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SKULL CHARACTERS AND THE CLADISTIC RELATIONSHIPS OF THE HISPANIOLAN DWARF TWIG ANOLIS

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ABSTRACT: Skull characters were examined and combined with postcranial osteological, external, allozyme, DNA sequence, and chromosome data from the literature to estimate the phylogenetic relationships of the Hispaniolan dwarf twig *Anolis* (*A. sheplani*, *A. insolitus*, and *A. placidus*). A survey of most species of *Anolis* species for which skeletons are available found two osteological character states unique to these species, a convex parietal roof and crenulated parietal edges, thus suggesting that the Hispaniolan twig dwarfs form a monophyletic group. To assess this hypothesis of monophyly and to estimate the phyletic placement of these species in the genus *Anolis*, parsimony analyses were undertaken including all proposed close relatives of the Hispaniolan twig dwarfs and a taxonomically and geographically diverse sample of congeners. Diagnostic synapomorphies found in this analysis were surveyed more widely in *Anolis*. Characterization difficulties of the skull data were addressed by using three coding methods to differentially code intraspecific and continuous variation. Confidence in the Hispaniolan twig dwarf relationships was assessed with the bootstrap, the test of Templeton, and the agreement between results from the three coding methods. The monophyly of the Hispaniolan twig dwarfs was strongly supported. The nearest relatives of the Hispaniolan twig dwarfs appear to be twig species from Hispaniola (*A. darlingtoni*), Puerto Rico (*A. occultus*), and South America (*tigrinus* group, i.e., *A. solitarius*), and *Phenacosaurus*. Wider taxonomic and character sampling is needed to assess the robustness of these clades, but present evidence suggests an invasion of Hispaniola or Puerto Rico from South America and, counter to the usual opinions of ecomorph occurrence by intra-island adaptive radiation, a clade of twig species on three different land masses.

Key words: *Anolis placidus*; *Anolis sheplani*; *Anolis insolitus*; Character coding; Cladistics; Skulls; Phylogeny; Twig ecomorph

IN 1983, Ernest Williams coined the term "ecomorph" to refer to species of *Anolis* of similar ecology and morphology that belong to separate phyletic lines and occur on different Caribbean islands. The "twig" ecomorph is characterized by short limbs, a long snout, a short prehensile tail, and cryptic coloration and behavior (Hedges and Thomas, 1989; Rand and Williams, 1969; Williams, 1983). Twig anoles are known to occur on Jamaica (*A. valencienni*), Hispaniola (*A. fowleri*, *A. darlingtoni*, *A. sheplani*, *A. insolitus*, and *A. placidus*), Puerto Rico (*A. occultus*), Cuba (*A. angusticeps*), and probably in northern South America (*tigrinus* series species: i.e., *A. tigrinus* and *A. solitarius*). Evolutionary relationships of the twig species are not well known, with one exception. The Jamaican species *A. valencienni* has been suggested to be part of a monophyletic, apparently adaptive intra-island radiation (Hedges and Burnell, 1990; Shochat and

Dessauer, 1981); other twig species as well as other ecomorphs also are believed to evolve as part of adaptive intra-island radiations (Hedges and Thomas, 1989; Losos, 1994). The monophyly of the Jamaican series, which includes ecomorph types seen on other islands, demonstrates that ecomorph convergence has occurred (Williams, 1983).

Examination of most of the skulls of *Anolis* at Harvard University's Museum of Comparative Zoology (200+ species) revealed that the Hispaniolan twig dwarf species [Williams (1983) differentiated between twig giants and twig dwarfs] *A. insolitus*, *A. sheplani*, and *A. placidus* share two osteological character states apparently unique in *Anolis*, namely, a convex parietal roof and crenulated parietal edges. The aims of this paper are (1) to assess the monophyly suggested by these apparently unique character states, (2) to gain a preliminary assessment of the phyletic position of the Hispaniolan dwarf twig species within the genus *Anolis*, and (3) in the

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context of these analyses, gain a preliminary estimate of the higher level phylogeny of *Anolis*.

Previous workers have suggested that the Hispaniolan twig dwarfs are not monophyletic. In their allozyme studies, Hedges and Thomas (1989) and Burnell and Hedges (1990) postulated a sister species relationship of *A. sheplani* and *A. placidus* in their *sheplani* series, but grouped *A. insolitus* with other twig species *A. fowleri* in their *christophei* series. In his taxonomic summary based on osteological, karyotypic, and external data, Williams (1976a) placed *A. darwingtoni* with *A. insolitus* in his *darwingtoni* series, and grouped *A. sheplani* with *A. occultus* in his *occultus* series. However Williams (1976a) did not perform phylogenetic analyses, so the monophyly of these series and of his higher level groupings has not been established. Savage and Guyer (1989; based on Guyer and Savage, 1986) placed the Hispaniolan dwarf twig species in their genus *Anolis* (sensu stricto), recognizing the *darwingtoni* and *occultus* series of Williams (1976a,b) within this. This generic assignment apparently was based on their inclusion of Williams' (1976a) *darwingtoni* series as a terminal taxon (which was miscoded for two characters; personal observation). The Guyer and Savage (1986, 1992) taxonomy is not followed here for the reasons outlined in Cannatella and de Queiroz (1989) and Williams (1989).

The monophyly and relationships of the Hispaniolan twig dwarfs would be best evaluated with a phylogenetic analysis of all species of *Anolis*. However, because of the unwieldy size of the genus *Anolis* (~400 species), it is not feasible to analyze simultaneously all species of *Anolis*. Because of the uncertainty regarding higher-level relationships of *Anolis* species and the relationships of the Hispaniolan dwarf twig species, it is not possible to be certain that a more limited ingroup is monophyletic. To address these difficulties, given constraints of time and material, the relationships of the Hispaniolan dwarf twig *Anolis* were assessed with the following methods.

First, parsimony analyses were conduct-

ed including all suggested close relatives of the Hispaniolan dwarf twig species as well as representatives of all series (= small informal grouping of species) recognized by Etheridge (1959), Williams (1976a,b), and Burnell and Hedges (1990) except Williams' *laevis* series. Species were selected from these series to correspond with published analyses in order to maximize the amount of data used (e.g., I tried to use species scored for DNA data by Hass et al., 1993). This is the first study since Etheridge (1959) to incorporate representatives from each series. Methodologically compatible data from diverse sources (DNA sequences, allozymes, chromosomes, osteology, scales) were combined with skull characters collected for this paper in parsimony analyses [Kluge's (1989) "total evidence"]. Because of continuous and intraspecific variation, alternative characterizations were equally justifiable for most skull characters. Therefore, alternative codings of the skull data were undertaken and the resulting effects on hypothesized relationships were examined (Gift and Stevens, 1997). These alternative codings served to assess the robustness of recovered relationships; clades that are insensitive to alteration of coding assumptions are considered to be more strongly supported. Bootstrap parsimony analyses and the test of Templeton (1983) also were used to assess Hispaniolan twig dwarf monophyly.

In addition, diagnostic synapomorphies discovered in these analyses were surveyed more widely in *Anolis* to assess the likelihood that recovered clades will withstand addition of more taxa and characters. This approach has disadvantages relative to including all species of *Anolis* in phylogenetic analyses, for example the possibility that inclusion of more species will affect hypothesized relationships (e.g., Gauthier et al., 1988). However this approach is adopted as an informative compromise to the time-intensive option of including all 350 species of *Anolis* and the less conclusive option of doing just the parsimony analyses with only the species studied here.

MATERIALS AND METHODS

Phylogenetic relationships of the Hispaniolan dwarf twig anoles were first investigated with cladistic parsimony analyses. Species analyzed that were previously grouped with the Hispaniolan twig dwarfs include *A. darlingtoni* (Williams, 1976a), *A. occultus* (Burnell and Hedges, 1990; Williams, 1976a), *A. monticola*, and *A. fowleri* (Burnell and Hedges, 1990). Specimens examined are listed in Appendix I.

Skulls were examined for systematic characters. Discrete coding is required for the operations of standard character analysis, with presence of a recognizable morphological gap the preferred criterion for delimiting character states and selecting characters (Stevens, 1991). However, in this study, virtually all characters examined exhibit continuous variation, including those used by Etheridge (1959) and Guyer and Savage (1986). Characters were used that could be coded objectively (i.e., "contact" vs. "non-contact" was acceptable but "long" vs. "short" was not) or for which a recognizable gap occurred between morphological states. Alternate coding methods were employed to address characterization difficulties and to explore alternative possible transformations, as explained below. Examples of characterization difficulties are given in the character descriptions.

This approach allowed for the use of characters that varied intraspecifically and, or, continuously. The boundaries between continuous and discrete and between intraspecifically variable and invariant are unclear (Thiele, 1993), but some explanation for including these character "types" that historically have been avoided on theoretical grounds may still be warranted. Intraspecifically variable characters were used because they have been shown in some cases to be congruent with intraspecifically invariant characters (Campbell and Frost, 1993) and to have hierarchical signal (Wiens, 1995). Continuously varying characters were used because they have in some cases been shown to be congruent with more traditional characters (Thiele, 1993) and because they should be tested

with the same criteria as other characters (i.e., congruence). Furthermore, the use of continuous and polymorphic characters is not actually novel, as many purportedly discrete characters used in cladistic analyses are in fact continuously valued characters rendered discrete by creative description (reification: Stevens, 1991), and many authors probably use intraspecifically varying characters without acknowledging them as such (Wiens, 1995).

In the following discussion, Jardine's (1969) terminology is adopted, whereby an "attribute state" as a condition of an individual organism (postfrontal absent, parietal Y-shaped) and a "character state" is a characterization of a taxon (here, essentially a condition of a species that corresponds to a cladistic matrix state: e.g., 50% of individuals with a postfrontal). Cladistic character states were based on first identifying one or more boundaries (i.e., presence/absence of a bone) delimiting attribute states. These attribute states served as character state codings for intraspecifically invariant characters. For intraspecifically variable characters, character states were applied to taxa according to three methods: frequency (Wiens, 1995), unscaled, and any-instance (Campbell and Frost, 1993).

Because gaps between attribute states generally were not evident, the frequency, unscaled, and any-instance methods were used here to erect alternative boundaries along more or less continuous variation. Because the variation is continuous, the frequencies of the traits for each species generally correlates with the morphological or attribute states for those species. For example, in species with a percentage of individuals lacking a postfrontal bone, that bone is invariably tiny. Conversely, in species in which all specimens have a postfrontal, that bone is generally larger. No attempt was made to code these differences in size because erecting a dividing line between "large" and "small" bones is difficult, especially so when comparing species of the disparate sizes seen in this analysis (see, e.g., character 10). However it is easy to tell when a bone is present or absent, so the presence/absence boundary

is used even though there may be no more evolutionary significance to this boundary than any of the potential large/small boundaries. Using this attribute state boundary, then, alternative cladistic character codings (frequency, any-instance, unscaled) were tried in an attempt to offer alternative characterizations of the observed morphologies.

The frequency bins method approximates "smooth" scaling by assigning different states (32 states in PAUP; 0-9-a-v) to polymorphic species based on the frequency of an attribute state within a species with character states ordered and all characters scaled to equal weight for changes from fixation for one attribute state to fixation for another attribute state (Wiens, 1995). Wiens and Servedio (1997) found that frequency methods performed best in evaluation of different coding methods for discrete, intraspecifically variable characters.

The unscaled approach (Campbell and Frost, 1993) assigns an intermediate character state to intraspecifically varying species [e.g., A → (A or B) → B becomes 0 → 1 → 2, where A and B are attribute states and 0-2 are character states] and does not scale characters to equal weight; that is, e.g., for binary characters, changes between extremes of variation occur at a cost of one step when there is no intraspecific variation and at two steps when intraspecific variation occurs. A threshold of one specimen is used. This method was recommended by Campbell and Frost (1993).

The any-instance approach (Campbell and Frost, 1993) combines all apomorphic conditions, such that both intraspecifically variable species and invariantly apomorphic species are assigned the same derived state. Characters that could not be polarized a priori were excluded from an initial analysis and then coded according to the distribution of states in that analysis (Campbell and Frost, 1993); that is, if an unambiguous state could be determined at the ingroup/outgroup node, that state was considered plesiomorphic and other states were combined. Characters that could not be polarized (for which primitive states

could not be determined) or for which an intermediate state was found to be plesiomorphic were coded according to the unscaled method. The any-instance approach is extended here to ordered multistate characters that change continuously [e.g., A → B → C is coded as 0 (A) → 1 (B, C)]. See Wiens (1995) and Campbell and Frost (1993) for description and discussion of the frequency, any-instance, and unscaled coding methods for discrete variation. These methods were applied only to the skull data (characters 86–116) which were collected for this paper and partially to the postcranial osteological and external data, as discussed below. The different coding methods could not be applied to most characters from the literature because information on intraspecific variation was not available.

I am using three different coding methods to assess the sensitivity of phylogeny estimates to changes in coding assumptions, and I am not certain which of these is the best way of the three, theoretically, to code variation. That stated, I prefer the frequency method for the following reasons. First, it is less sensitive to sampling error than the other methods (Swofford and Berlocher, 1993). Second, it retains the most phylogenetic information (Wiens, 1995). Third, the frequency method offers a convenient and objective way to recognize intermediate morphologies as separate character states. In the case of continuous variation (virtually all skull characters in this analysis), "variable" species tend to have states that are morphologically intermediate between "fixed" species. The frequency method recognizes these differences and weights changes based on the degree of difference in frequency (and thus morphology). The other methods erect essentially arbitrary character state boundaries along a continuum of states. This approach may be reasonable when there is some evolutionary significance to the boundary. For example, it is probably more difficult evolutionarily to gain a particular allele (change from 0% to any percent) than it is to increase frequency of that allele from, say, 20–21%. But in con-

tinuously varying morphological characters, such clear boundaries do not exist.

Leiocephalus and the polychrotid genera *Enyalius*, *Urostrophus*, *Anisolepis*, and *Polychrus* were included as outgroups. Frost and Etheridge (1989) found these species (except *Leiocephalus*) to be closest relatives of *Anolis*. *Leiocephalus* was included to help root the DNA sequence data (Hass et al., 1993). This analysis is concerned solely with ingroup relationships. Synapomorphies were not sought for anole monophyly.

Additional characters were obtained from the external data of Williams et al. (1995) and others (listed in text), the postcranial osteological data set of Etheridge (1959), the DNA sequence data of Hass et al. (1993), the allozyme data sets of Burnell and Hedges (1990) and Hedges and Burnell (1990), and the chromosomal data of Webster et al. (1972), Webster (1974), and Gorman (1973). These characters were used in an attempt to incorporate all methodologically compatible data [the "total evidence" of Kluge (1989)].

In addition to Etheridge's (1959) skull characters re-examined here, this study uses only his characters of interclavicle shape (no. 9 of Guyer and Savage, 1986, 1992), number of inscriptional ribs (10a), number of attached inscriptional ribs (10b), caudal autotomy (14), and caudal processes (15). Other postcranial characters used by Etheridge (1959) and then Guyer and Savage (1986, 1992) were omitted because they are invariant for these species (Guyer and Savage, 1992: their appendix 3) or because of coding ambiguities due to "some variation in all species" (Etheridge, 1959). Although this study makes liberal use of intraspecifically variable characters, it is difficult to code intraspecifically variable characters from the literature without information on how many specimens are variable. One of Etheridge's (1959) skull characters, jaw sculpturing, was not used here because of characterization difficulties. Assessment of homology is difficult for this character (Etheridge, 1959), and inter- and intraspecific variation in degree of sculpturing among

males made erection of a character state boundary difficult.

External characters from Williams et al. (1995) were coded as discrete states or using Thiele's (1993) gap-weighting method. Although means (e.g., Thiele, 1993) or modes (e.g., Mabee, 1993) may be most appropriate as cladistic states, medians were used as character states (e.g., Mickovich and Johnson, 1976), because Williams et al. (1995) gave only the range for scale counts. If the data approximate a normal distribution, which is not unlikely, all of these statistics should give about the same values. Some have argued against the use of "quantitative" data in cladistics (Farris, 1990). However quantitative and qualitative are simply methods of expression of variation rather than properties of variation (Thiele, 1993). The variation in these quantitatively coded characters is no different from that in continuously varying qualitative characters such as shape of the parietal or presence/absence of the postfrontal. Thiele's method, like frequency coding, simply recognizes finer differences.

Data matrices of 116 characters were analyzed using PAUP version 3.1 (Swofford, 1993) under the conditions of the three analyses. Character evolution was examined across most parsimonious trees (mpts) from the frequency analysis using PAUP. Clade support was assessed with the differing character change assumptions, the test of Templeton (1983), and the bootstrap (Felsenstein, 1985), with special reference to the Hispaniolan twig dwarf species. Although significance values for the accuracy of the bootstrap depend on the evolutionary processes at work (Hillis and Bull, 1993), this measure still is used to assess relative clade support, under the assumption that clades with higher bootstrap values are more likely to withstand addition of more taxa and characters in future analyses.

After these initial parsimony analyses, synapomorphies found to diagnose dwarf twig anole relationships were examined in 143 species of *Anolis*. This survey was undertaken to assess whether other species are likely to occur in the clades found in

this study when more species are analyzed. If the synapomorphies found to delimit Hispaniolan dwarf twig species clades in the parsimony analyses of this paper are common in species of *Anolis* not included here, then other species of *Anolis* are likely to occur in clades recovered in this analysis when more species are analyzed. In that case, little could be said about relationships within these clades. For example, if other species are found to share the synapomorphies that delimit a (*A. insolitus*, *A. placidus*, and *A. sheplani*) clade in the parsimony analyses of this paper, then a conclusion of this paper would be that the Hispaniolan dwarf twig species may not be monophyletic. Conversely, if these synapomorphies are nonexistent in species not analyzed here, the monophyly of the Hispaniolan dwarf twig clade is likely to withstand the addition of more species.

Characters

The following character descriptions describe the attribute states recognized in individual organisms. Cladistic character states, listed in appendices II (frequency), III (unscaled), and IV (any-instance), are based on these descriptions. Thus, for intraspecifically variable characters, numbered states in the character descriptions do not necessarily correspond to the matrix entries but rather to conditions on individual organisms from which the matrix codings are based. But for reference, the attribute state assigned "0" in the character description is always coded as "0" in the cladistic matrix (the alternative state could be "1", "v", or some other letter or number depending on the states and the particular analysis; see below). Individuals with bilateral variation were scored as having half of each state. Figures for these characters (Figs. 1–14) generally depict extreme conditions; intra- and interspecific variation occur between the states shown in most cases.

Continuously varying multistate characters were considered ordered. Thus, change between more similar morphologies was assumed to be evolutionarily easier. Ordered or additive coding is indicated by an arrow (\leftrightarrow ; double edged to signify

reversibility of states) between states in the character descriptions, unordered or non-additive coding is signaled by a semicolon (;). Characters noted as "variable" have some species with two or more attribute states and are coded differently in the three analyses. Intraspecifically variable characters with two attribute states (most skull characters) are coded as follows. (1) *Frequency*: scored as an ordered (additive) character with states 0 to v, with each cladistic coding corresponding to a percentage of specimens with a given state and scaled such that change between 0 and v (the extremes) costs one step (e.g., Wiens, 1995). (2) *Unscaled* (Campbell and Frost, 1993): coded as three ordered states ($0 \leftrightarrow 1 \leftrightarrow 2$), with states 0 and 2 corresponding to "fixation" for a species, and state 1 indicating that at least one specimen has a different attribute state than the others of that species. Change between 1 and either state costs one step, change between 0 and 2 costs two steps. (3) *Any instance*: plesiomorphic conditions are assigned one state (0 or v—these symbols were selected for convenience, any PAUP symbols could be used so long as the character is left unordered and unscaled) and all apomorphic conditions, including intraspecific variation, are assigned the alternative state (0 or v). Variable characters that were not coded according to this scheme (i.e., intraspecifically variable characters with multiple recognized attribute states) are described in the character descriptions. For continuously varying quantitative characters (those coded with gap weighting), extreme conditions are listed. Gap weighting, which is dependent on the extreme values of the group analyzed, was instituted without reference to the outgroups. If outgroup values were outside of the range seen in the ingroup, the outgroup species was assigned whatever extreme state was closest to its value. Citations are listed for characters that have previously been scored in analyses including *Anolis*.

