

# Biology and Zoogeography of the Amphibians and Reptiles of the Western Australian Wheatbelt

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## Abstract

One hundred and ten species of reptiles and 17 species of frogs are recorded from the Western Australian wheatbelt. Data presented on distributions within the wheatbelt and adjacent areas indicate zoogeographic affinities with both the arid-zone and mesic south-west; the arid-zone component is predominant. The concept of a south-west biogeographic province does not accord particularly well with most distributions recorded; a much smaller region encompasses the distinct south-west elements of the herpetofauna. No reptiles or amphibians are endemic to the wheatbelt. Data on soil types suggest that reptile distributions are not as edaphically determined as previously thought. Woodlands are a major habitat for reptiles in the wheatbelt. Most reptiles were found to breed in spring to early-summer.

## Introduction

The wheatbelt is the cereal producing area of Western Australia. It is located in the south-west of the State (Figure 1) between the 28-58 cm isohyets in an area of mild, wet winters and hot dry summers. The wheatbelt boundaries are taken from the 1968 Land Use map of Western Australia published by the Department of Lands and Surveys. The Esperance sandplain and Salmon Gums district are excluded because they are not contiguous to the rest of the wheatbelt and they were not examined by us.

The vegetation of the wheatbelt consists of woodland, mallee, shrubland, heath, breakaway, lithic complex (including granite outcrops) and salt complex (samphire) vegetation formations as defined by Muir (1977). Characteristic of the vegetation and soil types is the tight mosaic in which formations occur with all types often in close proximity, the effects of which were examined by Kitchener *et al.* (1980). Muir (pers. comm.) suggests that prior to clearing for cereal production woodland occupied as much as 60% of the wheatbelt. Much woodland was cleared because it occurred on soil considered most suitable for cereal production and it is now poorly represented on wheatbelt reserves.

Extensive clearing of the natural vegetation did not commence until *ca* 1900. Since then there have been two main waves of expansion. One followed the 1914-18 War when land grants were made to returning servicemen, and the

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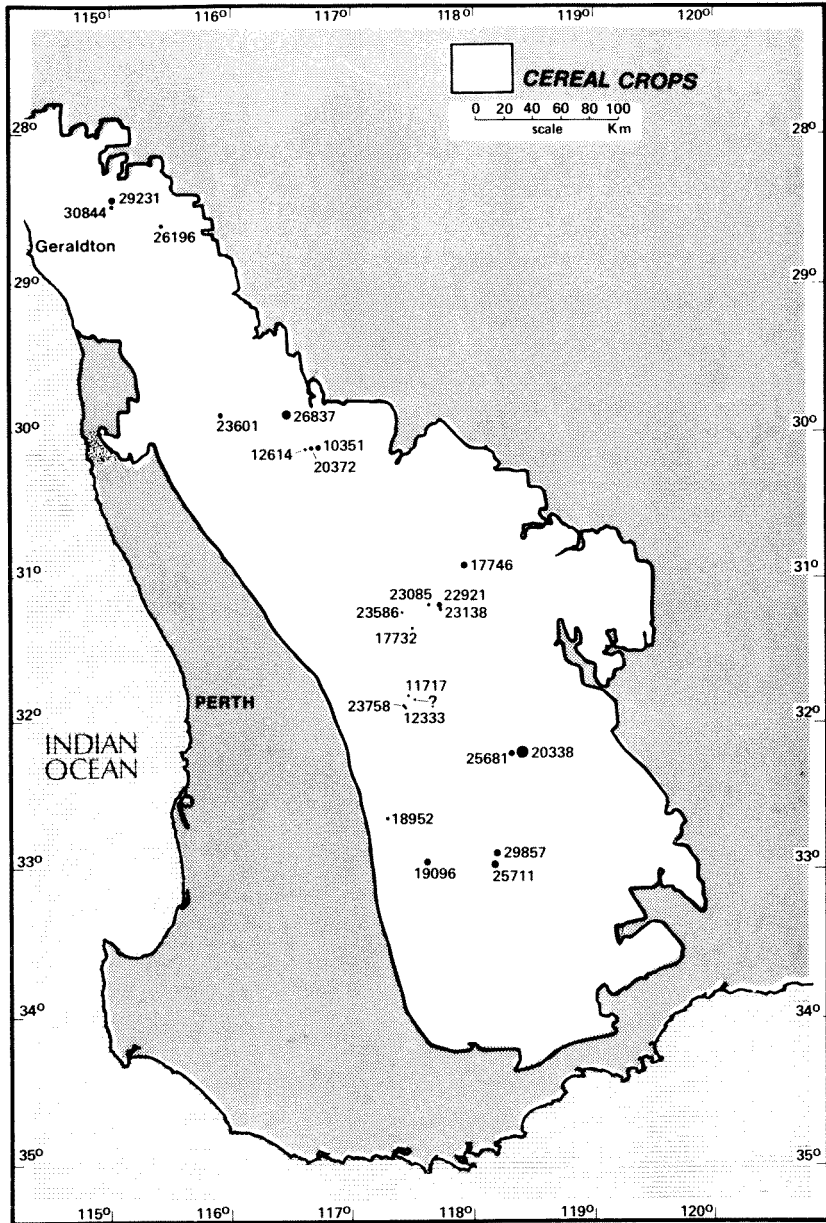


Figure 1 Map of south-west Western Australia showing the distribution of reserves selected by the Biological Survey of the Western Australian Wheatbelt. Reserves are identified by number and are listed on Table 1; their relative size is indicated by size of spot. The wheatbelt is outlined as in the 1968 Land Use Map of Western Australia.

second was in the 1950s when introduction of trace elements made sandplain arable. Today the wheatbelt occupies some 14 million hectares. Currently there are about 500 nature reserves within the region with a total area of 330,000 hectares or 2.4% of the area. Some of these are quite small; three-quarters of them are less than 500 ha in area. Figures are not available, but most of the uncleared land in the wheatbelt is privately owned farmland.

Between 1971 and 1976 the Western Australian Museum biological survey unit undertook a series of vertebrate and vegetation surveys of 24 nature reserves in the Western Australian wheatbelt. The objectives of these surveys and a brief description of the zoogeographic nature of the wheatbelt are given in Kitchener (1976). The results have been published in a series of 13 reports which are listed in Table 1 together with the size and coordinates of the reserves. The locations of these reserves are indicated in Figure 1. The fauna surveys were supplemented by vegetation studies which resulted in the vegetation formations (including area of each, species lists, soil types, drainage and fire history) being described for each reserve. A system of vegetation classification with emphasis on faunal utilisation of habitat was developed for the project (Muir 1977).

Prior to this survey the number of species comprising the herpetofauna of the wheatbelt was reasonably well known. Of the 125 species now known to occur 120 had already been recorded. Knowledge of the wheatbelt herpetofauna was greatly assisted by past Museum policy of encouraging country people, particularly school children, to collect, preserve and have specimens identified. Because the wheatbelt is the most closely settled of the non-metropolitan areas it resulted in considerable collections being made from the region. However, very little accurate information was available on the distribution of species within the wheatbelt and virtually nothing was known of their ecology and reproductive biology.

This contribution is a summary of existing knowledge of the distribution and biology of the herpetofauna of the wheatbelt region. It complements Kitchener *et al.* (1980) who describe aspects of the conservation of the wheatbelt lizard fauna in terms of the species/area relationship and biogeographic theory.

### Methods

Reptiles and frogs were surveyed on the 24 reserves concurrently with the mammal and bird surveys. Each reserve was visited twice, once each in autumn and spring, for a minimum of five days each season. Twice as long was spent on larger reserves. Except for *Varanus gouldii*, *Tiliqua rugosa* and *T. occipitalis* (large species which are readily identified in the field) all data in this paper are derived from the 2005 specimens collected and lodged in the Western Australian Museum. Specimens included are those accessed to 31 December 1978.

Specimens were obtained by shooting with 0.22 calibre dust shot, by hand, by digging out burrows and by turning over leaf litter, roadside spoil, rubbish etc.

Some were collected in pit-fall traps set primarily to catch mammals. Geckos and frogs were collected at night with the aid of a head torch. Collection sites were described so that vegetation, soil type, and drainage data were available for each specimen. Terminology of woodland, mallee, shrubland and heath follows Muir (1977) and that of soils follows Northcote (1971). Specimens were fixed in the field in 10% formalin and later preserved in 75% alcohol. Laboratory procedures included measuring snout-vent length (SVL), *in situ* examination and measurement of reproductive organs, and examination of stomach contents. To gain a better understanding of the reproductive cycle additional material from the Museum collection was examined.

Table 1 List of reserves studied during biological survey of wheatbelt with co-ordinates, size of reserve and authors of published reports.

Reserve	Location	Area ha	Published Survey Report
1 East Yuna (29231)	28°24'S,115°13'E	1717	Dell <i>et al.</i> 1981
2 Bindoo Hill (30844)	28°20'S,115°14'E	486	Dell <i>et al.</i> 1981
3 Wilroy (26196)	28°38'S,115°38'E	332	Dell <i>et al.</i> 1979b
4 Marchagee (23601)	29°58'S,116°05'E	495	Dell <i>et al.</i> 1979c
5 Buntine (26837)	29°58'S,116°34'E	3147	Kitchener <i>et al.</i> 1979
6 East Nugadong (20372)	30°12'S,116°53'E	772	Kitchener <i>et al.</i> 1979
7 Nugadong (12614)	30°13'S,116°49'E	400	Kitchener <i>et al.</i> 1979
8 Nugadong Forest (10351)	30°13'S,116°58'E	364	Kitchener <i>et al.</i> 1979
9 Billyacatting (17746)	31°03'S,118°01'E	2075	Chapman <i>et al.</i> 1981
10 Durokoppin (23138)	31°24'S,117°45'E	1030	Muir <i>et al.</i> 1978
11 East Yorkrakine (23085)	31°24'S,117°39'E	81	Chapman <i>et al.</i> 1980
12 Yorkrakine Rock (23586)	31°26'S,117°31'E	158	Chapman <i>et al.</i> 1980
13 Kodj Kodjin (22921)	31°27'S,117°48'E	204	Muir <i>et al.</i> 1978
14 North Bungulla (17732)	31°32'S,117°35'E	104	Chapman <i>et al.</i> 1980
15 Yoting Water (11717)	31°52'S,117°33'E	34	Muir <i>et al.</i> 1980
16 Yoting Town	31°58'S,117°35'E	61	Muir <i>et al.</i> 1980
17 Badjaling (23758)	31°59'S,117°30'E	272	Muir <i>et al.</i> 1980
18 South Badjaling (12333)	32°01'S,117°31'E	41	Muir <i>et al.</i> 1980
19 Bendering (20338)	32°21'S,118°30'E	5119	Kitchener <i>et al.</i> 1977
20 West Bendering (25681)	32°24'S,118°22'E	1602	Kitchener <i>et al.</i> 1977
21 Yornaning (18952)	32°45'S,117°23'E	247	Dell <i>et al.</i> 1979a
22 North Tarin Rock (29857)	33°00'S,118°15'E	1415	Kitchener <i>et al.</i> 1976
23 Tarin Rock (25711)	33°06'S,118°13'E	2011	Kitchener <i>et al.</i> 1976
24 Dongolocking (19096)	33°04'S,117°41'E	1061	Chapman <i>et al.</i> 1978

## Results

### Nature and composition of the fauna

The herpetofauna of the Western Australian wheatbelt comprises 13 species of leptodactylid frogs, and 4 species of hylid frogs, 1 turtle, 17 geckos, 10 legless lizards, 14 agamids, 35 skinks, 5 monitors, 7 blind snakes, 3 pythons and 18 elapid snakes. These are listed in Table 2 and their distribution indicated on Figures 2-88 (Appendix I). None is restricted to the region.



Wheatbelt Amphibians and Reptiles

Table 2 (continued)

	Fig. Number	East Yuna	Bindoo Hill	Wilroy	Marchagee	Buntine	East Nugadong	Nugadong	Nugadong Forest	Billyacatting	Durokoppin	East Yorkrakine	Yorkrakine Rock	Kodj Kodjin	North Bungulla	Yoting Water	Yoting Town	Badjaling	South Badjaling	Bendering	West Bendering	Yornaning	North Tarin Rock	Tarin Rock	Donglocking	Wandana	Karroun Hill	Dragon Rocks	Lake Grace/Chinocup	Lake Magenta	Lake Cairlocup	Lake Bryde	Other Reserves	Other Localities			
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33			
<b>PYGOPODIDAE</b>																																					
<i>Aprasia repens</i>	22				X																																
<i>Delma australis</i>	23	X	X		X					X	X									X			X	X			X									X	
<i>D. fraseri</i>	24									X	X	X	X					X			X	X	X	X												X	
<i>D. grayii</i>	25				X	X									X										X											X	
<i>D. nasuta</i>	24	X																								X										X	
<i>D. tincta</i>	25																																			X	
<i>Lialis burtonis</i>	26	X						X			X										X				X	X	X									X	
<i>Pletholax gracilis</i>	23																																			X	
<i>Pygopus lepidopodus</i>	27	X	X		X						X	X	X										X													X	
<i>P. nigriceps</i>	22	X			X																																
<b>AGAMIDAE</b>																																					
<i>Ctenophorus cristatus</i>	28										X	X	X							X	X		X		X						X	X	B		X		
<i>C. inermis</i>	28		X																						X											X	
<i>C. isolepis citrinus</i>	29																																			X	
<i>C. m. maculatus</i>	30	X	X																							X										X	
<i>C. m. griseus</i>	30				X	X					X	X		X						X	X		X	X												X	
<i>C. ornatus</i>	31									X	X	X	X										X				X	X								B/D	X
<i>C. reticulatus</i>	32	X									X	X	X		X												X									X	
<i>C. salinarum</i>	34				X															X																X	
<i>C. scutulatus</i>	33	X	X	X		X	X	X																		X	X									X	
<i>Gemmatophora longirostris</i>	34	X																																		X	
<i>Moloch horridus</i>	35	X	X		X	X	X												X							X										X	
<i>Pogona m. minor</i>	36	X	X		X	X			X	X	X			X					X		X	X	X		X	X	X	X	X	X	X	X	X	X		X	
<i>Tympanocryptis a. adalaidensis</i>	29				X																															X	
<i>T. a. chapmani</i>	29																						X				X		X							X	
<i>T. cephalo</i>	34																																			X	
<b>SCINCIDAE</b>																																					
<i>Cryptoblepharus carnabyi</i>	37	X	X	X																																	
<i>C. plagiocephalus</i>	37		X	X	X		X		X	X	X	X	X								X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	B	X
<i>Ctenotus alleni</i>	38	X																																			X
<i>C. atlas</i>	38																																				X
<i>C. fallens</i>	39				X																																X
<i>C. gemmula</i>	38																																				X
<i>C. impar</i>	40																				X	X		X	X		X	X								X	
<i>C. mimetes</i>	41	X	X						X																	X	X									X	
<i>C. p. pantherinus</i>	42		X							X	X	X							X	X																X	
<i>C. schomburgkii</i>	43		X	X		X	X			X	X	X							X	X				X												X	
<i>C. u. uber</i>	41		X					X																			X									X	
<i>Egernia carinata</i>	44																					X						X		X						X	
<i>E. depressa</i>	45		X																																	X	
<i>E. inornata</i>	46	X			X	X																															X
<i>E. kingii</i>	47																																			X	
<i>E. multiscutata bos</i>	46																			X	X						X	X	X							X	
<i>E. stokesii badia</i>	45				X																															X	
<i>Eremiascincus richardsonii</i>	48																					X														X	
<i>Hemiergus i. initialis</i>	49																												X	X	X					X	
<i>H. peronii</i>	50																													X	X					X	
<i>Lerista distinguenda</i>	51				X									X								X	X		X		X	X								X	
<i>L. elegans</i>	53				X																							X	X	X						X	
<i>L. gerrardii</i>	52								X																											X	



## Leptodactylidae

*Neobatrachus* has 4 species of which *N. pelobatoides* is restricted to south-western Australia; *N. sutor*, *N. centralis* and *N. wilsmorei* are widely distributed in arid Australia. The 3 *Heleioporus* species, *albopunctatus*, *eyrei* and *psammophilus*, are all endemic to south-western Australia. *Pseudophryne guentheri* is endemic to south-western Australia; in the south-eastern wheatbelt it overlaps with the wide-ranging semiarid *P. occidentalis*. *Limnodynastes* is an Australia-wide genus represented in the wheatbelt by the south-western endemic *L. dorsalis*. *Myobatrachus gouldi* is also endemic to south-western Australia. *Ranidella*, a temperate and tropical genus, is represented in the wheatbelt by the south-western endemic *R. pseudinsignifera*. *Crinia georgiana* is confined to humid south-western Australia, in the wheatbelt it is only found in the far south.

## Hylidae

The three south-western endemic species of *Litoria* are confined to the more humid coastal regions. Two species, *L. cyclorhynchus* and *L. adelaidensis*, occur in the extreme south of the wheatbelt, and *L. moorei* occurs both in the extreme south and in the north-western wheatbelt near Geraldton. *Cyclorana platycephalus* is a marginal wheatbelt species, being present at Morawa.

## Gekkonidae

*Diplodactylus*, which is widespread in arid Australia, has 9 species in the wheatbelt. Two northern species *D. michaelsoni* and *D. alboguttatus*, are found only in a few localities on the northern and western margins of the wheatbelt. Apart from *D. spinigerus*, which is endemic to south-western Australia, the remaining species have relatively wide distributions in the southern arid zone.

The remaining gecko genera are represented in the wheatbelt by one species each: *Crenadactylus ocellatus* (2 subspecies), *Gehyra variegata*, *Heteronotia binoei*, *Oedura reticulata*, *Phyllodactylus marmoratus*, *Phyllurus milii* and *Rhynchoedura ornata*. With the exception of *Oedura reticulata* (which is restricted to the semiarid woodlands of the wheatbelt and to the east) and *Phyllodactylus marmoratus* (which is found in southern Australia from Western Australia to Victoria and New South Wales) the other 5 species are widespread in Australia.

## Pygopodidae

*Delma* has 5 species: *D. grayii* has a relatively restricted west coast distribution, the remainder are widespread in arid and tropical (in the case of *D. tincta*) Australia. *Pygopus lepidopodus* and *P. nigriceps* have widespread southern and northern distributions respectively but have an area of sympatry in the northern wheatbelt (both occur together on 2 reserves). *Lialis burtonis* is widespread in Australia being absent only in southern Victoria and Tasmania. *Aprasia repens* is a south-western representative of a widespread genus. *Pletholax gracilis* is an endemic south-western monotypic genus and occurs only marginally in the wheatbelt.



