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PHYLOGENETIC RELATIONSHIPS WITHIN IGUANIDAE INFERRED USING MOLECULAR AND MORPHOLOGICAL DATA AND A PHYLOGENETIC TAXONOMY OF IGUANIAN LIZARDS

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ABSTRACT: We present phylogenetic analyses of 42 new partial mitochondrial-DNA sequences in combination with 28 previously published sequences representing all eight major groups of the lizard clade Iguanidae (sensu lato). These sequences include 1838 aligned positions (1013 parsimony informative for ingroup taxa) extending from the protein-coding gene *ND1* (subunit one of NADH dehydrogenase) through the genes encoding $tRNA^{Ile}$, $tRNA^{Gln}$, $tRNA^{Met}$, ND2 (NADH dehydrogenase subunit two), $tRNA^{Trp}$, $tRNA^{Ala}$, $tRNA^{Asn}$, $tRNA^{Cys}$, $tRNA^{Tyr}$, to the protein-coding gene *COI* (subunit I of cytochrome c oxidase). These data, analyzed in combination with 67 previously published morphological characters, provide statistical support for monophyly of iguanid clades Corytophaninae, Crotaphytinae, Hoplocercinae, Iguaninae, Oplurinae, and Phrynosomatinae. Monophyly is neither supported nor statistically rejected for Polychrotinae and Tropidurinae. Polychrotinae* and Tropidurinae* may be recognized as metataxa, to denote the fact that evidence for their monophyly is equivocal, or replaced by recognizing constituent groups whose monophyly has stronger empirical support. A phylogenetically (non-ranked) based, statistically robust taxonomy of iguanian lizards is proposed. The Old World lizard clade, Acrodonta, is composed of Chamaeleonidae and Agamidae* with the Agaminae, Amphibolurinae, Draconinae, Hydrosaurinae, Leiolepidinae, and Uromastycinae nested within Agamidae*. The predominately New World clade, Iguanidae, contains the groups Corytophaninae, Crotaphytinae, Hoplocercinae, Iguaninae, Oplurinae, Phrynosomatinae, Polychrotinae*, and Tropidurinae*; with *Anolis*, Leiosaurini (composed of the Leiosaurae and Anisolepae), and *Polychrus* as the subgroups of Polychrotinae*; and *Leiocephalus*, Liolaemini, and Tropidurini as the subgroups of Tropidurinae*.

Key words: Iguania; Iguanidae; Metataxon; Phylogenetic taxonomy; Polychrotinae; Squamata; Topology test; Tropidurinae

TAXONOMY of the predominantly New World lizard clade Iguanidae has been revised numerous times. For almost half a century, the suborder Iguania contained three families, Agamidae, Chamaeleonidae, and Iguanidae (sensu lato) (Camp, 1923). Using morphological characters, Etheridge and de Queiroz (1988) hypothesized eight major groupings within Iguanidae. Frost and Etheridge (1989) examined higher level relationships among iguanian lizards and were unable to find support for monophyly of either Iguanidae or Agamidae (sensu Estes et al., 1988). Thus, they recognized the eight major groups of Iguanidae identified by Etheridge and de Queiroz (1988) as eight families and placed Agamidae in synonymy with the family Chamaeleonidae. Based on combined molecular and morphological data supporting monophyly of Iguanidae (sensu lato), Macey et al. (1997*a*) recommended that the eight families of Frost and Etheridge (1989) be recognized as the iguanid subfamilies Corytophaninae, Crotaphytinae, Hoplocercinae, Iguaninae, Oplurinae, Phrynosomatinae, Polychrotinae, and Tropidurinae.

Macey et al. (1997*a*) demonstrated strong support for monophyly of Iguanidae (sensu lato), but their sampling was not adequate to establish monophyly of the eight proposed subfamilies. Schulte et al. (1998) sampled 10 additional species in Iguanidae, including multiple representatives of Crotaphytinae, Iguaninae, Phrynosomatinae, and Tropidurinae*. Combined and separate analyses of DNA sequence and morphological data revealed strong support for monophyly of Iguanidae (sensu lato), consistent with the results of Macey et al. (1997*a*) and subsequent analyses of nuclear DNA data (Harris et al., 2001; Saint et al., 1998). Strong support was found for monophyly of Crotaphytinae and

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Phrynosomatinae; however, monophyly of Iguaninae was weakly supported, and the three major groups of Tropidurinae (*Leiocephalus*; *Ctenoblepharys*, *Liolaemus*, and *Phymaturus*; *Microlophus*, *Plica*, *Stenocercus*, *Tropidurus*, *Uracentron*, and *Uranoscodon*—included in the analyses presented here) did not form a monophyletic group, although monophyly of this group could not be rejected statistically. For that reason, Schulte et al. (1998) presented a modified definition for the metataxon concept (Estes et al., 1988; Gauthier et al., 1988) to provide a more stable taxonomy for iguanid lizards. Tropidurinae* was designated as a metataxon, which is defined as a traditionally recognized group whose monophyly is statistically equivocal. This metataxon definition adds a statistical criterion to its usage as discussed by Schwenk (1994).

Recent molecular phylogenetic studies have addressed the relationships among taxa within the presumed clades Iguaninae (Petren and Case, 1997; Rassmann, 1997; Sites et al., 1996; Wiens and Hollingsworth, 2000), Oplurinae (Titus and Frost, 1996), Phrynosomatinae (Reeder, 1995; Reeder and Wiens, 1996), Polychrotinae (Frost et al., 2001*a*), and Tropidurinae* (Frost et al., 2001*b*). These studies include outgroups from four or fewer representatives of the other major iguanid groups. Although not the intention of the original studies, rigorous testing of monophyly of these presumed clades was precluded with this limited outgroup sampling.

Separate analyses of molecular and morphological data by Frost et al. (2001*a*) revealed, respectively, nonmonophyly and monophyly of Polychrotinae relative to one scleroglossan and three iguanid outgroups. Combined analysis of these data failed to recover a monophyletic Polychrotinae, with *Basiliscus basiliscus* forming the sister taxon to a clade containing *Anolis* and *Polychrus*. However, no attempt was made to test the alternative hypothesis of monophyly using statistical tests. Based on these results and those of previous studies, Frost et al. (2001*a*) proposed another revision of iguanian taxonomy. Briefly, their taxonomy removed Agamidae from the Chamaeleonidae; synonymized Iguanidae (sensu lato) with Pleurodonta; elevated Leiocephalinae, Liolaeminae, and Tropidurinae to familial status; redefined Polychrotidae to include only *Anolis* and *Polychrus*; and created three additional taxa, Leiosauridae (South American leiosaurs, *Enyalius*, and para-anoles), Leiosaurinae (leiosaurs), and Enyaliinae (*Enyalius* and para-anoles).

To investigate relationships among the major lineages of iguanid lizards, we present 42 new mitochondrial-DNA sequences analyzed in combination with 28 previously published sequences (Macey et al., 1997*a*; Schulte et al., 1998, 2000) representing all eight previously recognized major groups of Iguanidae. Sequences reported here extend from the mitochondrial-encoded protein-coding gene *ND1* (subunit one of NADH dehydrogenase) through the genes encoding $tRNA^{Ile}$, $tRNA^{Gln}$, $tRNA^{Met}$, ND2 (NADH dehydrogenase subunit two), $tRNA^{Trp}$, $tRNA^{Ala}$, $tRNA^{Asn}$, $tRNA^{Cys}$, $tRNA^{Tyr}$, to the protein-coding gene *COI* (subunit I of cytochrome c oxidase). These data are analyzed in combination with previously published morphological data (Frost and Etheridge, 1989; Schulte et al., 1998). Higher level iguanian lizard taxonomy follows the recommendations of Macey et al. (1997*a*, 2000) and Schulte et al. (1998).

Materials and Methods

Specimen Information

Museum numbers and approximate localities for voucher specimens from which mitochondrial DNA was extracted and GenBank accession numbers are presented in Appendix 1 for 42 newly sequenced ingroup taxa followed by GenBank accession numbers for the 25 previously published ingroup sequences and 3 outgroup sequences. The ingroup taxon sampling includes 38 genera and 67 species within Iguanidae.

Laboratory Protocols

Genomic DNA was extracted from liver or muscle using the Qiagen QIAamp tissue kit. Amplification of genomic DNA was conducted using a denaturation at 94 C for 35 s, annealing at 50 C for 35 s, and extension at 70 C for 150 s with 4 s added to the extension per cycle for 30 cycles. Negative controls were run on all amplifications to check for contamination.

Amplified products were purified on 2.5% Nusieve GTG agarose gels and reamplified under the conditions described above. Reamplified double-stranded products were purified on 2.5% acrylamide gels (Maniatis et al., 1982). Template DNA was eluted from acrylamide passively over 3 d with Maniatis elution buffer (Maniatis et al., 1982). Cycle-sequencing reactions were run using either the Promega fmol DNA sequencing system with a denaturation at 95 C for 35 s, annealing at 45–60 C for 35 s, and extension at 70 C for 1 min for 30 cycles or ABI Prism Big Dye Terminator DNA Sequencing Kit (Perkin-Elmer) with a denaturation at 95 C for 15 s, annealing at 50 C for 1 s, and extension at 60 C for 4 min for 35–40 cycles. Sequencing reactions were run on Long Ranger sequencing gels for 5–12 h at 38–40 C and ABI 373 or MJ Research Basestation sequencers.

Amplifications of the ND1 gene to the *COI* gene from genomic DNA were done with different primer combinations. Most samples were amplified with L3002, L3914, or L4160 in combination with H4980. In addition, all samples were amplified with L4437 in combination with H5934 or H6159. Both strands were sequenced using L3914, L4160, L4221a, L4221b, H4419a, H4419c, L4437, H4557, H4629, H4617, L4645, L4831b, L4882a, L4882b, L5549a, L5549b, L5556, H5617b, L5638b, H5692, H5689, H5934, and H6159. The DNA sequence data from *Stenocercus doellojuradoi* was amplified also using the primer pairs L4882a and H5692, and L5549b and H6159, to yield smaller fragments of DNA. Most primers are as described by Macey et al. (1997*b*) except L3914, which is erroneously reported in Macey et al. (1998) as L3878. Additional primers used include L4160 (Kumazawa and Nishida, 1993), L4882a (Macey et al., 1999), H4419c, H5689, H4629 (Macey et al., 2000), L4882b (Schulte et al., 1998), L5549a (Townsend and Larson, 2002), and H6159 (Weisrock et al., 2001). Five primers are new to this study: L4221b 5′-AAGGGNTACTTTGATAGAGT-3′; H4557 5′-TGAR TTGGCYTAGAGATAAAYAC-3′; H4617 5′-CCACGAGCNACAGAAGCCGCAACAA -3′; L4831b 5′- TGACTACCAGAAGTNCTACAA GG -3′; and L5549b 5′- AACCAAGRGCCTT CAAAG-3′. Primer numbers refer to the 3′ end on the human mitochondrial genome (Anderson et al., 1981), where L and H denote primers whose extension produces the light and heavy strands, respectively. Sixty-seven morphological characters from Frost and Etheridge (1989) were analyzed in combination with DNA sequences (Appendix II). Morphological character states for *Sator* are from Schulte et al. (1998). Character state data and aligned DNA sequences are available in TreeBASE (Study accession S847; Matrix accession number M1365).

