

A Taxonomic Revision of the *Cyclodomorphus branchialis* Species Group (Squamata: Scincidae)

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ABSTRACT. The *Cyclodomorphus branchialis* species group is defined on synapomorphies of scalation. Within this complex, five allopatric species, one with three subspecies, are recognised on morphological grounds: *C. branchialis* (Günther) of the lower west coast and hinterland, *C. maximus* (Storr) of the Kimberley, *C. melanops melanops* (Stirling & Zeitz) widespread in spinifex habitats of the arid north-west, and *C. m. elongatus* (Werner) widespread in spinifex habitats of the arid south and east of the continent, together with two new species, one from the lower west coast and the other from South Australia, and a new subspecies of *C. melanops* from chenopod habitats along the southern fringe of the Nullarbor Plain. The morphology, distribution, habitat preferences and reproduction of the seven taxa are described. All primary type specimens are illustrated. A key to the species and subspecies in the genus *Cyclodomorphus* is provided. *Cyclodomorphus branchialis*, considered on previous taxonomic opinion to be widespread in arid Australia, is restricted to a small area in Western Australia and is considered vulnerable.

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Closely allied to the large bluetongue skinks of the genus *Tiliqua* Gray, 1825 is a group of smaller species that have variously been considered as congeneric with *Tiliqua*, or placed in a separate genus, for which the names *Omolepida* Gray, 1845 or *Cyclodomorphus* Fitzinger, 1843 have been used (Shea, 1990). Two of the species of *Cyclodomorphus*, *C. casuarinae* (Duméril & Bibron, 1839) and *C. gerrardii* (Gray, 1845) are readily identifiable and confined to the moist coast and ranges of eastern Australia (see Shea [1995] for a

revision of variation in the former species, and the recognition of two new species). The remaining taxa within *Cyclodomorphus* are inhabitants of the dry interior and west coast of Australia, and have posed taxonomic problems for over a century. This latter group, differentiated from the other *Cyclodomorphus* species by having broadly contacting nasal scales, separated prefrontal scales, a distinct postnasal groove and paravertebral scales much broader than adjacent dorsal body scales, is here referred to as the *Cyclodomorphus*

branchialis species group. At least the first two characters are synapomorphies in the context of its relatives, the *Egernia* group of genera (Greer, 1979).

Boulenger (1887) recognised only one species in the *branchialis* group, *Lygosoma (Homolepida) branchiale* (Günther, 1867) from Western Australia, relegating the other described species, *Lygosoma muelleri* Peters, 1878, described from South Australia, to the synonymy of *L. casuarinae*. Stirling & Zeitz (1893) described a third taxon, *Lygosoma (Homolepida) melanops*, from northern South Australia but, following Boulenger (1887), the standard reference of that era, compared it only with *L. branchiale*. Boulenger (1898), without reference to Stirling & Zeitz (1893), described *Lygosoma gastrostigma* from north-west Western Australia.

Zeitz (1920), without explanation, referred *L. melanops* to the synonymy of *L. branchialis*, but retained *L. gastrostigma* as distinct. Sternfeld (1919, 1925) synonymised *L. gastrostigma* with *L. melanops*, and recognised that *Lygosoma muelleri* was both clearly distinct from *L. casuarinae* and *L. branchialis* and a junior homonym of *Scincus muelleri* Schlegel (1839) (then, as most skinks, in *Lygosoma*), and proposed *Lygosoma (Homolepida) petersi* as a replacement name, although basing his redescription on new material from Hermannsburg Mission, in the Northern Territory. The description by Werner (1910) of *Lygosoma branchiale* var. *elongatum* from a single specimen collected at Boorabbin, Western Australia, by Michaelsen and Hartmeyer's Hamburg expedition passed unnoticed by Sternfeld and Zeitz, and indeed by most subsequent authors, including Michaelson (1914) in a summary of the expedition's findings. Proctor (1923) described an insular species, *L. (H.) woodjonesii*, from Saint Francis Island, comparing it with *L. branchialis* and *L. gastrostigma*.

Sternfeld's and Zeitz's largely unsupported conclusions were criticised by Loveridge (1934, 1938), who resurrected *Lygosoma (Omolepida) melanops* from the synonymy of *L. branchialis* without explanation, placing *Lygosoma gastrostigma* in its synonymy, and reduced *Lygosoma petersi*, which he treated as a new species rather than a *nomen novum*, to a subspecies of *L. casuarinae*. The motivation for this latter action is unclear, but is possibly a reflection of Boulenger's (1887) earlier opinion. Smith (1937) listed only three species, *branchiale*, *gastrostigma* and *woodjonesi* [sic], when he transferred *Cyclodomorphus* (then *Lygosoma [Omolepida]*) to *Tiliqua*.

Mitchell (1950), in the first complete revision of the genus *Tiliqua* (in which he included *Cyclodomorphus*) since Boulenger (1887), reduced *L. woodjonesii* to a subspecies of *Tiliqua branchialis*, and placed both *L. melanops* and *L. gastrostigma* in the synonymy of *T. branchialis*, noting that he could find "no valid structural differences, the only variation being in coloration as is indicated by the various published descriptions... The colour variation does not appear to be correlated in any way with the other variable features, viz. the relative size of the ear opening, body proportions and distribution". However, he still retained *L. petersi* as a race of *T.*

casuarinae despite giving the type locality (incorrectly) as Hermannsburg Mission yet identifying specimens he had examined from this locality as *T. branchialis*.

Mitchell apparently subsequently changed his mind on the synonymy of *L. melanops*, for Warburg (1965) quotes a communication from Mitchell that his material listed in 1950 as *C. branchialis* should be *C. melanops*.

Glauert (1960, 1961) recorded three species from Western Australia, *Tiliqua branchialis*, which he restricted to the vicinity of the type locality, *T. melanops* from Perth through to South Australia, and *T. gastrostigma*, from the Pilbara, although noting that all were structurally almost identical and may only be subspecifically distinct. Worrell (1963) retained the same three species, together with *T. casuarinae petersi* and *T. woodjonesii*, although noting that further revision might result in the synonymy of *T. woodjonesii* and *T. c. petersi*.

Storr (1976) placed all previous names in the synonymy of *Omolepida branchialis*, and described a new species, *O. maxima*. This arrangement was accepted by Cogger (1979), although *Omolepida* was returned to the synonymy of *Tiliqua*.

Wells & Wellington (1984, 1985) recognised five species: *C. branchialis*, *C. gastrostigma* (confined to the west coast of Western Australia), *C. maxima*, *C. melanops* (confined to central Australia) and *C. woodjonesii* (confined to Nuyts Archipelago), but gave no justification for their taxonomy, which left a number of populations in nominate.

Schwaner *et al.* (1985) recorded two species, *T. branchiale* [sic] and *T. melanops* on the Nuyts Archipelago and Eyre Peninsula respectively.

Most recently, Wilson & Knowles (1988) recognised four species in the complex: *C. branchialis*, *C. maxima*, *C. melanops* and an undescribed species, providing distribution maps for each of the described taxa, while Ehmann (1992) recognised only *C. branchialis* (including "*O. b. melanops*" and other "forms"), *C. maximus* and the undescribed species.

Our work on this group indicates that, contrary to the assertions of Mitchell (1950), body proportions, coloration and ear aperture size, together with body scalation, are geographically correlated, and the recent collection of several of these geographic forms in close proximity, though never in exact sympatry, suggests specific status.

Materials and Methods

All specimens of the *C. branchialis* species group in Australian museum collections have been examined, together with all available type material and a few additional specimens in European and American collections, a total of over 1200 specimens. Collection abbreviations are Australian Museum, Sydney (AM), Australian National Wildlife Collection, Canberra (ANWC), Natural History Museum, London (formerly British Museum [Natural History]) (BMNH), Central Australian Wildlife Collection, Alice Springs (CAWC) (now lodged in Northern Territory Museum), H.F.W.

Ehmann private collection (to be lodged in SAM and WAM) (HFWE), Museum of Comparative Zoology, Harvard University, Massachusetts (MCZ), Museum of Victoria, Melbourne (MV), Naturhistorisches Museum, Vienna (NHMW), Northern Territory Museum, Darwin (NTM), Queensland Museum, Brisbane (QM), Senckenberg Museum, Frankfurt (SMF), South Australian Museum, Adelaide (SAM), Western Australian Museum, Perth (WAM), Zoologisches Museum, Berlin (ZMB) and Zoologisches Museum, Hamburg (ZMH).

Listed localities enclosed within quotation marks are property names. State names are abbreviated.

Species and subspecies definitions. The species and subspecies recognised in this revision are all geographically allopatric, and hence the biological species definition (Mayr, 1963) cannot be used. Further, the morphological characters that are used to define some species are of uncertain polarity due to variation among species in the most proximate outgroups (*Cyclodomorphus casuarinae* complex, *Cyclodomorphus gerrardii*, *Tiliqua* and *Egernia*), and hence the phylogenetic species concept (Frost & Hillis, 1990; Kluge, 1990), which defines species on the basis of synapomorphies, cannot be uniformly applied. Nonetheless, the geographic variation in morphological characters within the species-group is non-continuous, with abrupt discontinuities in the distribution of otherwise continuously varying characters, and the discontinuities in many characters are geographically concordant. We use the evolutionary species concept (Wiley, 1978) in recognising these morphological discontinuities as species boundaries.

In two cases, the geographic discontinuities in morphology are less clear-cut, either due to evidence of morphological intermediacy between two taxa in some part of the distribution, despite the maintenance of abrupt differences in other regions of geographic proximity, or to limited evidence of an abrupt but possibly continuous change over a short geographic distance between two otherwise homogeneous morphotypes. We recognise these two pairs of taxa as subspecies. In the latter case, between *C. melanops elongatus* and a newly described subspecies, synapomorphies of the temporal scalation and coloration link the two taxa. In the former case, however, between *C. m. melanops* and *C. m. elongatus*, there is as yet no evidence for monophyly of the two subspecies, and hence some workers may prefer to recognise these two taxa as species.

The diagnoses preceding each description list those characters which in combination distinguish the taxon. Further, more detailed comparisons between each taxon and those described before it are provided in comparisons with other taxa in each account.

Geographic variation. Within each of the geographically widespread taxa recognised in this study there is further geographic variation in morphology, in some instances involving characters used in diagnosing taxa. To further explore this geographic variation, we divided the overall

distribution of each taxon, based on the available samples, into smaller geographic units, which we term "populations". Available material was unevenly distributed, with large samples from some small areas, and small, scattered samples from other much larger areas. Consequently, some grouping of samples was unavoidable (Thorpe, 1976). In delimiting populations, we initially used geographic gaps between known localities. These may reflect real geographic discontinuities or a lack of collecting effort. In an attempt to avoid the second possibility, we preferentially used distributional discontinuities that reflected changes in geography, such as topographic features (drainage systems, ranges) or changes in vegetation or substrate. Adequately sampled insular populations were generally treated as discrete populations. Some residual large areas of homogeneous or gradually changing geography, lacking any clear gaps between localities, were arbitrarily sectioned into smaller units.

Geographic variation in scalational characters was explored by one-way analysis of variance, followed by pairwise comparison of means using Gabriel's approximation to the GT-2 method at a 5% level of significance (Sokal & Rohlf, 1981).

Character definitions. Head shield nomenclature follows Taylor (1935: 71). Head shields are counted on both sides, except for palpebrals, counted only on the left side, and are numbered from rostral to caudal. Where two figures are given for a specimen, the first figure is for the left side. Temporal scale configuration falls into one of two patterns. In all *Cyclodomorphus* species, the last supralabial is divided into an upper and lower scale, the upper scale thus forming a second "lower secondary temporal" (Shea, 1990). In members of the *C. branchialis* species group, this scale may be either of a height corresponding to the height of the primitive entire last supralabial, and permitting contact between the primary and true lower secondary temporal, here termed the α -configuration, or may be of greater height, contacting the upper secondary temporal and preventing contact between the primary and true lower secondary temporal, here termed the β -configuration (compare Figs 7 and 24 respectively). The latter condition is apomorphic. In a few cases, the contact between the spurious lower secondary and upper secondary temporal is so broad that the β -configuration is not immediately obvious. However, even these cases can be identified by the upper secondary temporal overlapping four scales (vs three) along its ventral and caudal margins.

Midbody scales are counted around the body at the mid-point of the axilla-groin interval. Paravertebral scales are counted, generally on the left side, from the first scale caudal to the parietals, to the last scale cranial to the level of the cranial margin of the hindlimbs. Subcaudal scales are counted, on original tails only, from the cranialmost scale approximately equal in size to adjacent lateral caudal scales, caudal to and including the terminal caudal scale. Subdigital lamellae are counted



Fig. 1. A live *Cyclodomorphus branchialis* from Galena, WA.

bilaterally on the fourth toe from the first scale just beyond the edge of the sole, to and including the scale bordering the claw.

With individual exceptions as noted in taxon accounts, the following scalational characters of taxonomic importance in skinks were invariant in the *C. branchialis* species group: rostral projecting slightly between nasals; nasals in moderate to broad contact, widely separating rostral and frontonasal; nostril rostroventral in nasal; postnasal groove present but weak; supra- and postnasals absent; prefrontals moderately separated; frontal large, longer than wide, broadest rostrally; frontoparietals paired; parietal eye spot present, just caudal to centre of interparietal; loreals two bilaterally, subequal; supraoculars three, rostral two in contact with frontal, second largest; presuboculars two; lower eyelid scaly; primary temporal single; usually one, rarely two scales intercalated between upper secondary temporal and first pair of nuchals; first pair of chin shields in broad contact; second pair of chin shields separated medially by one scale; third pair of chin shields longitudinally divided, separated medially by three scales; body scales smooth; preanal scales subequal.

Non-cephalic measurements follow Greer (1982) and Cogger (1986). Head length is from the rostral margin of the ear to the tip of the snout; head width is across the widest point of the head, rostral to the ear, and head depth is vertically from the highest point of the parietal table. Head measurements were made with dial calipers

to the nearest 0.1 mm. All other measurements were made to the nearest 0.5 mm with a steel rule. The following measurement abbreviations are used throughout the text: SVL, snout-vent length; AGL, axilla-groin length; TL, tail length; FLL, forelimb length; HLL, hindlimb length; HL, head length; HW, head width; HD, head depth. Because of the significant allometry in all measurements, data are presented in two forms: the more traditional range of ratios, allowing comparison with previous studies, and allometric regressions, expressing the degree of allometry and allowing more detailed comparisons between sexes and taxa. Sexual dimorphism in metric characters was assessed by analysis of covariance, using the SYSTAT statistical package (Wilkinson, 1987).

In each taxon, most specimens for which date of collection was known, and which were larger than obviously immature material (less than approximately 60 mm), were sexed by gross examination of the gonads. Minimum mature size was taken as the smallest male with enlarged turgid testes or opaque vasa deferentia, and the smallest female with enlarged yolking ovarian follicles, unshelled oviducal eggs or embryos, and all sexed animals larger than the minimum mature size were assumed mature.

Growth rates are inferred in *C. celatus*, *C. m. melanops* and *C. m. elongatus* from the seasonal distribution of body sizes. This method is useful for species which show rapid growth and seasonal

reproduction (Shine, 1978), and indicated at least a clear first year cohort in the species studied here.

In summarising habitat data associated with specimens examined, we have only cited registration numbers for detailed data we have quoted. For less detailed data common to a number of records, only the sample size is given.

Subscripts give degrees of freedom for statistical tests, and the superscripts *, **, *** indicate significance at 5%, 1% and 0.1% levels respectively. T-tests and Mann-Whitney U tests are two tailed.

Systematics

Cyclodomorphus branchialis (Günther, 1867)

Figs 1–3

Hinulia branchialis Günther, 1867: 47.

Diagnosis. The smallest member of the species group (maximum known SVL 88 mm), *C. branchialis* differs from other members in the combination of a mode of 24 midbody scales, 62–70 paravertebral scales, 57–64 subcaudal scales, usually a β -configuration of the secondary temporal scales, three large, black, vertically ovoid patches on the sides of the neck between ear and axilla, and a yellow-brown to grey-brown or reddish dorsal ground colour.

Description. Postnarial groove rarely absent (11.1%, $n = 9$); parietals completely separated by interparietal; interparietal broadest rostrally, approximately $\frac{3}{4}$ length and breadth of frontal in adults, slightly larger in juveniles; transversely enlarged nuchals 0–4 on each side ($\bar{x} = 2.8$, $SD = 0.71$, $n = 32$), usually three (71.9%); supraciliaries 5–7 ($\bar{x} = 6.0$, $SD = 0.45$, $n = 36$), usually six (80.6%), first and last largest, third-last usually projecting between second and third supraocular, remainder moderate, subequal; postsuboculars 2–4 ($\bar{x} = 2.6$, $SD = 0.54$, $n = 36$), usually three (58.3%), lower values often due to loss of uppermost postsubocular through fusion with last supraciliary; upper palpebrals 7–9 ($\bar{x} = 8.1$, $SD = 0.54$, $n = 11$); lower palpebrals 7–10 ($\bar{x} = 9.1$, $SD = 1.04$, $n = 11$); secondary temporals usually in β -pattern (86.1%, $n = 36$), rarely in α -pattern (13.9%); supralabials 7–8 ($\bar{x} = 7.1$, $SD = 0.29$, $n = 34$), usually seven (91.2%), third-last below centre of eye, separating pre- and postsuboculars; infralabials 5–7 ($\bar{x} = 6.2$, $SD = 0.48$, $n = 34$), usually six (73.5%); usually first two (84.8%, $n = 33$), rarely first three, infralabials contacting postmental; ear small, approximately half height of eye, usually (94.1%, $n = 34$) with a single small rounded lobule along rostral margin.

Body scales in 22–26 ($\bar{x} = 24.1$, $SD = 1.08$, $n = 18$) longitudinal rows at midbody; scales in paravertebral rows much broader than adjacent lateral dorsal scales, 62–70 ($\bar{x} = 65.2$, $SD = 1.99$, $n = 18$); subcaudal scales

57–64 ($\bar{x} = 60.4$, $SD = 2.12$, $n = 11$); lamellae below fourth toe 9–12 ($\bar{x} = 10.8$, $SD = 0.72$, $n = 32$), each with a narrow to broad light to mid-brown callus.

SVL 51–88 mm; AGL/SVL 52.6–63.9% ($\bar{x} = 58.5\%$, $n = 17$), TL/SVL 69.6–87.3% ($\bar{x} = 81.2\%$, $n = 10$); FLL/SVL 15.0–18.5% ($\bar{x} = 17.2\%$, $n = 15$); HLL/SVL 19.2–24.6% ($\bar{x} = 21.6\%$, $n = 16$); FLL/HLL 71.4–83.3% ($\bar{x} = 79.0\%$, $n = 15$); HL/SVL 16.6–20.9% ($\bar{x} = 18.7\%$, $n = 16$); HW/HL 64.4–81.3% ($\bar{x} = 72.2\%$, $n = 16$); HD/HL 44.5–59.2% ($\bar{x} = 54.6\%$, $n = 16$).

Presacral vertebrae 37–38 ($\bar{x} = 37.2$, $SD = 0.41$, $n = 6$); postsacral vertebrae 32–35 ($\bar{x} = 33.8$, $SD = 1.26$, $n = 4$); phalangeal formula of manus and pes 2.3.4.4.3.

Allometry. Due partly to the small sample size, relationships between most of the morphometric characters did not show statistically significant departures from isometry, despite a magnitude and direction of allometry similar to that seen in taxa represented by larger samples. AGL showed significant positive allometry in relation to SVL, while FLL and HL showed significant negative allometry compared to SVL (Table 1). Strong trends were apparent towards positive allometry in TL and negative allometry in HLL with respect to SVL.

Coloration (in preservative). Yellow-brown, brown or grey-brown dorsally and laterally, body and tail usually with short broad black spots centrally on many dorsal and lateral scales caudal to axilla, tending to align transversely, especially on tail. Black spots begin at base of scale, and may or (more commonly) may not reach free margin. Nape and head dorsum immaculate or with a few dark flecks or spots. Nape laterally with three large solid or nearly solid black vertical bars, cranialmost lying dorsocaudal to ear, caudalmost above axilla and sometimes dorsally forked. Head laterally with irregular dark margins to some labial scales, particularly the subocular supralabial, and temporal scales. Dark pattern on body and tail absent or almost absent, especially dorsally, on a few of the longer-preserved specimens.

Venter yellow, immaculate on body, throat with (especially laterally) or without dark spots forming weak vermiculations, tail sometimes with a few dark spots extending lateral pattern ventrad. Palms yellow.

Coloration (in life) (Fig. 1). Two live individuals from Galena (one AM R134998) were examined. Both had orange red irides, black pupils, slightly blue-grey tinged oral mucosa and dark blue-black tongues. The throat and body and tail venter had orange macules centrally on individual scales, while the non-black spotted lateral and dorsal body and tail scales had an orange flush. In other respects, the coloration was similar to preserved material.

Distribution. Lower west coast and hinterland of WA, from the Murchison River at Galena in the north, inland to 56 km south-east of Yalgoo, and south to the Irwin River (Fig. 4).

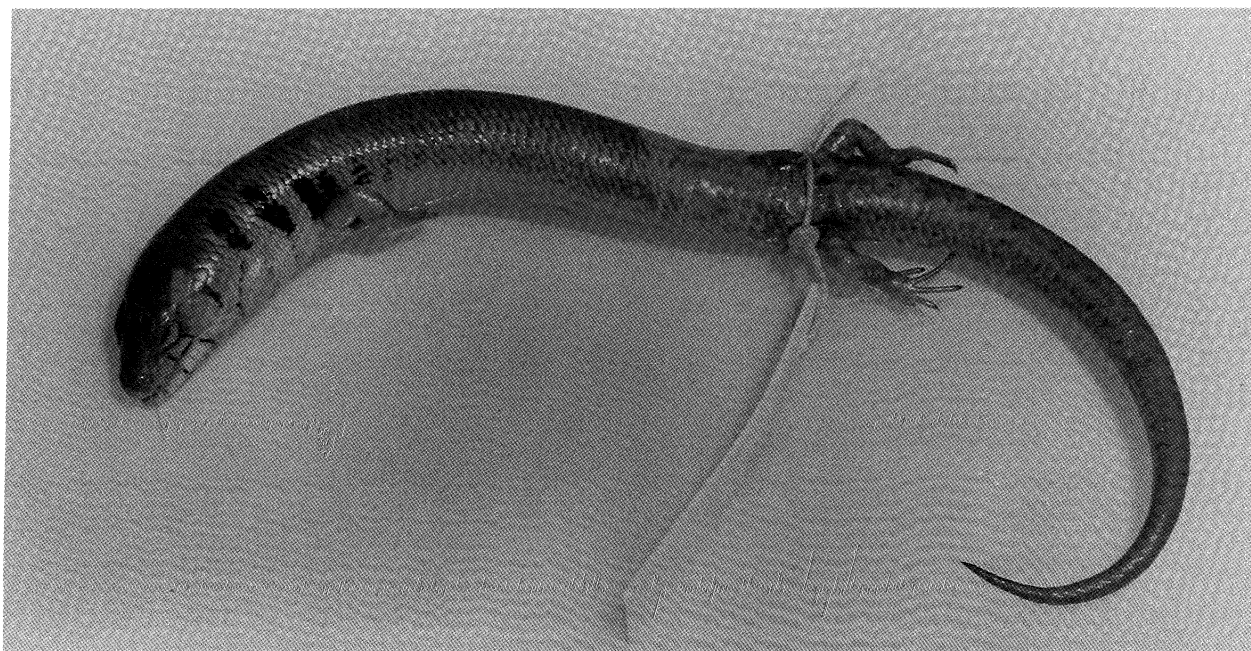


Fig. 2. Lectotype of *Hinulia branchialis* Günther (BMNH 1946.8.19.48).

The early Coolup record (MV D4605; donated H.M. Giles 26.i.1927) is probably in error. While the specimen is typical of *C. branchialis*, the locality is 420 km south of the next nearest record, and is unsupported by more recent collections in this region, which is close to Perth. As the MV collection also includes a specimen of *Egernia napoleonis* (D4192), a species not known from north of the Jurien Bay region, of similar age with locality Champion Bay [= Geraldton], it is assumed that some error in data recording has occurred.

The locality Swan River associated with the NHMW specimens, received in 1870 from the entomologist Boucard, probably represents a shipping point rather than accurate collection data.

Type material. *Hinulia branchialis* was described by Günther (1867) from three specimens from Champion Bay, "north-west coast of Australia". The latter is presumed to be a *lapsus* for "Western Australia", as given earlier in Günther's paper (p. 45). The city of Geraldton is now situated on the shores of Champion Bay.

Of the three syntypes (BMNH 1946.8.19.47–49), Wells & Wellington (1985) designate 1946.8.19.48 as lectotype. We have examined all three types, and all are typical of the taxon described here. The lectotype (Figs 2,3) has the following combination of characters: supraciliaries six, postsuboculars two (uppermost of usual three fused with last supraciliary), nuchals 3/2, supralabials seven, infralabials six, upper palpebrals eight, lower palpebrals nine, α -configuration of secondary temporals, midbody scales 22, paravertebral scales 64, subcaudal scales 64, subdigital lamellae 11, SVL 65 mm, AGL 38.5 mm, TL 55 mm, FLL 12 mm, HLL 15 mm, HL 11.5 mm, HW 8.6 mm, HD 6.4 mm.

Habitat. Little is known of the habitat preferences of this taxon. The two Galena specimens (AM R134998, WAM R71052) were taken under tin in *Acacia* scrub on hard red clay soils and "under rock in wash area, below flood level" respectively, while the specimen from near Mingenew (WAM R48638) was found under laterite boulders on top of a limestone ridge in *Acacia* scrub. Two specimens from Galena held in captivity spent most of the daylight hours buried below the surface in gravelly sand and leaf litter.

Predation. The easternmost specimen (WAM R89448) was taken, together with another tail of the same species, from the gut of the snake *Pseudechis butleri* (WAM R25815).

Reproduction. MCZ 33249 (SVL = 73 mm) collected 20.ix.1931, is a mature male with grossly enlarged turgid testes. Most of the other specimens examined either lack collection dates, or are in poor condition or obviously immature and were not dissected.

Conservation status. Despite occurring close to relatively large population centres, very few specimens of this taxon have been collected in recent years. Of the 18 known specimens, 14 were collected prior to 1940, while only four have been collected since 1960. Much of the known range lies in the northern part of the Western Australian wheatbelt, where the natural habitat has been badly degraded by clearing for agriculture and by grazing, and it is probable that this taxon is declining. None of the known localities lie in or close to the few nature reserves in this area.

Cogger *et al.* (1993) used a quantified objective ranking system to categorise the conservation status of

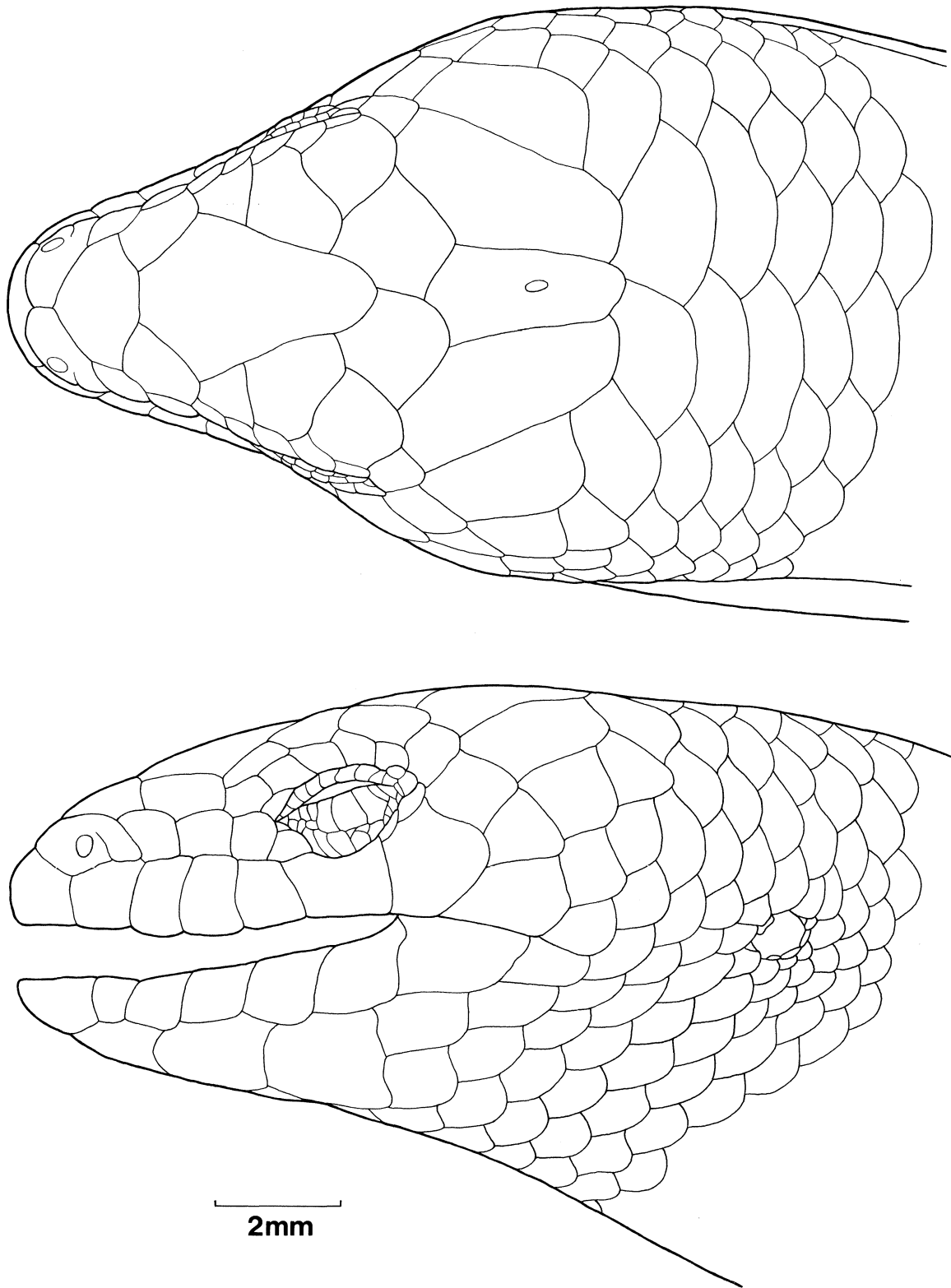


Fig. 3. Head shields of lectotype of *Hinulia branchialis*.

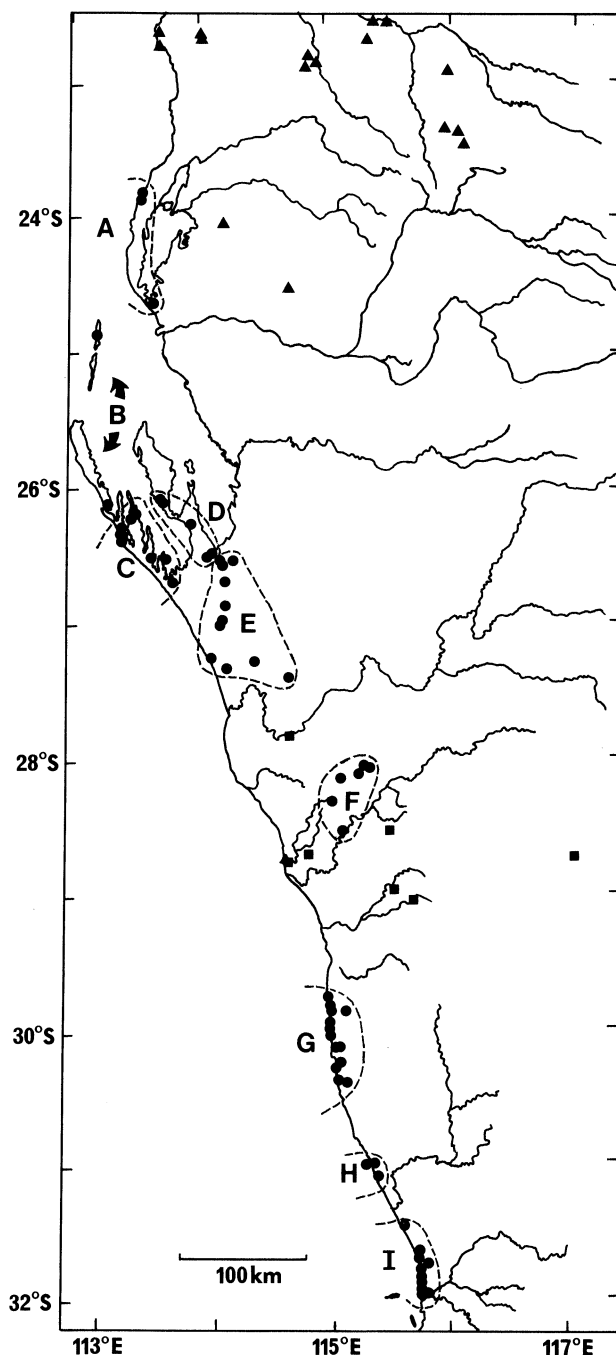


Fig. 4. Distribution of *Cyclodomorphus branchialis* (squares) and *C. celatus* (dots) along lower west coast of Western Australia. Nearest records of *C. m. melanops* are indicated by triangles. Dashed lines and letters indicate populations of *C. celatus* used in describing geographic variation, as follows: A, Gnaraloo; B, Dirk Hartog Island; C, Edel Land; D, Peron Peninsula; E, Zuytdorp; F, Yuna; G, Jurien; H, Lancelin; I, Perth.

Australian reptiles. Using their system, we determine the following score for *C. branchialis*: Biological Variables: 1b, 2b, 3c, 4c, 5d, 6Ab, 6Bc, 7Ab, 7Bb, 7Cc, score 32; Action Variables: 1b, 2a, 3a, 4b, score 30; Supplemental

Variables: 1c, 2b, 3b, 4a, 5d, score 17. Using the criteria adopted by Cogger *et al.* (1993), this species should be considered VULNERABLE.

Specimens examined (all localities are in Western Australia): AM R134998, WAM R71052, Galena; BMNH 1946.8.19.47–49, Champion Bay (LECTOTYPE and PARALECTOTYPES); 69.5.25.2–3, WA; MCZ 33247, Nannekine; 33248–49, Mullewa; MV D4605, Coolup (in error); NHMW 10137a–b, Swan River (in error); WAM R1724–25, R1727, Newmarracarra; R48638, 36 km north-north-east Mingenew; R89448, 56 km south-east Yalgoo.

Cyclodomorphus celatus n.sp.

Figs 5–7

Type material. HOLOTYPE: WAM R93111, Ledge Point, WA, collected by M. Peterson, G. Shea and B. Coulson on 26.v.1985. PARATYPES: all other specimens listed below as examined.

Diagnosis. *Cyclodomorphus celatus* differs from all other members of the *C. branchialis* species group in the combination of a mode of 22 midbody scales, 61–77 paravertebral scales, 61–74 subcaudal scales, interparietal scale $\frac{3}{4}$ length and breadth of frontal, a small, usually vertically slit-like ear aperture, pale grey to mid grey-brown dorsal ground with black streaks centrally on most dorsal body scales, and three or more series of black streaks arranged in vertical bars on the sides of the neck, but not fused into solid black patches.

Description. Parietals completely separated by interparietal (94.6%, $n = 205$), or in point to broad contact caudally (5.4%); interparietal broadest rostrally, approximately $\frac{3}{4}$ length and breadth of frontal in adults, slightly larger in juveniles; transversely enlarged nuchals 0–5 on each side ($\bar{x} = 3.1$, $SD = 0.66$, $n = 418$), usually three (68.4%); loreals rarely three unilaterally (1.4%, $n = 210$), one unilaterally (2.9%), or one bilaterally (1.4%); supraoculars rarely two unilaterally (1.5%, $n = 205$), or bilaterally (0.5%), or four bilaterally (0.5%), reduction to two due to fusion of first supraocular and first supraciliary ($n = 1$), first and second supraocular ($n = 2$) or second and third supraocular ($n = 1$), increase to four due to division of third supraocular; supraciliaries 3–7 ($\bar{x} = 6.0$, $SD = 0.38$, $n = 415$), usually six (91.6%), first and last largest, third-last usually projecting between second and third supraocular, remainder moderate, subequal; presuboculars rarely three unilaterally (0.5%, $n = 210$), or one unilaterally (1.0%) or bilaterally (1.4%); postsuboculars 2–4 ($\bar{x} = 3.2$, $SD = 0.43$, $n = 416$), usually three (78.4%); upper palpebrals 7–10 ($\bar{x} = 8.5$, $SD = 0.70$, $n = 191$); lower palpebrals 7–12 ($\bar{x} = 9.1$, $SD = 0.82$, $n = 191$); secondary temporals usually in α -pattern (93.5%, $n = 418$), rarely in β -pattern (6.5%); supralabials 6–8 ($\bar{x} = 7.0$, $SD = 0.28$, $n = 442$), usually seven (92.3%), usually third-last (99.3%) below



Fig. 5. A live *Cyclodomorphus celatus* from Ledge Point, WA (photo: M. Peterson).

centre of eye, separating pre- and postsuboculars, rarely second last, when last two fused; infralabials 5–8 ($\bar{x}$ = 6.0, SD = 0.35, n = 418), usually six (88.3%); usually first two (96.0%, n = 420), rarely first three, infralabials contacting postmental; ear small, approximately half height of eye, very narrow, usually covered rostrally by 1–2 overlapping scales, which may overlay 1–2 small acute lobules, and often with a shallow groove behind.

Body scales in 20–24 ($\bar{x}$ = 21.8, SD = 0.85, n = 222), usually 22 (73.4%) or fewer (19.4%), longitudinal rows at midbody; scales in paravertebral rows much broader than adjacent lateral dorsal scales, 61–77 ($\bar{x}$ = 69.1, SD = 2.69, n = 210); subcaudal scales 61–74 ($\bar{x}$ = 66.4, SD = 2.62, n = 91); lamellae below fourth toe 10–15 ($\bar{x}$ = 11.9, SD = 1.02, n = 429), each with a narrow to broad light to mid-brown callus.

SVL 38–121 mm; AGL/SVL 60.8–77.3% ($\bar{x}$ = 68.3%, n = 210), TL/SVL 69.2–109.3% ($\bar{x}$ = 90.1%, n = 87); FLL/SVL 10.7–21.2% ($\bar{x}$ = 14.8%, n = 209), HLL/SVL 14.0–24.7% ($\bar{x}$ = 19.8%, n = 207); FLL/HLL 66.7–90.0% ($\bar{x}$ = 75.0%, n = 207); HL/SVL 13.1–22.6% ($\bar{x}$ = 15.9%, n = 210); HW/HL 60.8–77.3% ($\bar{x}$ = 68.3%, n = 210); HD/HL 45.4–65.4% ($\bar{x}$ = 55.7%, n = 210).

Presacral vertebrae 40–42 ($\bar{x}$ = 40.6, SD = 0.63, n = 29); postsacral vertebrae 36–41 ($\bar{x}$ = 37.9, SD = 1.19, n = 13); phalangeal formula of manus and pes 2.3.4.4.3.

Allometry. With respect to SVL, both AGL and TL showed positive allometry, while limb lengths and HL

showed negative allometry. With respect to HL, HD showed significant positive allometry, while HW was nearly isometric (Table 2).

