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A NEW SPECIES OF *MORETHIA* (LACERTILIA: SCINCIDAE) FROM NORTHERN AUSTRALIA, WITH COMMENTS ON THE BIOLOGY AND RELATIONSHIPS OF THE GENUS

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ABSTRACT

Morethia is a genus of lygosomine skinks endemic to Australia. This paper provides a description of a new species of *Morethia* from northern Australia, a diagnosis of the genus, and a discussion of its intra and intergeneric relationships. It also includes a key to the eight currently recognized species of *Morethia* and notes on their colour pattern, reproduction, behaviour, habitat and distribution.

A NEW SPECIES OF *MORETHIA*

In his revision of the Western Australian species of the endemic Australian genus *Morethia*, Storr (1972) noted that the form *ruficauda* was "replaced by an undescribed race" in the far north of the Northern Territory. A few years later while reviewing the genus, I "rediscovered" this undescribed form and interpreted it as a distinct species. Dr Storr has graciously allowed me to describe this species, and in appreciation of his original contribution to the taxonomy of the genus (Storr 1972), I take pleasure in naming it

Morethia storri New Species

Figs 1, 2 (top), and 9

HOLOTYPE: Northern Territory Museum R 1815 — 4.5 km. S. of Noonamah, Northern Territory (12°40' S., 131°04' E.). Collected by Messrs G. F. Gow and R. W. Wells on 10 November 1975.

PARATYPES: Unless specifically mentioned otherwise, all localities are in the extreme northern part of the Northern Territory.

Australian Museum: R 12384 — Yirrkala; R 17411 — Port Keats Mission; R 37225 — Koongarra, Mt. Brockman Range; R 41960 — Maningrida Settlement; R 71991 — Yirrkala; R 72862 — approx. 16 km. S.E. of Daly River Police Station (by road); R 88631, 88791, 88850 and 88988 — Jabiluka Project Area (12°33' — 12°35'S., 132°55' — 132°57'E.).

Australian National Wildlife Collection: R 695 — Leanyer Swamp, RAAF Bombing Range, Darwin; R 1826 — Berrimah, Darwin.

South Australian Museum: R 1117 — Groote Eylandt; R 1130 A-B — Roper River (it is uncertain whether the township or the river is meant, *vide* Dr T. Houston in letter of 29 March 1977); R 13535 — Bing Bong Station near Boorroloola.

Northern Territory Museum: R 2715 — Berry Springs Reserve; R 2731-2732 — 32.5 km. S.E. of Noonamah; R 2864 — Millner, Darwin.

United States National Museum: 128635 — Yirrkala.

Western Australian Museum: R 23481 — Nightcliff, Darwin; R 23517 — Rapid Creek, Darwin; R 58498 — Lombadina Creek, Western Australia (16°34'S., 122°48'E.).

DIAGNOSIS: *Morethia storri* differs from all other *Morethia* in the following combination of characters: supranasal scale fused to nasal without trace of suture; lower Records of The Australian Museum, 1980, Vol. 33 No. 2 89-122 Figures 1-12

eyelid completely fused to underside of supraocular shelf (i.e., no palpebral slit); supraciliaries five (first four large and last small) and projecting behind first, second, and third supraoculars, and colour pattern consisting of a more or less uniform plain or faintly longitudinally striped dorsum and a distinct dark lateral stripe bordered above by a thin light dorsolateral stripe.

DESCRIPTION: In general aspect *storri* is a small (maximum snout-vent length = 38 mm), pentadactyl, spectacle-eyed skink with either a uniformly brown or faintly longitudinally striped dorsum and a distinct dark lateral stripe bordered above and below by more or less distinct, narrow white stripes.

Rostral prominent in dorsal view, its posterior edge slightly convex; frontonasal slightly wider than long, usually forming a narrow suture with the rostral (frequency = .94) and a narrow suture with the frontal (.85); prefrontals large and either narrowly separated (.85) or in contact (.15); frontal longer than wide; frontoparietals and interparietal fused into a single scale which bears a parietal eye spot in its posterior lobe; parietals narrow, in medial contact behind the fused frontoparietal — interparietal; parietals bordered posterolaterally by the single upper secondary temporal and the enlarged anterior nuchal.

Supranasal fused anteriorly to nasal without trace of a suture or groove and fused posteriorly to postnasal with a horizontal groove which may indicate the position of the former suture; loreals two; anterior loreal much deeper than long, posterior loreal much lower than anterior loreal and slightly longer than deep; preoculars two, suboculars none and postoculars three; supraciliaries five, first four large, fifth very small; second supraciliary projects medially to partially separate first and second supraoculars, third supraciliary projects to partially separate second and third supraoculars and fourth supraciliary separates third and fourth supraoculars; lower eyelid with a large clear spectacle surrounded by small periocular scales; no palpebral slit; primary temporals two, subequal; secondary temporals two, upper much larger than lower; supralabials seven or, rarely, eight with fifth or, rarely, sixth below centre of eye; mental followed by postmental and two chin scales in medial contact; postmental in contact with first two infralabials on each side; external ear opening vertically suboval, approximately one-quarter to one-third size of spectacle, without projections.

A single pair of transversely enlarged nuchal scales; body scales smooth, subequal in size dorsally and in 24-28 (\bar{X} = 26.2, mode = 26) longitudinal rows at midbody; scales in paravertebral row 54-58 (\bar{X} = 56.1) counted from level of posterior edge of thigh forward to parietals; medial pair of preanals only slightly larger than most immediately adjacent preanals; limbs pentadactyl; fourth toe covered by a single row of scales above and by 17-21 (\bar{X} = 19.4) obtusely keeled lamellae below.

Snout-vent length = 17-38 mm; foreleg .25-.35 times and rear leg .36-.47 times SVL (N = 14), respectively; complete tail 1.32-1.76 times SVL (N = 3).

COLOUR IN PRESERVATIVE: Dorsum of head and body usually more or less uniform medium brown but occasionally, dorsum of body faintly light and dark striped; sides of head and body with a distinct narrow light dorsolateral stripe extending from above eye onto base of tail, a distinct dark brown lateral stripe from loreals to base of tail, and a distinct narrow light lower lateral stripe from labials to rear leg; venter immaculate; lower labials with a few scattered brown spots; a small white post-femoral spot at junction of rear leg and base of tail.

COLOUR IN LIFE: Details on the colour of *storri* in life come from three sources: a transparency taken by Dr H. G. Cogger of a female from Koongarra (A.M. R 37225); the

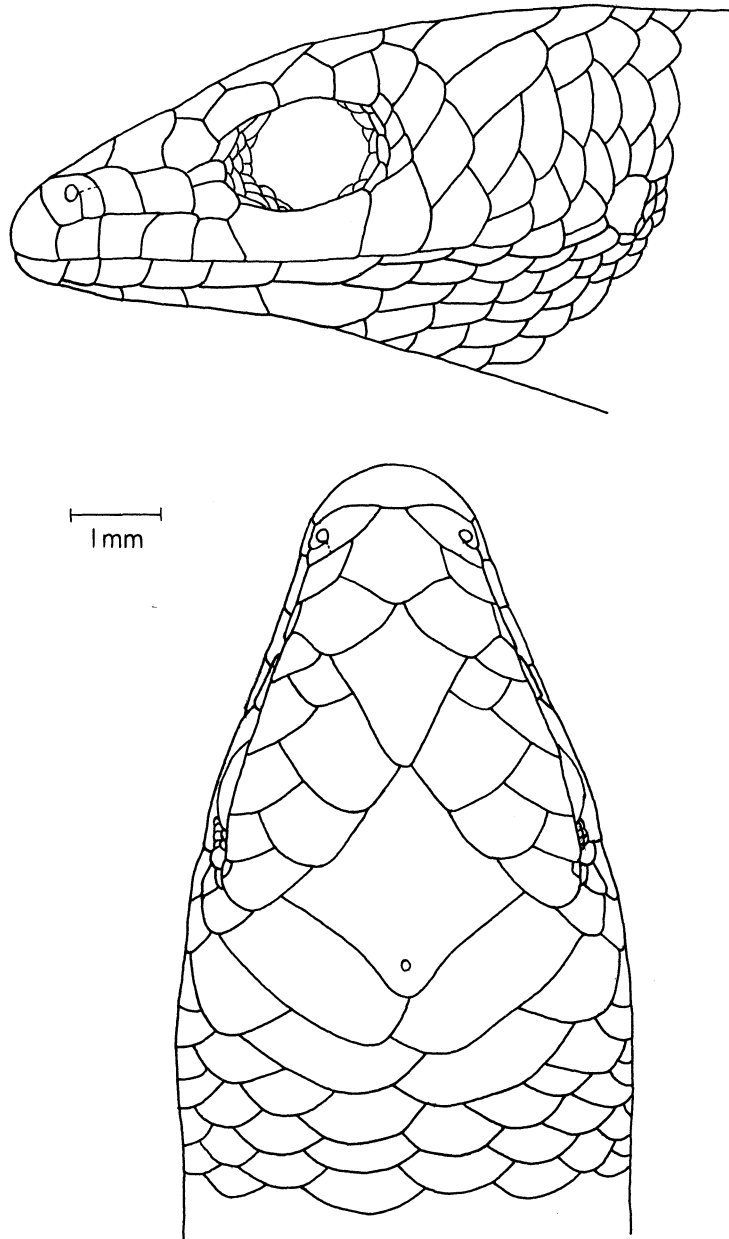


Fig. 1. Dorsal and lateral views of the head of *Morethia storri* (S.A.M. R 13535) from Bing Bong Station, near Borroloola, N.T.

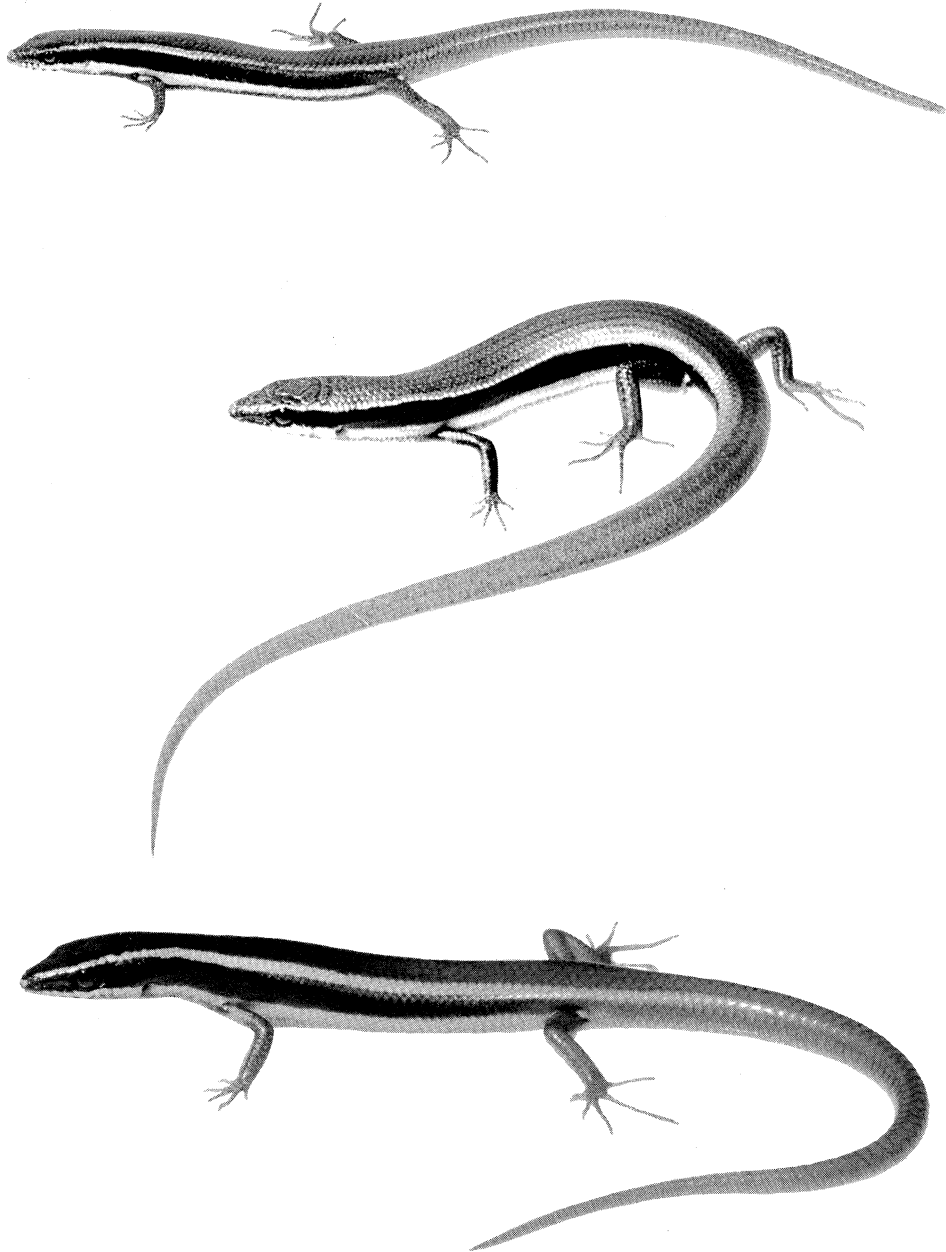


Fig. 2. Photographs of *Morethia storri* and its two most similar relatives. Top: *M. storri* (A.M. R 37225) from Koongarra, Mt. Brockman Range, N.T.; middle: *M. taeniopleura* from Townsville, Qld., and bottom: *M. ruficauda* from 16 km. S.E. Daly River Police Station, N.T.

