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SHORT COMMUNICATION

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Phylogeography of Australia's king brown snake (*Pseudechis australis*) reveals Pliocene divergence and Pleistocene dispersal of a top predator

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Abstract King brown snakes or mulga snakes (*Pseudechis australis*) are the largest and among the most dangerous and wide-ranging venomous snakes in Australia and New Guinea. They occur in diverse habitats, are important predators, and exhibit considerable morphological variation. We infer the relationships and historical biogeography of *P. australis* based on phylogenetic analysis of 1,249 base pairs from the mitochondrial cytochrome *b*, NADH dehydrogenase subunit 4 and three adjacent tRNA genes using Bayesian, maximum-likelihood, and maximum-parsimony methods. All methods reveal deep phylogenetic structure with four strongly supported clades comprising snakes from New Guinea (I), localities all over Australia (II), the Kimberleys of Western Australia (III), and north-central Australia (IV), suggesting a much more ancient radiation than previously believed. This conclusion is robust to different molecular clock estimations indicating divergence in Pliocene or Late Miocene, after landbridge dispersal to New Guinea had occurred. While members of clades I, III and IV are medium-sized, slender snakes, those of clade II attain large sizes and a robust build, rendering them top predators in their ecosystems. Genetic differentiation within clade II is low and haplotype distribution largely incongruent with geography or colour morphs, suggesting Pleistocene dispersal and recent ecomorph evolution. Significant haplotype diversity exists in clades III and IV, implying that clade IV comprises two species. Members of clade II are broadly sympatric with members of both northern Australian clades. Thus, our data support the recognition of at least five species from within *P. australis* (auct.) under various criteria. We discuss biogeographical, ecological and medical implications of our findings.

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Introduction

Molecular techniques have proven to be crucial for the characterization of morphologically conservative species. Many recent studies revealed a common pattern of phylogenetic segregation according to geographic breaks and not morphology or life history (Bonett and Chippindale 2004), parallel evolution of ecomorphs (Keogh et al. in press), and discordance with taxonomic concepts based on phenetic similarity, especially subspecies classifications (Burbrink et al. 2000). Various studies demonstrated deep genetic structure indicating a long history of isolation, but the possibility that cryptic species occur in sympatry throughout much of their range has rarely been addressed (Olson et al. 2004). In the case of venomous snakes, this may be of great medical importance because the composition, biological activities and antigenic properties of snake venoms can vary dramatically between species (Chippaux et al. 1991).

King brown snakes (*Pseudechis australis*) are Australia's largest venomous snakes, attaining maximum lengths in excess of 3 m and considerable bulk (3–6 kg body mass at 2–2.5 m total length; Maryan 1997). Their

diet consists of reptiles including venomous snakes, mammals, and frogs (Shine 1998). Large specimens have few natural enemies and are often remarkably tolerant of human interference (Shine 1998). If cornered and fully aroused, however, they can be aggressive and extremely dangerous (Gow 1989). The variability of *P. australis* venom is extensive (Mebs 2001), and regional colour morphs (Smith 1982) as well as differences in growth rates, adult size and body stature have been noted (Maryan 1997). As a consequence of morphological variation and their wide distribution in Australia and southern New Guinea, these snakes have had a complicated taxonomic history (Smith 1982). Several species and subspecies have been named or revalidated from within *P. australis* over the past 20 years, but these publications were criticized for their paucity of data and lack of taxonomic scrutiny (reviewed in Hoser 2001; Wüster et al. 2001). Science has thus been reluctant to accept these proposed changes, continuing to recognize only a single monotypic species (Cogger 2002). Here we identify deep phylogenetic structure, ancient and recent dispersal, ecomorph evolution, and broad sympatry of cryptic species within *P. australis*.

Materials and methods

DNA was isolated from shed snake skins using laundry detergent (Kuch et al. 1999), and from muscle and liver tissue by proteinase K digestion and phenol–chloroform extraction. Prolonged digestion and dithiothreitol treatment were used for tissue from preserved museum specimens (Kuch et al. in press). We amplified the first 378 nucleotides of the mitochondrial (mt) cytochrome *b* (cytb) gene using primers L14910 (de Queiroz et al. 2002) and H15175 (Kocher et al. 1989), and an 871-bp region of mtDNA including 697 bp of the NADH dehydrogenase subunit 4 (ND4) and 174 bp of the $tRNA^{His,\ Ser,\ Leu}$ genes using primers ND4 and Leu (Forstner et al. 1995). PCR, cycle sequencing and sequence analysis was carried out as described in Kuch et al. (in press). Sequencing reactions for cytb used the amplification primers. Three internal primers were designed to sequence overlapping portions of the ND4 and tRNA fragment (see S1). S2 includes sequence accession numbers with geographic and specimen information. The sequences were aligned and concatenated (EMBL-Align database accession number: ALIGN_000750).

