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The origin of snakes (Serpentes) as seen through eye anatomy

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Snakes evolved from lizards but have dramatically different eyes. These differences are cited widely as compelling evidence that snakes had fossorial and nocturnal ancestors. Their eyes, however, also exhibit similarities to those of aquatic vertebrates. We used a comparative analysis of ophthalmic data among vertebrate taxa to evaluate alternative hypotheses concerning the ecological origin of the distinctive features of the eyes of snakes. In parsimony and phenetic analyses, eye and orbital characters retrieved groupings more consistent with ecological adaptation rather than accepted phylogenetic relationships. Fossorial lizards and mammals cluster together, whereas snakes are widely separated from these taxa and instead cluster with primitively aquatic vertebrates. This indicates that the eyes of snakes most closely resemble those of aquatic vertebrates, and suggests that the early evolution of snakes occurred in aquatic environments. © 2004 The Linnean Society of London, *Biological Journal of the Linnean Society,* 2004, **81**, 469–482.

ADDITIONAL KEYWORDS: adaptation – Alethinophidia – ophthalmic morphology – parsimony analysis – Scolecophidia – vertebrate evolution.

INTRODUCTION

Limbless, snake-like bodies evolved independently among numerous squamate lineages, many of which exhibit terrestrial and fossorial or semifossorial ecologies (Wiens & Slingluff, 2002). One might infer from these observations that similar ecologies produced limblessness in snakes, but recent fossil discoveries (Caldwell & Lee, 1997; Lee, Caldwell & Scanlon, 1999; Rage & Escuillie, 2000; Scanlon & Lee, 2000; Tchernov *et al*., 2000) revived an alternative hypothesis that snake ancestors lived in marine environments (Cope, 1869; Nopsca, 1923; McDowell, 1972). Specifically, Cretaceous marine snakes with hind limbs, hypothesized to be transitional between lizard and snake body plans, provided the impetus for new phylogenetic analyses of snakes and their relatives. Some studies found these limbed marine snakes to be basal snakes, supporting a marine origin (Caldwell & Lee, 1997; Lee *et al*., 1999; Rage & Escuillie, 2000; Scanlon & Lee, 2000). Others concluded that they were not primitive but advanced (macrostomatan) snakes (Zaher, 1998; Zaher & Rieppel, 1999; Rieppel *et al*., 2003) that had re-evolved legs (Tchernov *et al*., 2000; Zaher & Rieppel, 2000). The latter analyses placed the extant, burrowing blindsnakes and anilioids as the most basal snakes, thus reaffirming the traditional view of a burrowing origin of snakes.

Other evidence relevant to question of snake origins comes from comparative vertebrate ophthalmology (Fig. 1). Specifically, the extreme structural and

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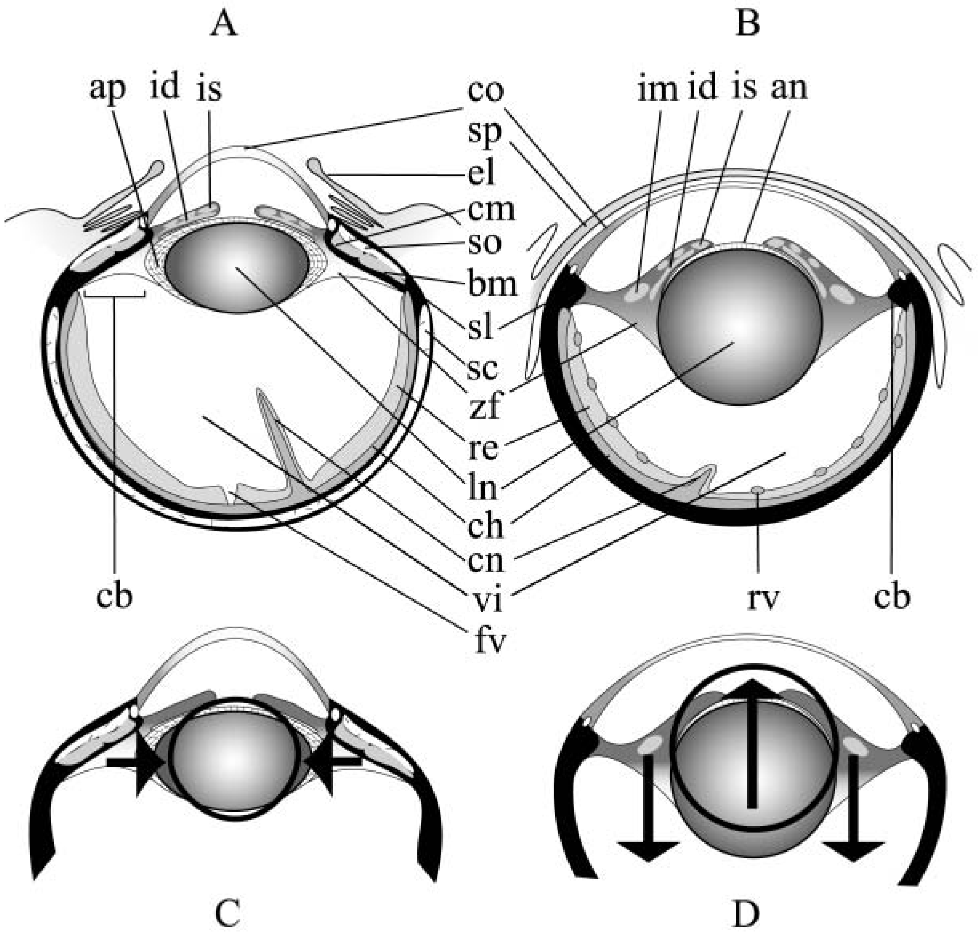

Figure 1. Functional anatomy of lizard (A) and snake (B) eyes, illustrating major differences between the two general types. C, lizards focus by contracting large ciliary muscles (bm, cm) anchored to scleral ossicles (so) thereby applying pressure to the lateral surface of the lens (ln) via the annular pad (ap). D, snakes focus by moving their lens forward via increased pressure on the vitreous (vi) due to peripheral iris muscle (im) contraction. *Abbreviations:* an, anterior pad; bm, Brücke's ciliary muscle; cb, ciliary body; ch, choroid; cm, Crompton's ciliary muscle; cn, conus papilliaris; co, cornea; el, eye lid; fv, fovea; id, iris dilator muscle; is, iris sphincter muscle; ln, lens; re, retina; sc, scleral cartilage; sl, sclera; sp, spectacle; vi, vitreous; zf, zonular fibres.

functional differences between the eyes of lizards (Fig. 1A, B) and those of snakes (Fig. 1C, D) implies that snake eyes were dramatically altered during their origin from lizard ancestors (Walls, 1940). The most substantial differences involve the structures directly associated with focusing an image onto the retina. Snakes focus by applying pressure to the vitreous body via enlarged peripheral iris muscles, thus forcing a rigid, spherical lens forward within the eyeball. Relaxation of those muscles results in passive retraction of the lens (Michel, 1933; Sivak, 1977). That contrasts with the lizard mechanism in which robust ciliary muscles embedded in the choroid and anchored to bony elements in the sclera squeeze a thick annular pad bounding the soft, flattened lens (Walls, 1942).

