AMERICAN MUSEUM
Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024
Number 3343, 38 pp., 6 figures, 1 table, 4 appendices June 22, 2001

Total Evidence, Sequence Alignment, Evolution of Polychrotid Lizards, and a Reclassification of the Iguania (Squamata: Iguania)

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ABSTRACT

Using the techniques of direct optimization and sensitivity analysis, the phylogenetics of polychrotid lizards were examined on the basis of both molecular and morphological data (ca. 1040 bp of 12S rDNA, valine tDNA, and 16S rDNA, and 82 characters of morphology). A sensitivity analysis of sequence alignment and morphological change cost functions demonstrated that equal weighting provided the most parsimonious solution for all data. The Polychrotidae is found not to be monophyletic, containing instead the Corytophanidae as the sister taxon of *Anolis* plus *Polychrus.* Based on these and other results over the last 12 years, the taxonomy of the Iguania is reformulated, with the Iguania composed of two subsidiary taxa, Acrodonta and Pleurodonta, the Acrodonta containing the likely paraphyletic and basally unresolved ''Agamidae'' as well as the Chamaeleonidae, and the Pleurodonta containing the Corytophanidae, Crotaphytidae, Hoplocercidae, Iguanidae, Leiocephalidae (newly elevated from its former status as a subfamily of the Tropiduridae), Leiosauridae (new taxon including *Anisolepis, Aperopristis, Diplolaemus, Enyalius, Leiosaurus, Pristidactylus,* and *Urostrophus*), Liolaemidae (newly elevated from its former status as a subfamily of the Tropiduridae), Opluridae, Phrynosomatidae, Polychrotidae (restricted to *Anolis* and *Polychrus*), and Tropiduridae (excluding the former subfamilies Leiocephalinae and Liolaeminae).

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 ISSN 0003-0082 / Price $4.70

INTRODUCTION

The polychrotids form a large component of the lizard taxon Iguania, of which the largest amniote genus *Anolis*[5] (>300 species) is the polychrotids' most conspicuous member in terms of local abundance, species diversity, and distribution, being found from the southeastern United States and northwestern Mexico south through the Antilles and Central and South America to Bolivia, Paraguay, and Brazil. Nevertheless, *Anolis* (sensu lato) is only one genus in this group, with six other smaller genera found primarily in austral South America. Most similar in general appearance to *Anolis* is *Polychrus,* which is the only putative anole relative not restricted to southern South America. *Polychrus* is composed of six species distributed from Nicaragua to southern Brazil, Uruguay, and northern Argentina. Much less conspicuous in the literature (and in collections) are the leiosaur polychrotids of southern South America: *Enyalius, Diplolaemus, Leiosaurus,* and *Pristidactylus. Enyalius* contains six to nine species, depending on author (Etheridge, 1969; Jackson, 1978), and is found in central and southern Brazil. *Diplolaemus* contains three poorly distinguished Patagonian species. *Leiosaurus* has three species found in arid Argentina, and *Pristidactylus,* found in western Argentina and central Chile, contains seven species (Etheridge and de Queiroz, 1988; Etheridge and Williams, 1985). Also found in southern South America are the para-anoles (*Urostrophus* and *Anisolepis*). *Urostrophus* has two species found disjunctly in southern Bolivia to northern Argentina and in southeastern Brazil, and *Anisolepis* has three species in southeastern Brazil, Uruguay, northeastern Argentina, and central Paraguay (Etheridge and Williams, 1991).

The polychrotid iguanians were first proposed as a monophyletic group (as the anoloid iguanids) by Etheridge and de Queiroz (1988), even though the notion of such a group had currency somewhat earlier (e.g., Etheridge *in* Paull et al., 1976). Subsequently, of course, Frost and Etheridge (1989) recognized that taxon formally as the Polychrotidae.

Because of its ubiquity, diversity, and availability in collections, *Anolis* has enjoyed considerable attention regarding its taxonomy and phylogeny (e.g., Cannatella and de Queiroz, 1989; Etheridge, 1959; Guyer and Savage, 1986; Hass et al., 1993; Jackman et al., 1997, 1999; Poe, 1998). The remaining taxa within the polychrotid clade have not received much taxonomic attention in the last 30 years (subsequent to the summary of Peters and Donoso-Barros, 1970). Paull et al. (1976), Etheridge and de Queiroz (1988), Williams (1988), Frost and Etheridge (1989), Macey et al. (1997), and Schulte et al. (1998) addressed these taxa (at least in part) as part of larger problems of iguanian relationships. Etheridge and Williams (1991) reported on the para-anoles. Jackson (1978) reviewed the systematics of *Enyalius,* and Etheridge and Williams (1985) provided a preliminary summary of *Pristidactylus.* Other than these contributions, the remaining taxonomic summaries in the last 30 years have been more restricted taxonomic papers: Cei (1973a) on generic limits among pristidactylines (i.e., *Leiosaurus, Diplolaemus, Pristidactylus,* and [at that time recognized] *Cupriguanus*), Cei and Castro (1975) on the serology of *Cupriguanus* (= *Pristidactylus*), and Lamborot and Diaz (1987) on speciation of *Pristidactylus* in Chile, as well as single species studies (Cei, 1973b, on *Pristidactylus fasciatus*), species descriptions (Donoso-Barros, 1975, of *Cupriguanus* [= *Pristidactylus*] *alvaroi*; Lamborot and Diaz, 1987, of *Pristidactylus volcanensis*), and regional faunal works (Cei, 1986, 1993; Avila-Pires, 1995). The major thrust of this study is to provide a basic cladogram of the nominal species of non-anole polychrotids so that progress in the study of the subsidiary taxa can be promoted. Nevertheless, like any such paper our objectives are several:

(1) We test the monophyly of the Polychrotidae, which although it has been considered monophyletic by most recent authors (e.g., Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989), others (e.g., Williams, 1988) have disputed this.

(2) We provide an improved approximation of phylogeny and a taxonomy consistent

[5] For our purposes we use *Anolis* (sensu lato) to include *Chamaelinorops, Chamaeleolis, Norops,* and *Phenacosaurus* (Hass et al., 1993; Poe, 1998).

with that phylogeny for the polychrotids not only to elucidate relationships within this poorly known group, but also to provide a more highly corroborated outgroup structure for further studies by others on the huge taxon *Anolis.* Etheridge and de Queiroz (1988) and Frost and Etheridge (1989) provided a first and second estimate on the intergeneric phylogeny, but these were clearly preliminary.

(3) We provide the morphological evidence in table form, also providing our sequences through GenBank, so that others may evaluate our results.

(4) We comment briefly on various aspects of systematic methods as they present themselves. In particular these issues are verificationism in systematics, the assumptions of sequence alignment, and the justification for cost functions of molecular changes as they relate to analysis of morphology. The use of sensitivity analyses as an empirical tool is also explored.

(5) We also discuss the progress in understanding iguanian lizards and the classificatory solutions so far offered. We suggest a classification that we think will promote continued research.

The data sets used reflect comparative differences of mitochondrial DNA and morphology, analyzed, we think in a new way, at least for herpetologists, that allows truly simultaneous analysis of molecular sequence and morphology data.

MATERIALS AND METHODS

Molecular Data

Mitochondrial DNA sequences were obtained for 16 ingroup terminals (and four outgroup taxa) representing all nominal genera (see appendix 1 for GenBank accession numbers). *Eumeces egregius* (as a surrogate for the Scleroglossa, all noniguanian squamates), *Basiliscus basiliscus* (Corytophanidae), *Oplurus cychlurus* (Opluridae), and *Leiocephalus barahonensis* (Tropiduridae: Leiocephalinae) were chosen as out-taxa to maximize the test of monophyly of the Polychrotidae (see discussion below under Choice of Out-taxa). Ingroup taxa selected for molecular analysis were *Anisolepis longicauda, Anolis carolinensis, A. fuscoauratus, A. meridionalis, A. ortonii, A. roquet, Diplolaemus darwini, Enyalius bilineatus, E. leechii, Leiosaurus catamarcensis, L. paronae, Polychrus acutirostris, P. femoralis, P. gutturosus, P. marmoratus, Pristidactylus scapulatus,* and *Urostrophus gallardoi.*

Mitochondrial genes encoding the 12S rDNA, valine tDNA, and the 5′ end of the 16S rDNA were amplified using the polymerase chain reaction. Genomic DNA extraction, primers, and amplification protocols were identical to those in Titus and Frost (1996). Amplified DNA was electrophoresed on 1% agarose gels and purified for sequencing using the Geneclean II kit (Bio 101, Inc.). Thermal cycle sequencing was done following Titus and Frost (1996). Automated sequencing was performed in the University of Oregon Molecular Biology Sequencing Facility utilizing the Big Dye Terminator Cycle Sequencing Kit with AmpliTaq FS (Perkin-Elmer) and an ABI PRISM 377 DNA Sequencer (Perkin-Elmer) following the manufacturer's specifications.

All sequences have been deposited with GenBank (see appendix 1 for accession numbers).

Morphological Data

Skeletons, alcoholics, hemipenes, and cleared and double-stained specimens of most non-anole ingroup taxa were examined for interspecific variation that could be hypothesized to be apomorphies relative to the outgroups (see Analytical Methods). Comparison of specimens yielded 82 characters (numbered 0–81 in appendix 2 to allow easy interpretation of our results) that were analyzed separately and jointly with the molecular data. (See appendix 2 for individual discussion of transformation series, and appendix 3 for the morphological data matrix.) Although every attempt was made to get representatives of all non-anole polychrotid species, some absences are notable. We did not have complete skeletal material for *Enyalius bibroni* (although notes of R. E. Etheridge allowed some of the cells to be filled in), *Pristidactylus alvaroi, Pristidactylus valeriae,* and *Pristidactylus fasciatus* (although x-rays and a mandible were available). We did not attempt to discriminate the three spe-

cies of *Diplolaemus*. The monophyly of the genus is easily supported, but the species are similar, and the species limits are murky at best. *Anolis* (sensu lato) was not sampled densely. Instead, we used taxa that we hope sit near the base of the taxon and which will not affect either the placement of *Anolis* in our tree(s) or the character distributions that diagnose these taxa.

Choice of Out-taxa

Out-taxa were selected on the basis of various lines of evidence of evolutionary proximity and on their ability as potential falsifiers of polychrotid monophyly (Frost and Etheridge, 1989; Hallermann, 1994; Macey et al., 1997; Titus and Frost, 1996; Schulte et al., 1998). These taxa included (1) oplurids (inducted for purposes of morphology from *Chalarodon* + *Oplurus* [Blanc, 1977; Titus and Frost, 1996], with the molecular evidence tied to this hypothetical taxon being *Oplurus cychlurus*); (2) *Leiocephalus* (coded morphologically as the ancestor of *Leiocephalus* as hypothesized by Pregill, 1992), with the molecular evidence being derived from *Leiocephalus barahonensis*; and (3) corytophanids (inducted as the ancestor of *Basiliscus* + [*Corytophanes* + *Laemanctus*] on the basis of Lang [1989] and independent specimen examination) being represented for molecular evidence by *Basiliscus basiliscus*. Finally, a noniguanian out-taxon was included to help root the entire network, with this being coded as the inducted ancestral scleroglossan for morphology (based on our observations and those of Estes et al., 1988) and represented by *Eumeces egregius* (Scincidae) for purposes of molecular evidence. Many of the morphological characters employed here fail to be definable far away from the ingroup, so many cells in the scleroglossan line were left as question marks where homology was dubious. A number of morphological characters that corroborate the monophyly of the Iguania were not included (Estes et al., 1988) for no reason other than they were not needed to support the ingroup relationship with the near outgroups.

Analytical Methods

The general analytical method employed is a parsimony analysis (Kluge and Farris, 1969; Farris, 1983; Farris and Kluge, 1985, 1986) of molecular and morphological data for most non-anole polychrotids and several out-taxa. The usual procedure for mixed morphology and molecular data analysis is to align the DNA strands and employ either character or taxonomic congruence to reconcile the data sets on a single set of solutions, character congruence being preferred for a number of reasons (Kluge, 1989). Nevertheless, the procedure of alignment, regardless of method used (e.g., CLUSTAL [Higgins et al., 1992], MALIGN [Wheeler and Gladstein, 1994], or ''by eye'', which is least satisfactory because it is not repeatable), optimizes cost functions (i.e., the cost to the parsimony measure of changes by transversions, transitions, and insertions/deletions) on a single implied tree. When this aligned molecular data set is combined with another data set, such as from morphology, the final tree obtained may actually have more efficient alignments available for that particular summary tree than allowed by the initial ($\approx$ locally optimal) alignment. In other words, the ''distortion'' by the morphological data to the implied tree of aligned sequences may allow more parsimonious sequence solutions than are allowed by the initial alignment estimate of site homologies. This additional analytical step of alignment being followed by inclusion for general analysis with another data partition such as morphology has generally been considered unavoidable. Nevertheless, the standard method of combining aligned sequences with morphology retains a component of taxonomic congruence (sensu Kluge, 1989) that is not appropriate if we are serious about a total-evidence approach to analysis.

To avoid this particular problem, in this study we employed the method of direct optimization (Wheeler, 1996) as implemented by the computer program POY (Gladstein and Wheeler, 1997–2001; Janies and Wheeler, 2000), which allows morphological changes to be simultaneously optimized with the molecular classes of change (transversions, transitions, indels) on multiple potential trees. This simultaneous analysis allows morphological characters to influence alignment optimization directly, thereby allowing more efficient solutions the transformations

implied by separate alignment and analysis. Put another way, POY optimizes cost functions for *all* of the data onto various topologies and calculates total parsimony costs for all cost functions. POY therefore has the capacity to find more parsimonious trees than does the procedure of alignment followed by total evidence analysis. (For documentation, a summary of this method, and access to the program and command scripts see ftp.amnh.org/pub/molecular/poy [Janies and Wheeler, in press].)

POY also allows simultaneous analysis of data partitions under various cost regimes. That is, different weighting functions for morphological change, transversions, transitions, and indels can be applied to allow the general exploration of data partitions. In the case of this analysis, various differential weights of alignment cost functions were investigated in a sensitivity analysis to discover at what alignment cost functions incongruence between morphology and molecules was minimized (Wheeler, 1995).

