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Phylogenetics of the Lizard Genus *Tropidurus* (Squamata: Tropiduridae: Tropidurinae): Direct Optimization, Descriptive Efficiency, and Sensitivity Analysis of Congruence Between Molecular Data and Morphology

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By use of the technique of direct optimization the phylogenetics of the cis-Andean lizard genus *Tropidurus* were examined on the basis of both molecular (ca. 1.04 kb of sequences from 12S rDNA, valine tDNA, and 16S rDNA) and morphological (93 characters) data. Although equal weighting of all parsimony cost functions logically must maximize descriptive efficiency and explanatory power of all evidence, a sensitivity analysis demonstrated that equal weighting of indels, transitions, transversions, and morphological change provided the most congruent solution between the molecular and the morphological data partitions. The position of *Uranoscodon* is resolved as the sister taxon of the remaining members of the Tropidurinae. *Plica, Uracentron,* and *Strobilurus,* previously considered synonyms of *Tropidurus,* are resurrected; the group of these three genera form the sister taxon of the former *Tropidurus nanuzae* group (herein named *Eurolophosaurus*) plus *Tropidurus* sensu stricto (composed of the *T. bogerti, T. semitaeniatus, T. spinulosus,* and *T. torquatus* groups, herein diagnosed). © 2001 Elsevier Science

INTRODUCTION

From 1931 (Burt and Burt, 1931) until 1979 (Vanzolini and Gomes, 1979), the systematics and taxonomy of *Tropidurus* were very stable, indeed, nearly moribund. From 1979 to the present, however, effort on the elucidation of the systematics of the taxon has increased, seemingly exponentially. In 1979, Vanzolini and Gomes started the dismemberment of the former "*T. torquatus*," a beginning upon which Rodrigues (1981, 1984, 1986, 1987, 1988a, b) built, with the recognition of many resurrected and newly described species of the *T. torquatus* group from Brazil and all three species of the newly recognized *T. nanuzae* group. Etheridge and de Queiroz (1988) provided the first estimate of the phylogeny of the group within the context of broader issues of iguanian relationships, and Frost (1992) subsequently provided the first detailed phylogenetic analysis of the *Tropidurus* group, in which he placed the cis-Andean (Amazonian) genera *Plica, Strobilurus,* and *Uracentron* into *Tropidurus* to prevent the latter's paraphyly. Frost also placed the former trans-Andean and Galapagos species of *Tropidurus* (the *T. occipitalis* and *T. peruvianus* groups of Dixon and Wright, 1975) into *Microlophus* and *Plesiomicrolophus.* That analysis was based entirely on morphological characters, and only very weak resolution was obtained among the species of the paraphyletic *T. torquatus* group. Subsequently, Harvey and Gutberlet (1988, 2000) described three additional species of *Tropidurus* and suggested rearrangements in the cladogram of the Tropidurini on the basis of new evidence from microscopic scale surface structure, including the synonymy of *Plesiomicrolophus* with *Microlophus.* They further suggested that *Uranoscodon,* previously considered by Frost (1992) to be the sister taxon of *Tropidurus* plus *Microlophus,* was likely deeply imbedded in the *Tropidurus* clade as the sister taxon of *T. umbra,* a species of inarguably similar external appearance to *Uranoscodon* (see figs. 38 and 44 of Frost, 1992). Nevertheless, they did not make any taxonomic recommendations based on this result because of serious character conflict within the lines of morphological evidence.

In an attempt to resolve the evidentiary issues of *Tropidurus* cladogeny we simultaneously analyze the morphological characters from Frost (1992), with corrections and additional characters noted here and by others, including those of Harvey and Gutberlet (2000), along with mtDNA sequence data for most of the species of *Tropidurus.*

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We employ the iguanian taxonomy suggested by Frost *et al.* (2001) and will also use the following collective terms: (1) *T. nanuzae* group [*T. amathites, T. divaricatus,* and *T. nanuzae*]; (2) *T. plica* group [the species formerly placed in *Strobilurus* (*T. strobilurus*), *Uracentron* (*T. azureus* and *T. flaviceps*), and *Plica* (*T. lumarius, T. plica,* and *T. umbra*)]; (3) *T. semitaeniatus* group [*T. helenae, T. pinima,* and *T. semitaeniatus*]; (4) *T. spinulosus* group [*T. callathelys, T. guarani, T. melanopleurus, T. spinulosus,* and *T. xanthochilus*]; and (5) *T. torquatus* group [*T. chromatops, T. cocorobensis, T. erythrocephalus, T. etheridgei, T. hispidus, T. hygomi, T. insulanus, T. itambere, T. montanus, T. mucujensis, T. oreadicus, T. psammonastes,* and *T. torquatus*].

MATERIALS AND METHODS

Morphological Data

Skeletons, alcoholics, hemipenes, and cleared and double-stained specimens of most ingroup taxa were examined (see Appendix 1 for specimens beyond those listed by Frost, 1992) for interspecific variation that could be hypothesized to be apomorphies relative to the outgroups. Most of these characters were previously discussed in detail by Frost (1992) and will not be further discussed here, except where specifically warranted. Species excluded from this part of the analysis were *T. helenae* and *T. pinima,* because for purposes of the analysis of morphology they are identical to *T. semitaeniatus* and we lack pertinent molecular data. In addition, those characters discussed by Harvey and Gutberlet (2000) and a few other features noted by other authors were included where possible. Comparison of specimens yielded 93 characters (numbered 0–92 in Appendix 2 to allow easy interpretation of our results).

In several cases noted below, Harvey and Gutberlet (2000) treated additive multistate characters of Frost (1992) as nonadditive or partially additive (as discussed by Campbell and Frost, 1993). We have retained the original coding additivity where developmental intermediacy justified it, especially in light of the fact that the unordering of multistates did not affect the topology of resultant trees in Harvey and Gutberlet's analysis. We have also noted with the individual character descriptions the implied characters that were rendered transparent to the parsimony measure by Harvey and Gutberlet's treatment.

Harvey and Gutberlet (2000) also included several characters of frequency (62, 74, and 75 in our list). However, for purposes of simplicity and to provide the strongest possible effect in the analysis, we applied to the polymorphic characters of Harvey and Gutberlet (2000), as appropriate, "unscaled" and "any instance" coding (sensu Campbell and Frost, 1993). (To foreshadow our results, this made no difference in the analysis.)

Molecular Data

Mitochondrial DNA sequences were obtained for 28 ingroup and outgroup taxa. Mitochondrial genes encoding the 12S rDNA, the valine tDNA, and the 5′ end of the 16S rDNA were amplified with 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 with 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 with the Big Dye Terminator Cycle Sequencing Kit with Ampli*Taq* FS (Perkin–Elmer) and an ABI PRISM 377 DNA Sequencer (Perkin–Elmer) following manufacturer's specifications.

All sequences have been deposited with GenBank (see Appendix 1 for accession numbers). We were not able to obtain DNA samples for *Microlophus occipitalis, T. chromatops, T. guarani, T. helenae, T. insulanus, T. melanopleurus, T. pinima,* or *T. xanthochilus.* Because *T. semitaeniatus, T. pinima,* and *T. helenae* form such an obviously tight monophyletic group, *T. pinima* and *T. helenae* were excluded from the analysis. In the case of the remaining species, these were included but coded as unknown for the molecular component of the data.

Choice of Out-Taxa

Out-taxa used were selected on the basis of their suspected abilities to be potential falsifiers of *Tropidurus* monophyly, as inferred from previous phylogenetic studies (Frost and Etheridge, 1989; Frost, 1992): (1) *Stenocercus* (inducted for purposes of morphology from species cited in Frost (1992) and with the molecular evidence tied to this hypothetical taxon being derived from *Stenocercus roseiventris*) and (2) *Leiocephalus* (coded for morphology as the ancestor of *Leiocephalus* as hypothesized by Pregill, 1992) with the molecular evidence being derived from *Leiocephalus barahonensis.*

Analytical Methods

General methods. The general analytical method employed is a parsimony analysis (Kluge and Farris, 1969; Farris, 1983; Farris and Kluge, 1985, 1986). 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 (Hig-

gins *et al.,* 1992), MALIGN (Wheeler and Gladstein, 1994), or least satisfactorily because it is not repeatable, "by eye"], optimizes cost functions (i.e., the cost to the parsimony measure of changes by transversions, transitions, and insertions/deletions) on an implied tree. In other words, there is no such thing as a tree-free sequence alignment procedure and any procedure that is not explicit on the material being maximized or minimized by its optimality criterion is not repeatable or consistent. When the aligned molecular data are combined with another data set, such as from morphology, the final tree obtained may actually have a more efficient alignment available for that particular summary tree than that allowed by the initial (i.e., optimal for the molecular-only partition) alignment. In other words, under the "distortion" caused by nonmolecular data to the implied tree of aligned sequences, solutions more parsimonious than those allowed by the initial alignment estimate of site homologies may be available (Wheeler, 2000). This additional analytical step of alignment 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, 1983) that is not appropriate if we are really 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, 2001), which allows morphological changes to be simultaneously optimized with the molecular classes of change (transversions, transitions, insertions–deletions [indels]) on multiple trees. This simultaneous analysis allows morphological characters to influence alignment optimization directly, thereby allowing more efficient solutions for all of the transformations implied by separate alignment and analysis. Put another way, POY optimizes cost functions for all of the data onto various topologies, calculates total parsimony costs for all cost functions, and employs the congruence test to simultaneously select the hypotheses that best explain available observations from the finite (albeit very large) pool of competing tree topologies and DNA homologies. POY therefore has the capacity to find more parsimonious trees than the procedure of alignment followed by total-evidence analysis. [For brief documentation, a summary of this method, and access to POY, related programs, and command scripts, see ftp.amnh.org/pub/molecular/poy (Janies and Wheeler, 2001).]

Maximum-likelihood approaches have not been employed because these have been demonstrated to converge on parsimony estimates when no general model of evolution is assumed (Tuffley and Steel, 1997; Steel and Penny, 2000) and, more to the point, because we think that the knowledge claims of processes inherent in maximum-likelihood approaches that assume particular models of evolution are severe. 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.

Sensitivity analysis. The majority of contemporary molecular systematics studies employ a priori differential weighting of transversion, transition, and indel costs. This arbitrary arrangement of necessarily unique events into discrete, universal classes is most commonly defended on the grounds that our knowledge of molecular biology indicates that certain kinds of events are more or less probable than others. Whereas this may be so, the statistical probability that a universal class of event may occur in the future is logically unrelated to the assessment of whether or not a particular event did occur in the past. Some workers (e.g., Simmons and Ochoterena, 2000) hold that multiple sequence alignment occurs independent of any tree, which, if true, would allow differential costs to be employed during alignment without it being necessary to invoke the argument that classes really exist in nature [see Frost (2000) for discussion]. However, because automated multiple sequence alignment is tree dependent (Phillips *et al.,* 2000) (as is the procedure of a by-eye tweaking of preliminary Clustal alignments), this line of argumentation fails. Therefore, for epistemological reasons, the only defensible "weighting" scheme for the testing of molecular homologies is equal weighting of all hypothesized transformations, including indels. This approach renders the highest degree of descriptive efficiency and maximizes the explanatory power of all lines of evidence (i.e., characters).

