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

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.

Chapter 1

General Introduction

Whitehead (1990) expressed concern for the perception of systematics within the general biological community, suggesting that the discipline is regarded by many as having limited theoretical and practical relevance. He attributed this view to misunderstanding concerning the goals and methodology of systematics and the failure of systematists to communicate the significance of their work (see also Keogh, 1995).

In the most general sense, systematics refers to 'the ordering of entities into systems', where 'a system is a more inclusive entity (whole) whose existence depends on some natural process through which its elements (component parts) are related' (de Querioz, 1988, p. 241; see also Hennig, 1966; Griffiths, 1974). It is widely accepted that evolutionary, or phylogenetic, descent is the process upon which biological systematics (the ordering of living entities) should be based (e.g. Hennig, 1966; McDowell, 1987; de Queiroz, 1988). Thus, the goal of biological systematics (systematics in its usual, more restricted, sense) is to produce a system (*sensu* de Queiroz, 1988) that reflects evolutionary history (phylogeny). It is now widely recognised that such a system provides a necessary basis for comparative studies (see, for example, Harvey and Pagel, 1991, especially their Chapter 2; see also Felsenstein, 1985) and hence our understanding of the general (mechanistic) principles governing biological evolution. The importance of systematics also extends to real-world, practical issues that affect people's lives and well being. For example, decisions concerning the relative conservation value of particular habitats usually depend on the diversity and endemicity of the organisms they contain, and so incorporate systematic considerations (e.g. Crozier, 1997). Moreover, knowledge of the historical relationships of groups of organisms may assist in the discovery of new pharmaceutical products and food sources (Keogh, 1995). The results of systematic research may also provide information that is valuable in moderating the impact of economically and/or medically important groups of organisms.

As Wiens and Penkrot (2002, p. 69) noted, systematics involves two primary activities, 'delimiting species and reconstructing their phylogenetic relationships'. Although considerable effort has been invested in developing a theoretically consistent methodological basis for inferring phylogenetic relationships, comparatively little attention has been given to the data and methods employed in delimiting species. Thus, '[f]ew specific criteria or methods for species delimitation have been proposed ... and these criteria are rarely stated explicitly by empirical workers' (Wiens and Penkrot, 2002, p. 69). The lack of an explicit, widely accepted methodology for delimiting species has (in conjunction with other issues, discussed in Chapter 2) prompted some authors (Pleijel, 1999; Pleijel and Rouse, 2000) to propose that the species category should be abandoned in systematics, and is perhaps largely responsible for the derisive perception of systematics among biologists brought forward by Whitehead (1990).

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 is generally considered to be poorly resolved. In doing so, I attempt to demonstrate that species level systematics can be practiced in a scientific manner, and that proposals to discard the species category based on the contention that this is rarely the case are unfounded. The thesis is divided into three chapters. A reply to critics of the species category, in which I consider the nature of species and develop a perspective of species level systematics consistent with that of scientific endeavour generally, is presented in Chapter 2. The ideas discussed in this reply are subsequently applied in Chapter 3 in reviewing brown snake systematics.

Chapter 2

A Reply to Critics of the Species Category with a Consideration of Methodology in Species Level Systematics

2.1 Introduction

Recently, Ereshefsky (1999), Mishler (1999), and Pleijel and Rouse (2000; see also Pleijel, 1999) have proposed that the species category should be abandoned in systematics. These authors, all of whom advocate a system of biological nomenclature in which names refer only to recovered monophyletic groups, provide three primary arguments in support of their proposal: (1) species are not ontologically distinct from higher taxa and therefore should not be recognised as such (Ereshefsky, 1999; Mishler, 1999); (2) in many cases, species are non-monophyletic, so that their inclusion in taxonomic schemes results in a loss of historical information (Pleijel and Rouse, 2000); and (3) systematists are rarely able to provide sufficient empirical evidence to justify the acceptance of hypotheses of species limits (Pleijel and Rouse, 2000). Here, I attempt to answer each of these arguments in turn. In doing so, I consider the nature of species and develop a view of species level systematics consistent with that of scientific endeavour generally, providing a background for the review of hydrophiine brown snake systematics presented in the following chapter.

2.2 Ontology, Species, and Higher Taxa

Ereshefsky (1999) and Mishler (1999) contend that no ontological distinction exists between species and higher taxa. Thus, they consider that species and higher taxa are not fundamentally different kinds of entity and, accordingly, argue that the recognition of species as a distinct taxonomic category is arbitrary and misleading and therefore should be rejected. (This is the same rationale underlying the proposal, endorsed by Ereshefsky and Mishler, that supraspecific categories [i.e. genus, family, order, etc] should be abandoned in taxonomy [see, for example, de

Queiroz and Gauthier, 1992; Ereshefsky, 2001].) Insofar as there is no ontological basis for distinguishing species from higher taxa, I would agree with this argument. Accordingly, I am concerned here only with Ereshefsky's and Mishler's ontological claim.

Previous discussions of ontology in systematics have emphasised the distinction between individuals and classes (e.g. Frost and Hillis, 1990; Frost et al., 1992; Frost and Kluge, 1994; Ghiselin, 1974, 1987, 1997; Hull, 1976, 1980; Mayden, 1997; Wiley, 1978, 1980, 1981, 1989), the prevailing opinion being that biological taxa (i.e. species and monophyletic groups of species) are individuals. Nonetheless, some authors (e.g. Wiley, 1980, 1981, 1989; Ghiselin, 1987, 1997) have noted an important distinction aside from the individuals-class dichotomy, namely, that between cohesive and historical individuals (*sensu* Ghiselin, 1987, 1997). This distinction clarifies what I consider to be significant ontological differences between species and higher taxa and, accordingly, is discussed below.

2.2.1 Cohesive and historical individuals

In everyday discourse, the term individual is commonly used to refer to particular organisms, usually particular humans. However, there is a broader sense of the term, referring approximately to those particular material entities existing in the surrounding universe. Some familiar examples include particular chairs (such as the one I am presently sitting on), the Amazon Basin, and Jupiter. Mishler and Brandon (1987) identified four properties that have been ascribed to individuals in this broader sense: (1) spatial boundaries, (2) temporal boundaries, (3) integration, and (4) cohesion. They noted a distinction between properties (1)-(2), which refer to patterns, and properties (3)-(4), which refer to the action of processes.

Spatial and temporal boundaries have been considered by the majority of authors to be necessary properties of individuals (e.g. Ghiselin, 1974, 1987, 1997; Hull, 1976, 1980; Mayden, 1997; Wiley, 1978, 1980, 1981, 1989; see, however, Mishler and Brandon, 1987, p. 402). Thus, individuals are usually considered to have a beginning and ending (at least potentially in the case of contemporary individuals) in space and time and to display continuity between these. These properties in conjunction render an entity particular (i.e. unique; Hull, 1976). The spatial and

temporal boundaries of individuals may appear distinct or indistinct, depending on the scale of perception (see, for example, Eldredge, 1985). Thus, while an organism may appear to us to be a discrete entity having distinct spatial boundaries, at the molecular level these boundaries become indistinct. Similarly, although the origin of a chain of mountains may seem to us to be a protracted event, when considered on a temporal scale of billions of years it appears nearly instantaneous. One consequence of defining individuals as spatiotemporally bounded entities is that a particular individual may undergo considerable change during the course of its existence without losing its identity (e.g. Ghiselin, 1974, 1997; Hull, 1976, 1980; Wiley, 1980, 1989). In regarding organisms as paradigmatic individuals, this makes intuitive sense; generally, we would consider a particular adult moth to be the same individual as the (obviously morphologically dissimilar) larva from which it metamorphosed. Because individuals may change throughout their existence, it also follows that particular individuals can not be defined by stating a list of necessary and sufficient properties; they may only be defined ostensively (e.g. Ghiselin, 1974, 1997; Hull, 1976, 1980; Mayden, 1997; Wiley, 1980, 1989).

As defined by Mishler and Brandon (1987), integration and cohesion have commonly been conflated in discussions of individuality (Mishler and Brandon, 1987, p. 402). Integration refers to 'active interaction among parts of an entity' (Mishler and Brandon, 1987, p. 400). The tissues comprising a metazoan organism, for example, interact in numerous physiological processes, such as muscle contraction, involving the interaction of nervous tissue and skeletal muscle. Likewise, the atoms composing a chair interact in forming electrostatic bonds. Cohesion refers to 'situations where an entity behaves as a whole with respect to some process' (Mishler and Brandon, 1987, p. 400). For example, a chair, when pushed, responds as a whole in moving. Obviously, these two properties are potentially related; interaction among the parts of an entity may enable it to behave as a whole with respect to processes. Nonetheless, integration and cohesion are at least partly independent. Thus, for example, a field of heliotropic plants turning to face the sun may be considered to behave as a whole (and therefore to be cohesive), however, the concerted movement of individual plants does not depend on their causal interaction (M. Lee, pers. comm.). Additionally, where the parts of more than one entity interact only infrequently, these entities, while exhibiting some degree of integration, may be insufficiently integrated to act as a whole (it is important to note,

however, that the simultaneous interaction of all parts of an entity is not necessary to render it cohesive; it is only necessary that sufficient interaction occurs that the entity can be considered to respond as a whole relative to some process [see Sober, 1993]).

It is difficult (if not impossible) to conceptualise an integrated, cohesive entity that is spatiotemporally unrestricted (cf. Mishler and Brandon, 1987, p. 402). It would seem therefore that spatiotemporal localisation is a prerequisite for integration and cohesion. The converse is not so, however; a spatiotemporally localised entity need not display integration or cohesion (cf. the following paragraph). A group of (integrated, cohesive) entities connected only by historical relations is spatiotemporally localised, having a beginning coincident with that of the ancestral entity from which it is derived and a potential ending (when all of its component entities cease to exist), however, it lacks integration and does not act as a whole. Wiley (1981) referred to such entities as historical groups (also historical entities; Wiley, 1980), reserving the term individual for those spatiotemporally localised entities displaying integration and cohesion. Ghiselin (1987, 1997) preferred to refer to all spatiotemporally localised entities as individuals, distinguishing between cohesive individuals (those individuals exhibiting integration and cohesion) and historical individuals (those individuals whose parts share only historical relations and which therefore lack integration and cohesion). Here I follow Ghiselin's terminology as it emphasises the distinction between spatiotemporally localised entities (i.e. individuals) and classes, which are abstract generalisations having no spatial or temporal limits (e.g. the concepts 'helium' and 'herbivore'; see, for example, Ghiselin, 1997). However, regardless of the terminology employed, it is important to note that there is a fundamental ontological distinction between cohesive and historical individuals; while the former derive their existence from the causal interaction of their parts (which need not be historically related) and their resulting ability to act as a whole, the latter derive their existence from historical connections among their parts.

In a recent paper, Lee and Wolsan (2002) argued that integration is a necessary property of individuals if they are to be spatiotemporally localised. They noted that permitting individuals to lack integration effectively renders them eternal as their ultimate parts (elementary particles) presumably will never cease to exist. Thus, they considered that the spatiotemporal boundaries of

individuals must be defined by the development and loss of integration. Lee and Wolsan's argument initially would appear to deny the notion of a historical individual developed above. However, this apparent contradiction can be resolved if we consider that at some level of organisation the parts comprising historical individuals are connected by history, and that each of these parts is necessarily an integrated, cohesive individual, coming into existence and ceasing to exist as it develops and loses integration, respectively. Thus, it is possible to define the limits of historical individuals with respect to the integration of their historically connected parts; any particular historical individual has a beginning coincident with the development of integration in the ancestral individual from which it is derived and a potential ending coincident with the loss of integration in all individuals derived from that ancestor.

2.2.2 The ontological distinction between species and higher taxa

It is evident from the preceding discussion that higher taxa (monophyletic groups of species) are historical individuals. They have a beginning coincident with that of a particular ancestral species and a potential ending (corresponding with the extinction of all species descended from that ancestral species), and display continuity between these. However, there is no convincing evidence that higher taxa are integrated or cohesive (Kluge, 1990). Thus, the majority of authors have considered that the species composing a higher taxon share only historical connections (e.g. Wiley, 1980, 1981; Ghiselin, 1987; Kluge, 1990). In this section, I argue that species, in contrast, are integrated, cohesive individuals and, accordingly, that species and higher taxa should be regarded as ontologically distinct. Before proceeding with this argument, however, it is necessary to consider exactly what species are.

Despite a proliferation of seemingly disparate species concepts in the evolutionary and systematic literature (reviewed by Mayden, 1997), Frost and Kluge (1994) proposed that the notion of species is not a problematic theoretical issue. It extends from the provision that species are fundamental entities in an evolutionary system. Considering that the recoverable aspects of evolution are predominantly hierarchical (Hennig, 1965, 1966), we would want to identify as species the largest entities within the preserve of evolutionary theory lacking long term internal hierarchical structure. In the case of sexual organisms, these entities correspond to independently evolving

population lineages (Frost and Kluge, 1994, p. 275). The idea that species are population lineages has been espoused by several authors (e.g. Simpson, 1951; Wiley, 1978, 1981; Ridley, 1989; Frost and Kluge, 1994; de Queiroz, 1998, 1999; Wiley and Mayden, 2000a). Indeed, de Queiroz (1998, 1999) has argued cogently that all contemporary definitions of species derive from this view.

Wiley (1979, 1981; see also de Queiroz, 1999; Wiley and Mayden, 2000a) has emphasised that species, as lineages, are individuals; they originate with the division of an existing lineage and cease to exist when they either go extinct or themselves divide. That species can cease to exist when they divide implies that they are, moreover, integrated individuals; it is the significant loss of integration accompanying division that results in an individual ceasing to exist upon dividing. In regarding species as integrated, cohesive entities, many authors have considered interbreeding to constitute the decisive interaction among their parts (individual organisms and demes; e.g. Mayr, 1970; Ghiselin, 1987, 1997). As a result of interbreeding, novel states spread among the parts of a lineage with the dispersal of organisms and union of entire demes, so that the lineage as a whole can be considered to evolve. Insofar as this is the case, it would seem difficult to argue that species are not cohesive individuals. Nonetheless, Ereshefsky (1999) and Mishler (1999) maintain that interbreeding is an inadequate basis on which to distinguish species and higher taxa.

Although Ereshefsky (1999) does not dispute that interbreeding can integrate and thereby impart cohesion to groups of organisms, he argues that not all species are integrated: 'suppose, as many biologists do, that asexual organisms form species taxa. The members of such species are not bound by interbreeding but by such processes as selection, genetic homeostasis, and developmental canalisation .... Such processes cause a group of organisms to belong to a single species without requiring any causal interaction among those organisms' (Ereshefsky, 1999, p. 288). In attempting to formulate a universal, theoretically significant concept of species, evolutionary biologists and systematists have considered asexual organisms to be especially problematic (see Wiley, 1978; Templeton, 1989; Hull, 1997). As Van Valen (1976; see also Hull, 1980) noted, however, there is no reason to expect that such a concept can be formulated. If we are to regard integration (in conjunction with an associated ability to undergo anagenesis as a whole) as a distinctive property of species (relative to higher taxa), and if processes such as selection, genetic homeostasis, and

developmental canalisation do not produce integration (which they patently do not), it follows that asexual organisms do not form species (for similar views see Hull, 1980; Frost and Kluge, 1994; Ghiselin, 1997; Lee, 2003). It should be noted, however, that this does not preclude the possibility of a universal system of biological nomenclature (see de Queiroz and Gauthier, 1992); such a system merely would include only clade names for asexual taxa.

Even if we agree that asexual organisms do not form species, Ereshefsky (1999) considers that the distinction between species and higher taxa remains problematic. According to Ehrlich and Raven (1969) and Templeton (1989), many species are composed of local populations (i.e. demes) among which little or no gene flow occurs for extended periods. Ereshefsky (1999, p. 289) proposes that 'the unity of such species may be the result of interbreeding within local populations, or their unity may be due to processes that independently affect organisms, such as selection or genetic homeostasis'. Thus, he considers that, although local populations are rendered cohesive through interbreeding, in many cases the species they comprise are not. In evaluating this argument, it is important to consider the temporal scale on which significant reproductive interactions among local populations take place. As noted above (see Cohesive and historical individuals), it is not necessary that all parts of an individual are interacting at every instant for that individual to be cohesive; it is only necessary that sufficient interaction occurs to allow the individual to respond as a whole with respect to some process. In the case of species, reproductive interactions among local populations must be realised sufficiently often that those local populations evolve (i.e. undergo anagenesis) as a whole. The temporal scale on which such interactions occur will vary, depending on generation times, selective pressures, and population sizes (all of which affect the rate at which an allele becomes fixed within a population). Thus, the fact that the local populations comprising a species do not exchange genetic material for extended periods may affect the cohesion of that species no more than the fact that milliseconds may elapse during the conduction of neural signals affects the cohesion of an organism. Nonetheless, should the frequency of interbreeding among local populations be insufficient to maintain the cohesion of the (nominal) species of which they are a part, there is no reason that these local populations can not be divided into more than one cohesive entity (i.e. species); that a group of organisms is presently referred to as a single species does not necessitate that this is the case.

Mishler (1999, p. 308) argues against the significance of interbreeding in distinguishing species from higher taxa on the basis that 'in most groups, the probability of intercrossability decreases gradually as more and more inclusive groups are compared'. That is, he considers that 'there usually is no distinct point at which the possibility of reticulation drops precipitously to zero' (Mishler, 1999, p. 308). This argument presupposes that the significance of interbreeding is considered to result from its restriction within species. Thus, Mishler contends that, because reproductive interactions may occur among the parts of separate species, interbreeding is not a defining property of species and, accordingly, should not be considered to differentiate species and higher taxa. However, according to the argument presented here, it is not interbreeding *per se* that defines species (with respect to higher taxa) but cohesion resulting from interbreeding. Consequently, the fact that the possibility of interbreeding decreases gradually as more inclusive groups of organisms are compared is extraneous; what is significant is that some frequency of interbreeding exists above which groups of organisms will evolve as a whole and below which they will evolve independently.

2.3 Hierarchy and Monophyly

Pleijel and Rouse (2000, p. 628) contend that the majority of existing species concepts should be rejected as they permit species to be non-monophyletic; that is, they permit situations where, for example, the local populations comprising a species share a sister group relationship with one or more local populations constituting part of a second species (here the latter species is considered to be paraphyletic; more elaborate scenarios can be constructed that would render some species polyphyletic by this reasoning). In their view, such concepts are unacceptable as they may lead systematists to disregard historical information. Thus, they would admit only those concepts that equate species with recovered monophyletic groups. Under such concepts, however, there is no ontological basis for distinguishing species from higher taxa and therefore for recognising species as a distinct taxonomic category (see Ontology, Species, and Higher Taxa above; see also Lee, 2003).

Contrary to the view of some authors (e.g. de Queiroz and Donoghue, 1988, 1990), I do not consider that the concepts of monophyly, paraphyly, and polyphyly can be applied to systems in

which relationships are predominantly or exclusively non-hierarchical (as is the case in systems of demes and sexually reproducing organisms; for similar views see, for example, Nixon and Wheeler, 1990; Goldstein and DeSalle, 2000). Nonetheless, even if such an application of these terms is permitted, I argue that Pleijel and Rouse's (2000) objection to non-monophyletic species (in the sense discussed above) is unfounded, extending from a failure to consider the hierarchical organisation of biological individuals and processes.

With the presumed exception of elementary particles, individuals (in the broad sense discussed above; see Cohesive and historical individuals) are necessarily composed of parts that are also individuals (as opposed to classes, which have instances rather than parts, these being either individuals or other classes; e.g. Eldredge and Salthe, 1984; Frost and Kluge, 1994; Ghiselin, 1974, 1997; Hull, 1976, 1980). Consequently, the organisation of the material universe is inherently hierarchical; higher taxa, for example, are composed of species, which in turn are composed of demes, which in turn are composed of organisms, etc. As a result of their differing scales of spatial and temporal organisation, individuals at different hierarchical levels do not participate in the same processes (Eldredge and Salthe, 1984; for the sake of simplicity, I ignore cases where individuals can be referred to more than one hierarchical level [e.g. unicellular organisms] in this discussion). An organism, for example, may participate in ecological and reproductive processes, however, it does not participate in DNA replication. Similarly, a somatic cell may undergo mitosis, however, it does not undergo speciation. While processes operating at a particular hierarchical level may affect individuals at more or less inclusive levels, they do so only indirectly, by constraining the processes in which those individuals interact (Eldredge and Salthe, 1984). An organism's ability to forage and reproduce will be limited by the rate at which energy is made available in cellular respiration, however, organisms themselves do not directly interact in the latter process. Thus, the individuals occupying particular hierarchical levels and the processes in which they participate may be regarded as discrete systems (Bunge, 1979, cited by Eldredge and Salthe, 1984).

Lidén (1990, p. 183) noted that '[e]ven if monophyly is a universal concept, it is in a particular case meaningful only in relation to the conceptual singularities [i.e. individuals] in the model [i.e. system] concerned'. As hypotheses of common descent, claims of monophyly

necessarily implicate some reproductive process; the notion that a group of somatic cells is descended from a common ancestor is meaningful only insofar as it may be related to some process by which cells are supposed to give rise to descendants, in this case mitosis or schizogony. Considering that individuals at different hierarchical levels do not interact in the same processes (including reproductive processes; see above), it follows that particular claims of monophyly can refer only to individuals at a single hierarchical level. Thus, if we are concerned with establishing whether a group of somatic cells is monophyletic or not, any (non-operational; see below) consideration of organisms is extraneous, since organisms do not undergo mitosis or schizogony and, accordingly, are incapable of being either ancestors or descendants of cells. Similarly, any consideration of demes (i.e. local populations) is extraneous if our concern is the historical relationships of species, since demes do not undergo speciation. Accordingly, the fact that the demes comprising a species may share a sister group relationship with one or more demes constituting part of a second species is irrelevant if our goal is to develop a phylogenetic system (i.e. a system based on the historical relationships of species; Hennig, 1965, 1966).

The difficulty with Pleijel and Rouse's (2000) position is evident if we consider that some of the organisms comprising a deme may be more closely related to organisms of other demes than to one another. Applying Pleijel and Rouse's reasoning, such demes are either paraphyletic or polyphyletic, depending on whether they contain the most recent common ancestor(s) of their component organisms or not. Perhaps, then, systematists should attempt to discover monophyletic groups of organisms rather than demes. Alternatively, they might focus on discovering monophyletic groups of cells, since many organisms are paraphyletic when considered at the cellular level (see, for example, Wiley and Mayden, 2000a). The point is that individuals at a number of hierarchical levels form monophyletic groups. Furthermore, because the reproductive processes in which these individuals interact are largely independent (see above), patterns of historical relationship at different hierarchical levels also are largely independent, so that in many cases they will not coincide. Perhaps the most familiar example of this is the potential discordance of gene and population level trees (see, for example, Pamilo and Nei, 1988; Wu, 1991; Brower *et al.*, 1996); processes such as DNA replication and gene duplication operate independently of processes such as vicariance and dispersal, so that the histories of genes and populations will not necessarily concur.

As historical relationships at a particular hierarchical level need not coincide with those at more or less inclusive levels, a single account of the history of biological individuals encompassing all hierarchical levels (or even more than one hierarchical level) is unattainable. Thus, historical accounts can deal only with individuals at a single hierarchical level in any particular instance. Accordingly, in developing a phylogenetic system, the decision to exclude information on the historical relationships of demes, rather than being ahistorical, is necessitated by the hierarchical organisation of biological individuals and the processes in which they interact.

2.4 A Consideration of Methodology in Species Level Systematics

Pleijel and Rouse (2000, p. 629) propose that '[i]n virtually all cases, the connection between the named species and the empirical evidence that justifies its status is weak or non-existent'. Thus, they consider that systematists are rarely able to provide sufficient empirical justification for accepting the hypothesis that a group of organisms constitutes part of an integrated lineage. This, supposedly, is particularly evident where species are described from limited preserved material. Hence, Pleijel and Rouse (2000, p. 629) consider the decision 'that a few dead specimens represent a species' to be 'an extravagant extrapolation having no place in science' and, accordingly, propose that systematists should not be required to make such decisions in order to classify newly discovered organisms. In a recent paper (Pleijel and Rouse, 2003), they contend that this constitutes perhaps the most significant argument for abandoning the species category in systematics.

As Chalmers (1999) has discussed, the perceived role of empirical evidence in science has shifted in the past half century from that of establishing the truth or falsity (or the probability) of hypotheses to that of providing a basis for comparing alternative hypotheses in the context of theories of scientific progress. Thus, I am concerned here with the ability of systematists to provide empirical evidence that would allow species level systematics to progress in a manner consistent with progress in science generally, rather than with their ability to establish the value of specific hypotheses in any absolute sense. I begin by presenting a general view (or theory) of progress in science that has been widely accepted by philosophers of science and scientific researchers. Subsequently, I argue that species level systematics can be practiced in accordance with this view

and that Pleijel and Rouse's (2000) contention that systematists are rarely able to provide sufficient empirical justification for accepting hypotheses of species limits, accordingly, is unfounded.

2.4.1 Sophisticated falsification and progress in science

According to the influential 'falsificationist' perspective of Popper (e.g. 1959, 1963, 1983), science consists in the proposition and critical appraisal of hypotheses intended to explain some aspect of the surrounding universe. Popper (1959, pp 32-34) considered that the process of critically evaluating hypotheses (and, accordingly, of science itself) always proceeds as follows. A series of conclusions is derived from a hypothesis by means of logical deduction. The compatibility of these conclusions with relevant observational statements (i.e. statements describing observed events) is assessed and a decision concerning the tenability of the hypothesis made accordingly. Where the conclusions and observational statements are consistent, we have no reason to reject the hypothesis and, following Popper's (1983, pp 223-227) terminology, consider it to be corroborated. Conversely, where the conclusions and one or more observational statements are inconsistent, the hypothesis is considered to have been falsified and, accordingly, is abandoned. 'Falsificationism' is based on the premise that hypotheses, insofar as they concern unobserved events, can not be proved but can only be disproved (i.e. falsified). A corroborated hypothesis is thus accepted only tentatively (since it may subsequently be falsified) and is continually reevaluated as empirical evidence becomes available.

While 'falsificationism' has been widely adopted within the scientific community, there are two related difficulties with the 'naïve' formulation described above (see, for example, Kuhn, 1970; Lakatos, 1970, 1977; Rieppel, 1988, pp 13-14). Firstly, the history of science provides numerous examples of hypotheses having been retained despite their inconsistency with one or more observational statements. Indeed, Lakatos (1978, p. 6) noted that 'all [research] programmes grow in a permanent ocean of anomalies'. Secondly, observational statements are themselves fallible and so can never decisively refute a hypothesis. Considering these criticisms of 'naïve falsificationism', Popper formulated a refined, 'sophisticated falsificationist' perspective of scientific methodology, elaborated by Lakatos (1970). According to this perspective, a hypothesis, h, is considered to be falsified only when a second hypothesis, h^*, has been proposed that (1) is consistent with all relevant

observational statements that are consistent with h and (2) predicts one or more observational statements that are improbable under h, especially those that would be considered by the 'naïve falsificationist' to refute h (see Lakatos, 1970, p. 116). Consequently, a hypothesis that is inconsistent with empirical evidence may be retained if there is no alternative hypothesis having the properties of h^* to replace it. Furthermore, progress in science no longer consists in disproving hypotheses by exposing their inconsistency with observational statements (a logical impossibility considering the fallability of observational statements), but instead consists in formulating hypotheses having greater explanatory power.

There has been some disagreement concerning the applicability of 'falsificationism' in historical sciences, including systematics. Mayr and Ashlock (1991, p. 221) asserted that 'falsification refers to theories based on universal laws. Since classifications are not such theories, falsification is an inappropriate consideration'. However, Popper did not consider (sophisticated) falsification to be restricted to universal statements, noting that 'the description of unique [i.e. historical] events can very often be tested by deriving from them testable predictions or retrodictions' (Popper, 1980, p. 611). Where testable predictions (or retrodictions) can be derived from a hypothesis, it is possible to assess its compatibility with empirical evidence and competing hypotheses. Consequently, the hypothesis may falsify an existing hypothesis (where one or more of the predictions derived from it are empirically consistent and improbable under the existing hypothesis) or be falsified by a novel hypothesis (where it is incompatible with one or more empirically consistent predictions derived from the novel hypothesis). Thus, the fact that classifications are not universal statements does not preclude their appraisal within the context of 'sophisticated falsificationism'. Rather, to the extent that classifications are intended as explicit representations of our contingent knowledge of phylogeny, they constitute testable hypotheses that can be readily evaluated according to 'sophisticated falsificationist' principles (see, for example, Wiley, 1975; Farris, 1983; Kluge, 1997a).

2.4.2 Sophisticated falsification in species level systematics

Considering the preceding discussion of methodology and progress in science, the issue of concern here is whether or not the statement that a series of specimens constitutes part of an

integrated lineage entails testable conclusions (i.e. conclusions that can be confirmed or disconfirmed by observational statements). In particular, if it is possible to identify potentially observable conditions or events, the realisation of which would be improbable except under a specific hypothesis of species limits, there is no reason to expect that species level systematics can not be practiced in accordance with the 'sophisticated falsificationist' account of science.

Although some authors (e.g. Sokal and Crovello, 1970; Mayr, 1982) have claimed that definitions equating species with independently evolving lineages (specifically, the evolutionary species concepts of Simpson [1951] and Wiley [1978, 1981]) have virtually no empirical implications, Wiley and Mayden (2000b, p. 147) noted that 'the concept of an independently evolving lineage is linked to all sorts of testable phenomena'. This is evident if we consider a generalised scenario in which an ancestral population lineage divides to produce two descendant lineages. As de Queiroz (1998) has discussed, the division of the ancestral lineage is associated with several related events or processes. Alleles originate, change in frequency, become fixed and/or go extinct in one or both of the descendant lineages, producing similar changes in the states of qualitative phenotypic characters and shifts in the frequency distributions of quantitative characters. Consequently, the epiphenotypes (*sensu* Wiley, 1981, p. 61) of the organisms composing each lineage diverge. The extinction of alleles in the descendant lineages also results in their progression through stages in which their component alleles comprise polyphyletic, paraphyletic, and reciprocally monophyletic groups (e.g. Avise and Ball, 1990; Avise, 1994, 2000). In some cases, changes in the states of characters affect the ability of organisms to interbreed, so that, as the descendant lineages diverge, they at some point become intrinsically reproductively isolated. Each of these events or processes can be investigated empirically; the level of epiphenotypic divergence of two groups of organisms may be estimated by comparing inter- and intragroup variation in genetic and/or phenotypic characters, the historical relationships of their component alleles can be inferred from amino acid or nucleotide sequences using phylogenetic methods, and their intrinsic reproductive isolation may be revealed by character state distributions in areas of sympatry, crossing experiments, or the observation of major chromosomal differences. Thus, hypotheses of the limits of independently evolving lineages (which may be rephrased as hypotheses of lineage division events) can be connected to a number of testable predictions (e.g. that a group of organisms, thought to

represent part of an independently evolving lineage, has diverged epiphenotypically from a second group of organisms, thought to represent part of a different lineage).

de Queiroz (1998) considered that observational statements following from the occurrence of those events or processes associated with the separation of lineages (e.g. that a group of organisms can be diagnosed by one or more character states or contains a monophyletic group of alleles at a particular locus; see above) may provide evidence for hypotheses of species limits. It is evident that a particular hypothesis of species limits may explain such observational statements (see above), however, if systematists are to contend that the acceptance of a hypothesis results in increased explanatory power (i.e. if systematists are to make progress in the 'sophisticated falsificationist' sense) these observational statements should not be equally explicable under alternative hypotheses (see above).

Given that a group of organisms is separable into two subgroups, each of which is diagnosed by one or more character states, we might propose that it contains parts of two independently evolving lineages. However, although the observation of diagnosable subgroups may be explained as the result of epiphenotypic divergence associated with lineage separation (and hence the existence of two lineages), it also is consistent with the presence of two or more alleles within a single lineage. Nonetheless, under the latter hypothesis it is improbable that either subgroup would possess diagnostic states for multiple unlinked characters, the distributions of which are expected to be independent among interbreeding organisms (assuming an absence of selection). Thus, the observation of correlated patterns of variation in unlinked characters would appear to provide supporting evidence for (i.e. corroborate) the hypothesis that a group of organisms contains parts of more than one independently evolving lineage. A similar argument can be made for disjunctive patterns of variation in quantitative characters, which are usually assumed to exhibit an approximately normal distribution within populations (Hartl and Clark, 1997).

As with the possession of diagnostic character states, the observation that two subgroups of a group of organisms contain reciprocally monophyletic assemblages of alleles (i.e. haplotypes), although explained by the existence of two independently evolving lineages, also is consistent with

the existence of a single lineage. Indeed, the presence of multiple haplotype clades within a lineage in many cases would be expected, especially when examining rapidly evolving, non-recombining genetic elements, such as some mitochondrial genes (see, for example, Avise *et al.*, 1987; Avise, 1994, 2000). Avise (1994, p. 247) considered that '[m]onophyletic groups [of alleles] distinguished by large phylogenetic gaps usually arise from long-term extrinsic (biogeographic) barriers to gene flow'. Thus, where two reciprocally monophyletic assemblages of alleles are separated by a large number of nucleotide substitutions (or resulting changes in amino acid sequences), we might contend that the subgroups (of organisms) containing them have been subject to long term isolation, especially where they are geographically localised. This has prompted some authors to argue that such subgroups are likely to constitute parts of independently evolving lineages and, accordingly, that they should be recognised as distinct species (e.g. Densmore *et al.*, 1992; Rodríguez-Robles and De Jesús-Escobar, 2000; Rodríguez-Robles *et al.*, 2001). However, even if we disregard the possibility of distinct haplotype clades arising in the absence of extrinsic reproductive barriers (see Avise, 2000, p. 138; this would seem reasonable where such clades are geographically localised), the fact that subgroups (local populations) within a species are isolated for extended periods does not necessitate that they are evolving independently (see The ontological distinction between species and higher taxa above). Furthermore, even where a group of organisms does include parts of more than one independently evolving lineage, lineage sorting of divergent ancestral alleles may result in a lack of correspondence between these parts and subgroups containing distinct, reciprocally monophyletic assemblages of alleles. Nonetheless, although the observation that two subgroups contain distinct haplotype clades is consistent with the existence of a single integrated lineage or multiple lineages, one or more of which contain paraphyletic or polyphyletic assemblages of alleles, it is improbable under either hypothesis that these subgroups would contain monophyletic assemblages of alleles at unlinked loci; the former hypothesis would necessitate the chance association of alleles (those comprising haplotype clades at each locus) in all individuals, while the latter hypothesis, additionally, would necessitate the chance correspondence of patterns of lineage sorting for multiple loci. Conversely, the independent extinction of alleles within two or more lineages and the associated development of reciprocal monophyly at unlinked loci is an expected outcome of their separation (see above). Thus, the hypothesis that a group of organisms incorporates parts of two or

more lineages would appear to be corroborated by the observation of subgroups containing distinct, reciprocally monophyletic assemblages of alleles at multiple unlinked loci.

In contrast with the observation that subgroups of a group of organisms possess diagnostic character states or contain reciprocally monophyletic assemblages of alleles, evidence for intrinsic reproductive isolation is inconsistent with the existence of a single lineage. Because interbreeding is the only known process that can integrate species (de Queiroz and Donoghue, 1988, pp 321-322; see also The ontological distinction between species and higher taxa above), an inability of the organisms comprising two subgroups to interbreed ensures that they are not parts of a more inclusive group capable of evolving as an integrated whole. Accordingly, the hypothesis that a group of organisms contains parts of more than one independently evolving lineage is corroborated by the observation of intrinsically reproductively isolated subgroups. As noted above, intrinsic reproductive barriers may be revealed by a number of potentially observable conditions or events. Richardson *et al.* (1986, p. 47; see also Baverstock and Moritz, 1996) noted that 'a single fixed genetically determined ... difference between sympatric populations of a diploid sexually reproducing species is sufficient to both recognise and characterise two co-existing ... species'. A fixed difference exists between two groups of organisms where they share no alleles at a particular locus and would be expected only in the absence of interbreeding (where organisms of two groups are interbreeding we would expect to observe all combinations of alleles, assuming an absence of selection). Although such differences may be apparent in patterns of morphological, physiological, or ecological variation, they have typically been revealed in allozyme electrophoretic studies, the results of which can usually be interpreted directly in terms of Mendelian genotypes at particular loci (Richardson *et al.*, 1986; Avise, 1994; see Adams *et al.*, 1982; Baverstock *et al.*, 1984; Hutchinson and Donnellan, 1999; James *et al.*, 2001 for examples of the use of allozyme data in inferring intrinsic reproductive barriers). An absence of interbreeding among sympatric groups of organisms may also be revealed by consistent differences in unlinked characters or disjunctive patterns of variation in quantitative characters, as discussed above. Additionally, direct evidence for intrinsic reproductive isolation may be provided by breeding studies or the observation of chromosomal differences that have been demonstrated to disrupt meiosis in hybrid progeny, including those

resulting from multiple independent fusions involving homologous chromosomes or changes in ploidy (see Sites and Moritz, 1987; Orr, 1990).

It is evident that a number of testable predictions can be derived from the hypothesis that a series of specimens constitutes part of an independently evolving lineage. Furthermore, the realisation of at least some of these predictions is probable only under the hypothesis that a distinct lineage is present and therefore would falsify (in the 'sophisticated falsificationist' sense) the alternative hypothesis that the proposed lineage incorporates parts of one or more recognised lineages. Accordingly, species level systematics may be considered to progress in a manner consistent with the 'sophisticated falsificationist' view of scientific progress generally. This is the case even where systematists are provided with only limited preserved material. Here it is possible to test predictions of consistent differences in unlinked characters or disjunctive patterns of variation in quantitative characters, so that the proposition that 'a few dead specimens represent a species', instead of being 'an extravagant extrapolation having no place in science', may falsify alternative hypotheses and, accordingly, constitutes a legitimate scientific hypothesis.

2.5 Conclusion

The 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. 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 an inadequate appreciation of the hierarchical organisation of biological individuals and processes. Just as any consideration of the historical relationships of somatic cells is extraneous if we are concerned with the relationships of organisms, so any consideration of the historical relationships of demes is

extraneous if our concern is developing a system based on the relationships of species. 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 on the basis of their relative explanatory power and, consequently, either accepted or rejected according to the same criteria as all hypotheses in science.

Chapter 3

A Systematic Review of Hydrophiine Brown Snakes (*Pseudonaja*)

3.1 Introduction

In the preceding chapter, I presented a view of species level systematics consistent with that of scientific endeavour generally (Lakatos, 1970; Popper, 1959, 1983). I argued that hypotheses of species limits can be connected to a number of testable predictions that are unlikely to be realised under alternative hypotheses and that they can therefore be assessed in the same manner as all hypotheses in science. In this chapter, I apply these ideas in reviewing the species level systematics of *Pseudonaja*, a group of hydrophiine snakes (*sensu* Slowinski and Keogh, 2000), commonly called brown snakes, the classification of which has been regarded as especially problematic.

Pseudonaja is distributed throughout mainland Australia and southern New Guinea, occurring in all major terrestrial habitats except closed forest (Cogger, 1992; O'Shea, 1996; Greer, 1997). Typically, individuals are various shades of brown dorsally (hence the commonly used vernacular name), however, colouration is variable and may be greyish, yellowish, or nearly black (see, for example, Mirtschin and Davis, 1983, pp 52-60; see also below). The group contains among the most highly venomous snakes in the world and all nominal species except one (*P. modesta*) are considered dangerous to humans (Broad *et al.*, 1979; Cogger, 1992). The primary food of brown snakes consists of small mammals, birds, lizards, and frogs (Shine, 1989, 1991), and prey are subdued by constriction as well as envenomation (Shine and Schwaner, 1985). All species are oviparous, with clutch size varying from two to 38 (Shine, 1989). Male-male combat has been observed in some species (Fleay, 1943; Shine, 1989). *Pseudonaja* is one of the few groups of snakes to have benefited from European settlement in Australia, due largely to the introduction of the house mouse, *Mus musculus* (Shine, 1989).

The species level systematics of *Pseudonaja* has remained poorly resolved despite significant implications for public health. Brown snakes are responsible for the majority of cases of

snake bite and snake bite fatality reported in Australia each year (Sutherland, 1992). Clinical assessment of bite victims indicates that there is considerable variation in the degree of coagulopathy and response toantivenom treatment displayed by patients (Williams and White, 1997). Williams and White (1997) reported intra- and interspecific variation in the procoagulant activity (the agent producing coagulopathy in snake bite victims) of venom samples from *P. textilis* and *P. nuchalis* specimens. Similarly, Williams *et al.* (1994) reported variation in procoagulant activity among venom samples from *P. affinis*, *P. inframacula*, *P. nuchalis*, and *P. textilis* specimens. Nonetheless, considering the uncertainty associated with the present classification, it is difficult to attribute this variation to differences at the individual, demic, or species level. Thus, the lack of a well founded classification for *Pseudonaja* impedes further understanding of the factors responsible for variation in patient response to envenomation.

3.2 Historical Review and Objectives

In 1858, Günther erected the name *Pseudonaja* for three specimens in the collection of the British Museum, which he described as a new species, *P. nuchalis*. Boulenger (1896) later referred *Pseudonaja* to the synonomy of *Diemenia* (emended to *Demansia* by Fry [1914]), an arrangement adopted by the majority of authors (e.g. Loveridge, 1934; Kinghorn, 1956) until Worrell (1961) revived the name for all of the currently recognised species (except *P. inframacula*; see below). Worrell (1961) did not discuss in detail the reasons for his decision, stating only that it had been based 'on skull characters' (Worrell 1961, p. 20), however, his separation of *Pseudonaja* and *Demansia* was later supported by evidence from venom-gland musculature (McDowell, 1967) and has been recognised by all subsequent authors (Mengden, 1983).

Pseudonaja is diagnosed by several derived character states, including the presence of fused temporolabial and posterior supralabial scales (Cogger, 1992; Greer, 1997) and unique chromosome (Mengden, 1985a,b) and hemipenis (Keogh, 1999) morphology, and the majority of authors have considered the group to be monophyletic (e.g. Worrell, 1961; McDowell, 1967; Mengden, 1985a,b; Hutchinson, 1990; Greer, 1997; Keogh, 1999; see however, Wallach, 1985; Keogh *et al.*, 1998). Seven species are recognised currently (*P. affinis*, *P. guttata*, *P. inframacula*, *P. ingrami*, *P. modesta*,

P. nuchalis, and *P. textilis*), however, there is general agreement that some of these species include more than one taxon. Cogger (1992, p. 668), for example, proposed that the existing 'classification is uncertain and unreliable' and that 'most species are probably composite'. Likewise, Hutchinson (1990, p. 402) noted that the 'alpha taxonomy [of *Pseudonaja*] is presently very unsatisfactory'. In particular, the geographically widespread species *P. nuchalis*, which exhibits considerable variation in colour pattern, has been considered by many authors to incorporate several species (e.g. Mengden, 1985b; Mengden and Fitzgerald, 1987; Wilson and Knowles, 1989; Shine, 1991; Greer, 1997; see, however, Bush, 1989a,b; Orange, 1992 and below).

While there is some consensus that the classification of *Pseudonaja* is in need of revision, the group has received little detailed study. Gillam (1979) redescribed those recognised species of *Pseudonaja* occurring in the Northern Territory, considering several characters, such as the colour of the mouth lining and iris, that previously had not been examined. Although no changes to the existing classification were recommended in this study, Gillam proposed that reputedly isolated populations of *P. textilis* from the MacDonnell Ranges, Barkly Tableland, and Victoria River District would probably be recognised as distinct species with further research. Gillam also described 12 different forms of *P. nuchalis* on the basis of dorsal colour pattern, although the taxonomic implications of this were not discussed.

In their controversial revision of the Australian herpetofauna, Wells and Wellington (1984, 1985) revived a number of previously recognised species names for *Pseudonaja* as well as describing six new species from central and northern Australia. As with many of their taxonomic propositions, Wells and Wellington provided no justification for the nomenclatural changes, which have been heavily criticised by some authors (e.g. Mengden, 1985b, p. 202), and seemingly ignored variation present in the characters mentioned in their descriptions. Nonetheless, the International Commission on Zoological Nomenclature (1991) has rejected an application requesting suppression of their works and, accordingly, their propositions are considered as hypotheses to be examined where possible in the present study.

Mengden (1985b) examined chromosome morphology in all nominal species of *Pseudonaja*, providing a clearer understanding of several problems concerning the classification of the group, particularly those regarding *P. nuchalis*. Seven different karyomorphs were identified within this species, two of these possessing characteristic diploid chromosome numbers and a third exhibiting what Mengden (1985b, p. 198) considered to be 'substantial' chromosomal differences when compared with the other karyomorphs. These karyomorphs were reported to exhibit distinct dorsal colour patterns, several corresponding to those described by Gillam (1979), and in a number of cases to be broadly sympatric (see Mengden, 1985b, his Fig. 7). Furthermore, an investigation of allozyme variation at 23 loci in three karyomorphs revealed that they are at least as divergent genetically as some of the other species of *Pseudonaja* (Mengden, 1985b, his Figs 2 and 3). Thus, Mengden proposed that at least four species are currently referred to *P. nuchalis* (Table 3.1), with the caveat that one of these species (the 'Southern' morph) may be composite. Mengden also showed that *P. inframacula* is diagnosed by a unique karyotype and, accordingly, proposed that this taxon should be recognised as separate from *P. textilis*, to which it previously had been referred as a subspecies.

While Mengden (1985b) did much to clarify the problems concerning the classification of *Pseudonaja*, he refrained from presenting any formal nomenclatural changes, suggesting that a broader study incorporating more material would be necessary before this could be advocated. In particular, he emphasised the need for further investigation of the variation he observed within the 'Southern' *P. nuchalis* group. To this it may be added that Mengden's chromosome data are alone insufficient to support his conclusions concerning species limits within *Pseudonaja*. While Mengden considered that at least some of the chromosomal differences he observed, which are largely the result of pericentric inversions and single Robertsonian rearrangements, may present a barrier to interbreeding, the effect of such differences on reproductive compatibility is difficult to predict (see Sites and Moritz, 1987). Thus, it is possible that these differences reflect intraspecific, as opposed to interspecific, variation (see Chapter 2). Although Mengden presented observations of colour pattern and allozyme variation, the former were discussed only generally, with little regard to individual or geographical variation, while the latter were available for only a subset of the species he proposed. Furthermore, Mengden presented his data in summary format, with no reference to the material he

Table 3.1. Mengden's (1985b) *Pseudonaja nuchalis* morphs. The 'Darwin', 'Pale head, grey nape', 'Orange with black head', and 'Southern' morphs were considered by Mengden to constitute distinct species.

Morph	Karyotype	Colour Pattern
'Darwin'	2N = 30; autosome pairs 4-14 gradually decreasing in size; sex chromosomes equal in size.	'... uniform light brown (in summer). The snout is often paler followed by a dark interocular region. The nuchal area is often flecked with a few dark scales, sometimes forming a narrow band on the neck' (Mengden, 1985b, p. 202).
'Pale head, grey nape'	2N = 34; autosome pairs 4-16 separable into two distinct size classes; sex chromosomes differ markedly in size.	'... possesses a pale head, dark interocular region, grey nape and herringbone pattern on the posterior two-thirds of the body' (Mengden, 1985b, p. 198).
'Orange with black head'	2N = 32; autosome pairs 4-15 gradually decreasing in size; sex chromosomes equal in size.	'... orange ... with herring-bone pattern and black head and nape' (Mengden, 1985b, p. 198).
'Southern'		
'Southern'	2N = 34; autosome pairs 4-16 separable into two distinct size classes; sex chromosomes equal in size.	'... may be either monotonal [brown] or possess a darker brown or black head and a few black scales on the nape. This is also sometimes accompanied by dark diagonal markings on the posterior dorsolateral surfaces' (Mengden, 1985b, p. 202).
'Southern with black nuchal band'	2N = 34; autosome pairs 4-16 separable into two distinct size classes; sex chromosomes equal in size.	As for the 'Southern' morph but with a broad dark brown or black band on the neck.
'Southern with black bands'	2N = 34; autosome pairs 4-16 separable into two distinct size classes; sex chromosomes differ markedly in size.	As for the 'Southern' morph but with a series of broad dark brown or black bands on the body. 'The ground colour may be pale orange to brown' (Mengden, 1985b, p. 202).
'carinata'	2N = 34; autosome pairs 4-16 separable into two distinct size classes; sex chromosomes equal in size.	'... with brown head, and a few dark spots on a paler brown nape. The posterior two-thirds of the body has eleven black saddles interspaced with slightly larger pale areas. These pale areas are each crossed by three to four narrow (one scale length) well defined brown bands' (Mengden, 1985b, p. 200, describing the holotype of *Diemenia carinata*).

examined, so that it is difficult to assess how robust the reported correspondence of karyotype and colour pattern is. Accordingly, there is not only a need to conduct a broader study incorporating more material, but also incorporating explicit data on independent (with respect to the reported chromosome differences) characters.

In response to Mengden (1985b), Bush (1989a,b) and Orange (1992) published observations of *P. nuchalis* in Western Australia that prompted them to query the supposed composite nature of this taxon. They reported considerable ontogenetic variation in colour pattern, with some individuals being referrable to different colour morphs depending on age. Furthermore, they noted that individuals may exhibit colour patterns that are intermediate between those of two or more colour morphs (see, for example, Bush's [1989b] Fig. 4, which depicts a specimen that may be regarded as an intermediate of the 'Pale head, grey nape' and 'Orange with black head' morphs) and that different colour morphs (e.g. the 'Pale head, grey nape' and 'Orange with black head' morphs, and '*carinata*' and conspicuously banded individuals) exhibit similar colouration as juveniles. Perhaps most significantly, however, Bush (1989b) observed successful crosses involving two 'Pale head, grey nape' specimens, and a male specimen that may be regarded as a 'Pale head, grey nape'-'Orange with black head' intermediate (see Bush's [1989b] Fig. 4) and a female 'Orange with black head' specimen, the former yielding juveniles referrable to the 'Pale head, grey nape', 'Orange with black head', and '*carinata*' morphs (see Bush's [1989b] Fig. 2) and the latter yielding juveniles referrable to the 'Pale head, grey nape' and 'Orange with black head' morphs. These observations led Bush and Orange to conclude that, in southern Western Australia, '*P. nuchalis* is a single species, albeit a highly variable one' (Orange, 1992, p. 23) and that 'one should err on the side of conservatism when considering ... [its] taxonomic dismemberment' (Bush, 1989b, p. 30; also quoted by Orange, 1992, p. 29).

It is evident that several questions concerning the species level systematics of *Pseudonaja* remain to be resolved: (1) Is there independent evidence, corroborating Mengden's (1985b) chromosome data, that nominal *P. nuchalis* includes more than one species? (2) If so, are the species limits proposed by Mengden corroborated by independent evidence? (3) Should the evolutionary independence of the 'Southern' *P. nuchalis* group be supported, is there evidence that the four

karyomorphs within this group (see Table 3.2) constitute distinct species? (4) Do the reputedly isolated populations of *P. textilis* constitute distinct species, as Gillam (1979) supposed? (5) Is there evidence for the evolutionary independence of the remaining species of *Pseudonaja* presently recognised? (6) Is there evidence for independently evolving lineages (i.e. species) within *Pseudonaja* that have not been made apparent by traditional scale and colour pattern characters and chromosome morphology (Mengden 1985b)? As Mengden's data were presented in summary format, without reference to the material he examined, they can not be incorporated in a broader study, so that much of Mengden's work must be repeated if many of the above questions are to be addressed.

Previous taxonomic studies of *Pseudonaja* (e.g. Gillam, 1979; see also Mengden and Fitzgerald, 1987; Cogger, 1992) indicate that traditional scale and colour pattern characters are, in the majority of cases, unlikely to exhibit diagnostic states at the species level, being subject to considerable individual variation. Conversely, it is probable that nucleotide sequences, which have been employed in investigations focusing on all levels of biological organisation, would provide a large number of suitable characters, assuming an appropriate marker is selected. On account of its relatively high rate of evolution, maternal and effectively haploid inheritance (and thus the relatively brief period over which mutations become fixed within a population [see, for example, Moore, 1995]), and high copy number (facilitating isolation and amplification), mitochondrial DNA is employed in the present study to identify groups of specimens containing distinct, monophyletic assemblages of alleles (i.e. groups of specimens that are potentially extrinsically and/or intrinsically isolated; see Chapter 2). Subsequently, the evolutionary independence of these groups is tested using allozyme electrophoretic and morphometric data, both of which have been employed extensively in elucidating species limits where traditional morphological characters exhibit confounding patterns of variation (for examples see Chapter 2 and below). Additionally, scale and colour pattern attributes are examined in the light of the mitochondrial DNA sequence data in an attempt to identify either previously recognised or novel diagnostic character states. Finally, chromosome data obtained for a number of individuals (in conjunction with observations of colour pattern) allow the mitochondrial DNA sequence, allozyme electrophoretic, and morphological data to be related to the conclusions of Mengden (1985b).

Adopting the above approach, I attempt to provide a well-founded hypothesis of species limits within *Pseudonaja*, supported by multiple lines of evidence. In doing so, I address the aforementioned questions concerning the species level systematics of the group and, where possible, the taxonomic propositions of Wells and Wellington (1984, 1985; these are considered in the Species Accounts).

3.3 Materials and Methods

3.3.1 Ingroup sampling and outgroups

The following comments on ingroup sampling and the selection of outgroups concern the mitochondrial DNA sequence analysis, which included all individuals considered in this study and served as a basis for the other analyses (see the previous section and below). Brief remarks on sampling for the allozyme electrophoretic, morphological, and chromosomal analyses are provided in the relevant sections below.

Mitochondrial DNA sequences were obtained for 189 individuals, representing all nominal species of *Pseudonaja* except *P. ingrami*, and the seven colour morphs of *P. nuchalis* identified by Mengden (1985b) as possessing distinctive karyotypes. As larger specimens were used in morphological comparisons (see below), sequence data for juvenile specimens, or for which specimens could not be located, were included only where appropriately preserved tissues (see below) were available from otherwise unsampled geographical areas. Individuals were sampled from throughout the distributions of most species, however, limited material was available from northern Australia (see Species Accounts).

Although the nominal species of *Pseudonaja* have been considered by many authors to comprise a clade (see Introduction), the results of several previous studies indicate that the group is paraphyletic. Mengden's (1985b, his Fig. 3) hypothesis of phylogenetic relationships among a limited number of hydrophiines shows *Oxyuranus* nested within *Pseudonaja*. Likewise, Keogh *et al.*'s (1998) parsimony analyses consistently placed *P. modesta* as the sister lineage to a clade containing *P. textilis* and *O. microlepidotus* (*P. modesta* and *P. textilis* were the only species of

Pseudonaja included in these analyses). Thus, mitochondrial DNA sequences obtained for two individuals of *O. microlepidotus* and three individuals of *O. scutellatus* were included in the analysis presented here to test the monophyly of *Pseudonaja*.

According to Wallach's (1985, his Fig. 5) preferred hypothesis of terrestrial hydrophiine relationships, the sister group to *Pseudonaja* and *Oxyuranus* is a clade consisting of *Demansia* and *Pseudechis*. Keogh's (1999, his Fig. 8) phylogenetic hypothesis, similarly, indicates a close affinity among these taxa (see, however, Greer, 1997; Keogh *et al.*, 1998), although his arrangement differs, with *Demansia* appearing as the sister lineage to *Pseudonaja*, exclusive of *Oxyuranus* and *Pseudechis* (cf. the previous paragraph). A close relationship among *Pseudechis*, *Pseudonaja*, and *Oxyuranus* has also been proposed by Mengden (1985a, his Fig. 5), however, he considered *Demansia* to be only distantly related with this group. Considering the inconsistency in these studies with regard to the exact relationships of *Pseudonaja* and *Oxyuranus*, both *Pseudechis* and *Demansia* were employed as outgroup taxa in the phylogenetic analysis performed here. Mitochondrial DNA sequences were obtained for three individuals of *P. australis* and two individuals of *D. papuensis*.

3.3.2 Specimens and tissues

Storage and collection details for all specimens and tissues are listed in Appendix 1. The material used was obtained from the following institutions: Australian Biological Tissue Collection (ABTC, South Australian Museum, Adelaide), Australian Museum (AM, Sydney), Evolutionary Biology Unit (EBU, Australian Museum, Sydney), Northern Territory Museum (NTM, Darwin), South Australian Museum (SAM, Adelaide), Western Australian Museum (WAM, Perth). All of the specimens examined had been fixed with 10% formalin and were stored in 70% ethanol. Tissues consisted of liver, heart, kidney, or skeletal muscle and had been either stored at -80°C or preserved in a 1:1 solution of absolute ethanol and 0.85% saline.

