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Molecular phylogeny of viviparous Australian elapid snakes: affinities of *Echiopsis atriceps* (Storr, 1980) and *Drysdalia coronata* (Schlegel, 1837), with description of a new genus

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Abstract

The rare Australian venomous elapid snake '*Echiopsis*' *atriceps* has been the subject of considerable taxonomic instability with the five known specimens assigned to four genera by various authorities. Phylogenetic affinities of the rare *Elapognathus minor* also are poorly understood and have been the subject of some disagreement. To examine the phylogenetic affinities of these two rare taxa, a molecular data set comprising 1680 base pairs of mtDNA was assembled from a representative of each of the terrestrial Australian viviparous elapid genera and two species of *Drysdalia*, a genus about which there also has been phylogenetic controversy. A total of 936 base pairs of 12S rRNA, 454 base pairs of 16S rRNA and 290 base pairs of cytochrome *b* mtDNA were sequenced for 15 species. The Asian elapid *Naja naja* was used as the outgroup. These mtDNA regions provided 195, 38 and 72 parsimony informative sites, respectively, for a total of 315 parsimony informative characters. Unweighted phylogenetic analyses were performed under both parsimony and neighbour-joining criteria. Parsimony analyses of the unweighted, combined data set resulted in a single fully resolved most parsimonious tree 1225 steps long. The neighbour-joining tree differed by only a single weakly supported branch. These data strongly support a sister group relationship between '*Echiopsis*' *atriceps* and the Australian broadheaded snakes of the genus *Hoplocephalus* with a bootstrap value of 99%. Templeton tests soundly reject all previous taxonomic arrangements for this species. Our data also strongly support a sister group relationship between *Elapognathus minor* and *Drysdalia coronata* with a bootstrap value of 98%. Importantly, *Drysdalia coronata* and *Drysdalia coronoides* do not form a monophyletic group, supporting some previous studies. Based on our results, we allocate '*Echiopsis*' *atriceps* to a new monotypic genus and re-describe *Elapognathus* to include '*Drysdalia*' *coronata*.

Key words: elapid snake, mitochondrial DNA, taxonomy, Australia

INTRODUCTION

The taxonomy of Australian elapid snakes has been particularly unstable, due almost entirely to the lack of a well-resolved phylogeny for the radiation (Mengden, 1983; Cogger, 1985; Keogh & Smith, 1996). While a number of authors have attempted to provide a phylogenetic framework for the Australian elapids based on data sets as diverse as morphology (McDowell, 1967, 1969, 1970; Wallach, 1985; Keogh, 1999), immunological distance (Schwaner *et al*., 1985), allozymes and karyology (Mengden, 1985) and DNA sequences (Keogh, 1998; Keogh, Shine & Donnellan, 1998), phylogenetic relationships are still not well resolved. Despite the lack of phylogenetic information, taxonomic shuffling of taxa among genera has proceeded unabated (reviewed in Keogh, 1999). In this paper we consider the phylogenetic affinities of one such species, '*Echiopsis*' *atriceps*, and also consider the affinities of the monotypic *Elapognathus minor*, and *Drysdalia coronata* and *D. coronoides*, based on DNA sequence data.

The Australian elapid snake '*Echiopsis*' *atriceps* is currently known from only five preserved museum specimens, all collected in the area of Lake Cronin in south-central Western Australia (32°23′S, 119°45′E). Due in part to the intermediate nature of commonly used diagnostic characteristics, but more importantly to the lack of rigorous comparative study, this species has been assigned to several genera. When describing the new species, Storr (1980) tentatively placed it in *Brachyaspis* with *B. curta*, but subsequently

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'shoehorned' both species into separate genera as *Notechis curtus* (Storr, 1982) and *Denisonia atriceps* (Storr, 1984).

Storr's (1982) concept of *Notechis* also included the species of *Austrelaps*, *Elapognathus* and *Drysdalia*, though his revision treated only species occurring in Western Australia. The oldest generic name for this assemblage is *Echiopsis* Fitzinger, 1843 which, though overlooked by Boulenger and many subsequent authors, was reinstated by Cogger (1975). *Brachyaspis* Boulenger, 1896 is unavailable as the name was preoccupied (Storr, 1982; Cogger, Cameron & Cogger, 1983). Storr (1982) regarded *Echiopsis* as a *nomen oblitum* and therefore unavailable, despite wide currency and acceptance of Cogger's classification outside Western Australia. In contrast to Storr, Cogger (1983, 1992), Cogger *et al*. (1983), Wells & Wellington (1984, 1985) and Golay (1985) retained both *atriceps* and *curta* in the genus *Echiopsis*; however, the use of the word 'stumpy' in Coggers (1983) generic diagnosis does not suggest familiarity with specimens of *atriceps*. Storr's (1984) expanded *Denisonia* also includes three species that most others refer to *Suta* (*S. fasciata*, *S. ordensis* and *S. suta*), and Storr, Smith & Johnstone (1986), Wilson & Knowles (1988) and Ehmann (1992) followed this classification of *atriceps*. Hutchinson (1990) also supports this close relationship to some members of *Suta*, and Golay *et al*. (1993) took this a step further, formally placing *atriceps* in *Suta* (otherwise with the same content as in Hutchinson, 1990 and Cogger, 1992).

It should be made clear that none of the above taxonomic decisions was accompanied by phylogenetic analyses of any kind. Wallach (1985) carried out a morphological study and phylogenetic analysis of most species of terrestrial Australian elapids, and while he did not report any data on *atriceps* or mention it in the text, he did include it in a 'hypothetical phylogeny' (his fig. 5; the caption states 'Taxa indicated by (?) were not available for examination' but no taxa were so marked in the figure). Wallach represented *Echiopsis curta* and '*E.*' *atriceps* as sister groups to members of *Notechis*, *Tropidechis* and *Hoplocephalus* (Fig. 1). More recently, Greer (1997) has performed another phylogenetic analysis on Australian elapids but these analyses did not shed any light on the relationships of *atriceps*.

