

Systematics of Hydrophiine Brown Snakes (*Pseudonaja*)

Adam W. Skinner

A thesis submitted in fulfilment of the
requirements for the degree of

Master of Science

Department of Environmental Biology

The University of Adelaide

June 2003

Table of Contents

Table of Contents.....	i
Abstract.....	iv
Declaration.....	vi
Acknowledgements.....	vii
Chapter 1. General Introduction.....	1
Chapter 2. A Reply to Critics of the Species Category with a Consideration of Methodology in Species Level Systematics.....	3
2.1 Introduction.....	3
2.2 Ontology, Species, and Higher Taxa.....	3
2.2.1 Cohesive and historical individuals.....	4
2.2.2 The ontological distinction between species and higher taxa.....	7
2.3 Hierarchy and Monophyly.....	10
2.4 A Consideration of Methodology in Species Level Systematics.....	13
2.4.1 Sophisticated falsification and progress in science.....	14
2.4.2 Sophisticated falsification in species level systematics.....	15
2.5 Conclusion.....	20
Chapter 3. A Systematic Review of Hydrophiine Brown Snakes (<i>Pseudonaja</i>).....	22
3.1 Introduction.....	22
3.2 Historical Review and Objectives.....	23
3.3 Materials and Methods.....	29
3.3.1 Ingroup sampling and outgroups.....	29

3.3.2 <i>Specimens and tissues</i>	30
3.3.3 <i>Mitochondrial DNA</i>	30
3.3.3.1 DNA extraction, amplification, and sequencing.....	30
3.3.3.2 Testing for nuclear paralogues.....	32
3.3.3.3 Phylogenetic analysis.....	33
3.3.4 <i>Allozyme electrophoresis</i>	34
3.3.5 <i>Morphology</i>	35
3.3.6 <i>Chromosomes</i>	37
3.4 Results	38
3.4.1 <i>Mitochondrial DNA</i>	38
3.4.2 <i>Allozyme electrophoresis</i>	41
3.4.3 <i>Morphology</i>	44
3.4.4 <i>Chromosomes</i>	55
3.5 Discussion	57
3.5.1 <i>Species limits</i>	57
3.5.2 <i>Phylogenetic relationships</i>	70
3.6 Species Accounts	71
3.7 Conclusions	91
References	93
Appendices	
Appendix 1.....	111
Appendix 2.....	120
Appendix 3.....	141
Appendix 4.....	144
Appendix 5.....	150
Appendix 6.....	158
Appendix 7.....	167

Appendix 8.....170

Abstract

In this thesis, I review the species level systematics of *Pseudonaja*, a group of medically important hydrophiine snakes, commonly called brown snakes, the classification of which has been regarded as especially problematic. In doing so, I attempt to demonstrate that species level systematics can be practiced in a scientific manner, and that proposals to abandon the species category based on the contention that this is rarely the case are unfounded.

Recent arguments presented by Ereshefsky (1999), Mishler (1999), and Pleijel and Rouse (2000) for abandoning the species category in systematics are unconvincing. As independently evolving population lineages, species derive their existence from the causal interaction of their component parts (interbreeding organisms) and their resulting ability to act as a whole (in undergoing anagenesis). Thus, contrary to the claim of Ereshefsky (1999) and Mishler (1999), species are ontologically distinct from higher taxa, the component parts of which (species) do not interact but are united by historical connections, and so may be justifiably recognised as such. Pleijel and Rouse's (2000) concern that, in permitting the recognition of non-monophyletic groups of demes, the inclusion of species in taxonomic schemes may result in a loss of historical information is unfounded, extending from a failure to consider the hierarchical organisation of biological individuals and processes. Also unfounded is Pleijel and Rouse's (2000) contention that systematists are rarely able to provide sufficient empirical justification for accepting hypotheses of species limits. Such hypotheses can be connected to a number of testable predictions that are unlikely to be realised under alternative hypotheses, so that they may be assessed in the same manner as all hypotheses in science.

A consideration of mitochondrial DNA sequence, allozyme electrophoretic, morphological, and chromosomal evidence reveals that the species level systematics of *Pseudonaja* is perhaps not as poorly resolved as previously supposed. As delimited here, *P. affinis*, *P. inframacula*, and *P. textilis* are largely coincident with recognised taxa, while the status of *P. guttata* and *P. modesta* as

evolutionarily independent entities is corroborated. Nonetheless, specimens presently referred to *P. nuchalis* represent at least three distinct species, two of these corresponding with the 'Darwin' and 'Southern' morphs described by Mengden (1985b), and the third incorporating Mengden's 'Pale head, grey nape' and 'Orange with black head' morphs. Additionally, it is probable that further investigation will reveal the presence of unrecognised taxa within *P. modesta* and perhaps *P. textilis*.

This work contains no material that has been accepted for the award of any other degree or diploma in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text.

I give consent to this copy of my thesis, when deposited in the University Library, being available for loan and photocopying.

Adam W. Skinner

June 2003

Acknowledgements

The work presented in this thesis was completed at the South Australian Museum under the supervision of Steve Donnellan and Mark Hutchinson, whom I thank for their advice, encouragement, and, especially, patience. Mike Lee gave up a substantial amount of time in providing editorial and motivational comments during the writing stage, and I am grateful for his support. The following people granted access to specimens and/or tissues in their care: Dennis O'Meally and Ross Sadlier (Australian Museum), Gavin Dally and Paul Horner (Northern Territory Museum), and Brad Maryan and Laurie Smith (Western Australian Museum). Peter Mirtschin, Rex Neindorf, Dave O'Connor, and Sharon from Snakes N.T. also made available valuable specimens and/or tissues. Steve Donnellan, Alison Fitch, Mark Hutchinson, and Mike Lee read drafts of one or more chapters. Mike Lee's comments on Chapter 2 were particularly insightful. All members of the Evolutionary Biology Unit contributed to a genial study environment. I am in debt to Russ Baudinette, Margaret Davies, Steve Donnellan, and Mark Hutchinson, without whose intervention I would have been unable to undertake this project as a Master of Science.

This project was funded by grants from the Australia and Pacific Science Foundation and the Ethel Mary Read Research Grant Fund.