### Agamidae

The arid and semiarid *Moloch horridus* is widespread in the wheatbelt. The northern *Gemmatophora longirostris* is only marginally a wheatbelt species. *Tympanocryptis adelaidensis* is an endemic south-western species, as are *Ctenophorus ornatus* and *C. maculatus*. *C. salinarum*, *C. reticulatus*, *C. scutulatus* and *Pogona minor* are widespread outside the wheatbelt.

### Scincidae

The genus *Ctenotus* is prominent in the wheatbelt with 9 species. *C. alleni*, *C. gemmula* and *C. impar* are endemic to south-western Australia; of these only *C. gemmula* extends into the extreme south-west. *C. atlas*, *C. fallens*, *C. pantherinus*, *C. schomburgkii* and *C. uber* are wide-ranging in the arid zone, and *C. mimetes* extends north to the Ashburton. *Lerista* has 8 species in the wheatbelt. *L. distinguenda* and *L. gerrardii* are endemic to south-western Australia; *L. planiventralis*, *L. praepedita*, *L. elegans* and *L. lineopunctulata* have extensive west coastal distributions; and *L. muelleri* and *L. macropisthopus* are wide-ranging in the arid zone. *Egernia*, which is widely distributed in Australia, has 6 wheatbelt species. With the exception of *E. kingii*, a south-western species which is only marginally present in the wheatbelt, all have relatively wide distributions in the semiarid and arid zone. The 3 *Morethia* species are largely allopatric and all extend well outside south-western Australia. Storr (1972) used the observation of allopatry to support his suggestion of their evolution *in situ*. *Cryptoblepharus*, *Menetia* and *Tiliqua* each have two species, *Eremiascincus* and *Omolepida* each have one; all range widely outside the wheatbelt.

### Varanidae

*Varanus caudolineatus* and *V. eremius* are arid species which occur south to the northern margin of the wheatbelt; *V. gouldii* and *V. tristis* range throughout arid, tropical and temperate regions; *V. rosenbergi* has a southern distribution.

### Typhlopidae

The genus *Ramphotyphlops* is Australia-wide; *R. australis*, *R. bituberculatus*, *R. pinguis* and *R. waitii* are wide-ranging but *R. hamatus* and *R. leptosoma* are south-western endemics (Storr 1981).

### Elapidae

The elapid fauna of the wheatbelt is quite diverse and contains several prominent genera. *Vermicella* is Australia-wide and 4 widespread arid and semiarid species occur in the wheatbelt. *Rhinoplocephalus* has 4 species; two, *R. nigriceps* and *R. bicolor*, have a southern distribution; *R. monachus* and *R. gouldii* have wide arid and semiarid zone distributions. *Pseudonaja* has three species; *P. modesta* is wide-ranging, *P. nuchalis* is widely distributed in arid and tropical Australia, and *P. affinis* appears to be a recently evolved sibling with a restricted distribution in south-western Australia. *Pseudechis australis* and *Demansia reticulata* are widely

distributed, the former also occurs in the tropics. *Notechis curtus*, *N. scutatus*, and *N. coronatus* are southern species; in the wheatbelt they only occur on the coastal margins. *Acanthopis antarcticus*, *A. pyrrhus* and *Furina ornata* have only a few wheatbelt records.

#### Boidae

*Python spilotos* is widely distributed in tropical, arid and temperate Australia excluding only the extreme south-east. *Aspidites ramsayi* is widely distributed in arid Australia, and *Liasis childreni* is widely distributed in northern Australia; they occur at their most southerly in the wheatbelt.

Having put the wheatbelt herpetofauna in its Australian perspective it is instructive to examine faunal variation within the region. There is a distinct attenuation from north to south, see also Table 5 in Kitchener *et al.* (1980). This is probably influenced by (a) zoogeography — the northern wheatbelt is closer to the areas of origin of the fauna than the south, (b) climate — cold is probably more involved than drought and (c) geomorphology and soil type — the south of the wheatbelt, including the Albany/Esperance block (Johnstone *et al.* 1973) is deficient in lateritic sandplains and dissected laterites — a prominent feature of the northern and central wheatbelt (Mulcahy 1973). The following data were derived by superimposing latitude 30°00'S and 32°30'S on the species distribution maps and counting all distribution records within the northern, central and southern zones.

#### Number of species of:

	Frogs	Geckos	Pygopodids	Agamids	Skinks	Varanids	Snakes
Northern	11	14	9	9	25	4	17
Central	10	15	6	9	23	3	18
Southern	10	9	6	6	16	2	12

Southern restricted species include *Litoria cyclorhynchus*, *Hemiernis peronii*, *Hemiernis initialis*, *Ctenopus gemmula*, *Notechis curtus*, *N. scutatus*, *Rhinoplocephalus bicolor*. These mainly belong to genera with strong south-eastern representation. In addition *Varanus rosenbergi*, *Egernia carinata*, *Egernia multiscutata* *bos*, *Ctenopus impar* and *Pseudonaja affinis* are not found in the far north of the wheatbelt.

#### Habitat Selection

Examination of the habitat data in this study indicates that the wheatbelt herpetofauna is non-specialist in its habitat utilisation. Only three species are habitat specialists, *Oedura reticulata* (only on trunks of eucalypt trees), *Ctenophorus ornatus* (only on granite outcrops with exfoliations), and *Ranidella pseudinsignifera* (only in rock pools and seepages associated with granite outcrops).

Using data from this study Kitchener *et al.* (1980) identified woodland as being particularly important for wheatbelt lizards, in spite of poor representation on reserves. In particular, more species are found in woodland, though not necessarily restricted to it, than any other vegetation formation. Additionally, the relationship between number of species and area is more highly correlated for woodland than other formations. Woodlands frequently have a high degree of structural complexity including lower strata, micro-environments of hollow spouts and refugia under bark within the trees themselves, as well as abundant leaf litter, humus and dead fallen and standing timber. In addition to those lizard groups examined by Kitchener *et al.*, woodland is a prominent formation for frogs and snakes, but less important than for lizards. The percentage of each family occurring in each vegetation formation is shown in Figure 89.

Table 3 shows the percentage of species of each family in different vegetation formations. Although woodland only represented 11.1% of formation area of reserves it provided habitat in most families for over 50% of species. The only family well represented on salt complex was Leptodactylidae.

Table 3 indicates the percentage of captures of each species in the different vegetation formations on wheatbelt reserves. It also shows the percentage of captures on each of the soil texture groups (Northcote 1971) recorded on the reserves. The relative abundance of each soil texture group can be gauged by the number of times it was recorded.

Seventeen species were predominantly (>50% of specimens collected) woodland inhabiting, 7 were predominantly mallee-inhabiting, 12 were predominantly shrubland-inhabiting, 6 were predominantly heath-inhabiting and 6 were predominantly lithic-inhabiting (Table 3). Only two species, *Heleioporus eyrei* and *Ctenophorus salinarum* were collected predominantly on salt complex.

Table 3 also indicates preferences by some reptile groups for certain soil texture groups. For example leptodactylid frogs had a high percentage of individuals on sandy loams and a low percentage preference for the more clayey soils. As a group the agamids showed preference for sandier soils, with sands and sandy loams having a high percentage of species and individuals.

Many individual species show a high degree of tolerance of different soil type. For example, 22% of the 73 species for which we have adequate data occur on 5 of the 6 texture groups, which range from Sands (5-10% clay content) to Heavy Clays (75% clay content). Most species were recorded on a range of soil types but tended to avoid extremely sandy or clayey soils. The following were only collected on sandier soils, i.e. Sands and Sandy Loam texture groups: *Diplodactylus ornatus*, *Diplodactylus squarrosus*, *Lialis burtonis*, *Tympanocryptis a. adelaidensis*, *T. a. chapmani*, *Ctenophorus inermis*, *C. m. maculatus*, *Omolepida branchialis* and *Heleioporus psammophilus*. The distributions of some of these species correspond quite nicely with the extent of 'sandplains' in a broad sense; however some, e.g. *D. squarrosus* and *Lialis burtonis* are not readily recognisable

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as sandplain species. For these species sampling error might be high as few were collected by us.

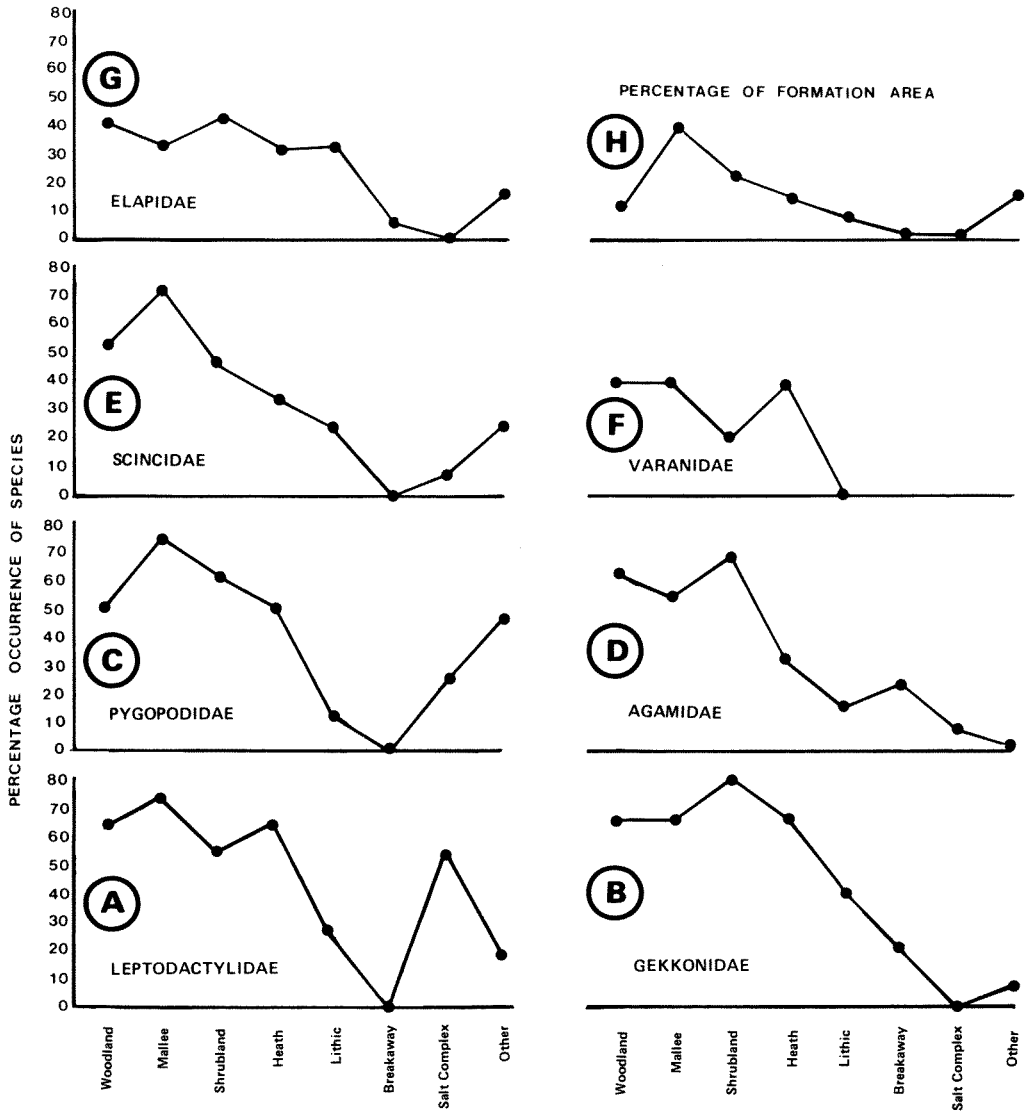


Figure 89 Percentage occurrence of each family (A-G) in the 7 vegetation formations recorded on wheatbelt reserves. The percentage of each vegetation formation is also indicated (H).

In contrast to the sandier soils no species was only recorded on the Light Clay and Medium-Heavy Clay texture groups. In fact all species which occur on the Medium-Heavy Clays also occur on Sands and most texture groups in between. There may, however be habitat or niche specificity in another component. For example, although *Oedura reticulata* is recorded from all six soil texture groups, it was only recorded from the trunks of eucalypt trees. These data suggest that for some species soil type may be less important in determining reptile and frog distributions than previously thought, see for example Storr (1964). However, lighter rather than heavier soils may limit the distribution of some species.

Pianka (1970) in his work on the genus *Ctenotus* has shown that as many as 7 species may occur in ecological sympatry. In that study, species partitioned the niche components place, food and time to avoid competitive exclusion. In the wheatbelt the following *Ctenotus* species occur in potential ecological sympatry (Table 3) on the basis of soil type and vegetation formation (including height and projective foliage cover of the upper stratum): *C. impar* and *C. schomburgkii*, *C. schomburgkii* and *C. pantherinus*, *C. schomburgkii* and *C. alleni*. Although *C. schomburgkii* and *C. alleni* overlap in distribution they have not been recorded from the same reserve. The other two pairs however have been recorded together at exactly the same sites. We assume that size disparity between these species is an important factor in minimising competition.

Some agamids are quite specific in their vegetation and soil type preference, and few are found in ecological sympatry. Of the four potentially ecologically sympatric taxa only *Ctenophorus scutulatus* and *Pogona minor* were actually recorded from the same site. Our data indicate some dietary preferences between these species with *P. minor* eating mainly centipedes and caterpillars (Geometridae) (Chapman and Dell 1978) compared to ants, bees, weevils, flies, moths, scarabid beetles, bugs, lacewings, crickets, centipedes and spiders for *C. scutulatus* (Dell and Chapman 1979).

Geckos of the genus *Diplodactylus* show the greatest degree of ecological sympatry. *D. maini*/*D. pulcher*/*D. granariensis* occurred together frequently, *D. maini*/*D. spinigerus*/*D. granariensis* and *D. pulcher*/*D. squarrosus*/*D. granariensis* occurred together once. *D. ornatus*/*D. michaelsoni* also occurred together once. There is a high degree of dietary difference between *D. pulcher* and *D. maini* with *D. maini* eating mainly spiders (families Clubionidae, Ctenidae and Gnaphosidae) and Pseudoscorpionidae. In addition lepidopteran larvae, crickets, moths, termites, flies, ants and isopods were eaten to a lesser extent, (Chapman and Dell 1979a and Chapman and Dell 1979c). *D. pulcher* on the other hand eats mainly termites (*Eutermes* sp.) (Dell and Chapman 1978 and Dell and Chapman 1979). Both can be collected on the same night in the same woodland, and both occupy lycosid spider burrows. *D. granariensis* eats spiders (Clubionidae and Mygalomorphae) and termites as well as lepidopteran larvae, cockroaches, ants, weevils and isopods (Dell and Chapman 1979 and Dell and Harold 1979).

Wheatbelt Amphibians and Reptiles

Table 3 List of wheatbelt reptiles and amphibians showing number of specimens collected during wheatbelt survey, percentage of captures on each vegetation formation type, and percentage of captures on each soil texture group recorded on wheatbelt reserves.

The combined percentage of each vegetation formation and the number of times each soil texture group was recorded are indicated.

	No. Specimens	Percent recorded in formation								No. of soil records					
		Woodland Formation 1.1%	Mallee 39.8%	Shrubland 23.3%	Heath 13.6%	Lithic Complex 8.8%	Breakaway Complex 1.3%	Salt Complex 1.4%	Other 0.1%	Sands 90	Sandy Loams 547	Loams 247	Clay Loams 51	Light Clays 89	Medium-Heavy Clays 23
<b>LEPTODACTYLIDAE</b>															
<i>Heleioporus albopunctatus</i>	74	48	8	3	20	9		5	7	29	27	23	5	14	2
<i>H. eyrei</i>	3		34					66					34*		
<i>H. psammophilus</i>	5	60			40						100				
<i>Limnodynastes dorsalis</i>	26	42	13	4	33			8			57	28	7		8
<i>Myobatrachus gouldii</i>	6	20	40		40					20	40	20*			
<i>Neobatrachus centralis</i>	26	29	25	8	16			12			19	6	21	54	
<i>N. pelobatoides</i>	42	66	18	11				5			45	2	36	15	2
<i>N. sutor</i>	11			60	40						77	23			
<i>N. wilsmorei</i>	1		100								100				
<i>Pseudophryne guentheri</i>	78	13	19	27	4	30		3	4	4	58	20		16	2
<i>Ranidella pseudinsignifera</i>	17					100									
<b>GEKKONIDAE</b>															
<i>Crenadactylus o. ocellatus</i>	98	47	15	8	20	7	3			26	46	4	8	14	2
<i>Diplodactylus alboguttatus</i>	32		15	85							14	79		7	
<i>D. granariensis</i>	146	68	9	15	6	2				3	35	10	10	35	7
<i>D. maini</i>	138	50	6	25	19						47		10	40	3
<i>D. michaelsoni</i>	7		20	20	60						80	20			
<i>D. ornatus</i>	15		66	14	8				12		20	80			
<i>D. pulcher</i>	49	30	10	40	13	7				6	66	3	8	17	
<i>D. spinigerus</i>	15	7	7	7	79					8	84		8		
<i>D. squarrosus</i>	2		50	50							100				
<i>Gehyra variegata</i>	236	62	8	7	1	20	2			1	22	35		35	7
<i>Heteronotia binoei</i>	28	45		10		45									
<i>Nephrurus levis occidentalis</i>	13			100							100				
<i>Oedura reticulata</i>	67	100								3	40	13		36	8
<i>Phyllodactylus marmoratus</i>	10	90			10					10	90				
<i>Phyllurus milii</i>	21	29				66	5				50		50		
<b>PYGOPODIDAE</b>															
<i>Aprasia repens</i>	2		50		50						50		50		
<i>Delma australis</i>	22	21	28	43	8					9	54		28	9	
<i>D. fraseri</i>	35	39	4	21	7	29				21	35	7	37		
<i>D. grayii</i>	5		25	25	25			25			66		34		
<i>D. nasuta</i>	8		50						50						
<i>Lialis burtonis</i>	8	38		12					50	25	75				
<i>Pygopus lepidopodus</i>	9	13	25	62							50	12	13	25	
<i>P. nigriceps</i>	3							33#	67						

Table 3 (continued)

