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The relationship of the Taipan, *Oxyuranus scutellatus,* and the Small-scaled Snake, *Oxyuranus microlepidotus* (Serpentes: Elapidae)

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ABSTRACT

The external and cranial morphology, venom, head musculature, hemipenis morphology, behaviour, and karyotypes of *'Parademansia' microlepidota* and *Oxyuranus scutellatus* are so similar that the two species are considered congeneric. *Parademansia* Kinghorn 1955 is, therefore, a junior subjective synonym of *Oxyuranus* Kinghorn 1923. *Oxyuranus* is redefined to accommodate both species. Specific differences between *O. microlepidotus* and *O. scutellatus* are listed.

INTRODUCTION

The Small-scaled (or Fierce) snake, *Oxyuranus microlepidotus* (Plate 1), has had an unstable generic history. It was described as *Diemenia microlepidota* McCoy 1879. The species has variously been treated as one of the 'Brown' snakes (*Pseudonaja* spp.), as one of the 'Black' snakes (*Pseudechis* spp.), as *Parademansia microlepidota,* as a junior subjective synonym of *Oxyuranus scutellatus,* and as *Oxyuranus microlepidotus.*

Boulenger (1886), Waite (1898), and Kinghorn (1929) placed *O. microlepidotus,* which was known only from the two type specimens, in *Pseudechis,* along with the species now assigned to that genus and *O. scutellatus.* Kinghorn (1923) described *Oxyuranus* to accommodate *scutellatus* and, later (1955), *Parademansia* to accommodate *microlepidotus.* The characteristics of each genus as described by Kinghorn (1923, 1955) are summarized in Table 1. Worrell (1963, quoting unpublished work by Brazenor on the type specimens of *Diemenia microlepidotus*) synonymized *O. microlepidotus* with *O. scutellatus.* With the rediscovery of the species in far southwestern Queensland and northeastern South Australia, Covacevich and Wombey (1976) recognized the species as *Parademansia microlepidota,* the name under which it has also been discussed by Cogger (1975); Sutherland, Broad, Tanner and Covacevich (1978); and Broad, Sutherland, Tanner and Covacevich (1979). Broad *et al.* concluded that the external and cranial morphology and venom of *'Parademansia'* suggested that it most closely resembled *Oxyuranus,* shared some features with *Pseudonaja,* and least resembled *Pseudechis.* Fohlman (1979), following detailed work on the venom of both *microlepidota* and *scutellatus,* proposed that they were congeneric. He noted '. . . the similarity of the gel filtration patterns, the occurrence of a direct prothombin activator, and a presynaptic neurotoxin with three subunits . . . the name *Oxyuranus microlepidotus* would then seem appropriate . . .'.

Examination of the external and cranial morphology, venom, cranial musculature, hemipenal morphology, behaviour, and karyotypes of the two species confirms the suggestion by Fohlman (1979) that *scutellatus* and *microlepidotus* are congeneric. Following a comparison of these seven features in *scutellatus* and *microlepidotus,* the genus *Oxyuranus* Kinghorn 1923 is expanded to accommodate both species, and the differences between *O. microlepidotus* and *O. scutellatus* are summarized.

COMPARISON BETWEEN *O. MICROLEPIDOTUS* AND *O. SCUTELLATUS*

External Features

Body scales and eye size are compared for *O. microlepidotus* and *O. scutellatus* in Table 2.

