A Concern for Evidence and a Phylogenetic Hypothesis of Relationships Among Epicrates (Boidae, Serpentes)

Arnold G. Kluge

Systematic Zoology, Vol. 38, No. 1 (Mar., 1989), 7-25.

Stable URL:
http://links.jstor.org/sici?sici=0039-7989%28198903%2938%3A1%3C7%3AACFEAA%3E2.0.CO%3B2-T

Systematic Zoology is currently published by Society of Systematic Biologists.

Syst. Zool., 38(1):7–25, 1989

A CONCERN FOR EVIDENCE AND A PHYLOGENETIC HYPOTHESIS OF RELATIONSHIPS AMONG *EPICRATES* (BOIDAE, SERPENTES)

ARNOLD G. KLUGE

Museum of Zoology, and Department of Biology, University of Michigan, Ann Arbor, Michigan 48109

Abstract.—Character congruence, the principle of using all the relevant data, and character independence are important concepts in phylogenetic inference, because they relate directly to the evidence on which hypotheses are based. Taxonomic congruence, which is agreement among patterns of taxonomic relationships, is less important, because its connection to the underlying character evidence is indirect and often imperfect. Also, taxonomic congruence is difficult to justify, because of the arbitrariness involved in choosing a consensus method and index with which to estimate agreement.

High levels of character congruence were observed among 89 biochemical and morphological synapomorphies scored on 10 species of *Epicrates*. Such agreement is consistent with the phylogenetic interpretation attached to the resulting hypothesis, which is a consensus of two equally parsimonious cladograms: (*cenchria* (*angulifer* (*striatus* ((*chrysogaster*, *exsul*) (*inornatus*, *subflavus*) (*gracilis* (*fordii*, *monensis*)))))). Relatively little (11.4%) of the character incongruence was due to the disparity between the biochemical and morphological data sets. Each of the clades in the consensus cladogram was confirmed by two or more unique and unreversed novelties, and six of the eight clades were corroborated by biochemical and morphological evidence. Such combinations of characters add confidence to the phylogenetic hypothesis, assuming the qualitatively different kinds of data are more likely to count as independent than are observations drawn from the same character system. Most of the incongruence occurred in the skeletal subset of characters, and much of that independent evolution seemed to be the result of paedomorphosis. [Biochemical data; character congruence; character independence; *Epicrates*; evidence; morphological data; paedomorphosis; phylogenetic systematics; taxonomic congruence; total evidence.]

The goals of cladistics and phenetics are different. The former estimates phylogeny (Hennig, 1966), the latter seeks stability and convenience in classification (Sokal, 1986:424). Unfortunately, these objectives have become confused, especially where stability is concerned. For example, Hillis (1987:35) stated that "[c]lassifications are best based on information in common among multiple data sets (i.e., consensus trees), whereas the best estimate of phylogeny and best estimate of character evolution are represented in the analysis of the combined data sets." The importance of a conservative information storage-retrieval system is undeniable (e.g., International Code of Zoological Nomenclature, 1985:3), and pheneticists sought justification for their methods in this simple truth (Sokal and Sneath, 1963). Even cladists attributed some significance to stability per se, because the lack of it confounds attempts to discover the single historical pattern (Schuh and Farris, 1981).

Not unexpectedly, cladists responded (e.g., Farris, 1971) to the proposition that phenetic methods produce more stable classifications (e.g., Sokal and Sneath, 1963: 264). Analytical precision was demanded by the contestants, and an incredible array of consensus methods and indexes were developed (see lists below). It is important to bear in mind that only information on taxonomic grouping can be used to evaluate the pheneticists' claims, because character congruence is difficult to judge in phenetic analyses.

Eventually, the controversy over stability became a relative issue, with cladists arguing greater stability for classifications produced by their methods, as if stability was a goal of phylogenetic systematics. Further, Nelson and Platnick (1981:219; see also Nelson, 1979) attempted to justify cla-

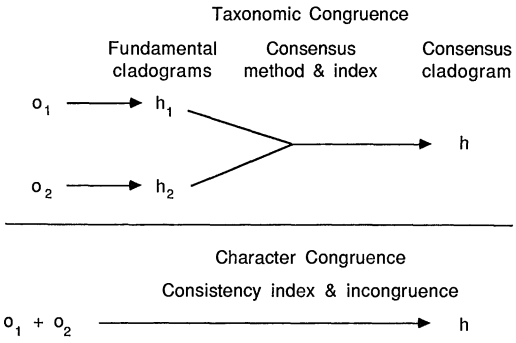

FIG. 1. The distinction between taxonomic and character congruence is illustrated in terms of the nature of the evidence employed in forming the consensus cladogram. $o_1 + o_2$ is the total evidence available; whereas o_1 and o_2 are the parts of that total. h_1, h_2, and h are the resulting cladograms.

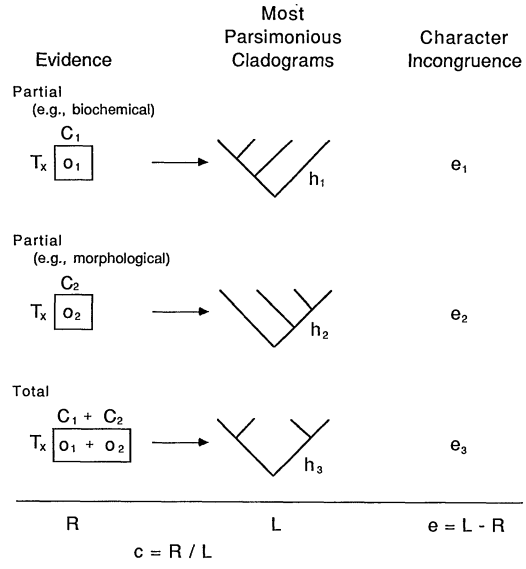

FIG. 2. The relationship between evidence, most parsimonious cladograms and character incongruence. For a given set of taxa, T_x, three sets of character data are analyzed, C_1, C_2, and $C_1 + C_2$. These data sets are denoted o_1, o_2, and $o_1 + o_2$, respectively. There is one or more most parsimonious cladograms, h_1, h_2, and h_3, and incongruence or extra number of steps, e_1, e_2, and e_3, for each data set. R is the minimum number of synapomorphies in a data set, and L is the number of transformations necessary to explain all of the evidence simultaneously on a cladogram. c is the consistency index. See text for further explanation.

distic parsimony with stability, viz., being able "to reach the same phylogenetic hypotheses from different evidential starting points" (Sober, 1988:chapt. 4, p. 73). As Sober succinctly put it (1988:chapt. 4, pp. 75 and 77), "Stability bears on the standing of *hypotheses*, not on the *methods* used to select them." Moreover, "phylogenetic hypotheses should not be stable under the addition of new characters, if those characters in fact suffice to undermine the phylogenies that were accepted earlier." Thus, it seems that stability of classification has been a red herring for cladists.

During this diversion, many phylogeneticists lost sight of the importance of character congruence. In addition, other concepts pertaining to evidence, such as the principle of total evidence and character independence, were given little attention. I will take this opportunity to review these topics, and apply the relevant ideas and methods to estimating the phylogeny of boid snakes belonging to *Epicrates*.

CONGRUENCE

Taxonomic congruence involves deriving a consensus object from a comparison of two or more fundamental topologies (Nelson, 1979), and measuring the agreement of the taxonomic groups in the fundamental branching patterns (Fig. 1). Consensus methods are used in the former operation, consensus indexes are used in the latter (Day and McMorris, 1985). The actual character evidence on which the fundamental topologies are based does not enter into either enterprise. Fundamental topologies may be the product of different clustering algorithms (phenetic, cladistic), qualitatively different data sets (biochemical, morphological; Fig. 2), or random samples of characters from the same data set. A fundamental topology may be compared to a hypothetical, fully unresolved, pattern of taxonomic relationships, viz., one totally lacking information on grouping.

A large number of consensus methods and indexes have been used to judge taxonomic congruence (Day, 1985; Day and McMorris, 1985). Adams (Adams, 1972), Nelson (Nelson, 1979; Sokal and Rohlf, 1981), Majority Rule (Margush and McMorris, 1981), M_1 (McMorris and Neu-

mann, 1983), Generalized Intersection (Neumann, 1983), and s-Consensus (Stinebrickner, 1984) constitute the different consensus methods developed thus far. Consensus indexes are even more numerous, and it is convenient to group them into functional classes: informative component metrics (Nelson, 1979; Colless, 1980; Day, 1983; Stinebrickner, 1984), distortion coefficients (Farris, 1973; Mickevich, 1978; Nelson, 1979; Schuh and Farris, 1981; Rohlf, 1982), distance metrics (Rohlf, 1982), probabilistic measures (Nelson, 1979; Rohlf, 1982), and matrix correlations (Sneath and Sokal, 1973). Some of these consensus methods and indexes are implemented in Swofford's (1985) Contree computer program.

Like phenetic algorithms, consensus methods and indexes do not always give the same result when applied to a particular data set. This means that it is difficult to claim repeatability, and there appears to be no biological criterion for choosing a particular consensus method or index. If objective choices are made at all they are based on avoiding unacceptable mathematical properties attributed to some consensus methods and indexes (Rohlf, 1982; Day and McMorris, 1985).

