

Molecular phylogeography and systematics of the arid-zone members of the *Egernia whitii* (Lacertilia: Scincidae) species group

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Received 6 November 2003; revised 16 June 2004

Available online 25 September 2004

Abstract

We assembled a molecular phylogeny for the arid-zone members of the *Egernia whitii* species group to test Pianka's [Zoogeography and speciation of Australian desert lizards: an ecological perspective, Copeia (1972) 127–145] hypothesis that habitat specificity to the three major arid-zone vegetation communities is the primary cause of lizard speciation within the arid interior of Australia. This hypothesis predicts that species should exhibit phylogeographic structuring concordant with the major arid-zone vegetation types. Sequence data were obtained from four of the five arid-zone members of the *E. whitii* species group, and from across the ranges of the ecologically generalized *E. inornata* and *E. multiscutata* and the more specialized *E. striata*. We targeted a fragment (696 base pair (bp)) of the mitochondrial genome comprising the 3' half of the ND4 gene. We analysed the data using parsimony, maximum likelihood and Bayesian methods. Our phylogeny confirms the monophyly of the arid-zone members of the species group, although the phylogenetic relationships among species were not fully resolved. Although our topology does not support the recognition of the existing subspecies within *E. multiscutata*, there is a substantial phylogeographic break between South Australian/Victorian (Clade 1) and Western Australian (Clade 2) populations. We found considerable phylogeographic structure within *E. inornata*, with six major clades identified. However, these clades were not concordant with the distribution of habitat types in the arid-zone. Phylogeographic structure was also observed in the more specialized *E. striata*, although our analysis revealed close phylogenetic affinities between the sympatric species *E. striata* and *E. kintorei*. Shimodaira–Hasegawa topology tests were equivocal in regard to whether the phylogeographic structure within *E. striata* was in accordance with Pianka's predictions. Although our data failed to provide strong support for the suggestion that ecological and habitat factors are responsible for the diversification of arid-zone lizards, most *E. inornata* and *E. striata* populations had similar habitats, indicating that adaptation to particular habitats may have some role in the speciation of lizards in the Australian arid-zone.

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Keywords: ND4; Arid Australia; Phylogeography; Lizard; Speciation; Sympatry

1. Introduction

Approximately 70% of the Australian continent is classified as arid or semi-arid, and intriguingly these regions are characterized by a diverse and distinctive vertebrate fauna (reviewed in Barker and Greenslade,

1982). However, rather than representing an expansive homogenous environment, the dry interior of Australia is remarkably heterogenous, comprising a diverse range of distinct vegetation communities, soil types and geographic features (Nix, 1982; Northcote and Wright, 1982; Wasson, 1982; Williams, 1982). Several distinct biogeographic regions exist within arid Australia (e.g. Pianka, 1972; Cracraft, 1991; Crisp et al., 1995). However, relatively few major geographic barriers exist within the interior of the continent; therefore it has been

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suggested that habitat barriers are likely to have shaped the present and historical distributions of faunas in the region (Pianka, 1972; reviewed in Barker and Greenslade, 1982).

The arid interior of Australia contains a large and diverse reptilian fauna, with several regions characterized by an inordinate number of coexisting species (Pianka, 1972, 1981, 1984; Witten, 1982; Cogger, 2000; James and Shine, 2000). Many desert lizards have been demonstrated to have highly specific habitat requirements, and the distributions of numerous taxa are closely linked with particular vegetation or soil types (Pianka, 1972, 1981, 1984; James and Shine, 2000). Several authors have attempted to correlate the biogeographic and distributional patterns observed in arid-zone lizard taxa to a variety of features in order to elucidate the mechanisms responsible for the observed diversification and species diversity within the arid-zone (Pianka, 1972, 1981, 1984; James and Shine, 2000). Pianka (1972) proposed a model for lizard diversification and speciation based on adaptation to local vegetation communities, with dispersal between habitats restricted to a limited number of corridors. He hypothesized that the diversification and eventual speciation of lizards within the arid interior of the continent was the result of the historical fluctuation of the boundaries of the major habitat types to which lizards had become adapted. Although much is known about the biogeography of the arid-zone lizards, there have been relatively few attempts to examine Pianka's (1972) hypothesis using phylogenetic information. However, it should be possible to use a phylogeographic approach to test the hypothesis of Pianka (1972), with the predication that arid-zone lizards should exhibit phylogeographic structuring concordant with the distribution of the major vegetation communities in central Australia. Here we present such an approach using a group of arid-zone scincid lizards.

The Australian scincid genus *Egernia* comprises 30 species of medium to large sized lizards, several of which occur within the arid-zone (Cogger, 2000; Chapple, 2003). The *Egernia whitii* species group comprises 11 species and forms a clade within the genus (Chapple, 2003; Chapple and Keogh, 2004; Donnellan et al., unpublished data). Five species within this species group are obligate-burrowers, four of which have distributions restricted to the arid-zone (*E. inornata*, *E. kintorei*, *E. striata*, *E. slateri*; Cogger, 2000; Chapple, 2003; Fig. 1). Although *E. multiscutata* occurs in semi-arid habitats in certain parts of its range, it is primarily found in coastal areas and on offshore islands (Cogger, 2000; Chapple, 2003; Fig. 1). All five species exhibit several adaptations for living in arid conditions such as the construction of burrows and reduced rates of evaporative water loss compared to the more temperate members of the species group (Henzell, 1972, 1982). *Egernia inornata*, *E. kintorei* and *E. striata* also display restricted

activity patterns (i.e. crepuscular or nocturnal; Henzell, 1972, 1982), and the latter two species possess an elliptical eye to enable them to forage at night (Cogger, 2000; Pearson et al., 2001; Chapple, 2003).

Egernia multiscutata is composed of two subspecies, *E. m. multiscutata*, which is restricted to Greenly Island, South Australia (Mitchell and Behrndt, 1949), and *E. m. bos*, which occurs in the remainder of the range (Storr, 1960, 1968, 1978). However, the validity of these two subspecies has been questioned recently (Donnellan et al., 2002). A disjunct population of *E. multiscutata* occurs in north-western Victoria and is currently listed as critically endangered in Victoria (Coventry and Robertson, 1980; Chapple, 2003); however, the taxonomic affinities of this population are currently unknown.

Despite earlier suggestions that the arid-zone members of the *E. whitii* species group arose as a result of multiple periods of colonization by more temperate species (e.g. Horton, 1972), it appears that the four arid-zone species arose from a single common ancestor, which was presumably closely related to the coastal or semi-arid *E. multiscutata* (Chapple and Keogh, 2004). These five obligate-burrowing species constitute a well-supported subgrouping within the species group (Chapple and Keogh, 2004) enabling examination of speciation and biogeographic patterns within a phylogenetic framework.