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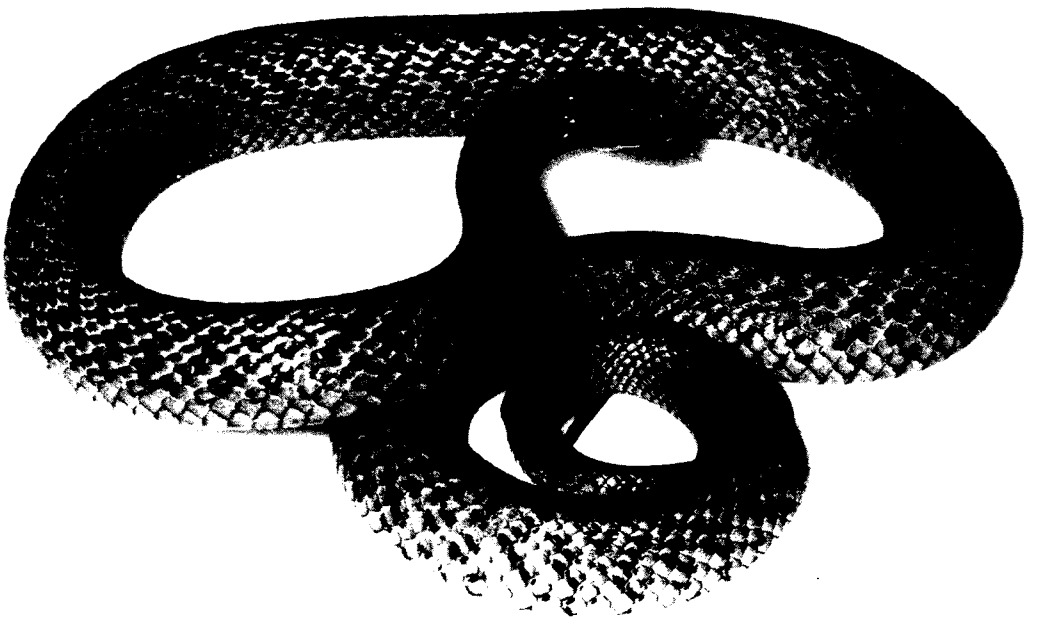

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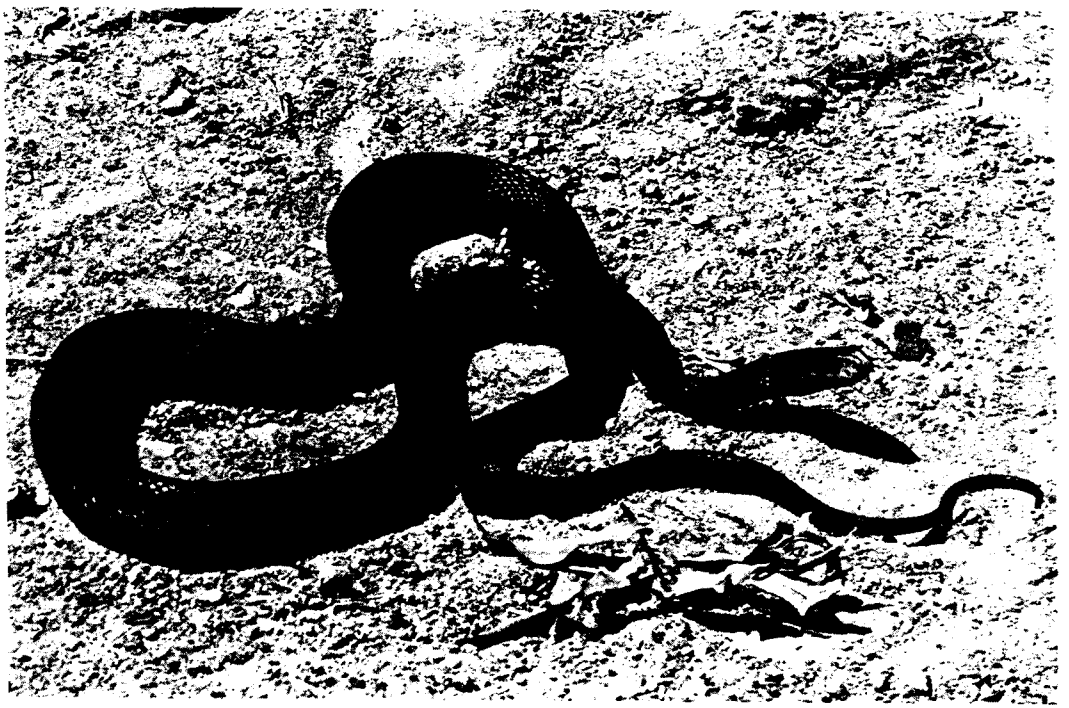

PLATE 1 (photography by A. J. Easton, Queensland Museum)

Fig. a *Oxyuranus microlepidotus* from the Windorah area, southwestern Queensland

Fig. b *Oxyuranus scutellatus* from Rolleston, northeastern Queensland

Table 1. SUMMARY OF GENERIC CHARACTERS OF *OXYURANUS* AND *PARADEMANSIA*, FROM KINGHORN (1923, 1955).

