A Taxonomic Revision
of the *Cyclodomorphus casuarinae* Complex
(Squamata: Scincidae)

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ABSTRACT. Univariate and multivariate analyses of geographic variation in morphological characters indicate that *Cyclodomorphus casuarinae* consists of three geographically distinct taxa, which are recognised as species: one in Tasmania (*C. casuarinae*), a new species in the Australian Alps, and the third at lower altitudes in mainland Australia (*C. michaeli*). These three species are described, and data on habitat and reproduction provided for each.

The she-oak skink, *Cyclodomorphus casuarinae*, is a poorly known, secretive and uncommonly collected species from south-eastern Australia and Tasmania. Although this large and spectacular species occurs in close proximity to two state capital cities (Sydney and Hobart), and has been known to science for over a century and a half, it has received almost no attention, either taxonomically or ecologically (Shea, 1988; Shine & Hutchinson, 1991). The species is considered to be rare and under threat in at least the Victorian part of its range (Ahern *et al.,* 1985; Cherry *et al.,* 1987; MacFarlane *et al.,* 1987).

With two exceptions (Peters, 1875; Wells & Wellington, 1984), no author has suggested that the taxon consists of other than a single monotypic species. However, until now, no author has examined representative series of specimens from throughout the range of the taxon. Indeed, there are only three redescriptions based on more than a single specimen: by Gray (1845) based on five unlocalised Tasmanian specimens, by Boulenger (1887) based on 16 unlocalised Tasmanian specimens and a single Sydney specimen, and by Mitchell (1950) based on six unlocalised Tasmanian specimens. None of these accounts were able to consider geographic variation.

Although it has broad altitudinal limits, from sea level up to the Australian Alps (Loveridge, 1934), and has been reported from a number of different habitats, including dry sclerophyll forest, woodlands, heathlands, swamplands, tussock grasslands, coastal plains and grazing lands, sand dunes, river flats, valleys and ranges (Cogger, 1986; Wilson & Knowles, 1988; Ehmann, 1992), *C. casuarinae* has a fragmented distribution, with several geographic isolates (Rawlinson, 1974; Wells & Wellington, 1984, 1989; MacFarlane *et al.,* 1987; Mansergh & Bennett, 1989; Swan, 1990; Richards *et al.,* 1990; Bennett *et al.,* 1991; Ehmann, 1992). This distribution is unlike that of any other species of

Australian reptile. In this paper, I explore geographic variation in the external morphology of these populations, and recognise and define three species each currently referred to by the name *Cyclodomorphus casuarinae*.

Materials and Methods

All specimens in most Australian museum collections were examined, together with type material held in European museums. Collection acronyms are: AM – Australian Museum, Sydney; ANWC – Australian National Wildlife Collection, Canberra; MNHP – Museum Nationale d'Histoire Naturelle, Paris; MV – Museum of Victoria, Melbourne; NTM – Northern Territory Museum, Darwin; QM – Queensland Museum, Brisbane; QVM – Queen Victoria Museum, Launceston; SAM – South Australian Museum, Adelaide; TM – Tasmanian Museum, Hobart; ZMB – Zoologisches Museum, Berlin.

Character definitions. Head shield nomenclature follows Taylor (1935: 71) and Shea (1992). In the case of presubocular scales, three scales were usually present in this region. However, there was much variation in the size of the second scale, from a large element completely separating the first and third scales and reaching the supralabial series, to a small element lying dorsal to the third scale, or even absent. In order to standardise the counts for this character, I counted as presubocular scales only those scales contacting the supralabial series, thus excluding this second scale in many cases. The nomenclature for temporal scale configurations follows Shea & Miller (in press). Head shields were counted on both sides where possible, with the exception of palpebrals, counted only on the left side, and are numbered from rostral to caudal. Where two counts are given for an individual, the first count is for the left side.

Midbody scales were counted around the body at the mid-point of the axilla-groin interval. Paravertebral scales were 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 were 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 were counted bilaterally on the fourth toe from the first scale just beyond the edge of the sole, to and including the scale bordering the claw.

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 acro-
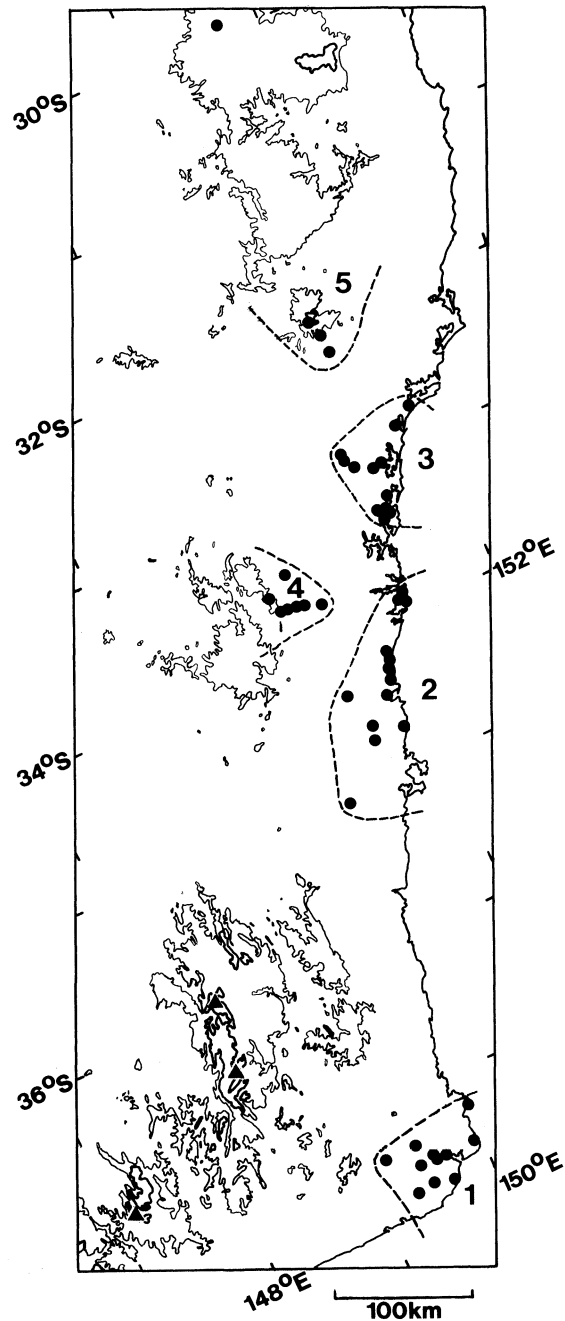

Fig. 1. Distribution of members of the *C. casuarinae* complex on mainland Australia. Dots are *C. michaeli*, triangles are *C. praealtus*. Dashed lines and numbers indicate populations of *C. michaeli* used for analysing geographic variation, as follows: 1, Eden; 2, Illawarra; 3, Central Coast; 4, Blue Mountains; 5, Barrington Tops. Thin solid lines represent 1000 m contour; thicker solid lines represent 1500 m contour.

nyms 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 significant allometry in all measurements, data are presented in two forms: the more traditional range of ratios, allowing comparison with previous
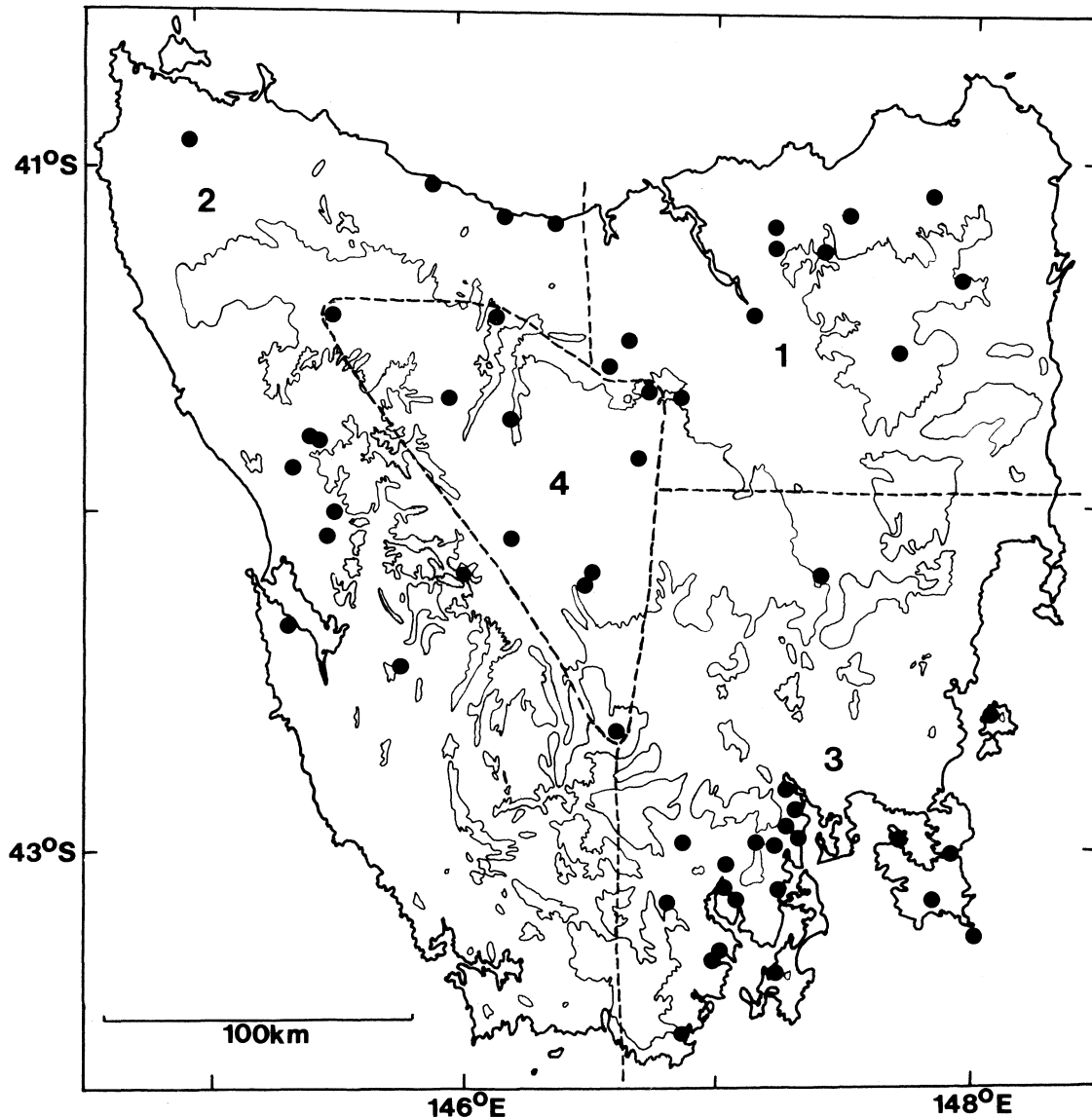
Fig. 2. Distribution of *C. casuarinae* in Tasmania. Dashed lines and numbers indicate populations used for analysing geographic variation, as follows: 1, north-east; 2, north-west; 3, south-east; 4, central. Solid lines represent 500 m contour.

studies, and allometric correlations, expressing the degree of allometry and allowing more detailed comparisons between sexes and taxa.

Geographic variation. For analysis of geographic variation, specimens were grouped into geographic subunits (populations) in two ways. On the mainland, specimens were grouped on the basis of geographic proximity and the existence of collecting gaps. From the large number of specimens of other reptiles from these intervening regions available in museum collections, I consider these gaps to represent real regions of absence rather than a lack of collecting effort. Six

mainland populations were recognised: an alpine population (Australian Alps), three largely coastal populations (from south to north: Eden, Illawarra and Central Coast), a Blue Mountains population, and a Barrington Tops population (Fig. 1). The latter population includes a single specimen from much further north, near Ben Lomond on the New England tableland. In Tasmania, no distributional discontinuities were apparent, and four populations were eventually arbitrarily differentiated by altitude, latitude and longitude to give three almost exclusively lowland populations (below 500 m a.s.l.) in the north-east, north-west and south-east and a central highland population above 500 m a.s.l. (Fig. 2).

Quantitative scalational characters were tested for geographic variation by one-way analysis of variation (ANOVA). Where significant variation was present, multiple pairwise comparisons of all pairs of populations were made by Gabriel's approximation to the GT2 method (Sokal & Rohlf, 1981) at a 5% level of significance.

Two qualitatively-scored scalational characters (degree of separation/contact of nasal and prefrontal shields) were re-scored as follows: separated – 1; point to narrow contact – 2; moderate to broad contact – 3. Analysis of variance and multiple pairwise comparisons were then carried out on these scores.

Minimum SVL at maturity was determined for three population groups (Tasmania, Australian Alps and other mainland groups) by the presence of enlarged, turgid testes 6 mm or more in length in males and oviducal embryos or enlarged yolking oviducal follicles 5.5 mm or more in diameter in females. All animals greater than the minimum mature size were considered mature. Differences in adult size were assessed by Mann-Whitney U tests, treating sexes separately.

Other morphometric characters showed allometric growth compared to SVL. The effects of allometric growth were removed by the following steps. All metric characters were converted to natural logs. Characters were regressed against SVL using the allometric growth formula $\ln(y) = a \ln(x) + b$, where y is the allometric variable and x is SVL (Thorpe, 1975), for each of the following three groups: Tasmanian populations, Australian Alps and other mainland populations. Allometric character states were then adjusted to the values they would assume if the specimen were of uniform body size by fitting the mean value of a for the three groups and the overall mean SVL (100 mm) to the equation (Thorpe, 1975)

$$y = e^{\ln(yi) - a(\ln(xi) - \ln(x))}$$

where y is the adjusted dependent variable, yi is the unadjusted dependent variable, xi is the SVL for that individual, and x is the mean SVL (100 mm) (see also Sokal & Rohlf, 1969: 442–445). Analysis of variance and multiple pairwise comparisons were then carried out on the adjusted values.

Initial univariate analyses indicated that tail characters (number of subcaudal scales and tail length) gave complete or nearly complete separation of three groups of populations (see below). However, as these characters were only scorable on some animals, a canonical variates analysis was performed, using specimens as units, scores for all other characters showing geographic variation (except palpebrals, which were not scored on many animals), and the ten populations as *a priori* groups.

Sexual dimorphism in all scalational characters showing geographic variation was tested by t-tests within species. Sexual dimorphism in metric characters was tested by analysis of covariance.

Analysis of variance was carried out by the statistical package MICROSTAT Ver. 4.1 (Ecosoft, 1984), while analysis of covariance and canonical variates analysis were carried out by SYSTAT Ver. 4.0 (Wilkinson, 1987).

In presenting the results of statistical tests, subscripted values indicate degrees of freedom, while the superscripts *, **, *** indicate significance at 5%, 1% and 0.1% levels respectively. All t-tests and Mann-Whitney U tests are two-tailed.

Geographic variation

Significant geographic variation was not detected in head depth. All other characters tested for geographic variation had significant variation.

Nasals: ANOVA: $F_{9,221} = 5.495^{***}$. Means for quantitatively-scored degree of separation/contact ranged from 1.2 (north-east Tasmania) to 2.4 (north-west Tasmania). Significant differences were detected only between the four highest means and four lowest means, and then only between some pairs: north-west Tasmania *vs* north-east Tasmania, Eden (1.3), south-east Tasmania and Blue Mountains (1.6); Alps (2.3) *vs* south-east and north-west Tasmania and Eden; Central Coast (1.9) and Illawarra (1.8) *vs* north-west Tasmania).

Prefrontals: ANOVA: $F_{9,221} = 5.714^{***}$. Means for quantitatively-scored degree of separation/contact were mostly between 2.7 (Alps, central Tasmania) and 3.0 (Barrington, Central Coast), with only the three lowland Tasmanian populations lower (north-west Tasmania, 2.2; north-east and south-east Tasmania, 2.4). The only significant differences detected were between the latter three populations *vs* Central Coast, Illawarra (2.9) and Blue Mountains (2.8), and between south-east Tasmania and Eden (2.9). Thus, there was a trend towards more narrowly contacting prefrontals in Tasmania.

Nuchals: ANOVA: $F_{9,444} = 9.214^{***}$. Two groups of means were apparent. North-east, central and south-east Tasmania had low means (2.1–2.3) while mainland populations, together with north-west Tasmania, had high means (2.6 [Barrington] – 3.2 [Central Coast]). Significant differences were found between the three low Tasmanian means and Central Coast, Blue Mountains, north-west Tasmania and Eden, and in the case of north-east and central Tasmania, also with Australian Alps and Illawarra.

Presuboculars: ANOVA: $F_{9,450} = 5.222^{***}$. Means ranged from 2.0 (Barrington, Central Coast, Eden) to 2.4 (Illawarra), with the only significant differences between Illawarra *vs* Central Coast and Eden *vs* south-east Tasmania (2.1).

Postsuboculars: ANOVA: $F_{9,448} = 4.386^{***}$. Means ranged from 3.2 (Eden, Alps) to 3.7 (north-west Tasmania). The alpine population differed significantly from Illawarra (3.6), north-west Tasmania and south-east Tasmania (3.6). The Eden population also differed significantly from Illawarra and north-west Tasmania, while the Central Coast (3.3) differed significantly from Illawarra.

