The Systematics and Reproduction of Bluetongue Lizards of the Genus Tiliqua (Squamata: Scincidae)

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Summary

The systematics of the genus *Tiliqua* are explored using univariate and multivariate analyses of morphological characters. Within each species and subspecies, adult size, the seasonality of reproduction, fecundity and offspring size are assessed from morphological variation in the reproductive tracts of both males and females.

A suite of 19 synapomorphies, including both external and osteological characters, identifies a restricted genus *Tiliqua* and its sister-genus, *Cyclodomorphus*, together forming the *Tiliqua* lineage. The relationships of this lineage are probably with the genus *Egernia*. The genus *Trachydosaurus* is placed in the synonymy of *Tiliqua*, and the genera *Hemisphaeriodon* and *Omolepida* placed in the synonymy of *Cyclodomorphus*.

Within the restricted genus *Tiliqua*, seven Recent species are identified on the basis of external characters. Each species is formally redescribed, and geographic variation in morphology is examined.

Tiliqua adelaidensis is a small species, probably recently extinct, known only from a restricted area around Adelaide.

Tiliqua multifasciata is a moderate-sized species largely restricted to *Triodia* grasslands in arid parts of northern and central Australia. It shows little geographic variation in morphology compared to other species.

Tiliqua nigrolutea is a moderate to very large species restricted to cool climates in Tasmania and south-eastern Australia. Although there is much geographic variation, with both size and coloration suggesting a division into a southern lowland morph and a northern highland morph, patterns of variation in different characters are not concordant, and formal taxonomic division is not recommended.

Tiliqua occipitalis is a large species inhabiting semi-arid habitats, particularly mallee habitats, in southern Australia, and showing relatively little geographic variation.

Tiliqua rugosa is a highly apomorphic, moderate to large species inhabiting open semi-arid habitats. Geographic variation in morphology is extensive, and concordant patterns of variation in different characters, including scalation, adult size and coloration identify four subspecies: *T. r. rugosa* in south-western Australia, *T. r. asper* in south-eastern and eastern Australia, *T. r. konowi* on Rottnest I. and a newly-described race, *T. r. palarra*, in the Shark Bay region. Limited hybrid zones are identified between the southern mainland taxa towards the western side of the Hampton Tableland, and between the north-western and south-western subspecies in the Murchison River district.

The *Tiliqua* with elongate temporal scales are divided into two allopatric species, *T. scincoides* and *T. gigas*, each of which is further divided into three subspecies. Within *T. scincoides*, the nominate race is distributed through open grassland and woodland habitats of south-eastern and eastern Australia, as far north as Cape York Peninsula. *T. s. intermedia* is distributed through savannah habitats of northern Australia, west of north-central Queensland. A new subspecies, *T. s. chimaerea*, is described to accomodate populations from the Babber and Tenimbar Islands in Indonesia that were formerly referred to *T. gigas*. Within *T. gigas*, the nominate race is restricted to the Moluccas and north coastal New Guinea east to the Huon Peninsula, and *T. g. keyensis* is restricted to the Kei and Aru Islands. A new subspecies, *T. g. evanescens*, is erected for other New Guinean populations.

Zones of sympatry between Australian *Tiliqua* species were studied to provide evidence for species status. Hybridisation was limited, and confined to three taxa: *T*. *nigrolutea*, *T*. *rugosa* and *T*. *scincoides*.

A detailed account of the osteology of *T*. *s*. *scincoides* and comparative data for other *Tiliqua* are provided. A set of apomorphic osteological and external characters was analysed cladistically, and the following scheme of intrageneric relationships hypothesised: ((*gigas*, *scincoides*) (*adelaidensis* ((*nigrolutea*, *rugosa*) (*multifasciata*, *occipitalis*)))). On the basis of this hypothesis, a model of speciation in *Tiliqua* is developed.

All *Tiliqua* species and subspecies for which data on reproduction are available appear to be seasonal breeders, with the possible exception of *T*. *g*. *gigas*. Mating occurs in late spring for southern species, and earlier in northern taxa. Only *T*. *nigrolutea* appears to normally breed less frequently than annually. Litter size and offspring size are unusually variable for skinks. The hypothesis of cladistic relationships suggests that large litters have evolved twice in *Tiliqua*, in *T*. *multifasciata* and *T*. *scincoides*, while small litters, and correspondingly large young, have evolved once, in *T*. *rugosa*. The pattern of variation in litter size in *Tiliqua* does not unequivocally support either density-based or demographic-based models for the evolution of litter size.

An annotated bibliography of the genera *Tiliqua* and *Cyclodomorphus* is appended.

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Chapter 1 Introduction

The family Scincidae, with over 1,000 species (Halliday & Adler, 1986), is the most species-rich family of lizards, and after the probably polyphyletic family Colubridae is the most species-rich family of terrestrial vertebrates. The Australopapuan region is a major centre of scincid diversity, with 357 described species in Australia (*pers*. *obs*.) and over 120 more species in New Guinea (Whitaker *et al*., 1982; Brown, 1991). Amongst the most familiar of these skinks are the bluetongues of the genus *Tiliqua*. Their combination of large size, ease of capture and ease of captive maintenance has meant that they are both frequently seen and kept as pets, and an ideal experimental subject for physiological and biochemical research. Consequently, the literature on bluetongues is vast, with over 2,000 citations (Appendix B), covering everything from general descriptions, history of human interactions and captive requirements, through such topics as diet and predation, to specific details of the anatomy, histology, karyotype, neurophysiology, endocrinology and biochemistry of certain species. This extensive literature, however, is misleading, familiarity creating an illusion of knowledge. In particular, there remain two major deficiencies in our knowledge of bluetongues: ecology and systematics. An understanding of both the ecology and evolutionary history of bluetongues is not only an end in itself, but also an essential prerequisite for interpretation of the published data on comparative physiology, biochemistry and anatomy, much of which is based on a premise that the bluetongue is a “typical” reptile.

Ecological studies of bluetongue species, particularly the shingleback, *Tiliqua rugosa*, are now beginning to appear (Bamford, 1980; Bull, 1987; Dubas, 1987; Dubas & Bull, 1991; Fergusson & Algar, 1986; Henle, 1990; MacMillan *et al*., 1989; Satrawaha & Bull, 1981; Shea, 1989; Yeatman, 1988). However, bluetongue systematics remain almost untouched in recent times. With most of the currently recognised species described last century, and the most recent complete revision of the genus in 1950 (Mitchell, 1950), *Tiliqua* remains almost the only Australian lizard genus that has not been subject to significant attention by systematists in the last 30 years. This is despite their being known to European science for over 200 years, and familiar to the Aborigines even before that.

Bluetongues were used as food by the Aborigines (Bennett, 1834; Berndt & Berndt, 1942; Foley, 1985; Fyfe, 1985; Gibson, 1986; Hale & Tindale, 1925, 1930; Krefft, 1866d; Lampert, 1971; Lindgren, 1961; Mulvaney, 1960; Mulvaney *et al*., 1964; Roff, 1983; Roth, 1899; Thomson & Hosmer, 1963). They are a totem species for various tribes (Mountford, 1965; Fyfe, 1985), and feature in their mythology (Mountford, 1965; Stirling & Waite, 1919) and artwork (Dunbar, 1943–44; McCarthy, 1976). There is clear evidence from the use of different names that the Aborigines recognised different “species” of bluetongues. Thus, in the Lyons River district, *Tiliqua rugosa* is known as “palarra” while *T*. *occipitalis* is “yaralla” (Alexander, 1921). In the Ayer's Rock region, *T*. *occipitalis* is known as “mita” while *T*. *multifasciata* is “lungata” (Fyfe, 1985). In the Pangkala language, *T*. *rugosa* is “kalla”, while *T*. *scincoides* is “karrenye” (Johnston, 1943), while in the Kalkatungu language, *T*. *rugosa* is “milimanu”, while other bluetongues (not specifically identifiable) are “pankara” and “tumparara” (Blake, 1969). Similar cases were reported by Mathews (1902b) and Hercus (1969).

One of the first Europeans to visit Australia and make observations on the fauna was the English pirate William Dampier. In an account (Dampier, 1729) reprinted by numerous subsequent authors (e.g., Alexander, 1914; Douglas & Ride, 1962; Flinders, 1814; Glauert, 1954; Greer, 1989; B. Main, 1967; Serventy, 1965, 1970; Serventy & Raymond, 1974b; Stanbury, 1978, 1987; Stanbury & Phipps, 1980; Whitley, 1970), he described from Shark Bay a lizard that is undoubtedly *Tiliqua rugosa*. Dampier, however, did not take his specimens back to Europe, apparently preferring to eat them.

The first bluetongues to reach Europe were presumably some large banded skinks reported in Dutch private collections (Boddaert, 1783; Gevers, 1787; Houttuyn, 1787). At least the former two specimens were from Ambon, and the specimens presumably reached Europe as part of the Dutch East Indies trade. None of these accounts constitute a formal naming of the species. As the specimens can no longer be identified in collections, if indeed they are still extant, there is no proof that all three accounts refer to the same species, or even to bluetongues at all. However, all three accounts were considered to refer to the same species by Schneider (1801), who named the taxon *Scincus gigas*, using the non-binomial name applied by Boddaert. There is no evidence that Schneider had examined any specimens.

Meanwhile, Cook's third voyage to the Pacific (1776–1780) visited Adventure Bay in Tasmania, where the surgeon, William Anderson, recorded the collection of a large lizard, described as “above fifteen inches long and six round, elegantly clouded with black and yellow”. A painting of this specimen by John Webber, artist to the expedition, is now in the collection of the British Museum (Whitley, 1970). While Anderson provided a name, *Lacerta tarda*, for this specimen, his manuscript account was not published in full until 1967 (Beaglehole, 1967), although the description of the specimen was published without the name by Eden (1787). Although the specimen has not been located in any European collection, the description is clearly of the later named *Tiliqua nigrolutea*.

The establishment of the first settlement in Australia in 1788 resulted in the collection of the first bluetongues to be examined by biologists in Europe. The surgeon of the First Fleet, John White, collected two specimens, presumably from the vicinity of Sydney Town, which were sent to the anatomist John Hunter. Hunter's account of his dissection of one of these specimens was published, in part and anonymously, in the Natural History appendix of White's (1790) *Journal of a Voyage to New South Wales*, under the binomen *Lacerta scincoides*. Hunter's full account, which included the earliest observation of herbivory in bluetongues, and probably in skinks in general, was unfortunately not published in full until 1860, after Hunter's death, and it has been overlooked by all subsequent systematists, who have assumed that the account in White's Journal was written by White himself (e.g., Boulenger, 1887; Cogger *et al*., 1983) or by George Shaw, then Assistant Keeper of Natural History at the Natural History Museum, London (e.g., Sherborn, 1891; Mitchell, 1950).

Shaw twice referred to *Lacerta scincoides*. In 1794, Shaw and Nodder provided a Latin diagnosis of the species, and reprinted the illustration Nodder had prepared for White's (1790) *Journal*. Shaw (1802) provided the same illustration, with brief descriptive comments, but considered the species a variety of his *Lacerta occidua* (now *Celestus occiduus*, and placed in the family Anguidae; Strahm & Schwartz, 1977).

Daudin (1802) considered *Lacerta scincoides* to be a variety of the African *Scincus officinalis*, possibly following the suggestions of Shaw and Nodder (1794), but *Scincus gigas* Schneider to be a distinct species, although he gave no indication that he had examined specimens of either Hunter's or Schneider's species. Cuvier (1817) recognised *Lacerta scincoides* as a distinct species, but did not mention *Scincus gigas*.

Merrem (1820) recognised both *L. scincoides* and *S. gigas* as distinct species, placing both in the genus *Scincus*. However, he applied the unnecessary new name *Scincus tuberculatus* to *L. scincoides*.

In presenting some preliminary herpetological results of the Baudin expedition to Australia, Lacépède (1804) described *Scincus crotaphomelas*. Lacépède did not compare his species to either *Lacerta scincoides* or *Scincus gigas*. Although recognised as valid by Cuvier (1829) and Gray (1831), Merrem (1820) suggested *S. crotaphomelas* was a synonym of *L.*

scincoides. It was subsequently formally synonymised by Duméril and Bibron (1839) and has remained in synonymy since.

The Baudin expedition, the most successful of the 19th century biological surveys of Australia, collected more than one bluetongue species. Unfortunately, the zoological results of the expedition were never published, due to the untimely death of the expedition's last remaining zoologist, Francois Péron, in 1810. However Péron's (1807) general account of the expedition contains some preliminary zoological data. On Bernier I., in Shark Bay, the expedition encountered the same species that Dampier had encountered in 1699. Péron's account ("l'une des plus grandes de ce genre, et dont la queue très-courte et très-grosse fait paraître, au premier instant, cet animal comme ayant deux têtes"), accompanied by the name *Scincus Tropisurus*, is enough to clearly identify the shingleback. Unfortunately, Péron's account was overlooked until 1962 (Douglas & Ride, 1962), and the name must be considered a *nomen oblitum*.

Although the shingleback was also seen by Vancouver (1798) and Flinders (1814) in the vicinity of King George's Sound, it was not until the collection of a specimen from that locality by P.P. King's 1818–1822 coastal survey that the species was formally described in the recognised literature. Gray (1825), in listing and diagnosing the genera of reptiles, erected the genus *Trachydosaurus* for a species *T. rugosus*. At the same time, he erected the genus *Tiliqua* for *Lacerta scincoides* (as *sincoides*) and a species *Tiliqua tuberculatus* Gray. However, it is clear that it was not Gray's intention to describe either *Trachydosaurus rugosus* or *Tiliqua tuberculatus* in 1825. Gray (1827), in the zoological appendix to King's *Narrative*, provided extensive descriptions of both taxa: the former, as *Trachysaurus rugosus*, named as a new species; the latter, although with both *Lacerta scincoides* and *Scincus tuberculatus* Merrem in its synonymy, not conspecific with them. However, the delay in publication of King's *Narrative* meant that Gray's (1825) brief account saw both the erection of the genera *Tiliqua* and *Trachydosaurus*, and also the naming of the species *Trachydosaurus rugosus*. This led to much confusion over the next century and a half over the usage of the generic names *Trachydosaurus* and *Trachysaurus*.

Meanwhile, Quoy and Gaimard (1824) had described another species of bluetongue, as *Scincus nigroluteus*, from two specimens from the Blue Mountains collected by the ill-fated de Freycinet expedition of 1817–1820. This species was also mentioned by Cuvier (1729), along with *Scincus scincoides* and *S. crotaphomelas*.

Fitzinger (1826) recognised both *Trachydosaurus* and *Tiliqua* as distinct genera, but considered *Trachydosaurus* to be in his family Cordyloidea, rather than the Scincoidea. In listing the material in the collection of the then Zoologischen Museum in Vienna, he added *Scincus gigas* Daudin and *Tiliqua fasciata* [now *Diploglossus fasciatus*, an anguid] to *Tiliqua*. Fitzinger apparently had not examined *T. rugosus*, and like Gray (1825), did not mention Quoy and Gaimard's species.

Wagler (1828) described and illustrated a new species, *Cyclodus flavigularis*, from an unknown locality. In so doing, he erected the genus *Cyclodus*. In 1830 (Wagler, 1830), he added Gray's genus *Tiliqua* to the synonymy of *Cyclodus*, added Quoy and Gaimard's species, and synonymised *Scincus tuberculatus* Merrem with *Lacerta scincoides*, thus giving four species in the genus: *Cyclodus flavigularis*, *C. gigas*, *C. nigroluteus* and *C. scincoides*. Wagler (1830) also recognised Gray's (1827) *Trachysaurus*, including in it only the species *T. rugosus*, but placing in its synonymy a manuscript name, *Scincus peronii*, applied to specimens in the Museum d'Histoire Naturelle, Paris. Wagler (1833) subsequently changed his mind about the validity of the name *Scincus peronii*, when he described *Trachysaurus peronii*, placing Gray's species in its synonymy. Wiegmann (1834), in a revised classification of the lizards, followed Wagler in recognising the two genera *Trachysaurus* and *Cyclodus*.

Gray (1831), in another listing of genera and species of reptiles, again recognised *Trachydosaurus* and *Tiliqua*, both as skinks. In *Trachydosaurus*, he still included only the single species *T. rugosus*, but placed in its synonymy the name *Scincus pachyurus*, derived from a Péron manuscript. In *Tiliqua*, Gray included *Lacerta scincoides* (under the unnecessary replacement name *Tiliqua Whitii*), *T. nigroluteus* and *T. crotaphomelas*. He further noted that Wagler's *Cyclodus flavigularis* was similar to *L. scincoides*, but failed to mention *Scincus gigas*. However, Gray (1831) also greatly expanded his concept of *Tiliqua* by placing in it a large number of unrelated skinks, including species now placed in such phylogenetically distant genera as *Mabuya* and *Ctenotus*, and even some anguids.

Smith (1835), apparently unaware of Gray's *Trachydosaurus*, described a new genus and species, *Brachydactylus typicus*, from two specimens from the Swan River district. This was synonymised with *Trachydosaurus* (as *Tachysaurus*, presumably an error) by Gray (1838), in yet another listing of genera and species. Gray (1838) maintained his expanded concept of *Tiliqua*, including in it the bluetongue species *T. Whitii* and *T. nigrolutea*.

Swainson (1839) considered *Trachydosaurus* and *Tiliqua* to be subgenera of *Scincus*, one of five genera in his family Scincidae.

The same year saw the publication of the volume on the Scincidae in the *Erpétologie Générale* (Duméril & Bibron, 1839). They recognised two genera, *Trachysaurus* (for *T. rugosus*) and *Cyclodus*. In *Cyclodus* were placed *S. nigroluteus*, *L. scincoides* and *S. gigas* (the latter two and their synonyms combined under the new name *Cyclodus boddaertii*). Also added to *Cyclodus* was a new species, *C. casuarinae*, described from a specimen collected by Péron and Lesueur from Bruny I. (Duméril & Duméril, 1851; Roux-Esteve, 1974). This is presumably the lizard described by Péron (1807) as “quelques beaux lézards analogues aux Scinques, différant toutefois essentiellement des animaux de celle famille par l'élégance des formes et le rapport des proportions”. From the first, this species was noted to be rather different from the other bluetongues, lacking ear lobules and a postnarial groove.

Charles Darwin, during his time in Tasmania on the Beagle voyage, collected both *T. nigrolutea* and *C. casuarinae* in February 1836. However, his manuscript observations remained unpublished until recently (Nicholas & Nicholas, 1989; Shine & Hutchinson, 1991). Only the *C. casuarinae* specimen was described and illustrated in the herpetological volume of the zoology of the voyage (Bell, 1843).

Gray (1841), in a catalogue of the reptiles and amphibians of Australia, recognised the two genera *Trachysaurus* and *Tiliqua*. In *Trachysaurus*, he recognised two species, resurrecting Smith's *Brachydactylus typicus* as specifically distinct from *T. rugosus*. Gray maintained his extended concept of the genus *Tiliqua*, but included in it three bluetongue species: *Tiliqua casuarinae*, *T. nigrolutea* and *T. whitei*, including in the latter taxon all other named bluetongue taxa, including *Scincus gigas*, which he had not previously considered. The same list of recognised species, without synonyms, was reprinted by Gray (1842).

Fitzinger (1843) proposed a reclassification of the reptiles, based on a numerical pattern of divisions into groups of three and five (Adler, 1989). In his family Eumecae, he recognised the genera *Trachysaurus* and *Cyclodus*, dividing the latter into three subgenera: *Cyclodus*, *Cyclodomorphus* and *Sphenomorphus*. Unfortunately, Fitzinger never published a full list of the species in his genera, only listing the type species of his subgenera. His concept of the genus *Cyclodus* is, however, apparently closer to Gray's expanded *Tiliqua* than the more restricted genera of Wagler and Duméril and Bibron, including as it does the subgenus *Sphenomorphus* (type species *Lygosoma melanopogon*). As type species of *Cyclodomorphus*, Fitzinger nominated *Cyclodus casuarinae*, although he did not provide a diagnosis for the subgenus.

In 1845, Gray published his *Catalogue of the Specimens of Lizards in the collection of the British Museum*. In it, he finally dismembered his expanded and by then unwieldy genus *Tiliqua*. Like Fitzinger, he considered *Cyclodus casuarinae* distinct from the other bluetongues, and erected the genus *Omolepida* for it. *Trachydosaurus* he retained as a distinct genus, but added to it a new species, *T. asper*, while relegating all previously described shinglebacks to the synonymy of *T. rugosus*. The remaining described bluetongue species he retained together in a distinct genus. However, in a bizarre twist, he apparently overlooked his own original concept of *Tiliqua*, using instead Wagler's *Cyclodus* for the bluetongues, while retaining *Tiliqua* (attributing the name to Fitzinger) for a small genus composed of species today placed in *Mabuya* and *Dasia*. Gray (1845) recognised only two species of *Cyclodus*: *C. nigroluteus* and *C. gigas*, placing all other published names in the synonymy of the latter. However, Gray's concept of *C. gigas* was apparently based solely on Australian material, as there were no non-Australian bluetongues in the British Museum collection at that time. Both Gray (1845) and Duméril and Bibron (1839) distinguished *C. nigroluteus* and *C. gigas* primarily on the combination of coloration and shape of the anterior temporal scales.

Gray's actions were not adopted by Duméril and Duméril (1851), who instead retained the arrangement of genera and species used by Duméril and Bibron (1839) for the bluetongues, adding only Gray's *T. asper* to their genus *Trachysaurus*. *T. asper* was also recognised by Peters (1864), Krefft (1866c), Sauvage (1875) and von Fischer (1882), although doubt was cast on the validity of Gray's diagnostic characters by Haacke (1883).

In describing collections made by various expeditions, Girard (1858) and Steindachner (1869) followed the actions of Gray (1845) in recognising only one species of *Cyclodus* with elongate temporals, calling the species *C. gigas*. Steindachner (1869), however, agreed with Duméril and Bibron (1839) in not considering *C. casuarinae* generically distinct, while Fitzinger (1860), describing the same collection as Steindachner, maintained the use of *Cyclodomorphus* for *C. casuarinae* and used the combination *Cyclodus scincoides*.

Albert Günther, Gray's successor at the Natural History Museum, London, recognised a distinction between Australian and non-Australian bluetongues with elongate temporals following the acquisition of two specimens from Seram. However, under the misapprehension that the name *C. gigas* referred to the Australian taxon, he named the Seram specimens as a new species, *Cyclodus carinatus* (Günther, 1863), later referring additional material from Cape York and the Torres Strait islands to this taxon (Günther, 1877). Von Martens (1876) suggested that *C. carinatus* and *C. flavigularis* may be synonymous.

Lütken (1863), on the basis of a stuffed and mounted specimen from Australia, described a new species, *Cyclodus fasciatus*, carefully comparing it to *C. gigas*, *C. nigroluteus* and *C. casuarinae*. Lütken and subsequent authors were apparently unaware that his name was unfortunately preoccupied in *Tiliqua* by *Tiliqua fasciata* Gray, 1831 (now *Diploglossus fasciatus*, an anguid; Peters & Donoso-Barros, 1970).

Working with a collection of specimens received from Richard Schomburgk, of Buchsfelde, SA, and apparently unaware of Lütken's paper, Peters (1864b) described two new species of *Cyclodus*: *C. occipitalis* and *C. adelaidensis*, and identified in the same collection *C. gigas* and *Trachysaurus asper*.

On the question of the generic status of Gray's *Omolepida* (emended to *Homolepida* by Lütken, 1863), Peters (1866) adopted a position intermediate between that of Gray and the Dumérils, recognising it as a subgenus of *Cyclodus*, and adding to it a new species, *Cyclodus* (*Omolepida*) *luctuosus*, and later still (Peters, 1875) another new species,

Cyclodus (*Homolepida*) *nigricans*. Peters (1872) subsequently changed his mind on the generic position of *C. luctuosus*, placing it in a monotypic genus, *Lissolepis*.

Strauch (1866) revised the genus *Cyclodus*, recognising ten species in three subgenera: *C. gigas*, *C. carinatus*, *C. petersi* sp. nov., *C. fasciatus*, *C. occipitalis*, *C. nigroluteus* and *C. adelaidensis* in *Cyclodus*, *C. casuarinae* and *C. luctuosus* in *Omolepida*, and *C. Brandtii* sp. nov. in *Otolepis* subgen. nov. The latter species was subsequently transferred to the synonymy of *Scincopus fasciatus* by Boulenger (1887). Within the subgenus *Cyclodus*, Strauch recognised four subgroups. The first, consisting of *C. gigas*, *C. carinatus* and *C. petersi*, was diagnosed on the presence of elongate anterior temporals. The second group, consisting of *C. fasciatus* and *C. occipitalis*, was diagnosed on the presence of four rows of occipital shields, while *C. nigroluteus* and *C. adelaidensis* were placed in monotypic groups. Strauch apparently based much of his revision on the available literature, as he had access to only eight specimens in his own collection (three *C. gigas*, one *C. petersii*, one *C. fasciatus*, two *C. nigroluteus* and one *C. brandtii*).

Cyclodus carinatus was synonymised with *C. gigas* (*sensu lata*) by Peters and Doria (1878).

Gray (1845) described in *Hinulia*, a polyphyletic genus of species now assigned mostly to *Sphenomorphus*, *Ctenotus* and *Cyclodina*, a new species, *Hinulia gerrardii*, from two stuffed and mounted specimens. A general similarity between this species and *Cyclodus* was first noted by Lütken (1863). On access to preserved material of this species, Peters (1867) also commented on the phenetic similarity to *Cyclodus*, and transferred the species to a monotypic genus, *Hemisphaeriodon*, diagnosed on the presence of grossly enlarged molariform teeth. Macleay (1885), unaware of Peters' (1867) reclassification, described *Hinulia picta* from a single specimen from north-east Queensland, noting its affinity with *Hinulia gerrardii*. De Vis (1888) unwittingly also recognised the affinity between *Hemisphaeriodon* and the bluetongues when he described *Tiliqua longicauda*, a species subsequently synonymised with *H. gerrardii* by Longman (1915), an action confirmed by Loveridge (1934).

In the second catalogue of the lizards in the British Museum, Boulenger (1887) resolved many of the anomalies resulting from the contradictory actions of previous workers. After examining rather larger samples that previously available to other workers, he resurrected the name *Tiliqua* for five species: *T. scincoides*, *T. gigas*, *T. nigrolutea*, *T. occipitalis* and *T. adelaidensis*, synonymising *C. petersi* with *T. gigas* and *C. fasciata* with *T. occipitalis* (although not realising that Lütken's description predated Peters'). *T. gigas* was differentiated from *T. scincoides* on the basis of a lower number of scales at midbody and longer forelimbs. *Cyclodus luctuosus* was removed from *Tiliqua* and placed in *Egernia*. In *Trachysaurus*, he recognised only one species, *T. rugosus*. He recognised *Hemisphaeriodon* as a distinct monotypic genus, placing it close to *Tiliqua* in his classification, and synonymising *Hinulia picta* with *H. gerrardii*. *Cyclodus casuarinae* (with *Cyclodus nigricans* and *Lygosoma muelleri* Peters, 1878 in its synonymy) he placed with several other elongate, short-limbed skinks, including *Hinulia branchialis* Günther, 1867 (as *Lygosoma branchiale*), in a subgenus, *Omolepida*, of the genus *Lygosoma*. Boulenger's monumental work, placing under the one set of covers for the first time since Duméril and Bibron's *Erpétologie Générale* descriptions and keys for identification of most of the lizards then described, had a stabilising effect on lizard systematics for many years. In particular, his enormous polyphyletic genus *Lygosoma* was accepted by most biologists for almost 50 years, despite his own stated view that a number of discrete lineages could be identified within it (“I trust that the arrangement of the species in one or more series within a genus, passing from forms with well-developed pentadactyle limbs and lacertiform physiognomy to such as have rudimentary limbs, or even none at all, markes a great improvement upon the artificial classifications in use down to the present day”). Cope (1892a), who considered Boulenger's

“series” as suprageneric categories, was possibly the only biologist of this period to hold an alternative view. Cope recognised as genera *Trachysaurus*, *Tiliqua*, *Hemisphaeriodon* and *Homolepida*, but gave no indication of their content.

Despite this stagnation at the generic level, most of the changes in bluetongue systematics over this period involved the species assigned to the *Omolepida* section of *Lygosoma* by Boulenger (1887).

Frost and Lucas (1894) described *Hemisphaeriodon tasmanicum* from the Tasmanian highlands, but later (Lucas and Frost, 1896a) synonymised this species with *Homolepida casuarinae*, thus, though inadvertantly, being the first to recognise a relationship between *Hemisphaeriodon* and *Omolepida*.

Several species with apparent affinities to *Lygosoma branchialis* were added in the 50 years after 1887: Stirling and Zeitz (1893) described *Lygosoma melanops* from two specimens from central Australia; Boulenger (1899) added *Lygosoma* (*Homolepida*) *gastrostigma*, described from a single specimen from north-west Australia and Proctor (1923) added *Lygosoma* (*Homolepida*) *wood-jonesii*, described from three specimens from the Nuyts Archipelago. Sternfeld (1919, 1925) added *Lygosoma petersi* as a replacement name for the preoccupied *Lygosoma mülleri* Peters, 1878, basing his redescription on three specimens from central Australia and noting that *Lygosoma mülleri* Peters, although placed in the synonymy of *L. casuarinae* by Boulenger (1887) was more probably related to the *branchialis* complex. He further (Sternfeld, 1925) suggested that *Cyclodus nigricans* Peters, 1874 might also prove to be a synonym of *Lygosoma melanops*. Zeitz (1920) synonymised *L. melanops* with *L. branchialis*, but retained *L. gastrostigma* as distinct. In contrast, Loveridge (1934) recognised *L. melanops* as distinct from *L. branchialis* while synonymising *L. gastrostigma* with the former. Loveridge also reduced *Lygosoma petersi* to a race of *Omolepida casuarinae*, and expressed doubts as to the identity of *L. mülleri*. He later considered these doubts unfounded, following his examination of a specimen from northern South Australia (Loveridge, 1938). Amongst these wildly differing opinions, the description of *Lygosoma* (*Homolepida*) *branchiale* var. *elongatum* from Boorabbin, W.A. by Werner (1910) passed unnoticed.

Malcolm Smith (1937) finally attacked the problem of Boulenger's (1887) polyphyletic and unwieldy *Lygosoma*, and removed *L. casuarinae* and the complex of species close to *L. branchialis*, synonymising them with *Tiliqua* on the basis of tooth morphology and the separation of the parietal shields, although retaining them in a separate division of the genus on the basis of an incomplete subocular row of scales and a longer tail. Smith recognised in this group only the species *casuarinae*, *branchiale*, *wood-jonesi* and *gastrostigma*, apparently following the classification of Zeitz (1920).

Amongst the large bluetongues, changes were relatively few in the half-century after Boulenger (1887).

The question of the status of *T. gigas vis-à-vis T. scincoides* remained unresolved. Although Boulenger (1887) had recognised *T. gigas* as specifically distinct, he based his concept of the species only on material from the Moluccas. Boulenger (1895, 1897) subsequently assigned material from New Guinea to this species, as did a number of other authors (Boettger, 1893, 1897; De Jong, 1930; de Rooij, 1915, 1919; De Rooy, 1909, 1922; De Vis, 1890a,b, 1892b, 1893; Méhelÿ, 1898; Vogt, 1911a,b, 1912; Wandolleck, 1911), although most did little more than list material collected by various expeditions. Werner (1901) considered that *T. gigas* was more similar to *T. nigrolutea* than to *T. scincoides*.

Oudemans (1894) described a subspecies, *T. gigas* var. *keyensis* from the Key Islands in the Arafura Sea, basing his description on two specimens collected by the Wertheim expedition of 1888. The race was diagnosed on the basis of the combination of a tail length like *T. gigas*, limb lengths and temporal scalation like *T. scincoides*, an intermediate number of midbody, paravertebral and ventral scales, and coloration differences. In making comparisons to *T. scincoides* and *T. gigas*, he noted the great variability in the cephalic scalation in these taxa. Additional material of *T. g. keyensis* was reported by Roux (1910), who unnecessarily emended the subspecies name to *keiensis*.

The subspecific validity of *T. g. keyensis* (as *keiensis*) was accepted by Barbour (1912) and de Rooij (1915), who also only reported the species from the Kei Islands. Subsequently, Kopstein (1926) and Brongersma (1933a) reported the subspecies from the Tenimbar and Babber Islands to the west.

Burt and Burt (1932) provided the first morphometric and scalational data on the eastern New Guinean populations, noting that the forelimb length was shorter than previously reported for *T. gigas*, and more similar to *T. g. keyensis*. They suggested that with further material, it may be possible to apply that name to eastern New Guinean populations.

Loveridge (1948) went even further, using the combination in *T. gigas keyensis* of characters otherwise typical of either *T. gigas* or *T. scincoides* to reduce *T. gigas* to a race of *T. scincoides*.

The 1894 Horn Expedition to central Australia collected two lizards from northern South Australia that were identified as *Tiliqua occipitalis* by Lucas and Frost (1896b), although several differences in coloration and scalation were noted. The same form was independently described as a subspecies of *T. occipitalis* three times in the next 35 years: Sternfeld (1919) described *T. o. multifasciata* from four specimens from Hermannsburg; Glauert (1923) described *T. o. nossiteri* from four from Wallal, W.A., while Kinghorn (1931) described *T. o. auriculare* from a specimen from Broome. Although Sternfeld (1919) merely provided a description without comparisons with *T. occipitalis*, comparisons were given by Sternfeld (1925), who also suggested that eastern and western populations of *T. o. occipitalis* may be subspecifically distinct. Glauert (1960) synonymised his subspecies with that of Sternfeld, while Kinghorn's subspecies was synonymised by Loveridge (1934).

An inability by local herpetologists to locate additional material of *T. adelaidensis* led to some doubt as to its identity. Lucas and le Souef (1909) noted claims by Peters (1864a) and Strauch (1866) that the types were juveniles and suggested that the name had been applied to juveniles of another species. This suggestion was also carried by Waite (1929) (who erroneously attributed it to Lucas and Frost). However, material collected in 1947 and reported by Mitchell (1948) led to a redescription of the species, as part of a complete revision of the genera *Tiliqua* and *Egernia* (Mitchell, 1950).

Mitchell (1950) used the combination of tooth shape and an osteological character, the exclusion of the suture between the palatine and pterygoid from the infraorbital vacuity by the palatine process of the ectopterygoid, to separate *Tiliqua* from *Egernia*. An emphasis on the palatine process of the ectopterygoid, however, led to the return of *Cyclodus luctuosus* to *Tiliqua* and uncertainty over the position of some members of the *Egernia whitii* species group, which showed a less developed process. Mitchell resolved this apparent intermediacy by suggesting that the *E. whitii* group was “archaic”, and that *Tiliqua* and the other *Egernia* were “recent” independent derivations from the primitive condition. Mitchell accepted Smith's (1935) transfer of *Omolepida* to the synonymy of *Tiliqua*, and added *Hemispheriodon*, noting that the enlarged molariform teeth of the latter were also present in subadults of some *Tiliqua* species. He also considered the characters previously employed to distinguish

Trachysaurus from *Tiliqua* (presence of an azygous occipital, divided subdigital lamellae, and a short, blunt tail; he failed to mention the thick osteoderms (Gray, 1825) or the conical teeth (Wagler, 1830)) to be of no use for a generic separation, and synonymised it with *Tiliqua*. Thus, Mitchell's concept of the genus was the broadest of all workers.

Mitchell recognised nine species and an additional five subspecies in *Tiliqua*: *T. luctuosa*, *T. rugosa*, *T. adelaidensis*, *T. s. scincoides*, *T s. gigas*, *T. s. keiensis*, *T. nigrolutea*, *T. o. occipitalis*, *T. o. multifasciata*, *T. b. branchiale*, *T. b. woodjonesii*, *T. gerrardii*, *T. c. casuarinae* and *T. c. petersi*. He synonymised with *T. branchiale* both *Lygosoma melanops* and *L. gastrostigma* and accepted Loveridge's views on the relationship of *L. petersi* with *T. casuarinae*, although going even further by suggesting that the differences between the two were slight. For *T. scincoides*, he retained Loveridge's (1948) subspecific arrangement, although not rejecting the possibility of specific differentiation.

While Mitchell examined larger series of some taxa than previous authors, he examined very few characters. Consequently, his redescriptions were extremely scanty, and lack adequate assessment of variation. For example, his examination of 32 *T. s. scincoides*, all but four from South Australia, resulted only in a range of variation for midbody scales and dark bands on body and tail, values of snout-vent length and tail length for an “average adult”, the observation that the prefrontals were in contact and the nasals usually in contact, and a comment that the four non-local specimens (from Queensland and Groote Eylandt) were longer than local material and possessed a distinctive color pattern. His morphological description of *T. nigrolutea* (based on three specimens) is even briefer: “midbody scales 28 or 30; four supraoculars; five or six supraciliaries. Measurements of an average adult. 376 (251 + 125) mm.”

The generic level changes proposed by Mitchell were not accepted by all subsequent workers. The *Egernia luctousa* complex (with a second species, *E. coventryi*, described by Storr, 1978b) was retained in *Tiliqua* by Glauert (1960) and Worrell (1963). However, Mitchell's retention of the group in *Tiliqua* has been universally rejected by subsequent workers (Cogger, 1975; Greer, 1979a, 1989; Horton, 1972; Hutchinson, 1981; Rawlinson, 1969; Storr, 1978b). Phenetically, both species are similar to other *Egernia* species, and very different to bluetongues. The only grounds ever advanced for their association with *Tiliqua* have been the complete subocular row and a robust palatine process of the ectopterygoid. However, both characters are also seen in other *Egernia* species, and there seems to be little doubt that the *Egernia luctuosa* complex is not, or only distantly, related to the bluetongues (see Chapter 3).

The synonymy of *Trachydosaurus* has been more controversial. Copland (1953) wished to retain *Trachydosaurus* “if only on the grounds of its gross scalation”. Mertens (1958a) informally resurrected *Trachydosaurus*, but reserved his justification for publication in a report on his 1957 Australian expedition. This appears not to have been published. Glauert (1960) used the blunt tail as a diagnosis for the genus, while Worrell (1963) used both the tail and the rugose scalation. Cogger (1975) noted the short tail, rugose scalation and mostly divided subdigital lamellae. Cogger (1983b) justified his continuing recognition of *Trachydosaurus* by stating “I believe . . . that the available morphological, biological and geographic evidence suggests that the shingle-back/blue-tongue divergence was earlier than, rather than approximately contemporaneous with, the radiation of the blue-tongued lizards in Australia”, apparently hypothesising a sister-group relationship with *Tiliqua* (inclusive of *Omolepida*/*Cyclodomorphus* and *Hemisphaeriodon*). However, no evidence was advanced in support of this hypothesis. *Trachydosaurus* was also recognised by Wells and Wellington (1984, 1985), who did not diagnose the genus. In contrast, *Trachydosaurus* has been considered synonymous with *Tiliqua* by several other authors (Storr, 1965a,b; Rawlinson, 1966; Greer, 1979a; Hutchinson, 1981).

Most authors have continued to regard *Hemisphaeriodon* as synonymous with *Tiliqua*. However, Wells and Wellington (1984, 1985) and Cogger (1989a) have resurrected the genus without diagnosis, and Czechura (1986) placed *gerrardii* with *Cyclodomorphus*.

Omolepida (or as it should be correctly known, *Cyclodomorphus*) was resurrected from the synonymy of *Tiliqua* by Storr (1964, 1976). Storr (1976) differentiated *Omolepida* from *Tiliqua* by the fragile tail, absence of occipital scales, and unpigmented (rather than blue-black) tongue, although he apparently based his diagnosis solely on the Western Australian taxa, and not on the type species, *C. casuarinae*. *Cyclodomorphus* was also recognised by Cogger (1989a), Czechura (1986), Shea and Wells (1985), Shea (1988), Wells and Wellington (1984, 1985) and Wilson and Knowles (1988), although none of these authors diagnosed the genus. It was not recognised by Greer (1979a, 1989), Hutchinson (1981) and Cogger (1983b). Of these three, Greer did not offer any justification. Cogger (1983b) stated "there is a continuum of character states linking the extreme expression of *Tiliqua* via *Hemisphaeriodon* with that of *Omolepida* (=*Cyclodomorphus*)", although he did not provide any analysis of characters to support this view.

Of all of the authors assessing Mitchell's generic arrangement, only Hutchinson (1981) has provided any new data. Using serum immunoelectrophoresis with a single *T. rugosa* antiserum. he found little antigenic difference between *T. rugosa* and *T. scincoides*, a greater divergence between *T. rugosa* and *T. casuarinae*, and *T. gerrardii* the most divergent. Hence, he concluded, "to separate *T. rugosa* or *T. casuarinae* [from *Tiliqua*], and not *T. gerrardii*, as has been suggested [by Storr, 1976], is quite inconsistent with the IEP results". By comparison with *Egernia*, which showed greater intrageneric variation to *E. cunninghami* antiserum than occurred between *T. rugosa* and *T. gerrardii*, yet was still treated as a monophyletic unit, *Cyclodomorphus* was regarded as synonymous with *Tiliqua*.

Below the generic level, there have been few recent changes to the taxonomy advanced by Mitchell.

Although northern Australian material of *T. scincoides* had been available to herpetologists for many years (Gray, 1845; Boulenger, 1887; Lönnberg & Andersson, 1913), only Macleay (1888) had suggested (though even then not explicitly) that more than one taxon occurred in Australia. Following the collection of additional material from Arnhem Land, Mitchell (1955, 1964) reassessed his earlier (Mitchell, 1950) comments on the variation in size and coloration, and described a northern Australian race, *T. s. intermedia*. However, although he had previously noted that north-eastern Queensland specimens were similar to Northern Territory material, he only described his new race from the more recent Groote Eylandt and Arnhem Land material, and did not compare it to non-Australian taxa. While Glauert (1960) reported the race from Western Australia, the identity of the north Queensland populations, and their relationship to New Guinean populations, remains unclear. Most authors have informally recognised *T. gigas* as specifically distinct (Cogger, 1972b, 1975; Greer, 1979a; Pernetta, 1983; Scott *et al*., 1977; Shea, 1982a; Whitaker *et al*., 1982), although Zweifel (1980) retained it as a subspecies. None of these authors, however, offer any justified reassessment of the taxonomic status of the taxon. There has also been some suggestion, again unsupported, that *T. s. intermedia* warrants specific status (Wells and Wellington, 1984; Hoser, 1989). Within eastern Australia, geographic variation has been reported in *T. scincoides* (Worrell, 1963; Frauca, 1973; Covacevich, 1987; Wilson & Knowles, 1988; Hoser, 1989), and Wells and Wellington (1985) diagnosed a new species (*Tiliqua macroscincoides*) on the basis of a single specimen from near Mt Carbine in Queensland.

Worrell (1963, 1966) reported two geographically distinct morphs of *T. nigrolutea*, a northern, high altitude form and a southern, low altitude form, differentiated on the basis of coloration and size. The same pattern of variation has also been reported by Bustard (1970), Swanson

(1976), McPhee (1979), Jenkins and Bartell (1980) and Griffiths (1984), culminating in the naming of the western mainland population of the lowland morph as *Tiliqua milleri* by Wells and Wellington (1985). Although they designated a holotype, they based their concept of the taxon on Worrell's (1963) labelled illustration.

Geographic variation has also been reported in *T. rugosa*. Werner (1910) described the distinctive coloration of the Rottnest I. population, while the extensive geographic and individual variation in coloration on the mainland has been noted by many (e.g., Bustard, 1970; Cogger, 1975; Swanson, 1976; Wilson & Knowles, 1988; Worrell, 1963). Mertens (1958a) described the Rottnest I. population as a distinct race, *T. r. konowi*, and suggested that the mainland populations could be divided into two races, *T. r. rugosa* and *T. r. asper*, although his justification for the latter suggestion was never published. Cogger (1979a) accepted Merten's statement, although inadvertantly transposing the names (H.G. Cogger, *pers. comm.*). Wells and Wellington (1984) raised all three subspecies to species level. Significant differences in morphology between eastern and western populations in Western Australia were noticed by Bamford (1980). McIlroy *et al*. (1985) report marked differences between eastern and western populations in sensitivity to the poison 1080, while Joger *et al*. (1986) report preliminary electrophoretic data indicating a difference in mobility of albumin between populations, which they interpreted as warranting subspecies recognition. Most recently, comparisons between South Australian insular populations and the adjacent mainland using both electrophoresis (Sarre *et al*., 1990) and external morphology (Sarre & Dearn, 1991) have demonstrated significant geographic variation, even between adjacent islands.

The subspecific status of *T. o. multifasciata* has been challenged within the last 25 years by reports of overlapping geographic distributions and actual sympatry with the nominate race (Cawood, undated; Burbidge *et al*., 1976; Pianka, 1972; Shea & Peterson, 1981; Fyfe, 1980a, 1985), and *T. o. multifasciata* was raised to a full species by Pianka (1969, 1971, 1972). This action has received universal support.

Mitchell's (1950) treatment of the *T. branchialis* complex was not accepted by Glauert (1960) and Worrell (1963). Glauert recognised three species in Western Australia: *T. branchialis*, restricted to the type locality; *T. melanops*, from Perth to South Australia, and *T. gastrostigma*, from the Pilbara, although noting that the three taxa may be only subspecifically distinct. Worrell (1963) retained the same three species, together with *T. woodjonesii* (raised to species level) and *T. casuarinae petersi*, although noting that further revision might result in the synonymy of the latter two taxa. Mitchell himself apparently subsequently altered his opinion on the synonymy of *melanops* with *branchialis*, for Warburg (1965b) quotes a communication from Mitchell to the effect that his material listed in 1950 as *T. branchialis* should be *T. melanops*.

Storr (1976) placed all previous names in the *branchialis* complex in the synonymy of *Omolepida branchialis*, and described a new species, *O. maxima* from the northern Kimberley. He further suggested that there remained much geographic variation in *O. branchialis*, some of which may warrant subspecific recognition. Further undescribed taxa were reported in the complex by Ehmann (1983) and Schwaner (1982).

In summary, there remain several unresolved issues in bluetongue systematics. At the generic level, there is a core of six species or subspecies that have consistently been associated in the one genus: *Lacerta scincoides* [Hunter], 1790; *Scincus gigas* Schneider, 1801; *Scincus nigroluteus* Quoy and Gaimard, 1824; *Cyclodus adelaidensis* Peters, 1864, *Cyclodus occipitalis* Peters, 1864 and *Tiliqua occipitalis multifasciata* Sternfeld, 1919. The relationships to this core (*Tiliqua* s.s.) of the species assigned to *Trachydosaurus*,

Hemispheriodon and *Cyclodomorphus* remain contentious. Even within the core, relationships have not been explored.

If one excludes the unsubstantiated proposals of Wells and Wellington (1984, 1985), several taxa within these groups have been consistently recognised as panmictic: *T. adelaidensis*, *T. occipitalis*, *T. multifasciata*, *Hemisphaeriodon gerrardii* and *Cyclodomorphus casuarinae*. There is known to be geographic variation in *Tiliqua nigrolutea* and *Trachydosaurus rugosus*, although the extent of the variation and its taxonomic relevance remains unknown. There remains confusion over species and subspecies boundaries within the *Cyclodomorphus branchialis* complex and between *T. scincoides* and *T. gigas* and their described subspecies.

Much of the lack of resolution and confusion would appear to be a direct consequence of a lack of data. The largest sample used in the initial description of any nominal species or subspecies in the group is six specimens, for *T. s. intermedia*. Many of the taxa were described from single specimens. Outside of the work of Storr (1976) on the *C. branchialis* complex, the largest stated sample used in redescribing any taxon, or for comparison with a newly described taxon is 43 (*T. rugosa*, Mitchell, 1950), and even this sample is very geographically restricted.

Small sample sizes and geographically restricted samples were acceptable to the typological philosophy in effect last century and early this century. However, the 40 years since the time of Mitchell's (1950) revision have seen a revolution in biological thinking. Foremost in this have been the change to a population-based approach in evaluating and defining species (e.g., Mayr, 1963), and the advent and subsequent development of a cladistic approach to the inference of relationships and the recovery of evolutionary history (Hennig, 1966; Eldredge & Cracraft, 1980; Wiley, 1981).

While the typological approach is maintained in the system of binomial nomenclature, various formal definitions have since been applied to the species category, all of which recognise that the species category defines naturally-occurring groups of individual animals, i.e., populations and groups of populations. Such concepts include the biological species concept (Mayr, 1963), and the related recognition concept (Lambert & Paterson, 1984; Paterson, 1985), the evolutionary species concept (Wiley, 1978, 1981) and the phylogenetic species concept (Nelson & Platnick, 1981; Donoghue, 1985).

The cladistic approach to estimating phylogenies is based on recognition of the fact that characters shared by members of a monophyletic group may have evolved in the immediate ancestor of that group (synapomorphies) or may have been retained from a more remote ancestor (symplesiomorphies) (Hennig, 1966). Logically, only synapomorphies provide evidence of relationship. Ultimately, the cladistic approach uses sets of synapomorphies to reduce the relationships between taxa to a nested set of three taxon statements of the type “taxon A is more closely related to taxon B than either is to taxon C” (Eldredge & Cracraft, 1980).

Neither modern species concepts nor a cladistic approach to phylogenetic reconstruction have previously been applied to bluetongue systematics. Further, it is clear that to apply these two approaches to bluetongue systematics requires a larger data base than has been previously compiled or analysed. New characters must be identified, and their consistency within and between populations must be examined. In particular, species must be examined throughout their geographic distributions.

The primary purpose of this thesis, then, is to address the systematics of the bluetongues, to attempt to resolve the conflicting opinions of previous workers, and to provide a sound basis

for the construction of hypotheses of relationship. In particular, I see three phases to the primary objective:

- 1. The demonstration of the monophyletic nature of the bluetongues as a group (Chapter 3). This serves two purposes. Firstly, it defines the scope of the subsequent investigation, by restricting the study to the members of a single lineage, and examining all taxa within that lineage. Secondly, recognition of a monophyletic group permits one to use that lineage as a taxonomic unit, and hence, from a systematic viewpoint, to subsequently hypothesize the relationships of that unit. This in turn defines outgroups which can be used to assess the polarity of characters used in estimating intragroup phylogenetic relationships.
- 2. The evaluation and definition of the taxonomic units (species and subspecies) within the genus by examining geographic variation within taxa and the morphology of different taxa in regions of sympatry (Chapters 4–10). Without such identifiable taxonomic units, the final phase of the project cannot be undertaken.
- 3. The estimation of evolutionary relationships between the taxa within the lineage (Chapter 11).

The results of these analyses can be interpreted and applied in three ways. Firstly, at the purest level, the project studies evolution, one of the bases of biological science. Secondly, the dissertation provides a well-corroborated phylogenetic framework on which the present and future ecological, biochemical, physiological and anatomical data of other workers can be usefully interpreted. Finally, a corroborated phylogenetic hypothesis at low taxonomic level, such as the genus and below in this case, can be used to reduce or remove the effect of one parameter, phylogeny, in testing ecological hypotheses (Shine, 1985; Tinkle & Gibbons, 1977; Stearns, 1983; Dunham & Miles, 1985; Dunham *et al*., 1988). In an Australian context, the bluetongue radiation provides a potentially ideal model to test ecological hypotheses, as various species encompass almost the entire range of terrestrial conditions on the continent, occurring almost throughout Australia, from the northern (Cape York) to the southern (Tasmania) tip, from the east to the west coast, altitudinally from sea level up to the Australian Alps, and from the most mesic habitats (rainforests) to the most xeric (deserts). Amongst the most obvious differences in the ecology of the bluetongue species are reproductive parameters, particularly litter size and size of young (Shine, 1985). This makes the bluetongue radiation a valuable test of hypotheses of the evolution of brood size in lizards (Greer, 1989). As reproduction is an important component of a taxonomic revision of the lineage, to assess the effect of sex on morphological variation, and as part of an assessment of reproductive compatability, this project was felt to be an opportune moment to apply the reproductive data to the derived phylogenetic hypotheses, and hence to test (Chapter 12) theories of the evolution of brood size (Stearns, 1976; Ballinger, 1978).

Chapter 2 Materials And Methods

2.1 Approach

Approaches to systematic studies have developed along two lines. The traditional approach has used morphological data. More recently, molecular data has been used to resolve systematic problems. Each approach has some advantages over the other (Hillis, 1987). The morphological approach, based on comparative anatomy, has had much the longer history. Material for morphological studies has generally been stored in museum collections, and represent the combined results of several generations of collectors. Consequently, potential sample sizes are greater and geographic representation is often more complete. Unlike most molecular approaches, workers are not dependent on the acquisition of fresh material collected specifically for the project.

Additionally, the reconstruction of phylogenetic history requires comparative data on related outgroups to give direction to the pattern of character states used to infer relationships. Comparative morphological data, both specimen-based and literature-based, is much more extensive than comparative molecular data.

Hillis (1987) outlines four advantages of molecular methods over morphology: size of the data set, more extensive phylogenetic limits, detection of cryptic species and the reduced extent of nonheritable variation.

I do not believe that any of these proposed advantages are applicable to bluetongue systematics.

While the potential data base available from molecular data, particularly DNA sequencing, is enormous, in practical terms there are very few such data presently available for reptiles, and even fewer for closely related groups of reptiles. The only sequencing data published for skinks are small-unit ribosomal RNA sequences for *Tiliqua rugosa* and the distantly related *Ctenotus robustus* (Baverstock *et al*., 1991).

Secondly, at low phylogenetic levels, as in the present study, an extended phylogenetic scale to the data is of no relevance.

Allozyme electrophoresis has been used to great effect in detecting cryptic species (e.g. for skinks, Daugherty *et al*., 1990; Donnellan & Aplin, 1989; Donnellan & Hutchinson, 1990; Harris & Johnston, 1977; Hutchinson & Schwaner, 1991; Mather, 1990). However, despite these apparent successes, my experience with skinks has been that given samples adequate for determining the extent of morphological variation, many of the “cryptic” species initially detected by allozyme electrophoresis are morphologically well-differentiated, and that the “success” of the technique in many cases simply reflects an absence of detailed comparative morphological research. For example, although Donnellan (1991b) described *Lampropholis* species as “intractable small brown skinks”, and attempted to resolve the alpha-systematics of the genus with karyotypic data, the literature on morphology is limited to the initial descriptions of species, with no attempt to explore geographic variation. Indeed, application of electrophoresis in detecting cryptic species has largely been limited to those complexes that have “a wide geographical or altitudinal range, occupy several habitats, or show unaccountable morphological variation” (Donnellan & Aplin, 1990). Recognition of such attributes has largely been morphology-based.

Finally, nonheritable variation in morphology, while common in invertebrates, appears to be rare in reptiles, at least to the point where it has not been demonstrated to be a significant problem in systematic studies.

Therefore, there appear to be no clear advantages to the use of biochemical techniques. Indeed, with regard to bluetongue systematics, there are disadvantages to a molecular-based approach. Most obvious, particularly from the point of view of distinguishing taxa, is the problem of availability of material representing all parts of the distribution. At least one modern species of *Tiliqua*, *T. adelaidensis*, is apparently now extinct (Ehmann, 1983). Many populations in remote areas, such as those in Indonesia, New Guinea and central Australia, cannot be readily sampled at the present time. Of the Indonesian populations, the Babber, Tenimbar, Kei and Aru Island *Tiliqua* have not been sampled since the early part of the century, through the combination of geographic remoteness and political instability. Further, from the point of view of inferring phylogenetic relationships, while the morphology of the outgroup taxa is reasonably well studied, molecular data are lacking.

I believe that any future molecular studies of *Tiliqua* will be best served by a present-day morphology-based systematic study.

Consequently, for this study, a morphological approach has been used. Four main character systems were examined: scalation, external proportions, coloration and osteology. These four systems were chosen on the basis of the ease of collection of data, and the availability of data (both literature-based and specimen-based) on character states from outgroups. The first three character systems are external characters, readily studied on whole individuals, both live and preserved, while the latter system represents hard tissues, readily dissected, and for which there is a reasonable body of comparative data. Soft tissue characters were not examined, due to the almost complete absence of comparative data for outgroups. Karyotypic data were also not studied. Karyotypes of most *Tiliqua* species have been presented by King (1973a,b), De Smet (1981a) and Donnellan (1985, 1991a). The uniformity of the karyotype, within *Tiliqua* and its nearest outgroups, renders it uninformative at the level of this study.

2.2 Materials

This study is based mostly on whole preserved museum specimens. All available specimens of seven large *Tiliqua* species (*T. adelaidensis*, *T. gigas*, *T. multifasciata*, *T. nigrolutea*, *T. occipitalis*, *T. rugosa*, *T. scincoides*) in Australian museum collections were examined, together with all identifiable types and some non-type material in European and U.S. museum collections. A total of approximately 3150 specimens of these taxa was examined.

Preliminary investigations suggested that these seven species formed a monophyletic group, with the other taxa variably referred to *Tiliqua* (*casuarinae*, *gerrardii* and the *branchialis* complex) being the sister group to *Tiliqua* (see Chapter 3). Consequently, only representative samples of the latter taxa were examined in this study, for the purposes of diagnosing the genera (Chapter 3), and for outgroup comparisons (Chapter 11). A more thorough investigation of the alpha-systematics of the *branchialis* complex is being made by Shea and Miller (in prep.).

Limited series of other skink species, particularly *Egernia* species, were also examined for outgroup comparisons.

Material from the following institutions was examined (acronyms in parentheses): American Museum of Natural History, New York (AMNH); Australian Museum, Sydney (AM); Australian National Wildlife Collection, Canberra (ANWC); Bernice P. Bishop Museum, Honolulu (BPBM); Brigham Young University, Salt Lake City (BYU); Central Australian Wildlife Collection, Alice Springs (CAWC; collection now held in Northern Territory Museum); Field Museum of Natural History, Chicago (FMNH); Macleay Museum, University of Sydney (MMus); Museum National d'Histoire Naturelle, Paris (MNHP); Museum of Comparative

Zoology, Harvard University, Cambridge (MCZ); Museum of Victoria, Melbourne (MV); Nationaal Natuurhistorisch Museum, Leiden (RMNH; formerly Rijksmuseum van Natuurlijke Historie); National Museum of Natural History, Washington (USNM); Natural History Museum, London (BMNH; formerly British Museum (Natural History)); Naturhistorisches Museum, Basel (NHMB); Naturhistorisches Museum, Vienna (NHMW); Northern Territory Museum, Darwin (NTM); Queensland Museum, Brisbane (QM); Queen Victoria Museum, Launceston (QVM); South Australian Museum, Adelaide (SAM); Tasmanian Museum, Hobart (TM); Western Australian Museum, Perth (WAM); Zoological Institute, Academy of Sciences of the USSR, Leningrad (ZIL); Zoologische Museum, Universiteit van Amsterdam, Amsterdam (ZMA); Zoologisches Museum, Universität Humboldt, Berlin (ZMB).

Some additional material was collected from the field.

Dry and alizarin-stained wet osteological preparations were either borrowed already-prepared from museums (AM, AMNH, QM, QVM, SAM), or prepared from wet or dry museum and field-collected material. Some osteological data was obtained from radiographs of whole preserved animals.

While most data were gathered during the course of candidature for this degree, some unpublished data for *T. rugosa* gathered by the author from WAM specimens between 1980 and 1983 were also incorporated. With a few exceptions (mostly incidental), these specimens were not re-examined specifically for this project, to save time. The full range of characters could not be scored on such specimens, as some characters were added since 1985.

2.3 Preparation of Specimens

Live field-collected specimens were euthanased with diluted Sodium Pentobarbitone euthanasia solution, fixed with 10% formalin injected intraperitoneally and into large muscle masses, and stored in 75% ethanol. Specimens were set with body and tail stretched out in a straight line, and brachium and thigh at right angles to the axis of the body (Cogger, 1986). Some specimens were set with mouth open, to facilitate examination of the dentition and oral cavity.

Dry osteological material was prepared from either preserved museum material or field-collected dried specimens. Dried carcasses were macerated in water for several days prior to preparation. In both preserved museum specimens and soaked dry material, the skin was dissected free, and most soft tissue removed manually from the skeleton by picking away with forceps and scalpel. When most soft tissue had been removed, the skeleton was soaked in a dilute bleach solution to dissolve the remaining soft tissue and bleach the bones. Bones were then washed in water and left to dry in a warm place. Some osteological preparations were fully disarticulated, some partially articulated.

In order to examine the relationships of sesamoids and carpal, tarsal, metapodial and digital elements, some limbs were removed whole from preserved specimens and prepared as cleared and stained specimens. Such specimens were double stained with alcian blue and alizarin red for cartilage and bone, using the methods of Hankin and Wassersug (1981).

Some osteological data (particularly vertebral and phalangeal counts) were also gathered from radiographs. Whole specimens were radiographed, using an industrial X-ray unit ("Eresco"; Rich. Seifert & Co.) and Agfa Stucturix DP4 film. Typical dosages for small specimens were 30kV, 5mA and a 40sec exposure.

To test an assumption that seasonal changes in testis size were related to sperm production (see also sections 2.4.5 and 2.5, and chapters 9, 12), histological sections of testes and epididymides of selected *T. s. scincoides* were examined. A 3–4mm thick transverse section from the middle of the right testis, and a similar mid-length section of epididymis were cut with a scalpel. Samples were dehydrated through graded alcohols, cleared in chloroform and embedded in paraffin wax using standard techniques. Sections were cut at 5–7µm, mounted on glass slides and stained with Harris' haematoxylin and eosin (N. Kelly, *pers. comm.*).

2.4 Selection And Definitions Of Characters

2.4.1 Scalation

The large, regular head shields and imbricate body scales of skinks have provided a range of characters widely used by systematists. Scalational characters used in this study were selected initally from this range, with particular emphasis on those previously used to differentiate *Tiliqua* species.

As this project developed, some additional scalation characters showing geographic and interspecies variation were noted. Where possible, such characters were added to the list of those scored for each specimen, although in the case of some characters added late in the study, it was impractical to re-examine all material previously seen. A few head scale abnormalities seen in occasional specimens were also noted, although not scored for each specimen.

The following 28 scalation characters were examined for each specimen:

1. Nasal scales: Bilaterally paired scales dorsolaterally on the snout, characterised by the presence of a nostril (Peters, 1964). The degree of separation of the nasal scales on the dorsal midline has been widely used in skink systematics (e.g., Storr, Smith & Johnstone, 1981; Cogger, 1986; Greer & Cogger, 1985). In the present study, the degree of separation (by contact of rostral and frontonasal) or the length of the suture of contact was subjectively estimated using the following range of states: broadly separated, moderately separated, narrowly separated, point contact, narrow contact, moderate contact, broad contact. All *Tiliqua* modally have the nasal scales separated.

2. Postnasal: Many relatively primitive skinks have the nasal scale bordered dorsally by a narrow supranasal scale and caudally by a narrow postnasal scale. In *Tiliqua*, supranasal scales are absent (presumably fused to the nasal), while only the ventral end of the postnasal scale is distinct, leaving the compound nasal scale with a vertical suture from its ventral margin, bordering the caudal margin of the nostril. The presence of a postnarial suture is a character often used in skink systematics (e.g., Storr, 1978b), and has previously been used in bluetongue systematics by several authors (e.g., Duméril & Bibron, 1839; Smith, 1937; Mitchell, 1950). For this study, three states were scored: postnasal completely distinct from nasal (i.e., suture extends to dorsal margin of nasal); postnasal fused dorsally to nasal/supranasal (i.e., suture ends dorsally within scale, usually towards caudodorsal margin of nostril), and postnasal completely fused to nasal/supranasal (i.e., no suture).

3. Prefrontals: Bilaterally paired scales dorsally on head, immediately bordering rostral margin of frontal, and lying slightly rostral to level of orbit (Peters, 1964). The degree of separation or contact of the prefrontals has been widely used in skink systematics (e.g., Storr, Smith & Johnstone, 1981; Ingram & Covacevich, 1989; Greer, 1990). The degree of separation (by contact of frontal and frontonasal) or contact of prefrontals was subjectively estimated using the following range of states: broadly contacting, moderately contacting, narrowly contacting, point contact, narrowly separated, moderately separated, broadly separated. All *Tiliqua* species modally have the prefrontals in contact.

4. Supraoculars: Enlarged shields dorsally on head, covering the dorsum of the orbit (Peters, 1964). Although the number of supraoculars and their relationship with the frontal shield has been widely employed in skink systematics, often at the generic level (e.g., Greer, 1974), there is some disagreement in the literature as to which scales should be termed supraoculars (Mitchell, 1950, for bluetongues). In this study, the supraoculars form a broad, low triangle of scales, with apex directed medially. The scales in the series lie in a longitudinal line, with lateral extremities level, although the long axis of each scale is transverse. The first supraocular is roughly triangular and contacts the frontal medially, usually the prefrontal rostrally, and the supraciliary row laterally. The last supraocular, also roughly triangular, contacts the frontoparietals and parietals medially and caudally, and the supraciliaries laterally (Fig. 1A). Both the number of supraoculars on each side, and the number of supraoculars contacting the frontal were scored.

5–7. Supraciliaries: A longitudinal row of small scales, lying lateral to the supraoculars, and bordering the dorsal margin of the orbit (Peters, 1964). The first supraciliary rostrally contacts the prefrontal and the second loreal. Although there is disagreement as to the caudal extent of the supraciliary row, I treat the last supraciliary as the generally slightly larger scale bordering, and projecting between, the last supraocular and the parietal (Fig. 1A). This scale is not included as part of the supraciliary row by some authors (e.g., Greer, 1982a, 1983a; Sadlier, 1986; Storr, Smith & Johnstone, 1981), although my treatment is the same as that used by Taylor (1935). Three aspects of the supraciliary scales were examined and scored in this study: 1. the number of supraciliaries on each side; 2. the degree of separation or contact of the first supraciliary and the frontal, and 3. the degree of separation or contact of the last supraciliary and the frontoparietal (the latter two characters subjectively estimated). Although there was some variation in the number, size, shape and relationships of the supraciliary scales, a modal number of supraciliaries with a consistent pattern of relationships to surrounding scales was apparent in most taxa.

8. Frontoparietals: Bilaterally paired scales on the dorsum of the head, immediately caudal to the level of the orbit, and between the frontal and the parietals (Peters, 1964). The presence of fused frontoparietals is a commonly used diagnostic character in skink systematics (e.g., Greer, 1974; Hutchinson *et al*., 1990). Frontoparietals are paired in all *Tiliqua*. However, the degree of contact between frontoparietals is variable within and between *Tiliqua* species, with separation occurring in some *T. multifasciata* (Mitchell, 1950). The degree of contact or separation of the frontoparietals was subjectively assessed using the following range of states: broadly contacting, moderately contacting, narrowly contacting, point contact, narrow separation, moderate to broad separation.

9. Occipitals: Head scales caudal to and bordering the parietals and interparietal (Peters, 1964). Although many skinks have a pair of transversely dilated scales (nuchals) caudally bordering the parietals and interparietal, bluetongues either lack scales sharply differentiated from succeeding body scales, or have longitudinally expanded scales in this region. The number of scales bordering the parietals has been employed as a taxonomic character in skinks (e.g., Greer, 1979a; Greer & Kluge, 1980). I count occipitals on each side of the dorsal midline as those scales contacting the parietal, extending rostrolaterally to the rather larger upper secondary temporal scale, which lies lateral to the parietal (Fig. 1A). Additionally, the presence of an azygous median occipital, bordering the interparietal, was noted.

10. Loreals: Shields laterally on the snout, in an area bounded by the nasal/postnasal complex rostrally, frontonasal and prefrontal dorsally, first supraciliary and presuboculars caudally, and supralabials ventrally (Peters, 1964). Most skinks, including bluetongues, modally have two loreals, one rostral, one caudal. Variants scored in bluetongues include a

single loreal, three loreals in horizontal series, and vertical division of one or both loreals into an upper and lower scale.

11. Presuboculars: There is much disagreement amongst herpetologists as to the nomenclature for the scales forming the rostroventral part of the scaly orbit (for examples of conflicting opinions, see Greer, 1982a; Peters, 1964; Rankin, 1979; Sadlier, 1984; Storr, 1978a, 1991; Storr, Smith & Johnstone, 1981), although the arrangement of the scales in this region is of systematic importance. Most skinks have an incomplete ring of scales around the ventral margin of the orbit, with the ring broken ventral to the eye by at least one supralabial scale. The subocular ring of scales is thus clearly divided into a presubocular and postsubocular series. In the bluetongues, which have a complete subocular ring of scales, I define as presubocular scales those scales ventrally contacting the supralabial series, from the first scale caudal to the loreal series to the last scale contacting both the subocular supralabial (see below) and the supralabial immediately rostral to it (Fig. 1B). The first presubocular lies below the first supraciliary, and may or may not contact it. A presubocular series defined in this way seems to be most nearly homologous to the distinct presubocular series in the closest outgroups, in which the caudalmost presubocular dips between the subocular supralabial and its antecessor.

12. Suboculars: I define the suboculars as the scale or scales of a complete subocular ring bordering only the subocular supralabial, but not the preceding or succeeding supralabial. In other words, they lie between and link the presubocular and postsubocular series (Fig. 1B).

13. Postsuboculars: A curved line of small scales forming the caudoventral and caudal margin of the orbit (Fig. 1B). The number of scales in this series (which as defined here also includes the lower pretemporal scale of Greer, 1983a), has rarely been used in skink systematics.

14–16. Supralabials: The number of supralabial scales is one of the most commonly scored characters in skink systematics. Supralabials are a longitudinal series of scales bordering the margin of the upper lip (Peters, 1964). The first supralabial lies immediately caudal to the rostral scale, and is followed by a series of similarly sized scales until the subocular region, which in many skinks (but not bluetongues) is notable for a longer supralabial scale. Immediately caudal to the subocular supralabial in most skinks are two larger, taller scales, followed beyond the commissure of the lips by several much smaller scales which grade into the lateral cervical scalation. The more caudal of the two large supralabials is usually taken to be the last supralabial. In *Tiliqua* species, this scale is much lower than the supralabial preceding it, and is bordered above by a similarly sized scale. Together, these scales are similar to, and probably the homologues of the last supralabial of other skinks.

With the development in *Tiliqua* of heavy, rigid osteoderms in the more caudal supralabials, several species have apparently extended the labial commissure more caudally, and the distinction between the last supralabial and more caudal scales has been lost. This modification is presumably necessary to allow wide opening of the mouth, which would otherwise be constrained by the limited stretch of the skin between the heavy scales. To maintain homologies, the caudal limit of the supralabial series in these taxa was defined as the second supralabial caudal to the subocular supralabial.

Three aspects of the supralabial scalation were scored: the number of scales in the series, division of the penultimate supralabial, and division of the last supralabial (in the latter two states, leaving a lower scale subequal in height to the more rostral scales in the series).

17. Primary temporals: The temporal scales are those caudal to the postsuboculars, between the parietal and the supralabials. In keeping with traditional usage, I have identified

as primary temporals those lying dorsal to the first postocular supralabial and overlapped by it, and contacting the postsuboculars, while the temporal scale actually bordering the parietal is the upper secondary temporal (Fig. 1B). In *Tiliqua*, the primary temporal may be single, double, or absent.

18. Lower secondary temporals: Defined as the second series of temporal scales ventral to, and cranially overlapped by, the upper secondary temporal, and dorsal to, and cranioventrally overlapped by, the last supralabial (or its upper part, when divided) (Fig. 1B). In *T. gigas* and *T. scincoides*, there is only a single series of elongate scales in place of primary and lower secondary temporals. Although these have been called anterior temporals (Boulenger, 1887; Mitchell, 1950; Cogger, 1986), I consider them to be lower secondary temporals that have invaded and replaced the primary temporals. Some *T. nigrolutea* show an intermediate condition, with very reduced primary temporals.

19. Posttemporals: The number of small scales in a horizontal line between the caudal extremity of the lower secondary temporal (or either of its component parts) and the rostral margin of the ear (Fig. 1B). This character does not appear to have been previously used in skink systematics.

20. Rostral ear lobules: A series of small to moderate sized scales lying along the rostral margin of the ear and projecting into the external auditory meatus. Lobules are often inset compared to the other scales forming the margin of the ear aperture. The number and shape of ear lobules has frequently been used in skink systematics (e.g. Greer, 1974; Ingram & Covacevich, 1988, 1989; Storr, Smith & Johnstone, 1981). In *Tiliqua*, the shape of the lobules is variable, even within individuals, although the central lobules, which are largest, usually have rounded free margins. Only the number of lobules was scored in this study, and only the lobules along the rostral margin of the ear were counted (lobules around other parts of the margin were not consistently present). Lobules were not identifiable in *T. rugosa*, in which all the scales around the rostral margin of the ear were nodular and bony.

