Do Dietary Habits Predict Scale Counts in Snakes?

RICHARD SHINE, *Biological Sciences A08, University of Sydney, New South Wales 2006, Australia; E-mail: rics@bio.usyd.edu.au*

Although studies on the biomechanical basis of feeding in snakes have revealed many links between dietary composition and feeding structures (e.g., Pough and Groves, 1983; Cundall, 1987), the strength and generality of such links have rarely been examined quantitatively. In this paper, I explore a simple ecomorphological question: can the type of prey eaten by a snake species be used to predict two aspects of its scale counts (the numbers of supralabial scales and dorsal scale rows)? The idea was first expressed more than 50 years ago by an innovative German scientist, Rudolf Mell (see Zhao and Adler, 1993). Based on his research in China, Mell noted that snake species eating larger prey (e.g., mammals rather than reptiles) had more supralabial scales and more midbody scale rows (Mell, 1929a,b). Mell suggested that an increased number of scale rows provides greater flexibility, enabling the skin between the scales to stretch over a large prey item.

More recent authors have repeated this suggestion. For example, Gans (1974) interpreted the increased number of scale rows on the neck of egg-eating snakes in this way. Pough and Groves (1983) interpreted high supralabial and midbody scale-row counts in viperid snakes (compared to colubrids) in the same fashion. Mell's original formulation was simplistic, however, and recent analyses of snake feeding provide more sophisticated views on these topics. For example, Greene (1983, 1997) has pointed out that prey items can be "large" in a number of ways; Mell's hypothesis relies upon prey being large in diameter rather than (for example) mass. Equally, it is a gross oversimplification to rate all mammals that are consumed by snakes as being larger (relative to the snake's size) than are all reptiles. Last, elasticity of the body could be enhanced by changing the structure of the skin, or increasing the amount of skin between scales, rather than by simply increasing the number of scale rows (Jayne, 1988). Given these issues, was Mell correct in suggesting an association between scale counts and dietary habits in Chinese snakes? And if so, how can this be true given the oversimplifications embedded in his assumptions?

I used Pope's (1935) tabulation of data on scale counts and prey types to test Mell's hypothesis on Chinese snakes. To examine the validity of the idea for a different assemblage, I also collated data on scale characters, body sizes and dietary composition for all terrestrial Australian snake species. Information on scale counts was obtained from publications by Wallach (1985), Storr et al. (1986), Barker and Barker (1994), O'Shea (1996), and Greer (1997). I recorded the mean (or modal, if no mean was reported) number of dorsal scale rows (the number of scales encircling the body, counted halfway between head and tail) and the number of supralabial scales (i.e., the scales along the top of the lip). Information on dietary composition and mean adult body sizes of snakes came from dissection and measurement of museum specimens (Shine, 1991, 1994). Diets were quantified in terms of the proportion of identifiable prey items falling into each major group (invertebrate, fish, amphibian, reptile, bird, mammal). Mean adult body size was calculated as the average of mean snout–vent lengths for adult males and adult females.

Three kinds of analysis were carried out on these data. First, I treated each species as a statistically independent unit and looked for the predicted correlations between the two types of scale characters (dorsal scale rows and supralabials) and between these traits and dietary composition (e.g., proportion of mammals in the diet). Second, because I found strong correlations between scale counts and body size (see below), I also compared dietary composition to size-corrected scale counts. To calculate size-corrected scores for each of the scale characters, I used residual scores from the general linear regressions of scale count versus mean body length. Thus, a species with a positive residual score for dorsal scale-rows would be one that had more scale-rows than would be expected for a species of that mean body size. Last, I combined the data with a putative phylogeny for these snakes (Fig. 1). This phylogenetic hypothesis was assembled by combining published suggestions about relationships among various subsets of the species involved (Kluge, 1991, 1993; Greer, 1997; Keogh et al., 2000; S. Keogh, pers. comm.). Hence, the resultant phylogeny (Fig. 1) is speculative and is not the result of any explicit phylogenetic analysis. Then I used this composite phylogeny to conduct a comparative analysis using independent contrasts (Purvis and Rambaut, 1995). This method overcomes the problem that many traits are highly conservative, so that correlations among traits may reflect phylogenetic inertia rather than functional relationship (Harvey and Pagel, 1991). Evolutionary changes in one variable (such as the proportional composition of the diet) within a clade can be compared to simultaneous changes in other traits (such as scalation) within the same clade. In the absence of reliable data on branch lengths within phylogenies, I assumed constant branch lengths (i.e., punctuated speciation events). Phylogenetically corrected relationships among variables were assessed by linear regression through the origin (Purvis and Rambaut, 1995). Statistical analyses were performed using CAIC (Purvis and Rambault, 1995) and Statview 5 on an Apple Macintosh G4 computer. Prior to analysis, data were tested for conformity with assumptions of normality required for tests.