Supraciliaries: ANOVA: $F_{9,449} = 9.703^{***}$. Means for all but one population were in the range 5.7 (Illawarra) to 6.0 (Barrington, all four Tasmanian populations) with mode six. The alpine population had mode five and mean 5.3, significantly different to all other populations. The only other significant differences were between Illawarra and north-west/south-east Tasmania.

Infralabials: ANOVA: $F_{9,445} = 4.826^{***}$. Means for all but two populations were in the range 7.1 (Central Coast) to 7.5 (central Tasmania), only Eden (6.7) and Barrington (7.8) being outside this range. The only significant differences were between Eden and most other populations (all but Central Coast; $\bar{x}s = 7.2$–7.8), and between Barrington *vs* Eden and Central Coast *vs* the Blue Mountains (7.2)

Upper palpebrals: ANOVA: $F_{9,172} = 3.243^{**}$. Means ranged from 7.3 (Alps) to 8.8 (Barrington, Central Coast), with the only significant differences between the alpine population *vs* Central Coast and Blue Mountains (8.2).

Lower palpebrals: ANOVA: $F_{9,171} = 9.022^{***}$. Means for all but the alpine population (8.1) were in the range 9.1 (central Tasmania) to 10.5 (Barrington, Central Coast). Significant differences were detected between the alpine population and other mainland populations, together with north-east and south-east Tasmania ($\bar{x}s = 9.3$–10.5), and between Central Coast and all four Tasmanian populations ($\bar{x}s = 9.1$–9.9).

Midbody scales: ANOVA: $F_{9,213} = 19.296^{***}$. Means for all but the alpine population (25.0) were in the range 22.4 (north-east Tasmania, Central Coast, Blue Mountains, Eden) to 23.7 (south-east Tasmania). The alpine mean was significantly different to all other populations. Significant differences were also detected in most possible pairwise comparisons between two groups: north-east/highland/south-east Tasmania ($\bar{x}s = 23.3$–23.7) and Central Coast/Blue Mountains/ Illawarra/Eden/north-west Tasmania ($\bar{x}s = 22.4$–22.5), only the Eden comparisons with north-east and central Tasmania being non-significant.

Paravertebral scales: ANOVA: $F_{9,211} = 15.442^{***}$. Two main groups of populations were apparent. Most mainland populations (Barrington, Central Coast, Blue Mountains, Illawarra) had high means ($\bar{x}s = 70.9$–73.4), while the four Tasmanian populations had low means ($\bar{x}s = 65.9$–67.5). All sixteen possible pairwise comparisons of populations between these two groups were significant. The alpine (68.9) and Eden (69.5) means were intermediate between these two groups, with the alpine mean significantly different to the Central Coast (72.3) and Blue Mountains (72.4) means.

Subcaudal scales: ANOVA: $F_{9,125} = 206.210^{***}$. Three groups of populations were apparent. The alpine population had a mean of 53.1 and a range of 48–57, the four Tasmanian populations had means of 73.5–79.5 and an overall range of 68–84, and the five non-alpine mainland populations had means of 89.5–99.1 and an overall range of 83–108. Significant

differences were detected between all possible combinations of population means between these groups, but only between Barrington (89.5) *vs* Central Coast (99.1) and Blue Mountains (97.6), and between north-east (79.5) *vs* central Tasmania (73.5) within these groups. On the mainland, the low mean for the Barrington population was the result of a low value for the sole New England animal (83), with the only value available for the true Barrington animals being 96.

The New England locality, six miles north-north-west Ben Lomond, is potentially mistakeable for a mountain of the same name in Tasmania, within the known range of the Tasmanian population (e.g., QVM 1972.3.188). Such a mistake would explain the low subcaudal scale count for the New England specimen. However, the specimen is recorded as collected by G. Webb and J. Parmenter, at the time based at the University of New England, with the same collectors recorded as collecting material of several non-Tasmanian reptile species on the same date from nearby localities. On this basis, I consider the record valid.

Subdigital lamellae: ANOVA: $F_{9,405} = 17.403^{***}$. Populations from the middle of the range had low means (Illawarra, Eden, Alps, north-east Tasmania; $\bar{x}s = 10.1$–10.7), significantly different to most populations to the north and south (all *vs* Central Coast, Blue Mountains, north-west and south-east Tasmania, $\bar{x}s = 11.5$–11.9; Alps also *vs* Barrington, central Tasmania, $\bar{x}s = 11.2$–11.5).

Snout-vent length: There were no significant differences for either males or females in adult SVL between Tasmanian and mainland Australian material other than the Australian Alps population. Females of the alpine population were significantly smaller than either the Tasmanian (Mann-Whitney U test, $z = 4.879^{***}$) or other mainland groups (Mann-Whitney U test, $z = 4.752^{***}$). Too few males of the alpine population were available to assess the extent of any differences for that sex.

Axilla-groin length: ANOVA: $F_{9,226} = 13.470^{***}$. The Tasmanian populations had generally shorter bodies than mainland populations. Significant differences were detected between north-east and south-east Tasmania *vs* all mainland populations, central Tasmania *vs* Central Coast, Blue Mountains, Illawarra and Eden, and north-west Tasmania *vs* Eden.

Tail length: ANOVA: $F_{9,125} = 52.190^{***}$. Variation was similar to that in subcaudal scales, with three groups of populations: Tasmania, Australian Alps and other mainland populations. The alpine population, with a very short tail, was significantly different to all other populations, while the four Tasmanian populations had significantly shorter tails than all other mainland populations except Barrington (represented by only two values, one the New England record discussed above).

Forelimb length: ANOVA: $F_{9,225} = 22.575^{***}$. In general the Tasmanian populations had long forelimbs, significantly different to all mainland
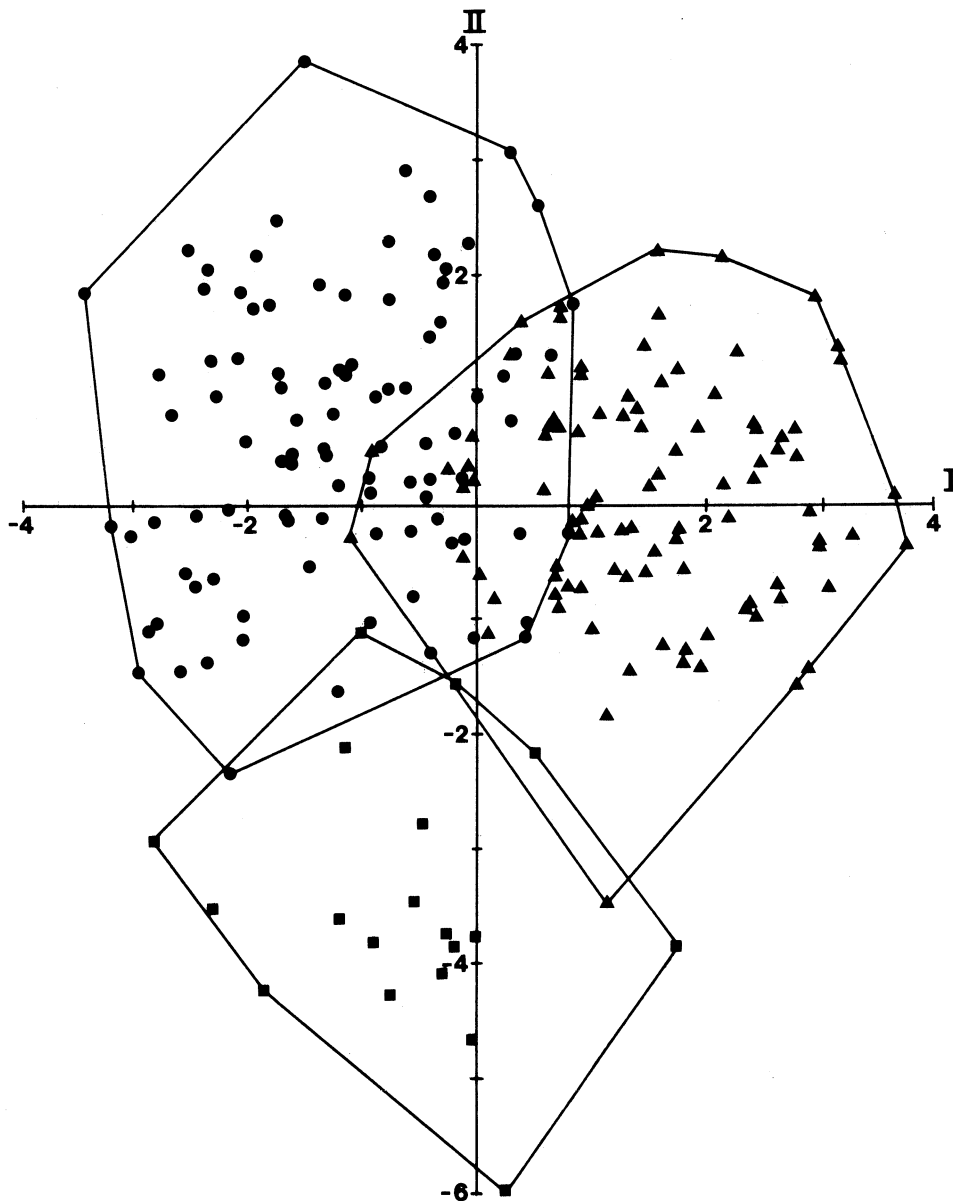
Fig. 3. Ordination of members of the *C. casuarinae* complex on the first two discriminant functions. Dots are *C. michaeli*, triangles are *C. casuarinae*, squares are *C. praealtus*.

populations other than Barrington (in all comparisons) and Central Coast (in the case of north-west Tasmania). The Eden population had significantly shorter forelimbs than all other populations.

Hindlimb length: ANOVA: $F_{9,216}$ = 18.108***. The pattern of geographic variation was almost identical to that of forelimb length, although Eden was not significantly different to the alpine population and Central Coast was not significantly different to north-east Tasmania but was significantly different to north-west Tasmania.

Head length: ANOVA: $F_{9,226}$ = 19.107***. In general, Tasmanian populations had proportionally longer heads than mainland populations, with significant differences between south-east Tasmania and all mainland populations, north-east and central Tasmania *vs* all mainland populations except Barrington, and north-west Tasmania *vs* Eden. Within Tasmania, there were significant differences between north-west Tasmania (short) *vs* north-east and south-east Tasmania (long). Amongst mainland populations the only significant difference was between Central Coast (long) and Eden (short).

Head width: ANOVA: $F_{9,217} = 13.130^{***}$. In general, Tasmanian populations had broader heads than mainland populations, with significant differences between north-east and south-east Tasmania *vs* all mainland populations but Barrington, central Tasmania *vs* all mainland populations but Barrington and Australian Alps, and north-west Tasmania *vs* Eden.

Canonical variates analysis: A combination of 16 characters (SVL, AGL, FLL, HLL, HL, HW, nasals, prefrontals, presuboculars, postsuboculars, supraciliaries, infralabials, nuchals, midbody scales, paravertebral scales, subdigital lamellae) was used in this analysis.

Overall, the combination of the six significant functions extracted gave reasonable assignment of animals to populations (Table 1), with 67.5% of animals correctly identified (population range 55.0–100.0%). Standardised canonical coefficients and character correlations with canonical functions for the six functions are presented in Table 2. The first two functions identified the same three geographic groups of populations as were identified on number of subcaudal scales and tail length (Fig. 3): Tasmania, Australian Alps and non-alpine mainland Australia.

These two functions alone resulted in correct geographic group identification of 77.3% of Tasmanian animals, 84.2% of alpine animals and 69.8% of other mainland animals. When all functions were considered, the proportion of correct group assignment rose to 91.8% for the Tasmanian group and 90.6% for non-alpine mainland animals, and 88.9% overall. Of the 20 animals incorrectly identified to group, 12 had original tails and could be unequivocally identified to the correct group on subcaudal counts, while an additional four animals had the next greatest probability in the canonical analysis of correct group identification (to the correct population in three cases).

Discussion

The identification of the same three groups of populations by multivariate analysis as were found by an independently analysed character (number of subcaudal scales), and the geographic cohesiveness of these three groups lead me to recognise these three groups as taxonomically distinct. In the absence of sympatry to test for reproductive isolation, I use the almost complete lack of overlap between these three taxa in number of subcaudal scales (the most geographically remote record of the non-alpine mainland taxon had the only value overlapping with the Tasmanian range, while the alpine taxon did not overlap with either other taxon) to identify them as distinct species under the evolutionary species concept (Frost & Hillis, 1990).

Of the three species, the name *Cyclodomorphus casuarinae* is available for the Tasmanian species and the name *Cyclodomorphus michaeli* is available for the non-alpine mainland taxon, while no name is available for the alpine species, described as new below.

Systematics

The three species in the *C. casuarinae* complex may be differentiated from the other species of *Cyclodomorphus* by the following combinations of characters. Contacting prefrontal shields (plesiomorphic) and absence of a postnarial groove (apomorphic) differentiate it from the *C. branchialis* species group, while the postmental usually contacting two infralabials on each side (plesiomorphic) and 26 or fewer midbody scales and 14 or fewer subdigital lamellae (apomorphic) distinguish it from *C. gerrardii*. However, in that the absence of a postnarial groove is shared with *C. gerrardii*, while the latter two apomorphies are shared with the *C. branchialis* species group, it is likely that one or more of the apomorphies represent reversals or convergences.

Unless otherwise noted, the following scalational characters of taxonomic importance in skinks were invariant in the *C. casuarinae* complex: supranasals, postnasals and postnarial groove absent; frontal large, longer than wide, broadest rostrally; frontoparietals paired; parietals separated by interparietal (rarely in narrow contact); interparietal broadest rostrally; parietal eye spot present; lower eyelid scaly; primary temporal single; one or more 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 divided, the two scales on each side separated by three scales; body scales smooth; preanal scales subequal.

Cyclodomorphus casuarinae (Duméril & Bibron, 1839)

Cyclodus Casuarinae Duméril & Bibron, 1839: 749. Lectotype: MNHP 7131, Bruny Island, Tasmania (Péron & Lesueur).
Cyclodus nigricans Peters, 1875: 621. Holotype: ZMB 8193, Australia (Flower).
Hemisphaeriodon tasmanicum Frost & Lucas, 1894: 227. Lectotype: MV D2087, Tasmania (C. Frost).

Diagnosis. A moderately large *Cyclodomorphus* (maximum SVL 174 mm), differing from all other species in the genus in the combination of prefrontals usually contacting, postnarial groove absent, postmental usually contacting two infralabials on each side, subcaudal scales 68–84, and dorsal colour pattern often present and complex in adults (dark edges to scales and dark streaks basally and centrally on scales).

Description. Nasals usually broadly to narrowly separated (55.6%, n = 117), less commonly in point to narrow contact (21.4%) or moderate to broad contact (20.5%), rarely a median internasal present (2.6%); prefrontals usually in moderate to broad contact (55.2%, n = 116), less commonly in narrow contact (31.0%), rarely in point contact (1.7%), narrowly to broadly separated (10.3%), or separated by a small median scale

(1.7%); transversely enlarged nuchals 0–6 on each side ($\bar{x}$ = 2.4, sd = 1.08, n = 225), usually three (48.0%) or two (26.2%); loreals two bilaterally; supraoculars usually three bilaterally, rostral two in contact with frontal, second largest (98.3%, n = 116), rarely two unilaterally (1.7%), reduction due to fusion of first and second supraoculars (n = 1) or second and third supraoculars (n = 1); supraciliaries 5–7 ($\bar{x}$ = 6.0, sd = 0.29, n = 232), usually six (91.8%); presuboculars 1–3, usually two (82.2%, n = 231), rarely one (0.4%); postsuboculars 2–5 ($\bar{x}$ = 3.6, sd = 0.56, n = 231), usually four (55.4%); upper palpebrals 7–12 ($\bar{x}$ = 8.2, sd = 1.00, n = 69); lower palpebrals 7–12 ($\bar{x}$ = 9.3, sd = 0.95, n = 68); secondary temporals usually in α-configuration bilaterally, rarely in β-configuration unilaterally (n = 2) or bilaterally (n = 1); supralabials 6–8 ($\bar{x}$ = 7.0, sd = 0.30, n = 232), usually seven (90.9%), third-last below centre of eye, separating pre- and postsuboculars; infralabials 6–9 ($\bar{x}$ = 7.4, sd = 0.56, n = 227), usually seven (56.4%) or eight (40.1%); usually first two infralabials contacting postmental (n = 110), rarely one only unilaterally (n = 4) or bilaterally (n = 1); ear small, usually with a single small lobule along rostral margin (81.2%, n = 218), rarely two (6.4%) or lobules absent (12.4%).

Body scales in 22–26 ($\bar{x}$ = 23.3, sd = 1.00, n = 108) longitudinal rows at midbody; scales in paravertebral rows not or only slightly broader than adjacent scales, 61–73 ($\bar{x}$ = 66.7, sd = 2.87, n = 107); subcaudal scales 68–84 ($\bar{x}$ = 76.9, sd = 3.89, n = 69); lamellae below fourth toe 9–14 ($\bar{x}$ = 11.5, sd = 1.03, n = 201).

