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Systematics of the Reduce-limbed and Limbless Skinks Currently Assigned to the Genus *Anomalopus* (Lacertilia: Scincidae)

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**ABSTRACT.** The genus *Anomalopus*, as currently recognized, harbours many of the reduce-limbed and limbless skinks of eastern Australia. In this paper the genus is argued to be polyphyletic and, on the basis of shared derived character states, is subdivided into three genera, one with two subgenera. The taxa are: *Anomalopus* (*Anomalopus*) *mackayi* n. sp., *A.* (*A.*) *verreauxii* Duméril & Duméril, 1851 and *A.* (*A.*) *leuckartii* Weinland, 1862; *Anomalopus* (*Vermiseps*) *swansoni* n. subgen., n. sp., *A.* (*V.*) *pluto* Ingram, 1977, *A.* (*V.*) *gowi* n. sp. and *A.* (*V.*) *brevicollis* n. sp.; *Ophioscincus truncatus* Peters, 1876, *O. ophioscincus* Peters, 1873 and *O. cooloolensis* n. sp.; *Coeranoscincus reticulatus* Günther, 1873 and *C. frontalis* De Vis, 1888. Data on distribution, habitats, habits and mode of reproduction are given for all taxa as available, and inter- and intrageneric relationships are discussed. Morphological trends within each genus or subgenus are discussed. Keys are provided to the genera of reduce-limbed skinks of Australia and the limbless lygosomines of the world.

**KEYWORDS:** Australia, Scincidae, limbless, lizards.

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Skinks are renowned for the frequency with which they undergo limb reduction and loss. If one takes as the end point of this process the total absence of any external trace of limbs, then non-scincid lizards (three-quarters of all lizard species) have lost the limbs (on a very conservative estimate) at least three or four times whereas skinks (about one-quarter of all lizard species) have lost them at least thirteen times. Within skinks the loss has not been uniform across major taxonomic groups. The scincines, acontines and feylines together account for about one-fourth of all skink species and have lost their limbs at least eight times, whereas the lygosomines, accounting for three-fourths of the species, have lost them at least five times (once in the Asian genus Isopachys and once each in the Australian genera Anomalopus (s.s.), Coeranoscincus, Lerista and Ophioscincus).

The number of limbless lygosomine species described and recognized as valid to date is eight. However, for several years four additional species, all from eastern Australia, have been known but undescribed. All of these have either been formally or informally assigned to the genus Anomalopus (see Cogger, 1973, for first use of the current generic concept), a member of the Sphenomorphus group of lygosomines (Greer, 1979). This genus also contains one informally recognised but undescribed reduce-limbed species. The primary purpose of this paper is to describe these five new species and to review their morphology and relationships, and hence make them more readily available to other studies, especially those concerned with limb reduction and loss. Furthermore, as the current diagnosis of Anomalopus comes very close to 'all those greatly reduce-limbed Australian skinks with no clear affinities elsewhere', a second, but related, purpose of the paper is to test the monophyly of the group. Finally, to facilitate the identification of reduce-limbed skink genera in Australia and limbless lygosomine species worldwide, keys are presented to both groups.

Materials and Methods

The specimens examined in this study comprise most of the Australian material and much of the overseas material. These have been studied as intact specimens in alcohol, dried skeletons, cleared (KOH and trypsin) and stained (alcian and alizarin) specimens and from X-rays.

Non-obvious head scale designations are given on figures of relatively primitive representatives of each genus and subgenus (Figs 2, 10, 24 and 35). Paravertebral scales are counted in a single row starting from the first scale, in either row, that falls completely beyond an imaginary line drawn along the posterior edges of the thighs, extended at right angles to the body and ending at and including the scale bordering the parietal. In limbless species the count begins with the paravertebral at the level of the anterior edge of the enlarged preanals, a level equivalent to that in limbed species. The digits of reduce-limbed forms are given sequence numbers on the basis of their inferred homologies.

Measurements of the head, body and appendages were made by adpressing the part against a stationary steel rule graduated in 0.5 mm. Measurements of scales were made with an ocular micrometer. Proportions were based on maximum widths and midline lengths. Tail lengths were based on complete tails as determined from X-rays. Brood sizes were determined by dissection of gravid females.

All diagnoses of supraspecific taxa are written for the hypothetical ancestor of the taxon, i.e., they represent the suite of the most conservative derived character states displayed within the taxon vis à vis the Sphenomorphus group. Descriptions of external morphology for the new species include details of all characters currently recognized as potentially useful in the alpha taxonomy of lygosomines. Descriptions of skeletal characters for all species are limited to characters that either vary intraspecifically or are useful in inferring relationships.

Species synonymies follow Cogger et al. (1983). Descriptive, institutional and statistical abbreviations that are not obvious are as follows:

AM Australian Museum, Sydney
AMNH American Museum of Natural History, New York
ANWC Australian National Wildlife Collection, Canberra
BMNH British Museum (Natural History), London
CAS California Academy of Sciences, San Francisco
FMNH Field Museum of Natural History, Chicago
GZM Giessener Zoologischen Museum, Giessener, Germany
MNHN Musée National d’Histoire Naturelle, Paris
MCG Museo Civico di Storia Naturale di Genova ‘Giacomo Doria’, Genova
MCZ Museum of Comparative Zoology, Cambridge, Massachusetts
MV Museum of Victoria, Melbourne
QM Queensland Museum, Brisbane
QNPWS Queensland National Parks and Wildlife Service, Townsville, Queensland
SAM South Australian Museum, Adelaide
SD standard deviation
SVL snout-vent length
WAM Western Australian Museum, Perth
seen in burrowers (see pp. 13, 33 and 41). In Anomalopus epidermis. close above orbit; fenestra rotunda reduced to vertical character states that are derived currently construed, shows the following suite of Anomalopus is a problem in that it is a list of character states that hence is likely to inspire confidence in the concept of This approach has led to the conclusion that there are three monophyletic, generic-level taxa within the current concept of Anomalopus and that one of these, Anomalopus (s.s.), is probably more closely related to a group outside Anomalopus (s.l.) than to one within, and that the relationships of the other two taxa, Ophioscincus new genus and Coeranoscincus, while for the present obscure, are by no means necessarily with each other. Hence the answer to the question posed above is that Anomalopus, as it has been construed to date, is probably not a clade of burrowers but rather a grade.


Diagnosis. Anomalopus differs from all other members of the Sphenomorphus group in the following combination of derived character states: prefrontals separated; last 2 supraoculars partially separated by a superciliary (usually the sixth); supralabials 6, fourth (or suture between fourth and fifth) below centre of eye; external ear opening absent; front and rear limb ≤ 0.07 x and ≤ 0.09 x SVL, respectively. Premaxillary teeth ≤ 7; ectopterygoid process present; postorbital absent; quadrate conch absent. Manus lacks distal carpals 1 and 5, metacarpal 1, and has phalanges reduced to 0.2.3.2.0; pes lacks metatarsal 1 and has phalanges reduced to 0.2.2.0.0; presacral vertebrae ≥ 47; sternal ribs ≤ 2; medial ends of ischia separated.

Comments. This genus brings together all those Sphenomorphus group species that, in addition to having the ‘Anomalopus’ suite of burrowing modifications, also show the following non so obviously burrowing-associated features: last two supraoculars partially separated by a superciliary; premaxillary teeth ≤ 7; ectopterygoid process present; postorbital absent.

Subgenera. Anomalopus Duméril & Duméril comprising the limbed forms, and Vermiseps n. subgen. comprising the limbless forms.


Distribution. Eastern Australia from Cape York Peninsula to central New South Wales (Figs 3,8,12).

Habitat and habits. Low closed forest (vine thicket) through open forest and woodland (various types) to open heath; apparently only rarely in tall closed forest (rainforest) and then generally in openings and clearings. Cryptozoic; generally found under surface cover.

Reproduction. Oviparous (three species) and ovoviviparous (one species). The only known ovoviviparous species (A. swansoni) is also the most southern, providing yet another example of the association of this mode of reproduction with life in cooler climates.

Relationships. Anomalopus shares three of its four non-burrowing derived character states with the genus Lerista, and it would share all four if the failure of the last two supraoculars to be separated partially by a supraciliary were secondarily derived instead of primitive in L. microtis. Lerista is a large genus, widespread in the arid, semi-arid and seasonally dry parts of Australia, with its most primitive members in the temperate zone (pers. obs.). Anomalopus, as represented by the most primitive species in each of its two subgenera, A. mackayi in Anomalopus and A. swansoni in Vermiseps, is similar to Lerista in being

<table>
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<tr>
<th>Institution</th>
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<tr>
<td>ZMA</td>
<td>Zoologisch Museum, Amsterdam</td>
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<td>ZMB</td>
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* statistical mean

significance levels for statistical tests of 0.05, 0.01 and 0.001, respectively
distributed in relatively open habitats (e.g. woodland) and in having its most primitive species restricted to the temperate zone.

Key to Species of Anomalopus

1. Limbs present .................................................. subgenus *Anomalopus* ...... 2
   — Limbs absent ............................................. subgenus *Vermiseps* ..... 4
   2. Three toes on front limb. .................................... 3
   — Two toes on front limb. ..................................... *A.(A.) leuckartii*
   3. Two toes on rear limb. ...................................... *A.(A.) mackayi*
   — Styliform rear limb. ....................................... *A.(A.) verreauxii*
   4. Nasals separated (rarely in contact in *A. swansoni*); prefrontals present. .... 5
   — Nasals in contact; prefrontals absent. .......................... 6
   5. Nasal extends to lip (through fusion with ‘first’ supralabial?) .................. *A.(V.) pluto*
   — Nasal separated from lip by first supralabial. .................. *A.(V.) swansoni*
   6. Supraoculars usually 3 (84%), occasionally 2 (16%); frontoparietals meet; supralabials 6; paravertebrals 86–102. .......... *A.(V.) brevicollis*
   — Supraoculars 2; frontoparietals usually separate (89%); supralabials usually 5 (90%), occasionally 6 (10%); paravertebrals 108–116. .......... *A.(V.) gowi*

Subgenus *Anomalopus* Dumeril & Duméril

Type-species. As for genus.

Diagnosis. There are three derived character states that will diagnose this group as a distinct lineage *vis a vis* the subgenus *Vermiseps*: larger size (maximum SVL of smallest species = 123 mm vs maximum SVL of largest species of *Vermiseps* = 108 mm), dedifferentiation of the transversely enlarged nuchal scales (mode = 0), and reduction of fenestra rotunda to a small foramen. For purposes of rapid identification it may be distinguished from this group by the retention of limbs.

Species (3). *Anomalopus leuckartii* Weinland, 1862; *A. mackayi* n. sp.; and *A. verreauxii* Dumeril & Duméril, 1851.

Distribution. Central eastern Australia from southeast Queensland to central eastern New South Wales (Figs 3,8).

Habitat and habits. Closed and open forests, woodlands and open paddocks. Generally found under cover (rocks and logs) over loose or semi-consolidated substrates; generally tries to escape by undulating/crawling laterally into the surface litter instead of diving into the substrate.

Reproduction. Oviparous (two species).

*Anomalopus mackayi* n. sp.

Figs 1–2

Type-material. HOLOTYPE. Australian Museum R 3834: Eurora, Walgett, N.S.W.; collected by ‘Mr. Raven’ and presented to the museum by C.N. Vaughan; no date of collection available; male.

PARATYPES. AM R 2383: locality unknown; R 3834, 13138: Old Burren, N.S.W.; R 14007: Gnowerry Station, Goodooga, N.S.W.; R 16902: Burren Junction, N.S.W.; R 17712, 21006: Bellata, N.S.W.; R 66665: Culgoora, N.S.W.

FMNH 73852: Wee Waa, N.S.W.; 75142, 75144: locality unknown.

QM J 8516: Allora, Qld; J 42433: Bongeen area, 20 km S of Cecil Plains, Qld; J 42531: 24 km NNW of Oakey (by road), Qld.

Diagnosis. Differs from all other *Anomalopus* and indeed all other lygosomines in having a digital formula of 3–2.

Description. A moderately long, attenuate skink with small front and rear limbs and a plain brown colour pattern.

Snout bluntly rounded; rostral with broad, moderately deep median lobe projecting between nasals to make narrow contact with frontonasals; frontonasal wider than long (1.4–1.8 x); prefrontals well developed but widely separated; frontal slightly longer than wide (1.2–1.4 x) and slightly shorter than midline length of frontoparietals and interparietal; supraoculars 4, first 2 in contact with frontal; frontoparietals paired, in contact, each shorter and broader than interparietal; interparietal distinct, with distinct parietal eye spot; parietals meet behind interparietal; each parietal bordered posterolaterally by large upper secondary temporal and 2 to 3 more-or-less equally sized body scales; transversely enlarged nuchals 0–1.

Nasals large and separated, nostril situated slightly forward and below centre point; loreals 2,
Fig. 1. *Anomalopus mackayi* n. sp. from 24 km NNW of Oakey (by road), Qld. Photo: A.E. Greer.

approximately equal in size and proportions; preoculars 2, lower much the larger; supraoculars 6 to 7, first separated from frontal, penultimate occasionally projects slightly medially between third and fourth supraoculars, and ultimate projects medially between last supraocular and pretemporals; suboculars large and forming a continuous row comprised of 1 presubocular, 2 suboculars and 1 postocular; lower eyelid scaly; pretemporals 2; primary temporal single; secondary temporals 2, upper very long and overlapping lower which is about equal in size to primary temporal; tertiary temporal single; external ear opening absent, represented by an anteriorly dipping, shallow auricular crease; supralabials 6 or 7, fourth smallest and situated directly below centre of eye; postsupralabials 2; infralabials 6 or 5; mental large, wider than long (1.7–2.3 x); postmental much wider than long, in contact with first two infralabials on each side; enlarged pairs of chin scales 3, first in contact, second separated by 1 scale row and third separated by 3.

Body scales smooth, in 18–20 longitudinal rows at midbody; paravertebral scales only slightly wider than those in more lateral rows, 97–116 in a single row; inner preanals overlap outer, medial pair enlarged; median row or subcaudals equal in size to immediately adjacent rows.