Given that lizards are ancestral to snakes, and that many superficially snake-like lizards are burrowers, one explanation for these ophthalmic observations was that snakes went through a burrowing phase in their origin, and in that low-light environment lost the typical lizard mechanism for precise image focusing. After the functional and structural degeneration of their eyes, snakes re-colonized light-rich environments and evolved a totally different focusing mechanism. That explanation is widely cited, with some reservations and modifications (Bellairs & Underwood, 1951; Underwood, 1970) as compelling evidence that early snakes had greatly reduced eyes and fossorial ancestors (Greene, 1997; Coates & Ruta, 2000; Zaher & Rieppel, 2000). The functional degeneration of snake eyes during their early evolution also is consistent with the similar fusion or loss of neural layers in the optic tectum observed in snakes and squamate species with reduced visual function (Senn & Northcutt, 1973).

Snake eyes, however, also bear many intriguing similarities to the eyes of aquatic vertebrates. Primitively aquatic animals, such as fishes and amphibians, have a rigid spherical lens that focuses by movement, usually toward the cornea, accomplished using one or more subsets of iridial musculature directly attached to the lens epithelium (Walls, 1942; Fernald, 1990). Secondarily aquatic animals, including mammals and birds, also have more spherical lenses than their terrestrial relatives (Walls, 1942; Sivak, 1975). Among aquatic mammals, whales accommodate by forward lens movement (Supin, Popov & Mass, 2001), and a similar mechanism was proposed for pinnepeds (West *et al*., 1991). Aquatic turtles and diving birds such as cormorants use robust iris sphincter muscles to squeeze the anterior surface of the lens to focus underwater.

In proposing similarities between the eyes of snakes and burrowing reptiles, Walls (1940) did not compare the eyes of snakes to those of the only extant marine lizard, the Galapagos marine iguana, *Amblyrhynchus cristatus* (Bell), whose eyes remain unstudied, nor did he compare them to other aquatic vertebrates. Similarly, aquatic species in general and the marine iguana, in particular, have yet to be investigated with regard to visual centres in the brain. Thus, the marine origin hypothesis has never been evaluated using comparative ophthalmic data. Here, we apply parsimony and phenetic clustering methods to ophthalmic and orbital data across a wide range of vertebrate taxa to investigate the probable ecological conditions responsible for snake eye anatomy.

MATERIAL AND METHODS

We constructed a matrix containing 69 ophthalmic and orbital characters (see Appendix) coded for 53 vertebrate taxa and compiled from extensive literature (Walls, 1942; Rochon-Duvigneaud, 1943; Duke-Elder, 1958; Underwood, 1970; Sillman, 1973; Sivak, 1977; Fite & Lister, 1981; Fernald, 1990; Murphy *et al*., 1990; Schmid, Howland & Howland, 1992; Pardue, Sivak & Kovacs, 1993; Supin *et al*., 2001). These were subjected to parsimony analysis (which unites taxa based on derived similarity) and phenetic analysis (which groups taxa based on overall similarity).

In the parsimony analyses, 11 multistate characters were treated as ordered (according to morphoclines) and the remainder as unordered. Additionally, we performed analyses with all multistate characters treated as both ordered and unordered. Prior to this, we identified and removed seven cladistically uninformative characters. Multiple searches on the resulting matrix were performed using the Parsimony Ratchet (Nixon, 2000) in the tree-searching program NONA (Goloboff, 1999). In Winclada (Nixon, 2002), we scanned the trees produced by the Parsimony Ratchet for unsupported nodes (which were collapsed) and created a strict consensus of the remaining trees. We expected snakes to align either with varanoid lizards, if eye characters reflected mainly shared ancestry, or unrelated fossorial or aquatic taxa if the characters reflected mainly convergent adaptation.

To determine which characters were responsible for each cluster in the consensus tree, the distribution of each of the 62 informative characters was analysed separately under accelerated and delayed optimization strategies. Next, we assembled several vertebrate trees from other studies (Sibley & Ahlquist, 1990; Helfman, Collette & Facey, 1997; Lee, 2000; Murphy *et al*., 2001; Scally *et al*., 2001; Zug, Vitt & Caldwell, 2001) and synthesized a traditional (though not universally accepted) topology for vertebrates. Using that tree, we performed character optimization using our ophthalmic data to identify lineages at the end of long branches, i.e. which had undergone extensive eye evolution.

Finally, we converted the matrix to binary data for each character state and constructed a distance matrix from those data in SPSS (2002) statistical software, using the ‘pattern difference’ algorithm for calculation of dissimilarity. The distance matrix was inspected directly, rather than forced into a cluster diagram (phenogram), because such clustering usually distorts phenetic distances. We subdivided taxa into four ecological categories – aquatic, amphibious, terrestrial, and fossorial – and then ranked distances between each taxon and separately for scolecophidians (blindsnakes) and alethinophidians (advanced snakes). We also calculated the median rank for the distances within each ecological category as a score of overall similarity between taxa in that category and either blindsnakes or advanced snakes.

RESULTS

In the consensus tree from the analysis with selected characters ordered (Fig. 2A), taxa tend to align with each other based upon similar ecologies rather than accepted phylogenetic relationships. In particular, mammals and reptiles with reduced eyes emerge at the base of the tree. Snakes, which might be expected to align either with lizards, or with eye-reduced forms, instead cluster with aquatic forms, nesting deeply within fishes and caecilian amphibians.

Three characters that unite snakes with primitively aquatic taxa (fishes and caecilians) are a flattened cornea, a thickened corneal margin, and a spherical lens.