3.3.3 Mitochondrial DNA

3.3.3.1 DNA extraction, amplification, and sequencing

Total cellular DNA was extracted using DNAzol (Life Technologies) following a protocol modified from the manufactuer's instructions. 0.2-0.5 g of tissue was homogenised in 1 mL of

DNAzol then 10 µL of Proteinase K (20 $mgmL^{-1}$) added and the mixture either incubated at 56 °C for 2 hr or left at room temperature overnight. Ethanol-preserved tissue was washed with distilled water prior to homogenisation. Following Proteinase K digestion, insoluble tissue debris, RNA, and excess polysaccharides were pelleted by centrifuging at 11000 rpm for 12 min. DNA was precipitated from 500-750 µL of supernatant with 0.5 × vol of absolute ethanol at –20 °C for at least 20 min. Precipitated DNA was pelleted by centrifuging at 12000 rpm for 15 min then washed in 70% ethanol, air-dried for at least 15 min, and resuspended in 100-300 µL of 1 × TE buffer.

An approximately 770 bp mitochondrial DNA fragment, including the 3′ end of the protein coding gene *ND4* (668 bp) and the adjacent tRNAs, $tRNA^{His}$ and $tRNA^{Ser}$ (approximately 102 bp; see Arévalo *et al.*, 1994), was amplified using the polymerase chain reaction (PCR; Saiki *et al.*, 1985, 1988). PCR conditions were as follows: 50-100 ng template DNA, 0.1 µL AmpliTaq Gold polymerase (Perkin Elmer), 4 mM $MgCl_2$, 2.5 µL GeneAmp 10 × PCR buffer (Perkin Elmer), 0.8 mM dNTPs, and 0.5 µM primers in a total volume of 25 µL. Light and heavy strand primer sequences are ND4 5′-TGA CTA CCA AAA GCT CAT GTA GAA GC-3′ (Forstner *et al.*, 1995) and Leu 5′-TTT TAC TTG GAT TTG CAC CA-3′ (Arévalo *et al.*, 1994) respectively. PCRs were carried out on a Corbett Research PC-960G Thermal Cycler with the following cycling conditions: one cycle of 92 °C for 9 min, 55-58 °C for 1 min, and 72 °C for 1 min, 34 cycles of 92 °C for 45 sec, 55-58 °C for 45 sec, and 72 °C for 1 min, and one cycle of 72 °C for 6 min. 1.5% agarose gel electrophoresis and ethidium bromide staining were used to visualise PCR products.

PCR products were purified using UltraClean PCR clean-up columns (Mo Bio Laboratories) following the manufacturer's instructions. Both strands were then cycle sequenced using the ABI PRISM BigDye Terminator Cycle Sequencing Ready Reaction Kit with the same primers used for PCR amplification. Sequencing was carried out on either a Hybaid Omn-E Thermal Cycler or a Corbett Research PC-960G Thermal Cycler with the following reaction and cycling conditions: 70-100 ng template DNA, 3 µL Ready Reaction Premix, and 0.5 µM primers in a total volume of 10 µL; 25 cycles of 92 °C for 30 sec, 50 °C for 15 sec, and 60 °C for 4 min and one cycle of 60 °C for 4 min. DNA was precipitated from the extension products with 75% isopropanol at room temperature

for at least 15 min. Precipitated DNA was then pelleted, washed in 75% isopropanol, air-dried, and run on an ABI 3700 capillary sequencer.

3.3.3.2 Testing for nuclear paralogues

The incorporation of duplicated sections of the mitochondrial genome into the nuclear genome (hence the term nuclear paralogues) is a well known phenomenon, having been reported for a large number of groups, including hydrophiines (recently reviewed by Bensasson *et al.*, 2001; see Keogh, 1998 for examples from hydrophiines). Such incorporations can present a considerable difficulty when inferring population- or higher-level phylogeny from mitochondrial DNA sequences, as preferential amplification of the incorporated sections may occur inadvertently, resulting in a data set consisting of paralogous, as opposed to orthologous, sequences (Zhang and Hewitt, 1996; Bensasson *et al.* 2001).

The potential for the primers used here to amplify nuclear paralogues was assessed using a method similar to that described by Donnellan *et al.* (1999). DNA was extracted from mitochondria-enriched homogenates for three individuals (ABTC numbers 35983, 56907, and 56281) following Welter *et al.* (1989). Serial dilutions (neat to 10^{-6}) of the mitochondrial DNA-enriched extracts served as template DNA in two sets of PCRs, one in which the ND4 and Leu primers were used, the other in which 'universal' primers designed to amplify an approximately 400 bp fragment of the nuclear 18S rRNA gene (light and heavy strand primer sequences are 5′-GGT TGA TCC TGC CAG TAG-3′ and 5′-AGG CTC CCT CTC CGG AAT CGA A-3′, respectively [modified from Hillis and Dixon, 1991]) were used. Reaction and cycling conditions were as above (see DNA extraction, amplification, and sequencing), except that the amount of template DNA varied (1 μL of diluted extract was used in each reaction) and an annealing temperature of 48 °C (as opposed to 55-58 °C) was used in the latter set of PCRs (i.e. those in which the 18S rRNA primers were used). In all cases, it was possible to identify an extract concentration for which DNA fragments could be amplified with the ND4 and Leu primers but not with the 18S rRNA primers. DNA fragments amplified from extracts of this concentration were presumed to be of mitochondrial origin and were cycle sequenced as described above. Where sequences could not be distinguished from those derived

from total genomic DNA (extracted using DNAzol; see above) it was concluded that inadvertent amplification of nuclear paralogues was unlikely to have occurred.

In addition to performing the above procedure, all protein coding sequences (i.e. *ND4* sequences) were translated using Se-Al (Version 1.0 alpha 1; Rambaut, 1996) and examined for unexpected stop codons. In metazoans, duplicated fragments of mitochondrial DNA typically lose their function when incorporated into the nuclear genome (Gellissen and Michaelis, 1987) and, consequently, are unconstrained in the mutations they can accumulate. Thus, while the presence of stop codons within protein-coding regions would not be expected for functional mitochondrial genes (these, presumably, would be removed from natural populations through selection), it would not be unexpected for nuclear paralogues.

3.3.3.3 Phylogenetic analysis

Raw sequences were edited using SeqEd (Version 1.0.3, ABI) then aligned by eye. *ND4* sequences initially were aligned against published sequences for the hydrophiine *Pelamis platurus* and the elapines *Bungarus fasciatus* and *Micrurus fulvius* (GenBank accession numbers AAC27874, AAC27861, and AAL66806, respectively). Insertions/deletions (indels) are absent in this region and the alignments were unambiguous. tRNA sequences were aligned against the secondary structure model of Macey and Verma (1997), optimising the correspondence between the aligned sequences and conserved structural elements, including stems and anticodons. This resulted in the restriction of indels to the length-variable loop regions. Aligned sequences are presented in Appendix 2.

The aligned sequence data were subjected to a parsimony analysis, performed using PAUP* (Version 4.0 b8; Swofford, 1999). Where identical sequences were obtained for more than one individual, a single representative individual was included in the analysis to reduce computation time. All substitutions were weighted equally (see Kluge, 1997b for arguments against differential character weighting in phylogenetic inference). Inferred indels were coded using the 'simple indel coding' method of Simmons and Ochoterena (2000; see Appendix 3). Due to the large number of sequences included in the analysis (and the corresponding large number of possible tree topologies), a heuristic search strategy was employed, using the random stepwise addition (100 replicates) and

tree-bisection-reconnection branch swapping options. Bremer support values (Bremer, 1988, 1994), calculated using Autodecay (Version 4.0; Eriksson, 1998), were employed as a measure of support for individual clades. Values of seven or greater were considered to indicate strong support, following Frost *et al.* (2001). Bootstrap values are not presented for reasons discussed by Kluge and Wolf (1993, pp 194-195).

3.3.4 Allozyme electrophoresis

The allozyme electrophoretic data presented here derive from a preliminary survey of allozyme variation within *Pseudonaja* undertaken by M. Adams (Evolutionary Biology Unit, SAM) prior to the commencement of the present study. Data were available for 44 individuals (although more than 170 individuals were included in M. Adams' preliminary investigation, only those for which mitochondrial DNA sequence data had been obtained were considered), representing all species of *Pseudonaja* except *P. ingrami*, and the 'Pale head, grey nape', 'Orange with black head', and 'Southern' colour morphs of *P. nuchalis*. Thirty-six loci were assayed following Richardson *et al.* (1986; Appendix 4).

A phylogenetic analysis was performed using PAUP* (Version 4.0 b8; Swofford, 1999), treating loci as characters and alleles as unordered character states. Prior to performing the analysis, individuals were grouped using the 'Filter Taxa' function in MacClade (Version 3; Maddison and Maddison, 1992), selecting the 'consider taxa redundant even if states are not identical, as long as a resolution of missing or uncertain data could make them identical' option. Where a group included more than one individual, a single representative individual was selected for inclusion in the analysis. This procedure reduced the number of individuals included in the analysis to 28 (see Results), decreasing considerably an otherwise prohibitively large computation time. A single individual of *P. australis* included in M. Adams' preliminary survey was employed as the outgroup. Heterozygosity was accommodated using the 'polymorphic' option for multistate taxa, as recommended Kornet and Turner (1999). As with the mitochondrial DNA sequence analysis (see above), a heuristic search strategy was employed, using the random stepwise addition (100 replicates) and tree-bisection-reconnection branch swapping options. Bremer support values were employed as a measure of support for individual clades (see Mitochondrial DNA above).

3.3.5 Morphology

The multivariate statistical methods employed in the present study are similar to those described by Wüster and Thorpe (1989, 1992) and Wüster *et al.* (1995). Generally, specimens were partitioned into (morphologically homogeneous) geographical groups, the relations of which were investigated using discriminant function analysis (canonical variates analysis). This approach has been used effectively in elucidating patterns of morhological variation in a number of groups, including snakes (reviewed by Thorpe, 1976; for additional examples concerning snakes, see Thorpe and McCarthy, 1978; Thorpe, 1980; Wüster and Thorpe, 1989, 1992; Wüster *et al.*, 1995, 1997; Slowinski and Wüster, 2000; Burbrink, 2001).

A series of continuous variables, many of which relate to scale dimensions, was measured on available specimens of nominal *P. affinis*, *P. inframacula*, *P. nuchalis*, and *P. textilis* for statistical analyses. These species have proved to be the most problematic with regard to the classification of *Pseudonaja* (see Introduction and Discussion) and preliminary analysis of the mitochondrial DNA sequence data indicated that they comprise a strongly supported clade. The variables measured are listed in Table 3.2. Snout-vent length and tail length were measured to the nearest 1 mm using a string and ruler. The remaining variables were measured to the nearest 0.01 mm using a dial calliper. In an initial effort to obviate any effect of variation associated with allometric growth (see below), only measurements for specimens with a snout-vent length greater than 300 mm were included in statistical analyses. Raw measurements are presented in Appendix 5.

Prior to performing statistical analyses, measurements were scaled to the mean snout-vent length for all specimens (874 mm) according to the function $Y_i^* = Y_i[X_o/X_i]^b$, where Y_i^* and Y_i are the scaled and observed values for each measurement respectively, X_o is the designated body size to which all measurements are scaled, X_i is the observed body size, and b is a constant (Lleonart *et al.*, 2000). This procedure removes all, potentially confounding, variation among measurements resulting from allometric growth (e.g. Gould, 1966; Thorpe, 1976; Reist, 1985). In practice, the value of b is usually estimated as the slope of the linear regression line obtained when $\ln Y_i$ is regressed against $\ln X_i$ (see Thorpe, 1976; Lleonart *et al.*, 2000). Values of b for each variable were estimated separately for males and females using pooled measurements from all individuals.

Table 3.2. Continuous variables measured on available specimens of nominal *Pseudonaja affinis*, *Pseudonaja inframacula*, *Pseudonaja nuchalis*, and *Pseudonaja textilis* for multivariate statistical analyses. Means are of the left and right sides.

Snout-vent length
Tail length
Length of frontal
Width of frontal
Distance from rostral to frontal
Length of prefrontal suture
Mean length of supraoculars
Mean length of parietals
Length of parietal suture
Distance from snout tip to posterior end of parietal suture
Mean distance from snout tip to posterior end of mandible
Interocular distance
Head width (measured between corners of mouth from ventral aspect)
Mean eye diameter
Mean distance from eye to nostril
Internarial distance

Although this method assumes that a similar pattern of allometric growth obtains for all geographical groups (and, accordingly, for all species), its use was necessitated by small sample sizes for the majority of groups.

Geographical groups were delimited on the basis of collecting gaps and presumed physiographical barriers (e.g. Great Dividing Range, Spencer Gulf). The homogeneity of each group was assessed using principle components analysis. Separate analyses were performed for male and female specimens, negating any effect of sexual dimorphism (see Thorpe, 1976, p. 411). Where geographical groups were observed to exhibit internal heterogeneity (i.e. where principle components analysis indicated the presence of more than one morphologically distinct group), specimens were partitioned into morphologically homogeneous subgroups. In a number of cases, geographical groups (or subgroups) contained specimens of more than one major mitochondrial DNA clade (see Results). These groups were divided (still) further according to the mitochondrial DNA clades in which specimens were placed, thereby allowing specimens of different mitochondrial DNA clades to

assort independently in the discriminant function analyses. A more detailed account of the procedure employed in delimiting geographical groups is presented in Appendix 6.

Discriminant function analyses were performed using Statistica (Version 5; StatSoft, 1997). For all analyses, geographical group served as the *a priori* grouping variable. In presenting canonical variate plots (see Results), however, specimens were identified according to the mitochondrial DNA clade in which they were placed, allowing patterns of morphological variation to be easily related to the results of the mitochondrial DNA sequence analysis. Again, separate analyses were performed for male and female specimens to negate any influence of sexual dimorphism.

In addition to the continuous variables included in the discriminant function analyses, the following scale counts were recorded for nominal *P. affinis*, *P. inframacula*, *P. nuchalis*, and *P. textilis* specimens in the SAM: number of ventrals (counted according to Dowling [1951]); number of subcaudals; number of dorsal rows at the level of the first ventral; number of dorsal rows on the neck, one head length posterior to the parietals; number of dorsal rows at midbody; number of dorsal rows one head length anterior to the vent; and number of dorsal rows at the level of the anal (Appendix 7). The size and shape of the rostral were also examined. Notes on colouration were taken for specimens in the SAM and WAM. The colour of the mouth lining, which tends to deteriorate with prolonged storage in ethanol (see Gillam, 1979, p. 3), was recorded from freshly killed or recently preserved specimens.

3.3.6 Chromosomes

Chromosome data were obtained for 11 individuals (SAM R numbers 56719, 56720, 56722, 56723, 56724, 56770, 56771, 56772, 56773, 56774, 567750; these individuals were acquired live during the course of this study), representing nominal *P. inframacula* and *P. textilis*, and the 'Darwin', 'Pale head, grey nape', and 'Orange with black head' colour morphs of *P. nuchalis*. Mitotic chromosome spreads were prepared by R. Hutchinson (Women's and Children's Hospital, Adelaide) from lymphocyte or fibroblast tissue cultures. Autosome pairs are numbered in order of decreasing size.

3.4 Results

3.4.1 Mitochondrial DNA

Typically, DNA fragments could be amplified from mitochondrial DNA-enriched extracts to dilutions of 10^{-3} and 10^{-2} using the ND4 and Leu, and 18S rRNA primers, respectively. In all cases, sequences derived from dilutions of 10^{-3} and total genomic DNA (with the ND4 and Leu primers) could not be distinguished. Furthermore, unexpected stop codons are absent in all protein coding sequences. Accordingly, it was concluded that inadvertent amplification of nuclear paralogues was unlikely to have occurred and all sequences were presumed to be orthologous.

Of the 770 aligned sites, 428 are invariable, 320 are parsimony-informative, and 22 are variable but uninformative under parsimony (see Appendix 2). Seven of nine inferred indels are parsimony-informative, the remaining two indels being observed in only a single haplotype (see Appendix 3). Including four outgroup haplotypes, 98 haplotypes were discovered, 27 of which are shared by more than one individual (see Appendix 1; Figs 3.1 and 3.2). Parsimony analysis yielded 28944 equally parsimonious trees (1017 steps), the strict consensus of which is presented in Figure 3.1. Several conclusions can be derived from this conservative hypothesis: (1) monophyly of the ingroup is strongly supported; (2) the two nominal species of *Oxyuranus* comprise a moderately supported clade, although their relationship to the remaining parts of the ingroup is unresolved; (3) *Pseudonaja* consists of at least eight moderately to strongly supported clades, of which five (the *P. affinis*, *P. guttata*, *P. inframacula*, *P. modesta*, and *P. textilis* clades) are largely consistent with presently recognised species (considering the nominal taxa to which individuals had previously been referred); the remaining three clades are composed predominantly of individuals that could be assigned to the *P. nuchalis* colour forms described by Mengden (1985b; the *P. nuchalis* 'Pale/black headed'clade [see Figs 3.1 and 3.2] includes both the 'Pale head, grey nape' and 'Orange with black head' colour forms); (4) moderately to strongly supported subclades are present within the *P. modesta* and *P. textilis* clades; and (5) *P. affinis*, *P. inframacula*, *P. textilis*, and the three *P. nuchalis* lineages comprise a strongly supported clade (hereafter referred to as the *P. textilis* group), within which only the relationships (*P. inframacula*, *P. nuchalis* 'Southern') and (*P. nuchalis* 'Darwin', *P. nuchalis* 'Pale/black headed') are resolved.

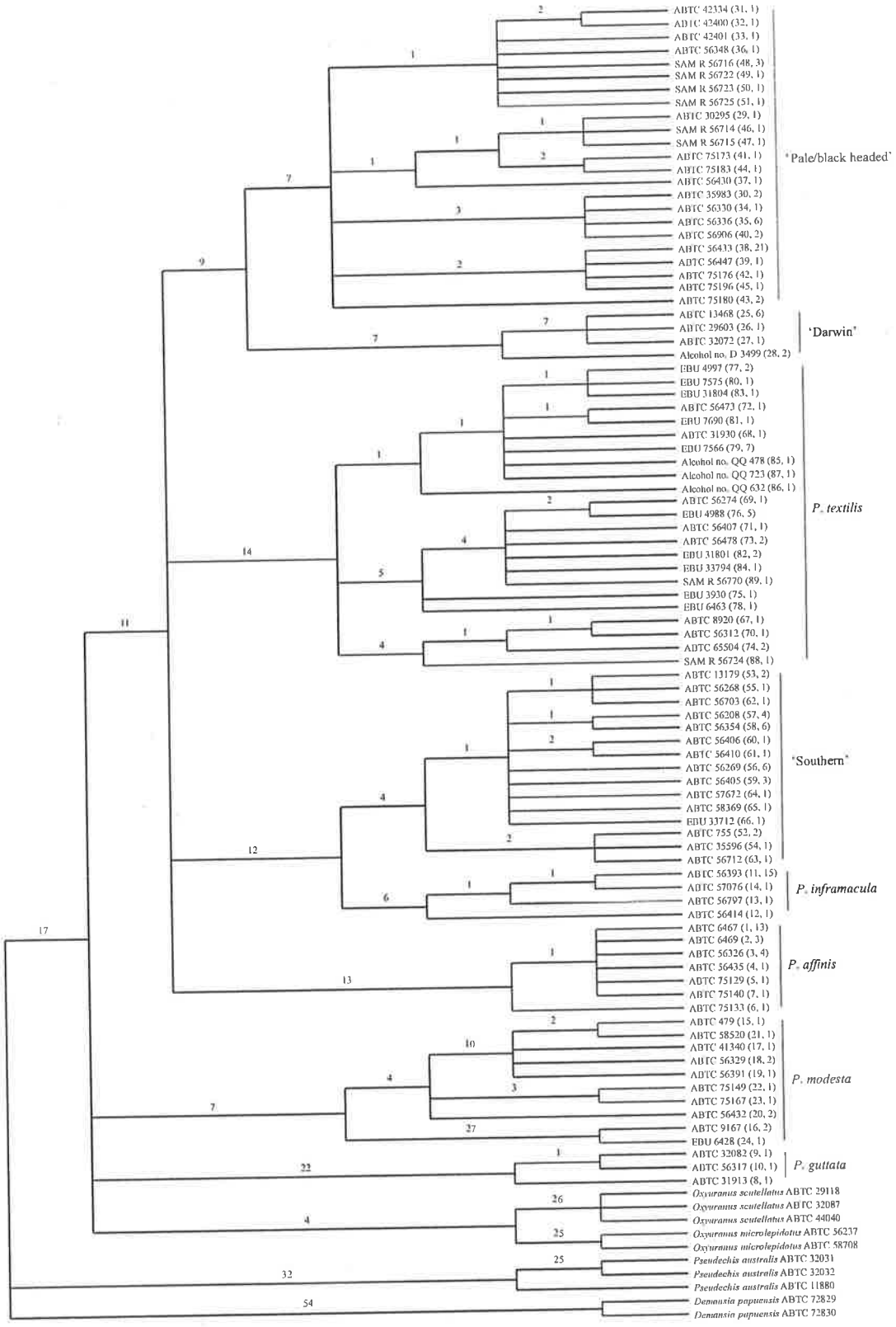


Fig. 3.1. Strict consensus of 28944 equally parsimonious trees obtained in a parsimony analysis of the mitochondrial DNA sequence data. For *Pseudonaja* specimens, ABTC numbers are followed by a haplotype number and the number of individuals for which that haplotype was observed in parentheses. Numbers above branches are Bremer support values.

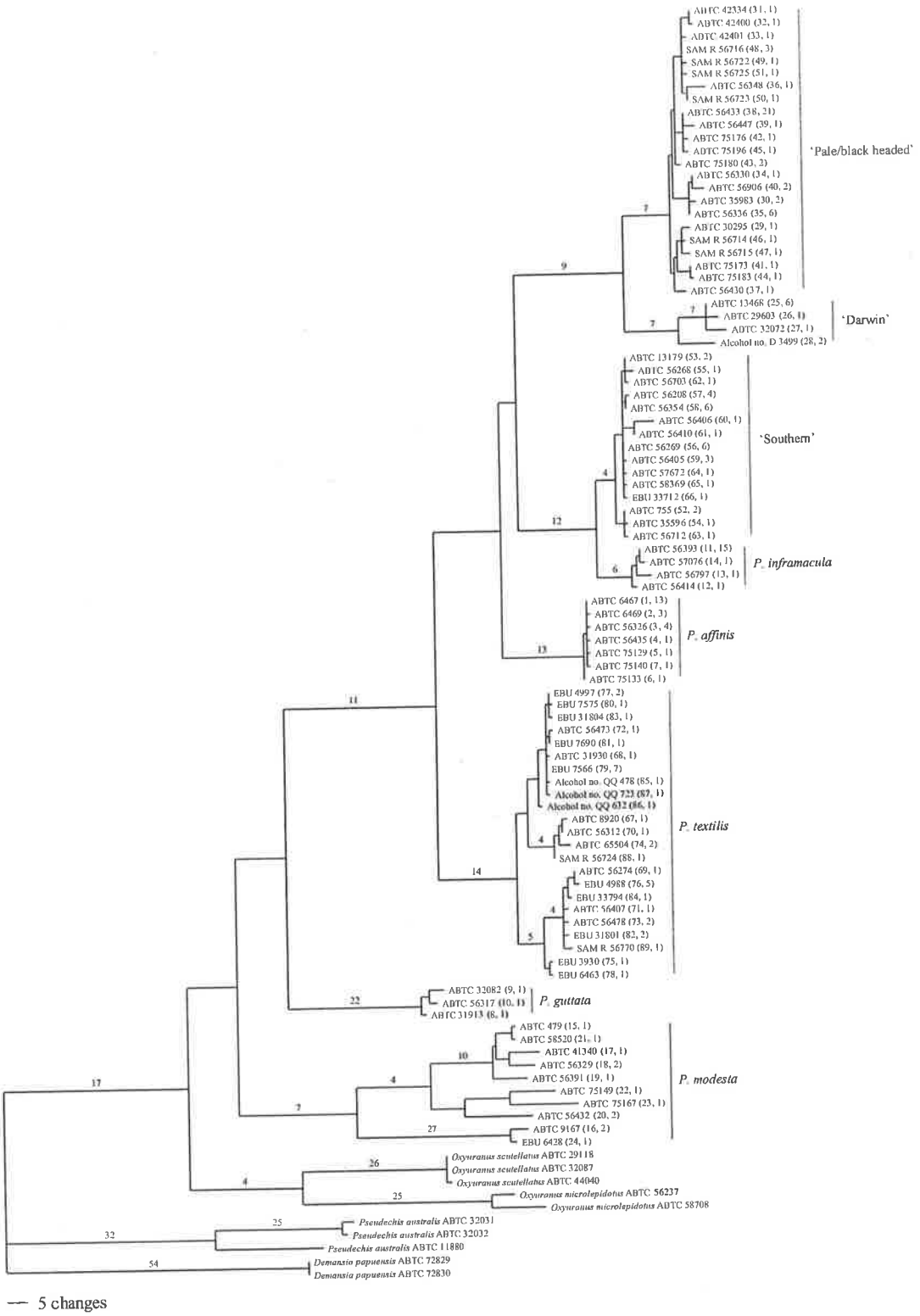


Fig. 3.2. One of 28944 equally parsimonious trees obtained in a parsimony analysis of the mitochondrial DNA sequence data. For *Pseudonaja* specimens, ABTC numbers are followed by a haplotype number and the number of individuals for which that haplotype was observed in parentheses. Haplotype numbers correspond with those in Appendix 1. Numbers above branches are Bremer support values.

The eight major clades of *Pseudonaja* identified in the strict consensus (see Fig. 3.1) are separated by comparatively long branches (Fig. 3.2) and, with the exception of the *P. modesta* clade (see below), uncorrected percent sequence divergence within clades (0.2-1.7%; excluding *P. modesta*) is generally lower than that among clades (2.3-14.5%; Table 3.3). Comparatively long branches also separate the strongly-supported subclades of the *P. modesta* clade (Fig. 3.2), which display comparable levels of interclade sequence divergence (10.4% between the two most strongly supported clades) to those observed for the major clades (see Table 3.3).

3.4.2 Allozyme electrophoresis

Of the 36 loci examined, seven are invariable, 13 are parsimony-informative, and 16 are variable but uninformative under parsimony (see Appendix 4). Parsimony analysis yielded 126 equally parsimonious trees (98 steps), the strict consensus of which is presented in Figure 3.3. This conservative hypothesis contains relatively few resolved relationships (as would be expected considering that more individuals were included in the analysis than there are parsimony-informative characters) and Bremer support values are generally low. Nonetheless, the following observations can be made: (1) the placement of *P. guttata* is unresolved, however, the remaining parts of the ingroup comprise a clade; (2) the *P. nuchalis* 'Pale/black headed' and *P. textilis* clades in Figure 3.1 (the strict consensus obtained in the mitochondrial DNA sequence analysis) are present, as is the *P. inframacula* clade, excluding ABTC 56449; (3) individuals of the *P. affinis*, *P. modesta*, *P. nuchalis* 'Pale/black headed', and *P. nuchalis* 'Southern' clades in Figure 3.1, and ABTC 56449 comprise a clade, the relationships within which are largely unresolved; and (4) the single individual of *P. modesta* forms a clade with two *P. nuchalis* 'Southern' individuals.

With the exception of the *P. affinis* and *P. inframacula* clades, and the *P. affinis* and *P. nuchalis* 'Southern' clades, at least one fixed difference exists between the major clades of the *P. textilis* group identified in Figure 3.1 (see Appendix 4). Loci for which fixed differences were observed are as follows: *P. affinis* and *P. nuchalis* 'Pale/black headed' – *Gapd*; *P. affinis* and *P. textilis* – *Srdh*; *P. inframacula* (excluding ABTC 56449) and *P. nuchalis* 'Pale/black headed' – *Gapd*, *Gda*, *Mpi*; *P. inframacula* (excluding ABTC 56449) and *P. nuchalis* 'Southern' (including ABTC 56449; see Morphology below) – *Gda*, *Mpi*; *P. inframacula* (excluding ABTC 56449) and *P.*

Table 3.3. Uncorrected percent sequence divergence among and within the major mitochondrial DNA clades of *Pseudonaja*. Values are means of all pairwise comparisons.

Interclade sequence divergence

	Pseudonaja affinis	*Pseudonaja guttata*	*Pseudonaja inframacula*	*Pseudonaja modesta*	*Pseudonaja nuchalis* 'Darwin'	*Pseudonaja nuchalis* 'Pale/black headed'	*Pseudonaja nuchalis* 'Southern'
Pseudonaja guttata	11.9						
Pseudonaja inframacula	7.0	12.6					
Pseudonaja modesta	13.9	13.0	13.3				
Pseudonaja nuchalis 'Darwin'	9.4	13.6	9.1	14.1			
Pseudonaja nuchalis 'Pale/black headed'	7.9	13.4	9.1	14.5	5.1		
Pseudonaja nuchalis 'Southern'	7.2	12.8	2.3	13.8	9.0	8.7	
Pseudonaja textilis	8.7	12.3	7.9	14.0	10.3	9.2	8.1

Intraclade sequence divergence

Pseudonaja affinis	0.2
Pseudonaja guttata	0.8
Pseudonaja inframacula	0.5
Pseudonaja modesta	6.5
Pseudonaja nuchalis 'Darwin'	1.4
Pseudonaja nuchalis 'Pale/black headed'	1.0
Pseudonaja nuchalis 'Southern'	0.5
Pseudonaja textilis	1.7

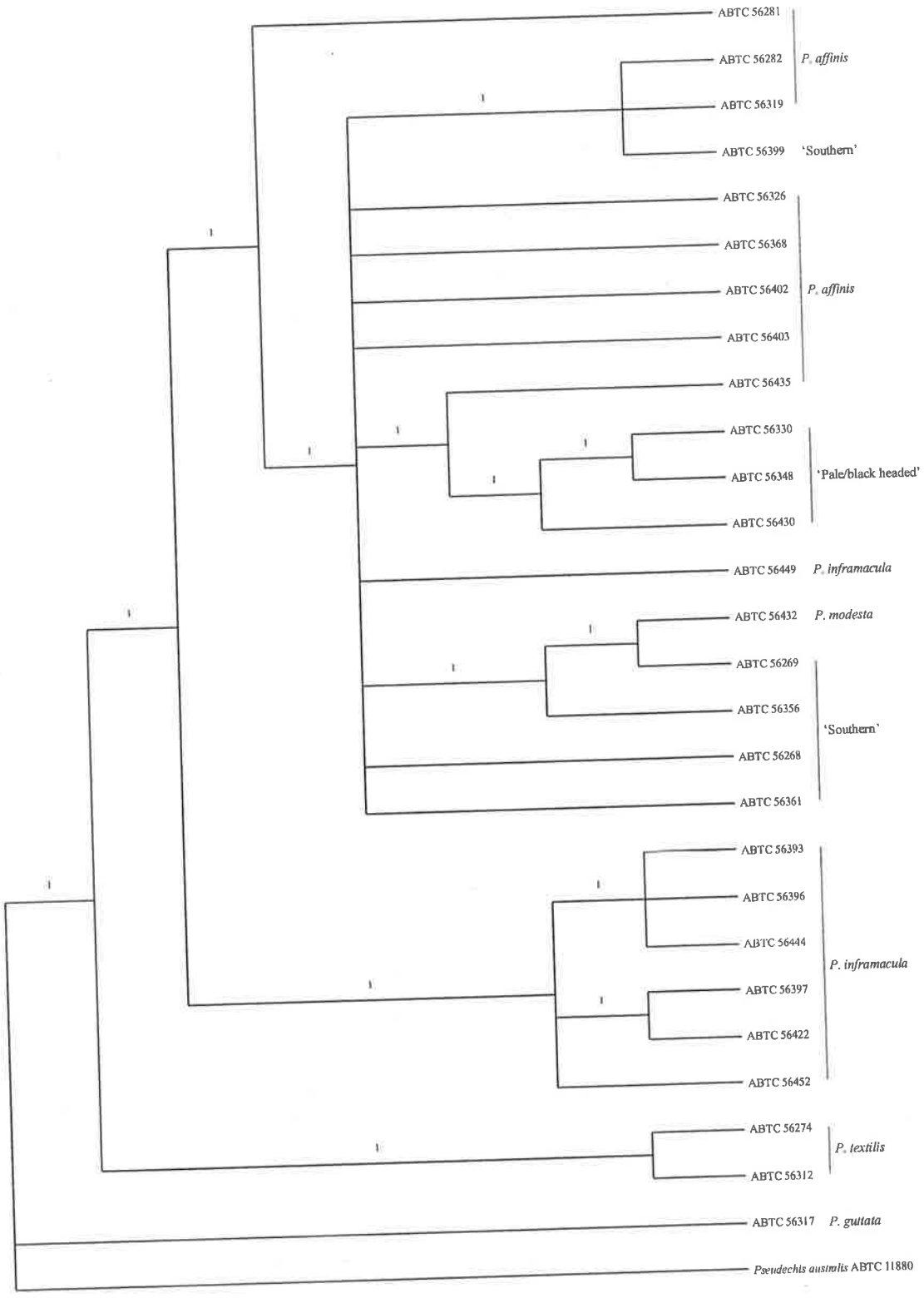


Fig. 3.3. Strict consensus of 126 equally parsimonious trees obtained in a parsimony analysis of the allozyme electrophoretic data. Numbers above branches are Bremer support values.

textilis – *Pep-C*, *Srdh*; *P. nuchalis* 'Pale/black headed' and *P. nuchalis* 'Southern' (including ABTC 56449) – *Gapd*; *P. nuchalis* 'Pale/black headed' and *P. textilis* – *Gapd*, *Gda*, *Mpi*; *P. nuchalis* 'Southern' (including ABTC 56449) and *P. textilis* – *Gda*, *Mpi*, *Pep-C*.

3.4.3 Morphology

Discriminant function analysis of the scaled measurements for all male specimens yielded 15 canonical variates. Canonical scores for the first two canonical variates (which account for 44.2% and 21.3% of the total variance, respectively; Appendix 8) are plotted in Figure 3.4. Two major groups are separated along the first canonical variate, one consisting of specimens of the *P. inframacula* and *P. textilis* clades (excluding SAM R 28559 [ABTC 56449]; Fig. 3.1) and SAM R 24807 (ABTC 56402, which is placed in the *P. affinis* clade in Fig. 3.1), the other consisting of the

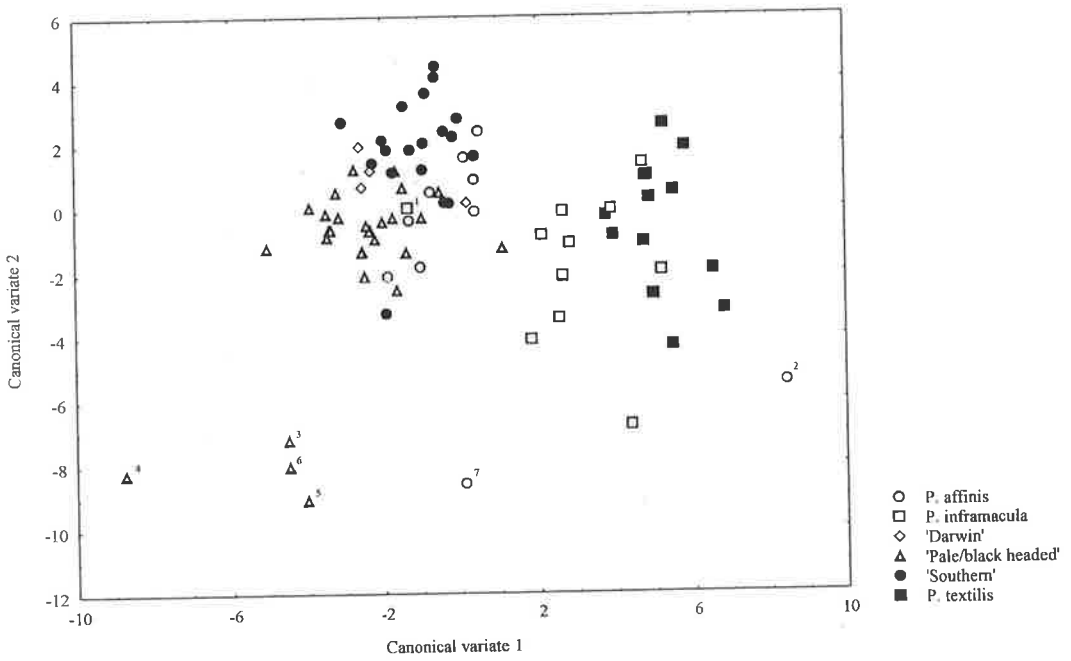


Fig. 3.4. Plot of canonical scores for the first two canonical variates extracted in a discriminant function analysis including all male specimens. The first and second canonical variates account for 44.2% and 21.3% of the total variance, respectively. Numbers identify specimens referred to in the text: 1 – SAM R 28559, 2 – SAM R 24807, 3 – SAM R 21025, 4 – WAM R 115182, 5 – WAM R 115183, 6 – WAM R 115276, 7 – SAM R 29468.

remaining specimens. Within the former group, specimens of the *P. inframacula* and *P. textilis* clades are incompletely separated along the first canonical variate, while SAM R 24807 is distinct from specimens of both clades. Within the latter group, SAM R 21025, WAM R 115182, WAM R 115183, WAM R 115276 (ABTC numbers 56336, 75197, 75198, and 75199, respectively; these specimens are placed in the *P. nuchalis* 'Pale/black headed' clade in Fig. 3.1), and SAM R 29468 (ABTC 56435, which is placed in the *P. affinis* clade in Fig. 3.1) are separated from the remaining specimens along the second canonical variate.

A further analysis was performed with specimens of the *P. inframacula* and *P. textilis* clades (excluding SAM R 28559 [ABTC 56449]), SAM R 24807, SAM R 21025, WAM R 115182, WAM R 115183, WAM R 115276, and SAM R 29468 (see the previous paragraph) omitted, to elucidate patterns of morphological variation among the remaining specimens. This analysis yielded eight canonical variates. Canonical scores for the first two canonical variates (which account for 59.2% and 12.6% of the total variance, respectively; Appendix 8) are plotted in Figure 3.5. The first canonical variate nearly completely separates specimens of the *P. nuchalis* 'Pale/black headed' and *P. nuchalis* 'Southern' clades (Fig. 3.1). Specimens of the *P. affinis* clade (Fig. 3.1) generally exhibit higher canonical scores for the first and second canonical variates than those of the *P. nuchalis* 'Southern' clade and, with the exception of WAM R 119550, are distinct from specimens of the *P. nuchalis* 'Pale/black headed' clade. The second canonical variate incompletely separates specimens of the *P. nuchalis* 'Darwin' (Fig. 3.1) and *P. nuchalis* 'Pale/black headed' clades, while specimens of the *P. nuchalis* 'Darwin' clade are completely separated from specimens of the *P. affinis* clade (exclcuding WAM R 119550), and nearly completely separated from specimens of the *P. nuchalis* 'Southern' clade, along the first canonical variate. SAM R 28559 (ABTC 56449, which is placed in the *P. inframacula* clade in Fig. 3.1) is placed among specimens of the *P. nuchalis* 'Southern' clade.

Discriminant function analysis of the scaled measurements for all female specimens yielded eight canonical variates. Canonical scores for the first two canonical variates (which account for 52.9% and 24.0% of the total variance, respectively; Appendix 8) are plotted in Figure 3.6. With the

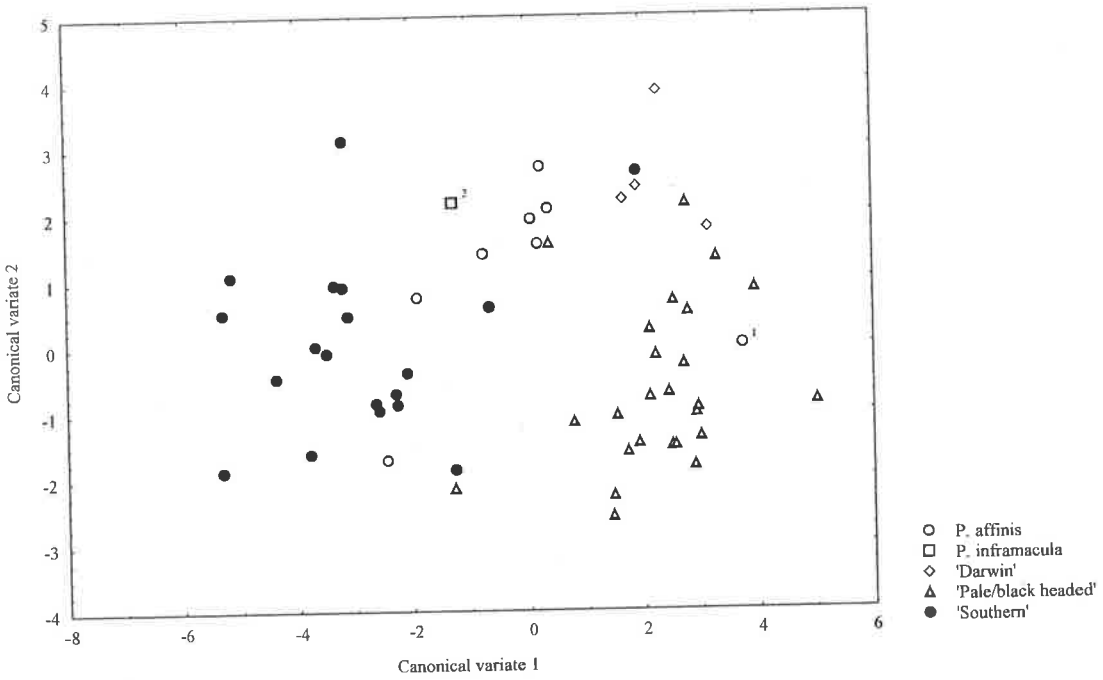


Fig. 3.5. Plot of canonical scores for the first two canonical variates extracted in a discriminant function analysis including male specimens of the *Pseudonaja affinis*, *Pseudonaja nuchalis* 'Darwin', *Pseudonaja nuchalis* 'Pale/black headed', and *Pseudonaja nuchalis* 'Southern' clades (excluding SAM R 21025, SAM R 24807, SAM R 29468, WAM R 115182, WAM R 115183, and WAM R 115276; see Fig. 3.4 and the discussion in the text), and SAM R 28559. The first and second canonical variates account for 59.2% and 12.6% of the total variance, respectively. Numbers identify specimens referred to in the text: 1 – WAM R 119550, 2 – SAM R 28559.

exception of the *P. nuchalis* 'Darwin' clade, the first and second canonical variates completely or nearly completely separate specimens of the major *P. textilis* group clades (Fig. 3.1). The single specimen of the *P. nuchalis* 'Darwin' clade is distinct from specimens of the *P. nuchalis* 'Pale/black headed' and *P. nuchalis* 'Southern' clades, emerging among specimens of the *P. affinis* clade.

Variation in scale counts within the major *P. textilis* group clades (Fig. 3.1) is summarised in Table 3.4. Specimens of the *P. affinis* clade generally possess a greater number of ventrals than those of the P. *inframacula* and *P. nuchalis* 'Darwin' clades (excluding SAM R 28559 [ABTC 56449]; see below). *Pseudonaja nuchalis* 'Southern' specimens (including SAM R 28559) also tend to possess a greater number of ventrals than *P. inframacula* specimens (excluding SAM R 28559)

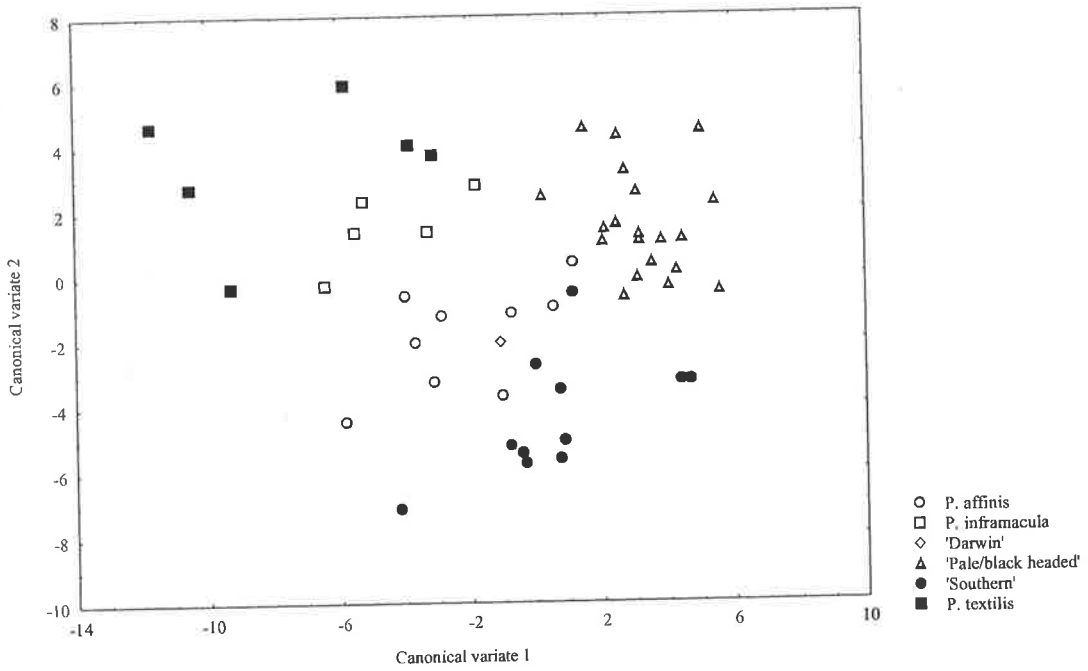


Fig. 3.6. Plot of canonical scores for the first two canonical variates extracted in a discriminant function analysis including all female specimens. The first and second canonical variates account for 52.9% and 24.0% of the total variance, respectively.

and consistently possess a greater number of ventrals than *P. nuchalis* 'Darwin' specimens. Variation in the number of ventrals within the *P. nuchalis* 'Pale/black headed' and *P. textilis* clades is similar to that observed for the remaining clades collectively. *Pseudonaja textilis* specimens generally possess a greater number of subcaudals than specimens of the remaining clades, while *P. nuchalis* 'Southern' specimens tend to possess a relatively low number of subcaudals. Specimens of the *P. nuchalis* 'Darwin' clade generally possess a greater number of dorsal rows at the level of the first ventral and on the neck (one head length posterior to the parietals) than those of the remaining clades, and consistently possess a greater number of dorsal rows on the neck than *P. inframacula* specimens (excluding SAM R 28559). In nearly all cases, *P. nuchalis* 'Pale/black headed' specimens possess 17 dorsal rows on the neck (23 of 24 specimens; see Appendix 7), and on that basis are largely separable from *P. nuchalis* 'Southern' specimens, the majority of which possess 18 or 19 dorsal rows on the neck (25 of 29 specimens; see Appendix 7), and *P. nuchalis* 'Darwin' specimens, which consistently possess 19 or more dorsal rows on the neck. With the exception of

Table 3.4. Variation in scale counts. Mean values are followed by ranges in parentheses.

Species	Ventrals	Subcaudals	Dorsal rows at first ventral	Dorsal rows one head length posterior to parietals	Dorsal rows at midbody	Dorsal rows one head length anterior to vent	Dorsal rows at anal
Pseudonaja affinis	215.4 (204-223)	59.4 (55-63)	22.1 (20-23)	17.9 (17-19)	17.9 (17-19)	14.4 (13-15)	15.6 (15-17)
*Pseudonaja inframacula**	201.5 (195-208)	60.3 (55-66)	20.5 (19-23)	17	17	13.1 (13-15)	15.2 (15-16)
Pseudonaja nuchalis 'Darwin'	198.8 (194-204)	59.6 (57-62)	23.8 (23-25)	19.8 (19-21)	17	15 (14-16)	15.4 (15-17)
Pseudonaja nuchalis 'Pale/black headed'	208.2 (199-224)	56.5 (49-63)	20.7 (19-23)	17.1 (17-19)	17	13.5 (13-15)	15.4 (13-17)
Pseudonaja nuchalis 'Southern'**	214.2 (207-226)	53 (47-63)	21.7 (19-23)	18.6 (17-19)	17	13.1 (13-15)	15.3 (13-18)
Pseudonaja textilis	206.6 (194-229)	65.3 (62-70)	20.7 (19-23)	17.4 (17-19)	17	14.1 (13-15)	15.9 (15-17)

* Excluding SAM R 28599 (ABTC 56449)

** Including SAM R 28599 (ABTC 56449)

the *P. affinis* clade, specimens of all clades possess 17 dorsal rows at midbody. *Pseudonaja affinis* specimens from Western Australia and SAM R 26268 (ABTC 6467) possess 19 dorsal rows at midbody, while in SAM R 21955 (ABTC 56359) and SAM R 31704 (ABTC 56484), there is an increase from 17 dorsal rows on the neck to 19 dorsal rows on the anterior body followed by a decrease to 17 dorsal rows at midbody (these specimens were recorded as possessing 19 midbody dorsal rows). The remaining *P. affinis* specimens possess 17 dorsal rows at midbody. Variation in the number of dorsal rows both one head length anterior to the vent and at the level of the anal is similar for all clades. *Pseudonaja nuchalis* 'Southern' specimens possess a strap-like rostral, so that the snout appears chisel shaped when viewed from above. The rostral of specimens of the remaining clades is normal, the snout appearing rounded in dorsal view.

Below, I describe variation in colour pattern within each of the major *P. textilis* group clades (Fig. 3.1) in turn (patterns of variation among clades are considered explicitly in the Discussion). The majority of the colour patterns described are illustrated in the Species Accounts.

Pseudonaja affinis. The dorsum is typically pale to dark brown or greyish-brown, commonly grading to lighter brown or grey laterally. In WAM R 77743, the dorsum is medium yellowish-brown. There is occasionally a pattern of darker brown or greyish-brown oblique bands, 1-3 dorsals wide, on the body. This pattern may be discernable only laterally. A subtle black reticulated pattern is present poterolaterally in SAM R 21955. Often, an indistinct (rarely distinct) darker brown or greyish-brown band, 9-16 dorsals wide, is present on the neck. The anterior margin of this band lies 15-20 dorsals posterior to the parietals. A number of specimens from Western Australia (WAM R 115297, WAM R 119172, and WAM R 136095) exhibit a pattern of darker greyish-brown bands, approximately 20 dorsals wide, alternating with sets of 4-5 indistinct dark grey or black bands, approximately one dorsal wide, on the posterior body. (These specimens possess 17 dorsal rows at midbody.) There are commonly numerous dark or partially dark scales on the body, these occasionally forming large blotches. Conspicuous darker brown blotches are often present on the head. Darker brown mottling is present on the neck in SAM R 52360. The head and neck of SAM R 31704 are black, contrasting with the body. The venter is medium to dark brown, or dirty cream or pale yellow. Occasionally, there are lighter brown or grey (rarely darker brown) crescent

shaped markings on the ventrals laterally. The posterior margins of the ventrals of some specimens are darker brown. A series of subtle darker brown or greyish-brown ventral blotches is often discernable. Nearly all specimens possess a contrasting dark grey or (less commonly) dark brown throat. The chin is commonly cream. The lining of the mouth is predominantly dark bluish-grey or black.

WAM R 119550 is unusual, resembling specimens of the 'Pale head, grey nape' colour form of *P. nuchalis* (see *P. nuchalis* 'Pale/black headed' below). The dorsum is medium brown with a pattern of greyish-brown oblique bands over nearly the entire body. A dark greyish-brown band, approximately 15 dorsals wide, is present on the neck, grading posteriorly to the dorsal ground colour. The head and neck (anterior to the dark nuchal band) are contrasting pale yellowish-brown. Several dark scales are present on the body. (This specimen possess 19 dorsal rows at midbody.)

Pseudonaja inframacula (excluding SAM R 28559 [ABTC 56449]). The dorsum is typically light to very dark brown (nearly black in some specimens), occasionally grading to lighter brown laterally and/or anteriorly. Where the body is lighter brown anteriorly, the head is usually darker, being similar in colour to the posterior body. The dorsum is medium coppery-brown in SAM R 25702. A subtle black reticulated pattern is discernable posteriorly in SAM R 29026. Conspicuous black bands, tapering laterally from 2-4 dorsals to one dorsal wide, are present on the body of SAM R 57076. Often, there are numerous dark or partially dark scales on the body, these being concentrated dorsomedially in may specimens. There are commonly darker brown or black blotches on the head. An indistinct darker brown band, approximately ten dorsals wide, is present on the neck, immediately posterior to the parietals, in SAM R 29026. The venter is typically medium to dark grey, occasionally grading to dark brown posteriorly. Laterally, there are often pale to medium brown or lighter grey crescent shaped markings on the ventrals. The venter is pale bluish-grey in SAM R 26474 and SAM R 31698. In SAM R 26474, there are contrasting dark brown crescent shaped markings on the ventrals laterally. The chin is commonly cream. The lining of the mouth is predominantly dark bluish-grey or black.

Pseudonaja nuchalis 'Darwin'. The dorsum is light to medium brown, commonly grading to greyish-brown laterally. The majority of specimens possess a darker brown interocular area and nape (where this condition is realised, the parietal area is slightly lighter, although still darker than the body). Often, there are also darker brown 'tear marks' below the eyes. These darker brown markings on the head and nape are presumably retained from the juvenile semaphoront (see *P. nuchalis* 'Pale/black headed' and *P. nuchalis* 'Southern' below), however, observations of ontogenetic variation in colouration are necessary to confirm this. The snout is pale to light brown, in many cases contrasting with the posterior portion of the head. There are invariably scattered dark scales on the neck. The venter is cream or yellowish-cream. There are medium brown or greyish-brown crescent shaped markings on the ventrals laterally. In SAM R 56774, these markings extend medially along the posterior margins of the ventrals, forming bars. Often, a series of subtle to conspicuous salmon-coloured ventral blotches is present. These blotches are usually more prominent anteriorly. The chin is cream. The lining of the mouth is predominantly dark bluish-grey or black.

Pseudonaja nuchalis 'Pale/black headed'. Nearly all specimens could be assigned unambiguously to one of two distinct colour forms, these corresponding to the 'Pale head, grey nape' and 'Orange with black head' morphs described by Mengden (1985b; see Introduction above). Among 53 specimens examined, the 'Pale head, grey nape' colour form is represented by 37 specimens and the 'Orange with black head' colour form by 14 specimens (two specimens could not be referred to either colour form; see below). A series of eight specimens collected from Alice Springs over an approximately two week period (SAM numbers 56714, 56715, 56716, 56719, 56720, 56722, 56723, 56725) contains three 'Pale head, grey nape' specimens and five 'Orange with black head' specimens. Specimens that might be considered intermediates of these two colour forms were not observed (see, however, the Introduction above).

The dorsum of specimens of the 'Pale head, grey nape' colour form is pale to dark-medium brown or yellowish brown, occasionally grading to greyish-brown laterally and/or darker brown anteriorly. The body is lighter brown laterally in SAM R 29288. A subtle to conspicuous black reticulated pattern is commonly present on the body. In many specimens, this pattern is discernable only posterolaterally. Additionally, a subtle pattern of darker brown or greyish-brown bands,

approximately two dorsals wide, may be present on the posterior body. A number of specimens from Western Australia (WAM R 103924, WAM R 116498) exhibit a pattern of conspicuous dark brown bands, 10-15 dorsals wide, alternating with sets of 3-7 indistinct to distinct darker brown or greyish-brown bands, approximately one dorsal wide, on the posterior body. This pattern resembles that of the '*carinata*' morph described by Mengden (1985b; see Introduction above). Nonetheless, these specimens are otherwise very similar to the remaining 'Pale/head grey nape' specimens. Typically, a dark-medium grey or darker brown band, 6-18 dorsals wide, is present on the neck, grading posteriorly to the dorsal ground colour. Often, this band is bordered anteriorly by several dark or partially dark scales, these commonly forming a chevron. The head and neck (anterior to the nuchal band) are pale to medium brown or yellowish brown, usually contrasting with the darker nuchal band. Often, the interocular area and anterior portion of the parietals are darker brown and there are darker brown 'tear marks' below the eyes. Some specimens also possess an indistinct darker brown band, approximately three dorsals wide, on the nape. Comparable, although more conspicuous, darker brown markings are present on the head and nape of juvenile specimens (WAM R 115182, WAM R 115183, WAM R 115276), and these presumably fade during ontogeny to produce the observed condition in larger specimens. Darker greyish-brown mottling is present on the nape in SAM R 36954 and SAM R 51516. The venter is cream or yellow. Laterally, there are often medium to dark brown blotches on the posterior margins of the ventrals, these occasionally extending medially to form bars. In SAM R 29288, there are medium brown crescent shaped markings on the ventrals laterally. A series of subtle to (less commonly) conspicuous salmon-coloured or grey ventral blotches is often present (these blotches differ from those on the posterior margins of the ventrals, being distributed medially, rather than laterally, and apparently randomly with respect to the ventral margins). The chin is cream. The lining of the mouth is predominantly dark bluish-grey or black.