The measure used to optimize congruence was the Mickevich-Farris extra steps index (MFES) (Mickevich and Farris, 1981), which measures the number of extra steps that occur in an analysis of combined data versus separate analysis of individual partitions. As character incongruence among data partitions increases, MFES increases. The number of extra steps is normalized by the length of the combined analysis so when parameter sensitivity analyses (Wheeler, 1995) are conducted on the same data partitions (as in this study), MFES scores are comparable despite different weighting schemes.

Of course, the issue of differential weighting and sensitivity analysis has exposed among us some philosophical disagreements. Frost and Janies are of somewhat different minds about the cost functions to employ in POY. Frost favors morphology, transversions, transitions, and indels to mutually interact with a relative cost of 1 inasmuch as he sees these all as marks of history and not ''kinds'' of characters. He regards anything else as an attempt to reduce evidentiary ambiguity rather than provide a logically and philosophically sound framework for analysis. Janies, on the other hand, argues that character partition congruence must be used as the optimality criterion for choosing among various topologies that are produced and for choosing costs that minimize incongruence among data sets inasmuch as there is no other empirical justification for cost functions. Janies suggests that there is no theoretical reason for picking any particular set of cost functions for sequence alignment and that minimizing incongruence between morphology and molecular sequence data may provide a general means of empirically investigating optimal alignment costs among different analyses. To foreshadow the results, our difference of opinion ultimately made no difference in this particular study.

POY is implemented at the American Museum of Natural History on a cluster of 256 UNIX-based work-stations integrated into a parallel virtual machine (Geist et al., 1993). A total of 12 parameter sets were explored. The ratio of weights among indels and transversion or transition weights ranged from 1 to 4. The transversion : transition ratios ranged from 0.5 to 2. Some parameter sets were set specifically to examine transversion parsimony (i.e., transitions were set at 0 cost yielding a transversion: transition ratio of ∞). Changes in morphological data were pegged to the cost of indels. Sequence data were also analyzed separately. The addition of taxa (including putative outgroups) was randomized during the build and swapping processes for molecular data and during swapping for molecular and morphological data. Tree searches included TBR and SPR swapping.

The g_1 statistic was not employed as a measure of information content for reasons detailed by Kallersjö et al. (1992). Maximum likelihood approaches have also not been employed in this analysis because these equate to parsimony estimates when no general model of evolution is imposed (Tuffley and Steel, 1997; Steel and Penny, 2000), the assumption of evolutionary process that we think the most conservative. The measure of tree stability here employed is Bremer support (or decay index) (Bremer, 1994). Inasmuch as all measures of tree stability are fundamentally rules-of-thumb, Bremer support has the advantage of not appearing to be a parametric statistic as do bootstrap values. Nevertheless, like Wilkinson et al. (2000), we appreciate that problems exist with Bre-

mer values also, so these numbers should be considered carefully within the context of discussion.

RESULTS

We will discuss the molecular-only and morphological-only results briefly before moving on to the combined analysis and discussion of previous hypotheses.

Molecular-Only Analysis

The molecular results shown (fig. 1) are based on relative cost functions of 1:1:1 (transversion : transition : indel). (The reason for this approach will be provided in the discussion of the morphology plus molecular data sensitivity analysis below.) Only one tree was obtained for the 21 terminals (length = 2332; CI = 0.23; RI = 0.68). If we arbitrarily take a Bremer support of 7 and above as ''strong'' and below 7 as ''moderate to weak'', we can make the following observations with declining levels of confidence on the molecular evidence alone:

The monophyly of the polychrotids is rejected by the molecular evidence. *Leiocephalus, Basiliscus,* and *Oplurus* (all nonpolychrotids) were suggested by Etheridge (*in* Paull et al., 1976), Etheridge and de Queiroz (1988), and Frost and Etheridge (1989) to be distantly related to the polychrotids, but in this analysis are imbedded within the Polychrotidae, being most closely related to *Polychrus* by apparently strong evidence. On the face of it, this suggests that, as worried about by other authors (most notably by Williams, 1988), *Polychrus* has little to do with the other ''polychrotids''. Furthermore, *Anolis,* never considered a controversial member of the group, is placed outside the remaining polychrotids, oplurids, leiocephalines, and corytophanids.

The leiosaurs plus the para-anoles (*Urostrophus, Anisolepis, Enyalius, Leiosaurus, Pristidactylus* and *Diplolaemus*) are a highly corroborated group with a decay index of 32, an enormous number. *Urostrophus* plus *Anisolepis* is placed as the sister taxon of *Enyalius,* and *Diplolaemus* is placed as the sister taxon of *Leiosaurus* plus *Pristidactylus.*

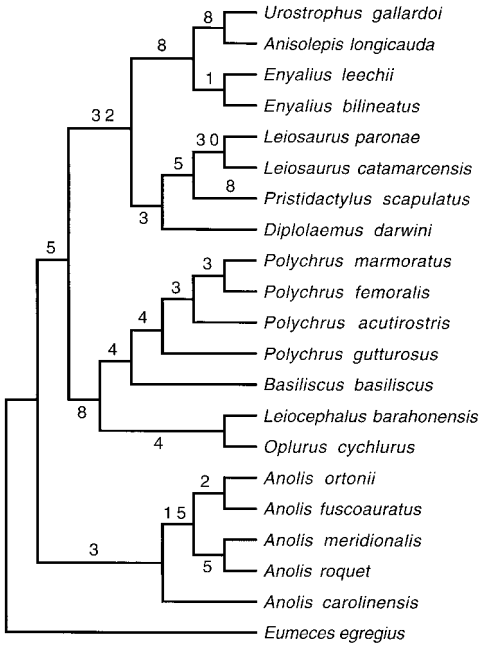

Fig. 1. Single tree obtained on molecular-only data (length = 2332; CI = 0.23; RI = 0.68). Numbers on branches are Bremer values.

Morphology-Only Analysis

The morphology-only analysis (fig. 2) generally exposes much lower Bremer support numbers than those found in the molecular analysis. Beyond being irrelevant, because the numbers are not necessarily comparable between the molecular and morphological analyses, this pattern of low Bremer numbers is not due especially to conflict, but to low numbers of characters along many of the stems, which is the normal turn of events in morphological studies in which individuation of character states tends to be the central problem. The number of equally parsimonious trees obtained was 192 (length = 276; CI = 0.443; RI = 0.74). Salient features of the morphology-only analysis are:

The Polychrotidae obtains as a monophyletic group under the most parsimonious arrangement. With a Bremer support of 3 on the critical stem according to our arbitrary cutoff, this is not highly corroborated.

Anolis is most parsimoniously placed as the sister taxon of *Polychrus,* with the evidence for this being moderate. The structure discovered within *Anolis* and *Polychrus* is

substantially different from that obtained in the molecule-only analysis, although the number of morphological characters critical to this structure is low.

The leiosaurs plus para-anoles group is only weakly united, although the leiosaurs form a monophyletic group (with an alternative rooting of their component of the overall network found in the molecule-only analysis). The Chilean species of *Pristidactylus* (*P. alvaroi, P. torquatus, P. valeriae, P. volcanensis*) plus *P. fasciatus,* from Argentina, are found to be a monophyletic subgroup of the genus.

No particular structure within *Enyalius* was discovered, nor were the para-anoles recovered consistently as a monophyletic group. Much of this lack of intrageneric resolution was due seemingly to a lack of firmly placed near neighbors in the analysis.

Morphological plus Molecular Data Analysis

As described above a sensitivity analysis was performed. A text summary of the results of the sensitivity analysis is provided in table 1, but more intelligibly these data are provided graphically in figure 3. In this graphic, as the color goes to red (color corresponds to the z-axis, which represents data set congruence), the congruence metric for the best trees among the morphological and molecular data set increases. In this case maximum congruence between the molecular and morphological data sets is achieved when the ratios of change costs of transversions, indels, transitions, and morphological change are all equal to one.[6] Because the equal-weighting analysis shows the most congruence by far between molecular evidence and morphological evidence, this will be the only analysis discussed here (and previously in the molecular-only analysis).

Figure 4 shows the strict consensus of the three most parsimonious trees (length of each tree = 2617; CI = 0.25; RI = 0.69) discovered by the combined analysis, as well as the corresponding Bremer support for these stems, and figure 5 shows this same tree with the taxa (internal stems and terminals) identified to correspond to the summary of change presented in appendix 4. To abbreviate discussion, the reader is referred to this table for a summary of the morphological evidence as well as the number and kind of molecular characters in support of each stem.

As expected, the complementarity of the molecular and morphological data is evident in the resolution obtained. With the exception of lack of resolution at two nodes in *Enyalius* (5 and 6), three nodes in *Pristidactylus* (20, 23, and 24), and the decisive node for *Leiosaurus* monophyly (16), resolution of the 43 terminal taxa is dichotomous. Again, assuming an arbitrary number of 7 for Bremer support, virtually all stems meet the criterion for strong support.

Polychrotid Monophyly. The most immediate result of the total evidence analysis is that the Polychrotidae as hypothesized by Etheridge and de Queiroz (1988) and Frost and Etheridge (1989) is not monophyletic, with the Corytophanidae (or basiliscines) being imbedded within it. This result is hardly bewildering. There are rather few truly arboreal clades of iguanian lizards, and to find the otherwise enigmatic corytophanids in

[6] This result has some rather serious implications about the justification for a priori character weighting based on notions of inherent rates of change in particular classes of modification (e.g., routinely weighting transversions over transitions because of their generally average lower rate of appearance), particularly because there is no logical basis to assume that the *average* rate of change in such classes as transversions and transitions should translate into differential weights for these classes of character change (see Broughton et al., 2000). The critical reader will nevertheless have noted that we also use classes of characters in our sensitivity analysis (i.e., transversions, transitions, indels, and morphological character shifts), a central and seemingly inescapable aspect of all scientific generalizations and methods (Frost and Kluge, 1994; Frost, 2000).

One possible explanation for why a posteriori differential character weighting could be arrived at by a sensitivity analysis of the interaction of morphology and molecular evidence extends from sampling density of terminal taxa/patristic distance among terminal. As taxon sampling density increases, one expects that long branches will be partitioned, and that the partitioned components will become increasingly informative (i.e., more and more apomorphies will be correctly identified), thereby bringing the ratio of various costs back to one. The number of studies so far that have performed sensitivity analyses is small (e.g., Edgecomb et al., 1999; Giribet et al., 2000; Janies and Mooi, 1999; O'Leary, 1999; Wheeler, 1995) thus, conjecture aside, we look forward to informed generalizations to be made as the set of examples expands.

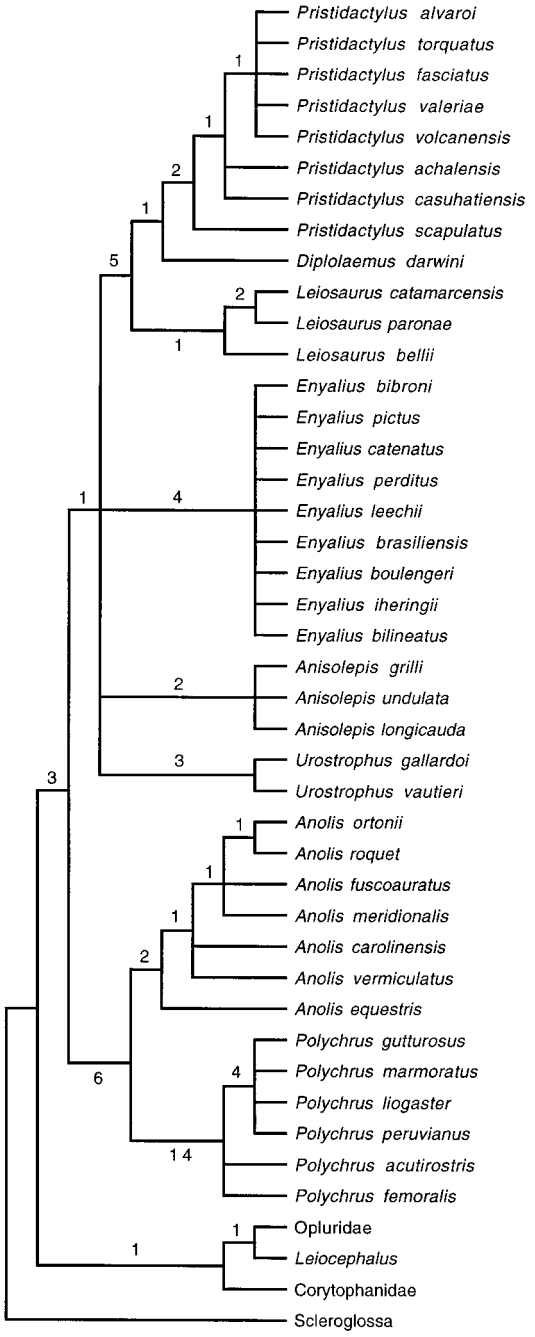

Fig. 2. Strict consensus of 192 equally parsimonious trees based on morphology alone (length = 276; CI = 0.443; RI = 0.74). Numbers on branches are Bremer values.

this position is not surprising. Indeed, in overall external appearance *Laemanctus*, the most generally plesiomorphic member of the corytophanids, is very similar in general body plan and habitus to some species of *Polychrus*, and young *Basiliscus* are routinely misidentified in research collections as *Anolis* spp., a similarity explained in this arrangement by homology rather than convergence. Furthermore, the propensity for skull casquing in corytophanids and polychrotids is explained by this relationship. The stem (39, fig. 5) supporting the Corytophanidae (*Basiliscus basiliscus* as the molecular surrogate for this taxon) with *Anolis* and *Polychrus* is supported by morphological characters 14.2 (fragmented suboculars) and, trivially, 33.2 (multicarinate subdigitals) and by 8 molecular transitions, 6 insertions, and 7 transversions. The loss of the standard polychrotid synapomorphy, calcified endolymphatic sacs extending into the nuchal musculature (55.1), in the corytophanids, we judged to have been discovered as well as the loss of the typical polychrotid scale microstructure (which is also lacking in *Polychrus*). Although the evidence in support of a monophyletic Corytophanidae plus the Polychrotidae (stem 26, fig. 5) is not well corroborated by Bremer support of 5 we consider this a very interesting result further supporting the special relationship of corytophanids and polychrotids first suggested by Hallermann (1994).