Although we prefer to maximize descriptive efficiency and explanatory power on the basis of equal weighting, a sensitivity analysis is included in this study because many systematists remain unconvinced by the logic of epistemology. Within that paradigm of probabilistic assumptions, it is often argued that transitions are more probable (i.e., observed more frequently) and should therefore deserve a lower cost (or no cost at all, as in transversion parsimony) than transversions. However, no consensus has been reached for the appropriate cost ratio, and an arbitrary choice is required. The only empirical operation designed to attack this problem is sensitivity analysis (Wheeler, 1995), wherein different weighting functions for morphological change, transversions, transitions, and indels can be applied to allow the general exploration of data partitions. In this case various differential weights of alignment cost functions were investigated in a sensitivity analysis to discover at which alignment

cost functions incongruence between the data partitions of morphology and molecules was minimized (Wheeler, 1995). (We do not subscribe to the notion that data partitions are natural classes, but they are used herein solely as heuristics to explore alignment cost functions.) 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 compared to 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; thus, when parameter sensitivity analyses (Wheeler, 1995) are conducted on the same data partitions (as is done in this study), MFES scores are roughly comparable, despite different weighting schemes. [Wheeler and Hayashi (1998) have noted that the MFES may decrease artifactually as weights between partitions become increasingly disproportionate. This renders the test of the 1:1:1:1 ratio of change costs that we prefer apparently more severe.]

Thirteen parameter sets were examined to thoroughly explore the trends in our data. The weights of morphological changes were set so that molecular characters were never upweighted relative to morphology. Some parameter sets were selected to examine transversion parsimony (i.e., transitions were set at 0 cost yielding a transversion:transition ratio of ∞). The ratio of weights among morphology, indels, and transversion or transition weights ranged from 1 to 4. The transversion:transition ratios ranged between 0.5 and 2.

Tree searches. Molecular-only and morphology plus molecular analyses were done in POY, which we implemented on a cluster of 256 UNIX-based work-stations integrated into a parallel virtual machine (Geist *et al.*, 1993). Polymorphic cells were converted to POY-readable symbols in HEN2POY. Multiple Wagner trees were generated through random addition sequences and submitted to a combination of SPR and TBR branch swapping (the default in POY). Although this appears redundant, the way that it is programmed in POY greatly increases search efficiency by the use of SPR to narrow the searches before TBR (W. Wheeler, personal commun.). *Leiocephalus* was kept as the root during all searches with the command-*norandomize-outgroup*. Three commands were employed to reduce error derived from the heuristic operations: *-slop*, *-checkslop*, and *-exact* (Wheeler, 2001). The command *-slop* verifies the length of all cladograms within "*n*" tenths of a percent of the current optimal length during all stages of the search by performing a complete down-pass on those trees. The command *-checkslop* has the same function, but it checks lengths by adding an extra round of TBR swapping, which allows concentration on the TBR stage of the search by employing a higher value for *-checkslop* than for *-slop*. For most analyses, we used *-slop* 5 and *-checkslop* 10. The command *-exact* checks tree length by performing a full Sankoff optimization of the implied alignment whenever a better or equal tree is found.

Bremer values were obtained first by the generation of a group inclusion matrix (with JACK2POY) for the best tree or strict consensus, next by the saving of each column (group) as a separate constraint file in WinClada (Nixon, 1999), and then by the searching in POY for shortest trees that do not include the specified group (command *-disagree*). POY also performs a simultaneous Bremer search (*-bremer*) based on a general constraint file, but it is less exhaustive and can grossly overestimate support. For very large trees, the simultaneous Bremer search can be used as a first pass, and nodes with questionable Bremer values can be reexamined individually more exhaustively.

Trees were visualized in WinClada. Tree lengths were verified by rediagnosis of the binary representation of the best tree(s) in POY and by optimization of the implied alignments onto the respective tree in WinClada (for equal weights) or PHAST (for Sankoff transformations; Goloboff, 1998).

Morphology-only analyses were done in NONA version 2.0 (Goloboff, 1993) spawned from WinClada. Heuristic searches were performed by the submission of Wagner trees generated through random addition sequence to a round of TBR branch swapping and the collapsing of branches of minimum length 0 (default, command *ambiguous-*). Bremer support was estimated in NONA by the search for trees of increasing length and the holding of as many trees as possible (100,000) in memory. Bremer values >3 are only approximate because the large number of trees prohibited completion of the searches.

RESULTS

Morphology-Only Analysis

A parsimony analysis of the morphological data provided six equally parsimonious trees at 235 steps (CI = 0.49; Fig. 1). Under the assumption for purposes of this discussion that a rule of thumb Bremers support value of 6 represents strong evidence, that 3–5 represents moderate evidence, and that 1–2 constitutes weak evidence, we can see that morphology provides strong evidence for the reality of the Tropidurinae (stem A, Fig. 1) and former *Uracentron* (*T. azureus* + *T. flaviceps*) (stem B), but only moderate evidence for *Microlophus* (stem C) and the placement of *T. bogerti* with *T. semitaeniatus* (stem D) as for the group composed of *T. plica* and *T. lumarius* (stem E), species which are quite different from congeners and nearly identical to each other. The association of *T. umbra* with *Uranoscodon superciliosus* (stem F) is supported by all of the mor-

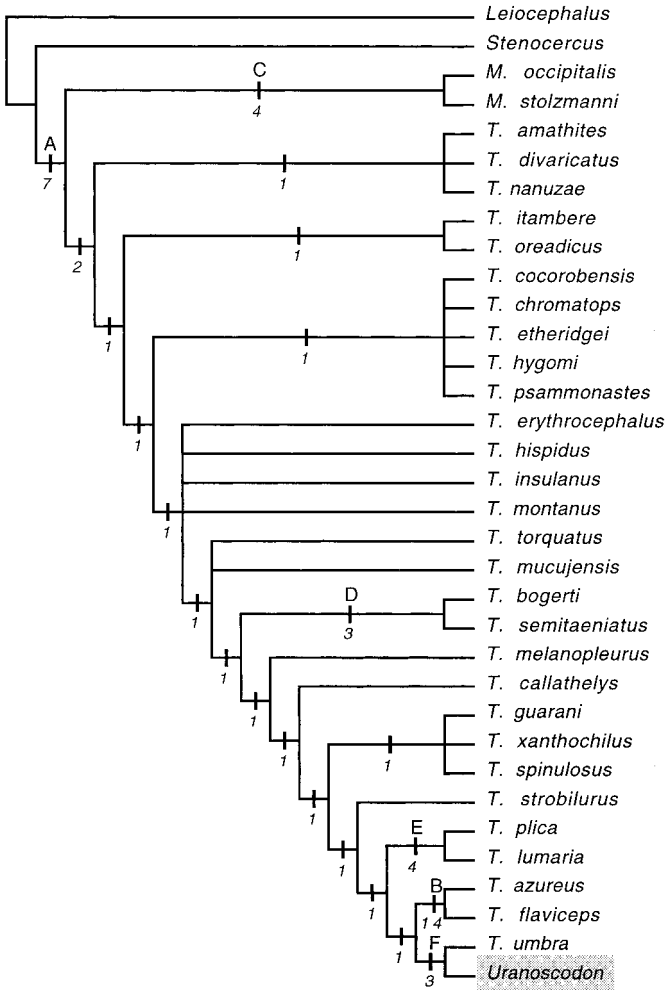

FIG. 1. Tree based on morphology only. Strict tree of six component trees. Length = 235 steps; CI = 0.49. A–F represent internal stems discussed in text. Italic numbers below the stems represent Bremer support.

phological evidence (contra Frost, 1992; Fig. 2), but only moderately.

A comparison with the tree suggested by Harvey and Gutberlet (2000) (Fig. 3) shows broad agreement with this result. (Note that Harvey and Gutberlet treated *T. cocorobensis, T. etheridgei, T. chromatops,* and *T. psammonastes* for purposes of their analysis as identical to *T. hygomi,* treated *T. divaricatus* and *T. amathites* as identical to *T. nanuzae,* and, like us, excluded *T. helenae* and *T. pinima* as identical to *T. semitaeniatus.*) *Uranoscodon* is placed as the sister taxon of *T. umbra,* the Tropidurinae is found to be monophyletic (stem A), and the former *T. torquatus* group is broadly paraphyletic with respect to the *T. spinulosus* group, which in turn is paraphyletic to the group composed of former *Plica* (*T. plica, T. lumarius, T. umbra*), *Strobilurus* (*T. strobilurus*), and *Uracentron* (*T. azureus* and *T. flaviceps*). We find the group *T. callathelys* + *T. melanopleurus* of Harvey and Gutberlet (2000) to be paraphyletic (although the degree of sexual dichromatism shared by these species suggests that this may be wrong), this being due to a difference between these two species in Harvey and Gutberlet's character 78 (our 75), preocular–canthal contact.

Other differences are noted, such as the placement of *T. itambere, T. oreadicus,* and *T. erythrocephalus,* but these differences are due to single characters and all should be considered equivocal inasmuch as the evidence in support of any particular topology within the *T. torquatus* group is weak.

Molecular-Only Analysis

The molecular evidence provided two trees (length = 2274 steps; CI = 0.54) under relative costs of 1:1:1 (transversion cost:transition cost:indel cost) as shown in the consensus tree in Fig. 4. (The reason for reporting just this set of relative cost parameters will be provided in the discussion below of the sensitivity analysis of congruence between the morphology and the molecular data partitions.) As in the morphology-only analysis we arbitrarily considered Bremer support numbers of 1–2 weak evidence, 3–5 moderate evidence, and 6 or greater strong evidence for a particular clade. The salient feature is that the molecular evidence supports strongly the monophyly of the Tropidurinae (Fig. 4, stem A) and the placement of *Uranoscodon* as the sister taxon of the remaining Tropidurinae (Fig. 4, stem B). *Microlophus* is placed as the sister taxon of *Tropidurus* (sensu lato). Other strongly supported

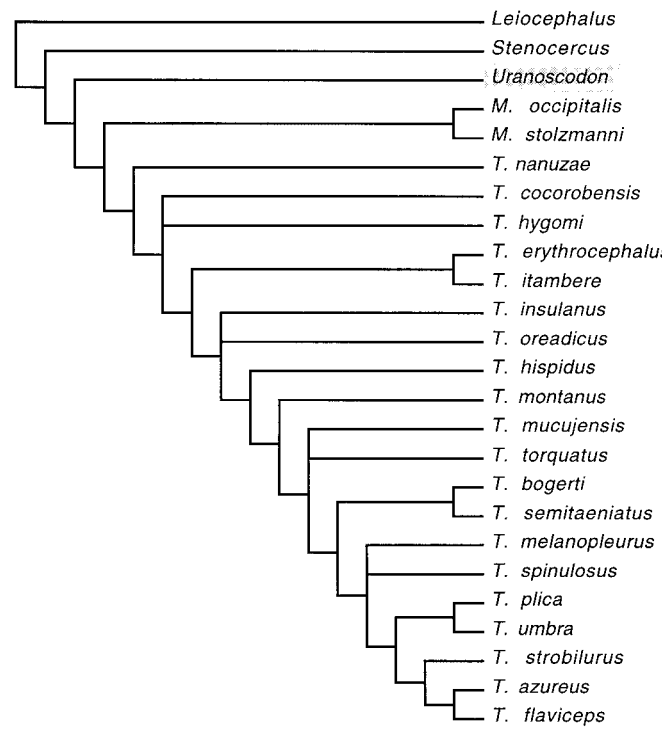

FIG. 2. Tree suggested by Frost (1992).

