PHYLOGENETIC RELATIONSHIPS AMONG AUSTRALIAN ELAPID SNAKES: THE SOFT ANATOMICAL DATA RECONSIDERED

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On the basis of an extensive set of visceral and scale characters, Wallach (1985) proposed a detailed phylogenetic scheme for all the Australian elapids, down to species level. The shortest tree found in that analysis is here shown to contain 592 steps. However, a re-analysis of the same data using PAUP 3.1.1 reveals that there are 258 most parsimonious trees, each with only 578 steps. The strict consensus of these trees is much less resolved than Wallach's tree, and has a different topology. For example, *Echiopsis* is most closely related to *Suta fasciata* rather than to the *Notechis* lineage, and *Demansia* is more closely related to advanced elapids (such as the *Notechis* lineage) than to *Oxyuranus* and *Pseudonaja*. Many of the larger (suprageneric) groupings proposed by Wallach are paraphyletic in the PAUP consensus tree. Almost all the groupings in this tree, however, can be collapsed with the addition of a single extra step. There are more than 32 000 cladograms at 579 steps, one step longer than the 258 most parsimonious cladograms. A strict consensus tree of cladograms 578 and 579 steps long is almost completely unresolved. The visceral and external morphological traits, therefore, are not as phylogenetically informative as previously proposed, at least with respect to the Australian elapid radiation. These types of characters might not be very phylogenetically informative at higher (intergeneric) levels, although much more data are required to test this hypothesis.

INTRODUCTION

Elapid (proteroglyphous) snakes have undergone a rapid and diverse adaptive radiation in Australia, and form the largest single component (approximately half) of the continent's snake fauna (e.g. Shine, 1985). This contrasts strongly with the snake faunas of other continents, which are dominated by colubrids. The Australian elapid radiation therefore represents an unusual and intriguing evolutionary event. However, phylogenetic relationships among these snakes have been subjected to few detailed studies and are still rather poorly known.

The only studies of Australian elapid phylogeny which sampled a broad range of taxa and characters were published together in a symposium volume. Schwaner et al. (1985) used immunological distances, Mengden (1985) used electrophoretic and chromosomal traits, and Wallach (1985) considered internal soft anatomical (visceral) and external (scale) characters. Of these studies, Wallach's data set was by far the most extensive in terms of number of characters and number of taxa sampled. It was also the only study that adopted an explicitly cladistic approach. Wallach's conclusions have resulted in taxonomic changes (e.g. Hutchinson, 1990) and have been used, along with other studies (e.g. Mengden, 1985), as the basis for ecological inferences (e.g. Shine, 1985, 1994). It is therefore important that the study is critically evaluated.

Because of the size of Wallach's data matrix, the parsimony programs available at the time could not evaluate it effectively. Analysis of the same data set using PAUP 3.1.1 (Swofford 1993), shows that the most parsimonious trees are very different to the tree proposed in Wallach (1985), and further shows that the phylogenetic signal is extremely weak. Also, some ambiguities regarding character codings in Wallach's data set are clarified.

THE DATA SET

Wallach's data matrix (his Appendix C) is reproduced here as Table 1. In Wallach's matrix, taxa were ordered, not by genera, but alphabetically by specific name (the second part of the binomial). Thus, species of different genera were shuffled together. Here, the species have been grouped according to genera, and similar genera also grouped together, making visual comparisons of character states in similar taxa easier.

In Wallach's study, 63 species of Australian elapids were examined, representing all recognized genera and the majority of recognized species. 50 potentially informative characters were identified, mostly involving the viscera and external morphology. These characters were polarized by outgroup comparison, using chiefly the African elapid *Naja melanoleuca*. Myological characters were not used, nor were skeletal characters, apart from tooth counts.

However, in Wallach's data matrix there were 72 characters. This discrepancy was not explained, and several colleagues (e.g. Scanlon pers. comm., Shea pers. comm.) have had problems interpreting this matrix. The reason for this discrepancy is that Wallach ordered his multistate characters into morphoclines (Wilkinson, 1992; Slowinski, 1993). Multistate characters that formed bifurcating series (i.e. two divergent morphoclines from the primitive condition) were recoded as two separate characters, one for each morphocline. This procedure is discussed in Wiley *et al.* (1991). There were 22 such characters in the 50

TABLE 1. The computer data matrix of Wallach (1985). The order of taxa has been modified so that species are grouped according to genera, and similar genera have been grouped together. The 72 characters are discussed in the text. The correspondence between the 72 characters in Wallach's computer data matrix (Appendix C), and the 50 characters in Wallach's text and Appendix B, is shown in the top two rows.

CHARACTERS (APP. C)	1234567891111111111222222222223333333333444444444455555555556666666666777
	0123456789012345678901234567890123456789012345678901234567890123456789012

CHARACTERS (APP. B & TEXT)	<1<2<3<4<5<6<78911111<1<1<1<11<2<2<222<2<2<222333333<3333444<44<4<44<445
	01234 5 6 7 89 0 1 234 5 6 789012345 6789012 34 5 67 890