The dorsum of specimens of the 'Orange with black head' colour form is typically pale to dark yellow or orange-yellow. The dorsum is medium brown in SAM R 56723. Often, there is a subtle to conspicuous black reticulated pattern on the body. This pattern is occasionally discernable only posterolaterally and, in many specimens, is absent on the anterior body. A subtle pattern of darker brown bands, approximately two dorsal wide, is present posteriorly in SAM R 56723. The

head and neck are contrasting dark brown or black. Black scales are present on the neck in SAM R 21414 and SAM R 56714 (in both of these specimens, the head and neck are dark brown), these forming a broad chevron in SAM R 56714. The venter is cream or yellow. Laterally, there are commonly medium to dark brown blotches on the posterior margins of the ventrals, these occasionally extending medially to form bars. In SAM R 56723, there are medium brown crescent shaped markings on the ventrals laterally. Often, a series of conspicuous salmon-coloured, dark brown, or grey ventral blotches is present (as with the 'Pale head, grey nape' form, these blotches differ from those on the posterior margins of the ventrals; see above). The chin and throat are, independently, cream, dark grey, or black. The lining of the mouth is predominantly dark bluish-grey or black.

SAM R 28531 and SAM R 29407 could not be referred unambiguously to either of the colour forms described above. SAM R 28531 resembles specimens of the 'Orange with black head' colour form, except that a series of conspicuous dark brown bands, 9-16 dorsals wide, is present on the body. These bands extend onto the ventrals, where they break up into a mottled pattern. The dorsum in SAM R 29407 is uniformly dark brown, grading to lighter brown laterally. The snout is lighter brown and there are darker brown 'tear marks' below the eyes. The venter is yellow, grading to orange-yellow posteriorly. Laterally, there are contrasting dark-medium brown crescent shaped markings on the ventrals.

Pseudonaja nuchalis 'Southern' (including SAM R 28559 [ABTC 56449]). The dorsum is typically pale to medium brown, often grading to lighter brown laterally. The dorsum is medium coppery-brown in SAM R 24410. Often, there is a subtle pattern of darker brown or greyish-brown oblique bands, approximately one dorsal wide, on the body. This pattern is usually more pronounced posterolaterally and is especially prominent in smaller specimens. A subtle black reticulated pattern is present on the posterior body in AM R 157294. Occasionally, an indistinct to distinct darker brown or black band, 16-30 dorsals wide, is present on the neck. This band commonly extends onto the throat, where it breaks up into a pattern of irregular blotches (specimens exhibiting this darker nuchal band correspond to Mengden's [1985b] 'Southern with black nuchal band' morph [see Introduction above]). A series of indistinct to distinct darker brown or black bands, 15-20 dorsal

wide, is present on the body in some specimens (these specimens correspond to the 'Southern with black bands' morph described by Mengden [1985b; see Introduction above]). There are commonly scattered black scales on the body and nape. Often, the interocular area and anterior portion of the parietals are darker brown and there are darker brown 'tear marks' below the eyes. SAM R 18598 and SAM R 36352 also possess a darker brown band, 5-8 dorsal wide, on the nape, immediately posterior to the parietals (this band differs from the considerably broader nuchal band described above, the anterior margin of which typically lies 20-25 dorsals posterior to the parietals). Conspicuous dark brown or black markings comparable to these are present on the head and nape of juvenile specimens (SAM R 21432-5), and these presumably fade during ontogeny to produce the observed condition in larger specimens. Occasionally, the head is contrasting dark brown. The head and neck are uniformly grey in SAM R 24411, and black in SAM R 47059. The venter is dirty cream or yellow, or medium brown, occasionally grading to darker brown or pale to medium grey anteriorly. There are often darker brown crescent shaped markings on the ventrals laterally. These markings commonly extend medially along the posterior margins of the ventrals, forming bars. Conspicuous darker grey mottling is present on the mid and posterior portions of the venter in SAM R 18598 and SAM R 40759, respectively. Some juvenile specimens (SAM R 21432, SAM R 21434) exhibit a series of grey ventral blotches anteriorly. The chin is typically cream or yellowish-cream. The lining of the mouth is predominantly dark bluish-grey or black.

SAM R 28559 is very similar in appearance to specimens of the *P. nuchalis* 'Southern' clade (in particular, those of the 'Southern with black bands' colour form). The dorsum is light brown with a subtle pattern of darker greyish-brown oblique bands, 1-2 dorsals wide, posterolaterally. A series of conspicuous dark brown bands, 15-20 dorsals wide, is present on the body. The interocular area and anterior portion of the parietals are darker brown and there are darker brown 'tear marks' below the eyes. Scattered black scales are present on the body. The venter is dirty cream.

Pseudonaja textilis. The dorsum is typically pale to dark-medium brown, grading to lighter brown laterally. The dorsum is dark-medium coppery-brown in SAM R 31701. In SAM R 25070, the first dorsal row and lateral portions of the ventrals are greyish-brown. The dorsals of some

specimens exhibit a concentration of darker pigment posteriorly. Occasionally, dark or partially dark scales are present on the body or neck. An indistinct darker brown band, 1-2 dorsals wide, is present on the nape, immediately posterior to the parietals, in SAM R 25070. SAM R 18605 possesses a darker brown band, approximately 10 dorsals wide, on the neck, its anterior margin lying approximately 8 dorsals posterior to the parietals. In SAM R 19943, the neck, from approximately 3-15 dorsals posterior to the parietals, is contrasting dark brown. The venter is dirty cream, yellowish cream, or yellow, occasionally grading to dirty medium brown or greyish-brown posteriorly. There are medium brown crescent shaped markings on the ventrals laterally in some specimens. Commonly, the posterior margins of the ventrals are darker brown. Nearly all specimens exhibit a series of moderately to highly conspicuous dark grey or medium to dark brown ventral blotches anteriorly. The chin is commonly cream. The lining of the mouth is pink.

3.4.4 Chromosomes

Representative karyotypes are presented in Figure 3.7. Consistent with Mengden's (1985b) observations, the diploid chromosome number is 36 in the single *P. inframacula* specimen and 38 in the two *P. textilis* specimens. Furthermore, the sex chromosomes of the *P. inframacula* specimen differ considerably in size, the W chromosome being nearly 50% larger than the Z chromosome (see Mengden, 1985b, p. 196). The karyotypes of the Alice Springs and Yorke Peninsula *P. textilis* specimens (the former representing the reputedly isolated MacDonnell Ranges population) are not obviously dissimilar. All *P. nuchalis* 'Darwin' specimens exhibit a diploid chromosome number of 30, with chromosome pairs 4-14 gradually decreasing in size, and, on that basis, can be referred to Mengden's 'Darwin' karyomorph (see Mengden, 1985b, p. 198 and his Table 1; see also Table 3.1). However, the sex chromosomes of the single female *P. nuchalis* 'Darwin' specimen are subequal in size, rather than equal in size as Mengden (1985b, see his Table 1) reported, the W chromosome being larger than the Z chromosome. The 'Orange with black head' *P. nuchalis* 'Pale/black headed' specimens can be referred to Mengden's 'Orange with black head' karyomorph, exhibiting a diploid chromosome number of 32, with chromosome pairs 4-15 gradually decreasing in size, and, in the two female specimens, possessing sex chromosomes that are approximately equal in size (see Mengden, 1985b, p. 198 and his Fig. 1; Table 3.1). The karyotypes of the 'Pale head, grey nape' *P. nuchalis* 'Pale/black headed' specimens could not be consistently differentiated from those of the 'Orange

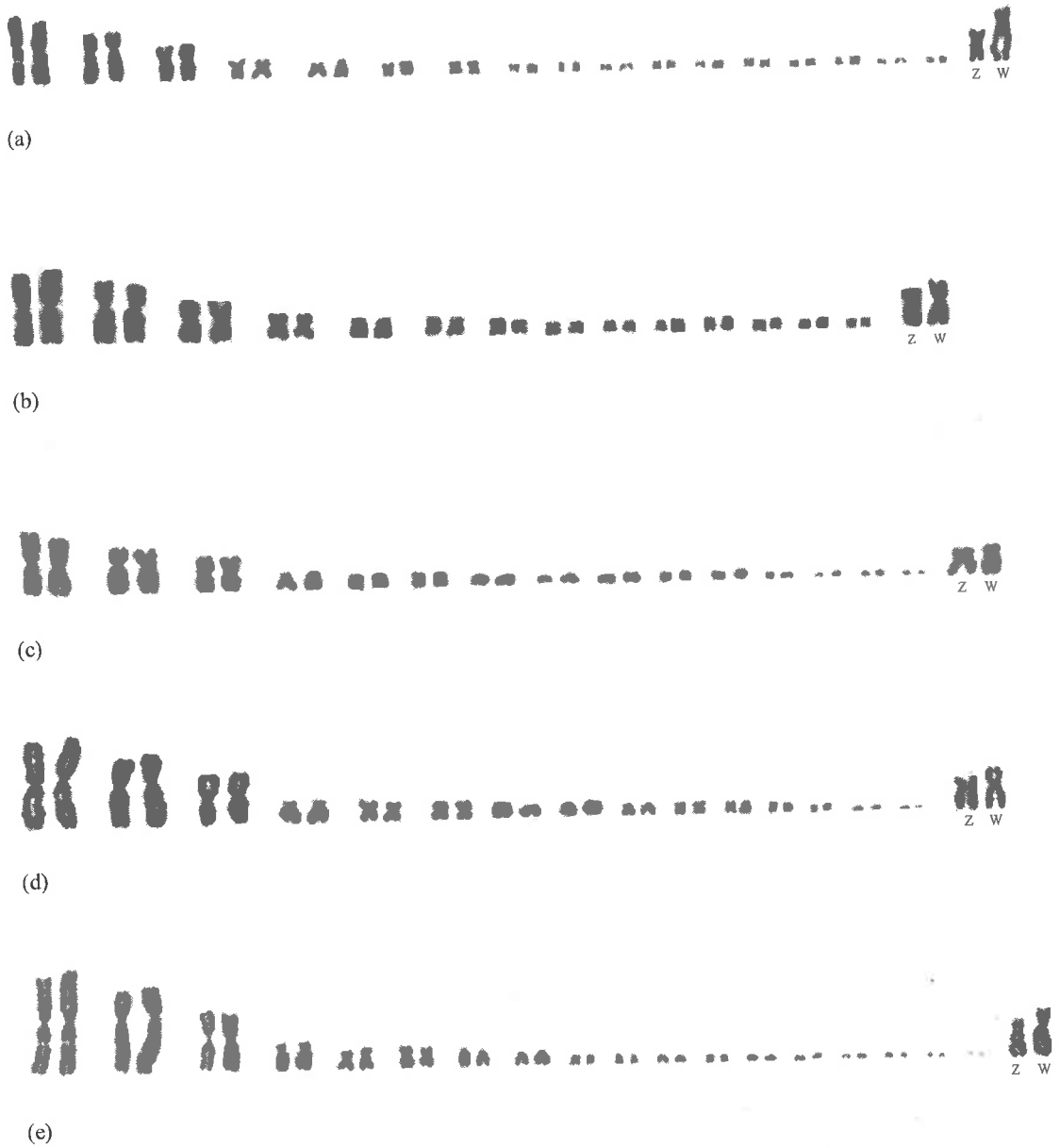


Fig. 3.7. Gross karyotypes: (a) *Pseudonaja inframacula* (SAM R 56771), (b) *Pseudonaja nuchalis* 'Darwin' (SAM R 56772), (c) *Pseudonaja nuchalis* 'Orange with black head' (SAM R 56720), (d) *Pseudonaja nuchalis* 'Pale head, grey nape' (SAM R 56722), and (e) *Pseudonaja textilis* (SAM R 56724). Sex chromosomes are labelled.

with black head' specimens, contrary to Mengden's observations (see Mengden, 1985b, p. 198 and his Table 1).

3.5 Discussion

3.5.1 Species limits

As discussed in the preceding chapter, the notion of species is not a problematic theoretical issue; as fundamental entities in a hierarchical evolutionary system, species correspond to independently evolving population lineages, rendered cohesive by reproductive interactions among their component organisms. Furthermore, contrary to the view of some authors (Pleijel, 1999; Pleijel and Rouse, 1999, 2000), there is no reason to expect that the task of delimiting species can not be undertaken in a scientific manner. Specific hypotheses of species limits can be connected to a number of testable predictions that are unlikely to be realised under alternative hypotheses, so that their acceptance may be demonstrated to entail an increase in explanatory power (where one or more such predictions are confirmed). In particular, it is improbable that a group of organisms would incorporate subgroups that can be diagnosed on the basis of consistent differences in unlinked characters or differentiated with respect to one or more quantitative characters, or that contain reciprocally monophyletic assemblages of alleles at multiple unlinked loci, except under the hypothesis that it contains parts of at least two independently evolving lineages (i.e. species). Moreover, the observation of intrinsically reproductively isolated subgroups is consistent only with the hypothesis that more than one lineage is present. Thus, adopting the widely held 'sophisticated falsificationist' view that scientific endeavour consists in evaluating alternative hypotheses on the basis of their relative explanatory power, hypotheses of species limits can, and should, be assessed and either accepted or rejected according to the same criteria as all hypotheses in science (see Chapter 2).

In view of the above, the results presented here provide supporting evidence for the presence of at least eight independently evolving lineages (i.e. species) within *Pseudonaja*. These lineages are largely coincident with the major mitochondrial DNA clades (Figs 3.1 and 3.2), although there are some exceptions, discussed below. In all cases, specimens appearing in the *P.*

guttata and *P. modesta* clades had previously been referred to nominal *P. guttata* and *P. modesta*, respectively. Both of these taxa differ from other nominal species of *Pseudonaja* in morphology (Gillam, 1979; Cogger, 1995), karyotype (Mengden, 1985b; Mengden and Fitzgerald, 1987), and ecology (Shine, 1989), and their status has been regarded as unproblematic by all recent authors (at least at the species level; see Wallach, 1985 and below). In that the results of the mitochondrial DNA sequence analysis imply an association of mitochondrial DNA haplotypes and, presumably unlinked, morphological, chromosomal, and ecological character states, they support the hypothesis that *P. guttata* and *P. modesta*, as presently conceptualised, are evolutionarily independent entities (species or perhaps, in the case of *P. modesta*, monophyletic groups of species [considering that at least some of the diagnostic haplotype differences are apomorphies]; see below). Specimens composing the major *P. textilis* group clades (disregarding the few exceptions to be discussed below) are largely separable with respect to the quantitative variables included in the multivariate analyses and, in the majority of cases, exhibit consistently different alleles at one or more allozyme loci, as well as differences in diploid chromosome number and/or chromosome morphology. Additionally, specimens of some clades can be diagnosed on the basis of scale attributes and/or colour pattern. These differences in quantitative and qualitative characters persist in areas of sympatry where these occur, providing evidence for the intrinsic reproductive isolation of specimens of some clades. Furthermore, the discovery of corresponding clades in the mitochondrial DNA sequence and allozyme electrophoretic analyses indicates that the specimens composing these clades contain monophyletic assemblages of alleles at two or more unlinked loci (a single mitochondrial DNA locus and at least one allozyme locus). Below, I discuss in detail the evidence for each of the *P. textilis* group lineages, considering *P. affinis*, *P. inframacula*, and *P. textilis*, which, as delimited here, largely correspond with recognised taxa, and the three *P. nuchalis* lineages in turn.

With the exception of SAM R 24807, SAM R 29468, and WAM R 119550 (for the sake of brevity, individuals are hereafter referred to only by their specimen number; see Appendix 1), the quantitative variables included in the multivariate analyses largely separate specimens of the *P. affinis* clade from those of the remaining *P. textilis* group clades (Figs 3.4-3.6). When compared with specimens of the *P. nuchalis* 'Pale/black headed' and *P. textilis* clades, specimens of the *P. affinis* clade also exhibit consistently different alleles at at least one allozyme locus. Furthermore,

they generally possess a greater number of ventrals than specimens of the *P. inframacula* and *P. nuchalis* 'Darwin' clades and, in nearly all cases, can be diagnosed by a contrasting dark grey or dark brown throat. Although chromosome data are unavailable for the specimens considered here, Mengden (1985b) reported a diploid chromosome number of 34 for *P. affinis*, with autosome pairs 4-16 gradually decreasing in size. Thus, considering that all specimens previously referred to nominal *P. affinis* were placed in the *P. affinis* clade, it is probable that the specimens composing this clade differ from those of the *P. inframacula*, *P. nuchalis* 'Darwin', *P. nuchalis* 'Pale/black headed', and *P. textilis* clades in diploid chromosome number (Fig. 3.7; see, however, the discussion of chromosome data for *P. nuchalis* 'Pale/black headed' below), and from specimens of the *P. inframacula*, *P. nuchalis* 'Southern', and *P. textilis* clades in possessing autosomes that are separable into only two (as opposed to three) distinct size classes (see Mengden, 1985b, his Table 1). Specimens of the *P. inframacula and P. textilis* clades (excluding SAM R 28559) are separable from those of the remaining *P. textilis* group clades, and largely separable from one another, with respect to the quantitative variables included in the multivariate analyses (Figs 3.4 and 3.6). Furthermore, specimens of both clades exhibit characteristic diploid chromosome numbers (see Fig. 3.7 and Mengden, 1985b), and are separable from specimens of the *P. nuchalis* 'Pale/black headed' and *P. nuchalis* 'Southern' clades, as well as from one another, in possessing consistently different alleles at one or more allozyme loci. Specimens of the *P. textilis* clade also possess consistently different alleles at at least one allozyme locus when compared with specimens of the *P. affinis* clade. It should be noted, however, that allozyme data are available for only two specimens of the *P. textilis* clade, so that observed fixed differences might reasonably be explained as artefacts of sampling. In nearly all cases, specimens of the *P. inframacula* clade can be diagnosed by a medium to dark grey venter, this condition often being observed in conjunction with pale to medium brown or lighter grey crescent shaped markings on the ventrals laterally. These specimens also differ from specimens of the *P. nuchalis* 'Darwin' clade in possessing 17, as opposed to 19 or more, dorsal rows on the neck, and from specimens of the *P. nuchalis* 'Darwin', *P. nuchalis* 'Pale/black headed', *P. nuchalis* 'Southern', and *P. textilis* clades in possessing sex chromosomes that differ markedly in size (see Fig. 3.7 and Mengden, 1985b). Specimens of the *P. textilis* clade tend to possess a greater number of subcaudals than those of the remaining *P. textilis* group clades, and can be diagnosed by an entirely pink mouth lining. Although specimens of more than one *P. textilis* group clade were collected from

the same locality in only two instances (eight *P. nuchalis* 'Pale/black headed' specimens and a single *P. textilis* specimen were collected from Alice Springs, and two *P. nuchalis* 'Pale/black headed' specimens and a single *P. nuchalis* 'Southern' specimen were collected from Roxby Downs; see Appendix 1 and the Species Accounts below), several likely areas of sympatry can be identified (see the distribution figures in the Species Accounts below). It is probable that specimens of the *P. affinis*, *P. inframacula*, and *P. nuchalis* 'Southern' clades are sympatric on Eyre Peninsula, while specimens of the *P. affinis* and *P. nuchalis* 'Pale/black headed' clades are potentially parapatric or sympatric in southern Western Australia and south-western South Australia. Specimens of the *P. textilis* and *P. nuchalis* 'Pale/black headed' clades co-occur in the Alice Springs region (see above) and are likely to be sympatric in eastern South Australia and western New South Wales. Furthermore, it is probable that specimens of the *P. textilis* clade are sympatric with specimens of the *P. nuchalis* 'Southern' clade in eastern South Australia and western and central New South Wales, and with specimens of the *P. nuchalis* 'Darwin' clade in southern central Queensland. Thus, the hypothesis that specimens of the *P. affinis*, *P. inframacula*, and *P. textilis* clades (excluding SAM R 28559, SAM R 24807, SAM R 29468, WAM R 119550, and possibly WAM R 115297, WAM R 119172, and WAM R 136095 [see below]) constitute parts of independently evolving lineages (or perhaps, in the case of *P. textilis* specimens, monophyletic groups of lineages [considering that these specimens share numerous molecular apomorphies]; see below) is supported by multiple lines of evidence. In addition to containing a monophyletic assemblage of mitochondrial DNA haplotypes, the specimens composing each of these clades, when compared with those of other *P. textilis* group clades, are largely or completely separable with respect to the quantitative variables included in the multivariate analyses, in the majority of cases exhibit consistently different alleles at one or more allozyme loci, and can be diagnosed on the basis of differences in diploid chromosome number, chromosome morphology, scalation, and/or colour pattern (see below for further differences between specimens of these and the *P. nuchalis* clades). This remains the case in presumed areas of sympatry, providing evidence for the intrinsic reproductive isolation of specimens of some clades. Furthermore, the *P. inframacula*, and *P. textilis* clades (excluding SAM R 28559) were recovered in the allozyme electrophoretic analysis, so that the specimens comprising these clades contain monophyletic assemblages of alleles at at least one allozyme locus (see, however, cautionary note for *P. textilis* above).

It is probable that SAM R 24807 and SAM R 29468 are *P. affinis* specimens. They can be differentiated from specimens of the *P. inframacula*, *P. nuchalis* 'Pale/black headed', *P. nuchalis* 'Southern', and *P. textilis* clades in possessing consistently different alleles at one or more allozyme loci (in all cases, these alleles are present in at least some other *P. affinis* specimens; loci for which differences were observed are as follows: *P. inframacula* [excluding SAM R 28559] – *Est-1* [SAM R 29468 only], *Gda* [SAM R 24807 only], *Mpi*, *Pep-C*; *P. nuchalis* 'Pale/black headed' – *Gapd*, *Gda* [SAM R 24807 only]; *P. nuchalis* 'Southern' [including SAM R 28559] – *Est-1* [SAM R 29468 only], *Pep-C*; *P. textilis* – *Est-1* [SAM R 29468 only], *Gda* [SAM R 24807 only], *Mpi*, *Pgm-2*, *Srdh* [see, however, cautionary note above]; see Appendix 4) and are widely separated geographically from specimens of the *P. nuchalis* 'Darwin' clade (see Appendix 1 and the Species Accounts below). Furthermore, SAM R 29468 possesses 19 dorsal rows at midbody, a condition observed only (although not ubiquitously) in *P. affinis* specimens (Table 3.4). The anomalous placement of these specimens in Figure 3.4 (the canonical variate plot for all male specimens) may be attributable to the procedure employed in scaling measurements prior to performing the multivariate analyses. As noted above (see Materials and Methods), small sample sizes for many geographical groups necessitated the use of pooled measurements for all specimens in estimating the value of the constant *b* in the scaling function. Thorpe (1976, p. 412 and his Fig. 1) noted that where patterns of allometric growth (specifically, the value of *b*) and/or body size differ among geographical groups (as is potentially the case where more than one species is being considered) this procedure is likely to produce spurious estimates of *b*, thereby affecting the reliability of scaled measurements. This is particularly the case where specimens are considerably smaller or larger than the designated body size to which measurements are scaled (measurements for such specimens are modified to a greater extent in scaling than those for specimens closer to the standard body size). Considering this, it is significant that SAM R 24807 and SAM R 29468 are juvenile specimens, being notably smaller than the remaining *P. affinis* specimens and the mean body size to which measurements were scaled (see Appendix 5), and that scaled measurements for both specimens are generally considerably higher than those for other specimens. Although neither specimen exhibits a contrasting dark grey or dark brown throat, considered here to diagnose *P. affinis* specimens, this condition may be subject to ontogenetic variation (Bush, 1989b; Mengden and Fitzgerald, 1987).

The placement of WAM R 119550 in the multivariate analyses (see Fig. 3.5) is not as readily explained as an artefact of the scaling procedure employed as that of SAM R 24807 and SAM R 29468, as this specimen is close to the designated body size to which measurements were scaled (see Appendix 5). Considering that, as well as being placed among specimens of the *P. nuchalis* 'Pale/black headed' clade in Figure 3.5, WAM R 119550 exhibits a colour pattern resembling that of 'Pale head, grey nape' *P. nuchalis* 'Pale/black headed' specimens, but possesses 19 dorsal rows at midbody, this specimen is possibly a *P. affinis-P. nuchalis* 'Pale/black headed' hybrid. This may also be the case for WAM R 115297, WAM R 119172, and WAM R 136095, which display a colour pattern similar to that of some 'Pale head, grey nape' *P. nuchalis* 'Pale/black headed' specimens and possess 17 dorsal rows at midbody (unusually among Western Australian specimens of the *P. affinis* clade), but are placed among other specimens of the *P. affinis* clade in the multivariate analyses (see Appendix 8 and Figs 3.5 and 3.6; WAM R 115297 was not included in these analyses due to missing data). Nonetheless, in the absence of allozyme electrophoretic data, any proposal that these specimens (i.e. WAM R 119550, WAM R 115297, WAM R 119172, and WAM R 136095) constitute *P. affinis-P. nuchalis* 'Pale/black headed' hybrids can only be regarded as speculative.

As presently conceptualised, *P. nuchalis* clearly incorporates more than one species. The majority of nominal *P. nuchalis* specimens (i.e. those that previously had been referred to *P. nuchalis*) are placed in three distinct mitochondrial DNA clades (with the exception of SAM R 28559 [see below], the remaining specimens appear in the *P. affinis* clade and are almost certainly parts of *P. affinis*, as this species is delimited here), these forming either a paraphyletic or polyphyletic assemblage, depending on their relationship to *P. affinis* and *P. textilis*. Two of these clades are composed predominantly of specimens that can be referred to the 'Darwin' and 'Southern' *P. nuchalis* groups of Mengden (1985b) on the basis of colour pattern and, in the case of *P. nuchalis* 'Darwin' specimens, diploid chromosome number and chromosome morphology. Nearly all specimens of the third clade can be assigned to Mengden's (1985b) 'Pale head, grey nape' and 'Orange with black head' colour morphs. With the exception of SAM R 21025, WAM R 115182, WAM R 115183, and WAM R 115276, specimens of the *P. nuchalis* 'Pale/black headed' clade are largely separable from those of the *P. nuchalis* 'Darwin' clade, and nearly completely separable from

those of the *P. nuchalis* 'Southern' clade, with respect to the quantitative variables included in the multivariate analyses (Figs 3.5 and 3.6). Additionally, these variables nearly completely separate specimens of the *P. nuchalis* 'Darwin' and *P. nuchalis* 'Southern' clades (Figs 3.5 and 3.6). Although chromosome data are unavailable for specimens of the *P. nuchalis* 'Southern' clade, Mengden (1985b) reported a diploid chromosome number of 34 for the 'Southern' *P. nuchalis* group, with autosome pairs 4-16 falling into two distinct size classes. Thus, specimens of the three *P. nuchalis* clades exhibit different diploid chromosome numbers (see, however, the discussion of chromosome data for the *P. nuchalis* 'Pale/black headed' clade below), while specimens of the *P. nuchalis* 'Darwin' and *P. nuchalis* 'Pale/black headed' clades are further separable from those of the *P. nuchalis* 'Southern' clade in possessing autosomes that can be partitioned into only two (as opposed to three) distinct size classes (see Fig. 3.7). Specimens of the *P. nuchalis* 'Southern' clade can be diagnosed by a strap-like rostral that imparts a chisel shape to the snout in dorsal view. Furthermore, they exhibit consistently different alleles at at least one allozyme locus when compared with specimens of the *P. nuchalis* 'Pale/black headed' clade, possess a greater number of ventrals than specimens of the *P. nuchalis* 'Darwin' clade (as well as the majority of *P. inframacula* specimens), and tend to possess a relatively low number of subcaudals. In the majority of cases, specimens of the *P. nuchalis* 'Pale/black headed' clade are separable from those of the *P. nuchalis* 'Darwin' and *P. nuchalis* 'Southern' clades in possessing fewer dorsal rows on the neck, while specimens of the *P. nuchalis* 'Darwin' clade generally posses a greater number of dorsal rows at the level of the first ventral than those of the remaining clades. Specimens of the *P. nuchalis* 'Pale/black headed' and *P. nuchalis* 'Southern' clades co-occur in the Roxby Downs area (see Appendix 1 and the Species Accounts below) and are likely to be sympatric in central and eastern South Australia and western New South Wales. Thus, a number of lines of evidence support the hypothesis that specimens of the *P. nuchalis* 'Darwin', *P. nuchalis* 'Pale/black headed', and *P. nuchalis* 'Southern' clades constitute parts of independently evolving lineages. These specimens, as well as containing monophyletic assemblages of mitochondrial DNA haplotypes, are largely separable with respect to the quantitative characters included in the multivariate analyses and can be diagnosed on the basis of differences in diploid chromosome number, chromosome morphology, scalation, and/or colour pattern. Additionally, specimens of the *P. nuchalis* 'Pale/black headed' and *P. nuchalis* 'Southern' clades exhibit consistently different alleles at at least one allozyme locus. Differences in quantitative

and qualitative characters between *P. nuchalis* 'Pale/black headed' and *P. nuchalis* 'Southern' specimens persist in probable areas of sympatry, providing evidence for their intrinsic reproductive isolation. Furthermore, the *P. nuchalis* 'Pale/black headed' clade was recovered in the allozyme electrophoretic analysis, so that the specimens composing this clade contain a monophyletic assemblage of alleles at two or more unlinked loci. In addition to the results presented here, direct evidence for the intrinsic reproductive isolation of *P. nuchalis* 'Darwin' and *P. nuchalis* 'Southern' individuals has been provided by M. Fitzgerald (see Mengden, 1985b), who observed two crosses of a male *P. nuchalis* 'Darwin' specimen and a female *P. nuchalis* 'Southern' specimen, both yielding 'hard, yellow, obviously infertile "slug[s]"' (Mengden, 1985b, p. 204) and infertile, but otherwise apparently normal, eggs.

As with SAM R 24807 and SAM R 29468, the anomalous placement of SAM R 21025, WAM R 115182, WAM R 115183, and WAM R 115276 in the multivariate analyses may be attributable to the procedure employed in scaling measurements. These specimens are notably smaller than the remaining *P. nuchalis* 'Pale/black headed' specimens and the mean body size to which measurements were scaled (see Appendix 1), and scaled measurements for each specimen are generally considerably higher than those for other specimens. The remaining *P. nuchalis* 'Pale/black headed' specimens form reasonably cohesive groups in Figures 3.5 and 3.6, within which there is no apparent differentiation of specimens of the 'Pale head, grey nape' and 'Orange with black head' colour forms. Specimens referable to these colour forms also can not be differentiated with respect to the allozyme electrophoretic data or scalation and, contrary to Mengden's (1985b) observations, possess similar karyotypes. The discrepancy between Mengden's chromosome data and that presented here may reflect individual or geographical variation within the *P. nuchalis* 'Pale/black headed' lineage in conjunction with limited sampling. Although chromosome data were obtained for eight *P. nuchalis* 'Pale/black headed' specimens in the present study, these were collected from a single locality (Alice Springs; see Materials and Methods and Appendix 1), while it is unclear how many specimens were available to Mengden or from where these specimens were collected. If Mengden was able to obtain chromosome data for only a small and/or geographically restricted series of specimens, the differences between our results may be explained as an artefact of sampling. Considering this, it is noteworthy that Mengden (1985b, p. 207) considered that '[t]he "orange with

black head" morph ... most resembles the "pale head, grey nape morph" chromosomally'. Alternatively, Mengden's 'Pale head, grey nape' karyomorph may represent a distinct lineage, not considered here, composed of individuals exhibiting a colour pattern similar to that of 'Pale head, grey nape' *P. nuchalis* 'Pale/black headed' specimens but possessing a different karyotype. A further (although perhaps improbable) possibility is that Mengden obtained chromosome data for one or more *P. nuchalis* 'Southern' specimens (which possess a karyotype not dissimilar to that reported for 'Pale head, grey nape' specimens; see Mengden's [1985b] Table 1), mistakenly believing them to represent the 'Pale head, grey nape' group. Specimens of these groups are broadly sympatric (see above) and in some cases may be difficult to distinguish on the basis of colour pattern, as noted by Shine (1989, p. 196). If this were the case, the differences Mengden observed between the 'Pale head, grey nape' and 'Southern' karyotypes (which concern the morphology of autosome pairs 4-16 and the sex chromosomes) would represent further variation within the *P. nuchalis* 'Southern' lineage (see below). Given Mengden's failure to provide details of the material he examined, it is difficult to evaluate the above explanations. It should be noted however, that none of these explanations entails the existence of corresponding patterns of variation in colour pattern and karyotype within the *P. nuchalis* 'Pale/black headed' lineage (as at least some 'Pale head grey nape' specimens are known to possess the 'Orange with black head' karyotype reported by Mengden; see Fig. 3.7), so that all are consistent with the conclusion that specimens of the *P. nuchalis* 'Pale/black headed' clade are parts of a single integrated lineage exhibiting more than one distinct colour form. Such marked intraspecific variation in colour pattern has been reported for a number of species of snakes (see Mattison, 1995, pp 124-125). Thus, the evidence presented here allows the conclusions of Mengden (1985b) and Bush (1989a,b) and Orange (1992) to be largely reconciled; while nominal *P. nuchalis* incorporates more than one species, as proposed by Mengden, Bush's and Orange's observations of *P. nuchalis* in Western Australia (see Historical Review and Objectives above) were almost certainly based on *P. nuchalis* 'Pale/black headed' specimens and so, as they concluded, concern only a single species.

There is no apparent differentiation of specimens of the 'Southern with black nuchal band', 'Southern with black bands', and typical 'Southern' colour forms in Figures 3.5 and 3.6 (the canonical variate plots). Furthermore, these specimens can not be consistently differentiated with

respect to the allozyme electrophoretic data or scalation. Although Mengden (1985b) observed distinctive karyotypes for each of these colour forms, he noted that the differences between them are relatively minor, concerning the morphology of autosome pairs 4-16 and the sex chromosomes, and are unlikely to present a barrier to interbreeding. While this does not limit their value as potentially diagnostic character states, it is unclear how robust the reported correspondence of colour pattern and karyotype is and, consequently, whether these differences provide supporting evidence for the presence of more than one species or represent intraspecific variation. It is possible that Mengden obtained chromosome data for only a single specimen of each colour form, so that the reported correspondence may be an artefact of sampling. Thus, in the absence of information on the material available to Mengden, there is no unequivocal evidence for correlated patterns of variation in colour pattern and karyotype, and hence the existence of multiple taxa, within the *P. nuchalis* 'Southern' lineage. The conclusion that specimens of the 'Southern', 'Southern with black nuchal band', and 'Southern with black bands' colour forms are parts of a single integrated lineage is supported by the observation that bands on the neck and body (which characterise the 'Southern with black nuchal band' and 'Southern with black bands' colour forms, respectively) vary from highly conspicuous (as illustrated in Mengden's [1985b] Plate 1F and 1G) to scarcely discernable, and may fade considerably over a relatively brief period (1-2 years; P. Mirtschin, pers. comm.).

Mengden (1985b, p. 207) considered that '[t]he "carinata" morph ... is chromosomally similar to the "southern" morph and may be capable of interbreeding with it', and implied that these morphs may be conspecific (see Mengden, 1985b, p. 198). A number of specimens considered here exhibit the '*carinata*' banding pattern described and illustrated by Mengden, however, these specimens are placed in the *P. nuchalis* 'Pale/black headed' clade and almost certainly represent the 'Pale head, grey nape' form of the *P. nuchalis* 'Pale/black headed' lineage (see the discussion of colour pattern variation in the Results above). Thus, both the *P. nuchalis* 'Pale/black headed' and *P. nuchalis* 'Southern' lineages may contain individuals referable to the '*carinata*' morph. Alternatively, Mengden's '*carinata*' karyomorph may in fact form part of the *P. nuchalis* 'Pale/black headed' lineage (rather than the *P. nuchalis* 'Southern' lineage). The differences Mengden observed between the 'Pale head, grey nape' and '*carinata*' karyotypes are not great, concerning the morphology of autosome pairs 4-16 and the sex chromosomes, and he did not consider them to be

'such as to guarantee a strong genetic barrier to reproduction' (Mengden, 1985b, p. 207). Accordingly, if Mengden's 'Pale head, grey nape' karyomorph is conspecific with the 'Pale head, grey nape' and 'Orange with black head' specimens considered here (see previous paragraph), it is plausible that these differences reflect further variation within the *P. nuchalis* 'Pale/black headed' lineage. Another possibility is that Mengden's '*carinata*' karyomorph represents a distinct lineage, not considered here, the component individuals of which exhibit a colour pattern similar to that of some 'Pale head, grey nape' *P. nuchalis* 'Pale/black headed' specimens. Nonetheless, in the absence of mitochondrial DNA sequence and morphological data for typical '*carinata*' specimens and/or chromosome data for 'Pale head, grey nape' *P. nuchalis* 'Pale/black headed' specimens exhibiting the '*carinata*' banding pattern, it is difficult to assess the above possibilities and hence the status of Mengden's '*carinata*' group.

SAM R 28559 is almost certainly part of the *P. nuchalis* 'Southern' lineage. Although this specimen appears in the *P. inframacula* mitochondrial DNA clade, it is placed among specimens of the *P. nuchalis* 'Southern' clade in the multivariate analyses, exhibits and allozyme genotype nearly identical (identical at diagnostic loci) to that of other *P. nuchalis* 'Southern' specimens, possesses a strap like rostral (considered here to diagnose specimens of the *P. nuchalis* 'Southern' lineage), and is very similar in appearance to 'Southern with black bands' *P. nuchalis* 'Southern' specimens. Furthermore, this specimen possesses 19 dorsal rows on the neck (as opposed to 17 in *P. inframacula*) and a relatively low number of subcaudals (fewer than all *P. inframacula* specimens examined; see Appendix 7). The placement of SAM R 28559 in the mitochondrial DNA sequence analysis is intriguing, and may reflect incomplete lineage sorting of ancestral mitochondrial DNA haplotypes. Considering this, it is significant that uncorrected percent sequence divergence between the *P. inframacula* and *P. nuchalis* 'Southern' clades is relatively low, suggesting that *P. inframacula* and the *P. nuchalis* 'Southern' lineage (which are sister taxa; see Results above) separated comparatively recently, a situation conducive to observing incomplete lineage sorting (e.g. Avise and Ball, 1990; Avise, 1994, 2000).

In the light of the above conclusions concerning species limits within *Pseudonaja*, it is evident that at least some of the confusion regarding the classification of this group has resulted from

a reliance by systematists on characters that are variable within species and/or exhibit states that are shared among species. Consider the number of dorsal rows at midbody. Previous authors (e.g. Mirtschin and Davis, 1983; Wilson and Knowles, 1988; Cogger, 1992) have regarded the possession of 19 midbody dorsal rows as a distinctive attribute of *P. affinis* specimens, serving to differentiate them from specimens of *P. inframacula*, *P. nuchalis*, and *P. textilis*. As delimited here, however, *P. affinis* incorporates specimens from Eyre Peninsula and south-western South Australia possessing 17 midbody dorsal rows, so that the number of midbody dorsal rows is variable within this taxon. The recognition of 19 midbody dorsal rows as a diagnostic trait of *P. affinis* specimens is likely to have prompted Mengden and Fitzgerald's (1987, p. 467) claim that *P. affinis* and the 'Southern' morph of *P. nuchalis* may hybridise in south-western South Australia. This claim is based on a specimen from Penong, illustrated by Mengden (1985b, his Plate 1H) and Mengden and Fitzgerald (1987, p. 466), for which Mengden (1985b) obtained chromosome data. Mengden (1985b, p. 197) considered that this specimen, which almost certainly possesses 17 midbody dorsal rows, exhibits an 'aberrant black pattern ... and karyotype, and may represent an intergrade'. However, the 'aberrant black pattern', which consists of numerous dark blotches on the dorsum, including the head, and indistinct oblique bands on the body, is similar to that of some Western Australian *P. affinis* specimens (and typical of specimens from south-western South Australia), while the observed karyotype is nearly indistinguishable from that reported for *P. affinis* (see Mengden, 1985b, his Table 1). Thus, it is doubtful that Mengden (1985b) would have regarded this specimen as a '*P. affinis* cross' had it possessed 19 midbody dorsal rows. According to the 'traditional classification' presented by Cogger (1992, p. 668), specimens of *P. inframacula*, *P. nuchalis*, and *P. textilis* are separable in exhibiting, respectively, scattered black scales on the body, these usually being concentrated dorsomedially, but occasionally covering nearly the entire dorsum, regular or irregular banding, or at least some dark sclaes on the nape, and uniform pale to dark brown dorsal colouration. Nonetheless, *P. inframacula* specimens may lack dark scales on the body, while these are commonly observed in *P. nuchalis* 'Southern' specimens, and occasionally in *P. textilis* specimens. Additionally, some *P. nuchalis* 'Pale/black headed' and *P. nuchalis* 'Southern' specimens exhibit neither banding nor dark scales on the nape, while conspicuous dark bands may be present in *P. inframacula* specimens (although these bands are distinctive in tapering laterally; see discussion of colour pattern variation in the Results above). Thus, these supposedly diagnostic colour pattern elements are not only variable within

species, but are, in a number of cases, shared among species. Cogger (1992, p. 668) also considered that specimens of *P. nuchalis* can be differentiated from those of *P. affinis* in possessing a large, strap like rostral that is 'higher than broad and conspicuous when viewed from above'. However, although the rostral of nominal *P. nuchalis* specimens is usually conspicuous in dorsal view, it is strap like only in *P. nuchalis* 'Southern' specimens (at least as this condition is considered here; see Results above). Furthermore, the rostral of *P. affinis* specimens is often large and is typically conspicuous when viewed from above.

Considering that moderately to strongly supported mitochondrial DNA clades separated by comparatively long branches are present within *P. modesta* and *P. textilis*, these taxa may incorporate more than one independently evolving lineage (i.e. species). Although the observation of distinct mitochondrial DNA clades is, in itself, consistent with the presence of one or multiple lineages, and so insufficient to justify the acceptance of either hypothesis (see Chapter 2), it may, as an expedient, be considered to indicate the existence of potentially isolated (extrinsically and/or intrinsically) groups of organisms whose evolutionary independence may be tested using evidence from unlinked characters (indeed, this is the approach that has been employed in the present study). Donnellan *et al.* (1993) have suggested that those species with extensive geographical distributions and/or exhibiting considerable morphological variation are most likely to incorporate unrecognised taxa (although Donnellan *et al.* were concerned specifically with the Australian herpetofauna, it would seem that their suggestion may be reasonably extended to other faunas; see also Frost and Hillis, 1990, p. 93). Both *P. modesta* and *P. textilis* are widely distributed, occurring throughout western and central Australia and eastern Australia, respectively (see, for example, Cogger, 1992 and the Species Accounts below). Furthermore, a number of authors (e.g. Gillam, 1979; Mirtschin and Davis, 1983; Cogger, 1992) have noted considerable variation in colouration among *P. textilis* specimens. Thus, it would perhaps be unsurprising if further investigation revealed the presence of more than one species within these taxa. Nonetheless, the single *P. textilis* specimen from Alice Springs (SAM R 56724) appears in a moderately supported clade with specimens from north-eastern South Australia and western Queensland and two specimens from Merauke in Irian Jaya, so that the mitochondrial DNA sequence data do not support Gillam's (1979) supposition that *P. textilis* specimens from the MacDonnell Ranges are parts of a distinct species.

3.5.2 Phylogenetic relationships

Although the mitochondrial DNA sequence data do not resolve the placement of *Oxyuranus* with respect *Pseudonaja* (see Fig. 3.1), they indicate that these taxa comprise a clade, controverting Wallach's (1985) proposal that *P. modesta* should be referred to *Hemiaspis* (there is general agreement that, within Hydrophiinae, *Hemiaspis* is distantly related to *Pseudonaja* and *Oxyuranus*; see, for example, Mengden, 1985a; Wallach, 1985; Greer, 1997; Keogh *et al.*, 1998; Keogh, 1999). Mengden (1985b) and Keogh (1999) have similarly disputed Wallach's proposal, concluding on the basis of chromosome and hemipenis morphology, respectively, that *P. modesta* is part of *Pseudonaja*. Mengden's (1985b, his Fig. 3) conclusion that *P. affinis*, *P. textilis*, and the 'Darwin', 'Orange with black head', and 'Southern' morphs of *P. nuchalis* share an ancestor not shared with *P. guttata* (*P. inframacula*, *P. ingrami*, and *P. modesta* were not included in Mengden's analysis) is supported by the mitochondrial DNA sequence data, however, these data are inconsistent with the conclusion that *P. nuchalis* 'Pale/black headed' (represented by the 'Orange with black head' morph in Mengden's analysis) and *P. nuchalis* 'Southern' are sister lineages (see Fig. 3.1). The conclusion that *P. affinis*, *P. textilis*, and at least the *P. nuchalis* 'Pale/black headed' and *P. nuchalis* 'Southern' lineages form a clade, exclusive of *P. guttata*, is also supported by the allozyme electrophoretic data (see Fig. 3.3). In comparing Figures 3.1 and 3.3, however, it is evident that the mitochondrial DNA sequence and allozyme electrophoretic data are otherwise largely incongruent (at least with regard to phylogenetic relationships; cf. the discussion of species limits above). This incongruence may be attributable to persistent ancestral variation in the allozyme electrophoretic data set; if the rate of allozyme evolution within *Pseudonaja* were sufficiently slow that variation observed within and among lineages existed prior to their separation, this variation would not be expected to contain information relevant to recovering phylogentic relationships (see, for example, Frost *et al.*, 1998). That *P. affinis* and *P. inframacula*, and *P. affinis* and *P. nuchalis* 'Southern' exhibit no fixed allozyme differences, and that the number of fixed allozyme differences observed among the remaining species is relatively low, implies that the rate of allozyme evolution within *Pseudonaja* is indeed slow, supporting this explanation.

3.6 Species Accounts

In this section, I provide brief accounts for the *P. textilis* group species discussed above. Specimens of these species are separable from those of *P. guttata* in possessing 17, as opposed to 19 or 21, dorsal rows at midbody or 19 dorsal rows at midbody and six, as opposed to seven, infralabials (see Gillam, 1979), and from specimens of *P. modesta* in possessing a greater number of ventrals (more than 180; Gillam, 1979; Cogger, 1992). It is probable that *P. ingrami* is part of the *P. textilis* group (see Wallach, 1985, his Fig. 5), however, this species was not considered here (due to an absence of suitable material; see Materials and Methods above) and, although I regard the available morphological (Gillam, 1979; Phillips, 1993) and chromosomal (Mengden, 1985b) evidence as sufficient to justify its recognition, I do not present an account below. Specimens of *P. ingrami* are separable from those of *P. affinis*, *P. inframacula*, *P. textilis*, and the three *P. nuchalis* lineages in possessing seven, as opposed to six, infralabials and an indistinct 'dull orange brown' iris (Gillam, 1979, p. 17). Comments regarding nomenclature are provided where appropriate. Synonymies are in Cogger *et al.* (1983).

Pseudonaja affinis Günther, 1972

Figure 3.8

Holotype

British Museum of Natural History (BMNH, London) 1946.1.19.77, collected from Australia.

Diagnosis

Specimens of *P. affinis* are separable from those of the remaining *P. textilis* group species in exhibiting a contrasting dark grey or dark brown throat. (Although the throat may be dark grey or black in 'Orange with black head' *P. nuchalis* 'Pale/black headed' specimens, this is invariably associated with a dark brown or black head and neck.) Additionally, *P. affinis* specimens differ from *P. inframacula*, *P. nuchalis* 'Darwin', *P. textilis*, and at least some (perhaps all; see the Discussion above) *P. nuchalis* 'Pale/black headed' specimens in possessing a diploid chromosome number of 34; from specimens of *P. inframacula*, *P. nuchalis* 'Southern', and *P. textilis* in possessing

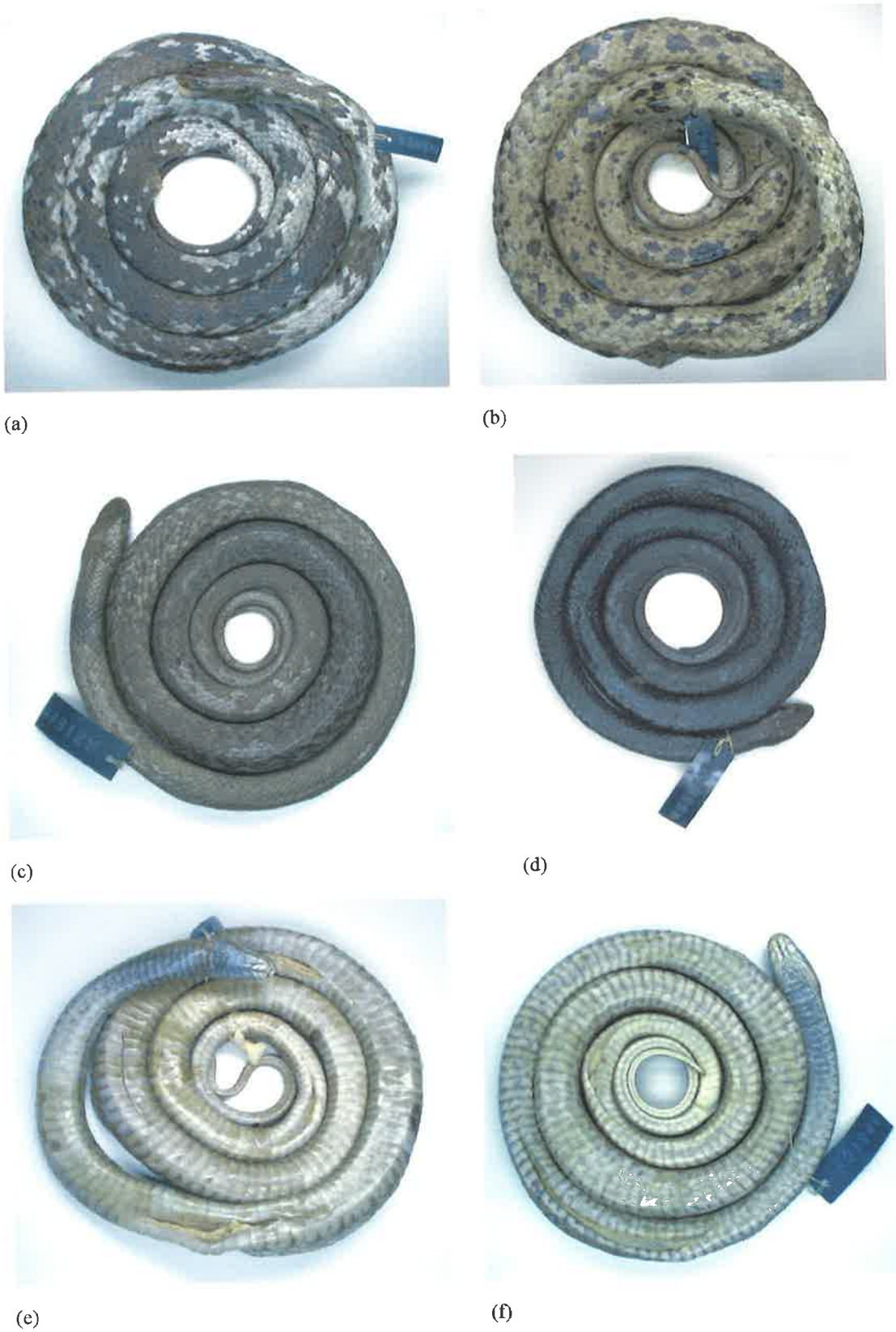


Fig. 3.8. *Pseudonaja affinis*: (a) SAM R 23000, dorsal view; (b) SAM R 20605, dorsal view; (c) SAM R 21955, dorsal view; (d) SAM R 18995, dorsal view; (e) SAM R 20605, ventral view; (f) SAM R 21955, ventral view.

Fig. 3.9. Geographical distribution of *Pseudonaja affinis* individuals considered in this study.

autosomes that can be partitioned into only two (rather than three) distinct size classes; from specimens of *P. inframacula* in exhibiting a medium to dark brown, or dirty cream or pale yellow venter; from specimens of *P. nuchalis* 'Southern' in possessing a normal, as opposed to strap like, rostral; and from specimens of *P. textilis* in exhibiting a predominantly dark bluish-grey or black mouth lining. *Pseudonaja affinis* specimens also tend to possess a greater number of ventrals than *P. inframacula* and *P. nuchalis* 'Darwin' specimens.

Distribution

The individuals considered in this study were collected in southern Western Australia and south-western South Australia, from the Perth area to Lake Gillies on Eyre Peninsula (Fig. 3.9).

Pseudonaja inframacula (Waite, 1925)

Figure 3.10

Syntypes

SAM, not found (Cogger *et al.*, 1983), collected from northern end of Coffin Bay Peninsula, west coast of Eyre Peninsula, South Australia.

Diagnosis

Specimens of *P. inframacula* are separable from those of the remaining *P. textilis* group species in exhibiting a medium to dark grey (rarely pale bluish-grey) venter and a diploid chromosome number of 36. Additionally, *P. inframacula* specimens differ from specimens of *P. nuchalis* 'Darwin', *P. nuchalis* 'Pale/black headed', *P. nuchalis* 'Southern', and *P. textilis* in possessing sex chromosomes that differ markedly in size; from specimens of *P. affinis*, *P. nuchalis* 'Darwin', and *P. nuchalis* 'Pale/black headed' in possessing autosomes that can be partitioned into three (rather than only two) distinct size classes; from specimens of *P. affinis* in lacking a contrasting dark grey or dark brown throat (the colour of the throat is similar to that of the belly, and hence not contrasting); from specimens of *P. nuchalis* 'Darwin' in possessing 17, as opposed to 19 or more, dorsal rows on the neck (one head length posterior to the parietals); from specimens of *P. nuchalis* 'Southern' in possessing a normal, as opposed to strap like, rostral; and from specimens of *P. textilis*

Fig. 3.10. *Pseudonaja inframacula*: (a) SAM R 24755, dorsal view; (b) SAM R 26474, dorsal view; (c) SAM R 29026, dorsal view; (d) SAM R 57076, dorsal view; (e) SAM R 24755 ventral view; (f) SAM R 26474, ventral view.

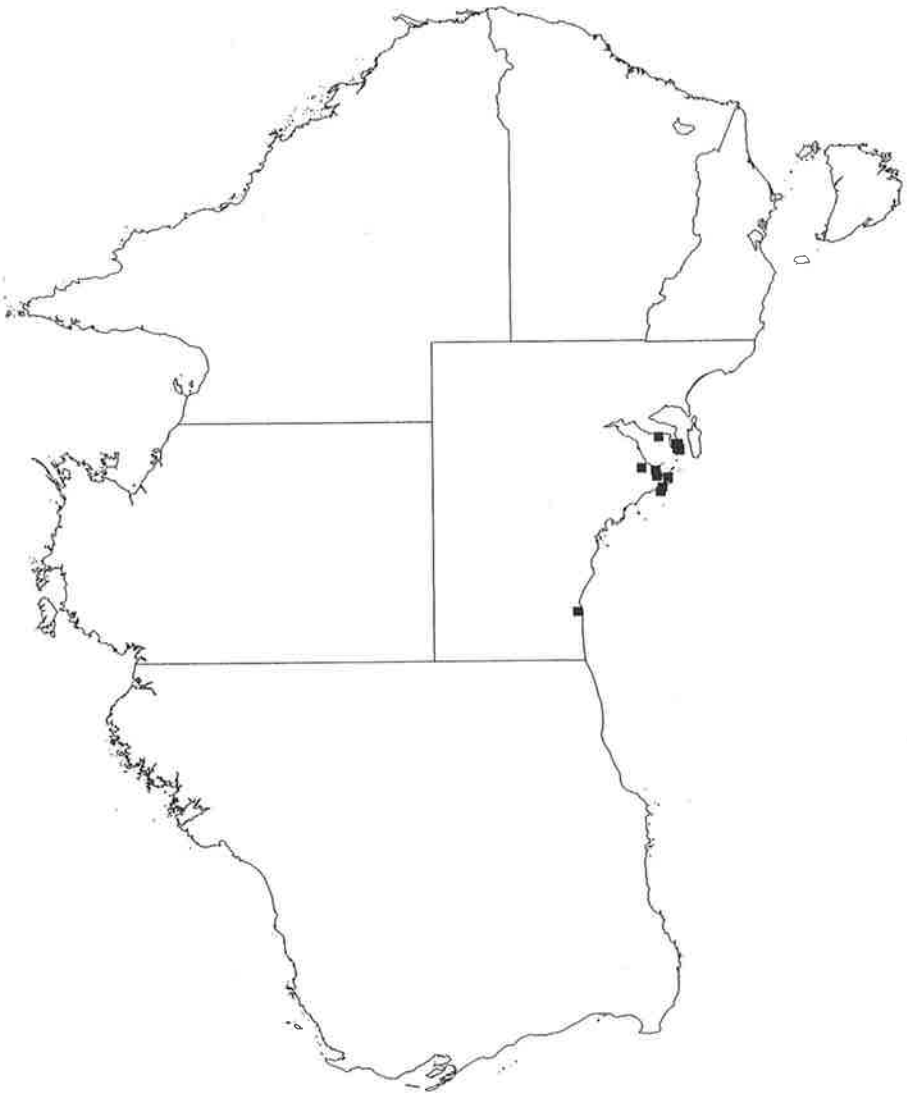


Fig. 3.11. Geographical distribution of *Pseudonaja inframacula* individuals considered in this study.

in exhibiting a predominantly dark bluish-grey or black mouth lining. *Pseudonaja inframacula* specimens also tend to possess fewer ventrals than *P. affinis* and *P. nuchalis* 'Southern' specimens.