SVL 41.5–174 mm (n = 114); AGL/SVL 51.8–69.1% ($\bar{x}$ = 62.0%, n = 112); TL/SVL 63.6–133.6% ($\bar{x}$ = 103.9%, n = 70); FLL/SVL 12.7–21.4% ($\bar{x}$ = 15.8%, n = 114); HLL/SVL 17.5–26.2% ($\bar{x}$ = 21.5%, n = 114); FLL/HLL 64.2–85.7% ($\bar{x}$ = 73.6%, n = 115); HL/SVL 13.6–24.6% ($\bar{x}$ = 17.2%, n = 113); HW/HL 57.9–75.2% ($\bar{x}$ = 67.9%, n = 113); HD/HL 40.4–61.1% ($\bar{x}$ = 50.8%, n = 112).

Coloration (in preservative). Adult coloration variable.

Dorsal ground colour olive-grey to green, rarely reddish. Rarely immaculate, usually with narrow to broad dark brown or black lateral margins to most dorsal body and tail scales, giving solid to broken narrow dark stripes on body and at least tail base. Many individuals also with multiple fine mid brown-grey or russet streaks basally and centrally on most scales, which may in extreme development obscure the dark stripes and ground colour. Some individuals with a few dorsal body and tail scales also dark brown to black edged apically, in rare extreme development leading to irregularly defined narrow dark bands across back and tail.

Head dorsum usually immaculate, but in some strongly patterned individuals with dark flecks or spots along margins of some head shields.

Laterally, body and tail with dorsal ground colour and predominantly striped pattern grading evenly into ventral colour and predominantly banded pattern.

Face olive-grey or green, sutures black edged, espe-

cially subocular supralabials and less commonly other circumocular scalation, giving a dark mask about eyes.

Venter olive-green to blue-grey, rarely immaculate, usually with scattered scales black, especially along apical and lateral margins, sometimes with cream bases, aligned to give a series of narrow dark bands, usually in the form of irregular vermiculations on the body, more regular and on alternate scale rows on tail. Throat variably patterned, from immaculate through a few scattered dark flecks or spots, to three or four solid narrow dark bands cranial to level of forelimbs.

Limbs above with dorsal ground, ventrally with ventral ground, with varying development of dark markings corresponding to dorsal and ventral patterns.

Soles and palms yellow, occasionally with light brown calli or low tubercles.

Rare individuals entirely melanistic, or in one case (MV D11218) with dorsal pattern and ground colour largely obscured by broad, black, nearly confluent bands.

Juveniles with red to olive-green dorsal ground, body dorsum with dark scales and/or scale margins tending to align transversely to give narrow, closely spaced dark bands on body and at least tail base. Nape with two similar but broader and more pronounced dark bands, the more cranial extending rostroventrolaterally towards ears, continuing below ears as one or two narrower bars. Head dorsum of neonates often with a dark brown wash, especially over parietal shields. Subocular supralabial and usually some adjacent circumocular shields solid black, giving a black mask over eyes. Coloration otherwise as adults. Dark nape bands are the most long-lasting element of juvenile coloration, but rarely persist as solid elements beyond SVL 50 mm.

Coloration (in life). Three lizards (AM R65206–08) had a faint lavender tint to the sides of the body, the smallest individual having the throat and body and tail venter yellowish-brown (A. Greer field notes). An individual from Mount Wellington (Fig. 4) had the pale parts of the body venter and flanks yellow, the iris mid-brown and the tongue dark blue-black.

Allometry (Table 3). With respect to SVL, AGL and TL show positive allometry, while HL and limb lengths show negative allometry. With respect to HLL, FLL shows negative allometry, while HD shows negative allometry with respect to HL.

Sexual dimorphism. No significant differences were detected in the degree of separation/contact of nasals or prefrontals, or in mean number of nuchals, presuboculars, postsuboculars, supraciliaries, lower palpebrals, supralabials, infralabials, midbody scales, subcaudal scales or subdigital lamellae (t-tests). Significant differences were detected between males and females in mean number of upper palpebrals (males: $\bar{x}$ = 7.9, sd = 0.60, n = 25; females: $\bar{x}$ = 8.4, sd = 1.10, n = 42; t_{65} = 2.06*) and paravertebral scales (males: $\bar{x}$ = 65.4, sd = 2.51, n = 33; females: $\bar{x}$ = 67.5, sd = 2.90, n = 57; t_{88} = 3.44***).

Fig. 4. A live *C. casuarinae* from Mt Wellington, Tasmania.

Mature females (SVL 103–174 mm; x̄ = 127.6 mm, sd = 16.97, n = 48) were much larger than mature males (85–126 mm, x̄ = 107.8 mm, sd = 12.48, n = 21; Mann-Whitney U test, z = 4.416***).

Females have significantly longer bodies, shorter tails and legs and shorter but broader heads than males, although the differences in proportions are slight in most characters (Table 4).

Distribution. Northern, central and eastern Tasmania, from sea level to the central plateau (Fig. 2). Also Betsy (Green & Rainbird, 1993), Bruny, Maria and Tasman Islands on the east coast. Although there are no specimen-based records from the south-west of Tasmania, sight records exist for Mount Anne and Mount Melaleuca (A. Dudley, M. Hutchinson, pers. comm.).

Type material. *Cyclodus casuarinae* was described by Duméril & Bibron (1839) mostly from a single MNHP specimen from Nouvelle Hollande. A second specimen, in the collection of the Zoological Society of London, is mentioned in their description of coloration. Duméril and Bibron did not specifically designate a holotype. However, the Paris specimen (MNHP 7131) has consistently been considered the holotype (Duméril & Duméril, 1851; Guibé, 1954; Brygoo,

1985; Cogger *et al.,* 1983), and must therefore be considered to be lectotype, nominated by assumption of holotype status (Article 74b of the Code of Zoological Nomenclature). The lectotype has been subsequently identified as collected by Péron and Lesueur from Bruny Island during the Baudin Expedition of 1801–04 (Duméril & Duméril, 1851; Guibé, 1954; Brygoo, 1985). This specimen is presumably one of the "quelques beaux lézards analogues aux Scinques, différant toutefois essentiellement des animaux de celle famille par l'élégance des formes et le rapport des proportions" observed by Péron (1807) on Bruny Island between mid January and early February 1802 (see also MacFarlane & Triebel, 1937, for a reprint of Péron's account). The whereabouts of the Zoological Society of London paralectotype are unknown. That collection was largely dispersed to other national and provincial collections in 1852, and the remaining specimens disposed of in 1856 (Sclater, 1901).

The lectotype of *C. casuarinae* (Fig. 5) has the following combination of character states: nasals narrowly separated; prefrontals in narrow contact; supraoculars three; presuboculars two; postsuboculars three; supraciliaries six; supralabials seven; infralabials 7/8, first two contacting postmental; nuchals three;
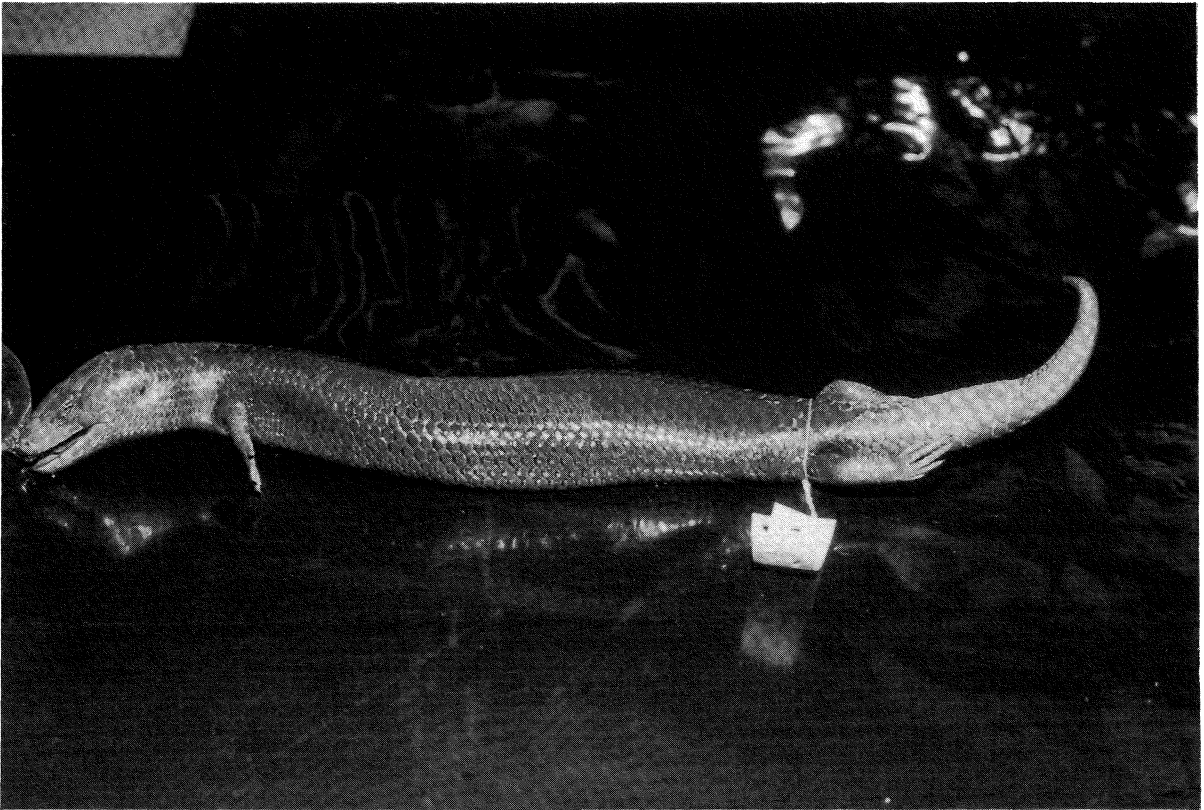
Fig. 5. Lectotype of *Cyclodus casuarinae* Duméril & Bibron, 1839 (MNHP 7131).

Fig. 6. Holotype of *Cyclodus nigricans* Peters, 1875 (ZMB 8193).

temporals in α-configuration; midbody scales 24; paravertebral scales 68; tail regenerated from 12th subcaudal; subdigital lamellae 14/13; SVL 145 mm; AGL 95.5 mm; TL 25.5 mm (original part) + 28 mm (regenerate); FLL 20 mm; HLL 26 mm; HL 21.2 mm; HW 15.2 mm; HD 11.1 mm. Although the specimen has been eviscerated, the large size suggests that it was female. Most of the measurements and scalational characters are in close agreement with those given in the type description, only the tail length (62 mm *vs* 53.5 mm) being noticeably different.

While the type description does not give a precise locality for the lectotype and the regenerated tail precludes use of subcaudal counts to accurately assign it to a population, the more precise locality given by Duméril & Duméril (1851) and subsequent authors, based on MNHP catalogue data, is sufficient to assign the name to the Tasmanian taxon.

The description of *Cyclodus (Homolepida) nigricans* by Peters (1875) is brief, mentioning only the dark coloration, 7/6 supralabials, two loreals longer than high, 25 midbody scales, and 70 scales along the body between lower jaw and vent. Peters considered that the combination of these features and a long snout differentiated his species from *C. casuarinae*, although he gave no comparative data for the latter species. *Cyclodus nigricans* was placed in the synonymy of *C. casuarinae* by Boulenger (1887).

Peters did not give any locality for his species, nor did he explicitly indicate the extent of his type series or its provenance or repository. Although he states at the end of the description that he found additional specimens of the species in collections sent to him by Prof. Flower of the Royal College of Surgeons in London, it is clear from the single set of scale counts and the asymmetry reported in supralabial scales (seven left, six right) that he described his species from only a single specimen. A single specimen (ZMB 8193; Australia; pre: Flower) is identified as the type in Berlin, and in coloration and the direction of asymmetry of the supralabial shields agrees with Peters' description, although Peters counts one fewer supralabial and 25 midbody scales rather than the 24 that I count. The holotype of *C. nigricans* (Figs 6, 7) has the following combination of character states: nasals in moderate contact; prefrontals in moderate contact; supraoculars three; presuboculars two; postsuboculars 3/4; supraciliaries 6/7; supralabials 8/7; infralabials 8/9, first two contacting postmental; rostral ear lobules one; nuchals three; temporals in α-configuration; upper and lower palpebrals nine; midbody scales 24; paravertebral scales 67; tail regenerated from 34th subcaudal; subdigital lamellae 13; SVL 148 mm; AGL 97 mm; FLL 21 mm; HLL 30 mm; HL 22.9 mm; HW 16.3 mm; HD 11.7 mm. The coloration is uniformly dark brown/black dorsally and dark but with evidence of darker macules centrally on scales ventrally. Although the gonads have not been examined to confirm the sex, the large size of the specimen suggests that it is female. As with *C. casuarinae*, the regenerated tail of this specimen precludes use of

the sole completely diagnostic character to assign the name to this species. However, the canonical variates analysis (Fig. 3) unequivocally (98.9% probability) identifies the type as Tasmanian (67.6% probability of being from south-east Tasmania). Further, I am aware of two other individuals with uniformly dark coloration, both from Tasmania (A. Dudley, pers. comm.).

Hemisphaeriodon tasmanicum was described by Frost & Lucas (1894) from material collected by Baldwin Spencer from Lake St Clair. They initially only compared their species with *Cyclodomorphus gerrardii* (then in the monotypic genus *Hemisphaeriodon*), but later (Lucas & Frost, 1896), after examining additional material, recognised its affinities with *C. casuarinae* and placed their species in its synonymy.

Although Frost and Lucas did not indicate the number of specimens on which their description was based, it is clear from the variation expressed ("one to four pairs of nuchals", ventral surface "greyish or brownish") that more than one individual was involved. This is further borne out by their later (Lucas & Frost, 1896) mention of "specimens" from Lake St Clair. No indication was given of the repository of their material, and no types were located by Cogger *et al.* (1983). Amongst the material examined for this paper are five MV specimens from Frost's collection (D2087–90, D2092, Tasmania, received 12 October, 1915, but not registered until 23 June, 1943; A.J. Coventry, pers. comm.) and a single AM specimen (R4142) from Lake St Clair, collected by Spencer and donated by Lucas. The AM animal forms part of a collection from Lucas that includes a syntype of *Ablepharus rhodonoides*, described by Lucas & Frost (1896) in the same paper that synonymised *H. tasmanicum*. Frost & Lucas (1894) placed *tasmanicum* in *Hemisphaeriodon* on the basis of enlarged maxillary teeth, while Lucas & Frost (1896) synonymised it partly on palatal osteology. The mouths of both R4142 and D2087 have been opened subsequent to preservation, in the former case by fracturing the mandibles, in the latter by transecting the adductor musculature, and the palatal mucosa has been stripped back, allowing access to the palatal elements. Both specimens are similar in coloration and in position and condition of preservation. The measurements and scalation of D2087 are very close to those presented by Frost & Lucas (1894), only the midbody count (24) being outside the variation given in the description (26). However, counts of 26 midbody scales are very rare in *C. casuarinae* (only seen in two of 108 specimens examined) and it is possible that the count provided by Frost and Lucas is erroneous. On the basis of collection data and the dissection of the oral cavity, I believe that AM R4142 is certainly a syntype, and on the basis of the similarity between this specimen and D2087, and between the latter and the type description, that MV D2087 is also a syntype. Of the other four MV specimens from Frost's collection, three (D2088–89, D2092) are strongly patterned, and cannot be syntypes (Frost and Lucas emphasised the unpatterned dorsum of their species). The other specimen, D2090, while unpatterned, has been more neatly set, is in a
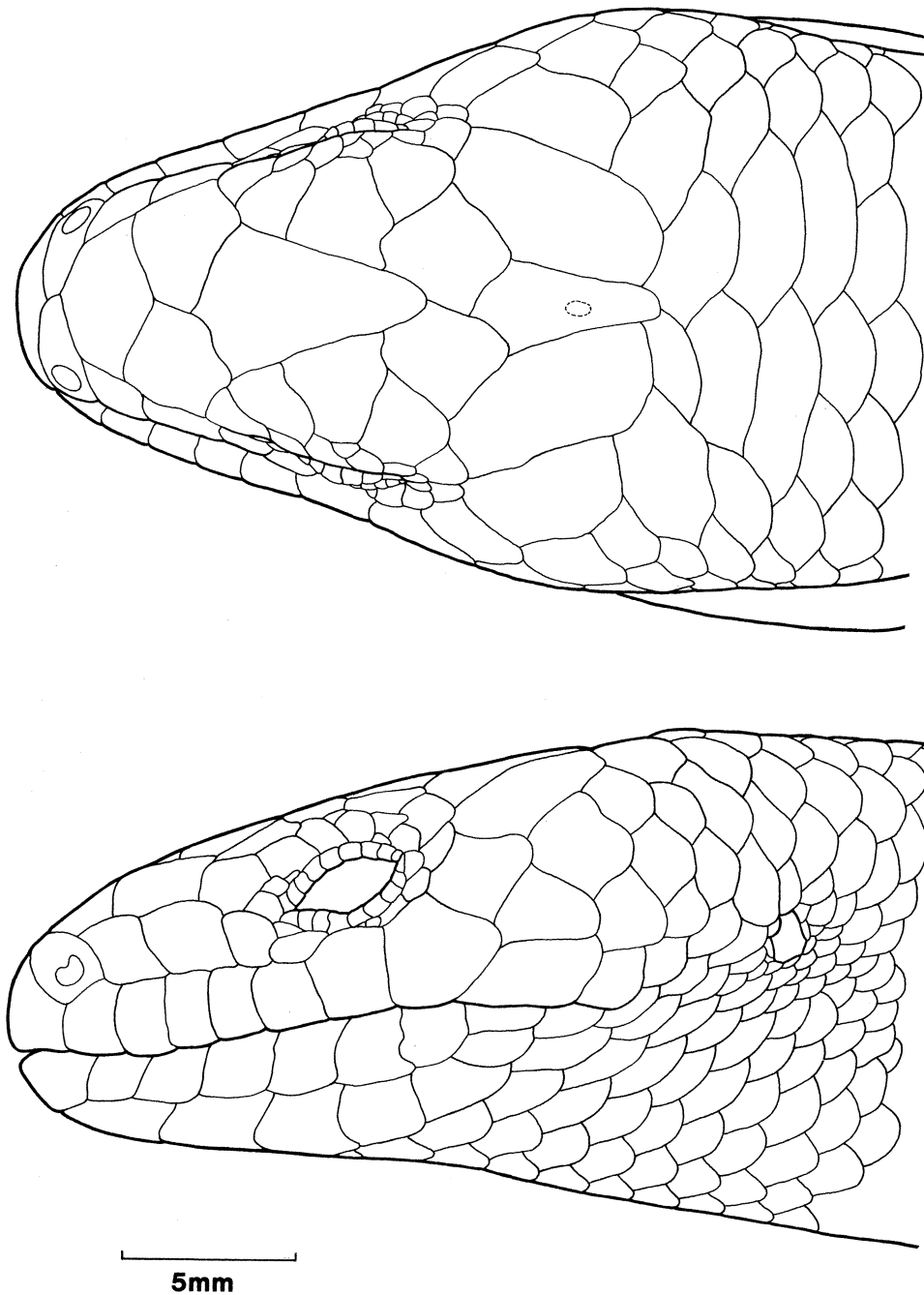
Fig. 7. Dorsal and lateral views of head shields of holotype of *Cyclodus nigricans*.

much better state of preservation, and has clearly been treated very differently to the two identifiable syntypes.