Phylogenetic Analysis

The DNA sequences were aligned initially by eye. Positions encoding part of ND1, all of ND2, and part of COI were translated to amino acids using MacClade 4.03 (Maddison and Maddison, 2001) for confirmation of alignment. Alignments of sequences encoding tRNAs were based on secondary structural models (Kumazawa and Nishida, 1993; Macey and Verma, 1997). Secondary structures of tRNAs were inferred from primary structures of the corresponding tRNA genes using these models. Unalignable regions were excluded from phylogenetic analyses (see Results).

Phylogenetic trees were estimated using PAUP* beta version 4.0b8 (Swofford, 2001) with 200 heuristic searches featuring random taxon addition using maximum parsimony (MP). Bootstrap resampling (Felsenstein, 1985*a*) was applied to assess support for individual nodes using 1000 bootstrap replicates with 10 random taxon additions per replicate. Decay indices (= "branch support" of Bremer, 1994) were calculated for all internal branches using TreeRot.v2b (Sorenson, 1999). Maximum-likelihood (ML) analyses also were performed on the molecular data. Simultaneous optimization of ML parameters and phylogenetic hypotheses for this data set was computationally impractical. To reduce computation time, ModelTest v3.06 (Posada and Crandall, 1998) was used to find the best fitting model of sequence evolution for the tree from unweighted parsimony analysis of these molecular data. Posada and Crandall (2001) found that the starting tree did not significantly influence the estimated parameters found by ModelTest. The best fitting model parameters were fixed, then used in 25 heuristic searches with random addition of taxa to find the overall best likelihood topology. Bootstrap analysis of

the maximum-likelihood tree was computationally intractable. To evaluate support for branches of the ML tree, each branch on the highest likelihood tree was individually collapsed to form a polytomy. The likelihood score of each tree with one collapsed node was compared to the highest likelihood tree using a likelihood ratio tested against a chi-squared distribution with one degree of freedom (Rice, 1995). This method is similar to that described by Slowinski (2001) and yields almost identical results. In our evaluation of branch support strength, we consider a bootstrap value of 95% and above as strongly supported (Felsenstein and Kishino, 1993), 95–70% as moderately supported, and below 70% as poorly supported.

Bayesian analysis was used to estimate a phylogenetic tree using many of the default values in MrBayes 2.1 (Huelsenbeck and Ronquist, 2001). All analyses were initiated from random starting trees and run for 2,000,000 generations using four incrementally heated Markov chains. Values of the likelihood model selected from the best-fit model of nucleotide substitution using ModelTest were estimated from the data and initiated using flat priors. Trees were sampled every 100 generations resulting in 20,000 saved trees. To ensure that Bayesian analyses reach stationarity, the first 5000 saved trees were discarded as "burn-in" samples following Leaché and Reeder (2002). Three analyses were run independently, beginning with different starting trees, to check that searches did not become trapped on local optima. For all three runs, log-likelihood scores converged on similar values. Sampled trees from all three runs were combined to yield 45,000 saved trees. These trees were used to generate a 50% majority-rule consensus tree in PAUP* and the percentage of trees having a particular clade represented that clade's posterior probability (Huelsenbeck and Ronquist, 2001).

Wilcoxon signed-ranks (WSR) tests (Felsenstein, 1985*b*; Templeton, 1983) were used to examine statistical significance of the shortest tree relative to alternative hypotheses. This test determines whether the most parsimonious tree is significantly shorter than an alternative tree or whether their differences in length are statistically indistinguishable (Larson, 1998). Wilcoxon signed-ranks tests were conducted as two-tailed tests (Felsenstein, 1985*b*). Tests were conducted using PAUP* (Swofford, 2001), which incorporates a correction for tied ranks. Goldman et al. (2000) criticized the application of the WSR test as applied in this study. Therefore, Shimodaira-Hasegawa (SH) tests (Shimodaira and Hasegawa, 1999), as advocated by Goldman et al. (2000), also were performed to test the shortest tree relative to the shortest alternative hypotheses using 10,000 resampling estimated log-likelihood (RELL) approximations in PAUP* as a comparison with the results of WSR tests.

Alternative phylogenetic hypotheses for WSR tests were tested using the most-parsimonious phylogenetic topologies compatible with them. To find the most-parsimonious tree(s) compatible with a particular phylogenetic hypothesis, phylogenetic topologies were constructed using MacClade (Maddison and Maddison, 2001) and analyzed as constraints using PAUP* (Swofford, 2001) with 200 heuristic searches with random addition of sequences. Alternative ML topologies used for SH tests were found as above except that a maximum-likelihood search using the overall shortest parsimony tree with a given constraint was used as a starting tree for branch swapping to obtain the alternative tree with the highest likelihood. Alternative trees are available from the first author upon request.

Three sets of phylogenetic analyses were performed. The first was an analysis of the molecular data alone using MP, ML, and Bayesian methods. The second set of analyses combined molecular and morphological characters into a single data set that was analyzed using MP. However, morphological data were available for only 33 taxa sampled here. Frost and Etheridge (1989) used the largest monophyletic groups within Iguania that could be corroborated as their terminal taxa. Morphological characters with states of uncertain "ancestral" status for terminal taxa were coded as unknown following the criteria of Frost and Etheridge (1989). The combined data set was analyzed in two ways. An analysis was performed with only those 33 taxa that had complete data for both molecules and morphology. For the analysis presented here, a single, representative mitochondrial DNA sequence was chosen from each of the 30

presumed monophyletic iguanid groups and three outgroup taxa and indicated in Appendix I. The second combined data set included all taxa sampled for DNA sequences. As with the previous combined analysis, morphological data for each presumed monophyletic group were combined with its representative DNA sequence as above. Two coding schemes were used for the morphological data set to determine if the resultant topology would be affected by inclusion of missing data: (1) data coded as missing (question marks) for those taxa not selected as representatives in the combined analysis (see Appendix I) and (2) all taxa in each presumed monophyletic group of Frost and Etheridge (1989) coded with the morphological data for that group. Finally, we analyzed the morphological characters alone from the 33 presumed monophyletic groups of Frost and Etheridge (1989) used in the combined data set as discussed above.

The four-taxon *S*-test of Felsenstein (1985*b*) was used, following Jackman et al. (1999) to distinguish between simultaneous or near simultaneous branching from a common ancestral lineage (hard polytomy) and sequential branching of lineages that have short internodes (soft polytomy) in poorly supported areas of the phylogenetic hypothesis. This technique evaluates whether removing taxa that subdivide internal branches increases support for phylogenetic groupings of the remaining taxa. Significant decay-index values for four-taxon statements were obtained from Jackman et al. (1999) and Weisrock et al. (2001).

Additional tests of phylogenetic signal (Archie, 1989; Faith and Cranston, 1991; Hillis, 1991) were conducted to evaluate weakly supported branches in Iguanidae. The distribution of informative characters (sequence data) on a hard polytomy should be random (Jackman et al., 1999); in contrast, on a soft polytomy, the distribution of informative characters is expected to differ significantly from random. We employed a permutation tail probability test (PTP) using representatives from well supported groups with 1000 randomizations. This test randomizes the data among the taxa sampled and then optimizes this randomized data set on the phylogenetic hypothesis from the original data. If more than 5% of the randomized data sets yields tree lengths lower than the one from the original data set, then the null hypothesis of no phylogenetic signal is not rejected. A second test used was the skewness test (g_1; Hillis and Huelsenbeck, 1992) of the frequency distribution of 10,000 randomly generated trees, obtained using MacClade, with the constraint that weakly supported branches among iguanid lineages form a hard polytomy. Therefore, significant skewness of randomly generated trees using these lineages was not expected if the data were random with respect to those lineages. Finally, likelihood-ratio tests (LRTs) were performed as discussed above to identify branches in the ML tree that were significantly different from zero-length.

Results

Sequence Alignment and Character Homology

Of the 1838 aligned positions, 221 positions were judged unsuitable for phylogenetic analysis. Protein-coding genes were alignable for most regions, but amino acids encoded at the C-terminal ends of ND1 and ND2 (positions 76–94, 1351–1372) were excluded from some regions because of questionable alignment.

All iguanids sequenced had the typical vertebrate mitochondrial gene order (Macey et al., 1997*a*,*b*). *Chamaeleo* and *Leiolepis* have the genes for $tRNA^{Ile}$ and $tRNA^{Gln}$ switched in order (Macey et al., 1997*a*). These gene sequences in *Chamaeleo* and *Leiolepis* were changed to the typical vertebrate gene order to align with the ingroup taxa (for *Chamaeleo* GenBank U82688, positions 72–151 are placed after position 219; for *Leiolepis* GenBank U82689, positions 81–165 are placed after position 235). Among tRNA genes, several loop regions were unalignable, as were noncoding regions between genes. Various nucleotide positions in the dihydrouridine (D) and TΨC (T) loops for the genes encoding $tRNA^{Ile}$ (positions 109–116, 149–156), $tRNA^{Met}$ (positions 271–273, 307–312), $tRNA^{Trp}$ (positions 1386–1395, 1428–1434), $tRNA^{Ala}$ (positions 1477, 1510–1512), $tRNA^{Cys}$ (positions 1698–1704, 1659–1666), and $tRNA^{Tyr}$ (positions 1742–1746, 1781–1788) were excluded from the analyses. *Basiliscus plumifrons* has an unusual $tRNA^{Asn}$ in which the variable loop is seven bases (Macey et al., 1997*a*) instead of the standard 3–5 bases, making this loop

unalignable (positions 1561–1567). The variable loops of the $tRNA^{Trp}$ (positions 1418–1422) and $tRNA^{Cys}$ genes (positions 1672–1676) were not alignable. A short portion of D-loop was excluded from the genes encoding $tRNA^{Gln}$ (positions 223–228) and $tRNA^{Asn}$ (positions 1590–1593). Noncoding sequences between the genes encoding $tRNA^{Ile}$ and $tRNA^{Gln}$ (positions 169–171), $tRNA^{Gln}$ and $tRNA^{Met}$ (positions 243–255), $tRNA^{Met}$ and ND2 (positions 326–327), $tRNA^{Trp}$ and $tRNA^{Ala}$ (positions 1448–1457), $tRNA^{Ala}$ and $tRNA^{Asn}$ (positions 1528–1535), $tRNA^{Cys}$ and $tRNA^{Tyr}$ (positions 1717–1728), and $tRNA^{Tyr}$ and *COI* (positions 1802–1808) were not used.