Outgroup (Naja melanoleuca)	000000000000000000000000000000000000000000000000000000000000000000000000
Demansia atra	0000000100101000001010100000000000000011011000000001000002100010120022012 0
Demansia olivacea	0000000001100010000000100000000000000011001010100000100000210001012000201 20
Demansia psammophis	00000000011000101100000000000000010001100101000000100000210001012000201 20
Demansia torquata	0000000000100110111101000000000010000000101010000101100210001012000201 20
Pseudechis australis	00000000100000100000000101000100000000000000000000001000001110100110001002 1
Pseudechis guttatus	000000010000000000000001000000000000001100000000000100000011100011000100 20
Pseudechis porphyriacus	001001001010100001000000101100100010000000000000001000001110100110001002 1
Oxyuranus microlepidotus	10001010001001100000000000001000100100110000100000110100000200010100101 20
Oxyuranus scutellatus	100010100010001010001000000000001001001100000000010111000000200110100201 20
Pseudonaja affinis A	10001010011000120000000000000000100100000000011001100000010001010000101 20
Pseudonaja affinis B	100010101010001011010000010000010010100000001100110110000000101000001012 0
Pseudonaja guttata	10001010000000101010001010000001001001000000011001110000010001000000101 20
Pseudonaja modesta	000000000100001011111001010001000110100101001100110000011000101000110110
Pseudonaja nuchalis	101010100010001000001000000000010010000000001001100100010001010000101 20
Pseudonaja textilis	10001010000001101001101000000000110101100000001001100000111101010000101 20
Acanthophis antarcticus	010001010010001000002100101101011010000101001101000110100110011001101000 102 1
Acanthophis pyrrhus	00000000000001121101200000010101101000010100110101000010010000001000102 1
Austrelaps superbus	00000001000001000000101000010100001000010100000001000002020010110001102 1
Notechis scutatus	100010000000001100002010000101000010010101000000010000000200010100110 21
Notechis ater	0000001001101000001000101011010000100001010010000100000002000101001102 1
Tropidechis carinatus	10001000011010000010001100001000010000101001101000000000210001011010111
Hoplocephalus bitorquatus	0000000000000100000101100000100010000000001100021000000020000001200010 1
Hoplocephalus bungaroides	10001010011010000010001000010000100100010110002100000002000000110001 01
Hoplocephalus stephensii	00001000001000000110000100000100001000100011000210000000210000120001 01
Denisonia maculata	010001010110011001101000000001010000000010120000100000102000000101110 01
Denisonia devisii	01010101010000100100200000010110010000001010110000100000102000000101110 01
Hemiaspis damelii	000000000110011000001010000101100000010101001000010010011200101200110011
Hemiaspis signata	000001010100001001002011000011001000001010010000100000112001012001100 11
Echiopsis curtus	100010100100000201102000000010100000001010110000100010120000101001101 1
Suta fasciata	100110100110101210102001010001010100000101011000011000010200011001110 01
Suta flagellum	000100000110101211112100010001010110000101002000010000010200001100100001
Suta gouldii	0000000001010112111120010100010100011010101100001100102020000110010000 1
Suta monachus	00000000011000121111100001000100010001000101012100010000020200001100100001
Suta nigriceps	000000000101001010002100000001010010100100110001000002020001100100001
Suta punctata	00000000011000121100200000000101101011010101200001000002020001100111001
Suta suta	00010000010000101111100000000101000000010101100011000002000011001000 01
Drysdalia coronata	00000000011000100100000000000101000000001010020000100000202000101011001 1
Drysdalia coronoides	01000001010001001101001000001000000010101102000000000021200001000110011
Drysdalia mastersii	010001011000001001102010001001000000001010020000100000202000010001100 11
Drysdalia rhodogaster	0010010001000000010001010000010000000001011020000100000202000010001100 11
Rhinoplocephalus bicolor	101000000100010000102011010001001000100101201001010002020000120011000 1
Rhinoplocephalus boschmai	000000001000000100100000000101001000001010912000110000202000011001000 01
Rhinoplocephalus nigrescens	0000000001000110010010110100010100000000101100001000002120001000120001
Rhinoplocephalus nigrostriat.	000000010010011100002010000001010000001001010000101000202000011001000 01
Rhinoplocephalus pallidiceps	00000001010100000100011000010100100101010101201000010000202000010001100 01
Elapognathus minor	000000101000100010020100011010000100001001020000100000202000110001100 01

TABLE 1. (continued...)

Cacophis harriettae	0100010101000012110100010000010101000001010121000110000210011010001000000
Cacophis krefftii	0000000001100012110110010000110100000101010121000100000210010110001000000
Cacophis squamulosus	0100010100000110110100000001010101000001010101110001000002100110100010000000
Furina barnardi	0000000001100110011021000100110100000001010121000010000210000000000100000
Furina diadema	0000000001001000011020010000010101000001010121000010000210010000000100000
Furina dunmalli	0100010001010110010000000000101001000010101100001100000100001000001000000
Furina ornata	0000000001100012110100000100110100000100000020000110000100010000000100000
Furina tristis	0101010000100012010001000000010110100001010010000110000111010000001000000
Simoselaps australis	1001100010101002010000110100010100010010101012100010000011100010000200000
Simoselaps bertholdi	0100010101010112011000100001010101001001010121000100000210000100002000000
Simoselaps bimaculatus	1000101001000110011000110100110100011000010121000200000210010100001000000
Simoselaps calanotus	0010010101000110011000110100101100010010101210001000000210010100001000000
Simoselaps fasciolatus	0001000100000112011000110000010100000001010121000110010110001000020000000
Simoselaps roperi	0010010001000012010020010100110100001001010121000200001021001010000200000
Simoselaps semifasciatus	0000010101000112111110010100010100101001010121000100000110010100002000000
Simoselaps warro	1010001001100002000020000100010110100001010121000110000210000000001000000
Vermicella annulata	1000101001000010011020001010011010001100001011110020000210010100002000100

characters described in the text. These 22 characters were each re-coded as two characters in the data matrix (Appendix C), giving a total of 72 characters.

The definitions for the character states for the 72 re-coded characters were not listed. However, they can be inferred by comparing the original descriptions for the 50 characters with the data matrix. The order of characters was kept the same in both; however, as bifurcating characters in the descriptions were each re-coded as two characters in the computer matrix, the numbering sequence was different. The correspondence between the two sets of characters is shown in Table 1. Inspection of the data matrix, and comparisons with specimens, revealed that, where bifurcating characters were re-coded as two characters, usually the first of the re-coded characters corresponded to the *second* direction of change mentioned in the character description, and the second re-coded character to the *first* direction of change. For instance, character 1 in the descriptions (ratio of right lung length to snout-vent length) is bifurcating and was re-coded as two characters. The morphoclines mentioned in the description are: low (0.311-0.422), intermediate (0.423-0.519) and high (0.52-0.74). Thus, the first of the recoded characters (character 1 in the matrix, see Table 1) refers to the presence/absence of the second change, towards the derived state of a high ratio: i.e. primitive (0), ratio 0.519 or less; derived (1), ratio 0.52 or more. The second of the re-coded characters (character 2 in the matrix, see Table 1) refers to the presence/absence of the first change, towards the derived state of a low ratio: i.e. primitive (0), ratio 0.423 or greater; derived (1), ratio 0.422 or less.

Because the alternative character states for the 72 recoded characters were not stated by Wallach, and have posed some problems for other workers, they are listed below. The original numbering system in the text (50 characters) is shown in brackets after each character number. However, the details of each measurement (e.g. how each ratio is calculated) were clearly discussed by Wallach, and thus are not repeated.

1 (1a). Right lung / snout-vent ratio. 0.519 or less, 0. 0.52 or more, 1.

2 (1b). Right lung / snout-vent ratio. 0.423 or more, 0. 0.422 or less, 1.

3 (2a). Vascular portion of right lung / snout-vent ratio. 0.112 or more, 0. 0.111 or less, 1.

4 (2b). Vascular portion of right lung / snout-vent ratio. 0.16 or less, 0. 0.161 or more, 1.

5 (3a). Avascular portion of right lung / snout-vent ratio. 0.374 or less, 0. 0.375 or more, 1.

6 (3b). Avascular portion of right lung / snout-vent ratio. 0.296 or more, 0. 0.295 or less, 1.

7 (4a). Position of caudal tip of right lung along snout-vent axis, measured as the ratio - snout to tip of right lung / snout-vent length. 0.763 or less, 0. 0.764 or more, 1.