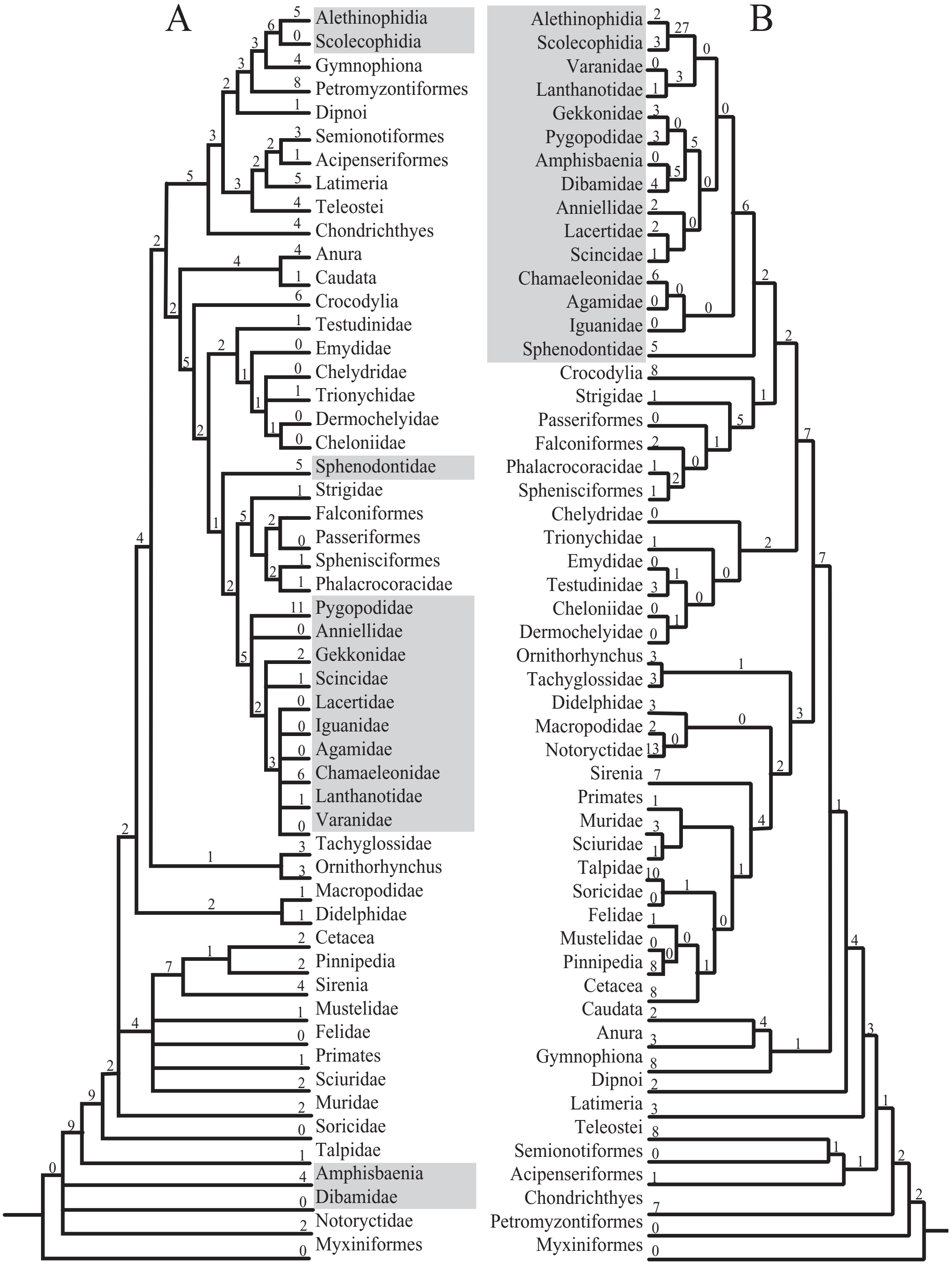

Figure 2. A, strict consensus of 12 most parsimonious trees from the matrix of 69 ophthalmic and orbital characters, each with length = 295, consistency index = 0.35, retention index = 0.77, shows how ophthalmic characters reflect common ecology, rather than common ancestry, among vertebrates. B, a traditional vertebrate phylogeny synthesized from other studies and data (Sibley & Ahlquist, 1990; Helfman *et al.*, 1997; Lee, 2000; Murphy *et al.*, 2001; Scally *et al.*, 2001; Zug *et al.*, 2001): length = 405, consistency index = 0.25, retention index = 0.64. In both trees, the two groups of snakes are at the top. Grey boxes show the distribution and relationships within the lepidosaur clade for both trees. Numbers above each branch length indicate that length for optimized ophthalmic and orbital characters. Branch lengths of zero indicate nodes unsupported by ophthalmic characters.

These characters are shared by all primitively aquatic animals, and also are expressed in secondarily aquatic animals to a greater degree than in their terrestrial relatives (Walls, 1942; Sivak, 1975). They thus appear to be associated with aquatic habits. Another character uniting snakes with the aquatic clade is the presence of blood vessels on the surface of the retina. These vessels on the inner surface of the retina nourish the vitreous humour and retina. In snakes, they are likely to represent the arrest of a developmental programme (Jokl, 1923; Walls, 1942), but as they are not also expressed in secondarily aquatic forms, the correlation of this character with aquatic habits is less compelling.

Three other characters uniting snakes with the aquatic clade are losses (in snakes) of various land vertebrate synapomorphies: the lachrymal gland, nictitans, and retractor bulbi muscles. Lachrymal glands, which usually secrete an aqueous fluid, were lost by numerous tetrapod lineages including some whales, murid rodents, penguins, some owls, *Sphenodon*, some geckos, pygopodids (legless geckoes), and snakes. The nictitans, or nictitating membrane also was lost by numerous taxa of varying ecologies: whales, echidnas, opossums, marsupial moles, largely burrowing squamates such as pygopodids, amphisbaenians, and dibamids, as well as chameleons and snakes. Retractor bulbi muscles are also synapomorphic for tetrapods and were subsequently lost by snakes and birds, and co-opted by caecilian amphibians to manipulate their tentacles. The broad ecological distribution of these three characters makes them ambiguous regarding the ecological origin of snakes.

Branch lengths on the synthesized vertebrate phylogeny (Fig. 2B) were calculated for those data optimized only for unambiguous changes. The longest branch (length = 27) leads to snakes (Scolecophidia plus Alethinophidia). The next three longest branches include those for dibamid and amphisbaenian squamates (length = 17), marsupial moles (length = 13), and talpid moles (length = 10). Both delayed and accelerated optimization identified the same long branches. Thus, snakes have indeed undergone substantial ophthalmic change, as have some burrowing forms. However, the previous results show that the actual nature of the changes is very different. Also, many of the nodes in Figure 2B are unsupported by any synapomorphies in ophthalmic characters, further demonstrating the lack of correlation between eye anatomy and phylogeny.

In the phenetic analysis, the eyes of blindsnakes and advanced snakes were, as expected, most similar to one another. When compared to other taxa, the eyes of advanced snakes shared the greatest similarity with mainly aquatic taxa: sharks, whales, sirenians, gars and lampreys, as well as caecilians, shrews, mice, and opossums (Table 1). The eyes of blindsnakes were most similar to those of caecilians, shrews, mice, lungfishes, echidnas, lampreys, hagfishes, dibamids, and sirenians (Table 1). The median ranks (Table 2) for distances between both advanced snakes and blindsnakes with the remaining taxa subdivided into ecological categories were least (nearest) for aquatic animals, indicating greatest overall similarity to aquatic taxa. The next greater median between blindsnakes and the remaining taxa was for fossorial groups, followed by amphibious taxa, and lastly terrestrial forms. For advanced snakes, the next greatest medians were for fossorial and terrestrial groups (tied), and lastly by amphibious taxa. Thus, the eyes of both groups of snakes are most similar to the eyes of aquatic rather than fossorial taxa, though the eyes of blindsnakes are also somewhat similar to those of fossorial species, as is expected given other convergent features (Lee, 1998).

