

4). For the form of additive binary coding in which it is the branches that are coded, there must be a branch placed below the bottom-most character state, and that branch must contribute a derived code for all of the states in the tree (i.e., the minimum pathlength from each of the character states to the base of the tree passes through that branch). O'Grady and Deets (1987) remarked that altered additive binary coding requires one fewer column of tree-encoding characters than does standard additive binary coding; but this reduction is eliminated with the placement of a branch below the bottom-most character state.

We conclude by noting that, at the base of the multistate character tree, only one of the tree-encoding characters should change states. With nonredundant linear coding, for example, the topology of the tree could also be maintained by assigning a primary derived code to *all* of the tree-encoding characters at the base. Such a practice, however, would create problems with unjustified weighting.

ACKNOWLEDGMENTS

We thank Richard Pimentel, Rhonda Riggins, Mary Mickevich, and David Swofford for their continually stimulating discussions and writings about multistate characters in cladistic analysis. Paula Mabee gave insightful comments on coding methods. Financial support was provided to R.O'G. by the Smithsonian Institution, and to G.B.D. by the Friends of the British Columbia Provincial Museum.

REFERENCES

- BROOKS, D. R. 1981. Hennig's parasitological method: A proposed solution. *Syst. Zool.*, 30:229-249.
- CAMIN, J. H., AND R. R. SOKAL. 1965. A method for deducing branching sequences in phylogeny. *Evolution*, 19:311-326.
- FARRIS, J. S., A. G. KLUGE, AND M. J. ECKARDT. 1970. A numerical approach to phylogenetic systematics. *Syst. Zool.*, 19:172-191.
- O'GRADY, R. T., AND G. B. DEETS. 1987. Coding multistate characters, with special reference to the use of parasites as characters of their hosts. *Syst. Zool.*, 36:268-279.
- PIMENTEL, R. A., AND R. RIGGINS. 1987. The nature of cladistic data. *Cladistics*, 3:201-209.
- SOKAL, R. R., AND P. H. SNEATH. 1963. *Principles of animal taxonomy*. W. H. Freeman and Co., San Francisco.

Received 18 February 1988; accepted 17 August 1988.

Phylogenetic Systematics of the Anoles: Is a New Taxonomy Warranted?

DAVID C. CANNATELLA AND KEVIN DE QUEIROZ

*Department of Zoology and Museum of Vertebrate Zoology,
University of California, Berkeley, California 94720*

The diverse radiation of squamate reptiles called anoles has been of particular interest to systematic biologists, serving as a fruitful system for studies of phylogenetic relationships (Etheridge, 1960; Gorman and Atkins, 1969; Gorman et al., 1980; Wyles and Gorman, 1980; Shochat and Dessauer, 1981; Guyer and Savage, 1987;

Case and Williams, 1988), character evolution (Peterson, 1983; Losos, 1988), biogeography (Etheridge, 1960; Williams, 1969; Guyer and Savage, 1987), ecology (Schoener, 1968; Roughgarden et al., 1983), and faunal evolution (Williams, 1972, 1983). Over the past 25 years, anole taxonomy has been based largely on the work of Ether-

TABLE 1. Alternative taxonomies of anoles.

Guyer and Savage (1987)	Traditional
<i>Chamaeleolis</i>	<i>Chamaeleolis</i>
<i>Phenacosaurus</i>	<i>Phenacosaurus</i>
<i>Chamaelinorops</i>	<i>Chamaelinorops</i>
	<i>Anolis</i>
	alpha section
	<i>punctatus</i> subsection
<i>Dactyloa</i>	<i>latifrons</i> series
<i>Semiurus</i>	<i>cuvieri</i> series
<i>Ctenonotus</i>	<i>bimaculatus</i> series
	<i>crisatellus</i> series
	<i>cybotes</i> series
<i>Anolis</i>	<i>carolinensis</i> subsection
	<i>alutaceus</i> series
	<i>angusticeps</i> series
	<i>carolinensis</i> series
	<i>chlorocyanus</i> series
	<i>equestris</i> series
	<i>darlingtoni</i> series
	<i>lucius</i> series
	<i>monticola</i> series
<i>Norops</i>	beta section
	<i>auratus</i> series
	<i>fuscoauratus</i> series
	<i>grahami</i> series
	<i>meridionalis</i> series
	<i>onca</i> series
	<i>petersi</i> series
	<i>sagrai</i> series

idge (1960) and Williams (1976a, b) who, in their most recent arrangements, recognized four genera of anoles: *Anolis*, *Chamaeleolis*, *Phenacosaurus*, and *Chamaelinorops*. The speciose genus *Anolis* is divided into two sections, alpha and beta (in turn divided into various subsections and series), diagnosed by the morphology of their caudal vertebrae and supposedly representing a primary dichotomy within *Anolis*.

Although some form of the Etheridge-Williams taxonomic arrangement has, until recently, been widely followed, Etheridge (1960:131) himself noted problems with the alpha-beta dichotomy in the form of character incongruence. Subsequent biochemical studies (Gorman et al., 1980; Wyles and Gorman, 1980; Shochat and Dessauer, 1981) also yielded data inconsistent with this arrangement. A reevaluation and synthesis of available data was attempted by Guyer and Savage (1987). Us-

ing numerical cladistic methods, these authors analyzed three data sets, Etheridge's (1960) osteological characters, Gorman's (1973) karyological data, and Shochat and Dessauer's (1981) immunological distance data. Based on their phylogenetic conclusions, Guyer and Savage (1987) proposed a new taxonomy of the anoles in which *Anolis* was restricted to the *carolinensis* subsection of the alpha section, and the remaining species were partitioned among four genera (Table 1). Guyer and Savage's (1987) effort is a welcome contribution to the phylogenetic systematics of the anoles. Nevertheless, it also has problems, some of which undermine their new taxonomy.

OSTEOLOGICAL ANALYSIS

Original data set.—Guyer and Savage's principal data set was a group of sixteen osteological characters derived from Etheridge's (1960) classic thesis on the relationships of the anoles. These data were analyzed using the PHYSYS program of J. S. Farris and M. F. Mickevich. Unweighted data and the global branch-swapping option were used to produce cladograms, but these were not presented. Instead, the tree presented (their fig. 5, our Fig. 1) was generated using the successive weighting procedure (Farris, 1969), which yielded a single "diagnostically most-efficient tree . . ." (p. 514) that served as the primary basis for their new taxonomy.