Pianka (1972) identified eight biogeographic regions within the arid-zone, but believed that sand ridge, shrub-*Acacia* and sand plain-*Triodia* (spinifex) were particularly important habitats due to large numbers of species that have become specialized to these habitats. Here we consider three members of the *E. whitii* species group that have distributions restricted entirely to the arid-zone (Cogger, 2000; Wilson and Swan, 2003). Pianka (1972) listed *E. striata* and *E. kintorei* as habitat specialists restricted to sand plain-*Triodia* regions and *E. inornata* as a more generalized species with a primarily southern arid-zone distribution across several habitat types. *Egernia striata* and *E. kintorei* occur sympatrically and are restricted to arid sand plains and inter-dunes in close association with spinifex (*Triodia*) grasslands (Cogger, 2000; Wilson and Swan, 2003). Both species presumably have a continuous distribution (present or historic) from the central interior of Western Australia to southern Northern Territory and northwest Western Australia (Cogger, 2000; McAplin, 2001; Wilson and Swan, 2003; Fig. 1). *E. inornata* has a wide distribution that extends from the southern interior of Western Australia to southern Northern Territory, South Australia, north-western Victoria, western New South Wales and south-west Queensland (Cogger, 2000; Wilson and Swan, 2003; Fig. 1). However, *E. inornata* occurs across a wide range of habitats, but is primarily associated with semi-arid to arid sand ridges or sand plains in hummock grasslands and mallee woodland (Cogger, 2000; Wilson and Swan, 2003).

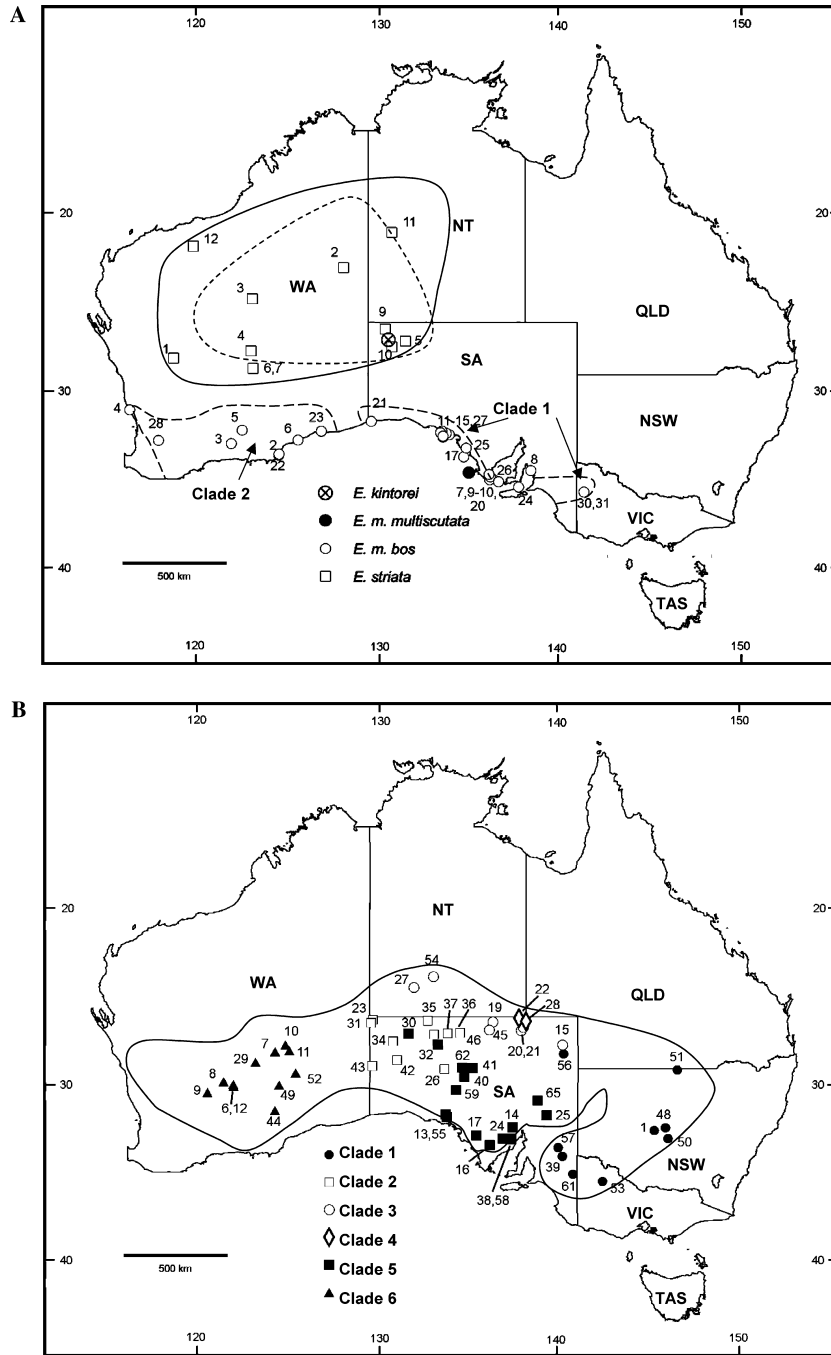


Fig. 1. Map showing the collecting localities of the tissue samples from the arid-zone members of the *Egernia whittii* species group presented in Table 1. (A) Locality of tissue samples for *E. multiscutata*, *E. striata* and *E. kintorei*. The distributions of *E. striata* (solid line), *E. kintorei* (short-dashed line) and *E. multiscutata* (long-dashed line) are shown (adapted from Wilson and Swan, 2003). The distribution of populations within the two major clades of *E. multiscutata* are indicated, with the split between clades occurring near the South Australian–Western Australian border (refer to Table 1 and Fig. 3 for more detail). (B) Locality of tissue samples for *E. inornata* showing the approximate distribution of each of the 6 clades identified in Fig. 3 and Table 2. The overall distribution of *E. inornata* is shown (adapted from Wilson and Swan, 2003). State codes are: WA, Western Australia; NT, Northern Territory; SA, South Australia; QLD, Queensland; NSW, New South Wales; VIC, Victoria; TAS, Tasmania.

Pianka (1972) proposed that local adaptation to the three important vegetation communities within the arid-zone (Fig. 2), and the subsequent diversification of taxa within each region, are the primary mechanisms responsible for the diversification of arid-zone reptiles.

If this hypothesis is correct then *E. inornata* (southern arid-zone generalist) and *E. striata* (sandplain-*Triodia* specialist) should exhibit phylogeographic structuring concordant with the major vegetation communities in the arid-zone. Specifically, adaptation to alternative

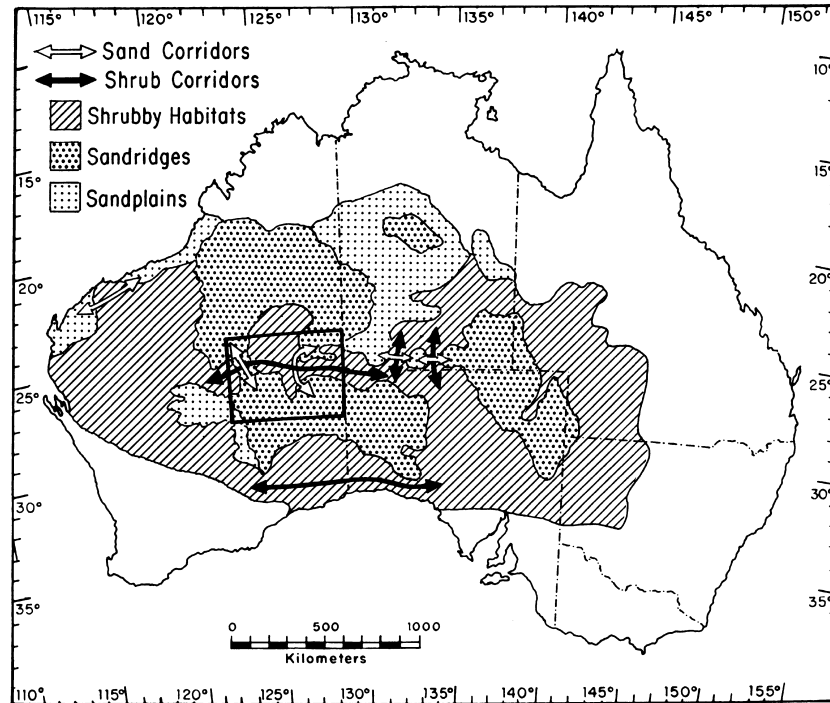


Fig. 2. Pianka's (1972) map displaying the distribution of sandplains, sandridges, and shrub–*Acacia* habitats in the Australian arid-zone. The presumed dispersal corridors between habitats are shown. Note. The northern horizontal solid line represents the Giles Corridor. (Figure reproduced with permission from the American Society of Ichthyologists and Herpetologists.)