A one-factor ANOVA on Pope's 1935 data (his table LX) with prey type as the factor and number of scale rows as the dependent variable, confirms Mell's (1929a,b) assertion that dietary habits correlate with scale counts within the Chinese snake fauna ($F_{5,112} = 3.88$, $P < 0.003$). Posthoc (Fishers' PLSD) tests show that species that eat mammals have significantly more

Ramphotyphlops pinguis
Ramphotyphlops bituberculatus
Ramphotyphlops australis
Ramphotyphlops endoterus
Ramphotyphlops polygrammicus
Ramphotyphlops guentheri
Ramphotyphlops affinis
Ramphotyphlops proximus
Ramphotyphlops ligatus
Ramphotyphlops nigrescens
Ramphotyphlops weidii
Ramphotyphlops diversus
Antaresia (3 species)
Antaresia perthensis
Liasis olivaceus
Liasis fuscus
Morelia spilota
Morelia amethistina
Chondropython viridis
Aspidites ramsayi
Aspidites melanocephalus
Tropidonophis mairii
Cerberus rynchops
Enhydris polylepis
Myron richardsoni
Fordonia leucobalia
Dendrelaphis punctulata
Dendrelaphis calligastra
Stegonotus cucullatus
Boiga irregularis
Simoselaps calonotus
Simoselaps (8 species)
Simoselaps anomalus
Simoselaps bertholdi
Simoselaps littoralis
Vermicella annulata
Simoselaps bimaculatus
Demansia (4 species)
Cacophis (3 species)
Furina (3 species)
Furina diadema
Furina ornata
Acanthophis antarcticus
Denisonia devisii
Denisonia maculata
Echiopsis curta
Drysdalia mastersi
Drysdalia rhodogaster
Drysdalia coronoides
Hemiaspis damelii
Hemiaspis signata
Hoplocephalus bungaroides
Hoplocephalus bitorquatus
Hoplocephalus stephensii
Austrelaps labialis
Austrelaps ramsayi
Austrelaps superbus
Tropidechis carinatus
Notechis scutatus
Elapognathus minor
Elapognathus coronatus
Suta (11 species)
Rhinoplocephalus (3 species)
Pseudechis australis
Pseudechis butleri
Pseudechis colletti
Pseudechis guttatus
Pseudechis porphyriacus
Pseudonaja (10 species)
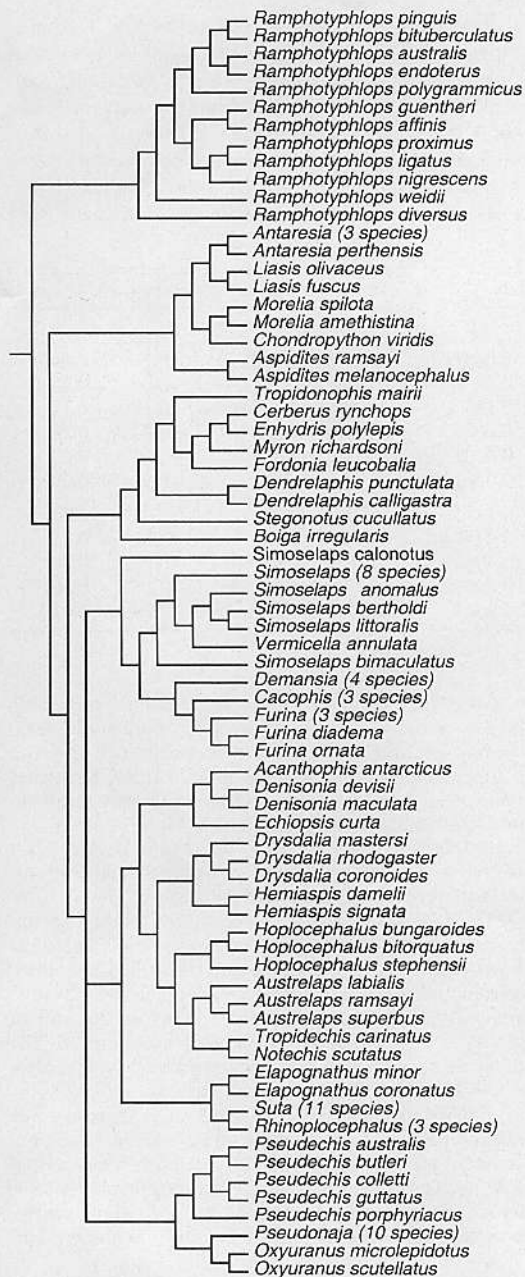Oxyuranus microlepidotus
Oxyuranus scutellatus

