whitii*, which were collected subsequent to the initial allozyme screen, were scored only for diagnostic markers at eight loci.

Initial analysis of the allozyme data involved examination of multi-locus genotypes of individual lizards from a single locality. The presence of two or more species in sympatry is often, in our experience, evident from the presence of fixed allelic differences at one or more loci where the genotypic classes are concordant among individuals (see Richardson *et al.* (1986) and Adams *et al.* (1987) for a more detailed explanation). In the present study, where evidence of departure from Hardy–Weinberg expectations, as detailed above, was observed at one or more loci, individuals were classified into OTUs (Operational Taxonomic Units) within which there was no departure from Hardy–Weinberg expectations. Thus at some locations more than one OTU was designated, e.g. Mt Scabby, New South Wales. Geographically proximate OTUs between which no fixed allelic differences were observed were pooled. On this basis, 21 OTUs were designated (Appendix). Cavalli-Sforza and Edwards (1967) chord distances (CSE) between OTUs were calculated with the BIOSYS-1 program (Swofford and Selander 1981). Trees were constructed by the Neighbour-Joining

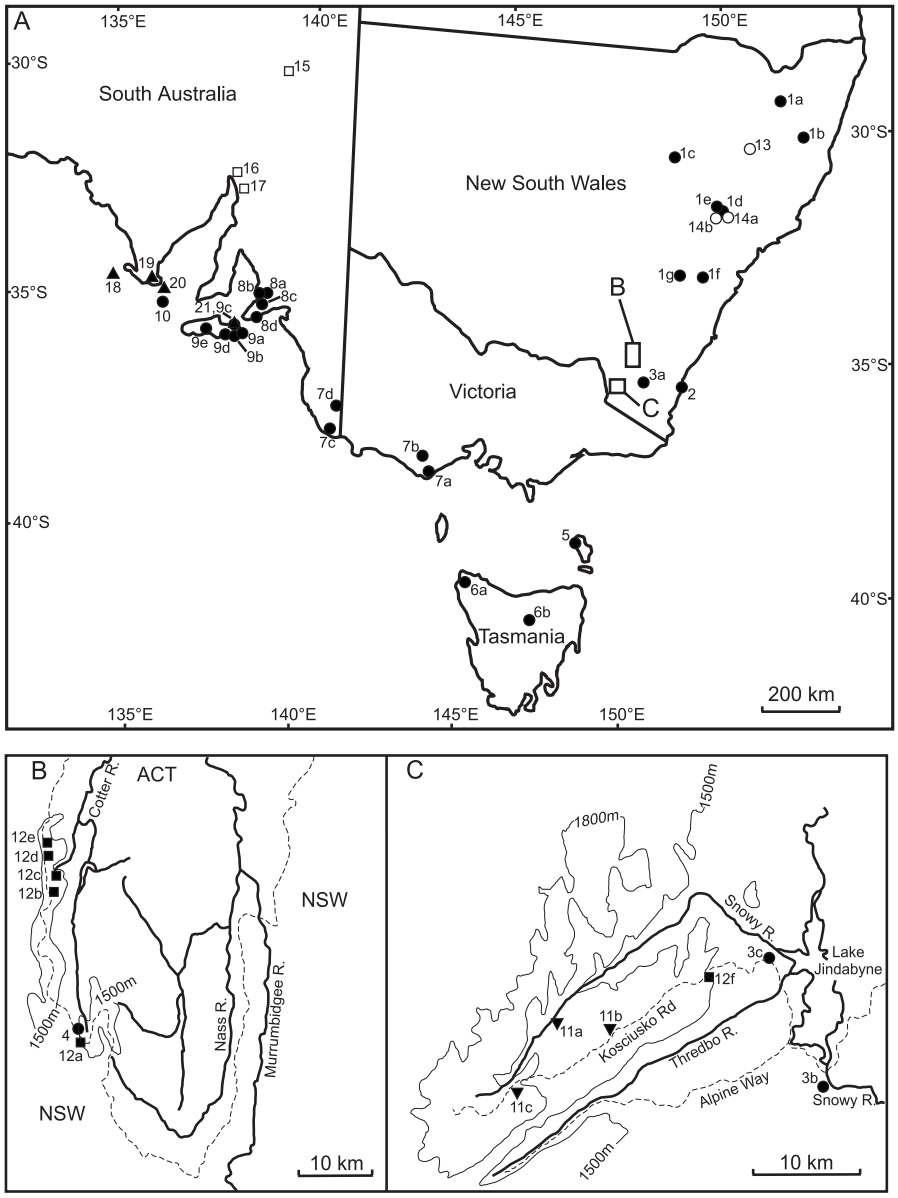

Fig. 1. Map showing the collection localities for specimens of the *Egernia whitii* species group in south-eastern Australia. Numbers refer to localities and OTUs listed in the Appendix. Symbols are: ▼ – *E. guthega*; □ – *E. margaretae*, ○ – *E. modesta*; ■ – E. montana; ▲ – *E. multiscutata*; and ● – *E. whitii*.

algorithm (NJ) using the NEIGHBOUR routine in PHYLIP version 3.5c (Felsenstein 1993). Wiens (2000) has shown that for allozyme data the construction of trees from CSE distances with NJ is generally more accurate than by parsimony methods.

The external morphology of the specimens used in the allozyme study was studied with reference to characters and methods used in earlier studies of the systematics of *E. whitii* and other scincids (e.g. Storr 1968, 1978; Horton 1972; Hutchinson and Donnellan 1992). Additional material in the South Australian Museum, Adelaide (SAMA), Museum Victoria, Melbourne (NMV), Australian National Wildlife

Table 1. Allele frequencies expressed as a percentage, in 21 OTUs of *Egernia* at 39 loci

Alleles are designated alphabetically, with 'a' being the most cathodally migrating allele. Where enzymes are encoded by more than one locus, the loci are designated numerically in order of increasing electrophoretic mobility. Where the allele frequencies are not given, the frequency is 100. See the Appendix for an explanation of the OTU codes. The sample size for each OTU is given at the head of each column. The loci *G3pdh*, *Lgl*, *Ldh-1*, *Np*, *Pgam* and *Tpi* were invariant

					whitii						*guthega*	*montana*	*modesta*			*margaretae*				*multiscutata*		
OTU	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**
Locus	11	2	7	4	5	6	7	6	25	1	5	7	2	10	1	1	2	1	1	2	1
Aat-1	b	d(50) b(50)	d(7) b(93)	d(37) b(63)	d(10) c(60) b(30)	d(8) b(92)	b	b	b(96) a(4)	b	b	d	b	b	b	b	d(25) b(75)	b	b	b	b
Aat-2	c	c	c	c	d c(20)	d (67)	c	c(84) b(8) a(8)	c(98) b(2)	c	d(30) c(70)	c	c	c	c	c	c	c	c	c	c
Acoh	d(5) c(95)	c	c	c	c	c	c	c	d(10) c(90)	d(50) c(50)	c	c	c(50) b(50)	b	d	d	d	a	c	c	c
Adh-1	d(5) b(18) a(77)	a	a	b(12) a(88)	b	b(92) a(8)	b(50) a(50)	a	d(6) b(42) a(52)	b	b	b	c	c	c	c	c	a	d	d	d
Adh-2	c(10) a(90)	c(25) a(75)	c(93) a(7)	c(75) a(25)	c	c	d(9) c(83) a(8)	d(10) c(90)	d(4) c(96)	c	c	c	b	b	c	c	c	c	c	d(25) c(75)	d
Ca	b	b	b	b	a	a	a	a	b(2) a(98)	b(50) a(50)	a	b(64) a(36)	b	b	b	b	b	a	a	a	a
Cap	c(86) b(9) a(5)	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c	c(75) a(25)
Dia	d(9) c(91)	c	c	c	c	c	c(57) b(43)	c(92) b(8)	c(98) b(2)	c	c	c	c	c	c	a	c	c	c	c	c
Eno	b	b	b	b	b	b	b	b	b	b	b	b	a	a	b	b	b	b	b	b	b
Est-1	c	c	c	c	c	c	c	c	c	c	b	a	c	c	d	d	d(50) c(50)	c	c	c	c
Est-2	c(9) a(91)	a	a	a	a	a	a	a	c(2) a(98)	a	a	a	a	a	a	a	a	d	d(50) b(50)	d(75) b(25)	b
Fbp	c	c	c	c	c	c	c(72) b(21) [2] a(7)	c	c	c	c	c	c	c	c	c	c	c	c	c	c(50) a(50)
Fumh	a	a	b(14) a(86)	a	a	a	a	a	a	a	a	a	b(25) a(75)	a	a	a	a	c(50) b(50)	b	a	a
Gda	b(14) a(86)	a	a	a	a	a	b(62) a(38)	b(20) a(80)	a	a	a	a	a	a	a	a	a	-	a	a	a
Gpdh	b(95) a(5)	b	b	b	b	b	b	b(92) a(8)	b(92) a(8)	b	b	c(7) b(93)	b	b	b	b	b	b	b	b	c(50) b(50)