habitats should act to reduce gene flow between habitat types resulting in more genetic divergence between rather than within habitat types. To test this hypothesis we utilized mtDNA sequence data to generate a phylogeny for the obligate-burrowing and arid-zone members of the *E. whitii* species group. Our aim was to examine the phylogenetic relationships between geographic subdivisions within *E. inornata*, *E. striata* and *E. multiscutata* and to utilize the phylogenetic information generated to infer speciation and biogeographic patterns within the Australian arid-zone and test the predictions of Pianka's (1972) habitat model of speciation. We also sought to resolve several systematic issues within the *E. whitii* species group, including the: (1) validity of the two recognized subspecies of *E. multiscutata*; and (2) taxonomic status of the critically endangered Victorian population of *E. multiscutata*.

2. Materials and methods

2.1. Taxonomic sampling

We obtained tissues samples from four of the five obligate-burrowing species within the *E. whitii* species group (Table 1). Samples were obtained primarily from museum tissue collections, although three additional tail-clip samples obtained from live animals were included (Table 1). No tissue samples were available for

either subspecies of *E. slateri* (*E. s. virgata* is presumed extinct), which is listed as critically endangered and has disappeared from most of its previously known localities (Chapple, 2003). Likewise, we included only one sample from *E. kintorei*, which is listed nationally as endangered (Chapple, 2003). However, we obtained samples that encompassed the entire range of *E. multiscutata* (28 samples), *E. striata* (11 samples) and *E. inornata* (55 samples) (Table 1, Fig. 1). Several of the *Egernia* species included as part of this study also were included in a broader phylogenetic study of relationships within the *Egernia* group (Donnellan et al., unpublished data). Based on that work, we chose two *Egernia* species (*E. saxatilis* and *E. major*) as outgroups, and we also included a more distantly related (see Reeder, 2003) Australian Sphenomorphus Group skink (*Eulamprus heatwolei*) as the outgroup in all analyses (Table 1).

2.2. DNA extraction, amplification and sequencing

Total genomic DNA was extracted from liver, toe or tail samples using a modified hexadecyl-trimethylammoniumbromide (CTAB) protocol. For each sample we targeted an approximately 700 bp DNA fragment of the mitochondrial genome, which included the 3' half of the ND4 gene and most of the tRNA cluster containing the Histidine, and Serine tRNA genes. This region was targeted because work at comparable taxonomic levels in other squamate groups has indicated useful lev-

Table 1
Museum registration numbers, GenBank accession numbers and locality data for taxa used in this study

