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PHYLOGENETIC RELATIONSHIPS WITHIN THE AUSTRALASIAN VENOMOUS SNAKES OF THE GENUS *PSEUDECHIS*

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ABSTRACT: The six species of this monophyletic assemblage of large terrestrial proteroglyphous snakes are widely distributed through Australia and southern New Guinea. Data on cytogenetics, scalation, general morphology, and electrophoretic patterns of blood proteins were used to investigate relationships within this group. Chromosomally, *P. australis* (2N = 38) differs from other Australian taxa (2N = 36), but it is most similar to *P. butleri* in detailed morphology of the sex chromosomes. *P. colletti* and *P. guttatus* also are closely related whereas *P. porphyriacus* is divergent. The same groupings are apparent from electrophoretic studies of 18 protein systems (representing 27 presumed genetic loci) and in morphological analyses. Morphological data ally the New Guinea species, *P. papuanus*, with *P. colletti*.

Results from the various techniques are congruent, and they shown an ancestral stock differentiated into two groups: (1) *P. porphyriacus*, a viviparous diurnal species from cool and mesic habitats in eastern Australia, and (2) the other five species, which are oviparous, primarily crepuscular or nocturnal, and restricted to warm (often arid) environments throughout Australia and southern New Guinea. Within the oviparous radiation, two species of extreme xeric areas (*P. australis*, *P. butleri*) are closely related to each other. *Pseudechis guttatus* is intermediate between this group and another species-pair (*P. colletti* and *P. papuanus*). Despite their widely different habitats, the *Pseudechis* species are conservative in morphology, karyology, and general ecology. Subdivision of the genus is not recommended.

Key words: Elapidae; Snake; Cladistics; Phylogeny; *Pseudechis*; Australia; Viviparity; Chromosomes; Electrophoresis

PROTEROGLYPHOUS snakes are a major component of the snake fauna throughout tropical and subtropical areas of the world. However, the phylogeny and biology of most elapid species remain poorly known, in comparison to information on colubrid and viperid groups. A recent review of proteroglyph relationships (Mengden, 1983) concluded that most studies to date have concentrated upon the use of morphological data to identify species groups and have not attempted to examine inter- or intra-generic relationships. A notable exception is the work of McDowell (1967, 1970) using data on venom gland musculature and hemipenial morphology. More recently, several studies utilizing immunological analyses of blood serum and venoms have attempted to discern phylogenetic relationships within proteroglyphous taxa (e.g., Cadle and Sarich, 1981; Mengden, 1985*a*,*b*; Minton, 1981; Saint Girons and Detrait, 1980; Schwaner et al., 1985; Tamiya, 1985). One genus of particular interest is *Pseudechis*, an Australian group of large terrestrial elapids. Studies of microcomplement fixation and internal anatomy suggest that this genus is a distinctive lineage within the Australian elapids (Schwaner et al., 1985; Wallach, 1985). Immunoelectrophoretic studies on venoms suggest that *Pseudechis* may be a basal group for the elapid radiation, because they share several characteristics with Asian elapids (Saint Girons and Detrait, 1980). *Pseudechis* also is of interest from an ecological and zoogeographic perspective; not only do its component species occur in very different habitats and climatic types (e.g., Cogger, 1983), but the species differ also in reproductive mode

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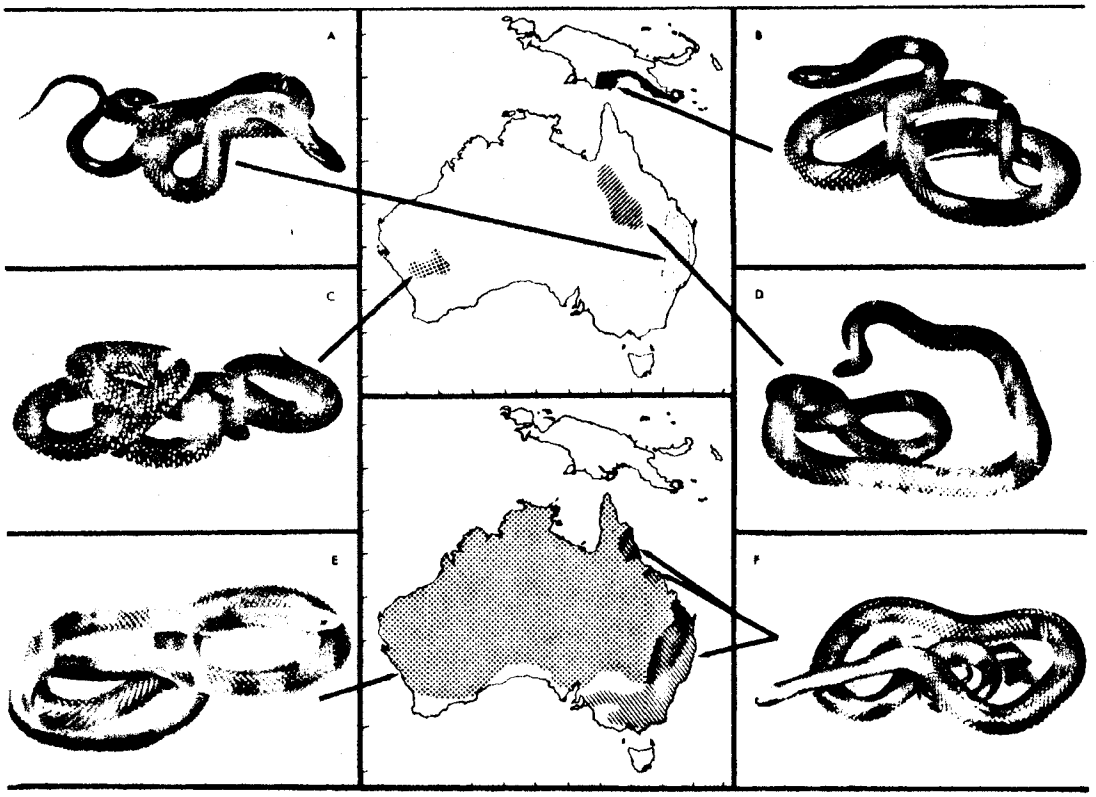

FIG. 1.—Gross morphology and distribution of *Pseudechis* species. (A) *P. guttatus*, color variable. Morphs include: black; black speckled with yellow or white; brown with darker and lighter spots. S.E. Queensland and N.E. New South Wales, except coastal areas. (B) *P. papuanus*, black with white throat. Coastal, southern Papua New Guinea. (C) *P. butleri*, black with extensive yellow and yellow-green speckling. Central Western Australia. (D) *P. colletti*, black with brilliant orange to yellow-brown blotches. Central inland Queensland. (E) *P. australis*, color variable, yellow-brown in the north with increasingly brown-tipped scales southward. Dark brown in peninsular South Australia and dark brown with yellow-orange lateral neck markings in western New South Wales. Found throughout Australia except cooler southern regions. Also reported from the southern border between Irian Jaya and Papua New Guinea. (F) *P. porphyriacus*, black dorsally, red ventrally. Eastern Australia.

