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PHYLOGENETIC RELATIONSHIPS OF HOPLOCERCID LIZARDS: CODING AND COMBINING MERISTIC, MORPHOMETRIC, AND POLYMORPHIC DATA USING STEP MATRICES

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ABSTRACT: Hoplocercidae is a small (10 species, 3 genera), poorly known but pivotal family of Central and South American iguanian lizards that has never been the subject of a focused phylogenetic study or systematic revision. We undertake the first rigorous phylogenetic analysis of hoplocercid lizards. We also use our analysis to demonstrate how meristic, morphometric, and polymorphic morphological characters can be coded and combined for phylogenetic analyses using step matrices, which allow continuous variation to be treated as continuous. Parsimony analysis of 46 informative external and skeletal characters (17 qualitative and fixed, 19 qualitative and polymorphic, 8 meristic, and 2 morphometric) yields very different topologies, depending on how the meristic characters are scaled (weighted). Use of between-state scaling yields a phylogeny in which *Hoplocercus* is at the base of the hoplocercid tree, and *Morunasaurus* is paraphyletic with respect to a monophyletic *Enyalioides*. Scaling between characters produces a tree in which *Enyalioides* is paraphyletic with respect to a clade containing *Morunasaurus* and *Hoplocercus*, and *Morunasaurus* is paraphyletic with respect to *Hoplocercus*. We also propose a third, "mixed" approach to scaling, which we marginally prefer over the other two methods. This method yields a tree in which *Hoplocercus* and a monophyletic *Morunasaurus* make up the sister group to a monophyletic *Enyalioides*. We discuss the implications of these results for hoplocercid biogeography and evolutionary ecology, tropical speciation, and the phylogenetic analysis of morphological data.

Key words: Character coding; *Enyalioides*; Hoplocercidae; *Hoplocercus*; Iguania; Morphology; *Morunasaurus*; Phylogeny; Squamata

THE FAMILY Hoplocercidae is a pivotal but poorly known group of Central and South American iguanian lizards. Formerly known as the morunasaurs (Etheridge and de Queiroz, 1988), an informal subgroup of Iguanidae, the 10 species and 3 genera of hoplocercids were recognized as a distinct family by Frost and Etheridge (1989; but see Schulte et al. [1998] for a recent dissenting opinion). Frost et al. (2001*a*) recently recognized three additional families of iguanian lizards, bringing to 11 the total number of families derived from the former Iguanidae (Corytophanidae, Crotaphytidae, Hoplocercidae, Iguanidae, Leiocephalidae, Leiosauridae, Liolaemidae, Opluridae, Phrynosomatidae, Polychrotidae, and Tropiduridae). Hoplocercids are pivotal in that they have been considered to be one of the most basal lineages within the Iguania (Etheridge and de Queiroz, 1988; Schulte et al., 1998) and Iguania is the putative sister group of all other squamates (Estes et al., 1988; Lee, 1998). Thus, hoplocercids may be critical in determining the primitive character states of morphological, ecological, behavioral, and physiological characters for both iguanians and squamates.

Hoplocercids collectively range from Panama to southeastern Brazil, but reach their greatest species diversity in the lowland rainforests of Ecuador and adjacent countries (Peters and Donoso-Barros, 1970). The genus *Hoplocercus* consists of a single species (*H. spinosus*) from the Mato Grosso region of Brazil (and adjacent Bolivia). The genus *Morunasaurus* contains two species, *M. annularis* from Amazonian Colombia and Ecuador and *M. groi* from Panama and Colombia (Corredor et al., 1985). The genus *Enyalioides* consists of seven species. Two species occur on the Pacific side of the Andes: *E. heterolepis* is found from Panama to Ecuador and *E. oshaughnessyi* occurs in Ecuador. Five species are distributed in the northwestern Amazonian region (*E. cofanorum*, *E. laticeps*, *E. microlepis*, *E. palpebralis*, and *E. praestabilis*).

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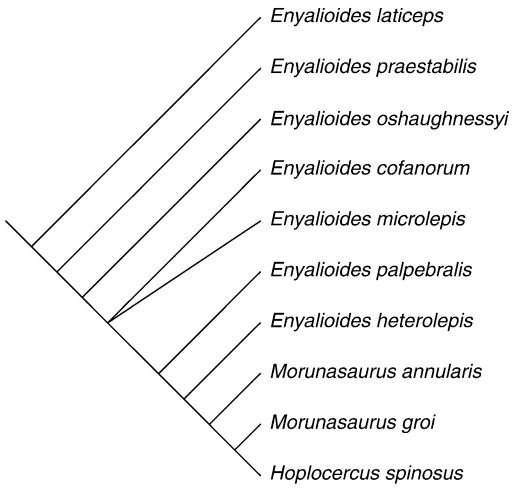

FIG. 1.—Phylogenetic relationships of hoplocercid lizards as postulated by Etheridge and de Queiroz (1988).

Considerable progress has been made in resolving phylogenetic relationships within the families of Iguania, including Agamidae (Macey et al., 2000), Chamaeleonidae (Raxworthy et al., 2002), Corytophanidae (Lang, 1989), Crotaphytidae (McGuire, 1996), Iguanidae (Hollingsworth, 1998; Sites et al., 1996; Wiens and Hollingsworth, 2000), Leiosauridae (Frost et al., 2001*a*), Leiocephalidae (Pregill, 1992), Liolaemidae (Etheridge, 1995; Schulte et al., 2000), Opluridae (Titus and Frost, 1996), Phrynosomatidae (Reeder and Wiens, 1996; Wiens and Reeder, 1997; Wilgenbusch and de Queiroz, 2000), Polychrotidae (Jackman et al., 1999; Frost et al., 2001*a*), and Tropiduridae (Frost, 1992; Frost et al., 2001*b*; Harvey and Gutberlet, 1999). However, relationships among these families remain uncertain (Frost and Etheridge, 1989; Frost et al., 2001*a*; Schulte et al., 1998). Hoplocercids are unique among iguanian families in that they have never been the subject of a focused phylogenetic study, or even a more traditional systematic revision. A preliminary tree described verbally by Etheridge and de Queiroz (1988) suggested that the species of *Enyalioides* formed a paraphyletic grade of lineages leading up to a clade containing *Morunasaurus* and the monotypic genus *Hoplocercus*, and that *Morunasaurus* was paraphyletic with respect to *Hoplocercus* (Fig. 1). In the present study, we conduct the first rigorous phylogenetic analysis of hoplocercid lizards. We also use our analysis of hoplocercid phylogeny as a case study for applying new methods for coding and combining different types of morphological variation.

A large gap exists between morphological variation as reported in most phylogenetic analyses and morphological variation that exists in nature. Morphological phylogenetic studies typically report variation as a matrix of simple 0s, 1s, and 2s for each species and character, whereas morphological variation in nature includes continuous variation in shape (morphometric characters); variation in counts of discrete, serially homologous traits with values that often overlap between species (meristic characters); and qualitative traits that vary within as well as between species (polymorphic characters). Trying to close this gap represents a major challenge to morphological systematists. In this analysis, we use relatively new methods for coding meristic, morphometric, and polymorphic characters that allow continuous variation to be treated as more-or-less continuous through the use of step matrices (Wiens, 1999, 2001). Data from the present study were utilized in a previous paper (Wiens, 2001) describing some of these methods.

MATERIALS AND METHODS

Morphological data for hoplocercid lizards were obtained from museum specimens (Appendix I). The characters (Appendix II) describe variation in external morphology (scalation, coloration, proportions) and osteology. We tried to include all potentially independent characters (following Poe and Wiens, 2000) and did not exclude characters on the grounds that they were polymorphic, meristic, or morphometric. However, we excluded some morphometric variables because we considered them likely to be correlated with other variables. Most osteological preparations were made by hand by R. Etheridge. Sample sizes were generally very small for osteological characters, primarily because most hoplocercids are relatively uncommon in collections and are rarely represented by more than a few individuals per locality. Nonetheless, we were able to obtain skeletal data from at least one individual of every species of hoplocercid.

We used all 10 of the previously recognized species in the family as terminal units in the phylogenetic analysis (Duellman, 1973; Peters and Donoso-Barros, 1970). However, there are a number of alpha-taxonomic issues in Hoplocercidae, all within the genus *Enyalioides* (discussed in Appendix III). The most prominent of these problems is that the species many herpetologists have considered to be *Enyalioides microlepis* is actually *E. oshaughnessyi*, and vice versa.

The phylogeny of Hoplocercidae was rooted by inclusion of several outgroup taxa. These were initially selected based on the morphological phylogenetic analysis of Frost and Etheridge (1989; their figure 7). In their analysis, the iguanids, polychrotids, and acrodonts were supported as possible sister groups of Hoplocercidae, either alone or in various combinations. We included two or three species from each of these higher taxa as terminal units in our analysis (following Nixon and Carpenter, 1993), although, in a few cases, external and skeletal data from congeners were combined into a single taxon (when both types of data were not available from the same species). The monophyly of each of these higher taxa was then constrained in the phylogenetic analyses, but the relationships among them were not. A more recent molecular study (Schulte et al., 1998) has placed Hoplocercidae as relatively basal within the Iguania, just above Acrodonta and just below a clade that includes polychrotids and corytophanids (the latter clade is the sister group of the remaining iguanians). We consider our use of acrodonts, iguanids, leiosaurids, and polychrotids as outgroups to be reasonable, regardless of which hypothesis is more accurate. The recent hypothesis that corytophanids are nested inside polychrotids (Frost et al., 2001*a*) should not significantly impact our results. Following Sites et al. (1996), we constrained *Brachylophus* to be basal within iguanids relative to *Ctenosaura* and *Dipsosaurus*.

Monophyly of Hoplocercidae was proposed by Etheridge and de Queiroz (1988) and assumed by Frost and Etheridge (1989). In our analyses, we left unconstrained the monophyly of Hoplocercidae relative to the outgroups to provide a more rigorous test of the monophyly of the family.

Phylogenetic analyses were performed using PAUP* (version 4.0b10; Swofford, 2002). Shortest trees were sought using heuristic searches, with 50 random taxon-addition sequence replicates per search and tree-bisection-reconnection (TBR) branch swapping. Support for individual clades was evaluated using non-parametric bootstrapping (Felsenstein, 1985), using 500 pseudoreplicates per analysis with five random addition sequences per pseudoreplicate. Our cut-off for considering results as strongly supported was a bootstrap value of 70% or higher (based on Hillis and Bull, 1993; but see their caveats).

Intraspecific variation in qualitative characters was coded using the frequency parsimony method described by Wiens (1995) and Berlocher and Swofford (1997). For a given character, each taxon with a unique set of trait frequencies was given a unique character state in the data matrix. The cost of a transition between each pair of character states was then entered into a step matrix; the cost was based on the Manhattan distance between the frequencies of each pair of taxa. The Manhattan distance for a given character for a pair of taxa A and B is defined as

$$D_{AB} = \frac{1}{2}\sum_{i=1}^{K} |p_{Ai} - p_{Bi}|,$$

where p_{Ai} and p_{Bi} are the frequencies of a given trait (or character state, as traditionally used) in taxa A and B, and K is the total number of traits per character (after Berlocher and Swofford, 1997). Although the use of frequency-based methods to code polymorphic data has been controversial, there are concordant results from real and simulated data sets that suggest that frequency-based methods are generally as accurate or more accurate than other coding methods (see review by Wiens, 1999).

Quantitative characters (meristic and morphometric) were coded using step matrix gap-weighting (Wiens, 2001), which is a modification of the gap-weighting method of Thiele (1993). For meristic characters, intraspecific variation for a given character for a given species was summarized using trait means. For each character, the mean trait value (x) for a given species was converted to a score (x_S) between 0 and 999 by range-standardizing the

data according to the following formula (modified from Thiele, 1993)

$$x_S = \frac{x - \min}{\max - \min} \times 999,$$

where "min" is the minimum (lowest) mean species value of the trait across all species and "max" the maximum. The cost of a transition between each character state (or taxon) in the step matrix was simply the difference between these scores. The pros and cons of the gap-weighting approach (including more philosophical objections) are addressed by Thiele (1993), Smith and Gutberlet (2001), and Wiens (2001).