In the successive weighting procedure, an initial tree is generated from unweighted data, and the consistency index of each character (or average of indices from several trees) is used as a character weight in a second analysis. Consistency indices (C-ratios) from the second analysis are used as weights in a third run, and so on to a specified stopping point (usually until the tree stabilizes or only one tree is found). Although this is a convenient way of reducing the number of equally parsimonious topologies resulting from unweighted analysis, it obscures alternative hypotheses of relationships that result from incongruent characters. Furthermore, while we do not reject out-of-hand the use of character weighting, doing so on the basis of

the fit of characters to a tree derived from these same characters can be criticized on the grounds that this practice reduces the independence of characters.

Guyer and Savage noted that the length of their "most-parsimonious" tree derived from weighted data was 31, in contrast with a length of 51 for the best-fit tree of unweighted osteological data. The shorter length of the weighted tree does not necessarily indicate a better fit to the unweighted data, because the character weights, which are ≤ 1.0 , contribute to the calculation of tree length. Given the concerns expressed above about successive weighting algorithms and that the most parsimonious unweighted tree(s) was not presented, we sought to reconstruct their unweighted tree using the IBM PC version of the Phylogenetic Analysis Using Parsimony program (PAUP, Version 2.4) of D. Swofford. Patterns of character evolution were examined using the MacClade program of W. Maddison and D. Maddison (Version 2.1). Unless otherwise stated, specific epithets refer to a series, the terminal taxa of Guyer and Savage's analysis. Before proceeding with the results of the analysis, we note some discrepancies in their data matrix.

(1) Character 4 of *crstatellus* is coded as state 2, but their table 2 indicates only states 0 and 1 for this character. In any case, state 2 is autapomorphic, and although recoding it to 1 would not affect the tree topology, we left it unchanged so that tree lengths could be compared directly. (2) The state of character 7 in *Chamaeleolis* is given as 1, but despite the requirement by the tree (their fig. 5) that state 1 be convergent in *Chamaeleolis*, no convergence in this state is indicated. The genus is described as having "unique parietal cresting" (p. 523), implying that it is autapomorphic. Regardless, this state does not affect the topology of the trees, so we left it unchanged. (3) Guyer and Savage stated that system 3 of character 15 (a priori coding of independent derivation of caudal transverse processes in *Chamaelinorops* and the beta anoles) was used, but comparison of states on the cladogram with those in the matrix in-

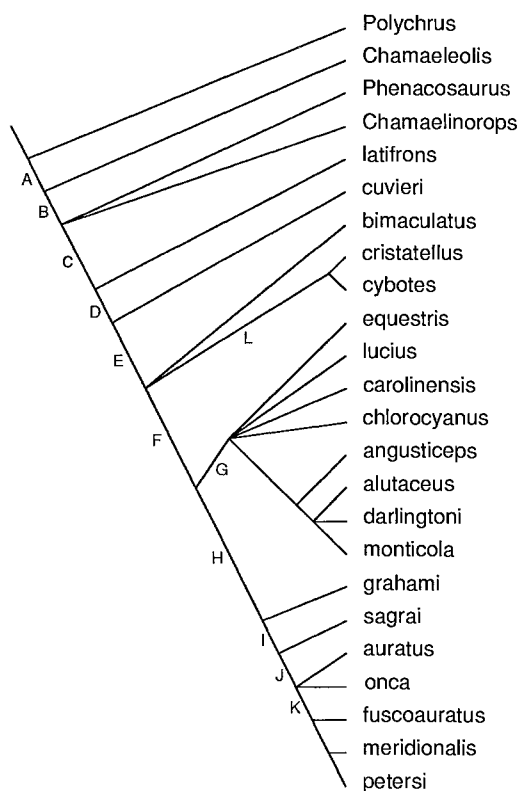


FIG. 1. Phylogeny of anoles based on successively weighted osteological data (Guyer and Savage, 1987).

dicates that system 2 (beta derived from alpha) was employed. (Additionally, this character seems to be scored incorrectly; in their table 3, *Chamaelinorops* is 0 and the alpha anoles are 1 for system 3, but the scoring is reversed in the matrix.) We adopted system 2 in the re-analysis of their data.

Our analysis of the data yielded 100 trees (the limit of the MAXTREE option of the IBM PC version of PAUP) of 52 steps each. More trees were doubtless possible, but many of the trees were the result of "different" topologies that reduced to the same polytomous tree because of the absence of characters at certain nodes. Using MacClade, we examined alternative possibilities for the evolution of character-states in trees with differing topologies. Ignoring rearrangements within the beta section, there are 12 different equally parsimonious trees, including topologies with nodes

TABLE 2. Data matrix derived from modifications of table 3 in Guyer and Savage (1987), as discussed in text. Character numbers with an asterisk are unordered.

Character	1	2	3	4	5	6	7*	8	9	10a	10b	11	12	13	14	15*
ANCESTOR	?	0	0	0	0	—	0	—	0	?	0	0	0	?	0	0
<i>Phenacosaurus</i>	0	1	0	0	0	—	0	—	0	0	0	2	0	?	0	1
<i>Chamaeleolis</i>	1	0	0	0	0	—	1	—	0	1	0	0	0	?	0	1
<i>Chamaelinorops</i>	0	1	1	0	0	—	0	—	1	1	0	0	0	?	0	?
<i>bimaculatus</i>	0	1	0	0	0	—	1	—	0	3	1	0	0	1	1	1
<i>crystalellus</i>	0	1	0	2	1	—	1	—	0	3	2	1	0	1	1	1
<i>cuvieri</i>	0	1	0	0	0	—	1	—	0	2	1	0	0	1	1	1
<i>cybotes</i>	0	1	0	1	1	—	1	—	0	3	2	0	0	1	1	1
<i>latifrons</i>	0	1	0	0	0	—	0	—	0	3	0	0	0	1	1	1
<i>alutaceus</i>	0	1	1	0	0	—	1	—	1	3	1	0	3	1	1	1
<i>angusticeps</i>	0	1	1	0	2	—	1	—	1	3	2	0	2	1	1	1
<i>carolinensis</i>	0	1	1	0	0	—	1	—	1	3	1	0	1	1	1	1
<i>chlorocyanus</i>	0	1	1	0	0	—	1	—	1	3	0	0	1	1	1	1
<i>equestris</i>	0	1	0	0	0	—	1	—	1	3	1	1	1	0	1	1
<i>auratus</i>	0	1	1	0	1	—	2	—	1	3	2	1	0	1	1	2
<i>fuscoauratus</i>	0	1	1	0	0	—	2	—	1	3	1	0	0	1	1	2
<i>grahami</i>	0	1	1	0	2	—	1	—	1	3	1	0	0	1	1	2
<i>meridionalis</i>	0	1	1	0	1	—	2	—	1	2	1	0	0	0	1	2
<i>onca</i>	0	1	1	0	1	—	2	—	1	3	2	0	0	1	1	2
<i>petersi</i>	0	1	1	0	1	—	2	—	1	2	1	0	0	1	1	2
<i>sagrai</i>	0	1	1	0	0	—	1	—	1	3	2	0	0	1	1	2

supported by ambiguous character placement. We could not find a 51-step tree, as Guyer and Savage claimed to have found using unweighted data. However, either of the discrepancies noted in characters 4 and 7 would account for the difference of 1 step.