Coloration (in preservative). Pale grey-white or white to mid grey-brown dorsally and laterally, body and tail usually with longitudinal black streaks (often cream-edged on darker specimens) centrally on most dorsal and dorsolateral body scales caudal to axilla, often forming irregular black stripes on tail. Black streaks extend length of scale, and may be single or paired. Nape with similar but weaker and sparser dark streaks, arranged on side of neck to form 3–4 weak vertical bars, usually one rostral to ear, 2–3 between ear and axilla. Head dorsum with or without black spotting, especially along margins of head shields. Head laterally with irregular dark margins to shields, particularly subocular supralabial.

Venter cream, with or without dark spots on chin and throat, forming weak vermiculations, and with or without fine dark flecks on body and tail. Palms cream with greyish to light brown calli.

Juveniles often with dorsal and ventral ground more yellow-brown or red-brown, reduced dark streaks, dark grey head and white centres to dorsal and lateral scales. Dorsal ground extends ventrolaterally in bars on side of neck, equivalent to dark bars of adults.

Coloration (in life) (Fig. 5). Two small individuals (AM R88482–83, SVL 62–65 mm) had pale straw yellow

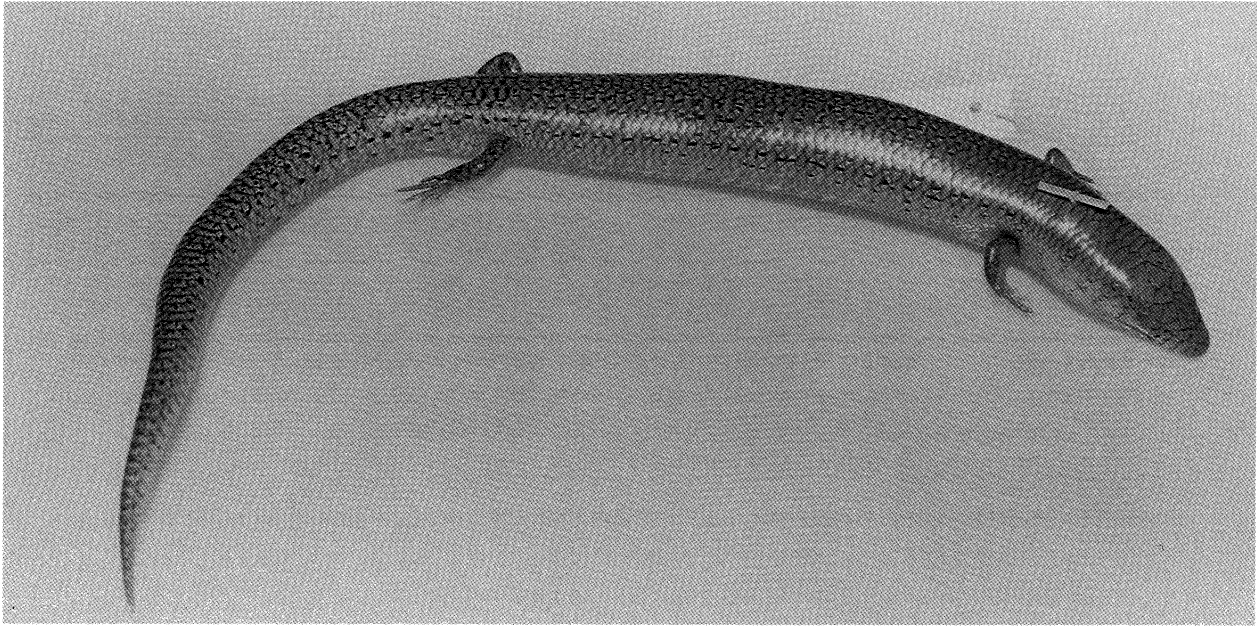


Fig. 6. Holotype of *Cyclodomorphus celatus* (WAM R93111).

venters, while a larger individual from the same locality showed little or no trace of such coloration. A fourth individual from a nearby location had venter and cranial flanks pale peach. The iris of the first three specimens was noted as pale coppery yellow, while that of the fourth was noted as coppery red. The iris in AM R102669–75 was described as a rich dark copper colour (A.E. Greer, pers. comm.).

The iris in five other specimens we examined was coppery-red.

Details of holotype. The holotype (Figs 6,7) has the following character states: supraciliaries 6/5; postsuboculars three; nuchals 4/3; supralabials seven; infralabials six; upper palpebrals eight; lower palpebrals nine; α -configuration of secondary temporals; midbody scales 22; paravertebral scales 69; subcaudal scales 64; subdigital lamellae 13; SVL 93 mm, AGL 59 mm; TL 88 mm; FLL 14 mm; HLL 18.5 mm; HL 14.8 mm; HW 9.4 mm; HD 5.4 mm.

Sexual dimorphism. Mature males were slightly smaller (82–115 mm, $\bar{x}$ = 96.4 mm, SD = 7.88, n = 56) than mature females (SVL 84–121 mm, $\bar{x}$ = 100.3 mm, SD = 8.19, n = 44; Mann-Whitney U test, z = 2.36*). In general, males had longer tails, limbs and heads, but shorter bodies than females (Table 3), although head shape was not sexually dimorphic. While some of this variation was probably due to the effect of the shorter body of males on SVL, used as the measure of overall size in all comparisons, it was not solely an artifact of this effect. For example, HLL in males was much greater than in females, even at maximum size (42.9% [n = 63] of males had HLL ≥ 20 mm, and up to 23 mm, while only one of 50 females had HLL even reaching 20 mm).

Overall, males additionally had slightly more

numerous subdigital lamellae below the fourth toe (10–14, $\bar{x}$ = 12.1, SD = 0.96, n = 118 vs 10–15, $\bar{x}$ = 11.7, SD = 1.03, n = 93, t_{210} = 2.88**) than females, although the difference was not significant within the populations examined.

No significant differences were detected between males and females in mean number of midbody scales, paravertebral scales, subcaudal scales, supralabials, infralabials, postsuboculars, supraciliaries, nuchals, upper palpebrals or lower palpebrals.

Distribution. Coastally and near-coastally along the lower west coast of WA, from “Gnaraloo” south to the north bank of the Swan River, including Bernier, Dirk Hartog, Baudin and Lancelin Islands, and inland as far as the Yuna district (Fig. 4). There is only a single unconfirmed record (WAM R31545, presumably near Geraldton, collected by a local resident) from the coastal strip and hinterland between “Gie Gie” Outcamp, north of the Murchison River, and Beagle Point, and it is possible that there is some geographic disjunction in this area between the northern and southern parts of the range. The population in the Yuna district is probably isolated from the coastal populations, as is the Gnaraloo population with respect to the Shark Bay mainland populations, with unsuitable hard soils in much of the intervening area in both cases.

Records from Albany (SAM R26128–30) are almost certainly in error. Albany is 440 km south-east of the nearest records, and on the southern rather than the western coast.

Storr, Smith & Johnstone (1981) illustrate an individual of *C. celatus* from Dorre Island. We have been unable to locate any specimen from this locality in the WAM collection to verify this record.

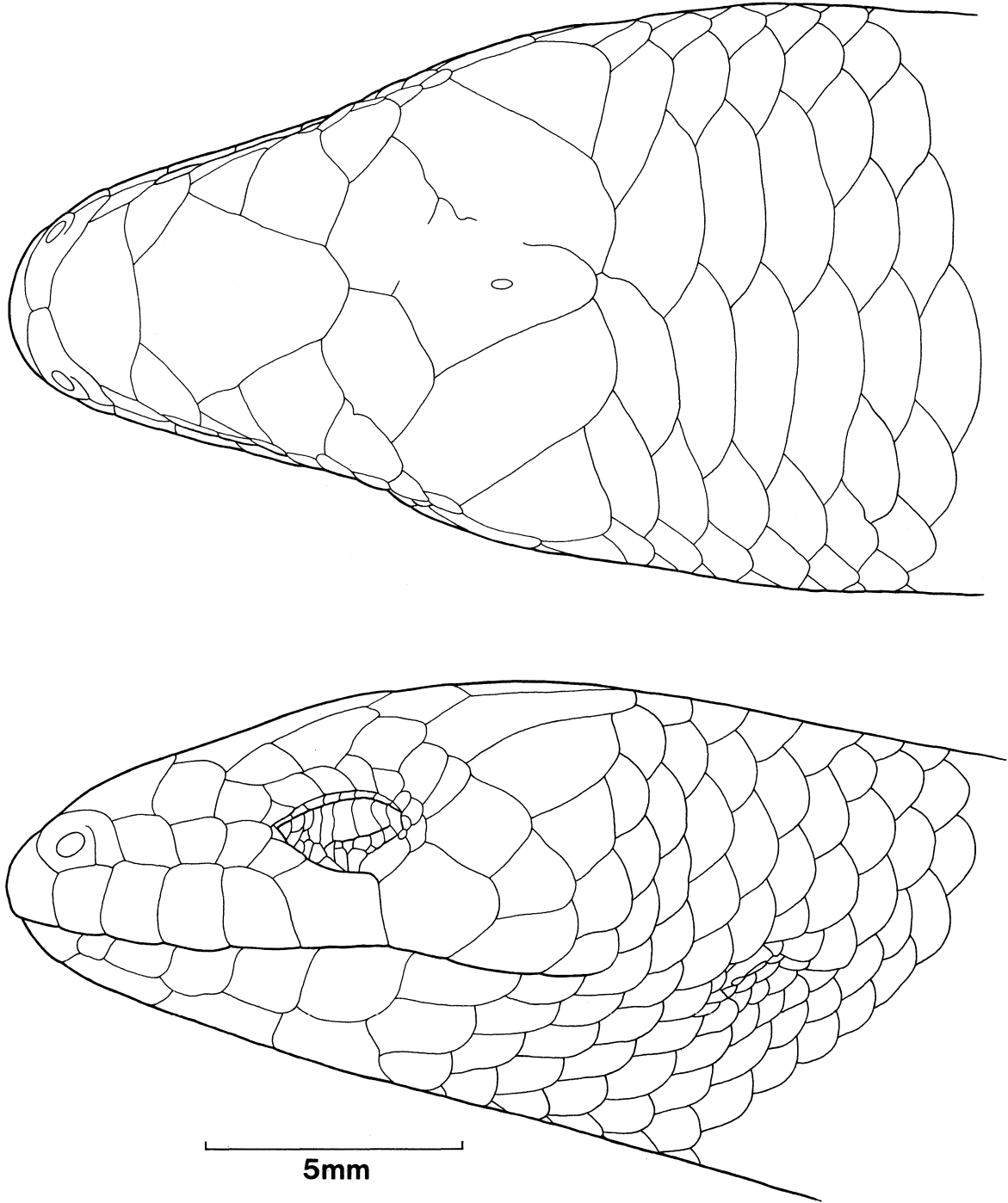


Fig. 7. Head shields of holotype of *Cyclodomorphus celatus*.

Geographic variation. For the purposes of describing geographic variation, the overall distribution of *C. celatus* was divided into nine subunits, named, from north to south, Gnarlaloo, Dirk Hartog Island, Edel Land, Peron Peninsula, Zuytdorp, Yuna, Jurien, Lancelin and Perth (Fig. 4). Samples from Bernier Island ($n = 1$), Baudin Island ($n = 1$) and Lancelin Island ($n = 11$) were included in the Dirk Hartog Island, Edel Land and

Lancelin populations, respectively. Analysis of variance did not reveal significant variation in mean number of supraciliaries, nuchals or upper palpebrals. Statistically significant variation in other scalational characters was relatively minor, and showed no consistent pattern.

Paravertebral scales. ANOVA: $F_{8,198} = 3.548^{**}$. Population means ranged from 66.4 (Gnarlaloo) to 70.6 (Peron Peninsula), with only the Gnarlaloo value below

68.6, and showing significant differences with other populations (Peron Peninsula, Yuna, Lancelin, all with means above 70.3).

Midbody scales. ANOVA: $F_{8,210} = 3.574^{***}$. Means ranged from 21.4 (Jurien) to 22.1 (Peron Peninsula, Lancelin, Perth). Only Jurien had a significantly different mean to other populations (Lancelin, Yuna, Perth), although the mode in each case was 22. Only in the two southern populations were counts of 24 seen more than once.

Subcaudal scales. ANOVA: $F_{8,80} = 8.692^{***}$. Means ranged from 63.3 (Perth) to 69.8 (Peron Peninsula), with only the latter population, Zuytdorp ($\bar{x} = 68.6$) and Edel Land ($\bar{x} = 67.9$), all northern mainland populations, having means above 66.5. Significant differences were detected between these three populations and several populations with low means (all were different to Perth, Lancelin and Dirk Hartog ($\bar{x} = 64.3$ for latter two), Peron Peninsula also different to Jurien ($\bar{x} = 66.1$) and Yuna ($\bar{x} = 66.2$)).

Subdigital lamellae. ANOVA: $F_{8,412} = 7.065^{***}$. Means ranged from 11.4 (Perth) to 12.7 (Lancelin), with only the former less than 11.6 and only the latter greater than 12.1. Only these two extreme values showed significant differences to other populations, with the Lancelin mean significantly greater than all other means, and the Perth mean significantly lower than Lancelin, Edel Land ($\bar{x} = 12.1$) and Jurien ($\bar{x} = 12.0$).

Supralabials. ANOVA: $F_{8,429} = 4.360^{***}$. Means ranged from 6.9 (Lancelin) to 7.2 (Gnaraloo), with significant differences only between these two extremes, and between Gnaraloo and Jurien ($\bar{x} = 7.0$).

Infralabials. ANOVA: $F_{8,405} = 2.581^{**}$. Means ranged from 5.8 (Lancelin) to 6.2 (Zuytdorp), with significant differences only between these two extremes, and Lancelin and Yuna ($\bar{x} = 6.1$).

Postsuboculars. ANOVA: $F_{8,403} = 8.640^{***}$. Means ranged from 3.0 (Edel Land) to 3.8 (Gnaraloo), with only the latter population and Peron Peninsula ($\bar{x} = 3.6$) having means above 3.4, and modes of four. These two populations had means significantly greater than Edel Land, Zuytdorp, Yuna, and all populations further south (all with $\bar{x}$ in the range 3.0–3.1).

Lower palpebrals. ANOVA: $F_{8,180} = 2.203^*$. Means ranged from 8.8 (Edel Land) to 9.6 (Perth). The only significant difference was between these two extreme values.

Coloration. There was marked geographic variation in coloration, with an apparent correlation with substrate colour, animals from darker substrates (red to brown sands) being more grey-brown dorsally, while animals from white sands had a paler dorsum (see also habitat account).

Specimens from "Gnaraloo", Dirk Hartog Island, and some Edel Land material had a darker dorsal ground and broader cream-edged dark streaks, giving a darker and very mottled appearance. Dirk Hartog Island juveniles had similar coloration to adults. Peron Peninsula material (both adults and juveniles) had a more grey-brown dorsum and weaker dark streaks. Adults from Edel Land

and the Zuytdorp coastline had little or no flecking on the head dorsum, grey-brown body dorsum and vertical bars on the side of the neck usually strongly developed, but occasionally absent. Edel Land juveniles (fig. 4, pl. 19 in Storr, Smith & Johnstone, 1981) were mid red-brown above with a prominent white spot caudally and fine black peppering on the caudal half of each dorsal body scale. Head and face were dark grey, unmarked, lips cream with dark margins to labial scales. The venter was cream-yellow with white centres to many scales.

Material from the vicinity of Yuna was grey to brown dorsally, usually with very reduced dark streaking on body dorsum, and head, nape and throat unmarked. The dark flecks were slightly more prominent laterally. Juveniles of this population resembled *C. melanops* juveniles, being mid-brown above, with no dark flecks, but a white spot on each body scale. They differed, however, in their dark grey heads and bars of dorsal ground laterally on neck.

Southern populations (Jurien and Lancelin) were very pale, with white to grey-white dorsal ground, but narrow black dorsal and lateral streaks still prominent, while Perth adults were light grey above with very weak dark streaks. Juveniles were yellowish to red-brown above with darker grey-brown head, white spots on body and tail scales, vertical bars on sides of neck weak, and usually with dark streaks dorsally and laterally.

Comparison with other taxa. *Cyclodomorphus celatus* is geographically very close to *C. branchialis*, almost surrounding it. However, the two taxa remain allopatric. Although there are records of both from the Geraldton/Champion Bay area, it is likely that these records are imprecise. The Champion Bay records of *C. branchialis* (the type series) date from the 1860's, the specimens being presented to the BMNH collection by the entomologist F.H. Duboulay. Although Duboulay lived in the Champion Bay district at the time, he and his brother lived on "Minnannooka" Station, away from the coast (Musgrave, 1932), and on the harder soils characteristic of more recent localities for the taxon. The accuracy of the Geraldton record of *C. celatus* is discussed above, under Distribution. Leaving aside these records, the nearest approaches of the two taxa are 46 km, between the Murchison River at Galena and 46 km to the north, and approximately 35 km, between Mullewa and East Yuna Reserve. The specimens of each species from these localities are typical and show no signs of introgression.

Cyclodomorphus celatus may be readily differentiated from *C. branchialis* by the lack of solid dark "gill" markings on the neck (although there are vertically aligned series of dark longitudinal streaks in corresponding positions), and by having usually the α -configuration of temporals (*vs* β -), a mode of 22 midbody scales (*vs* 24), and a much longer body and tail. The more elongate body of *C. celatus* may be seen in morphometrics (AGL/SVL and TL/SVL; Tables 1,2), scalation (paravertebral scales $\bar{x} = 69.1$ *vs* 65.2; subcaudal scales $\bar{x} = 66.4$ *vs* 60.4) and osteology

(presacral vertebrae 40–42 vs 37–38; postsacral vertebrae 36–41 vs 32–35). Additionally, the ear of *C. celatus*, while small as in *C. branchialis*, has the rostral edge covered by overlapping scales, which cover any lobules along this margin. This feature is an autapomorphy of the species.

Etymology. The specific epithet is derived from the Latin verb *celare*, to conceal or hide, and alludes to the small, partially covered ear, the propensity for this species (and some other members of the species group) to shelter in loose sand, and the failure of previous authors to recognise the differentiation between this species and *C. branchialis*.

Habitat. Storr (1976) suggested that *C. celatus* (as *Omorepida branchialis*) was largely confined to coastal limestones, while *C. melanops* was a *Triodia* inhabitant, and it was partly on the presence of a *celatus*-like *Triodia*-inhabiting population from Yuna that he refrained from recognising the two as distinct. However, the many observations on microhabitat usage accumulated since then (partly summarised in the herpetofaunal survey reports of Storr & Harold, 1978, 1980, 1984 and Storr *et al.*, 1983) indicate that *C. celatus* inhabits a wide range of vegetation and soil types, and shows distinct geographic trends in microhabitat preferences.

The WAM specimens of the northernmost population (Gnaraloo) were taken in *Acacia* litter in *Acacia coriacea* shrubland on pinkish sand. Specimens from other northern populations, including Bernier Island (n = 1), Peron Peninsula (n = 7) and the southern part of Edel Land (n = 4) and adjoining Zuytdorp region (n = 4) have been taken from *Triodia* and *Plectrachne* clumps. The Dirk Hartog Island population may also inhabit hummock grasses, specimens being taken from “*Acacia ligulata* scrub, scattered *Plectrachne*, on white-pink sand” (WAM R57085–86) and “low shrubland of *Acacia*, *Diplolaena*, *Triodia* and *Thryptomene*” (WAM R60875), although other specimens for which specific data are available were taken “under tin on samphire flat” (WAM R59706) and pit-trapped in an area of open sparse ground cover. Populations inhabiting hummock grasslands may also utilise other microhabitats, AM R101805–06 being taken from under litter mats below low trees in shrubland/low scrub with a *Triodia* understory. Substrate types for such hummock grass-inhabiting populations on the mainland include light brown soil, red to yellow-red sands, and brown to red-brown loamy sandplains.

Other non-coastal northern specimens have been taken in a variety of shrub and scrub habitats, including in litter in “mallee on yellow sand” (WAM R59005) and “*Banksia* shrubland on yellowish sand” (WAM R64408), in spoil in “*Hakea* shrubland on reddish soil” (WAM R64409, R64413) and “low, moderately dense *Banksia* shrubs/heath on yellowish sand” (WAM R64338) and “under tin in open *Acacia* on reddish-brown sand” (WAM R54536–40).

In contrast, coastal populations in Edel Land and along the Zuytdorp coastline inhabit a distinctly different set of habitats and microhabitats, mainly limestone slabs and exfoliations (n = 5) and coastal grasses (especially *Spinifex longifolius*) on white sand dunes (n = 3), other specimens being taken under tin (AM R102661), “within pile of sticks” (WAM R54747–48, R54759) and from a claypan surrounded by *Acacia* on gently rolling grey sandy soil hills (AM R101975–77, R102715–16, R102728–30). One specimen (WAM R66376) was taken from a habitat combining the coastal and inland features (“burnt from *Spinifex longifolius* in shrubland on red-brown sandplain”).

The Yuna population, like other northern inland populations, usually inhabits *Triodia* and *Plectrachne* (Storr, 1976; Burbidge *et al.*, 1978; WAM R57514, AM R105626). However, Dell & Chapman (1981) record three specimens from East Yuna Reserve, “one under *Plectrachne danthonioides* ... [WAM R48271]; 1 under roadside spoil in mallee ... [WAM R48102]; 1 active in daytime in shrubland ... near top of breakaway where there were surface sandstone fragments [WAM R56995]”, suggesting that the population is not restricted to hummock grasses.

The three southern populations (Jurien, Lancelin and Perth), like the Edel Land population in the north, are largely confined to coastal and near-coastal white sand dunes and sandplains.

About Jurien, most specimens were taken under rubbish, tin, boards, etc. (n = 4) in low coastal heath on white sand dunes (n = 23), although several specimens have been taken on or at the edge of salt/samphire flats (Dell & Chapman, 1977; n = 6), two of these (WAM R49059–60) found under fallen bark below *Casuarina obesa*. WAM R72986–87 were taken in “*Acacia* scrub behind coastal dunes”, while WAM R72907–08 were dug from beneath loose soil in *Banksia* heath. One specimen (WAM R71942) was found crossing a track at 1030hrs in *Acacia/Melaleuca* heath on sandy soil. A few specimens (n = 5) were found under limestone or concrete slabs.

The Lancelin and Lancelin Island populations appear to mostly shelter beneath limestone slabs (Ford, 1963; n = 9). AM R102665–68 and R102685 were found under loosely consolidated sand slabs on white sand hillocks with scattered shrubs over grass.

Most specimens from the coast north of Perth were taken in heath on consolidated coastal dunes, although one (WAM R83075) was taken from an *Acacia* thicket on grey sand. Most were taken under rubbish (n = 5), although one (WAM R59318) was taken under a sedge clump. Sorrento specimens were taken from “under scrub on limestone” (WAM R51159) and “under dead log in *Banksia* scrub” (WAM R53710–11), while two Wanneroo specimens (WAM R78472–73) were taken in “*Banksia*, tuart woodland with occasional jarrah; limestone pinnacles”, and one (WAM R61750) from Mullaloo from “under limestone rock in garden”.

Captive specimens we have observed have readily burrowed in loose sand, and spend their inactive periods below the surface.

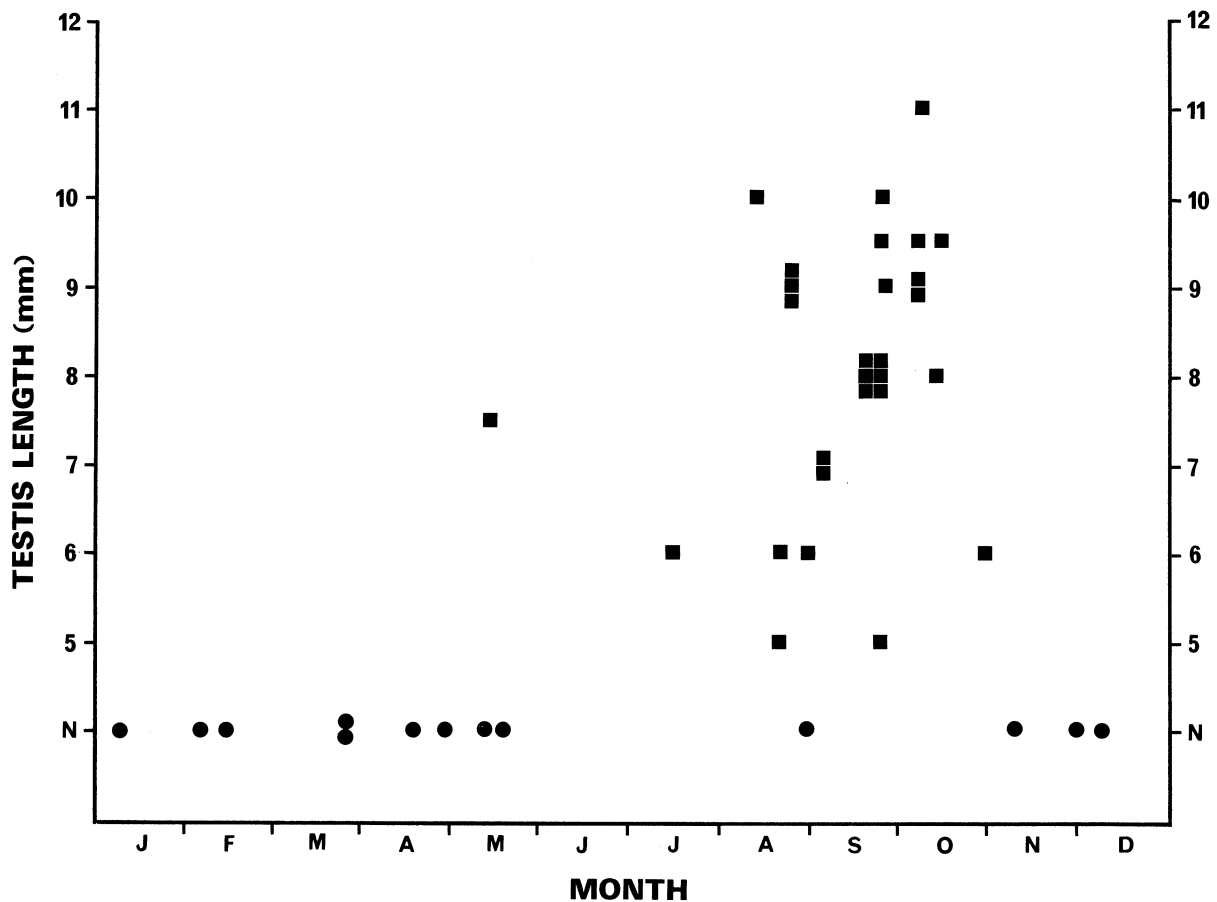


Fig. 8. Seasonal variation in length of turgid testes, and the occurrence of flaccid testes in *Cyclodomorphus celatus*. N represents small testes less than 5 mm long and assumed to be non-spermatogenic.

Reproduction. Male reproductive cycles in *C. celatus* are strongly seasonal (Fig. 8). Enlarged turgid testes ≥ 5.0 mm in length were present in most mature-sized males collected between 15 July and 31 October, while testes of mature-sized males collected outside that period were mostly small and flattened.

Female reproductive cycles are similarly seasonal (Fig. 9). None of the mature-sized females (SVL ≥ 84 mm, $n = 15$) collected between March and 9 September were gravid, although some August and September females had noticeably larger ovarian follicles than autumn females. Enlarged yolking ovarian follicles were present between 26 September and 18 November, with a single record for 2 January, while unshelled oviducal eggs or developing embryos were present between 22 October and 31 December. One litter from a wild-caught gravid female was born between 11–12 January.

We conclude from the above data that spermatogenic activity reaches a peak in October, coinciding with mating and fertilisation, and young are born in January, following approximately 3 months gestation.

Only four of 26 mature-sized females collected between 26 September and 2 January were not gravid, suggesting that breeding generally occurs annually.

Gravid females carried 3–5 ($\bar{x} = 3.8$, mode = 4 (57%), $n = 21$) enlarged yolking ovarian follicles, unshelled oviducal eggs or fully developed embryos. Litter size was not significantly related to maternal SVL ($r = 0.2304$, $P = 0.315$).

Growth rates: Seasonal distribution of body sizes in the material examined (Fig. 10) indicates a clear year 1 cohort, and suggests that a SVL of about 82–84 mm (size at maturity) is reached in the second or third year.

Sex ratio. The sex ratio of mature-sized material examined is 56 males : 44 females, a ratio not significantly different from 1:1 ($\chi^2_1 = 1.21$, n.s.). However, the sex ratio of the September sample (13 males : 2 females) is significantly different from 1:1 ($\chi^2_1 = 6.67^{**}$). Sex ratios of other monthly samples are not significantly different from 1:1, and when the September sample is removed, the overall sex ratio is 43:42, a ratio very close to 1:1. The increased proportion of males in the September sample may reflect an increase in male mobility just prior to the mating season.

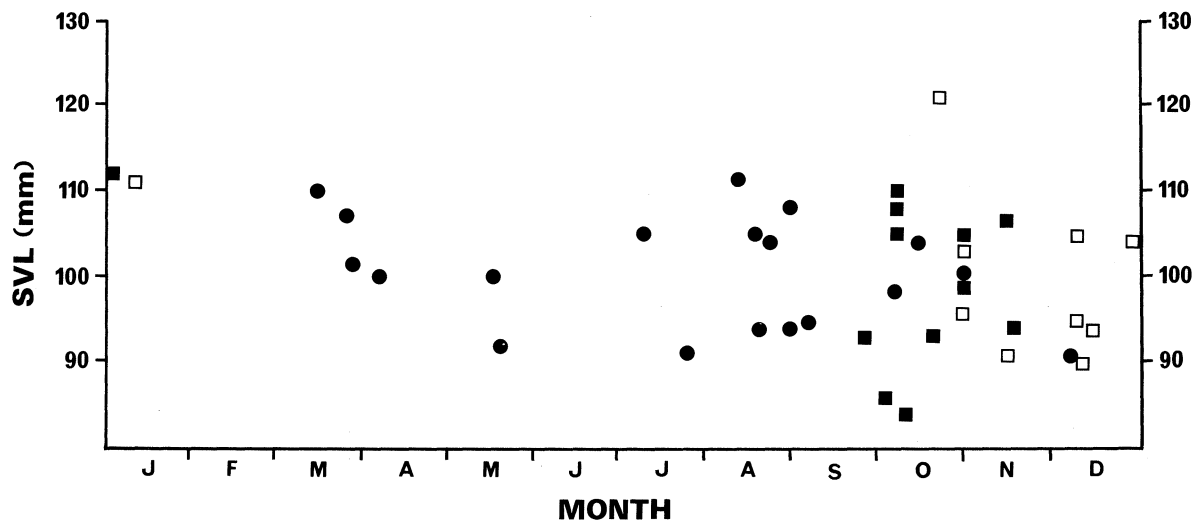


Fig. 9. Seasonal occurrence of non-vitellogenic follicles (dots), yolking ovarian follicles (squares) and oviducal embryos (open squares) in *Cyclodomorphus celatus*.

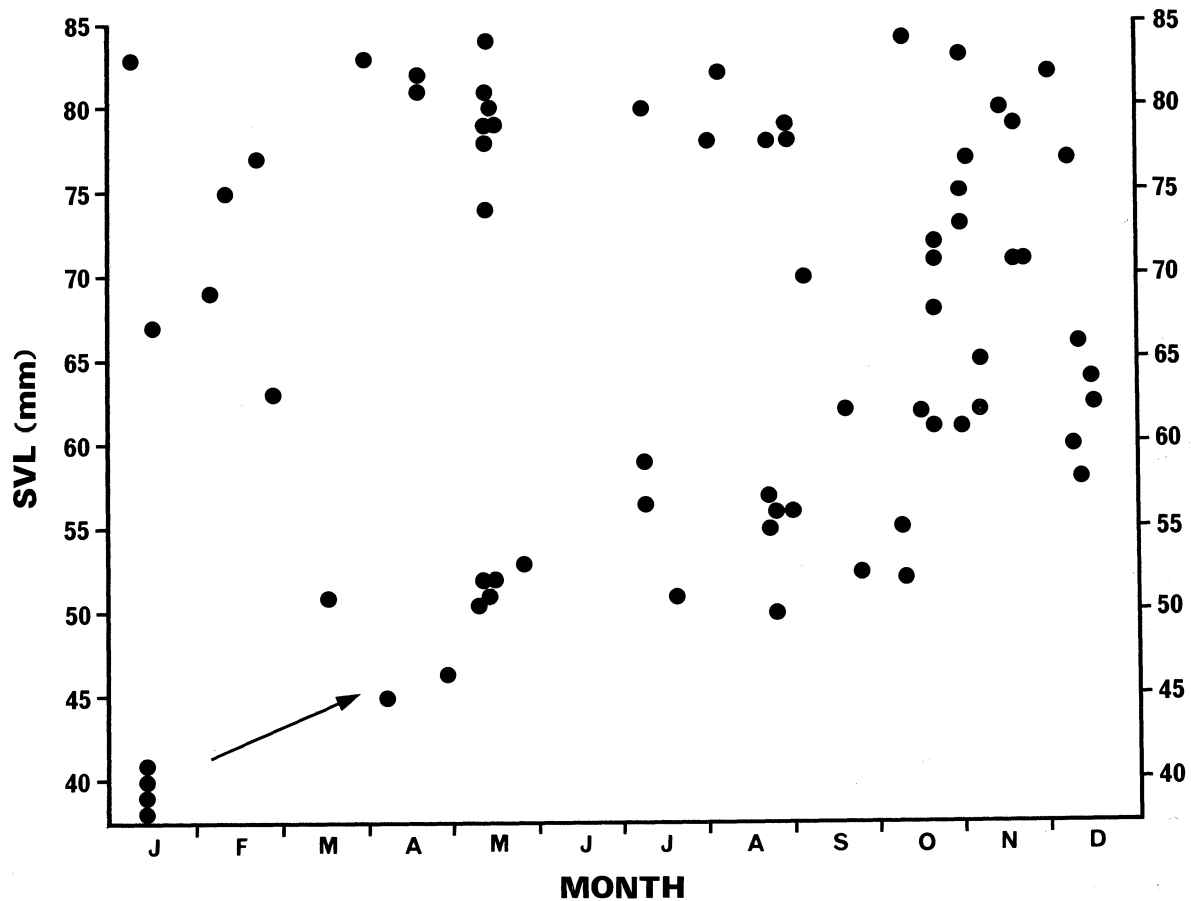


Fig. 10. Seasonal variation in SVL of immature *Cyclodomorphus celatus*. Arrow indicates inferred growth of first year cohort.

Diet. Gut contents of specimens we have examined have been largely arthropods. One specimen (WAM R47540) had eaten a skink, *Menetia surda*.

Specimens examined (all localities are in WA). **GNARALOO:** AM R134357–59, 3.0 km north “Gnaraloo” HS via Gnaraloo Bay track; WAM R76762, 1 km south “Gnaraloo”; R76888–89, 0.5 km south “Gnaraloo”; R88644, 13 km west-north-west “Boolathana”. **BERNIER ISLAND:** WAM R20497. **DIRK HARTOG ISLAND:** WAM R42371–73, R59706, R60875; R57085–86, 3 km north Cape Ransonnet; R70812–13, 4.3 km 352° Cape Ransonnet. **EDEL LAND:** AM R101975–77, R102715–16, R102728–34, “Tamala” tip; AM R102661, north-east side False Entrance; WAM R25735, Baudin Island, Freycinet Estuary; R39029, R54747–48, R54759, R91707, False Entrance Well, “Carrarang”; R54536–40, 1 km south “Tamala”; R54608–09, R54612, 10 km north-west Useless Loop; R54720, Editarra Well, “Carrarang”; R54774, 3 km south False Entrance Well, “Carrarang”; R55080, 3 km south-west False Entrance Well, “Carrarang”; R55109–12, 4 km south Useless Loop; R58793, 3 km south Sandhill Well; R64560, Zuytdorp Point; R92856, 17 km south-south-east “Nilemah” Outstation; R93921, R93923, 7 km south “Nilemah” Outstation. **PERON PENINSULA:** AM R101805–06, 5.6 km west Denham–Overlander Roadhouse road via Useless Loop road; R105735, 28.3 km north “Nanga” turnoff on Denham road; SAM R29378, 24 km south Denham; WAM R54489–90, R54610–11, 25 km south Denham; R55081, 8 km south-east “Nanga”; R64408, 48 km west Overlander Roadhouse; R81780, 26 km south-south-east Denham. **ZUYTDORP:** WAM R34040, “Gie Gie” Outcamp, 21 miles north-north-west “Murchison House”; R59005, 46 km north Murchison River on North-West Coastal Hwy; R64338, 51 km north-north-west Kalbarri; R64409, R64413, 31 km south-west “Nerren Nerren”; R66360–61, 23 km 237° “Cooloomia”; R66374–75, 17 km 240° “Cooloomia”; R66376, 15 km 302° “Cooloomia”; R88645, 20 km west-south-west “Cooloomia”; R91659, 16 km west “Coburn”; R92671, R92844, R92850, 17 km south-south-west “Hamelin”; R92494–95, 15 km south “Hamelin”. **YUNA:** AM R105626, 23.7 km north-north-east by road of Yuna; WAM R26496, 20 miles north-east Yuna; R47522–45, R56995, Yuna Flora & Fauna Reserve; R47700, Yuna; R48102, R48271, R49922–23, East Yuna Reserve, 30 km south-south-east Yuna; R57514, 40 km north-east Yuna. **JURIEN:** AM R102669–75, R105621, old Jurien tip, 0.5 km east Jurien; ANWC R3149, Leeman; WAM R13413, Stockyard Gully, Jurien Bay; R15859, mouth of Hill River; R19757–59, Beagle Point, 40 miles south Dongara; R30480, 5 miles north-east Jurien Bay; R30494–96, 2.5 miles east Jurien Bay; R31545, presumably Geraldton; R37719, R47803–06, R59658–59, R67337–38, R73104, Green Head; R46576, c. 7 km east Jurien; R48448–51, 5 km west “Padbury”; R48804, nr “Padbury”; R49059–60, R56071, R56094, 5 km east Green Head; R57596, Jurien Bay; R59656–57, 10 km north Green Head; R71942, 5 km north Coolimba; R72907–08, 16 km east Coolimba; R72974, 10 km north Coolimba; R72978–79, 15 km east Coolimba; R72986–87, 8 km south Leeman; R73109, 9 km south Leeman; R73118, Coolimba; R93147, 11 km north-north-east Cervantes. **LANCELIN:** AM R102665–68, R102685, south-east outskirts of Lancelin; SAM R13047a–b, Moore River, 56 miles north Perth; WAM R16544–48, R17878–79, R52102–05, R93715, Lancelin Island; R16549–50, Lancelin; R93109, 5 km south Lancelin; R93110–11, Ledge Point. **PERTH:** AM R47486–89, WAM R10664, R12645, City Beach; AM R88482–83, east of West Coastal Hwy and south of Whitfords Ave, nr junction; MV D9800, WAM R416, R444, Perth; SAM R22872–73,

WAM R59318, Burns Beach; SAM R29420, Scarborough Beach; WAM R4783, R21272, North Beach; R11002, One Tree Hill, betw. Wanneroo & Yanchep; R12914, Dalkeith; R41784, R78472–73, Wanneroo; R46130, Marmion; R48160–61, Scarborough; R50129, R51159, R53710–11, Sorrento; R61750, Mullaloo; R73728, Swanbourne; R83074, 3 km north Burns Beach; R83075, 4 km north-north-east Burns Beach; R83083, 3 km north-north-east Burns Beach; R83871, Two Rocks; R90506, Bold Park. **ERRONEOUS LOCALITIES:** SAM R26128–30, Albany.