In the few cases where an individual exhibited different traits on different sides (asymmetry), each side was counted separately (as one half of an individual) in calculations of the frequency or mean of that character for that species (following Wiens and Reeder, 1997). This convention makes sense biologically in that individuals that exhibit bilateral variation presumably have intermediate conditions for whatever genetic and/or ontogenetic mechanisms control the expression of the trait.

Two morphometric characters were included (relationship between hindlimb length and snout–vent length and between parietal width and length). Raw trait values were $\log_{10}$-transformed prior to further analysis. For each character, data from all individuals for all species were entered into a simple linear regression analysis of the two measurements to obtain residuals for each specimen (using Statview version 4.51; Roth et al., 1995). For a given species and character, the raw data were the averages of the residuals for conspecific individuals. Use of residuals to obtain indices of shape for phylogenetic analysis may be problematic in that residuals are affected by the other species included in the regression analysis and their phylogenetic relatedness. Ratios of trait values do not suffer from this problem, but have problems of their own (i.e., difficulty in summarizing ratios from across individuals using means). Analysis of these morphometric data using ratios gave very similar overall results (Wiens, 2001).

The maximum cost of a transformation in each of the polymorphic, meristic, and morphometric characters was 999. This value is the maximum allowed by step matrices in MacClade (Maddison and Maddison, 1992), which was used to make the matrices. PAUP* allows one additional step. To give the fixed, qualitative characters equivalent weight, each was weighted by 999. We also treated the maximum cost of a transformation in a given morphometric character as equivalent to the maximum weight of a binary qualitative character (fixed or polymorphic).

For meristic characters, "equal weighting" can be obtained in at least two different ways: either by scaling between different characters or between the states of different characters (Wiens, 2001). Between-character scaling gives all characters the same maximum length (equal to 1), regardless of the number of states (Wiens, 2001). Between-state scaling assumes that the common currency of weighting should be based on changes between fixed, adjacent character states, rather than the maximum length of the character (Wiens, 2001). For example, if the number of vertebrae in different species in a group of organisms varies from 21 to 24 (assume for the sake of simplicity that each species is fixed for a single vertebral number) and between-character scaling is used, then the cost of going from 21 to 22 vertebrae will be one third of a step (where a step equals a change from 0 to 1 in a fixed character) and will decrease to one fourth if a taxon with 25 vertebrae is found. In contrast, if between-state scaling is used, the cost of going from 21 to 22 vertebrae remains the same (equal to a change from 0 to 1 in a fixed character) regardless of the number of vertebrae in other taxa. Thus, between-state scaling treats meristic characters as ordered, multistate characters. This method is implemented by weighting each meristic character by the difference between the maximum and minimum of the mean values of the species (i.e., the range). Both methods have some disadvantages. Between-character scaling potentially downweights the cost of transition between discrete traits (Wiens, 2001) and is highly sensitive to inclusion of taxa. Nevertheless, meristic characters with very large ranges of trait values may be problematic for between-state scaling (i.e., a trait with mean species values ranging from 10 to 100 may have an overwhelming impact on an analysis). Furthermore, larger ranges may be indicative of

greater variability in these characters, which may be associated with greater homoplasy (e.g., Campbell and Frost, 1993; Wiens, 1995). However, the size at which these ranges are likely to become problematic is unclear. We analyzed our data using both between-character scaling and between-state scaling.

We herein propose a third approach, which combines between-state and between-character scaling and which we refer to as "mixed scaling." With this approach, we coded those meristic characters with a range of mean-species trait values <5.0 using between-state scaling, and those with ranges >5.0 using between-character scaling. This mixed scaling approach treats meristic characters with low ranges of trait values as equivalent to polymorphic, multistate characters and those with high ranges of trait values as equivalent to continuous characters. We acknowledge that a cut-off value of five is arbitrary. This number roughly corresponds to the largest number of states typically used to code discrete, multistate characters. Because this mixed approach should combine the advantages of between-state and between-character scaling, we (a priori) consider results obtained using this method to provide the current best estimate of hoplocercid phylogeny, but acknowledging the problem of the arbitrary cut-off value. We found that use of a larger cut-off value (i.e., 10.0) gives results (not shown) that are very similar to those from between-state scaling.

In theory, meristic characters could also be analyzed using "generalized frequency coding," (GFC) a method for analyzing ordered polymorphic multistate characters that incorporates detailed information on trait frequencies (Smith and Gutberlet, 2001). Because GFC is similar to Thiele's (1993) gap-weighting method), we would expect GFC and step-matrix gap weighting to yield very similar results. However, GFC is somewhat less precise than use of step matrices (i.e., frequencies of 96% and 100% share the same state) and considerably more cumbersome to implement. We, therefore, do not apply GFC to our data. We note that the problem of scaling of meristic characters is also an important issue for GFC (Smith and Gutberlet, 2001).

Fixed, qualitative, multistate characters were ordered (if possible) based on morphological intermediacy (following Wilkinson, 1992); otherwise, these characters were left unordered. In a few cases, characters that involved continuous variation in features that were difficult to measure or quantify were included by describing them qualitatively in terms of morphological landmarks (i.e., relative lengths of structures or contact between structures; characters 43, 44, and 47). We prefer to include these characters qualitatively rather than exclude them entirely. Two autapomorphic characters (characters 39 and 55) that involved variation in shape were difficult to measure or describe in terms of qualitative landmarks; for these characters, states were defined in terms of an obvious gap between the variation observed in these taxa and all others.

Results

A total of 56 variable morphological characters was scored (Appendix II); 46 were parsimony-informative. The 46 informative characters consisted of 31 from external morphology (scalation = 24, coloration = 5, tail shape = 1, limb proportions = 1) and 15 of osteology (cranial = 11, postcranial = 4). Of these 46 characters, 17 were qualitative and fixed, 19 were qualitative and polymorphic, 8 were meristic, and 2 were morphometric. Frequencies of qualitative characters (fixed and polymorphic) and means of quantitative characters (meristic and morphometric) are given in Table 1; the data matrix is presented in Appendix IV.

The analyses from between-state, between-character, and mixed scaling each yielded a fully resolved tree within hoplocercids (Figs. 2, 3, 4). Monophyly of Hoplocercidae was supported in all three trees. The trees from between-state and mixed scaling are radically different from the tree postulated by Etheridge and de Queiroz (1988; shown in Fig. 1 of this paper), but are more consistent with current taxonomy. In the tree from between-state scaling (Fig. 2), *Hoplocercus spinosus* is the sister taxon of all other hoplocercids, rather than being nested within *Enyalioides* and *Morunasaurus*. *Morunasaurus* is paraphyletic with respect to a monophyletic *Enyalioides*. The monophyly of *Enyalioides* is strongly supported, as is the monophyly of the family,

TABLE 1.—Matrix of trait frequencies and mean species values for polymorphic, meristic, and morphometric characters. Characters are described in Appendix II. Generic abbreviations: E = *Enyalioides*, H = *Hoplocercus*, M = *Morunasaurus*.

	2	3	5	6	7	9	12	13	14	16	17	18
Leiolepis	1.00	0	4.00	2.00	6.00	0	—	—	—	0	0	0
Physignathus	1.00	0	3.00	2.00	—	0	0	0	0	0	0	0
Pristidactylus	1.67	0	2.00	2.00	5.00	0	—	—	—	0	0	0
Polychrus	0.00	0	0.00	2.50	3.00	0	—	—	—	0	0	0
Brachylophus	—	0	1.00	5.00	—	0	0	0	0	0	0	0
Ctenosaura	1.00	0	2.00	4.00	7.00	0	0	0	0	0	0	0
Dipsosaurus	1.00	0	3.00	4.00	5.00	50%	100%	0	0	0	0	0
H. spinosus	1.00	0	2.25	4.00	5.25	0	—	—	—	100%	100%	100%
M. annularis	0.64	0	1.29	2.00	3.86	0	100%	—	—	100%	100%	100%
M. groi	1.00	0	0.43	2.00	4.5	0	—	—	—	100%	100%	100%
E. cofanorum	2.50	100%	1.00	2.25	2.75	100%	0	100%	0	100%	100%	100%
E. heterolepis	2.56	55.6%	1.00	2.11	2.50	100%	0	16.7%	0	100%	100%	83.3%
E. laticeps	2.21	50.0%	1.11	2.00	3.64	100%	100%	0	0	16.7%	0	0
E. microlepis	2.79	100%	1.18	2.43	3.42	100%	0	92.9%	0	100%	0	21.4%
E. oshaughnessyi	2.54	100%	0.85	2.08	2.85	23.1%	0	7.7%	0	84.6%	0	100%
E. palpebralis	3.00	100%	1.79	2.86	2.43	71.4%	14.1%	0	85.7%	100%	85.7%	100%
E. praestabilis	2.90	80%	1.02	2.35	3.25	100%	0	20%	5%	95%	0	25%

but otherwise relationships are not well supported. In the tree from mixed scaling (Fig. 4), all three genera are monophyletic, and *Hoplocercus* is well supported as the sister taxon of *Morunasaurus*. Monophyly of *Enyalioides* is well supported, but relationships within the genus are not.

In contrast to the trees from between-state and mixed scaling, the ingroup tree from between-character scaling (Fig. 3) is similar to the tree described by Etheridge and de Queiroz (1988), but is less consistent with current taxonomy: *Enyalioides* is paraphyletic, *Enyalioides laticeps* is at the base of the family, *Enyalioides heterolepis* is the sister taxon of a clade containing *Morunasaurus* and *Hoplocercus*, and *Morunasaurus groi* is the sister taxon of *Hoplocercus spinosus*. The major departure from the tree estimated by Etheridge and de Queiroz (1988) is that five of the seven species of *Enyalioides* form a monophyletic group in the tree from between-character scaling in this study, whereas no species of *Enyalioides* are closest relatives to each other in the tree of Etheridge and de Queiroz (1988). In general, relationships in the tree from between-character scaling are only weakly supported, with the exception of the monophyly of the family and the *Hoplocercus* + *Morunasaurus* clade.

In the following paragraphs, we describe some of the synapomorphies supporting various internal branches in the trees based on between-state, between-character, and mixed scaling. For the sake of brevity, we mention only synapomorphies that have a weight of at least 500 steps (i.e., equivalent to a 50% change in frequency of a binary qualitative character) under both ACCTRAN and DELTRAN optimizations; a complete listing of character state changes is given in Appendix V. In the tree based on between-state scaling, the monophyly of Hoplocercidae (stem A) is supported by synapomorphies that include: presence of a series of enlarged dorsolateral scales (16.1), enlarged dorsal scales (17.1), enlarged flank scales (18.1), spines on the dorsal surface of the thigh (20.1), a reduction in the mean number of femoral pores (22), heterogeneous caudal scales (23.1), caudal spines (24.1), a black collar that is continuous with the gular patch (29.1), a black gular patch (30.1), and an increase in the number of pterygoid teeth (50). The clade of Hoplocercidae above *Hoplocercus* (stem B) is supported by reductions in the mean numbers of lorilabials (5), scales contacting the rostral (7) and femoral pores (22), and increases in the mean number of caudal scales per segment (26) and premaxillary teeth (49). The clade consisting of *Morunasaurus annularis* and *Enyalioides* (stem C) is supported by further reduction in the mean number of scales contacting the rostral (7), acquisition of

Table 1.—Extended.