Snout-vent length 63–123 mm; front leg with 3 very short, clawed toes of which middle is longest, 0.05–0.07 x SVL; rear leg with 2 very short clawed toes of which second is longer, 0.04–0.08 x SVL; tail pointed, 1.03–1.21 x SVL.

Presacral vertebrae 51–58; complete inscriptive chevrons 11–13; sternal/mesosternal ribs 2/2.

Manus comprises radiale, ulnare and pisiform (intermedium could not be assessed); centrale; distal carpals 2–4; metacarpals 2–5, and phalanges 0.2.3.2.0.

Pes comprises fused astragalus and calcaneum; distal tarsals 3–4; metatarsals 2–5; phalanges 0.2.2.0.0.

**Colour.** In preservative the ground colour of the dorsum ranges from light, greyish brown to dark-brown.
and the venter from off-white to light-brown. The dorsal pattern is uniform in New South Wales specimens but consists of rows of dark-brown dots or dashes through the centres of the dorsal and lateral scales in the Queensland specimens. The venters are unpatterned in most specimens but consists of rows of dark spots like the dorsum in one Queensland specimen (QM J 8516).

Details of holotype. The holotype (AM R 3834; Fig. 2) has 7 supralabials on left side and 6 on right; 18 midbody scale rows; 104 paravertebral scales; SVL 110 mm, and tail regenerated.


Distribution. The 12 specimens of A. mackayi with locality data are from a relatively small area just west of the Dividing Range in northeastern New South Wales and southeastern Queensland (Fig. 3).

Habitat, habits and reproduction. Nothing known.

**Anomalopus verreauxii** Dumeril & Duméril
Figs 4-5


*S. simplex* Cope, 1864: 229. Type-locality: Australia. Type(s): unknown.


Material examined. Localities have been omitted for this common and widespread species in order to save space (Fig. 3).
Fig. 4. Anomalopus verreauxii from approximately 4.2 km SW of Maleny, Qld. Photo: A.E. Greer.

hence frontonasal shorter and broader; supraoculars generally 4, but occasionally reduced to 3, first two always in contact with frontal; transversely enlarged nuchals 0–2.

Nasal slightly larger, nostril situated slightly forward of centre; infralabials 5; mental slightly larger and extending more posteriorly, hence shorter and broader overall; paravertebral scales more numerous, 110–129; snout-vent length appreciably greater, 44–185 mm; front and rear legs relatively shorter (0.03–0.06 and 0.01–0.03 x SVL, respectively); rear leg styliform, clawless.

Presacral vertebrae 53–57; postsacral vertebrae 57–62; complete inscriptive chevrons 12–14; sternal/mesosternal ribs 3/2–2/2.

Manus comprises radiale, intermedium (sometimes absent), ulnare and pisiform; centrale; distal carpals 2–5; metacarpals 2–5, and phalanges 0.1.2.2.0 (basal 2 phalanges may fuse in digits 3–4 in older specimens).


Colour. In preservative, A. verreauxii is generally uniformly brown to dark-grey above and off-white to pale ‘dirty’ brown below; a light nuchal collar is very distinct in juveniles but becomes suffused with pigment in adults. In life, the nuchal collar and venter of the chin, throat and anterior body may be various shades of yellow (Fig. 4; see McPhee 1979, plate 50, for colour photograph of live specimen).

Distribution. Anomalopus verreauxii ranges along the east coast from the vicinity of Proserpine, Qld, south to Red Rocks, N.S.W. (Fig. 3). Despite its widespread distribution on the coast it is apparently known from only two islands: Great Keppel (MV D 42598) and Bribie (QM J 3422). The most inland locality which can be reliably accepted is Palm Gorge Fauna Reserve, Qld (QM J 37065) approximately 225 km from the coast. In the north, the range roughly coincides with the arid corridor that comes to the coast between Bowen and Townsville while in the south, it appears to coincide with the southern edge of the Clarence Basin.

Three localities associated with museum specimens have been omitted from the distribution map (Fig. 3) due to the fact that they are well outside the range as determined from more-or-less contiguous records. These are Wyong, N.S.W. (SAM 3931), 6.4 km W of Armidale (AM R 51693) and Charleville, Qld (QM J 1553).

Variation. Occasional specimens of A. verreauxii have a reduced number of digits on the front foot that appears to be due to normal variation instead of disease or injury. These are as follows: QM J 11831 — locality uncertain: 2 toes on left front foot, 3 on right (2–3); QM J 11837 — 32 km N of Dayboro, Qld: 2–2; QM J 22289–90 — Bulburin Forest Camp, Qld: 2–3 and 3–2, respectively and AM R 33035 — Rockhampton district, Qld: 2–2. QM J 11831 and J 22289–90 are reliably assigned to A. verreauxii on the basis of their having three toes on at least one front foot, and large size (SVL = 170, 176 and 182 mm, respectively vs a maximum of 137 mm for A. leuckartii), and J 22289–90 at least came from a population known to include three-toed animals. QM J 11837 is probably an A. verreauxii on the basis of its occurrence well within the range of this species (and far from the nearest A. leuckartii) and the fact that it was taken with a three-toed specimen (QM J 11836). AM R 33035 is assigned to A. verreauxii on the basis of its large size (SVL = 143 mm), but it could be interpreted as an exceptionally large A. leuckartii.

A light nuchal collar, albeit only faintly expressed in some large specimens, has been found in every specimen.
Fig. 5. Skull of *Anomalopus verreauxii* (AM R 6437).

examined for the trait (N = 115) except one: AM R 114092 from Mount Morgan. This specimen is especially significant because it is a juvenile, and in such young specimens the nuchal collar is usually very sharp.

**Habitat.** *Anomalopus verreauxii* occurs in habitats ranging from large man-made clearings through dry sclerophyll forest and woodland to closed forest (where it is most often found in openings and clearings). The species has been collected at three sites in the Australian Museum and Queensland Museum’s joint faunal survey of eastern Australian rainforests (Anonymous, 1976; Broadbent & Clark, 1976; and Covacevich, 1977). At Bulburin State Forest it was found in wet complex notophyll vine forest (adjacent to site 1) and moist low
microphyll vine forest (adjacent to site 3). *Ophiocircus ophiocyclus* was also found in the same habitats at both sites. *Anomalopus verreauxii* has also been taken at Marlaybrook in the Bunya Mountains (site 57). This is a semi-evergreen vine thicket with *Brachychiton*.

**Habits.** Cryptozoic, generally found under surface cover, e.g. rocks, logs and debris; 'commonly discovered under piles of rubbish in many of the suburbs of Brisbane' (Dale, 1973).

Longman (1916) notes that 'when a living *L.*[Lygosoma] verreauxii is placed on the ground, the stumps are moved with remarkable speed and vigor in the endeavour to promote locomotion over a comparatively smooth surface'.

In small specimens the claws of the front foot are usually relatively long and sharply pointed; however, in larger specimens the claws are often worn down, sometimes to skin level (pers. obs.).

**Reproduction.** Oviparous (Dale, 1973). We have found five gravid female *A. verreauxii* in the collections examined. All are from southeastern Queensland. One of these contains 11 very large ovarian eggs or recently ovulated oviducal eggs, and the other four contained 3–11 shelled oviducal eggs. Snout-vent lengths of the four measurable specimens range 128–182 mm and the two available dates of collection are 6 and 12 November. S.J. Copland reports (field notes for S.J.C. 3812–17) finding a clutch of six eggs at Hortons Creek, N.S.W., which hatched in the period 11–13 March.

**Taxonomic comments.** The following species have been assigned to the synonymy primarily on the basis of the unique (to lygosomines) digital formula of 3/1. The type of *'S. simplex'* Cope, 1864, has not been found (Cogger, pers. obs.) but Cope's description of a digital formula of 3/1 and a 'yellowish occipitonuchal collar' can only pertain to *Anomalopus* *verreauxii* within the Australian herpetofauna. All other parts of Cope's description also accord well with this species.

The two syntypes of *Anomalopus Godeffroyi* Peters, 1867, have not been examined by us, but because Peters himself noted it was distinguished from *A. verreauxii* only by the presence of a scaly eyelid (the eyelid being described as 'transparent' in the original description of the latter), and only provisionally recognized it as a distinct species, we feel confident in relegating *A. Godeffroyi* to the synonymy of *A. verreauxii*.

One of us (H.G.C.) has examined the holotype of *Chelomeles pseudopodus* Günther, 1873. Its digital formula of 3/1, light (albeit faint) nuchal collar, lack of an external ear opening, 20 midbody scale rows and large size (SVL ca 189 mm) make it clearly assignable to *Anomalopus verreauxii*.

**Anomalopus leuckartii** Weinland
Figs 6–7


**Diagnosis.** The only species of *Anomalopus* with the digital formula 2–1, the front leg bearing 2 very short clawed toes and the rear leg represented by a clawless nubbin (clawed on the right side in AM R 47480). Differences with this species (also see Table 1).

**Description.** Like *A. verreauxii*, *A. leuckartii* is very similar to *A. mackayeii* and may be described in terms of its differences with this species (also see Table 1).

Rostral appreciably larger and projecting more dorsally, hence frontonasal shorter and relatively broader; supraoculars 2–4, the first 2 or only the first in contact with frontal; transversely enlarged nuchals 0–4; nasal appreciably larger, nostril situated well forward of centre; anterior loreal appreciably larger than posterior loreal; supraciliaries 6–7 (mode = 6); fourth supralabial invariably situated below centre of eye; infralabials 6; mental much larger, extending more posteriorly, hence postmental shorter and relatively broader; paravertebral scales more numerous 108–128; snout-vent length slightly greater, 39–137 mm; fore and rear legs relatively shorter (0.03–0.04 and 0.01 or less, respectively); forelimb didactyl, inner digit shorter than outer; rear limb styloform, clawless.

Presacral vertebrae 51–55; postsacral vertebrae 50–54; complete inscriptional chevrons 10–14; sternal/mesosternal ribs 2/2–2/1.

Manus comprises radiale, ulnare and pisiform; distal
carpels 2–4, metacarpals 2–4 and phalanges 0.1.2.0.0.

Pes comprises astragalus and calcaneum.

**Colour.** In preservative, *A. leuckartii* is light-brown to grey-brown dorsally and off-white to pale ‘dirty’ brown ventrally (Fig.6). A light nuchal collar occurs commonly in Queensland populations (see below); these specimens can be distinguished from similarly patterned *A. verreauxii* by the 2 digits on the front foot, instead of 3, and the relatively shorter hindlimb. In life, the venter of the body may be uniform light-yellow (pers. obs. A.E.G.).

**Distribution.** *Anomalopus leuckartii* ranges from the Rockhampton district in southeastern Queensland (AM R 33034), south to Muswellbrook (AM R 15758-15759), Kandos (AM R 52992) and Cumnock (AM R 8986) in central eastern New South Wales (Fig.8).

**Variation.** There is only one specimen that has other than 2 toes on the front foot: AM R 26109 with a single clawed digit on each front foot. The specimen is one of nine from Crows Nest, Qld, and the other eight have 2 clawed toes on each front foot. There is also a single specimen with a claw on each styliform rear limb: AM R 47480 from the Warrumbungle Mountains, N.S.W.

A light nuchal collar — similar to that in *A. verreauxii* — occurs in many populations north of the granite belt in Queensland. The type of *Lygosoma leuckartii* and one of the types of *Lygosoma verreauxii biunguiculata* are specimens from such populations. The nuchal area is uniformly coloured in all southern populations (Fig.6). The species range is greatly constricted at the approximate demarcation point between these two groups (Fig.8).

**Habitat and habits.** To judge from both the general locality records and the many specific habitat observations for *A. leuckartii*, it appears as if the species is confined almost exclusively to sclerophyll forest and woodland.

Cryptozoic, generally found under surface cover, e.g. rocks and logs.

Respiration involves axillary expansion and contraction (Greer, pers. obs.).

The critical thermal maximum temperature as determined for one specimen was 35.8°C (Greer, 1980).

**Reproduction.** Oviparous (‘embryos removed from eggs’: AM R 15759 a-c). We have found four gravid females in collections; three have locality data and are from northeastern New South Wales. The females measure 107, 113, 129 and 134 mm and carry 3, 4, 4 and 4 ovarian (N = 1) or oviducal eggs (N = 3). The specimens with data were collected 25 Nov., 5 Dec. and 6 Dec., respectively.

**Taxonomic comments.** Species have been assigned to the synonymy of *Anomalopus leuckartii* primarily on the understanding that it is the only Australian species with a digital formula of 2/1. In the following accounts we comment specifically on digital formula and also on the nuchal collar which is variable within the species.

The two syntypes of *Brachymeles Leuckartii* Weinland, 1862, appear to have been destroyed during the World War II (W. Böhme in litt., 10 January and 6 February 1985). However, the type-description is fairly complete and specifically mentions two toes on the front foot and a styliform rear leg. It says nothing about a nuchal collar and hence implies a uniformly coloured nuchal area.

The type(s) of *Anomalopus lentiginosus* De Vis, 1888, are presumably lost (Covacevich, 1971) but the original description mentions a didactyl forelimb and a minute, undivided hindlimb. It also says ‘a trace of a pale band across the occipital conspicuous in the young.’ The type-locality of Brisbane is odd in that the species does not occur there (G. Czechura, in litt., 10 January 1985). We regard De Vis’ specimens as having erroneous locality data, but it is also possible that they were actually *A.
Anomalopus verreauxii with the digits of the forelimb miscounted or truly variable. *Anomalopus verreauxii* is common in the Brisbane area (Dale, 1973; Czechura & Miles, 1983).

Because Weinland's *A. leuckartii* had never once been used as the valid name for this taxon, whereas De Vis' *A. lentiginosus* has frequently been used in the literature, Cogger et al. (1983) regarded *Brachymeles Leuckartii* as a nomen oblitum and continued to use the long-accepted junior name *A. lentiginosus*, consistent with Article 23 (a–b) of the International Code of Zoological Nomenclature. However, it is clear that with the loss of the types of both species, it becomes important to fix the species long known as *A. lentiginosus* by designation of a neotype. However, as such a neotype could not be consistent with both the locality and the morphology of *A. lentiginosus*, as cited in the original description (see above), we prefer to resurrect the name *A. leuckartii* Weinland, 1862, for this species, and to designate as neotype AM R 44677. This specimen has two toes on the front foot and a styliform hind limb, a uniformly coloured nuchal area, 22 midbody scale rows, 113 paravertebrals, a snout-vent length of 99 mm and a tail length of 114 mm, of which 7 mm is regenerated.