21. Infralabials: A longitudinal series of scales bordering the margin of the lower lip. The first infralabial lies immediately caudal to the mental (Peters, 1964). The infralabial row, unlike the supralabial series, is not differentiated from more caudal scales in the cervical region. The last in the series was here taken to be the caudalmost scale partly or completely overlapped by the last supralabial with the mouth closed. In *Tiliqua* species, the more caudal scales in the infralabial series are irregularly paired. Only the scales actually contacting the margin of the lip are counted for this character.

22. Infralabials contacting postmental: A widely used character in skink systematics (e.g., Greer, 1983b, 1989). In most skinks, the first two infralabials contact the postmental. The number is variable in *Tiliqua*, from one to three, and often asymmetrical.

23. Midbody scales: The number of longitudinal rows of scales at midbody is one of the most commonly scored characters for skinks. It was first employed in *Tiliqua* systematics by Duméril and Bibron (1839). Because of the oblique orientation of the body scale rows immediately behind the axilla, and the higher number of rows in this region, the count was consistently taken at the midpoint of the axilla-groin interval.

24. Paravertebral scales: The scales along the dorsal midline of the neck and body are paired in most skinks. For this study, paravertebral scales were counted along one or the other longitudinal row from the first scale bordering the parietal/interparietal complex, extending caudally to the last scale cranial to the level of the cranial margin of the hindlimbs when held at right angles to the body. Variation in the count reflects both scale size and the degree of body elongation.

The paravertebral scale count used here differs from that used by other authors (e.g., Brown, 1991; Greer, 1982; Hikida, 1982; Kiester, 1982; Sadlier, 1986; Zweifel, 1972).

The number of paravertebral scales has only recently been regularly examined by skink systematists. However, it was used in *Tiliqua* systematics by Günther (1863), although overlooked by later workers.

25. Axilla-groin scales: In *T. multifasciata* and *T. occipitalis*, the paravertebral scales in the nuchal region are small and very different from more caudal paravertebral scales. In an attempt to isolate the effect of these small, more cranial scales, a second paravertebral count was made, over the trunk only. The count, performed immediately after the total paravertebral count, but in reverse, so as to return over the same path as the former count, was made from the first paravertebral scale cranial to the level of the hindlimbs, cranially to the last scale caudal to the level of the caudal margin of the forelimbs, when held at right angles to the body. In deep-bodied specimens, it was necessary to assess the cranial limit from a lateral aspect.

26. Ventral scales: Counted along the mid-ventral line from the first medial scale caudal to the second pair of chin shields, caudal to the vent. Most recent skink systematists have used ventral scales (e.g., Heyer, 1972; Inger & Hosmer, 1965; Ingram & Covacevich, 1988; Patterson & Daugherty, 1990) or paravertebral scales (e.g., Brown, 1991; Greer, 1982; Greer & Cogger, 1985; Hikida, 1982; Hutchinson & Donnellan, 1988; Kiester, 1982; Zweifel, 1972, 1979), but not both. Despite both reflecting degree of body elongation, the counts show different patterns of variation in *Tiliqua*, possibly due to the hypertrophy of the dorsal scalation in some taxa.

27. Subcaudal scales: Counted, on complete original tails only, along the tail mid-venter, from the first scale caudal to the vent, subequal in size to more lateral scales, distal to and including the terminal sheathing scale. The more proximal scales in the series are paired, while the others are single. Regenerated tails were easily identified by the irregular, often very short scales in the cranialmost transverse series on the regenerated part.

Subcaudal scale counts have been widely used in snake systematics. However, with the exception of one paper (Heyer, 1972), they have not previously been employed in skink systematics, despite the common use of tail length as a diagnostic character in skinks. I have found them of great use in differentiating species of *Tiliqua* and *Egernia*.

28. Subdigital lamellae: The number of lamellar scales below the fourth digit of the pes is a commonly scored character in lizard systematics. The fourth toe is traditionally used because this is the longest toe in lizards with non-reduced limbs, although in *Tiliqua* species the fourth and third toes are of similar length. In many individuals, the lamellae below the toe grade imperceptibly into the palmar granules. In order to standardise counts, I have begun the count from the level of the lowest point of the skin fold between third and fourth digits, and extend the count distally to the terminal lamella bordering the claw. In *T. rugosa*, the more proximal lamellae are irregularly paired, or even divided into three. In this taxon, I have counted each pair or triad of scales as one lamella.

2.4.2. Coloration

Coloration is, without doubt, the most widely used character system employed by reptile systematists in differentiating taxa. There are very few Australian skinks species that cannot be differentiated from close relatives in the basis of aspects of color and color pattern. Despite this, coloration remains difficult to quantify. Although there have been attempts to

quantify the size of single elements of pattern (e.g. pale spots, dark nuchal collars) on snakes by counting the number of scales covered by the element (Thorpe, 1975), and mathematical models for the generation of relatively simple patterns on snakes have been devised (Murray & Myerscough, 1991), the complex, frequently asymmetrical, and ontogenetically variable patterns seen in *Tiliqua* species have proven difficult to quantify. A further complication has been the very different patterns seen in different taxa, which have largely prevented the use of a uniform set of pattern parameters across the genus. Consequently, for each taxon studied, a series of approximately half a dozen major elements of color pattern was derived from preliminary examination of a few specimens from different parts of the geographic range.

The most consistently scored characters across taxa were:

1. The number of dark dorsal bands on body (quantitative)
2. The number of dark dorsal bands on the tail (quantitative)
3. The intensity and form of dark markings on the body venter (qualitative)
4. The intensity and form of dark markings on the head dorsally (qualitative)
5. The pigmentation of the soles of the feet (qualitative)

Other characters scored for some taxa included the presence and strength of a dark temporal streak, forelimb pattern, hindlimb pattern and throat pattern.

Although most authors (e.g., Storr, Smith & Johnstone, 1981; Cogger, 1986; Greer, 1982a) have described color pattern in terms of the presence and position of pale markings on a dark ground colour, I have used the dark markings as characters. There are two reasons for this. Firstly, when there is ontogenetic variation in the expression of dark and light elements, particularly dorsally, my impression has been that the dark elements invade and replace the light elements. Secondly, it is only dorsally on body and tail where the dark elements predominate. Ventrally, and dorsally on the head, the pale markings have the greater extent, and it is the dark markings that show the greater variation in intensity and extent.

The only occasion when I did not use the dark markings to score characters was in the dorsal pattern of *T. rugosa*, in which pale markings were either absent, or when present, and in the form of bands, were often weak and in the form of transversely aligned series of variegations rather than solid bands. In this case, the presence and number of pale bands proved easier to score.

In the case of pale markings, variations in hue were apparent within and between taxa. I have only used broad color categories (e.g., blue, green, yellow, red, blue-green) to describe these, due to the use in this study of preserved material of varying age and preservation history, which has resulted in inconstant alterations to the coloration in life.

2.4.3. Morphometrics

Morphometric characters selected were initially all those commonly used in the skink systematic literature: snout-vent length, axilla-groin length, tail length, fore- and hindlimb lengths, head length and head width.

Preliminary examination of material suggested that there were noticeable differences between taxa in the shape of the head not expressed by the combination of head length and width, and several cephalic measurements were added to attempt to quantify these differences. Size of ear aperture had previously been used as a diagnostic character in

Tiliqua (Kinghorn, 1931; Mitchell, 1950), while relative size and shape of the frontal and interparietal scales had been found useful in *Egernia* (Mitchell & Behrndt, 1949; Storr, 1968) and other skinks (Sadlier, 1986), and variation in these characters was also explored.

At the other end of the body, significant variation in width of the hip was noted by Bamford (1980) for different populations of *T. rugosa*. This character was applied to all *Tiliqua* species in this study. Finally, in *T. rugosa*, the width of the tail showed clear geographic variation. This character was not measured in other *Tiliqua* species, due to the even taper of the tail.

In total, 18 morphometric characters were examined for all taxa, with tail diameter also measured for *T. rugosa*. Definitions of these characters are as follows:

1. Snout-vent length (SVL): Measured along venter, with lizard pressed flat and long axis straightened, from tip of snout to caudal margin of preanal plate.
2. Axilla-groin length (AGL): Measured in same position as for SVL, from level of caudal margin of brachium, to level of cranial margin of hindlimb, with limbs held at right angles to body (Fig. 2).
3. Tail length (TL): Measured along tail venter, with tail held straight, from caudal edge of preanal plate to tail tip.
4. Forelimb length (FLL): Measured ventrally, with limb fully extended at right angle to body, from end of axillary crease to tip of claw of longest digit of forelimb (Fig. 2).
5. Hindlimb length (HLL): Measured ventrally, with limb fully extended at right angle to body, from end of postfemoral crease to tip of claw of longest digit of hindlimb (Fig. 2).
6. Hip width (Hip): Measured from dorsally, with the calipers placed across the largely parallel wings of the ilia, which were obvious externally.
7. Head length (HL): Measured laterally, obliquely from tip of rostral scale to rostral margin of ear.
8. Head width (HW): Measured dorsally, width across widest point of head (just rostral to ear).
9. Head depth (HD): Measured laterally, at right angles to longitudinal axis, at highest point of parietal table.
10. Interocular interval (IOC): Measured dorsally, at right angles to longitudinal axis, between lateral margins of supraciliary rows, at level of second supraciliary (a distinct notch was usually present between this supraciliary and the next).
11. Eye-naris interval (E–N): Measured laterally, from caudal margin of nostril to rostral margin of orbit, at level of medial canthus of eye.
12. Eye-ear interval (E–E): Measured laterally, obliquely, as minimum distance between caudal margin of scaly orbit and rostral margin of ear.
13. Eye diameter (Eye): Measured laterally, from medial canthus to lateral canthus of eye.
14. Ear diameter (Ear): Measured laterally, obliquely, along long axis of external ear aperture.
15. Interparietal length (IparL): Length of interparietal scale along midline.
16. Interparietal width (IparW): Maximum width of interparietal, measured at right angle to length.
17. Frontal length (FrontL): Maximum length of frontal scale along midline. Some populations of *T. rugosa* showed frequent division of the frontal scale into a large rostral scale and a smaller caudal scale, sometimes with further division of the caudal scale. Preliminary measurements showed that this condition was more than simple division of the scale, as the combined length was greater than for single frontals. Consequently, three frontal lengths are presented for *T. rugosa*. FrontL(a) is the length of undivided frontals. FrontL(b) is the length of the rostral frontal in the paired state. FrontL(c) is the total length of both scales in the paired state.
18. Frontal width (FrontW): Maximum width of frontal, measured at right angle to length. In *T. rugosa*, proportions of frontal width: length were only calculated for animals with single frontals.

19. Tail diameter: In *T. rugosa*, measured dorsally, at right angles to long axis, across widest point of tail.

2.4.4 Osteology

As only a few skeletons of each species could be examined, osteological data were not used in species definitions, but were only employed in hypothesising phylogenetic relationships between taxa.

Although the osteology of skinks is better studied than other aspects of the internal anatomy, much of the data is in the form of surveys of single characters across taxa. There are comparatively few descriptions of the osteology of single species, and very few that provide descriptions of fine details of bone sculpture, foraminae and contact patterns of the bones of the skull. In addition, while most of the major bones are consistently named in the recent literature, there is no consistently applied nomenclature for structures of individual bones. In order to address these deficiencies, a detailed osteological description of one taxon, *T. scincoides scincoides*, was prepared, and variation from this taxon was described for other taxa, comparisons made on a bone-by-bone basis (Appendix A). Taxon-specific variation was extracted from this descriptive account for use in a cladistic analysis of relationships (Chapter 11).

In naming structures, I have adopted the following principles, which are based on those used in the Nomina Anatomica Veterinaria (1973):

1. Names should be as short and simple as possible
2. Terms should have descriptive value; consequently, processes of bones are mostly named according to either direction (e.g. lateral process of . . .) or the bone which they contact (e.g., maxillary process of . . . .), and foraminae are mostly named according to their position or for the structures passing through them
3. Differentiating adjectives should generally be opposites, as lateral and medial, cranial and caudal.

In cases where a name is in wide use in the literature (e.g., Meckelian fossa), this name was used to maintain consistency.

2.4.5 Reproduction

Sex was determined by examination of gonads. Although hemipenes were everted on many specimens, I did not use partly-everted hemipenes for identifying males, as a few specimens with female reproductive tracts (ovaries, oviducts, in one case gravid) had some indication of eversion of a tubular, hemipene-like structure from the caudal wall of the cloaca.

Data taken from preserved material examined was used to explore two facets of reproduction:

1. seasonal timing of male and female reproductive cycles
2. number and size of young

The following reproductive characters were scored on specimens:

Males:

1. length of right testis (or left, when right damaged or absent), measured to the nearest 0.5mm.

2. a subjective estimate of testis condition, using the following three-state classification:

I. testis elongate, narrow and flattened ("straplike")

II. testis elongate, moderately laterally expanded, but flattened ("flaccid")

III. testis elongate, laterally and dorsoventrally expanded ("turgid")

3. for selected *T. s. scincoides*, width and depth of right testis at midlength, measured to 0.1mm, from a segment of testis extracted for histological examination (see below).

Females:

1. diameter of largest ovarian follicle, measured to the nearest 0.5mm. Ovarian follicle diameter was not measured for females with oviducal masses.

2. number of enlarged, yolking ovarian follicles (enlargement taken as being ≥10mm diameter) in left and right ovaries.

3. number of oviducal masses in left and right ovaries. Oviducal masses include recently ovulated eggs, early embryos, fully developed and pigmented embryos, and inspissated, yellow masses that were assumed to be infertile ova.

4. on an opportunistic basis (depending on accessibility of ovaries in females with oviducal masses), number of corpora lutea in left and right ovaries.

In order to test an assumption that testis size and shape was related to sperm production, histological examination of selected testes and epididymides of one taxon, *T. s. scincoides*, was made (see also section 2.5). The following characters were scored from stained sections: diameter, epithelial thickness and number of cell layers in the epithelium of ten seminiferous tubules in cross-section, diameter and wall thickness of the largest ten sections of epididymal duct, and the presence of spermatozoa in both tubules and ducts, on a subjective scale from 1 (spermatozoa absent) to 4 (maximum amounts of spermatozoa present).

2.4.6 Museum Collection Data

Where available, the following data for each specimen were obtained from museum registers:

1. locality, with latitude and longitude
2. date of collection, and of preservation, if available (with their large size, some bluetongues were held alive in captivity for some time, even several years, after collection)
3. any habitat, microhabitat or activity time data recorded

2.5 Method of Data Collection

While some specimens were borrowed from museums to allow simultaneous comparisons across a large number of specimens within taxa, the large size of bluetongues and transport costs prevented many museums from loaning large series. Consequently, data on external characters were generally gathered by visiting each collection. The high cost of interstate and overseas travel and time limitations on such visits (which were made during university vacations) meant that, for the most part, each specimen could only be examined on one occasion.

In general, all specimens of a taxon in a collection were examined on one occasion, on a specimen-by-specimen basis. To minimize the effect on analysis of geographic variation of any inadvertent shifts in scoring scalation characters with time, or an unconscious bias in scoring characters for samples from different areas, no attempt was made to group specimens on a geographic basis prior to examination, other than that grouping inherent in examining material in largely state-based collections. In many museums, I adopted a deliberate policy of not examining collection data until after specimen examination.

Scalation and coloration characters were scored from gross examination of specimens in good lighting conditions. Juveniles, and some fine-detail characters on adults (e.g., subdigital lamellae) were examined under a binocular dissecting microscope.

Following the scoring of scalation and coloration characters, morphometric characters were measured. The following measurements were made with stainless steel rulers, to either the nearest mm, or (in small specimens) 0.5mm: SVL, AGL, TL, FLL, HLL. All other measurements were made with dial calipers, to the nearest 0.1mm.

Finally, sex and reproductive condition of most specimens were examined through a ventral midline incision into the body cavity. The incision was made from the liver (junction of cranial and middle thirds of axilla-groin interval) to the pelvis. Testis and ovarian follicle measurements were made with dial calipers. Number of corpora lutea was estimated grossly, with ovaries *in situ*.

2.6 Taxonomic Assumptions and Operational Definitions
2.6.1 Working Hypothesis of Valid Species-Group Taxa

To give some order to the exploration of the alpha-systematics of the genus, I divided the material examined into smaller, more readily-handled groups. To do this, I assumed the six species consistently recognised by recent authors were identifiable, valid species-group taxa, and sorted specimens into these groups, using the diagnoses of Cogger (1986), who gives the following combination of characters:

T. adelaidensis: rostral temporals subequal to others, not much longer than broad; 36–42 midbody scale rows; at most single row of enlarged scales between interparietal and smaller scales on neck; three supraoculars; dorsal colour pattern does not involve bands on body.

T. multifasciata: rostral temporals subequal to others, not much longer than broad; 38–46 midbody scale rows; three or more rows of enlarged hexagonal scales between interparietal and smaller body scales on neck; 2–3 supraoculars; dorsal colour pattern involves nine or more irregular orange-brown bands on body.

T. nigrolutea: rostral temporals subequal to others, not much longer than broad; 28–32 midbody scale rows; four supraoculars; dorsal pattern involves pale blotches on dark brown to black ground colour.

T. occipitalis: rostral temporals subequal to others, not much longer than broad; 38–42 midbody scale rows; 2–4 rows of enlarged hexagonal scales between interparietal and smaller body scales on neck; 2–3 supraoculars; dorsal colour pattern involves 4–6 broad dark bands on body.

T. rugosa: body/tail scales grossly enlarged, rugose; head shields usually partly fragmented, only vaguely symmetrical; tail short, depressed, blunt-ended; subdigital lamellae mostly divided.

T. scincoides/*gigas* complex: rostral temporals much larger than others, longer than broad; four supraoculars; dorsal colour pattern involves 7–9 dark bands on a grey to brown ground colour.

Geographic variation was subsequently explored in each of these groups to determine if any were composite. Following the determination of the morphological limits of each of the recognisable taxa within these "species", the initial assumption of species status for each group was tested by exploration of zones of geographic overlap (Chapter 10) for evidence of reproductive isolation.

2.6.2 Definition of Species

The dominant species concept of recent decades has been the "biological species concept" (Mayr, 1963), which defines species as "groups of interbreeding natural populations that are reproductively isolated from other such groups". This definition suffers from some operational problems, such as the evaluation of reproductive isolation in naturally allopatric populations, and its inapplicability to uniparental populations. Further, in this form, Mayr's definition is ambiguous when applied to sympatric taxa showing occasional hybridisation, as Mayr (1982: 285) subsequently stated that "the two species in such a case remain 'reproductively isolated' in the sense that they do not fuse into a single population". Such an extension of the reproductive isolation concept of a species has not been without critics (e.g., Key, 1981; Barton & Hewitt, 1985). In addition, philosophically, the biological species concept, based on reproductive compatibility between populations, which is a plesiomorphic character and hence not informative in assessing evolutionary "relatedness", is logically inconsistent with the study of its underlying process, evolution (Frost & Hillis, 1990, and references therein). While this difficulty is overcome to some extent by focussing on the evolution of "isolating mechanisms" that maintain species independence, such mechanisms (particularly post-mating mechanisms that produce sterility), although by definition adaptations and hence apomorphies, are logically incompatible with allopatric models of speciation, and hence must be incidental to the process of speciation (Lambert & Paterson, 1983; Paterson, 1978, 1982, 1985, 1988). Because of these operational and philosophical defects, various other species concepts have been developed.

Some of the operational and logical defects of the biological species concept, such as its emphasis on *ad hoc* "isolating mechanisms", and its inability to deal with uniparental taxa, were overcome by Paterson (1978, 1982, 1985, 1988), with the development of a recognition concept of species. Under this concept, while interbreeding is still emphasised as a fundamental property of species, attention is focussed on the maintenance of species integrity by the evolution of specific-mate recognition systems, which are apomorphies. However, Paterson's model for the evolution and stabilisation of specific-mate recognition systems has been criticised on ethological grounds by Verrell (1988). Further, while the evolution of specific-mate recognition systems can be invoked to delimit daughter species, such apomorphies cannot be applied to the delimitation of an ancestral species with respect to its descendents. Following speciation events, the specific-mate recognition systems of the

ancestral species are likely to be retained in and shared with subsequent daughter species, and hence they may lack specificity at the species level.

An independently-derived species concept is the evolutionary species concept of Wiley (1978, 1981), defined as “a single lineage of ancestral-descendant populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate” (Wiley, 1978: 18). Wiley's concept is based on an earlier evolutionary species concept by Simpson (1961), although functionally it is significantly different. While Wiley's concept overcomes some of the philosophical incongruities of the biological species concept by concentrating on evolution as a process, it has severe operational difficulties in terms of identification of evolutionary systems. Failing to recognise polytypic species, it cannot deal with subsequent reconsolidation of former geographic isolates (Frost & Hillis, 1990).

Both the biological species concept and the evolutionary species concept consider the species as a taxon fundamentally different from taxa at other categorical levels. In such concepts, “species, unlike other taxa, are not only an outcome of evolution, they actually function in a direct way in the evolutionary process” (de Queiroz & Donoghue, 1988).

On the other hand, many phylogenetic systematists do not accept this difference, maintaining that there is no basic difference between species and other taxa. All taxa represent monophyletic groups, some more inclusive than others. Consequently, species must be defined as “the smallest detectable samples or populations with unique sets of characters” (the phylogenetic species concept; Frost & Hillis, 1990), although there is some disagreement over application of this definition (Rosen, 1978; Cracraft, 1983; Donoghue, 1985; Frost & Hillis, 1990).

Like the evolutionary species concept, the phylogenetic species concept, in its various guises, is consistent with the recovery of evolutionary history. However, if strictly applied, the phylogenetic species concept has operational difficulties, through recognising and delimiting the “smallest” detectable sample or population (Frost & Hillis, 1990). Further, as with Wiley's evolutionary species concept, the phylogenetic species concept cannot recognise paraphyletic groups, only monophyletic ones.

The biological, evolutionary and phylogenetic species concepts have recently been reviewed by Frost & Hillis (1990), who adopt for the species category a modification of Wiley's evolutionary species concept. They use the species category to:

> “carry names of lineages whose components (if distinguishable) are not incontrovertibly on different phylogenetic trajectories (i.e., sublineages, if distinguishable, are reproductively compatible), as long as these sublineages do not form a paraphyletic group in recovered history. The species category would carry names of single populations or monophyletic groups of populations that are either unresolved or estimated to be interacting through time.”

While accepting this modified evolutionary species concept, they reject the biological species concept. However, as argued by Smith (1990), the biological species concept, when applied only to geographically contiguous and overlapping biparental populations (Smith's Modified Biological Species Concept), is not incompatible with the Frost and Hillis model (which Smith considers an approximation to a Universal Species Concept) but merely a component of it.

For the purposes of this thesis, I make the assumption that operational difficulties of the biological species concept related to uniparental or dichopatric biparental populations are irrelevant with regard to *Tiliqua*. There is no suggestion from available data, either for *Tiliqua* or other members of the *Egernia* group of genera, that any populations are either uniparental or dichopatric, with both sexes represented within and throughout the range of each

recognised taxon (*pers*. *obs*.). Further, there is evidence of naturally occurring sympatry between the various species of *Tiliqua* presently recognised (e.g., Shea & Peterson, 1981; Thompson, 1973; see Chapter 10 for a full survey of the literature) that would permit a test of the biological species concept. Consequently, in recognising species of *Tiliqua*, I utilise the reproductive isolation principle of Mayr (1963) wherever it can be applied.

Like Frost and Hillis (1990) and Smith (1990), I agree that the species category should be consistent with recovered phylogenetic history. However, unlike Frost and Hillis (1990), I believe that the species category can include paraphyletic groups, and that such paraphyletic groups can be historically consistent. In so doing, I follow the model of de Queiroz and Donoghue (1988: 329–330), though not all their conclusions (de Queiroz & Donoghue, 1988: 332) and accept that ancestral species can occur, although their recognition is difficult. A similar view has also been advanced by Eldredge & Cracraft (1980). Provided that cladistic analysis places all sublineages hypothesised to belong to one species in a clade consisting only of that species and at most one other diagnosably monophyletic taxon, I am willing to accept that group of interbreeding (or in the case of insular taxa potentially interbreeding) sublineages as a species. I believe (see below) that identifiable sublineages within such paraphyletic species can be adequately recognised by the subspecies category.

2.6.3 Definition of Subspecies

The subspecies concept, which has generally been employed to geographically subdivide a species, has been the subject of much controversy in recent times (for reviews, see Wilson & Brown, 1953; Pimentel, 1958; Mayr, 1963; Thorpe, 1987, and references therein). Much of this controversy derives from the traditional subjective approach to the naming of subspecies. This approach, a natural extension of the typological approach to species identification, and a consequence of the former availability of only small, geographically scattered samples, was based on a central question of whether the sample was different. In general, one or a few characters were arbitrarily selected to delimit a small section of the range of a species. With the subspecies a subset of the morphological species, the differences between subspecies within a species usually had to be less than those between species.

In an attempt to remove the subjectivity from this approach, various formal statistical measures of morphological divergence were proposed, such as the 75% rule (Amadon, 1949), where subspecies were warranted when 75% of one populations could be differentiated from 75% of other. Even these were subject to controversy over their application (for review, see Pimentel, 1958; Sokal, 1965). Pimentel (1958) recommended a separation based on 84% of individuals from one population separated from 84% of the other as a conservative rule for differentiating subspecies, using a parametric approach, with confidence levels based on means and standard deviations. However, as noted by Sokal (1965), attempts to define subspecies by the overlap method confused a measurement of the level of differentiation with statements about the significance of the difference, and the approach retained the emphasis on the separation of *a priori* groups.

A second difficulty with both the “conventional” subspecies (Thorpe, 1987) and the overlap methods of delimiting subspecies (Sokal, 1965) was the lack of congruence between the patterns of variation seen in different characters. Thus, each character or set of characters gave a different breakup of the geographic range of the species. The advent of multivariate methods of analysis has provided a partial solution to this difficulty (Thorpe, 1987), and has changed the nature of the “level-of-differentiation” problem from confidence limits and

degrees of overlap to a discrimination problem, with the differences between populations expressed as a classification error (Sokal, 1965).

A further criticism of the conventional subspecies derives from its purely morphological and geographic nature, without differentiating between geographic patterns of morphological variation due to past history (phylogenesis) or current ecology. Most modern authors recommend that the subspecies category not be used for geographic variation that merely reflects local adaptation to the present environment (Thorpe, 1984, 1987, for review). This approach is in keeping with an evolutionary view that subspeciation is a logical extension of allopatric models of species formation (Pimentel, 1958; Mayr, 1963), with subspecies the result of incomplete speciation, most clearly seen when the allopatric populations regain contact. Such restriction of the subspecies category, while justifiable on the basis of its relation to evolutionary history, has proven difficult to use, due to problems in differentiating the effects of historical and current forces.

Thorpe (1987) recommends against the use of the conventional subspecies, restricting the application of trinomials to a restricted set of circumstances:

> 1. The pattern of geographic variation should give distinct races, such as categorical variation ("stepped clines") or very divergent isolates, such that they can be objectively delimited in geographic space by their characteristics. Trinomials should not be used where substantial introgression between lineages results in reticulation and loss of the categorical pattern. In particular, efforts should be made to avoid the subjective sectioning of clinal patterns of variation.
> 2. The subspecies should be predictive, with variation in the diagnostic characters predicting variation in other, independent, sets of characters. The congruence between data sets required for this principle is more likely to occur when historical events have been the cause of the geographic variation, than when the variation is a consequence of one or a few current ecological parameters.
> 3. The use of trinomials should be restricted to just below the species level, identifying only the main categories or lineages within a species, rather than sublineages.

This set of criteria has been adopted for this project.

Given that karyotypic variation in *Tiliqua* is minimal, the process of speciation must be assumed to be via the allopatric model (Mayr, 1963) of differentiation during geographic isolation. Hence, the possibility of the occurrence of geographical subspecies must be considered in this project.

2.7 Analysis of Data

2.7.1 Statistical Conventions

In presenting statistics, I have used the following abbreviations and symbols:

$\overline{X}$: mean

sd: standard deviation

cv: coefficient of variation

n: sample size

n.s.: not significant (probability >0.05) superscripts *, **, ***: probability levels <0.05, <0.01, <0.001 respectively

subscripts: degrees of freedom

Where not otherwise stated, X^2 tests have one degree of freedom.

All t-tests used are two-tailed tests for the difference of two means (Snedecor & Cochran, 1967).

In a few places in the text, apparent printing defects have occurred in the presentation of statistical data. These are due to minor incompatibilities between the printer and the word-processing package used in the production of this thesis (Vu-Writer) and could not be avoided. They occur when two or more non-standard symbols occur in different places on the same line.

2.7.2 External Morphology

2.7.2.1 Morphometrics

Ratios have traditionally been used in skink systematics to express variation in proportions (e.g., Storr, Smith & Johnstone, 1981; Cogger, 1986), despite the well-known inadequacy of ratios to account for allometric growth (e.g., Packard & Boardman, 1988; Sokal, 1965; Sneath & Sokal, 1973). To maintain current usage, simple ratios are presented in taxon accounts. However, to more adequately explore variation in morphometric characters between taxa, relative growth (Huxley, 1932) was taken into account.

While bivariate regression analysis has traditionally been the method of choice for exploring relative growth, multivariate techniques (particularly principal components analysis) have recently become fashionable (e.g., Jolicoeur, 1963; B. Shea, 1985; Somers, 1986, and references therein) in differentiating the effects of size (i.e., variation within a single metric variable) and shape (the relationship between two variables). In this technique, the first component is usually assumed to represent overall size, although it has been shown that in fact the technique does not differentiate the two factors (Somers, 1986). Somers (1986) attempted to modify the analysis to extract a first axis related to size alone, although this has not been without criticism (Sundberg, 1989; Somers, 1989; Bookstein, 1989; James & McCulloch, 1990).

In bivariate regression, use of the least-squares regression calculation (Snedecor & Cochran, 1967; Sokal & Rohlf, 1969; Peters, 1983) is widespread. However, least-squares regressions have been considered inappropriate for morphometric data by several authors (e.g., Dodson, 1975; McArdle, 1988; Seim & Saether, 1983) because both the dependent and independent variable are subject to random error (Model II regression; Sokal & Rohlf, 1969). This has led to a considerable literature discussing the relative merits of alternative techniques, including the major axis, reduced major axis (Gould, 1966; Harvey & Mace, 1982; Plotnick, 1989), and standard minor axis (McArdle, 1988) techniques, as well as nonparametric techniques such as Bartlett's best fit (Sokal & Rohlf, 1969; Dodson, 1975). However, as with multivariate relative growth techniques, there remains considerable disagreement as to the most appropriate technique, with each method making different, but equally restrictive mathematical assumptions that cannot be fulfilled by biological data (McArdle, 1988; Seim & Saether, 1983; Witten, 1985). Because of this disagreement, and as the different bivariate techniques give similar results when correlations are high (Sokal, 1965; Gould, 1966; McArdle, 1988), as in most of the morphometric regressions performed

in this study, I have used the traditional least-squares technique, which is the simplest, and is widely available in computer statistical packages (see also Peters, 1983).

Although violation of the least-squares assumption that the independent variable is measured without error has occurred, the calculated regression lines provide a sufficiently close fit to the data to provide a useful approximation for comparison of different taxa at fixed sizes or points in life history (e.g., Witten, 1985; Witten & Coventry, 1984).

Prior to calculation of regression lines, the range of ratios was examined, and extreme outliers rejected. Such outliers were most likely to be the result of errors in measurement, due to distortion of specimens, misreading of dial calipers or errors in data recording. Because of difficulties in re-examining material (see Section 2.5), it was not possible to verify outlying data points, although comparison with measurements for similar sized specimens often suggested that the extreme value was due to either misreading of calipers (e.g., measurement difference approximately 5mm, the range of values available on the caliper dial) or to errors in transcribing data (e.g., SVL 175 *vs* 275mm, with the specimen mature). Such outliers were relatively rare, and never represented more than 1% of data for any taxon.

Huxley's (1932) general relative growth formula $y = bx^a$, where x is the independent variable (a measure of size), y is the dependent variable, a is the allometric coefficient, and b is a constant, was used as a mathematical model for allometric growth. All morphometric data were transformed to natural logarithms, allowing use of simple linear regression analysis to calculate values of a and b for the relationship $\ln(y) = a.\ln(x) + \ln(b)$. For all calculations, the MGLH subprogram of SYSTAT Ver. 4.0 (Wilkinson, 1987) was used. For non-cephalic measurements, SVL was used as the independent variable, while for cephalic measurements, HL was used (see Witten, 1985, for a justification of the use of these measurements). For measurements of the two large median cephalic scales (frontal and interparietal), scale widths were regressed against scale lengths, while scale lengths were regressed against HL, and in the case of IparL, agains FrontL, to assess differences in the relative size of the two scales.

The relationship between a metric character and the independent metric was assumed to be allometric if the allometric coefficient (a) differed from 1.00 by more than two standard errors (Zar, 1974; Witten, 1985).

For the purposes of comparison between taxa, proportions (y/x) were calculated at three sizes (represented by SVL): size at birth, mean of ♂/♀ minimum size, and maximum size. These represent three relatively fixed points in the life history.

2.7.2.2 Asymmetry

A number of the cephalic scalation characters scored, and subdigital lamellae, were bilateral, and were scored on both sides of the head. While most authors have simply treated the score for each side as independent, resulting in an increase in the sample size, it is likely that left and right counts are not independent, being based on the same gene pool. Evidence for this comes from the rare occurrence of low and high extremes on opposite sides of the head, compared to the occurrence of the same extreme on opposite sides.

Alternatives to the use of bilateral counts, such as using counts for only one side, the sum of the two sides, or the mean value for both sides of each specimen, were considered and rejected for univariate analyses, for the following reasons:

1. A number of the specimens examined were road-kills, and a count could only be made on one side of the head.
2. Use of only a single side gives no indication of the variation on the other side, which could potentially exceed that on the side scored (Werner *et al*., 1991).
3. Use of mean values, resulting in frequent fractional scores, is not consistent with the determination of modal values, which are integers. I have used modal values as character states in cladistic analyses.

Apart from the likely interdependence of left and right counts, the possibility of directional asymmetry (Soulé, 1967; Werner *et al*., 1991), resulting in increased heterogeneity, and affecting subsequent analyses of variation, needs to be considered. As asymmetries in cephalic characters within individuals were often common, directional asymmetry was tested for within taxa by use of a two-tailed t-test for comparison of the means of the two sides (Snedecor & Cochran, 1967), prior to analysis of sexual dimorphism (Section 2.7.2.3) and geographic variation (Section 2.7.2.4). Initially, only asymmetrical pairs of scores were tested, to determine whether asymmetry was directional. When the results of these comparisons were significant, statistics for all pairs of scores were compared to assess the degree of the asymmetry and its potential effect on subsequent analyses.

2.7.2.3 Sexual Dimorphism

Sexual dimorphism in characters was explored for two reasons. Firstly, the presence and direction of sexual dimorphism has been used as a character in systematic studies (e.g., Arnold, 1973, 1989; Good, 1988; Griffith, 1991). Secondly, extensive sexual dimorphism can confound the results of studies of geographic variation. Consequently, the presence and magnitude of sexual dimorphism in all variable characters within taxa was assessed, to determine whether the sexes should be kept separate in geographic variation analyses.

Significant differences in mean values of meristic characters between males and females were tested for by two-tailed t-tests (Snedecor & Cochran, 1967). For categorical non-numeric data, X^2 contingency tests (Seigel, 1956) were used.

Sexual dimorphism in morphometric characters was tested for by covariance analysis (Snedecor & Cochran, 1967), using the MGLH subprogram of SYSTAT Ver. 4.0 (Wilkinson, 1987), for characters where the sample size and distribution of data points was adequate for testing. Where a significant difference in either slope or intercept was detected, the data was partitioned by sex, regression lines recalculated, and predicted proportions at mean size at maturity and maximum size of the smaller sex calculated to determine the direction of dimorphism.

Sexual dimorphism in adult size (SVL) was tested for by Mann-Whitney U tests (Seigel, 1956), due to the non-random, truncated nature of the samples inherent in the imposition of a lower limit for mature size.

2.7.2.4 Geographic Variation

Purpose and Approach

I analysed geographic variation for the purpose of determining and delimiting subspecies. I used the assumption that subspecies are relatively few in number for each species, and that the geographic range of each subspecies is relatively extensive, at least, in the case of isolated populations, equal in size to the compound localities, or in the case of contiguous

mainland populations, equal to or greater than two or more compound localities. These assumptions appear justified on the basis of subspecies recognised in closely related groups (*pers. obs.*).

Studies of geographic variation have generally focussed on one or other of two approaches: detection of areas of homogeneity, or detection of areas of abrupt change (Gabriel & Sokal, 1969; Barbujani *et al.*, 1989). My approach to partitioning geographic variation involves the recognition of concordant patterns of abrupt geographic change in different characters, with the use of multivariate techniques to further delimit and explore such areas.

2.7.2.4.2 Pooling of Samples

Ideally, studies of geographic variation should use samples of equal size collected over short time periods from single selected localities arranged in a regular pattern (Pimentel, 1958; Gabriel & Sokal, 1969). However, this is rarely possible in real life (Thorpe, 1976). In the case of this study, which is mostly reliant on previously collected museum material, samples of several specimens or more from single localities are rare. The taxa involved do not occur in the high densities necessary for such sampling, nor are they homogeneously distributed across all habitats. Consequently, grouping of specimens from different localities to produce compound localities is necessary to produce samples of sufficient size for statistical analysis (Thorpe, 1976).

I have grouped localities on the basis of several factors, including the existence of collecting gaps separating geographically discrete clusters of localities, and topographic features likely to be related to patterns of geographic variation, such as drainage patterns, altitudinal barriers (both ranges and valleys) and water barriers. Samples from insular populations were generally treated as distinct (except for some groups of inshore islands, where each island was represented by a single specimen). In general, compound groups were sufficiently numerous and well-scattered to account for simple clinal variation due to latitude, longitude, altitude and distance from the coast.

Because of variation in the numbers of specimens available from different area, it was not possible for all compound localities to be of similar geographic size or evenly scattered. Thus, there is a general trend for closely packed, small area groups to occur close to cities and in topographically varied regions, such as the east coast, while widely spaced, large area groups, often represented by few specimens, are generally found in arid area, particularly areas with fairly uniform topography. While localities were initially grouped solely on geographic considerations, in a few cases subsequent data transcription to sheets representing the pooled localities suggested bimodal variation within the groups. Such groups were further subdivided to take this variation into account. Thus, I distinguish two phases to producing compound localities: initial grouping on geographic grounds and subsequent subdivision of groups on morphological grounds.

A priori grouping of localities has been criticised (Pimentel, 1958; Sokal, 1965; Hiernaux, 1972; Thorpe, 1976) on a variety of statistical and biological grounds. The most serious of these criticisms appear to be:

1. compound localities do not distinguish between variance within samples and variance between samples
2. the compound localities may group two races without recognition
3. the compound localities may section a cline so as to produce a series of subspecies.

I believe that criticisms 1 and 3 reflect problems of scale. In the case of differentiating between variances, even “within locality” variance can have subdivisions within it, due to variation in microhabitat utilisation. Further, as noted by Thorpe (1976), the level of acceptable within-group variation must be determined with reference to the between-group variation. Criticism 3 can be largely overcome given sufficient compound localities to section areas of homogeneity and differentiate them from areas of abrupt change. The second criticism has been overcome by Thorpe (1976) by use of cluster analysis to assess the overall similarity between individual specimens within compound localities. Cluster analysis was not used in this study, due to time constraints and the large number of compound localities recognised. However, given the pattern of between-subspecies variation assumed (Section 2.5.1.4.1), I believe this criticism is of little significance for the actual analysis of variation. A single compound locality including two species or subspecies with differences in the character being examined, would have values for that character intermediate between the compound localities containing only one taxon, and hence would occupy an intermediate position that the groups representing each taxon. Such intermediate values, when geographically intermediate as well, suggest zones of overlap or intergradation that can be subsequently re-evaluated using several characters.

It is important to note that for simplicity in descriptive accounts, I refer to both the compound localities and the samples from these groups as “populations”, although recognising the statistical and biological differences between populations and samples from those populations.

2.7.2.4.3 Univariate Analyses

All quantitative scalation and coloration characters that showed sufficient variation overall to be potentially geographically variable were tested for geographic variation by one-way analysis of variation, using the ANOVA subprogram of MICROSTAT Ver. 4.1 (Ecosoft, 1984). The null hypothesis in this case was of no difference in means between populations. Although ANOVA, like the simple two sample situation, assumes equality of variance between groups, which was not tested because of time constraints, Sokal (1965) notes that relatively marked departures from this assumption will not unduly affect the result of the ANOVA.

Where ANOVA showed significant geographic variation, *a posteriori* tests of all pairs of population means were made, using a range simultaneous test procedure (Sokal & Rohlf, 1969). Because of the extreme variation in sample sizes (2 to >150), the GT-2 method of pairwise comparisons (Sokal & Rohlf, 1981) was used, with Gabriel's (1978) approximation to simplify calculations, which were made on a Casio FX-550 scientific calculator in the absence of a statistical package that included the method. A minimum of 17 and maximum of 61 populations were compared in such analyses, giving a range of 136 to 1830 pairwise tests for each character. I consistently used a 5% level of significance for these pairwise tests, despite the high potential for Type I errors with such a large number of tests (Gabriel, 1964). My purpose in comparing populations is not merely to determine which populations are significantly different from each other, but to describe broad patterns of variation. In other words, I am attempting to demonstrate a non-random distribution of means (Sokal, 1965). As noted by Sokal (1965: 349):

“given the genetic diversity of most animal and plant populations and given sufficiently large population samples with consequent reduction of the standard error, any two populations can be shown to be significantly different for almost any character or statistic. We must therefore clearly distinguish between the *significance* of differences and their *magnitude* and *importance*” (see also Mayr, 1963).

Population means and significant differences between adjacent populations were plotted on a network diagram of geographic relations between populations (Thorpe, 1976) to assess and describe patterns of geographic variation in means, and to define partitions (Gabriel & Sokal, 1969).

Geographic variation in qualitative, categorical characters, such as degree of separation of nasals and coloration differences, were investigated less rigorously. Frequencies of occurrence of commonly occurring states were plotted on a network diagram of geographic relationships between populations and sharply differing figures for adjoining populations tested by X^2 contingency tests (Seigel, 1956).

The comparatively small samples available for most populations were insufficient to determine adult body size (SVL) on the same population basis as for other characters. Consequently, where adult size was considered to be potentially geographically variable, populations were roughly clustered geographically on the basis of similar size of the largest specimens, and on the basis of other geographically discrete character variation, and SVL at maturity determined for these clusters of populations. Adult SVL for these groups was compared by Mann-Whitney U tests (Seigel, 1956) on a pair-wise basis, using a 5% level of significance.

Geographic variation in morphometric characters other than SVL was not attempted for most taxa, as the manipulation of data to remove the effects of allometric growth, involving sophisticated multivariate techniques, such as multiple-group principal components analysis, or use of pooled within-group slopes in bivariate comparisons (e.g., Thorpe, 1976, 1979) was beyond the computing capabilities and time limitations of this project. Instead, morphometric characters were simply used to describe taxa recognised on the basis of other characters. The only exception was in the case of *T. rugosa*, where there was obvious geographic variation in some morphometric characters, such as head width, ear diameter and tail length and width. A rough assessment of the pattern of variation in such characters was made by use of mean values of ratios for populations. However, due to the presence of allometry and the unusual statistical properties of ratios (Sokal, 1965), formal statistical analyses of the patterns of variation in these characters were not carried out.

Univariate methods have been criticised as incapable of indicating the affinites between populations, due to discordance in patterns of variation between characters (Thorpe, 1976; Willig *et al.*, 1986), although they remain popular in studies of geographic variation, particularly when multiple-comparison techniques are employed (Sokal, 1965; Thorpe, 1976; Sokal & Rohlf, 1981). As noted by Thorpe (1987), it is character congruence that is of central importance to the study of geographic variation. Personally, I find the patterns of variation of individual characters easier to interpret than variation in multivariate characters. Further, in this study, discordance in patterns of variation was not a major problem, with the characters showing the greatest amount of variation often revealing similar zones of change.

2.7.2.4.4 Multivariate Analyses

Most of the geographic variation was of a minor nature, and showed discordant patterns of variation for different characters. In the two taxa (*T. rugosa*, the *T. scincoides* complex) in which univariate analyses of geographic variation revealed strongly concordant patterns of variation, multivariate analyses of variation were undertaken.

Following the recommendations of Thorpe (1980), two separate multivariate analyses were made on each of these taxa. R-mode (between-characters) principal components analysis (PCA), using mean values for populations as cases, was used in conjunction with an

average taxonomic distance matrix of standardised values (Sneath & Sokal, 1973) to group populations, and detect zones of abrupt change that may represent contact zones between genetically differentiated populations. Canonical variates analysis (CVA), using populations as *a priori* groups and individual specimens as cases grouped populations and classified specimens, and also, by use of geographic transects of factor scores (Thorpe, 1976, 1979) permitted the finer resolution and examination of zones of abrupt change.

Although all populations were used for PCA, only selected populations could be used for CVA, due to limitations in computing facilities, and the small sample sizes (n = 1–2) used for a few populations. However, the populations selected for CVA included all those close to apparent zones of abrupt change, sufficient populations on either side of such zones to extend geographic transects, and other populations represented by large samples, in order to explore intrapopulation variation.

The characters selected for both analyses were those that showed the greatest geographic variation (high F values in ANOVA; sharp discontinuities in the case of qualitative characters) and concordance in their patterns of variation. Other characters, with patterns of variation non-concordant with the general pattern, had low F values in ANOVA. In both *T. rugosa* and the *T. scincoides* complex, the number of characters used was seven or more. In random resampling experiments using the snake *Natrix natrix* as a model, Thorpe (1985) suggested that approximately 8–10 characters gave a close approximation to the racial patterns revealed by analysis of 71 characters, while Thorpe (1989) showed that the pattern derived from six or more scalation characters gave a high correlation (>0.85) with the pattern of variation derived from all characters.

To avoid the problem of mixing unilaterally and bilaterally scored characters, the mean value for the two sides on each specimen was used for bilateral characters. Qualitative characters (e.g., degree of separation of nasals) and presence/absence-type characters (e.g., division of frontal) were scored on ordinal scales.

Multivariate analyses were performed using SYSTAT Ver. 4.0 (Wilkinson, 1987), using the FACTOR subprogram for PCA and the MGLH subprogram for CVA.

2.7.2.5 Exploration of Contact Zones

In order to test the assumption that the initial taxa recognised were reproductively isolated, and specifically distinct, specimens from zones of geographic overlap between pairs of these taxa were examined for phenetic intermediacy between the two morphotypes. If two species are involved, hybridisation in contact zones should be absent or restricted (Mayr, 1963, 1982). The presence of phenetic intermediates may indicate hybridisation between taxa (although conversely, hybrids, while genetically intermediate, may not be phenotypically intermediate; Barton & Hewitt, 1985). If such phenetic intermediates are common in the overlap zone, to the point where there is loss of the distinction between two phenotypes, then one can infer that the initial assumption that two species are involved has been violated.

To test the assumption, specimens of the two phenotypes from the zone of overlap were differentiated on the basis of diagnostic aspects of coloration and adult size occurring elswhere in the range of each taxon. The two *a priori* groups were then run through a two-group CVA, using selected characters from a different character system (scalation) to confirm that the two groups were distinct.

Where known captive-bred hybrids were available, these were run through the same discriminant function to determine with which of the parental phenotypes (if either) they grouped. Three wild-caught specimens from south-eastern SA that did not agree with the diagnoses for the taxa occurring in the area were also run through the discriminant functions and compared with captive-bred hybrids of known parentage.

2.7.3 Reproduction

2.7.3.1 Adult Size

Minimum size at maturity for each sex was determined graphically from the relationship between gonad size and SVL. For males, testis length and condition were plotted against SVL, and a sharp increase in testis length and the appearance of turgid testes (type III testes; Section 2.4.5) taken as indicative of the onset of maturity. For females, diameter of the largest ovarian follicle, and the occurrence of oviducal masses were plotted against SVL, and a sharp increase in follicle diameter or the appearance of oviducal masses taken as indicative of maturity.

In general, all animals larger than the minimum size at maturity were assumed to be mature, although a few animals only slightly larger than the smallest mature individuals, but with seemingly immature gonads, collected during the breeding season, were excluded from the mature sample.

2.7.3.2 Seasonality of Reproduction

The seasonality of the reproductive cycle was assessed graphically from the relationship between gonad size, presence of oviducal masses, and date of collection. Specimens known or suspected to have been preserved more than one month after collection were not included in the assessment, while date of preservation was used as the independent variable in the case of specimens preserved within one month of collection. Specimens for which only month of collection was available were arbitrarily assumed to have been collected on the 15th of the month for graphical purposes.

For females, a seasonal increase in diameter of the largest ovarian follicle was assumed to represent vitellogenesis. The period of birth was inferred from the seasonal disappearance of oviducal masses.

For males, an increase in testis length and change in condition of the testes, from type I to type III, was assumed to be due to spermiogenesis. Most authors using gross testis measurements to infer the seasonality of the male reproductive cycle (e.g., for skinks, Tanner, 1957; Mount, 1963; Robertson *et al.*, 1965; Davidge, 1980; Schwaner, 1980; Simbotwe, 1980, 1985; James & Shine, 1985) have apparently made this assumption, often based on correlations reported in the literature on phylogenetically distant taxa. However, Barwick (1965) found that in the skink *Egernia cunninghami*, mean testis length varied only slightly on a seasonal basis, while testis volume and mass varied markedly in association with sperm production. Conversely, in the skinks *Bassiana trilineatum* and *Eulamprus tympanum*, rapid increase in testis mass in autumn is due to spermatocytogenesis, and is not correlated with spermiogenesis and the onset of mating (Pengilley, 1972). To check the assumption of a relationship between testis size and spermiogenesis, the seasonal pattern of testis size and shape (the latter subjectively estimated) in *T. s. scincoides* was visually compared to corresponding graphical representations of seasonal variation of two indices of overall testis size ($\sqrt{}$testis length x width, 3 testis length x width x depth$_3\sqrt{}$; roots taken to reduce the relationship with raw testis length to linearity), and several histological

parameters: seminiferous tubule diameter, height of seminiferous epithelium, epididymal duct diameter, height of epididymal duct epithelium (all based on mean values for ten counts for each animal) and the presence of spermatozoa in seminiferous tubules and epididymal ducts. Statistical correlations between the various parameters were precluded by varying sample sizes for the different parameters.

The mating season was inferred from the correspondence between the peaks in testis size and ovarian follicle diameter.

2.7.3.3 Litter Size

Litter size was determined from the number of enlarged, yolking ovarian follicles, oviducal masses (ova or embryos), or young born to captive-held females. The correspondence between litter size based on number of follicles and on oviducal masses was checked by comparison of mean values by two-tailed t-tests, against a null hypothesis of equality of means. Asymmetry between left and right oviducts was checked by means of t-tests and X^2 tests, against a null hypothesis of equality of means in the former case, and of equality of frequency of right and left dominated totals in the latter.

The effect of maternal size on litter size was assessed by means of least-squares regression of number of follicles or oviducal masses against maternal SVL.

2.7.3.4 Size of Young at Birth

Size of young at birth, as quantified by SVL, was assessed from two lines of evidence: SVL of captive-born neonates and minimum SVL of wild-caught individuals, especially those collected around the presumed normal period of birth, as determined by the disappearance of gravid females from the population.

The limited data presented for a few taxa on mass of young at birth and relative litter mass was determined from raw data in the literature and from litters born to captive-held females, both due to captive breeding and collection of gravid females from the wild. Relative litter mass was defined as total mass of young (at birth)/female mass immediately postpartum.

2.7.3.5 Sex Ratio

Mature sex ratio was determined for individuals equal to or larger than the minimum mature size for each sex. Departures from parity were tested for by X^2 tests, and for seasonal variation by contingency X^2 tests (Seigel, 1956), against null hypotheses of a 1:1 ratio for the former, and no difference in frequencies between seasons in the latter.

2.7.4 Phylogenetic Relationships

2.7.4.1 Approach

A cladistic approach to the estimation of relationships (Arnold, 1981; Eldredge & Cracraft, 1980) has been adopted for this thesis. This approach recognises special similarity (as opposed to general similarity) as a principle for the selection of characters on which to infer relationships, and uses character congruence and parsimony to produce a nested series of three-taxon statements (a cladogram). While the resultant cladogram is strictly speaking merely a summary of the pattern of shared possession by taxa of apomorphic character

states, it has generally been inferred to represent the phylogenetic relationships of the included taxa (Eldredge & Cracraft, 1980).

The cladistic method involves three main steps (Weston, 1988):

1. the formulation of hypothetical unpolarised character transformation series on the basis of structure and function
2. the polarisation of these transformation series
3. the construction of a cladogram from the character phylogenies

The methods used in step 2 are discussed in Section 2.7.4.2 and 2.7.4.3, while the methods used for step 3 are discussed in Section 2.7.4.4.

2.7.4.2 Selection of Method for Determination of Polarities

Three major sources of data for the determination of the polarity of a transformation sequence have been proposed: paleontology, ontogeny and outgroup comparison (Eldredge & Cracraft, 1980; Stevens, 1980; Arnold, 1981; Maddison *et al.*, 1984). Application of all three data sources aims to identify the plesiomorphic state as the state represented by the data source.

Use of the fossil record to polarise characters has been popular with those who take the view that the fossil record is the key to the history of life, with phylogeny only determinable by direct empirical observation of the historical record (Eldredge & Cracraft, 1980). However, this idealistic view is not only not applicable given the fragmentary nature of the fossil record, but makes the unwarranted assumption that stratigraphically earlier taxa will have primitive character states.

In any case, use of the fossil record is not possible in the case of *Tiliqua*. With the exception of two partial dentaries from Miocene deposits at Riversleigh, soon to be described as a new species of *Tiliqua* (Shea & Hutchinson, in press), and statements of the occurrence of *Tiliqua* material from middle Miocene deposits in South Australia (Estes, 1984) and Pliocene deposits in NSW (Hand *et al.*, 1988), the fossil record for the genus consists solely of Pleistocene or Recent material, either uncategorised or referrable to modern taxa (Krefft, 1867b, 1870b, 1871; Stirling, 1889; Hale & Tindale, 1930; Tindale, 1933; Cook, 1960, 1963; Mulvaney, 1960; Mulvaney *et al.*, 1964; Trezise, 1970; Lampert, 1971; Thorne, 1971; Marshall, 1973; Bowdler, 1974; Ryder, 1974; M.J. Smith, 1976, 1982; Bartholomai, 1977; Hope *et al.*, 1977; Archer & Brayshaw, 1978; Molnar, 1978, 1982; Williams, 1980; Hope, 1981; M.A. Smith, 1982; Wells *et al.*, 1984).

Even if this material were sufficient for and capable of determining the plesiomorphic condition, its restriction to hard tissue (bones, osteoderms) would restrict the range of characters which could be used for estimating relationships.

The ontogenetic criterion for determination of polarities is based on the observations of the embryologist von Baer that during development specialised characters develop in a sequential manner, resulting in the gradual morphological divergence of the developing embryo from the form represented by the embryos of ancestors (de Beer, 1958). While one school of cladists has advocated the use of ontogenetic criteria as theory-neutral and hence assumption-free, this argument has been criticised (e.g., Kluge, 1985), and the method has fallen into disfavour with many systematists (Sneath & Sokal, 1973; Nelson, 1973; Stevens, 1980; de Queiroz, 1985; Weston, 1988). In any case, there are as yet no developmental

data available for external morphology and osteology in *Tiliqua*, that would permit use of the ontogenetic criterion.

The final method, outgroup comparison, while indirect and not theory-neutral, is an extension of general cladistic principles and methodology, and has been recommended as the technique of choice by many authors (e.g., Arnold, 1981; Eldredge & Cracraft, 1980; Farris, 1982; Kluge, 1991; Maddison *et al.*, 1984; Watrous & Wheeler, 1981; Weston, 1988). Outgroup comparison has been used for the determination of polarities in this project.

The outgroup method operates on the principle that those character states occurring in other taxa within a larger hypothesised monophyletic group that includes the monophyletic group under study as a subset can be hypothesised to be primitive (modified from Eldredge & Cracraft, 1980: 63). This method clearly requires the adoption of two working hypotheses:

1. the ingroup is monophyletic relative to proposed outgroups
2. a hypothesis of relationships between the ingroup and outgroups (often based on a framework of traditional classifications; Weston, 1988).

The first hypothesis is advanced and examined in Chapter 3. Choice of outgroups on the basis of previously advanced hypotheses of relationships within the Scincidae is discussed below (Section 2.7.4.3).

2.7.4.3 Selection of Outgroups

Determination of transformation series polarity cannot be determined from only a single outgroup. A series of nested outgroups (at least two) are necessary (Watrous & Wheeler, 1981; Maddison *et al*. 1984; Bauer 1989; A. Kluge, *pers. comm*.). This is particularly important within the Scincidae, due to the widespread occurrence of parallelism, convergence and reversal (e.g., Greer, 1970, 1974, 1979a; Greer & Cogger, 1985; Hutchinson *et al*., 1990; Sadlier, 1990).

For the purpose of determining polarity of characters used to define the ingroup under study (Chapter 3), I used three successively more distant outgroups:

1. the genus *Egernia*
2. other non-attenuate skinks of the subfamily Lygosominae, especially *Mabuya*
3. non-attenuate scincine skinks, with emphasis on *Eumeces*

My rationale for the selection of these outgroups is explained below.

Egernia has consistently been considered the genus closest to *Tiliqua* (*sensu lato*) by most authors from Gray (1845) on. Although Boulenger (1887) and Cope (1892a) separated *Tiliqua* and *Egernia* on the basis of separation or contact of palatine bones, Waite (1929) noted that this character was invalid in the form expressed by Boulenger. In both genera, the palatine bones are usually separated on the midline. Mitchell (1950) believed that the two genera “separated relatively recently from a common stock and have developed along two monophyletic lines”, although no characters of any utility were advanced to define this relationship. The two genera were separated on the basis of the presence or absence of contact of the medial palatine process of the ectopterygoid with the palatines, and tooth shape, but difficulty was experienced in assigning the *Egernia whitii* group, which has narrow contact between palatine and ectopterygoid process.

A close relationship between *Egernia* and *Tiliqua* was also implicit in the classifications proposed and argued by other workers in subsequent years (for review, see Hutchinson, 1981). Greer (1979a) considered the two genera, along with the monotypic *Corucia*, a lineage (the *Egernia* group) within the subfamily Lygosominae, diagnosed on the basis of a single character: a reduced modal number of premaxillary teeth (7–8 *vs* the primitive 9). Three other synapomorphies were employed in inferring a sister-group relationship between the *Egernia* and *Eugongylus* groups: closure of Meckel's groove in the dentary, loss of pterygoid teeth and loss of a distinct postorbital, although the latter two characters were not employed in diagnosing lineages as they "were not completely diagnostic for all groups". However, if the loss of pterygoid teeth and loss of a distinct postorbital be considered less than diagnostic, so too must the sole synapomorphy for the *Egernia* group, as three species of *Egernia*, *E. coventryi*, *E. luctuosa* and *E. major*, have a mode of nine premaxillary teeth (Greer, 1979a; *pers. obs.*). Further, loss of pterygoid teeth is not a synapomorphy for the combined *Egernia*/*Eugongylus* group lineage, as they are present in both *Leiolopisma telfairii* and *L. mauritianus* of the *Eugongylus* group (Arnold, 1980) and in *Corucia zebrata* in the *Egernia* group (*pers. obs.*).

Despite this, there remain four fairly clear lines of evidence for the monophyly of the *Egernia* group. *Tiliqua*, *Egernia* and *Corucia* share a distinctive karyotype, with diploid number 2n = 32, nine pairs of macrochromosomes, and pair six smaller than pair five (King, 1973a,b; Donnellan, 1985, 1991a). This karyotype is not known from any other lygosomine, scincid or scincomorph group. While it is not possible to determine the direction of karyotypic evolution within the family Scincidae, as no group has a demonstrably primitive karyotype as determined by outgroup comparison, each karyomorph may be uniquely derived (Donnellan, 1985). Secondly, immunoelectrophoretic studies (Hutchinson, 1981) have indicated that *Egernia* and *Tiliqua* are each other's closest relatives, with *Corucia* slightly more distant. Thirdly, microcomplement fixation using serum albumin (Baverstock & Donnellan, 1990) in one-way comparisons with antisera generated to each of the three major suprageneric groups proposed by Greer (1979a) has placed *Tiliqua* (represented by *T. rugosa*) closer to *Egernia* (represented by *E. frerei* antiserum) than to other lygosomines. Finally, intergeneric hybridisation has been reported between captive *E. cunninghami* and *T. gigas* (Rose, 1985), further suggesting that the genetic distance between the two genera is not great.

Although *Corucia* is a member of this lineage, I have not included it with *Egernia* in the first outgroup. *Corucia* displays a combination of recognisably very primitive characters (e.g., pterygoid teeth, double row of supradigital scales) with a number of bizarre autapomorphies (e.g., loss of central supraciliaries, extremely elongate last supralabial, separation of first pair of chin shields, grossly enlarged frontonasal scale, cuspidate teeth, distal end of tail forming a slight hook), at least some recognisably the result of a unique ecology (arboreal herbivory) amongst skinks. Immunological evidence has suggested that it is more distantly related to *Tiliqua* than is *Egernia* (Hutchinson, 1981), and I have consequently relegated it to the second outgroup, where its influence on determination of polarities is diluted.

The *Egernia* lineage has been placed in the subfamily Lygosominae (Greer, 1970a). This assignment has withstood critical evaluation, and the monophyly of the subfamily successfully defended (Donnellan, 1985, 1991a; Greer, 1986a) against criticism (King, 1973b; Rawlinson, 1974; Hutchinson, 1981). Within the Lygosominae, many lineages have undergone convergent evolution towards a fossorial lifestyle (Greer & Cogger, 1985; Heyer, 1972), with a number of derived characters, especially those associated with burrowing, having evolved a number of times. Complete loss of limbs has evolved at least five times within the subfamily (Greer & Cogger, 1985), with some loss of phalanges and an increase in the number of presacral vertebrae occurring in many other genera (Greer, 1991). The resulting "noise" hampers use of a uniform outgroup composed of all non-*Tiliqua* lygosomines. Greer (1977, 1979a, 1983b) has attempted to block this "noise" by placing

emphasis on character states in *Mabuya*, as “the genus that seems to comprise the most generally structurally primitive species among the lygosomines . . . ” (Greer, 1979a: 340). However, of the many plesiomorphies advanced in support of this view (Greer, 1979a), most are also present in *Tiliqua*, *Egernia* and most other non-attenuate lygosomines. Only in the presence of supranasal scales, postorbital bones, and pterygoid teeth is *Mabuya* as a whole notably more primitive than *Egernia* and many other lygosomines. Further, Greer's (1989) implicit placement of *Mabuya* in the *Egernia* group, while still accepting his earlier (Greer, 1979a) hypothesis of relationships between the Australian lygosomines (Greer, 1989: 128) is at variance with the concept of *Mabuya* as primitive within the Lygosominae. Consequently, I have not placed as much emphasis on character states in *Mabuya* as Greer, but instead have attempted to filter out the influence of convergence in fossorial and cryptozoic species by only considering those lygosomine genera which possess the primitive number of presacral vertebrae (n = 26; Hoffstetter & Gasc, 1969), or only a slight elevation above this (n ≤ 30). Fifty-eight genera or species groups are in this category (Table 2.1) and these are used as the second outgroup.

Three other subfamilies of the Scincidae have been proposed by Greer (1970a). Two of these, the Acontinae and the Feyliniinae, are composed of attenuate burrowing species with markedly elevated numbers of presacral vertebrae. The remaining subfamily, the Scincinae, is plesiomorphic *vis-à-vis* the Lygosominae (Greer, 1970a, 1986a; Hutchinson, 1981; Estes, 1983). Within the Scincinae, most genera show marked limb reduction and body elongation, and I have excluded these from the third outgroup, for the same reason as given above. Six scincine genera or subgenera (*Amphiglossus* (*Madascincus*), *Eumeces*, *Janetaescincus*, *Pamelaescincus*, *Scincus* and *Scincopus*), however, have a primitive or near-primitive number of presacral vertebrae (El-Toubi, 1938; Brygoo, 1981; A.E. Greer, *pers. comm.*), and this group is used as the third outgroup. Brygoo (1981) also lists *Gongylomorphus* as having 26 presacral vertebrae, but two Australian Museum specimens (R73340–41) of *G. b. bojeri* have 32, and I have therefore not included *Gongylomorphus* in this outgroup. Within the Scincinae, *Eumeces* is recognisably the most primitive genus (Greer, 1970a, 1974, 1979a), as well as the largest. Fortuitously, it is also the genus for which the greatest body of literature on scalation and osteology exists (Taylor, 1935; Kingman, 1932; Nash & Tanner, 1970; Hikida, 1978), and I have consequently placed most emphasis on this genus within the third outgroup.

For the purposes of defining character polarity within the ingroup (the genus *Tiliqua* sensu stricto), to infer intrageneric relationships (Chapter 11), the genus *Cyclodomorphus* was used as the first outgroup (see Chapter 3 for justification), and *Egernia*, other non-attenuate lygosomines, and non-attenuate scincines as the second to fourth outgroups.

2.7.4.4 Treatment of Characters and Choice of Terminal Taxa and Computation Procedures

Because the definition of species used in this project accepted polytypic and paraphyletic species, but not polyphyletic species, it was necessary to infer relationships between the recognised subspecies, despite the absence of osteological data for some taxa. Consequently, I ran an initial cladistic analysis using external characters alone, to assess the validity of my conclusions (Chapters 8,9) on intraspecies relationships in the *T. scincoides* complex and in *T. rugosa*.

A second analysis, using both external and osteological characters, was then run, using species as terminal taxa.

There has been disagreement of late between use of ordered (additive) and unordered (non-additive) linear multistate characters in cladistic analysis (Farris *et al*., 1970; Mickevich,

1982; Pimentel & Riggins, 1987; Hauser & Presch, 1991; Kluge, 1991), much of which is based on acceptance or otherwise of *ad hoc* assumptions of patterns of transformation *vs* potential loss of synapomorphies. In the most recently presented argument (Hauser & Presch, 1991), use of nonadditive characters could either increase or decrease parsimony and tree resolution. Consequently, for this project, I initially treated linear multistate characters as additive, and then examined the effect on the resultant trees of treating such characters as non-additive.

Non-linear (branched) multistate characters for which polarity was able to be inferred prior to the analysis were broken into two or more two-state characters or linear multistate characters.

Modal values were used as character states for external characters, provided that the modal value predominated (modal value in more than 40% of cases, and more than 75% more common than the next most common state).

Where a number of equally parsimonious trees were produced, character weighting on the basis of the consistency index of the individual characters was used to choose between trees (Carpenter, 1988).

All cladistic analyses were performed with Hennig86 (Farris, 1988), using the exact “implicit enumeration” algorith (ie). This program was found to be superior to other available cladistic inference programs (Platnick, 1989).

Chapter 3 Recognition and Diagnosis of the Genus *Tiliqua*

3.1 Introduction and Conventions

This chapter defines the subsequent scope of the thesis by identifying and diagnosing a monophyletic unit to which the name *Tiliqua* is applied. Characters used in diagnosing the genus were chosen following perusal of the anatomical and systematic literature on the group (Appendix B), and preliminary examination of the osteology of the species assigned to the genus by previous workers.

For convenience within the context of this chapter, the four groups of species identified by previous authors are generally referred to by the generic names available for them: *Trachydosaurus* (for *rugosa*), *Hemisphaeriodon* (for *gerrardii*), *Cyclodomorphus* (for *casuarinae*, *maximus* and the *branchialis* complex) and *Tiliqua* (for the other species).

3.2 Determination of Character Polarities

1. Presacral vertebrae. The primitive number of presacral vertebrae in skinks is 26 (Hoffstetter & Gasc, 1969). *Corucia* and all *Egernia* have a mode of 26 presacral vertebrae, while the range for *Cyclodomorphus*, *Hemisphaeriodon*, *Tiliqua* and *Trachydosaurus* is 32–44 (Siebenrock, 1895; *pers. obs*.).
2. Phalangeal formula of manus. A phalangeal formula of 2.3.4.5.3 is considered primitive for all lepidosaurs (Romer, 1956; Greer, 1983b, 1987). All *Egernia* species and 44 of 53 genera in the next two outgroups have this configuration, while only nine genera have a different formula, involving loss of phalanges in all but *Scincus* (El-Toubi, 1938). *Cyclodomorphus*, *Hemisphaeriodon* and *Tiliqua* have a manus formula of 2.3.4.4.3 (i.e., loss of one phalanx in the fourth finger), while *Trachydosaurus* has 2.3.3.3.2 (loss of a further three phalanges, one each from digits 3–5). These are assumed to be successive derivations from the primitive condition.
3. Phalangeal formula of pes. A phalangeal formula of 2.3.4.5.4 is considered primitive for lepidosaurs. All *Egernia* species and 50 of 53 genera in the next two outgroups have this configuration. *Cyclodomorphus*, *Hemisphaeriodon* and *Tiliqua* have a pes formula of 2.3.4.4.3 (i.e., loss of one phalanx in each of the fourth and fifth toes) while *Trachydosaurus* has 2.2.3.3.2 (loss of a further four phalanges, one each from digits 2–4). As with the manus, these are assumed to be successive derivations from the primitive condition.
4. Medial margin of orbit. In most skinks the prefrontal and postfrontal bones are widely separated along the lateral margin of the frontal, the separation generally equal to or greater than the smallest width of the frontal. Within *Egernia*, a slightly narrower separation occurs in *E. major*, while in the members of the second and third outgroups examined, only in *Corucia*, *Macroscincus*, *Leiolopisma* (sensu stricto) and the *Sphenomorphus fasciatus* group is the separation narrower. Broad separation of prefrontal and postfrontal bones is considered primitive, and the narrow separation to broad contact seen in *Cyclodomorphus*, *Hemisphaeriodon*, *Tiliqua* and *Trachydosaurus* (Fig. 3) derived. In *T. adelaidensis*, the separation is greater than in other species, but this is most likely to be a reversal.
5. Upper temporal arch. In most skinks the jugal and squamosal are narrowly to moderately separated along the lateral edge of the postorbital or postfrontal, while in only a few is there direct contact between jugal and squamosal. Within *Egernia*, distinct contact occurs only in most members of the *E. whitii* species group. In other non-attenuate lygosomines examined, the two bones are separated. In scincines, separation occurs in *Scincus* (El-Toubi, 1938) and moderate separation to variable point contact in 11 of the 13 *Eumeces* species for which data is available (Kingman, 1932; Nash & Tanner, 1970; Hikida, 1978), while narrow to moderate contact has been reported for two *Eumeces* species (Kingman, 1932). Separation of the jugal and squamosal is assumed primitive for skinks, and the consistent narrow to broad contact seen in *Cyclodomorphus*, *Hemisphaeriodon*, *Tiliqua* and *Trachydosaurus* (Fig. 4) derived.