Cyclodomorphus maximus (Storr, 1976)

Figs 11–13

Omolepida maxima Storr, 1976: 169.

Diagnosis. *Cyclodomorphus maximus* differs from all other members of the *C. branchialis* species group in the combination of a mode of 22 mid body scales, interparietal scale $\frac{1}{2}$ – $\frac{2}{3}$ length and $\frac{1}{3}$ – $\frac{1}{2}$ breadth of frontal, red-brown dorsal ground with white bars on most dorsal body scales, and large size (maximum known SVL 231 mm).

Description. Parietals separated by interparietal (50.0%, $n = 18$) or in narrow to moderate contact caudally (50.0%); interparietal broadest rostrally, approximately $\frac{1}{2}$ – $\frac{2}{3}$ length and $\frac{1}{3}$ – $\frac{1}{2}$ width of frontal in adults (slightly larger in juveniles); transversely enlarged nuchals 2–4 on each side ($\bar{x} = 3.5$, $SD = 0.56$, $n = 38$), usually four (58.3%); loreals rarely one unilaterally (10.5%, $n = 19$), due to fusion of the two loreals; supraciliaries 5–7 ($\bar{x} = 6.2$, $SD = 0.45$, $n = 36$), usually six (77.8%), first and last largest, third-last usually flat-topped or projecting slightly between second and third supraocular, remainder moderate, subequal; presuboculars rarely one unilaterally (5.6%, $n = 18$); postsuboculars 3–5 ($\bar{x} = 4.1$, $SD = 0.55$, $n = 34$), usually four (70.6%); upper palpebrals 9–12 ($\bar{x} = 10.3$, $SD = 0.70$, $n = 16$); lower palpebrals 10–13 ($\bar{x} = 11.0$, $SD = 0.97$, $n = 16$); secondary temporals in α -pattern; supralabials 7–8 ($\bar{x} = 7.2$, $SD = 0.38$, $n = 36$), third-last below centre of eye, separating pre- and postsuboculars; infralabials 6–7 ($\bar{x} = 6.3$, $SD = 0.45$, $n = 38$), first two contacting postmental; ear moderately open, approximately equal to eye height, with 1–4 ($\bar{x} = 2.4$, $SD = 0.60$, $n = 34$), usually two (52.9%), rounded lobules along rostral margin, uppermost two generally largest.

Body scales in 20–22 ($\bar{x} = 21.8$, $SD = 0.50$, $n = 19$), usually 22 (94.4%) longitudinal rows at midbody; scales in paravertebral rows much broader than adjacent lateral dorsal scales, 61–67 ($\bar{x} = 64.5$, $SD = 1.71$, $n = 19$); subcaudal scales 95–101 ($\bar{x} = 97.0$, $SD = 2.08$, $n = 7$); lamellae below fourth toe 14–17 ($\bar{x} = 15.4$, $SD = 0.98$, $n = 34$).

SVL 62.5–231 mm ($n = 19$); AGL/SVL 56.0–67.4% ($\bar{x} = 61.6\%$, $n = 19$); TL/SVL 92.8–105.1% ($\bar{x} = 99.6\%$, $n = 6$; sample comprises juveniles only); FLL/SVL 13.4–

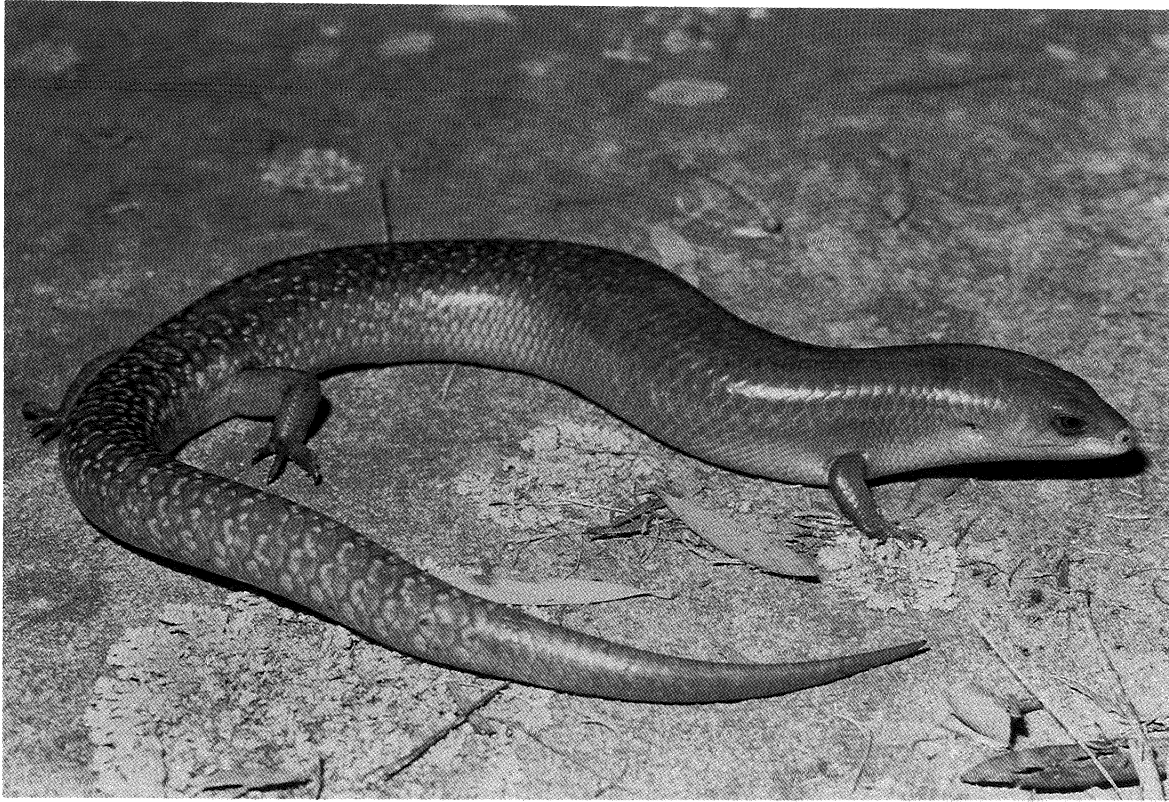


Fig. 11. A live *Cyclodomorphus maximus* from Barnett River Gorge, WA.

21.2% ($\bar{x}$ = 17.0%, n = 19); HLL/SVL 18.4–25.6% ($\bar{x}$ = 21.8%, n = 19); FLL/HLL 69.7–87.5% ($\bar{x}$ = 77.3%, n = 19); HL/SVL 13.1–21.8% ($\bar{x}$ = 16.8%, n = 19); HW/HL 65.5–76.9% ($\bar{x}$ = 72.4%, n = 19); HD/HL 48.2–57.9% ($\bar{x}$ = 52.1%, n = 19).

Presacral vertebrae 40–42 ($\bar{x}$ = 41.3, SD = 0.60, n = 16); postsacral vertebrae 54–55 ($\bar{x}$ = 54.6, SD = 0.53, n = 7); phalangeal formula of manus and pes 2.3.4.4.3.

Allometry. With respect to SVL, limb lengths and HL showed negative allometry, while AGL showed positive allometry. With respect to HL, both HW and HD showed significant positive allometry (Table 4).

Coloration (in preservative). Yellow-brown, caramel-brown or red-brown dorsally and laterally, with white to cream markings caudally on many scales, tending to align transversely, beginning between $1/4$ – $1/2$ length of body, and extending over basal $2/3$ – $3/4$ of tail, where most prominent. Pale markings on a scale generally consist of two broad, widely separated longitudinal streaks, frequently joined by a narrow to broad transverse bar, forming an open rectangle. Head dorsum immaculate; laterally immaculate except for dark brown clouding forming a narrow ring around orbit. Pattern may be obscure in large adults.

Venter light cream-brown to orange-yellow, immaculate or with a few light brown flecks laterally. Palms cream.

Juveniles yellow-brown dorsally and laterally, body

and tail with closely spaced narrow cream bands, formed by wholly or largely pale scales alternating with yellow-brown scales. Nape with broader alternating light and dark bands as follows: a 3–4 scale wide pale band behind parietals, extending laterally to venter, followed by an equally wide light brown band, clouded with dark brown laterally, at and caudal to level of ear, broken behind ear, but reappearing ventrocaudal to ear; a narrow 2–3 scale wide pale band extending laterally to venter, followed by a similarly narrow light brown band, clouded with darker brown laterally, at and slightly cranial to level of forelimbs, followed by an obscure narrow pale band (first band of the body pattern).

Head dorsum yellow-brown, more yellow on snout, darker on crown. Face yellow-brown with a narrow dark circumocular ring; lips cream with brown edges to some scales, temples with a cream patch, extending up from lips.

Venter cream, vent and tail with narrow brown transverse lines, throat and chin with narrow brown vermiculations. Soles of feet unpigmented.

Coloration (in life) (Fig. 11): Data are available for one Mitchell Plateau adult (Wilson & Knowles, 1988), the Barnett River Gorge adult (HFWE 2144) and one of the juveniles in the series 2288–94. Adults are red-brown dorsally, with the pale “horseshoe” markings light yellow-green to cream. Head dorsum a little paler and greyer than body ground. Laterally body and tail light

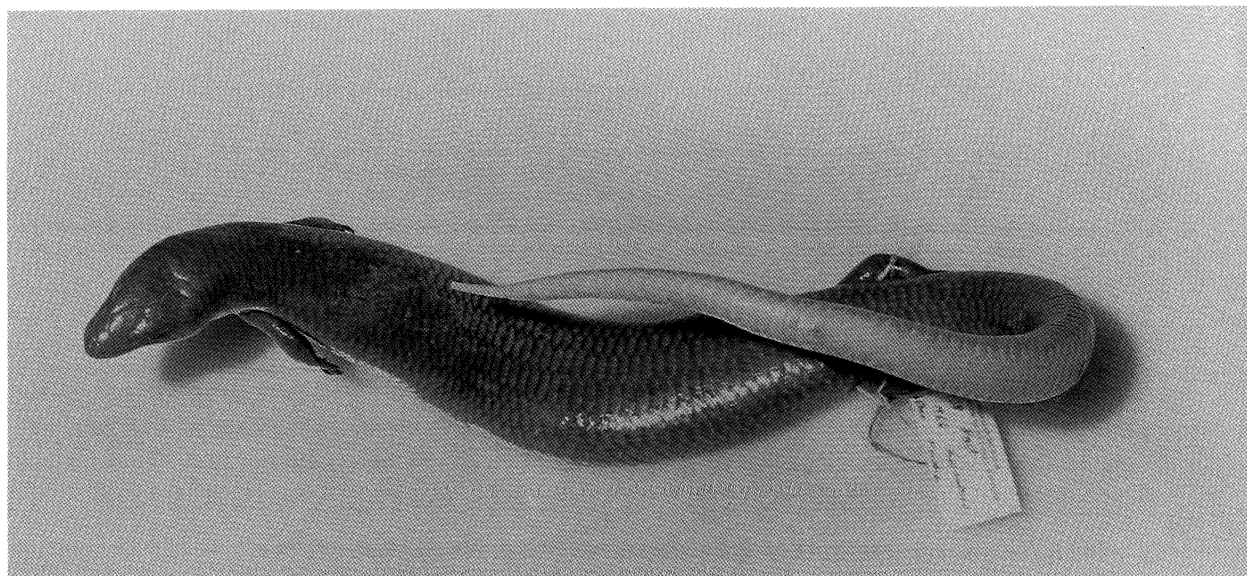


Fig. 12. Holotype of *Omolepida maxima* Storr (WAM R27760).

green-grey, with pale markings less distinct; face yellow-brown, cream-yellow over lips. Circumocular ring dark brown. Tip of snout grey-white. Ventrally pale cream-yellow, becoming more yellow on throat. Ventral colour extends dorsally behind axilla and around ventral half of ear. Palms unpigmented. Iris orange-red; tongue blue.

The juvenile had dorsal ground orange-brown with pale markings light yellow, tail yellow distally. Laterally, orange scales become yellowish grey-green, yellow scales remain unchanged, producing an overall grey-yellow hue. Head grey-brown dorsally, more yellow over snout. Bands on nape yellow and orange, the latter clouded with black, especially laterally. Face cream-yellow, with dark brown markings as above. Venter unpigmented, with narrow dark brown bands on tail, and dark brown vermiculations on throat. Iris orange; tongue blue.

Sexual dimorphism. Mature-sized males (SVL 155–231 mm, $\bar{x}$ = 193.8 mm, SD = 29.19, n = 6) were similar in size to mature-sized females (SVL 159–224 mm, $\bar{x}$ = 184.0 mm, SD = 35.0, n = 3; Mann-Whitney U test: U = 7, n.s.). The available material was too scanty to assess sexual dimorphism in other metric characters.

No significant differences were detected between males and females in mean number of paravertebral scales, subcaudal scales, subdigital lamellae, supralabials, infralabials, postsuboculars, supraciliaries, nuchals, lobules, upper palpebrals or lower palpebrals, or in frequency of contact of parietals.

Distribution. *Cyclodomorphus maximus* is restricted to the north-west Kimberley of WA, from Koolan Island in the west to Kalumburu in the east, and south to the Barnett River Gorge (Fig. 14).

Geographic variation. The female and litter from Barnett River Gorge, the southernmost locality, have significantly fewer lower palpebrals ($\bar{x}$'s = 10.3 vs 11.6, t_{14} = 3.16**), paravertebral scales ($\bar{x}$'s = 63.0 vs 65.3, t_{17} = 3.58**) and subdigital lamellae ($\bar{x}$'s = 14.5 vs 15.9, t_{32} = 4.86**), and a higher proportion of parietals contacting caudal to the interparietal (7:0 vs 2:8; Fisher Exact Probability Test, $p < 0.05$) than other material.

Type material. The holotype of *C. maximus* (WAM R27760; Figs 12,13) has supraciliaries six, postsuboculars four, nuchals 3/4, supralabials seven, infralabials 6/7, upper palpebrals 11, lower palpebrals 11, rostral ear lobules two, midbody scales 22, paravertebral scales 65, subdigital lamellae 15, SVL 231 mm, AGL 153 mm, tail regenerated, FLL 31 mm, HLL 42.5 mm, HL 30.2 mm, HW 22.2 mm, HD 16.6 mm.

Comparison with other taxa. *Cyclodomorphus maximus* differs from all other taxa in the *C. branchialis* species group in its much greater size, from neonates (minimum size 62.5 mm vs 38 mm) to adults (maximum size 231 mm vs 132 mm, for *C. m. melanops*), much longer tail with correspondingly more numerous subcaudal scales (95–101 vs ≤ 87) and postsacral vertebrae (54–55 vs ≤ 46), more numerous ear lobules (modally 2 vs 0 or 1) and shorter, narrower interparietal scale, in relation to frontal scale. The overall size and the small interparietal at least are autapomorphies of the species.

Cyclodomorphus maximus is similar to *C. celatus* in possessing 20–22 midbody scales, but differs markedly from this species and *C. branchialis* in having more numerous postsuboculars (modally 4 vs 3 in most populations), upper palpebrals ($\bar{x}$'s = 10.3 vs 8.5, 8.1), lower palpebrals ($\bar{x}$'s = 11.0 vs 9.1 for both) and subdigital lamellae (14–17, $\bar{x}$ = 15.3 vs 10–15, $\bar{x}$ = 11.9

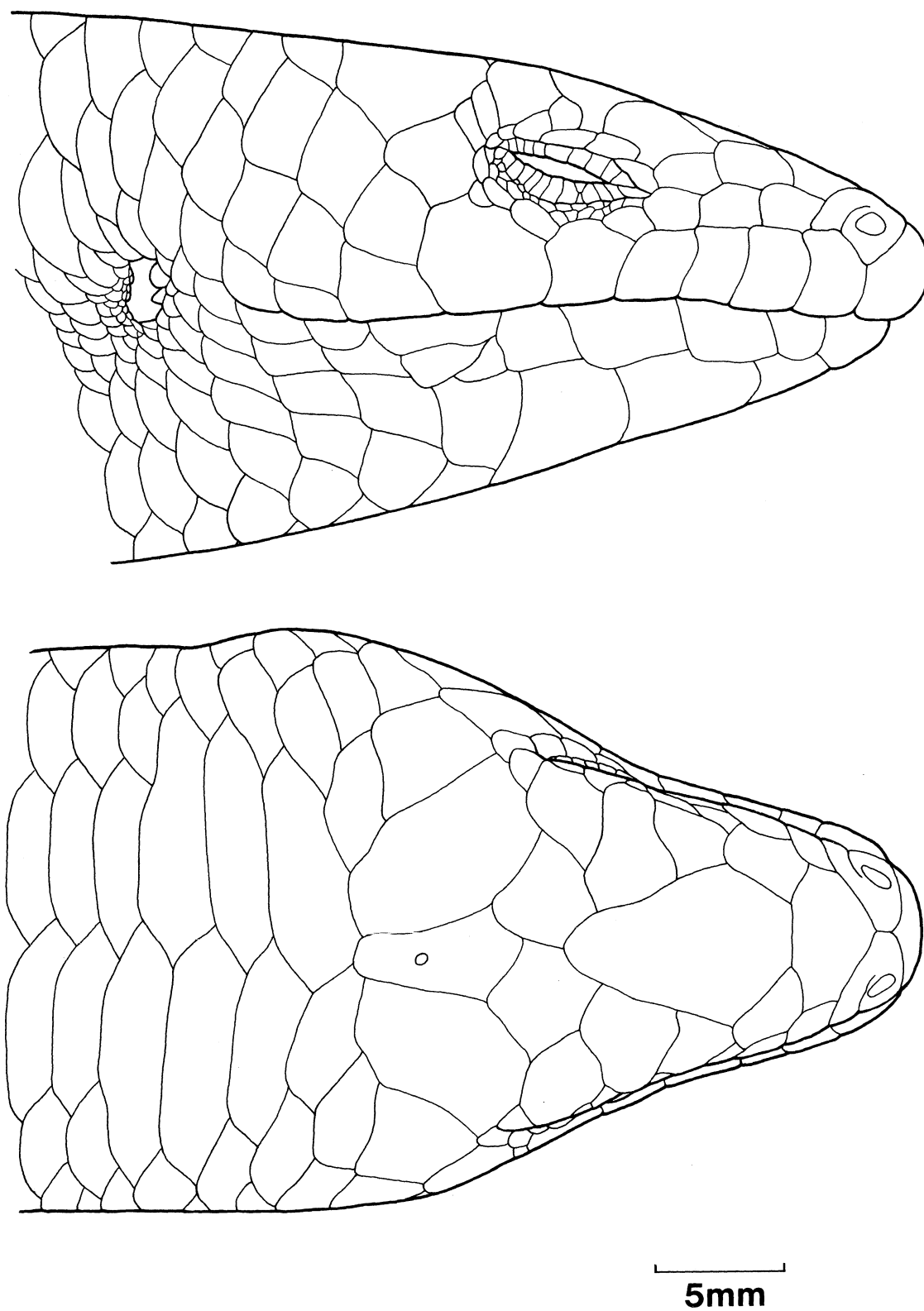


Fig. 13. Head shields of holotype of *Omolepida maxima* Storrs.

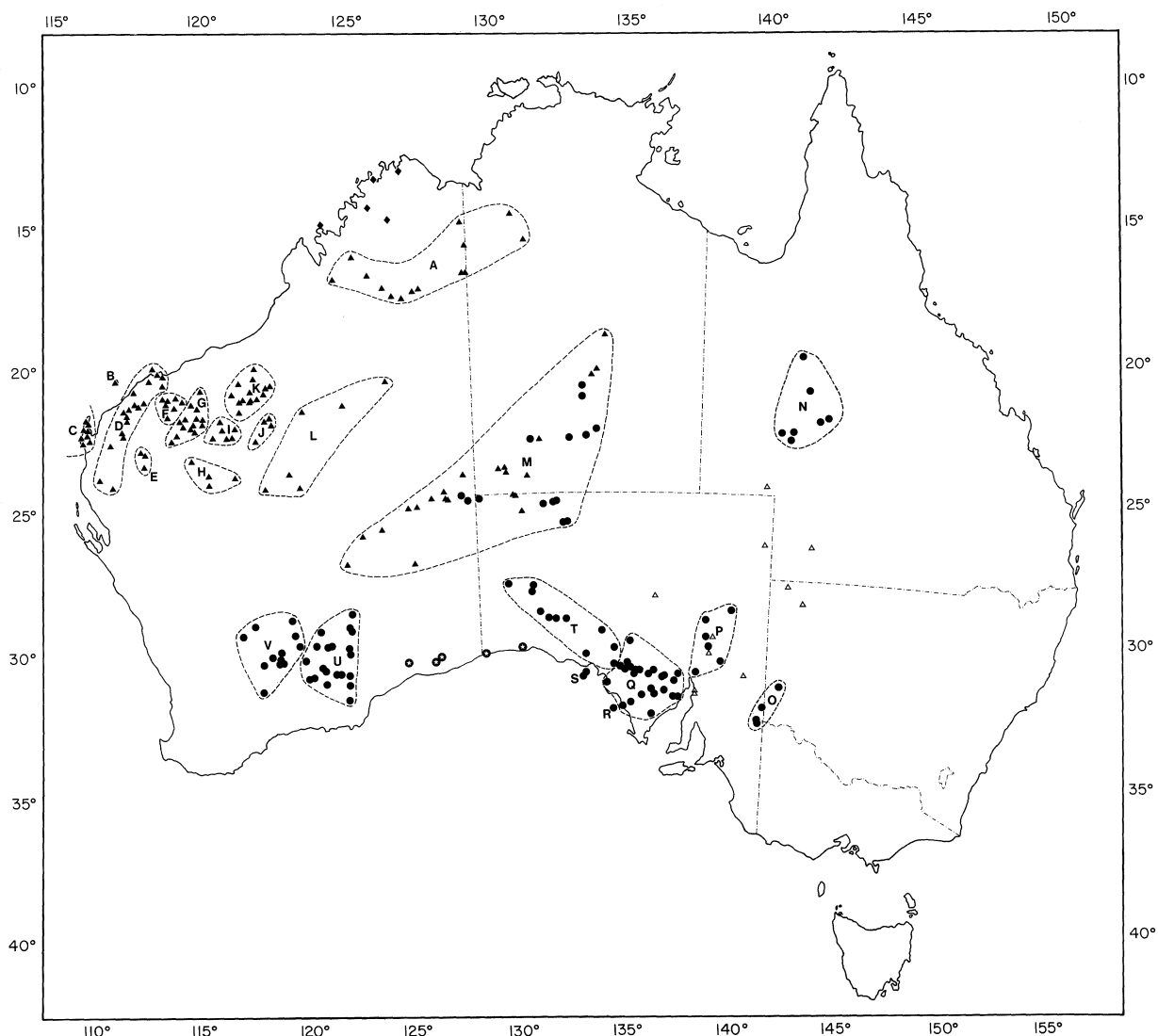


Fig. 14. Distribution of some members of *Cyclodomorphus branchialis* species group: *C. maximus* (diamonds); *C. m. melanops* (closed triangles); *C. m. elongatus* (dots); *C. m. siticulosus* (starred dots); *C. venustus* (open triangles). Dashed lines and letters delimit and identify populations used in defining geographic variation in *C. m. melanops* and *C. m. elongatus*, as follows: A, Kimberley; B, Barrow Island; C, Exmouth; D, Onslow; E, Lower Ashburton; F, Millstream; G, Hamersley; H, Upper Ashburton; I, Mt Newman; J, Talawana; K, Oakover; L, Great Sandy Desert; M, Centralian (both subspecies); N, Queensland; O, NSW; P, Flinders Ranges; Q, Eyre Peninsula; R, Flinders Island; S, Nuyts Archipelago; T, Ooldea; U, Zanthus; V, Boorabbin.

and 9–12, $\bar{x} = 10.8$), a broader but shallower head (Tables 1,2,4), dorsal ground more brown than grey, without dark streaks, and a prominent dark circumocular ring. It also has fewer midbody scales than *C. branchialis* (mode 22 vs 24).

Habitat. Storr (1976) records *C. maximus* from “sandstone plateaux of north-west Kimberley”, while Ehmann (1992) states that the species “inhabits loose leaf and humus debris that lies between boulders and rocks that are partly overgrown with vines, figs and fringing spear

grass tussock and hummock grass”, in “escarpments of ... sandstone plateaux ... especially around gorges and escarpment outcroppings with extensive broken up and exposed boulder reefs. Vegetation of straggling vines, thickets and figs on these reefs and edges provides deep loose leafy litter and humus in the labyrinths of crevices and tunnels. Adjacent vegetation includes low open eucalypt woodland with figs and boabs”. Specific habitat data are available for most specimens. The holotype was burnt from spinifex on sandstone. The Prince Regent River specimen was taken at site W6 (Youwanjela Creek)

of the WA Department of Fisheries and Wildlife Survey (Miles & Burbidge, 1975), where it was taken in sandstone/spinifex (Storr & Smith, 1975). Site W6 is described by Miles *et al.* (1975: 24): "the slopes of the valley consist of a series of steps made by strongly bedded sandstones supporting a low open-woodland of *Eucalyptus* spp., *Ficus* spp., and Baobab (*Adansonia gregorii*) trees with a ground cover of spinifex hummock grasses. The northern side is much steeper with several ridges along the lower parts and a high vertical rampart at the upper part. Under some of these ridges the vegetation becomes more dense with some vine thicket present ... Upstream from the main campsite about 1.5 km a major fork occurs in Youwanjela Creek ... The valley ridge on either side supports a low woodland of *Eucalyptus* spp. and *Acacia* sp. trees with spinifex hummock grasses."

The Lone Dingo specimen was taken in semi-deciduous vine thicket (Dense Low Forest) on laterite (J. Dell, pers. comm.), while the Walsh Point series was taken in "deciduous vine thicket, between beach and volcanic [basaltic] cliff ... Stratum 1: *Melaleuca leucadendron*, *Ficus platypoda*, *Terminalia petiolaris*, *Albixia lebbek*. Stratum 2: *Gardenia* sp., *Pouteria sericea*, *Calytrix brachychaeta*, *Bombax* sp. Stratum 3: *Flagellaria indica*, *Erythrophleum chlorostachys*" (Kitchener *et al.*, 1981). Both sites have numerous variable size boulders and considerable leaf litter (J. Dell, pers. comm.).

The Barnett River Gorge adult was found under a grass tussock at the entrance to the gorge, near vine thickets (H. Ehmann, pers. comm.).

Reproduction. One female (HFWE 2144; SVL 224 mm) gave birth to seven young (HFWE 2288–2294) in early January 1983 (Ehmann, 1992, pers. comm.) although Wilson & Knowles (1988) erroneously report the date as late February. Other apparently mature males ($n = 6$) and females ($n = 2$) were non-reproductive.

Sex ratio. The ratio of mature-sized males: mature-sized females in the sample examined is 6:3.

Diet. Ehmann (1992) records snails, slugs, cockroaches, isopods, plant material and fruits in the diet, presumably on the basis of captive feeding experiments on the Barnett River Gorge material he collected. Shells of small land snails were the only identifiable remains in the gut of WAM R77631, R77637 and R96112.

Specimens examined (all localities are in WA). WAM R27760 (HOLOTYPE) Kalumburu; R46885 (PARATYPE) Youwanjela Creek, Prince Regent River Reserve (15°34'S 125°25'E); R77022, Lone Dingo, Mitchell Plateau; R77042, R77192–93, R77592, R77631, R77637, Walsh Point, Port Warrender; R95558, Mitchell Plateau (14°35'S 125°45'E); R96112, R103732, Koolan Island; HFWE 2144, 2288–2294, Barnett River Gorge.

Cyclodomorphus melanops melanops (Stirling & Zeitz, 1893)

Figs 15–19

Lygosoma melanops Stirling & Zeitz, 1893: 173.

Lygosoma gastrostigma Boulenger, 1898: 918.

Diagnosis. *Cyclodomorphus m. melanops* differs from all other members of the *C. branchialis* species group in the combination of a mode of 24 or more midbody scales, 62–80 paravertebral scales, 66–87 subcaudal scales, moderately large, open ear aperture, usually α -temporal configuration, grey, grey-brown, yellow-brown or red-brown dorsal ground and black spots at least ventrally, but usually dorsally and laterally as well.

Description. Prefrontals rarely narrowly separated (0.5%, $n = 440$) or in narrow contact (0.2%); parietals completely separated by interparietal (98.2%, $n = 439$) or in narrow to broad contact caudally (1.8%); interparietal broadest rostrally, approximately $2/3$ – $9/10$ length and breadth of frontal; transversely enlarged nuchals 0–5 on each side ($\bar{x} = 2.8$, $SD = 0.70$, $n = 878$), usually three (65.8%); loreals rarely three unilaterally (0.5%, $n = 429$), one unilaterally (2.1%) or one bilaterally (1.2%); supraoculars rarely two unilaterally (0.9%, $n = 439$), or four unilaterally (0.2%) or bilaterally (0.5%); reduction to two due to fusion of first and second supraocular ($n = 2$) or second and third supraocular ($n = 1$); supraciliaries 4–7 ($\bar{x} = 6.0$, $SD = 0.27$, $n = 875$), usually six (93.1%), first and last largest, third last usually projecting between second and third supraocular, remainder moderate, subequal; presuboculars rarely one bilaterally (0.5%, $n = 440$) or unilaterally (0.2%) or three unilaterally (0.5%); postsuboculars 1–5 ($\bar{x} = 3.9$, $SD = 0.42$, $n = 874$), usually four (83.9%); upper palpebrals 7–13 ($\bar{x} = 9.7$, $SD = 1.07$, $n = 421$); lower palpebrals 7–14 ($\bar{x} = 10.9$, $SD = 1.08$, $n = 419$); secondary temporals usually in α -pattern (96.8%, $n = 876$), rarely in β -pattern (3.2%); supralabials 6–8 ($\bar{x} = 7.4$, $SD = 0.49$, $n = 875$), usually seven (61.3%), third-last below centre of eye, separating pre- and postsuboculars; infralabials 5–8 ($\bar{x} = 6.3$, $SD = 0.49$, $n = 875$), usually six (68.2%), usually first two (92.8%, $n = 878$), rarely first three (6.9%) or first (0.2%) infralabials contacting postmental; ear moderate, $2/3$ –1 times height of eye, open, oval, with 0–3 ($\bar{x} = 1.1$, $SD = 0.27$, $n = 872$), usually one (92.7%), rounded lobules along rostral margin.

Body scales in 22–28 ($\bar{x} = 25.4$, $SD = 1.07$, $n = 434$), usually 26 (54.5%) longitudinal rows at midbody; scales in paravertebral rows broader than adjacent lateral dorsal scales, 62–80 ($\bar{x} = 70.0$, $SD = 3.54$, $n = 432$); subcaudal scales 66–87 ($\bar{x} = 74.3$, $SD = 3.87$, $n = 144$); lamellae below fourth toe 10–18 ($\bar{x} = 14.1$, $SD = 1.30$, $n = 782$), each with a narrow to broad grey to mid-brown callus.

SVL 41–132 mm ($n = 427$); AGL/SVL 51.2–70.4% ($\bar{x} = 63.0\%$, $n = 424$); TL/SVL 78.3–138.8% ($\bar{x} = 103.8\%$, $n = 134$); FLL/SVL 11.9–22.3% ($\bar{x} = 16.7\%$,

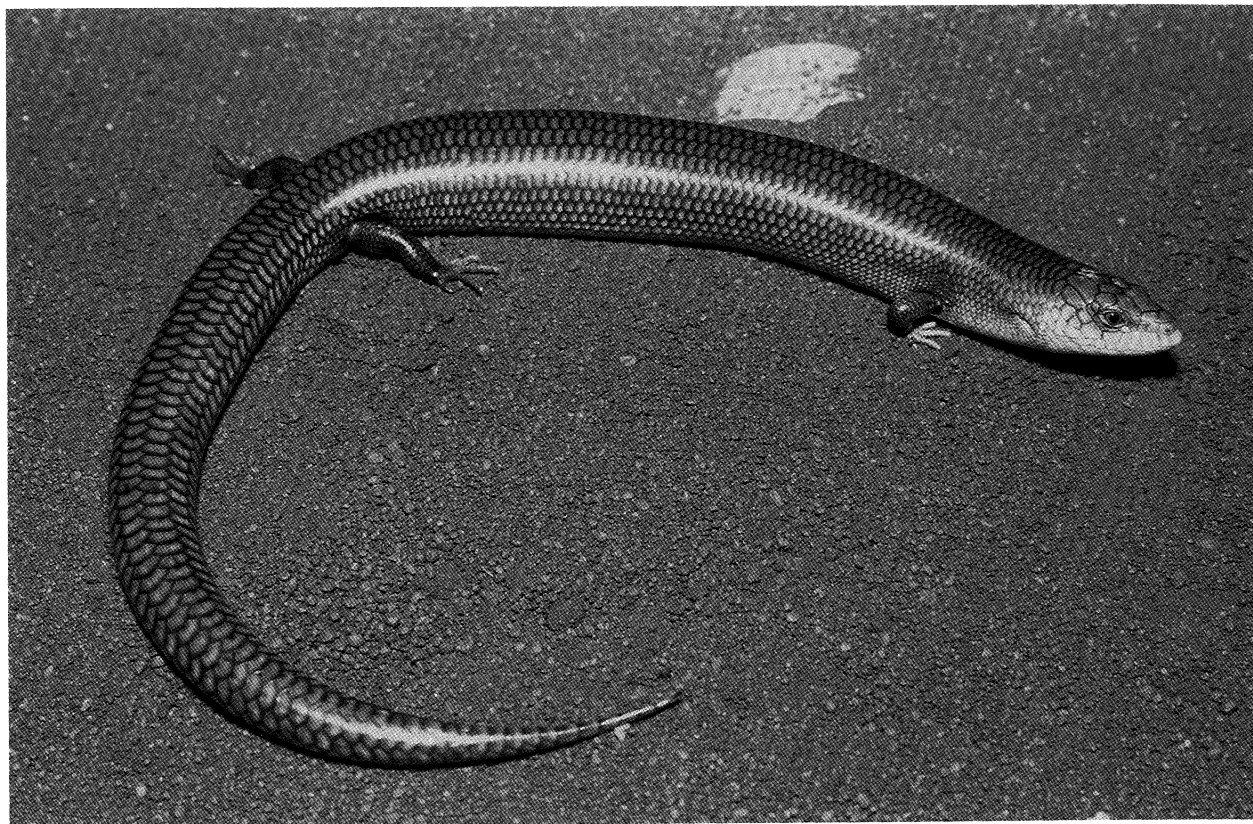


Fig. 15. A live *Cyclodomorphus melanops melanops* from Cane River, WA.

$n = 414$); HLL/SVL 16.0–28.0% ($\bar{x} = 21.8\%$, $n = 414$); FLL/HLL 65.0–90.9% ($\bar{x} = 76.7\%$, $n = 414$); HL/SVL 12.1–23.4% ($\bar{x} = 15.7\%$, $n = 426$); HW/HL 59.3–85.6% ($\bar{x} = 73.5\%$, $n = 431$); HD/HL 45.8–67.1% ($\bar{x} = 56.5\%$, $n = 430$).

Presacral vertebrae 38–42 ($\bar{x} = 39.9$, $SD = 1.14$, $n = 24$); postsacral vertebrae 35–46 ($\bar{x} = 40.6$, $SD = 3.55$, $n = 7$); phalangeal formula of manus and pes 2.3.4.4.3.

Allometry. With respect to SVL, AGL and TL showed positive allometry, while limb lengths and HL showed negative allometry. With respect to HL, both HW and HD showed slight but significant positive allometry (Table 5).

Coloration (in preservative). Light to mid olive brown, red-brown, yellow-brown or grey-brown dorsally, often with a central dark fleck or spot in many body and tail scales. Ventral ground cream to yellow usually with varying degrees of dark brown flecking or spotting, most prominent caudally.

Head and neck immaculate or weakly spotted dorsally, often strongly spotted laterally and on throat. Upper lip usually pale, often with dark streaks and flecks. Orbit sometimes clouded with dark grey-brown.

Palms cream to yellow to light brown with light cream-brown to dark brown calli and tubercles.

Juveniles as adults, but usually with head darker grey-

brown, and white spots midcaudally on many body and tail scales, often aligned in vertical bars laterally and on tail.

Coloration (in life) (Fig. 15): Data are available on iris, tongue and mouth colour for a series of 27 Barrow Island specimens (SVL 69–110 mm; L.A. Smith pers. comm.). Iris colour was described as yellow ($n = 11$), yellowish ($n = 15$) and reddish-yellow ($n = 1$). Tongue colour was described as inky-blue ($n = 22$), purplish-blue ($n = 3$), blue-black ($n = 1$) and purplish-red ($n = 1$). Mouth colour was noted as whitish ($n = 2$), pinkish-white ($n = 3$), pinkish ($n = 6$), pink ($n = 3$) and grey ($n = 1$). In WAM R84069, the iris was described as yellowish.

AM R52077 was described as “venter: ground colour pale yellow, becoming white under head, numerous tiny black spots all over; dorsal ground colour greyish-brown with numerous tiny black and white flecks all over; head light grey, becoming darker on sides; legs grey” (P. Rankin field notes).

Sexual dimorphism. Mature-sized males (82–126 mm, $\bar{x} = 95.1$ mm, $SD = 8.98$, $n = 88$) were generally slightly smaller than mature-sized females (83–132 mm, $\bar{x} = 97.0$ mm, $SD = 9.17$, $n = 125$), although the difference was not significant (Mann-Whitney U test, $z = 1.401$). Males also had generally shorter bodies, but proportionally longer limbs and heads than females, although females had slightly broader heads (Table 6).

Females had significantly greater numbers of paravertebral scales (62–80, $\bar{x}$ = 70.8, SD = 3.83, n = 141 vs 62–75, $\bar{x}$ = 68.9, SD = 3.16, n = 102; t_{241} = 4.08***) but fewer subdigital lamellae (10–18, $\bar{x}$ = 13.9, SD = 1.31, n = 257 vs 11–18, $\bar{x}$ = 14.4, SD = 1.35, n = 183; t_{438} = 3.89**) than males.

There were no significant differences between males and females in mean number of midbody scales, subcaudal scales, supralabials, infralabials, postsuboculars, supraciliaries, nuchals or upper or lower palpebrals.

Distribution (Fig. 14). *Cyclodomorphus m. melanops* occurs as three discrete and possibly geographically isolated populations: the southern fringe of the Kimberley, from Jasper Gorge, NT, in the east to “Mt Anderson”, WA in the west; central Australia, from 62 km east Neale Junction and 8 km west-north-west Point Salvation in the south-west to Davenport Range, NT, in the north-east, and the Pilbara and adjacent fringe of the Great and Little Sandy Deserts, including the coastal plain and North-West Cape, from Roebourne east to “Warrawagine” and Tobin Lake, south to Carnarvon Range, and west to Kumarina, the Ashburton drainage system, Mt Cahill outcamp and Point Cloates. It also occurs on Barrow Island and Dolphin Island off the Pilbara coastline.