LEIOSAURS PLUS PARA-ANOLES. Substantial evidence suggests that leiosaurs and the equally austral para-anoles form a monophyletic group (stem 14; Bremer support of 11). This taxon is composed of two major groups, the arboreal *Enyalius* plus para-anoles (stem 9; Bremer support of 13) and the seemingly *primitively* terrestrial pristidactylines: *Leiosaurus, Diplolaemus,* and *Pristidactylus* (stem 17; Bremer support of 14). The phylogenetic transition from *Leiosaurus, Diplolaemus,* and Argentinian *Pristidactylus* (*P. scapulatus, P. fasciatus, P. casuhatiensis*) to the Chilean *Pristidactylus* (*P. torquatus, P. valeriae, P. volcanensis,* and *P. alvaroi*) is unexpected inasmuch as both Etheridge (*in* Paull et al., 1976: 15) and Etheridge and de Queiroz (1988) suggested on the basis of

TABLE 1

Sensitivity Analysis Under 12 Different Weighting Regimes

Gap cost = cost of adding a gap into the sequence; tv cost = cost of making a transversion; ts cost = cost of making a transition; tv/ts = ratio of transversion and transition costs; $\log_2$ tv/ts = log (base 2) of tv/ts; gap/change = ratio of gap cost to maximum cost of tv or ts change; $\log_2$ gap/change = log (base 2) of gap/change; mm = length of morphological + molecular data on the shortest tree(s) based on analysis of combined morphological and molecular data; mol = length of molecular data on the shortest tree(s) based on analysis of molecular data only; morph = length of morphological data on the shortest tree(s) based on analysis of morphological data only; MFES = Mickevich-Farris extra steps index (0 = no extra steps; lowest MFES score is shown in boldface). See figure 3.

Gap cost	tv cost	ts cost	tv/ts	Log_2 tv/ts	Gap/ change	Log_2 gap/ change	mm	Mol	Morph	MFES
2	1	2	0.5	−1	1	0	4171	3581	552	0.009110525
1	1	1	1	0	1	0	2613	2320	276	**0.006505932**
2	2	1	2	1	1	0	3848	3248	552	0.012474012
4	4	0	∞	∞	1	0	5238	4031	1104	0.019663994
4	1	2	0.5	−1	2	1	4822	3668	1104	0.010369141
2	1	1	1	0	2	1	2998	2416	552	0.010006671
4	2	1	2	1	2	1	4927	3750	1104	0.014816318
8	4	0	∞	∞	2	1	7360	5011	2208	0.019157609
8	1	2	0.5	−1	4	2	6397	4084	2208	0.016413944
4	1	1	1	0	4	2	3788	2619	1104	0.017159451
8	2	1	2	1	4	2	6608	4313	2208	0.01316586
16	4	0	∞	∞	4	2	10866	6163	4416	0.026412663

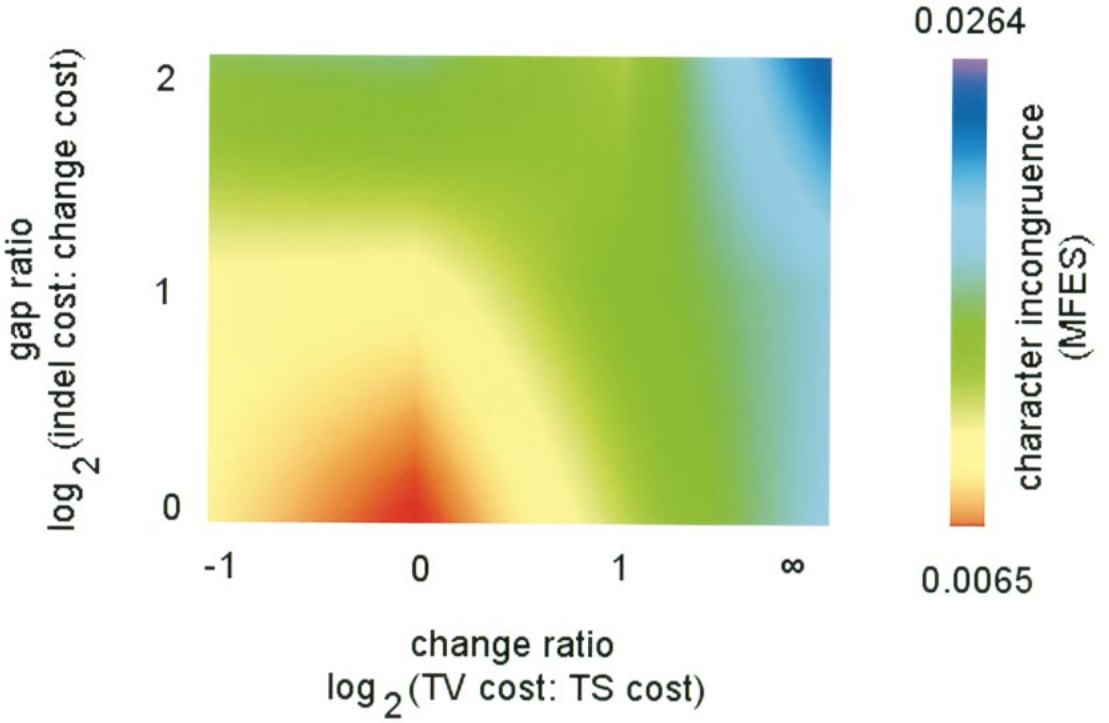

Fig. 3. Sensitivity analysis graphic. Y-axis represents the logarithm of the ratio of transversion: transition weights. The x-axis represents the logarithm of the ratio of the indel cost versus the maximal cost of a molecular change. The colors represent the z-axis, which is congruence between the molecular and morphological data partitions. Red is good, blue is bad.

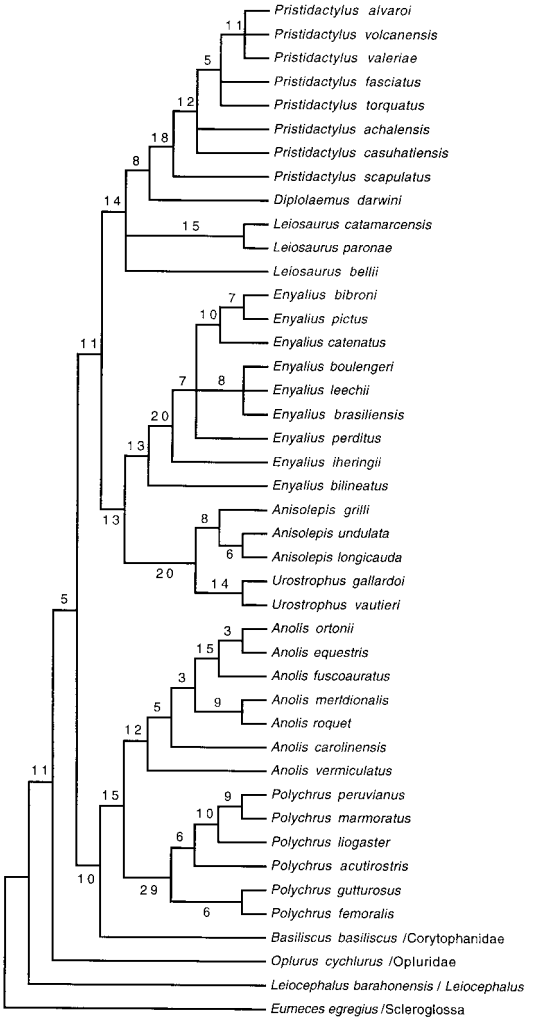

Fig. 4. Strict consensus of the three most parsimonious trees (length = 2617; CI = 0.25; RI = 0.69) for all data, showing Bremer support.

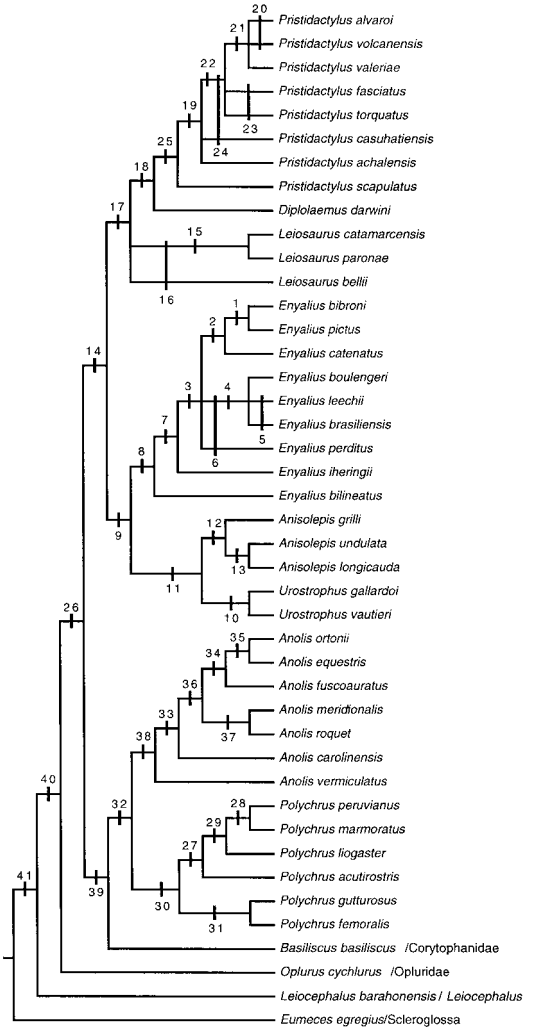

Fig. 5. The same consensus as shown in figure 4, with stems and taxa identified for ready comparison with evolutionary changes presented in appendix 4 (change list). Stems 5, 6, 16, 20, 23, 24 represent alternative relationships not rejected by the data.

very preliminary evidence that the Chilean species were plesiomorphic within *Pristidactylus* because they tend ecologically toward arboreality, arguably the primitive habit of the group. Nevertheless, the data support appears strong for our conclusion that pristidactylines are primitively terrestrial and secondarily arboreal. The inability to obtain a decisively monophyletic *Leiosaurus* (sensu lato) is also unexpected. Without molecular data or a more strenuous look at the anatomy of *L. bellii*, we have no way of resolving this polytomy (see comment in Conclusions).

The *Enyalius* + para-anole clade (stem 9; Bremer support of 13) is also well supported. With the exception of the placement of *Anisolepis grilli* as the sister taxon of the remaining *Anisolepis* (stem 13; Bremer support of 6), all other stems within the para-anoles are well supported (fig. 4). Nevertheless, this arrangement is hardly unexpected and is supported by one unambiguous morphological character. Structure within *Enyalius* (stem 8;

Bremer support of 13) is less resolved than in other taxa, and our suspicion is that regardless of the levels of support for various taxa, considerable work remains in the group to delimit species. The results of our analysis of *Enyalius* correspond roughly to the taxonomy suggested by Jackson (1978), although his preferred phylogeny is so much at variance with ours that detailed discussion is not warranted. (We note, however, that our phylogeny is roughly comparable to his phenetic network based on his meristic-morphometric data set, when rooted between *E. bilineatus* and *E. iheringii*, and not on his analysis of cranial measures; likely because ontogenetic variation in his osteological samples vitiated any results he obtained.) Jackson (1978) looked at most of the available alcoholic material of *Enyalius* at the time of his writing and suggested that *E. bibroni*, *E. pictus*, and *E. catenatus* were intergrading subspecies of one species, as were *E. boulengeri* and *E. brasiliensis*. In the first case our data do not reject that view. In the second case, however, our data indicate that *E. leechii* is imbedded within that second group, suggesting that a conservative species taxonomy is warranted.

Anolis and *Polychrus*. *Anolis* monophyly is corroborated (stem 38; Bremer support of 12) as is that of *Polychrus* (stem 30; Bremer support of 29).

Polychrus, despite being the perennial example of an enigmatic taxon (e.g., Vanzolini, 1983; Williams, 1988) composed in part of poorly diagnosed species has not attracted the kind of attention that it warrants. As far as we know, this is the first phylogenetic hypothesis of the component species in this highly corroborated monophyletic taxon. Nevertheless, except for the firm association of the western species *P. peruvianus*, *P. marmoratus*, and *P. liogaster*, we think that the last word has hardly been said about the phylogenetics of and species limits within this taxon.

Anolis (sensu lato) is, not surprisingly, monophyletic and highly corroborated (fig. 5: stem 38, Bremer support = 12) by this analysis. Our primary focus in this study was on the relationships of the non-anole polychrotids, so we did not attempt to exhaust the possibilities for morphological characters or to make substantial taxonomic sampling. Our purpose to was to assure the appropriate placement of *Anolis* within the larger phylogenetic framework and we think this has been accomplished.

CONCLUSIONS

Direct Optimization. We think that the method of direct optimization has performed well, especially with its ability to *truly* simultaneously cooptimize morphological and molecular sequence data. That the empirical results of this study indicated that the congruence of the molecular and morphological data was minimized by setting analytical costs at 1 for all changes (morphological change, insertions and deletions, transversions, and transitions) should make a number of workers reevaluate what the logical justification is for differential weighting schemes and assertions of general models of evolution. We do not expect to have a large impact on the verificationist approach to phylogenetic inference which is increasingly popular and seems to reflect the effects of many population biologists entering the field and bringing with them epistemologically inappropriate ways of thinking about historical problems. Nevertheless, the ratio of 1:1:1:1 is an empirical result of this study that should not be dismissed casually. Furthermore, we suggest that because direct optimization consistently finds globally more parsimonious resolutions for all data under consideration, it has a bright future.