Gpi	a	a	a	a	a	a	b(8)	b(2)	a	b(40)	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
							a(92)	a(98)		a(60)																					
Gtdh	b	b	b	b	b	b	b	b	b(98)	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b
									a(2)																						
Idh	a	a	a	a	a	a	a	a	a	a	b(70)	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
											a(30)																				
Idh-1	b	b	b	b	b	b	c(7)	b(83)	c(2)	b	b	b	b	b	b	b	d	d	d	d	d	b	b	b	b	b	b	b	b	b	b
							b(93)	a(17)	b(98)																						
Idh-2	b(95)	b	b	b	b	c(8)	b	b	b	a	d(7)	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b(50)	a		
	a(5)					b(92)					b(50)																	a(50)			
											a(43)																				
Ldh-2	a	a	a	a	b(20)	a	a	a	a	a	a	c	c	c	a	a	a	a	a	c	c	c	c	c	c	c	c	c	c	c	c
					a(80)																										
Mdh-1	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	b(50)	a		
																												a(50)			
Mdh-2	a	a	a	a	a	a	a	a	a	a	b	b	b	b	a	a	a	a	a	a	a	a	a	a	a	a	a	b(25)	a		
																												a(75)			
Mdhp	c	c	c(57)	c(87)	c(20)	b	c	c	d(2)	c	f	f(7)	d	d	c	c	c	c	c	d	d	d	d	d	d	d	d	d	d	d	d
			a(43)	a(13)	b(80)				c(98)			e(93)																			
Mpi	d(18)	c	c	c	c	c	c	c	c	c	c	c	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b
	c(77)																														
	a(5)																														
PepA	d(4)	b	b	b	b	b	b	b	b(98)	c	b	e(7)	c(25)	c(40)	a	a	a	b(50)	b	b	b	b	b	b	b	b	b	b	b	b	b
	c(5)								a(2)			c(93)	b(75)	b(60)				a(50)													
	b(91)																														
PepB	f(9)	e	e(71)	e	e	e	g(14)	e	g(2)	e	f	f(79)	e(50)	b(70)	e	e	e(50)	e	e	e	e	e	e	e	e	e	e	e	e	e	e
	e(91)		c(29)				e(86)		e(98)			e(7)	b(50)	a(30)			d(50)														
												d(14)																				
PepD	e(73)	e	e	e	e	e	e(79)	e(92)	g(4)	e	e(10)	b(14)	d	d	d	d	d	d	d	d	d	d	d	d	d	d	d	d	d	d	d
	c(27)						c(21)	c(8)	f(14)		c(90)	a(86)																			
									e(78)																						
									d(4)																						
Pgdh	b	b	b	b	b	c(8)	b	b	b	b	b	b	b	b	b	b	b	b	b	-	a	b(50)	a								
						b(92)																a(50)									
Pgk	b(95)	b	b	b	b	b	c(14)	b	b	b	b	b	b	b	b	b	b	b	b	a	a	a	a								
	c(5)						b(86)																								
Pgm-1	b	b	b	b	b	b	b	c(17)	c(2)	b	b	b	b	c(5)	b	c(50)	b	b	b	b	b	b	b								
								b(83)	b(94)							b(50)															
									a(4)																						
Pgm-2	c(95)	c	c	c	d(40)	c	c	e(8)	c	c	c	c(93)	c	c	c	c	c	c	c	c	c	c	c								
	b(5)				c(60)			c(92)				a(7)																			
Sod	b	b	b	b	b	b	b	b	b	b	b	b	b	b	a	a	a	a	b	b	b	b	b								

Collection, Canberra (ANWC), and Australian Museum, Sydney (AMS) were also examined to increase sample sizes for morphological data and to determine distribution limits for the taxa. Ecological data regarding habitat and microhabitat preferences, where unreferenced, are based on personal observations by the authors.

Results

Analysis of variation among the 39 loci scored for the 21 OTUs revealed six major genetically differentiated groups (Table 1, Fig. 1). Analysis of morphological characters, as detailed in the species descriptions that follow, demonstrated variation concordant with the genetically defined groups especially for colour patterns. These data taken, together with the distributions of each group, support the recognition of each group as separate species under the evolutionary species concept (Simpson 1951). Four of these species are the currently recognised *E. margaretae*, *E. modesta*, *E. multiscutata* and *E. whitii*, but two are unnamed and formal taxonomic descriptions are presented herein. Details of the allozyme evidence supporting the delineation of species boundaries follow the taxonomic descriptions.

Systematics

Egernia whitii (Lacepède, 1804)

(Fig. 2)

Synonymy

Scincus whitii Lacepède 1804: 209. Lectotype (Wells and Wellington, 1985; present work): MNHN 2988 A, Péron et Lesueur, Kangaroo Island, SA.

Scincus compressicauda Quoy & Gaimard, 1824: 180. Lectotype (present work): MNHN2989, 'Nouvelle Hollande'.

Tiliqua leucopsis Gray, 1838: 291. Syntypes in British Museum from New Holland. Lectotype identified by Cogger *et al.* [1983; 'holotype (probable)'], BMNH xv.17a, Kangaroo Island, SA.

Gongylus (*Lygosoma*) *moniligera* Duméril & Bibron, 1839: 736. Lectotype (this work): MNHN 2989 (type of *Scincus compressicauda*).

Scincus ocellatus Duméril & Bibron, 1839: 736. (*Nomen nudum*, from unpublished Peron manuscript.)

Scincus leuwinensis Duméril & Bibron, 1839: 736. (*Nomen nudum*, from unpublished Peron manuscript.)

Liopholis moniligera Fitzinger, 1843: 22.

Hinulia whitii Gray, 1845: 79.

Lygosoma whitei Peters, 1863: 230.

Egernia whitii Boulenger, 1887: 135.

Egernia whitei tenebrosa Condon, 1941: 111. Holotype: SAMA R02161, Flinders Chase, Kangaroo Island, SA.

Liopholis coplandi Wells & Wellington, 1985: 32. Holotype: AMS R76863 (formerly AM field series 14610), Cooma Airstrip, 17 km S of Cooma, NSW.