In contrast to '*Echiopsis*' *atriceps*, the monotypic *Elapognathus minor* has been the subject of very little taxonomic shuffling since the separation of this species from the greatly expanded *Hoplocephalus* of Günther (1858) by Boulenger (1896) based on the lack of maxillary teeth behind the fang. Nevertheless, systematic studies in which *E. minor* has been included have come to very different conclusions as to the affinities of this species. Based largely on venom gland musculature, McDowell (1967) placed *Elapognathus minor* in his '*Glyphodon*' group, the members of which he considered to share the primitive condition. This diverse group contained a number of Australian elapids, but also American and Asian coral snakes and Afro-Asian *Naja*. Storr (1982) did not comment on

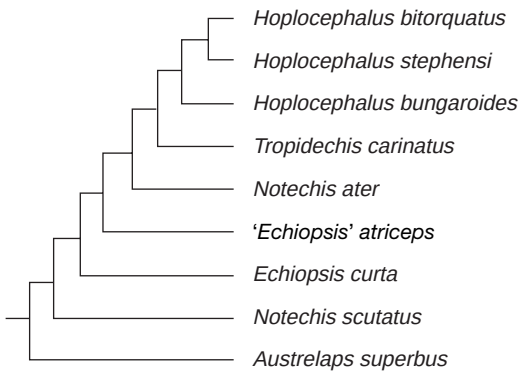

Fig. 1. Part of a hypothesized phylogeny for the taxa relevant to this study from Wallach (1985). This clade was part of a larger phylogeny which included virtually all species of Australian elapid and is based on a cladistic analysis of 50 primarily morphological characters.

McDowell's placement of *Elapognathus* but he did feel that the lack of maxillary teeth was too correlated with diet to be of taxonomic use and so synonymized *Elapognathus* (along with *Echiopsis*, *Drysdalia* and *Austrelaps*) with *Notechis* based only on a few external morphological characters. Wallach's (1985) morphologically based phylogenetic analysis nests *Elapognathus* within a clade formed by species that are now part of *Rhinoplocephalus* and *Suta* (after the classification of Hutchinson, 1990). A study of chromosomal morphology showed that *E. minor* possessed a '*Pseudechis* karyomorph' with a diploid chromosome number of 36 (Mengden, 1985). However, taxa included in this group are morphologically and phylogenetically diverse and not necessarily closely related based on independent data (and Mengden's own data). Mengden (1985) proposed that these taxa posses the ancestral karyomorph and this is why apparently unrelated forms all display the 'ancestral' condition. Mengden's (1985) electrophoretic data showed that *E. minor* was closest to *Acanthophis*, but biochemically still quite distinct from all other Australian elapids (based on his fig. 3). Hutchinson (1990) considered the published phylogenetic data cited above and concluded that *Elapognathus* was both morphologically and biochemically distinct with no obvious sister taxon, and recognized its monotypic generic status, as did Cogger (1992). Wells & Wellington (1984, 1985) and Ehmann (1992) adopted what is apparently a compromise classification between those of Storr (1982, 1984) and Cogger (1983); *Drysdalia* is synonymized with *Elapognathus*, and Ehmann suggested the latter genus was closely related to *Denisonia*, *Echiopsis* and *Hemiaspis*.

Clearly, the phylogenetic affinities of both '*E.*' *atriceps* and *E. minor* are poorly understood. To address this problem we have assembled a large molecular data set to complement previously published molecular data sets on the Australian elapid radiation (Keogh, 1998; Keogh *et al*., 1998). Together these data are used to elucidate phylogenetic relationships of these taxa and on the basis

of our results we are able to make well supported taxonomic changes.

MATERIALS AND METHODS

Mitochondrial DNA

A 290 base pair portion of the cytochrome *b* mitochondrial gene and a 490 base pair portion of the 16S rRNA gene were sequenced from one specimen of '*Echiopsis*' *atriceps* (Western Australian Museum R124882, from Elenora Peak, Western Australia, 32°57′, 121°09′) and one *Elapognathus minor* (Western Australian Museum R121344, from 32 km south of Rocky Gully, Western Australia) according to protocols described elsewhere for other elapid species (Keogh, 1998). These sequences were added to a data set comprising homologous sequences from a diverse range of Australo-Papuan elapid snake species with which other authors have suggested or implied close affinities of both *Echiopsis atriceps* and *Elapognathus minor* including *Acanthophis antarcticus*, *Austrelaps superbus*, *Drysdalia coronata*, *D. coronoides*, *Denisonia devisi*, *Echiopsis curta*, *Hemiaspis signata*, *Hoplocephalus bungaroides*, *Notechis ater*, *Rhinoplocephalus bicolor*, *Suta suta*, and *Tropidechis carinatus*. This selection of taxa also includes a representative of each of the viviparous Australian elapid genera (except *Pseudechis porphyriacus* which represents a separate evolution of viviparity (Mengden, Shine & Moritz, 1986)). The Asian cobra *Naja naja* was used as the outgroup. The individuals used in the analyses presented here are the same as those used in Keogh (1998) and Keogh *et al*. (1998) and marked as individual '1' in those papers. See those papers for locality data and voucher information.