8 (4b). Position of caudal tip of right lung along snout-vent axis, measured as the ratio - snout to tip of right lung / snout-vent length. 0.674, 0. 0.673 or less, 1.

9 (5a). Ratio of dense to spare parenchyma on right lung. 5 or less, 0. 5.1 or more, 1.

10 (5b). Ratio of dense to spare parenchyma on right lung. 2.5 or more, 0. 2.4 or less, 1.

11 (6a). Lung diameter / coelom diameter ratio. 0.75 or less, 0. 0.8 or more, 1.

12 (6b). Lung diameter / coelom diameter ratio. 0.5 or more, 0. 0.4 or less, 1.

13 (7a). Tracheal membrane / tracheal ring ratio. 1.9 or less, 0. 2 or more, 1.

14 (7b). Tracheal membrane / tracheal ring ratio. 1 or more, 0. 0.9 or less, 1.

15 (8). Left lung / snout-vent ratio. 0.01 or more, 0. 0.009 or less, 1.

16 (9). Tracheal entry. Subterminal, 0. Paraterminal or quasiterminal, 1. Terminal, 2.

17 (10). Left lung. Present, 0. Absent, 1.

18 (11). Left bronchus. Present, 0. Absent, 1.

19 (12). Free tips on tracheal rings. Absent, 0. Present, 1.

20 (13). Orifice for left lung. Present, 0. Absent, 1.

21 (14). Tracheal lung. Absent, 0. Small, 1. Moderate, 2.

22 (15a). Snout-heart / snout-vent ratio. 0.277 or less, 0. 0.278 or more, 1.

23 (15b). Snout-heart / snout-vent ratio. 0.233 or more, 0. 0.232 or less, 1.

24 (16a). Liver length / snout-vent ratio. 0.265 or less, 0. 0.266 or more, 1.

25 (16b). Liver length / snout-vent ratio. 0.212 or more, 0. 0.211 or less, 1.

26 (17a). Liver-gall bladder distance / snout-vent ratio. 0.398 or less, 0.399 or more, 1.

27 (17b). Liver-gall bladder distance / snout-vent ratio. 0.306 or more, 0. 0.305 or less, 1.

28 (18a). Kidney-vent distance / snout-vent ratio. 0.184 or less, 0. 0.185 or more, 1.

29 (18b). Kidney-vent distance / snout-vent ratio. 0.132 or more, 0. 0.131 or less, 1.

30 (19). Hyoid length / snout-vent ratio. 0.096 or less, 0. 0.097 or more, 1.

31 (20a). Position of umbilicus. Number of ventrals from umbilical to preanal scute / total number of ventrals. 0.187 or less, 0. 0.188 or more, 1.

32 (20b). Position of umbilicus. Number of ventrals from umbilical to preanal scute / total number of ventrals. 0.142 or more, 0. O.141 or less, 1.

33 (21a). Heart-liver distance / snout-vent ratio. 0.076 or less, 0. 0.077 or more, 1.

34 (21b). Heart-liver distance / snout-vent ratio. 0.048 or more, 0. 0.047 or less, 1.

35 (22a). Total kidney length (right plus left) / snout-vent ratio. 0.137 or less, 0. 0.138 or more, 1.

36 (22b). Total kidney length (right plus left) / snout-vent ratio. 0.085 or more, 0. 0.084 or less, 1.

37 (23). Distance between systemic arch junction and heart apex / snout-vent ratio. 0.01 or more, 0. 0.009 or less, 0.

38 (24). Diameter of right systemic arch / diameter of left systemic arch. 0.5 or more, 0. 0.4 or less, 1.

39 (25a). Number of ventral scutes. 228 or fewer, 0. 229 or more, 1.

40 (25b). Number of ventral scutes. 192 or more, 0. 191 or fewer, 1.

41 (26a). Number of subcaudal scales. 74 or fewer, 0. 75 or more, 1.

42 (26b). Number of subcaudal scales. 54 or more, 0. 53 or fewer, 1.

43 (27a). Tail length / total length ratio. 0.2 or less, 0. 0.21 or more, 1.

44 (27b). Tail length / total length ratio. 0.15 or more, 0. 0.14 or less, 1.

45 (28). Maximum total length. 1500 mm or more, 0. 1499 mm-600 mm, 1. 599 mm or less, 2.

46 (29). Temporolabial scale. Present, 0. Absent, 1.

47 (30). Internasal scale. Paired, 0. Fused, 1.

48 (31). Dorsal scales. Without carinae, 0. With carinae, 1.

49 (32). Ventral scales. Without keels, 0. Weakly keeled, 1. Strongly keeled and notched, 2.

50 (33). Number of supralabials. Seven, 0. Six, 1. Five, 2.

51 (34). Nasal-preocular contact. Present, 0. Absent, 1.

52 (35). Preocular scales. One, 0. Two, 1.

53 (36a). Postocular scales. Two or one, 0. Three, 1.

54 (36b). Postocular scales. Two or three, 0. One, 1.

55 (37). Subocular scales. Absent, 0. Present, 1.

56 (38). Mid-body dorsal scale rows. 23-19, 0. 17, 1. 15, 2.

57 (39). Anal plate. Single, 0. Divided, 1.

58 (40). Subcaudal scales. All paired, 0. Both paired and single, 1. All single, 2.

59 (41). Prey. All ectotherms, 0. 25-50% endotherms, 1. All endotherms, 2.

60 (42). Posterior scale row reduction. Present, 0. Absent, 1.

61 (43a). Maxillary teeth. Seven or fewer, 0. Eight or more, 1.

62 (43b). Maxillary teeth. Three or more, 0. Two or fewer, 1.

63 (44). Hemipenis. Forked, spinose, 0. Single, calyculate, 1.

64 (45a). Venom gland musculature. *Glyphodon* or *Oxyuranus* type, 0. *Pseudechis* type, 1. *Demansia* type, 2. This character refers to presence of the *Pseudechis* or *Demansia* type of musculature.

65 (45b). Venom gland musculature. *Glyphodon,. Pseudechis,* or *Demansia* type, 0. *Oxyuranus* type, 1. This character refers to presence of the *Oxyuranus* type of musculature.

66 (46a). Ecology. Terrestrial, sub-fossorial, or fossorial, 0. Semi-arboreal, 1. Arboreal, 2.

67 (46b). Ecology. Terrestrial, semi-arboreal, or arboreal, 0. Sub-fossorial, 1. Fossorial, 2.

68 (47). Sexual dimorphism. Females larger, 0. No dimorphism, 1. Males larger, 2.

69 (48a). Body shape. Moderate or thin, 0. Thick, 1.

70 (48b). Body shape. Moderate or thick, 0. Thin, 1.