Because of its closer correspondence to the measurements provided by Frost & Lucas (1894), I nominate MV D2087 as lectotype, leaving AM R4142 the only identifiable paralectotype.

The lectotype of *H. tasmanicum* (Figs 8, 9) has the following combination of character states: nasals separated; prefrontals in narrow contact; supraoculars three; presuboculars two; postsuboculars four; supraciliaries six; supralabials six; infralabials seven, first two contacting postmental; nuchals three; upper palpebrals eight; lower palpebrals nine; temporals in α-configuration; midbody scales 24; paravertebral scales 62; subcaudal scales 71; subdigital lamellae 11/10; SVL 101 mm; AGL 63 mm; TL 101 mm; FLL 17 mm; HLL 22.5 mm; HL 15.9 mm; HW 11.9 mm; HD 7.6 mm. Both the type locality (Lake St Clair) and the morphology of the two type specimens clearly identify the name as belonging to the Tasmanian taxon.

Habitat and habits. Rawlinson (1974) describes *C. casuarinae* as terrestrial, commonest in clearings bordered or surrounded by dense arboreal vegetation, and using exposed patches of low vegetation or litter for basking sites and microenvironments under fallen logs and in deep litter for periods of inactivity. In his tabulation of habitat preferences (Rawlinson, 1974, table 11.5) he records the species from savanna woodland, dry sclerophyll forest and wet sclerophyll forest.

Three more general publications give probably composite accounts of the ecology of members of the *C. casuarinae* complex, although the authors of all three have had some experience with the Tasmanian species. Wilson & Knowles (1988) describe the species as crepuscular to nocturnal, sheltering in grass tussocks and beneath leaf-litter, logs and surface debris in dry sclerophyll forest, woodlands, heathlands and swamplands, particularly where ground cover is dominated by tussock grasses. Ehmann (1992) records the species from "coastal plains, dunes, river flats, valleys and ranges. Vegetation of forests, woodlands, heathlands and tussock grasslands. In relatively closed vegetation structures, the species inhabits clearings, edges and other natural canopy openings that are invaded by dense low ground cover, especially spreading tussock grass." The species "shelters under embedded fallen logs, deep litter, stones and the procumbent spreading apron around the base of large tussock grasses and low bushes. It forages during the day and on warm nights, stalking and ambushing insects, snails, grubs and small lizards under partial cover." Cogger (1986) reports the species from a wide variety of habitats, from "coastal heaths and sand dunes to the dry sclerophyll forests of the ranges. Common in coastal grazing lands. Normally crepuscular to nocturnal, it is usually found during the day in leaf-litter or under fallen timber."

Specific data are available for few specimens. Green (1977) reported the species to be uncommon at his Maggs Mountain study site, with only three records. One adult was collected by a roadside in wet sclerophyll forest. Among the material examined for this study, habitat and microhabitat data are available for AM R65206–08 (under pieces of thin wood/timber which were very dry underneath, on a north-east facing grassy slope with lots of timber and large dead trees scattered about the paddocks; A. Greer field notes), AM R65209–10 (under dry rubbish in a cleared south-facing sloping paddock with rock outcrops, boards, rubbish and tree pieces scattered throughout, below a eucalypt forest; A. Greer field notes) and AM R70069–72 (under sheet iron in grassland bordered by dry sclerophyll forest; G. Stephenson field notes).

For a series of six lizards, Rawlinson (1974) reported a voluntary thermal minimum of 27.1°C, a voluntary thermal maximum of 39°C and a mean active temperature of 32.6°C.

Fleay (1952) reports predation by the Tasmanian Devil, *Sarcophilus harrisii*.

Reproduction. Adult females are available only from between October and March (Fig. 10). In this period, females with grossly enlarged ovarian follicles were only present between late October and early December, while oviducal yolks and embryos were present between early November and March. Between January and March, non-gravid females with small ovarian follicles were also collected. The data, being pooled over many years, are insufficient to determine whether the occurrence of both gravid and non-gravid material in summer reflects non-annual reproduction or variation in the timing of parturition. However, I suspect from the occurrence of enlarged ovarian follicles over almost a two month period, the occurrence of fully scaled and pigmented embryos in females collected as early as 19 January (TM C127) and as late as March (QVM 1972.3.17b), and the existence of neonates born January and March (MV D39151–56, SVL 41.5–44.5 mm, born to D39139, collected 31 January, 1967; QVM 1984.3.13b–g, SVL 42.5–45 mm, born after 4 weeks captivity to 1984.3.13a, collected 9 February, 1984; SAM R8784–8785, SVL 42 mm; collected January, 1967) that the latter is the case. Rawlinson (1974) reported parturition in mid to late February.

Mature males have turgid testes throughout the year (Fig. 11). The largest testes were seen in males collected 27 May, 30 September and December. The latter two dates correspond to the inferred timing of ovulation, but the May date is well before this period. Rawlinson (1974) stated that copulation occurs in Spring.

Females (SVL 103–174 mm, $\bar{x}$ = 127.6, sd = 16.90, n = 25) carried from 4–14 ($\bar{x}$ = 7.6, sd = 3.06, n = 26) enlarged yolking ovarian follicles or oviducal yolks or embryos. There was a significant positive correlation between litter size and maternal SVL (litter = 0.117SVL − 7.219; r = 0.655***).

There are several literature reports of litter size for *C. casuarinae*, although in the absence of associated locality data most could refer to any of the three species here recognised. Worrell (1963) reported "about six young", Frauca (1966) a litter of six, Peters (1967) 6–8 young, Bustard (1970) a litter of 19, Swanson (1976) around five young, Wilson & Knowles (1988) 2–17, usually about four, and Ehmann (1992) up to 19, usually about seven. More precise figures are given by Rawlinson (1974), Greer (1989) and Shine & Greer (1991), who give 2–7 ($\bar{x}$ = 4.1, n = 15), 4–14 ($\bar{x}$ = 6.8, n = 8) and 4–14 ($\bar{x}$ = 6.87, n = 8) respectively.

Sex ratio. Overall, the ratio of mature males:females was 21:49, significantly different to 1:1 (χ_1^2 = 10.41***), although animals were only available between September and May. Seasonally, there was a significant difference in sex ratio between the gestation period and other months (male:female; November–March, 9:29; April–October, 6:3; χ_1^2 = 6.05*).
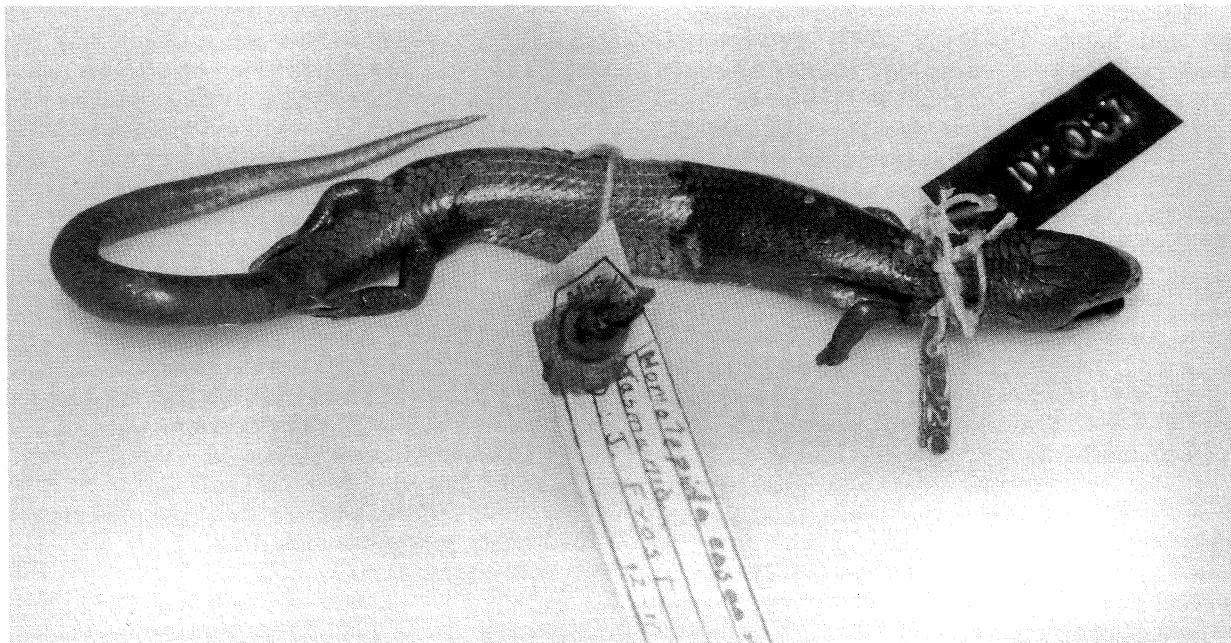
Fig. 8. Lectotype of *Hemisphaeriodon tasmanicum* Frost & Lucas, 1894 (MV D2087).

Specimens examined. 1. NORTH-EAST TASMANIA: MV D1051, Scottsdale; D39139, D39151–56, 16 km SSW Scottsdale; QVM 1006, Launceston; 1940.302, Montana; 1942.220, Deloraine; 1943.142, Hill Street, Launceston; 1944.76, Lebrina; 1962.3.28a–b, 1963.3.12–13, Winnaleah; 1969.3.8.a–b, Sideling, Launceston-Scottsdale road; 1972.3.188, south-east slope Ben Lomond; 1981.3.96, North Lilydale; 1984.3.13a–g, Liffey; 1987.3.74, Dairy Plains; TM C48, St Columba Falls, Pyengana. 2. NORTH-WEST TASMANIA: AM R37702–03, Zeehan; R37704–06, 4 miles west Queenstown; MV D915, Emu Bay; D39138, 24 km east Marrawah; D39140, 25 km south-east Zeehan; D39142, 17 km south-west Smithton; D39143, 6.4 km east Queenstown; D39144, Collingwood River, 44 km east Queenstown; QM J41561, Franklin River, below Goodwins Peak; J41562, south side Macquarie Harbour; QVM 1958.3.7, Burnie; 1969.3.13, near Devonport; 1972.3.19, Ulverstone; 1972.3.121, Renison Bell. 3. CENTRAL TASMANIA: AM R4142 (paralectotype of *H. tasmanicum*), Lake St Clair; R65206–08, 17.4 km north Breona via Highway 5; R65209–10, north-east side Bronte Lagoon, just north Lyell Highway; MV D56347–49, Mount Field; D56658, 2.6 km south Bronte Lagoon; NTM R9292, Cradle Mountain; QVM 1962.3.40, Erriba; 1964.3.3, Waratah - Hellyer Spur road; 1972.3.17a–b, Great Lake; 1976.3.22, Maggs Mountain; 1979.3.37, 1979.3.39, Maggs Mountain Hut; SAM R8784–85, south extreme, Lake Sinclair [St Clair]; R8798, Lake Sinclair [St Clair]. 4. SOUTH-EAST TASMANIA: AM 4785, Ouse River; R10053, Catamaran; R68001, Russell Falls National Park; R70069–72, Russell River, 5 km north Judbury in Huon Valley; R107594, Eaglehawk Neck; ANWC R3071, Huon River, 14 km east Judbury; MNHP 7131, Bruny Island (type of *C. casuarinae*); MV D29, Port Arthur; D2593, Port Esperance; D5733–34, Tasman Island; D7919–20, Kingston; D7991, Ridgeway; D11218, Huon Valley; D39128, 9.6 km west Geavestown; D39133, Coal Mines; D39141, 11.3 km south Huonville; D39145, 5.6 km east-south-east Longley; QVM 1972.3.16, Antill Ponds; TM C39, Kettering; C114, Lunawanna, South Bruny Island; C126–27, Lower Longley; C258, Dover; C267a–b, Cygnet; C273, Maria Island; C305, West Moonah; C318,

Counsel Creek, Maria Island; C997, Wellesley Street, South Hobart. UNLOCALISED: AM R2917, no data; R14402, north Tasmania; MV D1611, D2087 (lectotype of *H. tasmanicum*), D2088–90, D2092, D4919, QM J13774, QVM 1950.3.1, SAM R2231, R6131, Tasmania; SAM R59, "South Australia"; ZMB 8193, Australia (type of *C. nigricans*).

Cyclodomorphus michaeli Wells & Wellington, 1984

Cyclodomorphus michaeli Wells & Wellington, 1984: 89. Holotype: AM R111948, Mount Victoria, NSW (C.R. Wellington) (cited as AM field series 28007 in original description).

Diagnosis. A moderately large *Cyclodomorphus* (maximum SVL 174 mm), differing from all other species in the combination of prefrontals usually contacting, postnarial groove absent, postmental usually contacting two infralabials on each side, subcaudal scales 91–108, midbody scales 20–24 (usually 22), supraciliaries modally six and dorsal colour pattern in adults, when present, usually restricted to narrow dark edges to scales.