Types

The types of the older names available for this species were examined by the late P. A. Rawlinson and his extensive notes (held by the Herpetology Section, South Australian Museum) form the basis of the following discussion. Lacepède (1804) gave no details of specimens examined, but clearly stated that his descriptions were based on collections made during the Baudin expedition which had been lodged at the Muséum National d'Histoire Naturelle, Paris. That institution identifies MNHN 2988 (two specimens) as syntypes of

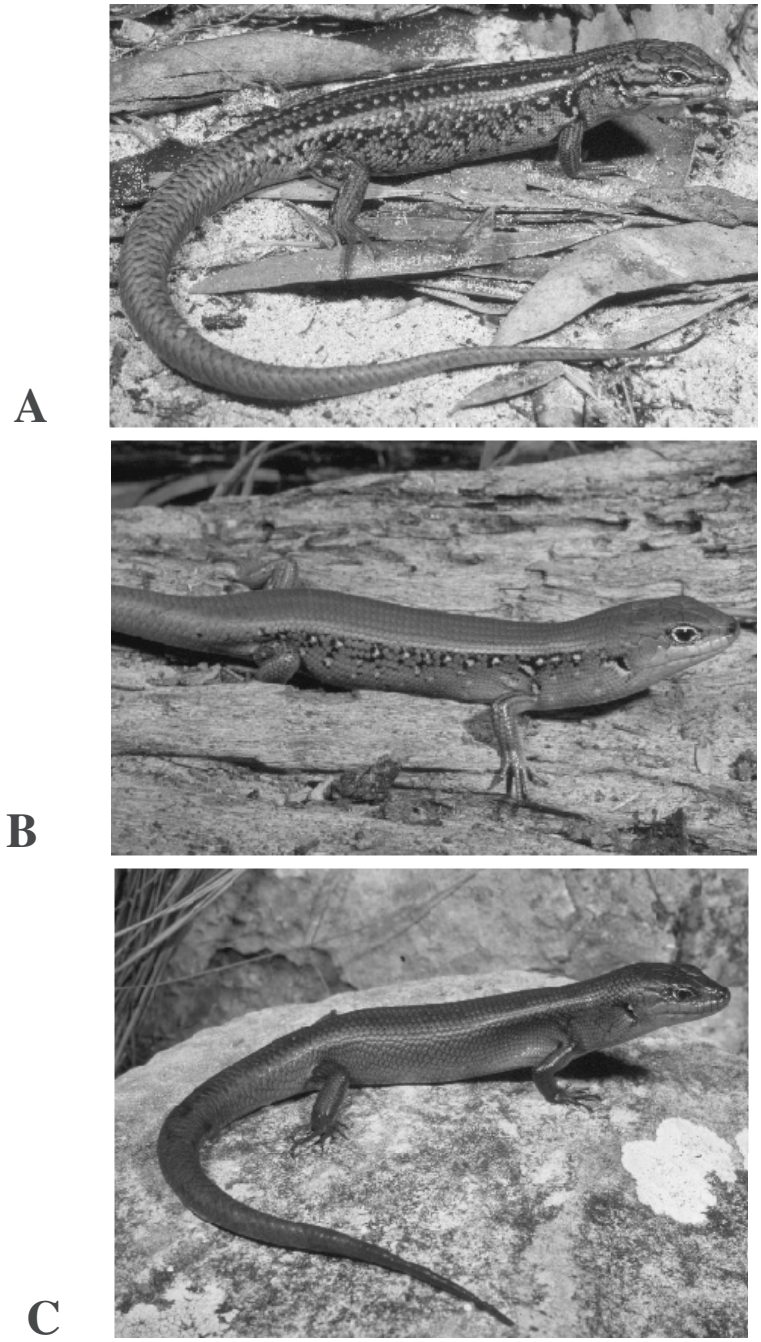

Fig. 2. *A*, *Egernia whitii* (Lacepède, 1804) from the type locality, Kangaroo Island, South Australia (specimen from Antechamber Bay), showing the 'patterned' dorsal colouration. *B*, *Egernia whitii* (Kilmore Reservoir, Mt Disappointment, Victoria) showing the 'plain back' dorsal colouration. *C*, *Egernia whitii* (Cape Hart, Kangaroo Island, South Australia) lacking both dorsal and lateral patterns.

Lacepède's *Scincus whitii*, the oldest available name. Although the type locality was published only as Nouvelle Hollande, data with 2988 identify them as collected by Péron and Lesueur from Île Decrès (= Kangaroo island, SA). Wells and Wellington (1985) suggested that 'the larger' of the two syntypes be designated as lectotype, without providing any data on the specimen. The larger syntype, designated MNHP 2988A in the collection, is a suitable choice as it is in better condition than the smaller (numbered 2988, no suffix) which is marred by a gash across the body. MNHN 2988A has a SVL of 89 mm, the tail is broken off, leaving a 9-mm stump, the midbody scales are smooth and in 36 longitudinal rows, the 25 subdigital lamellae are smooth, the lateral markings are in the form of black-bordered ocelli and there is a complex dorsal pattern including a pair of dorsolateral stripes, each bearing a series of white spots. The colour pattern of the specimens is consistent with their stemming from Kangaroo Island.

Quoy and Gaimard (1824) described *Scincus compressicauda* from Port Jackson, New South Wales, again without reference to particular specimens, and no type was identified by Guibé (1954). However, the only specimen of *E. whitii* in the MNHP collected by these workers, 2989, is identified in the catalogue and notes accompanying the specimens as the type of *S. compressicauda*. We therefore designate MNHN 2989 as the lectotype of *Scincus compressicauda* Quoy & Gaimard, 1824. This specimen has only 'Nouvelle Hollande' as locality data, but its dorsal colour pattern, with discontinuous dark paravertebral stripes, is consistent with an origin on the New South Wales coast.

When Duméril and Bibron (1839) described *Gongylus* (*Lygosoma*) *moniligera*, they stated that their specimens had been collected by Péron and Lesueur and by Quoy and Gaimard. Guibé (1954) identified MNHP specimens 2988, 2989 and 2992 as syntypes. Cogger *et al.* (1983) suggested that several other specimens may also be types (including MCZ 2133), but only those noted by Guibé are in the collection of the MNHN and attributable to the collectors nominated by Duméril and Bibron. Measurements given by Duméril and Bibron for this species correspond almost exactly to MNHN 2989 (the type of *S. compressicauda*), and we therefore designate this specimen as lectotype also of *Gongylus* (*Lygosoma*) *moniligera* Duméril & Bibron. MNHP 2992 (two specimens) are examples of the 'plain back' colour-pattern morph and were referred to as 'varieté B' by Duméril and Bibron, as opposed to the patterned morph, or 'varieté A'.

Tiliqua leucopsis was described by Gray (1838), evidently from a series of specimens (he makes reference to individual variation in ear lobule number), with no locality data other than New Holland. Rawlinson's notes identify the specimen as a possible lectotype based on it being the first in a series (xv.17a, d–m) that matches the BM collection available to Gray (1845). Cogger *et al.* (1983) identified BMNH xv.17a as the probable holotype; given the implication that Gray had a series of specimens, BMNH xv.17a should be regarded as a lectotype. The specimen's provenance, received from the Paris Museum and coming from Kangaroo Island, ensures that *Tiliqua leucopsis* is a junior synonym of *Scincus whitii*.

The description by Condon (1941) of a new subspecies from Kangaroo Island was clearly based on a misconception regarding the type locality of *whitii*. His subspecies *tenebrosa* is based on SAMA R02161, a plain patterned colour phase typical of many Kangaroo Island specimens.

Wells and Wellington's *Liopholis coplandi* is based on a type series from near Cooma, New South Wales; all specimens have been examined and their morphology indicates that they are conspecific with *E. whitii*.

Diagnosis

A member of the *Egernia whitii* species group (Storr 1968), distinguished by a combination of smooth dorsal scales, an ocellate lateral pattern, dorsal pattern (when present) including a rusty brown vertebral stripe and blackish dorsolateral stripes enclosing single series of cream spots or dashes, moderate midbody scale row counts, normally proportioned interparietal and smooth subdigital lamellae. Geographically proximate (south-eastern highlands) populations further distinguished from the two new species described below by smaller size (maximum SVL 90 mm versus 111 mm).