Farris (1979, 1980a, b, 1982) and Mickevich (1978, 1980) related stability to phylogenetic systematics by way of descriptive efficiency (informativeness) and explanatory power (Miyamoto, 1985). However, as they pointed out (Mickevich and Farris, 1981:364), the details of how information on taxonomic grouping is assessed is less important than evaluating the degree of conflict in the evidence itself. This is obvious from the fact that stability alone is not a sufficient criterion (Sober, 1988): a stable classification can always be obtained by pact, if that taxonomy need not appeal to any observations and underlying theory.

Cladists justify their use of character congruence (Fig. 1) by relating characters and their states to more inclusive theories of homology and phylogeny. Cladists take the position that congruent characters confirm a phylogenetic hypothesis, *provided they are independent*. The more independent congruent characters there are for a clade, the better supported it is as a phylogenetic hypothesis.

Character congruence is usually evaluated in phylogenetic studies with cladistic parsimony, and the consistency index (c) estimates how well all of the character evidence in a given study fits a hypothesis of taxonomic relationships (Fig. 2; Kluge and Farris, 1969). This measure of goodness of fit is calculated as the minimum number of synapomorphies in the data set (R), where each character's hypothesized history is considered separately, divided by the minimum number of transformations necessary to explain all of the evidence simultaneously on a cladogram (L). The absolute difference between R and L is the number of extra steps (Fig. 2), hypothesized independently evolved traits, and the larger the consistency index the better the hypothesis of relationships is said to fit the evidence embodied in the data set. All hypotheses have a consistency index. The most parsimonious hypothesis of relationships has the largest consistency index.

It has become standard practice to eliminate all autapomorphies when calculating the consistency index, because novelties that are coded as unique in a data set do not have the potential to contribute extra steps on the cladogram. The number of autapomorphies *must* be held constant when comparing the consistencies of different data sets, although I doubt such a practice can be justified, because the index is positively correlated with the number of autapomorphies.

Character congruence has two aspects, confirmation (corroboration) and disconfirmation. The latter is usually referred to as incongruence, and it is measured in terms of number of extra steps. As exemplified below, more detailed assessments of incongruence and confirmation are possible when different sets of characters are compared (e.g., biochemical and morphological) and when it is reasonable to assume their independent evolution, respectively.

The F-ratio (derived from the f-statistic

of Farris, 1972) and the D-measure (Brooks et al., 1986) have also been used to assess goodness of fit of data to phylogenetic hypotheses. The relationship of the consistency index to parsimony, one of the cornerstones of phylogenetic inference, is evident in the minimization of the number of extra steps; however, equally convincing justifications for the F-ratio and the D-measure are not obvious. While Brooks et al. (1986:571) claimed that the latter criterion measures "historical constraint," a property previously identified with parsimony algorithms that interpret as many shared derived conditions as homologues as is possible, it remains to be demonstrated that these two uses of constraint are conceptually equivalent. I doubt the strict equivalence, because the optimum values extracted from these three goodness of fit criteria are not always associated with the same cladogram. Minimally, I am forced to conclude that the three metrics differ in their ability to measure constraint accurately. In any case, Brooks et al. (1986) recommended that the F-ratio and D-measure be used as the bases for choosing among equally most parsimonious hypotheses of relationship identified with the consistency index. Furthermore, it must be recognized that there will be a range of F-ratio and D-measure values for phylogenetic hypotheses, even the most parsimonious patterns, when character histories cannot be optimized unambiguously on those cladograms.

Character congruence is concerned with *patterns among characters*, whereas taxonomic congruence focuses on *patterns among taxa*. From another perspective, character congruence and taxonomic congruence differ in terms of amount of evidence and resolution involved (Miyamoto, 1985). Character congruence seeks a fully resolved hypothesis based on all the evidence, whereas taxonomic congruence looks for a less resolved hypothesis that two or more sets of evidence agree about. Consider the hypothetical example in Fig. 2, which consists of three sets of synapomorphies (o_1, o_2, and $o_1 + o_2$) and three corresponding best fitting cladograms (h_1, h_2, and h_3). o_1 and o_2 confirm each other if h_3 is not much different from h_1 or from h_2. If the consensus of h_1 and h_2 contains many clades then o_1 and o_2 will be to that extent congruent; however, the consensus of h_1 and h_2 need not be the same as h_3.

TOTAL EVIDENCE AND CHARACTER INDEPENDENCE

Carnap (1950:211) stated that "the total evidence available must be taken as a basis for determining the degree of confirmation." This rule of the methodology of induction forms a "partial explication of conditions governing rational belief and rational choice" (Hempel, 1965:66). "Broadly speaking, we might say that according to this requirement, the credence which it is rational to give to a statement at a given time must be determined by the degree of confirmation, or the logical probability, which the statement possesses on the total evidence available at the time. Alternatively, that credence may be determined by reference to any part of the total evidence which gives to the statement the same support or probability as the total evidence: In this case, the omitted portion of the total evidence is said to be *inductively irrelevant* to the statement, relative to the evidence actually used" (Hempel, 1965:64). Good (1983:178–180) used a simple mathematical theorem to demonstrate that the principle of total evidence follows from the principle of rationality.

The principle of total evidence is an important maxim in phylogenetic systematics, because alternatives to using all available evidence must be carefully considered. For example, in order to exclude logically consistent evidence (e.g., biochemical or morphological data; extinct or extant taxa: Gauthier et al., 1988), the investigator must argue that "the premises constitute either the total evidence e available at the time or else a part of e which supports the conclusion to the same extent as does e" (Hempel, 1965:64). Thus, even less severe weighting, as well as partitioning evidence, requires justification. Furthermore, including all relevant evidence can be seen as a harmless activity, unless one is pre-

pared to argue a priori that certain evidence will confound the analysis and must therefore be eliminated.

The assumption of independence of evidence exists in all empirical sciences. Ideally in phylogenetic systematics, each synapomorphy in the character matrix is assumed to count as a *separate* piece of evidence, viz., has the potential to confirm, or disconfirm, taxonomic relationships independent of all other synapomorphies considered. This is important, because choice of a phylogenetic proposition is based on the largest number of synapomorphies that can be hypothesized as homologues. In actual practice, independence of evidence can be viewed as a weighting criterion—the phylogenetic hypothesis confirmed with the largest number of synapomorphies with the greatest likelihood of independence is preferred.

Obviously in the context of phylogenetic systematics, character independence doesn't mean that the characters will be uncorrelated, because independent characters may be correlated due to common descent. The term separate seems to imply that two or more novelties cannot have been the result of the same biological process or mechanism. Unambiguous dependent change occurs instantaneously, and responsible mechanisms may include (1) genetic factors, such as pleiotropy, gene associations (linkage), and polyploidy, (2) ontogenetic factors, such as allometry and paedomorphosis, and (3) compensatory functional changes (Lauder, 1983). It is extremely difficult to test hierarchic patterns of character covariation rigorously for such causation, and phylogenetic systematists have tended to ignore the assumption of independence.

Kluge (1983) thought it might be fruitful to evaluate competing phylogenetic hypotheses in terms of consilience. As Whewell wrote many years ago (1847, vol. 2, p. 469); "the consilience of inductions takes place when an induction, obtained from one class of facts, coincides with an induction, obtained from another *different class*. This consilience is a test of the truth of the theory in which it occurs" (my italics). I believe Whewell was emphasizing independence of evidence when he referred to different classes of facts. A phylogenetic hypothesis derived from character evidence intrinsic to the organism might be tested with evidence extrinsic (non-genetic) to the species in question, and thus with evidence that is more likely to be independent. Parasites (or hosts, if the truth of the parasite cladogram is at issue) and earth history are two sources of extrinsic evidence. Of course, a comparison of intrinsic and extrinsic observations is meaningful only insofar as one can reasonably assume a general theory of association by descent (e.g., host–parasite coevolution, or the theory that the organic–inorganic worlds coevolved). The *Epicrates* species relationships identified in this paper will be tested elsewhere with a hypothesis of earth history (Kluge, manuscript).

PHYLOGENETIC METHODS

For reasons discussed above, the phylogenetic relationships of *Epicrates* will not be judged with taxonomic congruence applied to fundamental cladograms. Where the inference of phylogeny is at issue I seek the hypothesis that best fits all of the relevant evidence available, that is, one of maximum character congruence (Fig. 1). However, methods will be applied to equally most parsimonious cladograms derived from the same data set, which I refer to as secondary cladograms, in order to reach a consensus (Fig. 3). Such consensus cladograms are used in the present study, because they are an efficient means of summarizing alternative hypotheses. They are effective in focusing attention on multichotomies, which may be due to lack of data or conflict in the available evidence, and the need for further research. The fact that Adams' (1972) and Nelson's (1979) consensus methods give nearly identical topologies when applied to the secondary cladograms discovered in this paper tends to diminish the taint of arbitrariness in choosing a method. More importantly, consensus indexes are not used to estimate agreement among the secondary clado-

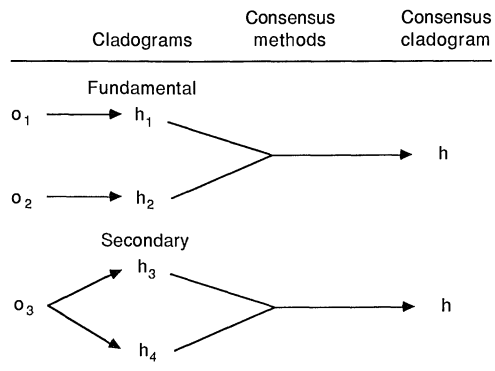

FIG. 3. A consensus cladogram derived from either fundamental or secondary cladograms illustrates two uses of consensus methods. o_1 and o_2 are data sets from which single most parsimonious cladograms, h_1 and h_2, are derived. o_3 is a data set from which two, h_3 and h_4, or more most parsimonious cladograms are derived. h is the consensus cladogram.

grams. Rather, attention is focused on agreement among the characters, as it is throughout this paper, and the consistency index is used as a global measure of that congruence. The F-ratio and D-measure will not be employed, because they are considered ancillary to the consistency index, and are at best applicable only under limited conditions.