Characters 1–12 are external data collected from the literature, mainly from Williams et al. (1995). In cases of conflict between Williams et al. (1995) and original

species descriptions (e.g., Williams et al. (1995) listed *A. insolitus* as having keeled or smooth supradigitals, the original description lists just smooth), specimens were checked if available. If specimens could not be examined, the data in the original character description were followed. Characters coded using Thiele's (1993) gap weighting method were natural-log transformed prior to coding (Thiele, 1993). Variable characters that were not gap-weighted (Nos. 1, 3, 4) could not be scored according to frequency because this information is not available in the literature; such characters still were scored such that change between extremes cost one step in the frequency analysis. Several of the scale characters in Williams et al. (1995) were not used because of suspected nonindependence. Independence was evaluated by examining bivariate scatterplots comparing scale counts. Near-perfect correlation was grounds for exclusion of a character, whereas a cloud of points suggested complete independence. Intermediate conditions were judged individually ("significant" correlations were not necessarily grounds for exclusion of a character; one expects some correlation due to phylogeny). Scatterplots of bivariate comparisons are available on request.

1. Ventral scales smooth (0) \leftrightarrow keeled (1). Variable. Williams et al. (1995). Species that Williams et al. coded as "weakly keeled" are included in state (1). Because the intermediate state was found to be plesiomorphic, this character is coded identically in the any instance and unscaled analyses.

2. Toepads overlapping first phalanx (0) \leftrightarrow not distinct from first phalanx (1). Williams et al. (1995). The adhesive pad under phalanges two and three may extend distally under the proximal ventral digital scales of the first phalanx (0), or extension may be lacking (1).

3. Supradigital scales smooth (0) \leftrightarrow multicarinate (1). Variable. Williams et al. (1995). Because the intermediate state was found to be plesiomorphic, this character is coded identically in the any instance and unscaled analyses.

4. Number of sublabials zero (0) \leftrightarrow two

(1). Variable. Williams et al. (1995). All species of *Anolis* in this study are either fixed for zero, fixed for two, or variable between zero, one, and two postmentals. Because the intermediate state (in this case, having 0, 1, or 2 sublabials) was found to be plesiomorphic, this character is coded identically in the any instance and unscaled analyses.

5. Enlarged postanal scales present in males (0) \leftrightarrow absent in males (1). Williams et al. (1995). In most species of *Anolis*, enlarged postanal scales are present in males but not in females (state 0). In some species, neither sex has enlarged postanals (state 1).

6. Median number of scales from nasal to rostral 0 (0) \leftrightarrow 2.5 (v). Williams et al. (1995). Gap weighted.

7. Median number of postmental scales 4 (0) \leftrightarrow 8 (v). Gap weighted. Williams et al. (1995).

8. Median number of loreal scale rows 2 (0) \leftrightarrow 9.5 (v). Gap weighted. Williams et al. (1995). The first row of loreals is counted, directly in front of the preoculars usually below the second canthal.

9. Median number of scales across snout between second canthals 3.5 (0) \leftrightarrow 12.5 (v). Gap weighted. Williams et al. (1995).

10. Maximum male snout-vent length 38 mm (0) \leftrightarrow 188 mm (v). Gap weighted. Williams et al. (1995). Mean snout-vent length of sexually mature animals is probably a better measure than maximum. But, information on means and sexual maturity is much less readily available than information on maximums, and these two measures should give very similar codings.

11. Ratio of maximum female snout-vent length to maximum male snout-vent length 0.569 (0) \leftrightarrow 1.063 (v). Gap weighted.

12. Row of enlarged middorsal scales separated by smaller scales absent (0) \leftrightarrow present (1). Hedges and Thomas (1989). *A. sheplani* and *A. placidus* share this dorsal scalation pattern that apparently is unique in *Anolis* (Hedges and Thomas, 1989).

Characters 13–71 are ribosomal DNA sequence data. Hass et al. (1993) amplified an approximately 450 base pair segment of

the 16S region using the polymerase chain reaction. Sites that are informative under parsimony for species analyzed here are included. All changes are weighted equally.

13–71. 16S ribosomal RNA sequence data. A (0); C (1); G (2); T (3). Hass et al. (1993).

Characters 72–78 are allozyme characters collected by Burnell and Hedges (1990:72–76) and Hedges and Burnell (1990:77 and 78). See Burnell and Hedges (1990) for definitions and methods. Loci that were informative for these species were included, with each locus an unadditive character and each allele a character state.

- 72. Aspartate aminotransferase (Aat)
- 73. Carboxylesterase-D (Esd)
- 74. Lactate dehydrogenase (Ldh-1)
- 75. Lactoyl-glutathione lyase (Lgl)
- 76. Pyruvate kinase (Pk)
- 77. Acid phosphatase (Acp)
- 78. Malate dehydrogenase (Mdh)

Characters 79–83 are postcranial osteological characters from Etheridge (1959). Discussion and descriptions of these characters are available in Etheridge (1959, 1965, 1967). Codings are adapted from Guyer and Savage (1986, 1992) as altered by Cannatella and de Queiroz (1989) and Williams (1989), with minor changes to allow for different species used. These characters were not examined in detail here. Rather, states were taken as described by Etheridge (1959) and others.

The level of variation in these characters for these species has not been published. Therefore, with a few exceptions (discussed below), the postcranial skeletal characters are entered as intraspecifically invariant in all analyses.

Character number from Guyer and Savage (1992) is given parenthetically. Outgroup states were obtained from Etheridge and de Queiroz (1988), Etheridge and Williams (1991), and Frost and Etheridge (1989).

79. (9) Interclavicle arrow-shaped (0) ↔ T-shaped (1). In state 0, the lateral aspects of the interclavicle are not in contact with the clavicle, whereas in state 1 the

interclavicle is in contact with the clavicle over its entire anterior margin.

80. (10a) Number of postxiphisternal inscriptive ribs four (0) ↔ five (1) ↔ six (2) ↔ seven (3). Postxiphisternal inscriptive ribs do not contact the sternum, instead forming a ventral "chevron" as the left and right ribs join posterior to the sternal ribs (Etheridge, 1965). *Anolis occultus*, *A. solitarius*, and *A. darwini* vary intraspecifically in number of inscriptive ribs (personal observation), although the extent of this variation was not determined.

In the frequency analysis, the character is scaled such that change between four and seven ribs is worth one step, and cladistic coding is: four (0) ↔ five (a) ↔ six (l) ↔ seven (v). Cases of intraspecific variation are coded as separate, perfectly intermediate states (e.g., a species showing variation between 5 and 6 ribs is coded as f, which is intermediate between a and l—states could not be coded by frequency because such information was not available).

In the any-instance and unscaled analyses, all changes (including those from "fixation" to variable) count as one step: four (0) ↔ four or five (1) ↔ five (2) ↔ five or six (3) ↔ six (4).

81. (10b) Number of attached postxiphisternal inscriptive ribs 2 (0) ↔ 3 (1) ↔ 4 (2) ↔ 5 (3) ↔ 6 (4). "Attached" postxiphisternal inscriptive ribs are those that suture with dorsal ribs (*sensu* Etheridge, 1965). As above, some species vary intraspecifically in number of attached inscriptive ribs (Etheridge, 1959; personal observation).

In the frequency analysis, the character is scaled such that change between two and six attached ribs is worth one step, and cladistic coding is: 2 (0) ↔ 3 (7) ↔ 4 (f) ↔ 5 (n) ↔ 6 (v). Any cases of intraspecific variation are coded as separate, perfectly intermediate states (e.g., a species showing variation between 3 and 4 attached ribs is coded as b, which is exactly between 7 and f).

In the any-instance and unscaled analyses, all changes (including those from "fixation" to variable) count as one step: two (0) ↔ three (1) ↔ three or four (2)

\leftrightarrow four (3) \leftrightarrow five or six (4). Some out-group species show variation between two and three attached ribs (Etheridge and Williams, 1991). Because this paper is concerned only with ingroup relationships, this condition is coded as 0/1 instead of as a separate intermediate state.

82. (14) Caudal autotomy septa absent (0) \leftrightarrow present (1). Fracture planes are visible on the caudal vertebrae of species with state 1. In state 0, the septa are not present, having fused or never formed.

83. (15) Transverse processes on posterior caudal vertebrae absent (0); Present (1); Outgroup state (2). Outgroups have transverse processes on their caudal vertebrae, however, these are not considered homologous (Etheridge, 1959; Etheridge and de Queiroz, 1988). State 0 is the alpha-anole state of Etheridge (1959), state 1 is the beta condition. Guyer and Savage (1986, 1992) and Cannatella and de Queiroz (1989) coded this character as above but recognized a third *Anolis* state (presence of reduced transverse processes) in their discussions of generic diagnoses. I follow the a priori coding of these authors.

84–85. Chromosome characters from Guyer and Savage (1992). Chromosome data were taken from Webster (1974), Webster et al. (1972), and Gorman (1973). Cladistic use of sex chromosomes and microchromosomes follows Guyer and Savage (1992:appendix 3). Number of macrochromosomes, which was also used as a character in Guyer and Savage (1992), was not included here because of problems of homology (Williams, 1989) and because this character is not independent of number of microchromosomes (Gorman, 1972).

84. Condition of sex chromosomes absent (0); xy (1); xxy (2);

85. Number of microchromosomes 24 (0); 20 (1); 16 (2); 14 (3); 8 (4);

Characters 86–116 were collected from dry skulls.

86. Skull dimensions, width/length (average for each species) 0.39 (0) \leftrightarrow 0.80 (1). Gap weighted. Length is measured from tip of snout to occipital condyle, width is measured at the widest point of the skull,

between the posteroventral corners of the jugals.

87. Parietal crests form a trapezoid (0) \leftrightarrow V (1) \leftrightarrow Y (2) \leftrightarrow Y with parietal spur (3). (Fig. 1). Variable. (Etheridge, 1959). "Trapezoid" (Fig. 1a), "V" (Fig. 1b,c), and "Y" (Fig. 1d–g) describe the appearance of the lateral boundaries of the parietal roof, as viewed from above. In the case of the Y-shaped parietal, a posteriorly directed median crest forms the stem of the Y. "Parietal spur" (Williams, 1992) refers to a posterior knoblike protrusion of the stem of the Y beyond the supratemporal processes (Fig. 1h,i). The ontogenetic transformation of this character is well documented and mirrors this hypothesized evolutionary transformation (Etheridge, 1959:Fig. 9; Cannatella and de Queiroz, 1989:Fig. 3).

This character varies continuously and intraspecifically in *Anolis* (Fig. 1). The difficulties and dangers in making continuous characters discrete are exemplified in this character—*A. monticola* and *A. polylepis* have practically identical parietals, but Etheridge (1959) (followed by Guyer and Savage, 1986) listed *A. monticola* as having Y shaped crests and *A. polylepis* with V ("V" in summary p. 164, "V or Y" in his Table XIII). If larger specimens can be assumed to be further along in ontogeny, then the intraspecific variation in *A. monticola* depicted in Fig. 1 (compare Fig. 1c,e) is not attributable to size or, if size is a reliable measure of ontogeny, ontogenetic differences. The "V" specimen—Fig. 1c—is actually larger than the "Y" specimen—Fig. 1e (52 mm SVL vs. 49 mm), which is counter to the pattern seen in ontogeny.

In the frequency analysis, the character is scaled such that change from a trapezoidal parietal roof to a Y-shaped roof with a spur is worth one step, and cladistic coding is: trapezoid (0) \leftrightarrow V (a) \leftrightarrow Y (k) \leftrightarrow Y with parietal spur (v). Cases of intraspecific variation are coded as intermediate states according to the percentage of individuals with a given state (e.g., a species with 67% of individuals with a Y-shaped parietal and 33% of individuals with a V-

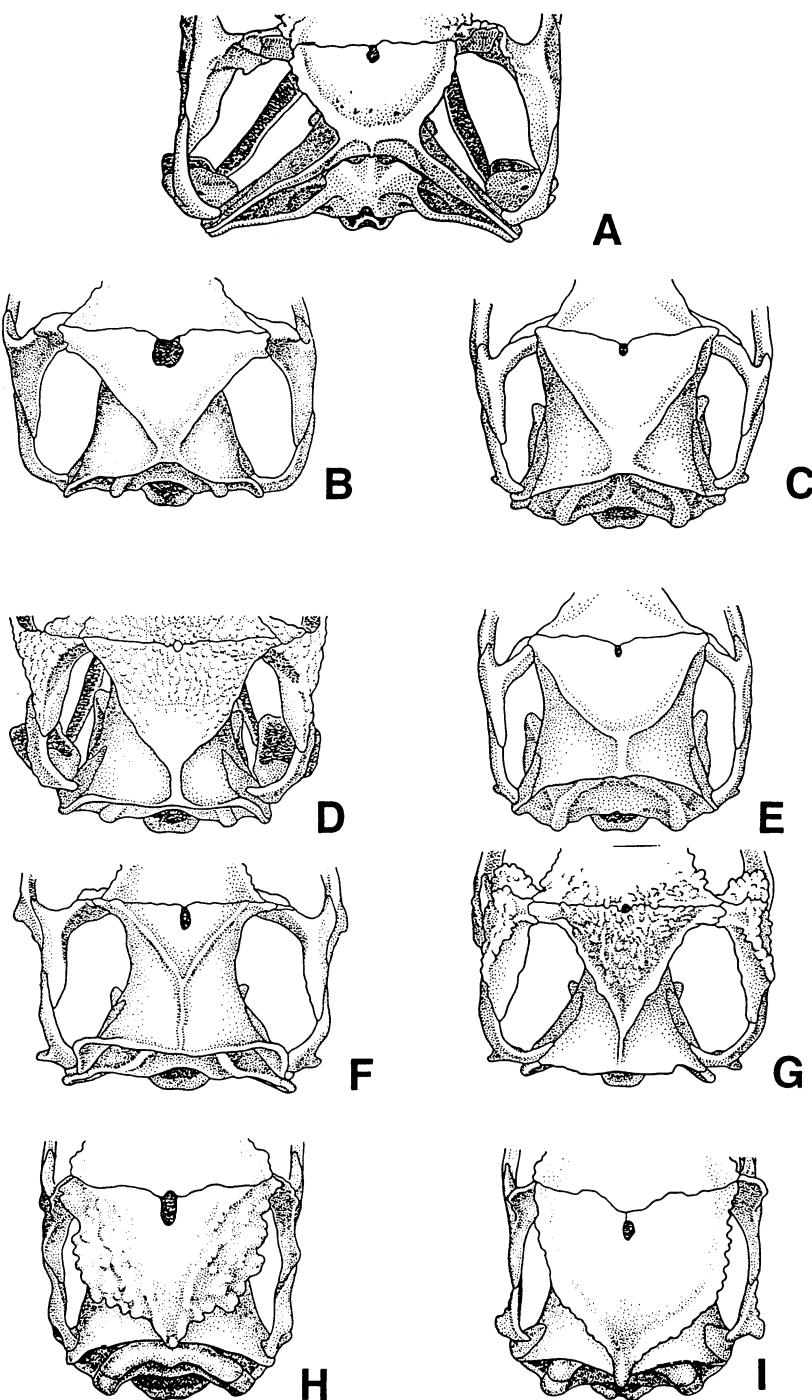


FIG. 1.—Dorsal view of posterior skull, showing variation in structure of parietals and position of pineal foramen. (A) *A. griseus*; (B) *A. fowleri*; (C) *A. monticola*; (D) *A. darlingtoni*; (E) *A. monticola*; (F) *A. bimaculatus*; (G) *A. cuvieri*; (H) *A. placidus*; (I) *A. insolitus*.

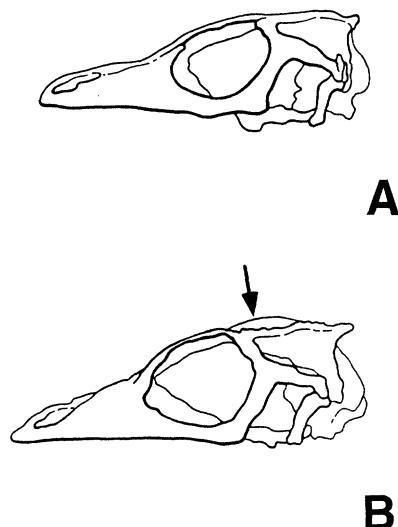


FIG. 2.—Lateral view of skull, showing convex (indicated by arrow) and flat parietals. (A) *A. solitarius*; (B) *A. insolitus*; (from Williams, 1992).

shaped parietal is coded as g, which is 67% of the “distance” between a and k).

In the unscaled analysis, all changes (including those from “fixation” to variable) count as one step: trapezoid (0) \leftrightarrow trapezoid or V (1) \leftrightarrow V (2) \leftrightarrow V or Y (3) \leftrightarrow Y (4) \leftrightarrow Y with parietal spur (5).

In the any instance analysis, apomorphic conditions are collapsed into a single state: trapezoid (0) \leftrightarrow V, Y, or Y with a spur (v).

88. Parietal crenulation absent (0) \leftrightarrow present (1) (Fig. 1). *Anolis insolitus*, *A. sheplani*, and *A. placidus* display horizontally aligned crenulations on the lateral crests of the parietal which extend from the parietal roof (Fig. 1h,i). In other *Anolis* in this study the parietal borders are smooth (Fig. 1a–g). Some *Anolis equestris* and *Phenacosaurus heterodermus* have rugose parietal edges. These do not appear to be homologous to the twig dwarf anole condition; in *A. equestris* and *Phenacosaurus*, the rugosity appears to spread over from the dorsal surface of the skull, whereas in the dwarf twig anoles the actual edges of the parietal appear to be scalloped.

89. Parietal roof flat (0) \leftrightarrow convex (1) (Fig. 2). In *A. insolitus*, *A. sheplani*, and *A. placidus* the parietal roof is domelike (Fig. 2b). This condition is not attributable

to small size; other small *Anolis* (e.g., adult *A. occultus*, juvenile *A. bonairensis*) do not have this condition (personal observation).

90. Pineal foramen at parietal/frontal suture (0) \leftrightarrow in parietal (1) (Fig. 1). (Etheridge, 1959). Guyer and Savage (1986) coded this character as three states (parietal/frontal \leftrightarrow anterior edge of parietal \leftrightarrow parietal), whereas Williams (1989) coded two. Pineal foramen location varies intraspecifically and continuously in *Anolis* (personal observation), so choice of character state boundary is arbitrary. In state 1, the foramen is oval and predominately in the parietal (Fig. 1i); the anterior border of the foramen is completely formed by the parietal or the anterior borders converge. State 0 describes states in which the foramen is circular or U-shaped and at the parietal/frontal suture; the frontal forms the entire anterior border of the foramen (Fig. 1a–h).