Description

(From Storr 1968; combines his *E. w. whitei* and *E. w. tenebrosa* descriptions, based on 16 specimens of the former and 262 specimens of the latter.) Longitudinal scale rows at midbody number 30–43 ($\bar{x}$ = 35.3, n = 278), scales smooth. Subdigital lamellae under fourth toe number 17–20 ($\bar{x}$ = 21.5); lamellae often paired under basal phalanx; palms and soles smooth to weakly granular. Nasals separated. Prefrontals separated or in point to broad contact. Frontoparietals paired. Interparietal similar in shape and only slightly smaller than frontal, much longer than wide, separating parietals. Each parietal bordered posteriorly by an enlarged nuchal scale and laterally by an elongate upper secondary temporal scale, this scale separated from the nuchal by a smaller tertiary temporal contacting the posterolateral corner of the parietal. Supraciliaries 5–9, usually 8 ($\bar{x}$ = 6.9). Supralabials 7–9 ($\bar{x}$ = 7.4), the sixth and seventh subocular. Subocular supralabials separated from granular scales of the eyelid by a row of small subocular scales.

SVL 51–113 mm ($\bar{x}$ = 71.2). Hind limb 30–48% SVL ($\bar{x}$ = 37.9%). Tail length/SVL (n = 122) 120–183% ($\bar{x}$ = 1151%).

Colour (in preservative) is light grey to grey brown, most individuals with a complex dorsal colour pattern. Dorsally, there is a reddish tan to brown narrow vertebral stripe from nape to base of tail, flanked on each side by broad blackish laterodorsal stripes. These typically enclose a longitudinal series of cream to yellow spots (Fig. 2*A*). Sometimes the pale spots take the form of dashes, and coalesce to form a longitudinal streak. The sides are grey, variably mottled with blackish flecks. Overlain on this is a pattern of ocelli, each ocellus consisting of several cream scales bordered by an irregular ring of black. A cluster of these markings rises from the axilla (Fig. 2*A*, *B*). The eyelids are creamy yellow, made more prominent by a shadowing of blackish colouring around the eye. A cream streak runs along the upper labials. This colour-pattern element varies in expression, some specimens, especially those from eastern New South Wales, having the stripe very prominent, while many southerly specimens show little trace of it. Animals of the 'plain back' colour morph (Fig. 2*B*) have a completely unmarked dorsum, coloured reddish tan to chocolate brown. Animals with the 'patternless' morph are uniform medium grey, with the back tinged with tan or brown. Young are similar to adults, although often more brightly coloured.

Storr's (1968) account of this species still serves as a complete description of this species, including major patterns of intrapopulation and geographic variation. In size and scalation *E. whitii* completely overlaps the two new species, which show a narrower range of morphological variation commensurate with their narrower geographic and ecological distributions. Storr's material included only a single specimen of one of the new species (NMV D1089).

Colour pattern distinguishes *E. whitii* from the two new species described below. The most consistent difference between *E. whitii* and the other two species is the nature of the lateral pattern with the characteristic ocellate markings. In both of the new species, the sides

have an upper lateral blackish zone forming a longitudinal stripe. Overlying this are one or more roughly longitudinal series of small cream or white spots. There is never an ocellate pattern to these markings. Patternless *E. whitii* are completely unmarked laterally (Fig. 2*C*), which distinguishes them from unpatterned *E. montana*, which also lack lateral spots, but still show a blackish upper lateral stripe.

Distribution

Temperate south-eastern Australia, from south-eastern Queensland, through New South Wales and Victoria, inland to about upper western slopes of the Great Dividing Range, to south-eastern South Australia, as far west as Wedge Island, Spencer Gulf. Also found on many of the Bass Strait islands and through northern and eastern Tasmania.

Ecology

Egernia whitii occupies a wide range of vegetation types, including eucalypt-dominated open-forest, woodland, tussock grassland and open heathland. Most sites where the species has been recorded have rock present in the form of boulders, rock slabs or partially buried blocks. However, this species can also be found in sandy coastal communities and in heavy, cracking soils that lack rocky outcrops. In sandy terrain, *E. whitii* digs burrow systems similar to, but less complex than, those dug by desert *Egernia* species (Pianka and Giles 1982). Studies of the species' ecology have been carried out in Tasmania (Hickman 1960) and Queensland (Milton 1990). This species usually lives in small colonies associated with suitable habitats. It is not unusual to find an adult and juvenile using the same burrow, and much of the species' daily activity is centred on the burrow.

Storr (1968), in discussing geographic variation of *E. whitii* (as currently conceived), partitioned it into two subspecies, *E. w. whitii* for the New South Wales coastal plain from Sydney northwards to Grafton, and *E. w. tenebrosa* from the rest of the species' range. Storr also included his new subspecies, *E. w. modesta*, but this is now regarded as a distinct species (Milton *et al.* 1983). As the above discussion of type material shows, the name *whitii* is based on Kangaroo Island, not east coast populations, and *tenebrosa* is a junior synonym of *whitii*. Cogger *et al.* (1983) continued Storr's subspecific division, correctly applied *whitii* to the southern subspecies, but applied the name *moniligera* to the east coast populations. As the lectotype of *moniligera* is probably an east coast specimen, it would be appropriate to apply this name to an east coast subspecies. However, the senior synonym, *compressicauda*, should replace *moniligera* if an east coast subspecies is recognised. We find little support for such a distinction and prefer not to recognise subspecies of *E. whitii* (see section on *Allozyme variation* below).

Egernia guthega, new species

(Fig. 3*A*)

Holotype

SAMA R37782, collected by W. Osborne, Charlotte Pass, NSW, 36°26′, 148°19′, on 31 October 1988.

Paratypes

New South Wales. SAMA R37781, R37813, same data as holotype; R37772, Guthega, Kosciusko National Park, 36°21′S, 148°25′E, 17 March 1988; R37779–80, Smiggins Holes, 36°24′S, 148°26′E, 31 October 1988; NMV D33986–87, Smiggins Holes, 9 March 1965; D33989, Smiggins Holes, 3 January 1968; D34022–29, Smiggins Holes, 26 March 1966.

Victoria. NMV D15003, Ruined Castle, 36°53′S, 147°16′E; D70909, Pretty Valley Track, 1.2 km SE of Mt McKay, 29 February 2000; D70910–12, Cope Saddle Track, 2.8 km SSE of Mt McKay, 1 March 2000.

Diagnosis

A member of the *Egernia whitii* species group, very similar in most respects to *E. whitii*, but distinguished by the presence of a blackish upper lateral stripe usually overlain by two or three roughly longitudinal series of light grey or cream dots. Adults with complex back pattern similar to that of *E. whitii*, but with only two colours, a greyish background colour and blackish brown pattern. Further distinguished by low numbers of subdigital lamellae (mode <20, cf. >20 for *E. montana* and *E. whitii*) and shorter tail (<140% SVL, cf. >140% SVL)

Description

Longitudinal scale rows at midbody number 35–40 ($\bar{x}$ = 36.2, n = 22), scales smooth. Paravertebral scales number 58–72 ($\bar{x}$ = 63.3). Subdigital lamellae under fourth toe number 17–20 (mode 19); lamellae often paired under basal phalanx; palms and soles smooth. Nasals separated. Prefrontals usually in point to broad contact (frequency of separated prefrontals 20%). Frontoparietals paired. Interparietal similar in shape and only slightly smaller than frontal, much longer than wide, separating parietals. Each parietal bordered posteriorly by an enlarged nuchal scale and laterally by an elongate upper secondary temporal scale, this scale separated from the nuchal by a smaller tertiary temporal contacting the posterolateral corner of the parietal. Supraciliaries 6–10, usually 8 ($\bar{x}$ = 8.0). Supralabials 7–8 ($\bar{x}$ = 7.9), the sixth and seventh subocular. Subocular supralabials separated from granular scales of the eyelid by a row of small subocular scales.

Mean adult size (arbitrarily >75 mm) SVL 97.5 mm (n = 13). Maximum snout–vent length 111 mm. Hind limb (adults) 28–37% SVL ($\bar{x}$ = 33%). Tail length/SVL (subadult to adults, n = 4) 119–131% ($\bar{x}$ = 125%).