A strict consensus tree (Rohlf, 1982) (Fig. 2) of the 100 trees was generated using the CONTREE program of D. Swofford (Jan. 86 version). Six of the nodes on Guyer and Savage's osteological tree are unresolved in the consensus tree. The lack of resolution results from either alternative topologies caused by character discordance or unresolved topologies resulting from absence of synapomorphies. Stem B collapses because of alternative topologies. Of the 15 possible trees describing bifurcating relationships among the four taxa *Phenacosaurus*, *Chamaelinorops*, *Chamaeleolis*, and *Anolis* (sensu lato), there are six 52-step trees that have either *Phenacosaurus* or *Chamaeleolis* as the sister-group to all other anoles; the other nine trees have 53 steps. Of the six shortest trees, five lack any synapomorphies that would resolve relationships among the three remaining taxa (*Phenacosaurus*, *Chamaelinorops*, and *Anolis*; or *Chamaeleolis*, *Chamaelinorops*, and *Anolis*), and

one (*Chamaeleolis* (*Phenacosaurus* (*Chamaelinorops*, *Anolis*))) depends on choosing one among the alternative interpretations of states 1 and 2 of character 10a.

Stem E is collapsed because there are no unambiguous synapomorphies that support any of the 15 four-taxon arrangements of *bimaculatus*, *cuvieri*, *cybotes-cristatellus*, and the remaining *Anolis* (stem F). One subset of 3 trees in which *cuvieri* is the sister-group of the other three taxa depends on choosing among alternative interpretations of states 3 and 4 of character 10a.

Stem G collapses because two equally parsimonious placements of *equestris* exist. In one, *equestris* is the sister-group of the beta section + the *carolinensis* subsection. In the second, *equestris* is in a basal polytomy with the members of the *carolinensis* subsection. A consensus of these two alternatives places *equestris* in a large polytomy comprised by the beta section and various members of the *carolinensis* subsection (Fig. 2). The difference in placement of *equestris* depends on equally parsimonious interpretations of characters 3 and 12 (splenial and number of lumbar vertebrae).

Lastly, although the beta section (stem H) remains monophyletic, three stems (I,

J, K) within that group collapse because of rearrangements involving characters 5 and 7. Also, all trees examined showed a relationship not presented in Guyer and Savage's tree, namely, that *auratus* and *onca* are sister-groups as evidenced by state 4 of character 10b.

Additionally, Guyer and Savage's osteological tree (Fig. 1) has a length of 53 steps for the unweighted data compared to 52 found for other trees in the present analysis, indicating that their tree does not provide a best fit to these data.

In conclusion, phylogenetic analysis of the unweighted osteological data yielded a much less resolved tree than that resulting from the successive weighting procedure.

Modified data set.—In addition to the analytical problems discussed above, there are problems with the characters on which the analysis was based. Although Guyer and Savage claimed to have accepted Etheridge's "coding of polarities," except in the case of the caudal vertebrae (character 15), discrepancies exist between their characters and Etheridge's in terms of both polarities and definitions.

1) Palatine teeth: absent (0), present (1). In contrast with Guyer and Savage, Etheridge (1960:107) considered the presence of palatine teeth to be ancestral for iguanids and anoles and their absence derived. *Polychrus*, used as the outgroup by Guyer and Savage, lacks palatine teeth, but these teeth are present in some leiosaurs and some para-anoles, taxa that may be more closely related to anoles than is *Polychrus* (Etheridge in Paull et al., 1976; Etheridge and de Queiroz, 1988). If the polarity used by Guyer and Savage is correct, then the character is irrelevant to anole phylogeny, because the derived condition occurs only in *Chamaeleolis*. We treated this character as unpolarized.

2) Angular: present (0), absent (1). Unchanged.

3) Splenial: present (0), absent (1). Unchanged.

4) Jaw sculpturing: absent (0), present (1). Unchanged.

5) Pineal (parietal) foramen: fronto-pa-

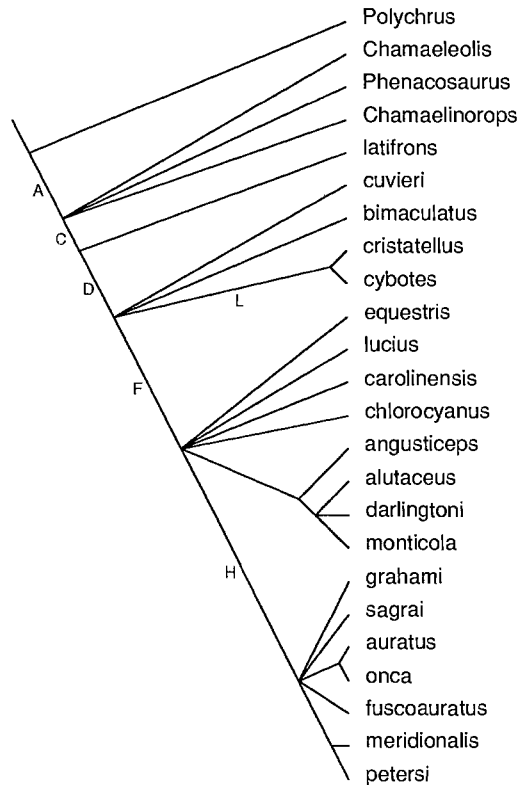


FIG. 2. Strict consensus tree derived from analysis of unweighted osteological data (Guyer and Savage 1987:table 3).

rietal suture (0), anterior edge of parietal (1), parietal (2). Unchanged.

6-8) Parietal shape: trapezoidal (0), triangular (1). Parietal crest: none or U-shaped (0), Y-shaped (1), V-shaped (2). Occipital: exposed (0), half-funnel (1). Although treated as three separate characters by Guyer and Savage, these are redundant. Parietal shape (character 6) refers to the shape of the parietal roof, that is, the superficial portion of the parietal directly underlying the skin (Fig. 3). The parietal roof is bounded laterally by the parietal crests (character 7), which separate this superficial component from the deeper lateral surfaces that serve as the site of origin for the jaw adductor muscles.