Oxyuranus	*Parademansia*
anterior edge of maxillary in front of tip of palatine	anterior portions of maxillary and palatine level
1 or 2 pairs large grooved fangs	—
1 small grooved posterior maxillary tooth	3 small maxillary teeth behind fang
anterior portion of palatine toothless, a needle-like projection	anterior portion of palatine normal, not a needle-like projection
5-6 palatine teeth	—
8-9 pterygoid teeth	—
head not or slightly distinct from neck	—
nostril in divided nasal	—
no loreal	—
body cylindrical	—
scales smooth	scales smooth, 23 around mid-body
ventrals rounded	—
2 rows of subcaudals	2 rows of subcaudals.

Table 2. A COMPARISON OF SOME EXTERNAL FEATURES OF *O. MICROLEPIDOTUS* AND *O. SCUTELLATUS*.

Feature	*O. microlepidotus*	*O. scutellatus*
mid-body	23[a]	21-23[b]
anal	single	single
ventrals	211-224	220-248
sub-caudals	paired[c], 54-66	48-76, paired
rostral	broader than deep	deep as broad, or slightly broader than deep
internasals	shorter (about $\frac{1}{2}$) than prefrontals	shorter than prefrontals
frontal	broader than supraocular; one and a half times as long as broad	about as broad as supraocular; twice as long as broad
canthus rostralis[d]	no canthal ridge	pronounced canthal ridge
postoculars	2	2
upper labials	6, 3 & 4 enter eye	6, 3 & 4 enter eye
neck scales	long, narrow; smooth	long, narrow; smooth
eye size	diameter less than its distance from mouth	diameter exceeds its distance from mouth

a 1 live specimen held by C.T. has 25 mid-body scales.

b in a sample of 10 Q.M. specimens 3 had 21, 7 had 23 mid-body scales

c subcaudals 3-5 are single in one specimen.

d in live specimens.

Table 3. COMPARISON OF THE SKULLS OF *O. SCUTELLATUS* AND *O. MICROLEPIDOTUS*[1]

Feature	*O. microlepidotus*	*O. scutellatus*
TL[2]	25.6-35.0 mm	30.0-50.7 mm
Breadth[3]	8.5-12.0 mm	8.9-13.6 mm
TL/B	2.9-3.1	3.3-3.7
Fang length	3.5-6.2 mm	7.9-12.1 mm
TL/fang length	5.4-9.9	3.9-4.8
Palatine length	6.6-10.9 mm	12.4-19.5 mm
Palatine projection	0.5-1.2 mm	2.9-5.0 mm
PL/PP	7.4-13.4	3.0-4.2
Pterygoid length	17.6-25.9 mm	24.7-37.8 mm
Pterygoid length/ palatine length	2.2-2.9	1.9-2.1
Pterygoid length/pterygoid tooth row length	approx. 1.8	approx. 1.8
Posterior maxillary teeth[4]	3-5 (3)	1-2 (1)
Palatine teeth	8-12	6-7 (5-6)
Pterygoid teeth	16-22	10-17 (8-9)
Dentary teeth	17-20	14-17
Temporal line	deep V, deeper than $\frac{1}{2}$ parietal length	shallow V, not as deep as $\frac{1}{2}$ parietal length
Sagittal crest	$>\frac{1}{2}$ parietal length	$<\frac{1}{2}$ parietal length

[1] based on Queensland Museum specimens (*O. scutellatus* J8335, J8342, J22192, J26935, J27314, and 1 unregistered specimen; *O. microlepidotus* J22514, J24391, J24436, J26515, J26540, J28776, J28778). Characteristics from Kinghorn's generic descriptions (1923, 1955) in brackets.

[2] tip of premaxilla to foramen magnum along mid-line.

[3] across the parietal at the widest part, just posterior to the parietal/postocular suture.