Geographic variation. For the purposes of describing geographic variation, the overall distribution was divided into 13 populations, named, from approximately west to east, Barrow Island, Exmouth, Onslow, Millstream, Hamersley, Lower Ashburton, Upper Ashburton, Newman, Talawana, Oakover, Great Sandy, Kimberley and Centralian (Fig. 14). The Onslow, Millstream, Hamersley, Lower Ashburton, Upper Ashburton, Newman, Talawana and Oakover populations are collectively referred to as the Pilbara populations. Significant geographic variation was not detected in mean number of supraciliary scales. In significantly varying characters, the only general trends were for fewer scales (midbody scales, subdigital lamellae, supralabials, palpebrals) in the east, and either fewer (paravertebral scales, midbody scales, supralabials) or more (subcaudals, subdigital lamellae) scales in the most peripheral populations in the west and north.

Paravertebral scales. ANOVA: $F_{12,419} = 24.235^{***}$. Means ranged from 66.6 (Barrow Island) to 73.0 (Millstream). The Pilbara, Great Sandy and Centralian populations had similar means, from 69.3 (Upper Ashburton) to 73.0. Within the Pilbara, significant differences were only detected between the means for Upper Ashburton and Millstream, Hamersley, Oakover and Onslow, with only Hamersley adjoining Upper Ashburton. In contrast, the Kimberley, Barrow Island and Exmouth populations ($\bar{x}$'s = 66.6–68.0), on the northern and western periphery of the distribution, had significantly lower means than most other populations (Table 7), including the nearest populations.

Midbody scales. ANOVA: $F_{12,421} = 12.150^{***}$. Means ranged from 24.4 (Barrow Island) to 26.3 (Talawana). All populations except Barrow Island and Centralian

(mode = 24) had a mode of 26 midbody scales and means above 25.0. With the exception of a significantly lower mean for Kimberley ($\bar{x}$ = 25.2) than Hamersley and Oakover ($\bar{x}$'s = 25.8–25.9), only the Centralian ($\bar{x}$ = 24.5) and Barrow Island populations were significantly different from other populations (Barrow Island vs all but Lower Ashburton, Centralian and Great Sandy; Centralian vs Kimberley, Hamersley, Millstream, Newman, Oakover, Onslow and Talawana).

Subcaudal scales. ANOVA: $F_{11,131} = 13.678^{***}$. No data were available for the Lower Ashburton population. Means ranged from 69.6 (Centralian) to Kimberley and Exmouth ($\bar{x}$ = 78.1), with only the latter two and Onslow ($\bar{x}$ = 76.2), all associated with the northern and western periphery of the distribution, above 74.6. All significant differences involved these three high means (Kimberley and Exmouth vs Millstream, Oakover, Upper Ashburton and Centralian; Onslow vs the latter two also).

Subdigital lamellae. ANOVA: $F_{12,770} = 24.731^{***}$. Means ranged from 12.6 (Centralian) to 15.2 (Exmouth), with a clinal decrease in mean from the north and west (Exmouth, Barrow Island, Onslow, Millstream, Kimberley; $\bar{x}$'s = 13.9–15.2) to the east (Centralian, Great Sandy; $\bar{x}$'s = 12.6–12.8). The intervening eastern and southern Pilbara populations had intermediate means ($\bar{x}$'s = 13.2–13.9). Significant differences were detected between a number of populations with high and low means, with the Exmouth population having a higher mean than all other populations, and a number of other significant differences involving geographically proximate populations (Table 8).

Supralabials. ANOVA: $F_{12,862} = 22.317^{***}$. Means ranged from 7.0 (Kimberley, Centralian) to 7.9 (Lower Ashburton). In general, higher means and modes of eight supralabials occurred in the Pilbara populations and those nearby, while low means and modes of seven supralabials occurred in peripheral populations (Barrow Island, Great Sandy, Centralian, Kimberley; $\bar{x}$'s = 7.0–7.3). With few exceptions, significant differences involved these low means compared to high Pilbara means (Table 9). In particular, the Centralian and Kimberley populations had lower means than most other populations.

Infralabials. ANOVA: $F_{12,864} = 7.018^{***}$. Means ranged from 6.1 (Kimberley) to 6.6 (Exmouth) and 6.7 (Newman). Only these extreme means were significantly different to other means (Exmouth vs Barrow Island, Hamersley, Oakover, Upper Ashburton, Centralian and Kimberley; Newman vs the latter three; Kimberley vs Barrow Island, Hamersley, Millstream, Oakover and Onslow), with few of the significantly different pairs involving geographically proximate populations.

Postsuboculars. ANOVA: $F_{12,862} = 5.336^{***}$. Four postsuboculars was modal for all populations. Means for most populations ranged from 3.7 (Talawana) to 4.0 (Lower Ashburton, Newman), without significant differences between populations. Only Upper Ashburton ($\bar{x}$ = 3.5) had a significantly lower mean than other populations (vs all but Great Sandy and Talawana).

Nuchals. ANOVA: $F_{12,865} = 8.770^{***}$. Three nuchals was modal for all populations. Means ranged from 2.5

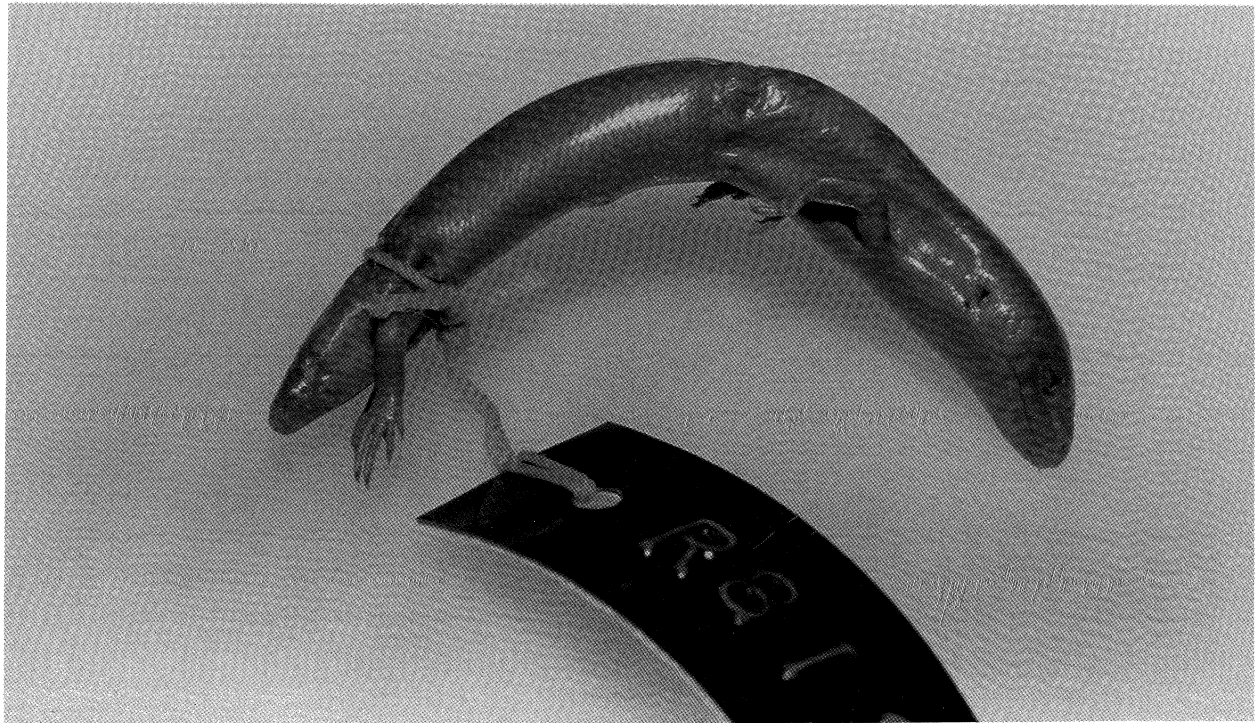


Fig. 16. Paratype of *Lygosoma melanops* Stirling & Zeitz (SAM R8139).

(Kimberley) to 3.2 (Barrow Island), with only these two peripheral populations significantly different to any others (Kimberley vs Barrow Island, Exmouth, Hamersley, Millstream, Oakover, Onslow and Upper Ashburton; Barrow Island vs Centralian, Exmouth, Hamersley and Oakover).

Upper palpebrals. ANOVA: $F_{12,408} = 8.789^{***}$. Means ranged from 8.5 (Lower Ashburton) to 10.4 (Kimberley), with most in the range 9.2–10.1 and without significant differences. With the exception of the Kimberley population (significantly different to Oakover and Upper Ashburton), all significant differences involved the three lowest means (Lower Ashburton, Barrow Island, Centralian; $\bar{x}$'s = 8.5–9.2), all three significantly different to Kimberley, Exmouth, Hamersley, Millstream and Onslow, Centralian also different to Oakover. Apart from the peripheral Lower Ashburton mean, none of the significantly different pairs involved geographically contiguous populations.

Lower palpebrals. ANOVA: $F_{12,406} = 7.490^{***}$. Means ranged from 9.4 (Great Sandy) to 11.7 (Talawana), with only these and the Centralian mean ($\bar{x} = 9.7$) outside the range 10.0–11.5. Apart from Onslow ($\bar{x} = 11.5$) vs Barrow Island, Lower Ashburton and Upper Ashburton ($\bar{x}$'s = 10.0–10.6), the only significant differences involved the Centralian and Great Sandy populations, both in the extreme east of the distribution, with lower means than Exmouth, Hamersley, Kimberley, Millstream, Oakover, Onslow and Talawana, and also Newman and Barrow Island in the case of the Centralian population.

Snout-vent length. Exmouth animals were generally larger than in other populations (mature-sized individuals, 91–132 mm vs 82–128 mm).

Coloration. There was much geographic variation in dorsal ground and degree of dark spotting. Kimberley animals were mid to dark brown dorsally and laterally, the dark flecks usually weak or absent on the body. When present, the flecks were usually restricted to the caudal half of the body, rarely over the whole dorsum, and were located in the middle of the scales, either over the caudal half, or full-length. Dark flecks continued onto the tail, where they were more prominent, and often occurred in pairs on a single scale. The venter had dark flecks from throat to tail tip, sometimes aligned to form stripes on the throat, and often prominent on lips and face. The pale juvenile spots persist to subadults.

Barrow Island individuals were olive-brown, occasionally grey-brown dorsally, pale yellow below. The dorsum usually had scattered very fine dark flecks, on body scales in the middle of the cranial half, but on tail scales in the middle of the distal half. The venter was as for the Kimberley population.

Pilbara material was usually mid grey-brown dorsally, head and cranial half of body often immaculate, sometimes with dark body spots, caudal half of body and tail with weak to strong broad dark spots cranially in many body and tail scales. The dorsal body scales often had darker margins, forming a weak dark reticulum. The venter was cream, usually with, occasionally without dark flecks and streaks, most prominent caudally, very weak (if present) on chin and throat. Juveniles were mid-brown to yellow-brown above with weak dark spots, pale spots on every second body scale caudal to nape, face and lower lips with black clouding. Adults from the Kumarina series differed in their weaker dark flecking, largely confined to the tail, and ventrally to tail and pelvis,

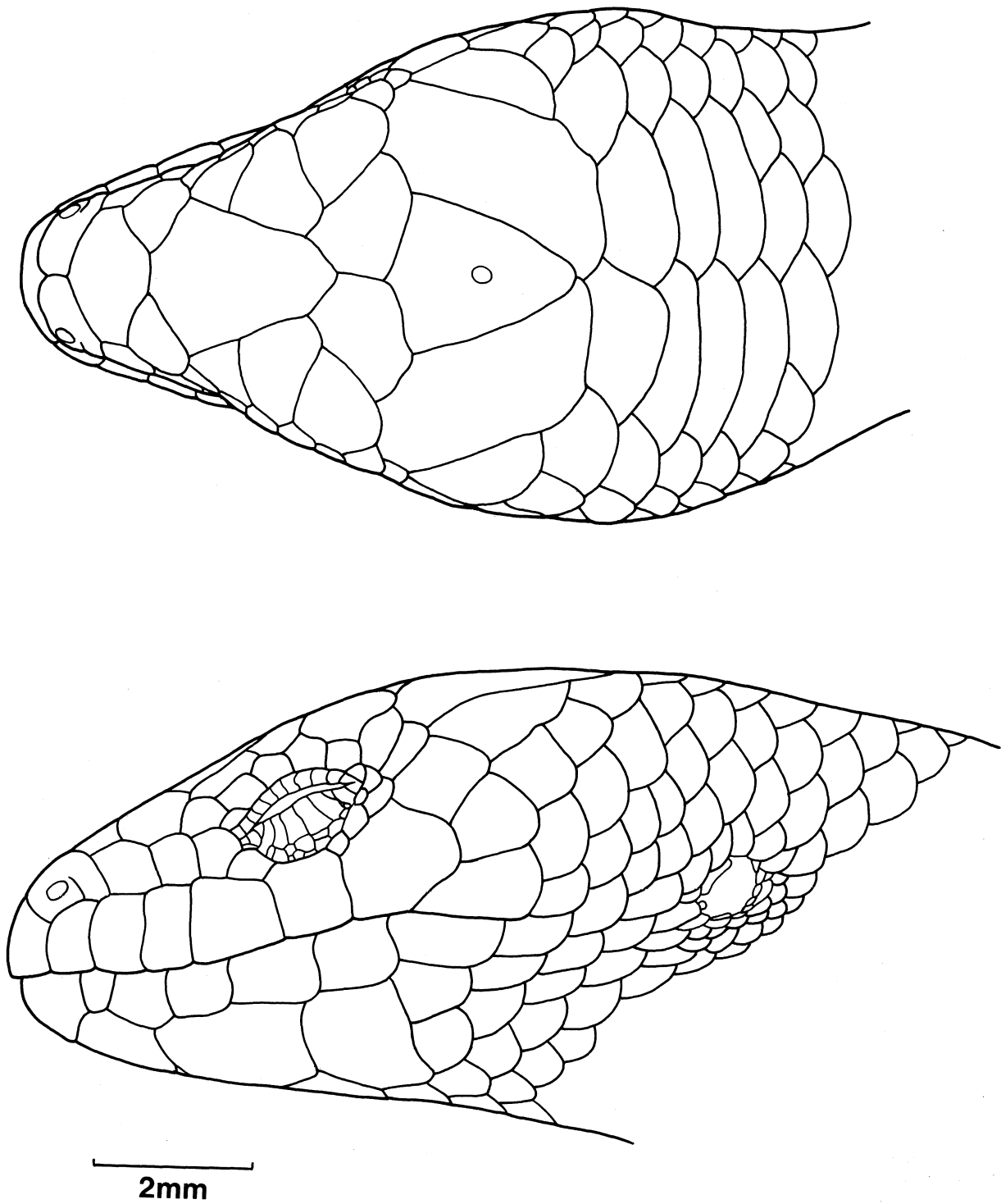


Fig. 17. Head shields of paralectotype of *Lygosoma melanops*.

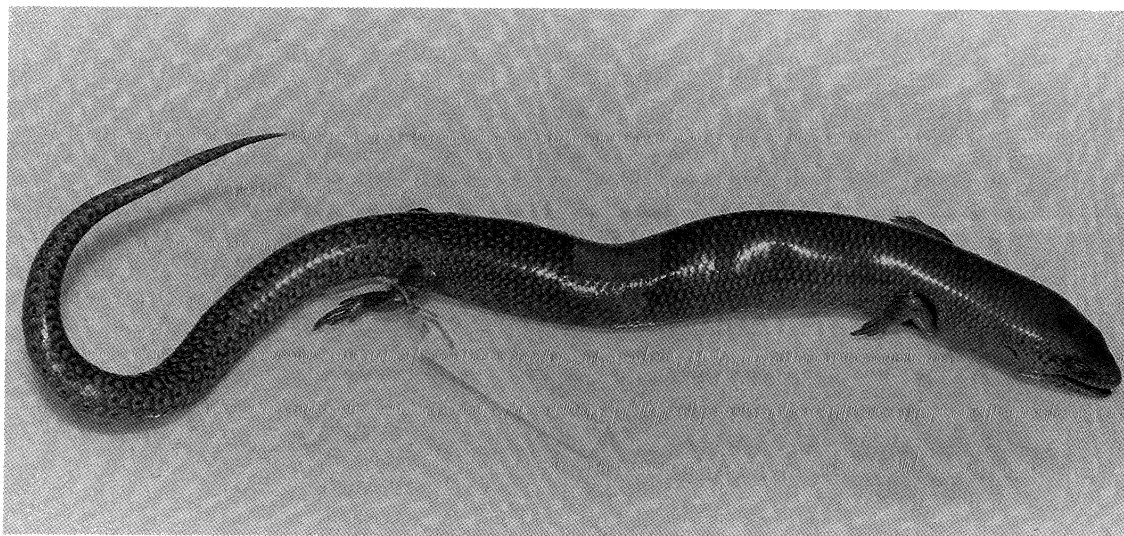


Fig. 18. Holotype of *Lygosoma gastrostigma* Boulenger (BMNH 1946.8.9.87).

although juveniles had more prominent dark flecking, extending more cranially, sometimes to the chin ventrally.

Exmouth material was usually grey-brown, rarely mid-brown dorsally, head and body usually immaculate, occasionally with a few dark spots cranially in scales on caudal half of body. The tail usually had similar dark spots on every second or third scale. The venter was cream, frequently with dark spots from mid-body to tail, occasionally with dark flecks on chin and throat. Juveniles had pale spots on tail, less prominently on caudal half of body.

Centralian animals were light to mid-brown or yellow-brown dorsally, tail yellowish, with strong dark cranially-situated streaks or spots on most body and tail scales. Venter and lips were cream to pale yellow, with numerous dark flecks and macules, smaller and sparser than on dorsum, weakest on throat, where often aligned in obscure stripes. Juveniles had very prominent pale spots.

Type material. *Lygosoma melanops* Stirling & Zeitz, 1893 was described from two specimens collected by the Elder Expedition between the Everard and Barrow Ranges, without specific holotype designation. The description of both adult and juvenile coloration implies that the two syntypes are adult and juvenile, although only the measurements of the adult are provided. Mitchell (1950) identified two specimens, both registered SAM R2732 as types, and provided an illustration of the head of the "holotype". Houston (1976), however, only records a single specimen, which could not be located, under SAM R2732, with a juvenile (SAM R8139) identified as a "paratype". Recent thorough searches of the SAM collection by the authors have also failed to find SAM R2732.

The original register entry for R2732 refers to a single specimen as "type specimen". This has been later corrected in pencil to two type specimens, and "(syntypes)" added after the entry. The register entry for R8139,

registered in 1966, provides a date, 24.vi.1891, and describes the specimen as a paratype. Amongst Mitchell's notes on SAM *Tiliqua* and *Egernia* material, on which his 1950 paper was based, only a single set of data is recorded for R2732: 24 midbody scales, snout-forelimb into axilla-groin, $2\frac{1}{3}$ – $2\frac{1}{2}$ times, colour bleached white, scalation typical, measurements 148 (83 + 65) mm. The measurements recorded by Mitchell, particularly the tail length, are similar to those recorded by Stirling and Zeitz.

The simplest explanation for the discrepancies between the type description, SAM registers, Mitchell's notes and 1950 paper, and Houston's (1976) listing is that at the time Mitchell was gathering data for his paper, he was initially only able to locate the adult type, which he registered in series with other *Tiliqua* and *Egernia* material, but subsequently found the juvenile, which he also included under that number, as was his registration policy, necessitating the pencilled corrections to the register entry. Subsequent to 1950, the juvenile was probably found separated from the adult, and re-registered as paratype, following Mitchell's (1950) labelling of the head drawing as "holotype". The erroneous labelling of this drawing appears to qualify as lectotype designation (Article 74[b] of the Code of Zoological Nomenclature). We have examined SAM R8139, and it is clear that the head drawing is not of this specimen. Presumably, Mitchell's illustration is of the adult specimen SAM R2732, and the lectotype must be presumed lost. Despite this loss, it is possible to unambiguously assign the name *Lygosoma melanops* to the taxon here described. The description and plate provided by Stirling & Zeitz (1893) clearly note a spotted rather than streaked colour pattern, while Mitchell's (1950) figure illustrates the α -temporal condition.

The paralectotype, SAM R8139, was invalidly designated lectotype by Wells & Wellington (1985). This specimen (Figs 16,17) is also representative of the

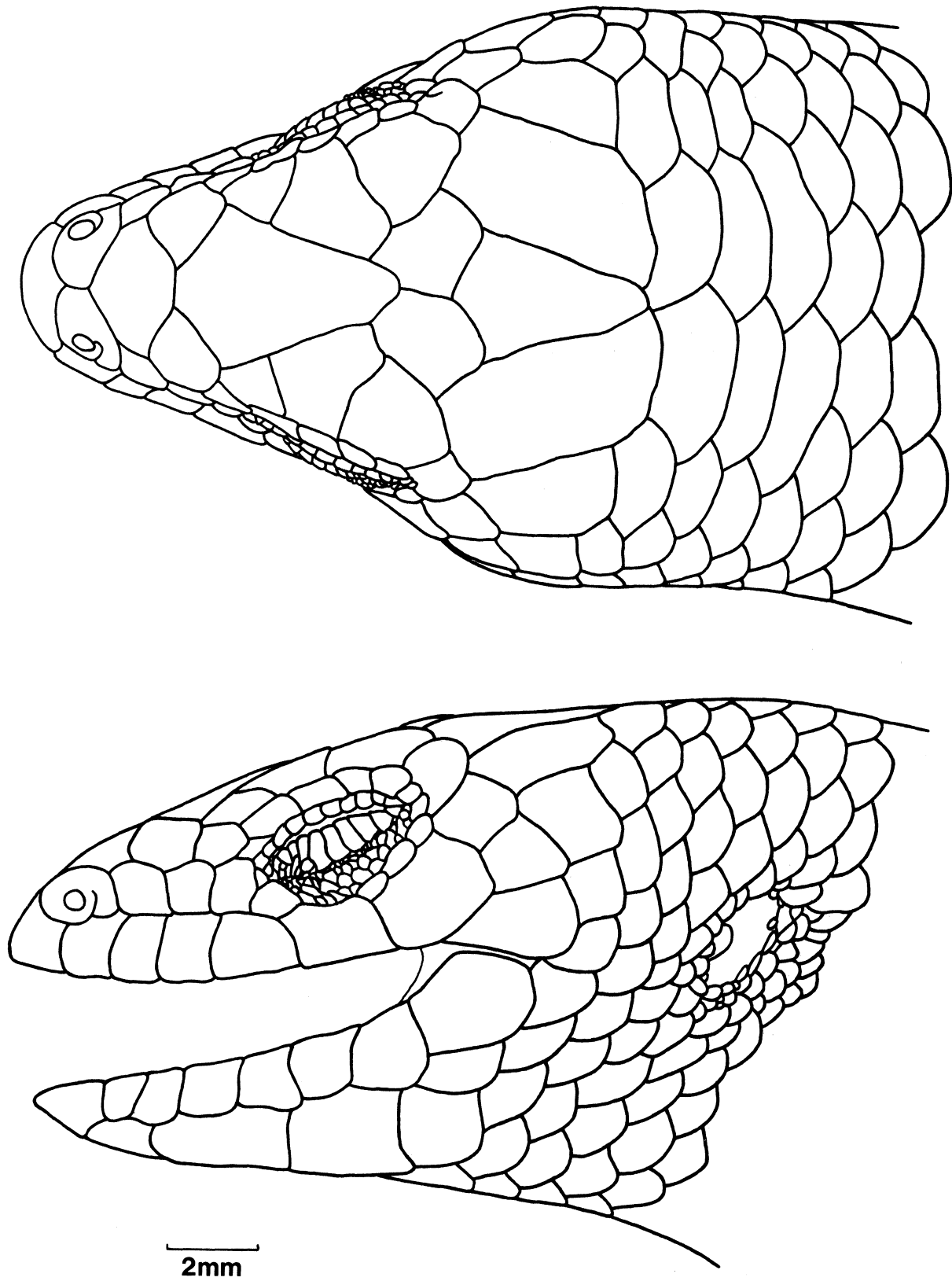


Fig. 19. Head shields of holotype of *Lygosoma gastrostigma*.

subspecies here described, and has supraciliaries six, postsuboculars four, nuchals 4/3, supralabials seven, infralabials six, upper palpebrals ten, lower palpebrals ten, α -configuration of secondary temporals, midbody scales 24, paravertebral scales 70, subdigital lamellae 12, presacral vertebrae 40, SVL 49.5 mm, AGL 29 mm, tail regenerated FLL 9.5 mm, HLL 11.5 mm, HL 9.1 mm, HW 6.6 mm, HD 5.4 mm. Approximately 10 mm caudal to the axilla is a deep constriction, possibly where another tag was previously tied. Such a missing tag could explain the date assigned to this specimen in the register, which is not mentioned in other literature. On 24.vi.1891, the main party of the Elder Expedition, including the naturalist, Richard Helms, travelled from Camp 8 to Camp 9, at Turner Hill, SA, between 0900–1000hrs, then spent the rest of the day about Camp 9 (Lindsay, 1893). No mention is made of the vegetation at this locality, but the habitat to the north-west of Camp 8 consisted primarily of spinifex on red sand ridges and plains, suitable for *C. m. melanops*. Accordingly, we restrict the type locality for *Lygosoma melanops* to the vicinity of Turner Hill, SA (27°20'S 130°52'E).

Lygosoma (Homolepida) gastrostigma Boulenger, 1898 was described from a single specimen from Sherlock River, Nicol [sic] Bay, WA, collected by Dr E. Clement. The holotype (BMNH 1946.8.9.87; Figs 18,19) agrees well with the type description and figures, and is representative of the Onslow population of *C. m. melanops*. The holotype has supraciliaries six, postsuboculars 4/3, nuchals three, supralabials 7/8, infralabials seven, upper palpebrals 10, lower palpebrals 11, α -configuration of secondary temporals, midbody scales 26, paravertebrals 75, subcaudal scales 77, subdigital lamellae 14/13, presacral vertebral 42, postsacral vertebrae 43, SVL 112 mm, AGL 74 mm, TL 119 mm, FLL 17.5 mm, HLL 23 mm, HL 15.4 mm, HW 11.8 mm, HD 9.5 mm. The difference between the total length as measured by Boulenger (1898) and ourselves (245 mm vs 231 mm) is undoubtedly due to a "soft" section at midbody, allowing stretching of the specimen.

Comparison with other taxa. *Cyclodomorphus m. melanops* differs from *C. branchialis* in possessing more numerous postsuboculars ($\bar{x}$ = 3.9 vs 2.6), upper palpebrals ($\bar{x}$ = 9.7 vs 8.1), lower palpebrals ($\bar{x}$ = 10.9 vs 9.1), paravertebral scales ($\bar{x}$ = 70.0 vs 65.2), subcaudal scales (66–87 vs 57–64) and subdigital lamellae ($\bar{x}$ = 14.1 vs 10.8), usually an α -configuration of the secondary temporals, a generally slightly larger ear aperture, and in lacking dark "gill" markings laterally on the neck. The differences in paravertebral and subcaudal counts are paralleled by differences in axilla-groin length and tail length, and in pre- and postsacral vertebrae. *Cyclodomorphus m. melanops* is a much larger taxon than *C. branchialis* (maximum SVL 132 mm vs 88 mm). The two taxa are separated by the Gascoyne drainage, which has hard soils and lacks *Triodia*, and is generally unsuitable for either taxon. The coastal districts between the distributions of the two are occupied by *C. celatus*.

Cyclodomorphus m. melanops differs from *C. celatus* in having a mode of 26 (24 on Barrow Island and in Central Australia) midbody scales (vs 22; ranges and means 22–28, $\bar{x}$ = 25.4 vs 20–24, $\bar{x}$ = 21.8), a larger, more open ear aperture, more numerous subdigital lamellae (10–18, $\bar{x}$ = 14.1 vs 10–15, $\bar{x}$ = 11.9), a longer tail and slightly broader head (Tables 2,5), dark markings usually absent on head and nape, and in the form of spots rather than streaks on body (vs nape and body, and often head, with dark streaks), and in many populations, a greater mean number of supralabials.

The coloration differences are less obvious in juveniles, with their reduced dark flecks, and in the Centralian adults, which are often similar to *C. celatus*. Juveniles can be differentiated by the extension of the dark head "hood" ventrally over the sides of the neck in *C. celatus*, while the Centralian adults have a more brown to yellow dorsum (vs usually grey in *C. celatus*), either lack the streaked "gill" markings or have them very reduced or disrupted, and have the dorsal markings generally in the form of spots rather than streaks.

The two taxa approach each other in the Lake Macleod region, where *C. celatus* has been recorded as far north as 0.5 km south of "Gnaraloo", along the coastal strip, while *C. m. melanops* extends as far south as Point Cloates coastally, and 6 km south-east of "Manberry" and "Mt Cahill" Outcamp to the east of Lake Macleod, a separation of only 125 km and 75 km respectively (Fig. 4).

The seven *C. celatus* from "Gnaraloo" and "Boolathana" have 7–8 ($\bar{x}$ = 7.2) supralabials, 21–22 ($\bar{x}$ = 21.9) midbody scales, 10–13 ($\bar{x}$ = 11.6) subdigital lamellae, the characteristically small, slit-like ear, and head, nape and body heavily dark streaked on a light grey dorsal ground. The largest specimen has SVL = 105 mm.

The three *C. m. melanops* from Point Cloates and "Ningaloo" have 8, 8 and 7/8 supralabials, 26 midbody scales, 12–16 ($\bar{x}$ = 14.3) subdigital lamellae, a large, open ear, and head and neck immaculate. The largest has SVL = 127 mm, typical of the Exmouth population.

The five *C. m. melanops* from "Manberry" and "Mt Cahill" Outcamp have 7–8 ($\bar{x}$ = 7.4) supralabials, 24–27 ($\bar{x}$ = 25.2) midbody scales, 13–17 ($\bar{x}$ = 14.9) subdigital lamellae and additionally have dorsal ground much more brown than the "Gnaraloo" *C. celatus*.

Cyclodomorphus m. melanops is the geographically closest taxon to *C. maximus*, and the most geographically proximate population, Kimberley, shows a slight trend towards *C. maximus* in a number of characters, including low numbers of paravertebral scales, midbody scales, supralabials, infralabials and nuchals, high numbers of subcaudal scales, subdigital lamellae and upper palpebrals, reduction in degree of dark dorsal spotting and flecking, and the frequent retention of pale spots in subadults. However, in addition to the marked differences in overall size, tail length, number of ear lobules and interparietal proportions, *C. m. melanops* differs from *C. maximus* in having a higher modal number of midbody scales (24 or 26 vs 22), dark dorsal spots but no pale dorsal spots

in adults, and a slightly deeper head (Tables 4,5). Known localities for the two taxa are separated by approximately 165 km (Barnett River Gorge vs “Napier Downs”).

Habitat. *Cyclodomorphus m. melanops* appears to be primarily a *Triodia*-inhabiting form (Butler, 1970; Smith, 1976; Storr & Hanlon, 1980; Heatwole & Butler, 1981; Johnstone, 1983; Storr & Harold, 1985). Of 234 specimens for which microhabitat was recorded, 220 (94.0%) were taken from dead or living *Triodia* or *Plectrachne* tussocks, or from bulldozed *Triodia* spoil, while an additional 16 records were collected in habitats noted as containing *Triodia*. Of the 14 records not taken from hummock grasses, four (WAM R47549, R52946, R63124, R63158) were taken under rubbish, three (WAM R80176, R80247, R85040) in “spoil” (not further described), three (WAM R68360–62) in post-cyclone flood debris, one (WAM R80253) under “litter” in *Triodia* habitat, one (WAM R74882) under a soft-grass tussock, one (WAM R47552) from *Spinifex longifolius* and one (AM R100679) from an *Acacia* litter mat in *Triodia* habitat.

The substrate, topography and extra-*Triodia* vegetation associations inhabited by *C. m. melanops* are quite varied. The Kimberley and Pilbara populations mostly occur on stony to rocky substrates ($n = 50$), both on plains ($n = 4$) and slopes ($n = 5$; WAM R58250: “limestone range”), although it has also been recorded from other substrates (WAM R51717: red sandy soil; WAM R51723: reddish sandy loam; WAM R73972: sandy colluvium; WAM R74074–79: slightly stony, loamy soil; WAM R73941–44: loamy flat; WAM R74882: clay flat), and about the margins or floodplains of seasonally dry rivers and streams ($n = 6$). The vegetation of such substrates is varied, and includes mulga/*Triodia* or *Plectrachne* ($n = 4$) or other *Acacia* species (WAM R80798: “*Acacia xiphophila*, hummock grass on gravelly soil”), mallee/*Triodia* (WAM R73149: “open shrub mallee over *Triodia basedowii* on gibber and loam”) and other eucalypts (WAM R81366–70: “sparse eucalypts over spinifex on stony red soil”). Other described vegetations include “open shrubland/woodland with spinifex, on hard pebble, red sand” (AM R100679); “open savannah grassland on red sandy soil” (CAWC R805–06, WAM R60229–33) and “low shrubs/*Triodia* on red sandy loam” (WAM R71651).

Further to the west, the Onslow and Exmouth populations largely occur on sandy substrates, both dunes ($n = 6$; WAM R61109–12: “light soil behind coastal dunes”: AM R101631: “red sand dunes with locally outcropping limestone”) and plains ($n = 2$; WAM R61248–50: “light yellowish soil plain”), with a variety of vegetation associations (WAM R71487–89: “*Acacia* *Triodia* on red dune”; WAM R76421, R78944: “hummock grassland dominated by *T. angusta* on sandy substrate”; WAM R80176: “*Eucalyptus camaldulensis* woodland over open shrubs on brown sandy loam”; WAM R80247: “sparse low shrubs on red sandy loam”; WAM R85040: “open *Eucalyptus microtheca* over open *Acacia* and *Triodia* on red loam”). One specimen was recorded from harder substrates (WAM R81306: stony red clay).

To the east of the Pilbara, the Great Sandy Desert and more western Centralian populations also largely inhabit sandy substrates ($n = 1$), both dunes ($n = 6$; WAM R63539: “desert oaks over spinifex on dune slope”) and plains (WAM R63947: “mallee over mulga over spinifex, sandy loam plain with anthills”), although harder substrates have been recorded, particularly for the more eastern Centralian populations (AM R52074–76: sandstone hills; “rocky ground at foot of range”: Smith & Johnstone, 1979; WAM R63771: “mallee over shrubs over mulga over melaleuca; loamy sand, gravel and pebbles”; WAM R20790: “mulga flat”: CAWC R1017: “sandy burnt area of *Thryptomene maisonneuvei*; spinifex on occasional sandstone outcrops”).

Reproduction. There has been little published on reproduction in *C. m. melanops*. Smith (1976) recorded reproductive activity in gonads of Barrow Island specimens collected 17 August–13 September, with up to 5 enlarged ovarian follicles, while Heatwole & Butler (1981) record a single full-term embryo in a Barrow Island female collected 6 February. Pianka (1986) records a single litter of 3.

Male reproductive cycles in *C. m. melanops* are strongly seasonal (Fig. 20). Enlarged turgid testes ≥ 5.0 mm in length were present in most mature-sized males collected between May and September, with testis length peaking in late August–early September. Testes of mature-sized males collected outside this period were generally small and flattened.

Female reproductive cycles are similarly seasonal (Fig. 21). Only one of 34 mature-sized females collected between 12 March and 18 August showed signs of reproductive activity. Most females collected in late August–early September showed an increase in size of ovarian follicles, and enlarged yolking ovarian follicles were present between 22 September and 26 November. Unshelled oviducal eggs and developing embryos were present between 17 October and January, with a single record of full-term young on 8–11 March, although all late January and February specimens were non-gravid, suggesting that parturition had generally occurred by then.

We conclude from the above data that spermatogenic activity reaches a peak in late August, coinciding with mating and fertilisation, and young are born in January, following approximately 4 months gestation.

Only four of 24 mature-sized females collected in October and November were not gravid, suggesting that breeding generally occurs annually.

Gravid females carried 1–4 ($\bar{x} = 2.6$, mode 3 [46.4%], $n = 31$) enlarged yolking ovarian follicles, unshelled oviducal eggs or fully developed embryos. Litter size was not significantly related to maternal SVL ($r = 0.2270$, $P = 0.245$).

Growth rates. Seasonal distribution of body sizes in the material examined (Fig. 22) indicates a clear year 1 cohort, and suggests that a SVL of about 82–83 mm

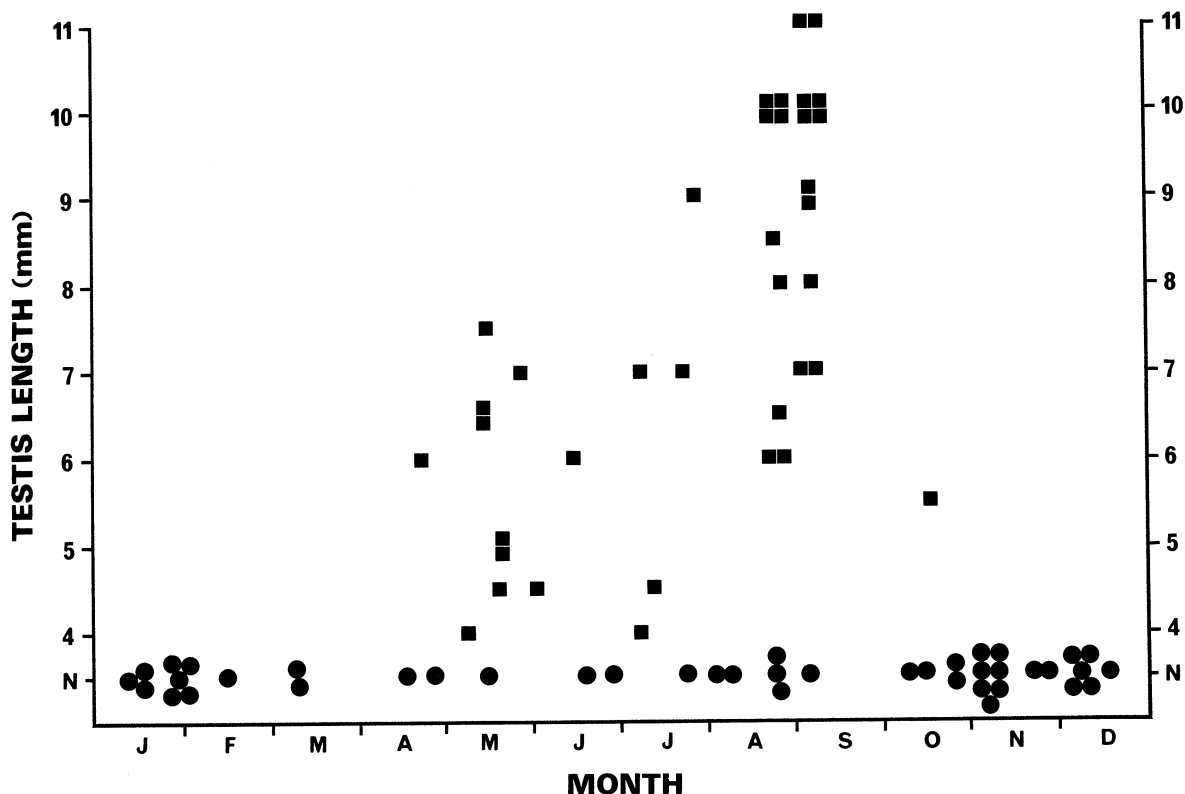


Fig. 20. Seasonal variation in length of turgid testes, and the occurrence of flaccid testes in *Cyclodomorphus melanops melanops*.