6. Coronoid process of dentary. In the majority of skinks examined, the coronoid process of the dentary articulates with only the rostral margin of the dorsal process of the coronoid, although in most *Egernia* species the articulation also extends slightly over the rostrolateral face of the coronoid in *Cyclodomorphus*, *Hemisphaeriodon*, *Tiliqua* and *Trachydosaurus*, the coronoid process of the dentary largely covers or completely overlaps the dorsal process of the coronoid laterally (Hoffstetter, 1949; *pers*. *obs*.). Articulation of the coronoid process of the dentary with only the rostral or rostrolateral margin of the coronoid is considered primitive, and extended lateral overlap of the coronoid (Fig. 5) derived.
7. Lacrimal bone. A distinct lacrimal forming the lateral margin of the lacrimal foramen is present in most skinks, though often very reduced in size and thickness in very small species. Despite a claim of absence in *E. whitii* (Siebenrock, 1892), a well-developed lacrimal was seen in all *Egernia* species examined (n = 20), including *E. whitii* and covering all species groups within the genus. Within the other outgroups, a distinct lacrimal was not found only in *Geomyersia* (Greer, 1982b), *Ristella* (A. Greer, *pers. comm*.), *Menetia* and one species of *Lobulia* (*pers. obs*.). The presence of a lacrimal is considered primitive, and the absence of a distinct lacrimal seen in *Cyclodomorphus*, *Hemisphaeriodon*, *Tiliqua* and *Trachydosaurus* (Fig. 6) derived.
8. Palatine process of the ectopterygoid. A palatine process of the ectopterygoid, bordering the medial margin of the infraorbital fenestra, has been considered a derived character amongst skinks (Fuhn, 1969; Greer, 1970a,b, 1976; Greer & Cogger, 1985). Within *Egernia*, a long palatine process of the ectopterygoid, reaching the palatine, was seen in nine of the 20 species examined. However, these nine species represented only three of nine recognisable species groups within the genus (Shea, *in prep*.). In the second outgroup, the process is lacking in 23 genera and species groups, present but not contacting the palatine in three, present and contacting the palatine in nine, and variably present (i.e., present in only some species) in three. Within *Mabuya*, the process has only been seen in five species (Greer, 1976; *pers. obs*.). In the third outgroup, the process is lacking in all genera. Absence of a palatine process of ectopterygoid is considered primitive, and its presence in *Cyclodomorphus*, *Hemisphaeriodon*, *Tiliqua* and *Trachydosaurus* (Fig. 7) derived.
9. Heterodonty. Most skinks have a homodont dentition, with marked heterodonty only reported in *Cyclodomorphus*, *Hemisphaeriodon*, *Tiliqua*, *Trachydosaurus* and one species each of *Eumeces* and *Lerista* (Siebenrock, 1892; Estes & Williams, 1984). *Egernia*, *Mabuya*, other *Eumeces* species, and all other species examined within the outgroups have homodont dentition. Although there is variation in the degree of heterodonty in adults, juveniles of all *Cyclodomorphus*, *Hemisphaeriodon*, *Tiliqua* and *Trachydosaurus* species have a single markedly enlarged tooth in the maxillary (position number 7 or 8) and dentary (position 10) arcades (*pers. obs*.). Homodonty is considered primitive and juvenile heterodonty derived (Estes & Williams, 1984).
10. Scales over temporal region. The majority of skinks have two supralabials caudal to the subocular supralabial, a single primary temporal dorsally between these, a single lower secondary temporal caudodorsal to the last supralabial, and a single upper secondary temporal dorsally, bordering parietal, primary temporal and lower secondary temporal, overlapping the latter scale. Generally, the last two supralabials are subequal in height, and both higher than the preceding supralabials (Fig. 8). This is assumed to be the primitive temporal configuration. All *Egernia* species, over two-thirds of the genera in the second outgroup, and *Eumeces*, *Scincus* and *Scincopus* in the third outgroup show this arrangement, although some genera in the *Sphenomorphus* group (e.g., *Lerista*, *Calyptotis*, *Notoscincus*, *Ctenotus*) and a few *Eumeces* species have reversed the overlap of upper and lower secondary temporals. Other genera in the second and third outgroups show a variety of modifications to this pattern, mostly apparently involving subdivision of scales, particularly the lower secondary temporal and last supralabial scales. In *Cyclodomorphus*, *Hemisphaeriodon* and *Tiliqua*, the last supralabial is divided into an upper and a lower scale by a suture, leaving a single low “last supralabial” bordering the lip. Most *Tiliqua* species, and occasional *Hemisphaeriodon* specimens additionally show further subdivisions of the primary and lower secondary temporal

scales. In *Trachydosaurus*, the number and pattern of division of the supralabial and temporal scales is variable. However, the consistently low last two supralabials, frequent irregularity of the caudal margin of the "lower secondary temporal" and the number and pattern of overlap of surrounding scales suggests that the upper scale of the last supralabial pair and the lower scale of the lower secondary temporal pair have usually fused, sometimes incorporating the upper scale of the lower secondary temporal pair as well (Fig. 8K), as part of a general reduction in number of scales in this species.

11. Supraciliary scales. Most species in the first two outgroups modally have eight or more supraciliaries, although most *Mabuya* have 5–6 supraciliaries. In the third outgroup, *Amphiglossus* (*Madascincus*), *Janetaescincus*, *Pamelaescincus* and over 70% of *Eumeces* species have modes of seven or more supraciliaries. Seven to nine supraciliaries is considered primitive for skinks, and modes of six or fewer derived. *Cyclodomorphus*, *Hemisphaeriodon* and *T. scincoides* usually have six supraciliaries, *T. gigas* has high frequencies of both six and seven supraciliaries, while other *Tiliqua* and *Trachydosaurus* usually have five or fewer supraciliaries (Fig. 7).

12. Tongue colour. Although this character has been relatively little studied in skinks, most Australian lygosomines I have examined in life (including 14 species of *Egernia*) have pink to light grey tongues. *Corucia* also has a pink tongue. Consequently, I believe that a pink or only lightly melanised tongue is primitive and the dark blue-black to bright blue tongues of *Cyclodomorphus*, *Hemisphaeriodon*, *Tiliqua* and *Trachydosaurus* are derived. Although *Hemisphaeriodon* variably has a pink or blue tongue as an adult, the tongue is dark blue-black in juveniles. Tongue colour in life is not known for *T. adelaidensis*, although long-preserved material shows no pigmentation of the tongue.

13. Colour pattern. Broad patterns of dorsal and lateral coloration have been frequently used in skink systematics at the generic level (Greer, 1970b, 1974, 1979b). The majority of taxa within the outgroups, including most *Eumeces*, *Mabuya* and *Egernia* species, show strong indications of a longitudinally striped pattern dorsally and laterally, generally with some or all of the following elements: continuous dark dorsal stripes, longitudinally aligned dark dorsal streaks, a broad dark upper lateral stripe and a pale midlateral stripe. In contrast, strongly banded colour patterns are uncommon in all outgroups (Greer, 1970b, 1979b). A dominance of longitudinal elements of pattern is considered primitive, and strongly banded patterns derived. *Hemisphaeriodon*, most *Tiliqua*, and many *Trachydosaurus* have a dorsal and lateral body and tail pattern of strongly contrasting light and dark bands. Two species (*T. nigrolutea*, some *Trachydosaurus*) have the transverse elements obscured by expansion of the dark-pigmented areas, while *T. adelaidensis* has a back pattern of broken narrow dark vermiculations on a light background. *Cyclodomorphus* species have either narrow alternating light and dark bands (most *C. casuarinae*) or a pattern of dark and light spots (*C. branchialis*, *C. maximus*), which are most prominent in juveniles. However, in *C. branchialis* and *C. maximus*, the light spots are predominantly transversely aligned, while in *T. adelaidensis* there does not appear to be any predominant orientation. I believe that the pattern in these cases is most simply explained as a secondary reduction of the broad-banded motif.

14. Subocular scale row. The presence of a complete row of enlarged subocular scales, separating the lower eyelid from the supralabials, has variously been considered primitive (Fuhn, 1969; Greer & Cogger, 1985) or derived (Greer, 1982b; Sadlier, 1987) within skinks. In attempting to survey this character, I have experienced occasional difficulties in differentiating subocular scales from enlarged granules on the ventral margin of the lower eyelid. In these cases, I have defined a complete subocular scale row as existing only when fewer than three moderate to large scales border the subocular supralabial between presubocular and postsubocular series. Within *Egernia*, a complete subocular row is present only in the *E. luctuosa* species group, *E. major*, *E. rugosa* and a few members of the *E. whitii* species group. In the second and third outgroups, a complete subocular row is consistently present in 16 genera, variably present in four (and then only in a few species) and absent in 39 genera. Most *Eumeces* and *Mabuya* species have an incomplete subocular row. The incomplete subocular scale row seen in *Cyclodomorphus* and *Hemispheriodon* is primitive and the complete, even subocular row, with 0–1 scales

interposed between presubocular and postsubocular series, seen in *Tiliqua* and *Trachydosaurus* (Fig. 10) is derived.

15. Nuchal scales. In general, transversely enlarged nuchal scales exhibit three patterns in skinks: absent (i.e., scales bordering the caudal margin of parietals not noticeably wider than succeeding scales, the caudal edge of each overlapping three scales), a single pair present (the caudal edge of each overlapping four or more scales), or a variable number of multiple pairs present (Fig. 11). The first condition is rare in the first three outgroups, and is considered derived. However, it is more difficult to determine the relative polarities of the other two conditions. In *Egernia*, a single pair of nuchals is characteristic of the *E. whitii* group, while most other groups have multiple pairs of nuchal scales. Within the second outgroup, a single pair of nuchals characterises most members of the *Eugongylus* group, *Mabuya*, *Macroscincus* and *Dasia*, while multiple pairs of nuchals are characteristic of most members of the *Sphenomorphus* group and *Lamprolepis*. Within the third outgroup, *Eumeces*, *Scincus* and *Scincopus* have multiple pairs of nuchals, while *Janetaescincus* and *Pamelaescincus* lack nuchals. Because of the more widespread occurrence of multiple nuchals in *Egernia* and the third outgroup, I am inclined to consider multiple nuchals primitive within the *Tiliqua* lineage. *Cyclodomorphus* and *Hemisphaeriodon* have multiple pairs of nuchals, while most *Tiliqua* and *Trachydosaurus* lack nuchals (Fig. 11). The exception, *T. adelaidensis*, has a variably expressed single pair of slightly enlarged nuchals often separated by a median occipital. The nuchals in this species are never as large and clearly defined as in the *E. whitii* species group, the only other member of the *Egernia* group to possess a single pair of nuchals, and are probably not homologous.

16. Temporal process of jugal bone. The temporal process of the jugal is long and slender in all of the outgroups, generally much narrower than the adjoining jugal process of the maxilla, although in some *Egernia* species and a few other skinks the caudoventral angle bears a narrow spur to support the quadratojugal ligament. A narrow temporal process, rounded in cross-section, as occurs in *Hemisphaeriodon* and *Cyclodomorphus*, is considered primitive. In *Tiliqua* and *Trachydosaurus*, the temporal process is much more robust (Fig. 12), apparently largely due to expansion of its caudal free margin, producing a flattened cross-section. This expansion of the caudal margin is particularly evident at the dorsal and ventral extremities, which are expanded into two caudally-directed flanges. *C. branchialis* and *Hemisphaeriodon* show some trend in this direction, but in both the expansion is less than in *Tiliqua* and *Trachydosaurus*, as is evidenced by the lack of expansion of the caudoventral angle (the caudal process) beyond the maxilla, and in *Hemisphaeriodon* by the rounded cross-section and the very narrow, straight dorsal extremity.

17. Rostral margin of frontal bone. In most skinks the frontal extends superficially a variable distance laterally along the nasals, forming lateral frontal processes between the nasals, prefrontals, and often the maxillae. These processes are consistently present, and usually long, in the outgroups, and in *Tiliqua* and *Trachydosaurus*, although in *Eugongylus*, they extend into the nasals rather than along their lateral border. In *Cyclodomorphus* and *Hemisphaeriodon* they are either completely absent, or when present in some individuals, short and less developed than the opposing caudomedial frontal processes of the maxillae. Consequently, I believe that the presence of superficial lateral rostral frontal processes, forming a W-shaped rostral frontal margin, is primitive, and their absence, replaced by caudomedial processes from the maxillae, and leaving a Λ-shaped frontal margin (Fig. 13), is derived.

18. Supraocular scales. Four supraoculars, the first two contacting the frontal, has been considered the primitive condition for skinks (Greer, 1974; Perret, 1975; Greer & Cogger, 1985). This configuration occurs in all *Egernia* species, and in at least some species in 46 of 51 genera in the second outgroup, although most *Mabuya* species have the first three supraoculars contacting the frontal. In the third outgroup, *Amphiglossus* (*Madascincus*), *Janetaescincus* and *Pamelaescincus* have four supraoculars (although fusion of frontoparietals and frontal makes it impossible to determine the pattern of frontal contact), *Scincus* and *Scincopus* have multiple supraoculars, and most *Eumeces* have four supraoculars with the first three contacting the frontal, although some species have

the 4(2) configuration. The evidence suggests that the 4(2) configuration is primitive for lygosomines at least, and reduction either in total number or number contacting the frontal is derived. In *Tiliqua, T. gigas, T. nigrolutea* and *T. scincoides* usually have the primitive condition, while *T. multifasciata, T. occipitalis* and *T. rugosa* usually have the first and second supraoculars fused, leaving only a single supraocular contacting the frontal. *T. adelaidensis, Cyclodomorphus* and *Hemisphaeriodon* have only three supraoculars, but two contacting the frontal (Fig. 9). On the basis of the supraciliary contact pattern, it appears that the second and third supraoculars have fused in these taxa. However, in that *T. adelaidensis* modally has only five supraciliaries, like most *Tiliqua*, while *Cyclodomorphus* and *Hemisphaeriodon* have the more primitive six, I believe that fusion of the second and third supraoculars has occurred independently in the former species. A few *T. scincoides* and *T. gigas* also show the 3(2) supraocular configuration.

19. Ear lobules. Most generally primitive skinks have a moderate to large external ear, with several rounded to acute lobules along the rostral margin (Perret, 1975; Greer, 1982b), although lobules are generally lacking in those taxa which have a greatly reduced external ear. Of those taxa which have a moderate to large ear, several moderate to large lobules are present in all *Egernia* species and consistently present in half (24 of 48) of the genera in the second outgroup (including *Corucia*, most *Mabuya*, and most members of the *Eugongylus* group). In the third outgroup, ear lobules are generally present in *Eumeces* and *Scincopus*, but absent in *Janetaescincus* and *Pamelaescincus*. Although the evidence is not conclusive, the condition shown by *Egernia, Corucia*, *Mabuya* and *Eumeces*, several moderate to large lobules along the rostral margin of the ear, is considered primitive, and the 0–2 small rounded lobules seen in *Cyclodomorphus, Hemisphaeriodon* and *T. adelaidensis*, derived. It is difficult to assess the condition of the rostral margin of the ear in *Trachydosaurus*, as the scales are thick and bony, and evenly grade into smaller bony scales deep within the external auditory meatus, but these thickened bony scales may be derived from the lobules of other *Tiliqua* species.

3.3 Diagnosis of the Tiliqua *Lineage*

The species variously assigned to *Cyclodomorphus, Hemisphaeriodon*, *Tiliqua* and *Trachydosaurus* share the derived condition in characters 1–13, and constitute a lineage, which may be defined as follows:

Osteology: prefrontal and postfrontal narrowly separated or in contact (except in *T. adelaidensis*); jugal and squamosal in contact; lacrimal absent; medial palatine process of ectopterygoid strong, broadly contacting palatine; coronoid process of dentary laterally overlapping coronoid; single grossly enlarged tooth in maxilla (position 7 or 8) and dentary (position 10) in juveniles; presacral vertebrae 32–44; phalangeal formula of manus and pes 2.3.4.4.3/2.3.4.4.3 or fewer.

Scalation: caudalmost supralabial divided into an upper and a lower scale; supraciliaries modally six or fewer (except in some populations of *T. gigas*).

Coloration: tongue deeply pigmented, at least in juveniles, blue-black to bright blue (except in *T. adelaidensis*?); dorsal and lateral pattern on body and tail, when present, predominantly consists of narrow to broad bands or transversely aligned vermiculations or spots, at least in juveniles (except in *T. adelaidensis*).

3.4 The Holophyly and Relationships of the Tiliqua *Lineage*[1]

There seems little doubt that the *Tiliqua* lineage is monophyletic. Two characters seem particularly telling in this regard: the increase in number of presacral vertebrae and the pattern of phalangeal loss. Within the *Egernia* group, these characters readily separate the *Tiliqua* lineage from both *Egernia* and *Corucia*, with no evidence of intermediacy. The *Egernia luctuosa* species group is clearly not a member of the *Tiliqua* lineage on both characters, having the primitive number of presacral vertebrae and phalanges.

No skinks currently outside of the *Egernia* group appear to be members of the *Tiliqua* lineage or likely close relatives. The genera in the cluster closest to the *Egernia* group, the *Eugongylus* group, rarely show marked increases in number of presacral vertebrae or phalangeal loss, apart from the loss of the first finger in *Carlia, Lygisaurus*, *Menetia, Ristella* and *Saproscincus tetradactyla* (Greer, 1974, 1979a, 1991), a synapomorphy that does not occur within the *Egernia* group. The only two exceptions to this pattern are *Graciliscincus*, which has a similar number of presacral vertebrae to the *Tiliqua* lineage while still retaining the primitive phalangeal configuration, and *Nannoscincus*, in which there is a mosaic of taxa with elevated numbers of presacral vertebrae and phalangeal loss (Sadlier, 1987, 1990), including the combination seen in the *Tiliqua* lineage. However, it is apparent that this similarity between *Nannoscincus* and the *Tiliqua* lineage is due to convergence, as *Nannoscincus* is both monophyletic and clearly a member of the *Eugongylus* group rather than the *Egernia* group (Greer, 1974; Sadlier, 1987, 1990; Hutchinson *et al.*, 1990), and otherwise shows little resemblance to *Tiliqua*.

Although *Egernia* has been shown to be the genetically closest genus to the *Tiliqua* lineage (Hutchinson, 1981), the nature of the relationship has not previously been determined. Three types of relationship are possible:

1. *Egernia* and the *Tiliqua* lineage are sister-groups, each monophyletic
2. *Egernia* is primitive, possibly ancestral to the *Tiliqua* lineage, and hence paraphyletic
3. the *Tiliqua* lineage is primitive, possibly ancestral to *Egernia*, and hence paraphyletic.

The latter hypothesis was favoured by Horton (1972). At first glance, the third hypothesis seems untenable, given the above argument for the holophyly of the *Tiliqua* lineage. However, given the high frequency of parallel evolution and character reversal with the Scincidae, if the third alternative were the case, use of *Egernia* (then an ingroup) as the primary outgroup would be inappropriate, potentially assigning erroneous character polarities. However, exclusion of the first outgroup does not result in reversal of the inferred polarity of any character, and hence confirms the highly derived nature of the *Tiliqua* lineage.

In contrast, I have been unable to identify any synapomorphies with which to diagnose *Egernia vis-à-vis* the *Tiliqua* lineage. Previous diagnoses have also failed to demonstrate a sister-group relationship between the two groups. The modern concept of *Egernia* is derived from Boulenger (1887), who placed in one genus a range of species formerly spread over at least five genera. Boulenger's diagnosis utilises only two derived characters compared to

[1] I use holophyletic in the sense of Ashlock (1971), as a term for a monophyletic group containing all the descendents of a common ancestor, although for operational reasons rather than the philosophical arguments presented by Ashlock, which have been discussed and criticised by others (e.g., Farris, 1990). I see the I use holophyletic in the sense of Ashlock (1971), as a term for a monophyletic group containing all the descendents of a common ancestor, although for operational reasons rather than the philosophical arguments presented by Ashlock, which have been discussed and criticised by others (e.g., Farris, 1990). I see the recognition of an initial monophyletic group (in which the intragroup relationships can then be explored by cladistic principles) as a two-step procedure. Firstly, a set of synapomorphies must be accumulated to provide evidence for the historical reality of the group of species under consideration as monophyletic. Secondly, that set of synapomorphies must be used for wider comparison to check that the hypothetical monophyletic group contains all of the known species that should be included in the group. It is following the completion of this second stage that I use the term holophyly.

generally primitive lygosomine skinks: pterygoid teeth “few or absent” and lack of supranasal scales. Although Hoffstetter (1949) also records pterygoid teeth in *Egernia*, I have been able to identify them only in one specimen of *E. cunninghami*. Both characters are shared with *Tiliqua*, and the second also with *Corucia*. Hence, at best the second character merely supports the monophyly of the *Egernia* group, and the first the monophyly of *Egernia*+*Tiliqua*. Mitchell (1950), Cogger (1975) and Storr (1978) have subsequently attempted to diagnose *Egernia*. However, none of these diagnoses offer any synapomorphies for the genus.

On present knowledge, therefore, the second hypothesis, that *Egernia* is primitive, possibly ancestral to the *Tiliqua* lineage, and potentially a paraphyletic assemblage, seems to be the most likely. Although there are arguments for not recognising paraphyletic taxa (e.g., Hutchinson & Maxson, 1987), the interrelationships of the recognisable lineages within *Egernia* remain obscure (Horton, 1972; Storr, 1978b; Wells & Wellington, 1984, 1985; *pers. obs*.) and in the absence of resolution of the relationships within this assemblage, and of evidence relating the *Tiliqua* lineage to any one of these other lineages, I prefer to retain the *Egernia* assemblage as a generic unit distinct from the *Tiliqua* lineage.

3.5 Recognition of two Genera within the Tiliqua *Lineage*

On the basis of characters 14–19, I believe that two sister-taxa can be recognised within the *Tiliqua* lineage. The first of these, comprising the species formerly placed in *Tiliqua* (s.s.) and *Trachydosaurus* and for which the name *Tiliqua* is available, may be diagnosed as follows:

Tiliqua Gray, 1825

Tiliqua Gray, J.E. (1825). A Synopsis of the Genera of Reptiles and Amphibia, with a Description of some new Species. *Annals of Philosophy* (2)10(3): 193–217 [201].
Type species: *Lacerta scincoides* [Hunter], 1790, by subsequent designation (Cogger *et al.*, 1983).

Trachydosaurus Gray, J.E. (1825). A Synopsis of the Genera of Reptiles and Amphibia, with a Description of some new Species. *Annals of Philosophy* (2)10(3): 193–217 [201].
Type species: *Trachydosaurus rugosus* Gray, 1825, by monotypy.

Trachysaurus Gray, J.E. (1827). Reptilia. pp. 424–434 *in*, King, P.P. *Narrative of a survey of the intertropical and western coasts of Australia*. *Performed between the years 1818 and 1822*. Vol. II. John Murray, London (637pp.) [430].
Unjustified emendation *pro Trachydosaurus*

Cyclodus Wagler, J. (1828). *Descriptiones et icones amphibiorum*. J.G. Cottae, Monachii, Stuttgartiae et Tubingae. Part 1, fig. 6.
Type species: *Cyclodus flavigularis* Wagler, 1828, by monotypy.

Brachydactylus Smith, [A.] (1835). [untitled]. *South African Quarterly Journal* 2(2): 143–144 + pl.
Type species: *Brachydactylus typicus* Smith, 1835, by monotypy.

Tiligua Duméril, [A.M.C.] (1837). Rapport sur un ouvrage manuscrit de M. le docteur Cocteau, ayant pour le titre: Tabulae synopticae Scincoideorum. *Comptes Rendus hebdomadaires des séances de l'Académie des Sciences*, *Paris* 4(1): 14–17. [16]
Lapsus pro Tiliqua.

Keneaux Duméril, [A.M.C.] (1837). Rapport sur un ouvrage manuscrit de M. le docteur Cocteau, ayant pour le titre: Tabulae synopticae Scincoideorum. *Comptes Rendus hebdomadaires des séances de l'Académie des Sciences*, *Paris* 4(1): 14–17. [16]
Nomen nudum. Originally proposed without included species, *ex* Cocteau MS.

Tachydosaurus Gray, J.E. (1838). Catalogue of the Slender-tongued Saurians, with Descriptions of many new Genera and Species. *Annals and Magazine of Natural History* (2)2(10): 287–293.
Lapsus pro Trachydosaurus.

Diagnosis: Moderate to very large skinks, with a complete subocular row of evenly enlarged scales separating supralabials from lower eyelid; nuchals either a single variably expressed pair or absent; temporals usually divided (except in *T. adelaidensis*), and jugal broad, with an expanded winglike temporal process.

Content: *Cyclodus adelaidensis* Peters, 1864a, *Scincus gigas* Schneider, 1801, *Tiliqua occipitalis multifasciata* Sternfeld, 1919, *Scincus nigroluteus* Quoy & Gaimard, 1824, *Cyclodus occipitalis* Peters, 1864a, *Trachydosaurus rugosus* Gray, 1825, *Lacerta scincoides* [Hunter], 1790. See Chapters 4–9 for species synonymies and diagnoses.

Nomenclatural notes: Although *Tiliqua* and *Trachydosaurus* were both erected by Gray (1825), Mitchell (1950), acting as first reviser in the sense of Article 24(b) of the Code of Zoological Nomenclature, selected *Tiliqua* to have precedence over *Trachydosaurus*.

The second genus, comprising the species variably placed in *Omolepida*, *Cyclodomorphus* and *Hemisphaeriodon*, for which *Cyclodomorphus* is the earliest available name, may be diagnosed as:

Cyclodomorphus Fitzinger, 1843.

Cyclodus (*Cyclodomorphus*) Fitzinger, L. (1843). *Systema reptilium*. *Fasciculus primus Amblyglossae*. Braümuller et Seidel, Vindobonae. (106 + ix pp.) [23].
Type species: *Cyclodus casuarinae* Duméril & Bibron, 1839, by original designation

Omolepida Gray, J.E. (1845). *Catalogue of the specimens of lizards in the collection of the British Museum*. Edward Newman, London. (xxviii + 289pp.) [71,87].
Type species: *Cyclodus casuarinae* Duméril & Bibron, 1839, by monotypy

Hemisphaeriodon Peters, W. (1867). Herpetologische Notizen. *Monatsbericht der königlich preussischen Akademie der Wissenschaften zu Berlin* 1867: 13–37 [24].
Type species: *Hinulia gerrardii* Gray, 1845, by monotypy.

Homolepida Lütken, C. (1863). Nogle nye Krybdyr og Padder. *Videnskagelige Meddelelser fra den naturhistoriske Forening i Kjoberhaun* 1862(20–22): 292–311 [294].
Lapsus pro Omolepida.

Omolepidota Lucas, A.H.S. & Frost, C. (1896). Description of a new species of *Ablepharus* from Victoria, with critical notes on two other Australian lizards. *Proceedings of the Linnean Society of New South Wales* 21(3): 281–283 [281].
Lapsus pro Omolepida.

(erroneously cited as Frost, C. & Lucas, A.H.S. (1894). Proc. Linn. Soc. N.S.W. (2)8(2): 227–228 by Shea, G.M. (1991)).

Diagnosis: Small to moderately large skinks lacking lateral rostral projections of frontal bone, or with them very reduced, leaving a Λ-shaped rostral margin to frontal superficially on intact skull; second and third supraoculars fused, leaving only three supraoculars, first two contacting the frontal; lobules along rostral margin of ear very reduced (both in size and number) or absent.

Content: *Hinulia branchialis* Günther, 1867, *Cyclodus casuarinae* Duméril & Bibron, 1839, *Hinulia gerrardii* Gray, 1845a, *Omolepida maxima* Storr, 1976. See Cogger *et al*. (1983) for species synonymies. *Cyclodomorphus branchialis* as currently recognised (Storr, 1976; Cogger, 1986) is polytypic, and can be divided into five taxa, of which three deserve species rank; G. Shea & B. Miller, *in prep*.).

Nomenclatural notes: Although *Cyclodomorphus*, a senior objective synonym of *Omolepida*, has been formally used only eight times in the 148 years since its erection (Fitzinger, 1860; Wells & Wellington, 1984, 1985; Shea & Wells, 1985; Czechura, 1986; Shea, 1988; Wilson & Knowles, 1988; Cogger, 1989), while *Omolepida* (or its emendation *Homolepida*) has been frequently used as an available generic or subgeneric name over the same period, I do not believe that recognition of the priority of *Cyclodomorphus* over *Omolepida* disturbs stability or causes confusion (Articles 23(b) and 79(c) of the Code). Mitchell (1950), Hutchinson (1981) and Cogger *et al*. (1983), while placing both names into the synonymy of *Tiliqua*, clearly recognised the priority of *Cyclodomorphus* over *Omolepida*. In the previous fifty years, *Omolepida* has been formally used only once in combination with the type species (Storr, 1976), although frequently used as the generic name for the *C. branchialis* complex and *C. maximus* in Western Australia. Use of *Cyclodomorphus* here recognises the rather different concept of the genus I have proposed, and clearly distinguishes this version from that to which the name *Omolepida* has formerly been applied.

Romer (1956) and Cogger *et al*. (1983) list three additional names in the synonymy of *Tiliqua* and *Trachydosaurus*: *Rachites*, *Homolepides* and *Silubolepis*. All are apparently derived from an unpublished manuscript, *Tabulae synopticae Scincoideorum*, by J.-T. Cocteau, submitted to the Académie des Sciences in Paris, and described by Duméril (1837). All three names appear to be unavailable. *Rachites* was published without any included species or description (Duméril, 1837; Duméril & Bibron, 1839: 523). There appears to be no justification for associating *Rachites* with *Tiliqua* other than the inclusion of both, along with *Euprepis* Wagler, 1830, *Keneaux*, *Psammites*, *Heremites* and *Arne* (the latter four similarly *nomina nuda*) as subgenera of the vernacular Scléroblépharides by Duméril (1837). *Keneaux* Duméril, 1837 was subsequently associated with *Tiliqua* by the inclusion of two of Cocteau's vernacular names, Kéneaux de l'Uranie and Kéneaux de Boddaert, in the synonymy of *Cyclodus nigroluteus* and *C. boddaertii* (Duméril & Bibron, 1839). *Homolepides* Agassiz, 1846 was based, again without included species, on Cocteau's vernacular Omolépides. There is no indication provided by Duméril (1837) as to the status assigned to this name, other than that it was six divisions below a tribe and, in turn, three divisions above *Tiliqua*. Consequently, there appears to be no basis for associating *Homolepides* with the *Tiliqua* lineage. *Silubolepis* Duméril & Bibron, 1839, a name assigned to Cocteau, appears only in the synonymy of *Trachysaurus*, and is not therefore available (Article 11(c)).

An alternative classification reflecting the same relationships as inferred here would be to recognise *Tiliqua* and *Cyclodomorphus* as subgenera within an expanded *Tiliqua*. This would emphasise the sister-group relationship between the two taxa. However, I prefer generic separation for three reasons. Firstly, the larger *Tiliqua* are frequently used as experimental subjects in comparative physiological and biochemical research. Generic

separation simplifies a nomenclature frequently used by non-taxonomists. Secondly, with the generic status of *Egernia* still undetermined, generic status adds two diagnosable monophyletic groups to an *Egernia* group otherwise having the monotypic *Corucia* as its only other diagnosable genus. Finally, the two genera are also ecologically distinct, and generic status more clearly expresses this (Greer & Haacke, 1982). With the exception of *T. adelaidensis*, a small, probably extinct species of largely unknown habits (Ehmann, 1983), *Tiliqua* comprises large, mostly diurnally active species that forage widely in largely open habitats, while *Cyclodomorphus* species are mostly of small to moderate size and secretive habits in generally "closed" habitats and microhabitats, from closed forest (*C. gerrardii*) to *Triodia* tussocks (*C. branchialis*).

3.6 Assessment of Previous Arguments for the Synonymy of Cyclodomorphus *with* Tiliqua

Arguments for the synonymy of *Cyclodomorphus* with *Tiliqua* have been based on two lines of evidence: morphology (Duméril & Bibron, 1839; Duméril & Duméril, 1851; Strauch, 1866; Smith, 1937; Mitchell, 1950; Cogger, 1983b) and immunology (Hutchinson, 1981). With the exception of the claims of Cogger (1983b) I do not consider that any of these arguments are incompatible with the sister-group relationship I have hypothesised above.

Hutchinson's (1981) immunological results (see Chapter 1) were interpreted in the light of Storr's (1976) concept of *Omolepida*, which did not include *C. gerrardii*, and on an assumption of monophyly for *Egernia*. However, as noted above, evidence for the monophyly of *Egernia* is wanting, and hence his comparison of the extent of antigenic variation within the *Tiliqua* lineage and *Egernia* is invalid. The classification proposed here satisfies Hutchinson's other major criticism by separating both *C. gerrardii* and *C. casuarinae* from *Tiliqua*. Indeed, Hutchinson's criticism of Storr's concept of *Omolepida* is flawed. Although Storr did not specifically include *gerrardii* in *Omolepida* (perhaps due to a lack of familiarity with the species), it possesses all of the diagnostic characters Storr proposed for the genus, and clearly should have been included.

Of the morphological arguments for the synonymy of *Cyclodomorphus* with *Tiliqua*, those of Duméril and Duméril (1851) and Strauch (1866) are not explicit, but appear to be largely based on the combination of overall phenetic similarity and the synapomorphy of enlarged, molariform teeth, while one of the two characters employed by Smith (1937), complete separation of the parietals by the interparietal, is a symplesiomorphy (Greer, 1979a) and hence of no use in inferring relationships. Most authors advocating synonymy on morphological grounds have recognised a basic division within *Tiliqua* (s.l.). Duméril and Bibron (1839) and Duméril and Duméril (1851) separated *C. casuarinae* from the two other *Cyclodus* species then recognised (*nigroluteus*, *boddaertii*) in the first couplet of their keys, on the basis of lack of ear lobules. Strauch (1866) separated the subgenus *Omolepida* on the basis of lack of a postnarial groove. Smith (1937) and Mitchell (1950) separated *casuarinae* and the *branchialis* complex from other *Tiliqua* on the basis of a longer tail and incomplete subocular scale row. Using these criteria, *C. gerrardii* comes out with *C. casuarinae* (Mitchell, 1950). The generic separation advocated here does not contradict any of these proposed classifications, but merely alters the level at which the distinction is made.

The view of Cogger (1983b: 8) that "there is a continuum of character states linking the extreme expression of *Tiliqua* via *Hemisphaeriodon* with that of *Omolepida* (=*Cyclodomorphus*)", although incompatible with the dichotomy presented here, was not presented with the support of any specific data, and hence cannot be considered on its own merits. However, I do not believe that Cogger's argument can be justified. *Hemisphaeriodon* shows all of the synapomorphies used to define *Cyclodomorphus vis-à-vis Tiliqua*, most notably the supraocular pattern and the shape of the suture between frontal and surrounding bones, and is plesiomorphic *vis-à-vis Tiliqua* in all diagnostic characters. Within

Cyclodomorphus, *gerrardii* shares with *casuarinae* one synapomorphy unique within the *Tiliqua* lineage, loss of the postnarial groove, and another synapomorphy rare in other taxa, extreme reduction of the single ear lobules, such that it is barely evident in many individuals. a behavioural synapomorphy also links the two taxa: tongue-flickering, used in both food location and defence (Shea, 1988, *pers. obs.*), in contrast to simple tongue protrusion and licking in other species. Both species are primitive within the *Tiliqua* lineage in possessing a mode of eight premaxillary teeth (Greer, 1979a; *pers. obs.*). These characters in combination suggest to me that *C. casuarinae* and *C. gerrardii* are sister-species, and that any apparent phenetic similarity between *C. gerrardii* and *Tiliqua* is due to a position for *C. gerrardii* close to the basal stock of the lineage.

Cogger appears to have reversed his earlier opinion, as he has recently (Cogger, 1989a) used both *Hemisphaeriodon* and *Cyclodomorphus* as distinct genera, although again without offering any argument.

3.7 Assessment of Previous Arguments for the Recognition of Trachydosaurus

T. rugosa possesses all of the synapomorphies listed above for *Tiliqua*, or further modifications from these, and is clearly a member of the *Tiliqua* (s.s.) radiation. From a phylogenetic viewpoint, the only justification that could be offered for recognition of *Trachydosaurus* as distinct from *Tiliqua* would be a hypothesis of relationships that identified *T. rugosa* as the sister taxon to a rest-of-*Tiliqua* clade, each taxon diagnosable on the basis of derived character states. With the possible exception of an unsupported, and hence unassessable, statement by Cogger (1983b) (see Chapter 1), this has not explicitly been the basis of any of the arguments advanced for the recognition of *Trachydosaurus*, all of which have rested on only a few characters.

Gray (1825), in describing *Trachydosaurus*, used two characters: thick, bony scales on head and body, and a short, depressed tail. Wagler (1830) added to these a difference in dentition: conical teeth in *Trachydosaurus vs* rounded, obtuse crowns in *Cyclodus*. These three characters were used by all authors for over sixty years (Gray, 1827, 1831, 1838, 1845a; Wiegmann, 1834; Duméril & Bibron, 1839; Duméril & Duméril, 1851; McCoy, 1885), although Peters (1864a) noted that the teeth of *T. adelaidensis* had conical rather than rounded crowns. Boulenger (1887) recognised all three characters, and added a further two: presence of an azygous occipital scale and mostly divided subdigital lamellae. These five characters are the only morphological evidence formally offered for the recognition of *Trachydosaurus*.

Of these five characters, the conical teeth and azygous occipital scale are invalid for diagnosing the genus, as they also occur in other *Tiliqua* species. Within *Tiliqua*, there is marked interspecific and ontogenetic variation in tooth shape (Shea, *in prep.*). Only *T. gigas* and *T. scincoides*, the first two described species, have the rounded tooth crowns noted by Wagler (1830). The other species have more conical crowns, those of *T. nigrolutea* being more conical than in *Trachydosaurus*.

The presence of a median occipital is variable in *Trachydosaurus*, although it is present in most individuals. Presence of a median scale caudal to the interparietal is an apomorphy in skinks (Greer, 1968) and has previously been used as the major diagnostic character in one genus, *Geomyersia*. However, a median occipital also occurs in many *T. adelaidensis* and *T. nigrolutea*, while asymmetry in the scales bordering the caudal margin of the parietal/interparietal complex, a possible precursor to the differentiation of a median occipital, is common in other *Tiliqua* species.

Similarly, although the grossly enlarged, thickened osteoderms characteristic of *Trachydosaurus* are a unique apomorphy within the Scincidae, *T. nigrolutea* also displays a trend in this direction. Enlargement of body scales can also be expressed as a reduction in number of scales, assuming similar body shapes. The ranges for midbody, paravertebral and ventral scales for *T. rugosa*, while generally higher than for other *Tiliqua*, are overlapped by *T. nigrolutea* in the case of midbody and ventral scales, and are approached by *T. nigrolutea* in the case of paravertebral scales.

The short, depressed, blunt-tipped tail of *Trachydosaurus* is also apomorphic. However, there is geographic variation in tail length in *T. rugosa* (Chapter 8), with the longest tails occurring in the south-west of Western Australia. Moreover, some Western Australian individuals have a distinctly conical tail tip. *T. nigrolutea* again shows some trend in the direction of *Trachydosaurus*, with a short, thick tail, showing a tendency to depression in emaciated individuals.

The division of subdigital lamellae seen in *Trachydosaurus* is an autapomorphy within the *Egernia* group.

A number of other differences between *T. rugosa* and other *Tiliqua* (usually as represented by *T. scincoides*) have been noted in the course of more general comparative studies, though not previously utilised for formal taxonomic separation (Arnold, 1984; Camp, 1923; Cope, 1892b; Greer, 1979a; Hoffstetter, 1949; Lécuru, 1968a–c; Parker, 1868; Renous-Lécuru, 1973; Siebenrock, 1892, 1895; M.J. Smith, 1976, 1982). The generality of these differences, within and between species, has not previously been assessed in most cases. I have examined most of these characters, and in almost all cases, the purported differences are less than diagnostic, either due to variation within *T. rugosa* or the *T. rugosa* condition occurring in other *Tiliqua* species. Only in the further reduction of phalangeal formula (Siebenrock, 1895; Hoffstetter, 1949), again an apomorphy for *T. rugosa*, is the difference from all other *Tiliqua* clear-cut and consistent.

In summary, on previously reported data, *T. rugosa* is characterised by several autapomorphies, although there is a trend in some other *Tiliqua* in the direction of *T. rugosa* in some of these characters. However, there is as yet no analysis of relationships that identifies *T. rugosa* as the sister-taxon of other *Tiliqua*, and hence as yet, there can be no argument for the recognition of a monotypic genus *Trachydosaurus*. Phylogenetic relationships within *Tiliqua* are considered further in Chapter 11.

3.8 Conclusion

The data presented in this chapter provides evidence for the monophyletic nature of a restricted genus *Tiliqua*, consisting of the species consistently referred to the genus by other authors, and *T. rugosa*, and hypothesises a sister-group relationship between *Tiliqua* (s.s.) and *Cyclodomorphus*, the latter incorporating *Hemisphaeriodon*.

The species and subspecies within *Tiliqua* (s.s.) will be considered further in the following chapters.

Chapter 4 *Tiliqua adelaidensis*

4.1 Synonymy Tiliqua adelaidensis (Peters, 1864a).

Cyclodus adelaidensis Peters, W. (1864a). Übersicht der von Hrn. Richard Schomburgk an das zoologische Museum eingesandten Amphibien, aus Buchsfelde bei Adelaide in Südaustralien. *Monatsbericht der Königlichen Preussischen Akademie der Wissenschaften zu Berlin* 1863: 228–236 [232].

Lectotype (designated by Wells and Wellington, 1985): ZMB 4710a (SVL 72mm)

4.2 Diagnosis

A very small species of *Tiliqua* (maximum SVL 98mm), with three supraoculars, the first two contacting the frontal, frontoparietals nearly reaching or contacting last supraciliary, primary temporal and lower secondary temporal usually single and subequal, and dorsal pattern of narrow broken vermiculations on a green-grey dorsal ground.

4.3 Description

Nasals usually moderately separated (52.6%, n = 19), less commonly narrowly separated (21.1%) or in point (5.3%) to narrow (21.1%) contact; supranasals absent; postnasals usually fused dorsally to nasals, separated ventrally by a postnarial suture, rarely completely distinct unilaterally (5.3%, n = 19); prefrontals in broad to moderate contact (n = 19); supraoculars three, with first two contacting frontal (n = 19); supraciliaries 4–6 ($\overline{X}$ = 5.05, sd = 0.32, n = 38), usually five (89.5%), first a little longer than tall, contacting prefrontal and first supraocular, second much longer than tall, contacting and projecting slightly between first and second supraocular, third a little longer than tall, contacting and projecting slightly between second and third supraoculars, fourth subequal to third, contacting third supraocular, fifth a little taller than long, contacting and projecting strongly between third supraocular and parietal; first supraciliary broadly to moderately separated from frontal; last supraciliary usually narrowly separated from (41.2%, n = 17) or contacting (35.3%) frontoparietals bilaterally, less commonly moderately separated (11.8%) or asymmetrically contacting and narrowly separated (11.8%); frontoparietals paired, in broad to moderate contact (n = 17); frontoparietals rarely longitudinally divided unilaterally (n = 1); occipitals 2–4 ($\overline{X}$ = 2.97, sd = 0.30, n = 34), usually three (91.2%); median azygous occipital present (17.6%, n = 17) or absent; loreals two in horizontal series; subocular ring complete; presuboculars 2–3 ($\overline{X}$ = 2.09, sd = 0.28, n = 35), usually two (91.4%); suboculars 0–1 ($\overline{X}$ = 0.06, sd = 0.24, n = 35), usually absent; postsuboculars 3–4 ($\overline{X}$ = 3.57, sd = 0.50, n = 35), usually four (57.1%); supralabials 7–9 ($\overline{X}$ = 8.16, sd = 0.55, n = 38), usually eight (68.4%), antepenultimate below centre of eye, penultimate entire, last vertically divided into at least two scales bilaterally; primary temporal present, usually entire bilaterally (n = 16), rarely (n = 1) vertically paired; upper secondary temporal single; lower secondary temporal apparently single (possibly a small scale frequently present caudal to the upper part of the last supralabial represents a lower fragment of this scale, rather than a third fragment of the last supralabial, although the overlap pattern between this and the lower portion of the last supralabial is variable); posttemporals 4–6 ($\overline{X}$ = 5.00, sd = 0.25, n = 33), usually five (93.9%); rostral ear lobule single (n = 36); infralabials 7–9 ($\overline{X}$ = 8.21, sd = 0.47, n = 38), usually eight (73.7%); usually first two infralabials contacting postmental, rarely first three unilaterally (n = 1).

Midbody scales 34–37 ($\bar{x}$ = 34.9, sd = 0.99, n = 19); paravertebral scales 71–83 ($\bar{x}$ = 76.4, sd = 2.69, n = 19), between axilla and groin 49–57 ($\bar{x}$ = 52.5, sd = 1.86, n = 18); ventral scales 77–90 ($\bar{x}$ = 84.3, sd = 3.44, n = 18); subcaudal scales 55–60 ($\bar{x}$ = 57.9, sd = 1.27, n = 17); lamellae below fourth toe unpaired, 9–12 ($\bar{x}$ = 10.38, sd = 0.76, n = 37), mode = 10 (45.9%).

SVL 44–98mm (n = 19); AGL/SVL 46.5–57.1% ($\bar{x}$ = 51.9%, n = 19); TL/SVL 57.9–74.1% ($\bar{x}$ = 63.9%, n = 17); FLL/SVL 17.4–23.9% ($\bar{x}$ = 20.9%, n = 19); HLL/SVL 19.5–27.3% ($\bar{x}$ = 22.9%, n = 19); Hip/SVL 6.6–8.8% ($\bar{x}$ = 7.6%, n = 15); HL/SVL 20.5–25.2% ($\bar{x}$ = 22.7%, n = 18); HW/HL 61.3–76.7% ($\bar{x}$ = 69.0%, n = 18); HD/HL 49.3–64.1% ($\bar{x}$ = 55.8%, n = 17); IOC/HL 36.2–48.8% ($\bar{x}$ = 40.7%, n = 18); E–N/HL 25.2–29.7% ($\bar{x}$ = 27.0%, n = 18); E–E/HL 41.3–49.2% ($\bar{x}$ = 45.6%, n = 17); Eye/HL 16.9–25.1% ($\bar{x}$ = 21.6%, n = 18); Ear/HL 6.7–12.8% ($\bar{x}$ = 9.8%, n = 18); IparL/HL 23.5–29.3% ($\bar{x}$ = 26.4%, n = 15); FrontL/HL 27.5–33.1% ($\bar{x}$ = 29.6%, n = 14); IparL/FrontL 76.2–94.1% ($\bar{x}$ = 88.9%, n = 14); IparW/IparL 55.4–89.9% ($\bar{x}$ = 68.3%, n = 15); FrontW/FrontL 47.9–61.8% ($\bar{x}$ = 55.5%, n = 14).

4.4 Allometry

Allometric values and calculated values for morphometric characters are presented in Table 4.1. While most characters showed apparent allometry, of similar magnitude to other *Tiliqua* species, in many cases the allometric coefficient was not significantly different from 1.000. This is probably due to the combination of the small sample size and large standard error for some relationships. Axilla-groin length showed positive allometry, while limb lengths, head length, interocular width, frontal length and interparietal width showed negative allometry. The degree of allometry in other characters was not significant.

4.5 Coloration (Fig. 14)

Dorsal ground colour light green-grey; head dorsum and distal two-thirds of tail more light brown-green to yellow-brown. Body dorsum from just behind parietals to at least tail base, rarely almost to tail tip (especially laterally) with narrow (1–2 scale wide) largely broken dark brown vermiculations, tending to align in a longitudinal series of dark macules vertebrally, and broken transverse bars dorsolaterally. Dark markings weakest (sometimes absent) paravertebrally on body, and vertebrally on tail base. Dark markings leave exposed *ca*2–6 scale wide patches of ground color.

Laterally on body and tail base, ground color more blue-grey and dark markings a little narrower, tending to form ocelli on the neck and to be transversely aligned between axilla and groin.

Head dorsum and face either immaculate, or rarely with weak dark margins to the caudal head shields.

Throat yellow, especially mentally, usually immaculate or with obscure fine dark vermiculations caudally. Body venter with blue-grey ground color, with or without weak fine broken dark grey vermiculations. Tail ventrally yellow, immaculate.

Limbs light green-grey to yellow, immaculate. Palmar granules and subdigital lamellae yellow, sometimes with poorly defined broad light brown calli.

Juveniles with similar pattern to adults.

4.6 Asymmetry

The small sample sizes available were insufficient for a statistical analysis of the degree of asymmetry in scalational characters. However, in the characters (n = 10) for which asymmetry was recorded, the frequency of asymmetries (5.3–29.4%) was similar to other species.

4.7 Sexual Dimorphism

The few sexed specimens did not permit an analysis of sexual dimorphism in this species.

4.8 Distribution

Unfortunately, most specimens lack precise locality data. However, four localities (Marion, North Burra, Dry Creek and the Buchsfelde area) are probably reasonably accurate (see Ehmann [1983] for a dissenting view), while the “Seven Hills nr Melbourne” locality is probably Seven Hills near Adelaide (see below). All localities are from a small area close to Adelaide, from Marion in the south to the Burra district in the north-east (Fig. 15), a distance of only 155km.

4.9 Geographic Variation

Because of the restricted distribution of this species, and the few precise locality data, a discussion of geographic variation is not possible.

4.10 Comparison with Other Species

Small size, unbanded colour pattern dominated dorsally by pale ground colour, usually undivided temporal scales and contact or narrow separation of the last supraciliary and frontoparietal each readily distinguish *T. adelaidensis* from all other *Tiliqua* species. The last-mentioned character is an autapomorphy for the species. In addition, it has much higher paravertebral and ventral scale counts than *T. nigrolutea* and *T. rugosa*, and lower midbody scale counts than *T. occipitalis* and *T. multifasciata*. The presence of a large primary temporal scale further differentiates it from all subspecies of *T. gigas* and *T. scincoides*. Although the head scalation is similar in some respects to *Cyclodomorphus* species (particularly the three supraoculars, temporal configuration and reduced ear lobules) the head shields are more rugose than in *Cyclodomorphus*, the nuchals are dedifferentiated (multiple pairs in *Cyclodomorphus*, there are usually only five supraciliaries (*vs* modally six for all *Cyclodomorphus*), and the body scales are much smaller than in *Cyclodomorphus* (midbody scales in particular being more numerous).

4.11 Habits and Habitats

There are virtually no first-hand ecological data for this species. Richard Schomburgk, who apparently was most familiar with the taxon, made the comment “Kommt nur auf sandigem, steinigem Terrain vor” (found only on sandy, stony terrain) (Peters, 1864a). The Dry Creek specimen is noted as “taken opposite railway station under stone” (SAM register data). Ehmann (1983) has suggested, on the basis of these data, the local habitat and the ecology of similar reptiles, that the species was “a diurnal terrestrial/fossorial inhabitant of

compacting or crusty sandy soils carrying mallee scrub and chenopodiaceous understory with hollow mallee lignotubers and associated low stump hollows and near-surface kunkar limestone sheet, outcropping or large slab floaters; a burrower into moisture pockets/depressions on or between kunkar sheeting, under outcroppings and slabs, between mallee lignotubers and sheeting and into insect-hollowed lignotubers and trunks; a user of relatively short and hard-rimmed refuges in wood and stone", although all of this is supposition. Ehmann also provides data on the stomach contents of the SAM specimens.

4.12 Taxonomic History and Type Material

Cyclodus adelaidensis was described by Peters (1864a) from two specimens ("die beiden . . . Exemplare") collected by Richard Schomburgk, who lived at Buchsfelde, S.A. at the time. Although no precise locality for the two specimens was given by Peters, and only "South Australia" is recorded in the Berlin collection, the collection presented by Schomburgk on that occasion has been presumed to be of the local fauna (Peterson & Shea, 1987). Buchsfelde, no longer a name in use, is now known as Loos, and is 4.8km WSW of Gawler, S.A. (Ehmann, 1983).

The two syntypes were not identified by registration number by Peters, but the two specimens under ZMB 4710 are identified as syntypes by bottle labels, and are the earliest representatives of *T. adelaidensis* in that collection. Wells and Wellington (1985), without examining either specimen, nominated "ZMB 4710, being the largest of the two syntypes registered under this number" as lectotype. Both specimens are typical of the species.

The larger specimen (Figs. 16–17; sex male) has the following combination of characters, of those variable for the species: nasals in narrow contact; prefrontals in broad contact; supraciliaries five; last supraciliary in narrow contact with frontoparietals; occipitals three; presuboculars two; suboculars absent; postsuboculars three; supralabials eight; infralabials nine; posttemporals five; midbody scales 36; paravertebral scales 76, between axilla and groin 52; ventral scales 82; subcaudal scales 59; subdigital lamellae 10/11; SVL 72mm; AGL 37mm; TL 46mm; FLL 15mm; HLL 16mm; HL 16.0mm; HW 11.4mm; HD 8.4mm; IOC 6.4mm; E–N 4.3mm; E–E 7.2mm; Eye 3.5mm; Ear 1.7mm.

The paralectotype is much smaller, with SVL 56.5mm.

Peters noted in particular the small size of the two syntypes, suggesting that both were immature. This suggestion was carried further by Lucas and le Souef (1909) and Waite (1929) who suggested that *T. adelaidensis* was not a valid taxon, but instead the juvenile of another species, Waite noting that he had been unable to identify this species in the SAM collection (although at least four specimens were present in the collection by that date [Mitchell, 1950; Ehmann, 1983]). With the exception of a redescription by Strauch (1866), the mention by Günther (1867) of a South Australian specimen donated by Gerard Krefft to the Natural History Museum, London and its subsequent description by Boulenger (1887), nothing additional was published on this species until 1948, when Mitchell (1948) noted the recent collection of additional specimens from near Adelaide. These, together with four older specimens subsequently located in the SAM collection, were described by Mitchell (1950), who confirmed the small size of the species, but was unable to recognise any relationships to other *Tiliqua* species. Since 1948, the species has only been collected on one occasion, when two specimens (SAM R4307, R4307a) were found at Marion, a southern suburb of Adelaide, in October 1959, during building operations. Despite much fieldwork in the Adelaide area by a number of herpetologists since that time, no further specimens have been located, and the species is now believed to be endangered (Ride & Wilson, 1982; Ehmann, 1983; Jenkins, 1985; Ehmann & Cogger, 1985) and possibly extinct.

Ehmann (1983) has examined the history of the 11 specimens known to him, and concluded that the BMMN specimen and possibly the “central South Australia” specimens in the SAM were obtained from Schomburgk, subsequent to the type description. Of the additional nine specimens in the MV, NHMW and ZMB collections, which were not known to Ehmann, NHMW 20272.1–3 are registered as from “Seven Hills, near Melbourne”, presented by Ferdinand von Müller, ZMB 5938 was presented by E.G. Waterhouse, ZMB 15950 presented by Schomburgk, and MV D1325 and ZMB 43365–67 have no useful collection data, the latter specimens having become dissociated from labels during World War II, and subsequently re-registered.

I can find no record of a Seven Hills in Victoria, and presume that the locality is the Seven Hills in South Australia, near Burra, which is a known locality for the species. Müller, although living in Melbourne later in life (where he was Government Botanist), collected botanical specimens throughout the Adelaide region, from the Mt Lofty Ranges to the Murray Mallee and north to the Flinders Ranges, between 1847 and 1852 (Willis, 1949). Waterhouse was the first curator of the South Australian Museum, between 1860–1882 (Hale, 1956). Both Müller and Waterhouse were contemporaries of Schomburgk, who was both curator of the Gawler Institute Museum and director of the Adelaide Botanic Gardens in the 1860s (Ehmann, 1983) and it is therefore possible that all of the NHMW and ZMB material, together with the BMNH and some of the SAM material, was originally derived from Schomburgk. The relative abundance of *T. adelaidensis* specimens in European collections (compared to the representation of other South Australian reptile species accessioned in that period) suggests that the species was formerly common.

4.13 Reproduction

It has been possible to determine sex by dissection and examination of gonads in only a few specimens, due to the rarity of the material. Reproductive data for the six SAM specimens which were not eviscerated are presented by Ehmann (1983). The two females (SVL 92–95mm; my measurements) are apparently both mature, but non-reproductive. The three largest of the four males (SVL 72–81mm) are apparently mature, the two smaller of these mature males (SVL 72–77mm) apparently reproductively active, with enlarged turgid testes and opaque epididymides.

The holotype (SVL 72mm) is also male, and on the basis of size probably also mature, while a radiograph of the BMNH specimen (SVL 73mm) reveals two large radio-opaque abdominal masses. These are too large and rounded to be testes, and are probably either grossly enlarged yolky ovarian follicles, or oviducal egg masses.

The smallest specimen, NHMW 20472–3 (SVL 44mm) has a well-marked umbilical scar, and is clearly immature

4.14 Specimens Examined

BMNH 64.10.27.18, South Australia; MV D1325, Australia?; NHMW 20472.1–3, “Seven Hills, nr Melbourne” [Seven Hills, SA?]; SAM R2227, R8588–89, Central South Australia; SAM R2228, R8587, N. Burra, SA; SAM R2229, Dry Creek, SA; SAM R4307, R4307a (latter cleared and stained), Marion, SA; ZMB 4710a–b [lectotype and paralectotype], [Buchsfelde], South Australia; 5938, South Australia; 15950, Adelaide, SA; 43365–67, no locality.

Chapter 5 *Tiliqua multifasciata*

5.1 Synonymy

Tiliqua multifasciata Sternfeld, 1919.

Tiliqua occipitalis multifasciata Sternfeld, R. (1919). Neue Schlangen und Echsen aus Zentralaustralien. *Senckenbergiana* 1(3): 76–83 [79].

Lectotype (designated by Mertens, 1967): SMF 14037

Tiliqua occipitalis nossiteri Glauert, L. (1923). Contributions to the Fauna of Western Australia No. 3. Annotated List of Lizards from Wallal. *Journal of the Royal Society of Western Australia* 9(1): 57–60 [59].

Lectotype (designated by Wells & Wellington, 1985): WAM R1013.

Tiliqua occipitalis auriculaire Kinghorn, J.R. (1931). Herpetological notes. No. 2. *Records of the Australian Museum* 18(3): 85–91 [88]. Holotype: AM R10080.

5.2 Diagnosis

A moderately large species of *Tiliqua* (maximum SVL 289mm), with only one supraocular contacting the frontal, primary temporals present and paired, elongate, narrow occipital scales, very small body scales (midbody scales 37–46), a large ear aperture, short tail, only 5–8 unpaired subdigital lamellae, and a dorsal colour pattern involving many (9–15) narrow yellow to orange bands on the body.

5.3 Description

Nasals broadly separated (82.8%, n = 238) to moderately separated (17.2%); supranasals absent; postnasals usually fused dorsally to nasals, separated ventrally by a postnarial suture, rarely completely distinct from nasals bilaterally (6.3%, n = 237); prefrontals usually in broad to moderate contact (86.6%, n = 238), rarely in narrow (5.0%) or point contact (1.3%) or narrowly to moderately separated (4.6%); rarely an azygous median scale separating prefrontals (2.5%); supraoculars usually two, rarely three unilaterally (n = 2) or four unilaterally (n = 1), first largest and in contact with frontal, second not contacting frontal (except in single case of four supraoculars, when first two supraoculars contacted frontal); supraciliaries 3–7 ($\overline{X}$ = 5.02, sd = 0.32, n = 477), usually 5 (92.0%), with first taller than long, dorsally bordering prefrontal and first supraocular, second low, elongate, bordering first supraocular, third short, pentagonal, projecting between first and second supraoculars, fourth low, slightly longer than tall, bordering second supraocular, last much taller than long, bordering caudal margin of last supraocular and parietal; first supraciliary usually moderately to broadly separated from frontal (90.8%, n = 239), rarely narrowly separated (7.9%), or in point, moderate or broad contact (each 0.4%); last supraciliary broadly to moderately separated from frontoparietals; frontoparietals paired, usually in narrow contact (48.9%, n = 237), less commonly in moderate contact (19.4%), point contact (4.6%) or narrowly to moderately separated (26.6%), rarely in broad contact (0.4%); occipitals 2–5 ($\overline{X}$ = 3.55, sd = 0.53, n = 475), usually 4 (55.4%) or 3 (43.2%); median azygous occipital absent; loreals usually two in horizontal series, rarely one unilaterally (n = 2) or bilaterally (n = 1) or three unilaterally (n = 1); rostral loreal rarely vertically paired unilaterally (n = 1) or bilaterally (n = 2); subocular ring complete; presuboculars 1–4 ($\overline{X}$ = 2.77, sd = 0.51, n = 476), usually 3 (72.7%) or 2 (23.3%); subocular usually absent (77.0%, n = 474) or single (22.2%), rarely

two present (0.8%); postsuboculars 3–6 ($\overline{X}$ = 4.42, sd = 0.55, n = 474), usually 4 (55.5%) or 5 (41.6%); supralabials 7–9 ($\overline{X}$ = 8.08, sd = 0.40, n = 477), usually 8 (83.4%), antepenultimate below centre of eye, penultimate usually single, rarely (n = 1) vertically divided unilaterally, last vertically paired; primary temporal usually vertically divided into a pair of scales (93.7%, n = 238), rarely single unilaterally (2.5%), single bilaterally (0.8%) or divided into three unilaterally (1.7%) or bilaterally (1.3%), in one case, upper scale fused to upper secondary temporal unilaterally, in another, lower scale fused to upper scale of last supralabial unilaterally; upper secondary temporal single; lower secondary temporal vertically divided into a pair of scales; posttemporals 2–3 ($\overline{X}$ = 2.2, sd = 0.36, n = 474); rostral ear lobules 2–7 ($\overline{X}$ = 4.19, sd = 0.81, n = 466), usually 4 (44.4%) or 5 (33.7%); infralabials 7–11 ($\overline{X}$ = 8.94, sd = 0.71, n = 471), usually 9 (54.8%) or 8 (25.3%), caudal part of row irregularly paired; usually first two infralabials contact postmental, rarely first only unilaterally (n = 2) or bilaterally (n = 1) or first three unilaterally (n = 6);

Midbody scales 37–46 ($\overline{X}$ = 40.8, sd = 1.76, n = 232), mode = 40 (29.7%); paravertebral scales 55–75 ($\overline{X}$ = 63.2, sd = 3.09, n = 232), between axilla and groin 39–55 ($\overline{X}$ = 45.4, sd = 2.61, n = 239); ventral scales 69–88 ($\overline{X}$ = 78.5, sd = 3.93, n = 225); subcaudal scales 36–46 ($\overline{X}$ = 40.8, sd = 2.19, n = 214), mode 40; lamellae below fourth toe unpaired, 5–8 ($\overline{X}$ = 6.77, sd = 0.65, n = 466), mode = 7 (55.2%).

SVL 70–289mm (n = 235); AGL/SVL 46.2–64.3% ($\overline{X}$ = 58.4%, n = 234); TL/SVL 33.8–55.7% ($\overline{X}$ = 46.0%, n = 213); FLL/SVL 16.8–30.0% ($\overline{X}$ = 20.7%, n = 233); HLL/SVL 18.1–29.3% ($\overline{X}$ = 22.2%, n = 233); HipW/SVL 8.0–14.1% ($\overline{X}$ = 12.3%, n = 235); HL/SVL 15.7–25.9% ($\overline{X}$ = 18.1%, n = 232); HW/HL 84.5–118.4% ($\overline{X}$ = 105.1%, n = 231); HD/HL 53.1–82.1% ($\overline{X}$ = 68.5%, n = 229); IOC/HL 41.0–64.1% ($\overline{X}$ = 45.6%, n = 232); E–N/HL 23.8–33.3% ($\overline{X}$ = 27.8, n = 232); E–E/HL 41.1–57.2% ($\overline{X}$ = 50.6, n = 231); Eye/HL 16.8–28.3% ($\overline{X}$ = 21.0%, n = 232); Ear/HL 18.9–34.5% ($\overline{X}$ = 27.8%, n = 232); IparL/HL 23.2–37.2% ($\overline{X}$ = 28.1%, n = 232); FrontL/HL 23.2–37.9% ($\overline{X}$ = 28.7%, n = 233); IparL/FrontL 77.6–127.7% ($\overline{X}$ = 98.3%, n = 233); IparW/IparL 35.6–69.6% ($\overline{X}$ = 48.7%, n = 233); FrontL/FrontW 55.4–89.4% ($\overline{X}$ = 69.5%, n = 234).

5.4 Allometry

All proportions examined showed significant allometry, with the exception of interparietal length/frontal length (Table 5.1). In most cases, allometry was negative. However, all characters relating to the caudal part of the head (head width, head depth, eye-ear) showed significant positive allometry, indicating that the postocular regions of the head are proportionally larger in adults than juveniles. This may suggest an increase in the temporal musculature of adults. Positive allometry was also seen in axilla-groin length, tail length and hip width.

5.5 Coloration (Fig. 18)

Dorsal ground yellow to cream to grey. Head dorsum immaculate or with dark brown to black edging to median shields, most prominently and commonly on the interparietal and median occipitals. Body dorsum usually with 9–15 ($\overline{X}$ = 11.5, sd = 1.12, n = 178, mode 12 (39.5%)), 2–5 scale wide, yellow to orange transverse bands, usually first just behind head, second

over nape between forelimbs; tail dorsum with or without 9–15 ($\overline{X}$ = 11.5, sd = 1.25, n = 65, mode 11 (33.8%)) similar bands, most prominent in juveniles (SVL < 180mm, banded:unbanded 35:5, SVL >180mm, 29:162; contingency $X_1^2 = 86.2^{***}$). Bands extend ventrally to ventrolateral margin of body and tail.

Face laterally with a very prominent, sharp but irregularly-edged black temporal stripe, from lateral canthus of eye, caudally to dorsal margin of ear, covering ventral margin of upper secondary temporal and subsequent scales, entire upper scale of primary temporal, lower secondary temporal and subsequent scales, dorsal edge of lower scale of primary temporal, and upper half of lower scale of lower secondary temporal and subsequent scales. Usually a weak to prominent brown to black smudge on side of neck, being the continuation of, though separated from, the dark temporal stripe.

Body and tail venter straw-yellow to cream, usually immaculate, or with alternating slightly paler and darker scales, rarely with faint light grey to dark brown flecks, variegations or lateral bars (n = 10); throat immaculate (23.7%, n = 228) or with 1–3 narrow light grey to dark brown bands, scattered light grey to dark brown flecks or spots, or grey to brown streaks, occasionally extending to a grey wash over throat.

Forelimb usually dark dorsally over brachium and at least proximal antebrachium, rarely (n = 1 adult, 2 juveniles) with dark patch very reduced in extent and intensity; ventrally as body venter. Palmar granules with dark brown to black-tipped tubercles.

Hindlimb dorsally orange to light brown, with narrow pale bands (two on thigh, two or three on calf), usually at least partly obscured by a dark brown smudge; ventrally as body venter. Plantar granules with dark brown to black-tipped tubercles.

5.6 Asymmetry

Although asymmetries of head shield configurations were commonly seen, these generally had no significant effect on pooled counts. No significant differences were detected between means for left and right sides (t-tests) in number of supraciliaries, presuboculars, supralabials, infralabials, occipitals or rostral ear lobules. A significant difference exists between left and right sides in mean number of postsubocular scales (L: 3–6, $\overline{X}$ = 4.36, sd = 0.54, n = 238; R: 3–6, $\overline{X}$ = 4.48, sd = 0.56, n = 238; $t_{494} = 2.38^{*}$); although the mode for both sides is 4, and the magnitude of the difference is so low that it is only of significance in very large samples.

5.7 Sexual Dimorphism

There were no significant differences between males and females in mean number of presuboculars, suboculars, postsuboculars, supralabials, infralabials, occipitals, rostral ear lobules, midbody scales, paravertebral scales, ventral scales, subcaudal scales, subdigital lamellae or dark body bands (t-tests) or degree of separation of nasals, prefrontals or frontoparietals (contingency X^2). Significant differences were noted between males and females in mean number of supraciliaries (range 3–7, $\overline{X}$ = 4.98, sd = 0.42, mode = 5, n = 203 *vs* range 5–6, $\overline{X}$ = 5.07, sd = 0.25, mode = 5, n = 182; $t_{383} = 2.52^{*}$) and paravertebral scales between axilla and groin (range 39–55, $\overline{X}$ = 44.9, sd = 2.49, n = 103 *vs* range 39–55, $\overline{X}$ = 45.8, sd = 2.72, n = 91; $t_{192} = 2.15^{*}$), although the magnitude of the difference is so low that it is only of significance in very large samples, and does not prevent pooling of the sexes in analyses of geographic variation.

Mature females are slightly larger than mature males (see Section 5.13.1). However, significant sexual dimorphism in body proportions was only detected in tail length. The allometric growth curve for TL/SVL in females was significantly different to that of males (♀♀: TL = $0.215SVL^{1.135}$; ♂♂: TL = $0.155SVL^{1.212}$; slopes: $F_{1,172} = 2.074$, n.s.; intercepts: $F_{1,173} = 7.129^{**}$), females having shorter tails than males.

5.8 Distribution

T. multifasciata occurs through much of the arid northern, western and central *Triodia* grasslands of Australia, from the west coast between 62mi N of Carnarvon and Derby, through the northern Pilbara, Great Sandy Desert, Great Victoria Desert (south to Plumridge Lakes), southern Kimberley, Northern Territory south of Willeroo and the Roper River, to western Qld (east to Burketown, Torrens Ck and the Adavale district) and the southern edge of the Sturt Stony Desert in SA (Fig. 19). There are two sight records for NSW, from the vicinity of Camerons Corner in the extreme north-west of the state (M. Sharpe, *in litt*. to H.G. Cogger; Swan, 1990). *T. multifasciata* is apparently absent from the Simpson Desert and most of South Australia (except the extreme north-west and north-east).

5.9 Geographic Variation

For the purposes of analysing geographic variation, the overall range of *T. multifasciata* was divided into 17 geographic subunits (Fig. 19).

One-way ANOVA did not provide any indication of significant geographic variation in mean number of presuboculars, supraciliaries, infralabials, occipitals, paravertebral scales, either overall or between axilla and groin, or ventrals.

In a further three characters minimally significant differences were detected by analysis of variance (supralabials, $F_{16,434} = 1.912^{*}$; subcaudal scales, $F_{16,189} = 1.903^{*}$; subdigital lamellae, $F_{16,423} = 2.011^{*}$) but no significant differences were identified by pairwise comparisons, probably due to the variation in sample sizes. Mean number of supralabials for populations ranged from 7.9 (populations 5, 8, 16) to 8.3 (populations 1, 15), with the mode consistently 8; mean number of subcaudal scales ranged from 39.2 (population 17) to 42.0 (population 9), while mean number of subdigital lamellae ranged from 6.4 (population 1) to 7.1 (populations 11, 14, 15), with mode usually 7 (except populations 5 and 6, where mode = 6).

In other meristic characters, significant geographic variation was detected, as follows:

5.9.1 Postsuboculars:

ANOVA-1: $F_{16,432} = 2.359^{**}$. Means ranged from 4.0 (population 1) to 4.8 (population 2). Significant differences at the 5% level were detected between populations 1 *vs* 2, and 1 *vs* 11 ($\overline{X}$ = 4.6). The majority of populations had mode = 4, but mode = 4,5 was observed in populations 2, 10, 11, 15 and 17.

5.9.2 Anterior ear lobules:

ANOVA-1: $F_{16,425} = 2.710^{***}$. Means ranged from 3.7 (population 16) to 4.6 (populations 9, 11). Significant differences at the 5% level were detected between population 16 and populations 10 ($\overline{X}$ = 4.4), 11 ($\overline{X}$ = 4.6), 13 ($\overline{X}$ = 4.4) and 15 ($\overline{X}$ = 4.5). Most populations

had mode = 4, but mode = 5 in populations 8–11, and 3 in population 16.

5.9.3 Midbody scales:

ANOVA-1: $F_{16,205} = 3.728^{***}$. Means ranged from 39.4 (population 17) to 42.1 (population 10). Significant differences at the 5% level were detected between population 10 and populations 6 ($\overline{X}$ = 40.3), 7 ($\overline{X}$ = 40.0), 13 ($\overline{X}$ = 39.5), 16 ($\overline{X}$ = 39.6) and 17.

5.9.4 Coloration:

The East Kimberley population (8) had a noticeably high proportion of individuals in which the body bands as well as the tail bands were indistinct (71.4%, n = 14). The two south-westernmost populations (14 and 16) had a slightly greater number of dark body bands (10–15, modes 14 *vs* 9–14, modes 11, 12 for other populations).

It is clear from the above that geographic variation in *T. multifasciata* is of a minor and random nature. No population appears to be geographically isolated, and there appear to be no grounds for subspecific recognition of any population or group of populations.

5.10 Comparison with Other Species

Comparison with *T. adelaidensis* has already been made (Section 4.10). *T. multifasciata* differs from all other *Tiliqua* in having only 5–8 unpaired subdigital lamellae below the fourth toe, frontoparietals usually narrowly contacting or separated, and large numbers of narrow bands dorsally on the body, all three characters being autapomorphies of the species. *T. multifasciata* further differs from all races of both *T. gigas* and *T. scincoides* by its more numerous midbody scale rows (37–46 *vs* 26–38), single supraocular contacting the frontal, narrow, elongate occipitals (usually 3–4 on each side *vs* usually two), and presence of paired primary temporals. It further differs from *T. nigrolutea* and *T. rugosa* by its more numerous, less rugose scales (midbody scale counts non-overlapping), narrow, elongate occipitals, predominantly pale dorsal coloration, pale venter, dark temporal streak, and relatively large ear aperture with several rostral ear lobules.

T. multifasciata is similar to *T. occipitalis* in the orientation of the occipital and temporal shields, single supraocular contacting the frontal, pale venter, dark temporal streak and dark granules on the soles of the feet. However, in addition to the autapomorphies listed above, it may be readily separated from *T. occipitalis* in having a dark patch dorsally on the brachium, a very large ear aperture with more rostral ear lobules, fewer supralabials, and fewer ventral and subcaudal scales.

5.11 Habits and Habitats

The presence of *Triodia* appears to be a major determinant of the distribution of *T. multifasciata*. Habitat data associated with museum specimens specifically noted *Triodia* or “hummock grasses” in 39 cases, while in most other cases, the habitat described was likely to include *Triodia*. In 12 of these cases, the specimen was found in or under a clump of *Triodia*. In only three instances did the data not mention *Triodia* and indicate a habitat where *Triodia* was unlikely to be a feature: black soil plains (NTM R3624, WAM R87184) and tropical savannah woodland (NTM R3378), although the latter specimen was reported to have “retreated into grass”. Fyfe (1980c) further noted that *T. multifasciata* was only found in

unburnt *Triodia* habitats around Ayer's Rock, while Gibson and Cole (1988) report it from dunes vegetated with *Zygochloa paradoxa* and *Triodia basedowii*.