fading colour in an unsexed specimen from Berrimah (A.N.W.C. R 1826) preserved five weeks prior to observation, and notes made by Mr Ross Sadlier on a male from the Jabiluka Project Area (A.M. R 88631). The specimen in the transparency shows russet to dull brick red colour on the dorsal surfaces of the tail and hind legs; the tail colour is most intense distally and diminishes rapidly over the base. The preserved specimen shows raspberry pink colour over all but the very basal part of the tail. This colour is also evident, albeit more diffusely, over the rear legs and distal half of the foreleg. No other colour is evident in either specimen. The specimen noted in life had pinkish orange colour on the tail (less intense anteriorly), throat and tip of snout.

DETAILS OF THE HOLOTYPE: The holotype shows the following characters: prefrontals just meet at their medial corners; midbody scale rows, 26; paravertebral scales, 58; subdigital lamellae on fourth toe, 18-19; SVL, 37 mm; unregenerated portion of tail, 32 mm; regenerated portion of tail, 8 mm; length of foreleg, 9.5 mm; length of rear leg, 14 mm.

DISTRIBUTION: The new species is known to date from northern Dampier Land in Western Australia and the broad coastal plain and certain offshore islands in the far northern part of the Northern Territory (Fig. 9). All the known localities are below 150 metres (approx. 500 feet) elevation.

FIELD NOTES: There is relatively little information on the habitat associations of *storri*. According to Mr R. W. Wells (pers. comm.), the holotype (N.T.M. R 1815) was in the roadside verge of a grassy open woodland with scattered cycads. At the time of collection at the end of the dry season, the scattered low clumps of "dormant" Spear Grass (*Sorghum* sp.) were separated by broad intervals of very dry, firm lateritic soil consisting of small ironstone pebbles. A later visit to this site during the wet season of 1977, however, showed that grass cover may reach a height of 2-3 metres and become extremely dense. Mr Wells also notes that the Berry Springs specimen (N.T.M. R 2715) was in a similar habitat but the soil was locally sandy. According to Dr H. G. Cogger the Koongarra specimen (A.M. R 37225) was found in an *Eucalyptus* woodland on the slightly rolling upper reaches of Deaf Adder Creek. The field notes associated with various specimens also give some indication of the habitats occupied: the Western Australian specimen (W.A.M. R 58498) was found in *Acacia* leaf litter at the edge of vine scrub; the Leanyer Swamp specimen (A.N.W.C. R 695) was found in open grassland on sandy soil while the Berrimah specimen (A.N.W.C. R 1826) was found "under a log in wet grass."

Mr R. Sadlier (pers. comm.) found both *storri* (A.M. R 88631, 88791, 88850 and 88988) and *ruficauda* (R88523, 88663, 88665, 88674-88675, 88836, 88846, 88848, 88949, 88954-88955) in broad sympatry in the Jabiluka Project Area of the Northern Territory but in different habitats: *storri* in open woodland on the sandy and lateritic/sandy soils of the alluvial flats of the Magela drainage and *ruficauda* in woodland on the stony soils of an outlier of the Arnhemland sandstone plateau.

There is one interesting behavioural observation available for *storri*. Mr Wells informs me that the Berry Springs specimen buried itself in loose soil while being pursued. This may be a characteristic evasion response in *Morethia* as I have noted it in *adelaidensis*, *boulengeri*, *butleri*, *lineoocellata*, *obscura* and *taeniopleura*.

REPRODUCTION: The two females from "Roper River" (S.A.M. R 1130 A-B) are gravid with shelled oviducal eggs which indicate that the species is oviparous, as are all other *Morethia* (see Notes section). One of these females measures 36 mm SVL and contains three eggs, and the other measures 38 mm SVL and contains two eggs. No collection date is available for either specimen.

COMPARISONS WITH OTHER MORETHIA: *Morethia storri* shows greatest overall similarity to *taenioleura* and *ruficauda* but in certain points of squamation it is most similar to *lineoocellata* and *adelaidensis*. Three characters serve to ally *storri* with *taenioleura* and *ruficauda*. These are (1.) a lower eyelid which is completely fused to the underside of the supraocular shelf instead of only partially fused; (2.) a relatively small body size with a maximum snout-vent length of less than 46 mm instead of 57 mm or more, and (3.) a colour pattern featuring a distinct dark brown lateral stripe bordered above by a distinct light dorsolateral stripe and a relatively uniformly coloured or only faintly longitudinally striped mid-dorsal area¹ instead of a more or less diffuse dark brown lateral stripe or area with no light dorsolateral stripe² and usually a mottled, blotched or ocellated mid-dorsal area.

Storri is closest to *taenioleura* in colour pattern in that both species have a thin light dorsolateral stripe separated from its fellow by approximately six scale rows whereas *ruficauda* has a rather wide light dorsolateral stripe separated from its fellow by only three to five scale rows. Furthermore, in both *storri* and *taenioleura* the dorsolateral light stripes end above the eye whereas in *ruficauda* the stripes run forward to converge on the snout.

Storri is more similar to *ruficauda* than *taenioleura*, however, in the relative size of the supraciliaries; both *storri* and *ruficauda* usually have four very large supraciliaries followed by a very small fifth whereas *taenioleura* usually has five relatively large supraciliaries (Fig. 3).

Storri may be readily distinguished from both *ruficauda* and *taenioleura* in having the anterior part of the supranasal fused to the nasal instead of completely separate and in having the supraciliaries projecting behind the first, second and third supraoculars instead of just the first and second (Table 1 and Fig. 3).

In showing these last two characters in combination, *storri* is similar to *lineoocellata* of Western Australia, but *storri*'s uniform or only faintly striped brown dorsum, distinct light dorsolateral stripe and distinct dark lateral stripe will instantly distinguish it from *lineoocellata* with its olive-grey or olive-brown and often variegated dorsum, usual absence of a light dorsolateral stripe, and only vague dark lateral stripe or area.

Storri is also similar to *adelaidensis* in having the supraciliaries projecting behind the first, second, and third supraoculars (Fig. 3), but it differs from this species in having the anterior part of the supranasal fused to the nasal instead of completely separate and a distinct dark lateral stripe bordered above by a distinct light dorsolateral stripe instead of an only ill-defined dark lateral area and no distinct light dorsolateral stripe.

A key to all the currently recognized species and subspecies of *Morethia* comprises a separate later section of this paper.

DIAGNOSIS OF THE GENUS MORETHIA

The genus *Morethia* is a member of the *Eugongylus* subgroup of the *Eugongylus* group of lygosomine skinks (Greer 1979). This subgroup is centred over the Australian Region and comprises the following genera in addition to *Morethia*: *Anotis*, *Cryptoblepharus*, *Emoia*, *Eugongylus*, *Leiolopisma* (including *Pseudemoia*), *Phoboscincus*, *Proablepharus* and *Tachygyia*.

1. The distinct light mid-dorsal stripe of *ruficauda exquisita* is an exception, but it is in no way similar to the mid-dorsal colour pattern of the other *Morethia*.
2. A few *lineoocellata* have a distinct light dorsolateral stripe.

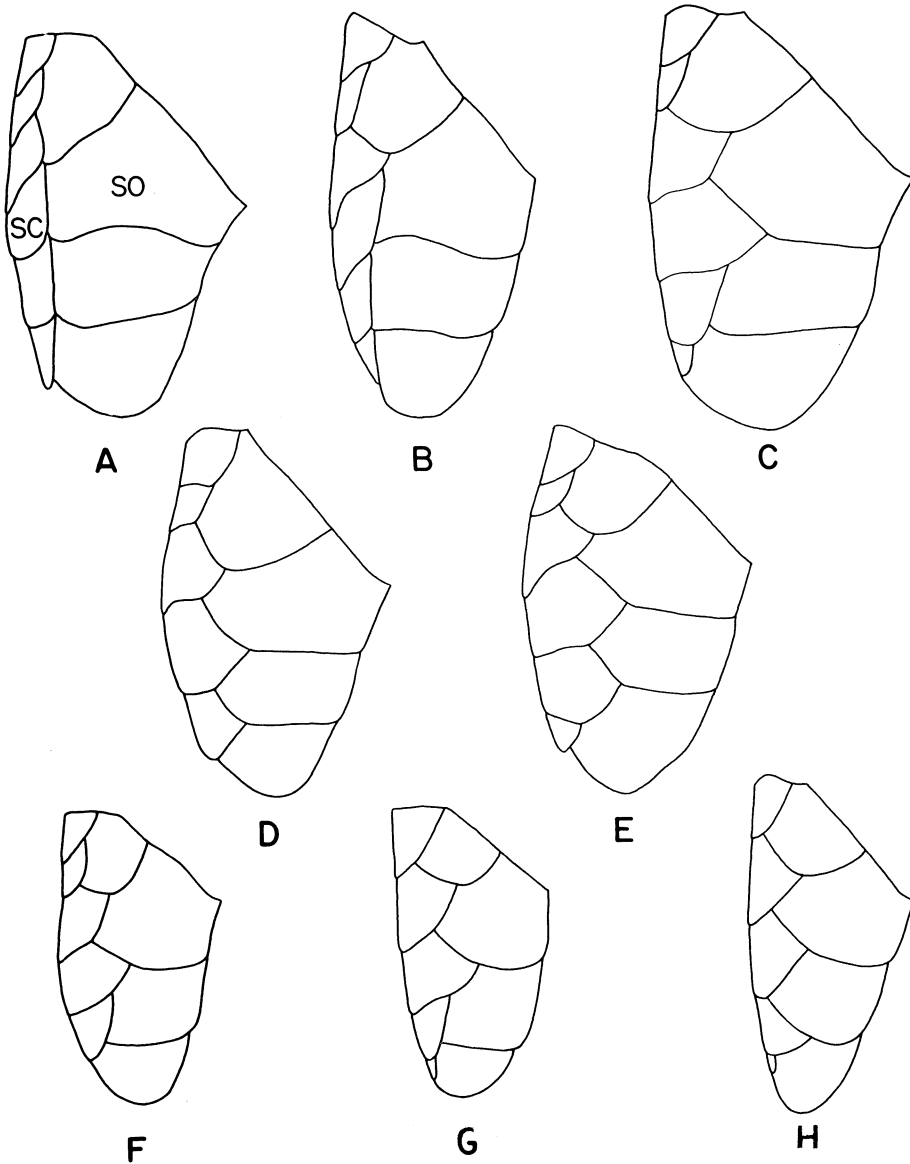


Fig. 3. Line drawings of the supraocular (SO) and supraciliary (SC) scales on the left side of the head in the eight species of *Morethia*. The species are as follows: A — *butleri*, B — *boulengeri*, C — *obscura*, D — *adelaidensis*, E — *lineocellata*, F — *taeniopleura*, G — *ruficauda*, H — *storri*.