[4] all tooth counts based on erect functional teeth or sockets; small, unattached teeth excluded.

The colour descriptions below are based on Thomson (1933), Covacevich and Wombey (1976), Covacevich (in press), and on recent observations of captive live specimens.

O. scutellatus: unmarked light olive to dark russet brown dorsally (specimens from the Tully area, NE.Q., almost black); head usually lighter coloured, especially in the rostral and labial regions; ventrally cream, usually with pink or orange flecking; buccal cavity pink; eye reddish.

O. microlepidotus: pale to very dark brown dorsally, often with dark flecks which may form distinct bands posteriorly; head glossy black in most freshly collected specimens (this sometimes fades with captivity); ventrally (behind the black neck region) mustard yellow without flecks; buccal cavity in dark specimens blue grey shading to pink, in lighter coloured specimens greyish pink shading to off-white; eye black. *O. scutellatus* is a larger snake than *O. microlepidotus* (maximum size 3.0 m *vs* 2.0 m).

Skull Morphology (Plate 2, Figs. a-d; Plate 3, Figs. A-f)

Skull measurements, ratios, and dental characteristics in eight specimens of *O. microlepidotus* and five specimens of *O. scutellatus* are compared in Table 3. The skulls are more similar to each other than either is to skulls of *Pseudechis* or *Pseudonaja,* the other genera to which *O. microlepidotus* and *O. scutellatus* have been referred. They differ, however, in size and proportion, and there are minor differences in the number of teeth. The fangs in *O. scutellatus* are very large (*vs* moderate in *O. microlepidotus*), but there are no other significant differences in the maxillary teeth. In *O. scutellatus* all posterior maxillary teeth are solid, with a groove (apparently similar to that on the fang) which varies from deep to very shallow. There is much greater variation in these teeth in *O. microlepidotus.* In J26515 two of the posterior maxillary teeth appear to be fully functional fangs. They have hollow bases and

PLATE 2

Fig. a anterior tip of palatine of *Oxyuranus microlepidotus* showing short blunt projection

Fig. b three posterior maxillary teeth of *Oxyuranus microlepidotus* showing two functional ('fangs') and one solid grooved tooth

Fig. c anterior tip of palatine of *Oxyuranus scutellatus* showing long narrow projection