For each of the above individuals we also sequenced a 936 base pair portion of the 12S rRNA gene. The 12S fragment was amplified using the primers tRNA-Phe (5′–AAA GTA TAG CAC TGA AAA TGC TAA GAT GG–3′) and tRNA-Val (5′–GTC GTG TGC TTT AGT GTA AGC TAC–3′). Reactions were 40 µl in volume and contained 20 pmol of each primer, 10 mM Tris-HCl (pH 8.318), 50 mM KCl, 318 mM $MgCl_2$, 0.5 mM dNTPs and 2 units of *Taq*-polymerase (*Amplitaq* DNA polymerase, Perkin-Elmer). PCR amplification of double-stranded product was done using a Corbett PC-960C cooled thermal cycler using a step-down cycling profile. Reactions were initially denatured at 94 °C for 5 min, followed by an annealing step at 65 °C for 20 s and extension at 72 °C for 1.5 min. This was followed by a further round of denaturation at 94 °C for 15 s, annealing at 65 °C for 20 s and extension at 72 °C for 1.5 min. The annealing temperature was then dropped by 5 °C in the next 2 rounds of cycling. This 'stepping-down' in annealing temperature was repeated until a final annealing temperature of 50 °C was reached. The next 25 cycles then were performed with this annealing temperature. A final extension step at 72 °C was done for 7 min. PCR products were gel purified using the BESAclean kit (Geneworks) following manufacturer's instructions.

Direct sequencing of purified products was done with the ABI PRISM BigDye Terminator Cycle Sequencing Ready Reaction Kit. Reactions were done using half the amount of Ready Reaction Premix and 1.6 pmol of each amplification primer. Approximately 10–15 ng of PCR template was used. Reactions (final volume 10 µl) were overlaid with 10 µl of mineral oil. Cycle sequencing was done using the following profile for 25 cycles: 96 °C for 30 s; 50 °C for 15 s; 60 °C for 4 min. Ramping was set for 1 °C/s. On completion of cycle, 25 reactions were brought to 4 °C. Extension products then were removed from under the oil, placed in 1.5 ml tubes and the volume brought to 20 µl with deionised water. Purification of extension products was done using the manufacturer's ethanol/sodium acetate precipitation protocol. Dried extension products were resuspended in 3–4 µl of loading dye. Sequences were electrophoresed on 5.2% denaturing polyacrylamide (PAGE-PLUS, Amresco) gels (36 cm well-to-read) and analysed on the ABI 377XL automated DNA sequencer. Sequence data were edited using Sequencher 3.0 (Gene Codes Corporation).

Sequence alignment

The cytochrome *b* data were aligned easily by eye. The 16S rRNA data set contains a hyper-variable region ranging in length from 15–35 base pairs across the Australo-Papuan elapid radiation (Keogh, 1998; Keogh *et al*., 1998). The region was unalignable across all the taxa included in this study and so was excluded from phylogenetic analyses because site homology could not be confidently ascertained. The 12S data set also contains a number of indels but these sections were alignable and thus included in our analyses. The DO COMPLETE ALIGNMENT option of ClustalX (Thompson, Higgins & Gibson, 1994) was used to generate a multiple alignment of 12S DNA sequences. Default parameters for pairwise and multiple alignments were used. Pairwise alignments were done using dynamic programming ('slow but accurate'). Pairwise gap opening and extension penalties were 10.0 and 0.1 respectively. The IUB DNA weight matrix was used to assign scores to matches and mismatches. Gap opening and extension penalties for the multiple alignment were 10.0 and 0.05 respectively. The DELAY DIVERGENCE SEQUENCES option was set at 40% identity. The default DNA transition weight was 0.50. The IUB DNA weight matrix was used for the final multiple alignment. These sequences will be deposited in GenBank upon publication.

Phylogenetic analysis

The cytochrome *b*, 16S and 12S data sets were combined into a single large data set and all analyses were

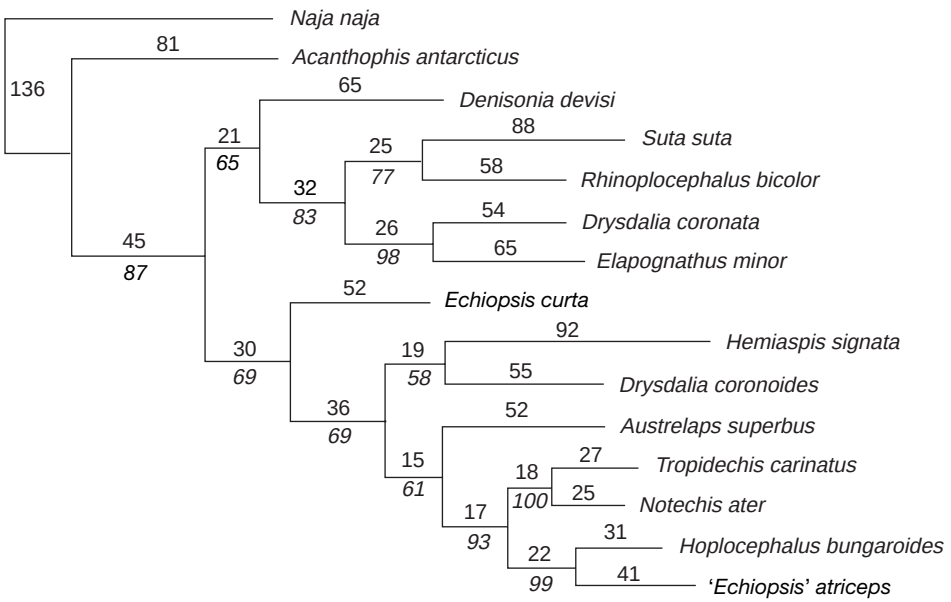

Fig. 2. Single most parsimonious phylogram generated from the unweighted analysis of a combined data set comprised of cytochrome *b*, 16S rRNA and 12S rRNA mitochondrial DNA sequences. See text for details. Numbers above terminal branches and internodes represent branch lengths, numbers below internodes represent bootstrap values from 1000 pseudoreplicates.

performed on the combined data. The resulting data set was subjected to unweighted maximum parsimony and neighbour-joining analyses with the computer program PAUP* 4.0d65 (Swofford, 1999). Indian spectacled cobra *Naja naja* sequences were used to root the trees in all analyses. Because of the large number of taxa and consequent large number of possible trees, heuristic searches were used for all analyses and replicated 30 times with the random-stepwise-addition and tree-bisection-reconnection branch swapping options of PAUP. All analyses were followed by 1000 bootstrap pseudoreplicates.