Fig. 4. Plate showing throat colour in an adult male *Morethia lineocellata* from Rottnest Island, W.A. (top) and an adult male *Leiopisma trilineatum* from Augusta, W.A. (bottom).

Within this subgroup, *Morethia* is most similar to *Cryptoblepharus* and *Proablepharus* in having an ablepharine eye. *Morethia* differs from *Proablepharus*, however, in having the frontoparietal and interparietal scales fused into a single scale instead of having all three scales distinct or the interparietal distinct from the fused frontoparietals. *Morethia* also usually has a distinct dark lateral stripe or area which *Proablepharus* lacks.

Most *Morethia* can be distinguished from most *Cryptoblepharus* by the presence of supranasal scales and by supraciliary scales which interdigitate with the supraocular scales rather than make linear contact with them. These convenient characters are not universal, however, in that some *Morethia* lack distinct supranasals (i.e., some *lineoocellata* and all *storri*) or have a linear contact between the supraciliaries and supraoculars (i.e., *butleri*) while some *Cryptoblepharus* have distinct supranasals (e.g., some *africanus*, *eximius*, *poecilopleurus* and *novocaledonicus*, *vide* Mertens 1931 and pers. obs.).

Morethia and *Cryptoblepharus* can be readily distinguished from each other on the basis of a number of slightly more subtle but nonetheless significant characters. *Morethia*, for example, has a moderately deep head and body, a relatively long frontal scale, no enlarged upper periocular scales and, in most species, red colour in the tail during some stage of ontogeny, whereas *Cryptoblepharus* has a depressed head and body, a relatively short frontal, generally three large upper periocular scales, and no red in the tail.

THE INTRAGENERIC RELATIONSHIPS OF *MORETHIA*

There are seven characters — five morphological and two colour — that are variable within *Morethia* and useful in inferring phylogenetic relationships within the genus. These seven characters are briefly analyzed below.

(A) EYE COVERING: All *Morethia* have an immovable clear spectacle permanently covering the eye, but in some species there is a distinct palpebral slit while in others the spectacle is completely fused to the underside of the supraocular shelf¹. The palpebral slit is most logically viewed as an intermediate stage (A) in the evolution of the completely fused spectacle (a) and as such may be taken as the more primitive condition (Schwarz — Karsten 1933, Smith 1935 and 1937, Underwood 1970 and Greer 1974).

(B) SUPRANASAL SCALES. Most species of *Morethia* have the supranasals distinct from the nasals (B) whereas others have them fused to the nasals (b). The former condition appears to be primitive in lygosomines and the latter derived (Greer 1974).

(C) NUMBER AND RELATIVE SIZE OF SUPRACILIARY SCALES: The different species of *Morethia* have one of the following four character states: six relatively large supraciliaries (C), five large supraciliaries and a smaller sixth (c), five large supraciliaries only (c'), or four large supraciliaries and a very small fifth (c''). In that six relatively large supraciliaries is closest to the number seen in the more generally primitive members of the *Eugongylus* group, e.g., *Eugongylus*, *Leiolopisma spenceri*², *L. palfreymani* and an undescribed species of *Leiolopisma* from southwestern Australia, it is taken as the

1. Rawlinson (1976:28) states that the "immovable transparent disc (is) fused to the eye surface." This is incorrect; there is an easily probeable space (through the palpebral slit) between the disc and the surface of the eye.

2. Rawlinson (1976:40) discounts my suggestion that *Leiolopisma spenceri* "would make a morphologically reasonable hypothetical ancestor" for the line leading to *Morethia* and its relatives (Greer 1974). His reason is that virtually all of the descendant taxa are oviparous whereas *Leiolopisma spenceri* is viviparous, and viviparity is clearly the more derived mode of reproduction. My own view of a taxon's morphology excludes its mode of reproduction, but I suppose a very broad view of morphology could include it. Be that as it may, the fact that viviparity in Australian skinks is so obviously an ecological phenomenon (Greer, in prep.) means that viviparity, even as a derived character, can count for little in phylogenetic inference. With this in mind, it does not seem unreasonable to speculate about a form morphologically similar to *Leiolopisma spenceri* but with an oviparous mode of reproduction.

primitive condition and the lower numbers of large supraciliaries are taken as progressive reductions.

(D) DEGREE OF INTERDIGITATION BETWEEN SUPRACILIARY AND SUPRAOCULAR SCALES: A straight-edged line of contact between the supraciliary and supraocular scales is the rule in lygosomines and as far as I know the interdigitating contact seen in all *Morethia*, except *butleri*, is unique within the *Eugongylus* group. For this reason, I take the straight-edged contact as the primitive condition (D) and the projection of the supraciliaries behind the first (d), first and second (d'), and first, second and third (d'') supraoculars as progressive derivations.

(E) SUBDIGITAL LAMELLAE: Most species of *Morethia* have smooth or only bluntly keeled subdigital lamellae, and as this is the condition seen in the more primitive members of the *Eugongylus* group, e.g., *Eugongylus* and *Leiolopisma*, it is taken as primitive (E) while the more unusual sharply keeled lamellae seen in only two species of *Morethia* is taken as derived (e).

(F) VENTRAL COLOUR: Ventral colour on the head and body is present in most of the species of the more primitive genera in the *Eugongylus* subgroup, e.g., *Eugongylus* and *Leiolopisma*¹. This indicates that the presence of ventral colour is probably primitive in the subgroup as a whole and its absence derived.

The most primitive ventral colour pattern in *Morethia* is probably the extensive reddish-orange wash that develops seasonally on the chin and throat in the males of most species of *Morethia* (see Notes section and Fig. 4). The reason for thinking this is that this is the only ventral colour pattern shared with other members of the *Eugongylus* subgroup, i.e., the *trilineatum* species group of *Leiolopisma* and perhaps also the genus *Proablepharus* (see below), and at least in certain characters, i.e., a movable lower eyelid in the *trilineatum* species group and distinct frontoparietals and interparietals in *Proablepharus*, these relatives are more primitive than *Morethia*. This means that these taxa may have had a common ancestor with red throat colour and that they inherited this colour pattern as a primitive trait from the ancestor (F)². The fringing reddish-orange ventral colour of *adelaidensis* (see Notes section) is probably derived (f), as it is unique in the *Eugongylus* group, and as reasoned above, the absence of any ventral colour in *ruficauda* is derived (f'), probably independently from the primitive condition.

(G) TAIL COLOUR: Most species of *Morethia* have a bright red tail as hatchlings and then lose this colour as they grow. Three species, however, apparently never have tail colour (see Notes section). The fact that most of the more generally primitive members of the *Eugongylus* subgroup, e.g., *Eugongylus* and *Leiolopisma*, lack tail colour would suggest that this is the primitive character state. Opposed to this, however, is the fact that there is one genus in the *Eugongylus* subgroup — the Australian *Proablepharus* — which shares a red tail with *Morethia* but is more primitive in having the frontoparietals and interparietal distinct instead of fused into a single scale. This latter consideration raises the possibility that red tail colour in both *Morethia* and *Proablepharus* was inherited from a common ancestor and is therefore primitive in both genera (G) and that the absence of red tail colour in *Morethia* is secondarily derived (g). It is difficult to decide which of these

1. Note, however, that ventral colour is apparently lacking in the very primitive *L. spenceri* (Rawlinson 1974 and pers. obs.).

2. The fact that red throat colour occurs in both sexes and all age groups in the *trilineatum* species group (Rounsevell 1978 and pers. obs.) but only in adult male *Morethia* makes little difference to the phylogenetic analysis. Red throat colour in males is the common feature in both taxa and hence almost certainly characterized their hypothetical common ancestor.

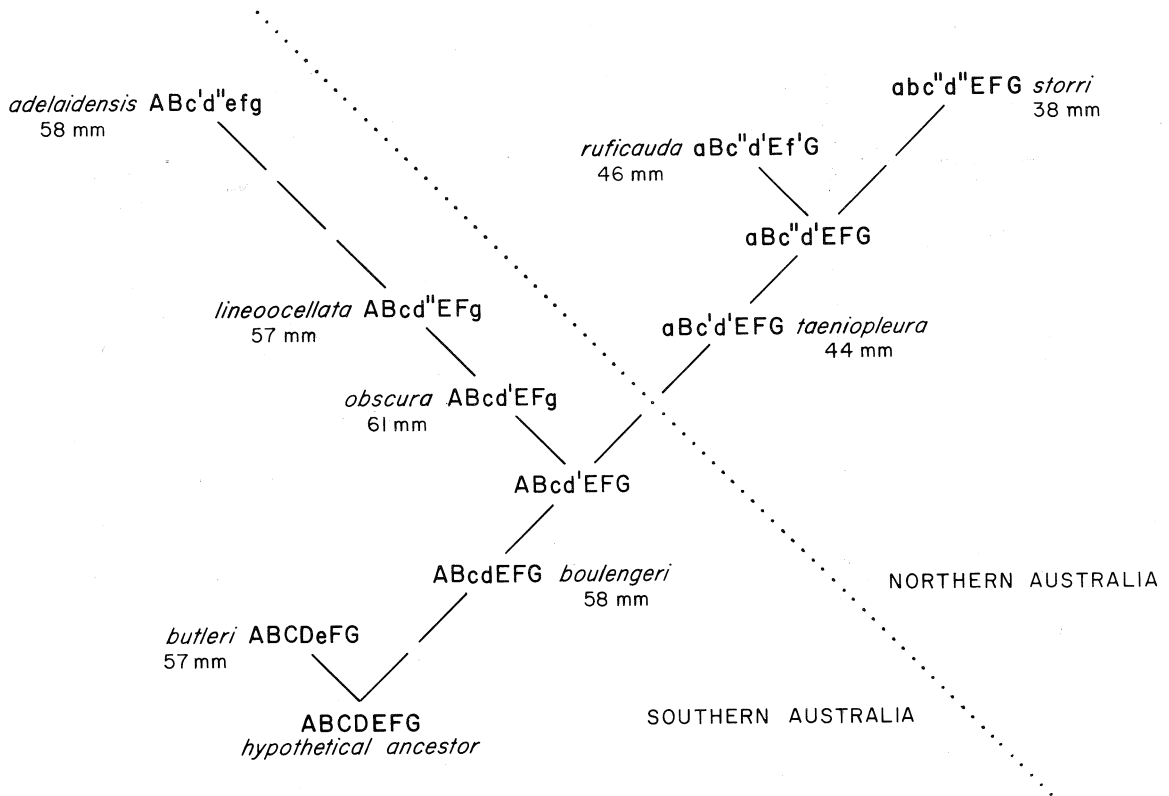


Fig. 5. A schematic representation of the inferred relationships of the eight living species of *Morethia* as determined from an analysis of seven characters (for which, see text) represented by letters A-G. In those cases in which a character state is variable within a species, the more primitive state is taken to represent the species. The distance between each taxon in the diagram is proportional to the number of character state changes separating it from its nearest relatives. The number below the name of each species is the maximum known snout-vent length (mm) for the species.

two possibilities is correct, but I prefer the second.

Utilizing the seven characters discussed above, it is possible to construct a phylogeny that is maximally parsimonious in that it hypothesizes no retrogressive events and only three convergent events. These are (1) the loss of the small sixth supraocular from a condition of five large supraoculars and a smaller sixth in two lineages, (2) the projection of the supraciliaries behind the third supraocular from a condition in which the supraciliaries project behind the first two supraoculars in two lineages, and (3) the acquisition of sharply keeled subdigital lamellae in two lineages (Fig. 5).