	Percent recorded in formation									No. of soil records					
	No. Specimens	11.1%	39.8%	23.3%	13.6%	8.8%	1.3%	1.4%	0.1%	90	547	247	51	89	23
	Woodland Formation	Mallee	Shrubland	Heath	Lithic Complex	Breakaway Complex	Salt Complex	Other	Sands	Sandy Loams	Loams	Clay Loams	Light Clays	Medium-Heavy Clays	
<b>AGAMIDAE</b>															
<i>Ctenophorus cristatus</i>	16	64	29			7			49	44		7			
<i>C. inermis</i>	2			100					100						
<i>C. m. maculatus</i>	8			50	50				100						
<i>C. m. griseus</i>	45	4	18	39	36		3			80	12			8	
<i>C. ornatus</i>	38					100									
<i>C. reticulatus</i>	8	43	14	29			14				40	20	40		
<i>C. salinarum</i>	6	8	9		33		50			17					49#
<i>C. scutulatus</i>	18	7	27	59	7					56	11		33		
<i>Gemmatophora longirostris</i>	2	100													
<i>Moloch horridus</i>	10	10	10	80						67	33				
<i>Pogona m. minor</i>	28	32	15	32	21				26	53	16		5		
<i>Tympanocryptis a. adalaidensis</i>	2			100						100					
<i>T. a. chapmani</i>	2			100					100						
<b>SCINCIDAE</b>															
<i>Cryptoblepharus carnabyi</i>	7		14					86							
<i>C. plagiocephalus</i>	52	86	11			3			16	37		9	19	19	
<i>Ctenotus alleni</i>	9		33	33	34					85	15				
<i>C. fallens</i>	1				100			100		100					
<i>C. impar</i>	13	8	34		58				20	40	40				
<i>C. mimetes</i>	5		20	40				40			20*				
<i>C. p. pantherinus</i>	18	13	19	68						66	11	23			
<i>C. schomburgkii</i>	29	28	8	28	32			4	11	66		23			
<i>C. u. uber</i>	33	33	33	33						33				66	
<i>Egernia carinata</i>	2	100										100			
<i>E. depressa</i>	1		100							100					
<i>E. inornata</i>	3		50	50						100					
<i>E. multiscutata bos</i>	15	7	13		33	47				33	67				
<i>E. stokesii badia</i>	1	100											100		
<i>Eremiascincus richardsonii</i>	1					100									
<i>Lerista distinguenda</i>	23	46		23	31				80		20				
<i>L. elegans</i>	2							100							
<i>L. gerrardii</i>	1							100							
<i>L. macropisthopus</i>	1					100									
<i>L. muelleri</i>	33	37	27	33	3					30		40	30		
<i>L. praepectata</i>	1		100												
<i>Menetia greyii</i>	67	54	11	14	6	8		7	4	70	9		13	4	
<i>M. surda</i>	13		100												
<i>Morethia butleri</i>	8	43	57							13*					
<i>M. lineocellata</i>	2		50					50		50*					
<i>M. obscura</i>	63	34	21	16	26	3			19	66	4		7	4	
<i>Omolepida branchialis</i>	3		66	34						100				3	
<i>Tiliqua occipitalis</i>	28	13	41	33	13				11	61	5	5	18		
<i>T. rugosa</i>	29	24	17	41	13	3		2	9	60	8	3	21		

Wheatbelt Amphibians and Reptiles

Table 3 (continued)

	Percent recorded in formation									No. of soil records					
	No. Specimens	11.1%	39.8%	23.3%	13.6%	8.8%	1.3%	1.4%	0.1%	Sands	Sandy Loams	Loams	Clay Loams	Light Clays	Medium-Heavy Clays
<b>VARANIDAE</b>															
<i>Varanus caudolineatus</i>	2			100											
<i>V. eremius</i>	1		100											100	
<i>V. gouldii</i>	2	50		50							100				
<i>V. rosenbergi</i>	1	100													
<i>V. tristis</i>	1					100									
<b>TYPHLOPIDAE</b>															
<i>Ramphotyphlops australis</i>	18	29	6		53	12									
<i>R. waitii</i>	8														
<b>BOIDAE</b>															
<i>Python spilotos</i>	1		100								100				
<b>ELAPIDAE</b>															
<i>Denisonia fasciata</i>	1	100													
<i>Notechis curtus</i>	3		33												66
<i>Rhinoplocephalus gouldii</i>	33	12	8	36	28	16				13	60		20		7
<i>R. monachus</i>	5			80		20									
<i>R. nigriceps</i>	2		50		50							50	50		
<i>Pseudechis australis</i>	3		25	50		25							50*		
<i>Pseudonaja affinis</i>	7	20			60		20				100				
<i>P. modesta</i>	2			100											50*
<i>P. nuchalis</i>	7	40		40		20						67	33		
<i>Vermicella bertholdi</i>	4	100										50		50	
<i>V. bimaculata</i>	2														100
<i>V. s. semifasciata</i>	2				100							100			

\* Other data not recorded

# Ecotone

Reproduction

This study provides reproductive data on 44 reptile species (Table 4). The usual situation is that animals are gravid in spring and/or summer with juveniles and subadults present the following autumn. There is some indication that breeding is earlier in the north than in the south. To the north of the wheatbelt at Shark Bay and Kalbarri the agamids *Ctenophorus m. maculatus* and *C. reticulatus* were gravid in August compared with northern wheatbelt *Pogona minor* and *C. scutulatus* which were gravid in September (Dell and Chapman 1979). North of the wheatbelt, Bradshaw (1981) has reported earlier oviducal eggs in *Pogona minor* and *C. ornatus*. In the central and southern wheatbelt October is the earliest date for gravid specimens of the agamids *Tympanocryptis adelaidensis chapmani* and *Moloch horridus* and the geckos *Gehyra variegata*, *Heteronotia binoei* and



Table 4 List of wheatbelt reptile species for which reproductive data are available showing snout-vent length of males, females, and gravid females, clutch size and months during which females had yolky follicles and oviducal eggs.

	Snout Vent Length (mm) $\bar{x} \pm S.E. (n)$			Clutch size $\bar{x} \pm SD (n)$	Sept Oviducal eggs Yolky follicles	Oct Oviducal eggs Yolky follicles	Nov Oviducal eggs Yolky follicles	Dec Oviducal eggs Yolky follicles	Jan Oviducal eggs Yolky follicles	Feb Oviducal eggs Yolky follicles	Other Oviducal eggs Yolky follicles
	Males	Females	Gravid ♀♀								
<i>Crenadactylus o. ocellatus</i>	31.25 ± 2.45 (8)	32.19 ± 0.67(21)	31.43 ± 0.16 (7)	2 ± 0 (6)		x	xx	x			
<i>Diplodactylus alboguttatus</i>	45.83 ± 0.57(18)	44.0 ± 1.36 (4)	48.0 (1)	2 ± 0 (2)					x	x	
<i>D. granariensis</i>	46.85 ± 0.91(56)	51.77 ± 0.80(45)	52.07 ± 0.89(17)	2 ± 0(17)	x		xx				
<i>D. maini</i>	41.13 ± 0.72(51)	44.64 ± 0.57(53)	46.88 ± 0.76(11)	2 ± 0(11)		x	xx		x	x	
<i>D. pulcher</i>	46.2 ± 0.80(18)	47.0 ± 0.66(17)	48.66 ± 0.97 (3)	2 ± 0 (3)	x		xx				
<i>D. spinigerus</i>	57.16 ± 1.63 (6)	60.0 ± 3.10 (4)	70.0 (1)	2 ± 0 (1)			x				
<i>D. squarrosus</i>			53.0 (1)		x						
<i>Phyllurus milii</i>	78.66	76.0 - 85.0 (2)	78.0 (1)	2 ± 0 (1)			x	x			
<i>Gehyra variegata</i>	42.80 ± 0.61(67)	44.83 ± 0.36(59)	45.20 ± 0.95(17)	1 ± 0(17)		x	xx				
<i>Heteronotia binoei</i>	47.0 - 50.0 (2)	47.3 ± 1.05(10)	45 (1)	2 ± 0 (1)			xx		x		
<i>Oedura reticulata</i>	58.42 ± 1.69(14)	61.72 ± 1.95(11)	64.33 ± 1.78 (3)	2 ± 0 (3)		x	x				
<i>Delma australis</i>	60.33 ± 1.34 (6)	71.42 ± 2.40 (7)	70.0 (1)	2 ± 0 (3)		x		x			
<i>D. fraseri</i>	87.33 ± 4.19(12)	105.5 ± 4.95 (6)	120 (1)	2 ± 0 (1)			xx				
<i>D. grayii</i>	80.0 ± 3.30 (3)	97.6 ± 3.31 (3)	105 (1)	2 ± 0 (1)			x				
<i>D. nasuta</i>	75.0 ± 5.31 (3)	81.25 ± 4.08 (4)									
<i>Lialis burtonis</i>	115.66 ± 6.6 (3)	183.33 ± 11.81(9)	195-220 (2)	1 ± 0 (1)			x				
<i>Pygopus lepidopodus</i>			180 (1)				xx				
<i>Ctenophorus cristatus</i>	76.41 ± 5.35(12)	89.76 ± 2.71(17)	85-95 (2)	3 ± 1.41 (2)			xx	x			
<i>C. maculatus maculatus</i>	50.54 ± 1.71(12)	49.75 ± 1.59(15)	59.0 ± 1.69 (3)	2 ± 0 (3)							
<i>C. maculatus griseus</i>	48.39 ± 1.55(28)	53.21 ± 1.95(23)	56.25 ± 2.88 (4)	4 ± 0 (4)	x		xx				
<i>C. ornatus</i>	76.61 ± 2.42(26)	76.76 ± 1.31 (30)	84.66 ± 3.34 (3)	2.9 ± 0.71 (3)		x	xx	x	x	x	
<i>C. reticulatus</i>	73.3 ± 3.07(16)	66.37 ± 1.48(16)	72 (1)	4 ± 0 (1)			x				

Table 4 (continued)

	Snout Vent Length (mm)			Clutch size $\bar{x} \pm SD$ (n)	Sept Oviducal eggs Yolky follicles	Oct Oviducal eggs Yolky follicles	Nov Oviducal eggs Yolky follicles	Dec Oviducal eggs Yolky follicles	Jan Oviducal eggs Yolky follicles	Feb Oviducal eggs Yolky follicles	Other Oviducal eggs Yolky follicles
	Males	Females	Gravid ♀♀								
<i>C. salinarum</i>		55.5 ± 2.99 (4)	55.67 ± 3.18 (3)	3 ± 0 (1)	x						
<i>C. scutulatus</i>	83.0 ± 6.89 (9)	72.8 ± 8.11 (5)	90-97 (2)	3.5±0.7 (2)							
<i>Moloch horridus</i>	73.5 ± 7.08 (4)	90.6 ± 3.61 (5)	97.00 ± 1.00 (3)	6.5±1.29 (3)		x	x				x April
<i>Pogona m. minor</i>	99.28 ± 3.63(14)	99.92 ± 3.25(28)	106.12 ± 4.0 (8)	7 ± 1.38 (8)	x	x	x				
<i>Cryptoblepharus plagio-</i> <i>cephalus</i>	36.27 ± 1.72(11)	39.14 ± 0.79 (7)	41 (1)	2 ± 0 (1)				x			
<i>Ctenotus alleni</i>			89 (1)			x					
<i>C. impar</i>	48.8 ± 3.09 (5)	41.33 ± 2.87 (3)	63 (1)	2 ± 0 (1)			x				
<i>C. mimetes</i>	63 (1)	80 (1)	80 (1)	6 ± 0 (1)	x						
<i>C. p. pantherinus</i>	73.28 ± 2.29 (7)	73.84 ± 4.17 (7)	83 (1)	3 ± 0 (1)			x				
<i>C. schomburgkii</i>	37.72 ± 1.16(11)	40.10 ± 1.19(19)	40 (1)				x				
<i>Egernia depressa</i>			85 (1)		x						
<i>E. inornata</i>	74 (1)	74 (1)	74 (1)	3 ± 0 (1)				x			
<i>E. multiscutata bos</i>	83 (1)	68.66 ± 6.13 (1)	82 (1)	1 ± 0 (1)				x			
<i>Lerista distinguenda</i>	37.11 ± 0.63 (9)	40.66 ± 1.18 (3)									
<i>L. muelleri</i>	36.20 ± 0.76(15)	39.53 ± 1.09(13)	39.0 (1)								
<i>Menetia greyii</i>	25.16 ± 1.79 (6)	29.34 ± 0.56(35)	30.77 ± 1.39(13)	1.8±0.98(11)		x	x				
<i>Morethia butleri</i>	46.58 ± 1.04(12)	49.0 ± 0.56 (5)							x		
<i>M. obscura</i>	42.36 ± 0.95(22)	41.90 ± 1.23(21)	45.20 ± 2.01 (5)	3 ± 0.82 (4)	x	x	xx				
<i>Tiliqua rugosa</i>	163.0 ± 7.17 (5)	200-230 (2)	200-230 (2)				x				
<i>Varanus gouldii</i>	NA	NA	300 (1)	12 ± 0 (1)			x				x May
<i>Rhinoplocephalus gouldii</i>	304.44 ± 16.48(9)	296.06 ± 11.47(6)	303.33 ± 17.64(3)			xx					

*Phyllodactylus marmoratus*. Some skinks breed later than agamids and geckos as *Morethia butleri*, *M. lineocellata*; *Ctenotus fallens* and *C. schomburgkii* and *Cryptoblepharus plagiocephalus* were only gravid in summer.

The only instances of any reproductive activity in autumn were one *Moloch horridus* and one *Tiliqua rugosa* which had enlarged yolky ovarian follicles. The possibility of sperm storage cannot be ignored as Smyth (1968) and Philipp (1979) have presented data on sperm storage in *Hemiergis peronii* and *Moloch horridus*.

Our data indicate that *Pogona minor*, *Ctenophorus salinarum* and *Moloch horridus* take more than one year, probably two, to achieve sexual maturity. *C. maculatus* appears to breed in its first year and this probably applies to many of the smaller skinks, geckos and agamids.

### Discussion

Several authors have commented on the zoogeography of south-western Australia: Serventy and Whittell (1976) commented on birds; Storr (1964), Keast (1959) and Cogger and Heatwole (1981) have dealt with reptiles; and Main (1965) and Main *et al.* (1958) with frogs. Storr's main contribution was to recognise the distinctness of the south-west for reptiles as others had done for other vertebrate groups. In addition he identified the geographical factors contributing to the south-west's herpetofauna distinguishing it from both the arid zone and temperate south-east Australia, and recognised that different factors influence different vertebrate groups; in particular that bird and reptile faunas are different. Unlike Main *et al.* (1958) Storr believes that geographical influences in the south-west, particularly the laterites of the forest block, which adjoins the western margin of the wheatbelt, could account for speciation in both reptiles and frogs.

Consideration of the nature and composition of the wheatbelt herpetofauna confirms the concepts of Storr (1964) for the south-west; that is that the fauna is a blending of arid-adapted elements from the north and east and meso-temperate elements from the extreme south-east of Australia. The diversity of wheatbelt herpetofauna is largely due to the arid-adapted groups — *Ctenophorus* (8 spp.), *Ctenotus* (9 spp.), *Diplodactylus* (9 spp.), *Lerista* (8 spp.) and *Neobatrachus* (4 spp.). These genera are poorly represented in the mesic south-east and south-west regions of Australia. Conversely three genera which have radiated widely on the east coast, *Oedura*, *Sphenomorphus* and *Leiolopisma* are poorly represented in the south-west; and *Anomalopus*, *Pseudemoia* and *Saiphos* are not represented in the south-west. The leptodactylid genera *Crinia* and *Ranidella* and the skink genus *Leiolopisma*, which identify the south-west with the south-east are, with the exception of *R. pseudinsignifera*, absent from the wheatbelt.

The case for a south-west phytogeographic province has recently been reviewed and consolidated by Beard (1980). However the evidence for a faunal south-west province is not as conclusive. Serventy and Whittell (1976) indicated that the south-west avifauna is a mixture of Bassian and Eyrean components in terms

of the traditional terminology of Baldwin Spencer (1896). Keast (1959) was unable to reconcile any of the biogeographic distribution patterns to reptile distributions. Our data and those of Cogger (1979) show that few reptile or amphibian distributions accord with the south-west province boundary as usually drawn from the mouth of the Murchison River ( $27^{\circ}43'S$ ,  $114^{\circ}10'E$ ) to Israelite Bay ( $33^{\circ}37'S$ ,  $123^{\circ}32'E$ ). Many species with wide distributions in arid Australia extend well to the south and west of this line but exclude the extreme south-west. Conversely other species, most of which do not occur in the wheatbelt, have rather restricted distributions in the extreme south-west. In particular there is a hiatus along a line drawn between Perth and Albany; of 109 species of wheatbelt reptiles only 35 extend south and west of this line. Agamids and geckos are particularly poorly represented south of this line with two and four species respectively. This is reminiscent of the situation in south-east Australia, where Tasmania has one agamid and no geckos.

In summary, the distributions of reptiles and amphibians in south-west Western Australia do not readily accord with the concept of a south-west province based on a line between the Murchison River and Israelite Bay. To encompass the 'distinctness' of the south-west herpetofauna in terms of most endemic species and isolated endemic genera, e.g. *Pseudemydura*, *Pletholax*, *Aclys*, *Elapognathus*, *Rhinoplocephalus* and *Metacrinia* a much smaller region should be envisaged. It would include the coastal plain south from Geraldton and east to the vicinity of Esperance ( $33^{\circ}52'S$ ,  $121^{\circ}53'E$ ) and inland to the eastern margins of the forest block.

Except for a few species our data do not support the suggestion of Keast (1959) that the south-west has, 'given rise to major faunal components in reptiles'.

It is relevant to compare the herpetofauna of the Western Australian wheatbelt and Victorian 'mallee'; these areas are similar in rainfall seasonality, incidence and variability, land use and vegetation (though the wheatbelt probably had more woodland than its Victorian counterpart). Seventy-three species of reptile are recorded from the 'mallee' (Rawlinson 1966) compared to 109 for the Western Australian wheatbelt, and there is no endemism. In this latter sense the two regions are similar, Rawlinson states that the mallee cannot be considered a separate faunal division and draws attention to the similarity between the 'mallee' and south-western Australia.

*Hemiergus initialis initialis* and *Ranidella pseudinsignifera* are interesting cases of species of apparent mesic origin which have made considerable inroads into the semiarid zone in Western Australia. The former is found north and east to Fraser Range; *R. pseudinsignifera* occurs north to Kalbarri and east to the vicinity of Balladonia, it survives in a mesic microenvironment by virtue of its occurrence in seepages and soaks around granite outcrops. Heatwole (1976) has postulated a similar situation in south-west Western Australia for the genus *Egernia*.

Mulcahy (1973) has reviewed the formation of landscape in the south-west and Bettenay and Hingston (1964) and Mulcahy and Hingston (1961) have examined

pedogenesis in two localised areas within the wheatbelt. The erosion of dissected laterites into sandplains has been a prominent feature of the evolution of landscape here. It is tempting to postulate the incursion of a sand-adapted herpetofauna from the central deserts into the wheatbelt concurrent with the evolution of sandplains. However this is unlikely as the development of sandplains from the weathering of lateritic duricrust in the central deserts and in the wheatbelt were probably simultaneous events, probably in the mid Miocene or Oligocene epochs, see Johnstone *et al.* (1973), Mulcahy and Hingston (1961) and Towner and Gibson (1980). Additionally, Pianka (1972) has shown abundantly clearly that of the 'desert' species which also occur in the wheatbelt 90% are on the heavier soils of the 'shrub — *Acacia* species' category. Only *Ctenophorus isolepis* and *Varanus eremius* (which are only marginally wheatbelt species) belong to Pianka's 'sand-ridge' and 'Triodia-sandplain' category. Some distributions suggest that there has been incursion of sandplain species into the south-west via the west coast south of North West Cape. The distributions of *Ctenopus fallens*, *Diplodactylus alboguttatus* and *Ctenophorus maculatus* suggest that this might be the case.