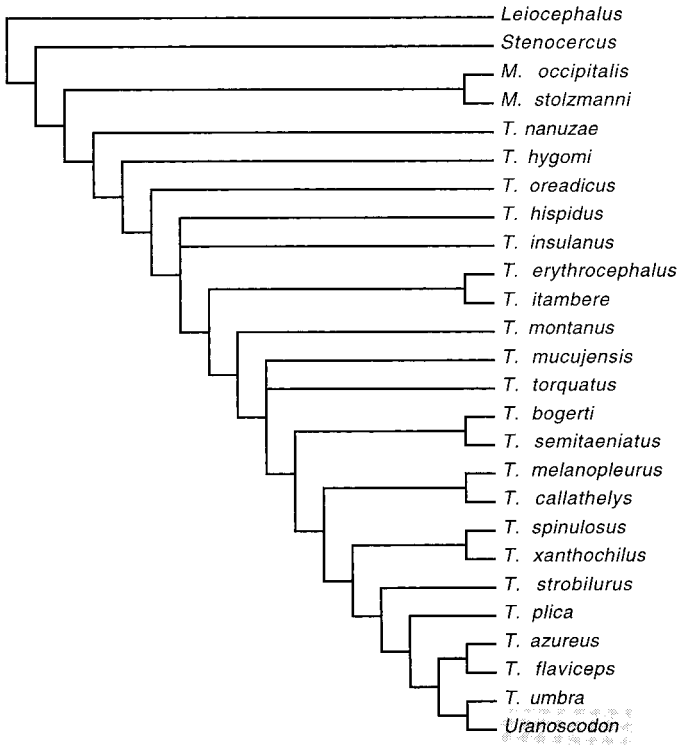

FIG. 3. Tree suggested by Harvey and Gutberlet (2000).

clades include *T. callathelys* and *T. spinulosus* (stem C; *T. melanopleurus, T. guarani,* and *T. xanthochilus* lack molecular data and are not shown in this analysis), *T. plica* plus *T. lumarius* (stem D), the *T. nanuzae* group (stem E), and most stems within the group composed of *T. semitaeniatus* and the *T. torquatus* group (stem F). The most immediate differences between the molecular-only analysis and the morphology-only analysis are (1) the placement of *Uranoscodon,* (2) the position of the *T. nanuzae* group, and (3) the placement of a group composed of *T. callathelys, T. spinulosus, T. bogerti,* and the former members of *Uracentron* (*T. flaviceps*) and *Plica* (*T. umbra, T. plica,* and *T. lumarius*).

The placement of *Uranoscodon* outside of the remainder of the Tropidurinae is well supported in the sense that *Microlophus* + *Tropidurus* has a Bremer support of 6 and this would have to be vitiated to allow *Uranoscodon* to move to a position closer to *T. umbra,* the result from the morphology-only analysis.

The *T. nanuzae* group is placed by the molecular evidence more closely to *T. semitaeniatus* and the *T. torquatus* group (which is obtained as monophyletic by the molecular evidence) than to *T. bogerti* and the *T. spinulosus* and *T. plica* groups. Nevertheless, the Bremer support for this is weak.

Morphological Plus Molecular Data Analysis

Sensitivity analysis. As described above a sensitivity analysis was performed to evaluate congruence between molecular and morphological partitions under various alignment costs. The reason for this is not, as explained above, because we think that congruence between arbitrary data partitions is some kind of criterion of goodness, but rather to evaluate whether there is any reason implied by the available data for the a priori character weighting (such as transversion weighting) that has become so popular, seemingly for little empirical reason. A summary of the results of the analysis are provided in Table 1 and graphically presented in Fig. 5. In this graphic, as the color goes to green (color corresponds to the z axis representing data set congruence as measured by the Mickevich–Farris Extra Steps Index; Mickevich and Farris, 1981) the congruence level among the morphological and molecular data partitions increases. In this case, maximum congruence between the molecular and the morphological partitions is achieved when the ratio of change costs of transversions, transitions, indels, and morphological changes are all equal to one. Because the equally weighted analysis is by far the analysis that shows the most congruence between the molecular and the morphological partitions this will be the only analysis discussed here (and previously in the molecular-only analysis).

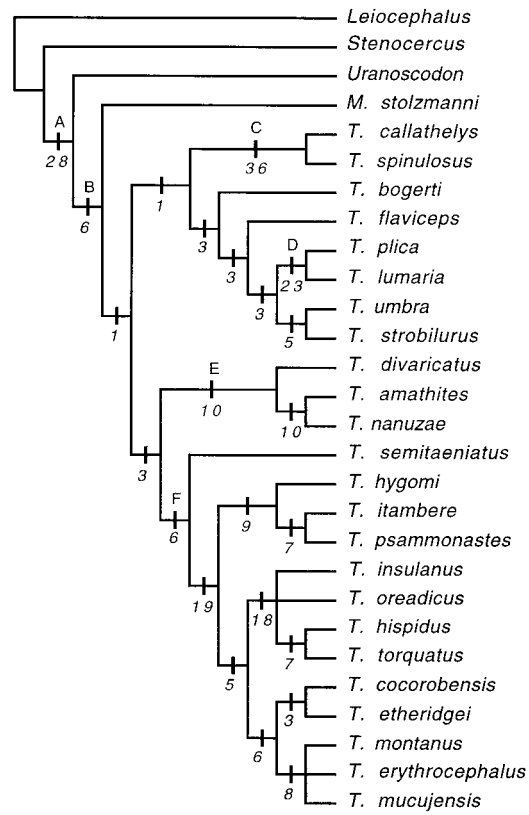

FIG. 4. Tree based on molecular evidence only. Consensus of two trees. Length = 2274 steps; CI = 0.54. A–E represent internal stems discussed in text. Italic numbers below the stems represent Bremer support.

TABLE 1

Numerical Summary of Sensitivity Analysis Composed of 13 Analyses under Different Weighting Regimes

Morph cost	Gap cost	tv cost	ts cost	tv/ts	log 2 tv/ts	Gap/ change	log 2 gap/ change	mm	mol	Morph	MFES
1	1	1	0	∞	∞	1	0	1328	1046	235	0.035391566
1	**1**	**1**	**1**	**1**	**0**	**1**	**0**	**2545**	**2274**	**235**	**0.014145383**
2	1	1	0	∞	∞	1	0	1582	1046	470	0.041719343
2	1	1	1	1	0	1	0	2812	2274	470	0.024182077
2	2	1	0	∞	∞	2	1	1898	1351	470	0.040569020
2	2	1	1	1	0	2	1	3147	2604	470	0.023196695
2	2	1	2	0.5	−1	2	1	4152	3600	470	0.019749518
2	2	2	1	2	1	1	0	3908	3347	470	0.023285568
4	2	1	1	1	0	2	1	3659	2604	940	0.031429352
4	2	2	1	2	1	1	0	4433	3347	940	0.032934807
4	2	1	0	∞	∞	2	1	2401	1351	940	0.045814244
4	4	1	2	0.5	−1	4	2	5220	4114	940	0.031800766
4	4	2	1	2	1	2	1	5084	3982	940	0.031864673

Note. Morph cost, the cost of the making of a morphological character change; gap cost, the cost of the adding of a gap into the sequence; tv cost, the cost of the making of a transversion; ts cost, the cost of the making of a transition; tv/ts, ratio of transversion and transition costs; log 2 tvs/ts, log (base 2) of the transgression cost/transition cost; gap/change, ratio of the gap cost and the maximum cost of tv or ts; log 2 gap/change, log (base 2) of the gap cost/maximum cost of tv or ts change cost; mm, length of the morphological + molecular data on the shortest tree(s); mol, length of molecular data on the shortest tree(s); MFES, Mickevitch–Farris Extra Steps Index (0 = no extra steps; lowest MFES score is in boldface). See Fig. 5.

Results. Figure 6 shows the single most parsimonious tree of all evidence (morphology and molecular partitions) under equal cost functions for the alignment parameters (transversions, transitions, and indels) and morphological changes (length = 2545 steps; CI = 0.52). In this figure the internal taxa are numbered (which corresponds to Appendix 4—a change list by stem) or, if terminal, named. It is notable that half of the stems show strong Bremer support. Moderate support is found on stem 5 (support for former *Plica*), stem 7 (support for *Tropidurus* above the *T. nanuzae* group), stem 24 (the association of *T. xanthochilus* with

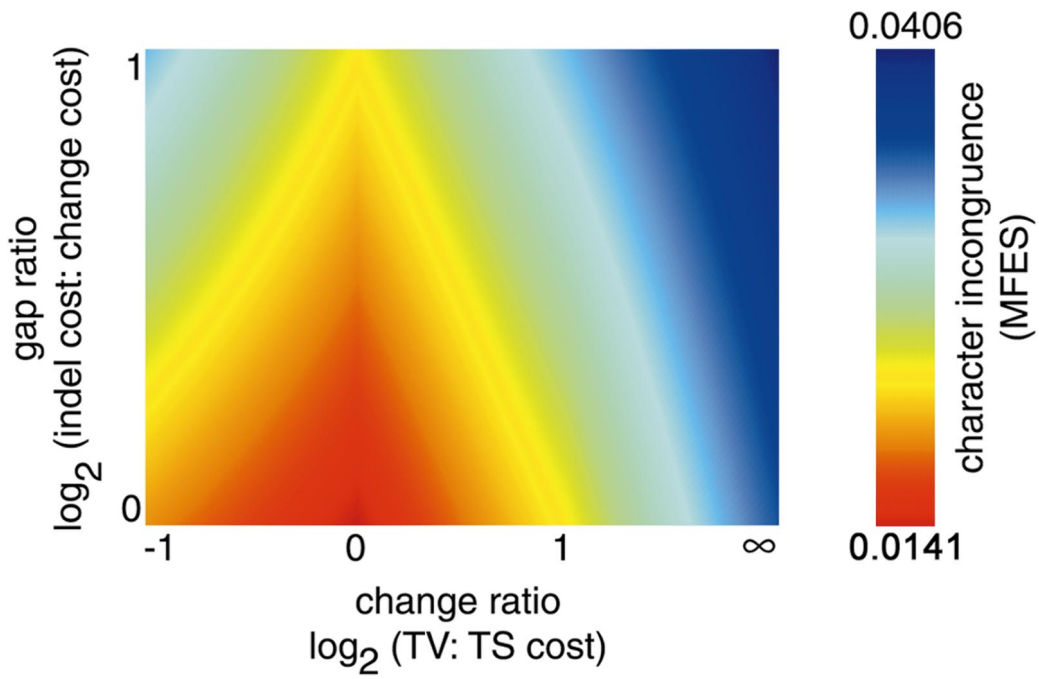

FIG. 5. Sensitivity analysis. The y axis represents the logarithm of the ratio of transversion:transition weights. The x axis represents the logarithm of the ratio of the indel cost to the maximal cost of a molecular change. The colors represent a z axis, which is congruence between the molecular and the morphological data partitions. Red is good congruence.

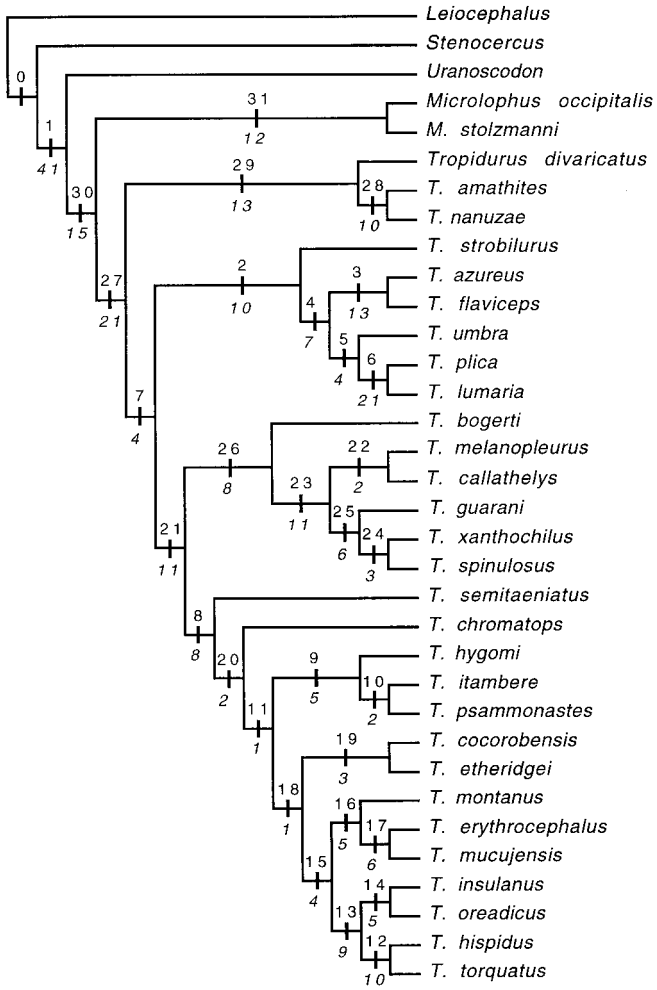

FIG. 6. Evidence of combined morphology and molecular data with transversion, transition, and indel alignment costs set at 1. Numbers above stems refer to apomorphy lists in Appendix 4, a change list. Italic numbers below the stems refer to Bremer support.

