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MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 178

Boine Snake Phylogeny and Research Cycles

by
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ABSTRACT

Kluge, A.G. 1991. Boine snake phylogeny and research cycles. Misc. Publ. Mus. Zool., Univ. Michigan, 178:1–58, 14 figs. A cladistic analysis of 79 morphological characters delimits the following group and subgroups of snakes, collectively referred to as boines, on the best-fitting hypothesis of relationships: (*Candoia* (*Corallus* (*Boa* (*Epicrates, Eunectes*)))). This hierarchy obtains under either the assumption of character state additivity or nonadditivity. *Xenoboa* is synonymized with *Corallus* in order to maintain the monophyly of the latter taxon, and *Acrantophis* and *Sanzinia* are placed in the synonymy of *Boa*. The latter action makes the taxonomy more informative by reducing the number of monotypic genera, and it also emphasizes a South America-Madagascar vicariance hypothesis. The general nature of research cycles in phylogenetic inference and their importance in reaching a consensus hypothesis are discussed. In particular, the individuality of the ingroup and the relationships of its most inclusive taxa are emphasized. That boine monophyly and the basal dichotomies within that group are strongly corroborated are expected to impact significantly on the next round of research on the higher classification of snakes.

Key words: *Boines,* Acrantophis, Boa, Candoia, *cladistics,* Corallus, Epicrates, Eunectes, *phylogeny, research cycles,* Sanzinia, *snakes, taxonomy,* Xenoboa.

CONTENTS

ILLUSTRATIONS

FIGURE PAGE

TABLES

TABLE PAGE

INTRODUCTION

There is little agreement in the last 50 years' research concerning snake higher classification, viz., the phylogeny and taxonomy of the major groups. The following sample of references contain some of the most different hypotheses: H. M. Smith and Warner (1948, fig. 2), Schmidt (1950, fig. 1), Bellairs and Underwood (1951, fig. 9), Dowling (1959, fig. 2), Frazzetta (1959, fig. 10; 1975, fig. 2), Haas (1962, fig. 14), Underwood (1967:8–11; 1976, figs. 7–8), Langebartel (1968, fig. 19), Gasc (1974, fig. 1), McDowell (1975, 1979, 1987, table 1–1), H. M. Smith, R. B. Smith, and Sawin (1977:117–119), Dowling and Duellman (1978, table 100.1), Groombridge (1979a,b,c, 1984), Rieppel (1979b, fig. 1; 1979d, fig. 5; 1988, fig. 3), Hecht (1982, fig. 7), Rage (1984, figs. 35–37; 1987, fig. 2–1), Cadle (1987, fig. 3–1), and Dowling and Jenner (1988). Also, there appears to be no consensus concerning relationships within the most familiar major groups of snakes, such as boines (Figs. 1–3; see also Branch [1981]). Thus, the search for the history of snakes continues, and it seems prudent to identify the reasons why there has been so little progress to date (Arnold, 1990). The latter findings may benefit the study of other taxa.

All of the major systematic philosophies and methodologies, cladistics, phenetics, and syncretism, are present in the aforementioned studies of snake higher classification, and no doubt such variety contributed to the different systematic conclusions. The effects of using overall similarity instead of special similarity (Farris, 1977:836), paraphyletic as opposed to monophyletic taxa (Hennig, 1966), and taxonomic congruence rather than character congruence (Kluge, 1989b) are well documented. Some have also argued (e.g., McDowell [1987]) that snakes are so specialized that there is too little evidence on which to base a classification and/or independent evolution is so pervasive the unique pattern of historical relationships is effectively destroyed. Cladistics is now generally accepted as the philosophy and methodology of choice in phylogenetic inference and taxonomy (Hull, 1988), and I adopt its principles, special similarity, monophyly, and character congruence, in my studies of snake higher classification. The claim that snakes are too specialized and homoplastic will be examined empirically below.

Another factor that seems to have contributed significantly to the lack of consensus is the emphasis previous students of snake higher classification placed on certain, relatively few, characters. That such extreme forms of *a priori* weighting can give different results is well known. In the present study, I do not discern classes of characters and character bearers, nor do I prejudge the phylogenetic informativeness of different characters on the basis of process explanations. Quite the contrary, I attempt to consider all the relevant available evidence. As a first approximation, congruence is used to identify hierarchical patterns of character covariation, and in doing so I pursue the ideal of total evidence (Kluge, 1989b). Doubtless, I have overlooked some relevant characters and misjudged the polarity and trans-

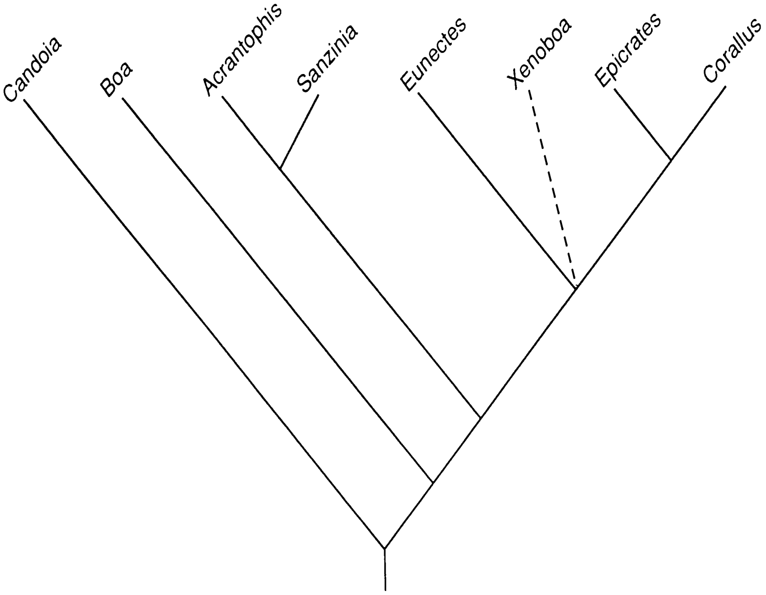

FIG. 1. The morphology-based hypothesis of relationships of extant boine snakes figured by Underwood (1976, fig. 8). Underwood's placement of *Xenoboa* was tentative.

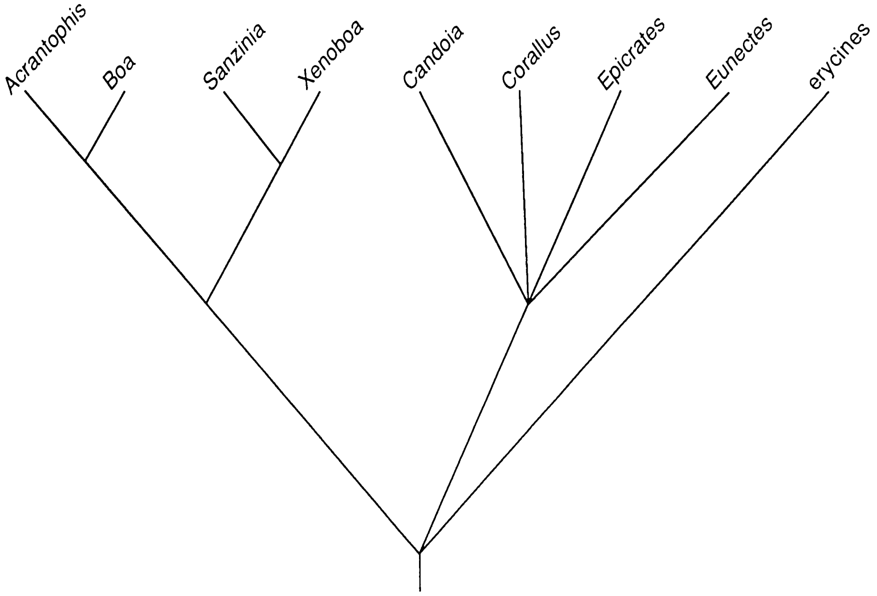

FIG. 2. The morphology-based hypothesis of relationships of boine snakes (including erycines) discussed by McDowell (1979). McDowell did not figure the phylogenetic conclusions he described in the text.

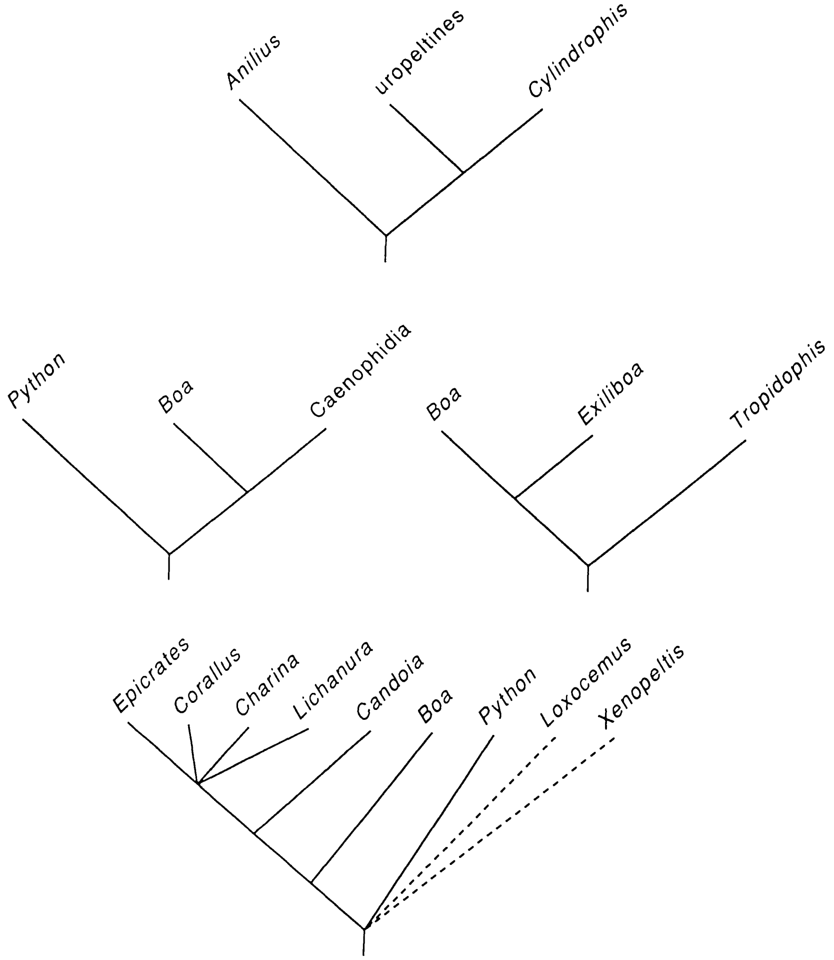

FIG. 3. Hypotheses of relationship among booid snakes. These propositions of sister group relationship were extracted from the general discussion of immunological evidence summarized by Dessauer et al. (1987); the branching patterns do not imply relative rates of evolution. The placement of *Loxocemus* and *Xenopeltis* is inferred from Schwaner and Dessauer (1981).

formation series of some of those employed. However, such shortcomings do not obviate the goal of total evidence because additions and corrections can be easily made to the data base I explicitly summarize (Table 1).

RESEARCH CYCLES

Yet another factor that may contribute to lack of consensus in classification, especially in diverse, speciose groups like snakes (see also Kluge

[1989b]), is failure to check the reliability of working hypotheses (assumptions), one's own propositions or someone else's. Surprisingly, these failures are not limited to the earliest studies of snake classification. While there is a broad spectrum of reliability, ranging from well-founded to merely expedient propositions, all assumptions must be scrutinized eventually. In effect, systematics, like science generally, is a recursive enterprise, and Hennig (1966:148) acknowledged the importance of these research cycles in his discussion of the principle of reciprocal clarification (illumination).

There are several research cycles in phylogenetic inference. One of the most obvious is the ingroup cycle, where the researcher assumes, as an expedient, the historical reality (= individuality) of each of the terminal taxa and perhaps the ingroup itself. For example, in a preliminary investigation of snake higher classification (Figs. 4–5), I assumed that *Acrantophis, Boa, Candoia, Corallus, Epicrates, Eunectes, Sanzinia* and *Xenoboa* are individuals, and that together they form the ingroup I label boines. Other important research cycles include functional outgroup analysis (Watrous and Wheeler, 1981), character state optimization (Swofford and Maddison, 1987), character weighting (Carpenter, 1988), and transformation series analysis (Mickevich, 1982; see also below). Working toward the ideal of total evidence (Kluge, 1989b) involves more than the discovery of new characters. Previously proposed synapomorphies should be reexamined for accuracy of ingroup taxonomic generality and additivity.

The reliability of the assumptions that terminal taxa are real evolutionary entities can be investigated by delimiting the parts of two or more terminal taxa and proceeding with a cladistic analysis at that level of taxonomic generality. When the weight of evidence indicates that a part of one terminal taxon (**A**) is the sister group of a part of another terminal taxon (**B**), then the assumed individuality of taxon **B** is unfounded according to the evidence at hand. Examining the assumption that the ingroup is an historical entity is judged likewise with synapomorphies, the assumption being unrealistic when the simplest interpretation of the evidence indicates that an outgroup is nested within the ingroup.

Evaluating the assumptions of group individuality is important because organisms are character bearers, and the diagnostic content of clades and their relationships can be affected by included (or excluded) parts. For example, consider the hypothetical example in which all parts of terminal taxon **A,** an assumed individual, may exhibit derived state 1 of character **x,** and **A** and **B** are hypothesized sister taxa based on **x.** However, if the individuality of **A** is not supported by further research, one may find that including the missing parts of other terminal taxa bearing different states of **x** will change the diagnosis of **A** and its relationships to **B.** The consequences of such research may not always be minor. In fact, an entirely unexpected pattern of historical relationships can obtain, especially when multiple research cycles and plesiomorphic sister taxa are involved (see for example Gauthier et al. [1988] and Donoghue et al. [1989]).

My ultimate goal in snake systematics is a cladistic analysis of the major groups. I accept tentatively Rieppel's (1988) and Schwenk's (1988; see also McDowell [1972]) conclusions that snakes are monophyletic and that the snake lineage is the sister group to Varanidae, respectively. From a survey of the literature, I recognized 36 ingroup terminal taxa and scored 139 characters. The result is a preliminary hypothesis of the higher classification of snakes (Fig. 4). Of particular interest are the three speciose taxa, denoted informally as boines, erycines and pythonines. Each of these three is only weakly diagnosed in the preliminary study, and their relationships might be expected to change if the hypothesized history within each group is altered. The unresolved placement of erycines is most likely to be affected by further research. Thus, I believe it is important to reexamine the individuality of the boine group and each of its terminal taxa (Fig. 5) and to evaluate interspecific relationships cladistically (the comparable research cycles on erycines and pythonines will be published separately; Kluge, ms.). I have already investigated interspecific relationships in the most diverse boine genus group, *Epicrates,* as part of a more limited research cycle (Fig. 6; Kluge, 1989a,b; see also Tolson [1987]). One of the most important contributions that particular cycle makes to the present study is the identification of basal sister taxa in *Epicrates* (Fig. 6; see also below).

BOINE TERMINAL TAXA AND NOMENCLATURE

The following abbreviated taxonomy summarizes the boine species group entities accepted in the present study. I have no *a priori* reason to doubt the individuality of most of these terminal taxa, and I make no attempt to diagnose them. The (*Epicrates cenchria* (*E. angulifer* (*E. striatus,* all other *Epicrates* species))) pattern of relationships (see Fig. 6; Kluge, 1989b) was used to estimate the common ancestral state of the terminal taxon *Epicrates.* The absence of material of *Eunectes barbouri,* other than the holotype (Petzold, 1984), implies that it may not be a valid species (Kluge, 1990). Corroborated patterns of character variation among some geographical parts of *Corallus annulatus* (Colombia and Ecuador; see characters 59 and 61 below) suggest the existence of an additional species. The previously noted (Kluge, 1989b) discordant variation among the insular parts of *Epicrates striatus* may also indicate the assumed individuality of this species is unjustified. With the exception of *Corallus,* the genus group names in the following list are monophyletic taxa contingent upon my phylogenetic hypothesis of boine relationships (Fig. 7). I use *Xenoboa* in the character descriptions, although I ultimately place that genus group name in the synonymy of *Corallus* because there is overwhelming evidence that *C. caninus* and *X. cropanii* are sister species. Likewise, I use *Acrantophis* and *Sanzinia,* although I conclude that they should be synonymized with *Boa.* Complete genus and species group synonymies of boines can be found in Stimson (1969), Peters and Orejas-Miranda (1970) and McDowell (1979).

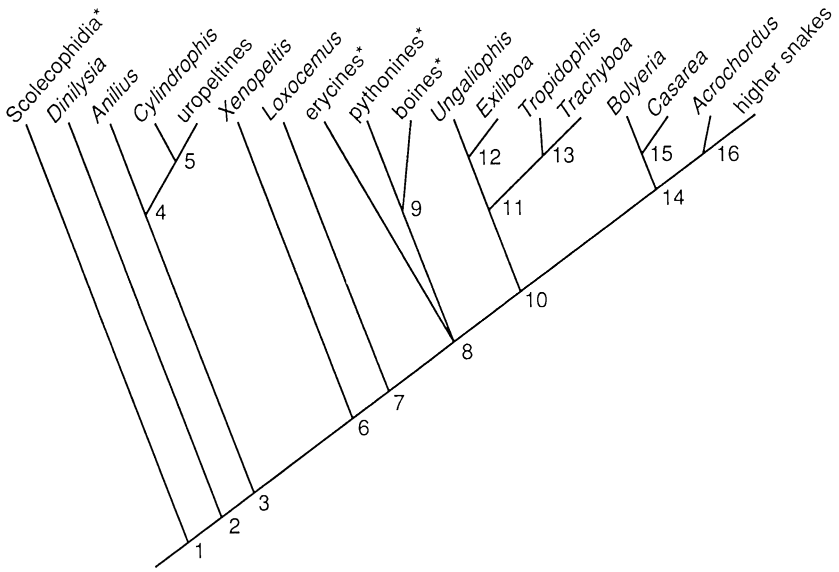

FIG. 4. A preliminary hypothesis of relationships of the major groups of snakes based on 139 characters, **M** = 194. Twenty-one equally parsimonious trees (**S** = 389, **C** = 0.50, **R** = 0.72) were found on the first run using the **m*** and **bb*** heuristic parsimony algorithms in Hennig86. The **xs w** weighting option reduced those 21 trees to six on the second run (**C** = 0.75, **R** = 0.86), which is summarized here as a Nelson consensus tree. The range of variation in the amount of evidence supporting the numbered clades is as follows: 1 = 26–35, 2 = 4–14, 3 = 10–23, 4 = 3–9, 5 = 5–9, 6 = 17–21, 7 = 5–9, 8 = 10–15, 9 = 3–9, 10 = 7–14, 11 = 3–8, 12 = 7–10, 13 = 14–19, 14 = 4–9, 15 = 5–7, 16 = 17–25 (the character list is available from the author). The affinities discovered within Scolecophidia, erycines, and pythonines are (Anomalepidae (Leptotyphlopidae, Typhlopidae)), (*Calabaria* ((*Charina, Lichanura*) ((*Eryx colubrinus, E. jaculus, E. jayakari, E. johnii, E. tataricus*) *Gongylophis conicus*))), and (*Aspidites melanocephalus* ((*Liasis albertisii, L. boa, L. childreni, L. mackloti*) (*Chondropython viridis, Morelia spilota*) (*Python amethistinus, P. boeleni, P. curtus, P. molurus, P. regius, P. reticulatus, P. sebae, P. timoriensis*))), respectively. The preliminary boine relationships are illustrated in Fig. 5. For explanation of boldface abbreviations, see Methods and Materials section.

Schwartz and Thomas (1975) provide a complete taxonomy of *Epicrates* species. I follow Underwood and Stimson (1990; see also L. A. Smith [1981a,b, 1985]) on pythonine nomenclature (except where I refer to my preliminary research on the higher classification of snakes, as in the legend to Fig. 4), even though I anticipate several name changes in the near future resulting from my own study of that group. I use Stimson's (1969) species and genus group names for the remaining outgroup taxa.

Acrantophis Jan

1860 *Acrantophis* Jan, *in* Jan and Sordelli, 1860–1881, Icon. Gén. Ophidiens, livr. 1, pl. 2.
Type species: *Acrantophis dumerili* Jan (by monotypy).
Geographic range: Madagascar and Réunion.

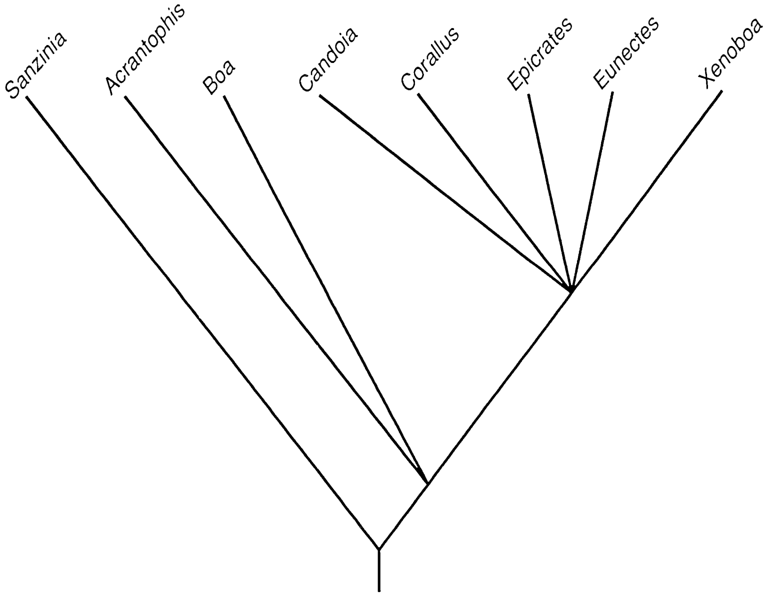

FIG. 5. A preliminary hypothesis of relationships of boine snakes (see Fig. 4 for outgroup history).