Distribution

The majority of individuals considered in this study were collected from southern Eyre Peninsula and southern Yorke Peninsula. Two individuals (SAM R 31572 and SAM R 31599) were collected from Wardang Island, while SAM R 25702 was collected near Nullarbor Station, west of Eyre Peninsula (Fig. 3.11).

Pseudonaja nuchalis 'Darwin'

Figure 3.12

Diagnosis

Specimens of *P. nuchalis* 'Darwin' are separable from those of the remaining *P. textilis* group species in possessing a diploid chromosome number of 30. Additionally, *P. nuchalis* 'Darwin' specimens differ from specimens of *P. inframacula*, *P. nuchalis* 'Southern', and *P. textilis* in possessing autosomes that can be partitioned into only two (rather than three) distinct size classes; from specimens of *P. affinis* in lacking a contrasting dark grey or dark brown throat; from specimens of *P. inframacula* in exhibiting a cream or yellowish-cream venter, possessing sex chromosomes that are approximately equal in size, and possessing 19 dorsal rows on the neck; from specimens of *P. nuchalis* 'Southern' in possessing fewer ventrals and a normal, as opposed to strap like, rostral; and from specimens of *P. textilis* in exhibiting a predominantly dark bluish-grey or black mouth lining. *Pseudonaja nuchalis* 'Darwin' specimens also tend to possess a greater number of dorsal rows at the level of the first ventral than specimens of the remaining *P. textilis* group species, in the majority of cases possess a greater number of dorsal rows on the neck than *P. nuchalis* 'Pale/black headed' specimens, and generally possess fewer ventrals than *P. affinis* specimens.

Distribution

The majority of individuals considered in this study were collected north of 13°S in the Northern Territory. ABTC 32072 (no specimen) was collected from Nardoo Station in southern central Queensland (Fig. 3.13).

(a) (b)

(c)

Fig. 3.12. *Pseudonaja nuchalis* 'Darwin': (a) SAM R 56775, dorsal view; (b) SAM R 56775, dorsal view of head; (c) SAM R 56773, ventral view.

Comments

According to Mengden (1985b, p. 202), there is no available name for the '"Darwin" morph'. It is probable that the geographical distribution of *P. nuchalis* 'Darwin' incorporates the collection locality for the lectotype of *Pseudonaja nuchalis* Günther, 1858 (BMNH 1946.1.20.41, collected from Port Essington, Northern Territory), however, this specimen exhibits a colour pattern considerably different to that of the *P. nuchalis* 'Darwin' specimens examined here (see Mengden's [1985b] Figs 4A and 4A′) and may represent a distinct species. The holotype of *Pseudonaja jukesi* Wells and Wellington, 1985 (NTM R 1186, collected from Oenpelli, Northern Territory) is almost

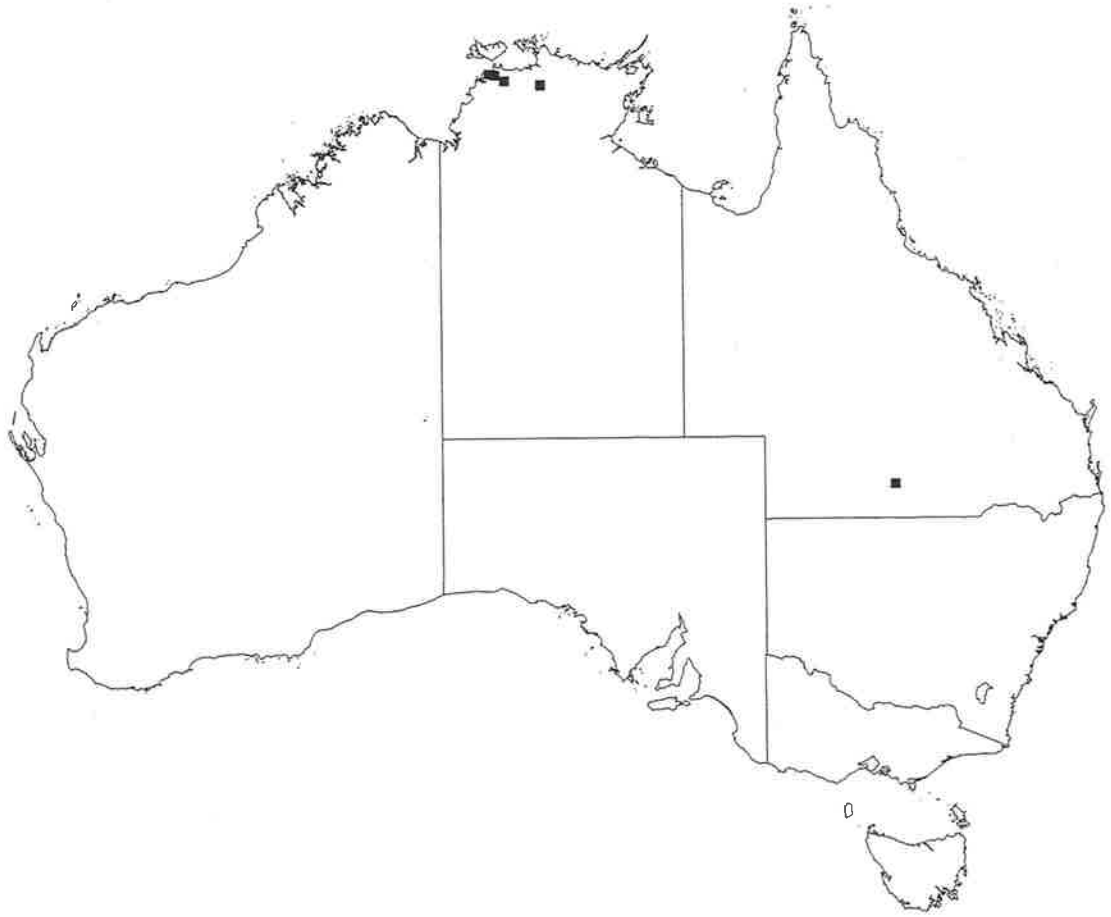


Fig. 3.13. Geographical distribution of *Pseudonaja nuchalis* 'Darwin' individuals considered in this study.

certainly a specimen of *P. nuchalis* 'Darwin' (I have examined all of the Wells and Wellington holotypes), so that the name *jukesi* could be ascribed to this lineage.

Pseudonaja nuchalis 'Pale/black headed'

Figures 3.14-3.16

Diagnosis

At least some (perhaps all; see the Discussion above) specimens of *P. nuchalis* 'Pale/black headed' are separable from specimens of the remaining *P. textilis* group species in possessing a diploid chromosome number of 32. Additionally, *P. nuchalis* 'Pale/black headed' specimens differ from specimens of *P. inframacula*, *P. nuchalis* 'Southern', and *P. textilis* in possessing autosomes that can be partitioned into only two (rather than three) distinct size classes (see, however, Mengden, 1985b); from specimens of *P. affinis* in lacking a contrasting dark grey or dark brown throat (see Diagnosis for *P. affinis* above); from specimens of *P. inframacula* in exhibiting a cream or yellow venter, and possessing sex chromosomes that are approximately equal in size (see, however, Mengden, 1985b); from specimens of *P. nuchalis* 'Southern' in possessing a normal, as opposed to strap like, rostral; and from specimens of *P. textilis* in exhibiting a predominantly dark bluish-grey or black mouth lining. The majority of *P. nuchalis* 'Pale/black headed' specimens also possess fewer dorsal rows on the neck than *P. nuchalis* 'Darwin' and *P. nuchalis* 'Southern' specimens.

Distribution

The individuals considered in this study were collected throughout western and central Australia, from near Carnarvon in Western Australia to Mootwingee National Park in western New South Wales (Fig. 3.17).

Comments

Mengden (1985b, p. 200) noted that the holotype of *Pseudelaps bancrofti* De Vis, 1911 (Queensland Museum, Brisbane, J 187, collected from Stannary Hills, Queensland) 'seems to resemble, in its head markings, the "pale head, grey nape" morph. Its posterior markings are not unlike those of *Diemenia carinata*' (the holotype after which Mengden named the '*carinata*' morph). A number of *P. nuchalis* 'Pale/black headed' specimens considered here exhibit colouration similar

Fig. 3.14. *Pseudonaja nuchalis* 'Pale/black headed', 'Pale head, grey nape' form: (a) SAM R 51592, dorsal view; (b) SAM R 20981, dorsal view; (c) SAM R 56725, dorsal view; (d) SAM R 56725, dorsal view of head; (e) SAM R 20981, ventral view; (f) SAM R 56725, ventral view.

Fig. 3.15. *Pseudonaja nuchalis* 'Pale/black headed', 'Orange with black head' form: (a) SAM R 42333, dorsal view; (b) SAM R 21414, dorsal view; (c) SAM R 56723, dorsal view; (d) SAM R 56714, dorsal view of head; (e) SAM R 21414, ventral view; (f) SAM R 56714, ventral view.

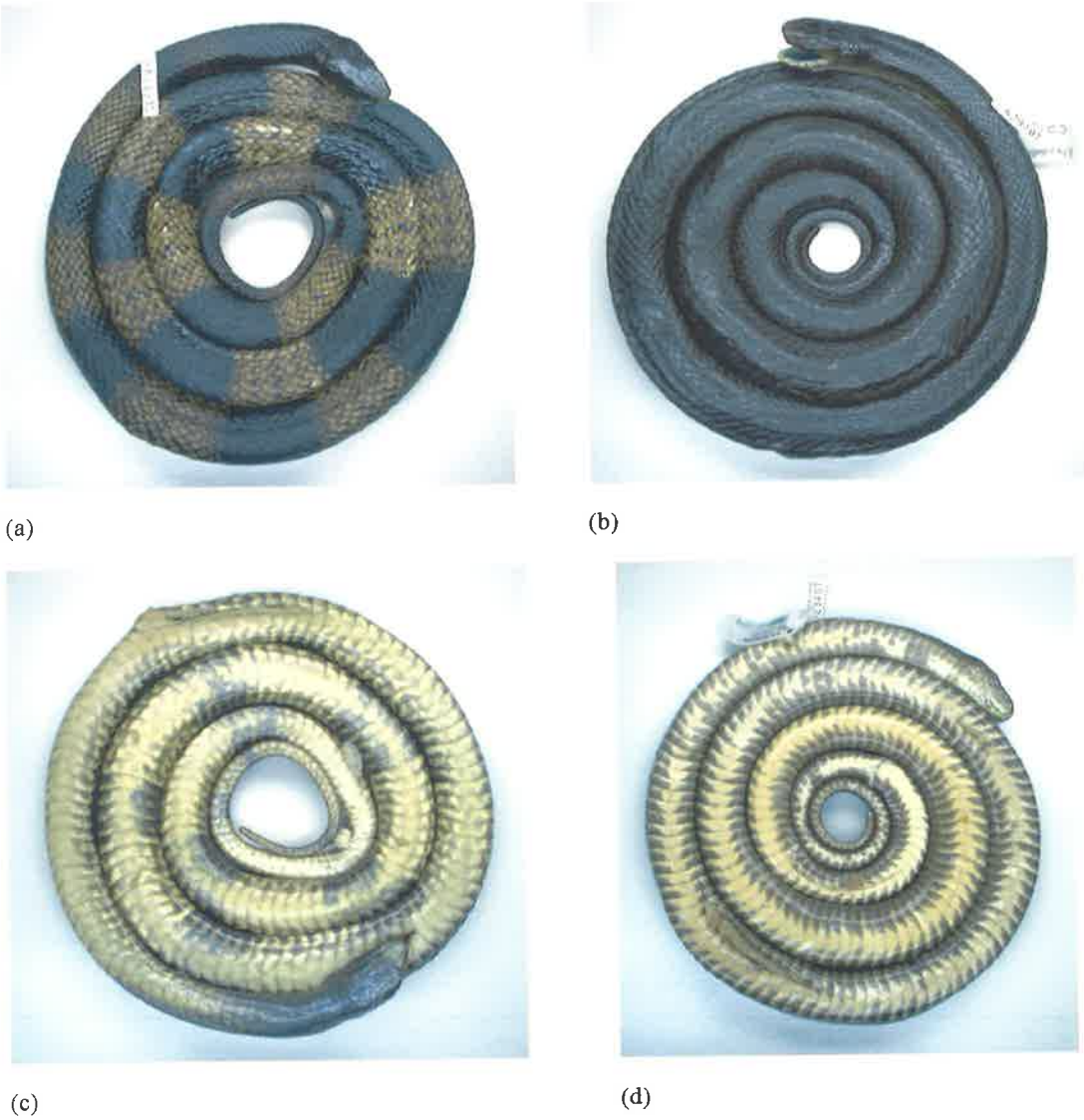


Fig. 3.16. *Pseudonaja nuchalis* 'Pale/black headed': (a) SAM R 28531, dorsal view; (b) SAM R 29407, dorsal view; (c) SAM R 28531, ventral view; (d) SAM R 29407, ventral view.

to this, displaying '*carinata*'-type banding on the posterior body but otherwise resembling typical 'Pale head, grey nape' specimens (see the discussion of colour pattern variation in the Results above and the Discussion). Thus, I tentatively propose that the name *bancrofti* should be ascribed to the *P. nuchalis* 'Pale/black headed' lineage, noting that I have only examined photographs of the holotype provided by Mengden (1985b, his Figs 4D and 4D′).

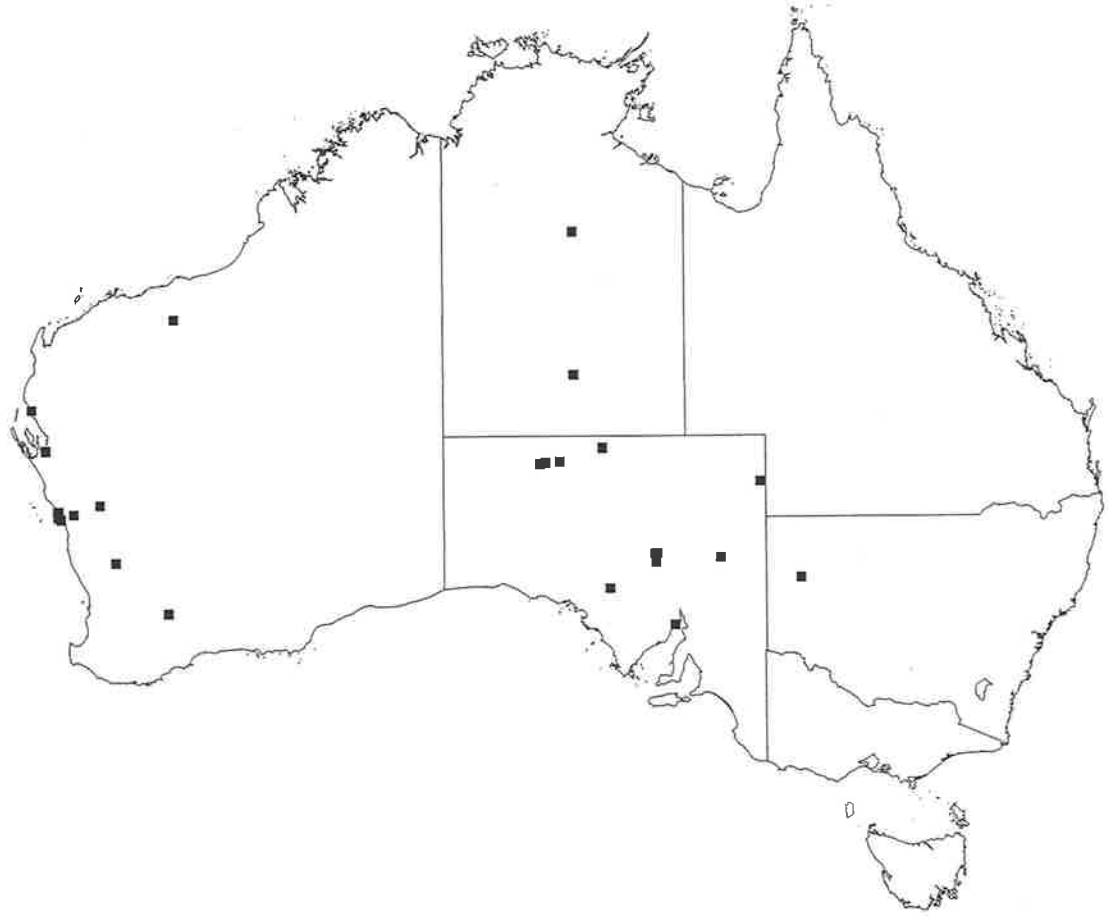


Fig. 3.17. Geographical distribution of *Pseudonaja nuchalis* 'Pale/black headed' individuals considered in this study.

The holotypes of *Pseudonaja kellyi* Wells and Wellington, 1985 (NTM R 1689, collected on Stuart Highway, 160 km north of Ayres Rock turnoff, Northern Territory) and *Pseudonaja vanderstraateni* Wells and Wellington, 1985 (NTM R 0371, collected 100 km north of Katherine, Northern Territory), and the holotype of *Pseudonaja mengdeni* Wells and Wellington, 1985 (NTM R 1989, collected 2 km east of Maryvale, Northern Territory) are specimens of the 'Orange with black head' and 'Pale head, grey nape' colour forms of *P. nuchalis* 'Pale/black headed', respectively. Accordingly, the names *kellyi*, *mengdeni*, and *vanderstraateni* should be regarded as junior synonyms of *bancrofti*.

Pseudonaja nuchalis 'Southern'

Figure 3.18

Diagnosis

Specimens of *P. nuchalis* 'Southern' are separable from those of the remaining *P. textilis* group species in possessing a strap like rostral that imparts a chisel shape to the snout in dorsal view (in specimens of the remaining *P. textilis* group species, the rostral is normal, the snout appearing rounded when viewed from above). Additionally, *P. nuchalis* 'Southern' specimens differ from *P. inframacula*, *P. nuchalis* 'Darwin', *P. textilis*, and at least some (perhaps all; see the Discussion above) *P. nuchalis* 'Pale/black headed' specimens in possessing a diploid chromosome number of 34; from specimens of *P. affinis*, *P. nuchalis* 'Darwin', and *P. nuchalis* 'Pale/black headed' in possessing autosomes that can be partitioned into three (rather than only two) distinct size classes; from specimens of *P. affinis* in lacking a contrasting dark grey or dark brown throat; from specimens of *P. inframacula* in exhibiting a dirty cream or yellow, or medium brown venter, and possessing sex chromosomes that are approximately equal in size; from specimens of *P. nuchalis* 'Darwin' in possessing a greater number of ventrals; and from specimens of *P. textilis* in exhibiting a predominantly dark bluish-grey or black mouth lining. *Pseudonaja nuchalis* 'Southern' specimens also tend to possess a greater number of ventrals than *P. inframacula* specimens, in the majority of cases possess a greater number of dorsal rows on the neck than *P. nuchalis* 'Pale/black headed' specimens, and generally possess fewer subcaudals than specimens of the remaining *P. textilis* group species.

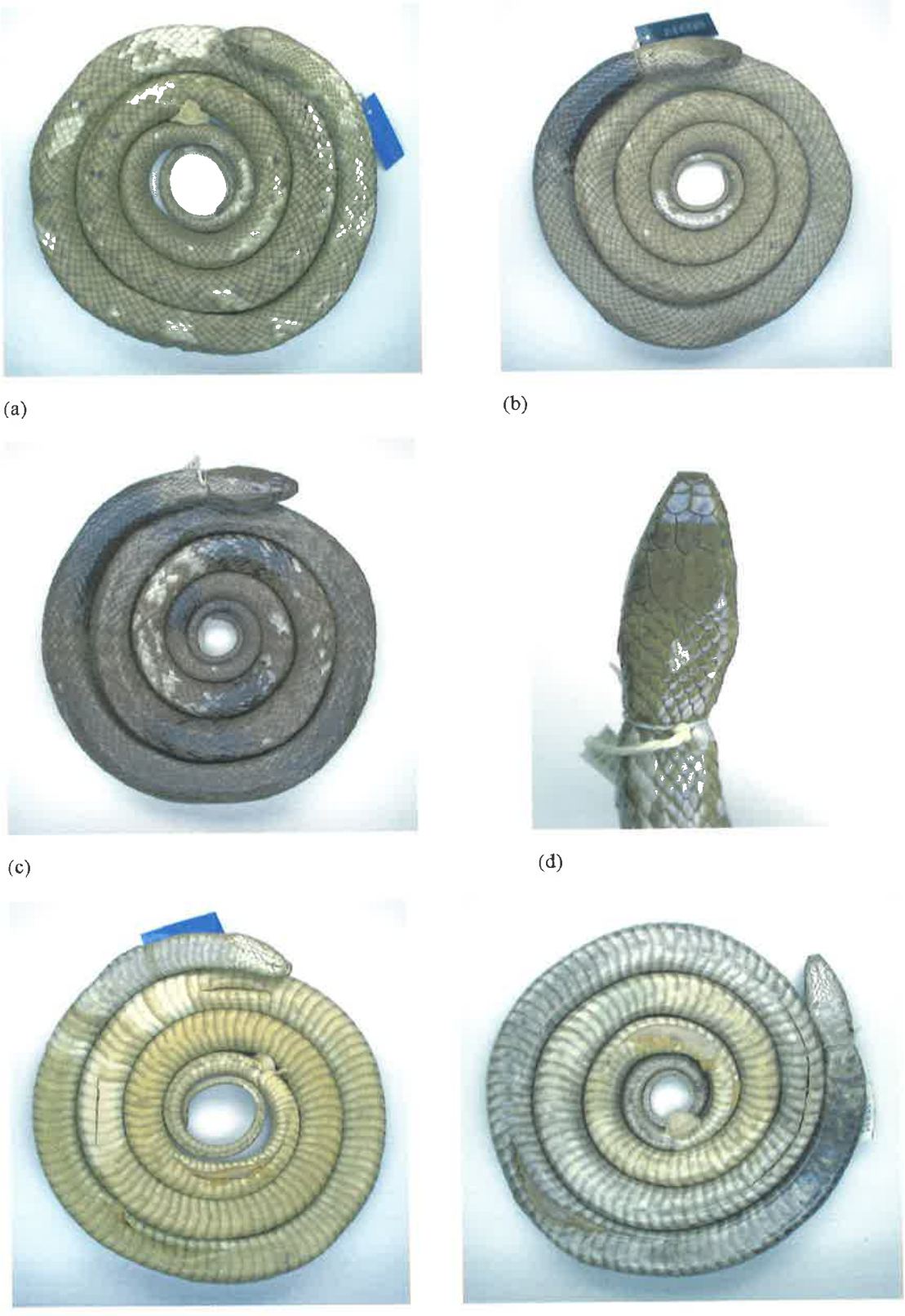


Fig. 3.18. *Pseudonaja nuchalis* 'Southern': (a) SAM R 18599, dorsal view; (b) SAM R 18860, dorsal view; (c) SAM R 21163, dorsal view; (d) SAM R 21163, dorsal view of head; (e) SAM R 18599, ventral view; (f) SAM R 18860, ventral view.

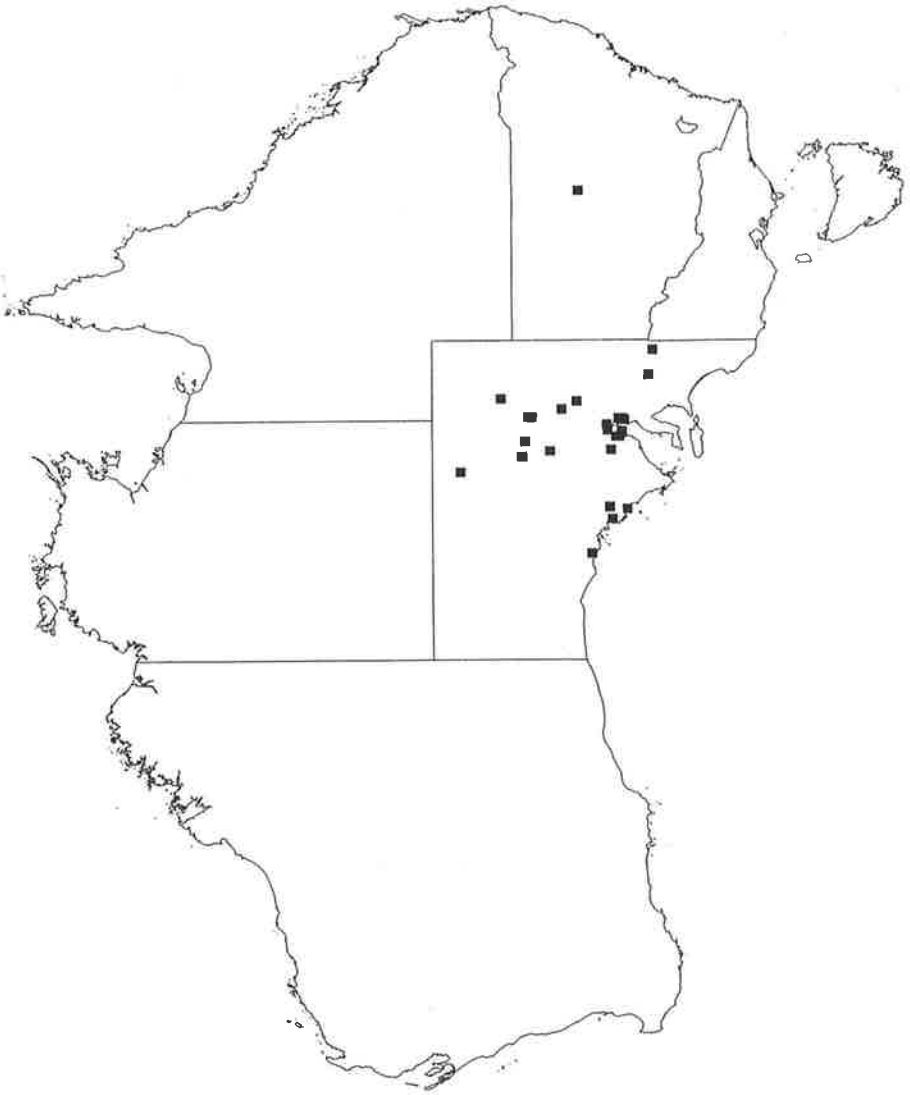


Fig. 3.19. Geographical distribution of *Pseudonaja nuchalis* 'Southern' individuals considered in this study.

Distribution

The individuals considered in this study were collected south of 27°S, from near Penong, west of Eyre Peninsula, to near Hermidale in central New South Wales (Fig. 3.19).

Comments

Mengden (1985b, p. 200) considered the holotype of *Diemenia aspidorhyncha* McCoy, 1879 (National Museum of Victoria, Melbourne, D 12352, collection locality unknown, presumably restricted to junction of Murray and Darling Rivers, Victoria [Coventry, 1970]), 'although badly faded and discoloured', to be 'most like the ... "Southern" morph'. An evaluation of Mengden's (1985b) Figure 4C' reveals that this specimen possesses a large strap like rostral, considered here to diagnose *P. nuchalis* 'Southern' specimens (see above). Thus, I tentatively agree with Mengden's (1985b) proposition that the name *aspidorhyncha* should be ascribed to this species.

Mengden (1985b) also referred the holotype of *Demansia acutirostris* Mitchell, 1951 (SAM R3133, collected from island in Lake Eyre, South Australia) to the 'Southern' morph. I have examined this specimen and also consider it to be a part of the *P. nuchalis* 'Southern' lineage. Accordingly, the name *acutirostris* should be regarded as a junior synonym of *aspidorhyncha*.

Pseudonaja textilis (Duméril, Bibron, and Duméril, 1854)

Figure 3.20

Holotype

Muséum National d'Histoire Naturelle, Paris, 3944 (not found [Cogger *et al.*, 1983]), collected from Australia.

Diagnosis

Specimens of *P. textilis* are separable from those of the remaining *P. textilis* group species in exhibiting an entirely pink mouth lining and a diploid chromosome number of 38. Additionally, *P. textilis* specimens differ from specimens of *P. affinis*, *P. nuchalis* 'Darwin', and *P. nuchalis* 'Pale/black headed' in possessing autosomes that can be partitioned into three (rather than only two) distinct size classes; from specimens of *P. affinis* in lacking a contrasting dark grey or dark brown

Fig. 3.20. *Pseudonaja textilis*: (a) SAM R 31701, dorsal view; (b) SAM R 31692, dorsal view; (c) SAM R 56724, dorsal view; (d) SAM R 19943, dorsal view; (e) SAM R 31701, ventral view; (f) SAM R 31692, ventral view.

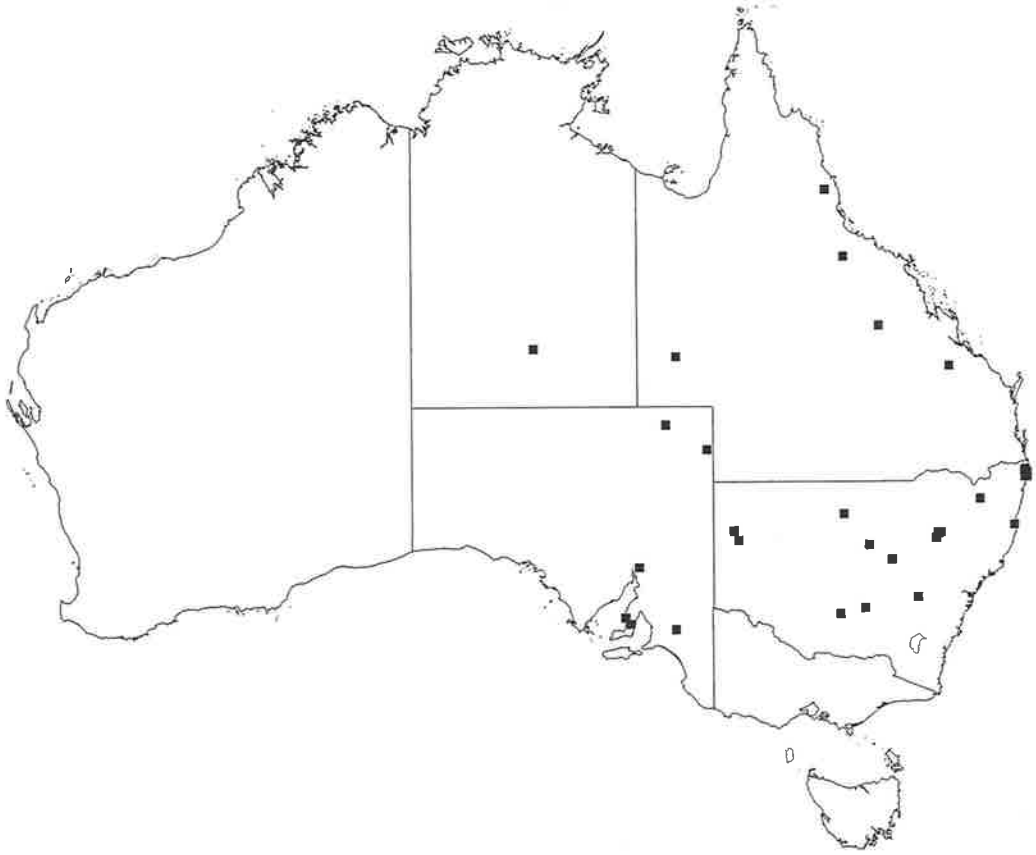


Fig. 3.21. Geographical distribution of *Pseudonaja textilis* individuals considered in this study. Two individuals from Merauke in Irian Jaya (AM R 147652 and AM R 147659) are not shown.

throat; from specimens of *P. inframacula* in exhibiting a dirty cream, yellowish-cream, or yellow venter, and possessing sex chromosomes that are approximately equal in size; and from specimens of *P. nuchalis* 'Southern' in possessing a normal, as opposed to strap like, rostral. *Pseudonaja textilis* specimens also tend to possess a greater number of subcaudals than specimens of the remaining *P. textilis* group species.

Distribution

The majority of individuals considered in this study were collected throughout eastern Australia, from near Malanda in northern Queensland to south-eastern South Australia. SAM R 56724 was collected from Alice Springs, while two specimens (AM R 147652 and AM R 147659) were collected from Merauke in Irian Jaya (Fig. 3.21).

Comments

The holotype of *Pseudonaja ohnoi* Wells and Wellington, 1985 (NTM R 1970, collected from Alice Springs, Northern Territory) is a MacDonnell Ranges specimen of *P. textilis*. Considering that none of the supposedly diagnostic attributes listed by Wells and Wellington (1985, pp 48-49) differentiate this specimen from eastern Australian specimens of *P. textilis*, I propose that the name *ohnoi* should be regarded as a junior synonym of *textilis*, recognising that the MacDonnell Ranges population of this species may be found to constitute part of a distinct species with further research (see the Discussion above).

3.7 Conclusion

The species level systematics of *Pseudonaja* is perhaps not as poorly resolved as previous authors (e.g. Hutchinson, 1990; Cogger, 1992) have 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 supported by mitochondrial DNA sequence data. 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. A number of avenues of study remain to be pursued. In particular, the status of Mengden's (1985b) '*carinata*' morph remains unresolved, as does the possibility of unrecognised taxa within *P. modesta* and *P. textilis* (a more detailed survey of variation within *P. modesta* is in progress), and the issue of *Pseudonaja* monophyly. Progress in these areas, as well as in brown snake systematics generally, will depend on the acquisition of new material and data, and a consideration of additional sources of evidence (e.g. nuclear gene sequences, osteology, soft anatomy).

While systematists have largely been unconcerned with the data and methods employed in delimiting species (see Wiens and Penkrot, 2002; Chapter 1), there is no reason to expect that species level systematics can not be practiced in a scientific manner. As I have emphasised in this thesis, specific hypotheses of species limits can be connected to a number of testable predictions that are unlikely to be realised under alternative hypotheses, so that they may be assessed on the basis of their relative explanatory power and thus either accepted or rejected according to the same criteria as all hypotheses in science. Nonetheless, although I consider that this perspective dispels the claim that systematists are rarely able to provide sufficient empirical justification for accepting hypotheses of species limits (see Chapter 2), it is undoubtedly in need of elaboration. It is my hope that future workers will further develop this (or a similar) view, so that a detailed, coherent methodology for delimiting species may eventually emerge.

References

(References associated with type specimens are listed only where they were referred to elsewhere in the text. Those not listed are in Cogger *et al.* [1983]).

Adams, M., P.R. Baverstock, C.R. Tidemann, and D.P. Woodside, 1982. Large genetic differences between sibling species of bats, *Eptesicus*, from Australia. Heredity 48: 435-438.

Arévalo, E., S.K. Davis, and J.W. Sites, Jr., 1994. Mitochondrial DNA sequence divergence and phylogenetic relationships among eight chromosome races of the *Sceloporus grammicus* complex (Phrynosomatidae) in central Mexico. Systematic Biology 43: 387-418.

Avise, J.C., 1994. Molecular Markers, Natural History, and Evolution. Chapman and Hall, New York.

Avise, J.C., 2000. Phylogeography: The History and Formation of Species. Harvard University Press, Cambridge.

Avise, J.C., J. Arnold, R.M. Ball, Jr., E. Bermingham, T. Lamb, J.E. Neigel, C.A. Reeb, and N.C. Saunders, 1987. Intraspecific phylogeography: the mitochondrial DNA bridge between population genetics and systematics. Annual Review of Ecology and Systematics 18: 489-522.

Avise, J.C., and R.M. Ball, Jr., 1990. Principles of genealogical concordance in species concepts and biological taxonomy. Oxford Surveys in Evolutionary Biology 7: 45-67.

Baverstock, P.R., M. Adams, and M. Archer, 1984. Electrophoretic resolution of species boundaries in the *Sminthopsis murina* complex (Dasyuridae). Australian Journal of Zoology 32: 823-832.

Baverstock, P.R., and C. Moritz, 1996. Project design. Pp 17-28. In Hillis, D.M., C. Moritz, and B.K. Mable (eds). Molecular Systematics. Sinauer, Sunderland.

Bensasson, D., D-X. Zhang, D.L. Hartl, and G. Hewitt, 2001. Mitochondrial pseudogenes: evolution's misplaced witnesses. Trends in Ecology and evolution 16: 314-321.

Boulenger, G.A., 1896. Catalogue of the Snakes in the British Museum (Natural History), Vol. 3. British Museum of Natural History, London.

Bremer, K., 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. Evolution 42: 795-803.

Bremer, K., 1994. Branch support and tree stability. Cladistics 10: 295-304.

Broad, A.J., S.K. Sutherland, and A.R. Coulter, 1979. The lethality in mice of dangerous Australian and other snake venoms. Toxicon 17: 661-664.

Brower, A.V.Z., R. DeSalle, and A. Vogler, 1996. Gene trees, species trees, and systematics: a cladistic perspective. Annual Review of Ecology and Systematics 27: 423-450.

Bunge, M., 1979. Treatise on Basic Philosophy, Vol. 4., A World of Systems. D. Reidel, Dordrecht.

Burbrink, F.T., 2001. Systematics of the eastern ratsnake complex (*Elaphe obsoleta*). Herpetological Monographs 15: 1-53.

Bush, B., 1989a. Ontogenetic colour change in the gwarder, *Pseudonaja nuchalis*. Western Australian Naturalist 18: 25-29.

Bush, B., 1989b. Polymorphism in captive bred siblings of the snake, *Pseudonaja nuchalis*. Herpetofauna 19: 28-32.

Chalmers, A.F., 1999. What is this Thing Called Science? University of Queensland Press, St Lucia.

Cogger, H.G., 1992. Reptiles and Amphibians of Australia. Reed Books, Chatswood.

Cogger, H.G., E.E. Cameron, and H.M. Cogger, 1983. Zoological Catalogue of Australia. Vol. 1, Amphibia and Reptilia. Bureau of Flora and Fauna, Canberra.

Coventry, A.J., 1970. Reptile and amphibian type specimens housed in the National Museum of Victoria. Memoirs of the National Museum of Victoria 31: 115-124.

Crozier, R.H., 1997. Preserving the information content of species: genetic diversity, phylogeny, and conservation worth. Annual Review of Ecology and Systematics 28: 243-268.

Densmore, L.D., III, F.L. Rose, and S.J. Kain, 1992. Mitochondrial DNA evolution and speciation in water snakes (genus *Nerodia*) with special reference to *Nerodia harteri*. Herpetologica 48: 60-68.

dc Queiroz, K., 1988. Systematics and the Darwinian revolution. Philosophy of Science 55: 238-259.

de Queiroz, K., 1998. The general lineage concept of species, species criteria, and the process of speciation: a conceptual unification and terminological recommendations. Pp 57-75. In Howard, D.J., and S.H. Berlocher (eds). Endless Forms: Species and Speciation. Oxford University Press, Oxford.

de Queiroz, K., 1999. The general lineage concept of species and the defining properties of the species category. Pp 49-89. In Wilson, R.A. (Ed). Species: New Interdisciplinary Essays. MIT Press, Cambridge.

de Queiroz, K., and M.J. Donoghue, 1988. Phylogenetic systematics and the species problem. Cladistics 4: 317-338.

de Queiroz, K., and M.J. Donoghue, 1990. Phylogenetic systematics and species revisited. Cladistics 6: 83-90.

de Queiroz, K., and Gauthier, J., 1992. Phylogenetic taxonomy. Annual Review of Ecology and Systematics 23: 449-480.

Donnellan, S., M. Adams, M. Hutchinson, and P.R. Baverstock, 1993. The identification of cryptic species in the Australian herpetofauna: a high research priority. Pp 121-126. In Lunney, D., and D. Ayers (eds). Herpetology in Australia. A Diverse Discipline. Royal Zoological Society of New South Wales, Sydney.

Donnellan, S.C., M.N. Hutchinson, and K.M. Saint, 1999. Molecular evidence for the phylogeny of Australian gekkonoid lizards. Biological Journal of the Linnean Society 67: 97-118.

Dowling, H.G., 1951, A proposed standard system of counting ventrals in snakes. British Journal of Herpetology 1: 97-99.

Eldredge, N., 1985. The ontology of species. Pp 17-20. In Vrba, E.S. (Ed). Species and Speciation. Transvaal Museum, Pretoria.

Eldredge, N., and S.N. Salthe, 1984. Hierarchy and evolution. Oxford Surveys in Evolutionary Biology 1: 184-208.

Ehrlich, P., and P. Raven, 1969. Differentiation of populations. Science 165: 1228-1232.

Ereshefsky, M., 1999. Species and the Linnaean Hierarchy. Pp 285-305. In Wilson, R.A. (Ed). Species: New Interdisciplinary Essays. MIT Press, Cambridge.

Ereshefsky, M., 2001. The Poverty of the Linnaean Hierarchy. A Philosophical Study of Biological Taxonomy. Cambridge University Press, Cambridge.

Eriksson, T., 1998. Autodecay, Version 4.0 (program distributed by the author). Department of Botany, Stockholm University, Stockholm.

Farris, J.S., 1983. The logical basis of phylogenetic analysis. Pp 7-36. In Platnick, N.I., and V.A. Funk (eds). Advances in Cladistics, Vol. 2. Columbia University Press, New York.

Felsenstein, J., 1985. Phylogenies and the comparative method. The American Naturalist 125: 1-15.

Fleay, D., 1943. The brown snake – dangerous fellow. Victorian Naturalist 59: 147-152.

Forstner, M.R.J., S.K. Davis, and E. Arévalo, 1995. Support for the hypothesis of anguimorph ancestry for the suborder Serpentes from phylogenetic analysis of mitochondrial DNA sequences. Molecular Phylogenetics and Evolution 4: 93-102.

Frost, D.R., H.M. Crafts, L.A. Fitzgerald, and T.A. Titus, 1998. Geographic variation, species recognition, and molecular evolution of cytochrome oxidase I in the *Tropidurus spinulosus* complex (Iguania: Tropiduridae). Copeia 1998: 839-851.

Frost, D.R., R. Etheridge, D. Janies, and T. Titus, 2001. Total evidence, sequence alignment, evolution of polychrotid lizards, and a reclassification of the Iguania (Squamata: Iguania). American Museum Novitates 3343: 1-38.

Frost, D.R., and D.M. Hillis, 1990. Species in concept and practice: herpetological applications. Herpetologica 46: 87-104.

Frost, D.R., and A.G. Kluge, 1994. A consideration of epistemology in systematic biology, with special reference to species. Cladistics 10: 259-294.

Frost, D.R., A.G. Kluge, and D.M. Hillis, 1992. Species in contemporary herpetology: comments on phylogenetic inference and taxonomy. Herpetological Review 23: 46-54.

Fry, D.B., 1914. On a collection of reptiles and batrachians from Western Australia. Records of the Western Australian Museum and Art Gallery 1: 174-210.

Gellissen, G., and G. Michaelis, 1987. Gene transfer: mitochondria to nucleus. Annals of the New York Academy of Sciences 503: 391-401.

Ghiselin, M., 1974. A radical solution to the species problem. Systematic Zoology 23: 536-554.

Ghiselin, M., 1987. Species concepts, individuality, and objectivity. Biology and Philosophy 2: 127-143.

Ghiselin, M., 1997. Metaphysics and the Origin of Species. State University of New York Press, Albany.

Gillam, M.W., 1979. The genus *Pseudonaja* (Serpentes: Elapidae) in the Norhtern Territory. Territory Parks and Wildlife Research Bulletin 1: 1-28.

Goldstein, P.Z., and R. DeSalle, 2000. Phylogenetic species, nested hierarchies, and character fixation. Cladistics 16: 364-384.

Gould, S.J., 1966. Allometry and size in ontogeny and phylogeny. Biological Reviews 41: 587-640.

Greer, A.E., 1997. The Biology and Evolution of Australian Snakes. Surrey Beatty and Sons, Chipping Norton.

Griffiths, G.C.D., 1974. On the foundations of biological systematics. Acta Biotheoretica 23: 85-131.

Günther, A., 1858. Catalogue of Colubrine Snakes in the Collection of the British Museum. British Museum, London.

Hartl, D.L., and A.G. Clark, 1997. Principles of Population Genetics. Sinauer, Sunderland.

Harvey, P.H., and M.D. Pagel, 1991. The Comparative Method in Evolutionary Biology. Oxford University Press, Oxford.

Hennig, W., 1965. Phylogenetic systematics. Annual Review of Entomology 10: 97-116.

Hennig, W., 1966. Phylogenetic Systematics. University of Illinois Press, Urbana.

Hillis, D.M., and M.T. Dixon, 1991. Ribosomal DNA: molecular evolution and phylogenetic inference. The Quarterly Review of Biology 66: 411-453.

Hull, D.L., 1976. Are species really individuals? Systematic Zoology 25: 174-191.

Hull, D.L., 1980. Individuality and selection. Annual Review of Ecology and Systematics 11: 311-332.

Hull, D.L., 1997. The ideal species concept – and why we can't get it. Pp 357-380. In Claridge, M.F., H.A. Dawah, and M.R. Wilson (eds). Species: The Units of Biodiversity. Chapman and Hall, London.

Hutchinson, M.N., 1990. The generic classification of the Australian terrestrial elapid snakes. Memoirs of the Queensland Museum 28: 397-405.

Hutchinson, M.N., and S.C. Donnellan, 1999. Genetic variation and taxonomy of the lizards assigned to *Ctenotus uber orientalis* Storr (Squamata: Scincidae) with description of new species. Records of the South Australian Museum 32: 173-189.

International Commission on Zoological Nomenclature, 1991. Decision of the Commission. Three works by Richard W. Wells and C. Ross Wellington: proposed suppression for nomenclatural purposes. Bulletin of Zoological Nomenclature 48: 337-338.

James, B.H., S.C. Donnellan, and M.N Hutchinson, 2001. Taxonomic revision of the Australian lizard *Pygopus nigriceps* (Squamata: Gekkonoidea). Records of the South Australian Museum 34: 37-52.

Keogh, J.S., 1995. The importance of systematics in understanding the biodiversity crisis: the role of biological educators. Journal of Biological Education 29: 293-299.

Keogh, J.S., 1998. Molecular phylogeny of elapid snakes and a consideration of their biogeographic history. Biological Journal of the Linnean Society 63: 177-203.

Keogh, J.S., 1999. Evolutionary implications of hemipenial morphology in terrestrial Australian elapid snakes. Zoological Journal of the Linnean Society 125: 239-278.

Keogh, J.S., R. Shine, and S. Donnellan, 1998. Phylogenetic relationships of terrestrial Australo-Papuan elapid snakes based on cytochrome *b* and 16S rRNA sequences. Molecular Phylogenetics and Evolution 10: 67-81.

Kinghorn, J.R., 1956. The Snakes of Australia. Angus and Robertson, Sydney.

Kluge, A.G., 1990. Species as historical individuals. Biology and Philosophy 5: 417-431.

Kluge, A.G., 1997a. Testability and the refutation and corroboration of cladistic hypotheses. Cladistics 13: 81-96.

Kluge, A.G., 1997b. Sophisticated falsification and research cycles: consequences for differential character weighting in phylogenetic systematics. Zoological Scripta 26: 349-360.

Kluge, A.G., and A.J. Wolf, 1993. Cladistics: what's in a word? Cladistics 9: 183-199.

Kornet, D.J., and H. Turner, 1999. Coding polymorphism for phylogeny reconstruction. Systematic Biology 48: 365-379.

Kuhn, T.S., 1970. Logic of discovery or psychology of research? Pp 1-23. In Lakatos, I., and A. Musgrave (eds). Criticism and the Growth of Knowledge. Cambridge University Press, Cambridge.

Lakatos, I., 1970. Falsification and the methodology of scientific research programmes. Pp 91-196. In Lakatos, I., and A. Musgrave (eds). Criticism and the Growth of Knowledge. Cambridge University Press, Cambridge.

Lakatos, I., 1978. Science and pseudoscience. Pp 1-7. In Worrall, J., and G. Currie (eds). Imre Lakatos, Philosophical Papers, Vol. 1: The Methodology of Scientific Research Programmes. Cambridge University Press, Cambridge.

Lee, M.S.Y., 2003. Species concepts and species reality: salvaging a Linnaean rank. Journal of Evolutionary Biology 16: 179-188.

Lee, M., and M. Wolsan, 2002. Integration, individuality, and species concepts. Biology and Philosophy 17: 651-660.

Lidén, M., 1990. Replicators, hierarchy, and the species problem. Cladistics 6: 183-186.

Lleonart, J., J. Salat, and G.J. Torres, 2000. Removing allometric effects of body size in morphological analysis. Journal of Theoretical Biology 205: 85-93.

Loveridge, A., 1934. Australian reptiles in the Museum of Comparative Zoology. Bulletin of the Museum of Comparative Zoology 77: 241-383.

Macey, J.R., and A. Verma, 1997. Homology in phylogenetic analysis: alignment of transfer RNA genes and the phylogenetic position of snakes. Molecular Phylogenetics and Evolution 7: 272-279.

Maddison, W.P., and D.R. Maddison, 1992. MacClade. Analysis of Phylogeny and Character Evolution, Version 3. Sinauer, Sunderland.

Mayden, R.L., 1997. A hierarchy of species concepts: the denouement in the saga of the species problem. Pp 381-424. In Claridge, M.A., H.A. Dawah, and M.R. Wilson (eds). Species: The Units of Biodiversity. Chapman and Hall, London.

Mayr, E., 1970. Populations, Species, and Evolution. Harvard University Press, Cambridge.

Mayr, E., 1982. The Growth of Biological Thought. Diversity, Evolution, and Inheritance. Belknap Press, Cambridge.

Mayr, E., and P.D. Ashlock, 1991. Principles of Systematic Zoology. McGraw-Hill, New York.

McDowell, S.B., 1967. *Aspidomorphus*, a genus of New Guinea elapid snakes of the family Elapidae, with notes on related genera. Journal of Zoology, London 151: 497-543.

McDowell, S.B., 1987. Systematics. Pp 3-50. In Seigel, R.A., J.T. Collins, and S.S. Novak (eds). Snakes: Ecology and Evolutionary Biology. McGraw Hill, New York.

Mengden, G.A., 1983. The taxonomy of Australian elapid snakes, a review. Records of the Australian Museum 35: 195-222.

Mengden, G.A., 1985a. Australian elapid phylogeny: a summary of the chromosomal and electrophoretic data. Pp 185-192. In Grigg, G., R. Shine, and H. Ehmann (eds). Biology of Australasian Frogs and Reptiles. Royal Zoological Society of New South Wales, Sydney.

Mengden, G.A., 1985b. A chromosomal and electrophoretic analysis of the genus *Pseudonaja*. Pp 193-208. In Grigg, G., R. Shine, and H. Ehmann (eds). Biology of Australasian Frogs and Reptiles. Royal Zoological Society of New South Wales, Sydney.

Mengden, G.A., and M. Fitzgerald, 1987. The paradoxical brown snakes. Pp 459-470. In Covacevich, J., P. Davie, and J. Pearn (eds). Toxic Plants and Animals : A Guide for Australia. Queensland Museum, Brisbane.

Mirtschin, P., and P. Davis, 1983. Dangerous Snakes of Australia: An Illustrated Guide to Australia's Most Venomous Snakes. Rigby, Adelaide.

Mishler, B.D., 1999. Getting rid of species? Pp 307-315. In Wilson, R.A. (Ed). Species: New Interdisciplinary Essays. MIT Press, Cambridge.

Moore, W.S., 1995. Inferring phylogenies from mtDNA variation: mitochondrial-gene trees versus nuclear-gene trees. Evolution 49: 718-726.

Nixon, K.C., and Q.D. Wheeler, 1990. An amplification of the phylogenetic species concept. Cladistics 6: 211-23.

O'Shea, M., 1996. A Guide to the Snakes of Papua New Guinea. Independent, Port Moresby.

Orange, P., 1992. Colour morphs in *Pseudonaja nuchalis* (Serpentes: Elapidae) – variations on a theme? Herpetofauna 22: 22-23.

Orr, H.A., "Why polyploidy is rarer in animals than in plants" revisited. The American Naturalist 136: 759-770.

Pamilo, P., and M. Nei, 1988. Relationships between gene trees and species trees. Molecular Biology and Evolution 5: 568-583.

Pleijel, F., 1999. Phylogenetic taxonomy, a farewell to species, and a revision of *Heteropodarke* (*Hesionidae*, *Polychaeta*, *Annelida*). Systematic Biology 48: 755-789.

Pleijel, F., and G.W. Rouse, 2000. Least-inclusive taxonomic unit: a new taxonomic concept for biology. Proceedings of the Royal Society, Biological Sciences, Series B 267: 627-630.

Pleijel, F., and Rouse, G.W., 2003. Ceci n'est pas une pipe: names, clades, and phylogenetic nomenclature. Zoological Scripta (in press).

Popper, K., 1959. The Logic of Scientific Discovery. Routledge, London.

Popper, K., 1963. Conjectures and Refutations: The Growth of Scientific Knowledge. Routledge, London.

Popper, K., 1983. Realism and the Aim of Science. Routledge, London.

Rambaut, A., 1996. Se-Al. Sequence Alignment Editor, Version 1.0 alpha 1. Department of Zoology, University of Oxford, Oxford.

Reist, J.D., 1985. An empirical evaluation of several univariate methods that adjust for size variation in morphometric data. Canadian Journal of Zoology 63: 1429-1439.

Richardson, B.J., P.R. Baverstock, and M. Adams, 1986. Allozyme Electrophoresis. A Handbook for Animal Systematics and Population Studies. Academic Press, Sydney.

Ridley, M., 1989. The cladistic solution to the species problem. Biology and Philosophy 4: 1-16.

Rieppel, O.C., 1988. Fundamentals of Comparative Biology. Birkhäuser Verlag, Basel.

Rodríguez-Robles, J.A., and J.M. De Jesús-Escobar, 2000. Molecular systematics of new world gopher, bull, and pinesnakes (*Pituophis*: Colubridae), a transcontinental species complex. Molecular Phylogenetics and Evolution 14: 35-50.

Rodríguez-Robles, J.A., G.R. Stewart, and T.J. Papenfuss, 2001. Mitochondrial DNA-based phylogeography of North American rubber boas, *Charina bottae* (Serpentes: Boidae). Molecular Phylogenetics and Evolution 18: 227-237.

Saiki, R.K., T.L. Bugawan, G.T. Horn, K.B. Mullis, and H.A. Erlich, 1985. Analysis of enzymatic amplified beta-globin and HLA-DQalpha DNA with allele-specific oligonucleotide probes. Nature 324: 163-166.

Saiki, R.K., D.H. Gelfand, S. Stoffel, S.J. Scharf, R. Higuchi, G.T. Horn, K.B. Mullis, and H.A. Erlich, 1988. Primer-directed enzymatic amplification of DNA with a thermostable DNA polymerase. Science 239: 487-491.

Shine, R., 1989. Constraints, allometry and adaptation: food habits and reproductive biology of Australian brownsnakes (*Pseudonaja*: Elapidae). Herpetologica 45: 195-207.

Shine, R., 1991. Australian Snakes: A Natural History. Reed Books, Chatswood.

Shine, R., and T. Schwaner, 1985. Prey constriction by venomous snakes: a review, and new data for Australian species. Copeia 1985: 1067-1071.

Simmons, M.P., and H. Ochoterena, 2000. Gaps as characters in sequence-based phylogenetic analyses. Systematic Biology 49: 369-381.

Simpson, G.G., 1951. The species concept. Evolution 5: 285-298.

Sites, J.W., Jr., and C. Moritz, 1987. Chromosomal evolution and speciation revisited. Systematic Zoology 36: 153-174.

Slowinski, J.B., and J.S. Keogh, 2000. Phylogenetic relationships of elapid snakes based on cytochrome *b* mtDNA sequences. Molecular Phylogenetics and Evolution 15: 157-164.

Slowinski, J.B., and W. Wüster, 2000. A new cobra (Elapidae: *Naja*) from Myanmar (Burma). Herpetologica 56: 257-270.