Colour (in preservative) is light grey to grey brown, with a complex dorsal colour pattern similar to that in *E. whitii*, but differing in several respects. The pattern is more irregular, with the margins of light and dark longitudinal stripes blurred by flecks and intrusions of the alternate colour. The upper lateral zone is black, as in *E. montana* but unlike *E. whitii*. Overlying the black is one or more longitudinal series of white spots. Young are almost solidly black on the back and sides, with indistinct pale brown vertebral and dorsolateral lines, this pattern overlain by longitudinal series of intense white dots (pink in at least some living animals), but as animals mature these spots and the longitudinal brown lines expand and blur, changing to the dorsal background shade of grey-brown.

Distribution

Known from the Snowy Mountains in the vicinity of Mt Kosciusko, New South Wales, and from the Bogong High Plains, Victoria.

Ecology

Egernia guthega appears to be restricted to high-altitude areas. It has not been recorded below 1600 m altitude and has been observed as high as 1940 m altitude on the Ramshead Range near Mt Kosciusko. The region occupied by this species is the coldest and amongst the wettest on mainland Australia and includes subalpine (1500–1800 m) and alpine environments (above the tree-line, about 1800 m: Costin *et al.* 1979) that are subject to

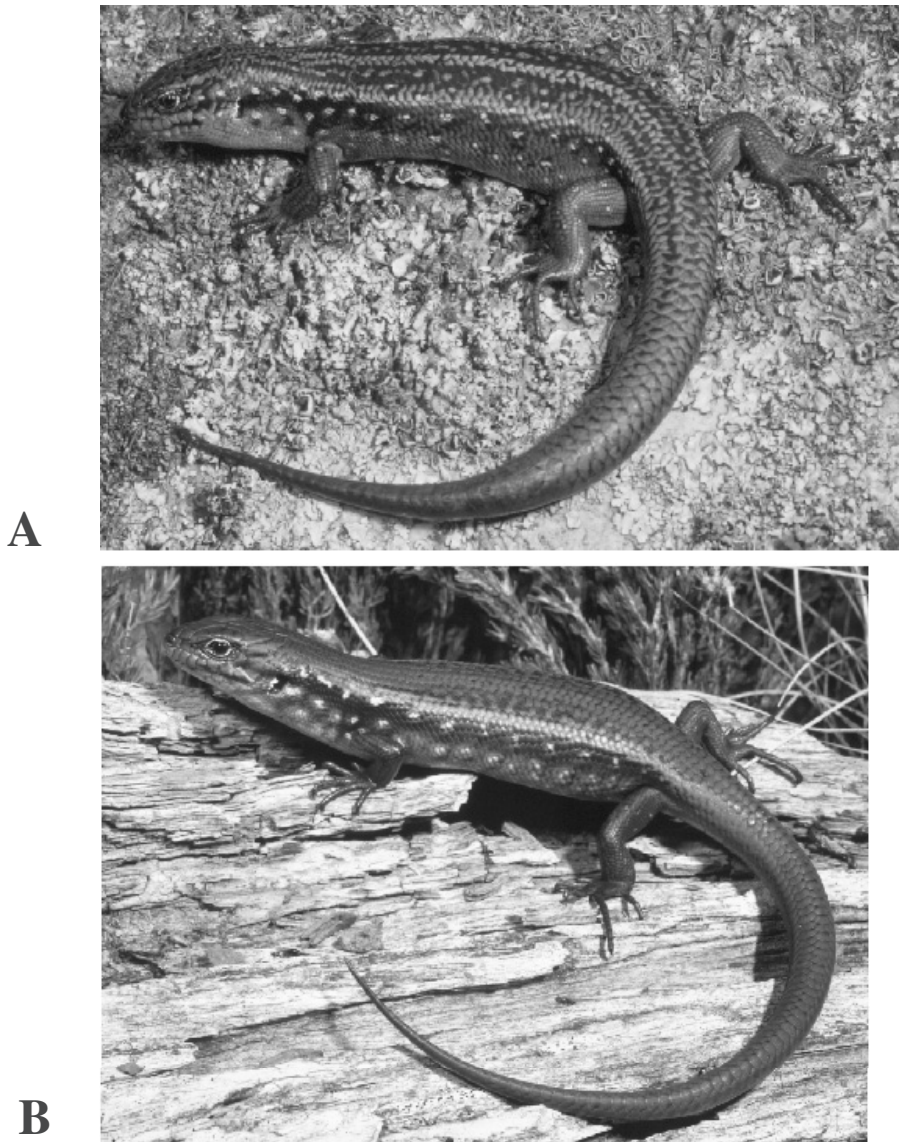

Fig. 3. *A*, *Egernia guthega*, sp. nov., from Smiggin Holes, New South Wales (paratype, SAMA R37780). *B*, *Egernia montana*, sp. nov., from the Mt Hotham area, Victoria (paratype, NMV D56468).

prolonged snow cover in winter. The alpine zone in the Snowy Mountains is characterised by a continuous snow cover for at least four months of the year and 6–8 months with minimum temperatures below freezing (Costin 1957).

Areas preferred by the species are usually rocky or have sub-surface boulders hidden beneath soil or thick vegetation. Such situations include granite rock outcrops, and glacial and peri-glacial deposits such as moraines, boulder fields and blockstreams. Individuals have been recorded in a range of vegetation types, including open snow gum (*Eucalyptus pauciflora*) woodland with grassy or shrubby understoreys, dry tussock grassland, and tall

and short heath. In these areas the lizards live in extensive colonies associated with a deep burrow network that is constructed in the eroded granite and humus soil beneath boulders and shrubs. Both the soil and winter snow cover provide good insulation from cold at these altitudes (Green and Osborne 1994, as the 'Snowy Mountains Rock Skink').

The alpine water skink (*Eulamprus kosciuskoi*) *shares* the same disjunct distribution pattern, with populations in the Snowy Mountains and the Bogong High Plains, although it prefers wet microhabitats (Shea and Peterson 1985; Hutchinson and Rawlinson 1995).

In the morning, when air and substrate temperatures are low, the lizards typically bask at ground level on bare ground, grass tussocks, or open mats of vegetation near their burrow entrances. Later in the day they often bask on the surface of granite boulders, where their dorsal colour pattern provides good camouflage. Known predators include the Australian kestrel (*Falco cenchroides*) and highlands copperhead (*Austrelaps ramsayi*).

The two litters we have observed each comprised three young.

Etymology

Guthega is a Snowy Mountains locality that has yielded a specimen of this species. The specific name is treated as a noun in apposition. Pronunciation stress is on the first syllable.

Egernia montana, new species

(Fig. 3*B*)

Synonymy

Egernia whitei tenebrosa (part) Storr, 1968: 55.

Holotype

SAMA R37767, collected by W. Osborne at Mt Gingera, Brindabella Ranges, ACT, 35°35′S, 148°46′E, on 8 March 1989.

Paratypes

Australian Capital Territory. SAMA R37768, same data as holotype; R37769, Mt Ginini, 35°32′S, 148° 46′E, 8 March 1989; R37770, Ginini Flats, 35°31′S, 148°46′E, 8 March 1989; R37771, Little Ginini, 35°38′S, 148°47′E, 8 March 1989; R37773–74, Mt Scabby summit, 35°46′S, 148°52′E, 17 March 1988; NMV D39220, Mt Ginini, 35°32′S, 148°46′E, 26 January 1971.

New South Wales. SAMA R37809, R37812, Rennix Gap, 36°22′S, 148°31′E, 11 March 1991.

Victoria. SAMA R55349–50, NE Slope of Mt Bogong, 36°44′S, 147°19′E, 6 March 2001; NMV D1089, Upper Yarra, 37°42′S, 145°53′E, March 1873; D33999–34000, Sawyers Hill, 35°54′S, 148°34′E, 2 March 1959; D44844, Bryces Gorge, Licola, 37°38′S, 146°38′E, 30 December 1972; D51135, 1 km E of Saltlick Saddle, 37°18′00″S, 146°28′18″E; D51139, 0.5 km S of The Nobs, Nobs Spur track, 37°20′S, 146°29′E, 19 April 1978; D52832, 7.25 km SE of Stockmans Reward, 37°34′S, 146°04′E, 18 March 1979; D56468, 1.5 km SW of Mt Lock, 1.7 km NE of Mt Hotham, 36°57′S, 147°08′E, 2 January 1983; D56489–90, 0.8 km W of junction of Crowsfoot and Waratah tracks, Rodger River catchment, 37°16′S, 148°32′E, 20 February 1983; D57442, 3.5 km SW of Mt Bendoc, 37°10′S, 148°54′E, 5 November 1984; D57457, 0.3 km NE of Mt Wombargo, 36°56′S, 148°10′E, 2 February 1965.