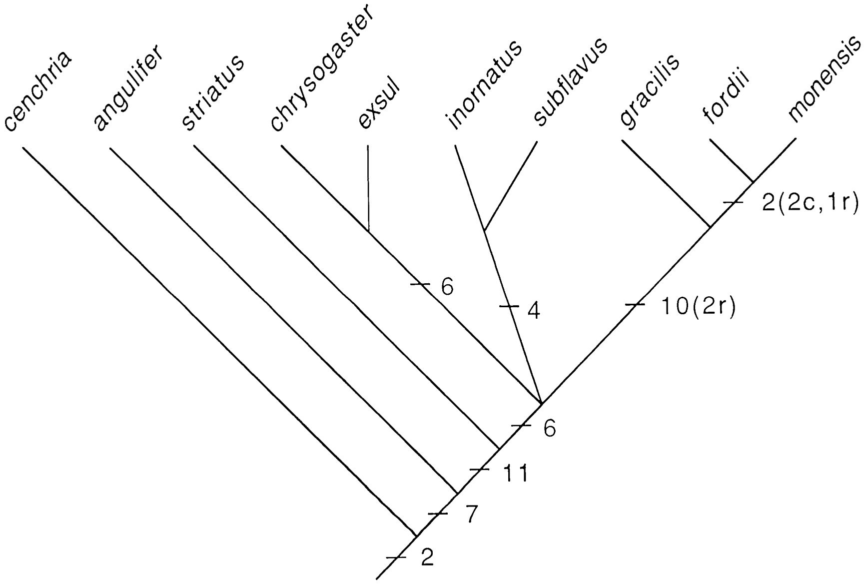

FIG. 6. Interspecific relationships in *Epicrates* (**S** = 133, **C** = 0.67; Kluge, 1989a, fig. 6). The number of apomorphies supporting each clade is indicated (those numbers without parentheses are unique and unreversed within *Epicrates*, those within parentheses are homoplastic; c = convergence/parallelism, r = reversal).

Acrantophis dumerili Jan

1860 *Acrantophis Dumerili* Jan, *in* Jan and Sordelli, 1860–1881, Icon. Gén. Ophidiens, livr. 1, pl. 2.
Holotype: Museo Civico di Storia Naturale, Milan.
Type locality: Unknown.
Geographic range: South and southwest Madagascar and Réunion (the latter may be due to human agency according to Branch [1981]).

Acrantophis madagascariensis (Duméril and Bibron)

1844 *Pelophilus madagascariensis* Duméril and Bibron, Erpétol. Gén., 6, p. 524.
Syntypes: MHNP 3133, 7275 and 8636.
Type locality: Madagascar.
Geographic range: West, north, northeast and east Madagascar.

Boa Linnaeus

1758 *Boa* Linnaeus, Syst. Nat., 10th ed., 1, p. 214.
Type species: *Boa constrictor* Linnaeus (by subsequent designation: Fitzinger [1843:24]).
Geographic range: From northern Sonora, Mexico, through South America north of lat. 35 degrees S; Lesser Antilles.

Boa constrictor Linnaeus

1758 *Boa constrictor* Linnaeus, Syst. Nat., 10th ed., 1, p. 215.
Syntypes: NRS (2 specimens). Other syntypes not located.
Type locality: "Indiis."
Remarks: Several subspecies have been recognized (see Stimson [1969] and Langhammer [1983]).

Candoia Gray

1842 *Candoia* Gray, Zool. Misc., p. 43.
Type species: *Boa carinata* ["Merrem"] Schneider (by monotypy).
Geographic range: Sulawesi (Celebes), north and south Moluccas, Telaud, Sangihe and Tanimbar islands, eastward through New Guinea and the Bismarck Archipelago; through the Solomon, Santa Cruz, Banks, New Hebrides, Loyalty, Fiji and Samoan islands; northward to Palau. Appears to be absent from the Philippines, Marshall, Ellice, Gilbert, Aru, Kei, and Lesser Sunda islands, New Caledonia and Australia, including Torres Strait islands (after McDowell [1979]).

Candoia aspera (Günther)

1877 *Erebophis asper* Günther, Proc. Zool. Soc. London, p. 132.
Holotype: BMNH 1946.1.10.33.
Type locality: Duke of York Island, Bismarck Archipelago.
Geographic range: New Guinea and adjacent islands; Manus group, Admiralty Islands; New Britain, Duke of York, New Ireland, and New Hanover, Bismarck Archipelago (after McDowell [1979]).

Candoia bibroni (Duméril and Bibron)

1844 *Enygrus Bibroni* Duméril and Bibron, Erpétol. Gén., 6, p. 483.
Syntypes: MHNP 1313, 3276, 3277, 61 and 61A.
Type locality: Viti Levu, Fiji Islands (see Stimson [1969]).
Geographic range: Eastern Solomon Islands; Banks Islands; New Hebrides; Loyalty Islands; Fiji Islands; Western and American Samoa islands (after McDowell [1979]).

Candoia carinata (Schneider)

1801 [*Boa*] *Carinata* Schneider, Hist. Amph., 2, p. 261.

Syntypes: None traced by Stimson (1969; see however McDowell [1979:27–28]).
Type locality: Unknown (see further explanation by McDowell [1979:28]).
Geographic range: Sulawesi; Sangihe and Telaud Islands; northern and southern Moluccas; central Palau Group; probably all New Guinea and adjacent islands; Manus Island; all Bismarck Archipelago; probably all the Solomon Islands (after McDowell [1979]).

Corallus Daudin

1803 *Corallus* Daudin, Hist. Nat. Gén. Rept., 5, p. 256.
Type species: *Corallus obtusirostris* Daudin [= *Corallus enydris* (Linnaeus)] (by monotypy).
Geographic range: Southern Nicaragua to Brazil and northern Bolivia; the Windward Islands.

Corallus annulatus (Cope)
1876 *Xiphosoma annulatum* Cope, J. Acad. Nat. Sci. Philad., (n.s.) 8, p. 129, pl. 28, fig. 6.
Holotype: USNM 32480.
Type locality: Costa Rica.
Geographic range: Southern Nicaragua through western Colombia and eastern Ecuador.
Remarks: Three subspecies are recognized (Peters and Orejas-Miranda, 1970).

Corallus caninus (Linnaeus)
1758 *Boa canina* Linnaeus, Syst. Nat., 10th ed., 1, p. 215.
Holotype: NRS Lin 8.
Type locality: "America."
Geographic range: Amazon Basin of Colombia, Venezuela, Guianas, Brazil, Ecuador, Peru, Bolivia.

Corallus enydris (Linnaeus)
1758 *Boa Enydris* Linnaeus, Syst. Nat., 10th ed., 1, p. 215.
Holotype: Uppsala University.
Type locality: "America."
Geographic range: Nicaragua through northern and western Brazil, Amazonian Ecuador, Peru and Bolivia; the Windward Islands.
Remarks: Two subspecies are currently recognized (Peters and Orejas-Miranda, 1970).

Epicrates Wagler

1830 *Epicrates* Wagler, Nat. Syst. Amph., p. 168.
Type species: *Boa cenchria* Linnaeus (by subsequent designation).
Geographic range: Costa Rica through Argentina, including Trinidad and Tobago; Greater Antilles and northern Lesser Antilles.
Remarks: *Epicrates* includes the following species (Schwartz and Thomas, 1975)—*E. angulifer* Cocteau and Bibron (1840); *E. cenchria* (Linnaeus) (1758); *E. chrysogaster* Cope (1871); *E. exsul* Netting and Goin (1944); *E. fordii* Günther (1861); *E. gracilis* Fischer (1888); *E. inornatus* Reinhardt (1843); *E. monensis* Zenneck (1898); *E. striatus* Fischer (1856); *E. subflavus* Stejneger (1901). Only *E. angulifer, E. exsul, E. inornatus* and *E. subflavus* are currently recognized as monotypic (Schwartz and Thomas, 1975).

Eunectes Wagler

1830 *Eunectes* Wagler, Nat. Syst. Amph., p. 167.
Type species: *Boa scytale* Linnaeus [= *Eunectes murinus* (Linnaeus)] (by subsequent designation: Fitzinger [1843:24]).
Geographic range: South America.

Eunectes barbouri Dunn and Conant
1936 *Eunectes barbouri* Dunn and Conant, Proc. Acad. Nat. Sci. Philad., 88, p. 504.
Holotype: ANSP 20892.
Type locality: Marajo Island, Brazil.
Geographic range: Known only from the type locality.

Eunectes deschauenseei Dunn and Conant
1936 *Eunectes deschauenseei* Dunn and Conant, Proc. Acad. Nat. Sci. Philad., 88, p. 505.
Holotype: ANSP 20891.
Type locality: Marajo Island, Brazil.

Eunectes murinus (Linnaeus)
1758 *Boa murina* Linnaeus, Syst. Nat., 10th ed., 1, p. 215.
Holotype: NRS Lin 9.
Type locality: "America."
Geographic range: Venezuela and Colombia to Bolivia.
Remarks: Two subspecies are recognized currently (Peters and Orejas-Miranda, 1970).

Eunectes notaeus Cope
1862 *Eunectes notaeus* Cope, Proc. Acad. Nat. Sci. Philad., (1862), p. 70.
Holotype: USNM 4707.
Type locality: Paraguay River and its tributaries.
Geographic range: Bolivia, Paraguay, Uruguay, western Brazil, and northeastern Argentina.

Sanzinia Gray

1849 *Sanzinia* Gray, Cat. Snakes Brit. Mus., p. 98.
Type species: *Xiphosoma madagascariense* Duméril and Bibron (by monotypy).
Geographic range: Throughout Madagascar.

Sanzinia madagascariensis (Duméril and Bibron)
1844 *Xiphosoma Madagascariense* Duméril and Bibron, Erpétol. Gén., 6, p. 549.
Syntypes: MHNP 43 and 7329 (3 specimens).
Type locality: Madagascar.

Xenoboa Hoge

1953 *Xenoboa* Hoge, Mem. Inst. Butantan, São Paulo, 25, p. 27.
Type species: *Xenoboa cropanii* Hoge (by monotypy).
Geographic range: State of São Paulo, Brazil.

Xenoboa cropanii Hoge

1953 *Xenoboa cropanii* Hoge, Mem. Inst. Butantan, São Paulo, 25, p. 27.
Holotype: Instituto Butantan no. 15.200.
Type locality: Miracatu, State of São Paulo, Brazil.

FOSSILS

Numerous fossilized remains of snakes, the vast majority of which are isolated vertebrae (Harding and Holman, 1982), have been referred to as "boids" (Underwood, 1976; Rage, 1984, 1987; Albino, 1986, 1987). Based on overall similarity, Johnson (1955) claimed that "boid" trunk vertebrae can be distinguished from comparable vertebrae taken from several other major groups of snakes; however, he was unable to separate boine from pythonine vertebrae (see also Mosauer [1935]). Unfortunately, I have been unable to discover diagnostic features of boines or "boids" in the postcranial skeleton (see below; also Rage [1984:15]), and there is no evidence to indicate which, if any, of the many fossil vertebrae are relevant to the present study. Even the relationships of *Boavus,* the extinct "boid" represented by the most cranial material, cannot be resolved. A right mandible and quadrate (USNM 129890) have been referred to as *B. occidentalis,* and *B. idelmani* consists of a nearly complete skeleton, although the skull is badly crushed and only a poorly prepared cast of the holotype is available (AMNH 3850). I am unaware of any *Boavus* species that can be diagnosed as a boine (see Underwood [1976], McDowell [1979] and my preliminary research reported below). Moreover, the available material suggests that *Boavus* may not be monophyletic (see also Holman [1979]). For example, the size of the surangular and the relative positions of the splenial, coronoid, and articular involve apomorphic conditions shared with unrelated alethinophidians (Gilmore, 1938, figs. 4, 10). My review (Kluge, 1988a) of the remaining North American Tertiary boines (Holman, 1979) indicated that *Paraepicrates* is an erycine, and that at least some of the fossil vertebrae referred to *Pseudoepicrates* (cf. *P. barbouri*) cannot be distinguished from those of *Boa constrictor.*

While a resolved classification of the fossil "boids" is assumed to be impossible at this time, it seems best to defer final judgment on their history until the relationships within and among all the major groups of extant snakes have been reexamined. Once these several cycles of research have been completed, the phylogeny of all monophyletic terminal taxa, extant and extinct, will be examined (*sensu* Gauthier et al. [1988], Donoghue et al. [1989] and Kluge [1989b]).

METHODS AND MATERIALS

I began my search for relevant evidence with a review of the literature, and the following articles provided background information on many potential characters (Zacharias, 1897; Beddard, 1904a,b 1906a,b, 1908; Mosauer, 1935; H. M. Smith and Warner, 1948; Bellairs and Boyd, 1950; Johnson, 1955; Auffenberg, 1958; Frazzetta, 1959, 1966, 1975; Hoffstetter, 1962, 1968; Gasc, 1966, 1974, 1981; Genest-Villard, 1966; Underwood, 1967, 1976; Langebartel, 1968; Hoffstetter and Gasc, 1969; McDowell, 1972, 1979, 1987; Rieppel, 1976, 1977a, 1978a, 1979a,b,c,d, 1980a, 1987, 1988; Groombridge, 1979a,b,c, 1984; Bellairs and Kamal, 1981; Branch, 1981; Jayne, 1982; Shine, 1985; Kluge, 1989b). One entire class of observations, genetic distances (e.g., Domergue et al. [1969], Schwaner and Dessauer [1981], and Dessauer et al. [1987]; Fig. 3), had to be rejected because they cannot be analyzed in terms of character congruence and total evidence (see above). Some individual characters were also discarded because they became too variable when several representatives of boine terminal taxa were examined. Some believe (Sober, 1988) that choosing the most conservative characters is a requirement for applying parsimony algorithms in phylogenetic inference (Farris, 1988). Those characters which were continuously variable and exhibited no gaps between states had to be abandoned (e.g., Underwood's [1976] respiratory characters, nos. 20–21), and autapomorphies were not considered as well. Numerous other character descriptions were modified in order to apply to boine relationships and to maximize the likelihood of character independence. It is impossible to say how many new variables were actually discovered during the course of my survey. The cladistically informative characters are summarized below in the approximate order in which I found it convenient to score them in the data matrix (Table 1).

Almost all of the characters employed are qualitative. While only the most obvious states are recognized, the size of the gaps between them varies within and among characters, and it is rarely, if ever, true that specimens recorded as having the same state are actually identical. Thus, to minimize observational error more than one representative of most species was at hand when the different conditions were scored. It is recommended that those wishing to check the taxonomic generality and comparability of the states that I recorded have at least one adult specimen of each species in front of them.

The skeletal material examined in the present study is listed in the Appendix. Repository abbreviations are AMNH = American Museum of Natural History; ANSP = Academy of Natural Sciences, Philadelphia; BMNH = British Museum of Natural History; CAS = California Academy of Sciences; CM = Carnegie Museum; DU = Duke University; FMNH = Field Museum of Natural History; IB = Instituto Butantan; KU = University of Kansas Museum of Natural History; MCZ = Museum of Comparative Zoology, Harvard University; MNHP = Muséum National d'Histoire Naturelle, Paris; NRS (and NRS Lin) = Naturhistoriska Riksmuseet, Stockholm; MVZ = Museum of Vertebrate Zoology, University of California at Berkeley; FSM = Florida State Museum, University of Florida; UMMZ = University of Michigan Museum of Zoology; USNM = National Museum of Natural History; UTACV = University of Texas at Arlington.

The issue of which anatomical name to apply arises repeatedly in my studies of snake higher classification, especially when specimens representing distantly related and highly modified lineages are compared. As a rule, I have given the same name to anatomically similar structures, even though the best supported phylogenetic hypothesis suggests the identically named structures may not be homologues. Thus, I emphasize the concept of synapomorphy instead of homology, the former being an estimator, the latter the parameter (Patterson, 1982). In this regard, it is important to remember that while all homologues are synapomorphies, not all synapomorphies are homologues.

Several of the characters I use have been the subject of controversy. Most of the differences of opinion concern homology, and most of those opinions have been expressed without the benefit of a historical hypothesis. The controversies are usually accompanied by arguments relating to idealized adaptive modes, such as functional optima (e.g., Frazzetta [1975]). I have nothing to say about those arguments because they lack historical content. Homology is dealt with only indirectly by character congruence, the ultimate arbiter of character history (Patterson, 1982).

The anatomical nomenclature employed mostly follows that of Frazzetta (1959, 1966, 1975), Genest-Villard (1966), Hoffstetter and Gasc (1969), Bellairs and Kamal (1981), and Cundall and Irish (1989). A few new names are coined, when the structures are obviously dissimilar and are highly likely to have had an independent history. I have also taken the liberty of renaming a few structures whose infrequently used nomenclature does not describe anatomical location accurately. I give synonyms in those cases where I break from an obvious tradition. My renaming follows either of two conventions, anatomical location (e.g., anterodorsal process of the . . .) or the structure it contacts (e.g., the vomerine process of the premaxilla).

The outgroup criterion was used to infer polarity, and I was successful in discovering an unambiguous hypothesis of plesiomorphy for most characters (only nos. 2, 7, 23, and 66 remain unpolarized). Those unfamiliar with the outgroup criterion should see Farris (1982) for a discussion of parsimony in outgroup character state optimization, and Maddison et al. (1984) for the importance of the doublet rule in finding the best-fitting outgroup hypothesis. I did not discard unpolarized characters because all matches can count (Donoghue, 1990; *contra* Nelson [1989:294]). The respective ambiguous and unambiguous histories of polarized character 4 and unpolarized character 2 illustrate this point.

The outgroup criterion is more general than the ontogeny rule (Kluge, 1985; Kluge, 1988b; Kluge and Strauss, 1985), and in any case, except for three boine terminal taxa (*Boa constrictor,* UMMZ 184028–42; *Corallus enydris,* UMMZ 184240–48; *Epicrates* species, see Kluge [1989b]), a wide range of semaphoronts, including neonates, were unavailable. Bony crests and processes are especially subject to ontogenetic variation, and therefore only the largest specimens were used to decide the states of those characters.

According to my preliminary study (Fig. 4), pythonines are the proximate outgroup to boines. The unresolved trichotomy in the preliminary analysis is a function of the unstable position of erycines; that lineage was the sister group to the (boine, pythonine), (tropidophiine (bolyeriine (*Acro-*

chordus, colubroid))), or ((boine, pythonine) (tropidophiine (bolyeriine (*Acrochordus,* colubroid)))) clades.[1] Thus, the erycine and (tropidophiine (bolyeriine (*Acrochordus,* colubroid))) assemblages shared equally in estimating the second outgroup state. This lack of resolution is unfortunate because some polarity decisions are shifted to more distantly related lineages where the comparability of character states is more tenuous. In order to simplify the following text, the (tropidophiine (bolyeriine (*Acrochordus,* colubroid))) lineage is hereafter referred to as the "advanced snake" clade. The outgroup classification will be reexamined following the study of relationships among the boines, erycines and pythonines.

Fig. 4 indicates that *Loxocemus, Xenopeltis,* and (*Anilius* (*Cylindrophis,* uropeltines)) are the third, fourth and fifth outgroups to boines, respectively, and they were employed in polarity decisions when variation in the first and second outgroups would not permit an unambiguous estimate of boine plesiomorphy. The (*Anilius* (*Cylindrophis,* uropeltines)) clade is usually abbreviated as anilioids in the text to follow, and it does not include *Anomochilus* (*contra* Welch [1988]). The hypothesized common ancestral state of the advanced snake clade was usually a function of the condition observed in bolyeriines (*Bolyeria, Casarea*) and tropidophiines ((*Exiliboa, Ungaliophis*) (*Trachyboa, Tropidophis*)), rarely *Acrochordus,* and never colubroids (caenophidians of some authors; e.g., Underwood [1967]). Occasionally, it was impossible to discover a unique plesiomorphic state for the advanced snake clade because of the considerable variation observed among its parts.

According to my preliminary assessment of the higher classification of snakes, (*Chondropython viridis, Morelia spilota*) is considered the most derived pythonine clade, and the several states they share with boines are interpreted as homoplastic (see however, Frazzetta [1975:471]). Also, in the preliminary study, *Aspidites* and *Calabaria* are the sister lineages to all other pythonines and erycines, respectively. The complicated dichotomous and trichotomous pattern of outgroup relationships (Fig. 4) required that polarity be estimated on a character-by-character basis, and a brief statement of outgroup variation is included in each character description. The inferred common ancestral condition is listed in the data matrix (Table 1).

The hypothesized order of the apomorphic states of a multistate character is of concern because there is a potential conflict between number of assumptions and phylogenetic informativeness (Farris et al., 1970). A nonadditive (unordered) hypothesis of character evolution admits that a state could have evolved from any other state, but such propositions do not contain the synapomorphic information that resides in an additive (ordered), hierarchical, treatment. However, to consider multistate characters as additive requires one or more *ad hoc* assumptions about processes

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[1] The content of the group designated colubroid follows Marx and Rabb (1970; see also Rieppel's [1988] definition).

TABLE 1
CHARACTER BY TAXON MATRIX

	Taxa*															
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P
1.	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
2.	N†	0	0	0	1	1	1	1	1	1	1	1	1	1	0	1
3.	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0
4.	0	1	1	1	1	1	1	0	0	0	1	1	1	1	0	0
5.	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1
6.	0	1	1	2	0	1	0	2	2	2	2	2	2	2	1	1
7.	?‡	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1
8.	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0
9.	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0
10.	0	0	0	0	1	1	1	0	0	1	0	0	0	0	1	1
11.	0	1	1	1	0	0	0	1	1	1	1	1	1	1	1	1
12.	0	1	1	1	0	0	0	1	1	1	1	1	1	1	1	1
13.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
14.	0	1	1	1	0	0	0	1	1	1	1	1	1	1	1	1
15.	1	2	2	2	1	0	0	2	1	1	2	2	2	2	2	1
16.	0	1	1	1	0	N	N	0	0	0	1	1	1	1	0	0
17.	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0
18.	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0
19.	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1
20.	0	0	0	0	0	0	0	1	2	1	0	0	0	0	0	2
21.	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1
22.	0	1	1	1	0	0	0	1	1	1	1	1	1	1	1	1
23.	N	2	2	2	1	2	1	2	2	2	1	0	1	0	1	2
24.	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1
25.	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1
26.	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0
27.	1	3	3	0	1	3	1	2	2	0	0	0	0	0	3	2
28.	0	1	1	1	0	1	0	1	1	1	1	1	1	1	1	1
29.	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0
30.	0	1	1	0	0	0	0	0	0	0	1	0	0	0	1	1
31.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
32.	0	1	1	1	0	0	0	2	1	1	2	2	2	2	2	1
33.	0	0	0	0	0	0	0	1	2	2	0	0	0	0	1	2
34.	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1
35.	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1
36.	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
37.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
38.	0	2	2	N	0	1	0	0	0	0	1	1	1	1	0	0
39.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
40.	0	0	0	0	0	0	0	1	2	1	0	0	0	0	0	2
41.	0	1	1	1	1	1	1	1	1	1	1	0	0	0	1	1
42.	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
43.	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1
44.	1	0	0	0	1	1	1	1	2	1	0	0	0	0	0	2
45.	0	1	1	1	0	0	0	2	2	2	1	1	1	1	1	2
46.	0	1	1	0	0	0	0	2	2	2	1	1	1	1	1	2
47.	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1
48.	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1
49.	0	1	1	1	0	0	0	0	0	0	1	1	1	1	1	0
50.	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

TABLE 1 (continued)
CHARACTER BY TAXON MATRIX

	Taxa*															
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P
51.	0	2	2	2	1	1	1	0	0	0	1	1	1	1	2	?
52.	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
53.	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
54.	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0
55.	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
56.	0	2	2	1	0	0	0	1	1	1	2	2	2	2	0	1
57.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
58.	0	1	1	1	0	0	0	0	0	0	1	1	1	1	0	0
59.	0	1	1	0	0	0	0	?	1	1	0	0	0	0	0	1
60.	0	0	0	0	0	1	1	0	1	1	0	0	0	0	0	1
61.	0	0	0	?	1	1	1	?	1	1	0	0	0	0	0	1
62.	0	1	1	1	0	0	0	1	1	1	0	0	0	0	1	1
63.	0	2	2	1	0	0	0	0	0	0	0	0	0	0	2	0
64.	0	1	1	1	0	0	0	1	1	1	1	1	1	1	1	1
65.	0	0	0	1	1	0	0	2	2	2	0	1	1	1	0	2
66.	N	1	1	0	0	0	0	0	0	0	0	2	0	2	1	0
67.	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0
68.	0	?	1	1	0	0	0	1	1	1	?	1	1	1	1	1
69.	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	1
70.	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0
71.	0	0	0	1	1	1	1	2	2	2	0	0	0	0	2	1
72.	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0
73.	0	0	0	1	0	0	0	2	2	2	1	0	0	0	2	2
74.	0	2	1	2	2	2	2	1	1	1	1	1	1	1	1	1
75.	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0
76.	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	0
77.	0	0	?	1	1	1	1	?	?	1	1	?	0	?	0	?
78.	0	1	1	0	1	1	1	0	0	0	0	0	0	0	1	?
79.	0	1	1	0	1	1	1	0	0	0	0	0	0	0	1	?