Sober, E., 1993. Philosophy of Biology. Westview Press, Boulder.

Sokal, R.R., and Crovello, T.J., 1970. The biological species concept: a critical evaluation. The American Naturalist 104: 127-153.

Statsoft, 1997. Statistica, Version 5. Statsoft, Tulsa.

Sutherland, S.K., 1992. Deaths from snakebite in Australia, 1981-1991. The Medical Journal of Australia 157: 740-746.

Swofford, D.L., 1999. PAUP*. Phylogenetic Analysis Using Parsimony (* and Other Methods). Sinauer, Sunderland.

Templeton, A.R., 1989. The meaning of species and speciation a genetic perspective. Pp 3-27. In Otte, D., and J. Endler (eds). Speciation and its Consequences. Sinauer, Sunderland.

Thorpe, R.S., 1976. Biometric analysis of geographic variation and racial affinities. Biological Reviews 51: 407-452.

Thorpe, R.S., 1980. A comparative study of ordination techniques in numerical taxonomy in relation to racial variation in the ringed snake *Natrix natrix* (L.). Biological Journal of the Linnean Society 13: 7-40.

Thorpe, R.S., and C. McCarthy, 1978. A preliminary study, using multivariate analysis, of a species complex of African house snakes (*Boaedon fuliginosus*). Journal of Zoology 184: 489-506.

Van Valen, L., 1976. Ecological species, multispecies, and oaks. Taxon 25: 233-239.

Wallach, V., 1985. A cladistic analysis of the terrestrial Australian Elapidae. Pp 223-253. In Grigg, G., R. Shine, and H. Ehmann (eds). Biology of Australasian Frogs and Reptiles. Royal Zoological Society of New South Wales, Sydney.

Wells, R.W., and C.R. Wellington, 1984. A synopsis of the class Reptilia in Australia. Australian Journal of Herpetology 1: 73-129.

Wells, R.W., and C.R. Wellington, 1985. A classification of the Amphibia and Reptilia of Australia. Australian Journal of Herpetology, Supplementary Series 1: 1-61.

Welter, C., S. Dooley, and N. Blin, 1989. A rapid protocol for the purification of mitochondrial DNA suitable for studying restiction fragment length polymorphisms. Gene 83: 169-172.

Whitehead, P., 1990. Systematics: and endangered species. Systematic Zoology 39: 179-184.

Wiens, J.J., and T.A. Penkrot, 2002. Delimiting species using DNA and morphological variation and discordant species limits in spiny lizards (*Sceloporus*). Systematic Biology 51: 69-91.

Wiley, E.O., 1975. Karl R. Popper, systematics, and classification: a reply to Walter Bock and other evolutionary taxonomists. Systematic Zoology 24: 233-243.

Wiley, E.O., 1978. The evolutionary species concept reconsidered. Systematic Zoology 27: 17-26.

Wiley, E.O., 1980. Is the Evolutionary species fiction? – A consideration of classes, individuals, and historical entities. Sytematic Zoology 29: 76-80.

Wiley, E.O., 1981. Phylogenetics: The Theory and Practice of Phylogenetic Systematics. John Wiley and Sons, New York.

Wiley, E.O., 1989. Kinds, individuals, and theories. Pp 289-300. In Ruse, M. (Ed). What the Philosophy of Biology Is. Kluwer Academic, Boston.

Wiley, E.O., and R.L. Mayden, 2000a. The evolutionary species concept. Pp70-89. In Wheeler, Q.D., and R. Meier (eds). Species Concepts and Phylogenetic Theory: A Debate. Columbia University Press, New York.

Wiley, E.O., and R.L. Mayden, 2000b. A critique from the evolutionary species concept perspective. Pp 146-158. In Wheeler, Q.D., and R. Meier (eds). Species Concepts and Phylogenetic Theory: A Debate. Columbia University Press, New York.

Williams, V., and J. White, 1997. Snake venom and snakebite in Australia. Pp 205-218. In Thorpe, R.S., W. Wüster, and A. Malhotra (eds). Venomous Snakes: Ecology, Evolution, and Snakebite. The Zoological Society of London, Oxford.

Williams, V., J. White, and P.J. Mirtschin, 1994. Comparative study on the procoagulant from the venom of Australian brown snakes (Elapidae; *Pseudonaja* spp.). Toxicon 32: 453-459.

Wilson, S.K., and D.G. Knowles, 1988. Australia's Reptiles. Collins, Sydney.

Worrell, E., 1961. Herpetological name changes. Western Australian Naturalist 8: 18-27.

Wu, C.-I., 1991. Inferences of species phylogeny in relation to segregation of ancient polymorphisms. Genetics 127: 429-435.

Wüster, W., M.G. Salomão, R.S. Thorpe, G. Puorto, M.F.D. Furtado, S.A. Hoge, R.D.G. Theakston, and D.A. Warrell, 1997. Systematics of the *Bothrops atrox* complex: new insights from multivariate analysis and mitochondrial DNA sequence information. Pp 99-113. In Thorpe, R.S., W. Wüster, and A. Malhotra (eds). Venomous Snakes: Ecology, Evolution, and Snakebite. The Zoological Society of London, Oxford.

Wüster, W., and R.S. Thorpe, 1989. Population affinities of the asiatic cobra (*Naja naja*) species complex in south-east Asia: reliability and random resampling. Biological Journal of the Linnean Society 1989: 391-409.

Wüster, W., and R.S. Thorpe, 1992. Asiatic cobras: population systematics of the *Naja naja* species complex (Serpentes: Elapidae) in India and central Asia. Herpetologica 48: 69-85.

Wüster, W., R.S. Thorpe, M.J. Cox, P. Jintakune, and J. Nabhitabhata, 1995. Population systematics of the snake genus *Naja* (Reptilia: Serpentes: Elapidae) in Indochina: multivariate morphometrics and comparative mitochondrial DNA sequencing (cytochrome oxidase I). Journal of Evolutionary Biology 8: 493-510.

Zhang, D-X., and G.M. Hewitt, 1996. Nuclear integrations: challenges for mitochondrial DNA markers. Trends in Ecology and Evolution 11: 247-251.

Appendices

Appendix 1

Storage and collection details for material used in this study. Mitochondrial DNA haplotype numbers correspond to those in Figures 3.1 and 3.2.

Species	Tissue Number	Specimen Number	Collection Locality	mtDNA Haplotype Number	Latitude	Longitude
Pseudonaja affinis	ABTC 6467	SAM R 26268	10 km NE Border Village, SA	1	31 36 50 S	129 06 20 E
	ABTC 6469	SAM R 26347	50 km W Yalata Roadhouse, SA	2	31 25 50 S	131 16 50 E
	ABTC 56281	SAM R 18995	Yalata Mission, SA	2	31 29 S	131 50 E
	ABTC 56282	SAM R 18996	Yalata Mission, SA	2	31 29 S	131 50 E
	ABTC 56319	SAM R 20605	24 km S Ceduna, SA	1	32 16 S	133 52 E
	ABTC 56326	SAM R 20807	Near Corrobinnie Hill, SA	3	32 58 S	135 45 E
	ABTC 56359	SAM R 21955	Lake Gilles, SA	3	32 46 S	136 29 E
	ABTC 56368	SAM R 22974	Wilsons Inlet, Denmark, WA	1	34 58 S	117 21 E
	ABTC 56371	SAM R 23000	65 km W Esperance, WA	1	33 45 S	121 15 E
	ABTC 56402	SAM R 24807	Hambidge CP, SA	3	33 28 S	136 02 E
	ABTC 56403	SAM R 24808	Hambidge CP, SA	3	33 28 S	136 02 E
	ABTC 56435	SAM R 29468	2 km E Ravensthorpe, WA	4	33 35 S	120 03 E
	ABTC 56484	SAM R 31704	Yumbarra CP, SA	1	31 46 46 S	133 25 53 E
	ABTC 58893	SAM R 52360	11 km E Ceduna, SA	1	32 07 47 S	133 47 56 E
	ABTC 61786	WAM R 104272	Maida Vale, WA	1	31 57 00 S	116 00 00 E
	ABTC 75102	WAM R 77743	Toolina Rockhole, WA	1	32 37 40 S	124 50 40 E
	ABTC 75121	WAM R 115146	Unknown	1		
	ABTC 75129	WAM R 119550	Cardup, WA	5	32 15 00 S	116 00 00 E
	ABTC 75132	WAM R 121141	Figure of Eight Island, WA	1	34 02 00 S	121 37 00 E
	ABTC 75133	WAM R 121144	7 km NW Frankland, WA	6	34 21 00 S	117 01 00 E

Species	Tissue Number	Specimen Number	Collection Locality	mtDNA Haplotype Number	Latitude	Longitude
	ABTC 75140	WAM R 125640	Wanneroo, WA	7	31 45 00 S	115 48 00 E
	ABTC 75143	WAM R 136095	Cardup, WA	1	32 15 00 S	116 00 00 E
	ABTC 75262	WAM R 115297	Woodvale, WA	1	31 47 00 S	115 47 00 E
	ABTC 75263	WAM R 119172	Trigg, WA	1	31 52 00 S	115 46 00 E
Pseudonaja guttata	ABTC 31913		Tarcombe and Depot Glen Stn., QLD	8	24 04 S	143 23 E
	ABTC 32082		Longreach, QLD	9	23 28 S	144 14 E
	ABTC 56317	SAM R 20582	Goyder Lagoon, SA	10	26 46 S	139 08 E
Pseudonaja inframacula	ABTC 56393	SAM R 24751	Shell Beach, Innes NP, SA	11	35 16 S	136 51 E
	ABTC 56394	SAM R 24752	Inneston Ruins, SA	11	35 16 S	136 54 E
	ABTC 56396	SAM R 24755	19 km E Marion Bay, SA	11	35 13 S	137 05 E
	ABTC 56397	SAM R 24756	33 km SW Warooka, SA	11	35 08 S	137 06 E
	ABTC 56398	SAM R 24757	Inneston Ruins, SA	11	35 16 S	136 54 E
	ABTC 56413	SAM R 25422	Coffin Bay NP, SA	11	34 34 S	135 18 E
	ABTC 56414	SAM R 25702	7 km NW Nullarbor Stn., SA	12	31 25 S	130 49 46 E
	ABTC 56422	SAM R 26474	Eyre Peninsula, SA	11		
	ABTC 56444	SAM R 28457	Coffin Bay area, SA	11	34 38 S	135 28 E
	ABTC 56452	SAM R 29026	Lincoln NP, SA	11	34 50 S	135 50 E
	ABTC 56459	SAM R 31572	Wardang Island, SA	11	34 30 S	137 22 E
	ABTC 56464	SAM R 31599	Wardang Island, SA	11	34 30 S	137 22 E
	ABTC 56479	SAM R 31698	24 km W Stenhouse Bay, SA	11	35 11 S	136 54 E
	ABTC 56797	SAM R 36588	4 km E Hincks CP, SA	13	33 51 S	136 12 E
	ABTC 57104	SAM R 38193	2 km E Koppio, SA	11	34 26 S	135 53 E
	Unregistered	SAM R 57076	Tumby Bay, SA	14	34 23 S	136 06 E
	Unregistered	SAM R 56771	1 km W Inneston, SA	11	35 16 41 S	136 53 25 E

Species	Tissue Number	Specimen Number	Collection Locality	mtDNA Haplotype Number	Latitude	Longitude
Pseudonaja modesta	ABTC 479	SAM R 35874	1 km S Hamilton homestead, SA	15	26 44 S	135 04 E
	ABTC 9167	SAM R 42921	142 km E Windorah, QLD	16	26 10 S	143 29 E
	ABTC 31967		Longreach, QLD	16	23 28 S	144 14 E
	ABTC 41340		134 km ENE Laverton, WA	17	28 44 S	122 29 E
	ABTC 56329	SAM R 20859	Olympic Dam, Roxby Downs, SA	18	30 27 S	136 53 E
	ABTC 56391	SAM R 24656	7 km N King Lookout, SA	19	26 53 S	140 36 E
	ABTC 56432	SAM R 29347	Wooramel homestead, WA	20	25 44 S	114 18 E
	ABTC 58520	SAM R 48586	5 km NNE Mt. Cheesman, SA	21	27 22 01 S	130 21 06 E
	ABTC 64356	SAM R 31930	8 km W Pinjarra Dam, Yumbarra, SA	18	32 08 41 S	134 43 51 E
	ABTC 75149	WAM R 96631	Lochada homestead, WA	22	29 12 00 S	116 33 00 E
	ABTC 75155	WAM R 117097	Carey Downs Stn., WA	20	25 37 00 S	115 28 00 E
	ABTC 75167	WAM R 138971	West Angelas, WA	23	23 11 46 S	118 31 10 E
	EBU 6428	AM R 155038	Wanaaring, NSW	24	29 41 59 S	144 08 35 E
Pseudonaja nuchalis 'Darwin'	ABTC 13468		Arnhem Highway, NT	25	12 42 S	131 25 E
	ABTC 29603	NTM R 21673	Palmerston Woodroofe, NT	26	12 28 S	130 58 E
	ABTC 32072		Nardoo Stn., QLD	27	27 47 S	145 52 E
	ABTC 56264	NTM R 10685	40 km S Howard Springs, NT	25	12 30 S	131 04 E
	ABTC 56360	SAM R 22291	Unknown	25		
	Unregistered	(Alcohol no. D 3499)	Kakadu, NT	28	12 52 S	132 45 E
	Unregistered	SAM R 56772	Darwin, NT	25	12 27 S	130 50 E
	Unregistered	SAM R 56773	Darwin, NT	25	12 27 S	130 50 E
	Unregistered	SAM R 56774	Darwin, NT	25	12 27 S	130 50 E
	Unregistered	SAM R 56775	Darwin, NT	28	12 27 S	130 50 E
Pseudonaja nuchalis 'Pale/black headed'	ABTC 30295	NTM R 18321	118 km N Three Ways, NT	29	18 25 66 S	133 51 21 E

Species	Tissue Number	Specimen Number	Collection Locality	mtDNA Haplotype Number	Latitude	Longitude
	ABTC 35983	SAM R 46920	3 km W Top Camp Well, SA	30	26 27 39 S	134 55 37 E
	ABTC 42334	SAM R 51516	4 km E Indulkana, SA	31	26 57 55 S	133 20 59 E
	ABTC 42400	SAM R 51591	11 km WSW Mimili, SA	32	27 01 36 S	132 36 08 E
	ABTC 42401	SAM R 51592	11 km E Mimili, SA	33	26 59 33 S	132 48 48 E
	ABTC 56330	SAM R 20981	Olympic Dam, Roxby Downs, SA	34	30 22 S	136 56 E
	ABTC 56336	SAM R 21025	Olympic Dam, Roxby Downs, SA	35	30 43 S	136 53 E
	ABTC 56347	SAM R 21413	7 km NE Innamincka, SA	35	27 40 S	140 48 E
	ABTC 56348	SAM R 21414	Lake Everard Stn., SA	36	31 40 S	135 10 E
	ABTC 56349	SAM R 21415	Olympic Dam, Roxby Downs, SA	35	30 22 S	136 56 E
	ABTC 56404	SAM R 24821	Whyalla, SA	35	33 02 S	137 35 E
	ABTC 56430	SAM R 29288	Near Carnarvon, WA	37	24 53 S	113 40 E
	ABTC 56433	SAM R 29360	Hamelin homestead, WA	38	26 26 S	114 11 E
	ABTC 56434	SAM R 29407	1 km S Drummond, WA	38	28 40 S	114 36 E
	ABTC 56447	SAM R 28531	68 km E Mullewa, WA	39	28 26 S	116 11 E
	ABTC 56906	SAM R 36953	Roxby Downs, SA	40	30 23 S	136 51 E
	ABTC 56907	SAM R 36954	Roxby Downs, SA	40	30 23 S	136 51 E
	ABTC 57660	SAM R 42333	Balcanoona Creek, SA	35	30 32 S	139 18 E
	ABTC 75173	WAM R 102045	Karratha, WA	41	32 30 S	118 43 00 E
	ABTC 75175	WAM R 103848	Geraldton, WA	38	28 46 00 S	114 37 00 E
	ABTC 75176	WAM R 103849	Ballidu, WA	42	30 36 00 S	116 46 00 E
	ABTC 75180	WAM R 103923	Captive bred	43		
	ABTC 75181	WAM R 103924	Captive bred	43		
	ABTC 75183	WAM R 104187	Woodstock, WA	44	21 36 34 S	118 59 16 E
	ABTC 75188	WAM R 114659	24 km E Mt. Michael, WA	38	28 46 00 S	115 12 00 E
	ABTC 75190	WAM R 114661	Buller River, WA	38	28 52 00 S	114 37 00 E
	ABTC 75192	WAM R 114663	Buller River, WA	38	28 52 00 S	114 37 00 E

Species	Tissue Number	Specimen Number	Collection Locality	mtDNA Haplotype Number	Latitude	Longitude
	ABTC 75193	WAM R 115021	Utakarra, Geraldton, WA	38	28 47 00 S	114 39 00 E
	ABTC 75194	WAM R 115062	Utakarra, Geraldton, WA	38	28 47 00 S	114 39 00 E
	ABTC 75195	WAM R 115063	Rangeview, WA	38	28 46 00 S	114 37 00 E
	ABTC 75196	WAM R 115180	Sunset Beach, Geraldton, WA	45	28 43 30 S	114 37 30 E
	ABTC 75197	WAM R 115182	Spalding Park, Geraldton, WA	38	28 39 00 S	114 38 00 E
	ABTC 75198	WAM R 115183	Spalding Park, Geraldton, WA	38	28 39 00 S	114 38 00 E
	ABTC 75199	WAM R 115276	Greenough, WA	38	28 57 00 S	114 44 00 E
	ABTC 75200	WAM R 115607	Webberton, Geraldton, WA	38	28 46 00 S	114 37 00 E
	ABTC 75201	WAM R 115608	Sunset Beach, Geraldton, WA	38	28 46 00 S	114 37 00 E
	ABTC 75202	WAM R 115609	Mt. Scott, Geraldton, WA	38	28 46 00 S	114 37 00 E
	ABTC 75203	WAM R 115610	Karloo, Geraldton, WA	38	28 46 00 S	114 37 00 E
	ABTC 75205	WAM R 115751	Sunset Beach, Geraldton, WA	38	28 46 00 S	114 37 00 E
	ABTC 75206	WAM R 115752	Rangeway, Geraldton, WA	38	28 46 00 S	114 37 00 E
	ABTC 75211	WAM R 116498	Geraldton area	38	28 46 00 S	114 37 00 E
	ABTC 75216	WAM R 119293	Geraldton area	38	28 46 00 S	114 37 00 E
	ABTC 75218	WAM R 119526	Geraldton area	38	28 46 00 S	114 37 00 E
	EBU 6616	AM R 150262	Mootwingee NP, NSW	35	31 17 S	142 18 E
	Unregistered	SAM R 56714	Alice Springs, NT	46	23 42 S	133 52 E
	Unregistered	SAM R 56715	Alice Springs, NT	47	23 42 S	133 52 E
	Unregistered	SAM R 56716	Alice Springs, NT	48	23 42 S	133 52 E
	Unregistered	SAM R 56719	Alice Springs, NT	48	23 42 S	133 52 E
	Unregistered	SAM R 56720	Alice Springs, NT	48	23 42 S	133 52 E
	Unregistered	SAM R 56722	Alice Springs, NT	49	23 42 S	133 52 E
	Unregistered	SAM R 56723	Alice Springs, NT	50	23 42 S	133 52 E
	Unregistered	SAM R 56725	Alice Springs, NT	51	23 42 S	133 52 E

Species	Tissue Number	Specimen Number	Collection Locality	mtDNA Haplotype Number	Latitude	Longitude
Pseudonaja nuchalis 'Southern'	ABTC 755	SAM R 40497	Beltana Ruins, SA	52	30 49 S	138 25 E
	ABTC 13179	SAM R 49359	30 km SW Lake Harry Ruins, SA	53	29 36 00 S	138 07 00 E
	ABTC 35596	SAM R 46467	14 km SSW Beresford Bore, SA	54	29 22 17 S	136 37 25 E
	ABTC 56268	SAM R 18598	10 km S Marree	55	29 44 S	138 06 E
	ABTC 56269	SAM R 18599	10 km SW Port Augusta, SA	56	32 31 S	137 37 E
	ABTC 56270	SAM R 18600	Snake Creek Bore, SA	53	27 04 S	136 03 E
	ABTC 56280	SAM R 18994	Whyalla, SA	57	33 02 S	137 35 E
	ABTC 56342	SAM R 21163	Middleback Stn., SA	57	32 57 S	137 23 E
	ABTC 56354	SAM R 21432	Weeroona Island, 8 km N Port Pirie, SA	58	33 08 S	138 01 E
	ABTC 56355	SAM R 21433	Port Germein Gorge, SA	58	33 01 S	138 00 E
	ABTC 56356	SAM R 21434	Port Germein Gorge, SA	58	33 01 S	138 00 E
	ABTC 56357	SAM R 21435	Port Germein Gorge, SA	58	33 01 S	138 00 E
	ABTC 56361	SAM R 22545	Telowie beach, SA	58	33 03 S	138 04 E
	ABTC 56363	SAM R 22746	Cungena, SA	56	32 35 S	134 43 E
	ABTC 56389	SAM R 24410	Eba Island CP, SA	56	32 41 S	134 16 E
	ABTC 56390	SAM R 24411	Eba Island CP, SA	56	32 41 S	134 16 E
	ABTC 56399	SAM R 24778	Baroota Reservoir, SA	58	32 55 S	138 04 E
	ABTC 56405	SAM R 24828	Oraparinna homestead, SA	59	31 22 S	138 43 E
	ABTC 56406	SAM R 25058	Morgan CP, SA	60	34 03 S	139 41 E
	ABTC 56410	SAM R 25295	Cooltong Dam, SA	61	34 12 30 S	140 38 E
	ABTC 56449	SAM R 28559	Lake Gilles Tanks, SA	11	32 38 S	136 53 E
	ABTC 56471	SAM R 31690	100 km S William Creek, SA	52	29 29 S	137 12 E
	ABTC 56472	SAM R 31691	Near Roopena Stn., SA	57	32 49 S	137 23 E
	ABTC 56703	SAM R 36306	Roxby Downs, SA	62	30 23 S	136 51 E
	ABTC 56721	SAM R 36352	Near Cooper Creek Ferry Crossing, SA	63	28 35 S	138 49 E
	ABTC 57459	SAM R 40758	Stirling North, SA	64	32 29 S	137 50 E

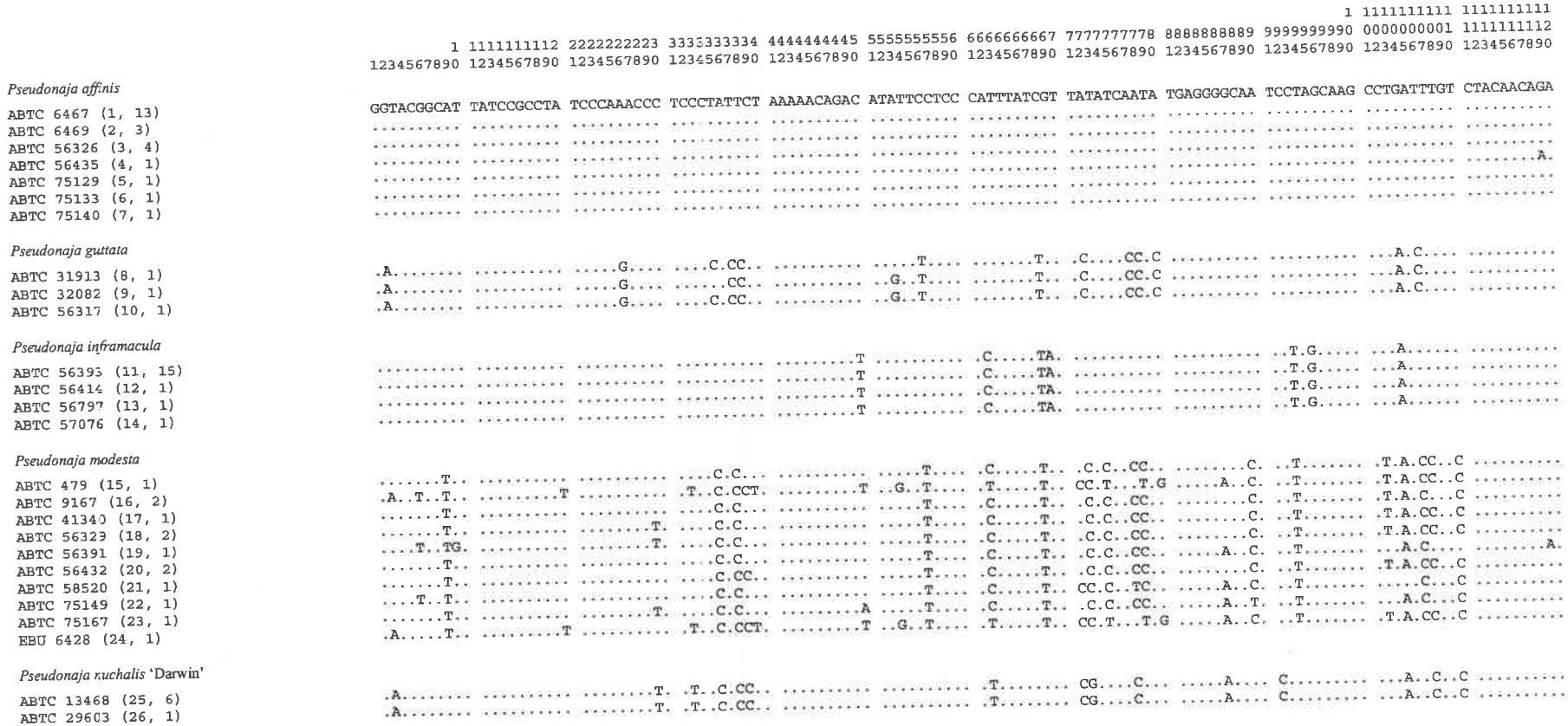
Species	Tissue Number	Specimen Number	Collection Locality	mtDNA Haplotype Number	Latitude	Longitude
	ABTC 57460	SAM R 40759	Stirling North, SA	59	32 29 S	137 50 E
	ABTC 57671	SAM R 42409	Venus Bay CP, SA	56	33 14 S	134 38 E
	ABTC 57672	SAM R 42410	Venus Bay CP, SA	64	33 14 S	134 38 E
	ABTC 57779	SAM R 43080	3 km SW Whyalla, SA	57	33 03 S	137 31 E
	ABTC 58369	SAM R 46513	2 km W Penong, SA	65	31 55 S	132 59 E
	EBU 33712	AM R 157294	Collaroy Stn., 10 km NW Hermidale, NSW	66	31 28 S	146 39 E
	EBU 33714	AM R 157295	Collaroy Stn., 10 km NW Hermidale, NSW	56	31 28 S	146 39 E
Pseudonaja textilis	ABTC 8920	SAM R 42663	Bedourie to Boulia, QLD	67	24 01 S	139 33 E
	ABTC 31930		26 km S Clermont, QLD	68	22 49 S	147 38 E
	ABTC 56274	SAM R 18605	10 km E Mannum, SA	69	34 53 S	139 30 E
	ABTC 56312	SAM R 19943	Goyder Lagoon, SA	70	26 46 S	139 08 E
	ABTC 56407	SAM R 25070	Richman Valley, SA	71	32 24 S	138 03 E
	ABTC 56473	SAM R 31692	Innamincka, SA	72	27 44 S	140 46 E
	ABTC 56478	SAM R 31697	Point Pearce, SA	73	34 25 S	137 29 E
	ABTC 56482	SAM R 31701	Near Point Pearce, SA	73	34 25 S	137 30 E
	ABTC 65504	AM R 147652	Merauke, Irian Jaya	74	8 30 S	140 30 E
	ABTC 65511	AM R 147659	Merauke, Irian Jaya	74	8 30 S	140 30 E
	EBU 3930	AM R 141106	Buddigower NR, NSW	75	34 03 S	147 01 45 E
	EBU 4988	AM R 142766	Mandurama, NSW	76	33 38 S	149 07 45 E
	EBU 4997	AM R 142827	Near Narromine, NSW	77	32 07 S	148 06 45 E
	EBU 6247	AM R 149264	2 km N Nyngan, NSW	77	31 32 S	147 11 E
	EBU 6463	AM R 148735	Scotts Head, NSW	78	30 45 S	153 00 45 E
	EBU 7401	AM R 151551	Mullaley area, NSW	76	31 03 S	150 02 E
	EBU 7566	AM R 153025	North Ballina, NSW	79	28 50 S	153 31 E
	EBU 7570	AM R 153008	Alstonville, NSW	79	28 50 S	153 26 E

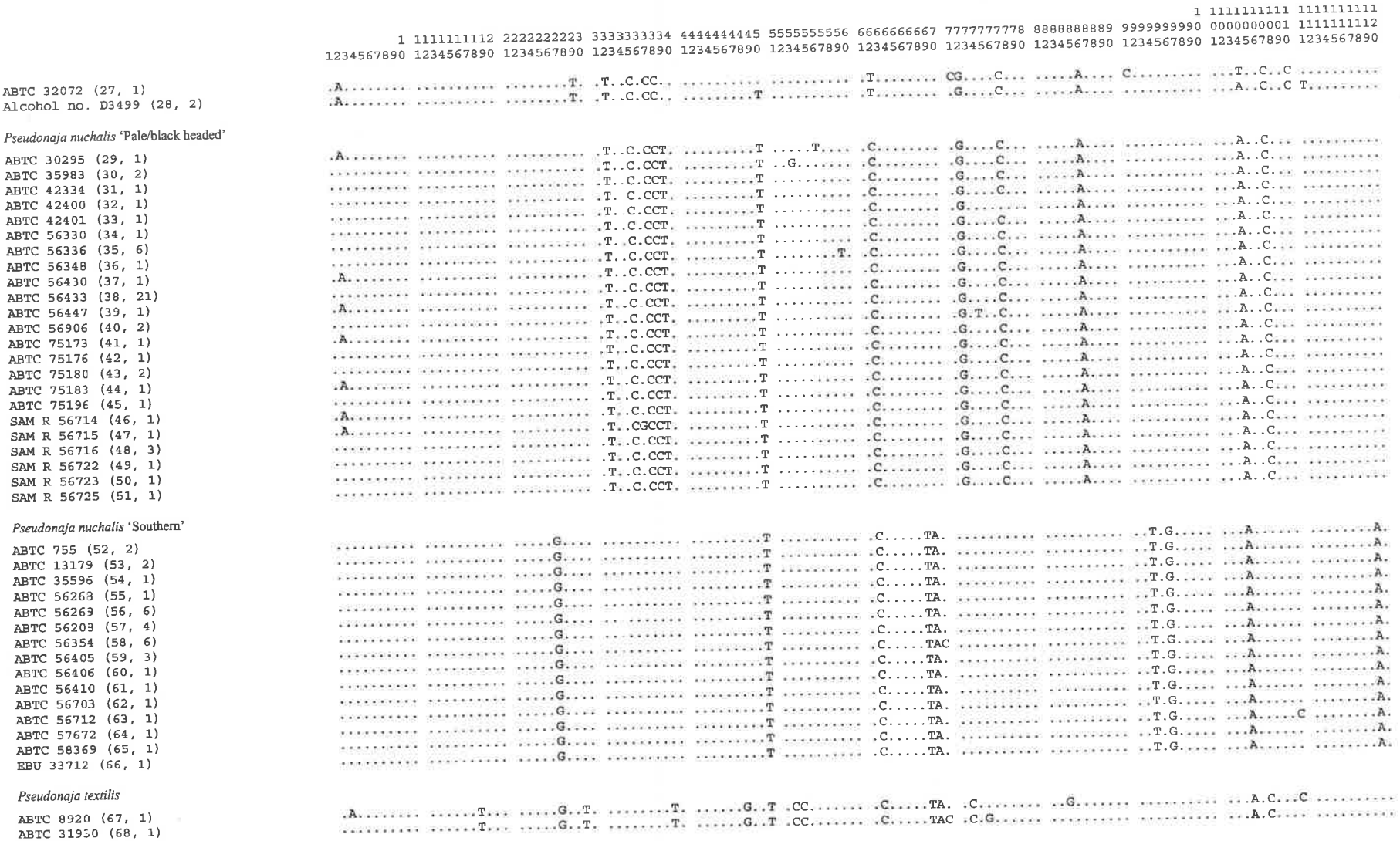
Species	Tissue Number	Specimen Number	Collection Locality	mtDNA Haplotype Number	Latitude	Longitude
	EBU 7575	AM R 151570	200 km S Tibooburra, NSW	80	30 58 S	141 48 33 E
	EBU 7690	AM R 151699	Near Mootwingee NP, NSW	81	31 21 30 S	141 59 33 E
	EBU 31287		Bendemeer Stn., NSW	76	30 18 S	146 13 E
	EBU 31801	AM R 152279	Mullaley, NSW	82	31 06 S	149 55 E
	EBU 31802	AM R 152280	Mullaley area, NSW	76	31 03 S	150 02 E
	EBU 31803	AM R 152281	Mullaley area, NSW	82	31 16 S	149 50 E
	EBU 31804	AM R 152282	Mullaley, NSW	83	31 03 S	149 55 E
	EBU 31926	AM R 152761	2 km E Bangalow, NSW	79	28 40 52 S	153 32 E
	EBU 31943	AM R 152790	Coopers Chute, NSW (?)	79		
	EBU 33253	AM R 156908	11 km W Glen Innes	76	29 43 S	151 38 E
	EBU 33262	AM R 156942	Mullumbimby Creek, NSW	79	28 32 S	153 28 E
	EBU 33751	AM R 157781	Goonengerry, NSW	79	28 35 45 S	153 25 E
	EBU 33794	AM R 158564	Griffith, NSW	84	34 17 S	146 02 E
	Unregistered	(Alcohol no. QQ 402)	Near Biloela, QLD	79	24 25 04 S	150 25 58 E
	Unregistered	(Alcohol no. QQ 478)	North QLD	85		
	Unregistered	(Alcohol no. QQ 632)	Near Malanda, QLD	86	17 24 03 S	145 31 18 E
	Unregistered	(Alcohol no. QQ 723)	Charters Towers, QLD	87	20 06 32 S	146 14 40 E
	Unregistered	SAM R 56724	Alice Springs, NT	88	23 42 S	133 52 E
	Unregistered	SAM R 56770	4 km W Minlaton, SA	89	34 40 S	137 42 45 E
Oxyuranus microlepidotus	ABTC 56237	SAM R 20583	Goyder Lagoon, SA		26 46 S	139 08 E
	ABTC 58708	SAM R 49883	20 km NE Coober Pedy, SA		28 51 S	134 53 E
Oxyuranus scutellatus	ABTC 29118	NTM R 17009	Bathurst Island, NT		16 02 S	123 32 E
	ABTC 32087		Mt Ossa, QLD		20 58 S	148 50 E
	ABTC 44040	AM R 119562	Port Moresby, PNG		9 30 S	147 07 E

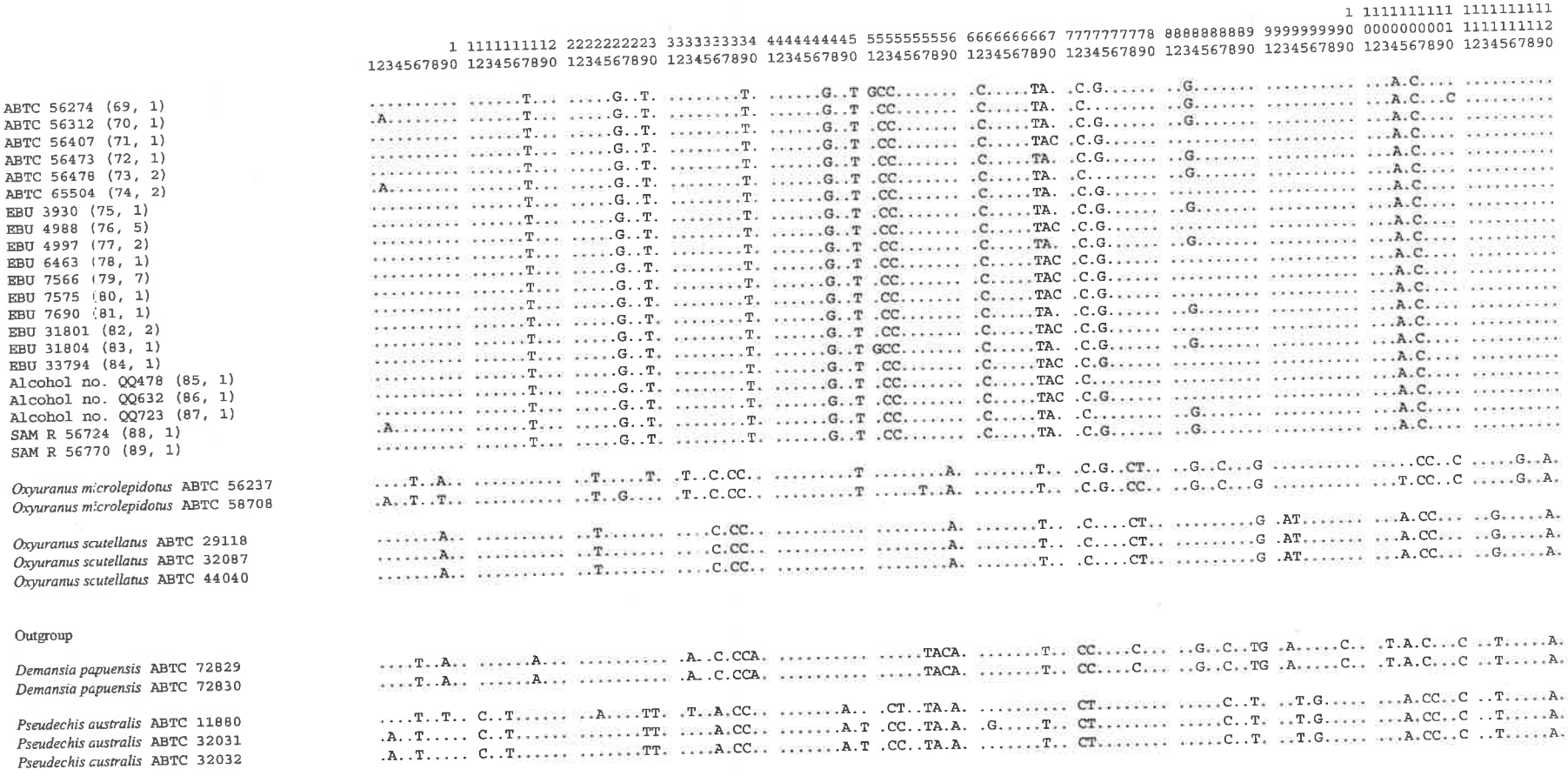
Species	Tissue Number	Specimen Number	Collection Locality	mtDNA Haplotype Number	Latitude	Longitude
Outgroup						
Demansia papuensis	ABTC 72829	SAM R 54427	13 km ENE Karumba turnoff, QLD		17 25 28 S	141 18 11 E
	ABTC 72830	SAM R 54397	41 km ENE Karumba turnoff, QLD		17 18 46 S	141 31 21 E
Pseudechis australis	ABTC 11880	SAM R 34179	46 km SW Borroloola, NT		16 21 S	136 05 E
	ABTC 32031		Ban Ban Stn., QLD		24 07 S	143 42 E
	ABTC 32032		Arrilalah, QLD		23 41 S	143 53 E

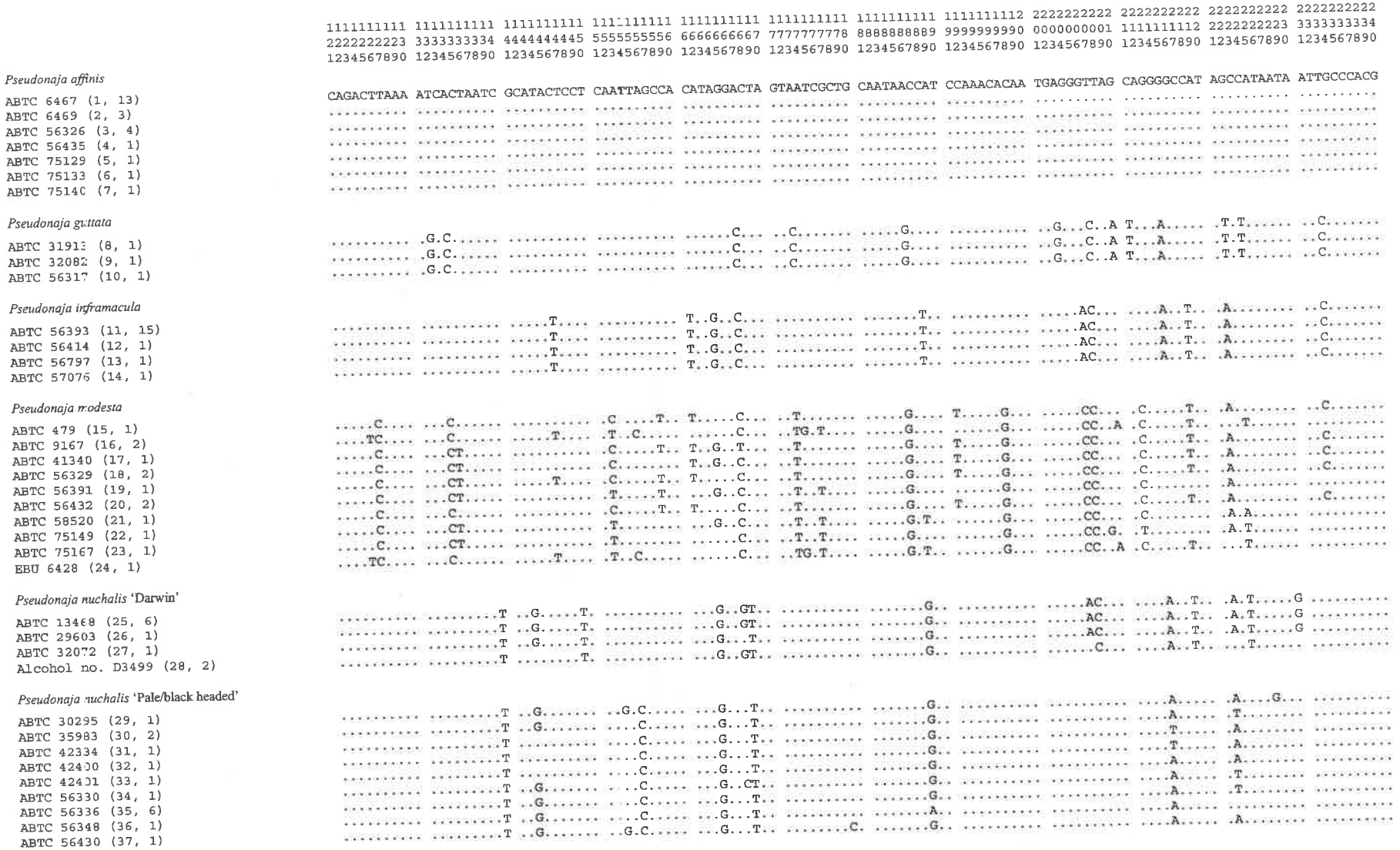
Appendix 2

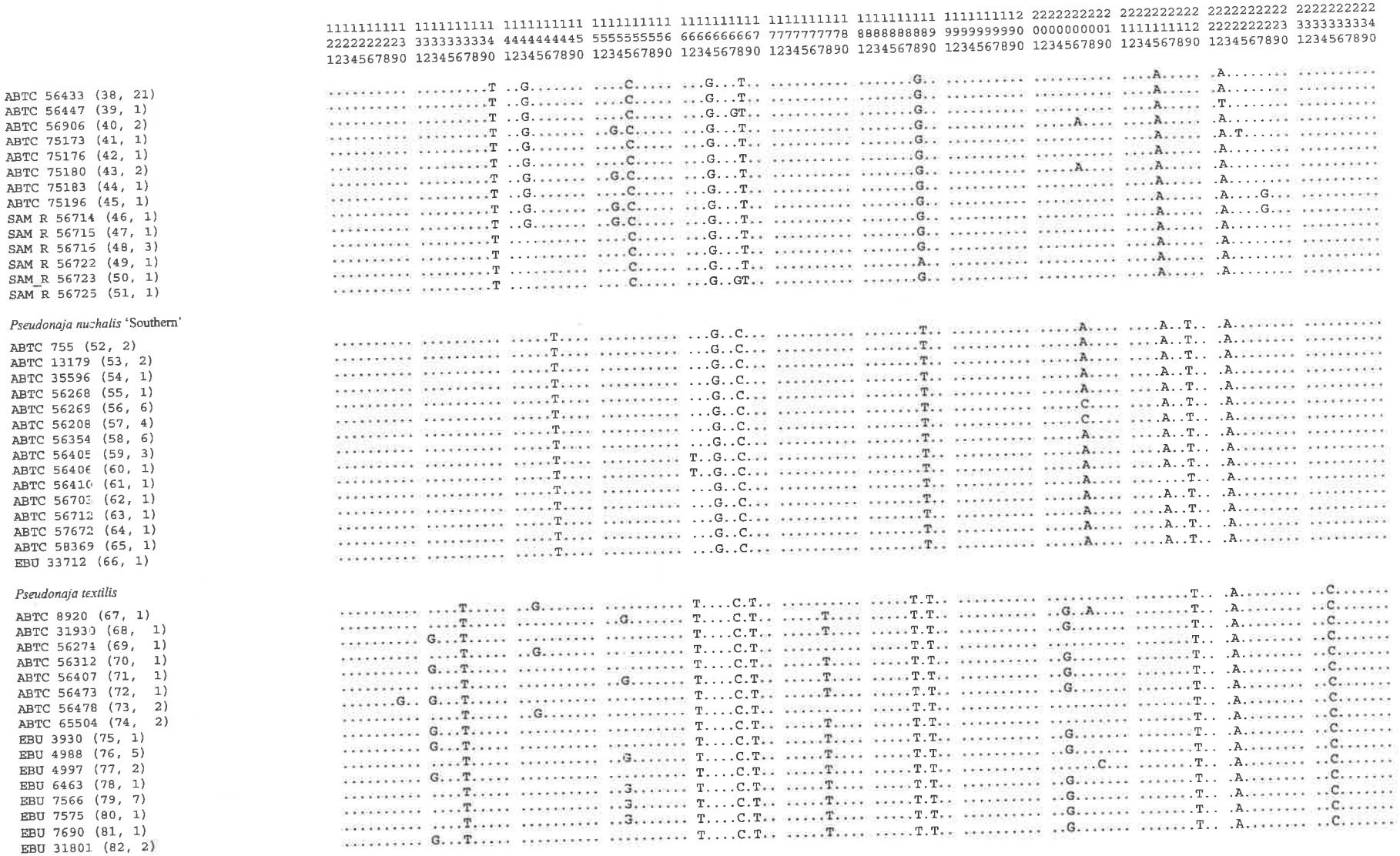
Mitochondrial DNA sequence data. ABTC numbers are followed by a haplotype number and the number of individuals for which that haplotpype was observed. Haplotype numbers correspond to those in Appendix 1.

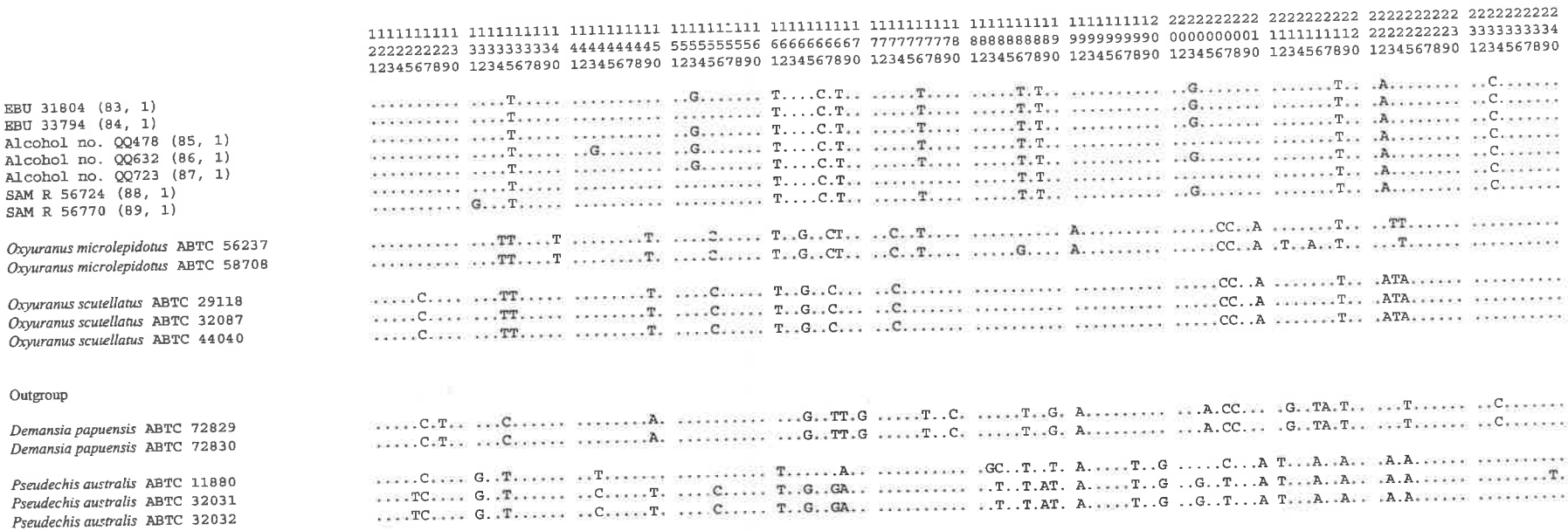


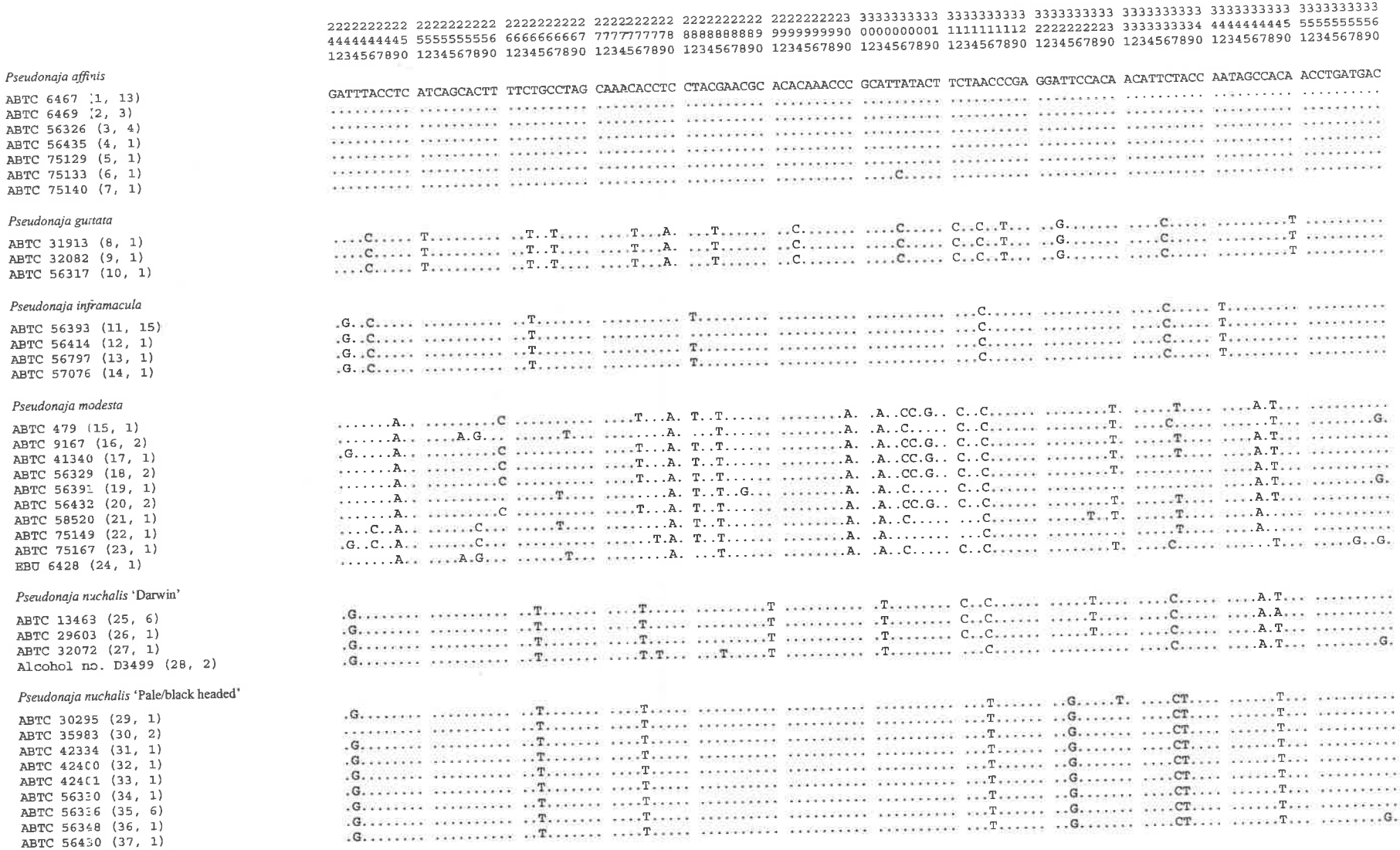

1 1111111112 2222222223 3333333334 4444444445 5555555556 6666666667 7777777778 8888888889 9999999990 0000000001 1111111112
1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890
1 1111111111 1111111111
ABTC 32072 (27, 1)
Alcohol no. D3499 (28, 2)
Pseudonaja nuchalis 'Pale/black headed'
ABTC 30295 (29, 1)
ABTC 35983 (30, 2)
ABTC 42334 (31, 1)
ABTC 42400 (32, 1)
ABTC 42401 (33, 1)
ABTC 56330 (34, 1)
ABTC 56336 (35, 6)
ABTC 56348 (36, 1)
ABTC 56430 (37, 1)
ABTC 56433 (38, 21)
ABTC 56447 (39, 1)
ABTC 56906 (40, 2)
ABTC 75173 (41, 1)
ABTC 75176 (42, 1)
ABTC 75180 (43, 2)
ABTC 75183 (44, 1)
ABTC 75196 (45, 1)
SAM R 56714 (46, 1)
SAM R 56715 (47, 1)
SAM R 56716 (48, 3)
SAM R 56722 (49, 1)
SAM R 56723 (50, 1)
SAM R 56725 (51, 1)
Pseudonaja nuchalis 'Southern'
ABTC 755 (52, 2)
ABTC 13179 (53, 2)
ABTC 35596 (54, 1)
ABTC 56263 (55, 1)
ABTC 56269 (56, 6)
ABTC 56209 (57, 4)
ABTC 56354 (58, 6)
ABTC 56405 (59, 3)
ABTC 56406 (60, 1)
ABTC 56410 (61, 1)
ABTC 56703 (62, 1)
ABTC 56712 (63, 1)
ABTC 57672 (64, 1)
ABTC 58369 (65, 1)
EBU 33712 (66, 1)
Pseudonaja textilis
ABTC 8920 (67, 1)
ABTC 31950 (68, 1)