There are two interesting points in this phylogeny that are worth discussing briefly. First, there appear to be two distinct subgroups within *Morethia* based on morphology, colour pattern and distribution. The first, which comprises *adelaidensis*, *boulengeri*, *butleri*, *lineocellata* and *obscura*, is characterized by an incompletely fused spectacle, relatively large body size (maximum SVLs from 57 to 61 mm) and a colour pattern featuring an ocellated, variegated or blotched mid-dorsal area, usually no distinct light dorsolateral stripe and usually a somewhat indistinct dark lateral stripe or area. This group is southern and temperate in distribution (Figs 6-8). The second group comprises *ruficauda*, *storri* and *taeniopleura* and is characterized by a completely fused spectacle, relatively small body size (maximum SVLs from 38 to 46 mm), and a colour pattern featuring a relatively patternless mid-dorsal area (the striking light mid-dorsal stripe of *ruficauda exquisita* is an exception but different from the pattern in the first group), a distinct light dorsolateral stripe and a distinct dark lateral stripe. This group is northern and tropical in distribution (Fig. 9). It may be noted here that Rawlinson (1976) has also suggested that the genus can be broken into two "geographical and evolutionary groups" along the same lines as suggested in this analysis, but he has given no reasons other than geography.

The second interesting point related to the phylogeny presented here is that the three most primitive species in the genus, i.e., *boulengeri*, *butleri* and *obscura*, are centred over temperate woodland and shrubland habitats (see Notes section below) — a fact which suggests that these habitats may be primitive for the genus. If this is true, *lineocellata* can be viewed as occupying, at least over much of its range, the same kind of habitats, whereas *adelaidensis* and the northern group can be interpreted as having shifted into habitats that differ markedly either in structure, e.g., *adelaidensis*' low, halophytic (chenopod) shrubland, or in climate, e.g., the northern group's tropical distribution.

THE BIOLOGY OF THE PRIMITIVE *MORETHIA*

Before proceeding to an analysis of *Morethia*'s intergeneric relationships, it will be useful to review various aspects of the biology of the common ancestor of all living *Morethia*. It is this ancestor that is of interest in trying to determine *Morethia*'s relatives. On the basis of the analysis in the preceding section and taking into account certain features found in all living *Morethia*, it seems likely that the primitive *Morethia* had the following morphology: supranasal present and distinct from nasal; lower eyelid with a clear window and fixed in the up position but not completely fused to the underside of the supraocular shelf; six subequally-sized supraciliary scales in linear contact with the supraoculars; frontoparietals and interparietal fused into a single scale; subdigital lamellae smooth or only bluntly keeled; chin and throat of adult males bright reddish-orange, at least seasonally; tail bright red, at least in the young, and a dark lateral stripe or area bordered below by a light stripe.

It is also probable that, like all living species, the primitive *Morethia* was both

terrestrial and diurnal, and that it was oviparous with a variable number of eggs per clutch (see Notes section below). It also seems likely on the basis of the habitats occupied by the three most primitive species in the genus that the primitive *Morethia* occupied a temperate woodland or shrubland habitat (see above).

THE INTERGENERIC RELATIONSHIPS OF *MORETHIA*

Morethia is clearly a member of the *Eugongylus* subgroup (Greer, 1979 and above), and the search for its relatives can be made with reference to both the characters and the taxa of this subgroup. The most reliable basis for inferring relationships is shared derived character states, and *Morethia* displays four character states which current knowledge suggests are either almost certainly or very likely to be derived within the *Eugongylus* subgroup. These are the fused frontoparietal and interparietal scales (Greer 1974 and 1977), a spectacle (see above), red throat colour, and red tail colour. These last two character states are presumed to be derived in the *Eugongylus* subgroup due to their restricted taxonomic occurrence. In the following discussion I compare *Morethia* with each of the genera in the *Eugongylus* subgroup using these derived character states. I also introduce certain other morphological characters, as well as data on ecology and distribution, in order to corroborate the evidence of the derived character states.

Eugongylus comprises three species which are centred over the islands of the southwest Pacific. It is the most generally primitive genus in the subgroup (Greer 1974) and shares no derived character states with *Morethia*. In fact, in the case of the two morphological characters of interest, each of which has three sequential states, *Eugongylus* shows the most primitive condition (frontoparietals and interparietal distinct and lower eyelid movable and scaly) whereas *Morethia* shows the characters in their most derived condition (frontoparietals and interparietal fused and the lower eyelid a spectacle). *Eugongylus* also differs greatly from *Morethia* in size; the maximum snout-vent length of the smallest species of *Eugongylus*, for example, is 162 mm (*mentovaria*, *fide* an unpublished MS by F.A.C.B. Adema) whereas the maximum SVL of the largest *Morethia* is only 61 mm. The two genera also differ in ecology and distribution. *Eugongylus* is a shade-dwelling to crepuscular inhabitant of mesic habitats (Messrs F. Parker and M. McCoy, pers. comms) on islands in the tropical Pacific whereas *Morethia* is a diurnal inhabitant of arid and semi-arid, continental Australia. These differences suggest that the relationship between *Eugongylus* and *Morethia* is not close.

Phoboscincus (two species) and *Tachygyia* (one species) appear to be independent derivatives of *Eugongylus* in the New Caledonian-Loyalty Islands Archipelago and the Tonga Islands, respectively (Greer 1974 and Böhme 1976). Both genera have fused frontoparietals and hence are one derived character state closer to *Morethia*¹ than is *Eugongylus*, but they differ from *Morethia* in the same way that *Eugongylus* does in all other morphological characters discussed, including size. Nothing is known of the ecology of either genus, as both are extremely rare, but *Phoboscincus* has pointed, recurved teeth which suggests that it has unusual feeding habits. The remote oceanic island distribution of the two genera, but especially the Tongan *Tachygyia*, is a further point of contrast with *Morethia* and may be taken, along with the other evidence, to indicate that neither genus is particularly closely related to *Morethia*.

1. This is assuming that the fused frontoparietal and interparietal scales of *Morethia* were reached via an intermediate stage in which the frontoparietals were fused and the interparietal distinct and that this intermediate stage occurred in an immediate ancestor of *Morethia* (see below).

Böhme (1976) has recently described a new species of skink from New Caledonia and placed it in the genus *Eugongylus* along with *Phoboscincus* and *Tachygyia*. I believe that this species is rightly allied with *Eugongylus*, *Phoboscincus* and *Tachygyia*, but I also think that along with these other taxa, it merits separate generic rank. Be that as it may, the new species differs from *Morethia* in all the ways that *Eugongylus* does, plus others such as the absence of supranasals. It also probably has an even more distinctive ecology since the two known specimens were found inside a rotting log in moist rainforest. There is, therefore, nothing in the biology of this species that would indicate that it is closely related to *Morethia*.

Anotis comprises five species: two in Australia and three in New Caledonia (Greer 1974). The genus is slightly more plausible as a possible close relative of *Morethia* than any of the preceding taxa in that it shares fused frontoparietals (in one species), small size and an Australian distribution. Opposed to this, however, is the fact that *Anotis* shares no other derived character states with *Morethia* and the one species that does have fused frontoparietals is New Caledonian and not Australian. The genus is also highly cryptozoic and mesic adapted, to judge from the better known Australian species, and hence is quite distinct from the surface dwelling, xeric adapted *Morethia*. There seems to be little reason, therefore, to accept the notion that *Anotis* and *Morethia* might be close relatives.

In an earlier paper (Greer 1974), I suggested that *Morethia* was perhaps most closely related to the *Emoia*→*Cryptoblepharus* line and that it was possibly even derived from a *Cryptoblepharus*-like ancestor. When I made these suggestions, I only knew the animals on the basis of preserved specimens and was ignorant of them as living organisms. In the intervening six years, however, I have had an opportunity of seeing many of the animals and their relatives alive, and I have also considered their morphology in greater detail. As a result, I now think that the relationship between *Morethia* and the *Emoia*→*Cryptoblepharus* line is not particularly close. The reasons for my changed views are, briefly, as follows.

My original reason for allying *Morethia* with the *Emoia*→*Cryptoblepharus* lineage was that both groups had supranasals and fused frontoparietals. This is not a particularly convincing reason, however, as the former character state is primitive (Greer 1974) and hence not useful for inferring relationships and the latter character state has evolved many times in skinks and hence, by itself, does not provide strong evidence of relationship.

Detailed comparisons between each of the two genera in the lineage and *Morethia* also make it difficult to accept the notion that either is particularly closely related to *Morethia*. *Emoia* (approximately 36 species), for example, shares only the one derived character state with *Morethia*, i.e., fused frontoparietals¹, and the two genera differ greatly in ecology and distribution. *Emoia* is a basically mesic adapted taxon with its centre of diversity, and hence probable area of origin, in the islands of the southwest Pacific whereas *Morethia* is a basically xeric adapted taxon that probably originated in temperate, continental Australia (see above).

In addition to fused frontoparietals, *Cryptoblepharus* (approximately 36 species) shares a spectacle with *Morethia* and both taxa are broadly sympatric over much of arid and semi-arid Australia. These similarities are intriguing, but they are counterbalanced, I think, by substantial differences in morphology, colour and ecology. *Cryptoblepharus*, for example, has a very depressed head and body, a relatively small frontal, virtually no chromatic colour, and is almost exclusively arboreal and saxicolous. In contrast, *Morethia*

1. *Emoia ruficauda* from the Philippines is an exception in that it has a bright red tail like *Morethia*. Given the great geographical distance separating these two taxa, however, it is unlikely that they shared a common ancestor.

has a typically deep head and body, a relatively large frontal, red colour in both the throat (in males) and tail (at least in juveniles), and is almost exclusively terrestrial. Furthermore, despite the fact that the two genera are now broadly sympatric in Australia, *Cryptoblepharus* probably evolved in tropical and subtropical habitats (Greer 1974) whereas *Morethia* appears to have evolved in temperate habitats (see above).

Leiolopisma is a diverse group of approximately 42 species distributed from the Chatham Islands, New Zealand and New Caledonia west through southern Australia to Round Island just north of Mauritius. The *trilineatum* species group is one of the most distinctive subgroups in the genus and is characterised by a slightly elongate body, the absence of a distinct supranasal scale and red throat colour. The species group comprises two or three species and is restricted to Australia: *platynotum* in the south-east and *trilineatum* with disjunct populations, that may have reached species status, in the southwest and southeast (Cogger 1975 and Fig. 10, this paper).

The fact that the *trilineatum* species group shares red throat colour and fused frontoparietals with *Morethia* (Fig. 4) suggests that the two taxa may be closely related. This hypothesis is also supported by the fact that the species group is similar to *Morethia* in general size (maximum SVLs range from 69 to 80 mm), shape and colour pattern (all forms have a dark lateral stripe or area and in some *trilineatum* at least this is bordered below by a light lateral stripe). The group is also somewhat similar to *Morethia* in ecology and distribution in that it is diurnal, terrestrial and oviparous and narrowly overlaps or abuts the distribution of the two most primitive living species of *Morethia*, i.e., *butleri* and *boulengeri* (compare Figs 6 and 10).

Proablepharus, the last genus in the *Eugongylus* group to be discussed, also appears to be closely related to *Morethia*. This genus occurs throughout most of mainland Australia and comprises three species: *reginae* in the west, *kinghorni* in the east and *tenuis* in the far north (Storr 1975, Cogger 1975 and Fig. 11, this paper).

Proablepharus is similar to *Morethia* in having a spectacle (which is incompletely fused), red tail colour at least in juveniles¹, and some reddish-orange colour on the head². It is also similar in having the same general size (maximum SVLs range from 32 to 47 mm) and shape. Furthermore, *Proablepharus* is extremely similar to *Morethia* in ecology and distribution. It is diurnal, terrestrial and oviparous (known for *reginae* and *tenuis* — Mr B. Bradshaw and pers. obs., respectively) and is widespread in the arid and semi-arid parts of Australia (Fig. 11).

1. *Proablepharus reginae* has bright red tail colour in hatchlings but loses this colour with age (Mr B. Bradshaw, pers. comm.). *P. kinghorni* has bright red tail colour in small individuals and the colour largely persists in larger individuals (pers. obs.). *P. tenuis* has a dull red wash on the tail in small individuals but this appears to be lost in larger animals (pers. obs.).

2. *P. reginae* has a reddish-orange wash along the side of the face and neck (Messrs B. Bradshaw and L. A. Smith, pers. comm.). *P. kinghorni* apparently has this colour confined to the snout and anterior labial area (colour transparencies taken by Mr H. F. W. Ehmann and pers. obs.). It should be emphasised that the head colour in *Morethia* also extends to both these regions, at least in certain species, e.g. *lineoocellata* (Fig. 4). *P. tenuis* has an orange suffusion on the head and nape which is most intense over the snout and supraciliaries (Mr R. Sadlier, pers. comm.).