91. Supratemporal processes leave supraoccipital exposed above (0) \leftrightarrow extend over supraoccipital (1) (Fig. 1). Variable. (Etheridge, 1959). In the plesiomorphic state, a supratemporal process extends posterolaterally from each posterior corner of the parietal roof such that together they create a 120 degree angle (as viewed from above) and the supraoccipital is completely exposed above (Etheridge, 1959). In apomorphic states, the anterior ends of the supratemporal processes join and arch posteriorly over the supraoccipital. Etheridge (1959) called this derived state the “half-funnel”, a term which describes the hollow and rounded structure seen in extremely posteriorly extended supratemporal processes. This character varies continuously: *Anolis cuvieri* has an advanced half-funnel and *A. griseus* displays no posterior extension at all, but intermediate stages exist in the small sample of *Anolis* taxa examined in this study alone. Erection of an attribute state boundary therefore requires strict criteria. In this study, state 0 includes all specimens in which the entire dorsal surface of the supraoccipital ridges is visible in a dorsal view (Fig. 1a), whereas state 1 indicates that the supratemporal processes extend over the supraoccipital such that some or all of the

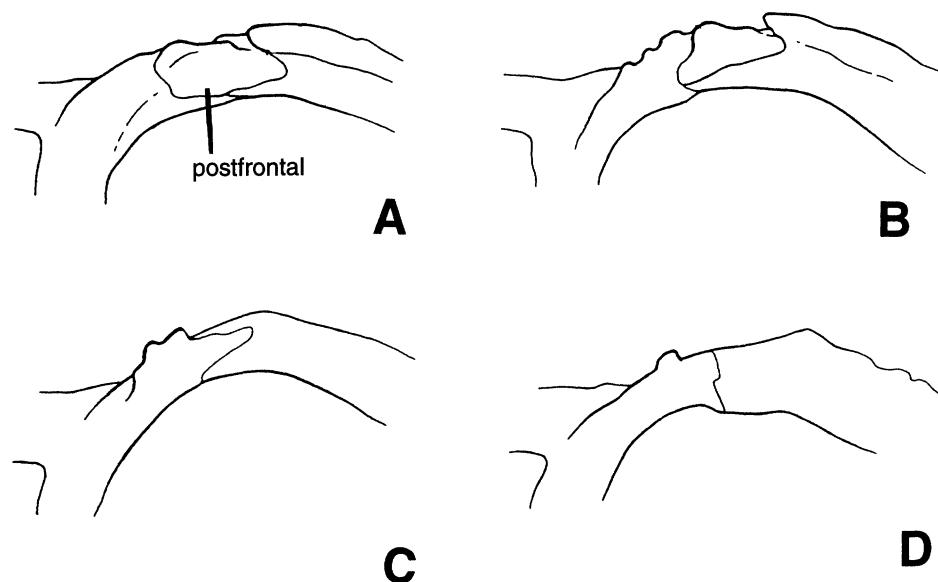


FIG. 3.—Oblique ventral view posterodorsal rim of orbit, showing postfrontal present or absent. Anterior is to the right. (A) *A. griseus*; (B) *A. placidus*; (C) *A. insolitus*; (D) *A. sheplani*.

supraoccipital ridges are not visible from above (Fig. 1b–i). This character is not nonindependent of character 87 (see matrix), but it probably is not completely independent either (Cannatella and de Queiroz, 1989).

92. Postfrontal present (0) ↔ absent (1) (Fig. 3). Variable. (Etheridge and de Queiroz, 1988). Variation in the size of the postfrontal occurs but could not be objectively coded.

93. Prefrontal contacts nasal (0) ↔ is separated from nasal by frontal and maxilla (1) (Fig. 4). Variable. All outgroups have state 0. In some specimens the prefrontal contacts the nasal between the frontal and the maxilla (state 0; Fig. 4a), whereas in others such contact is prevented by the anterior extension of the frontal suturing with the maxilla (state 1; Fig. 4b). Any contact between prefrontal and nasal was scored 1.

94. Gap between nasals and frontal absent (0) ↔ present (1). In *A. occultus* and *A. solitarius* the nasals diverge posteriorly and do not suture with the frontal medially (state 1), thus leaving a dorsal hole.

95. Dorsal process of jugal terminates on posterior or medial aspect of postorbital (0) ↔ on lateral aspect of postorbital

(1) (Fig. 5). Variable. The end of the dorsal process of the jugal may suture on the lateral (state 1; Fig. 5b) or medial (state 0; Fig. 5a) surface of the postorbital. In state 1, the blunt dorsal end of the jugal is visible in a lateral view of the skull. The morphologically intermediate state of a posterior suture is included with state 0 to minimize intraspecific variation (*A. insolitus* and *A. placidus* show both posterior and medial sutures).

96. Jugal/squamosal contact absent (0) ↔ present (1) (Frost and Etheridge, 1989). All outgroups have state 0. In some species the jugal extends dorsally far enough to contact the anterior end of the squamosal (state 1), whereas in others it terminates further ventrally (state 0).

97. Pterygoid-lacrimal contact absent (0) ↔ present (1). Variable. The pterygoid may extend laterally in the anteroventral region of the orbit to contact the lacrimal (state 1). The intraspecifically variable condition was found to be the plesiomorphic state; thus this character was coded identically in the unscaled and any-instance analyses.

98. Jugal extends superiorly to form anterior border of lacrimal (0) ↔ or abuts ventral edge of lacrimal (1). This character

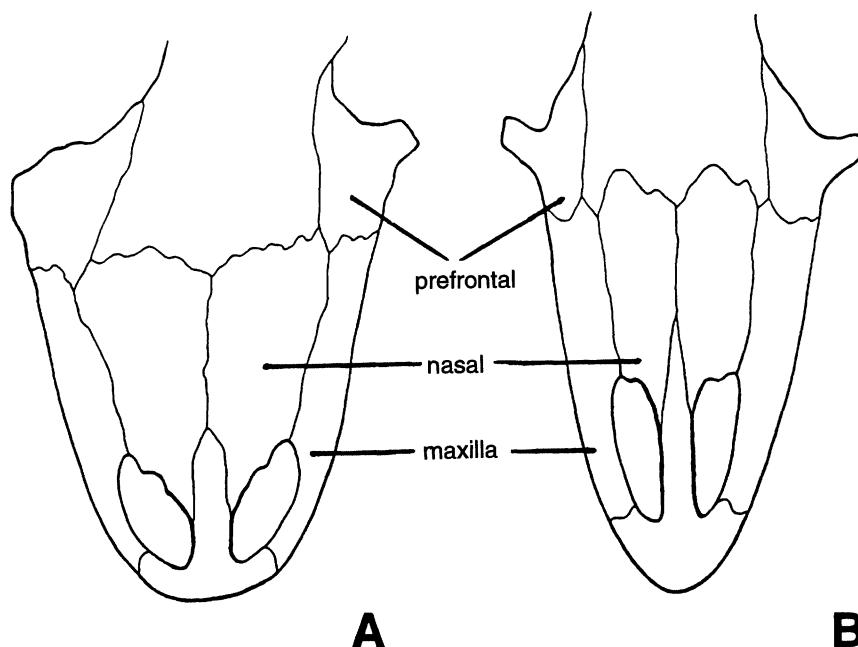


FIG. 4.—Dorsal view of anterior skull, showing contact or non-contact of prefrontal and nasal. (A) *A. fowleri*; (B) *A. insolitus*.

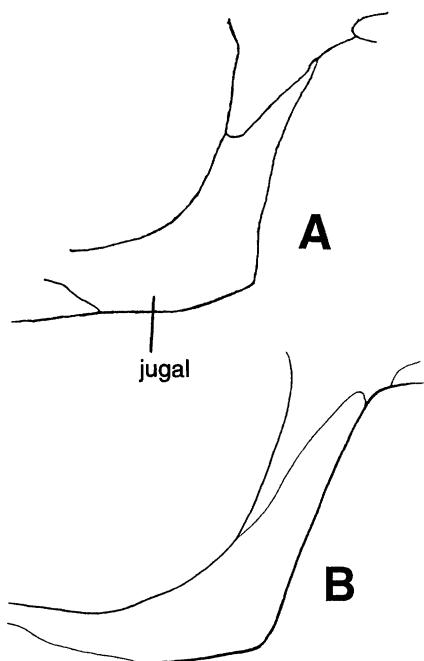


FIG. 5.—Lateral view of posterior orbit, showing medial (A) or lateral (B) sutures of the dorsal process of the jugal. Anterior is to the left. (A) *A. darlingtoni*; (B) *A. insolitus*.

is judged by inspection of the lateral view of the skull at the anterior edge of the orbit. The intraspecifically variable condition was found to be the plesiomorphic state; thus this character was coded identically in the unscaled and any-instance analyses.

99. Epitygoid contacts parietal (0) ↔ does not contact parietal (1). Variable. The parietals found in the outgroups do not extend as far ventrally as those in *Anolis*, so the above character may not be comparable between these two groups as presently coded.

100. Dorsum sella concave, facing anteriorly (0) ↔ flat, facing dorsally (1) (Fig. 6). Variable. The dorsum sella, or anterior face of the basisphenoid, usually displays an anteriorly directed crista sellaris which gives the structure a cylindrically concave and vertical appearance (Fig. 6b). In state 1, the crista sellaris is low and faint, and the entire dorsum sella is aligned more horizontally than vertically (Fig. 6a).

101. Pterygoid teeth present (0) ↔ absent (1). Variable. (Etheridge, 1959). Pterygoid teeth may occur in a single row along the medial edge of the pterygoid, or

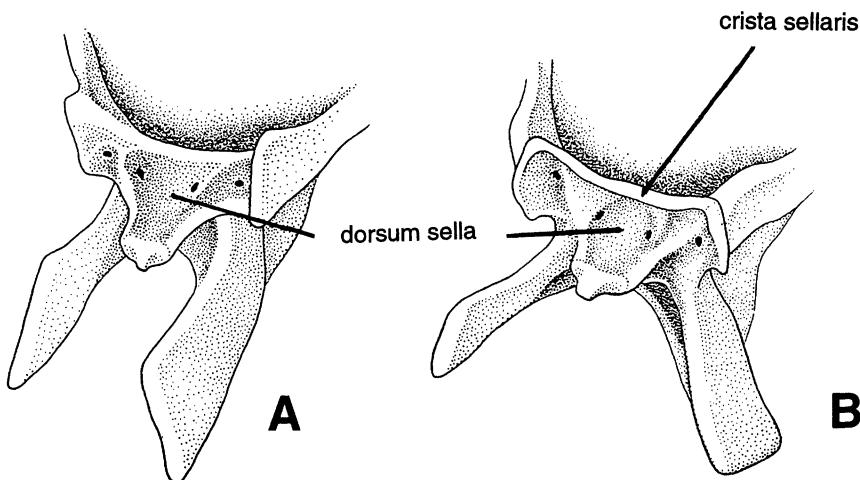


FIG. 6.—Anterior view of basisphenoid, showing flat (A) or concave (B) dorsum sella. (A) *A. darlingtoni*; (B) *A. fowleri*.

they may be clumped there in a ball like stubby pins in a pincushion. The latter condition is exemplified in *A. grahami*, and may not be homologous with the other state. However continuous and intraspecific variation makes characterization difficult, and the simplest operational coding is as presence or absence.

102. Palatine-vomer suture is oriented posterolaterally and located posteriorly, with vomer flared laterally (0); oriented transversely and located anteriorly, with vomer and palatine of equal width (1); oriented transversely with vomer and palatine of equal width and with anterolateral processes (2) (Fig. 7). In most *Anolis*, the vomer extends laterally into the fenestra exochoanalis and sutures diagonally near its posterior border (state 0; Fig. 7b). In state 1, the vomer and palatine are of equal width and meet in a straight transverse suture near the middle of the fenestra exochoanalis (Fig. 7a). State 2 is similar to state 1 but with lateral extensions of the vomer imparting an arrow shape to the palate. Damage prevented scoring this character for many *Anolis*.

103. Maxilla extends posteriorly to ectopterygoid (0) \leftrightarrow beyond ectopterygoid (1). (Fig. 8). Variable. [Frost and Etheridge (1989) compared maxillary extent to the frontoparietal suture]. The maxilla extends most posteriorly on the ventral edge

of the jugal. State 1 includes all specimens in which the maxilla clearly extends beyond the posterior edge of the lateral head of the ectopterygoid (Fig. 8b). Amount of posterior extension varies continuously between species; for convenience, the posterior end of the lateral head of the ectopterygoid is chosen as the attribute state boundary.

104. Basipterygoid crest absent (0) \leftrightarrow present (1). In all *A. sagrei* and *A. cristatellus*, a crest extends between the basipterygoid processes of the basisphenoid anterior to the dorsum sella. This character shows discrete, intraspecifically invariant variation.

105. Supraoccipital cresting continuous across supraoccipital (0) \leftrightarrow lateral processes distinct from supraoccipital crest (1) (Fig. 9). Variable. State 1 describes two distinct lateral processes extending upward from the supraoccipital (Fig. 9b). In state 0 these processes are joined in a crest across the supraoccipital (Fig. 9a). Any cresting between the processes was coded as state 0. Considerable variation occurs within each state, i.e., in height of crest in state 0 and width of lateral processes in state 1. Within-state variation could not be objectively coded.

106. Quadrate lateral shelf absent (0) \leftrightarrow present (1) (Fig. 10). Variable. *Anolis* with state 1 have a shelf-like crest extend-

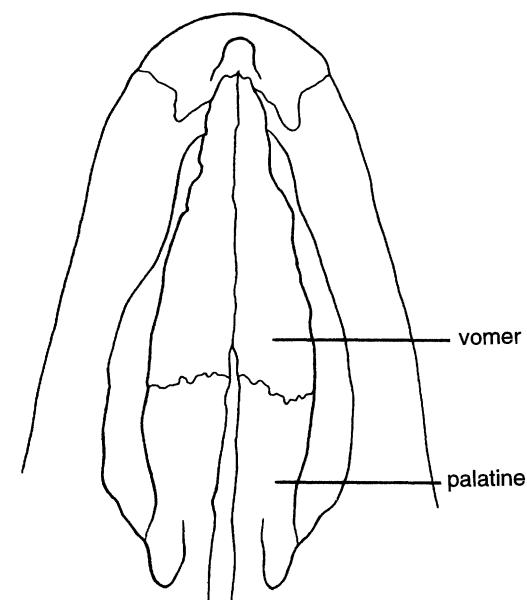
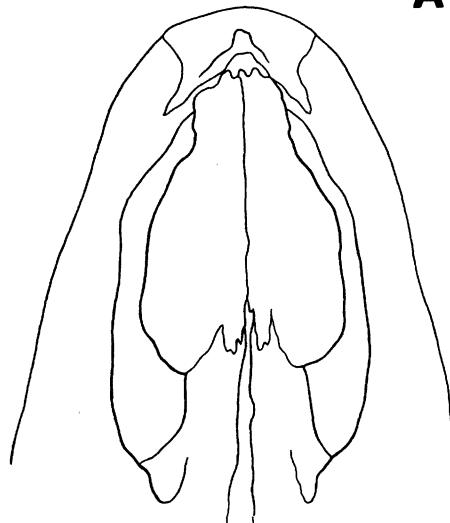
**A****B**

FIG. 7.—Ventral view of anterior skull, showing variation in structure of vomers and position and orientation of palantine-vomer suture. (A) *A. darlingtoni*; (B) *A. griseus*.

ing laterally from the posteriorly directed lateral crest of the quadrate (Fig. 10a).

107. Posteroventral process of the squamosal extends ventrally into auditory cup of quadrate (0) \leftrightarrow squamosal excluded

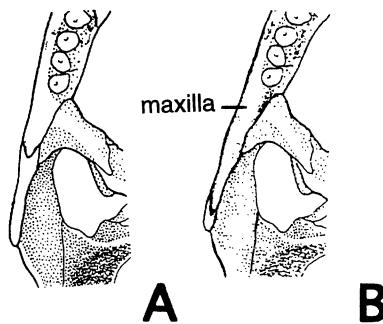
**A****B**

FIG. 8.—Ventral view of lateral skull, showing variable posterior extension of the maxilla. (A) *A. griseus*; (B) *A. fowleri*.

from auditory cup by dorsal surface of quadrate (1). Variable.

108. Posteroventral process of squamosal contacts supratemporal (0) \leftrightarrow extends above supratemporal to contact parietal (1). Variable. The posterior end of the squamosal abuts the supratemporal, which is flush with the parietal. The dorsal process of this posterior end may extend above the supratemporal to contact the parietal (state 0).

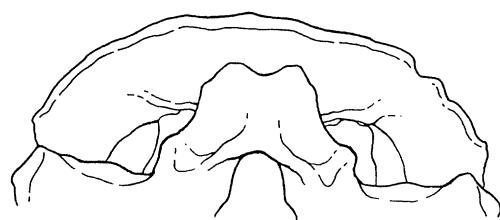
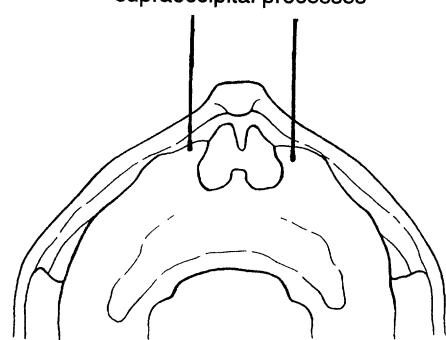
**A****B**

FIG. 9.—Posterior view of skull, showing supraoccipital crest with continuous crest (A) or distinct supraoccipital processes (B). (A) *A. griseus*; (B) *A. insolitus*.

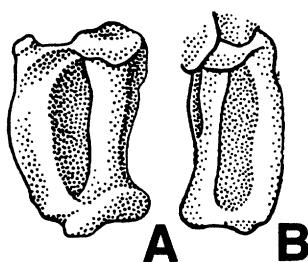
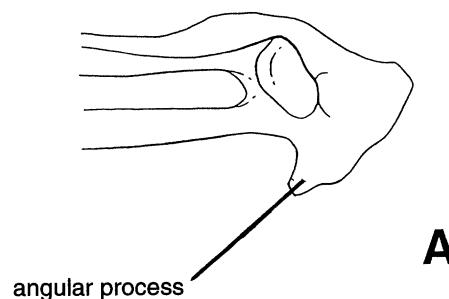
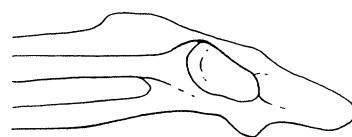


FIG. 10.—Posterior view of quadrate, showing presence (A) or absence (B) of a lateral shelf. (A) *A. fowleri*; (B) *A. darlingtoni*.



angular process



B

FIG. 11.—Dorsal view of posterior mandible, showing variable size of angular process (see Fig. 14 also). (A) *A. griseus*; (B) *A. placidus*.

109. Posteriormost tooth is at least partially posterior to anterior mylohyoid foramen (0) \leftrightarrow posteriormost tooth is at least partially anterior to anterior mylohyoid foramen (1) \leftrightarrow posteriormost tooth is completely anterior to anterior mylohyoid foramen (2). Variable.

In the frequency analysis, states 0, 1, and 2 above correspond to states 0, f, and v, with intraspecific variation coded according to the percentage of individuals with a given state (as in the parietal character).

In the unscaled analysis, the character is coded as follows, with each change at a cost of one step: Posteriormost tooth is at least partially posterior to anterior mylohyoid foramen (0) \leftrightarrow part posterior or part anterior (1) \leftrightarrow part anterior (2) \leftrightarrow part anterior or completely anterior (3) \leftrightarrow completely anterior (4).

In the any instance analysis, apomorphic conditions are collapsed: Posteriormost tooth is at least partially posterior to anterior mylohyoid foramen (0) \leftrightarrow posteriormost tooth is variably partially posterior or partially anterior or completely anterior to anterior mylohyoid foramen (v).

110. Angular process of articular present, large (0) \leftrightarrow reduced or absent (1) (Fig. 11). Variable. (Williams, 1989). Continuous variation appears minimal in state 0 among these species, but some variation occurs within state 1. For example, *A. occultus* has no angular process at all, whereas *A. solitarius* has a small bump where the angular process is seen in other species (Fig. 11b). In spite of these difficulties, the character is retained because, for this sam-

ple of species, there is an obvious gap between states 0 and 1.

111. Posterior suture of dentary pronged (0) \leftrightarrow blunt (1) (Fig. 12). Variable. In labial view, the posterior border of the dentary may form a blunt, undifferentiated suture with the surangular (state 0; Fig. 12a). Alternately, two distinct processes of the dentary may be evident posteriorly (state 1; Fig. 13b,c). Variation in the relative lengths of the processes is common, however coding these differences as separate states created unmanageable levels of variation (e.g., 4 states occurring in a single species).

112. Anterior aspect of posterior border of dentary is anterior to mandibular fossa (0) \leftrightarrow within mandibular fossa (1). Variable. Posterior extent of the dentary varies in *Anolis*. For convenience, the mandibular fossa is used as the attribute state boundary.