(Charles et al., 1980, 1983; Fitzgerald and Mengden, 1985; Fitzgerald and Pollitt, 1981; Shine, 1977). Such examples of intrageneric diversity in reproductive mode are relatively rare (Shine, 1985). Hence, this situation stimulated our interest in the phylogenetic relationships within the group. The fossil record for *Pseudechis* is meager (Smith, 1976), so we were forced to rely on information from present-day species. We attempted to determine relationships among species with a combination of electrophoretic, karyotypic, morphological, ecological and behavioral data.

As currently recognized (Cogger et al., 1983), the genus *Pseudechis* comprises a group of six species of large venomous front fanged (proteroglyphous) snakes endemic to Australia and New Guinea. Since its original description, the composition and size of the genus has fluctuated markedly. Although the genus was erected in 1830 by Wagler to accommodate a single species (*P. porphyriacus*), the component species numbered eight by the time of Boulenger's (1896) classical work. By 1933, the genus included 14 taxa, but this total was reduced to five by a series of synonymies culminating in the work of Mackay (1955). The recent description of a new form from Western Australia (*P. butleri*

TABLE 1.—Running buffers and conditions for electrophoretic systems run on *Pseudechis* samples. This table lists the abbreviation for each protein system, its name, number of scorable loci, the electrophoretic commission number (EC No.) for each system, tissue used (E = erythrocyte; P = plasma), and the buffers and conditions employed for each system. Key to buffers: (1) 0.05 M Tris-EDTA-maleate, pH 7.8, 1 mM $MgCl_2$, 5 mM EDTA; (2) 0.1 M Tris-maleate, pH 7.8, 1 mM $MgCl_2$; (3) 0.015 M Tris-EDTA-maleate, pH 7.8, 1 mM $MgCl_2$, 5 mM EDTA; (4) 0.015 M Tris-EDTA-borate, pH 7.8, 1 mM $MgCl_2$, 5 mM EDTA; (5) 0.1 M Tris-citrate, pH 8.2; (6) 0.01 M citrate-phosphate, pH 6.4; (7) 0.04 M sodium-barbital, pH 9.9. All gels run at 10–13 V/cm at 4 C.

	Protein	Loci	EC no.	Tissue	Buffer and conditions
ACP	acid phosphatase	2	3.1.3.2	E	6; 3 h
ACON	aconitase	1		E	6; 1 h 20 min
GA_3PD	glyceraldehyde-3-phosphate dehydrogenase	1	1.2.1.12	E	1; 3 h 20 μg NAD added
GDA	guanine deaminase	1	3.5.4.3	E	1; 30 min
GOT	aspartate aminotransferase	2	2.6.1.1	E	5; 2 h
GP	general protein	4		P	7; 1 h
GPI	glucose-phosphate isomerase	1	5.3.1.9	E	4; 3 h 20 μg NAD added
GPT	alanine aminotransferase	1	2.6.1.2	E	5; 1 h
Hb	hemoglobin	1		E	3 or 5; up to 3 h
IDH	isocitrate dehydrogenase	1	1.1.1.42	E	5; 2 h
LDH	lactate dehydrogenase	2	1.1.1.27	E	1; 3 h 20 μg NAD added
MDH	malate dehydrogenase	2	1.1.1.37	E	1; 3 h 20 μg NAD added
PEP-LP	peptidase—substrate = leucyl-proline	1	3.4.13.9	E	2; 2 h
PEP-LA	peptidase—substrate = leucyl-alanine	2	3.4.11/13	E	2; 2 h
6PGD	6-phosphogluconate dehydrogenase	1	1.1.1.44	E	4; 1 h 30 min 10 μg NADP added
PGK	phosphoglycerate dehydrogenase	1	2.7.2.3	E	5; 2 h
PGM	phosphoglucomutase	1	2.7.5.1	E	3; 2 h
SOD	superoxide dismutase	1	1.15.1.1	E	1; 3 h
TPI	triosephosphate isomerase	1	5.3.1.1	E	1; 3 h 20 μg NAD added

Smith, 1982) resulted in a genus composed of six species. The dorsal coloration, gross morphology, and geographic distributions of these six taxa are illustrated in Fig. 1.

MATERIALS AND METHODS

Localities for the specimens examined karyologically and electrophoretically in this study are listed in Appendix I. Chromosomal data were obtained from air-dried slides of cell suspensions derived from both short term blood cultures (Mengden, 1983) and direct preparation from peripheral blood (Mengden, 1982). The C-banding technique follows the modifications described by Mengden (1981). G-banding was accomplished by a technique similar to that of Wang and Federoff (1972) using 0.01% trypsin in Hank's basal salt solution at 30 C. Chromosome pairs are numbered in decreasing size order including the Z.

The specimens indicated by an asterisk in Appendix I were examined by electrophoretic methods. Although the sample sizes for each of the five species of *Pseudechis* examined and the outgroup, *Pseudonaja nuchalis*, were small, this should have a negligible effect on phylogenetic reconstructions if (1) the number of loci analyzed is sufficiently large, (2) the level of individual heterozygosity is low, and (3) the genetic distances between the studied taxa are large (Baverstock et al., 1977; Gorman and Renzi, 1979; Nei, 1978). The affinities between *Pseudechis* and the other genera of Australian elapids are not clear. However, *Pseudonaja* was the obvious choice as an outgroup, because its members appear similar to *Pseudechis* in terms of general morphology, distribution, ecology and behavior