Hopper (1979) has shown that the 'transitional rainfall zone' which corresponds approximately to the wheatbelt is particularly rich in plant species and he invokes Tertiary-Quaternary climatic fluctuation and subsequent landscape developments as a factor promoting plant speciation in the region. While the evidence for similarly directed speciation in reptiles is not extensive there are several interesting cases. The distributions of *Tympanocryptis adelaidensis adelaidensis* and *T. a. chapmani* correspond approximately to the northern and southern occurrences of extensive sandplains in the wheatbelt. Both subspecies have only been recorded on sandplains and it is possible that the intervening 'heavier', i.e. with a greater clay content, soils may be a geographical barrier promoting reproductive isolation. A similar situation may prevail in the Coorow-Mt. Lesueur district where a distance of 50-60 km with laterite overlain by shallow sand apparently separates *Ctenophorus maculatus maculatus* on the coast from *C. m. griseus* in the wheatbelt (Dell and Chapman, 1977). In addition Storr (1972) has inferred *in situ* speciation for 3 species of *Morethia* which occur largely in allopatry in the wheatbelt. Storr (1976) has also implied that woodland on laterite of the forest block is a geographical barrier between *Lerista elegans* and *L. distinguenda* which occur on the coastal plain and precambrian shield respectively.

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Appendix I  
 Figures 2–88

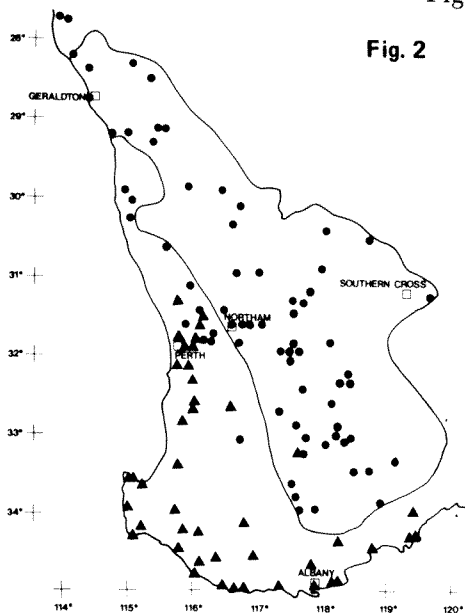


Fig. 2

*Heleioporus albopunctatus* ●  
*Crinia georgiana* ▲

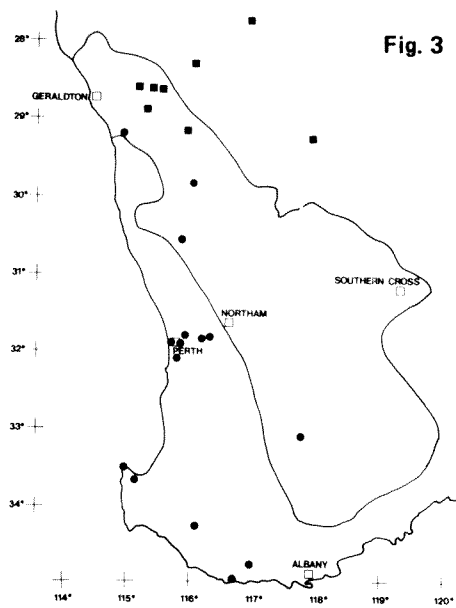


Fig. 3

*Heleioporus psammophilus* ●  
*Neobatrachus wilsmorei* ■

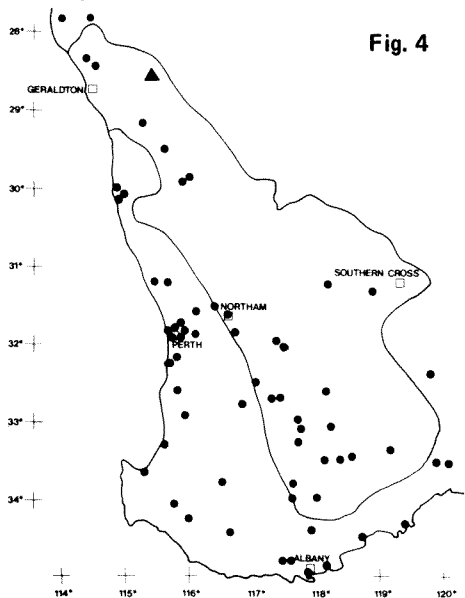


Fig. 4

*Cyclorana platycephala* ▲  
*Limnodynastes dorsalis* ●

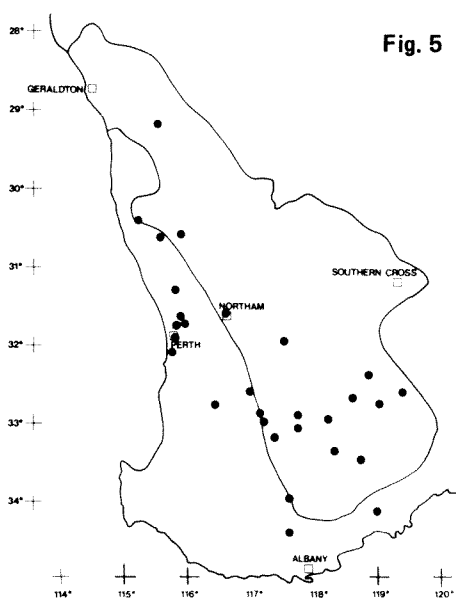


Fig. 5

*Myobatrachus gouldii* ●

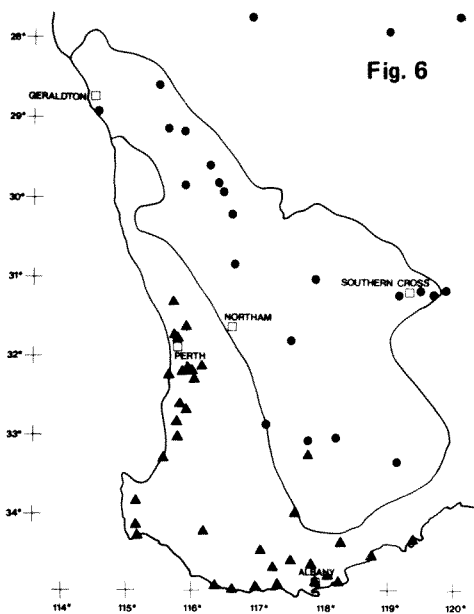


Fig. 6

*Neobatrachus centralis* ●  
*Litoria adelaidensis* ▲

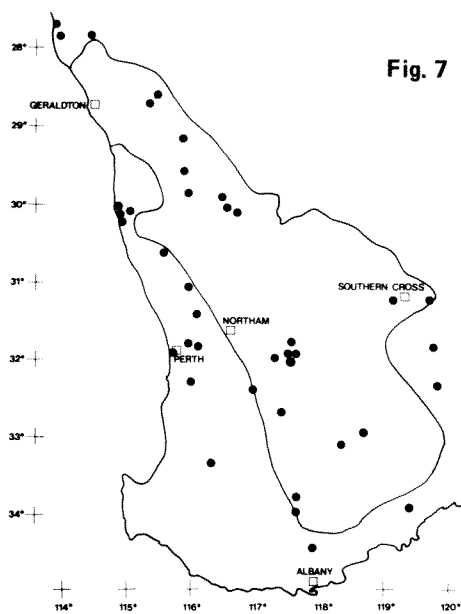


Fig. 7

*Neobatrachus pelobatoides* ●

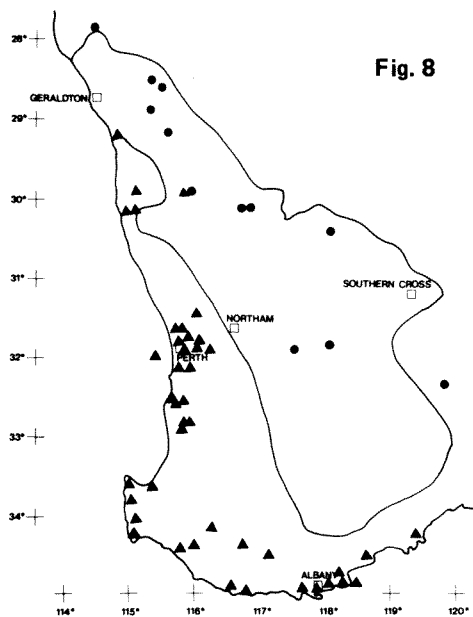


Fig. 8

*Neobatrachus sutor* ●  
*Heleioporus eyrei* ▲

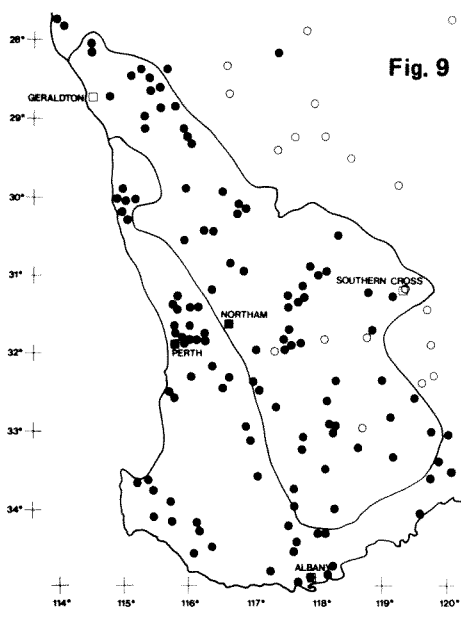


Fig. 9

*Pseudophryne guentheri* ●  
*Pseudophryne occidentalis* ○

Wheatbelt Amphibians and Reptiles

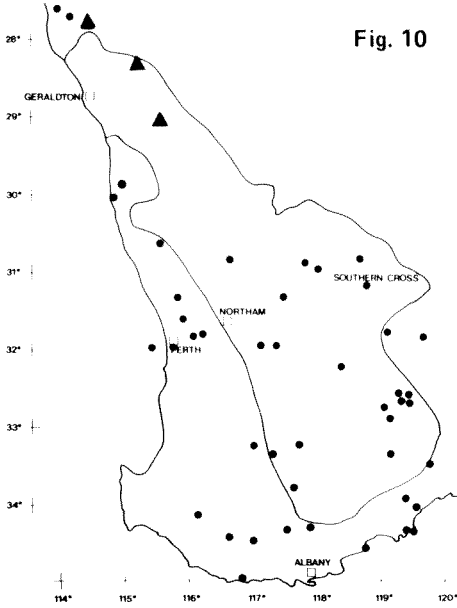


Fig. 10

*Ranidella pseudinsignifera* ●  
*Chelodina steindachneri* ▲

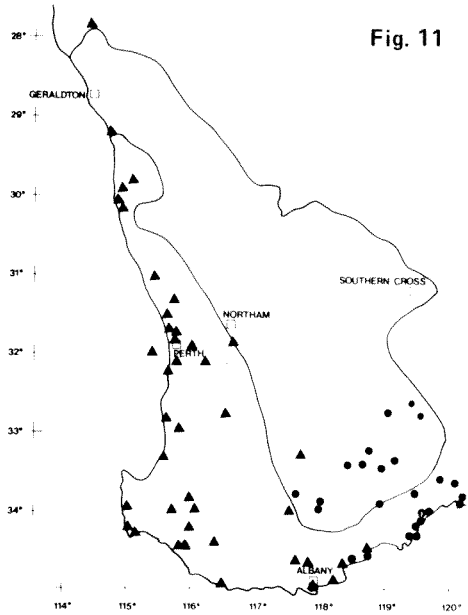


Fig. 11

*Litoria moorei* ▲  
*Litoria cyclorhynchus* ●

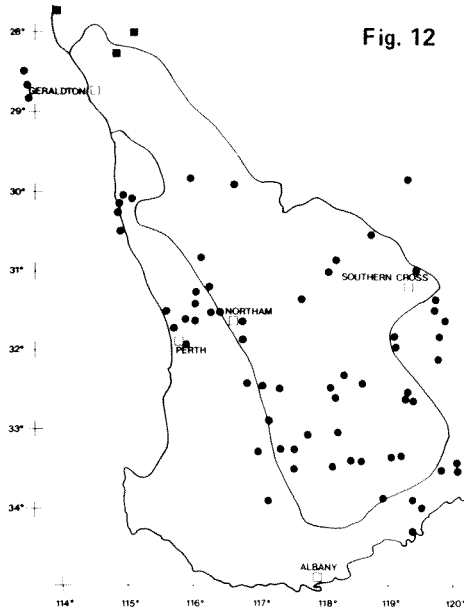


Fig. 12

*Crenadactylus o. ocellatus* ●  
*Crenadactylus o. horni* ■

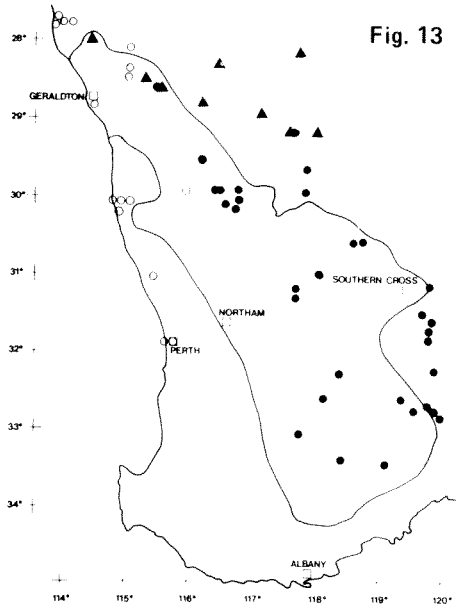


Fig. 13

*Diplodactylus albuguttatus* ○  
*Diplodactylus squarrosus* ▲ *D. maini* ●

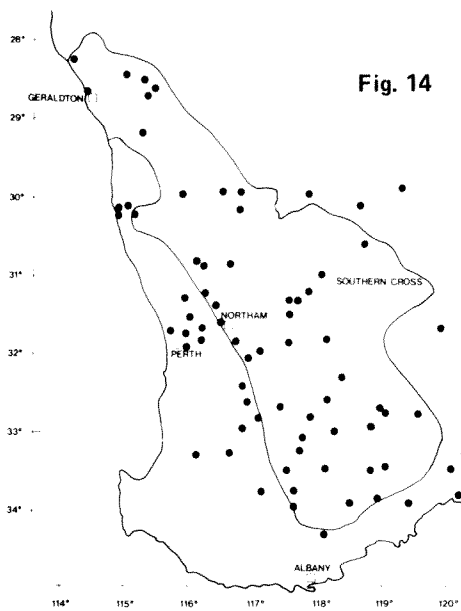


Fig. 14

*Diplodactylus granariensis* ●

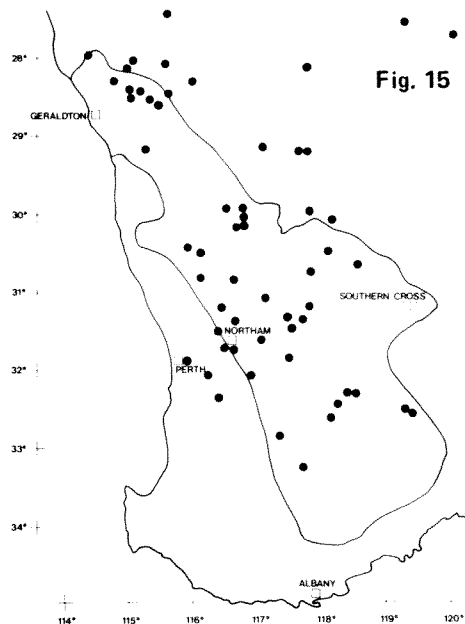


Fig. 15

*Diplodactylus pulcher* ●

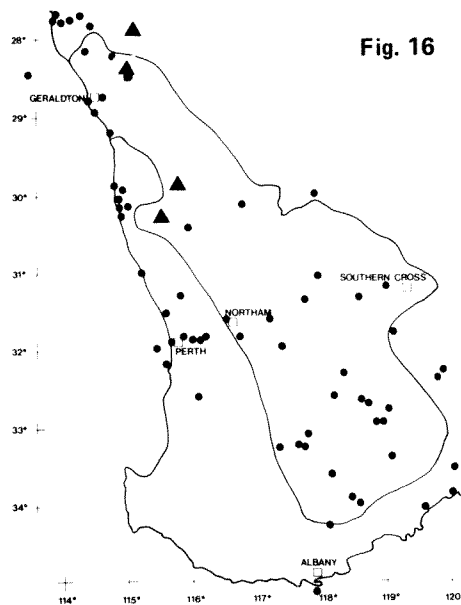


Fig. 16

*Diplodactylus michaelsoni* ▲  
*Diplodactylus spinigerus* ●

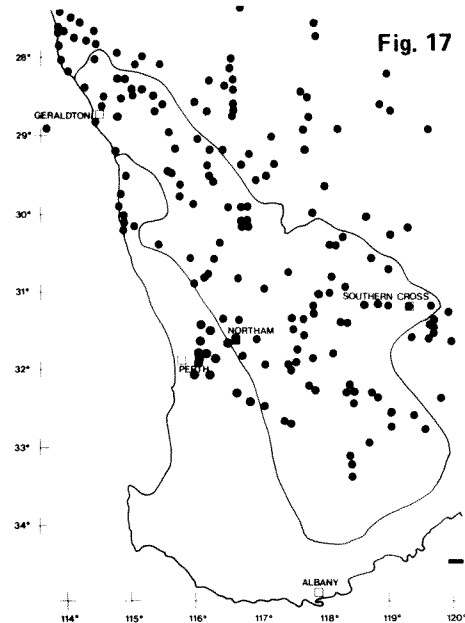
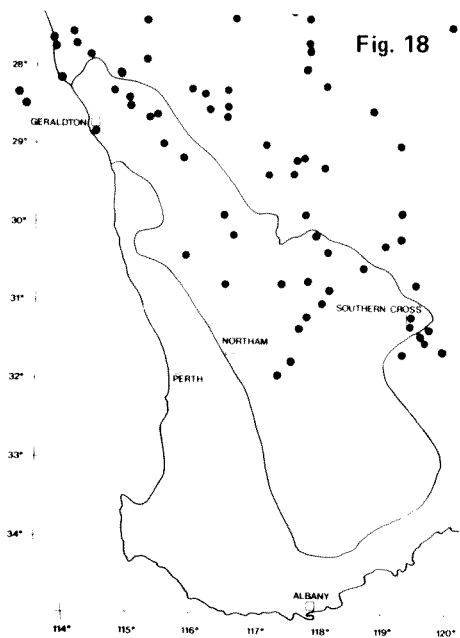