T. spinulosus, for which molecular data were absent for *T. xanthochilus* and *T. guarani*), stem 19 (*T. cocorobensis* plus *T. etheridgei*), stem 15, and stem 16.

Weak evidence was found only on stem 20 (*Tropidurus* above the level of *T. semitaeniatus*), stem 11 (which no doubt reflects that we had no molecular data for *T. chromatops*), stem 10 (*T. itambere* plus *T. psammonastes*), and Stem 18.

The salient features of the combined tree are that *Uranoscodon* is firmly placed as the sister taxon of *Tropidurus* plus *Microlophus*, as suggested by Frost (1992), and that the *T. nanuzae* group (stem 29) is placed more weakly as the sister taxon of the remaining *Tropidurus*. Unlike the earlier analyses of Frost (1992), Harvey and Gutberlet (2000), and the morphology analysis in this paper, the *T. plica* group (stem 2) does not render the *T. torquatus* group broadly paraphyletic; instead, it forms the sister taxon of all *Tropidurus* with the exception of the *T. nanuzae* group. Unlike the analysis of Frost (1992), but similar to both the morphology-only and the molecular-only analyses in this paper, *T. strobilurus* is placed as the sister taxon of the former *Uracentron* (stem 3) plus the former *Plica* (stem 5). The alternatives therefore are that the armed tails of *Uracentron* and *T. strobilurus* evolved on stem 2 and were lost on stem 5 or that they were evolved independently in *T. strobilurus* and *Uracentron*.

The placement of the enigmatic *T. bogerti*, previously considered the sister taxon of *T. semitaeniatus* by Frost (1992) and Harvey and Gutberlet (2000), adjacent to the *T. spinulosus* group (stem 23) suggests that the crevice-dwelling morphologies of *T. bogerti* and *T. semitaeniatus* are convergent. It also suggests that the isolated species *T. bogerti* in southern Venezuela has been long isolated from its near relatives, the *T. spinulosus* group, in austral South America.

The *T. torquatus* group, considered by Frost (1992) and Harvey and Gutberlet (2000) to be paraphyletic with respect to the *T. plica* group (stem 2 of Fig. 6), is demonstrated to be monophyletic on the basis of the total evidence, a result suspected for some time by M. T. Rodrigues and his associates. Although the placement of *T. chromatops* is suggestive, it's placement and that of *T. semitaeniatus* are not strongly supported, and additional work is needed.

Having provided the descriptive summary of all of the evidence we note also that this result leaves considerable numbers of morphological convergences between *Uranoscodon* and *T. umbra* (for instance elevation of the skull and breakup of the subocular scale), the source of much of the previous confusion. Interestingly, character 60, that of the forward direction of scale imbrication on the head, is a synapomorphy at the level of stem 7 and is reversed as a synapomorphy of the *T. torquatus* group (stem 8).

CONCLUSIONS

Sensitivity Analysis and Direct Opimization

For those unimpressed by the scientific priorities of descriptive efficiency and explanatory power, the sensitivity analysis demonstrated unambiguously that in this study equal weighting maximizes congruence between the morphological and the molecular data partitions. Nevertheless, workers should be aware that the MFES can render spuriously inflated measures of congruence as differential weights among partitions are increased (Wheeler and Hayashi, 1998; T. Reeder, personal commun.). In this case, because the highest congruence between the morphology and the molecular partitions is at a mutual relative weight of 1, we can safely assume that the tendency of the MFES in some circumstances to report artifactual increases in congruence with differential weighting was not a problem.

As noted previously by Frost *et al.* (2001), sensitivity analysis has provided an empirical basis for alignment costs not being tied to a particular view of how the evolutionary process must occur and so far has not justified the a priori weighting popular among other authors. Further, that it arrived at a most congruent solution for the morphological and molecular data partitions with relative costs of 1:1:1:1 suggests that previous a priori weighting schemes need to be seriously reconsidered. (See also the paper by Broughton *et al.*, 2000.) Direct optimization has provided parsimonious solutions for alignment regardless of the topology preferred, a great improvement over other techniques. Having praised POY as representing a great conceptual breakthough we must caution users that it continues to be experimental software, subject to frequent and undocumented changes, lagging documentation, and occasional lack of stability.

Comparison with Previous Hypotheses

Although representing progress over the first cladogram of the group (Etheridge and de Queiroz, 1988), Frost's (1992) arrangement was more successful in deep structure than it was for structure among members of the *T. torquatus* group and for the position of the *T. spinulosus* and *T. plica* groups, both of which were considered to render the *T. torquatus* group paraphyletic. Nevertheless, Frost (1992, p. 40, his alternative tree and associated discussion) noted considerable instability in the cladogram and the rampant character conflict in this region of the tree. Addition of characters from surface microstructure (Harvey and Gutberlet, 2000) for the most part had a salutary effect. However, their inclusion most trenchantly was illustrated in the placement of *Uranoscodon* as the sister taxon of *T. umbra;* this arrangement was not corroborated by the addition of molecular data, which placed firmly *Uranoscodon* as the sister taxon of the remaining Tropidurinae.

Taxonomic Conclusions

Obviously, the taxonomy as proposed by Frost (1992), wherein *Tapinurus* (= the *T. semitaeniatus* group), *Plica, Strobilurus,* and *Uracentron* were placed in the synonymy of *Tropidurus,* could be retained and is logically consistent with the most parsimonious cladogram. Nevertheless, there is an enormous amount of literature unassociated with systematics that uses the generic names *Plica* and *Uracentron* and we would be remiss if we did not take the opportunity to resurrect those names if their recognition is logically consistent with the recovered phylogeny, which, in this case it is. In addition, their resurrection has been personally lobbied for by Roy W. McDiarmid. This resurrection requires only that the previously enigmatic *T. nanuzae* group (*T. nanuzae, T. amathites,* and *T. divaricatus*) be placed in a new taxon, here coined as *Eurolophosaurus.* *Microlophus* (including *Plesiomicrolophus*) and *Uranoscodon* are, of course, retained, and *Plica, Strobilurus,* and *Uracentron* are resurrected. The name *Tropidurus* is restricted to the *T. bogerti, T. semitaeniatus, T. spinulosus* and *T. torquatus* groups (content defined below).

Tropidurinae Bell, 1843

Diagnosis: As provided by Frost (1992, p. 44) for Tropidurini (elevated to Tropidurinae by Frost *et al.*, 2001). See Appendix 4, stem 30, for an apomorphy list.

Content: Eurolophosaurus new; *Microlophus* Duméril and Bibron, 1837 (including *Plesiomicrolophus* Frost, 1992, fide Harvey and Gutberlet, 2000); *Plica, Strobilurus, Tropidurus, Uracentron, Uranoscodon.*

Genus *Uranoscodon* Kaup, 1825

Tree diagnosis: See *Uranoscodon* in Appendix 4 for list of apomorphies.

Comparative diagnosis: (1) skull highly elevated at the level of the orbits; (2) premaxilla broad; (3) nutritive foramina of maxilla not striking enlarged; (4) lingual process of dentary absent, not extending over ling dentary process of coronoid; (5) angular not strongly reduced; (6) medial centrale present; (7) "flash" marks on undersides of thighs absent; (8) circumorbitals not distinct from other small supraorbital scales; (9) lateral fringe developed on both sides of fourth toes; (10) enlarged middorsal scale row present; (11) tail terete, elongate, not mucronate; (12) hemipenes attenuate, without apical disks.

Content. Uranoscodon superciliosus (Linnaeus, 1758).

Distribution. Amazonian and Guianan regions from eastern Colombia and southern Venezuela, south to extreme northern Bolivia, and east to Maranhão, Brazil.

Genus *Microlophus* Duméril and Bibron, 1837

Tree diagnosis: See stem 31 for list of apomorphies in Appendix 4.

Comparative diagnosis: (1) skull not highly elevated at the level of the orbits; (2) premaxilla not broad; (3) nutritive foramina of maxilla not striking enlarged; (4) lingual process of dentary absent, not extending over ling dentary process of coronoid; (5) angular not strongly reduced; (6) medial centrale present; (7) "flash" marks on undersides of thighs absent; (8) circumorbitals distinct from other small supraorbital scales; (9) lateral fringe not developed on both sides of fourth toes; (10) enlarged middorsal scale row present (except in part of the *M. peruvianus* group: *M. atacamensis, M. heterolepis, M. quadrivittatus, M. theresiae*); (11) tail terete, not strongly mucronate; (12) hemipenes with apical disks (except in *M. koeckeorum*).

Content: Microlophus albemarlensis (Baur, 1890); *M. atacamensis* (Donoso-Barros, 1966); *M. bivittatus* (Peters, 1871); *M. delanonis* (Baur, 1890); *M. duncanensis* (Baur, 1890); *M. grayii* (Bell, 1843); *M. habelii* (Steindachner, 1876); *M. heterolepis* (Wiegmann, 1834); *M. koepckeorum* (Mertens, 1956); *M. occipitalis* (Peters, 1871); *M. pacificus* (Steindachner, 1876); *M. peruvianus* Lesson, 1831; *M. quadrivittatus* (Tschudi, 1845); *M. stolzmanni* (Steindachner, 1891); *M. tarapacensis* (Donoso-Barros, 1966); *M. theresiae* (Steindachner, 1901); *M. thoracicus* (Tschudi, 1845); *M. tigris* (Tschudi, 1845); *M. yanezi* (Ortiz-Zapata, 1980).

Distribution: Galapagos Islands; South America west of the Andes from southern Ecuador to northern Chile; east of the continental divide only in the Huancabamba Depression Region of northern Peru.

Comment: Although two species groups have been used, i.e., the *M. occipitalis* and *M. peruvianus* groups (Dixon and Wright, 1975; Frost, 1992), no evidence has yet suggested that the *M. occipitalis* group is monophyletic.

Genus *Eurolophosaurus* New

Etymology: Greek: Euro- (eastern), lopho- (ridge), sauros (lizard), referring to the association of this group of species with the Serra da Espinhaço ridge of mountains in eastern Brazil.

Tree diagnosis: See stem 29 for list of apomorphies in Appendix 4.

Comparative diagnosis: (1) skull highly elevated at the level of the orbits; (2) premaxilla not broad; (3) nutritive foramina of maxilla striking enlarged; (4) lingual process of dentary present, extending over ling dentary process of coronoid; (5) angular strongly reduced; (6) medial centrale absent; (7) "flash" marks on undersides of thighs present; (8) circumorbitals distinct from other small supraorbital scales; (9) lateral fringe not developed on both sides of fourth toes; (10) enlarge middorsal scale row present; (11) tail terete, not strongly mucronate; (12) hemipenes attenuate, without apical disks.

Type species: Tropidurus nanuzae Rodrigues, 1981.

Distribution: The Serra Espinhaço ridgeline and nearby areas of Bahia and Minas Gerais, Brazil.

Content: Eurolophosaurus amathites (Rodrigues, 1984); *E. divaricatus* (Rodrigues, 1986); *E. nanuzae* (Rodrigues, 1981).