While I have no interest in debating the relative stability of classifications derived from phenetic and cladistic algorithms, a consideration of the congruence of biochemical and morphological data has merit (Fig. 2). The reason concerns the fact that there is a growing tendency to attribute greater importance to biochemical characters (Anonymous, 1974; Avise, 1974; Maxson and Wilson, 1974, 1975; Nei, 1975; Frelin and Vuilleumier, 1979; Highton, 1981; Palmer, 1987; Woese, 1987), and especially on the grounds that such evidence exhibits relatively little homoplasy (Gould, 1985; Dessauer et al., 1987:1, 19; Sibley and Ahlquist, 1987; Jansen and Palmer, 1988). The expectation from cladistic theory is that there will be congruence between different character sets, and contradictory claims concerning homoplasy must be tested empirically (see also Mickevich and Johnson, 1976; Miyamoto, 1983, 1984). The methods I use to test for character congruence require the analysis of separate biochemical and morphological data sets; however, the two sets of evidence are combined in assessing the phylogeny of *Epicrates* species (Fig. 2).

The issue of character independence is being faced, if only indirectly, as the search for evidence broadens. For example, data taken from different character systems are explicitly or implicitly assumed to be independent; presumably the more different, the less likely they are to be the product of the same process or mechanism. Biochemical and morphological traits are frequently mentioned as independent character sets, while those observed on cranial and postcranial bones, bones and muscles, muscles and nerves, etc., are rarely considered independent. In my analysis of the phylogenetic relationships of *Epicrates* species, I will assume that biochemical and morphological classes of characters are more likely to be independent than are the characters within each class.

The branch and bound algorithm (Hendy and Penny, 1982) in Swofford's PAUP software package (1985) was used to find the cladograms that best fit the evidence. Swofford's Contree program was used to compute a consensus cladogram for a given data set when equally parsimonious hypotheses were observed (Fig. 3). All multistate characters (Table 1) were treated as unordered to avoid biasing the phylogenetic conclusions in terms of traditional hypotheses of character evolution. Both Farris (1970) and deltran (Swofford and Maddison, 1987) optimization routines were employed. The former minimizes convergences/parallelisms over reversals whenever possible, the latter minimizes reversals over convergences/parallelisms.

THE DATA

Tolson's (1987) survey of *Epicrates'* skin and scent gland lipids constitutes the biochemical data. The lipid characters are really the presence or absence of a secondary product, which may be the result of several enzymes acting in concert, as opposed to primary gene products, such as enzymes or proteins, or gene sequences. In this re-

gard the lipid characters may be intermediate between strictly molecular and strictly morphological characters. The binary states of Tolson's 24 lipid characters are summarized in Table 1, which is identical to part of his table 3, except the taxa have been rearranged in alphabetical order. Characters 1–7 are skin neutral, 8, 9 skin polar, 10–17 scent gland neutral, and 18–24 scent gland polar lipids.

Tolson (1987) employed a few external phenotypic features, and these make up part of the morphological data set summarized in Table 1. There are eight binary transformations (characters 25–29 and 31–33) and one three-state variable (30). This array is equivalent to part of Tolson's table 3, except the taxa have been rearranged in alphabetical order. The characters were extracted from Sheplan and Schwartz's (1974) study of geographic variation. Tolson used large gaps between sample modes as the basis for delimiting most character states. The following describes the nature of these characters (see Tolson, 1987, for further comments): 25. Labial pits present (0), or absent (1); 26. Juvenile coloration reddish or orange-brown (0), or gray or gray-brown (1); 27. Adult snout-vent length greater (0), or less (1) than one meter; 28. Number of subcaudal scales fewer than 55 (0), or greater than 75 (1); 29. Lorilabial scale row present (0), or absent (1); 30. Number of intersupraocular scales three or more (0), two (1), or one (2); 31. Number of scale rows at midbody more (0), or less (1) than 50; 32. Number of supralabial scales more (0), or less (1) than 12; 33. Number of infralabial scales more (0), or less (1) than 16.

I surveyed more than 250 *Epicrates* skeletons housed in the University of Michigan Museum of Zoology, and as a result 44 characters, 34–77, were added to the morphological data set. The taxonomic distributions of the character states are summarized in Table 1. Characters 35, 38, 42, 43, 46, 55, 56, 60, 62, 70, and 71 consist of three states, the remainder are binary. The nature of each transformation series is described in Appendix A. While observations were made on hatchlings, juveniles, subadults and adults of all species, the skeletal characters were scored only on adults in order to maintain comparability to Tolson's lipid data. An analysis of the ontogenetic variation and the use of the ontogeny criterion for polarizing characters will be reported elsewhere.

Variation in a terminal taxon is coded with a slash in Table 1, the inferred primitive state being placed first. The symbol N signifies "not applicable." The 0/1 variation (characters 69 and 72) recorded in *E. striatus* suggests that this taxon is not monophyletic. A synapomorphy analysis of additional evidence corroborates that possibility (Kluge, in prep.). Thus, the relationships of only the most primitive member of "*striatus*," from Hispaniola, is analyzed in this paper.

The monophyly of *Epicrates* is supported by the arrangement of prefrontal bones (Boulenger, 1893), and general habitus, coloration, and one skin neutral lipid according to Tolson (1987:table 9). Additional evidence will be considered in Appendix B.

A hypothetical common ancestor of the *Epicrates* species was reconstructed according to the outgroup criterion and parsimony optimization. (*Corallus* (*Eunectes*, *Epicrates*)) was the immediate outgroup cladogram employed. Several characters diagnose this group as a historical entity (see review by McDowell, 1979:4–5). The Cenozoic *Paraepicrates* and *Pseudoepicrates* were found to be distantly related to this assemblage (Kluge, 1988a). *Xenoboa cropanii* is considered a part of *Corallus* (Kluge, in prep.). The (*Eunectes*, *Epicrates*) clade is delimited by the narrowness of the anterior edge of the nasal septum of the premaxilla, and the postorbital contacting both the frontal and parietal.

Tolson (1987) chose *Corallus*, rather than *Eunectes*, as the proximate outgroup to *Epicrates*. I have not examined the effects of his outgroup classification; however, a single lineage difference is not likely to be important, because the lipid components were coded as present or absent, and they are largely absent in *Epicrates cenchria* (the most primitive sister lineage in that taxon, as judged by morphological traits alone),

TABLE 1. Biochemical (1-24) and morphological (25-77) characters for *Epicrates* species (characters 1-33 from Tolson, 1987:table 3; see Appendix A for descriptions of characters 34-77; * = unordered).

Character	ancestor	*angulifer*	*cenchria*	*chryso-gaster*	*exsul*	*fordii*	*gracilis*	*inornatus*	*monensis*	*striatus*	*subflavus*
1.	0	1	1	1	1	1	1	1	1	1	1
2.	0	1	0	1	1	1	1	1	1	1	1
3.	0	1	0	1	1	1	1	1	1	1	1
4.	0	0	0	1	1	0	0	0	0	0	0
5.	0	0	0	1	1	0	0	0	0	0	0
6.	0	0	0	0	0	1	0	0	0	1	0
7.	0	0	0	1	0	1	1	1	1	0	1
8.	0	1	0	1	1	1	1	1	1	1	1
9.	0	0	0	0	0	1	0	0	1	0	0
10.	0	0	0	0	0	1	1	0	1	0	0
11.	0	0	0	0	0	1	1	0	1	0	0
12.	0	0	0	0	0	1	1	0	1	0	0
13.	0	0	0	0	0	0	0	1	0	0	1
14.	0	1	0	1	1	1	1	1	1	1	1
15.	0	0	0	0	0	1	1	1	1	0	0
16.	0	0	0	0	0	1	1	0	1	0	0
17.	0	0	0	0	0	1	1	0	1	0	0
18.	0	0	0	1	1	1	1	1	1	1	1
19.	0	0	0	1	1	1	1	1	1	1	1
20.	0	0	0	0	0	1	0	0	1	1	0
21.	0	0	0	1	1	0	0	0	0	0	0
22.	0	0	0	1	1	0	0	0	0	0	0
23.	0	0	0	1	1	0	0	0	0	0	0
24.	0	0	0	1	1	0	0	0	0	0	0
25.	0	0	0	1	1	1	1	1	1	1	1
26.	0	0	0	0	0	1	0	0	1	0	0
27.	0	0	0	0	0	1	1	0	1	0	0
28.	0	0	0	1	1	1	1	1	1	1	1
29.	0	0	0	1	1	1	1	1	1	0	1
30.*	0	0	0	1	1	2	2	2	2	1	2
31.	0	0	0	1	1	1	1	1	1	0	1
32.	0	0	0	0	0	0	0	1	0	0	1
33.	0	0	0	1	1	1	1	1	1	0	1
34.	0	1	0	1	1	1	1	1	1	1	1
35.*	0	0	0	2	2	2	2	2	2	2	1
36.	0	1	0	1	0	0	0	0	0	1	0
37.	0	1	0	1	1	0	0	0	0	1	0
38.*	0	0	0	1	1	2	1	1	1	1	1
39.	0	0	0	0	0	0	0	1	0	0	1
40.	0	0	0	1	1	1	1	1	1	1	1
41.	0	0	0	1	1	1	1	1	1	1	1
42.*	0	0	0	0	1	2	2	1	2	0	1
43.*	0	2	1	2	2	2	2	2	2	2	2
44.	0	0	0	0	0	0	0	1	0	0	1
45.	0	0	0	1	1	1	1	0	1	0	0
46.*	0	0	0	0	0	2	2	0	1	0	0
47.	0	0	0	1	1	1	1	1	1	1	1
48.	0	0	0	1	1	1	1	1	1	1	1
49.	0	0	0	1	1	1	0	0	1	1	0
50.	0	1	0	0	0	0	0	1	0	1	1
51.	0	1	0	1	1	1	1	1	1	1	1
52.	0	1	0	1	1	0	0	1	0	1	1
53.	0	0	0	0	0	1	1	0	1	0	1
54.	0	1	0	1	1	1	1	0	1	1	1
55.*	0	1	0	2	2	2	2	2	2	1	2
56.*	0	1	0	1	1	1	2	1	1	2	0
57.	0	0	0	0	0	1	1	0	1	0	0
58.	0	0	0	0	0	1	1	0	1	0	0