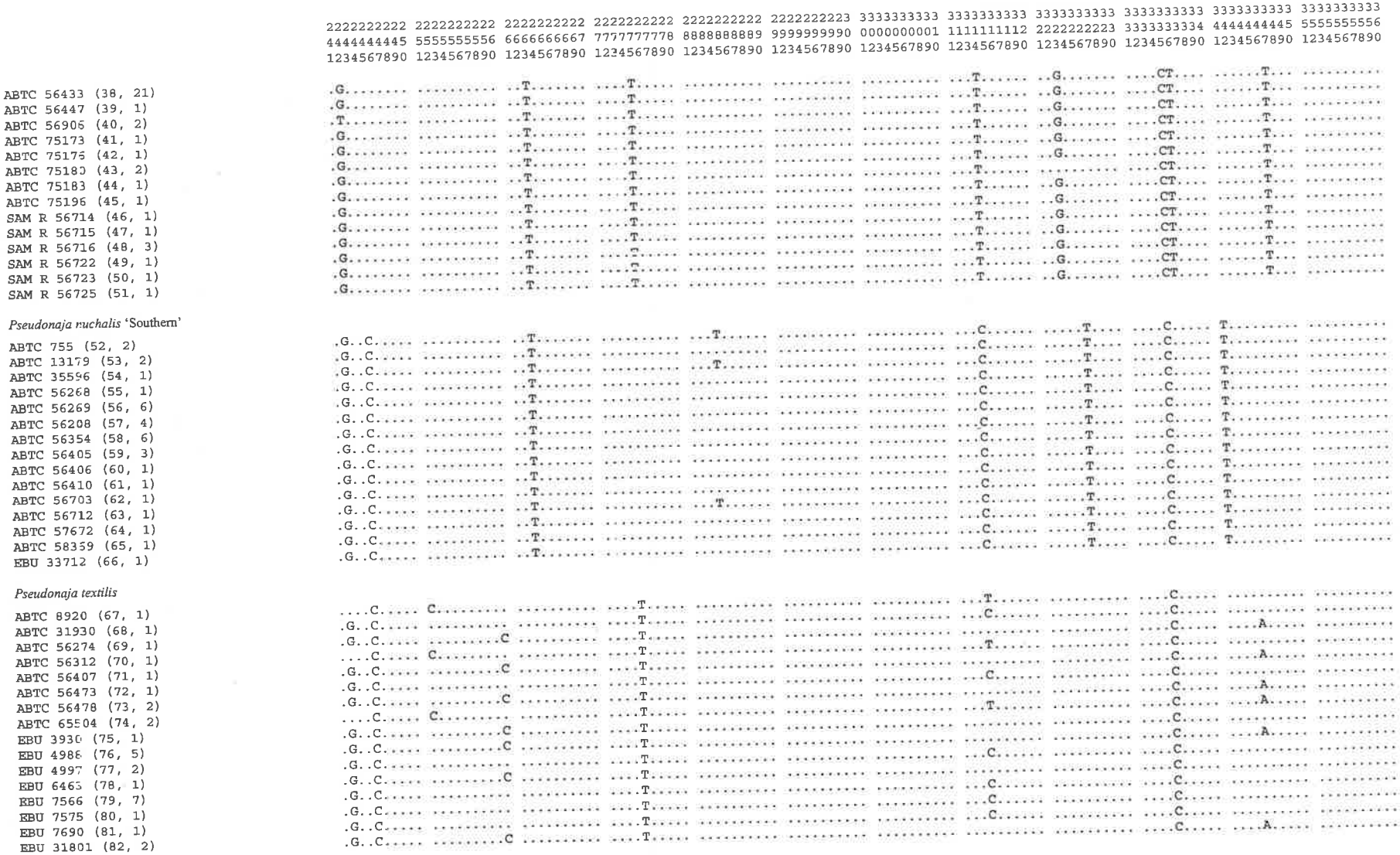

1 1111111112 2222222223 3333333334 4444444445 5555555556 6666666667 7777777778 8888888889 9999999990 0000000001 1111111112
1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890
ABTC 56274 (69, 1)
ABTC 56312 (70, 1)
ABTC 56407 (71, 1)
ABTC 56473 (72, 1)
ABTC 56478 (73, 2)
ABTC 65504 (74, 2)
EBU 3930 (75, 1)
EBU 4988 (76, 5)
EBU 4997 (77, 2)
EBU 6463 (78, 1)
EBU 7566 (79, 7)
EBU 7575 (80, 1)
EBU 7690 (81, 1)
EBU 31801 (82, 2)
EBU 31804 (83, 1)
EBU 33794 (84, 1)
Alcohol no. QQ478 (85, 1)
Alcohol no. QQ632 (86, 1)
Alcohol no. QQ723 (87, 1)
SAM R 56724 (88, 1)
SAM R 56770 (89, 1)
Oxyuranus microlepidotus ABTC 56237
Oxyuranus microlepidotus ABTC 58708
Oxyuranus scutellatus ABTC 29118
Oxyuranus scutellatus ABTC 32087
Oxyuranus scutellatus ABTC 44040
Outgroup
Demansia papuensis ABTC 72829
Demansia papuensis ABTC 72830
Pseudechis australis ABTC 11880
Pseudechis australis ABTC 32031
Pseudechis australis ABTC 32032

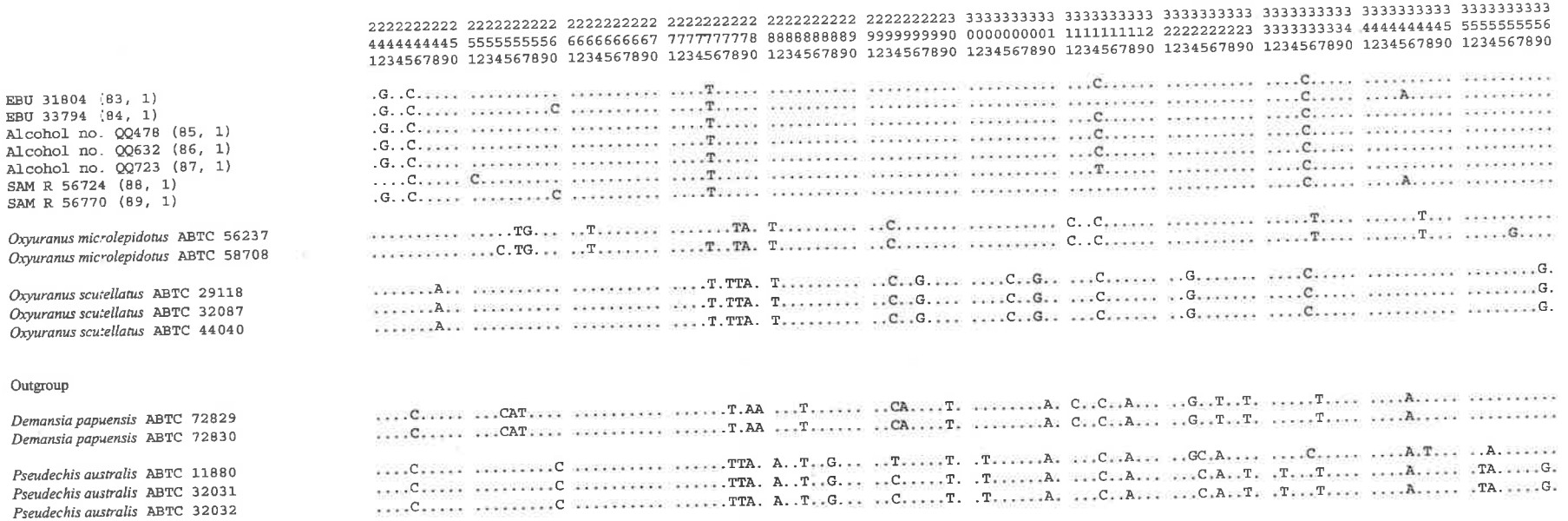

1111111111 1111111111 1111111111 1111111111 1111111111 1111111111 1111111111 1111111112 2222222222 2222222222 2222222222 2222222222
2222222223 3333333334 4444444445 5555555556 6666666667 7777777778 8888888889 9999999990 0000000001 1111111112 2222222223 3333333334
1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890
CAGACTTAAA ATCACTAATC GCATACTCCT CAATTAGCCA CATAGGACTA GTAATCGCTG CAATAACCAT CCAAACACAA TGAGGGTTAG CAGGGGCCAT AGCCATAATA ATTGCCCACG
Pseudonaja affinis
ABTC 6467 (1, 13)
ABTC 6469 (2, 3)
ABTC 56326 (3, 4)
ABTC 56435 (4, 1)
ABTC 75129 (5, 1)
ABTC 75133 (6, 1)
ABTC 75140 (7, 1)
Pseudonaja guttata
ABTC 31913 (8, 1)
ABTC 32082 (9, 1)
ABTC 56317 (10, 1)
Pseudonaja inframacula
ABTC 56393 (11, 15)
ABTC 56414 (12, 1)
ABTC 56797 (13, 1)
ABTC 57076 (14, 1)
Pseudonaja modesta
ABTC 479 (15, 1)
ABTC 9167 (16, 2)
ABTC 41340 (17, 1)
ABTC 56329 (18, 2)
ABTC 56391 (19, 1)
ABTC 56432 (20, 2)
ABTC 58520 (21, 1)
ABTC 75149 (22, 1)
ABTC 75167 (23, 1)
EBU 6428 (24, 1)
Pseudonaja nuchalis 'Darwin'
ABTC 13468 (25, 6)
ABTC 29603 (26, 1)
ABTC 32072 (27, 1)
Alcohol no. D3499 (28, 2)
Pseudonaja nuchalis 'Pale/black headed'
ABTC 30295 (29, 1)
ABTC 35983 (30, 2)
ABTC 42334 (31, 1)
ABTC 42400 (32, 1)
ABTC 42401 (33, 1)
ABTC 56330 (34, 1)
ABTC 56336 (35, 6)
ABTC 56348 (36, 1)
ABTC 56430 (37, 1)

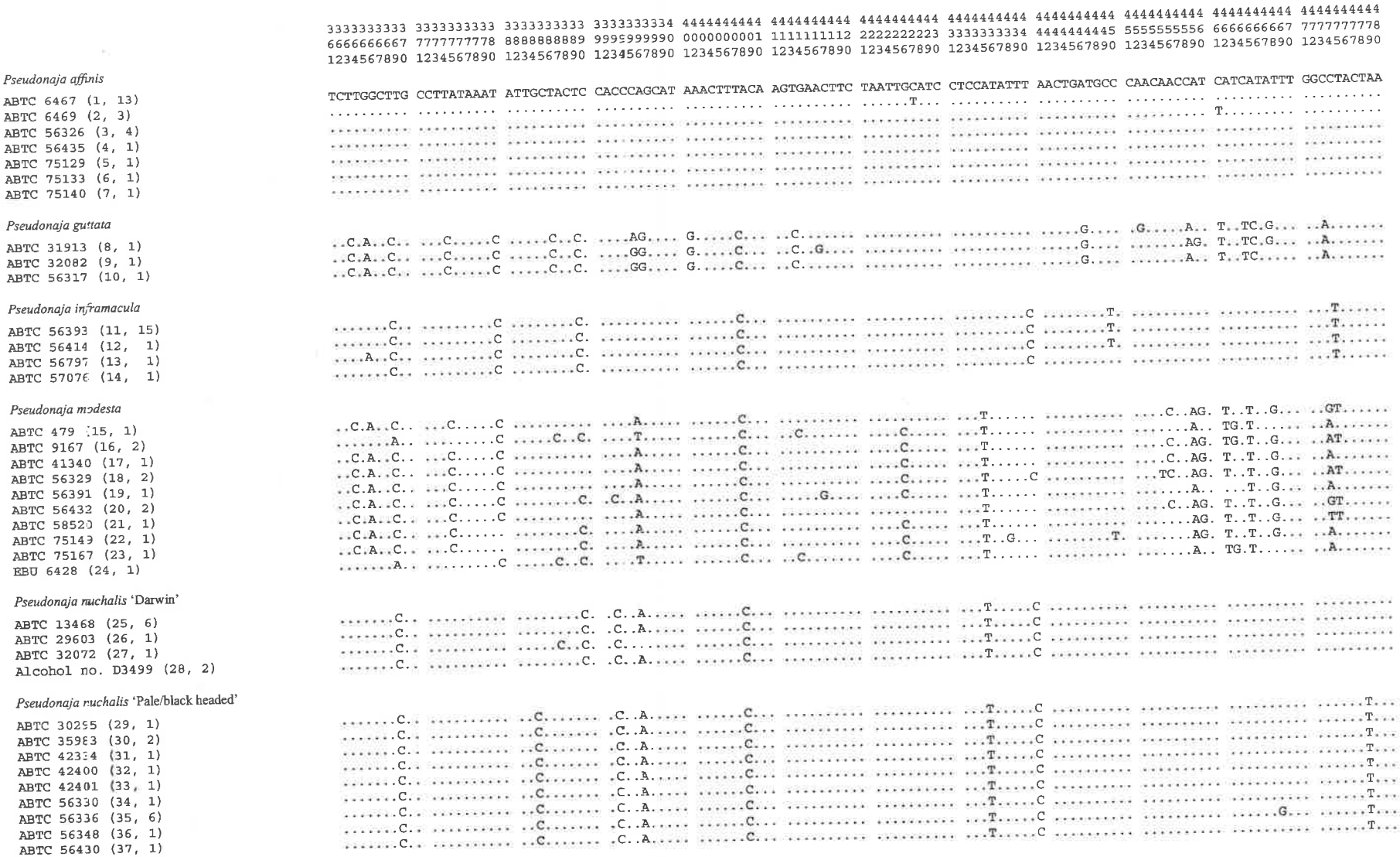

1111111111 1111111111 1111111111 1111111111 1111111111 1111111111 1111111111 1111111112 2222222222 2222222222 2222222222 2222222222
2222222223 3333333334 4444444445 5555555556 6666666667 7777777778 8888888889 9999999990 0000000001 1111111112 2222222223 3333333334
1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890
ABTC 56433 (38, 21)
ABTC 56447 (39, 1)
ABTC 56906 (40, 2)
ABTC 75173 (41, 1)
ABTC 75176 (42, 1)
ABTC 75180 (43, 2)
ABTC 75183 (44, 1)
ABTC 75196 (45, 1)
SAM R 56714 (46, 1)
SAM R 56715 (47, 1)
SAM R 56716 (48, 3)
SAM R 56722 (49, 1)
SAM_R 56723 (50, 1)
SAM R 56725 (51, 1)
Pseudonaja nuchalis 'Southern'
ABTC 755 (52, 2)
ABTC 13179 (53, 2)
ABTC 35596 (54, 1)
ABTC 56268 (55, 1)
ABTC 56269 (56, 6)
ABTC 56208 (57, 4)
ABTC 56354 (58, 6)
ABTC 56405 (59, 3)
ABTC 56406 (60, 1)
ABTC 56410 (61, 1)
ABTC 56703 (62, 1)
ABTC 56712 (63, 1)
ABTC 57672 (64, 1)
ABTC 58369 (65, 1)
EBU 33712 (66, 1)
Pseudonaja textilis
ABTC 8920 (67, 1)
ABTC 31930 (68, 1)
ABTC 56274 (69, 1)
ABTC 56312 (70, 1)
ABTC 56407 (71, 1)
ABTC 56473 (72, 1)
ABTC 56478 (73, 2)
ABTC 65504 (74, 2)
EBU 3930 (75, 1)
EBU 4988 (76, 5)
EBU 4997 (77, 2)
EBU 6463 (78, 1)
EBU 7566 (79, 7)
EBU 7575 (80, 1)
EBU 7690 (81, 1)
EBU 31801 (82, 2)

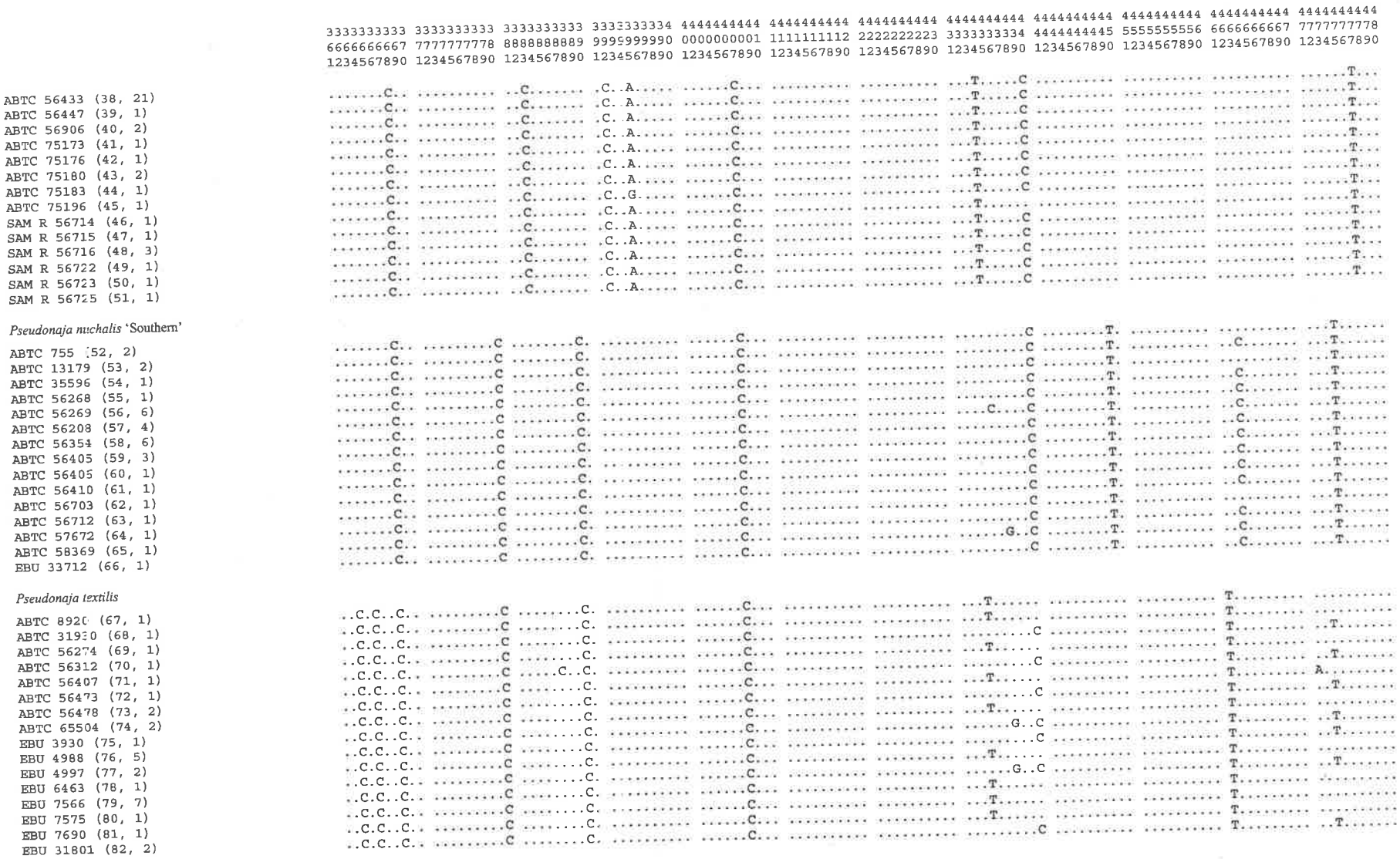

1111111111 1111111111 1111111111 1111111111 1111111111 1111111111 1111111111 1111111112 2222222222 2222222222 2222222222 2222222222
2222222223 3333333334 4444444445 5555555556 6666666667 7777777778 8888888889 9999999990 0000000001 1111111112 2222222223 3333333334
1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890
EBU 31804 (83, 1)
EBU 33794 (84, 1)
Alcohol no. QQ478 (85, 1)
Alcohol no. QQ632 (86, 1)
Alcohol no. QQ723 (87, 1)
SAM R 56724 (88, 1)
SAM R 56770 (89, 1)
Oxyuranus microlepidotus ABTC 56237
Oxyuranus microlepidotus ABTC 58708
Oxyuranus scutellatus ABTC 29118
Oxyuranus scutellatus ABTC 32087
Oxyuranus scutellatus ABTC 44040
Outgroup
Demansia papuensis ABTC 72829
Demansia papuensis ABTC 72830
Pseudechis australis ABTC 11880
Pseudechis australis ABTC 32031
Pseudechis australis ABTC 32032

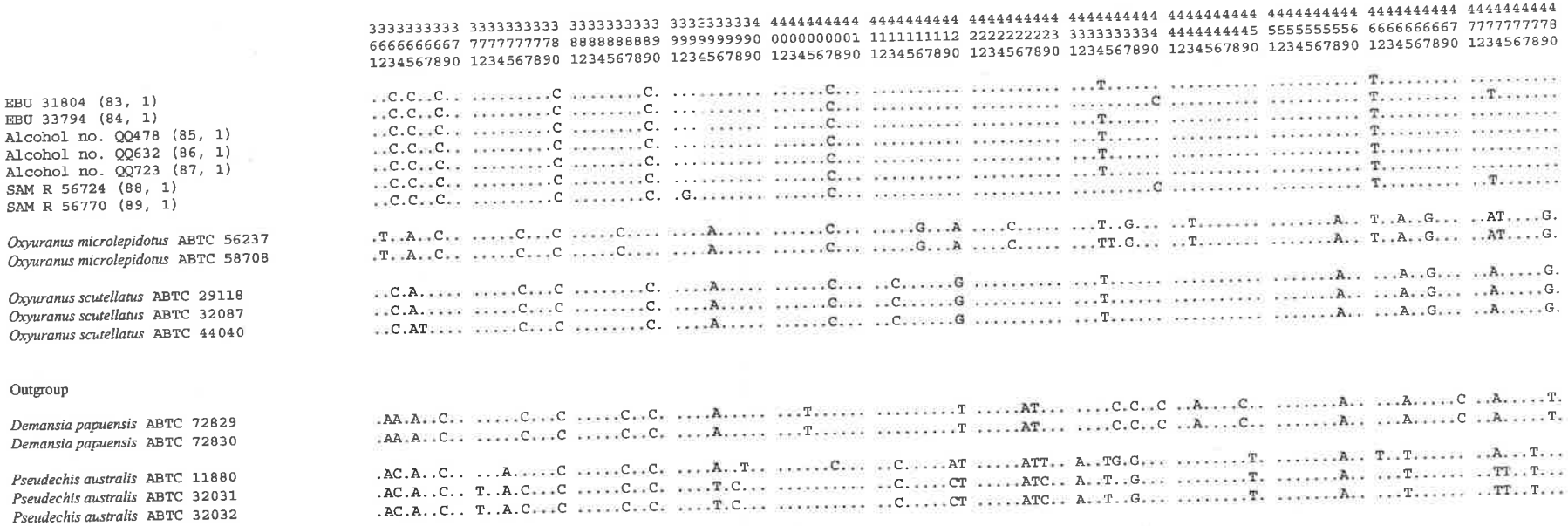

2222222222 2222222222 2222222222 2222222222 2222222222 2222222223 3333333333 3333333333 3333333333 3333333333 3333333333 3333333333
4444444445 5555555556 6666666667 7777777778 8888888889 9999999990 0000000001 1111111112 2222222223 3333333334 4444444445 5555555556
1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890
GATTTACCTC ATCAGCACTT TTCTGCCTAG CAAACACCTC CTACGAACGC ACACAAACCC GCATTATACT TCTAACCCGA GGATTCCACA ACATTCTACC AATAGCCACA ACCTGATGAC
Pseudonaja affinis
ABTC 6467 (1, 13)
ABTC 6469 (2, 3)
ABTC 56326 (3, 4)
ABTC 56435 (4, 1)
ABTC 75129 (5, 1)
ABTC 75133 (6, 1)
ABTC 75140 (7, 1)
Pseudonaja guttata
ABTC 31913 (8, 1)
ABTC 32082 (9, 1)
ABTC 56317 (10, 1)
Pseudonaja inframacula
ABTC 56393 (11, 15)
ABTC 56414 (12, 1)
ABTC 56797 (13, 1)
ABTC 57076 (14, 1)
Pseudonaja modesta
ABTC 479 (15, 1)
ABTC 9167 (16, 2)
ABTC 41340 (17, 1)
ABTC 56329 (18, 2)
ABTC 56391 (19, 1)
ABTC 56432 (20, 2)
ABTC 58520 (21, 1)
ABTC 75149 (22, 1)
ABTC 75167 (23, 1)
EBU 6428 (24, 1)
Pseudonaja nuchalis 'Darwin'
ABTC 13463 (25, 6)
ABTC 29603 (26, 1)
ABTC 32072 (27, 1)
Alcohol no. D3499 (28, 2)
Pseudonaja nuchalis 'Pale/black headed'
ABTC 30295 (29, 1)
ABTC 35983 (30, 2)
ABTC 42334 (31, 1)
ABTC 42400 (32, 1)
ABTC 42401 (33, 1)
ABTC 56330 (34, 1)
ABTC 56336 (35, 6)
ABTC 56348 (36, 1)
ABTC 56430 (37, 1)

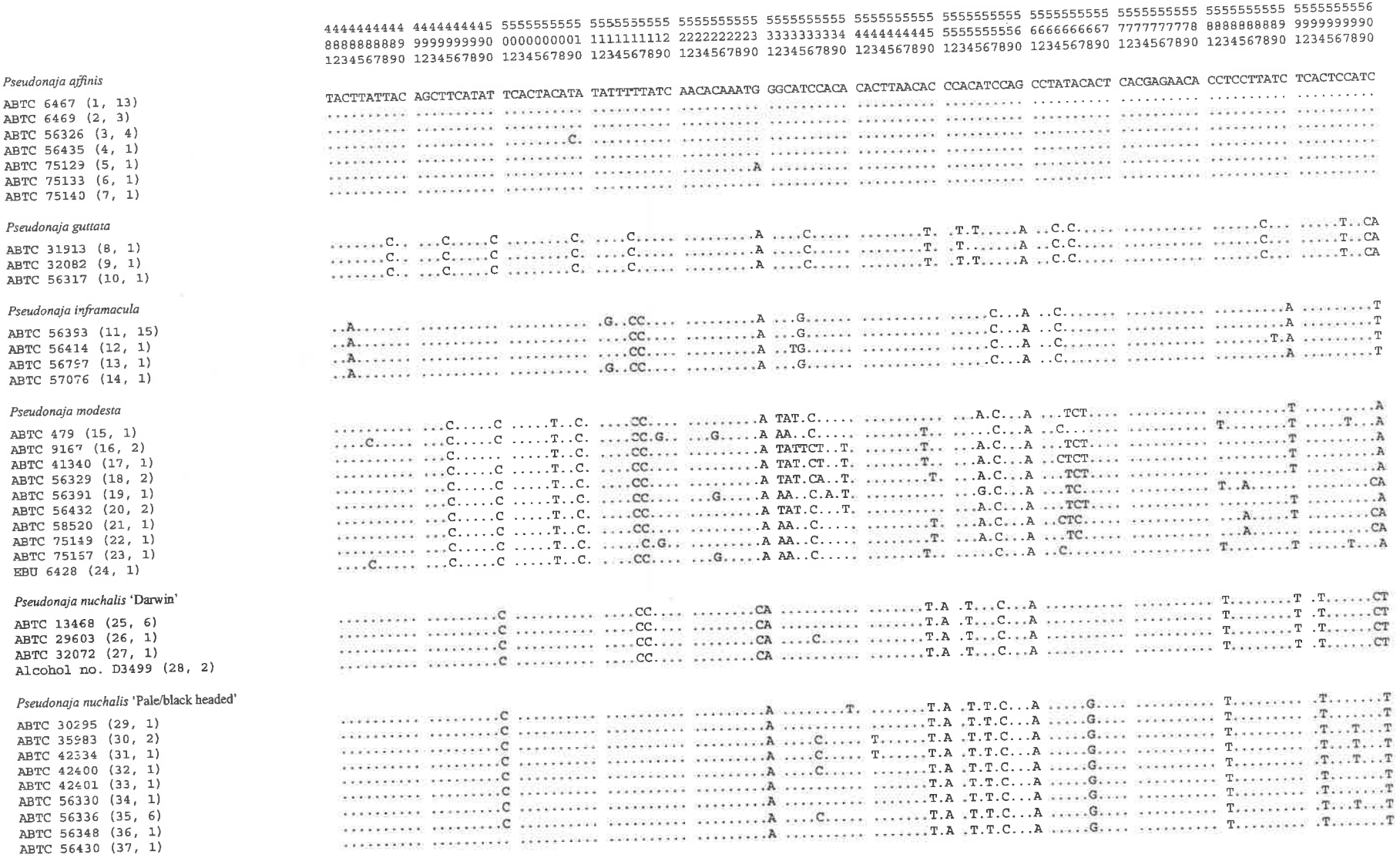

2222222222 2222222222 2222222222 2222222222 2222222222 2222222223 3333333333 3333333333 3333333333 3333333333 3333333333 3333333333
4444444445 5555555556 6666666667 7777777778 8888888889 9999999990 0000000001 1111111112 2222222223 3333333334 4444444445 5555555556
1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890
ABTC 56433 (38, 21)
ABTC 56447 (39, 1)
ABTC 56905 (40, 2)
ABTC 75173 (41, 1)
ABTC 75175 (42, 1)
ABTC 75180 (43, 2)
ABTC 75183 (44, 1)
ABTC 75196 (45, 1)
SAM R 56714 (46, 1)
SAM R 56715 (47, 1)
SAM R 56716 (48, 3)
SAM R 56722 (49, 1)
SAM R 56723 (50, 1)
SAM R 56725 (51, 1)
Pseudonaja nuchalis 'Southern'
ABTC 755 (52, 2)
ABTC 13179 (53, 2)
ABTC 35596 (54, 1)
ABTC 56268 (55, 1)
ABTC 56269 (56, 6)
ABTC 56208 (57, 4)
ABTC 56354 (58, 6)
ABTC 56405 (59, 3)
ABTC 56406 (60, 1)
ABTC 56410 (61, 1)
ABTC 56703 (62, 1)
ABTC 56712 (63, 1)
ABTC 57672 (64, 1)
ABTC 58359 (65, 1)
EBU 33712 (66, 1)
Pseudonaja textilis
ABTC 8920 (67, 1)
ABTC 31930 (68, 1)
ABTC 56274 (69, 1)
ABTC 56312 (70, 1)
ABTC 56407 (71, 1)
ABTC 56473 (72, 1)
ABTC 56478 (73, 2)
ABTC 65504 (74, 2)
EBU 3930 (75, 1)
EBU 4986 (76, 5)
EBU 4997 (77, 2)
EBU 6463 (78, 1)
EBU 7566 (79, 7)
EBU 7575 (80, 1)
EBU 7690 (81, 1)
EBU 31801 (82, 2)

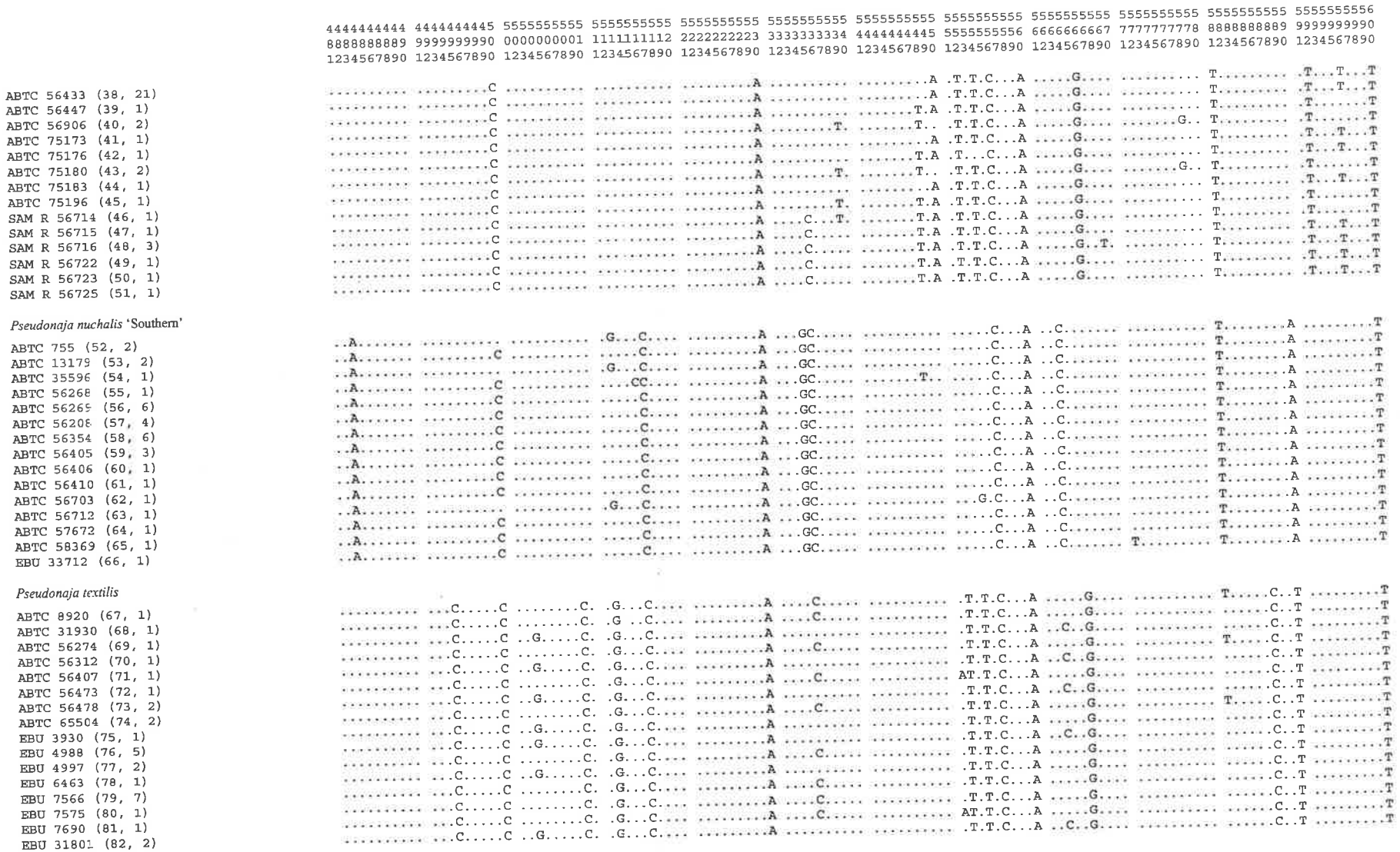

2222222222 2222222222 2222222222 2222222222 2222222222 2222222223 3333333333 3333333333 3333333333 3333333333 3333333333 3333333333
4444444445 5555555556 6666666667 7777777778 8888888889 9999999990 0000000001 1111111112 2222222223 3333333334 4444444445 5555555556
1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890
EBU 31804 (83, 1)
EBU 33794 (84, 1)
Alcohol no. QQ478 (85, 1)
Alcohol no. QQ632 (86, 1)
Alcohol no. QQ723 (87, 1)
SAM R 56724 (88, 1)
SAM R 56770 (89, 1)
Oxyuranus microlepidotus ABTC 56237
Oxyuranus microlepidotus ABTC 58708
Oxyuranus scutellatus ABTC 29118
Oxyuranus scutellatus ABTC 32087
Oxyuranus scutellatus ABTC 44040
Outgroup
Demansia papuensis ABTC 72829
Demansia papuensis ABTC 72830
Pseudechis australis ABTC 11880
Pseudechis australis ABTC 32031
Pseudechis australis ABTC 32032

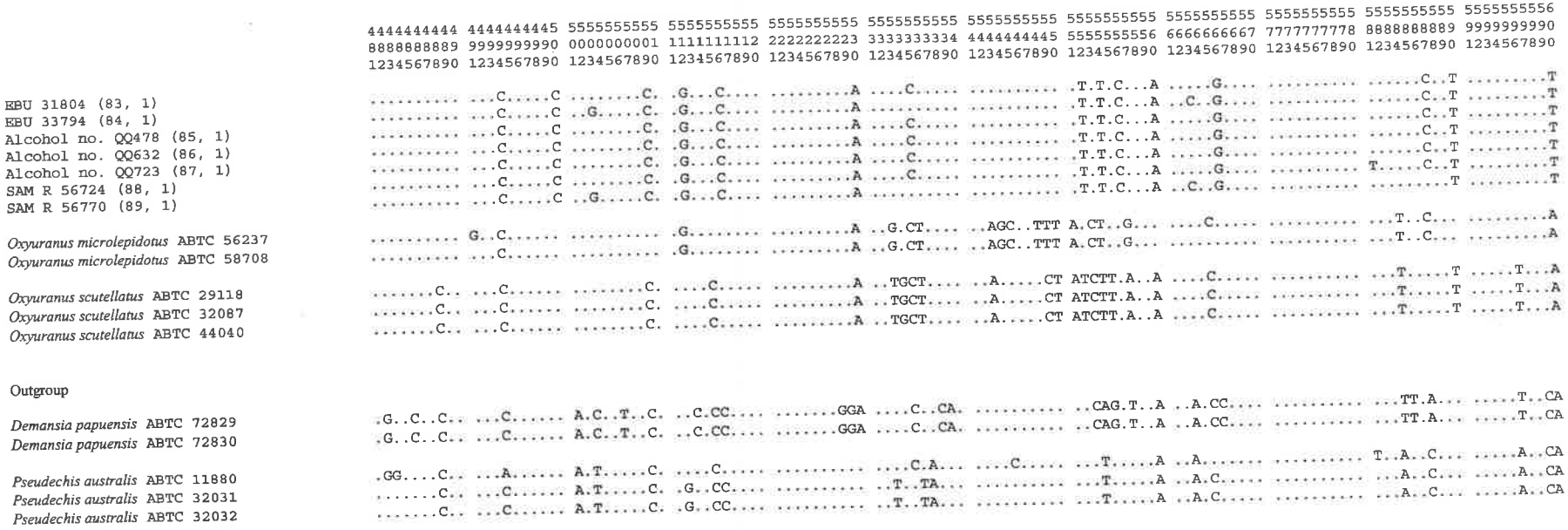

3333333333 3333333333 3333333333 3333333334 4444444444 4444444444 4444444444 4444444444 4444444444 4444444444 4444444444 4444444444
6666666667 7777777778 8888888889 9999999990 0000000001 1111111112 2222222223 3333333334 4444444445 5555555556 6666666667 7777777778
1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890
TCTTGGCTTG CCTTATAAAT ATTGCTACTC CACCCAGCAT AAACTTTACA AGTGAACTTC TAATTGCATC CTCCATATTT AACTGATGCC CAACAACCAT CATCATATTT GGCCTACTAA
Pseudonaja affinis
ABTC 6467 (1, 13)
ABTC 6469 (2, 3)
ABTC 56326 (3, 4)
ABTC 56435 (4, 1)
ABTC 75129 (5, 1)
ABTC 75133 (6, 1)
ABTC 75140 (7, 1)
Pseudonaja guttata
ABTC 31913 (8, 1)
ABTC 32082 (9, 1)
ABTC 56317 (10, 1)
Pseudonaja inframacula
ABTC 56393 (11, 15)
ABTC 56414 (12, 1)
ABTC 56797 (13, 1)
ABTC 57076 (14, 1)
Pseudonaja modesta
ABTC 479 (15, 1)
ABTC 9167 (16, 2)
ABTC 41340 (17, 1)
ABTC 56329 (18, 2)
ABTC 56391 (19, 1)
ABTC 56432 (20, 2)
ABTC 58520 (21, 1)
ABTC 75143 (22, 1)
ABTC 75167 (23, 1)
EBU 6428 (24, 1)
Pseudonaja nuchalis 'Darwin'
ABTC 13468 (25, 6)
ABTC 29603 (26, 1)
ABTC 32072 (27, 1)
Alcohol no. D3499 (28, 2)
Pseudonaja nuchalis 'Pale/black headed'
ABTC 30295 (29, 1)
ABTC 35983 (30, 2)
ABTC 42334 (31, 1)
ABTC 42400 (32, 1)
ABTC 42401 (33, 1)
ABTC 56330 (34, 1)
ABTC 56336 (35, 6)
ABTC 56348 (36, 1)
ABTC 56430 (37, 1)

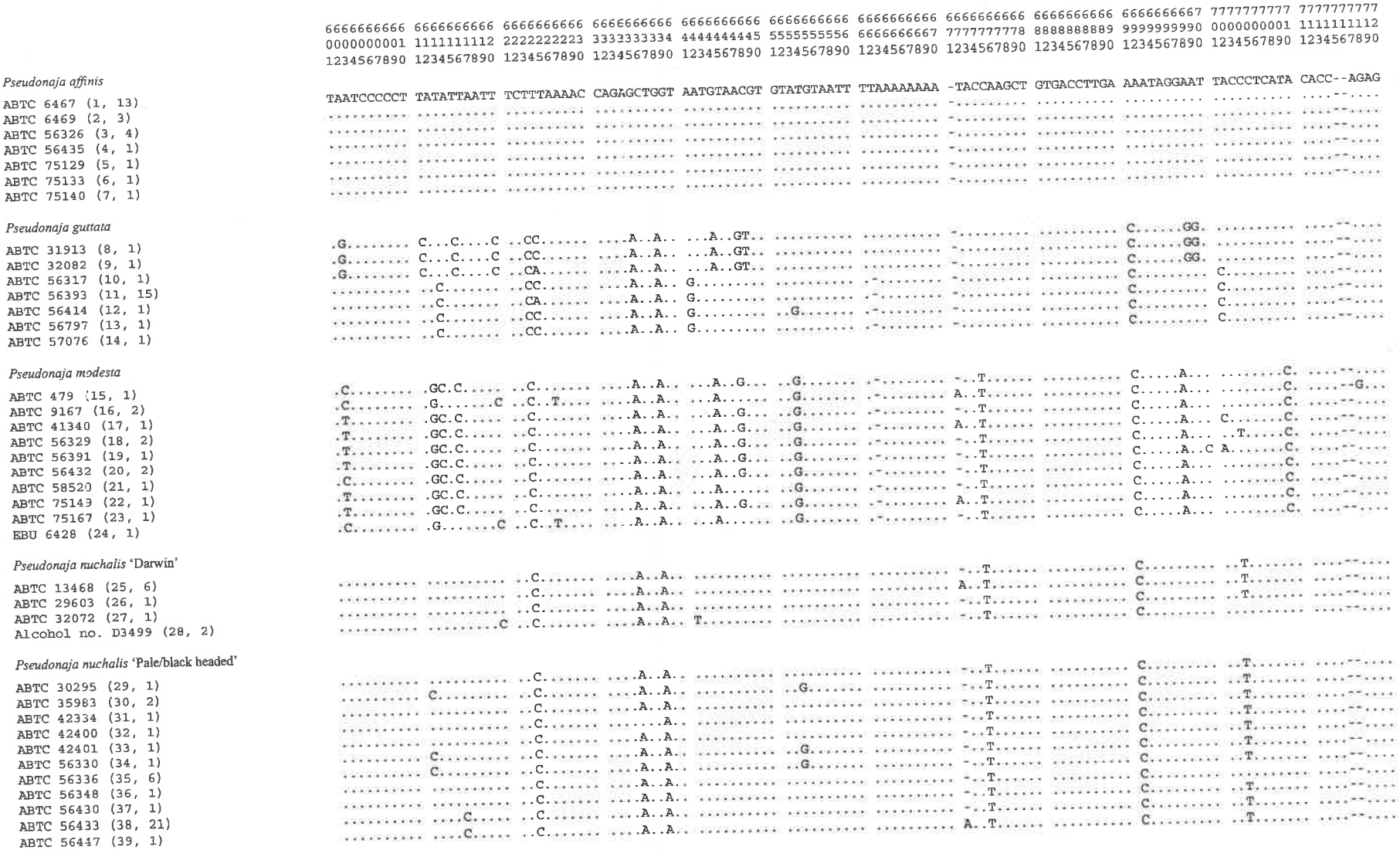

3333333333 3333333333 3333333333 3333333334 4444444444 4444444444 4444444444 4444444444 4444444444 4444444444 4444444444 4444444444
6666666667 7777777778 8888888889 9999999990 0000000001 1111111112 2222222223 3333333334 4444444445 5555555556 6666666667 7777777778
1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890
ABTC 56433 (38, 21)
ABTC 56447 (39, 1)
ABTC 56906 (40, 2)
ABTC 75173 (41, 1)
ABTC 75176 (42, 1)
ABTC 75180 (43, 2)
ABTC 75183 (44, 1)
ABTC 75196 (45, 1)
SAM R 56714 (46, 1)
SAM R 56715 (47, 1)
SAM R 56716 (48, 3)
SAM R 56722 (49, 1)
SAM R 56723 (50, 1)
SAM R 56725 (51, 1)
Pseudonaja nuchalis 'Southern'
ABTC 755 (52, 2)
ABTC 13179 (53, 2)
ABTC 35596 (54, 1)
ABTC 56268 (55, 1)
ABTC 56269 (56, 6)
ABTC 56208 (57, 4)
ABTC 56354 (58, 6)
ABTC 56405 (59, 3)
ABTC 56405 (60, 1)
ABTC 56410 (61, 1)
ABTC 56703 (62, 1)
ABTC 56712 (63, 1)
ABTC 57672 (64, 1)
ABTC 58369 (65, 1)
EBU 33712 (66, 1)
Pseudonaja textilis
ABTC 8920 (67, 1)
ABTC 31930 (68, 1)
ABTC 56274 (69, 1)
ABTC 56312 (70, 1)
ABTC 56407 (71, 1)
ABTC 56473 (72, 1)
ABTC 56478 (73, 2)
ABTC 65504 (74, 2)
EBU 3930 (75, 1)
EBU 4988 (76, 5)
EBU 4997 (77, 2)
EBU 6463 (78, 1)
EBU 7566 (79, 7)
EBU 7575 (80, 1)
EBU 7690 (81, 1)
EBU 31801 (82, 2)

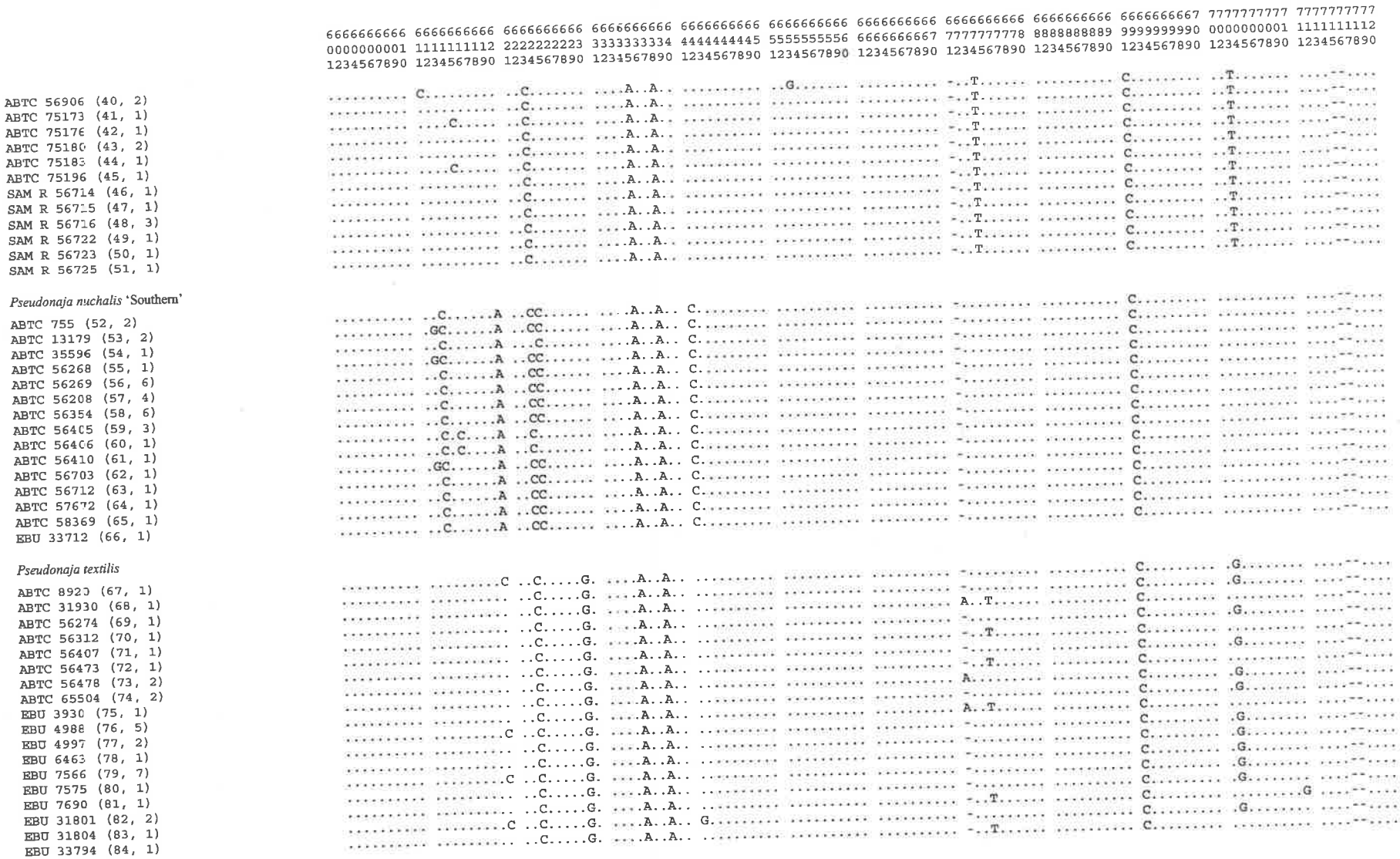

3333333333 3333333333 3333333333 3333333334 4444444444 4444444444 4444444444 4444444444 4444444444 4444444444 4444444444 4444444444
6666666667 7777777778 8888888889 9999999990 0000000001 1111111112 2222222223 3333333334 4444444445 5555555556 6666666667 7777777778
1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890
EBU 31804 (83, 1)
EBU 33794 (84, 1)
Alcohol no. QQ478 (85, 1)
Alcohol no. QQ632 (86, 1)
Alcohol no. QQ723 (87, 1)
SAM R 56724 (88, 1)
SAM R 56770 (89, 1)
Oxyuranus microlepidotus ABTC 56237
Oxyuranus microlepidotus ABTC 58708
Oxyuranus scutellatus ABTC 29118
Oxyuranus scutellatus ABTC 32087
Oxyuranus scutellatus ABTC 44040
Outgroup
Demansia papuensis ABTC 72829
Demansia papuensis ABTC 72830
Pseudechis australis ABTC 11880
Pseudechis australis ABTC 32031
Pseudechis australis ABTC 32032

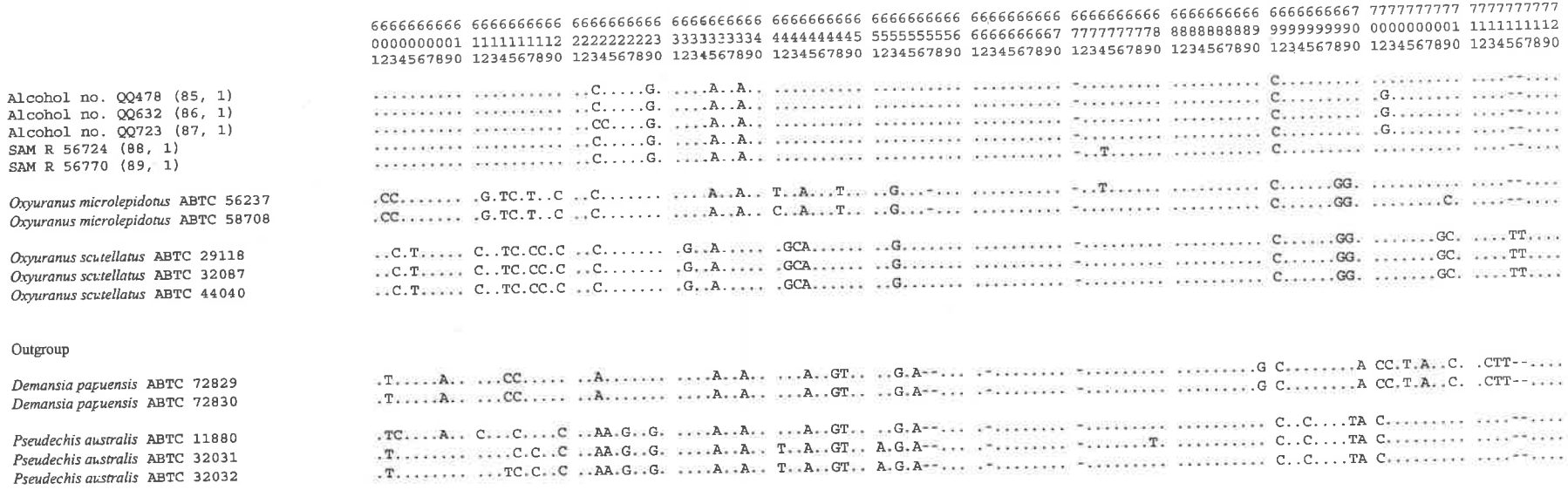

4444444444 4444444445 5555555555 5555555555 5555555555 5555555555 5555555555 5555555555 5555555555 5555555555 5555555555 5555555556
8888888889 9999999990 0000000001 1111111112 2222222223 3333333334 4444444445 5555555556 6666666667 7777777778 8888888889 9999999990
1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890
TACTTATTAC AGCTTCATAT TCACTACATA TATTTTTATC AACACAAATG GGCATCCACA CACTTAACAC CCACATCCAG CCTATACACT CACGAGAACA CCTCCTTATC TCACTCCATC
Pseudonaja affinis
ABTC 6467 (1, 13)
ABTC 6469 (2, 3)
ABTC 56326 (3, 4)
ABTC 56435 (4, 1)
ABTC 75129 (5, 1)
ABTC 75133 (6, 1)
ABTC 75140 (7, 1)
Pseudonaja guttata
ABTC 31913 (8, 1)
ABTC 32082 (9, 1)
ABTC 56317 (10, 1)
Pseudonaja inframacula
ABTC 56393 (11, 15)
ABTC 56414 (12, 1)
ABTC 56797 (13, 1)
ABTC 57076 (14, 1)
Pseudonaja modesta
ABTC 479 (15, 1)
ABTC 9167 (16, 2)
ABTC 41340 (17, 1)
ABTC 56329 (18, 2)
ABTC 56391 (19, 1)
ABTC 56432 (20, 2)
ABTC 58520 (21, 1)
ABTC 75149 (22, 1)
ABTC 75157 (23, 1)
EBU 6428 (24, 1)
Pseudonaja nuchalis 'Darwin'
ABTC 13468 (25, 6)
ABTC 29603 (26, 1)
ABTC 32072 (27, 1)
Alcohol no. D3499 (28, 2)
Pseudonaja nuchalis 'Pale/black headed'
ABTC 30295 (29, 1)
ABTC 35983 (30, 2)
ABTC 42334 (31, 1)
ABTC 42400 (32, 1)
ABTC 42401 (33, 1)
ABTC 56330 (34, 1)
ABTC 56336 (35, 6)
ABTC 56348 (36, 1)
ABTC 56430 (37, 1)


4444444444 4444444445 5555555555 5555555555 5555555555 5555555555 5555555555 5555555555 5555555555 5555555555 5555555555 5555555556
8888888889 9999999990 0000000001 1111111112 2222222223 3333333334 4444444445 5555555556 6666666667 7777777778 8888888889 9999999990
1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890
ABTC 56433 (38, 21)
ABTC 56447 (39, 1)
ABTC 56906 (40, 2)
ABTC 75173 (41, 1)
ABTC 75176 (42, 1)
ABTC 75180 (43, 2)
ABTC 75183 (44, 1)
ABTC 75196 (45, 1)
SAM R 56714 (46, 1)
SAM R 56715 (47, 1)
SAM R 56716 (48, 3)
SAM R 56722 (49, 1)
SAM R 56723 (50, 1)
SAM R 56725 (51, 1)
Pseudonaja nuchalis 'Southern'
ABTC 755 (52, 2)
ABTC 13179 (53, 2)
ABTC 35596 (54, 1)
ABTC 56268 (55, 1)
ABTC 56269 (56, 6)
ABTC 56208 (57, 4)
ABTC 56354 (58, 6)
ABTC 56405 (59, 3)
ABTC 56406 (60, 1)
ABTC 56410 (61, 1)
ABTC 56703 (62, 1)
ABTC 56712 (63, 1)
ABTC 57672 (64, 1)
ABTC 58369 (65, 1)
EBU 33712 (66, 1)
Pseudonaja textilis
ABTC 8920 (67, 1)
ABTC 31930 (68, 1)
ABTC 56274 (69, 1)
ABTC 56312 (70, 1)
ABTC 56407 (71, 1)
ABTC 56473 (72, 1)
ABTC 56478 (73, 2)
ABTC 65504 (74, 2)
EBU 3930 (75, 1)
EBU 4988 (76, 5)
EBU 4997 (77, 2)
EBU 6463 (78, 1)
EBU 7566 (79, 7)
EBU 7575 (80, 1)
EBU 7690 (81, 1)
EBU 31801 (82, 2)


4444444444 4444444445 5555555555 5555555555 5555555555 5555555555 5555555555 5555555555 5555555555 5555555555 5555555555 5555555556
8888888889 9999999990 0000000001 1111111112 2222222223 3333333334 4444444445 5555555556 6666666667 7777777778 8888888889 9999999990
1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890
EBU 31804 (83, 1)
EBU 33794 (84, 1)
Alcohol no. QQ478 (85, 1)
Alcohol no. QQ632 (86, 1)
Alcohol no. QQ723 (87, 1)
SAM R 56724 (88, 1)
SAM R 56770 (89, 1)
Oxyuranus microlepidotus ABTC 56237
Oxyuranus microlepidotus ABTC 58708
Oxyuranus scutellatus ABTC 29118
Oxyuranus scutellatus ABTC 32087
Oxyuranus scutellatus ABTC 44040
Outgroup
Demansia papuensis ABTC 72829
Demansia papuensis ABTC 72830
Pseudechis australis ABTC 11880
Pseudechis australis ABTC 32031
Pseudechis australis ABTC 32032