The ability of our sequence data set to reject alternative phylogenetic hypotheses of others was examined further with a series of non-parametric Templeton (Wilcoxon signed-rank) tests (Templeton, 1983) in PAUP*. This test examines if there is a significant difference between the shortest tree and alternative topologies. A member of each clade in which either *E. atriceps* or *E. minor* did not occur in the shortest tree was made the sister group to these species in various constraint trees. Alternative topologies also were constructed for the *Drysdalia* species. These trees then were compared to the shortest tree.

RESULTS

The cytochrome *b* data set comprised 290 aligned sites of which 125 were variable and 86 informative under parsimony. After exclusion of the hyper-variable region, the 16S data set comprised 454 aligned sites of which 72 were variable and 38 informative under parsimony. The 12S data set comprised 936 aligned sites of which 306 were variable and 195 informative under parsimony. Thus the total data set comprised 315 parsimony informative sites. Jukes–Cantor (1969) interspecific genetic distances for each individual data set and the total data set are presented in Table 1. The distributions of 10 000 randomly generated trees from each of the cytochrome *b*, 16S rRNA, 12S rRNA and combined data sets were left-skewed indicating strong phylogenetic signal in the data (Hillis, 1991; Hillis & Huelsenbeck, 1992): cytochrome *b* $g_1 = -0.434$ ($P < 0.01$); 16S rRNA $g_1 = -0.169$ ($P < 0.05$); 12S rRNA $g_1 = -0.487$ ($P < 0.01$); combined $g_1 = -0.532$ ($P < 0.01$).

Analyses of the unweighted, combined data set resulted in a single most parsimonious tree (Fig. 2; length = 1225 steps, CI = 0.55, RI = 0.42, RC = 0.23, HI = 0.44). Neighbour-joining (NJ) analyses resulted in a single tree that differed from the parsimony tree only in the placement of *Denisonia devisi*. The NJ analysis placed *D. devisi* as the sister group to the *Drysdalia coronata*/*Elapognathus minor* clade. However, this arrangement was supported by a low bootstrap value (59%). The arrangement produced by the parsimony analyses is more congruent with other independent data sets (see Discussion), and therefore we refer to the parsimony tree in all further discussion.

Bootstrap values were generally very high for most nodes, particularly the more terminal nodes. In particular, these data very clearly resolve the phylogenetic affinities of both '*Echiopsis*' *atriceps* and *Elapognathus minor*. '*Echiopsis*' *atriceps* and *Hoplocephalus bungaroides* form a clade supported by a bootstrap value of 99%. Importantly, *Drysdalia coronata* and *D. coronoides* do not form a monophyletic group. While *D. coronoides* and *Hemiaspis signata* form a weakly supported clade, *D. coronata* and *Elapognathus minor* form a very well supported clade with a 98% bootstrap value. The close relationship between *Notechis* and *Tropidechis* is confirmed with a bootstrap value of 100%. *Suta suta* and

Table 1. Pair-wise Jukes–Cantor (1969) genetic distances for taxa used in phylogenetic analyses. Cytochrome *b* distances are presented above the diagonal and 16S rRNA distances are presented below the diagonal in the upper panel. In the lower panel, 12S rRNA distances are presented above the diagonal and the total genetic distances for all three data sets combined is presented below the diagonal. The smallest genetic distances between '*Echiopsis*' *atriceps* and *Elapognathus minor* and other Australian elapids are in bold