71 (49). Circadian activity. Nocturnal, 0. Crepuscular, 1. Diurnal, 2.

72 (50). Reproduction. Oviparous, 0. Viviparous, 1.

Wallach (1985) analysed the data set using three different algorithms of the PHYSYS program (see Wallach, 1985 for full details). Multistate characters were ordered in all three analyses, and each character state change was given a weighting of one. The "Wagner" and "Pimentel" algorithms were alternative methods that attempted to find the most parsimonious tree(s), assuming characters were reversible. The WISS algorithm attempted to find the most parsimonious tree, under the assumption of irreversibility. The three trees found in these analyses are shown in Fig. 1.

I re-analysed the data set using the phylogenetic package PAUP 3.1.1 (Swofford, 1993) on a MacIntosh Quadra 700 computer. Because of the size of the data matrix, only the heuristic search option could be used.
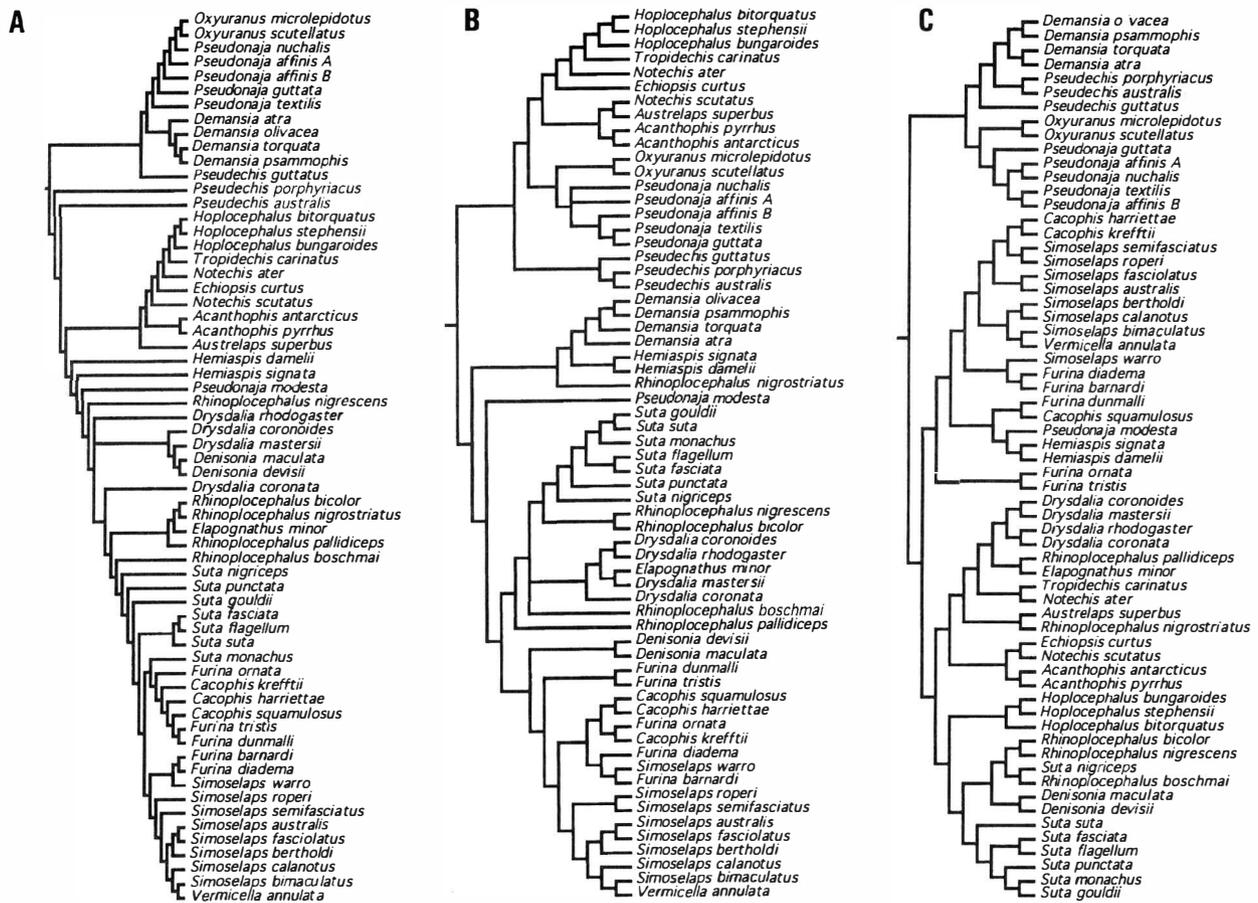
A

Oxyuranus microlepidotus
Oxyuranus scutellatus
Pseudonaja nuchalis
Pseudonaja affinis A
Pseudonaja affinis B
Pseudonaja guttata
Pseudonaja textilis
Demansia atra
Demansia olivacea
Demansia torquata
Demansia psammophis
Pseudechis guttatus
Pseudechis porphyriacus
Pseudechis australis
Hoplocephalus bitorquatus
Hoplocephalus stephensii
Hoplocephalus bungaroides
Tropidechis carinatus
Notechis ater
Echiopsis curtus
Notechis scutatus
Acanthophis antarcticus
Acanthophis pyrrhus
Austrelaps superbus
Hemiaspis damelii
Hemiaspis signata
Pseudonaja modesta
Rhinoplocephalus nigrescens
Drysdalia rhodogaster
Drysdalia coronoides
Drysdalia mastersii
Denisonia maculata
Denisonia devisii
Drysdalia coronata
Rhinoplocephalus bicolor
Rhinoplocephalus nigrostriatus
Elapognathus minor
Rhinoplocephalus pallidiceps
Rhinoplocephalus boschmai
Suta nigriceps
Suta punctata
Suta gouldii
Suta fasciata
Suta flagellum
Suta suta
Suta monachus
Furina ornata
Cacophis krefftii
Cacophis harriettae
Cacophis squamulosus
Furina tristis
Furina dunmalli
Furina barnardi
Furina diadema
Simoselaps warro
Simoselaps roperi
Simoselaps semifasciatus
Simoselaps australis
Simoselaps fasciolatus
Simoselaps bertholdi
Simoselaps calanotus
Simoselaps bimaculatus
Vermicella annulata