A wide range of substrate types and topographies have been reported for this species, from sand dunes and sandplains to gravelly sand and even stony hills and rocky ranges (Burbidge, 1983; Cogger, 1975; Fyfe, 1985; Gibson & Cole, 1988; Smith & Johnstone, 1979; Storr & Smith, 1981). Data associated with museum specimens support this assessment. Specimens have been collected from sand dunes (n = 7), plains and steppes (n = 5), gravelly or stony soils and laterites (n = 7), on a stony rise (WAM R69891), on sandy colluvium (WAM R73996–98) and in a gully with red sand and river pebbles (WAM R63854). Soil colour is similarly variable, from red sand to sandy loam (n = 8) and yellow loam (WAM R86782), through grey sandy soil (WAM R58487) to black soil (n = 2).

The vegetation overstory is also variable, though usually involving acacias, especially mulga (NTM R11085; WAM R63231–32, R63275, R63294, R64226, R69511, R75752; WAM R58487, *Melaleuca* and *Acacia*; R87185, *Acacia* and *Lysiphyllum* over grasses), or eucalypts (WAM R48987, open eucalypt woodland; WAM R63538, scattered bloodwoods; WAM R70746, open mallee; WAM R70755, open low eucalypt woodland over *E. gamophylla* open shrub mallee over *Triodia basedowii* mid-dense hummock grass; substrate of gibbers interspersed with fans of shallow loam, litter, *Triodia* and mallee; WAM R86782, *E. youngiana*) or combinations of the two (WAM R63374, R63854). One specimen (WAM R63432) was taken amongst “scattered *Hakea*, *Lorea* and wattles”.

Although *Triodia* is commonly used for shelter, specimens have been reported from other situations, including a shallow burrow (Loveridge, 1934), logs (Lucas & Frost, 1898), and tin and other debris (n = 8 specimens examined in this study). Stammer (1976) describes a “run” with numerous tunnels through matted native passionfruit and Mitchell and buffel grass.

Christian (1977) reports a seasonally variable activity pattern, with the species inactive over winter (mid May to mid August), maximum activity and a diurnal pattern in early spring (mid August to late September), and decreased activity with a crepuscular shift between late September and March. However, Cogger (1975) and Loveridge (1934) describe the species as diurnal, while Swanson (1976) states that it is active in early morning, late afternoon and night, and Lucas and Frost (1898) note that the Horn Expedition did not find the species active by day.

Data accompanying museum material supports the view that there is a seasonal shift in activity time, although activity was not recorded in the early morning. Specimens collected in the early morning were invariably found under shelter. Of 23 specimens collected when active (mostly crossing roads) for which time of day was recorded, all but two were collected after 1400hrs, the two exceptions being 1140hrs and 1230hrs, on 10–11 August. Two other August specimens were taken in “late afternoon” and 2000hrs, and four September specimens between 1455hrs and 1745hrs, the latter record being at dusk. Two December specimens were collected between 2022hrs and 2110hrs, and one January specimen at 2030hrs. Of three February specimens, two were active by day and one by night. One March specimen was found at 2000hrs, seven April specimens between 1520hrs and 1735hrs, one May specimen at 1735hrs, and one July specimen collected by day.

T. multifasciata is a significant food resource for central Australian aboriginals (Fyfe, 1985; Lindgren, 1961; Roff, 1983; Thomson and Hosmer, 1963), and is locally known by several names including “lungata” (variously also spelt as lungkata, lungkala and lungkuta; Fyfe, 1985; Gibson, 1986; Lindgren, 1961; data accompanying WAM R40606, R40872), “lulga” (Loveridge, 1934), “culameer” (Loveridge, 1938), “jidna” (Mitchell, 1950) and “looma” (Gibson, 1986; data accompanying NTM R230).

5.12 Taxonomic History and Type Material

Tiliqua multifasciata was first noted by Lucas and Frost (1898) who referred specimens from Oodnadatta and Charlotte Waters to *T. occipitalis*, but noted that their specimens differed from Boulenger's (1887) account of *T. occipitalis* in having 5 *vs* 3 ear lobules, a shorter forelimb, more numerous body bands (11–12 *vs* 5) and forelimb dark dorsally. All four characters remain diagnostic for *T. multifasciata.*

Sternfeld (1919) also recognised a close affinity between *T. multifasciata* and *T. occipitalis* when he described *T. occipitalis multifasciata*. His description was based on four specimens, two adult and two juvenile, from Hermannsburg Mission, NT, collected by Friar Leonhardi between 1907–1910. Sternfeld's (1919) description was brief, and did not specifically compare his material with *T. occipitalis*. However, Sternfeld (1925) subsequently rectified this, noting the greater number of bands on body and tail, and the shorter tail and limbs of adults. Sternfeld did not designate a holotype from his type series, and Mertens (1967) designated SMF 14037 (formerly 6147a) as lectotype. A label in the jar containing this specimen gives the locality as Finke River, although the label on the jar reads Hermannsburg.

The lectotype and paralectotypes are typical of the species, the lectotype (Fig. 20A) having the following combination of character states: nasals broadly separated; postnasals dorsally fused to nasals; prefrontals in point contact; supraoculars two; supraciliaries 4/5, first broadly separated from frontal, last broadly separated from frontoparietal; frontoparietals in narrow contact; occipitals three; loreals two; presuboculars three; suboculars absent; postsuboculars four; supralabials eight; infralabials 8/7, first two contacting postmental; primary and lower secondary temporals, and last supralabial vertically paired; posttemporals two; rostral ear lobules four; midbody scales 38; paravertebrals 62, between axilla and groin 44; ventral scales 75; subcaudal scales 38; subdigital lamellae six; SVL 215mm; AGL 128mm; TL 98mm; FLL 43mm; HLL 43.5mm; Hip 29.4mm; HL 41.5mm; HW 41.1mm; HD 25.3mm; IOC 17.2mm; E–N 11.0mm; E–E 22.0mm; Eye 7.9mm; Ear 9.4mm; IparL 10.7mm; IparW 5.1mm; FrontL 11.6mm; FrontW 7.4mm. The lectotype is gutted and could not be sexed. Of the three paralectotypes (SMF 14038–40), one is an adult female with small ovarian follicles, but grossly dilated oviducts, and is apparently post-parturient, while the other two are neonates. It is possible that the two neonates were born to the female.

Glauert (1923) described *T. occipitalis nossiteri* from four specimens collected from Wallal, WA, by a Perth Observatory expedition. His description notes four morphological and four coloration differences between his specimens and Boulenger's (1887) account of *T. occipitalis*. Four of these (the same as noted by Lucas and Frost (1898)) still remain diagnostic. Measurements were provided for one syntype (WAM R1013), but no registration numbers were provided for the remaining specimens, and no specimen was designated holotype. According to the WAM registers, the remaining syntypes are WAM R1014–16. Of these, WAM R1015 is noted as missing in an entry in the WAM register in Glauert's handwriting (L.A. Smith, *pers. comm.*). I have examined the remaining three specimens.

Although Glauert did not specifically designate a holotype in his description, WAM R1013 is listed as holotype by Anon (1961). Under Article 74(b) of the Code of Zoological Nomenclature, this constitutes lectotype designation. However, the anonymity of the action prevents its recognition (Article 14). Wells and Wellington (1985) have formally designated WAM R1013 as lectotype. This specimen (Figs. 20B, 21), a mature female, has: nasals broadly separated; prefrontals in point contact; supraciliaries 6/5, first broadly separated from frontal, last broadly separated from frontoparietals; frontoparietals narrowly separated; occipitals four; presuboculars three; suboculars absent; postsuboculars five; supralabials 8/9; temporal pattern typical; posttemporals two; rostral ear lobules 4/5; infralabials nine;

midbody scales 38; paravertebral scales 58, between axilla and groin 41; ventral scales 75; subcaudal scales 40; subdigital lamellae seven; SVL 198mm; AGL 110mm; TL 90mm; FLL 44mm; HLL 46mm; HL 35.6mm; HW 37.8mm; HD 24.9mm; IOC 16.1mm; E–N 9.3mm; E–E 18.3mm; Eye 7.5mm; Ear 10.9mm; IparL 11.0mm; IparW 4.8mm; FrontL 11.3mm; FrontW 7.1mm.

The lectotype and both extant paralectotypes are typical of *T. multifasciata*.

Glauert (1960) synonymised *T. o. nossiteri* with *T. multifasciata*, an action followed by Cogger *et al.* (1983), while Wells and Wellington (1984), without explanation, resurrected it from synonymy and raised it to species status. As noted above, I can find no justification for formal division of *T. multifasciata*, and hence support Glauert's (1960) action.

Kinghorn (1931), apparently unaware of both Sternfeld's and Glauert's prior descriptions, described *T. occipitalis auriculare* from a single specimen collected at Broome, WA in 1929 by Mr A.A. Livingstone. Kinghorn noted particularly the very large ear, reduction of toes and dorsal color pattern as distinguishing his subspecies from *T. occipitalis*. Loveridge (1934) placed *T. o. auriculare* in the synonymy of *T. multifasciata*, an action followed by Mitchell (1950), Cogger (1979b) and Cogger *et al.* (1983), while Wells and Wellington (1984), again without explanation, resurrected *T. o. auriculare* and raised it to species status. I have examined the holotype (AM R10080), and as with *T. o. nossiteri*, I support the synonymy of this name with *T. multifasciata*. The holotype (Figs. 20C, 22) has: presuboculars three, suboculars one, postsuboculars three, supraciliaries five, supralabials eight, infralabials 10/9, rostral ear lobules five, posttemporals two, occipitals four, frontoparietals narrowly separated, midbody scales 42, paravertebral scales 71 (51 between axilla and groin), ventral scales 85, subcaudal scales 41, subdigital lamellae seven, SVL 238mm, AGL 135mm, TL 118mm, FLL 48.5mm, HLL 50.5mm, HL 41.6mm, HW 43.2mm, HD 29.7mm, IOC 19.0mm, E–N 11.3mm, E–E 21.4mm, Eye 8.5mm, Ear 11.2mm, Hip 29.2mm, IparL 12.5mm, IparW 7.3mm, FrontL 11.6mm, FrontW 8.9mm.

Prior to 1970, all authors continued to treat *T. multifasciata* as a race of *T. occipitalis*. Pianka (1971), in a book review, claimed species status for *T. multifasciata*, following his earlier listing (Pianka, 1969) of the same combination, but gave no justification for his statement. Pianka (1972) provided spot distribution maps for both *T. multifasciata* and *T. occipitalis*, suggesting an overlap in their geographic distribution. Further evidence for overlapping distributions was provided by Burbidge *et al.* (1976) and Cawood (undated), while Shea and Peterson (1981) and Fyfe (1980a, 1985) documented local sympatry in the Laverton district of WA and the southern NT respectively, confirming Pianka's claims (see also Chapter 10).

5.13 Reproduction

5.13.1 Size at maturity:

Mature males had SVL 201–257mm, $\bar{x}$ 227.3, sd = 13.74, n = 83, while mature females were slightly larger, with SVL 203–289mm, $\bar{x}$ = 233.6, sd = 16.81, n = 77 (Mann-Whitney U test, z = 2.25*) (Figs. 23–24). Mature animals from eastern populations were slightly larger than those from western populations (Populations 1–7 *vs* 8–17, ♂♂: 202–257mm, $\bar{x}$ = 233.4, sd = 15.09, n = 29 *vs* 201–247mm, $\bar{x}$ = 224.1, sd = 11.63, n = 48; Mann-Whitney U test, z = 2.91**; ♀♀: 206–289mm, $\bar{x}$ = 241.0, sd = 17.26, n = 34 *vs* 203–259mm, $\bar{x}$ = 227.1, sd = 13.74, n = 38; Mann-Whitney U test, z = 3.58***). Although the direction and degree of sexual dimorphism in body size within both eastern and western populations was the same as in the overall pooled sample, sample sizes were too small for significance (eastern: z = 1.76; western: z = 0.68, n.s.). Gravid females were similar in size to other, non-gravid,

mature females (SVL 212–259mm, $\overline{X}$ = 235.1, sd = 12.94, n = 21 *vs* 203–289mm, $\overline{X}$ = 233.5, sd = 17.96, n = 56). The range of sizes for mature females determined here is similar to that (210–250mm SVL) reported by How *et al.* (1991).

5.13.2 Male reproduction:

Testis length did not increase isometrically with body size, as estimated by SVL (Fig. 23), and consequently testis length, rather than a gonosomatic index, was used to indicate seasonal patterns of reproduction.

Testis length increases from January to June. During the same period, the proportion of narrow, flattened testes decreases. Between August and November, testis length decreases, although testis condition changes little over this period (Fig. 25). Data are completely lacking for December, and mostly lacking for June and July. Despite the pooling of samples from throughout the distribution, covering a wide range of climatic regimes, and over many years, the relationship between testis length and date of collection is close.

The data suggest that spermiogenesis begins about January–February, increases to a peak in July–August, and thereafter decreases until November–December.

5.13.3 Female reproductive activity (Fig. 26):

Between December and August, follicle diameter increases only very gradually. Between July and early October, follicle diameter increases much more rapidly, and the larger follicles become very yolky. The first oviducal eggs appear in early October, while one female with fully scaled and pigmented embryos was collected 1 January. Corpora lutea were obvious grossly throughout embryonic development. The smallest juveniles for which specific dates of collection are available have SVL = 99–106.5mm and were collected between 4 January and 4 February.

The data suggest that follicular development is slow in the first half of the year, followed by a short period of rapid vitellogenesis between August and September. Ovulation occurs in early October, and young are born in early January. Birth has been recorded in captive-bred populations in late December and early January (Christian, 1977; Barnett, 1977c), while How *et al.* (1991) collected reproductively active females in September–October, but not in February. There is no indication that more than a single litter is produced each year.

5.13.4 Mating season:

The peak in testis size about August, together with the onset of rapid vitellogenesis in August, followed by ovulation in early October agrees well with the reported mating season between mid-August and late September (Christian, 1977).

5.13.5 Frequency of reproduction:

Between October and November, 11 of 13 mature females were gravid, suggesting that reproduction is normally annual.

5.13.6 Litter size:

Of 21 females with either enlarged yolky ovarian follicles (> 10mm diameter) or oviducal "eggs" or embryos, the number of follicles or young could be counted in 20 cases. Litter size in these instances was 3–12, mode = 7 (25%), $\overline{X}$ = 7.35, sd = 2.41. Mean litter size based on number of enlarged follicles did not differ significantly from the mean based on oviducal "eggs" ($\overline{X}$ = 8.2, sd = 1.72, n = 6 *vs* $\overline{X}$ = 7.0, sd = 2.63, n = 14; t_{18} = 0.976, n.s.).

More follicles and young were generally present on the right side (in total, 75 *vs* 64; R>L:R=L:R<L = 9:5:5), although these differences are non-significantly different from 1:1 (totals, X^2 = 0.87; individual inequalities (9:5), X^2 = 1.14).

There is little evidence for extra-uterine transfer of ova or loss of ova at ovulation. In those cases where the number of corpora lutea was estimated grossly (n = 10), the number and distribution of corpora lutea was usually the same (n = 7) as that of oviducal masses. In only one case was the number of corpora lutea (2L:3R) greater than the number of oviducal eggs present (1L/3R), and this was in a female with resorbing eggs held in captivity for several months post-capture. In the other two instances, the number of corpora lutea grossly visible was less than the number of developing young, and with the same distribution as oviducal young. The number of corpora lutea could have been underestimated in these cases due to difficulties in thoroughly examining ovaries. In another case, two of three ova in the left oviduct were apparently infertile, although the third ovum and the four ova in the right oviduct appeared normal.

With the exception of two females, there was a tight positive correlation between litter size and maternal SVL (Fig. 27; litter size = 0.110SVL - 17.934, r = 0.670**, n = 18). One of the two exceptions is the captive referred to above, which may have lost at least one ovum prior to preservation. I am unable to suggest an explanation for the low clutch size in the other specimen.

Litter size has previously been reported as 2–7, $\overline{X}$ = 4 (Christian, 1977), 3–6, $\overline{X}$ = 4.4, n = 5 (Barnett, 1977c), 2–4 (Swanson, 1976), 5, n = 1 (Mitchell, 1950) and $\overline{X}$ = 4.5, n = 2 (How *et al.*, 1991). Cogger (1975) estimated litter size as up to about 10, while Frauca (1982) states "said to produce 10 young". Mitchell's record is based on SAM R2746, also examined in the present study, although I have only been able to locate three juveniles under this number, and consequently have not included this record in my analyses. All previous studies underestimate litter size. In the first two cases, this may be due to the stresses of captivity, as both are based on captive studies.

5.13.7 Size of young at birth.

Although the smallest field-collected young for which dates of collection are available had SVL 99–106.5mm, several slightly smaller juveniles have been recorded (SVL 70–85mm, $\overline{X}$ = 78.0, sd = 4.62, n = 7). Christian (1977) and Barnett (1977c) record marked variation in total length and mass of live-born and apparently healthy neonates, both within and between litters. Mass overall was reported to range from 5–29.5g, although the latter figure is suspiciously large, almost 50% greater than the mass of the largest *T. s. scincoides* neonate known. Using the raw data of Barnett (1977c), within five litters, maximum mass and total length were 116–192% and 104–115% of the minimum respectively, while the overall maxima were 590% and 161% of the minima. Some indication of such variation was seen in the present study. In one specimen (WAM R23993), the two early oviducal masses on the

left side were very much larger than the five on the right (approximate diameter 26mm *vs* 15.5mm).

5.13.8 Sex ratio:

The overall adult sex ratio in the material examined was 84:77, slightly biased towards males (1.09:1), although the ratio is not significantly different to 1:1 ($X^2 = 0.30$, n.s.). Seasonal sex ratios were non-significantly different to each other (summer 9:14; autumn 21:18; winter 14:9; spring 23:16; 4 x 2 contingency table $X^2_3 = 2.84$, n.s.).

5.14 Specimens Examined

Population 1 (south/central Qld)

AM R20996, 1mi E Quilpie; R50218, Torrens Ck; ANWC R1623, Opalton; QM J5466, Adavale; J8526, “Darriveen”, via Longreach; J24837, Wakes Lagoon, 89km SW Adavale; J27518, between Morella and Muttaburra; J41859, Terriboah Waterhole, Coorabulka.

Population 2 (north-west Qld)

AM R13711, Burketown; R15674, R18664, R28446, R64701, R64888, R75057, NTM R979, R1156, Mt Isa; NTM R8798, Cloncurry; QM J39060, 43km W Mt Isa on Barkly Hwy.

Population 3 (Lake Eyre, SA)

MV D1087, Lake Eyre; SAM R2736, “Kilalpaninna”; R29584, Coongie Lakes area.

Population 4 (north-east NT)

AM R48649, 10mi N Macarthur R. Base Camp; R48655, 35km N Macarthur R. Base Camp; R55034, 33km N Macarthur R. Base Camp; R55035, Surprise Ck; R60168, 29km N Barkly Hwy on Borroloola rd; R117074, 1.2km W Roper Bar Store; NTM R3624, 5km S “Anthony's Lagoon”; R3633, “Anthony's Lagoon”; R5464, 23km E Frewena; R5465, 16km E Frewena; R5766, R6419, Frewena; R8795, 24.2km E Frewena; QM J32261, 40mi E Barry Caves via Camooweal.

Population 5 (north-west NT)

AM R73326, Jasper Gorge; NTM R19, R3734, “Willeroo”; R850, Top Springs; R3378, 165.0km E Top Springs on Buchanan Hwy; R3607, 1.2km S Dunmarra; R5319, 26.7km E Stuart Hwy on Barkly Stock Route; R6535, R6536, Wave Hill.

Population 6 (central NT)

AM R60169, North Star Mine, nr Three Ways; R84861, 14km S Barrow Ck on Stuart Hwy; R98002, 10km S Barrow Ck on Stuart Hwy; ANWC R1440, MV D68, NTM R1287–88, SAM R2744, R 2746a–c, R2747a–c, Tennant Ck; CAWC R1059, Bonney Ck; NTM R1581, 28km S Tennant Ck; R1582, 37km S Tennant Ck; R5731–32, Whycliffe Well; R8504, 42km S Tennant Ck; R9755, “Phillipp Ck”.

Population 7 (southern NT and environs)

AM R14361, road between Curtin Springs and Ayers Rock, NT; R51658, 60.2km W Ayer Rock, NT; R99394, Aileron, NT; R125059–62, Mt Liebig, NT; R128331–32, “Utopia”, NT; CAWC R166, Conners Well, 60mi N Alice Spring, NT; MV D164, D39226, Alice Springs, NT; NTM R394, Jessie Gap, NT; R522, “Alcoota”, NT; R718 Finke River township, NT; R719, 4km N Kulgera, NT; R720, 49km E Kulgera, NT; R721, “New Crown”, NT; R11085, 22km W Wallara Ranch, George Gill Ranges, NT; SAM R323, MacDonnell Ranges, NT; R3569, Yuendumu rd, NT; R29554, 11.8km W Mt Crombie, SA; R29888, 7km along Mulga Park rd, SSE Curtin Spring, NT; R29910, 10km along Mulga Park rd, SSE Curtin Spring, NT; R29926, 26km along Mulga Park rd, SSE Curtin Spring, NT; SMF 14037–40, Hermannsburg; WAM R17786, R31365, Warburton Mission, WA; R22024, presumably Warburton Mission, WA.

Population 8 (eastern Kimberley, WA)

NTM R6881, 18.5km W WA border, Victoria Hwy; R7290, WAM R58844, Turkey Ck; SAM R16338, “Mt Elizabeth”; WAM R23071, 20mi S “Dunham River” HS; R23099, 8km SE Wyndham; R25087–88, 38mi SSE Wyndham; R44790, vicinity of Main Dam, Lake Argyle; R58843, Bow R. crossing, Great Northern Hwy; R70679, 10.8km 253° New “Lissadell” HS; R75549, 12km W New “Lissadell” HS; R86923–24, Lake Argyle.

Population 9 (central Kimberley, WA)

NTM R230, “Gordon Downs”; WAM R23046, 9km E “Bohemia Downs”; R26032, Christmas Ck; R40872, 4mi S Wolf Ck Meteor Crater; R63269, 28km 200° Halls Ck P.O.; R87184, 0.5km W Fitzroy Crossing.

Population 10 (Dampier Land, WA)

AM R10080 (holotype of *T. occipitalis auriculare* Kinghorn), WAM R14053, R31197, Broome; R98686, 0.5km S Coulomb Point Fauna and Flora Sanctuary, Coulomb Point; R102738, 8.9km E Broome; R117393, 91.1km E Broome via Great Northern Hwy; WAM R14941, R23001, R26832, R31038, R42472, Derby; R15824, Langey Crossing, Fitzroy River; R27745, 70mi N Broome; R27746, Cape Leveque; R28135, 40mi ENE Broome; R54026, Edgar Ranges; R54178, 8km N Logues Spring; R58487, 5km N Coulomb Point; R70027, 9,5km 120° Mt North; R83685, 30km NE Camballin; R87185, R87343, Cable Beach, Broome.

Population 11 (Ninety-Mile Beach, WA)

WAM R1013–14, R1016, (types of *T. occipitalis nossiteri* Glauert), R5002, “Wallal”; R27742, Badur Hill, “La Grange”; R27743, “Frazier Downs”; R27744, “La Grange”; R27747, “Anna Plains”; R46516, 16mi NE McLarty Hills; R63231, 16km 68° “Frazier Downs” HS; R63232, 14km 90° “La Grange”; R68982, 51km NE Sandfire Roadhouse; R69511, Ankatell Ridge; R71740, 28mi N Sandfire Roadhouse; R75752, 35km E Lyngett Well.

Population 12 (Tanami Desert, NT/WA)

CAWC R2164, Tanami Sanctuary, 19°57'S 130°35'E, NT; NTM R426, Refridgerator Bore, NT; R1485, 20.6km W Rabbit Flat, NT; WAM R8712–13, Well 48, Canning Stock Route, WA; R21944, Balgo Mission, WA; R63275, 52km 112° Balgo Mission, WA; R63294, 26km 280° Balgo Mission, WA; R63374, Djaluwon Ck, WA; R63432, Twin Heads, WA; R63636, 8km 223° Lens Bore, WA; R64060, Bungabiddy Well, WA; R64084, Lens Bore, WA; R69891, Bishop Range, WA.

Population 13 (Little Sandy Desert, WA)

AM R111503, R123942, south of Roy Hill junction on rd to Meekatharra, nr “Bulloo Downs”; WAM R15841, 17mi NNE Weld Spring, Canning Stock Route; R40606, Wari Soak, 90mi N Carnegie; R51902–05, R51918–19, Carnarvon Range; R51934, Durba Hills; R63538, 2km 36° Murgaga Well (No. 39, Canning Stock Route); R63854, 4km S Talbot Soak; R94966, Well No. 39, Canning Stock Route.

Population 14 (Exmouth district, WA)

WAM R11757, R12241, Mardie; R13278, 12km N “Mt Stuart” HS; R14015, Wogatti Well; R21774, 37km NE Ningaloo; R22405–06, 6km S Learmonth; R22507, 9km S “Yardie Ck” HS; R22946, 62mi N Carnarvon; R30369, “Koordarrie” HS.

Population 15 (Pilbara coast, WA)

NTM R9990, 28km N Pt Hedland; WAM R13084–87, R13453, R94632, Woodstock; R16537, mouth of Turner River; R16538, Roebourne district; R19220, Comet Mine, Marble Bar; R71877, 1km NE Woodstock; R73996–98, 5km ENE Kurrana Well; R79152, 23km ENE “Pardoo” HS; R82602 Carawine Pool.

Population 16 (northern Pilbara, WA)

WAM R13284, Dales Gorge; R13641, R94883, “Jigalong”; R23993, 10mi S Mt Newman; R30919, Mt Newman; R34749, 5mi W Wittenoom; R36174, Ethel Ck; R42292, Nyiahihya Rockhole, 12mi SE “Jigalong”; R52675, Marandoo minesite, Mt Bruce; R70746, 10km N Mt Bruce; R70755, 30.2km 238° “Marillana” HS; R73746, 22km W Tom Price; R78990, 34km ENE “Prairie Downs”.

Population 17 (Wiluna/Laverton, WA)

ANWC R2128–29, Desert Farm, Wiluna; R2194, “Millbillillie”; WAM R28481, Wiluna district; R48987, Plumridge Lakes area; R62775, 7km NNW “Erlistoun”; R62776, 20km SE Mt Keith; R79353, 5km SSE White Cliffs; R86782, 10km ENE Mt Luck.

Poor or unidentifiable localities:

AM R18675, R18758, ANWC R1546, MV D2015, D8013, NTM R3514–16, no locality; SAM R2737, NT; R8318, Mt Cannon, NT; WAM R36136, 120mi SE Wallal, WA.

Additional specimens not found, but listed in collection registers:

ANWC R177, 61MI E Wittenoom, WA; WAM R11105, Bamboo Ck, WA; R11599, Mardie, WA R13729, Dunmarra, NT; R14107, Broome, WA; R28136–37, 40mi ENE Broome, WA; R52674, Marandoo minesite, Mt Bruce, WA; R64226, 15km S Well No. 33, Canning Stock Route, WA; R73008, 15km NNE Kumarina Roadhouse, WA.

Chapter 6 *Tiliqua nigrolutea*

6.1 Synonymy

Tiliqua nigrolutea (Quoy & Gaimard, 1824).

Scincus nigro-luteus Quoy, [J.R.C.] & Gaimard, [P.] (1824). Zoologie. *In*, de Freycinet, L. (ed.). *Voyage autour du monde*, *Entrepris par Ordre du Roi*, *sous le ministère et conformément aux instructions de s. exc. m. le vicomte du Bouchage*, *secrétaire d'etat au Département de la Marine*, *Exécuté sur les corvettes de S.M. l'Uranie et la Physicienne*, *pendant les années 1817*, *1818*, *1819 et 1820*. Pillet Aîné, Imprimeur-Libraire, Paris. (712pp.) [176, pl. 41]
Lectotype (designated by Wells and Wellington, 1985): MNHP 7134.

Cyclodus gigantea Anon (1888). Narrative of the expedition. pp. 146–162 *in*, Campbell, A.J. (ed.). Expedition to King Island, November, 1887. *Victorian Naturalist* 4(9): 129–164 [159]. (*lapsus pro Cyclodus gigas*, misidentification of *T. nigrolutea*?)

Lacerta tarda Anderson, W. (1967). A journal of a voyage in His Majestys Sloop Resolution. pp. 723–986. *In*, Beaglehole, J.C. (ed.). *The Journals of Captain James Cook on his voyages of discovery. Vol. III. The voyage of the* Resolution *and* Discovery *1776–1780. Part Two.* Cambridge University Press & Hakluyt Society, Cambridge. (1647pp.) [793].
Holotype: not found.

Tiliqua milleri Wells, R.W. & Wellington, C.R. (1985). A Classification of the Amphibia and Reptilia of Australia. *Australian Journal of Herpetology* Suppl. Ser. (1): 1–61 [40].
Holotype: AM R92696.

6.2 Diagnosis

A moderate to very large species of *Tiliqua* (maximum SVL 368mm), differentiated from all others by the combination of a dorsal colour pattern dominated by broad dark bands and longitudinal stripes, leaving exposed blotches of paler coloration; solid dark temporal streak absent; dark markings present on venter; primary temporals present and paired; supraoculars usually four, first two contacting frontal, and paravertebral scales 41–57.

6.3 Description

Nasals usually moderately separated (86.9%, n = 359), less commonly broadly separated (3.3%), narrowly separated (8.1%), rarely in point to narrow contact (0.8%) or separated by a median internasal (0.8%); supranasals absent; postnasals usually fused dorsally to nasals, separated ventrally by a postnarial suture, rarely completely distinct from nasals unilaterally (1.1%, n = 358); prefrontals usually in broad to moderate contact (63.9%, n = 357), less commonly in narrow contact (17.6%) or narrowly (6.4%) to moderately (7.6%) separated, rarely in point contact (0.6%) or with an azygous median scale (3.9%); supraoculars usually four bilaterally, with first two contacting frontal (91.4%, n = 359), rarely five with first two contacting frontal unilaterally (0.8%), three with first two contacting frontal unilaterally (5.2%) or bilaterally (1.4%), three with only first contacting frontal unilaterally (0.6%), two with first contacting frontal bilaterally (0.3%), or fused into a single scale (0.3%); where a reduction to three with first two contacting frontal, due to fusion of second and third (n = 15) or third and fourth (n = 3) supraoculars; supraciliaries 3–8 ($\overline{X}$ = 4.82, sd = 0.60, n = 714), usually 5 (68.5%), first as tall as long, projecting between prefrontal and first supraocular, second long and low, contacting first, second, and sometimes third supraocular, usually projecting slightly between first and second supraocular, third smallest, contacting third and sometimes second

supraocular, fourth a little longer than tall, contacting and projecting between third and fourth supraocular, fifth relatively tall and narrow, projecting between fourth supraocular and parietal; first supraciliary broadly to moderately separated from frontal; last supraciliary broadly to moderately separated from frontoparietals; frontoparietals paired, usually in broad (32.3%, n = 359) to moderate (62.4%) contact, rarely in narrow contact (4.7%) or narrowly (0.3%) or broadly (0.3%) separated; frontoparietals rarely longitudinally divided bilaterally (n = 19) or unilaterally (n = 4); parietals rarely longitudinally divided bilaterally (n = 3) or unilaterally (n = 1); occipitals 1–4 ($\overline{X}$ = 2.52, sd = 0.67, n = 712), usually 2 (46.9%) or 3 (43.1%); median azygous occipital present (44.2%, n = 355) or absent; loreals usually two in horizontal series, rarely one unilaterally (n = 13) or bilaterally (n = 10), or three unilaterally (n = 1); rostral loreal rarely vertically paired unilaterally (n = 8) or bilaterally (n = 16); caudal loreal rarely vertically paired unilaterally (n = 5) or bilaterally (n = 10); rarely both loreals vertically paired bilaterally (n = 3); subocular ring complete; presuboculars 1–4 ($\overline{X}$ = 2.25, sd = 0.53, n = 717), usually 2 (77.0%); suboculars 0–2 ($\overline{X}$ = 0.55, sd = 0.55, n = 715); postsuboculars 3–5 ($\overline{X}$ = 4.11, sd = 0.47, n = 717), usually 4 (77.0%); supralabials 6–9 ($\overline{X}$ = 7.95, sd = 0.47, n = 719), usually 8 (79.3%), antepenultimate below centre of eye, penultimate usually single, rarely (n = 1) vertically divided unilaterally; last usually vertically divided into two scales bilaterally (n = 342), rarely divided into three unilaterally (n = 11) or bilaterally (n = 5), fragmented (n = 1), or entire bilaterally (n = 1); primary temporal usually vertically divided into a pair of scales (n = 174), or into three scales unilaterally (n = 58) or bilaterally (n = 85), or with other rare combinations (upper scale only present bilaterally [n = 23] or unilaterally [n = 4], lower scale only present unilaterally [n = 2], divided into 4/3 scales [n = 6], multiple fragmentation [n = 1], 3/fragmented [n = 1], 4/2 [n = 1], 3/upper scale only present [n = 1], entire unilaterally [n = 1], absent bilaterally [n = 1], or absent/upper scale only [n = 1]); upper secondary temporal single; lower secondary temporal usually vertically divided into a pair of scales bilaterally (n = 346), rarely divided into three scales unilaterally (n = 7) or bilaterally (n = 4), entire unilaterally (n = 1), fragmented bilaterally (n = 1) or divided into 4/3 scales (n = 1); lower scale rarely intruding between, and separating, upper and lower primary temporals unilaterally (n = 11) or bilaterally (n = 6), or separating lower primary temporal from penultimate supralabial unilaterally (n = 1); upper scale rarely excluded from contact with primary temporals unilaterally (n = 4); posttemporals 2–4 ($\overline{X}$ = 2.98, sd = 0.34, n = 715), usually 3 (88.1%); rostral ear lobules 1–3 ($\overline{X}$ = 1.98, sd = 0.37, n = 710), usually 2 (86.2%); infralabials 6–10 ($\overline{X}$ = 8.34, sd = 0.70, n = 719), usually 8 (50.2%) or 9 (36.9%), scales in caudal part of row irregularly paired; usually first two infralabials contacting postmental, rarely first only unilaterally (n = 4) or bilaterally (n = 1), first three unilaterally (n = 3), or not contacting postmental unilaterally (n = 1).

Midbody scales 26–35 ($\overline{X}$ = 30.3, sd = 1.51, n = 359); paravertebral scales 41–57 ($\overline{X}$ = 49.1, sd = 3.03, n = 357), between axilla and groin 31–43 ($\overline{X}$ = 36.4, sd = 2.46, n = 357); ventral scales 54–83 ($\overline{X}$ = 71.8, sd = 4.19, n = 353); subcaudal scales 26–45 ($\overline{X}$ = 37.0, sd = 3.21, n = 324); lamellae below fourth toe unpaired, 6–10 ($\overline{X}$ = 8.17, sd = 0.80, n = 706), mode = 8 (49.9%).

SVL 76.5–368mm (n = 361); AGL/SVL 49.0–67.3% ($\overline{X}$ = 60.6%, n = 357); TL/SVL 29.3–55.1% ($\overline{X}$ = 45.1%, n = 322); FLL/SVL 15.4–26.8% ($\overline{X}$ = 19.1%, n = 356); HLL/SVL 15.2–27.0% ($\overline{X}$ = 20.4%, n = 361); Hip/SVL 7.5–13.1% ($\overline{X}$ = 10.5%, n = 357); HL/SVL 14.3–27.4% ($\overline{X}$ = 18.1%, n = 353); HW/HL 75.5–101.2% ($\overline{X}$ = 87.7%, n = 352); HD/HL 47.2–72.6% ($\overline{X}$ = 60.5%, n = 352); IOC/HL 38.4–53.0% ($\overline{X}$ = 45.6%, n = 355); E–N/HL 24.4–

34.6% ($\bar{x}$ = 28.0%, n = 355); E–E/HL 34.9–47.9% ($\bar{x}$ = 43.1%, n = 355); Eye/HL 16.9–25.6% ($\bar{x}$ = 20.7%, n = 361); Ear/HL 5.4–18.1% ($\bar{x}$ = 11.2%, n = 354); IparL/HL 15.3–27.9% ($\bar{x}$ = 21.2%, n = 351); FrontL/HL 17.0–29.6% ($\bar{x}$ = 23.1%, n = 355); IparL/FrontL 66.1–130.4% ($\bar{x}$ = 92.1%, n = 351); IparW/IparL 36.5–89.6% ($\bar{x}$ = 58.6%, n = 351); FrontW/FrontL 40.6–107.8% ($\bar{x}$ = 78.4%, n = 356).

6.4 Allometry

Because of the difference in adult size between highland and lowland populations of *T. nigrolutea* (see Section 6.9.16), data were analysed separately for the two groups. Allometric values and calculated values for morphometric characters are presented in Tables 6.1–6.2. In lowland populations, all characters except the relationship between frontal length and head length showed allometric growth, while in the highland morph, for which sample sizes were much smaller, the relationships between head width and head length, and between ear diameter and head length were not significantly different from isometry. In both morphs, axilla-groin length, tail length, head depth, and eye-ear interval showed positive allometry, as did head width and ear diameter in the lowland morph. All other characters showed negative allometry. The positive allometry in characters related to the caudal part of the head, compared to the negative allometry in characters related to the rostral part of the head may suggest an increase in the temporal musculature in larger specimens.

6.5 Coloration (Fig. 28).

Dorsal ground colour variable, from light grey through blue-grey, light olive-green, cream and yellow to salmon pink; head dorsum generally more brownish; where dorsum yellow, often more blue-grey laterally. Dorsal ground largely obscured by a variably expressed combination of dark grey, brown or black bands and stripes. Dark stripes on body and tail base mostly due to broad dark lateral margins to body scales; most prominent and consistent is a broad dark vertebral stripe, equal to or greater in width than a dorsal body scale, from nape (beginning several scales behind head shields) to tail base, sometimes enclosing narrow streaks of dorsal body ground colour. On side of nape, a consistent narrow to broad dark stripe from just caudodorsal to ear, over forelimb, extending onto body to merge with other dark markings. Remaining, more lateral dark dorsal stripes variably leaving exposed 1–3 narrow to broad blotches of ground colour on either side of midline, with or without additional small spots or flecks. Dark dorsal bands approximately 3–5 scales wide, first usually across nape midway between level of parietals and forelimbs, 3–9.5 ($\bar{x}$ = 5.4, sd = 1.08, n = 331) between axilla and groin, last either over or immediately cranial to hips. Rarely, dark bands absent on cranial part of body, leaving broad stripes of ground colour. Dark bands continue to tail tip, sometimes largely obscuring dorsal ground colour, 5–11 ($\bar{x}$ = 7.1, sd = 1.13, n = 312).

Laterally on body and tail, dark markings generally narrower and more oblique, often enclosing an irregular array of streaks or macules of lateral ground colour.

Head dorsum ranges from immaculate, to very heavily reticulated with dark vermiculations, more solid on margins of temporal shields; lips generally a little paler and more yellow, with reduced dark vermiculations (when present).

Throat yellow, with or without dark flecks or spots, or a grey-blue flush encroaching from sides. Body and tail venter ranges from yellow with strong, sharply margined 1/2–2 scale-

wide dark streaks and broken bands forming a coarse reticulum, through yellow-blue with an obscure darker reticulum, to evenly blue-grey.

Limbs similarly patterned to body in strongly marked individuals, but with exposed macules and streaks of ground colour much finer. In duller, blue-grey individuals, hindlimbs finely but densely speckled with dark grey, forelimbs largely immaculate.

Palmar granules and subdigital lamellae with broad glossy dark brown to black calli, in extreme cases leaving whole palmar surface black.

Juveniles with similar pattern to adults, but duller and with paler, more cream-brown ground.

6.6 Asymmetry

Although asymmetry was common in individuals, significant asymmetry was not detected in mean number of presuboculars, suboculars, supraciliaries, infralabials, rostral ear lobules, posttemporals, occipitals, or subdigital lamellae (t-tests of asymmetrical cases). Significant asymmetry was detected in mean number of supralabials (asymmetrical cases only: L: $\overline{X}$ = 7.90, sd = 0.754, n = 77; R: $\overline{X}$ = 8.14, sd = 0.720, n = 77; $t_{152} = 2.071^{*}$) and postsuboculars (asymmetrical cases only: L: $\overline{X}$ = 4.05, sd = 0.693, n = 88; R: $\overline{X}$ = 4.32, sd = 0.653, n = 88; $t_{174} = 2.683^{**}$). In the case of supralabials, the difference is minor, and only of significance when very large samples are involved, while in the case of postsuboculars, the difference becomes minor when all cases are included (L: $\overline{X}$ = 4.08, sd = 0.470, n = 358; R: $\overline{X}$ = 4.14, sd = 0.467, n = 358, $t_{714} = 1.72$, n.s.).

6.7 Sexual Dimorphism

Sexual dimorphism was not detected in mean number of presuboculars, suboculars, postsuboculars, infralabials, rostral ear lobules, posttemporals, occipitals, midbody scales, subcaudal scales, or dark bands between axilla and groin (t-tests), or in degree of separation or contact of nasals, prefrontals or frontoparietals, or presence of a median occipital (X^2 tests).

Sexual dimorphism was detected in mean number of supraciliaries (♂♂: $\overline{X}$ = 4.94, sd = 0.659, n = 284; ♀♀: $\overline{X}$ = 4.79, sd = 0.569, n = 279; $t_{561} = 2.75^{**}$), supralabials (♂♂: $\overline{X}$ = 8.01, sd = 0.442, n = 288; ♀♀: $\overline{X}$ = 7.92, sd = 0.490, n = 280; $t_{566} = 2.27^{*}$), paravertebral scales, both between head and groin (♂♂: $\overline{X}$ = 48.8, sd = 3.01, n = 143; ♀♀: $\overline{X}$ = 49.7, sd = 3.14, n = 139; $t_{280} = 2.67^{**}$) and axilla and groin (♂♂: $\overline{X}$ = 36.0, sd = 2.40, n = 144; ♀♀: $\overline{X}$ = 37.0, sd = 2.63, n = 139; $t_{281} = 3.24^{**}$), ventral scales (♂♂: $\overline{X}$ = 71.4, sd = 3.52, n = 142; ♀♀: $\overline{X}$ = 72.4, sd = 4.30, n = 138; $t_{278} = 2.13^{*}$), subdigital lamellae (♂♂: $\overline{X}$ = 8.26, sd = 0.778, n = 287; ♀♀: $\overline{X}$ = 8.06, sd = 0.801, n = 271; $t_{556} = 2.99^{**}$), and dark tail bands (♂♂: $\overline{X}$ = 7.34, sd = 1.079, n = 131; ♀♀: $\overline{X}$ = 7.03, sd = 1.086, n = 117; $t_{246} = 2.24^{*}$). In the case of number of supraciliaries, supralabials, paravertebral and ventral scales and number of dark tail bands, the differences are trivial compared to the range of variation within sexes, while in the case of subdigital lamellae, despite the difference between the means, the mode for both sexes was 8 (48.8% *vs* 51.3% respectively). Consequently, I have not separated the sexes in analysing geographic variation in meristic characters.

There is significant geographic variation, correlated with altitude, in adult body size in *T. nigrolutea* (see Section 6.9.16). Consequently, highland and lowland populations were analysed separately for sexual dimorphism in morphometric characters.

Mature-sized females are larger than mature-sized males in both the lowland (♂♂: 227–300mm, $\overline{X}$ = 260.2mm, sd = 16.82, n = 89; ♀♀: 239–328mm, $\overline{X}$ = 269.5mm, sd = 19.90, n = 82; Mann-Whitney U test: z = 2.789**) and highland (♂♂: 242–368mm, $\overline{X}$ = 296.6mm, sd = 24.11, n = 31; ♀♀: 280–368mm, $\overline{X}$ = 313.1mm, sd = 23.77, n = 27; Mann-Whitney U test: z = 2.362*) morphs.

In the lowland morph, adult and subadult females had proportionally longer bodies, shorter tails, limbs and heads (the latter possibly due to the longer body), and very slightly broader hips, but shorter snouts than males at any given SVL (Tables 6.3–6.4). Significant sexual dimorphism was also detected in head width and ear diameter in this morph, but the degree and polarity varied with size. In the highland morph, for which sample sizes were much smaller, adult and subadult females similarly had proportionally longer bodies and shorter tails, limbs and heads (Tables 6.5–6.6).

6.8 Distribution

South-eastern Australia (Fig. 29), including low and moderate elevations in northern and eastern Tasmania, and both the western (Hunter, King Is.) and eastern (Swan, Clarkes, Cape Barren, Flinders, Babel, East Sister, West Sister, Deal and Hogan Is.) Bass Strait islands. On the mainland, lowlands along the southern coast and hinterland from Cape Jaffa, S.A. (Yeatman, 1989) east to 3km W Seaspray, Vic., and up to 80km inland (Mt Tanjil), including three islands (Phillip, French and Quail Is.) in Westernport Bay. Further north, following the highlands of the Great Dividing Range from Eildon and the Strathbogie Ranges, Vic., in the south-west, to Batlow and Captains Flat, NSW in the north-east, with a probable isolate in the Blue Mountains and adjacent southern highlands of NSW, above 500m, from 9km east of Laggan north to Newnes Plateau. Altitudinally, extends from sea level up to approximately 1600m in the Snowy Mtns (Copland, 1947; P. Harlow, *pers. comm.*), and possibly slightly higher in the Victorian highlands (Mt Cobberas). Also recorded, but without specimen records, from Great Dog I. in eastern Bass Strait (Mackay, 1955, as Big Dog I.; Skira & Brothers, 1988).

6.9 Geographic Variation

For the purposes of analysing geographic variation, the overall distribution was subdivided into 25 populations (Fig. 29). Bass Strait islands were treated as separate populations, while the three small islands in Westernport Bay, for which only small samples were available were grouped as one population. Populations 1–19 represent lowland material (below approximately 500m) while 20–25 are highland samples (above approximately 500m). Populations 4–12 are eastern Bass Strait islands, while 13–14 are western Bass Strait islands. Population 20, although geographically apparently part of population 21, was separated due to differences in coloration apparent during data collection.

The altitudinal distinction used here is designed to test the perception frequently mentioned in the literature over the past 30yrs that there are two distinct morphs, one highland, one lowland, differing in size and coloration (Worrell, 1963, 1966; Bustard, 1970; Swanson, 1976; McPhee, 1979; Jenkins & Bartell, 1980; Wells & Wellington, 1985).

6.9.1 Supraciliaries:

ANOVA-1: $F_{24,641 = 7.326}^{***}$. Means ranged from 4.6 (populations 10, 17–20) to 6.0 (population 9). Most populations had mode 5 and means between 4.6 and 5.1. However, three of the northern eastern Bass Strait islands (Hogan [12], Deal [11], East Sister [9] Is.), together with Clarkes I. [5] to the south and Hunter I. in western Bass Strait, had much higher means, and in the case of East Sister and Hogan Is., a mode of 6. The means for the three northern islands were significantly different at the 5% level to most other populations, including the adjacent mainland (population 19) and most of the nearest islands (Table 6.7).

6.9.2 Occipital scales:

ANOVA-1: $F_{24,639} = 3.966^{***}$. Means for most populations were between 2.0 (population 23) and 3.0 (populations 4, 9, 13), although East Sister I. (population 8, $\overline{X} = 1.3$) had a much lower mean. In general, mainland highland populations and nearby lowland populations had low means, and mode 2, while Tasmanian and nearby island populations had high means and mode 3, with population 8 the most divergent. Relatively few significant differences were detected at the 5% level (Table 6.8), and only between populations 8 and 9 were these differences between adjacent populations.

6.9.3 Presuboculars:

ANOVA-1: $F_{24,644} = 14.801^{***}$. Most populations had means between 2.0 (populations 5, 8, 10, 23) and 2.4 (populations 22, 24), with a mode of 2, and without significant differences between means. Four eastern Bass Strait island populations, however, had higher means, and modes of 3. Hogan I. (population 12, $\overline{X} = 3.4$) had the highest mean, significantly different at the 5% level to all other populations except East Sister I. (population 9, $\overline{X} = 3.0$), itself significantly different to most other populations (Table 6.9), including nearby West Sister I. (population 10, $\overline{X} = 2.0$). Deal I. (population 11, $\overline{X} = 2.6$), between Hogan and East Sister Is., also had a high mean, while Swan I. (population 4, $\overline{X} = 2.8$), in the south, had a significantly different mean to both the adjacent Tasmanian population (2, $\overline{X} = 2.1$) and Clarkes I (5, $\overline{X} = 2.0$) to the north.

6.9.4 Suboculars:

ANOVA-1: $F_{24,642} = 5.538^{***}$. Means ranged from 0.0 (population 10) to 1.3 (population 13). In general, southern and western populations (including Tasmania, the western Bass Strait islands, the extreme western mainland [population 15] and Swan, Clarkes, Cape Barren and Flinders Is. in eastern Bass Strait) usually had a single subocular, while the remaining mainland and eastern Bass Strait populations more frequently lacked a subocular. Although a number of significant differences at the 5% level were detected between the more extreme means (Table 6.10), only West Sister I. (population 10) was significantly different to some adjacent populations (East Sister I. [9] and Flinders I. [7]).

6.9.5 Postsuboculars:

ANOVA-1: $F_{24,644} = 2.605^{***}$. Means ranged from 3.9 (populations 18, 21–22) to 4.7 (population 11), with most populations having a mode of 4. The latter mean was significantly different at the 5% level from the lowest means (populations 18, 21–22; 1, 17, 20 [$\overline{X}$ = 4.0]; 2, 3, 15, 17 and 24 [$\overline{X}$'s = 4.1]) while population 4 ($\overline{X}$ = 4.4) was significantly different to population 21. None of these pairs are, however, geographically proximate.

6.9.6 Supralabials:

ANOVA-1: $F_{24,646} = 6.861^{***}$. Means ranged from 7.5 (populations 3, 13) to 8.5 (population 10). Most populations had means between 7.9 and 8.1. There was a slight tendency for western populations (in Tasmania, the Bass Strait islands and on the mainland) to have slightly lower means. Mode for most populations was 8, although in population 10 (West Sister I.), the frequencies of 8 and 9 were equal, while in population 13 (Hunter I.), the frequencies of 7 and 8 were equal. Significant differences at the 5% level were detected between several high and low means (Table 6.11), although the only significant difference between adjacent populations was between 2 and 3.

6.9.7 Infralabials:

ANOVA-1: $F_{24,646} = 5.053^{***}$. Means ranged from 7.6 (populations 10, 14) to 8.8 (population 24). Most populations have mode 8, except for populations 5, 8, 11, 20–21 and 24–25, which have mode 9, population 23, which has mode 8=9, and population 14, with mode 7. No clear geographic pattern is obvious, although south-west populations (Tasmania and western Bass Strait islands) have low means. Significant differences at the 5% level were detected between the lowest means and a number of other populations (Table 6.12), but only King I. (14) was significantly different from proximate populations (mainland populations 15, 16). The eastern Bass Strait islands had the greatest variation in means, but sample sizes were too small for significance.

6.9.8 Rostral ear lobules:

ANOVA-1: $F_{24,638} = 2.852^{***}$. Means ranged from 1.8 (populations 3, 17) to 2.4 (populations 5–6), with almost all in the range 1.8–2.2, with mode 2. Only four eastern Bass Strait islands (Clarkes [population 5], Cape Barren [population 6], Babel and Deal, $\overline{X}$'s = 2.3, Babel and Cape Barren with mode 3) have higher means. Significant differences at the 5% level were detected between population 6 and populations 3, 17 ($\overline{X}$'s = 1.8), 16, 25, 15 and 21 ($\overline{X}$'s = 1.9) and between populations 11 ($\overline{X}$ = 2.3), 5 and 12 on one hand and 3 and 17 on the other, although none of these are geographically proximate.

6.9.9 Posttemporals:

ANOVA-1: $F_{24,642} = 1.975^{**}$. Means ranged from 2.7 (population 7) to 3.3 (population 13), with mode consistently 3. Probably due to the extreme means being for islands from which only small samples were available, no significant differences at the 5% level were detected in multiple pairwise comparisons.

6.9.10 Midbody scales:

ANOVA-1: $F_{24,311} = 6.671^{***}$. Means ranged from 27.9 (population 3) to 31.6 (populations 4, 18). No geographic trends were evident. Significant differences at the 5% level were detected between population 3 and most other populations (1–2, 4–6, 9–12, 15–22, 24–25), between population 12 ($\overline{X}$ = 31.5) and populations 1–2, 14, 16 and 25, between population 4 and 1–2, 14 and 25, between population 18 and 1 and 13 and population 14 and 21. Only the north–west Tasmanian population (3) was significantly different to surrounding populations within landmasses, while the Swan I population was significantly different to the adjacent north-east Tasmanian population.

6.9.11 Paravertebral scales:

ANOVA-1: $F_{24,309} = 8.176^{***}$. Means ranged from 45.6 (population 3) to 53.1 (population 12). In general, low means occurred in the south and west, while the highest means occurred in the southern (Swan, Clarkes, Cape Barren Is.) and northern (East Sister, Deal and Hogan Is.) eastern Bass Strait islands. The two extreme values were significantly different at the 5% level from most other means, while a number of other significant differences were detected between high and low values (Table 6.13). However, the only significant differences between surrounding populations within landmasses were between north-west and north-east Tasmania (populations 3 and 2), and between Melbourne (population 17) and populations to the east (populations 19, 21). Although the greatest differences between means occurred in the eastern Bass Strait islands, sample sizes were too small for significance.

6.9.12 Axilla-groin scales:

ANOVA-1: $F_{24,309} = 5.270^{***}$. Means ranged from 33.5 (population 14) to 39.3 (population 12). The pattern of geographic variation is similar to that in paravertebral scales, with generally low means in the west, and generally high means in the east, on the mainland and eastern Bass Strait islands. Significant differences at the 5% level were detected between several of the highest and lowest means (Table 6.14), although the only significant difference between adjacent populations occurred between populations 22 ($\overline{X}$ = 38.6) and 23 ($\overline{X}$ = 35.8) in the highlands.

6.9.13 Ventral scales:

ANOVA-1: $F_{24,305} = 7.957^{***}$. Means ranged from 63.0 (population 8) to 76.6 (population 6). The pattern of geographic variation was similar to that for paravertebral scales, with generally low means in Tasmania, the western Bass Strait islands, and the western part of the mainland distribution, and higher means in the eastern highland populations and the northern (Hogan, Deal Is.) and southern (Cape Barren, Clarkes, Swan Is.) eastern Bass Strait islands. The two lowest means, for populations 8 and 3 ($\overline{X}$ = 65.4) were significantly different at the 5% level to most other populations, while significant differences were also detected between several other populations with high and low means (Table 6.15). However, the only significant differences between adjacent populations within a landmass were between northwest Tasmania (population 3) and the other two Tasmanian populations. Although the greatest differences between means occurred in the eastern Bass Strait islands, sample sizes were too small for significance.

6.9.14 Subcaudal scales:

ANOVA-1: $F_{24,281} = 7.639^{***}$. Means ranged from 30.7 (populations 7,8) to 39.9 (population 21), with all but the two lowest means within the range 33.5–39.9. No obvious pattern of variation is apparent, although mainland populations and some eastern Bass Strait islands (Clarkes, Cape Barren, Deal Is.) have the highest means, and the highland populations generally have the highest means on the mainland. Significant differences at the 5% level were detected between many of the highest and lowest means (Table 6.16), although the only significant differences between proximate populations were between the two northern Tasmanian populations (2 and 3), and between Hogan I. (population 12) and the adjacent south Gippsland mainland (population 19).

6.9.15 Subdigital lamellae:

ANOVA-1: $F_{24,635} = 5.514^{***}$. Means range from 7.4 (population 12) to 9.4 (population 6). High means were largely confined to Bass Strait islands (means for most within the range 8.4–9.4) while most mainland and Tasmanian populations had low means (range 7.8–8.5), although the two eastern Bass Strait islands closest to the mainland and Tasmania (Hogand and Swan respectively) had low means, as did Babel I., in the middle of the chain. Although the two extreme means were significantly different at the 5% level to most other means, and several other significant differences between pairs of means were detected (Table 6.17), the only significant differences between adjacent populations occurred between populations 19 and 21 (lowland *vs* highland) and 11 and 12 (Deal I. *vs* Hogan I.).

6.9.16 Snout-vent length:

The six highland populations (20–25) attained significantly greater sizes than the lowland and island populations (mature-sized ♂♂: pooled highland 242–368mm, $\overline{X}$ = 296.6mm, sd = 24.11, n = 31; pooled lowland 227–300mm, $\overline{X}$ = 260.2mm, sd = 16.82, n = 89; Mann-Whitney U test, $z = 6.51^{***}$; mature-sized ♀♀: pooled highland 280–368mm, $\overline{X}$ = 313.1mm, sd = 23.77, n = 27; pooled lowland 239–328mm, $\overline{X}$ = 269.5mm, sd = 19.90, n = 82; Mann-Whitney U test, $z = 6.55^{***}$).

6.9.17 Other morphometric characters:

Probably due to the difference in overall size, significant differences in the allometric relationships between most morphometric characters were detected between highland and lowland morphs (Tables 6.1–6.2, 6.18). However, despite the difference in size, the relationship between tail length and SVL, head depth and head length, interocular width and head length, and interparietal length, width and head length were not significantly different between the two morphs.

6.9.18 Dark dorsal bands between axilla and groin:

ANOVA-1: $F_{24,287} = 12.013^{***}$. Means ranged from 4.4 (populations 23, 25) to 8.0 (population 9, East Sister I.), with significant differences between a number of means (Table 6.19). In general, the highland populations (20–25), and the adjacent Melbourne population (17), had relatively low means (4.4–5.3), significantly different at the 5% level to the nearest population

to the south (19, $\overline{X}$ = 6.2), although not to the west (17 *vs* 16, $\overline{X}$ = 5.6). Similarly low means were also found for eastern Tasmania (populations 1–2, $\overline{X}$ = 4.8–5.1), though in this case not significantly different to the nearest populations. The eastern Bass Strait islands showed the greatest variation in means, from 5.3 (Flinders I., population 7, similar to Tasmanian means), to 7.3 (Hogan I., population 12) and 8.0 (East Sister I., population 9), although due to the small sample sizes, the only significant differences between adjacent populations were between East Sister and Flinders I., and between Hogan I. and the adjacent South Gippsland mainland.

6.9.19 Presence of a dark nape band:

A dark nape band was usually absent in Tasmanian populations (pooled Tasmanian: n = 56, 71.4%), variably present on Bass Strait islands (modally absent on Hunter, Swan, Clarkes, Babel and Hogan Is., total n = 24, 87.5%; modally present on King, Cape Barren, Flinders, East and West Sister and Deal Is., total n = 27, 77.8%), and usually present on the mainland (pooled populations 15–25, n = 204, 93.6%).

6.9.20 Dark tail bands:

ANOVA-1: $F_{24,268} = 9.590^{***}$. Means ranged from 6.0 (populations 22, 25) to 9.2 (Hogan I., population 12). The pattern of variation was similar to that for dark body bands, with generally low means (6.0–6.8) in the highland populations (20–25) and adjacent Melbourne population (17), significantly different at the 5% level from South Gippsland ($\overline{X}$ = 7.8), but with Melbourne not significantly different from the Otways (16, $\overline{X}$ = 7.6), and with similarly low means (6.7–6.8) in eastern Tasmania. Again, the greatest variation occurred in the eastern Bass Strait islands, with generally high means in the south (Swan, Clarkes and Cape Barren Is., populations 4–6, $\overline{X}$'s = 8.5–8.7), and the north (West Sister, East Sister, Hogan Is., populations 9–10, 12, $\overline{X}$'s = 8.5–9.2), but much lower in the remaining islands (Flinders, Babel, Deal Is., populations 7–8, 11, $\overline{X}$'s = 6.8–7.5), although the small sample sizes meant that only Hogan I. was significantly different at the 5% level, from both Deal I. to the south and S. Gippsland to the north (Table 6.20).

6.9.21 Dorsal ground color:

Tasmanian and Bass Strait island populations generally had a green to blue dorsal and lateral ground (pooled populations 1–14, n = 112, green 70.5%, blue 24.1%). Blue to green dorsal grounds also occurred in low frequencies (<15%) in mainland populations 15–19, although in all, the dominant dorsal ground was cream to tan (pooled populations 15–19, n = 112, 62.5%), and a high proportion had a combination of tan to orange dorsally and green to blue laterally (pooled populations: 30.6%). In population 20, such mixtures were the dominant form (n = 11, 72.7%), while in the highland populations (21–25), the predominant dorsal ground color was yellow (pooled populations 21–24, n = 59, 86.4%) or even yellow-orange to salmon pink (population 25, n = 27, 48.1%).

6.9.22 Body venter:

Tasmanian, Bass Strait island, and extreme western mainland (15) populations usually had green-grey to blueish venters, usually clouded, speckled or obscurely banded with darker flecks. In other lowland mainland populations (16–19), the venter was more commonly spotted with larger flecks, or variegated with narrow dark vermiculations, and the ventral ground color ranged from greenish to blue-yellow and cream or yellowish. In contrast, the highland populations (21–25) typically had bright yellow venters moderately to heavily variegated with black.

6.9.23 Head markings:

Only two of 121 Tasmanian and Bass Strait island specimens had an indication of variegations on the head, and then only in a minor degree. Only slightly more lowland mainland specimens had variegated heads (6 of 114), again only weakly variegated with brown. In contrast, strongly dark variegated heads were the norm amongst the some high altitude populations (21: n = 29, strongly variegated 72.4%, moderately variegated 27.6%; 25: n = 27, strongly variegated 100%), but not in others at intermediate altitudes (20: n = 11, immaculate 72.7%; 24: n = 19, immaculate 57.9%, weakly to moderately variegated 20.8%).

6.9.24 Summary of geographic variation:

The extreme difference in size between highland and lowland populations of *T*. *nigrolutea* was only partly accompanied by coloration differences. Most of the coloration differences were more clinal in nature, from poorly-contrasting, reduced patterns in Tasmania, to brightly-contrasting, complex patterns in the populations at highest altitudes. Geographic variation in scalation was typically greatest in the isolates in Bass Strait, but less on the mainland, and in no case showed a clear division between highland and lowland morphs concordant with that in overall size. In contrast, size and coloration (apart from number of dark bands) showed little variation on the Bass Strait islands. The only potential mainland isolate, in the Blue Mountains, showed few morphological differences to the nearest populations. The lack of concordance between the geographic patterns of variation from different morphological systems, and the lack of any clear division between adjoining populations, apart from size between highland and lowland morphs, makes it impossible to recognise subspecies within *T*. *nigrolutea* at the present time. Instead, it seems likely that the great variation seen in the species reflects local adaptation to the combination of the variety of habitats and altitudes inhabited by the species on landmasses, and its occurrence on a number of isolated, often small Bass Strait islands, presumably in relatively small populations that would encourage the rapid genetic fixation of scalational peculiarities.

6.10 Comparison with other Species

Comparisons with *T*. *adelaidensis* and *T*. *multifasciata* have already been made (Sections 4.10, 5.10). *T*. *nigrolutea* is readily differentiated from all other *Tiliqua* by the dorsal colour pattern, although occasional lowland specimens may have the pale blotches laterally confluent, and slightly resembling the dorsal colour pattern of *T*. *scincoides*.

T. *nigrolutea* can be readily differentiated from *T*. *gigas* and *T*. *scincoides* by the presence of paired primary temporal scales, and fewer subcaudal scales, ventral scales, supraciliaries and presuboculars, and further, from *T*. *s*. *scincoides*, with which it is sympatric, by possessing dark ventral markings, a yellow throat, and fewer paravertebral scales, midbody scales, supralabials and posttemporals, and in lacking a dark temporal stripe.

T. nigrolutea may be differentiated from *T. occipitalis* by the very different dorsal color pattern, in having dark ventral markings, fewer supralabials, presuboculars, rostral ear lobules, body scales (midbodies, paravertebrals, ventrals) and subcaudals, but more supraoculars, and lacking a dark temporal streak.

T. nigrolutea shows some resemblance to *T. rugosa* in the relatively large, thick body scales. However, it may be differentiated from all subspecies of *T. rugosa* by the dorsal colour pattern, and in having a conical tail with more subcaudal scales, more paravertebral scales, more supraoculars and undivided subdigital lamellae.

6.11 Habits and Habitats

T. nigrolutea has been reported to inhabit a wide range of forested and open grassland habitats within its distribution, including open forest, both dry and (in warmer areas) wet, montane sclerophyll woodland of *Eucalyptus pauciflora, E. dalrympleana, E. rubida, E. stellulata*, and *E. camphosa* and *E. stellulata*, tall open montane forest of *E. fastigata*, *E. viminalis*, open montane forest, montane wet woodland, dry sclerophyll forest of *E. dives/radiata, E. rubida, E. cypellocarpa*, and of *E. obliqua*, riparian open forest, dry upslope forest, valley sclerophyll forest, subalpine snow gum woodland, woodlands of foothills and coasts, softwood plantations, heaths and coastal scrubs, *Leptospermum* thickets and agricultural lands (Brown *et al.*, 1989; Carr *et al.*, 1984; Cherry *et al.*, 1987; Chesterfield *et al.*, 1983, 1988; Chisolm, 1924; Earl *et al.*, 1989; Emison *et al.*, 1975, 1978; Gillespie *et al.*, 1990; Gilmore, 1977; Gilmore *et al.*, 1979; Horrocks *et al.*, 1987a,b; Hutchinson, 1979; Land Conservation Council, 1972a, 1973a,b, 1974a,b, 1976, 1977, 1979, 1980a,b, 1982a,b, 1984, 1985a; Lunt *et al.*, 1987; Norris *et al.*, 1979, 1983; Opie *et al.*, 1984, 1987, 1990; Smales, 1981; Webb, 1991; Westaway *et al.*, 1990; Yugovic *et al.*, 1990). Although several authors have suggested that it is absent from moister and more closed forests, such as wet sclerophyll forest and temperate rainforest (Emison *et al.*, 1975; Hewer, 1948; Land Conservation Council, 1976; Norris *et al.*, 1979), it has been reported to occur, sometimes commonly, in wet sclerophyll forest by Brown *et al.* (1986, 1989), Cherry *et al.* (1986), Chesterfield *et al.* (1988), Henry *et al.* (1988a,b) and Pyrke *et al.* (1988). Thompson and Tyler (1983) consider the extreme western mainland populations to be largely restricted to dense vegetation near swamps.

Rawlinson (1974) states that it is most active in clearings bordered or surrounded by dense heath or arboreal vegetation, using exposed patches of ground as basking sites.

T. nigrolutea is reported to shelter by burrowing into deep litter layers (Norris *et al.*, 1983; Rawlinson, 1974) or under boulders and grass tussocks (Keast, 1966; MacFarlane *et al.*, 1987). Baehr (1976) suggests that Tasmanian populations shelter up to 0.5m below ground, but never under timber, unlike mainland populations, while Smales (1981) reports two cases of specimens found in hollow logs during winter on the mainland. Mackay (1955) notes that specimens encountered in the open on Babel I. attempted to shelter in Mutton-bird burrows.

There are virtually no field data associated with museum specimens examined in this study. SAM R17014 was found foraging on a coastal dune, R23102 amongst *Gahnia* and intermittent grassland and R23103 in grazed grassland.

6.12 Taxonomic History and Type Material

Scincus nigro-luteus was described by Quoy and Gaimard (1824) from material they collected during the 1817–1820 French expedition commanded by de Freycinet. It is not clear from their account whether they base their description on one or two specimens. Although they state that two specimens were collected (“nous nous en procurâmes deux

individus"), the ship carrying the zoological material was wrecked in the South Atlantic, and only some of the collection was saved. Quoy and Gaimard state "ce bel animal est le seul objet d'histoire naturelle échappé au naufrage, qui puisse rappeler à l'un de nous le fatigant voyage qu'il fit au-delà des Montagnes-bleues de la Nouvelle-Hollande" [This fine animal is the only object of natural history saved from the shipwreck, that strongly recalls to one of us the tiring trip that he made beyond the Blue Mountains of New Holland], and provide one set of measurements and meristic data, and an excellent color plate that clearly identifies the type as of the northern morph, all suggesting only a single holotype. However, Duméril and Duméril (1851) report the presence of "types" in the MNHP collection, from King George Sound, and Brygoo (1987) lists three specimens, MNHP 3023, 3024 and 7134, as types, noting their identification as types, collected by Quoy and Gaimard, in the oldest register for the collection. Of these three specimens, only 7134 can be the specimen described and illustrated by Quoy and Gaimard, who give a total length of 18" (459mm), a tail length of 5" (128mm), 32 teeth in the lower jaw (indicating an open mouth) and 6L/5R "quadrilateral and vertical" supralabials. MNHP 7134 has a total length of 449mm (SVL 303mm, TL 146mm), a partially open mouth, and one more supralabial on the left than on the right (although I count the "quadrilateral and vertical" supralabials [those between penultimate supralabial and rostral?] as 7L/6R). The other two specimens are far too small (3023: SVL 162mm, TL 47.5mm; 3024: SVL 272mm, TL 126mm) and have inappropriate supralabial counts (6/6, 6/7 respectively, counted as above) to be Quoy and Gaimard's specimen. Wells and Wellington (1985) designate MNHP 7134 as lectotype, although they did not examine any of the MNHP material, and give no reason for their lectotype selection. The lectotype (Fig. 30A) has the following combination of character states: nasals moderately separated; prefrontals in narrow contact; presuboculars two; suboculars 0/1; postsuboculars 4/5; supraciliaries five; supralabials 9/8; infralabials 8/9; rostral ear lobules two; primary temporal divided into three scales; posttemporals three; occipitals 2/3; midbody scales 34; paravertebral scales 50, between axilla and groin 36; ventral scales 82; subcaudal scales 41; subdigital lamellae nine; SVL 303mm; AGL 187mm; TL 146mm; FLL 58mm; HLL 61mm; HL 54.3mm; HW 43.6mm; HD 34.7mm; IOC 22.7mm; E–N 14.6mm; E–E 19.1mm; Eye 9.5mm; Ear 4.5mm; Hip 30.5mm; IparL 11.3mm; IparW 5.2mm; FrontL 12.3mm; FrontW 9.0mm. All three specimens are conspecific with and typical of the species here described. The head shield configuration of a topotypic specimen is illustrated in Fig. 31.

Scincus nigro-luteus was placed in *Cyclodus* by Wagler (1830) and *Tiliqua* by Gray (1831).

Quoy and Gaimard were not the first zoologists to collect *T. nigrolutea*, however. William Anderson, who acted as zoologist during Cook's third expedition (1776–1780), in the *Resolution* and *Discovery*, noted in his manuscript diary the collection of a specimen at Adventure Bay, Tasmania, on 30 January 1777: " . . . a large Lizard[g] above fifteen inches long and six round, elegantly clouded with black and yellow was kill'd,. . . . [g]Lacerta tarda", the species name being given as a note on the facing page, and keyed to the text (Beaglehole, 1967). This diary was eventually published in whole by Beaglehole (1967), although the same description, without the associated name, was also published by Eden (1787).

Despite the 190 years delay in publication, the name *Lacerta tarda* appears to be available under the Code, with the size, coloration and locality sufficient to identify the species. It could be argued that as Beaglehole, in his editorial annotations, identified *Lacerta tarda* as *T. nigrolutea*, the name was first published as a junior synonym and hence unavailable (Article lle). However, I do not believe that such an argument can be sustained, as Anderson is clearly the author of the binomen, and Beaglehole's action in identifying it as *T. nigrolutea* must be a subsequent synonymy, even though printed on the same page. Consequently, I treat *Lacerta tarda* Anderson as an available name, with date 1967 and type locality Adventure Bay, Tasmania. The current depository of the type, if still extant, is unknown.

Whitehead (1969) suggested that reptile material from Cook's voyages ended up in the British Museum, via Sir Joseph Banks and the Royal College of Surgeons, although no such material can now be identified in the BMNH collection. Conversely, Whitley (1970), quoting Keevil (1933), suggested that much of Anderson's material was left in Russia, and may now be in St Petersburg or Moscow. However, it was not amongst the material in St Petersburg listed by Strauch (1866). Whitley (1970) also notes that a drawing of the specimen was made by the artist J. Webber, the illustration now held in the British Museum Prints and Drawings Department at Bloomsbury (Whitehead, 1969).