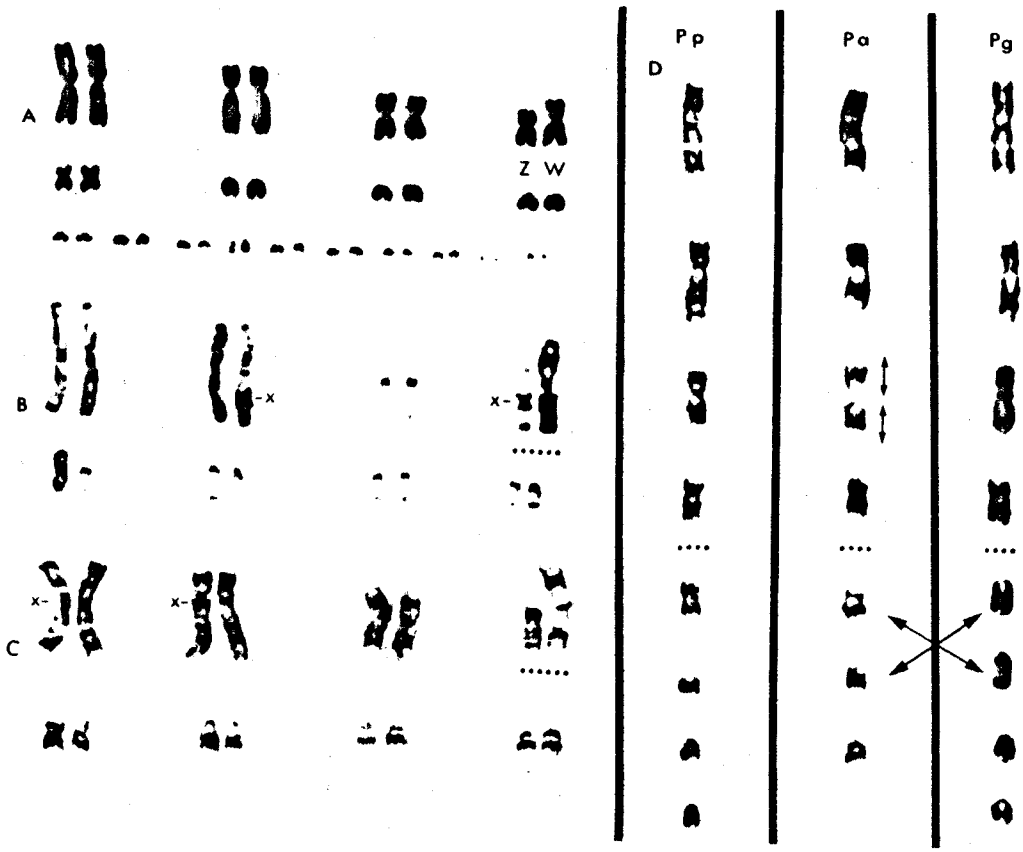

FIG. 2.—Chromosomes of *Pseudechis*. Sex chromosomes are labelled and underlined. Overlapping chromosomes in the original preparations are indicated by an "x" and these areas are omitted from banding comparisons. (A) Karyotype of *P. porphyriacus* (2N = 36; 16M/20m; 3 pairs of telocentric macrochromosomes). (B) G-banded macro elements of *P. porphyriacus*. (C) G-banded preparation from *P. porphyriacus*. (D) G-banded comparisons of the macrochromosomes of: Pp = *P. porphyriacus*; Pa = *P. australis*; Pg = *P. guttatus*. Pairs 5 and 6 of *P. australis* (2N = 38; 18M/20m) are involved in a Robertsonian type rearrangement relative to pair 3 of the other *Pseudechis* species (2N = 36; 16M/20m).

(Cogger, 1983), and *Pseudechis* has been shown to be monophyletic relative to *Pseudonaja* by other studies (Mengden, 1985*b*; Schwaner et al., 1985). The choice of *P. nuchalis*, rather than *textilis* or *ingrami*, was based on wide geographic distribution. However, this is not crucial because these *Pseudonaja* species are more similar to each other electrophoretically (Mengden, 1985*a*) than to any of the other genera of large Australian elapids.

Erythrocytes and plasma were separated by centrifugation of whole blood immediately after it was obtained from the specimens, and the resultant fractions were stored at −170 C. Prior to electrophoresis, the erythrocytes were lysed in a pH 7.0 solution consisting of 0.1 M Tris, 0.001 M EDTA, 0.005 M NADP and 5 μl of beta mercaptoethanol per 10 ml of solution (Selander et al., 1971). The electrophoresis was conducted on Cellogel (Chemetron, Milan), and the appropriate buffers and conditions for each protein assayed are given in Table 1. The staining techniques were modified for Cellogel from Harris and Hopkinson (1976). Data analysis was facilitated by the BIOSYS computer package for phylogenetic interpretation of electrophoretic data (D. L. Swofford and R. B. Selander, 1981, University of Illinois at Urbana, USA).