	N.n.	*A.a.*	*A.s.*	*D.c.*	*D.c.*	*D.d.*	*E.c.*	*H.s.*	*H.b.*	*N.a.*	*R.b.*	*S.s.*	*T.c.*	*E.a.*	*E.m.*
Naja naja	–	.19591	.20492	.20040	.19591	.21404	.15242	.20947	.19145	.19145	.16092	.20040	.19591	.18701	.23262
Acanthophis antarcticus	.06682	–	.19591	.20492	.22327	.20492	.18701	.23262	.16952	.16092	.19591	.22327	.16521	.19591	.23733
Austrelaps superbus	.05937	.05199	–	.15666	.13571	.17821	.15242	.16521	.10733	.07998	.16521	.16092	.10336	.10336	.20040
'*Drysdalia*' *coronata*	.06184	.04468	.03745	–	.19145	.15666	.16521	.19591	.18701	.16521	.15242	.15666	.17385	.18701	**.12749**
Drysdalia coronoides	.05717	.04240	.03996	.03273	–	.19591	.17385	.16092	.13571	.14402	.16092	.19145	.14821	.13985	.21404
Denisonia devisi	.05690	.04955	.03028	.03266	.03995	–	.13571	.17821	.15666	.15242	.13985	.18260	.15666	.18701	.14821
Echiopsis curta	.05690	.04711	.02554	.03505	.03519	.03505	–	.14821	.14402	.13571	.14821	.15666	.13571	.17385	.17821
Hemiaspis signata	.07687	.05937	.03505	.04711	.04968	.04955	.03745	–	.17385	.17821	.17385	.17821	.16092	.18260	.19591
Hoplocephalus bungaroides	.05690	.03985	.03028	.03266	.02794	.03505	.02791	.04468	–	.08769	.14402	.17821	.08383	**.08769**	.20492
Notechis ater	.06682	.05444	.02791	.03985	.04240	.03266	.03266	.03745	.03028	–	.14821	.16521	.03892	.09941	.17385
Rhinoplocephalus bicolor	.06932	.05690	.03985	.03505	.03755	.03505	.03745	.05690	.04468	.04468	–	.14821	.16521	.15242	.17385
Suta suta	.06184	.04955	.03266	.03266	.02807	.03985	.03505	.03505	.03745	.03985	.03985	–	.15666	.17821	.18260
Tropidechis carinatus	.05937	.04711	.02083	.03028	.02801	.03266	.03028	.02791	.02319	.01849	.03985	.02554	–	.11132	.17821
'*Echiopsis*' *atriceps*	.05690	.05199	.03266	.03266	.03274	.03505	.03266	.04711	**.02319**	.02791	.04468	.03745	.02554	–	.20492
Elapognathus minor	.06433	.05937	.03985	**.03505**	.04475	.03985	.03745	.05199	.04955	.03985	.03985	.04711	.03745	.04226	–
	N.n.	*A.a.*	*A.s.*	*D.c.*	*D.c.*	*D.d.*	*E.c.*	*H.s.*	*H.b.*	*N.a.*	*R.b.*	*S.s.*	*T.c.*	*E.a.*	*E.m.*
Naja naja	–	.15716	.15808	.17242	.16092	.15735	.14581	.17522	.17051	.17001	.15411	.16350	.17560	.17004	.16291
Acanthophis antarcticus	.13784	–	.14579	.13418	.14465	.11953	.12719	.15581	.13928	.13871	.13960	.13556	.14236	.13332	.13769
Austrelaps superbus	.13760	.12732	–	.11827	.08621	.10971	.09462	.10899	.07730	.07296	.10858	.11107	.07393	.07902	.12495
'*Drysdalia*' *coronata*	.14598	.12102	.10245	–	.13475	.10141	.13341	.14133	.12361	.12391	.10540	.11814	.13261	.13297	**.07732**
Drysdalia coronoides	.13771	.12825	.08165	.11571	–	.10896	.09584	.09793	.09003	.07303	.12171	.13849	.07905	.08672	.12755
Denisonia devisi	.13792	.11379	.09850	.09199	.10380	–	.11493	.13381	.12756	.12536	.11966	.12764	.12759	.12634	.10709
Echiopsis curta	.12147	.11435	.08475	.11136	.09175	.09581	–	.11914	.09066	.08160	.11242	.13492	.09424	.09625	.13426
Hemiaspis signata	.15338	.14141	.09813	.12477	.09566	.11782	.10148	–	.12447	.11569	.12961	.12709	.11052	.12495	.14856
Hoplocephalus bungaroides	.14128	.11593	.06932	.10885	.08034	.10609	.08197	.11077	–	.05861	.10477	.12158	.06441	**.04302**	.13798
Notechis ater	.14452	.11838	.06160	.10761	.07645	.10344	.07699	.10459	.05569	–	.11988	.13373	.03732	.06435	.11918
Rhinoplocephalus bicolor	.13100	.12534	.09868	.09409	.10438	.09895	.09717	.11706	.09441	.10344	–	.10543	.12516	.11717	.10408
Suta suta	.14193	.12676	.09854	.10094	.11699	.11316	.11128	.12583	.10843	.11356	.09544	–	.14112	.12974	.12437
Tropidechis carinatus	.14552	.11897	.06416	.11095	.07638	.10542	.08328	.09622	.05628	.03237	.10757	.11185	–	.06818	.12827
'*Echiopsis*' *atriceps*	.14023	.12054	.07022	.11394	.08053	.11038	.09121	.11313	**.04515**	.06019	.10258	.11284	.06360	–	.13623
Elapognathus minor	.14753	.13302	.11457	**.07460**	.11970	.09644	.11539	.13095	.12525	.10723	.09891	.11347	.11217	.12216	–

Table 2. Results of Templeton (Wilcoxon signed-rank) tests of alternative sister group relationships for '*Echiopsis*' *atriceps*, *Elapognathus minor*, '*Drysdalia*' *coronata* and *Drysdalia coronoides* respectively. *N* represents the number of additional steps required to accommodate the alternative sister group relationship (Fig. 2). A significant *p* value indicates that the alternative topology is significantly different from the shortest tree based on our data

Constraint tree	Tree length	*N*	*z* score	*p* value
Shortest tree	1225			
'*Echiopsis*' *atriceps* +				
Suta suta	1288	63	5.6727	0.0001
Denisonia devisi	1290	65	6.1973	0.0001
Echiopsis curta	1269	44	5.0248	0.0001
Hemiaspis signata	1265	40	4.5680	0.0001
Notechis ater	1254	29	4.1563	0.0001
Elapognathus minor +				
Rhinoplocephalus bicolor	1249	24	2.8960	0.0014
Denisonia devisi	1247	22	2.8242	0.0020
Drysdalia coronoides	1285	60	5.1074	0.0001
Notechis ater	1300	75	6.0699	0.0001
Acanthophis antarcticus	1278	53	5.5559	0.0001
'*Drysdalia*' *coronata* +				
Drysdalia coronoides	1289	64	5.6130	0.0001
Drysdalia coronoides +				
'*Drysdalia*' *coronata*	1290	65	5.5065	0.0001

Rhinoplocephalus bicolor form a well-supported clade with a bootstrap of 77%. *Acanthophis* appears to be rather distantly related to other viviparous Australian elapids with a long internode length and high bootstrap value of 87%.