*A = ancestor, B = *Acrantophis dumerili*, C = *Acrantophis madagascariensis*, D = *Boa constrictor*, E = *Candoia aspera*, F = *Candoia bibroni*, G = *Candoia carinata*, H = *Corallus annulatus*, I = *Corallus caninus*, J = *Corallus enydris*, K = *Epicrates*, L = *Eunectes deschauenseei*, M = *Eunectes murinus*, N = *Eunectes notaeus*, O = *Sanzinia madagascariensis*, P = *Xenoboa cropanii*.

†N = not applicable.

‡? = cannot be determined unambiguously at this time.

(Mabee, 1989). For example, it is usually implied that extreme conditions occur at the beginning or end of a transformation, the usual assumption being that evolution must proceed orthogenetically, through intermediate states, because small increments of change are most likely to be adaptive and to become fixed in lineages. Numerous specific examples of multistate additivity exist in the literature, and the most common classes concern size and number (e.g., a medium size process occurred historically between small and large processes, and 2 teeth occurred between 1 and 3 teeth). Recent interest in macroevolution, and heterochrony in particular, has called into question many of these kinds of process assumptions. My solution to the conflict between minimizing *ad hoc* assumptions and losing synapomorphies is purely pragmatic. Initially, I treat all characters as additive and then I reanalyze the data matrix under the condition of nonadditivity to see what differences in cladistic relationships, if any, result. Only those synapomorphies unambiguously diagnostic of the same clade under both assumptions of additivity and nonadditivity are interpreted as homologues.

All cladistic analyses are performed with Farris's (1988) phylogenetic inference software, Hennig86. The exact "implicit enumeration" (**ie**) algorithm is used to find the best-fitting phylogenetic hypotheses. Fit to data is measured in terms of consistency and retention indices. Character consistency, **c,** is defined as **m/s,** where **s** is the minimum number of steps a character can exhibit on a particular tree hypothesis, and **m** is the minimum number of steps that character can show on any tree hypothesis (Kluge and Farris, 1969). Character retention, **r,** is defined as **(g-s)/(g-m),** where **g** is the greatest number of steps a character can have on any tree (Farris, 1989; Seberg, 1989; Steve Farris, pers. comm.). The ensemble consistency, **C,** and ensemble retention, **R,** indices are simply the quantities for a single character, **m, g,** and **s,** summed over all characters in the matrix, thus yielding corresponding totals, **M, G,** and **S.** Therefore, **C = M/S,** and **R = (G-S)/(G-M).** The successive weighting algorithm (**xs w**) in Hennig86 is used "to determine which of the equally parsimonious cladograms found are best supported by the most consistent characters" (Platnick, 1989:149; see also Carpenter [1988]). A character's weight is the product of its consistency and retention indices. The effectiveness of this weighting coefficient is owing to its close approximation to a concave bounded function (see Farris [1969, fig. 4]). Swofford and Olsen's (1990:499–500) negative comments concerning the *a posteriori,* successive approximations, form of weighting used herein seem to be ill-founded (Farris, et al., ms.). In any case, Swofford and Olsen's (p. 499) "extreme [counter] example" does not relate to the **xs w** algorithm.

BOINE PHYLOGENY

CHARACTER DESCRIPTIONS

The following 79 characters are employed in my study of boine phylogeny (Table 1, Figs. 7–8). Characters 1–70 are osteological, the remainder concern various aspects of the external and internal soft anatomy. There are 19 three state characters (nos. 6, 15, 20, 23, 32, 33, 38, 40, 44, 45, 46, 51, 56, 63, 65, 66, 71, 73 and 74), and one four state transformation (no. 27). The total size (**M**) of the data set is 100. Ambiguous variation within the ingroup terminal taxa is noted; however, only unambiguous variation among those terminal taxa is recorded in Table 1.

1. Premaxilla (Fig. 9): The ascending process of the premaxilla (Frazzetta, 1959,

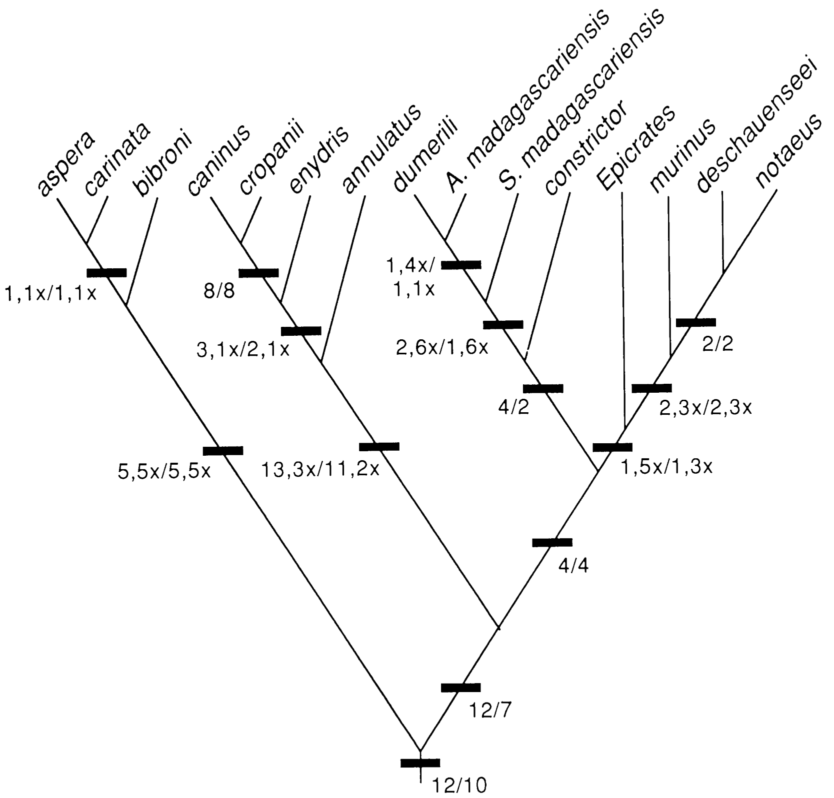

FIG. 7. The single best-fitting hypothesis of interspecific relationships among boines based on the synapomorphies summarized in Table 1. See text for a discussion of the weighting protocol which leads to the completely resolved cladogram (pp. 17) and the effect of relaxing the assumption of character state additivity (pp. 16–17). The number of unambiguous apomorphies supporting each clade is indicated (x = homoplasy; those numbers without the x suffix are unique and unreversed within boines). The array preceding the slash results when all multistate characters are treated as additive, whereas the array succeeding the slash results when all multistate characters are treated as nonadditive.

fig. 3) is absent (0) or present (1). All boines possess the ascending process, including *Candoia carinata* which has a markedly depressed snout. In that species, the ascending process rests on top of the nasal process, which is short. The advanced snake clade appears to be characterized by state 0; however, the process is present in *Exiliboa* and *Ungaliophis.* All the remaining tropidophiines, and the bolyeriines (see however Anthony and Guibé [1952, figs. 2, 4] and Rieppel [1978a, fig. 6]), seem to exhibit state 0. All other outgroups also possess the 0 state. Among those taxa, *Xenopeltis* most closely approaches the boine condition; however, its premaxilla is shallow and there is no bone dorsal to the nasal process. Among erycines, *Lichanura* is superficially similar to the boine condition, but the extra margin of bone its premaxilla exhibits seems to be due to the presence of tall transverse

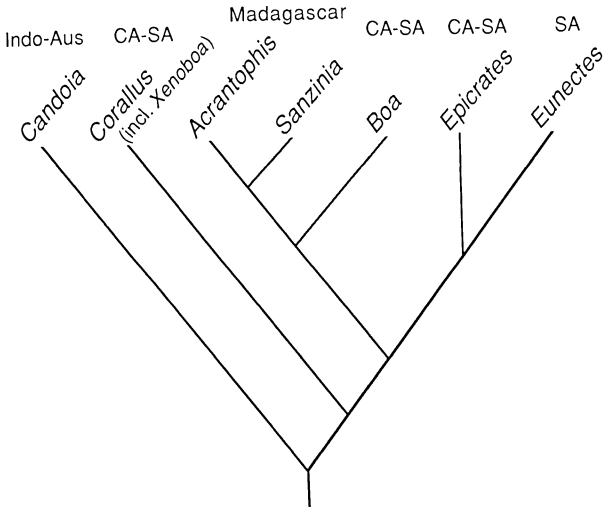

FIG. 8. Relationships among boine genera, according to Fig. 7. The following abbreviations describe the geographic distribution of each of the terminal taxa: CA = Central America; Indo-Aus = Indoaustralian Archipelago in the broad sense (see geographic distribution of *Candoia* in Taxonomy section); SA = South America. The "Madagascar" label includes Réunion.

processes (the lateral wing terminology of Underwood [1976:156]) rather than additional bone on the midline. While I agree with Frazzetta (1975) that the ascending process diagnoses boines, I do not accept the adaptationist-morphocline (fig. 5) approach he used to determine polarity. Variation in the outgroups clearly indicates that absence of the process is plesiomorphic.

2. *Premaxilla (Fig. 9): The dorsal-anterodorsal margin of the ascending nasal process of the premaxilla is slightly (0) or considerably (1) wider than the body of the process.* This character cannot be polarized because the ascending process of the premaxilla appears to be unique to boines (see character 1). My definition attempts to capture the sense of Underwood's (1976) character 36, which he attributed to Frazzetta (1959). In *Xenopeltis*, the dorsal-anterodorsal margin of the nasal process is slightly or considerably wider than the body of that process, depending on where the observation is made along the margin, which is superficially similar to the boine states (0 and 1).

3. *Premaxilla (Fig. 9): The dorsal margin of the transverse process of the premaxilla (Frazzetta, 1975, fig. 3), adjacent to the nasal process, is thick and little, if at all, elevated (0) or the margin forms a thin high wall which is noticeably curved posteriorly (1).* State 0 is assumed to be plesiomorphic because it occurs in most outgroups. Some erycines (*Calabaria, Charina* and *Lichanura*) exhibit the derived condition; however, that similarity to boines is most parsimoniously interpreted on Fig. 4 as independently evolved.

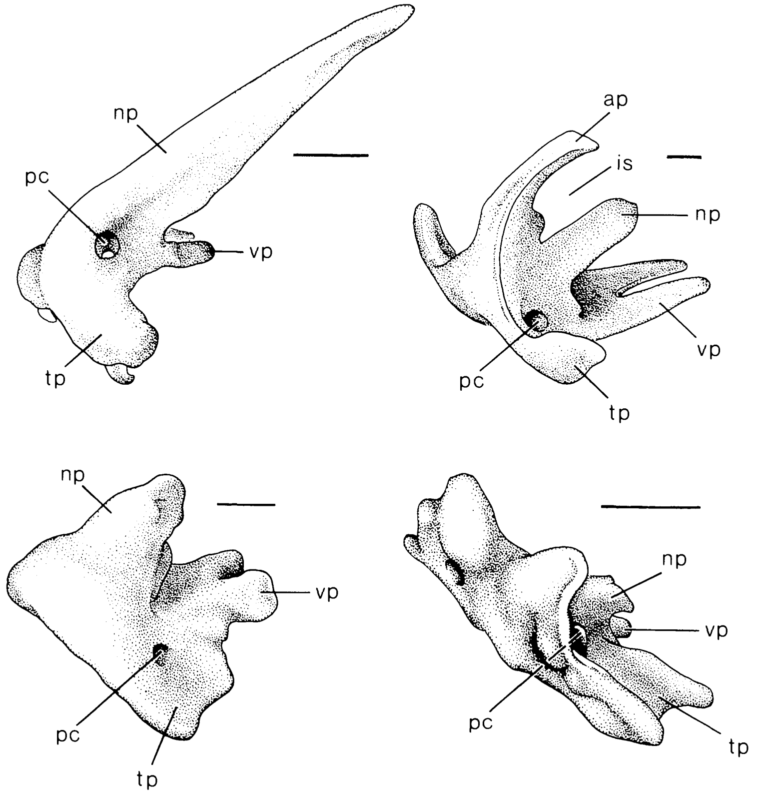

FIG. 9. Left dorsolateral view of the premaxilla of *Anilius scytale* (UMMZ 149661), upper left; *Eunectes murinus* (UMMZ 130169), upper right; *Clelia clelia* (UMMZ 149692), lower left; and *Calabaria reinhardtii* (UMMZ 149642), lower right. Scale equals 2 mm; ap = ascending process, is = internarial septum, np = nasal process, pc = premaxilla channel, tp = transverse process, vp = vomerine process (terminology largely after Frazzetta [1959, 1975]).

4. Premaxilla (Figs. 9–11): The transverse process of the premaxilla is short (0) or long (1). The process in *Sanzinia* is recorded as plesiomorphic; however, its unique shape (markedly down-turned) makes it difficult to compare to other boines and the relevant outgroups. Most outgroups have a short process, which in many instances is located entirely within the rostral arc established by the medially curving tip of the maxilla. *Eryx* is an exception.

5. Premaxilla (Fig. 9): The transverse process of the premaxilla is directed horizontally or downward (0), or upward (1). The derived conditions in *Epicrates* and *Eunectes* and in *Xenoboa* (Table 1) are probably not comparable because the process is long and short, respectively. The upturned state appears to be restricted to a few boines; it is absent in the outgroups.

6. Premaxilla (Figs. 9–11): The internarial septum is completely mineralized, or *nearly so, such that a fenestra is absent (0), or a small (1) or large (2) opening is present.* The internarial septum, not to be confused with the nasal septum of the premaxilla, a chondrocranial element (Bellairs and Kamal, 1981), is formed by the ascending and nasal processes of the premaxilla (Frazzetta, 1959, 1975). Frazzetta (1959, figs. 3C, 4C) and McDowell (1975:18) drew attention to the presence of a fenestration in the septum, which appears to be absent in the outgroups. There may be some intraspecific internarial septum variation in *Candoia aspera* and *C. carinata;* however, additional cleared and stained material is required to assess its extent. This character may not be independent of the variation in the anterior margin of the nasal (see character 11).

7. Premaxilla (Fig. 9): The internarial septum is long and projects far posteriorly between and/or beneath the nasals (0), or the septum is short and separates little, if any, of the nasals (1). I have recorded the plesiomorphic state as ambiguous because a long septum is present in anilioids, *Loxocemus,* almost all pythonines, and *Xenopeltis;* however, it seems the septum is short in erycines and in most parts of the advanced snake clade.

8. Premaxilla (Fig. 9): The base of the nasal process of the premaxilla (Frazzetta, 1959, fig. 3) is narrow and abuts nearly vertically, or it inserts between, the nasal laminae (0) or the base of the premaxilla is wide and rests on top of, but does not insert between, the nasal laminae which are equally wide at that point (1). Another distinctive correlate of the derived state is the considerable distance the lateroventral corner of a nasal lamina undercuts the premaxilla. State 1 is restricted to some boines; state 0 was observed in the outgroups.

9. Premaxilla (Fig. 9): The floor of the premaxilla, the horizontal area formed by the united anterior portion of the vomerine processes, is narrow (0) or wide (1). The size of the floor is evaluated relative to the lateral margin of the opening for the duct of Jacobson's organ, the *fenestra vomeronasalis externa* (Groombridge, 1979c, fig. 1). A few *Corallus caninus* approach the derived state, but most resemble the plesiomorphic condition. Among the ingroup and outgroups, state 1 appears to be restricted to *Candoia* species.

10. Premaxilla: The vomerine processes (the palatine processes of Frazzetta [1959, fig. 3]), projecting posteriorly from the floor of the premaxilla, are long (0) or short to absent (1). Length is assessed at the midline, where the processes diverge from the floor of the premaxilla. There is considerable size variation among some of the ingroups. The plesiomorphic condition includes a variety of shapes and sizes of processes which require further study (see for example Frazzetta [1975] and Rieppel [1979d, fig. 5]). A few specimens of *Candoia bibroni* are plesiomorphic; however, the majority of the material examined are obviously derived. There is little variation in the outgroups, except *Calabaria* possesses the derived state.

11. Nasal (Figs. 10–11): The anterior margin of the ventral lamina of the nasal (Underwood, 1976:158), viewed laterally, is more or less even (0) or indented (1). The margin in question is usually vertical; however, it may be horizontal in those outgroups whose nasals curve downward to meet the base of the premaxilla (e.g., *Aspidites* and *Calabaria*). Characters 6 and 11 are reason-

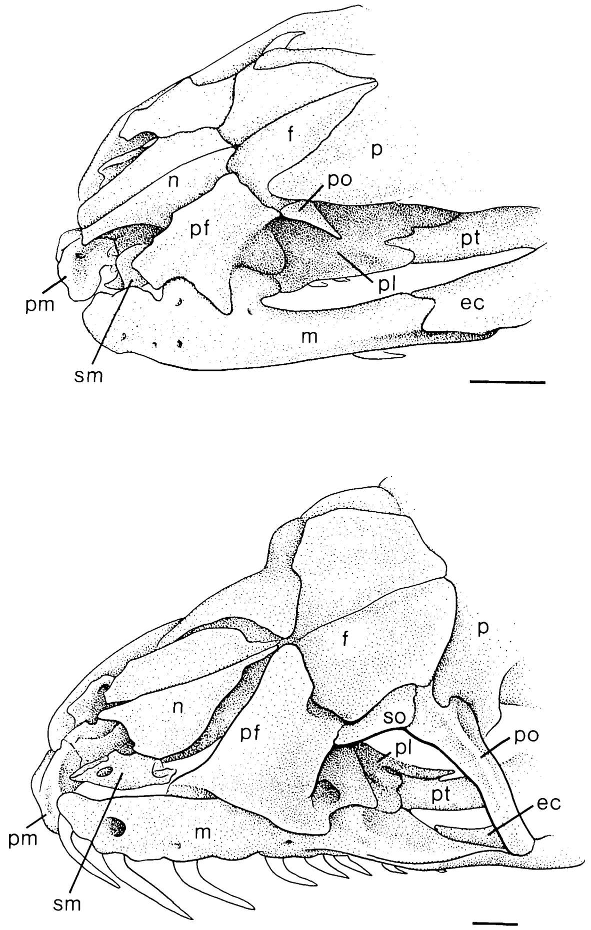

FIG. 10. Left dorsolateral view of the snout of *Cylindrophis rufus* (UMMZ 155827), top; and *Morelia viridis* (UMMZ 149644), below. Scale equals 2 mm; ec = ectopterygoid, f = frontal, m = maxilla, n = nasal, p = parietal, pf = prefrontal, pl = palatine, pm = premaxilla, po = postorbital, pt = pterygoid, sm = septomaxilla, so = supraorbital (terminology after Frazzetta [1959, 1966]).

ably well correlated (Table 1) and may not be independent because together they pertain to the shape of the internarial fenestra. State 0 characterizes the first and second outgroups.

12. Nasal (Figs. 10–11): The anterolateral margin of the horizontal lamina of the nasal, viewed dorsally, gradually tapers (0) or the margin is noticeably indented (1). Underwood (1976:157) referred to the horizontal lamina as the wing of the nasal. Anilioids, erycines, *Loxocemus* and *Xenopeltis* exhibit state 0. There is considerable variation among pythonines; however, the plesiomorphic state for the group appears to be state 0.

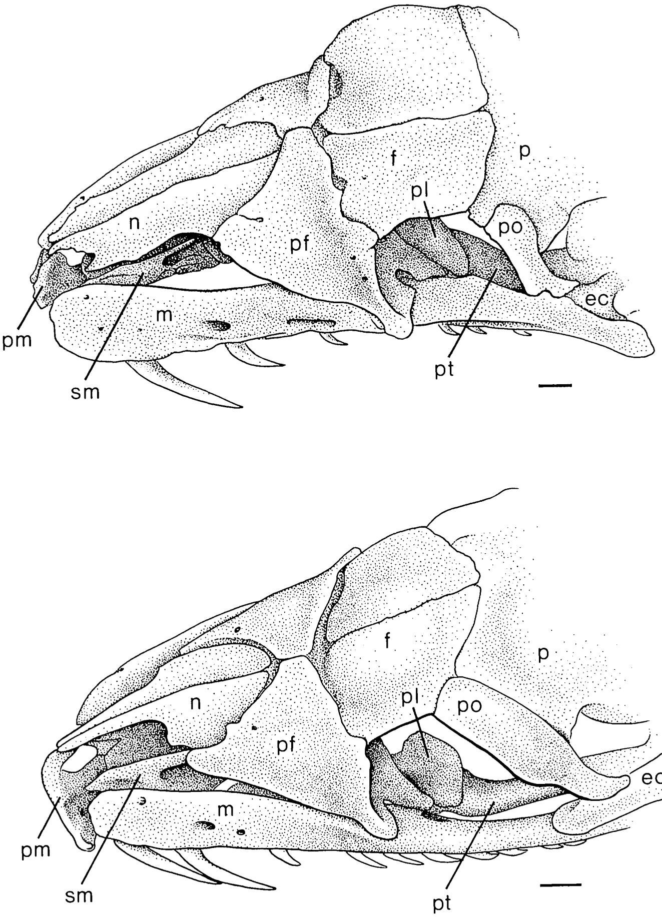

FIG. 11. Left dorsolateral view of the snout of *Corallus caninus* (UF 56081; the septomaxilla is from UMMZ 176798), top; and *Epicrates cenchria* (UMMZ 155341), below. Scale equals 2 mm; ec = ectopterygoid, f = frontal, m = maxilla, n = nasal, p = parietal, pf = prefrontal, pl = palatine, pm = premaxilla, po = postorbital, pt = pterygoid, sm = septomaxilla (terminology after Frazzetta [1959, 1966]).