113. Splenial present (0) \leftrightarrow absent (1). (Fig. 14). Variable. (Etheridge, 1959). Wil-

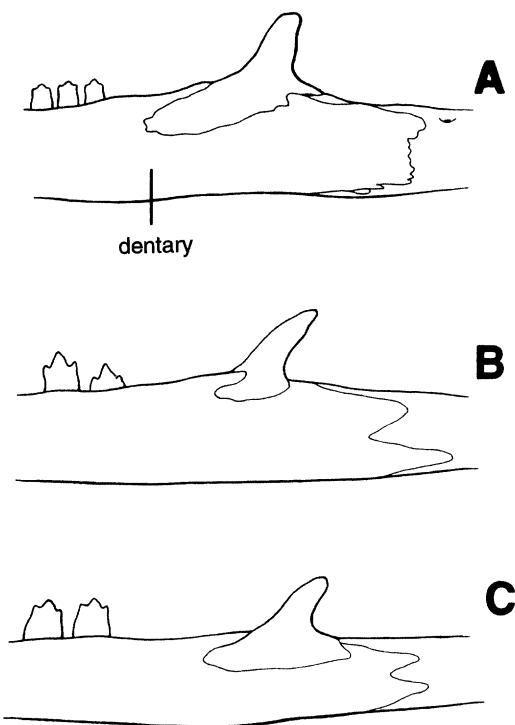


FIG. 12.—Lateral view of mandible, showing blunt or pronged posterior suture of dentary. (A) *A. bimaculatus*; (B) *A. darwini*; (C) *A. insolitus*.

liams (1989) suggested additional states wherein the position of the splenial is recognized in addition to its presence or absence. Continuous variation precluded the use of these alternative states.

114. Anteromedial process of coronoid extends anteriorly (0) \leftrightarrow ventral aspect of anteromedial process projects posteriorly (1) (Fig. 14). Variable. The posterior margin of the anteromedial leg of the coronoid may slope smoothly forward (state 0; Fig. 14a) or jut posteriorly at its ventral end (state 1; Figs. 14b, 11c). This character could not be polarized in the preliminary any instance analysis. Thus it is coded identically in the any instance and unscaled analyses.

115. Surangular foramen completely in surangular (0) \leftrightarrow bordered laterally by dentary (1) (Fig. 13). Variable. The surangular foramen may be located exclusively in the surangular (state 0; Fig. 13b), or it may be bordered on one side by the dentary (state 1; Fig. 13a) (The coronoid may superficially

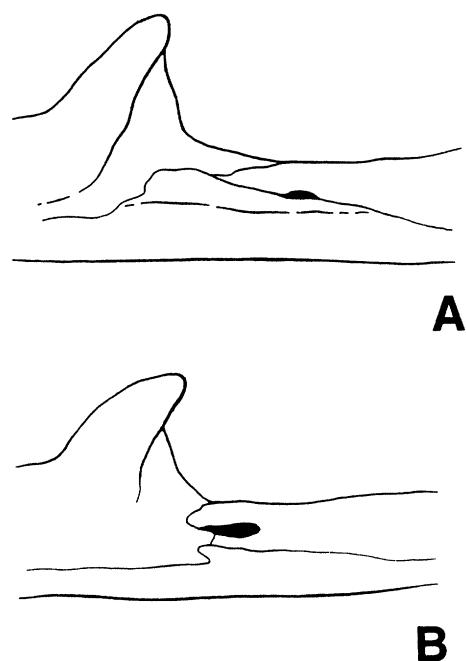


FIG. 13.—Medial view of mandible, showing variable borders for the surangular foramen. (A) *A. polylepis*; (B) *A. cuvieri*.

also contact this foramen, e.g., Fig. 13b, but in these cases it overlays state 0 or state 1). For convenience, the transition from state 0 to state 1 is erected where the opening of the foramen is formed equally by the dentary and the surangular.

116. Coronoid labial process absent (0) \leftrightarrow present (1) (Etheridge and de Queiroz, 1988). The coronoid may extend antero-labially on the dentary (state 1) or this process may be nonexistent (state 0). Continuous variation between and within species occurs in state 1, the labial leg extending far anteriorly or hardly at all. This variation could not be objectively coded. Figure 13 shows various conditions of state 0 (state 1 is not figured). All species except *A. occultus* and the outgroups show state 1.

RESULTS

Parsimony Analyses

The any-instance analysis resulted in six most parsimonious ingroup trees (Fig. 15) of length 578.8, consistency index (CI; Kluge and Farris, 1969) of 0.35, and retention index (RI; Farris, 1989) of 0.49

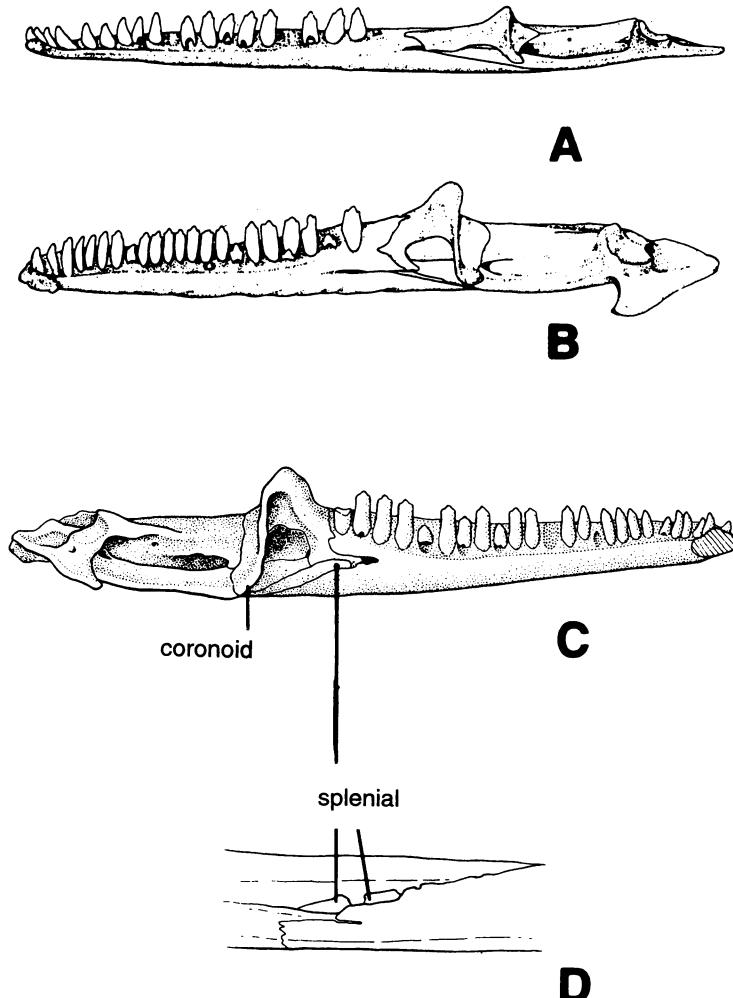


FIG. 14.—Medial (a, b, c) and ventral (d) views of dentary, showing variable conditions of the anterior and posterior coronoid processes, and variable splenials. (A) *A. occultus*; (B) *A. cuvieri*; (C) *A. darlingtoni*; (D) *A. bimaculatus*.

(five outgroup topologies were found, for a total of 30 optimal trees). The unscaled analysis produced a single most parsimonious ingroup tree of length 699.9, CI = 0.32, and RI = 0.50 (Fig. 16). The frequency approach yielded a single most parsimonious tree of length 518.8, CI = 0.36 and RI = 0.47. Figure 17 depicts this tree with bootstrap values. Figure 18 shows the relationships common to all three analyses. The Hispaniolan dwarf twig species are monophyletic in each analysis, and in all analyses *A. sheplani* and *A. insolitus* are sister species. The mono-

phyly of the Hispaniolan twig dwarfs was supported at a bootstrap value of 94% in the frequency analysis. In the preferred frequency analysis under both character change optimizations offered in PAUP (ACCTRAN, or accelerated change, and DELTRAN, or delayed character change), the Hispaniolan twig dwarf clade is diagnosed by two unique unreversed synapomorphies: parietal crenulation (character 88), and convex parietal roof (89). Additional unambiguous synapomorphies (present under all possible optimizations) include increased number of scales be-

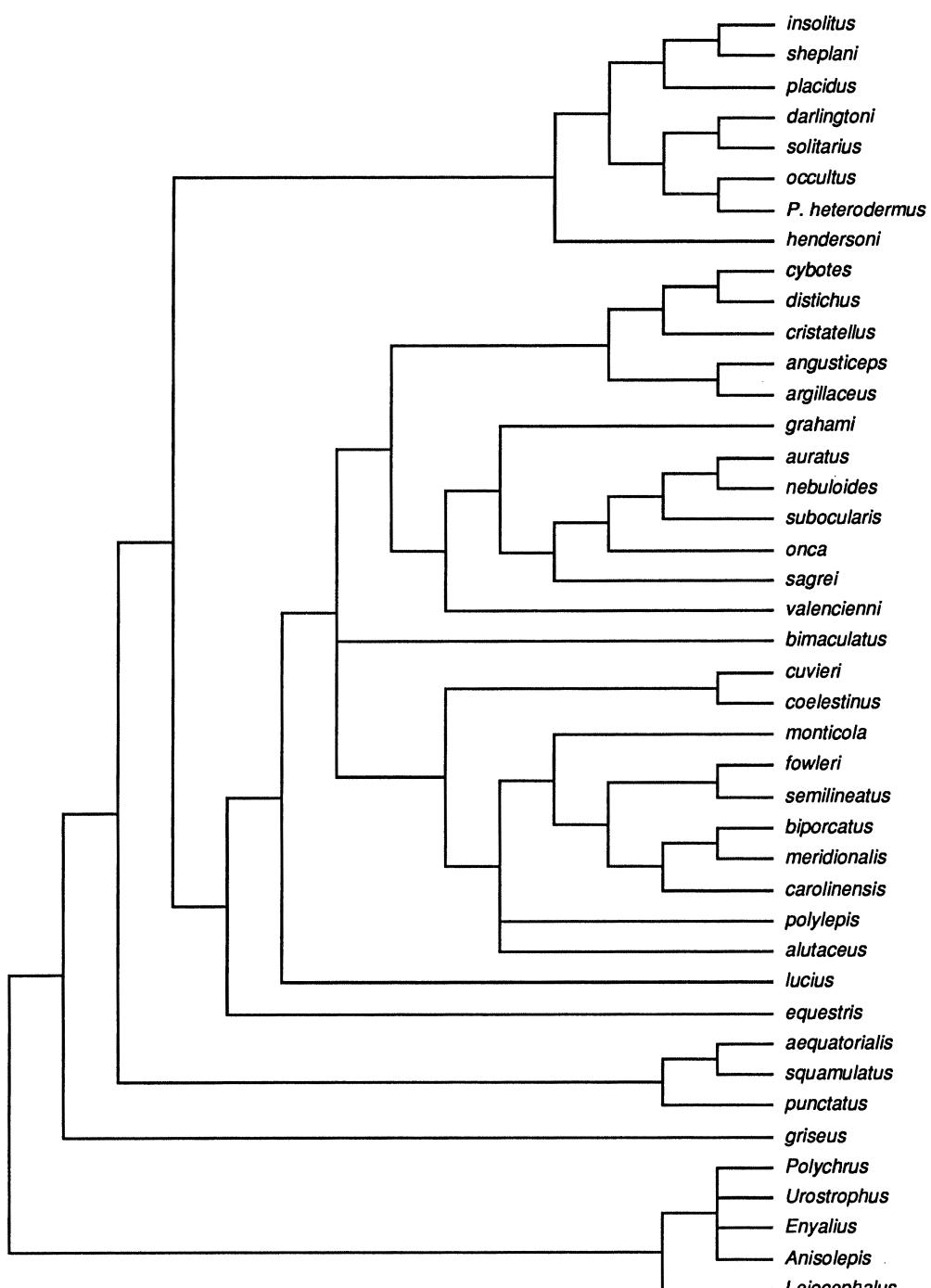


FIG. 15.—Strict consensus of two most parsimonious ingroup trees from any-instance analysis.

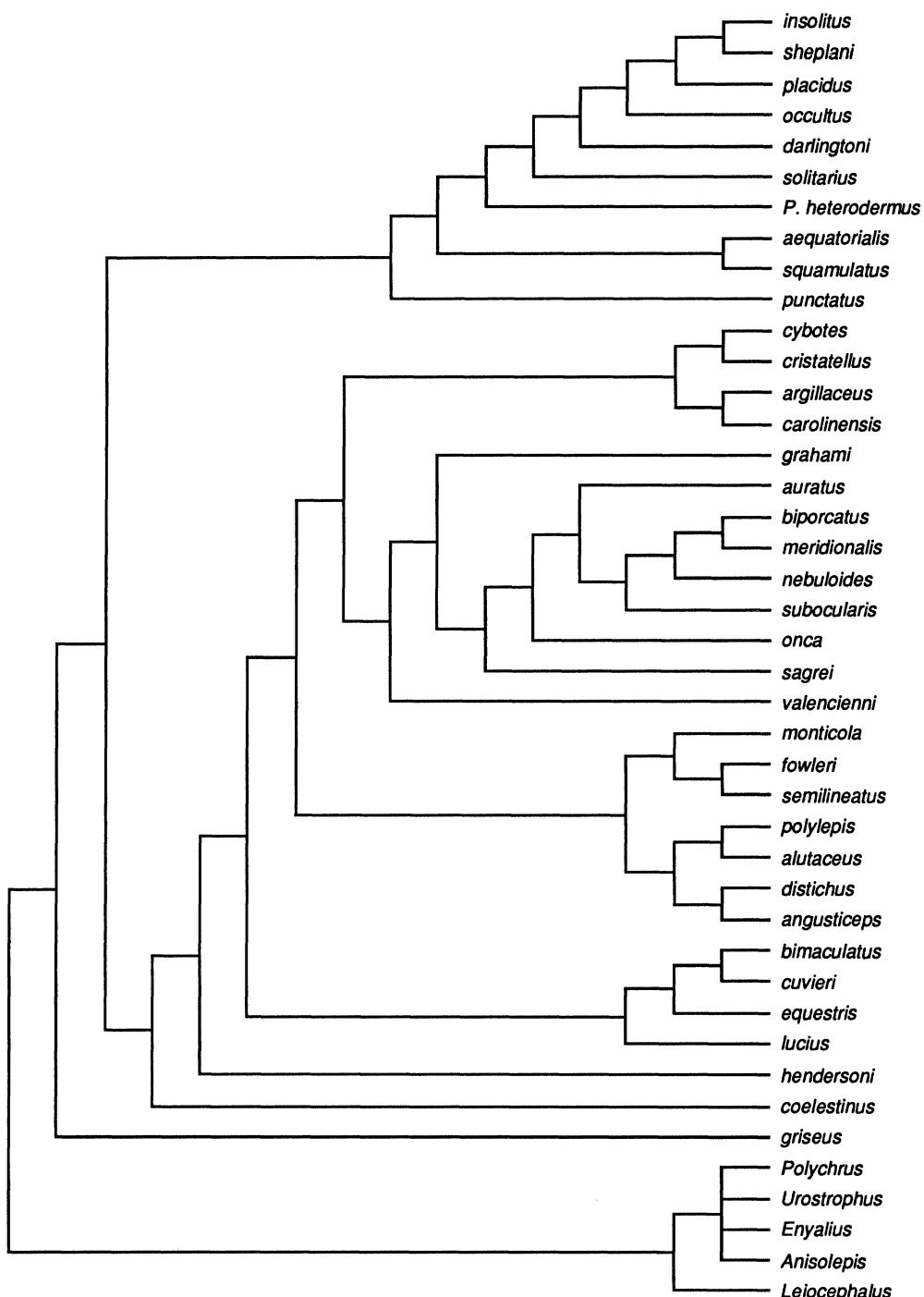


FIG. 16.—Single most parsimonious ingroup tree from unscaled analysis.

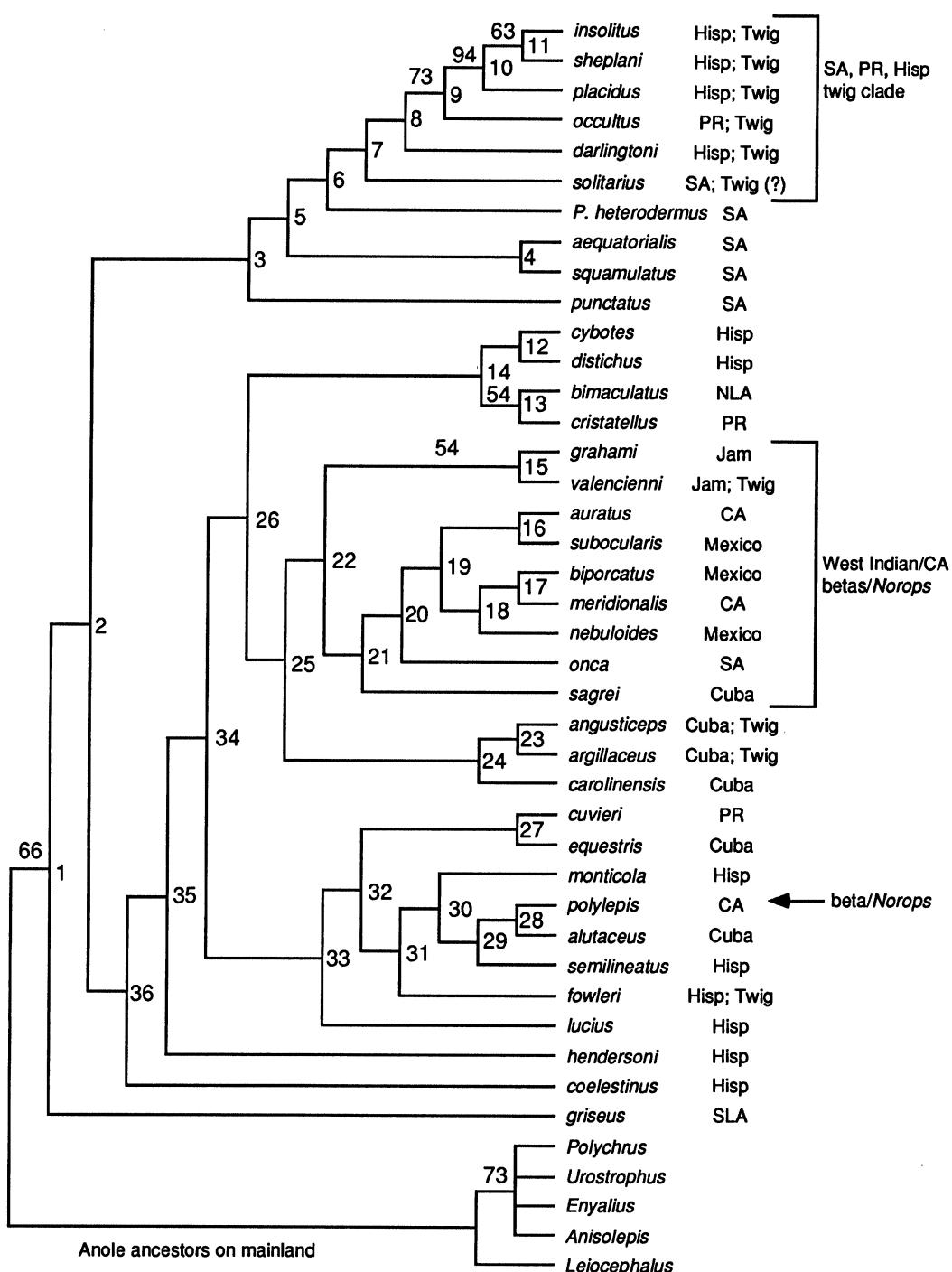


FIG. 17.—Preferred estimate of relationships. Single most parsimonious ingroup tree from frequency analysis. Numbers above clades are bootstrap values. Numbered nodes refer to apomorphies listed in Appendix V. Hisp (Hispaniola), PR (Puerto Rico), SA (South America), NLA (Northern Lesser Antilles), SLA (Southern Lesser Antilles), Jam (Jamaica), CA (Central America), Cuba, and Mexico are localities. “Twig” indicates the twig ecomorph.