One of us (H.G.C.) has examined the two syntypes of *Lygosoma verreauxii biunguiculata* Oudemans, 1894.

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**Fig. 7.** Skull of *Anomalopus leuckartii* (AM R 43949).
Morphological Trends and Species Relationships within the Subgenus *Anomalopus*.

Theoretically, one might expect that as the components of limbed locomotion declined in importance, the components of the potentially complementary trunk locomotion (lateral undulation) might increase. Indeed, there are preliminary results and statements in the literature to suggest that such is the case (Sewertzoff, 1931; Presch, 1975; Lande, 1979; Renous & Gasc, 1979). As the three species of the subgenus *Anomalopus* show different degrees of limb reduction, they provide an opportunity to test this relationship.

Within *Anomalopus*, limb reduction, whether it be measured by digit number, total number of limb bones, absolute length or relative length, forms the following transformation series: *A. mackayi* — *A. verreauxii* — *A. leuckartii*. However, segmentation and elongation of the trunk, the former measured by paravertebral scales and presacral vertebrae, and the latter by snout-vent length, form the series: *A. mackayi* — *A. leuckartii* — *A. verreauxii*. Hence the theoretical relationship between limb reduction and trunk elongation and segmentation does not seem to hold. Indeed, it would seem as if the functional significance of trunk segmentation probably has more to do with trunk elongation, i.e. size increase, than limb function. Trunk segmentation may be the method of increasing size, while maintaining the suppleness required for efficient lateral undulation. Size increase in *Anomalopus* may relate to ecology: to judge from general distribution, size increases from xeric (inland) to mesic (near coastal) habitats (Figs 3, 8).

The only clear correlation with limb loss in *Anomalopus* is midbody scale row increase. The functional significance of this relationship is obscure.

All the morphological trend data above can be interpreted to support the hypothesis of a close relationship between *A. verreauxii* and *A. leuckartii*.

### *Vermiseps* n. subgen.

**Type-species.** *Anomalopus (Vermiseps) swansoni* n. sp.

**Diagnosis.** Differs from the subgenus *Anomalopus* in the following combination of derived character states: nasals greatly enlarged; supraoculars 3 or fewer, only first in contact with frontal; supraciliaries 4 or fewer; postsupralabial single; tail bluntly rounded; ventral hues lacking.

Pre- and postfrontal bones in contact above orbit; limbs totally lacking.

**Etymology.** From *vermes* — worm, and *seps* — lizard. The name is meant to draw attention to the limbless, and hence ‘worm-like’, appearance.

**Species (4).** *A. brevicollis* n. sp.; *A. gowi* n. sp.; *A. pluto* Ingram, 1977 and *A. swansoni* n. sp.

**Distribution.** Eastern Australia, from Cape York Peninsula to central New South Wales (Fig. 12).
**Habitat and habits.** Low, closed forest (vine thicket) and open forest, woodland and open heath. When uncovered, these skinks almost invariably try to escape by 'swimming' into the substrate.

**Reproduction.** Oviparous (one species) and ovoviviparous (one species).

**Anomalopus swansoni** n. sp.

Figs 9–11

**Type-material.** **HOLOTYPE.** Australian Museum R 67162: Raymond Terrace area, N.S.W.; R. Wells and R. Cook; 2 December 1973; female.

**PARATYPES.** All localities are along the central coast of New South Wales. AM R 6961, 15183, 16433–34, 115676: locality unknown; R 3648: Pitt Town via Windsor; R 4820, 6078: Milson I., Hawkesbury R.; R 4915: Pokolbin; R 9277–8, 107551–53: Raymond Terrace; R 11558, 17921: Newcastle; R 12505, 30290: Merewether; R 13788: Tuggerah; R 13894: Jones Beach, Gosford; R 14355, 67163: Toukley; R 14885, 21040–41, 29962–63, 112413–15: Norah Head; R 15083: Broken Bay; R 21042–44: N.S.W. central coast; R 28552–53: Hamilton, Newcastle; R 32717: The Entrance; R 32718, 57121, 69198, 69204, 71324: Sandy Hollow; R 39009; Muogamarra Nature Reserve, near Berowra; R 49100, 52995: 29 km S of Singleton via Putty Road; R 54282: Waratah, near Newcastle; R 57120: Belmont; R 65236: near Sandy Hollow; R 76612–15: Myall Range; R 89120, 112024: Denman; R 89273–75: 8.1 km S of Bulga PO via Hwy 69; R 98693: Myall National Park; R 106102–04: ca 3 km E of Raymond Terrace; R 106639–40: Little Cattai Ck, 2.0 km N of Cattai. CAS 94471: near Catherine Hill Bay. QM J 44236: Sandy Hollow.

**Diagnosis.** Differs from all other *Anomalopus* in the following combination of characters: limbs totally lacking; supraciliary row complete; loreals 2.

**Description.** A medium-sized, limbless skink with predominantly light to dark dorsal ground colour but with slight aggregations of pigment in the centre of each dorsal scale giving a punctate or striped pattern.

Rostral trilobed with blunt, round medial lobe projecting partially or completely between nasals to level just posterior to nostril and 2 lateral lobes projecting to same level; frontonasal wider than long (1.6–2.3 x); prefrontals moderate in size, widely separated; frontal slightly wider than long (1.1–1.3 x) supraoculours usually 3, rarely 2, only first in contact with frontal; frontoparietals distinct, in contact, each shorter than interparietal; interparietal distinct with dark parietal eye evident at base of posterior lobe; parietals meet behind interparietal, each bordered posterolaterally by large, upper secondary temporal, nuchal and 2 scales intercalated between; nuchals undifferentiated (i.e., not enlarged).

Nasals greatly enlarged, usually narrowly separated but rarely in contact; nostril situated slightly below and well forward of centre; loreals 2, anterior larger; preoculars 2; supraoculars 4, in continuous series, first separated from frontal, third interdigitates between second and third supraoculours when these scales distinct; suboculars 4, large, in continuous series and interdigitating with supralabials; lower eyelid movable and scaly; pretemporals 2, first usually not contacted by frontoparietal (86.5%, N = 89) but occasionally so (13.5%); primary temporal single; secondary temporals 2, upper overlaps lower; external ear opening completely covered by scaly epidermis, its former position indicated by shallow vertical depression; supralabials 6, first by far largest, fourth smallest and generally situated below centre of eye, although occasionally suture between third and fourth supralabials subocular; postsupralabial single; infralabials 6, first 2 in contact with postmental; mental large, wider than long (1.4–1.5 x); postmental very much wider than long; 3 pairs of enlarged chin scales, first pair usually slightly separated by 1 scale, second pair well separated by 1 scale and third pair by 3 scales.

Body scales smooth, in 22–26 longitudinal rows at midbody; paravertebral scales same size as more lateral scales, 115–138 in a single row; inner preanals overlap outer, medial pair of preanals enlarged; medial row of subcaudals same size as more lateral rows.

Snout-vent length 44–107 mm; tail bluntly rounded 0.64–0.84 x SVL; limbs totally lacking.

**Colour.** In both life and preservative generally light-brown to dark, greyish brown above and immaculate below; dark pigment tends to concentrate in centres of dorsal scales thereby creating a very diffuse spotted or striped effect; tip of tail black (see Cogger, 1983, fig. 137 for colour photograph of live specimen).
PRETEMPORALS  POSTSUPRALABIALS

SUPRACILIARIES  PRETEMPORALS  POSTSUPRALABIALS

PREOCULARS

INFRAOCULARS

Fig. 10. Head of Anomalopus swansoni (AM R 11558) with certain head scales labelled.

Details of holotype. The holotype (AM R 67162) has 3 supraoculars, 26 midbody scale rows; 138 paravertebral scales; 56 presacral vertebrae, 42 postsacral vertebrae; SVL 96 mm and TL 76 mm (complete).

Distribution. Confined to an area bordered by the lower reaches of the Hunter River Valley in the north, and the northern half of the adjacent Hawkesbury River Valley in the south (Pitt Town and the Berowra area just north of the greater Sydney metropolitan area are the two southernmost known localities). Sandy Hollow, approximately 130 km from the coast in the upper Hunter River Valley, is the most inland locality (Fig. 12).

Etymology. Named for Stephen C. Swanson, photographer, natural historian and author.

Habitat and habits. Known only from fairly open forest on well-drained soils. Generally encountered under surface objects, e.g. rocks and logs, but occasionally found in rotting logs and stumps.

Reproduction. Ovoviparous. A 'no data' specimen prepared for clearing and staining (AM R 21042) contained two developing young (AM R 21043–44), and a specimen from Norah Head (AM R 112413) gave birth to two young (AM R 112414–15). The holotype (AM R 67162) contains three oviducal 'eggs' and AM R 106103 contains 3 enlarged ovarian eggs; these last two specimens measure 96 mm and 107 mm SVL and were collected on 2 Dec. and 4 Oct., respectively. Mean litter size for these four specimens is 2.5.

Anomalopus pluto Ingram

Figs 13–15

Anomalopus pluto Ingram, 1977: 52. Type-locality: McDonald Crossing, Cockatoo Ck, 115 km S of Bamaga, Cape York, Qld at 11°33'S, 142°27'E. Holotype: QM J 26261.

Material examined. In addition to the type, we have examined the following specimens. All localities are in northern Cape York Peninsula.

AM R 94360: McDonnell Ck area, 1 km E of the main N-S Peninsula Developmental Road, at 11°33'S, 142°27'E; R 94361-62, 94484-85, 112004: 15 km E of Heathlands Homestead via road to Captain Billy Beach, at 11°45'S, 142°41'E.

Diagnosis. This is the only species of Anomalopus, indeed the only species of Australian skink, in which the nasal extends ventrally to the upper lip (apparently through fusion with the first supralabial). It is also unique within Vermiseps in having the presubocular absent, the pretemporal single and the surangular fused (presumably) to the prearticular.

Description. In view of Ingram’s (1977) recent description and figure of A. pluto, we provide only a few additional comments on the species’ external morphology.

First, the most distinctive scale character of the species is the large nasal which extends ventrally to the lip. It seems virtually certain that this nasal is a complete scale resulting from the fusion of the nasal with the first supralabial. Indeed, there is a small inflection along the nasal’s suture with the anterior loreal that probably represents the posterior point of the old suture between the nasal and first supralabial. If such a fusion has occurred, it means that there are really 6 supralabials instead of 5 and that the one situated directly below the centre of the eye is the fourth and not the third.

Second, there seems to be little doubt that what Ingram calls the first supraciliary is really the prefrontal. The relationship of this scale with the surrounding scales leaves little room for any other conclusion, and it is a conclusion that Ingram granted as possible.

Third, Ingram (1977, fig. 1) figures the second loreal as entering the anterior corner of the eye. In reality, there is a more-or-less vertical suture separating the second loreal from a relatively large lower preocular. It is this preocular, not the second loreal, that enters the corner of the eye (Fig. 14).
Fourth, we see only 1 large posterior supraciliary, not 2 as seen and figured by Ingram. There are thus a total of 3 free supraciliaries; the first 2 are separated from the third by the second supraocular.

For additional character states in comparison with other species of the subgenus *Vermiseps* see Table 2.

**Distribution.** Northern Cape York Peninsula (Fig. 12).

**Habitat and habits.** The holotype of *A. pluto* was “uncovered under leaf litter in a small patch of monsoon forest” (Ingram, 1977). A second specimen (AM R 94360), found near the type-locality (1 km E), was under a piece of wood on the verge of the road bordering a “vine and scrub thicket”. Five other specimens (AM R 94361–62, 94484–85) were found in a very different habitat: low dense heath on white sand. These specimens were found beneath a lignotuber (N = 1) and pile of debris (N = 4) alongside a rough track. Also found in this pile of debris were *Nactus arnouxii*, *Stegonotus* sp. and *Unechis nigrostriata* (R. Sadlier, pers. comm.).

**Reproduction.** Nothing known.

**Anomalopus gowi n. sp.**

Figs 16–18

**Type-material.** **Holotype,** Queensland Museum J 42615 (formerly AM R 63128): SW side of ‘Forty Mile Scrub’, approximately 1.8–2.9 km NNE of Gulf Hwy via Kennedy Hwy; 18°07’S, 144°49’E; A.E. Greer; 19 June 1977.

**Paratypes.** All localities are in Queensland. AM R 32719: Minnamoolka Station, Mt Garnet; R 62465–62466, 63125–63127, 63129–30: SW side of ‘Forty Mile Scrub’ (approx. 1.8–2.9 km NNE of Gulf Hwy via Kennedy Hwy); R 113837: approx. 19.2 km E of Kennedy Hwy via Gulf Hwy; R 113885–89, 115248–50: approx. 7.3 km E of Woodstock PO.

**BMNH AMF 35365:** SW side of ‘Forty Mile Scrub’; AMF 35474–79: same data as AM R 113885–89. (BMNH numbers refer to field tags.)

**QM J 27617:** Hervey Range, 10 km S and 35 km W of
Fig. 12. Distribution of the four species in the subgenus *Vermiseps* of the genus *Anomalopus*: *A. brevicollis* (open triangles), *A. gowi* (closed triangles), *A. pluto* (open circles), and *A. swansoni* (closed circles).

**Diagnosis.** Differs from all other species of *Anomalopus* in the following combination of characters: limbs totally lacking, nasals in broad contact, and supraoculars 2.

**Description.** A medium-sized, limbless skink of predominantly light-tan to sandy ground colour but with the head and end of tail very dark-brown, and dark spots running through the centres of each longitudinal scale row.

Rostral trilobed with an acutely angular medial lobe projecting between nasals (which are in broad contact) to level just posterior to nostrils, and labial lobes projecting to midlength level of nasals; frontonasal much wider than long (approximately 2 x); prefrontals small, wider than long and widely separated; frontal slightly wider than long (1.2–1.3 x); supraoculars 2, first contacts frontal; frontoparietals distinct, in contact or separated; interparietal distinct, slightly larger in area than either frontoparietal and with light parietal eye spot situated centrally; parietals in short contact behind interparietal, each bordered posterolaterally by upper secondary temporal, anteriormost transversely enlarged nuchal and often a smaller scale intercalated between the two; transversely enlarged nuchals 1–4.