Anon (1888), based on notes provided by W.B. Spencer, Mr Campbell and Mr Cornwall, notes “the large blue-tongued *Cyclodus gigantea*” observed during a Field Naturalists Club of Victoria expedition to King Island. Earlier in the same expedition report, le Souef (1888) lists *Cyclodus nigro-luteus*, noting that “numerous specimens of the blue-tongued lizard were seen”. *Cyclodus gigantea* is presumably a misspelling for *Cyclodus gigas* (which at the time included *T. scincoides*), and a misidentification of *T. nigrolutea*, and I prefer to treat it as such. However, under the Code, it may also be possible to treat it as a new name, depending on whether “large blue-tongued . . . ” be considered sufficient description.

Wells and Wellington (1985) described *Tiliqua milleri* as a partial solution to the highland/lowland morph concept frequently mentioned in the literature, basing their concept on Worrell's (1963) labelled illustration. However, their concept of the species is not precisely congruent with the lowland morph of other authors, as they restrict the species to south-eastern SA, regarding other lowland populations (e.g., the illustration provided by Gans [1975]) as other members of the group (presumably different, unnamed species). Wells and Wellington nominated a holotype (AM R92696), but did not describe it. The holotype (Figs. 30B, 32) has the following combination of character states: nasals broadly separated; prefrontals in broad contact; presuboculars two; subocular one; postsuboculars four; supraciliaries four; supralabials eight; infralabials 9/8; rostral ear lobules two; primary temporal divided into three scales; posttemporals three; occipitals, two on each side, separated by a median occipital; midbody scales 32; paravertebral scales 48, between axilla and groin 38; ventrals 68; subcaudals 38; subdigital lamellae 8/9; SVL 203mm; AGL 124mm; TL 94mm; FLL 40mm; HLL 41mm; HL 36.3mm; HW 32.5mm; HD 22.4mm; IOC 16.9mm; E–N 10.1mm; E–E 15.2mm; Eye 7.6mm; Ear 5.5mm; Hip 22.6mm; IparL 8.0mm; IparW 4.3mm; FrontL 8.2mm; FrontW 6.1mm; sex ♀ (immature).

As noted under geographic variation, the available evidence appears insufficient for recognition of even a distinct subspecies for the lowland morph. Further, even if subspecies were recognised, Anderson's name predates that proposed by Wells and Wellington.

6.13 Reproduction
6.13.1 Size at maturity.

As noted above, there is considerable geographic variation in size at maturity, with highland populations larger than lowland population. Consequently, I have determined size at maturity for these two forms separately. In the small lowland morph, mature-sized males had SVL 227–300mm, $\bar{X}$ = 260.2mm, sd = 16.82, n = 89, while mature-sized females were larger, with SVL 239–328mm, $\bar{X}$ = 269.5mm, sd = 19.90, n = 82 (Mann-Whitney U test, z = 2.79**) (Figs. 33–34). In the highland morph, the direction of sexual dimorphism was the same, with mature-sized males 242–368, $\bar{X}$ = 296.6mm, sd = 24.11, n = 31, and mature-sized females 280–368mm, $\bar{X}$ = 313.1mm, sd = 23.77, n = 27 (Mann-Whitney U test, z = 2.36*) (Figs. 35–36). Gravid females were similar, and not significantly different in size to other, non-gravid, mature females (lowland: gravid: 247–328mm, $\bar{X}$ = 271.6mm, sd = 21.06, n = 34; non-

gravid: 239–321mm, $\overline{X}$ = 268.1mm, sd = 19.12, n = 48; Mann-Whitney U test, z = 0.64n.s.; highland: gravid: 284–368mm, $\overline{X}$ = 319.3mm, sd = 25.66, n = 12; non-gravid: 280–339mm, $\overline{X}$ = 308.2mm, sd = 21.76, n = 15; Mann-Whitney U test, U = 113.5, n.s.).

6.13.2 Male reproduction.

Testis length did not increase isometrically with body size, as estimated by SVL (Fig. 33), and consequently testis length, rather than a gonosomatic index, was used to infer seasonal patterns of reproduction.

Testis length increases through spring, peaking in late October–November, and decreases through summer. As testis length decreases, condition also changes, with an increase in the frequency of flaccid testes (Fig. 37). Data are largely lacking for the cooler months (May to mid September). There is much variation in the data, many late spring individuals showing no enlargement (length 15–24mm) at the same time as others are grossly enlarged (up to 39mm long). However, the seasonal pattern of variation is similar in both highland and lowland morphs.

The data suggest that spermiogenesis peaks in late spring.

6.13.3 Female reproduction.

The pattern of variation in follicle diameter is similar in both the southern lowland and northern highland morphs. Follicle diameter increases gradually between late winter (August) and late spring (November), with the largest follicles occurring in late November and December. The earliest female with oviducal eggs was collected 9 November, and oviducal eggs and embryos were present until 27 March. During this period, non-breeding females show little increase in follicle diameter, while follicle diameter in April, following parturition, is similar to the diameter in summer (Fig. 38). Unfortunately, data are lacking for May–July. Corpora lutea were obvious grossly throughout embryonic development.

These results are consistent with the limited literature available. Gravid or possibly gravid females have been reported in late summer and autumn (Booth, 1981, 29 February; Green, 1984, 6 March; Green & McGarvie, 1971, 26 February; Horrocks *et al.*, 1987, 8–16 January; Thomas & Gilmore, 1976, late February), while young have also mostly been reported or estimated to be born in late summer or autumn (Anon, 1893, 12 April; D. Clutterbuck, *pers. comm.*, 2–17 March (n = 4); Fleay, 1931, late March; Longley, 1941, 7 February; Rawlinson, 1974, April-early May; Weigel, 1988, summer to early autumn), although both Jenkins & Bartell (1980) and Wilson & Knowles (1988) suggest that young are born in summer. The Clutterbuck records of birth followed mating between 14–17 October.

Taken as a whole, the data suggest that vitellogenesis occurs in spring, ovulation in late spring-early summer (November–December), and young are born in autumn, following approximately 4–4.5 months gestation. There is no evidence that more than one litter can be produced in a year.

6.13.4 Mating season.

Rawlinson (1974) states that copulation occurs in spring, while Fleay (1937, 1951) states that the breeding season in October–November, and is accompanied by fierce fighting

between males. Longley (1941) also reports captive males fighting on 9–10 October. Male captives held outdoors in southern Victoria (Anglesea) chase females and fight with other males from late October through to December, with actual mating observed between 14–17 October, while local wild males have been observed chasing other males over distances of up to 15m during the same period (D. Clutterbuck, *pers. comm.*). Bartlett (1984a) reports mating activity in northern hemisphere captives on warm evenings in February and March, equivalent to August/September in the southern hemisphere. An October–November breeding season is consistent with the timing of appearance of enlarged ovarian follicles and oviducal eggs in females and enlarged testes in males.

D. Clutterbuck (*pers. comm.*) describes a distinct courtship ritual for this species as follows: "he will walk normally in that lovely fluid flowing motion but about [60cm] from an adult female he starts [a] stilted, jerky robotic motion where instead of taking one step in one go his, say, right front leg will be jerked forward along with the left hind leg up to four times before completing the step, and starting with the left front leg and right hind. Often the pupils will be noticeably dilated. If the female is too young or not ready she will take off before he gets within touching distance. Sometimes he pursues, and if he catches up and bites the ribs or neck there is a skirmish with the female making strenuous efforts to escape, attempting to bite a portion of the male's body she can reach. If the female is receptive, as he gets a few inches away from her, her tail will start to twitch and writhe. She lets him get alongside her. He may have given her a few nudges and pushes with his head and then he will quickly grasp her high up on the rib cage. Usually the females make a token gesture of escaping by unhurriedly trying to walk away. I have noticed once a male is biting a female they may stay like that for up to an hour with no mating taking place. Sometimes [the male] makes no attempt to position his rear end alongside and underneath her at all, just grabs her and hangs on in a trance. . . . The few times I have [seen mating] it takes only about 3–5 minutes from actual grabbing of the female to his penetrating her and then they may be joined for up to half an hour, I suspect as long as an hour or more sometimes. The males seem to favour the right side of the female to grab".

6.13.5 Frequency of reproduction.

Between 15 December and 15 March (i.e., the middle of the period when gravid females are present in the population), only 24 of 50 mature-sized females had either developing oviducal eggs or grossly enlarged ovarian follicles, suggesting non-annual, and possibly biennial reproduction in females. This pattern was present in both lowland (14 of 33 females) and highland (9 of 15 females), and involved females of all sizes. It is therefore unlikely that the high proportion of non-gravid females is due to misclassification of immature specimens as mature. Similarly, although the largest, most turgid testes were found in October–November, many of the mature males collected at this time had testes of similar size to late summer and autumn males. Taken together, the data suggest that *T. nigrolutea* does not consistently breed annually in the wild, although captives have been reported to breed annually (D. Clutterbuck, *pers. comm.*).

6.13.6 Litter size.

Of 46 females with either countable enlarged yolky ovarian follicles (≥12.5mm), oviducal "eggs" or embryos, or litters of young born before preservation, the number of follicles or young was 3–10 ($\bar{X}$ = 6.1, sd = 1.61), with mode 6 (26.1%). Mean litter size based on number of enlarged follicles did not differ significantly from the mean based on oviducal "eggs" or young in either lowland or highland morphs (lowland: $\bar{X}$ = 5.4, sd = 1.69, n = 8 *vs*

$\overline{X}$ = 6.4, sd = 1.55, n = 27, t_{33} = 1.718, n.s.; highland: $\overline{X}$ = 5.0, sd = 1.414, n = 2 *vs* $\overline{X}$ = 5.8, sd = 1.64, n = 9, t_9 = 0.665, n.s.).

More follicles and young were generally present on the right side than the left (in total, 133 *vs* 118; R>L:R=L:R<L = 18:13:10), although these differences are non significantly different from 1:1 (totals, X^2 = 0.90, n.s.; individual inequalities (18:10), X^2 = 2.29, n.s.).

There was little evidence for extra-uterine transfer of ova or loss of ova at ovulation. In those cases where the number of corpora lutea was estimated grossly (n = 14), the number and distribution of corpora lutea was usually either the same as for the oviducal eggs (n = 6) or fewer than the number of oviducal eggs, but with the same distribution (n = 6), the latter situation probably due to difficulties in examining ovaries deep within a body cavity full of embryos. In one of the remaining two cases, there was one more corpus luteum than oviducal masses, but with much free yolk scattered through the body cavity, while in the other, there were 3L/3R corpora lutea, but only 3L/1R oviducal eggs.

There was no evidence for a correlation between litter size and maternal SVL (Fig. 39), either overall, or in lowland or highland morphs (overall, r = 0.1341, n = 44; lowland, r = 0.2665, n = 34; highland, r = 0.4710, n = 10, all values non-significant). In pairwise comparisons of mean litter size in Tasmanian, Bass Strait island, lowland mainland and highland mainland populations, the only significant difference was between the two extremes, Tasmania and lowland mainland populations ($\overline{X}$ = 6.7, sd = 1.63, n = 19 *vs* $\overline{X}$ = 5.1, sd = 1.55, n = 8, t_{25} = 2.36*).

Litter sizes have previously been reported by several authors (Table 6.21). Results from captive breedings have generally suggested smaller litters than found here, possibly due to captive stress, while statements in the older general texts have overestimated litter size.

6.13.7 Size of young at birth.

There seems to be little variation, either geographic or individual, in size of young at birth. The 11 smallest non-embryonic Tasmanian specimens have SVL 86–104mm ($\overline{X}$ = 94.6, sd = 7.86), with dates of collection, where known, between 29 December and March. A date of 8 November associated with two specimens may have been date of collection of the parent. The 7 smallest mainland lowland specimens have SVL 76.5–104mm ($\overline{X}$ = 94.1, sd = 10.90), the only date of collection being 8 June for a 96mm specimen, although two with SVL 100–103mm are recorded as being less than 2 days old. The 6 smallest highland specimens have SVL 89.5–103mm ($\overline{X}$ = 95.8, sd = 5.75), none having any date of collection, although the three smallest (SVL 89.5–93mm) were born in captivity, and three slightly larger specimens (SVL 118–119mm) are known to have been 4–7.5months old at death. These results indicate smaller young than reported by most previous authors (Griffiths, 1984, total length 160mm; Jenkins & Bartell, 1980, 150mm total length; Longley, 1941, 4 x 172mm, 1 x 140mm total length), although the young reported by Bartlett (1984a) (SVL 84–93mm, total length 116–128mm, n = 2) and D. Clutterbuck (*pers. comm.*; 90–113mm total length, n = 26 young from four litters) are close to the size inferred here.

6.13.8 Observations on birth.

Neonates regularly eat the yolk sac and fetal membranes following birth (Davey, 1944; Bartlett, 1984a; Giddings, 1984; D. Clutterbuck, *pers. comm.*). Females have been observed

to be aggressive during parturition (Davey, 1944), and to show interest in neonates, often turning around and licking at emerging young (D. Clutterbuck, *pers. comm.*).

6.13.9 Longevity.

T. nigrolutea is potentially long-lived. One captive female acquired as an adult died after 25yrs in captivity (M. Shea, 1991), two captive males collected as large adults are still alive 10yrs after capture (D. Clutterbuck, *pers. comm.*), and a captive female in my possession died recently ten years after collection as an adult. Flower (1925) reports five longevity records, the longest being 11yrs 6mo 25d, while Anon (1984) states that the species lives to 10 years in captivity.

6.13.10 Sex ratio.

Overall, the ratio of mature-sized males:females was 119:113, a ratio not significantly different to parity ($X^2 = 0.16$, n.s.). Sex ratios for lowland and highland morphs were similar, and also not significantly different to parity when seasons were pooled (lowland: 89:85; highland, 30:28). However, in both forms, more females than males were collected in March-April, and more males than females in November, although significant differences between seasons were only present when the two morphs were pooled (using categories Dec-Feb, Mar-Jun, Aug-Nov; lowland: 35:39, 8:14, 30–19; highland: 10:12, 1:3, 10:5; pooled: 45:51, 9:17, 40:24, $X^2_2 = 7.27^*$). Possibly, this seasonal variation is due to increased activity by males seeking mates in spring, and basking by gravid females in autumn. The lack of material during winter is consistent with previous studies. Green (1977) observed *T. nigrolutea* only between November and March at Maggs Mtn in Tasmania, during monthly visits spanning several years, while Norris *et al.* (1983) noted that roadkilled *T. nigrolutea* were common between October and February in the Gippsland Lakes region of Victoria.

6.14 Specimens Examined

Population 1 (southern Tasmania)
AM 4841, Ouse R.; R15892, Mt Field National Park; R67930, 15.7km N Nive R. at Tungatinah, via Lyell Hwy; R67931, 4.0km S Pt Arthur (P.O.) via rd to Remarkable Caves; R67937, 13.4km N MacLaines Ck at Triabunna via Hwy 3; R80334, Glen Huon; R100035, Russel R., near Glen Huon; MV D2591–92, Pt Esperance; D33181–82, Coalmines, 3.2km N Saltwater Ck; QVM 1961/3/21, Oatlands; TM C128a–b, Ridgeway; C129, Bagdad; C130, Lunawanna, Bruny I.; C251, Lymington; C392, Moogara.

Population 2 (north-east Tasmania)
QVM 1947/3/1, Prospect, Launceston; 1961/3/10–11, Launceston; 1962/3/1–3, Tatana; 1962/3/30a–c, Winnaleah; 1962/3/33a–c, Punchbowl, Launceston; 1972/3/203, Kelso; 1972/3/205, Green's Beach; 1976/3/26, Nabowla; 1978/3/89, Tommahawk; 1982/3/15, Shelly Beach; 1983/3/21, Reatta rd, Launceston; 1984/3/16, Mt Arthur; 1985/3/5, Underwood; TM C281, Bicheno.

Population 3 (north–west Tasmania)
AM R37756–57, Rosebery; MV D33042, D39225, Strahan aerodrome; D33180, 9.7km W Rosebery; NTM R9293–94, Cradle Mtn; QVM 1975/3/2, 1975/3/27, 1975/3/29, 1975/3/31–33, 1976/3/1, 1977/3/15, 1978/3/8, 1978/3/46, 1978/3/101, 1980/3/6, 1983/3/5, Maggs Mtn; 1981/3/27, 1981/3/78, Brooks Ck.

Population 4 (Swan I.)
MV D42510–17.

Population 5 (Clarkes I.)
MV D56775–76, MacLaines Bay, Clarkes I.; D56777, Clarkes I.; D56778, plateau nr Green Hill, Clarkes I.

Population 6 (Cape Barren I.)
MV D14307–11.

Population 7 (Flinders I.)
MV D14675, N. Pats R., Flinders I.; D38670, D42211, NTM R6943, Flinders I.

Population 8 (Babel I.)
AM R14470–72.

Population 9 (East Sister I.)
MV D12275, D42518.

Population 10 (West Sister I.)
MV D12276–77, D13857, D14312.

Population 11 (Deal I.)
MV D39108, 1.6km E East Cove, Deal I.; D39109, D42212, D42508–09, D44885, Deal I.

Population 12 (Hogan I.)
MV D42482–90, D42493, D42501–07.

Population 13 (Hunter I.)
QVM 1973/3/28–29, SAM R3674.

Population 14 (King I.)
AM R8012, R42168, MV D2618, D38659–62, King I.; QVM 1968/3/4, Pegarah Forestry Reserve.

Population 15 (south-west Victoria/south-east South Australia)
AM R41273, Portland, Vic.; AM R66114, NTM R290, R1097, SAM R1801, Mt Gambier, SA; AM R92696–97, tip at Pt MacDonnell, SA; MV D14677, Marp, Vic.; MV D14736–39, Johnstone's Ck, Kentbruck Heath, Vic.; D17809, Casterton rd, 51km N Portland, Vic.; D17825–26, Pines rd, 2.4km SW Hotspur, Vic.; D17827, 3 Waterholes rd, 0.8km E Portland-Hamilton rd, Vic.; D17979, South Portland, Vic.; D39104, Mt Richmond National Park, Vic.; D39105, Bats Ridge Wildlife Refuge, nr Portland, Vic.; D39111–12, 9.7km NE Nelson, Vic.; D55005–06, Alcoa site, Portland, Vic.; QM J20208, Tyrendarra, nr Portland, Vic.; SAM R2748, Robe, SA; R3205, Nelson, Vic.; R3654, Kalangadoo, SA; R4081, 10mi W Lucindale, SA; R13010, 38°01'S 140°35'E, SA; R13042, 37°46'S 140°42'E, SA; R13043, 37°48'S 140°47'E, SA; R17014, Canunda National Park, SA; R23102, Bool Lagoon Reserve, SA; R23103, “Tuckers Land”, W boundary of Bool Lagoon Reserve, SA; R23215, 37°40'S 140°53'E, SA; R23924, Woolwash Ck, SA; R28629, 37°22'S 140°45'E, nr Penola, SA.

Population 16 (Otway Ranges and hinterland, Victoria)
MV R13817, Torquay; D2824, Lorne; D8115, Blanket Bay; D12233, Gellibrand; D12234, Johanna turnoff, Lavers Hill; D12357, Gellibrand R. (Yaugher 21A); D33044–45, Echlin

South; D38667, Anglesea; D39095–97, Naringal East; D39113, Broken Head, 8km ESE Pt Campbell.

Population 17 (Melbourne district, Victoria)
AM R66111, Melbourne; MV D592, D1045–46, Macedon; D622, Lilydale; D890, Dandenong; D974, Yarra Junction; D1028, D38701, Oakleigh; D1504, D3464, Ringwood; D2985, nr Melbourne; D4360, Mordialloc; D18258, Gisborne; D33008, 6.4km E No. 1 camp, Mt Disappointment; D33031–35, Wallan; D33039, D40028–29, East Warburton; D33041, 9.6km S Glenburn; D38663–64, The Basin; D38666, Montrose; D55079, Bonbeach; D55353, 5km SSE Yellingbo Ck on Cockatoo Ck.

Population 18 (Westernport Bay islands)
MV D33038, Ventron Rd, Phillip I.; D33043, Causeway Rd, French I.; D38669, Smiths Beach, Phillip I.; D49365, D59482, French I.; D52599, D52697, Quail I.

Population 19 (south Gippsland, Victoria)
AM R106903, R111498–502, The Gurdies, 0.5km E on Woodleigh rd from turnoff on Bass Hwy; MV D5699, Flinders; D16582, D52698, Tooradinn; D17992, 0.8km N Rye Ocean Beach; D33040, Shoreham; D33289, St Kilda Junction, Wilsons Promontory; D38668, D50946, Tidal R.; D38671, 4km N Tidal R.; D38672, 11.3km N Darby R.; D38673, D38787, 19.3km N Darby R.; D38674, 27.4km NW Korumburra; D38700, DT-D1251, Shady Ck, nr Warragul; D39110, 1.6km E Wonthaggi; D40200, Waratah Bay; D47299, 14km ESE Carrajung; D47663–64, Point Smythe; D48738, 2.2km WSW Blackwarry; D48739, 4km SE Balook; D48965, 3km W Seaspray; D50947, Cape Liptrap; D51315, 0.5km S Mt Tanjil; D55187, Gelliondale; D56443, Tarwin.

Population 20 (Omeo district, Victoria)
MV D38786, Omeo; D40018–22, D40024–25, Omeo-Hotham-Tongio West junction; D40023, D40026–27, Kalorama.

Population 21 (Victorian highlands)
MV D7868, D7929, Gelantipy; D12018, Howqua Hills; D12021, Eildon; D17165, Whitfield; D17298, Escreets Rd, S of Mt Buggaree; D17304–05, Shelley Forestry Camp; D17333, Burrowye Rd, between Burrowye Ck and Pines Track; D17336, Pines Track, Koetong Forestry Commission Pine Plantation; D17416, Spring Ck Track, Blue Range Forestry Commission Pine Plantation; D17417, Old Tolmie Rd, Blue Range Forestry Commission Pine Plantation; D17501, Tiger Hill, nr Tatong; D33007, 11.3km SW Bonang; D33046, Dandongadale; D33047, Suggan Buggan; D33287, 3.2km NW Harrietville; D38665, Frys, Howqua R.; D40285, Dargo High Plains rd, 1.4mi S Pattys Track; D40991, 5km N Omeo; D41399, 6km SSE junction of Gibbo and Mitta Mitta Rivers; D41634, 2km SSE junction of Mitta Mitta R. and Toakes Ck; D41716, 3.2km N new Dartmouth; D42116, 1km W Mt Murphy mining camp; D42130, Tom Groggin Track, 3km NE Buenba Hut; D47536, 1.5km N Fantail Falls; D48559, Mt Cobberas; D59515, Cravensville Track, SSE Corryong; D60868, 1.5km E junction Chapmans and Stems Roads, Boho, Strathbogie Range.

Population 22 (Snowy Mtns, NSW)
AM R59904, 4mi from Hotel Kosciusko on Jindabyne rd; R96196, 36km NW Cooma on Snowy Mtns Hwy; R102853, Khancoban; ANWC R180, Kosciusko; MV D33048, D39107, Illawong Peninsula, Lake Eucumbene, 4mi W Adaminaby; D33049, Adaminaby.

Population 23 (Monaro tablelands, NSW)
AM R17094, Bombala; R70430, Bondi Forest Rd, Bondi State Forest; R95500–01, R99300, Bombala tip; R96321, 17.2km N Nimmitabel; R96322, 1.5km SE Bibbenluke; R96585, intersection of Snowy Mtns and Monaro Highways, 42km N Bombala; R96586, ca4km S

Bombala on Cann Valley Hwy; R97905, 1.7km E Bibbenluke on Cathcart rd; R98006, 2km N Bondi Work Camp, Bondi State Forest; R99301–02, between Cathcart and Bibbenluke; ANWC R611, 2mi S Nimmitabel; R1223, ca7mi S Nimmitabel; R2868, Captains Flat; R3599, Coolumbooka, 15km E Bombala; MV D11219, Bondo; D33036, 1mi W Bobundara.

Population 24 (South-West Slopes, NSW)
AM R42165–67, Batlow; ANWC R229, Lob's Hole, Tumut R.; R2869, Albury.

Population 25 (Blue Mountains region, NSW)
AM R3892–93, R10062, MV D7866, Blackheath; AM R8263, R26255, R27496, R33137, Oberon; R14392, Hampton; R28494, Wiseman's Ck, Oberon; R33202, Kanangra Walls; R59905, 10mi N Abercrombie R. on Porters Retreat rd; R59906, 3mi from Edith on Jenolan Caves rd; R66109, NTM R1117, Katoomba; AM R66110, R66112, Wentworth Falls; R66113, Mt Boyce; R66119, Lithgow district; R76878, ca7mi N Lithgow on Prison Farm rd; R80087, Site U14, Newnes Plateau; R97935, Bell; R98375, ca9km E Laggan, 29km from Taralga; R104063, Bolong Ck (trib. of Abercrombie R.), “Kiaora”, Colspie; R106743, Wentworth Falls Lake; R120949, 7.3km N Oberon on Tarana rd; MNHP 3023–24, 7134, Blue Mountains [possible syntypes of *Scincus nigroluteus*]; NTM R218, Tarana.

Not assigned to populations:
AM R3349, MV D2095, QVM 1946/3/1, 1947/3/2, SAM R28994, Tasmania; AM R11633a–b, R11634a–b, R12486, R12709, R12802, NSW; R13098, Warrawee; R69101–02, Dunedoo-Uarbry; MV D616, D1592, D3465, Victoria; D1765, “Mallee”; D2868, Big Hill; D2890–91, D3068, D4208, D4239, no locality; QVM 1972/3/204, probably north Tasmania

Chapter 7 *Tiliqua occipitalis*

7.1 Synonymy

Tiliqua occipitalis (Peters, 1864a)

Cyclodus fasciatus Lütken, C. (1863). Nogle nye Krybdyr og Padder. *Videnskabelige Meddelelser fra den Naturhistoriske Forening i Kjobenhaun* 1862(20–22): 292–311. [292]. (*non Tiliqua fasciata* Gray, 1839 = *Diploglossus fasciatus*).
Holotype: UZM R47563

Cyclodus occipitalis Peters, W. (1864a). Übersicht der von Hrn. Richard Schomburgk an das zoologische Museum eingesandten Amphibien, aus Buchsfelde bei Adelaide in Südaustralien. *Monatsberichte der Koniglichen Preussischen Akademie der Wissenschaften zu Berlin* 1863: 228–236 [231].
Holotype ZMB 4709.

7.2 Diagnosis

A moderately large *Tiliqua* (maximum SVL 320mm) with dorsal body and tail pattern of broad dark brown bands on a pale ground, a pale venter, dark temporal streak, only first supraocular contacting frontal, occipitals narrow and elongate, primary temporals present and paired, usually nine or more supralabials and 37–44 midbody scale rows.

7.3 Description

Nasals usually moderately separated (73.5%, n = 253), less commonly narrowly separated (13.4%), rarely broadly separated (0.4%) or in point (4.3%), narrow (5.5%) or moderate (2.8%) contact; supranasals absent; postnasals usually fused dorsally to nasals, separated ventrally by a postnarial suture, rarely completely distinct from nasals unilaterally (3.8%, n = 264) or bilaterally (1.5%); prefrontals usually in broad to moderate contact (45.9%, n = 255) or narrow contact (29.8%), less commonly in point contact (5.5%) or narrowly (11.4%) to moderately (7.5%) separated; an azygous median scale separating prefrontal scales seen in one specimen; supraoculars two (57.7%, n = 534) or three (41.0%), rarely four unilaterally (n = 2) or bilaterally (n = 2) or five unilaterally (n = 1), first largest and in contact with frontal, second and third (when present) successively smaller, not contacting frontal (except in four specimens having 3–5 supraoculars, when first two contacting frontal, first small); supraciliaries 4–7 ($\overline{X}$ = 5.05, sd = 0.45, n = 532), usually 5 (83.4%), with first as tall as long, dorsally bordering prefrontal and first supraocular, second low, elongate, bordering first supraocular, third short, low, rectangular or slightly pentagonal, bordering first and second supraoculars, fourth short, pentagonal or rectangular, weakly projecting between second and third supraoculars (or bordering second when only two present), last taller than long, bordering last supraocular and parietal; first supraciliary usually moderately to broadly separated (59.0%, n = 266) or narrowly separated (19.9%) from frontal, or in point to broad contact (21.0%); last supraciliary broadly to moderately separated from frontoparietals; frontoparietals paired, usually in broad to moderate contact (92.7%, n = 137), rarely in narrow contact (5.1%), or separated by an azygous median scale (2.2%); occipitals 2–5 ($\overline{X}$ = 3.02, sd = 0.58, n = 528), usually 3 (68.0%); median azygous occipital usually absent, rarely (n = 5) present; loreals usually two in horizontal series, rarely one unilaterally (n = 1) or three unilaterally (n = 2); rostral loreal rarely vertically paired bilaterally (n = 2); subocular ring complete; presuboculars 2–5 ($\overline{X}$ = 3.28, sd = 0.54, n = 531), usually 3 (66.3%) or 4 (29.2%); subocular usually absent (97.7%, n = 532), rarely one (2.1%) or two (0.2%) present; postsuboculars 4–6 ($\overline{X}$ = 4.61, sd = 0.58, n = 532), usually 5 (52.1%) or 4 (43.4%);

supralabials 8–11 ($\bar{x}$ = 9.62, sd = 0.65, n = 531), usually 10 (55.2%) or 9 (35.0%), antepenultimate below centre of eye; penultimate usually single, rarely (n = 1) bilaterally vertically divided; last usually vertically paired, rarely unilaterally (n = 1) or bilaterally (n = 1) divided into three scales; primary temporal usually vertically divided into a pair of scales (89.1%, n = 266), rarely divided into three unilaterally (6.8%) or bilaterally (4.1%) or into three on one side, four on the other (0.4%); upper secondary temporal single; lower secondary temporal usually divided into two scales (98.5%, n = 266), rarely to three scales unilaterally (1.1%) or bilaterally (0.4%); single fusions between temporal scales or with supralabial scales rare (1.5%, n = 266); posttemporals 2–4 ($\bar{x}$ = 2.80, sd = 0.45, n = 532), usually three (76.1%); rostral ear lobules 2–5 ($\bar{x}$ = 3.57, sd = 0.64, n = 523), usually four (50.7%) or three (41.1%); infralabials 8–13 ($\bar{x}$ = 10.55, sd = 0.86, n = 523), usually 11 (41.9%) or 10 (35.8%), caudal part of row irregularly paired; usually first two infralabials contact postmental, rarely first only unilaterally (n = 5) or bilaterally (n = 2), or first three unilaterally (n = 24) or bilaterally (n = 3).

Midbody scales 37–44 ($\bar{x}$ = 40.3, sd = 1.62, n = 267), mode = 40 (27.3%); paravertebral scales 56–75 ($\bar{x}$ = 64.8, sd = 3.51, n = 266), between axilla and groin 41–57 ($\bar{x}$ = 47.0, sd = 2.86, n = 266); ventral scales 78–104 ($\bar{x}$ = 92.5, sd = 4.66, n = 259); subcaudal scales 41–54 ($\bar{x}$ = 47.0, sd = 2.44, n = 247); lamellae below fourth toe unpaired, 7–12 ($\bar{x}$ = 9.7, sd = 0.94, n = 515), mode = 10 (38.6%).

SVL 85–320mm (n = 257); AGL/SVL 48.2–64.5% ($\bar{x}$ = 58.2%, n = 257); TL/SVL 35.4–55.6% ($\bar{x}$ = 45.4%, n = 238); FLL/SVL 16.8–31.2% ($\bar{x}$ = 21.0%, n = 256); HLL/SVL 18.4–29.1% ($\bar{x}$ = 22.3%, n = 256); Hip/SVL 9.1–12.6% ($\bar{x}$ = 10.5%, n = 256); HL/SVL 16.1–27.4% ($\bar{x}$ = 18.8%, n = 257); HW/HL 76.8–102.5% ($\bar{x}$ = 90.0%, n = 262); HD/HL 50.1–68.4% ($\bar{x}$ = 58.3%, n = 261); IOC/HL 34.2–48.2% ($\bar{x}$ = 40.7%, n = 264); E–N/HL 25.1–34.8% ($\bar{x}$ = 30.0%, n = 265); E–E/HL 38.8–50.6% ($\bar{x}$ = 46.0%, n = 265); Eye/HL 15.0–26.3% ($\bar{x}$ = 19.9%, n = 264); Ear/HL 12.4–22.8% ($\bar{x}$ = 18.5%, n = 263); IparL/HL 18.3–26.7% ($\bar{x}$ = 22.9%, n = 266); FrontL/HL 21.3–32.6% ($\bar{x}$ = 27.1%, n = 266); IparL/FrontL 65.4–107.1% ($\bar{x}$ = 84.9%, n = 266); IparW/IparL 30.9–58.9% ($\bar{x}$ = 42.6%, n = 266); FrontW/FrontL 54.3–91.1% ($\bar{x}$ = 71.2%, n = 266).

7.4 Allometry

All proportions examined showed significant allometry (Table 7.1). In most cases, allometry was negative. However, all characters relating to the caudal part of the head (HW/HL; HD/HL; E–E/HL) showed significant positive allometry, indicating that the postocular region of the head is proportionally larger in adults than juveniles. This may indicate an increase in the temporal musculature of adults. Positive allometry was also seen in AGL/SVL, TL/SVL and Hip/SVL.

7.5 Coloration (Fig. 40)

Dorsal ground cream to light brown. Head dorsum immaculate, often a little darker than body dorsum. Body dorsum with 3–8 ($\bar{x}$ = 4.6, sd = 0.81, n = 262), approximately 5–9 scale wide, mid to dark brown transverse bands, first over nape and shoulders (sometimes partially or completely divided into two narrower bands); tail dorsum with 3–6 ($\bar{x}$ = 4.2, sd =

0.61, n = 254) similar bands, usually including a dark tip to tail. Body bands extend ventrally to ventrolateral margin of body, often laterally curving more caudally and sometimes tapering slightly; tail bands often with faint continuation ventrally. Dark body bands often contain scattered single or multiple paler scales, especially medially, while pale interspaces may enclose narrower dark patches laterally, sometimes extending across back to form a second series of narrow dark bands. Often dark lateral and medial margins of pale body scales giving some indication of narrow dark stripes dorsally, from nape to at least tail base.

Face laterally with a broad, irregularly edged, dark brown to black temporal streak (often obscured in individuals with dark heads) from lateral canthus of eye, caudally to immediately above ear, covering lower half of upper secondary temporal and subsequent scales, entire upper scale of primary and lower secondary temporals and subsequent scales, all or most of lower scale of primary and lower secondary temporals and subsequent scales, usually rostrodorsal part of penultimate supralabial, and often dorsal margin of upper scale of last supralabial and subsequent scales. Generally some indication of a cranial extension of ventral margin of dark nuchal band passing towards the temporal streak.

Body and tail venter cream to light yellow, usually immaculate, or with scattered brown scales, mostly on the throat (where they may be aligned transversely) and lateral margins of the body, more common in juveniles than adults ($X_2^2 = 10.03^{**}$).

Forelimbs pale, cream, light grey or light brown dorsally, rarely with a weak darker wash; more yellow ventrally. Palmar granules and subdigital lamellae pale with dark brown to black-tipped tubercles.

Hindlimb dorsally with dorsal ground, weakly to very heavily variegated with dark brown or black, especially caudally. On thigh, dark markings may take form of bands, or be reduced to a dark patch; on calf, usually more irregular and diffuse. Plantar granules and subdigital lamellae yellow with dark brown to black tipped calli.

Iris brown or orange to greyish with an orange tinge; oral mucosa with a blue to purple tint, or pale pink; tongue dark purple-blue.

7.6 Asymmetry

Although asymmetries of head shields were common, these generally had no effect on pooled counts. No significant differences were detected between means for left and right sides (t-tests) in cases of asymmetry of supraoculars, supraciliaries, presuboculars, postsuboculars, supralabials, posttemporals or infralabials.

A significant difference between sides in mean number of occipital scales was detected in asymmetrical cases (L: $\overline{X} = 3.16$, sd = 0.70, n = 81; R: $\overline{X} = 2.83$, sd = 0.69, n = 81, $t_{160} = 3.00^{**}$), although the mode for both sides was three. A significant difference in mean number of rostral ear lobules in asymmetrical cases was also detected (L: $\overline{X} = 3.47$, sd = 0.73, n = 86; R: $\overline{X} = 3.74$, sd = 0.74, n = 86; $t_{170} = 2.39^{*}$), with mode three on the left and four on the right, although the ranges for both sides were equal.

7.7 Sexual Dimorphism

There were no significant differences between males and females in mean number of supraoculars, supraciliaries, occipitals, presuboculars, postsuboculars, supralabials, rostral ear lobules, infralabials, midbody scales, paravertebral scales, ventral scales, subcaudal

scales, subdigital lamellae or dark body or tail bands (t-tests) or in degree of separation of prefrontals, frontal from first supraciliary, or contact of frontoparietals (contingency X^2).

Significant differences were detected between sexes in three scalation characters:

a. Degree of separation of nasal scales (using categories broadly-moderately separated, narrowly separated, point contact and narrow-moderate contact, contingency $X^2_3 = 11.72^{**}$). Although the relative frequency of separated *vs* contacting nasals was almost identical between the sexes, when the nasals are in contact, they are more broadly in contact in males.

b. Mean number of posttemporals (♂♂: $\overline{X} = 2.86$, sd = 0.41, n = 234; ♀♀: $\overline{X} = 2.73$, sd = 0.48, n = 190, $t_{422} = 2.96^{**}$), although the mode is three in both sexes.

c. Mean number of paravertebral scales between axilla and groin (♂♂: range 41–57, $\overline{X} =$ 46.5, sd = 2.96, n = 118; ♀♀: range 42–54, $\overline{X} = 47.4$, sd = 2.63, n = 95; $t_{211} = 2.32^{*}$).

In the latter two cases, the magnitude of the difference is so low that it is only significant in samples of the size of the pooled sample, and does not invalidate pooling of the sexes in describing geographic variation.

There is significant sexual dimorphism in a number of morphometric characters (Tables 7.2–7.3). Females had proportionally longer bodies, shorter tails, limbs and heads (the latter possibly an artefact of the longer body), broader and deeper heads, and slightly larger eyes than males.

7.8 Distribution

Arid and semi-arid parts of southern Australia (Fig. 41). Western and southern Western Australia, from the west coast and hinterland between 145km N Carnarvon and just S of Perth (Whitby Falls), and the south coast east of 3mi E Nornalup (i.e., excluding the moist extreme south-west and Darling Range), inland to “Muggon”, 5mi N Maroubra, 14km NE Bungalbin Hill, and the Wiluna district (i.e., excluding the upper Murchison and Gascoyne drainages), east through the Hampton Tableland, Nullarbor Plain and southern and eastern Great Victoria Desert to the Gawler Ranges and Eyre Peninsula in South Australia. Possibly isolated populations in central Australia (western SA/NT border region), Yorke Peninsula and coastal Adelaide Plains, Murray Mallee of South Australia and the adjacent parts of N.S.W. and Victoria, Little Desert of Victoria and adjacent parts of South Australia, and Olary Spur of South Australia, and a probable isolate in central N.S.W. (Round Hill).

7.9 Geographic Variation

For the purposes of analysing geographic variation, the overall range of *T. occipitalis* was divided into 22 geographic subunits (Fig. 41).

One-way analysis of variance did not provide evidence of significant geographic variation in mean number of midbody scales. However, significant variation was detected in all other characters examined, as follows:

7.9.1 Supraciliaries:

ANOVA-1: $F_{21,472} = 4.052^{***}$. Means ranged from 4.7 (population 21) to 5.4 (population 5). Significant differences at the 5% level were detected between population 5 and populations 7, 16 ($\overline{X}$'s = 5.0), 8–9, 15, 17–18 ($\overline{X}$'s = 4.9), 14, 20 ($\overline{X}$'s = 4.8), 13 and 21 ($\overline{X}$'s = 4.7), although the mode was five in all populations. Apart from the high mean for population 5 (Perth), which lies on the southwestern periphery of the overall distribution, there was no suggestion of clinal or stepped variation.

7.9.2 Occipitals:

ANOVA-1: $F_{21,468} = 2.747^{***}$. Means ranged from 2.6 (populations 2, 19) to 3.3 (populations 3,5). Significant differences at the 5% level were only detected between the extremes (population 2 *vs* populations 3,4 [$\overline{X}$ = 3.2] and 5). The mode was three in all populations. Away from the west coast, population means were similar.

7.9.3 Presuboculars:

ANOVA-1: $F_{21,471} = 2.408$, $P = 0.0005^{***}$. Means ranged from 2.8 (population 14) to 3.8 (population 19). Significant differences at the 5% level were only detected between the extremes (population 14 *vs* populations 13 [$\overline{X}$ = 3.6] and 19). Most populations had modes of three, although 13 and 19 had mode four.

7.9.4 Postsuboculars:

ANOVA-1: $F_{21,472} = 3.439^{***}$. Means ranged from 4.3 (populations 1, 9) to 5.3 (population 20). Significant differences at the 5% level were mainly between three of the six highest means and four of the five lowest means (Table 7.4).

Modes varied from four to five in parallel with the means. However, no overall clinal trend was apparent, although the extreme eastern populations consistently had high means, with the highest mean in the peripheral Round Hill isolate.

7.9.5 Supralabials:

ANOVA-1: $F_{21,472} = 3.872^{***}$. Means ranged from 8.9 (population 1) to 10.0 (population 5). Significant differences at the 5% level were detected mainly between extreme values (population 1 *vs* populations 5, 18 [$\overline{X}$ = 9.9], 6 [$\overline{X}$ = 9.8], 4, 7 and 13 [$\overline{X}$'s = 9.7]; population 5 *vs* populations 14 [$\overline{X}$ = 9.1] 2, 16 and 22 [$\overline{X}$'s = 9.3]; population 18 *vs* populations 2 and 16). The two extreme means are at north and south ends of the west coast, and a clinal increase from north to south was apparent between these. Elsewhere, however, such a trend was only suggested by low means for a few northern populations. Modes for all populations were either nine or ten.

7.9.6 Posttemporals:

ANOVA-1: $F_{21,472} = 3.190^{***}$. Means ranged from 2.5 (population 9) to 3.1 (population 1). Significant differences at the 5% level were only detected between population 9 and the highest means (populations 1, 12 [$\overline{X}$ = 3.1], 3 and 22 [$\overline{X}$ = 3.0] and 4 [$\overline{X}$ = 2.9]) and between populations 1 and 17 ($\overline{X}$ = 2.6).

7.9.7 Rostral ear lobules:

ANOVA-1: $F_{21,463} = 4.276^{***}$. Means ranged from 2.8 (population 11) to 4.1 (population 19). Significant differences at the 5% level were detected between some of the 9 highest and 8 lowest means (Table 7.5), and of these, only 11 and 22 amongst adjacent populations had significantly different means. Variation was largely of a random nature, with no clear geographic trend emerging, although most central, western and southern W.A. populations had very similar means ($\overline{X}$'s = 3.4–3.6). Modes varied between three and four in parallel with the means.

7.9.8 Infralabials:

ANOVA-1: $F_{21,465} = 4.189^{***}$. Means ranged from 9.6 (population 14) to 10.9 (populations 13, 18). Significant differences at the 5% level were detected between some of the five highest and five lowest means (Table 7.6), although the only significant difference between adjoining populations was between populations 13 and 22. Population modes were either 10 or 11. South-western populations (5–8, 11, 13) have relatively high means, while central, southern and north-western populations (1–2, 9, 12, 14–17, 22) have relatively low means. However, this trend does not continue further east.

7.9.9 Paravertebral scales:

ANOVA-1: $F_{21,225} = 3.895^{***}$. Means ranged from 60.7 (population 13) to 67.5 (population 8). Significant differences at the 5% level were detected between population 13 and populations 8, 12 ($\overline{X}$ = 67.3), 11 ($\overline{X}$ = 67.0), 6 and 7 ($\overline{X}$'s = 66.9), between population 15 ($\overline{X}$ = 61.0) and populations 6–8 and 11, and between population 18 ($\overline{X}$ = 63.0) and populations 6–7 and 11. The only significant difference between adjacent populations occurred between populations 11 and 13. In general, the highest means were in south-western populations (5–8, 11–12, 22), while inland and central populations had low means.

7.9.10 Axilla-groin scales:

ANOVA-1: $F_{21,224} = 3.689^{***}$. Means ranged from 43.2 (population 15) to 49.8 (population 12). Significant differences (at the 5% level) were restricted to between extreme means (populations 13 [$\overline{X}$ = 43.6] and 15 *vs* populations 12, 8 [$\overline{X}$ = 48.8], 6 [$\overline{X}$ = 48.6], 5 [$\overline{X}$ = 48.5] and 7 [$\overline{X}$ = 48.2]). None of these differences were between adjacent populations. The pattern of variation was similar to that for paravertebral scales, with highest means in the south-west (populations 5–8, 11–12, 22) and lowest means in the interior (populations 10, 13–15).

7.9.11 Ventral scales:

ANOVA-1: $F_{21,219} = 2.919^{***}$. Means ranged from 89.0 (population 2) to 97.5 (population 7), with significant differences at the 5% level between population 7 and populations 2, 3 ($\overline{X}$ = 90.1), 4 ($\overline{X}$ = 91.9), 12 ($\overline{X}$ = 90.0), 16 ($\overline{X}$ = 92.1) and 18 ($\overline{X}$ = 92.5). Of these, only 12 is adjacent to 7. In general, the highest means were in south-western populations.

7.9.12 Subcaudal scales:

ANOVA-1: $F_{21,206} = 2.944^{***}$. Means ranged from 43.7 (population 22) to 50.3 (population 19), with the former significantly different at the 5% level to populations 19, 1 ($\overline{X}$ = 48.3), 5 ($\overline{X}$ = 48.3), 10 ($\overline{X}$ = 48.2), 7 ($\overline{X}$ = 48.1), 3 ($\overline{X}$ = 47.4), 6 ($\overline{X}$ = 47.1) and 4 ($\overline{X}$ = 46.9), although none of these populations are adjacent to population 22. No clear geographic trend is apparent, although the highest means are at the eastern and western ends of the distribution.

7.9.13 Subdigital lamellae:

ANOVA-1: $F_{21,460} = 3.082^{***}$. Means ranged from 8.7 (population 1) to 10.3 (population 18), with significant differences at the 5% level between these two, the former and populations 5, 17 ($\overline{X}$'s = 9.9), 6 ($\overline{X}$ = 9.8) and 4 ($\overline{X}$ = 9.7) and the latter and populations 9 ($\overline{X}$ = 9.2), 15 and 22 ($\overline{X}$'s = 9.3). The only broad geographic trend apparent is for low means to be concentrated in a belt from the Nullarbor northwest to Shark Bay and Carnarvon (populations 1–2, 9, 13, 15, 22).

7.9.14 Dark body bands:

ANOVA-1: $F_{21,222} = 28.172^{***}$. Means range from 3.9 (population 13) to 6.6 (population 22). Most populations have four broad dark bands between neck and tail base. However, south-western populations (3–8, 11–12, 22) show a clinal increase from north to south in number of dark bands. The extreme high value of population 22, significantly different at the 5% level to all other populations, is accompanied by irregularity of the bands, narrowing of the pale interspaces (almost absent in one individual), and in many specimens by a paling of the bands from rich brown to light grey. Of the remaining south-western populations listed above, the means for populations 5–8 and 11–12 are significantly different at the 5% level to those of populations 1–3, 9–10 and 13–21, with population 7 also different to 4. Population 4 also had a significantly different mean to populations 1–2, 9, 13 and 15–18. In addition to this cline in number of broad dark bands, most individuals in eastern populations (15–21) had additional narrow dark body bands (often reduced to lateral dark patches) interposed between the broad bands. These additional bands were not included in the band counts.

7.9.15 Dark tail bands:

ANOVA-1: $F_{21,214} = 7.391^{***}$. Means ranged from 3.3 (population 14) to 5.2 (population 22). Most populations have 3–4 broad dark bands (scoring a dark tail tip as a band), although south-western populations (3–8, 11–12) show a clinal increase in number of bands from north to south. The mean for population 22 is significantly different at the 5% level from all but populations 6–8 and 12. Populations 4–8 were significantly different to populations 13–

14 and 18, with populations 6–8 also different to 17, and 7 also different to 9–10 and 15–16. As with body bands, additional narrow dark bands between the broad bands were present only in eastern populations (15–21).

7.9.16 Other aspects of coloration:

Although not quantified, eastern populations often have a more brown dorsal ground than western populations, while the presence of irregular narrow dark stripes, due to dark margins to dorsal scales, is most commonly seen in western populations. The Nullarbor population (22) was noticeable for the common occurrence of irregular, asymmetrical dark bands.

7.9.17 Conclusions:

In summary, although significant geographic variation was present in most characters, it was generally of a minor nature and random, and gave no evidence for a division of populations into two or more groups. The potentially isolated far eastern and centralian populations did not differ in any consistent way from the main body of the distribution. Only in coloration (number of body bands and presence of narrow dark bands in the intervals) was there any suggestion of marked differentiation between populations, and even this showed pronounced clinal rather than step-wise variation. Consequently, I have not recognised subspecies in *T. occipitalis*.

7.10 Comparison with Other Species

Comparisons have already been made with *T. adelaidensis*, *T. multifasciata* and *T. nigrolutea* (Sections 4.10, 5.10, 6.10).

T. occipitalis may be readily differentiated from *T. rugosa*, *T gigas* and *T. scincoides* by the much greater number of midbody scales (37–44) and the presence of narrow, elongate occipital scales. From *T. rugosa* it is further differentiated by color pattern (both dorsal and ventral) and by having a narrow, tapering tail; a much more gracile head; smaller, smoother body scales (reflected in higher values for all counts), and more, undivided subdigital lamellae. From both *T. gigas* and *T. scincoides*, it may be further differentiated by having only the first supraocular contacting the frontal, paired primary temporals, and usually fewer supraciliaries (modally five, *vs* usually six or more).

7.11 Habits and Habitats

T. occipitalis has generally been considered a mallee habitat specialist (Bustard, 1970; Cogger, 1975, 1989b; Land Conservation Council, 1985b, 1987; Licht *et al.*, 1966; Robertson *et al.*, 1989; Schwaner *et al.*, 1985; Shea & Peterson, 1981; Specht, 1981). Most specific literature records support this assessment, with specimens being recorded from mallee/heath, shrub mallee, mallee with a *Plectrachne* or *Triodia* understory, mallee woodland, broombush-mallee mallee-*Callitris*, *Eucalyptus leptopoda* mallee, *E. oldfieldii* low woodland, *E. longicornis* open woodland and *E. transcontinentalis* mallee habitats (Arnold *et al.*, 1987; Burbidge *et al.*, 1978; Chapman & Dell, 1978, 1979, 1980a; Dell & Chapman, 1981; Dell & How, 1988; How *et al.*, 1988; Morris & Rice, 1981; Robertson *et al.*, 1989). However, there are some records from other habitats, especially in coastal or near-coastal situations (shrubland, woodland: Chapman & Dell, 1977, 1980a,b; heath on sandplain with travertine outcrops: Dell & Chapman, 1977; well-vegetated coastal dunes, sandplains, saltbush flats: Storr *et al.*, 1983; mixed scrub: White, 1982; near coastal swamps: True & Reidy, 1981; lignum swamp: Brooker & Wombey, 1978). Of 28 specimens collected in WA

wheatbelt reserves, 41% were collected in mallee, 33% in shrubland, and 13% each in woodland and heath (Chapman & Dell, 1985).

Towards the inland limits of its distribution, *T. occipitalis* also occurs in mulga (Fyfe, 1985; Storr & Harold, 1978) and other *Acacia* habitats (*A. coolgardiensis* tall shrubland: Dell & How, 1985; *Acacia resinomarginea* shrubland: Dickman *et al.*, 1991).

T. occipitalis seems to prefer sandplains and sandy loam substrates (Chapman & Dell, 1980a,b; Dell & Chapman, 1977; Dell & How, 1985, 1988; How *et al.*, 1988; Storr & Harold, 1978), but rarely sand dunes (Fyfe, 1985). Of the 28 WA wheatbelt specimens, 61% were found on sandy loams, 18% on light clays, 11% on sands, and 5% each on loams and clay loams (Chapman & Dell, 1985).

Open eucalypt habitats, including mallee heath and scrub, eucalypt woodland, wandoo woodland, wodjil/mallee/sheoak, eucalypt woodland with spinifex, *Melaleuca* or *Callitris* and mallee/*Triodia* habitats were also well represented amongst the data accompanying specimens examined for this project, with 14 records. However, a relatively large number of specimens were recorded from *Acacia* habitats, including *Acacia* scrub, shrublands and heaths, mulga/saltbush, *Acacia/Hakea* shrubland, *Acacia/Casuarina* scrub, myall over grasses, a claypan surrounded by *Acacia* scrub, and *Acacia/Callitris/Melaleuca/Casuarina* heath over dwarf scrub of *Thryptomene/Baeckea/Verticordia* (n = 13). Other specimens were recorded from open heaths and sandheaths (n = 7), myrtaceous heath (n = 1), shrublands (n = 4), shrubland with spinifex, spinifex, a *Banksia prionotes* sandplain, a tea tree thicket, jarrah/*Banksia*, woodland, *Melaleuca*/bluebush heath and mallee/*Acacia/Casuarinae* (each with one record).

All specimens for which substrate and topography were recorded were taken from flat or only slightly undulating ground, often from sandplains or sandy loams, although the colour of the sand varied from grey (n = 2), white (n = 3), white-yellow (n = 1) or yellow (n = 7), through yellow-orange (n = 1), brown-yellow (n = 1) and pink (n = 1), to red (n = 10) or brown (n = 1). Only four records were from heavier substrates, such as limestone (n = 1) or “soil” (n = 3).

In summary, *T. occipitalis* seems to prefer flat open habitats, both eucalypt and *Acacia* dominated with a reasonably dense understory, on sandy or sandy loam substrates.

While most specimens were collected on roads or in various traps, a few were taken from shelter sites. Most (n = 8) were found under tin or other rubbish, but two were found under leaf litter mats below bushes, one was under a log, and another was burnt from *Triodia*. Dell and Chapman (1979) record specimens from under *Triodia* and *Plectrachne* tussocks. A few specimens have been excavated from burrows (Kinghorn, 1924; Robinson, 1987; Wilson & Swan, 1972; data accompanying AM R98687), lending some support to Swanson's (1976) claim that the species often inhabits rabbit warrens.

7.12 Taxonomic History and Type Material

Tiliqua occipitalis was described as *Cyclodus occipitalis* by Peters (1864a) from a single specimen in a collection of reptiles and amphibians sent to Berlin by R. Schomburgk of Buchsfelde, near Adelaide in S.A. Although no precise locality for the holotype was given by Peters or Schomburgk, and only “South Australia” is recorded on the specimen bottle in Berlin, the collection presented by Schomburgk in 1863 has been presumed to be of the local fauna (Peterson & Shea, 1987).

Peters gave only a description without diagnosis or comparisons, although he recorded a number of features diagnostic of the species, including small primary temporals, four rows of occipital scales, three supraoculars with first largest, 40 midbody scales, and dorsal color pattern. The presence of narrow dark bands in the pale zones agrees with the putative South Australian origin. The presumed holotype (ZMB 4709; Figs. 42–43) has the following combination of character states: nasals moderately separated, postnarial groove present, incomplete; prefrontals in narrow contact; supraoculars three; supraciliaries five, first moderately separated from frontal, last broadly separated from frontoparietal; frontoparietals in moderate contact; occipitals three; presuboculars three; postsuboculars four; supralabials 10/9; temporals typical; posttemporals three; rostral ear lobules 3/4; infralabials ten, first two contacting postmental; midbody scales 40; paravertebral scales 66, between axilla and groin 50; ventral scales 96; subcaudal scales 47; subdigital lamellae 11/10; SVL 267mm; AGL 170mm; TL 116mm; FLL 52mm; HLL 53.5mm; HL 44.5mm; HW 42.1mm; HD 26.6mm; IOC 17.5mm; E–N 12.6mm; E–E 19.9mm; Eye 8.7mm; Ear 9.1mm; Hip 27.9mm; IparL 10.0mm; IparW 8.7mm; FrontL 11.9mm; FrontW 8.2mm. Broad dark body bands four, with narrow dark bands in interspaces; dark tail bands four.

At about the same time, Lütken (1863) described *Cyclodus fasciatus* from a single dry stuffed specimen in the Zoologisk Museum, Universitets Kobenhaven, Copenhagen (UZM), purchased from a dealer in Hamburg, giving the locality only as “Nova Hollandia”. Although I have not examined the putative holotype (UZM R47563, *vide* Cogger *et al.*, 1983), the description and illustration are thorough, the diagnosis mentioning 40 midbody scales, non-elongate temporal scales, four rows of occipitals, and brown transverse bands dorsally, five on the body, three on the tail. This combination of characters is unique to *T. occipitalis*. The number of dark body bands, the presence of narrow dark edges to the lateral margins of the dorsal body scales, and the probable lack of narrow dark bands between the broad body bands (at least, they are not mentioned in Lütken's otherwise thorough description) each suggest that the specimen came from south-west W.A., most probably from the Perth region (although other taxa described in the same paper are certainly from S.A.).

Strauch (1866) recognised both species as distinct, although, without examining specimens, apparently basing his opinion on the different number of supraocular scales (two *vide* Lütken, three *vide* Peters), and the presence of narrow dark bands between the dark dorsal bands. Both characters are now known to be variable in *T. occipitalis*, and consequently I support the synonymy of *Cyclodus fasciatus* with *T. occipitalis*.

Boulenger (1887) placed *C. fasciatus* in the synonymy of *T. occipitalis*, believing that the date of publication for both was 1863. All subsequent authors have followed Boulenger's nomenclature. Parker (1956) and Kluge (1974), however, dealing with the pygopodids described in the same two papers, recognised that Peters' paper was published in 1864, giving Lütken's description priority. This discrepancy was noted by Cogger (1983b) who preferred to maintain existing usage. However, *C. fasciatus* Lütken is, in *Tiliqua*, a junior secondary homonym of *Tiliqua fasciatus* Gray, 1831 (= *Diploglossus fasciatus* (Gray, 1831) *vide* Peters & Donoso-Barros, 1970), and consequently an unavailable name.

Two authors (Waite, 1920; McFarland & McFarland, 1977) have used the combination *Tiliqua occidentalis*, apparently in error for *T. occipitalis*, probably due to the common name Western Bluetongue often applied. In both cases the name is a *nomen nudum*.

7.13 Reproduction

7.13.1 Size at maturity:

Mature males had SVL 231–320mm, $\overline{X}$ = 265.3, sd = 16.55, n = 95, while mature females were slightly larger, with SVL 245–307mm, $\overline{X}$ = 272.7, sd = 13.20, n = 73 (Mann-Whitney U test, z = 3.28***) (Figs. 44–45). Gravid females were similar in size to other, non-gravid females (SVL 258–299mm, $\overline{X}$ = 277.2, sd = 10.54, n = 17 *vs* 245–307mm, $\overline{X}$ = 271.3, sd = 13.69, n = 56; Mann-Whitney U test, z = 1.65, P > 0.05).

7.13.2 Male reproduction:

Testis length did not increase isometrically with body size, as estimated by SVL (Fig. 44) and consequently testis length, together with a subjective estimate of testis shape, rather than a gonosomatic index, was used to infer the seasonality of reproduction.

Testis length increases slightly from January to September (Fig. 46), while between October and December, testis length decreases. Data are lacking for March, June and July, and are few for April and May. During December and January, testes are not only small, but narrow and flattened as well. Maximum size and turgidity of testes occurs in September–October, with the few records of poorly developed testes in this period being from four small October males (SVL 238–244mm), possibly attaining mature size too late to begin reproductive activity in that season.

The data suggest that spermiogenesis begins about March–April, following a summer refractory period, and increases to peak in September–October.

7.13.3 Female reproductive activity:

Between February and September, follicle diameter increases only gradually (Fig. 47). Although one May female had three grossly enlarged (20mm) follicles in one ovary, and one July female a single moderately enlarged (13mm) follicle, the other follicles in each case were only slightly enlarged. In October, very large, yolky ovarian eggs are present in many females. The first oviducal eggs appear in early November, while scaled and pigmented embryos are present in two females collected in January and February. Corpora lutea were obvious grossly in most females carrying oviducal young. The six smallest juveniles for which specific dates of collection are available have SVL = 112–129mm and were collected between 8 February and 14 May, with the smallest individual collected earliest. A wild-caught gravid female held in captivity for several months gave birth between 31 January and 3 February.

The data suggest that follicular development is slow through late summer, autumn and winter, followed by a short period of rapid vitellogenesis between September and October. Ovulation occurs in early November, and young are born in February. Chapman & Dell (1975) report a December female with oviducal eggs, while Ehmann (1973) and Wilson & Knowles (1988) state that young are born in mid to late summer and summer respectively. There is no indication that more than a single litter is produced each year.

7.13.4 Mating season:

The peak in testis size in September–October, together with the rapid follicular development in October, suggests that mating occurs in mid-spring.

7.13.5 Frequency of reproduction:

Between November and January, 4 of 7 mature females were gravid. This may indicate that reproduction is often not annual, although more data are needed to confirm this suggestion.

7.13.6 Litter size:

If the two females (mentioned above) with enlarged follicles collected outside the normal breeding season are excluded, the number of enlarged yolky ovarian follicles (≥13mm) or oviducal "eggs" or embryos in the 16 females in which they could be counted was 2–7 ($\overline{X}$ = 5.2, sd = 1.42), with mode 5 (31%). Mean litter size based on number of enlarged follicles did not differ significantly from the mean based on number of oviducal masses ($\overline{X}$ = 5.3, sd = 1.86, n = 6 *vs* $\overline{X}$ = 5.1, sd = 1.20, n = 10; t_{14} = 0.25, P > 0.05).

More follicles were generally present on the right side (in total 44 *vs* 32; R > L:R = L:R < L 9:4:2). Although the totals are not significantly different from equality (X^2_1 = 1.89, P > 0.05), the individual inequalities (9:2) are (X_1^2 = 4.45*).

Although the largest litters were seen only in the larger females, there was no significant correlation (Fig. 48) between litter size (number of follicles or oviducal masses) and maternal SVL (r = 0.087, n = 16, P > 0.05).

Litter size for *T. occipitalis* has previously been reported as 3–5 (Bustard, 1970), 4–8 (Ehmann, 1973), and 4–10, usually five (Wilson & Knowles, 1988). Specific litter sizes reported in the literature are seven (Chapman & Dell, 1975) and five (Swanson, 1976), the former record also included in the material here examined. Zoo breeding records include seven born at Melbourne Zoo in 1974 (Zoological Society of London, 1976), two at Perth Zoo in 1973 (Zoological Society of London, 1975), one at Perth Zoo in 1982, 1983 and 1989 (Main, 1982, 1983, Zoological Society of London, 1986; Slavens & Slavens, 1990), five at Perth Zoo in 1986 (Roberts, 1986), and either one (Main, 1984) or four (Zoological Society of London, 1987) at Perth Zoo in 1984, although it is not recorded whether these refer to single litters. Generally, the published data is in agreement with the data reported here.

7.13.7 Size of young at birth:

The four smallest individuals examined (SAM 2740d–g) had SVL = 85–87mm. However, the next ten smallest individuals had SVL = 107.5–115mm, this sample including a specimen with collection date 8 February 1973. A further seven specimens have SVL 117–120mm, and a further six, 122–125mm. Consequently, I infer the normal size at birth to be approximately 110mm.

7.13.8 Longevity:

The only published record of longevity for *T. occipitalis* in captivity is 7yrs 5mo (Slavens & Slavens, 1990). However, there does not seem to be any indication that the species is much shorter-lived than other large *Tiliqua*.

7.13.9 Sex ratio:

The overall adult sex ratio in the material examined was 95:75, slightly biased towards males (1.26:1), although the ratio is not significantly different to 1:1 (X^2_1 = 2.35, n.s.). Seasonal sex ratios (pooling autumn and winter, due to insufficient sample sizes) were almost significantly different to each other (summer 11:10, autumn/winter 6:10; spring 56:28; 3 x 2 contingency table, X^2_2 = 5.56, n.s.), while in the spring sample, there is a significant excess of males (X^2_1 = 9.33**).

7.14 Specimens Examined

Population 1 (Gascoyne River, WA)
SAM R2722, between Ashburton and Gascoyne Rivers; R4372, WAM R37898, R71519, Carnarvon; WAM R41226, “Callagiddy”; R51025, 14km E Carnarvon; R51709, 145km N Carnarvon.

Population 2 (Shark Bay, WA)
AM R101999, 2.7km W NW Coastal Hwy via “Coburn” track; R102736, “Tamala” tip; WAM R22759, Denham; R54985, R55011–12, “Peron” HS; R66283, “Muggon”; R96655, Zuytdorp Cliffs.

Population 3 (Geraldton region, WA)
AM R111551, Geraldton rubbish tip; WAM R16539, 5mi N Balline; R16925, R43887, Balline; R30320, 8mi W Ajana; R33769–70, llmi S Kalbarri; R33895, Red Bluff, 3mi S Kalbarri; R48279, R49907, East Yuna Nature Reserve, 30km SE Yuna; R56987–88, 35km NE Yuna; R57550, 25km NE Yuna; R57551, 31km NE Yuna; R57714, Wilroy Nature Reserve, 19km S Mullewa; R96683, Hardabut Pool.

Population 4 (Jurien region, WA)
WAM R1295, Dalwallinu; R1556, Damboring; R2158, Ballidu; R2848, Pithara; R3454, Morawa; R6548, Moora WA; R14943, cliff head, 20mi S Dongara; R16540, 30mi NE Wubin; R16541, 5mi N Maroubra; R22879, Caron; R29814, 4mi E Jurien; R30471, 6.5mi NE Jurien; R30472, 4.5mi NE Jurien; R43649–50, R44920, Buntine Nature Reserve; R48438, 5km W “Padbury” HS; R48499, R59695, Green Head; R49159, 2km E Green Head; R50990, Wongan Hills; R57817, 15km N Marchagee; R58205, 20km NE Dalwallinu; R60076, 40km W Watheroo; R68915, Badgingarra National Park; R71940, 8km S Leeman; R96613, 5km SW Darrinkobbin Hill.

Population 5 (Perth region, WA)
MV R950, R952–93, Perth; WAM R160, Osborne Park; R193, Perth (City Markets); R809, Beechboro; R1185, Whitby Falls; R1217, Carlisle; R2139, Greenmount; R2148, R3750, West Swan; R2253, Claremont; R3425, R5051, Victoria Park; R3460–61, South Perth; R8652, Armadale; R9131, R24091, Como; R13377, Upper Swan; R14942, Lancelin; R24092, Scarborough; R51558, Mussel Pool, 15km NNE Perth; R54284, Duncraig.

Population 6 (central Wheatbelt, WA)
WAM R1354, Corrigin; R14013, R16543, Wyalkatchem; R14665, Brookton; R16542,

Mukinbudin; R31515, 13mi SE Dowerin; R43451, Bendering Fauna Reserve, 5mi E Bendering; R43462, Bruce Rock; R49202, R52265, 17km NW Kellerberrin; R52177, Yorkrakine Nature Reserve; R52272, 29km N Kellerberrin; R52485, Badjaling Nature Reserve, 11km E Quairading; R52598, 8km NE Bendering; R56536, *ca*22km N Kellerberrin; R56663, *ca*25km N Kellerberrin; R71834, R71840, 20.5km 76° Toomey Hills.

Population 7 (southern Wheatbelt, WA)
WAM R994, Toolibin; R1218, Dumbleyung; R5358, Newdegate; R6351, Woodanilling; R11842, Dinninup; R28134, Mt Madden; R28147, Kuender; R30833, 25mi NNE Lake King; R40094, Tarin Rock Reserve; R43485, Lake Chinocup, nr Pingrup; R49786–89, Dongolocking Nature Reserve; R65234, 6km ENE Lake Cronin; R71187, 7.0km 287° Forrestonia crossroad; R78406, Frank Hann National Park; R93564, 15km SSW Round Top Hill.

Population 8 (Albany region, WA)
AM R105591, 0.4km E Fitzgerald River crossing; WAM R1123, Bremer Bay; R1614, Borden; R3386, Tambellup; R4526, Chorkerup; R22532, 3mi E Nornalup; R36038, Cheyne Beach; R44867, Phillips River, 16mi W Ravensthorpe.

Population 9 (northern Goldfields, WA)
AM R98687, 32.3km S Agnew via Leonora Rd; ANWC R1756, Lake Way, “Millbillillie”; R1778, “Lake Violet”, E Wiluna; R2193, between “Millbillillie” HS and Uramurdah Ck crossing; WAM R1208, Laverton; R17679, Mt Margaret Mission; R28390, Wiluna; R37786, Kathleen Valley; R39701, 14mi W Cosmo Newberry; R62774, 10.5km NW Mt Windarra.

Population 10 (central Goldfields, WA)
WAM R12999, Karonie; R58727, 2km S Queen Victoria Spring; R72652, 6.5km NE Comet Vale; R78487, 1km NE Yowie Rockhole; R86832, Kanandah; R86955, 7km E Coonana.

Population 11 (southern Goldfields, WA)
AM R102735, 18.4km S Norseman P.O. via Hwy 1; SAM R2718, R2720, Fraser Range; WAM R58074, 4km NE Jyndabinbin Rockhole; R58075, 5km E Boingaring Rocks; R81856, Norseman.

Population 12 (Esperance region, WA)
SAM R22942, Pink Lake, Esperance; WAM R9779, Esperance; R14173, Israelite Bay; R31087, 8km W Israelite Bay; R42529, Cape le Grand National Park: 1mi W Frenchman Peak; R93329, Sheoaks Hill.

Population 13 (Great Victoria Desert, WA/SA)
MV R8219, Ooldea, SA; SAM R14953, 26km W Tarcoola, SA; R15492, 35km SE Emu, SA; R15572, 87mi W Vokes Hill Corner, SA; R18577, 28°56'S 130°24'E NW Churina Native Well, SA; WAM R48988, 29°35'S 125°59'E, Plumridge Lakes area, WA; R93205, 102km NNW Forrest, WA.

Population 14 (central Australia)
MV D10993, Ernabella Mission, SA; NTM R395, 27.5mi E Ayers Rock, NT; SAM R29887, 17km NNW “Curtin Springs” HS, NT; WAM R21491, Tennant Ck area, NT [locality probably in error].

Population 15 (Gawler Range, SA)
MV D3470, Gawler Range; D39229, Iron Knob; SAM R28391, 28km NW Iron Knob; R28408, 118km ENE Minnipa; R28433, 41.3km NNE Minnipa; R28436, 45.5km NNE Minnipa.

Population 16 (southern Eyre Peninsula, SA)
AM R79765, *ca*2km SE Coffin Bay; R79766, E side Port Lincoln; R79831, Coffin Bay; R110512, R110632, Cowell area; MV D9524, Sheringa; D9525, D9533, Lock; D38652, 12mi S Arno Bay; D38653, D39227–28, Port Lincoln; SAM R6594, 12mi N Cowell; R18374, Tumby Bay; R18606, W side Sleaford Mere; WAM R27360, 17mi W Port Lincoln.

Population 17 (Yorke Peninsula and Adelaide Plains, SA)
AM R123943, Site 7, NCSSA Yorke Peninsula Vegetation Survey; MV D39230, 4mi W Warooka; SAM R2741a–b, Balhannah; R2811, Dublin; R3010, Port Parham; R13956, Port Gawler; R14307, R15906, R16344, Redcliff, 23.5km S, 7.5km E Port Augusta; R16979, 11km S Warooka on Stenhouse Bay Rd; R23925, nr Dublin; R24758, 9.2km S jcn between Warooka and Daly Hundred Rds; R24932, 20km SW Warooka; R27459, nr Sailing Club, Port Augusta; ZMB 4709, Buchsfelde, nr Adelaide (holotype of *Cyclodus occipitalis*).

Population 18 (Murray Mallee, SA/Vic/NSW)
AM R116030, 13.3mi S Bow Hill on Murray Bridge Rd, SA; R66115, MV D12725, Hattah, Vic; MV R4552, R4857, D1525, Purnong Landing, SA; R5187, Murray Bridge, SA; D745, Ouyen, Vic; D8604, Red Cliffs, Vic; D48368, Lake Boga, Vic; D56350, Hattah Lakes area, Vic; D58429, 5.7km N Round Swamp, Vic; D58556, 5km SE Mt Crozier (nr Pink Lakes State Park), Vic; D60547, D60855, 16.6km W Sunset Tank, Vic; SAM R394, Strathalbyn, SA; R2740a–g, Murray Scrub, SA; R2743, “Avoca”, Wentworth, NSW; R28529, Milang, SA.

Population 19 (Little Desert, Vic/SA)
MV D11156, 25mi NW Kaniva, Vic; D51625, 8km S Kiata, Vic; D53937, 4.7km ENE Chinaman Well, Vic; SAM R28423, Ngarkat Conservation Park, 20km S Lameroo, SA.

Population 20 (Round Hill, NSW)
AM R31797, R33284, R64780, Round Hill Nature Reserve; R32755, “Yaddra”.