We used the yellow-bellied blacksnake (*Pseudechis butleri*) and the red-bellied blacksnake (*Pseudechis porphyriacus*) as outgroups (Keogh et al. 1998). Levels of saturation were examined for all codon positions and mutation types of cytb and ND4. Saturation graphs suggest that the ingroup sequences and *P. butleri* are essentially unaffected by saturation (see S3). To estimate the relative rate of sequence divergence of cytb and ND4 for our data, we calculated all possible pairwise uncorrected (*p*) distance comparisons, and plotted ND4 distances against the corresponding cytb distances (see S3). The regression slope of 1.08 suggests that these gene regions evolve at approximately the same rate in the studied taxa, rendering their divergence rates comparable.

The best-fitting model of molecular evolution for the data was determined by hierarchical log-likelihood ratio tests using MODELTEST 3.06 (Posada and Crandall 2001). Pairwise relative rate tests using the linearized tree method (Takezaki et al. 1995; implemented through PHYLTEST; Kumar 1996) were carried out to test if rates of nucleotide substitution differ between clades. We used *p*-distances and K80+G distances, grouped sequences by clade, and used *P. butleri* as the outgroup.

Pairwise distances were calculated for the combined protein-coding gene regions of the ingroup taxa, first without rate-correction, and then using the best-fitting model for these data (HKY85+G). Maximum and minimum pairwise distances were used to calculate divergence ranges. To infer approximate temporal boundaries for lineage divergences, we used three different molecular clock estimations. For *p*-distances we used the rates of 1.09–1.77% per million years ($Myears^{-1}$) (combined cytb and ND4 of pitvipers, calibration point 3.5 Myears ago (MYA); Wüster et al. 2002), and the 2% $Myears^{-1}$ clock (based on primate mtDNA, calibration point 5 MYA; Brown et al. 1979). Since the use of under-corrected distances leads to estimated dates of divergence that are biased toward the calibration point (Arbogast et al. 2002), we also employed for comparison HKY85+G distances with the much greater estimate (5.18% $Myears^{-1}$) obtained by Arbogast and Slowinski (1998) for primate cytb using the best-fit HKY85+G model and the calibration of Brown et al. (1979).

Bayesian analysis was performed with MRBAYES 3.0b4 (Huelsenbeck and Ronquist 2001) using the best-fitting model for the combined data and the default settings. Three runs of 5.5 million generations were performed, saving the current tree every 100 generations. The first 5,000 trees were discarded as the "burnin" phase and the last 50,000 trees were used to estimate posterior clade probabilities. Maximum-parsimony (MP) and maximum-likelihood (ML) analyses were performed using PAUP* 4.0b10 (Swofford 2003). MP analyses used the branch-and-bound search algorithms and assumed equal weights for all transformation series. Support values for clades in MP analyses were calculated from 2,000 bootstrap pseudo-replicates obtained by heuristic searches, each of which was performed with 100 random addition-sequence replicates. ML analyses were performed as heuristic searches (as-is stepwise addition followed by TBR branch swapping) under the best-fit model of molecular evolution, and using the substitution parameters and gamma parameter estimated by MODELTEST. Clade support in ML analyses was calculated from 100 bootstrap pseudo-replicates obtained as above. Species concept and species criteria follow de Queiroz (1998).

Results

Among the combined data of *P. australis*, we identified 19 unique haplotypes. Three haplotypes were represented more than once (Figs. 1, 2). Sequence divergence is summarized in Table 1. In the combined data matrix of 1,249 bp, 882 sites were constant, 367 variable and 213 parsimony informative. Tree topologies from Bayesian analyses were congruent, and posterior probability estimates derived from three independent runs were almost identical ($\leq$1% variation). Figure 2a shows the 50% majority-rule consensus tree of the 150,000 Bayesian trees from the three runs. Parsimony searches resulted in a single shortest tree (Fig. 2b). ML analysis resulted in a single tree of –log-likelihood 4309.83 (Fig. 2c). In all analyses, the same four strongly supported clades (I–IV; Fig. 2) were recovered. Clade II haplotypes are genetically poorly differentiated (Table 1), however, three moderately to strongly supported clades within II were recovered by all methods.