6666666666 6666666666 6666666666 6666666666 6666666666 6666666666 6666666666 6666666666 6666666666 6666666667 7777777777 7777777777
0000000001 1111111112 2222222223 3333333334 4444444445 5555555556 6666666667 7777777778 8888888889 9999999990 0000000001 1111111112
1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890
TAATCCCCCT TATATTAATT TCTTTAAAAC CAGAGCTGGT AATGTAACGT GTATGTAATT TTAAAAAAAA -TACCAAGCT GTGACCTTGA AAATAGGAAT TACCCTCATA CACC--AGAG
Pseudonaja affinis
ABTC 6467 (1, 13)
ABTC 6469 (2, 3)
ABTC 56326 (3, 4)
ABTC 56435 (4, 1)
ABTC 75129 (5, 1)
ABTC 75133 (6, 1)
ABTC 75140 (7, 1)
Pseudonaja guttata
ABTC 31913 (8, 1)
ABTC 32082 (9, 1)
ABTC 56317 (10, 1)
ABTC 56393 (11, 15)
ABTC 56414 (12, 1)
ABTC 56797 (13, 1)
ABTC 57076 (14, 1)
Pseudonaja modesta
ABTC 479 (15, 1)
ABTC 9167 (16, 2)
ABTC 41340 (17, 1)
ABTC 56329 (18, 2)
ABTC 56391 (19, 1)
ABTC 56432 (20, 2)
ABTC 58520 (21, 1)
ABTC 75149 (22, 1)
ABTC 75167 (23, 1)
EBU 6428 (24, 1)
Pseudonaja nuchalis 'Darwin'
ABTC 13468 (25, 6)
ABTC 29603 (26, 1)
ABTC 32072 (27, 1)
Alcohol no. D3499 (28, 2)
Pseudonaja nuchalis 'Pale/black headed'
ABTC 30295 (29, 1)
ABTC 35983 (30, 2)
ABTC 42334 (31, 1)
ABTC 42400 (32, 1)
ABTC 42401 (33, 1)
ABTC 56330 (34, 1)
ABTC 56336 (35, 6)
ABTC 56348 (36, 1)
ABTC 56430 (37, 1)
ABTC 56433 (38, 21)
ABTC 56447 (39, 1)


6666666666 6666666666 6666666666 6666666666 6666666666 6666666666 6666666666 6666666666 6666666666 6666666667 7777777777 7777777777
0000000001 1111111112 2222222223 3333333334 4444444445 5555555556 6666666667 7777777778 8888888889 9999999990 0000000001 1111111112
1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890
ABTC 56906 (40, 2)
ABTC 75173 (41, 1)
ABTC 75176 (42, 1)
ABTC 75180 (43, 2)
ABTC 75183 (44, 1)
ABTC 75196 (45, 1)
SAM R 56714 (46, 1)
SAM R 56715 (47, 1)
SAM R 56716 (48, 3)
SAM R 56722 (49, 1)
SAM R 56723 (50, 1)
SAM R 56725 (51, 1)
Pseudonaja nuchalis 'Southern'
ABTC 755 (52, 2)
ABTC 13179 (53, 2)
ABTC 35596 (54, 1)
ABTC 56268 (55, 1)
ABTC 56269 (56, 6)
ABTC 56208 (57, 4)
ABTC 56354 (58, 6)
ABTC 56405 (59, 3)
ABTC 56406 (60, 1)
ABTC 56410 (61, 1)
ABTC 56703 (62, 1)
ABTC 56712 (63, 1)
ABTC 57672 (64, 1)
ABTC 58369 (65, 1)
EBU 33712 (66, 1)
Pseudonaja textilis
ABTC 8920 (67, 1)
ABTC 31930 (68, 1)
ABTC 56274 (69, 1)
ABTC 56312 (70, 1)
ABTC 56407 (71, 1)
ABTC 56473 (72, 1)
ABTC 56478 (73, 2)
ABTC 65504 (74, 2)
EBU 3930 (75, 1)
EBU 4988 (76, 5)
EBU 4997 (77, 2)
EBU 6463 (78, 1)
EBU 7566 (79, 7)
EBU 7575 (80, 1)
EBU 7690 (81, 1)
EBU 31801 (82, 2)
EBU 31804 (83, 1)
EBU 33794 (84, 1)


6666666666 6666666666 6666666666 6666666666 6666666666 6666666666 6666666666 6666666666 6666666666 6666666667 7777777777 7777777777
0000000001 1111111112 2222222223 3333333334 4444444445 5555555556 6666666667 7777777778 8888888889 9999999990 0000000001 1111111112
1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890 1234567890
Alcohol no. QQ478 (85, 1)
Alcohol no. QQ632 (86, 1)
Alcohol no. QQ723 (87, 1)
SAM R 56724 (88, 1)
SAM R 56770 (89, 1)
Oxyuranus microlepidotus ABTC 56237
Oxyuranus microlepidotus ABTC 58708
Oxyuranus scutellatus ABTC 29118
Oxyuranus scutellatus ABTC 32087
Oxyuranus scutellatus ABTC 44040
Outgroup
Demansia papuensis ABTC 72829
Demansia papuensis ABTC 72830
Pseudechis australis ABTC 11880
Pseudechis australis ABTC 32031
Pseudechis australis ABTC 32032

```
                         7777777777 7777777777 7777777777 7777777777 7777777777
                         2222222223 3333333334 4444444445 5555555556 6666666667
                         1234567890 1234567890 1234567890 1234567890 1234567890
```

Pseudonaja affinis

```
ABTC 6467 (1, 13)        GGGGTTACAA GACCTGCTAA CTCTTTAACC TGGTACTAAA A-CCCAGCCC
ABTC 6469 (2, 3)         .......... .......... .......... .......... .-........
ABTC 56326 (3, 4)        .......... .......... .......... .......... .-........
ABTC 56435 (4, 1)        .......... .......... .......... .......... .-........
ABTC 75129 (5, 1)        .......... .......... .......... .......... .-........
ABTC 75133 (6, 1)        .......... .......... .......... .......... .-........
ABTC 75140 (7, 1)        .......... .......... .......... .......... .-........
ABTC 31913 (8, 1)        .......... .......... .......... .......... .A........
ABTC 32082 (9, 1)        .......... .......... .......... .......... .A........
ABTC 56317 (10, 1)       .......... .......... .......... .......... .A........
```

Pseudonaja inframacula

```
ABTC 56393 (11, 15)      .......... .......... .....C.... .....T.... .-........
ABTC 56414 (12, 1)       .......... .......... .....C.... .....T.... .-........
ABTC 56797 (13, 1)       .......... .......... .....C.... .....T.... .-........
ABTC 57076 (14, 1)       .......... .......... .....C.... .....T.... .-........
```

Pseudonaja modesta

```
ABTC 479 (15, 1)         .......... .......... .....C.... ...A...... .A........
ABTC 9167 (16, 2)        .....C.... .......... A....C.... ...C...... .A........
ABTC 41340 (17, 1)       .......... .......... .....C.... ...G...... .A...G....
ABTC 56329 (18, 2)       .......... .......... .....C.... ...A...... .A........
ABTC 56391 (19, 1)       .......... .......... .....C.... ...A...... .A........
ABTC 56432 (20, 2)       ....CC.T.. .......... .....C.... ...A...... .A........
ABTC 58520 (21, 1)       .......... .......... .....C.... ...A...... .A........
ABTC 75149 (22, 1)       .......... .......... .....C.... ...A...... .A.......T
ABTC 75167 (23, 1)       .......... ..T....... .....C.... ...A...... .A.......T
EBU 6428 (24, 1)         .....C.... .......... A....C.... ...C...... .A........
```

Pseudonaja nuchalis 'Darwin'

```
ABTC 13468 (25, 6)       .A........ .......... ........T. ...C.T.... .-........
ABTC 29603 (26, 1)       .A........ .......... ........T. ...C.T.... .-........
ABTC 32072 (27, 1)       .A........ .......... ........T. ...C.T.... .-........
Alcohol no. D3499 (28, 2) .A........ .......... ........T. ...C.T.... .-........
```

Pseudonaja nuchalis 'Pale/black headed'

```
ABTC 30295 (29, 1)       .A........ .......... ........T. ...C.T.... .-........
ABTC 35983 (30, 2)       .A........ .......... ........T. .....T.... .-........
ABTC 42334 (31, 1)       .A........ .......... ........T. ...C.T.... .-........
ABTC 42400 (32, 1)       .A........ .......... ........T. ...C.T.... .-........
ABTC 42401 (33, 1)       .A........ .......... ........T. ...C.T.... .-........
ABTC 56330 (34, 1)       .A........ .......... ........T. .....T.... .-........
ABTC 56336 (35, 6)       .A........ .......... ........T. .....T.... .-........
ABTC 56348 (36, 1)       .A........ .......... ........T. ...C.T.... .-........
ABTC 56430 (37, 1)       .A........ .......... ........T. ...C.T.... .-........
ABTC 56433 (38, 21)      .A........ .......... ........T. ...C.T.... .-........
ABTC 56447 (39, 1)       .A........ .......... ........T. ...C.T.... .-........
```

```
                          7777777777 7777777777 7777777777 7777777777 7777777777
                          2222222223 3333333334 4444444445 5555555556 6666666667
                          1234567890 1234567890 1234567890 1234567890 1234567890
ABTC 56906 (40, 2)        .A........ .......... ........T. .....T.... .-........
ABTC 75173 (41, 1)        .A........ .......... ........T. ...C.T.... .-........
ABTC 75176 (42, 1)        .A........ .......... ........T. ...C.T.... .-........
ABTC 75180 (43, 2)        .A........ .......... ........T. ...C.T.... .-........
ABTC 75183 (44, 1)        .A........ .......... ........T. ...C.T.... .-........
ABTC 75196 (45, 1)        .A........ .......... ........T. ...C.T.... .-........
SAM R 56714 (46, 1)       .A........ .......... ........T. ...C.T.... .-........
SAM R 56715 (47, 1)       .A........ .......... ........T. ...C.T.... .-........
SAM R 56716 (48, 3)       .A........ .......... ........T. ...C.T.... .-........
SAM R 56722 (49, 1)       .A........ .......... ........T. ...C.T.... .-........
SAM R 56723 (50, 1)       .A........ .......... ........T. ...C.T.... .-........
SAM R 56725 (51, 1)       .A........ .......... ........T. ...C.T.... .-........

Pseudonaja nuchalis 'Southern'

ABTC 755 (52, 2)          .......... .......... .....C.... .....T.... .-........
ABTC 13179 (53, 2)        .......... .......... .....C.... .....T.... .-........
ABTC 35596 (54, 1)        .......... .......... .....C.... .....T.... .-........
ABTC 56268 (55, 1)        .......... .......... .....C.... .....T.... .-........
ABTC 56269 (56, 6)        .......... .......... .....C.... .....T.... .-........
ABTC 56208 (57, 4)        .......... .......... .....C.... .....T.... .-........
ABTC 56354 (58, 6)        .......... .......... .....C.... .....T.... .-........
ABTC 56405 (59, 3)        .......... .......... .....C.... .....T.... .-........
ABTC 56406 (60, 1)        ...-...... .......... .....-C... .....T.... .-........
ABTC 56410 (61, 1)        .......... .......... .....C.... .....T.... .-........
ABTC 56703 (62, 1)        .......... .......... .....C.... .....T.... .-........
ABTC 56712 (63, 1)        .......... .......... .....C.... .....T.... .-........
ABTC 57672 (64, 1)        .......... .......... .....C.... .....T.... .-........
ABTC 58369 (65, 1)        .......... .......... .....C.... .....T.... .-........
EBU 33712 (66, 1)         .......... .......... .....C.... .....T.... .-........

Pseudonaja textilis

ABTC 8920 (67, 1)         .......A.. .......... ........T. ...C.T.... .-........
ABTC 31930 (68, 1)        .......A.. .......... ........T. .....T.... .-........
ABTC 56274 (69, 1)        .......... .......... ........T. .....T.... .-........
ABTC 56312 (70, 1)        .......A.. .......... ........T. ...C.T.... .-........
ABTC 56407 (71, 1)        .......... .......... ........T. .....T.... .-........
ABTC 56473 (72, 1)        .......A.. .......... ........T. .....T.... .-........
ABTC 56478 (73, 2)        .......... .......... ........T. .....T.... .-........
ABTC 65504 (74, 2)        .......A.. .......... ........T. ...C.T.... .-........
EBU 3930 (75, 1)          .......... .......... ........T. .....T.... .-........
EBU 4988 (76, 5)          .......... .......... ........T. .....T.... .-........
EBU 4997 (77, 2)          .......A.. .......... ........T. .....T.... .-........
EBU 6463 (78, 1)          .......... .......... ........T. .....T.... .-........
EBU 7566 (79, 7)          .......A.. .......... ........T. .....T.... .-........
EBU 7575 (80, 1)          .....A.A.. .......... ........T. .....T.... .-........
EBU 7690 (81, 1)          .......A.. .......... ........T. .....T.... .-........
EBU 31801 (82, 2)         .......... .......... ........T. .....T.... .-........
EBU 31804 (83, 1)         .......A.. .......... ........T. .....T.... .-........
EBU 33794 (84, 1)         .......... .......... ........T. .....T.... .-........
```

```
                                7777777777 7777777777 7777777777 7777777777 7777777777
                                2222222223 3333333334 4444444445 5555555556 6666666667
                                1234567890 1234567890 1234567890 1234567890 1234567890

Alcohol no. QQ478 (85, 1)       .......A.. .......... ........T. .....T.... .-........
Alcohol no. QQ632 (86, 1)       .......A.. .......... ........T. .....T.... .-........
Alcohol no. QQ723 (87, 1)       .......A.. .......... ........T. ....T.... .-........
SAM R 56724 (88, 1)             .......A.. .......... ........T. ...C.T.... .-........
SAM R 56770 (89, 1)             .......... .......... ........T. .....T.... .-........

Oxyuranus microlepidotus ABTC 56237  .......... .......... .....C..T. ...C...... .A........
Oxyuranus microlepidotus ABTC 58708  .......... .......... .....C..T. ...C...... .A........

Oxyuranus scutellatus ABTC 29118  .....C.T.. .......... .....A..T. ...A...... .A........
Oxyuranus scutellatus ABTC 32087  .....C.T.. .......... .....A..T. ...A...... .A........
Oxyuranus scutellatus ABTC 44040  .....C.T.. .......... .....A..T. ...A...... .A........

Outgroup

Demansia papuensis ABTC 72829   .T........ .......... .......... ....TA.... .-........A
Demansia papuensis ABTC 72830   .T........ .......... .......... ....TA.... .-........A

Pseudechis australis ABTC 11880  .......... .......... ........T. ...A.T.... .A-..G....
Pseudechis australis ABTC 32031  .......... .......... .......... ...A.T.... .A-......T
Pseudechis australis ABTC 32032  .......... .......... .......... ...A.T.... .A-......T
```

Appendix 3

Inferred indels were coded using the 'simple indel coding' method of Simmons and Ochoterena (2000), in which particular indels are treated as two state characters, the alternative states being 'present' or 'absent'. Where an indel observed for a terminal, A, completely overlaps one or more smaller indels observed for another terminal, B, A is coded as 'present' for the first indel and 'inapplicable' for the smaller indels, while B is coded as 'absent' for the first indel and 'present' for the smaller indels. Simmons and Ochoterena (2000) discuss the theoretical basis for this procedure.

Distribution of indels among mitochondrial DNA haplotypes observed in this study. 0 = absent, 1 = present, - = inapplicable. Haplotype numbers correspond to those in Appendix 1.

		Indel (position[s] in alignment)								
Species	Haplotype	656-657	657	662	671	715-716	724	746	762	763
Pseudonaja affinis	1	0	0	0	1	1	0	0	1	0
	2	0	0	0	1	1	0	0	1	0
	3	0	0	0	1	1	0	0	1	0
	4	0	0	0	1	1	0	0	1	0
	5	0	0	0	1	1	0	0	1	0
	6	0	0	0	1	1	0	0	1	0
	7	0	0	0	1	1	0	0	1	0
Pseudonaja guttata	8	0	0	0	1	1	0	0	0	0
	9	0	0	0	1	1	0	0	0	0
	10	0	0	0	1	1	0	0	0	0
Pseudonaja inframacula	11	0	0	1	1	1	0	0	1	0
	12	0	0	1	1	1	0	0	1	0
	13	0	0	1	1	1	0	0	1	0
	14	0	0	1	1	1	0	0	1	0
Pseudonaja modesta	15	0	0	1	1	1	0	0	0	0
	16	0	0	1	0	1	0	0	0	0
	17	0	0	1	1	1	0	0	0	0
	18	0	0	1	0	1	0	0	0	0
	19	0	0	1	1	1	0	0	0	0
	20	0	0	1	1	1	0	0	0	0
	21	0	0	1	1	1	0	0	0	0
	22	0	0	1	1	1	0	0	0	0
	23	0	0	1	0	1	0	0	0	0

Species	Haplotype	Indel (position[s] in alignment)								
		656-657	657	662	671	715-716	724	746	762	763
Pseudonaja nuchalis 'Darwin'	24	0	0	0	1	1	0	0	1	0
	25	0	0	0	0	1	0	0	1	0
	26	0	0	0	1	1	0	0	1	0
	27	0	0	0	1	1	0	0	1	0
Pseudonaja nuchalis 'Pale/black headed'	28	0	0	0	1	1	0	0	1	0
	29	0	0	0	1	1	0	0	1	0
	30	0	0	0	1	1	0	0	1	0
	31	0	0	0	1	1	0	0	1	0
	32	0	0	0	1	1	0	0	1	0
	33	0	0	0	1	1	0	0	1	0
	34	0	0	0	1	1	0	0	1	0
	35	0	0	0	1	1	0	0	1	0
	36	0	0	0	1	1	0	0	1	0
	37	0	0	0	1	1	0	0	1	0
	38	0	0	0	0	1	0	0	1	0
	39	0	0	0	1	1	0	0	1	0
	40	0	0	0	1	1	0	0	1	0
	41	0	0	0	1	1	0	0	1	0
	42	0	0	0	1	1	0	0	1	0
	43	0	0	0	1	1	0	0	1	0
	44	0	0	0	1	1	0	0	1	0
	45	0	0	0	1	1	0	0	1	0
	46	0	0	0	1	1	0	0	1	0
	47	0	0	0	1	1	0	0	1	0
	48	0	0	0	1	1	0	0	1	0
	49	0	0	0	1	1	0	0	1	0
	50	0	0	0	1	1	0	0	1	0
Pseudonaja nuchalis 'Southern'	51	0	0	0	1	1	0	0	1	0
	52	0	0	0	1	1	0	0	1	0
	53	0	0	0	1	1	0	0	1	0
	54	0	0	0	1	1	0	0	1	0
	55	0	0	0	1	1	0	0	1	0
	56	0	0	0	1	1	0	0	1	0
	57	0	0	0	1	1	0	0	1	0
	58	0	0	0	1	1	0	0	1	0
	59	0	0	0	1	1	1	1	1	0
	60	0	0	0	1	1	0	0	1	0
	61	0	0	0	1	1	0	0	1	0
	62	0	0	0	1	1	0	0	1	0
	63	0	0	0	1	1	0	0	1	0
	64	0	0	0	1	1	0	0	1	0
	65	0	0	0	1	1	0	0	1	0

Species	Haplotype	Indel (position[s] in alignment)								
		656-657	657	662	671	715-716	724	746	762	763
Pseudonaja textilis	66	0	0	0	1	1	0	0	1	0
	67	0	0	0	1	1	0	0	1	0
	68	0	0	0	0	1	0	0	1	0
	69	0	0	0	1	1	0	0	1	0
	70	0	0	0	1	1	0	0	1	0
	71	0	0	0	1	1	0	0	1	0
	72	0	0	0	1	1	0	0	1	0
	73	0	0	0	0	1	0	0	1	0
	74	0	0	0	1	1	0	0	1	0
	75	0	0	0	0	1	0	0	1	0
	76	0	0	0	1	1	0	0	1	0
	77	0	0	0	1	1	0	0	1	0
	78	0	0	0	1	1	0	0	1	0
	79	0	0	0	1	1	0	0	1	0
	80	0	0	0	1	1	0	0	1	0
	81	0	0	0	1	1	0	0	1	0
	82	0	0	0	1	1	0	0	1	0
	83	0	0	0	1	1	0	0	1	0
	84	0	0	0	1	1	0	0	1	0
	85	0	0	0	1	1	0	0	1	0
	86	0	0	0	1	1	0	0	1	0
	87	0	0	0	1	1	0	0	1	0
	88	0	0	0	1	1	0	0	1	0
Oxyuranus microlepidotus	ABTC 56737	0	1	0	1	1	0	0	0	0
Oxyuranus microlepidotus	ABTC 58708	0	1	0	1	1	0	0	0	0
Oxyuranus scutellatus	ABTC 29118	0	0	0	1	0	0	0	0	0
Oxyuranus scutellatus	ABTC 32087	0	0	0	1	0	0	0	0	0
Oxyuranus scutellatus	ABTC 44040	0	0	0	1	0	0	0	0	0
Outgroup										
Demansia papuensis	ABTC 72829	1	-	1	1	1	0	0	1	0
Demansia papuensis	ABTC 72830	1	-	1	1	1	0	0	1	0
Pseudechis australis	ABTC 11880	1	-	1	1	1	0	0	0	1
Pseudechis australis	ABTC 32031	1	-	1	1	1	0	0	0	1
Pseudechis australis	ABTC 32032	1	-	1	1	1	0	0	0	1

Appendix 4

Allozyme electrophoretic data. Locus abbreviations, proteins, and enzyme commission numbers are in Richardson *et al.* (1986). Alleles are designated alphabetically, with 'a' being the most cathodally migrating allele.

		Locus																
Species	Tissue Number	*Aco-1*	*Aco-2*	*Ada*	*Adh-1*	*Enol*	*Est-1*	*Fdp*	*Fum*	*Gapd*	*Gda*	*Glo*	*Got-1*	*Gpd*	*Gpi*	*Gpt*	*Gsr*	*Idh-1*	*Idh-2*
Pseudonaja affinis	ABTC 56281	bb	cc	cc	bb	bb	bd	aa	aa	bb	ad	bb	aa	aa	aa	dd	bb	bb	bb
	ABTC 56282	bb	cc	cc	bb	bb	bd	aa	aa	bb	cc	bb	aa	aa	aa	dd	bb	bb	bb
	ABTC 56319	bb	cc	cc	bb	bb	bd	aa	aa	bb	ac	bb	aa	aa	aa	de	bb	bb	bb
	ABTC 56326	bb	cc	cc	bb	bb	bb	aa	aa	bb	aa	bb	aa	aa	aa	cc	ab	bb	bb
	ABTC 56359	bb	cc	cc	bb	bb	bb	aa	aa	bb	aa	bb	aa	aa	aa	cc	aa	bb	bb
	ABTC 56368	bb	cc	cc	bb	bb	bd	aa	aa	bb	dd	bb	aa	aa	aa	cc	bb	bb	bb
	ABTC 56402	bb	cc	cc	bb	bc	bb	aa	aa	bb	aa	bb	aa	aa	aa	cc	bb	bb	bb
	ABTC 56403	bb	cc	cc	bb	bb	bb	aa	aa	bb	ac	bb	aa	aa	aa	cc	bb	bb	bb
	ABTC 56435	bb	cc	cc	bb	bb	dd	aa	aa	bb	cd	bb	aa	aa	aa	cc	ab	bb	bb
Pseudonaja guttata	ABTC 56317	aa	cc	ee	aa	bb	bb	aa	cc	cc	dd	aa	aa	aa	bb	bb	bb	bb	cc
Pseudonaja inframacula	ABTC 56393	bb	cc	cc	bb	bb	bb	aa	aa	bb	dd	bb	aa	aa	aa	de	ab	bb	bb
	ABTC 56394	bb	cc	cc	bb	bb	bb	aa	aa	bb	dd	bb	aa	aa	aa	de	ab	bb	bb
	ABTC 56396	bb	cc	cc	bb	bc	bb	aa	aa	bb	dd	bb	aa	aa	aa	ee	bb	bb	bb
	ABTC 56397	bb	cc	cc	bb	bb	bb	aa	aa	bb	dd	aa	aa	aa	aa	dd	bb	bb	bb
	ABTC 56398	bb	cc	cc	bb	bb	bb	aa	aa	bb	dd	ab	aa	aa	aa	ee	ab	bb	bb
	ABTC 56413	bb	cc	cc	bb	bb	bb	aa	aa	bb	dd	ab	aa	aa	aa	ce	bb	bb	bb
	ABTC 56422	bb	cc	cc	bb	bb	bb	aa	aa	bb	dd	bb	aa	aa	aa	de	bb	bb	bb

Species	Tissue Number	Locus																
		Aco-1	*Aco-2*	*Ada*	*Adh-1*	*Enol*	*Est-1*	*Fdp*	*Fum*	*Gapd*	*Gda*	*Glo*	*Got-1*	*Gpd*	*Gpi*	*Gpt*	*Gsr*	*Idh-1*	*Idh-2*
	ABTC 56444	bb	cc	cc	bb	bb	bb	aa	aa	bb	dd	ab	aa	aa	aa	ee	bb	bb	bb
	ABTC 56449	bb	cc	cc	bb	bb	aa	aa	aa	bb	cc	bb	aa	aa	aa	cc	bb	bb	bb
	ABTC 56452	bb	cc	cc	bb	bb	bb	aa	aa	bb	dd	ab	aa	aa	aa	dd	bb	bb	bb
Pseudonaja modesta	ABTC 56432	bb	ac	dd	bb	bb	bb	aa	aa	bb	cc	bb	aa	aa	aa	cc	bb	bb	bb
Pseudonaja nuchalis 'Pale/black headed'	ABTC 56330	bb	cc	cc	bb	bb	dd	aa	aa	aa	cc	bb	aa	aa	aa	cc	bb	bb	bb
	ABTC 56336	bb	cc	cc	bb	bb	dd	aa	aa	aa	cc	bb	aa	aa	aa	cc	bb	bb	bb
	ABTC 56347	bb	cc	cc	bb	bb	dd	aa	aa	aa	cc	bb	aa	aa	aa	cc	bb	bb	bb
	ABTC 56348	bb	cc	cc	bb	bb	bd	aa	aa	aa	cc	bb	aa	aa	aa	cc	bb	bb	bb
	ABTC 56349	bb	cc	cc	bb	bb	bd	aa	aa	aa	cc	bb	aa	aa	aa	cc	bb	bb	bb
	ABTC 56404	bb	cc	cc	bb	bb	dd	aa	aa	aa	cc	bb	aa	aa	aa	cc	bb	bb	bb
	ABTC 56430	bb	cc	cc	bb	bb	dd	aa	aa	aa	cc	bb	aa	aa	aa	cc	bb	bb	bb
	ABTC 56434	bb	cc	cc	bb	bb	dd	aa	aa	aa	cc	bb	aa	aa	aa	cd	bb	bb	bb
	ABTC 56447	bb	cc	cc	bb	bb	dd	aa	aa	aa	cc	bb	aa	aa	aa	cc	bb	bb	bb
Pseudonaja nuchalis 'Southern'	ABTC 56268	bb	cc	cc	bb	bb	ab	aa	aa	bb	cc	bb	aa	aa	aa	cc	bb	bb	bb
	ABTC 56269	bb	cc	cc	bb	bb	ab	aa	aa	bb	cc	bb	aa	aa	aa	cc	bb	bb	bb
	ABTC 56270	bb	cc	cc	bb	ab	ad	aa	aa	bb	cc	bb	aa	aa	aa	cc	bb	bb	bb
	ABTC 56280	bb	ac	cc	bb	bb	aa	aa	aa	bb	cc	bb	aa	aa	aa	cc	bb	bb	bb
	ABTC 56342	bb	cc	cc	bb	bb	aa	aa	aa	bb	cc	bb	aa	aa	aa	ac	ab	bb	bb
	ABTC 56354	bb	cc	cc	bb	bb	bb	aa	aa	bb	cc	bb	aa	aa	aa	cd	bb	bb	bb
	ABTC 56356	bb	cc	cc	bb	bb	bb	aa	aa	bb	cc	bb	aa	aa	aa	cc	bb	bb	bb
	ABTC 56357	bb	cc	cc	bb	bb	bb	aa	aa	bb	cc	bb	aa	aa	aa	cc	bb	bb	bb
	ABTC 56361	bb	cc	cc	bb	bb	ab	aa	aa	bb	cc	bb	aa	aa	aa	cc	bb	bb	bb

Species	Tissue Number	Locus																
		Aco-1	*Aco-2*	*Ada*	*Adh-1*	*Enol*	*Est-1*	*Fdp*	*Fum*	*Gapd*	*Gda*	*Glo*	*Got-1*	*Gpd*	*Gpi*	*Gpt*	*Gsr*	*Idh-1*	*Idh-2*
	ABTC 56389	bb	cc	cc	bb	ɒb	ab	aa	aa	bb	cc	bb	aa	aa	aa	cc	bb	bb	bb
	ABTC 56390	bb	cc	cc	bb	bb	aa	aa	aa	bb	ac	bb	aa	aa	aa	cc	bb	bb	bb
	ABTC 56405	bb	cc	cc	bb	bb	aa	aa	aa	bb	cc	bb	aa	aa	aa	cc	bb	bb	bb
	ABTC 56399	bb	cc	cc	bb	bb	bb	aa	aa	bb	cc	bb	aa	aa	aa	dd	ab	bb	bb
Pseudonaja textilis	ABTC 56274	bb	cd	cc	bb	bb	bb	aa	aa	bb	dd	bb	aa	aa	aa	cc	bb	bb	bb
	ABTC 56312	bb	ee	bc	bb	bb	bb	aa	aa	bb	dd	bb	aa	aa	aa	dd	bb	bb	bb
Outgroup																			
Pseudechis australis	ABTC 11880	bb	cc	ee	bb	bb	bd	aa	bb	bb	cc	bb	aa	bb	aa	ab	bb	bb	bb

Species	Tissue Number	Locus																
		Ldh-1	*Ldh-2*	*Mdh-1*	*Mdh-2*	*Mpi*	*Np*	*Pep-A*	*Pep-B*	*Pep-C*	*Pep-D*	*Pgam*	*6-Pgd*	*Pgk*	*Pgm-1*	*Pgm-2*	*Sod*	*Srdh*	*Tpi*
Pseudonaja affinis	ABTC 56281	aa	bb	aa	aa	bb	bb	bb	bb	cc	bc	bb	cc	aa	cc	dd	bb	dd	aa
	ABTC 56282	aa	bb	aa	aa	bb	bb	bb	bb	ee	bb	bb	cc	aa	cc	dd	bb	dd	aa
	ABTC 56319	aa	bb	aa	aa	bb	bb	bb	bb	ee	bb	bb	cc	aa	cc	fg	bb	dd	aa
	ABTC 56326	aa	bb	aa	aa	bc	bb	bb	bb	ce	bb	bb	cc	aa	cc	dd	bb	dd	aa
	ABTC 56359	aa	bb	aa	aa	bb	bb	bb	bb	cc	bc	bb	cc	aa	cc	dd	bb	dd	aa
	ABTC 56368	aa	bb	aa	aa	bb	bb	bb	bb	ce	bb	bb	cc	aa	cc	dd	bb	ee	aa
	ABTC 56402	aa	bb	aa	aa	bb	bb	bb	bb	cc	bb	bb	cc	aa	cc	dd	bb	dd	aa
	ABTC 56403	aa	bb	aa	aa	cc	bb	bb	bb	ce	bb	bb	cc	aa	cc	dd	bb	dd	aa
	ABTC 56435	aa	bb	aa	aa	bb	bb	bb	bb	cc	bb	bb	ce	aa	cc	dd	bb	dd	aa
Pseudonaja guttata	ABTC 56317	aa	bb	aa	aa	bb	bb	bb	dd	cc	bb	bb	cc	bb	ff	gg	bb	dd	aa
Pseudonaja inframacula	ABTC 56393	aa	bb	aa	aa	cc	bb	bb	bb	dd	bb	bb	cc	aa	cc	bf	bb	de	aa
	ABTC 56394	aa	bb	aa	aa	cc	bb	bb	bb	dd	bb	bb	cc	aa	cc	df	bb	de	aa
	ABTC 56396	aa	bb	aa	aa	cc	bb	bb	bb	dd	bb	bb	cc	aa	ac	bd	bb	dd	aa
	ABTC 56397	aa	bb	aa	aa	cc	bb	bb	bb	dd	bb	bb	cc	aa	ac	bb	bb	dd	aa
	ABTC 56398	aa	bb	aa	aa	cc	bb	bb	bb	dd	bb	bb	cc	aa	cc	df	bb	dd	aa
	ABTC 56413	aa	bb	aa	aa	cc	bb	bb	bb	dd	bb	bb	cc	aa	cc	dd	bb	dd	ab
	ABTC 56422	aa	bb	aa	aa	cc	bb	bb	bb	de	bb	bb	cc	aa	cc	bb	bb	dd	aa
	ABTC 56444	aa	bb	aa	aa	cc	bb	bb	bb	dd	bb	bb	cc	aa	cc	dd	bb	dd	ab
	ABTC 56449	aa	bb	aa	aa	bb	bb	bb	bc	ee	bb	bb	bc	aa	cc	dd	bb	dd	aa
	ABTC 56452	aa	bb	aa	aa	cc	bb	bb	bb	dd	bb	bb	cc	aa	cc	dd	bb	dd	aa
Pseudonaja modesta	ABTC 56432	aa	bb	bb	aa	bb	bb	bb	cc	cc	bb	bb	de	ab	cc	ff	bb	dd	aa

Species	Tissue Number	Locus																
		Ldh-1	*Ldh-2*	*Mdh-1*	*Mdh-2*	*Mpi*	*Np*	*Pep-A*	*Pep-B*	*Pep-C*	*Pep-D*	*Pgam*	*6-Pgd*	*Pgk*	*Pgm-1*	*Pgm-2*	*Sod*	*Srdh*	*Tpi*
Pseudonaja nuchalis 'Pale/black headed'	ABTC 56330	aa	bb	aa	aa	bb	bb	bb	aa	ce	bb	bb	ac	aa	cc	dd	bb	dd	aa
	ABTC 56336	aa	bb	aa	aa	bb	bb	bb	aa	ce	bb	bb	cc	aa	cc	dd	bb	dd	aa
	ABTC 56347	aa	bb	aa	aa	bb	bb	bb	aa	ee	bb	bb	cc	aa	cc	df	bb	dd	aa
	ABTC 56348	aa	bb	aa	aa	bb	bb	bb	ab	cc	bb	bb	cc	aa	cc	dd	bb	dd	aa
	ABTC 56349	aa	bb	aa	aa	bb	bb	bb	aa	cc	bb	bb	ac	aa	cc	df	bb	dd	aa
	ABTC 56404	aa	bb	aa	aa	bb	bb	bb	aa	ee	bb	bb	cc	aa	cc	dd	bb	dd	aa
	ABTC 56430	aa	bb	aa	aa	bb	bb	bb	bb	ce	bb	bb	cc	aa	cc	df	bb	dd	aa
	ABTC 56434	aa	bb	aa	aa	bb	bb	bb	bb	cc	bb	bb	cc	aa	cc	dd	bb	dd	aa
	ABTC 56447	aa	bb	aa	aa	bb	bb	bb	bb	cc	bb	bb	cc	aa	cc	dd	bb	dd	aa
Pseudonaja nuchalis 'Southern'	ABTC 56268	aa	bb	aa	aa	bb	bb	bb	bb	ee	bb	bb	cc	aa	cc	dd	bb	dd	aa
	ABTC 56269	aa	bb	aa	aa	bb	bb	bb	cc	ee	bb	bb	cc	aa	cc	ff	bb	dd	aa
	ABTC 56270	aa	bb	aa	aa	bb	bb	bb	bc	ee	ab	bb	cc	aa	cc	dd	bb	dd	aa
	ABTC 56280	aa	bb	aa	aa	bb	bb	bb	bc	ee	bb	bb	cc	aa	cc	df	bb	dd	aa
	ABTC 56342	aa	bb	aa	aa	bb	bb	bb	bc	ee	bb	bb	cc	aa	cc	df	bb	dd	aa
	ABTC 56354	aa	bb	aa	aa	bb	bb	bb	bb	ee	bc	bb	cc	aa	cc	df	bb	dd	aa
	ABTC 56356	aa	bb	aa	aa	bb	bb	bb	cc	ee	bb	bb	cc	aa	cc	dd	bb	dd	aa
	ABTC 56357	aa	bb	aa	aa	bb	bb	bb	bc	ee	bb	bb	cc	aa	cc	df	bb	dd	aa
	ABTC 56361	aa	bb	aa	aa	bb	bb	bb	bb	ee	bb	bb	cc	aa	cc	--	bb	bd	aa
	ABTC 56389	aa	bb	aa	aa	bb	bb	bb	bc	ee	bb	bb	cc	aa	cc	df	bb	dd	aa
	ABTC 56390	aa	bb	aa	aa	bb	bb	bb	bc	ee	bb	bb	cc	aa	cc	df	bb	dd	aa
	ABTC 56405	aa	bb	aa	aa	bb	bb	bb	bc	ee	bc	bb	cc	aa	cc	bd	bb	dd	aa
	ABTC 56399	aa	bb	aa	aa	bb	bb	bb	bb	--	bb	bb	cc	aa	cc	df	bb	bd	aa
Pseudonaja textilis	ABTC 56274	aa	bb	aa	aa	cc	bb	bb	bb	cc	bb	bb	cc	bb	cc	ff	bb	bb	aa
	ABTC 56312	aa	bb	aa	aa	cc	bb	bb	bb	cc	bb	bb	cc	ab	cc	ff	bb	bb	aa

Species	Tissue Number	Locus																
		Ldh-1	*Ldh-2*	*Mdh-1*	*Mdh-2*	*Mpi*	*Np*	*Pep-A*	*Pep-B*	*Pep-C*	*Pep-D*	*Pgam*	*6-Pgd*	*Pgk*	*Pgm-1*	*Pgm-2*	*Sod*	*Srdh*	*Tpi*
Outgroup																			
Pseudechis australis	ABTC 11880	aa	bb	bb	aa	cc	cc	aa	bb	bb	cc	bb	aa	bb	dd	ee	aa	aa	aa

Appendix 5

Raw measurements recorded for available specimens of nominal *Pseudonaja affinis*, *Pseudonaja inframacula*, *Pseudonaja nuchalis*, and *Pseudonaja textilis* for multivariate statistical analyses. All measurements are in millimetres. Measurements for specimens having a snout-vent length less than 300 mm cr for specimens for which one or measurements could not be recorded were not included in analyses and are not presented.

Species	Specimen Number	Snout-vent length	Tail length	Length of frontal	Width of frontal	Distance from rostral to frontal	Length of prefrontal suture	Mean length of supraoculars	Mean length of parietals	Length of parietal suture	Distance from snout tip to posterior end of parietal suture	Mean distance from snout tip to posterior end of mandible	Interocular distance	Head width	Mean eye diameter	Mean distance from eye to nostril	Internarial distance
Pseudonaja affinis																	
Male																	
	SAM R 18996	734	126	6.01	3.50	2.96	2.20	5.21	8.46	6.18	17.16	23.98	9.11	13.33	3.73	4.67	5.11
	SAM R 20605	1093	194	8.27	5.05	4.06	2.79	7.05	11.76	7.96	23.20	33.58	12.29	17.87	4.71	6.12	7.30
	SAM R 20807	1234	197	8.40	4.64	5.03	3.03	7.38	12.35	8.78	25.21	35.28	13.01	19.11	4.32	6.77	7.01
	SAM R 24807	460	91	5.36	2.31	3.34	2.41	4.72	6.10	4.61	14.01	18.79	7.39	8.01	3.37	3.43	3.75
	SAM R 24808	662	123	6.34	3.86	2.69	1.67	5.25	8.17	6.01	16.34	21.79	8.88	10.31	3.53	4.34	5.14
	SAM R 26268	818	156	6.49	3.42	3.69	2.30	5.76	8.53	6.09	18.52	26.18	9.53	13.66	4.14	4.86	5.71
	SAM R 29468	396	69	4.30	2.65	2.39	1.80	3.79	5.54	4.27	12.38	16.15	6.16	6.65	2.97	3.10	3.45
	SAM R 52360	1299	225	8.43	5.12	4.71	3.25	7.34	11.91	8.52	24.15	34.81	12.63	19.03	4.90	6.52	7.65
	WAM R 115146	373	65	4.40	2.31	2.15	1.37	3.81	5.70	4.35	12.14	15.85	6.15	6.70	2.85	2.86	3.11
	WAM R 119172	925	149	6.65	4.17	3.65	2.54	5.94	8.96	6.60	19.19	27.13	9.80	12.69	4.11	5.21	5.67
	WAM R 119550	710	140	6.44	3.62	3.29	2.51	5.68	8.57	6.62	18.47	25.58	8.83	13.09	3.80	4.76	5.18
	WAM R 121144	1252	205	8.47	5.20	5.68	3.65	7.47	11.56	9.06	26.80	35.63	14.14	17.76	4.73	7.22	8.35
Female																	
	SAM R 18995	728	127	5.36	3.05	3.35	2.67	5.02	7.90	6.63	17.50	23.19	8.93	12.33	3.73	4.62	5.26
	SAM R 21955	701	142	6.17	3.56	3.19	1.98	5.24	8.49	6.17	17.40	23.97	8.65	12.00	3.68	4.38	5.15

Species	Specimen Number	Snout-vent length	Tail length	Length of frontal	Width of frontal	Distance from rostral to frontal	Length of prefrontal suture	Mean length of supraoculars	Mean length of parietals	Length of parietal suture	Distance from snout tip to posterior end of parietal suture	Mean distance from snout tip to posterior end of mandible	Interocular distance	Head width	Mean eye diameter	Mean distance from eye to nostril	Internarial distance
	SAM R 23000	1130	181	7.05	3.85	4.45	2.95	6.45	10.90	8.20	23.24	32.54	11.67	14.45	4.73	6.24	6.15
	SAM R 26347	865	155	6.56	4.25	3.75	2.53	5.79	9.54	6.87	19.21	26.50	10.11	14.10	4.09	4.79	5.78
	SAM R 31704	1017	181	7.74	4.76	3.97	2.69	6.56	10.74	7.29	21.71	31.88	11.42	15.40	4.71	5.97	6.47
	WAM R 77743	575	109	4.89	2.84	3.03	1.79	4.53	6.49	4.72	14.60	20.27	7.50	10.09	3.42	3.70	4.50
	WAM R 104272	712	114	5.39	2.94	2.96	2.01	4.83	7.47	5.30	15.71	21.93	7.75	10.00	3.56	4.07	4.39
	WAM R 125640	1199	204	7.62	3.83	3.48	3.35	7.11	10.76	8.25	23.67	33.02	11.83	14.84	4.65	6.41	6.64
	WAM R 136095	917	162	6.17	3.70	3.87	2.47	5.84	9.21	6.70	20.30	29.27	9.89	15.11	3.74	5.05	6.06
Pseudonaja inframacula																	
Male																	
	SAM R 24751	1188	195	7.33	4.15	5.15	3.32	6.49	10.03	7.38	23.02	30.38	12.27	12.21	5.01	5.92	7.30
	SAM R 24752	877	164	6.90	3.73	4.91	2.87	5.49	8.97	6.60	19.79	26.56	9.68	11.77	4.31	5.29	6.07
	SAM R 24755	953	187	6.84	3.65	4.92	2.85	6.02	9.58	6.81	21.13	29.01	10.15	12.25	4.35	5.43	5.74
	SAM R 24756	1179	223	8.37	4.38	5.90	4.10	7.32	11.21	7.98	24.98	34.80	12.45	16.46	5.17	6.67	7.77
	SAM R 24757	457	89	4.99	2.52	3.20	2.09	4.08	5.85	4.14	13.20	16.99	6.46	7.26	3.11	3.27	3.77
	SAM R 25702	1023	181	7.77	4.18	4.79	2.62	6.91	10.90	7.97	22.29	30.25	11.82	13.17	4.77	5.26	6.65
	SAM R 26474	1174	189	7.87	4.47	6.74	3.86	6.67	10.64	7.46	23.91	33.03	12.10	15.85	4.80	6.22	7.14
	SAM R 28457	777	142	6.55	3.24	4.49	2.55	5.93	9.21	6.81	19.46	26.70	10.19	11.98	4.28	5.07	5.70
	SAM R 29026	742	154	6.16	3.49	4.63	2.64	5.44	8.06	5.60	17.76	25.88	9.32	12.32	4.16	4.58	5.65
	SAM R 31599	634	126	5.12	3.08	4.12	2.50	4.45	7.07	5.36	15.95	21.63	8.22	11.24	3.37	4.12	4.40
	SAM R 31698	879	158	6.80	3.74	5.06	3.10	5.83	8.62	5.89	20.03	27.17	11.19	14.55	4.24	5.10	6.36
Female																	
	SAM R 25422	706	149	6.29	3.20	3.95	2.50	5.63	8.45	5.92	18.10	24.62	9.55	12.79	4.12	4.78	5.46

Species	Specimen Number	Snout-vent length	Tail length	Length of frontal	Width of frontal	Distance from rostral to frontal	Length of prefrontal suture	Mean length of supraoculars	Mean length of parietals	Length of parietal suture	Distance from snout tip to posterior end of parietal suture	Mean distance from snout tip to posterior end of mandible	Interocular distance	Head width	Mean eye diameter	Mean distance from eye to nostril	Internarial distance
	SAM R 36588	687	153	6.17	3.32	3.77	2.55	4.89	7.78	5.52	17.61	23.94	8.76	12.94	3.81	4.47	4.96
	SAM R 38193	779	168	6.42	3.22	3.83	2.18	5.59	8.93	6.33	18.60	24.30	9.29	10.75	3.91	4.42	5.32
	SAM R 56771	948	177	6.90	3.41	4.59	2.88	5.76	9.24	6.03	19.89	28.09	10.04	12.77	4.45	5.03	5.33
	SAM R 57076	921	191	6.09	3.31	4.13	2.52	5.30	8.33	6.00	18.28	24.57	8.91	11.08	3.68	4.44	4.97
Pseudonaja nuchalis 'Darwin'																	
Male																	
	NTM R 10685	1116	224	8.53	4.24	4.34	2.15	7.66	11.81	8.54	26.40	37.45	12.26	17.72	5.64	7.18	8.16
	SAM R 56773	991	190	7.73	4.44	4.06	2.43	6.02	10.51	7.44	22.90	30.66	11.00	13.39	4.62	6.02	6.00
	SAM R 56774	859	148	6.76	3.72	2.89	1.79	5.28	8.99	6.38	19.41	27.38	9.40	13.25	3.96	4.57	5.70
	SAM R 56775	977	189	7.45	4.03	3.21	1.73	5.90	10.20	7.60	21.70	29.95	10.72	14.63	4.33	5.67	6.37
Female																	
	SAM R 56772	1092	205	7.76	3.89	3.67	1.86	6.38	9.55	7.15	22.42	31.61	10.75	13.25	4.42	5.94	6.19
Pseudonaja nuchalis 'Pale/black headed'																	
Male																	
	SAM R 20981	815	172	6.35	3.56	3.41	2.30	4.97	9.78	7.16	19.16	25.25	9.31	12.96	3.85	4.86	5.87
	SAM R 21025	484	98	4.31	2.50	2.88	1.86	3.87	6.85	4.96	13.80	18.37	6.67	9.19	2.83	3.55	3.70
	SAM R 21413	787	162	6.17	3.26	3.90	2.72	5.35	8.77	6.64	18.96	26.50	8.65	12.90	4.08	5.07	5.67
	SAM R 21414	835	146	6.64	3.10	4.13	2.36	5.68	9.29	6.79	18.84	26.59	9.53	14.27	3.55	5.25	5.14
	SAM R 24821	608	119	5.84	3.08	2.77	1.86	4.98	7.17	4.95	15.76	21.38	7.91	11.26	3.13	4.30	4.65
	SAM R 28531	1028	189	7.09	4.05	3.70	2.27	5.99	11.08	7.99	22.75	31.57	10.95	14.48	3.69	6.06	7.42

Species	Specimen Number	Snout-vent length	Tail length	Length of frontal	Width of frontal	Distance from rostral to frontal	Length of prefrontal suture	Mean length of supraoculars	Mean length of parietals	Length of parietal suture	Distance from snout tip to posterior end of parietal suture	Mean distance from snout tip to posterior end of mandible	Interocular distance	Head width	Mean eye diameter	Mean distance from eye to nostril	Internarial distance
	SAM R 29360	999	181	7.14	4.32	5.15	3.40	6.22	10.25	7.54	22.10	30.10	10.51	14.15	4.40	6.05	6.75
	SAM R 51516	794	143	5.66	3.29	3.34	2.31	5.30	8.74	6.76	17.63	23.93	7.67	11.39	3.42	4.55	4.35
	SAM R 51591	769	146	5.93	3.46	3.17	1.71	5.05	8.30	6.14	17.70	23.38	8.19	11.84	3.56	4.53	5.20
	SAM R 51592	799	156	6.35	3.07	3.19	2.14	5.44	8.92	6.61	17.45	24.06	8.34	12.56	3.72	4.63	4.86
	SAM R 56714	1007	174	7.14	3.92	3.66	2.26	5.93	10.41	6.95	21.20	29.90	9.55	14.50	3.98	5.82	5.59
	SAM R 56715	876	157	5.92	3.18	3.80	2.47	4.80	9.13	6.03	18.59	25.92	8.94	14.01	3.50	4.94	5.35
	SAM R 56723	1012	178	6.91	3.88	3.96	2.59	5.71	10.03	7.11	21.48	29.46	9.83	13.01	3.92	5.85	6.24
	SAM R 56725	1067	186	6.32	3.97	3.91	2.47	5.55	10.90	7.77	21.47	29.15	9.43	12.76	3.80	5.58	6.08
	WAM R 103848	659	123	5.73	2.83	3.25	1.51	4.43	7.22	5.24	16.31	22.98	8.04	12.73	3.05	4.32	4.82
	WAM R 103849	946	172	6.43	4.01	3.50	2.60	5.53	10.52	7.35	20.15	26.54	9.26	13.67	3.31	5.22	5.58
	WAM R 103923	588	123	5.27	2.94	2.75	1.75	4.39	7.35	5.36	15.76	20.71	7.66	10.49	3.27	3.86	4.34
	WAM R 104187	776	155	6.20	3.41	3.30	2.44	4.98	9.17	7.21	19.89	25.59	8.61	10.45	3.71	4.71	5.31
	WAM R 115021	842	146	6.28	3.78	3.20	1.89	4.74	8.75	5.78	17.87	25.03	8.66	12.91	3.17	4.76	5.33
	WAM R 115062	896	175	6.68	3.92	3.90	2.43	5.55	9.76	6.70	19.80	26.96	9.60	14.34	3.46	5.32	5.66
	WAM R 115063	841	158	6.03	3.20	3.72	2.40	5.10	8.98	6.25	18.99	26.09	9.06	14.23	3.54	5.13	5.65
	WAM R 115180	827	151	5.90	3.35	3.20	2.25	5.00	8.22	5.40	17.65	24.56	8.90	12.25	3.22	4.70	5.06
	WAM R 115182	322	51	3.75	1.98	1.46	0.85	2.99	5.08	3.65	10.28	13.13	4.71	6.50	2.28	2.37	2.70
	WAM R 115183	333	62	3.80	1.80	1.95	1.25	3.07	5.07	3.80	10.64	13.15	5.15	6.00	2.30	2.50	3.41
	WAM R 115276	386	76	4.15	2.20	2.23	1.39	3.20	5.20	3.49	11.50	15.76	5.80	8.36	2.25	2.91	3.46
	WAM R 115607	699	125	5.26	3.03	3.19	2.16	4.68	7.36	5.62	15.82	22.29	7.88	12.15	3.00	4.24	4.52
	WAM R 115609	874	168	6.35	3.45	3.25	2.32	5.23	9.34	6.30	19.81	26.92	9.88	14.61	3.56	5.10	5.77
	WAM R 115751	693	129	5.54	2.67	2.97	1.53	4.29	7.20	4.66	15.80	21.43	7.84	11.70	2.84	4.23	4.71
	WAM R 115752	800	147	5.75	3.34	3.53	2.44	5.05	8.46	6.00	17.73	24.55	8.35	12.59	3.23	4.64	5.31
	WAM R 119293	666	106	5.88	2.94	1.99	1.92	4.35	7.91	5.69	16.84	22.79	7.81	10.92	3.16	4.11	5.68

Species	Specimen Number	Snout-vent length	Tail length	Length of frontal	Width of frontal	Distance from rostral to frontal	Length of prefrontal suture	Mean length of supraoculars	Mean length of parietals	Length of parietal suture	Distance from snout tip to posterior end of parietal suture	Mean distance from snout tip to posterior end of mandible	Interocular distance	Head width	Mean eye diameter	Mean distance from eye to nostril	Internarial distance
Female																	
	AM R 150262	103	103	4.25	2.26	2.75	1.44	3.93	6.96	5.09	13.46	17.51	5.69	8.80	2.82	3.47	3.47
	NTM R 18321	621	116	4.85	2.69	2.44	1.43	4.07	7.55	6.00	15.78	20.25	7.31	14.70	3.03	4.11	4.48
	SAM R 21415	667	118	4.88	2.26	3.29	2.14	4.90	8.03	6.38	16.51	21.49	7.44	11.08	3.45	4.23	4.38
	SAM R 29288	977	166	6.36	3.64	4.15	2.70	5.27	10.08	6.69	20.01	27.28	10.26	13.67	3.58	5.11	5.95
	SAM R 29407	973	176	6.80	3.79	3.84	2.27	5.54	10.88	7.92	21.34	28.81	10.38	14.81	3.77	6.16	6.60
	SAM R 36953	809	186	6.11	3.53	3.64	2.32	5.25	9.17	6.33	18.80	25.37	8.81	14.42	3.61	5.01	5.55
	SAM R 42333	792	138	5.32	2.67	3.20	2.01	4.52	8.33	6.76	17.54	23.19	8.14	11.66	3.33	4.50	5.31
	SAM R 46920	705	121	5.32	2.60	2.84	1.83	5.00	7.74	5.34	15.14	19.58	7.15	8.87	2.98	3.65	4.24
	SAM R 56716	866	143	5.56	3.23	3.15	1.54	4.76	9.24	6.66	18.14	25.35	8.69	13.39	3.23	4.70	5.05
	SAM R 56720	995	157	6.25	3.64	3.43	2.36	5.58	9.95	6.94	20.09	27.94	8.98	12.07	3.60	5.35	5.53
	SAM R 56722	839	158	5.72	3.20	3.03	1.48	4.56	8.41	5.91	17.91	24.74	8.10	11.42	3.23	4.84	5.08
	WAM R 102045	755	150	5.94	3.05	3.40	2.40	5.21	8.47	6.65	18.37	24.93	8.30	12.20	3.72	4.88	4.85
	WAM R 103924	634	114	4.99	2.50	2.39	1.46	3.86	6.84	4.91	14.75	19.88	6.85	10.45	2.85	3.70	4.10
	WAM R 114659	933	162	5.96	3.70	3.32	2.10	5.23	9.76	7.44	20.25	27.08	9.28	14.51	3.76	4.82	5.53
	WAM R 114661	935	169	6.35	3.28	2.97	2.00	5.18	8.81	6.30	18.90	26.22	8.57	13.72	3.63	5.01	5.63
	WAM R 114663	892	164	5.32	3.26	3.01	1.80	4.83	8.65	6.65	18.05	25.13	8.55	14.38	3.39	4.68	5.03
	WAM R 115608	601	111	4.89	2.69	2.46	1.66	4.21	6.69	4.82	14.40	20.16	6.99	10.25	2.67	3.63	4.64
	WAM R 115610	990	177	6.65	3.45	3.65	2.27	5.42	8.15	6.80	19.96	27.59	9.29	15.54	3.64	4.98	5.91
	WAM R 116498	733	136	5.65	2.87	3.07	1.83	4.73	7.76	6.22	16.80	21.56	7.81	12.78	3.16	4.33	4.45
	WAM R 119526	1077	206	7.35	4.06	3.29	2.32	5.75	11.02	7.57	21.59	29.11	9.55	12.90	3.89	5.49	5.78