The comparative morphological analysis utilized 10 characters identified by our

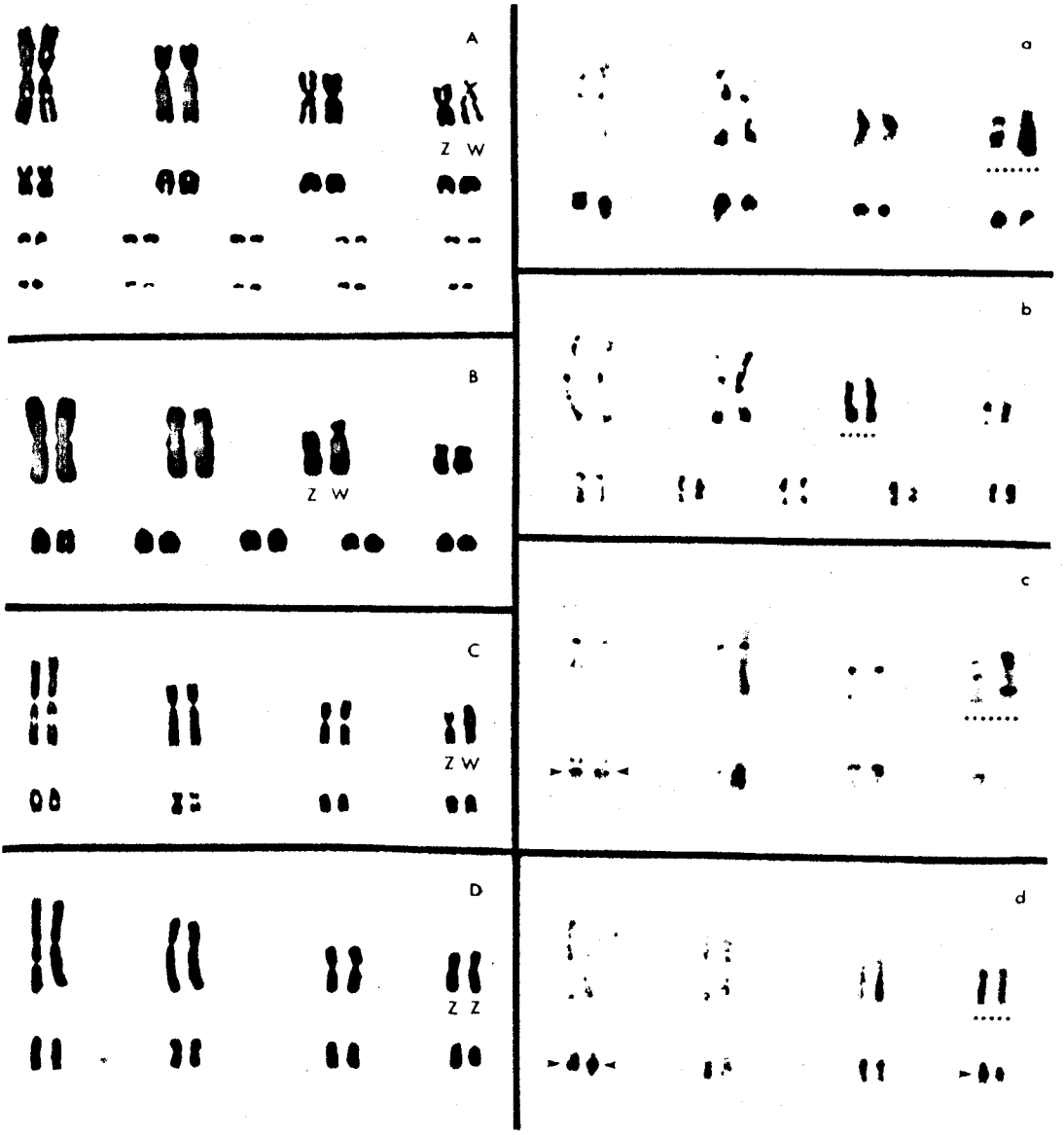

FIG. 3.—Chromosomes of *Pseudechis*. (A) Gross karyotype and (a) C-banded preparations from *P. butleri* (2N = 36; 16M/20m). Note the subtelocentric W chromosome similar to that seen in *P. australis*. (B and b) Gross karyotypic and C-band preparations of *P. australis* (2N = 38; 18M/20m, 5 pairs of telocentric macrochromosomes). The sex chromosomes are the third largest pair of chromosomes in descending size order. This condition results from a Robertsonian rearrangement of the metacentric pair 3 seen in other *Pseudechis*, yielding two smaller pairs of telocentric chromosomes in *P. australis* (see G-band comparisons Fig. 2D). (C and c) Gross karyotype and C-banded macrochromosomes of *P. guttatus*. (D and d) Gross karyotype and C-banded macrochromosomes of *P. colletti*. Note that both *P. guttatus* and *P. colletti* possess an interstitial heterochromatic addition to the largest of the three pairs of telocentrics (arrowed) resulting in the observed increase in the size of this pair.

preliminary observations as showing species-specific variation. These characters included absolute numbers of scales (at midbody; in contact with parietals; number of ventrals), ratios of scale counts and lengths (length-to-width ratios of frontal, parietal, and chin-shields; proportion of left and right anterior chin-shields

in contact with each other; ratio of divided to undivided subcaudals), and relative proportions of different parts of the body (relative eye size; relative head size). Measurements were taken on six preserved adult specimens of each taxon (see Table 4). Means were calculated for each variable for each species (Table 4 below), and this matrix was then normalized such that the sum of squares of each character vector over the species equalled unity. A matrix of Euclidean distances between the taxa was computed, and phenograms were generated from this matrix using average linkage (Orloci, 1978) and nearest-neighbor single linkage (Davis, 1971).

Results

Chromosomal Data

We examined chromosomes from all five of the currently recognized Australian *Pseudechis* species, but not from the New Guinean *P. papuanus*. Apart from *P. australis*, all the Australian species of *Pseudechis* have similar karyotypes except for species-specific variations in the morphology and banding character of the W chromosome (Mengden, 1981) and some differences in the C-band character of the autosomes (Figs. 2, 3). *Pseudechis porphyriacus, P. butleri, P. colletti* and *P. guttatus* all possess a diploid number of 36 with 16 macro- and 20 microchromosomes. The three largest autosomal pairs are similar to those of most other Australian terrestrial elapids (Mengden, 1982) being respectively metacentric, submetacentric and metacentric in descending order of size. The Z chromosome, which is the fourth largest pair, is metacentric in *P. porphyriacus* and *P. butleri* while it appears slightly submetacentric in *P. guttatus*. The W chromosome is larger than the Z, being the third largest element in all species of *Pseudechis* studied. The W is metacentric in *P. porphyriacus*, subtelocentric in *P. butleri*, and telocentric in *P. guttatus*. The remaining four pairs of macrochromosomes include one metacentric pair and three pairs of telocentrics. Metacentric pair 5 and telocentric pair 6 are very similar in overall length, and the telocentric pair even appears slightly longer than the metacentric in some preparations of *P. colletti* and *P. guttatus* (Fig. 3). The 20 microchromosomes are all telocentric or subtelocentric in all species.

All species exhibit a secondary constriction on one arm of pair 1 and this constriction is C-band positive. Prominent centromeric heterochromatin is present on all macrochromosomes. Small telomeric blocks are evident on pairs 1, 2 and the Z (Figs. 2, 3). In addition, *Pseudechis guttatus* and *P. colletti* possess a procentric C-block on telocentric pair 5, which explains the slightly larger relative size of this chromosome mentioned above (Fig. 3). Such an interstitial C-block is not evident in most other Australian elapids. It clearly represents a derived condition, probably the result of heterochromatic addition. *Pseudechis butleri* appears to display a relatively greater overall amount of heterochromatin, having particularly large heterochromatic blocks in the centromeric regions of the small metacentric pair and the three telocentric pairs (Fig. 3). The majority of microchromosomes in this species appear almost completely heterochromatic. G-band data for the *Pseudechis* species are illustrated in Fig. 2.

Pseudechis australis differs from all other species in the genus in possessing a diploid number of 38, with 18 macrochromosomes and 20 microchromosomes (Fig. 3). This distinctive karyotype is the result of a Robertsonian rearrangement involving the metacentric pair 3 observed in the other species of *Pseudechis*. Thus *P. australis* possesses two small pairs of acrocentrics (pairs 5 and 6 of *P. australis*) in place of the metacentric pair 3 of the other species. The sex chromosome pair consequently is the third rather than the fourth largest pair though the Z is equivalent in size (and gross morphology) to that of *P. butleri* relative to the length of pair 1. G-band analysis unequivocally confirms the homology between pairs 5 and 6 of *P. australis* and pair 3 of the other *Pseudechis* species (Fig. 2).