In some anoles, the shape of the parietal crests, and concomitantly the shape of the roof that they bound, undergoes considerable change in postembryonic ontogeny

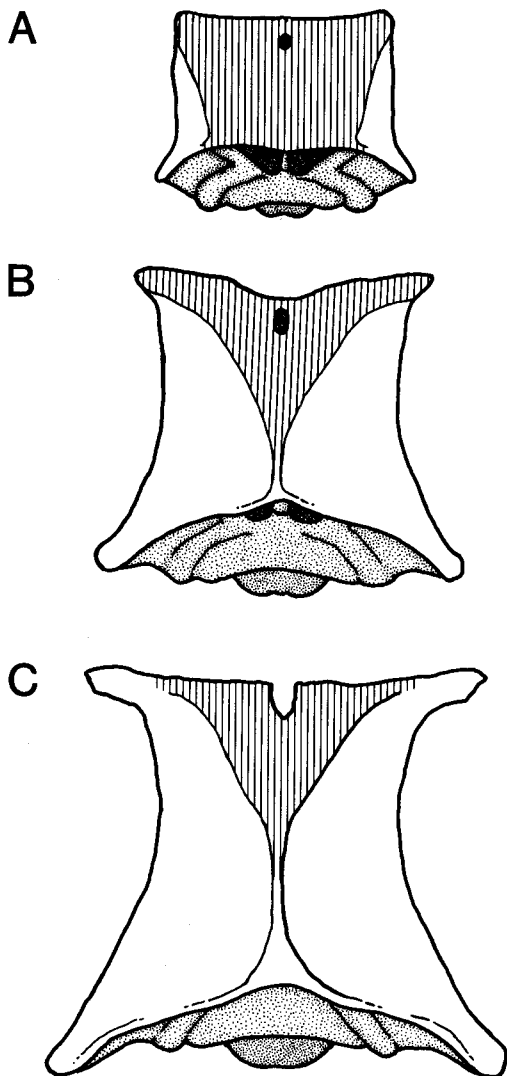


FIG. 3. Parietal regions of an ontogenetic series of *Anolis carolinensis*. Parietal roof hatched; occipital region stippled.

(Fig. 3) (Etheridge, 1960). In juveniles, the right and left crests are separated throughout their lengths and the shape of the parietal roof is trapezoidal. The lateral crests meet a transverse occipital crest on the posterior edge of the parietal table and hence, the crests on this bone form the shape of a U (Fig. 3a). During ontogeny, the parietal crests converge posteriorly until they meet to form the shape of a V, and the roof is therefore triangular (Fig. 3b). Further de-

velopment results in formation of a median crest through union of the lateral crests posteriorly. The crests thus take the shape of a Y, although the parietal roof remains triangular (Fig. 3c). Different anoles terminate their ontogenies at various stages along this trajectory.

In short, the information contained in character 6 is encompassed completely by character 7. This redundancy is supported by Guyer and Savage's character matrix; taking into consideration that the derived state of character 7 has been subdivided, the distributions of ancestral and derived states of these two characters correspond exactly.

Character 8, "Occipital" of Guyer and Savage, is also related to ontogenetic changes in the parietal described above (Fig. 3). Early in ontogeny, the parietal of anoles does not extend posteriorly over the occipital portion of the skull (Fig. 3a). In some anoles this condition persists throughout ontogeny, but in others the parietal extends posteriorly during ontogeny to cover the occipital region dorsally (Fig. 3c, "half-funnel" refers to the tapering, concave ventral surface of the parietal in forms in which this bone is extensive posteriorly). The posterior convergence and union of the lateral parietal crests is related to the posterior development of the parietal.

Guyer and Savage's matrix suggests that character 8 is independent of characters 6 and 7 in that *Chamaeleolis* is scored derived for the latter characters but ancestral (i.e., occipital exposed) for the former. This is an error. In fact, *Chamaeleolis* is among the most extreme of the anoles in terms of the posterior extension of the parietal over the occipital region. But if *Chamaeleolis* is scored 1 for character 8, as it should have been, then the derived states of characters 6 (and 7) and 8 have the same taxonomic distribution, and given their morphological interdependence, they should not be scored as separate characters.

Because all of the information contained in characters 6 and 8 is also contained in character 7, we eliminated the former two characters. Guyer and Savage's ordering of

the derived states of character 7 does not agree with Etheridge's (1960:187), and it cannot be justified by outgroup comparison. Indeed, the V-shaped crests, not the Y-shaped ones, are morphologically intermediate between the outgroup condition (U-shaped) and the Y-shaped condition in some anoles. We treated this character as unordered so as not to preclude Guyer and Savage's ordering of this state.

9) Interclavicle: arrow-shaped (0), T-shaped (1). Unchanged.

10a) Total number of parasternal ribs: >seven (0), seven (1), six (2), five (3), four (4). Guyer and Savage considered more than seven parasternal ribs, the condition in *Polychrus*, to be ancestral, but this condition does not occur in any anole nor does it occur in leiosaurs, para-anoles, or more distantly related iguanids (Etheridge, 1965). Hence, Guyer and Savage's interpretation of character polarity is based on the inappropriate practice of treating outgroup as ancestor (i.e., as if the outgroup cannot have derived characters of its own). In any case, state 0 is irrelevant to relationships among the anoles.

Although Etheridge (1960) seems to have considered high numbers of parasternal ribs to be ancestral for anoles, the seven parasternal ribs of *Phenacosaurus*, highest in the anoles, may be derived. First, the presence of five parasternal ribs in leiosaurs and some para-anoles (others have seven) (Etheridge, 1965) calls into question the interpretation that seven is ancestral. Second, *Phenacosaurus* (and *Polychrus*) appear to be derived in having only two ribs with sternal attachments (Etheridge, 1960; Etheridge and de Queiroz, 1988). The cartilaginous ventral portions of the ribs attaching to the sternum are serially homologous with similar cartilaginous portions of the xiphisternal ribs as well as with the parasternal ribs (Etheridge, 1965). Therefore, loss of a connection between sternum and what was primitively the third pair of sternal ribs, with maintenance of two xiphisternal attachments (as occurs in *Phenacosaurus* and *Polychrus*), should result in addition of an anterior parasternal element, that is, an increase in the number of par-

asternal ribs. In light of the above considerations, we recoded character 10a as seven (0), six (1), five (2), and four (3), but treated the polarity as unknown.

10b) Number of attached parasternal ribs: >six (0), five (1), four (2), three (3), two (4). Here again, some of the variation encoded in the character is irrelevant to relationships among the anoles. According to Guyer and Savage's character matrix only four, three, and two attached parasternal ribs occur in anoles, and we recoded these as states 0, 1, and 2, respectively. In this case, however, we retained Guyer and Savage's polarity.