TABLE 1. Continued.

Character	ancestor	*angulifer*	*cenchria*	*chryso-gaster*	*exsul*	*fordii*	*gracilis*	*inornatus*	*monensis*	*striatus*	*subflavus*
59.	0	0	0	0	0	1	1	0	0	0	0
60.*	0	2	0	2	1	0	0	1	1	2	1
61.	0	0	0	0	0	1	1	0	0	0	0
62.*	0	0	0	1	1	1	2	1	2	0	1
63.	0	0	0	1	1	1	1	1	1	0	1
64.	0	1	0	1	0	0	0	0	0	1	0
65.	0	0	0	0	1	1	1	0	1	0	0
66.	0	1	0	1	0	0	0	1	0	1	1
67.	0	0	0	0	1	1	1	0	1	0	0
68.	0	0	0	0	0	1	1	0	1	0	0
69.	0	0	0	1	0	0	1	1	1	0/1	0
70.*	0	1	0	0	0	0	0	1	1	2	1
71.*	0	1	1	2	1	2	2	1	1	0	1
72.	0	0	0	1	1	1	1	1	1	0/1	1
73.	0	0	0	0	0	0	1	1	0	0	1
74.	0	0	0	1	1	0	1	1	0	0	0
75.	0	0	0	0	0	1	0	0	1	1	0
76.	0	0	0	1	1	0/N	1	1	0/N	0/N	1
77.	0	0	0	1	1	0	0	1	0	0	1

Corallus and other boids (Tolson, 1987). I have found no reason to alter Tolson's morphological character polarizations in light of my assuming that *Eunectes*, rather than *Corallus*, is the sister lineage to *Epicrates*.

PHYLOGENETIC RESULTS

Ten equally parsimonious (c = .857) cladograms resulted from an analysis of the biochemical data set (Table 1, characters 1–24), and these patterns are illustrated as a Nelson consensus cladogram in Figure 4. The number of expected transformations (R) was 24, the number observed (L) was 28. Analysis of the morphological data (Table 1, characters 25–77) resulted in only two equally parsimonious cladograms (c = .650; R = 65; L = 100), which are summarized in Figure 5. The two equally most parsimonious cladograms (c = .669; R = 89; L = 133) obtained from an analysis of the combined data sets (Table 1, characters 1–77) are shown as a consensus cladogram in Figure 6. The quantitative aspects of these three analyses are summarized in Table 2.

Miyamoto (1985:188) suggested weighting the subsets of characters in a combined analysis in such a way that the set of more numerous transformations does not overwhelm the other set, by virtue of its sheer numbers (Kluge, 1983). Implementing this idea may be warranted when incongruence is high and the resulting unweighted cladograms are markedly different. In the present study (Table 2), the number of morphological transformations (65) is more than twice the number of biochemical novelties (24). However, transforming the sets

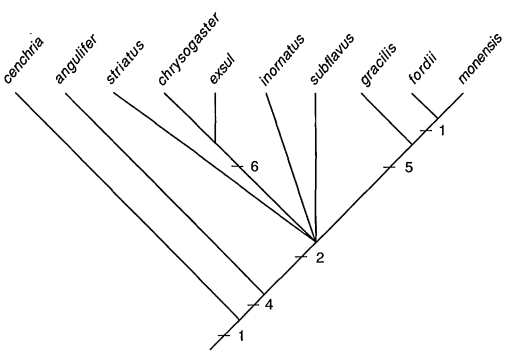

FIG. 4. The Nelson consensus cladogram based on 10 equally parsimonious secondary cladograms (c = .857) extracted from the biochemical data summarized in Table 1, characters 1–24 (see Fig. 3). The Adams (1972) consensus cladogram for these data is identical, except the pentachotomy is partially resolved into the following dichotomy and trichotomy: ((*chrysogaster, exsul*) (*inornatus, subflavus* (*gracilis* (*fordii, monensis*)))). The number of unique and unreversed diagnostic synapomorphies is given for each nonterminal clade.

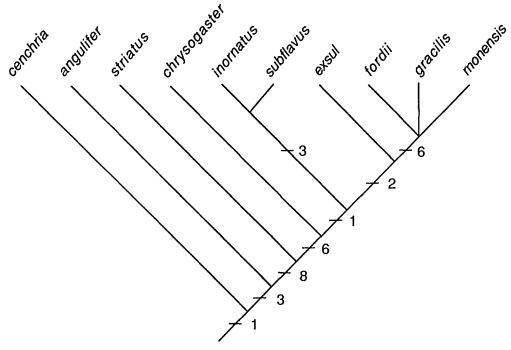

FIG. 5. The Nelson consensus cladogram based on two equally parsimonious secondary cladograms (c = .650) extracted from the morphological data summarized in Table 1, characters 25–77 (see Fig. 3). The number of unique and unreversed diagnostic synapomorphies is given for each nonterminal clade.

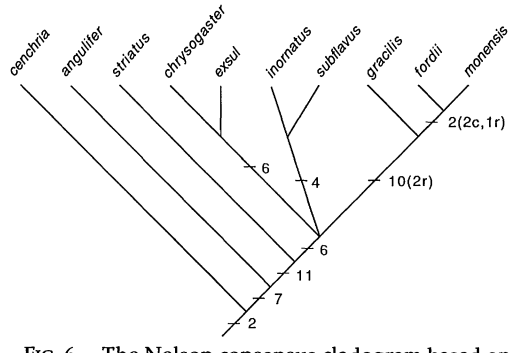

FIG. 6. The Nelson consensus cladogram based on two equally parsimonious secondary cladograms (c = .669) extracted from the combined biochemical and morphological data summarized in Table 1, characters 1–77 (see Fig. 3). The number of unique and unreversed diagnostic synapomorphies is given for each nonterminal clade, followed by the number of unambiguous and consistent homoplasious novelties (c = convergence/parallelism, r = reversal; see text for further explanation).

of characters onto the same scale does not change the taxonomic relationships from those illustrated in Figure 6. This is not surprising given the similarity of the cladograms resulting from the combined (Fig. 6) and separate data set analyses (Figs. 4, 5).

INCONGRUENCE

Mickevich and Farris (1981:366–367) formulated an ingenious definition of character incongruence, and I apply the corresponding metric they developed to *Epicrates*. When the biochemical and morphological data are combined there is a total of 44 extra steps on the best fitting cladograms (R = 89; L = 133; Fig. 6), which is defined as total character incongruence. Four of those extra steps are required to explain the biochemical data on the best fitting cladograms extracted from that data set (R = 24; L = 28; Fig. 4), and 35 of these extra steps are required of the morphological data (R = 65; L = 100; Fig. 5). These 39 extra steps explain the character incongruence in the separate data sets, which leaves five additional extra steps originating from incongruence between the character sets. Only 11.4% (5/44) of the total character incongruence is due to the disparity between data sets (i_{MF}; Table 3). The total in the combined data sets (Fig. 6), as judged from the consistency index, is .669 (R = 89; L = 133). That due to the incongruence between characters within data sets is .293 (R = 39; L = 133), and that due to incongruence between character sets is .038 (R = 5; L = 133). Thus, disagreement between the biochemical and morphological characters is small relative to incongruence among the characters within each set. The two qualitatively independent sources of

TABLE 2. Summary of information on *Epicrates* congruence.

Character type	Biochemical	Morphological	Combined
Character numbers	1–24	25–77	1–77
Minimum number of synapomorphies (R)	24	65	89
Number of equally most parsimonious cladograms	10	2	2
Length of most parsimonious cladogram (L)	28	100	133
Number of extra steps (e)	4	35	44
Consistency indexes (c)	.857	.650	.669
Figure illustrating consensus cladogram	4	5	6

information are not strikingly contradictory in this example.