Electrophoretic Data

In total, 18 protein systems representing 27 presumed genetic loci were analyzed.

TABLE 2.—Allele frequency from electrophoretic data. "N" refers here to null activity at the loci for the taxa run under these conditions (see Materials and Methods).

Locus		*P. australis*	*P. guttatus*	*P. butleri*	*P. colletti*	*P. porphyriacus*	*Ps. nuchalis*
	$n =$	6	3	3	4	3	3
ACP-1	1.32						100
	1.25					100	
	1.00	100	100	100	100		
ACP-2	1.11					100	
	1.00	100	100	100	75		
	0.91				25		
	N						100
ACON	1.08						100
	1.00	91		100		67	
	0.93	9	100		100	33	
GA_3PD	1.00	100	100	100	100		
	0.88					100	
	0.82						100
GDA	1.00	100	100	100	100		
	N					100	100
GP-1	1.00	100	100	100			
	0.95				100		
	0.92					100	
	N						100
GP-2	1.12						50
	1.08					100	50
	1.04		100	100			
	1.00				100		
GP-3	1.06			100			
	1.00	100	100		100	100	100
GP-4	1.00	63	100				100
	0.96				100	100	
	0.91	37		100			
GPT	1.13						100
	1.00	100	100	100		100	
	0.89				100		
Hb	1.00	100	100	100	100		
	0.94					100	
	0.89						100
MDH-2	1.00	100	100	100	100		
	0.95						100
	0.90					100	
PEP-LP	1.00	100	100	100	100		
	0.90					100	100
PEP-LA-1	1.21		67		100		
	1.00	100	33	100			
	0.93						100
	0.88					100	
PEP-LA-2	1.32					100	
	1.05				100		
	1.00	100	100				
	N			100			
PGK	1.00	100	100	100	100		
	0.96					100	
	0.90						100
SOD	1.38						100
	1.00	100		100		100	
	0.88		100		100		

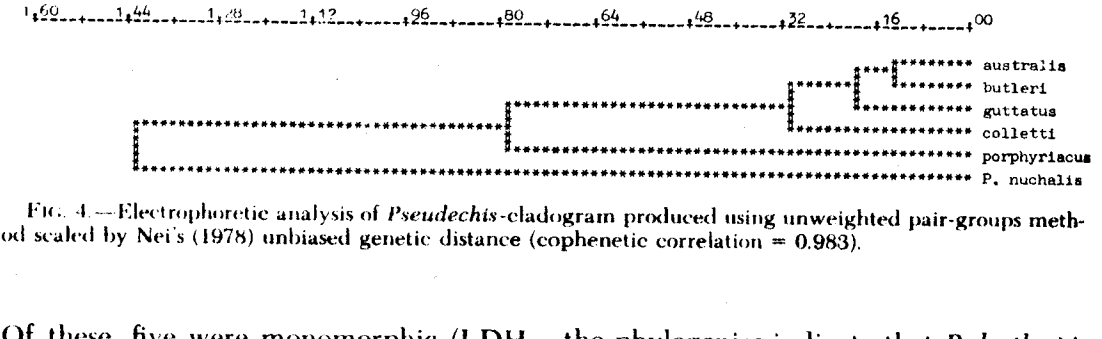

FIG. 4.—Electrophoretic analysis of *Pseudechis*-cladogram produced using unweighted pair-groups method scaled by Nei's (1978) unbiased genetic distance (cophenetic correlation = 0.983).

Of these, five were monomorphic (LDH 1 and 2, GPI, TPI and ICD) and an additional five showed no variation within the species of *Pseudechis* examined (PGM, MDH-1, GOT 1 and 2, 6PGD). The allele frequencies for the remaining 16 loci are given in Table 2. The alleles are designated by their mobility relative to the condition in *P. australis*. However, at four loci (ACP-2, GDA, GP-1 and PEP LA-2), the alleles in at least one species (usually the outgroup) could not be visualized under these conditions. Since this phenomenon could not be attributed to the low activity of the samples concerned, the absence of activity has been regarded as an additional character state in preference to excluding these loci from the analysis.

The genetic distance estimates (Nei, 1978; Rogers, 1972) between the species are presented in Table 3. The Nei genetic distances were used to generate a dendrogram by the UPGMA clustering procedure (Sneath and Sokal, 1973) and an outgroup-rooted distance-Wagner tree (Farris, 1972) was constructed from the Nei distance estimates (Fig. 4). Although the phylogenetic relationships determined by these two methods were fully concordant, it should be recognized that the chosen outgroup shared few alleles with *Pseudechis* (Table 2). These data were not considered suitable for the construction of an accurate phylogenetic tree by Hennigian cladistic procedures, because few shared-derived characters could be determined.

The dendrogram and distance-Wagner trees show that three species (*P. australis*, *P. butleri* and *P. guttatus*) form a closely related group within the genus. Although the phylogenies indicate that *P. butleri* is closer to *P. australis* than is *P. guttatus*, it should be noted that these two species are equidistant from *P. australis* using the Nei genetic distances. On the basis of the available electrophoretic data, these three species should be regarded as an unresolved trichotomy. In contrast, *P. colletti* is differentiated from the above species at four loci (GPT, GP-1, GP-2 and PEP LA-2; Table 2) and represents a distinct lineage.

The Nei genetic distance among these four species ranges from 0.135–0.411, which is considerably lower than those between *P. porphyriacus* and all other species of *Pseudechis* so far examined (range 0.660–0.766, Table 3). Thus, relative to the genetic differences between the other four species, *P. porphyriacus* is a highly divergent member of the genus.

Morphological Data

The two algorithms used (single linkage, average linkage) produced identical results. Two species-pairs were identified: *colletti-papuanus* (similarity 0.995) and *australis-butleri* (similarity 0.994). These two groups together then formed the next most similar cluster of species (average similarity 0.991), with *P. guttatus* falling just outside this group (0.985). The remaining species, *P. porphyriacus*, was very divergent from all the others (0.961).

Ecological Data

Pseudechis porphyriacus is viviparous, with limited placental nutrient transfer (Shine, 1977). In contrast, oviparity characterizes all of the remaining species: *P. australis* (Fitzgerald and Pollitt, 1981), *P. butleri* (Fitzgerald and Mengden, 1986),

TABLE 3.—Matrix of genetic similarity and/or distance coefficients. Below the diagonal is Nei's (1978) unbiased genetic distance. Above the diagonal is Rogers' (1972) genetic distance.