(size at maturity) is reached in the second or third year.

Sex ratio. The sex ratio of mature-sized material examined is 87 males : 127 females, significantly different from 1:1 ($\chi^2_1 = 7.11^{**}$). An excess of females is present in both northern (Kimberleys; 12:14) and southern material (Pilbara, 48:73, Barrow Island, 18:26, Centralian and Great Sandy 9:14) and in southern seasonal samples (summer 8:17, autumn 11:15, winter 27:43, spring 27:38). Seasonal sex ratios are not significantly different to each other (4×2 contingency table, $\chi^2_3 = 0.81$, n.s.).

Diet. The diet of the Barrow Island population includes annelids, spiders, roaches, termites, lepidoptera and beetles (Smith, 1976), while the stomachs of six Centralian specimens contained 54% termites, 16% grasshoppers/crickets, 13% beetles, 8% bugs, 4% roaches, 2% lepidoptera, 3% unidentified arthropods, and <0.5% each of spiders, ants, insect larvae and vertebrates (Pianka, 1986).

Specimens examined. **KIMBERLEYS:** AM R45605–07, MV D42000–02, WAM R47490–501, R47504–15, Lake Argyle, WA; AM R76648, Jasper Gorge, NT; CAWC R805–06, WAM R60229–33, Spring Ck, c. 58 km north “Wave Hill”, NT; NTM R6652–60, Nicholson River Gorge, “Nicholson”, WA; R7032–

34, between Fitzroy Crossing and Halls Creek, WA; R7277–81, 167 km east Fitzroy Crossing, WA; WAM R23038–39, 26 km south-south-east “Gogo”, WA; R27759, “Mt Anderson”, WA; R46051–54, 76 miles south-west Halls Creek, WA; R46111–12, “Margaret River”, WA; R57121, 22 km north “Mistake Creek”, NT; R57161, 67 km south-west Halls Creek, WA; R58250, “Napier Downs”, WA; R60292, 3 km south-east “Nicholson”, WA; R70489–90, 64.0 km 265° “Louisa Downs”, WA; R79064–65, “Brooking Springs”, WA. **BARROW ISLAND, WA:** WAM R27757–58, R28460, R28684–91, R47546–84, R47850, R56678–86. **EXMOUTH, WA:** AM R81284, Yardie Creek camp; R101631, just west of “Bullara”; R101959, “Yardie Creek”; WAM R13199, R13232, Point Cloates; R21767–69, 25 miles north-east “Ningaloo”; R22402, 8 miles south Learmonth; R22403, 5 miles south Learmonth; R22404, 3 miles south Learmonth; R27752–55, “Yardie Creek”, 40 miles south homestead; R31416, presumably vicinity of Exmouth; R32029, 2 miles east Norwegian Bay, “Ningaloo”; R51013–14, Exmouth; R51015, “Bullara”, R52932, Shothole Canyon, Cape Range; R52946, Vlaming Head Lighthouse, Exmouth; R61109–12, 9 km north Yardie Creek; R61248–50, 14 km north Yardie Creek; R61271, R88634, 3 km north-west “Bullara”; R61426–27, R88619, Yardie Creek mouth; R83154–61, “Yardie Creek”.

PILBARA, WA: ONSLOW: AM R49082, Roebourne; R123076–77, 6.7 km south Cane River crossing on hwy; BMNH 1946.8.9.87, Sherlock River, Nickol Bay (type of *Lygosoma gastrostigma*); SAM R22881, 12 km south Barradale

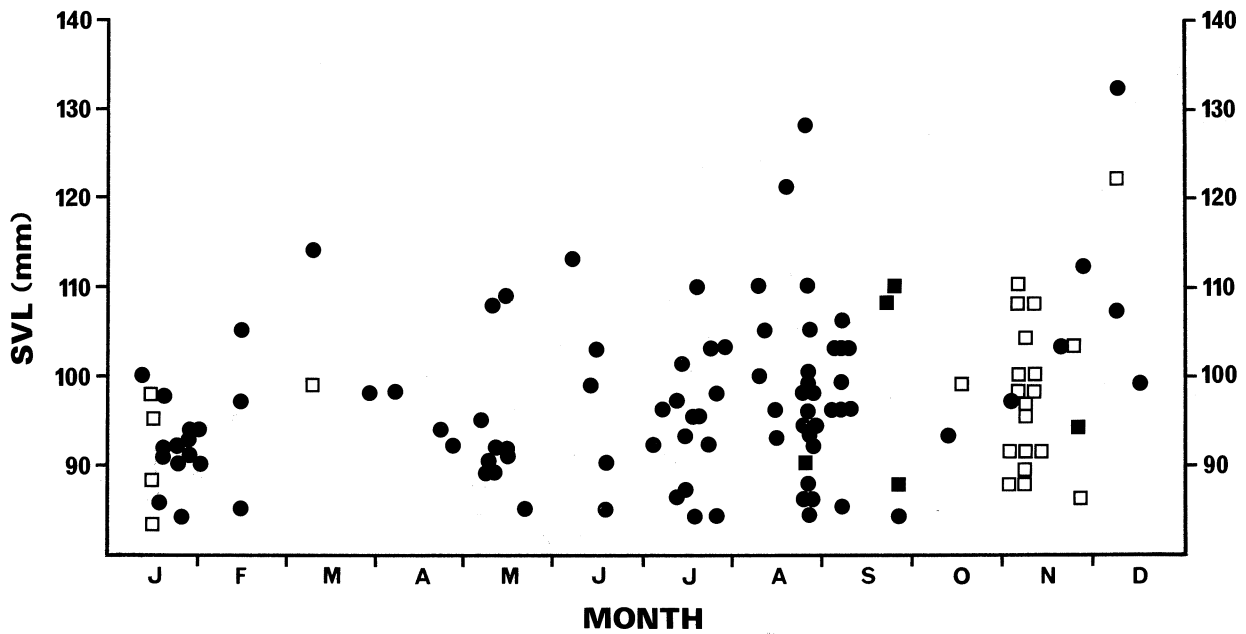


Fig. 21. Seasonal occurrence of non-vitellogenic follicles (dots), yolking ovarian follicles (squares) and oviducal embryos (open squares) in *Cyclodomorphus melanops melanops*.

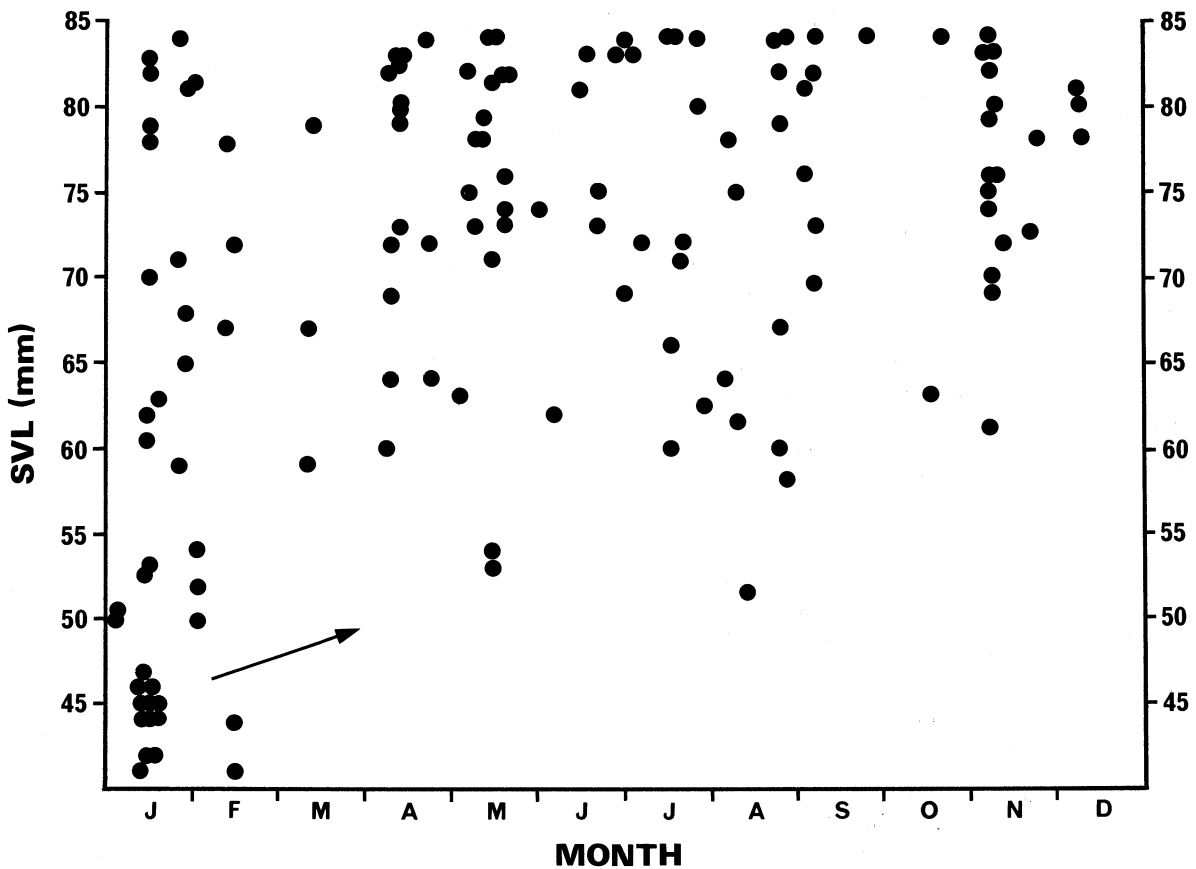


Fig. 22. Seasonal variation in SVL in immature *Cyclodomorphus melanops melanops*. Arrow indicates inferred growth of first year cohort.

Roadhouse; WAM R13862, "Mardie"; R14277, Dolphin Island, Dampier Archipelago; R22933, Karratha; R25631, 17 miles east "Yarraloola"; R25641, 10 miles east "Yarraloola"; R25647, R25656, 16 miles east "Yarraloola"; R25651–52, 10 miles north "Peedamulla"; R25653, 10 miles west "Peedamulla"; R25659–60, 15 miles east "Yarraloola"; R61543–45, R96785, Myaree Pool; R61581, Jundalaya Hill, 15 km west "Nanutarra"; R61594–97, Cattle Pool, Cane River; R68332, Pannawonica; R71487–89, 6 km south-east "Manberry"; R71592–93, "Mt Cahill" Outcamp, 16 km south-east "Mardathuna"; R76421, Harding River, c. 52 km south-east Karratha; R78944, Harding River, 32 km south-east Karratha; R80176, R81306, 2 km south Barradale Roadhouse; R80247, 4 km west Barradale Roadhouse; R80253, 9.5 km north-west Barradale Roadhouse; R80739, 1 km south Nanutarra Roadhouse; R84263, Burrup Peninsula; R85040, 11 km north-north-west "Uaroo"; R91137, Harding River Dam; R94389–91, 3 km north-north-west "Cane River". **LOWER ASHBURTON:** AM R15482, WAM R25355, Kookhabinna Gorge, Barlee Range; AM R15484–87, "Ullawarra"; WAM R25265, 13 miles north-west "Ullawarra"; R84069, "Glenflorrie" HS. **MILLSTREAM:** SAM R4569, R4573, WAM R20170–74, R20176–77, R20182, R20186, R94607, "Millstream"; SAM R4570, WAM R20175, 28 miles south "Kangiangi"; SAM R4571, WAM R20179, R20185, 3 miles east Mt Ulric; SAM R4574, Mt Ulric Gorge; SAM R4582–83, Fortescue Creek, "Millstream"; SAM R4584, WAM R20178, "Tambrey"; SAM R4585, WAM R20184, 5 miles north "Kangiangi"; WAM R20181, "Coolawanyah" aerodrome; R51717, 100 km north-west Wittenoom; R74915–18, "Mt Brockman"; R81366–70, 3 km east "Millstream"; R88667, 2 km north-east "Millstream". **HAMERSLEY:** SAM R4572, R4576, WAM R20183, Asbestos Creek; WAM R13090, R13327, R27751, R82718, "Woodstock"; R13322, Dale Gorge, Wittenoom; R34731, Kyan Pool, "Hooley"; R37071, 6 miles north Wittenoom; R37086, Hancock Gorge, 9 miles south Wittenoom; R54381, R55908–09, R56837, R69767–68, Marandoo; R55987, 3 km west East Ore Body, Paraburdoo; R55988, Paraburdoo; R69681–82, c. 10 km east Marandoo; R69713–15, 4 km west Marandoo; R69736, north-east side Mt Bruce; R69748, R69766, Coppin Pool, Turee Creek; R73564, nr Barnett Creek, 30 km north-north-west Tom Price; R73745, R73750, 22 km west Tom Price; R74882, 10 km south-south-east Mt Bruce; R74897, 10 km south-west "Rocklea"; R76538, 20 km north-west Tom Price; R76555, 24 km north-north-west Tom Price; R76558, 4 km west Tom Price; R76562, 4 km north-north-west Tom Price; R80798, Milli Milli Spring, Hamersley Range. **UPPER ASHBURTON:** AM R100679, WAM R23953–64, R25188–92, Kumarina; WAM R22701, "Mulgul"; R22804–05, Nichol Spring, 30 miles south "Mt Vernon" on Ethel Creek; R25235, 18 miles north-west "Mt Vernon". **MOUNT NEWMAN:** AM R76228, camp on Weeli Wolli Creek, nr "Marillana"; WAM R25176, R29742, Mt Newman; R27756, "Poonda", 28 miles south-west "Roy Hill"; R67898, 34 km south-east Mt Meharry; R71651, 21 km west-south-west "Marillana"; R73149, 24 km south-west "Marillana"; R73939, Weeli Wolli Spring; R91660, 38 km west-north-west Newman. **TALAWANA:** WAM R19850, "Balfour Downs"; R25187, 20 miles east Jigalong; R39129–30, "Talawana"; R42232–33, Junction Well, Oakover River. **OAKOVER:** WAM R13198, R13239, R83170–71, Burramine; R13237, R83162–66, Budjan Creek, 8 km south "Corunna Downs"; R13238, R83167–69, Ripon Hills; R13242, R84988–92, Mosquito Creek-Eastern Creek; R36337, 10 miles south Nullagine; R45761–62, 3 miles south-east "Mt Edgar"; R51723, 24 km north "Roy Hill"; R58962–63, 65 km north "Roy Hill"; R63109, 15 km c. 125° Nullagine; R63119–20, 2 km 156°

Italy Bore; R63124, R74087, Rove Hills Mine; R63143–46, Woody Woody Mine; R63158, 5 km 336° Skull Spring; R68360–62, between Nullagine and "Roy Hill"; R73941, 16 km south-east Nullagine; R73942–44, R73972–91, 5 km east-north-east Kurrana Well; R74074–79, 7 km east-north-east Kurrana Well; R74090–92, Skull Spring, Davis River; R74097–99, 16 km south Upper Carawine Pool; R83881–84, "Warrawagine"; R94679, Carawine Gorge.

GREAT SANDY DESERT, WA: WAM R15842, 17 miles north Weld Spring, Canning Stock Route; R53634, south end Carnarvon Range; R63459, Tobin Lake; R63539, 2 km 36° Murguga Well (Canning Stock Route No. 39); R63771, 1 km north Talbot Soak; R63947, 12 km north-north-east Well 29, Canning Stock Route; R94712, "Glenayle".

CENTRALIAN: AM R17257–59, 20 miles east Piltadi, Mann Range, SA; R26399–401, nr Peterman Range, 61 miles from WA border, NT; R52074–76, Stuart Hwy, 18 miles south-west Barrow Creek, NT; R52077, Barrow Creek, NT; CAWC R835, Ayer's Rock, NT; R1017, nr Mereenie, Well No. 1; CAWC R1105, "McLaren Creek", NT; NTM R1706, Armstrong Creek, 100 km west Ayer's Rock, NT; NTM R12109–10, 7 km south-west Bull Creek Bore, Davenport Range, NT; SAM R343, Central Australia; R25882, north-west tip Cavenagh Range, 1 km south-east Linton Bore, WA; R29549, Mt Crombie, SA; WAM R15157, 8 miles south-south-east Warburton Range Mission, WA; R16554, 20 miles south-west Warburton Range Mission, WA; R20708–09, 11 miles south-west Muggan Rock Hole, WA; R20736, Cavenagh Range, WA; R20752, 23 miles south-east Giles, WA; R20790, 27 miles west-north-west Mt Olga, NT; R20958–59, 28 miles west "Musgrave Park", SA; R20991, 9 miles west Cavenagh Range, WA; R20999, Mt Palgrave, Barrow Range, WA; R22176, 5 miles south Warburton Range Mission, WA; R24355, 6 miles south-west Barrow Creek, NT; R24362, 15 miles south-west Barrow Creek, NT; R28992, Jameson Range, WA; R40142, Davenport Range, NT; R46552–53, 6 miles south-west Nullie, WA; R60158, 62 km east Neale Junction, WA; R85667–68, R85670, 8 km west-north-west Point Salvation, WA.

Cyclodomorphus melanops elongatus
(Werner, 1910)

Figs 23–28

Lygosoma (*Lygosoma*) *muelleri* Peters, 1878: 191.

Lygosoma (*Homolepida*) *branchiale elongatum* Werner, 1910: 479.

Lygosoma (*Homolepida*) *petersi* Sternfeld, 1919: 81. [*nom. nov. pro. Lygosoma muelleri*, at that time a junior homonym of *Scincus muelleri* Schlegel, 1839].

Lygosoma (*Homolepida*) *woodjonesii* Proctor, 1923: 80.

Diagnosis. *Cyclodomorphus m. elongatus* differs from all other members of the *C. branchialis* species group in possessing a mode of 24 or more midbody scales, 61–85 paravertebral scales, 58–77 subcaudal scales, moderately large, open ear aperture, usually β -temporal configuration, and mid grey-brown to dark olive green dorsum without dark spots.

Description. Prefrontals rarely in narrow to moderate contact (1.1%, n = 378), fused to frontonasal unilaterally

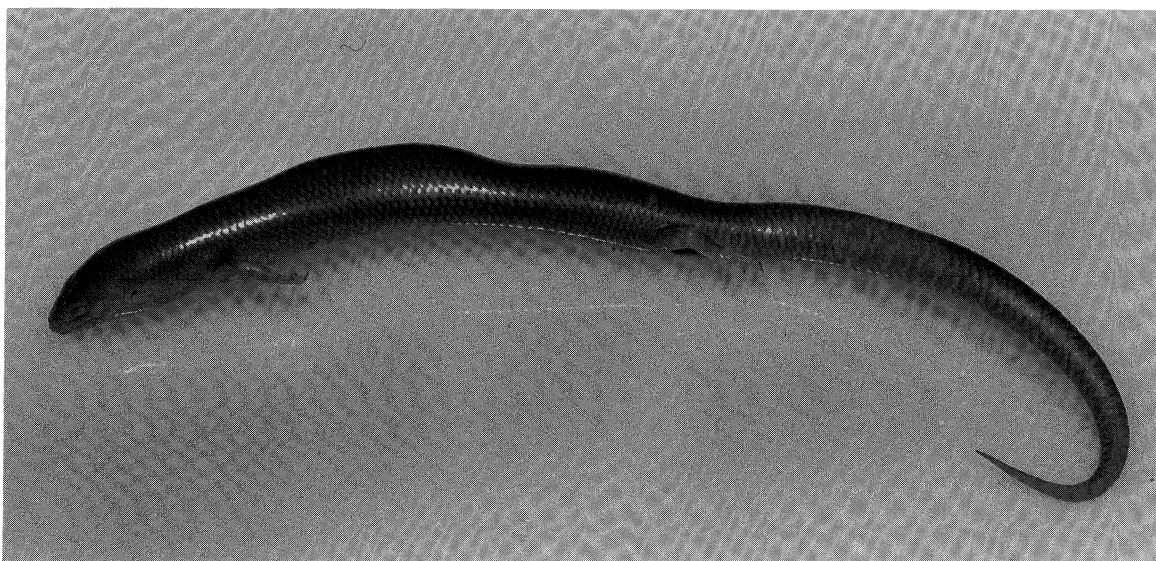


Fig. 23. Lectotype of *Lygosoma muelleri* Peters (ZMB 9373).

(0.3%) or bilaterally (0.3%) or fused to frontal unilaterally (0.3%); parietals completely separated by interparietal (94.4%, $n = 372$), or in point to moderate contact caudally (5.6%); interparietal broadest rostrally, approximately $2/3$ – $9/10$ length and breadth of frontal; transversely enlarged nuchals 0–5 on each side ($\bar{x} = 2.9$, $SD = 0.70$, $n = 753$), usually three (64.7%); loreals rarely three unilaterally (1.1%, $n = 366$) or bilaterally (0.3%), one unilaterally (1.1%) or bilaterally (0.6%) or absent unilaterally (0.3%); supraoculars rarely four unilaterally (0.5%, $n = 377$), two unilaterally (1.3%) or one unilaterally (0.3%), reduction to two due to partial fusion of first and second ($n = 1$) or fusion of second and third ($n = 2$); supraciliaries 4–8 ($\bar{x} = 6.0$, $SD = 0.38$, $n = 752$), usually six (89.2%), first and last largest, third-last usually projecting between second and third supraocular, remainder moderate, subequal; presuboculars rarely three unilaterally (0.3%, $n = 354$) or one unilaterally (0.3%); postsuboculars 2–4 ($\bar{x} = 3.4$, $SD = 0.51$, $n = 753$), usually three (60.2%); upper palpebrals 7–11 ($\bar{x} = 8.7$, $SD = 0.88$, $n = 348$); lower palpebrals 8–12 ($\bar{x} = 9.7$, $SD = 0.87$, $n = 348$); secondary temporals usually in β -configuration (88.2%, $n = 768$), rarely in α -configuration (11.8%); supralabials 6–9 ($\bar{x} = 7.2$, $SD = 0.44$, $n = 747$), usually seven (76.8%), usually third-last (99.1%) below centre of eye, separating pre- and postsuboculars, rarely fourth last (0.4%) or second last (0.5%); infralabials 5–8 ($\bar{x} = 6.2$, $SD = 0.43$, $n = 750$), usually six (80.4%); usually first two (94.5%, $n = 752$), rarely first three (4.8%) or first (0.7%) infralabials contacting postmental; ear moderate, oval, usually subequal in height to eye, with 0–3 ($\bar{x} = 1.09$, $SD = 0.33$, $n = 708$), usually one (89.0%), small to large rounded lobules along rostral margin.

Body scales in 22–29 ($\bar{x} = 25.1$, $SD = 1.27$, $n = 385$), usually 24 (42.1%) or more (55.3%), longitudinal rows at midbody; scales in paravertebral rows moderately broader than adjacent lateral dorsal scales, 61–85 ($\bar{x} =$

72.1, $SD = 4.41$, $n = 386$); subcaudal scales 58–77 ($\bar{x} = 68.2$, $SD = 3.90$, $n = 173$); lamellae below fourth toe 9–17 ($\bar{x} = 12.6$, $SD = 1.27$, $n = 699$), each with a narrow to broad light to mid-brown callus.

SVL 41–125 mm ($n = 401$); AGL/SVL 50.0–76.3% ($\bar{x} = 63.6\%$, $n = 389$); TL/SVL 69.1–110.3% ($\bar{x} = 93.9\%$, $n = 182$); FLL/SVL 10.9–23.5% ($\bar{x} = 16.6\%$, $n = 397$); HLL/SVL 15.3–29.3% ($\bar{x} = 21.5\%$, $n = 393$); FLL/HLL 66.7–92.0% ($\bar{x} = 77.1\%$, $n = 392$); HL/SVL 12.3–22.5% ($\bar{x} = 15.5\%$, $n = 392$); HW/HL 60.8–85.1% ($\bar{x} = 72.7\%$, $n = 393$); HD/HL 45.9–67.6% ($\bar{x} = 55.9\%$, $n = 392$).

Presacral vertebrae 38–44 ($\bar{x} = 41.7$, $SD = 1.23$, $n = 115$); postsacral vertebrae 35–45 ($\bar{x} = 39.4$, $SD = 1.90$, $n = 42$); phalangeal formula for manus and pes 2.3.4.4.3.

Allometry. With respect to SVL, AGL and TL showed positive allometry, while limb lengths and HL showed negative allometry. With respect to HL, both HW and HD showed positive allometry (Table 10).

Coloration (in preservative). Dorsum mid grey-brown to dark olive green, venter cream. Body scales usually with slightly darker edges, forming an obscure dark reticulum. Soles cream, with light grey to dark grey-brown tubercles and calli. Upper lips and sides of neck usually cream, with grey margins to scales.

Juveniles, and occasional subadults, as for adults, but with a single cream to pale yellow fleck in most dorsal and lateral body and tail scales, aligned laterally to form vertical bars.

Coloration (in life). AM R111032–33 were light greyish-green above, becoming cream with a greenish tinge ventrolaterally and cream ventrally; greenish edges to ventral scales forming a reticulum; tail and vent with a very weak yellowish flush; head greenish-grey, slightly darker than body dorsum; yellowish tint around ear;

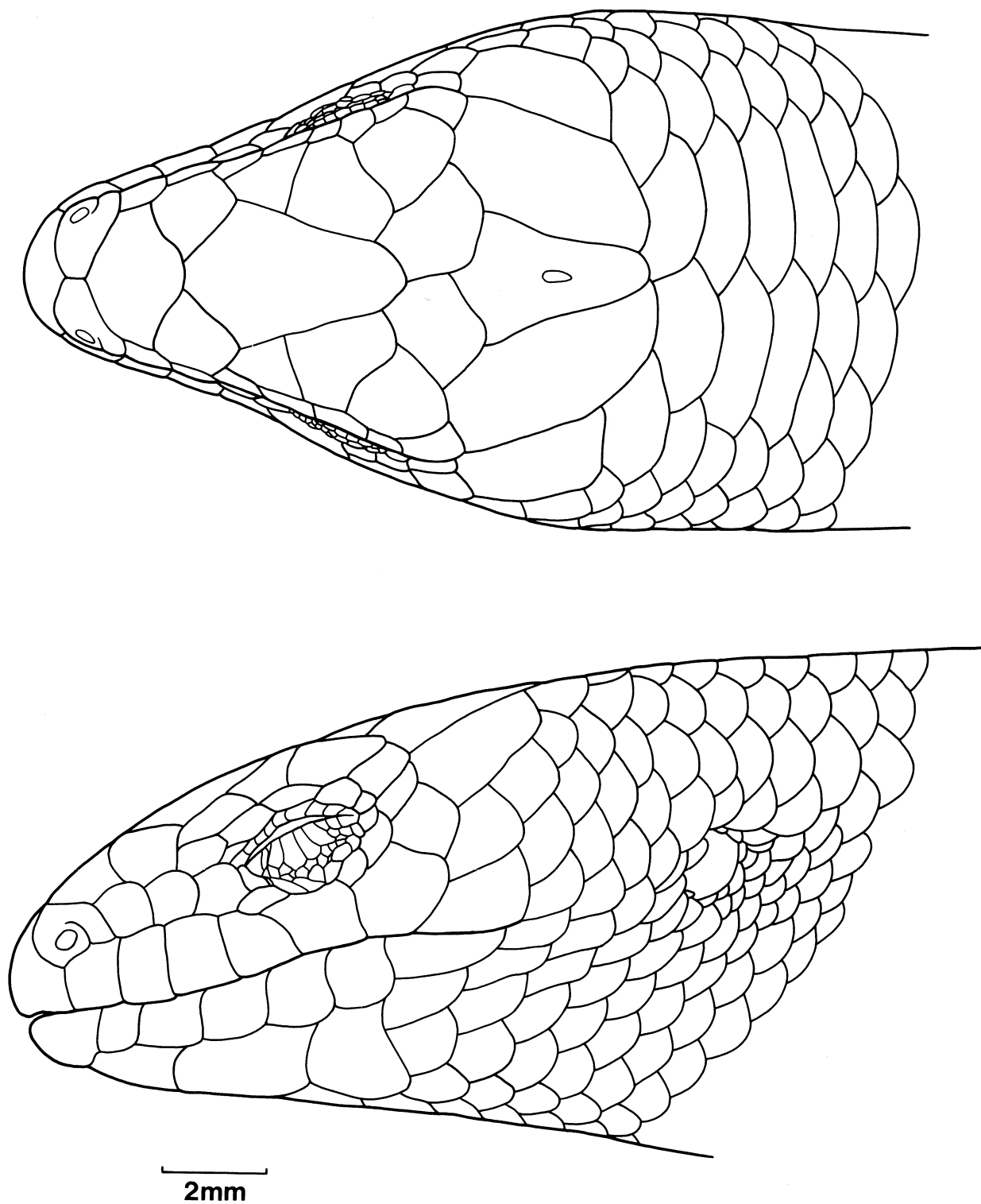


Fig. 24. Head shields of lectotype of *Lygosoma muelleri*.

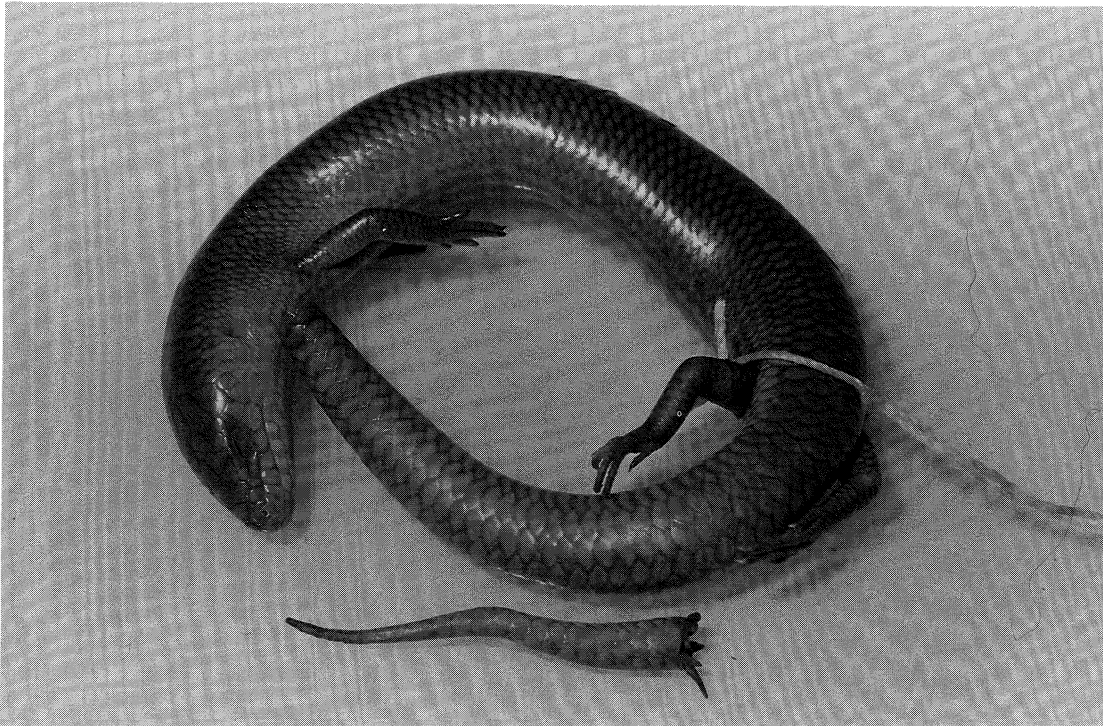


Fig. 25. Holotype of *Lygosoma (Homolepida) branchiale elongatum* Werner (ZMH R03961).

palms cream; pupil black; mouth lining pink.

Both specimens, as well as AM R107954–56, R121029 and two live specimens from 12.5 km north “Coombah”, had irides orange and tongue dark blue-black. In AM R105443 and R105446, the irides were orange, tongue blue-brown and venter green-white, with an orange flush over the belly and tail base (Shea & Wells, 1985).

Sexual dimorphism. Mature-sized males (SVL 71–111 mm, $\bar{x}$ = 87.2 mm, SD = 9.15, n = 134) were significantly smaller than mature-sized females (SVL 75–122 mm, $\bar{x}$ = 93.3 mm, SD = 9.82, n = 148; Mann-Whitney U test, z = 5.015***). Males additionally had shorter bodies, but longer tails, limbs and heads than females at a given SVL (Table 11).

Females had a greater number of paravertebral scales (61–85, $\bar{x}$ = 73.5, SD = 4.41, n = 174 *vs* 61–81, $\bar{x}$ = 70.7, SD = 4.22, n = 140; t_{312} = 5.66***) and subcaudal scales (61–77, $\bar{x}$ = 68.8, SD = 3.41, n = 71 *vs* 60–76, $\bar{x}$ = 67.3, SD = 3.41, n = 72; t_{141} = 2.55*) than males.

No significant differences were found between sexes in mean number of midbody scales, subdigital lamellae, supralabials, infralabials, supraciliaries, postsuboculars, nuchals, upper palpebrals or lower palpebrals.

Distribution. *Cyclodomorphus m. elongatus* occurs through the *Triodia* deserts and semiarid areas of southern Australia (Fig. 14), from 1 km west Lake Cronin and 70 km north Bullfinch, WA in the west, through the Western Australian Goldfields, Great Victoria Desert, northern Eyre Peninsula, Gawler and Flinders Ranges to 12.5 km north “Coombah”, NSW in the east,

with outlying populations in western Queensland (“Diamantina Lakes” north to 41 km south Dajarra, and south-east to 5 km west “Fermoy”), central Australia (Blackstone Mining Camp and Bell Rock Range, WA in the south-west to “Ti Tree”, NT in the north-east) and Nuyts Archipelago, SA (St Francis, Fenellon and Lacy Is.).

Four old specimens (SAM R2728a–c, R2729) recorded from Flinders Island, SA (Hudson *et al.*, 1981) are not supported by recent collections from that island, and may have come from the Nuyts Archipelago, which population they most closely resemble. For the purposes of exploring geographic variation, however, the records are considered valid. A single record from Kangaroo Island (SAM R2730) is unsupported by subsequent collections from this herpetologically well-known island (Houston & Tyler, 1979) and is considered erroneous.

Geographic variation. For the purposes of describing geographic variation, the overall distribution of *C. m. elongatus* was divided into nine subpopulations, named, approximately from west to east, Boorabbin, Zanthus, Centralian, Ooldea, Nuyts, Eyre Peninsula, Flinders Island, Flinders Ranges, NSW and Queensland (Fig. 14). Statistically significant variation was present in all scalational characters assessed. In general, the most different populations were peripheral, particularly those on the eastern and northern periphery, with in many cases, greater numbers of scales in the eastern (Flinders Ranges, Queensland, NSW) populations.

Paravertebral scales. ANOVA: $F_{9,373} = 33.056^{***}$. Means ranged from 68.3 (Zanthus) to 77.7 (Flinders Ranges). A trend towards higher means in the east and

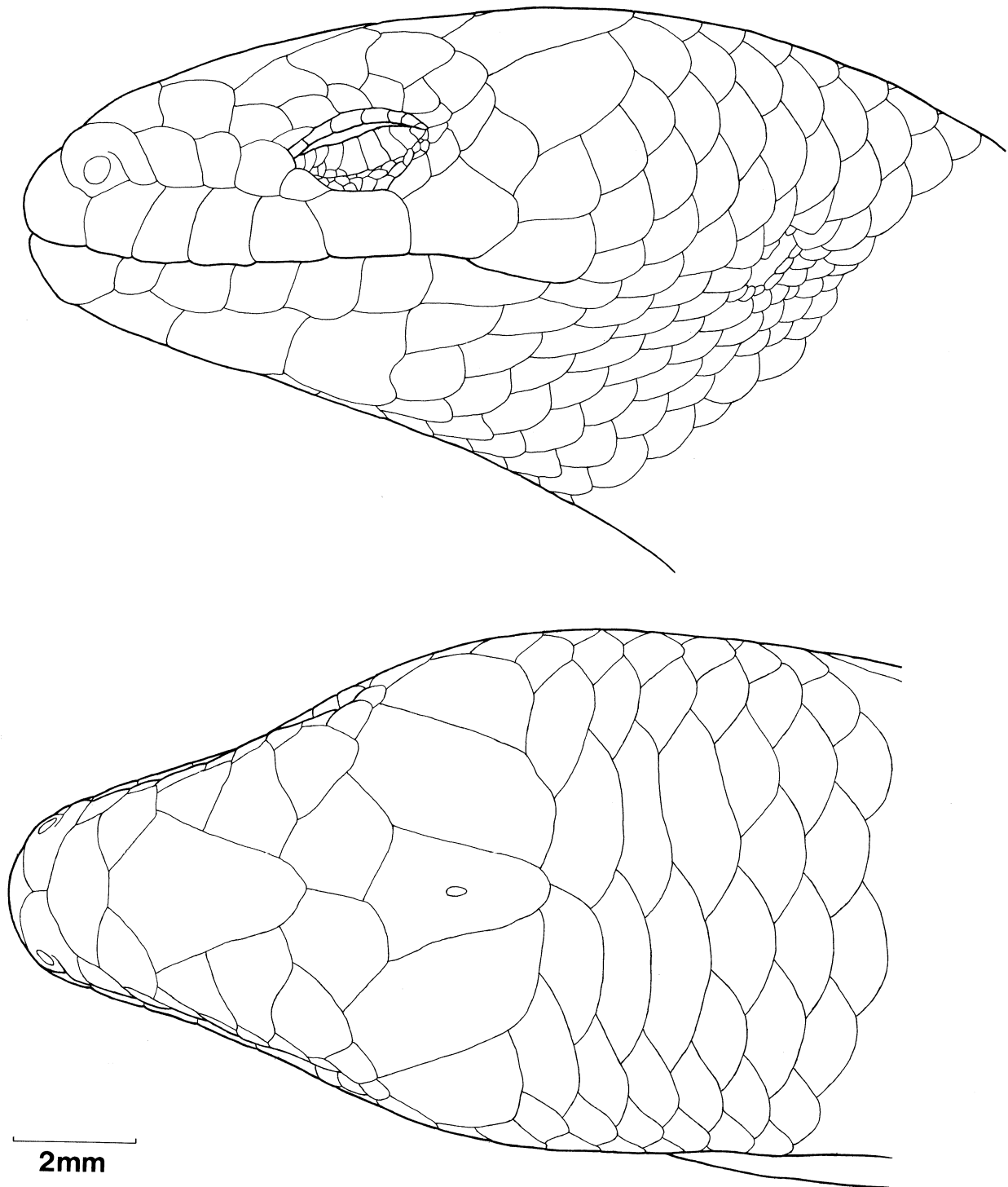


Fig. 26. Head shields of holotype of *Lygosoma (Homolepida) branchiale elongatum*.