DISCUSSION

It is not surprising that previous workers (Walls, 1940; Bellairs & Underwood, 1951; Underwood, 1970) considered the highly modified snake eye as evidence of a fossorial or sheltering ancestor, given that ophthalmic and orbital characters show the greatest degree of change among burrowing taxa and snakes (Fig. 2B). However, the exact nature of the changes in snakes, and in burrowing taxa, are very different (Fig. 2A). Previous studies only compared snake eyes with those of lizards, and thus overlooked the striking ocular similarities between snakes and a variety of primarily aquatic vertebrates.

The placement of caecilians with snakes in our parsimony consensus tree reflects the ambiguity that has plagued attempts to understand the ecological forces that moulded the unique snake body plan. Caecilians contain species that are either burrowing, aquatic, or both and this cluster thus fits predictions of either an aquatic or burrowing origin of snakes. Indeed, these hypotheses are not mutually exclusive (Nopsca, 1923; McDowell, 1972; Rieppel, 1988). However, the nesting of the snake-caecilian ‘clade’ within a plexus of aquatic vertebrates (fish) strongly supports the aquatic hypothesis for snake origins. None of the characters supporting the fish–caecilian–snake cluster are shared with exclusively burrowing taxa. In contrast, three characters are shared with exclusively aquatic or amphibious taxa: the flattened cornea, thickened corneal margin, and spherical lens. Moreover, the loss of the retractor bulbi muscles in snakes, resulting in a condition convergent with primitively aquatic animals, does not necessarily imply visual reduction, since a similar loss has occurred in large-eyed forms with great visual acuity (birds). Overall, these oph-

Table 1. Pairwise distances comparing Alethinophidia (advanced snakes) and Scolecophidia (blindsnakes) to other vertebrate taxa. Distances are shown in ascending order (i.e. decreasing similarity) for advanced snakes

Taxa	Alethinophidia	Scolecophidia	Taxa	Alethinophidia	Scolecophidia
Alethinophidia	0.000	0.004	Dibamidae	0.026	0.012
Scolecophidia	0.004	0.000	Sphenisciformes	0.028	0.024
Chondrichthyes	0.015	0.023	Talpidae	0.030	0.017
Gymnophiona	0.017	0.006	Sphenodontidae	0.030	0.024
Muridae	0.017	0.010	Pygopodidae	0.030	0.019
Soricidae	0.018	0.009	Strigiformes	0.030	0.025
Cetacea	0.018	0.015	Amphisbaenia	0.031	0.015
Mustelidae	0.019	0.017	Phalacrocoracidae	0.031	0.024
Sirenia	0.019	0.014	Falconiformes	0.032	0.029
Petromyzontiformes	0.021	0.011	Teleostei	0.034	0.038
Semionotiformes	0.021	0.016	Cheloniidae	0.034	0.020
Didelphidae	0.021	0.013	Chelydridae	0.034	0.020
Felidae	0.021	0.017	Dermochelyidae	0.034	0.020
Dipnoi	0.022	0.010	Emydidae	0.034	0.024
Tachyglossidae	0.022	0.010	Testudinidae	0.036	0.022
Pinnipedia	0.022	0.020	Trionychidae	0.036	0.022
Sciuridae	0.022	0.016	Passeriformes	0.037	0.030
Anura	0.023	0.027	Gekkonidae	0.039	0.039
Crocodylia	0.023	0.017	Scincidae	0.041	0.036
Latimeria	0.024	0.014	Anniellidae	0.041	0.039
Ornithorhyncus	0.024	0.016	Chamaeleonidae	0.048	0.039
Macropodidae	0.024	0.015	Varanidae	0.053	0.044
Primates	0.024	0.018	Lanthanotidae	0.054	0.045
Myxiniformes	0.025	0.011	Lacertidae	0.055	0.045
Acipenseriformes	0.025	0.014	Iguanidae	0.055	0.047
Caudata	0.026	0.021	Agamidae	0.056	0.046
Notoryctidae	0.026	0.016			

Table 2. Medians of ranked pairwise distances from blindsnakes and advanced snakes for vertebrate taxa grouped by ecology

	Aquatic	Amphibious	Terrestrial	Fossorial
Alethinophidia	11.500	32.500	29.500	29.500
Scolecophidia	11.000	30.000	38.000	17.500

thalmic characters add strength to the hypothesis that snakes had aquatic ancestors.

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APPENDIX

CHARACTER STATES

Numbers correspond to the character numbers (columns) in the character by taxon matrix. Numbers in parentheses represent character states. *indicates characters coded as ordered. All remaining characters were unordered. †indicates characters found to be uninformative for our parsimony analysis.