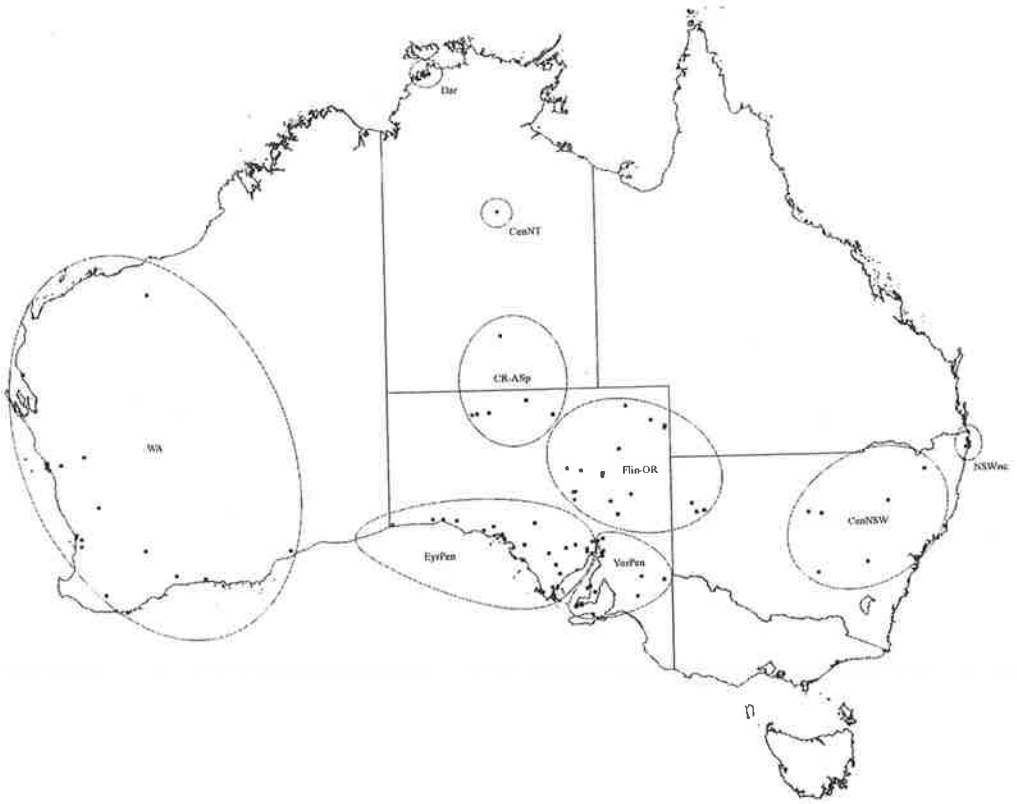
Species	Specimen Number	Snout-vent length	Tail length	Length of frontal	Width of frontal	Distance from rostral to frontal	Length of prefrontal suture	Mean length of supraoculars	Mean length of parietals	Length of parietal suture	Distance from snout tip to posterior end of parietal suture	Mean distance from snout tip to posterior end of mandible	Interocular distance	Head width	Mean eye diameter	Mean distance from eye to nostril	Internarial distance
Pseudonaja nuchalis 'Southern'																	
Male																	
	AM R 157294	864	138	6.49	3.41	2.89	1.50	5.44	7.91	6.09	18.35	26.25	8.78	13.38	3.60	4.76	5.48
	SAM R 18598	1022	144	6.90	3.28	3.04	1.98	5.73	9.23	6.86	19.41	26.79	9.75	13.29	4.05	5.13	6.10
	SAM R 18599	992	153	6.65	3.87	4.24	2.68	6.20	9.69	6.94	20.76	28.48	10.51	15.04	3.87	5.46	6.64
	SAM R 21163	853	133	6.84	3.27	3.16	2.01	5.16	8.56	6.16	18.46	25.03	8.97	12.98	3.70	4.93	5.66
	SAM R 22746	1054	119	6.64	3.89	3.40	2.00	5.77	9.48	6.98	19.95	28.47	10.44	15.26	3.84	5.13	6.12
	SAM R 24778	1276	199	8.19	4.30	4.31	2.64	6.69	12.26	8.11	24.77	33.04	13.16	17.81	4.03	6.55	7.75
	SAM R 24828	850	109	5.93	3.65	2.03	2.03	5.16	8.09	6.03	17.66	23.92	9.42	13.31	3.36	4.51	5.69
	SAM R 25295	1226	194	7.30	4.16	3.63	2.39	6.52	10.48	7.94	22.75	30.65	11.37	16.45	4.29	5.89	6.93
	SAM R 28559	850	124	5.91	3.44	3.34	2.33	5.37	8.69	6.15	18.26	26.04	9.20	13.80	3.85	4.46	5.66
	SAM R 31690	745	117	5.92	2.94	3.12	2.31	5.11	7.98	5.82	16.48	23.40	8.38	11.35	3.40	4.23	5.14
	SAM R 31691	918	137	6.62	3.13	3.48	2.50	5.27	9.36	6.42	19.14	26.24	9.14	13.65	4.05	4.97	6.61
	SAM R 36306	1098	172	7.59	4.20	3.92	2.54	6.59	11.05	7.94	22.52	29.99	10.38	15.46	4.08	6.02	7.27
	SAM R 40497	854	133	6.36	3.50	2.70	1.45	5.48	8.58	6.49	18.35	25.00	9.60	10.90	3.94	4.56	5.89
	SAM R 40758	526	89	4.69	2.69	2.48	1.56	4.18	6.04	4.34	13.58	18.61	7.07	10.14	2.97	3.45	4.13
	SAM R 40759	896	169	6.24	3.77	2.80	2.33	5.30	8.56	5.86	13.12	26.20	9.68	12.74	3.63	5.05	6.17
	SAM R 42409	1165	147	6.96	4.24	4.06	2.85	6.36	9.76	7.81	21.89	31.36	11.32	15.16	4.02	5.71	7.21
	SAM R 42410	908	136	6.24	3.80	3.41	2.47	5.45	8.57	6.54	18.30	25.76	10.14	14.15	3.70	4.86	5.79
	SAM R 46467	1112	175	6.99	3.83	3.94	2.35	5.79	9.88	6.97	20.91	26.59	10.67	15.66	3.82	5.63	7.10
	SAM R 46513	1158	182	7.11	4.49	3.92	2.65	5.98	10.78	7.79	22.81	32.03	11.80	17.26	3.79	6.24	7.30
	SAM R 49359	848	131	6.49	3.06	3.44	1.94	5.31	8.83	6.12	18.67	26.23	9.37	14.09	3.64	4.99	5.81
Female																	
	AM R 157295	735	116	5.67	3.28	3.07	1.86	5.00	7.04	5.34	16.48	22.81	8.16	14.06	3.57	4.32	4.41

Species	Specimen Number	Snout-vent length	Tail length	Length of frontal	Width of frontal	Distance from rostral to frontal	Length of prefrontal suture	Mean length of supraoculars	Mean length of parietals	Length of parietal suture	Distance from snout tip to posterior end of parietal suture	Mean distance from snout tip to posterior end of mandible	Interocular distance	Head width	Mean eye diameter	Mean distance from eye to nostril	Internarial distance
	SAM R 18600	1056	169	7.53	3.65	2.67	1.50	5.84	9.52	6.69	20.31	27.45	9.92	15.39	3.96	5.50	6.16
	SAM R 18994	562	85	4.81	2.31	2.32	1.32	4.16	6.51	4.50	13.78	18.95	6.82	10.95	3.25	3.35	4.15
	SAM R 21432	552	90	5.24	2.68	2.76	1.47	4.13	6.75	4.96	14.83	19.42	7.21	8.61	2.94	3.90	4.14
	SAM R 21433	468	70	4.46	2.09	2.56	1.54	3.94	5.99	4.14	13.16	16.66	6.61	8.35	3.00	3.31	4.09
	SAM R 21434	462	71	4.01	2.22	2.38	1.76	3.54	6.02	3.81	12.59	17.28	6.19	7.77	2.94	3.30	3.77
	SAM R 21435	341	49	4.15	1.79	1.64	0.81	3.06	4.59	3.80	10.79	13.74	5.15	6.26	2.48	2.70	3.17
	SAM R 24410	1101	151	7.32	3.76	3.30	1.98	6.35	9.63	7.37	20.48	27.24	10.78	12.16	4.25	5.26	6.71
	SAM R 24411	1040	157	7.54	3.61	3.30	2.01	5.83	9.30	6.67	19.80	27.70	10.39	13.85	4.15	5.29	6.10
	SAM R 25058	1090	183	6.60	3.44	3.31	2.26	6.56	9.74	7.16	20.33	28.40	10.34	15.26	4.37	5.13	6.17
	SAM R 36352	986	143	6.21	3.25	3.41	1.95	5.24	8.37	6.04	18.93	25.66	9.16	14.20	3.97	5.24	5.96
Pseudonaja textilis																	
Male																	
	AM R 141106	562	120	6.13	2.51	2.97	2.01	4.64	6.60	4.59	15.34	21.24	8.26	8.33	3.52	3.72	4.21
	AM R 149264	1052	216	8.41	4.10	5.38	3.99	7.33	11.12	7.86	25.07	34.52	12.72	16.18	5.19	6.41	7.00
	AM R 151551	1495	221	10.69	5.11	6.20	4.29	9.70	13.49	10.47	31.93	42.56	15.96	19.16	6.72	8.02	8.54
	AM R 151570	1115	222	8.32	4.14	5.30	4.00	7.49	11.02	8.06	24.45	33.41	12.36	15.48	5.34	6.32	6.93
	AM R 151699	1181	228	9.30	4.19	5.67	3.97	8.41	11.70	8.04	27.01	37.44	13.85	18.83	6.21	6.84	7.71
	AM R 152761	1402	206	10.10	4.90	6.65	4.50	9.10	14.47	10.09	30.92	42.96	16.28	20.29	6.47	8.55	9.19
	AM R 152790	1251	234	9.90	4.96	6.26	4.16	8.49	12.59	8.56	27.38	38.61	14.10	17.97	5.76	7.16	7.60
	AM R 153025	1367	210	9.90	5.11	6.66	4.25	8.27	13.36	9.23	29.15	39.78	14.40	17.55	5.78	7.85	7.25
	AM R 156908	863	174	7.84	4.01	4.71	2.47	6.13	9.16	6.26	19.80	27.97	11.22	15.07	4.22	5.51	5.84
	AM R 156942	1572	254	11.25	5.28	7.09	4.78	9.34	13.78	8.19	30.26	44.77	16.04	21.04	6.83	8.43	9.63
	SAM R 25070	837	172	7.67	3.77	4.80	3.55	7.05	10.24	6.96	22.10	28.18	11.35	12.74	4.67	5.55	6.81

Species	Specimen Number	Snout-vent length	Tail length	Length of frontal	Width of frontal	Distance from rostral to frontal	Length of prefrontal suture	Mean length of supraoculars	Mean length of parietals	Length of parietal suture	Distance from snout tip to posterior end of parietal suture	Mean distance from snout tip to posterior end of mandible	Interocular distance	Head width	Mean eye diameter	Mean distance from eye to nostril	Internarial distance
	SAM R 31692	803	151	6.95	3.01	4.11	3.24	5.99	8.68	6.13	19.60	27.13	9.75	13.41	4.11	5.06	5.36
	SAM R 31701	874	189	7.37	3.68	5.20	3.72	6.89	9.39	6.75	22.18	30.72	11.40	15.69	4.82	5.81	6.51
	SAM R 56770	964	212	8.30	3.98	6.45	4.24	7.10	10.24	7.07	23.34	33.20	12.26	15.44	4.90	6.07	7.23
Females																	
	AM R 142766	770	166	6.55	3.45	4.70	3.30	6.44	8.44	6.09	19.20	28.16	10.36	13.51	4.59	5.24	5.76
	AM R 153008	934	208	7.50	3.65	5.11	3.20	6.59	10.07	6.70	22.16	30.92	10.75	14.64	4.69	5.83	5.78
	SAM R 18605	937	226	7.79	3.87	5.16	3.75	6.76	9.51	6.26	15.64	29.70	11.14	14.80	4.64	5.56	6.21
	SAM R 19943	1415	273	9.82	4.27	6.94	4.72	8.90	12.97	8.90	21.24	44.08	15.06	22.66	6.00	8.17	8.45
	SAM R 31697	830	182	7.52	3.38	4.66	3.32	6.70	9.34	7.10	21.21	28.38	11.21	13.95	4.77	5.08	5.73
	SAM R 56724	1002	192	7.26	3.47	4.37	2.87	5.87	8.83	6.18	20.31	27.83	9.91	13.75	4.12	5.12	5.95

Appendix 6

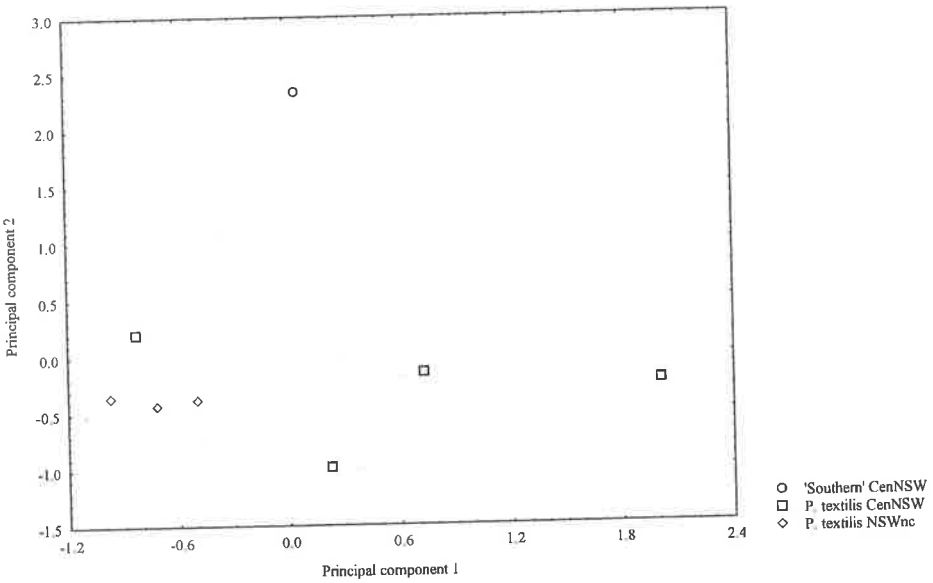
Geographical groups were delimited on the basis of collecting gaps and presumed physiographical barriers (e.g. Great Dividing Range, Spencer Gulf).



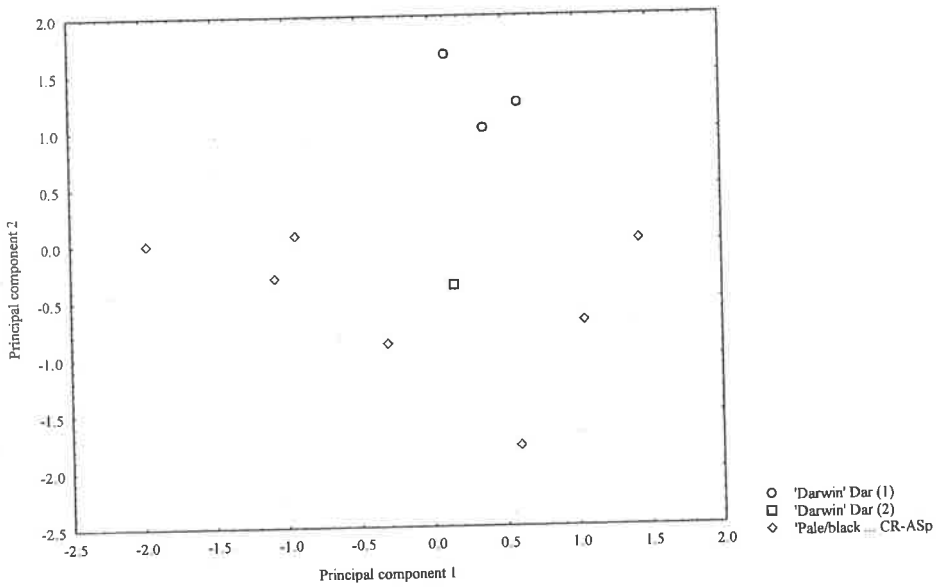
Geographical groups delimited on the basis of collecting gaps and presumed physiographical barriers. Abbreviations are: CenNSW – central NSW, CenNT – central NT, CR-Asp – central ranges and Alice Springs, Dar – Darwin, EyrPen – Eyre Peninsula, Flin-OR – Flinders and Olary Ranges, NSWnc – NSW north coast, YorPen – Yorke Peninsula.

The homogeneity of each group was assessed using principal components analysis. Separate analyses were performed for male and female specimens, negating any effect of sexual dimorphism. Where geographical groups were observed to exhibit internal heterogeneity (i.e. where principal components analysis indicated the presence of more than one morphologically distinct group), specimens were partitioned into morphologically homogeneous subgroups. In a number of cases, geographical groups (or subgroups) contained specimens of more than one major

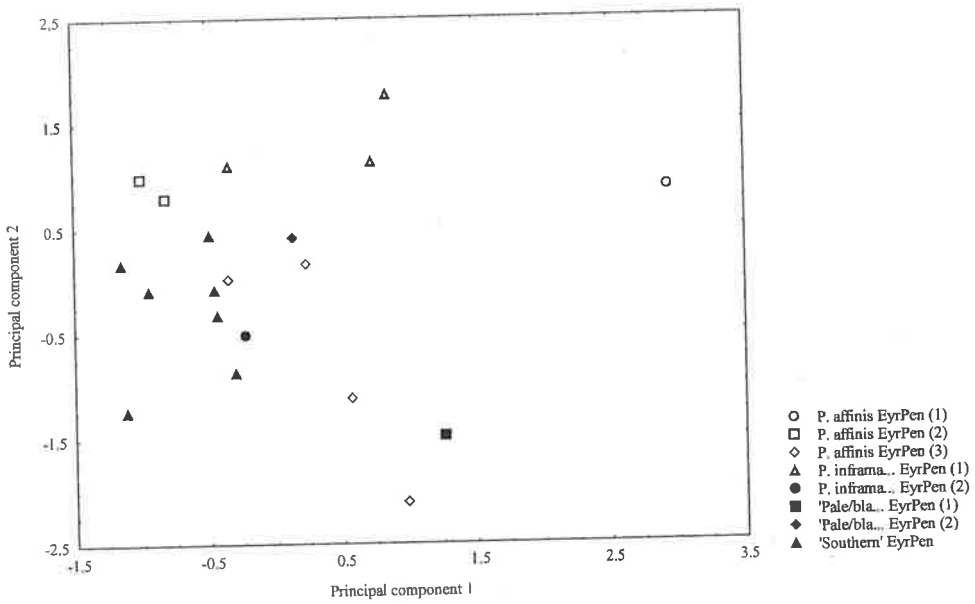
mitochondrial DNA clade. These groups were divided (still) further according to the mitochondrial DNA clades in which specimens were placed.



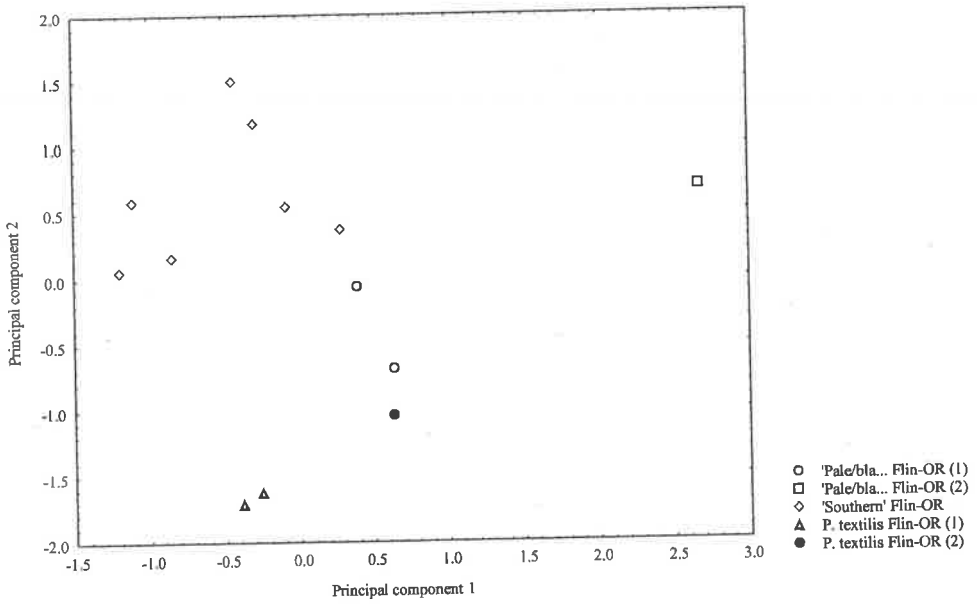
Principal component plot for male specimens of the central NSW (CenNSW) and NSW north coast (NSWnc) groups (see above). Specimens are identified according to the final geographical group in which they were placed.



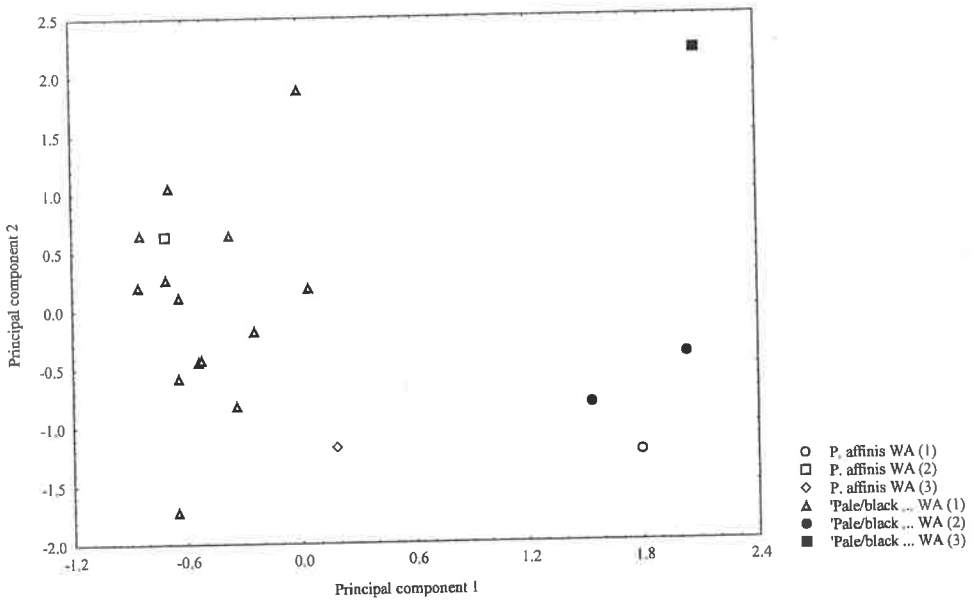
Principal component plot for male specimens of the central ranges and Alice Springs (CR-Asp), and Darwin (Dar) groups (see above). Specimens are identified according to the final geographical group in which they were placed.



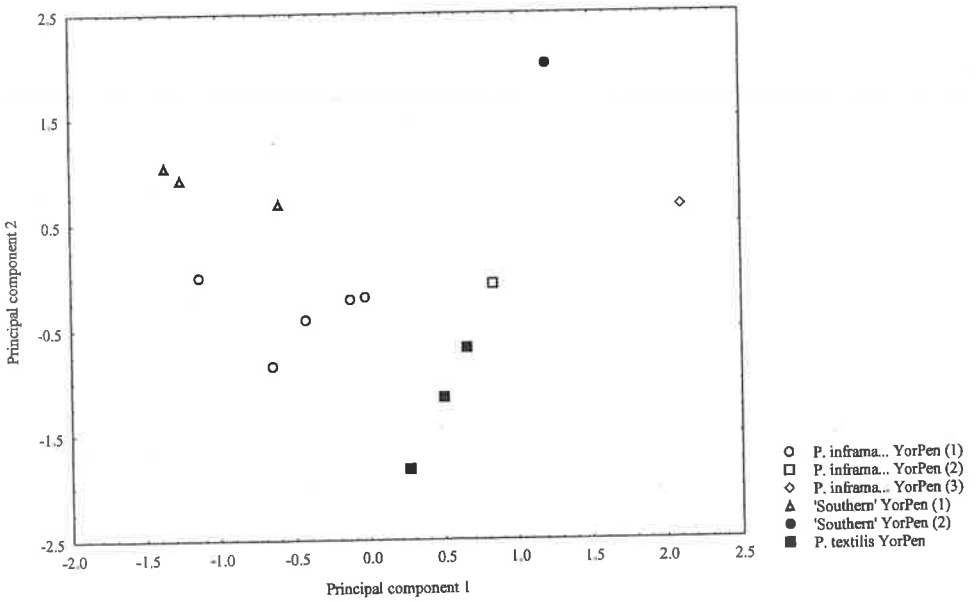
Principal component plot for male specimens of the Eyre Peninsula (EyrPen) group (see above). Specimens are identified according to the final geographical group in which they were placed.



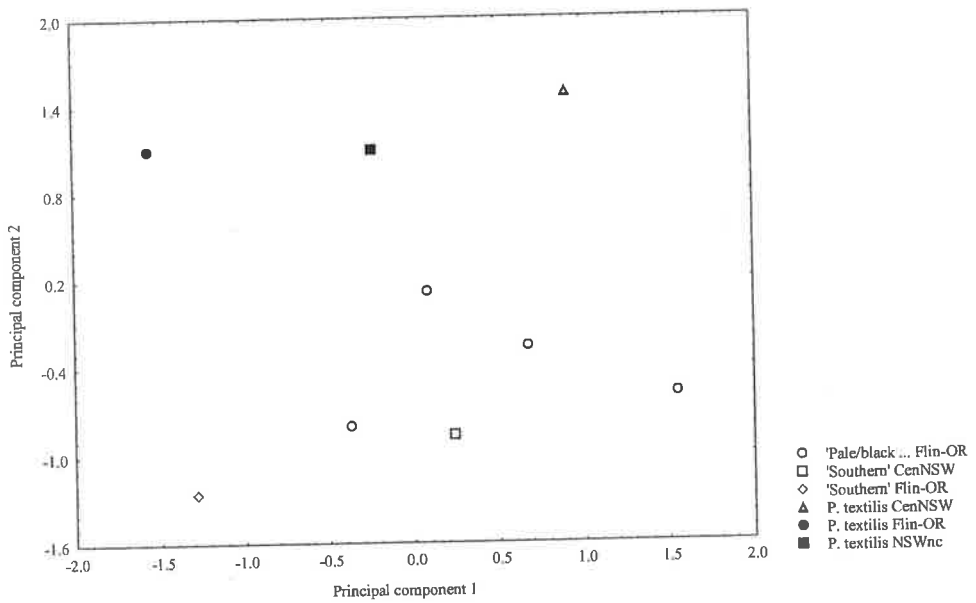
Principal component plot for male specimens of the Flinders and Olary Ranges (Flin-OR) group (see above). Specimens are identified according to the final geographical group in which they were placed.



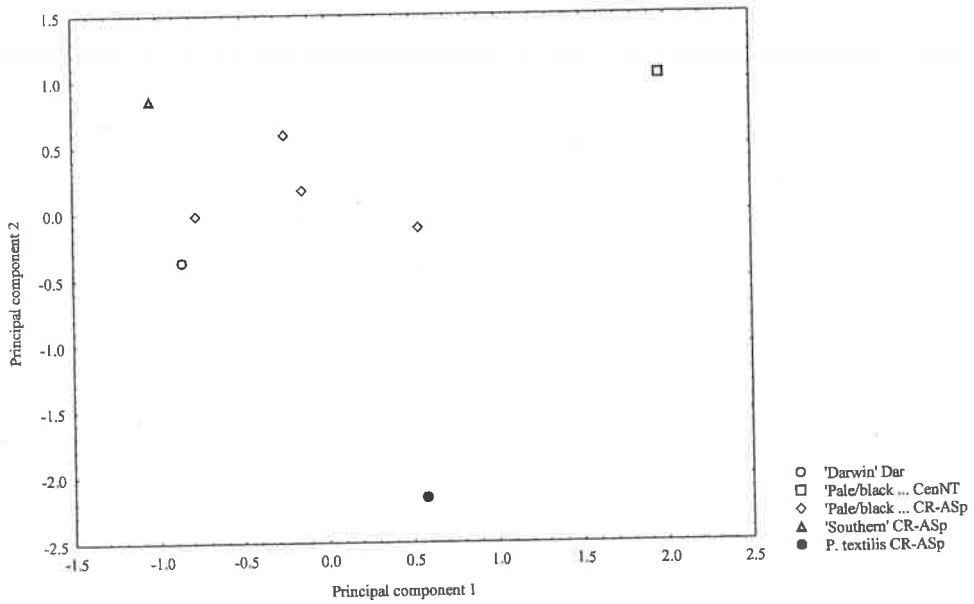
Principal component plot for male specimens of the WA group (see above). Specimens are identified according to the final geographical group in which they were placed.



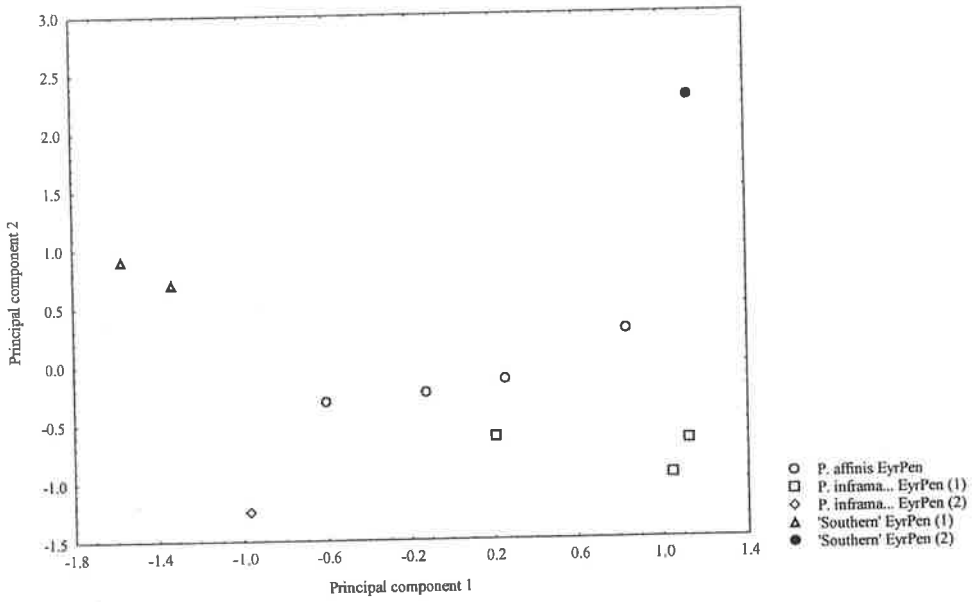
Principal component plot for male specimens of the Yorke Peninsula (YorPen) group (see above).. Specimens are identified according to the final geographical group in which they were placed.



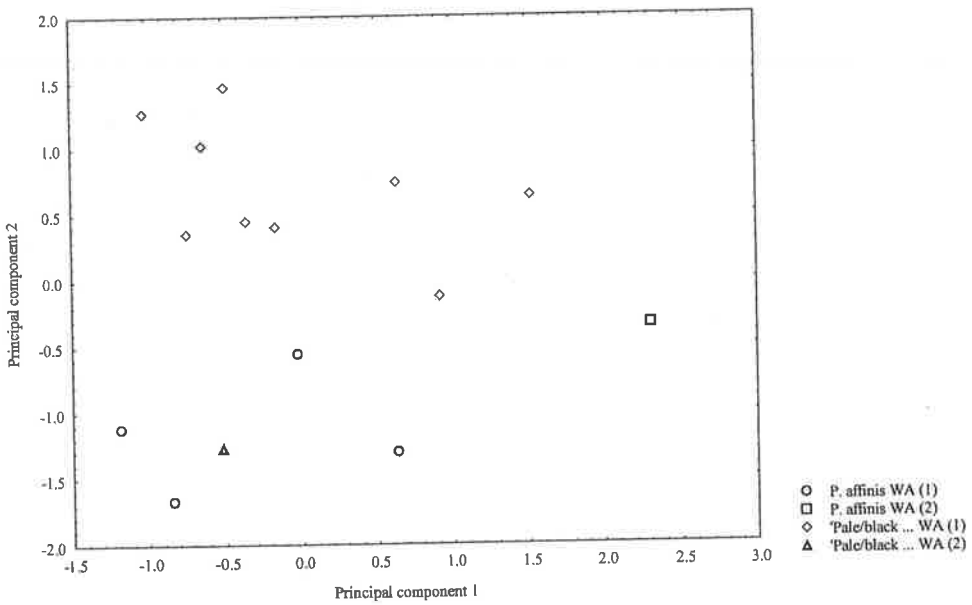
Principal component plot for female specimens of the central NSW (CenNSW), Flinders and Olary Ranges (Flin-OR), and NSW north coast (NSWnc) groups (see above). Specimens are identified according to the final geographical group in which they were placed.



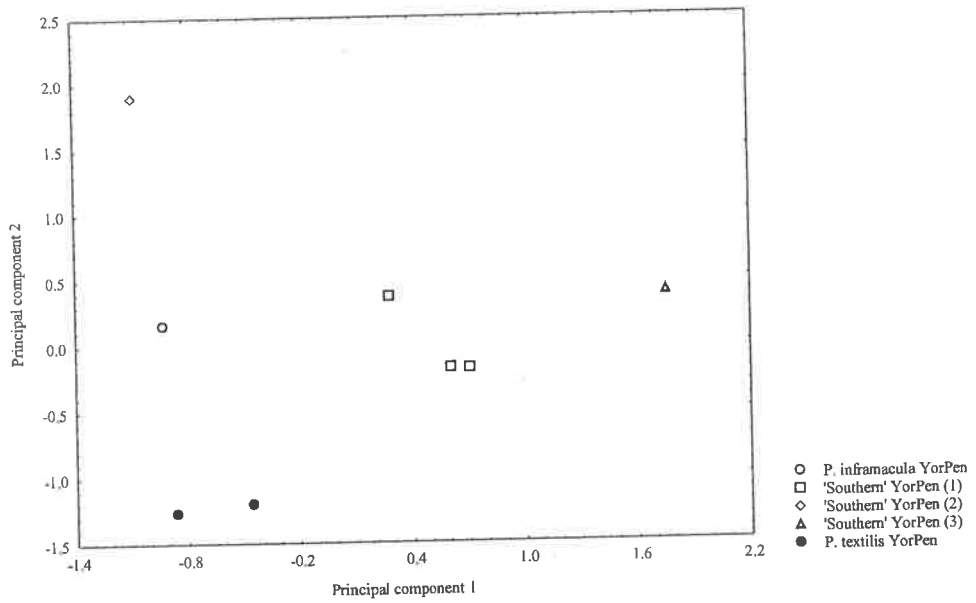
Principal component plot for female specimens of the central NT (CenNT), Darwin (Dar), and central ranges and Alice Springs (CR-Asp) groups (see above). Specimens are identified according to the final geographical group in which they were placed.



Principal component plot for female specimens of the Eyre Peninsula (EyrPen) group (see above). Specimens are identified according to the final geographical group in which they were placed.



Principal component plot for female specimens of the WA group (see above). Specimens are identified according to the final geographical group in which they were placed.



Principal component plot for female specimens of the Yorke Peninsula (YorPen) group (see above). Specimens are identified according to the final geographical group in which they were placed.

The final geographical groups employed are listed below.

Final geographical groups. Abbreviations are: CenNSW – central NSW, CenNT – central NT, CR-Asp – central ranges and Alice Springs, Dar – Darwin, EyrPen – Eyre Peninsula, Flin-OR – Flinders and Olary Ranges, NSWnc – NSW north coast, YorPen – Yorke Peninsula.

Mitochonrial DNA Clade	Geographical Group	Included Specimens
Pseudonaja affinis		
Male		
	EyrPen (1)	SAM R 24807
	EyrPen (2)	SAM R 20807, SAM R 52360
	EyrPen (3)	SAM R 18996, SAM R 20605, SAM R 24808, SAM R 26268
	WA (1)	SAM R 29468
	WA (2)	WAM R 119172
	WA (3)	WAM R 119550
Female		
	EyrPen	SAM R 18995, SAM R 21955, SAM R 26347, SAM R 31704

Mitochonrial DNA Clade	Geographical Group	Included Specimens
	WA (1)	SAM R 23000, WAM R 104272, WAM R 125640, WAM R 136095
	WA (2)	WAM R 77743
Pseudonaja inframacula		
Male		
	EyrPen (1)	SAM R 25702, SAM R 28457, SAM R 29026
	EyrPen (2)	SAM R 28559
	YorPen (1)	SAM R 24751, SAM R 24752, SAM R 24755, SAM R 24756, SAM R 31698
	YorPen (2)	SAM R 31599
	YorPen (3)	SAM R 24757
Female		
	EyrPen (1)	SAM R 25422, SAM R 36588, SAM R 38193
	EyrPen (2)	SAM R 57076
	YorPen	SAM R 56771
Pseudonaja nuchalis 'Darwin'		
Male		
	Dar (1)	NTM R 10685, SAM R 56774, SAM R 56775
	Dar (2)	SAM R 56773
Female		
	Dar	SAM R 56772
Pseudonaja nuchalis 'Pale/black headed'		
Male		
	CR-Asp	SAM R 51516, SAM R 51591, SAM R 51592, SAM R 56714, SAM R 56715, SAM R 56723, SAM R 56725
	EyrPen (1)	SAM R 24821
	EyrPen(2)	SAM R 21414
	Flin-OR (1)	SAM R 20981, SAM R 21413
	Flin-OR (2)	SAM R 21025
	WA (1)	SAM R 28531, SAM R 29360, WAM R 103848, WAM R 103849, WAM R 104187, WAM R 115021, WAM R 115062, WAM R 115063, WAM R 115180, WAM R 115607, WAM R 115609, WAM R 115751, WAM R 115752, WAM R 119293
	WA (2)	WAM R 115183, WAM R 115276
	WA (3)	WAM R 115182
Female		
	CenNT	NTM R 18321
	CR-Asp	SAM R 46920, SAM R 56716, SAM R 56720, SAM R 56722
	Flin-OR	AM R 150262, SAM R 21415, SAM R 36953, SAM R 42333

Mitochonrial DNA Clade	Geographical Group	Included Specimens
	WA (1)	SAM R 29288, SAM R 29407, WAM R 102045, WAM R 114659, WAM R 114661, WAM R 114663, WAM R 115608, WAM R 115610, WAM R 116498
	WA (2)	WAM R 119526
Pseudonaja nuchalis 'Southern'		
Male		
	CenNSW	AM R 157294
	EyrPen	SAM R 18599, SAM R 21163, SAM R 22746, SAM R 31691, SAM R 42409, SAM R 42410, SAM R 46513
	Flin-OR	SAM R 18598, SAM R 24828, SAM R 31690, SAM R 36306, SAM R 40497, SAM R 46467, SAM R 49359
	YorPen (1)	SAM R 24778, SAM R 25295, SAM R 407549
	YorPen (2)	SAM R 40758
Female		
	CenNSW	AM R 15729
	CR-Asp	SAM R 18600
	EyrPen (1)	SAM R 24410, SAM R 24411
	EyrPen (2)	SAM R 18994
	Flin-OR	SAM R 36352
	YorPen (1)	SAM R 21432, SAM R 21433, SAM R 21434
	YorPen (2)	SAM R 25058
	YorPen (3)	SAM R 21435
Pseudonaja textilis		
Male		
	CenNSW	AM R 141106, AM R 149264, AM R 151551, AM R 156908
	Flin-OR (1)	AM R 151570, AM R 151699
	Flin-OR (2)	SAM R 31692
	NSWnc	AM R 152761, AM R 153025, AM R 156942
	YorPen	SAM R 25070, SAM R 31701, SAM R 56770
Female		
	CenNSW	AM R 142766
	CR-Asp	SAM R 56724
	Flin-OR	SAM R 19943
	NSWnc	AM R 153008
	YorPen	SAM R 18605, SAM R 31697

Appendix 7

Scale counts recorded for nominal *P. affinis*, *P. inframacula*, *P. nuchalis*, and *P. textilis* specimens in the SAM.

Species	Specimen number	Number of ventrals	Number of subcaudals	Number of dorsal rows at first ventral	Number of dorsal rows one head length posterior to parietals	Number of dorsal rows at midbody	Number of dorsal rows one head length anterior to vent	Number of dorsal rows at anal
Pseudonaja affinis	SAM R 18995	223	58	20	17	17	15	15
	SAM R 18996	220	61	22	17	17	13	15
	SAM R 20605	212	62	21	17	17	13	16
	SAM R 20807	212	59	23	17	17	14	15
	SAM R 21955	219	63	23	17	19	15	15
	SAM R 22974	209	55	22	19	19	15	17
	SAM R 23000	220	56	23	19	19	15	17
	SAM R 24807	204	60	22	19	17	13	16
	SAM R 24808	219	61	23	18	17	15	15
	SAM R 26268	221	63	21	19	19	13	16
	SAM R 26347	222	60	22	17	17	15	16
	SAM R 29468	211	58	21	19	19	15	15
	SAM R 31704	211	57	23	17	19	15	15
	SAM R 52360	213	59	23	18	17	15	15
Pseudonaja inframacula	SAM R 24751	208	59	19	17	17	13	16
	SAM R 24752	204	58	20	17	17	13	16
	SAM R 24755	199	62	19	17	17	13	15
	SAM R 24756	195	63	19	17	17	13	15
	SAM R 25702	200	61	21	17	17	13	15
	SAM R 26474	198	58	21	17	17	13	15
	SAM R 28457	195	58	21	17	17	13	15
	SAM R 29026	200	64	21	17	17	13	16
	SAM R 31698	200	55	20	17	17	13	15
	SAM R 31599	201	62	20	17	17	13	15
	SAM R 24757	208	66	20	17	17	13	15
	SAM R 25422	204	60	22	17	17	15	15
	SAM R 31599	202	62	21	17	17	13	15
	SAM R 36588	202	62	20	17	17	13	15
	SAM R 38193	199	56	21	17	17	13	15
	SAM R 57076	205	61	21	17	17	13	15
	SAM R 56771	205	58	23	17	17	13	15
Pseudonaja nuchalis 'Darwin'	SAM R 56772	204	57	24	19	17	15	15
	SAM R 51138	199	62	24	19	17	14	15
	SAM R 56774	198	58	23	21	17	15	17
	SAM R 56775	194	60	25	21	17	16	15
	SAM R 56773	199	61	23	19	17	15	15

Species	Specimen number	Number of ventrals	Number of subcaudals	Number of dorsal rows at first ventral	Number of dorsal rows one head length posterior to parietals	Number of dorsal rows at midbody	Number of dorsal rows one head length anterior to vent	Number of dorsal rows at anal
Pseudonaja nuchalis 'Pale/black headed'	SAM R 56723	203	55	20	17	17	13	15
	SAM R 56725	206	59	21	19	17	15	16
	SAM R 56714	205	56	21	17	17	13	15
	SAM R 28531	210	58	21	17	17	13	15
	SAM R 29360	212	63	21	17	17	13	15
	SAM R 56715	199	55	21	17	17	13	15
	SAM R 56716	203	49	19	17	17	13	15
	SAM R 56719	206	-	19	17	17	15	17
	SAM R 56720	204	50	20	17	17	13	15
	SAM R 56722	205	62	21	17	17	15	15
	SAM R 46920	215	51	21	17	17	14	15
	SAM R 36953	211	56	21	17	17	13	17
	SAM R 21414	206	55	19	17	17	13	14
	SAM R 21415	204	52	21	17	17	13	15
	SAM R 51516	210	56	21	17	17	13	16
	SAM R 51591	209	58	-	-	17	13	16
	SAM R 51592	207	58	21	17	17	13	15
	SAM R 20981	208	58	21	17	17	13	16
	SAM R 21025	210	61	21	17	17	13	15
	SAM R 21413	203	58	23	17	17	13	13
	SAM R 24821	201	58	21	17	17	15	15
	SAM R 29288	221	58	21	17	17	15	17
	SAM R 29407	214	59	21	17	17	15	17
	SAM R 36954	-	-	20	17	-	-	-
	SAM R 42333	224	54	21	17	17	13	15
Pseudonaja nuchalis 'Southern'	SAM R 18598	223	56	19	17	17	13	15
	SAM R 18599	210	59	21	19	17	13	16
	SAM R 18600	219	56	22	19	17	13	15
	SAM R 18994	221	48	21	17	17	13	15
	SAM R 21163	209	53	23	19	17	13	15
	SAM R 21432	215	52	23	19	17	15	18
	SAM R 21433	226	49	22	19	17	13	15
	SAM R 21434	218	52	22	19	17	13	16
	SAM R 21435	217	49	20	19	17	13	15
	SAM R 22746	211	-	22	19	17	13	15
	SAM R 24410	219	47	21	19	17	13	14
	SAM R 24411	209	50	22	18	17	13	15
	SAM R 24778	209	56	23	19	17	13	16
	SAM R 24828	214	47	21	18	17	13	15
	SAM R 25058	220	55	22	19	17	13	15
	SAM R 25295	215	56	23	19	17	13	15
	SAM R 28559	210	53	21	19	17	13	15
	SAM R 31690	208	50	22	19	17	14	16
	SAM R 31691	212	54	23	19	17	13	15

Species	Specimen number	Number of ventrals	Number of subcaudals	Number of dorsal rows at first ventral	Number of dorsal rows one head length posterior to parietals	Number of dorsal rows at midbody	Number of dorsal rows one head length anterior to vent	Number of dorsal rows at anal
	SAM R 36306	212	52	22	17	17	13	15
	SAM R 36352	224	50	20	17	17	13	15
	SAM R 40497	213	54	21	18	17	13	13
	SAM R 40758	210	54	22	19	17	13	17
	SAM R 40759	207	63	21	19	17	13	15
	SAM R 42409	212	51	23	19	17	13	14
	SAM R 42410	219	57	23	19	17	13	15
	SAM R 46467	208	54	21	18	17	13	16
	SAM R 46513	212	56	22	19	17	14	16
	SAM R 49359	209	52	20	19	17	13	17
Pseudonaja textilis	SAM R 25070	199	63	23	17	17	13	15
	SAM R 31692	210	64	21	17	17	14	15
	SAM R 31701	194	65	19	17	17	15	17
	SAM R 56770	203	68	21	17	17	13	16
	SAM R 31697	203	64	20	17	17	15	15
	SAM R 18605	205	70	19	19	17	15	17
	SAM R 19943	210	62	21	17	17	13	17
	SAM R 42663	-	-	21	19	-	-	-
	SAM R 56724	229	66	21	17	17	15	15

Appendix 8

Canonical scores for the first two canonical variates extracted in a discriminant function analysis including all male specimens.

Mitochondrial DNA Clade	Specimen Number	Canonical variate 1	Canonical variate 2
Pseudonaja affinis	SAM R 18996	-1.30	-0.36
	SAM R 20605	-0.74	0.52
	SAM R 20807	0.15	1.60
	SAM R 24807	8.43	-5.44
	SAM R 24808	-1.01	-1.81
	SAM R 26268	0.41	-0.10
	SAM R 29468	0.11	-8.56
	SAM R 52360	0.52	2.40
	WAM R 119172	0.40	0.89
	WAM R 119550	-1.87	-2.09
Pseudonaja inframacula	SAM R 24751	4.72	1.39
	SAM R 24752	2.81	-1.10
	SAM R 24755	2.10	-0.85
	SAM R 24756	3.89	-0.04
	SAM R 24757	4.39	-6.79
	SAM R 25702	2.64	-0.11
	SAM R 28457	2.63	-2.11
	SAM R 28559	-1.33	0.04
	SAM R 29026	2.53	-3.43
	SAM R 31599	1.81	-4.09
	SAM R 31698	5.18	-1.95
Pseudonaja nuchalis 'Darwin'	NTM R 10685	-2.30	1.19
	SAM R 56773	0.21	0.17
	SAM R 56774	-2.54	0.68
	SAM R 56775	-2.59	1.94
Pseudonaja nuchalis 'Pale/black headed'	SAM R 20981	-2.53	-1.30
	SAM R 21025	-4.52	-7.18
	SAM R 21413	-1.38	-1.36
	SAM R 21414	-0.51	0.52
	SAM R 24821	-1.63	-2.52
	SAM R 28531	-3.93	0.05
	SAM R 29360	1.10	-1.22
	SAM R 51516	-3.16	-0.24
	SAM R 51591	-3.42	-0.64
	SAM R 51592	-1.64	1.19
	SAM R 56714	-2.74	1.24
	SAM R 56715	-1.72	-0.27
	SAM R 56723	-1.46	0.66

Mitochondrial DNA Clade	Specimen Number	Canonical variate 1	Canonical variate 2
	SAM R 56725	-3.23	0.52
	WAM R 103848	-3.47	-0.87
	WAM R 103849	-3.37	-0.64
	WAM R 104187	-2.48	-2.09
	WAM R 115021	-3.50	-0.14
	WAM R 115062	-2.20	-0.93
	WAM R 115063	-2.32	-0.64
	WAM R 115180	-0.97	-0.27
	WAM R 115182	-8.73	-8.23
	WAM R 115183	-4.05	-9.06
	WAM R 115276	-4.51	-8.00
	WAM R 115607	-2.35	-0.68
	WAM R 115609	-1.99	-0.40
	WAM R 115751	-2.43	-0.51
	WAM R 115752	-2.56	-1.34
	WAM R 119293	-5.04	-1.20
Pseudonaja nuchalis 'Southern'	AM R 157294	-3.05	2.71
	SAM R 18598	-0.60	4.10
	SAM R 18599	-0.37	0.20
	SAM R 21163	-0.91	2.05
	SAM R 22746	-1.42	3.20
	SAM R24778	-0.13	2.24
	SAM R 24828	-1.98	2.14
	SAM R 25295	-0.85	3.60
	SAM R 31690	-0.25	0.17
	SAM R 31691	-0.95	1.22
	SAM R 36306	-2.25	1.44
	SAM R 40497	-1.25	1.83
	SAM R 40758	-1.92	-3.26
	SAM R 40759	-0.57	4.45
	SAM R 42409	-0.01	2.80
	SAM R 42410	0.41	1.64
	SAM R 46467	-0.37	2.40
	SAM R 46513	-1.86	1.83
	SAM R 49359	-1.72	1.14
Pseudonaja textilis	AM R 141106	6.52	-1.95
	AM R 149264	4.74	-1.07
	AM R 151551	5.25	2.61
	AM R 151570	4.89	0.28
	AM R 151699	5.49	0.50
	AM R 152761	4.79	0.97
	AM R 153025	4.83	0.99
	AM R 156908	3.75	-0.23
	AM R 156942	5.80	1.91
	SAM R 25070	5.45	-4.31

Mitochondrial DNA Clade	Specimen Number	Canonical variate 1	Canonical variate 2
	SAM R 31692	3.94	-0.86
	SAM R 31701	4.98	-2.70
	SAM R 56770	6.82	-3.18

Canonical scores for the first two canonical variates extracted in a discriminant function analysis including male specimens of the *Pseudonaja affinis*, *Pseudonaja nuchalis* 'Darwin', *Pseudonaja nuchalis* 'Pale/black headed', and *Pseudonaja nuchalis* 'Southern' clades (excluding SAM R 21025, SAM R 24807, SAM R 29468, WAM R 115182, WAM R 115183, and WAM R 115276), and SAM R 28559.

Mitochondrial DNA Clade	Specimen Number	Canonical variate 1	Canonical variate 2
Pseudonaja affinis	SAM R 18996	0.35	2.06
	SAM R 20605	0.17	1.53
	SAM R 20807	-2.45	-1.72
	SAM R 24808	0.06	1.91
	SAM R 26268	0.23	2.70
	SAM R 52360	-1.90	0.74
	WAM R 119172	-0.76	1.39
	WAM R 119550	3.73	0.00
Pseudonaja inframacula	SAM R 28559	-1.26	2.17
Pseudonaja nuchalis 'Darwin'	NTM R 10685	2.28	3.83
	SAM R 56773	3.14	1.75
	SAM R 56774	1.91	2.38
	SAM R 56775	1.66	2.19
Pseudonaja nuchalis 'Pale/black headed'	SAM R 20981	3.28	1.32
	SAM R 21413	3.93	0.85
	SAM R 21414	-1.28	-2.15
	SAM R 24821	2.91	-1.03
	SAM R 28531	1.45	-2.27
	SAM R 29360	0.77	-1.16
	SAM R 51516	2.77	0.51
	SAM R 51591	2.75	2.14
	SAM R 51592	0.37	1.54
	SAM R 56714	2.52	0.67
	SAM R 56715	2.21	-0.15
	SAM R 56723	1.53	-1.06
	SAM R 56725	2.11	0.25

Mitochondrial DNA Clade	Specimen Number	Canonical variate 1	Canonical variate 2
	WAM R 103848	2.88	-1.83
	WAM R 103849	2.49	-1.52
	WAM R 104187	5.01	-0.86
	WAM R 115021	2.94	-0.94
	WAM R 115062	2.98	-1.39
	WAM R 115063	2.43	-0.71
	WAM R 115180	2.11	-0.78
	WAM R 115607	1.71	-1.61
	WAM R 115609	2.70	-0.29
	WAM R 115751	1.91	-1.48
	WAM R 115752	2.55	-1.52
	WAM R 119293	1.44	-2.58
Pseudonaja nuchalis 'Southern'	AM R 157294	-0.66	0.59
	SAM R 18598	-5.16	1.07
	SAM R 18599	-2.64	-0.86
	SAM R 21163	-2.29	-0.71
	SAM R 22746	-5.32	0.51
	SAM R 24778	-3.79	-1.62
	SAM R 24828	-3.69	0.01
	SAM R 25295	-3.20	0.90
	SAM R 31690	-2.59	-0.97
	SAM R 31691	-3.12	0.47
	SAM R 36306	-2.26	-0.88
	SAM R 40497	-3.18	3.11
	SAM R 40758	1.91	2.61
	SAM R 40759	-3.35	0.93
	SAM R 42409	-5.33	-1.88
	SAM R 42410	-3.49	-0.10
	SAM R 46467	-4.39	-0.47
	SAM R 46513	-1.26	-1.87
	SAM R 49359	-2.08	-0.40

Canonical scores for the first two canonical variates extracted in a discriminant function analysis including all female specimens.

Mitochondrial DNA Clade	Specimen Number	Canonical variate 1	Canonical variate 2
Pseudonaja affinis	SAM R 18995	-2.89	-1.22
	SAM R 21955	-4.00	-0.59
	SAM R 23000	-0.74	-1.15
	SAM R 26347	-3.69	-2.03

Mitochondrial DNA Clade	Specimen Number	Canonical variate 1	Canonical variate 2
	SAM R 31704	-3.13	-3.24
	WAM R 104272	-1.04	-3.68
	WAM R 125640	0.55	-0.96
	WAM R 136095	1.15	0.40
	WAM R 77743	-5.84	-4.45
Pseudonaja inframacula	SAM R 25422	-6.43	-0.27
	SAM R 36588	-5.52	1.37
	SAM R 38193	-5.25	2.31
	SAM R 56771	-3.28	1.37
	SAM R 57076	-1.79	2.80
Pseudonaja nuchalis 'Darwin'	SAM R 56772	-1.08	-2.04
Pseudonaja nuchalis 'Pale/black headed'	AM R 150262	5.02	4.46
	NTM R 18321	5.42	2.27
	SAM R 21415	2.52	4.30
	SAM R 29288	2.04	1.06
	SAM R 29407	3.81	1.08
	SAM R 36953	1.50	4.52
	SAM R 42333	2.73	3.23
	SAM R 46920	3.51	0.39
	SAM R 56716	4.27	0.15
	SAM R 56720	5.55	-0.47
	SAM R 56722	4.01	-0.32
	WAM R 102045	0.24	2.45
	WAM R 103924	3.08	-0.07
	WAM R 114659	2.10	1.44
	WAM R 114661	4.44	1.12
	WAM R 114663	3.14	1.08
	WAM R 115608	2.67	-0.64
	WAM R 115610	2.47	1.60
	WAM R 116498	3.14	1.25
	WAM R 119526	3.07	2.56
Pseudonaja nuchalis 'Southern'	AM R 157295	0.73	-5.63
	SAM R 18600	4.37	-3.24
	SAM R 18994	-0.01	-2.73
	SAM R 21432	-0.33	-5.77
	SAM R 21433	-0.79	-5.21
	SAM R 21434	-0.43	-5.44
	SAM R 21435	-4.19	-7.12
	SAM R 24410	0.85	-5.08
	SAM R 24411	0.72	-3.51
	SAM R 25058	1.13	-0.54
	SAM R 36352	4.64	-3.24

Mitochondrial DNA Clade	Specimen Number	Canonical variate 1	Canonical variate 2
Pseudonaja textilis	AM R 142766	-9.31	-0.32
	AM R 153008	-3.83	4.04
	SAM R 18605	-11.68	4.63
	SAM R 19943	-5.79	5.88
	SAM R 31697	-10.53	2.74
	SAM R 56724	-3.10	3.72