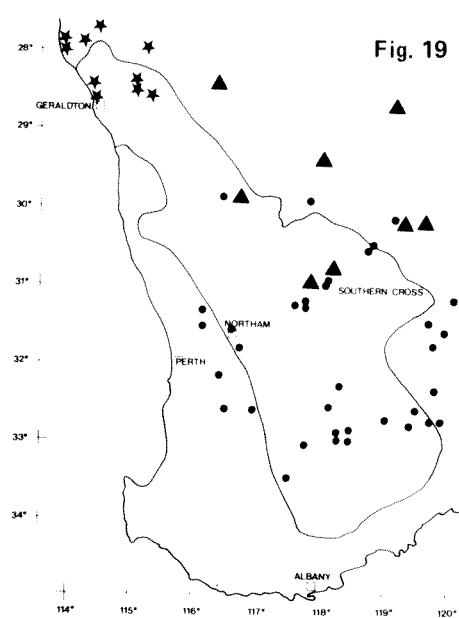
Fig. 17

*Gehyra variegata* ●

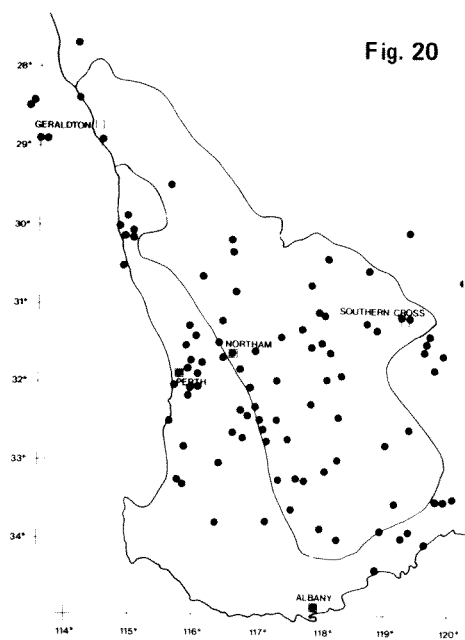
Wheatbelt Amphibians and Reptiles



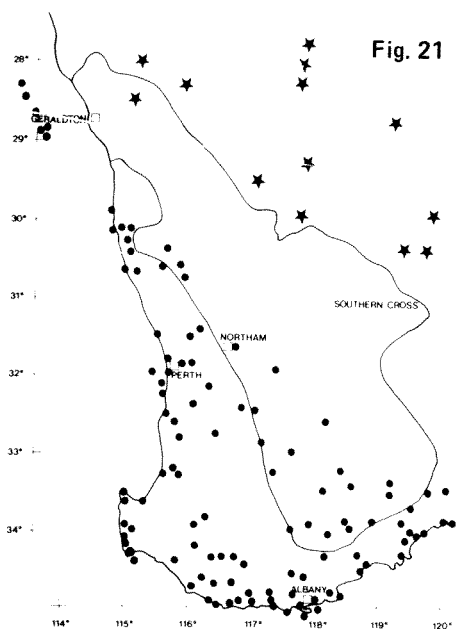
*Heteronotia binoei* ●



*Oedura reticulata* ● *Nephurus vertebralis* ▲  
*Nephurus levis occidentalis* ★



*Phyllurus milii* ●



*Rhynchoedura ornata* ★  
*Phyllodactylus marmoratus* ●

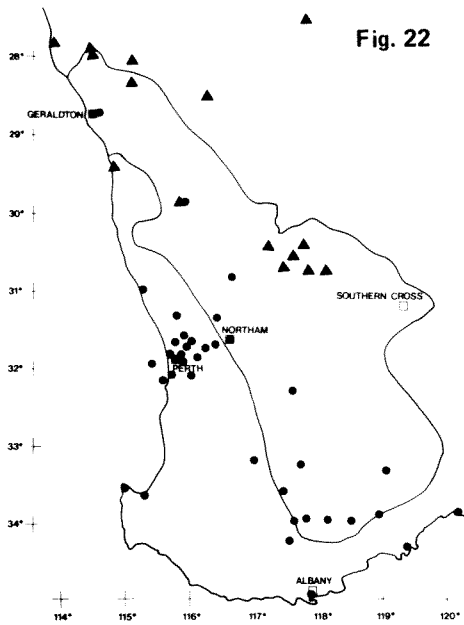


Fig. 22

*Aprasia repens* ●  
*Pygopus nigriceps* ▲

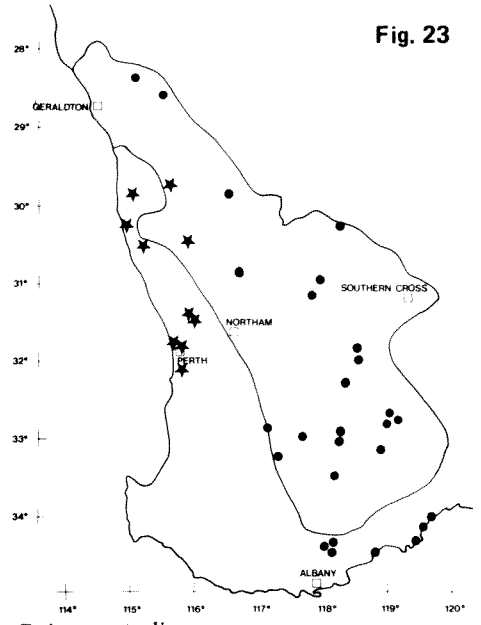


Fig. 23

*Delma australis* ●  
*Pletholax gracilis* ★

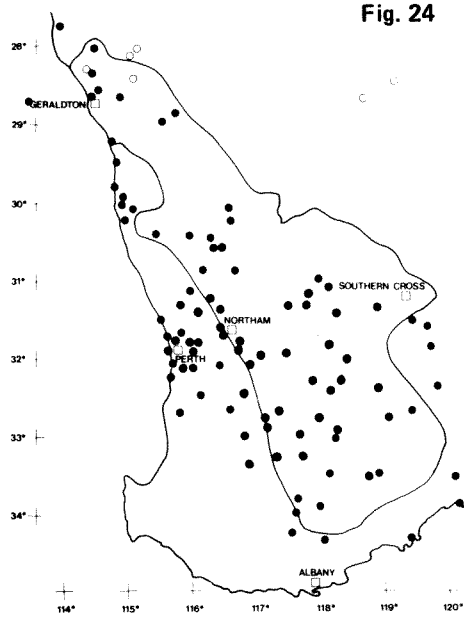


Fig. 24

*Delma nasuta* ○  
*Delma fraseri* ●

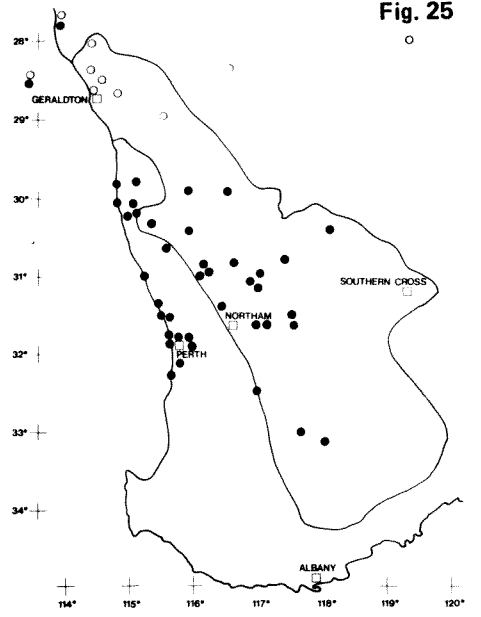


Fig. 25

*Delma grayii* ●  
*Delma tincta* ○

Wheatbelt Amphibians and Reptiles

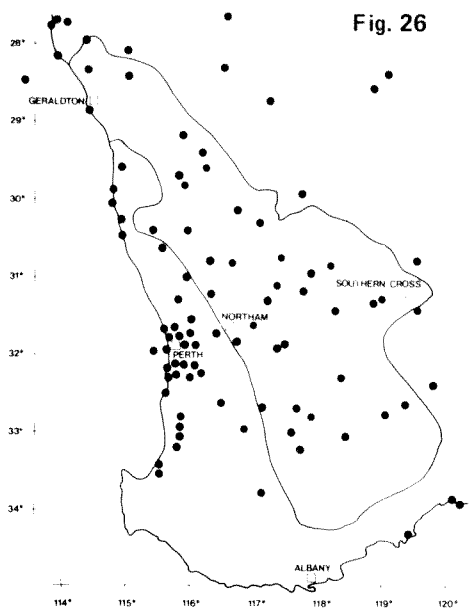


Fig. 26

*Lialis burtonis* ●

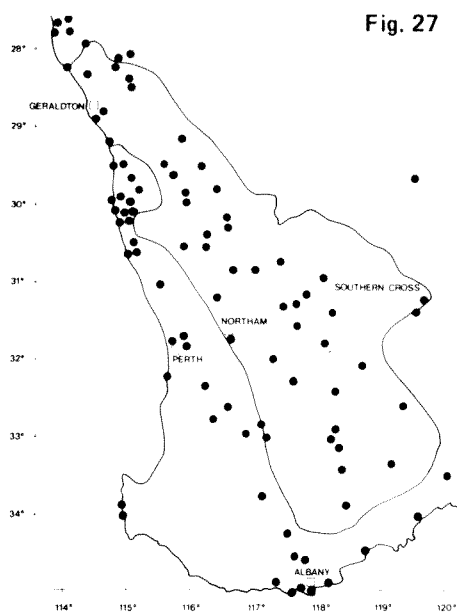


Fig. 27

*Pygopus lepidopus* ●

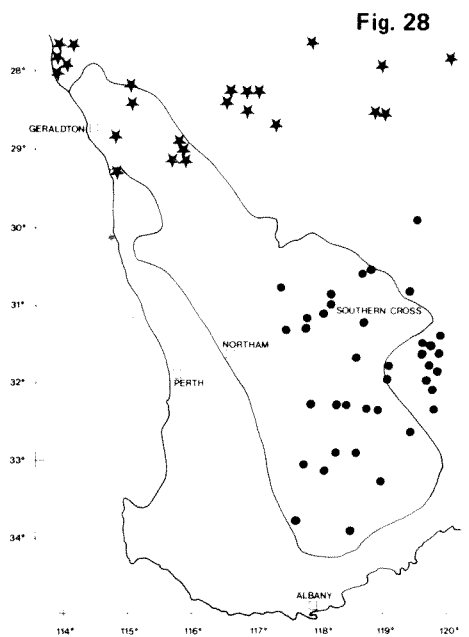


Fig. 28

*Ctenophorus inermis* ★  
*Ctenophorus cristatus* ●

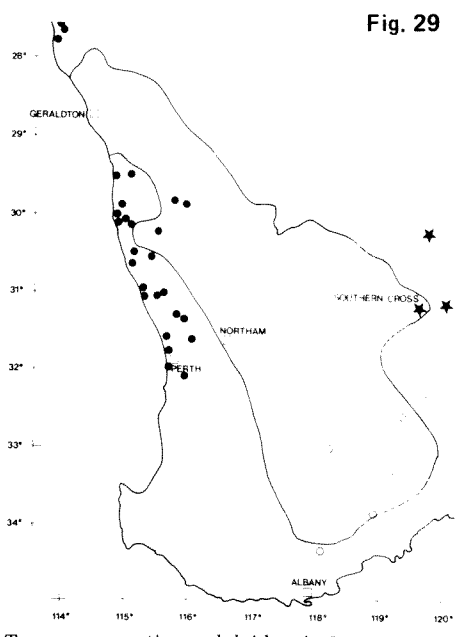


Fig. 29

*Tympanocryptis a. adelaidensis* ●  
*Tympanocryptis a. chapmani* ○  
*Ctenophorus isolepis citrinus* ★

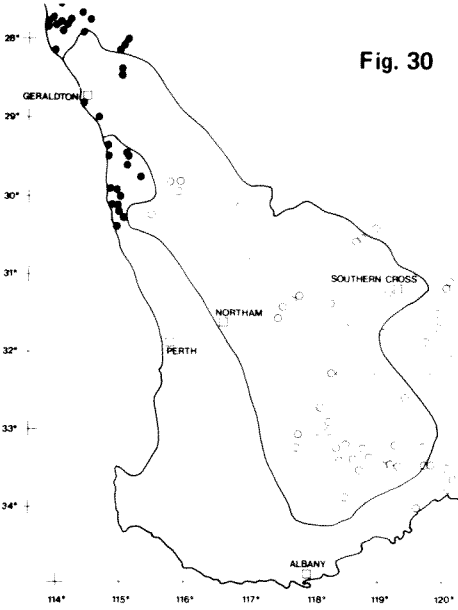


Fig. 30

*Ctenophorus m. griseus* ○  
*Ctenophorus m. maculatus* ●

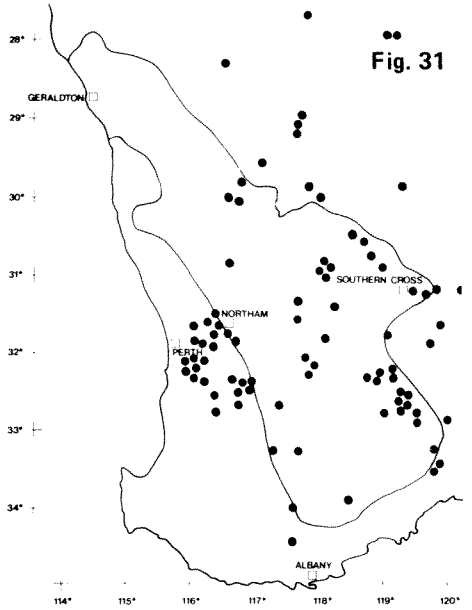


Fig. 31

*Ctenophorus ornatus* ●

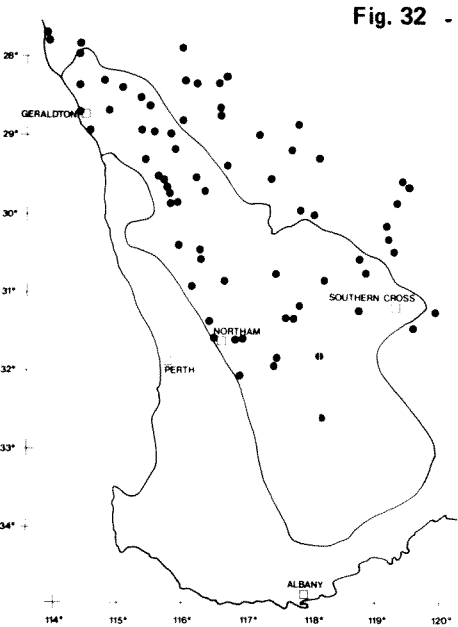


Fig. 32

*Ctenophorus reticulatus* ●

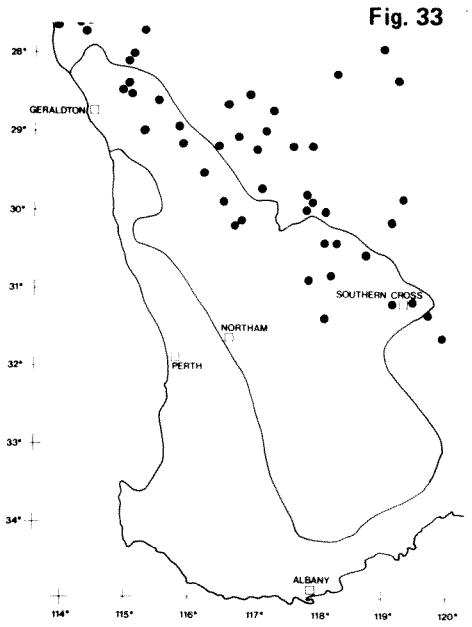


Fig. 33

*Ctenophorus scutulatus* ●



Wheatbelt Amphibians and Reptiles

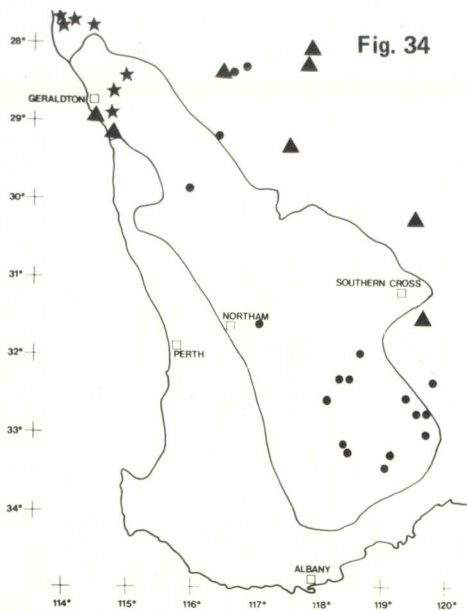


Fig. 34

*Ctenophorus salinarum* ○  
*Tymanocryptis cephalo* ▲  
*Gemmatophora longirostris* ★