The relative rate tests showed the four clades not to differ significantly (P=0.05) in their levels of combined cytb and ND4 sequence divergence from *P. butleri*, suggesting that the rate of sequence evolution is equal across these clades. Using *p*-distances and substitution rates of 1.77–2% $Myears^{-1}$ dates divergences among the four

Table 1 Percent divergence of concatenated cytochrome *b* and NADH dehydrogenase subunit 4 sequences (378+697 bp) between *Pseudechis australis* clades I–IV and among haplotypes within clade II, expressed as mean±SD (range), number of pairwise comparisons of HKY85+G corrected distances (*above diagonal*) and pairwise uncorrected (*p*)-distances (*below diagonal*). The highest and lowest of all possible pairwise distances between clades were used to infer temporal boundaries of lineage divergences for clades I–IV

	Clade I	Clade II	Clade III	Clade IV
Clade I		17.19±0.50 (16.13–17.97) *n*=26	20.24±0.28 (19.93–20.68) *n*=4	20.04±1.96 (17.61–22.15) *n*=4
Clade II	9.50±0.19 (9.13–9.78) *n*=26		15.75±0.88 (14.20–17.33) *n*=26	17.87±1.19 (16.04–19.50) *n*=26
Clade III	10.47±0.16 (10.28–10.71) *n*=4	9.04±0.37 (8.38–9.68) *n*=26		16.20±0.68 (15.19–17.05) *n*=4
Clade IV	10.14±0.56 (9.43–10.76) *n*=4	9.54±0.28 (8.99–10.06) *n*=26	8.98±0.27 (8.57–9.31) *n*=4	

Clade II, intraclade distance: 0.89±0.40 (0.09–1.71) (HKY85+G); 0.85±0.37 (0.09–1.58) (*p*); *n*=78