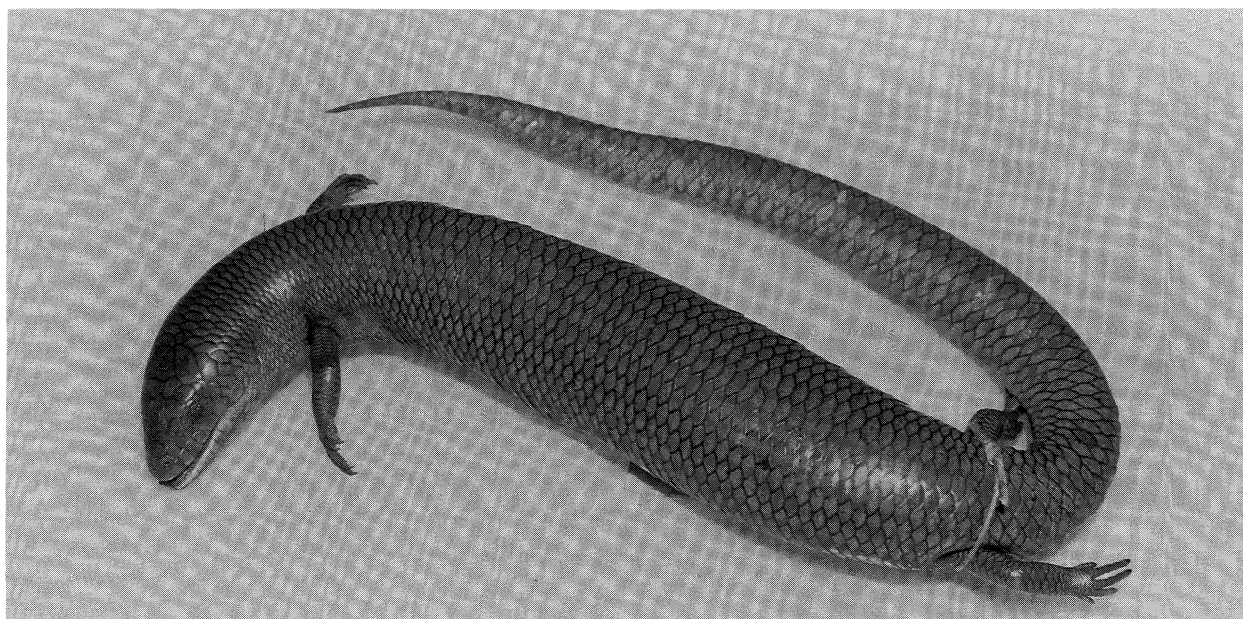


Fig. 27. Lectotype of *Lygosoma (Homolepida) woodjonesii* Proctor (BMNH 1946.8.17.97).

north was apparent, with the four highest means (Centralian, Flinders Ranges, NSW, Queensland; $\bar{x}$'s = 74.1–77.7) significantly different to many other populations, including the most geographically proximate populations (Centralian, Flinders Ranges, Queensland vs Boorabbin, Eyre Peninsula, Flinders Island, Ooldea and Zanthus; former two also vs Nuyts; NSW vs Boorabbin and Zanthus). Amongst the other populations, the only significant differences were between the three extreme means (Zanthus vs Eyre Peninsula and Nuyts; $\bar{x}$'s = 71.4–71.5).

Midbody scales. ANOVA: $F_{9,373} = 18.239^{***}$. Means ranged from 24.5 (Ooldea, Queensland) to 27.1 (NSW, Nuyts), with only the latter and the Centralian population having means greater than 25.0 and modes greater than 24 (26 in Centralian, 28 in NSW, Nuyts). These three populations, all peripheral, have significantly greater means than most other populations (all vs Boorabbin, Eyre Peninsula, Ooldea, Queensland and Zanthus; NSW and Nuyts also vs Centralian and Flinders Ranges).

Subcaudal scales. ANOVA: $F_{8,162} = 15.747^{***}$. No data were available for the Flinders Island sample. Means ranged from 65.3 (Boorabbin) to 74.4 (Queensland), with only the latter and Flinders Ranges ($\bar{x} = 71.8$) above 69.3. A general trend for higher means in the east and north of the distribution was apparent, with the Queensland mean significantly greater than all but the Flinders Ranges mean, while the Eyre Peninsula, Zanthus and Boorabbin means, the three lowest ($\bar{x}$'s = 65.3–66.7), were significantly lower than the Queensland, Flinders Ranges and Centralian means.

Subdigital lamellae. ANOVA: $F_{9,684} = 46.196^{***}$. Means varied from 11.6 (Eyre Peninsula) to 14.7 (Queensland), although only the latter mean was greater than 13.2. The Queensland mean was significantly greater than all other means, while the three lowest means (Ooldea,

Flinders Ranges, Eyre Peninsula, $\bar{x}$'s = 11.6–12.2), all from the central part of the subspecies' distribution, had significantly lower means than most other populations, including those immediately adjacent (all vs NSW, Nuyts, Queensland and Zanthus; Flinders Ranges and Eyre Peninsula also vs Centralian; Eyre Peninsula also vs Boorabbin).

Supralabials. ANOVA: $F_{9,735} = 11.687^{***}$. Means ranged from 7.1 (Boorabbin, Queensland) to 7.9 (NSW), although only the latter and Flinders Ranges ($\bar{x} = 7.7$) had means above 7.4 and modes other than seven. These two high means were significantly different to most other populations (both vs Boorabbin, Centralian, Eyre Peninsula, Ooldea, Queensland and Zanthus; NSW also vs Nuyts). The only significant difference between other populations was between Nuyts ($\bar{x} = 7.4$) and Queensland.

Infralabials. ANOVA: $F_{9,736} = 8.404^{***}$. Most populations had mode six and means of 6.0 (Boorabbin, Zanthus) to 6.4 (Flinders Island), with significant differences between only Boorabbin and Centralian, and Zanthus and Centralian and Queensland. The NSW population ($\bar{x} = 6.8$, mode seven) had a significantly greater mean than all but the Flinders Island population.

Supraciliaries. ANOVA: $F_{9,736} = 4.211^{***}$. Six supraciliaries was modal for all populations. Means ranged from 5.9 (Boorabbin) to 6.5 (Flinders Island), with only the latter mean and Flinders Ranges ($\bar{x} = 6.3$) greater than 6.1. The Flinders Island and Flinders Ranges means were significantly different to the Centralian, Zanthus and Boorabbin means, with the Flinders Island mean also different to the Ooldea and Eyre Peninsula means. The only other significant difference was between the Boorabbin and Queensland means. In no cases did these differences involve contiguous populations.

Postsuboculars. ANOVA: $F_{9,737} = 12.129^{***}$. Means

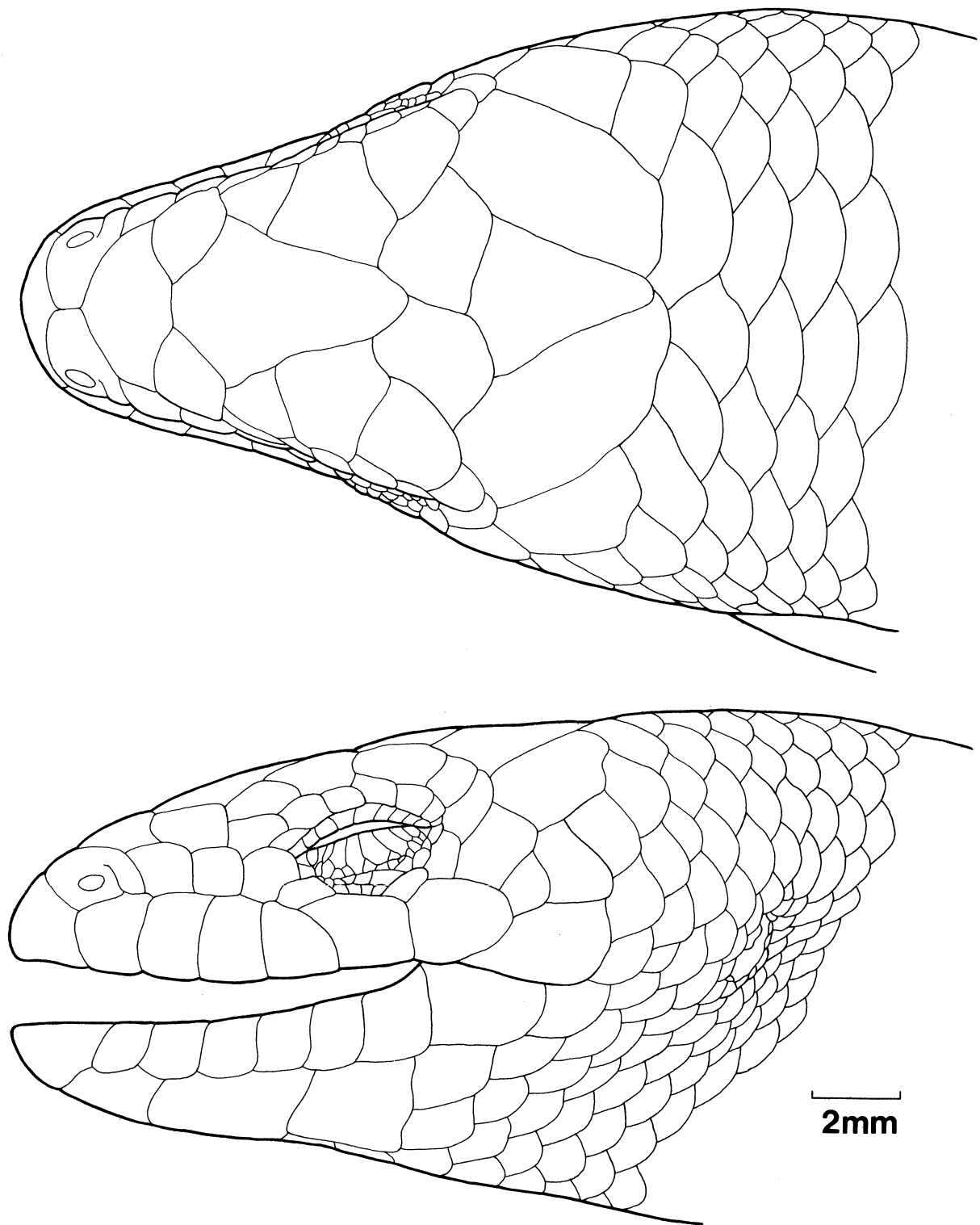


Fig. 28. Head shields of lectotype of *Lygosoma (Homolepida) woodjonesii*.

ranged from 3.1 (Boorabbin) to 3.8 (Flinders Island, Nuyts). In general, the easternmost populations (NSW, Queensland; $\bar{x}$ = 3.7) and insular populations had greater means and modes (four in all) than elsewhere in the distribution (all *vs* Boorabbin, Zanthus and Centralian; Queensland and Nuyts also *vs* Eyre Peninsula, Ooldea).

Nuchals. ANOVA: $F_{9,740} = 9.732^{***}$. All populations had mode three. Means ranged from 2.2 (NSW) to 3.4 (Queensland), although all other means were within the range 2.5–3.0. The two extreme values, both from populations at the extreme east of the distribution, were significantly different to most other means (Queensland *vs* Boorabbin, Centralian, Eyre Peninsula, Flinders Ranges, NSW, Nuyts and Zanthus; NSW *vs* Boorabbin, Centralian, Eyre Peninsula, Ooldea and Zanthus). The only significant differences elsewhere in the distribution were between Zanthus ($\bar{x}$ = 3.0), and Eyre Peninsula and Nuyts ($\bar{x}$'s = 2.5–2.7).

Upper palpebrals. ANOVA: $F_{9,335} = 8.543^{***}$. Means ranged from 8.5 (Boorabbin, Zanthus, Eyre Peninsula, Flinders Island and Flinders Ranges) to 10.0 (Queensland), with only the latter mean above 8.9. The high Queensland mean was significantly different to all other means.

Lower palpebrals. ANOVA: $F_{9,335} = 6.833^{***}$. Means ranged from 9.3 (Boorabbin) to 10.6 (Queensland). Only the latter population and Nuyts ($\bar{x}$ = 10.2) had means greater than 10.0, and were significantly different to other populations (both *vs* Eyre Peninsula, Zanthus and Boorabbin; Queensland also *vs* Centralian and Flinders Ranges).

Secondary temporals. Queensland had a much higher proportion of the α -configuration (41:17) than the other populations (pooled, 17:660; $\chi^2_1 = 207.0^{***}$).

Snout-vent length. The Queensland population attains a larger size than other populations (mature-sized males: SVL 98–111 mm, $\bar{x}$ = 105.3 mm, n = 6 *vs* 71–107 mm, $\bar{x}$ = 86.4 mm, n = 128, Mann-Whitney U test, z = 3.84^{***}; mature-sized females: SVL 98–122 mm, $\bar{x}$ = 108.8 mm, n = 5 *vs* 75–119 mm, $\bar{x}$ = 92.8 mm, n = 143, Mann-Whitney U test, z = 3.05^{**}).

Coloration. Queensland and Nuyts Archipelago specimens generally had paler grey-brown dorsums, while southern mainland (Boorabbin, Zanthus, Ooldea, Eyre Peninsula, NSW) specimens generally had dark olive-green dorsums.

Type material. *Lygosoma muelleri* Peters, 1878 was described from two specimens from South Australia, presented by Baron Ferdinand von Müller to the Royal Cabinet of Stuttgart, and has usually been placed in the synonymy of *C. casuarinae*, most recently by Cogger *et al.* (1983), who list ZMB 9373 as “syntypes”. We have examined a single specimen bearing this number (Fig. 23, 24), corresponding well to the type description, and find it typical of the form described here. Accordingly, we designate this specimen lectotype. This specimen has the locality Murray River, and is presumably from the population near Renmark. The specimen has the following combination of characters: supraciliaries 5/6;

postsuboculars three; nuchals 3/4; supralabials seven; infralabials six; β -configuration of secondary temporals; upper palpebrals nine; lower palpebrals ten; midbody scales 24; paravertebral scales 69; subcaudal scales 70; subdigital lamellae 11/12; SVL 96 mm; AGL 63 mm; TL 96 mm; FLL 13.5 mm; HLL 17.5 mm; HL 13.1 mm; HW 9.8 mm; HD 7.6 mm.

Lygosoma muelleri Peters is a junior subjective homonym of *Scincus muelleri* Schlegel, 1839 [= *Sphenomorphus muelleri*, *vide* Loveridge, 1948], placed in *Lygosoma* between 1839 (Duméril & Bibron, 1839) and 1930 (de Jong, 1930). Sternfeld (1919, 1925) proposed the replacement name *Lygosoma (Homolepida) petersi* for *L. muelleri*, though basing his redescription on material from Hermannsburg, NT. Subsequent authors (Loveridge, 1934, 1948; Mitchell, 1950; Worrell, 1963) inexplicably reduced *L. petersi* to a central Australian subspecies of the mesic south-eastern species *C. casuarinae*, although possibly on the basis of Boulenger's (1887) earlier synonymy.

Lygosoma (Homolepida) branchiale var. *elongatum* Werner 1910 was erected, almost parenthetically, on the basis of a single specimen collected by Michaelsen and Hartmeyer at Boorabbin on 3 July 1905, the only specimen of the *C. branchialis* complex collected by their expedition. Cogger *et al.* (1983) did not locate the holotype. Of the collections known to house reptile material from the Michaelsen and Hartmeyer collection (NHMW, SMF, ZMB, ZMH; Cogger *et al.*, 1983), there are no specimens of *C. melanops* in the former three with appropriate data to be the holotype. A single ZMH specimen (R03961; formerly 3500), not identified as the type (and hence surviving the Second World War bombing that destroyed the ZMH type collections) bears printed Michaelsen and Hartmeyer labels corresponding to the type description, as well as a handwritten label giving Werner's determination of the specimen as *Lygosoma (Homolepida) branchiale* (H.-W. Koepcke, pers. comm.) and is here presumed to be the holotype. This specimen (Figs 25,26) has the following combination of characters: supraciliaries six; postsuboculars three; nuchals three; supralabials seven; infralabials six; upper palpebrals seven; lower palpebrals nine; β -configuration of secondary temporals; midbody scales 24; paravertebral scales 72; subcaudal scales 60; subdigital lamellae 15/14; SVL 76.5 mm; AGL 51 mm; AGL 51 mm; TL 61.5 mm (distal part of tail broken off but retained); FLL 12 mm; HLL 16.5 mm; HL 12.0 mm; HW 8.2 mm; HD 6.5 mm. The measurements correspond reasonably closely to those provided by Werner (1910): SVL 80 mm; TL 64 mm; FLL 14 mm; HLL 15 mm; HL 14 mm; HW 9 mm. Differences are probably due to differences in reference points for making measurements, and possibly to subsequent shrinkage of the specimen.

Lygosoma (Homolepida) woodjonesii Proctor, 1923 was described from three syntypes from St Francis Island in the Nuyts Archipelago, collected by F. Wood-Jones, and distinguished from other members of the *C. branchialis* species group primarily on the basis of a higher midbody scale count (28 *vs* 26). However, of the

three syntypes (BMNH 1946.8.17.97–99) the adult female mentioned by Proctor (BMNH 1946.8.17.97) has 29 midbody scales, while the other two have 26. Wells & Wellington (1985) nominate BMNH 1946.7.17.97 as lectotype. This specimen (Figs 27,28), a gravid female with three full-term embryos, has the following combination of characters: supraciliaries 6/7; postsuboculars four; nuchals 0/1; supralabials 7/8; infralabials 7/6; β -configuration of secondary temporals; upper palpebrals nine; lower palpebrals eleven; paravertebral scales 74; tail regenerated; subdigital lamellae 13; presacral vertebrae 39; SVL 111 mm; AGL 73; FLL 17.5 mm; HLL 22 mm; HL 16.0 mm; HW 11.4 mm; HD 9.7 mm.

The two paralectotypes have (counts for BMNH 1946.8.17.98 first) supraciliaries six, 6/7; postsuboculars four, 4/3; nuchals 2/3, 3/2; supralabials eight, 7/8; infralabials 6/7, six; α - and β -configuration of secondary temporals; upper palpebrals eight, nine; lower palpebrals 11; paravertebral scales 69; subcaudal scales 66, 70; subdigital lamellae 12/13, 12/11; presacral vertebrae 40; postsacral vertebrae 38, 40; SVL 84.5, 82 mm, AGL 52, 51 mm, TL 77, 82.5 mm, FLL 17.5, 16 mm, HLL 22, 19.5 mm, HL 13.4, 13.2 mm, HW 9.6, 9.5 mm, HD 8.1, 7.6 mm.

Comparison with other taxa. Recognition of *C. m. elongatus* as distinct from *C. m. melanops* is based largely on the occurrence of both forms in central Australia. To the east of the Stuart Highway, the two forms are quite distinct, with the nominate subspecies, occurring in the west and north, having heavy dark spotting on a generally light yellow-brown to red-brown ground, and usually the α -configuration of the lower secondary temporals, while *C. m. elongatus*, in the east and south, has an immaculate dark olive-green to olive-brown dorsum and the β -configuration. The two forms appear to be nowhere syntopic, yet approach to within 36 km in the north (Mereenie Well No. 1 vs No. 6) and approximately 45 km in the west (Blackstone Mining Camp vs Cavenagh Range). The large series from Erliwunyawunya Rockhole is exclusively of the *elongatus* form, while all three specimens from 20 miles east of Piltadi, in the Mann Ranges, are typical of nominal *melanops*. Only two specimens (WAM R20858–59, 28 miles west “Musgrave Park”) appear to combine the characters of the two races, being pale with numerous dark spots, yet both having the β -configuration. Additionally, Centralian *elongatus* have a higher number of midbody and paravertebral scales and a lower number of postsuboculars than Centralian *melanops* (midbody scale modes 26 (57.4%) vs 24 (65.6%); paravertebral scales 66–85, $\bar{x}$ = 75.4 vs 64–76, $\bar{x}$ = 70.2, t_{130} = 7.11***; postsuboculars mode 3 (74.0%), $\bar{x}$ = 3.2 vs mode 4 (78.5%), $\bar{x}$ = 3.8; t_{267} = 9.36***). However, to the east of the Stuart Highway, in the Davenport Ranges, the differences are less obvious, particularly in coloration. The four specimens from this area (CAWC R1105, NTM R12109–10, WAM R40142) have the α -configuration, while the dorsum is pale grey, and the dark spotting

very reduced to absent, persisting longest on the venter. We identify these specimens as *C. m. melanops* on the basis of the temporal configuration, the presence of dark spots ventrally on some specimens, and their proximity to typical *C. m. melanops* around Barrow Creek. Further east again, the Queensland population is homogeneous in coloration, with dorsum grey-brown and lacking dorsal or ventral spots, yet has both temporal conditions. Indeed, our placement of the apparently isolated Queensland population with *C. m. elongatus* rather than the nominal subspecies is largely arbitrary, the uniform dorsal coloration, lack of dark flecks and high numbers of paravertebral scales tipping the balance in favour of *C. m. elongatus*. It is this apparent breakdown of the diagnostic characters in the extreme east that leads us to identify these two taxa as only subspecifically distinct, despite the absence of any synapomorphy linking the two taxa.

Outside of central Australia and Queensland, the differences in coloration and temporal configuration between the two subspecies are clearly defined, with all southern populations having a uniform dorsum, and almost always an immaculate venter, together with the β -configuration of the secondary temporals, and all north-western populations having the states described for *C. m. melanops*. Additionally, most *C. m. elongatus* populations have lower mean numbers of subcaudal scales ($\bar{x}$'s = 65.3–74.7, only Flinders and Queensland being greater than 69.2 vs $\bar{x}$'s = 69.6–78.1) and a shorter tail (Tables 5,10).

Cyclodomorphus m. elongatus differs from *C. branchialis* in having a uniform olive-green to olive-brown dorsum (vs cream to grey or reddish with dark spots, and solid dark “gill” markings on the sides of the neck). It also has generally more paravertebral (61–85 vs 62–70) and subcaudal (58–77 vs 57–64) scales and subdigital lamellae (9–17, $\bar{x}$ = 12.6 vs 9–12, $\bar{x}$ = 10.8). It is separated from *C. branchialis* by approximately 260 km (70 km north Bullfinch vs 56 km south-east Yalgoo).

Cyclodomorphus m. elongatus differs from *C. celatus* in coloration (uniform olive dorsum vs cream to grey with dark streaks, neck with several vertically-aligned series of dark longitudinal streaks) and in having a greater number of midbody scales (modes 24 or more for all populations vs 22), modally β - vs α -configuration of secondary temporals, and a more open external ear, usually with a large, low, rounded rostral lobule. *Cyclodomorphus m. elongatus* is separated from *C. celatus* by approximately 360 km (70 km north Bullfinch vs the Jurien district), with much of the intervening area being unsuitable for either species, having hard soils and lacking hummock grasses.

In addition to the differences in body size, tail length, number of rostral ear lobules and interparietal shape differentiating *C. m. melanops* from *C. maximus* (see above), *C. m. elongatus* differs from *C. maximus* in having more midbody scales (mode 24 or 26 vs 22) and paravertebral scales (61–85, $\bar{x}$ = 72.1 vs 61–67, $\bar{x}$ = 64.4), fewer subdigital lamellae (9–17, $\bar{x}$ = 12.6 vs 14–

17, $\bar{x} = 15.3$), and postsuboculars (modes 3 vs 4), modally β - vs α -configuration of secondary temporals, a slightly deeper head (Tables 4,10), and immaculate olive-green to grey dorsum (vs red-brown with pale spots, and a dark circumocular ring).

Habitat. Mainland populations of *C. m. elongatus* appear to be primarily *Triodia* inhabitants (White, 1976; Dell & How, 1984, 1985; Shea & Wells, 1985). Of 164 specimens for which microhabitat is recorded, 154 (93.9%) were taken in or under *Triodia* or unidentified "spinifex", and a further 32 specimens were taken from unspecified microhabitats in *Triodia*-dominated habitats. Of the ten specimens not collected from *Triodia*, four (WAM R55362, R71174, R72387–88) were taken in or under spoil, three (WAM R72287–89) under *Casuarina* leaf litter, and one each in sedges (WAM R78775), in leaf litter on stony soil (WAM R64759) and under litter (WAM R65465).

The majority of specimens from southern mainland populations come from mallee-*Triodia* habitats on various soil types, although a number of other vegetation associations are also inhabited.

The Boorabbin population inhabits mallee-*Triodia* and eucalypt woodland/*Triodia* formations ($n = 1$; WAM R64760: "very open tree mallee over spinifex"; WAM R64786: "open eucalypts over shrubland over spinifex on red earth"; WAM R71174: "sparse eucalypt woodland on white-red loamy sand"; WAM R78679: "*Eucalyptus formanii*, *E. lesouefii* and *E. campaspe* over *Triodia* on yellow sand"; WAM R78721: "open eucalypt woodland over mallee over spinifex and shrubs"), mallee heath habitats ($n = 3$), *Acacia/Triodia* and other *Acacia* associations ($n = 1$; WAM R71863, R71866, R78813: "*Acacia* shrubland over spinifex"; WAM R78723: "*Acacia* shrubland near granite outcrop"; WAM R78775: "open sedges and grasses on granitic soils, some *Acacia* to 3m"), *Callitris* heath ($n = 5$) and a variety of intermediate habitats (WAM R64751, R64758: "mallee over mulga, other shrubs and spinifex on red earth"; WAM R64759: "open tree mallee over scrub *Acacia* over open low grass on stony soil of range outwash"; WAM R70902: "base of red sandy dune with low woodland of *Casuarina* and mulga over sparse scrub and herbs"; WAM R72720: "mallee/mulga/spinifex"; WAM R78664: "*Eucalyptus campaspe*, *Acacia* and *Triodia* on red earth").

The adjacent Zanthus population largely inhabits mallee/*Triodia* habitats ($n = 9$; WAM R70891: "open shrub mallee over heath and open/low/dwarf scrub over open spinifex and very low grass on buff gravelly sand"; WAM R72538–39, "*Eucalyptus oleosa* mallee/*Triodia*") and open *Triodia* plains ($n = 11$; WAM R57975: "spinifex and bluebush on a saltlake island"; WAM R59808: "spinifex and sedges"), the latter sometimes with scattered emergents (AM R107954–56: "*Triodia* field with few scattered *Acacia* and *Atriplex* on stony red soil").

The Ooldea population inhabits mixed mallee/*Triodia* associations on a variety of substrates ($n = 1$; SAM R14223: "spinifex-fixed dunes with eucalypt scrub";

SAM R31870: "*Eucalyptus pyriformis*, *Grevillea* open shrubland in rocky gullies and ridges"; SAM R31900–02: "open mallee woodland over *Triodia* on sand dune"; SAM R31948: "open mallee over *Triodia/Melaleuca* on sandy plain with underlying calcrete"; SAM R32067–68: "mallee/*Callitris* open woodland over *Acacia/Eremophila*/spinifex on calcareous interdune"; SAM R32135–36: "low mallee/*Casuarinae*/*Heterodendron* open woodland over sparse shrubs and *Triodia* on sandy interdune"; SAM R32147: "open mallee over *Acacia/Eremophila*/sparse *Triodia* on sand plain with minor dunes").

Few data are available for the Eyre Peninsula, Flinders Ranges and NSW populations. Specimens have been recorded from mallee/*Triodia* habitats ($n = 1$; AM R105522–31: "mallee woodland with *Triodia* on red sand"; Shea & Wells [1985]: "open mallee woodland [*Eucalyptus socialis*, *Acacia burkitti* and *Dubosia hopwoodii* association] with an understory of *Triodia* cf. *irritans* and *Calotis* sp. on red sandy soil with scattered pieces of calcrete") and a wide range of substrates and topography (SAM R14685: "base of hill"; SAM R14912: "arid low scrub, spinifex, rocky red soil"; SAM R15206: "sandridge"; SAM R19925–27: "rocky hillside").

Most Queensland specimens come from lateritic substrates in "jump-up" country ($n = 21$; AM R110550: "gidyea woodland and spinifex on red gravel"), although one specimen was taken from *Triodia* on "red soil with eucalypt emergents" (WAM R55575).

Centralian specimens have been recorded from both plains (SAM R13229a–b, R29543) and in association with harder substrates and hills (WAM R20847–48: "stony bank of Hugh River"; WAM R31696: "foot of granite tor"; WAM R31697: "foot of stony hill"). One specimen (CAWC R1014) was taken from low tussock grassland (*Enneapogon arenaceus*) under *Acacia aneura* and *A. estrophiolata*.

In contrast to the *Triodia*-dominated habitats preferred on the mainland, the limited data available suggest different preferences for the Nuyts Archipelago population. Robinson & Smyth (1976) describe it as common in litter and around buildings, while SAM R22483 was taken "under limestone rocks".

Reproduction. Male reproductive cycles in *C. m. elongatus* are seasonal (Fig. 29). Enlarged turgid testes ≥ 5.0 mm in length were present in most mature-sized males collected between April and September, with some indication of an increase in mean length during this period. In October and November, both enlarged, turgid and small, flattened testes occurred in approximately equal numbers, while between December and March, most testes were small and flattened.

Female reproductive cycles are similarly seasonal (Fig. 30). None of the mature-sized females collected between February and 10 August were gravid. Enlarged yolking ovarian follicles were present between 12 August and 26 October, while unshelled oviducal eggs or developing embryos were present between 25 September and January.

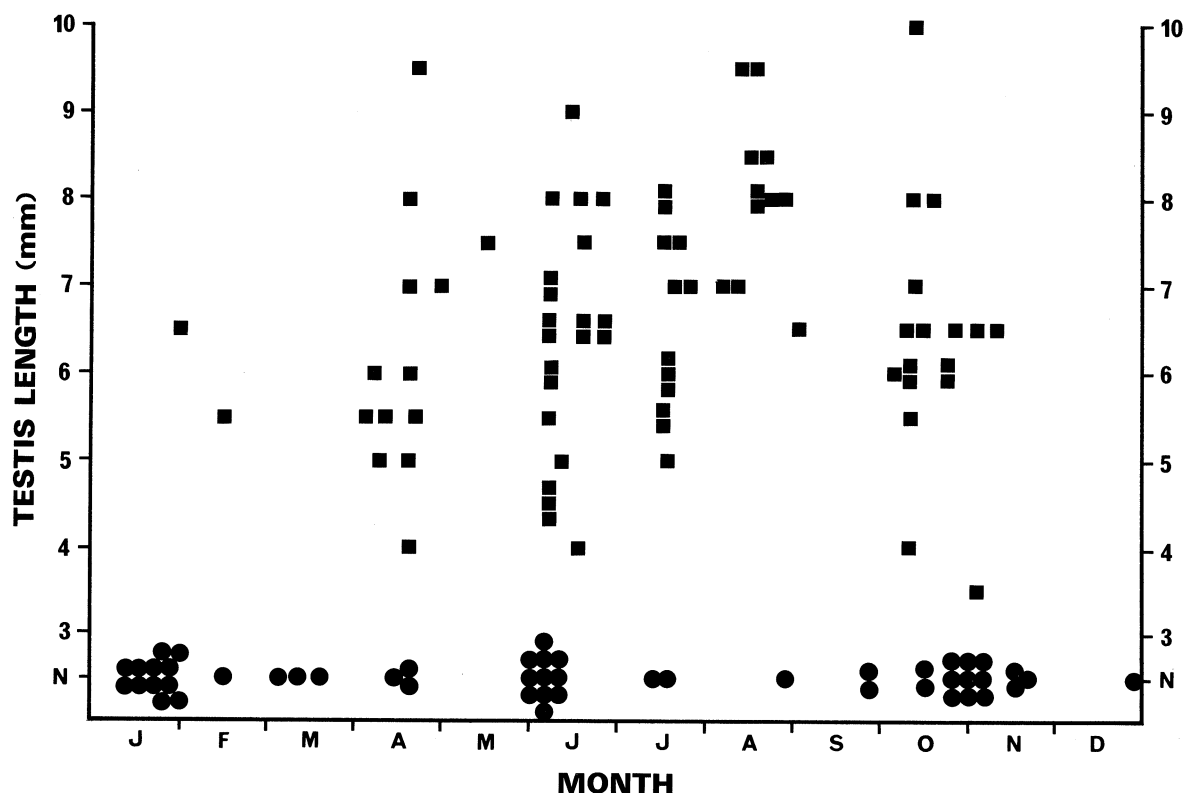


Fig. 29. Seasonal variation in length of turgid testes, and the occurrence of flaccid testes in *Cyclodomorphus melanops elongatus*.

The smallest juveniles (SVL 40.5–42 mm) were collected 27 January.

We conclude from the above data that spermatogenic activity reaches a peak about September, coinciding with mating and fertilisation, and young are born in January.

Of 28 mature-sized females collected between 15 September and 31 November, 13 (46.4%) were gravid, suggesting that reproduction is generally less frequent than annual.

Gravid females carried 2–4 ($\bar{x}$ = 2.4, mode = 2 (62.5%), n = 16) enlarged yolking ovarian follicles, unshelled oviducal eggs or fully developed embryos. Litter size was not significantly related to maternal SVL (r = 0.3055, P = 0.250).

Growth rates. Seasonal distribution of body sizes in the immature material examined (Fig. 31) suggests that mature size is certainly not reached in the first year, and probably not until at least the third year.

Sex ratio. The sex ratio of mature-sized material examined was 134 males:148 females, not significantly different to 1:1 (χ^2_1 = 0.70, n.s.). Seasonal male:female ratios were also not significantly different to equality (summer 17:13, χ^2_1 = 0.53, autumn 22:32, χ^2_1 = 1.85, winter 47:64, χ^2_1 = 2.60, spring 35:32, χ^2_1 = 0.13), or to each other (4×2 contingency table, χ^2_3 = 3.59, n.s.).

Diet and predation. Stomach contents of specimens we have examined are mainly arthropods, although one specimen (WAM R20980) had eaten a skink, *Proablepharus reginae*.

A second specimen (WAM R41142) is recorded as taken from the gut of a road-killed snake, *Pseudechis australis*.

Specimens examined. QUEENSLAND: AM R72028–37, R73325, 92 km west Winton; R110550, R111032, 14 km north-east Scotts Tank, “Diamantina Lakes”; R111033, Scotts Tank, “Diamantina Lakes”; ANWC R1618, R1644, QM J28598–600, “Opalton”; HFWE 0632, within 1 km of Sulieman Creek, 41 km south Dajarra; QM J40188–89, “Diamantina Lakes”; J41828–35, Ooridra area, “Diamantina Lakes”; WAM R55575, 5 km west “Fermoy”. NEW SOUTH WALES (including adjacent SA): AM R16110, Renmark, SA; R105443, R105446, 12.5 km north “Coombah”, NSW, R121029, 166 km north Wentworth, NSW; R130982, 12.4 miles north Coombah Roadhouse via Silver City Hwy, NSW; R130983, 8.4 miles north Coombah Roadhouse via Silver City Hwy, NSW; NTM R5025, Wentworth road, nr Rotten Lake, SA; SAM R15988, R16666a–b, R17125, Danggali Conservation Park, SA. FLINDERS RANGES, SA: SAM R3321, Mt Aroona, 6 miles south-west Copley; R5611, 5 miles west “Arkaroola”; R10943–44, R10956–57, Paralana Hot Springs; R14912, “Baratta”; R15953a–b, Parachilna; R17457, nr summit Mt Sunderland, Flinders Ranges National Park; R22304–05, Middle Gorge nr Quom. EYRE PENINSULA, SA: AM R105522–31, 31.5 km east-north-east Kimba; MV D10015, “Yardea”; D56659, 28

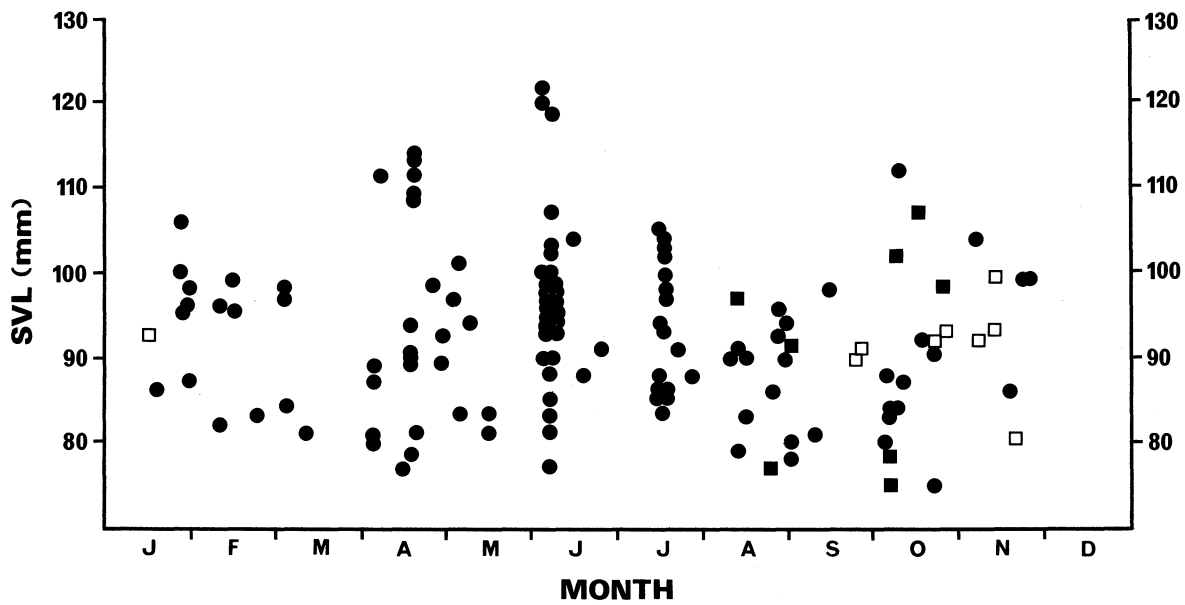


Fig. 30. Seasonal occurrence of non-vitellogenic follicles (dots), yolking ovarian follicles (squares) and oviducal embryos (open squares) in *Cyclodomorphus melanops elongatus*.