All taxa used for phylogenetic analysis appear to have a recognizable origin for light-strand replication (O_L) between the $tRNA^{Asn}$ and $tRNA^{Cys}$ genes by the criteria outlined in Macey et al. (1997*b*). However, the outgroups, *Chamaeleo* and *Leiolepis*, have unusual stem-and-loop structures that contain a shortened stem of 7–8 base pairs in length (Macey et al., 1997*a*). In addition, the O_L stem is nearly invariant (positions 1611–1612 could not be adequately aligned and were excluded) in the ingroup and the O_L loop is not alignable; therefore, this region (positions 1623–1636) was excluded. Coding regions other than the anticodon stem and loop in the *Chamaeleo* and *Leiolepis* $tRNA^{Cys}$ gene (positions 1646–1676, 1694–1716) were coded as missing data because this gene contains a D-arm replacement loop instead of a D-stem, and the AA- and T-stems may shift as a result (Macey et al., 1997*c*). Excluded regions comprise 12% (221 of 1838) of the aligned sequence positions. The aligned sequences have been deposited in GenBank and TreeBASE.

Genetic and Morphological Variation

Forty-two new mitochondrial DNA sequences range in size from 1720–1746 bases and are aligned with 3 outgroup and 9 ingroup sequences from Macey et al. (1997*a*), 10 ingroup sequences from Schulte et al. (1998), and 6 additional ingroup sequences from Schulte et al. (2000) for a total of 1838 aligned positions. Sequences reported here are inferred to be authentic mitochondrial DNA, based on the criteria of Macey et al. (1997*a*,*b*). All sequences show strong strand bias against guanine on the light strand (G = 10.9–13.5%, T = 22.2–29.8%, A = 31.1–36.3%, and C = 24.5–33.1%), which is characteristic of the mitochondrial genome but not the nuclear genome. In the phylogenetic analysis of 1617 unambiguous sites in 70 aligned sequences, 1200 (1132 ingroup only) are variable and 1062 (1013 ingroup only) are phylogenetically informative (parsimony criterion) (Table 1). The morphological data contribute 63 (56 ingroup only) informative characters.

Phylogenetic Relationships

Analysis of the 67 morphological characters produced 12 equally most-parsimonious trees, each with a length of 194 steps (Fig. 1). Crotaphytinae, Iguaninae, Phrynosomatinae, and Oplurinae were recovered as monophyletic groups with fairly good heuristic support (Crotaphytinae—96% bootstrap, decay index 5; Iguaninae—89% bootstrap, decay index 4; Oplurinae—92% bootstrap, decay index 5; Phrynosomatinae—97% bootstrap, decay index 6). Hoplocercinae contained only one representative, *Enyalioides laticeps*, so monophyly of this group could not be assessed. Corytophaninae, Polychrotinae, and Tropidurinae* were monophyletic in the consensus tree, but their support was weak (Corytophaninae—52% bootstrap, decay index 2; Polychrotinae—63% bootstrap, decay index 4; Tropidurinae*—<50% bootstrap, decay index 1).

Analysis of DNA sequence data produced a single most-parsimonious tree of 13,096 steps (Fig. 2). As with previous molecular phylogenetic analyses, Iguanidae (sensu lato) receives strong support (100% bootstrap, decay index 31). Corytophaninae, Crotaphytinae, Hoplocercinae, Oplurinae, and Phrynosomatinae are recovered as monophyletic groups with strong support (Corytophaninae—100% bootstrap, decay index 39; Crotaphytinae—100% bootstrap, decay index 48; Hoplocercinae—100% bootstrap, decay index 20; Oplurinae—100% bootstrap, decay index 51; Phrynosomatinae—100% bootstrap, decay index 29). Iguaninae is also monophyletic, albeit with marginal support (76% bootstrap, decay index 8).

Both Polychrotinae and Tropidurinae* are nonmonophyletic; each group is split into three subgroups in the parsimony analysis of molecular data. *Anolis*, *Leiocephalus*, and *Polychrus* receive strong support for their monophyly (98% bootstrap, decay index 20;

TABLE 1.—Distribution of phylogenetically informative and variable positions.

	ND1 codon positions			$tRNA^{Ile}$*		$tRNA^{Gln}$†		$tRNA^{Met}$*	
	1st	2nd	3rd	Stem	Non-stem	Stem	Non-stem	Stem	Non-stem
Informative sites	17	11	25	30	7	25	10	20	4
Variable sites	19	14	25	34	7	31	12	25	7
	ND2 codon positions			$tRNA^{Trp}$*		$tRNA^{Ala}$*		$tRNA^{Asn}$†	
	1st	2nd	3rd	Stem	Non-stem	Stem	Non-stem	Stem	Non-stem
Informative sites	235	157	334	29	2	24	9	32	7
Variable sites	264	200	339	31	4	31	12	35	9
	$TRNA^{Cys}$*		$tRNA^{Tyr}$*		*COI* codon positions				
	Stem	Non-stem	Stem	Non-stem	1st	2nd	3rd		
Informative sites	21	5	31	14	4	2	7		
Variable sites	29	5	36	16	5	3	7		
	Protein coding codon positions			tRNA					
Total	1st	2nd	3rd	Stem	Non-stem	Morphological data	All aligned sequence		
Informative sites	256	170	366	212	58	63	1062		
Variable sites	288	217	371	252	72	65	1200		

* Not including D- and T-loops, which were excluded from the analyses.
† Not including part of the D-loop, which was excluded from the analyses.

100% bootstrap, decay index 49; 100% bootstrap, decay index 38; respectively), but their relationships to other iguanids are equivocal. The leiosaurs, *Enyalius*, and para-anoles of Polychrotinae form a strongly supported group (100% bootstrap, decay index 40). The major lineages of tropidurines (Macey et al., 1997*a*) are recovered; former Liolaeminae of Frost and Etheridge (1989) (composed of *Ctenoblepharys*, *Liolaemus*, and *Phymaturus*) receives weak support (62% bootstrap, decay index 8); and *Liolaemus* and *Phymaturus* are joined with moderate support (93% bootstrap, decay index 15). Former Tropidurinae of Frost and Etheridge (1989) (composed of *Microlophus*, *Plica*, *Tropidurus*, *Uracentron*, and *Uranoscodon* analyzed here) is grouped with moderate support (77% bootstrap, decay index 8), and a group containing all taxa except *Stenocercus* is well supported (98% bootstrap, decay index 21). All nodes connecting the major groups of polychrotines and tropidurines receive weak support.

The combined molecular and morphological data using coding scheme one recovered a single most-parsimonious tree of 13,327 steps (Fig. 3). Analysis of combined data according to coding scheme two produced 10 equally most-parsimonious trees, one of which was the topology produced from coding scheme one (results not shown). Differences in tree topology were confined to branches with decay indices of <2; therefore, further analyses are performed using analyses of coding scheme one to simplify results. The topology of this tree is similar to that from the molecular data alone, except for relationships among the major lineages deep in the tree. Support for individual nodes is similar to that obtained from the molecular data alone. Three groups increased in support: Iguaninae (96% bootstrap, decay index 11); monophyly of the Liolaeminae of Frost and Etheridge (1989) (87% bootstrap, decay index 10); and monophyly of Tropidurinae of Frost and Etheridge (1989) (94% bootstrap, decay index 11). Only one group noticeably decreased in support; the decay index for a sister-taxon relationship of *Anolis* and *Leiocephalus* dropped from 11 to 4.

The combined analysis using only those taxa with the full complement of morphological and molecular data produced five equally most-parsimonious trees, each with lengths of 7380 steps (Fig. 4). In general, results are similar to those from combined analysis of all taxa sampled here. Corytophaninae, Crotaphytinae, Iguaninae, Oplurinae, and Phrynosomatinae are recovered as monophyletic groups with rather strong heuristic support (Corytophaninae—100% bootstrap,