Population	1	2	3	4	5	6
P. australis	—	0.147	0.137	0.261	0.486	0.748
P. guttatus	0.135	—	0.210	0.207	0.539	0.731
P. butleri	0.135	0.226	—	0.343	0.531	0.810
P. colletti	0.287	0.214	0.411	—	0.540	0.769
P. porphyriacus	0.660	0.764	0.747	0.766	—	0.718
Ps. nuchalis	1.379	1.327	1.674	1.484	1.258	—

P. colletti (Charles et al., 1983), *P. guttatus* (Charles et al., 1980) and *P. papuanus* (present study: based on shelled oviducal eggs in MCZ specimen R-129207).

Dissection of 870 museum specimens, combined with detailed field studies on *P. porphyriacus*, permit the following generalizations about the ecology of *Pseudechis* (Shine, 1977, 1979; Shine and Allen, 1980; Shine and Bull, 1979; Shine et al., 1981): All of the *Pseudechis* species are similar in adult body sizes and in the direction and degree of sexual size dimorphism (males grow much larger than females). Male combat has been recorded in *P. australis*, *P. guttatus* and *P. porphyriacus*. All species have generalized diets, with geographic variation; major prey items are frogs in wetter areas, reptiles and mammals in drier regions. All species appear to be similar in seasonal timing of reproduction (oviposition or parturition in summer), fecundity, incubation period (in the oviparous forms), and hatchling size. *P. porphyriacus* is diurnal and is restricted to mesic habitats, whereas the oviparous forms within Australia are primarily nocturnal (especially in northern areas) and are in relatively xeric to extremely xeric habitats.

DISCUSSION

The cytogenetic, morphological and electrophoretic data are broadly consistent with each other. The monophyletic nature of this group is evidenced by the extensive morphological and cytogenetic similarities between all *Pseudechis* species (see above), similarities in internal anatomy (Wallach, 1985), and the strong cross-reaction between all Australian *Pseudechis* species so far tested, relative to other Australian proteroglyphs, in microcomplement fixation studies (Schwaner et al., 1985). In attempting to erect the most parsimonious hypothesis of phylogenetic relationships within *Pseudechis*, one would ideally rely only on characters in which primitive and derived states could be identified. In this way, a purely cladistic approach could be pursued. This can be done with the karyotypic data, because there is good evidence as to the primitive karyomorph within the group (Mengden, 1982, 1985*b*). However, our electrophoretic and morphological data only provide estimates of overall similarity. In practice, a combination of these data sets provides an unambiguous picture of *Pseudechis* phylogeny.

The electrophoretic analysis has proven especially valuable in resolving the phylogeny of this group. It seems clear from these data that *P. porphyriacus* is very divergent from the other taxa. On the other hand, *P. australis* and *P. butleri* are close to each other, with *P. guttatus* also related to these two. *Pseudechis colletti* represents a distinct lineage. We will now discuss each of these groups identified by electrophoresis, adding data from cytogenetics, morphology and ecology.

Pseudechis porphyriacus

The electrophoretically distinctive nature of *P. porphyriacus* could be interpreted in two different ways. First, this species may have split off from the lineage leading to the other species at a very early stage in the evolution of the genus. Second, rates of allelic substitution at the analyzed structural gene loci may vary remarkably between lineages (Baverstock et al., 1979). Thus, it is possible that *P. por-*

TABLE 4.—Morphology of *Pseudechis* species based on examination of six preserved adult specimens for each taxon. The table gives the $\bar{x}$ with 1 SD in brackets. Specimens examined for morphological data (AM = Australian Museum; QM = Queensland Museum; MCZ = Museum of Comparative Zoology, Harvard; WAM = Western Australian Museum; EG = Eric Gibson private collection). *P. australis:* AM—R26408, R31801, R52367, R98617, R101357, R101998. *P. butleri:* WAM—R5372, R7627, R12919, R13703, R25978, R26815. *P. colletti:* AM—R74512, R25883; QM—J11520, J41485, J41489, J41490. *P. guttatus:* AM—R13132, R15595, R18333, R37369, and two unnumbered EG specimens. *P. papuanus:* MCZ—59065, 59072, R137526, Y129207, AM—R15396; QM—J32938. *P. porphyriacus:* AM—R84232, R103818, R103819, R103828, R104004.

Character	*P. australis*	*P. butleri*	*P. colletti*	*P. guttatus*	*P. papuanus*	*P. porphyriacus*
Number of midbody scale rows	17.0 (0.0)	17.0 (0.0)	19.0 (0.0)	19.0 (0.0)	19.0 (0.0)	17.0 (0.0)
Number of scales in contact with parietal scale	11.5 (1.5)	11.2 (1.0)	14.0 (0.9)	11.2 (0.8)	13.8 (0.4)	11.3 (0.5)
Ratio of length to width of frontal scale	1.83 (0.16)	1.52 (0.23)	1.59 (0.09)	1.55 (0.17)	1.59 (0.23)	1.61 (0.18)
Ratio of length to width of parietal scale	1.91 (0.12)	1.79 (0.12)	1.63 (0.11)	1.92 (0.14)	1.75 (0.20)	1.48 (0.12)
Ratio of length to width of chin shield	2.82 (0.60)	3.29 (0.51)	2.23 (0.56)	3.12 (0.42)	2.19 (0.27)	2.55 (0.20)
Proportion of left and right chin shields in contact with each other	0.69 (0.19)	0.54 (0.28)	0 (—)	0.46 (0.25)	0.66 (0.02)	0.54 (0.08)
Ratio of eye diameter to head length (snout to tip of quadrate)	0.12 (0.03)	0.13 (0.01)	0.12 (0.02)	0.12 (0.01)	0.11 (0.01)	0.15 (0.01)
Ratio of divided to undivided subcaudals	0.30 (0.28)	0.65 (0.36)	0.22 (0.10)	0.67 (0.28)	0.89 (0.44)	7.88 (2.98)
Number of ventral scales	205.2 (7.1)	214.2 (1.8)	220.3 (3.3)	193.7 (4.6)	222.2 (3.7)	187.2 (1.7)
Ratio of head length to snout–vent length	0.038 (0.005)	0.037 (0.003)	0.032 (0.004)	0.040 (0.003)	0.033 (0.003)	0.036 (0.002)

phyriacus is a recently derived species that has been subject to extremely rapid electrophoretic change. It is possible to distinguish between these alternatives on the basis of the electrophoretic data; *P. porphyriacus* is more similar to the outgroup (*Pseudonaja*) than are any of the other *Pseudechis* species, suggesting a relatively ancient divergence of *P. porphyriacus* from its congeners. The other data sets show that *P. porphyriacus* is unique also in its large metacentric W chromosome and in several aspects of scalation and bodily proportions (Table 4). These additional differences, in unrelated characters, support the hypothesis of an early divergence of *P. porphyriacus* from the major *Pseudechis* lineage. Ecological data also support this conclusion: *P. porphyriacus* differs strongly from all of its congeners in geographic distribution, habitat preference, activity time and reproductive mode. Further evidence for the unique status of this species comes from the coagulating properties of its venom, as opposed to those of *P. australis* and *P. colletti* (Chester and Crawford, 1982).