Description. Nasals usually moderately to narrowly separated (49.1%, n = 114), less commonly in point to narrow contact (30.7%), or moderate to broad contact (20.2%); prefrontals usually in moderate to broad contact (92.0%, n = 113), less commonly in narrow contact (6.2%), rarely in point contact (0.9%) or narrowly separated (0.9%); transversely enlarged nuchals 0–12 on each side ($\bar{x}$ = 3.1, sd = 1.12, n = 225), usually three (62.2%), only two counts of more than six; loreals usually two bilaterally (99.1%, n = 114), rarely one
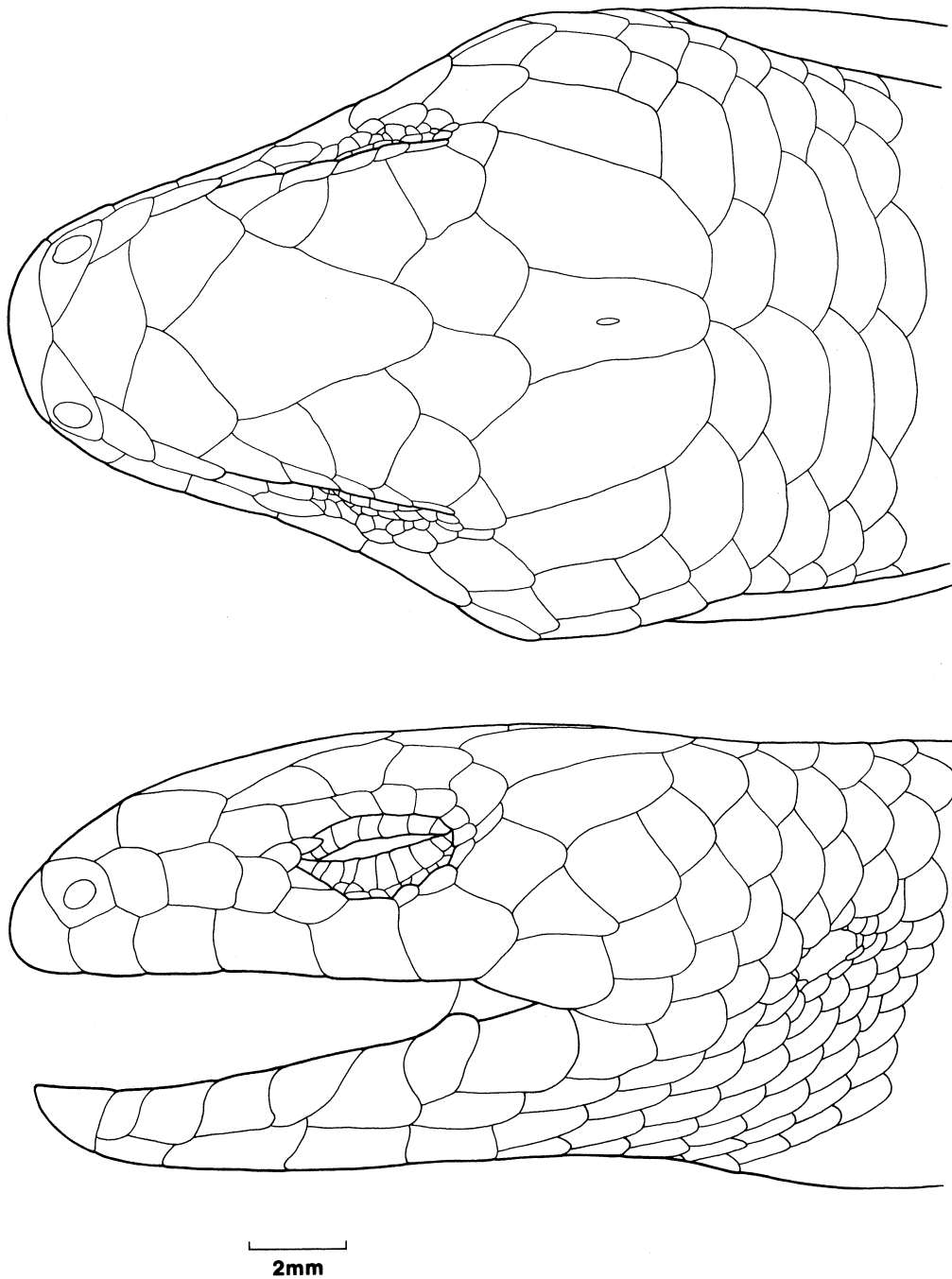
Fig. 9. Dorsal and lateral views of head shields of lectotype of *Hemisphaeriodon tasmanicum.*

bilaterally (0.9%); supraoculars usually three bilaterally, rostral two in contact with frontal, second largest (95.5%, n = 112), rarely two unilaterally (2.7%) or bilaterally (1.8%), reduction due to fusion of first and second supraoculars (n = 4) or first supraocular and first supraciliary (n = 1); supraciliaries 4–7 (x̄ = 5.8, sd = 0.55, n = 225), usually six (76.4%); presuboculars 2–3, usually two (79.3%, n = 227); postsuboculars 2–5 (x̄

= 3.4, sd = 0.54, n = 224), usually three (54.0%); upper palpebrals 6–12 (x̄ = 8.2, sd = 0.98, n = 103); lower palpebrals 8–13 (x̄ = 10.0, sd = 1.04, n = 104); secondary temporals usually in α-configuration bilaterally, rarely in β-configuration unilaterally (n = 5) or bilaterally (n = 1); supralabials 6–8 (x̄ = 7.0, sd = 0.31, n = 226), usually seven (90.3%), third-last below centre of eye, separating pre- and postsuboculars; infralabials
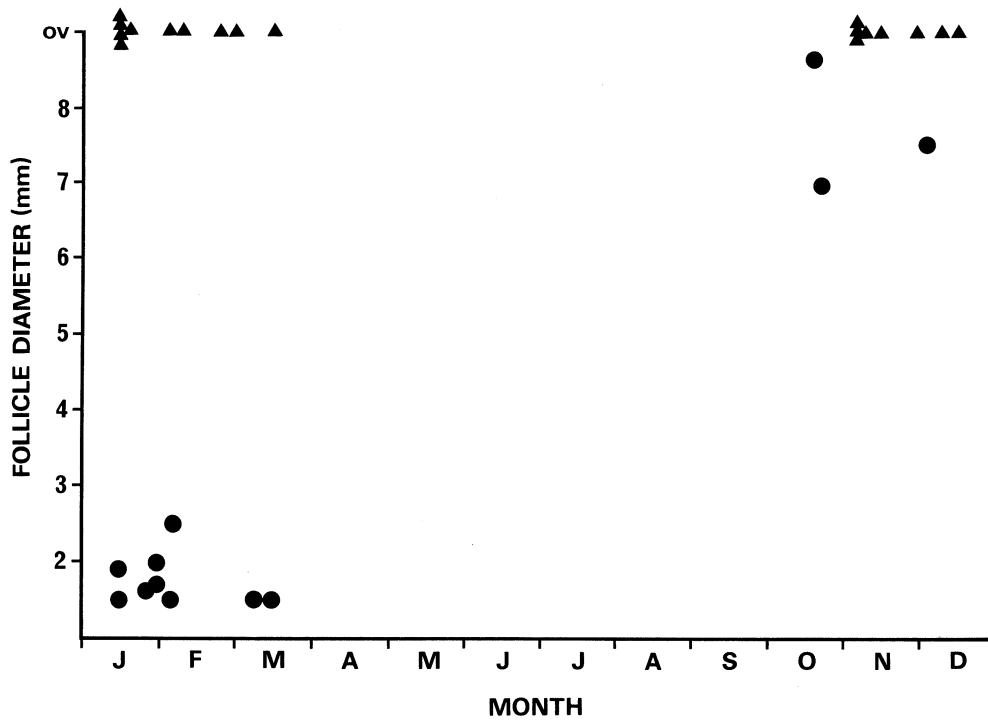
Fig. 10. Seasonal variation in size of largest ovarian follicle, and occurrence of oviducal embryos (ov) in *C. casuarinae.*
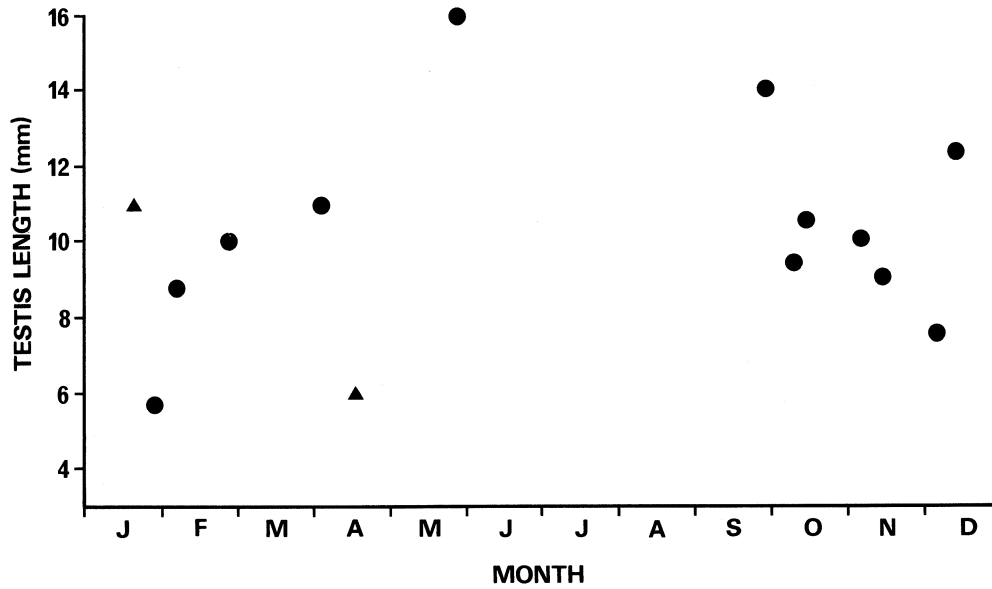

Fig. 11. Seasonal variation in testis length in *C. casuarinae.* Dots are turgid rounded testes, triangles are flaccid or flattened testes.

6–9 ($\bar{x}$ = 7.2, sd = 0.68, n = 225), usually seven (51.6%) or eight (32.8%); usually first two infralabials contacting postmental (n = 107), rarely one only unilaterally (n = 2) or bilaterally (n = 3) or first three unilaterally (n = 2); ear small, usually with a single small lobule along rostral margin (82.1%, n = 218), rarely lobules absent (17.9%).

Body scales in 20–24 ($\bar{x}$ = 22.5, sd = 0.91, n = 113) longitudinal rows at midbody; scales in paravertebral rows not or only slightly broader than adjacent scales, 62–82 ($\bar{x}$ = 71.6, sd = 3.57, n = 112); subcaudal scales 83–108 ($\bar{x}$ = 97.2, sd = 4.11, n = 56), only one less than 91; lamellae below fourth toe 8–14 ($\bar{x}$ = 11.1, sd = 1.07, n = 210).

SVL 29.5–174 mm (n = 111), smallest neonate 39.5 mm; AGL/SVL 50.8–72.8% ($\bar{x}$ = 64.5%, n = 111); TL/SVL 78.0–163.6% ($\bar{x}$ = 128.5%, n = 54); FLL/SVL 10.8–20.6% ($\bar{x}$ = 14.2%, n = 110); HLL/SVL 13.8–24.2% ($\bar{x}$ = 19.2%, n = 110); FLL/HLL 62.5–86.7% ($\bar{x}$ = 73.6%, n = 111); HL/SVL 12.1–27.5% ($\bar{x}$ = 15.8%, n = 111); HW/HL 57.3–79.1% ($\bar{x}$ = 66.6%, n = 104); HD/HL 45.0–64.7% ($\bar{x}$ = 53.9%, n = 110).

Coloration (in preservative). Coloration variable. Adults with dorsal ground colour usually olive green, sometimes red to blue-grey. Dorsal pattern on body and tail usually either absent or limited to narrow dark brown or black lateral edges to individual scales, aligning to give narrow dark stripes, often zigzagging finely due to scale overlap pattern. Dorsum rarely with more extensive dark edges to apical margins of scales, giving a less regular, predominantly narrow-banded pattern. Very rarely a few fine brown streaks basally on scales (e.g., AM R54802), as in *C. casuarinae.*

Head dorsum usually immaculate, rarely, in most strongly patterned individuals, with a few dark flecks or spots aligned along margins of median head shields.

Laterally, body and tail with dorsal ground color and predominantly striped pattern (when present) blending evenly with ventral ground color and predominantly banded pattern (when present). Lateral pattern usually weakly developed.

Face olive green or brown to blue-grey, usually immaculate, sometimes with weak narrow dark edges to some subocular and circumocular head shields, slightly obscuring ocular region.

Venter blue-green to olive yellow-green, occasionally immaculate, more commonly body and tail (but rarely throat) with varying intensities and densities of dark scales, pigmentation especially apically on scales. Markings tend to be transversely aligned into vermiculations on body and narrow dark bands on alternate scale rows of tail.

Limbs with ground color and pattern corresponding to body dorsum and venter, although ventrally usually immaculate or only weakly spotted.

Soles and palms yellow to mid-brown.

Juveniles and some subadults (up to 70 mm SVL) with strong solid dark nape bands, the most cranial often several scales wide, extending rostroventrolaterally to ears, then continuing below ears as one or two narrower dark bars. Head dorsum often with a dark grey-brown flush, particularly caudally. Circumocular scalation and subocular supralabial black, giving a solid dark vertical bar over eye. Throat often with a few narrow dark bands. Body dorsum of neonates often with apical dark margins to scales pronounced, leading to a dominant pattern of narrow, closely spaced bands dorsally and laterally.

Coloration (in life). Timms (1977) records adult and juvenile coloration of animals from the Cooranbong area. An adult had "back and sides... almost uniform olive-brown... most scales had darker edges... a slight yellow tinge under the chin and a definite orange colouration on the belly. The obvious checkerboard pattern (due to every second scale being half white and half black) on the belly gave way to definite stripes underneath the tail. The legs were longitudinally striped. The inside of the mouth and tongue were blue." Juveniles were either striped or banded (ratio 6:7 in a litter of eleven) with ground colour "grey (which had a yellowish-green tinge for 24 hours post birth) and the blotches and stripes... black. The characteristic large black blotches on the head... extended from the nose to behind the ear with lobes down over the eyes and ears. In the vertically striped [banded] individuals this was followed by a complete stripe, then by numerous thinner stripes, often incomplete, but on the tail they formed complete rings. In the longitudinally striped individuals there were 4–6 narrow black stripes on the back extending down the tail. The [sides] were blotched in incomplete vertical stripes, much the same as those in the previous pattern. The belly scales in both patterns were somewhat transparent."

Rankin (1973) described juveniles from the Martinsville area with "a broad black band on the nape and another on the neck, while the frontal area of the head is greyish-brown. There is also a vertical black streak through the eye. Between the bands on the nape and neck and around the auricular region is a distinct orange tinge. The body is olive coloured with black edged scales...".

Three animals from five miles east of Nerriga (one AM R75966) showed variation in coloration from deep russet to grey with black checks on dorsum (P. Rankin field notes).

Allometry (Table 5). With respect to SVL, AGL and TL show positive allometry, while HL and limb lengths show negative allometry. With respect to HLL, FLL shows negative allometry, while HW shows negative allometry with respect to HL.

Sexual dimorphism. No significant differences were detected in the degree of separation/contact of nasals or prefrontals, or in mean number of nuchals, presuboculars, postsuboculars, supraciliaries, upper or lower palpebrals, supralabials, infralabials, midbody scales, subcaudal scales or subdigital lamellae (t-tests). Significant differences were detected between males and females in mean number of paravertebral scales (males: $\bar{x}$ = 70.5, sd = 3.64, n = 51; females: $\bar{x}$ = 72.6, sd = 3.28, n = 47; t_{96} = 2.96**).

Fig. 12. A (above) – a live adult *C. michaeli* from Mt Cambewarra, NSW. B (below) – a live juvenile *C. michaeli* from Mt Victoria, NSW.

Mature females (101–174 mm, x̄ = 126.0 mm, sd = 16.45, n = 34) were much larger than mature males (73.5–127.5 mm, x̄ = 107.8, sd = 14.32, n = 32; Mann-Whitney U test, z = 4.24***).

Females have significantly longer bodies, but shorter tails, legs and heads than males, although the proportional differences are slight in most cases (Table 6).

Distribution. Eastern New South Wales and extreme north-eastern Victoria (Fig. 1), from the following six apparently isolated populations: eastern Gippsland, near-coastally from Little Ram Head north to Cape Green and inland to Chandler's Creek; the Illawarra region and southern Sydney, from five miles east Nerriga north to Sydney Harbour (Darlinghurst, Centennial Park, Rose Bay); the Blue Mountains, from Glenbrook, north-west to Mount Victoria and north to Mount Irvine; the central coast and hinterland, from the Hawkesbury River north to 13 km east Raymond Terrace; the Barrington Tops region, and a single record from the New England tableland (six miles north-north-east Ben Lomond).

Additional literature records are for Awabakal Nature Reserve (Parks & Tasoulis, 1984), Martinsville (Rankin, 1973), Tianjara (Slater, 1978), Narrabarba Nature Reserve (Pyke & O'Connor, 1991), the Betka River Rapids in Croajingolong National Park, Link Camp Creek in Croajingolong and Alfred National Parks, and Burglars Gap in Coopracambra State Park (Mansergh & Watson, 1984), although a literature record of "*Tiliqua casuarinae*" from Queensland (Shine, 1984) cannot be confirmed and is presumably in error. Swan (1990) maps two localities just south of the headwaters of the Shoalhaven River, well outside the known range of this taxon. One of these is based on AM R6803 (Inglewood, Colo Vale), which he assumed to be the Inglewood at 35°54'S 149°22'E, very distant from Colo Vale. The other record is based on a sight observation from Braidwood by W. Osborne (G. Swan, pers. comm.).

Also known, but without museum voucher specimens, from the Kanangra Plateau south-west of the Blue Mountains (a single individual from along Whalania Fire Road, Kanangra Boyd National Park, 33°52'S 150°03'E; S. Blomberg, pers. comm.) and as far north coastally as Tea Gardens (J. Scanlon, pers. comm.).

Type material. Wells & Wellington (1984) described *Cyclodomorphus michaeli* from a single specimen from Mount Victoria, NSW, without making any attempt to differentiate it morphologically or genetically from *C. casuarinae*, which they considered to be restricted to Tasmania. Initially, they considered their species to be restricted to "post-glacial montane refugia of New South Wales from the Snowy Mountains to the Hunter River valley", but subsequently (Wells & Wellington, 1985) restricted it to "the Blue Mountains Plateaux", resurrecting *Cyclodus nigricans* from the synonymy of *C. casuarinae* and applying the name to "the population in Victoria and south-eastern New South Wales". Still more recently (Wells, 1988; Wells & Wellington, 1988a,b, 1989) they have reduced their taxon to a subspecies of

C. casuarinae, and referred to it individuals from Ourimbah State Forest on the central coast (Wells, 1988) and populations on the south coast from South Head to Helensburgh and on the Woronora and Hornsby Plateaux (Wells & Wellington, 1989). None of the taxonomic and nomenclatural actions made by Wells and Wellington are formally supported by presentation of new data or re-interpretation of existing data.