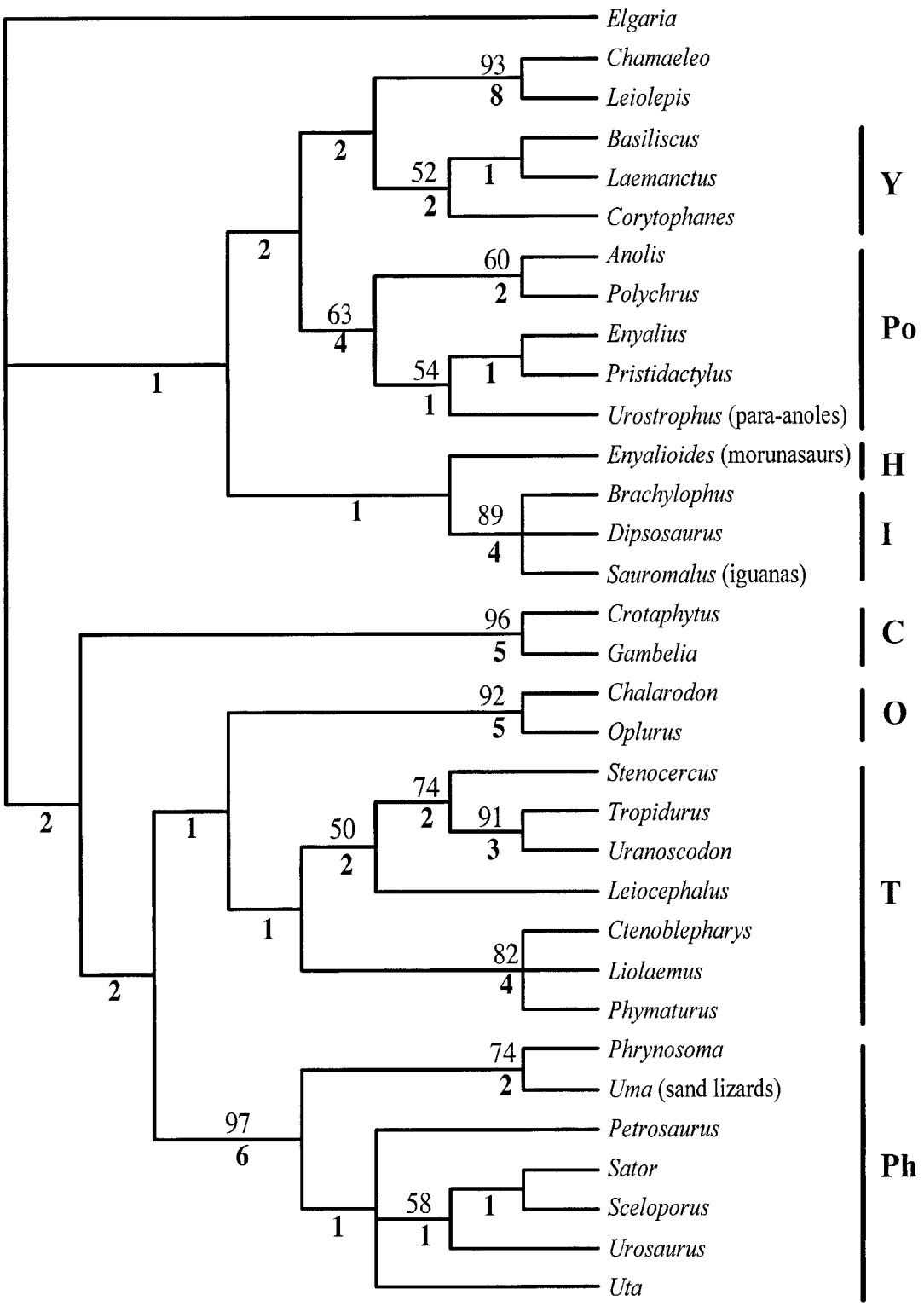

FIG. 1.—Strict consensus of 12 equally most-parsimonious trees generated from analysis of morphological data (length = 194). Bootstrap values are presented above branches and decay indices are shown in bold below branches. Major iguanid clades are labeled as follows: Y, Corytophaninae; Po, Polychrotinae*; H, Hoplocercinae; I, Iguaninae; C, Crotaphytinae; O, Oplurinae; T, Tropidurinae*; Ph, Phrynosomatinae. Monophyly of the Polychrotinae* and Tropidurinae* is weakly supported.

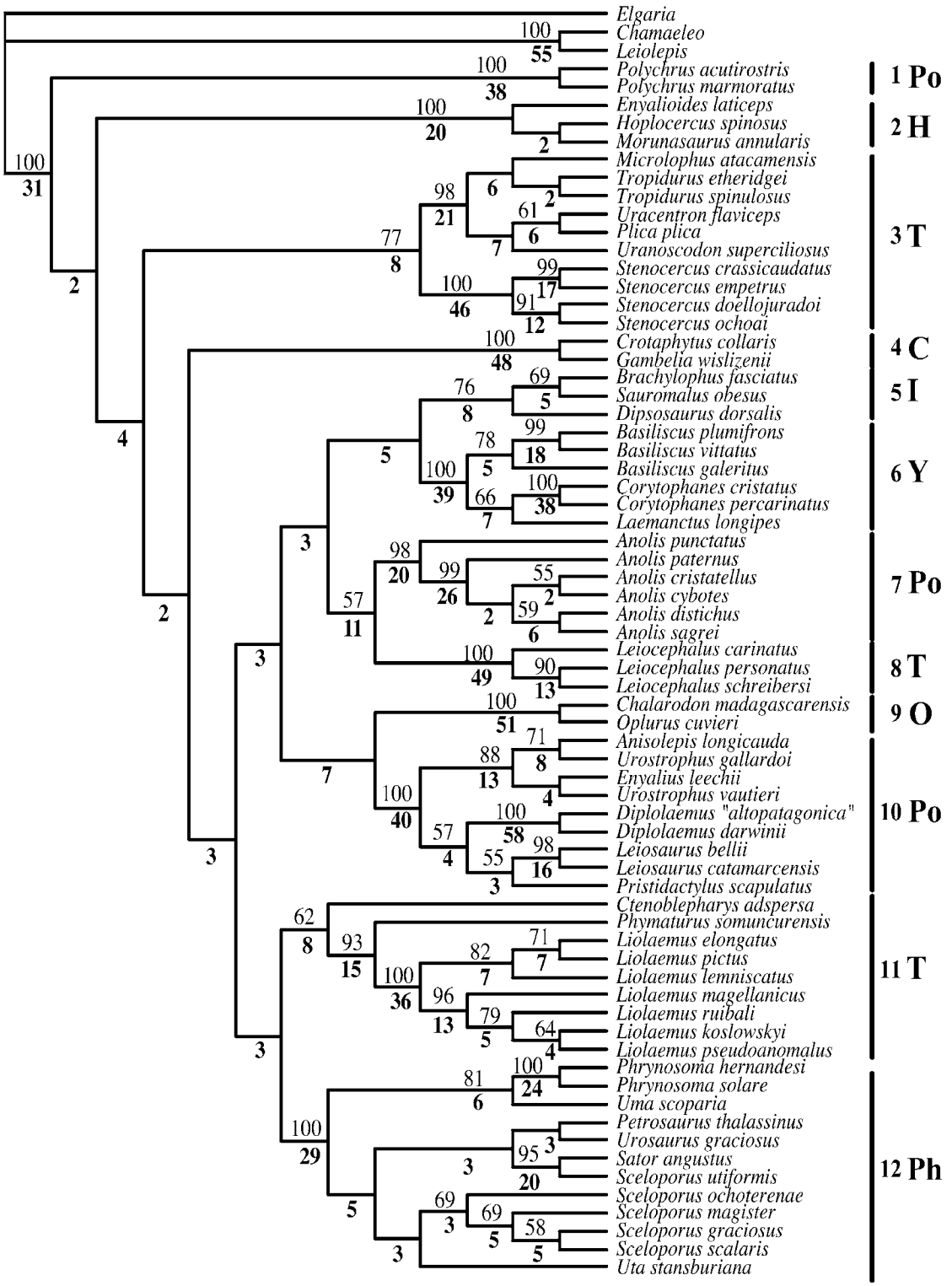

FIG. 2.—Phylogenetic relationships among iguanid lizards based on analysis of molecular data (length = 13,096). Bootstrap values are presented above branches and decay indices are shown in bold below branches. Iguanid clades are labeled as in Figure 1. Numbered bars indicate the 12 lineages used in tests for hard polytomy, g_1-statistic, PTP test, and four-taxon subsampling.

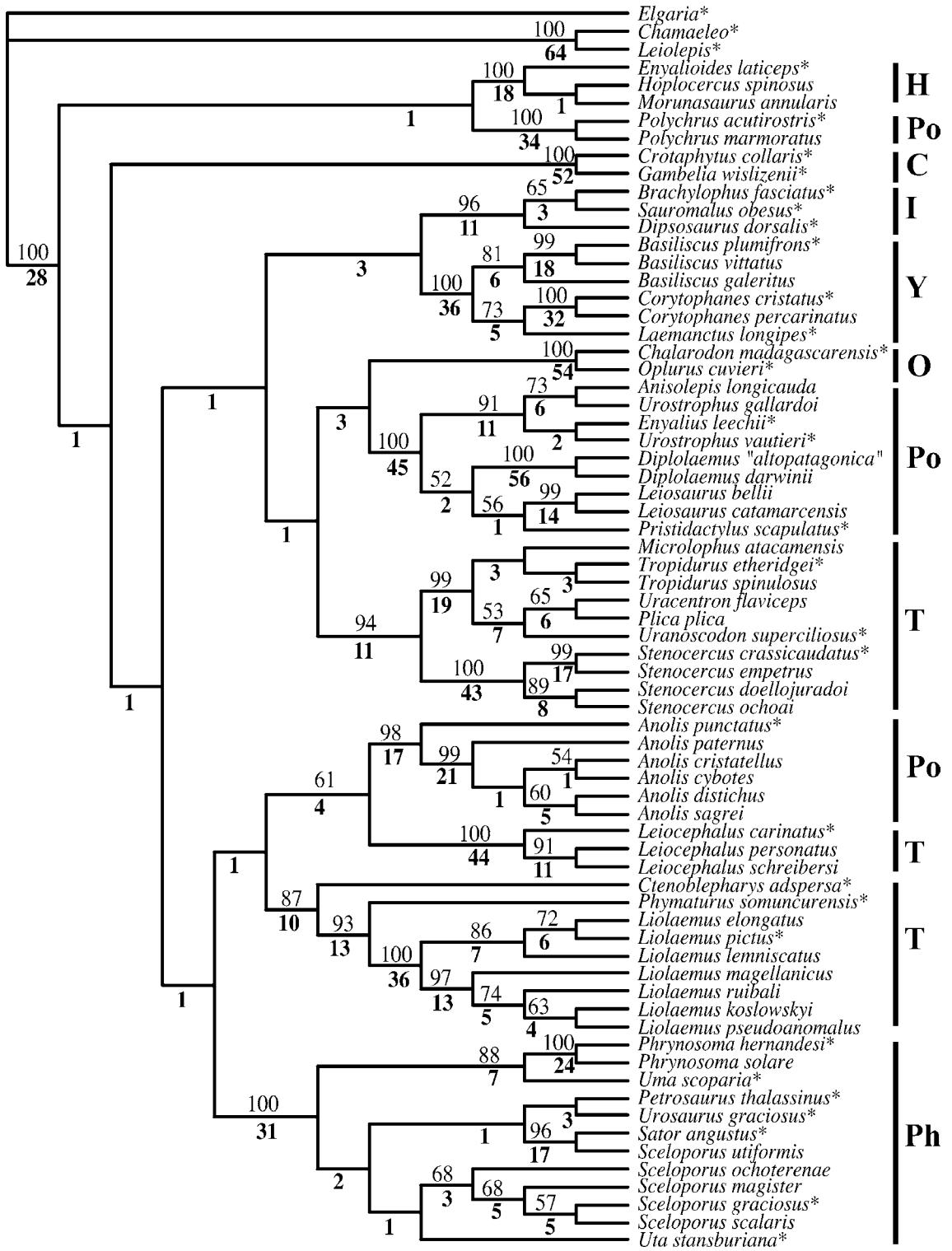

FIG. 3.—Phylogenetic relationships among iguanid lizards based on analysis of combined data including all taxa sampled (length = 13,327). Specific taxa used as representatives of larger monophyletic groups to combine with morphological data are denoted with an asterisk. Bootstrap values are presented above branches and decay indices are shown in bold below branches. Clade labels follow Figure 1.

decay index 28; Crotaphytinae—100% bootstrap, decay index 54; Iguaninae—92% bootstrap, decay index 12; Oplurinae—100% bootstrap, decay index 49; Phrynosomatinae—100% bootstrap, decay index 26), and Polychrotinae and Tropidurinae* are recovered as nonmonophyletic with weak support for branches deep in the phylogenetic tree.