Species	Museum Tissue No.	Voucher No.	GenBank Accession No.	Locality
<i>Egernia inornata</i> (EI1)	ANWC 5588		AY612922	Yathong NR, 130 km S Cobar, NSW
<i>Egernia inornata</i> (EI6)	WAM 103905		AY612926	Comet Vale, WA
<i>Egernia inornata</i> (EI7)	WAM 84526		AY612924	Cosmo Newberry, WA
<i>Egernia inornata</i> (EI8)	WAM 108240		AY612935	Riverina HS, WA
<i>Egernia inornata</i> (EI9)	WAM 126439		AY612930	Bungalbin Sandplain, WA
<i>Egernia inornata</i> (EI10)	WAM 84578		AY612929	North Lake Throssell, WA
<i>Egernia inornata</i> (EI11)	WAM 114536		AY612907	Yeo Lake HS, WA
<i>Egernia inornata</i> (EI12)	WAM 129954		AY612917	Goongarrie Station, WA
<i>Egernia inornata</i> (EI13)	ABTC 53869	SAMAR 31965	AY612910	Yumberra CP, SA
<i>Egernia inornata</i> (EI14)	ABTC 53888	SAMAR 19917	AY612934	Cariewerloo Station, Eyre Peninsula, SA
<i>Egernia inornata</i> (EI15)	ABTC 53960	SAMAR 53960	AY612903	Coopers Creek Area, SA
<i>Egernia inornata</i> (EI16)	ABTC 53963	SAMAR 24809	AY612905	SE corner Hambidge NP, SA
<i>Egernia inornata</i> (EI17)	ABTC 53993	SAMAR 28475	AY612898	30 km NNE Minnipa, SA
<i>Egernia inornata</i> (EI19)	ABTC 524	SAMAR 35936	AY612928	0.5 km W Purni Bore, SA
<i>Egernia inornata</i> (EI20)	ABTC 38593	SAMAR 51383	AY520465	22.5 km WSW Haines Hill Simpson Desert, SA
<i>Egernia inornata</i> (EI21)	ABTC 38673	SAMAR 51346	AY612901	13.6 km WNW Beal Hill Simpson Desert, SA
<i>Egernia inornata</i> (EI22)	ABTC 38733	SAMAR 51408	AY612937	13.1 km WNW Approdinna Attora Knolls, SA
<i>Egernia inornata</i> (EI23)	ABTC 58277	SAMAR 45970	AY612939	26 km S Pipalyatjara, SA
<i>Egernia inornata</i> (EI24)	ABTC 58320	SAMAR 46017	AY612925	Lake Gilles CP, SA
<i>Egernia inornata</i> (EI25)	ABTC 58557	SAMAR 48623	AY612946	1.5 km NW Kunoths Dam, SA
<i>Egernia inornata</i> (EI26)	ABTC 884	SAMAR 42546	AY612927	11.5 km ENE Tallaringa Well, SA
<i>Egernia inornata</i> (EI27)	ABTC 12609		AY612909	28 km S Kings Creek HS, NT
<i>Egernia inornata</i> (EI28)	ABTC 38373	SAMAR 50957	AY612920	12.7 km ESE Carruthers Hill, SA
<i>Egernia inornata</i> (EI29)	ABTC 41326		AY612908	134 km ENE Laverton, WA
<i>Egernia inornata</i> (EI30)	ABTC 41749	SAMAR 45431	AY612947	14.2 km ESE Maryinna Hill, SA
<i>Egernia inornata</i> (EI31)	ABTC 41820	SAMAR 46097	AY612945	18 km SE Kunatjara, SA
<i>Egernia inornata</i> (EI32)	ABTC 41912	SAMAR 47454	AY612914	1.4 km E Oolarinna East Bore, SA
<i>Egernia inornata</i> (EI34)	ABTC 42090	SAMAR 48824	AY612948	4.5 km NE Mt. Cheesman, SA
<i>Egernia inornata</i> (EI35)	ABTC 42234	SAMAR 50219	AY612916	0.7 km WNW Donald Well Hill, SA
<i>Egernia inornata</i> (EI36)	ABTC 42312	SAMAR 51241	AY612897	9.4 km SSW Granite Downs HS, SA
<i>Egernia inornata</i> (EI37)	ABTC 42445	SAMAR 51627	AY612911	31.5 km ENE Mimili, SA
<i>Egernia inornata</i> (EI38)	ABTC 57028	SAMAR 37954	AY612915	2 km N Mt. Middleback North, SA
<i>Egernia inornata</i> (EI39)	ABTC 57155	SAMAR 38356	AY612942	Pooginook CP, 2.3 km W of NE corner, SA
<i>Egernia inornata</i> (EI40)	ABTC 57332	SAMAR 39985	AY612913	Lake Phillipson on Long Creek, SA
<i>Egernia inornata</i> (EI41)	ABTC 59633	SAMAR 43808	AY612923	2 km W Dog Fence, SA
<i>Egernia inornata</i> (EI42)	ABTC 59643	SAMAR 43826	AY612938	41 km W Vokes Hill Junction, Unnamed CP, SA
<i>Egernia inornata</i> (EI43)	ABTC 59645	SAMAR 43803	AY612904	Serpentine Lakes Edge, SA
<i>Egernia inornata</i> (EI44)	ABTC 61607	SAMAR 65868	AY612944	1.1 km NE Buningtonia Springs, WA
<i>Egernia inornata</i> (EI45)	ABTC 73565	SAMAR 52799	AY612949	27.5 km SE Oolgawa Waterhole, SA
<i>Egernia inornata</i> (EI46)	ABTC 73579	SAMAR 52829	AY612900	12.6 km NNE Lambina Station, SA
<i>Egernia inornata</i> (EI48)	ABTC 3656	SAMAR 33520	AY612902	Round Hill, NSW
<i>Egernia inornata</i> (EI49)	ABTC 10483		AY612943	Officer Basin, 300 km NE Kalgoorlie, WA
<i>Egernia inornata</i> (EI50)	ABTC 11442	AMSR 97887	AY612899	Mt. Hope, NSW
<i>Egernia inornata</i> (EI51)	ABTC 11445	AMSR 106840	AY612933	Widgee Downs, NSW
<i>Egernia inornata</i> (EI52)	ABTC 21742	WAMR 92005	AY612941	60 km SE Blue Robin Hill, WA
<i>Egernia inornata</i> (EI53)	ABTC 23246	NMVD 66575	AY612936	Wathe Fauna Reserve, VIC
<i>Egernia inornata</i> (EI54)	ABTC 30281	NTMR 18298	AY612912	Finke Gorge NP, NT
<i>Egernia inornata</i> (EI55)	ABTC 35091	SAMAR 45573	AY520466	3.5 km SE Inila Rockwater, SA
<i>Egernia inornata</i> (EI56)	ABTC 35484	SAMAR 46022	AY612931	Approx. 30 km SE Moomba Gas Field, SA
<i>Egernia inornata</i> (EI57)	ABTC 39867	SAMAR 41669	AY612918	Hideaway Hut, SA
<i>Egernia inornata</i> (EI58)	ABTC 57449	SAMAR 40717	AY612940	Cooks North, Middleback Ranges, SA
<i>Egernia inornata</i> (EI59)	ABTC 57901	SAMAR 44350	AY612906	Mulgathing Station, SA
<i>Egernia inornata</i> (EI61)	ABTC 58100	SAMAR 45249	AY612921	E boundary Karte CP, SA
<i>Egernia inornata</i> (EI62)	ABTC 58792	SAMAR 51143	AY612919	Mabel Creek Station, SA
<i>Egernia inornata</i> (EI65)	ABTC 74047		AY612932	5.5 km W Warraweena HS, SA
<i>Egernia kintorei</i> (EO6)	ABTC 67672		AY520468	Pitlands Survey, SA
<i>Egernia multiscutata multiscutata</i> (EU19)	ABTC 17379	SAMAR 38268	AY520481	Greenly Island, SA
<i>Egernia multiscutata bos</i> (EU2)	WAM 77912		AY612972	Point Dempster, WA
<i>Egernia m. bos</i> (EU3)	WAM 140942		AY612968	Peak Eleanor, WA
<i>Egernia m. bos</i> (EU4)	WAM 108949		AY612962	Lancelin Island, WA

(continued on next page)

Table 1 (continued)

Species	Museum Tissue No.	Voucher No.	GenBank Accession No.	Locality
<i>Egernia m. bos</i> (EU5)	WAM 135225		AY612973	Norseman, WA
<i>Egernia m. bos</i> (EU6)	WAM 77762		AY612979	Toolinna Rockhole, WA
<i>Egernia m. bos</i> (EU7)	ABTC 53829	SAMAR 27529	AY612970	Thistle Island, SA
<i>Egernia m. bos</i> (EU8)	ABTC 53851	AMSR 115708	AY612967	Port Prime, SA
<i>Egernia m. bos</i> (EU9)	ABTC 53861		AY612961	Williams Island, SA
<i>Egernia m. bos</i> (EU10)	ABTC 53882	SAMAR 19407	AY612963	Taylor Island, SA
<i>Egernia m. bos</i> (EU11)	ABTC 53907	SAMAR 21730	AY612980	Franklin Island East, SA
<i>Egernia m. bos</i> (EU12)	ABTC 53912	SAMAR 21808	AY612977	Evans Island, SA
<i>Egernia m. bos</i> (EU13)	ABTC 53917	SAMAR 21874	AY612975	Purdie Island, SA
<i>Egernia m. bos</i> (EU14)	ABTC 53919	SAMAR 21884	AY612974	Goat Island, SA
<i>Egernia m. bos</i> (EU15)	ABTC 53921	SAMAR 21924	AY612981	Fenelon Island, SA
<i>Egernia m. bos</i> (EU16)	ABTC 53952	SAMAR 23194	AY612965	North Island, Gambier Group, SA
<i>Egernia m. bos</i> (EU17)	ABTC 54015	SAMAR 31315	AY612971	Flinders Island, SA
<i>Egernia m. bos</i> (EU20)	ABTC 69271	SAMAR 53552	AY612976	13 km ESE Port Lincoln, SA
<i>Egernia m. bos</i> (EU21)	ABTC 1300	AMSR 107938	AY612983	16 km E SA/ WA Border, SA
<i>Egernia m. bos</i> (EU22)	ABTC 11459	AMSR 96632	AY612966	Near Israelite Bay, WA
<i>Egernia m. bos</i> (EU23)	ABTC 21716	WAMR 92010	AY520480	6 km N Eyre, WA
<i>Egernia m. bos</i> (EU24)	ABTC 33356	SAMAR 37405	AY612960	Kangaroo Island, SA
<i>Egernia m. bos</i> (EU25)	ABTC 57583	SAMAR 41967	AY612969	Venus Bay CP, SA
<i>Egernia m. bos</i> (EU26)	ABTC 57608	SAMAR 42091	AY612982	Wedge Island, SA
<i>Egernia m. bos</i> (EU27)	ABTC 58895	SAMAR 52362	AY612964	East end St. Francis Island, SA
<i>Egernia m. bos</i> (EU28)	ABTC 63470	WAMR 132277	AY612978	Dryandra, WA
<i>Egernia m. bos</i> (EU30)			AY612984	Wyperfeld NP, VIC
<i>Egernia m. bos</i> (EU31)			AY612985	Wyperfeld NP, VIC
<i>Egernia striata</i> (ES1)	WAM 127245		AY612953	130 km NW Mt. Magnet, WA
<i>Egernia striata</i> (ES2)	WAM 131145		AY612958	Pollock Hills, WA
<i>Egernia striata</i> (ES3)	WAM 102790		AY612954	Little Sandy Desert, WA
<i>Egernia striata</i> (ES4)	WAM 132191		AY612956	Duketon, WA
<i>Egernia striata</i> (ES5)	ABTC 58180	SAMAR 45402	AY612959	10.5 km E Ampeinna Hills, SA
<i>Egernia striata</i> (ES6)	ABTC 41247		AY612952	38 km ENE Laverton, WA
<i>Egernia striata</i> (ES7)	ABTC 41342		AY612950	134 km ENE Laverton, WA
<i>Egernia striata</i> (ES9)	ABTC 42030	SAMAR 48701	AY520469	1.8 km NNW Mt. Lindsay, SA
<i>Egernia striata</i> (ES10)	ABTC 42092	SAMAR 48829	AY612955	15.7 km NW Mt. Cheesman, SA
<i>Egernia striata</i> (ES11)	ABTC 60818		AY612951	30 km SW Sangster's Bore, NT
<i>Egernia striata</i> (ES12)	ABTC 61870	WAMR 103994	AY612957	Woodstock Station, WA
<i>Egernia major</i> (EO1)	ANWC 5298		AY520464	Nana Creek, near Coffs Harbour, NSW
<i>Egernia saxatilis</i> (EO2)			AY520463	Booroomba Rocks, ACT
<i>Eulamprus heatwolei</i> (EH40807)	ABTC 57494	SAMAR 40807	AY520462	20.3 km N Abercrombie River, NSW