Nasals greatly enlarged, in medial contact for approximately one-third their entire maximum length and with nostrils situated well forward; loreal single, deeper than long; preoculars 2, lower much the larger; supraciliaries usually 3 + 1 (rarely 2 + 1), first 3 or 2 separated from last by second, or second and third, supraoculare which project laterally into supraciliary row; postoculars 2; suboculars 3, first and third largest; lower eyelid scaly; pretemporals 2, first contacted by frontoparietal; primary temporal single; upper secondary temporals 2, upper equal in size to primary and slightly larger than lower secondary; external ear opening completely covered by scaly dermis, its former position indicated by slight bulge; supralabials usually 5, rarely 6 with usually third, rarely fourth subocular; mental almost as wide or as wide as long (0.9–1.0 x); postmental much wider than long, in contact with first two infralabials; first pair of chin scales separated.

Body scales smooth, in 18–20 longitudinal rows at midbody; paravertebrals not transversely enlarged, 105–117 in a single row; inner preanals overlap outer, medial pair enlarged; subcaudals of medial and immediately adjacent rows equal in size.

Snout-vent length 49–108 mm; tail bluntly rounded, 0.75–0.94 x SVL; limbs totally lacking.

Premaxillary teeth 4–5 (x = 4.7, N = 15); presacral vertebrae 53–57; post sacral vertebrae 48–52.

**Colour.** The ground colour of the dorsal part of the body and most of the tail is light-tan to pale-straw; the venter of the body is light-gray. The head and end of tail are dark-brown. Between these dark extremities extend longitudinal rows of dark-brown spots, one per scale; these spots are largest on the tail and smallest on the venter. The regenerated tip of the tail has a ‘dipped in ink’ appearance.

In life, the iris is dark-brown and virtually indistinguishable from the pupil, and the venter has a pink suffusion due to the blood showing through the translucent scales.
Fig. 13. *Anomalopus pluto* from 15 km E of Heathlands Settlement on Captain Billy Creek Rd, Qld.

Fig. 14. Head of *Anomalopus pluto* (AM R 94362).

Fig. 15. Skull of *Anomalopus pluto* (AM R 94362).
Fig. 16. *Anomalopus gowi* from Forty Mile Scrub, Qld. Photo: H.G. Cogger.

Fig. 17. Head of *Anomalopus gowi* (AM R 63128).

Fig. 18. Skull of *Anomalopus gowi* (AM R 63130).
Details of holotype. The holotype (QM J 42615) has a single pair of transversely enlarged nuchal scales, 4 premaxillary teeth and 57 presacular vertebrae; SVL 91 mm, TL 71 mm.

Distribution. Known only from two general areas: the vicinity between Mt Garnet and Mt Surprise and the vicinity just west and south of Townsville. Probably widespread in the drier inland area between Mt Garnet and Townsville.

Intrapopulation variation. The 15 specimens collected randomly, on the same date, at the locality just east of Woodstock, provide insight into intrapopulation variation. There are 5 males and 10 females; a sex ratio not significantly different ($\chi^2 = 0.86, NS$) from 1:1. Females may attain larger size than males, as the largest female measures 108 mm SVL and the largest male 103 mm. Compared to males, females have more paravertebral scales (111–117, $\overline{X} = 113.9, SD = 2.56$ vs 106–114, $\overline{X} = 109.6, SD = 2.97; t = 5.06*** and more presacular vertebrae (54–56, $\overline{X} = 54.6, SD = 0.70$ vs 52–53, $\overline{X} = 52.8, SD = 0.45; t = 5.13***). Both trends are not uncommon in attenuate lygosomines.

Interpopulation variation. Animals from the southern end of the range appear to be larger than those from the north, and to have fewer postascral vertebrae. The largest specimen of the ten known from ‘Forty Mile Scrub’ in the north measures only 90 mm SVL, whereas the largest of 15 known from Woodstock in the south measure 108 mm SVL and all but two are larger than 90 mm. The four Woodstock specimens with complete tails (1♂, 3♀♀♀) have 46–48 postascals whereas the six ‘Forty Mile Scrub’ specimens with complete tails (2♀♀♀, 4 indeterminate) have 49–52 postascals. Inability to determine sex in most of the ‘Forty Mile Scrub’ animals precludes a comparison of presacular vertebrae (which, because of the sexual dimorphism demonstrated above, must be made within sexes). No other differences between northern and southern populations are evident in the data.

Comparison with similar species. In lacking limbs and having the enlarged nasals in broad contact, a single loreal, 18–20 midbody scale rows, 1–4 transversely enlarged nuchal and a longitudinally spotted pattern, *Anomalopus gowi* is similar to *A. brevicollis*. It differs from this species, however, in being larger (max. SVL = 108 mm vs 83 mm) and in having 2 supraoculars instead of 3; frontoparietals usually (89 %) separate instead of always in contact; 5 supralabials instead of 6; 4 infralabials instead of 5; more paravertebrals (105–116 vs 87–104) and a lighter ground colour (see also Table 2).

Etymology. The species is named after Graeme F. Gow.

Habitat and habits. The species has been found in both sclerophyll woodland (several localities) and evergreen vine forest (‘Forty Mile Scrub’).

It is almost always found by turning ground cover such as rocks, logs and debris. At ‘Forty Mile Scrub’ it occurs primarily inside the forest under basalt rocks. At this locality it is much less common than a slightly smaller but similarly attenuate and small-limbed *Sphenomorphus* n. sp. (Greer, in press).

Reproduction. The specimens collected on 30 September 1984 from just east of Woodstock provide some insight into reproduction. Seven of the ten females in the sample of 15 are gravid. These specimens measure 99–108 mm SVL ($\overline{X} = 101.9$ mm) and contain 1–3 ($\overline{X} = 2.1$) enlarged ovarian (N = 1) or thinly shelled oviducal eggs (N = 6); of the non-gravid specimens, two, measuring 71 and 78 mm SVL, are clearly immature and the third, measuring 103 mm, is spent with two corporea lutea in the left ovary. There was no correlation between female SVL and clutch size ($r = -0.57$ NS). The shells surrounding the oviducal eggs indicate that the species is oviparous.

*Anomalopus brevicollis* n. sp.

Figs 19–21

Type-material. HOLOTYPE. Queensland Museum J 42616 (formerly AM R 96212): 1.0 km E of Frenchville Road via Pilbeam Drive (main road to summit of Mt Archer), Rockhampton, QLD; 23°21’S, 150°34’E; A.E. Greer; 21 August 1976.

PARATYPES. All localities are in Queensland.

AM R 13820: 32 km W of Capella; R 89277, 96200–96208, 113374–90: same locality data (different date) as holotype; R 96209–96211, 96213: same data as holotype; R 113364, 113392–95: 16.1 km N of Fitzroy R. at Rockhampton via Bruce Hwy; R 113501–04, 113790, 115245–47: 0.3 km from E end of Frenchville Rd via dirt track, Rockhampton. ANWC 4506: Rockhampton.

BMNH AMF 35183–88: same locality data as holotype; AMF 35191–94: same data as AM R 113364 and 113392–95; AMF 35330–31, 35363, 35411: same data as AM R 113501–04, 113790 (BMNH numbers refer to field tags).

CAS 77118–77120: 32 km W of Capella.

MCZ 141079: The Diggings Rd, 6.4 km S and 1.6 km W of Eungella.

QM J 4561: Castle Ck, Dawson Valley; J 33863: ‘Honeymare’ (21°24’S, 148°33’E); J 33870: bank of Oakey Ck, ‘Honeymare’; J 34056: Finch Hatton National Park in 21°24’S, 148°38’E; J 38740: Mimosa Creek, Blackdown Tableland; J 41997–41998: Cracow; J 42454: 0.3 km ENE of Old Corry Rd turnoff, via Retro.

QNPWS N 58056: Blackdown Tableland.

Diagnosis. Differs from all other species of *Anomalopus* in the following combination of characters: limbs totally lacking, nasals in broad contact, and paravertebral scales 84–102. It is also unique among *Anomalopus* in having the first sternal rib arising from the eighth presacular vertebra instead of the ninth, and unique in *Vermiseps* in having the frontal and maxilla bones in contact (thereby separating the prefrontal and nasal).

Description. A medium-sized, limbless skink of predominantly light-brown ground colour but with slightly darker head and tail and dark-brown spots running through the centers of all but the midventral scale rows.
Rostral trilobed with an angular medial lobe projecting slightly between nasals (which are in broad medial contact) to approximately level with nostrils, and labial lobes projecting to midlength level of nasals; frontonasal wider than long (2.0–2.5 x); prefrontals absent; frontal wider than long (1.2–1.7 x), slightly shorter than midline length of frontoparietals and interparietals; supraoculars usually 3, rarely 2, only first contacts frontal; frontoparietals paired, usually in contact, rarely separated, each approximately equal in size to interparietal; interparietal distinct, with light parietal eye spot slightly posterior of centre; parietals in short contact behind interparietal; each parietal bordered posterolaterally by upper secondary temporal, anteriormost transversely enlarged nuchal and often a smaller scale intercalated between the two; transversely enlarged nuchals 1-4.

Nasals greatly enlarged, in broad medial contact, with nostril situated well anteriorly; loreal single, deeper than long; preoculars 2, lower much larger than upper; supraciliaries 3+1 or 2+1, first 3 or 2 separated from last by second and third, or third only, supraoculars which project laterally into supraciliary row; preoculars 2; lower eyelid scales extend into subocular row but suboculars proper absent; postocular single; lower eyelid scaly; pretemporals 2, first contacted by frontoparietal; primary temporal single; secondary temporals 2, upper either similar in size to lower or about twice its size; external ear opening absent, its former position indicated by a shallow vertical crease; supralabials 6, first largest, third or suture between third and fourth below centre of eye; postsupralabial single; infralabials 5, usually first two (rarely first only) in contact with postmental on each side; mental very large, wider than long (1.2–1.3 x); postmental much wider than long, in contact with first two (93%) or first only (7%); 3 pairs of enlarged chin scales, first pair separated by 1 scale row, second pair by 1 row and third pair by 3 rows.

Body scales smooth, in 18–20 longitudinal rows at midbody; paravertebral scales not transversely enlarged, 84–102 in a single row; inner preanals overlap outer, median pair enlarged; subcaudals of medial and adjacent rows equal in size.

Snout-vent length 39–83 mm; tail bluntly rounded, 0.86–1.17 x SVL; limbs totally lacking.

Premaxillary teeth 5–6 (N = 6); presacral vertebrae 46–49; postsacral vertebrae 48–52; cervical vertebrae 8 (instead of the more usual and primitive 9).

Colour. In preservative, the dorsal ground colour is dark, greyish brown on the head, fawn to medium-brown on the body, and medium brown becoming darker posteriorly on the tail (the tip is nearly uniform black). Pigment tends to be concentrated at the base of individual scales giving a uniform, slightly linear, pattern of spots to the top and sides of the body and base of the tail. This spotting extends onto the chin, throat, lateral edges of the venter and underside of the tail (where it becomes increasingly dense posteriorly) but the midventral area is generally unspotted or with only a few randomly scattered spots.
In life, the iris is as dark as the pupil and the venter light-grey or off-white with a pink suffusion due to the blood showing through the translucent scales.

**Details of holotype.** The holotype (QM J 42616) has 2 infralabials in contact with the postmental; 18 midbody scale rows; 3 pairs of transversely enlarged nuchals; 88 paravertebral scales; 47 pre- and 48 postsacral vertebrae; SVL 72 mm and TL 73 mm.

**Distribution.** Known from widely scattered localities in the area bounded roughly by Finch Hatton in the north, Clermont in the west and Theodore in the south, i.e. basically the northern half of the Mackenzie-Dawson drainage basin.

**Comparison with similar species.** For a comparison with the very similar *Anomalopus gowi* see this section under that species and also Table 2.
Fig. 21. Skull of *Anomalopus brevicollis* (QM J 33863).

**Etymology.** The name *brevicollis* derives from the Latin for ‘short neck’ and calls attention to reduced number of cervical vertebrae (8 instead of 9).

**Habitat.** *Anomalopus brevicollis* has been found in a variety of habitats ranging from dry sclerophyll forest through monsoon rainforest to permanently moist rainforest. The specimen collected by Mr Graeme Gow near Mt Garnet (AM R 32719) was ‘in open sclerophyll forest’, and on the basis of general vegetation distribution, it seems likely that the specimens from both Castle Creek (QM J 4561) and 32 km W of Capella (AM R 13820) were from some kind of dry forest or woodland habitat.

The species has been collected at two sites in the Australian Museum and Queensland Museum’s joint faunal survey of eastern Australian rainforests. At the Homevale site (number 10) it was found in seasonally dry, semi-evergreen vine thicket and at the Finch Hatton site (number 9) it was in moist, complex notophyll vine forest (Anonymous, 1976; Broadbent & Clark, 1976). The three localities around Rockhampton are associated with closed forests of various kinds. One is in fairly tall, dense forest in a rocky south-facing gully at the base of Mt Archer; another is in a short, dense forest (vine thicket) on a limestone hill (this type of habitat is very common in The Caves area, north of Rockhampton), and the third (the type-locality) is in a depauperate forest on an eroded limestone reef in a northwest-facing gully on the lower slopes of Mt Archer. In all cases the closed forests stood out starkly against the surrounding dry sclerophyl woodlands. In all three habitats the animals were generally found in association with pockets of friable soil.

**Habits.** The critical thermal maximum temperature of five specimens ranged from 35.2 – 37.0°C ($\bar{x} = 35.8$, SD = 0.65) (Greer, 1980 as *Anomalopus* sp.1)

**Reproduction.** The only known gravid specimens are five from the Rockhampton area (AM R 96203–04, 96210, 113389, 114084) collected in the period 21 Aug.–27 Sept. in various years. They measure 72–81 mm SVL ($\bar{x} = 76.4$) and contain 1–2 ($\bar{x} = 1.8$) ovarian eggs.