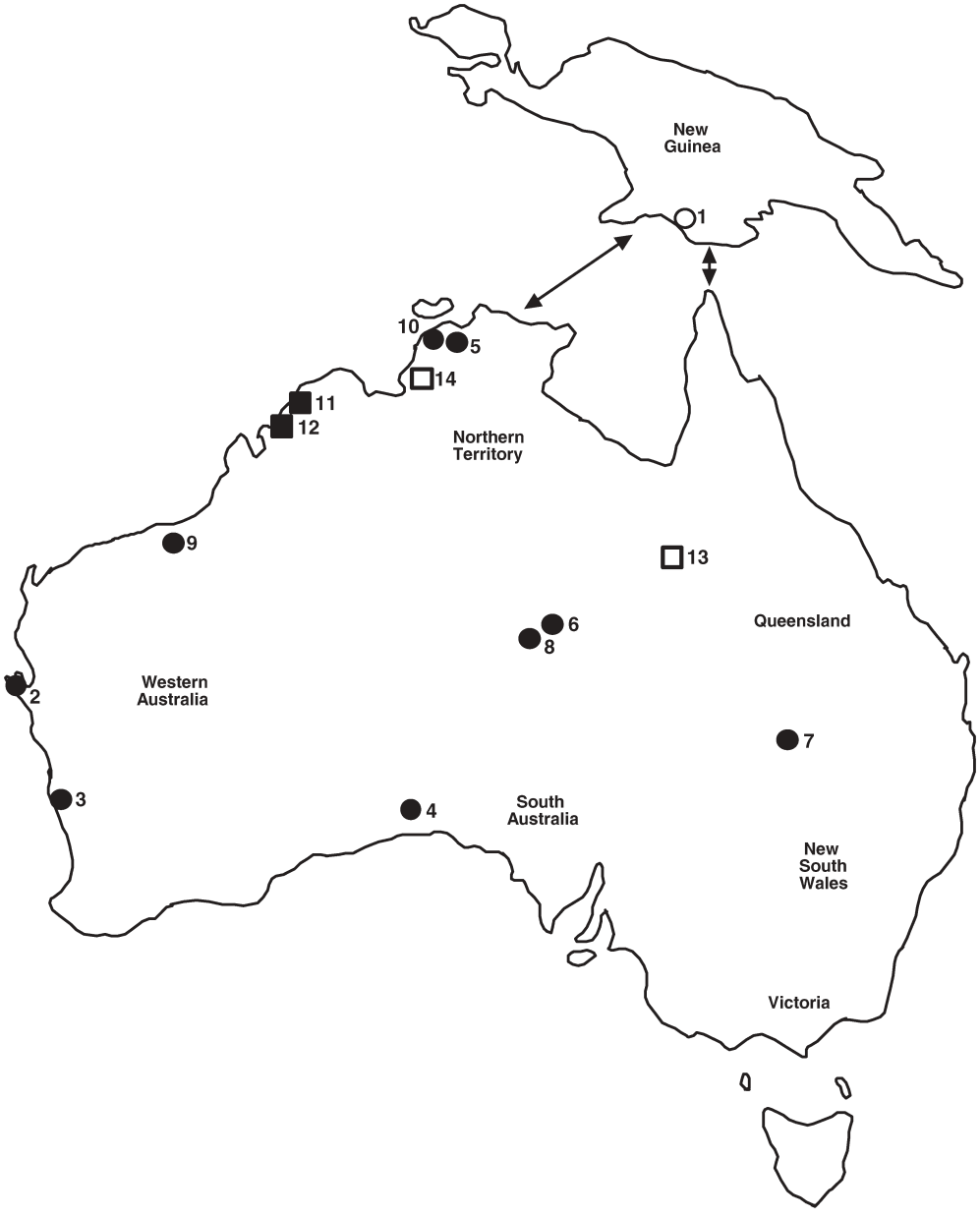


Fig. 1 Map of Australia and New Guinea showing collecting localities of king brown snake specimens used in this study. *Numbers* correspond to those in Fig. 2; symbols to clades I (▮), II (●), III (■), IV (❑) in Fig. 2. Possible corridors for faunal exchange during periods of low sea levels are indicated by *arrows* (*left* across the exposed Arafura Sill; *right* across the Torres Strait), much of the intervening area being occupied by Lake Carpentaria (Torgersen et al. 1985)