Although the age and sexual distribution of the head colour in *Proablepharus* is unknown, the available evidence is not incompatible with the hypothesis that the colour is restricted to adult males. The only specimen of *P. reginae* which showed head colour and which has been sexed is a male (Mr L. A. Smith, pers. comm.). Of the six specimens of *P. kinghorni* for which there are colour notes, three are males (SVL = 35 mm or >), all with colour and three are females (SVL = 34 mm or >), all without colour. The only specimen of *P. tenuis* noted to have head colour is a large male (SVL = 31 mm) with very enlarged testes.

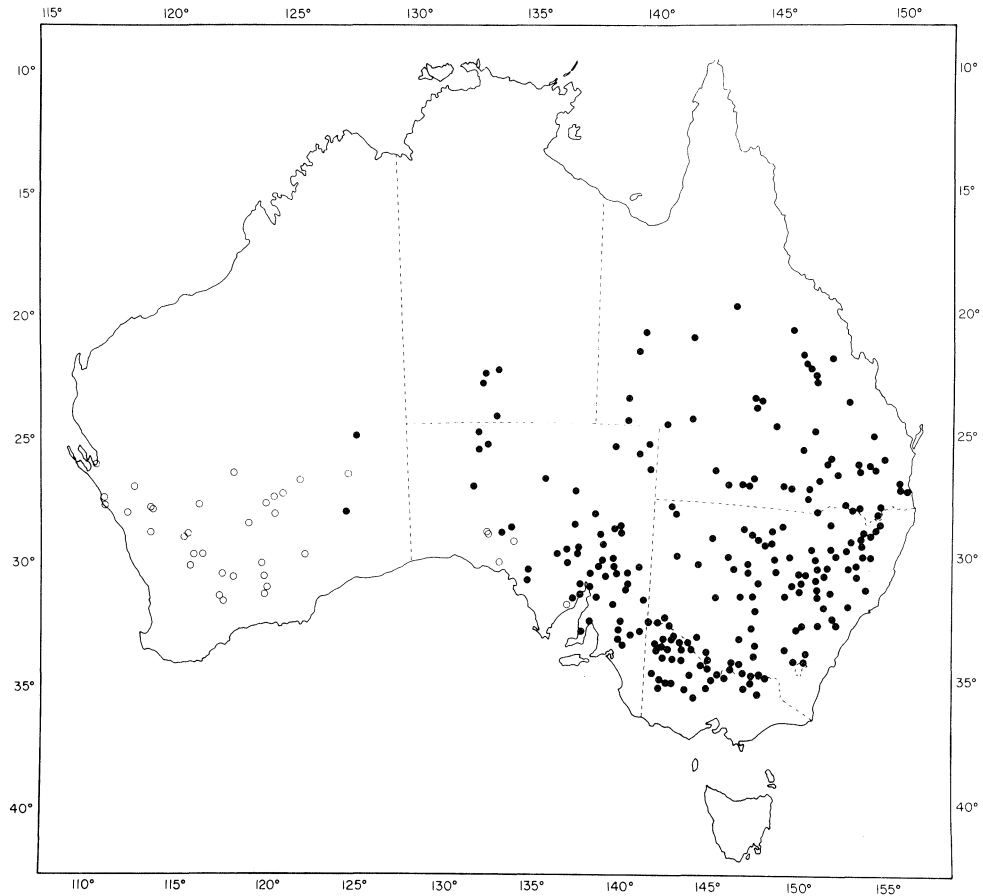


Fig. 6. Map showing the known distribution of *Morethia butleri* (open circles) and *M. bouleengeri* (black dots).

Although the *trilineatum* species group and *Proablepharus* both appear to be fairly closely related to *Morethia*, I believe that the sum of the evidence actually favours *Proablepharus* as *Morethia*'s closest living relative. The reason for this is that *Proablepharus* and *Morethia* share three derived character states and are broadly sympatric whereas the *trilineatum* species group and *Morethia* share only two derived character states and are only broadly parapatric.

If *Proablepharus* and *Morethia* are each other's closest living relatives, what can be said of their common ancestor? If one agrees that this ancestor can be "reconstructed" by combining the primitive character states unique to each taxon with the character states common to both, then the following picture emerges. Morphologically, this ancestor was a small skink with a distinct supranasal scale (inherited by *Morethia*), distinct frontoparietal and interparietal scales (inherited by *Proablepharus*), a spectacle, red tail, and some aspect of red throat colour (probably most like *Morethia* in its distribution for reasons that become apparent below). Ecologically, this ancestor was diurnal, terrestrial and oviparous and probably resident in a temperate, semi-arid habitat.

How is the *trilineatum* species group to be related to the *Morethia-Proablepharus* lineage? The most parsimonious hypothesis is that the two groups had a common ancestor which had a red throat at least in males (the only derived character state common to both groups), a distinct supranasal scale and distinct frontoparietal and interparietal scales (inherited by the ancestor of the *Morethia-Proablepharus* group), a movable lower eyelid with a clear window, and a dark-coloured tail (inherited by the *trilineatum* species group). In addition, this ancestor was probably diurnal, terrestrial, and oviparous and occupied a temperate, woodland habitat on the mesic periphery of a semi-arid area (features common to both groups).

If the relationships between *Morethia*, *Proablepharus* and the *trilineatum* species group are correct as described above (summarised in Fig. 12), then two cases of parallel evolution must be hypothesised. First, there is the independent loss of the supranasal scale in both *Proablepharus* and the *trilineatum* species group. It is unknown whether this loss in *Proablepharus* occurred by reduction or by fusion to the nasal, but in the *trilineatum* species group the loss has apparently occurred by fusion. The evidence for this is the bilateral presence in a single specimen of *platynotum* (AM R 39979) of a composite supranasal-postnasal that is partially set off from the nasal by fairly deep sutures. The second case of parallel evolution is the independent fusion of the frontoparietals in the line leading to *Morethia* on the one hand and to the *trilineatum* species group on the other. Independent evidence for the fusion of the frontoparietals within the *trilineatum* species group lineage is provided by the observation that in rare specimens the frontoparietals may be only partially fused (e.g., in the eastern form of *trilineatum* — AM 4705 and R 64715). It should also be mentioned that the phylogenetic relationships of these three taxa suggests that extensive red throat colour may have once occurred in the *Proablepharus* line but was reduced prior to the evolution of the living species in the genus.

The movable lower eyelid of the common ancestor of *Morethia*, *Proablepharus* and the *trilineatum* species group would have caused it to be identified as a species of *Leiopisma* if it were alive today, and the supranasals and distinct frontoparietals and interparietal would have marked it as an extremely primitive species at that. In view of these facts, it is interesting to note that there are two species of *Leiopisma* living in Australia today which show the structural characters just described: *L. spenceri* from southeastern Australia and an undescribed species from southwestern Australia known from only a single specimen (Western Australian Museum R 44969; Greer, in prep.). As alluded to several times above, however, *L. spenceri* appears to differ from this hypothetical ancestor in several other aspects of its biology, viz., it is arboreal and

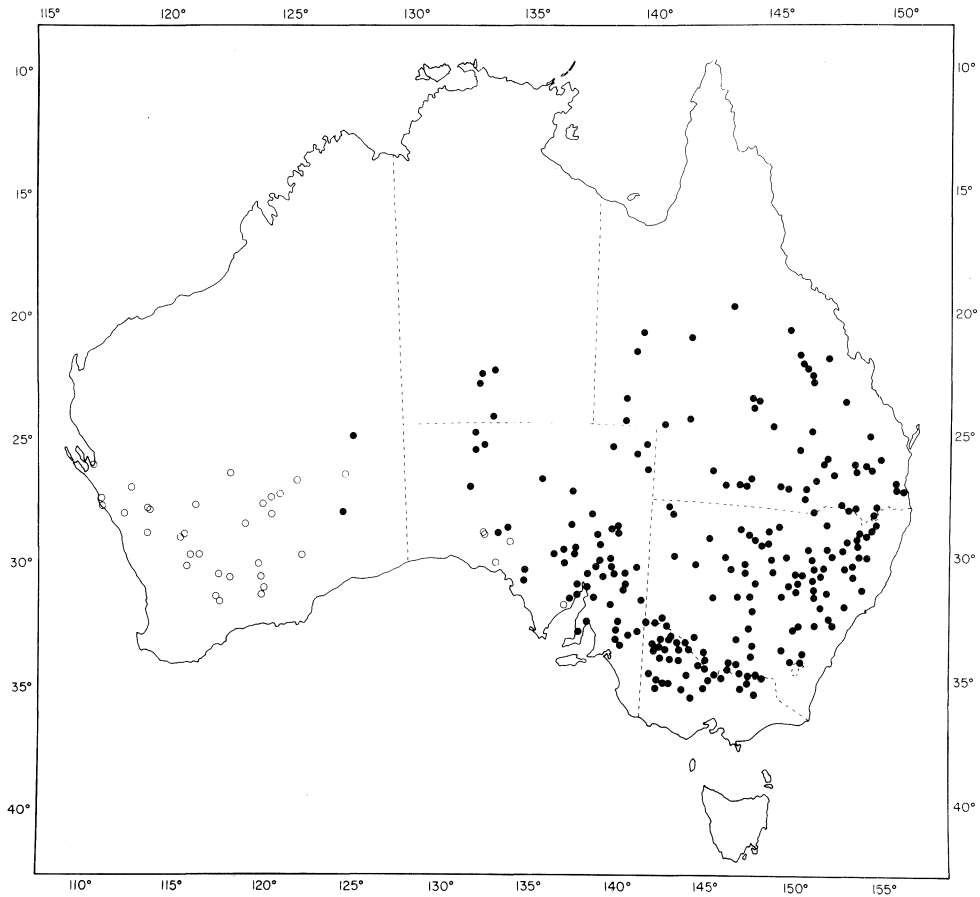


Fig. 7. Map showing the known distribution of *Morethia lineocellata* (open circles) and *M. adalaidensis* (black dots).

[A corrected map was published at a later date,
see last page of this PDF, Editor]

saxicolous, live-bearing and lacks throat colour (Rawlinson 1974 and pers. obs.) whereas the common ancestor of *Morethia*, *Proablepharus* and the *trilineatum* species group was probably terrestrial, oviparous and had a red throat, at least in males. It is unfortunate that nothing is known of the biology of the undescribed species, except that the single known specimen was found on the ground; needless to say, it would be interesting to know the mode of reproduction and colour pattern in this species.

A KEY TO THE SPECIES AND SUBSPECIES OF *MORETHIA*

- (1.) A distinct brown to black lateral stripe bordered above by a very distinct white dorsolateral stripe; no palpebral slit; maximum snout-vent length = 46 mm; northern Australia 2
 A dark lateral stripe of varying distinctness bordered above by at best an indistinct white dorsolateral stripe or area; a distinct palpebral slit; maximum snout-vent length of smallest species = 57 mm; southern Australia 5
- (2) Supranasal distinct from nasal; supraciliaries project behind first and second supraoculars only 3
 Supranasal fused anteriorly to nasal; supraciliaries project behind first, second and third supraoculars *storri*
- (3) Four large supraciliaries and a smaller fifth that might be taken for a postocular; dorsolateral light stripe broad, separated from its fellow by three to five scale rows 4
 Five large supraciliaries; dorsolateral light stripe narrow, separated from its fellow by six scale rows *taenioleura*
- (4) A distinct light mid-dorsal stripe *ruficauda exquisita*
 No light mid-dorsal stripe *ruficauda ruficauda*
- (5) Supraciliaries project behind at least one supraocular, resulting in a zig-zag border between the supraciliaries and supraoculars 6
 Supraciliaries do not project behind any supraocular, therefore there is a straight border between the supraciliaries and supraoculars *butleri*
- (6) Supraciliaries project behind more than the first supraocular 7
 Supraciliaries project behind the first supraocular only *boulengeri*
- (7) Supraciliaries project behind the first, second and third supraoculars 8
 Supraciliaries project behind the first and second supraoculars only *obscura*
- (8) Supranasal often fused to nasal anteriorly; five large supraciliaries plus a smaller sixth; toe lamellae smooth or obtusely keeled; ventral colour consists of a bright reddish-orange restricted to the throat of breeding males *lineoocellata*
 Supranasal distinct from nasal; five large supraciliaries; toe lamellae sharply keeled; ventral colour consists of a continuous reddish-orange fringe to the throat, chest and belly of breeding males *adelaidensis*

NOTES ON THE BIOLOGY OF *MORETHIA*

The preceding discussion of the intra and intergeneric relationships of *Morethia*

introduced certain observations on the colour, reproduction, behaviour, habitat and distribution of the genus that may be elaborated on here.