19	20	22	26	27	28	29	30	33	34	35	36	40	41	49	50	51	52
0	0	15.50	—	0	0	0	0	—	0	0.022	0	100%	−0.050	2.00	0	0	66.7%
0	0	5.50	—	100%	0	0	0	—	0	0.069	0	0	−0.002	3.67	0	0	66.7%
0	0	7.00	—	0	0	100%	0	—	0	−0.004	0	0	−0.082	6.00	1.33	0	0
100%	0	10.00	—	0	0	0	0	—	100%	0.083	100%	100%	−0.020	11.00	0	100%	0
100%	0	14.00	—	100%	0	0	0	—	0	0.112	0	—	0.002	0	0	100%	0
0	0	5.75	3.00	0	0	0	0	—	0	0.055	0	0	0.022	7.00	17.67	100%	0
0	0	21.50	4.00	100%	0	0	0	—	0	0.033	0	0	0.001	7.00	1.00	100%	0
0	100%	4.38	2.00	0	0	100%	100%	25%	50%	0.012	0	0	0.053	6.00	6.62	0	0
0	100%	2.14	5.50	0	0	100%	100%	100%	57.1%	0.020	25%	100%	0.116	9.00	1.25	100%	0
0	100%	2.86	5.17	0	0	100%	100%	—	0	−0.012	0	0	0.052	8.00	5.00	50%	100%
100%	0	1.12	7.25	100%	25%	0	100%	—	100%	−0.029	0	100%	−0.021	11.00	6.00	50%	0
33.3%	100%	2.09	8.06	100%	0	23.1%	100%	0	94.4%	−0.041	0	0	0.000	7.33	10.50	100%	100%
71.4%	0	2.05	5.91	0	0	0	100%	—	0	−0.006	0	0	−0.041	10.00	9.17	62.5%	0
100%	0	2.00	6.85	100%	0	0	100%	—	23.1%	−0.013	0	100%	−0.015	9.00	12.00	100%	0
100%	0	1.12	6.38	100%	0	0	100%	—	16.7%	0.035	0	0	−0.060	9.00	10.0	0	0
100%	100%	0.00	5.57	100%	0	0	0	—	57.1%	−0.030	100%	100%	0.008	8.00	10.00	100%	0
15%	5%	1.32	5.47	95%	94.7%	0	85.7%	—	73.7%	−0.008	0	33%	0.035	9.00	6.50	0	0

a mid-dorsal crest of enlarged scales (10.1), a reduction in the mean number of femoral pores (22), and an increase in the mean number of premaxillary teeth (49). Monophyly of *Enyalioides* (stem D) is supported by pointed, conical head scales (1.1), an increase in the number of circumorbital scales (2), presence of raised scales posterior to the superciliaries (3.1), conical gular scales (8.1), keeled dorsal scales (9.1), loss of enlarged dorsal scales between the dorsolateral and mid-dorsal scale rows (17.0), loss of spines on the dorsal surface of the thigh (20.0), loss of caudal spines (24.0), loss of a black gular collar (29.0), and an increase in the mean number of pterygoid teeth (50). The clade of *Enyalioides* above *E. praestabilis* (stem E) is supported by keeled ventral scales (19.1) and an increase in the mean number of pterygoid teeth (50). The clade consisting of *E. cofanorum*, *E. heterolepis*, *E. microlepis*, *E. oshaughnessyi*, and *E. palpebralis* (stem F) is supported by a further increase in the mean number of pterygoid teeth (50). The clade consisting of *E. oshaughnessyi*, *E. cofanorum*, and *E. palpebralis* (stem G) is supported by a decrease in the mean number of femoral pores (22) and by an angular posterior margin of the clavicle (53.1). The clade consisting of *E. cofanorum* and *E. palpebralis* (stem H) is supported by the presence of enlarged dorsal scales between the dorsolateral and mid-dorsal scale rows (17.1), loss of the parietal foramen (40.1), and medial separation of the vomerine processes of the palatines (43.1). The clade of *E. heterolepis* and *E. microlepis* (stem I) is supported by a decrease in the mean number of pterygoid teeth (50).

In the tree based on between-character scaling, the monophyly of Hoplocercidae (stem A) is supported by the following synapomorphies: pointed, conical head scales (1.1), raised scales posterior to superciliaries (3.1), conical gular scales (8.1), paired, mid-dorsal crest scales on tail (15.1), black gular patch (30.1), and a palatine process of the pterygoid that extends well forward to the anterior margin of the inferior orbital fenestra (44.1). Hoplocercids above *E. laticeps* (stem B) are supported by the presence of a series of enlarged dorsolateral scales (16.1) and heterogeneous caudal scales (23.1). The clade of *E. praestabilis*, *E. microlepis*, *E. oshaughnessyi*, *E. cofanorum*, and *E. palpebralis* (stem C) is supported by synapomorphies that include a transition from slightly expanded to strongly expanded posterior marginal teeth (48.2). The clade of *E. microlepis*, *E. oshaughnessyi*, *E. cofanorum*, and *E. palpebralis* (stem D) is supported by keeled ventral scales (19.1). The clade of *E. oshaughnessyi*, *E. cofanorum*, and *E. palpebralis* (stem E) is supported by the presence of enlarged flank scales (18.1) and an angular or hooked posterior margin of the clavicle (53.1). The clade of *E. cofanorum* and *E. palpebralis* (stem F) is supported by the

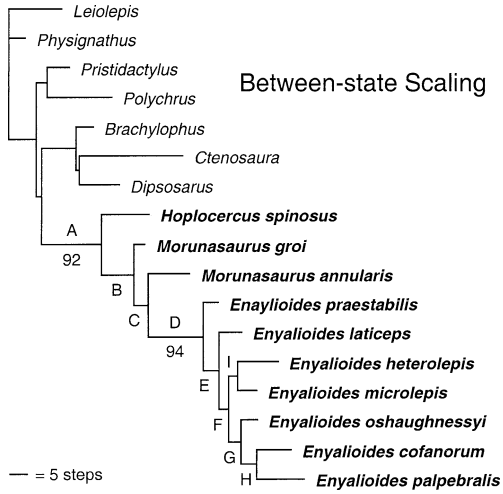

FIG. 2.—Phylogenetic relationships of hoplocercid lizards (boldface taxa) based on between-state scaling of meristic characters (length = 265.8 [265846.63], consistency index = 0.4463, consistency index [excluding uninformative characters] = 0.4274, retention index = 0.5434). Support for internal branches (labeled A to I) is listed in Appendix V. Numbers associated with internal branches are bootstrap values (values <50% not shown). The length of each branch is drawn proportional to the amount of evolutionary change estimated by parsimony with ACCTRAN optimization. Note that the raw tree lengths are much higher than in other studies because of the use of step matrices (lengths are divided by 999, to make them comparable to those reported in other studies; raw lengths are given in brackets).

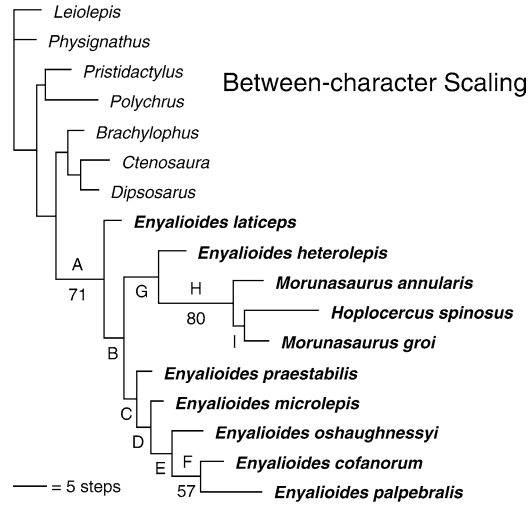

FIG. 3.—Phylogenetic relationships of hoplocercid lizards (boldface taxa) based on between-character scaling of meristic characters (length = 132.1 [131972], consistency index = 0.4376, consistency index [excluding uninformative characters] = 0.3915, retention index = 0.5541). Support for internal branches (labeled A to I) is listed in Appendix V. Numbers associated with internal branches are bootstrap values (values <50% not shown). The length of each branch is drawn proportional to the amount of evolutionary change estimated by parsimony, with ACCTRAN optimization.

presence of enlarged dorsal scales (17.1), medial contact of the vomerine processes of the palatine (43.1), and a reversal from strongly expanded to slightly expanded cusps of the posterior marginal teeth (48.1). The clade consisting of *E. heterolepis*, *Morunasaurus*, and *Hoplocercus* (stem G) is supported by synapomorphies including the presence of enlarged dorsals (17.1), enlarged flank scales (18.1), spines on the dorsal surface of the thigh (20.1), spines on the foot (21.1), and a black belly (32.1). The monophyly of the clade of *Morunasaurus* + *Hoplocercus* (stem H) is supported by a reversal to flat, rounded head scales (1.0), loss of raised scales posterior to the superciliaries (3.0), reversion to smooth gular scales (8.0), reversion to smooth dorsal scales (9.0), presence of caudal spines (24.1), and acquisition of a white bordered black collar (29.1). The clade consisting of *M. groi* and *Hoplocercus spinosus* (stem E) is supported by the loss of the mid-dorsal crest of enlarged scales (10.0).

In the tree from mixed scaling (Fig. 4), the monophyly of Hoplocercidae (stem A) is supported by synapomorphies including a black gular patch (30.1) and a palatine process of the pterygoid that extends well forward to the anterior margin of the inferior orbital fenestra (44.1). Monophyly of *Enyalioides* (stem B) is supported by the presence of pointed, conical head scales (1.1), an increase in the mean number of scales separating the circumorbitals medially (2), raised scales posterior to the superciliaries (3.1), a decrease in the mean number of scales contacting the rostral (7), conical scales in the gular region (8.1), and keeled dorsal scales (9.1). The clade of *Enyalioides* species exclusive of *E. laticeps* (stem C) is supported by a laterally compressed tail (27.1). The clade consisting of *E. heterolepis*, *E. oshaughnessyi*, *E. cofanorum*, and *E. palpebralis* (stem D) is supported by the presence of enlarged scales

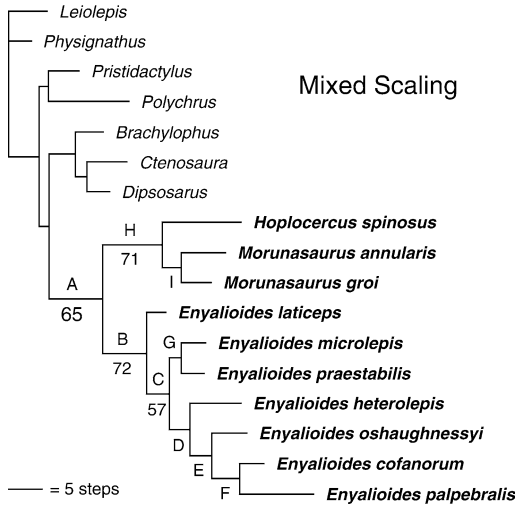

FIG. 4.—Phylogenetic relationships of hoplocercid lizards (boldface taxa) based on mixed scaling of meristic characters (length = 155.9 [155740.47], consistency index = 0.4386, consistency index [excluding uninformative characters] = 0.4001, retention index = 0.5509). Support for internal branches (labeled A to I) is listed in Appendix V. Numbers associated with internal branches are bootstrap values (values <50% not shown). The length of each branch is drawn proportional to the amount of evolutionary change estimated by parsimony, with ACCTRAN optimization. This tree is one of the three shortest trees from this analysis. These trees differ only in relationships among the outgroup families and have the topologies: (Acrodonta (Iguanidae (Polychrotidae + Hoplocercidae))) and (Acrodonta (Hoplocercidae (Iguanidae + Polychrotidae))).

on the flanks (18.1). The clade of *E. oshaughnessyi*, *E. cofanorum*, and *E. palpebralis* (stem E) is supported by an angular posterior margin of the clavicle (53.1). Monophyly of the species pair *E. cofanorum* and *E. palpebralis* (stem F) is supported by loss of the parietal foramen (40.1) and separation of the vomerine processes of the palatines (43.1). The species pair *E. microlepis* and *E. praestabilis* (stem G) is supported by strongly expanded posterior marginal teeth (48.2). The clade consisting of the genera *Hoplocercus* and *Morunasaurus* (stem H) is supported by the presence of enlarged dorsal scales between the dorsolateral and mid-dorsal scale rows (17.1), enlarged scales on the flanks (18.1), enlarged spines on the dorsal surface of the thigh (20.1), and caudal scales that are developed into distinct spines (24.1). Monophyly of *Morunasaurus* (stem I) is supported by presence of spines on the foot (21.1) and by the dentary extending posteriorly above the anterior surangular foramen (46.0).