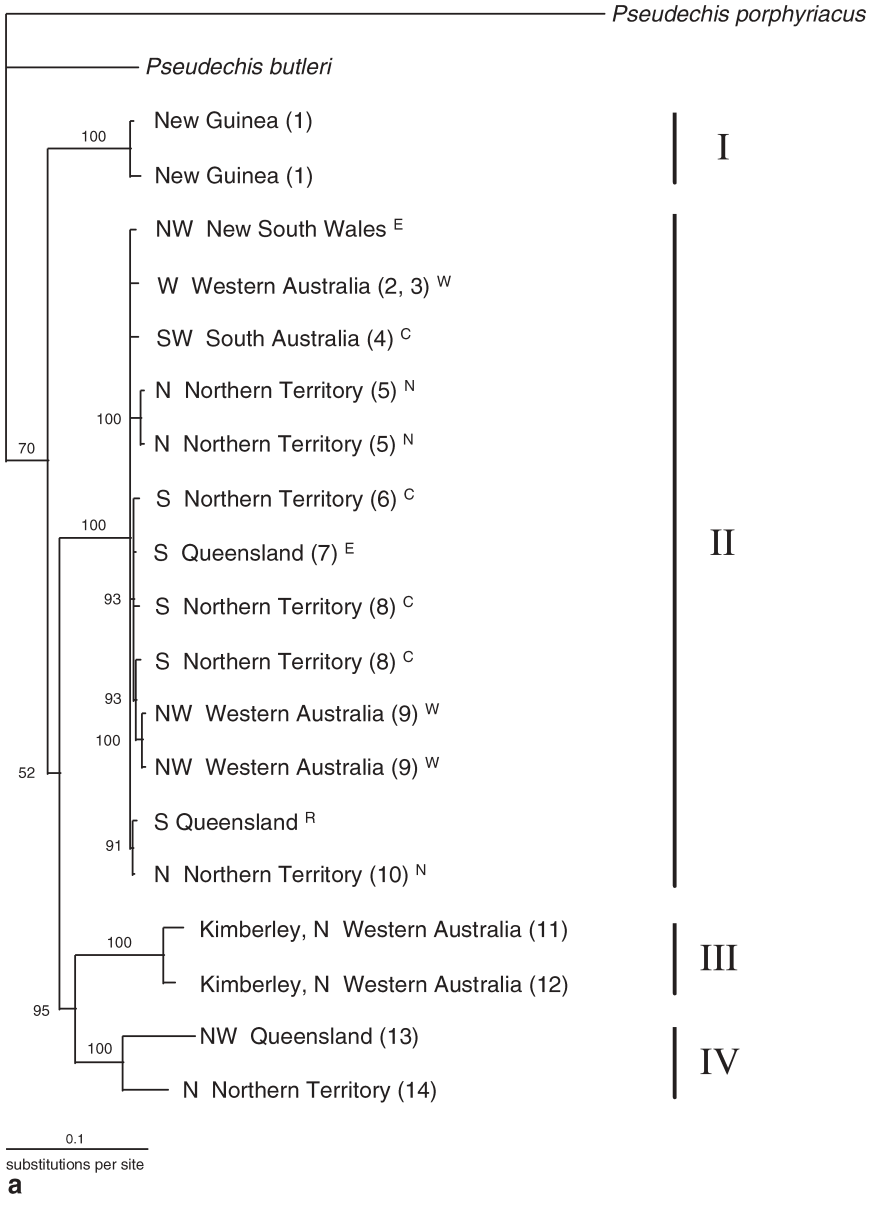


Fig. 2a–c Relationships among evolutionary lineages of *Pseudechis australis* inferred by phylogenetic analysis of 1,249 bp of mitochondrial DNA. Haplotypes are identified by collecting area; *numbers in parentheses* correspond to localities in Fig. 1. *Roman numerals* are clade numbers. *Superscript letters* designate regional colour morphs within clade II [central desert (*C*); eastern (*E*); northern (*N*); "red" form (*R*); western (*W*); see S4). **a** 50% majority-rule consensus calculated from 150,000 Bayesian trees. *Numbers along internodes* are posterior probability values. **b** Most parsimonious tree from maximum-parsimony analysis (589 steps; consistency index excluding uninformative sites, 0.730; retention index, 0.739). *Numbers along internodes* are bootstrap values >50%. *Light grey branches* indicate small body size