Hierarchical likelihood-ratio tests, as implemented in ModelTest, find that the most complex model (GTR + I + Γ) best explains the DNA sequence data and topology of the overall most-parsimonious tree. Model parameters are as follows: $\alpha = 0.529$; proportion of invariant sites = 0.210; substitution rates R(a) = 0.177, R(b) = 3.565, R(c) = 0.275, R(d) = 0.251, and R(e) = 1.908; and estimated base frequencies A = 0.419, C = 0.342, G = 0.043, and T = 0.197. A single optimal tree is found (Fig. 5) with a negative log-likelihood of 51,306.7. Topological differences between results of parsimony and likelihood analyses are restricted to branches that are not strongly supported by parsimony. Monophyly is recovered for Corytophaninae, Crotaphytinae, Hoplocercinae, Iguaninae, Oplurinae, and Phrynosomatinae by likelihood analysis, as is nonmonophyly for Tropidurinae* and Polychrotinae, consistent with the results of parsimony.

Bayesian analysis performed using the GTR + I + Γ nucleotide substitution model and parameters estimated from the sequence data includes 60,000 saved trees, 15,000 of which are considered "burn-in," leaving 45,000 trees. A 50% majority-rule consensus tree of the 45,000 trees has an almost identical topology as the maximum-likelihood tree with a mean log-likelihood of –51495.80 and variance of 86.54 (Fig. 5). All groupings that received strong heuristic support from parsimony and likelihood analyses occurred in 100% of the 45,000 trees from the Bayesian analysis. Comparison of branch support, as assessed using parsimony, and Bayesian criteria is consistent with the suggestion that Bayesian posterior probabilities generally overestimate support for branches in the tree (Suzuki et al., 2002).

Monophyly of Taxonomic Groups

All analyses showed monophyly of Corytophaninae. However, only molecular data could statistically reject the alternative hypothesis of a nonmonophyletic Corytophaninae (Tables 2, 3). The WSR tests applied to the combined data set using both taxon-sampling methods showed that a nonmonophyletic Corytophaninae was significantly less parsimonious than the overall shortest tree (Table 2).

All data sets produced trees with a monophyletic Crotaphytinae. The WSR test using molecular and both combined data sets each showed that the shortest alternative trees with Crotaphytinae constrained not to be monophyletic are significantly longer than the overall shortest trees (Table 2). The SH test applied to the molecular data also rejected the alternative hypothesis of crotaphytine nonmonophyly (Table 3). When the WSR test was applied to the morphological data set, the shortest alternative tree showing a nonmonophyletic Crotaphytinae could be rejected in favor of the overall shortest tree.

Only the molecular and combined data set containing all taxa included more than one representative of Hoplocercinae. When the WSR test was applied to each of these data sets, the alternative phylogenetic hypothesis of a nonmonophyletic Hoplocercinae could be rejected with the combined data (Table 2) but not with the molecular data alone (Table 2), although the SH test using molecular data could reject this alternative (Table 3).

All data sets produced trees with a monophyletic Iguaninae with moderate to strong heuristic support. However, only the WSR test applied to the combined data set including all taxa could reject the alternative phylogenetic hypothesis showing a nonmonophyletic Iguaninae (Table 2).

Monophyly of Oplurinae was suggested by all analyses with strong heuristic support. The WSR test applied to all data sets showed that each of the shortest alternative phylogenetic trees constraining Oplurinae to be nonmonophyletic were significantly longer than the overall most-parsimonious trees (Table 2).

All data sets produced trees showing a monophyletic Phrynosomatinae with high bootstrap values and decay indices. Using the morphological data and combined data set including only taxa with complete character sampling, the shortest tree showing a nonmonophyletic Phrynosomatinae was rejected with the WSR test. When this test was applied to the molecular data set, the alternative hypothesis of a nonmonophyletic Phrynosomatinae was significantly longer than the overall shortest tree.

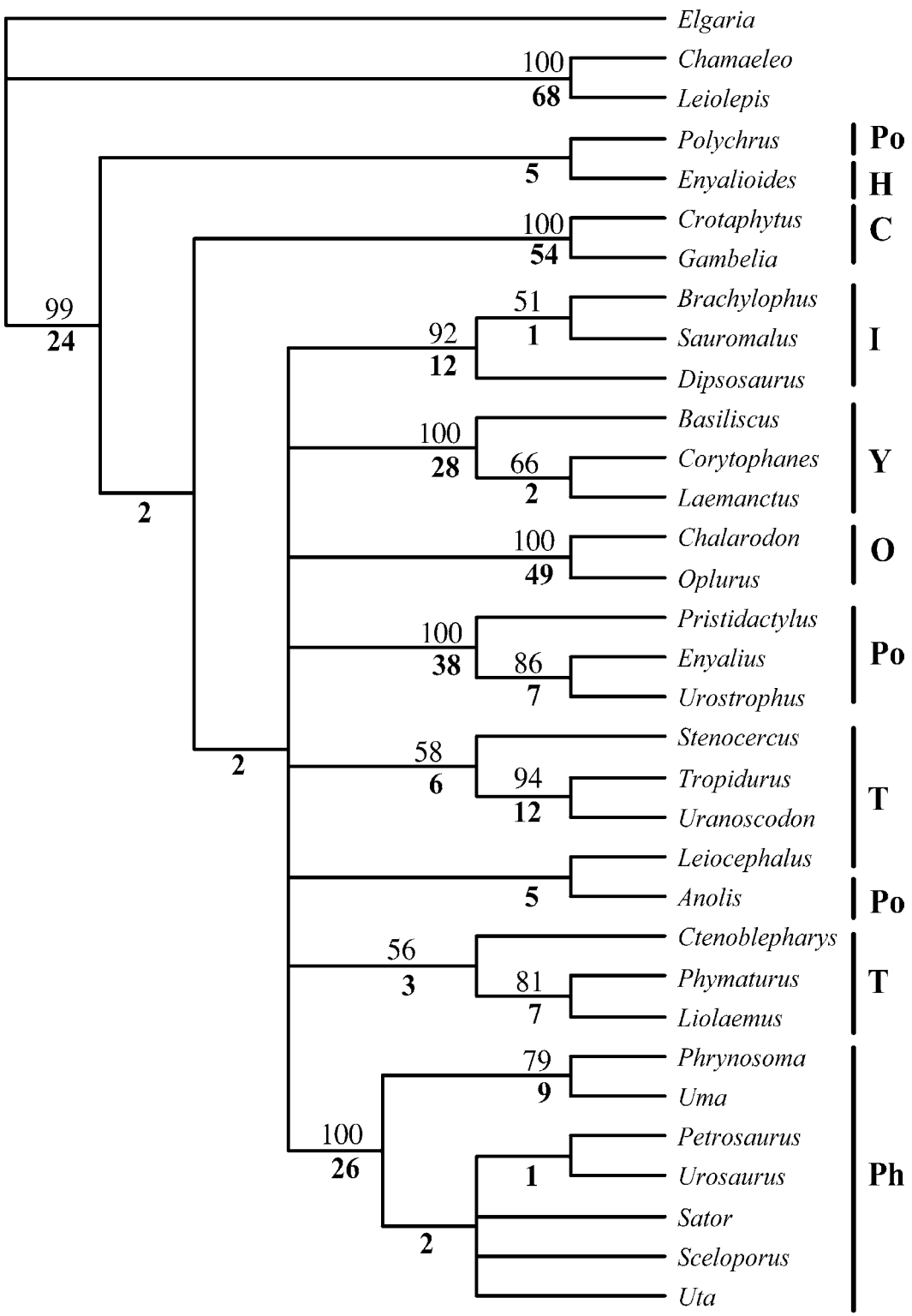

FIG. 4.—Strict consensus of five equally most-parsimonious trees generated from combined analysis of only 33 taxa that were complete for both molecular and morphological data (length = 7380). Bootstrap values are presented above branches and decay indices are shown in bold below branches. Clade labels follow Figure 1.

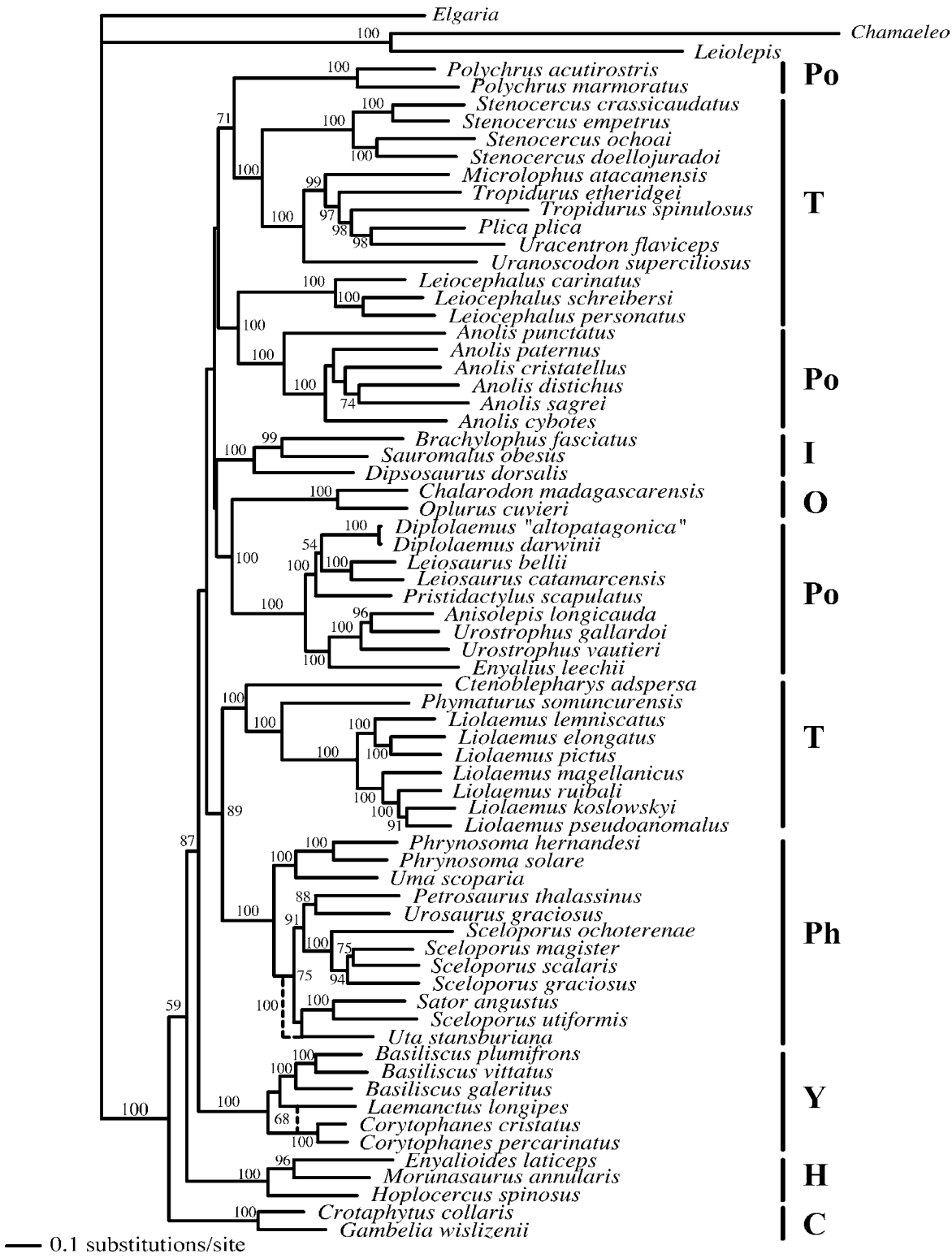

FIG. 5.—Phylogenetic relationships among iguanid lizards based on maximum likelihood using the GTR + I + Γ model (log likelihood = –51,306.7). All maximum likelihood LRTs conducted for individual nodes on this tree as discussed in the text were significant. Numbers adjacent to branches are percentages calculated from 45,000 Bayesian trees representing posterior probability values. Dotted lines denote the alternative position of taxa in the topology from Bayesian analysis. Clade labels follow Figure 1.