FIG. 1. Phylogenetic hypothesis for Australian snakes, as used in the present study. See text for list of sources for this phylogeny.

midbody scale rows than those that eat reptiles, frogs or invertebrates ($P < 0.05$ in each case).

Data were obtained for 108 Australian species, comprising 11 pythonids, nine colubrids, 76 elapids and 12 typhlopids. Mean adult snout–vent length ranged from 17–212 cm, midbody scale rows from 13–67, and supralabial scale counts from 4–14. The proportion of the diet composed of various prey types also varied widely (from 0–100% for each of fishes, reptiles, and mammals; from 0–97% for amphibians; 0–36% for birds).

Overall, my analyses for the Australian taxa revealed the same general pattern as noted by Mell for Chinese snakes but cast substantial doubt on the mechanism that he suggested to explain this pattern. Table 1 summarizes results from statistical tests of three predictions from Mell's hypothesis.

Number of Midbody Dorsal Scale-Rows Is Positively Correlated with Number of Supralabial Scales.— As predicted, species with high numbers of midbody dorsal scale rows also had many supralabial scales (Fig. 2, Table 1). However, both of the scale counts also showed strong positive correlations with mean adult body size. These relationships differed among families. For example, at any given body size, pythons have more supralabial scales than elapids, and colubrids are intermediate in this respect (Fig. 3). The correlation between dorsal and labial counts remained high even after the effects of body size were removed (Table 1). That is, the trend for species with high numbers of scale-rows to also have many supralabial scales is not an indirect consequence of body size.

Comparative analysis further supported the notion of a functional relationship between scale numbers around the body versus along the upper lip. Increases in midbody scale rows during phylogeny were consistently associated with increases in supralabial counts (Table 1). After removing body-size effects from the comparative analysis, shifts in relative numbers of midbody dorsal scale-rows (i.e., residual scores) were associated with shifts in relative numbers of supralabial scales (i.e., residual scores; $N = 70$, $r = 0.65$, $P < 0.0001$).

Species that Eat Larger Prey Types Have More Dorsal Scale Rows.—As in the Chinese fauna, Australian snake species that feed on birds and mammals tend to have more dorsal scale rows than do other species (Table 1; Fig. 4). When the effects of body size on scale counts are removed, however, none of the probability values for these analyses attain the conventional level of significance ($P < 0.05$) after Bonferroni corrections are applied (Table 1).

Phylogenetically based analysis revealed a consistent association between dorsal scale rows and the proportion of mammalian prey in the diet but not for the other prey groups (Table 1). Using size-corrected scores (i.e., residual values from scale counts versus SVL) greatly weakened the apparent link between scalation and diet: no dietary proportions were significantly correlated with size-corrected scale counts ($P > 0.10$ in all cases).

Species that Eat Larger Prey Types Have More Supralabial Scales.—Patterns for this variable are similar to those for dorsal scale rows (above), as might be expected from the high correlation between the two traits (Fig. 2). Species that feed on birds and mammals have more supralabial scales than do species that feed on ectotherms (Fig. 4), but this pattern disappears after body-size effects are removed from the analysis (Table 1). Phylogenetic shifts in supralabial counts were correlated (albeit weakly) with shifts in the proportion of mammalian prey (Table 1), but this effect disappeared when size-corrected values were used in the analysis (all $P > 0.10$).

TABLE 1. Relationsihps among scale characters and dietary composition in Australian snakes. The table provides results from linear regression analysis of three types of data. First, values for each species were used as independent datapoints ("raw data"). Then, because both types of scale counts were highly correlated with overall body size, the effects of size were removed by calculating residual scores from the general linear regressions of the scale trait against mean adult snout–vent length ("size-corrected data"). Third, comparative analysis using independent contrasts was used to remove the effects of phylogenetic conservatism. Sample size was 108 for the first two types of tests and 70 for the comparative analysis. The table shows the correlation coefficient (r) and its associated probability (P). **Boldface** shows results that are statistically significant ($P < 0.05$) after Bonferroni correction.