Diagnosis

A member of the *Egernia whitii* species group, very similar in most respects to *E. whitii*, but distinguished by the presence of a blackish upper lateral stripe usually overlain by two or three roughly longitudinal series of small white or cream dots. Spotted back pattern absent except in some juveniles. Dorsal patterning in adults absent or restricted to two paravertebral zones marbled with brown.

Description

Longitudinal scale rows at midbody number 31–37 ($\bar{x}$ = 34.3, n = 23), scales smooth; 57–62 ($\bar{x}$ = 59.1) paravertebral scales; 19–25 (mode 22) subdigital lamellae under fourth toe; lamellae undivided and palms and soles smooth. Nasals separated. Prefrontals in point to broad contact (one of 23 with separated prefrontals, frequency 4%). Frontoparietals paired. Interparietal distinctly narrower than frontal, much longer than wide, separating parietals. Each parietal bordered posteriorly by an enlarged nuchal scale and laterally by an elongate upper secondary temporal scale, this scale separated from the nuchal by a smaller tertiary temporal contacting the posterolateral corner of the parietal. Supraciliaries 7–9, usually 8 ($\bar{x}$ = 8.1). Supralabials 8, rarely 7 ($\bar{x}$ = 7.9), the sixth and seventh subocular. Subocular supralabials separated from granular scales of the eyelid by a row of small subocular scales.

Adult size attained at approximately 74 mm (smallest breeding female). Mean adult SVL 92.3 mm. Maximum snout–vent length 111 mm. Hind limb 28–41% SVL ($\bar{x}$ = 36%). Tail length/SVL (subadult to adults, n = 8) 145–185% ($\bar{x}$ = 161%).

Colour (in preservative): this species shows weak development of the pattern dimorphism found in the *E. whitii* species group. The basic colour of the head, body, limbs and tail is grey-brown. Most animals are plain-backed with a reddish brown dorsum generally divided by a lighter or more greyish vertebral zone. The patterned morph has a series of dorsolateral blotches or vermiculations, occasionally being sufficiently continuous to outline spots of the underlying brown colouring. Some juveniles and subadults have a longitudinal pattern of alternating dark lines and series of white spots in the dorsolateral area. The upper lateral zone is black, fading to grey ventrolaterally. Running along the upper edge of the black zone is a row of white spots, and a second, even a third series, may also be present. The venter is greyish white. The pattern is highly contrasting in the young, with the pale spots being intense white and the black markings well demarcated, but this diminishes ontogenetically, adults having more obscure patterns.

Distribution

Mountainous areas of the Southern Highlands of New South Wales and the Australian Capital Territory, extending along the Great Dividing Range into Victoria, as far west as the upper Yarra River valley.

Ecology

Egernia montana is apparently a rare species, distributed in a series of isolated pockets. In the north of its range it is found only at high montane and subalpine altitudes, i.e. above 1400 m and as high as 1800 m in the Australian Capital Territory. Specimens from Victoria indicate that at higher latitudes, the species descends to lower altitudes, approximately to about 900 m above sea level.

To date, *E. montana* has been found mostly in areas with granitic geology and has been observed in a wide range of vegetation including tall open-forest, open-forest, woodland and heath (Green and Osborne 1994, as the 'Tan-backed Rock Skink'). Most specimens have been collected from somewhat open areas, for example on the rain-shadowed side of a ridge, with out-cropping boulders or slabs (NMV D56489–90), or on rock screes (NMV D57457). This species lives in colonies and shelters in deep burrow networks that are constructed beneath rocks.

A gravid specimen from Mt Gingera, Australian Capital Territory, gave birth to four young on 16 February 1989. Neonate dimensions were SVL 39.0, 39.5, 39.5, 38.0; tail L 55.0, 57.0, 54.0, 52.0).

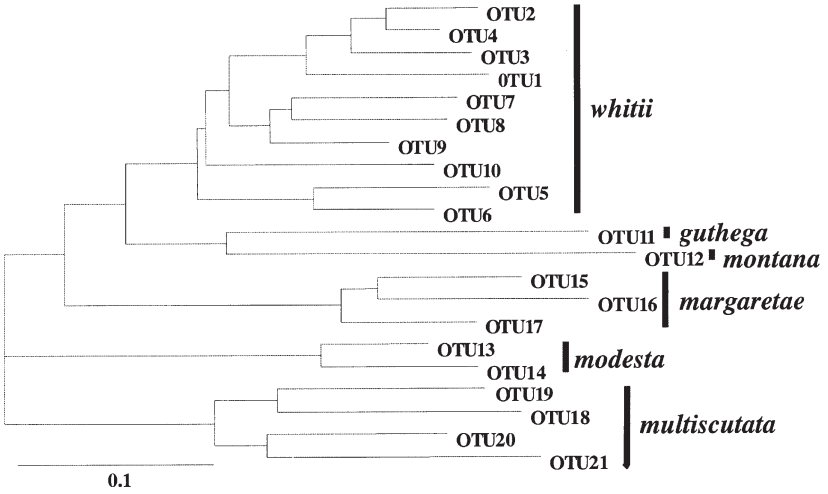

Fig. 4. A Neighbour-Joining phylogram of CSE distances among 21 OTUs of the *Egernia whitii* species group from south-eastern Australia.

Etymology

The Latin adjective *montana* means 'belonging to the mountains'.

Allozyme variation

Allele distributions at the 39 loci resolved are shown in Table 1. These data were converted into matrices of percentages of loci showing fixed differences and CSE distances between OTUs. A fixed difference occurs at a locus when the two populations being compared share no alleles (Richardson *et al.* 1986). Fig. 4 is a neighbour-joining phylogram constructed from CSE distances among OTUs. In the absence of any knowledge about outgroup relationships, the network was rooted at the mid-point of the longest branch, an often-used practice. The OTUs form four groups that reflect current species boundaries within the *E. whitii* species-complex in south-eastern Australia: '*E. whitii*' OTUs 1–12; *E. modesta* OTUs 13–14; *E. margaretae* OTUs 15–17; and *E. multiscutata* OTUs 18–21.

Within the *E. whitii* group, three lineages of OTUs 1–10, 11 and 12, are the most divergent and represent, respectively, *E. whitii*, and the two new species, *E. guthega* and *E. montana*. The patterns of allozyme variation give strong support to the conclusion that OTUs 11 (*E. guthega*) and 12 (*E. montana*) are indeed specifically distinct from each other as well as from *E. whitii*. Four *E. whitii* and three *E. montana* specimens were collected within 200 m of each other on Mt Scabby at the southern end of the Brindabella Range on the Australian Capital Territory–New South Wales border. Our approach to the study of allozyme variation assumes, as a null hypothesis, that the seven individuals were sampled from a single population of a single species in Hardy–Weinberg equilibrium (Richardson *et al.* 1986). We found that the two morphological phenotypes had fixed differences at six loci (Table 1), implying estimated allele frequencies at each locus of p = 0.57 and q = 0.43. The expected proportion of heterozygotes is 2pq, in this case 2 × 0.57 × 0.43 = 0.49. The probability of not obtaining any heterozygotes in a sample of seven individuals simultaneously at the six loci showing fixed allelic differences is $(1 - 0.49)^{6\times7} = 5.2 \times$

Table 2. Genotypes of specimens from Perisher Valley, New South Wales, scored for diagnostic loci only