TABLE 2.—Results from Wilcoxon Signed-Rank Tests for monophyly of presumed iguanid clades.†

Data set	Monophyletic Corytophaninae	Monophyletic Crotaphytinae	Monophyletic Hoplocercinae	Monophyletic Iguaninae	Monophyletic Oplurinae	Monophyletic Phrynosomatinae	Nonmonophyletic Polychrotinae	Nonmonophyletic Tropidurinae
Morphological data	n = 6–10 Ts = 7–22 $P < 0.41$–0.53	n = 5–7 Ts = 0–4 $P < 0.025$–0.059*	N/A	n = 6–7 Ts = 3.5–7 $P < 0.103$–0.206	n = 5 Ts = 0 $P < 0.025$**	n = 6–8 Ts = 0–4.5 $P < 0.014$–0.034**	N/A	N/A
Molecular data	n = 171–266 Ts = 5734.5–15317.5 $P < 0.03$–0.005**	n = 142 Ts = 3360.5 $P < 0.001$**	n = 99–158 Ts = 1980–5505.5 $P < 0.048$–0.125	n = 28–107 Ts = 145–2675 $P < 0.131$–0.446	n = 175–238 Ts = 5456–11357 $P < 0.003$–0.001**	n = 219–222 Ts = 10537–10884 $P < 0.071$–0.084*	n = 259 Ts = 15620.5 $P < 0.28$	n = 142–170 Ts = 4369–6397 $P < 0.088$–0.132
Combined data [all taxa]	n = 267 Ts = 15688.5 $P < 0.056$*	n = 146–263 Ts = 3506.5–14151 $P < 0.004$–0.001**	n = 56 Ts = 541.5 $P < 0.016$**	n = 39 Ts = 280 $P < 0.08$*	n = 136 Ts = 2835 $P < 0.001$**	n = 243 Ts = 13301.5 $P < 0.133$	n = 258–310 Ts = 16020–23227.5 $P < 0.533$–0.568	n = 144 Ts = 4776 $P < 0.321$
Combined data [culled taxa]	n = 209–215 Ts = 9567.5–10163 $P < 0.070$–0.073*	n = 232–281 Ts = 10554.5–16297.5 $P < 0.004$–0.001**	N/A	n = 111 Ts = 2775 $P < 0.261$	n = 267 Ts = 14865 $P < 0.008$**	n = 136–163 Ts = 3767.5–5637 $P < 0.023$–0.048**	n = 318 Ts = 24998.5 $P < 0.812$	n = 247 Ts = 14345 $P < 0.337$

† The null hypothesis is that the shortest trees showing monophyly versus nonmonophyly of the group in question are equally parsimonious. Column headings denote the hypothesis that would be favored by a statistically significant result. Two-tailed probabilities are shown. A single asterisk denotes significance using a one-tailed test; a double asterisk denotes significance using a two-tailed test.

TABLE 3.—Results from Shimodaira-Hasegawa tests for monophyly of presumed iguanid clades.†

Hypothesis	Δ −ln L	*P*
Monophyletic Corytophaninae	104.04	0.001*
Monophyletic Crotaphytinae	42.00	0.013*
Monophyletic Hoplocercinae	54.01	0.009*
Monophyletic Iguaninae	17.49	0.180
Monophyletic Oplurinae	38.90	0.064
Monophyletic Phrynosomatinae	26.26	0.158
Nonmonophyletic Polychrotinae	20.91	0.184
Nonmonophyletic Tropidurinae*	31.83	0.076

† The null hypothesis is that the maximum-likelihood trees showing monophyly versus nonmonophyly of the group in question are equally good explanations of the data. Row headings denote the hypotheses favored by a statistically significant result indicated by * on the *P* value. One-tailed probabilities are shown.

Based on the results presented in Table 2, the combined data set including all taxa has the best statistical power among the four data sets, rejecting the alternative hypothesis of nonmonophyly for five out of the six major clades.

Only the morphological data set produced trees compatible with a monophyletic Polychrotinae and Tropidurinae*. When the WSR test was applied to the molecular and two combined data sets, the alternative hypotheses of a monophyletic Polychrotinae and Tropidurinae* could not be rejected in favor of the overall shortest trees, which depict nonmonophyly (Table 2). The WSR test applied to the morphological data set could not reject the alternative hypothesis of nonmonophyly of Polychrotinae or Tropidurinae* (Table 2). The SH tests also failed to reject the alternative hypotheses of polychrotine and tropidurine monophyly (Table 3).

Polytomy Tests

Taxon subsampling is used to test whether the 12 major iguanid lineages on the overall most-parsimonious tree (Fig. 2) form a hard polytomy. The outgroup, *Chamaeleo*, plus the 67 species of iguanid lizards that form the polytomy contain 34,382 taxon quartets. Of these quartets, 2851 (8.0%) have significant decay-index values. Thus, the hypothesis that the poorly supported iguanid lineages represent a hard polytomy is not supported using a 95% significance criterion. Likelihood-ratio tests (LRTs) applied to the maximum-likelihood tree found all branches significantly different from a polytomy.

In contrast to the previous tests, a permutation test comparing the tree lengths of 999 randomized data sets with that of the most-parsimonious tree obtained from analysis of the empirical data could not reject the null hypothesis of no phylogenetic signal (P = 0.338) among the 12 iguanid lineages (Fig. 2). The hypothesis that iguanid lineages 1–12 (Fig. 2) form a hard polytomy also could not be rejected by the frequency distribution of tree lengths for 10,000 randomly sampled trees using both molecular data alone and combined with morphological data for all taxa (g_1 = –0.085, $P > 0.05$; g_1 = –0.091, $P > 0.05$, respectively); a normal distribution would be expected for a hard polytomy. These critical values are conservative because we used significance values for 500 variable characters (maximum value given by Hillis and Huelsenbeck, 1992), whereas our results are for 1200 and 1265 variable characters in the molecular and combined data sets, respectively. Hillis and Huelsenbeck (1992, their figure 7) report very little change in critical values for four-state character data beyond 10 taxa and 500 characters. The LRTs, four-taxon subsampling techniques, permutation test (PTP), and the test for skewness of tree-length distributions were unable to distinguish between a hard and soft polytomy among 12 major iguanid lineages.

Discussion

Phylogenetic Relationships Among Iguanian Lizards

Statistical support is found for monophyly of Corytophaninae, Crotaphytinae, Hoplocercinae, Oplurinae, and Phrynosomatinae, and we recommend continued taxonomic recognition of these iguanid clades. Strength of support for Iguaninae varies among the measures and statistical tests used. Only the WSR test, using the combined data set with all taxa included, could reject the alternative hypothesis of nonmonophyly. However, all analyses and relevant data demonstrate monophyly of this group, so it remains the best working hypothesis of relationships for the included lineages.

Polychrotinae and Tropidurinae* appear monophyletic in the analysis of morphological data but nonmonophyletic in analyses of molecular and combined data sets. However, the molecular and combined data sets are unable statistically to reject the hypothesis of monophyly. Frost et al. (2001*a*) also recovered a nonmonophyletic Polychrotinae with weak support in an analysis of molecular and combined data. Their sampling included representatives from only three other iguanid clades, and, thus, it was an inadequate test of polychrotine monophyly. This is important as it is likely that additional data will not recover *Anolis* and *Polychrus* as sister taxa, a result consistent with our analyses except the morphological data alone and the analysis of molecular data by Frost et al. (2001*a*). Because monophyly is equivocal, the taxon names Polychrotinae* and Tropidurinae* may be retained as a metataxa (Estes et al., 1988; Gauthier et al., 1988; Schwenk, 1994; Schulte et al., 1998).

Several phylogenetic hypotheses for the relationships among the major lineages of iguanian lizards have been published since the cladistic analysis of morphological data presented by Etheridge and de Queiroz (1988) and Frost and Etheridge (1989). An important motivation for the latter study to suggest such a radical taxonomic revision was the lack of morphological evidence to support monophyly of Iguanidae and Agamidae*. This proposal generated a flurry of discussion in the literature (reviewed in Schwenk, 1994). Nonetheless, the eight family system for the former Iguanidae was gradually embraced by the herpetological community, whereas their proposal to combine Agamidae* and Chamaeleonidae into one family has never become established.

Less than a decade later, Macey et al. (1997*a*) and Schulte et al. (1998), using combined and separate analyses of morphological and molecular data, found strong support for monophyly of Iguanidae, with the former study recommending a return to the traditional recognition of a single family Iguanidae (sensu lato) and considering the families of Frost and Etheridge (1989) as subfamilies. Macey et al. (1997*a*) also recommended resurrecting Agamidae* as a metataxon (sensu Schwenk, 1994) to denote its equivocal status of monophyly based on the available evidence.

A similarity between all previous studies is the lack of topological resolution and support for relationships among the major lineages of iguanid lizard branches ancestral to clades numbered 1–12 in Fig. 2. This result was consistent in our analyses, whether the data

were analyzed using maximum parsimony, maximum likelihood, or Bayesian analyses. The hypothesis that the major lineages of iguanid lizards as defined here experienced a rapid radiation also was equivocal based on four different tests for a hard polytomy. Therefore, it remains unclear whether the lack of resolution is due to character incongruence, lack of phylogenetic structure in the data, or lack of sufficient information among the internal branches of the tree. Another possibility is that the phylogenetic hypothesis inferred here might be different from the haplotype tree of the mitochondrial sequences (Page and Charleston, 1997). Additional data and more sophisticated polytomy tests are required to distinguish between these alternative hypotheses. Harris et al. (2001) analyzed multiple lineages of iguanian lizards using a small fragment of the nuclear gene C-*mos* and found moderately high bootstrap support between a few major lineages of iguanid lizards, although this was not statistically significant when subjected to a WSR or SH test (results not shown). Perhaps with additional nuclear DNA markers, statistical support for interclade relationships may be found.