11) Number of presacral vertebrae: 25 (0), 24 (1), 23 (2), 22 (3). Guyer and Savage treated the outgroup as a direct ancestor and coded 25 presacral vertebrae, the condition in *Polychrus*, as primitive. The high number of presacral vertebrae in this taxon is almost certainly derived (Etheridge and de Queiroz, 1988), but it is irrelevant to the problem at hand since no anole has more than 24. We retained Guyer and Savage's polarity but recoded the states as follows: 24 (0), 23 (1), 22 (2).

12) Number of lumbar vertebrae: ≤two (0), three (1), three or four (2), four (3), five (4). Again, one of the states does not occur in any anole and is therefore irrelevant. We retained Guyer and Savage's polarity but recoded the states as follows: three (0), three or four (1), four (2), five (3). Their state 2 is inappropriately defined as possession of three *or* four lumbar vertebrae seemingly implying that every species in the series is intermediate between those series scored 1 and 3; in fact, some species are derived and others primitive.

13) Number of aseptate caudal vertebrae: >eight (0), ≤eight (1). Etheridge made no statement about the polarity of this character. Guyer and Savage seem to have used the condition in *Polychrus* to determine polarity, but this presents a problem.

In those lizards possessing autotomy septa in their caudal vertebrae, the anteriormost caudal (postsacral) vertebrae are aseptate. The number of such vertebrae in *Anolis* varies among species with most hav-

ing fewer than eight, but with some having eight or more (Etheridge, 1960). Other anoles (*Chamaeleolis*, *Chamaelinorops*, and *Phenacosaurus*) and *Polychrus* lack autotomy septa entirely. Guyer and Savage scored these completely aseptate taxa state 0; however, any animal with more than eight caudal vertebrae and lacking autotomy septa necessarily has more than eight aseptate caudal vertebrae. The character would be described more accurately as the number of caudal vertebrae anterior to the first autotomic vertebra. Therefore, we scored the taxa that lack septa entirely as missing and left the polarity of this character undetermined.

14) Caudal autotomy septa: absent (0), present (1). Guyer and Savage score the absence of autotomy septa as ancestral, their presence derived. In contrast, Etheridge (1960) considered the presence of autotomy septa ancestral for both iguanids (his table VI) and anoles (his fig. 10). Nevertheless, autotomy septa are absent in *Polychrus*, para-anoles, and some leiosaurs, suggesting that Guyer and Savage's polarity is correct.

15) Caudal vertebrae: System 1: *Polychrus* (0), beta (1), alpha (2); System 2: *Polychrus* (0), alpha (1), beta (2); System 3: alpha (1), *Chamaelinorops* (0), beta (2). Etheridge (1960) considered the caudal vertebrae of anoles to fall into two classes, and he designated the sections of *Anolis* that they characterized alpha and beta. Both classes exhibit derived features relative to the caudal vertebrae of other iguanids: the alpha type in its loss of transverse processes from the autotomic vertebrae, and the beta type in having the transverse processes of the autotomic vertebrae oriented anterolaterally. Both types share the derived feature of having the autotomy septa shifted anteriorly, that is, anterior to the transverse processes when both septa and processes are present. According to Etheridge, *Chamaelinorops* possesses vertebrae of the beta type, but the vertebrae of *Chamaelinorops* are highly modified, and others have questioned this conclusion (e.g., Forsgaard, 1983; Williams in Peterson, 1983).

Etheridge considered the alpha type to

be derived from the beta type, but he noted problems (i.e., character incongruence) with this interpretation. Guyer and Savage discussed several alternative interpretations and, therefore, performed separate analyses with this character coded in three different ways. Nevertheless, their three alternatives ignore other possibilities (e.g., alpha and beta types derived independently). We left this character unordered and scored *Chamaelinorops* missing.

These data were analyzed using PAUP and MacClade as before, using a hypothetical ancestor to root the trees. A strict consensus tree (Fig. 4) differs in only one feature from the consensus tree derived from the original data of Guyer and Savage (Fig. 2). *Chamaeleolis* is placed unambiguously as the sister-group to all other anoles, the latter group united by state 1 of character 2 (absence of the angular) and, under one interpretation, by state 0 of character 1. As noted above, analysis of the unmodified data set yielded this arrangement and one other: *Phenacosaurus* as the sister-group to all other anoles, the latter group diagnosed by state 1 of character 10a (6 or fewer parasternal ribs). We did not find Guyer and Savage's interpretation of the ancestral state of character 10a to be supportable (see Modified Data Set). Because the ancestral state was scored conservatively as unknown, the presence of only six parasternal ribs is not interpreted as a derived feature allying *Chamaeleolis*, *Chamaelinorops* and *Anolis* to the exclusion of *Phenacosaurus*. Therefore, in all of the shortest trees *Chamaeleolis* is the sister-group to other anoles.

Although the unmodified and modified consensus trees differ in the resolution of only one node, both differ from Guyer and Savage's tree in that the latter has five more resolved nodes. Additionally, the use of a hypothetical ancestor reconstructed using multiple outgroups to root the modified tree (rather than treating *Polychrus* as if it were a direct ancestor) yields a different interpretation of the synapomorphies, especially at node A. The modified tree is not, however, inconsistent with that of Guyer and Savage.

OTHER DATA SETS

In addition to the reanalysis of Etheridge's (1960) osteological characters, Guyer and Savage also analyzed karyological and immunological data sets. They claimed that "the three data sets are congruent, except for the placement of the *carolinensis* subsection and their failure to resolve the relations of the beta section, the *bimaculatus* series, and the *crstatellus* series" (p. 518). The congruencies and incongruencies are more involved than indicated by Guyer and Savage, and the consensus of the three analyses is considerably less resolved than the consensus of the trees resulting from the osteological characters alone.

Karyological phylogeny.—Guyer and Savage's most parsimonious karyotype tree (their fig. 6) is congruent with the osteological tree (Fig. 1) in having the beta section derived from within the alpha section (paraphyly of the alpha section); in particular, in having the *crstatellus* and *bimaculatus* series closer to the beta section than are *Chamaeleolis*, *Chamaelinorops*, *Phenacosaurus*, and the *latifrons* and *cuvieri* series. Beyond this, congruence between osteological and karyological trees is better described as plesiomorphic lack of incongruence. For example, *Chamaeleolis*, *Chamaelinorops*, and *Phenacosaurus* retain a primitive karyotype. This evidence is consistent (i.e., not incongruent) with the phylogenetic position of these taxa, but because the primitive karyotype also occurs in some *Anolis*, it does not imply that these taxa are outside of a monophyletic *Anolis*.