Museum acronyms as follows: ABTC, Australian Biological Tissue Collection; SAM, South Australian Museum, Adelaide; WAM, Western Australian Museum; ANWC, Australian National Wildlife Collection, CSIRO, NTM, Northern Territory Museum and Art Gallery, Darwin, NMV, Museum Victoria, Melbourne.

els of variability (Benabib et al., 1997; Forstner et al., 1995; Scott and Keogh, 2000; Keogh et al., 2003).

The primers used to amplify this region were EgND4(L), EgtRNA-Ser(H) (Chapple and Keogh, 2004), ND4 and Leu (Forstner et al., 1995). Sequencing was performed as described in Chapple and Keogh (2004). Sequence data were edited using Sequencher 3.0 (Genes Codes Coporation), and provisionally aligned using the default parameters of ClustalX (Thompson et al., 1997) and refined by eye. Following elimination of alignment gaps, aligned sequences then were translated into amino acid sequences using the vertebrate mitochondrial genetic code. This was done to determine if these data were truly mitochondrial in origin. No premature stop codons were observed therefore we conclude that all sequences obtained are true mitochondrial copies.

2.3. Phylogenetic analyses

We took a broad approach to analysing the data and used a variety of phylogenetic techniques. We used unweighted and weighted parsimony, maximum-likelihood (ML) and Bayesian approaches to analyse the data and looked for agreement among the various alternative methods. For our weighted parsimony analyses we used the empirical Ti/Tv ratio of 4:1. We used the objective criteria provided by the computer program ModelTest 3.06 (Posada and Crandall, 1998) with the Hierarchical Likelihood Ratio Test (hLRT) to select the most appropriate model of molecular evolution for our data. We used the ModelTest estimates of the empirical nucleotide frequencies, substitution rates, gamma distribution, and proportion of invariant sites (I) in our ML analyses implemented in PAUP* (Swofford, 2002).

We used the computer program MrBayes (v3.0b4; Huelsenbeck and Ronquist, 2001) for our Bayesian analyses. Using the identical data set as our ML analyses, the General Time Reversible (GTR) + gamma distribution + proportion of invariant sites parameters were all estimated from the data during the run. We used the default value of four Markov chains per run and also ran the full analysis five times to make sure overall tree-space was very well sampled and to avoid getting trapped in local optima. We ran our analysis for a total 2,000,000 generations and sampled the chain every 100 generations, resulting in 20,000 sampled trees. Log-likelihood values reached a plateau after approximately 200,000 generations, and we discarded the first 4000 trees as the burn-in phase and used the remaining trees to estimate Bayesian posterior probabilities.

We used the bootstrap values and Bayesian posterior probabilities to assess branch support. Our data set was too large to do ML bootstraps, and so we performed a weighted parsimony bootstrap using the observed ti/tv ratio of 4:1 with 1000 pseudoreplicates. In addition, Bayesian analysis provided posterior probabilities for branches. The use of posterior probabilities to assess branch support is still rather new (Holder and Lewis, 2003), and some issues have been raised with regard to how they compare to bootstrap values (Suzuki et al., 2002; Douady et al., 2003; Alfaro et al., 2003), but they serve as an additional source of information on branch support and may represent a better estimate of phylogenetic accuracy (Wilcox et al., 2002; Reeder, 2003). As a rough guide, we consider branches supported by bootstrap values greater than or equal to 70% (Hillis and Bull, 1993) and posterior probability values greater than or equal to 95% (Wilcox et al., 2002) to be significantly supported by our data, but acknowledge that there are diverse opinions concerning how to interpret these values (Simmons et al., 2004).

2.4. Hypothesis testing

We tested the significance of log-likelihood differences between our optimal ML/Bayesian tree (using ML–ln L) and topologies representing various alternative hypotheses with the Shimodaira–Hasegawa test in PAUP* (Shimodaira and Hasegawa, 1999; see also Goldman et al., 2000) using full optimisation and 1000 replicates. We tested hypotheses relating to the subspecies status of *E. multiscutata* and assessed the support for the various *E. striata* and *E. inornata* topologies predicted under Pianka's (1972) habitat model of arid-zone speciation. We tested alternative topologies where:

(1) The existing subspecies *E. multiscutata multiscutata* (Greenly Island, EU19) and *E. m. bos* (remainder of the range) were sister clades (i.e. valid subspecies).

(2) *E. striata* comprised three clades corresponding to the three major arid-zone habitats identified in Fig. 2 (shrub habitat, sandridges, sandplains).

(3) *E. striata* sandplain/sandridge populations north and south of the shrub corridor (see Fig. 2) each formed clades;

(4) *E. inornata* comprised three clades corresponding to the three major arid-zone habitats identified in Fig. 2 (shrub habitat, sandridges, sandplains).

3. Results

The edited alignment comprised 696 characters and of these, 321 (46%) were variable and of these variable sites, 237 (34%) were informative under parsimony. Within the ingroup only, 286 characters were variable of which 228 were informative under parsimony.

The hLRT from ModelTest supported the general time reversible (GTR) plus invariant sites (+I) plus gamma shape (+G) model as the best-fit substitution model for the data and gave a $-\ln L = 5476.1206$. The estimated parameters were as follows: nucleotide frequencies $A = 0.3673$, $C = 0.3158$, $G = 0.0915$, $T = 0.2254$; substitution rates $A \leftrightarrow C$ 0.8805, $A \leftrightarrow G$ 20.6963, $A \leftrightarrow T$ 0.6825, $C \leftrightarrow G$ 0.5328, $C \leftrightarrow T$ 7.8919, $G \leftrightarrow T$ 1.0000; proportion of invariant sites = 0.4453; gamma shape parameter = 1.0768. The Bayesian analysis produced parameter estimates that were very similar to those produced by ModelTest.