1† Eyeball shape: hemispherical (0), flattened tubular (1).
2* Lachrymal gland: absent (0), small (1), large (2)
3* Harderian gland: absent (0), small (1), large (2)
4 Orbital drainage: none (0), soft tissue canal (1), bony canal (2)
5 Eyelid mobility: both mobile (0), reduced mobility in one lid (1), reduced mobility in both (2), lids fused (3)
6 Eyelid transparency: both opaque (0), one eyelid transparent (1), both eyelids transparent (2)
7 Nictitating membrane: none (0), actively mobile (1), passively mobile (2), immobile (3)
8 Inferior oblique: absent (0), present (1)
9 Superior oblique: absent (0), present (1)
10 Inferior rectus: absent (0), present (1)
11 Superior rectus: absent (0), present (1)
12 Medial rectus: absent (0), present (1)
13 Lateral rectus: absent (0), present (1)
14 Retractor bulbi: absent (0), present (1), co-opted (2)
15 Levator bulbi: absent (0), present (1), co-opted (2)
16 Bursalis: absent (0), present (1), co-opted (2)
17 Protractor lentis (transversalis): absent (0), present (1)
18† Retractor lentis: absent (0), present (1)
19 Spectacle: none (0), primary (1), secondary (2), tertiary (3)
20 Choroid and sclera: fused (0), separate (1)
21 Corneal curvature: flattened (0), convex but little or no sulcus (1), extremely convex with distinct sulcus (2)
22 Corneal margin: as thick as centre (0), thicker than centre (1)
23 Corneal epithelium: stratified squamous (0), cornified stratified squamous (1)
24 Descemet's lamina and mesothelium: absent (0), present (1)
25 Corneal substantia propria: absent (0), present (1)
26 Autochthonous layer of cornea: absent (0), present (1)
27† Corneal pigment: none (0), present (1)
28 Pectinate or annular ligament: absent (0), present (1)
29† Aqueous production: diffusion through cornea (0), secreted internally (1)
30 Aqueous drainage: indirect diffusion (0), general lymphatic (1), canal of Schlemm (2)
31* Scleral cartilage: absent (0), reduced (1), robust (2)
32* Scleral ossicles: absent (0), reduced (1), robust (2)
33 Iris muscle fibres: absent (0), smooth (1), striated (2)
34 Pupillary contraction: none (0), slow dilation, slow contraction (1), slow dilation, fast contraction (2), fast dilation and contraction (3)
35 Lens attachment: none (0), zonular fibres only (1), distinct ringwulst (2), reduced ringwulst (3), anterior pad (4)
36* Lens shape: spherical (0), slightly lenticular (1), markedly lenticular (2) subspherical along the equatorial axis (3)
37 Lens pigment: none (0), yellow (1)
38 Lens sutures: absent (0), present (1)
39* Pigment epithelium: amelanistic (0), sparsely melanized (1), heavily melanized (2)
40 Photomechanical response of pigment epithelium: absent (0), present (1)
41* Central fovea: absent (0), shallow (1), deep central (2)
42 Rods: absent (0), present (1)
43 Cone: absent (0), present (1)
44 Double cones: absent (0), present (1)
45 Double rods: absent (0), present (1)
46 Myoid contractility: none (0), present (1)
47 Oil droplets: absent (0), present (1)
48 Parabaloids: absent (0), present (1)
49 Rhodopsin or porphyropsin: absent (0), present (1)
50* Optic nerve condition: fascicular (0), some septa (1), no septa (2)
51† Choroidal vasculature: none (0), present (1)
52 Retinal vasculature: none (0), present (1)
53* Conus papilliaris or pecten absent (0), small or simple (1) large or elaborate (2)
54 Corneal blood vessels: none (0), present (1)
55 Tapetum: absent (0), choroidal (1), retinal (2)
56 Accessory focus: absent (0), lens deformation by iris sphincter (1), stenopaic pupil (2)
57* Temporal fovea: absent (0), shallow (1), deep (2)
58 Pupil shape when dilated: round (0), vertical ellipse (1), horizontal ellipse (2)
59† Pupillary operculum: absent (0), present (1)

60* Iris sphincter: absent (0), normal (1), robust (2)

61 Iris dilator: absent (0), present (1)

62 Pupil shape when contracted: round (0), vertical slit (1), horizontal slit (2)

63 Lens deformation: none (0), squeezed by ciliary contraction (1), elastic recoil during ciliary contraction (2)

64 Lens movement rearward: none (0), passive (1), active (2)

65 Lens movement forward: none (0), passive (1), active (2)

66 Deformation of eyeball: none (0), external muscles (1), internal muscles (2)

67 Brücke's ciliary muscle: absent (0), smooth (1), striated (2)

68 Crompton's ciliary muscle: absent (0), smooth (1), striated (2)

69 Muller's circular ciliary muscle: absent (0), present (1)

DATA MATRIX

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Myxiniformes	0	0	0	–	–	–	0	0	0	0	0	0	0	0
Petromyzontiformes	0	0	0	–	–	–	0	1	1	1	1	1	1	0
Chondrichthyes	0	0	0	–	0	0	1	1	1	1	1	1	1	0
Acipenseriformes	0	0	0	–	–	–	0	1	1	1	1	1	1	0
Semionotiformes	0	0	0	–	–	–	0	1	1	1	1	1	1	0
Latimeria	0	0	0	–	–	–	0	1	1	1	1	1	1	0
Dipnoi	0	0	0	–	–	–	0	1	1	1	1	1	1	0
Teleostei	[02]	0	0	–	0	2	0	1	[12]	1	[12]	[12]	[12]	0
Anura	0	0	[01]	1	[01]	0	2	1	1	1	1	1	1	1
Caudata	0	1	1	1	[012]	0	[02]	1	1	1	1	1	1	1
Gymnophiona	0	0	2	?	–	–	0	1	1	1	1	2	1	2
Ornithorhyncus	0	1	2	2	0	0	2	1	1	1	1	1	1	1
Tachyglossidae	0	1	1	2	0	0	0	1	1	1	1	1	1	1
Didelphidae	0	1	1	2	0	0	0	1	1	1	1	1	1	1
Macropodidae	0	1	1	2	0	0	2	1	1	1	1	1	1	1
Notoryctidae	0	?	?	?	2	0	0	0	0	0	0	0	0	0
Soricidae	0	2	1	2	1	0	3	1	1	1	1	1	1	1
Talpidae	0	2	1	2	2	0	3	0	0	0	0	0	0	0
Primates	0	2	1	2	1	0	3	1	1	1	1	1	1	1
Felidae	0	2	1	2	1	0	2	1	1	1	1	1	1	1
Mustelidae	0	2	1	2	1	0	2	1	1	1	1	1	1	1
Sirenia	0	0	2	0	2	0	2	1	1	1	1	1	1	1
Pinnipedia	0	1	2	0	1	0	2	1	1	1	1	1	1	1
Cetacea	0	[01]	2	0	[12]	0	0	1	1	1	1	1	1	1
Sciuridae	0	2	1	2	1	0	3	1	1	1	1	1	1	1
Muridae	0	0	2	2	1	0	3	1	1	1	1	1	1	1
Cheloniidae	0	2	2	2	1	0	1	1	1	1	1	1	1	1
Chelydridae	0	1	2	2	1	0	1	1	1	1	1	1	1	1
Dermochelyidae	0	2	2	2	1	0	1	1	1	1	1	1	1	1
Emydidae	0	1	2	2	1	0	1	1	1	1	1	1	1	1
Testudinidae	0	1	2	2	1	0	1	1	1	1	1	1	1	1
Trionychidae	0	1	2	2	1	0	1	1	1	1	1	1	1	1
Sphenodontidae	0	0	2	2	1	0	1	1	1	1	1	1	1	1
Scincidae	0	1	2	2	[13]	[012]	[01]	1	1	1	1	1	1	1
Anniellidae	0	1	2	2	0	0	?	1	1	1	1	1	1	1
Lacertidae	0	2	2	2	1	[01]	1	1	1	1	1	1	1	1
Dibamidae	0	?	?	?	–	–	0	0	0	0	0	0	0	0
Amphisbaenia	0	0	2	2	–	–	0	0	0	0	0	0	0	0
Iguanidae	0	2	2	2	1	[01]	1	1	1	1	1	1	1	1
Agamidae	0	2	2	2	1	[01]	1	1	1	1	1	1	1	1
Chamaeleonidae	0	2	2	2	2	0	0	1	1	1	1	1	1	1
Pygopodidae	0	0	2	2	3	2	0	1	1	1	1	1	1	1
Gekkonidae	0	[01]	2	2	[123]	[012]	[01]	1	1	1	1	1	1	1
Lanthanotidae	0	2	2	2	1	1	1	1	1	1	1	1	1	1
Varanidae	0	2	2	2	1	0	1	1	1	1	1	1	1	1
Scolecophidia	0	0	2	2	3	2	0	1	1	1	1	1	1	0
Alethinophidia	0	0	2	2	3	2	0	1	1	1	1	1	1	0
Crocodylia	0	1	2	2	1	0	1	1	1	1	1	1	1	1
Passeriformes	0	2	1	2	0	0	1	1	1	1	1	1	1	0
Strigiformes	2	[01]	2	2	0	0	1	1	1	1	1	1	1	0
Falconiformes	0	2	2	2	0	0	1	1	1	1	1	1	1	0
Phalacrocoracidae	0	1	2	2	0	0	1	1	1	1	1	1	1	0
Sphenisciformes	0	0	2	2	0	0	1	1	1	1	1	1	1	0