Comment: Eurolophosaurus represents the monophyletic group formerly referred to as the *T. nanuzae* group (Rodrigues, 1986).

Genus *Plica* Gray, 1831

Tree diagnosis: See stem 5 in Appendix 4 for a list of apomorphies.

Comparative diagnosis: (1) skull highly elevated at the level of the orbits in *P. umbra,* not in other species; (2) premaxilla broad; (3) nutritive foramina of maxilla striking enlarged; (4) lingual process of dentary present, extending over ling dentary process of coronoid; (5) angular strongly reduced; (6) medial centrale absent; (7) "flash" marks on undersides of thighs present (except in *P. umbra*); (8) circumorbitals distinct from other small supraorbital scales; (9) lateral fringe not developed on both sides of fourth toes; (10) enlarged middorsal scale row present; (11) tail terete, not heavily mucronate; (12) hemipenes attenuate, without apical disks.

Content: Plica plica (Linnaeus, 1758); *P. lumaria* Donnelly and Myers, 1991; *P. umbra* (Linnaeus, 1758).

Distribution: Tropical forest regions of northern South America east of the Andes, south to central Bolivia and Rondonia and Pará in Brazil.

Genus *Strobilurus* Wiegmann, 1834

Tree diagnosis: See *Tropidurus strobilurus* (= *Strobilurus torquatus*) in Appendix 4 for list of apomorphies.

Comparative diagnosis: (1) skull not highly elevated at the level of the orbits; (2) premaxilla broad; (3) nutritive foramina of maxilla striking enlarged; (4) lingual process of dentary present, extending over ling dentary process of coronoid; (5) angular strongly reduced; (6) medial centrale absent; (7) "flash" marks on undersides of thighs present; (8) circumorbitals distinct from other small supraorbital scales; (9) lateral fringe not developed on both sides of fourth toes; (10) enlarged middorsal scale row present; (11) tail terete but heavily mucronate and short; (12) hemipenes attenuate, without apical disks.

Content: Strobilurus torquatus Wiegmann, 1834 (= *Tropidurus strobilurus* Frost, 1992).

Distribution: Atlantic forests of southern Brazil.

Genus *Tropidurus* Wied-Neuwied, 1825

Tree diagnosis: See stem 21 in Appendix 4 for list of apomorphies.

Comparative diagnosis: (1) skull not highly elevated at the level of the orbits; (2) premaxilla not broad; (3) nutritive foramina of maxilla striking enlarged; (4) lingual process of dentary present, extending over ling dentary process of coronoid; (5) angular strongly reduced; (6) medial centrale absent; (7) "flash" marks on undersides of thighs present; (8) circumorbitals distinct from other small supraorbital scales; (9) lateral fringe not developed on both sides of fourth toes; (10) enlarged middorsal scale row present or absent; (11) tail terete; (12) hemipenes attenuate, without apical disks.

Content: T. bogerti Roze, 1958; *T. callathelys* Harvey and Gutberlet, 1988; *T. chromatops* Harvey and Gutberlet, 1988; *T. erythrocephalus* Rodrigues, 1987; *T. etheridgei* Cei, 1982; *T. guarani* Alvarez *et al.*, 1991; *T.*

helenae (Manzini and Abe, 1990); *T. hispidus* (Spix, 1825); *T. hygomi* Reinhardt and Lütken, 1861; *T. insulanus* Rodrigues, 1987; *T. itambere* Rodrigues, 1987; *T. melanopleurus* Boulenger, 1902; *T. montanus* Rodrigues, 1987; *T. mucujensis* Rodrigues, 1987; *T. oreadicus Rodrigues, 1987; T. pinima* (Rodrigues, 1984); *T. psammonastes* Rodrigues *et al.*, 1988; *T. semitaeniatus* (Spix, 1825); *T. spinulosus* (Cope, 1862); *T. torquatus* Wied-Neuwied, 1825; *T. xanthochilus* Harvey and Gutberlet, 1988.

Distribution: From southern Venezuela east through the Guianas to northeastern Brazil, from there west south of the Amazon region to eastern Bolivia, extreme northern Uruguay, and central Argentina.

Comment on species groups: We formally at this time diagnose the four species groups within *Tropidurus,* the *T. spinulosus* group, the *T. bogerti* group, the *T. semitaeniatus* group, and the *T. torquatus* group.

The *T. spinulosus* group corresponds to the group subtended by stem 23 (Appendix 4) and is diagnosed by having thigh flash marks colored yellow or white (rather than brown or black as in the other groups), a strong antegular fold (absent in the other species groups), poorly defined postmental scale series (well-defined in the other groups), and some frequency of two rows of circumorbital scales (63, single row in the other groups) and a middorsal scale row (absent in the other groups). The content of this group is *T. melanopleurus, T. callathelys, T. spinulosus, T. xanthochilus,* and *T. guarani.*

The *T. bogerti* group contains solely *T. bogerti.* We could have included this far-flung Venezuelan species in the *T. spinulosus* group (which is otherwise found only far south of the Amazon) on the basis of molecular evidence, but we think that a species group, a rather rough and ready taxonomic grouping, is best formulated on easily observable morphological characters. The *T. bogerti* group corresponds to *T. bogerti* in Appendix 4 and is diagnosed by lateral gulars imbricating posteriorly (rather than laterally as in the other groups) and by having a depressed habitus (less so in the other groups, except for the *T. semitaeniatus* group, which is extremely flattened). Additionally, it is also unique in having a color pattern of white dots on a black background; a similar but not identical pattern is found only in *T. mucujensis.*

The *T. semitaeniatus* group (corresponding to *T. semitaeniatus* in Appendix 4) is characterized by extreme flattening of the body and head and various other attributes associated with this flattening. (Other groups are not extremely flattened.) The content of this group is *T. helenae, T. pinima,* and *T. semitaeniatus.*

The *T. torquatus* group (corresponding to stem 20, Appendix 4) is equivalent to the *T. torquatus* group of Rodrigues (1987) and is characterized by lacking an enlarged middorsal scale row and in not being extremely flattened. The content of this group is *T. chromatops, T. cocorobensis, T. erythrocephalus, T. etheridgei, T. hispidus, T. hygomi, T. insulanus, T. itambere, T. montanus, T. mucujensis, T. oreadicus, T. psammonastes,* and *T. torquatus.*

Genus *Uracentron* Kaup, 1826

Tree diagnosis: See stem 3 in Appendix 4 for a list of apomorphies.

Comparative diagnosis: (1) skull not highly elevated at the level of the orbits; (2) premaxilla broad; (3) nutritive foramina of maxilla striking enlarged; (4) lingual process of dentary present, extending over ling dentary process of coronoid; (5) angular strongly reduced; (6) medial centrale absent; (7) "flash" marks on undersides of thighs absent; (8) circumorbitals distinct from other small supraorbital scales; (9) lateral fringe not developed on both sides of fourth toes; (10) middorsal scale row not present; (11) tail very short, heavily mucronate, and spatulate; (12) hemipenes attenuate, without apical disks.

Content: Uracentron azureum (Linnaeus, 1758), *U. flaviceps* (Guichenot, 1855).

Distribution: Amazon Basin of southeastern Colombia, eastern Ecuador, and eastern Peru (and likely northern Bolivia) east to Surinam, French Guiana, and Maranhão, Brazil.

APPENDIX 1

Specimens Examined

DNA vouchers. Sequence data (and associated voucher information) from this article have been deposited with the AMBL/GenBank Data Libraries: *Microlophus stolzmanni* (BankIt391492; AF362518), *Plica lumaria* (BankIt 391494; AF362519), *P. plica* (BankIt 391501; AF362520), *P. umbra* (BankIt391502; AF362521), *Stenocercus roseiventris* (BankIt391504; AF362522), *Strobilurus torquatus* (BankIt391505; AF362523), *Tropidurus amathites* (BankIt391509; AF362525), *T. bogerti* (BankIt391508; AF362526), *T. callathelys* (BankIt391510; AF362527), *T. cocorobensis* (BankIt391511; AF362528), *T. divaricatus* (BankIt391513; AF362529), *T. erythrocephalus* (BankIt391514; AF362530), *T. etheridgei* (BankIt391515; AF362531), *T. hygomi* (BankIt391516; AF362532), *T. insulanus* (BankIt391517; AF362533), *T. itambere* (BankIt391518; AF362534), *T. montanus* (BankIt391519; AF362535), *T. mucujensis* (BankIt391520; AF362536), *T. nanuzae* (BankIt391521; AF362537), *T. oreadicus* (BankIt391792; AF362538), *T. psammonastes* (BankIt391793; AF362539), *T. semitaeniatus* (BankIt391506; AF362524), *T. spinulosus* (BankIt391794; AF362540), *T. torquatus* (BankIt391795; AF362541), *Uracentron flaviceps* (BankIt391796; AF362542), *Uranoscodon superciliosus* (BankIt391800; AF362543).

Morphological specimens. Many of the specimens cited in Frost (1992) were reexamined for purposes of this study. The following should be added to the specimens examined for morphological characters listed in Frost (1992). All are whole alcoholic specimens unless otherwise noted: *Plica lumaria:* AMNH 136177 (subsequently prepared as a dry skull and cleared and double-stained postcrania), 136178, 136182–83, 136186, 136189. *Tropidurus amathites:* AMNH 138808, 138809 (subsequently prepared as a dry skull and cleared and double-stained postcranium), 138810, MZUSP 78624–25, 78630. *T. callathelys:* UTA R-39611 (subsequently prepared as a dry skull and cleared and double-stained postcrania), 39616–20, 39622–23, 39625, 39627. *T. chromatops:* UTA R-39603-04 (alcoholic and X ray). *T. divaricatus:* AMNH 138814–15, 133816 (subsequently prepared as a dry skull and cleared and double-stained postcranium), 138817–19; MZUSP 78.633–34, 78.643 (skeleton). *T. guarani:* AMNH 138858–59 (subsequently prepared as a dry skull and cleared and double-stained postcranium); MHNP unnumbered [11 specimens]; USNM 30299–300, 319758, 342058–59–62. *T. mucujensis:* NZUSP 78.661–62 (skeletons); 66.210–66.212; 68.608; 68.610. *T. psammonastes:* AMNH 138850, 138851, 138850 (subsequently prepared as a skin, dry skull, and cleared and double-stained postcranium). *T. spinulosus:* AMNH 101489–96, 141502–14, 141733–42, USNM 342040–57, UTA R-38052. *T. xanthochilus:* UTA R-38054–55 (X rayed).

APPENDIX 2

Morphological Transformation Series

General nomenclature of squamation follows Smith (1949) and most transformation series come directly from Frost (1992), where they are illustrated and discussed in considerably more detail. Modifications and additions to that character list are noted. Because POY starts counting characters with "0," rather than the traditional "1," we have also started our numbering convention with 0 so as to make direct interpretation of output (Appendix 4) relatively straightforward.

Cranial Osteology

0. Skull size: (0) adult males with head length <23% of snout–vent length; (1) adult males with head length >23% of snout–vent length.

1. Skull elevation: (0) skull not elevated at level of orbits (skull height <39% of skull length—postorbital bone not rotated to form a flange; (1) skull elevated at level of orbits (skull height >39% of skull length)—postorbital bone rotated outward to form a flange.

2. Skull compression: (0) not compressed—skull height >30% of skull length; (1) compressed—skull height ≤25% of skull length.

3. Rostrum length: (0) long; (1) shortened.

4. Premaxilla: (0) nasal spine narrow—dentigerous part of premaxilla broad; (1) nasal spine broad—dentigerous part of premaxilla narrow.