DISCUSSION

Hoplocercid Phylogeny

We present the first explicit phylogenetic analysis of the lizard family Hoplocercidae. Our phylogenetic conclusions are highly sensitive to how meristic characters are scaled (weighted) relative to each other and to other characters in the analysis. Whether our results are unusually sensitive remains unclear, because ours is the only study that we are aware of that directly contrasts the results of these scaling methods (also reported in Wiens, 2001). The uncertainty does beg the question: what is the actual phylogeny of hoplocercids? We marginally prefer the results from the mixed-scaling approach, because between-state scaling may be unduly influenced by meristic traits with large ranges of trait values and between-character may unduly down-weight meristic characters with low ranges of trait values (which are essentially equivalent to polymorphic multistate characters). Therefore, we consider this tree (Fig. 4) to be our preferred estimate of hoplocercid phylogeny. However, it is clear that all three trees are relatively weakly supported, especially with regards to relationships within *Enyalioides*.

All three trees imply considerable homoplasy, but in different sets of characters. For example, the tree based on between-state scaling suggests that some of the character states shared by *Hoplocercus* and *Morunasaurus* (enlarged dorsal scales, spines on the thigh, caudal spines, and black collar) were gained in the common ancestor of the family and lost in the common ancestor of *Enyalioides*. The tree based on between-character scaling requires that many of the distinctive synapomorphies of *Enyalioides* be lost in *Hoplocercus* and *Morunasaurus*, including the pointed head scales, raised scales posterior to the superciliaries, conical gular scales, and increased number of scales between the circumorbitals. The preferred tree (based on mixed scaling) treats the unusual characteristics shared by *Hoplocercus* and *Morunasaurus* as unreversed synapomorphies and treats the distinctive synapomorphies of *Enyalioides* as unreversed as well. We find this result to be intuitively appealing.

However, our choice of this topology as "preferred" is based on our slight preference for the mixed-scaling method rather than an affinity for the resulting topology.

All three of our hypotheses differ considerably from the previous hypothesis for the group (Fig. 1; Etheridge and de Queiroz, 1988). Our analysis included many of the characters used by Etheridge and de Queiroz (1988), especially those characters shared by *Hoplocercus* and *Morunasaurus* (and, for some characters, some *Enyalioides*). We have added several characters as well, including synapomorphies uniting all or most species of *Enyalioides*. Not surprisingly then, the major difference between all three of our trees and the hypothesis of Etheridge and de Queiroz (1988) is our placement of most (between-character scaling) or all (between-state and mixed-scaling) species of *Enyalioides* in a single clade.

The tree of Etheridge and de Queiroz (1988) and those from two of our analyses (between-state and between-character scaling) suggest that the current generic-level taxonomy of hoplocercid lizards does not reflect their phylogenetic relationships. If our tree from between-state scaling is correct, then the genus *Morunasaurus* is paraphyletic; whereas, if the tree from between-character scaling is correct, then both *Enyalioides* and *Morunasaurus* are non-monophyletic. However, our preferred results, from mixed scaling, suggest that all three genera are monophyletic. Although we remain uncertain about the monophyly of *Enyalioides* and *Morunasaurus*, our current data suggest that the current taxonomy may adequately reflect hoplocercid phylogeny.

Biogeography and Historical Ecology

The preferred phylogeny generated by this study (Fig. 4) suggests some interesting biogeographical and evolutionary patterns. We mapped distributions of species onto this phylogeny using parsimony, with MacClade (version 3.04; Maddison and Maddison, 1992) with unordered states for Amazonian South America, Pacific South America, Brazilian grasslands, Central America (including North America for some taxa), and Oceania + Asia. This analysis (results not shown) suggests that the ancestor of the Hoplocercidae occurred in the tropical rainforests in the Amazon basin of northwestern South America and that the disjunct species from the grasslands of western Brazil (*Hoplocercus spinosus*) represents a more recent biogeographical and ecological transition. Recent authors have focused on the possible role of ecotones in generating high species richness in tropical regions (Moritz et al., 2000), particularly ecotones between rainforest and adjacent open forest/grassland (e.g., Schneider et al., 1999; Smith et al., 1997). In hoplocercids, it appears that the rainforest-grassland ecotone is relatively unimportant in speciation and that, instead, most speciation has been confined to the rainforests.

The mechanism of speciation for rainforest hoplocercid species is uncertain. Although some taxa are clearly allopatric (e.g., those on opposite sides of the Andes), there is extensive sympatry or near sympatry among species of hoplocercids in northwestern South America. *Enyalioides oshaughnessyi* and *E. heterolepis* occur together in western Ecuador and Colombia; *M. groi* and *E. heterolepis* are found in close proximity in Panama and Colombia; and *M. annularis*, *E. cofanorum* (or *E. microlepis*), *E. laticeps*, and *E. praestabilis* may occur in sympatry in eastern Ecuador and parts of Colombia and Peru. *Enyalioides palpebralis* seems to occur south of the other species, and *E. microlepis* and *E. cofanorum* appear to be allopatric with respect to each other. At least one pair of putative sister taxa are sympatric (*E. microlepis* and *E. praestabilis*), although their relationships are weakly supported and sensitive to scaling methods. This geographic pattern suggests that there has either been some sympatric speciation in the group or, perhaps more likely, extensive dispersal subsequent to speciation. These two hypotheses are not mutually exclusive and are difficult to distinguish given available data. The coexistence of these closely related hoplocercid species, especially the large number of species found together in Amazonian Ecuador, could be an interesting topic for future ecological and evolutionary studies. For example, it is not clear if, and to what extent, these species are ecologically or microgeographically segregated and if this segregation might play a role in speciation.

The preferred tree (and our two other trees) suggests that species from the Pacific side of the Andes (*E. heterolepis* and *E.*

oshaughnessyi) do not form a monophyletic group relative to the species on the Amazonian slopes of the Andes (*M. annularis*, *E. cofanorum*, *E. laticeps*, *E. microlepis*, *E. palpebralis*, and *E. praestabilis*). Because the Andes likely form an impassable barrier to dispersal by hoplocercids (which are all lowland tropical species), our results suggest that hoplocercid species were widely distributed and speciating prior to the major uplift of the Andes (approximately 14–11 million years ago; see recent review in Zamudio and Greene, 1997). This result is hardly surprising, however, given that hoplocercids may be a relatively old lineage among the iguanian families.

The limited ecological data available for hoplocercids, coupled with the preferred phylogeny (Fig. 4), suggest a major evolutionary transition within the family from a terrestrial, burrowing ecology to semi-arboreality (the latter defined based on at least some use of upright plants as diurnal or nocturnal perches). *Hoplocercus* and *Morunasaurus* contain terrestrial species that utilize burrows as nocturnal retreats (*H. spinosus* [G. Colli, M. Rodrigues and L. Vitt, personal communication]; *M. annularis* [J. Cadle, personal communication]; and *M. groi* [Dunn, 1933]). In contrast, most species of *Enyalioides* are generally found both on the ground and in arboreal settings by day (*E. heterolepis* [K. Miyata and R. McDiarmid, field notes]; *E. laticeps* [Duellman, 1978; Vitt and de la Torre, 1996; R. Etheridge, personal observation]; *E. microlepis* [K. Miyata and R. McDiarmid, field notes]; and *E. oshaughnessyi* [R. McDiarmid, field notes]). Further, all *Enyalioides* species for which data are available are known to sleep on trunks and branches at night (*E. cofanorum* [Duellman, 1978]; *E. heterolepis* [R. McDiarmid, field notes]; *E. microlepis* [listed as *E. cofanorum* by Duellman and Mendelson, 1995; K. Miyata, field notes]; *E. laticeps* [Duellman, 1978; Vitt and de la Torre, 1996; J. Wiens, personal observation]; *E. palpebralis* [R. McDiarmid, field notes]; *E. praestabilis* [W. Duellman, field notes]; unknown for *E. oshaughnessyi*). Three species of *Enyalioides* have so far only been found on the ground by day, but this may reflect the ease of finding these taxa on the ground (relative to finding them high in trees) or limited observations rather than their actual habits (*E. cofanorum* [Duellman, 1978]; *E. palpebralis* [L. Vitt, personal communication]; *E. praestabilis* [J. Peters, field notes]). The exact phylogenetic placement of the transition between terrestriality and semi-arboreality depends on the tree and optimization among the limited sampling of outgroup taxa. One hypothesis is that the ancestor of Hoplocercidae was terrestrial and that arboreality evolved in the ancestor of *Enyalioides* (supported by between-state scaling and some optimizations of mixed scaling). The alternate hypothesis is that arboreality is ancestral and that the *Hoplocercus* + *Morunasaurus* clade is secondarily terrestrial (supported by between-character scaling and some optimizations under mixed scaling).

Coding Morphological Variation

Our study demonstrates that step matrices can be used to code meristic, morphometric, and polymorphic characters in a way that allows continuous variation in mean trait values and trait frequencies to be treated as continuous. The use of step matrices allows the maximum possible information to be extracted from these data and avoids the use of arbitrary cut-offs. Furthermore, we demonstrate that step matrices can allow meristic, morphometric, and polymorphic data to be combined and analyzed simultaneously, along with more traditional characters (i.e., fixed and qualitative).

Our study also shows that different ways of scaling meristic data can lead to very different hypotheses of phylogeny, even for clades that are strongly supported under one or more scaling methods (see also Wiens, 2001). This is surprising given that the coding of the data sets is identical. It remains to be seen how sensitive phylogenetic conclusions will be in general to the application of these scaling methods. We note that most morphological analyses implicitly require making a decision about how meristic characters are scaled—we have simply treated this decision in a more formal and quantitative manner (Wiens, 2001).

Finally, our study demonstrates that rigorous phylogenetic analysis of morphological data can be quite complex, especially in groups (such as hoplocercids) in which many of the morphological characters show overlapping trait values between species. We have

employed relatively sophisticated, time-intensive methods for coding characters (using step matrices) and have found that the details of these methods (e.g., scaling meristic characters) can have a major impact on the estimated trees. Clearly, it would be simpler and easier to use qualitative descriptions and arbitrary cutoffs in defining and delimiting character states. Yet, the traditional approach also involves decisions that can impact phylogenetic conclusions (e.g., where exactly to define character state boundaries). The important difference is that, in the traditional approach, the decision making process is rarely explained and is, therefore, much less explicit and repeatable. We argue that including and coding meristic, morphometric, and polymorphic characters as continuous variables using step matrices is an important way to increase the character data available in phylogenetic analyses and to make morphological phylogenetics more explicit and rigorous.

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Literature Cited

Berlocher, S. H., and D. L. Swofford. 1997. Searching for phylogenetic trees under the frequency parsimony criterion: an approximation using generalized parsimony. Systematic Biology 46:211–215.

Campbell, J. A., and D. R. Frost. 1993. Anguid lizards of the genus *Abronia*: revisionary notes, descriptions of four new species, phylogenetic analysis, and key. Bulletin of the American Museum of Natural History 216:1–121.

Corredor, V., J. M. Renjifo, and S. C. Ayala. 1985. Discovery of *Morunasaurus groi* Dunn (Sauria, Iguanidae) in northwestern Colombia. Journal of Herpetology 19:162–164.

Duellman, W. E. 1973. Descriptions of new lizards from the Upper Amazon Basin. Herpetologica 29:228–231.

———. 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. Miscellaneous Publications of the University of Kansas Museum of Natural History 65:1–352.

Duellman, W. E., and J. R. Mendelson III. 1995. Amphibians and reptiles from northern Departamento Loreto, Peru: taxonomy and biogeography. The University of Kansas Science Bulletin 55:329–376.