B

Hoplocephalus bitorquatus
Hoplocephalus stephensii
Hoplocephalus bungaroides
Tropidechis carinatus
Notechis ater
Echiopsis curtus
Notechis scutatus
Austrelaps superbus
Acanthophis pyrrhus
Acanthophis antarcticus
Oxyuranus microlepidotus
Oxyuranus scutellatus
Pseudonaja nuchalis
Pseudonaja affinis A
Pseudonaja affinis B
Pseudonaja textilis
Pseudonaja guttata
Pseudechis guttatus
Pseudechis porphyriacus
Pseudechis australis
Demansia olivacea
Demansia psammophis
Demansia torquata
Demansia atra
Hemiaspis signata
Hemiaspis damelii
Rhinoplocephalus nigrostriatus
Pseudonaja modesta
Suta gouldii
Suta suta
Suta monachus
Suta flagellum
Suta fasciata
Suta punctata
Suta nigriceps
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Rhinoplocephalus bicolor
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Drysdalia rhodogaster
Elapognathus minor
Drysdalia mastersii
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Rhinoplocephalus pallidiceps
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Denisonia maculata
Furina dunmalli
Furina tristis
Cacophis squamulosus
Cacophis harriettae
Furina ornata
Cacophis krefftii
Furina diadema
Simoselaps warro
Furina barnardi
Simoselaps roperi
Simoselaps australis
Simoselaps fasciolatus
Simoselaps bertholdi
Simoselaps calanotus
Simoselaps bimaculatus
Vermicella annulata

C

Demansia o vacea
Demansia psammophis
Demansia torquata
Demansia atra
Pseudechis porphyriacus
Pseudechis australis
Pseudechis guttatus
Oxyuranus microlepidotus
Oxyuranus scutellatus
Pseudonaja guttata
Pseudonaja affinis A
Pseudonaja nuchalis
Pseudonaja textilis
Pseudonaja affinis B
Cacophis harriettae
Cacophis krefftii
Simoselaps semifasciatus
Simoselaps roperi
Simoselaps fasciolatus
Simoselaps australis
Simoselaps bertholdi
Simoselaps calanotus
Simoselaps bimaculatus
Vermicella annulata
Simoselaps warro
Furina diadema
Furina barnardi
Furina dunmalli
Cacophis squamulosus
Pseudonaja modesta
Hemiaspis signata
Hemiaspis damelii
Furina ornata
Furina tristis
Drysdalia coronoides
Drysdalia mastersii
Drysdalia rhodogaster
Drysdalia coronata
Rhinoplocephalus pallidiceps
Elapognathus minor
Tropidechis carinatus
Notechis ater
Austrelaps superbus
Rhinoplocephalus nigrostriatus
Echiopsis curtus
Notechis scutatus
Acanthophis antarcticus
Acanthophis pyrrhus
Hoplocephalus bungaroides
Hoplocephalus stephensii
Hoplocephalus bitorquatus
Rhinoplocephalus bicolor
Rhinoplocephalus nigrescens
Suta nigriceps
Rhinoplocephalus boschmai
Denisonia maculata
Denisonia devisii
Suta suta
Suta fasciata
Suta flagellum
Suta punctata
Suta monachus
Suta gouldii

FIG. 1. The trees proposed for the data set in Table 1 (Wallach, 1985). A, tree found using the WAGNER algorithm of PHYSYS. Characters assumed to be reversible. B, tree found using the Pimentel algorithm of PHYSYS. Characters assumed to be reversible. C, tree found using the WISS algorithm of PHYSYS. Characters assumed to be irreversible.

Thus, as in the previous analysis, multistate characters were ordered, and each character state change (e.g. 0-1, or 2--1) was given a weighting of one. This has the undesirable effect that finely subdivided characters (those with more states) contribute more to tree length, and could have been eliminated by scaling all characters to unity. Also, some characters appear to be correlated (e.g. characters 19, tracheal rings with 21, tracheal lung). However, in order that my results be directly comparable to the previous study, no attempt has been made at this stage to modify the raw data set. In future, a more exhaustive study would need to increase sample sizes for many taxa, employ different outgroups, use organ mid-points rather than ends as landmarks, employ recent methods for coding continuous variables, consider character correlations, and investigate the effects of scaling all characters to unity (Wallach pers. comm., Underwood pers. comm.).

The analysis was run assuming that all characters were reversible (this corresponded to the Wagner and Pimentel analyses in PHYSYS). Two heuristic searches were performed: one using simple stepwise addition, and the other using 500 replicates of random stepwise addition. The latter is more time consuming but is usually better at finding all the most parsimonious trees.

A second analysis was run assuming irreversibility (this corresponded to the WISS analysis in PHYSYS). A heuristic search using simple stepwise addition was performed. Because PAUP is very slow when operating under this constraint, a search using random stepwise addition could not be performed (see Results).

RESULTS AND DISCUSSION

The re-analysis of Wallach's data set using PAUP 3.1.1, assuming reversibility, found a total of 258 equally-parsimonious trees, each of 578 steps. The search involving simple stepwise addition found only 27 trees, while the search involving random stepwise addition found 258 trees, including the 27 found in the former search. Thus, the analysis using random stepwise addition proved superior at finding the most parsimonious trees. All 258 trees were found in the first 200 random stepwise addition replicates, and the remaining 300 replicates only found trees already discovered in previous replicates. Thus, further replicates of random stepwise addition are unlikely to discover other equally-parsimonious (or even more parsimonious) trees, increasing one's confidence that all the most parsimonious trees were found.

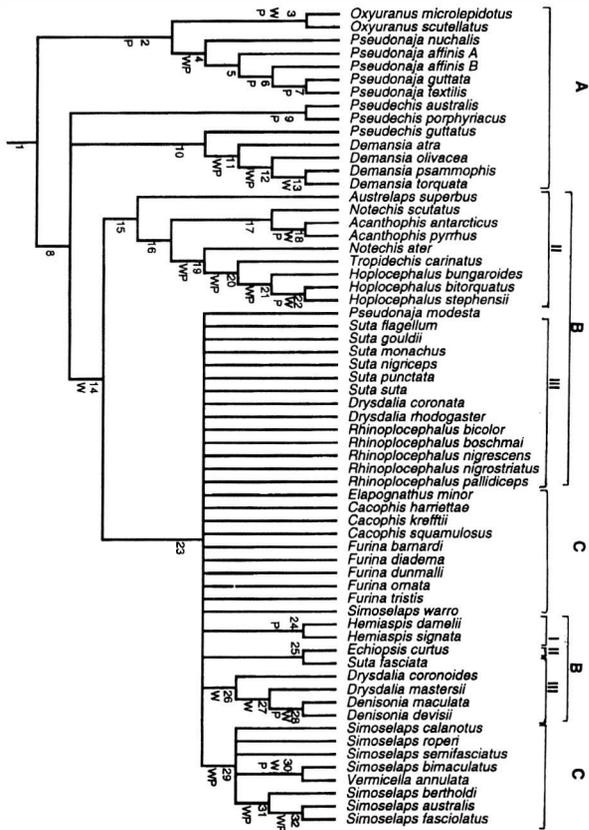The consistency index (0.147) and retention index (0.576) are both low, even when the number of taxa is

FIG. 2. Strict component consensus of the 258 most-parsimonious trees for the data set in Table 1, found using PAUP 3.1.1. The most parsimonious trees are each 578 steps long, c.i. 0.147, r.i. 0.576. Diagnoses for the numbered clades are presented in Table 2. "W" indicates a clade found in the corresponding Wagner tree (Fig. 1A), "P" indicates a clade found in the corresponding Pimentel tree (Fig. 1B). The taxa included in Wallach's divisions (A, BI, BII, BIII, C) are also indicated along the top of the cladogram.

taken into account (Sanderson & Donoghue, 1989), implying much character incongruence within the data set. The strict component consensus tree - which depicts only those clades common to all most-parsimonious trees (Wilkinson, 1994) - is shown in Figure 2A. Characters were optimized under delayed transformation, and characters diagnosing each grouping are listed in Table 2. It should be emphasized that, because of the amount of homoplasy in the data set, many characters can optimize in many different ways equally parsimoniously.