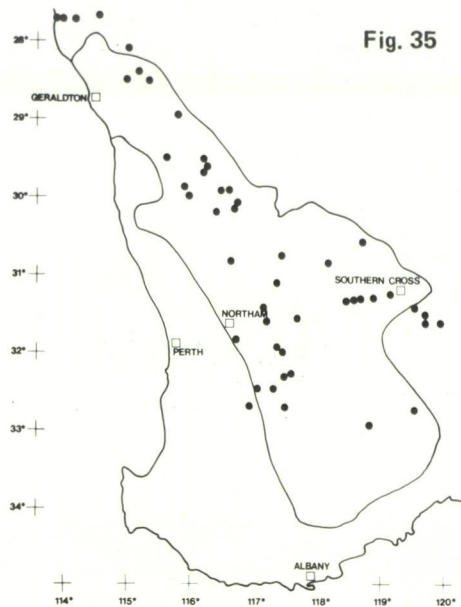


Fig. 35

*Moloch horridus* ●

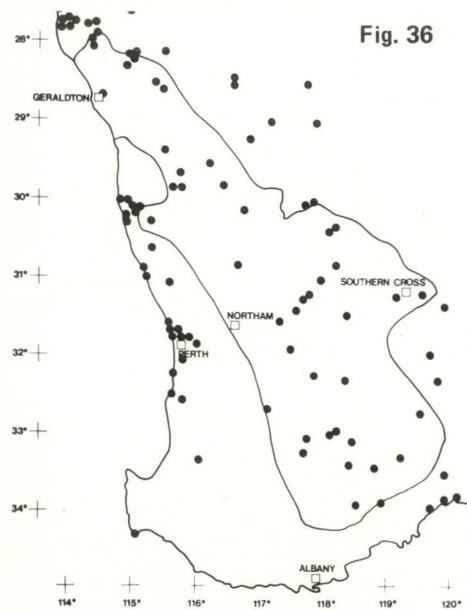


Fig. 36

*Pogona m. minor* ●

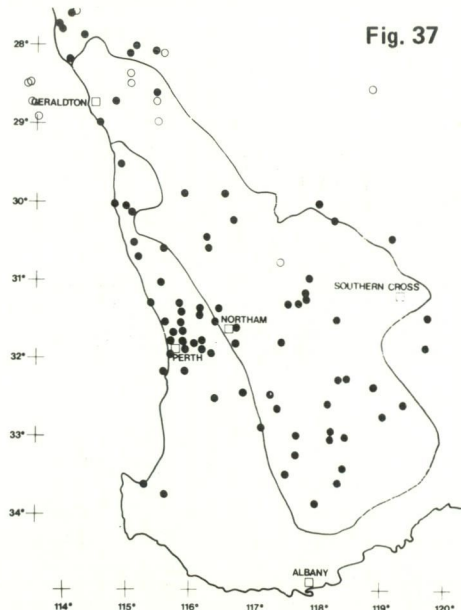


Fig. 37

*Cryptoblepharus carnabyi* ○  
*Cryptoblepharus plagioccephalus* ●

Wheatbelt Amphibians and Reptiles

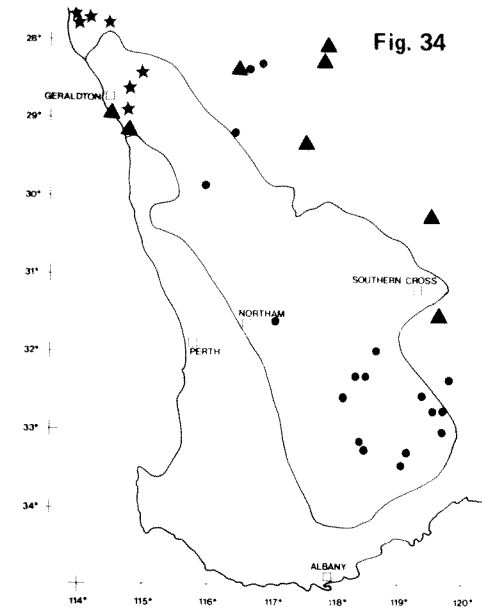


Fig. 34

*Ctenophorus salinarum* ○  
*Tymanocryptis cephalo* ▲  
*Gemmatophora longirostris* ★

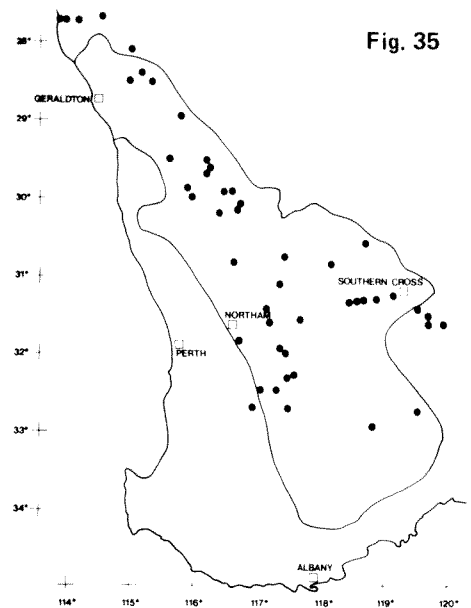


Fig. 35

*Moloch horridus* ●

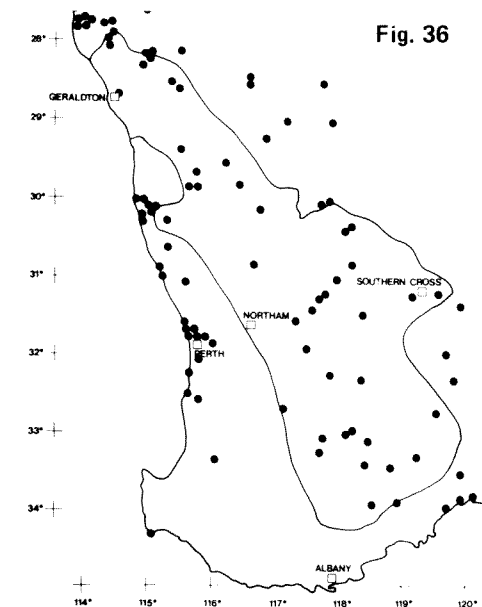


Fig. 36

*Pogona m. minor* ●

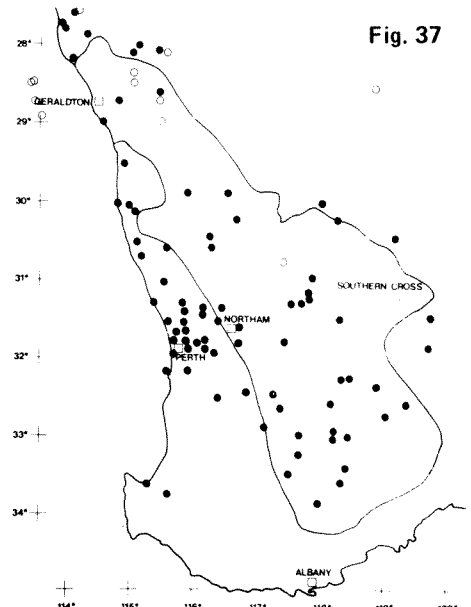


Fig. 37

*Cryptoblepharus carnabyi* ○  
*Cryptoblepharus plagiocephalus* ●

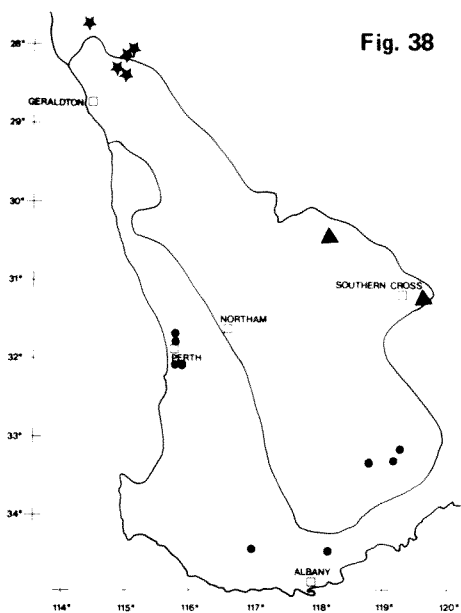


Fig. 38

*Ctenotus alleni* ★ *Ctenotus atlas* ▲  
*Ctenotus gemmula* ●

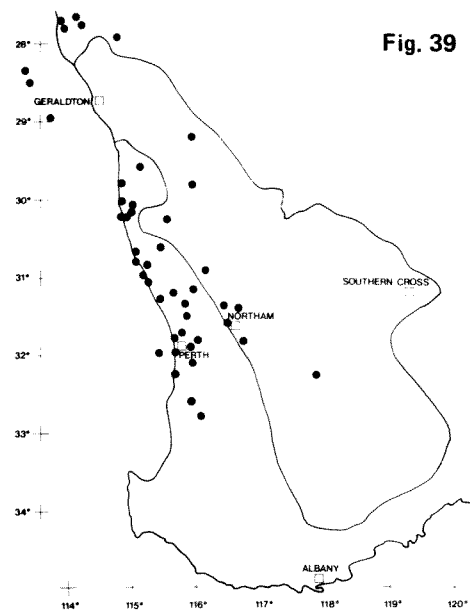


Fig. 39

*Ctenotus fallens* ●

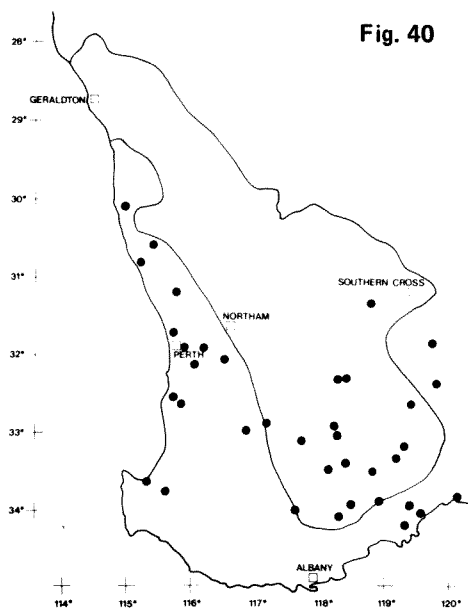


Fig. 40

*Ctenotus impar* ●

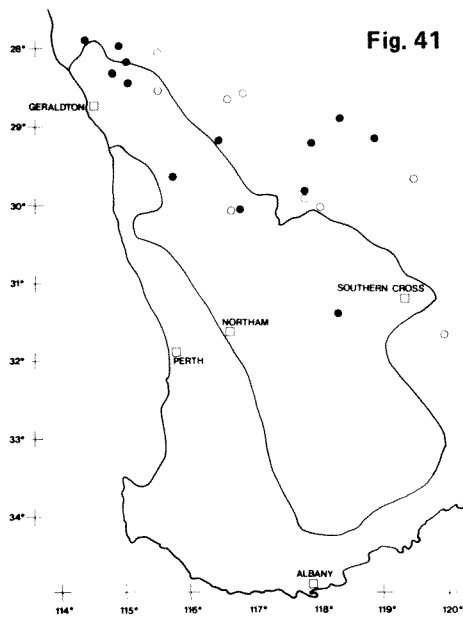
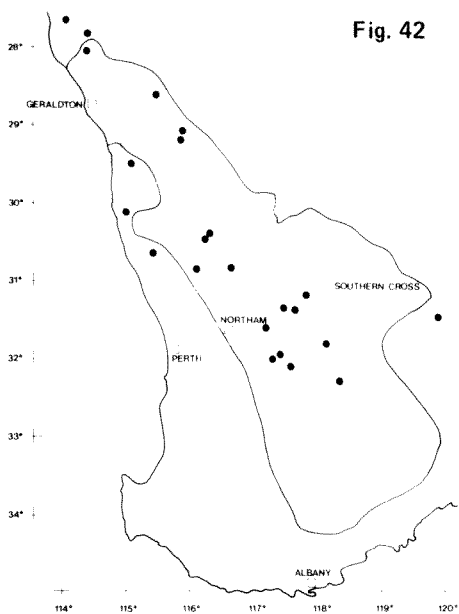
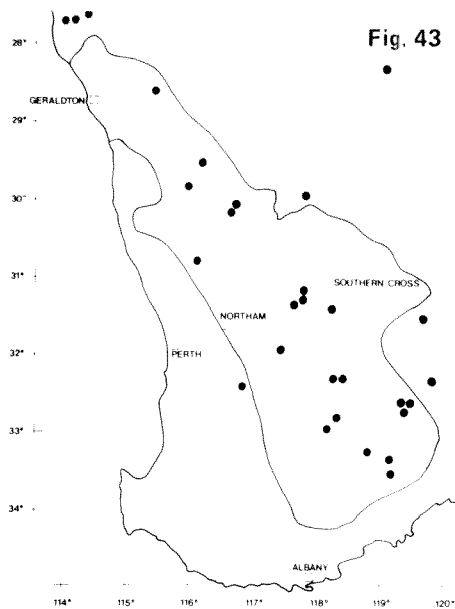


Fig. 41

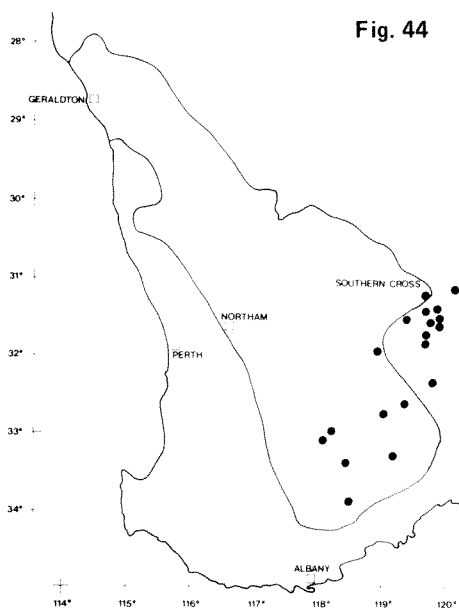
*Ctenotus mimetes* ●  
*Ctenotus uber* ○



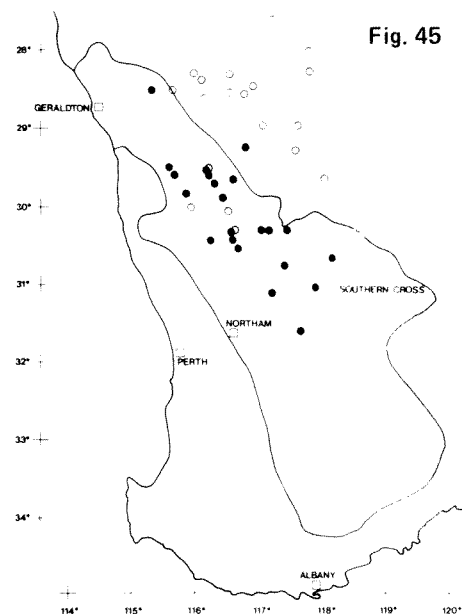
*Ctenotus p. pantherinus* ●



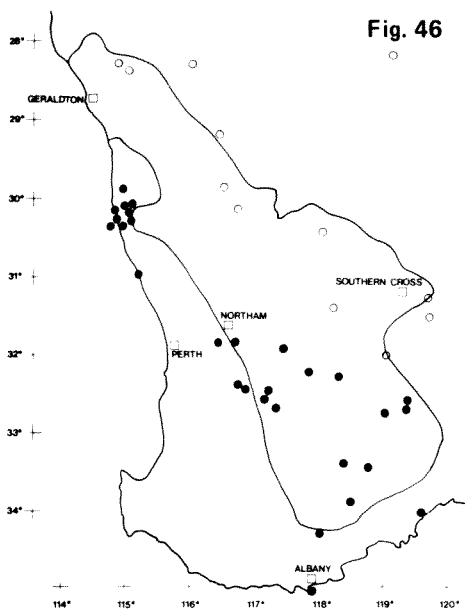
*Ctenotus schomburgkii* ●



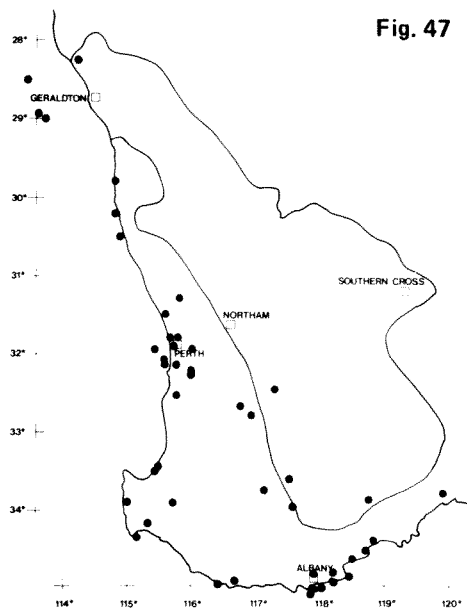
*Egernia carinata* ●



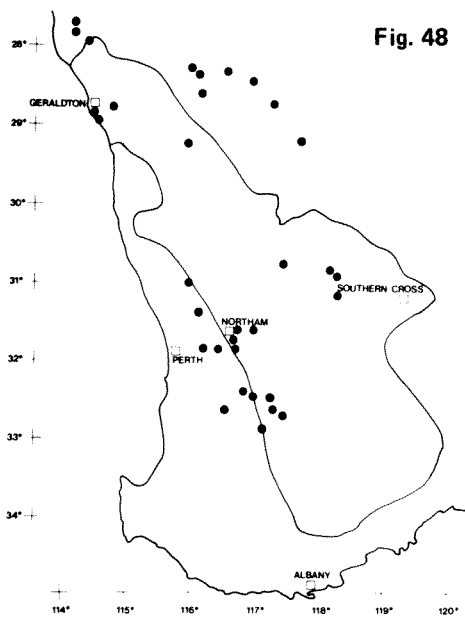
*Egernia depressa* ○  
*Egernia stokesii badia* ●



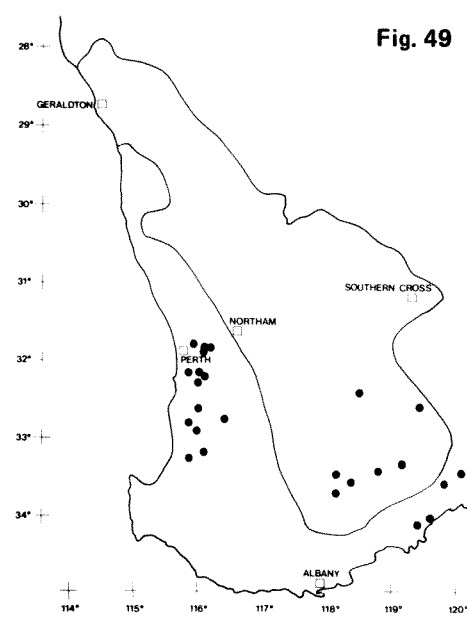
*Egernia inornata* ○  
*Egernia multiscutata bos* ●