Dunn, E. R. 1933. Amphibians and reptiles from El Valle de Anton, Panamá. Occasional Papers of the Boston Society of Natural History 8:65–79.

Estes, R., K. de Queiroz, and J. A. Gauthier. 1988. Phylogenetic relationships within Squamata. Pp. 119–281. *In* R. Estes and G. K. Pregill (Eds.), Phylogenetic Relationships of the Lizard Families. Stanford University Press, Stanford, California, U.S.A.

Etheridge, R. 1995. Redescription of *Ctenoblepharys adspersa* Tschudi, 1845, and the taxonomy of Liolaeminae (Reptilia: Squamata: Tropiduridae). American Museum Novitates 3142:1–34.

Etheridge, R., and K. de Queiroz. 1988. A phylogeny of Iguanidae. Pp. 283–368. *In* R. Estes and G. K. Pregill (Eds.), Phylogenetic Relationships of the Lizard Families. Stanford University Press, Stanford, California, U.S.A.

Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39:783–791.

Frost, D. R. 1992. Phylogenetic analysis and taxonomy of the *Tropidurus* group of lizards (Iguania: Tropiduridae). American Museum Novitates 3107:1–68.

Frost, D. R., and R. Etheridge. 1989. A phylogenetic analysis and taxonomy of iguanian lizards (Reptilia: Squamata). Miscellaneous Publications of the University of Kansas Museum of Natural History 81:1–65.

Frost, D. R., R. Etheridge, D. Janies, and T. A. Titus. 2001*a*. Total evidence, sequence alignment, evolution of polychrotid lizards, and a reclassification of the Iguania (Squamata: Iguania). American Museum Novitates 3343:1–38.

Frost, D. R., M. T. Rodrigues, T. Grant, and T. A. Titus. 2001*b*. Phylogenetics of the lizard genus *Tropidurus* (Squamata: Tropiduridae: Tropidurinae): direct optimization, descriptive efficiency, and sensitivity analysis of congruence between molecular data and morphology. Molecular Phylogenetics and Evolution 21:352–371.

Harvey, M. B., and R. L. Gutberlet. 1999. A phylogenetic analysis of the tropidurine lizards (Squamata: Tropiduridae), including new characters of squamation and epidermal microstructure. Zoological Journal of the Linnean Society 128:189–233.

Hillis, D. M., and J. J. Bull. 1993. An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. Systematic Biology 42: 182–192.

Hollingsworth, B. D. 1998. The systematics of chuckwallas (*Sauromalus*) with a phylogenetic analysis of other iguanid lizards. Herpetological Monographs 12:38–191.

Jackman, T. R., A. Larson, K. de Queiroz, and J. B. Losos. 1999. Phylogenetic relationships and tempo of early diversification in *Anolis* lizards. Systematic Biology 48:254–285.

Lang, M. A. 1989. Phylogenetic and biogeographic patterns of basiliscine iguanians (Reptilia: Squamata: "Iguanidae"). Bonner Zoologische Monographien 28: 1–172.

LEE, M. S. Y. 1998. Convergent evolution and character correlation in burrowing reptiles: towards a resolution of squamate relationships. Biological Journal of the Linnean Society 65:369–453.

LEVITON, A. E., R. H. GIBBS, JR., E. HEAL, AND C. E. DAWSON. 1985. Standards in herpetology and ichthyology: Part 1. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. Copeia 1985:802–832.

MACEY, J. R., J. A. SCHULTE II, A. LARSON, N. B. ANANJEVA, Y. WANG, R. PETHIYAGODA, N. RASTEGAR-POUYANI, AND T. J. PAPENFUSS. 2000. Evaluating trans-Tethys migration: an example using acrodont lizard phylogenetics. Systematic Biology 49:233–256.

MADDISON, W. P., AND D. R. MADDISON. 1992. MacClade Ver. 3.04. Analysis of Phylogeny and Character Evolution. Sinauer Associates, Sunderland, Massachusetts, U.S.A.

MCGUIRE, J. A. 1996. Phylogenetic systematics of crotaphytid lizards (Reptilia: Iguania: Crotaphytidae). Bulletin of the Carnegie Museum of Natural History 32: 1–143.

MORITZ, C., J. L. PATTON, C. J. SCHNEIDER, AND T. B. SMITH. 2000. Diversification of rainforest faunas: an integrated molecular approach. Annual Review of Ecology and Systematics 31:533–563.

NIXON, K. C., AND J. M. CARPENTER. 1993. On outgroups. Cladistics 9:413–426.

PETERS, J. A., AND R. DONOSO-BARROS. 1970. Catalogue of the Neotropical Squamata. Part II. Lizards and Amphisbaenians. United States National Museum Bulletin 297:1–293.

POE, S., AND J. J. WIENS. 2000. Character selection and the methodology of morphological phylogenetics. Pp. 20–36. *In* J. J. Wiens (Ed.), Phylogenetic Analysis of Morphological Data. Smithsonian Institution Press, Washington, D.C., U.S.A.

PREGILL, G. K. 1992. Systematics of the West Indian lizard genus *Leiocephalus* (Squamata: Iguana: Tropiduridae). Miscellaneous Publications of the University of Kansas Museum of Natural History 84:1–69.

RAXWORTHY, C. J., M. R. J. FORSTNER, AND R. A. NUSSBAUM. 2002. Chameleon radiation by oceanic dispersal. Nature 415:784–787.

REEDER, T. W., AND J. J. WIENS. 1996. Evolution of the lizard family Phrynosomatidae as inferred from diverse types of data. Herpetological Monographs 10:43–84.

ROTH, J., K. HAYCOCK, J. GAGNON, C. SOPER, AND J. CALDAROLA. 1995. Statview version 4.51. Abacus Concepts Inc., Berkeley, California, U.S.A.

SCHNEIDER, C. J., T. B. SMITH, B. LARISON, AND C. MORITZ. 1999. A test of alternative models of diversification in tropical rainforests: ecological gradients vs. rainforest refugia. Proceedings of the National Academy of Sciences USA 96:13869–13873.

SCHULTE, J. A. II, J. R. MACEY, A. LARSON, AND T. J. PAPENFUSS. 1998. Molecular tests of phylogenetic taxonomies: a general procedure and example using subfamilies of the lizard family Iguanidae. Molecular Phylogenetics and Evolution 8:367–376.

SCHULTE, J. A. II, J. R. MACEY, R. E. ESPINOZA, AND A. LARSON. 2000. Phylogenetic relationships in the iguanid lizard genus *Liolaemus*: multiple origins of viviparous reproduction and evidence for recurring Andean vicariance and dispersal. Biological Journal of the Linnean Society 69:75–102.

SITES, J. W., JR., S. K. DAVIS, T. GUERRA, J. B. IVERSON, AND H. L. SNELL. 1996. Character congruence and phylogenetic signal in molecular and morphological data sets: a case study in the living iguanas (Squamata: Iguanidae). Molecular Biology and Evolution 13:1087–1105.

SMITH, E. N., AND R. L. GUTBERLET. 2001. Generalized frequency coding: a method of preparing polymorphic multistate characters for phylogenetic analysis. Systematic Biology 50:156–169.

SMITH, T. B., R. K. WAYNE, D. J. GIRMAN, AND M. W. BRUFORD. 1997. A role for ecotones in generating rainforest biodiversity. Science 276:1855–1857.

SWOFFORD, D. L. 2002. PAUP*: Phylogenetic analysis using parsimony*, version 4.0b10. Sinauer Associates, Sunderland, Massachussetts, U.S.A.

THIELE, K. 1993. The holy grail of the perfect character: the cladistic treatment of morphometric data. Cladistics 9:275–304.

TITUS, T. A., AND D. R. FROST. 1996. Molecular homology assessment and phylogeny in the lizard family Opluridae (Squamata: Iguania). Molecular Phylogenetics and Evolution 5:49–62.

VITT, L. J., AND S. DE LA TORRE. 1996. A research guide to the lizards of Cuyabeno. Museo de Zoologia, Centro de Biodiversidad y Ambiente, Pontificia Universidad Catolica del Ecuador, Monografía 1:1–165.

WIENS, J. J. 1995. Polymorphic characters in phylogenetic systematics. Systematic Biology 44:482–500.

———. 1999. Polymorphism in systematics and comparative biology. Annual Review of Ecology and Systematics 30:327–362.

———. 2001. Character analysis in morphological phylogenetics: problems and solutions. Systematic Biology 50:689–699.

WIENS, J. J., AND B. D. HOLLINGSWORTH. 2000. War of the iguanas: conflicting molecular and morphological phylogenies and long-branch attraction in iguanid lizards. Systematic Biology 49:69–85.

WIENS, J. J., AND T. W. REEDER. 1997. Phylogeny of the spiny lizards (*Sceloporus*) based on molecular and morphological evidence. Herpetological Monographs 11:1–101.

WILGENBUSCH, J., AND K. DE QUEIROZ. 2000. Phylogenetic relationships among the phrynosomatid sand lizards inferred from mitochondrial DNA sequences. Systematic Biology 49:592–612.

WILKINSON, M. 1992. Ordered versus unordered characters. Cladistics 8:375–385.

ZAMUDIO, K. R., AND H. W. GREENE. 1997. Phylogeography of the bushmaster (*Lachesis muta:* Viperidae): implications for neotropical biogeography, systematics, and conservation. Biological Journal of the Linnean Society 62:421–442.

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APPENDIX I

Specimens Examined

Institutional abbreviations follow Leviton et al. (1985), with the addition of RE (personal collection of Richard Etheridge). Sample sizes (individuals examined per

species) are given for preserved hoplocercids only. Localities are given for hoplocercids only, with elevations in parentheses (if known).

Preserved Specimens

Hoplocercidae

Hoplocercus spinosus (*n* = 13).—BOLIVIA: Santa Cruz: Velasco, El Refugio, UTA 38071. BRAZIL: Mato Grosso: Barra do Tapirapes, CAS 93081–87, 93804–05, CM 65047, SDSU 2118, UTA 30931.

Morunasaurus annularis (*n* = 14).—COLOMBIA: Putumayo: Puesto de Bombeo de Guamez (1000 m), KU 140396. ECUADOR: Napo: Cabeceras del Río Arajuno, tributary of Río Napo, USNM 200736, 200738–39, 200741–47, 200751–52. Pastaza: La Cabaceras del Río Bobonaza, KU 209799.

Morunasaurus groi (*n* = 7).—PANAMA: Cocle: El Valle de Antón, CAS 98280, CM 6637, FMNH 22978, 178119, KU 76060 (560 m), MCZ 34876. Panama: El Valle de Antón, CAS 7507.

Enyaliodes cofanorum (*n* = 4).—ECUADOR: Napo: Santa Cecilia (340 m), KU 105342, 122118, 147584, 175308.

Enyalioides heterolepis (*n* = 18).—COLOMBIA: Cauca: Gorgona Island FMNH 165387–88. Chocó: Río San Juan between Cucurrupi and Noanama Buenaventura, Valle, MCZ 139485. Boca de la Raspadura, approximately 12 km NNW Istmina, AMNH 18278. ECUADOR: Esmeraldas: Río Palabi, USNM 211081; San Lorenzo, USNM 211085. Pichincha: 4 km ESE of El Esfuerzo, MCZ 171865; Río Blanco, below the mouth of Río Toachi, USNM 211088; Santo Domingo de los Colorados, USNM 211090; Quinindé to Santo Domingo de los Colorados, Km 30, USNM 211091; Centro Científico Río Palenque, 47 km S Santo Domingo de los Colorados (150–220 m), USNM 285449, 285451-52, 285454; Palma Real, USNM 211092. PANAMA: Darién: southern base of Cerro Tacarcuna (approximately 800 m), AMNH 119365. Panama: Cerro Azul region, Río Piedra, AMNH 119868–69.