Pseudechis australis *and* P. butleri

Pseudechis australis has a remarkably wide geographic distribution, covering all of mainland Australia except for the southeastern corner (e.g., Cogger, 1983). There is considerable geographic variation in body sizes (northern specimens attain much larger sizes) and dorsal coloration. For example, northern specimens are uniformly sandy brown, central desert specimens are strongly "speckled" with a white spot on each scale, and southern specimens tend to be very dark in overall color. Extensive clinal variation can be demonstrated both in coloration and in scalation (Smith, 1982). These geographic differences have led in the past to the recognition of several species within *P. australis* (*darwiniensis*—Macleay, 1878; *cupreus*—Boulenger, 1896; *denisonioides*—Werner, 1909; *platycephalus*—Thomson, 1933; *brunnea*—Mitchell, 1951). These species were synonymized on morphological grounds (see Mackay, 1955; Cogger et al., 1983 for synonymy), but recently three of these taxa were resurrected without explanation by Wells and Wellington (1983). Our electrophoretic and chromosomal data give no support to this view (Table 2, Figs. 2 and 3), and we consequently relegate *cuprea*, *brunnea* and *denisonioides* back to the synonymy of *Pseudechis australis*. However, we recognize that detailed population studies using electrophoresis would be needed to more fully resolve the problem.

As well as their electrophoretic similarity, geographically distant *P. australis* share a similar and distinctive karyomorph. All of the other Australian *Pseudechis* show a diploid number of 36 (16 macro/20 micro), with the three smallest macrochromosomes telocentric. This condition is seen in a diverse array of Australian elapid species, and it has been proposed to be the ancestral condition for this entire group (Mengden, 1982, 1985*b*). In contrast, *P. australis* has a modified karyomorph (presumably, a derived condition relative to the other *Pseudechis*) where fission of the pair 3 metacentric has given rise to two pairs of medium-sized telocentric chromosomes.

As is common in other elapid species (Mengden, 1981), the W chromosome shows species-specific variation within *Pseudechis* both in gross morphology and in C-band characteristics. Significantly, however, two species (*P. australis* and *P. butleri*) have almost identical W chromosomes (Fig. 2). These data support the conclusion, from electrophoresis and morphology, that *P. australis* and *P. butleri* are closely related. Also, the derived autosomal condition in *P. australis* affords additional information on its placement on the *Pseudechis* phylogenetic tree: *P. australis* is not likely to be directly ancestral to any other species in the genus (Mengden, 1985*b*).

Morphological data emphasize the close resemblance between *butleri* and *australis*, despite their differences in coloration (Table 4). This meristic similarity also is highlighted by the excellent study of Smith (1982). However, we disagree with Smith's

suggestion that *butleri* is most closely related to *porphyriacus*. Although it is true that *butleri* and *porphyriacus* both have 17 scale-rows, and that there are superficial similarities in coloration, our data unequivocally place *butleri* near *australis* rather than *porphyriacus*. Similarities between the two, as opposed to *porphyriacus*, include: blood proteins, W chromosome characteristics, coagulant properties of the venoms, oviparity, gracile build, arid habitat, geographic contiguity, high proportion of undivided subcaudals, crescent-shaped black markings on anterior edge of each ventral scale (versus posterior edge in *porphyriacus*), higher ventral counts, small relative eye size, lack of distinct canthus rostralis, and shape of the parietal scale (Table 4). Although some of these characters (e.g., oviparity) are primitive features and hence afford no information on relationships, most others appear to be shared derived conditions.

Pseudechis guttatus

The affinities of *P. guttatus* are clearly with the other oviparous species rather than with *P. porphyriacus*, but its exact placement is problematical. The electrophoretic data place *P. guttatus* slightly closer to the *australis-butleri* group than to *P. colletti* (Nei, 1978, unbiased genetic distances of 0.23 and 0.14, versus 0.21), but the difference is trivial. Karyotypic and morphological data are more revealing. Possession of a shared derived chromosomal character (interstitial heterochromatic addition to telocentric pair 5) unequivocally allies *P. guttatus* with *P. colletti*. Also, *Pseudechis guttatus* and *P. colletti* both have 19 mid-body scale-rows, whereas *butleri* and *australis* have 17 rows. Thus, if *guttatus* shares a more recent common ancestor with *butleri* and *australis* than with *colletti*, one must invoke two independent evolutionary increases in number of mid-body scale rows: one in the lineage to *P. guttatus* and one to *P. colletti* (or, two separate reductions—one in *butleri-australis* and one in *porphyriacus*). While such changes could occur, the chromosomal data make it more reasonable to assume that *guttatus* is more closely related to *colletti* than to *butleri-australis*. Then, the phylogenetic tree is consistent with a primitive number of mid-body scale rows (17, now shown by *butleri, australis*, and *porphyriacus*) evolving to a higher number (19) only once, in the lineage leading to *colletti, guttatus*, and *papuanus*). This putative relationship between *guttatus* and *colletti* is also supported by their contiguous geographic distributions, and their similarity in color pattern and scalation (Fig. 1, Table 4).

Pseudechis colletti *and* P. papuanus

Although we have argued for a relatively closer relationship of *guttatus* to *colletti* than to *australis-butleri*, it is clear from the electrophoretic data that *P. colletti* is a distinct and well-differentiated taxon (Tables 2 and 3). In contrast, some earlier authors have treated *colletti* and *guttatus* as subspecies (e.g., Worrell, 1963).

In the absence of electrophoretic and cytogenetic data on *P. papuanus*, the affinities of this New Guinean form remain ill-defined. However, examination of preserved specimens strongly suggests that its affinities lie with *P. colletti*. These two species form the closest pair morphologically, being more similar to each other than either was to any other species, for seven of the 10 characters scored. This putative relationship also seems reasonable on zoogeographic grounds, although the habitat preferences are very different.