Comparison with Previous Hypotheses. Only two studies have dealt specifically with the phylogeny of all polychrotid genera: Etheridge and de Queiroz (1988) and Frost and Etheridge (1989). The results of these studies are presented in figure 6, and because they present a natural evolution of increasing data, suffice it to say that we think we have made progress. The Etheridge and de Queiroz (1988) cladogram was done prior to easy computational analysis. The Frost and Etheridge (1989) analysis was done with a second-generation computer program (PAUP 2.4.1; Swofford, 1985), and the lack of resolution in that study is salutary only in that it pointed the way to further research. More recent molecular studies by Macey et al.

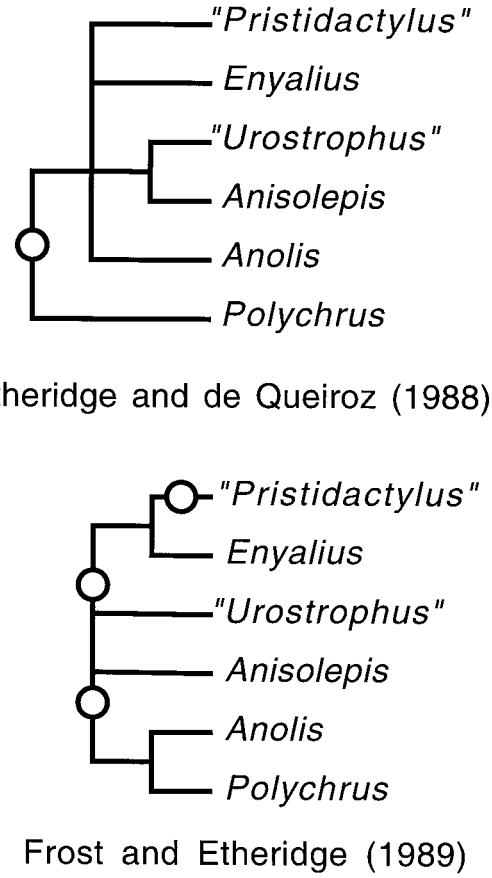

Fig. 6. Phylogenetic hypotheses for the Polychrotidae of Etheridge and de Queiroz (1988), and Frost and Etheridge (1989). Circles represent hypothesized rooting points.

(1997) and Schulte et al. (1998) dealt with a restricted set of terminal taxa, but beyond providing evidence for the pleurodont iguanians being monophyletic, they did provide molecular evidence in support of Hallermann's (1994) earlier suggestion that the corytophanids were intimately involved with the polychrotids. We think that all of these studies show increasing understanding of the phylogenetics of the group.

TAXONOMIC CONCLUSIONS. Inasmuch as evidence for a monophyletic Polychrotidae sensu Frost and Etheridge (1989) is lacking, we cannot continue its recognition in its original form. (See comment on Iguanian phylogenetics and taxonomy, following this section for context.) We recognize the Leiosauridae (diagnosed by the features noted in appendix 4, stem 14) to contain ''*Leiosaurus*'', *Diplolaemus, Pristidactylus, Enyalius,* and the paranoles (*Anisolepis* and *Urostrophus*). Within this taxon we recognized two tribes: (1) Leiosaurinae (stem 17) to contain ''*Leiosaurus*'' (see below), *Diplolaemus,* and *Pristidactylus,* and (2) Enyaliinae (stem 9) to contain *Enyalius, Anisolepis,* and *Urostrophus.*

The issue of ''*Leiosaurus*'' is frustrating because we think that subsequent work will show this to be a monophyletic taxon. Nevertheless, at this juncture we do not have the evidence to reject the hypothesis of paraphyly. Rather than use the metataxon convention (Estes et al., 1988), which we believe has been abused to the point of now merely being a tool for promoting the recognition of paraphyletic groups (e.g., see Tudge [2000: 82–87], for the use of the metataxon convention in defense of recognizing unambiguously paraphyletic groups), our inclination is to return to the taxonomy of this group as it was before Gallardo (1961) and Etheridge and de Queiroz (1988) synonymized *Aperopristis* (*A. catamarcensis* and *A. paronae*) with *Leiosaurus* (*L. bellii*). This minor taxonomic change renders a non-misleading taxonomy, and one we hope will be changed in the near future.

The name Polychrotidae[7] is attached to stem 32 (fig. 5), subtending *Polychrus* and *Anolis* (sensu lato). Because this is at variance with previous taxonomy, at this point the issue of Iguanian taxonomy in general must be addressed.

COMMENTS ON IGUANIAN PHYLOGENETICS AND TAXONOMY. Twelve years ago Frost and Etheridge (1989) noted that no evidence for the monophyly of the Iguanidae (sensu lato; Boulenger, 1885) existed, nor was there decisive evidence for the monophyly of the Agamidae with respect to the chameleons. Their (our) solution was to render a scientifically conservative taxonomy in the sense of sticking close to the evidence rather than bending to social conservatism. The strength of the study was that the ''dirty laundry'' of Iguanian systematics was displayed for all to see and to invite fur-

[7] We consider Polychrotidae Fitzinger (1843) to have priority over Corytophanidae Fitzinger (1843), under provisions of article 24.2 (First Revisor Principle) of the International Code of Zoological Nomenclature (1999).

ther scrutiny. This approach met with some criticism, most of which was related to discomfort with phylogenetic systematics (e.g., Böhme, 1990), but for the most part it was met with considerable enthusiasm and adopted wherever monophyly was taken seriously, which we were gratified to see was in most of the Western Hemisphere. The first *scientific* criticism of this arrangement was that of Macey et al. (1997) in which they presented molecular evidence for the monophyly of the Iguanidae (sensu lato). We applaud this effort and for those who wish to reclaim the older taxonomy on this basis, we have no scientific reason to dispute this reclamation. Nevertheless, in the intervening years since 1989, the family-group names of Frost and Etheridge (1989) have widespread acceptance and usage. Further, we suspect strongly that additional work on the fossil record will make for added ambiguity in the phylogenetic record regarding the status of the Iguania as well as the evidence of monophyly of the Iguanidae (sensu lato). So, as long as the canon of monophyly is not violated, the choice of ranks is entirely a subjective decision dependent upon what we believe will lead to the least confusion and make for the most progress. We therefore recommend the resurrection of the name Pleurodonta (Cope, 1864) for the monophyletic group formerly known as the Iguanidae (sensu lato; Boulenger, 1885). This provides symmetry with the Acrodonta (Cope, 1864), its putative sister taxon and, if pleurodont iguanian monophyly is falsified, or found to be unlikely (under the approach promoted by Macey et al., 1997), we will not have to make major changes in our taxonomy. Further, the molecular evidence presented by Titus and Frost (1996), Macey et al. (1997), and Schulte et al. (1998) suggests that the weak morphological evidence for the monophyly of the Tropiduridae is deeply questionable and certainly rejected by the molecular evidence, so we will not persist in recognizing that nominal taxon. Obviously, in the future, fossils will have to be taken into account, and the set of possible terminals will have to be sampled densely, both with respect to molecular and morphological characters analyzed simultaneously, before we can arrive at a comprehensive taxonomy. We still consider Iguanian phylogenetics to be largely an open field (indeed, we think this extends to squamates generally—see Northcutt, 1978, and Harris et al., 1999), and suggest that the following taxonomy (for living taxa) of iguanian lizards makes the best provision for promoting further progress as well as the best statement of the state of our understanding of the phylogeny of the group. (Where the group content is the same as in Frost and Etheridge, 1989, no notations are provided.)

Iguania Cope, 1864
- Acrodonta Cope, 1864 (= Chamaeleonidae of Frost and Etheridge, 1989).
  - Chamaeleonidae Rafinesque, 1815 (= Chamaeleoninae of Frost and Etheridge, 1989)
  - ''Agamidae'' (*see note at end of list*) Spix, 1825 (= Leiolepidinae plus Agaminae of Frost and Etheridge, 1989; diagnostically equivalent to the Acrodonta as well as the Chamaeleonidae sensu Frost and Etheridge, 1989)
- Pleurodonta Cope, 1864 (= Iguanidae sensu Boulenger, 1885)
  - Corytophanidae Fitzinger, 1843
  - Crotaphytidae Smith and Brodie, 1982
  - Hoplocercidae Frost and Etheridge, 1989
  - Iguanidae Oppel, 1811
  - Leiocephalidae Frost and Etheridge, 1989 (= Leiocephalinae of the Tropiduridae of Frost and Etheridge, 1989)
  - Leiosauridae *New*
    - Leiosaurinae *New*
    - Enyaliinae *New*
  - Liolaemidae Frost and Etheridge, 1989 (= Liolaeminae of the Tropiduridae of Frost and Etheridge, 1989).
  - Opluridae Moody, 1983
  - Phrynosomatidae Fitzinger, 1843
  - Polychrotidae Fitzinger, 1843 (as defined above)
  - Tropiduridae Bell, 1843 (= Tropidurinae of the Tropiduridae of Frost and Etheridge, 1989)

NOTE ON ''AGAMIDAE.'' Macey et al. (1997) argued that within the framework of systematic confidence estimates that the Agamidae (in the sense of nonchameleon acrodont iguanians) should be considered a metataxon (cf. Estes, 1988). We suggest that the

metataxon convention does not apply, and that this issue of taxonomic disarray can be addressed more clearly by applying the quotation convention for paraphyly developed by Wiley (1981: 213). Frost and Etheridge (1989) found no decisive evidence for a monophyletic Agamidae to the exclusion of the chameleons. In one of their two most parsimonious topologies, chameleons were imbedded within the Agamidae (in the traditional sense of nonchameleon acrodonts). In the other arrangement, chameleons were the sister taxon of other living acrodonts; in other words, only one of two topologies supported the Agamidae in the sense of Macey et al. (1997). If this were the only basis on which to derive a taxonomy, we suppose that authors could have opted for applying the metataxon convention, which, at least as originally formulated, was to be applied in cases of evidentiary conflict as in this example. However, Macey et al. (1997: fig. 5a, b) presented new molecular evidence for ''agamid'' paraphyly and none for its monophyly. So, even though they reformulated the notion of metataxon in the form of a confidence measure, the metataxon convention is not appropriate (at least in a deductive approach), because the evidence pointed to ''agamid'' paraphyly more strongly in 1997 than it did in 1989. Formulating a taxonomy that suggests something different is not conservative in any evidentiary sense and, further, no one attached to the canon of monophyly would formulate the taxonomy of acrodonts still adhered to by so many. The base of the cladogram of acrodonts is poorly understood, and we consider it unlikely that future work will render the ''agamids'' monophyletic with respect to the chameleons, especially when fossils are finally taken into account. For this reason we suggest that as an evidentiarily conservative taxonomy that the ''Agamidae'' be placed in quotations to denote its paraphyletic status (Wiley, 1981: 213), pending resolution of the placement of the problematic taxa, *Uromastyx, Leiolepis, Physignathus* (including *Hydrosaurus*), and the species of ''*Hypsilurus*'', not to mention a relatively large number of fossil taxa including *Mimeosaurus, Isodontosaurus, Priscagama,* and *Arretosaurus.*

ACKNOWLEDGMENTS

We thank J. Faivovich, T. Grant, M. Mahoney, G. Pregill, W. Wheeler, and especially B. Hollingsworth and M. Donnelly for constructive criticism of the manuscript and to G. Giribet and W. Wheeler for advice on the use of POY. K. de Queiroz provided advice regarding appropriate exemplars of *Anolis* (sensu lato) to represent that taxon in our more general analysis. Access to morphological specimens was provided by L. Coloma (Escuela Politécnica Nacional, Quito, Ecuador); D. B. Wake and B. Stein (Museum of Vertebrate Zoology, University of California [MVZ]); J. Cadle and J. Rosado (Museum of Comparative Zoology, Harvard University [MCZ]; R. McDiarmid, R. I. Crombie, and R. Reynolds (National Museum of Natural History, U.S. Geological Survey and Smithsonian Institution [USNM]); E. N. Arnold and B. Clarke (Natural History Museum, London [BM]); L. Vitt and J. Caldwell (Oklahoma State Museum of Natural History [OMNH]); M. T. Rodrigues and H. Zaher (Museu de Zoologia, Universidade de São Paulo [MZUSP]); A. Almendariz (Politécnica Universidad Católica, Quito, Ecuador [PUC]); A. G. Kluge, R. I. Nussbaum, and G. Schneider (Museum of Zoology, University of Michigan [UMMZ]); W. E. Duellman and J. Simmons (Museum of Natural History, University of Kansas [KU]); R. Laurent and F. Lobo (Instituto Miguel Lillo, Tucumán, Argentina [FML]); R. Inger and H. Voris (Field Museum of Natural History [FMNH]); and Juan Carlos Ortiz (Departamento de Zoología, Universidad de Concepción, Chile [IZUC]).

Tissues were graciously supplied by W. E. Duellman and C. Raxworthy (KU), C. J. Cole and C. Myers (AMNH), D. Dittman (Museum of Natural Science, Louisiana State University [LSU]), M. T. Rodriguez (MZUSP), F. B. Cruz and S. E. Torres (FML), B. Alvarez de Avanza (Universidad Nacional del Nordeste, Corrientes, Argentina [UNNEC]), L. Vitt and J. Caldwell (OMNH), and L. Fitzgerald (Texas A&M University [TCWC]). J. Williams (Museo de La Plata, Argentina) and M. R. Cabrera (Universidad Nacional de Córdoba, Argentina) provided information on life history and behavior in

Urostrophus and *Anisolepis*. This project was funded in part by National Science Foundation grant DEB-9220870 to D. Frost and T. Titus, and by National Aeronautical and Space Administration grants NAG5-8443 to D. Frost and W. Wheeler and NAG2-1339 to D. Janies and W. Wheeler.

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APPENDIX 1

Specimens Examined, Molecular Data Vouchers, and GenBank Accession Numbers

MORPHOLOGICAL SPECIMENS. Anatomical specimens of ingroup taxa examined by Frost and Etheridge are noted below. In addition to these listed specimens, other specimens of the genera *Diplolaemus, Leiosaurus, Pristidactylus, Anisolepis, Urostrophus, Enyalius,* and *Anolis* (sensu lato) examined by Etheridge previously (and the source of a considerable volume of notes) are listed in Etheridge (1959, 1969), Etheridge and de Queiroz (1988), and Etheridge and Williams (1985, 1991). Outgroup taxa specimens are listed in Frost and Etheridge (1989) and Titus and Frost (1996) as

well as those available in AMNH and REE (R. E. Etheridge osteology; now mostly in the AMNH) collections.