5. Nasal bones: (0) not reduced—external choana does not approach level of anterior extent of prefrontal; (1) reduced—excavated to a point approaching the anterior part of the prefrontal in *T. bogerti* and *T. amathites;* (2) excavated to a point where the prefrontal contacts the margin of the external choana in *T. semitaeniatus*. Harvey and Gutberlet (2000, p. 195) treated this transformation as nonadditive. We have retained the original coding for the reason that to treat this as nonadditive would have allowed excavation of the nasals to happen twice (characters 1 and 2) without any cost to the parsimony measure.

6. Nutritive foramina of maxillary: (0) small, inconspicuous; (1) enlarged, conspicuous.

7. Maxillopalatine foramen: (0) much smaller than lacrimal foramen; (1) enlarged and dorsoventrally expanded—frequently subequal in size to lacrimal foramen.

8. Squamosal shape and skull width: (0) squamosal bone relatively straight, reflected in the posterior apex of the temporal fenestra forming an acute angle; (1) squamosal bone curved around the posterior end of the temporal fenestra—the posterior apex of the temporal fenestra forming a smooth curve.

9. Superior fossa of quadrate: (0) relatively small, a process of the squamosal fitting into the fossa like a peg in a hole; (1) relatively enlarged, the squamosal not penetrating the fossa.

10. Alveolar shelf of mandible: (0) forming a well-defined ridge; (1) alveolar ridge rounded—erosion of thickness of mandible below level of alveolar ridge; (2) alveolar ridge poorly defined—medially approaches ventral margin of mandible. Harvey and Gutberlet (2000, p. 195) treated this transformation as nonadditive, although this would not have allowed the development of the implied homology "eroded alveolar ridge" to have taken place twice without any cost to the parsimony measure.

11. Lingual coronoid process of dentary: (0) not overlapping anterior lingual "leg" of coronoid; (1) overlapping anterior lingual "leg" of coronoid.

12. Posterior extent of dentary: (0) dentary extending <50% of the length from apex of coronoid to anterior edge of articular; (1) extending >50% of the length from the apex of the coronoid to the anterior edge of the articular.

13. Anterior surangular foramen: (0) not captured by contact of the coronoid and dentary posterior to the foramen; (1) "captured" by contact of the coronoid and surangular posterior to the anterior surangular foramen.

14. Angular condition: (0) large, distinct; (1) reduced (limited to below surangular–prearticular suture) or lost.

15. Posterior mylohyoid foramen, osseous contact: (0) posterior mylohyoid foramen penetrating angular or between dentary and angular; (1) between denatary and splenial.

16. Posterior mylohyoid foramen, position: (0) at the level of anterior end of mandibular fossa; (1) placed more posteriorly, about 33% of the length of the mandibular fossa back from the anterior end.

17. Premaxillary teeth, number: (0) 6 or 7; (1) 4 or 5.

18. Anterior maxillary teeth, enlargement: (0) not or only feebly enlarged in older adults; (1) enlarged in older adults, forming caniniform teeth.

19. Posterior maxillary and dentary teeth, crown flaring: (0) shaft parallel-side with crowns not or weakly flared; (1) crowns flared.

20. Posterior maxillary teeth, elevations: (0) posterior maxillary teeth apparently hypsodont, extending above the edge of the maxilla more than the width of a tooth; (1) posterior maxillary teeth brachydont, not extending far above the level of the maxilla.

21. Posterior maxillary teeth, orientation: (0) posterior maxillary teeth set obliquely on the maxilla; when viewed from the ventral side most of the length of the individual teeth can be seen; (1) posterior maxillary teeth set more vertically on maxilla (not to be confused with recurving of the teeth as seen in some other taxa such as some *Leiocephalus*); when viewed from the ventral side, much of the length of the tooth is hidden from view; additionally, the orbital margins of the jugal form "cheeks" that, as evidenced by their outward rotation, are structurally part of the inward rotation of the dental row.

22. Pterygoid teeth: (0) present; (1) absent.

Postcranial Osteology

23. Clavicle: (0) strongly flanged, frequently fenestrate; (1) weakly flared or cylindrical, never fenestrate.

24. Sternum, fenestration: (0) single fenestration present; (1) fenestra absent. *T. divaricatus* is coded as polymorphic because of intraspecific variation.

25. Posterior process of the interclavicle anterior to the sternum: (0) "free" part of the posterior process of the interclavicle $>25\%$ of the total length of the sternum, (i.e., the sternum is small); (1) "free" part of the posterior process of the interclavicle $<25\%$ of the total length of the sternum (i.e., the sternum is enlarged).

26. Interclavicle median process: (0) posterior process of the interclavicle extending as a broad process posteriorly well beyond the posterolateral corners of the sternum; (1) posterior process of the interclavicle not extending posteriorly beyond the posterolateral corners of the sternum.

27. Scapular deflection and fenestration of scapulocoracoid: (0) scapular fenestra present, large, and scapula not bent; (1) scapular fenestra present, reduced, and scapula weakly bent; (2) scapular fenestra absent, with no room for fenestra in scapula because extremely bent. Harvey and Gutberlet (2000) treated this transformation as nonadditive, although this would provide for no cost to the parsimony measure for deflection of the scapula occurring independently in conditions 1 and 2.

28. Suprascapular fenestrations: (0) absent, or very tiny; (1) large.

29. Rib formula: (0) five ribs in contact with the sternum and xiphisternum: 3 sternal ribs + 2 xiphisternal ribs; (1) six ribs in contact with the sternum and xiphisternum (3 sternal ribs + 3 xiphisternal ribs, or 4 sternal ribs + 2 xiphisternal ribs), with the insertion of the fourth sternal rib being very close to the insertion of the xiphisternal rods or, conversely in the case of only three sternal ribs, the first xiphisternal rib inserting very close to the insertion of the xiphisternal rods on the sternum.

30. Recurved xiphisternal–pectoral ribs: (0) absent or present as short spurs associated with the medial part of the pectoralis musculature; (1) present, long, associated with entire origin of the pectoralis musculature.

31. Humerus, head: (0) articular surface scroll-like; (1) somewhat elevated, ovate; (2) ball-shaped and very elevated. Harvey and Gutberlet (2000, p. 195) treated this transformation as nonadditive, although this approach loses the implied character "elevated humeral head" as measurable by the parsimony metric.

32. Medial centrale: (0) present; (1) absent.

33. Fourth metacarpal and first phalanx of fourth finger: (0) fourth metacarpal distinctly shorter than third metacarpal—first phalanx of fourth finger distinctly shorter than first phalanx of third finger; (1) fourth metacarpal equal to length of third metacarpal—first phalanx of fourth finger distinctly shorter than first phalanx of third finger; (2) fourth metacarpal equal to length of third metacarpal—first phalanx of fourth finger subequal to first phalanx of third finger. Harvey and Gutberlet (2000, p. 195) treated this transformation as nonadditive, although this loses the implied character "fourth metacarpal equal to length of third metacarpal," shared by conditions 1 and 2, as measurable by the parsimony metric.

34. Claw of first toe: (0) weakly flexed; (1) strongly flexed, recurved.

35. Fringe on fourth toe: (0) absent; (1) present.

36. Pubic symphysis, anterior margin: (0) acute; (1) flattened.

37. Anterior caudal vertebrae, neural spines: (0) moderate to high; (1) very depressed.

38. Caudal vertebrae, autotomy fracture planes: (0) present; (1) absent.

External Morphology

39. Nostrils: (0) exposed posterolaterally and keyhole shaped or some other modification thereof; (1) exposed laterally and widely open; (2) directed anteri-

orly or anterolaterally and unconstricted. This transformation is treated as nonadditive because the conditions form no discernible developmental sequence.

40. Ventral thigh pigmented region (Rodrigues, 1987): (0) thighs without a well-defined ventral pigmented spot; (1) thigh region with a well-defined white, yellow, greenish, brown, or black spot.

41. Color of thigh and preanal pigmented region: (0) white or creme; (1) greenish to yellow; (2) dark brown or black. Taxa without a pigmented region in the thigh are coded as unknown to not weight additionally the transformation illustrated by character 40. This transformation is considered nonadditive because we cannot discern a developmental sequence among the states.

42. Hemipenes, condition: (0) no terminal disks on hemipenial lobes; (1) terminal disks present on hemipenial lobes.

43. Hemipenes, length of lobes: (0) short; (1) long.

44. Hemipenes, ornamentation: (0) calyces start below crotch between lobes; (1) calyces start at a level well above the crotch between the hemipenial lobes. *Leiocephalus* may not have well-defined lobes, but the ornamentation does extend well down the shaft of the hemipenis. In "*Stenocercus*" the lobes are quite short, but the ornamentation does not extend below the level of the bifurcation of the sulcus.

45. Gular fold: (0) incomplete medially; (1) complete medially.

46. Antegular fold: (0) absent or weak and variable; (1) present, strong, well anterior to gular fold; (2) present, strong, closely approximating or overlapping gular fold. Harvey and Gutberlet (2000) partially ordered this transformation (sensu Campbell and Frost, 1993). We have retained the original additivity, because to do otherwise would have excluded the implied character "antegular fold present" as a character that could be detected by the parsimony measure, although, like the other multistates examined, this is an effect of this assumption.

47. Antegular-oblique neck fold mite pockets, condition: (0) weak single mite pocket; (1) no mite pocket, complex neck folding; (2) a well developed mite pocket in the upper position (see following transformation); (3) ventrolateral mite pockets; (4) no mite pockets although weak depressions are in the ventrolateral side of antegular fold; (5) no mite pocket, no depressions, scales enlarged to the point of obscuring any folds or pockets. *Leiocephalus* and *Stenocercus* are both coded as 0/2 because of interspecific variability. Harvey and Gutberlet (2000, p. 194) combined this character with the following to avoid "unknown" cells in the data matrix. We retain the original coding, although we note that coding of this particular morphology is particularly difficult to individuate.

48. Oblique neck fold mite pocket, condition: (0) two mite pockets separated by a distinct fold; (1) a single well-developed mite pocket in the upper position indicated; (2) single, very enlarged mite pocket, apparently resulting from the fusion of the two primordial pockets. Species that lack mite pockets (or the pockets that they occur in) are coded as unknown. This character is nonadditive.

49. Mite pocket in antehumeral fold: (0) absent; (1) present laterally; (2) present ventrolaterally in antehumeral–antegular fold. This character is treated as nonadditive because of the strikingly different nature of the apomorphic characters. Nevertheless, it could have been treated as partially ordered if we had thought that "mite pocket in antehumeral" fold should have been coded as a hypothesized homology. *Leiocephalus* and *Stenocercus* are both coded as 0/1 becuase of interspecific variation.

50. Tufts of spines on sides of neck: (0) absent; (1) present.

51. Rictal fold: (0) absent; (1) present.

52. Axillary pocket, presence: (0) absent; (1) present. Harvey and Gutberlet (2000, p. 192) corrected this character by noting that *T. oreadicus* was miscoded by Frost (1992) as having a mite pocket, when, in fact, they do not. They also noted that "good" *T. hispidus* have single pockets, not double pockets (this character likely applying to a cryptic species north of the Amazon River).

53. Axillary pocket, condition: (0) present, single; (1) multiple, usually 3, sometimes only 2.

54. Inguinal granular pocket: (0) absent or represented solely by a fold; (1) present and deep.

55. Rostral scale, height: (0) rostral scale 1.5 to 2× height of adjacent supralabials; (1) rostral scale height reduced, less than 1.5× height of adjacent supralabials.

56. Mental scale: (0) enlarged, extending posteriorly well beyond level of adjacent infralabials; (1) reduced, not extending posteriorly well beyond level of adjacent infralabials.

57. Postmental series: (0) well defined; (1) poorly defined or absent. Harvey and Gutberlet (2000, p. 209) add another character (their 79; 76 of this list), which is the degree of contact between the postmentals and the infralabials. One could quibble about the logical relationship of these two characters, but definition and contact do not seem to be necessarily causally related and we have retained them as independent characters for this reason.