DISCUSSION

Phylogenetic affinities of '*Echiopsis*' *atriceps*

Our analyses clearly nest '*Echiopsis*' *atriceps* within what is often referred to as the tiger snake or *Notechis* lineage comprising *Notechis*, *Austrelaps*, *Tropidechis* and *Hoplocephalus*. While Wallach (1985) places '*E.*' *atriceps* in this group as well, *E. curta* is also shown as the sister group to '*E.*' *atriceps* and so his analysis did not result in a rejection of a hypothesized close relationship between '*E.*' *atriceps* and *E. curta*. Templeton tests on our data allow us to soundly reject all taxonomic and phylogenetic arrangements previously hypothesized for '*E.*' *atriceps*. When each of the species *Suta suta*, *Denisonia devisi*, *Echiopsis curta*, *Acanthophis antarcticus* and *Hemiaspis signata* were made the sister group to '*E.*' *atriceps* in individual constraint trees respectively, each of these trees were significantly longer than the shortest tree (all $P < 0.0001$, Table 2). Even though members of the '*Notechis*' lineage are relatively closely related (Table 1), Templeton tests also reject *Notechis ater* as an equally likely sister group to '*E.*' *atriceps* ($P < 0.0001$, Table 2). Thus, the taxonomic arrangements that have put '*E.*' *atriceps* in *Echiopsis* (Storr, 1980; Cogger, 1983, 1992), *Denisonia* (Storr, 1982; Wilson & Knowles, 1988; Ehmann, 1992) or *Suta* (Hutchinson, 1990; Golay *et al*., 1993) can each be rejected. Genetic distance data also strongly support the close relationship of '*E.*' *atriceps* to *Hoplocephalus bungaroides*. The genetic distances between these species are smaller than between *H. bungaroides* and any other species included in this data set, for all three genes (8.7% for cytochrome *b*, 2.3% for 16S, 4.3% for 12S and 4.5% for the entire data set combined, see Table 1). Finally, this sister group relationship between '*E.*' *atriceps* and *Hoplocephalus* is corroborated by preliminary results of a large cladistic analysis of morphological characters (primarily skull; Scanlon & Lee, pers. comm.).

Our results have important taxonomic implications. Given the strong support for a sister group relationship between '*E.*' *atriceps* and *Hoplocephalus* and the lack of support for all previous taxonomic arrangements for '*E.*' *atriceps*, a new arrangement is warranted. Our molecular data suggest that the only named genus '*E.*' *atriceps* could reasonably be referred to is *Hoplocephalus*. While '*E.*' *atriceps* does share important morphological characteristics with *Hoplocephalus*, the three members of *Hoplocephalus* are strongly morphologically derived with respect not only to other members of the '*Notechis*' lineage but also all other Australo-Papuan elapids. Further, while '*E.*' *atriceps* is nested well within the '*Notechis*' group, it is sufficiently morphologically divergent from all these taxa that it would make re-defining any of these genera to include *atriceps* difficult. While some have suggested that the '*Notechis*' group perhaps should be lumped into a single large genus (i.e. Storr, 1982 for the Western Australian taxa; Wallach, 1985), the vast majority have continued to recognize each of these genera for both morphological and medical reasons (i.e. Wilson & Knowles, 1988; Hutchinson, 1990; Cogger, 1992; Keogh, 1999). The members of each of these genera feature significantly in Australia's snakebite toll each year; thus taxonomic stability is viewed as being of paramount importance. Despite Storr's suggestion to the alternative, each of these genera is morphologically well

defined and we also support their retention. This leaves us with only one taxonomic option. Given the morphological distinctiveness of '*E.*' *atriceps* from *Hoplocephalus* and also other members of the *Notechis* lineage, this species must be recognized as a monotypic genus.

If *atriceps* is the immediate sister taxon to *Hoplocephalus* as our results indicate, these two taxa presumably represent the products of a vicariance event between eastern and western populations of a widespread ancestral species. Since *Hoplocephalus* spp. occupy mainly mesic, near-coastal environments (like the close outgroups *Tropidechis*, *Notechis*, *Austrelaps*, etc.), the semi-arid, inland environment of *atriceps* can be regarded as 'autapomorphic' for this species. Coupled with the extremely small extent of its range, this indicates that while *atriceps* is an evolutionary relict of a formerly widespread lineage, it has also undergone significant independent evolution by adapting to a habitat unavailable to any of its close relatives (approached most closely by *H. bitorquatus* in inland Queensland). The saxicoline and arboreal habits seen in *Hoplocephalus* spp., and an observation implying that *atriceps* is also a tree-climber (Ehmann, 1993) suggest that climbing habits and adaptations in their common ancestor may have acted as preadaptations for more arid habitats (cf. Greer, 1989 on arid adaptation in *Cryptoblepharus*, Scincidae).

Phylogenetic affinities of *Elapognathus minor* and *Drysdalia* monophyly

Elapognathus minor is a small and little known snake found only in the south-western portion of Western Australia. Since it was split off into a monotypic genus by Boulenger (1896) based on the lack of maxillary teeth behind the fang, only a few studies have considered its affinities, and these studies have not consistently identified the same sister group. McDowell (1967) was the first to really consider Australo-Papuan elapid relationships based on venom gland musculature and hemipenial morphology. McDowell (1967) placed *Elapognathus* into his '*Glyphodon* type' group, one of four groups he identified based on the condition of the *adductor externus superficialis* muscle. This large group contains most American elapids (*Micrurus*), plus the Asian *Calliophis*, African elapid genera (except *Dendroaspis*), Afro-Asian *Naja*, most sea snakes and 11 of the Australo-Papuan elapid genera (*sensu* Hutchinson, 1990). McDowell considered this character state to be the plesiomorphic condition and he provided few additional comments specifically about *Elapognathus* affinities which we could test. However, it is worth noting that the only other viviparous terrestrial taxa McDowell (1967) assigned to his '*Glyphodon*' group were *D. coronoides*, *Rhinoplocephalus pallidiceps* and *R. nigrescens*.

As noted above for '*Echiopsis*' *atriceps*, based on few data and no phylogenetic analysis, Storr (1982) lumped *Elapognathus* and several other genera into a greatly expanded *Notechis*. Templeton tests on our molecular data reject Storr's hypothesis of *Elapognathus* affinities. When *Elapognathus* is made the sister group to either *Notechis ater* or *Drysdalia coronoides* in respective constraint trees, these trees are considerably longer than the shortest tree (both $P < 0.0001$, Table 2). Our data also allow us to reject Wallach's (1985) implied hypothesis of relationship. Wallach's (1985) cladistic analysis of morphological data nests *E. minor* within a large group of species now placed in *Rhinoplocephalus* and *Suta* (*sensu* Hutchinson, 1990). While our data strongly support a close relationship between the *E. minor*/'*D.*' *coronata* clade and the *Rhinoplocephalus*/*Suta* clade with a bootstrap of 83%, Templeton tests show that placing *E. minor* in the *Rhinoplocephalus*/*Suta* clade results in a significantly longer tree ($P < 0.0014$, Table 2). Finally, Mengden's (1985) karyological and allozyme studies did not clearly identify an *Elapognathus* sister group among Australian elapids, but his allozyme data showed that *Elapognathus* was closest to both *Acanthophis* and '*D.*' *coronata*, but still biochemically quite distinct from other Australian elapids (based on his fig. 3). Templeton tests also allow us to reject a close relationship between *E. minor* and both *Acanthophis* and *Denisonia* ($P < 0.0001$, Table 2). While Mengden (1985) placed both *Elapognathus minor* and '*D.*' *coronata* in his large '*Pseudechis*' karyomorph group with 14 other species and seven other genera, he implies a close relationship between the two species in his summary of the karyological data in his fig. 2. So based on both karyological and allozyme data, Mengden (1985) supported a close relationship between *E. minor* and '*D.*' *coronata*. Our results strongly corroborate this conclusion based on independent molecular data.