**Morphological Trends within the Subgenus *Vermiseps.***

Three components of trunk segmentation have been assessed for the four species of *Vermiseps*: paravertebral scales, presacral vertebrae and complete inscriptive chevrons. These, plus relative tail length, increase in the series: *A. brevicollis* → *A. gowi* → *A. swansoni* → *A. pluto*. In contrast to *Anomalopus*, the trend in trunk segmentation does not follow size, as snout-vent length increases in the series *A. pluto* → *A. brevicollis* → *A. swansoni* → *A. gowi*.

**Species Relationships within the Subgenus *Vermiseps.***

The phylogenetic relationships of the four species of *Vermiseps* have been inferred from a cladistic analysis of 15 characters (Table 3), the polarity of the character states having been determined with reference to the more generally primitive subgenus *Anomalopus*. The results of this analysis are presented in Figure 22.

### Genus *Ophioscincus* Peters

*Ophioscincus* Peters, 1873: 746. Type-species: *Ophioscincus australis* Peters, 1873 (= *Lygosoma ophioscincus* Bouleneger, 1887), by monotypy.

*Coloscincus* Peters, 1876: 532. Type-species: *Coloscincus truncatus* Peters, 1876, by monotypy.

**Diagnosis.** *Ophioscincus* differs from all other members of the *Sphenomorphus* group in Australia in the following combination of derived character states: nasals slightly enlarged; prefrontals separate; supraoculars 3, only first in contact with frontal; first supraciliary contacts frontal; supralabials 5, third subocular; external ear opening absent, its former position indicated by oblique crease; postsupralabial single; infralabials 5; tail $\leq 0.95$ x SVL. Pre- and postfrontal bones in contact above orbit; postorbital absent; orbitosphenoid well ossified; quadratal conch reduced to small flange; palatal rami of pterygoids with slight to deep recurved processes;
crows of teeth squared off with distinct apical groove and rotated slightly postero-medially.

Presacral vertebrae ≥ 43; post-sacral vertebrae ≤ 42; sternum with two attached ribs (from 9th and 10th vertebrae); mesosternum with one rib; complete inscriptive chevrons ≥ 11; front limb lacks all elements distal to single proximal carpal; rear limb lacks all elements distal to single proximal tarsal; ischia form acute angle at symphysis with shafts paralleling those of pubes.

Parietal peritoneum lacks pigment.

Although the list of derived character states for this genus is long, the only distinctly non-burrowing feature is the peculiar shape of the tooth crowns.

**Species (3).** *Ophioscincus cooloolensis* n. sp.; *O. ophioscincus* (Boulenger, 1887); *O. truncatus* (Peters, 1876).

**Distribution.** Coastal and near coastal areas of southeastern Queensland and northeastern New South Wales (Fig. 26).

**Habitat and Habits.** Closed forest (all species) and wallum (*O. cooloolensis* and *O. truncatus*). Cryptozoic; generally found under surface cover.

**Reproduction.** Oviparous (two species).

**Relationships.** All but one of the derived character states of *Ophioscincus* can be interpreted as a burrowing modification and the one exception — the peculiar shape and orientation of the tooth crowns — occurs in no other member of the *Sphenomorphus* group. On the basis of this observation, all that can be said is that the possible relationships are very broad indeed and range from a relatively primitive member of the *Sphenomorphus* group (discounting burrowing related features) to a highly modified burrower (accepting these features at face value).

With regard to the latter possibility, it is significant that the genus *Isopachs* (three species) from southeast Asia shows all the derived character states of *Ophioscincus*, or their obvious further modification, except for the tooth morphology. Hence, the diagnosis above for *Ophioscincus*, less the tooth morphology, could serve equally well to diagnose an *Ophioscincus–Isopachys* group, the generic name for which would be *Ophioscincus*. This is precisely the suggestion made by Smith (1935) when the only Australian species known was *O. australis* (= *ophioscincus*), but this idea was never widely accepted (Heyer, 1972; Greer, 1977; Cogger, 1983, but see Mittleman, 1952).

Does this proposal have validity? This depends, of course, on the significance of characters that may be convergent within burrowers. In this case the list of shared ‘burrowing features’ is particularly long, and hence the possibility of close relationship should be considered seriously. On the other hand, given enough trials with burrowing, and there have been many in skinks, a few are likely to show remarkable similarity. The dilemma remains unresolved. The ‘solution’ offered here is to keep the two genera distinct. This is the conservative taxonomic position, which seems appropriate in the face of uncertainty, and it is the one that accords well with our strong suspicions about the degree of convergence amongst burrowing skinks.

**Key to Species of Ophioscincus**

1. Limbs present

   —— Limbs absent

2. Prefrontals present; loreals 2; midbody scale rows 20–24

   —— Prefrontals absent; loreal single; midbody scale rows 18–19

**Ophioscincus truncatus** (Peters)

Figs 23–25

*Coloscinus truncatus* Peters, 1876: 532, fig. 1. Type-locality: Pea I., Moreton Bay, Qld. Holotype: ZMB 8932.


**Material examined.** AM (all specimens from N.S.W. unless designated otherwise): R 6376, 115677: locality unknown; R 16872: Wai Wai State Forest, Macksville; R 18587: Wilson’s Peak, Qld; R 19022–4: Victoria Park via Ballina; R 35187: Five Day Ck near Comara; R 44774–96, 89270: Red Scrub Flora Reserve, Whian Whian State Forest; R 44774: Brindle Ck, Wiangaree State Forest; R 44797–805: 18 km NE Wiangaree via Wiangaree State Forest Rd; R 60767: Dorrigo; R 61169–71, 71434: Brinerville area; R 96445: Mt Warning; 5 unregistered specimens: 5.1 km SE of Maleny, Qld.

MV D 1285: Qld.

QM (all specimens from Qld unless designated otherwise): J 2221: P.J. War Signal Station, Moreton I.; J 5202–4; National Park (= Lamington National Park); J 6898: Maleny; J 14143, 14148–9: no locality data; J 16872: on track to Blue Lagoon, Moreton I.; J 16873–4: near The Hut, Ocean Beach, Moreton I.; J 21942: Mary Cairncross Park via Maleny; J 21983: Point Lookout, Stradbroke I.; J 22275: Moreton I.;
Fig. 23. *Ophioscincus truncatus* from approximately 5.1 km SSE of Maleny, Qld.

**Fig. 24.** Head of *Ophioscincus truncatus* (QM J 5203) with certain head scales labelled.


**Diagnosis.** Differs from all other *Ophioscincus* in each of the following character states: limbs visible externally, sacral diapophyses fused and ischia joined medially.

**Description.** Peters (1876) gave a good description and figure of *O. truncatus* in his original description and even compared it with what we recognize here as one of the species’ congers, *O. australis* (= *ophioscincus*). Copland (1952) gave his usual detailed account of the species, accompanied by a figure and photograph, when he sought to distinguish the Mt Wilson population (*O. monswilsonensis*) from the Moreton Bay populations. In light of these previous accounts and accompanying figures, we forgo a redescription of the species. For a tabular comparison between this and the other two species in the genus see Table 4.

**Distribution.** *Ophioscincus truncatus* is known to range from the area around Maleny in southeastern Queensland, south to Way Way State Forest just south of Macksville in northeastern New South Wales. The most inland locality is Mt Wilson on the Queensland–New South Wales border, approximately 100 km from the coast. The species is also known from Peel, Moreton and North Stradbroke Islands in Moreton Bay (Fig. 26).

**Habitat.** *Ophioscincus truncatus* occurs in two remarkably different habitats: rainforest and wallum (Covacevich & Ingram, 1977). Most of the mainland records are associated with rainforest while the Moreton Bay island and a few of the coastal records, e.g. Coolum, are from wallum — a dry heath and sclerophyll formation especially well developed on sandy soils. The species is notably rare or absent in ‘intermediate’ dry
sclerophyll habitats on the mainland; it is here that *O. ophioscincus* appears to be widespread.

**Reproduction.** The species is probably oviparous to judge from the shelled oviducal eggs in the only two gravid females discovered (QM J 5202–5203). These two females measured 79 and 77 mm SVL and contained three and two eggs respectively. Both specimens were from Lamington National Park, Qld; no date of collection is available.

**Intrapopulation variation.** Twenty-one of the 25 specimens collected at random from one locality in Whian Whian State Forest, New South Wales on 21 April 1976 are large enough to be sexed reliably. They show that females (N = 15) compared to males (N = 6) have more paravertebral scales (85–95, \( \bar{x} = 88.8 \), SD = 3.54 vs 79–86, \( \bar{x} = 82.9 \), SD = 2.47; \( t = 3.71^{**} \)) and more presacral vertebrae (47–50, \( \bar{x} = 48.0 \), SD = 1.10 vs 45–47, \( \bar{x} = 46.5 \), SD = 0.64; \( t = 3.26^{**} \)).

**Ophioscincus cooloolensis** n. sp.

*Type-material.* **HOLOTYPE.** Queensland Museum J 31573: National Parks Headquarters on 'A' road, Fraser I., Qld; G.B. Monteith; 13 Oct. 1978.

**PARATYPES.** All localities are in Queensland.

AM R 64071: Tallow Wood Hill, Fraser I.; R 89276: approx 4.8 km SW Rainbow Beach PO via Gympie Rd, then 3.9 km SE via Forestry Rd.

ANWC 2541: Happy Valley, E shore of Fraser I.
QM J 27381–5: Cooloola National Park via Gympie; J 31574: same data as holotype; J 31578: Poona Lake, Cooloola; J 40092: Kroombit Creek, Kroombit Tops; J 40223: Poona Lake, Cooloola National Park; J 40224: 8 km along Freshwater Rd (from Rainbow Beach end), Cooloola State Forest; J 40225: Poona Scrub (Seary's Scrub), Cooloola; J 40226: Inskip Point (near Rainbow Beach township).
Fig. 27. *Ophioscincus cooloolensis* from Cooloola State Forest, Qld. Photo: A.E. Greer.

**Diagnosis.** Differs from all other *Ophioscincus* in the following two characters states, both of which are unique: prefrontals absent and presacral vertebrae ≪ 44.

**Description.** Snout bluntly rounded; rostral trilobed with broad, rounded medial lobe projecting between nasals to contact frontonasal broadly, and 2 relatively narrow labial lobes, each projecting posteriorly below nasal; frontonasal wider than long (1.6–1.9 x), wider than frontal; prefrontal absent; frontal wider than long (1.2–1.4 x) and considerably shorter than midline length of frontoparietals and interparietal; supraoculars 3 or 2, only first in contact with frontal; frontoparietals distinct, in contact; interparietal distinct, larger than each frontoparietal; parietal eye spot located just posterior of centre in frontoparietal; parietals meet behind interparietal, each bordered posterolaterally by first transversely enlarged nuchal and upper secondary temporal; transversely enlarged nuchals 2–5.

Nasals moderately large, separated medially, with nostril well forward and slightly ventral of centre; loreal one; preoculars 2, lower much larger and in contact with first supralabial; subocular row narrowed or interrupted below centre of eye, presuboculars 1–2, postsuboculars 2; postoculars 2, lower much the larger; supraciliaries 3, anterior 2 separated from posterior one by second and third supraoculars; lower eyelid moveable, scaly; pretemporals 2, lower larger; primary temporal single; secondary temporals 2, upper much larger than lower, and lower only slightly smaller than primary; external ear opening absent, its former position indicated by a slightly forward-dipping vertical crease; supralabials 5, third situated below centre of eye and bordering scales of lower eyelid; postsupralabial single; infralabials 4; mental wider than long (1.6–1.7 x); postmental much wider than long (2.3–2.7 x) usually in contact with first two infralabials (92%), occasionally only first (8%). 3 pairs of enlarged chin scales, first pair in medial contact or just separated, second pair separated by single scale row and third pair by 3 rows.

Scales smooth, in 18–19 longitudinal rows at midbody; paravertebral scales 77–83, only slightly larger than those in more lateral rows; inner preanals overlap outer, medial pair appreciably larger than surrounding scales; median row of subcaudals slightly larger than more lateral rows.

Snout-vent length 54–69 mm; limbs absent, tail 0.77–0.93 x SVL, tip rounded.

**Colour.** In preservative, dorsum light-tan to light-brown with scattered dark-brown motting on head and dark-brown spots (one per scale) running longitudinally...
Fig. 28. Head of *Ophioscincus cooloolensis* (QM J 31573).
on body and tail; sides with well defined, dark-brown stripe which forms a dense mottling on head and neck but a solid band over body and tail; ventral light-tan to off-white except for some dark mottling on chin and throat (which is continuous with mottling of anterior part of lateral stripe), and some solid dark colour on posterior part of tail (which is continuous with colour of posterior part of lateral stripe).

In life, one specimen (AM R 89276) was noted to have had the venter of the body (from about the pectoral area back) and tail papaya orange in colour (Greer, pers. obs.).

Details of holotype. The holotype (QM J 31573) has 2 supraoculars on the left side and 3 on the right, 2 infralabials in contact with the postmental on each side, first pair of chin scales in medial contact, 3 pairs of transversely enlarged nuchals, 18 midbody scale rows, 80 paravertebral scales, 43 presacral vertebrae, SVL 62 mm and tail regenerated.

Etymology. Named after the Cooloolo area of Queensland where the species is best known.

Distribution. Known only from the coastal localities of Fraser Island and the adjacent mainland just to the south (Cooloolo), and from the inland locality of Kroombit Tops in southeastern Queensland (Fig. 26).

Habitats and habits. Generally found under cover in rainforest growing on white coastal sands; also in wallum (G. Czechura; pers. comm.). 'Swims' into the substrate when uncovered.

Reproduction. A single gravid female (QM J 40902) collected on 20 January contains three enlarged ovarian eggs.

Comment. Some specimens of Ophioscincus truncatus have the posterior loreal truncated ventrally by the anterior loreal and lower preocular. This may be an indication of the reduction process that led to the single loreal in O. cooloolensis.

Ophioscincus ophioscincus Boulenger
Figs 30–32

Ophioscincus australis Peters, 1873: 747, fig. on page 746. Type-locality: Port Bowen (= Port Clinton), Queensland. Holotype: ZMB 8046.