58. Infralabials, expansion: (0) infralabials not ventrally expanded; (1) infralabials greatly expanded ventrally.

59. Lateral gular scales: (0) imbricate posteriorly; (1) imbricate laterally.

60. Scales of frontonasal region: (0) imbricate posteriorly or no imbrication evident; (1) weakly imbricate anteriorly; (2) all head shields strongly imbricate anteriorly. Harvey and Gutberlet (2000, p. 195) treated this transformation as nonadditive, although this does

not allow the implied character shared by 1 and 2, "scales of frontonasal region imbricate anteriorly," to act as a putative homology whose behavior can be measured by a parsimony metric.

61. Superciliary scales: (0) not or only weakly produced vertically to form a longitudinal crest; (1) produced vertically to form a longitudinal crest.

62. Circumorbital series: (0) in one row between the supraoculars and the median head shield; (1) two partial to complete rows occurring at some frequency in populations; (2) two complete rows of supraoculars at least posteriorly in all members of a population. Harvey and Gutberlet (2000, p. 192) noted in *T. melanopleurus* and *T. callathelys* a low frequency of a double row of circumorbitals. We have coded these using the unscaled method of Campbell and Frost (1993) to reflect this intermediacy. Because in *Uranoscodon* a circumorbital series is autapomorphically indistinguishable from the small supraoculars, this species was coded "unknown" in the analysis.

63. Circumorbitals: (0) small; (1) enlarged at the expense of the supraoculars.

64. Interparietal: (0) not enlarged, smaller than interorbital distance; (1) enlarged, larger than interorbital distance.

65. Interparietal length: (0) subequal to significantly less than width; (1) significantly longer than wide.

66. Rows of scales between subocular and supralabials: (0) 0–1; (1) 2 or more.

67. Subocular: (0) entire—0–1 preoculars; (1) divided—at least 2 preoculars in contact with the orbit; (2) subocular–preocular series so fragmented as to be obscure. Harvey and Gutberlet (2000, p. 195) treated this transformation as nonadditive, rejecting intermediacy as a reason for the assumption of additivity. Inasmuch as this coding scheme rejects the implied character "subocular divided" as a potential homology shared by characters 1 and 2, we retain the original coding.

68. Preauricular fringe: (0) present, ear canal deep, a continuous fringe of scales partially to nearly completely covering ear opening; (1) reduced, ear canal deep; (2) auricular scales reduced, ear canal deep, a lower lobule with several short spines present; (3) auricular fringe absent, ear canal shallow.

69. Middorsal scale row: (0) present; (1) absent.

70. Paravertebral scales of males: (0) keeled; (1) not keeled. See discussion by Harvey and Gutberlet (2000, p. 192) for correction. We have accepted the suggested change from granular and juxtaposed to granular and juxtaposed in both sexes, following Harvey and Gutberlet (2000, p. 192), although we suggest that their recognition of the process which resulted in their being able to distinguish the nonhomology of these conditions is a posteriori given the tree published by Frost (1992).

71. Caudal scales: (0) tail unarmed, longer than head + body; (1) tail armed with heavy mucrons, tail roughly terete and subequal to length of head + body; (2) tail armed with heavy mucrons, tail dorsoventrally flattened and shorter than head + body. Harvey and Gutberlet (2000, p. 195) treated this transformation as nonadditive, although this rejects "tail scales heavily armed" as an implied potential homology whose behavior in the analysis can be measured by the parsimony metric. We retain the original coding scheme.

72. Ventral scales: (0) smooth; (1) keeled. *Leiocephalus* is coded as unknown because of ambiguity in the root of that taxon.

73. Upper thigh scales: (0) not heavily mucronate; (1) heavily mucronate.

New Characters of Squamation and Epidermal Microstructure from Harvey and Gutberlet (2000)

74. Preocular–canthal contact (Harvey and Gutberlet, 2000, p. 209; their character 78): (0) posterior canthal contacting preocular; (1) canthal and preocular separated at some frequency within a population; (2) canthal and preocular always separated by rectangular scale. Harvey and Gutberlet (2000, p. 209) coded this as (a) posterior canthal contacting preocular; (b–x) intermediate frequencies [*T. itambere*—m; *T. oreadicus*—e, *T. torquatus*—c); (y) canthal and preocular always in contact. We have coded this in an "unscaled" form (Campbell and Frost, 1993) to assure that all hypotheses of homology are given equal weight.

75. Postmental–infralabial contact (Harvey and Gutberlet, 2000, p. 209; their character 79): (0) one or no postmentals contacting infralabials; (1) some intermediate frequency of contact between two postmentals and infralabials; (2) two or more postmentals contacting infralabials. Harvey and Gutberlet (2000, p. 209) coded this as (a) 1 or no postmentals contacting infralabials—Ancestor, *Uranoscodon, M. occipitalis, M. stolzmanni*]; (b) *T. chromatops;* (c) *T. torquatus;* (f) *M. peruvianus;* (m) *T. bogerti;* (n) *T. hispidus;* (q) *T. semitaeniatus;* (y) 2 or more postmentals contating infralabials [*T. melanopleurus, T. callathelys*]. As in the previous character we have made all initial hypotheses of homology of equal weight. *T. plica, T. lumarius, T. umbra, T. azureus,* and *T. flaviceps* are coded as unknown for reason of the characterization being inapplicable (Harvey and Gutberlet, 2000, p. 209).

76. Type of coarse microstructure (Harvey and Gutberlet, 2000, p. 210; their character 80): (0) very low, rectangular macrohoneycomb; (1) well developed, imbricate macrohoneycomb.

77. Caudal wall of macrohoneycomb on dorsals (Harvey and Gutberlet, 2000, p. 210; their character 81): (0) caudal wall lacking a jagged projection of the oberhautchen; (1) caudal wall having a jagged projection of the oberhautchen on at least some portions of the scale.

78. Distribution of macrohoneycomb on dorsals (Harvey and Gutberlet, 2000, p. 210; their character

82): (0) poorly developed to absent on the caudal two-thirds of the scale; (1) well-developed over entire surface of dorsals except for distal surface of keel. The presence of both characters within *Stenocercus* and the low relief of scale microstructure in *Leiocephalus* require that those taxa be coded as unknown.

79. Distribution of coarse microstructure on supralabials (Harvey and Gutberlet, 2000, p. 210; their character 83): (0) coarse microstructure distributed in a narrow band along dorsal edge of the scale; (1) coarse microstructure distributed across most of the scale surface, edge bordering the buccal commissure smooth. Harvey and Gutberlet (2000, p. 201) suggested that *T. nanuzae* exhibits an intermediate condition of irregular patches of macrohoneycomb extending across portions of the lower two-thirds of the supralabial, but coded this taxon as "1." We have retained the coding of Harvey and Gutberlet (2000) because we have not examined the character in question.

80. Distribution of coarse microstructure on supraoculars (Harvey and Gutberlet, 2000, p. 210; their character 84): (0) restricted to the edge of the supraocular scales, dorsal surface lacking coarse microstructure; (1) coarse microstructure extending across entire surface of supraocular scales except for the surfaces of macroscopic ridges and keels.

81. Distribution of coarse microstructure on ventrals (Harvey and Gutberlet, 2000, p. 211; their character 85): (0) confined to hinge region of scale; (1) distributed over most or all of the scale.

82. Type of coarse microstructure on the inner surface zone of dorsals (Harvey and Gutberlet, 2000, p. 211; their character 86): (0) macrohoneycomb or macrohoneycomb and lamellae; (1) lamellae only; (2) inner surface zone reduced to a narrow strip precluding evaluation for coarse microstructure. Harvey and Gutberlet (2000) considered the condition "2" to equate to unobservable. We, however, consider the reduction of the inner surface to be part of the nonadditive character.

83. Regional expression of spinules (Harvey and Gutberlet, 2000, p. 211; their character 87): (0) present on all scales; (1) absent from ventrals. Harvey and Gutberlet (2000, p. 211) code "absent from all scales" as inapplicable but we would have retained this as a character as part of a multistate for reason that "absent from all scales" necessarily includes character 1. Nevertheless, we have retained their coding because we cannot distinguish in their paper between lacking spinules and the observation not having been made. Unlike Harvey and Gutberlet (2000, p. 211) we have coded *Uranoscodon* as unknown for reason that to code them as having spinules requires that the large, widely spaced papillae occurring on all scales (also found in *T. plica* in addition to spinules) be derived from spinules. *Stenocercus* is coded as unknown because of variation among species in the taxon. Likewise, *Leiocephalus* is coded as unknown because it has spines and pits.

84. Presence of a morphotypic series of pits, pit and groove, and spinules on dorsals and surpraoculars (Harvey and Gutberlet, 2000, p. 211; their character 88): (0) series present and occupying more than two rows of macrohoneycomb chambers; (1) series truncated or absent, scales uniformly spinulate or lacking spinules only on the anteriormost edge of the scale; (2) series absent, scales uniformly pitted.

85. Large, widely spaced papillae occurring on all scales (Harvey and Gutberlet, 2000, p. 203; their character 89): (0) absent; (1) present. Harvey and Gutberlet (2000, p. 203) report *U. superciliosus* and *T. plica* as sharing the microstructure characteristic of large, widely spaced papillae occurring on all scales but did not include this as a character under analysis.

86. Position of scale organs on paravertebrals (Harvey and Gutberlet, 2000, p. 211; their character 90): (0) behind or beside keel; (1) on surface of keel, near caudal tip.

87. Scale organs on ventral scales (Harvey and Gutberlet, 2000, p. 211; their character 91): (0) single, tiny, near caudal tip of scale; (1) sometimes paired, lateral to keel, larger and more developed.

88. Caudal notch on ventrals (Harvey and Gutberlet, 2000, p. 212; their character 92): (0) absent; (1) present on some ventral scales.

89. Position of scale organs on enlarged supraoculars (Harvey and Gutberlet, 2000, p. 212; their character 93): (0) scale organs arranged in a row along caudal edge of scale; (1) scale organs distributed across scale surface seemingly at random. *Stenocercus* is coded as unknown because of interspecific variability.

New Characters from Other Sources

90. Spots in supraocular region (Rodrigues, 1986; Martins, 1995). (0) absent; (1) present. Reported in *T. amathites* and *T. divaricatus*, not in any member of the *T. torquatus* group.

91. Position of the nucleolar organizer region (NOR) (Martins, 1995): (0) two NORs on the proximal centromeric region of an acrocentric pair of microchromosomes; (1) on chromosome six. *T. amathites*, *T. nanuzae*, and *T. divaricatus* all exhibit the NOR in secondary constrictions near the centromere of the sixth (submetacentric) chromosome. In *T. nanuzae* and *T. amathites* the NOR is in the long arm and in *T. divaricatus* it is in the short arm, presumably due to a pericentric inversion. *T. spinulosus* also has the NOR in the sixth chromosome, but the position is telomeric. We have considered only the chromosome location of the NOR as a character, although position on this chromosome (i.e., centromeric-short arm, centromeric-long arm, telomeric) involves either nonhomology or subsequent inversions.

92. Sex chromosomes (Pellegrino *et al.*, 1994; Kasahara *et al.*, 1986a,b): (0) XY:XX system; (1) X1X2Y:X1X2X2 system. The development of the derived condition involves the centric fusion of the Y chromosome and an autosome (Kasahara *et al.*, 1996). We have assumed that the $m = 36$ karyotype reported for *Leiocephalus* (Paull *et al.*, 1976) represents the plesiomorphic condition. *T. plica* and *T. umbra* have been reported to have, respectively, $2n = 40$ and $2n = 38$ or 39.