The strong support our data show for the close relationship of *E. minor* and '*D.*' *coronata* also has important implications for *Drysdalia* monophyly. Our analyses clearly support the notion that *Drysdalia* in the traditional sense is polyphyletic. The polyphyly of *Drysdalia* has long been suspected. Though Coventry & Rawlinson (1980) outlined characters that appear to support monophyly of this genus, long ago McDowell (1967) noted the anatomical distinctiveness of *D. coronata* from its congeners (as does Wallach, 1985), suggesting that it was more closely related to the *Notechis* lineage. McDowell (1967: p. 540) went so far as to say 'I believe *coronata* is a genuine evolutionary intermediate and may merit generic distinction'. While McDowell may have been wrong in the lineage to which he assigned '*D.*' *coronata*, the electrophoretic data of Mengden (1985, his fig. 3) united *D. coronoides*, *D. mastersi* and *D. rhodogaster* with the *Notechis* lineage while *D. coronata* grouped with *E. minor*. Thus our sequence data corroborate the morphological distinctiveness of '*D.*' *coronata* from other *Drysdalia* (as did analyses based on fewer sequence data in Keogh *et al.*, 1998) and the close affinity between '*D.*' *coronata* and *E. minor* on the one hand and other *Drysdalia* with the *Notechis* lineage on the other, indicated by electrophoretic data.

Templeton tests used on our data also strongly support *Drysdalia* paraphyly. Forcing monophyly of '*D.*' *coronata* and *D. coronoides* (in either direction) resulted in much longer trees that are significantly different from the shortest tree ($P < 0.0001$, Table 2).

It is worth noting three other pieces of corroborating evidence with regard to *Drysdalia* affinities. First, '*D.*' *coronata* is part of the same karyomorph group as *E. minor* whereas the other three species of *Drysdalia* share a karyomorph type with *Denisonia* (Mengden, 1985). Second, '*D.*' *coronata* and *E. minor* have similar diets comprised of approximately half lizards and half frogs whereas the other three species of *Drysdalia* are lizard specialists (Shine, 1981, 1986). Finally, '*D.' coronata* and *E. minor* both occur in the same habitat type and have roughly the same biogeographic distribution in Western Australia whereas the other three *Drysdalia* occur in eastern Australia and into south-eastern Western Australia (Wilson & Knowles, 1988; Cogger, 1992). Based largely on the results of Mengden (1985) and this other corroborating evidence, several have already taken the taxonomic step of using the name *Elapognathus coronatus* (Wells & Wellington 1984, 1985; Ehmann, 1992; Scanlon, 2000). Based on all the available evidence, it is clear that '*D.*' *coronata* should be referred to *Elapognathus*. Below we re-describe *Elapognathus* to include this species.

A new genus of Australian elapid snake

Brief synonymies of included species follow Cogger *et al.* (1983), and also give first uses of additional synonyms subsequent to that work.

PAROPLOCEPHALUS NEW GENUS

Type species: *Brachyaspis atriceps* Storr, 1980 (*Denisonia atriceps* Storr, 1982, *Echiopsis atriceps* Cogger *et al.*, 1983, *Suta atriceps* Golay in Golay *et al.*, 1993)

Etymology: From Greek *para*, beside, and the generic name *Hoplocephalus* Wagler, 1830, in reference to the close relationship and morphological similarity between the two genera. (While Greek *hoplon* can refer to any implement, tool, or weapon, it was commonly used in classical texts to refer to the heavy shield carried by Greek foot-soldiers or 'hoplites' (Liddell & Scott, 1871) so Waglers intended sense of *hoplocephalus* was presumably 'shield-head' in reference to the broad, angular head shape of *H. bungaroides* seen from above.)

Diagnosis: Terrestrial hydrophiine elapid snake with anal and all subcaudals undivided; dorsal scales smooth but not highly glossed; head moderately broad and distinct from the neck; eye large, pupil vertically elliptical; 3 noncanaliculate maxillary teeth behind a diastema; temporal scales usually 2 + 2 + 3, but up to 2 + 3 + 5 (formula follows definition in Scanlon, 2000); preocular without canthus rostralis, contacts undivided nasal and 2nd supralabial; usually 6 supralabials, sometimes 7 when temporolabial (lower anterior temporal) reaches lip between 5th and last; parietal separated from lower postocular; 7 infralabials. '*Oxyuranus* type' of venom-gland musculature (*sensu* McDowell, 1967; main dorsal portion of *m. adductor externus* superficialis completely covering *m. adductor externus* medialis, reaching transverse crest of supraoccipital and overlapping anterior part of *m. depressor mandibulae*, but not attaching to quadrate). Neck and posterior trunk slender, and body somewhat laterally compressed; ventral scales extend to lower lateral surface of body, and their posterior edges arcuate (lateral parts concave; see Ehmann, 1993). Scale rows 21–23 at first ventral, sometimes reducing to 17 on neck, 19 at midbody; three reductions (19 − 17 − 15 − 13) posterior to midbody, increasing again to 15 rows at or just before last ventral. Ventrals more than 170, less than 190. Iris pale (golden orange in life; Storr, 1980); body reddish brown (paler ventrally); head dull black or dark grey with pale spots on upper and lower labials, and denser black collar on neck, pale-edged posteriorly; dorsal bands or blotches absent; oral lining pale, tongue dark. Largest specimen examined is a female (WAM R132047) with snout–vent length (SVL) 490 mm, tail length 79 mm (16.1% SVL); the largest male (WAM R126978) has SVL 459, tail 85 mm (18.5%). Presumed viviparous, but reproduction and natural diet unknown.