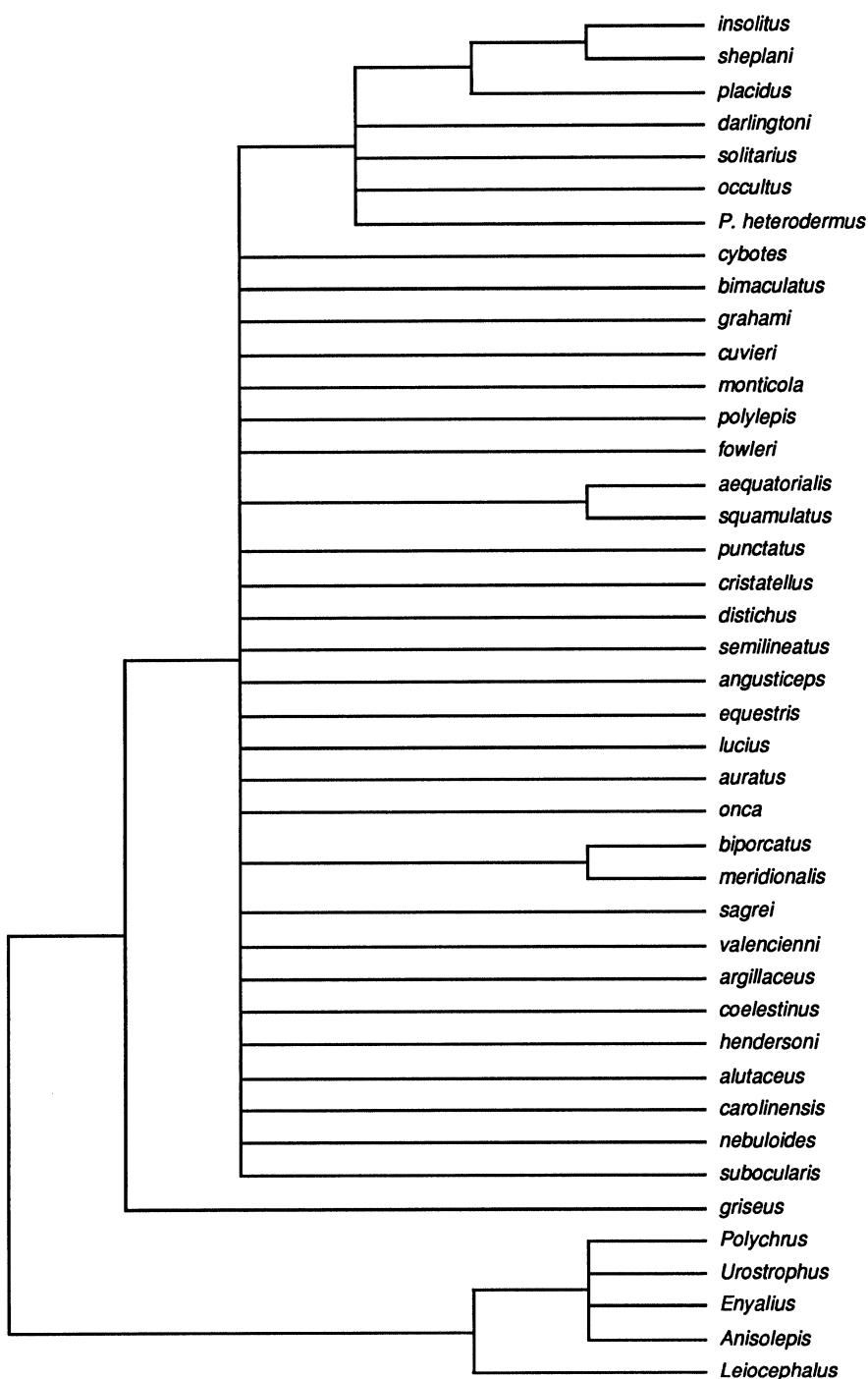


FIG. 18.—Strict consensus of most parsimonious trees from any-instance, unscaled, and frequency analyses.

tween nasal and rostral (6) and parietal crests Y-shaped with a spur (87). The *A. sheplani* + *A. insolitus* clade is consistently diagnosed by increased number of postmentals (7), loss of the postfrontal (92), and pineal foramen in the parietal (90). The Templeton test did not find the Hispaniolan twig dwarf species to be significantly monophyletic ($n = 6$; $P = 0.17$).

The following discussion concerns character evolution on the frequency analysis, unless otherwise noted. The sister species to the Hispaniolan twig dwarfs was Puerto Rican dwarf twig species *A. occultus* (also in unscaled analysis), supported by the unambiguous synapomorphies of smooth supradigitals (3), small size (10), narrow skull (86), lack of prefrontal nasal contact (93), maxilla extends to ectopterygoid (103), short mandibular toothline (109), short dentary (112), loss of splenial (113). All of these characters are homoplastic. In the frequency analysis (and in the unscaled analysis), the closest relatives of these twig dwarfs were hypothesized to be twig species from Hispaniola (*A. darlingtoni*) and northern South America (*A. solitarius*; although no detailed ecological studies have involved *A. solitarius*, evidence suggests that this species fits the twig ecomorph; Williams, 1992), and *Phenacosaurus heterodermus*, the ecology of which has not been studied. This clade was diagnosed by eleven unambiguous synapomorphies, including reduced numbers of loreals (8) and scales between second canthals (9), decrease in SVL (10), increase in number of inscriptive ribs (80), narrow skull (86), dorsal process of jugal sutures posterior or medial to postorbital (95), jugal does not form anterior border of lacrimal (98), shortened epitygoid (99), straight and anterior palatine-vomer suture (102; scoreable only in *A. solitarius*, *P. heterodermus*, and *A. darlingtoni* among species in this clade), short toothline (109), reduced angular process (110). All of these characters are homoplastic except for the palatine-vomer suture (112). However this character (112) could not be scored for several species because of damage (some smaller *Anolis*) or unavailability.

The clade of the Hispaniolan twig dwarf

species plus *A. occultus*, *A. darlingtoni*, and *A. solitarius* was supported by ten unambiguous synapomorphies, including increase to two sublabials (4), (very slightly) larger ratio of female to male length (11), reduced number of attached ribs (81), narrow skull (86), Y-shaped parietal crest (87), dorsal process of jugal sutures posterior or medial to postorbital (95; above change was v to 4, this change is 4 to 0), less jugal-squamosal contact (96), lack of contact between pterygoid and lacrimal (97), flattened dorsum sella (100), anteriorly oriented anteromedial process of coronoid (114). All of these characters are homoplastic except the flattened dorsum sella.

Character support in the frequency analysis is listed in Appendix V, including details on the degree of change in the above discussed clades and in other clades.

Survey of Anolis

In order to assess whether other *Anolis* will be placed in dwarf twig *Anolis* clades when more species are rigorously analyzed, from 1–3 MCZ specimens each of 143 species (MCZ numbers were not recorded) were examined for the character states of a convex parietal (character 89), crenulated parietal edges (88), flattened dorsum sella (100, abbreviated below as ds), shortened epitygoid (99, e), reduced angular process (110, ap), straight and anterior palatine-vomer suture (102, pvs), and medial or posterior termination of the dorsal process of the jugal (95, j). These characters were selected from those discussed above because 1) they were synapomorphies in dwarf twig monophyly or for their wider relationships (including *A. occultus*, *A. darlingtoni*, *A. solitarius*, *P. heterodermus*) under both ACCTRAN and DELTRAN optimization, and 2) they appear to be uncommon in *Anolis*. Thus, characters such as narrowness of the skull were not surveyed because they are known to be common in *Anolis*.

The following *Anolis* species were examined for the character states listed above. Synapomorphies found in each species are listed in parentheses.

Anolis aeneus, *aequatorialis*, *agassizi*, *ahli*, *aliniger*, *allisoni*, *allogus*, *altavelen-*

sis, alumina, alutaceus, "anchicaye", angusticeps, anisolepis, antoni, apollinaris, argenteolus, argillaceus, auratus, baharuccensis, baleatus (j), baracoae (e), barkeri, bartschi, bitectus, blanquillanus, boettgeri, bombiceps, bonairensis, bourgeai, bremeri, brevirostris, brunneus, calimae (e, ap), capito, caudalis, chloris, chlorocyanus, chocorum, christophei, chrysolepis (e), clivicola, cobanensis, concolor, conspersus, cooki, cyanopleurus, danieli, deschensis, dolichocephalus, dunni, ernestwilliamsi, etheridgei, eugenegrahami, eulaemus, evermanni, extremus, fasciatus, ferreus, festae (ap), fitchi, forresti, fraseri, frenatus, fuscoauratus, gadovi (e), garmani, gemmosus (e), gingivinus, gracilipes, granuliceps, gundlachi, haguei, hui-lae (pvs), humilis, insignis (e), jacare (ap, ds), latifrons (j), limifrons, lineatopus, lineatus, lionotus, lividus, longiceps (pvs), longitibialis, loveridgei, loysiana, luciae, lucius, maculigula, marcanoi, marsupialis, medemi, megapholidotus, menta (e, ap), mestrei, microtus, monensis, nebulosus, nelsoni, nigropunctatus (ap), noblei, olsomni, opalinus, ophiolepis, ortoni, oxylophus, parvaauritus, paternus, pentaprion, peraccae, petersi, pinchoti, poecilopus, pogus, polyrhachis, poncensis, porcatus (j), princeps, pulchellus, quadriocellifer, quercorum, reconditus, "robertoi", ruizi (j, ds, ap), santamartae (ap), schwartzzi, sericeus, shrevei, smaragdinus, sminthus, strahmi, transversalis (ap), aeneus × trinitatus, uniformis, urraoi, vanidicus, vaupesianus (e, ap), ventrimaculatus.

As found previously, two of the Hispaniolan twig dwarf synapomorphies (88, 89) were not observed. Although none of the other twig synapomorphies is unique in *Anolis*, some of them are very rare individually, and were observed in combination only in species from the *tigrinus* series (*A. ruizi*, *A. vaupesianus*, *A. menta*, *A. calimae*), of which *A. solitarius* is a member.

DISCUSSION

Hispaniolan Twig Dwarf Species

Hispaniolan dwarf twig species monophyly and relationships.—The monophyly of the Hispaniolan twig dwarf species was

strongly supported in this study by parsimony analyses under different character codings (Fig. 18), bootstrap parsimony analyses (Fig. 17), and by the presence of two character states not seen in the wider survey of *Anolis*. This result contrasts with those of other studies that considered these species (Burnell and Hedges, 1990; Williams, 1976a). This difference may be due to the expanded character base of this study, differences in taxa sampled, or methodological differences. Burnell and Hedges (1990) used distance and parsimony methods to analyze 12 characters and 49 West Indian taxa. They erected groups based on their recovered trees and on other evidence (e.g., *A. sagrei* was nested in the *grahami* series in their trees, but was excluded from this group because of immunological data and suspected convergence; Hedges and Burnell, 1990:20). Williams (1976a,b) erected a taxonomy for all known *Anolis*, drawing mainly from Etheridge's (1959) data. In this study, 116 informative characters and 38 taxa from the West Indies and the mainland were analyzed with parsimony.

The Templeton test did not find the Hispaniolan twig dwarf species to be significantly monophyletic. However as implemented, this test may have a high type II error rate. Like the bootstrap, it requires several synapomorphies to attain significance (even if there is no conflict), and achievement of this level may be difficult with only 116 informative characters (most of which were incompletely scored) and changing a single clade, as was done here.

In recognition of the strong support for the (*A. placidus* + *A. sheplani* + *A. insolitus*) clade, I recommended that *A. insolitus* be placed in a series called the *insolitus* series with *A. placidus* and *A. sheplani* rather than in the *darlingtoni* (Williams, 1976a) or *christophei* series (Burnell and Hedges, 1990). Because it is a well supported clade, this group is suitable for use as a terminal unit in phylogenetic analyses involving a larger sample of the genus. The monophyly of *A. insolitus* and *A. sheplani*, although strongly supported in this analysis, should be

viewed with caution, as the characters that support this clade are variable in other species, and could not be scored for many specimens of these species.

In parsimony trees from all analyses, the Hispaniolan twig dwarfs were found to form a clade with Hispaniolan *A. darlingtoni*, Puerto Rican *A. occultus*, Colombian *A. solitarius*, and Colombian *P. heterodermus* (Fig. 18), all of which have been assigned to the twig ecomorph (except the unstudied *Phenacosaurus*, which is sister species to the other species of this clade in the preferred frequency analyses). Although it does not include the Hispaniolan twig species *A. fowleri* or some other twig species on other islands, this clade excluding *Phenacosaurus* will hereafter sometimes be referred to as the "twig clade" mostly for convenience but also to emphasize the ecomorphic aspect of these lizards' similarity (Fig. 17).

Clearly, wider taxonomic sampling and more characters are needed to assess the robustness of this clade, and these relationships will not be conclusive until cladistic analyses have included more *Anolis* species and more characters. Still, the results of this study suggest that *A. sheplani*, *A. insolitus*, *A. placidus*, *A. occultus*, *A. darlingtoni*, *A. solitarius*, and *P. heterodermus*, together with some or all of the other *tigrinus* group species (and, presumably, other *Phenacosaurus*, which were not surveyed), represent a monophyletic assemblage: First, this clade occurred in all parsimony analyses. Second, in the wider survey of *Anolis*, five of the diagnostic synapomorphies for this clade were found in combination only in *tigrinus* group species believed to be closely related to *A. solitarius* (Etheridge, 1959; Williams, 1992; other *Phenacosaurus* were not examined). If it can be assumed that species with more of the synapomorphies of this clade are more likely to be phylogenetically closer to this clade than are species with one or none of these synapomorphies, then the *tigrinus* group species are likely to be close relatives of this clade. Similarities between the Hispaniolan twig species and *tigrinus* group *Anolis* have previously been noted by Williams (1992), Ayala et al. (1984), and

Etheridge (1959). However, these were rejected as convergence by those authors, probably because of the considerable overwater distance separating these species (~700 km).

Within this group of twig species, the monophyly of the Hispaniolan (*A. insolitus*, *A. sheplani*, *A. placidus*, *A. darlingtoni*) and Puerto Rican (*A. occultus*) twig species (excluding *A. fowleri*) relative to other Caribbean *Anolis* is suggested by the absence of caudal autotomy (reversal in *A. occultus*; present in *Phenacosaurus* and several South American *Anolis*), which is not found in other Caribbean *Anolis* (Williams, 1976a), and the posterodorsal termination of the jugal (not seen in the *tigrinus* group, including *A. solitarius*, but present in *P. heterodermus*) and flattened dorsum sella, which were not observed in Caribbean species in the wider survey, as well as the general rarity of the diagnostic synapomorphies according to the wider survey.

Potential biogeographic and ecomorphic implications.—The above relationships suggest the possibility of an invasion of twig *Anolis* to Hispaniola or Puerto Rico from Colombia, and presence of a monophyletic group of twig species in Puerto Rico, Hispaniola, and South America. The Colombia to Hispaniola (or Puerto Rico) scenario may be more plausible than the alternative (a Hispaniola to Colombia invasion, with ancestors of the *tigrinus* group in the West Indies) for two reasons: first, this paper and work by Etheridge (1959), Williams (1976a,b) and Guyer and Savage (1986) suggests that the *tigrinus* group and *Phenacosaurus* are parts of sister groups to most *Anolis* (i.e., "primitive" groups) and strongly implicates South America as the origination of *Anolis*. Second, the few *tigrinus* group species that could be examined had some but not all of the rare synapomorphies that support this clade, thus suggesting they are sequential outgroups to this clade rather than monophyletic with just *A. solitarius* (additional *Phenacosaurus* species were not examined). These alternatives could not be investigated conclusively because the *tigrinus* series is among the least known groups of *Anolis*.

(Williams, 1992). The possibility of this Colombia to Hispaniola invasion has probably escaped notice because the *tigrinus* group species, and the South American species in general, have been so meagerly studied (Williams, 1989; Hass et al., 1993), and because of the extreme overwater distance mentioned above. If the closest relatives of the Hispaniolan and Puerto Rican twig species are in South America, as appears to be the case, then this may help explain why knowledge of their relationships has been so elusive. Etheridge (1959) (who examined no other twig species examined here) considered *A. darlingtoni* to be "of uncertain position in the alpha section" (p. 154), although he did recognize similarities to unspecified species in his *latifrons* series (p. 155), of which *A. solitarius* is a member.

This discussion assumes dispersal (e.g., Hedges et al., 1992), but vicariant explanations are also possible. For example, the anole fauna of Hispaniola could have reached its present diversity by collision of tectonic plates that each contained a community of anoles (Roughgarden, 1995). Recent expositions on the geologic history of the Caribbean do not suggest that Hispaniola and Northeastern South America have ever been in direct contact, but that Puerto Rico and Hispaniola (indeed, virtually all of the Caribbean) may have been linked during the Cretaceous (Stehli and Webb, 1985; Roughgarden, 1995). If these hypotheses are accepted, than a vicariant origin for *A. occultus* relative to *A. insolitus*, *A. sheplani*, *A. placidus*, and *A. darlingtoni* is possible, but the origin of these species from the northeastern South American *tigrinus* group is not easily explained by vicariance.

The monophyly of twig species on three different land masses contradicts the usual notions of convergent ecomorph evolution suggested between Puerto Rico and Jamaica by Williams (1983) and Losos (1992, 1994) (who recognized the possibility that the Hispaniolan situation was probably more complex than that seen in the comparatively simple radiations on Puerto Rico and Jamaica; 1992:405). The result of the Hispaniolan-Puerto Rican-South Amer-

ican twig clade suggests that specialized ecomorphs on separate islands do not always arise by convergence, but rather that they can occur as independent invaders without being part of an intraisland adaptive radiation. *Anolis* ecomorphs were originally defined in terms of convergent evolution (Williams, 1972), and the existence of the adaptive radiation on Jamaica suggests that ecomorph convergence between land masses could be a general rule [see Williams (1983), Hedges and Thomas (1989), Losos (1992, 1994)]. Losos, for example, has stated concerning the greater Antilles that "it is clear that evolutionary radiations have occurred more or less independently on the four islands" and that "the same 'ecomorph' types have evolved on all four islands, producing apparently convergent assemblages" (Losos, 1992: 405). But, the correlations between morphology, ecology, and behavior that define the same ecomorph on different islands could also occur by common ancestry, as appears to be the case with the twig clade.

Relationships of Representative Anolis

Because only 38 of a potential 350 species were included in the parsimony analyses and deep branches of the recovered trees were only weakly supported, conclusions are necessarily speculative. However some comment is warranted. Unless otherwise stated, the following discussion refers to the preferred frequency analysis. Refer to Fig. 17 as a guide.

Weakly supported clades.—It is apparent from the bootstrap analysis (Fig. 17) and the consensus tree (Fig. 18) that most of the relationships in these analyses are not well supported. The regions of the tree that were not robustly resolved (almost all relationships except the twig clade) all involve relatively deep branches. All species except those in the twig clade were selected as exemplars of larger groups (the informal "series" of previous authors); these exemplars presumably are more closely related to members of their own series than they are to other species included in these analyses. Perhaps the monophyly of smaller groups in *Anolis* is relatively easy to discern whereas the re-

relationships among these smaller groups are more difficult. In addition to this paper, this pattern is seen in previous phylogenetic analyses in *Anolis* (Etheridge, 1959; Shochat and Dessauer, 1981; Burnell and Hedges, 1990; Hass et al., 1993). This lack of support in the deep branches could be due to character conflict, a paucity of collected characters, a rapid radiation causing a dearth of informative variation, or some other factor. Although a rapid radiation is an attractive explanation, these possibilities are difficult to distinguish without many more characters and better coverage across species.