*Egernia kingii* ●



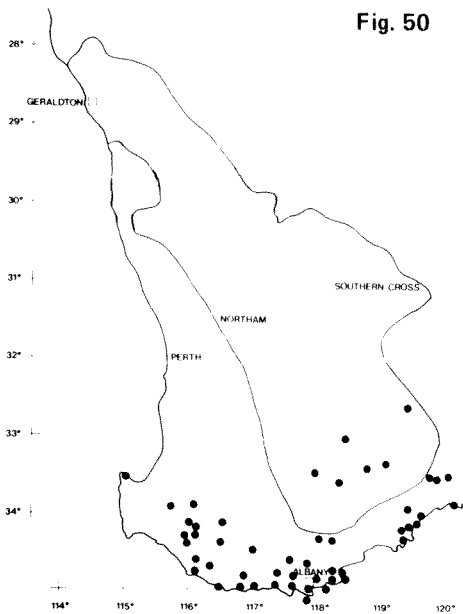
*Eremiascincus richardsonii* ●



*Hemiergis i. initialis* ●

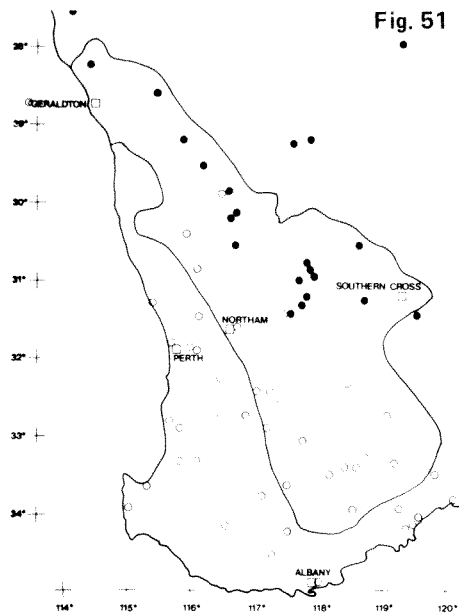
Wheatbelt Amphibians and Reptiles

Fig. 50



*Hemiergis peronii* ●

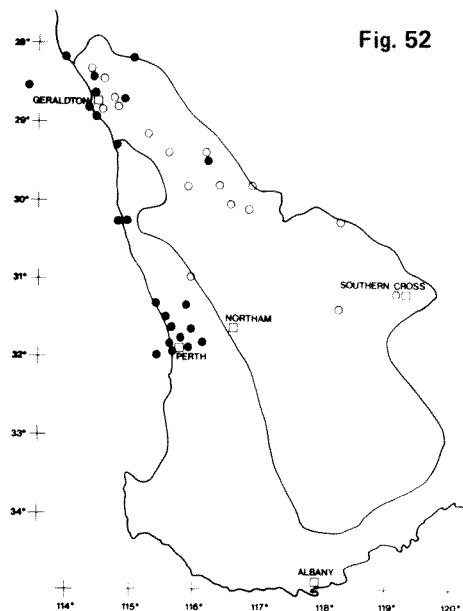
Fig. 51



*Lerista muelleri* ●

*Lerista distinguenda* ○

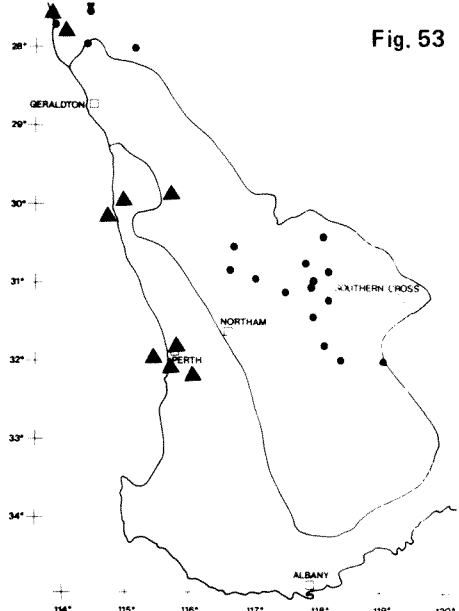
Fig. 52



*Lerista lineopunctulata* ●

*Lerista gerrardii* ○

Fig. 53



*Lerista macropisthopus* ●

*Lerista elegans* ▲

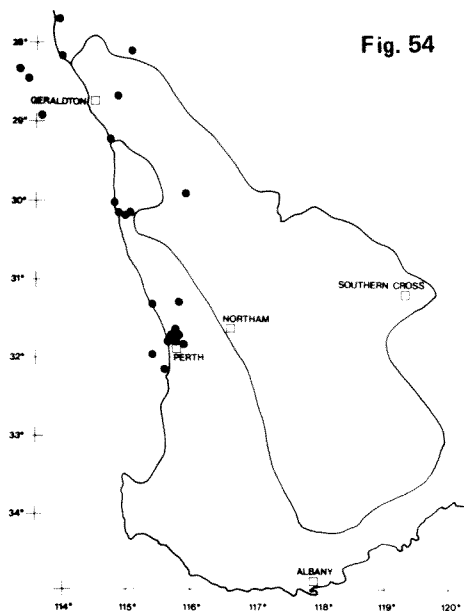


Fig. 54

*Lerista praepedita* ●

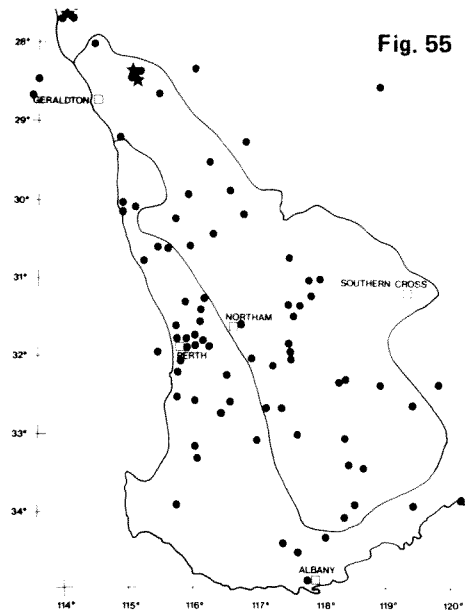


Fig. 55

*Menetia greyii* ●  
*Menetia surda* ★

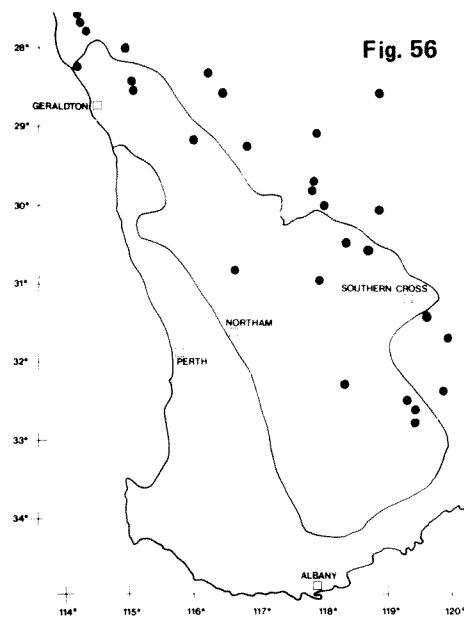


Fig. 56

*Morethia butleri* ●

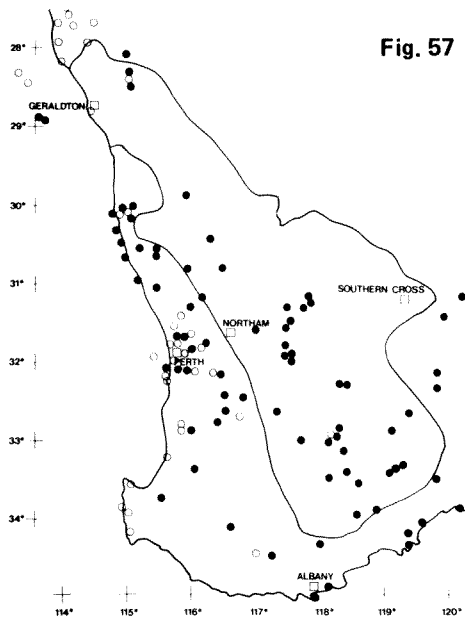


Fig. 57

*Morethia lineoocellata* ○  
*Morethia obscura* ●

Wheatbelt Amphibians and Reptiles

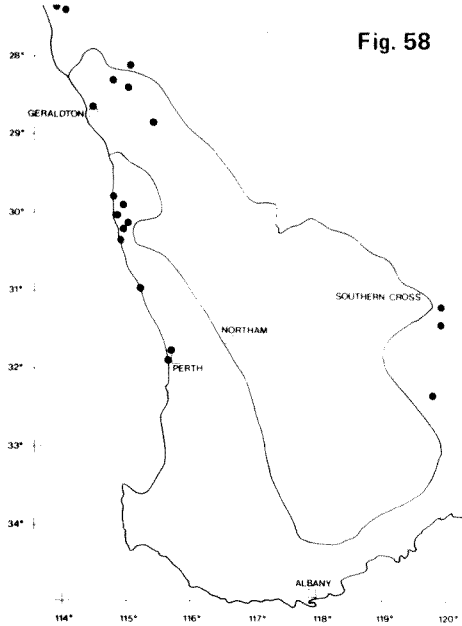


Fig. 58

*Omolepida branchialis* ●

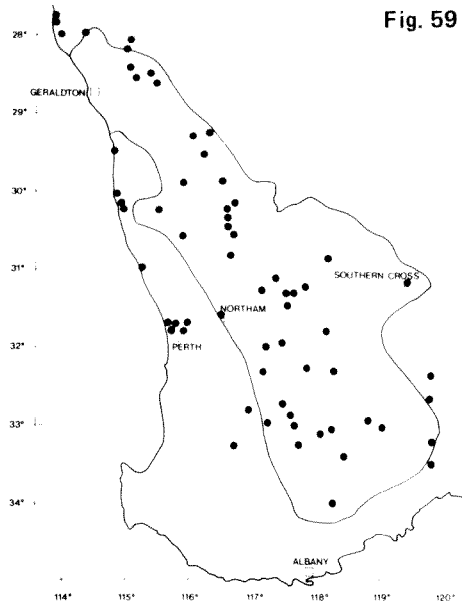


Fig. 59

*Tiliqua occipitalis* ●

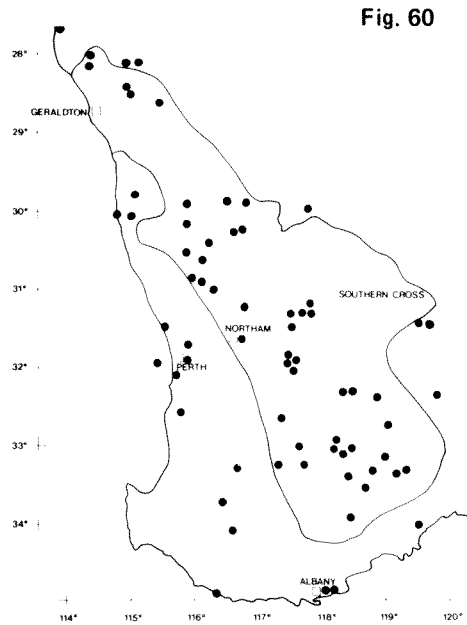


Fig. 60

*Tiliqua rugosa* ●

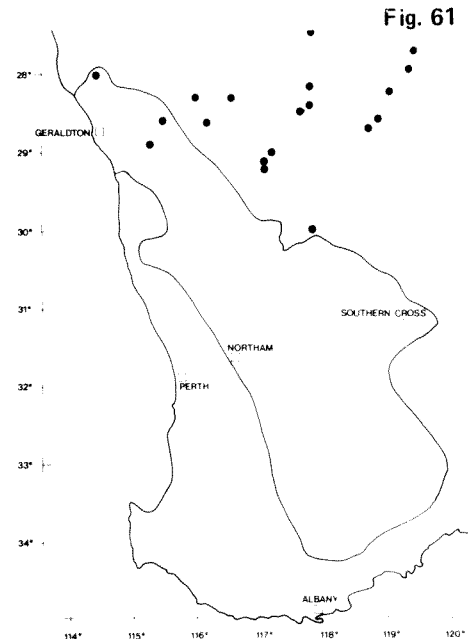
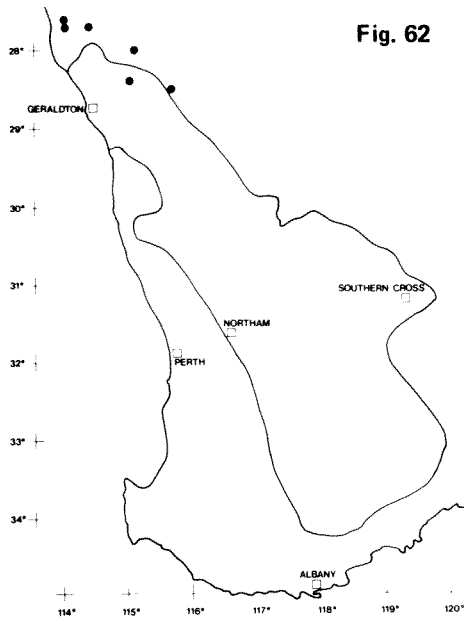


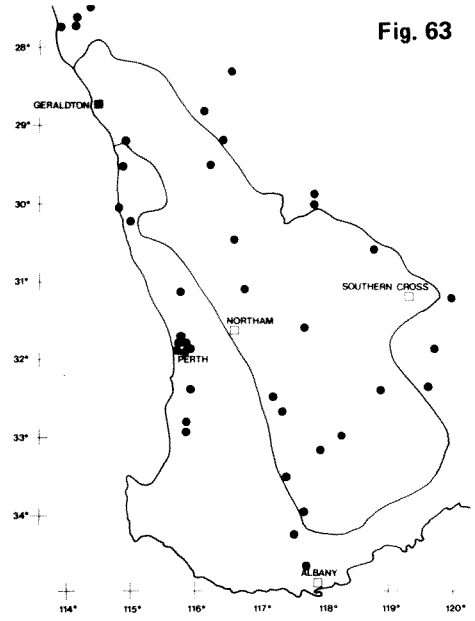
Fig. 61

*Varanus caudolineatus* ●

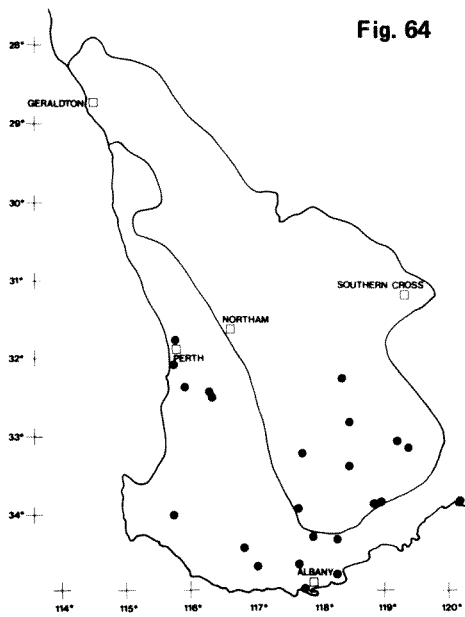




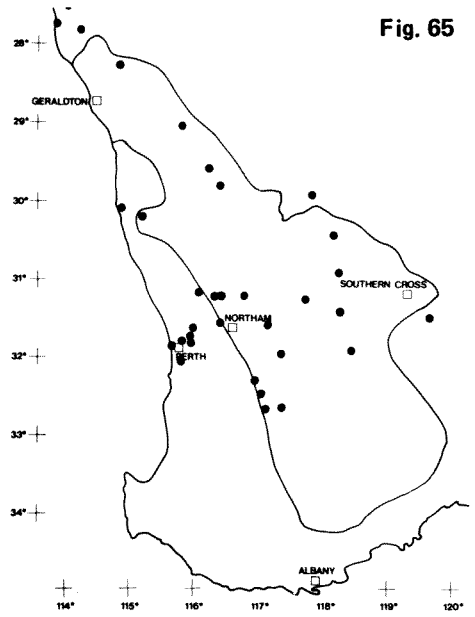
*Varanus eremius* ●



*Varanus gouldii* ●

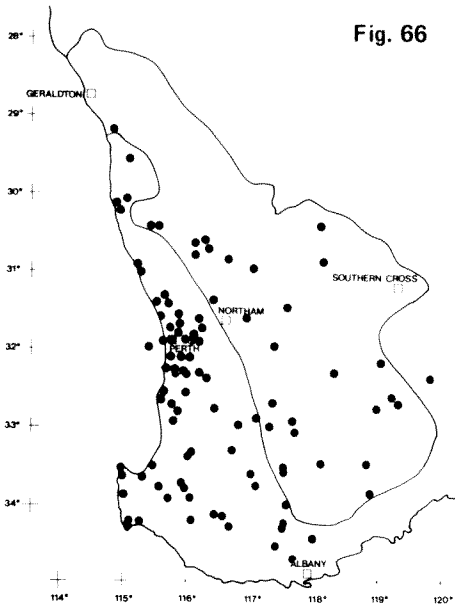


*Varanus rosenbergi* ●

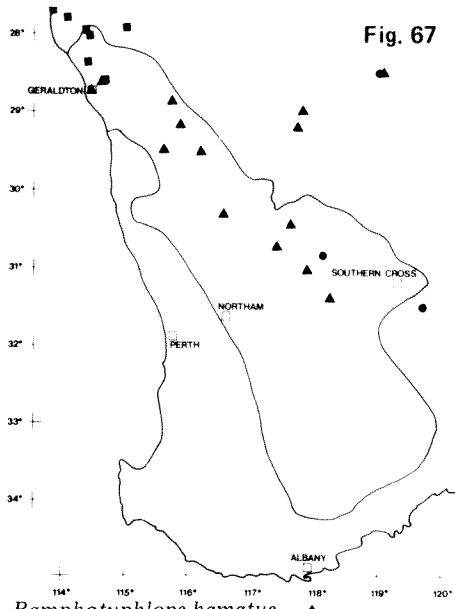


*Varanus tristis* ●

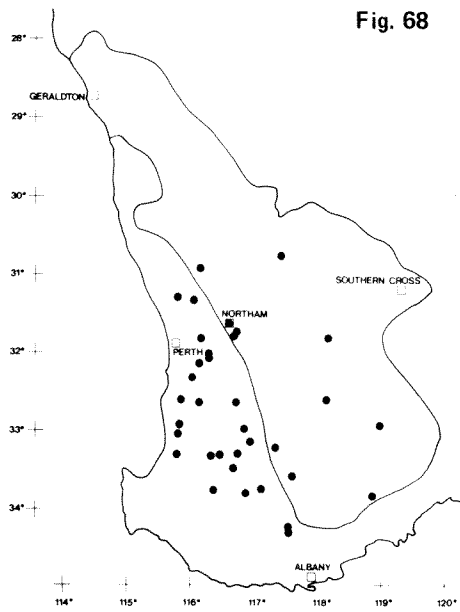
Wheatbelt Amphibians and Reptiles



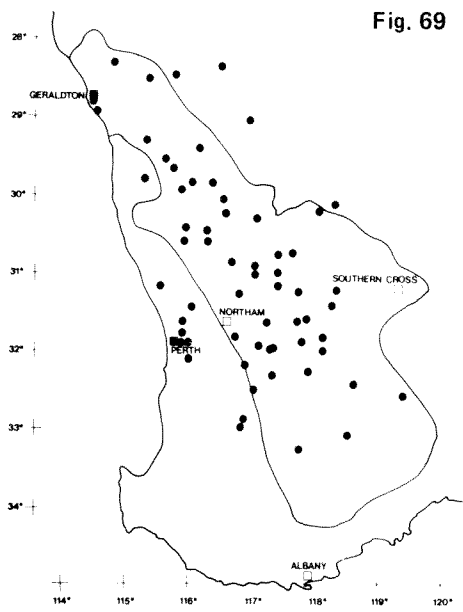
*Ramphotyphlops australis* ●



*Ramphotyphlops hamatus* ▲  
*Ramphotyphlops leptosoma* ■  
*Ramphotyphlops bituberculatus* ●