Traits being compared	Raw data		Size-corrected data		Comparative analysis	
	r	P	r	P	r	P
Dorsal scale rows vs supralabial scales	**0.82**	**0.0001**	**0.71**	**0.0001**	**0.70**	**0.0001**
Dorsal scale rows vs. % fishes	0.03	0.77	0.09	0.35	0.09	0.45
Dorsal scale rows vs % frogs	−0.15	0.13	0.09	0.35	−0.19	0.11
Dorsal scale rows vs % reptiles	**−0.28**	**0.0004**	−0.22	0.026	−0.04	0.75
Dorsal scale rows vs % birds	**0.43**	**0.0001**	0.21	0.028	0.14	0.23
Dorsal scale rows vs % mammals	**0.49**	**0.0001**	−0.02	0.85	**0.31**	**0.008**
Supralabial scales vs % fishes	0.13	0.18	0.22	0.03	0.04	0.77
Supralabial scales vs % frogs	0.01	0.92	−0.01	0.93	−0.07	0.55
Supralabial scales vs % reptiles	−0.05	0.60	0.16	0.11	0.05	0.70
Supralabial scales vs % birds	**0.41**	**0.0001**	0.20	0.04	0.13	0.30
Supralabial scales vs % mammals	**0.46**	**0.0001**	−0.03	0.79	**0.28**	**0.02**

The end result of these analyses is that three traits (body size, dietary habits, and scale counts) are significantly intercorrelated. Although it is difficult to distinguish direct from indirect effects within such constellations of traits, partial correlation offers a partial solution. I used this technique to evaluate the correlation between dietary habits and one variable (such as scale-row number) when another factor (such as body size) was held constant. Two sets of these analyses were conducted, one on the raw data and one on phylogenetic contrasts. In both cases, partial-correla-

tion analyses suggested that dietary habits were more highly associated with body-size than with scale counts. For the raw data, the proportion of the diet composed of mammals was significantly correlated with mean adult SVL when either scale-row numbers or supralabial counts were held constant ($N = 108$, $r = 0.63, 0.71$, respectively, $P < 0.001$ in both cases) but neither of the scale characters was correlated with dietary habits if SVL was held constant ($N = 108$, $r = −0.03, 0.05$, respectively, $P > 0.50$). No other partial correlations between dietary habits and morphological traits were statistically significant ($P < 0.05$) after Bonferroni correction for multiple tests. The comparative analysis (independent contrasts) provided an almost identical result. The proportion of mammals in the diet was correlated with mean adult SVL when either of the scale characters was held constant ($N = 70$, $r = 0.56, 0.55$, respectively, $P < 0.001$ in both cases) but not with either of the scale counts when SVL was held constant ($N = 108$, $r = −0.13, −0.04$, respectively, $P > 0.50$). These results suggest that the correlations between scale counts and diet are secondary consequences of body-size effects on both scalation and diet.

If indeed we could find strong links between ecological traits (such as dietary composition) and morphological features (such as the numbers of dorsal scale-rows), such associations would be of considerable value. For example, we have quantitative information on dietary composition for only a small proportion of snake species. Unfortunately, my study is not encouraging with respect to inferring diet from scalation (or vice versa). There are at least three processes that might generate a correlation between dietary composition and scale counts in snakes. First, interspecific divergences in dietary habits (especially, relative prey size) might have imposed selection on scale-row numbers as envisaged by Mell. Second, the
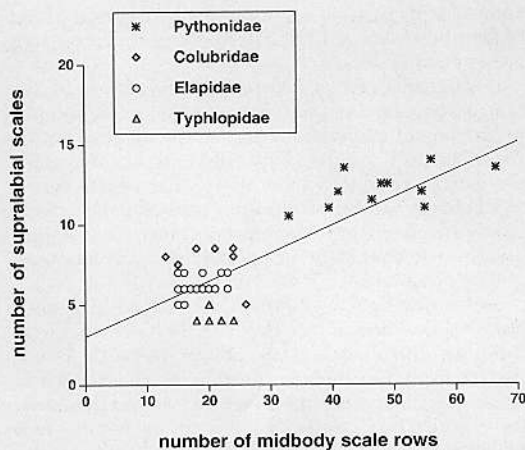