The unweighted parsimony analysis, the weighted parsimony analysis, the ML analysis using the above parameters and the Bayesian analysis all yielded almost identical optimal trees (ML – ln L = 5585.61145, Bayesian –ln L was higher at 5788.71; Fig. 3, only ML tree shown). Fig. 3 shows a conservative tree with weak branches collapsed. The monophyly of each of the four recognized species (*E. inornata*, *E. multiscutata*, *E. striata* and *E. kintorei*) within the obligate-burrowing subgroup was supported by extremely high bootstrap values (92–99%) and posterior probabilities (99–100%). However, these data fail to resolve the phylogenetic relationships among species, apart from confirming the close relationship between *E. striata* and *E. kintorei* (bootstrap value 92%, posterior probability 100%). There appears to be a substantial degree of genetic differentiation between the obligate-burrowing species with each species separated by genetic distances between 8.5% and 16.1% (Table 2).

Considerable phylogeographic structure is evident in *E. inornata*, *E. multiscutata* and *E. striata*. Six major clades are identified within *E. inornata* (Figs. 1 and 3). Genetic divergence between the clades of *E. inornata* is in the range of 3.5–6.1% (Table 2), while the divergence observed within each clade is around

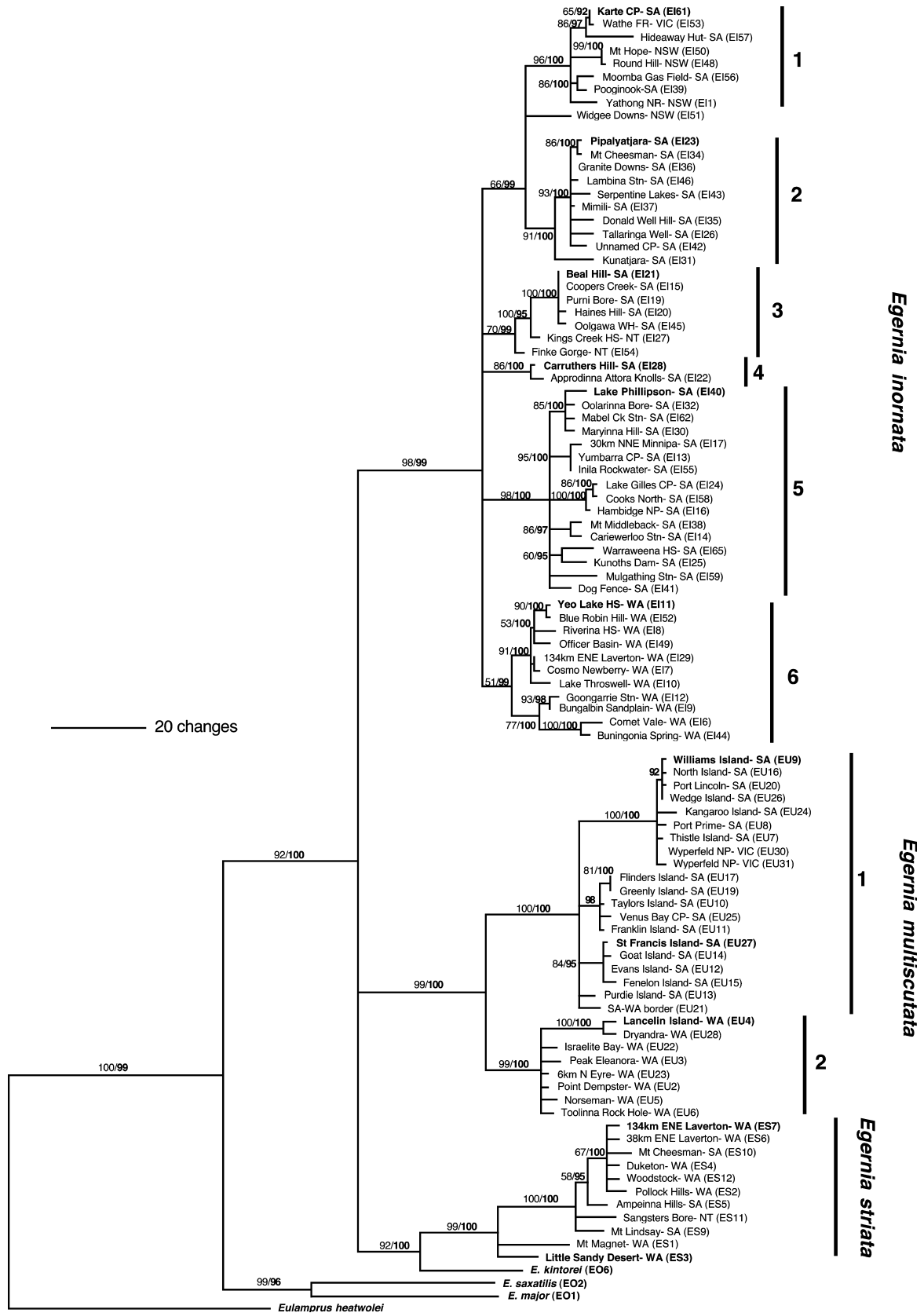


Fig. 3. Conservative phylogram from maximum likelihood analyses for the arid-zone members of the *Egermia whitii* species group based 696 bp of the ND4 mitochondrial gene. Parsimony bootstrap values are shown in plain-text and Bayesian posterior probabilities are shown in bold. Six clades are identified within *E. inornata* and two clades within *E. multiscutata* (see Fig. 1; Tables 1–3).

Table 2
Jukes-Cantor distance matrix for representatives (bold individuals) from each clade identified in Fig. 3

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1 <i>Eulamprus heatwolei</i>	—													
2 <i>Egernia saxatilis</i> (EO2)	0.256	—												
3 <i>E. major</i> (EO1)	0.286	0.153	—											
4 <i>E. inornata</i> (EI21)-clade 3	0.265	0.182	0.202	—										
5 <i>E. inornata</i> (EI11)-clade 6	0.275	0.195	0.198	0.041	—									
6 <i>E. inornata</i> (EI40)-clade 5	0.279	0.185	0.181	0.058	0.058	—								
7 <i>E. inornata</i> (EI28)-clade 4	0.279	0.200	0.209	0.035	0.041	0.058	—							
8 <i>E. inornata</i> (EI61)-clade 1	0.279	0.194	0.202	0.051	0.057	0.061	0.044	—						
9 <i>E. inornata</i> (EI23)-clade 2	0.270	0.181	0.196	0.048	0.048	0.061	0.041	0.042	—					
10 <i>E. kintorei</i> (EO6)	0.288	0.185	0.187	0.108	0.107	0.108	0.110	0.125	0.119	—				
11 <i>E. striata</i> (ES7)	0.288	0.193	0.193	0.113	0.120	0.123	0.128	0.135	0.124	0.085	—			
12 <i>E. multiscutata bos</i> (EU9)	0.285	0.198	0.217	0.156	0.140	0.140	0.162	0.147	0.157	0.144	0.162	—		
13 <i>E. m. bos</i> (EU4)	0.283	0.200	0.196	0.144	0.134	0.130	0.149	0.140	0.146	0.135	0.154	0.084	—	
14 <i>E. m. bos</i> (EU27)	0.290	0.196	0.209	0.142	0.137	0.140	0.156	0.142	0.151	0.134	0.151	0.043	0.076	—

Table 3
Range of Jukes-Cantor genetic distances within clades identified in Fig. 3