Anisolepis grilli: USNM 73504 (alcoholic); MCZ 13319; BMNH 1946.8.12.38, REE 1952 (skeletons); AMNH 120468 (skull and cleared and double-stained postcranium). *A. longicauda:* BMNH 1946.8.9.2 (alcoholic); BMNH 98.11.3.1 (skeleton). *A. undulata:* BMNH 1946.8.5.90–91, USNM 65545 (alcoholics); MCZ 84033, 59273, 59274 (skeletons). *Anolis carolinensis:* AMNH (many alcoholic specimens); AMNH 70089, 70102–05, 75749, 141111 (skeletons). *A. equestris:* AMNH 57962, 58352–53, 78074, 78147, 89355 (alcoholics); AMNH 72634, 73848, 74278–79, 1141137 (skeletons); AMNH 74618 (skull); AMNH 126049 (skull and cleared and double-stained postcranium). *A. fuscoauratus:* AMNH 125135–52 (alcoholics); AMNH 101383 (skull and cleared and double-stained postcranium). *A. meridionalis:* AMNH 98413–25 (alcoholics); AMNH 98421, 98424 (skulls and cleared and double-stained postcrania). *A. ortonii:* AMNH 64860–61, 91637, 125354 (alcoholics); AMNH 56886, 114923 (skulls and cleared and double-stained postcrania). *A. roquet:* AMNH 100458–92 (alcoholics); AMNH 93806, 94598 (skeletons); AMNH 100472, 100476 (skulls and cleared and double-stained postcrania). *A. vermiculatus:* AMNH 76521–26, 144670–82 (alcoholics); AMNH 70093 (skeleton); AMNH 63062 (skull and cleared and double-stained postcranium). *Aperopristis catamarcensis:* SDSU 1005 (alcoholic); MCZ 96709 (skeleton); FML 0670.2 (skull and cleared and double-stained postcranium). *A. paronae:* MCZ 162923 (skeleton); FML 00035 (alcoholic/subsequently skull and cleared and double-stained postcranium). *Diplolaemus bibroni:* AMNH 80042, 46427–29 (alcoholic). *Diplolaemus darwini:* AMNH 17005 (alcoholic); MVZ 93047, 93035–36, 200505–06 (skeletons). *Enyalius bibroni:* AMNH 131861 (alcoholic). *E. bilineatus:* AMNH 120471, UMMZ 65946 (alcoholics); REE 1658, 1958, MZUSP 43019, 43022–25 (skeletons). *E. boulengeri:* MCZ 79025 (alcoholic); MCZ 163781; MCZ 163781, MZUSP 17452–54, 43020 (skeletons). *E. brasiliensis:* AMNH 62143, MCZ 3317, 4251, UMMZ 108627 (lot of 3) (alcoholics); MZUSP 3232, 43023, REE 1960 (skeletons); MZUSP 43046 (skull). *E. catenatus:* MCZ 7320, 3717, 4251, UMMZ 204084 (alcoholics); REE 1961; MZUSP 43016, 78382 (skeletons). *E. iheringii:* SDSU 2222–23, AMNH 74964, 120469, UMMZ 108628–29, 204085 (alcoholics); MCZ 6316, REE 1959, MZUSP 702, 43024, 43025, 42701, 80630 (skeletons). *E. leechii:* BMNH 1946.8.9.7, OMNH 36690–92 (alcoholics) (36690 subsequently cleared and double-stained with dry skull). *E. perditus:* AMNH 133744–47 (alcoholics); MCZ 163788, USNM 247877, MZUSP 43017–18 (skeletons); AMNH 119749 (skull); AMNH 119749 (postcranial skeleton). *E. pictus:* SDSU 2221, AMNH 131859–60 (alcoholics); MZUSP 8826, 59183–85 (skeletons); MCZ 163784 (skull); MZUSP 42686 (skull). *Leiosaurus bellii:* SDSU 2228, 2230, AMNH 17004 (alcoholics); REE 2410 (skeleton). *Pristidactylus achalensis:* SDSU 2380–81, 2385–86 (alcoholics); MCZ 86628, REE 2488, MVZ 92966–69, 93006 (skeletons). *P. alvaroi:* IZUC 8632, 12104 (alcoholics). *P. casuhatiensis:* MCZ 162925 (alcoholic); MCZ 162924 (skeleton). *P. fasciatus:* MVZ 127058, 127061 (alcoholics); REE 127061 (mandible only). *P. scapulatus:* SDSU 3392–93, 3395–96 (alcoholics); REE 2381–82, 2509 (skeletons). *P. torquatus:* SDSU 2249, 2251, AMNH 131856–57 (alcoholics); MCZ 3586, REE 2766–2767; MZUSP 6982–84, 65667–78 (skeletons). *P. valeriae:* USNM 165602, IZUC 12037, 12440–41 (alcoholics). *P. volcanensis:* MCZ 169549 (alcoholic); MCZ 169550 (skeleton).

Polychrus acutirostris: AMNH 17006, 104547–49, 62141–42, 75303–04, AMNH 82299, 75303–04, 101461, 17006, 90274, 104546, 101462, 38806 (alcoholics); AMNH 104549 (skull and cleared and double-stained postcranium); REE 568, 4412, 4488 (skeletons). *P. femoralis:* FMNH 34303, 81404–05, (alcoholics); FMNH 81405, PUC 7302 (skulls and cleared and double-stained postcrania). *P. gutturosus:* AMNH 13426, 13518, 32674–77, 108990, 13424–25, 13536, 103744, 104527, 120009, 16338, 16391 (alcoholics); AMNH 32675–76 (skulls and cleared and double-stained postcrania). *P. liogaster:* AMNH 1679, 6764–65, 22509, 23141, 37812,, 56416, 101452, 101459–60 (alcoholics); AMNH 101460 (skull and cleared and double-stained postcranium). *P. marmoratus:* AMNH 13420–23, 13415–16, 29326, 32279–81, 57211–15, 57217–23, 57225, 57227–30 (alcoholics); REE 346, 2283, 2496, MVZ 174843; AMNH 141084, 141130 (skeletons); AMNH 71170–71 (skulls). *P. peruvianus:* AMNH 28633–35 (alcoholics); MVZ 82413 (skeleton). *Urostrophus gallardoi:* BMNH 1902.5.22.4 (alcoholic); MCZ 162920 (skeleton). *U. vautieri:* BMNH 57.10.28.66 (alcoholic); MCZ 7319, 84036, REE 2507, BMNH 94.9.15.3 (skeletons).

MOLECULAR VOUCHERS AND GENBANK ACCESSION NUMBERS. *Anisolepis longicauda:* UNNEC 891 (GenBank AF338336). *Anolis carolinensis:* T. Jackman unnumbered from Bimini, 12 April 1992 (GenBank AF338324). *A. fuscoauratus:* KU 214946 (W. E. Duellman 57670) (GenBank AF338337). *A. meridionalis:* USNM Field (Lee

Fitzgerald) 166692 (GenBank AF338332). *A. ortonii:* Mus. Javier Prado, Lima, unnumbered (W. E. Duellman 57705) (GenBank AOU39561). *A. roquet:* AMNH (C. J. Cole 6387) (GenBank AF338339). *Aperopristis paronae:* FML unnumbered (S. Torres) (GenBank AF338328). *A. catamarcensis:* FML unnumbered (S. Torres) (GenBank AF338341). *Basiliscus basiliscus*: MVZ 137675 (GenBank AF338330). *Diplolaemus darwini:* MVZ (R. D. Sage 13041) (GenBank AF33826). *Eumeces egregius:* GenBank AB016606. *Enyalius bilineatus:* MZUSP unnumbered (M. Rodrigues LG814) (GenBank AF338340). *E. leechii*: LSU H13958 (formerly L. Vitt) (GenBank AF338342). *Leiocephalus barahonensis:* T. Titus unnumbered (GenBank AF338327). *Oplurus cychlurus:* UMMZ 197023 (GenBank AF338334). *Polychrus acutirostris:* UNNEC 1368 (GenBank AF338331). *P. femoralis:* L. A. Coloma 2568 (GenBank AF338335). *P. gutturosus:* OMNH unnumbered (J. P. Caldwell 10187) (GenBank AF338338). *P. marmoratus:* AMNH (C. J. Cole 6513) (GenBank AF338329). *Pristidactylus scapulatus:* SDSU 3448 (GenBank AF338333). *Urostrophus gallardoi:* FML unnumbered (S. Torres) (GenBank AF338325).

APPENDIX 2

Morphological Transformation Series

Morphological characters were drawn from direct observation of alcoholic, dry skeletal and double cleared-and-stained specimens (see appendix 1). General nomenclature of squamation follows Smith (1949). Because POY treats all characters showing multistate cells (polymorphism) as nonadditive, where this might have presented a problem in analysis, we transformed additive multistates into sequentially numbered bistate characters. This is reflected in the numbering system of the characters below. Also, because POY starts counting characters with ''0'' rather than with the traditional ''1'', we also started our numbering convention with 0 so as to make direct interpretation of output (appendix 4) relatively straightforward.

Squamation and Form of Head

0. Rostral sutures (Etheridge and de Queiroz, 1988): (0) rostral scale without sutures, undivided; (1) rostral scale with a pair of posterior sutures; (2) rostral scale divided medially. The rostral scale is divided medially into a pair of scales subequal to the adjacent anterior supralabials in *Leiosaurus catamarcensis* and *L. paronae.* In *Polychrus acutirostris* the rostral scale exhibits posterior sutures that do not partition the rostral. Because we had no ontogenetic reason to assume a morphocline, this character is treated as nonadditive.

1. Snout, orbit relative lengths (Etheridge, 1969): (0) snout length greater than orbital diameter; (1) orbital diameter greater than snout length. The length of the snout (as measured from the anterior border of the rostral to the anterior corner of the orbit, as determined by the ciliary–preorbital scale contact zone) is less than the maximum longitudinal diameter of the orbit (as measured from the anterior to the posterior margin of the ciliary patch) in *Enyalius.* The reverse is true in all other taxa.

2. Mental scale (Williams, 1988; Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989): (0) undivided; (1) divided. In *Polychrus* and the anoles the mental scale is partly or completely divided by a median groove. In *Leiosaurus paronae* the mental is so reduced in size, or fragmented, that it is not evident whether a mental scale is present so it is coded as unknown.

3. Nasal scale–canthus rostralis: (0) canthus rostralis relatively straight with nasal scale definitely below it; (1) anteriorly the canthus deflected medially, with the anteriormost canthals reduced; no development of a postnasal/subnasal ridge involving anterior loreals; (2) canthal ridge involves anteriormost loreals to form a ridge posterior to the nasal scale; canthals either very weakly ridged or no trace of anteriormost canthal ridge; (3) canthus obsolete. Although an argument could be made for ordered 0–1–2, condition 3 cannot be placed in this series and could conceivably be intercalated between any two of the other characters. We have therefore treated this set of characteristics as nonadditive.

4. Nasal scale–postrostral scale contact: (0) in contact; (1) separated. Contact is intraspecifically variable in *Pristidactylus achalensis* and *P. torquatus.*

5. Nasal–labial contact: (0) nasal scale not in broad contact with supralabial(s); (1) nasal scale in broad contact with second or third supralabial scales.

6. Nasal scale, nostril: (0) nasal scale with rounded margin; except for suture with suprala-

bial, nostril almost as large as scale; (1) nasal scale polygonal, nostril much smaller than scale. In species of *Polychrus*, except for *P. femoralis*, the nasal scale is very large with respect to the size of the nostril and is quite unlike the condition found in other polychrotids.

7. Nasal scale position: (0) entire nasal scale closer to anterior tip of rostral than to anterior border of orbit; (1) center of nasal scale roughly equidistant to anterior border of orbit and anterior border of rostral.

8. Superciliary scales (Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989): (0) imbricate and elongate; (1) nonimbricate and short.

9. Supraocular scales (Etheridge, 1969): (0) not carinate or very weakly carinate (may be rugose or swollen); (1) strongly longitudinally carinate or ''pyramidal.''

10. Eyelids: (0) not fused at anterior and posterior corners of the meatus, iris clearly visible around the pupil; (1) partly fused, constricting the ocular meatus to roughly the size of the pupil. *Polychrus* is unique in pleurodont iguanians in having this characteristic.

11. Frontal region (Etheridge and de Queiroz, 1988): (0) flat or slightly convex; (1) concave.

12. Head scale *striae*: (0) fine, linear rugosities on head scales absent; (1) fine, linear rugosities (*striae*) present on lateral gulars, infra- and supralabials, and scales of the snout, present or not on other head scales. Linear *striae* may be obscured in large adults, especially in *Polychrus peruvianus*, by large, swollen rugosities.

13. Interparietal scale and ''eye'': (0) interparietal scale differentiated, with a distinct, opalescent ''eye''; (1) interparietal scale and ''eye'' differentiated in juveniles, obscure or absent in adults; (2) interparietal scale and eye undifferentated in juveniles and adults. We have treated this transformation as additive because condition 1 is developmentally intermediate between 0 and 2.

14. Subocular scales (Etheridge and de Queiroz, 1988): (0) one greatly elongate, more than three times longer than any other; (1) one or more moderately elongate, none three times longer than wide; (2) subequal, none elongate. The holotype of *Enyalius bibronii* has state 2, but according to Jackson (1978), one subocular usually is longer than the others, so we have treated this as interspecifically variable. Other species that are interspecifically variable are *Enyalius pictus* and *Polychrus peruvianus* (1–2), *Diplolaemus* (0–1), and *Pristidactylus achalensis* and *P. torquatus* (0–1–2). The transformation is treated as nonadditive for reason that intraspecific variation suggests multiple means of transitioning between states.