Biochemical and morphological data sets with the combination of markedly different consistency indices and relatively little incongruence are not unusual. For example, Wyss et al. (1987) examined the relationships among the major groups of mammals ("orders") with one morphological and four amino acid sequence data matrices (alpha crystallin A, myoglobin, and alpha and beta hemoglobin). Consistency indices for the morphological and combined biochemical data sets are .833 and .534, respectively (.600 for all data combined), according to calculations made by David Polly (pers. comm.) on the 12 taxa described by most of the characters. The total incongruence between the morphological and combined biochemical data sets is 70 extra steps, and the sum of the extra steps in the separate suites of evidence is 69, 7 and 62. Thus, only 1.4% (1/70) of the total incongruence is due to the disparity between the data sets (i_{MF}; Table 3), and this is another example where the cladist's expectation of congruence is upheld.

One of the important features of the Mickevich-Farris metric for calculating incongruence is that it employs total evidence ($o_1 + o_2$). This is not the case for all measures of incongruence. Again, consider the hypothetical example in Figure 2 of three data sets, o_1, o_2 and $o_1 + o_2$, and corresponding most parsimonious cladograms, h_1, h_2 and h_3. In addition, each hypothesis has a number of extra steps (incongruence), e_1, e_2 and e_3. According to the Mickevich-Farris metric, the incongruence due to the disparity between o_1 and o_2 is equal to $e_3 - (e_1 + e_2)$. The total evidence, $o_1 + o_2$, forms the basis for determining e_3, on h_3. The following is an alternative technique for measuring incongruence (M. Miyamoto, pers. comm.), which does not take into account total evidence. In this case e_4 results when o_1 is optimized on h_2, and e_5 when o_2 is optimized on h_1, and the incongruence due to the disparity between o_1 and o_2 is equal to $(e_4 + e_5) - (e_1 + e_2)$. Notice, the total evidence is not involved in these calculations.

TABLE 3. Summary of congruence parameters for three types of data scored on *Epicrates* and mammals. c = consistency index; e = extra steps; i_{MF} = Mickevich-Farris incongruence metric.

	Biochemical	Morphological	Combined
Epicrates			
c	.857	.650	.669
e	4	35	44
i_{MF} = 11.4%	(5/44)		
Mammals			
c	.534	.833	.600
e	62	7	70
i_{MF} = 1.4%	(1/70)		

CONFIRMATION

I believe character confirmation provides an additional basis on which to judge congruence. The number of synapomorphies marking a clade is a measure of the confirmation of that part of the cladogram (=patristic distance; Kluge and Farris, 1969), and more general synapomorphies further secure less general shared apomorphies. In phylogenetic studies, attention is focused only on confirmation of the inclusive clades, because it is difficult to judge the evidence for the individuality of terminal taxa. Unless the systematist seeks both autapomorphies and synapomorphies, only homoplasies will confirm terminal taxa.

Table 4 summarizes the number of unique and unreversed biochemical and morphological synapomorphies delimiting each clade in the separate and combined analyses. All of the nonterminal clades in the combined analysis (Fig. 6) are confirmed by two or more synapomorphies, and both biochemical and morphological characters mark six of those eight clades.

Table 5 suggests that the numbers of unique and unreversed biochemical and morphological novelties diagnostic of all clades in the separate analyses (Figs. 4, 5) are not significantly different from the numbers in the combined analysis (Fig. 6). Thus, I conclude that confirmation of biochemical and morphological synapomorphies indicates a high level of congruence in the hypothesis of *Epicrates* species relationships.

TABLE 4. Summary of unique and unreversed diagnostic states. (clade)[a]: character number; see Table 1.

Biochemical data (Fig. 4)
Characters 1-24
(3, 4):4, 5, 21, 22, 23, 24
(5, 8):9
(5, 6, 8):10, 11, 12, 16, 17
(3-10):18, 19
(1, 3-10):2, 3, 8, 14
(1-10):1
Morphological data (Fig. 5)
Characters 25-77
(7, 10):32, 39, 44
(5, 6, 8):27, 42, 46, 57, 58, 68
(4-6, 8):65, 67
(4-8, 10):42
(3-8, 10):29, 31, 33, 55, 63, 72
(3-10):25, 28, 35, 38, 40, 41, 47, 48
(1, 3-10):34, 51, 55
(1-10):43
Combined data (Fig. 6)
Biochemical/morphological characters
(3, 4):4, 5, 21, 22, 23, 24/
(7, 10):13/32, 39, 44
(5, 8):9/26
(5, 6, 8):10, 11, 12, 16, 17/27, 46, 57, 58, 68
(3-8, 10):/29, 31, 33, 55, 63, 72
(3-10):18, 19/25, 28, 30, 35, 38, 40, 41, 47, 48
(1, 3-10):2, 3, 8, 14/34, 51, 55
(1-10):1/43

[a] *angulifer* = 1; *cenchria* = 2; *chrysogaster* = 3; *exsul* = 4; *fordii* = 5; *gracilis* = 6; *inornatus* = 7; *monensis* = 8; *striatus* = 9; *subflavus* = 10.

Tolson (1987:37-39) mentioned additional color and color pattern characters, which confirm some of the clades identified in the final phylogenetic hypotheses of *Epicrates* (Fig. 6). According to Tolson, the (*fordii, monensis*) clade is corroborated by the configuration and boldness of the adult color pattern, and the unique neonate color; the (*inornatus, subflavus*) clade, also recognized by Sheplan and Schwartz (1974), is distinguished by another neonate color pattern; and the (*chrysogaster, exsul*) clade is diagnosed by a peculiar ontogeny of color.

Additional confirmation may be sought in homoplasious traits providing they can be unambiguously optimized and are consistently placed on all equally parsimonious phylogenetic hypotheses. A character whose history can be mapped parsimoniously only one way on a phylogenetic hypothesis is said to be unambiguous. In the present study, characters 6, 20, 42, 52, 54, 56, 60, 62, 75, and 76 exhibit states with these properties (assuming either Farris or deltran optimization; see Fig. 6). Of those, 20, 52, 60, 75, and 76 mark nonterminal clades. All of the unique and unreversed and the unambiguous and consistent character states diagnosing each nonterminal clade in the phylogenetic hypothesis derived from the combined data sets (Fig. 6) are described in Appendix B.

TABLE 5. Number of unique and unreversed states confirming all clades on the consensus hypotheses (see Table 4).

	All clades			
	Biochemical	Morphological		
Separate	19[a]	30		
Combined	20	28	$\chi^2 = .169$	NS

[a] Value lower than might be expected, because of the large number of equally parsimonious cladograms (10), which reduced the number of clades present on the Nelson consensus cladogram (Fig. 4).

DISCUSSION

Measures of incongruence and confirmation suggest that biochemical and morphological data are highly consistent with a phylogenetic hypothesis of *Epicrates* species relationships (Tables 2, 3; Fig. 6). Such a finding does not appear to be unusual (Mickevich and Johnson, 1976; Miyamoto, 1983, 1984), and it does not support the claim that one class of evidence should be favored over another. Until there are several examples to the contrary, phylogenetic inference should be carried out in the context of total evidence. Necessarily, all of that evidence will have to be of the same form if it is to be analyzed together. For example, character and distance data cannot be mixed.

I conclude that the phylogenetic hypothesis for *Epicrates* based on all of the available evidence (Fig. 6) is robust. The combined intrinsic evidence, biochemical and morphological, examined quantitatively in this study has a high consistency index (c = .669). All of the clades are confirmed by two or more unique and unreversed transformations, and six of the eight

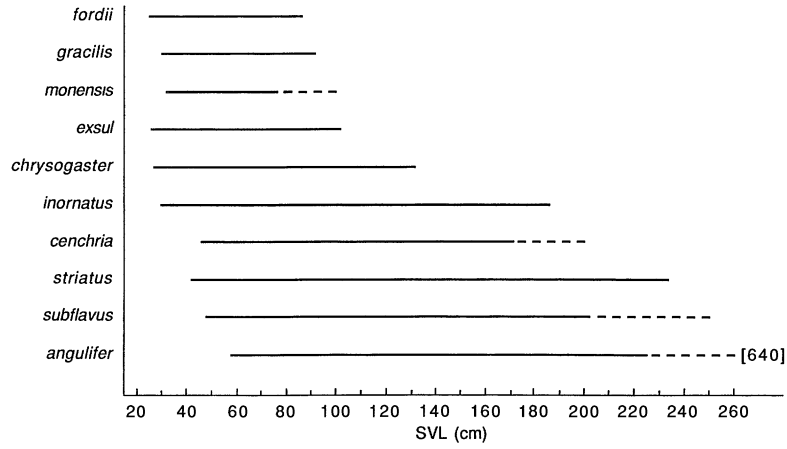

FIG. 7. Size of *Epicrates*. The spans estimate average snout to vent length (SVL) at birth (left extreme) and maximum adult SVL (right extreme) for each species. All observations from the literature have been confirmed, except those represented by dashed lines (Pete Tolson, pers. comm.). The 640 cm SVL *angulifer* is probably erroneous.

groups are corroborated by both biochemical and morphological characters. The latter finding is particularly significant, assuming the two classes of evidence are likely to be independent. Additional confirmation exists in unambiguously optimized and consistent homoplasious characters (involving both convergence and reversal) for two of the nonterminal clades.