The validity of the numerous new names and other nomenclatural actions proposed by Wells & Wellington (1984, 1985) has been questioned by several authors (e.g., Cogger, 1986; Australian Society of Herpetologists, 1987; Shea, 1987; Hutchinson & Donnellan, 1992). However, the International Commission on Zoological Nomenclature has refused to make any formal ruling on a petition to suppress the Wells and Wellington works (Anon., 1991). I believe that *Cyclodomorphus michaeli*, like other species described in the first Wells and Wellington publication, is a validly published name for the purposes of the Code of Zoological Nomenclature, and that there is no case for refusing to apply it to the present species. However, it should be noted that although I use their name, I apply it to a species with different limits to that proposed by Wells and Wellington (1984) or any of their subsequent restrictions.

The holotype of *Cyclodomorphus michaeli* (AM R111948; Figs 13, 14) has the following combination of character states: nasals narrowly separated; prefrontals in moderate contact; supraoculars three; presuboculars two; postsuboculars three; supraciliaries six; supralabials 8/7; infralabials seven, first two contacting postmental; rostral ear lobules absent; nuchals 2/3; temporals in α-configuration; upper palpebrals eight; lower palpebrals nine; midbody scales 22; paravertebral scales 74; subcaudal scales 96; subdigital lamellae 11; SVL 166 mm; AGL 119 mm; TL 216 mm; FLL 18.5 mm; HLL 25.5 mm; HL 20.6 mm; HW 14.0 mm; HD 10.8 mm. While the gonads have not been examined to confirm the sex, the very large size of the specimen indicates that it is female. In several features, the measurements and scale counts I make on this specimen differ from those provided in the type description. Most of these (e.g., postnasal absent, loreals two *vs* postnasal present, loreal one; supraoculars three, supraciliaries six *vs* supraoculars four, supraciliaries five; subdigital lamellae 11 *vs* 14) presumably reflect different operational definitions of various characters, which were not indicated by Wells & Wellington (1984). However, they also identify the tail as regenerated, although radiographs indicate that it is original and complete.

Habitat and habits. There are several literature records of habitat for *C. michaeli*. Swan (1990) reports the species from dry sclerophyll forest, coastal grazing lands and sandy heaths, while Slater (1978) reports it from heath. Wells & Wellington (1984) consider that the species occurs "mainly in *Danthonia* tussock grasses of montane forests, but... also... wet sclerophyll and rain-forests of some areas as well as coastal heaths and grasslands. It is largely crepuscular... and is quite
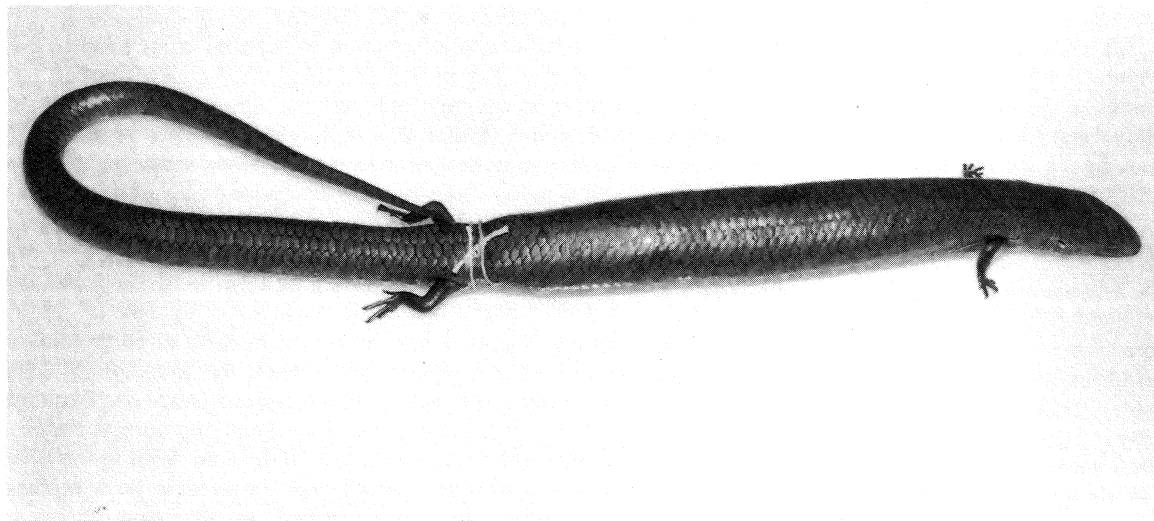
Fig. 13. Holotype of *Cyclodomorphus michaeli* Wells & Wellington, 1984 (AM R111948).

secretive, being more often found beneath objects on grass." In the Hunter River region, Waterhouse (1981) considers the species common in swamp oak forests on the edge of wetlands, where it is often found sheltering beneath loose bark or in swampside grass clumps. At nearby Cooranbong, Timms (1977; see also Cowled, 1974) describes it as inhabiting dry sclerophyll forest, grazing lands, gardens, and *Casuarina* leaf litter in coastal dunes, hiding under logs, stacks of timber and in long grass, and emerging mainly at night. Further south, on the Central Coast, Wells (1988) records an individual under a sheet of bark on grass and sandy soil in dense heath and forest, while juveniles have been found under sheets of ironbark and blocks of wood on the ground (Rankin, 1973). In the Blue Mountains, it has been reported from leaf litter and fallen timber in dry sclerophyll forest, grassy woodland and heath (Smith & Smith, 1990). In the Sydney region, the species has been reported under boards and sheet iron (Mackay, 1949), while at Dapto, Maddocks (in Shea, 1982) found several individuals active and feeding around 2300 hrs on a warm evening in August 1974. In Victoria, MacFarlane *et al.* (1987) record two individuals from under logs in heathland sites, one dominated by *Gahnia, Casuarina* and *Comesperma*, the other near a small stand of *Eucalyptus cephalocarpa* in heathland dominated by *Xanthorrhoae* (sic) and *Leptocarpus tenax*.

Habitat and microhabitat data are available for several of the animals examined in this study. Specimens from the Raymond Terrace and Newcastle districts have been found "beneath cardboard on sand and dry grass, 1015–1025 hrs" (AM R54802) and torpid in a short burrow under a rock in dense grassland bordering a swamp (AM R112395).

In the Watagan State Forest (P. Rankin field notes), animals have been found basking on the edge of sheet iron at 0730 hrs (AM R54715), sunning outside a hollow log in long grass at edge of road in wet/dry sclerophyll

forest (AM R68348), under a log in a clearing in wet sclerophyll forest (AM R75956), in curled up bark in a roadside clearing in wet sclerophyll forest (AM R75967) and under bark (AM R76516).

An Ourimbah animal was found in a hole in the ground in wet sclerophyll forest (AM R73287).

In the Sydney region, animals from La Perouse have been found in coastal heath (AM R93762) and under sheets of roofing iron in long grass surrounded by eucalypts and banksias (AM R102945–46).

The specimen from near Nerriga (AM R75966) was found, together with two other individuals, basking or under tin in an open grassy area with basalt rocks (P. Rankin field notes).

A Victorian animal (AM R57875) was found under a flat piece of wood lying in undergrowth among twigs and other litter (S.J. Copland, field notes).

Captive specimens of this species (and possibly other members of the *C. casuarinae* complex) have proven to be aggressive to other lizards and both captive and wild-caught animals readily bite when handled (Peters, 1967; Rankin, 1973; Timms, 1977; see also Swanson, 1976; Swan, 1990).

Predation by the highland copperhead *Austrelaps ramsayi* has been reported by Shine (1987). A record of a sheoak skink from the stomach of a Queensland *Cryptophis nigrescens* (Shine, 1984) cannot be confirmed (R. Shine, pers. comm.) and given the locality is presumably in error.

Reproduction. Mature females were available for all months except April and June-September (Fig. 15). Enlarged yolking follicles were present in all three October animals, but not at other times of the year, while oviducal yolks and embryos were present from late November to early January. The data suggest that ovulation occurs in mid/late Spring, gestation takes 2–3 months, and young are born in mid Summer.
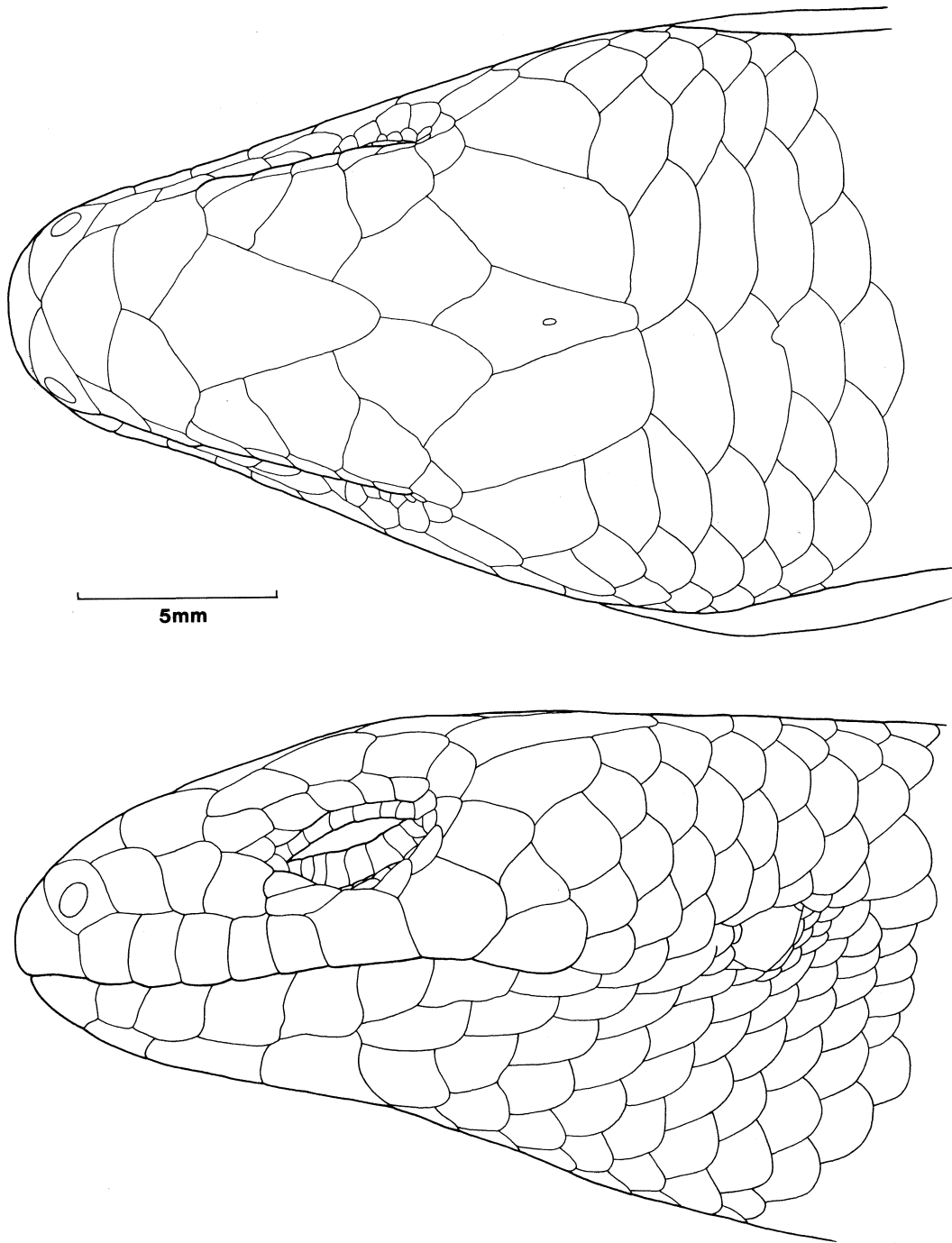
Fig. 14. Dorsal and lateral views of head shields of holotype of *Cyclodomorphus michaeli.*

Mature males with turgid testes were collected throughout the year (Fig. 16). However, the largest testes were seen in three males collected in August and early September, while three males collected in October and March had collapsed testes. These data may suggest that mating occurs in late Winter or early Spring, prior to ovulation.

Females (SVL 101–157.5 mm, x̄ = 124.5, sd = 14.51,

n = 16) carried from 4–16 (x̄ = 8.3, sd = 3.32, n = 16) enlarged yolking ovarian follicles or oviducal yolks or embryos. There was a significant positive correlation between litter size and maternal SVL (litter = 0.153SVL − 10.801; r = 0.6693**). Timms (1977) reports a litter of 13 born on 24 and 26 January (n = 11,2 respectively) to a female (SVL 158 mm) from Cooranbong, NSW, collected on the former date. Relative litter mass

Fig. 15. Seasonal variation in size of largest ovarian follicle, and occurrence of oviducal embryos (ov) in *C. michaeli*.

Fig. 16. Seasonal variation in testis length in *C. michaeli*. Dots are turgid rounded testes, triangles are flaccid or flattened testes.

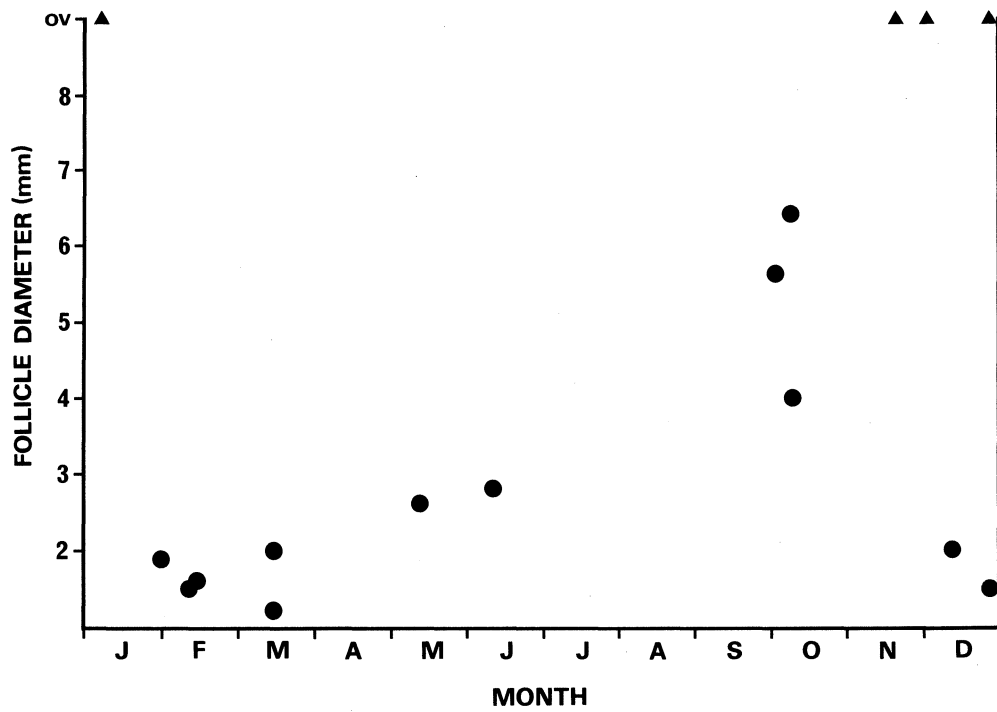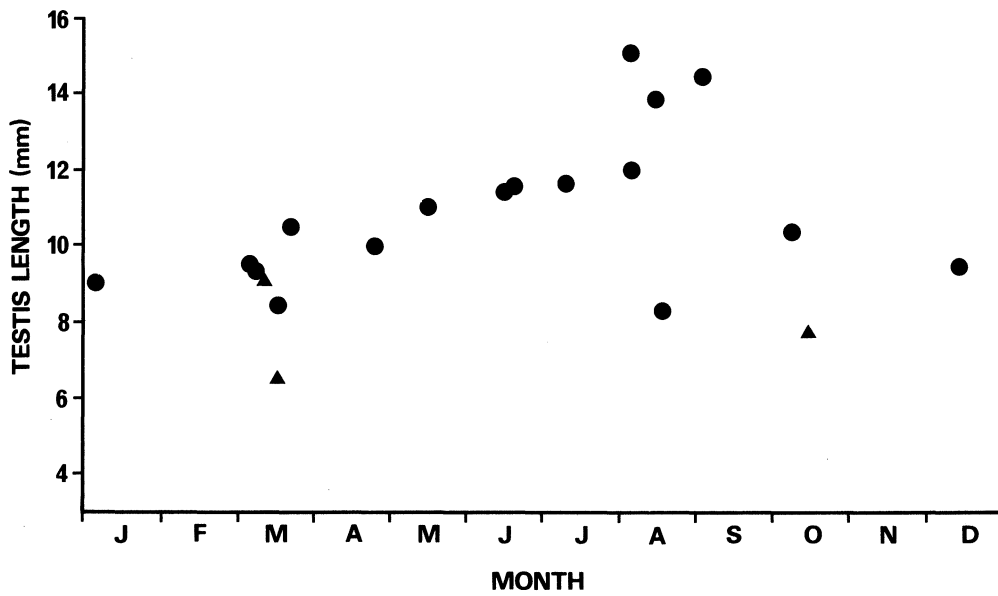(progeny mass/post-parturient female mass) was 0.302, with individual offspring having SVL 41–46 mm ($\bar{x}$ = 43.7 mm) and mass 0.75–1.44 g ($\bar{x}$ = 1.10 g). A similarly extended parturition was reported by Palmer (1888) for a female presumably from near Sydney, which gave birth to six young, "three on each of two consecutive days". Other literature records of litter size for this species are eleven and four (Rankin & Maddocks, in Shea, 1982). Swan (1990) reports litter size for NSW members of the *C. casuarinae* complex as 4–19, born late January to early February, with young about 44 mm SVL.