The Wagner tree (Fig. 1A) published in Wallach (1985) entails 592 steps. The Pimentel tree (Fig. 1B) is even less parsimonious, entailing 612 steps. Both trees are thus substantially longer than the most parsimonious trees (578 steps) found in this analysis. In addition, as noted by Wallach, they also differ very substantially from each other.

Both Wallach's trees are almost completely resolved, with only one or two trichotomies, while the consensus tree found in the current PAUP analysis is much more poorly resolved, with a 28-way polytomy. This polytomy mainly involves species in the genera

TABLE 2. Diagnoses of the clades identified in the PAUP analysis, when characters are optimized under delayed transformation. The numbered clades are shown in Fig. 2. Unless stated otherwise, changes are from 0-1. The consistency index for each character is also indicated in parentheses, characters with a relatively high index (0.33 or greater) are highlighted in bold. It will be clear that nearly all the characters are highly homoplastic.

1. 50 (0.22), 63 (0.083), 68 (0.111), 71 (0-2, 0.154).
2. 1 (0.111), 5 (0.125), 7 (0.167), 11 (0.048), 15 (0.067), 32 (0.1), 35 (0.067), 70 (0.2).
3. 38 (0.071), 39 (0.5), 51 (0.071), 59 (0-2, 0.286), 65 (0.2).
4. 46 (0.077), 49 (0.5), 57 (0.056), 61 (0.125).
5. 45 (0.095).
6. 17 (0.059).
7. 11 (1-0, 0.048), 23 (0.062), 38 (0.071).
8. 56 (0.095), 58 (0.074).
9. 9 (0.25), 57 (0.056), 60 (0.111), 64 (0.118), 72 (0.077).
10. 23 (0.062), 37 (0.091), 38 (0.071), 57 (0.056), 64 (0.118).
11. 11 (0.048), 41 (1.0), 56 (1-2, 0.095), 58 (1-0, 0.074), 61 (0.125), 64 (1-2, 0.118), 68 (1-2, 0.111), 70 (0.2).
12. 15 (0.067), 43 (0.2).
13. 17 (0.059), 18 (0.083), 33 (0.125).
14. 21 (0.056), 30 (0.5), 40 (0.167), 42 (0.2), 58 (1-2, 0.074). 72 (0.077).
15. 23 (0.062), 28 (0.1), 35 (0.067), 69 (0.2).
16. 56 (1-0, 0.095), 65 (0.2).
17. 15 (0.067), 21 (1-2, 0.056).
18. 23 (1-0, 0.062), 32 (0.1), 33 (0.125), 45 (0.095), 46 (0.077), 48 (0.333), 55 (0.5), 58 (2-1, 0.074), 68 (1-0. 0.111).
19. 10 (0.091), 11 (0.048), 13 (0.125), 19 (0.053), 21 (1-0. 0.056), 45 (0.095).
20. 5 (0.125), 66 (1.0), 69 (1-0, 0.2), 70 (0.2), 71 (2-1. 0.154).
21. 40 (1-0, 0.167), 44 (0.071), 49 (0-2, 0.5), 63 (1-0. 0.083), 68 (1-0, 0.111), 71 (1-0, 0.154).
22. 10 (1-0, 0.091), 13 (1-0, 0.125), 24 (0.059), 28 (1-0. 0.1), 42 (1-0, 0.2), 66 (1-2, 1.0).
23. 10 (0.091), 15 (0.067), 18 (0.083), 32 (0.1), 44 (0.071). 45 (0-2, 0.095), 56 (1-2, 0.095), 67 (0.286), 68 (1-0. 0.111), 71 (2-0, 0.154).
24. 23 (0.062), 31 (0.333), 32 (1-0, 0.1), 44 (1-0, 0.071), 45 (2-1, 0.095), 56 (2-1, 0.095), 57 (0.056), 61 (0.125), 64 (0-2, 0.118), 68 (0.111), 71 (0.154).
25. 1 (0.111), 5 (0.125), 7 (0.167), 16 (0-2, 0.062), 19 (0.053), 21 (1-2, 0.056), 45 (2-1, 0.095), 51 (0.071), 56 (2-1, 0.095), 68 (0.111), 69 (0.2).
26. 2 (0.143), 8 (0.067), 19 (0.053), 32 (1-0, 0.1), 68 (0.111).
27. 6 (0.083).
28. 56 (2-1, 0.095), 63 (1-0, 0.083), 65 (0.2), 69 (0.2).
29. 6 (0.083), 14 (0.053), 19 (0.053), 24 (0.059), 26 (0.067), 37 (0.091), 46 (0.077), 57 (0.056), 58 (2-0, 0.074), 60 (0.111), 62 (0.2), 63 (1-0, 0.083), 67 (1-2, 0.286), 72 (1-0, 0.077).
30. 1 (0.111), 5 (0.125), 6 (1-0, 0.083), 7 (0.167), 29 (0.2). 36 (0.5), 40 (1-0, 0.167), 50 (1-2, 0.222).
31. 16 (0-2, 0.062), 21 (1-0, 0.056), 23 (0.062), 60 (1-0. 0.111).
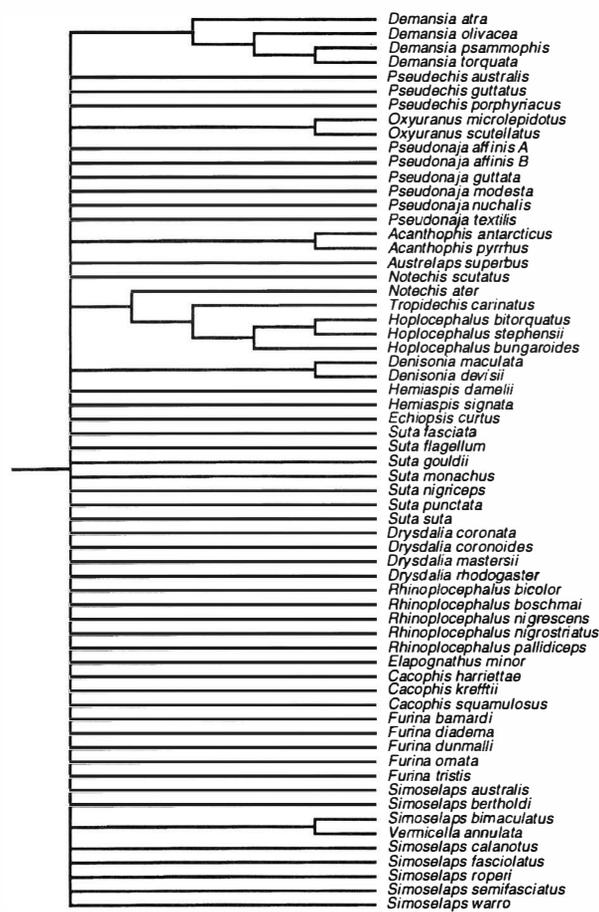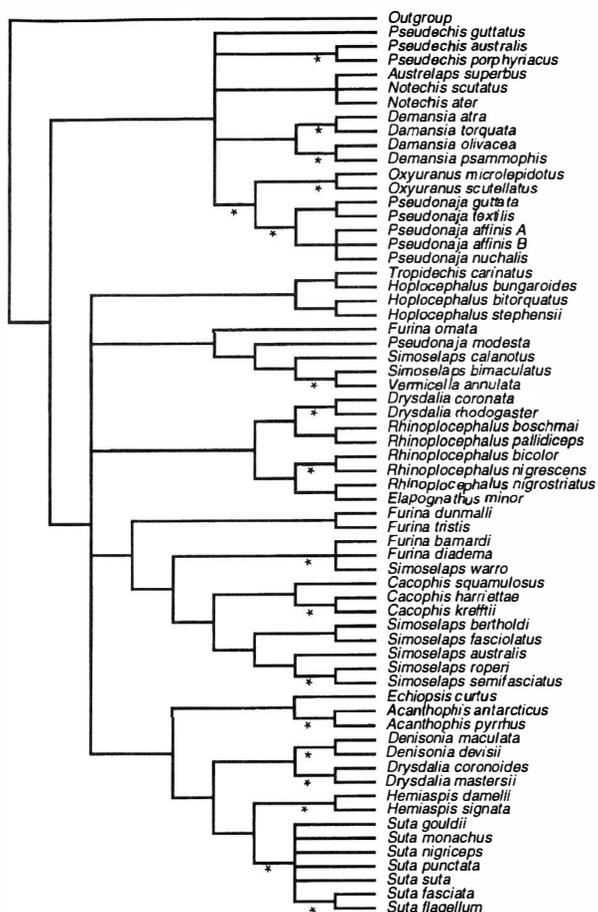32. 4 (0.167), 6 (1-0, 0.083), 10 (1-0, 0.091), 56 (2-1. 0.095).