Colour

In his revision of the South Australian species of *Morethia* Smyth (1972) asserted that during the breeding season adult male *boulengeri* and *obscura* (his *lineoocellata*) develop a bright orange or orange-pink throat colour. He also noted that male *adelaidensis* in "breeding condition develop an orange colour all around the edges of the ventral surfaces, extending onto the inside surfaces of both fore and hind limbs and being particularly prominent around the vent and under the anterior part of the tail." In a later, more detailed study of *boulengeri* in an area just north of Adelaide, Smyth and Smith (1974) showed that the throat colour appeared in males in August and faded by mid-January and that changes in throat colour occurred in parallel with the testicular cycle.

My own observations support Smyth's observations on the location of ventral colour in male *Morethia* and indicate that male *butleri*, *lineoocellata* and *taenioleura* are similar to *boulengeri* and *obscura* in having reddish-orange colour on the chin and throat. As noted above *storri* also has pinkish orange throat colour. It is also evident that in certain species, e.g. *lineoocellata*, the throat colour can extend up onto the snout and upper labials (Fig. 4).

In contrast, however, it seems as if *Morethia ruficauda* lacks ventral colour on the head and body. My own limited observations indicate that this is true and none of the people with whom I have spoken can recall having seen ventral colour on the head or body of this species (Dr H. G. Cogger, Mr M. Gillam, Mr G. F. Gow, Mr P. R. Rankin, Dr G. M. Storr and Mr R. Wells).

Previously published work (Smyth 1972, Storr 1972 and Rawlinson 1976) plus my own and other people's observations indicate that all species of *Morethia*, except probably *adelaidensis*, *lineoocellata* and *obscura*, have bright red tail colour, at least during the juvenile stages. Adult and hatching *adelaidensis* and *obscura* definitely lack red tail colour (pers. obs.). Adult *lineoocellata* also lack red tail colour (pers. obs.), and the late Mr P. R. Rankin, who had collected young *lineoocellata*, could find no indication in his field notes that these specimens had red colour in the tail, nor did the specimens themselves show any trace of it after having been in preservative for only a few months.

Reproduction

Smyth and Smith (1974) provided a detailed analysis of the events in the reproductive cycle of *Morethia boulengeri* in an area north of Adelaide. Among other things, this study showed that the species is oviparous, with a clutch size ranging from 2-5 (mean = 3.7, N = 28) and that there was a positive correlation between clutch size and female size.

Rawlinson (1976) noted that *adelaidensis*, *boulengeri* and *obscura* are oviparous and that clutch sizes in *boulengeri* range from 3-5 (mean = 3.5, N = 11).

In an effort to learn more about the mode of reproduction and clutch size in *Morethia*, I examined all the state museum collections plus my own collection (now in the Australian Museum) for females gravid with either enlarged, yolky ovarian eggs or oviducal eggs. For each gravid female I noted SVL and clutch size.

Females gravid with oviducal eggs were found for each of the eight species of *Morethia* and all had shelled eggs which appeared as if they would have been laid. Hence it may be concluded that the genus as a whole is oviparous.

There was a positive correlation between female size and clutch size within each

species for which sample sizes were reasonably large (Table 2), and not surprisingly, there was also a positive correlation between mean size of gravid females and mean clutch size between species ($r = .90$, $P < .01$).

On 14 January 1979 I found a communal nest of *Morethia adelaidensis* on Reevesby Island in the Sir Joseph Banks Group off Eyre Peninsula, South Australia. The nest comprised 20 near term eggs plus one recently vacated shell. The eggs were partially buried in a crevice 8-12 cm beneath a granite boulder just above the high tide mark. If the mean clutch size for the species as a whole (3.2, Table 2) pertains to the Reevesby Island population, the nest could have represented the clutches of five to seven females. Some of the eggs hatched during collection and all had hatched by 24 January. None of the hatchlings showed any sign of red throat or tail colour.

Behaviour

There are relatively few observations in the literature on the behaviour of *Morethia*, and many of those that are available are of diminished value since they date from the time when all of the southern species were regarded as conspecific. The following is a brief review of what seems to be the more important published observations, supplemented with some personal observations.

Bustard (1968) reported that *boulengeri* (as *lineo-ocellatus anomalus* in his paper) "is a voracious feeder and will consume any insect which can be forced through its jaws", but he gives no data or observations. Bustard also reports that in northcentral New South Wales, the species has a "long active season and some bask throughout the winter."

Symth and Smith (1975) provided a fairly detailed analysis which showed that *boulengeri* "eats almost exclusively arthropods taken on the ground, and probably takes any animal of appropriate size it can catch."

Rawlinson (1976) described *boulengeri* as "heliothermic" and "insectivorous" but gave no details to support his assertion. He also said that this species has "high thermal preferences compared to other skinks from other temperate areas", but the other species he referred to are from obviously cooler habitats and hence the differences in thermal preferences are not surprising. Mr M. Gillam notes (in a letter of 10 January 1978) that *ruficauda* generally selects large exposed boulders for basking and that it is often active in high midday temperatures.

Smith (1976) reported that *ruficauda* "feeds by standing motionless in the open while curling its brilliant red tail horizontally back and forth as a lure." Due to the fact that these observations were obviously made in the presence of a potential predator, however, it is possible that what Smith has interpreted as feeding behaviour may have actually been some form of predator distraction behaviour.

All seven species with which I am familiar (all except *storri*) appear to be diurnal but generally cryptozoic during their activity period. The two northern species *ruficauda* and *taeniopleura* seem to be especially secretive, but this may simply be due to the fact that their small size causes them to be more easily overlooked.

Morethia is virtually completely terrestrial, but I have found *taeniopleura* a short distance above the ground in projecting portions of rotting timber.

Most species, perhaps all, sand swim quite readily, and will do so both as a means of escape and casual refuge. This sand swimming behaviour is especially interesting because it may provide a functional basis for the deep interdigitation of the supraocular and supraciliary scales seen in all species except *butleri*. This arrangement of the two parallel interlocking rows of scales may serve to resist the shearing forces induced by friction along the line of contact during forward motion under the surface.

Habitat and Distribution

Adelaidensis. The general distribution of this species covers a large part of southcentral Australia (Fig. 7), but due to the fact that it is associated almost exclusively with chenopod shrubs, its distribution is likely to be as scattered and spotty as this plant community is itself.

Adelaidensis is apparently very tolerant of halophytic conditions. In South Australia, for example, I have found it beneath the first shrubs bordering the dry salt bed of Lake Everard, and Mr Glen Ingram tells me that in southwestern Queensland he has found it in the salt bush vegetation around salinas (see also Storr 1972).

The general distribution of *adelaidensis* (Fig. 7) broadly overlaps the distribution of *boulengeri* (Fig. 6) and *obscura* (Fig. 8), but I suspect that its close association with chenopod shrubs separates it locally from these species, both of which appear to prefer habitats with taller shrubs and trees (see below).

Boulengeri. This species occurs widely throughout the southeastern quarter of Australia (Fig. 6) in a variety of habitats ranging from open forest to medium height shrubland (Bustard 1968 and pers. obs.). In some of its habitats, such as the *Callitris* forests of northcentral New South Wales, it has been described as the "most common terrestrial skink" (Bustard 1968). Despite its wide geographical distribution and habitat diversity, however, the species rarely occurs near the coast, and it is unknown from any offshore island.

There are two problems with regard to the general distribution of *boulengeri* that merit mention. First, there is the problem of the three specimens in the Australian Museum (Palmer Register No. 4764 a-c) collected by Mr George Masters and registered as having come from "Port Lincoln", presumably at the tip of Eyre Peninsula in South Australia. Rawlinson (1976) accepted this record as valid, but I believe there are good reasons for questioning it. First, is the fact noted above that *boulengeri* rarely occurs at coastal localities. Second, no further specimens have been collected anywhere in the southern half of Eyre Peninsula (pers. obs. on all *boulengeri* in all Australian state museums), and Port Lincoln is in the far south end of the peninsula. And third, there is confusion with regard to at least two other localities involving Masters' specimens from southcentral South Australia: (1) the type of *Notechis ater* (Krefft 1866) was stated as having come from "Flinder's Range, South Australia" whereas the original register entry reads "Port Lincoln" and (2) the types of *Drysdalia masteri* (Krefft 1866) were registered as having come from "Flinder's Range" but this species, as it is currently understood, is not otherwise known from the Flinders Ranges (Mr H. F. W. Ehmann, pers. comm.).

The second problem with regard to the general distribution of *boulengeri* is that there are several areas in what could be considered the general distribution of the species, where, in fact, it is not known whether the species occurs or not. The two most important of these areas are the Simpson Desert and the Great Victoria Desert. Clearly our understanding of the species' habitat associations and its spatial relations with congeners could vary greatly depending on its distribution in these areas.

The distribution of *boulengeri* either overlaps or interdigitates with the distribution of five other species of *Morethia*. In the northeast and northwest *boulengeri* overlaps narrowly with *taeniopleura* and *ruficauda*, respectively, and in the far west and southwest it narrowly overlaps or interdigitates with *butleri*. In none of these cases, however, is the nature of the habitat separation between the species known.

Boulengeri appears to occur in fairly broad sympatry with *adelaidensis* and *obscura* in parts of southeastern South Australia, southwestern New South Wales, and northwestern Victoria. I know of no instance, however, where even two of the species have been found together in an area of uniform habitat. This is no doubt due to the fact that the

general habitat associations of the three species are somewhat different (pers. obs.). *Boulengeri*, for example, appears to be closely associated with relatively heavily wooded habitats such as brigalow and dense shrubland, whereas *obscura* seems to occur in more open shrub habitats such as mallee, and *adelaidensis* is largely associated with open, low shrub habitats such as chenopod communities.

Butleri. Based on current information, this species appears to occur in two disjunct areas: the largely interior parts of the southern third of Western Australia, and the central part of southern South Australia (Fig. 6)¹. It is uncertain, however, whether this disjunction is real or not. In my experience *butleri* appears to be strongly associated with woodland and tall shrub habitats and is generally absent from open low shrub habitats (see also Pianka 1969). It is possible therefore that while the species is absent from the more or less accessible parts of the intervening Nullarbor Plain, it is continuously distributed in the relatively inaccessible mallee belt north of the Plain.

It is also uncertain how the distributions of *butleri* and *boulengeri* relate to each other. On the very broadest scale, they would appear to overlap widely, but they may, in fact, interdigitate or form a mosaic. Either of these latter possibilities would not be surprising as the two species appear to be morphologically and ecologically similar (Storr 1972).

The only species with which *butleri* does broadly overlap is *obscura*. I have collected both species at a locality just south of Norseman, Western Australia, in a woodland of medium height and little ground cover, but I formed no impression of any microhabitat differences.

Lineoocellata. The distribution of this species is largely centred over the coastal plain of midwestern and southwestern Western Australia (Fig. 7) (Storr 1972). The few inland populations are presumably relict.

Despite the species' restricted geographical distribution, it seems to have a fairly broad habitat range. On Rottneest Island, for example, I have seen it on the samphire flats bordering the salt lakes just behind the main settlement, and in the vicinity of Busselton, I have collected it both on sparsely vegetated dunes and in heavily wooded Tuart Forest. Elsewhere these habitats might have been typically occupied by *adelaidensis*, *obscura* and *boulengeri*, respectively.

An investigation of the habitats occupied by the isolated inland populations would be very interesting, especially with regard to how they may differ from any neighbouring habitats occupied by the closely related (Storr 1972) and widespread *obscura*.