Enyaliodes laticeps (*n* = 14).—ECUADOR: Napo: Lago Agrío, SDSU 2117. Pastaza: Sarayacu, Río Bobonaza, USNM 211122; upper Río Bobonaza, USNM 211134; Teresa Mama, Río Bobonaza, USNM 211137; Río Huiyayacu, tributary of Río Conambo, USNM 21127–28; Río Conambo, near mouth of Río Romarizo, USNM 211138; Río Conambo, USNM 211139; Río Pindo, tributary of Río Tigre, USNM 211143–44; upper Río Oglan, USNM 211146; Cabaceras del Río Arajuno, tributary of Río Napo, USNM 211135. PERU: Loreto: Colonia Calleria, Río Calleria, 15 km from Ucayali, CAS 93246. Junín: Pan de Azucar, Río Izcosazín SDSU 2116.

Enyaliodes microlepis (*n* = 14).—ECUADOR: Morona-Santiago: Río Llushin, N of Arapicos, USNM 211069; Río Liguiño, Río Bobonaza, USNM 211071; below Montalvo, USNM 211073. Pastaza: Sarayacu, AMNH 37562; Andoas, AMNH 113634; mouth of Río Capahuari, MCZ 156936. PERU: Amazonas: approximately 0.8 km N of Huampami on the Río Cenepa, USNM 316717–18; vicinity of San Antonio on the Río Cenepa, USNM 316720; vicinity of Kayamas, on the Río Cenepa, USNM 316721; vicinity of Súa on the Río Cenepa, USNM 316722–23. Loreto: San Jacinto (175 m), KU 222163. Barranca, Marañón River Valley, (142 m), AMNH 56417.

Enyalioides oshaughnessyi (*n* = 13).—ECUADOR: Guayas: 11 km E Manglaralto, Cordillera de Coloche, CM 9928. Los Ríos: Estación Biológica Río Palenque, 56 km N Quevedo (220 m), KU 152597. Pichincha: Santo Domingo de los Colorados (500 m), KU 109630, USNM 211109; 2 km E and 1 km S Santo Domingo de los Colorados (600 m), KU 179416; 5 km W of Santo Domingo de los Colorados, USNM 21107; Finca Victoria S of Santo Domingo de los Colorados, MCZ 145269; Finca La Esperanza, near Santo Domingo de los Colorados, USNM 21106; Centro Científico Río Palenque, 47 km S of Santo Domingo de los Colorados, USNM 285457; Puerto Quito, MCZ 164509; Tandapi, MCZ 164789; Silanchi, Río Blanco, USNM 211102. LOCALITY UNCERTAIN: USNM 211101.

Enyaliodes palpebralis (*n* = 7).—PERU: Cuzco: Marcapata, Hacienda Cadena (1000 m), FMNH 59185; Tono, FMNH 229575. Madre de Dios: ridge above Hacienda Amazonia, near Río Alto (780 m), FMNH 218569–70; Zona Reservada Tambopata-Candamo, W bank of Río Tambopata, Colpa de Guacamayo, USNM 332467; 57 km (airline) NW of mouth of Río Manu, on Río Manu, Pakitza Reserve Zone, Manu National Park, USNM 342870. San Martin: Río Cainrache, 33 km NE Tarapoto on road to Yurimaguas, KU 209512.

Enyaliodes praestabilis (*n* = 20).—COLOMBIA: Putumayo: 10.3 km W El Pepino (1440 m), KU 169854. ECUADOR: Morona-Santiago: Misión Bomboiza (840 m), KU 147183–84; Chiguaza, USNM 211152, 211154. Napo: Avila, Río Napo, CAS 8260; Concepción, USNM 211156; S slope Cordillera del Due above Río Coca (1150 m), KU 122117; Lumbaquí, MCZ 164901–02; San José de Sumaco, AMNH 28894. Pastaza: Alto Curaray, MCZ 156937; Palmera, Pastaza River Valley, AMNH 37554; Pastaza River (1000 m), UMMZ 90803; Cabaceras del Río Arajuno, tributary of Río Napo, USNM 211159–60; immediate vicinity of Arajuno, USNM 211165; Hacienda Madrid, 5 km SSE of Puyo, USNM 211161; Río Villano, USNM 211164.

Acrodonta

Leiolepis belliana.—SDSU 2588-89.
Physignathus concincinus.—SDSU 2665.

Iguanidae

Brachylophus fasciatus.—CM 4287.
Ctenosaura similis.—SDSU 2628, 2629.
Dipsosaurus dorsalis.—SDSU 3121, 3123.

Leiosauridae

Pristidactylus torquatus.—CM 64692, 147621; SDSU 2250.

Polychrotidae

Polychrus marmoratus.—SDSU 2233, 2234.

Skeletal Specimens

Hoplocercidae

Hoplocercus spinosus.—BRAZIL: Santa Philomena, MCZ 20677, 20679. NO LOCALITY DATA: RE 1263, 1502.

Morunasaurus groi.—PANAMA: Cocle: El Valle de Anton, KU 76061, MCZ 34876 (no skull).

Morunasaurus annularis.—ECUADOR: Morona-Santiago: Río Santiago, Valle, RE 1956. Napo: Cabaceras del Río Arajuno, tributary of Río Napo, USNM 200735, 200740. Pastaza: Cabaceras del Bobonaza, USNM 203842.

Enyalioides cofanorum.—ECUADOR: Napo: Santa Cecilia (340 m), KU 147587.

Enyalioides heterolepis.—PANAMA: Isthmus of Panamá, MCZ 28384. ECUADOR: Esmeraldas: Río Cachavi, USNM 211079; San Javier, USNM 211083.

Enyalioides laticeps.—ECUADOR: Pastaza: Pastaza River, Canelos to Marañón River, MCZ 37287; mouth of Río Capahuari, USNM 211123; Río Huiyayacu, tributary of Río Conambo, USNM 211126. NO LOCALITY DATA: RE 1957.

Enyalioides oshaughnessyi.—ECUADOR: Pichincha: 5 km W of Santo Domingo de los Colorados, USNM 211108.

Enaylioides palpebralis.—PERU: (no other locality data), FMNH 40008.

Enyalioides praestabilis.—ECUADOR: Pastaza: road to Puyo, MCZ 163653. Pastaza: Río Villano, USNM 211162; region of Alto Río Curaray, USNM 211168.

Acrodonta

Leiolepis belliana.—RE 1907, 1908, 1993.
Physignathus lesuerii.—RE 1272, 1364, 1849.

Iguanidae

Brachylophus fasciatus.—RE 1866, 1888.
Ctenosaura similis.—RE 469, 2233, 2238.
Dipsosaurus dorsalis.—RE 356, 359, 484, 661.

Leiosauridae

Pristidactylus achalensis.—RE 2490, 2491.

Polychrotidae

Polychrus marmoratus.—RE 2863.

Appendix II

Characters Used in Phylogenetic Analysis

Characters are categorized as either fixed, polymorphic, meristic, or morphometric. Autapomorphies and ordering of multistate, fixed characters are also noted. The consistency index (ci) of each character is given, with the slash denoting the ci on the between-state scaling, between-character scaling, and mixed trees, respectively. Character states are designated as "0" or "1" for the purposes of description (not to indicate polarity), and polymorphic characters were coded in a more complex manner in the actual data matrix (using step matrices). For external morphology, references to various "enlarged" scales refers to the large size of these scales relative to the size of adjacent scales.

External Morphology

1. Dorsal head scales: (0) not pointed and conical, (1) some or all pointed and conical. Fixed and qualitative (ci = 1.000/0.500/1.000)
2. Minimum number of scales separating circumorbitals medially. Meristic (ci = 0.599/0.481/0.674). *Brachylophus fasciatus* was scored as unknown ("?") because the circumorbitals are poorly differentiated. Range of mean species values = 3.00
3. Raised, dorsally projecting scales just posterior to superciliaries, on lateral edge of skull roof: (0) absent, (1) present. Polymorphic (ci = 0.573/0.642/0.693)
4. Posterior superciliary scales: (0) not enlarged relative to adjacent scales, (1) enlarged, pointed, and projecting laterally. Fixed, uninformative (autapomorphy of *Enyalioides palpebralis*)
5. Minimum number of lorilabial scales separating subocular and supralabials (below eye). Meristic (ci = 0.429/0.392/0.403). Range of mean species values = 4.00
6. Number of scales contacting mental posteriorly (excluding labials). Meristic (ci = 0.425/0.434/0.447). Range of mean species values = 3.00
7. Number of scales contacting rostral (excluding labials). Meristic (ci = 0.501/0.436/0.482). Range of mean species values = 4.57
8. Scales in gular region (Frost and Etheridge, 1989): (0) smooth, (1) some or all distinctly conical. Fixed (ci = 0.500/0.333/0.500)
9. Dorsals: (0) smooth, (1) distinctly keeled. Polymorphic (ci = 0.281/0.247/0.281)
10. Mid-dorsal row of enlarged scales (Etheridge and de Queiroz, 1988): (0) absent, (1) present. Fixed (ci = 0.333/0.333/0.250)
11. Scales of mid-dorsal row: (0) not raised, (1) raised, projecting above surrounding scales. Fixed (ci = 0.500)
12. Mid-dorsal scale row: (0) extends onto tail, (1) absent or indistinct on anterior portion of tail. Polymorphic (ci = 0.318)
13. Mid-dorsal crest scales: (0) single row, (1) some scales paired in nuchal region. Not scored in *Morunasaurus annularis*, with poorly developed crest scales. Polymorphic (ci = 0.783/0.731/0.731)
14. Mid-dorsal crest: (0) continuous in nuchal region, (1) with distinct gap in nuchal region. Not scored in *Morunasaurus annularis*. Polymorphic (ci = 0.945)
15. Mid-dorsal crest scales: (0) single on tail, (1) paired on tail. Not scored in *Morunasaurus annularis*. Fixed (ci = 1.000)
16. Longitudinal series of enlarged dorsolateral scales (Etheridge and de Queiroz, 1988): (0) absent, (1) present. Polymorphic (ci = 0.492/0.832/0.492)
17. Enlarged dorsal scales between dorsolateral and mid-dorsal scale rows: (0) absent, (1) present. Polymorphic (ci = 0.250/0.500/0.333)
18. Enlarged scales on flanks, ventral to dorsolateral scale row: (0) absent, (1) present. Polymorphic (ci = 0.297/0.560/0.491)
19. Ventral scales at mid-body: (0) smooth, (1) some or all keeled. Polymorphic (ci = 0.273/0.257/0.236)
20. Irregularly placed, enlarged scales or spines on dorsal surface of thigh: (0) absent, (1) present. Polymorphic (ci = 0.250/0.488/0.328)

21. Spines or enlarged scales on foot over fourth and fifth metatarsals: (0) absent, (1) present. Fixed (ci = 0.333/0.500/0.500)
22. Femoral pores in males (one side). Meristic (ci = 0.494/0.470/0.470). Range of mean species values = 21.50
23. Caudal scales (Etheridge and de Queiroz, 1988): (0) homogeneous, (1) heterogeneous, scales increasing in size posteriorly within each segment. Fixed (ci = 0.333/0.500/0.333)
24. Caudal scales (Etheridge and de Queiroz, 1988): (0) not developed into distinct spines, (1) some scales developed into distinct spines. Fixed (ci = 0.500/1.000/1.000)
25. Tail (Etheridge and de Queiroz, 1988): (1) not short, flattened, and heavily spinous, (1) short, flattened, heavily spinous. Uninformative, autapomorphy of *Hoplocercus spinosus*
26. Number of rows of caudal scales per segment, measured one head length (tip of snout to posterior edge of retroarticular process) from level of posterior hind limb insertion and at roughly mid-height of tail. Meristic (ci = 0.515/0.462/0.450). Some outgroup taxa were scored as unknown because the limits of caudal segments were unclear. Range of mean species values = 6.05
27. Tail shape (Etheridge and de Queiroz, 1988): (0) rounded or flattened in cross-section, not laterally compressed, (1) laterally compressed. Polymorphic (ci = 0.202/0.200/0.247)
28. Coloration of dorsal surface of head scales: (0) not dark, or if dark lacking light spots, (1) dark, with a lighter colored spot on many scales. Polymorphic (ci = 0.791)
29. White-bordered black collar, continuous with gular patch: (0) absent, (1) present. Polymorphic (ci = 0.309/0.500/0.448)
30. Black gular patch (in males, in preservative): (0) absent, (1) present. Polymorphic (ci = 0.467)
31. Dark gular patch: (0) on throat, (1) in gular fold only. Uninformative, autapomorphy of *Enyalioides oshaughnessyi*
32. Black pigmentation on belly: (0) absent, (1) present. Fixed (ci = 0.333/0.500/0.333)
33. Black belly and gular patches: (0) separate, (1) continuous. Uninformative
34. Dark spot below eye: (0) absent, (1) present. Polymorphic (ci = 0.230/0.259/0.230)
35. Relationship between hind-limb length and snout–vent length (SVL). Hind-limb length measured from groin (angle formed by lateral surface of body and anterior surface of thigh) to distal extremity of digit IV (including claw). SVL measured from anterior margin of rostral to anterior margin of cloacal opening. Values were $\log_{10}$-transformed prior to analysis. Morphometric (ci = 0.375/0.355/0.372)