Taxon	Location	*n*	*Aat-1*	*Est-1*	*Fbp*	*Idh-2*	*Mdh-2*	*Mdhp*	*PepA*	*PepD*
whitii	Jindabyne	1	bb	cc	cc	bb	aa	aa	bb	ee
whitii	Jindabyne	1	bb	cc	cc	bb	aa	cc	bb	ee
whitii	Jindabyne	1	bb	cc	cc	bb	aa	ac	bb	ee
whitii	Jindabyne	1	bd	cc	cc	bb	aa	ac	bb	ee
whitii	Sawpit Ck	2	bd	cc	cc	bb	aa	ac	bb	ee
guthega	Charlottes Pass	1	bb	bb	cc	aa	bb	ff	ab	cc
guthega	Charlottes Pass	1	bb	bb	cc	aa	bb	ff	bb	ce
guthega	Charlottes Pass	1	bb	bb	cc	aa	bb	ff	bb	cc
guthega	Smiggin Holes	2	bb	bb	cc	aa	bb	ff	bb	cc
guthega	Guthega	1	bb	bb	cc	aa	bb	ff	bb	cc
montana	Rennix Gap	1	dd	aa	aa	aa	bb	ee	cc	aa
montana	Rennix Gap	1	dd	aa	aa	ab	bb	ee	cd	aa

10^{-11}%. Thus, the null hypothesis is not supported, and a reasonable alternative hypothesis is that two distinct species are represented. If they are different species, then we would expect that the fixed differences would be maintained at other sympatric localities. This expectation is met on the Ramshead Range, Kosciuszko National Park, where populations separated by 5 km showed fixed differences at the same six loci (Table 1).

All three species, *E. guthega*, *E. montana* and *E. whitii*, occur on the Ramshead Range, just east of Mt Kosciusko, New South Wales, between Sawpit Creek and Charlotte's Pass, a distance of approximately 25 km. Table 2 shows the genotypes of all individuals of the *E. whitii* complex sampled from this transect. These include five specimens collected subsequent to the main allozyme survey, which were typed for eight loci that were diagnostic of the three groups present in the southern highlands of New South Wales. *Egernia whitii* (Sawpit Creek) and *E. guthega* samples (Guthega and Smiggin Holes), collected 14 km apart, have fixed differences at five loci (Table 2). The same *E. guthega* samples have fixed differences at six loci compared with an *E. montana* sample collected at Rennix Gap, 9 km away.

Intraspecific variation

Egernia whitii can be subdivided into four groups on the basis of phenetic analysis of the allozyme data (Fig. 2): an eastern group (OTUs 1–4), including the samples from New South Wales (including Montague Island) and the ACT; a southern group (OTUs 5 and 6), including Flinders Island (Bass Strait) and Tasmania; a south-western group (OTUs 7–9) comprising western Victoria, South Australia and Kangaroo Island; and a fourth comprising the specimen from North Neptune Island (OTU 10). The eastern group has a fixed difference at *Ca* with the mainland populations of the south-western group, but there is a sampling gap of 650 km between the closest samples of each group (Jindabyne and Stoneyford respectively). Further sampling in the intervening region of eastern Victoria is needed to interpret the significance of this single fixed difference. The southern group also shows a fixed difference compared with the eastern group at *Ca*, and differs from both the eastern and the south-western group at *Mdhp*, where the most common allele in the southern group is also unique to that group. The isolated populations on Kangaroo Island and North Neptune Island are polymorphic for the *Ca* alleles that distinguish the eastern group from the remainder.

OTU 10 is represented by one individual with a very boldly contrasting colour pattern from an insular population, North Neptune Island. The Neptune island group includes some

Table 3. Genotypes of variable loci among striped and plain morph *Egernia whitii* from two locations on Kangaroo Island, South Australia

	Aat-1	*Aat-2*	*Acoh*	*Adh-1*	*Ca*	*Dia*	*Est-2*	*Gtdh*	*Gpdh*	*Idh-1*	*Mdhp*	*PepB*	*PepD*	*Pgm-1*
Penneshaw														
Plain (n = 6)	bb	cc	cd	bb	aa	cc	aa	ab	ab	bb	cc	ee	cc	bb
	bb	cc	cc	bb	aa	cc	aa	bb	bb	bb	cc	ee	cc	bb
	bb	cc	cc	ab	aa	cc	aa	ab	ab	bc	cc	ee	cc	bb
	bb	cc	cd	aa	aa	cc	aa	bb	bb	bb	cc	ee	cc	bb
	bb	cc	cc	ab	aa	cc	aa	bb	bb	bb	cc	ee	cc	bb
	bb	cc	cc	aa	–	cc	aa	bb	bb	bb	cc	ee	cc	ab
Striped (n = 3)	bb	cc	cc	bb	aa	cc	aa	bb	bb	bb	cc	ee	cc	bb
	bb	cc	dd	aa	aa	cc	aa	bb	ab	bb	cc	ee	cc	bb
	ab	cc	cc	dd	aa	cc	aa	bb	bb	bb	cc	eg	cc	bb
Dudley CP														
Plain (n = 5)	bb	cc	cc	aa	aa	cc	aa	bb	bb	bb	cc	ee	de	bb
	bb	cc	cc	aa	ab	bc	aa	bb	bb	bb	cc	ee	de	bb
	bb	cc	cc	aa	aa	cc	aa	bb	bb	bb	cc	ee	de	bb
	bb	cc	cc	ab	aa	cc	aa	bb	bb	bb	cc	ee	de	ab
	bb	cc	cc	bb	aa	cc	ac	bb	bb	bb	cc	ee	dd	bb
Striped (n = 5)	bb	cc	cc	bb	–	cc	aa	bb	bb	bb	cc	ee	ee	bb
	bb	bc	cc	ab	aa	cc	aa	bb	bb	bb	cc	ee	dd	bb
	bb	cc	cc	aa	aa	cc	aa	bb	bb	bb	cd	ee	de	bb
	bb	cc	cc	aa	aa	cc	aa	bb	bb	bb	cc	ee	dd	bb
	bb	cc	cc	ab	aa	cc	aa	bb	ab	bb	cc	ee	dd	bb

of the deepest water islets fringing south-eastern Australia and so have been isolated more often and for longer periods (Rawlinson 1974). Isolation, coupled with the small area of the islands may be a sufficient explanation for the differentiation. The strikingly contrasting colour pattern of the North Neptune specimens is almost identical to that of another isolated population restricted to the top of Mt Arapiles in western Victoria. Whether this similarity reflects close genetic relationship or represents convergent phenotypic evolution in similar rocky isolates will require genetic sampling of the Mt Arapiles population. At present, there are insufficient data to reject the hypothesis that the North Neptune and Mt Arapiles specimens are merely locally differentiated *E. whitii* (*sensu stricto*).

We investigated whether there is any genetic differentiation among sympatric samples of plain- and striped-morph *Egernia whitii* from two samples collected from Penneshaw and Dudley Conservation Park on Kangaroo Island. Table 3 summarises the genotypes of the 19 individuals for the 13 loci that were variable among these samples. There was no pattern of genetic heterogeneity that was concordant with dorsal colour pattern. However, there was a fixed difference at the *PepD* locus between the sample locations.

There was also heterogeneity within samples of *E. margaretae* and *E. multiscutata*, but the small sample sizes in each case are insufficient to assess the significance of the apparent fixed differences. There was no evidence to support the taxonomic distinction of the sample of *E. m. multiscutata* from the type locality, Greenly Island, from the other three populations sampled, currently referable to *E. m. bos*.

Discussion

The present study supports the recognition of six species within the *E. whitii* species-complex in south-eastern Australia. This is true regardless of whether the biological, phylogenetic or evolutionary species concept is used. The phenetic analysis of the allozyme data and instances of sympatric distributions demonstrate the presence of a minimum of three biological species within *E. whitii* as previously conceived. The

phylogenetic analysis of the allozyme data is consistent with the recognition of these species under an evolutionary species concept.