*Ramphotyphlops pinguis* ●



*Ramphotyphlops waitii* ●

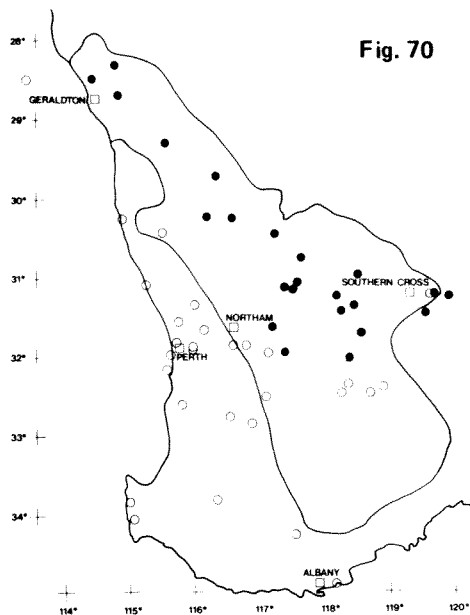


Fig. 70

*Python spilotes* ○  
*Aspidites ramsayi* ●

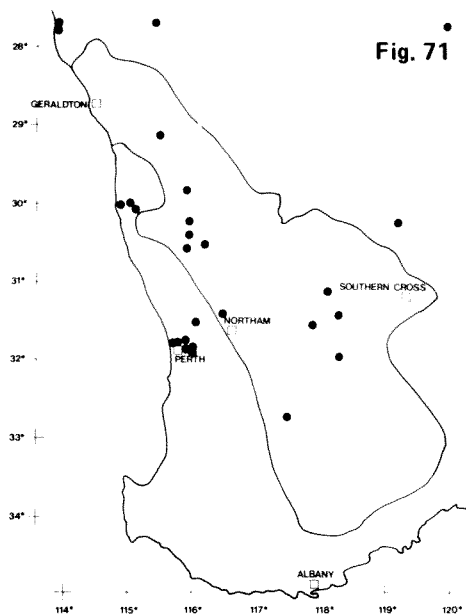


Fig. 71

*Liasis childreni* ●

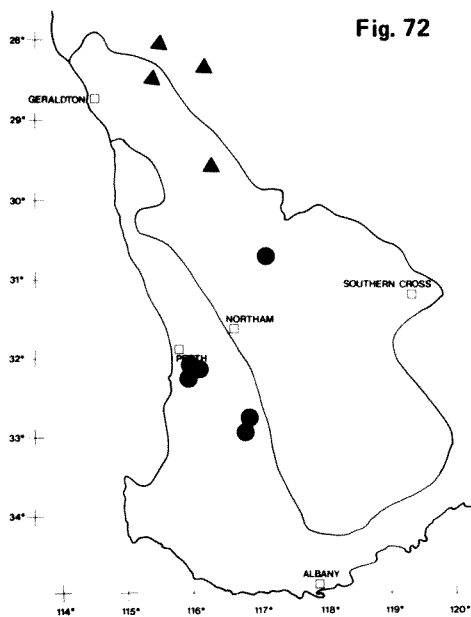


Fig. 72

*Acanthophis antarcticus* ●  
*Acanthophis pyrrhus* ▲

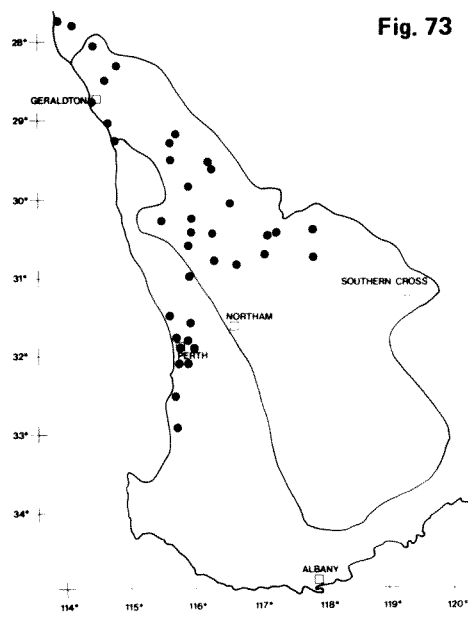
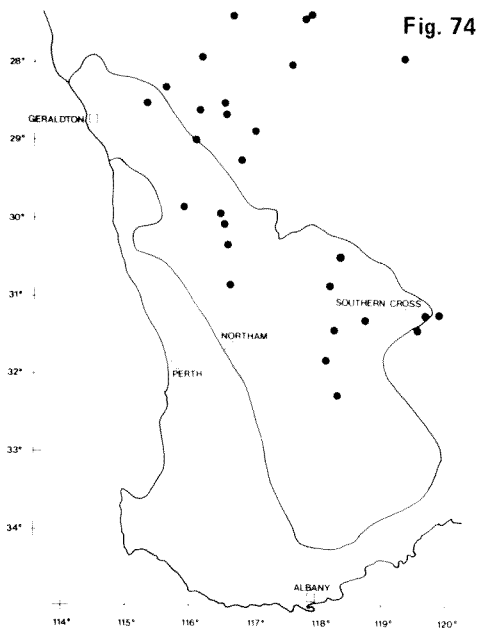


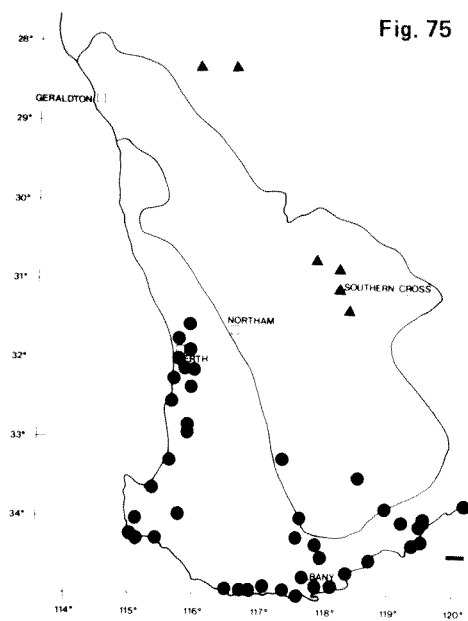
Fig. 73

*Demansia reticulata* ●

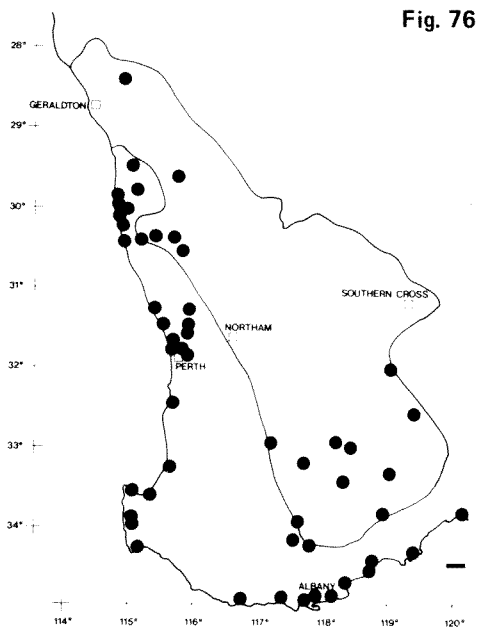
Wheatbelt Amphibians and Reptiles



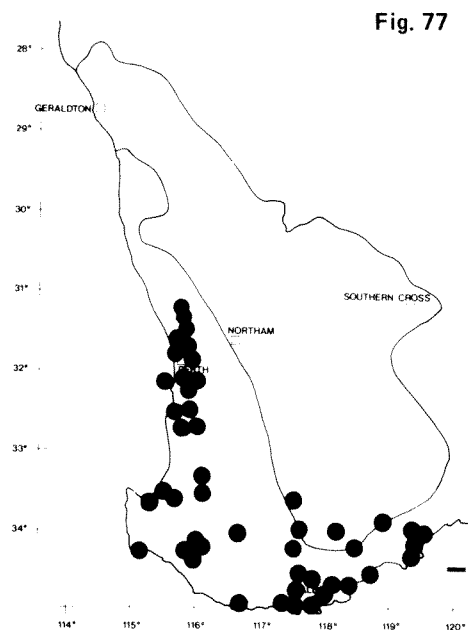
*Denisonia fasciata* ●



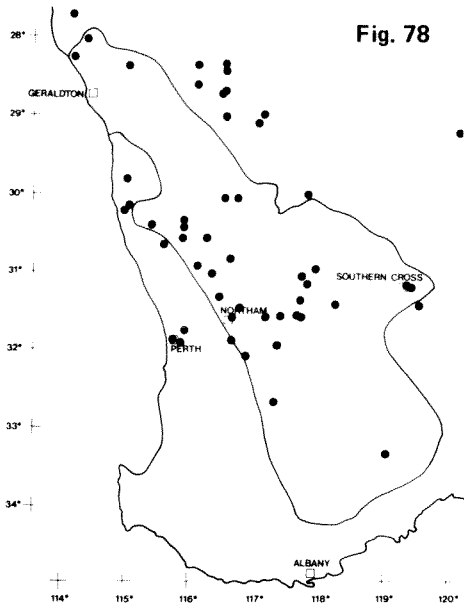
*Furina ornata* ▲  
*Notechis coronatus* ●



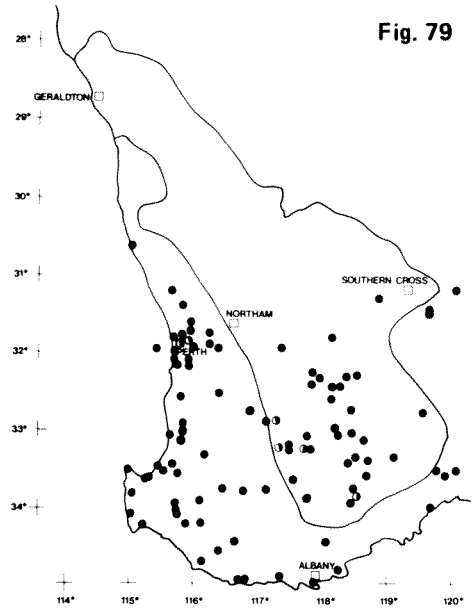
*Notechis curtus* ●



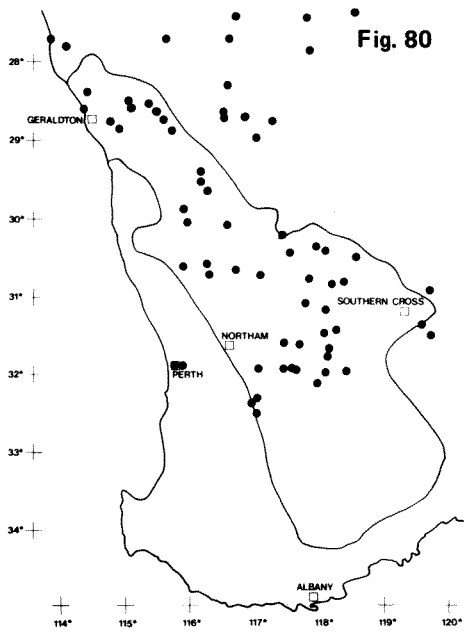
*Notechis scutatus* ●



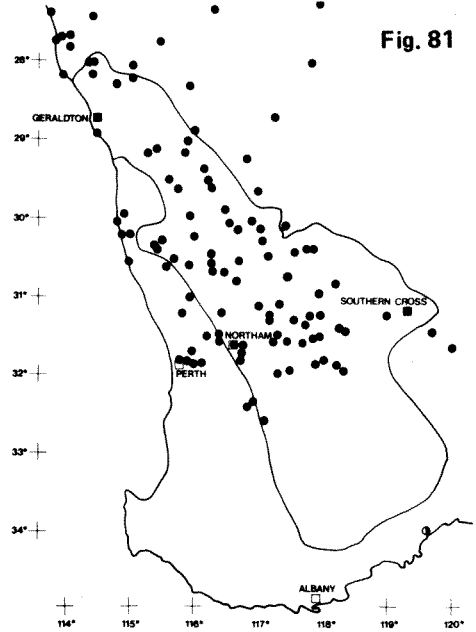
*Pseudechis australis* ●



*Pseudonaja affinis* ●

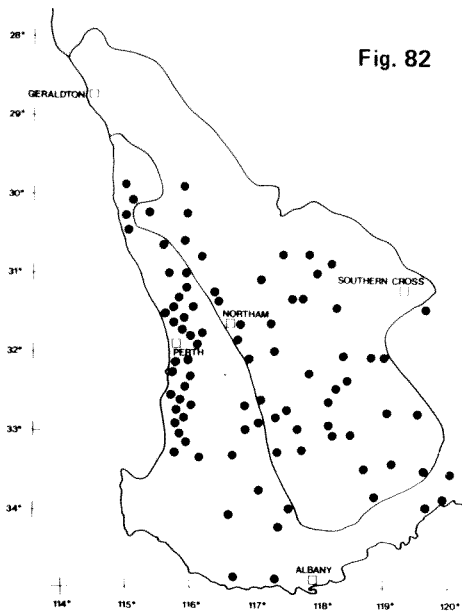


*Pseudonaja modesta* ●

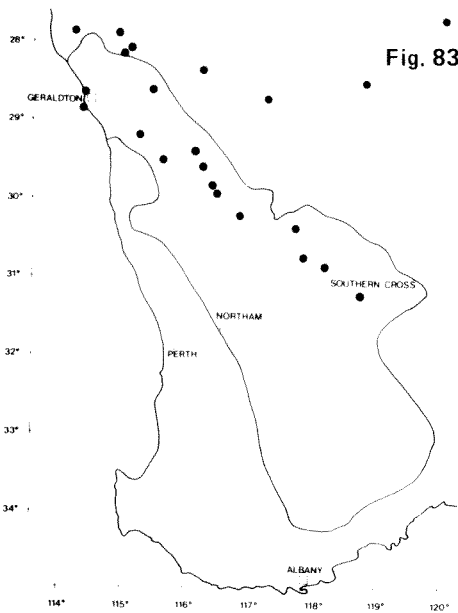


*Pseudonaja nuchalis* ●

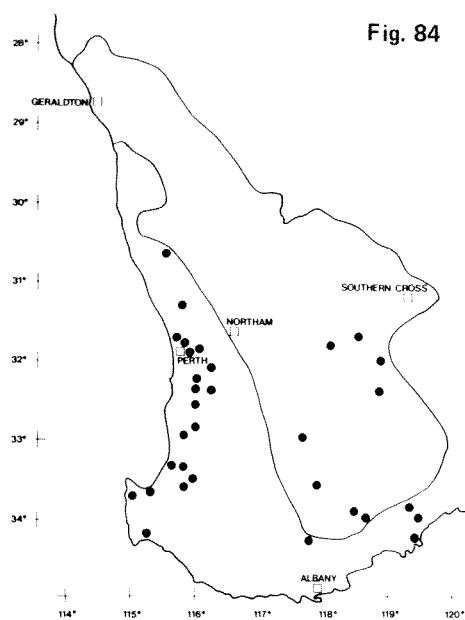
Wheatbelt Amphibians and Reptiles



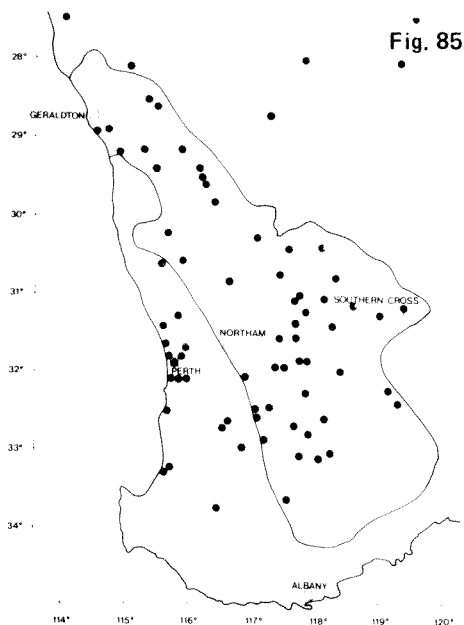
*Rhinoplocephalus gouldii* ●



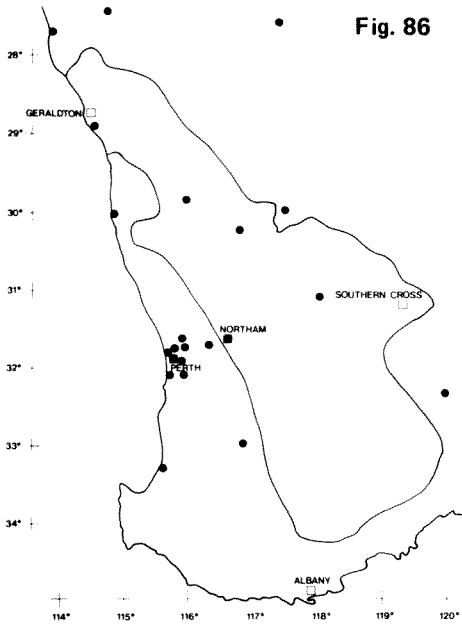
*Rhinoplocephalus monachus* ●



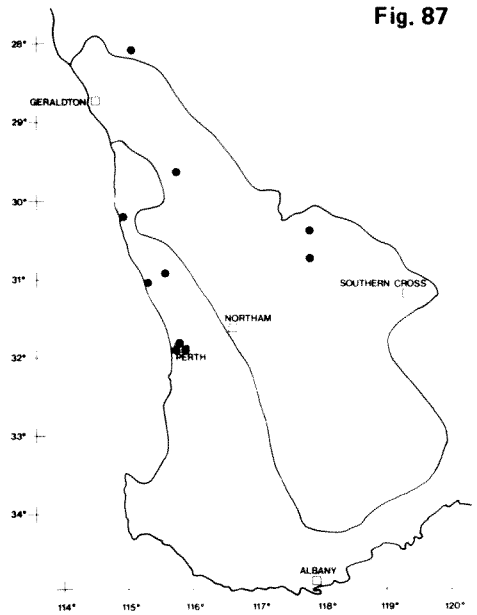
*Rhinoplocephalus nigriceps* ●



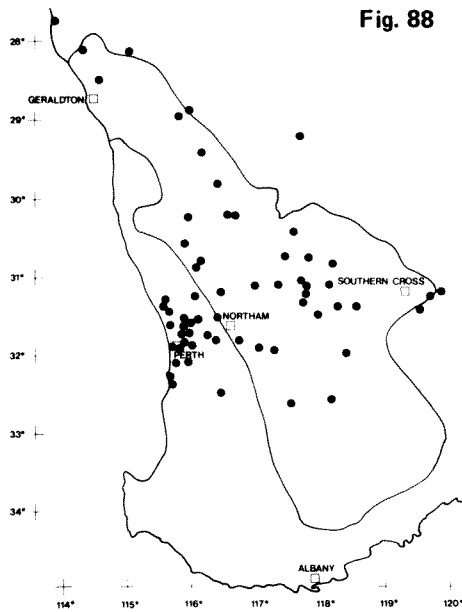
*Vermicella bertholdi* ●



*Vermicella bimaculata* ●



*Vermicella f. fasciolata* ●



*Vermicella semifasciata* ●