FIG. 3. The strict component consensus of the 840 trees, each 669 steps long, found in the PAUP analysis assuming irreversibility. The corresponding tree identified by the WISS algorithm in PHYSYS (Wallach, 1985) is very different (Fig. 1C): clades correctly identified in the WISS tree are indicated with an asterisk (*).

FIG. 4. The strict component consensus tree of the 32 700 cladograms of 578 or 579 steps in the heuristic search employing simple stepwise addition. The same tree was found in the search employing random stepwise addition. This tree is very poorly resolved.

Pseudonaja, Suta, Drysdalia, Rhinoplocephalus, Elapognathus, Cacophis, Furina, and *Simoselaps*. Another five-way polytomy involves mainly species of *Simoselaps*. When the trees are compared, of the 31 clades (clades 2-32 in Fig. 2A) identified in the PAUP analysis, only 13 were found in both the Wagner and Pimentel analyses. 3 were found in the Wagner analysis only, and 5 were found in the Pimentel analysis only. The correctly identified clades are shown in Figure 2A. It will be clear that the previous analyses were most accurate concerning relationships within the *Hoplocephalus-Austrelaps-Notechis* group and portions of the *Simoselaps-Vermicella* group. However, 10 of the clades in the PAUP consensus tree were not identified in either of Wallach's trees. In particular, many of the larger groupings found in the PAUP analysis (e.g. clades 8, 15, 23), representing the earliest and most basal divisions within Australian elapids, were not previously identified.

The PAUP analysis assuming irreversibility proved to be extremely slow. The heuristic search using simple stepwise addition took 242 hours (10 days) to complete. Extensive random stepwise addition would have taken much longer, and was therefore abandoned. The former analysis resulted in 840 equally-parsimonious

trees, each of 669 steps. The strict component consensus tree is shown in Fig. 3. The corresponding WISS tree produced by PHYSYS (Fig. 1C) published in Wallach (1985) entailed 686 steps (when characters were optimized assuming irreversibility). Thus, the PHYSYS analysis again failed to find the most parsimonious solution for the data set, this time under the assumption of irreversibility. Again, of the 48 clades found in this analysis (not counting the clade consisting of the entire ingroup), only 18 were correctly identified. These are indicated in Fig. 3.

The above results demonstrate that the computer package available at the time did not allow Wallach to find the most parsimonious trees consistent with his data matrix in any of his three analyses. This is understandable, considering the size of the data set and the primitive nature of computer parsimony programs at the time. The consensus tree in each analysis is of a different topology, and less well resolved, than those published in Wallach.

Based primarily on the three trees found in his PHYSYS analyses, Wallach proposed some suprageneric groupings of Australian elapids. The assumption of irreversibility in cladistic analyses cannot usually be justified, and I know of no recent cladistic

analyses of snake phylogeny that make this assumption. For this reason, in the following discussion, I will only compare in detail Wallach's proposed divisions with the PAUP consensus tree found for that data set assuming reversibility.

The major clades ("Divisions", divided into "Sections") proposed by Wallach are indicated in Fig. 2A, and discussed below.

Division A: *Pseudechis, Demansia, Pseudonaja* (excluding *P. modesta*) and *Oxyuranus*. This assemblage is paraphyletic in this analysis. While these taxa are similar, it appears that the similarities they share are all primitive for Australian elapids. As noted by Wallach, *Pseudonaja modesta* surprisingly comes out as being not closely related to other members of the genus. Rather, it is much more derived than any of the members of Division A, and has affinities with Division C.