13. Nasal (Figs. 10–11): Much of the lateral margin of the horizontal lamina of the nasal, anterior to the prefrontal, lies at an angle (0) or most of that margin lies parallel (1) to the midline. Among the outgroups, only some anilioids, *Loxocemus* and *Xenopeltis* approach the derived state.

14. Nasal (Fig. 12): The horizontal lamina of the nasal overlaps the dorsal surface of the frontal (0) or it does not (1). The pythonine clade is diagnosed as having state 0, although *Morelia viridis* approaches state 1. All erycines exhibit state 0, except *Charina* and *Lichanura.*

A conspicuous feature of most snakes is the prokinetic joint (nasofrontal joint of some authors; e.g., Frazzetta [1959]), which allows movement of the snout, at the juncture between the nasal and frontal bones (e.g., Riep-

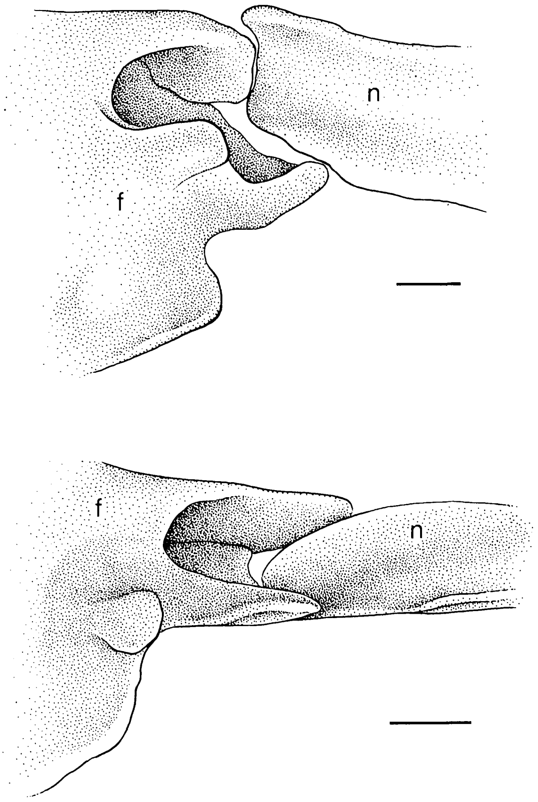

FIG. 12. Right lateral view of the nasofrontal joint in *Eunectes murinus* (AMNH 62559), top; and *Corallus caninus* (UMMZ 149650), below. Scale equals 1 mm; f = frontal, n = nasal.

pel [1977b, 1978a,b, 1979d]). The usual practice among snake systematists has been to describe the joint as one or two characters, with only a few qualitatively different states (e.g., see Underwood's [1976] character 40). Such an approach ignores independent variation, and assumes that all participating components are so highly integrated that they are incapable of independent evolution. At the risk of unduly weighting this region of anatomy, I delimit more than one character (nos. 14–16) because it allows me to test the latter proposition (Kluge, 1989b). Frazzetta (1959:469, fig. 4A-B; see also Underwood [1976]) considered additional variation which I believe is irrelevant to boine relationships.

15. Nasal (Fig. 12): The nasal contacts the frontal predominantly dorsal (0) or ventral (2) to the mesial frontal flange suture (Rieppel, 1979b, fig. 2), or the contact is nearly equally distributed above and below the suture (1). The mesial frontal flange suture forms on both sides of the midline as the result of the frontal surrounding the olfactory peduncle (Underwood, 1976:158; Rieppel, 1979b, fig. 2). I believe the "mesial processes" of Underwood (1976:158), and the "anterior medial pillars" and "medial processes" of Rieppel (1988:80, 90; see also McDowell [1975] and Groombridge [1979a]) are the same as the mesial frontal flanges. Pythonines have state 0, while state 1 characterizes all other outgroups, including erycines (except *Lichanura*), *Loxocemus,* and *Xenopeltis.* The suture seems to form more ventrally in erycines and some pythonines than in the other relevant outgroups. Further, the suture disappears in all adult erycines, including *Calabaria* (Underwood, 1976:158; *contra* Rieppel [1978b]), but there is little difficulty in discerning the presence of state 1. I assume state 1 is plesiomorphic for boines; however, this polarity may have to be changed to state 0 with a more detailed analysis of advanced snakes.

16. Nasal (Fig. 12): The posteroventral end of the nasal abuts the midventral edge of the frontal (0) or it curves significantly beneath the frontal (1). This character is not applicable to those taxa scored as state 0 in character 15. Almost all parts of the outgroup taxa exhibit state 0.

17. Maxilla (Figs. 10–11): The anterior 3–4 maxillary teeth are short, and if long they are curved posteriorly (0) or the anterior maxillary teeth are conspicuously long and nearly straight (1). I interpret the ingroup distribution of these states differently than McDowell (1979:4). The tooth-bearing margin of the maxilla is uneven in some species (e.g., *Candoia*); however, the different elevations are not at issue in determining the states of this character. Relatively short and straight anterior maxillary teeth are typical of the first and second outgroups. Some of the more apomorphic pythonine clades, and also *Epicrates* species (e.g, *E. angulifer*), have long but not especially straight teeth.

18. Maxilla: The lateral edge of the maxilla beneath the orbit is rounded or slightly (0) or markedly (1) inflected laterally. There is variation in *Eunectes notaeus* and the plesiomorphic state attributed to the species (Table 1) requires confirmation. Pythonines are variable, and the group cannot be characterized at this time. However, the fact that all the other relevant outgroups possess state 0 suggests that it is the plesiomorphic condition in boines.

19. Maxilla: The suborbital region of the maxilla is shallow (0) or deep (1). Pythonines are variable. The suborbital shelf is moderately well developed in some, but not all, species of *Morelia* and *Python,* and it is difficult to distinguish the condition in *Morelia viridis* from the state observed in *Corallus caninus* and *Xenoboa.* The other outgroups examined are characterized by the shallow state, and therefore it is assumed to be the plesiomorphic condition for boines.

20. Maxilla: The postorbital region of the maxilla is shallow, tapering gradually to a point, (0), or it is moderately (1) or very (2) deep. The end of the maxilla tends to be rounded in state 1, and it abruptly tapers to a point in state 2. *Morelia viridis* cannot be distinguished from the most derived state observed among *Corallus caninus* and *Xenoboa.* All other outgroups exhibit state 0.

21. Maxilla: From a dorsal view, the caudal end of the maxilla is directed posteriorly (0) or lateroposteriorly (1). The posterior one-third or more of the maxilla is turned outward in *Sanzinia,* as it is in some pythonines, such as *Morelia viridis;* however, this is not considered the same state as a reflected distal tip of the maxilla. All outgroups exhibit state 0.

22. Maxilla (Figs. 10–11): Most of the palatine process of the maxilla (Cundall and Irish, 1989, fig. 4) is located far anteriorly, at or beyond the anterior margin of the orbit, (0) or most of the process occurs posteriorly, within the orbit (1). The prefrontal and palatine often completely overlap the palatine process of the maxilla, and I suggest rotating between dorsal and ventral views when determining the position of the process relative to the orbit. Clearly, the condition in anilioids and *Loxocemus* is state 0. That state is also attributed to *Xenopeltis;* however, its score must be considered tentative because the palatine process is tiny (McDowell, 1975, fig. 1), if present at all. Pythonines and erycines are more like state 1, while the advanced snake clade is most simply diagnosed as state 0 (there is variation within *Tropidophis*). Thus, appealing to outgroups 3–5, state 0 is assumed to be plesiomorphic in boines.

I did not use this character in my preliminary study of snake higher classification, and as such it provides evidence for a (boine, erycine, pythonine) assemblage. If future cycles of research on the higher classification of snakes provide additional evidence for the (boine, erycine, pythonine) clade, then the 0 state in boines will have to be judged a reversal diagnostic of *Candoia.* Further, Frazzetta (1959:469), McDowell (1975:30, 32) and Underwood (1976, fig. 4) used other anatomical relations to define the position of the palatine process, such as size, shape and contact with the palatine and pterygoid, and those variables must be reexamined in future reviews of evidence. If the far anterior position of the maxillary process is finally judged primitive in alethinophidians, then its history might be considered decoupled from the evolution of the intramaxillary joint in bolyeriines. In any case, the position of the palatine process adds significantly to the dissimilarity in the palatomaxillary arch of bolyeriines and "pythonids," a point not stressed by Cundall and Irish (1989:593, fig. 6).

23. Prefrontal (Figs. 10–11): The median two-thirds of the dorsal lappet of the prefrontal (Frazzetta, 1966, fig. 18) is nearly at a right angle to the long axis of the skull (0), or it is slightly (1) or markedly (2) angled anteriorly. The condition is variable (states 0 and 1) among *Python* species; however, the 0 state appears to be plesiomorphic for pythonines as a whole. This character cannot be polarized because the dorsal lappet is small or absent in advanced snakes, anilioids, and erycines, and the peculiar double processes in *Loxocemus* and *Xenopeltis* are probably not comparable to dorsal lappets (see discussion of dorsal lappet variation in the Other Characters section).

24. Prefrontal: Viewed dorsally, the lateral foot process of the prefrontal (Frazzetta, 1966, fig. 18) lies within the boundary of the underlying maxilla (0) or the process extends well beyond the lateral edge of the maxilla (1). In the latter condition, the lateral foot process effectively wraps around the lateral margin of the maxilla. The first and second outgroups possess the 0 state.

25. Frontal (Figs. 10–11): The interorbital width of the frontals is narrow (0) or broad (1). The latter condition can be readily determined from a dorsal view because most if not all of the maxilla-ectopterygoid area of overlap (Frazzetta, 1966, fig. 51) is hidden. The narrower the interorbital width, the more the maxilla and ectopterygoid are exposed. McDowell (1975:32, 50) used frontal width to delimit groups of pythonines. My review indicates the narrow condition is plesiomorphic for the first and second outgroups, and thus for boines as well.

26. Frontal: The right and left supraorbital margins of the frontals are parallel or diverge (0), or they converge slightly anteriorly (1). Even though the supraorbital margin is indented in some *Eunectes* species and in *Corallus enydris,* the overall shape is one of anterior convergence (state 1). The first and second outgroups exhibit state 0.

27. Postorbital (Figs. 10–11): From a dorsal view, the postorbital broadly (0) or narrowly (1) contacts the frontal, or these two bones are narrowly (2) or broadly (3) separated by the parietal. The dorsal end of the pythonine postorbital is forked; the anterior lobe (Frazzetta, 1959:469, fig. 7) tends to lie ventral to the parietal and fills the space behind the supraorbital in that taxon. The presence of a posterior lobe, which lies dorsal to the parietal, appears to be a pythonine synapomorphy (Underwood, 1976, fig. 8, his character 45), and therefore its relationship to the frontal is irrelevant in determining the polarity of the present character. A few boines (e.g., *Candoia carinata,* BMNH 1964.1609; UMMZ 138820) and advanced snakes (e.g., *Tropidophis melanurus,* UMMZ 149664; *Ungaliophis continentalis,* UMMZ 149666) have a small lobe on the posterior margin of the postorbital, dorsal to the posteroventral edge of the postorbital process of the parietal, far removed from the frontoparietal suture (see character 28). The fact that many pythonines have that accessory lobe (e.g., *Aspidites*), as well as large anterior and posterior lobes (*sensu* Frazzetta [1959]), leads me to conclude that the small, second lobe observed in a few boines is not comparable to the large posterior lobe of pythonines. Thus, I believe the anterior lobe of the pythonine postorbital is comparable to the large, single lobe found in other alethinophidians, and it is almost always in narrow contact with the frontal (state 1), except in *Aspidites* which varies from narrow contact to narrow separation (states 1–2). The plesiomorphic erycine condition appears to be state 1, as exemplified by *Eryx* and *Lichanura;* state 3 occurs in *Calabaria,* and the postorbital is absent in *Charina.* The plesiomorphic state of the advanced snake clade also appears to be one of narrow contact between the postorbital and frontal. Given the interpretations of plesiomorphy for the first and second outgroups, state 1 is inferred to be plesiomorphic for boines.

28. Postorbital (Figs. 10–11): At least a major part of the dorsal one-third of the postorbital, above the accessory lobe (see character 27), is uniformly narrow (0) or broad (1). The plesiomorphic condition cannot be inferred in pythonines because their postorbital is widened considerably with the addition of the posterior lobe. A narrow postorbital is typical of the second (except *Calabaria*) and third outgroups, and this level of taxonomic generality suggests state 0 is plesiomorphic in boines.

29. Postorbital (Figs. 10–11): In lateral view, the ventral one-third of the postorbital is narrow (0) or wide (1). The optic foramen is visible in the former state, whereas it is completely obscured in the latter. Even though erycines are variable, the narrow condition is assumed to be plesiomorphic in boines because that state is typical of pythonines, the advanced snake clade, and *Loxocemus.*

30. Optic Foramen: The dorsal border of the optic foramen is formed nearly equally by the frontal and parietal (0) or it consists mostly of the parietal, the frontal forming only the anterior margin (1). State 0 is characteristic of all pythonines, except *Aspidites,* and the second outgroup. The frontal also contributes significantly to the foramen in *Loxocemus* and *Xenopeltis.* Thus, I assume state 0 is plesiomorphic in boines.

31. Optic Foramen: The posterior and dorsal margins of the optic foramen are flat or bounded by a low and rounded (0) or tall and sharply crested (1) wall. The former state is typical of outgroups 1 and 2, and it is assumed to be plesiomorphic in boines.

32. Ectopterygoid: The anterior end of the ectopterygoid (Rieppel, 1979b, fig. 6) consists of distinct (0) or indistinct (1) lateral and medial heads, or that end of the ectopterygoid is not indented (2). All pythonines (except *Morelia viridis*) have two distinct heads, whereas all erycines have none. The advanced snake clade also appears to be characterized by state 2; however, *Bolyeria* has two indistinct heads. Most *Loxocemus* have two recognizable processes (UMMZ 149657 is exceptional), as does *Xenopeltis.* The anilioid clade varies; *Cylindrophis* has two distinct heads, and *Anilius* and uropeltines have none (see Rieppel [1979b, fig. 6]). The simplest interpretation is that state 0 is plesiomorphic in boines.

33. Ectopterygoid: The ectopterygoid is long (0), of only modest length (1), or it is extremely short (2). A long ectopterygoid is typical of the first and second outgroups, and therefore I assume that state is plesiomorphic in boines.

34. Ectopterygoid: The ectopterygoid is oriented anteriorly (0) or anterolaterally (1). The first and second outgroups are characterized by the former condition, which therefore I assume is plesiomorphic in boines. The orientation in *Morelia spilota* and *M. viridis* is somewhat anterolateral, but it is not the severe angle observed in most *Corallus* and *Xenoboa* species.

35. Ectopterygoid: The ectopterygoid lies dorsal (0) or mostly lateral (1) to the maxilla. The dorsal condition is plesiomorphic in the first and second outgroups, and therefore I assume state 0 is also plesiomorphic in boines. The ectopterygoid of *Morelia viridis* and *Sanzinia* appears to lie somewhat lateral to the maxilla; however, that position seems to be due to the shape of the caudal end of the maxilla, rather than variation in the ectopterygoid itself.

36. Ectopterygoid: The posterior end of the ectopterygoid contacts the dorsal or *anterior (0) or lateral (1) surface of the pterygoid.* The contact is distinctly dorsal in all species of *Eryx,* and I interpret the minor lateral component to be secondarily derived; all other erycines exhibit an anteriorly directed joint. Some pythonines also exhibit partial lateral contact between the ectopterygoid and pterygoid. However, I consider this condition to be secondary as well because a reasonably large area of dorsal-ventral overlap exists between the two bones (best seen from a ventral view), and other pythonines such as *Aspidites* clearly possess the plesiomorphic condition. Hoffstetter (1960) claimed the ectopterygoid joined the pterygoid laterally in *Bolyeria* and *Casarea;* however, McDowell (1975:17) pointed out that the condition in those taxa was really one of dorsal overlap, similar to other advanced snakes (see Anthony and Guibé [1952, figs. 2 and 5]). Thus, I assume state 0 is plesiomorphic in boines.

37. Ectopterygoid: The area of contact between the ectopterygoid and the pterygoid is relatively simple, flat or composed of no more than one convex-concave facet (0) or it is complex, consisting of two or more such facets (1). While the joint is complicated in *Boa,* with projections from both the ectopterygoid and pterygoid, it is unlike the derived state observed in *Corallus caninus* and *Xenoboa* where the ectopterygoid is folded two or more times. The first and second outgroups exhibit state 0. I assume the complex joint in erycines is not equivalent to either state because the area of contact is anterior. A relatively simple facet also occurs in *Loxocemus* and *Xenopeltis,* the third and fourth outgroups. The simplest interpretation is that state 0 is plesiomorphic in boines.

38. Ectopterygoid: A mid-lateral prominence, when present, originates from the entire or dorsal margin of the ectopterygoid (0), or it originates from the ventral margin alone, and it is either slight (1) or prominent (2). The mid-lateral prominence in question usually occurs above the posterior end of the maxilla. It is not clear how much of the lower muscle sheath, quadrato-maxillary ligament and pterygoideus muscle attach to the prominence (Frazzetta, 1966, figs. 3–4, 25, 31). The prominence forms a distinct shelf of bone in state 2, but not state 1. Typically, a prominence is absent in the outgroups. However, one specimen of *Morelia albertisii* (FMNH 218609), a pythonine, appears to have state 1, which I assume to be convergent because all other pythonines possess the plesiomorphic condition. This character is scored as inapplicable in *Boa* because its ectopterygoid exhibits such a peculiar shape and orientation.

39. Parietal: The dorsolateral region of the parietal, between the postorbital and supratemporal, is bulbous (0) or flat (1). The first and second outgroups exhibit the former state. This character is subject to considerable ontogenetic change, and therefore must be judged only in adults.

40. Parietal: The anterolateral corner of the parietal extends much (0) or slightly (1) beyond the lateral margin of the frontal, or the two bones are approximately even (2). The first and second outgroups have state 0, and I assume that condition is plesiomorphic in boines. In treating this as an ordered transformation series, I assume the anterolateral corner of the parietal has been progressively shortened. However, the variation might be more accurately described in terms of frontal width, or some combination of change in the widths of the parietal and the frontal. That the postorbital process of the parietal diagnoses the (boine, pythonine) clade, or is more general (Rage, 1984:13; Rieppel, 1988:91–92), does not appear to affect these assumptions of polarity and transformation.

41. Parietal: From a dorsal view (Underwood, 1976, fig. 1E- F), the posterior margin of the parietal, on the midline, is slightly indented, nearly straight or slightly pointed (0) or the margin forms an extremely long process (1). While I recognize only two states, I believe this variable is consistent with Underwood's (1976:160) character 49. There is considerable variation among the first and second outgroups; however, it appears that all major lineages involved can be characterized by state 0. The slightly pointed conditions observed in *Cylindrophis, Lichanura, Morelia, Python* (e.g., *P. molurus* and *P. reticulatus*), *Trachyboa,* and *Tropidophis* are scored as plesiomorphic. The apomorphic states exhibited by *Eryx, Morelia amethistina* and *M. viridis* are interpreted as homoplastic because the plesiomorphic sister taxa in their respective groups, erycines and pythonines, have state 0. Thus, state 0 is assumed to be plesiomorphic in boines. The process is short in *Acrantophis madagascariensis;* however, the condition is treated as apomorphic because its length is more nearly like that of *A. dumerili* than it is the plesiomorphic state recorded for *Eunectes.*

42. Supraoccipital: A supraoccipital midsagittal crest is absent or only weakly developed (0) or the crest is tall and occupies most, if not all, of the length of the supraoccipital (1). I believe this transformation series, not 43 (below), is the same as Underwood's (1976:160) character 51. I use the term midsagittal, rather than sagittal (Frazzetta, 1966:247), crest for this prominence to distinguish it from parasagittal crests (the "lateral extension" of Underwood, 1976:160, his character 50). Some of the outgroups have tall parietal midsagittal crests but they are not considered apomorphic because those ridges of bone occupy little of the length of the supraoccipital (these crests are usually hidden beneath the flared parasagittal crests of the parietal). The apomorphic states observed in *Eryx* and *Morelia viridis* are interpreted as secondarily evolved because more plesiomorphic sister lineages in the erycine and pythonine clades exhibit state 0. The absence or weak development of a crest in boines is considered plesiomorphic.

43. Supraoccipital: The midsagittal crest of the supraoccipital is only partly (0) or at least nearly completely (1) covered by the parietal midsagittal crest. This variable does not appear to be the same as Underwood's (1976:160) character 51 because I refer to the amount of the supraoccipital that is covered by the parietal. State 0 is typical of the first and second outgroups, and I assume it is the plesiomorphic condition in boines. Some pythonines might appear to exhibit the derived state; however, I am inclined to consider these conditions incomparable to the boine apomorphy because the supraoccipitals are so different in the two taxa. The supraoccipital is much larger in boines, covers most of the dorsal surface of the exoccipitals and usually extends to the end of the skull, whereas the supraoccipital is tiny and the exoccipitals are fully exposed from above in pythonines.

44. Supratemporal: From a dorsal view, the supratemporals diverge (0), lie nearly parallel to each other (1), or they converge (2) lateroposteriorly (see Underwood, 1976, fig. 1E-F). This character (also character 45) may be affected by the state of preservation, and it is necessary to examine at least two specimens of each terminal taxon to be reasonably sure of obtaining an accurate determination. With few notable exceptions (e.g., Underwood [1976:160, fig. 1]), squamate systematists refer to this bone as the supratemporal, rather than the squamosal; however, that choice seems to be predicated on the choice of outgroups to snakes (Estes et al., 1970:53). Pythonines possess states 0 and 1, and I have been unable to diagnose that assemblage. However, all second and third outgroup taxa appear to be characterized by state 1, and therefore I assume it is plesiomorphic for boines.

45. Supratemporal: From a lateral view, the supratemporal is nearly horizontal (0), or it is inclined slightly (1) or markedly (2) dorsoposteriorly. The most apomorphic condition (state 2) results more from a strong upward curvature of the posterior portion of the supratemporal than it does from a reorientation of the entire supratemporal. A few specimens of *Boa* appear to exhibit the most upturned shape but there is little if any upward curvature in their supratemporal. The first and second outgroups can be characterized as having a nearly horizontal supratemporal, and that condition is considered plesiomorphic in boines. A derived condition (state 1) occurs in a few erycines (*Eryx colubrinus* and *E. conicus*).