Species/Clade	Genetic distance range
<i>Egernia inornata</i>	
Clade 1	0.0014–0.0369
Clade 2	0.0014–0.0293
Clade 3	0.0000–0.0219
Clade 4	0.0058
Clade 5	0.0000–0.0513
Clade 6	0.0015–0.0414
<i>Egernia multiscutata</i>	
Clade 1	0.0000–0.0475
Clade 2	0.0087–0.0339
<i>Egernia striata</i>	
	0.0059–0.0630

0–5.1% (Table 3). Topology tests provided no support for populations forming monophyletic groups by habitat type (Table 4). Two extremely well supported clades are evident within *E. multiscutata* (Fig. 3), with Clade 1 consisting of populations from South Australia and Victoria, and Clade 2 comprising populations from Western Australia (Fig. 1 and Table 1). Genetic divergence between these two clades is in the range of 7.5–8.3% (Table 2), with divergence within each clade between 0–4.7% (Table 3). There is no support for *E. m. multiscutata* (Greenly Island, SA) representing a separate clade from *E. m. bos* (remainder of the range)

within *Egernia multiscutata*. Importantly, the Victorian population of *E. multiscutata* is part of Clade 1, confirming its close affinity with the disjunct South Australian populations. However, topology tests were equivocal in regard to the validity of the existing *E. multiscutata* subspecies (Table 4). Genetic variation within *E. striata* was generally high, with the level of genetic divergence between populations around 0.5–6.3%. Results of the topology tests were equivocal regarding whether *E. striata* populations in different habitats represent clades or whether sandplain/sandridge populations have diverged genetically on either side of the shrub corridor (Table 4).

4. Discussion

We have produced a phylogeny for the obligate-burrowing species within the *E. whitii* species group, which clarifies the phylogenetic structure among populations in *E. inornata*, *E. multiscutata*, and *E. striata*. This is the first detailed examination of the phylogenetic relationships among populations in these three obligate-burrowing species, and the results have several taxonomic and biogeographic implications. We outline the taxonomic implications of our phylogeny first, before considering the implications of our study for the biogeography of arid-zone reptiles.

Table 4
Results of Shimodaira–Hasegawa tests of alternative topologies regarding *E. multiscutata* subspecies and predictions of Pianka’s (1972) habitat model of speciation for arid-zone reptiles

Alternative topology	–ln L	Difference in –ln L	P value
Optimal tree	5585.611		
Existing <i>E. multiscutata</i> subspecies valid	5635.685	50.074	0.480
<i>E. striata</i> habitat types monophyletic	5660.033	74.421	0.407
<i>E. striata</i> monophyletic groups either side of shrub corridor	5720.788	135.177	0.291
<i>E. inornata</i> habitat types monophyletic	6125.294	539.683	0.001

A significant P value (<0.05) indicates that the alternative topology is significantly different from the maximum likelihood (ML) tree.

4.1. Taxonomic implications

Our phylogeny does not support recognition of the existing subspecies within *Egernia multiscutata*. Mitchell and Behrndt (1949) originally described *E. multiscutata* from a single population on Greenly Island, off the coast of South Australia, while Storr (1960) later described the Western Australian populations as *E. bos*. As part of a major taxonomic revision of the *E. whitii* species group, Storr (1968) recognized two subspecies within *E. multiscutata*, with the nominate form restricted to Greenly Island and *E. m. bos* occurring in the remainder of the range. Although topology tests were equivocal regarding the status of the existing subspecies (Table 4), our phylogeny indicates that the nominate form of *E. multiscutata* (Greenly Island, SA) has close phylogenetic affinities with other geographically proximate populations from South Australia (Clade 1) and does not support the recognition of the existing subspecies in *E. multiscutata*.

Although the existing *E. multiscutata* subspecies do not have support, genetic structuring within *E. multiscutata* is evident. We found an extremely well-supported genetic break between the South Australian (Clade 1) and Western Australian (Clade 2) populations of *E. multiscutata*. The Western Australian clade is concordant with a recognized area of faunal and floral endemism in south-western Western Australia (Cracraft, 1991; Crisp et al., 1995). Likewise, the South Australia clade broadly corresponds to an area of endemism in south-eastern South Australia (Eyre Peninsula and Adelaide regions; Cracraft, 1991; Crisp et al., 1995). The two clades are separated by a distance of approximately 200 km, with the subdivision occurring near the South Australian–Western Australian border. This phylogenetic break is geographically concordant with the Nullarbor Cliffs and also corresponds to a break in the species range (records from the South Australian Museum and Western Australian Museum; Wilson and Swan, 2003; Fig. 1). Despite the significant genetic differentiation between the two clades (genetic distance 7.6–8.4%), there was the potential for continuity between the two clades across the expanded Roe plain south of the present coastline during the last glacial as recently as 10 000 years ago (Rawlinson, 1974; Hope, 1984). The east–west split in *E. multiscutata* may justify the designation of subspecies, more detailed sampling across this phylogenetic break is required to examine the validity of any such subdivision.

The disjunct population of *E. multiscutata* in Victoria is currently listed under state legislation as critically endangered (Victorian Natural Resources and Environment, 2000; Chapple, 2003). *Egernia multiscutata* in Victoria is known only from three localities in the vicinity of Chinaman Well and Moonlight Tank near the western boundary of Wyperfeld NP (Coventry and Robertson, 1980; Victorian Natural Resources and

Environment, 2000). It is evident from our topology that the Victorian population exhibits close phylogenetic affinities to populations around the Gulf of St Vincent and Spencer Gulf in South Australia, from which it is separated by a distance of about 200 km (Fig. 1). However, unlike the majority of South Australian populations that occur in coastal areas or on offshore islands, the Victorian population lives in burrows in large sand dunes in desert heath land habitat with sparse ground vegetation (Coventry and Robertson, 1980). Although there are sparse records of *E. multiscutata* occurring in heath land in the eastern part of South Australia, indicating that the Victorian population was once continuous with the other populations within Clade 1, the Victorian population represents one of the few localities within the eastern clade where *E. multiscutata* occurs in a non-coastal habitat (i.e. semi-arid habitat). We suggest that *E. multiscutata* should retain its conservation listing in Victoria due to the current state-based conservation approach in Australia. In addition, conservation of the Victorian population may be warranted using the criterion of Waples (1991); (reviewed in Crandall et al., 2000) due to the absence of recent records of *E. multiscutata* in equivalent suitable habitat on the South Australian side of the border (e.g. Kgarkat CP; records from the South Australian Museum).

4.2. Biogeography and speciation in the Australian arid-zone reptilian fauna

The pioneering research of Pianka (1969, 1972, 1981, 1984) on the Australian arid-zone reptilian fauna highlighted the extraordinary diversification and species diversity within the arid interior of the continent. Regions of Australia's spinifex (*Triodia*) grasslands are believed to contain the highest known reptilian species diversity in the world (Wilson and Swan, 2003). Such species diversity is intriguing given that there are very few major geographic barriers within arid Australia (Pianka, 1972; Barker and Greenslade, 1982). Consequently, researchers have searched for other potential mechanisms for the extensive speciation within the arid-zone (e.g. Pianka, 1972; James and Shine, 2000). Pianka (1969) demonstrated that Australian arid-zone lizards exhibit a high degree of habitat specificity. This fact, combined with the spatial patchiness of the major arid-zone habitat communities (Fig. 2), lead Pianka (1972) to propose a model of speciation whereby lizards become adapted to particular habitats, with speciation the result of historical fluctuations in the boundaries of each habitat. The distribution of arid-zone lizards and the regions of species abundance are consistent with this hypothesis (Pianka, 1972). However, the predictions inherent in Pianka's (1972) hypothesis have never previously been examined within a phylogeographic framework.