Population 21 (Olary-Barrier Ranges, NSW/SA)
AM R18458, Yunta, SA; R50619, 138.5km SW Broken Hill, SA; R102737, 28.5km SW Olary, SA.

Population 22 (Nullarbor Plain-Hampton Tableland, SA/WA)
AM R59470, 70mi W Eucla, WA; R102680, 45.6km W Madura, WA; R107942, 66.6km E WA/SA border via Eyre Hwy, SA; R117689, 23.9km W Eucla via Eyre Hwy, WA; R125941, vicinity of Nullarbor Roadhouse, SA; SAM R25722, R26331, 31km NW “Nullarbor”, SA; R26273, 54.5km N “Colona” HS, SA; R26369, 62km N “Colona” HS, SA; WAM R8235, 80mi E “Balladonia”, WA; R93192, 70km SE Forrest, WA.

Examined, but not assigned to populations:
AM R81297, R101986; MV D1080, D3469, WA; R8039, Vic; NTM R5065–66, R5135–38, Bredl's Zoo [Renmark, SA]; R701–02, R980–81, R1093, Renmark [probably from Bredl's Zoo]; SAM R1096, E–W railway; R3659, Bunora, Eyre Peninsula, SA; R24933, NT.

Additional specimens not found, but listed in collection registers:
MV D1816, Western District, Victoria; D3471, Victoria; WAM R1308, Badgebup, WA; R2384, Wembley, WA; R2385, West Leederville, WA; R2821, Wickepin, WA; R3745, Mt Barker, WA; R3776, Dumbleyung, WA; R5074, Queen's Park, WA; R9134, Mullewa, WA; R9494, Lake Matilda, WA; R10493, Kalgoorlie, WA; R12221, 7mi S Cunderdin, WA; R12841, Jurien Bay, WA; R13961, East Manning Park, WA; R19849, Dongara, WA; R22252, Lake Arrowsmith, WA; R27740–41, Contine, WA; R29815, 7mi E Jurien, WA; R49784–85, Dongolocking Nature Reserve, WA; R54396–97, Jurien, WA; R73089, 23km NNW

Carnarvon, WA; R73216, 1km 45° Yowie Rockhole, WA; R76207, 14km NE Bungalbin Hill, WA.

Chapter 8 *Tiliqua rugosa*

8.1 Introduction

T. rugosa is the most distinctive and readily identifiable of the *Tiliqua* species. The grossly enlarged, often irregular, dorsal body scales and the short, blunt tail are unique amongst skinks.

Analysis of geographic variation in *Tiliqua rugosa* revealed the existence of several discrete subspecies, as had been suggested by previous authors (Mertens, 1958a; Cogger, 1979a; Bamford, 1980; Joger *et al.*, 1986; see Chapter 1) and confirmed the distinctiveness of *T. r. konowi*, the Rottnest I. subspecies described by Mertens (1958a). Consequently, in this chapter, results of the analysis of geographic variation precede the formal description of these subspecies.

8.2 Geographic Variation

For the purposes of analysing geographic variation, the overall range of *T. rugosa* was divided into 56 geographic subunits (Fig. 49), numbered approximately from north-east to north-west. Populations 19–21, 24–28, 40–41, 47–48 and 53–55 are insular (respectively Troubridge, Wardang, Weerona, Reevesby, Duffield, Spilsby, Flinders, St Peters, North Twin Peaks + Salisbury + Middle, Mondrain, Garden, Rottnest, Dirk Hartog, Dorre and Bernier Is. Three of the Archipelago of the Recherche islands (North Twin Peaks, Salisbury and Middle Is.) were pooled into a single unit because each was represented by only a single specimen. All populations are considered natural, with the possible exception of the population on Troubridge I., as that island has only reformed within the last 89 years following complete destruction by an earthquake (Sarre *et al.*, 1990).

8.2.1 Univariate Analyses

8.2.1.1 Nasals:

Most populations of *T. rugosa* had the nasals modally separated, with frequencies of contacting nasals less than 10% (populations 1–23, 25–34, 36–50). Two further populations, 24 and 35, had slightly higher frequencies of contacting nasals (20.0–25.0%). In the latter case, this was due to three individuals with the nasals in only point contact.

In contrast, the five north-westernmost populations (52–56) had the nasals modally in contact (frequencies of contact 63.6–75.0%). The intervening population, 51, had a moderately elevated frequency of contact (34.6%). The overall frequency of contact for populations 52–56 was significantly greater than for both populations 1–50 pooled (2x2 contingency table; $X^2_1 = 370.4^{***}$) and population 51 ($X^2_1 = 8.23^{**}$), while the frequency for population 51 was in turn significantly greater than for populations 1–50 pooled ($X^2_1 = 68.5^{***}$), but not significantly different from the next greatest frequency (population 35; $X^2_1 = 0.36$, n.s.).

8.2.1.2 Supraoculars:

Two geographically discrete groups of populations were evident, although there was some variation between populations within each group. Most eastern Australian populations (1–28), west to Eyre Peninsula and its associated islands, modally had two supraoculars with the first only contacting the frontal, with this condition occurring in over 50% of cases. The next most common configuration was three supraoculars with only the first contacting the frontal. There were only two exceptions to this pattern in the east. The Reevesby I.

population (24) had only 23.5% of cases with the 2(1) configuration, and even fewer of the 3(1) pattern, due to a high frequency (44.1%, n = 34) of three supraoculars with the first two contacting the frontal. Elsewhere, the 3(2) configuration was rare, occurring in only 2.6% (n = 2049) of cases. The other exception was population 12, where the 3(1) pattern was slightly more common than the 2(1) pattern (52.8%, n = 36).

In contrast, western populations (29–56) had very low frequencies of the 2(1) configuration (0–50.0%), with only populations 35 (40.9%, n = 22), 38 (44.4%, n = 18) and 41 (50.0%, n = 14) having a frequency of over 23%. Indeed, in 16 populations, the frequency was below 10%.

Overall, the frequency of the 2(1) pattern was significantly different between the eastern and western groups ($X^2_1 = 692.1^{***}$), and also between the two nearest populations of the two groups, 22 and 29 ($X^2 = 17.7^{***}$).

8.2.1.3 Supraciliaries:

(ANOVA-1: $F_{54,1957} = 6.333^{***}$). Means ranged from 4.6 (population 3) to 6.1 (populations 24, 27, 30, 32, 35, 52), with most (80.0%, n = 55) in the range 5.4–6.1. Mode was usually 6 (76.4%, n = 55 populations). Low means (and corresponding modes of 5) were mostly confined to the north-east of the mainland distribution (population 1–6, 8, $\overline{X}$'s = 4.6–5.4) and to some islands (populations 19, 28, 40+41, 54, $\overline{X}$'s = 5.0–5.3). Significant differences between populations were few (Table 8.1), and the only significant difference involving adjacent populations between 3 and 7.

8.2.1.4 Degree of separation of frontal and first supraciliary:

Data were unavailable for two populations (41, 45). In most eastern Australian (1–34, 36–37) and southern western (42–44, 46–47) populations, the frontal was usually moderately to broadly separated from the first supraciliary. In these populations, the frequency of narrower separation or even contact between the two scales either unilaterally or bilaterally was generally less than 10%, although in a few populations (7, 23, 30, 36, 42–43) it was a little higher (14.3–25.0%). In one insular population (27), the scales were in contact in two of the four cases, although this character state was not seen in any specimen from the other seven islands off the South Australian coast.

In contrast, most central and northern Western Australian populations (35, 38–40, 48–54) had much greater frequencies of narrow separation or contact between the two scales (38.5–100.0%), although sample sizes are much smaller, as this character was only scored late in the study. The only exception to this pattern was in the extreme north (populations 55–56), where the two scales were separated in five of six cases.

Overall, the eastern and western groups differed significantly in the frequency of approach (narrow separation) or contact of the two scales (pooled populations 1–34, 36–37 *vs* 35, 38–54; $X^2_1 = 221.5^{***}$), as did the three nearest east and west populations pooled (34, 36–37 *vs* 35, 38–39; $X^2_1 = 8.40^{***}$).

8.2.1.5 Division of frontal:

The frontal may be either a single scale, as in other *Tiliqua*, or the more caudal portion may be separate, and often enlarged. In eastern mainland populations (1–18, 23), the frequency of divided frontals was 25.3% (n = 454), with the frequency within those populations represented by 10 or more specimens ranging from 7.1% (population 6) to 50.0% (population 16). Central mainland populations (22, 29–34) had much greater frequencies of division (overall 51.2%, n = 166; population frequencies 26.7–66.7%, only population 31 lower than 45.5%). In contrast, divided frontals were rare in western populations. On the south-western mainland (populations 37–39, 42–46, 49), they were present in only 5.2% of individuals (n = 213), with no population sample containing more than two cases, while in the north-west (populations 50–56), no divided frontals were found (n = 106). Populations 35–36, located between the high frequency central populations and low frequency western populations, had intermediate frequencies of divided frontals (16.7%, n = 12; 25.0%, n = 8 respectively).

The frequencies of divided frontals in each of these four groups were significantly different to the next group (eastern *vs* central: $X^2_1 = 37.4^{***}$; central *vs* south-west: $X^2_1 = 104.8^{***}$; south-west *vs* north-west: $X^2_1 = 5.78^{*}$).

Insular populations generally had higher frequencies of divided frontals than mainland populations, with the values for populations 19–21, 24–28, 40+41 and 47–48 from 25.0% (pooled populations 40+41) to 87.5% (population 26).

8.2.1.6 Occipitals:

ANOVA-1: $F_{50,1672} = 2.037^{***}$. Because of the absence of data for populations 40–41 and 45, these populations were not included in this analysis, while populations 53–54 were pooled because of small samples for this character. Means ranged from 1.8 (population 26) to 2.4 (populations 5, 24, 36), with mode consistently 2. The only significant differences between pairs of populations involved population 26 and populations 8, 10, 11, 15–16, 22, 24, 29, 36 and 48 ($\overline{X}$'s 2.1–2.4) and populations 13 ($\overline{X}$ = 2.0) and 24, none of these pairs geographically adjoining.

8.2.1.7 Presence of median occipital:

A median occipital was modally present in all populations except Rottnest I. In most populations (n = 36), it was present in over 80% of individuals. Lower frequencies were observed in four main areas: a band across south-eastern Qld, central NSW and eastern SA (populations 2, 5, 7–8, 10, 16; frequencies 72.7–78.1%); southern Eyre Peninsula and some of the adjacent islands (populations 23–25, 27; frequencies 80.0–58.8%); a band across southern WA from the southern Goldfields to the Esperance region (populations 35, 37, 39; 75.0–63.6%), and another band along the lower west coast and hinterland (populations 44, 46, 50; 76.5–64.1%). In addition, two Nullarbor populations (31, 33) had lower frequencies (78.6–73.3%). Rottnest I. material, on the other hand, usually lacked a median occipital (frequency of presence 34.5%), in contrast to the adjacent Garden I. population, where both individuals examined had a median occipital. The frequency of presence of a median occipital on Rottnest I. was significantly different from both the remaining populations pooled (2x2 contingency table, $X^2_1 = 86.5^{***}$) and from the adjacent mainland (population 46; $X^2_1 = 8.21^{**}$). In contrast, the population with the next lowest frequency (Reevesby I., 58.8%) was not significantly different to the adjacent mainland (population 23; $X^2_1 = 1.44$, n.s.).

8.2.1.8 Presuboculars:

ANOVA-1: $F_{55,2174} = 4.926^{***}$. Means ranged from 2.7 (populations 1, 56) to 3.9 (population 24), with most (76.8%) in the range 2.9–3.4, and mode 3. Means of 3.4 or above were mostly confined to islands (populations 21, 24, 26, 28, 41, 53), and to a band of mainland populations from southwestern Victoria, through Adelaide and Yorke Peninsula, north to the Birdsville area (populations 12, 14–18). The three lowest means were on peripheral populations and an island (population 47). Although there were few significant differences between pairs of populations (Table 8.2), the Reevesby I. population (24) had a higher mean than most, including the adjacent mainland, and significant differences were also detected on the mainland between population 11 and two populations (15, 16) to the west.

8.2.1.9 Suboculars:

ANOVA-1: $F_{55,2179} = 3.618^{***}$. Means ranged from 0 (populations 17, 24, 26, 28) to 1.0 (population 19), with most (75.0%) in the range 0.3–0.6. Low means were restricted to islands (Reevesby, Spilsby, St Peters, Rottnest, $\overline{X}$'s = 0.0–0.2) and the NSW/SA/Qld border area (populations 8, 16–17, $\overline{X}$'s = 0.0–0.2). The highest mean was also from an island (Troubridge I.), while other high means were present in the extreme north-east (populations 1, 4, $\overline{X}$'s = 0.8), the extreme north-west and adjacent islands (populations 53–54, 56, $\overline{X}$'s = 0.6–0.7), the Esperance region (population 39), and Garden I. (population 47, $\overline{X}$ = 0.8), despite the latter's proximity to Rottnest I. Significant differences were detected between only a few pairs of populations (Table 8.3), none being between adjacent populations.

8.2.1.10 Postsuboculars:

ANOVA-1: $F_{55,2180} = 4.486^{***}$. Means ranged from 3.5 (population 19) to 5.0 (population 53), with most (76.8%) in the range 3.9–4.4, with mode 4. Of the 13 populations with means outside this range, most (n = 10) are insular, eight of these with high means (populations 20, 21, 24, 28, 41, 47, 53, 54, $\overline{X}$'s = 4.5–5.0), the other two (19, 40) with low means. The remaining three mainland populations had means either slightly higher than usual (14, 17; $\overline{X}$ = 4.5) or lower than usual (38, $\overline{X}$ = 3.6). Significant differences between pairs of populations were few, and mostly involve extreme values (populations 24, 38, 53–54; Table 8.4). Only Reevesby I. (population 24) was significantly different to adjacent populations (23, 25).

8.2.1.11 Supralabials:

ANOVA-1: $F_{54,2170} = 4.496^{***}$. Means ranged from 8.0 (population 19) to 9.5 (population 53), with most (76.4%) in the range 8.6–9.1, and with mode 9. Of the twelve populations with means outside this range, eight are insular, five with higher means (populations 24, 26, 47, 53, 55, $\overline{X}$'s = 9.3–9.5), three with lower means (populations 19, 21, 48, $\overline{X}$'s = 8.0–8.5). Of the remaining four mainland populations, three from the extreme north-east of the distribution (1, 3, 5) had low means ($\overline{X}$'s = 8.2–8.4) while the other (population 17), with a high mean ($\overline{X}$ = 9.3), is also peripheral. Significant differences between pairs of populations mostly involved these extreme values (Table 8.5) with only Rottnest I. (population 48) and

Troubridge I. (population 19) having significant differences from adjacent populations (mainland populations 46 and 18 respectively).

8.2.1.12 Infralabials:

ANOVA-1: $F_{54,2175} = 6.859^{***}$. Means ranged from 8.2 (populations 1, 19) to 10.0 (populations 28, 53), although most (70.9%) were in the range 8.7–9.3, with mode 9. Outside that range were five populations from the extreme north-east of the mainland distribution, with low means (populations 1–3, 6–7, $\overline{X}$'s = 8.2–8.6), four of the five populations from the extreme north-west of the distribution, all with high means (populations 52–53, 55–56, $\overline{X}$'s = 9.6–10.0), the two lower west coast populations (46, 50, $\overline{X}$ = 9.6), and five insular populations from the south coast, four with high means (populations 24, 25, 28, 40+41, $\overline{X}$'s = 9.4–10.0), the other (population 19) with a low mean. Although significant differences were detected between a number of the extreme means (Table 8.6), none were between adjacent populations.

8.2.1.13 Posttemporals:

ANOVA-1: $F_{50,1693} = 10.681^{***}$. No data were available for populations 40, 41 and 45, while the data for populations 53–55 were pooled because of small samples. Means ranged from 2.0 (populations 35, 38, 47) to 3.5 (population 52), although most (62.7%) were in the range 2.2–2.7. A number of significant differences were detected between pairs of populations (Table 8.7), with obvious geographic trends.

North-western populations (50–56, $\overline{X}$'s = 2.8–3.5) had generally high means, with significant differences at the 5% level between most (90%, n = 10) of these populations and the two nearest populations (46, 49, $\overline{X}$'s = 2.1–2.3). Elsewhere, means were generally higher in the east than in the west. In eastern Australia, the highest means were in western NSW (populations 4, 6–8, 10–11, $\overline{X}$'s = 2.7–3.0), with significant differences between populations 10–11 and 12–13 to the south. The four lowest means in the east were for insular populations (19, 21, 25, 28, $\overline{X}$'s = 2.1–2.3).

In western Australia, excluding the north-western populations, means were higher in the south-west (populations 39, 42–44, $\overline{X}$'s = 2.7–2.8) than to the north and east (populations 32–38, 46–48, $\overline{X}$'s = 2.0–2.4), although the only significant difference between adjacent populations was between populations 38 and 39.

Although geographically situated between the eastern and western groups, populations 30–31 had high means (2.9), significantly different to populations 32 to the west, and a little higher than population 29 to the east.

8.2.1.14 Midbody scales:

ANOVA-1: $F_{54,1059} = 58.090^{***}$. Because of the small sample size for population 40, this population was pooled with population 41. Means ranged from 20.8 (population 1) to 31.8 (population 54). The general trend was for means to increase from east to north-west. However, two disjunctions were apparent on the mainland, giving three largely discrete

groups of populations. Eastern Australian populations (1–23, 27, 29–34) had low means ($\overline{X}$'s = 20.8–22.9), south-western populations (38–46, 49–51) had higher means (23.7–25.7), while north-western populations (52–56) had noticeably higher means (27.7–31.8). Within the eastern Australian group, only two pairs of means (23 and 31 *vs* 11) were significantly different at the 5% level, neither pair involving adjacent populations. The south-western group was similarly homogenous, with only population 44 significantly different to any other populations (50–51), both geographically distant. The north-western group was less homogeneous, with the three insular populations (53–55) having significantly, higher means than the two mainland populations (Table 8.8).

Three populations (35–37) between the eastern and south-western groups had intermediate means ($\overline{X}$'s = 22.9–23.4). With the exception of these populations, most (83.9%, n = 330) pairwise comparisons of populations between the two groups were significant (Table 8.9). Similarly, most (97.2%, n = 250) pairwise comparisons between the five northwestern populations and all other populations were significant (Table 8.8), including all comparisons involving the nearest population (51) to the south.

Off southern Australia, four insular populations (Reevesby, Spilsby, Duffield, St Peters Is., populations 24–26, 28, $\overline{X}$'s = 24.2–25.7) had higher means than most other eastern mainland populations (Table 8.10), including the adjacent mainland (populations 22–23). Similarly, off the west coast, Rottnest and Garden Is. (populations 47–48) had noticeably higher means ($\overline{X}$'s = 26.2–27.0) than south-eastern mainland populations, with significant differences between Rottnest I. and many other south-western mainland populations (38–39, 42–46, 49).

8.2.1.15 Paravertebral scales:

ANOVA-1: $F_{54,994} = 28.775^{***}$. Because of the small sample for population 40, this population was pooled with population 41. Means ranged from 21.9 (population 9) to 33.0 (population 55). As with midbody scales, the general pattern of geographic variation was for higher means in the west than the east, with disjunctions providing three major geographic groups: eastern (populations 1–23, 27, 29–34), with mostly low means; south-western (37–39, 42–46, 49–51), with slightly higher means, and north-western (52–56), with very high means.

Within the eastern group, means were less homogeneous than was the case for midbody scales, with a trend for higher means in the south. Most north-eastern populations (1–11, 16) had low means ($\overline{X}$'s = 22.2–23.1), while most southern mainland populations (12–15, 18, 22–23, 29) had higher means ($\overline{X}$'s = 23.6–24.6). Further west, means were again low (populations 31–34, $\overline{X}$'s = 22.1–22.9). Island populations off the south coast were more variable than the mainland populations, most with either higher (Wardang, $\overline{X}$ = 25.2; St Peters, $\overline{X}$ = 26.0; Sir Joseph Banks Group (Reevesby, Spilsby, Duffield), $\overline{X}$'s = 27.8–28.6) or lower (Troubridge, $\overline{X}$ = 22.3; Weerona, $\overline{X}$ = 23.5) means than adjacent populations. Despite this variation, and the number of significantly different pairs of means within eastern Australia (Table 8.11), the only significant differences between adjacent populations were for the three Sir Joseph Banks islands and the adjacent mainland (population 23).

Within the south-western group, there was much less variation between populations, with no significant differences between means on the mainland. The three offshore island populations, Archipelago of the Recherche, Garden and Rottnest, all had higher means than

any of the south-west mainland populations, with a significant difference at the 5% level between Rottnest I. and populations 37–39, 43–46, 49 and 51, and between the Archipelago of the Recherche and population 37.

The north-west group was similarly fairly homogeneous, with the only significant difference at the 5% level between the two extreme means (populations 55 and 56), although again, the three highest means were for the insular populations.

The populations in the north-west group all had significantly different means than all but one of the other mainland populations (Table 8.12), while 44.7% of pairwise comparisons between populations in the south-western and eastern groups were significantly different (Table 8.13).

8.2.1.16 Axilla-groin scales:

ANOVA-1: $F_{54,992} = 25.854^{***}$. Because of the small sample for population 40, this population was pooled with population 41. Means ranged from 14.5 (population 4) to 23.6 (population 55).

Geographic variation largely paralleled that for paravertebral scales, with an east to north-west increase in means, three more-or-less discrete groups on the mainland, and a trend for insular populations to have higher means than adjacent mainland populations.

As with paravertebral scales, the highest means in the eastern group were in the south, from Victoria across to Eyre Peninsula. While there were several significant differences between pairs of populations in eastern Australia (Table 8.14), mostly involving island populations, the only significant differences involving geographically adjacent populations were between Duffield and Spilsby Is. in the Sir Joseph Banks group, and the adjacent mainland (population 23).

Within the south-western group, the only population significantly different to others was the Rottnest I. population ($\overline{X}$ = 19.0) with significant differences at the 5% level between this population and populations 35, 37–39, 43–46 and 51 ($\overline{X}$'s = 16.8–17.6). While the mean for Garden I. was even greater than that for Rottnest I., the small sample size precluded significant differences.

Within the north-western group, the highest mean (Bernier I.) was significantly greater at the 5% level than the three lowest means (populations 52–53, 56).

In pairwise comparisons, 47.8% of the 312 possible pairs of east *vs* south-west mainland populations were significantly different, with the proportion only slightly lower (41.6%, n = 510) when insular populations were included (Table 8.15).

The north-west populations were even more distinct from other populations. If insular populations from elsewhere in the range are excluded from comparison (because of the general trend for higher means in these populations, and the usually small sample sizes), 89.7% of the 195 possible pairwise comparisons between north-western and other populations were significant (Table 8.16).

8.2.1.17 Ventral scales:

ANOVA-1: $F_{54,979} = 12.191^{***}$. The sample for population 40 was pooled with population 41. Means ranged from 57.4 (population 31) to 75.7 (population 54). In general insular populations had higher means than on the mainland, with the six highest means recorded from islands (Garden, Duffield, Spilsby, St Peters, Bernier and Dorre Is, in order of increasing mean). If islands are excluded, means ranged from 57.4 to 68.0 (population 17). On the mainland, the lowest means were on the Nullarbor Plain and hinterland (populations 30–34, $\overline{X}$'s = 57.4–60.5), while populations to the west had generally higher means than populations to the east.

The six island populations with high means (Table 8.17) and the five Nullarbor populations with low means (Table 8.18) were involved in most of the significant differences between pairs of means, with the only significant differences between adjoining populations involving island populations (24 and 26 *vs* 23; 24 *vs* 25–26; 28 *vs* 22; 54 *vs* 52). Curiously, while Duffield and Spilsby Is. in the Sir Joseph Banks group had high means ($\overline{X}$'s = 70.8–71.1) with Spilsby significantly higher than the mainland, Reevesby I. in the same group had an unusually low mean ($\overline{X}$ = 60.2), significantly lower than the other two islands, and the mainland. Significant differences between other pairs of populations (Table 8.19) were few.

8.2.1.18 Subcaudals:

ANOVA-1: $F_{54,895} = 66.847^{***}$. The small sample for population 40 was pooled with population 41. Means ranged from 12.3 (population 31) to 21.5 (population 47). Two largely discrete geographic groups of population means were apparent: eastern Australia (populations 1–34) and western Australia (populations 35, 37–56), with only population 36 intermediate between the two groups. Most (96.9%, n = 700) pairwise comparisons of populations between the two groups were significant (Table 8.20).

Within each group, there was little variation (Tables 8.21–8.22). None of the few significant differences between populations within groups involved geographically proximate populations.

8.2.1.20 Subdigital lamellae:

ANOVA-1: $F_{55,1958} = 11.448^{***}$. Means ranged from 5.2 (population 3) to 7.8 (population 47). Two partially discrete geographic groups were apparent. Eastern Australian populations (1–34, 36) had generally low means ($\overline{X}$ = 5.2–7.2), with only four insular populations (the three Sir Joseph Banks islands and St Peters I.) having means higher than 6.1. Western populations (35, 37–56) had generally high means ($\overline{X}$'s = 6.2–7.8), again with four of the five highest means from insular populations (Dorre, Rottnest, Garden and Middle/Salisbury/North Twin Peaks).

While only 28.3% (n = 735) of the possible pairwise comparisons between eastern and western populations were significant (Table 8.23), these accounted for 73.5% of the 283 significant differences detected between all possible pairs of populations.

Further, means within each of the groups were largely homogeneous. In the eastern group, if the four insular populations with high means are excluded from consideration, only 12 significant differences were detected between pairs of populations, with only one, between

populations 10 and 12, involving adjacent populations (Table 8.24). In the western group, the only significant differences detected at the 5% level involved Garden I. (significantly different to populations 37, 42–45 and 51) and Rottnest I. (significantly different to populations 37 and 43–44).

8.2.1.21 Dorsal body coloration:

Eastern populations were mostly dark to mid brown, either uniform, or mottled with various shades of brown, and with or without sparse to dense yellow flecking or spotting (often cream in strongly formalinised specimens). Occasionally, especially in juveniles, the spots are transversely aligned in weak to moderately strong but narrow bands. Countable bands were recorded in only 6.0% (n = 500) of individuals. The dark range of coloration was modal (91.6%) for populations 1–11 and 15–29, with most of the remainder having a light brown ground colour. Although the variation within this eastern coloration group was largely continuous, there were some apparent geographic trends. The easternmost populations (7, 9–10), particularly those from higher altitudes (population 9) were modally uniform dark brown dorsally, while material from Eyre Peninsula and the adjacent offshore islands (22–28) generally had a dense yellow speckling on a dark brown ground, especially in the south.

The remaining eastern populations, from the south-east (12–14), together with a few specimens from adjoining populations, were usually either dark brown with broad uniform tan bands or tan mottling, or paler, mottled mid to light brown (70.6%, n = 85), with most of the remainder more similar to other eastern material. However, even when banded, the lighter bands were solid.

On the Nullarbor (populations 30–34), coloration was more variable, although most individuals were irregularly mottled light to mid grey-brown or yellow-brown, often with blotches or spots of darker brown or cream. Cream markings were often aligned vertebrally. In most cases, there was no regular pattern. Pale transverse bands, in some cases restricted to the vertebral region, were recorded in 33.3% (n = 90) of cases.

To the west of the Nullarbor, most western populations (35–47, 49–51) had a light to dark brown dorsal ground, often even and with an olive tint, with paler transverse bands, usually composed of narrow cream or light grey to orange variegations, although in some boldly marked specimens, these bands were solid. This description fitted 94.4% (n = 301) of specimens from this region. Of the 17 exceptions, which lacked paler bands, 64.7% were from the north-westernmost population (51) of this south-western group. Within this group, there was some variation in the intensity of coloration, Goldfields material being particularly boldly marked with a dark brown dorsal ground and bright orange paler bands, and coastal specimens generally paler, with pale markings cream or light grey.

Further to the north-west (populations 52–56), a distinctive dorsal pattern was apparent, with all material olive mid to dark brown, either uniform and immaculate, or with narrow, short yellow (cream in formalin) longitudinal streaks, occasionally transversely aligned in juveniles. The population (51) between this coloration type and the more southern coloration showed much variation, some individuals with brightly contrasting cream bands, others with an immaculate dull brown dorsal ground, occasionally with a few paler flecks. Both color patterns were seen in specimens from around the Murchison River in the north of the population's range.

The Rottnest I. population (48) had a unique dorsal color pattern. All specimens had a mid to dark olive green to grey dorsal ground, largely obscured by a fine mesh of paler grey

vermiculations. There was little or no evidence of distinct bands across the back.

8.2.1.22 Ventral body coloration:

Overall, the ventral ground coloration ranged from yellow to bluish-yellow, patterned or obscured by varying degrees of light to dark brown spots, transverse bands or longitudinal stripes, or variegated. There was marked variation in the intensity and form of the dark pigmentation, and to a lesser extent, in the pale ground color. Eastern populations (1–29) almost invariably had a yellow venter, largely or completely obscured by dark brown to black variegations, often predominantly banded or striped (98.0%, n = 559), to the point where the venter was almost completely dark brown with a few yellow spots, or even completely dark. In two south-eastern populations (9–10), the venter was modally completely dark pigmented (80.0%, n = 50).

Immediately to the west, on the Nullarbor Plain and its hinterland (populations 30–34), the dark pigmentation was greatly reduced, with most (53.2%, n = 85) having a predominantly light venter, with or without a few light brown variegations, bands or stripes. None of the specimens from these populations had the venter completely dark, while only 3.5% had the venter so darkly pigmented that only a few yellow patches were exposed.

Further west (populations 35–47, 49–51), the ventral ground was often bluish-yellow or even blue-grey, especially laterally, while the dark pigmentation was generally less than in eastern Australia, with 34.6% (n = 243) scored as having a pale venter with dark streaks or flecks, and a further 4.1% having immaculate pale venters. Even where the venter was heavily pigmented, it was more commonly with mid-brown pigmentation than with the dark brown common in eastern Australia.

The extreme north-western populations (51–56) had the ventral ground yellow, heavily clouded or mottled with olive mid-brown, often concentrated medially. Reduced pigmentation, as commonly seen in more southern populations, was not seen in this group.

The Rottnest I. population (48) invariably had a blue-grey venter, densely marked with fine dark flecks and streaks, sometimes apparently obscuring traces of coarsely variegated pattern of irregular dark stripes and bands. A similar, though less intense pattern was seen in occasional specimens from the western mainland.

8.2.1.23 Head coloration:

The coloration of the head was variable. In eastern Australia, all individuals (n = 540) in populations 1–28 had dark to mid brown heads dorsally and laterally, either evenly pigmented, mottled with different shades of brown, or occasionally flecked or spotted with yellow (5.9%). On the Nullarbor and its hinterland (populations 29–33, n = 68), most individuals also had brown mottled heads, although there was a strong tendency for the pigmentation to be reduced to light brown with large irregular darker brown blotches and spots. In 20.6% of cases, this was carried to the point where the head was best described as yellow with a light brown mottle, although the head was always concolorous with the body dorsum.

In populations further west, there was a general trend for the head to be lighter than the body, often a different color, and usually immaculate rather than mottled. At a minimum, this was expressed as slightly paler temples, while at the most the entire face and head dorsum were immaculate cream-yellow to bright orange. For populations 35, 37–38, 40–47, 49 and

51, the frequency of dark brown or brown mottled heads was consistently lower than 15%, while overall, pale temples, faces or heads were recorded for 95.0% (n = 222) of individuals in these populations.

Populations 34, 36, 39 and 50 had a rather higher frequency of brown heads (54.5%, 25.0%, 31.6% and 37.5% respectively), although only in the geographically intermediate population 34 were heads modally brown rather than pale.

The unique color pattern of the Rottnest I. population extended to the head, with all specimens having a mid to dark brown or grey-brown head, usually with a finely variegated pattern.

In the north-west (populations 52–56, n = 51), the head was again dark, but usually either an immaculate even mid olive-brown (54.9%), or with slightly paler temples (43.1%). None of the specimens from these populations had evenly pale heads. Population 51, to the immediate south of this group, also showed a trend in this direction, with most (76.2%, n = 21) specimens having only the temples pale.

8.2.1.24 Pigmentation of soles of feet:

With the exception of Troubridge I., eastern populations (1–28) modally have the soles of the feet heavily pigmevnted dark to mid brown. On Troubridge I., two specimens had yellow soles while a third had dark brown soles. In none of the other eastern populations was the frequency of dark to mid brown soles less than 77%.

Pooling the data for these populations gave an overall frequency of 92.2% (n = 549) dark soles. An additional 2.7% had soles coarsely variegated with dark brown and yellow, while only 5.1% had yellow or light brown to grey soles.

To the west (populations 30–50), with the exception of the Archipelago of the Recherche (population 40), soles were modally yellow or only lightly pigmented with brown or grey. The single specimen representing population 40 had dark soles. In none of the other populations in this group was the frequency of heavily pigmented soles greater than 18%. Pooling the data from these populations gave an overall frequency of 94.9% (n = 214) of individuals with yellow, light brown to grey or variegated brown and yellow soles, and only 5.1% dark to mid brown soles. The frequencies of dark to mid brown soles for these two groups are highly significantly different (2x2 contingency table, $X^2_1 = 533.8^{***}$).

Between these two groups, population 29 was intermediate, with 36.4% of the 11 specimens having dark brown soles.

To the north of the western group, there was apparently a higher frequency of heavily pigmented soles, although this character was only assessed for a few specimens. In populations 51 and 52, 26.9% (n = 26) had heavily pigmented soles, although only one specimen had dark brown pigmentation. Of the eight specimens from populations 53–56 for which this character was recorded, five had dark brown soles, while the other three had yellow to light grey soles.

8.2.1.24 Adult body size:

There was marked geographic variation in SVL of adult *T. rugosa*. Adult size at maturity was inferred for seven groups of populations, based on the major color patterns evident, and on

differences in maximum size apparent during data collection: 1: populations 1–11; 2: 12–14; 3: 15–29; 4: 30–34; 5: 35–47, 49–51; 6: 52–56; 7: 47. Mean adult SVL amongst these groups was greatest in the north-east (group 1: 253–351mm, $\overline{X}$ = 293.9, n = 193), progressively less in the south-east (group 2: 236–317mm, $\overline{X}$ = 282.3, n = 65) and to the immediate west (group 3: 235–324mm, $\overline{X}$ = 271.4, n = 217) and least on the Nullarbor (group 4: 220–274, $\overline{X}$ = 248.0, n = 72) and on Rottnest I. (group 7: 201–260, $\overline{X}$ = 230.2, n = 55). To the west of the Nullarbor, mean adult SVL was greater (group 5: 216–303mm, $\overline{X}$ = 261.2, n = 228), and still greater again in the extreme north-west (Group 6: 242–300mm, $\overline{X}$ = 270.0, n = 26), although not as great as in the north-east. Highly significant differences between most pairs of these groups were detected (Table 8.25), although group 6, from the extreme north-west, was similar in size to groups 2 and 3, from the south-east.

There was some indication that small adult size was a feature of several insular populations, although sufficient material was only available for Rottnest I. to test this. Of the South Australian island material, the largest Troubridge I. specimen (n = 3) had SVL = 258mm, for Wardang I. (n = 10) 265mm, for Weerona I. (n = 6) 286mm, for Reevesby I. (n = 17) 283mm, for Duffield I. (n = 8) 290mm, for Spilsby I. (n = 8), 302mm, for Flinders I. (n = 4) 279mm and for St Peters I. (n = 3) 300mm. The largest of seven Mondrain I. specimens had SVL = 229mm. In the north-west, the largest Dirk Hartog I. specimen (n = 3) had SVL = 300mm, but for Dorre I. (n = 4) only 256mm, and for Bernier I. (n = 11) only 268mm.

8.2.1.25 Loss of digit 5 on pes:

Although the absence of digits was not specifically scored during data collection, two specimens from population 30, collected on different occasions, were noted to lack any traces of the fifth digit on the pes bilaterally.

8.2.1.26 Axilla-groin length:

There was a slight trend for western populations to have shorter bodies (as expressed by the ratio AGL/SVL) than eastern populations. Of populations 1–22, most (n = 16) had a mean AGL/SVL ratio of between 58.0–59.9%, with all but one of the remainder having even higher means (60.0–61.8%). The only exception was Reevesby I. (24), with a lower mean (57.9%). In contrast, of the 27 western populations (29–56, pooling populations 40 and 41), 18 had means between 56.0–57.9%, and a further two (31, 53: 54.8–55.6%) had even lower means. The remaining seven populations (35, 39, 42–43, 48, 51, 55) had means between 58.1–59.3%.

8.2.1.27 Tail length:

The ratio TL/SVL showed uneven clinal increases from north-east to south-west, and from north-west to south-west. Eastern Australian populations (1–33) showed only slight variation in mean values, from 18.3% (population 28) and 19.6% (populations 5, 19) to 22.8% (populations 29, 32–33). In southern Western Australia, however, the increase was more rapid, from 23.8% (population 34) and 25.4% (population 35) to 31.4% (population 43), with only the former two population means below 26.3%. In the north-west (populations 51–56), means were lower (24.2–26.6%) than in the south-west, though not as low as in eastern Australia.

8.2.1.28 Tail diameter:

As in tail length, the ratio TD/TL showed a clinal decrease from north-east to south-west, with the greatest change occurring on the western Nullarbor. Extreme north-eastern populations (1–8) had high means (70.4–80.7%), while more southern and central populations (9–34) mostly had lower means (60.3–69.2%), the only exceptions being three populations around Adelaide (15, 19, 21: 70.6–81.3%), Duffield and Flinders Is. (25, 27: 54.3–54.5%), St Peters I. (28: 72.8%), and one Nullarbor population (31: 73.9%). Western populations had markedly lower means, all below 52.0%, and all but three (35–36, 56) below 47.6%. The lowest means were in the south-west (populations 39, 41, 43, 46–48: 34.8–37.9%), and may be related to the relatively long tails of these populations.

8.2.1.29 Limb lengths:

Both fore- and hindlimb lengths showed little geographic variation. Central populations, particularly those on the Nullarbor (30–34) had slightly higher means for both FLL/SVL and HLL/SVL, as did north-western populations (52–56), while the lowest means were for South Australian insular populations.

8.2.1.30 Head length:

There was noticeable geographic variation in the ratio HL/SVL. All of the eastern populations (1–22) had means between 19.0–20.9%, while only three western populations (38, 48, 54: 20.4–20.7%) had similar means. Instead, western means were a little higher, with 18 in the range 21.0–21.9%, and the remaining six between 22.1–23.2%. The extreme values were clustered around the lower west coast and hinterland (populations 45–46, 49–50).

8.2.1.31 Head Width:

In general, eastern populations had broader heads than western populations. This was reflected in three ratios: HW/HL, IOC/HL and IparW/IparL. In HW/HL ratios, most eastern populations (1–34, 36) had a mean HW/HL of over 100%, the range of means being 100.8–109.9%, the only exceptions being five insular populations (19–20, 25–27) with means of 97.2–99.4%. In contrast, western populations (35, 37–56) all had means of less than 100%, with seven populations (41, 43, 46, 48, 52, 54–55) having means of less than 95% (90.6–94.9%).

In the ratio IOC/HL, the disjunction was not as sharp. Most eastern populations, west to southern Eyre Peninsula (populations 1–21, 23–27) had means of 42.0% or more (42.0–44.8%), the exceptions being populations 8 and 25–26, the latter two insular, with means 40.7–41.8%. Populations to the west of the Nullarbor (35–56) generally had lower means, most less than 39.9% (37.3–39.9%), the only exceptions being populations 38, 41 and 48–49, with means 40.1–41.1%. The intervening populations (22, 28–34) had intermediate means (40.4–41.6%).

Interparietal width showed a more clinal pattern of variation. The more eastern populations (1–21) mostly had mean IparW/IparL ratios of more than 80.0% (80.7–96.0%), with the only exceptions being the extreme north-east populations (1, 3: 71.0–76.0%), the extreme south-east population (14: 78.3%) and Yorke Peninsula (18: 79.0%). Central populations (22–34) mostly had lower means, between 70–80% (70.7–78.5%), the exceptions being higher means for northern Eyre Peninsula (22: 80.4%) and Reevesby I. (24: 85.0%), and lower

means for two Nullarbor populations (30–31: 67.6–68.6%). South-western populations (35–49) had still lower means, between 63–70% (63.4–69.7%), the two exceptions being higher means for Mondrain I. (41: 71.3%) and Garden I. (47: 77.5%). North-western populations (50–56) showed some reversal of the cline, with generally higher means (66.4–75.8%, only one [53] less than 70.0%).

8.2.1.32 Ear diameter:

In general, ear diameter (as reflected by the ratio Ear/HL) was greatest in the east, and least in the north-west. Reduction in population means was slight and gradual over southern Australia, from 13.5% in population 2, 14.5% in population 27, and 14.0% in population 29, to 10.0% in population 50. However, the north-western populations had markedly smaller ears, with the means for populations 52–56 being between 5.1% and 7.6%. Only the two specimens from Garden I. (population 47) had ears approaching this size ($\overline{X}$ = 8.3%).

8.2.1.33 Summary of univariate analyses:

Although there was much apparently random variation, the morphological data suggest the existence of three groups of populations on the mainland: an eastern group occurring east of the Nullarbor region; a south-western group occurring west of the Nullarbor region, and a north-western group occurring to the north of the Murchison River. However, the nature and position of the transition zones, particularly the east-west zone, is not clear from univariate analyses, with some incongruencies in the patterns of variation of different characters.

A second problem concerns the insular populations. While there are certain general trends apparent, such as a trend towards smaller body scales (high body scale counts), melanism and small size, there is also much variation between even geographically close islands in a number of characters that does not agree with the geographic proximity of the islands. A similar result was noted by Sarre and Dearn (1991) for several South Australian island populations.

8.2.2 Multivariate Analyses

8.2.2.1 Introduction:

Two multivariate analyses were undertaken to more clearly define the limits of the three mainland groups of populations, and to study the relationships of the insular populations to the mainland morphs. Ten quantifiable characters which maximally discriminated between populations were used in each analysis. Nine of these were scalational: number of supraocular, midbody, paravertebral, ventral and subcaudal scales, number of subdigital lamellae, occurrence of a median occipital (0 = absent, 1 = present) and a divided frontal (0 = whole, 1 = divided), and degree of separation of nasals (1 = moderately to broadly separated, 2 = narrowly separated, 3 = point contact, 4 = narrow to broad contact). The other character was morphometric: ear diameter, expressed as a proportion of head length to partially eliminate the effect of size. Use of a simple ratio produces a non-normal distribution, often corrected for by an arcsine transformation (Sokal & Rohlf, 1969), although this does not correct for allometry. However, of the two multivariate analyses used, principal components analysis does not make an assumption of normality for the variables analysed (Clifford & Stephenson, 1975; Thorpe, 1976; James & McCulloch, 1990), while although canonical variates analysis does assume multivariate normality, it is relatively robust to violations of this assumption (Sneath & Sokal, 1973). Allometry in ear diameter in *T. rugosa* is relatively minor compared to the variation between populations and between similar sized

individuals within populations, and the two major groups of populations differentiated by ear diameter show only minimal overlap in range of the ratio. Hence, I do not feel that use of a simple ratio in this instance invalidates the analyses.

8.2.2.2 Principal components analysis (PCA):

An R-mode PCA of populations, using standardised population means as individual scores, and pooling the data for population 40 (represented by a single specimen for some characters) with population 41, gave good separation of the populations. The first component explained over 55% of the variance, the first two components over 68% of the variance, and the first three components almost 79% (Table 8.26). For the first component, most variables were similarly weighted, the exceptions being the presence of an azygous occipital and frontal division. In the second component, the weighting was more uneven, with heaviest weighting for (successively) presence of an azygous occipital, subdigital lamellae, nasal contact, division of frontal, and number of supraoculars. The first two components (Fig. 50) separated three mainland groups of populations, an eastern group (populations ≤34), a south-western group (populations 35–51), and a north-western group (populations 52–56). In the north-west, island populations (53–55) grouped with the two mainland populations. In southern Australia, island populations were more divergent. Some islands (Troubridge, Weerona, Wardang, Flinders in the east, and the Archipelago of the Recherche in the west) grouped with the adjacent mainland, while others (Reevesby, Duffield, Spilsby and St Peters in the east and Garden and Rottnest in the west) had higher scores on both components, resulting in the eastern islands grouping with the western mainland populations, but the two western islands being distinct from everything else. The third (Fig. 50) and subsequent components, while further separating some populations, showed little correlation with geography, apart from inconsistently separating some of the insular populations.

An average taxonomic distance network (Fig. 51) using the same standardised data, showed a pattern of variation largely consistent with the PCA, with distances of more than 0.900 between eastern and western mainland groups, and north-western and south-western island groups, and distances of more than 0.800 between insular populations and the adjacent mainland populations. The only exception to this pattern was the separation of population 17, on the northern periphery of the eastern group, and represented by only three specimens, from the adjacent eastern populations (1, 4, 8, 16, average taxonomic distance 0.892–1.163).

8.2.2.3 Canonical variates analysis (CVA):

The same ten characters, this time unstandardised, were subjected to a CVA, using individual specimens as data points, and populations as operational taxonomic units (OTU's). The computing facilities used for this project were unable to handle the full set of 55 OTU's, and so to specifically explore the most problematic areas, most eastern populations were excluded, and a subset of 40 populations run. The OTU's chosen were populations 9–11, 13, 15–16, 18, 22–39, 40+41, 42–52, 53+54, 55–56. The eastern populations selected were chosen so as to give a rough transect across the continent. Populations 40+41 were pooled due to the full set of data being available for only one specimen from population 40, and populations 53+54 were pooled as each was represented by only two complete individuals. A total of 717 cases was run.

Of the ten canonical factors isolated, the first seven explained significant amounts of the variance at the 5% level. Factor 1 had a canonical correlation of 93.7%, factor 2 81.7% and factor 3 68.5%.

On the mainland, the CVA identified the same three geographically discrete groupings of OTU's as the PCA, although zones of intergradation across the western fringe of the Hampton Tableland and about the Murchison River were defined. Overall, while the CVA correctly assigned most individuals to these three groups, or to insular populations, it showed poor discrimination within these groups, with only 37.3% of individuals correctly identified to OTU (Table 8.27). As with the PCA, the first factor of the CVA separated eastern Australian and south-western material, while the combination of the first and second factors, but principally the second, separated the north-western material from the others (Fig. 52).

Using only these two factors, two completely distinct polygons enclosed almost all cases from mainland populations 33 and further east (99.7%, n = 361), and mainland populations 37 and further west (98.2%, n = 171). A third polygon completely enclosed all cases from populations 52–56, and only minimally overlapped with the polygon enclosing south-western mainland populations.

On the western fringe of the Hampton Tableland, all but one specimen from population 34 fell within the eastern group, while from population 36, four of the seven cases lay within the eastern group and three in the western, and from population 35, two were in the eastern group, six in the western group, and one intermediate between the two (Fig. 52A).

For population 51, between the south-western and north-western group, 15 specimens fell within the south-western polygon, one in the north-western polygon, and three outside both polygons, although on the Factor 2 score, one of these was a member of the north-western group, and the other two were intermediate (Fig. 52A).

The first factor provided the greatest separation between the eastern and south-western groups. Plotting the factor 1 scores for mainland populations between 9 and 50 against longitude gave a rough transect across Australia (Fig. 53). This transect showed limited variation east of 124°30'E, a marked rise in the scores between 122°30' and 124°30'E, then relative constancy again west of 122°30'E, with scores much higher than in the east. In the intervening zone, corresponding to the western fringe of the Hampton Tableland were individuals with high and low scores typical of both eastern and western groups, together with a cluster of scores within the range of both groups. Just outside this zone were also a few (n = 2 to the east, n = 3 to the west) specimens with scores outside the usual range for the respective morphs.

No coloration characters were used in the CVA. When the coloration of the individuals in the intergrade zone is considered, all specimens from population 34 were either similar to material from further east, or showed some trend towards the western coloration, although none were typical of the western coloration. All of these specimens had canonical scores typical or only slightly above those for eastern populations. In population 36, in the south-west of the intergrade zone, the three specimens with the lowest canonical scores (similar to eastern material) had coloration more similar to eastern material, while other material (with scores similar to western material) had coloration closer to the western morph. In population 35, the two specimens with the lowest canonical scores had coloration typical of the western form. Of the two specimens from west of 121°20'E with scores within the usual range of the eastern material, one (WAM R12916) had the all-black coloration typical of extreme eastern Australian material, and may either have an erroneous locality, or have been transported along the Trans-Australian railway line (along which it was purportedly found), while the other had coloration similar to other western material.

If WAM R12916 is excluded from consideration, the scalation and coloration data concur in indicating that there are two forms of *T. rugosa* on the southern Australian mainland, contacting and introgressing across the approximately 200km wide zone between about

122°30'E and 124°30'E, the introgression zone possibly a little further east in the north than in the south. The variability present in this zone, with both “typical” and intermediate phenotypes present, suggests that this region is one of secondary introgression (Mayr, 1963; Thorpe, 1979).

The second factor in the CVA provided the greatest separation between the north-western and south-western populations. When factor 2 scores were plotted against latitude, using populations 43–46 and 49–56, there was a gradual, but clinal increase in scores from the extreme south, north to about 28°10'S, a sharp increase between 28°10'S and 27°40'S, around the Murchison River, then consistently high scores further north (Fig. 54). The only exception to this pattern was a single individual (AM R102044) from Port Denison, which had a much higher score than other material from the same latitude, but had coloration typical of southern populations. Coloration showed the same pattern of variation as the mostly-scalation-based CVA. Typical southern animals were uniformly present north up to the transition zone. In the transition zone were individuals with typical southern coloration and low scores (e.g., AM R102001, 7.9km N Murchison River via North-West Coastal Hwy), and individuals with coloration intermediate between the southern and northern forms, but with variable factor 2 scores, from low to very high. The two northernmost specimens (WAM R33854, R34045), while having the highest factor 2 scores in the transition zone, had variably expressed pale bands on the dorsum, a character typical of southern populations, but rare in the northern material. The transition zone, about 80km wide, therefore appears to be again a zone of secondary intergradation.

Of the eight southern island populations included in the CVA (Fig. 52B), the south-western islands (Rottnest, Garden, Recherche Archipelago) grouped mostly with the south-western mainland populations on the first two factors, while the Flinders I. material fell within the eastern mainland variation on the same factors. The remaining four eastern island populations (Sir Joseph Banks Group, St Peters I.) formed a homogeneous group, largely distinct from other populations, on these factors, but overlapped both the eastern and south-western mainland polygons. Overall, the CVA correctly assigned all five eastern island populations to this group, and indeed correctly identified all of the Reevesby I. and Flinders I. specimens. In contrast, the CVA was less successful in distinguishing the three south-western islands. Of 8 Archipelago of the Recherche specimens, five were correctly identified, with the remainder identified as south-west mainland specimens. Of 52 Rottnest specimens, 65% were correctly identified, with the remainder identified as south-west mainland specimens, while one of the two Garden I. specimens was correctly identified, the other identified as from the mainland.

8.2.3 Conclusions

On the basis of these results, I recognise three subspecies of *T. rugosa* on the mainland. The nominate subspecies is the south-western form (type locality King George Sound), while the name *T. r. asper* (type locality Adelaide) is available for the eastern form. The north-western race, including the adjacent insular populations (Dirk Hartog, Dorre, Bernier Is.) I describe below as a new subspecies, *T. r. palarra*.

Of the southern insular populations, the most distinctive is the Rottnest I. population, which was differentiated by the PCA but not the CVA, and has a unique coloration and small adult size, two characters not used in the multivariate analyses. Further, the nearest insular population, Garden I., shows no trend in the direction of the Rottnest morphology. For these reasons, I believe the Rottnest I. population merits taxonomic recognition, as *T. r. konowi*. The other two south-western island populations, Garden I. and the Archipelago of the

Recherche, are generally similar to adjacent mainland populations. Consequently, I assign both to the nominate subspecies.

While the CVA distinguished the south-eastern insular populations from others, and clearly differentiated them from western insular populations, the PCA gave generally high scores on the first and second components to most southern islands, both eastern and western, resulting in some eastern islands clustering with *T. r. rugosa*. On the basis of coloration, which was not used in the multivariate analyses, the south-eastern islands were all more similar to *T. r. asper* than to the nominate race, and I believe that the similarity with *T. r. rugosa* indicated by the PCA results is due to a general trend for small scales in insular populations. CVA, which takes into account within-group covariance between characters (Thorpe, 1976), removes this effect. Consequently, I consider the eastern insular populations should be grouped with the eastern mainland populations rather than with *T. r. rugosa*. The question still remains, however, whether they should be accorded taxonomic recognition, as suggested by the clear differentiation seen in the CVA results. Although the eastern island populations were both grouped together, and differentiated from other populations by the CVA. I believe that the lack of uniformity across these islands seen in other characters not used in the multivariate analyses (e.g., circumocular scalation, supralabials; see also the electrophoretic and morphological results of Sarre *et al.*, 1990 and Sarre & Dearn, 1991) makes it difficult to recognise these island populations as one homogeneous taxon. This leaves two taxonomic alternatives: either to lump them with the adjacent mainland populations, or to recognise a number of subspecies for different island populations. To emphasise the perceived similarity of the south-eastern insular populations to the adjacent mainland, I have retained them in *T. r. asper*.

8.3 Specimens Examined

Note: a number of specimens listed in collection registers could not be located for this study. As there is little likelihood of misidentification of *T. rugosa*, I have included this unlocated material in the following lists, with the registration numbers followed by a superscripted star. A few specimens were represented by osteological material only. Such specimens are indicated by a superscripted dagger.

8.3.1 Tiliqua Rugosa Asper

Population 1 (central Qld)
AM R62436, Aramac tip; MV D13896, 6.6km S Aramac; QM J4132, Clermont; J8703, “Maneroo”, via Longreach; J24317, Emerald.

Population 2 (south-east Qld)
AM R59913, 2mi W Wallumbilla; QM J1268, Dulacca; J1290, J6387*, Chinchilla; J2008*–09*, Roma; J8849*, Jandowae; J21939, “The Gums”, via Tara.

Population 3 (St George region, Qld and NSW)
AM R10449, Cambo, NSW; R25846–49, Lightning Ridge, NSW; R31705, 9mi E Lightning Ridge, NSW; R31833–35, betw. Hebel, Qld and Angledool, NSW; R130562, 48km NW Lightning Ridge turnoff on Collarenebri-Angledool rd, NSW; R130563, old Angledool tip, NSW; MV D14033, 29km W Lightning Ridge, NSW; QM J10491, St George, Qld; J14295, Lussvale, Qld; J31914, Bollon, Qld.

Population 4 (central south Qld)
AM R49237*, 125km S Quilpie; R49238, 5km W Cunnamulla; R65297, “Gilruth Plains”, Cunnamulla; R90818, 37.6km N Thargomindah by rd; R90819, 44.8km N Thargomindah by

rd; R110581, 65km E Quilpie on Charleville rd; QM J2806*–07*, Charleville; J19438, “Rhondavale”, 5mi S Charleville.

Population 5 (north-west slopes, NSW)
AM R18851, Warialda, NSW; R33225, 30mi from Coonabarabran on Narrabri rd, NSW; R91932, 4mi S Yetman, NSW; QM J8394, Goondiwindi, Qld.

Population 6 (Bourke region, NSW)
AM R18327, Brewarrina; R29923, Yantabulla; R31706, “Nocoleche”, Wanaaring; R33115, R33119*, R33233–34, R90334–35, betw. Bourke and Yantabulla; R90817, 33.9km S Enngonia via Hwy 71; R97115, 10mi from Bourke, E of Hungerford rd; R104064, 10mi E Bourke on Hungerford rd; R123570, 21.6km from Wanaaring on Tilpa rd; R123572, 30.2km from Bourke on Wanaaring rd; R123583, 35.2km from Wanaaring on Bourke rd; R123584, 29.4km from Enngonia on Weilmoringle rd.

Population 7 (Cobar region, NSW)
AM R4909, R113117, Cobar; R11402–03, “Marra”, via Tilpa; R16789–90, Hermidale; R18837, R18839, Warren; R29926–28, 40mi E Cobar; R33164–69, Girilambone; R38314, 6mi S Hermidale; R49728, 123km W Nyngan; R70109†, 25mi NW Tilpa; R76647, 125km W Cobar (Manara); R91939–40, 6mi E Quambone on Baradine rd; R111906†, R127917†, Moura Ck, 18km NW Warren on western rd to Carinda; R114488, 51.9km E Cobar on Nyngan rd; R114489, 25km SW Cobar on Ivanhoe rd; R123569, 41.6km from Tilpa on Wanaaring rd; R123571, 11.7km along Tilpa rd from turnoff on Wilcannia-Cobar rd; R123582, 70.9km along Tilpa rd from turnoff on Wilcannia-Cobar rd; R124000, 1.3km W Warren-Carinda rd via Coolibah rd; R125940, 19.4km W Warren-Carinda rd via Coolibah rd; SAM R12057, 25mi W Nyngan.

Population 8 (north-west NSW)
AM R12963–64, R12965*, Tibooburra, NSW; R14645, Mootwingee, NSW; R31651, 37mi N Broken Hill, NSW; R31652, 8mi E Broken Hill, NSW; R31658–59, *ca*.10mi N Broken Hill, NSW; R31715–16, 84mi N Broken Hill, NSW; R33280–81, Cobham Lake [=Gnurntah Lake], NSW; R45504, nr Broken Hill, NSW; R49727, 95.5km E Broken Hill, NSW; R96326–29, Wilcannia district, NSW; R98688, 20km E Broken Hill, NSW; R123944, 20km S Broken Hill on Menindee rd, NSW; R130832, “Waka” Woolshed, 78.9km W Silver City Hwy on Cameron's Corner rd, NSW; MV D41506, “Benagerie” Stn area, SA; SAM R14890, 2km NE “Turley's House”, NSW/SA border; R27024*, Lake Bumbarlow, SA.

Population 9 (south-west slopes, NSW)
AM R8431, Abercrombie Ranges; R16891–93, Binda, nr Crookwell; R21456, R25955, Bathurst distr.; R25954, R33210, Fremantle, 20mi NW Bathurst; R33160, Force Rd, 20mi N Bathurst; R33178, bridle track, 18mi N Bathurst; R33200, Killongbutta, 30mi NW Bathurst; R44936–37, Cumnock; R59915, 7mi from Yass on Gunning rd; R66116, Tuena; R129115, 2.7km N Cumnock turnoff at Molong.

Population 10 (south-central NSW)
AM R10382*, Lake Cargelligo; R16788, Nymagee; R25843, Gidginbung; R26258–61, rd betw. Nymagee and Mt Hope; R31653, 15mi N Booberoi Ck; R31660–64, *ca*.20mi W Mt Hope; R32749–50, 5mi W Mt Hope; R32751, “Naradhan”, betw. Rankins Springs and Lake Cargelligo; R64779, R90336, Round Hill, via Mt Hope; R90333*, Mt Hope - Gilgandra [?Gilgunnia]; R90816, Griffith, nr Pioneer Peak; R94838–39, Yathong Nature Reserve; on Mt Hope rd; R95260†, betw. Mt Hope and Gilgunnia; R98689, 45km E Hay; R105426, Goolgowie tip, 2km N Goolgowie; R105427, 0.8km SW Goolgowie; R105429, 16.5km SW Gunbar South; R107961, R112007, 7km SW Gunbar South; R114144, 54.6km NE Hay on Goolgowie rd; R114145, 35km NE Hay on Goolgowie rd; R114398, 34.5km NW “Monia Gap”

HS on Hillston rd; R114399, 4.4km NW “Monia Gap” HS on Hillston rd; R125422, 2km N Nymagee (Condobolin turnoff) on Hermidale rd; R125423, 1.8km N Cobar-Condobolin rd on Nymagee rd.

Population 11 (Murray-Darling junction, NSW, SA and Victoria)
AM R31654–57, R32752–53, Kinchega National Park, NSW; R61213, 100km E Menindee on railway track, NSW; R105433, Lake Benanee, 14km NW Euston, NSW; R105436–37, Euston tip, 2.5km NW Euston, NSW; R105438, old tip, 2.5km ESE Wentworth, NSW; R105448, 5km W Wentworth, NSW; R105449, 6km NW Wentworth, NSW; R105450, 6.5km NW Wentworth, NSW; R105451, 26.5km W Wentworth, NSW; R105452, 34.5km W Wentworth, NSW; R105455–56, 13.5km WNW Rufus River, NSW; R105457, 14km NW Rufus River, NSW; R114147, 47.8km E Balranald on Hay rd, NSW; R114150, 29.2km E Balranald on Hay rd, NSW; R114151, 23.4km E Balranald on Hay rd, NSW; R114152, 10km N Balranald on Ivanhoe rd, NSW; R114165, 8km E “Mungo” HS on Walls of China rd, NSW; R114170–71, 27.5km ENE Silver City Hwy on “Arumpo” rd, NSW; R114173–74, 5.6km S “Old Arumpo” HS on “Bellnar” rd, NSW; R114175, 4.4km S “Old Arumpo” HS on “Bellnar” rd, NSW; R114176, 1.8km N “Old Arumpo” HS on “Mungo” rd, NSW; R114178, 7.8km NE “Old Arumpo” HS on “Mungo” then “Top Hut” rds, NSW; R114180, “Zanci” turnoff on “Mungo”-“Garnpang” rd, NSW; R114183–84, 3.8km NE “Gol Gol” HS on “Manfred” rd, NSW; R114185, 3.5km N “Top Hut” HS on “Mungo”-“Leaghur” rd, NSW; R114187, 1km E Red Top Dam, Mungo National Park, NSW; R114188, 2.1km W “Top Hut” HS on Pooncarie rd, NSW; R114189, nr “Zanci” turnoff on “Mungo”-“Garnpang” rd, NSW; R114191, 7km N “Prungle” on “Old Arumpo” rd, NSW; R114192, 21.5km N “Prungle” on “Arumpo” rd, NSW; R114193, 36.4km N “Prungle” on “Arumpo” rd, NSW; R114271, 8.2km N Sturt Hwy on “Prungle” rd, NSW; R114279, 0.4km S “Koorakee” turnoff on Euston-“Prungle” rd, NSW; R114325, 26.7km N Silver City Hwy on Pooncarie rd, NSW; R114326, 19.1km N Dareton turnoff on Wentworth-Pooncarie rd, NSW; R114327, 14.2km N “Wamberra” turnoff on Wentworth-Pooncarie rd, NSW; R114391, 3.3km S Poo Poo Tank, “Top Hut”, NSW; R114393, 4.9km E “Milton Grove” turnoff on “Gol Gol”-Ivanhoe rd, NSW; R114394, 7.3km W Ivanhoe-Balranald rd on “Gol Gol” rd, NSW; R114396, Willandra Ck crossing on Balranald-Ivanhoe rd, NSW; R114474, 7.6km SW “Garnpang” HS on “Leaghur” rd, NSW; R114530, junction “Balmoral” turnoff on “Garnpang”-“Gol Gol” rd, NSW; R123938, 8.4km N “Coombah” roadhouse on Silver City Hwy, NSW; R125429, 29km E Ivanhoe-Cobar rd on Trida rd, NSW; R125430, 26.3km S Ivanhoe on Balranald rd, NSW; R125452–54, Ivanhoe tip, NSW; R130813–14, 0.2km N old Broken Hill rd turnoff on Silver City Hwy at Popiltah Lake, NSW; R130833†, 19.7km N by rd of “Coombah” roadhouse, NSW; R133106, “Backwell” HS, E of Silver City Hwy on Lake Tandou rd, NSW; MV R4850, R4852, D4851, Ouyen. Vic.; D16485–86, “Neds Corner” Stn, Vic.; D38702–05, 14.4km NE “Chowilla”, SA; D38795–96, D38798, betw. Ouyen and Walpeup, Vic.; D39235–36, Mildura airport, Vic.; D58485, 30km WNW Kiamil, Vic.; SAM R27033*, Lake Menindee, NSW; R27495, Lake Limbra lunette, SA.

Population 12 (central Victoria)
MV D624, Findlay [?Finley], NSW; D8134, Mt Hope, Vic.; D38793, Mt Langhi Ghiran, Vic.; D47908, SW Buangor, Vic.; D48510, 15km SW Dunolly, Vic.; D48543, 3km E Avoca, Vic.; D48545, 3km NW Mt Langhi Ghiran, Vic.; D48817, 3km W Muckleford, Vic.; D48818, Mt Sugarloaf, Vic.; D50176, 3km NW Lexton, Vic.; D50290, 8km S Moliagul, Vic.; D50685, 2km E Navarre, Vic.; D50686, 1km W Landsborough, Vic.; D50756, 8km E Warrenmang, Vic.; D51415, 2km W Llanelly, Vic.; D51948, Pyramid Hill, Vic.; D56353, Mt Korong, Vic.; D57104, 0.5km S Benjeroop Primary School, Vic.

Population 13 (Little Desert region, Victoria and SA)
AM R96625, 60km S Pinnaroo, SA; MV R12091, R12109, R13783, D5697–98, Horsham, Vic.; D1079, Nhill, Vic.; D2984, D3466–67, D3573–74, 3575*, Kewell, Vic.; D3149, Wyperfeld, Vic.; D8008, Little Desert, Vic.; D14989–90, 11km S Broughton's Waterhole, Vic.;

D40046, D55744–45, Mt Arapiles, Vic.; D51373, 7km W Dimboola, Vic.; D51465, 2.5km W Broughton's Waterhole, Vic.; D51622, D51624, 27km S Kiata, Vic.; D51947, Wyperfeld National Park, Vic.; D52649, 4.5km ENE Chinaman Well, Vic.; D52952, 4.2km ENE Chinaman Well, Vic.; D53079, 2km N Chinaman Well, Vic.; D54559, 12.5km NE Chinaman Well, Vic.; D54750, 5.3km ENE Chinaman Well, Vic.; D54782, 2.8km NNW Chinaman Well, Vic.; D54909, 1.3km N Chinaman Well, Vic.; D54957, 4.9km NNW Chinaman Well, Vic.; D54991, 3.9km ENE Chinaman Well, Vic.; D55207, 14km N Nhill, Vic.; D55304, 5.2km 15°W of N from Chinaman Well, Vic.; D56749, 0.5km N Chinaman Well, Vic.; SAM R16184a–b, E of Box Flat, 25km S Lameroo, SA; R18539, 12km SW Narrung, SA; R21484, Tea Tree crossing, Coorong National Park, SA; R27228, Hensley Scrub, *ca*.8km NW Bordertown, SA.

Population 14 (southern Victoria and SA)
AM R6681–82, SAM R4084, Naracoorte, SA; AM R67932, SSE slope Mt Abrupt, 6.0km N Dunkeld, Vic.; R67933, 10.5km N Dunkeld, Vic.; R67934, 1.0km N Zumstein, Vic.; MV R11770, D47813, Grampians, Vic.; D14680, Marp, Vic.; D17822, Pines rd, 5.6km E Crawford River, Vic.; D17823, 22km SSW Casterton, Vic.; D17824, Pines rd, 4km E Crawford River, Vic.; D38792, nr Cavendish, Vic.; D38794, Lake Fyans, Vic.; D39237, 3.2km W Halls Gap, Vic.; D40012*–13*, Hamilton, Vic.; D47812, Glenisla Shelter, Victoria Range, Vic.; SAM R3783a–b, Avenue Range, SA; R4085, Naracoorte Caves, SA; R13009*, SE of SA (38°01'S 140°35'E); R18751, Naracoorte Conservation Park, SA; R18752, Penola Conservation Park, SA; R22772–73, Bucks Lake Game Reserve, SA; R23099, Bool Lagoon Game Reserve, SA; R23214, NE Mt Gambier, SA; R30595, N of Lucindale (36°43'S 140°19'E), SA.

Population 15 (Adelaide region, SA)
AM R7749–51, Murray Bridge; R15374, Blanchetown; R105479, 7km WSW Yacka; R105480, 1.8km NW Pt Germein; R105481–82, 1.5km SSE Warnertown; R105483, 9km W Booborowie; R105484, rail crossing, Pt Pirie, on Crystal Brook rd; R106776–77, 2.9km W Pt Wakefield rd via St Kilda rd; R106778, 0.5km W Dry Ck railway station; R115695, 13.3mi S Bow Hill on Murray Bridge rd; R115696, 8.0km S Bow Hill on Murray Bridge rd; R115699–700, 2.1mi E Two Wells on Gawler rd; R115707, 0.3mi S main NW bend on Pt Gawler rd; R115727, Pt Parham rubbish tip, N end of town; R115889, Hallett rubbish tip, E side of town; R115903, “Pandappa”: 1.2mi N Terowie-“Pandappa” HS rd, 14.1mi E Terowie; BMNH xv.81a–d (types of *Trachydosaurus asper*), Adelaide; MV R4545, Purnong Landing; R4546*, Purnong; D11609, 4.6km S Morgan; D12670, 8km S Yankalilla; D38797, 4km E Burra; SAM R1786, Adelaide; R15434, Laura; R16985a–b, *ca*.13.5km N Robertstown; R18540, “Glenforslan” Ranch; R18541, Blanchetown tip; R18542, *ca*.18km NE Mannum; R18590, Black Hill; R23523, Mt Remarkable National Park; R24138–39, WNW of Gawler (34°34'S 138°35'E); R24215, 11.2km N Dutton; R32415–16, Gunn St, Eudunda; R33402, WAM R82641–49*********, R91247, Mt Mary; SAM R33408, St Kilda; WAM R27307, 5mi S Pt Germein.

Population 16 (Flinders Ranges, SA)
AM R59914, betw. Hawker and Peterborough; R64809, Copley; MV D9842, Emu Creek Forest; QM J22738–39, D22750, Flinders Range; SAM R755–56, Devil's Village; R1277a–b northern Flinders Range; R3733, Maree Picnic Ground; R4323, “Beltana” HS; R16577, Flinders Ranges National Park; R16951, “Yudnapinna” HS; R18164, 37.5km S Parachilna on Hawker rd; R19013, “New Mulgaria” HS; R28082, 30km SW Hawker; WAM R55680, 16km NE Quorn.

Population 17 (SA-Qld border region)
AM R11856, R12176, Moonbah, SA; QM NJ9734, Birdsville, Qld.

Population 18 (Yorke Peninsula, SA)
AM R79624–28, 0.5–20km W Hillock Point; R115738, South Hummocks; R115771, 3.3mi W Kulpara on Paskeville rd; R115772, Site 1, N.C.S.S.A. Yorke Peninsula Vegetation Survey; R115799, Site 10, N.C.S.S.A. Yorke Peninsula Vegetation Survey; R115803, 4.9mi due NW Arthurton; SAM R1256, Maitland; R1393a–i, Pt Victoria; R1802a–b, Minlaton; R12050, 4mi N Pine Point; R12051, Pt Minlacowie; R12054, Stansbury; R16972, Shell Beach, Innes National Park; R30390–93, R31588, Point Pearce rubbish tip; R30394, Point Pearce mill; R30395–97, Point Pearce area; R31577, 3.9km N Point Pearce turnoff; R31578, R31590–91, 3km S Edithburgh; R31587, Point Pearce; R31589, 21.7km S Minlaton; R31592–93, 1.7km E Pt Victoria; WAM R82628–29, Tickera.

Population 19 (Troubridge I., SA)
SAM R20819, R31418–19, Troubridge I.

Population 20 (Wardang I., SA)
SAM R30388–89, R31037–38, R31479–81, R31594–96, Wardang I.

Population 21 (Weerona I., SA)
SAM R31618–19, R31622, Mt Ferguson; R31620–21, R31623, nr railway crossing.

Population 22 (northern Eyre Peninsula, SA)
AM R17586, Kingoonya; R49724, 8.4km W Ceduna; R49725, 28km E Ceduna; R49726, 47km E Ceduna; R90822, 5.9km SE Ceduna via Eyre Hwy; R90823, 7.1km SE Ceduna via Eyre Hwy; R90824, 0.8km E Wirrulla by rd; R90825, 10.2km E Wirrulla by rd; R90826–27, jcn Wirrulla-Kingoonya and Iron Knob-Kingoonya rds; R90828, 16.4km SE cutoff to "Morance" Stn; SAM R3192a–b, 6.5mi N Pimba; R16933, Streaky Bay; R27315, 22km S Pimba; R27317, R27321, E edge Kingoonya; R27319–20, 8.8km NW Kingoonya; R28378, 52km NE Minnipa; R28379, 38km NE Minnipa; R28384, R29206, 37.5km NE Minnipa; R28392, 27km NW Iron Knob; R28395, 25km NW Iron Knob; R28396, 28km NW Iron Knob; R28404, R28407, 118km ENE Minnipa; R28405, 126.8km ENE Minnipa; R28406, 126.3km ENE Minnipa; R28470, 36km NNE Minnipa; R28476, 119.3km NE Minnipa; R28507, R28604, 120km NE Minnipa; R28589, R28592, 73.3km NW Iron Knob; R28590, 47.5km NW Iron Knob; R28591, 49km NW Iron Knob; R28593, 73km N Minnipa; R28594, 125km ENE Minnipa; R28595, 130.8km ENE Minnipa; R28602, 101.8km ENE Minnipa; R28603, 102.5km ENE Minnipa; R28605, 118.5km NE Minnipa; R31472–73, 4.5km NE quarry nr Ceduna; R31868, 5km NE Mt Finke; R31941, 19.5km NNW Wallala Hill; R31954–55, S Inila Rock Waters, Yumbarra Conservation Park; R31926, 8km W Pinjarra Dam, Yumbarra Conservation Park; R33401, 6km N Buckleboo; WAM R15018*, 11mi W Ceduna; R15019*, 32mi E Ceduna; R23842–43, Ceduna; R23844–46, Smoky Bay; R24516–21, R24522*, R24523–25, Hiltaba.