Other relationships implied by Guyer and Savage's karyotype tree are neither congruent nor incongruent with the tree based on osteological characters, but some of these relationships bear on their proposed taxonomy. For example, the karyotype tree indicates that each of the *latifrons*, *auratus*, *petersi*, *grahami*, *fuscoauratus*, and *crstatellus* series are either paraphyletic or polyphyletic or both. In addition, the karyotype tree favors one of the possible arrangements of the trichotomy on the osteological tree between the *bimaculatus* and *crstatellus* series and the beta section.

Finally, at least four relationships im-

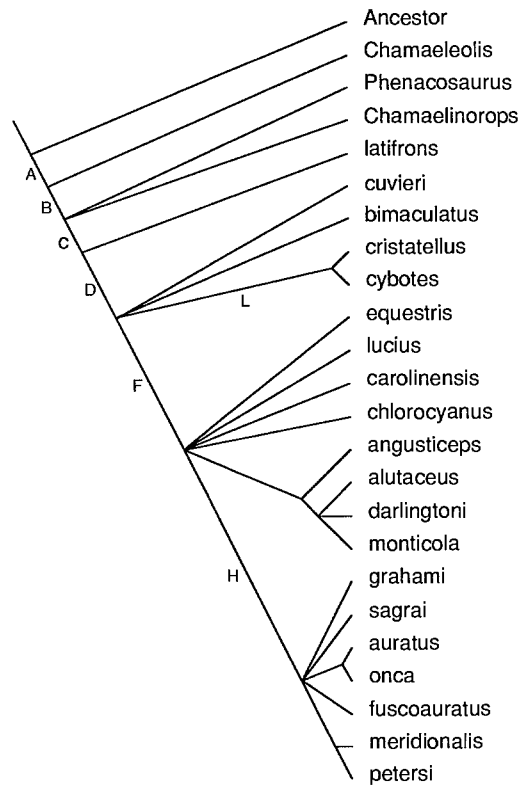


FIG. 4. Strict consensus tree derived from analysis of modified osteological data (Table 2).

plied by the karyotype tree are incongruent with those of the osteological tree. These include: (1) Closer relationship of the beta section to the *crstatellus* and *bimaculatus* series than to the *carolinensis* subsection (noted by Guyer and Savage). (2) Paraphyly of the beta section. This is contrary to Guyer and Savage's statement (p. 519) that "All data sets confirm that the beta section forms a distinct, monophyletic lineage. . . ." Guyer and Savage dismissed the paraphyly of the beta section on the karyotype tree as "a limitation of the data," arguing that the incongruencies with the osteological tree reflect the "homoplastic nature of these [karyotypic] characters." (3) Distant relationship between the *cybotes* and *crstatellus* series. The *cybotes* series is not shown on Guyer and Savage's karyotype tree, but its primitive karyotype (12V + 24m, no sex chromosome heteromorph-

ism) would place it outside the monophyletic group represented by their entire tree, within which *cratatellus* is deeply embedded. (4) Close relationship of some of the *latifrons* series to the group composed of the beta section and the *cratatellus* and *bimaculatus* series. This is contrary to Guyer and Savage's statement (p. 518) that "The three data sets agree on the positioning of the *latifrons* series at the base of the tree . . ." Their statement is an artifact of excluding the *carolinensis* subsection and the *cuvieri* and *cybotes* series (all of which have more primitive karyotypes than some members of the *latifrons* series) from the karyotype tree.

Immunological phylogeny.—Guyer and Savage's immunological tree is based on a small (six species) but taxonomically diverse (five series representing both alpha and beta sections) sample of taxa for which reciprocal distances are available (Shochat and Dessauer, 1981). As noted by Guyer and Savage, this tree is congruent with both the karyotype and osteological trees in having the beta section derived from within the alpha section, specifically, in having the beta section closer to the *cratatellus* and *bimaculatus* series than to the *latifrons* series. As they also noted, the immunological tree agrees with the karyotype tree but not with the osteological tree in having the beta section closer to the *cratatellus* and *bimaculatus* series than to the *carolinensis* subsection. The immunological tree is congruent with the osteological tree but incongruent with the karyotype tree in having the *latifrons* series outside of a monophyletic group composed of the beta section, the *carolinensis* subsection, and the *bimaculatus* and *cratatellus* series. The *carolinensis* subsection is not shown on their karyotype tree (and the data are omitted from their table 4), but the primitive karyotype of the *carolinensis* subsection (Gorman, 1973) would place it outside all taxa shown on the tree—including at least part of the *latifrons* series. The immunological tree is also incongruent with the karyotype tree, but only consistent with the osteological tree, in having the beta section closer to the *cratatellus* series than to the *bimaculatus* series.

CONSENSUS OF THE THREE DATA SETS

Guyer and Savage adopted a consensus approach to the results of the three different analyses. Although they did not present a consensus tree, they discussed congruence among the different trees and did not attempt to combine data into a single analysis. The consensus approach has been criticized on grounds of overall parsimony (Miyamoto, 1985); nevertheless, we produced a consensus tree in order to examine Guyer and Savage's claim of "an essential congruence among the several data sets" (p. 512).

A strict consensus tree (Fig. 5) for the relationships based on separate analyses of the three data sets, osteology, karyology, and immunology, was derived by eliminating resolution on the osteological consensus tree (Fig. 4) as follows. Stem H was collapsed because the beta section is paraphyletic with respect to *bimaculatus* and *cratatellus* on the karyotype tree. Close relationships between the beta section and the *cratatellus* and *bimaculatus* series on both the immunological and karyotype trees collapsed stem F. Although not shown on their tree, the primitive karyotypes of the *cuvieri* and *cybotes* series and the *carolinensis* subsection relative to some members of the *latifrons* series caused stems D and L to collapse. The consensus of all three data sets (Fig. 5) presents a considerably less resolved phylogeny than the consensus tree based on osteological characters alone (Figs. 2, 4) and serves as the basis for comments on Guyer and Savage's proposed taxonomy of anoles.