DATA MATRIX *Continued*

	15	16	17	18	19	20	21	22	23	24	25	26	27	28
Myxiniformes	0	0	0	0	?	0	1	–	–	–	–	–	–	0
Petromyzontiformes	0	0	0	0	1	1	0	1	0	1	0	0	0	1
Chondrichthyes	0	0	1	0	0	1	0	1	0	1	1	0	[01]	0
Acipenseriformes	0	0	1	0	0	1	0	1	0	1	1	0	0	1
Semionotiformes	0	0	1	0	0	1	0	1	0	1	1	1	0	1
Latimeria	0	0	0	0	0	1	0	0	?	?	?	?	1	?
Dipnoi	0	0	1	0	2	1	1	0	0	1	1	0	0	0
Teleostei	0	0	1	1	[23]	1	0	0	0	1	1	1	[01]	1
Anura	1	0	1	0	[01]	1	1	1	0	1	1	0	0	0
Caudata	1	0	1	0	[01]	1	[01]	1	0	1	1	0	0	0
Gymnophiona	2	0	0	0	1	1	1	0	0	1	1	0	0	0
Ornithorhyncus	0	0	0	0	0	1	1	1	0	1	1	0	0	0
Tachyglossidae	0	0	0	0	0	1	1	0	1	1	1	0	0	0
Didelphidae	0	0	0	0	0	1	2	0	0	1	1	0	0	0
Macropodidae	0	0	0	0	0	1	2	0	0	1	1	0	0	0
Notoryctidae	0	0	0	0	0	?	?	?	?	?	?	?	0	0
Soricidae	0	0	0	0	0	1	1	0	0	1	1	0	0	0
Talpidae	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Primates	0	0	0	0	0	1	2	0	0	1	1	0	0	0
Felidae	0	0	0	0	0	1	2	0	0	1	1	0	0	0
Mustelidae	0	0	0	0	0	1	2	0	0	1	1	0	0	0
Sirenia	0	0	0	0	0	1	1	0	1	1	1	0	0	0
Pinnipedia	0	0	0	0	0	1	0	0	1	1	1	0	0	1
Cetacea	0	0	0	0	0	1	0	1	1	1	1	0	0	0
Sciuridae	0	0	0	0	0	1	2	0	0	1	1	0	0	0
Muridae	0	0	0	0	0	1	2	0	0	1	1	0	0	0
Cheloniidae	1	0	1	0	0	1	1	0	0	1	1	0	0	0
Chelydridae	1	0	1	0	0	1	1	0	0	1	1	0	0	0
Dermochelyidae	1	0	1	0	0	1	1	0	0	1	1	0	0	0
Emydidae	1	0	1	0	0	1	1	0	0	1	1	0	0	0
Testudinidae	1	0	1	0	0	1	2	0	0	1	1	0	0	0
Trionychidae	1	0	1	0	0	1	1	0	0	1	1	0	0	0
Sphenodontidae	1	1	1	0	0	1	2	0	0	1	1	0	0	0
Scincidae	1	[01]	1	0	[03]	1	2	0	[12]	1	1	0	0	1
Anniellidae	1	1	1	0	0	1	2	0	0	0	1	0	0	1
Lacertidae	1	1	1	0	0	1	2	0	[12]	0	1	0	0	1
Dibamidae	0	0	0	0	3	0	1	0	0	0	1	0	0	0
Amphisbaenia	0	0	0	0	3	1	1	0	0	0	1	0	0	0
Iguanidae	1	1	1	0	0	1	2	0	[12]	0	1	0	0	1
Agamidae	1	1	1	0	0	1	2	0	[12]	0	1	0	0	1
Chamaeleonidae	0	0	1	0	0	1	2	0	[12]	0	1	0	0	1
Pygopodidae	0	0	1	0	3	1	1	0	0	0	1	0	0	1
Gekkonidae	1	[01]	1	0	[03]	1	[12]	0	[12]	0	1	0	0	1
Lanthanotidae	1	1	1	0	0	1	2	0	[12]	0	1	0	0	1
Varanidae	1	1	1	0	0	1	2	0	[12]	0	1	0	0	1
Scolecophidia	0	0	0	0	3	0	1	1	0	1	1	0	0	0
Alethinophidia	0	0	0	0	3	0	0	1	0	1	1	0	0	0
Crocodylia	?	?	0	0	0	1	1	0	0	1	1	0	0	0
Passeriniformes	0	0	0	0	0	1	2	0	0	1	1	0	0	0
Strigiformes	0	0	0	0	0	1	1	0	0	1	1	0	0	0
Falconiformes	0	0	0	0	0	1	2	0	0	1	1	0	0	0
Phalacrocoracidae	0	0	0	0	0	1	1	0	0	1	1	0	0	0
Sphenisciformes	0	0	0	0	0	1	0	0	0	1	1	0	0	0