and gracile build. In our phylogeny, a single ancestral reduction in body size followed by secondary evolution of gigantism in clade II is equally parsimonious to two convergent reductions in body size, in the ancestors of clades I and (III+IV). **c** Best tree from maximum-likelihood analysis. *Numbers along internodes* are bootstrap values >50%

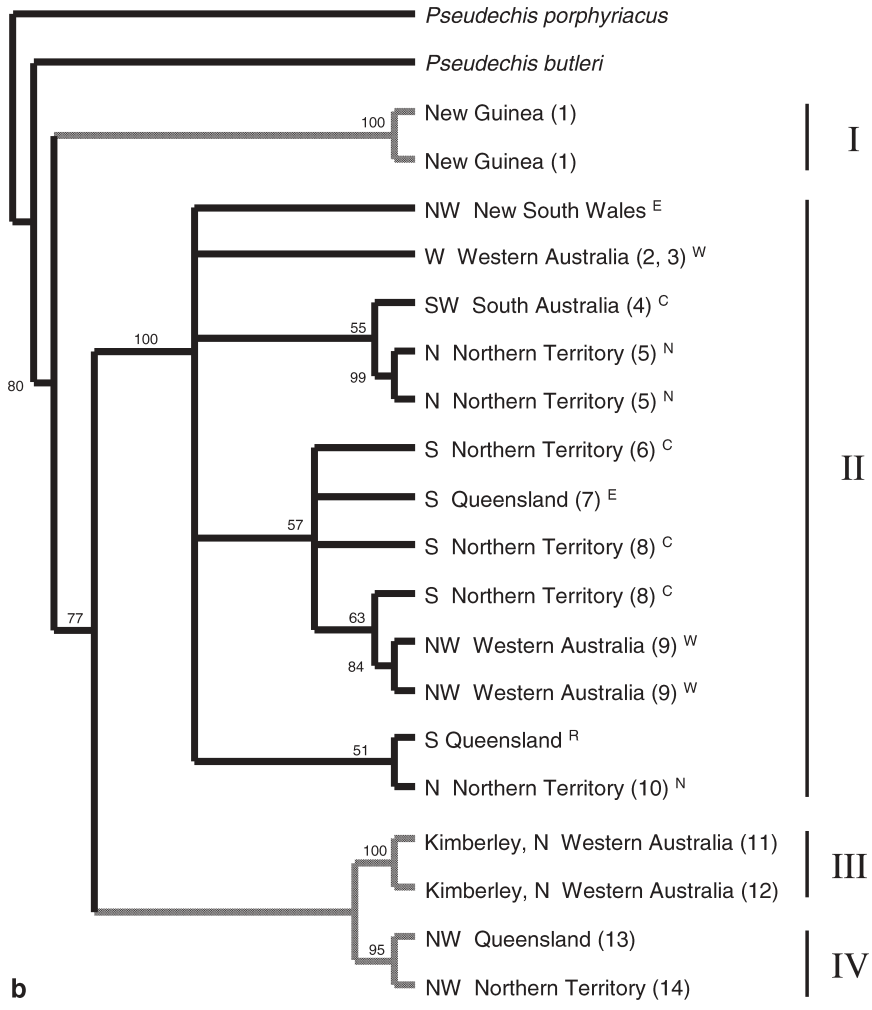
major clades to the Early Pliocene/Late Miocene (4–6 MYA), and lineage separations within clade II to the Mid- to Late Pleistocene (≤0.9 MYA). A low end estimate (1.09% Myears^{-1}) still dates these clades to the Late Miocene (~8–10 MYA; I–IV) and Early to Late Pleistocene (≤1.45 MYA; within II). Based on the best-fit model for the ingroup and the 5.18% Myears^{-1} clock, lineage divergence is dated to Mid- to Early Pliocene (2.7–4.3 MYA; I–IV) and Late Pleistocene (0.33 MYA; within II).