These considerations may be combined to produce an hypothesis on the overall phylogenetic relationships with *Pseudechis* (Fig. 5). Most aspects of this hypothesis are well supported: for example, the divergent position of *P. porphyriacus* and the close relationship of *australis* and *butleri* on the one hand, and *colletti* and *papuanus* on the other. Electrophoretic and cytogenetic data on *P. papuanus* would be of value. The phylogenetic hypothesis of Fig. 5 has interesting ecological and zoogeographical implications. The ancestral *Pseudechis* may be inferred to most closely resemble the present-day *P. butleri*, with characterisics such as oviparity, warm climatic zone, 17 midbody scale

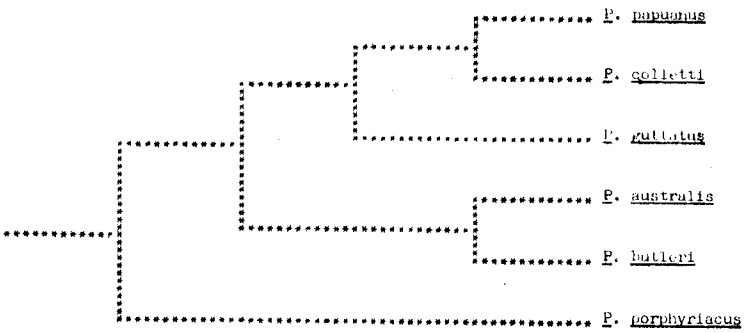

FIG. 5.—"Best guess" phylogeny of *Pseudechis* based on chromosomal, electrophoretic, morphological and ecological data presented here.

rows, and diploid number of 36 chromosomes. It appears that early in the history of the group, two stocks diverged. One of these led to an extensive radiation in warm climates, ranging from extreme aridity (*australis*, *butleri*), through to more mesic areas (*colletti*, *guttatus*) and to lowland tropical swamps (*papuanus*). All of these forms retained the primitive reproductive mode of oviparity, as is typical of most warm-climate reptiles (e.g., Shine and Berry, 1978; Tinkle and Gibbons, 1977). In contrast, the other basal *Pseudechis* stock produced a single surviving taxon (*P. porphyriacus*), which occupies montane eastern Australia. Primary adaptations of *P. porphyriacus* include viviparity (which apparently has evolved in cold climates in many reptilian lineages: Shine, 1985), diurnal activity, and utilization of riparian habitats. Although we are confident of the broad outlines of this hypothesis, several puzzles remain. Perhaps the most intriguing puzzle is the apparently rapid spread of a single species (*P. australis*) throughout most of mainland Australia. Both the electrophoretic and morphological data suggest that *P. australis* is extremely similar to *P. butleri*, and one might thus infer that their separation was relatively recent. *P. australis* has the more derived karyotype, so that it must have radiated into a diverse array of habitats, and evolved marked geographic variation in color pattern, over a short time-span relative to that separating most of the other species of *Pseudechis*. However, recent studies using microcomplement fixation suggest that the *Pseudechis* radiation has occurred over a much longer period than has been involved in speciation within many other genera of Australian proteroglyphs (Schwaner et al., 1985). Although the spread of *P. australis* may have been rapid compared to other events in the *Pseudechis* lineage, it may have occupied a long time relative to adaptive radiations in other genera of Australian elapids.

Although the genus *Pseudechis* has undergone a major adaptive radiation throughout the Australian continent, it would be misleading to stress only the differences between species. In many respects, *Pseudechis* is a conservative group. For example, interspecific differences are relatively minor with respect to scalation, size, general body form, karyology and ecology. These conclusions lead us to refrain from any formal subdivision of *Pseudechis*. It is clear that *P. porphyriacus* is quite divergent from the other taxa. However, the entire *Pseudechis* group undoubtedly is monophyletic, is very distinct from all other lineages of Australian elapids, and is conservative in many features. The substantial electrophoretic distance between *P. porphyriacus* and its congeners does not constitute a case for generic subdivision per se; many other reptile genera include species with equally great levels of genetic differentiation (Avise and Aquadro, 1982). Hence, we reject the recent suggestion (Wells and Wellington, 1983) that this genus should be divided into *Cannia* [containing *australis*, *colletti* and "*papuanis*" (sic)] and *Pseudechis*

(containing *butleri*, *guttatus* and *porphyriacus*). No reasons were given for this division, and it is clearly inconsistent with all of our data. Thus, we formally synonymize *Cannia* with *Pseudechis*. To divide this genus would be to obscure the biological reality of its adaptive radiation, rather than to illuminate it.

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APPENDIX I

Specimens Examined for Chromosomal and Electrophoretic Analysis

P. australis: GAM 14, N.L. Taronga Zoo; *GAM 112**, Cuddapan, Qld.; *GAM 217*, Doongan Stn., Kimberleys, W.A.; *GAM 283*, *GAM 344**, Alice Springs, N.T.; *GAM 252**, *GAM 292*, Mooney, Qld.; *GAM-TS 249**, N.L., S.A.; *GAM-TS 107**, Tierdya Sta., S.A.

*P. butleri: GAM-TS 174**, *GAM 205**, *GAM 267**, Yalgoo, W.A.

*P. colletti: GAM-TS 224**, *GAM-TS 225**, *GAM-TS 226**, *GAM 164**, Richmond, Qld.

P. guttatus: GAM 4, *GAM 204*, *GAM 267*, *GAM-TS 250**, *GAM-TS 467*, Oakey, Qld.; *GAM-TS 231**, *GAM-TS 232*, Forrest Hill, Qld.; *GAM-TS 208**, *GAM-TS 209*, *GAM-TS 210*, Dubbo, N.S.W.; *GAM 156*, *GAM 44*, *GAM 22*, *GAM 45*, N.L. captives.

P. porphyriacus: GAM 46, Casuarina Sands, A.C.T.; *GAM 245**, *GAM 317*, "Adnamira" via Dogtrap Rd., N.S.W.; *GAM 73*, *GAM 215*, N.L. captives; *GAM-TS 219*, *GAM-TS* 221*, Sandy Camp, Macquarie Marshes, N.S.W.; *GAM-TS 219*, Madden's Plains, N.S.W.; *GAM-TS 229*, Numinbah Valley, Qld.; *GAM-TS 250**, Docker's Creek, Qld.; *GAM-TS 468*, Eungella, Qld.

* Specimens examined for electrophoretic analysis.

N.L. = no locality.

GAM = Mengden collection.

GAM-TS = Mengden tissue sample from live specimen.