FIG. 2. The relationship between the numbers of dorsal scale rows and supralabial scale count in an interspecific comparison among Australian snakes. Each point represents one species. See Table 1 for results of a test of the statistical significance of this relationship.
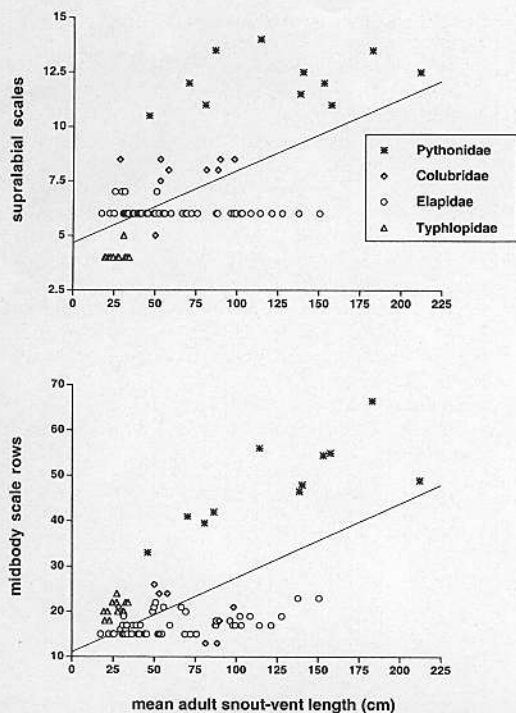
FIG. 3. The relationship between body size (mean adult snout–vent length) and scale counts in Australian snakes. Lower graph shows data for the number of dorsal scale rows, and upper graph shows the data for the number of supralabial scales. Each point represents one species. Linear regression for these datasets shows: dorsal scale rows, $N = 108$, $r = 0.65$, $P < 0.0001$; supralabial scales, $N = 108$, $r = 0.62$, $P < 0.0001$.
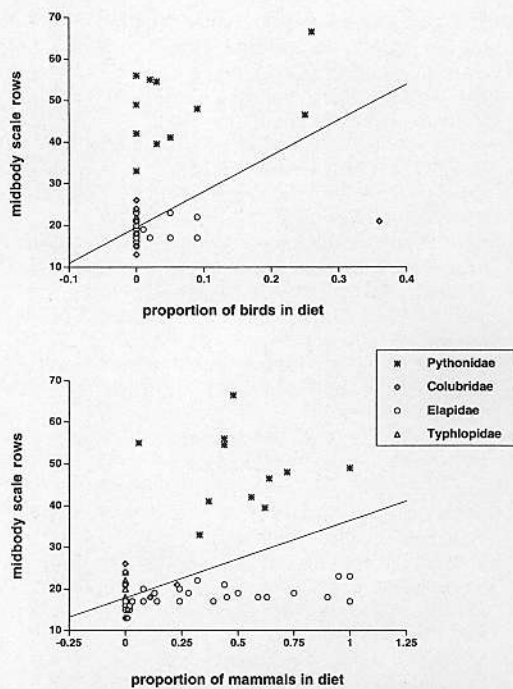
FIG. 4. Scale characteristics of Australian snakes in relation to dietary composition. Species that consume a higher proportion of birds and mammals tend to have more dorsal scale rows and more supralabial scales. See Table 1 for tests of the statistical significance of these relationships.

correlation between scale counts and dietary composition might be an artifact of phylogenetic inertia, because some lineages of snakes have low values for all three traits (supralabials, dorsal scale rows, and proportion of the diet composed of endotherms) whereas other lineages have high values for all three traits. This circumstance might have arisen early in snake phylogeny, and require no adaptive explanation in terms of selective forces during the radiation of species within lineages. In practice, phylogenetic shifts in the degree of reliance on mammalian prey were consistently accompanied by shifts in scale counts (Table 1), suggesting a functional association between the traits. Nonetheless, phylogenetic conservatism undoubtedly amplifies the strength of these correlations (Table 1, Fig. 4). Last, correlation does not imply causation. A third factor (mean adult body size) is known to correlate both with dietary habits (e.g., Fitch, 1960; Arnold, 1993; Shine, 1994) and with scale counts (e.g., Klauber, 1956; Lindell, 1994). Thus, a shift in food habits toward larger prey could favor the evolution of larger body size, which in turn could favor an increase in scale counts (because larger snakes have more scales: see Fig. 3). In keeping with this hypothesis, correlations between scale counts and dietary habits

generally disappeared when body-size effects were removed from the analysis (Table 1).