TAXONOMY

Based on their phylogenetic analysis, Guyer and Savage presented a purportedly cladistic taxonomy of anoles in which *Anolis* was dismantled into several genera (Table 1). Despite their claim of congruence among the several data sets, our analysis reveals sufficient incongruence that the resulting consensus tree is largely unresolved (Fig. 5). Such a tree provides little basis for erecting monophyletic taxa, much less a sequenced, phylogenetic arrange-

ment. Additionally, Guyer and Savage's taxonomy can be criticized for reasons that fall into three general categories:

1) Guyer and Savage applied names to single terminal taxa as if these were monophyletic, when their monophyletic status was not investigated, or was contradicted by the available data. This problem applies to the names proposed for the *latifrons* and *cuvieri* series. In the case of *latifrons*, there is only one derived state (four parasternal ribs; state 4 of character 10a) supporting monophyly on the osteological tree, but its placement here is ambiguous. It either arises convergently in *latifrons* and stem E, or arises at stem C and reverses to state 3 in *cuvieri*. Additionally, variation within the *latifrons* series in this character and character 10b (see their table 3), as well as karyotype features (their fig. 6), suggests that the group is paraphyletic. Furthermore, Guyer and Savage included in the genus ("*Dactyloa*") five series in addition to *latifrons* whose relationships were not analyzed. Finally, although they claim to "precisely diagnose groupings based on synapomorphic and autapomorphic characters" (p. 519), the characters listed in the diagnosis of this genus apply to virtually all *Anolis* (sensu lato).

The genus named for the *cuvieri* series ("*Semiurus*") is also supported by only one synapomorphy, state 3 of character 10a, but again, its placement is ambiguous. In this case, however, no other data presented suggest that the series is paraphyletic.

2) Guyer and Savage applied names to groups of terminal taxa whose monophyletic status is questionable according to their analysis, our re-analysis, or both. This criticism applies to names proposed for (1) the group composed of the *bimaculatus*, *crisatellus*, and *cybotes* series ("*Ctenonotus*"), (2) the *carolinensis* subsection ("*Anolis*"), and (3) the beta section ("*Norops*"). Monophyly of "*Ctenonotus*" is not supported on any of the osteological trees, and is contradicted by the karyological and immunological data. Monophyly of the *carolinensis* subsection is supported only by state 2 of character 12 on the weighted osteological tree and on some of the unweighted trees, but

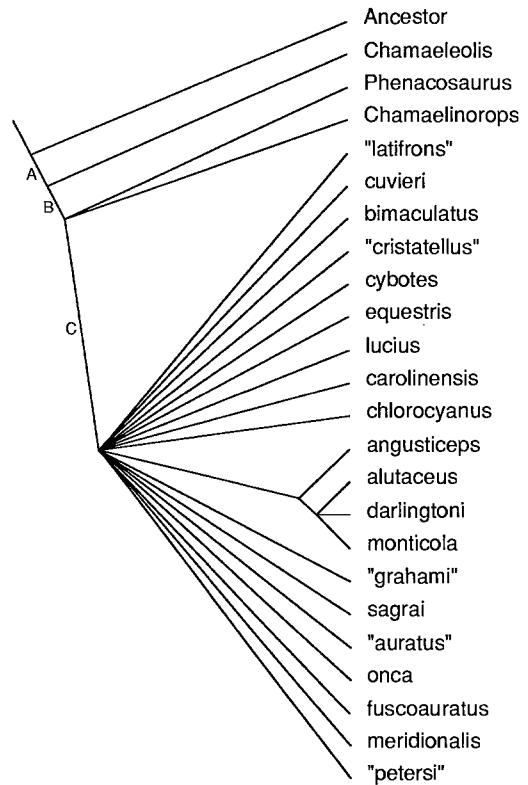


FIG. 5. Strict consensus tree derived from osteological, karyotype, and immunological data of Guyer and Savage (1987).

is not supported on the consensus of the osteological trees. Moreover, state 2 is inappropriately defined as three or four lumbar vertebrae, with the actual derived condition (four lumbar vertebrae) being found only in some species in the series. Lastly, monophyly of the beta section is contradicted by the karyological data.

3) Guyer and Savage proposed a new generic level taxonomy when their own analysis indicated that the traditional one was already consistent with their taxonomic principles. Although they provided evidence for the possible paraphyletic nature of the alpha section and *punctatus* subsection, their proposal for rectification unnecessarily partitioned *Anolis* into several genera. Savage and Talbot (1978) had already resurrected *Norops* for the beta section of *Anolis* and restricted *Anolis* to the alpha section, a taxonomy that has not

gained general acceptance. Guyer and Savage, in effect, have attempted to preserve *Norops* by rendering *Anolis* monophyletic through the exclusion of the *latifrons*, *bimaculatus*, *cuvieri*, *cybotes* and *crisatellus* series. In fact, the osteological tree (Fig. 1) on which their revision was based indicated that *Anolis* as traditionally conceived is a monophyletic taxon. Given that both taxonomic stability and an accurate depiction of phylogeny are desirable, then recognizing a single genus *Anolis* is preferable to resurrecting several genera and restricting the meaning of the name *Anolis*. A phylogenetic taxonomy could have been effected by reorganizing sections, subsections, and series within *Anolis*, without generic level re-arrangements.

CONCLUSIONS AND SUMMARY

To recapitulate, Guyer and Savage's use of a successive weighting algorithm arbitrarily biased the results of their cladistic analysis. Analysis of the unweighted, unmodified data yielded several trees whose incompatibilities resulted in a poorly resolved consensus tree. Analysis of the modified data set produced a similar consensus tree with one additional resolved node among the non-*Anolis* anoles. Neither consensus tree supported the generic partitioning of *Anolis*. Trees derived from the karyotype, immunological, and unmodified (or modified) osteological data sets are incongruent to the extent that their consensus results in a tree in which almost all of the series of *Anolis* form a unresolved polytomy. The lack of evidence for monophyly of several genera resurrected by Guyer and Savage precludes their recognition as phylogenetic taxa. We do not mean to imply that these taxa are not monophyletic, or that the relationships proposed by Guyer and Savage are incorrect, only that there are more incongruences than they acknowledged. Indeed, even if their hypothesis of relationships is accepted, a phylogenetic taxonomy could have been effected without dismantling of *Anolis*. We conclude that Guyer and Savage's proposed taxonomy is neither de-

manded by, nor consistent with, the results of phylogenetic analysis.

ACKNOWLEDGMENTS

We thank R. Etheridge, J. A. Gauthier, G. C. Gorman, H. W. Greene, S. B. Hedges, J. "Bonehead" Losos, D. B. Wake, and E. E. Williams for comments on the manuscript, and H. W. Greene and J. B. Losos for permission to skeletonize specimens used in Figure 3. E. E. Williams provided us a manuscript detailing his disagreements with Guyer and Savage's paper. J. S. Farris explained how successive weighting is done by PHYSYS. IBM hardware for phylogenetic analysis was provided by an IBM DACE grant to the Museum of Vertebrate Zoology. This study was supported in part by a NSF Postdoctoral Fellowship to the senior author.