15. Supraorbital semicircles (Etheridge, 1969): (0) separated by two to four rows of small scales (smaller than scales of supraorbital semicircles); (1) in narrow contact, or separated by a single row of small scales; (2) separated by a single row of large scales that are about as large as those of the supraorbital semicircles; (3) more than one pair of scales in broad contact. Although descriptions make the characteristics sound as if they are part of a single ordered series, there are a number of sources of variation that are confounded by them. For instance, in *Polychrus* the head shield is generally quite large with seeming reduced supraoculars, whereas in *Diplolaemus* the appearance is of widened supraorbital semicircles and in *Leiosaurus* is apparently associated with a general reduction of scale size. For this reason we consider this transformation nonadditive.

16, 17. Infralabial scale number: (0) 7–7 or fewer; (1) 8–8 to 12–12; (2) 14–14 or more. This ordered transformation was cast as two columns in the data matrix because of intergeneric variation within the Corytophanidae.

18. Mesoptychial scales (Etheridge, 1969): (0) not conical; (1) conical, with naked skin evident between. The mesoptychals of *Enyalius* are distinctly conical. In all other taxa they are convex or flat; in *Polychrus* they may be elongate.

19. Gular fold (Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989): (0) present; (1) absent. A gular fold (sensu Frost, 1992) is absent in *Anisolepis longicauda*, *Polychrus*, and anoles (except *Anolis vermiculatus*) but is present in all other taxa. *Anolis equestris* (especially evident in juveniles) exhibits a midventrally narrowly incomplete gular fold that is rendered incomplete by the well-developed dewlap. (The gular fold in *A. vermiculatus* apparently is ''allowed'' by the rather small dewlap.) *Polychrus femoralis* has a strongly developed antegular fold, which superficially looks like a gular fold. However, this fold is not confluent with the dorsolateral fold (which is normally confluent with the gular fold when present). Instead, it sits anterior to the position where a gular fold would, thus justifying our supposition that this is an antegular fold.

20. Gular crest: (0) absent; (1) a short midventral row of compressed, projecting gular scales that form a short anterior crest; (2) a long row of compressed, projecting scales extends most of the length of the dewlap. This transformation was treated as additive for the reason that condition 1 is developmentally intermediate between 0 and 2.

21. Antegular fold (Frost, 1992): (0) present; (1) absent.

22. Dewlap (Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989): (0) absent; (1) present, small, supported by second ceratobranchials that terminate at the antegular fold, below the level of the clavicles; (2) present, large, supported

by second ceratobranchials that extend well back below the sternum.

Squamation of Trunk and Tail

23. Middorsal scale row (Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989): (0) present, continuous or nearly so (middorsals may be separated by medial contact of occasional pairs of paravertebral scales at the level of the shoulders or hips), forming a distinguishable (if occasionally low) ridge of enlarged keeled scales; (1) present, but discontinuous; (2) absent (with occasional individuals in some taxa showing very weak development of a line of scales over the sacral region); in some taxa the appearance of a dorsal scale row is made by the linear enlargement of adjacent dorsalmost scales; (3) middorsal row formed of tubercles rather than of compressed, keeled, or convex scales. We have treated this set of characters as nonadditive because we can easily envision a rather large number of different processes producing the observed variation.

24. Paravertebral scale shape: (0) polygonal; (1) rounded (may be convex or tubercular). The paravertebral scales of the body are polygonal in *Enyalius* and *Anisolepis* and are rounded in *Pristidactylus, Diplolaemus, Leiosaurus,* and *Urostrophus.* Both states are present in individuals of *Polychrus liogaster* and *Enyalius iheringi.*

25. Paravertebral scale surface: (0) unicarinate; (1) tuberculate; (2) smooth; convex or flat; (3) mixed unicarinate and multicarinate. We have treated these characters as nonadditive due to our inability to discern any particular morphocline beyond setting the root on the unicarinate condition.

26. Lateral body scales: (0) not in oblique rows of rectangular scales; (1) in oblique rows of large, more-or-less rectangular scales with rounded corners, separated by skin beset with small, irregular thickenings. The dorsal body scales of these taxa are smooth or keeled, rounded and imbricate or nonoverlapping; however, the lateral body scales of *Polychrus* are nearly unique in their oblique arrangement, as also found in *Anolis equestris.*

27. Ventral body scales: (0) unicarinate; (1) smooth; (2) mixed unicarinate and multicarinate, or all multicarinate. Ventral scales are unicarinate in *Leiosaurus paronae* (Peracca, 1897), *Anisolepis* (Etheridge and Williams, 1991), and *Enyalius pictus* and *E. bibronii* (Etheridge, 1969). They are unicarinate in *Polychrus acutirostris,* tricarinate in *P. peruvianus,* and variably unicarinate, smooth or tricarinate in *P. marmoratus* and *P. gutturosus.* The ventrals are smooth in *Urostrophus* (Etheridge and Williams, 1991), *Pristidactylus* (Etheridge and Williams, 1985; Lamborot and Diaz, 1987), *Diplolaemus, Leiosaurus belli, L. catamarcensis,* and in *Enyalius catenatus, E. bilineatus, E. iheringii, E. perditus* and *E. brasiliensis* (Etheridge 1969, Jackson, 1978). We have treated this transformation as nonadditive due to our inability to perceive any kind of morphocline or developmental progression. *Leiocephalus* and oplurids are coded as unknown because of a cladistically basal dichotomy in this feature in their respective cladograms (Titus and Frost, 1996; Pregill, 1992).

28. Ventrolateral row of enlarged scales (Etheridge and Williams, 1991): (0) absent; (1) present, interrupted or continuous. In *Anisolepis* (*A. grilli* variably) a distinctive ventrolateral row of enlarged scales is evident.

29. Proximal caudal scales: (0) keeled; (1) smooth. The dorsal scales of the tail are keeled in *Enyalius* (weakly in *E. bibronii*), *Anisolepis,* and *Polychrus peruvianus,* and faintly keeled in *P. marmoratus, P. acutirostris,* and *P. guttrosus.* They are smooth on the dorsal surface of the proximal one third (or more) of the tail in *Pristidactylus, Diplolaemus, Leiosaurus belli,* and *Urostrophus.* In some *Diplolaemus* all caudal scales are smooth.

30. Caudal annuli: (0) regular, forming segments of four to six scale rows separated by nearly vertical scale sutures; (1) irregular, vertical sutures, if present confined to ventral half of scale. This character is largely congruent with the presence/absence of autotomy septa, except in *Diplolaemus,* in which partially fused septa are not accompanied with scale annuli on the tail.

31. Tail: (0) not prehensile; (1) prehensile. *Urostrophus vauteri* and *Anisolepis grilli* were reported to have a prehensile tail by Etheridge and Williams (1991). According to Cabrera (in litt.) the tail is prehensile in *Urostrophus gallardoi* and according to J. Williams (in litt.) the same is true for *Anisolepis longicauda.* Hoogmoed (1973: 183) rejected earlier reports of tail prehensility in *Polychrus.*

Squamation and Morphology of Limbs

32. Supradigital scale shape: (0) not all supradigitals of third phalanx of third finger at least twice as broad as postdigitals of third phalanx; (1) all supradigitals of third phalanx at least twice as broad as postdigitals of third phalanx. All polychrotids have expanded supradigitals, as do oplurids, with interspecific variation ranging from 1.5 to about 3 times wide than long. Individuating classes of variation more than twice the diameter of the supradigital scales proved impossible.

33. Supradigital scale keels: (0) smooth; (1)

unicarinate; (2) some or all multicarinate. We treat this set of characters as nonadditive due to variation in carination not forming a developmental series.

34. Postdigital scales of third finger: (0) single lateral row penetrating proximally to penultimate phalanx; (1) double postdigital row penetrating proximally to penultimate phalanx; (2) triple postdigital row penetrating proximally to penultimate phalanx.

35. Subdigital lamellae of toes (Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989): (0) most with three distinct keels; (1) usually a single, asymmetrical keel; (2) smooth; (3) most with four to six distinct keels. We treat this as nonadditive.

36. Proximal subdigital lamellae of third toe: (0) not swollen, or only weakly; (1) swollen and weakly projecting; (2) swollen and projecting to form a pectinate margin. The justification for treating this as an additive multistate is that the pectinate margin is necessarily a subset of the set of taxa showing swollen subdigital lamellae of the third toe.

37. Distal subdigital lamellae (Etheridge and de Queiroz, 1988): (0) not divided; (1) longitudinally grooved or divided. The distal subdigital scales are not divided in *Polychrus, Anisolepis, Urostrophus,* and in those species of *Enyalius* and *Leiosaurus* that have multicarinate subdigital lamellae. The distal subdigital lamellae are divided longitudinally, often with a median notch, in *Pristidactylus* (including *P. fasciatus,* which has keeled subdigital lamellae), *Leiosaurus belli,* and those *Enyalius* that have smooth subdigital lamellae, or subdigital lamellae with a single keel (Etheridge and Williams, 1985; Etheridge, 1969).

38. Digital pads: (0) absent; (1) present. The absence of a digital pad in *Anolis onca* and its reduction in *A. chrysolepis* and *A. auratus* are considered to be due to ''retrograde'' evolution by Peterson and Williams (1981), and in *Chamaelinorops* by Peterson (1983). We have accepted this view at face value for the purposes of this analysis.

39. Third toe length: (0) third toes distinctly shorter than fourth toe; (1); third and fourth toes of approximately equal length. *Polychrus* is characterized by its unusual possession of third and fourth toes of equal or subequal length. We have not been able to individuate characters beyond this, although note that the difference in length between the toes in question appears to be somewhat greater as a trend in *Enyalius* than in the remaining taxa.

40. Hindlimb length: (0) short; (1) medium; (2) long. The fourth toe of the adpressed hindlimb does not extend beyond the shoulder in *Polychrus, Diplolaemus, Pristidactylus fasciatus,* and *Urostrophus.* It extends to a point between the shoulder and the orbit in *Anisolepis, Pristidactylus* (except *P. fasciatus*), and *Leiosaurus* and to a point anterior to the middle of the orbit in *Enyalius.*

41. Femoral pores (Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989): (0) present; (1) absent. Femoral pores are present in *Polychrus,* and are absent in all other polychrotids.

Scale Organs

42. Scale organ of dorsum (Etheridge and de Queiroz, 1988): (0) without spinules; (1) spinules present.

43. Condition of spinulate scale organs of dorsum (Etheridge and de Queiroz, 1988): (0) with a tuft of mildly elongate spinules; (1) most or all with a long filament formed by many spinules twisted together; (2) spinulate but without a central tuft of more elongate spinules. The scale organs seen in *Enyalius leechii* are unique; that is, they are spinulate, with the spinules short and without a central tuft of elongate spinules. Taxa lacking scale organs were coded as unknown to avoid implicitly weighting in concert with the previous character transformation. We treat this set of characters as nonadditive because we have no compelling theory of transformation.

44. Subdigital surface microstructure (Peterson and Williams, 1981; Peterson, 1983): (0) honeycomb; (1) spinulate; (2) subdigital scale surface is covered with minute, rounded knobs, all with a blanket of short, blunt, minute projections (*Enyalius leechii*). We treat this set of characters as nonadditive because we lack a compelling theory of transformation.

General Body Plan and Coloration

45. Sexual size dimorphism: (0) males larger than females; (1) females larger than males. Maximum snout–vent lengths of males are greater in *Pristidactylus,* except for *P. volcanensis,* where it is unknown. Maximum adult size of females is greater in *Anisolepis, Urostrophus, Diplolaemus, Leiosaurus, Enyalius* (Etheridge, 1969; Jackson 1978), and *Polychrus* (except possibly *P. peruvianus,* which is coded as unknown).

46. Sexual dichromatism: (0) present; (1) absent. Marked sexual dicromatisim occurs in the Argentinean species of *Pristidactylus, P. torquatus* (Etheridge and Williams, 1985), and *P. valeriae.* It is apparently absent in *P. volcanensis* (Lamborot and Diaz, 1987) and is unknown in *P. alvaroi.* It is present in *Enyalius* except *E. bilineatus*; male *E. bibronii* are unknown (Etheridge, 1969; Jackson, 1978). Sexual dichromatism is ab-

sent in *Diplolaemus* and *Leiosaurus* (Etheridge and Williams 1985) and in *Anisolepis* and *Urostrophus* (Etheridge and Williams, 1991). Sexual dichromatism is present in *Polychrus acutirostris* and absent in *P. marmoratus* (Vanzolini, 1983).

47. Black antehumeral bar: (0) absent in adult males; (1) present in adult males. A conspicuous, wide, black vertical bar on each side in front of the shoulder is present in adult males of *Pristidacytlus scapulatus, P. achalensis, P. torquatus,* and *P. fasciatus*; the bars are present but narrower and partly hidden within the antehumeral fold in *P. casuhatiensis.* In *P. valeriae* the bars may be faint or absent but are evident in some individuals. *P. volcanensis* in our single alcoholic specimen appears to have a faint dark antehumeral bar.

48. Dorsal color pattern: (0) not fleur-de-lis; (1) fleur-de-lis. The species of *Leiosaurus* are conspicuous by their possession of a fleur-de-lis dorsal pattern.

Hemipenis

49. Hemipenis (Arnold, 1984; Frost and Etheridge, 1989; Böhme, 1988): (0) unicapitate; (1) bilobate.

Cranial Skeleton

50. Parietal foramen (Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989): (0) present; (1) absent.

51. Lacrimal bone (Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989): (0) on orbital rim; (1) excluded from orbital rim. Considerable variation exists in the morphology of the lacrimal region. In some cases exclusion of the lacrimal from the orbital margin is obtained by contact of the prefrontal and jugal on the orbital margin, even though the lacrimal bone is exposed laterally (*P. acutirostris*: REE 4412 and 568). The lacrimal bone is intraspecifically variable in its exclusion from the orbital margin in *P. marmoratus.* The condition is unknown in *Pristidactylus alvaroi* and *P. valeriae.*

52. Postfrontal bone (Etheridge and de Queiroz, 1988: 346; Frost and Etheridge, 1989): (0) present; (1) absent. Frost and Etheridge coded *Polychrus* as ''present'' in error. Listed as unknown in *E. bibroni, Pristidactylus alvaroi, P. fasciatus,* and *P. valeriae* due to unavailability of material.