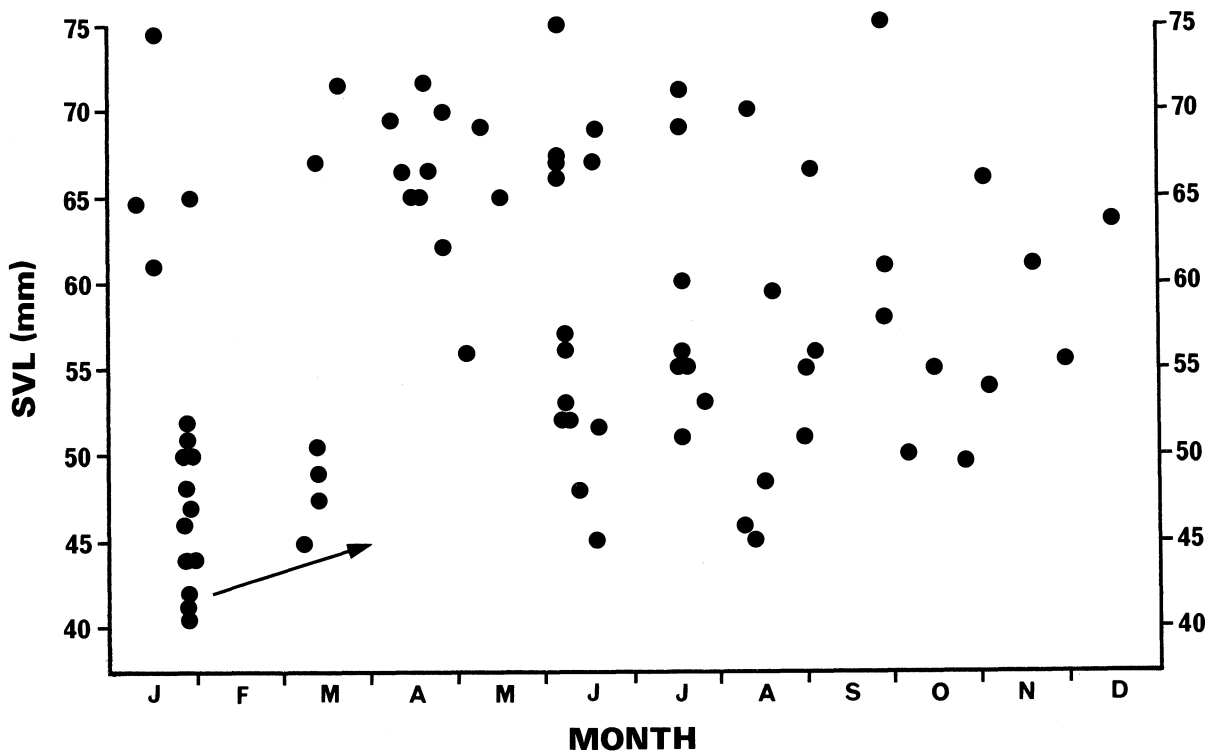


Fig. 31. Seasonal variation in SVL of immature *Cyclodomorphus melanops elongatus*. Arrow indicates inferred growth of first year cohort.

miles west-north-west Iron Knob; NTM R9243, 40 km east Whyalla; SAM R2733, west of Port Augusta; R3058a–c, nr Siam Woolshed, "Cariewerloo"; R3061a–h, Birthday Well, "Cariewerloo"; R3841a–b, Kokatha Hills; R3856a–f, 10 miles south "Yardea"; R3861a–d, "Kondoolka" turnoff, Gawler Ranges; R3870a–b, nr "Kokatha"; R5743, 3 miles east Ucontitchie, 5 miles west Warrambo; R5747a–b, behind Smooth Pool, Streaky Bay; R5767, Elliston; R10729–31, Mamblin; R12460–65, "Corunna"; R12486a–c, R12489a–d, Miccollo Hill, "Siam"; R12618, 5 miles north-west Wharminda; R14202, nr "Minaro Downs"; R14566, Lincoln Hwy, 45 km south-west Whyalla; R14685, R16355a–b, Gum Creek Gorge, Corunna Hills; R14865, "Mt Ive"; R15206, 28 km north-east Wirrulla; R17143, Pinkawillinie Reserve, nr Kimba; R17678, north-west "Yarker" shearing shed; R19925–27, nr Chinaman Dam, "Yardea"; R20613–17, 2 km north-west Corunna Hill North; R27839, Duchess Ridge; R28538–39, 77.5 km north Minnipa; R28541–42, 73 km north Minnipa; R28596, 120 km north-east Minnipa; WAM R24531, 23 miles east-north-east Wirrulla; R25566–67, 10 miles south Kimba. **FLINDERS ISLAND, SA:** SAM R2728a–c, R2729. **NUYTS ARCHIPELAGO, SA:** BMNH 1946.8.17.97–99 (LECTOTYPE and PARALECTOTYPES of *Lygosoma wadJonesii*), SAM R1198, R12879a–b, R21771–77, R22483, St Francis Island; R12864, R21923, Fenellon Island; R21823, Lacy Island. **OOLDEA, SA:** NTM R9202–03, R9287, SAM R17708a–b, R17715, Immarna; SAM R766, R17729, Ooldea; R2731, Barton; R2734a–b, between Ooldea and Talarinna; R14223, Childara Rock Holes; R14444, bomb site, Maralinga; R14957, Mt Finke; R15024a–b, 7 km west Immarna; R18190, 29°15'S 130°15'E; R18240, 29°28'S 130°10'E; R22255, 2 km east Ooldea; R31870, 0.5 km north-east Mt Finke; R31900–02, 14 km west Pinjarra Dam, Yumbarra Conservation Park; R31948, south of Inila Rock Waters, Yumbarra Conservation Park; R32067–68, 5.5 km south Immarna Siding; R32135–36, 9.7 km south-south-west Maralinga; R32147, 8 km south-west Maralinga; WAM R31862, 100 miles north Cook. **ZANTHUS, WA:** AM R107954–56, 45.1 km west by road of Newman Rocks turnoff on Eyre Hwy; WAM R12985–86, R12988, R13547, R16551, R39995, Queen Victoria Spring; R14232–33, Gordons Rocks, 4 miles north Karonie; R16552–53 Goddard Creek, 10 miles east Zanthus; R21654, 4 miles east Chiffley; R21689, 13 miles north-east Cundeelee Mission; R25562, 76 miles east Norseman; R26424–25, Uraryie Rock, Zanthus; R30693–701, 8 miles east Fraser Range; R30716; 13 km east Fraser Range; R30777, 5 miles east Norseman; R30847, Lake Widgiemooltha; R41142, 42 miles east Kalgoorlie; R51064–68, 4 miles north Norseman; R53457–58, Newman Rocks; R57927, 5.5 km north-north-west Clear Streak Well; R57948, 10 km east Boingarling Rocks; R57975, 12 km north-east Charlina Rock; R58050, R59859, R59886, 8 km north Clear Streak Well; R58070, 5 km east Boingarling Rocks; R58071, 4 km east Boingarling Rocks; R59808, 20 km east-south-east Mt Newmont; R59908–09, 12.5 km north-north-east Charlinna [sic] Rock; R62284, 31 km east Jindabinbin Rock Hole; R65423, 30.0 km north-west Heartbreak Ridge; R65465, R72387–88, 20 km north-west Heartbreak Ridge; R65504–07, c. 1 km south Buningtonia Spring; R65535, R65630, R72501, R74592, 3.5 km south-west Buningtonia Spring; R65543, 0.5 km south Buningtonia Spring; R70891, 1.0 km north-east Yowie Rock Hole; R72431, Buningtonia Spring; R72440–43, R74563–67, 1.5 km south-west Buningtonia Spring; R72478–79, R72511–12, 1.5 km south-east Buningtonia Spring; R72488–89, 9.0 km north-north-east Buningtonia Spring; R72538–39, 3.0 km south-west Buningtonia Spring; R74543–44, 15 km south-west Buningtonia Spring; R93424, 6 km north-north-east "Southern Hills";

R94040, R94076, 53 km north-north-east Queen Victoria Spring; R94213, 25 km east Newman Rocks. **BOORABBIN, WA:** WAM R19141–42, Red Lake, Coolgardie; R30692, 17 miles west Bulla Bulling; R33968, 16 miles south Karalee; R64751, R64758–60, R64786, Mt Manning Range; R70902, 5.5 km 145° Black Flag; R71174, c. 1 km west Lake Cronin; R71773, 32.5 km south Woolgangie Rail Siding; R71863, R71866, 15 km east Toomey Hills; R72252–53, R72287–89, 31°15'S 120°14'E, Boorabbin area; R72254, R72295–96, 31°13'S 120°13'E, Boorabbin area; R72292, 31°16'S 120°20'E, Boorabbin area; R72720, 6.5 km north-east Comet Vale; R72759, 3.5 km north-east Comet Vale; R73341, R78664–65, 7 km west Mt Manning Range (south-east peak); R78679, 5 km west Mt Manning Range (south-east peak); R78721, 34 km south-south-east Woolgangie; R78723, 21 km south Woolgangie; R78775, Boodarding Rock; R78813, 1 km north-east Boodarding Rock; R83994, 70 km north Bullfinch. **CENTRALIAN:** AM R17177, Mt Gillen, Alice Springs, NT; R17195–244, Erliwunyawunya Rock Hole, Musgrave Ranges, SA; R17339–55, R17361–66, "Mt Davies", Tomkinson Ranges, SA; R106833, "Ti Tree", NT; ANWC R3969, North-West Reserve, SA; CAWC R120, SAM R1569a–f, R2735, Hermannsburg, NT; CAWC R1014, Mereenie, Well No. 6, NT; CAWC R1651, Palm Valley, west end, NT; MV D5071, Central Australia; D51968, Everard Range, SA; SAM R3116a–d, Ernabella Mission, SA; R3721, Bell Rock Range, WA; R11735–36, "Everard Park", SA; R13229a–b, 31 miles south-west Ernabella Mission, SA; R13319, 7 miles east-north-east Ernabella Mission, SA; R29543, 1 km north Victory Well, SA; WAM R20847–48, Owen Springs, NT; R20861, Palm Valley, NT; R20980, 4 miles north-east Blackstone Mining Camp, WA; R31696, 8 miles north-west "Mt Davies" camp, SA; R31697, 5 miles north-west "Mt Davies" camp, SA; R44347, Blackstone Mining Camp, WA; R55362, 146 km north Alice Springs, NT. **OTHERS:** NTM R2986, no locality; SAM R2730, Kangaroo Island, SA [in error].

Cyclodomorphus melanops siticulosus n.subsp.

Figs 32,33

Type material. HOLOTYPE: SAM R26399, 15 km west "Nullarbor", in 31°26'S 130°43'E, collected by K. Casperson on 21.ix.1984. PARATYPES: AM R96633–34, 15 km east SA/WA border on Eyre Hwy, SA; R106834, "Arubiddy", WA; R107935, cliff edge 200 m south of Eyre Hwy, 16 km east of WA/SA border, SA; SAM R22979, 17 km east SA/WA border on Eyre Hwy, SA; R26255, 8 km south-east Border Village, SA; WAM R36165, Cave N59, c. 24 miles north-east Madura Pass (GR549083), WA; R36719, 8 miles north Madura, WA.

Diagnosis. *Cyclodomorphus m. siticulosus* differs from all other members of the *C. branchialis* species group in the combination of a mode of 24 midbody scales, 56–63 paravertebral scales, 60–62 subcaudal scales, β -temporal configuration, and an olive green to green-brown dorsum without dark spots.

Description. Parietals separated by interparietal; interparietal broadest rostrally, approximately $\frac{3}{4}$ length and breadth of frontal; transversely enlarged nuchals 2–

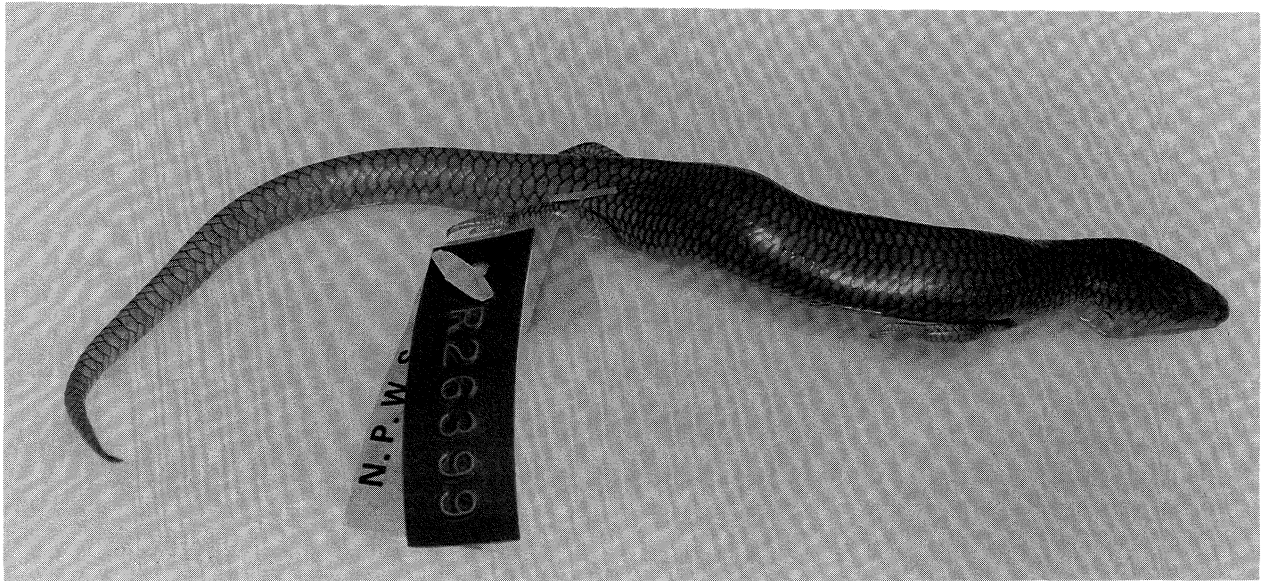


Fig. 32. Holotype of *Cyclodomorphus melanops siticulosus* (SAM R26399).

5 on each side ($\bar{x}$ = 3.1, SD = 0.73, n = 18), usually three (66.7%); loreals rarely one bilaterally (11.1%, n = 9); supraciliaries 5–7 ($\bar{x}$ = 6.1, SD = 0.42, n = 18), usually six (83.3%), first and last largest, third-last usually projecting between second and third supraocular, remainder moderate, subequal; postsuboculars 3–4 ($\bar{x}$ = 3.4, SD = 0.51, n = 18); upper palpebrals 8–9 ($\bar{x}$ = 8.2, SD = 0.44, n = 9); lower palpebrals 8–11 ($\bar{x}$ = 9.2, SD = 0.97, n = 9); secondary temporals in β -configuration; supralabials 7–8 ($\bar{x}$ = 7.1, SD = 0.32, n = 18), third-last below centre of eye, separating pre- and postsuboculars; infralabials 6–7 ($\bar{x}$ = 6.3, SD = 0.49, n = 18), usually first two (88.9%, n = 18), rarely first three infralabials contacting postmental; ear moderately large, vertically ovoid, with a single rounded lobule on rostral margin.

Body scales in 22–24 ($\bar{x}$ = 23.4, SD = 0.88, n = 9), usually 24 (66.7%) longitudinal rows at midbody; scales in paravertebral rows much broader than adjacent lateral dorsal scales, 56–63 ($\bar{x}$ = 58.8, SD = 2.59, n = 9); subcaudal scales 60–62 ($\bar{x}$ = 61.0, SD = 1.00, n = 3); lamellae below fourth toe 11–14 ($\bar{x}$ = 12.3, SD = 1.13, n = 18), each with a narrow to broad light to mid-brown callus.

SVL 66–94 mm (n = 9); AGL/SVL 52.4–63.3% ($\bar{x}$ = 59.0%, n = 9); TL/SVL 97.8–114.6% ($\bar{x}$ = 106.8%, n = 3); FLL/SVL 16.5–21.6% ($\bar{x}$ = 19.1%, n = 9); HLL/SVL 19.7–26.5% ($\bar{x}$ = 24.0%, n = 9); FLL/HLL 72.5–85.0%, $\bar{x}$ = 79.8%, n = 9); HL/SVL 16.0–19.1% ($\bar{x}$ = 17.8%, n = 9); HW/HL 67.3–75.8% ($\bar{x}$ = 72.1%, n = 9); HD/HL 52.3–59.9% ($\bar{x}$ = 55.8%, n = 9).

Presacral vertebrae 35–37 ($\bar{x}$ = 36.3, SD = 0.82, n = 6); postsacral vertebrae 35–36 (n = 2); phalangeal formula of manus and pes 2.3.4.4.3.

Allometry: Although samples are insufficient to determine the direction of allometry for most metric characters,

HLL is significantly negatively allometric in relation to SVL (Table 12).

Coloration (in preservative) (Fig. 32). Dorsum mid olive grey-brown; venter pale cream yellow to blue-yellow, more yellow on throat and tail, more blue-yellow on belly. Body scales with slightly darker edges, forming a dark reticulum. Soles cream, with light to mid grey-brown tubercles and calli. Upper lips and sides of neck cream to light grey-brown.

Coloration (in life). The iris in AM R96633–34 was orange. In other respects, coloration was not noticeably different to preserved material.

Details of holotype. Of the variable characters for the subspecies, the holotype (Figs 32,33) has supraciliaries 5/6, postsuboculars 3/4, nuchals 4/5, supralabials seven, infralabials 6/7, upper palpebrals eight, lower palpebrals nine, midbody scales 22, paravertebral scales 57, subcaudal scales 60, subdigital lamellae 11, presacral and postsacral vertebrae 35, SVL 82 mm, AGL 43 mm, TL 94 mm, FLL 16 mm, HLL 21 mm, HL 15.6 mm, HW 11.0 mm, HD 8.3 mm.

Sexual dimorphism. Mature-sized females (SVL 82–94 mm) were larger than mature-sized males (SVL 66–86 mm), although the sample sizes were too small for the differences to be significant (Mann-Whitney U test, U = 3, n.s.).

There were no significant differences between males and females in mean number of paravertebral scales, midbody scales, subcaudal scales, subdigital lamellae, postsuboculars, supraciliaries, supralabials, infralabials, nuchals, upper palpebrals or lower palpebrals, again at least partly due to the small sample sizes.

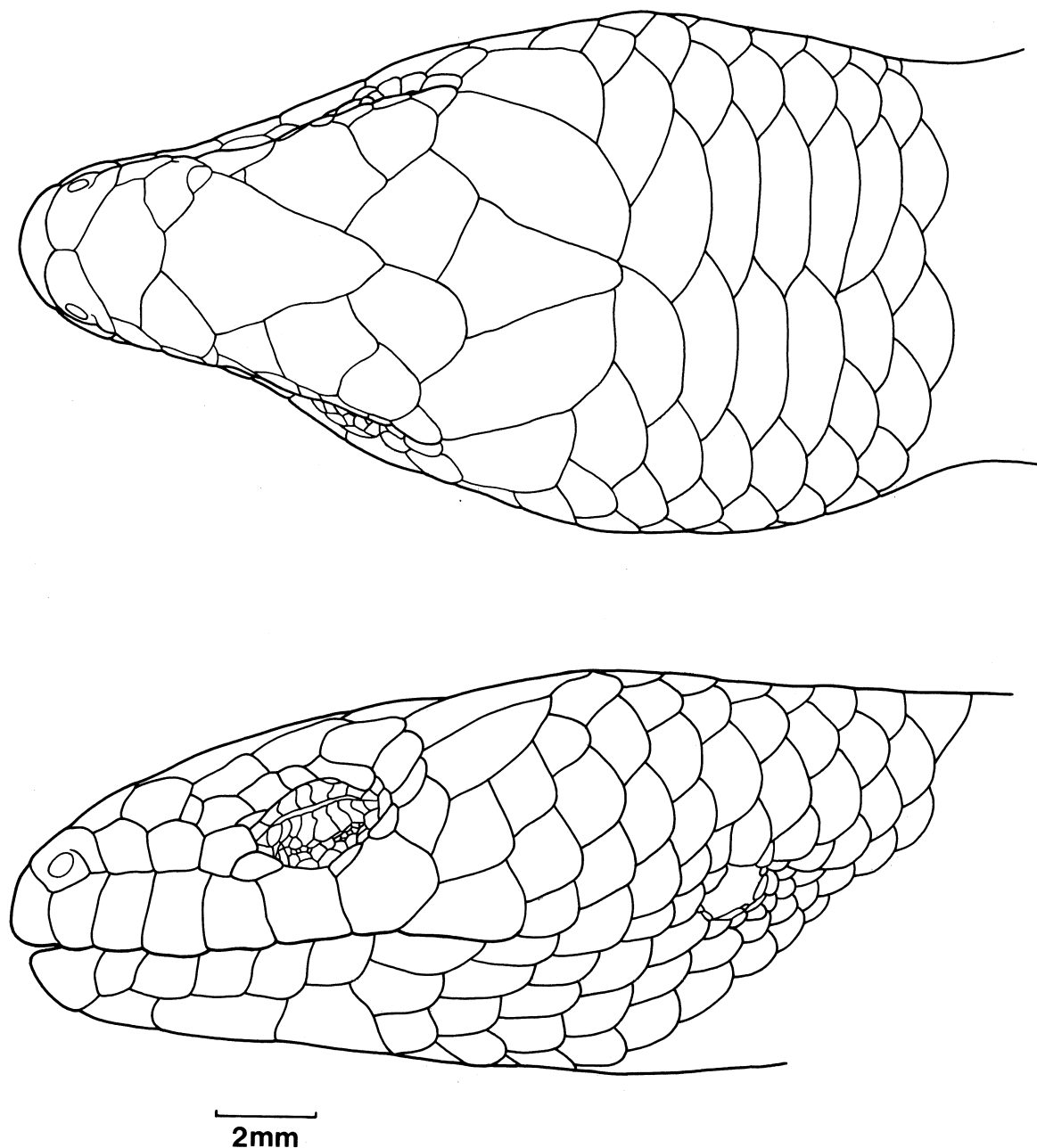


Fig. 33. Head shields of holotype of *Cyclodomorphus melanops siticulosus*.

Distribution. *Cyclodomorphus m. siticulosus* is confined to the limestones of the southern fringe and coastal cliffs of the Nullarbor Plain and Hampton Tableland, from “Arubiddy”, WA in the west to 15 km west “Nullarbor”, SA in the east (Fig. 14).

Comparison with other taxa. *Cyclodomorphus m. siticulosus* is very similar to the most geographically proximate race, *C. m. elongatus*, sharing with it the two major diagnostic characters of that race, the uniform olive dorsum and the b-configuration of the lower

secondary temporals, both apomorphic in the context of the *C. branchialis* species group. However, *C. m. siticulosus* is differentiated from *C. m. elongatus* by the very low number of paravertebral scales (56–63, $\bar{x}$ = 58.8 vs 61–85, $\bar{x}$ = 72.1), also reflected in a shorter body and consequently longer limbs and head (Table 11, 13) and by a very different habitat and microhabitat preference. The low number of paravertebral scales is an autapomorphy of *C. m. siticulosus*. The three nearest populations of *C. m. elongatus* have lower mean numbers of paravertebral scales than other populations, but even

these are very much higher than in *C. m. siticulosus* (vs Zanthus, 61–77, only 6% with fewer than 64, $\bar{x}$ = 68.3, t_{91} = 8.68***; vs Ooldea, 64–75, $\bar{x}$ = 70.0, t_{27} = 8.30***; vs Nuyts, 65–77, $\bar{x}$ = 71.4, t_{27} = 10.50***). However, the indication of a rapid clinal decrease in paravertebral scales leads us to treat *C. m. siticulosus* and *C. m. elongatus* as only subspecifically distinct.

Cyclodomorphus m. siticulosus is an inhabitant of the chenopod plains and low coastal heath on stony kunkar soils of the southern fringe of the Nullarbor Plain and Hampton Tableland, while *C. m. elongatus* is a *Triodia* inhabitant. Known localities for the two races are separated by 225 km in the west (“Arubiddy” vs Goddard Creek and 9 km north-north-east Buningonia Spring) and 150 km in the east (15 km west “Nullarbor” vs Ooldea), although the intervening areas have not been thoroughly surveyed.

Cyclodomorphus m. siticulosus differs from *C. m. melanops* in the same characters as *C. m. elongatus*: a uniform olive dorsum, β -configuration of lower secondary temporals, lower number of midbody scales (mode = 24, $\bar{x}$ = 23.4 vs mode = 26, $\bar{x}$ = 25.4) and subcaudal scales (60–62, $\bar{x}$ = 61.0 vs 66–87, $\bar{x}$ = 74.3), and additionally in the lower number of paravertebral scales, shorter body, and longer limbs and head (Tables 5,12).

Cyclodomorphus m. siticulosus differs from both *C. branchialis* and *C. celatus* in coloration (uniform olive green-brown vs greyish with dark streaks, the former also with solid dark “gill” markings on the neck), and further from the latter species in the more open external ear, β -configuration of temporals vs modally α -pattern, generally lower number of paravertebral scales, and shorter body and consequently longer limbs and head (Tables 1,12).

In addition to marked differences in size, tail length, number of ear lobules and shape of interparietal (as in other races of *C. melanops*), *C. m. siticulosus* differs from *C. maximus* in having a greater number of midbody scales (22–24, mode 24 vs 20–22, mode 22), fewer paravertebral scales (56–63 vs 61–67), presacral vertebrae (36–37 vs 40–42), subdigital lamellae (11–14 vs 14–17), upper palpebrals (8–9 vs 9–12) and lower palpebrals (8–11 vs 10–13), β - vs α -configuration of secondary temporals and immaculate olive green-brown dorsal ground (vs red-brown to yellow-brown with white spots). It is also shorter-bodied, longer-limbed and longer-headed, and slightly narrower-headed at comparable life-history stages (Tables 4,12).

Etymology. The subspecific epithet is derived from the Latin *siticulosus* (very dry, parched) in allusion to the lack of surface water in its habitat.

Habitat. Storr (1976) and Storr, Hanlon & Harold (1981), on the basis of the two WAM specimens, considered this race to be cave-inhabiting. However, specific habitat and microhabitat data are lacking for both specimens in the WAM registers, and the only basis

for assuming a cave-inhabiting ecology appears to be the collection of WAM R36165 at Cave N59. This site is notable on the chenopod/limestone plains of the Hampton Tableland for the presence of an isolated stand of mallee in the vicinity (Pilkington & Mott, 1986).

Specific habitat data are available for all of the South Australian specimens. The five specimens from between 8 km south-east Border Village and 17 km east of the SA/WA border all came from low open coastal heath on limestone at or near the top of the coastal cliffline. The most detailed habitat data are for AM R107935 (*Melaleuca* heath with scattered taller *Atriplex* and large expanses of bare limestone pavement with small boulders and exfoliations; soil, where present, thin, grey and of rocky/sandy texture) and SAM R26255, collected at Site ME1 of the joint Nullarbor Survey (McKenzie & Robinson, 1987). The photograph of this latter site (p. 322 in McKenzie & Robinson, 1987) shows low open coastal heath with low eucalypts and melaleucas on a stony plain with crusting loam. The dominant plant species were *Atriplex* spp., *Maireana erioclada*, *Melaleuca pauperiflora*, *M. quadrifaria*, *Rhagodia* spp., *Acacia erinacea*, *A. oswaldii* and mallee eucalypts (*E. brachycalyx*, *E. calcareana*, *E. diversifolia*, *E. gracilis*, *E. oleosa*, *E. rugosa*, *E. socialis*). Four of the five specimens are known to have been taken under limestone rocks and slabs. In the case of AM R107935, the lizard was occupying a short, shallow burrow beneath the rock.

The holotype was collected at Site CA1 of the Nullarbor Survey, “under loose bark, dead tree or log” at a bore (field data sheets stored at South Australian Museum). The photograph of this site (p. 338 in McKenzie & Robinson, 1987) shows low chenopod shrubland on hard clay soils strewn with pebbles, in a shallow depression. The dominant plant species at this site were *Atriplex nummularia*, *Maireana erioclada*, *M. sedifolia*, *Myoporum platycarpum*, *Rhagodia ulicina*, *Selenothamnus squamatus*, *Acacia oswaldii* and *A. papyrocarpa*.

Triodia is not recorded from any of the known localities for *C. m. siticulosus*.

Reproduction. WAM R36719 (SVL 66 mm; 17.x.1966) is a mature male with 6 mm semiturgid testes. SAM R26399 (SVL 82 mm; 21.ix.1984) has 7 mm turgid testes. Other male specimens ($n = 5$) are mature, but non-reproductive. SAM R22979 (SVL 94 mm; x.1982) is a gravid female with 1L/2R greatly enlarged yolking ovarian follicles, while AM R106834 (SVL 89 mm; v.1983) has moderately enlarged ovarian follicles. WAM R36165 (SVL 82 mm; 15–28.ii.1970) is a mature but non-reproductive female.

Sex ratio. The ratio of mature-sized males:females was 6:3.

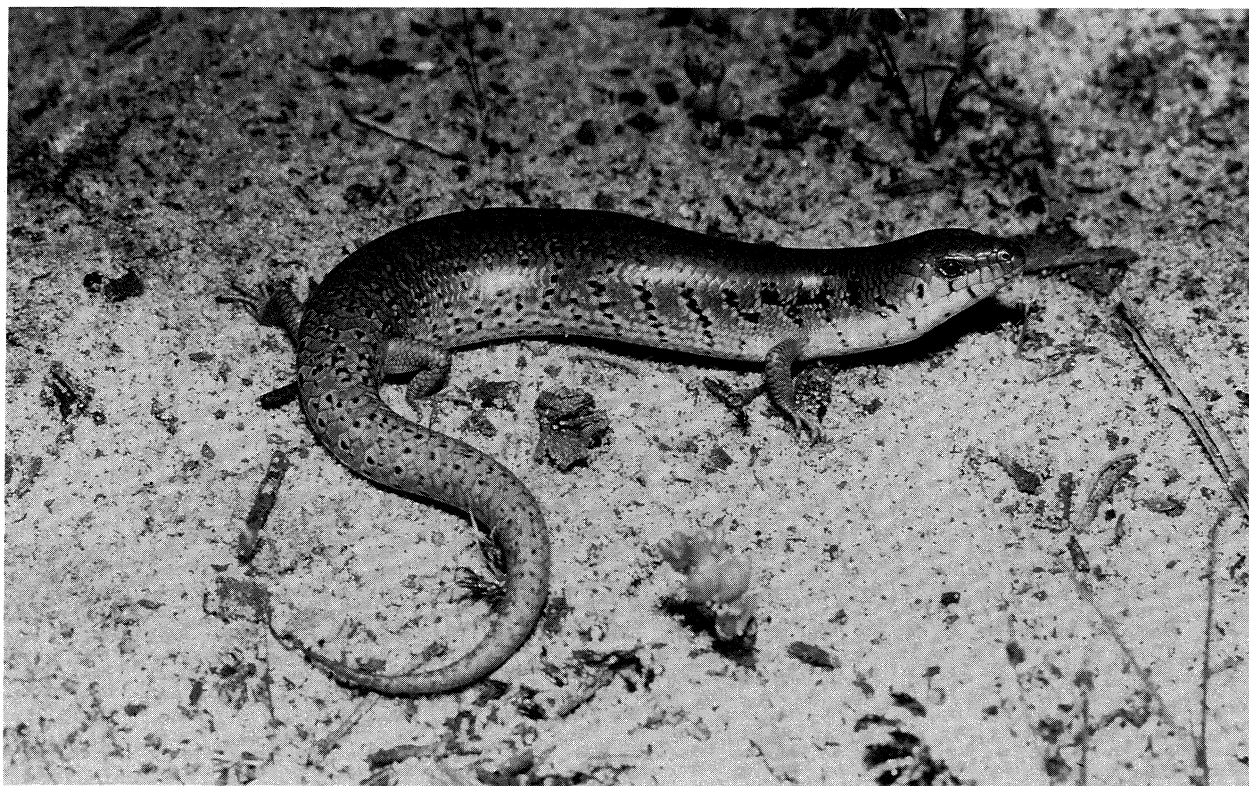


Fig. 34. A live *Cyclodomorphus venustus* from Port Germein, SA.

Cyclodomorphus venustus n.sp.

Figs 34–36

Type material. HOLOTYPE: SAM R18869, Port Germein, SA, in 33°01'S 138°00'E, collected by T.D. Schwaner on 27.xi.1980. PARATYPES: AM R107969–71, ANWC R2285, R2580, SAM R5370, R5451a–b, R8311, R10200, R11511, R21437, R22969, R24820, R25179–80, R26123–27, R26172–76, Port Pirie, SA; AM R125971, R130977–78, HFW 1624–25, MV D51967, D56351, SAM R17693, R21363, R22980, Port Germein, SA; MV D55887, 4.1 km north-east Manna Hill on Port Augusta–Broken Hill Hwy, SA; SAM R21024, 28 km north “Billa Kalina”, SA; R24415, Wilpena Pound, SA; R24519, Blinman, SA.

Diagnosis. *Cyclodomorphus venustus* differs from all other members of the *C. branchialis* species group in the combination of a mode of 24 midbody scales, 51–63 paravertebral scales, 44–54 subcaudal scales, three or more large, black, vertically ovoid patches on the sides of the neck, and a pale grey to red-brown dorsal ground.

Description. Parietals completely separated by interparietal (97.5%, $n = 40$) or in narrow contact caudally (2.5%); interparietal broadest rostrally, approximately $2/3$ – $3/4$ length and breadth of frontal; transversely enlarged nuchals 0–5 on each side ($\bar{x} = 2.8$, $SD = 0.74$, $n = 80$), usually three (72.5%); loreals rarely one unilaterally (5.0%, $n = 41$) or bilaterally (20.0%);

supraoculars rarely one unilaterally (2.5%, $n = 40$); supraciliaries 5–6 ($\bar{x} = 5.9$, $SD = 0.32$, $n = 80$), usually six (88.8%), first and last largest, third last usually projecting between second and third supraocular, remainder moderate, subequal; presuboculars rarely one unilaterally (2.5%, $n = 40$) or bilaterally ($n = 1$); postsuboculars 2–5 ($\bar{x} = 3.5$, $SD = 0.53$, $n = 80$), usually three (50.0%) or four (48.6%); upper palpebrals 6–10 ($\bar{x} = 7.9$, $SD = 0.84$, $n = 35$); lower palpebrals 7–10 ($\bar{x} = 8.3$, $SD = 0.79$, $n = 36$); secondary temporals in α - (51.4%, $n = 72$) or β - (48.6%) pattern; supralabials usually seven bilaterally (97.5%, $n = 40$), rarely eight unilaterally ($n = 1$); third last below centre of eye, separating pre- and postsuboculars; infralabials 5–7 ($\bar{x} = 6.1$, $SD = 0.37$, $n = 80$), usually six (85.0%), usually first two (96.3%, $n = 80$), rarely first three infralabials contacting postmental; ear small, vertically ovoid, approximately $2/3$ – $1 \times$ height of eye, usually with one (95.0%, $n = 80$), rarely two (5.0%) rounded to subacute lobules along rostral margin.

Body scales in 21–27 ($\bar{x} = 24.4$, $SD = 1.21$, $n = 39$), usually 24 (46.2%) or more (38.5%) longitudinal rows at midbody; scales in paravertebral rows broader than adjacent lateral dorsal scales, 51–63 ($\bar{x} = 59.2$, $SD = 2.50$, $n = 40$); subcaudal scales 44–54 ($\bar{x} = 48.3$, $SD = 1.95$, $n = 30$); lamellae below fourth toe 10–14 ($\bar{x} = 11.9$, $SD = 0.93$, $n = 78$), each with a narrow light grey-brown callus.

Presacral vertebrae 34–36 ($\bar{x} = 35.0$, $SD = 0.71$, $n = 9$); postsacral vertebrae 27–30 ($\bar{x} = 28.6$, $SD = 1.13$, $n = 7$); phalangeal formula of manus and pes 2.3.4.4.3.

SVL 40–101.5 mm ($n = 40$); AGL/SVL 51.1–64.7% ($\bar{x} = 58.8\%$, $n = 40$); TL/SVL 54.3–95.9% ($\bar{x} = 72.1\%$, $n = 32$), only one longer than 82.4%; FLL/SVL 11.7–25.0% ($\bar{x} = 18.7\%$, $n = 40$); HLL/SVL 18.5–26.9% ($\bar{x} = 22.3\%$, $n = 40$); FLL/HLL 60.0–100.0% ($\bar{x} = 83.8\%$, $n = 40$); HL/SVL 14.8–22.5% ($\bar{x} = 18.1\%$, $n = 40$); HW/HL 60.9–82.4% ($\bar{x} = 70.1\%$, $n = 40$); HD/HL 45.6–66.2% ($\bar{x} = 52.8\%$, $n = 40$).

Allometry. In relation to SVL, significant positive allometry was detected for AGL, while negative allometry was present for FLL, HLL and HL (Table 13). Other metric characters did not show statistically significant allometry, although a trend towards positive allometry of TL with respect to SVL was evident.

Coloration (in preservative) (Fig. 35). Light to mid grey, grey-brown to pink-brown dorsally and laterally, body and tail with heavy longitudinal black streaks centrally on many dorsal and lateral body scales, most prominent laterally, and aligned in transverse rows (occasionally longitudinally aligned on tail). Black streaks either restricted to base of scales or extend full length of scales, and may be single or paired. Nape dorsally with similar, though smaller and sparser black streaks; laterally with streaks coalescing to form 3–4 vertical black patches between ear and axilla. Head dorsum with only a few fine dark flecks, especially along margins of head shields; laterally with irregular dark margins to some labial scales, particularly the subocular supralabial.

Venter cream to pale yellow-blue, with or without black spots on chin and throat, aligned to form narrow irregular bands, and with or without black spots on body and tail. Pale ventral coloration may extend laterally and dorsally, particularly about transverse rows of black spots. Palms cream with cream to pale brown calli and tubercles.

Juveniles similar to adult, but with darker yellow-brown dorsal ground, and black spots on body and neck dorsum more prominent and tending to coalesce, particularly cranially, to form narrow black bands. Head dorsum slightly darker than body dorsum. Dark markings on body venter very reduced. Laterally, cream spots a little larger and more prominently transversely aligned.

Coloration (in life) (Fig. 34). Life colour notes are available for SAM R22969, AM R125971 and AM R130977–78. All had orange irides, blue-black tongues and pink mouth lining. Body coloration and pattern were similar to preserved specimens, except for ground colours (dorsum olive grey-brown becoming pink-red laterally and on tail; venter cream with yellow-orange scale margins forming a reticulum).

Details of holotype. Of the variable characters for the species, the holotype (Figs 35,36) has supraciliaries five, postsuboculars three, nuchals 2/3, supralabials seven, infralabials six, upper palpebrals six, lower palpebrals

seven, β -configuration of secondary temporals, rostral ear lobules two, midbody scales 24, paravertebral scales 59, subcaudal scales 47, subdigital lamellae 13/11, presacral vertebrae 35, postsacral vertebrae 27, SVL 92 mm, AGL 55 mm, TL 61 mm, FLL 13 mm, HLL 17 mm, HL 14.6 mm, HW 11.3 mm, HD 8.5 mm.

Sexual dimorphism. Mature-sized males were slightly larger than mature-sized females (SVL 79.5–101.5 mm, $\bar{x} = 89.3$ mm, SD = 9.44, $n = 5$ vs 74–98 mm, $\bar{x} = 86.1$ mm, SD = 7.04, $n = 18$) although the difference was not significant (Mann-Whitney U test, $U = 38$, n.s.). Males also had shorter bodies, longer hindlimbs and longer but shallower heads than females (Table 14). Due to the narrow size range for the female sample, the regressions of TL against SVL and FLL against both SVL and HLL were not significant in that sex. These relationships were not tested for sexual dimorphism.

Males had slightly more postsuboculars than females ($\bar{x}$'s = 3.8 vs 3.4, $t_{56} = 2.71^{**}$). There were no significant differences between males and females in mean number of paravertebral scales, midbody scales, subcaudal scales, subdigital lamellae, supralabials, infralabials, supraciliaries, nuchals, upper palpebrals or lower palpebrals.

Distribution. *Cyclodomorphus venustus* inhabits semi-arid habitats of central and eastern SA, from 28 km north “Billa Kalina” in the west, to 4.1 km north-east Manna Hill in the east, and south to Port Pirie (Fig. 14). Also tentatively associated with this taxon (but not included in the above description) are six specimens and a literature record from the vicinity of the SA/NSW/Qld border: Chunky Creek, nr Tibooburra, NSW (AM R106892), Innamincka, SA (NTM R6986), Betoota Hotel, Qld (QM J28851, J37673), Noccundra Hotel, Qld (AM R133211–12) and Rat Point, NSW (Becker, in Tipping, 1979).