46. Supratemporal: The posterior end of the supratemporal is rounded and not noticeably enlarged (0), or it is rounded but dilated (1) or markedly hooked (2) posteroventrally. The caudal end of the supratemporal is not swollen or hooked in the first and second outgroups, and I hypothesize that state 0 is plesiomorphic in boines.

47. Stapes: The stapes does (0) or does not (1) contact the quadrate. The point of contact on the quadrate is usually an oval, flat surface located on a process. The stapes is absent in the single specimen of *Xenoboa,* probably lost during preparation, and the apomorphic condition is inferred from the absence of a process on the quadrate. The two bones appear to contact in the plesiomorphic sister taxa of the first and second outgroups, and therefore such a state is inferred to be plesiomorphic in boines.

48. Vomer: The horizontal posterior lamina is horizontal (0) or more nearly vertical (1). Groombridge (1979c) distinguished between vertical and horizontal posterior laminae, and the vertical state I recognize should not be confused with the vertical lamina. All but one of the *Corallus enydris* examined exhibit the derived state. The horizontal condition is characteristic of most of the outgroups; *Lichanura, Morelia viridis* and *Python* species are exceptions. Therefore, state 0 is considered plesiomorphic in boines.

49. Septomaxilla: The lateroventral edge of the septomaxilla projects modestly, if at all, posterior to the fenestra vomeronasalis externa (Groombridge, 1979c, fig. 1), *the opening for the duct of Jacobson's organ, (0) or the edge forms a large blade posterior to the fenestra (1).* The variable area of the vomer is not to be confused with the lateral process (Frazzetta, 1959, fig. 4D), which lies dorsolaterally, beneath the apex of the prefrontal (Frazzetta, 1966, fig. 18). The outgroups appear to exhibit uniformly the 0 state, and therefore that condition must be treated as plesiomorphic in boines. Several pythonines (e.g., *Python molurus*) possess a well developed blade; however, this process appears to be incomparable to the derived state in boines because it is an extension of the lateroposterior wall of the nasal cavity and might therefore be reasonably interpreted as secondarily evolved.

50. Palatine (Fig. 13): The maxillary process of the palatine (Cundall and Irish, 1989, fig. 4) lies anterior to (0) or at (1) the level of the palatine-pterygoid joint. The character states can be inferred accurately in most cases from the position of the palatine process of the maxilla, as seen in ventral view; however, in taxa like *Morelia spilota* and *M. viridis* the palatine, pterygoid, and maxilla must be disarticulated and the connective tissue removed in order to see the exact relationship of the process and joint. Erycines are variable, but all other outgroups can be characterized by the anterior position of the maxillary process of the palatine. Thus, I assume state 0 is plesiomorphic in boines. I believe further research on erycine relationships is required before much confidence can be placed in the taxonomic level of generality of this apomorphy (see also character 52; Underwood, 1976, fig. 8). The derived condition in *Morelia amethistina* is a notable exception among pythonines.

51. Palatine (Fig. 13): The choanal process of the palatine (see Underwood's [1976:161] character 57) is long and continuous with the vomer (0), or it contacts the vomer by a thin, disarticulated section of mineralized tissue (1), or it is short and far removed from the vomer (2). The process in question lies dorsal to the choanal channel, or *ductus nasopharyngeus* (McDowell, 1972, fig. 20). *Epicrates* is variable (states 0 and 1); however, the disarticulated condition is assumed to be plesiomorphic because it occurs in the most basal sister taxa (Kluge, 1989b). Mineralization occurs throughout the length of the process before birth in *Epicrates.* Following parturition, there is either additional mineralization or loss of mineralization, both sets of events proceeding from near the base of the choanal process outward to the tip of the process, which is in contact with the vomer. The loss of mineralization appears to begin at the tip and move toward the base in *Eunectes.* The choanal process of the palatine in the single specimen of *Xenoboa* seems to have been destroyed during preparation, and its character state is left undetermined. Pythonines exhibit state 2, whereas erycines are variable (*Calabaria, Charina* and *Lichanura* have state 0, *Eryx* state 1). All other outgroups—advanced snakes, anilioids, *Loxocemus,* and *Xenopeltis*—have state 0. I assume the long and continuous palatine (state 0) is the plesiomorphic condition in boines, and that loss of contact with the vomer (state 2) evolved independently in boines and pythonines.

52. Palatine: The maxillary foramen (Underwood, 1976:161) lies completely

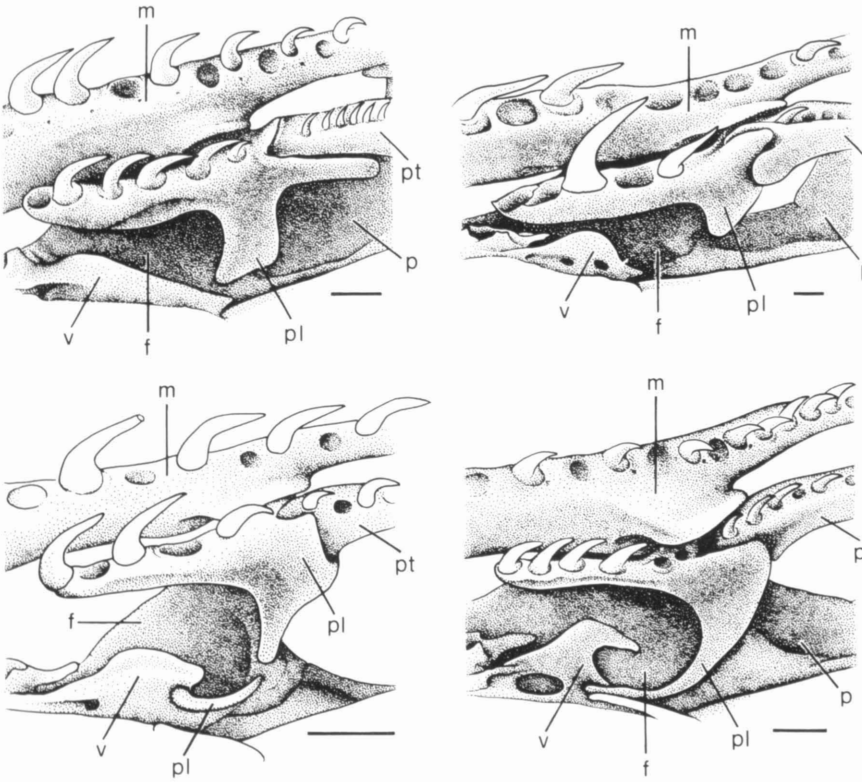

FIG. 13. Lateroventral view of the left side of the palate of *Python regius* (UMMZ 149660), upper left; *Boa constrictor* (UMMZ 155336), upper right; *Epicrates angulifer* (UMMZ 176921), lower left; and *Epicrates subflavus* (UMMZ 176911), lower right. Scale equals 2 mm; f = frontal, m = maxilla, p = parietal, pf = prefrontal, pl = palatine, pt = pterygoid, v = vomer (terminology after Frazzetta [1959, 1966]).

within the palatine (0) or it is not so enclosed (1). This is equivalent to Underwood's (1976) character 56 (see also Frazzetta [1959:469, fig. 6]); however, he seems to have referred to the opening as the palatine foramen (Underwood, p. 169, fig. 8). All outgroups, except erycines, can be characterized as having the foramen completely enclosed within the palatine. Therefore, state 0 is assumed to be plesiomorphic in boines. The open condition in *Morelia amethistina* is assumed to be convergent to the boine apomorphy. Underwood (1976, table 1, under the heading of Tropidophidae) listed *Bolyeria* and *Casarea* as having a deeply notched and wide open foramen, respectively; however, I believe both taxa exhibit the plesiomorphic closed condition, as do all tropidophiines, except *Ungaliophis*. The foramen in bolyeriines and most tropidophiines is relatively small and occupies a more central position, above the dentigerous portion of the palatine. Nonetheless, in those taxa, the foramen exits from the lateral side of the palatine, as it does in the outgroups where the foramen lies above the maxillary process of the palatine. I believe further research on erycine relationships is required before much confidence can be placed in the taxonomic level of generality of this apomorphy (see also character 50; Underwood, 1976, fig. 8).

53. Palatine (Fig. 13): The medioposterior pterygoid process of the palatine is long (0) or short (1). The process in question extends along the inner margin of the pterygoid, and Underwood (1976:161, his character 55; see also Frazzetta [1959:469]) referred to it as the posterior process. I prefer a more specific terminology because there is a lateroposterior pterygoid process of the palatine. All outgroups, except *Xenopeltis,* have the long condition. I assume state 0 is plesiomorphic in boines. In *Xenopeltis,* the process is somewhat shorter than in most other outgroups, and it is located dorsal, not lateral, to the pterygoid.

54. Pterygoid (Fig. 13): An anteromedial palatine process on the pterygoid is absent (0) or present (1). The palatine and pterygoid must be disarticulated when considering this character. A low ridge of bone occurs along the medial side of the pterygoid in most of those boines in which the process is absent, but the ridge does not continue forward along the side of the palatine. The process in question actually overlaps the palatine and thereby creates an additional area of articulation between the two bones. One specimen of *Candoia bibroni* possesses a tiny anteromedial projection, but it is located ventrally and does not overlap the palatine. The process was not observed in any outgroup. Thus, I assume the boines scored as state 0 are plesiomorphic.

55. Pterygoid: The palatine keel on the anterodorsal surface of the pterygoid is absent or long and shallow (0) or short and deep (1). This ridge lies near the middle of the pterygoid and is not to be confused with the anteromedial process (see character 54). Among boines, the keel is least prominent in *Eunectes.* With the exception of *Trachyboa* and *Tropidophis,* the 0 state typifies the first and second outgroups, and therefore that condition is assumed to be plesiomorphic in boines.

56. Basisphenoid: The parasphenoid wing (the basipterygoid process of Frazzetta [1959:470]) is absent or only weakly developed (0) or large and without (1) or with (2) a distinctly flattened (pedicellate) ventral surface. This transformation is consistent with Underwood's (1976) character 63. Curiously, the Madagascar boine taxa represent two extremes: *Acrantophis* has the most massive pedicellate process I observed among boines, whereas adult *Sanzinia* have no process whatsoever. If I assume such a process (the "*processus basitrabeculaire*" of Genest-Villard [1966, fig. 4]) is present early in development in *Sanzinia* then the ontogeny criterion suggests its absence in the adult semaphoront of that taxon is apomorphic (Kluge, 1988b). The wing is absent to short in the second outgroup (except *Bolyeria, contra* Anthony and Guibé [1952:193–194]), *Loxocemus* and *Xenopeltis.* The large process that occurs in several pythonines is interpreted as secondarily evolved because my preliminary study (Fig. 4) indicates that those groups are apomorphic sister taxa. The simplest interpretation is that state 0 is plesiomorphic in boines.

There is considerable disagreement concerning the homology of the basipterygoid process of lizards (Oelrich, 1956; Rieppel, 1980b) and the wing-like projection originating from the lateral margin of the parabasisphenoid in many snakes (Underwood, 1967, figs. 3–4; the "basi-parasphenoid" of Underwood [1976, fig. 5]). In fact, Rieppel (1978c) suggested that it is the parasphenoid component of the parabasisphenoid, not the basisphenoid component, from which the wings project. While I accept Rieppel's (1977a:154; 1988:45, 90) conclusion that the basipterygoid process and the lateral wing are not part of the same transformation series (*contra* Bellairs and Kamal [1981]), and must therefore be treated as separate characters, I do so for different reasons. Rieppel (1988) claimed that both process and wing were found in the same specimen of *Sanzinia,* and thus he argued that they cannot be homologous because the test of conjunction is failed (Patterson, 1982). In my opinion, *Sanzinia* does not have a parasphenoid wing (or basipterygoid process). I believe Genest-Villard's (1966, fig. 4) reference to a basitrabecular process (= basipterygoid process; Bellairs and Kamal, 1981:11), which Rieppel cited, is ambiguous. It is true that the projection labelled "processus basi-trabeculaire" in Genest-Villard's figure of a developmental stage of *Sanzinia* has the general appearance of the lizard basipterygoid process (compare to fig. 15 in Bellairs and Kamal [1981]); however, such a structure does not exist in adult *Sanzinia.* It is also important to note that the projection Genest-Villard labelled "nodule sub-trabeculaire" in his fig. 4 appears to be a separate center of chondrification rather than an outgrowth of the trabecula (Bellairs and Kamal, 1981, fig. 1; see however their figs. 61–62). In general, my reasons for thinking the parasphenoid wing and the basipterygoid process are incomparable is that they develop from the trabecula and the basal plate, respectively, are usually dissimilar in shape, approach the pterygoid from different angles, and the nature of the contact with the pterygoid is different (often there is a meniscus in lizards; Bellairs and Kamal, 1981, figs. 18, 40). Perhaps most importantly, I find no evidence that adult anilioids, *Loxocemus,* scolecophidians (*contra* McDowell and Bogert [1954:80–81];see also McDowell [1967:689–690, fig. 1]), and *Xenopeltis* (Fig. 4) have a pedicellate projection from the parabasisphenoid like that in lizards (see however, *Dinilysia;* Estes et al., 1970, figs. 2a, 5, 10). Thus, character congruence convinces me that the well-developed lateral wing of the parasphenoid in boines and pythonines and the basipterygoid of lizards have independent histories.

57. Basisphenoid: A midventral keel is absent to only moderately elevated on the basisphenoid (0) or the keel is extremely deep (1). Pythonines are variable; however, none of those taxa with the largest keel (e.g., *Python timoriensis*) approach the boine apomorph condition. The second, third, and fourth outgroups are characterized by state 0, which I assume is the plesiomorphic condition in boines. The extraordinarily massive midventral projection in *Bolyeria* bears no resemblance to a keel.

58. Basisphenoid: The right and left posterior vidian canals are approximately of equal size (0) or the right canal is larger than the left (1). Underwood (1976:163–164, his character 66; see also Underwood [1967:13, 15, 17], Rieppel [1977a] and Groombridge [1984]) pointed out that the left vidian canal is larger in pythonines and *Loxocemus,* and the right is larger than the left in erycines and boines. According to my observations (Table 1), I believe Underwood (1976, table 1) over-generalized concerning the asymmetry in boines (his Boini). Moreover, he mistakenly (1976, table 1; see also Underwood [1967:69]) recorded the vidian canals in *Calabaria* as invariably of equal size (even in the material he listed as having examined, BMNH 96.3.9.3 and 1911.10.28.17, the right side is 1.6 times wider than the left). Thus, among the outgroups, state 1 is present in all erycines, and state 0 typifies all others (the posterior vidian canal appears to be absent in *Trachyboa* and *Tropidophis;* Underwood, 1976:164). Given the variation in the outgroups, and according to Fig. 4, the simplest interpretation is that equal-sized canals is plesiomorphic in snakes (including boines). It also follows that the boine-erycine synapomorphy is one of convergence, as is the shared derived state in *Loxocemus* and pythonines.

59. Splenial (Fig. 14): The anterior edge of the splenial (Frazzetta, 1959) exhibits a noticeable indentation, a hooked condition, at the level of Meckel's groove (0) or the edge gradually tapers anteroventrally (1). Epicrates is variable; however, the plesiomorphic sister taxa, *E. angulifer* and *E. cenchria,* possess state 0. Colombian *Corallus annulatus* also have the 0 condition, but *C. annulatus* from Ecuador possess the alternative state. This and other jaw characters described below suggest that *C. annulatus* consists of more than one species lineage (Kluge, 1990). Unfortunately, I do not believe these entities can be satisfactorily characterized with the skeletal material available because most of the specimens are without specific locality data. Polarizing this character is problematical because of outgroup variation. For example, all pythonines exhibit state 0, bolyeriines state 1, and erycines and tropidophiines are variable. While *Cylindrophis* possesses the hooked condition, *Anilius, Loxocemus* and *Xenopeltis* exhibit the alternative state. Thus, I have left the ancestral state in boines as unknown.

60. Coronoid (Fig. 14): The coronoid (Frazzetta, 1959) contacts the splenial (0) or the two bones are separated (1). I assume Underwood's (1976) character 61 is covered by my variables 60–62. All bolyeriines and pythonines exhibit state 0, whereas only some erycines (*Eryx*) and anilioids (*Cylindrophis*) have that condition. The variation in tropidophiines is particularly interesting. The coronoid seems to be absent in *Exiliboa* and *Ungaliophis,* and therefore these taxa are not applicable in deciding this character's polarity. In the other tropidophiines, *Trachyboa* and *Tropidophis,* the coronoid, although tiny, contacts the splenial. *Loxocemus* and *Xenopeltis* possess state 1. Given this variation among the outgroups (see also Rieppel [1988:81]), and the preliminary hypothesis of relationships (Fig. 4), the simplest interpretation

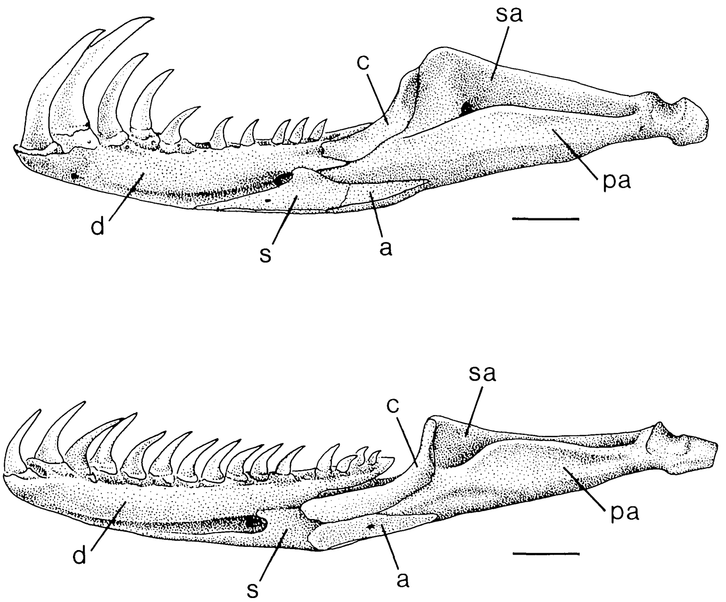

FIG. 14. Medial view of right mandible of *Corallus caninus* (UMMZ 149650), top; and *Eunectes deschauenseei* (USNM 135454), bottom. Scale equals 5 mm; a = angular, c = coronoid, d = dentary, pa = prearticular, s = splenial, sa = surangular (terminology after Frazzetta [1959, 1966]).

is that state 0 is plesiomorphic in boines. It must be emphasized that this interpretation of polarity in boines hinges on the condition of the tiny element in *Trachyboa* and *Tropidophis*.

61. Coronoid (Fig. 14): The coronoid contacts the angular (0) or the two bones are separated (1). The condition in *Boa* is scored as unknown because I observed nearly equal numbers of the two states in the available sample (state 0, 9 specimens; state 1, 7 specimens). *Corallus annulatus* is also variable; there is contact in Colombian *C. annulatus,* whereas those from Ecuador possess state 1. Like character 60, state 0 is tentatively considered plesiomorphic in boines. All bolyeriines and pythonines exhibit state 0, whereas only some erycines (*Eryx*) and anilioids (*Cylindrophis*) have that condition. As noted above, tropidophiines are variable; the coronoid seems to be absent in *Exiliboa* and *Ungaliophis,* and therefore these taxa are not applicable in deciding this character's polarity, but the coronoid is tiny and contacts the splenial in *Trachyboa* and *Tropidophis. Loxocemus* and *Xenopeltis* possess state 1.

62. Coronoid (Fig. 14): The anterodorsal margin of the coronoid is almost entirely concealed behind the surangular portion of the compound bone (0) or it extends slightly or well beyond the surangular, such that it is clearly exposed when viewed laterally (1). I use the term compound bone (see also Estes et al. [1970:45]) because the articular-prearticular and surangular are fused in adults. Pythonines are variable, but the basal lineages have state 1. *Loxocemus,* and those erycines and advanced snakes with a coronoid (see Rieppel [1988:81]), exhibit state 0. Thus, the latter condition is assumed to be plesiomorphic in boines.

63. Coronoid (Fig. 14): The apex of the coronoid (the dorsalmost point) lies at or below the surangular (0) or the apex extends slightly (1) or well (2) above the surangular. Pythonines are variable, but the plesiomorphic sister taxa in that group have state 0. *Loxocemus,* and those erycines and advanced snakes with a coronoid (see Rieppel [1988:81]), exhibit state 0. Thus, the latter condition is assumed to be plesiomorphic in boines.

64. Prearticular (Fig. 14): The dorsal margin of the prearticular, the area where the adductor posterior muscle inserts (Frazzetta, 1966, fig. 32), forms a low and nearly flat ridge (0) or it is noticeably curved upward (1). The ridge is low in all parts of the first and second outgroups, except some erycines (*Charina, Eryx,* and *Lichanura*) and *Tropidophis,* and I assume the 0 state is plesiomorphic in boines.

65. Surangular (Fig. 14): The lateroventral edge of the surangular, the margin where part of the adductor externus medialis and the adductor externus superficialis muscles insert (Frazzetta, 1966, fig. 32), is rounded or forms a narrow (0), wide (1) or extremely wide ledge (2). Little or no ledge appears to be present in the second and third outgroups. Pythonines are variable (it is wide in *Morelia spilota, M. viridis,* and most *Python* species). Therefore, I assume state 0 is plesiomorphic in boines.

66. Surangular (Fig. 14): The lateroventral ledge of the surangular (see character 65), when present, is long (0) or restricted to the anterior (1) or posterior (2) region of the surangular. This character cannot be polarized because the ledge is absent or reduced in most of the outgroups.

67. Teeth: There are small (0) or large (1) numbers of adult teeth (see Underwood's [1976] characters 52, 59–60). The smaller numbers of maxillary, dentary, and pterygoid teeth almost always average less than 22, 22, and 18, respectively, whereas the larger numbers usually average more than 26, 26, and 23, respectively. The fact that the numbers of maxillary, dentary, and pterygoid teeth covary significantly in boines suggests that they should not be treated as historically independent characters in that taxon. There is some increase in tooth number with specimen size (age), and my assessment of tooth number is based on reproductively mature individuals. Variation in palatine tooth number does not appear to divide into small and large categories, and it is excluded from this character. Among the ingroup taxa, only *Epicrates monensis* approaches the derived state. I assume this condition to be one of secondary evolution because *E. angulifer* and *E. cenchria,* the plesiomorphic sister species in that genus (Kluge, 1989b), exhibit smaller numbers of teeth. There is considerable variation among pythonines; however, smaller numbers of teeth characterizes the basal lineages. All bolyeriines, erycines, *Loxocemus,* and tropidophiines have relatively small numbers of teeth. Therefore, I assume state 0 is plesiomorphic in boines.