Lygosoma ophioscincus Boulenger, 1887: 343. Replacement name for Ophioscincus australis Peters, preoccupied in Lygosoma.

Material examined. All localities are in Queensland. AM R 47522, 47524, 47642−3, 47675, 47678, 57781, 60408, 96214−23: Bulburin State Forest.
MEG 27914: Port Bowen.

Diagnosis. Differs from all other Ophioscincus in the following character states, each of which is unique within the genus: supraciliary scale row complete; paravertebral scales ≥ 90; premaxillary teeth 7–8; jugal short and well separated from postfrontal; parietal eye and foramen absent; supratemporal fenestra completely obliterated by close apposition of supratemporal arch (postfrontal and squamosal) to parietal; orbitosphenoid strongly ossified; maxilla enters infraorbital vacuity only narrowly, due to apposition of palatine and ectopterygoid; medial ends of clavicle narrow, and pelvic girdle reduced to widely separated puboischial rods. Only the first of these character states is primitive within the genus.

Description. Although Peter’s (1873) original description of the species was accurate and accompanied by a good illustration, an expanded description will allow a more complete comparison with the species’ close relatives.
Snout bluntly rounded; rostral trilobed with broad, rounded rostral lobe projecting between nasals to contact frontonasal broadly, and 2 relatively narrow, angular labial lobes each projecting posteriorly below nasal; frontonasal wider than long (1.5–2.0 x), narrower than frontal; prefrontals well developed but widely separated; frontal wider than long (1.4–1.8 x) and slightly shorter than midline length of frontoparietals and interparietal; supraoculars 3 or 2, only first in contact with frontal; frontoparietals paired, in contact; interparietal distinct, slightly larger than each frontoparietal; parietal eye absent; parietals meet behind interparietal, each bordered posterolaterally by transversely enlarged nuchal and upper secondary temporal; transversely enlarged nuchals 0–4.

Nasals moderately large and separated, nostril situated well forward and slightly ventral of centre; loreals 2, first deeper than second; preoculars 2, lower larger; subocular row narrowed or interrupted below eye, presubocular 1, postsuboculars 2; supraciliaries 4, in continuous series, third and fourth projecting medially to varying degrees; lower eyelid moveable, scaly; pretemporals 2; primary temporal single; secondary temporals 2, upper much larger than and overlapping lower, which is about equal in size to primary; external ear opening absent, its former position indicated by vertical crease; supralabials 5, third situated below centre of eye and bordering scales of lower eyelid; postsupralabial single; infralabials 4; mental wider than long (1.7–2.1 x); postmental much wider than long (2.1–3.1 x), usually in contact with first infralabial only (98%), rarely with first two (2%); 3 pairs of enlarged chin scales, first and second pairs separated by single scale row, third pair by 3 scale rows.

Body scales smooth, in 20–24 longitudinal rows at midbody; paravertebral scales 94–113, only slightly wider than those in more lateral rows; inner preanals overlap outer, medial pair appreciably larger than surrounding scales; median row of subcaudals slightly larger than more lateral rows.

Snout-vent length 39–97 mm; limbs absent; tail 0.59–0.88 x SVL, tip bluntly rounded.

Colour. In preservative, dorsum is light to medium tan with scattered darker brown mottling on head and dark brown spots (one per scale) forming longitudinal lines on body and tail; sides with well defined, dark-brown stripe which begins as dense mottling on the head and neck but quickly coalesces to extend the length of the body and tail; venter light-tan to off-white except for dark mottling on chin and throat which is continuous with anterior part of lateral stripe, and dark-brown colour on posterior four-fifths of the tail which is continuous with solid, dark colour of posterior part of lateral stripe.

In life, small individuals (SVL = 37–46 mm, N = 4) were noted to have the light ventral areas pale-yellow, and large individuals (SVL = 57–89 mm, N = 5) orangish yellow (Greer pers. obs., on Bulburin State Forest specimens).

Distribution. Ophioscincus ophioscincus is known only from southeast Queensland in an area from Bulburin State Forest in the Many Peaks Range, south
Fig. 31. Head of Ophioscincus ophioscincus (QM J 13514).

Fig. 32. Skull of Ophioscincus ophioscincus (AM R 47642).

to the lower reaches of the Brisbane River Valley. The species has not been found on any of the offshore islands of southeast Queensland (Fig. 26).

Peters’ type-locality of Port Bowen, situated approximately 100 km NNE of Rockhampton at 22°29’S, 150°43’30”E (Wells, 1848), is approximately 230 km NNW of the nearest modern and well established locality at Bulburin State Forest. Because of this ‘disjunction’ and an even more egregious one for another Peters’ Port Bowen type (Lygosoma scutirostrum; see Greer, 1983: 42–44), the locality is taken to be in error.

The species ranges in altitude from near sea level to approximately 610 m at Bulburin State Forest.

Habitat. Rainforest, both within the forest and in clearings (pers. obs.).

Reproduction. We have found four gravid females in collections. All have shelled oviducal eggs indicating the species is oviparous. One female (QM J 7338) collected from the Brisbane area measured 68 mm SVL and contained three eggs; three others (QM J 30607, 31613–14) collected from Ravensbourne on 7–8 January 1978, measured 93, 97 and 97 mm SVL and contained 2, 3 and 2 eggs, respectively.

Morphological Trends within the Genus Ophioscincus.

Three measures of trunk segmentation have been assessed in the three species of Ophioscincus: paravertebral scales, presacral vertebrae, and complete inscriptive chevrons. All three, plus midbody scale rows, increase in the series O. coolooolensis → O. truncatus → O. ophioscincus. This series also follows an increase in snout-vent length but places the one limbed form between the two limbless (externally) forms. Thus, as in the case with Anomalopus, trunk segmentation seems to be more closely related functionally to size increase than to limb loss.

Species Relationships within the Genus Ophioscincus.

The phylogenetic relationships of the three species of Ophioscincus have been inferred from a cladistic analysis of eight characters (Table 5), the polarity of the character states being determined with reference to the character state in a generalized member of the
Sphenomorphus group. On the basis of this analysis O. cooloolensis and O. ophioscincus share the largest number of derived character states (characters E–H) and hence may be presumed to be each others closest living relatives. However, all, the characters indicating this relationship are postcranial and if one takes the attitude that they may be simply manifestations of a single, more general feature of limb reduction, this hypothesis fails, leaving as equally weak alternative hypotheses: either an O. truncatus–O. ophioscincus (characters A and D) or an O. truncatus–O. cooloolensis (characters B and C) relationship.

Genus Coeranoscincus Wells & Wellington

Coeranoscincus Wells & Wellington, 1984: 87. Type-species Ophioscincus frontalis De Vis, 1888, by original designation.

Diagnosis. Coeranoscincus differs from all other members of the Sphenomorphus group in Australia in the following combination of derived character states: snout slightly conical; nasals slightly enlarged; prefrontals separated (although often only barely in C. frontalis); supraoculars 3 (primary supraoculars 3 and 4 fused or one lost — cf. Anomalopus (Vermiseps) and Ophioscincus); first supraciliary contacts frontal; supraciliaries 6 or less; supralabials 6, fourth below centre of eye; infralabials 5; ear opening absent; size large (maximum size of smaller species = 195 mm).

Maxilla-frontal contact; pre- and postfrontals closely apposed above orbit; quadratal conch lacking; supratemporal fenestra obliterated by apposition of supratemporal arch to parietal; premaxillary teeth < 8; teeth pointed and recurved; palatal rami of pterygoids moderately separated.

Presacral vertebrae ≥ 52; complete inscriptive chevrons ≥ 12; manus lacks intermediate and pisiform, distal carpals 1 and 5 and metacarpal 1, and has phalanges reduced to 0.2.3.3.0 or less; pes has astragalus and calcaneum distinct, lacks metatarsal 1 and has phalanges reduced to 0.2.3.3.0; sternal ribs ≤ 2; mesosternal ribs 1.

Parietal peritoneum lacks pigment.

Three characters in the foregoing suite are not necessarily associated with burrowing and therefore provide the primary reason for hypothesizing the monophyly of the group: large size, premaxillary teeth < 8, teeth pointed and recurved, and palatal rami of pterygoids slightly separated medially.

It should be noted that this diagnosis differs substantially from that of Wells & Wellington (1984).

Species (2). O. frontalis (De Vis, 1888) and O. reticulatus (Günther, 1873).

Distribution. Widely disjunct along the coast and near coastal areas of eastern Australia: northeastern Queensland, southeastern Queensland and northeastern New South Wales (Fig. 37).

Habitat and habits. Tall open forest and closed forest (rainforest); primarily the latter. Cryptozoic; generally found under surface cover or in decaying logs.

Reproduction. Oviparous (one species).

Relationships. None of the characters, as understood at this time, offer any particularly cogent insight into the relationships of Coeranoscincus.

Key to Species of Coeranoscincus

1. Limbs present.................................C. reticulatus
   —Limbs absent................................C. frontalis

Coeranoscincus reticulatus (Günther)

Figs 33–36

Chelomeles reticulatus Günther, 1873: 146. Type-locality: Clarence River, N.S.W. Holotype: BMNH 1946.8.3.25.

Material examined. AM R 644; Clarence R., N.S.W.; R 2201: Tweed R., N.S.W.; R 3317, R 6375: locality unknown; R 4795: Clarence R., N.S.W.; R 17804: Richmond Range, N.S.W.; R 18707, 18742: Binnaburra, Qld; R 55066: Whian Whian State Forest, N.S.W.; R 57076: Grafton, N.S.W.; R 89096, 89281: Grady’s Ck Flora Reserve, Wiangaree State Forest, N.S.W.; R 98376: 0.5 km S Qld border via Mt Lion Rd, N.S.W.; R 111131: Grafton, N.S.W.

MV D 9056: Emu Vale, near Warwick, Qld.

QM J 4390: Tambourine Mt, Qld; J 6217: Beechmont, Qld; J 14507, 22692: Lamington National Park, Qld; J 22616: Binna Burra, Qld; J 24348: 6 km SE of Maleny, Qld; J 24407: Cooloola State Forest, Qld; J 24408–12: Lamington National Park, Qld; J 25409: Cunningham’s Gap National Park, Qld.

WAM R 43856: south of Lamington, Qld.

Diagnosis. Differs from all other lygosomines with a digital formula of 3/3 (Eumecia achietae (some), Hemiergis decresiensis, Lerista fragilis, L. haroldi, L. muelleri, L. terdigitata and Saiphos equalis) in having distinct prefrontals and 2 loreals instead of 1 (Saiphos), in having lost the external ear opening (Eumecia and Lerista), or in having a scaly lower eyelid instead of an eyelid with a clear window (Hemiergis). For a comparison with the only other species in the genus, see below and Table 6.

Description. As the last comprehensive description of this species was provided nearly a century ago (Boulenger, 1887) and the species is still somewhat rare in collections today, a redescription based on currently important characters may be useful.

In general appearance, a long, attenuate skink with small front and rear tridactyl limbs and a plain brown to dark, cross-banded colour pattern.

Snout, bluntly conical; rostral trilobed with moderately deep median lobe projecting between nasals to make contact with frontonasal, and two truncated lateral lobes ending at level of nostril; frontonasal slightly wider than long; prefrontals large but separated; frontal slightly longer than wide, approximately equal to, or slightly shorter than, midline length of frontoparietals and interparietal; supraoculars 3, first 2 in contact with frontal; frontoparietals distinct, each shorter than interparietal; interparietal distinct, with distinct parietal eye spot; parietals meet behind
Fig. 33. Coeranoscincus reticulatus from Wiangaree State Forest, N.S.W. Photo: A.E. Greer.

Fig. 34. Coeranoscincus reticulatus from Richmond R., N.S.W showing the reticulated ventral pattern which gives the species its name. Photo: H.G. Cogger.
interparietal, each bordered posterolaterally by upper secondary temporal and anterior nuchal, and often a third scale intercalated between the two; nuchals differentiated, 2–4 (mode = 4).

Nasals slightly enlarged, separated, with nostril situated well forward and slightly below centre; loreals 2; preoculars 2, lower much the larger; subocular scale row interrupted or narrowed appreciably below centre of eye; presuboculars usually 2, rarely 1; postsuboculars 2; supraciliaries 5–6 (mode = 6), first largest and in contact with frontal, last projects between last supraocular and first pretemporal; lower eyelid scaly; pretemporals two; primary temporal single; secondary temporals 2, upper much the larger and overlapped by lower; external ear opening absent, its former position indicated by a conical depression in a nearly vertical crease; supralabials 6, fourth subocular; postsupralabials usually 2, occasionally 1; mental moderate in size; postmental as large as mental, in contact with first 2 infralabials on either side; enlarged pairs of chin scales 3, first pair in contact, second pair separated by 1 scale row, and third by 3.

Body scales smooth, in 23–28 longitudinal rows at midbody; paravertebral scales only slightly wider than more lateral rows, 109–125 in a single row; inner preanals overlap outer, medial pair enlarged; median row of subcaudals slightly wider than immediately adjacent rows.

Snout-vent length 67–195 mm; front leg 0.04–0.07 x SVL, with 3 very short, clawed toes of which middle is largest; rear leg with 3 very short, clawed toes of which middle is largest, 0.04–0.09 x SVL; tail pointed, 0.98–1.47 x SVL.

**Colour.** Individuals approximately 70 mm SVL and shorter have very conspicuous dark crossbands which are large and distinct anteriorly but become broken and diffuse posteriorly. Generally, there is a rather broad dark crossband or blotch on the head extending down into the ocular area, a slightly narrower one across the nape, and numerous posterior bands which are still narrower and more variable. Adults never seem to retain the dark head band except as a dark ocular blotch, while the nape and body bands may be either retained throughout life (albeit against a generally darkening ground colour) or lost from back to front, the ultimate in this trend being the total loss of banding. The venter is usually heavily reticulated with dark colour.

In life, an adult male (AM R 89281) had the labial area and side of head and neck back to the ear suffused
counts were given. However, and no follicle three females with large ovarian follicles. The SVLs for these females ranged 135-164 of the eggs examined by me indicated that the eggs and may be the prey to which their pointed, recurved interesting because large earthworms are relatively common in the closed forest habitats of McDonald, 1977 and pers. obs.), but there is at least one record from “all open layered eucalyptus forest” (McDonald, 1977).