Division B: *Hemiaspis, Hoplocephalus, Tropidechis, Notechis, Austrelaps, Echiopsis, Acanthophis, Rhinoplocephalus* (including *Cryptophis*), *Suta* ("*Parasuta*"), *Drysdalia* and *Denisonia*. This grouping includes all the viviparous forms, with the exception of *Pseudechis porphyriacus*. As noted by Wallach, *Pseudonaja modesta* surprisingly comes out as part of this group, rather than being related to other species of *Pseudonaja*. The most parsimonious arrangement found in this study indicates that this group is paraphyletic with respect to Division C: *Simoselaps, Furina, Vermicella*, and *Cacophis*.

Division B, Section I: *Hemiaspis*. The monophyly, and distinctness, of this genus is supported here. It is not closely related to any other genus in Division B.

Division B, Section II: *Hoplocephalus, Tropidechis, Notechis, Austrelaps, Echiopsis, Acanthophis*. This grouping is largely supported by this analysis. All the genera, except for *Echiopsis*, form a clade. *Echiopsis* is not part of this lineage, but clusters with *Suta fasciata*.

Division B, Section III. *Rhinoplocephalus* (including *Cryptophis*), *Suta* ("*Parasuta*"), *Drysdalia* and *Denisonia*. Whether this grouping is monophyletic or paraphyletic cannot be ascertained; i.e. this is a "metataxon" (Archibald, 1994). This assemblage forms part of the 28-way polychotomy along with members of Division C.

Division C. *Simoselaps, Vermicella, Furina* (including *Glyphodon*), *Cacophis*. Monophyly or paraphyly of this group cannot be ascertained, this grouping is therefore another "metataxon" (Archibald 1994). Again, the contained taxa form part of the 28-way polychotomy along with members of Division B.

The soft anatomical data set therefore does not resolve the phylogenetic relationships of Australian elapids as fully as previously thought. Wallach (1985) was careful to emphasize that his results were tentative, because of the inadequate sample sizes of many taxa: most species were represented by only one or two specimens. Another source of error could not be detected at the time: the failure of the computer programs to find the most parsimonious tree. Most of the group-

ings found in Wallach's analyses, and proposed in his dicussion, are not found in the PAUP analysis. However, many of Wallach's groupings, including those above, have been accepted by later workers. For instance, Hutchinson (1990), in his taxonomic revision of generic names, cited Wallach's work as containing evidence for the monophyly of *Drysdalia*, the monophyly of *Furina*, the monophyly of *Pseudechis*, and a close relationship between *Echiopsis* and *Notechis*. The present study shows that Wallach's data set does not support any of these conclusions. However, Wallach's analyses managed to identify many of the clades present on the most parsimonious trees (Figure 2A).

Because the consistency index for this analysis was rather low (0.147), implying much character incongruence, it was decided to investigate the strength of the phylogenetic signal in the data. I first attempted to calculate the Bremer index for each clade. This index is the number of steps it takes to break up a clade (Bremer 1988). The procedure is discussed in Lee (1995, 1996). Briefly, in order to obtain the Bremer index of, for instance, the *Oxyuranus* clade, a constraint tree is entered into PAUP. In this tree, the two species of *Oxyuranus* form a clade, but relationships between the *Oxyuranus* clade and all other ingroup taxa, are unresolved. PAUP is then instructed to find the most parsimonius tree which is *not* consistent with this constraint tree (reverse searching). The difference between the length of this tree (584) and the most parsimonious tree (578 steps) is the Bremer index. It soon became apparent that the data set was too big for PAUP to find the most parsimonious tree during reverse searching, and thus Bremer indices could not be calculated. For instance, according to several different heuristic analyses in PAUP, the most parsimonious trees inconsistent with the *Oxyuranus* clade are each 584 steps, in which case the Bremer index is 6. However, this clade (Table 2) is only diagnosed by five characters, and hence can be broken by assuming, at most, 5 additional steps. Since all the characters are equivocal, one would expect to be able to break up the clade by assuming fewer than 5 additional steps. Thus, the most parsimonious tree inconsistent with *Oxyuranus* monophyly should have been 583 or fewer steps, and could not be the 584 calculated by PAUP's reverse search. For this reason, Bremer indices were not calculated via this method. However, it was possible to use another method to identify clades with a Bremer index of only 1 (see below).

Because of the number of taxa, it also did not prove possible to investigate the strength of the clades via bootstrapping (Felsenstein, 1985; Sanderson, 1995): an attempt was made, but was aborted after 24 hours elapsed and only three replicates (out of the minimum 100 needed) were completed.

One further test, however, could be performed to test the strength of the phylogenetic signal in the data set. The PAUP analysis (assuming reversibility) was rerun, and all most parsimonious trees, and those one step longer, were saved. Using simple stepwise addition, a

total of 32 700 trees (27 of 578 steps, the remainder of 579 steps), were identified before the computer ran out of memory, and the strict consensus tree of all these trees is almost totally unresolved (Fig. 4). An analysis employing random stepwise addition was also performed; in order to stop the computer memory from being filled with trees from a single replicate, PAUP was instructed to save no more than 1000 trees from each replicate. The strict consensus from this analysis was identical to the one found in the preceding analysis. Thus, almost all the clades identified in the analysis can be collapsed if one assumes only a single additional step, i.e., most clades have a Bremer index of only 1.

The above analyses demonstrate that this soft anatomical (visceral and external morphological) data set is much less phylogenetically informative than previously thought. They also show how the number of changes diagnosing a clade is often a poor indicator of the strength of the grouping: most of the groupings in this analysis collapse if one assumes a single additional step (Fig. 4), yet many of these are diagnosed by numerous changes (Table 2).

The weak and ambiguous phylogenetic signal in this data set means that one should avoid making evolutionary inferences or taxonomic changes based on the most parsimonious trees, or Wallach's published trees. It should be mentioned, though, that recent taxonomic reviews (Hutchinson, 1990) and ecological studies (Shine, 1994) of Australian elapids have not been based solely on Wallach's data, but have also considered other phylogenetic evidence (e.g. Mengden, 1985; Schwaner et al., 1985).

Nevertheless, Wallach's data set remains an extremely important body of work: in particular, it is one of the most comprehensive surveys of morphology and variability of the viscera in any group of snakes. The fact that it is not very phylogenetically informative is in itself a significant and potentially profound conclusion. It may be that the data were inadequately coded, and that a rigorous re-study might reveal a stronger phylogenetic signal. Alternatively, one might conclude that visceral and scale features, the bulk of the data set, are too labile to be very useful in constructing higher level (suprageneric) groupings, i.e. the poor signal is real rather than an artefact. However, many other studies of snakes have suggested the potential value of visceral and scale character data in higher-level squamate phylogeny, e.g. Underwood (1967), Rossman et al. (1982), Becker et al. (1989), Underwood & Stimson (1990). Much more work is necessary in order to test this hypothesis. For instance, a best fitting tree will need to be found from a combined analysis of osteological, myological, visceral, external, genetic, behavioural, and ecological traits, and relative amounts of homoplasy in each data set compared.

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