Population 23 (southern Eyre Peninsula, SA)
AM R79667, 1.5km from Yalunda Flat-Tumby rd via Pillawarta rd; R79717–19, old Elliston rubbish tip; R79738, *ca*.2–3km SE Mt Hope; R79763, Tumby; R79764, rubbish tip, S side Port Lincoln; R128944, WAM R25966, Elliston; AM R128945–48, SAM R4043, Port Lincoln; MV D5698, D7896, Whyalla; D39232–34, nr Sheringa; SAM R4773, Cleve; R18402–03, R18404*, R18405–06, Tumby Bay, N edge town to 2km inland; R18610, *ca*.2km S Tulka; R20587, nr Cowell; R20797, 9km W Base Camp; R27311, 25km SW Whyalla; R30481–82, 2km N Tumby Bay; R30483, Wanna; R30484, 5.3km N Wanna; R30485, 9.9km SW Memory Cove, Lincoln National Park; R30486, 2.5km SW Memory Cove, Lincoln National Park; R31555–59, 2km W Tumby Bay; R31560–62, rubbish tip, 2km N Port Kenny.

Population 24 (Reevesby I., SA)
SAM R18591–94, R30584–93, R31482, R31728, R31554, Reevesby I.

Population 25 (Duffield I., SA)
SAM R22771, R30468–74, Duffield I.

Population 26 (Spilsby I., SA)
SAM R30475–80, R31474–75, Spilsby I.

Population 27 (Flinders I., SA)
SAM R17275, R31301–03, Flinders I.

Population 28 (St Peters I., SA)
SAM R21944, R31477–78, St Peters I.

Population 29 (Penong region, SA)
AM R105545, 6.3km NNE “Glen Boree”; R107949, 15.6km E Nundroo via Eyre Hwy; R107953, 15.2km W Penong rail siding via Eyre Hwy; SAM R25604, Koonalda campsite No. 2, 12.6km NE “Colona” HS; R25615*, Koonalda campsite No. 1, 12.5km NE “Colona” HS; R25714, 60km N “Colona” HS; R26361, 14.2km NE “Colona” HS; R26368, 62km N “Colona” HS; R31837, 14km ESE Lake Bring; R31843, 5.8km ESE Lake Bring; R31855*, 15km SSE Mt Christie siding; R31996, 7km S Mitcherie Rockhole; R32096, 9.5km WNW Immarna siding; WAM R23847, 5mi NE Fowlers Bay.

Population 30 (eastern Nullarbor, SA)
AM R7642–45, R7695*, Fisher; R105546, 14km E Nullarbor Roadhouse; R107943, 25.1km W Nullarbor Roadhouse; SAM R15571, 10mi E Cook; R23074, 20km W “Nullarbor” HS; R25708, 50km W Yalata Roadhouse; R25715, R25719, 48km SE “Koonalda” HS; R25717, 52km SE “Koonalda” HS; R25718, R26317, 51km SE “Koonalda” HS; R25720–21, 7km NW “Nullarbor” HS; R26391, *ca*. 10km N Cook; WAM R15016–17, R37676, “Nullarbor” Stn; R36668, 15mi S Cook.

Population 31 (western Nullarbor, SA and WA)
AM R90820–21, 21.5km N “Koonalda” on Hughes rd, SA; R117690, *ca*. 5km W Eucla via Eyre Hwy, WA; SAM R18985–86, Eucla, WA; R25548, 6km N Koonalda Cave, SA; R25712, 30km N Koonalda Cave, SA; R25713, 15.9km NW Hughes, SA; R25716, R26254, 8km SE Border Village, SA; R26267, 10km NE Border Village, SA; R26392, 12km NW Hughes, SA; WAM R26431–32, 7mi N Eucla, WA; R67256, 10km NNW Eucla, WA; R67257, 40km SW Eucla, WA; R67476, “Koonalda” Stn, SA.

Population 32 (eastern Hampton tableland, WA)
AM R105916, 50.4km E Madura Roadhouse on Eyre Hwy; MV D38788–91, D40044, SAM R18990, WAM R23837, Madura; SAM R23071, 62km E Madura; WAM R36149–50, “Mundrabilla” track, 20mi NE Madura; R24738, Loongana; R29193, 15mi SW Loongana; R29487, 10mi S Loongana; R29488, Madura airstrip, 1mi N Madura Pass; R77885*, 19km S Mundrabilla; R91460, 6km S Mundrabilla Motel; R91527, 7km W Loongana; R91530, 98km N Loongana; R91547, 44km N Loongana; R91549, 19km N Loongana; R91551, 12km N Loongana; R91552–53, 12km S Loongana.

Population 33 (central Hampton tableland, WA)
AM R59471, 26mi E Cocklebiddy, 31mi W Madura on Eyre Hwy; R105877, Cocklebiddy Roadhouse rubbish tip; SAM R23075, 31km W Madura; WAM R37060, R34016, 70mi NE Rawlinna; R45779, 17.5mi E Cocklebiddy; R24737, R91524, Nurina; R23835, 30mi W Madura; R23836, 17mi E Cocklebiddy; R23838–39, 26mi W Madura; R23840, 8mi E Cocklebiddy; R23841, 12mi E Cocklebiddy; R77873*, 25km N “Eyre” HS; R91592, 3km SW Haig; R91593, 4km S Haig; R91594, 14km S Haig; R91596, 20km S Haig.

Population 34 (western Hampton tableland, WA)
AM R102681, Caiguna; R102683, 25km W Cocklebiddy; WAM R15015*, R25617, Naretha; R29191–92, 7mi E Rawlinna; R31960–62***, 70mi NNE Rawlinna; R37670, 37mi NE Rawlinna; R37790, “Kanandah” HS; R67255, 37km W Caiguna; R86828, 20km SSW “Premier Downs”; R86829, 12km NNE Rawlinna; R86833, 2km NW Kanandah; R86956, 18km W Naretha; R91519, 20km W Naretha; R91520, 13km W Naretha; R91521, 7km W Naretha.

Population 38a (Goldfields, WA)
WAM R12916, 3mi W Kalgoorlie

Specimens not assigned to populations
AM R5688, western NSW; R8592, Beecroft; R10140, Hyde Park; R10553, R10555, central Australia; R10584, Bellevue Hill; R48109, R48118, NSW; R49967, White Wells, SA; R71863, *ca*. 2km N Coffs Harbour; R130496, 30,8km N Colo River crossing on Putty rd; MV R1825, D1081, D1590, Victoria; D8910–11, west coast, SA; D39231, Werribee; D50040, Teddington Reservoir; QM J3503, Rocky Ck, Darling Downs; R1483, upper Warrego; R4533, Kingsthorpe; R14395, Gunnedah; SAM R22528, R27103–07, R27278, No data; WAM R18577–80, N Nullarbor Plain and S Great Victoria Desert.

8.3.2 Specimens From Hybrid Zone Between T. r. asper *and* T. r. rugosa*, Not Readily Assignable to Either Subspecies*

Population 35a (Zanthus region, WA)
WAM R65502, 6.5km N Buningonia Spring.

Population 36a (Balladonia region, WA)
AM R102682, 33km E Balladonia; R102684, 199km W Cocklebiddy; MV D40045, “Balladonia” HS; WAM R14172, Balladonia; R91639, Balladonia Rock.

8.3.3 Tiliqua rugosa rugosa

Population 35b (Zanthus region, WA)
WAM R12998*, R13000, Cundeelee; R14489–90, “Cowarna Downs”; R21661, R21662*, Zanthus; R70883, 1km 45° Yowie Rockhole; R72499, 6.5km SE Buningonia Ridge; R86686–87, 32km ENE Kanowna; R86688, 9km W Kurnaldi; R86691–92, 3km N Yindi.

Population 36b (Balladonia region, WA)
WAM R36270, mouth of Thomas River; R59901, 16KM N Charlina Rock; R77922*, 1.4km NNW Point Dempster; R89450, Cape Arid National Park, mouth of Thomas River; R93354, Bilbunya Dunes; R93671*, 6km E Breeboorinia Rock.

Population 37 (Norseman region, WA)
AM R59473, 47mi W Balladonia, 73mi E Norseman; R92694, 72.1km S Norseman P.O. via Hwy 1; R105559†, 68km S Norseman by rd; WAM R15013*, 8mi NE Norseman; R30767, 8mi E Fraser Range; R58002, 3km ENE Jyndabinbin Rocks; R58003, 23.5km ENE Jyndabinbin Rockhole; R62218, 12km from Dingo Rock; R62219, 4.5km N Jyndabinbin Rockhole; R62220, 13km from Dingo Rock; R62221, 19.5km E Jyndabinbin Rockhole; R64868, 37km ENE Clear Streak Well; R65414, R65433, 23km NE Heartbreak Ridge; R72383, R72326, 23km NE Heartbreak Ridge; R93422–23, “Southern Hills” HS; R93438, 17km NNE “Southern Hills” HS; R93445–47, “Fraser Range” HS.

Population 38b (Goldfields, WA)
MV D13402, Kamballa [?Kambalda]; WAM R12723, Woolgangie; R15014*, N of Kalgoorlie; R22559, 4mi W Callion; R37934*–35*, 18mi S Yellowdine; R65048*, 6.0km 290° Knapp Rock; R65266*, 6.3km SW McDermid Rock; R65315, 3.7km SSW McDermid Rock; R71760, 16km 184° Woolgangie rail siding; R72268, nr Boorabbin; R74285, 2.5km E McDermid Rock.

Population 39 (Esperance region, WA)
AM R92692–93, Esperance; R102319, 1.2km E Ravensthorpe P.O. via Hwy 1; R105563, R105566, southern outskirts, Ravensthorpe; R105582, old rifle range, Ravensthorpe; SAM R23072–73, Lort River, 65km W Esperance; R33406, 11km W Esperance; WAM R15002, 4mi W Ravensthorpe; R15003, 4mi E Ravensthorpe; R15004*, 11mi E Ravensthorpe; R15005, Oldfield River; R15006, Young River; R15007, Stokes Inlet; R15008, Lort River; R15009–10, lower Dalyup River; R15011, 12mi NW Esperance; R21996, 5mi E Gibson's Soak; R42527, nr Mt le Grand, Cape le Grand National Park; R78405*, Frank Hann National Park; R86970, nr Fanny Cove, Stokes Inlet; R93242, 20km ENE Munglinup.

Population 40 (miscellaneous Archipelago of the Recherche islands)
WAM R53067, North Twin Peaks I.; R76347, Salisbury I.; R84717, nr Coverdale Cove, Middle I.

Population 41 (Mondrain I.)
WAM R15012, R53113–14, R54459–60, R68175, R68373, Mondrain I.

Population 42 (Fitzgerald River region, WA)
AM R105592, Fitzgerald R. crossing on Eyre Hwy; R105594, 26.2km W Gairdner on Eyre Hwy; SAM R18978, R18987, 20km W Bremer Bay; WAM R12808, R12810, R12812, Ongerup; R21731, 7mi S Newdegate; R21734–35, 26mi SR Newdegate; R36777, R36913–14, lower Fitzgerald River; R39872–73, 6mi S Greenshields Soak; R45739, Lake Magenta Reserve; R64867, 7km W West Mt Barren, Fitzgerald River National Park; R69642, 17km S Pingrup; R86969, Gordon Inlet; R96780, Fitzgerald River National Park.

Population 43 (south-west WA)
AM R7640–41, Cranbrook; R7712–13, WAM R60486, Albany; AM R59472, Collie River, 15mi E Bunbury; R92695, 8.1km E Blackwood River at Alexander Bridge on Brockman Hwy; R102311, tip, *ca*. 3.3km E Boyanup (end of Gray Rd); R102316, R102593, Emu Point, Albany; R102317, E end, Catalina Rd, Albany; R102318, just N Ledge Point (by rd), King George Sound; R102320, Griffiths Rd, just S Golf Links Rd, Albany; R102594–95, rubbish tip, *ca*. 1.6km W Greenbushes (by rd); R105606, Hanrahan rubbish tip, Albany; SAM R18979–82, 18km E Mt Barker; R18988–89, 6km W Mt Barker; R18991–92, 40km S Mt Barker; WAM R14171, Scott River; R15001, 15mi E Albany; R31068, 7mi SW Boyup Brook; R36035–37, R54393, Cheyne Beach; R36371, Two Peoples Bay Reserve; R44993, R95468, Two Peoples Bay; R47797, betw. Perup and Tone Rivers; R47798, Woolbales, E of Broke Inlet; R62231, Balingup Pine Plantation; R71869, 0.5km SW Wallcliffe House; R71870, 8km WNW Dunsborough; R86971, NW side, Lake Muir; R93554*, Mt Clarence.

Population 44 (southern Wheatbelt, WA)
AM R125044†, R125045–55, Narrogin; WAM R2444, West Popanyinning; R12809, R12811, Dumbleyung; R14052, 15mi E Highbury; R14999–15000, 9mi E Pingelly; R40095, Tarin Rock Reserve; R44200, S end, Lake Grace Reserve; R44448, N Tarin Rock Nature Reserve; R49783, Dongolocking Nature Reserve; R69639, R69641, Woyaling Well, E of Pingelly; R69643, 16km NW Wickepin; R73126, Brookton.

Population 45 (central Wheatbelt, WA)
WAM R2812, Wadderin Hill; R12218–20, 7mi S Cunderdin; R41693, Hyden; R43408, Bendering Fauna Reserve, 5mi E Bendering; R43688, Bendering Flora Reserve, 3mi E Bendering; R44884, 1mi N Hyden; R52175–76, Yorkrakine Nature Reserve; R52266, 17km NW Kellerberrin; R52273–74, 29km N Kellerberrin; R52486*, Badjaling Nature Reserve, 11km E Quairading; R52515, Yoting Reserve, 20km E Quairading; R52516, 21km NE Quairading; R52597, 8km NE Bendering; R56535, *ca*. 22km N Kellerberrin; R58094, 7km E Bendering; R58095, 25km N Kellerberrin; R68973*, Yoting Water Reserve; R68974*, Badjaling Flora Reserve.

Population 46 (Perth region, WA)
AM R2180, SAM R12055, Perth; AM R102048–49, *ca*. 3.4km N Waroona via South-Western Hwy; MV D7930, Wembley; D8005 Wondong Gorge, Perth [?Wungong Reservoir]; SAM R33405, trig. opposite Scarborough Beach; WAM R8150*, Cottesloe; R12814, Bindoon; R12839, Brockman River, 1mi N Avon River; R12840, Walyunga, Avon River; R12861, Caversham; R13115*, Kalamunda; R13180, 11mi E The Lakes; R14989*, 7mi E Bindoon Hill; R14990, R41251, Crawley; R14991–92, Kings Park; R14993–97, Lesmurdie; R14998, Point Peron; R21346–47, Wooroloo; R21597*, Serpentine; R21722–23, Pelican Point; R27270*, Mahogany Creek; R29523, Northam Army Camp; R34324, Pinjarra; R39114, Bentley; R41247–50, R41253–55, R41257–60, West Coast Hwy, Perth; R41252, R41256, Jandakot Reserve; R51557, Mussel Pool, 15km NNE Perth; R59111, Melaleuca Park; R59157, Yanchep National Park; R60419–20, Jandakot; R73129, Scarborough.

Population 47 (Garden I., WA)
WAM R89982, R89996, Garden I., north end.

Population 49 (northern Wheatbelt, WA)
WAM R12813, Mogumber; R12923, Goomalling; R13408, New Norcia; R14037*, Buntine; R14038*, betw. Pithara and Buntine; R14154, Moonijin; R14978, 18mi NE Wubin; R14979, Miling; R14980, Walebing; R14981, 4mi NE Moora; R14982, 7mi N Watheroo; R17088, 8mi N Moora; R18581, 5mi S New Norcia; R25086, Fields Find; R43652–54, R44534–37, Buntine Nature Reserve; R50137–38, 20km NE Dalwallinu; R50220, Mt Matilda, Wongan Hills; R50221, Wongan Hills, 1.5km NE camp; R51106, 12km NE Dalwallinu; R57765, 15km N Marchagee; R58206*, 20km NE Dalwallinu; R71806, 2km W Konnongorring; R96609, 25km SSW “Mouroubra” HS.

Population 50 (Jurien region, WA)
AM R101997, 1.3km S Hill River via Brand Hwy; R102026–27, old tip just NE Jurien; R102028–29, *ca*.3km E Lancelin rd via K.W. rd; R102041, 34.2km W Brand Hwy via Jurien rd; R102042, 24.6km W Brand Hwy via Jurien rd; R102045–46, 20.3km W Brand Hwy via Jurien rd; R105620, 31.1km W Brand Hwy via Jurien rd; R105620†, 31.1km W Brand Hwy on Jurien rd; R105622, old tip, 0.5km E Jurien on N side of rd; WAM R13042, Jurien; R14983, Mimegarra; R14984, Wookawooka; R14985–87, 25km SE Lancelin; R14988, Lancelin; R25819, Eneabba; R48430, 2km E Mt Peron; R52151, 1.5km S Green Head; R59661*, Green Head; R68914, Badjingarra National Park; R73125, Jurien Bay.

Population 51a (Murchison River and hinterland, WA)
AM R102000, northern outskirts Geraldton; R102001, 7.9km N Murchison River via NW Coastal Hwy; R102002, 5.9km W NW Coastal Hwy via Kalbarri rd; R102043–44, S side, Pt Denison on South Beach rd; R102047, SE side Horrocks; R102978, Port Gregory; R105624†, Dongara tip, 2.6km from town on Golf Course rd; R105763, 14.3km N Northampton on NW Coastal Hwy; R107997†, 3.7km N Yuna turnoff on NW Coastal Hwy; R117819, 6.2km N Murchison River via NW Coastal Hwy; WAM R14975, 7mi N Northampton; R14976, Northampton; R14977, Naraling; R16918, 13mi NW Tenindewa;

R16924, 16mi NW Northampton; R16927, Balline; R17087, Ogilvie; R18594, R25817–18, Kalbarri; R41659, 0.5mi W Devlins Pool; R49906, East Yuna Nature Reserve, 30km SE Yuna; R51130, 19km S Mullewa; R57549, 30km NE Yuna; R57665, R57674, R57713, Wilroy Reserve, 19km S Mullewa; R96684, 13km W Mt View.

Not assigned to populations
AM R4949, MV D3468, SAM R1609, WA; AM R26601, Streaky Bay; R26602, between Esperance and Norseman; BMNH xv.77h, Abrolhos; BMNH unregistered (possible syntype of *Brachydactylus typicus*), no data; WAM R12930, R34003, no data.

8.3.4 Specimens From Hybrid Zone Between T. r. rugosa *and* T. r. palarra*, Not Readily Assignable to Either Subspecies*

Population 51b (Murchison River and hinterland, WA)
WAM R17085*–86*, R76392, Binnu; R33854, 4mi downstream, “Murchison House” HS; R34045, “Gie Gie” outcamp, 21mi NNW “Murchison House” HS.

8.3.5 Tiliqua rugosa palarra

Population 52 (Shark Bay, WA)
AM R102710–14, R112444, R129202†, field series 15160–65, “Tamala” HS; R108000†, WAM R22755–58, Denham; SAM R33404, 2km S Denham; WAM R22681, betw. Denham and Monkey Mia; R23879, 5km S “Tamala”; R53795, 45km S Denham; R54588, 5km S “Carrarang” HS; R54666, 21km N “Biddy Giddy” outcamp, “Carrarang”; R54757, 4km S Useless Loop; R54983*, “Peron” HS; R55259, 55km S Denham; R55260, 4km E Denham; R60609, R60712–13, 20km N Nanga; R64448, 1km S “Tamala” HS.

Population 53 (Dirk Hartog I., WA)
WAM R42375–76, R59704, Dirk Hartog I.

Population 54 (Dorre I., WA)
WAM R13280*, south end, Dorre I.; R13460, R69640, Dorre I.; R46547–48, White Beach, Dorre I.

Population 55 (Bernier I., WA)
WAM R13160, R13487–94********, R20496, R54394–95, R58815, R69644–45, R73127–28, R73130–31, Bernier I.

Population 56 (Gascoyne River region, WA)
AM R81388, 6km N Gascoyne River; R105690, 0.7km E Hwy on Gascoyne Junction rd; SAM R4371, WAM R69933*, R71467, Carnarvon; SAM R33403, Carnarvon area; WAM R16949, 10mi E Carnarvon; R22958, 1mi N Gascoyne River (E of Carnarvon); R41637, NW corner, “Callagiddy”; R62371, 7km W of NW Coastal Hwy, nr “Boolathana”; R67335, 5km N Gascoyne River on Coastal Hwy; R71097*, 23.0km, 2° Carnarvon; R80428, 20km SSE Carnarvon.

Not assigned to populations
RMNH 2842 (syntype of *Scincus pachyurus*), New Holland

8.3.6 Tiliqua rugosa konowi

Population 48 (Rottnest I., WA)
WAM R1952, R2350, R12713–15, R12721 (holotype of *T. r. konowi*), R12800–07, R12815, R12922, R13742, R13747, R14545, R14944–51, R14953–74, R15188–89, R15890–91, R16498–99, R60608, R60698–707, R95458, Rottnest I.

8.4 Tiliqua rugosa rugosa

8.4.1 Synonymy

Tiliqua rugosa rugosa (Gray, 1825)

Trachydosaurus rugosus Gray, J.E. (1825). A Synopsis of the Genera of Reptiles and Amphibia, with a Description of some new Species. *Annals of Philosophy* (2)10(3): 193–217 [201].
Holotype: BMNH 1946.8.5.1

Scincus peronii Wagler, J.G. (1830). *Natürliches System der Amphibien, mit vorangehender Classification der Säugthiere und Vögel*. J.G. Cotta, München, Stuttgarten und Tübingen. (354pp.) [163].
(*nom. nud*.; name introduced in synonymy of *Trachysaurus rugosus*).

Trachysaurus peronii Wagler, J. (1833). *Descriptiones et icones amphibiorum*. J.G. Cottae, Monachii, Stuttgartiae et Tubingae. [pl.36]
(*nom. nov. pro Trachydosaurus rugosus* Gray)

Brachydactylus typicus Smith, A. (1835). [untitled]. *South African Quarterly Journal* 2(2): 143–144 + pl. [144]
Syntype (?): BMNH, unregistered.

Scincus pachyurus Gray, J.E. (1831). A synopsis of the species of the Class Reptilia, pp. 1–110 *in*, Griffith, E. & Pidgeon, E., *The Animal Kingdom arranged in conformity with its organization, by the Baron Cuvier, member of the Institute of France, &c. &c. &c. with additional descriptions of all the species hitherto named, and of many not before noticed*. Volume 9. *The class Reptilia arranged by the Baron Cuvier, with specific descriptions*. Whittaker, Treacher, and Co., London. (481 + 110pp.) [67].
(*nom. nud*.; F. Peron ms. name introduced in synonymy of *Trachydosaurus rugosus*)

8.4.2 Diagnosis

T. rugosa differs from all other *Tiliqua* species in the combination of large, heavily ossified dorsal scales, a short, blunt tail and divided subdigital lamellae. The nominate subspecies differs from all other subspecies in the combination of a relatively longer, more slender tail, usually 16 or more subcaudal scales, usually 22–30 midbody scales, a relatively narrow head ($\overline{x}$ HW/HL = 95.4%), usual presence of a median occipital, usual separation of first supraciliary and frontal, usual separation of nasals, moderately large ear aperture ($\overline{x}$ Ear/HL 11.4%) and dorsal colour pattern usually involving bands composed of fine pale variegations.

8.4.3 Description

Nasals usually moderately separated (84.2%, n = 304), less commonly broadly separated (3.3%), narrowly separated (7.9%), in point contact (2.3%), narrow to moderate contact (2.0%), or fused with other head scales (0.3%); postnasals usually fused dorsally to nasals, separated ventrally by a postnarial suture, rarely completely distinct from nasals unilaterally (1.3%, n = 156) or bilaterally (1.9%), completely fused to nasals bilaterally (0.6%) or bilaterally distinct from nasals but fused to frontonasal (0.6%); prefrontals usually in broad to moderate contact (91.1%, n = 304), less commonly in narrow (3.6%) contact, narrowly to broadly separated (3.3%), with an interposed median scale (0.7%), or fragmented, fused to each other, to the frontonasal, or to several other head shields (0.3% each); supraoculars usually three (73.4%, n = 263) or two (12.5%) bilaterally, with first only contacting frontal, or asymmetrical (2/3) (7.2%), rarely four with first two contacting frontal bilaterally (1.5%), three with first two contacting frontal (0.4%), or asymmetrical (4/4(2/1), 0.4%; 4/3(2/2), 0.4%; 4/3(2/1), 2.7%; 4/3(1/1), 1.1%; 1/2(1/1), 0.4%); supraciliaries 4–7 ($\overline{X}$ = 5.69, SD = 0.72, n = 521), usually six (56.0%) or five (28.8%); when six supraciliaries, and three supraoculars, first supraciliary tall, a little narrower to a little broader than tall, penetrating strongly between prefrontal and first supraocular, second low, rectangular, a little longer than tall, tapering slightly caudally, contacting first supraocular only, third small, a little longer than tall, contacting and projecting slightly between first and second supraoculars, fourth subequal to third, squarish, contacting second and usually third supraoculars, sometimes projecting slightly between them, fifth small, square, contacting third and sometimes second supraocular, last large, as long as tall, projecting between third supraocular and parietal; first supraciliary usually broadly to moderately separated from frontal bilaterally (72.7%, n = 154), less commonly narrowly separated (14.9%), in narrow to broad contact (9.7%) or asymmetrical (broadly separated/narrowly separated; broadly separated/narrow contact; moderately separated/narrow contact; narrowly separated/narrow contact; 0.7% each); last supraciliary usually broadly to moderately separated from frontoparietals bilaterally (98.6%, n = 146), rarely in narrow contact (0.7%), or asymmetrical, moderately separated/narrowly separated (0.7%); frontoparietals paired, usually in broad to moderate contact (96.2%, n = 182), rarely in narrow contact (2.7%), separated (0.5%) or fragmented (0.5%); occipitals 1–3 ($\overline{X}$ = 2.15, sd = 0.39, n = 300), usually two (82.7%); median azygous occipital usually present (78.6%, n = 266), less commonly absent (21.4%); loreals usually two in horizontal series, rarely one unilaterally (n = 6) or bilaterally (n = 14), or three unilaterally (n = 7) or bilaterally (n = 3); reduction to one loreal commonly due to fusion of rostral loreal to frontonasal (n = 6); caudal loreal rarely vertically paired bilaterally (n = 1); subocular ring complete; presuboculars 2–5 ($\overline{X}$ = 3.07, sd = 0.59, n = 619), usually three (66.2%); suboculars 0–2 ($\overline{X}$ = 0.43, sd = 0.55, n = 620), usually absent (59.8%); postsuboculars 3–6 ($\overline{X}$ = 4.18, sd = 0.58, n = 622), usually four (66.2%); supralabials 7–10 ($\overline{X}$ = 8.83, sd = 0.66, n = 603), usually nine (56.6%), antepenultimate below centre of eye, penultimate and last usually single bilaterally, subequal in height (n = 146), rarely both paired bilaterally (n = 1); primary temporal usually paired bilaterally (n = 142), rarely entire unilaterally (n = 1) or divided into three scales unilaterally (n = 1) or bilaterally (n = 1), paired, with upper scale fused with lower secondary temporal and last supralabial bilaterally (n = 1), or paired, but with the upper scale absent unilaterally (n = 1); lower secondary temporal usually paired bilaterally (n = 93), less commonly single (refused?) unilaterally (n = 24) or bilaterally (n = 17), rarely divided into three scales unilaterally (n = 7) or bilaterally (n = 5), or with upper scale fused unilaterally to upper secondary temporal (n = 1); posttemporals 1–4 ($\overline{X}$ = 2.57, sd = 0.57, n = 312), usually three (51.0%) or two (44.9%); rostral ear lobules absent; infralabials 7–12 ($\overline{X}$ = 9.27, sd = 0.82, n = 601), usually nine (44.3%) or ten (32.6%), scales in caudal part of row irregularly paired; usually first two infralabials contacting postmental,

less commonly first three unilaterally (10.2%, n = 266) or bilaterally (15.4%), rarely one unilaterally (0.8%) or none/three (0.4%).

Midbody scales 20–30 ($\overline{X}$ = 24.4, sd = 1.39, n = 304), rarely (0.7%) less than 22; paravertebral scales 20–30 ($\overline{X}$ = 25.1, sd = 1.70, n = 264), rarely (0.8%) less than 22; paravertebral scales between axilla and groin 14–21 ($\overline{X}$ = 17.4, sd = 1.36, n = 267); ventral scales 55–76 ($\overline{X}$ = 65.8, sd = 3.79, n = 266), rarely (1.9%) below 58; subcaudal scales 14–25 ($\overline{X}$ = 19.1, sd = 1.79, n = 235), rarely (0.4%) below 16; lamellae below fourth toe 4–9 ($\overline{X}$ = 6.39, sd = 0.81, n = 513), mode six (44.4%), basally paired.

SVL 128–303mm; AGL/SVL 50.0–67.5% ($\overline{X}$ = 57.8%, n = 261); TL/SVL 20.7–37.2% ($\overline{X}$ = 29.0%, n = 269); TD/TL 24.9–70.8% ($\overline{X}$ = 40.1%, n = 268); FLL/SVL 15.1–25.8% ($\overline{X}$ = 20.2%, n = 258); HLL/SVL 16.2–24.8% ($\overline{X}$ = 20.8%, n = 259); Hip/SVL 10.7–15.6% ($\overline{X}$ = 13.1%, n = 260); HL/SVL 18.3–25.7% ($\overline{X}$ = 21.8%, n = 260); HW/HL 83.5–109.4% ($\overline{X}$ = 95.4%, n = 263); HD/HL 53.2–74.2% ($\overline{X}$ = 62.1%, n = 253); IOC/HL 32.6–46.6% ($\overline{X}$ = 38.7%, n = 265); E–N/HL 23.0–30.8% ($\overline{X}$ = 27.0%, n = 154); E–E/HL 40.2–53.6% ($\overline{X}$ = 47.5%, n = 262); Eye/HL 15.9–24.6% ($\overline{X}$ = 19.2%, n = 263); Ear/HL 7.0–16.0% ($\overline{X}$ = 11.4%, n = 262); IparL/HL 12.9–26.3% ($\overline{X}$ = 19.4%, n = 253); FrontL(a)/HL 14.6–26.4% ($\overline{X}$ = 20.6%, n = 239); FrontL(c)/HL 19.0–28.3% ($\overline{X}$ = 22.8%, n = 16); IparL/FrontL(a) 65.3–135.8% ($\overline{X}$ = 94.3%, n = 273); IparW/IparL 49.5–99.2% (67.2%, n = 291); FrontW/FrontL(a) 37.6–153.1% ($\overline{X}$ = 81.1%, n = 275).

8.4.4 Allometry

Allometric values and calculated values for morphometric characters are presented in Table 8.28. All characters except tail length and hip width (both regressed against SVL) showed significant allometric growth. Axilla-groin length (against SVL) and eye-ear interval (against head length) showed positive allometry, while all other characters showed negative allometry.

8.4.5 Coloration (Fig. 55)

Colour and pattern variable. Dorsal ground colour mid-brown on body and tail, usually even; ground colour interrupted by blue-grey, cream, yellow or even orange bands, each 1–1.5 scales wide, formed of fine vermiculations coalescing to varying degrees. Usually 2–7 ($\overline{X}$ = 5.1, sd = 0.77, n = 266) pale bands between nape and hindlimbs, 1–5 ($\overline{X}$ = 3.2, sd = 0.79, n = 243) on tail. Some individuals also with yellow to orange vertebral blotches variably expressed on centre of scales.

Head dorsum variable; cream, yellow or orange, variably obscured by brown body ground colour. At maximum exposure, no brown on head; at least exposure, pale coloration restricted to lower temporals, supralabials and preauricular region. Brown pigmentation most prominent peripherally on shields, pale coloration most prominent centrally.

Venter yellow to blue-grey (latter more dominant ventrolaterally), immaculate or more commonly with obscure to prominent mid-brown flecks and spots, tending to align medially to form narrow (1/4–1/2 scale wide) stripes along scale margins, laterally to form bands of equal width.

Throat with brown flecks and spots along scale margins, tending when prominent to coalesce into a brown clouding on mental region and two bands over gular region.

Laterally, disjunction between predominantly dark dorsal colour and predominantly pale ventral colour clear but irregular.

Limbs yellowish to blue-grey, with varying degrees of brown infiltration, weakest below, but usually more strongly developed dorsally, especially on antebrachium and crus; brown on thigh tending to be organised dorsally into bands, leaving pale band across mid-thigh.

Soles yellow to blue-grey, with or without light brown clouding. Dark clouding most prominent distally on digits.

8.4.6 Asymmetry

Although asymmetry was common in individuals in many characters (up to 47.8% [n = 301] in the case of infralabials), significant asymmetry was not detected in mean number of supraciliaries, presuboculars, suboculars, supralabials, infralabials, posttemporals or subdigital lamellae (t-tests of asymmetrical cases). Significant asymmetry was detected only in mean number of postsuboculars (asymmetrical cases only [n = 80]: L: $\overline{X}$ = 4.01, sd = 0.755; R: $\overline{X}$ = 4.36, sd = 0.716; $t_{158} = 3.01^{**}$), although even in this case the difference between the sides becomes insignificant when all cases are considered (n = 310; L: $\overline{X}$ = 4.13, sd = 0.582; R: $\overline{X}$ = 4.22, sd = 0.572; $t_{618} = 1.94$, n.s.).

8.4.7 Sexual Dimorphism

Sexual dimorphism was not detected in mean number of supraoculars, supraciliaries, occipitals, presuboculars, suboculars, supralabials, posttemporals, midbody scales, paravertebral scales, axilla-groin scales, ventral scales, subcaudal scales or subdigital lamellae (t-tests) or degree of separation/contact of nasals, prefrontals or frontoparietals or presence of an azygous occipital (X^2 tests).

Sexual dimorphism was detected in mean number of postsuboculars (♂♂: $\overline{X}$ = 4.23, sd = 0.556, n = 288; ♀♀: $\overline{X}$ = 4.12, sd = 0.576, n = 226; $t_{512} = 2.09^{*}$), infralabials (♂♂: $\overline{X}$ = 9.37, sd = 0.862, n = 292; ♀♀: $\overline{X}$ = 9.21, sd = 0.805, n = 224; $t_{514} = 2.26^{*}$), infralabials contacting the postmental (♂♂: $\overline{X}$ = 2.27, sd = 0.462, n = 255; ♀♀: $\overline{X}$ = 2.14, sd = 0.342, n = 193; $t_{446} = 3.43^{***}$), and separation of frontal and first supraciliary (using categories broad to moderately separated, narrowly separated, contacting; ♂♂: 61:12:16; ♀♀: 49:11:3; $X^2_2 = 6.67^{*}$). In all of these cases, the difference between the means is minor compared to the range of variation, and the modes are equal. Consequently, there was no need to separate the sexes in assessing geographic variation.

There was no detectable sexual dimorphism in SVL. Males and females had similar minimum mature, mean mature and maximum sizes (♂♂: 224–303mm, $\bar{X}$ = 262.5mm, sd = 16.82, n = 128; ♀♀: 216–288mm, $\bar{X}$ = 259.5mm, sd = 17.86, n = 100, with only one female from Mondrain I. smaller than 222mm), without significant differences between the sexes (Mann-Whitney U test, z = 0.772, n.s.).

Mature males had significantly shorter bodies, longer heads and limbs, a longer but narrower tail, narrower hips and a slightly greater interparietal/frontal length ratio than mature females (Tables 8.29–8.30). The narrower hips, longer, narrower tails and longer heads and legs of males have been previously noted by Butler (1977), Bamford (1980), Stettler (1981) and Gross (1989). However, a broader head in males noted by Bamford (1980), Gross (1989) and Twigg *et al*. (1988) is not borne out by the data in this study.

8.4.8 Distribution

Temperate and semi-arid parts of south-western Australia, from the lower Murchison River region in the north-west (where it intergrades with *T. r. palarra*), to approximately latitude 123°E in the east, (where it intergrades with *T. r. asper*) (Fig. 49). Occurs from the coast, inland as far as 30km NE Yuna, Fields Find, 4mi W Callion, 3km N “Yindi” and Cundeelee. Possibly absent from or rare in the extreme south-west coast, with only a single record from Woolbales (WAM R47798) (see also How *et al*., 1987). Also present on five of the largest seven islands off the adjacent coast: Garden, Mondrain, Middle, North Twin Peaks and Salisbury Is., the only exceptions being Bald I. (Storr, 1965b) and Rottnest I., the latter occupied by *T. r. konowi*.

8.4.9 Geographic Variation

Geographic variation in *T. r. rugosa* has previously been analysed in the context of *T. rugosa* as a whole. However, a brief summary of variation within the subspecies is given here.

The most obvious variation was in coloration and tail length.

Material from the eastern interior (Goldfields region) had bright orange heads and orange bands on the body and tail dorsum, while southern and eastern coastal specimens had pale green-grey to yellow heads and generally green-grey pale bands on the body dorsum. In the north-west, the head was often less distinctively pale than in the south, and the pale body bands were often reduced in extent and intensity. Ventrally, the pattern of dark pigment was most boldly defined in the arid material, while often diffusely clouded or irregularly mottled in the south.

The south-western coastal populations had the longest, narrowest tails, and also showed a tendency for narrower heads.

Variation in other characters, including scalation, was slight, and mostly related to introgression with neighbouring subspecies towards the contact zones in the east and north-west.

8.4.10 Comparison with Other Taxa

Comparisons between *T. rugosa* and *T. adelaidensis, T. multifasciata, T. nigrolutea* and *T. occipitalis* have already been made (Chapters 4–7). All subspecies of *T. rugosa* differ from all taxa in the *T. scincoides* complex in possessing large, heavy dorsal body scales (paravertebral scales ≤38 *vs* ≥46), a short, blunt tail, divided subdigital lamellae, primary temporal scales and usually only one supraocular contacting the frontal (*vs* two).

T. r. rugosa differs from *T. r. asper* in the combination of a mode of three supraoculars (73%; *vs* two, 57%), usually 11–16 subcaudal scales (*vs* usually 16–25), usually 22–30 midbody scales (*vs* usually 19–25), a colour pattern involving a pale head, or at least pale temples, and dorsal body and tail bands composed of fine pale variegations. In addition, *T. r. rugosa* has a generally narrower head (as evidenced by the ratios HW/HL, IOC/HL, IparW/IparL) and longer, narrower tail (Tables 8.28 *vs* 8.32–8.34).

T. r. rugosa differs from *T. r. konowi* in coloration (dorsal pattern of pale-variegated bands *vs* diffuse pale variegations on a dark ground colour; usually pale head *vs* dark head; venter, when pigmented, usually with coarse brown variegations, stripes or bands *vs* diffuse grey-green clouding), larger adult size (maximum SVL 303mm *vs* 260mm), usual presence of a median occipital (79%; *vs* usual absence, 66%) and usual separation of first supraciliary and frontal (88%; *vs* contact at least unilaterally in 71%).

T. r. rugosa differs from *T. r. palarra* in coloration (dorsal pattern of pale-variegated bands *vs* dorsal pattern, when best developed, of narrow pale streaks on a brown ground; head usually pale *vs* head evenly brown; venter, when pigmented, usually with brown streaks, stripes and bands *vs* usually a large brown patch medially), usual separation of nasal scales (96%; *vs* usual contact, 68%), larger ear aperture (Ear/HL, $\overline{X}$ = 11.4% *vs* 6.5%; see also Tables 8.28, 8.47), and fewer midbody (20–30, $\overline{X}$ = 24.4 *vs* 26–35, $\overline{X}$ = 29.3) and paravertebral (20–30, $\overline{X}$ = 25.1 *vs* 23–38, $\overline{X}$ = 30.0) scales.

8.4.11 Habits and Habitats

T. r. rugosa has been reported from a number of semi-arid and near-coastal open habitats, particularly farmland, heaths, shrublands (including *Allocasuarina campestris*, *Halosarca* shrublands), mallee (including mallee/*Casuarina*, *E. uncinata* and *E. transcontinentalis* mallee habitats) and open eucalypt woodlands (including wandoo, yarri, tuart, York gum, Salmon Gum, *E. salubris* and *E. oleosa* woodlands) (Arnold *et al*., 1987; Burbidge *et al*., 1978; Burbidge & Boscacci, 1989; Chapman & Dell, 1978, 1979, 1980a,b, 1985; Christensen & Liddelow, undated; Dell & Chapman, 1977, 1979b, 1981; Dell & Harold, 1977, 1979; Demarz, 1955; Dudley, 1989; How *et al*., 1988; Licht *et al*., 1966; Robinson *et al*. 1987; V. Smith, 1990; Storr *et al*., 1983; Worsley Alumina, 1985). It has also been reported from *Banksia* woodlands (How & Dell, 1989). The subspecies appears to be rare in wetter or more closed habitats (Christensen *et al*., 1985; Demarz, 1955), although there are some records from dry sclerophyll forests, including jarrah and even karri (Christensen & Liddelow, undated; Licht *et al*., 1966; Nichols & Bamford, 1985; Worsley Alumina, 1985) and also pine plantations (Christensen & Liddelow, undated).

The topography, when reported in the literature, has been mostly flat or only gently sloping, with sandplains, light clay or loamy soils or saline claypans the most common substrates (Burbidge & Boscacci, 1989; Chapman & Dell, 1980a,b, 1985; Dell & Chapman, 1977; Dell & Harold, 1977; How *et al*., 1988), although the subspecies also occurs on stony soils, such as calcrete and granulitic plains (Dell & How, 1984) and has even been reported from stony hills

and granite outcrops (Dell & Chapman, 1981; How *et al*., 1988).

8.4.12 Taxonomic History and Type Material

Trachydosaurus rugosus gen. et sp. nov. was described by Gray (1825) in a brief description that reads simply: “body fusiform; head shielded; back covered with hard bony scales, like the frontal shields in form; abdomen with thin scales; feet four; toes 5–5; femoral pores none; tail short depressed.” This uninformative account was clearly not intended to be the type description, as Gray (1827), in describing the zoological results of P.P. King's surveying expedition, provided a much more extensive description under the heading “*Trachysaurus rugosus*, (n.s.)”. Gray (1825) mentions only the locality New Holland and the collector P.P. King. However, Gray (1827), although apparently basing his description on a single specimen from King George the Third's Sound collected by King, lodged in the Natural History Museum, London, mentions the existence of a second specimen in the collection of the Linnean Society.

As Gray (1825) mentioned only the King specimen, this must be considered to be the holotype. This specimen (BMNH 1946.8.5.1; Fig. 56) was described by Gray (1827) as “considerably injured” due to the evaporation of the preservative. It has not improved with age. The present condition of the specimen suggests that it not only dessicated, but also decomposed due to inadequate preservation at the time of collection. Most of the muscle tissue has rotted away, together with large areas of the epidermis, leaving, for the most part, osteoderms attached to a skeleton held together by ligaments. Many of the osteoderms are missing and the right fore and left hind limbs have fallen off. The poor condition of the specimen makes it impossible to provide a full description of the scalation and morphometrics of the type. However, the following characters are discernable: nasals broadly separated; prefrontals in broad contact; frontal undivided; supraoculars two; supraciliaries five, first broadly separated from frontal, last broadly separated from frontoparietals; frontoparietals in broad contact; occipitals three; median occipital present; presuboculars three; suboculars one (L side only); postsuboculars four (L side only); supralabials 9/10; infralabials 10/11, first three contacting postmental (L side only); primary temporal divided (L side only); lower secondary temporal divided; paravertebral scales 28; subcaudal scales 20; subdigital lamellae eight (R side only); SVL *ca*268mm; TL 65.5mm; HL 48.4mm; HW 43.5mm; HD 30.3mm; IparL 11.7mm; IparW 5.5mm.

The head shield configuration of a typical topotypic individual (AM R102316) is illustrated in Fig. 57.

The combination of type locality (King George Sound is at Albany, WA), the relatively gracile form, long tail, and (in a few places where epidermis remains) traces of pale body bands verify the subspecific identity of the holotype.

Wagler (1830) mentions *Scincus Peronii* in the synonymy of *Trachysaurus rugosus*, attributing the name to “Dumer. in Mus. Paris”. Presumably, the name was a manuscript name provided by Duméril. As the name was published as a junior synonym, without description, it is unavailable as published by Wagler (1830). However, Wagler (1833) provides a description and illustration of *Trachysaurus peronii*. The description, while apparently based primarily on Gray's descriptions, includes some additional data. The measurements provided are those of Gray (1827). The illustration, however, is clearly not of the same species as the description (McCoy, 1885), as it shows a lizard with a moderately long, conical tail (certainly greater than 40% of SVL, as given by Gray's measurements) and long toes (although the description states “digiti . . . breviusculi”). The illustration is certainly not conspecific with *Trachydosaurus rugosus* Gray. Wagler (1833) noted the existence of

three specimens, in the “Museum Londinense”, “Museum Societatis Linneanae Londinensis” (both presumably based on Gray's (1827) description), and the “Museum Parisiense”. It is presumably this latter specimen that Wagler examined to obtain the additional characters, and from which the name “*Scincus peronii* Dumer.” is derived. If the illustration is representative of the Paris specimen, then the description must be a composite of two species. However, as Wagler (1830) places the name in the synonymy of *Trachysaurus rugosus*, and Wagler (1833) gives the same synonymy in reverse, the name *Trachysaurus peronii* must be considered at least an objective junior synonym of *Trachydosaurus rugosus* Gray, and probably merely an unwarranted replacement name.

Brachydactylus typicus gen. et sp. nov. was described by Smith (1835) from material from the Swan River. Although the description is brief and the accompanying illustration of a hideously distorted specimen, the combination of type locality, moderately long tail (for *T. rugosa*), and coloration indicate that this taxon is synonymous with *Trachydosaurus rugosus* Gray. Smith gave only a single set of measurements (SVL six inches [=152mm]; tail length two inches [=51mm]), but subsequently notes that he had examined a second specimen: “Dr. Smith remarked that, until he met with a second specimen of this Lizard, he had considered the peculiar appearance of the tail as depending upon its having been injured, but now he was satisfied from having minutely compared the two, that it was the natural form”. Clearly the type series must be regarded as consisting of two syntypes.

Smith did not give any indication as to the depository of his types. However, a single stuffed and mounted specimen in the BMNH collection bears the inscription “Rugose stump tail *Trachydosaurus rugosus Brachydactylus typicus* Smith S. African Quart Journ.”, and was regarded as the holotype by Cogger *et al*. (1983). This specimen cannot be the specimen on which Smith based his measurements, as it has SVL *ca*244mm and tail length *ca*63mm. It is not possible on present information to either confirm or deny that this specimen is the second specimen mentioned by Smith, and that it is therefore a syntype. If it can be positively identified as a syntype, it must be considered to have been designated lectotype by the actions of Cogger *et al*. (1983).

The specimen has the following combination of character states: nasals moderately separated; prefrontals in broad contact; frontal undivided; supraoculars two; supraciliaries five; occipitals two; median occipital present; presuboculars three; suboculars absent; postsuboculars four; supralabials 8/9; infralabials nine (L side only), first two contacting postmental; primary temporal paired; lower secondary temporal paired; posttemporals three; midbody scales 24; paravertebral scales 26; subcaudal scales more than 16; HL 46.6mm; HW 37.1mm; HD 26.7mm; IOC 17.2mm; E–N 13.8mm; E–E 21.6mm; Eye 6.4mm; Ear 4.2mm; IparL 10.2mm; IparW 5.7mm; FrontL(a) 8.5mm; FrontW 8.3mm; pale bands on body four.

8.4.13 Reproduction

8.4.13.1 Size at maturity:

Mature-sized males had SVL 224–303mm, $\bar{X}$ = 262.5mm, sd = 16.82, n = 128, while mature-sized mainland females had SVL 222–288mm, $\bar{X}$ = 260.3, sd = 17.14, n = 98 (Figs. 58–59). One smaller mainland female (WAM R54393; SVL 209mm) was gravid, with oviducal masses. However, this female was the only one of several mainland females below 222mm collected during the breeding season that showed any signs of reproductive activity. Hence I now believe that this individual reached maturity at an abnormally small size, although I had earlier (Shea, 1989) accepted its maturity in determining size at maturity in this taxon. Chapman and Dell (1985) report two gravid females with SVL 200–230mm.

These records are apparently based on specimens reported by Chapman and Dell (1980a,b), one of which had a grossly enlarged ovarian follicle, the other a single 10mm “yolky” follicle. However, I have only been able to accurately determine litter size from follicles larger than 16mm in this study, and hence I don't consider that a 10mm follicle confirms maturity. The two mature Mondrain I. females were also slightly smaller (both gravid, SVL 216–226mm) than mainland material. However, both with and without these two individuals, mature males and females were of similar and non-significantly different size.

Gravid females were similar, and not significantly different in size to other, non-gravid, mature females (gravid: 216–284mm, $\overline{X}$ = 259.4mm, sd = 19.04, n = 42; non-gravid: 225–288mm, $\overline{X}$ = 258.3mm, sd = 17.89, n = 54; Mann-Whitney U test, z = 0.266, n.s.).

8.4.13.2 Male reproduction:

Testis length did not increase isometrically with SVL (Fig. 58) and hence testis length, rather than a gonosomatic index, was used to infer seasonal patterns of reproduction.

Testis length and condition show marked seasonal variation (Fig. 60). Testes are small and shrunken in January, show a gradual increase in size through autumn and winter, and are largest and most turgid between October and early November. In late November and December, while testes remain long, then are mostly flaccid. Between December and April, most testes are flaccid or narrow and flattened (57.7%, n = 26) and even those that are turgid are mostly less than 19mm long (90.9%, n = 11). Between September and November, in contrast, only 9.8% (n = 61) of animals have non-turgid testes, while 70.9% of the turgid testes are more than 19mm long.

The data suggests that spermiogenesis peaks in mid-spring (October-early November) and is rapidly followed by a period of testicular regression. Winter and early spring spermiogenesis was also inferred by Bamford (1980) from dissection of winter-collected specimens.

8.4.13.3 Female reproduction:

Follicle diameter is minimal in summer (December-February) in non-gravid females. Follicles showed a gradual increase in size through autumn and winter, followed by a rapid increase in diameter from late September through to early November, with the largest yolky follicles in the first half of November. The earliest female with oviducal eggs was collected 2 November, and embryos were found in most females collected in summer, up to 22 February, with a single gravid female collected 29 April (Fig. 61).

This data is in agreement with literature records. Enlarged yolky ovarian follicles have been reported in November (Chapman & Dell, 1980b), ovulation has been reported to be in November (Fergusson & Bradshaw, 1991), while births have been reported in early autumn (Serventy, 1968, 1970; Holmes & Light, 1983), April (Anon, 1972c), March-April (Fergusson & Algar, 1986; Fergusson & Bradshaw, 1991) and 18–28 March (Bamford, 1980, 1982) in wild and local captive animals, and on 27 March and 11 April in northern hemisphere captives maintained in an Australian seasonal cycle (Gross, 1989; Slavens, 1988), although the subspecies for the latter record was not reported. Leake (1962) also notes that young are born about the end of March. The gestation period has been estimated as between 17–21 weeks (Bamford, 1980) and 4 months (Gross, 1989).

Taken together, the data suggest that vitellogenesis occurs in spring, peaking in late October-early November, ovulation occurs in November, and young are usually born in late March-early April, after approximately 5 months gestation.

With the long gestation period, it is not considered possible for more than one litter to be produced per year.

8.4.13.4 Mating season:

The mating season has been reported to be between October and November (Bradshaw, 1984; Fergusson & Algar, 1986; Visser & Horn, 1989). During the breeding season, males and females form pairs which remain together for several weeks, with the males fighting during this period (Leake, 1962; Serventy, 1969; Serventy & Raymond, 1974b; Bamford, 1980, 1982). Pairing was first noted for this subspecies by Nind (1832). Bamford (1980) observed pairs between 12 October and 11 November at a site near Perth, although Bamford (1982) states that the breeding season is September-October in this population.

An October–November mating season corresponds well to the peak in both male and female reproductive cycles.

8.4.13.5 Frequency of reproduction:

Between December and February (the middle of the period of gestation), 15 of 23 females (65.2%) had oviducal eggs or embryos. None of the eight females showed any signs of follicular enlargement, and presumably did not breed in that season. The frequency of non-breeding females is almost identical to that for *T. r. asper*.

8.4.13.6 Litter size:

Of 42 females with either countable enlarged ovarian follicles (≥16mm), oviducal egg masses or embryos, the number of follicles or young was 1–3 ($\overline{X}$ = 1.7, sd = 0.56), with mode two (59.5%). Mean litter size based on number of enlarged follicles did not differ significantly from the mean based on oviducal masses (1–3, $\overline{X}$ = 1.8, sd = 0.60, n = 23 *vs* 1–2, $\overline{X}$ = 1.6, sd = 0.51, n = 19; t_{40} = 1.15, n.s.).

More follicles and young were generally present on the right side than the left (follicles: in total, 25 *vs* 16; R>L:R=L:R<L = 9:10:4; oviducal masses: in total, 15 *vs* 11; R>L:R=L:R<L = 6:8:4) although in no case was the asymmetry significant (X^2 tests).

As in *T. r. asper*, there was evidence for extra-uterine transfer of ova. One of the two females in which the number of corpora lutea was estimated from gross examination had the same number and distribution as for oviducal young, while the other showed 2L/0R corpora lutea, but 1L/1R oviducal masses, indicating a left to right shift of one ovum.

There is some evidence for a relationship between litter size and maternal SVL. Only the largest females (SVL ≥267mm) had litters of three, although litters of one were also recorded for large females (Fig. 62). The correlation between litter size and maternal SVL is almost statistically significant (r = 0.245, n = 42, $F_{1,40}$ = 2.556, P = 0.12).

General statements that *T. rugosa* gives birth to between one and two young, usually two, and rarely three, are abundant in the literature (Angel, 1949; Anon, undated, c; Banks, 1980; Berridge, 1926; Bustard, 1970; Cogger, 1967, 1975, 1980a; Dale, 1973; Delean *et al.*, 1983; Drury, 1981; Fuhn, 1975; Goode & Cann, 1974; Honders, 1975; Hvass, 1961; Klingelhoffer, 1957; Mattison, 1989; Owner, 1970; Richmond, 1984; Sadleir, 1970; Saville-Kent, 1897; Seth-Smith, 1950; Serventy, 1965; Shine, 1985a; Spencer, 1900; Stanbury & Phipps, 1980; Stettler, 1981; Swanson, 1976; Switak, 1986; Terent'ev, 1961; Wilson & Knowles, 1988; Worrell, 1963). Most of these, however, are not supported by statistical data and are apparently secondary citations of other literature. Further, most records lack locality data and are hence impossible to assign to subspecies. Amongst the general statements referring specifically to *T. r. rugosa* are Anon (1972b), Bush (1981), le Souef (1900, 1907), Leake (1962), Serventy (1968, 1970) and Tingay and Tingay (1982). Most of these agree in giving a range of 1–2, although Leake (1962) gives a maximum of four and le Souef (1900, 1907) a mode of four.

Specific published data on litter size for *T. r. rugosa*, in contrast, are very few. Nind (1832) records two, Anon (1972c) a single case of two, Bamford (1980, 1982) a range of 1–2 ($\overline{X}$ = 1.4, n = 20), Chapman and Dell (1980b) a single large follicle in one female, and Gross (1989) a single young. Slavens (1988) and Slavens and Slavens (1990) report three litters of twins to an unspecified subspecies.

T. rugosa has been bred by a number of zoos (Table 8.31), although again, most records cannot be identified to subspecies. Most records are of 1–2 young born per year, suggesting single litters.

8.4.13.7 Size of young at birth:

The smallest wild-caught animal collected close to the normal time of birth (WAM R53114; 8.v.1976) had SVL 136mm, with three additional juveniles collected in May to June only slightly larger (SVL 146–151mm), and two juveniles without dates of collection with SVL 140–152mm. However, the smallest animal seen (WAM R44993; SVL 128mm; 9.x.1971) was collected well after the normal period of birth, and was presumably even smaller at birth. Bamford (1980, 1982) recorded SVL for three pairs of twins and six singletons. The twins were significantly smaller ($\overline{X}$ = 153.5mm, n = 6) than the singletons ($\overline{X}$ = 171.3mm, n = 6). In contrast, twins born in captivity to a wild-caught female from Coolgardie had SVL 168–179mm (*pers. obs.*), while a captive-bred singleton (Gross, 1989) had a total length of 170mm (equivalent to SVL of approximately 131mm; Table 8.28). Other records of neonate size are 17–18cm total length (n = 2; equivalent to 131–139mm SVL; Anon, 1972c), 7 inches total length (n = 1; equivalent to 137mm SVL; Serventy, 1968), and 18cm total length (equivalent to 139mm SVL; Serventy & Raymond, 1974b). Consequently, I infer normal size at birth to be approximately 145mm, but with marked variation, with minimum size 128mm or less.

Birth mass is also variable. Bamford (1980, 1982) records mean mass of twins as 100.1g (n = 6) and of singletons as 128.6g (n = 6). The Coolgardie twins were 84.6–101.4g, while the singleton reported by Gross (1989) had mass 75g. Serventy (1968) reports a singleton of 3 ounces (= 85g), while Serventy & Raymond (1974b) give 65g. Neonates eat the placenta and fetal membranes (Bamford, 1980) and it is possible that some of this variation is a reflection of weighing before or after placental ingestion. Condition of the gravid female in captivity may also play a role.

8.4.13.8 Relative litter mass:

There are few data on relative litter mass available for *T. r. rugosa*. Fergusson and Algar (1986), presuming birth from sudden decreases in mass of radiotracked wild gravid females during March and April, stated that "up to 40% of the weight carried by a pregnant female is due to the presence of one or more fetuses, associated membranes, and fluids". Using changes in mass estimated from their graphically presented data, I calculate relative litter mass for the four females that showed rapid weight loss as 62%, 45%, 44% and 39%. The Coolgardie female that gave birth to two young in captivity had a relative litter mass of 46% (*pers. obs*.). Bamford (1980) presented data on percentage weight loss for gravid females that gave birth to litters of one and two. Converting these figures to relative litter mass by the formula $((1-x/100)^{-1}-1)x100$ gives mean relative litter mass for twins of 45.1% (n = 3) and for singletons of 29.6% (n = 7).

8.4.13.9 Age at maturity:

Growth is rapid. Gross (1989) reports that a neonate grew in the first five months from 17 to 24cm total length, with mass increasing from 75 to 190g. Bamford (1980, 1982), on the basis of growth of captive neonates, and mark-recapture data, suggested that maturity was attained at the age of three years, although he estimated minimum size at maturity as 250mm SVL. This is larger than the figure determined in this study, and suggests that maturity might be reached in the second year in some specimens, as some two year olds had attained 235mm SVL.

8.4.13.10 Longevity:

Data on longevity in *T. rugosa* are mostly based on captive specimens, with no indication as to provenance to determine the subspecific identity. Flower (1925) gives five longevity records from 4yrs 6mo 16d to 7yrs 1mo 14d. Conant and Hudson (1949) give a record of 7yrs 11mo, Bowler (1977) and Slavens (1989) give 14yrs 6mo, Slavens and Slavens (1990) give 9yrs 7mo for a still-living animal, while Munsch (1979) kept the species for almost 10yrs. The oldest *T. r. rugosa* known to Bamford (1982) was at least 12yrs old. Holmes and Light (1983) suggest a rather greater maximum age based on a retained mass of shed skin in the ear of a large wild-caught specimen of *T. r. rugosa*. Assuming that shedding is annual, the estimate of 20 layers of shed skin in the mass suggests a minimum age of 20 years. However, while *T. rugosa* often sheds its skin in mid to late summer (Warburg, 1965a; Bull, 1978; Holmes & Light, 1983), some individuals, at least in captivity, can shed more frequently than annually (Shea, 1980, and references therein).

8.4.13.11 Sex ratio:

Overall, the adult sex ratio was slightly skewed towards males, with the ratio of mature-sized males:females 126:98, although this was not significantly different to 1:1 ($x^2_1 = 3.50$, n.s.). There were significant seasonal differences in adult sex ratio (summer: 18:24; autumn/winter: 18:19; spring: 69:39; $x^2_2 = 6.55^{*}$), with many more males than females collected in spring ($x^2_1 = 8.33^{**}$). This probably reflects increased activity of males searching for mates in spring. Increased activity in spring has been reported for this subspecies (August–October, McFarland & McFarland, 1977; October–November, Bradshaw, 1984), as with *T. r. asper*.

8.5 Tiliqua rugosa asper

8.5.1 Synonymy

Tiliqua rugosa asper (Gray, 1845a)

Trachydosaurus asper Gray, J.E. (1845a). *Catalogue of the Specimens of Lizards in the collection of the British Museum*. Trustees of the British Museum, London. (289pp.) [103].

Lectotype (designated by Wells and Wellington, 1985): BMNH 42.6.29.58.

8.5.2 Diagnosis

T. r. asper differs from all other *Tiliqua* species in the combination of large, heavily ossified dorsal scales, short, blunt tail and divided subdigital lamellae. It differs from all other subspecies of *T. rugosa* in having a very short, broad tail with few subcaudals (11–20, rarely >16), few midbody scales (19–27, rarely >25), few paravertebral scales 18–31, rarely >28), a broad head, moderate ear and dark head dorsum and in lacking pale variegated bands across the body dorsum.

8.5.3 Description

Nasals usually moderately separated (80.2%, n = 697), less commonly broadly separated (3.9%), narrowly separated (12.1%), in point contact (1.9%) or narrowly to moderately contacting (1.0%), or separated by an interposed median internasal (1.0%); postnasals usually fused dorsally to nasals, separated ventrally by a postnarial suture, rarely completely distinct from nasals unilaterally (3.8%, n = 660) or bilaterally (12.1%), or completely fused to nasals bilaterally (0.2%); prefrontals usually in broad to moderate contact (81.6%, n = 706), less commonly in narrow (13.0%) or point (0.3%) contact, narrowly to broadly separated (3.8%), or with an interposed median scale (1.3%); supraoculars usually two (57.0%, n = 670), or three (24.9%) bilaterally, with first only contacting frontal, or asymmetrical (2/3) (7.9%), rarely five with first two contacting frontal bilaterally (0.4%). four with first two contacting frontal bilaterally (2.5%), four with first contacting frontal bilaterally (0.3%), three with first two contacting frontal (3.4%), all fused (0.1%), or asymmetrical (5/4(2/2), 0.1%; 4/3(2/2), 0.6%; 4/3(2/1), 0.3%; 4/3(1/1), 0.3%; 3/3(2/1), 0.1%; 3/2(2/1), 1.3%; 2/1(1/1), 0.1%; 4/2(2/1), 0.1%; 4/2(1/1), 0.1%); supraciliaries 3–8 ($\overline{X}$ = 5.65, sd = 0.70, n = 1293), usually six (58.0%) or five (29.9%); when six supraciliaries, and two supraoculars, first supraciliary large, a little taller than long, projecting strongly between prefrontal and first supraocular, second low, longer than tall, tapering caudally, contacting first supraocular, third smallest, square, contacting first supraocular, fourth only a little larger than third, contacting and projecting slightly between first and second supraoculars, fifth subequal or slightly larger than fourth, contacting second supraocular, sixth large, a little taller than long, projecting strongly between second supraocular and parietal; reduction to five supraciliaries often due to fusion of third and fourth; first supraciliary usually usually broadly to moderately separated from frontal bilaterally (95.6%, n = 659), rarely narrowly separated (2.0%), in narrow to broad contact (1.7%), or asymmetrical (broadly separated/broad contact, 0.2%; narrowly separated/narrow contact, 0.2%; broadly separated/point contact 0.2%); last supraciliary usually broadly to moderately separated from frontoparietals bilaterally (99.4%, n = 657), rarely narrowly separated (0.3%), in broad contact ((0.2%) or asymmetrical (moderately separated/narrow contact, 0.2%); frontoparietals paired, usually in broad to moderate contact (82.6%, n = 679), less commonly in narrow contact (12.1%), or fragmented (4.4%), rarely narrowly to moderately separated (0.3%) or with an azygous scale interposed (0.6%); occipitals 1–3 ($\overline{X}$ = 2.14, sd = 0.40, n = 1302), usually two (81.8%); median azygous

occipital usually present (84.3%), rarely absent (15.7%); loreals usually two in horizontal series, rarely one unilaterally (n = 9) or bilaterally (n = 10), or three unilaterally (n = 2) or bilaterally (n = 2); rostral loreal rarely vertically paired unilaterally or bilaterally (n = 1 each); caudal loreal rarely vertically paired unilaterally (n = 4) or bilaterally (n = 21); subocular ring complete; presuboculars 2–5 ($\overline{X}$ = 3.26, sd = 0.61, n = 1396), usually three (59.0%) or four (31.9%); suboculars 0–2 ($\overline{X}$ = 0.38, sd = 0.52, n = 1402), usually absent (63.1%); postsuboculars 2–6 ($\overline{X}$ = 4.21, sd = 0.57, n = 1400), usually four (67.4%); supralabials 7–12 ($\overline{X}$ = 8.83, sd = 0.63, n = 1403), usually nine (60.0%) or eight (28.2%), antepenultimate below centre of eye, penultimate usually single bilaterally (n = 645), rarely vertically paired unilaterally (n = 1) or bilaterally (n = 1), last usually single bilaterally (n = 638), rarely vertically paired unilaterally (n = 3) or bilaterally (n = 6); primary temporal usually vertically paired bilaterally (n = 577), occasionally single unilaterally (n = 20) or bilaterally (n = 15), or divided into three unilaterally (n = 17) or bilaterally (n = 17), rarely divided into three scales on one side, four on the other (n = 1); upper secondary temporal usually vertically paired bilaterally (n = 362), less commonly single unilaterally (n = 86) or bilaterally (n = 139), occasionally divided into three scales unilaterally (n = 24) or bilaterally (n = 34), or rarely single/divided into three (n = 2); occasional identifiable abnormalities of temporal scales seen, including exclusion of upper scale of lower secondary temporal series from contact with primary temporals unilaterally (n = 11) or bilaterally (n = 2), fusion of upper scale of primary temporals with upper secondary temporal unilaterally (n = 2) or bilaterally (n = 5), fusion of upper scale of lower secondary temporals with upper secondary temporal unilaterally (n = 5) or bilaterally (n = 1) and fusion of upper scales of both primary and lower secondary temporals with upper secondary temporal bilaterally (n = 1); posttemporals 2–4 ($\overline{X}$ = 2.60, sd = 0.50, n = 1314), usually three (59.0%); rostral ear lobules absent; infralabials 7–12 ($\overline{X}$ = 8.92, sd = 0.76, n = 1405), usually nine (52.8%) or eight (25.8%), scales in caudal part of row irregularly paired; usually first two infralabials contacting postmental, less commonly first three unilaterally (12.0%, n = 684) or bilaterally (7.6%), rarely first only unilaterally (1.9%) or bilaterally (1.0%), or 3/1 (0.1%) or 0/2 (0.1%).

Midbody scales 19–27 ($\overline{X}$ = 22.1, sd = 1.42, n = 704), rarely (1.7%) more than 25; paravertebral scales 18–31 ($\overline{X}$ = 23.6, sd = 1.94, n = 685), rarely (2.0%) more than 28; paravertebral scales between axilla and groin 12–22 ($\overline{X}$ = 15.9, sd = 1.54, n = 684); ventral scales 52–76 ($\overline{X}$ = 62.9, sd = 4.18, n = 664), rarely (2.9%) above 71; subcaudal scales 11–20 ($\overline{X}$ = 13.8, sd = 1.27, n = 624), rarely (1.6%) above 16; exceptionally high values for all body scalation characters mostly restricted to some South Australian islands; lamellae below fourth toe 4–9 ($\overline{X}$ = 5.79, sd = 0.72, n = 1307, mode six (49.7%), basally paired.

SVL 107–341mm; AGL/SVL 48.3–69.9% ($\overline{X}$ = 59.1, n = 678); TL/SVL 14.5–30.2% ($\overline{X}$ = 21.5%, n = 648); TD/TL 39.4–103.7% ($\overline{X}$ = 66.2%, n = 644); FLL/SVL 16.5–25.3% ($\overline{X}$ = 20.0%, n = 668); HLL/SVL 16.6–25.3% ($\overline{X}$ = 21.0%, n = 668); Hip/SVL 11.3–17.5% ($\overline{X}$ = 13.8%, n = 680); HL/SVL 16.6–27.1% ($\overline{X}$ = 20.3%, n = 675); HW/HL 83.4–125.3% ($\overline{X}$ = 103.5%, n = 674); HD/HL 50.9–72.9% ($\overline{X}$ = 60.4%, n = 669); IOC/HL 35.8–52.4% ($\overline{X}$ = 42.5%, n = 668); E–N/HL 20.8–31.7% ($\overline{X}$ = 26.7%, n = 653); E–E/HL 41.0–55.4% ($\overline{X}$ = 48.0%, n = 672); Eye/HL 14.9–27.3% ($\overline{X}$ = 19.0%, n = 672); Ear/HL 7.6–18.8% ($\overline{X}$ = 12.4%, n = 656); IparL/HL 12.4–25.3% ($\overline{X}$ = 18.2%, n = 657); FrontL(a)/HL 13.5–26.6% ($\overline{X}$ = 19.2%, n = 436); FrontL(c)/HL 16.7–28.4% ($\overline{X}$ = 22.1%, n = 231); IparL/FrontL(a) 56.8–

132.3% ($\bar{X}$ = 97.2%, n = 442); IparW/IparL 52.1–130.9% ($\bar{X}$ = 81.4%, n = 680); FrontW/FrontL(a) 58.2–116.9% ($\bar{X}$ = 85.7%, n = 449).

8.5.4 Allometry

In order to minimise the potential effect of the marked geographic variation in adult size from the north-east to the west of the distribution, morphometric data was analysed in four sets: all data pooled, eastern populations (1–11), “southern” populations (12–29) and western populations (30–34). Although the “southern” group consists of two distinct color morphs (populations 12–14 and 15–29), minimum mature and maximum size were similar for both, and hence they were pooled. Allometric values for each data set, and calculated values for the latter three sets, are presented in Tables 8.32–8.35. All characters except tail length showed allometric growth. In all four data sets, the relationship between tail length and SVL was not significantly different from isometry. Statistically significant negative allometry, or (in a few cases) a non-significant trend towards negative allometry was consistently seen across all groups in most other characters. The only characters showing positive allometry were axilla-groin length (*vs* SVL: significant in all groups) and eye-ear interval (*vs* head length; significant in the pooled data and in southern populations, same direction of allometry in eastern and western groups). Head depth (compared to head length) showed slight but significant negative allometry in the eastern populations, a non-significant trend towards negative allometry in the pooled and western groups, but a non-significant trend towards positive allometry in the southern populations.

8.5.5 Coloration (Fig. 63)

Coloration variable, pattern usually irregular.

Pale dorsal ground color cream or pale to bright yellow, usually largely or completely obscured by light to dark brown, leaving only scattered pale flecks and blotches. At melanistic extreme, no trace of pale coloration, entire dorsum dark brown. Brown pigmentation usually of uneven darkness, darkest in centre of scales, paler about periphery. Exposed pale ground color ranges from randomly scattered fine yellow or white flecks to yellow blotches. Blotches most often on apices of scales, often largest on paravertebral scales, and occasionally transversely aligned, particularly in juveniles. When present, pale bands on body 4–7 ($\bar{X}$ = 5.3, sd = 0.66, n = 93), first either on nape or caudal to forelimbs, last cranial to forelimbs; pale bands on tail 1–4 ($\bar{X}$ = 3.0, sd = 0.82, n = 73), first just caudal to hindlimbs, and strongest.

Head dorsum and face mottled pale to dark brown; pale markings, when present, mostly restricted to sparse to moderately dense yellow flecks dorsally, more solid spotting on lips.