The main prediction stemming from Pianka's (1972) hypothesis is that arid-zone species such as *E. inornata* (southern arid-zone generalist) and *E. striata* (sandplain-*Triodia* specialist) should exhibit phylogeographic structuring concordant with the distribution of the major desert habitat types. Our Shimodaira–Hasegawa topology tests of this prediction provide conflicting results for *E. inornata* and *E. striata* (Table 4). The alternative topology where populations within different habitats formed clades within *E. inornata* was strongly rejected; however, the results for *E. striata* were equivocal (Table 4). Similarly, the results of our topology tests were equivocal in regard to the presence of significant genetic structure between sandplain/sandridge populations of *E. striata* on either side of the Giles shrub corridor (Fig. 2, Table 4). Thus, our data do not support the main predictions of Pianka's (1972) hypothesis.

Although our analyses have specifically tested for concordance between phylogenetic clades and broad-scale habitat communities, Pianka (1972) recognized that on a finer scale certain regions of the Australian desert form a mosaic of all three habitat types. In particular, large desert regions support a combination of alternating sandplain and sandridge habitats (e.g. Great Victoria Desert; Pianka, 1972). Thus, to test this hypothesis it is necessary to examine the concordance between clades and habitats on a finer scale to determine whether particular clades are distributed entirely within a single habitat community. Consequently, the genetic structuring evident within *E. inornata* has some important implications for the biogeographic patterns in arid-zone lizards. Although our topology indicates that the wide-ranging *E. inornata* is monophyletic, six distinct sub-clades are evident (Figs. 1 and 3).

Clade 1 comprises populations from New South Wales, Victoria, and the extreme south-east and north-east of South Australia. Although some populations within clade 1 are located beyond the eastern boundary of the area Pianka (1972) considered, these populations occur in mulga shrubland. The majority of populations within clade 1 inhabit shrubland, although one population occurs in sandridge habitat (EI56). Clade 2 comprises populations from north-western South Australia that occur in either shrubby habitats or sandplain regions. Interestingly, *E. inornata* populations within the Giles Corridor are included within clade 2. *Egernia inornata* populations in the Northern Territory are part of clade 3 and occur in sandplain regions, while the remainder of the clade occurs in sandridge habitats in north-eastern South Australia. Clade 4 comprises two sandridge populations in the Simpson desert region of north-eastern South Australia, adjacent to populations from clade 3. The distribution of clade 5 encompasses the majority of South Australia, except for the peripheral border regions already identified, with all populations confined to shrubby habitats. Interestingly, the

distribution of clade 5 extends up into the distribution of clade 3 in north-west South Australia, which may represent recent northward range expansion of clade 5, presumably along the Giles shrub corridor (Fig. 2). Clade 6 comprises all Western Australian populations that inhabit either shrubby habitat or sandridge regions.

Although the distribution of *E. inornata* clades within the arid-zone is complex, four of the clades are entirely or predominately confined within a single habitat type (Figs. 1 and 2). While this does not provide conclusive evidence at a finer scale for the predictions of Pianka (1972) it does highlight that habitat barriers and specialization to particular vegetation types may influence the distribution and biogeography of *E. inornata*. Indeed, *E. inornata*, like most other *Egernia* species, exhibits limited proclivity for dispersal and specific habitat requirements to construct its burrow system (Webber, 1979; Pianka and Giles, 1982; Daniel, 1998; Chapple, 2003). Burrows are constructed at the base of vegetation, generally shrubs (e.g. spinifex), with the root network stabilizing the sandy soil and maintaining the integrity of the burrow system (Webber, 1979; Pianka and Giles, 1982; Daniel, 1998; Chapple, 2003). However, microhabitat factors such as soil composition may also be a determining factor in the distribution of *E. inornata*. *E. inornata* exhibits a preference for constructing burrows in soft soil that is deep enough to burrow in, and generally avoids burrowing in clay or stony soils (Webber, 1979; Pianka and Giles, 1982; Daniel, 1998; M. Hutchinson, personal observation). For instance, in north-western South Australia where *E. inornata* is sympatric with *E. striata* and *E. kintorei* (Fig. 1), it may be micro-allopatric due to its preference for sand dunes, whereas the other two species prefer hard-packed sand dunes or swales (M. Hutchinson, personal observation).

Substantial phylogenetic structure and haplotype diversity were evident within *E. striata*; however, multiple well-supported clades were not recognized (Fig. 3). *Egernia striata* is a wide-ranging species that occurs throughout the sandy regions of the Tanami, Great Victoria, Great Sandy and Gibson Deserts (Cogger, 2000; Wilson and Swan, 2003), generally in close association with spinifex (*Triodia*) grasslands (Pianka, 1972). The vast majority of populations we sampled were from sandridge habitats, although populations from shrub (ES1, ES12) and sandplain (ES11) habitats also were included. We found little evidence of fine-scale concordance between habitat type and the phylogeographic structuring within *E. striata*.

Our phylogeny does reveal an interesting pattern within the sandy deserts (sand plain-*Triodia*) of the central-western region of the continent. Our analyses confirm that *E. kintorei* represents the sister species to *E. striata*. Although we included only one sample from the endangered *E. kintorei*, these two species occur

sympatrically throughout the majority of their range (Cogger, 2000; Wilson and Swan, 2003; Figure 1), and have similar diets, activity and habitat use (Chapple, 2003). In particular, both species are primarily crepuscular-nocturnal, possessing an elliptical eye (semi-elliptical in *E. kintorei*) to enable them to forage at night (Cogger, 2000; Pearson et al., 2001; Chapple, 2003). However, although both species have similar body proportions and body plans, *E. kintorei* weighs approximately five times more than *E. striata* and is about twice the length (190–200 mm SVL v 100–110 mm SVL; Henzell, 1972; Chapple, 2003).

Acknowledgment

We especially thank Chris Hayes her for assistance and encouragement in the laboratory and Ian Scott for developing the *Egernia* specific ND4 primers. We thank Nick Clemann, John Coventry, Greg Fyfe, Robert Henzell, Brad Maryan, Peter Robertson and Glenn Shea for providing tissue samples or useful information and/or discussions. Tissue samples were collected with approval of the Australian National University Animal Experimentation Ethics Committee (F.BTZ.36.01) under the Victorian Scientific Permit No: 10001624. We are grateful to the following museum personnel for providing tissue samples: Steve Donnellan, Terry Bertozzi (South Australian Museum), Ric How, Brad Maryan (Western Australian Museum), John Wombey and Robert Palmer (CSIRO Australian National Wildlife Collection). Funding was provided to D. Chapple from the following sources: Australian Geographic, Australian Society of Herpetologists (ASH) Student Research Grant, American Society of Ichthyologists and Herpetologists (ASIH) Gage Fund Award, Society for Systematic Biologists (SSB) Award for Graduate Student Research, Joyce W. Vickery Scientific Research Fund, Peter Rankin Trust Fund for Herpetology, Ecological Society of Australia (ESA) Student Research Grant. Financial support also was provided by a research grant from the Australian Research Council to Scott Keogh.

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