The combined data nearly completely resolve the species relationships (Fig. 6). Only a single trichotomy remains ((*chrysogaster, exsul*) (*inornatus, subflavus*) (*gracilis* (*fordii, monensis*))).The trichotomy is due to contradictory evidence, not lack of information, and the characters consistently in conflict under both Farris and deltran optimization are 30, 37, 45, 50, 70, and 71. Incongruence may be due to mosaic evolution and/or investigator error, and reexamination of the characters responsible for the polytomy suggests that it is a case of mosaic evolution. Thus, resolution will have to come from the discovery of new characters.

What biological processes might explain the many hypothesized independent evolutionary events, 44 extra steps, that had to be postulated in the final phylogenetic analysis of *Epicrates* (c = .669; Table 2; Fig. 6)? Most of the homoplasy was associated with the morphological characters (40 extra steps for 65 character state transformations, as opposed to four for 24 in the biochemical data; Table 2), and the morphological data set was responsible for all of the increased incongruence when the two classes of characters were combined (five extra steps). Moreover, Tolson's (1987) external phenotypic variables (25–33) contributed only one extra step; the remaining 39 involved the skeletal subset of morphological characters.

Paedomorphosis (Kluge and Strauss, 1985; Kluge, 1988b) may provide a biological explanation for some of the extra steps in the morphological data, especially in the skeletal characters. Adult *exsul, fordii, gracilis* and *monensis* are considerably smaller than all other species in *Epicrates* (Fig. 7; *chrysogaster* is of intermediate size), and in general they are similar to the subadults of the larger species (Fig. 8). The hypothesized phylogenetic relationships (Fig. 6) suggests that small adult size is derived in *Epicrates*. In this context, there are two possible causes for the extra steps—evolutionary reversal and the independent evolution of small size. Both types of mosaic evolution seem to apply.

The possibility of paedomorphosis was recognized at the outset of the study of the skeletal system (Fig. 8), and consequently I used only the outgroup criterion to po-

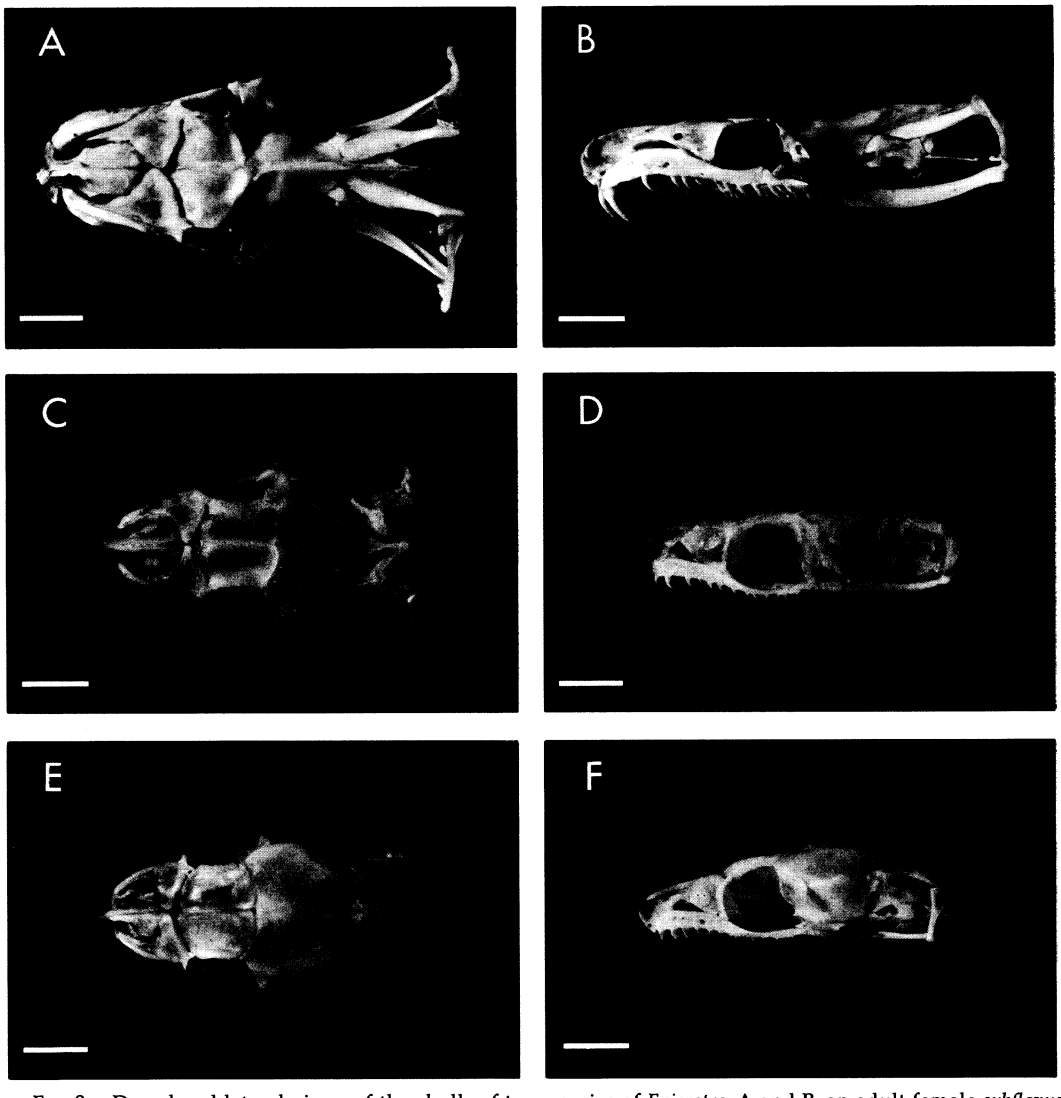

FIG. 8. Dorsal and lateral views of the skulls of two species of *Epicrates*. A and B, an adult female *subflavus* (snout to vent length [SVL] = 203 cm; UMMZ 181121). C and D, a neonate *subflavus*, of unkown sex (SVL = 39 cm; UMMZ 179329). E and F, an adult female *gracilis* (SVL = 76 cm; UMMZ 176918). The length of the horizontal bar in panels A and B is 1 cm; it is 3.3 mm in C–F.

larize character states (Kluge and Strauss, 1985). Evolutionary reversals are expected when paedomorphosis obtains, because those conditions must be interpreted and coded as symplesiomorphies in the data matrix. Indeed, the proportion of the homoplasy explained as evolutionary reversal was extraordinarily high in the final analysis (Fig. 6). Estimates varied from a conservative 32% (14/44 of the extra steps; Table 2) with deltran optimization, to a high of 82% (36/44) with Farris optimization, and almost all of the reversals occurred in the skeletal characters (32–80%). The high proportion of reversals persisted (60%) when only the unambiguous and consistent homoplasious states were considered (9/13), and all of those extra steps involved the skeletal characters.

The sister group relationships of *exsul*,

one of the four small species, changed more than any other lineage in the biochemical and morphological cladograms (Figs. 4, 5). According to the biochemical hypothesis, *exsul* evolved independently from a more primitive larger species (Fig. 4), whereas all of the small taxa had a single, highly derived, origin in the morphological hypothesis (Fig. 5). In the final analysis of the combined data (Fig. 6), the small *exsul* and (*gracilis* (*fordii, monensis*)) lineages are hypothesized to have evolved independently. Few extra steps are required to evolve *exsul* separately from the other small species. In the majority of the equally parsimonious trees and with different optimizations, only characters 65 and 67 appear convergently (two steps) and character 66 is a reversal that occurs twice (two steps). Thus, the independent evolution of small size contributes relatively little to the incongruence.

EPILOGUE

Phylogeny is estimated with characters interpreted as homologues (Darwin, 1859), and without knowing beforehand which are the marks of common ancestry one can do no better than consider all of the relevant evidence. Thus, the task of sorting through synapomorphies is great, and character congruence has proven to be an excellent screening device. Character congruence is stronger than the other tests of homology, such as conjunction and similarity, because it is more general (Patterson, 1982). Moreover, character congruence efficiently promotes critical re-evaluation, because incongruence signals homoplasy. Once the noise is identified it can be examined empirically for investigator error (Hennig, 1966:122) or the biological processes that might have been responsible for the independent evolution (Kluge and Strauss, 1985). In either case, the research program is extended, and the prospect for a better understanding of phylogeny grows. I believe such is evident in the study of *Epicrates* phylogeny. In light of these basic principles of phylogenetic systematics, I am left to wonder about those investigations which do not employ character data (e.g., genetic distance studies) or which emphasize agreement among fundamental cladograms. What marks of history do they employ, and how is the potential evidence re-evaluated? Does the inquiry simply end with the phylogenetic hypothesis? These questions arise from a concern for evidence. I suggest the answers be judged in the same context.

ACKNOWLEDGMENTS

I thank Doug Begle, Mike Donoghue, Steve Farris, Darrel Frost, Mary McKitrick, Richard O'Grady, Mike Miyamoto, David Polly, Elliott Sober, Ed Theriot, and Pete Tolson for their help. All of the skeletons used in this study are housed in the Division of Amphibians and Reptiles, University of Michigan Museum of Zoology, and most of that material was obtained by Pete Tolson. The research was supported by National Science Foundation grant BSR-83-04581.

REFERENCES

ADAMS, E. N. 1972. Consensus techniques and the comparison of taxonomic trees. Syst. Zool., 21:390–397.

ANONYMOUS. 1974. Trends, priorities, and needs in systematic and evolutionary biology. Syst. Zool., 23: 416–439.