Fig. d single solid posterior maxillary tooth of *Oxyuranus scutellatus*

Figs. e f hemipenis of *Oxyuranus microlepidotus*

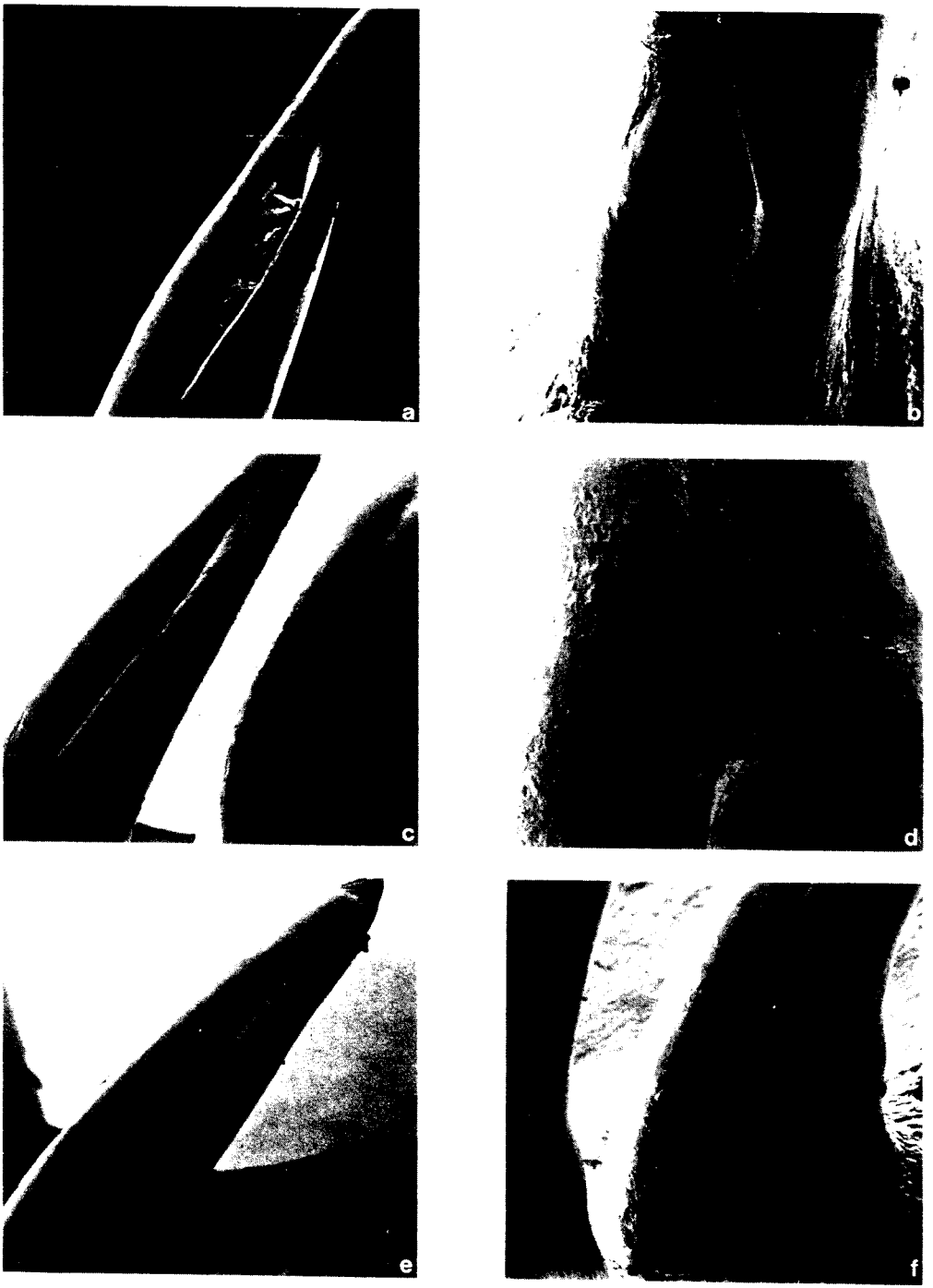

PLATE 3 Electron micrographs of maxillary teeth of *Oxyuranus microlepidotus* (J26515).

Fig. a. tip of fang.
Fig. b. base of fang.
Fig. c. tip of first posterior maxillary tooth
Fig. d base of first posterior maxillary tooth.
Fig. e tip of third posterior maxillary tooth.
Fig. f. base of third posterior maxillary tooth.

tips and, except for their smaller size, resemble the primary fangs. The third tooth is solid, with a shallow groove (Plate 3, Figs a-f). These apparently functional posterior maxillary 'fangs' are not however present in the remaining seven specimens of *O. microlepidotus* examined. In these specimens the posterior maxillary teeth bear folds which vary, as in *O. scutellatus,* from deep, well-formed grooves to shallow 'lines'.

Venom

The venoms of *O. microlepidotus* and *O. scutellatus* have been examined by Fohlman (1979), Broad, Sutherland, Tanner and Covacevich (1979) and Broad, Sutherland and Coulter (1979). They are very similar. Both have a direct prothombin activator and a presynaptic neurotoxin with three subunits. Further, their gel filtration patterns are very similar and are closer to each other than to those of any other large Australian elapid, despite differences in the relative proportions of the fractions. Fohlman (1979, Table 1) noted that the amino acid compositions of the neurotoxin subunits in paradoxin (from *O. microlepidotus*) and taipoxin (from *O. scutellatus*) are very similar. He concluded that, on the basis of venom comparisons alone, the two species were congeneric.

The venoms differ, however, in toxicity, hyaluronidase activity, and yield. The venom of *O. microlepidotus* has a lower LD_{50} than that of *O. scutellatus* (.413-.581 *vs* 1.61-2.46, Broad, Sutherland, Tanner and Covacevich, 1979) and a greater hyaluronidase activity (11.8 units/mg for a larger 'pool' of venom and a range of 12.0-15.0 units/mg *vs* 7.5, 3.0-8.7). The venom yield in *O. microlepidotus* is smaller than that of *O. scutellatus* (30-110 mg *vs* 120-400 mg: Broad, Sutherland, Tanner and Covacevich, 1979; Worrell, 1963).