DATA MATRIX *Continued*

	29	30	31	32	33	34	35	36	37	38	39	40	41	42
Myxiniformes	–	–	0	0	0	0	–	–	–	–	0	–	0	0
Petromyzontiformes	0	0	0	0	0	0	0	0	1	0	2	1	0	1
Chondrichthyes	1	0	2	0	1	[013]	1	1	[01]	1	0	–	0	1
Acipenseriformes	1	0	2	0	0	0	1	0	0	0	1	[01]	0	1
Semionotiformes	1	0	2	0	0	0	1	0	0	1	2	1	0	1
Latimeria	1	0	2	1	0	0	0	0	0	1	0	?	0	1
Dipnoi	1	0	1	0	0	1	0	0	0	1	2	?	0	1
Teleostei	1	0	[12]	[012]	[01]	[013]	1	[012]	[01]	1	[012]	[01]	[012]	1
Anura	1	2	[12]	[01]	1	1	1	[01]	0	1	2	1	0	1
Caudata	1	1	[012]	0	1	1	1	0	?	1	2	1	0	1
Gymnophiona	?	?	0	0	0	0	0	1	0	1	2	0	0	1
Ornithorhyncus	1	2	2		0	1	?	1	1	0	1	2	0	0
Tachyglossidae	1	2	2	0	1	?	1	2	0	1	2	0	0	1
Didelphidae	1	2	0	0	1	?	3	0	0	1	2	?	0	1
Macropodidae	1	2	0	0	1	?	3	2	0	1	2	?	0	1
Notoryctidae	?	?	1	0	0	0	–	–	–	–	?	?	0	0
Soricidae	1	2	0	0	1	3	1	1	0	1	1	0	0	1
Talpidae	1	2	0	0	1	3	1	1	0	1	1	0	0	1
Primates	1	2	0	0	1	3	1	2	[01]	1	1	0	[012]	1
Felidae	1	2	0	0	1	3	1	2	0	1	1	0	0	1
Mustelidae	1	2	0	0	1	3	1	1	0	1	1	0	0	1
Sirenia	1	2	0	0	1	3	1	2	0	1	1	0	0	1
Pinnipedia	1	2	0	0	1	3	1	0	0	1	1	0	0	1
Cetacea	1	2	0	0	1	3	1	0	0	1	1	0	0	1
Sciuridae	1	2	0	0	1	3	1	2	1	1	1	0	0	[01]
Muridae	1	2	0	0	1	3	1	1	0	1	1	0	0	1
Cheloniidae	1	2	2	2	2	0	3	0	0	0	2	1	0	1
Chelydridae	1	2	2	2	2	0	3	0	0	0	2	1	0	1
Dermochelyidae	1	2	2	2	2	0	3	0	0	0	2	1	0	1
Emydidae	1	2	2	2	2	0	3	1	0	0	2	1	[01]	[01]
Testudinidae	1	2	2	2	2	0	3	2	0	0	2	1	0	1
Trionychidae	1	2	2	2	2	0	3	0	0	0	2	1	1	1
Sphenodontidae	1	2	2	2	2	3	2	1	0	0	2	?	1	1
Scincidae	1	2	2	2	2	3	2	2	0	0	2	1	[01]	0
Anniellidae	1	2	2	2	2	3	2	1	0	0	2	1	0	0
Lacertidae	1	2	2	2	2	3	2	2	0	0	2	1	[01]	0
Dibamidae	1	2	0	0	0	0	–	–	–	–	1	?	0	0
Amphisbaenia	1	2	[12]	[01]	0	0	–	–	–	–	2	?	0	0
Iguanidae	1	2	2	2	2	3	2	2	0	0	2	1	[01]	0
Agamidae	1	2	2	2	2	3	2	2	0	0	2	1	[01]	0
Chamaeleonidae	1	2	1	2	2	3	2	2	0	0	2	1	2	0
Pygopodidae	1	2	2	2	2	3	[03]	0	0	0	2	1	0	0
Gekkonidae	1	2	[012]	[12]	2	3	2	2	[01]	0	2	1	0	[01]
Lanthanotidae	1	2	2	2	2	3	2	2	0	0	2	1	1	0
Varanidae	1	2	2	2	2	3	2	2	0	0	2	1	1	0
Scolecophidia	1	1	0	0	2	0	4	0	0	1	2	0	0	1
Alethinophidia	1	[12]	0	0	2	[023]	4	[01]	[01]	1	2	0	0	[01]
Crocodylia	1	2	2	0	2	2	3	1	0	?	2	0	0	1
Passeriformes	1	2	2	2	2	3	2	2	0	?	2	1	2	1
Strigiformes	1	2	2	2	2	3	2	1	0	?	2	1	0	1
Falconiformes	1	2	2	2	2	3	2	2	0	?	2	1	2	1
Phalacrocoracidae	1	2	2	2	2	3	2	1	0	?	2	1	2	1
Sphenisciformes	1	2	2	2	2	3	2	1	0	?	2	1	2	1

DATA MATRIX *Continued*

	43	44	45	46	47	48	49	50	51	52	53	54	55	56
Myxiniformes	0	0	0	–	–	–	?	2	?	?	0	–	–	0
Petromyzontiformes	1	0	0	0	0	0	1	2	1	0	0	0	0	0
Chondrichthyes	1	0	0	0	0	0	1	[012]	1	0	0	0	1	[02]
Acipenseriformes	1	[01]	0	?	1	1	1	2	1	[01]	0	0	1	0
Semionotiformes	1	1	0	1	1	1	1	2	1	1	0	0	2	0
Latimeria	1	0	0	?	1	1	1	2	1	1	0	0	1	0
Dipnoi	[01]	[01]	0	?	[01]	1	1	1	1	0	0	0	1	0
Teleostei	1	1	0	1	0	1	1	1	1	1	0	0	[12]	0
Anura	1	1	0	1	[01]	1	1	2	1	1	0	0	0	0
Caudata	1	1	0	1	0	1	1	1	1	0	0	[01]	0	0
Gymnophiona	[01]	0	0	0	0	0	?	0	1	0	0	0	0	0
Ornithorhyncus	1	1	1	0	0	1	0	?	1	1	0	0	0	?
Tachyglossidae	0	0	0	0	0	0	?	1	1	0	0	0	?	0
Didelphidae	1	1	0	?	1	0	?	1	1	1	0	0	2	0
Macropodidae	1	1	0	?	1	0	?	1	1	1	0	0	?	0
Notoryctidae	0	0	0	–	–	–	–	?	?	?	0	?	0	0
Soricidae	[01]	0	0	0	0	0	1	1	1	1	0	0	0	0
Talpidae	1	0	0	0	0	0	1	1	1	1	0	0	0	0
Primates	1	0	0	0	0	0	1	1	1	1	0	0	[01]	[02]
Felidae	1	0	0	0	0	0	1	1	1	1	0	0	1	[02]
Mustelidae	1	0	0	0	0	0	1	1	1	1	0	0	1	0
Sirenia	1	0	0	0	0	0	1	1	1	1	0	0	1	0
Pinnipedia	1	0	0	0	0	0	1	1	1	1	0	0	1	[02]
Cetacea	1	0	0	0	0	0	1	1	1	1	0	0	1	0
Sciuridae	1	0	0	0	0	0	[01]	1	1	1	0	0	0	0
Muridae	1	0	0	0	0	0	1	1	1	10	0	0	0	0
Cheloniidae	1	1	0	1	1	1	1	1	1	0	0	0	0	1
Chelydridae	1	1	0	1	1	1	1	1	1	0	0	0	0	1
Dermochelyidae	1	1	0	1	1	1	1	1	1	0	0	0	0	1
Emydidae	1	1	0	1	1	1	1	1	1	0	0	0	0	1
Testudinidae	1	1	0	1	1	1	1	1	1	0	0	0	0	0
Trionychidae	1	1	0	1	1	1	1	1	1	0	0	0	0	1
Sphenodontidae	1	0	1	?	1	1	1	0	1	0	0	0	0	0
Scincidae	1	1	0	1	1	1	0	2	1	0	1	0	0	0
Anniellidae	1	1	0	1	1	1	0	2	1	1	0	0	0	0
Lacertidae	1	1	0	1	1	1	0	2	1	0	2	0	0	0
Dibamidae	0	0	0	–	–	–	–	2	1	0	0	0	0	0
Amphisbaenia	1	0	0	0	[01]	[01]	0	2	1	0	0	0	0	0
Iguanidae	1	1	0	1	1	1	0	2	1	0	2	0	0	0
Agamidae	1	1	0	1	1	1	0	2	1	0	2	0	0	0
Chamaeleonidae	1	1	0	1	1	1	0	2	1	0	2	0	0	0
Pygopodidae	1	1	0	1	0	1	0	2	1	0	1	0	0	0
Gekkonidae	1	1	1	1	1	1	[01]	2	1	0	1	0	0	[02]
Lanthanotidae	1	1	0	1	1	1	0	2	1	0	2	0	0	?
Varanidae	1	1	0	1	1	1	0	2	1	0	2	0	0	0
Scolecophidia	[01]	0	0	0	0	0	1	0	1	1	0	1	0	0
Alethinophidia	[01]	[01]	0	0	0	0	1	0	1	1	[01]	1	0	[012]
Crocodylia	1	1	0	1	0	1	1	0	1	0	0	1	2	0
Passeriformes	1	1	0	1	1	1	1	1	1	0	2	0	0	0
Strigiformes	1	1	0	1	1	1	1	1	1	0	2	0	0	0
Falconiformes	1	1	0	1	1	1	1	1	1	0	2	0	0	[02]
Phalacrocoracidae	1	1	0	1	1	1	1	1	1	0	2	0	0	1
Sphenisciformes	1	1	0	1	1	1	1	1	1	0	2	0	0	0