Previously suggested relationships.—Some support was found for some of the genera of Guyer and Savage (1986, 1992) and the informal groupings of Williams (1976a) and Etheridge (1959). Guyer and Savage's *Ctenonotus* was monophyletic, with *A. bimaculatus* and *A. cristatellus* as sister species exemplars of their respective series. The presence of *A. distichus*, which is usually considered a member of the *cristatellus* series (e.g., Etheridge, 1959; Williams, 1976a), with *A. cybotes* exclusive of *A. cristatellus* suggests that the *Ctenonotus* complex of anoles should be studied in more detail and sampled more extensively. *Norops*, composed of Etheridge's (1959) beta anoles, was nearly monophyletic, as only *A. polylepis* was excluded. The Jamaican series of beta anoles was monophyletic (Etheridge, 1959; Shochat and Dessauer, 1981; Hedges and Burnell, 1991), although not convincingly so (Figs. 17, 18), and the mainland betas were monophyletic except for *A. polylepis*, and nested within Caribbean betas. *Dactyloa* (Etheridge's *latifrons* series) appears as a paraphyletic basal group of anoles (Fig. 17). *Anolis* sensu stricto (see Savage and Guyer, 1989) was polyphyletic and paraphyletic in all analyses. The monophyly of *Xiphosurus* (Williams' 1976 *cuvieri* series) was not tested. Williams' (1976a) *carolinensis* and *punctatus* subsections were not monophyletic in any of the parsimony trees. Lower level groupings of Etheridge (1959) and Williams (1976a,b) were not tested, as only representative species from these groups were included.

Names.—In all analyses, *Phenacosaurus heterodermus* was nested within *Anolis* (Fig. 18). Although the name *Phenacosaurus* has enjoyed continued use, this result is not novel; Etheridge (1959:Fig. 10) first suggested *Anolis* paraphyly relative to *Phenacosaurus*, a possibility reiterated in Etheridge and de Queiroz (1988). Because recognition of *Phenacosaurus* renders *Anolis* paraphyletic (Figs. 15–18) I recommend that *Phenacosaurus* be synonymized with *Anolis*.

Some of the relationships recovered in these analyses may eventually warrant formal taxonomic recognition (e.g.) as genera; likely candidates include the Hispaniolan–Puerto Rican–South American twig clade plus *Phenacosaurus* and Guyer and Savage's *Ctenonotus*. However recognition of these groups would be premature until 1) more species can be sampled to ensure the proper allocation of species (testing the monophyly of the series and species groups is critically important) and 2) relationships of other *Anolis* are more robustly resolved. Recognition of (e.g.) either of these clades would render *Anolis* paraphyletic, and naming the weakly supported clades in this analysis does not seem prudent for reasons of stability.

Potential biogeographic and ecomorphic implications.—The scheme in Figure 17 has some geographic coherence. A paraphyletic basal group of *Anolis* includes lineages that invades the West Indies by dispersal or vicariance once through the Southern Lesser Antilles (*A. griseus* of the *roquet* group) and twice through the Greater Antilles (the twig clade and a larger radiation). Back-invasion of the mainland occurred once (beta *Anolis*) or perhaps twice (if *A. polylepis* is correctly placed). The extent of intraisland radiation is impossible to judge without inclusion of more species, but it is evident that movement between islands has not been lacking.

If the relationships of any of the recovered trees (Figs. 15–17) are real, than intraisland adaptive radiation, or at least island monophyly, appears uncommon in *Anolis*. This lack of island monophyly has implications for views on *Anolis* ecomorph

evolution. For example, if Puerto Rican species *A. occultus*, *A. cuvieri*, and *A. cristatellus* are each part of separate evolutionary lines (Figs. 15–17), then the conclusions of Losos (1992) concerning convergent sequences of community structure are in need of re-examination. The hypothesized similarity of the sequences of ecomorph evolution on different islands depicted in Losos (1992:Figs. 6, 7) is predicated on the ecomorphs of Jamaica and Puerto Rico each evolving in succession *in situ* from their respective common ancestors. This condition is necessary to ensure that one is comparing the evolution of convergent communities (rather than just the existence of similar ecomorphs) and so that ancestral states can be reconstructed accurately. The parsimony trees of this paper, in which twig species *A. occultus*, crown-giant *A. cuvieri*, and trunk-ground species *A. cristatellus* are each part of separate phyletic lines that include many non-Puerto Rican species, contradict this assumption of Puerto Rican monophyly. One could still compare the Jamaican radiation to the radiation of the *cristatellus* group (which includes the Puerto Rican *Anolis* that are not *A. occultus* or *A. cuvieri*) on Puerto Rico, but results are less interesting. If the Jamaican species and the remaining Puerto Rican species (excluding *A. occultus* and *A. cuvieri*) are each monophyletic and endemic to those islands, then the Jamaican lineage contains the ecomorphs twig, trunk-ground, crown-giant, and trunk-crown, whereas the Puerto Rican *cristatellus* lineage contains the ecomorphs trunk-crown, trunk-ground, and grass-bush (with twig and crown-giant species invading separately). In this case, the two radiations share just two ecomorphs. If this lack of Puerto Rican monophyly holds in future study, the question of a convergent sequence of community evolution is moot, as there is little similarity even between which ecological niches are filled during these radiations. It is possible that the sequence of ecomorph invasions in Puerto Rico may mirror the radiation of ecomorphs in Jamaica, but this is a different question that is not answerable from phylogeny alone—one would need to

know the timing of the invasions. It is also possible that convergent structure in the evolution of complex communities may eventually be found between other islands in the Caribbean (Losos, 1994), or perhaps Jamaica "may be our only example of a complex anole fauna evolved within an island" (Williams, 1983:342).

Although the lack of island monophyly and the existence of the twig clade suggests that convergence of ecomorphs between islands should not be an assumption in evolutionary analyses of *Anolis*, it is apparent that ecomorph monophyly is no more the rule than is intraisland adaptive radiation. Some ecomorphs are not monophyletic even within islands (Williams, 1983; Losos, 1994; e.g., probably twig species *A. fowleri* is not part of the twig clade discussed above). No generalizations are currently possible concerning the evolution of *Anolis* ecomorphs. How a given ecomorph came to occur in an area should be evaluated on a case-by-case basis with a phylogenetic approach.

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APPENDIX I

Specimens Examined for Parsimony Analyses

Numbers are Museum of Comparative Zoology (MCZ) unless otherwise noted.

Anisolepis undulatus 59273, 59274, 84033, 133191; *Enyalius iheringi* 6316; *Leiocephalus melanochlorus* 37528, one additional specimen of unrecorded number; *Polychrus marmoratus* 6101, 46441, 74149, 74150, 74153, 147437, 74151, 74152, 131670–2, 173135; *Urostrophus gallardoi* 162920; *U. vautieri* 7319, 84036;

Anolis aequatorialis 100507, 107699, 156811, 176457; *A. alutaceus* 21860; *A. argillaceus* 42528, 42559, 173782; *A. angusticeps* 59245, 59248–50, 93354; *A. auratus* 77430, 77448, 133473–5, 133480–1, 133483–4; *A. bimaculatus* 10380i, 10380ii, 28717, 10384, 145814, 145813, 16531, 6156i, 6156ii, 57171; *A. biporcatus* 24396, 32206, 85556; *A. carolinensis* 57012, "PI", "PII", "PIII", 57385 (4 pairs of jaws); *A. coelestinus* 131572, 131574, 131994–5, 131999, 132000, 144780, 144795; *A. cristatellus* 35763, 35767, 130048, 131583, 132018–9, 140247; *A. cuvieri* 3598, 3587, 35985, 35979, 35986, 35981, 85472; *A. cybotes* 131278, 131274, 132865, 37471, 132864, 134012, 134015, 131277, 131298, 134013, 131301, 131281, 132868, 131297, 132867, 131601, 37474, 131280, 131272, 37473, 131286, 134014, 131603, 131289, 37470; *A. darwini* 173207; *A. distichus* 140063, 140234, 140237, 142512, 142514, 145319, 152483, 152488; *A. equestris* 55630, 55633, 66843, 131609–10; *A. fowleri* 166996, 135388; *A. grahami* 154135, 140225, 154134, 119707, 138509, 131624, 138508, 140224, 69832, 131625, 138511, 52305, 138510, 131626, 138504, 142518, 142520, 142519, 131623; *A. griseus* 82927, 82013, 82009, 81343, 82928, 81333; *A. hondurensis* 66030, 66037–8, 66042, 66045, 66050, 66056, 66069, 131268; *A. insolitus* 107015, 10717–8; *A. lucius* 55801–3, 67990, 68021, 68014, 68020–2; *A. meridionalis* 18089–90; *A. monticola* 120014, 124896, 124921, 124936, 124902, 124935, 124923, 120013, 121733, 124866, 63000, 121732, 124880, 124922, 124917, 124878, 124864; *A. nebuloides* 92965–7, 100379; *A. occultus* 83657, 131667, 146684, 83660, 146683, 35983; *A. onca* 57386, 110066, 110068, 140261–2, 140264, 144822, 145312; *A. placidus* 173209; *A. polylepis* 133824, 133828, 132873, 133825, 133827, 133870, 132872, 132871, 133826; *A. punctatus* 20630, 84050, 84052, 92537, 153994; *A. sagrei* 61106, 61107, 68149, 71577, 71590, 142509, 142511, 171990, 171997; *A. semilineatus* 63427, 63430–1, 64842, 64862, 79316, 152521–2; *A. sheplani* 140021, 125691; *A. solitarius* 24393, ICN 6153, ICN 6179; UMMZ 148935; *A. squamulatus* 66895, 159123; *A. subocularis* 167239, 167242; *A. valencienii* 7341, 7358, 45139, 68761, 73535, 140103, 145320–1; *Phenacosaurus heterodermus* 110133–4, 110136–8, 145324–5;

APPENDIX II

Matrix from Frequency Analysis: File from PAUP

```
BEGIN DATA;
DIMENSIONS NTAX=42 NCHAR=116;
FORMAT MISSING=? GAP=- SYMBOLS= "0 1 2 3 4 5 6 7 8 9 a~v";
OPTIONS MSTAXA=POLYMORPH;
[spaces are between the different data "types": external, DNA, allozyme, postcranial osteology, chromosome,
skull]
;

MATRIX
insolitus
00020ns904o0 ??????????????????????????????????????????????????????????
codgj?? 10700 00 0vvvvvv0f0fnvvv?00v000lv0vvl0v

sheplani
00020ng9alq1 ??????????????????????????????????????????????????????
fosbk?? ????? 00 ?vvvvvv0000vvv?00v0?0jv0vv0v

placidus
00020vd5a4r1 ??????????????????????????????????????????????????
?????? ?? 7vvv0v0v0000?vvv?00v000nv0?vv0v

darlingtoni
00220h993d?0 33100112102031011?3300003003333023102120030011210331310111
frnfi20 15b00 ?? hk000v000000vvv?0f0v0?0000f0v0v

solitarius
00220hdij6q0 ??????????????????????????????????????????????
?????? 05b00 ?? gv000v0lv0500v150v0v7v000v0v

occultus
00001h9fu2r0 3112011230210103333102000013333000102130033003000101130113
eubb(ei)?? 1fr00 00 5000007vv0000rvv?00v000sv0vv00

cybotes
002200vtgfg0 331001020013030111102200113333301332320210213000313130113
fdmbf00 00010 00 sk000vgs0v0i90060v02v0p00lvv05v

bimaculatus
000200slen00 3310011230330101011102010033333003302120010011200131130111
?????? 00710 24 sk00fv0v0vn000000s0p00vv4eev

grahami
101200nnrdj0 3300011230330101313300030003333303300321010113000133130113
flbbk11 10711 02 pk00vu0m0vgir0040000pf010qv4v

griseus
101210qnkp40 3112030232201123313102010003333300330210000103301011131011?
?????? 00f10 00 u000000000v0qf00v0000v00005006v

cuvieri
00210adnmppm0 3300013110330101113102000033333001102120030013000001130113
?????? 00710 00 uk000v070vhv10000t0010r004v3v0v

monticola
20210hqvo7g0 ??????????????????????????????????????????????
jrphd?? 10710 00 fe003l0g0v4bp00v0j0v010002vv2gv
```

polylepis

002100svt8n0 ???
?????? 10711 02 hf00j30h0vluv00v0u0v05300vvv3vv

fowleri

10220h9lger0 ???
colgf?? 10710 00 qa00vv000vvvv00v0f0vf?0000vvf0v

aequatorialis

01211hvvvhm0 ???
?????? 10f?0 ?? ka007v070vvfb00v0j00l0v00000r0v

punctatus

10110hnprhk0 ???
?????? 00f00 ?? mi00060mvv9mc00v0v0000000v0d0v

cristatellus

002200sncem0 3310011230330101112102101003333020302120010113202331130111
gnpbfo3 00010 24 rk00rv9v0v4pq0030vv0vf000lv007v

distichus

001200vlc8j0 1310330210330101111300233013331300133212001001121013311311
hnobe?? 00710 22 oh000o0e0vaj100v0v0aju0h0dv00mv

semilineatus

202100glh4n0 3310012110330121333102000111333000302120011113200331130311
cgdf?? 10710 00 7d00b7710v9rv00v0f0v3d020bvv10v

angusticeps

00110nsfe6h0 ???
?????? 10010 ?? ce00cj0p0sbs600v000ncp7j0pvvpbv

equestris

00020rdiavm0 ???
?????? 10710 00 vk000v000vfla002p00aav00000s0v

lucius

000200vpeck0 3310011230330301133102000033333003302120010013010101330113
?????? 10710 00 mk00hvc50vhjv000?v007aa00fv080v

auratus

21200hnrk7m0 ???
?????? 10011 02 eh0000vo0v0nb00v0l0d00020lvvnlv

onca

2?210vdphog0 ???
?????? 10011 12 pk000vvt0vmnm60r?v09b0a009vzb4v

biporcatus

20111rqvuiq0 ?????????????????????????????????
?????? 1a711 23 pa000f0v0fvv00v0v0vv0v00fv000v

sagrei

202200knge60 3312011230330101113330003000313130330032000213000131130313
clbbm12 10011 03 ok00vsno0kv300v0sv33ei00fvv73v

valencienni

00120aqcagk0 ?????????????????????????????????
albjn11 10011 02 lk003v0s0v5hp0030a03vv2005vv30v

argillaceus

00120hq955e0 3112211230330301131132200030333300122100010013032330130111
?????? 10010
?? lk00v00v0v00l00v0v0fvvf0lvvf0v

coelestinus

102100gnqfc0 ???
hmdbi?? 10f10 00 kj00000r0q0sk000000m43002vvv3v

hendersoni

002200vpe6n0 33100112102001011311020010133110103302320230013010131110011
gpdbf?? 10710 00 8f00v30h0v07k0000000000200v0cav

P._heterodermus

00110a505dp0 ???
?????? 0vf00 00 j0000v0c04mm0v0v100?00f4v0m042v

alutaceus

002100dmh0q0 1312213212330301133102033033333011300320010013000003330301
?????? 10710 ?? bk00v00v0v?vv?0v000v0v?0?fvv0vv

carolinensis

20220rnghcd0 ???
diebm14 10710 00 ik00070r0vvan0000v0f00vv0fvv0v

squamulatus

1021?advuiv0 ???
?????? 10f00 00 qk000v000vvfv00v0f0000v000v070v

meridionalis

21211hkmm8r0 ?????????????????????????????????????
?????? 1a701 ?? k000000v0vvv0000v0f00v007vv7fv

nebuloides

2022105kg6h0 ?????????????????????????????????
?????? 10011 11 k50000vv0vfbv00v0v0v007000vv0vv

subocularis

10210adihad0 ?????????????????????????????????
?????? 10011 12 j50000v0fv0ffv000v0v000000vvfnv

Polychrus

?????????0 1112230212200121111132200101033002132210101003321011111101
?????? 0??2 05 v000?0v0000mv00?00000v00060900

Leiocephalus

?????????pa?0 1310213232201101313102100101333323332101010033210311310113
?????? ??2 ?? v00000000v07000v?00000v?0000vfv

Urostrophus

0?0?0n0??9v0 ?????????????????????????????????
?????? ?f402 ?? v0000000000?????0?0000?????0?0?0?00

Enyalius

?????????c?0 ?????????????????????????????????
?????? ??2 00 v0000000000????0?0000?????0v?0v00

Anisolepis

2?1?0h0??8v0 ?????????????????????????????????
?????? ?va02 00 v0000000000????0?0000?????0?0?0v00

;
END;

BEGIN ASSUMPTIONS;

```
OPTIONS DEFTYPE=unord PolyTcount=MINSTEPS ;
TYPESET * UNTITLED = unord: 13-78 84-85 102, ord: 1-12 79-83 86-101 103-116;
wts * mercutio=1000:all, scale/basewt=1000: 1-11 80 81 86-101 103-116;
END;
```

APPENDIX III

Matrix from Unscaled Analysis: File from PAUP

BEGIN DATA;
 DIMENSIONS NTAX=42 NCHAR=116;
 FORMAT MISSING=? GAP=- SYMBOLS= "0 1 2 3 4 5 6 7 8 9 a~v";
 OPTIONS MSTAXA=POLYMORPH;

MATRIX

insolitus

00020ns904o0 ???
 codgj?? 10100 00 0511222201011222?00200031022101

sheplani

00020ng9alq1 ???
 fosbk?? ????? 00 9511222200002222?0020?031022201

placidus

00020vd5a4r1 ???
 ??????? ????? ?? 751102020000?222?002000310?2201

darlingtoni

00220h993d?0 33100112102031011?3300003003333023102120030011210331310111
 frnfi20 11200 ?? h4000200000022211020?000010201

solitarius

00220hdij6q0 ???
 ??????? 01200 ?? g500020110100212110200211000201

occultus

00001h9fu2r0 31120112302101033331020000133333000102130033003000101130113
 eubb(ei)?0 13400 00 5000001210000122?00200031022200

cybotes

00220vtgfg0 331001020013030111102200113333301332320210213000313130113
 fdmbf00 00010 00 s400021102011001020120100122011

bimaculatus

000200slen00 331001123033010101102010033333003302120010011200131130111
 ??????? 00110 24 s400120202100000010100221111

grahami

101200nnrdj0 3300011230330101313300030003333303300321010113000133130113
 flbbk11 10111 02 p400210102111001000011010122211

griseus

101210qnkp40 3112030232201123313102010003333300330210000103301011131011?
 ??????? 00310 00 u000000002011002000020000010011

cuvieri

00210adnmppm0 3300013110330101113102000033333001102120030013000001130113
 ??????? 00110 00 u400020102121000010010100121201

monticola

20210hqvo7g0 ???
 jrphd?? 10110 00 f300110102111002010201000122111

polylepis

002100svt8n0 ???
 ??????? 10111 02 h300110102112002010201100222121

fowleri

10220h9lger0 ???
colgf?? 10110 00 q20022000222200201021?000022101

aequatorialis

01211hvvhm0 ???
?????? 103?0 ?? k200120102211002010010200000101

punctatus

10110hnprhk0 ???
?????? 00300 ?? m30001011211100202000000020101

cristatellus

002200sncem0 3310011230330101112102101003333020302120010113202331130111
gnpbfo3 00010 24 r400121202111001021021000120011

distichus

001200vlc8j0 13103302103301011113002330133313001332120010011210133111311
hnobe?? 00110 22 o300010102111002020111030120011

semilineatus

202100glh4n0 33100121103301213331020001113330000302120011113200331130311
cgdif?? 10110 00 7300111102112002010211010122101

angusticeps

00110nsfe6h0 ?????????????????????????????????????
?????? 10010 ?? c300110101111002000111130122111

equestris

00020rdiavm0 ?????????????????????????????????
?????? 10110 00 v400020002121100210011200000101

lucius

000200vpeck0 331001123033030113310200003333003302120010013010101330113
?????? 10110 00 m400121102112000?20011100120101

auratus

21200hnrk7m0 ?????????????????????????????????????
?????? 10011 02 e30000210201100201010010122111

onca

2?210vdphg0 ?????????????????????????????????
?????? 10011 12 p40002210211101?20110100122111

biporcatus

20111rqvuiq0 ?????????????????????????????
?????? 12111 23 p200010202122002020220200120001

sagrei

202200kngc60 33120112303301011133300030003131303300320000213000131130313
clbbm12 10011 03 o4001110212100201111100122111

valencienni

00120aqcagk0 ?????????????????????????????
albjn11 10011 02 l400120102111001010122100122101

argillaceus

00120hq955e0 31122112303303011311322000030333300122100010013032330130111
?????? 10010 ?? l400200202001002020212220122101

coelestinus

102100gnqfc0 ?????????????????????????
hmdbi?? 10310 00 k300000101011000000011100122211

hendersoni

002200vpe6n0 33100112102001011311020010133110103302320230013010131110011
gpdbf? 10110 00 830021010201100000000010020111