Recently, Frost et al. (2001*a*) proposed resurrecting the name Pleurodonta for the clade we recognize as Iguanidae, with the families Corytophanidae, Crotaphytidae, Hoplocercidae, Iguanidae, Leiocephalidae, Liolaemidae (latter two elevated from subfamilies of Tropiduridae), Leiosauridae (new), Opluridae, Phrynosomatidae, Polychrotidae, and Tropiduridae as its major subgroups. Frost et al. (2001*a*) claim rejection of tropidurine monophyly by available molecular evidence (Macey et al., 1997*a*; Schulte et al., 1998; Titus and Frost, 1996). As reported here, morphological and molecular data are unable to distinguish between alternative hypotheses of monophyly for Tropidurinae* and Polychrotinae* using statistical tests rather than by weight of evidence alone. Finally, Frost et al. (2001*a*) cite Macey et al. (1997*a*) as providing strong support for agamid paraphyly, criticizing the application of the metataxon criteria in this case without considering that Macey et al. (2000) recovered Agamidae* as the sister group to the Chamaeleonidae with weak support. Available evidence remains ambiguous regarding monophyly of Agamidae*. Contrary to the assertion of Frost et al. (2001*a*), the application of metataxon in this case, as with Tropidurinae* and Polychrotinae*, emphasizes the point made by Schwenk (1994) that application of the metataxon when monophyly is equivocal is taxonomically conservative, yet highlights the need for additional phylogenetic information.

Proposed Phylogenetic Taxonomy of Iguanian Lizards

Based on our phylogenetic results, we propose the following taxonomic scheme for Iguania (Table 4) in which all the supraspecific taxa (and their names) are considered unranked. Monophyly of Iguanidae is strongly supported by previous analyses using morphological characters analyzed in combination with mitochondrial DNA sequence data, as well as mitochondrial and nuclear DNA sequence data alone (Harris et al., 2001; Macey et al., 1997*a*; Schulte et al., 1998). Therefore, we associate this name with the clade composed of the eight major groups included in Iguanidae by Etheridge and de Queiroz (1988), which corresponds with Pleurodonta of Frost et al. (2001*a*). Six of these eight groups received statistical support from our analyses and warrant continued recognition as clades nested within Iguanidae. These taxa are Corytophaninae, Crotaphytinae, Hoplocercinae, Iguaninae, Oplurinae, and Phrynosomatinae. Their content follows that given by Etheridge and de Queiroz (1988) and Frost and Etheridge (1989).

The taxonomic status of the groups Polychrotinae* and Tropidurinae* is less clear. At this time, we recognize these traditional groups as metataxa (Estes et al., 1988; Gauthier et al., 1988; Schulte et al., 1998) because statistical support for their monophyly is equivocal. We propose the following phylogenetic taxonomic arrangement to provide stable [consistent] names for their subgroups. The clades within Tropidurinae* are *Leiocephalus*, Liolaemini, and Tropidurini, which correspond respectively with the groups Leiocephalidae, Liolaemidae, and Tropiduridae of Frost et al. (2001*a*). The clades within Polychrotinae* are *Anolis*, Leiosaurini, and *Polychrus*, which correspond respectively with *Anolis* of Jackman et al. (1999; including *Chamaeleolis*, *Chamaelinorops*, *Norops*, and *Phenacosaurus*), Leiosauridae of Frost et al. (2001*a*; including the leiosaurs, *Enyalius*, and para-anoles of Etheridge and de Queiroz [1988]), and *Polychrus* of Peters and Donoso-Barros (1970; including *P.*

peruvianus [Noble, 1924]). In addition, the new taxon names Leiosaurae (for the leiosaurs of Etheridge and de Queiroz [1988]) and Anisolepae (for the clade of *Enyalius* and the para-anoles) are used instead of Leiosaurinae and Enyalinae of Frost et al. (2001*a*). These new names are proposed to minimize confusion related to the connotations concerning taxonomic rank and the position of these groups in our phylogenetic hypothesis as nested within the Leiosaurini, which, though here treated as unranked, has an ending (-ini) traditionally associated with the rank of tribe.

Monophyly of Acrodonta also is strongly supported by morphological characters and mitochondrial and nuclear DNA sequence data (Harris et al., 2001; Macey et al., 1997*a*; Saint et al., 1998), including a synapomorphy of rearrangement of two mitochondrial tRNAs (Macey et al., 1997*b*). Acrodonta is thus retained as circumscribed by Estes et al. (1988). Monophyly of Agamidae* is not statistically supported (Harris et al., 2001; Honda et al., 2000; Macey et al., 1997*a*, 2000). Until evidence statistically rejecting monophyly of Agamidae* is presented, this name is retained as a metataxon with the traditional circumscription (e.g., Estes et al., 1988; Macey et al., 1997*a*; Moody, 1980). Six clades nested within Agamidae* recognized by Macey et al. (2000) are retained as Agaminae, Amphibolurinae, Draconinae, Hydrosaurinae, Leiolepidinae, and Uromastycinae. Because Macey et al. (2000) were unable to sample all relevant taxa, the content of some of these groups is unclear. Specifically, the sampling of Agaminae and Draconinae are missing certain critical taxa that may be outside of the basal nodes recovered by previous sampling; for example, unpublished data for *Ptyctolaemus* places this taxon as the sister group to all South Asian taxa in Draconinae. Therefore, the content of these taxa follows Macey et al. (2000) until they can be more accurately circumscribed through denser sampling.

For over a century, herpetologists have recognized Iguanidae in the sense followed in this paper (Boulenger, 1884; Camp, 1923; Etheridge and de Queiroz, 1988). The eight-family taxonomy of Frost and Etheridge was proposed in 1989, was never fully accepted (Pough et al., 2001; Schwenk, 1994; Zug et al., 2001), and was subsequently rejected by Macey et al. (1997*a*), who provided evidence for monophyly of Iguanidae as traditionally circumscribed and recognized the eight taxa ranked as families by Frost and Etheridge (1989) as subfamilies. In addition, the taxonomic recommendation of Frost and Etheridge (1989) to place Agamidae* in synonymy with Chamaeleonidae has never been widely accepted (Barts and Wilms, 1997; Cogger, 2000; Manthey and Grossman, 1997). Macey et al. (1997*a*) also reversed this proposal by removing Agamidae* from synonymy with Chamaeleonidae, and that traditional arrangement was subsequently followed by Frost et al. (2001*a*).

TABLE 4.—Updated iguanian lizard phylogenetic taxonomy. See discussion for explanation of taxon names and content.

Higher-level iguanian taxonomy
Acrodonta
Chamaeleonidae
Agamidae*
Agaminae
Amphibolurinae
Draconinae
Hydrosaurinae
Leiolepidinae
Uromastycinae
Iguanidae
Corytophaninae
Crotaphytinae
Hoplocercinae
Iguaninae
Oplurinae
Phrynosomatinae
Polychrotinae*
Anolis
Leiosaurini
Leiosaurae
Anisolepae
Polychrus
Tropidurinae*
Leiocephalus
Liolaemini
Tropidurini

One of the goals of nomenclatural systems is to provide maximal utility of the names associated with particular taxa. The choice of ranks is ultimately a subjective decision and was a major thrust behind the development of a system of phylogenetic nomenclature not based on ranks (e.g., de Queiroz and Gauthier, 1992, 1994). The application of a phylogenetic concept of taxa (monophyly) and a statistical criterion of support for recognizing higher taxa of Iguania promotes stability and increases utility. Furthermore, use of the metataxon convention (sensu Schulte et al., 1998;

Schwenk, 1994) more precisely reflects our statistical and evidentiary confidence in the major subgroups of Iguania. Thus, our taxonomy maintains historical continuity in the context of a strict criterion of monophyly by naming strongly supported groups using morphological and molecular data. Current levels of confidence in the monophyletic status of taxa is reflected in the use of metataxon, indicating the need for additional data to test the monophyly of Agamidae*, Polychrotinae*, and Tropidurinae*. Finally, our proposal can readily accommodate new molecular, morphological, and fossil data as they are accumulated.

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APPENDIX I

Museum numbers and localities for voucher specimens from which DNA was obtained and GenBank accession numbers are presented: AMNH represents the American Museum of Natural History, New York; BWMC for Bobby Witcher Memorial Collection, Avila College, Kansas City, Missouri; BYU for Monte L. Bean Life Science Museum, Provo, Utah; FML for Fundación Miguel Lillo, Tucumán, Argentina; KU for Kansas Museum of Natural History, Lawrence, Kansas; LSUMZ for Louisiana State University Museum of Natural Science, Baton Rouge, Louisiana; MVZ for Museum of Vertebrate Zoology, University of California, Berkeley, California; OU for Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma; QCAZ for Museo de Zoología, Universidad Católica del Ecuador, Quito; SDSU for San Diego State University, San Diego, California; STLID# for a specimen currently in the care of St. Louis Zoo with an origin at the San Diego Zoo (SDID#); UNNEC for Colección Herpetológica de la Universidad Nacional del Nordeste-Corrientes, Corrientes, Argentina; USNM for National Museum of Natural History, Smithsonian Institution, Washington, D.C. Institutional abbreviations are as listed in Leviton et al. (1985). FBC and PT are acronyms of Félix B. Cruz field numbers for uncatalogued specimens being deposited in the Fundación Miguel Lillo, Tucumán, Argentina. JPV is the acronym for field numbers of J. P. Valladares for specimens being deposited in the Museo de Historia Natural, Santiago, Chile. REG is the acronym for Richard E. Glor for specimens to be deposited in National Museum of Natural History. RT is the acronym for Richard Thomas for specimens deposited at the University of Puerto Rico, Department of Biology, San Juan. The acronym followed by a dash JAS represents the field number of J. A. Schulte II for an uncatalogued specimen to be deposited in the Museum of Vertebrate Zoology. Specimens denoted with an asterisk by the GenBank number are those DNA sequences used as representatives in the culled combined phylogenetic analysis.