53. Dermal roof bone rugosities (Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989): (0) absent or weak, although indistinct rugosities may be present; (1) strong rugosities that correspond to scale outlines extend over parietal and frontal and adjacent dermal skull bones.

54. Osseus labyrinth (Etheridge and de Queiroz, 1988: 346; Frost and Etheridge, 1989): (0) superficial outline of osseous labyrinth distinctly above the level of the opisthotics, although only of low to moderate elevation; (1) high elevation of the osseous labyrinth above the level of the opisthotic.

55. Calcified nuchal endolymphatic sacs (Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989): (0) absent; (1) present.

56. Supratemporal bones (Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989): (0) mostly on lateral side of supratemporal process of parietal; (1) more-or-less equally on both sides of the supratemporal process of the parietal. *Enyalius* species have the anterior tip of the supratemporal moved posteriorly, causing a more medial exposure of the supratemporal on the paroccipital processes. Additionally, they may have a ventral groove on the paroccipital process, which makes evaluation of this feature difficult. Frost and Etheridge therefore coded *Enyalius* as ''0'' in error. *Urostrophus* and *Anisolepis* seem to have reduced supratemporals, but this is difficult to evaluate against the variation in *Enyalius.*

57. Crista ventrolateralis of basisphenoid and basioccipital in adults: (0) well developed and sharp on basioccipital and basisphenoid; (1) rounded or absent on basioccipital.

58. Sphenoccipital process: (0) long, extending to spheno-occipital tubercle; (1) absent or short, terminating well short of spheno-occipital tubercle. The sphenoccipital process extends posteriorly with ontogeny, so it must be evaluated in older adults.

59. Coronoid lateral process (Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989): (0) large, extending anterolaterally to overlap dentary; (1) absent or labial process of coronoid not extending anterolaterally, but posterolaterally along margin of dentary.

60. Splenial, anterior extent (Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989): (0) extends anteriorly more than 25% length of tooth row; (1) extremely short or absent, not extending anteriorly more than 25% length of tooth row.

61. Splenial, posterior extent (Frost and Etheridge, 1989): (0) terminates posteriorly anterior to anterior edge of mandibular fossa; (1) terminates posterior to anterior edge of mandibular fossa.

62. Angular (Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989): (0) moderate to large with suture line of contact with splenial on the lingual face of the mandible; (1) absent or reduced to splint; if present, suture or angular with splenial on the inferior margin of the mandible.

63. Dentary, posterior extent (Pregill, 1984; Etheridge and de Queiroz, 1988; Frost and Eth-

eridge, 1989): (0) short, more-or-less at level of coronoid apex; (1) extends beyond a point 30% of distance from coronoid apex to anterior edge of articular fossa.

64. Posterior mylohyoid foramen (Frost and Etheridge, 1989): (0) on medial face of mandible; (1) on ventral or ventrolateral face of mandible.

65. Retroarticular fossa: (0) well developed, occupies space greater than half the size of articular surface; (1) reduced, occupies less than half the size of articular surface. *Urostrophus* and *Polychrus* are coded as ''0'', but the condition they exhibit approaches ''1''.

66. Pterygoid teeth (Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989): (0) present; (1) absent. In addition to pterygoid teeth, polychrotids variably possess palatine teeth. Frost and Etheridge (1989) coded all polychrotids as possessing palatine teeth, excepting *Polychrus*. This is in error inasmuch as *Anisolepis* and *Urostrophus* (intraspecifically variably) lack palatine teeth, and the only *Pristidactylus* for which we have adequate samples (*P. achalensis*) is also variable as are all species of *Enyalius. Chamaeleolis* has palatine teeth, but *Anolis* does not. Therefore, widespread intraspecific variation and small sample sizes make us uncomfortable with coding palatine teeth or considering them as evidence for relationships.

67. Marginal teeth (Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989): (0) tricuspid with sides varying from parallel to moderately flared; (1) tapered blunt crown with reduced lateral cusps; (2) slender, sharp crown with reduced lateral cusps. Characterization of states within observed variation is made difficult by intraspecific and interindividual variation and many sources of variation. We treat this set of characters as nonadditive because we lack a compelling theory of transformation.

Postcranial Skeleton

68. Clavicle (Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989): (0) broad, with blade forming a sharp angle; (1) slender, with no distinctive lateral angular blade. *Diplolaemus* has its clavicle a little less flared than the rest of the leiosaurs, but not approaching condition 0.

69. Insertion of clavicle (Lang, 1989; Frost and Etheridge, 1989): (0) on suprascapula, although may contact scapula; (1) on scapula away from suprascapular margin.

70. Sternum, anterior extent (Frost and Etheridge, 1989): (0) sternum does not approach junction of posterior and lateral processes of interclavicle closely for more than 50% of length of anterior process anterior to the lateral horns of sternum; (1) sternum approaches junction of lateral and posterior processes of interclavicle closely.

71. Sternum, median sternal fontanelle (Frost and Etheridge, 1989): (0) absent; (1) median. The taxa here coded as having a median sternal fontanelle were coded as *not* having a median sternal fontanelle by Frost and Etheridge (1989), because of the difficulty of coding across all iguanian taxa. The apomorphy in that case was limited to the phrynosomatid condition of a very large median fontanelle. In this case the fontanelle is considerably smaller though definitely present.

72. Scapular fenestra (Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989): (0) absent; (1) present.

73. Posterior coracoid fenestra (Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989; Etheridge and Williams, 1991): (0) absent; (1) present, marginal and weak. Widely open posterior coracoid fenestrae are not found in the polychrotids. However, marginal and weak ones along the edge of the ''window'' where the fenestra ''should'' be are found in the coracoid.

74, 75. Sternal ribs (Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989): (0) four; (1) three, with posterior extremity of sternum not elongated to form parallel rods continuous with xiphisternal rods, and bearing third pair of ribs aticulating via synovial joints; (2) two, with posterior extremity of sternum elongated to form parallel rods continuous with xiphisternal rods, and last pairs of ribs aticulating via synovial joints. Because of intraspecific variation in species of *Anisolepis* and within genera (*Chalarodon* and *Oplurus*) in the Opluridae, this transformation had to be cast in two columns.

76. Postxiphisternal inscriptional ribs (Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989): (0) none midventrally continuous; (1) chameleon-like, with one or more forming midventrally continuous chevrons, even if laterally not confluent with ribs.

77. Postxiphisternal inscriptional chevrons that are attached to dorsal ribs: (0) 1–5; (1) 8–11. Terminal taxa that lack postxiphisternal inscriptional ribs attached to dorsal ribs are coded as unknown.

78. Transverse processes of caudal vertebrae (Etheridge and de Queiroz, 1988): (0) do not extend posteriorly beyond 16; (1) extend beyond 16.

79. Caudal autotomy fracture planes (Etheridge and de Queiroz, 1988; Frost and Etheridge, 1989): (0) present, although occasionally showing ventral fusion; (1) absent.

80, 81. Total caudal vertebrae: (0) 33–44; (1) 46–64; (2) 66–87. Because *Pristidactylus torquatus* varies across the 0–1 boundary it was coded as polymorphic, requiring that the transformation be cast into two columns.

APPENDIX 3

Data Matrix for Morphology

Taxon/Branch	1111111111222222222233333333334444444444555555555566666666667777777777888 12345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012
E. bibroni	0101100010010010101001000201000010120100211011100102?1?1??????????0?0?0?????101010 2
E. bilineatus	0100000010010000101001000000001000120100211011000100011110010001000100010100100110
E. boulengeri	0100100011010020101001000000000001100000211011000100011110010001000100010100100010 1
E. brasiliensis	0100100011010020101001000100000001100000211011000100011110010001000100010100100010 1
E. catenatus	0101100011010020101001000100000001120100211011000100011110010001000100010100100010
E. iheringii	0100100011010020101001000100001002120100211011000100011110010001000100010100100100 1 1
E. leechii	0100100011010020101001010000000002100000211221000100011110010001000100000100100110
E. perditus	0100100011010020101001000000000001120100211011000100011110010001000100010100100010 1
E. pictus	0101100010010010101001000201000001120100211011000100011110010001000100010100100010 2
L. catamarcensis	2002100010000020110001011101001012200000111011101100110101110001010100010100100100 2
L. paronae	20?2100010000020110001031100001012200000111011101100010101110001010100010100101100
L. bellii	0002100010000020110001011101011010201100111011101100100101110001010100010100101100 1 2
Diplolaemus	0002000010000003100001021201011010221100011011100100000101110001011100010100100000 1 1
P. achalensis	0002000010000001100001021201010010222100111010010100010101110001010000010100101 0?? 1 1 2
P. alvaroi	0002000010000001100001011201010010122100111010110 10??0?????????????1??0?????1??0??
P. casuhatiensis	0002100010000001100001021201010010212100111010010100010101111001?10100010100100000
P. fasciatus	0002100010000001100001021201010010132100011010010 10??1?1??????????????????????10?0??
P. scapulatus	0002100010000003100001021201010010222100111010010100010101110001010100010100101000
P. torquatus	0002000010000001100001011201010010122100111010010100010111001000101010001010010100 1 1 2 1 2
P. valeriae	0002000010000001100001021201010010122100110?1001010??0?????????????1??0?????1??0?? 1
P. volcanensis	0002000010000011000001021201010010122100110?1?110100000111?10001000000010100 10?0??
U. gallardoi	0002000010000010100000021201011100020000011011100100011100010001001000010100100110 2
U. vautieri	0001000010000011100000021201011100020000011011100100011100010001000000000100100110
A. grilli	0000000010000000100001020000001101020000111011100100011101110001000200010100101111 1 1
A. longicauda	0000000010000000100101020000101101020000111011100100011101110001000000000100101111 1
A. undulata	0000000010000001100000020000101?0102000011101110010000110111000100000000110101111
P. acutirostris	1013111110111012000100121010001000130001000?0110010111110011100010001110001111 0111 1
P. femoralis	0013110110111012000100120211001000130001000?0100010011110001100010001011001111 0111
P. gutturosus	0010111110111112000101221312001012130001000?0100011011110001100010001010001111 0111
P. peruvianus	0010111110111112000121200312001002130001000?0?000111111100011000100011100011110111 2
P. liogaster	0010111110111212000111220311001002130001000?0100011011110001100010001110001111 0111 1 1

APPENDIX 3—(*Continued*)

Taxon/Branch	1111111111222222222233333333334444444444555555555566666666667777777777888 12345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012
P. marmoratus	00101111101112120001112203120010121300010000?0110011011110001100010001110101111011 1
A. carolinensis	00121000100110221001012202010010020200101111100001000111011011111000001000111000 10
A. fuscoauratus	00121000100100201001012202010010020200102111100001000011011011111010101000111010 10
A. ortonii	00120000100100231001012202010110020200102111100001000011011011111010111000111000 10
A. meridionalis	00120000100110221001012200000010020200102111100001000011011011111010001000111010 10
A. roquet	00120000100100221001012201010110021200102111100001000011011011111010001000111000 10
A. equestris	00110000100101201001012002110100000200101111100001000111000011111011101000111000 00
A. vermiculatus	00121000100100201000012101000000021200102111100001000111001011111000011000111000 10 2
Opluridae	00020000000000021000000000000000010000001111001000000000100100010000000010001000 10 2 1 1 1 1 1
Leiocephalus	00020000000000030001000000000010000000000 10?001000000000000110010000000010100?0010 1 1
Corytophanidae	00000??000000020100001000?0000100201000021 0?001001000000000100000000000000000?0010 1 1 11 1
Scleroglossa	0000???0100000?3??000102??010?000?000?00?00?0?100?0000?0?001?????00?000??0000??000

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♾ This paper meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).

APPENDIX 4

Summary of Evidence on Each Stem (Terminal Taxon or Internal Branch)

Terminal taxa and internal branch numbers are shown in figure 5. ''Morphological character'' numbers correspond to the character numbers listed in appendix 2. ''Ancestral state'' is the condition of the character in the stem antecedent to the referenced terminal taxon or internal branch; the ''Descendant state'' in that taxon or stem is also noted. The ''Molecular changes'' column shows the number of different kinds of molecular changes along the referenced stem or terminal taxon. Asterisks indicate that characters (molecular or morphological) are ''Definite'' (i.e., placed on the stem or terminal taxon regardless of optimization).