Discussion

Distribution patterns of elapid snakes occurring in both New Guinea and Australia have long been proposed to reflect landbridge dispersal during periods of low sea levels in the Late Pleistocene (Covacevich 1989). However, our data show that ancestral king brown snakes dispersed to New Guinea much earlier (Pliocene to Late Miocene). In agreement with our findings, studies of freshwater fishes (McGuigan et al. 2000), pythons (Rawlings and Donnellan 2003), and rodents (Godthelp 2001) reveal a complex pattern of faunal exchanges with notable ecological and east–west distinctions (Rawlings et al. 2004; Smales and Spratt 2004; Fig. 1) during multiple periods of landbridge connections in Tertiary and Quaternary times, and not a generalized Pleistocene migration between Australia and New Guinea.

Whereas all other species of *Pseudechis* are large snakes with maximum total lengths in excess of 1.6 m (Gow 1989), members of clades I, III and IV are gracile and not known to exceed 1.2 m. Conversely, clade II members exceed all congeners in total length and body mass (Fig. 2b). A paucity of natural enemies, opportunistic habits, and a large proportion of reptilian prey

Fig. 2 (continued)



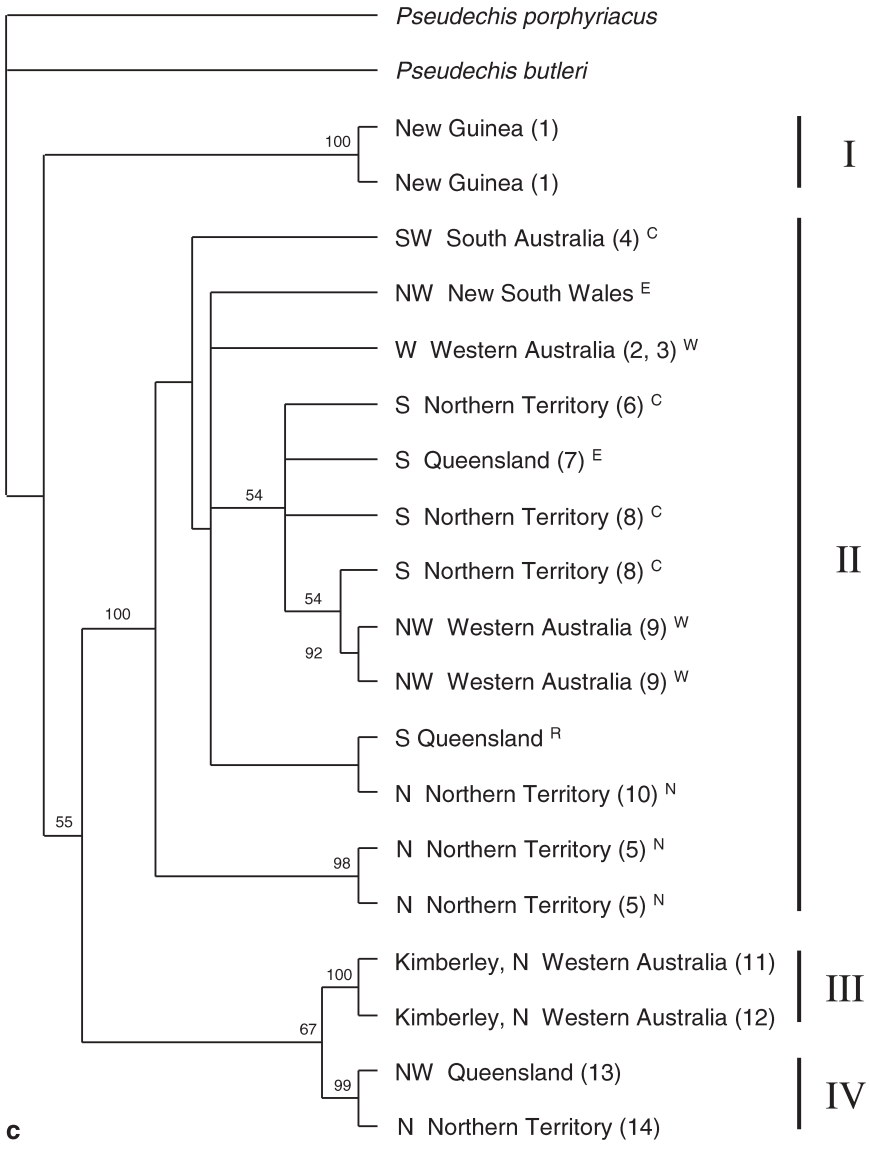
(Shine 1998) may have facilitated their dispersal into extremely xeric regions, or may have supported their resilience after contraction of woodlands. Very large body size and the acquisition of resistance to snake venoms may have allowed these animals to effectively exploit the ubiquitous food resource formed by other snakes. As evinced by the low degree of genetic differentiation (Table 1) and the notable incongruence between clade II haplotypes and geography (Figs. 1, 2), these snakes dispersed across most of Australia fairly recently in the Pleistocene. The same incongruence concerns the regional colour morphs represented in our study (see Figs. 1, 2a, S4), which reflect ecomorph evolution secondary to recent dispersal and/or climatic change. They are associated with substrate colour and crypsis (e.g. snakes of the "red form" occur on red sand), although dark colouration (Smith 1982) may play an important role in thermoregulation in southern populations.

Although our sampling of clade III and IV members was limited to four and two snakes, respectively, their haplotype diversity (up to 1.85 and 5.8% cytb *p*-divergence) exceeded that of clade II, suggesting significant phylogeographic structure. Moreover, comparison of the amount of sequence divergence within clade IV with that observed between three pairs of closely related elapid snake species in eastern Australia and Asia (2.3–3.1%: Keogh et al. 2003; Kuch et al. 2003; U. Kuch et al., unpublished data) indicates species-level genetic differentiation.

Our study contributes to the taxonomic debate in providing strong evidence for the recognition of several species from within *P. australis*: The distantly allopatric New Guinean population (clade I), the Australian clades II and III, and the two members of clade IV all are species using the criteria of apomorphy and diagnosability (de Queiroz 1998). Throughout their known ranges, clade III and IV members also occur in sympatry with clade II members. Pending the resolution of complex nomenclatural problems and the formal description of a new species (U. Kuch et al., unpublished data), we refrain from assigning names to these taxa at this time.

The implications of snake venom variability for clinical medicine are widely recognized (Chippaux et al. 1991). Mebs (2001) reported variability of venom phospholipases A_2 of king brown snakes from various localities in Australia. Due to an accelerated mode of molecular evolution, the structures and activities of these toxic enzymes can differ significantly at the intraspecific level.

Fig. 2 (continued)



Substantial differences in venom composition should be expected between the five species, which have been on separate evolutionary trajectories for several million years. The efficacy of diagnostic and therapeutic antibodies in recognizing and neutralizing the venoms of these species should thus be tested, and their venoms included in antivenom production if necessary.

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