Most similar to *Hoplocephalus* spp. in body form and scalation (also cranial morphology; Scanlon & Lee, pers. comm.); distinguished by vertically elliptical pupils (vs. round), lower numbers of ventrals (171–184 vs. 190–250) and usually of subcaudals (44–50 vs. 40–70), and only weakly angled and scalloped ventral scales (vs. usually distinctly keeled and notched as an adaptation for climbing). The difference in midbody scale rows, 19 vs. 21, is also reflected by more detailed counts: *Hoplocephalus* spp. have 25 or more scale rows at the first ventral, no reduction below 21 until midbody or beyond, and after reducing 21 − 19 − 17 − 15 may have from 13 to 17 at the last ventral. Midbody counts of 19 attributed to *H. bitorquatus* (Cogger, 1992), and 17 to *atriceps* (Storr *et al.*, 1986), may be miscounts due to reductions on neck or close to midbody.

Comments: The morphological data on *P. atriceps* are based on external examination (by JDS) of four specimens (WAM R67330 [holotype], R29770, R126978, and R132047), and preparation of the skull of R29770, the head of which had previously been skinned by another worker. The fifth known specimen, which was also used for the genetic study (WAM R124882), was examined by JSK.

Redescription of *Elapognathus*

ELAPOGNATHUS BOULENGER, 1896

Type species: *Hoplocephalus* minor Günther, 1863 (*Elapognathus minor* Boulenger 1896, *Notechis minor* Storr, 1982).

Referred species: *Elaps coronatus* Schlegel, 1837 (*Trimeresurus olivaceus* Gray, 1841; *Elaps melanocephalus* Gray & Neill, 1845; *Denisonia coronata* Boulenger, 1896; *Drysdalia coronata* Worrell, 1961; *Notechis coronatus* Storr, 1982; *Elapognathus coronata* Wells & Wellington, 1984; *Elapognathus resolutus* Wells & Wellington, 1985). Allopatric (e.g. island) populations exhibit geographic variation (Coventry & Rawlinson, 1980) but are regarded as conspecific.

Diagnosis: Small terrestrial hydrophiine elapid snakes with anal and all subcaudals undivided; dorsal scales smooth and matt; head slightly distinct from neck; eye large; pupil round; 0 to 4 noncanaliculate maxillary teeth behind diastema (usually none in *minor*, but one specimen with 3 posterior alveoli); temporal scales usually 2 + 2 + 3 (up to 3 + 3 + 4 in *coronatus*); preocular contacts undivided nasal and second supralabial; usually 6 supralabials (in *coronatus*, sometimes 7 when temporolabial reaches lip); parietal separated from lower postocular; 7 infralabials. Venom-gland musculature '*Oxyuranus* type' (*coronatus*) or *Glyphodon* type (*m. adductor externus superficialis* secondarily simplified and reduced in *minor*). Body form moderate to somewhat stout, round (or facultatively depressed) in cross-section; ventral scales not extending to lateral surface of the body and with uniformly curved free edge. Dorsal scale rows 19–23 at first ventral, 15 on neck and at midbody, a single bilateral posterior reduction to 13. Ventrals fewer than 160 (*minor* 116–129, *coronatus* 130–153). Iris dark with pale ring around pupil; body reddish or greenish grey or brown; top of head darker and with pale-edged dark collar (in *minor*, only on sides of neck); upper lip pale; dorsal bands or blotches absent; venter yellow or orange with dark speckles or transverse bars; oral lining pale, tongue dark. SVL less than 600 mm, adult males and females approximately equal in size; viviparous; diet includes more frogs than skinks. Tail moderately prehensile, used by both species to climb at least in low vegetation.

Most similar to species of *Drysdalia* (*coronoides*, *mastersii*, *rhodogaster*), but distinguished by the following apomorphic characters: dorsal laminae of nasal bones more extensive, clasping premaxilla and contacting frontal; anteromedial spine of prefrontal absent; lacrimal foramen may be transversely elongated rather than round; postorbital broad and 'strap-like' distally; adductor crests on parietal not meeting to form a sagittal crest posteriorly; neural spine not overhanging anteriorly; diet mainly frogs; tail prehensile and climbs in low vegetation. *Drysdalia* spp. further differ from *Elapognathus* in the following apomorphies: lower average number of dorsal scale rows at first ventral (range 17–21, vs. 19–23), and posterior reduction further behind midbody (15 to 13 rows at 76–88% ventral scale, vs. 63-88% in *Elapognathus*); posterior process of vomer subequal in length to capsule of Jacobsen's organ; frontal bones (and overlying scale) long, narrow between the orbits and expanded anteriorly; postorbital crest of parietal reduced; trigeminal foramen (V2) narrowly separated from parietal; retroarticular process in lateral view in line with compound; adductor fossa open laterally; surangular foramen one-third from anterior end of compound bone; one less pair of macrochromosomes (by fusion); Z sex chromosome modified and differing in relative length ('Group 5' vs. 'Group 1' karyomorph, Mengden, 1985).

Comments: Based on examination of specimens in the AM, WAM, SAM and QM (by JDS), and data in the literature. Concise diagnosis is made difficult by the fact that the two species of *Elapognathus* strongly resemble species of *Hemiaspis* and *Drysdalia* externally, but differ from each other internally more than do species of these or other comparable genera.

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