**Diet.** McDonald (1977) found stomach contents in four of the 18 specimens he examined. These comprised three earthworms, one coleoptera larva and one indeterminable insect. The earthworms are especially interesting because large earthworms are relatively common in the closed forest habitats of *Coeranoscincus* and may be the prey to which their pointed, recurved teeth are adapted.

**Reproduction.** McDonald (1977) examined four gravid females and I have examined one (WAM R 43856). These females ranged 100-192 mm SVL (x = 154 mm) and contained 2-6 oviducal eggs (x = 4.2). The dates of collection available for three females were in the period 20 Oct.-12 Dec. The thickness of the shells of the eggs examined by me indicated that the eggs would have been laid. McDonald (1977) also reported three females with large ovarian follicles. The SVLs for these females ranged 135-164 (x = 148 mm); no dates of collection were available, however, and no follicle counts were given.

*Coeranoscincus frontalis* De Vis

Figs 38-40


**Material examined.** All localities are in northeast Queensland.

AMNH 27295: Ravenshoe District; 83937: Malanda Falls. AM R 3823: Queensland; R 4006: Mt Bartle Frere; R 16627: Atherton; R 49086: Mt Speck; R 55074: Thornton Peak area; R 61297: Milpa Mill; R 89278-80: vicinity of “The Boulders”, West of Babinda; R 91063: Yuccabine Ck at Kirrama State Forest Rd (29.3 km W of Bruce Hwy via Kirrama State Forest Road).

ANWC 3454: Severin State Forest, Atherton; 4114: Atherton.

QM J 243, 11499: Geraldton (= Innisfail); J 5215: Aloomba; J 5336: Barrine; J 13139: Euramo; J 13139: Mt Kalorama; J 19737-19741, 22172: locality not known.

**Diagnosis.** Differs from the only other species of *Coeranoscincus* in being totally limbless.

**Description.** A long limbless skink with a dark lateral band in juveniles but this diminishes with age to give a plain, brown ground colour in adults. Snout bluntly conical; rostral trilobed with distinct median lobe projecting between nasals to contact frontonasal, and 2 slightly shorter, labial lobes extending to level of nostril; frontonasal about as long as wide; prefrontals large, narrowly to moderately separated; frontal longer than wide, approximately equal to midline length of frонтопаретального and interparietal; supraoculars 2 or 3, first 1 or 2 contact frontal; frontoparietals distinct, broadly contacting to narrowly separated, each smaller than interparietal; interparietal distinct, with distinct parietal eye spot; parietals meet behind interparietal, each bordered posterolaterally by upper secondary temporal, undifferentiated body scale or transversely enlarged nuchal and often a third scale intercalated between these 2; nuchals 0–4.

Nasals slightly enlarged, well separated, with nostril in ventral corner; loreals 2; preoculars 2; supralabials 4 or 5, first much the largest and in contact with frontal, penultimate projecting medio- laterally between last 2 supraoculars, and last projecting medio- laterally between supraocular and first pretemporal; subocular scale row complete, but anterior scales small, last 2 large; lower eyelid scaly; pretemporals 2; primary temporal single; secondary temporals 2, upper much the larger (long), overlapping lower which is about same size as primary; external ear opening absent, its former position indicated by a nearly vertical crease; supralabials 6, fourth subocular; postsupralabials 2; mental moderate in size; postmental about equal in size to mental, in contact with first 2 of 5 infralabials; enlarged pair of chin scales 3, members of first pair in contact, those of second pair separated by 1 scale row, and those of third by 3 rows.

Body scales smooth, in 26–34 longitudinal rows at midbody; paravertebral scales equal in size to more lateral row, 151–197 in single row; inner preanal overlap outer, medial pair enlarged; median row of subcaudals just slightly wider than more lateral rows.

Snout-vent length 70–291 mm; no external trace of limbs; tail 0.47–0.57 x SVL.

**Colour.** Specimens generally smaller than about 130 mm SVL have a distinct colour pattern. The dorsum of the body and tail is dark-brown, often with slightly darker longitudinal stripes as in the adults, but the top of the head, the nape and the sides of the neck are generally light-cream colour with the exception of dark pigment concentrated around the eyes and ears. A very distinct dark stripe begins on the side of the chin and extends posteriorly along the side of the throat to a point just posterior to the level of the ear where it turns slightly upward to just below the level of the ear and extends posteriorly to just past the vent before breaking up into a series of evenly spaced, dark, vertical dashes connected dorsally by a thin longitudinal stripe.

Depending on their size, adults retain elements of this pattern, but suffusion of dark pigment over the nape and head, and the loss of dark pigment from the lateral stripe results in a nearly uniformly coloured dorsum in...
Fig. 37. Distribution of the two species of Coeranoscincus: *C. reticulatus* (closed circles) and *C. frontalis* (open circles).

the largest individuals. There is no polymorphism as in *C. reticulatus*.

In life, the venter of juveniles below the dark lateral stripe can vary from pale, greenish yellow to a very bright orange. In adults the venter is a pale, pinkish yellow anteriorly, becoming increasingly yellow posteriorly until maximum intensity of pale-yellow is reached over the posterior third of the body and entire underside of the tail.

**Distribution.** *Coeranoscincus frontalis* is known only from the coastal ranges and lowlands of northeastern Queensland, and in an area between Thornton Peak in the north and Mt Speck in the south. The most inland locality is Atherton, approximately 55 km from the coast.

**Habitat.** The species is known only from moist rainforest where it is generally found in rotten logs or under surface cover such as logs and rocks.

**Habits.** Despite the species' extremely long, sharply pointed teeth, none of the specimens we have handled (*N* = 4) ever attempted to bite.

**Comparison of the Two Species of Coeranoscincus.**

Meristic features of the two species are compared in Table 6 and the non-meristic below.

The **prefrontal scales** are slightly larger and closer together in *C. frontalis* than in *C. reticulatus*.

The **upper secondary temporal** overlaps the lower secondary in *C. frontalis* but the reverse is true in *C. reticulatus*.

The total **number of premaxillary teeth** is eight in *C. reticulatus* (*N* = 2) and seven in *C. frontalis* (*N* = 1). In *C. reticulatus* the **crows of the teeth** are flattened, pointed and 'twisted' posteriorly. The edge of the flattened points have a very narrow groove rendering the tooth bicuspid. There is also a shallow groove running along the outer curvature of the tooth. In *C. frontalis* the teeth are conical, very sharply pointed and strongly recurved, i.e., fang-like. A very narrow apical groove is evident on some of the larger teeth, rendering them bicuspid, but there is no groove running along the outer length of the teeth.

A long thin **postorbital bone** extends posteriorly to the parietal in *C. reticulatus*, but there is no distinct postorbital in *C. frontalis*.

The dorsal (postfrontal) process of the **jugal** is well developed in *C. reticulatus* but is reduced to a tapering, thin 'wisp' in *C. frontalis*.

The **palatal rami of the pterygoids** are relatively 'thin' and diverge slightly from the midline in *C. frontalis* but they are 'heavy' and medially expanded in *C. reticulatus*.

There is a short, stout midventral ridge between the **basipterygoid processes** in *C. reticulatus* but no such ridge in *C. frontalis*.

The **fenestra rotunda** is large in *C. reticulatus* but reduced to a tiny foramen in *C. frontalis*.

The **surangular** is distinct in *C. frontalis* but it is fused to the articular and prearticular in *C. reticulatus*.

The **front limb** is tridactyl with a phalangeal formula of 0.2.3.3.0 in *C. reticulatus* but is reduced to a vestige of the humerus which is not visible externally in *C. frontalis*.

In *C. reticulatus* the **pectoral girdle** differs little from the primitive scincid condition; the major difference is that only two ribs (from the ninth and tenth presacral vertebrae) contact the sternum instead of three, and one or no rib contacts the mesosternum instead of two. In
Fig. 38. *Coeranoscincus frontalis* from near 'The Boulders' just west of Babinda, Qld.

Fig. 39. Head of *Coeranoscincus frontalis* (CAS 44130).
C. frontalis the pectoral girdle is highly modified: the clavicles are thin and rod-like; the interclavicle is absent; the sternum is assymetrical and more rectangular than rhomboidal; only one rib (from ninth presacral vertebrae) contacts the sternum and there is no mesosternum.

The rear limb is tridactyl with a phalangeal formula of 0.2.3.3.0 in C. reticulatus but is totally absent in C. frontalis.

The distal ends of the sacral diapophyses are in broad contact in C. reticulatus but separated in C. frontalis.

The pelvic girdle conforms to the primitive scincid condition in C. reticulatus but is reduced to a blade-like ilium with attached scale-like vestiges of the pubis.
and ischium in *C. frontalis*.

In most of the characters in which the two species of *Coeranoscincus* differ, and which can be fairly assessed in terms of primitive and derived character states (above and Table 8), *C. reticulatus* is more primitive and *C. frontalis* more highly derived. The only exceptions are the prefrontals, secondary temporals, palate and surangular; in these, *C. frontalis* is more primitive.

### Key to Skink Genera in Australia with Species Having a Reduced Number of Digits

1. Outer preanal scales overlap inner; digital formula 4–5. ........................................ 2
   —Inner preanal scales overlap outer; digital formula 4–4 or less. ............................... 5
2. Lower eyelid moveable. ......................................................................................... 3
   —Lower eyelid a spectacle. . ......................................................................................  Menetia
3. Prefrontals present. .............................................................................................. 4
   —Prefrontals absent. ................................................................................................. Anotis
4. Frontoparietals distinct. ......................................................................................  Saprososcincus
   —Frontoparietals fused. ........................................................................................ Carlia
5. External ear opening present. ................................................................................ Lerista
   —External ear opening absent. ................................................................................ 6
6. Lower eyelid scaly................................................................................................. 7
   —Lower eyelid with a clear window............................................................................. Hemiergis
7. Ectopterygoid process present. .............................................................................. 8
   —Ectopterygoid process absent. ................................................................................ 9
8. Digital formula 3–3; premaxillary teeth 8–9.........................................................  Saiphos
   —Digital formula 3–2 or less; premaxillary teeth ≤ 7. ............................................. Anomalopus
9. Supralabials 6, fourth subocular; frontal in contact with 2 (of 3) supraoculars. .......... Coeranoscincus
   —Supralabials 5, third subocular; frontal in contact with only 1 (of 3) supraoculars. ... Ophioscincus

### Key to Limbless Species of Lygosomite Skinks

1. External ear opening present (although minute). ................................................ 2
   —External ear opening absent. ................................................................................. 3
2. Eye covered by moveable eyelid. ........................................................................... Lerista ameles
   —Eye covered by fixed ocular scale. ...................................................................... Lerista apoda
3. Supralabials 6 ....................................................................................................... 4
   —Supralabials 5 or fewer (4% of *A. gowi* have 6). .................................................. 7
4. Nasal and first supralabial scale distinct. ............................................................... 5
   —Nasal and first supralabial scale fused. .................................................................. Anomalopus (*Vermiseps*) pluto
5. Paravertebral scales 84–138; size smaller, maximum SVL 107 mm. ....................... 6
   —Paravertebral scales 151–197; size larger, maximum SVL 291 mm. .......................  Coeranoscincus *frontalis*
6. Midbody scale rows 22–26; supraciliary scale row continuous; loreals usually 2 (8% with 1). .................................................... Anomalopus (*Vermiseps*) swansoni
Midbody scale rows 18–20; supraciliary scale row interrupted (last supraciliary separated from anterior supraciliaries by last 1 or 2 supraoculars); loreal one.

Anomalopus (Vermiseps) brevicollis

7. Prefrontal present .................................................. 8
   —Prefrontal absent ................................................ 10

8. Loreals 2 .............................................................. Ophioscincus ophioscincus
   —Loreals 1 ........................................................... 9

9. Midbody scale rows 22–26; supraciliary scale row continuous; pretemporal 1; a distinct dark lateral stripe; Asia. ...................... Isopachys anguinoides
   —Midbody scale rows 18–20; supraciliary scale row interrupted (last supraciliary scale separated from anterior supraciliaries by last 1 or 2 supraoculars); pretemporals 2; no distinct dark lateral stripe; Australia. .................................................. Anomalopus (Vermiseps) gowii

10. Supralabials 5; frontonasal distinct ...............................................

11. Frontoparietals in contact; pretemporals 2; mental and postmental distinct; Australia. .................................................. Ophioscincus cooloolensis

   —Frontoperietals separated; pretemporal 1; mental and postmental fused; Asia. .................................................. Isopachys roulei

ACKNOWLEDGEMENTS. We thank P. Koshland for drawing Figs 2, 5, 7, 10–11, 14–15, 17–18, 20–22, 24–25, 28–29, 31–32, 35–36 and 39–40; the New South Wales National Parks and Wildlife Service for permits to collect; J. Gates and D. Kent for typing the manuscript, and J. Paxton and two anonymous reviewers for critical reviews.

References


**Table 1.** Comparison of certain characters in the three species of the subgenus *Anomalopus* of the genus *Anomalopus*.

<table>
<thead>
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<th>Character</th>
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<td>0.93</td>
</tr>
<tr>
<td>1</td>
<td>–</td>
<td>1.00</td>
<td>–</td>
<td>0.07</td>
</tr>
<tr>
<td>Number of loreals</td>
<td>N</td>
<td>3</td>
<td>5</td>
<td>25</td>
</tr>
</tbody>
</table>

*Based on inference that first supralabial is fused to nasal

Table 2. Comparison of certain characters in the four species of the subgenus Vermiseps of the genus Anomalopus.