Earlier taxonomic practice established subspecies within *E. multiscutata* and *E. whitii*. We find no support for these taxonomic decisions. Re-examination of Storr's (1968) revision shows that the method of analysis (subjective groupings based on proportions and colour pattern) and sampling were unlikely to have succeeded in differentiating clinal from discontinuous variation. Storr (1968) established his east-coast subspecies of *E. whitii* on the basis of its larger size, longer appendages and more broken colour pattern. However, his data demonstrated that many size, colour and proportional changes were clinal in *E. whitii*. The bolder face markings, with prominent lip stripe, and more broken colour pattern seen in adults of coastal NSW populations is also seen in specimens from outside this area, although not usually in combination. Our analysis reveals that the weak evidence for an east-coast subspecies (a fixed difference at *Ca*) would also force the inclusion of other New South Wales populations that share the allele, but have morphologies more like southern *E. whitii* than east-coastal populations. The lack of concordance between the genetic and morphological groups weakens the case for Storr's subspecific arrangement.

Instead, we suggest a more informal treatment of *E. whitii* as a geographically variable species, with different patterns of geographically and genetically discrete variation within *E. whitii*. For example, the south-western and eastern groups are separated by a fixed difference at *Ca*; this disjunction matches a similar fixed difference between highland (eastern) and lowland (western) populations of the skink *Pseudemoia pagenstecheri* reported by Hutchinson and Donnellan (1992). This difference may prove to be illusory, as our samples are remote from each other (700 km apart). The southern group (Tasmania and Flinders Island) has a fixed difference with the eastern group at *Ca*, is nearly fixed for a unique allele at *Mdhp* and is monomorphic for dorsal colour pattern (plain variants absent). This population is also distinguished in having separated prefrontals as the modal condition (Storr 1968). At present, the minor morphological differences are only weakly supported by the allozyme data, given the small sample sizes and low level of allozyme differentiation. Larger samples for molecular genetic study would be required to resolve the status of the Bass Strait–Tasmanian *E. whitii* populations.

Another subdivision within *E. whitii* was that suggested by Milton (1990), who reported departures from random mating between samples of plain and striped-pattern morphs from several locations in eastern Australia. While our samples of plain and striped-pattern morph animals from two locations on Kangaroo Island were too small to reveal statistical differences of the magnitude detected by Milton (1990), they were consistent with random mating and revealed a considerable degree of divergence between locations. Indeed, if samples collected over a large local area were pooled to test for differences in allele frequencies between dorsal colour-pattern types, then statistical differences may be apparent due to population substructuring rather than assortative mating. Milton's (1990) data are not presented in a way that would allow a distinction between these hypotheses.

Our data on differentiation in *E. multiscutata* are scantier, but Storr's supposed differentiation of Greenly Island animals from the rest is not true for all animals we have examined. The colour pattern and hind limb features used by Storr (1968) are inconsistently present in both Greenly Island and other populations, making it impossible to accurately define Storr's subspecies. Storr himself was dubious regarding whether the recognition of subspecies was justified ('… the propriety of subdividing [*Egernia multiscutata*] is not yet certain.': Storr 1968, p. 57). Our genetic data, even though it includes several island

samples, shows no evidence that *E. multiscutata* populations have differentiated in any geographically cohesive way.

This study has largely clarified the systematics of the *E. whitii* species group in south-eastern Australia, leaving only the status of Tasmanian–Bass Strait populations and the degree of genetic differentiation between east-coast and southern Australian *E. whitii* as the two remaining issues to be resolved. A number of issues concerning relationships of populations of the *E. whitii* species group from the western half of the continent also remain to be resolved. Foremost among these are the taxonomic status of the two subspecies of *E. margaretae* and the phylogenetic relationships of the species with predominantly western distributions, *E. multiscutata* and *E. pulchra*, with their eastern relatives.

Acknowledgments

We thank M. Adams, B. Miller, J. Read, R. Sadlier, T. Schwaner, and G. Shea for supplying animals or tissues, Marnie Rawlinson and John Coventry for allowing us access to the papers of the late Peter Rawlinson, which contained data on types held in European museums, and J. Coventry (NMV), R. Sadlier (AMS) and J. Wombey (ANWC) for allowing us to access specimens. This work was supported in part by an Australian Research Council Grant No. D18416251 to M. Adams and P. Baverstock and a La Trobe University CTEC grant to M. Hutchinson. We thank the fauna authorities of the Australian Capital Territory, New South Wales, Victoria, Tasmania and South Australia for permission to collect specimens

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Appendix. Specimens examined electrophoretically

Institution code: AMS, Australian Museum, Sydney; MV, Museum of Victoria; SAMA, South Australian Museum, Adelaide.

Egernia whitii: **OTU 1**: Northern New South Wales: **1a** SAMA R33640, Glen Innes; **1b** SAMA R33641, Point Lookout; **1c** SAMA R34757, Coonabarabran; **1d** AMS R130084, Sandy Hollow; **1e** AMS R130062, Baerami; **1f** AMS R120848–9 Boyd River; **1g** AMS R133156–9, Black Springs. **OTU 2**: AMS R130072–3, Montague Island, NSW. **OTU 3** Snowy Mountains: **3a** SAMA R34684–6, Cooma; **3b** SAMA R37783–6, Jindabyne; **3c** SAMA R37810–1, Sawpit Creek. **OTU 4** ACT: SAMA R37775–8, Mt Scabby, NSW. **OTU 5**: MV D62223-7/9, near Emita, Flinders Island, Tas. **OTU 6**: Tasmania: **6a** MV D62234, 1 km E of West Point; **6b** MV D62230–3, 4 km S of Bracknell. **OTU 7**: Western Victoria/SE South Australia: **7a** MV D62064, Beech Forest, Vic.; **7b** MV D62061–3, Stoneyford, Vic.; **7c** SAMA R23929–30, Blanche Bay; **7d** SAMA R33294, Penola, SA. **OTU 8**: Fleurieu Peninsula, SA: **8a** SAMA R32962–3, 34533, Cherry Gardens; **8b** SAMA R32916, Mylor; **8c** SAMA R34521, Kyeema; **8d** SAMA R34530, Newland Head. **OTU 9**: Kangaroo Island, SA: **9a** SAMA R34781, Cape Hart; **9b** SAMA R34783–4, Cape Willoughby; **9c** SAMA R23572–5, 82/84–7, Penneshaw; **9d** SAMA R34782, 23718–22, 735–9, Dudley CP; **9e** SAMA R23488–9, Vivonne Bay. **OTU 10**: SAMA R27418, North Neptune Island, SA.

Egernia guthega: **OTU 11**: Snowy Mountains: **11a** SAMA R37772, Guthega; **11b** SAMA R37779–80, Smiggin Holes; **11c** SAMA R37781–2, R37813, Charlotte Pass.

Egernia montana: **OTU 12** ACT: **12a** SAMA R37773–4, Mt Scabby; **12b** SAMA R37769, Mt Ginini; **12c** SAMA R37771, Little Ginini; **12d** SAMA R37770, Ginini Flats; **12e** SAMA R37767–8, Mt Gingera; **12f** SAMA R37809/812, Rennix Gap.

Egernia modesta: **OTU 13**: SAMA R33577–8 Bendemeer, NSW. **OTU 14**: **14a** AMS R126118–25, Kings Ck, 10 km W of Denman, NSW; **14b** AMS R130063–4, Merriwa, NSW.

Egernia margaretae: **OTU 15**: SAMA R32943 Yudnamutana, SA. **OTU 16**: SAMA R18562, Devil's Peak, Flinders Ranges, SA. **OTU 17**: SAMA R23267/24815, Mt Remarkable, SA.

Egernia multiscutata: **OTU 18**: SAMA R23947, Greenly I., SA. **OTU 19**: MV D62114, Port Lincoln, SA. **OTU 20**: SAMA R25171–2, Hopkins I., SA. **OUT 21**: SAMA R23583, Penneshaw, Kangaroo I., SA.

Manuscript received 28 September 2001; accepted 13 February 2002