AVISE, J. C. 1974. Systematic value of electrophoretic data. Syst. Zool., 23:465–481.

BOULENGER, G. A. 1893. Catalog of snakes of the British Museum. Volume 1. Longman's, London.

BROOKS, D. R., R. T. O'GRADY, AND E. O. WILEY. 1986. A measure of information content of phylogenetic trees, and its use as an optimality criterion. Syst. Zool., 35:571–581.

CARNAP, R. 1950. Logical foundations of probability. Univ. Chicago Press, Chicago.

COLLESS, D. H. 1980. Congruence between morphometric and allozyme data for *Menidia* species: A reappraisal. Syst. Zool., 29:288–299.

DARWIN, C. R. 1859. The origin of species by means of natural selection. A. L. Burt, New York. (Reprinted from the sixth London edition, 1872, with all additions and corrections.)

DAY, W. H. E. 1983. The role of complexity in comparing classifications. Math. Biosci., 66:97–114.

DAY, W. H. E. 1985. Optimal algorithms for comparing trees with labeled leaves. J. Classif., 2:7–28.

DAY, W. H. E., AND F. R. MCMORRIS. 1985. A formalization of consensus index methods. Bull. Math. Biol., 47:215–229.

DESSAUER, H. C., J. E. CADLE, AND R. LAWSON. 1987. Patterns of snake evolution suggested by their proteins. Fieldiana, Zool., (34):1–34.

FARRIS, J. S. 1970. Methods for computing Wagner trees. Syst. Zool., 19:83–92.

FARRIS, J. S. 1971. The hypothesis of nonspecificity and taxonomic congruence. Ann. Rev. Ecol. Syst., 2:277–302.

FARRIS, J. S. 1972. Estimating phylogenetic trees from distance matrices. Am. Nat., 106:645–668.

FARRIS, J. S. 1973. On comparing the shapes of taxonomic trees. Syst. Zool., 22:50–54.

FARRIS, J. S. 1979. The information content of the phylogenetic system. Syst. Zool., 28:483–519.

FARRIS, J. S. 1980a. Naturalness, information, invariance, and the consequences of phenetic criteria. Syst. Zool., 29:360–381.

FARRIS, J. S. 1980b. The efficient diagnoses of the phylogenetic system. Syst. Zool., 29:386–401.

FARRIS, J. S. 1982. Simplicity and informativeness in systematics and phylogeny. Syst. Zool., 31:413–444.

FRELIN, C., AND F. VUILLEUMIER. 1979. Biochemical methods and reasoning in systematics. Z. Zool. Syst. Evol., 17:1–10.

GAUTHIER, J., A. G. KLUGE, AND T. ROWE. 1988. Amniote phylogeny and the importance of fossils. Cladistics, 4:105–208.

GOOD, I. J. 1983. The foundations of probability and its applications. Univ. Minnesota Press, Minneapolis.

GOULD, S. J. 1985. A clock of evolution. Nat. Hist., 4:12–25.

HEMPEL, C. G. 1965. Aspects of scientific explanation and other essays in the philosophy of science. Free Press, New York.

HENDY, M. D., AND D. PENNY. 1982. Branch and bound algorithms to determine minimal evolutionary trees. Math. Biosci., 59:277–290.

HENNIG, W. 1966. Phylogenetic systematics. Univ. Illinois Press, Chicago.

HIGHTON, R. 1981. Biochemical systematics and evolution. Evolution, 35:823–824.

HILLIS, D. M. 1987. Molecular versus morphological approaches to systematics. Ann. Rev. Ecol. Syst., 18: 23–42.

INTERNATIONAL CODE OF ZOOLOGICAL NOMENCLATURE. 1985. Third edition adopted by the XX General Assembly of the International Union of Biological Sciences. Univ. California Press, Berkeley, California.

JANSEN, R. K., AND J. D. PALMER. 1988. Phylogenetic implications of chloroplast DNA restriction site variation in the Mutisieae (Asteraceae). Am. J. Bot., 75:753–766.

KLUGE, A. G. 1983. Cladistics and the classification of the great apes. Pages 151–177 *in* New interpretations of ape and human ancestry (R. L. Ciochon and R. S. Corruccini, eds.). Plenum Press, New York.

KLUGE, A. G. 1988a. Relationships of the Cenozoic boine snakes *Paraepicrates* and *Pseudoepicrates*. J. Vert. Paleo., 8:229–230.

KLUGE, A. G. 1988b. The characterization of ontogeny. Pages 57–81 *in* Ontogeny and systematics (C. J. Humphries, ed.). Columbia Univ. Press, New York.

KLUGE, A. G. Manuscript. Parsimony in vicariance biogeography: A quantitative method and a Greater Antillean example. Syst. Zool., accepted for publication.

KLUGE, A. G. In preparation. The classification of primitive snakes.

KLUGE, A. G., AND J. S. FARRIS. 1969. Quantitative phyletics and the evolution of anurans. Syst. Zool., 18:1–32.

KLUGE, A. G., AND R. E. STRAUSS. 1985. Ontogeny and systematics. Ann. Rev. Ecol. Syst., 16:247–268.

LAUDER, G. V. 1983. Functional design and evolution of the pharyngeal jaw apparatus in euteleostean fishes. Zool. J. Linn. Soc., 77:1–38.

MARGUSH, T., AND F. R. MCMORRIS. 1981. Consensus n-trees. Bull. Math. Biol., 43:239–244.

MAXSON, L. R., AND A. C. WILSON. 1974. Convergent morphological evolution detected by studying proteins of tree frogs in the *Hyla eximia* species group. Science, 185:66–68.

MAXSON, L. R., AND A. C. WILSON. 1975. Albumin evolution and organismal evolution in tree frogs (Hylidae). Syst. Zool., 24:1–15.

MCDOWELL, S. B. 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.

MCMORRIS, F. R., AND D. A. NEUMANN. 1983. Consensus functions defined on trees. Math. Soc. Sci., 4:131–136.

MICKEVICH, M. F. 1978. Taxonomic congruence. Syst. Zool., 27:143–158.

MICKEVICH, M. F. 1980. Taxonomic congruence: Rohlf and Sokal's misunderstanding. Syst. Zool., 29:162–176.

MICKEVICH, M. F., AND J. S. FARRIS. 1981. The implications of congruence in *Menidia*. Syst. Zool., 30: 351–370.

MICKEVICH, M. F., AND M. S. JOHNSON. 1976. Congruence between morphological and allozyme data in evolutionary inference and character evolution. Syst. Zool., 25:260–270.

MIYAMOTO, M. M. 1983. Frogs of the *Eleutherodactylus rugulosus* group: A cladistic study of allozyme, morphological, and karyological data. Syst. Zool., 32:109–124.

MIYAMOTO, M. M. 1984. Central American frogs allied to *Eleutherodactylus cruentus*: Allozyme and morphological data. J. Herpetol., 18:256–263.

MIYAMOTO, M. M. 1985. Consensus cladograms and general classifications. Cladistics, 1:186–189.

NEI, M. 1975. Molecular population genetics and evolution. North-Holland, Elsevier, New York.

NELSON, G. 1979. Cladistic analysis and synthesis: Principles and definitions, with a historical note on Adanson's Familles des Plantes (1763–1764). Syst. Zool., 28:1–21.

NELSON, G., AND N. I. PLATNICK. 1981. Systematics and biogeography: Cladistics and vicariance. Columbia Univ. Press, New York.

NEUMANN, D. A. 1983. Faithful consensus methods for n-trees. Math. Biosci., 63:271–287.

PALMER, J. D. 1987. Chloroplast DNA evolution and biosystematic uses of chloroplast DNA variation. Am. Nat., 130:S6–S29.

PATTERSON, C. 1982. Morphological characters and homology. Pages 21–74 *in* Problems of phylogenetic reconstruction (K. A. Joysey and A. E. Friday, eds.). Academic Press, New York.

ROHLF, F. J. 1982. Consensus indices for comparing classifications. Math. Biosci., 59:131–144.

SCHUH, R. T., AND J. S. FARRIS. 1981. Methods for investigating taxonomic congruence and their application to the Leptopodomorpha. Syst. Zool., 30: 331–351.

SHEPLAN, B. R., AND A. SCHWARTZ. 1974. Hispaniolan boas of the genus *Epicrates* (Serpentes, Boidae) and their Antillean relationships. Ann. Carnegie Mus., 45:57–143.

SIBLEY, C. G., AND J. E. AHLQUIST. 1987. Avian phylogeny reconstructed from comparisons of the genetic material, DNA. Pages 95–121 *in* Molecules and morphology in evolution: Conflict or compromise (C. Patterson, ed.). Cambridge Univ. Press, New York.

SNEATH, P. H. A., AND R. R. SOKAL. 1973. Numerical taxonomy. Freeman, San Francisco.

SOBER, E. 1988. Reconstructing the past: Parsimony, evolution and inference. M.I.T. Press, Massachusetts.

SOKAL, R. R. 1986. Phenetic taxonomy: Theory and methods. Ann. Rev. Ecol. Syst., 17:423–42.

SOKAL, R. R., AND F. J. ROHLF. 1981. Taxonomic congruence in the Leptopodomorpha re-examined. Syst. Zool., 30:309–325.

SOKAL, R. R., AND P. H. A. SNEATH. 1963. Principles of numerical taxonomy. Freeman, San Francisco.