In summary, Mell was probably correct in recognizing a general association between scale counts and diets in snakes, but wrong about its cause. To fully understand the pattern identified by Mell 50 years ago, we will need to gather data on traits that relate much more closely to the actual selective pressures and functional challenges involved in prey ingestion. For example, many researchers in snake ecology still report only the species and mass of prey items, despite heartfelt appeals to take more extensive data (e.g., Greene 1997). Maximum prey diameter is simple to measure (even with partially digested prey) and is likely to be a better measure of the physical difficulty of ingesting the item than is prey mass. Until we have extensive datasets on such variables, many of the ideas espoused by visionaries like Rudolf Mell will remain untested.

LITERATURE CITED

ARNOLD, S. J. 1993. Foraging theory and prey-size-predator-size relations in snakes. *In* R. A. Seigel

and J. T. Collins (eds.), Snakes. Ecology and Behavior, pp. 87–116. McGraw-Hill, New York.

BARKER, D. G., AND T. M. BARKER. 1994. Pythons of the World. Vol. 1. Australia. Advanced Vivarium Systems, Lakeside, CA.

CUNDALL, D. 1987. Functional morphology. *In* R. A. Seigel, J. T. Collins, and S. S. Novak (eds.), Snakes: Ecology and Evolutionary Biology, pp. 106–142. MacMillan, New York.

FITCH, H. S. 1960. Autecology of the copperhead. University of Kansas Publications of the Museum of Natural History 13:85–288.

GANS, C. 1974. Biomechanics: An Approach to Vertebrate Biology. J. P. Lippincott, Philadelphia, PA.

GREENE, H. W. 1983. Dietary correlates of the origin and radiation of snakes. American Zoologist 23: 431–441.

———. 1997. Snakes. The Evolution of Mystery in Nature. University of California Press, Berkeley.

GREER, A. E. 1997. The Biology and Evolution of Australian Snakes. Surrey Beatty and Sons, Sydney, New South Wales, Australia.

HARVEY, P. H., AND M. D. PAGEL. 1991. The Comparative Method in Evolutionary Biology. Oxford Studies in Ecology and Evolution, Oxford University Press, Oxford.

JAYNE, B. C. 1988. Mechanical behaviour of snake skin. Journal of Zoology, London 214:125–140.

KEOGH, J. S., I. A. SCOTT, AND J. D. SCANLON. 2000. Molecular phylogeny of viviparous Australian elapid snakes: affinities of "*Echiopsis atriceps*" (Storr, 1980) and "*Drysdalia*" *coronata* (Schlegel, 1837), with description of a new genus. Journal of Zoology, London 252:317–326.

KLAUBER, L. M. 1956. Rattlesnakes. Their Habits, Life Histories and Influence on Mankind. University of California Press, Berkeley.

KLUGE, A. G. 1991. Boine snake phylogeny and research cycles. Miscellaneous Publications of the Museum of Zoology, University of Michigan 178: 1–58.

———. 1993. *Aspidites* and the phylogeny of pythonine snakes. Records of the Australian Museum, Supplement 19:1–77.

LINDELL, L. E. 1994. The evolution of vertebral number and body size in snakes. Functional Ecology 8: 708–719.

MELL, R. 1929a. Beitrage zur Fauna Sinica. IV. Grundzuge einer Okologie der Chinesischen Reptilien und einer Herpetologischen Tiergeographie Chinas. Walter de Gruyter, Berlin, Germany.

———. 1929b (1931). Preliminary contributions to an ecology of East Asiatic reptiles, especially snakes. Lingnan Science Journal 8:187–197.

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

POPE, C. H. 1935. The Reptiles of China. American Museum of Natural History, New York.

POUGH, F. H., AND J. D. GROVES. 1983. Specialization in the body form and food habits of snakes. American Zoologist 23:443–454.

PURVIS, A., AND A. RAMBAUT. 1995. Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analysing comparative data. Computer Applications in the Biosciences 11:247–251.

SHINE, R. 1991. Australian Snakes. A Natural History. A. H. and A. W. Reed, Sydney, New South Wales, Australia.

———. 1994. Allometric patterns in the ecology of Australian snakes. Copeia 1994:851–867.

STORR, G. M., L. A. SMITH, AND R. E. JOHNSTONE. 1986. Snakes of Western Australia. Western Australia Museum, Perth, Western Australia, Australia.

WALLACH, V. 1985. A cladistic analysis of the terrestrial Australian Elapidae. *In* G. C. Grigg, R. Shine and H. Ehmann (eds.), The Biology of Australasian Frogs and Reptiles, pp. 223–253. Royal Zoological Society of New South Wales, Sydney, New South Wales, Australia.

ZHAO, E., AND K. ADLER. 1993. Herpetology of China. Society for the Study of Amphibians and Reptiles, Oxford, OH.