Corytophaninae: *Basiliscus galeritus*, 100 m, Rio Cauque, E Pedernales via road from Pedernales to El Carmen, Prov. Manabi, Ecuador (MVZ 226111, AF528714); *Basiliscus vittatus*, 1300 m, 13° 53′ 29″ N, 89° 37′ 17″ W, Finca El Milagro, Departamento Santa Ana, El Salvador (KU 289791, AF528715); *Laemanctus longipes*, no locality (uncatalogued, AF528716*); *Corytophanes cristatus*, approximately 15 km S El Castillo on north bank Rio San Juan at Isla El Diamante, Departamento Rio San Juan, Nicaragua (OU 35887, AF528717*); *Corytophanes percarinatus*, 1080 m, 13° 39′ 34″ N, 88° 22′ 47″ W, Finca La Giralda, Departamento La Libertad, El Salvador (KU 289954, AF528718).

Hoplocercinae: *Enyalioides laticeps*, 8° 15′ 31″ S, 72° 46′ 37″ W, approximately 5 km N Porto Walker, Acre, Brazil (LSUMZH 13573, AF528719*); *Morunasaurus annularis*, Rio Cenepa, ridge on N side at Headwaters of the Rio Kagka, Departamento Amazonas, Peru (MVZ 163062, AF528720).

Iguaninae: *Brachylophus fasciatus*, Fiji (STLID# 920451, SDID# 189337, AF528721*).

Oplurinae: *Chalarodon madagascarensis*, Madagascar (uncatalogued, AF528722*).

Phrynosomatinae: *Phrynosoma solare*, White Stallion Ranch, Tucson, Arizona (uncatalogued, to be deposited in

MVZ, AF528739); *Sceloporus utiformis*, approximately 6 km E Uruapan (by the Patzcuaro–Uruapan Hwy), Jalisco, Mexico (BYU 45730, AF528740); *Sceloporus magister*, Whipple Mountains, San Bernardino County, California, U.S.A. (MVZ 182569, AF528741); *Sceloporus scalaris*, Rustler's Park, Chirichua Mountains, Cochise County, Arizona, U.S.A. (LSUMZ 48789, AF528742); *Sceloporus ochoterenae*, 12.0 km W Chilpancingo, Guerrero, Mexico (BYU 45517, AF528743).

Polychrotinae*: *Anolis cybotes*, Hotel Embajador, Santo Domingo, Dominican Republic (BWMC 6581, AF528723); *Anolis cristatellus*, PR 9973, 1.7 mi from intersection with PR 972, Naguabo, Puerto Rico (RT 13042, AF528724); *Anolis distichus*, Comendador, Dominican Republic (REG 648, AF528725); *Anolis punctatus*, 8° 20′ 47″ S, 65° 42′ 57.9″ W, Rio Ituxi at the Madeirera Scheffer, Prov. Amazonas, Brazil (OU 37172, AF528726*); *Anolis sagrei*, grounds IES, La Habana, Cuba (USNM 498107, AF528727); *Diplolaemus forma "Alto-patagonia,"* 40° 26′ 96″ S, 68° 22′ 61″ W, 2 km S Esperanza, Prov. Rio Negro, Argentina (FBC 55, AF528728); *Diplolaemus darwinii*, approximately 950 m, rock along Rta. 40, 23 km NNW Las Bayas, Departamento Norquino, Prov. Río Negro, Argentina (R. D. Sage 13041-MVZ uncatalogued, AF528729); *Leiosaurus bellii*, 2 km W Los Menucos, Prov. Río Negro, Argentina (PT 4782, AF528730); *Leiosaurus catamarcensis*, Castro Barros, Prov. La Rioja, Argentina (PT 4999, AF528731); *Pristidactylus scapulatus*, 40° 26′ 96″ S, 68° 22′ 61″ W, 2 km S Esperanza, Prov. Río Negro, Argentina (PT 4810, AF528732*); *Enyalius leechii*, approximately 101 km S and 18 km E Santarem, 3° 08′ 52″ N, 54° 49′ 58″ W, Agropecularia Treviso LTDT, Pará, Brazil (LSUMZ-H 13957, AF528733*); *Urostrophus vautieri*, Nova Ponte, Mato Grosso, Brazil (LSUMZ-H 13960, AF528734*); *Urostrophus gallardoi*, approximately 2 km S L. V. Marsilla, on Prov. Rta. 60, Prov. Córdoba, Argentina (FBC 36, AF528735); *Anisolepis longicauda*, Isla Yacyretá, Paraguay (UNNEC 906, AF528736); *Polychrus acutirostris*, no locality data (AMNH 10182, AF528737*); *Polychrus marmoratus*, approximately 101 km S and 18 km E Santarem, 3° 9′ 2.4″ S, 54° 50′ 32.9″ W, Agropecuaria Treviso LTDA, Pará, Brazil (OU 36693, AF528738).

Tropidurinae*: *Stenocercus doellojuradoi*, Finca Los Colorados, Departamento de Anta, Prov. Salta, Argentina (FML 9298, AF528744); *Stenocercus empetrus*, no locality data, northwest Perú (SDSU 4025, AF528745); *Stenocercus ochoai*, 2400 m, Machu Picchu Ruins, Departamento Cuzco, Perú (MVZ 199534, AF528746); *Uracentron flaviceps*, Laguna Grande, Reserva Faunistica Cuyabeno (RPF-Cuyabeno), Prov. Sucumbíos, Ecuador (QCAZ-2536, AF528747); *Plica plica*, approximately 5 km N Porto Walker, 8° 15′ 31″ S, 72° 46′ 37″ W, Prov. Acre, Brazil (OU 37036, AF528748); *Uranoscodon superciliosus*, 8° 20′ 47″ S, 65° 42′ 58″ W, Rio Ituxi at the Madeirera Scheffer, Prov. Amazonas, Brazil (OU 37182, AF528749*); *Tropidurus etheridgei*, 3 km S Cachi Yacu on Rta. 22, Prov. Córdoba, Argentina (PT 4808, AF528750*); *Tropidurus spinulosus*, Señor de la Peña, Departamento. Arauco, Prov. La Rioja, Argentina (FBC 116, AF528751); *Microlophus atacamensis*, Pan de Azucar, Region III, Chile (JPV 145, AF528752); *Leiocephalus schreibersi*, 16.4 km NW Duverge, 18° 23′ 66″ N, 71° 33′ 75″ W, Dominican Republic (REG 602, AF 528753); *Leiocephalus personatus*, 4.8 km SE Monte Cristi, 19° 49′ 27″ N, 71° 36′ 32″ W, Dominican Republic (REG 666, AF528754); *Ctenoblepharys adspersa*, approximately 30 km S Huacho, near Las Lomas, Perú (SDSU 3781, AF305784*).

Corytophaninae: *Basiliscus plumifrons* (U82680*)

Crotaphytinae: *Crotaphytus collaris* (U82681*); *Gambelia wislizenii* (U82682*)

Hoplocercinae: *Hoplocercus spinosus* (U82683)

Iguaninae: *Dipsosaurus dorsalis* (AF049857*); *Sauromalus obesus* (U82687*)

Oplurinae: *Oplurus cuvieri* (U82685*)

Phrynosomatinae: *Petrosaurus thalassinus* (AF049858*); *Phrynosoma hernandesi* (U82686*, previously recognized by Macey et al. (1997*a*) as *Phrynosoma douglassi* and corrected here following Zamudio et al. (1997); *Sator angustus* (AF049859*); *Sceloporus graciosus* (AF049860*); *Uma scoparia* (AF049861*); *Urosaurus graciosus* (AF049862*); *Uta stansburiana* (AF049863*).

Polychrotinae*: *Anolis paternus* (U82679)

Tropidurinae*: *Leiocephalus carinatus* (AF049864*); *Liolaemus elongatus* (AF099240); *Liolaemus koslowskyi* (AF099264); *Liolaemus lemniscatus* (AF099229); *Liolaemus magellanicus* (AF099243); *Liolaemus pictus* (U82684*); *Liolaemus pseudoanomalus* (AF099254); *Liolaemus ruibali* (AF099244); *Phymaturus somuncurensis* (AF049865*); *Stenocercus crassicaudatus* (AF049866*, misspelled in Schulte et al. (1998) as *S. crasicaudatus*)

Outgroups: Scelorglossa, *Elgaria panamintina* (U82692*); Acrodonta, Chamaeleonidae, *Chamaeleo fischeri* (U82688*); Acrodonta, Agamidae*, *Leiolepis belliana* (U82689*)

Appendix II

Morphological characters are as reported in Etheridge and de Queiroz (1988) and Frost and Etheridge (1989) and summarized below: 1. premaxilla-nasal relationship; 2. maxillae; 3. maxilla, posterior extent; 4. vomers; 5. lacrimal; 6. lacrimal foramen; 7. skull rugosity; 8. jugal, squamosal contact; 9. postfrontal; 10. parietal roof shape; 11. parietal foramen; 12. supratemporal; 13. osseous labyrinth; 14. endolymphatic sacs; 15. epiotic foramen; 16. dentary, expansion onto labial face of coronoid; 17. dentary, posterior extent; 18. coronoid labial blade; 19. anterior surangular foramen; 20. Meckel's groove; 21. splenial, anterior extent; 22. splenial, posterior extent; 23. angular, condition of contact with splenial; 24. posterior mylohyoid foramen; 25. crowns of marginal teeth; 26. posterior maxillary and dentary teeth; 27. palatine teeth; 28. pterygoid teeth; 29. ceratobranchials; 30. clavicle; 31. insertion of clavicle; 32. interclavicle; 33. sternum, anterior extent; 34. caudal vertebral type; 35. scapular fenestra; 36. posterior coracoid fenestra; 37. median enlarged sternal fontanelles(s); 38. cervical ribs; 39. number of sternal ribs; 40. postxiphisternal inscriptional ribs; 41. tail autotomy fracture planes; 42. interparietal scale; 43. interparietal coloration; 44. superciliary scales; 45. subocular scale; 46. mid-dorsal scale row; 47. gular fold; 48. femoral pores; 49. preanal pores; 50. distal subdigital scales; 51. subdigital scale surface macrostructure; 52. scale organs; 53. nasal chamber, sink trap; 54. nasal chamber, S-condition; 55. nasal chamber, fusion of nasal concha to roof of nasal chamber; 56. nasal chamber, anole condition; 57. nasal chamber, acrodontan condition; 58. ulnar nerve pathway; 59. dorsal shank muscle innervation; 60. hemipenis, posterior lobe; 61. hemipenis, capitation and sulci; 62. hemipenis, *m. retractor lateralis posterior*, division of; 63. hemipenis, *m. retractor lateralis posterior*, sheath position; 64. hemipenis, dorsal accessory sheath muscle; 65. colic septa; 66. paired ventrolateral belly patches; 67. reticular papillae on tongue.