P._heterodermus

00110a505dp0 ???
?????? 14300 00 j000020101110202100?00111010111

alutaceus

002100dmh0q0 1312213212330301133102033033333011300320010013000003330301
?????? 10110 ?? b400200202?22?02000202?0?122021

carolinensis

20220rnghcd0 ???
diebm14 10110 00 i400010102211000020100240122101

squamulatus

1021?advuiv0 ???
?????? 10300 00 q400020002212002010000200020101

meridionalis

21211hkmm8r0 ???
?????? ?? 12101 ?? k000000202222000020100200122111

nebuloides

2022105kg6h0 ???
?????? 10011 11 k100002202112002020200100022022

subocularis

10210adihad0 ???
?????? 10011 12 j10000210212000202000000222111

Polychrus

????????????0 111223021220012111132200101033002132210101003321011111101
?????? 0???2 05 v000?02000012100?00000200010100

Leiocephalus

?????????a?0 1310213232201101313102100101333323332101010033210311310113
?????? ???2 ?? v00000000201002?000002?0000211

Urostrophus

0?0?On0??9v0 ???
?????? ?3(01)02 ?? v0000000000??0?0000??0?0?0?00

Enyalius

?????????c?0 ???
?????? ?? ???2 00 v0000000000??0?0000??0?02?0200

Anisolepis

2?1?0h0?8v0 ???
?????? ?4202 00 v0000000000??200?0000??0?0?0200

;
END;

BEGIN ASSUMPTIONS;

```
OPTIONS DEFTYPE=unord PolyTcount=MINSTEPS ;
TYPESET * UNTITLED = unord: 13-78 84-85 102, ord: 1-12 79-83 86-101 103-116;
wts * mercutio=1000:all, scale/basewt=1000: 6-11 86;
END;
```

APPENDIX IV

Matrix from Any-instance Analysis: File from PAUP

```
BEGIN DATA;
DIMENSIONS NTAX=42 NCHAR=116;
FORMAT MISSING=? GAP=- SYMBOLS= "0 1 2 3 4 5 6 7 8 9 a~v";
OPTIONS MSTAXA=POLYMORPH;

MATRIX
insolitus
00020ns904o0 ??????????????????????????????????????????????????????????
codgi?? 10100 00 0vvvvvvv0v011vvv?00v000vv02v20v

sheplani
00020ng9a1q1 ??????????????????????????????????????????????????????
fosbk?? ????? 00 ?vvvvvv00002vvv?00v0?0vv02v20v

placidus
00020vd5a4r1 ??????????????????????????????????????????????????
?????? ????? ?? 7vvv0v0v0000?vvv?00v000vv0?v20v

darlingtoni
00220h993d?0 33100112102031011?3300003003333023102120030011210331310111
frnfi20 11200 ?? hv000v000000vv1v0v0?00001020v

solitarius
00220hdij6q0 ??????????????????????????????????????????????????
?????? 01200 ?? gv000v0vv0v0vv1v0v0vv00020v

occultus
00011h9fu2r0 311201123021010333102000013333000102130033003000101130113
eubb(ei) ?? 13400 00 500000vvv0000vvv?00v000vv02v200

cybotes
00220vtgfg0 3310010200130301111102200113333301332320210213000313130113
fdmbf 00 00010 00 sv000vvv0v01100v0v0vv0000v2v1vv

bimaculatus
000200slen00 3310011230330101011102010033333003302120010011200131130111
?????? 00110 24 sv00vv0v0v0210000000v0000v2v1vv

grahami
10120nnrdj0 3300011230330101313300030003333303300321010113000133130113
ffbbk11 10111 02 pv00vv0v0vv1100v0000vv0v0v2v2vv

cuvieri
00210adnmppm0 330001311033010111310200003333300110212003001300001130113
?????? 00110 00 uv000v0vv210000v00v0000v2v20v

monticola
20210hqvo7g0 ??????????????????????????????????????????????????
jrphd?? 10110 00 fv00vv0v0vv1100v0v0v000v2v1vv

polylepis
002100svt8n0 ??????????????????????????????????????????????
?????? 10111 02 hv00vv0v0vv1200v0v0v0v000v2v1vv
```

fowleri

10220h9lger0 ???
colgf?? 10110 00 qv00vv000vv2200v0v0v?00002v10v

aequatorialis

01211hvvvhm0 ???
?????? 103?0 ?? kv00vv0v0vv1100v0v00v0v0000010v

punctatus

10110hnprhk0 ???
?????? 00300 ?? mv000v0vvv1100v0v00000002010v

cristatellus

002200sncem0 3310011230330101112102101003333020302120010113202331130111
gnpbfo3 00010 24 rv00vvv0vv1100v0vv000v200vv

distichus

001200vlc8j0 13103302103301011113002330133313001332120010011210133111311
hnobe?? 00110 22 ov000v0vv1100v0v0vv0v0v200vv

semilineatus

202100glh4n0 33100121103301213331020001113330000302120011113200331130311
cgdif?? 10110 00 7v00vvv0vv1200v0v0vv0v0v2v10v

angusticeps

00110nsfe6h0 ???
?????? 10010 ?? cv00vv0v0vv1100v000vv0v0v2v1vv

equestris

00020rdiavm0 ???
?????? 10110 00 vv000v000vv21v002v00vv000010v

lucius

000200vpeck0 33100112303303011331020000033333003302120010013010101330113
?????? 10110 00 mv00vvv0vv12000?v00vv000v2010v

auratus

21210hnrk7m0 ???
?????? 10011 02 ev0000vv0v01100v0v0v000v0v2v1vv

onca

2?210vdphog0 ???
?????? 10011 12 pv000vvv0vv11v0v?v0vv0000v2v1vv

biporcatus

20111rqvuiq0 ???
?????? 12111 23 pv000v0vv2200v0v0vv0v0v2000v

sagrei

202200knge60 33120112303301011133300030003131303300320000213000131130313
clbbm12 10011 03 ov00vvv0vv2100v0vvvv000v2v1vv

valencienni

00120aqcagk0 ???
albjn11 10011 02 lv00vv0v0vv1100v0v0vv000v2v10v

argillaceus

00120hq955e0 31122112303303011311322000030333300122100010013032330130111
?????? 10010 ?? lv00vv0v0vv00100v0vvvv0v2v10v

coelestinus

102100gnqfc0 ?????????????????????????????????????
hmdbi?? 10310 00 lv00000v0v0110000000vv000v2v2vv

hendersoni

002200vpe6n0 33100112102001011311020010133110103302320230013010131110011
gpdhf? 10110 00 8v00vv0v0v0110000000000v00201vv

P. heterodermus

00110a505dp0 ???
?????? 14300 00 j0000v0v0vv10v0v100?000vv0101vv

alutaceus

002100dmh0q0 1312213212330301133102033033333011300320010013000003330301
?????? 10110 ?? bv00v0v0v?22?0v000v0v?0?v2v0vv

carolinensis

20220rmghcd0 ???
diebm14 10110 00 iv000v0v0vv110000v0v00vv0v2v10v

squamulatus

1021?advuiv0 ???
?????? 10300 00 qv000v000vv1200v0v0000v0002010v

meridionalis

21211hkmm8r0 ???
?????? 12101 ?? k000000v0vv220000v0v00v0v2v1vv

nebuloides

2022105kg6h0 ???
?????? 10011 11 kv0000vv0vv1200v0v0v0000002v0vv

subocularis

10210adihad0 ???
?????? 10011 12 jv0000vv0vv2000v0v000000v2v1vv

Polychrus

?????????????0 111223021220012111132200101033002132210101003321011111101
?????? 0??2 05 v000?0v000012v00?00000v00010100

Leiocephalus

??????????a?0 1310213232201101313102100101333323332101010033210311310113
?????? ???2 ?? v00000000v01000v?00000v?00002f

Urostrophus

0?0?On0??9v0 ???
?????? ?3(01)02 ?? v0000000000????0?0000????0?0?0?0?0

Enyalius

??????????c?0 ???
?????? ???2 00 v0000000000????0?0000????0v0200

Anisolepis

2?1?0h0??8v0 ???
?????? ?4202 00 v0000000000?0?0000????0?0?0?0?0

;

END;

BEGIN ASSUMPTIONS;

```
OPTIONS DEFTYPE=unord PolyTcount=MINSTEPS;
TYPESET * UNTITLED = unord: 13-78 84 85 87-96 99-111 113 115 116,
ord: 1-12 79-83 86 97 98 112 114;
wts * mercutio=1000:all, scale/basewt=1000: 6-11 86;
END;
```

APPENDIX V

Apomorphy list

Unambiguous changes (those insensitive to character change optimization) for frequency tree (Fig. 17). Parsimony cost of number of unweighted steps depends on weight of that character. Refer to PAUP files for character weights.

Branch	Character	Steps	CI	Change
outgroup node → node 1	10	7	0.212	a ↔ h
	13	1	0.333	1 ↔ 3
	17	1	0.500	2 ↔ 0
	38	1	0.333	1 ↔ 0
	40	1	0.667	1 ↔ 3
	46	1	0.500	2 ↔ 0
	53	1	0.500	1 ↔ 0
	60	1	0.200	2 ↔ 0
	83	2	0.500	2 ↔ 0
	86	1	0.230	v ↔ u
	108	28	0.109	v ↔ 3
node 1 → node 2	19	1	0.600	0 ⇒ 1
	22	1	0.500	2 ⇒ 0
	30	1	0.250	1 ⇒ 3
	52	1	0.667	0 ⇒ 2
	58	1	1.000	3 ⇒ 1
	64	1	0.400	1 ⇒ 3
	86	10	0.230	u ⇒ k
	87	18	0.195	0 ⇒ i
	93	17	0.144	0 ⇒ h
	112	26	0.220	5 ⇒ v
node 2 → node 3	91	3	0.139	3 ⇒ 6
	96	9	0.140	0 ⇒ 9
	98	3	0.137	f ⇒ c
	103	15	0.121	0 ⇒ f
	115	3	0.175	3 ⇒ 0
node 3 → node 5	11	5	0.217	k ⇒ p
	91	25	0.139	6 ⇒ v
	108	12	0.109	3 ⇒ f
node 5 → node 6	8	16	0.221	p ⇒ 9
	9	17	0.166	r ⇒ a
	10	4	0.212	h ⇒ d
	80	5	0.356	0 ⇒ 5
	86	1	0.230	k ⇒ j
	95	27	0.365	v ⇒ 4
	98	11	0.137	b ⇒ 0
	99	31	0.378	0 ⇒ v
	102	1	1.000	0 ⇒ 1
	109	4	0.316	0 ⇒ 4
	110	31	0.500	0 ⇒ v
node 6 → node 7	4	1	0.182	1 ⇒ 2
	11	1	0.217	p ⇒ q
	81	4	0.318	f ⇒ b
	86	3	0.230	j ⇒ g
	87	2	0.195	i ⇒ k
	95	4	0.365	4 ⇒ 0
	96	17	0.140	m ⇒ 5
	97	15	0.146	f ⇒ 0
	100	21	1.000	0 ⇒ 1
	114	18	0.114	d ⇒ v
node 7 → node 8	79	1	0.200	0 ⇒ 1
	96	5	0.140	5 ⇒ 0
	100	10	1.000	1 ⇒ v

APPENDIX V—Continued.

Branch	Char- acter	Steps	CI	Change
node 8 → node 9	108	15	0.109	f ⇒ 0
	3	2	0.125	2 ⇒ 0
	10	2	0.212	6 ⇒ 4
	86	11	0.230	g ⇒ 5
	93	10	0.144	l ⇒ v
	103	5	0.121	5 ⇒ 0
	109	16	0.316	7 ⇒ n
	112	16	0.220	f ⇒ v
	113	31	0.161	0 ⇒ v
node 9 → node 10	6	6	0.137	h ⇒ n
	87	11	0.195	k ⇒ v
	88	31	1.000	0 ⇒ v
	89	31	1.000	0 ⇒ v
node 10 → node 11	7	3	0.150	d ⇒ g
	90	31	0.124	0 ⇒ v
	92	24	0.177	7 ⇒ v
node 11 → insolitus	7	12	0.150	g ⇒ s
	9	10	0.166	a ⇒ 0
	11	2	0.217	q ⇒ o
	72	1	0.636	f ⇒ c
	75	1	0.833	b ⇒ g
	95	15	0.365	0 ⇒ f
	97	15	0.146	0 ⇒ f
	114	10	0.114	v ⇒ l
node 11 → sheplani	10	3	0.212	4 ⇒ 1
	74	1	0.800	d ⇒ s
	98	8	0.137	n ⇒ v
	109	2	0.316	l ⇒ j
node 10 → placidus	6	8	0.137	n ⇒ v
	8	4	0.221	9 ⇒ 5
node 9 → occultus	4	2	0.182	2 ⇒ 0
	5	1	0.250	0 ⇒ 1
	9	20	0.166	a ⇒ u
	10	2	0.212	4 ⇒ 2
	72	1	0.636	f ⇒ e
	74	1	0.800	d ⇒ b
	80	10	0.356	5 ⇒ f
	81	16	0.318	b ⇒ r
	87	20	0.195	k ⇒ 0
	91	31	0.139	v ⇒ 0
	94	31	0.333	0 ⇒ v
	99	4	0.378	v ⇒ r
	109	5	0.316	n ⇒ s
	116	31	0.500	v ⇒ 0
node 8 → darlingtoni	9	7	0.166	a ⇒ 3
	21	1	0.333	3 ⇒ 1
	25	1	0.667	0 ⇒ 3
	32	1	0.333	1 ⇒ 3
	34	1	0.333	2 ⇒ 0
	37	1	0.333	0 ⇒ 3
	46	1	0.500	0 ⇒ 2
	59	1	0.333	3 ⇒ 1
	60	1	0.200	0 ⇒ 2
	63	1	0.286	1 ⇒ 3
	74	1	0.800	d ⇒ n
	75	1	0.833	b ⇒ f
	93	21	0.144	l ⇒ 0
	103	10	0.121	5 ⇒ f
	109	7	0.316	7 ⇒ 0

APPENDIX V—Continued.

Branch	Character	Steps	CI	Change
node 7 → solitarius	110	31	0.500	v ⇒ 0
	87	11	0.195	k ⇒ v
	94	31	0.333	0 ⇒ v
	108	16	0.109	f ⇒ v
	112	15	0.220	f ⇒ 0
node 6 → P. heteroder-	7	4	0.150	9 ⇒ 5
	8	9	0.221	9 ⇒ 0
	9	5	0.166	a ⇒ 5
	80	26	0.356	5 ⇒ v
	87	18	0.195	i ⇒ 0
	103	5	0.121	5 ⇒ 0
	114	9	0.114	d ⇒ 4
	115	2	0.175	0 ⇒ 2
	8	6	0.221	p ⇒ v
	9	3	0.166	r ⇒ u
node 5 → node 4	79	1	0.200	0 ⇒ 1
	93	5	0.144	c ⇒ 7
	96	9	0.140	m ⇒ v
	108	16	0.109	f ⇒ v
	2	1	0.333	0 ⇒ 1
node 4 → aequatorialis	7	18	0.150	d ⇒ v
	9	1	0.166	u ⇒ v
	87	8	0.195	i ⇒ a
	90	7	0.124	0 ⇒ 7
	103	4	0.121	f ⇒ j
	106	21	0.135	0 ⇒ 1
	112	22	0.220	m ⇒ 0
	114	14	0.114	d ⇒ r
	10	1	0.212	h ⇒ i
	11	6	0.217	p ⇒ v
node 4 → squamulatus	86	6	0.230	k ⇒ q
	87	2	0.195	i ⇒ k
	93	7	0.144	7 ⇒ 0
	98	20	0.137	b ⇒ v
	114	6	0.114	d ⇒ 7
	93	5	0.144	h ⇒ m
	94	31	0.333	0 ⇒ v
	103	16	0.121	f ⇒ v
	108	3	0.109	3 ⇒ 0
	79	1	0.200	0 ⇒ 1
node 2 → node 36	98	5	0.137	f ⇒ k
	101	31	0.140	v ⇒ 0
node 36 → node 35	1	1	0.133	1 ⇒ 0
	9	12	0.166	q ⇒ e
	10	3	0.212	f ⇒ c
	76	1	0.889	i ⇒ f
	81	8	0.318	f ⇒ 7
	90	12	0.124	0 ⇒ c
	97	3	0.146	m ⇒ j
	114	1	0.114	d ⇒ c
	23	1	1.000	2 ⇒ 3
	24	1	1.000	0 ⇒ 3
node 35 → node 34	6	1	0.333	1 ⇒ 3
	87	1	0.195	j ⇒ k
	91	28	0.139	3 ⇒ v
	96	16	0.140	0 ⇒ g
	98	3	0.137	k ⇒ n
	103	31	0.121	0 ⇒ v

APPENDIX V—Continued.

Branch	Character	Steps	CI	Change
node 34 → node 26	107	6	0.179	4 ⇒ a
	108	7	0.109	3 ⇒ a
	11	4	0.217	k ⇒ g
	93	10	0.144	h ⇒ r
	101	4	0.140	0 ⇒ 4
node 26 → node 14	79	1	0.200	1 ⇒ 0
	106	16	0.135	c ⇒ s
	115	4	0.175	3 ⇒ 7
	7	3	0.150	s ⇒ v
	19	1	0.600	1 ⇒ 0
node 14 → node 12	35	1	0.400	0 ⇒ 2
	39	1	0.333	0 ⇒ 1
	47	1	0.286	3 ⇒ 1
	49	1	0.500	0 ⇒ 3
	65	1	0.500	1 ⇒ 3
node 12 → cybotes	90	12	0.124	c ⇒ 0
	98	14	0.137	n ⇒ 9
	101	2	0.140	4 ⇒ 6
	8	6	0.221	n ⇒ t
	10	1	0.212	e ⇒ f
node 12 → distichus	23	1	1.000	3 ⇒ 1
	26	1	0.250	1 ⇒ 3
	38	1	0.333	0 ⇒ 1
	45	1	0.500	0 ⇒ 3
	51	1	0.250	1 ⇒ 3
node 12 → punctatus	54	1	0.500	0 ⇒ 2
	57	1	0.400	0 ⇒ 2
	63	1	0.286	1 ⇒ 3
	64	1	0.400	3 ⇒ 1
	71	1	0.167	1 ⇒ 3
node 12 → aequatorialis	73	1	0.900	n ⇒ d
	86	1	0.230	r ⇒ s
	92	16	0.177	0 ⇒ g
	96	4	0.140	4 ⇒ 0
	97	1	0.146	j ⇒ i
node 12 → squamulatus	106	3	0.135	s ⇒ v
	107	14	0.179	e ⇒ 0
	108	15	0.109	a ⇒ p
	113	27	0.161	4 ⇒ v
	3	1	0.125	2 ⇒ 1
node 12 → solitarius	8	2	0.221	n ⇒ l
	9	2	0.166	e ⇒ c
	10	6	0.212	e ⇒ 8
	13	1	0.333	3 ⇒ 1
	17	1	0.500	0 ⇒ 3
node 12 → punctatus	18	1	0.333	1 ⇒ 3
	32	1	0.333	1 ⇒ 3
	34	1	0.333	2 ⇒ 0
	36	1	0.400	0 ⇒ 3
	37	1	0.333	0 ⇒ 3
node 12 → node 36	43	1	0.500	3 ⇒ 1
	59	1	0.333	3 ⇒ 1
	61	1	0.400	0 ⇒ 1
	67	1	0.333	3 ⇒ 1
	68	1	0.500	0 ⇒ 1
node 12 → node 35	69	1	0.500	1 ⇒ 3
	72	1	0.636	f ⇒ h
	76	1	0.889	f ⇒ e
	85	1	0.625	0 ⇒ 2

APPENDIX V—Continued.