DATA MATRIX *Continued*

	57	58	59	60	61	62	63	64	65	66	67	68	69
Myxiniformes	0	0	0	0	0	0	0	0	0	0	0	0	0
Petromyzontiformes	0	0	0	0	0	0	0	2	0	1	0	0	0
Chondrichthyes	0	[012]	[01]	1	1	[012]	0	1	2	0	0	0	0
Acipenseriformes	0	1	0	0	0	[01]	0	0	0	0	0	0	0
Semionotiformes	0	1	0	0	0	0	0	1	2	0	0	0	0
Latimeria	0	0	0	?	?	0	0	0	0	0	0	0	0
Dipnoi	0	0	0	0	0	[02]	0	0	0	0	0	0	0
Teleostei	[01]	[02]	[01]	1	1	[012]	0	2	1	0	1	0	0
Anura	0	[012]	0	1	1	[012]	0	1	2	0	1	0	0
Caudata	0	0	0	1	1	0	0	2	2	0	0	0	0
Gymnophiona	0	0	0	0	0	0	0	0	0	0	0	0	0
Ornithorhyncus	0	0	0	0	2	0	0	0	0	0	0	0	0
Tachyglossidae	0	0	0	2	0	0	0	0	0	0	0	0	0
Didelphidae	0	0	0	1	0	1	?	0	0	0	1	0	0
Macropodidae	0	0	0	1	0	2	?	0	0	0	1	0	0
Notoryctidae	0	0	0	0	0	0	–	–	–	0	1	0	0
Soricidae	0	0	0	1	0	0	0	0	0	0	0	0	0
Talpidae	0	0	0	1	0	0	0	0	0	0	0	0	0
Primates	0	0	0	1	1	0	2	0	0	0	1	0	1
Felidae	0	[01]	0	1	1	[01]	2	0	0	0	1	0	0
Mustelidae	0	[02]	0	1	1	[012]	2	0	0	0	1	0	0
Sirenia	0	2	0	2	1	2	0	0	0	0	0	0	0
Pinnipedia	0	[02]	0	2	1	1	2	0	[02]	0	1	0	1
Cetacea	0	2	[01]	2	1	2	[02]	0	[02]	0	[01]	0	[01]
Sciuridae	0	0	0	1	1	0	2	0	0	0	1	0	0
Muridae	0	0	1	0	0	0	0	0	0	1	0	0	
Cheloniidae	0	0	0	2	0	0	1	0	0	0	2	0	0
Chelydridae	0	0	0	2	0	0	1	0	0	0	2	0	0
Dermochelyidae	0	0	0	2	0	0	1	0	0	0	2	0	0
Emydidae	0	0	0	2	0	0	1	0	0	0	2	0	0
Testudinidae	0	0	0	2	0	0	1	0	0	0	2	0	0
Trionychidae	0	0	0	2	0	0	1	0	0	0	2	0	0
Sphenodontidae	0	0	0	1	1	1	1	0	0	0	2	0	0
Scincidae	[01]	0	0	1	1	0	[01]	0	0	0	2	2	0
Anniellidae	0	0	1	1	1	1	0	0	0	2	2	0	
Lacertidae	0	0	0	1	1	0	1	0	0	[02]	2	2	0
Dibamidae	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphisbaenia	0	0	0	0	0	0	0	0	0	0	0	0	0
Iguanidae	[01]	0	0	1	1	0	1	0	0	[02]	2	2	0
Agamidae	0	0	0	1	1	0	1	0	0	[02]	2	2	0
Chamaeleonidae	0	0	0	1	1	0	1	0	0	[02]	2	2	0
Pygopodidae	0	0	0	0	0	1	1	0	0	0	[02]	[02]	0
Gekkonidae	1	[01]	[01]	1	1	[01]	[01]	0	0	0	[02]	[02]	0
Lanthanotidae	0	0	0	1	1	0	1	0	0	0	2	2	0
Varanidae	0	0	0	1	1	0	1	0	0	0	2	2	0
Scolecophidia	0	0	0	0	0	0	0	0	0	0	0	0	0
Alethinophidia	1	[012]	0	[12]	1	[012]	0	1	2	0	0	0	0
Crocodylia	0	0	0	1	1	1	1	0	0	0	2	0	0
Passeriformes	[012]	0	0	1	1	0	1	0	0	2	2	2	0
Strigiformes	1	0	0	1	1	0	1	0	0	2	2	2	0
Falconiformes	1	0	0	1	1	0	1	0	0	2	2	2	0
Phalacrocoracidae	0	0	0	2	1	0	1	0	0	2	2	0	0
Sphenisciformes	0	0	0	2	1	0	1	0	0	2	2	0	0