Skeletal Morphology

36. Lacrimal bone (Etheridge and de Queiroz, 1988): (0) present, (1) absent. Polymorphic (ci = 0.444)
37. Prefrontal: (0) projects over lacrimal region, (1) does not project. Fixed (ci = 0.250/0.200/0.200)
38. Postorbital, posteriorly projecting squamosal process: (0) present, (1) absent. Uninformative, autapomorphy of *Enyalioides palpebralis*
39. Squamosal postorbital process: (0) relatively narrow, (1) relatively wide. Uninformative, autapomorphy of *Enyalioides palpebralis*
40. Parietal foramen (Etheridge and de Queiroz, 1988): (0) present, (1) absent. Polymorphic (ci = 0.188/0.200/0.200)
41. Relationship between parietal width and length. Parietal width is the distance between the distal extremities of the parietal at the frontoparietal suture. Parietal length is the distance between the anterior margin of the parietal (at the frontoparietal suture) and the distal (i.e. posterior) extremities of the paraoccipital processes of the parietal. Values were $\log_{10}$-transformed prior to analysis. Morphometric (ci = 0.440/0.455/0.440)
42. Paired, enlarged dermal tubercles on posterolateral surface of parietal roof: (0) absent, (1) present. Uninformative, autapomorphy of *Enyalioides palpebralis*
43. Medial contact of vomerine processes of palatines: (0) present, (1) absent. Fixed (ci = 0.500)
44. Palatine process of the pterygoid: (0) does not extend forward to the anterior margin of the inferior orbital fenestra, (1) extends well forward to the anterior margin of the inferior orbital fenestra. Fixed (ci = 0.333)
45. Vidian canal exit: (0) lateral to the sella turcica, (1) on the ventral surface of the parabasisphenoid. Uninformative, autapomorphy of *Hoplocercus spinosus*
46. Anterior surangular foramen (Frost and Etheridge, 1989): (0) dentary extends posteriorly above foramen, (1) dentary does not extend posteriorly above foramen. Fixed (ci = 0.200/0.200/0.250)
47. Splenial posterior extent (Frost and Etheridge, 1989): (0) terminates anterior to anterior edge of adductor fossa, (1) terminates at anterior edge of adductor fossa or more posteriorly. Fixed (ci = 0.500)
48. Posterior marginal teeth (Etheridge and de Queiroz, 1988): (0) tapered, tiny secondary cusps, (1) slightly expanded, large secondary cusps, (2) strongly expanded, low central cusp, small fourth cusp. Fixed and ordered (ci = 0.500/0.667/0.667)
49. Premaxillary tooth number. Meristic (ci = 0.482/0.435/0.435). Range of mean species values = 9.00
50. Pterygoid tooth number (per side). Meristic (ci = 0.449/0.372/0.408). Range of mean species values = 17.84
51. Scapular fenestra: (0) absent, (1) present. Polymorphic (ci = 0.195/0.182/0.178)
52. Clavicular fenestra (Etheridge and de Queiroz, 1988): (0) absent, (1) present. Polymorphic (ci = 0.375)
53. Posterior margin of clavicle (Etheridge and de Queiroz, 1988): (0) smooth curve, (1) angular or hooked, (2) irregular. Fixed and unordered (ci = 0.667)
54. Caudal autotomy (Etheridge and de Queiroz, 1988): (0) present, (1) absent. Fixed (ci = 0.200/0.167/0.167)
55. Sacral diapophyses: (0) robust and flattened, (1) slender and rounded. Uninformative, autapomorphy of *Hoplocercus spinosus*
56. Transverse processes of caudal vertebrae: (0) decrease in length throughout column, (1) increase in length

from first to fourth. Uninformative, autapomorphy of *Hoplocercus spinosus*

Appendix III

Alpha Taxonomy

There has been considerable confusion regarding *Enyalioides microlepis* and *E. oshaughnessyi* in the literature and in museum collections. Peters and Donoso-Barros (1970) listed *E. microlepis* as occurring in "Pacific lowlands of Ecuador" and *E. oshaughnessyi* as being found in "Amazonian Ecuador and Colombia." Yet, the type locality of *E. microlepis* is Sarayacu, a town in Amazonian Ecuador, and the type series of *E. microlepis* also includes a specimen (BMNH 58.7.25.17 [RR 1946.8.5.57]) from Guayaquil (on the Pacific coast). The type locality of *E. oshaughnessyi* is given only as "Ecuador." Specimens we have examined from northwestern Ecuador agree with the description and illustration of *E. oshaughnessyi* given by Boulenger in having a distinctly raised mid-dorsal crest, a distinct dewlap, scattered enlarged scales on the flanks, and a black gular fold (but no black coloration on the throat). In contrast, specimens we have examined from Amazonian Ecuador and Peru have a relatively low mid-dorsal crest, lack a distinct dewlap, have no enlarged scales on the flanks, and have black coloration on the throat but not in the gular fold, in accord with O'Shaughnessy's description and illustration of *E. microlepis*. Thus, we consider the Amazonian form to be *E. microlepis* and the Pacific form to be *E. oshaughnessyi*.

Another issue is the distinctness of *E. microlepis* and *E. cofanorum*. Duellman (1973) distinguished *E. cofanorum* from *E. microlepis* by the presence of flat scales between the dorsolateral and mid-dorsal scale rows in *E. microlepis* and conical scales in *E. cofanorum*. Our observations revealed that both *E. cofanorum* and *E. microlepis* have conical scales, although these scales are flat in *E. oshaughnessyi* (and this error may be attributed to the confusion surrounding *E. microlepis* and *E. oshaughnessyi*). In fact, there is relatively little to separate *E. cofanorum* and *E. microlepis*. Nevertheless, all specimens of *E. cofanorum* that we have examined have distinctly enlarged scales scattered between the mid-dorsal and dorsolateral scale rows. This character remains diagnostic even in a specimen of *E. microlepis* from Limoncocha (MCZ 156396), close to the type locality of *E. cofanorum* at Santa Cecilia in the province of Napo. Further collecting may show these two forms to be conspecific, but we tentatively consider them to be distinct. Based on our understanding, *E. cofanorum* is known only from the type locality, whereas *E. microlepis* ranges widely in Amazonian Ecuador and southward into Peru. Although our phylogenetic results do not place *E. cofanorum* and *E. microlepis* as sister taxa (supporting their treatment as distinct species), the possible relationships that we postulate for these taxa are only weakly supported, and we cannot rule out the possbility that they are actually conspecific based on these results.

In our study, we found two forms that may represent undescribed species, but we lack sufficient material and character evidence to describe these at the present time. One is represented by a single specimen (BMNH 89.12.16.18) from an unknown locality in Bolivia. This specimen is very similar to specimens of *E. palpebralis* from Peru (i.e., it shares the elongate superciliary horns and a gap in the mid-dorsal crest in the nuchal region). It differs from *E. palpebralis* in lacking enlarged scales between the dorsal midline and the dorsolateral tubercles (present in *E. palpebralis*) and in having smaller, more homogeneous temporal scales than *E. palpebralis*. However, we are hesitant to describe this species as new based on a single specimen from an unknown locality. We assume that future collecting in Bolivia will reveal more material and a known locality for this species.

We have also observed three specimens of what may represent an undescribed species from Amazonian Peru (AMNH 56400 [Upper Biabo Valley, Huallaga River Valley], CAS 135348 and FMNH 5593 [Tingo Maria]). This form is similar to *E. praestabilis*, but differs from most individuals of that species in having strongly keeled ventral and gular scales, lacking enlarged lateral gular scales, and having distinctly raised scales posterior to the superciliaries, scattered black spots on the venter, light bands on the dorsum, and an elongate light nuchal stripe. However, all of these characters show at least some variation within *E. praestabilis*. Furthermore, many of the characters of the Peruvian form (i.e., distinct head spines, black spots on the venter, light bands on the dorsum, elongate nuchal stripe) were observed in a sample of two individuals of *E. praestabilis* from southern Ecuador (KU 147183-84; Morona-Santiago Province: Mision Bomboiza), suggesting the possibility that the Peruvian form represents only geographic variation within *E. praestabilis*. Additional material, especially males of this potentially new taxon, may allow resolution of this problem, but we are hesitant to describe this form as new based only on currently available information.

Appendix IV

Data Matrix

Data matrix used in the phylogenetic analyses. Characters are described in Appendix II. Meristic, morphometric, and polymorphic characters are coded such that each taxon with a unique trait mean or frequency is given a unique state, and the cost of changes between these states are specified using a step matrix. The weighting commands for all three scaling methods are included, but only one was used in any given analysis. Generic abbreviations: E = *Enyalioides*, H = *Hoplocercus*, M = *Morunasaurus*.

```
#NEXUS
BEGIN DATA;
DIMENSIONS NTAX=17 NCHAR=56;
FORMAT MISSING=? GAP= -SYMBOLS= " 0 1 2 3 4 5 6 7 8 9 A B C D E F G " ;
MATRIX
[                    10         20         30         40         50     ]
Leiolepis        0200C0C000?????000000E000?0000?0?000100200010??00010100
Physignathus     0200B0?00110000000000900?2000?0?010000010000?0?10011100
Pristidactylus   030090A000?????000000B000A0020?0?0201000200000012300000 0
Polychrus        0000064100?????000400C000?0000?0?732000230000001803001 00
Brachylophus     0?0039?04110000000400D000?2000?0?040000040000?0?31300100
Ctenosaura       020098D00110000000000A10020000?0?050000050000000?3C300000
Dipsosarus       0200B8A02102000000000F00012000?0?060000060000000?31300000
H.spinosus       0200A8B000?????42402081110002201137010007001110027000111
M.annularis      010070800102???42402161105002201248100028011000162302000
M.groi           0200109000?????42402171103002200?090000090000000154120000
E.cofanorum      1540332141105014244001100B210200?7A00002A0110?0185101000
E.heterolepis    1720321141102014232215100C20120106B01000B00101114A320000
E.laticeps       1410507141120011003004000700020 0?0C00000C001010178200000
E.microlepis     1840656141103014014003100920020 0?2D01002D00101026B300000
E.oshaughness    1640213111100012044001100820021 0?1E00000E001011269001100
E.palpebralis    1A4187013111021414420010062000?0?4F20112F111000159301100
E.praestabilis   1930445141101113021102100412010 0?5G00001G00101026600?000
;
ENDBLOCK;
```

USERTYPE char2 STEPMATRIX = 11

	0	1	2	3	4	5	6	7	8	9	A
[0]	.	213	333	556	736	832	846	852	929	966	999
[1]	213	.	120	343	523	619	633	639	716	753	786
[2]	333	120	.	223	403	499	513	519	596	633	666
[3]	556	343	223	.	180	276	290	296	373	410	443
[4]	736	523	403	180	.	96	110	116	193	230	263
[5]	832	619	499	276	96	.	14	20	97	134	167
[6]	846	633	513	290	110	14	.	6	83	120	153
[7]	852	639	519	296	116	20	6	.	77	114	147
[8]	929	716	596	373	193	97	83	77	.	37	70
[9]	966	753	633	410	230	134	120	114	37	.	33
[A]	999	786	666	443	263	167	153	147	70	33	.