Head Musculature:

The head muscles of *'Parademansia'* are similar to those of *Oxyuranus.* In both, the dorsal venom gland muscle is very broad (the adductor externus superficialis pars dorsalis is so broad as to conceal the adductor externus medialis) and arises from the entire length of the parietal, even reaching the supraoccipital, but does not have any attachment to the quadrate. The pterygoideus superficialis is unusual, forming a flat ribbon of muscle fibres from the outer side of the retroarticular process of the lower jaw to the rear of the ectopterygoid, without attachment to the maxilla. (In most Australian elapids the pterygoideus superficialis forms a bulging spheroidal mass at the angle of the jaw and either attaches directly by tendon to the rear of the maxilla or attaches to the articular capsule of the maxilla-ectopterygoid joint. The pterygoideus superficialis can thus aid swallowing by pulling the maxilla backward. In *Oxyuranus, 'Parademansia'* (and the *Notechis* group) the maxilla is only a minor adjunct to the palatine and pterygoid, and the palatine-pterygoid articulation is not the simple tongue-in-groove joint seen in many elapids. It is a complex saddle joint. The rear of the palatine has lateral and medial lips that clasp the inner and outer surfaces of the anterior end of the pterygoid. The pterygoid has a short anterior finger clasping the ventral surface of the rear of the palatine, and a much longer finger which extends forward on the dorsal surface of the palatine. This prevents raising of the palatine above the horizontal and is present in *Oxyuranus, 'Parademansia', 'Demansia'* (including *Pseudonaja*) and *Pseudechis.*

Hemipenis Morphology:

The hemipenis in *Oxyuranus* and *'Parademansia'* is similar: moderately long, narrow, and simple (Plate 2, Figs. e-f). The sulcus is forked within the region of spinules and, proximal to the distal spinulose zone, there are more irregular transverse whorls of enlarged spines, fewer in *'Parademansia'* than in *Oxyuranus* (1 *vs* 3). Further, the small spines on the distal part of the organ of *'Parademansia'* are evenly spaced, but in *Oxyuranus* are arranged in groups of 3-5.

Behaviour:

Data available on the behaviour of *O. microlepidotus* and *O. scutellatus* are summarized in Table 4.

Karyotypes:

This information is based on Giemsa-stained, air dried preparations obtained from short term leukocyte cultures of one female and one male of *Oxyuranus* and one male of *'Parademansia'.* Gross karyotypic comparisons indicate that, in addition to sharing the same diploid number ($2n = 36$), the chromosomes of these two genera are similar in general morphology as indicated by centromere positions and arm ratios. By comparison many species of *Pseudonaja* have a diploid count of 38. Those species of *Pseudonaja* and *Pseudechis* which do have counts of 36 differ from *'Parademansia'* and *Oxyuranus* in the morphology and centromere position of one or more chromosomes.

However, before concluding that these similarities between *'Parademansia'* and *Oxyuranus* indicate a true genetic relationship, it

Table 4. ASPECTS OF BEHAVIOUR IN *O. MICROLEPIDOTUS* AND *O. SCUTELLATUS*

Feature	*O. microlepidotus*	*O. scutellatus*
'demeanour'	placid	alert, nervous
period of greatest activity	morning, 8.00 am—10.00 am; occasionally late afternoon and early night	mid-morning, 9.00 am-11.00 am; rarely late afternoon and very rarely night
ability to immobilize prey	fair	very quick and efficient
natural diet	mammals (especially *Rattus villosissimus*) and birds (?)	mammals (especially *Melomys* spp.)
breeding	oviparous	oviparous
clutch size	9-12	7-20
incubation period	66 days	66 days ± 2[a]
egg size	average 6 cm x 3.5 cm[c]	*5.0-6.2 cm* × 2.4-2.6 cm[b]
hatchlings	40 cm ± 3 cm	—

a R. W. Dunn (pers. comm.)
b Thomson (1935, p. 730)
c based on two clutches

is necessary to compare the chromosomes with those of other Australian elapids using the C and G banding techniques. Additionally it is important to examine larger sample sizes and to include both sexes.