68. Hyobranchium: The cornua of the hyobranchium are continuous (0) or discontinuous (1) anteriorly (see Underwood's [1976:163] character 64). The derived state recorded for *Acrantophis madagascariensis* (UMMZ 170396) and *Xenoboa* (AMNH 92997) must be confirmed with cleared and stained material. *Epicrates* has been scored as unknown (?) because the plesiomorphic condition for that terminal taxon cannot be coded unambiguously—the cornua are discontinuous in *E. cenchria* (Langebartel, 1968; Underwood, 1976), and continuous in all other species examined thus far: *E. angulifer* (Langebartel, 1968), *E. chrysogaster, E. exsul, E. monensis,* and *E. subflavus* (my observations on the last four species were based on cleared and stained specimens). I assume continuous cornua are plesiomorphic in boines. This inference is based almost entirely on the literature pertaining to the outgroups (Fürbringer, 1919; Warner, 1946; H. M. Smith and Warner, 1948; Anthony and Guibé, 1952; Kamal and Hammouda, 1965a,b,c; List, 1966; McDowell, 1967, 1975; Bogert, 1968; Langebartel, 1968; Groombridge, 1979a,b,d). I accept Groombridge's opinion (1979a, fig. 11; see also McDowell [1975:13]) that the cornua in *Ungaliophis* are continuous (*contra* Langebartel [1968]).

A problem confronted by all students of the snake hyobranchium is correctly identifying the parts of that obviously vestigial skeleton. I believe it is safe to assume that the plesiomorphic snake hyobranchium consisted of a lingual process, basihyal, and first ceratobranchial and epibranchial (Kluge, 1983). The presumed homologies identified in snakes are based in part on shape, position, and associated musculature. The entire snake hyobranchium is almost always cartilaginous, which makes it difficult to distinguish the separate and usually bony first ceratobranchial from the hyoid and second branchial arch elements. However, some typhlopids (List, 1966, plate 18, fig. 8) have both a cartilaginous lingual process-basihyal and a distinct bony element, which I believe is the first ceratobranchial. This exact configuration is present in some lizards (e.g., *Anniella;* see List [1966, plate 18, fig. 7]). The continuous cartilaginous branchia that remain in other snakes cannot be attributed convincingly to particular elements, and therefore I simply refer to them as cornua; all or part of a cornua might be a lingual process, basihyal, and/or first ceratobranchial and epibranchial. Like McDowell (1967:690), I believe the peculiar M-shaped hyobranchium of anomalepids (H. M. Smith and Warner, 1948) represents the first branchial arch. Given the associated musculature (Warner, 1946), it is unlikely to be the hyoid arch, *contra* the interpretations of List (1966), Langebartel (1968) and Underwood (1967). Even the shape of the anomalepid hyobranchium is vaguely similar to the first branchial arch of some lizards; the anterior projecting end of the cornua resembles the first epibranchial (Kluge, 1983).

69. Vertebrae: Paracotylar foramina are absent (0) or present (1) in mid-trunk vertebrae (see Underwood [1976, figs. 6 and 8, table 1] and his character 77). Paired foramina always seem to be present in *Boa, Candoia, Corallus annulatus* and *Xenoboa,* and the openings are especially large in the last two taxa.

Only one of 10 *Sanzinia* vertebrae sampled had a tiny foramen present (one side only) and that species was recorded as having the 0 state. Paracotylar foramina are absent in erycines (except *Lichanura;* Hoffstetter and Rage, 1972; Kluge, 1988a), *Loxocemus,* pythonines, a well diagnosed subgroup of tropidophiines (*Trachyboa, Tropidophis*), *Xenopeltis* (Underwood, 1976), and the remaining parts of the advanced snake clade (Underwood, 1976). There is considerable variation within and among *Lichanura* (e.g., in 22 and 23 midtrunk vertebrae taken from UMMZ 131053 and 189644, 9%, 32% and 59%, and 0%, 18% and 82% of the foramina were symmetrically present, asymmetrically present, or absent, respectively; Kluge, 1988a). While a hypothesis of independent evolution of these foramina in *Lichanura* seems warranted, the taxonomic level at which they evolved in the advanced snake clade is ambiguous (*contra* Underwood [1976, fig. 8]). Nonetheless, it is clear, based on the condition attributed to the other outgroups, that state 0 is the plesiomorphic condition in boines.

70. Vertebrae: Most trunk vertebrae have at best a weakly developed hypapophyseal keel (0) or a well developed keel is present throughout that region (1). This variable is equivalent to Underwood's (1976) character 76. *Boa* has the best developed hypapophyseal keel of all those ingroup taxa I scored as state 0. Rage (1984:15) stated that only bolyeriines and tropidophiines (*Trachyboa* and *Tropidophis* according to Underwood [1967:25]), among the first and second outgroups, have a hypapophysis. Thus, I assume the absence of a keel in the trunk is plesiomorphic in boines. The fact that *Acrochordus* and many colubroids have a hypapophyseal keel suggests the presence of a more general synapomorphy in the advanced snake clade. In that group, the hypapophysis consists of a long, thin blade of bone emanating mostly from the posterior part of the centrum. Such a hypapophysis is not part of the definition of the apomorphic state in extant boines.

71. General habitus: Body shape, in cross-section, and the distinctness of the head from the neck-trunk region are described as three states: the body is round and the head is not set off noticeably from the neck (0); the body is oval and the head is slightly larger than the neck (1); the body is distinctly laterally compressed and the head is much larger than the neck (2). The more plesiomorphic sister species in *Epicrates* appear to be state 0; however, the remaining taxa are state 1, including the arboreal *E. gracilis* (Tolson, 1987). Basal pythonine taxa seem to exhibit state 0, as do all erycines. While the plesiomorphic condition for the advanced snake appears to be ambiguous, *Loxocemus* and *Xenopeltis* are like erycines. Thus, I assume the 0 state is plesiomorphic in boines.

72. Eye: The eye is directed laterally (0) or dorsally (1). Among the first and second outgroups, only a few species of *Eryx* have dorsally directed eyes (*E. jayakari* and *E. miliaris*). Laterally directed eyes are assumed to be plesiomorphic in boines.

73. Labial pits: Macroscopically, labial pits are absent (0), shallow (1), or deep (2) in the labial scales. Physiology and micro- and neuroanatomy are not implied by these states (Barrett, 1970; Maderson, 1970; Meszler, 1970; Gamow and Harris, 1973; Gopalakrishnakone, 1984). Underwood (1976) employed three pit characters (his nos. 15–17), two of which referred to the number of upper (no. 15) and lower (no. 16) labial pits. I have not treated these as independent because there is significant correlation among boines. In *Epicrates,* the basal lineages exhibit state 1, while the cladistically more apomorphic sister taxa have state 0. Among the relevant outgroups, only some pythonines have pits. The simplest interpretation, given this pattern of outgroup variation and the hypothesis of relationships illustrated in Fig. 4, is that the absence of pits is plesiomorphic in boines. While character congruence and parsimonious reasoning alone suggest the history of pits is one of convergent acquisition in boines and pythonines, the different anatomical positions of the pits in the two clades (McDowell, 1975), between versus within the labial scales, respectively, is consistent with that process explanation (see Underwood's [1976] character 17).

74. Head scales: The dorsal and lateral head scales anterior to the parietal region (excluding the labials and rostral) are mostly, if not all, large and occur in pairs—viz., they are bilaterally symmetrical (0), a few scales may be large but these are usually unpaired (1), or almost all of the scales are small and there is little evidence of bilateral symmetry (2). The first and second outgroups are characterized by state 0 (exceptions are *Eryx, Morelia spilota,* and *M. viridis*). There is variation in *Epicrates,* with the most basal species exhibiting state 1, the more apomorphic sister taxa state 0 (see Zacharias [1897] and Guibé [1949]).

75. Body scales: Body scales are smooth (0) or keeled (1). This is equivalent to Underwood's (1976) character 14. I assume the smooth state is plesiomorphic in boines because most outgroups have that condition. All but one species of pythonine (*Morelia carinatus* L. A. Smith, 1981a) are smooth, as are most erycines (many *Eryx* species are keeled). Bolyeriines are keeled (Underwood, 1976), among tropidophiines only *Trachyboa* and some *Tropidophis* have keels, and *Loxocemus* and *Xenopeltis* are smooth scaled.

76. Rectal caecum: The rectal caecum is present (0) or absent (1). According to McDowell (1979:3), *Acrantophis, Boa, Sanzinia,* and *Xenoboa* exhibit a "well defined rectal caecum," whereas *Candoia, Corallus, Epicrates* and *Eunectes* lack it. My dissections of *Acrantophis madagascariensis* (UMMZ 170396), *Boa* (UMMZ 79785), *Candoia bibroni* (UMMZ 100015), *Corallus annulatus* (UMMZ 65782), *C. caninus* (UMMZ 123714), *C. enydris* (UMMZ 131314), *Epicrates cenchria* (UMMZ 148992), *Eunectes notaeus* (UMMZ 56863), and *Xenoboa* (AMNH 92997) confirm McDowell's conclusions concerning these taxa; however, I was unable to locate a "well defined" caecum in *Sanzinia* (BMNH 1961.2024; UMMZ 174414). To be sure, the anterodorsal end of the rectum is distinctive (it is much deeper than the small intestine and it projects beyond the rectum-small intestine junction) in *Sanzinia,* as it is in *Corallus annulatus,* but the condition in neither taxon counts as "well defined" (e.g., like *Boa*). In many snakes the caecum is small and closely bound by connective tissue to the digestive tract, which makes it easy to overlook the presence of the structure. McDowell (1979:4, 70) noted that the rectal caecum was generally present in snakes, but absent in tropidophiines. He also described the condition in colubroids as variable. I have determined that a rectal caecum is present in erycines; it was found in *Calabaria* (BMNH 1919.8.16.75), *Charina* (BMNH 1964.1992; see Cope [1900:692, plate 7]), *Eryx colubrinus* (BMNH 1902.12.13.70), *E. conicus* (BMNH 1921.6.15.9), *E. jaculus* (BMNH 64.8.23.50), *E. jayakari* (BMNH 1971.1655), *E. johnii* (BMNH IV.22.1.b, 1914.4.25.2), *E. miliaris* (BMNH 1962.852), *E. muelleri* (BMNH 1975.577), *E. somalicus* (BMNH 1949.2.1.46), *E. tataricus* (BMNH 73.7.24.3), and *Lichanura* (BMNH 1969.2695). Underwood (1967, fig. 14i) clearly showed a caecum in at least two of the major lineages of scolecophidians. These diverticula appear to diverge dorsally at the anterior end of the rectum. Luppa (1977:272–273) stated that "various reptiles may lack a caecum," and I am unaware of any lizard possessing such a structure (Bellairs, 1970; Fox, 1977). Thus, I assume the presence of a rectal caecum is plesiomorphic in boines.

77. Intercostal Artery Segmentation: Each posterior trunk intercostal artery usually supplies one (0) or more (1) body segments. This character is discussed at length elsewhere (Kluge, ms.). I accept Underwood's (1976) and Underwood and Stimson's (1990) hypothesis of polarity, state 0 being plesiomorphic in boines. *Candoia bibroni* (UMMZ 100015) exhibits the derived state and is like all other congeners (*contra* Underwood [1976]).

78. Hemipenis: A well-defined longitudinal flounce, with which the transverse flounces usually fuse and which travels obliquely distad over and around the arms delineating sulcal and asulcal fields, is absent (0) or present (1). This character is taken entirely from Branch (1981:98). I have been unable to confirm his observations and hypothesis of polarity (state 0 is plesiomorphic in boines) because of inadequate material. Further research on *Candoia* may be warranted because Branch (p. 94) dissected their hemipenes *in situ,* rather than observe them in the more natural everted position (see also McDowell [1979, fig. 2]).

79. Hemipenis: The sulcus terminates above (0) or below (1) the tips of the arms. This character is also taken entirely from Branch (1981:98; see character 78 above), and I tentatively accept his observations and hypothesis of polarity (state 0 is plesiomorphic in boines).

OTHER CHARACTERS

Underwood (1976:157, fig. 1A-D, his character 39) and McDowell (1979:3) used the extent of the gap between the prefrontals on the dorsal midline (Figs. 10–11), the dorsal lappets of Frazzetta (1966, fig. 18), as evidence of primitive snake relationships. The former author stated that there is a mesial line of contact between the lappets in *Corallus, Epicrates,* and *Eunectes,* and the latter author concluded that his Boini, consisting of *Acrantophis, Boa, Sanzinia,* and *Xenoboa,* could be diagnosed in terms of the prefrontal bones "extending close to [the] midline." I agree with Underwood that widely separated lappets, as in advanced snakes, anilioids, erycines, and *Loxocemus,* is the primitive alethinophidian condition; however, I find too much variation in most boine and pythonine species represented by large samples to reasonably identify more than one apomorph. For example, the prefrontals in *Boa constrictor* vary from broad contact (e.g, UMMZ 155336) to modest separation (e.g., UMMZ 155335). Further, even Underwood's (1976) quantification of only a few specimens indicates a nearly continuous pattern of interspecific variation. Thus, the only apomorph I recognize is that of the prefrontals approaching the midline, which is a derived condition shared by boines and pythonines. Underwood (1976:168–9, fig. 8) claimed the apomorph evolved independently in boines and pythonines, whereas I would interpret it as further evidence of their common ancestry (Fig. 4). *Xenopeltis* may also be interpreted as having the derived state.

Frazzetta (1959:470) distinguished boines from pythonines in terms of the former group having a longitudinal distance from the "basipterygoid" processes to the level of the quadrate-pterygoid joint more than 40% of the total skull length. Using the length of the lower jaw, instead of total skull length, I have been unable to confirm the distinction noted by Frazzetta.

Underwood (1976) observed a closed Meckel's groove at the anterior end of the dentary in all of the specimens of boines he examined (except *Candoia bibroni* and *C. carinata*), whereas he characterized the outgroups as having an open groove (his character 69). I have been unable to identify confidently the alternative states on the surface of the dentary, and future research might better concentrate on the exposed nature of Meckel's cartilage. It may also be necessary to compare only adults because Meckel's groove appears to vary markedly with size (age). Tentatively, I reject this character (see also Underwood [1976, the legend to his fig. 8]).

Underwood (1976) also identified two scale characters that might be useful in delimiting subgroups of boines, the number of ventral body and subcaudal scales (his characters 1 and 2). However, the counts covary significantly, and the two characters may be only a function of a change in the position of the vent. In addition to the issue of independence, larger samples must be surveyed, separated by sex, before this character(s) can be reconsidered.

According to Shaw and Campbell (1974), Shine (1985), McDowell (1987) and Mehrtens (1987), acrochordids, anilioids, all boines (*Xenoboa* is unknown), bolyeriines, *Charina, Eryx, Lichanura,* and tropidophiines (except *Trachyboa,* Van Wallach pers. comm.) are viviparous. *Anomochilus* (Brongersma and Helle, 1951), *Calabaria, Loxocemus,* all pythonines, almost all scolecophidians (M. A. Smith, 1943), and *Xenopeltis* are oviparous. Assuming erycines are variable, the polarity for boines is equivocal because equally parsimonious optimizations obtain on the accepted outgroup hypothesis (Fig. 4). I have no reason to prefer one possibility over the other, and I consider this character uninformative in the study of boine relationships.

Boines vary karyotypically; however, more extensive surveys of both ingroup and outgroup taxa must be completed before the taxonomic level of generality of the apomorphies can be determined accurately. For example, *Acrantophis dumerili, Corallus caninus, C. enydris,* and *Sanzinia madagascariensis* have 2n = 34, 44, 40 (not 42 as reported by De Smet [1978:109]) and 34, respectively, whereas 2n = 36 occurs in all other boines that have been examined (*Boa, Epicrates cenchria, E. striatus, Eunectes murinus*), *Loxocemus,* pythonines, and *Xenopeltis* (Fischman et al., 1972; Gorman, 1973; Mengden and Stock, 1980; Bickham, 1984). Erycines are also variable (2n = 34 and 36; Gorman, 1973; De Smet, 1978). Accepting Gorman and Gress's (1970) hypothesis that 2n = 36 is plesiomorphic, then there would appear to have been both a decrease (*Acrantophis* and *Sanzinia*) and increase (*Corallus* species) in diploid number in boines. The (*Acrantophis, Sanzinia*) clade is also delimited by several other synapomorphies (see below; Fig. 7), and the reduced diploid number would also be interpreted as diagnostic of that group. However, some cytotaxonomists might doubt the homologous nature of the (*Acrantophis, Sanzinia*) karyotype synapomorphy because C- and G-banding data for the two taxa are substantially different (Mengden and Stock, 1980). Perhaps the mechanisms of chromosome change, like ontogenetic trajectories (Kluge, 1988b:71-76), do not have to be identical for a conclusion of homology to apply.

The Reality of the Ingroup

Underwood (1976) recognized the boine group (Fig. 1), and McDowell's (1979:2–9) general discussion of relationships (Fig. 2) was at least consistent[2] with a hypothesis of boine individuality. However, the evidence thus far accumulated for the monophyly of boines is hardly overwhelming when the purported diagnostic characters are reexamined carefully. For example, Underwood (1976; see table 1 and legend to fig. 8) listed only two synapomorphies of boines: the prefrontals approach one another on the dorsal midline, and the posterior process of the palatine is lost (it is unclear why he omitted the closed Meckel's groove at the tip of the dentary, his character 69). In my opinion (see above), Underwood's first character does not provide evidence for the individuality of boines *per se* because the apomorphy diagnoses a larger clade, including pythonines (Fig. 7). That leaves Underwood's second feature as uncorroborated, which I accept as phylogenetically informative, assuming it is equivalent to my character 53 (see description).

In my unpublished preliminary study (Figs. 4–5), the boine group was delimited by five synapomorphies; however, now I can accept only one of these, the ectopterygoid's position lateral to the pterygoid (described as character 36 above). The other apomorphies were the (1) concavity in the anterior margin of the nasal septum, viewed laterally (= character 11 above), (2) discontinuity of the hyobranchial cornua (= character 68

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[2] My concept of logical consistency in phylogeny and taxonomy follows Hull (1964; see also Wiley, 1981).

above), (3) height of the frontal's olfactory canal suture (Rieppel, 1979b, fig. 2), and (4) widely separated vomerine processes of the premaxilla (Frazzetta, 1975). Apomorphies 1–2 no longer appear to be relevant to the individuality of boines. Consider that *Candoia* was hypothesized to have highly derived sister group relationships within boines in the preliminary study (Fig. 5), and its plesiomorphic states of those two characters were most simply explained as evolutionary reversals on that phylogenetic hypothesis. However, if *Candoia* is the sister group of all other boines, as suggested by the present research (Fig. 7), then the first two synapomorphies diagnose a subgroup of boines, but not boines as a whole. The variation in apomorphies 3-4 (above) in both the ingroups and outgroups is greater than recorded in my preliminary study, and whatever phylogenetic information remains, if any, does not diagnose the boine group.

While only two of the seven previously recognized synapomorphies of boines are retained (characters 36 and 53), at least eight more unambiguous transformations (characters 1, 41, 42, 50, 52, 55, 76, and 77), not assuming additivity or nonadditivity, are discovered in the present study. When all multistate characters are treated as additive, characters 71 and 74 can be added to the array of unambiguous evidence for the individuality of boines. Thus, the historical reality of boines is well supported (see Diagnoses section below for details).

RELATIONSHIPS AMONG THE PARTS OF THE INGROUP

Two equally best-fitting cladograms (**S** = 164, **C** = 0.61, **R** = 0.79) result from an exact analysis (the implicit enumeration algorithm in Hennig86) of the 79 characters summarized in Table 1, assuming additivity of the multistate characters. A single cycle of weighting (the **xs w** algorithm described in the Methods And Materials section; Table 2) leads to the fully resolved branching pattern illustrated in Fig. 7 (**C** = 0.81, **R** = 0.90). This hypothesis requires only 64 extra steps to explain the available evidence, whereas a completely unresolved topology requires 241 *additional* extra steps (Kluge, 1989b). An identical best-fitting topology is obtained when the assumption of additivity is relaxed for all multistate characters: four equally most parsimonious trees (**S** = 154, **C** = 0.65, **R** = 0.79) are discovered initially with exact implicit enumeration, and these topologies are then reduced, with one round of successive weighting, to the unique branching diagram shown in Fig. 7. Thus, particular assumptions concerning multistate character evolution do not have to be made in this study of boine phylogeny. However, all polarity propositions must be reexamined after the erycine and pythonine ingroup relationships have been reinvestigated, and the (boine, pythonine), erycine, and advance snake trichotomy has been resolved (Fig. 4).

All clades in the boine phylogenetic hypothesis are delimited by at least one unique and unreversed synapomorphy (viz., unique and unreversed within boines; Fig. 7). Also, each clade is corroborated by two or more

TABLE 2

CHARACTER METRICS*

	CHARACTERS																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
s	1	1	1	3	2	5	1	1	1	4	1	1	1	1	4	2	2
c	1.0	1.0	1.0	.33	.50	.40	1.0	1.0	1.0	.25	1.0	1.0	1.0	1.0	.50	.50	.50
r	1.0	1.0	1.0	.60	.75	.66	1.0	1.0	1.0	.40	1.0	1.0	1.0	1.0	.71	.83	.50
	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
s	1	1	2	1	1	4	1	1	2	9	2	1	3	1	4	3	1
c	1.0	1.0	1.0	1.0	1.0	.50	1.0	1.0	.50	.33	.50	1.0	.33	1.0	.50	.66	1.0
r	1.0	1.0	1.0	1.0	1.0	.71	1.0	1.0	.66	.57	.50	1.0	.50	1.0	.75	.83	1.0
	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51
s	1	1	1	4	1	2	2	1	1	2	2	3	1	1	1	1	3
c	1.0	1.0	1.0	.50	1.0	1.0	.50	1.0	1.0	1.0	1.0	.66	1.0	1.0	1.0	1.0	.66
r	1.0	1.0	1.0	.71	1.0	1.0	.66	1.0	1.0	1.0	1.0	.80	1.0	1.0	1.0	1.0	.83
	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68
s	1	1	1	1	4	1	2	2	3	2	2	2	1	5	3	1	1
c	1.0	1.0	1.0	1.0	.50	1.0	.50	.50	.33	.50	.50	1.0	1.0	.40	.66	1.0	1.0
r	1.0	1.0	1.0	1.0	.77	1.0	.83	.75	.50	.80	.85	1.0	1.0	.66	.80	1.0	1.0
	69	70	71	72	73	74	75	76	77	78	79						
s	4	1	6	1	5	4	1	4	3	2	2						
c	25	1.0	.33	1.0	.40	.50	1.0	.25	.33	.50	.50						
r	40	1.0	.55	1.0	.70	.50	1.0	.25	.33	.80	.80						

*The actual number of steps (**s**), and consistency (**c**) and retention (**r**) indices for each character (Table 1) used to construct the phylogenetic hypothesis illustrated in Fig. 7 (Kluge and Farris, 1969; Farris, 1989; Kluge, 1989b). See Methods and Materials section for further explanation. All multistate characters (see footnote 2) are assumed to be additive.

synapomorphies, regardless of the assumption of additivity. The quantity and quality of the evidence supporting each clade is summarized on Fig. 7, and the phylogenetically informative, unambiguous character states are listed in the Diagnoses section. Further research on *Candoia* and *Eunectes* is suggested because relationships among their congeners are the least well supported, and *E. barbouri* is not included in the present study.