Obscura. This species is widely distributed throughout southern Australia (Fig. 8), including most of the offshore islands.

In my experience, *obscura* is largely associated with open woodland and shrubland, although in certain areas such as along the south coast of Western Australia, it also occurs on the coastal plain (Storr 1972) in coastal heathland (pers. obs.).

1. Smyth (1972) assigned a specimen from Ooldea, South Australia to *butleri*, but noted that it differed slightly from Western Australian specimens in the squamation of the supraocular region. Perhaps for this reason, neither Smyth (1972) nor Rawlinson (1976) mapped *butleri* in South Australia. I have examined this Ooldea specimen and others subsequently acquired by the South Australian Museum and on this basis can confirm the presence of *butleri* in central-southern South Australia (Fig. 6).

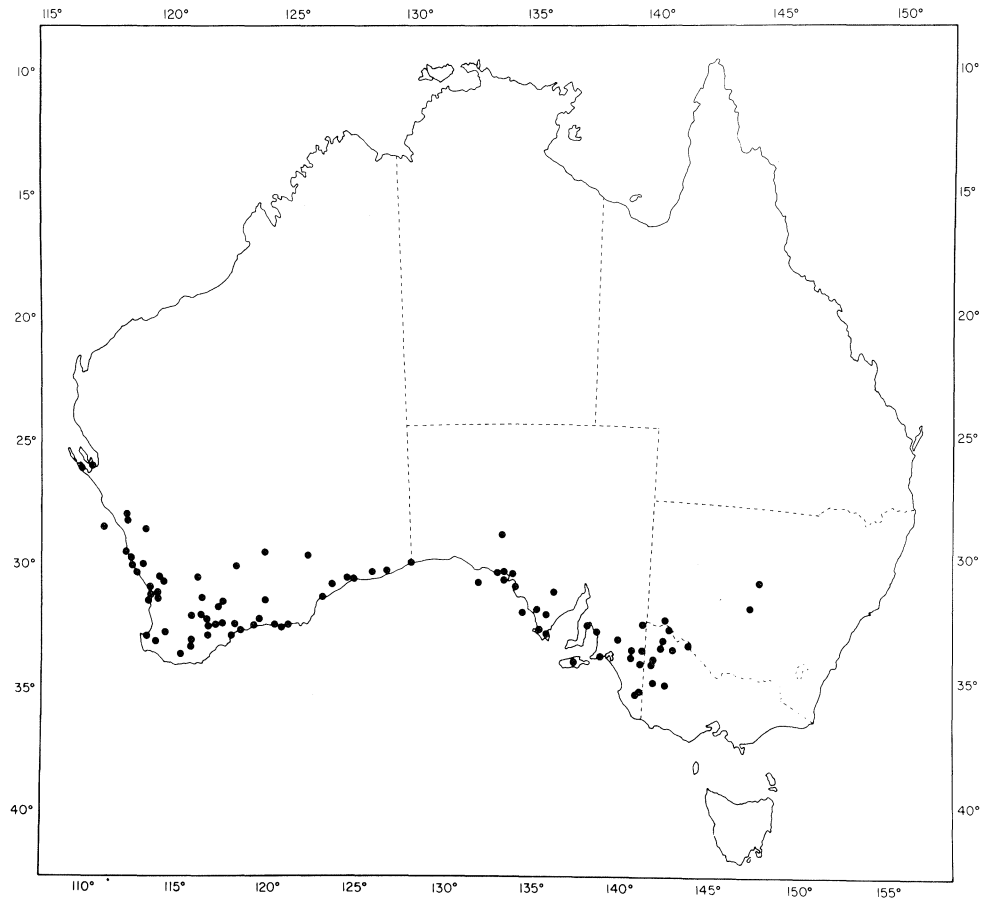


Fig. 8. Map showing the known distribution of *Morethia obscura*.

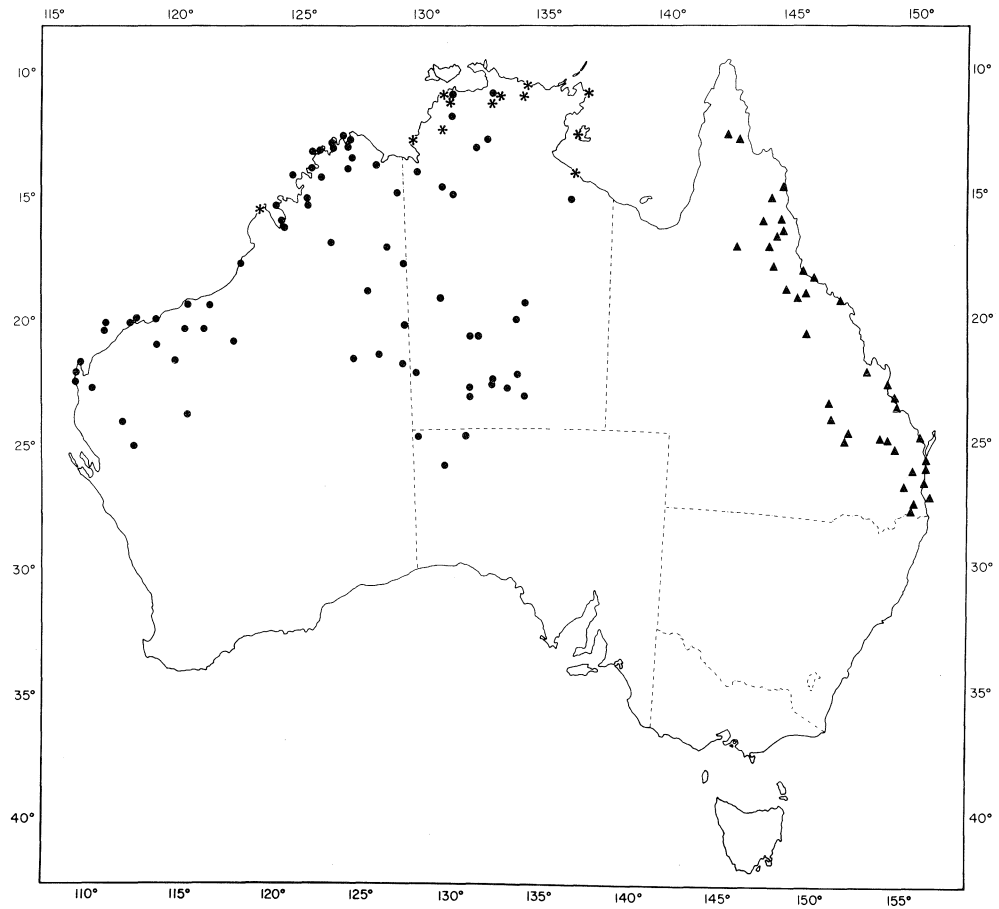


Fig. 9. Map showing the known distribution of *Morethia taeniopleura* (black triangles), *M. ruficauda* (black dots) and *M. storri* (asterisks).

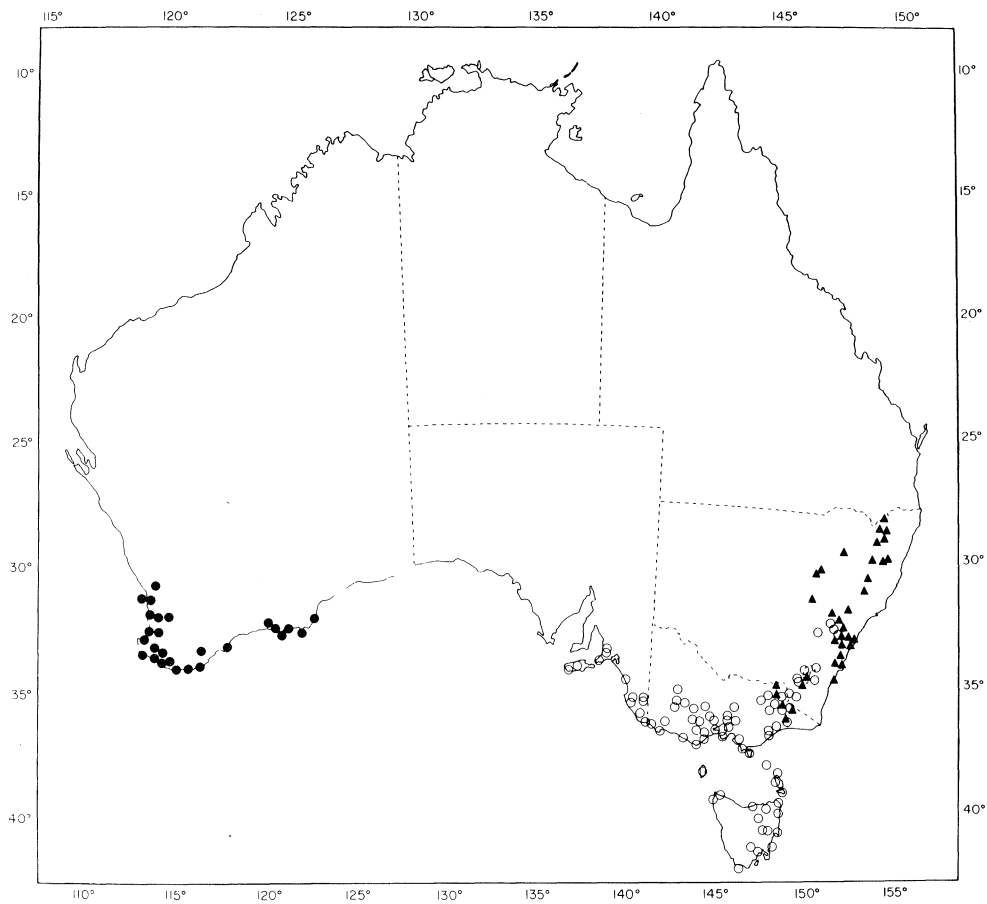


Fig. 10. The distribution of the three forms of the *trilineatum* species group of *Leiopisma*: *platynotum* (black triangles) and the eastern (open circles) and western (black dots) forms of *trilineatum*.

The populations mapped in central New South Wales are interesting in that they are generally distinguishable from all other populations in being uniformly coloured above instead of ocellate. Rawlinson (1976) has mapped these populations as being continuous with the rest of the species' distribution, but they may, in fact, be isolated. The populations inhabit an eastern outlier of the mallee-*Triodia* association (Dr H. G. Cogger, pers. comm.) which is more extensive to the southwest and which may have retreated from central New South Wales after the last dry period of the last glacial some 25000-13000 years B.P. (Bowler 1976). This same habitat also supports a relict population of *Amphibolurus fordi* (Cogger 1974).

Ruficauda. This species is widespread over the northwestern quarter of Australia (Fig. 9), and its distribution covers some of the most arid parts of the continent. It has been found in a variety of habitats ranging from woodland to open grassy flats. It occurs on both rocky and hard-packed sand substrates but appears to avoid loose sand dunes (Mr M. Gillam pers. comm. and pers. obs. for subspecies *ruficauda*, but note that Smith [1976] records the subspecies *exquisita* from "all habitats but mostly siliceous foredunes and consolidated dunes" on Barrow Island).

In certain areas along the periphery of its distribution, *ruficauda* is broadly sympatric with three other species of *Morethia*: *boulengeri* in the southern part of the Northern Territory and perhaps the northwest corner of South Australia, *lineocellata* in the northwest of Western Australia, and *storri* in the northern part of the Northern Territory. In none of these areas, however, is anything known about the habitat differences between the species.

It may be noted here that Pianka (1972) has suggested that this species (as *taeniopleura* in his paper) appeared to have isolates in the Central Ranges. Present information, however, indicates that the distribution of *ruficauda* in the Central Ranges is part of a continuous distribution to the north and west (Fig. 9).

Storri. This species is known at present from two disjunct areas in northern Australia: the near coastal regions of the northern part of the Northern Territory and Dampier Land in Western Australia (Fig. 9). This disjunction is almost certainly a collecting artifact, however, and additional field work will probably fill the gap. *Storri* appears to occur in a variety of habitats ranging from open woodland to open grassland (see species description above). It is broadly sympatric only with *ruficauda*, but the nature of the niche differences between the two species is little understood.