Terminal taxon or internal branch	Morphological character	Ancestral state	Descendant state	Molecular changes	Definite
41	41	{01}	1		
	80	{01}	1		
				Transversions = 57	*
				Transitions = 64	*
				Deletions = 29	*
				Insertions = 13	*
				Ambiguous changes = 57	
Leiocephalus barahonensis	3	{02}	2		
	8	{01}	0		
	16	{01}	0		
	19	0	1		*
	21	{01}	0		
	23	2	0		*
	30	{01}	1		
	60	{01}	1		
	74	0	1		*
				Transversions = 31	*
				Transitions = 31	*
				Insertions = 6	*
				Deletions = 5	*
				Ambiguous changes = 57	
40	15	3	{023}		
	16	{01}	1		
	42	0	{01}		
	76	0	1		*
				Transversions = 16	*
				Transitions = 12	*
				Insertions = 4	*
				Deletions = 1	*
				Ambiguous changes = 41	
Oplurus cychlurus	3	{02}	2		
	8	{01}	0		
	15	{023}	2		
	21	{01}	0		
	30	{01}	0		
	33	0	1		*
	42	{01}	1		
	56	0	1		*
				Transversions = 28	*
				Transitions = 19	*
				Insertions = 10	*
				Deletions = 1	*
				Ambiguous changes = 51	

APPENDIX 4—(*Continued*)

Terminal taxon or internal branch	Morphological character	Ancestral state	Descendant state	Molecular changes	Definite
26	15	{023}	{02}		
	21	{01}	1		
	25	0	{012}		
	30	{01}	1		
	35	0	2		*
	49	0	1		*
	53	0	1		*
	55	0	{01}		
	72	1	0		*
	79	0	{01}		
				Transversions = 12	*
				Transitions = 7	*
				Insertions = 2	*
				Deletions = 6	*
				Ambiguous changes = 63	
39	14	0	2		*
	25	{012}	{0123}		
	33	0	2		*
	63	1	{01}		
				Transversions = 7	*
				Transitions = 8	*
				Insertions = 6	*
				Ambiguous changes = 48	
Basiliscus basiliscus	3	{02}	{01}		
	8	{01}	0		
	15	{02}	0		
	23	2	0		*
	27	1	0		*
	35	2	1		*
	42	{01}	0		
	55	{01}	0		
	60	{01}	0		
	63	{01}	0		
	76	1	0		*
				Transversions = 29	*
				Transitions = 29	*
				Insertions = 8	*
				Deletions = 1	*
				Ambiguous changes = 26	
32	2	0	1		*
	4	0	1		*
	8	{01}	1		
	11	0	1		*
	19	0	{01}		
	22	0	{12}		*
	46	1	0		*
	54	0	1		*
	55	{01}	1		
	60	{01}	1		
	64	0	1		*
	70	0	1		*
	74	0	1		*
	75	0	1		*

APPENDIX 4—(*Continued*)

Terminal taxon or internal branch	Morphological character	Ancestral state	Descendant state	Molecular changes	Definite
32 (*continued*)				Transversions = 14	*
				Transitions = 8	*
				Insertions = 2	*
				Deletions = 3	*
				Ambiguous changes = 32	
38	3	{02}	2		
	38	0	1		*
	42	{01}	1		
	44	0	1		*
	58	0	1		*
	59	1	0		*
	61	0	1		*
	62	0	1		*
	63	{01}	1		
	79	{01}	0		
				Ambiguous changes = 85	
Anolis vermiculatus	15	{02}	0		
	19	{01}	0		
	25	{0123}	1		
	27	1	0		*
	30	1	0		*
	69	0	1		*
33	19	{01}	1		
	25	{0123}	{012}		
	57	0	1		*
				Ambiguous changes = 106	
36	4	1	{01}		
	53	1	0		*
	66	0	1		*
				Transversions = 13	*
				Transitions = 11	*
				Insertions = 4	*
				Deletions = 4	*
				Ambiguous changes = 26	
37	4	{01}	0		
	15	{02}	2		
				Transversions = 10	*
				Transitions = 7	*
				Insertions = 2	*
				Ambiguous changes = 15	
Anolis roquet	25	{012}	1		
	29	0	1		*
	34	0	1		*
				Transversions = 16	*
				Transitions = 41	*
				Insertions = 4	*
				Deletions = 3	*
				Ambiguous changes = 11	

APPENDIX 4—(*Continued*)

Terminal taxon or internal branch	Morphological character	Ancestral state	Descendant state	Molecular changes	Definite
Anolis meridionalis	12	0	1		*
	25	{012}	0		
	27	1	0		*
	78	0	1		*
				Transversions = 21	*
				Transitions = 34	*
				Insertions = 6	*
				Deletions = 6	*
				Ambiguous changes = 11	
34	15	{02}	0		
	25	{012}	2		
	68	0	1		*
				Tranversions = 9	*
				Transitions = 15	*
				Insertions = 3	*
				Deletions = 3	*
				Ambiguous changes = 13	
35	4	{01}	0		
	29	0	1		*
				Ambiguous changes = 42	
Anolis equestris	3	2	1		*
	13	0	1		*
	23	2	0		*
	26	0	1		*
	30	1	0		*
	33	2	0		*
	40	2	1		*
	53	0	1		*
	57	1	0		*
	58	1	0		*
	67	0	1		*
	80	1	0		*
Anolis ortonii	15	0	3		*
	69	0	1		*
				Ambiguous changes = 55	
Anolis fuscoauratus	4	{01}	1		
	78	0	1		*
				Transversions = 21	*
				Transitions = 37	*
				Insertions = 5	*
				Deletions = 5	*
				Ambiguous changes = 12	
Anolis carolinensis	12	0	1		*
	15	{02}	2		
	25	{012}	2		
				Transversions = 36	*
				Transitions = 33	*
				Insertions = 7	*
				Deletions = 3	*
				Ambiguous changes = 13	

APPENDIX 4—(*Continued*)

Terminal taxon or internal branch	Morphological character	Ancestral state	Descendant state	Molecular changes	Definite
30	3	{02}	{03}		
	5	0	1		*
	6	0	{01}		
	7	0	1		*
	10	0	1		*
	12	0	1		*
	14	2	1		*
	15	{02}	2		
	16	1	0		*
	19	{01}	1		
	25	{0123}	{023}		
	26	0	1		*
	35	2	3		*
	39	0	1		*
	40	{12}	0		*
	41	1	0		*
	42	{01}	0		
	45	0	1		*
	52	0	1		*
	63	{01}	0		
	68	0	1		*
	77	0	1		*
	79	{01}	1		
	81	0	1		*
				Transversions = 18	*
				Transitions = 12	*
				Insertions = 5	*
				Deletions = 3	*
				Ambiguous changes = 38	
31				Transversions = 5	*
				Transitions = 9	*
				Insertions = 1	*
				Deletions = 1	*
				Ambiguous changes = 14	
Polychrus gutturosus	3	{03}	0		
	6	{01}	1		
	13	0	1		*
	24	0	1		*
	25	{023}	3		
	27	1	2		*
	32	0	1		*
	50	0	1		*
				Transversions = 19	*
				Transitions = 23	*
				Insertions = 1	*
				Ambiguous changes = 20	

APPENDIX 4—(*Continued*)

Terminal taxon or internal branch	Morphological character	Ancestral state	Descendant state	Molecular changes	Definite
Polychrus femoralis	3	{03}	3		
	6	{01}	0		
	21	1	0		*
	25	{023}	2		
	33	2	0		*
	71	0	1		*
				Transversions = 12	*
				Transitions = 37	*
				Insertions = 4	*
				Deletions = 1	*
				Ambiguous changes = 18	
27	6	{01}	1		
	51	0	{01}		
	69	0	1		*
				Transitions = 4	*
				Deletions = 1	*
				Ambiguous changes = 17	
29	3	{03}	0		
	13	0	{12}		*
	20	0	1		*
	25	{023}	3		
	50	0	1		*
				Ambiguous changes = 66	
Polychrus liogaster	51	{01}	0		
28	27	1	2		*
				Ambiguous changes = 79	
Polychrus marmoratus	32	0	1		*
	46	0	1		*
	72	0	1		*
Polychrus peruvianus	20	1	2		*
	23	2	0		*
	51	{01}	1		
Polychrus acutirostris	0	0	1		*
	3	{03}	3		
	21	1	0		*
	24	0	1		*
	25	{023}	0		
	27	1	0		*
	33	2	0		*
	46	0	1		*
	51	{01}	1		
	58	0	1		*
				Transversions = 31	*
				Transitions = 30	*
				Insertions = 3	*
				Deletions = 6	*
				Ambiguous changes = 12	

APPENDIX 4—(*Continued*)

Terminal taxon or internal branch	Morphological character	Ancestral state	Descendant state	Molecular changes	Definite
14	8	{01}	1		
	15	{02}	0		
	37	0	{01}		
	42	{01}	1		
	43	1	0		*
	44	0	1		*
	45	0	1		*
	55	{01}	1		
	60	{01}	0		
	67	0	{01}		
	71	0	1		*
	73	0	1		*
				Transversions = 20	*
				Transitions = 23	*
				Insertions = 2	*
				Deletions = 4	*
				Ambiguous changes = 34	
17	3	{02}	2		
	4	0	{01}		
	24	0	1		*
	29	0	{01}		
	32	0	1		*
	34	{01}	2		*
	57	0	1		*
	58	0	1		*
	65	0	1		*
	67	{01}	1		
	78	0	1		*
	80	1	0		*
				Transversions = 8	*
				Transitions = 5	*
				Insertions = 2	*
				Ambiguous changes = 26	
18	15	0	3		*
	25	{012}	2		
	29	{01}	1		
	37	{01}	1		
	79	{01}	0		
				Transversions = 5	*
				Transitions = 9	*
				Ambiguous changes = 13	
25	4	{01}	1		
	30	1	0		*
	36	1	2		*
	45	1	0		*
	46	1	0		*
	47	0	1		*
				Transversions = 21	*
				Transitions = 21	*
				Insertions = 4	*
				Deletions = 4	*
				Ambiguous changes = 13	

APPENDIX 4—(*Continued*)

Terminal taxon or internal branch	Morphological character	Ancestral state	Descendant state	Molecular changes	Definite
Pristidactylus scapulatus					
19	15	3	1		*
24					
Pristidactylus casuhatiensis	35	2	1		*
	60	0	1		*
22	34	2	1		*
	56	0	1		*
	58	1	{01}		
23	57	1	{01}		
Pristidactylus torquatus	57	{01}	0		
	58	{01}	0		
Pristidactylus fasciatus	35	2	3		*
	40	1	0		*
21	4	1	0		*
	42	1	{01}		
	53	1	{01}		
	65	1	{01}		
Pristidactylus valeriae	42	{01}	0		
20	46	0	1		
	53	{01}	0		
Pristidactylus volcanensis	14	0	1		*
	16	1	0		*
	42	{01}	0		
	65	{01}	0		
	67	1	0		*
Pristidactylus alvaroi	23	2	1		*
	42	{01}	1		
Pristidactylus achalensis	67	1	0		*
Diplolaemus darwini	4	{01}	0		
	40	1	0		*
	53	1	0		*
	66	0	1		*
				Transversions = 18	*
				Transitions = 32	*
				Insertions = 4	*
				Deletions = 1	*
				Ambiguous changes = 14	
16	4	{01}	1		
	14	0	2		
	17	0	1		
	23	2	{12}		
	25	{012}	1		
	35	2	{02}		
	48	0	1		
	52	0	{01}		
	79	{01}	1		
				Ambiguous changes = 41	

APPENDIX 4—(*Continued*)

Terminal taxon or internal branch	Morphological character	Ancestral state	Descendant state	Molecular changes	Definite
Leiosaurus bellii	23	{12}	1		
	29	{01}	1		
	37	{01}	1		
	52	{01}	1		
	53	1	0		*
15	0	0	2		*
	29	{01}	0		
	33	0	2		*
	35	{02}	0		
	37	{01}	0		
				Ambiguous changes = 52	
Leiosaurus paronae	23	{12}	3		*
	27	1	0		*
	52	{01}	0		
				Transversions = 6	*
				Transitions = 16	*
				Insertions = 2	*
				Ambiguous changes = 6	
Leiosaurus catamarcensis	52	{01}	1		
	78	1	0		*
				Tranversions = 9	*
				Transitions = 13	*
				Insertions = 1	*
				Ambiguous changes = 7	
9	27	1	{01}		
	54	0	1		*
	79	{01}	1		
				Transversions = 8	*
				Transitions = 9	*
				Insertions = 1	*
				Deletions = 3	*
				Ambiguous changes = 26	
11	31	0	1		*
	37	{01}	0		
	67	{01}	0		
				Transversions = 7	*
				Transitions = 3	*
				Ambiguous changes = 28	
12	3	{02}	0		
	25	{012}	0		
	27	{01}	0		
	28	0	{01}		
	33	0	1		*
	57	0	1		*
	58	0	1		*
	74	0	{01}		
	78	0	1		*
	81	0	1		*
				Ambiguous changes = 71	

APPENDIX 4—(*Continued*)

Terminal taxon or internal branch	Morphological character	Ancestral state	Descendant state	Molecular changes	Definite
13	28	{01}	1		
	71	1	0		*
				Ambiguous changes = 84	
Anisolepis undulata	15	0	1		*
	21	1	0		*
	53	1	0		*
	74	{01}	1		
Anisolepis longicauda	19	0	1		*
Anisolepis grilli	67	0	2		*
10	3	{02}	{012}		
	14	0	1		*
	21	1	0		*
	24	0	1		*
	25	{012}	2		
	27	{01}	1		
	29	0	1		*
	40	1	0		*
				Ambiguous changes = 74	
Urostrophus vautieri	3	{012}	1		
	15	0	1		*
	71	1	0		*
Urostrophus gallardoi	3	{012}	2		
	66	0	1		*
				Ambiguous changes = 85	
8	1	0	1		*
	3	{02}	0		
	11	0	1		*
	18	0	1		*
	23	2	0		*
	27	{01}	0		
	37	{01}	1		
	40	1	2		*
	46	1	0		*
	56	0	1		*
	67	{01}	1		
				Transversions = 5	*
				Transitions = 7	*
				Insertions = 2	*
				Ambiguous changes = 14	
Enyalius bilineatus	25	{012}	0		
				Transversions = 15	*
				Transitions = 27	*
				Insertions = 2	*
				Deletions = 3	*
				Ambiguous changes = 17	

APPENDIX 4—(*Continued*)

Terminal taxon or internal branch	Morphological character	Ancestral state	Descendant state	Molecular changes	Definite
7	4	0	1		*
	9	0	1		*
	14	0	2		*
	33	0	{012}		
				Ambiguous changes = 77	
Enyalius iheringii	25	{012}	1		
	33	{012}	2		
3	30	1	0		*
	33	{012}	1		
	79	1	0		*
				Ambiguous changes = 102	
6	25	{012}	0		
Enyalius perditus					
4	35	2	0		*
	37	1	0		*
5					
Enyalius leechii	23	0	1		*
	33	1	2		*
	43	0	2		*
	44	1	2		*
	71	1	0		*
	79	0	1		*
Enyalius brasiliensis	25	0	1		*
Enyalius boulengeri					
2	3	0	1		*
Enyalius catenatus	25	{012}	1		
1	9	1	0		*
	25	{012}	2		
	27	0	1		*
Enyalius pictus					
Enyalius bibroni	32	0	1		*
	33	1	0		*
	46	0	1		*
	78	0	1		*
Eumeces egregius	3	{02}	0		
	8	{01}	1		
	21	{01}	1		
	30	{01}	0		
	41	{01}	0		
	80	{01}	0		