Given the large number of characters employed and the taxonomic resolution and high degree of character congruence obtained, I infer that boines are neither too specialized nor too homoplastic to be studied phylogenetically (*contra* McDowell [1987]). Of course, one can always assert that the discovered taxonomic pattern of relationships is controlled by homoplasy. However, I know of "no a priori reason to expect homoplasious characters, as a group, to be congruent" (Kluge, 1984:34). Thus, while homologues are expected to be congruent due to common ancestry, false synapomorphies are expected to be incongruent with homologues and nonhomologues alike.

The three previously available detailed hypotheses of relationships among boines provide substantially poorer fits to the present evidence (Table 1, Fig. 7). For example, the hypotheses of Underwood (1976; Fig. 1, **S** = 212, **C** = 0.47), of McDowell (1979; Fig. 2, erycines excluded, **S** = 224, **C** = 0.45), and of my own preliminary study (Fig. 5, **S** = 234, **C** = 0.43) exhibit 48, 60, and 70 additional extra steps, respectively. Bogert's (1968) contention that *Xenoboa* is closely related to *Epicrates* is not confirmed.

A Monophyletic Taxonomy

Almost all of the traditionally recognized genera of boines are monophyletic on the cladistic hypothesis discovered herein (Figs. 7-8). The single exception is *Corallus,* which would be paraphyletic if *Xenoboa* were recognized. Given the well supported sister group relationships of *C. caninus* and *X. cropanii* (Figs. 7–8), I synonymize *Xenoboa* with *Corallus* and thereby avoid a paraphyletic taxon.

The relationships among *Acrantophis, Boa,* and *Sanzinia* are resolved and the monophyly of that clade is confirmed, particularly so assuming additivity (Figs. 7–8; see also Brygoo [1982]). Further, that only four species are involved (*Boa* and *Sanzinia* are monotypic) allows for a simpler, and in some ways more informative, generic reclassification. There are two options given these considerations (Brygoo, 1982), either of which maintains monophyly: synonymize *Sanzinia* with *Acrantophis,* or both of those taxa with *Boa.* I prefer the latter because it emphasizes the unusual biogeographic hypothesis discussed below. In either case, *Acrantophis madagascariensis* and *Sanzinia madagascariensis* are homonyms, and one must be replaced. The Malagasy vernacular name for *Sanzinia madagascariensis,* the junior homonym according to page priority (Duméril and Bibron, 1844), is manditra (Brygoo, 1982; IUCN/UNEP/WWF, 1987), etymology unknown (Chris Raxworthy, pers. comm.), and I propose *manditra* as a replacement name for that species. Boulenger (1893) seems to have been the first to synonymize *Acrantophis* with *Boa* (Brygoo, 1982). While I cannot accept his placement of *Sanzinia* in the synonymy of *Corallus,* both sets of synonyms served as an early recognition of a geographic connection between the New World and Madagascar.

My recommendations for a formal higher classification of boines are postponed until the erycine and pythonine research cycles are completed and integrated with the present study. For the time being (see Diagnoses section below), the topology itself serves as the hierarchy for the genus group names I recognize. Synonymizing *Xenoboa* with *Corallus* and *Acrantophis* and *Sanzinia* with *Boa* (see above) results in the following classification: (*Candoia* (*Corallus* (*Boa* (*Epicrates, Eunectes*)))).

DIAGNOSES[3]

(*Candoia* (*Corallus* (*Boa* (*Epicrates, Eunectes*)))): 1, 36, 41, 42, 50, 52, 53, 55, [71], [74], 76, 77.

Candoia: 3, 9, 10c, 18, 69c, 70, *71c,* [74(2)c], 75, 78c, 79c.

C. (*aspera, carinata*): 23c, 67.

(*Corallus* (*Boa* (*Epicrates, Eunectes*))): 6(2), 11, 12, 14, 22, [32], [45], [46], [56], 64, 68, [73].

Corallus: 17, 20, 21, 24, 25, [33c], 34, 35, 40, 43, [45(2)], [46(2)], 48, 65(2), 71(2)c, 73(2)c.

C. (*caninus, cropanii, enydris*): 19, [33(2)], 47, 60c.

C. (*caninus, cropanii*): 13, 20(2), 31, 37, 39, 40(2), 44(2), 57.

(*Boa* (*Epicrates, Eunectes*)): 16, 44(0), 49, 58.

Boa: 2(0), [51(2)], 54, [63].

B. (*manditra* (*dumerili, madagascariensis*)): 6c, 27(3)c, 30c, [63(2)], 66, 77(0)x, 78c, 79c.

B. (*dumerili, madagascariensis*): 38(2), [56(2)c], 59c, [71(0)x], [73(0)x].

(*Epicrates, Eunectes*): 5c, 8, 23c, [32(2)c], *38c,* [56(2)c], [71(0)x].

Eunectes: 26c, 29, 41(0)r, *65c,* 72, [73(0)x].

E. (*deschauenseei, notaeus*): 23(0), 66(2).

BIOGEOGRAPHY

The phylogenetic hypothesis of boine relationships (Figs. 7–8) forms the basis for a limited number of conclusions concerning the group's geographic history. The simplest interpretations are that (1) boines have had a long and continuous presence in the New World, at least since the divergence of *Corallus* and (*Boa* (*Epicrates, Eunectes*)), (2) (*manditra* (*dumerili, madagascariensis*)) cladogenesis took place within the area encompassed by Madagascar and Rèunion, (3) the Madagascar-Rèunion radiation diverged from a New World ancestor, and (4) *Candoia*'s peculiar Indoaustralian Archipelago distribution is more likely to have been the result of vicariance in the Old World (*contra* Mertens [1972], Underwood [1976] and McDowell [1979]), assuming the sister group relationships between boines and the exclusively Old World pythonines is confirmed. The South America-Ma-

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[3] Only unambiguous diagnostic information is summarized for the boine taxonomy discussed in the section A Monophyletic Taxonomy. Numbers without parentheses refer to particular characters (1–79; see Character Descriptions and Table 1), those within parentheses specify character states. Character state 1 can be assumed, unless indicated otherwise. Lower-case letters c and r mean convergence/parallelism and reversal, respectively (x signifies c and r). Characters in brackets do not apply under the assumption of nonadditivity, those in italics apply only under that assumption. Character state evolution within boines can be assumed to be unique and unreversed in boines, unless indicated otherwise. Autapomorphies are omitted; 30c can be added to the diagnosis of *Epicrates* summarized by Kluge (1989b).

dagascar connection is repeated in iguanian lizards, where the Madagascar oplurines are the sister group to the South American tropidurines (and/or anoloids), not the African-Asian acrodonts (Branch, 1981; Frost and Etheridge, 1989), and in pelomedusid turtles of the genus *Podocnemis* which have a tropical America-Madagascar distribution (Underwood, 1976:172). Such geographic congruence, which may also be paralleled in a caecilian clade (Ron Nussbaum, pers. comm.), suggests a vicariance explanation; however, according to Mertens (1972; see also Underwood [1976]), the evolution of the (*manditra,* (*dumerili, madagascariensis*)) lineage was the result of a single transoceanic colonization subsequent to the breakup of Gondwanaland. To deny the vicariance explanation, in light of the hypothesis of boine relationships illustrated in Fig. 8, and the corroborating patterns claimed for three other, unrelated taxa, is unscientific because it gives up the opportunity to generalize as to common cause (Kluge, 1989a:320). Dispersal (like homoplasy) is a universal process explanation because it explains pattern and nonpattern alike, and as such it is empty of historical generalities if used before alternative interpretations are exhausted.

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REFERENCES

Albino, A.M. 1986. Nuevos Boidae Madtsoiinae en el Cretacico tardio de Patagonia (formacion Los Alamitos, Rio Negro, Argentina). Actas IV Congreso Argentino de Paleontología y Bioestratigrafía, Mendoza, 2:15–21.

———. 1987. Un nuevo Boidae (Reptilia: Serpentes) del Eoceno temporano de la provincia del Chubut, Argentina. Ameghiniana, 24:61–66.

Anthony, J., and J. Guibé. 1952. Les affinities anatomiques de *Bolyeria* et de *Casarea* (Boides). Mém. Inst. Sci. Madagascar, 7:189–201.

Arnold, E.N. 1990. Why do morphological phylogenies vary in quality? An investigation based on the comparative history of lizard clades. Proc. Royal Soc. London, 240:135–172.

Auffenberg, W. 1958. The trunk musculature of *Sanzina* [sic] and its bearing on certain aspects of the myological evolution of snakes. Breviora, (82):1–12.

Barrett, R. 1970. The pit organs of snakes. *In* Gans, C., and T.S. Parsons (eds.), Biology of the Reptilia. Vol. 2:277-300. Academic Press, New York.

Beddard, F.E. 1904a. Contributions to our knowledge of the circulatory system in the Ophidia. Proc. Zool. Soc. London, 1904:331–370.

———. 1904b. Notes upon the anatomy of certain snakes in the family Boidae. Proc. Zool. Soc. London, 1904:107-121.

———. 1906a. Contributions to the anatomy of the Ophidia. Proc. Zool. Soc. London, 1906:12–44.

———. 1906b. Contributions to the knowledge of the vascular and respiratory systems in the Ophidia, and to the anatomy of the genera *Boa* and *Corallus.* Proc. Zool. Soc. London, 1906:499–532.

———. 1908. A comparison of the Neotropical species of *Corallus, C. cookii,* with *C. madagascariensis;* and some points in the anatomy of *Corallus caninus.* Proc. Zool. Soc. London, 1908:135–158.

Bellairs, A.d.'A. 1970. The Life of Reptiles. Universe Books, New York.

———, and J.D. Boyd. 1950. The lachrymal apparatus in lizards and snakes. II. The anterior part of the lachrymal duct and its relationship with the palate and with the nasal and vomeronasal organs. Proc. Zool. Soc. London, 120:269–310.

———, and A.M. Kamal. 1981. The chondrocranium and the development of the skull of Recent reptiles. *In* Gans, C., and T.S. Parsons (eds.), Biology of the Reptilia. Vol. 11:1–263. Academic Press, New York.

———, and G. Underwood. 1951. The origin of snakes. Biol. Rev. Cambridge Philos. Soc., 26:193–237.

Bickham, J.W. 1984. Patterns and modes of chromosomal evolution in reptiles. *In* Sharma, A. K., and A. Sharma (eds.), Chromosomes in Evolution of Eukaryotic Groups: 13–40. CRC Press, Boca Raton, Florida.

Bogert, C.M. 1968. A new genus and species of dwarf boa from southern Mexico. Amer. Mus. Novit., 2354:1–38.

Boulenger, G.A. 1893. Catalogue of the snakes in the British Museum (Natural History). Vol. 1. Taylor and Francis, London.

Branch, W.R. 1981. Hemipenes of the Madagascan boas *Acrantophis* and *Sanzinia,* with a review of hemipeneal morphology in the Boinae. J. Herpetol., 15:91–99.

Brongersma, L.D., and W. Helle. 1951. Notes on Indo-Australian snakes. Proc. K. Ned. Akad. Wet., Ser. C, 54:3–10.

Brygoo, E.R. 1982. Les ophidiens de Madagascar. Mem. Inst. Butantan, 46:19–58.

Cadle, J.E. 1987. Phylogenetic relationships among advanced snakes: A molecular perspective. Univ. California Publ. Zool., 119:1–77.

Carpenter, J.M. 1988. Choosing among equally parsimonious cladograms. Cladistics, 4:291–296.

Cope, E.D. 1900. The crocodilians, lizards, and snakes of North America. Report U.S. Natl. Mus., 1900:155-1270.

Cundall, D., and F.J. Irish. 1989. The function of the intramaxillary joint in the Round Island boa, *Casarea dussumieri.* J. Zool., London, 217:569–598.

De Smet, W.H.O. 1978. The chromosomes of 23 species of snakes. Acta Zool. Pathol. Antverp., 70:85–118.

Dessauer, H.C., J.E. Cadle, and R. Lawson. 1987. Patterns of snake evolution suggested by their proteins. Fieldiana, Zool., 1376:1–34.

Domergue, C.A., A. Dodin, J.M. Pinon, and E.R. Brygoo. 1969. Première application des techniques sérologiques à l'étude de la systématique des serpents de Madagascar. Arch. Inst. Pasteur Madagascar, 38:175–180.

Donoghue, M.J. 1990. Why parsimony? Evol., 44:1121-1123.

———, J.A. Doyle, J. Gauthier, A.G. Kluge, and T. Rowe. 1989. The importance of fossils in phylogeny reconstruction. Annu. Rev. Ecol. Syst., 20:431–460.

Dowling, H.G. 1959. Classification of the serpentes: A critical review. Copeia, 1959:38–52.

———. 1975. The Nearctic snake fauna. 1974 HISS Yearbook of Herpetology: 191–202.

———, and W.E. Duellman. 1978. Systematic herpetology: A synopsis of families and higher categories. 1974–1978 HISS Publ., New York.

———, and J.V. Jenner. 1988. Snakes of Burma: Checklist of reported species and bibliography. Smithsonian Herpetological Information Service, 76:1–19.

Duméril, A.M.C., and G. Bibron. 1844. Erpétologie générale ou histoire naturelle complète des reptiles. Vol. 6. Librairie Encyclopédique de Roret, Paris.

Estes, R., T.H. Frazzetta, and E.E. Williams. 1970. Studies on the fossil snake *Dinilysia patagonica* Woodward: Part 1. Cranial morphology. Bull. Mus. Comp. Zool., Harvard Univ., 140:25–74.

Farris, J.S. 1969. A successive approximation approach to character weighting. Syst. Zool., 18:374–85.

———. 1977. On the phenetic approach to vertebrate classification. *In* Hecht, M.K., P. Goody, and B.M. Hecht (eds.), Major Patterns in Vertebrate Evolution: 823–850. Plenum, New York.

———. 1982. Outgroups and parsimony. Syst. Zool., 31:328-334.

———. 1988. Hennig. Hennig86 reference: Vers. 1.5. Privately printed.

———. 1989. The retention index and the rescaled consistency index. Cladistics, 5:417–419.

———, A.G. Kluge, and M.J. Eckardt. 1970. A numerical approach to phylogenetic systematics. Syst. Zool., 19:172–189.

———, ———, and J.M. Carpenter. ms. Successive and spectral weighting. Cladistics.

Fischman, H.K., J. Mitra, and H.G. Dowling. 1972. Chromosome characteristics of 13 species in the order Serpentes. Mammalian Chromosomes Newsletter, 13:7-9.

Fitzinger, L.J. 1843. Systema Reptilium. Braümuller and Seidel, Wien.

Fox, H. 1977. The urogenital system of reptiles. *In* Gans, C., and T.S. Parsons (eds.), Biology of the Reptilia. Vol. 6:1–157. Academic Press, New York.

Frazzetta, T.H. 1959. Studies on the morphology and function of the skull in the Boidae (Serpentes). Part 1. Cranial differences between *Python sebae* and *Epicrates cenchria.* Bull. Mus. Comp. Zool., Harvard Univ., 119:453–472.

———. 1966. Studies on the morphology and function of the skull in the Boidae (Serpentes). J. Morph., 118:217–296.

———. 1975. Pattern and instability in the evolving premaxilla of boine snakes. Amer. Zool., 15:469–481.

Frost, D.R., and R. Etheridge. 1989. A phylogenetic analysis and taxonomy of iguanian lizards (Reptilia: Squamata). Misc. Publ. Mus. Nat. Hist. Univ. Kansas, 81:1–65.

Fürbringer, M. 1919. Über das zungenbein der reptilien. Bijdr. Dierkd., Amsterdam and Leiden, 21:195–212.

Gamow, R.I., and J.F. Harris. 1973. The infrared receptors of snakes. Sci. Amer., 228:94–100, 102.

Gasc, J.-P. 1966. Les rapports anatomiques du membre pelvien vestigial chez les squamates serpentiformes. B. *Python sebae* (Seba). Bull. Mus. Natl. Hist. Nat. Paris, 38:99–110.

———. 1974. L'interprétation fonctionelle de l'appareil musculo-squelettique de l'axe vertébral chez les serpents (Reptilia). Mém. Mus. Natl. Hist. Nat. Paris, A 83:1–182.

———. 1981. Axial musculature. *In* Gans, C., and T.S. Parsons (eds.), Biology of the Reptilia. Vol. 11:355–453. Academic Press, New York.

Gauthier, J., A.G. Kluge, and T. Rowe. 1988. Amniote phylogeny and the importance of fossils. Cladistics, 4:105–209.

Genest-Villard, H. 1966. Développement du crâne d'un Boidé: *Sanzinia madagascariensis.* Mém. Mus. Natl. d'Hist. Nat. Paris, 40:207–262.

Gilmore, C.W. 1938. Fossil snakes of North America. Geol. Soc. Amer. Spec. Pap., (9):1–96.

Gopalakrishnakone, P. 1984. Light and scanning electron microscopic study of the pit organ of the reticulate python, *Python reticulatus.* Snake, 16:33–42.

Gorman, G.C. 1973. The chromosomes of the Reptilia, a cytotaxonomic interpretation. *In* Chiarelli, A.B., and E. Capanna (eds.), Cytotaxonomy and Vertebrate Evolution: 349–424. Academic Press, New York.

———, and F. Gress. 1970. Chromosome cytology of four boid snakes and a varanid lizard, with comments on the cytosystematics of primitive snakes. Herpetologica, 26:308–317.

Groombridge, B.C. 1979a. Variations in morphology of the superficial palate of henophidian snakes and some possible systematic implications. J. Nat. Hist., 13:447–475.

———. 1979b. Comments on the intermandibular muscles of snakes. J. Nat. Hist., 13:477–498.

———. 1979c. On the vomer in Acrochordidae (Reptilia: Serpentes), and its cladistic significance. J. Zool., London, 189:559–567.

———. 1979d. A previously unreported throat muscle in Scolecophidia (Reptilia: Serpentes), with comments on other scolecophidian throat muscles. J. Nat. Hist., 13:661–680.

———. 1984. The facial carotid artery in snakes (Reptilia, Serpentes): Variations and possible cladistic significance. Amphibia-Reptilia, 5:145–155.

Guibé, J. 1949. Révision des Boidés de Madagascar. Mém. Inst. Sci. Madagascar, 3:95–105.

Haas, G. 1962. Remarques concernant les relations phylogéniques de divers familles d'ophidiens fondées sur la différentiation de la musculature mandibulaire. Colloq. Int. Cent. Natl. Rech. Sci., 104:215–241.

Harding, J.H., and J.A. Holman. 1982. The paleohistory of snakes in North America - A brief review. Bull. Chicago Herpetological Soc., 17:33–45.

Hecht, M.K. 1982. The vertebral morphology of the Cretaceous snake, *Dinilysia patagonica* Woodward. Neues Jahrb. Geol. Palaeontol. Monatsh., 1982:523–532.

Hennig, W. 1966. Phylogenetic Systematics. Univ. Illinois Press, Chicago.

Hoffstetter, R. 1960. Sur la classification des boides de Madagascar et des Mascareignes. Bull. Mus. Natl. Hist. Nat. Paris, 32:131–138.

———. 1962. Revue des recéntes acquisitions concernant l'histoire et la systématique des Squamates. Colloq. Int. Cent. Natl. Rech. Sci., 104:25–74.

———. 1968. [Review of] A contribution to the classification of snakes, by G. Underwood. Copeia, 1968:201–213.

———, and J.-P. Gasc. 1969. Vertebrae and ribs of modern reptiles. *In* Gans, C., A.d'A. Bellairs, and T.S. Parsons (eds.), Biology of the Reptilia. Vol. 1:201–310. Academic Press, New York.

———, and J.-C. Rage. 1972. Les Erycinae fossils de France (Serpentes, Boidae). Compréhension et histoire de la sous-famille. Ann. Paléontol. (Vert.), 58:1–46.

Holman, J.A. 1979. A review of North American Tertiary snakes. Publ. Mus. Michigan State Univ. Paleontol. Ser., 1:200–260.

Hull, D.L. 1964. Consistency and monophyly. Syst. Zool., 13:1-11.

———. 1988. Science as a Process. University of Chicago Press, Chicago.

IUCN/UNEP/WWF. 1987. Madagascar, an environmental profile. Edited by M.D. Jenkins. IUCN, Gland, Switzerland.

Jayne, B.C. 1982. Comparative morphology of the semispinalis-spinalis muscle of snakes and correlations with locomotion and constriction. J. Morph., 171:83-96.

Johnson, R.G. 1955. The adaptive and phylogenetic significance of vertebral form in snakes. Evol., 9:367-388.

Kamal, A.M., and H.G. Hammouda. 1965a. On the laterosphenoid boine in Ophidia. Anat. Anz., 116:116–123.

———, and ———. 1965b. The development of the skull of *Psammophis sibilans*. J. Morph., 116:197–309.

———, and ———. 1965c. The chondrocranium of the snake *Eryx jaculus*. Acta Zool., Stockholm, 46:167–208.

Kluge, A.G. 1983. Cladistic relationships among gekkonoid lizards. Copeia, 1983:465–475.

———. 1984. The relevance of parsimony to phylogenetic inference. *In* Duncan, T., and T.F. Stuessy (eds.), Cladistics: Perspectives on the Reconstruction of Evolutionary History: 24–38. Columbia Univ. Press, New York.

———. 1985. Ontogeny and phylogenetic systematics. Cladistics, 1:13–27.

———. 1988a. Relationships of the Cenozoic boine snakes *Paraepicrates* and *Pseudoepicrates*. J. Vert. Paleontol., 8:229–230.

———. 1988b. The characterization of ontogeny. *In* Humphries, C.J. (ed.), Ontogeny and Systematics: 57–81. Columbia Univ. Press, New York.

———. 1989a. Parsimony in vicariance biogeography: A quantitative method and a Greater Antillean example. Syst. Zool., 37:315-328.

———. 1989b. A concern for evidence and a phylogenetic hypothesis of relationships among *Epicrates* (Boidae, Serpentes). Syst. Zool., 38:7–25.

———. 1990. Species as historical individuals. Biol. Philos., 5:417–431.

———. ms. Pythonine snake phylogeny.

———, and J.S. Farris. 1969. Quantitative phyletics and the evolution of anurans. Syst. Zool., 18:1–32.