Branch	Character	Steps	CI	Change
	87	3	0.195	k ⇒ h
	91	7	0.139	v ⇒ o
	93	14	0.144	s ⇒ e
	98	8	0.137	9 ⇒ 1
	101	25	0.140	6 ⇒ v
	105	8	0.190	2 ⇒ a
	107	16	0.179	e ⇒ u
	108	10	0.109	a ⇒ 0
	109	17	0.316	0 ⇒ h
	111	8	0.158	l ⇒ d
	115	15	0.175	7 ⇒ m
node 14 → node 13	85	1	0.625	0 ⇒ 4
	90	3	0.124	c ⇒ f
	93	3	0.144	s ⇒ v
	97	6	0.146	j ⇒ p
node 13 → bimaculatus	3	2	0.125	2 ⇒ 0
	8	2	0.221	n ⇒ l
	10	9	0.212	e ⇒ n
	11	16	0.217	g ⇒ 0
	29	1	0.333	1 ⇒ 0
	36	1	0.400	0 ⇒ 1
	39	1	0.333	0 ⇒ 3
	59	1	0.333	3 ⇒ 1
	86	1	0.230	r ⇒ s
	96	4	0.140	4 ⇒ 0
	97	6	0.146	p ⇒ v
	10	3	0.140	3 ⇒ 0
	103	31	0.121	v ⇒ 0
	107	14	0.179	e ⇒ 0
	108	15	0.109	a ⇒ p
	111	10	0.158	l ⇒ v
	114	14	0.114	0 ⇒ e
	115	7	0.175	7 ⇒ e
node 13 → cristatellus	9	2	0.166	e ⇒ c
	11	6	0.217	g ⇒ m
	31	1	0.400	1 ⇒ 2
	35	1	0.400	0 ⇒ 1
	37	1	0.333	0 ⇒ 1
	46	1	0.500	0 ⇒ 2
	47	1	0.286	3 ⇒ 0
	57	1	0.400	0 ⇒ 1
	62	1	0.500	0 ⇒ 2
	63	1	0.286	1 ⇒ 3
	90	12	0.124	f ⇒ r
	92	9	0.177	0 ⇒ 9
	98	3	0.137	n ⇒ q
	104	31	0.500	0 ⇒ v
	106	3	0.135	s ⇒ v
	107	1	0.179	e ⇒ f
	108	10	0.109	a ⇒ 0
node 26 → node 25	45	1	0.500	0 ⇒ 3
	76	1	0.889	f ⇒ m
	105	1	0.190	2 ⇒ 3
	113	27	0.161	4 ⇒ v
node 25 → node 22	32	1	0.333	1 ⇒ 3
	34	1	0.333	2 ⇒ 0
	50	1	0.500	2 ⇒ 0
	51	1	0.250	1 ⇒ 3
	71	1	0.167	1 ⇒ 3

APPENDIX V—Continued.

Branch	Character	Steps	CI	Change
	83	1	0.500	0 ⇒ 1
	85	1	0.625	0 ⇒ 2
node 22 → node 15	3	1	0.125	2 ⇒ 1
	98	2	0.137	n ⇒ p
	103	18	0.121	s ⇒ a
	106	13	0.135	c ⇒ p
	107	1	0.179	e ⇒ f
	108	8	0.109	a ⇒ 2
node 15 → grahami	9	11	0.166	g ⇒ r
	86	1	0.230	o ⇒ p
	90	19	0.124	c ⇒ v
	93	5	0.144	r ⇒ m
	98	2	0.137	p ⇒ r
	103	10	0.121	a ⇒ 0
	105	3	0.190	3 ⇒ 0
	108	2	0.109	2 ⇒ 0
	109	1	0.316	0 ⇒ 1
	111	11	0.158	f ⇒ q
	114	20	0.114	b ⇒ v
	115	1	0.175	3 ⇒ 4
node 15 → valencienni	8	11	0.221	n ⇒ c
	9	6	0.166	g ⇒ a
	10	3	0.212	d ⇒ g
	11	1	0.217	j ⇒ k
	72	1	0.636	f ⇒ a
	75	1	0.833	b ⇒ j
	86	3	0.230	o ⇒ 1
	90	9	0.124	c ⇒ 3
	91	1	0.139	u ⇒ v
	93	1	0.144	r ⇒ s
	96	11	0.140	g ⇒ 5
	97	1	0.146	i ⇒ h
	106	6	0.135	p ⇒ v
	107	16	0.179	f ⇒ v
	111	10	0.158	f ⇒ 5
	114	8	0.114	b ⇒ 3
	115	3	0.175	3 ⇒ 0
node 22 → node 21	1	1	0.133	1 ⇒ 2
	7	3	0.150	n ⇒ k
	92	23	0.177	0 ⇒ n
	97	5	0.146	i ⇒ n
	101	27	0.140	4 ⇒ v
node 21 → node 20	4	1	0.182	2 ⇒ 1
	9	4	0.166	g ⇒ k
	84	1	0.400	0 ⇒ 1
	90	12	0.124	c ⇒ 0
	92	8	0.177	n ⇒ v
	105	6	0.190	3 ⇒ 9
	107	14	0.179	e ⇒ 0
	115	1	0.175	3 ⇒ 4
node 20 → node 19	10	4	0.212	c ⇒ 8
	86	4	0.230	o ⇒ k
	87	15	0.195	k ⇒ 5
	91	28	0.139	s ⇒ 0
	106	3	0.135	3 ⇒ 0
	115	17	0.175	4 ⇒ 1
node 19 → node 16	86	1	0.230	k ⇒ j
	93	5	0.144	t ⇒ o
	98	11	0.137	m ⇒ b

APPENDIX V—Continued.

Branch	Character	Steps	CI	Change
node 16 → auratus	108	7	0.109	7 ⇒ 0
	111	12	0.158	9 ⇒ l
	114	4	0.114	b ⇒ f
	2	1	0.333	0 ⇒ 1
	4	1	0.182	1 ⇒ 0
	7	10	0.150	d ⇒ n
	8	5	0.221	m ⇒ r
	10	1	0.212	8 ⇒ 7
	11	5	0.217	h ⇒ m
	84	1	0.400	1 ⇒ 0
	86	5	0.230	j ⇒ e
	96	15	0.140	f ⇒ 0
	103	10	0.121	v ⇒ l
	109	2	0.316	0 ⇒ 2
node 16 → subocularis	114	8	0.114	f ⇒ n
	1	1	0.133	2 ⇒ 1
	8	4	0.221	m ⇒ i
	11	4	0.217	h ⇒ d
	93	9	0.144	o ⇒ f
	97	8	0.146	n ⇒ v
	98	11	0.137	b ⇒ 0
	105	13	0.190	d ⇒ 0
	111	10	0.158	l ⇒ v
	115	2	0.175	l ⇒ n
node 19 → node 18	5	1	0.250	0 ⇒ 1
	93	2	0.144	t ⇒ v
	98	9	0.137	m ⇒ v
	105	18	0.190	d ⇒ v
	114	11	0.114	b ⇒ 0
node 18 → node 17	9	2	0.166	k ⇒ m
	11	9	0.217	h ⇒ q
	80	10	0.356	0 ⇒ a
	81	7	0.318	0 ⇒ 7
	92	31	0.177	v ⇒ 0
	97	8	0.146	n ⇒ v
	108	24	0.109	7 ⇒ v
node 17 → biporcatus	3	1	0.125	2 ⇒ 1
	6	10	0.137	h ⇒ r
	7	6	0.150	k ⇒ q
	8	9	0.221	m ⇒ v
	9	8	0.166	m ⇒ u
	10	10	0.212	8 ⇒ i
	86	5	0.230	k ⇒ p
	91	15	0.139	0 ⇒ f
	106	31	0.135	0 ⇒ v
	113	31	0.161	v ⇒ 0
node 17 → meridionalis	115	15	0.175	f ⇒ 0
	2	1	0.333	0 ⇒ 1
	11	1	0.217	q ⇒ r
	82	1	0.333	1 ⇒ 0
	87	5	0.195	5 ⇒ 0
node 18 → nebuloides	96	16	0.140	f ⇒ v
	101	31	0.140	v ⇒ 0
	4	1	0.182	1 ⇒ 2
	6	17	0.137	h ⇒ 0
	7	8	0.150	d ⇒ 5
	8	2	0.221	m ⇒ k
	9	4	0.166	k ⇒ g
node 19 → angusticeps	10	2	0.212	8 ⇒ 6

APPENDIX V—Continued.

Branch	Character	Steps	CI	Change
node 20 → onca	97	12	0.146	n ⇒ b
	111	7	0.158	7 ⇒ 0
	115	10	0.175	l ⇒ v
	6	14	0.137	h ⇒ v
	8	2	0.221	n ⇒ p
	9	4	0.166	k ⇒ o
	10	5	0.212	c ⇒ h
	86	1	0.230	o ⇒ p
	91	3	0.139	s ⇒ v
	96	2	0.140	k ⇒ m
	99	6	0.378	0 ⇒ 6
	11	10	0.217	g ⇒ 6
	85	1	0.625	2 ⇒ 3
	90	19	0.124	c ⇒ v
node 21 → sagrei	93	3	0.144	r ⇒ o
	97	8	0.146	n ⇒ v
	98	19	0.137	m ⇒ 3
	104	31	0.500	0 ⇒ v
	108	8	0.109	a ⇒ i
	114	4	0.114	b ⇒ 7
	6	13	0.137	a ⇒ n
	8	7	0.221	n ⇒ g
	86	6	0.230	o ⇒ i
	91	21	0.139	s ⇒ 7
node 25 → node 24	105	12	0.190	3 ⇒ f
	109	19	0.316	0 ⇒ j
	3	1	0.125	2 ⇒ 1
	8	1	0.221	g ⇒ f
	10	6	0.212	c ⇒ 6
node 24 → node 23	98	2	0.137	n ⇒ l
	101	27	0.140	4 ⇒ v
	105	8	0.190	f ⇒ n
	107	11	0.179	e ⇒ p
	111	6	0.158	f ⇒ l
	114	4	0.114	b ⇒ f
	4	1	0.182	2 ⇒ 1
	7	2	0.150	q ⇒ s
	86	6	0.230	i ⇒ c
	87	6	0.195	k ⇒ e
node 23 → angusticeps	93	2	0.144	r ⇒ p
	95	3	0.365	v ⇒ s
	97	18	0.146	a ⇒ s
	98	15	0.137	l ⇒ 6
	103	31	0.121	v ⇒ 0
	108	24	0.109	v ⇒ 7
	111	4	0.158	l ⇒ p
	114	10	0.114	f ⇒ p
	115	11	0.175	0 ⇒ b
	8	6	0.221	f ⇒ 9
node 23 → argillaceus	9	9	0.166	e ⇒ 5
	10	1	0.212	6 ⇒ 5
	90	19	0.124	c ⇒ v
	91	7	0.139	7 ⇒ 0
	93	4	0.144	r ⇒ v
	96	11	0.140	b ⇒ 0
	97	10	0.146	a ⇒ 0
	105	8	0.190	n ⇒ v
	106	3	0.135	c ⇒ f
	107	6	0.179	p ⇒ v

APPENDIX V—Continued.

Branch	Character	Steps	CI	Change
node 24 → carolinensis	1	1	0.133	1 ⇒ 2
	6	4	0.137	n ⇒ r
	9	1	0.166	g ⇒ h
	11	1	0.217	e ⇒ d
	90	12	0.124	c ⇒ 0
	96	15	0.140	g ⇒ v
	101	4	0.140	4 ⇒ 0
	106	12	0.135	c ⇒ 0
	107	14	0.179	e ⇒ 0
	109	12	0.316	j ⇒ v
node 34 → node 33	64	1	0.400	3 ⇒ 0
	93	12	0.144	h ⇒ 5
	115	3	0.175	3 ⇒ 0
node 33 → node 32	6	17	0.137	0 ⇒ h
	7	15	0.150	s ⇒ d
	11	2	0.217	k ⇒ m
	19	1	0.600	1 ⇒ 3
	21	1	0.333	3 ⇒ 1
	39	1	0.333	0 ⇒ 3
	47	1	0.286	3 ⇒ 1
	63	1	0.286	1 ⇒ 0
	97	12	0.146	j ⇒ v
node 32 → node 27	10	11	0.212	e ⇒ p
	86	4	0.230	q ⇒ u
	90	11	0.124	b ⇒ 0
	98	10	0.137	v ⇒ l
	108	17	0.109	a ⇒ r
	114	13	0.114	f ⇒ s
node 27 → cuvieri	4	1	0.182	2 ⇒ 1
	9	6	0.166	g ⇒ m
	79	1	0.200	1 ⇒ 0
	106	6	0.135	7 ⇒ 1
	107	10	0.179	a ⇒ 0
	114	3	0.114	s ⇒ v
node 27 → equestris	3	2	0.125	2 ⇒ 0
	6	10	0.137	h ⇒ r
	8	4	0.221	m ⇒ i
	9	6	0.166	g ⇒ a
	10	6	0.212	p ⇒ v
	86	1	0.230	u ⇒ v
	93	5	0.144	5 ⇒ 0
	99	10	0.378	0 ⇒ a
	102	1	1.000	0 ⇒ 2
	106	3	0.135	7 ⇒ a
	108	4	0.109	r ⇒ v
	111	2	0.158	2 ⇒ 0
	112	31	0.220	v ⇒ 0
node 32 → node 31	1	1	0.133	0 ⇒ 1
	87	6	0.195	k ⇒ e
	101	31	0.140	0 ⇒ v
	103	10	0.121	p ⇒ f
	105	31	0.190	0 ⇒ v
	108	10	0.109	a ⇒ 0
	113	28	0.161	3 ⇒ v
node 31 → node 30	4	1	0.182	2 ⇒ 1
	9	1	0.166	g ⇒ h
	10	7	0.212	e ⇒ 7
	86	11	0.230	q ⇒ f
	91	10	0.139	v ⇒ 1

APPENDIX V—Continued.

Branch	Character	Steps	CI	Change
	106	7	0.135	7 ⇒ 0
	114	13	0.114	f ⇒ 2
node 30 → monticola	7	10	0.150	g ⇒ q
	8	9	0.221	m ⇒ v
	9	7	0.166	h ⇒ o
	11	7	0.217	n ⇒ g
	72	1	0.636	c ⇒ j
	76	1	0.889	f ⇒ d
	90	8	0.124	b ⇒ 3
	96	5	0.140	9 ⇒ 4
	97	16	0.146	r ⇒ b
	107	9	0.179	a ⇒ 1
node 30 → node 29	6	17	0.137	h ⇒ 0
	91	14	0.139	l ⇒ 7
	111	9	0.158	2 ⇒ b
node 29 → node 28	1	2	0.133	2 ⇒ 0
	87	1	0.195	e ⇒ f
	90	8	0.124	b ⇒ j
	91	4	0.139	7 ⇒ 3
	93	1	0.144	g ⇒ h
	111	4	0.158	b ⇒ f
	115	15	0.175	g ⇒ v
node 28 → polylepis	7	12	0.150	g ⇒ s
	8	9	0.221	m ⇒ v
	9	12	0.166	h ⇒ t
	10	4	0.212	4 ⇒ 8
	83	1	0.500	0 ⇒ 1
	86	6	0.230	b ⇒ h
	103	15	0.121	f ⇒ u
	107	8	0.179	d ⇒ 5
	111	16	0.158	f ⇒ v
	114	2	0.114	1 ⇒ 3
node 28 → alutaceus	7	3	0.150	g ⇒ d
	10	4	0.212	4 ⇒ 0
	11	3	0.217	n ⇒ q
	87	5	0.195	f ⇒ k
	90	12	0.124	j ⇒ v
	91	3	0.139	3 ⇒ 0
	93	14	0.144	h ⇒ v
	97	1	0.146	u ⇒ v
	103	15	0.121	f ⇒ 0
	107	18	0.179	d ⇒ v
	114	1	0.114	1 ⇒ 0
node 29 → semilineatus	8	1	0.221	m ⇒ l
	19	1	0.600	3 ⇒ 2
	27	1	0.333	0 ⇒ 2
	29	1	0.333	1 ⇒ 3
	38	1	0.333	0 ⇒ 1
	39	1	0.333	3 ⇒ 1
	40	1	0.667	3 ⇒ 1
	44	1	0.500	3 ⇒ 0
	47	1	0.286	1 ⇒ 0
	56	1	0.667	0 ⇒ 1
	57	1	0.400	0 ⇒ 1
	60	1	0.200	0 ⇒ 2
	63	1	0.286	0 ⇒ 3
	64	1	0.400	0 ⇒ 3
	86	4	0.230	b ⇒ 7
	87	1	0.195	e ⇒ d

APPENDIX V—Continued.

Branch	Character	Steps	CI	Change
node 31 → fowleri	92	7	0.177	0 ⇒ 7
	93	15	0.144	g ⇒ 1
	109	2	0.316	0 ⇒ 2
	7	4	0.150	d ⇒ 9
	8	1	0.221	m ⇒ l
	11	4	0.217	n ⇒ r
	74	1	0.800	p ⇒ l
	87	4	0.195	e ⇒ a
	90	20	0.124	b ⇒ v
	93	5	0.144	5 ⇒ 0
	96	14	0.140	h ⇒ v
	106	8	0.135	7 ⇒ f
node 33 → lucius	111	2	0.158	2 ⇒ 0
	3	2	0.125	2 ⇒ 0
	7	3	0.150	s ⇒ v
	8	2	0.221	n ⇒ p
	26	1	0.250	1 ⇒ 3
	66	1	0.200	1 ⇒ 3
	90	5	0.124	c ⇒ h
node 35 → hendersoni	92	12	0.177	0 ⇒ c
	114	3	0.114	b ⇒ 8
	7	3	0.150	s ⇒ v
	8	2	0.221	n ⇒ p
	10	6	0.212	c ⇒ 6
	11	3	0.217	k ⇒ n
	21	1	0.333	3 ⇒ 1
	37	1	0.333	0 ⇒ 1
	39	1	0.333	0 ⇒ 1
	42	1	0.500	3 ⇒ 1
node 1 → griseus	43	1	0.500	3 ⇒ 1
	44	1	0.500	3 ⇒ 0
	45	1	0.500	0 ⇒ 1

APPENDIX V—Continued.

Branch	Character	Steps	CI	Change
node 36 → coelestinus	51	1	0.250	1 ⇒ 3
	54	1	0.500	0 ⇒ 2
	69	1	0.500	1 ⇒ 0
	72	1	0.636	f ⇒ g
	73	1	0.900	o ⇒ p
	86	12	0.230	k ⇒ 8
	87	4	0.195	j ⇒ f
	90	19	0.124	c ⇒ v
	97	12	0.146	j ⇒ 7
	108	3	0.109	3 ⇒ 0
	109	2	0.316	0 ⇒ 2
	115	7	0.175	3 ⇒ a
node 1 → griseus	11	8	0.217	k ⇒ c
	72	1	0.636	f ⇒ h
	73	1	0.900	o ⇒ m
	93	10	0.144	h ⇒ r
	95	5	0.365	v ⇒ q
	97	6	0.146	m ⇒ s
	106	15	0.135	7 ⇒ m
	113	28	0.161	3 ⇒ v
	114	18	0.114	d ⇒ v
	5	1	0.250	0 ⇒ 1
node 1 → griseus	7	3	0.150	n ⇒ q
	10	8	0.212	h ⇒ p
	11	16	0.217	k ⇒ 4
	28	1	0.500	1 ⇒ 3
	36	1	0.400	0 ⇒ 1
	56	1	0.667	0 ⇒ 1
	97	4	0.146	m ⇒ q
	106	24	0.135	7 ⇒ v
	108	3	0.109	3 ⇒ 0
	114	13	0.114	d ⇒ 0