Geographic variation. For the purposes of describing geographic variation, the large sample from the two southernmost localities, Port Germein and Port Pirie, was compared to the four specimens from central SA (MV D55887, SAM R21024, R24415, R24519). These two populations are referred to as southern and central. The six atypical specimens from further north are discussed separately, and collectively referred to as the northern sample.

Significant differences occur between southern and central populations in mean number of subcaudal scales (44–51, $\bar{x} = 48.0$ vs 50–54, $\bar{x} = 52.0$; $t_{30} = 3.81^{***}$), infralabials ($\bar{x}$'s = 6.1 vs 6.4, $t_{78} = 2.03^*$) and nuchals ($\bar{x}$'s = 2.9 vs 2.0, $t_{78} = 3.56^{***}$), but not in number of midbody scales, paravertebral scales, subdigital lamellae, postsuboculars or supraciliaries. The single specimen from Wilpena Pound (SAM R24415), a male, is not only a little larger than other specimens (SVL 101.5 vs up to 98 mm) but is also very much more robust.

The northern sample is similar to *C. venustus* in having solid “gill” markings and a light dorsal ground

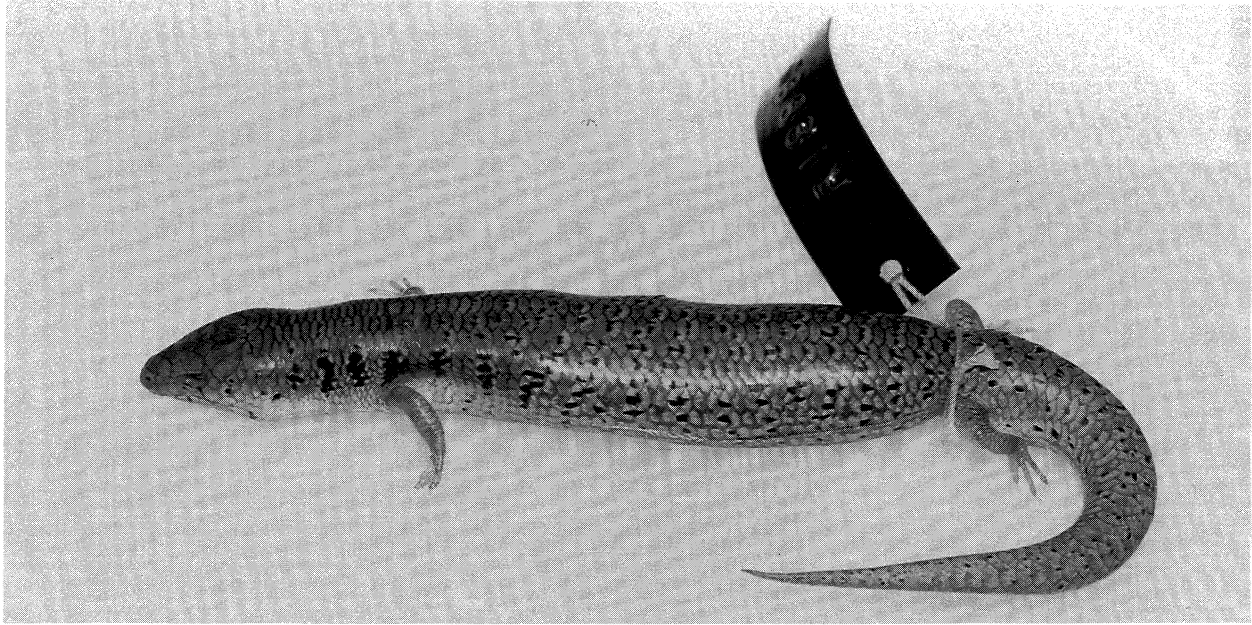


Fig. 35. Holotype of *Cyclodomorphus venustus* (SAM R18869).

(Fig. 37), but has fewer midbody scales (20–24, $\bar{x} = 22.3$; $t_{43} = 3.83^{***}$), postsuboculars (2–3, $\bar{x} = 2.8$, $t_{90} = 4.43^{***}$) and nuchals (0–3, $\bar{x} = 2.0$, $t_{90} = 3.23^{***}$), more paravertebral scales (58–64, $\bar{x} = 62.0$, $t_{44} = 2.58^*$), presacral vertebrae (37–40, $\bar{x} = 38.8$, $t_{11} = 6.30^{***}$) and subcaudal scales (69–74 in the two specimens with complete tails), a consistent α -configuration of secondary temporals, a longer tail (101.1–108.1% of SVL), and dorsal and lateral pattern very reduced (absent or almost so dorsally, reduced to sparse black spots, basal on scales laterally on body and tail, and lateral nuchal markings reduced to black or grey smudges; dorsal ground light sandy yellow-brown or grey-brown). Our assignment of this sample to *C. venustus*, despite its very different scalation in several characters, is largely on the basis of the synapomorphy of presence of dark “gill” markings, geographic proximity, and the suggestion of a clinal increase in subcaudal scales and a decrease in nuchal scales from south to north. Further collections, especially from intervening areas, may result in the recognition of this population as a distinct taxon.

Comparison with other taxa. *Cyclodomorphus venustus* (*sensu stricto*) differs from all other taxa in the *C. branchialis* species group in having only 44–54 subcaudal scales (minimum for other species 57, in *C. branchialis*), an autapomorphy in the context of the *C. branchialis* species group. This difference is also reflected in a shorter tail (Tables 1–6) and lower number of postsacral vertebrae (27–30 vs minimum of 32, in *C. branchialis*). In other respects, particularly in coloration, *C. venustus* is most similar to *C. branchialis*, although geographically separated from it by over 1870 km, with *C. m. elongatus* occupying much of the gap. Despite the almost identical colour pattern to *C. branchialis*, southern and central populations of *C. venustus* have fewer paravertebral (51–

63 vs 62–70) and subcaudal (44–54 vs 57–64) scales, but more numerous postsuboculars ($\bar{x} = 3.5$ vs 2.6, $t_{112} = 8.30^{***}$, modes three vs two) and subdigital lamellae ($\bar{x} = 11.9$ vs 10.8, $t_{108} = 6.02^{***}$), as well as a greater variation in the temporal configuration (49% vs 86% in β -pattern). Some of these differences (paravertebrals, subcaudals) are not maintained in the northern population of *C. venustus*, although the differences in mean number of postsuboculars ($\bar{x} = 2.8$, mode 3 [83.3%], $n = 12$) and subdigital lamellae (10–14, $\bar{x} = 11.9$, $n = 12$) remain, while the difference in the temporal configuration is enhanced (all six of the northern *venustus* have the α -pattern). Further, in the northern *venustus* the number of subcaudals (69–74, $n = 2$) is greater than in *C. branchialis*, while the coloration is paler, with the “gill” markings on the neck less developed, and the strong lateral and dorsal pattern present on most *C. branchialis* almost absent.

The presence of dark “gill” markings on the neck would seem to be a synapomorphy linking *C. branchialis* and *C. venustus*, and it is possible that they should be treated as subspecies of a single species. However, we believe that the extreme geographic separation of the two taxa, together with evidence of morphological differentiation in scalation and body proportions, constitutes a case for the two taxa being on distinct “phylogenetic trajectories” (Frost & Hillis, 1990: 90) and having “distinct evolutionary tendencies and historical fate” (Wiley, 1978: 18), and hence warranting distinct specific status using the evolutionary species concept.

Cyclodomorphus venustus differs from *C. celatus* in its smaller adult size (mature SVL 74–101.5 mm vs 82–121 mm), shorter body (AGL/SVL: Tables 2,13), longer limbs (Tables 2,13), greater number of midbody scales (mostly 24 or more, vs usually 22 or fewer), lower number of paravertebral scales (51–63 vs 61–77), and

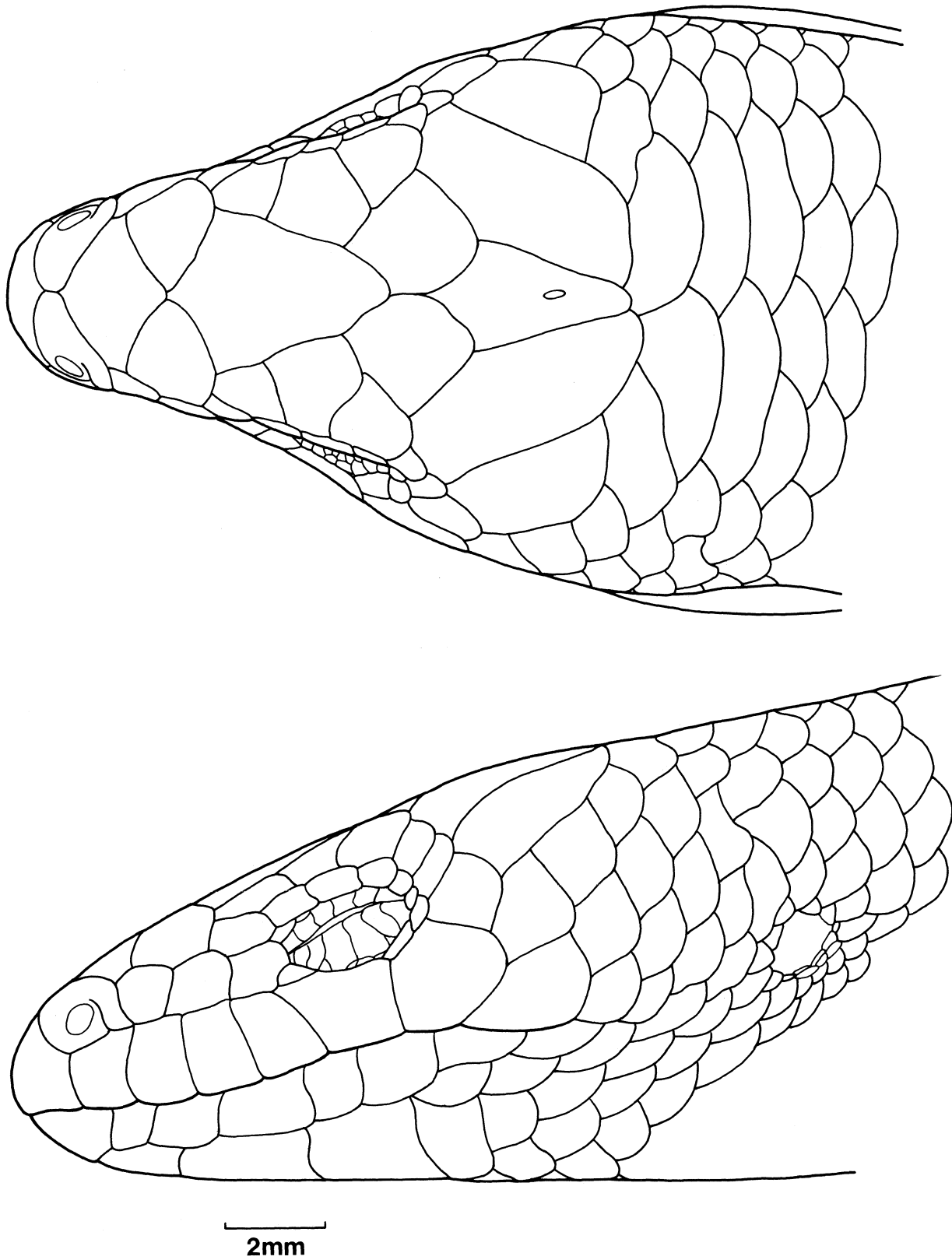


Fig. 36. Head shields of holotype of *Cyclodomorphus venustus*.



Fig. 37. A live individual of the northern form of *Cyclodomorphus venustus* from Noccundra Hotel, Qld.

in colour pattern, with fusion of the lateral nuchal markings to form solid black bars and reduction of the black streaks to basal spots. The reddish flush seen in many southern and central *C. venustus* has not been observed in *C. celatus*.

In addition to the marked differences in body size, tail length, number of ear lobules and shape of interparietal, *C. venustus* differs from *C. maximus* in its greater number of midbody scales (usually 24 or more vs mode 22), fewer paravertebral scales (51–63 vs 61–67), presacral vertebrae (34–36 vs 40–42), subdigital lamellae (10–14 vs 14–17), upper palpebrals (6–10 vs 9–12) and lower palpebrals (7–10 vs 10–13), shorter body (and therefore longer limbs and head) and narrower head (Tables 4,13), and in coloration (solid “gill” markings, strong dark spotting and streaking on body and tail vs no dark markings on body and tail, but pale spots and a dark circumocular ring present).

Cyclodomorphus venustus further differs from *C. m. melanops* in its very much smaller size (SVL to 101.5 mm vs 132 mm), shorter body (Tables 5,13), with fewer paravertebral scales (51–63 vs 62–80) and presacral vertebrae (34–36 vs 38–42), lower mean number of subdigital lamellae (10–14, $\bar{x}$ = 11.9 vs 10–18, $\bar{x}$ = 14.1), slightly lower mean numbers of upper palpebrals (6–10, $\bar{x}$ = 7.9 vs 7–13, $\bar{x}$ = 9.7) and lower palpebrals (7–10, $\bar{x}$ = 8.3 vs 7–14, $\bar{x}$ = 10.9), and possession of solid dark “gill” markings.

Cyclodomorphus venustus is geographically closest to *C. m. elongatus*. Within the Flinders Ranges, the two

taxa approach to within approximately 15 km between Wilpena Pound and Mt Sunderland and 27 km between Blinman and Parachilna. In addition to the shorter tail, *C. venustus* differs from *C. m. elongatus* in its smaller size (SVL to 101.5 mm vs 125 mm), shorter body (Tables 10,13), with fewer paravertebral scales (51–63 vs 61–85) and presacral vertebrae (34–36 vs 38–44), and strong colour pattern (absent or almost so in *C. m. elongatus*). Within the Flinders Ranges, *C. m. elongatus* has an even greater number of paravertebral scales (73–84, $\bar{x}$ = 77.7), suggesting character displacement.

Cyclodomorphus venustus and *C. m. siticulosus* are similar in size and body length, and in habitat preferences (chenopods and coastal heaths, often on stony soils). In addition to the difference in tail length, however, the two taxa differ in the complete lack in *C. m. siticulosus* of the strong colour pattern of *C. venustus*, and the variable temporal pattern of *C. venustus* (consistently β -in *C. m. siticulosus*). Geographically, the two taxa are separated by *C. m. elongatus* on Eyre Peninsula and in the Gawler Ranges.

Etymology. The specific epithet is from the Latin *venustus* (lovely, beautiful) in allusion to the bright coloration of this species.

Habits and habitats. The Port Pirie and Port Germein populations inhabit coastal samphire flats (SAM R26172–76) and low heath (pers. obs.). Most specimens have

been taken from under rubbish in dumps and tips. Ehmann (1992) reports the species (as *Cyclodomorphus* sp.) from “low-lying saline flats and old stranded foredunes above the influence of most high tides but subject to low, slow sheet flooding during extreme tides... or especially after very heavy rain. Soils are saline clays, often containing grit, especially on the coast. Also inland samphire plains... “. He also reports burrow construction in this species: “the Samphire Omolepida digs a home burrow which starts under a samphire bush and extends up to 1.5 metres more or less horizontally through the saline loamy... soil. The burrow has risers as well as air traps to retard entry of water due to flooding or high tides. It can remain submerged for up to an hour and is not distressed by being completely covered by water in a confined space. While foraging away from the home burrow, it shelters under more superficial cover such as matted and procumbent vegetation”. Individuals we have held in captivity have readily burrowed into loose sand, gravel and leaf litter, and spent much of the time below the surface.

Specific habitat data are available for all four specimens in the central sample. SAM R21024 was taken in a pitfall trap in gibber plains with cracking clay and low dense chenopods. MV D55887 was found under railway sleepers in an open saltbush-bluebush plain. SAM R24519 was found under tin on sandy soil by a ruined building, while SAM R24415 was taken under *Triodia* on a scree slope.

Of the northern material, QM J28851 was found under a small sheet of iron on a bare gibber plain (J. Covacevich, pers. comm.), and the Noccundra Hotel specimens were found under tin in a rubbish tip (L. Voigt, pers. comm.) while the habitat at Chunky Creek (AM R106892) has been described by Denny (1975): close to the creek, the dominant plants are “a mixture of sedge, *Leptochloa digitata* and a small bush (*Chenopodium* species) with a scattering of Coolabah trees (*Eucalyptus microtheca*) and an undergrowth of native clover (*Medicago* sp.)” on “red cracking soil”; successively more distant from the creek are “a vegetation complex of *Bassia quinquecupis* as the dominant species” and “a stand of grass containing such species as Mitchell, Flinders, Umbrella (*Chloris acicularis*) and Ray (*Sporobolus actinocladius*).”

Reproduction. Ehmann (1983) recorded a litter of two for this species, born 9.ii.1982. The young at birth were 41 and 42 mm SVL, with mass 1.28 and 1.19 g respectively. This record is based on HFWE 1624–25, born to a Port Germein specimen (H. Ehmann, pers. comm.). Ehmann (1992) subsequently reported a litter of three born in early February, possibly also based on the above record, and in error.

Males collected in September and October ($n = 4$) had enlarged, semiturgid to turgid testes 7–10 mm long.

Three gravid females (SVL 90.5–92 mm) were collected between 27 October and 27 November, and carried 2–4 ($n = 2$) unshelled oviducal eggs. Other

mature-sized females ($n = 15$) collected between 16 January and 29 October were non-gravid, although some of those collected in September and October had slightly enlarged ovarian follicles.

Sex ratio. The ratio of mature-sized males:females is 5:18, a ratio significantly different from equality ($\chi^2_1 = 6.26^*$).

Diet. The diet of this species has been reported to include “spiders, cockroaches, centipedes, snails, and smaller skinks”, captured by “stealth and ambush” (Ehmann, 1992).

Conservation status. Cogger *et al.* (1993) identify this species (as *Cyclodomorphus* sp. [Samphire, SA]) as RARE or INSUFFICIENTLY KNOWN in a national comparison of reptiles of conservation significance.

A Key to the Genus *Cyclodomorphus*

1. Postnarial groove absent; paravertebral scales not or only slightly broader than adjoining lateral dorsal scales 2
- Postnarial groove present; paravertebral scales noticeably broader than adjoining lateral dorsal scales 3
2. Postmental contacting a single infralabial on each side; 26–34 midbody scales; 14–17 subdigital lamellae; east coast NSW and Queensland *C. gerrardii*
- Postmental contacting two infralabials on each side; 20–26 midbody scales; 8–14 subdigital lamellae; Tasmania and coast and ranges of eastern Victoria and NSW *C. casuarinae* complex *
3. SVL up to 231 mm; interparietal much smaller than frontal ($\frac{1}{2}$ – $\frac{2}{3}$ length, $\frac{1}{3}$ – $\frac{1}{2}$ breadth in adults, slightly larger in juveniles); north-west Kimberley *C. maximus*
- SVL up to 132 mm; interparietal only a little smaller than frontal ($\frac{3}{4}$ – $\frac{9}{10}$ length; $\frac{2}{3}$ – $\frac{9}{10}$ breadth in adults, slightly larger in juveniles) 4
4. Three large solid black to grey, vertically ovoid patches on side of neck between ear and axilla; subcaudal scales 44–64 5
- Side of neck without solid dark ovoid markings; subcaudal scales 58–87 6
5. Subcaudal scales 44–54; paravertebral scales 51–63; South Australia *C. venustus*
- Subcaudal scales 57–64; paravertebral scales 62–70; Geraldton region, WA *C. branchialis*
6. Midbody scales usually 20–22; ear narrow, slit-like, usually without obvious lobules; sides of neck with 3–4 vertical series of short black streaks; west coast of WA, south of “Gnaraloo” *C. celatus*
- Midbody scales usually 24–29; ear open, usually with a single lobule on rostral margin; sides of neck immaculate or with scattered black spots (not streaks) 7
7. Secondary temporals usually in α -configuration; venter usually with black spots; dorsum with or without black spots; southern Kimberley, Pilbara, central Australia *C. m. melanops*
- Secondary temporals usually in β -configuration; body and tail immaculate, rarely with a few dark flecks ventrally 8
8. Paravertebral scales 61–85; *Triodia* habitats; WA Goldfields east to western NSW, western Qld, central Australia *C. m. elongatus*
- Paravertebral scales 56–63; chenopod habitats; Nullarbor Plains and Hampton Tableland *C. m. siticulosus*

* See Shea (1995) for a key to the three species in this complex.

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Table 1. Allometric equations and calculated values for cranial and somatic proportions in *Cyclodomorphus branchialis*. Values a and b solve the equation $y = bx^a$, r = correlation coefficient, s.e. = standard error of a, C_{51} , C_{88} are calculated percentage proportions (y/x) at SVL = 51 and 88 mm (minimum and maximum size of the material seen, although the minimum almost certainly does not represent neonate size). Sample sizes are as for ratios.

y	x	a	b	r	s.e.	C_{51}	C_{88}
AGL	SVL	1.1664	0.289	0.9893	0.0445	55.6	60.9
TL	SVL	1.2395	0.296	0.9468	0.1490	75.9	86.5
FLL	SVL	0.7497	0.496	0.9173	0.0903	18.5	16.2
HLL	SVL	0.8430	0.419	0.9141	0.1000	22.6	20.7
FLL	HLL	1.0440	0.700	0.9605	0.0839	78.0	79.5
HL	SVL	0.7749	0.484	0.9452	0.0716	20.0	17.7
HW	HL	1.1627	0.476	0.9334	0.1195	69.4	74.4
HD	HL	1.1458	0.375	0.9065	0.1426	52.6	55.9

Table 2. Allometric equations and calculated values for cranial and somatic proportions in *Cyclodomorphus celatus*. Values a and b solve the equation $y = bx^a$, r = correlation coefficient, s.e. = standard error of a, C_{38} , C_{83} , C_{121} are calculated percentage proportions (y/x) at SVL = 38, 83 and 121 mm (minimum, minimum mature and maximum size). Sample sizes are as for ratios.

y	x	a	b	r	s.e.	C_{38}	C_{83}	C_{121}
AGL	SVL	1.1229	0.373	0.9916	0.0101	58.3	64.2	67.2
TL	SVL	1.2784	0.270	0.9765	0.0306	74.3	92.4	102.6
FLL	SVL	0.6770	0.616	0.8960	0.0233	19.0	14.8	13.1
HLL	SVL	0.7615	0.566	0.9022	0.0254	23.8	19.7	18.0
FLL	HLL	0.8656	1.092	0.9646	0.0165	81.2	75.0	72.2
HL	SVL	0.6377	0.788	0.9575	0.0133	21.1	15.9	13.9
HW	HL	0.9755	0.727	0.9546	0.0211	69.1	68.2	67.8
HD	HL	1.0919	0.438	0.9434	0.0266	53.0	55.5	56.8

Table 3. Sexual dimorphism in cranial and somatic proportions in *Cyclodomorphus celatus*. Tests of significance (i) and allometric and calculated values for males (ii) and females (iii) in sexually dimorphic characters. Conventions for (ii) and (iii) as for Table 1, except for n (sample size). C_{83} and C_{115} are calculated proportions at SVL = 83, 115 mm (mean minimum size at maturity, and maximum size for males, the smaller sex).

(i)		Slopes			Intercepts		
y	x	F	d.f.	P	F	d.f.	P
AGL	SVL	0.004	1,112	n.s.	58.904	1,113	***
TL	SVL	0.003	1,28	n.s.	18.044	1,29	***
FLL	SVL	4.861	1,111	*	70.774	1,112	***
HLL	SVL	11.335	1,109	***	—	—	—
FLL	HLL	0.213	1,109	n.s.	0.501	1,110	n.s.
HL	SVL	4.701	1,112	*	134.486	1,113	***
HW	HL	0.722	1,112	n.s.	1.051	1,113	n.s.
HD	HL	0.195	1,112	n.s.	2.603	1,113	n.s.

(ii)		a	b	r	s.e.	n	C_{83}	C_{115}
AGL	SVL	1.115	0.378	0.971	0.035	65	62.8	65.2
TL	SVL	1.144	0.511	0.949	0.101	16	96.6	101.2
FLL	SVL	0.637	0.775	0.781	0.065	64	15.6	13.8
HLL	SVL	0.844	0.410	0.846	0.068	63	20.6	19.6
HL	SVL	0.750	0.490	0.929	0.038	65	16.2	15.0

(iii)		a	b	r	s.e.	n	C_{83}	C_{115}
AGL	SVL	1.118	0.389	0.984	0.029	51	65.5	68.1
TL	SVL	1.134	0.486	0.882	0.162	16	87.9	91.8
FLL	SVL	0.412	1.956	0.590	0.081	51	14.6	12.0
HLL	SVL	0.476	1.933	0.619	0.087	50	19.1	16.1
HL	SVL	0.631	0.782	0.918	0.039	51	15.3	13.6

Table 4. Allometric equations and calculated values for cranial and somatic proportions in *Cyclodomorphus maximus*. Values a and b solve the equation $y = bx^a$, r = correlation coefficient, s.e. = standard error of a, C_{62} , C_{157} , C_{231} are calculated percentage proportions (y/x) at SVL = 62, 157 and 231 mm (minimum, mean minimum mature and maximum size). Correlation between tail length and SVL not calculated due to limited data. Sample sizes are as for ratios.

y	x	a	b	r	s.e.	C_{62}	C_{157}	C_{231}
AGL	SVL	1.1201	0.344	0.9997	0.0071	56.5	63.1	66.1
FLL	SVL	0.6665	0.837	0.9952	0.0160	21.1	15.5	13.6
HLL	SVL	0.7897	0.599	0.9977	0.0130	25.1	20.7	19.1
FLL	HLL	0.8435	1.293	0.9968	0.0163	84.1	75.0	71.5
HL	SVL	0.6456	0.919	0.9954	0.0151	21.3	15.3	13.4
HW	HL	1.0700	0.585	0.9938	0.0289	70.1	73.1	74.4
HD	HL	1.1015	0.383	0.9926	0.0327	49.8	52.9	54.2

Table 5. Allometric equations and calculated values for cranial and somatic proportions in *Cyclodomorphus melanops melanops*. Values a and b solve the equation $y = bx^a$, r = correlation coefficient, s.e. = standard error of a, C_{41} , C_{83} , and C_{132} are calculated percentage proportions (y/x) at SVL = 41, 83, and 132 mm (minimum, minimum mature, and maximum size). Sample sizes are as for ratios.

y	x	a	b	r	s.e.	C_{41}	C_{83}	C_{132}
AGL	SVL	1.1419	0.335	0.9888	0.0084	56.7	62.7	67.0
TL	SVL	1.2476	0.351	0.9516	0.0351	88.0	104.8	117.6
FLL	SVL	0.6186	0.904	0.8699	0.0173	21.9	16.8	14.0
HLL	SVL	0.6832	0.886	0.8869	0.0175	27.3	21.9	18.9
FLL	HLL	0.8667	1.129	0.9394	0.0156	81.8	76.7	73.5
HL	SVL	0.6507	0.737	0.9071	0.0147	20.1	15.7	13.4
HW	HL	1.0708	0.611	0.9541	0.0162	71.0	73.3	74.9
HD	HL	1.1232	0.410	0.9372	0.0202	53.2	56.3	58.4

Table 6. Sexual dimorphism in cranial and somatic proportions in *Cyclodomorphus melanops melanops*. Tests of significance (i) and allometric and calculated values for males (ii) and females (iii) in sexually dimorphic characters. Conventions for (ii) and (iii) as for Table 3. C_{83} and C_{126} are calculated proportions at SVL = 83, 126 mm (mean minimum size at maturity, and maximum size for males, the smaller sex).

(i)

y	x	Slopes			Intercepts		
		F	d.f.	P	F	d.f.	P
AGL	SVL	2.621	1,235	n.s.	43.591	1,236	***
TL	SVL	0.069	1,63	n.s.	3.901	1,64	n.s.
FLL	SVL	4.349	1,230	*	36.560	1,231	***
HLL	SVL	6.669	1,230	**	—	—	—
FLL	HLL	0.072	1,231	n.s.	0.168	1,232	n.s.
HL	SVL	6.346	1,235	*	54.197	1,236	***
HW	HL	0.096	1,238	n.s.	8.933	1,239	**
HD	HL	0.674	1,238	n.s.	3.420	1,239	n.s.

(ii)

y	x	a	b	r	s.e.	n	C_{83}	C_{126}
AGL	SVL	1.034	0.536	0.960	0.030	101	62.3	63.2
FLL	SVL	0.663	0.765	0.770	0.056	99	17.3	15.0
HLL	SVL	0.674	0.959	0.760	0.058	100	22.7	19.8
HL	SVL	0.868	0.286	0.860	0.052	100	16.0	15.1
HW	HL	0.936	0.869	0.912	0.042	101	73.7	72.0

(iii)

AGL	SVL	1.098	0.412	0.963	0.026	138	63.5	66.2
FLL	SVL	0.491	1.581	0.579	0.060	135	16.7	13.5
HLL	SVL	0.464	2.328	0.580	0.057	134	21.8	17.4
HL	SVL	0.685	0.618	0.758	0.050	139	15.4	13.5
HW	HL	0.953	0.845	0.909	0.037	141	75.0	74.0

Table 7. Geographic variation in mean number of paravertebral scales in *Cyclodomorphus melanops melanops*. Pairwise comparisons between the ten highest means (horizontal) and the five lowest means (vertical). Means are in parentheses. Significant differences at the 5% level are indicated by asterisks. All other pairs of means not significantly different. Populations identified by the first letter(s) of their names.

	M	N	H	T	Oa	On	LA	GS	C	UA
	(73.0)	(72.8)	(72.2)	(72.2)	(67.7)	(71.9)	(71.7)	(70.6)	(70.0)	(69.3)
C (70.0)	*	—	—	—	*	—	—	—	—	—
UA (69.3)	*	—	*	—	*	*	—	—	—	—
K (68.0)	*	*	*	*	*	*	*	—	*	—
E (67.7)	*	*	*	*	*	*	*	—	*	—
BI (66.6)	*	*	*	*	*	*	*	*	*	*

Table 8. Geographic variation in mean number of subdigital lamellae in *Cyclodomorphus melanops melanops*. Pairwise comparisons between the seven highest means (horizontal) and all other means. Conventions as for Table 7.

	E	K	BI	M	H	On	Oa
	(15.2)	(14.6)	(14.5)	(14.4)	(13.9)	(13.9)	(13.7)
K (14.6)	*	—	—	—	—	—	—
BI (14.5)	*	—	—	—	—	—	—
M (14.4)	*	—	—	—	—	—	—
H (13.9)	*	*	*	—	—	—	—
On (13.9)	*	*	*	—	—	—	—
Oa (13.7)	*	*	*	*	—	—	—
N (13.7)	*	*	—	—	—	—	—
T (13.7)	*	—	—	—	—	—	—
UA (13.2)	*	*	*	*	—	—	—
LA (13.2)	*	*	*	*	—	—	—
GS (12.8)	*	*	*	*	—	—	—
C (12.6)	*	*	*	*	*	*	*

Table 9. Geographic variation in mean number of supralabial scales in *Cyclodomorphus melanops melanops*. Pairwise comparisons between the ten highest means (horizontal) and the seven lowest means (vertical). Conventions as for Table 7.

		LA (7.9)	E (7.7)	M (7.6)	N (7.6)	H (7.5)	On (7.5)	Oa (7.5)	T (7.4)	UA (7.3)	BI (7.3)
Oa	(7.5)	*	—	—	—	—	—	—	—	—	—
T	(7.4)	—	—	—	—	—	—	—	—	—	—
UA	(7.3)	*	*	—	—	—	—	—	—	—	—
BI	(7.3)	*	*	*	—	*	—	—	—	—	—
GS	(7.1)	*	*	*	—	*	—	*	—	—	—
C	(7.0)	*	*	*	*	*	*	*	—	*	*
K	(7.0)	*	*	*	*	*	*	*	*	*	*

Table 10. Allometric equations and calculated values for cranial and somatic proportions in *Cyclodomorphus melanops elongatus*. Values a and b solve the equation $y = bx^a$, r = correlation coefficient, s.e. = standard error of a, C_{41} , C_{73} and C_{125} are calculated percentage proportions (y/x) at SVL = 41, 73 and 125 mm (minimum, minimum mature and maximum size). Sample sizes are as for ratios.

y	x	a	b	r	s.e.	C_{41}	C_{73}	C_{125}
AGL	SVL	1.1407	0.342	0.9869	0.0095	57.7	62.5	67.5
TL	SVL	1.2240	0.354	0.9769	0.0200	81.3	92.6	104.4
FLL	SVL	0.5862	1.022	0.8344	0.0196	22.0	17.3	13.9
HLL	SVL	0.6674	0.928	0.8777	0.0185	27.0	22.3	18.6
FLL	HLL	0.8832	1.077	0.9558	0.0138	81.3	77.8	74.6
HL	SVL	0.6037	0.885	0.9243	0.0126	20.3	16.2	13.1
HW	HL	1.0878	0.581	0.9547	0.0172	70.0	72.2	74.2
HD	HL	1.0949	0.438	0.9229	0.0231	53.6	55.4	57.1

Table 11. Sexual dimorphism in cranial and somatic proportions in *Cyclodomorphus melanops elongatus*. Tests of significance (i) and allometric and calculated values for males (ii) and females (iii) in sexually dimorphic characters. Conventions for (ii) and (iii) as for Table 3. C_{73} and C_{111} are calculated proportions at SVL = 73, 111 mm (mean minimum size at maturity, and maximum size for males, the smaller sex).

(i)

y	x	Slopes			Intercepts		
		F	d.f.	P	F	d.f.	P
AGL	SVL	0.019	1,318	n.s.	31.845	1,319	***
TL	SVL	11.003	1,137	***	—	—	—
FLL	SVL	3.996	1,323	*	45.313	1,324	***
HLL	SVL	2.465	1,319	n.s.	77.910	1,320	***
FLL	HLL	2.159	1,318	n.s.	0.168	1,319	n.s.
HL	SVL	2.677	1,318	n.s.	63.412	1,319	***
HW	HL	0.765	1,319	n.s.	0.174	1,320	n.s.
HD	HL	0.118	1,318	n.s.	0.173	1,319	n.s.

(ii)

y	x	a	b	r	s.e.	n	C_{73}	C_{111}
AGL	SVL	1.099	0.405	0.981	0.018	152	61.9	64.6
TL	SVL	1.261	0.312	0.980	0.031	72	95.6	106.7
FLL	SVL	0.663	0.750	0.830	0.036	156	17.7	15.3
HLL	SVL	0.733	0.722	0.882	0.032	153	23.0	20.5
HL	SVL	0.685	0.631	0.915	0.025	152	16.3	14.3

(iii)

y	x	a	b	r	s.e.	n	C_{73}	C_{111}
AGL	SVL	1.103	0.409	0.979	0.018	170	63.6	66.4
TL	SVL	1.093	0.620	0.956	0.041	69	92.4	96.1
FLL	SVL	0.562	1.102	0.772	0.036	171	16.8	14.0
HLL	SVL	0.661	0.922	0.839	0.033	170	21.5	18.7
HL	SVL	0.633	0.757	0.925	0.020	139	15.7	13.4

Table 12. Allometric equations and calculated values for cranial and somatic proportions in *Cyclodomorphus melanops siticulosus*. Values a and b solve the equation $y = bx^a$, r = correlation coefficient, s.e. = standard error of a, C_{70} and C_{94} are calculated percentage proportions (y/x) at SVL = 70 and 94 mm (small adult and maximum size). Due to the narrow range of SVLs for the material known, small samples and the sexual dimorphism at this size, most correlations were non-significant in the pooled sample. Hence, this table presents only the allometric equations for males for all variables except AGL.

y	x	a	b	r	s.e.	C_{70}	C_{94}
AGL	SVL	1.3000	0.157	0.9168	0.2141	56.2	61.4
FLL	SVL	0.8482	0.390	0.8928	0.2140	20.5	19.6
HLL	SVL	0.6753	1.041	0.9168	0.1471	26.2	23.8
FLL	HLL	1.1440	0.519	0.8870	0.2978	78.9	81.2
HL	SVL	0.8756	0.323	0.9887	0.0665	19.0	18.4
HW	HL	0.8279	1.138	0.8567	0.2493	72.9	69.7
HD	HL	0.7712	1.014	0.8805	0.2076	56.1	52.9

Table 13. Allometric equations and calculated values for cranial and somatic proportions in *Cyclodomorphus venustus*. Values a and b solve the equation $y = bx^a$, r = correlation coefficient, s.e. = standard error of a, C_{40} , C_{74} and C_{101} are calculated percentage proportions (y/x) at SVL = 40, 74 and 101 mm (minimum, minimum mature and maximum size). Sample sizes are as for ratios.

y	x	a	b	r	s.e.	C_{40}	C_{74}	C_{101}
AGL	SVL	1.1396	0.320	0.9819	0.0357	53.6	58.4	60.9
TL	SVL	1.1017	0.462	0.9323	0.0780	67.2	71.6	74.6
FLL	SVL	0.5781	1.163	0.7450	0.0840	24.5	18.9	16.6
HLL	SVL	0.7287	0.724	0.8943	0.0592	26.6	22.5	20.7
FLL	HLL	0.8147	1.415	0.8556	0.0800	91.3	84.0	80.6
HL	SVL	0.6647	0.778	0.9120	0.0485	22.6	18.4	16.6
HW	HL	0.9817	0.734	0.9278	0.0640	70.5	70.0	69.7
HD	HL	1.0740	0.432	0.9040	0.0824	50.8	52.4	53.2

Table 14. Sexual dimorphism in cranial and somatic proportions in *Cyclodomorphus venustus*. Tests of significance (i) and allometric and calculated values for males (ii) and females (iii) in sexually dimorphic characters. Conventions for (ii) and (iii) as for Table 3. C_{77} and C_{98} are calculated proportions at SVL = 77, 98 mm (mean minimum size at maturity, and maximum size for females, the smaller sex). TL and FLL were not significantly correlated with SVL in females due to the small size range of the female sample.

(i)

y	x	Slopes			Intercepts		
		F	d.f.	P	F	d.f.	P
AGL	SVL	2.477	1,26	n.s.	5.762	1,27	*
HLL	SVL	3.774	1,26	n.s.	20.190	1,27	***
HL	SVL	14.710	1,26	***	—	—	—
HW	HL	0.273	1,26	n.s.	2.475	1,27	n.s.
HD	HL	0.217	1,26	n.s.	6.240	1,27	*

(ii)

y	x	a	b	r	s.e.	n	C_{77}	C_{98}
AGL	SVL	0.994	0.588	0.993	0.047	8	57.3	57.2
HLL	SVL	0.883	0.399	0.969	0.092	8	24.0	23.3
HL	SVL	0.892	0.312	0.979	0.076	8	19.5	19.0
HD	HL	0.891	0.677	0.989	0.055	8	50.4	49.2

(iii)

AGL	SVL	1.206	0.243	0.908	0.124	22	59.5	62.5
HLL	SVL	0.554	1.514	0.655	0.143	22	21.8	19.6
HL	SVL	0.439	2.048	0.727	0.093	22	17.9	15.6
HD	HL	1.033	0.497	0.591	0.316	22	54.2	54.4