———, and R.E. Strauss. 1985. Ontogeny and systematics. Annu. Rev. Ecol. Syst., 16:247–268.

Langebartel, D.A. 1968. The hyoid and its associated muscles in snakes. Illinois Biol. Monogr., 38:1–156.

Langhammer, J.K. 1983. A new subspecies of *Boa constrictor, Boa constrictor melanogaster,* from Ecuador (Serpentes: Boidae). Trop. Fish Hobbyist, 1983:70–79.

List, J.C. 1966. Comparative osteology of the snake families Typhlopidae and Leptotyphlopidae. Illinois Biol. Monogr., 36:1-112.

Luppa, H. 1977. Histology of the digestive tract. *In* Gans, C., and T.S. Parsons (eds.), Biology of the Reptilia. Vol. 6:225–313. Academic Press, New York.

Mabee, P.M. 1989. Assumptions underlying the use of ontogenetic sequences for determining character state order. Trans. Amer. Fisheries Soc., 118:151–158.

Maddison, W.P., M.J. Donoghue, and D.R. Maddison. 1984. Outgroup analysis and parsimony. Syst. Zool., 33:83-103.

Maderson, P.F.A. 1970. The distribution of specialized labial scales in the Boidae. *In* Gans, C., and T.S. Parsons (eds.), Biology of the Reptilia. Vol. 2:301–304. Academic Press, New York.

Marx, H., and G.B. Rabb. 1970. Character analysis: An empirical approach applied to advanced snakes. J. Zool., London, 161:525–548.

McDowell, S.B. 1967. Osteology of the Typhlopidae and Leptotyphlopidae: A critical review. Copeia, 1967:686–692.

———. 1972. The evolution of the tongue of snakes and its bearing on snake origins. *In* Dobzhansky, T., M.K. Hecht, and W.C. Steere (eds.), Evolutionary Biology. Vol. 6:191–273. Appleton-Century-Crofts, New York.

———. 1975. A catalogue of the snakes of New Guinea and the Solomons, with special reference to those in the Bernice P. Bishop Museum. Part II. Anilioidea and Pythoninae. J. Herpetol., 9:1–79.

———. 1979. A catalogue of the snakes of New Guinea and the Solomons, with special reference to those in the Bernice P. Bishop Museum. Part III. Boinae and Acrochordoidea (Reptilia, Serpentes). J. Herpetol., 13:1–92.

———. 1987. Systematics. *In* Seigel, R.A., J.T. Collins, and S.S. Novak (eds.), Snakes: Ecology and Evolutionary Biology: 3–50. Macmillan, New York.

———, and C.M. Bogert. 1954. The systematic position of *Lanthanotus* and the affinities of the anguinomorphan lizards. Bull. Amer. Mus. Nat. Hist., 105:1–142.

Mehrtens, J.M. 1987. Living Snakes of the World. Sterling, New York.

Mengden, G.A., and A.D. Stock. 1980. Chromosomal evolution in serpentes; a comparison of G and C chomosome banding patterns of some colubrid and boid genera. Chromosoma, 79:53–64.

Mertens, R. 1972. Madagaskars herpetofauna und die kontinentaldrift. Zool. Meded. (Leiden), 46:91–98.

Meszler, R.M. 1970. Correlation of ultrastructure and function. *In* Gans, C., and T.S. Parsons (eds.), Biology of the Reptilia. Vol. 2:305–314. Academic Press, New York.

Mickevich, M.F. 1982. Transformation series analysis. Syst. Zool., 31:461–478.

Mosauer, W. 1935. The myology of the trunk region of snakes and its significance for ophidian taxonomy and phylogeny. Publ. Univ. Calif. Los Angeles, Biol. Sci., 1:81–120.

Nelson, G. 1989. [Review of] Reconstructing the past: Parsimony, evolution, and inference, by Elliot Sober. Syst. Zool., 38:293–294.

Oelrich, T.M. 1956. The anatomy of the head of *Ctenosaura pectinata* (Iguanidae). Misc. Publ. Mus. Zool., Univ. Michigan, 94:1–122.

Patterson, C. 1982. Morphological characters and homology. *In* Joysey, K.A., and A.E. Friday (eds.), Problems in Phylogenetic Reconstruction: 21–74. Academic Press, New York.

Peters, J.A., and B. Orejas-Miranda. 1970. Catalogue of the Neotropical Squamata: Part I. Snakes. Bull. U.S. Natl. Mus., (297):1–347.

Petzold, H.-G. 1984. Die Anakondas: Gattung *Eunectes*. Ziemsen, Wittenberg.

Platnick, N.I. 1989. An empirical comparison of microcomputer parsimony programs, II. Cladistics, 5:145–161.

Rage, J.-C. 1984. Encyclopedia of Paleoherpetology. Serpentes. G. Fischer, New York.

———. 1987. Fossil history. *In* Seigel, R.A., J.T. Collins, and S.S. Novak (eds.), Snakes: Ecology and Evolutionary Biology: 51–76. Macmillan, New York.

Rieppel, O. 1976. The homology of the laterosphenoid bone in snakes. Herpetologica, 32:426–429.

———. 1977a. Studies on the skull of the Henophidia (Reptilia: Serpentes). J. Zool., London, 181:145–173.

———. 1977b. The naso-frontal joint in *Anilius scytale* (Linnaeus) and *Cylindrophis rufus* (Schlegel): Serpentes, Aniliidae. J. Nat. Hist., 11:545–553.

———. 1978a. The evolution of the naso-frontal joint in snakes and its bearing on snake origins. Z. Zool. Syst. Evolutionsforsch., 16:14–27.

———. 1978b. A functional and phylogenetic interpretation of the skull of the Erycinae (Reptilia, Serpentes). J. Zool., London, 186:185–208.

———. 1978c. The phylogeny of cranial kinesis in lower vertebrates, with special reference to the Lacertilia. Neues Jahrb. Geol. Palaeontol. Abhandl., 156:353–370.

———. 1979a. Ontogeny and the recognition of primitive character states. Z. Zool. Syst. Evolutionsforsch., 17:57-61.

———. 1979b. The classification of primitive snakes and the testability of phylogenetic theories. Biol. Zbl., 98:537–552.

———. 1979c. The evolution of the basicranium in the Henophidia (Reptilia: Serpentes). Zool. J. Linn. Soc., 66:411–431.

———. 1979d. A cladistic classification of primitive snakes based on skull structure. Z. Zool. Syst. Evolutionsforsch., 17:140-150.

———. 1980a. The sound-transmitting apparatus in primitive snakes and its phylogenetic significance. Zoomorphology, 96:45–62.

———. 1980b. The phylogeny of anguinomorph lizards. Denkschr. Schweiz. Naturforsch. Ges., 94:1–86.

———. 1987. Pattern and process: The early classification of snakes. Biol. J. Linn. Soc., 31:405–420.

———. 1988. A review of the origin of snakes. *In* Hecht, M.K., B. Wallace, and G.T. Prance (eds.), Evolutionary Biology. Vol. 22:37–130. Plenum, New York.

Schmidt, K.P. 1950. Modes of evolution discernible in the taxonomy of snakes. Evol., 4:79–86.

Schwaner, T.D., and H.C. Dessauer. 1981. Immunodiffusion evidence for the relationships of Papuan boids. J. Herpetol., 15:250–253.

Schwartz, A., and R. Thomas. 1975. A check-list of West Indian amphibians and reptiles. Carnegie Mus. Nat. Hist. Spec. Publ., 1:1–216.

Schwenk, K. 1988. Comparative morphology of the lepidosaur tongue and its relevance to squamate phylogeny. *In* Estes, R., and G. Pregill (eds.), Phylogenetic Relationships of the Lizard Families: Essays Commemorating Charles L. Camp: 569–598. Stanford Univ. Press, Stanford, California.

Seberg, O. 1989. The Seventh Annual Meeting of the Willi Hennig Society. Cladistics, 5:183–191.

Shaw, C.E., and S. Campbell. 1974. Snakes of the American West. Knopf, New York.

Shine, R. 1985. The evolution of viviparity in reptiles: An ecological analysis. *In* Gans, C., and F. Billett (eds.), Biology of the Reptilia. Vol. 15B:605–694. Wiley, New York.

Smith, H.M., R.B. Smith, and H.L. Sawin. 1977. A summary of snake classification (Reptilia, Serpentes). J. Herpetol., 11:115–121.

———, and R. Warner. 1948. Evolution of the ophidian hyobranchium and its bearing on classification. Herpetologica, 4:189–193.

Smith, L.A. 1981a. A revision of the python genera *Aspidites* and *Python* (Serpentes: Boidae) in Western Australia. Rec. West. Aust. Mus., 9:211–226.

———. 1981b. A revision of the *Liasis olivaceus* species-group (Serpentes: Boidae) in Western Australia. Rec. West. Aust. Mus., 9:227–233.

———. 1985. A revision of the *Liasis childreni* species-group (Serpentes: Boidae). Rec. West. Aust. Mus., 12:257–276.

Smith, M.A. 1943. The fauna of British India, Ceylon and Burma. Reptilia and Amphibia. Vol. 3, Serpentes. Taylor and Francis, London.

Sober, E. 1988. Reconstructing the Past: Parsimony, Evolution, and Inference. MIT Press, Cambridge, Massachusetts.

Stimson, A.F. 1969. Liste der rezenten amphibien und reptilien. Boidae (Boinae + Bolyeriinae + Loxoceminae + Pythoninae). Das Tierreich, 89:1–49.

Swofford, D.L., and W.P. Maddison. 1987. Reconstructing ancestral character states under Wagner parsimony. Math. Biosci., 87:199–229.

———, and G.J. Olsen. 1990. Phylogeny reconstruction. *In* Hillis, D.M., and C. Moritz (eds.), Molecular Systematics: 411–501. Sinauer Assoc., Sunderland, Massachusetts.

Tolson, P.J. 1987. Phylogenetics of the boid snake genus *Epicrates* and Caribbean vicariance theory. Occ. Pap. Mus. Zool., Univ. Michigan, 715:1–68.

Underwood, G. 1967. A contribution to the classification of snakes. Publ. Brit. Mus. (Nat. Hist.)., 653:1–179.

———. 1976. A systematic analysis of boid snakes. *In* Bellairs, A.d'A., and C.B. Cox (eds.), Morphology and Biology of Reptiles. Linn. Soc. Symp., 3:151–175.

———, and A.F. Stimson. 1990. A classification of the pythons (Serpentes, Pythoninae). J. Zool., London, 221:565–603.

Warner, R. 1946. Pectoral girdle vs. hyobranchia in snake genera *Liotyphlops* and *Anomalepis*. Science, 103:720–723.

Watrous, L.E., and Q.D. Wheeler. 1981. The out-group comparison method of character analysis. Syst. Zool., 30:1–11.

Welch, K.R.G. 1988. Snakes of the Orient: A Checklist. Krieger Publ. Co., Malabar, Florida.

Wiley, E.O. 1981. Convex groups and consistent classifications. Syst. Bot., 6:346–358.

Zacharias, H.C.E. 1897. Die phylogenese der kopfschilder bei den boiden. Zool. Jahrb., 10:56–90.

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APPENDIX[4]

SKELETAL MATERIAL EXAMINED

ANILIOIDS

Anilius scytale: KU 140152 (c/s); UMMZ 149661 (skull, mand.), 183253.
Cylindrophis rufus: UMMZ 129399, 149662 (skull, mand.), 155827.

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[4] Complete dried skeleton unless indicated otherwise. Abbreviations: c/s = cleared and stained; disart. = disarticulated; incomp. vert. col. = incomplete vertebral column; mand. = mandibles. See Materials and Methods section for abbreviations of repositories.

BOINES

Acrantophis dumerili: BMNH 92.2.29.20 (skull, mand.); FMNH 228340; UMMZ 190701–2, 190705–6.

Acrantophis madagascariensis: AMNH 60730 (skull, mand.).

Boa constrictor: UMMZ 130168, 130979, 134132, 149638–41, 149646–8, 155334–6, 155337–8 (skull, mand., incomp. vert. col.), 155339, 155347, 178660, 182031, 183481, 184028–42 (c/s), 189463 (skull, mand.).

Candoia aspera: AMNH 59078 (skull, mand.), 62474 (skull, mand.), 66344 (skull, mand.), 74508 (skull, mand.), 74992 (skull, mand.), 82342 (skull, mand.), 85660 (skull, mand.).

Candoia bibroni: AMNH 29248 (skull, mand.), 40413 (skull, mand.), 40439 (skull, mand.), 40451 (skull, mand.), 41742 (skull, mand.), 42004 (skull, mand.), 42160 (skull, mand.); UMMZ 190708; UTACV 7492 (c/s), 7580 (c/s).

Candoia carinata: AMNH 5070 (skull, mand.), 36404 (skull, mand.), 40406 (skull, mand.), 40433 (skull, mand.), 42041 (skull, mand.), 42056 (skull, mand.), 42062 (skull, mand.), 42067 (skull, mand.), 42205 (skull, mand.), 42240 (skull, mand.), 42247 (skull, mand.), 62473 (skull, mand.), 70645 (skull, mand.), 71512 (skull, mand.), 76667 (skull, mand.), 76686 (skull, mand.), 92068 (skull, mand.); UMMZ 138820, 170378, 181089, 181672–3 (c/s), 182529–33.

Corallus annulatus: AMNH 73252 (skull, mand.), 114496 (skull, mand., incomp. vert. col.); CM 91919 (disart.); MCZ 37862 (skull, mand., incomp. vert. col.); UMMZ 149649.

Corallus caninus: AMNH 57788 (skull, mand., incomp. vert. col.), 57816 (skull, mand., incomp. vert. col.), 63587 (skull, mand., incomp. vert. col.), 64417 (skull, mand.), 64562 (skull, mand., incomp. vert. col.), 73347 (skull, mand., incomp. vert. col.), 103851 (skull, mand., incomp. vert. col.); CM 49330, 91874 (skull, mand.), 116978; FMNH 22339 (skull, mand.), 31025 (skull, mand.), 223193, 229856; MVZ 79306, 96000; FSM 56081, 60830, 61486; UMMZ 149650, 169669, 176798, 190684; UTACV 939, 941–2.

Corallus enydris: AMNH 53400 (skull, mand., incomp. vert. col.), 57786 (skull, mand.), 57809 (skull, mand., incomp. vert. col.), 57812 (skull, mand., incomp. vert. col.), 74832 (skull, mand.), 118702 (skull, mand.); CM 38723; FMNH 4009 (skull, mand.), 31326 (skull, mand.), 98880, 229903–5; FSM 56402, 60831 (disart.), 63847; UMMZ 128028, 128062, 149651, 149652 (skull, mand.), 184240–48 (c/s).

Epicrates angulifer: UMMZ 174401 (skull, mand., incomp. vert. col.; pelvic region c/s), 174402 (c/s), 176921, 176923, (skull, mand., incomp. vert col.), 176928, 176934, 179399 (c/s).

Epicrates cenchria: AMNH 62577 (skull, mand.), 71153, 114716; UMMZ 146097, 149653–4, 155341, 168414, 169873, 174670, 176971–2, 180341, 190707, 190328–9.

Epicrates chrysogaster: UMMZ 173406, 173410 (c/s), 176916, 176919–20, 176925, 176927.

Epicrates exsul: UMMZ 176910, 176913, 176915, 176941, 176943–54, 177980–81, 177984, 177995, 179327, 179338–9 (c/s), 179368 (c/s), 179400 (c/s), 182285–6 (c/s).

Epicrates fordii: UMMZ 173415–8, 173426 (c/s), 173470, 173473 (c/s).

Epicrates gracilis: UMMZ 172160, 173436, 173469, 176917–8, 176926, 176970, 179389–91 (c/s).

Epicrates inornatus: UMMZ 173440, 176906–9, 176931, 176956, 176966–7, 176969, 176976–9, 177979, 177982–3, 177985, 177990, 177993, 177996–7, 178003, 179340 (c/s), 179344–5 (c/s), 179367 (c/s), 179392–3 (c/s), 179404–5, 180348, 180363, 180365–6, 180369.

Epicrates monensis: UMMZ 177006 (skull, mand., incomp. vert. col.), 183119–20 (c/s).

Epicrates striatus: UMMZ 131052, 149655–6, 151091–2, 173456 (skull, mand.), 173457–68, 175404, 176914, 176922, 176929–30, 176933, 176942, 176955, 176957–8, 176963–5, 176973, 176984, 178004–5, 178007, 178530, 178873, 179333, 179401, 180362, 180364, 180373–4, 181078–9, 182528 (c/s).

Epicrates subflavus: UMMZ 176911–2, 176932, 176935–8, 176939, 176940, 176959–62, 176968, 176983, 176985, 177986–9, 177991–2, 177994, 177998–800, 178576, 178874, 179328–31, 179335–7 (c/s), 179346–66 (c/s), 179369–88 (c/s), 179394–8 (c/s), 179402–3, 180342–7, 180367–8, 180416–22 (c/s), 180468 (c/s), 181080–1, 181121.

Eunectes deschauenseei: USNM 135453–4 (skull, mand., incomp. vert. col.).

Eunectes murinus: AMNH 29349–50 (skull, mand., incomp. vert. col.), 53572 (skull, mand., incomp. vert. col.), 54158 (skull, mand., incomp. vert. col.), 62559 (skull, mand.); CM 41222 (skull, mand., incomp. vert. col.), 61619 (skull, mand., incomp. vert. col.); FMNH 8546 (skull, mand.), 22776 (skull, mand.), 31665 (skull, mand.), 39465 (skull, mand.), 45700; MVZ 96003, 96004 (incomp. vert. col.); FSM 2210 (skull, mand., incomp. vert. col.), 20636 (skull, mand.), 21216 (skull, mand., incomp. vert. col.), 57041; UMMZ 130169, 130171; USNM 220301 (skull, mand.), 220302.

Eunectes notaeus: CM 112284; FMNH 9084 (skull, mand.), 229591, 229857–8, 229918 (skull, mand., incomp. vert. col.), 229919–21; UMMZ 182035–6.

Eunectes sp.: UMMZ 130868.

Sanzinia madagascariensis: UMMZ 131713, 149663 (skull, mand.).

Xenoboa cropanii: AMNH 92997 (skull, mand., incomp. vert. col.).

BOLYERIINES

Bolyeria multocarinata: BMNH 70.11.30.4A-B (skull, mand., 2 vert.).

Casarea dussumieri: BMNH 70.11.30.4C (skull, mand.).

CAENOPHIDIANS

Acrochordus granulatus: UMMZ 149667, 185885.

Acrochordus javanicus: UMMZ 128026, 128566, 155818–20, 169871, 169876.

Bothrops asper: UMMZ 155831.

Bungarus fasciatus: UMMZ 127306 (skull, mand., incomp. vert. col.).

Clelia clelia: UMMZ 149692.

Crotalus atrox: UMMZ 176246.

Drymarchon corais: UMMZ 169872.

Pelamis platurus: UMMZ 174479.

Spilotes pullatus: UMMZ 128030.

ERYCINES

Calabaria reinhardtii: FMNH 191123; UMMZ 149642 (skull, mand., incomp. vert. col.), 183242.

Charina bottae: UMMZ 135013–6, 149643, 170951 (c/s), 171470 (c/s), 171473 (c/s), 173360.

Eryx colubrinus: UMMZ 186019, 190339–40, 190384, 190412–3.

Eryx conicus: UMMZ 128037.

Eryx jaculus: BMNH 1930.5.8.19 (skull, mand.); UMMZ 190419–21 (c/s).

Eryx jayakari: BMNH 1909.10.15.8 (skull, mand).

Eryx johnii: BMNH 1930.5.8.34 (skull, mand.).

Eryx miliaris: UMMZ 190696–7.

Eryx tataricus: UMMZ 190414.

Lichanura trivirgata: UMMZ 131053, 134130, 189644; UTACV 9432 (c/s), 10062 (c/s).

PYTHONINES

Aspidites melanocephalus: AMNH 69302 (skull, mand.), 76200 (skull, mand.); BMNH 1924.1.24.15 (skull, mand.), 1946.8.1.2 (incomp. vert. col.); CAS uncatalogued (skull, mand., incomp. vert. col.); DU R-3619 (skull, mand.); UMMZ 190781 (skull, mand.).

Aspidites ramsayi: UMMZ 190782 (skull, mand.).

Morelia albertisii: FMNH 218609; UTACV 970 (c/s).

Morelia amethistina: DU R-3480 (skull, mand.), R-3768 (skull, mand.); UMMZ 132343, 132345.

Morelia boa: AMNH 44002 (skull, mand.); FMNH 21729; UMMZ 190703–4.

Morelia childreni: UMMZ 190779 (skull, mand.).

Morelia mackloti: KU 182381 (c/s).

Morelia maculosa: DU R-3639 (skull, mand.); UMMZ 190775 (skull, mand.), 190777 (skull, mand.).

Morelia olivacea: UMMZ 190780 (skull, mand.).

Morelia spilota: DU R-3610 (skull, mand.); UMMZ 131714 (skull, mand., incomp. vert. col.), 132348, 190710–13, 190784–7, 190788 (skull, mand., incomp. vert. col.).

Morelia viridis: UMMZ 128025, 128060, 149644–5, 150698, 151090.

Python anchietae: UMMZ 190773 (skull, mand.).

Python curtus: UMMZ 145019, 153087; UTACV 732 (c/s).

Python molurus: UMMZ 129407, 155835–6, 169895–6, 170385 (incomp. vert. col.), 181669–71.

Python regius: UMMZ 149660, 155833, 176805, 186004, 188066, 190111; UTACV 7330–31 (c/s), 8195 (c/s).

Python reticulatus: UMMZ 128051, 151095, 155332–3 (skull, mand., incomp. vert. col.), 173474; UTACV 8186 (c/s), 8206–7 (c/s).

Python sebae: UMMZ 61400 (disart. skull, mand.), 61410 (skull, mand.).

Python timoriensis: KU 158546 (c/s); UMMZ 190771–2 (skull, mand.); UTACV 6970 (c/s).

Python sp.: UMMZ 149659 (incomp. vert. col.).

TROPIDOPHIINES

Exiliboa placata: AMNH 102892 (skull, mand.); UMMZ 183573 (skull, mand.).

Trachyboa boulengeri: UMMZ 183143 (skull, mand., incomp. vert. col.).

Trachyboa gularis: AMNH 28982 (disart. skull).

Tropidophis melanurus: UMMZ 149664 (skull, mand., incomp. vert. col.), 182509–13 (c/s).

Tropidophis pardalis: UMMZ 149665 (skull, mand., incomp. vert. col.), 150788–90 (skull, mand., incomp. vert. col.).

Ungaliophis continentalis: UMMZ 149666 (skull, mand., incomp. vert. col.), 190698–700.

OTHER TAXA

Loxocemus bicolor: UMMZ 128027, 132051, 149657–8.

Xenopeltis unicolor: UMMZ 131952.