STINEBRICKNER, R. 1984. s-consensus trees and indices. Bull. Math. Biol., 46:923–935.

SWOFFORD, D. L. 1985. PAUP, phylogenetic analysis using parsimony. Version 2.4. Privately printed and distributed by author.

SWOFFORD, D. L., AND W. P. MADDISON. 1987. Reconstructing ancestral character states under Wagner parsimony. Math. Biosci., 87:199–229.

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

WHEWELL, W. 1847. The philosophy of the inductive sciences, founded upon their history. Parker, London.

WOESE, C. R. 1987. Macroevolution in the microscopic world. Pages 177–202 *in* Molecules and morphology in evolution: Conflict or compromise (C. Patterson, ed.). Cambridge Univ. Press, New York.

WYSS, A. R., M. J. NOVACEK, AND M. C. MCKENNA. 1987. Amino acid sequence versus morphological data and the interordinal relationships of mammals. Mol. Biol. Evol., 4:99–116.

Received 25 April 1988; accepted 10 August 1988

APPENDIX A

Skeletal Character Descriptions for Epicrates (see Table 1; characters 34–77)

A. Premaxilla:
   34. External surface of midbody flat (0), or markedly indented (1).
   35. External surface of nasal process flat (0), or slightly (1) or markedly (2) indented.
   36. Dorsal margin of maxillary process nearly horizontal (0), or tips markedly curved dorsally (1).
   37. Mid-labial margin of body slightly (0), or markedly (1) indented.
   38. Nasal process underlies nasals and weakly wedged between them (0), weakly abuts ends of nasals (1), or abuts ends of nasals and wedged between them (2).
   39. Internarial wall of premaxilla deeply indented (0), or more nearly vertical (1).
   40. Base of internarial septum, posterior to body, exhibits anteromedially converging, slightly notched margins (0), or even margins (1).
   41. Maximum anteroposterior length of base from labial margin to end of vomerine process (a), relative to greatest width of base (b): a > b (0), or a < b (1).
   42. Position of labial margin anterior (0), even (1), or slightly posterior (2) tip of nasal process.

B. Vomer:
   43. Point of contact with premaxilla blade-like (0), slightly swollen (1), or bulbous (2).
   44. Posterior wings wide (0), or narrow (1).

C. Septomaxilla:
   45. Anterodorsal process of premaxillary blade prominent (0), or weakly developed or absent (1).
   46. Posterolateral wing large (0), small (1), or tiny (2).

D. Palatine:
   47. Dorsomedian process discontinuous (0), or continuous (1).

E. Nasal:
   48. Anteroventral corner forms projection along side of internarial septum of premaxilla (0), or forms nearly vertical margin and abuts septum (1).

F. Prefrontal:
   49. Lateral Margin of lacrimal duct prominent pedicel (0), or not (1).

G. Maxilla:
   50. Ectopterygoid shelf projecting into ectopterygoid fossa absent or small (0), or large (1).

H. Ectopterygoid:
   51. Posterolateral overlap with maxilla extensive (0), or modest (1).
   52. Posterior end of maxillary facet shallow (0), or deep (1).
   53. Lateral projection, posterior to maxillary facet, large (0), or small or absent (1).

I. Postorbital:
   54. Anterior margin, near its contact with ectopterygoid, conspicuously notched (0), or not (1).
   55. Posterior margin slopes at approximately 45 degree angle (0), at a less acute angle (1), or is nearly vertical (2).

J. Frontal:
   56. Arcade ventral to frontoparietal foramen (also

contributed to by parietal) weakly developed, does not extend to level of parasphenoid (0), moderately large, approximately even with parasphenoid (1), or extends well below level of parasphenoid (2).

K. Parietal:
57. Width, posterior to postorbital, less than or equal to frontals (0), or much wider than frontals (1).
58. Anterolateral wings long (0), or short (1). One-half maximum parietal width, which includes wings, relative to maximum length of frontals is a useful quantitative comparison.

L. Basisphenoid:
59. Midventral keel between pterygoid processes: present (0), or absent (1).
60. Bony ridge connecting pterygoid processes: absent (0), weak (1), or strong (2).
61. Pterygoid process creates: deep (0), or shallow (1) depression between it and parietal.
62. Right posterior vidian foramen lies: anterior to, or opposite, maxillary foramen (0), between maxillary and mandibular foramina (1), or opposite mandibular foramin (2).

M. Pterygoid:
63. Medial blade: sharply (0), or gently (1) curved toward pterygoid process of basisphenoid.

N. Exoccipital:
64. Tuberosity dorsal to otic foramen absent or small (0), or large (1).
65. Ridge or pedicel(s) of bone on which supratemporal rests present (0), or absent (1).

O. Supraoccipital:
66. Midsagittal crest projects posterior: beyond occipitals (0), or not (1).

P. Supratemporal:
67. Posterior end dorsal to (0), or level with, or ventral to (1) anterior end.
68. Extends well beyond exoccipital (0), or not (1).

Q. Angular:
69. Contacts coronoid (0), or separated from it by prearticular (1).

R. Surangular:
70. Anteriorly, ventrolateral shelf absent or only weakly developed (0), moderately large (1), or very conspicuous (2).
71. Posteriorly, ventrolateral shelf very conspicuous (0), moderately large (1), or absent or only weakly developed (2).
72. Anterior margin of coronoid process forms acute (0), or gradual (1) angle with long-axis of lower jaw.

S. Mid-trunk vertebrae:
73. Dorsal surface of neural spine narrow (0), or wide (1).
74. Anterodorsal margin of neural spine rounded (0), or forked (1).
75. Midventral ridge on centrum conspicuous (0), or inconspicuous (1).
76. Sides of midventral ridge on centrum tapered (0), or more nearly vertical (1). The inconspicuous midventral ridge (see character 42) makes it difficult to determine the nature of the sides of that ridge in individual *E. fordii*, *E. monensis*, and *E. striatus* (thus, the 0/N coding in Table 4).

T. Axis:
77. Intercentrum 2 thick and projects posteriorly (0), or blade-like and projects downward (1).

APPENDIX B

Diagnoses of Nonterminal Clades in Epicrates[1]

(3, 4) Skin neutral lipids present at Rf .301 and .353 (fig. 9); scent gland polar lipids present at Rf .704 and .793, and absent at Rf .679 and .780 (fig. 14).

(7, 10) Scent gland neutral lipid present at Rf .581 (fig. 12); modal number of supralabial scales fewer than 12; internarial wall of premaxilla more nearly vertical than indented; posterior wings of vomer narrow.

(5, 8) Skin polar lipid present at Rf .529 (fig. 11); scent gland polar lipid present at Rf .440 (fig. 14); juvenile coloration gray or gray-brown; midventral ridge on mid-trunk centrum inconspicuous; side of midventral ridge on mid-trunk centrum more nearly vertical than tapered.

(5, 6, 8) Scent gland neutral lipids present at Rf .515 (fig. 12), .153 and .822 (fig. 13), or absent at .458 and .541 (fig. 12); adults less than one meter snout–vent length; posterolateral wing of septomaxilla relatively small; posterior end of maxillary facet of ectopterygoid shallow; parietal, posterior to postorbital, much wider than frontals; anterolateral wings of parietal short; basisphenoid bony bridge connecting pterygoid processes weak or absent; supratemporal does not extend well beyond exocciptal.

(3–8, 10) Lorilabial scale row absent; number of scale rows at midbody fewer than 50; modal number of infralabial scales fewer than 16; posterior margin of postorbital nearly vertical; medial blade of pterygoid curved toward pterygoid process of basisphenoid; anterior margin of coronoid process of surangular forms gradual angle with long axis of lower jaw.

[1] *angulifer* = 1; *cenchria* = 2; *chrysogaster* = 3; *exsul* = 4; *fordii* = 5; *gracilis* = 6; *inornatus* = 7; *monensis* = 8; *striatus* = 9; *subflavus* = 10. The clades are illustrated in Figure 6. Only unique and unreversed (Table 4) and unambiguous and consistent homoplasious states are used to diagnose the clades. See Tolson (1987) for further description of biochemical variables; figure citations refer to his publication. Rf is a measure of the relative mobility of a lipid in a given solvent system.

(3–10) Scent gland polar lipids present at Rf .201 and .223 (fig. 14); labial pits absent; modal number of subcaudal scales greater than 75; modal number of intersupraocular scales less than three; external surface of premaxilla slightly or markedly indented; nasal process of premaxilla weakly abuts ends of nasals, or abuts ends of nasals and wedged between them; base of internarial septum of premaxilla, posterior to body, with even margins; maximum anteroposterior length of base of premaxilla from labial margin to end of vomerine process narrower than greatest width of base; dorsomedian process of palatine continuous; anteroventral corner of nasal forms nearly vertical margin and abuts septum.

(1, 3–10) Skin neutral lipids present at Rf .169 and absent at .186 (fig. 9); skin polar lipid present at Rf .255 (fig. 11); scent gland neutral lipid present at Rf .754 (fig. 12); external midbody surface of premaxilla markedly indented; posterolateral overlap of ectopterygoid with maxilla modest; posterior end of maxillary facet of ectopterygoid deep; posterior margin of postorbital assumes angle less acute than 45 degrees.

(1–10) Skin neutral lipid present at Rf .126 (fig. 9); vomer-premaxilla point of contact slightly swollen or bulbous.