REFERENCES

- CASE, S. M., AND E. E. WILLIAMS. 1988. The cybotoid anoles and *Chamaelinorops* lizards (Reptilia: Iguanidae): Evidence of mosaic evolution. *Zool. J. Linn. Soc.*, 91:325-341.
- ETHERIDGE, R. 1960. The relationships of the anoles (Reptilia: Sauria: Iguanidae): An interpretation based on skeletal morphology. Ph.D. Dissertation, Univ. Michigan, Ann Arbor.
- ETHERIDGE, R. 1965. The abdominal skeleton of lizards in the family Iguanidae. *Herpetologica*, 21: 161-168.
- ETHERIDGE, R., AND K. DE QUEIROZ. 1988. A phylogeny of Iguanidae. Pages 283-368 in *Phylogenetic relationships of the lizard families* (R. Estes and G. K. Pregill, eds.). Stanford Univ. Press, Palo Alto, California.
- FARRIS, J. S. 1969. A successive approximations approach to character weighting. *Syst. Zool.*, 18:374-385.
- FORSGAARD, K. 1983. The axial skeleton of *Chamaelinorops*. Pages 284-295 in *Advances in herpetology and evolutionary biology: Essays in honor of E. E. Williams* (G. J. Rhodin and K. Miyata, eds.). Museum of Comparative Zoology, Harvard Univ., Cambridge, Massachusetts.
- GORMAN, G. C. 1973. The chromosomes of the Reptilia, a cytotoxic interpretation. Pages 349-424 in *Cytotaxonomy and vertebrate evolution* (A. B. Chiarelli and E. Capenna, eds.). Academic Press, London.
- GORMAN, G. C., AND L. ATKINS. 1969. The zoogeography of Lesser Antillean *Anolis* lizards—An analysis based on chromosomes and lactic dehydrogenase. *Bull. Mus. Comp. Zool.*, 138:53-80.
- GORMAN, G. C., D. G. BUTH, AND J. S. WYLES. 1980. *Anolis* lizards of the eastern Caribbean: A case study in evolution. III. A cladistic analysis of albumin immunological data, and the definitions of species groups. *Syst. Zool.*, 29:143-158.
- GUYER, C. AND J. M. SAVAGE. 1987 [1986]. Cladistic relationships among anoles (Sauria: Iguanidae). *Syst. Zool.*, 35:509-531.

- LOSOS, J. B. 1988. A phylogenetically based analysis of character displacement in Caribbean *Anolis* lizards. Manuscript.
- MIYAMOTO, M. M. 1985. Consensus cladograms and general classifications. *Cladistics*, 1:186-189.
- PAULL, D., E. E. WILLIAMS, AND W. P. HALL. 1976. Lizard karyotypes from the Galapagos Islands: Chromosomes in phylogeny and evolution. *Breviora*, 441:1-31.
- PETERSON, J. A. 1983. The evolution of the subdigital pad in *Anolis*. I. Comparisons among the anoline genera. Pages 245-283 in *Advances in herpetology and evolutionary biology: Essays in honor of E. E. Williams* (G. J. Rhodin and K. Miyata, eds.). Museum of Comparative Zoology, Harvard Univ., Cambridge, Massachusetts.
- ROHLF, F. J. 1982. Consensus indices for comparing classifications. *Math. Biosci.*, 59:131-144.
- ROUGHGARDEN, J., D. HECKEL, AND E. R. FUENTES. 1983. Coevolutionary theory and the biogeography and community structure of *Anolis*. Pages 371-410 in *Lizard ecology: Studies of a model organism* (R. B. Huey, E. R. Pianka, and T. W. Schoener, eds.). Harvard Univ. Press, Cambridge, Massachusetts.
- SAVAGE, J. M., AND J. J. TALBOT. 1978. The giant anoline lizards of Costa Rica and Western Panama. *Copeia*, 1978: 480-492.
- SCHOENER, T. W. 1968. The *Anolis* lizards of Bimini: Resource partitioning in a complex fauna. *Ecology*, 49:704-726.
- SHOCHAT, D., AND H. C. DESSAUER. 1981. Comparative study of albumins of *Anolis* lizards of the Caribbean islands. *Comp. Biochem. Physiol.*, 68A:67-73.
- WILLIAMS, E. E. 1969. The ecology of colonization as seen in the zoogeography of anoline lizards on small islands. *Q. Rev. Biol.*, 44:345-389.
- WILLIAMS, E. E. 1972. The origin of faunas: Evolution of lizard congeners in a complex island fauna—A trial analysis. *Evol. Biol.*, 6:47-89.
- WILLIAMS, E. E. 1976a. West Indian anoles: A taxonomic and evolutionary summary. I. Introduction and a species list. *Breviora*, 440:1-21.
- WILLIAMS, E. E. 1976b. South American anoles: The species groups. *Pap. Avulsos Zool.*, Sao Paulo, 29: 259-268.
- WILLIAMS, E. E. 1983. Ecomorphs, faunas, island size, and diverse end points in island radiations of *Anolis*. Pages 326-370 in *Lizard ecology: Studies of a model organism* (R. B. Huey, E. R. Pianka, and T. W. Schoener, eds.). Harvard Univ. Press, Cambridge, Massachusetts.
- WYLES, J. S., AND G. C. GORMAN. 1980. The classification of *Anolis*: Conflict between genetic and osteological interpretations as exemplified by *Anolis cybotes*. *J. Herpetol.*, 14:149-153.

Received 25 January 1988; accepted 31 May 1988.

Graphs and Generalized Tracks: Some Comments on Method

C. J. HUMPHRIES¹ AND O. SEBERG²

¹Department of Botany, British Museum (Natural History),
Cromwell Road, London SW7 5BD, England

²Botanical Laboratory, 140 Gothersgade, DK-1123 Copenhagen K, Denmark

Panbiogeography makes no assumptions about the nature of area relationships [Page, 1987:2].

For some years now, a number of workers from the Antipodes have extolled the virtues of Croizat's panbiogeographical method (e.g., Craw, 1982, 1983, 1984, 1985, 1987; Craw and Gibbs, 1984; Craw and Weston, 1984; Heads, 1985; Grehan and Henderson, in press). Originally, the form of explanation was to say that Croizat had been neglected in the literature and that other biogeographers, and particularly vic-

ariance biogeographers, have misunderstood or misrepresented his method and considered it a crude precursor of vicariance biogeography or the results as some form of phenetics (e.g., Ball, 1975; Patterson, 1981).

Page (1987) has recently identified the main issue of debate as the status of Croizat's actual method of analysis. He goes on to express his own view of what Croizat's method of analysis is about and develops panbiogeography into a quantified meth-