APPENDIX 3

Morphological Data Matrix

	0 5 10 15 20 25 30 35 40 45 50 55 58 63 68 73 78 83 88 93
Leiocephalus	00000000000001000001000000000000000000000?00000X?Y000?000000000000000000?000???010???00000?00
Stenocercus	00000000000000000000?000000000000000000000?00100X?Y000?000000000000000000000?010????00?0000????
Uranoscodon	01011000011000000100110001101000000100000?011114?0100?0101010?0100230001 0?01111110?211101000
M. occipitalis	00000000011100000000000001100001000000000?110000?0000?000001000010000000000000000000100001 00??
M. stolzmanni	00000000011100000000000001100001000000000?110010?0000?000001000010000000000000000000100001 00??
T. amathites	10000110012110110010110001101002100000011???0021100 0?00001000010000000000?????????????0?111
T. divaricatus	10000010012111110010010Y1101002100000000????005?0000?000001000010000000100 0?????????????0?111
E. nanuzae	10000010012111110010100011101002100000001101000211000?000001000010000000000011111000200001011
T. cocorobensis	10000010012111110010000101101002110000001 2?1?0020000 0?000010000100001000000?????????????0?000
T. chromatops	100000??0?2??????0100001011010021100000012011002000 00?000010000100001000001100000001000?????
T. etheridgei	10000010012111110010000101101002110000001201100200000?000001000010000100000000000000100001000
T. hygomi	10000010012111110010000101101002110000001201100200000?000001000010000100000000000000100001000
T. erythrocephalus	10000010012111110010000101101002110000001 2???0021000101000010000100001000000?????????????0?000
T. hispidus	10000010012111110011000101101102110000001201100210001000000100001000010000010000000100001000
T. insulanus	10000010012111110010000101101102110000001201?0021000100000010000100011000001?????????????0?0??
T. itambere	10000010012111110010000101101002110000001201100210000?100001000011000100001000010001001001
T. montanus	10000010012111110010000101101102110000001201100220001110000100001000010000000000000100001000
T. mucujensis	10000010012110111010000101101102110000001201100210101110000100001000001000001?????????????0?000
T. oreadicus	10000010012111110010000101101102110000001201100220000?000001000010000100001100011000100001000
T. psammonastes	10000010012111110010000101101002110000001201100200000?000001000010000100000?????????????001
T. torquatus	10000010012111110010000101101102110000001201100200101110000100001000010000110000000100001000
T. bogerti	10000110012110110010001101011102120001011201100 1?011111100 0?000100021000001000010202000?0??
T. melanopleurus	10000010012111110010000101111102120000011101101 3?0110?000101101010002000000200000010100001???
T. callathelys	10000010012111110010000101111102120000001101102 3?0110?000101101010002000002210000010000 0?0??
T. xanthochilus	100000??012??????0100001 01?1?102120000001101102 3?0110?001101102010002000002010111000100001???
T. guarani	10000010012111100010000101111102120000001101102 3?0110?001101102010002000001 0?????????????0?0??
T. spinulosus	10000010012111100010000101011102120000001001102 3?0110?001101102010002000002000111000100001 01?
Tapinurus semitaeniat	10100210012111111111001101121012120001011201100 1?011111000011000100021100001000000201000010?0
Plica plica	10001011112111110111110101101102120000021101112 3?2110?011101212010112000002?111111000110010 00
Plica lumaria	10001011112111110111110101101102120000021101112 3?2110?011101212010112000002?????????????1 0??
Plica umbra	11011011112111110011111001101102120000020?011023?0000?011101112010123000 10??111111000011010 00
Strobilurus	10001011012111110111011101101102120010021101100 0?110?000101102010012001012011111010200001000
U. azureum	10001011012111101111011001000102121010120?011111?0010?010010102111013112002?111111200 0?001???
U. flaviceps	10001011012111101111110001100102121010120?011111?0110?010010102111013102002?111111200 0?001???

Key to polymorphisms (morphology only): X = 0, 2; Y = 0, 1.

APPENDIX 4

Change List for Taxa Shown in Fig. 6

Stem refers to numbered internal stems or terminal taxa shown in Fig. 6. Morph, unambiguously placed morphological characters by stem; Tv, number of unambiguously optimized transversions; Tr, number of unambiguously optimized transitions; Ins, number of unambiguously optimized insertions; Del, number of unambiguously optimized deletions.

Stem 0—Mol: Tv = 65, Tr = 61, Ins = 27, Del = 21. **Stem 1**—Morph: 9.2, 10.1, 25.1, 26.1, 43.1, 59.1, 64.1; Mol: Tv = 15, Tr = 15, Ins = 4, Del = 3. **Stem 2**—Morph: 4.1, 7.1, 17.1, 19.1, 39.2, 62.2, 67.1, 74.2; Mol: Tv = 6, Tr = 4, Ins = 2, Del = 4. **Stem 3**—Morph: 15.0, 16.1, 28.0, 34.1, 38.1, 58.1, 59.0, 63.1, 65.1, 69.1, 71.2, 82.2. **Stem 4**—Morph: 46.1, 55.1, 81.1, 84.0; Mol: Tv = 9, Tr = 14, Ins = 8, Del = 10. **Stem 5**—Morph: 8.1, 46.2, 56.1, 61.1, 66.1; Mol: Tv = 4, Tr = 7, Ins = 5, Del = 1. **Stem 6**—49.2, 60.2; Mol: Tv = 10, Tr = 23, Ins = 7, Del = 1. **Stem 7**—Morph: 33.2, 50.1, 51.1, 60.1, 68.2; Mol: Tv = 14, Tr = 7, Ins = 4, Del = 4. **Stem 8**—Morph: 80.0; Mol: Tv = 10, Tr = 2. **Stem 9**—Mol: Tv = 3, Tr = 5, Ins = 5, Del = 1. **Stem 10**—Morph: 92.1; Mol: Tv = 1, Tr = 2, Del = 1. **Stem 11**—Morph: 75.0. **Stem 12**—Mol: Tr = 2, Tr = 2. **Stem 13**—Mol: Tv = 9, Tr = 5, Ins = 9, Del = 1. **Stem 14**—Mol: Tv =

1, Tr = 7. **Stem 15**—Morph: 29.1, 48.1, 52.1; Mol: Tv = 4, Tr = 2, Del = 2. **Stem 16**—Morph: 54.1; Mol: Tv = 2, Tr = 6, Ins = 2. **Stem 17**—Mol: Tr = 3, Ins = 1, Del = 1. **Stem 18**—Mol: Tv = 4, Tr = 2, Ins = 2, Del = 1. **Stem 19**—Mol: Tv = 1, Tr = 1. **Stem 20**—Morph: 33.1, 47.2, 50.0, 51.0, 60.0, 68.0. **Stem 21**—Morph: 75.1, 76.0, 78.0; Mol: Tv = 13, Tr = 6, Ins = 1, Del = 3. **Stem 22**—Morph: 75.2, 80.0, 82.1. **Stem 23**—Morph: 46.1–2, 47.3, 57.1, 62.1; Mol: Tv = 27, Tr = 27, Ins = 3, Del = 4. **Stem 24**—Morph: 74.2. **Stem 25**—Morph: 15.0, 56.1, 62.2, 75.0. **Stem 26**—Mol: Tv = 7, Tr = 4, Ins = 2, Del = 3. **Stem 27**—0.1, 6.1, 10.2, 12.1, 13.1, 14.1, 15.1, 18.1, 31.2, 32.2; Mol: Tv = 17, Tr = 10, Ins = 3, Del = 4. **Stem 28**—Morph: 20.1, 40.1, 47.2, 48.1, 49.1; Mol: Tv = 13, Tr = 13, Ins = 6, Del = 2. **Stem 29**—Morph: 91.1, 92.1; Mol: Tv = 9, Tr = 11, Ins = 1, Del = 1. **Stem 30**—Morph: 11.1, 31.1; Mol: Tv = 26, Tr = 16, Ins = 10, Del = 5. **Stem 31**—Morph: 42.1, 76.0, 78.0, 80.0, 83.1, 84.0, 88.1. ***Leiocephalus***—NA. ***Microlophus occipitalis***—NA. ***M. stolzmanni***—Morph: 46.1. ***Stenocercus***—Mol: Tv = 22, Tr = 17, Ins = 9, Del = 7. ***Tropidurus amathites***—Morph: 5.1, 13.0; Mol: Tv = 7, Tr = 26, Ins = 2, Del = 7. ***T. azureus***—Morph: 26.0, 50.0, 70.1. ***T. bogerti***—Morph: 5.1, 13.0, 26.0, 37.1, 39.1, 52.1, 54.1, 55.1, 59.0, 82.2; Mol: Tv = 16, Tr = 27, Ins = 4, Del = 3. ***T. callathelys***—Morph: 74.2, 76.1, 84.0. ***T. chromatops***—Morph: 76.1. ***T. cocorobensis***—Mol: Tv = 5, Tr = 21, Ins = 1. ***T. divaricatus***—Morph: 72.1, Tv = 23, Tr = 18, Ins = 4, Del = 4. ***T. erythrocephalus***—Morph: 29.0, 53.0; Mol: Tv = 6, Tr = 16, Ins = 4, Del = 1. ***T. etheridgei***—Mol: Tv = 3, Tr = 18, Ins = 1, Del = 1. ***T. flaviceps***—NA. ***T. guarani***—NA. ***T. hispidus***—Morph: 19.1; Mol: Tv = 2, Tr = 7, Del = 2. ***T. hygomi***—Mol: Tv = 9, Tr = 10, Ins = 2, Del = 2. ***T. insulanus***—Morph: 53.0, 68.1; Mol: Tv = 3, Tr = 21, Ins = 4, Del = 2. ***T. itambere***—Morph: 48.1, 54.1, 65.1, 74.1; Mol: Tv = 5, Tr = 22, Ins = 1. ***T. lumaria***—Mol: Tv = 8, Tr = 16, Ins = 3, Del = 1. ***T. melanopleurus***—Morph: 39.1. ***T. montanus***—Morph: 48.2; Mol: Tv = 5, Tr = 18, Ins = 1, Del = 2. ***T. mucujensis***—Morph: 13.0, 16.1, 50.1, 75.1: Mol: Tv = 3, Tr = 11. ***T. nanuzae***—Morph: 24.1; Mol: Tv = 14, Tr = 29, Ins = 3, Del = 1. ***T. oreadicus***—Morph: 48.2, 52.0, 74.1; Mol: Tv = 4, Tr = 6, Ins = 1, Del = 2. ***T. plica***—Mol: Tv = 17, Tr = 22, Ins = 1, Del = 2. ***T. psammonastes***—Mol: Tv = 5, Tr = 12, Ins = 3, Del = 1. ***T. semitaeniatus***—Morph: 2.1, 5.2, 16.1, 17.1, 19.1, 27.2, 30.1, 37.1, 39.1, 52.1, 54.1, 70.1, 82.2; Mol: Tv = 17, Tr = 21, Ins = 4, Del = 2. ***T. spinulosus***—Morph: 41.0. ***T. strobilurus***—Morph: 73.1, 82.1; Mol: Tv = 23, Tr = 24, Ins = 18, Del = 3. ***T. torquatus***—Morph: 48.0, 50.1, 54.1, 74.1; Mol: Tv = 1, Tr = 6. ***T. umbra***—Morph: 1.1, 3.1, 17.0, 50.0, 51.0, 67.2, 72.1, 87.1; Mol: Tv = 25, Tr = 23, Ins = 14, Del = 2. ***T. xanthochilus***—Morph: 76.1. ***Uranoscodon***—Morph: 1.1, 3.1, 4.1, 17.1, 20.1, 35.1, 45.1, 46.1, 47.4, 50.1, 55.1, 57.1, 61.1, 67.2, 68.3, 72.1, 81.1, 85.1, 86.1, 87.1; Mol: Tv = 27, Tr = 29, Ins = 10, Del = 8.

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