Taeniopleura. This species occurs in far eastern Queensland between the upper part of Cape York and the lower north slopes of the Macpherson Range (Fig. 9).

The species has been collected on the following islands: Magnetic, Curtis, Bribie and North Stradbroke. It has also apparently been seen but not collected on Fraser Island (Barry and Campbell 1977). There appear to be no records for any of the Whitsunday Islands, but this may be due to lack of collecting.

Taeniopleura occurs in fairly open and at least seasonally dry habitats ranging from large artificial grass clearings and wallum to open sclerophyll forests (pers. obs. and Covacevich and Ingram 1975). It has also been found associated with a semi-evergreen vine thicket (with *Brachychiton* emergent) in the Bunya Mountains (Covacevich 1977).

The range of *taeniopleura* overlaps that of *boulengeri* in southeastern Queensland, but there seems to be no information on how the habitat requirements of the two species differ in sympatry. I personally know of only one case of the two species having been found together at the same locality. This was around the rubbish tip at the Belyando Star

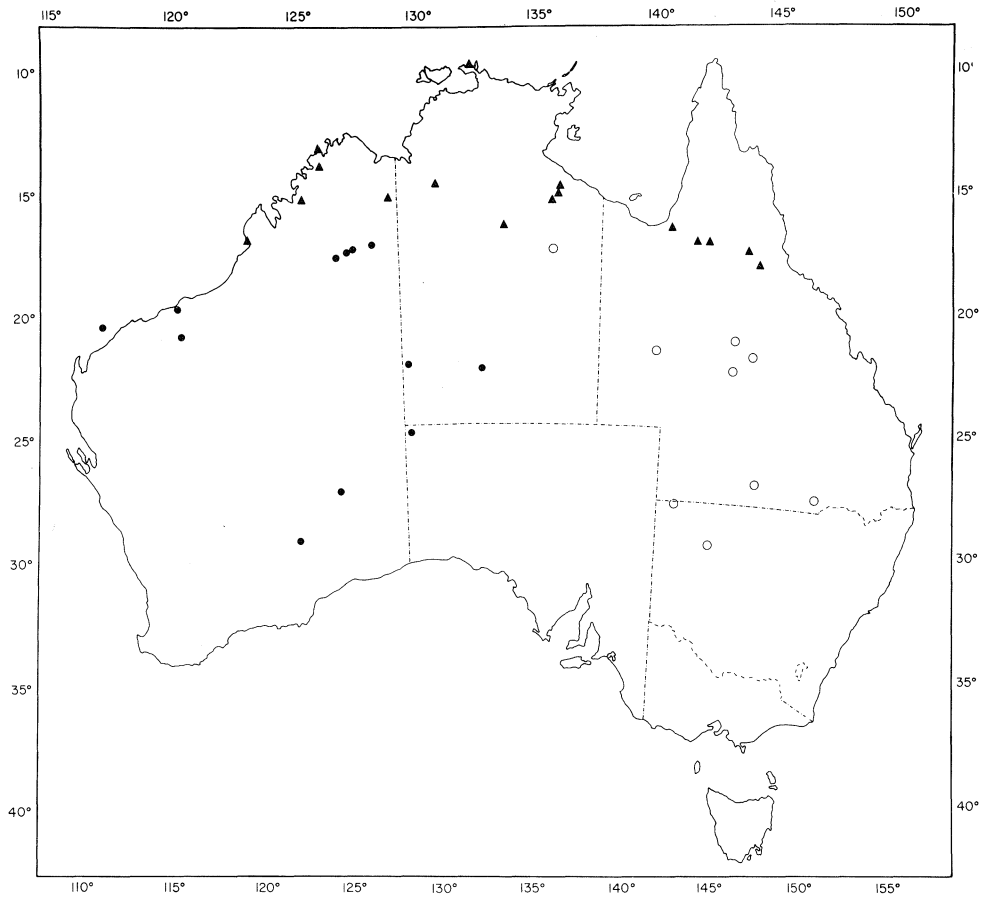


Fig. 11. The distribution of the three species of *Proablepharus*: *kinghorni* (open circles); *reginae* (black dots) and *tenuis* (black triangles).

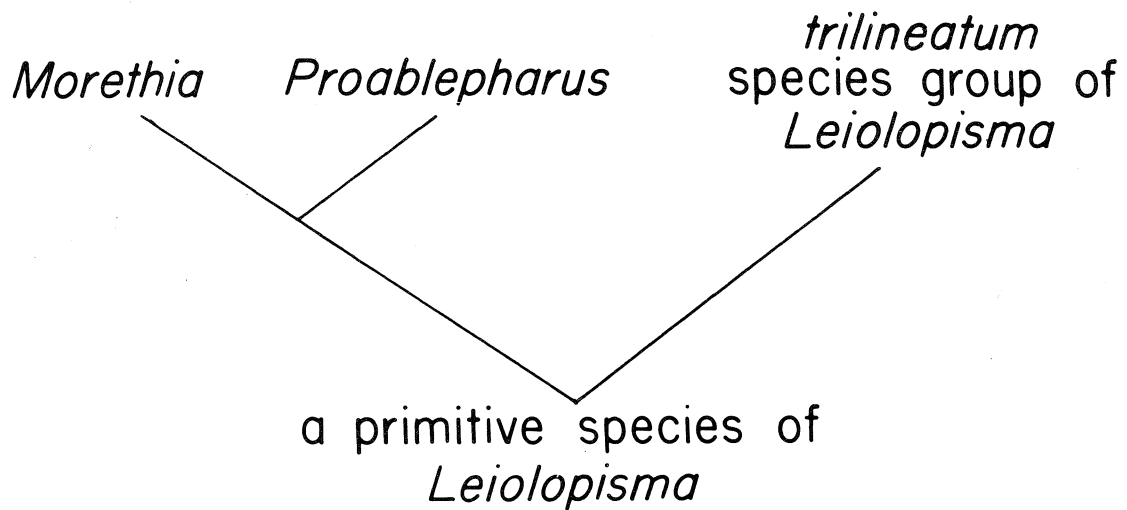


Fig. 12. A schematic representation of the phylogenetic relationship hypothesized for *Morethia*, *Proablepharus* and the *trilineatum* species group of *Leiolopisma*. See the text for the details and rationale.

Service Station on the Gregory Highway. The locality was in a grassy open forest and single specimens of each species were obtained during general collecting.

The long and relatively narrow, near coastal distribution of *taenioleura* parallels that of *lineoocellata* in Western Australia, and if very near coastal populations of *taenioleura* were chosen, the two species might provide some interesting comparisons of biogeographic trends.

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TABLE 1. A comparison of certain systematically important characters between *Morethia storri* new species and its two nearest relatives.

Character	<i>storri</i>	<i>taeniopleura</i>	<i>ruficauda</i>
Midbody scale rows			
Range	24-28	24-29	24-27
Mode	26	26	26
Mean	26.2	26.2	26.4
N	18	42	34
Paravertebral scales			
Range	54-58	55-64	54-58
Mean	56.1	59.7	56.6
S.D.	1.44	2.29	1.68
N	14	30	12
Subdigital lamellae (fourth toe)			
Range	17-21	18-22	17-23
Mean	19.4	20.2	20.0
S.D.	1.05	1.33	1.72
N	20	55	37
Supranasal fused anteriorly to nasal (+) or completely distinct (-)			
	+	-	-
Suparoculars bordered posteriorly by medially projecting supraciliaries			
	1-2-3	1-2	1-2
Supraciliaries			
	4 large, 1 small	5 large	4 large, 1 small
Width of mid-dorsal area between light dorsolateral lines (in scale rows)			
	6	6	3-5
Dorsolateral light stripe extends to snout (S) or eye (E)			
	E	E	S

Snout-vent length (mm)

Range	17-38	18-42	20-46
N	20	51	182

Length of foreleg/
snout-vent length

Range	.25-.35	.23-.29	.23-.32
N	14	11	16

Length of rear leg/
snout-vent length

Range	.36-.47	.33-.43	.33-.46
N	14	11	16

Tail length/
snout-vent length

Range	1.32-1.76	1.06-1.82	1.49-2.17
N	3	35	4

TABLE 2. Data on certain reproductive parameters in gravid *Morethia*.

Parameter	<i>adelaidensis</i>	<i>boulengeri</i>	<i>butleri</i>	<i>lineocellata</i>	<i>obscura</i>	<i>ruficauda</i>	<i>storri</i>	<i>taeniopleura</i>
SVL of gravid ♀♀ (mm)								
Range	44-58	40-54	49-57	38-57	39-55	31-42	36-38	36-44
Mean	49.0	47.5	53.3	46.1	47.4	36.2	37.0	39.2
N	33	74	11	32	52	12	2	14
Clutch size								
Range	2-6	1-6	2-5	2-5	1-5	1-3	2-3	2- 4
Mean	3.2	3.2	3.8	2.8	3.1	2.0	2.5	2.4
N	33	74	11	32	52	12	2	14
Correlation coefficient of clutch size us SVL								
	.58	.58	.30	.39	.55	.79	—	.57
	P < .001	P < .001	P > .05	P < .05	P < .001	P < .01	—	P < .05

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106

ALLEN E. GREER

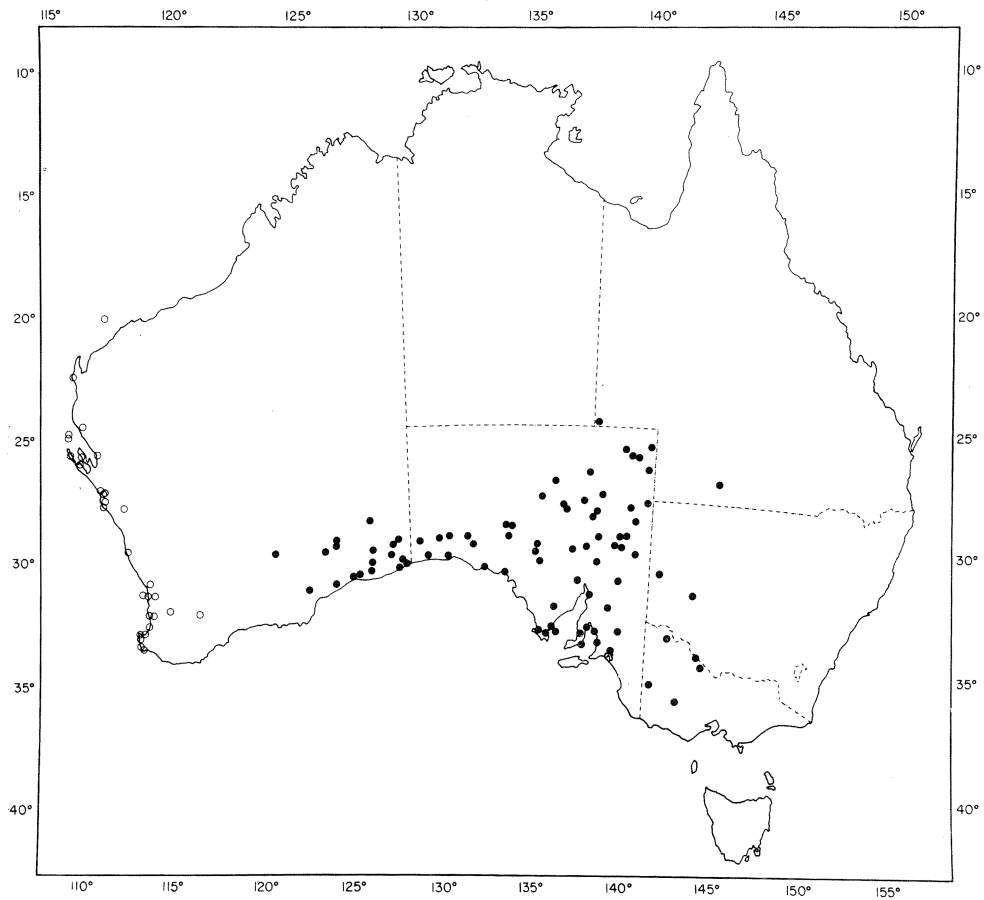


Fig. 7. Map showing the known distribution of *Morethia lineocellata* (open circles) and *M. adalaidensis* (black dots).