Sex ratio. Overall, the ratio of mature males:females was 32:35, close to 1:1, with animals collected from all months (n = 1–8). However, females predominated during the period of gestation, while males predominated in other months (Nov–Jan, 2:6; Feb–Oct 19:10), these two ratios being significantly different (χ^2_1 = 4.05*)

Specimens examined. 1. EDEN REGION, NSW/VIC: AM R57875, Chandlers Creek, 22 miles north Cann River, Vic; R64041, Nadgee Nature Reserve, NSW; MV D33721–23, Wroxham, Vic; D39127, D39129, Genoa, Vic; D39146, Gipsy Point, Vic; D39196, Little Ram Head, Vic; D50977, Cape Green, NSW; D51983, 19.6 km north-west Wingan Inlet, Vic; D57447, 10.5 km south-south-west Wangarabell, Vic; D65095, Hard-to-Seek Track, 300 m north-east southern crossing of Hard-to-Seek Creek, Vic; D66126, Stony Creek Track, 1 km east Nash Camp Track, Vic. 2. ILLAWARRA REGION, NSW: AM R1930, R9341–42, Wollongong; R3870, Randwick; R6803, Inglewood, Colo Vale; R7090, Austinmer; R8058, Darlinghurst; R10021, R13412, Centennial Park; R10996, Unanderra; R10998, Rose Bay; R11670, Botany, Mascot; R12314, Coniston via Wollongong; R12771, North Wollongong; R15194, Kangaroo Valley; R18483, Botany; R18766–67, Long Bay; R18770, Malabar; R30277, Wollongong district; R68002, R93762, NTM R0961, SAM R25922, La Perouse; AM R75966, 5 miles east Nerriga; R95721, c. 0.5 km north Macquarie Hill; R102945–46, La Perouse Golf Links; R103160, Mascot; R106832, Mount Cambewarra, near Nowra; R121017, Dapto; R130244, Victoria Street, Gerringong; MV D8572, Sydney; QM J32175, Darkes Forest. 3. BLUE MOUNTAINS, NSW: AM R10139, R11673, R12515, R12561, R12921, R13106, R27381, R65875, Lawson; R12728, R12751, Mount Irvine; R45846, Glenbrook Boys Home, Glenbrook; R45847, Three Sisters, Katoomba; R65870–71, R65876–77, Wentworth Falls; R65873, R67166–68, Katoomba district; R67164, R111948 (type of *C. michaeli*), Mount Victoria; R106362–63, 1.2 km east-south-east Mount Victoria; R106746, 0.5 km south Mount Victoria; R120855, Woodford; NTM R4829, Wentworth Falls township; R4830–32, Wentworth Falls Lake; SAM R8787–89, mountains behind Sydney. 4. CENTRAL COAST, NSW: AM R7099, Wyong; R8290–91, R8702, Somersby; R12251, Dora Creek; R16109, Gosford district; R16981, Cooranbong; R21216, Lisarow; R54715, R68348, hill above Boardinghouse Dam, Watagan State Forest, South Cessnock; R54802, 13 km east Raymond Terrace on Williamtown road; R68000, Ourimbah State Forest, north-east Wyong; R68003–04, Heaton Range; R68005, R99461, MV D39131, Gosford; AM R73287, Ourimbah; R75956, Watagan Range; R75967, R92690–91, 7.4 miles south Boardinghouse Dam on Wishing Well Road, Watagan State Forest; R76516, 7.8 km west of main road, on Mount Faulk Road, Watagan State Forest;

R112395, Shortland Swamp; R134999, Narara. 5. BARRINGTON TOPS/NEW ENGLAND, NSW: AM R16085, Barrington Tops; R18961, upper Allyn River; R51692, 6 miles north-north-west Ben Lomond; R139127, Chichester State Forest, east Mount Allyn on Mount Allyn Forest Road (Patterson Forest Road); SAM R8713, Lister Park, c. 30 miles north-east Singleton. UNLOCALISED: AM R14345, Mount Isa; R65872, R65874, Sydney region; MV D57466, no data.

Cyclodomorphus praealtus n.sp.

Figs 17–19

Type material. HOLOTYPE: MV D39148, Three Mile Dam, Kiandra, collected by W.A. Rawlinson on 3 November, 1967. PARATYPES: AM R57876, R64896, ANWC R5127–28, MV D8937, D39130, D39132, D39134–37, D39147, D39149–50, D39194–95, D50053, D56467, D56483.

Diagnosis. A small *Cyclodomorphus* (maximum SVL 114 mm), differing from all other species in the combination of prefrontals usually contacting, postnarial groove absent, postmental usually contacting two infralabials on each side, subcaudal scales 48–57, midbody scales 24–26, supraciliaries modally five and adult dorsal colour pattern complex, including dark edges to scales and scattered paler scales.

Description. Nasals usually in point to broad contact (80.0%, n = 20), rarely narrowly to moderately separated (20.0%); prefrontals usually in moderate to broad contact (75.0%, n = 20), less commonly in narrow contact (20.0%), rarely moderately separated (5.0%); transversely enlarged nuchals 2–5 on each side ($\bar{x}$ = 2.9, sd = 0.70, n = 40), usually three (57.5%); loreals usually two bilaterally (90.0%, n = 20), rarely one unilaterally (10.0%); rarely rostral loreal double unilaterally (n = 1); supraoculars three bilaterally, rostral two in contact with frontal, second largest; supraciliaries 4–6 ($\bar{x}$ = 5.3, sd = 0.53, n = 40), usually five (62.5%); presuboculars 2–3, usually two (71.8%, n = 39); postsuboculars 2–4 ($\bar{x}$ = 3.2, sd = 0.45, n = 40), usually three (77.5%); upper palpebrals 6–8 ($\bar{x}$ = 7.3, sd = 0.57, n = 18); lower palpebrals 7–9 ($\bar{x}$ = 8.1, sd = 0.70, n = 17); secondary temporals usually in α-configuration bilaterally, rarely (n = 1) in β-configuration unilaterally, or with only a single lower secondary temporal bilaterally (n = 1); supralabials 6–8 ($\bar{x}$ = 7.0, sd = 0.39, n = 40), usually seven (85.0%), third-last below centre of eye, separating pre- and postsuboculars; infralabials 6–8 ($\bar{x}$ = 7.2, sd = 0.68, n = 38), usually seven (50.0%) or eight (34.2%); usually first two infralabials contacting postmental, rarely first only unilaterally (n = 1); ear very small, usually with a single small lobule along rostral margin (76.3%, n = 38), rarely two (10.5%) or three (2.6%) or lobules absent (10.5%).

Body scales in 24–26 ($\bar{x}$ = 25.0, sd = 0.97, n = 20) longitudinal rows at midbody; scales in paravertebral rows not or only slightly broader than adjacent scales,

Fig. 17. A live individual of *Cyclodomorphus praealtus* from Smiggin Holes (photograph by W. Osborne).

62–75 ($\bar{x}$ = 68.9, sd = 3.58, n = 20); subcaudal scales 48–57 ($\bar{x}$ = 53.1, sd = 2.34, n = 11); lamellae below fourth toe 8–12 ($\bar{x}$ = 10.1, sd = 0.92, n = 40).

SVL 44–119 mm (n = 20); AGL/SVL 59.1–68.5% ($\bar{x}$ = 64.1%, n = 20); TL/SVL 47.7–77.6% ($\bar{x}$ = 67.3%, n = 11); FLL/SVL 12.3–16.7% ($\bar{x}$ = 13.8%, n = 20); HLL/SVL 15.5–22.7% ($\bar{x}$ = 18.5%, n = 20); FLL/HLL 69.8–81.3% ($\bar{x}$ = 74.7%, n = 20); HL/SVL 14.3–20.5% ($\bar{x}$ = 15.6%, n = 20); HW/HL 64.0–74.0% ($\bar{x}$ = 68.2%, n = 19); HD/HL 50.9–61.2% ($\bar{x}$ = 55.4%, n = 19).

Coloration (in preservative). Dorsal ground color yellow-brown to dull olive-green or grey. On body and tail, centres of individual scales a little darker, often with very fine mid-brown streaks, lateral parts of scales paler, sometimes cream; extreme lateral margins of most dorsal body and basal tail scales with dark brown to black edges, producing a series of weak, irregularly defined, often broken, narrow dark longitudinal stripes, extending onto base of tail, often continued by pale stripes distally as dark margins are reduced and disappear. On body, some transverse rows of scales (generally alternate) may be paler.

Head dorsum immaculate or (more commonly) with black flecks and spots along shield margins, tending to coalesce into dark margins to some shields.

Laterally, body and tail with dorsal ground color, gradually replaced ventrally by paler ventral ground colour. Many scales in alternate transverse scale rows largely black, especially centrally and apically, these dark macules often with cream edges laterally or basally, producing a series of roughly parallel, irregular, narrow dark bars, separated by one to three rows of unspotted scales.

Face with dorsal ground color, individual shields margined by black spots and flecks, especially around eye and adjacent supralabial shields.

Venter blue-grey to yellow, immaculate or with varying density and contrast of dark margins and central dark flecks to scales, leading to an often irregular pattern of narrow dark stripes or variegations on at least body, less commonly on throat and tail.

Limbs yellow-brown to green-grey above, grey-blue to yellow below, with fine dark streaks and spots. Soles yellow-brown, sometimes with slightly darker calli on granules and lamellae.

Juvenile coloration similar to adults, but with more prominent and contrasting dark and light markings on head, especially on face and sides of neck.

Coloration (in life) (Fig. 17). I have not examined any live individuals of this taxon. However, AM R57876 was reported to have had "much bright red,
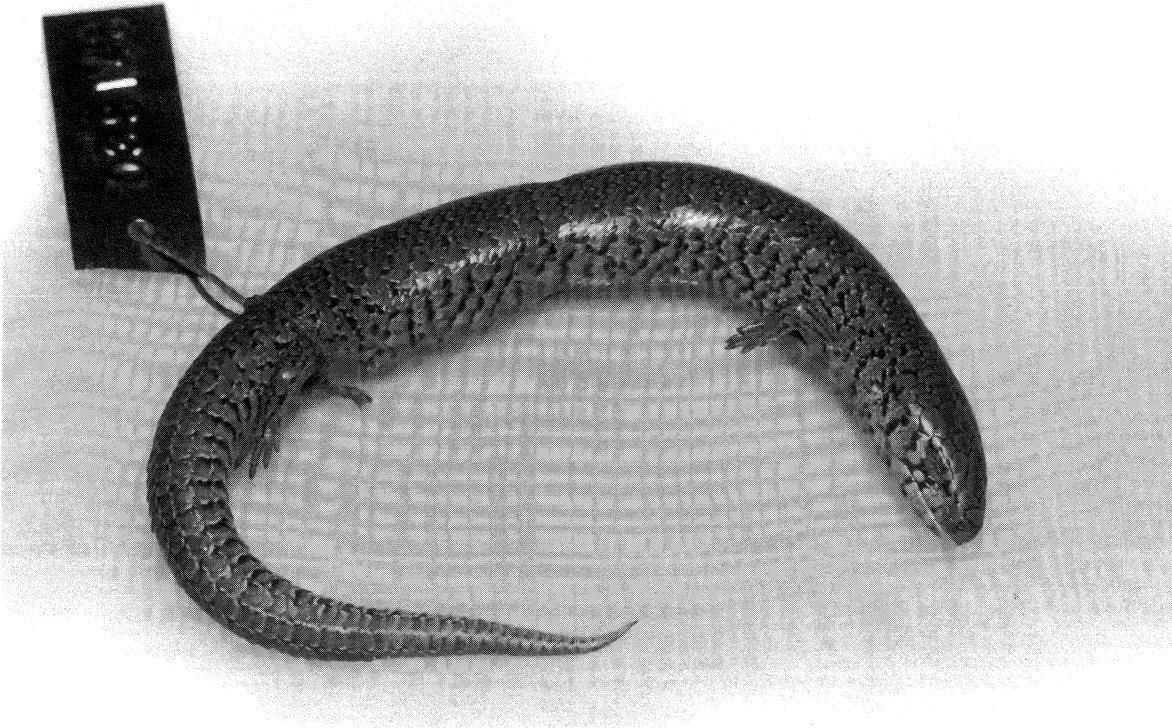
Fig. 18. Holotype of *Cyclodomorphus praealtus* n.sp. (MV D39148).

practically vermillion" ventrally (S.J. Copland field notes, on file in AM), a coloration not now present in this specimen. Colour transparencies of live individuals taken by W. Osborne show orange-red irides, and a dorsal and lateral ground colour suffused with red, particularly on a subadult.

Allometry (Table 7). With respect to SVL, AGL and TL show positive allometry, while FLL, HLL and HL show negative allometry. Neither HW and HD (with respect to HL) nor FLL (with respect to HLL) show significant departures from isometry.

Sexual dimorphism. Sample sizes for males are too small to adequately test for sexual dimorphism. In most cases, the magnitude and direction of difference between the mean values for males and females is similar to that seen in *C. casuarinae* and *C. michaeli*.

Distribution. Australian Alps, above 1500 m, from Kiandra in the north to Mount Hotham in the south (Fig. 1). In addition to the localities cited below, there are several literature records of *C. casuarinae* from the Australian Alps that are probably based on this species: Daner's Gap (Loveridge, 1934; see also Copland, 1947); Mount Buffalo National Park (Jenkins & Bartell, 1980) and Mount Higginbotham (Norris *et*

al., 1983). P. Harlow (pers. comm.) observed an individual of this species at 200 m east of Valentine Hut, on the banks of Valentine Creek at 1680 m in February 1990. This locality is about 10 km north of Guthega Power Station, NSW. W. Osborne (pers. comm.) has recorded the species from Smiggin Holes, Daner's Gap, Mount Blue Cow (36°23'S 148°23'E, 1550 m), Mount Gutherie (36°25'S 148°20'E, 1800 m) and Etheridge Range (36°27'S 148°16'E, 2020 m).

Details of holotype. The holotype (Figs 18, 19) is a gravid female with the following combination of character states: nasals in broad contact; prefrontals in moderate contact; presuboculars two; postsuboculars three; supraciliaries five; supralabials seven; infralabials seven; rostral ear lobules one; nuchals three; upper palpebrals 7/8; lower palpebrals 9/8; midbody scales 24; paravertebral scales 73; subcaudal scales 52; subdigital lamellae ten; SVL 93 mm; AGL 61 mm; TL 57 mm; FLL 11.5 mm; HLL 16 mm; HL 14.2 mm; HW 9.2 mm; HD 7.7 mm. There are 2L/3R oviducal egg masses.

Etymology. The specific epithet is from the Latin *praealtus*, very high, and alludes to the high altitudes inhabited by this species.
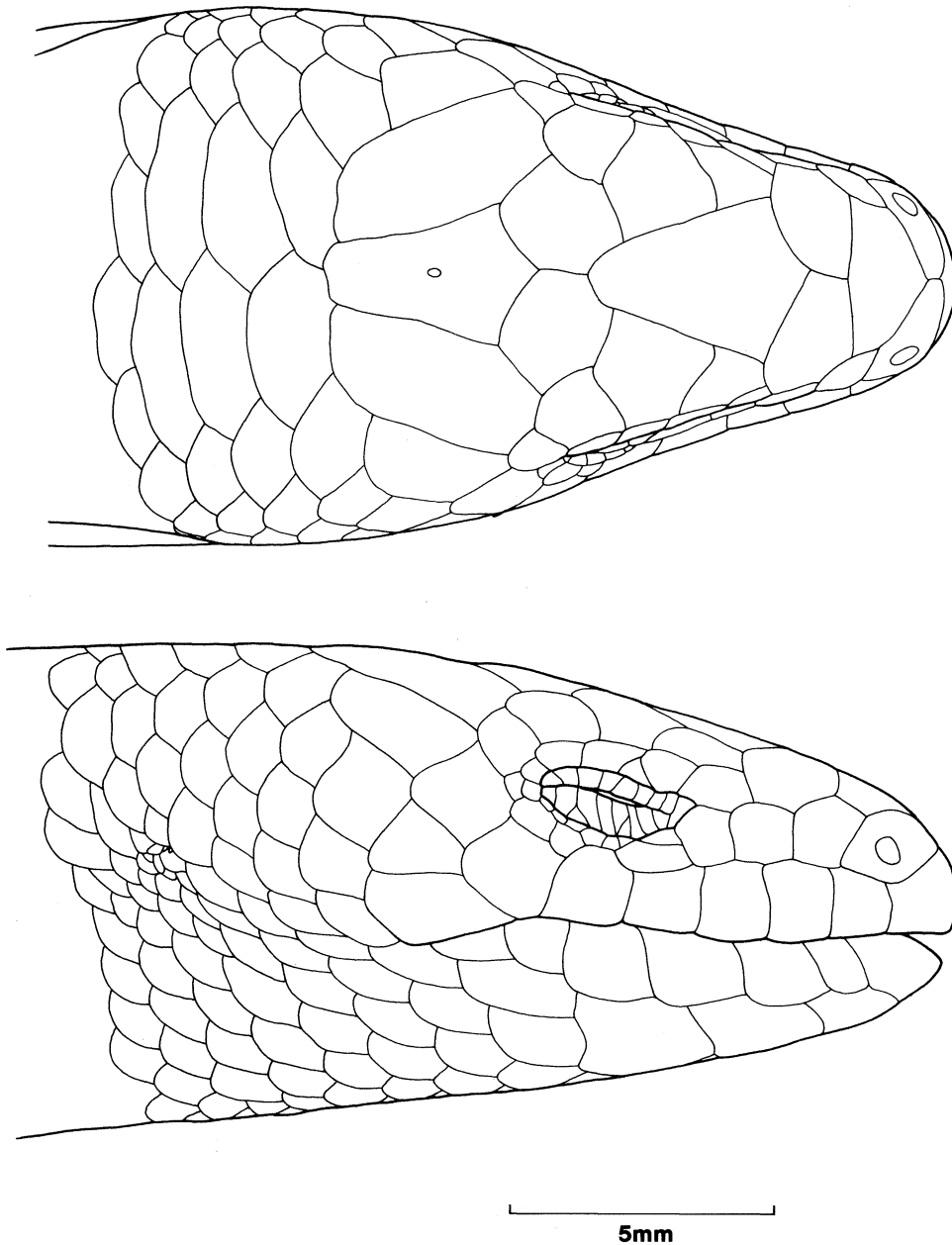
Fig. 19. Dorsal and lateral views of head shields of holotype of *Cyclodomorphus praealtus*.