<table>
<thead>
<tr>
<th>Character</th>
<th>A. swansoni</th>
<th>A. pluto</th>
<th>A. gowi</th>
<th>A. brevicollis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Midbody scale rows</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Range</td>
<td>22-26</td>
<td>22-23</td>
<td>18-20</td>
<td>18-20</td>
</tr>
<tr>
<td>x</td>
<td>23.6</td>
<td>22.2</td>
<td>19.0</td>
<td>18.4</td>
</tr>
<tr>
<td>SD</td>
<td>0.95</td>
<td>0.45</td>
<td>0.99</td>
<td>0.76</td>
</tr>
<tr>
<td>N</td>
<td>34</td>
<td>5</td>
<td>25</td>
<td>47</td>
</tr>
<tr>
<td>Paravertebrals</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Range</td>
<td>115-138</td>
<td>126-136</td>
<td>105-117</td>
<td>84-102</td>
</tr>
<tr>
<td>x</td>
<td>128.7</td>
<td>131.0</td>
<td>111.9</td>
<td>90.3</td>
</tr>
<tr>
<td>SD</td>
<td>7.12</td>
<td>3.90</td>
<td>3.81</td>
<td>4.73</td>
</tr>
<tr>
<td>N</td>
<td>14</td>
<td>6</td>
<td>24</td>
<td>41</td>
</tr>
<tr>
<td>Number of supraoculars</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>3</td>
<td>0.81</td>
<td>–</td>
<td>–</td>
<td>0.95</td>
</tr>
<tr>
<td>2</td>
<td>0.19</td>
<td>1.00</td>
<td>1.00</td>
<td>0.05</td>
</tr>
<tr>
<td>N</td>
<td>37</td>
<td>6</td>
<td>25</td>
<td>39</td>
</tr>
<tr>
<td>Number of supraciliaries</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>0.05</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>4</td>
<td>0.95</td>
<td>–</td>
<td>0.96</td>
<td>0.05</td>
</tr>
<tr>
<td>3</td>
<td>–</td>
<td>1.00</td>
<td>0.04</td>
<td>0.95</td>
</tr>
<tr>
<td>N</td>
<td>44</td>
<td>6</td>
<td>25</td>
<td>41</td>
</tr>
<tr>
<td>Number of loreals</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>0.97</td>
<td>1.00</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>1</td>
<td>0.03</td>
<td>–</td>
<td>1.00</td>
<td>1.00</td>
</tr>
<tr>
<td>N</td>
<td>37</td>
<td>7</td>
<td>25</td>
<td>39</td>
</tr>
</tbody>
</table>

Table 3. Distribution of character states used to infer the phylogenetic relationships of the four species of the subgenus Vermiseps. Primitive character states are indicated by an upper case letter, derived states by lower case letters and, if necessary, superscripts. If a character varies intraspecifically, only the most primitive character state is entered.

<table>
<thead>
<tr>
<th>Character</th>
<th>A. swansoni</th>
<th>A. pluto</th>
<th>A. gowi</th>
<th>A. brevicollis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nasals separated (A) or in contact (a)</td>
<td>A</td>
<td>A</td>
<td>a</td>
<td>a</td>
</tr>
<tr>
<td>Prefrontals present (B) or absent (b)</td>
<td>B</td>
<td>B</td>
<td>B</td>
<td>b</td>
</tr>
<tr>
<td>Supraoculars 4 (C) or 2 (c)</td>
<td>C</td>
<td>C</td>
<td>c</td>
<td>c</td>
</tr>
<tr>
<td>Posterior supraocular excluded from supraciliary row (D) or entering it (d)</td>
<td>D</td>
<td>D</td>
<td>d</td>
<td>d</td>
</tr>
<tr>
<td>Supraciliaries 5 (E) or fewer (e)</td>
<td>E</td>
<td>E</td>
<td>e</td>
<td>e</td>
</tr>
<tr>
<td>Posterior loreal present (F) or absent (f)</td>
<td>F</td>
<td>F</td>
<td>f</td>
<td>f</td>
</tr>
<tr>
<td>Subocular scale row large (G) or much reduced (g)</td>
<td>G</td>
<td>G</td>
<td>g</td>
<td>g</td>
</tr>
<tr>
<td>Infraciliaries 5 (H) or 4 (h)</td>
<td>H</td>
<td>H</td>
<td>h</td>
<td>H</td>
</tr>
<tr>
<td>Premaxillary teeth 7 (I) or &lt;6 (i)</td>
<td>I</td>
<td>I</td>
<td>i</td>
<td>i</td>
</tr>
</tbody>
</table>
### Table 3. continued

<table>
<thead>
<tr>
<th>Character</th>
<th>A. swansoni</th>
<th>A. pluto</th>
<th>A. gowi</th>
<th>A. brevicollis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Frontal’s ventral processes weak (J) or moderate to strong (j)</td>
<td>J</td>
<td>j</td>
<td>J</td>
<td>j</td>
</tr>
<tr>
<td>Fenestra rotunda moderate in size (K) or reduced to small foramen (k)</td>
<td>K</td>
<td>k</td>
<td>K</td>
<td>k</td>
</tr>
<tr>
<td>Sacral diapophyses fused (L) or separate (l)</td>
<td>L</td>
<td>l</td>
<td>L</td>
<td>l</td>
</tr>
<tr>
<td>Pubes present (M) or absent (m)</td>
<td>M</td>
<td>m</td>
<td>m</td>
<td>m</td>
</tr>
<tr>
<td>First supraciliary separated (N) or in contact (n) with frontal</td>
<td>N</td>
<td>n</td>
<td>n</td>
<td>n</td>
</tr>
<tr>
<td>Parietal peritoneum pigmented (O) or not (o)</td>
<td>O</td>
<td>o</td>
<td>o</td>
<td>O</td>
</tr>
</tbody>
</table>

### Table 4. continued

<table>
<thead>
<tr>
<th>Character</th>
<th>O. truncatus</th>
<th>O. cooloolensis</th>
<th>O. ophioscincus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of infralabials</td>
<td>5</td>
<td>0.36</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>0.64</td>
<td>1.00</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>28</td>
<td>11</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>22</td>
</tr>
<tr>
<td>Number of infralabials contacted by postmental</td>
<td>2</td>
<td>0.92</td>
<td>0.92</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>0.08</td>
<td>0.08</td>
</tr>
<tr>
<td></td>
<td>0</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>40</td>
<td>12</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>43</td>
</tr>
<tr>
<td>Anterior pair of chin scales</td>
<td>Contact</td>
<td>1.00</td>
<td>0.75</td>
</tr>
<tr>
<td></td>
<td>Separate</td>
<td>-</td>
<td>0.25</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>25</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>21</td>
</tr>
<tr>
<td>Snout-vent length (mm)</td>
<td>Range</td>
<td>34-79</td>
<td>54-69</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>36</td>
<td>13</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>37</td>
</tr>
<tr>
<td>Tail length/snout-vent length</td>
<td>Range</td>
<td>0.71-0.95</td>
<td>0.77-0.93</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>32</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>22</td>
</tr>
<tr>
<td>Presacral vertebrae</td>
<td>Range</td>
<td>45-50</td>
<td>43-44</td>
</tr>
<tr>
<td></td>
<td>X</td>
<td>47.2</td>
<td>43.6</td>
</tr>
<tr>
<td></td>
<td>SD</td>
<td>1.07</td>
<td>0.55</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>32</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>14</td>
</tr>
<tr>
<td>Postsacral vertebrae</td>
<td>Range</td>
<td>40-42</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>X</td>
<td>41.1</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>SD</td>
<td>0.54</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>11</td>
<td>-</td>
</tr>
<tr>
<td>Complete inscriptive chevrons</td>
<td>Range</td>
<td>12-15</td>
<td>11-12</td>
</tr>
<tr>
<td></td>
<td>X</td>
<td>13.4</td>
<td>11.3</td>
</tr>
<tr>
<td></td>
<td>SD</td>
<td>0.92</td>
<td>0.52</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>8</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>9</td>
</tr>
<tr>
<td>Siernal/splenosternal ribs</td>
<td>Range</td>
<td>2/1</td>
<td>0.89</td>
</tr>
<tr>
<td></td>
<td>2/0</td>
<td>0.11</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>1/1</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>1/0</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>9</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>10</td>
</tr>
</tbody>
</table>

### Table 4. A comparison of certain characters among the three species of *Ophioscincus*.

<table>
<thead>
<tr>
<th>Character</th>
<th>O. truncatus</th>
<th>O. cooloolensis</th>
<th>O. ophioscincus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Midbody scale rows</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Range</td>
<td>18-22</td>
<td>18-19</td>
<td>20-24</td>
</tr>
<tr>
<td>X</td>
<td>19.6</td>
<td>18.1</td>
<td>21.7</td>
</tr>
<tr>
<td>Mode</td>
<td>20</td>
<td>18</td>
<td>22</td>
</tr>
<tr>
<td>N</td>
<td>39</td>
<td>13</td>
<td>37</td>
</tr>
<tr>
<td>Paravertebrals</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Range</td>
<td>77-90</td>
<td>77-83</td>
<td>94-113</td>
</tr>
<tr>
<td>X</td>
<td>81.9</td>
<td>79.4</td>
<td>102.0</td>
</tr>
<tr>
<td>SD</td>
<td>4.08</td>
<td>2.23</td>
<td>5.28</td>
</tr>
<tr>
<td>N</td>
<td>9</td>
<td>12</td>
<td>13</td>
</tr>
<tr>
<td>Supraoculars</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>1.00</td>
<td>0.69</td>
<td>0.66</td>
</tr>
<tr>
<td>2</td>
<td>-</td>
<td>0.31</td>
<td>0.34</td>
</tr>
<tr>
<td>N</td>
<td>40</td>
<td>14</td>
<td>44</td>
</tr>
<tr>
<td>Number of loreals</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>0.92</td>
<td>-</td>
<td>1.00</td>
</tr>
<tr>
<td>1</td>
<td>0.08</td>
<td>1.00</td>
<td>-</td>
</tr>
<tr>
<td>N</td>
<td>40</td>
<td>10</td>
<td>44</td>
</tr>
<tr>
<td>Transversely enlarged nuchals</td>
<td>1-7</td>
<td>2-5</td>
<td>0-4</td>
</tr>
<tr>
<td>X</td>
<td>3.4</td>
<td>3.4</td>
<td>2.6</td>
</tr>
<tr>
<td>Mode</td>
<td>3</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>N</td>
<td>40</td>
<td>12</td>
<td>42</td>
</tr>
</tbody>
</table>
Table 5. Distribution of character states used to infer the phylogenetic relationships of the three species of genus Ophioscincus. Primitive character states are indicated by an upper case letter, derived states by lower case letters and, if necessary, superscripts. If a character varies interspecifically only the most primitive state is entered.

<table>
<thead>
<tr>
<th>Character</th>
<th>C. reticulatus</th>
<th>C. frontalis</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Character</strong></td>
<td>C. reticulatus</td>
<td>C. frontalis</td>
</tr>
<tr>
<td>Supraciliary row complete (A)</td>
<td>a</td>
<td>a</td>
</tr>
<tr>
<td>or interrupted (a)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Posterior edge process</td>
<td></td>
<td></td>
</tr>
<tr>
<td>of pterygoid weakly (B)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>or strongly (b) developed</td>
<td>B</td>
<td>B</td>
</tr>
<tr>
<td>Prefrontal and nasal bones in</td>
<td></td>
<td></td>
</tr>
<tr>
<td>contact (C) or maxilla and</td>
<td></td>
<td></td>
</tr>
<tr>
<td>frontal in contact (c)</td>
<td>C</td>
<td>C</td>
</tr>
<tr>
<td>Presacral vertebrae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>less than 44 (D) or &gt; 45 (d)</td>
<td>d</td>
<td>d</td>
</tr>
<tr>
<td>Front limb comprises</td>
<td></td>
<td></td>
</tr>
<tr>
<td>humerus, radial, ulna</td>
<td></td>
<td></td>
</tr>
<tr>
<td>and one carpel (E)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>or only a humeral fragment</td>
<td></td>
<td></td>
</tr>
<tr>
<td>or less (e)</td>
<td>e</td>
<td>e</td>
</tr>
<tr>
<td>Sacral diaphyses</td>
<td></td>
<td></td>
</tr>
<tr>
<td>fused (G) or separated (g)</td>
<td>g</td>
<td>g</td>
</tr>
<tr>
<td>Ischia joined (H) or</td>
<td></td>
<td></td>
</tr>
<tr>
<td>separated through reduction</td>
<td>H</td>
<td>H</td>
</tr>
<tr>
<td>Snout-vent length (mm)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Digital formula</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Complete inscriptive chevrons</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sternal/mesosternal ribs</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Midbody scale rows</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Range</td>
<td>23-28</td>
<td>26-34</td>
</tr>
<tr>
<td>SD</td>
<td>26.0</td>
<td>29.7</td>
</tr>
<tr>
<td>Mode</td>
<td>1.33</td>
<td>2.23</td>
</tr>
<tr>
<td>Posts acral vertebrae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Range</td>
<td>52-55</td>
<td>72-76</td>
</tr>
<tr>
<td>SD</td>
<td>54.4</td>
<td>73.4</td>
</tr>
<tr>
<td>Supraoculars</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Range</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>SD</td>
<td>1.00</td>
<td>0.36</td>
</tr>
<tr>
<td>N</td>
<td>1</td>
<td>1</td>
</tr>
</tbody>
</table>
Addendum

Since this paper went to press a few changes and additions in our understanding of *Anomalopus leuckartii* and *A. verreauxi* have occurred. These are discussed below. The maps in the text (Figs 3 and 8) conform to these revisions.

*Anomalopus verreauxi*. Re-examination of QM J 11837 from 32 km N of Dayboro, Qld shows it to conform completely with *A. leuckartii*. It is therefore accepted as this species and the locality record rejected as being in error; there are no other records of *A. leuckartii* from the lowlands of far southeast Queensland (aside from the types of *Anomalopus lentiginosus*).

Additional specimens examined of *A. verreauxi* are: QNPWS R 58, 230, 578, 720-21, 724-25, 745, N 11381, 17670, 17759, 17924-25, 17670, 58799.

The furthest inland specimen is not QM J 37065 from Palm Gorge Fauna Reserve, Qld, but QNPWS N 10892 from Clemantis Creek, at the boundary between Glenaughton and Nugga Nugga Stations; this locality is approximately 250 km from the coast.

*Anomalopus leuckartii*. QM J 11837 is accepted as this species and not *A. verreauxi*, its locality of 32 km N of Dayboro, Qld is rejected as in error (see above).

Although the species appears not to occur in the lowlands of far southeastern Queensland, a specimen from Tamborine Mt., Qld (QM J 13935) may represent an isolated, high elevation population in this area.

Accepted 21st February 1985