Discussion:

On the basis of the many similarities shown above in the external and skull morphology, venom, head muscles, hemipenis morphology, behaviour and karyology, it seems reasonable to treat *Parademansia* Kinghorn 1955 as a junior synonym of *Oxyuranus* Kinghorn 1923 and to modify *Oxyuranus* to include *'Parademansia' microlepidota.*

Genus *Oxyuranus* Kinghorn

Oxyuranus Kinghorn, 1923, p. 43 (Type species *Pseudechis scutellatus* Peters 1868 by monotypy).

Parademansia Kinghorn, 1955, p. 285 (Type species *Diemenia microlepidota* McCoy 1879 by monotypy).

Description:

Mid-body scales 21-25, anal single, subcaudals 48-76 and paired, ventrals 211-248; 1-5 pairs posterior maxillary teeth, 6-12 palatine teeth, 14-20 dentary teeth, 10-22 pterygoid teeth, fangs moderate (3.5-6.2 mm) to very long (7.9-12.1 mm).

A mid-body scale count of 21-25 sets *Oxyuranus* apart from all other genera of Australian elapids except *Pseudonaja, Tropidechis, Acanthophis*, and *Hoplocephalus. Oxyuranus* is readily distinguished from *Pseudonaja* in having fewer posterior maxillary teeth (1-5 *vs* 7-12). In *Oxyuranus* and *Tropidechis* the head muscles, hemipenis morphology, and skull morphology are similar. *Oxyuranus* may be distinguished from *Tropidechis* by the length of the pterygoid tooth row (less than half the pterygoid length *vs* more than half), maximum size (3.0 m *vs* 1.0 m), and in lacking keels on the dorsal scales. The dorsal scales in *Tropidechis* are always strongly keeled. *Oxyuranus* is easily distinguished from *Acanthophis,* which has a distinct viper-like body form, suboculars excluding the labials from the eye, mostly single subcaudals, and a quite different hemipenis. The hemipenis in *Acanthophis* is very elongated in its proximal smooth portion, has the sulcus forked within the zone of large spines (none of which is as large as the more proximal spines of *Oxyuranus*), and has the distal end of the organ conspicuously forked, with the tip of each lobe smooth. *Oxyuranus* differs from *Hoplocephalus* in lacking sharp angulation of the ventrals, in having divided subcaudals, and in hemipenis morphology. The hemipenis of *Hoplocephalus* is similar to that of *Acanthophis,* but lacks the conspicuous furcation and is merely bilobate distally.

The species of Oxyuranus: (Plate 1, Figs. a-b).

As redefined, *Oxyuranus* contains two species, *O. scutellatus* and *O. microlepidotus.* These are readily distinguished by the following features.

External features:

O. microlepidotus has a lower ventral scale count, a broader rostral, a shorter frontal and a

smaller eye than *O. scutellatus*. Further, it lacks a canthal ridge which is well developed in *O. scutellatus*.

Skull morphology:

The skull of *O. microlepidotus* is a smaller, more 'toothy' version of that of *O. scutellatus:* TL 25.6 mm-34.5 mm *vs* 30.0 mm-50.7 mm; $\frac{TL}{Breadth}$ 2.9-3.1 *vs* 3.3-3.7; palatine teeth 8-12 *vs* 6-7; pterygoid teeth 16-22 *vs* 10-17; dentary teeth 17-20 *vs* 14-17; posterior maxillary teeth 3-5 *vs* 1-2). The fangs of *O. microlepidotus* are moderate in size (3.5-6.2 mm). In *O. scutellatus* they are large (7.6-12.1 mm). See Table 3.

Venom:

O. microlepidotus produces less, but more toxic, venom which has a higher hyaluronidase activity than that of *O. scutellatus*.

Hemipenis:

In *O. microlepidotus* there are fewer transverse whorls of enlarged spines (1 *vs* 3) and the distal spines are evenly spaced (*vs* arranged in small groups).

Behaviour:

The minor differences between the two species are shown in Table 4.

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