Ventral ground color cream or pale to bright yellow, rarely immaculate, usually with mid to dark brown streaks and bands, which may, in extreme cases, coalesce to produce an evenly dark brown venter. Pale markings retained for longest on throat (but not chin) and laterally on body. Transverse dark elements 1–3 scales wide, longitudinal elements up to one scale wide.

Limbs yellow, with varying degrees of mid to dark brown variegation, at maximum evenly dark, at minimum with about half of fore- and hindlimb dorsum brown, some brown

vermiculations on hindlimb venters. Usually (except in melanistic individuals) a yellow band dorsally across thigh.

Soles yellow, usually with a heavy dark brown infiltration.

8.5.6 Asymmetry

Although asymmetry was commonly seen in individuals (up to 42.6% [n = 681] in the case of infralabials), statistically significant asymmetry was not detected in mean number of presuboculars, supralabials, infralabials, occipitals, posttemporals, or subdigital lamellae (t-tests of asymmetrical cases). Significant asymmetry was detected in mean number of suboculars (L: $\overline{X}$ = 0.45, sd = 0.54, n = 202; R: $\overline{X}$ = 0.66, sd = 0.56, n = 202; $t_{402} = 3.84^{***}$), postsuboculars (L: $\overline{X}$ = 4.28, sd = 0.70, n = 208; R: $\overline{X}$ = 4.48, sd = 0.74, n = 208; $t_{414} = 2.83^{**}$) and supraciliaries (L: $\overline{X}$ = 5.38, sd = 0.81, n = 154; R: $\overline{X}$ = 5.66, sd = 0.83, n = 154; $t_{306} = 3.00^{**}$). In all three variables, the difference between the sides was minor, and the modal value the same for both sides when all cases were compared. Further, when all cases were used, the difference became non-significant for postsuboculars and supraciliaries, and was only barely significant for suboculars (L: $\overline{X}$ = 0.35, sd = 0.50, n = 683; R: $\overline{X}$ = 0.41, sd = 0.53, n = 683; $t_{1364} = 2.13^{*}$).

8.5.7 Sexual Dimorphism

Statistically significant sexual dimorphism was not detected in the following meristic characters: supraoculars, supraciliaries, occipitals, presuboculars, postsuboculars, supralabials, infralabials, infralabials contacting postmental, posttemporals, midbody scales, subdigital lamellae (t-tests); degree of separation/contact of prefrontals, frontoparietals, or first supraciliary and frontal (X^2 tests), or presence of an azygous occipital or a distinct postnasal (X^2 tests).

Significant sexual dimorphism was detected in mean number of suboculars (♂♂: $\overline{X}$ = 0.41, sd = 0.53, n = 718; ♀♀: $\overline{X}$ = 0.34, sd = 0.49, n = 556; $t_{1272} = 2.33^{*}$), degree of separation of nasals (using categories broadly/moderately separated, narrowly separated, contacting; males with lower than expected frequencies of narrow separation; 2x3 contingency table; $X^2_2 = 7.68^{*}$), and in all scalation characters related to body and tail length (paravertebral scales: ♂♂: $\overline{X}$ = 23.4, sd = 1.82, n = 356; ♀♀: $\overline{X}$ = 23.9, sd = 2.14, n = 267; $t_{621} = 2.84^{**}$; axilla-groin scales: ♂♂: $\overline{X}$ = 15.8, sd = 1.34, n = 355; ♀♀: $\overline{X}$ = 16.3, sd = 1.74, n = 266; $t_{619} = 4.14^{***}$; ventral scales: ♂♂: $\overline{X}$ = 62.7, sd = 3.82, n = 355; ♀♀: $\overline{X}$ = 63.4, sd = 0.45, n = 266; $t_{619} = 2.03^{*}$; subcaudal scales: ♂♂: $\overline{X}$ = 14.0, sd = 1.28, n = 324; ♀♀: $\overline{X}$ = 13.6, sd = 1.28, n = 241; $t_{563} = 3.21^{**}$). In the case of suboculars, the difference is minor, and barely significant, considering the large sample size, with the mode for both sexes (0) the same, while in the case of the body and tail scalation characters, the differences are minor compared to the range of variation, both within populations and overall. Consequently, separation of the sexes in analysing geographic variation in meristic characters is not warranted.

There was no detectable sexual dimorphism in SVL. Males and females had similar sizes at maturity and maximum sizes in eastern (populations 1–11), southern (populations 12–14), central (populations 15–29) and western (populations 30–34) material (see below, under adult size), and there were no significant differences between mature-sized males and

females in any of these groups (Mann-Whitney U tests; P > 0.05). Sexual dimorphism in SVL in a single population was similarly not detectable by Bull (1988), although females were significantly heavier than males. However, Sarre *et al*. (1991) reported significant (though minimal) differences in SVL for South Australian offshore islands.

Sexual dimorphism in other morphometric characters was assessed for the same four groups as for allometry (Tables 8.36–8.43). Most characters showed significant sexual dimorphism in at least three of the four data sets, with the direction of the dimorphism constant in all data sets. The only exceptions were eye-naris interval (western males with significantly higher values than western females, but elsewhere, and in the overall sample, a non-significant trend for lower values for males), eye-ear interval (not significantly different in eastern, southern, and total sets, significantly different slopes in western material, with direction of dimorphism size-dependent), interparietal length (against head length, significant only for eastern data set, where males having lower values, trend in same direction for southern material, but in opposite direction in western material; against frontal length, significant only for western material, where regression line for females non-significant, but with males having slightly lower values than females in all data sets) and interparietal width (significant overall and in eastern material, males with higher values in east, trend in same direction in west, opposite direction in south).

In other morphometric characters, males consistently had shorter bodies, narrower hips, narrower (both at maximum width and interocular distance) and shallower heads, smaller eyes and ears and shorter frontals than females, but longer head and limbs, a broader frontal, and a longer but narrow tail. The sexual dimorphism in tail proportions has previously been noted (Haacke, 1883; Schneider, 1941; Horn, 1980; Sarre *et al*., 1991), while the trend to larger heads has been reported by Beste (1973) and Sarre *et al*. (1991). However, a trend for broader heads in males reported by Tyler (1962), Bourne *et al*. (1986a,b) and Bull (1988, 1990) is not apparent in the material examined here, with males having proportionally narrower heads. It is possible that the general trend towards lower ratios for head shape variables in males is a consequence of the greater head length in males.

8.5.8 Distribution

Dry parts of eastern Australia, south of a line through Clermont, Aramac, “Maneroo”, Birdsville, Maree, the Lake Bring region, Fisher, 16km NW Hughes, 98km N Loongana and 70mi NE Rawlinna. East to about the Great Dividing Range (Emerald, Jandowae, 4mi S Yetman, Gunnedah, Bathurst and district, Binda, 7mi E Yass, Finley, 3km W Muckleford, Crawford River region and Marp), and west to about 40km W Caiguna and the Naretha district, where it begins to intergrade with *T*. *r*. *rugosa* (Fig. 49). Possibly occurs further north in Queensland (“hills behind Mackay”; Anon, 1973). Also found on Weerona, Wardang, Reevesby, Spilsby, Duffield, Flinders and St Peters Is., and probably introduced to Troubridge Is. (Sarre *et al*., 1990). Also reported, without specimen records, from the following islands in the Sir Joseph Banks group: Hareby, Kirkby, Langton and Winceby (Tubb, 1938b). Reportedly introduced to Kangaroo I. in 1926 (Waite, 1927; Bartlett, in Terrill, 1948; Wheeler, 1960; Houston & Tyler, 1979; Thomson *et al*., 1987), although I have seen no specimens from that island. Occasional records from east of the Great Dividing Range (Beecroft, Hyde Park, Bellevue Hill, *ca* 2km N Coffs Harbour, 30.8km N Colo River crossing on Putty Rd, Werribee) have mostly been associated with major cities, and are probably escaped or released captives.

8.5.9 Geographic Variation

Geographic variation within *T. r. asper* has previously been discussed in the context of the species as a whole. However, a summary of the major features of morphological variation within *T. r. asper* is given here.

On the mainland, four regions may be defined on the basis of coloration and adult size. In the east, animals were melanistic and large, with the darkest animals associated with the western slopes of the Great Dividing Range in NSW. In the west, animals were small and pale, with a yellow dorsal ground colour partially obscured by brown spots and flecks, and a pale venter. Between these extremes, in eastern SA and western NSW, animals were of intermediate size, and predominantly dark to mid brown dorsally, with yellow flecks and spots, and yellow with brown variegations ventrally. Southeastern animals were similar in size to populations to the northwest (eastern South Australia) but differed in coloration, with a tendency to solid tan bands across the body dorsum. Variation in scalation in these mainland populations was relatively minimal. To the west of Eyre Peninsula, there was a higher frequency of three supraoculars and of contact between first supraciliary and frontal (although still much lower than in *T. r. konowi*), and a trend towards lower posttemporal and ventral scale counts. Eastern SA and southern Victorian populations, possibly associated with rangelands and their foothills, showed slightly elevated presubocular, postsubocular and paravertebral counts. Otherwise, the most divergent populations were about the northern and eastern periphery, with various combinations of lower supraciliary, supralabial, infralabial and subdigital lamellae, lower or higher subocular and higher postsubocular counts.

In contrast to the relative uniformity of scalation on the mainland, insular populations showed great variation in scalation and little uniformity between islands. The Sir Joseph Banks islands were characterised by smaller dorsal body scales (high midbody, paravertebral counts, the former shared with St Peters I.), yet only Spilsby, Duffield and St Peters I. had similarly elevated ventral counts, Reevesby I. having very low ventral counts. Within the Sir Joseph Banks group, there was relatively little uniformity, with Reevesby notable for an increased frequency of contacting nasals (absent on other islands) and first two supraoculars contacting the frontal, and increased numbers of pre- and postsuboculars (shared with St Peters I.), supralabials (shared with Spilsby I.) and infralabials (shared with St Peters and Duffield I.), but reduced numbers of suboculars (shared with Spilsby and St Peters I.).

The Troubridge I. population was also noticeable for its divergence from other populations in a number of characters, including reduced numbers of ventrals (shared with Reevesby I.) supraciliaries (shared with St Peters I.), posttemporals (shared with Weerona, St Peters and Duffield Is.), pre- and postsuboculars, supra- and infralabials, but constant presence of a subocular. The Flinders I. sample was notable for two of the four specimens having contact between first supraciliary and frontal, absent in other samples, while the St Peters I. population had an elevated subdigital lamellae count.

8.5.10 Comparison with other Taxa

Comparisons between *T. rugosa* and most other *Tiliqua* species have been made in previous chapters, while comparisons between *T. r. asper* and *T. r. rugosa* were made in Section 8.4.10.

T. r. asper is unique within *T. rugosa* in having a very short, broad, tail (Tables 8.33–8.35 *vs* Tables 8.44, 8.47), the mean value for TL/SVL being 21.5% and for TD/TL being 66.2% (c.f.

means of 25.2–28.6% and 37.0–45.1% for *T. r. konowi* and *T. r. palarra*). *T. r. asper* is also autapomorphic in having large body scales (midbody, paravertebral and subcaudal scale counts are the lowest for any *Tiliqua*; respectively mostly 19–25, mostly 18–28 and mostly 11–16 [higher values occur in less than 2.0% of cases] *vs* 24–30/26–35, 24–32/23–38 and 16–23/17–22 for *T. r. konowi* and *T. r. palarra*). It also differs from *T. r. konowi* in lacking the autapomorphies of that subspecies (high frequencies of absence of a median occipital, high frequencies of contact of first supraciliary and frontal, finely pale-variegated dorsal coloration), as well as in having a mode of two supraoculars (usually three or more) and three posttemporals (modally two). It further differs from *T. r. palarra* in lacking the autapomorphies of that subspecies (high frequency of contiguous nasals and small ear), as well as having a mode of two supraoculars (*vs* three or more), and in having a rather broader head, as indicated by both head width and interocular width (Tables 8.33–8.35 *vs* Table 8.47).

8.5.11 Habits and Habitats

It has been claimed that *T. r. asper* is a habitat generalist, occurring in all habitats within its range (Brooker & Wombey, 1978; Houston, 1980; McCann, 1983; McGreevy, 1987). It has been recorded in the literature from a variety of open semi-arid habitats, such as gresslands, xeric heaths, shrublands (including chenopod shrublands), mallee (including mallee-broombush and mallee-*Triodia* habitats), woodland (including brigalow, black box, river red gum, bull-oak, brown stringybark, scrub-pine, belah and yellowgum woodlands), *Eucalyptus sideroxylon* open forest and cleared agricultural and urban lands (Armstrong, undated; Bull, 1987; Congreve, 1985; Emison *et al.*, 1978; Gilmore *et al.*, 1979; Henle, 1987, 1989, 1990; Horn, 1980; Hudson *et al.*, 1981; James, 1974; Jenkins & Bartell, 1980; Krefft, 1866d; Land Conservation Council, 1978, 1979, 1980a, 1983, 1985b, 1987; Lucas & Frost, 1894; Menkhorst & Gilmore, 1979; Robertson *et al.*, 1989; Schnee, 1900; Specht, 1981; Storr, Hanlon & Harold, 1981; Vestjens, 1977; White, 1978a; Woinarski, 1989), although Henle (1989, 1990) suggested that it was absent from riverine gallery forests. Although it appears to prefer dry habitats (Brooker & Wombey, 1986), it has been recorded from around swamps in the south-east of the distribution (Reidy & Booth, 1981). Bamford (1982) reported it as absent from mallee on the Roe Plains, although abundant around nearby claypans.

T. r. asper appears to be most common on flatlands, although it seems to occur on a variety of substrate types, including loose sands, calcreted sands, stony soils and rocks, (Barrett, 1919; Chesson, 1977; Fowler, 1973; Horn, 1980; McGreevy, 1987). It has also been recorded from low sandridges, dunes and lunettes, and from low hills (Henle, 1989, 1990; Robertson *et al.*, 1989; Schnee, 1900).

The literature assessment corresponds well with specific habitat data associated with museum specimens. Specimens have been reported from grasslands (n = 14, including tussock grassland, *Enneapogon* grassland), chenopod steppes and shrublands (n = 18), coastal and saltlake chenopod/halophyte heaths (n = 3), coastal scrub (n = 3), open shrubland of *Grevillea treuriana/Eucalyptus pyriformis* (n = 1), mallee (n = 14; including mallee/*Triodia*, mallee/chenopod and mallee/*Acacia* habitats), *Banksia* and *Banksia*/broombush scrub (n = 2), and woodlands (n = 9, including *Callitris, Casuarina, Casuarina*/eucalypt, *Casuarina/Heterodendron*, eucalypt and *Acacia*/eucalypt woodlands).

Most specimens were found on flatlands, such as sandplains, calcareous sandplains, floodplains and saltlakes (n = 14), or other low-lying areas such as interdunes (n = 5), usually on red or grey sandy or loamy soils. Only a few specimens were found on dunes (n = 4) or associated with rocky hillslopes (n = 3).

A large number of specimens were found dead or alive on roads (n = 47). Where activity times were noted, most were found active in the late afternoon (1530–1750hrs; n = 5) or early morning (0845–0945hrs; n = 6), with relatively few found on roads during the middle of the day (1220–1501hrs, n = 3). Although *T. r. asper* appears to be diurnal, there is a single literature record of a live specimen found on a road at night (Armstrong, 1979a). Where shelter sites were noted, specimens were found under tin (n = 12), railway sleepers (n = 5), concrete (n = 1), cardboard (n = 1) or bushes and grass tussocks (n = 4).

8.5.12 Taxonomic History and Type Material

Trachydosaurus asper was described by Gray (1845a) from four specimens from "Adelaide, W. Australia" presented to the Natural History Museum, London by C.D.E. Fortnum. All four syntypes are dried, stuffed specimens mounted on boxwood bases. The taxon was differentiated from *T. rugosa* by the broader interparietal (as broad as long *vs* longer than broad), more rugose scalation (very rugose *vs* rather rugose) and coloration ("dark brown, with yellow tips to some of the scales of the back and sides in the young, of the sides only in the adult" *vs* "pale brown with broad rather irregular yellow cross bands").

Of the four syntypes of *Trachydosaurus asper* (BMNH xv.81.a–b, 42.6.29.58–59 *vide* Cogger *et al.*, 1983, but xv.81.a–d according to labels on the mounts, *pers. obs.*), Wells and Wellington (1985) designate 42.6.29.58 as lectotype. This specimen (Fig. 64), equivalent to BMNH xv.81.d (H.G. Cogger, *pers. comm.*), is the smallest of the type series, and has the following combination of characters for the taxon: nasals moderately separated, prefrontals in moderate contact; frontal divided; supraoculars three, first contacting frontal; supraciliaries six; frontoparietals in narrow contact; occipitals 2/3; azygous occipital present; presuboculars four; suboculars absent; postsuboculars 5/4; supralabials eight; infralabials 9/8, first two contacting postmental; primary temporals asymmetrical, 2/3; posttemporals three; midbody scales *ca*20; paravertebral scales 22, between axilla and groin 15; subcaudals *ca*15; SVL 245mm; AGL 145mm; TL 53mm; HL 46.3mm; HW 40.9mm; HD 32.8mm; IOC 19.3mm; E–N 13.6mm; E–E 24.1mm; IparL 8.1mm; IparW 7.0mm.

The head shield configuration of a typical topotypic specimen is illustrated in Fig. 65.

8.5.13 Reproduction

8.5.13.1 Size at maturity:

There is much geographic variation in adult size in this subspecies. Consequently, adult size was determined separately for four groups of populations, corresponding to populations 1–11, 12–14, 15–29 and 30–34. In the east (populations 1–11), mature-sized males had SVL 253–331 ($\overline{X}$ = 292.7mm, sd = 15.98, n = 110) while mature-sized females had SVL 253–341mm ($\overline{X}$ = 295.4mm, sd = 17.76, n = 83) (Figs. 66–67). In south-eastern populations (12–14), mature-sized males had SVL 236–302mm ($\overline{X}$ = 281.5mm, sd = 15.54, n = 43) while mature-sized females had SVL 248–317mm ($\overline{X}$ = 284.0mm, sd = 15.72, n = 22) (Figs. 68–69). In the central populations (15–29), mature-sized males had SVL 235–324mm ($\overline{X}$ = 271.4mm, sd = 20.12, n = 116) while mature-sized females had SVL 241–313mm ($\overline{X}$ = 271.5mm, sd = 17.84, n = 101) (Figs. 70–71). Western populations (30–34), the smallest animals, had mature-sized males with SVL = 220–273mm ($\overline{X}$ = 249.5mm, sd = 12.67, n = 44) and mature-sized females with SVL = 222–274mm ($\overline{X}$ = 245.7mm, sd = 14.02, n = 28)

(Figs. 72–73). Males were not significantly different in size to females in any of these groups (Mann-Whitney U tests, z = 0.124–0.775, P > 0.05).

Gravid females were similar in size to other, non-gravid, mature females. In the two groups of populations for which sample sizes were sufficiently large for a reasonable assessment, SVL for gravid and non-gravid females were either not significantly different (central populations [15–29]: gravid: 241–313mm, $\overline{X}$ = 271.7mm, sd = 17.01, n = 39; non-gravid: 241–312mm, $\overline{X}$ = 271.7mm, sd = 18.17, n = 62; Mann-Whitney U test, z = 0.06, n.s.) or only barely significantly different (eastern populations [1–11]: gravid: 269–341mm, $\overline{X}$ = 297.5mm, sd = 14.98, n = 42; non-gravid: 253–339mm, $\overline{X}$ = 293.3mm, sd = 20.20, n = 41; Mann-Whitney U test, z = 2.204*).

8.5.13.2 Male reproduction:

There is a distinct pattern of seasonal variation in both testis length and turgidity (Fig. 74). Narrow, flattened, and flaccid, laterally expanded testes predominated from December to March, especially in December and January, when only five of 36 adult males had turgid testes. While the testes became more swollen during late autumn and early winter (April to June), there was little increase in length, with few turgid testes more than 24mm long. From mid-winter (July) to mid spring (October), there was an increase in both the frequency of turgid testes and testis length. In October, only 10.3% (n = 78) of males had flaccid or shrunken testes, while 61.4% (n = 70) of males with turgid testes had testes over 24mm long. In November, while there were still many males with grossly enlarged turgid testes, the frequency of flaccid testes increased (25.9%, n = 58).

The data presented here agree closely with data on seasonal variation in testis size, sperm production and androgen secretion in Victorian and South Australian populations (Bourne *et al*., 1971; Bourne & Seamark, 1973a, 1975, 1978; Bourne, Taylor & Watson, 1986a,b).

Taken together, the data suggest that spermiogenesis peaks in spring, from October to November, and is followed by a period of testicular regression.

8.5.13.3 Female reproduction:

The pattern of seasonal variation in follicle diameter is similar throughout the distribution. Follicle diameter is minimal in summer (December–February), although only some females were not gravid at this time. Follicles showed a gradual increase in size through autumn and winter, followed by a rapid increase in diameter from late September to early November, with the largest yolky follicles occurring in November. The earliest female with oviducal eggs was collected 30 October, and oviducal eggs and embryos were found in females collected as late as 1 May, although most females collected from late March through to the end of April were non-gravid (Fig. 75). Litters have been born in captivity in Australia on 12 March (G. Husband, *pers. comm*.), 6 April and 23 April (B.W. Hart, *in litt*. to H. Hale, 30.iv.1946). The only exception to the above pattern was a single April female with one enlarged (23.5mm) follicle. All other follicles in the ovaries of this female were 6mm or less in diameter. Corpora lutea were obvious throughout embryonic development.

These results are consistent with the data available.

Gestation has variously been inferred to be around 4–5months (Tyler, 1962), 150d (Bourne, 1981), 119–125d (Hitz, 1983) and 140–170d, $\bar{X}$ = 168±18d (Bourne, Stewart & Watson, 1986), although Haacke (1883, 1885) estimated a rather shorter period: over 3 months.

Gravid females have been collected between October and April (Bourne, Stewart & Watson, 1986), while Haacke (1883) found late embryos in April females. Births have been reported in February to March (Bull, 1987), March (Bourne, 1981; McCoy, 1885; Haacke, 1885; Frauca, 1966), mid to late summer (Ehmann, 1973), summer to early autumn (Weigel, 1988), late autumn (Cole, 1930), between late March and early May in captive-held Victorian animals (Bourne, Stewart & Watson, 1986), but between late February and mid March in the wild in Victoria (P. Robertson *in* Bourne, Stewart & Watson, 1986). In northern hemisphere captives kept in a southern hemisphere climatic regime, young were born to two females between 5 and 15 March (Hitz, 1983), on 9 March (Hitz, 1985), to three females (collected gravid a few months before) between 9–27 April (Schneider, 1941; Roesch, 1956). Krefft (1871c) stated that young are born about the end of January, while Tubb (1938b) reports “very young” specimens in early December. Krefft's record is not supported by any specific data, and may be an inaccurate estimate, while it is likely that Tubb's specimens were born the previous season.

Taken together, the data suggest that vitellogenesis occurs in spring, ovulation in late spring (November) and young are born in autumn, mostly by March, but sometimes as late as April, after approximately 4.5–5months gestation. There is no evidence that more than one litter can be produced in a year.

8.5.13.4 Mating season and mating system:

The mating season has been reported to be in spring, during October in eastern South Australia and western NSW (MacGillivray, 1910; Bourne *et al.*, 1971; Bourne & Seamark, 1975; Bourne, 1981), in October–November in South Australia (Bull, 1988, 1990; Bull *et al.*, 1991), in September–October to the south, in Victoria (Bourne, Taylor & Watson, 1986a,b) and in August in the west (Bamford, 1982). Bull (1988) gave a more extensive mating season (September to December), although Bull (1987) actually observed copulation (n = 3) only between 19 October and 2 November, and Bull *et al.* (1991) inferred copulation in November, and observed three instances of copulation between 27 October and 10 November.

Males show increased aggression during the mating period (Bamford, 1982; Bourne, Taylor & Watson, 1986a; Bull, 1990). Fighting (sexes not known) was observed on 28 September (Howe & Tregellas, 1914), while captive males fought in spring (Malcolm, 1979). Bull (1990) reports nine instances of male-male aggression, all in October or November. Hill (1923) gives a detailed description of a fight between two males observed on 15 December. In northern hemisphere captives only recently imported, aggression was noted in October, and 13 matings between 30 October and 9 November (Hitz, 1983).

The mating system in this race has been studied by Bull (1987, 1988, 1990) and Bull *et al.* (1991) and is unusually complex for lizards. The otherwise solitary males and females pair for about 8 weeks before mating. During this period, the male appears to repeatedly test the receptivity of the female, touching the female with his head, occasionally biting her head and neck, and sometimes attempting to lift her tail. Mating has been described by Hitz (1983) for captives. Mate fidelity is strong, both within and across breeding seasons. Few males were displaced during breeding seasons, and a high proportion of pairs were recaptured over several breeding seasons (up to seven years; Bull, 1990). When males were displaced within seasons, it was usually by a similar sized or larger male. Bull (1988) observed pairs

only between September 1 and December 15 at his study site in South Australia, while Bull *et al.* (1991) reported the separation by 27 November of four pairs radiotracked since early October, and observed pairs from September. Pairs have similarly been observed in spring (MacGillivray, 1910; Cogger, 1967; Greer, 1989), in October and November (*pers. obs.*), between 29–30 September (Anstis & Peterson, 1973), in October (Greenup & Deveson, [1989]) and in early November (Reidy, 1979). Henle (1990) frequently noted "pre-mating behaviour" in September, but only rarely in November.

The timing of the mating season closely corresponds to the common peak in male and female reproductive cycles.

8.5.13.5 Frequency of reproduction:

From December to February (the middle of the period when gravid females are present in the population), 19 of 28 females (67.9%) had oviducal eggs or embryos. Seven of the nine non-gravid females had very small ovarian follicles, and presumably did not breed in that season, while the other two (both December collected) showed moderately enlarged, yolking follicles, and were probably too late in the season for successful mating, as testes during this period had begun to regress.

Bull (1987), however, recaptured females paired with males during three consecutive breeding seasons, Bull (1988) similarly found one female in a pair situation over five years, and Bull (1990) found one pair together over seven consecutive years, suggesting that at least some females are likely to breed annually over long periods.

The data suggest that female *T. r. asper*, although usually breeding annually, may skip a year. This could be due to two factors. Firstly, some females may not acquire a mate, either through a lack of free unpaired males, or asynchrony in the reproductive cycles. Secondly, some females, especially those that gave birth late in the previous season, may not have regained the fat reserves necessary to breed. Postparturient females are thin and have very reduced fat reserves, although they can rapidly regain condition after feeding (Schneider, 1941; Roesch, 1956).

8.5.13.6 Litter size:

Of 95 females with either countable enlarged yolky ovarian follicles (≥16mm), oviducal yolk masses or embryos, or litters of young born before preservation, the number of follicles or young was 1–4 ($\overline{X}$ = 2.2, sd = 0.68), with mode two (58.9%). The range of litter sizes was similar for both ovarian follicles and oviducal masses, and mean litter size was not significantly different between the two groups ($\overline{X}$ = 2.28, sd = 0.62, n = 57 *vs* $\overline{X}$ = 2.08, sd = 0.76, n = 37; t_{92} = 1.39, n.s.).

More follicles were generally present on the right side than the left (in total, 73 *vs* 56; R>L:R=L:R<L 23:22:12), although these differences are non-significantly different from 1:1 (totals, X^2 = 2.24, n.s.; individual inequalities (23:12), X^2 = 3.46, n.s.).

There was evidence for extra-uterine transfer of ova. In those cases where the number of corpora lutea was estimated grossly (n = 14), the number and distribution of corpora lutea was the same as for oviducal masses in nine cases, one fewer in one case (probably due to inability to clearly visualise one ovary), but different in four cases. In each of the four

exceptions, one more corpus luteum was present on the left side, and one more oviducal mass was present on the right, indicating a left to right transfer of ova.

There was some evidence for a positive correlation between litter size and maternal SVL (Fig. 76). Although the correlation was not significant within groups of populations (eastern: r = 0.027, n = 40; central [15–29]: r = 0.109, n = 38), when all data was pooled, the correlation was almost statistically significant (r = 0.180, n = 95, $F_{1,93}$ = 3.128, P = 0.08). Overall, the smallest females, from the west, had only 1–2 young in a litter, while only large females (SVL ≥282mm) had litters of four, although small litters of 1–2 were also seen in several large females.

Litter size for *T. rugosa* (by inference for *T. r. asper* for authors from eastern Australia) has been frequently stated to be 1–3, usually two (Barrett, 1939, 1943, 1955; Bustard, 1970; Cole, 1930; Frauca, 1966, 1982; Hoser, 1989; Hyett, 1961; Jenkins & Bartell, 1980; Krefft, 1871; McPhee, 1959; Tyler, 1962; Waite, 1925, 1929), although Kershaw (1927) gives the mode as one, and the range one to two. Some authors have suggested that up to four (Mincham, 1970; Weigel, 1988) or even five young (Ehmann, 1983) may be produced on occasion, while “An amateur naturalist” (1887) gives the range as 3–5. Despite the frequency of the “1–3, mode 2” statement, there are surprisingly few specific data on litter size in *T. r. asper* in the literature.

Krefft (1866d) reported two embryos in three individuals. Haacke (1883), erroneously claiming the first record of viviparity in this species, reported a range of 2–3 in six animals, and later (Haacke, 1885) gave the same range for a larger sample (n > 30), while McCoy (1885) reported a single embryo in one female. Waite (1929) and Tyler (1962) both erroneously claimed the first record of triplets.

In more recent times, Schneider (1941) reports two litters of three; Roesch (1956) a litter of two, Hitz (1983, 1985) two litters of two and one of one, Jones (1987) a range of 1–2 (sample size not given), Bull (1987) a range of 1–3 ($\overline{X}$ = 2.2, n = 9), and Bourne, Stewart and Watson (1986) a mean of 2.8 (sample size not given).

8.5.13.7 Size of young at birth:

There appears to be some geographic variation in size at birth in *T. r. asper*. In the populations with large adult size (1–11), the smallest specimen examined (AM R130814), a full-term embryo removed from a fresh road-killed female on 26.iii.1989, had SVL 153mm. Two further neonates or late embryos (MV D39235–36, 15.ii.1966), still with yolk sacs attached, had SVL 161–162mm. A further seven individuals, three collected between February and May, had SVL 155–173mm. A captive-bred neonate had SVL 185mm (G. Husband, *pers. comm.*)

In contrast, southern and western populations appear to have rather smaller neonates. The smallest “southern” (populations 12–29) definite neonates examined in this study (AM R6681–82, regressed umbilicus, food in gut) had SVL 127–132.5mm. A series of either late embryos or neonates (SAM R1393a–i) had SVL 118–140mm, two late embryos still in fetal positions (AM R7750–51) had SVL 127–132mm, and the eleven other smallest specimens (four collected April) examined had SVL 107–151mm. In the western region (populations 30–34), the smallest animal (SAM R25716, 5.iv.1984) had SVL 133mm, and had an ingested yolk sac in the stomach, indicating that it had only recently been born (Roesch, 1956; Hitz, 1983), while a second animal, collected 3d before (SAM R25548) had SVL 144mm.

Consequently, I infer minimum SVL at birth for *T. r. asper* to be about 153mm in the east, but only 127mm in the "south" and similarly 133mm or less in the west.

Limited published data are available on captive-bred animals of this subspecies. Roesch (1956) reports young with a total length of 14cm (equivalent to SVL approximately 115mm; Table 8.32). However, Hitz (1983) and Jones (1987) record somewhat larger young, 17–20cm total length (equivalent to approximately 140–165mm SVL) and 147–154mm (n = 2) respectively. The neonates reported by Jones are from eastern populations. McCoy (1885) and Frauca (1966) report neonates of "over five inches" (roughly equivalent to SVL 105mm). Jenkins and Bartell (1980) estimate total length of neonates to be about 150mm (SVL equivalent 124mm), Hoser (1989) estimates a total length of 160mm (SVL equivalent 132mm) while Hyett (1961) estimates about seven inches (SVL equivalent 146mm). The approximations provided by McCoy (1885) and Frauca (1966) are presumably gross underestimates.

Mean weight for 9 neonates was 71.6g (Bull, 1987), for three pairs of twins 69.2g (range 62.0–73.8g) and for a litter of three 63g (range 59.7–67.1g) (Tyler, 1962), similar to the approximations of Roesch (1956) (70g), although the three neonates reported by Hitz (1983) are considerably heavier (100–150g), while the neonates reported by Bourne, Stewart and Watson (1986) were noticeably lighter ($\bar{X}$ = 58g). A single captive-bred neonate of the large eastern form had a mass of 7 oz (= 198g) (G. Husband, *pers. comm.*). Neonates eat the placenta and foetal membranes (Roesch, 1956; Hitz, 1983), and it is possible that some of this variation is due to weighing before or after ingestion of the placenta.

8.5.13.8 Relative litter mass:

There are few data on relative litter mass. Bull *et al*. (1991) give a mean of 35% for five animals. Roesch (1956) gives the mass of a gravid female nine days before parturition as 750g, postparturient mass as 590g, and mean mass of the two neonates as approximately 70g. Assuming total mass of neonates (after ingesting the placenta) as 140g gives a relative litter mass of about 27%. Hitz (1983) gives data on neonate mass (including ingested placenta) and postparturient female mass for two captive females. Relative litter mass for a litter of two was 32%, while for a litter of one was 22%. For two litters of one born to eastern females, the figures were 19% and 26% (raw data from G. Husband, *pers. comm.*; *pers. obs.*). Across all ten records, the mean value was 30%.

8.5.13.9 Age at maturity:

Rapid growth has been noted by several authors (e.g., Roesch, 1956; Frauca, 1967; Hitz, 1983), mostly on the basis of captive observations. Inferred growth rates in the wild have been reported by Bull (1987) and Henle (1990). On the basis of mark-recapture studies, seasonal variation in minimum size, and a slowing of growth with increasing size, maturity has been estimated as being reached in the second (Henle, 1990) or third to fourth (Bull, 1987) year.

8.5.13.10 Longevity:

Captive longevity records for *T. rugosa* are mostly not associated with data as to locality of origin, and cannot be identified to subspecies. However, one captive-born *T. r. asper* lived for 6.5yrs (Schneider, 1941). Other records not identifiable to subspecies are given under the nominate subspecies. Bull (1987) reported 18 wild adult *T. r. asper* recaptured after six

years, and therefore at least 8.5 years old, and suggested that maximum age was over nine years. Bull (1990) reports mate fidelity for up to nine years. Assuming a minimum age at maturity of three years, this indicates a potential lifespan of at least ten years, and probably much longer.

8.5.13.11 Sex ratio:

Overall, the ratio of mature-sized males:females was 268:208, a ratio significantly different to parity ($X^2_1 = 7.56^{**}$), and biased towards males. The male bias was noticeable in all seasons, and in most months, except in January, when there were slightly more females collected than males (22:18), March, when there were equal numbers of males and females collected (3:3) and June, when there were again slightly more females (4:2), although the sample sizes are very small for the latter two months.

On a seasonal basis, the male bias was strongest and significant in spring (151:105; $X^2_1 = 8.27^{**}$), when by far the most animals were collected, and weakest in summer (39:36) and winter (19:17). A tendency for seasonal variation in activity patterns, with maximum activity in spring for males, and a female bias in captures in summer, has been previously noted (Warburg, 1965a; Bull, 1987; Henle, 1990; Bull *et al.*, 1991). It is probable that the increased frequency of male captures in spring reflects high male activity during the breeding season, while the increased frequency of female captures in summer reflects basking by the females during pregnancy (Bull *et al.*, 1991). The winter sample, presumably collected when animals were hibernating in shelter sites, may be a more accurate reflection of the adult sex ratio, and suggests that approximately equal numbers of adult males and females are present.

8.6 Tiliqua rugosa konowi

8.6.1 Synonymy

Tiliqua rugosa konowi (Mertens, 1958a)

Trachydosaurus rugosus konowi Mertens, R. (1958a). Neue Eidechsen aus Australien. *Senckenbergiana biologica* 39(1/2): 51–56 [52]. Holotype: WAM R12721.

8.6.2 Diagnosis

A small subspecies of *T. rugosa* (maximum SVL 260mm) with a relatively long, slender tail, 16 or more subcaudal scales, 24–30 midbody scales, a relatively narrow head ($\bar{X}$ HW/HL = 94.9%), usual absence of a median occipital, contact of first supraciliary and frontal and separation of nasals, a moderately large ear aperture ($\bar{X}$ Ear/HL = 11.4%) and dorsal colour pattern consisting of dark grey head, body and tail with fine pale vermiculations.

8.6.3 Description

Nasals moderately separated (n = 61); postnasals usually fused dorsally to nasals, separated ventrally by a postnarial suture, rarely completely distinct from nasals unilaterally (5.3%, n = 57); prefrontals in broad to moderate contact (n = 62); supraoculars usually three bilaterally, with first only contacting frontal (53.2%, n = 62), less commonly four, with first two contacting frontal unilaterally (14.5%) or bilaterally (12.9%), two, with first only contacting frontal unilaterally (6.5%) or bilaterally (8.1%), or with other unique patterns (4/2(2/1); 3/3(2/2); 4/3(2/2), 1.6% each); supraciliaries 3–7 ($\bar{X}$ = 5.8, sd = 0.66, n = 124), usually six

(65.3%) or five (23.4%); when six supraciliaries and three supraoculars, first supraciliary large, contacting and penetrating between prefrontal/frontal and first supraocular, second longer than tall, contacting first supraocular only, third and fourth smallest, third contacting first supraocular only, fourth contacting and projecting slightly between first and second supraocular, fifth a little larger, as tall as long, projecting between second and third supraoculars, sixth large, contacting and projecting between third supraocular and parietal; first supraciliary usually either in broad to moderate contact with frontal bilaterally (48.2%, n = 56) or broadly to moderately separated from frontal bilaterally (25.0%), less commonly in narrow contact bilaterally (7.1%), narrowly separated bilaterally (3.6%), or asymmetrical, with broad to moderate contact on one side and broad to moderate separation on the other (10.7%), narrow contact/narrow separation (3.6%) or point contact/moderate separation (1.8%); last supraciliary usually broadly separated from frontoparietals bilaterally (72.4%, n = 58), less commonly moderately separated (25.9%); frontoparietal paired, usually in broad (31.6%, n = 57) to moderate (64.9%) contact, rarely in narrow contact (1.8%) or narrowly separated (1.8%); occipitals 1–3 ($\overline{X}$ = 2.2, sd = 0.45, n = 114), usually two (77.2%); median azygous occipital usually absent (66.1%, n = 59); loreals usually two in horizontal series, rarely one unilaterally (n = 1) or bilaterally (n = 8), absent bilaterally (n = 1) or absent unilaterally/single unilaterally (n = 1), absence due to fusion to prefrontal, single loreals often due to rostral loreal fusing to frontonasal bilaterally (n = 3) or prefrontal unilaterally (n = 1) or bilaterally (n = 1); subocular ring complete; presuboculars 1–5 ($\overline{X}$ = 3.1, sd = 0.62, n = 134), usually three (66.4%); suboculars 0–2 ($\overline{X}$ = 0.1, sd = 0.38, n = 134), usually absent (85.8%); postsuboculars 3–5 ($\overline{X}$ = 4.1, sd = 0.48, n = 133), usually four (75.2%); supralabials 7–10 ($\overline{X}$ = 8.4, sd = 0.61, n = 134), usually eight (57.5%) or nine (35.8%), antepenultimate below centre of eye, penultimate single (n = 56), last single (n = 56); primary temporal usually vertically paired bilaterally (n = 52), rarely divided into three unilaterally (n = 3) or bilaterally (n = 1); upper secondary temporal single; lower secondary temporal usually vertically paired bilaterally (n = 55), rarely divided into three bilaterally (n = 1); posttemporals 2–3 ($\overline{X}$ = 2.2, sd = 0.41, n = 114), usually two (78.9%); infralabials 7–11 ($\overline{X}$ = 9.0, sd = 0.76, n = 134), usually nine (53.7%), scales in caudal part of row irregularly paired; usually first two infralabials contacting postmental, rarely first only unilaterally (n = 2) or first three unilaterally (n = 6) or bilaterally (n = 2).

Midbody scales 24–30 ($\overline{X}$ = 26.2, sd = 1.22, n = 67); paravertebral scales 24–32 ($\overline{X}$ = 27.1, sd = 1.64, n = 67), between axilla and groin 17–22 ($\overline{X}$ = 19.0, sd = 1.23, n = 62); ventral scales 54–73 ($\overline{X}$ = 66.2, sd = 3.25, n = 67); subcaudal scales 16–23 ($\overline{X}$ = 19.6, sd = 1.55, n = 64); lamellae below fourth toe 5–8 ($\overline{X}$ = 6.72, sd = 0.73, n = 128), mode 7 (55.5%), basal 1–6 ($\overline{X}$ = 4.37, sd = 0.96, n = 108) paired.

SVL 167–260mm; AGL/SVL 55.1–65.4% ($\overline{X}$ = 59.7%, n = 55); TL/SVL 22.8–37.0% ($\overline{X}$ = 28.6%, n = 51); TD/TL 28.2–45.7% ($\overline{X}$ = 37.0%, n = 52); FLL/SVL 18.0–22.6% ($\overline{X}$ = 19.8%, n = 55); HLL/SVL 18.6–22.6% ($\overline{X}$ = 20.6%, n = 54); Hip/SVL 11.1–14.3% ($\overline{X}$ = 12.8%, n = 54); HL/SVL 18.9–22.7% ($\overline{X}$ = 20.7%, n = 55); HW/HL 84.7–105.1% ($\overline{X}$ = 94.9%, n = 55); HD/HL 54.4–70.4% ($\overline{X}$ = 62.3%, n = 55); IOC/HL 35.9–44.5% ($\overline{X}$ = 40.1%, n = 55); E–N/HL 24.6–30.0% ($\overline{X}$ = 26.9%, n = 55); E–E/HL 44.9–52.7% ($\overline{X}$ = 47.7%, n = 55) Eye/HL 16.4–22.2% ($\overline{X}$ = 19.4%, n = 55); Ear/HL 8.4–14.6% ($\overline{X}$ = 11.5%, n = 55); IparL/HL 16.6–26.2% ($\overline{X}$ = 21.3%, n = 55); FrontL(a)/HL 15.5–26.2% ($\overline{X}$ = 21.6%, n = 39); FrontL(b)/HL 13.8–20.0% ($\overline{X}$ = 17.0%, n = 16); FrontL(c)/HL 20.5–26.4% ($\overline{X}$ = 23.6%, n =

16); IparL/FronL(a) 71.7–135.5% ($\overline{X}$ = 100.5%, n = 39); IparW/IparL 50.5–80.8% ($\overline{X}$ = 64.8%, n = 55); FrontW/FrontL(a) 68.8–113.2% ($\overline{X}$ = 81.2%, n = 39).

8.6.4 Allometry

Allometric values and calculated values for morphometric characters are presented in Table 8.44. Most characters showed allometric growth, the exceptions being the relationships between tail length and SVL, head length and SVL, head depth and head length, eye-ear interval and head length, interparietal length and head length, and interparietal width and length. Almost all characters showing allometry showed negative allometry, the exception being the relationship between axilla-groin length and SVL.

8.6.5 Coloration (Fig. 77)

Dorsal ground colour even dark olive grey to dark olive grey-brown, with fine light olive green-grey vermiculations over body and tail, tending to concentrate in a series of obscure 1–2 scale-wide bands, but also evident over dark areas between bands.

Head concolorous with body dorsum and with same fine pale vermiculations; face, lips and snout a little lighter.

Venter with pale olive green-grey to olive green-yellow ground colour, largely obscured, particularly on body and tail, by fine dark flecks which tend to concentrate laterally and caudally on each scale to produce a series of poorly defined narrow stripes (1/4-scale wide) and bands (1/2-scale wide), the latter particularly on tail. Dark flecks usually finer and sparser on throat.

Laterally, disjunction between predominantly dark dorsal coloration and pale ventral coloration clear but irregular, taking the form of alternating dark and light patches.

Limbs pale olive green-grey, with varying degrees of dark clouding and flecking, most strongly developed over tibial region dorsally.

Soles yellowish.

8.6.6 Asymmetry

Statistically significant asymmetry was not detected in mean number of presuboculars, suboculars, postsuboculars, supraciliaries, supralabials, infralabials, posttemporals, occipitals or subdigital lamellae (t-tests of asymmetrical cases), despite the high frequency of asymmetries in some characters (up to 52% [n = 67] in the case of infralabials).

8.6.7 Sexual Dimorphism

Sexual dimorphism was not detected in mean number of presuboculars, postsuboculars, supraciliaries, supralabials, infralabials, posttemporals, occipitals, midbody scales, paravertebral scales, ventral scales, subcaudal scales or subdigital lamellae (t-tests) or in degree of separation or contact of frontoparietals or of first supraciliary and frontal, or frequency of presence of an azygous median occipital (X^2 tests).

Slight, but significant sexual dimorphism was detected in mean number of suboculars (♂♂: $\bar{x}$ = 0.07, sd = 0.26, n = 54; ♀♀: $\bar{x}$ = 0.21, sd = 0.44, n = 78; t_{130} = 2.08*).

Mature-sized males and females were similar and not significantly different in size (see below). Females have longer bodies and slightly broader hips than males, but shorter limbs and head, and a slightly shorter snout (Tables 8.45–8.46).

8.6.8 Distribution

Restricted to Rottnest I., 18km off the lower west coast of Western Australia. Not known to be restricted to any one part of the island.

8.6.9 Comparison with Other Taxa

Comparisons between *T. rugosa* and most other *Tiliqua* species have been made in previous chapters. Comparisons between *T. rugosa* and the *T. scincoides* complex were made in Section 8.4.10, while *T. r. konowi* was compared with *T. r. rugosa* and *T. r. asper* in Sections 8.4.10 and 8.5.10.

T. r. konowi differs from *T. r. palarra* in a number of characters. It is smaller (maximum SVL 260mm *vs* 300mm), with a slightly more elongate body ($\bar{x}$ AGL/SVL 59.7% *vs* 56.9%), longer tail ($\bar{x}$ TL/SVL 28.6% *vs* 25.2%) but shorter limbs ($\bar{x}$ FLL/SVL 19.8% *vs* 22.0%; $\bar{x}$ HLL/SVL 20.6 *vs* 22.4%), and a much larger ear ($\bar{x}$ Ear/HL 11.5% *vs* 6.5%) (see also Tables 8.44, 8.47). *T. r. konowi* also has the nasal scales separated (100%; *vs* usually contiguous nasals, 68%), the first supraciliary usually contacting the frontal at least unilaterally (71%; *vs* usually separated bilaterally, 73%), frequent absence of a median occipital (66%; *vs* usually present, 98%), and generally fewer supralabials (mode eight [58%] *vs* nine [66%]), posttemporals (mode two [79%) *vs* three [52%]), and midbody scales ($\bar{x}$ = 26.2 *vs* 29.3). The coloration is also very different, *T. r. konowi* having fine pale vermiculations over a dark grey dorsal ground, while *T. r. palarra* has yellow streaks and spots over a brown dorsal ground.

8.6.10 Habits and Habitats

Apart from an observation of large numbers of individuals drinking from puddles after rain (Sadleir, 1958), nothing is known of the natural history of this race. The vegetation and physiography of Rottnest I. are described by Storr (1962) and Storr *et al*. (1959).

8.6.11 Taxonomic History and Type Material

The occurrence of *T. rugosa* on Rottnest I. was first reported by Werner (1910) and Glauert (1929). Werner provided a brief coloration description of his specimen, noting its difference from specimens from several mainland localities. No further notice of this population was made until Mertens (1958a) described the subspecies from five specimens (holotype WAM R12721; paratypes SMF 53202–05) collected by G. Konow and G.A. Phillip during Mertens' 1957 Australian expedition.

The holotype (Fig. 78) has the following combination of character states: nasals moderately separated; postnasals fused dorsally to nasals; prefrontals in moderate contact; supraoculars three, first contacting frontal; supraciliaries six, first broadly separated from frontal, last broadly separated from frontoparietal; frontoparietals in moderate contact; occipitals two; azygous occipital absent; loreals one (rostral loreal fused to prefrontal); presuboculars three; subocular absent; postsuboculars four; supralabials seven; primary temporals paired; lower secondary temporals paired; posttemporals three; infralabials 8/7, first two contacting postmental; midbody scales 24; paravertebrals 25, between axilla and groin 18; ventral scales 59; subcaudal scales 16; subdigital lamellae 7/6, apical three undivided; SVL 201mm; AGL 119.5mm; TL 55mm; TD 23.6mm; FLL 41.5mm; HLL 41.5mm; Hip 27.1mm; HL 44.5mm; HW 39.7mm; HD 27.0mm; IOC 17.9mm; E–N 12.0mm; E–E 21.2mm; Eye 8.2mm; Ear 4.7mm; IparL 9.0mm; IparW 6.0mm; FrontL 10.2mm; FrontW 8.1mm; coloration typical of race.

8.6.12 Reproduction

8.6.12.1 Size at maturity:

Mature-sized males had SVL 205–251mm, $\overline{X}$ = 233.3mm, sd = 12.99, n = 23, and were similar and not significantly different in size to mature-sized females, with SVL 201–260mm, $\overline{X}$ = 230.2mm, sd = 15.72, n = 32 (Mann-Whitney U test, z = 0.81 n.s.) (Figs. 79–80). Gravid females (SVL 213–250mm, $\overline{X}$ = 232.8mm, sd = 11.14, n = 12) were similar in size to other, non-gravid, mature females.

8.6.12.2 Male reproduction:

Although data are sparse and seasonally incomplete, the pattern of testicular enlargement and change in shape is consistent with the seasonal cycle in other subspecies. Males with enlarged turgid to flaccid testes were collected between 26 March and 23 November, testicular length increasing during this period (with the exception of a single March specimen with thin, narrow but very long testes), while most males collected in January (the only other month for which data are available) had thin, narrow testes (Fig. 81).

8.6.12.3 Female reproduction:

The pattern of variation in follicle diameter and presence of oviducal young is strongly seasonal, and parallels the inferred male cycle. Enlarged yolking ovarian follicles were present in females collected on 7 September (n = 2) and 1 November (n = 1), oviducal “egg masses” were present on 22 January (n = 3), while well-developed embryos were present in February (n = 2). Other females collected between January and early September (n = 16) had ovarian follicles ≤9mm in diameter, with the larger follicles occurring in winter and spring (Fig. 82).

The data suggest that vitellogenesis occurs in late winter and early spring, ovulation in spring, and young are born after February. There is no evidence that more than a single litter can be produced in a year.

8.6.12.4 Mating season:

There is no specific data on mating season in *T. r. konowi*, although the congruence between the peak in testicular length and turgidity, and the presence of yolking ovarian follicles suggest that mating occurs in early to mid spring (September–October).

8.6.12.5 Litter size:

Of 12 females with either countable enlarged yolky ovarian follicles (≥12mm), oviducal "eggs" or embryos, the number of follicles or young was 1–2 ($\overline{X}$ = 1.3, sd = 0.49, n = 12). There was no significant correlation between maternal SVL and litter size (r = 0.27, n = 12), nor was there a significant difference in SVL between females with one *vs* two young (Mann-Whitney U test, U = 10, n.s.), although the five smallest females had litters of one (Fig. 83).

8.6.12.6 Size of young at birth:

Although the smallest wild-caught specimen had SVL = 167mm, this individual was clearly not a neonate, and size at birth is presumably less than this size, possibly about SVL = 136mm, the size of the smallest wild-caught autumn specimen of *T. r. rugosa*.

8.6.12.7 Sex ratio:

The ratio of mature-sized males: females was 23:32, a ratio not significantly different to parity (X^2_1 = 1.47, n.s.).

8.7 Tiliqua rugosa palarra

8.7.1 Synonymy

Tiliqua rugosa palarra subsp. nov.

Scincus tropisurus Péron, F. (1807). *Voyage de Découvertes Aux Terres Australes, exécuté par ordre de Sa Majesté l'Empereur et Roi, Sur les Corvettes le Géographe, le Naturaliste, et la Goelette le Casuarina, Pendant les Années 1800, 1801, 1802, 1803 et 1804*. Vol. I. Imprimerie Impériale, Paris. (469pp.) [118]. (*nomen oblitum*)

Syntype (?): RMNH 2842, Nouvelle Hollande

Tiliqua rugosa palarra subsp. nov.

Holotype: AM R133199, Tamala rubbish tip, WA. Collected by A. Greer, R. Sadlier et al., 20 October, 1981.

Paratypes (58): AM R81388, R102710–14, R105690, R112444, R133197–98, R133200–01, RMNH 2842, SAM R4371, R33403–04, WAM R13160, R13460, R16949, R20496, R22681, R22755–58, R22958, R23879, R41637, R42375–76, R46547–48, R53795, R54394–95, R54588, R54607, R54666, R54757, R55259–60, R58815, R59704, R60609, R60712–13, R62371, R64448, R67335, R69640, R69644–45, R71467, R73127–28, R73130–31, R80428.

8.7.2 Diagnosis

A moderate-sized (maximum SVL 300mm), robust subspecies of *T. rugosa* with 17 or more subcaudal scales, 26–35 midbody scales, a relatively narrow head ($\overline{X}$ HW/HL 94.7%), usual presence of a median occipital, separation of first supraciliary and frontal and contiguous nasal scales, a small ear aperture ($\overline{X}$ Ear/HL = 6.5%), dorsal colour pattern consisting of yellow streaks and spots on an olive brown ground colour and a dark head.

8.7.3 Description

Nasals usually in narrow to moderate contact (59.3%, n = 59), less commonly moderately (20.3%) to narrowly separated (10.2%), rarely in point (6.8%) or broad (1.7%) contact, or separated by a median internasal (1.7%); supranasals absent; postnasals usually fused dorsally to nasals, separated ventrally by a postnarial suture, rarely completely distinct from nasals bilaterally (8.7%, n = 23); prefrontals usually in broad to moderate contact (98.3%, n = 59), rarely in narrow contact (1.7%); frontal undivided; supraoculars usually three bilaterally, with first only contacting frontal (86.3%, n = 51), rarely four, with first two contacting frontal bilaterally (3.9%) or unilaterally (3.9%), four, with first only contacting frontal bilaterally (2.0%), five, with first two contacting frontal bilaterally (2.0%), or two, with first only contacting frontal unilaterally (2.0%); supraciliaries 4–8 ($\overline{X}$ = 5.88, sd = 0.83, n = 104), usually six (50.0%) or five (32.7%); when supraciliaries six, and supraoculars three, first supraciliary very large, a little taller than long, projecting strongly between prefrontal and first supraocular, second much smaller, longer than tall, tapering caudally, contacting first supraocular only, third still smaller, slightly larger than tall, contacting and slightly projecting between first and second supraocular, fourth smallest or subequal to third, squarish, contacting second and sometimes third supraocular, fifth a little larger, square or slightly longer than tall, contacting third supraocular only, or projecting slightly between second and third, last large, subequal to or slightly smaller than first, projecting strongly between third supraocular and parietal; first supraciliary usually broadly to moderately separated (45.5%, n = 22) or narrowly separated (27.3%) from frontal, less commonly in point (4.5%), narrow (9.1%) or moderate contact (9.1%), or asymmetrical, moderately separated and in point contact (4.5%); last supraciliary usually broadly to moderately separated (95.7%, n = 23) from frontoparietals, rarely narrowly separated (4.3%); frontoparietals paired, in moderate to broad contact, rarely (n = 1) fragmented; occipitals 1–3 ($\overline{X}$ = 2.00, sd = 0.21, n = 46), usually two (95.7%); azygous occipital usually present (98.1%, n = 52) and large, rarely absent (1.9%); loreals usually two in horizontal series, rarely three bilaterally (n = 4) or unilaterally (n = 1) or one bilaterally (n = 1); caudal loreal rarely (n = 1) vertically paired bilaterally; subocular ring complete; presuboculars 2–4 ($\overline{X}$ = 2.92, sd = 0.46, n = 114), usually three (78.1%); suboculars 0–2 ($\overline{X}$ = 0.48, sd = 0.52, n = 114); postsuboculars 3–7 ($\overline{X}$ = 4.41, sd = 0.66, n = 114), usually four (57.0%); supralabials 8–11 ($\overline{X}$ = 8.99, sd = 0.61, n = 118), usually nine (66.1%), antepenultimate below centre of eye, penultimate and last undivided, taller than others; primary temporal present, usually paired bilaterally (n = 21), rarely undivided bilaterally (n = 1) or divided into three bilaterally (n = 1); upper secondary temporal single; lower secondary temporal usually paired bilaterally (n = 21), rarely divided into three unilaterally (n = 1) or bilaterally (n = 1); posttemporals 2–4 ($\overline{X}$ = 3.30, sd = 0.63, n = 46), usually three (52.2%); infralabials 8–11 ($\overline{X}$ = 9.64, sd = 0.70, n = 118), usually ten (50.8%) or nine (36.4%), scales in caudal part of row irregularly paired; usually first two infralabials contacting postmental bilaterally (n = 32), less commonly first three bilaterally (n = 12) or asymmetrically 2/3 (n = 8).

Midbody scales 26–35 ($\bar{X}$ = 29.3, sd = 1.77, n = 58); paravertebral scales 23–38 ($\bar{X}$ = 30.0, sd = 2.87, n = 51), between axilla and groin 17–27 ($\bar{X}$ = 20.8, sd = 2.21, n = 51); ventral scales 60–79 ($\bar{X}$ = 68.8, sd = 4.62, n = 51); subcaudal scales 17–22 ($\bar{X}$ = 18.8, sd = 1.40, n = 42); subdigital lamellae below fourth toe 3–10 ($\bar{X}$ = 6.46, sd = 1.18, n = 100), modally six (41.0%), basal lamellae paired.

SVL 151–300mm; AGL/SVL 46.4–63.4% ($\bar{X}$ = 56.9%, n = 50); TL/SVL 20.6–31.0% ($\bar{X}$ = 25.2%, n = 50); TD/TL 31.2–63.4% ($\bar{X}$ = 45.1%, n = 49); FLL/SVL 18.3–25.1% ($\bar{X}$ = 22.0%, n = 50); HLL/SVL 18.3–25.1% ($\bar{X}$ = 22.4%, n = 50); Hip/SVL 11.9–14.5% ($\bar{X}$ = 13.4%, n = 50); HL/SVL 19.3–25.5% ($\bar{X}$ = 22.3%, n = 50); HW/HL 87.5–107.4% ($\bar{X}$ = 94.7%, n = 51); HD/HL 53.5–73.0% ($\bar{X}$ = 62.4%, n = 49); IOC/HL 34.1–43.3% ($\bar{X}$ = 38.9%, n = 51); E–N/HL 25.8–30.1% ($\bar{X}$ = 28.2%, n = 22); E–E/HL 45.2–52.7% ($\bar{X}$ = 48.2%, n = 50); Eye/HL 15.1–24.1% ($\bar{X}$ = 18.6%, n = 51); Ear/HL 2.9–9.9% ($\bar{X}$ = 6.5%, n = 51); IparL/HL 12.3–20.7% ($\bar{X}$ = 16.9%, n = 51); FrontL/HL 16.8–26.6% ($\bar{X}$ = 21.3%, n = 51); IparL/FrontL 61.0–95.6% ($\bar{X}$ = 80.7%, n = 58); IparW/IparL 53.3–102.4% ($\bar{X}$ = 73.8%, n = 58); FrontW/FrontL 71.4–95.5% ($\bar{X}$ = 82.4%, n = 58).

8.7.4 Allometry

Allometric values and calculated values for morphometric characters are presented in Table 8.47. Half of the characters examined showed significant allometric growth, the exceptions being tail length, hip width and head length (all against SVL), tail width (against tail length), head width, head depth, eye-ear interval and ear diameter, (all against head length), interparietal length (against frontal length) and interparietal width (against interparietal length). Of these characters, tail width and ear diameter showed a noticeable trend towards allometry (magnitude of difference between allometric coefficient and 1.000 greater than minimum difference for significantly allometric relationships). Of the characters showing statistically significant allometry, all but the relationship between axilla-groin length and SVL showed negative allometry.

8.7.5 Coloration (Fig. 84)

Dorsal and ventral ground colour cream to pale yellow. Dorsal ground colour almost completely obscured by mid to very dark brown leaving only pale flecks or narrow streaks on body and tail dorsum. At maximum exposure of pale coloration, narrow (1/2 scale wide) pale longitudinal streaks up to 5–6 scales long scattered over dorsum, occasionally partially aligned in transverse series, and a narrow brown vertebral line on nape bordered laterally by pale streaks.

Head dorsum mid to dark brown, with or without obscure fine paler flecks or marbling; temporal region often slightly paler, due to increased dominance of pale ground colour.

Venter yellow, with moderate to heavy brown markings; on body and tail, dark markings mostly in form of narrow (1/2 scale wide) longitudinal stripes medially, narrow to broad (2–4 scale wide) transverse bars laterally. Some tendency for dark medial markings to coalesce into a solid patch. Throat moderately to strongly clouded with brown, at minimum

represented to dark caudal margins to scales, at maximum almost completely brown, especially over mental region.

Laterally, a weakly defined zone of demarcation between dorsal (brown dominated) and ventral (yellow dominated) patterns.

Limbs irregularly variegated brown and yellow, predominantly brown dorsally, yellow ventrally. Hindlimb dorsum with a weakly to strongly defined 2 scale wide pale band over thigh.

Soles yellow-brown to dark brown.

8.7.6 Asymmetry

Asymmetry was common to rarely present in number of occipitals, supraciliaries, presuboculars, suboculars, postsuboculars, supralabials, infralabials and subdigital lamellae, with up to 52.1% of individuals (in the case of subdigital lamellae) having asymmetries. However, there were no significant differences between left and right sides in any of these variables (t-tests of asymmetrical cases).

8.7.7 Sexual Dimorphism

Sexual dimorphism was not detected in mean number of supraoculars, occipitals, presuboculars, suboculars, postsuboculars, supralabials, infralabials (both overall and contacting postmental), posttemporals, midbodies, paravertebrals between axilla and groin, ventrals or subcaudals (t-tests), or in degree of separation or contact of nasals (contingency X^2).

Statistically significant sexual dimorphism was detected in mean number of supraciliaries (♂♂: $\overline{X}$ = 6.02, sd = 0.91, n = 50; ♀♀: $\overline{X}$ = 5.59, sd = 0.56, n = 32; $t_{80} = 2.40^{*}$), paravertebral scales (overall) (♂♂: $\overline{X}$ 30.7, sd = 3.25, n = 25; ♀♀: $\overline{X}$ = 28.6, sd = 2.31, n = 16; $t_{39} = 2.31^{*}$) and subdigital lamellae (♂♂: $\overline{X}$ = 6.72, sd = 1.25, n = 50; ♀♀: $\overline{X}$ = 6.16, sd = 0.884, n = 32; $t_{80} = 2.21^{*}$). In all three cases, the differences are trivial compared to the range of variation within the sexes, and consequently the sexes were not separated in analysing geographic variation.

Tests for sexual dimorphism in morphometric characters are presented in Tables 8.48–8.49. Possibly due to the small sample sizes, only hind limb length, head length and interparietal length showed statistically significant sexual dimorphism. In each case, females had the lower values, although the differences are relatively minor.

8.7.8 Distribution

Restricted to the Shark Bay region of Western Australia (Fig. 49). Occurs on Bernier, Dorre and Dirk Hartog islands, on both the Edel Land and Peron Peninsulas on the mainland, south to 5km S Tamala, and around the lower Gascoyne River drainage, from the coast inland to 10mi E Carnarvon, north to “Boolathana” and south to “Callagiddy”. Possibly occurs further south along the Zuytdorp coast (as defined by Storr and Harold, 1980) towards the Murchison River, where there is intergradation with the nominate race. The Zuytdorp

coastline remains largely inaccessible and uncollected.

8.7.9 Geographic Variation

Geographic variation within *T. r. palarra* has been explored elsewhere within the context of the species as a whole (Section 8.2–8.3). There is little geographic varition within *T. r. palarra* apart from a tendency for the insular populations to have smaller scales (higher midbody, and for some insular populations [at least two of three in each case], higher paravertebral, ventral, postsubocular and supralabial counts), and possibly for the two northern insular populations to be a little smaller than other populations (maximum SVL 268mm [n = 15] *vs* 300mm [n = 42], with 15 specimens >268mm).

8.7.10 Comparison with Other Taxa

Comparisons with all other *Tiliqua* taxa have been made in previous chapters and sections.

8.7.11 Habits and Habitats

The habitat preferences of *T. r. palarra* are poorly known. Storr and Harold (1978) report the mainland populations from low *Acacia* scrub on sandy soils, while the Carnarvon population is common in banana plantations (Storr & Harold, 1984). Douglas and Ride (1962) record the Bernier I. population from *Olearia* thickets and open steppe. Two individuals I have collected between Carnarvon and Gascoyne Junction have been in *Acacia* scrub on compacted red sandy soil close to the Gascoyne River. One was crossing the road late in the morning, the other was in leaf litter under an *Acacia*. The Tamala series was taken from under tin in a rubbish tip on a claypan surrounded by *Acacia* scrub on gently sloping limestone/sand hills (A. Greer, *pers. comm*.).

8.7.12 Taxonomic History and Type Material

The Shark Bay population of *Tiliqua rugosa* was the first population to be seen by Europeans. First noticed and described by Dampier (1729), prior to the introduction of binomial nomenclature, it was next collected by François Péron, during the Baudin expedition of 1800–1804. Unfortunately Péron died before completing the zoological results of the expedition, and no formal description appeared. However, in the general narrative of the expedition, when describing the period spent at the Barren Islands (= Bernier and Dorre Is.) Péron provided a name, *Scincus tropisurus*, with the brief annotation: “Les *Reptiles* ne comptoient qu'une espèce de *Scinque* (*Scincus Tropisurus N*.), l'une des plus grandes de ce genre, et dont la queue très-courte et très-grosse fait paroître, au premier instant, cet animal comme ayant deux têtes . . . ”

This comment appears to be sufficient to diagnose the species, and the name must be considered valid. However, due to the informal nature of the proposal of the new name, it was overlooked by all authors until 1962, when Douglas and Ride (1962) noted its existence.

Péron (1807) did not indicate the number of specimens collected. However, the leader of the expedition, Nicolas Baudin, in his posthumously published journal (Baudin, 1974) noted that two were collected, presumably between 27 June and 14 July 1801, when the expedition was at Bernier and Dorre Is. A specimen I located in the Nationaal Natuurhistorisch Museum, Leiden (RMNH 2842), although not identified as a type, appears to be one of the

specimens collected by Peron. The specimen is in spirit, in a permanently sealed jar, which bears two labels. The older label reads "*Scincus pachyurus* Per. *Trachysaurus rugosus* Gray. Voy. Peron. Nouv. Holl.", while the apparently more recent label reads "*Trachysaurus rugosus* (s.n. *Scincus pachyurus*, Pér.) Voyage Péron, Nieuw Holland". While the locality is not precise, the faded specimen is typical of the Shark Bay race of *T. rugosa*, and Péron (1807) did not report collecting specimens of *T. rugosa* anywhere outside of Shark Bay.

Consequently, I consider this specimen to be one of the syntypes of *Scincus tropisurus* Péron (1807). The species name *pachyurus* on the bottle labels (which also appears, attributed to Péron, in the synonymies of *Tiliqua rugosa* provided by Gray [1831, 1838, 1841, 1845] and Duméril and Bibron [1839]) is probably due to a later decision by Péron to formally name the species as such in the zoological results of the Baudin expedition, and emphasises the informal nature of the names proposed in the general narrative.

The specimen (Fig. 85) has the following combination of characters: nasals narrowly separated; supraoculars three; supraciliaries six, first narrowly contacting frontal; presuboculars three; suboculars 0/1; postsuboculars 4/5; supralabials nine; infralabials 11/10; first 3/2 infralabials contacting postmental; posttemporals three; occipitals two; midbody scales 29; paravertebrals scales 30, 21 between axilla and groin; ventral scales 73; subcaudal scales 21; subdigital lamellae seven; ear very small.

Although the specimen could not be measured, it appears to be a small adult, with SVL approximately 250mm.

Bonnemains *et al*. (1988), in publishing part of the natural history artwork from the Baudin expedition, includes a painting by the artist Lesueur of one of Péron's specimens of *T. rugosa*. This painting is of a typical Shark Bay animal, although it is not clear if it is of RMNH 2482, and provides further proof of the identity of *Scincus tropisurus*.

As pointed out by Douglas and Ride (1962), the name *Scincus tropisurus* is a senior synonym of *Trachydosaurus rugosus* by 18 years, and hence to recognise it as an available name for the subspecies is impossible without overturning more than 165 years of usage of *rugosa* as the species name, although Wilson and Knowles (1988) incorrectly use the combination *Tiliqua rugosa tropisurus*. Douglas and Ride (1962), followed by Cogger *et al*. (1983), recommend treating the name as a *nomen oblitum*. Under the third edition of the Code (1985), Douglas and Ride's (1962) action, which took place during the period of force of Article 23(b) of the previous edition, must be followed, and the name cannot be used unless approval has been obtained from the ICZN acting under its plenary powers (Article 79(c)(iii–iv)). As recommended by the Code, a formal request for the use of the plenary powers to suppress the name *Scincus tropisurus* is in preparation.

As the name *Scincus tropisurus* is unavailable for the Shark Bay subspecies, a new name must be proposed. Consequently, I propose the name *Tiliqua rugosa palarra*. "Palarra" is the Aboriginal name for *T. rugosa* in the Gascoyne River drainage area (Alexander, 1921).

The proposed holotype (AM R133199; Figs. 84, 86), a mature female with two 27.5mm yolking follicles in the right ovary, has the following combination of characters: nasals in narrow contact; supraoculars three; supraciliaries five, first narrowly separated from frontal; occipitals two, median occipital absent; presuboculars 2/3; suboculars absent; postsuboculars five; supralabials nine; infralabials ten, first two contacting postmental; temporal scalation typical; posttemporals four; midbody scales 30; paravertebral scales 29, 21 between axilla and groin; ventral scales 64; subcaudal scales 18; subdigital lamellae eight, basal 5/4 paired; SVL 286mm; AGL 178mm; TL 76mm; TD 34.2mm; Hip 41.1mm; FLL 62.5mm; HLL 62mm; HL 62.8mm; HW 56.6mm; HD 37.0mm; IOC 23.4mm; E–N 17.9mm;

E–E 29.6mm; Eye 11.8mm; Ear 4.9mm; IparL 10.9mm; IparW 7.5mm; FrontL 12.0mm; FrontW 9.7mm.

8.7.13 Reproduction

8.7.13.1 Size at maturity:

Mature-sized males had SVL 242–290mm, $\bar{X}$ = 265.3mm, sd = 16.22, n = 15, while mature-sized females were apparently a little larger, at SVL 259–300mm, $\bar{X}$ = 276.5mm, sd = 13.59, n = 11. However, the sample sizes were too small for statistical significance to be reached.

8.7.13.2 Male reproduction:

Samples were too limited in size and seasonal distribution to accurately assess the seasonality of the male reproductive cycle. However, the data available are not inconsistent with the spring peak in the cycle seen in other *Tiliqua*. Of the 15 adult males examined, eight were collected in October–November. All but one of these had turgid testes 13.5–25.5mm in length. Of six adults collected in July–August, only two had turgid testes (length 15.5–17mm), while the other four had flattened testes 12–21mm long. The only other specimen examined was collected in April, and had small flattened testes 12.5mm long.

8.7.13.3 Female reproduction:

Although the data are limited, vitellogenesis seems to peak in mid to late spring (October or a little later), and gestation lasts to at least February, possibly as late as April. Two of three adult females collected in October had enlarged yolking follicles 14.5–27.5mm, while the third had a largest follicle of 13mm. Six females collected between July and September had smaller follicles, the largest in each case between 6–10mm. A February female had oviducal eggs, while the sole April female had dilated oviducts, and was possibly postparturient.

8.7.13.4 Litter size:

Data on litter size are available for only three females. The smallest (SVL = 259mm) had one enlarged (17mm) yolking follicle in the left ovary, and a smaller (14.5mm) follicle beginning to deposit yolk in the right ovary. Of the two larger females (both SVL = 286mm), one had two 27.5mm yolking follicles in the right ovary, but none in the left, while the other had three oviducal masses, two in the right oviduct, one in the left. In the latter case, the three corpora lutea had the same distribution.

8.7.13.5 Size of young at birth:

The smallest individual seen had SVL = 151mm, and was collected 24 August 1976. If parturition occurs in April or before, as suggested by the mature female data, then size at birth is likely to be rather less than this. A neonate size of 136mm SVL for *T. r. rugosa* (SVL of smallest wild-caught autumn specimen) would seem to be a reasonable estimate for *T. r. palarra* as well.

8.7.13.6 Sex ratio:

Overall, the ratio of mature-sized males: females was 15:11, a ratio not significantly different to 1:1 ($\chi^2_1 = 0.62$, n.s.), although the sample size is probably too small for this to be reasonably assessed.