Habitat and habits. Little is known of the habitat preferences and habits of this species. The specimen from Daner's Gap reported by Loveridge (1934) was taken from a *Myrmecia* nest, the Mount Higginbotham record was found amongst ground litter in subalpine woodland (Norris *et al.,* 1983), the Lankey Plain specimen (MV D50053) was found frozen in snow (Cherry *et al.,* 1987; note, however, that the specimen is a neonate, not an adult as reported by Cherry *et al.*) in an alpine herbfield (Norris *et al.,* 1983) and AM R57876 was found under stones in grass (S.J. Copland

field notes), while the individual observed by Harlow was basking in a grass tussock by day.

W. Osborne (pers. comm.) has field data on six individuals: one from Mount Blue Cow disturbed from grass cover in open shrubland of *Grevillea australis, Prostanthera cuneata* and *Orites lancifolia* over *Poa*; one from Mount Gutherie captured in a small mammal trap in open shrubland with grassy ground cover; a subadult from Etheridge Range collected in a tall alpine herbfield dominated by *Poa*; a subadult from Daner's Gap was found active, moving over sod tussock grass-

land with scattered emergent shrubs; a gravid female from Smiggin Holes basking on grass surface in *Poa* grassland clearing in *Bossiae foliosa* open shrubland, and a second animal from the same locality disturbed from within a grass tussock in *Poa* tussock grassland in an area disturbed by clearing of trees and taller shrubs at the edge of a ski run. On the basis of his experience, Osborne considers the preferred habitat to be open shrubland with a thick ground cover of snow grasses (*Poa* spp.). The species appears to be absent from many alpine habitats, including snow gum forest, wet heath, bog, rock outcrops or wet grassland (W. Osborne, pers. comm.).

Preferred body temperatures of 27.8–33.0°C ($\bar{x}$ = 31.2°C) have been reported for a single animal from Kosciusko National Park (Bennett & John-Alder, 1986).

Reproduction. Of the 20 specimens examined, one was a neonate, three (SVL 89–97.5 mm) were mature males, and the remainder (81–119 mm; $\bar{x}$ = 102.9 mm, sd = 9.51, n = 16) were mature females. The two males for which dates of collection were known were collected 9–28 March, and had grossly enlarged, turgid testes 14 mm long. Of the females, 13 (SVL 81–119, $\bar{x}$ = 101.9 mm, sd = 10.32), collected 3 November (n = 4), 2–4 January (n = 5), 3 February (n = 2) and 2 March

(n = 2) were gravid, with 2–9 ($\bar{x}$ = 4.9, sd = 1.97) oviducal embryos, those collected in March being fully scaled and pigmented. All of the three non-gravid mature females (SVL 105–108 mm) were collected in January, although two were held in captivity for varying periods before death. Two gravid females collected by W. Osborne gave birth to litters of two and five young at the end of February.

There is a positive correlation between litter size and maternal SVL (litter = 0.126SVL – 7.96; r = 0.6595*).

Sex ratio. The adult sex ratio is heavily skewed towards females (3:16; χ_1^2 = 7.58**). A similar seasonal pattern to that seen in other species was apparent, with only females found between November and 2 March, during the gestation period, and two males collected on 9 and 28 March.

Specimens examined. AM R57876, MV D8937, Mount Hotham; AM R64896, ANWC R5127–28, MV D39130, D39132, D39134–37, Smiggin Holes; MV D39147–50, Three Mile Dam, Kiandra; D39194, Mount Hotham Hotel (top); D39195, Mount Hotham Ski Lodges (top); D50053, Lankey Plain; D56467, 0.7 km south-west Mount Loch; D56483, 0.3 km north Loch car park, Mount Hotham.

A key to the species of the *Cyclodomorphus casuarinae* complex

1. Tail short, subcaudals on original tails 57 or fewer; midbody scales 24 or more; Australian Alps .... *C. praealtus*

—— Tail moderate to long, subcaudals on original tails 68 or more; midbody scales usually 24 or fewer 2

2. Subcaudals on original tails 84 or fewer; dorsal colour pattern often complex; Tasmania .... *C. casuarinae*

—— Subcaudals on original tails usually 91 or more; dorsal colour pattern usually simple, either immaculate or with dark margins to scales; Victoria or New South Wales .... *C. michaeli*

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Table 1. Proportions of correct identification of specimens to populations and population groups by canonical variates analysis.

Population	n	correct popn	non-alpine mainland	alpine	Tasmanian
Barrington	3	100.0%	100.0%	–	–
Central Coast	22	63.6%	95.5%	–	4.5%
Blue Mountains	30	56.7%	93.3%	–	6.7%
Wollongong	30	56.7%	80.0%	3.3%	16.7%
Eden	11	100.0%	100.0%	–	–
Total	96	64.6%	90.6%	1.0%	8.3%
Alps	19	84.2%	5.3%	84.2%	10.5%
north-east Tas.	22	59.1%	13.6%	4.5%	81.8%
north-west Tas.	16	75.0%	–	–	100.0%
central Tas.	20	55.0%	15.0%	–	85.0%
south-east Tas.	30	76.7%	–	–	100.0%
unlocalised Tas.	9	–	11.1%	–	88.9%
Total	97	67.0%	7.2%	1.0%	91.8%
Grand total	203	67.5%			

Table 2. Standardised canonical coefficients (and correlations with canonical functions) for 16 characters from all ten populations of the *C. casuarinae* complex. Canonical coefficients standardised by within-groups standard deviations.

Function	I	II	III	IV	V	VI
SVL	0.330 (0.073)	-0.026 (0.046)	0.274 (0.194)	0.136 (0.072)	-0.162 (-0.111)	0.259 (0.528)
AGL	-0.205 (-0.558)	0.174 (0.024)	0.035 (0.103)	0.079 (0.264)	0.110 (-0.102)	0.384 (0.056)
FLL	0.220 (0.685)	0.435 (0.203)	0.852 (0.182)	-0.484 (-0.276)	0.475 (0.290)	-0.556 (-0.243)
HLL	0.302 (0.620)	-0.090 (0.213)	-0.303 (0.049)	0.422 (-0.048)	-0.142 (0.235)	-0.087 (0.009)
HL	-0.209 (0.634)	0.239 (0.014)	-0.288 (-0.034)	-0.762 (-0.411)	-0.107 (0.036)	0.829 (0.309)
HW	0.359 (0.522)	-0.107 (-0.021)	0.126 (0.038)	0.446 (-0.166)	0.083 (0.019)	-0.121 (0.058)
NAS	-0.096 (-0.042)	-0.053 (-0.116)	0.419 (0.422)	0.417 (0.447)	0.303 (0.228)	0.081 (0.141)
PFR	-0.429 (-0.323)	0.069 (0.048)	0.010 (0.136)	-0.252 (-0.247)	0.043 (0.019)	0.253 (0.274)
POS	0.030 (0.123)	0.189 (0.129)	-0.223 (-0.196)	0.176 (0.060)	0.466 (0.400)	0.156 (0.248)
PRS	-0.130 (-0.070)	-0.056 (-0.058)	0.146 (0.004)	-0.005 (0.033)	0.633 (0.543)	0.103 (0.115)
SCIL	0.146 (0.185)	0.388 (0.312)	-0.236 (-0.107)	0.095 (-0.069)	-0.072 (-0.017)	-0.191 (-0.256)
ILAB	0.013 (0.139)	-0.162 (-0.013)	0.061 (0.169)	-0.037 (-0.070)	0.390 (0.395)	0.236 (0.259)
NUCH	-0.074 (-0.268)	0.117 (0.099)	0.298 (0.267)	0.388 (0.345)	-0.106 (-0.203)	-0.230 (-0.240)
MB	0.284 (0.271)	-0.807 (-0.574)	0.331 (0.386)	0.005 (-0.277)	-0.224 (-0.168)	-0.051 (0.059)
PV	-0.324 (-0.458)	0.333 (0.201)	0.534 (0.464)	-0.650 (-0.289)	0.121 (-0.141)	-0.234 (0.012)
SUBLAM	0.178 (0.218)	0.493 (0.446)	0.220 (0.343)	0.276 (0.147)	-0.367 (-0.255)	0.408 (0.413)
Canonical Correlations	0.810	0.791	0.581	0.569	0.503	0.368

Table 3. Allometric equations and calculated values for cranial and somatic proportions in *C. casuarinae*. Values a and b solve the equation $y = bx^a$, r = correlation coefficient, s.e. = standard error of a, C_{42}, C_{103} and C_{174} are calculated percentage proportions (y/x) at SVL = 42, 103 and 174 mm (minimum, minimum mature female and maximum size). Sample sizes are as for ratios.

y	x	a	b	r	s.e.	C_{42}	C_{103}	C_{174}
AGL	SVL	1.150	0.313	0.998	0.007	54.8	62.7	67.9
TL	SVL	1.431	0.149	0.990	0.025	74.6	109.8	137.7
FLL	SVL	0.755	0.479	0.984	0.013	19.2	15.4	13.5
HLL	SVL	0.866	0.392	0.986	0.014	23.8	21.1	19.6
FLL	HLL	0.865	1.101	0.992	0.011	80.7	72.7	68.4
HL	SVL	0.653	0.818	0.982	0.012	22.4	16.4	13.7
HW	HL	0.976	0.723	0.980	0.019	68.5	67.6	67.0
HD	HL	0.931	0.613	0.972	0.022	52.5	50.4	49.3

Table 4. Sexual dimorphism in cranial and somatic proportions in *C. casuarinae*. 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. C_{85} and C_{126} are calculated proportions at SVL = 85, 126 mm (minimum mature and maximum SVL for males, the smaller sex).

(i)

y	x	slopes			intercepts		
		F	d.f.	P	F	d.f.	P
AGL	SVL	0.361	1,88	n.s.	13.646	1,89	***
TL	SVL	26.441	1,52	***	–	–	–
FLL	SVL	0.153	1,88	n.s.	12.797	1,89	***
HLL	SVL	6.552	1,88	*	–	–	–
HL	SVL	10.750	1,88	***	–	–	–
HW	HL	6.047	1,88	*	–	–	–
HD	HL	1.994	1,87	n.s.	0.871	1,88	n.s.
FLL	HLL	9.710	1,89	**	–	–	–

	y	x	a	b	r	s.e.	n	C_{85}	C_{126}
(ii)									
	AGL	SVL	1.139	0.324	0.997	0.015	35	60.1	63.5
	TL	SVL	1.531	0.102	0.996	0.031	24	107.9	133.0
	FLL	SVL	0.771	0.457	0.984	0.025	35	16.5	15.1
	HLL	SVL	0.949	0.283	0.993	0.020	35	22.6	22.1
	HL	SVL	0.661	0.801	0.986	0.020	35	17.8	15.5
	HW	HL	0.874	0.946	0.976	0.034	35	67.2	65.0
	FLL	HLL	0.812	1.271	0.992	0.018	35	72.9	68.0
(iii)									
	AGL	SVL	1.125	0.355	0.994	0.017	57	61.9	65.0
	TL	SVL	1.167	0.514	0.957	0.065	32	107.9	115.3
	FLL	SVL	0.786	0.405	0.958	0.032	57	15.7	14.4
	HLL	SVL	0.853	0.409	0.964	0.032	57	21.3	20.1
	HL	SVL	0.779	0.444	0.962	0.030	57	16.6	15.2
	HW	HL	1.006	0.668	0.957	0.041	57	67.9	68.0
	FLL	HLL	0.909	0.960	0.979	0.025	58	73.8	71.5

Table 5. Allometric equations and calculated values for cranial and somatic proportions in *C. michaeli*. Values a and b solve the equation $y = bx^a$, r = correlation coefficient, s.e. = standard error of a, C_{40}, C_{101} and C_{174} are calculated percentage proportions (y/x) at SVL = 40, 101 and 174 mm (minimum, minimum mature female and maximum size). Sample sizes are as for ratios.

y	x	a	b	r	s.e	C_{40}	C_{101}	C_{174}
AGL	SVL	1.159	0.313	0.998	0.007	56.3	65.2	71.1
TL	SVL	1.335	0.285	0.984	0.034	98.1	133.7	160.5
FLL	SVL	0.705	0.537	0.953	0.022	18.1	13.8	11.7
HLL	SVL	0.838	0.400	0.960	0.023	22.0	18.9	17.3
FLL	HLL	0.835	1.183	0.985	0.014	82.6	72.7	67.4
HL	SVL	0.611	0.914	0.970	0.015	21.8	15.2	12.3
HW	HL	0.923	0.818	0.970	0.023	69.2	66.3	64.6
HD	HL	0.959	0.600	0.958	0.028	54.9	53.6	52.9

Table 6. Sexual dimorphism in cranial and somatic proportions in *C. michaeli*. 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. C_{74} and C_{128} are calculated proportions at SVL = 74, 128 mm (minimum mature and maximum SVL for males, the smaller sex).

(i)

y	x	slopes F	slopes d.f.	slopes P	intercepts F	intercepts d.f.	intercepts P
AGL	SVL	0.016	1,98	n.s.	35.933	1,99	***
TL	SVL	14.406	1,47	***	–	–	–
FLL	SVL	7.136	1,98	**	–	–	–
HLL	SVL	8.815	1,98	**	–	–	–
HL	SVL	2.234	1,98	n.s.	44.584	1,99	***
HW	HL	0.173	1,91	n.s.	0.075	1,92	n.s.
HD	HL	1.696	1,97	n.s.	0.816	1,98	n.s.
FLL	HLL	0.282	1,99	n.s.	2.925	1,100	n.s.

	y	x	a	b	r	s.e.	n	C_{74}	C_{128}
(ii)	AGL	SVL	1.131	0.351	0.998	0.011	52	61.7	66.3
	TL	SVL	1.485	0.152	0.986	0.047	31	122.6	159.9
	FLL	SVL	0.814	0.341	0.966	0.031	52	15.3	13.8
	HLL	SVL	0.962	0.240	0.978	0.029	52	20.4	20.0
	HL	SVL	0.682	0.681	0.972	0.023	52	17.3	14.6
(iii)	AGL	SVL	1.133	0.358	0.998	0.010	50	63.5	68.3
	TL	SVL	1.254	0.394	0.992	0.037	20	117.6	135.1
	FLL	SVL	0.694	0.546	0.951	0.033	50	14.6	12.4
	HLL	SVL	0.834	0.386	0.967	0.032	50	18.9	17.3
	HL	SVL	0.639	0.777	0.983	0.017	50	16.4	13.5

Table 7. Allometric equations and calculated values for cranial and somatic proportions in *C. praealtus*. Values a and b solve the equation $y = bx^a$, r = correlation coefficient, s.e. = standard error of a, C_{44}, C_{81} and C_{119} are calculated percentage proportions (y/x) at SVL = 44, 81 and 119 mm (minimum, minimum mature female and maximum size). Sample sizes are as for ratios.

y	x	a	b	r	s.e.	C_{44}	C_{81}	C_{119}
AGL	SVL	1.113	0.382	0.992	0.033	58.6	62.8	65.6
TL	SVL	1.416	0.102	0.983	0.088	49.2	63.5	74.5
FLL	SVL	0.800	0.344	0.911	0.085	16.1	14.3	13.2
HLL	SVL	0.735	0.620	0.900	0.084	22.7	19.3	17.5
FLL	HLL	1.050	0.647	0.977	0.054	72.6	74.2	75.3
HL	SVL	0.646	0.783	0.947	0.052	20.5	16.5	14.4
HW	HL	1.069	0.565	0.963	0.073	65.8	67.6	68.7
HD	HL	0.980	0.584	0.951	0.077	55.9	55.4	55.2