;

USERTYPE char3 STEPMATRIX = 5

	0	1	2	3	4
[0]	.	500	556	800	999
[1]	500	.	56	300	499
[2]	556	56	.	244	443
[3]	800	300	244	.	199
[4]	999	499	443	199	.

;

USERTYPE char5 STEPMATRIX = 13

	0	1	2	3	4	5	6	7	8	9	A	B	C
[0]	.	107	212	250	255	277	295	322	447	500	562	749	999
[1]	107	.	105	143	148	170	188	215	340	393	455	642	892
[2]	212	105	.	38	43	65	83	110	235	288	350	537	787
[3]	250	143	38	.	5	27	45	72	197	250	312	499	749
[4]	255	148	43	5	.	22	40	67	192	245	307	494	744
[5]	277	170	65	27	22	.	18	45	170	223	285	472	722
[6]	295	188	83	45	40	18	.	27	152	205	267	454	704
[7]	322	215	110	72	67	45	27	.	125	178	240	427	677
[8]	447	340	235	197	192	170	152	125	.	53	115	302	552
[9]	500	393	288	250	245	223	205	178	53	.	62	249	499
[A]	562	455	350	312	307	285	267	240	115	62	.	187	437
[B]	749	642	537	499	494	472	454	427	302	249	187	.	250
[C]	999	892	787	749	744	722	704	677	552	499	437	250	.

;

USERTYPE char6 STEPMATRIX = 10

	0	1	2	3	4	5	6	7	8	9
[0]	.	27	37	83	117	143	166	286	666	999
[1]	27	.	10	56	90	116	139	259	639	972
[2]	37	10	.	46	80	106	129	249	629	962
[3]	83	56	46	.	34	60	83	203	583	916
[4]	117	90	80	34	.	26	49	169	549	882
[5]	143	116	106	60	26	.	23	143	523	856
[6]	166	139	129	83	49	23	.	120	500	833
[7]	286	259	249	203	169	143	120	.	380	713
[8]	666	639	629	583	549	523	500	380	.	333
[9]	999	972	962	916	882	856	833	713	333	.

;

USERTYPE char7 STEPMATRIX = 14

	0	1	2	3	4	5	6	7	8	9	A	B	C	D
[0]	.	15	70	92	125	179	216	264	313	452	562	616	780	999
[1]	15	.	55	77	110	164	201	249	298	437	547	601	765	984
[2]	70	55	.	22	55	109	146	194	243	382	492	546	710	929
[3]	92	77	22	.	33	87	124	172	221	360	470	524	688	907
[4]	125	110	55	33	.	54	91	139	188	327	437	491	655	874
[5]	179	164	109	87	54	.	37	85	134	273	383	437	601	820
[6]	216	201	146	124	91	37	.	48	97	236	346	400	564	783
[7]	264	249	194	172	139	85	48	.	49	188	298	352	516	735
[8]	313	298	243	221	188	134	97	49	.	139	249	303	467	686
[9]	452	437	382	360	327	273	236	188	139	.	110	164	328	547
[A]	562	547	492	470	437	383	346	298	249	110	.	54	218	437
[B]	616	601	546	524	491	437	400	352	303	164	54	.	164	383
[C]	780	765	710	688	655	601	564	516	467	328	218	164	.	219
[D]	999	984	929	907	874	820	783	735	686	547	437	383	219	.

;

USERTYPE char9 STEPMATRIX = 5

	0	1	2	3	4
[0]	.	231	500	714	999
[1]	231	.	269	483	768
[2]	500	269	.	214	499
[3]	714	483	214	.	285
[4]	999	768	499	285	.

;

USERTYPE char12 STEPMATRIX = 3

	0	1	2
[0]	.	141	999
[1]	141	.	858
[2]	999	858	.

;

USERTYPE char13 STEPMATRIX = 6

	0	1	2	3	4	5
[0]	.	77	167	200	929	999
[1]	77	.	90	123	852	922
[2]	167	90	.	33	762	832
[3]	200	123	33	.	729	799
[4]	929	852	762	729	.	70
[5]	999	922	832	799	70	.

;

USERTYPE char14 STEPMATRIX = 3

	0	1	2
[0]	.	50	857
[1]	50	.	807
[2]	857	807	.

;

USERTYPE char16 STEPMATRIX = 5

	0	1	2	3	4
[0]	.	167	846	950	999
[1]	167	.	679	783	832
[2]	846	679	.	104	153
[3]	950	783	104	.	50
[4]	999	832	153	50	.

;

USERTYPE char17 STEPMATRIX = 3

	0	1	2
[0]	.	857	999
[1]	857	.	142
[2]	999	142	.

;

USERTYPE char18 STEPMATRIX = 5

	0	1	2	3	4
[0]	.	214	250	833	999
[1]	214	.	36	619	785
[2]	250	36	.	583	749
[3]	833	619	583	.	166
[4]	999	785	749	166	.

;

USERTYPE char19 STEPMATRIX = 5

	0	1	2	3	4
[0]	.	150	333	714	999
[1]	150	.	183	564	849
[2]	333	183	.	381	666
[3]	714	564	381	.	285
[4]	999	849	666	285	.

;

USERTYPE char20 STEPMATRIX = 3

	0	1	2
[0]	.	50	999
[1]	50	.	949
[2]	999	949	.

;

USERTYPE char22 STEPMATRIX = 16

	0	1	2	3	4	5	6	7	8	9	A	B	C	D	E	F
[0]	.	52	61	93	95	97	99	133	204	256	267	325	465	650	720	999
[1]	52	.	9	41	43	45	47	81	152	204	215	273	413	598	668	947
[2]	61	9	.	32	34	36	38	72	143	195	206	264	404	589	659	938
[3]	93	41	32	.	2	4	6	40	111	163	174	232	372	557	627	906
[4]	95	43	34	2	.	2	4	38	109	161	172	230	370	555	625	904
[5]	97	45	36	4	2	.	2	36	107	159	170	228	368	553	623	902
[6]	99	47	38	6	4	2	.	34	105	157	168	226	366	551	621	900
[7]	133	81	72	40	38	36	34	.	71	123	134	192	332	517	587	866
[8]	204	152	143	111	109	107	105	71	.	52	63	121	261	446	516	795
[9]	256	204	195	163	161	159	157	123	52	.	11	69	209	394	464	743
[A]	267	215	206	174	172	170	168	134	63	11	.	58	198	383	453	732
[B]	325	273	264	232	230	228	226	192	121	69	58	.	140	325	395	674
[C]	465	413	404	372	370	368	366	332	261	209	198	140	.	185	255	534
[D]	650	598	589	557	555	553	551	517	446	394	383	325	185	.	70	349
[E]	720	668	659	627	625	623	621	587	516	464	453	395	255	70	.	279
[F]	999	947	938	906	904	902	900	866	795	743	732	674	534	349	279	.

;

USERTYPE char26 STEPMATRIX = 13

	0	1	2	3	4	5	6	7	8	9	A	B	C
[0]	.	165	330	523	572	577	588	645	722	800	824	866	999
[1]	165	.	165	358	407	412	423	480	557	635	659	701	834
[2]	330	165	.	193	242	247	258	315	392	470	494	536	669
[3]	523	358	193	.	49	54	65	122	199	277	301	343	476
[4]	572	407	242	49	.	5	16	73	150	228	252	294	427
[5]	577	412	247	54	5	.	11	68	145	223	247	289	422
[6]	588	423	258	65	16	11	.	57	134	212	236	278	411
[7]	645	480	315	122	73	68	57	.	77	155	179	221	354
[8]	722	557	392	199	150	145	134	77	.	78	102	144	277
[9]	800	635	470	277	228	223	212	155	78	.	24	66	199
[A]	824	659	494	301	252	247	236	179	102	24	.	42	175
[B]	866	701	536	343	294	289	278	221	144	66	42	.	133
[C]	999	834	669	476	427	422	411	354	277	199	175	133	.

;

USERTYPE char27 STEPMATRIX = 3

	0	1	2
[0]	.	950	999
[1]	950	.	49
[2]	999	49	.

;

USERTYPE char28 STEPMATRIX = 3

	0	1	2
[0]	.	250	947
[1]	250	.	697
[2]	947	697	.

;

USERTYPE char29 STEPMATRIX = 3

	0	1	2
[0]	.	231	999
[1]	231	.	768
[2]	999	768	.

;

USERTYPE char30 STEPMATRIX = 3

	0	1	2
[0]	.	857	999
[1]	857	.	142
[2]	999	142	.

;

USERTYPE char33 STEPMATRIX = 3

	0	1	2
[0]	.	250	999
[1]	250	.	749
[2]	999	749	.

;

USERTYPE char34 STEPMATRIX = 8

	0	1	2	3	4	5	6	7
[0]	.	167	231	500	571	737	944	999
[1]	167	.	64	333	404	570	777	832
[2]	231	64	.	269	340	506	713	768
[3]	500	333	269	.	71	237	444	499
[4]	571	404	340	71	.	166	373	428
[5]	737	570	506	237	166	.	207	262
[6]	944	777	713	444	373	207	.	55
[7]	999	832	768	499	428	262	55	.

;

USERTYPE char35 STEPMATRIX = 17

	0	1	2	3	4	5	6	7	8	9	A	B	C	D	E	F	G
[0]	0	307	169	399	587	216	72	65	13	222	333	411	182	228	85	339	195
[1]	307	0	476	92	281	91	235	372	320	528	639	717	489	534	222	645	501
[2]	169	476	0	567	756	385	241	104	156	53	164	242	13	59	254	170	26
[3]	399	92	567	0	189	183	327	464	412	620	731	809	580	626	314	737	593
[4]	587	281	756	189	0	372	515	652	600	809	920	998	769	815	502	926	782
[5]	216	91	385	183	372	0	144	281	229	438	548	626	398	444	131	554	411
[6]	72	235	241	327	515	144	0	137	85	294	405	483	254	300	13	411	267
[7]	65	372	104	464	652	281	137	0	52	157	268	346	117	163	150	274	130
[8]	13	320	156	412	600	229	85	52	0	209	320	398	169	215	98	326	182
[9]	222	528	53	620	809	438	294	157	209	0	111	189	40	6	307	117	27
[A]	333	639	164	731	920	548	405	268	320	111	0	78	151	105	418	6	138
[B]	411	717	242	809	998	626	483	346	398	189	78	0	229	183	496	72	216
[C]	182	489	13	580	769	398	254	117	169	40	151	229	0	46	267	157	13
[D]	228	534	59	626	815	444	300	163	215	6	105	183	46	0	313	111	33
[E]	85	222	254	314	502	131	13	150	98	307	418	496	267	313	0	424	280
[F]	339	645	170	737	926	554	411	274	326	117	6	72	157	111	424	0	144
[G]	195	501	26	593	782	411	267	130	182	27	138	216	13	33	280	144	0

;

USERTYPE char36 STEPMATRIX = 3

	0	1	2
[0]	.	250	999
[1]	250	.	749
[2]	999	749	.

;

USERTYPE char40 STEPMATRIX = 3

	0	1	2
[0]	.	333	999
[1]	333	.	666
[2]	999	666	.

;

USERTYPE char41 STEPMATRIX = 17

	0	1	2	3	4	5	6	7	8	9	A	B	C	D	E	F	G
[0]	0	243	161	152	263	364	258	519	837	514	147	252	46	177	50	293	429
[1]	243	0	404	91	20	121	15	277	594	272	96	9	197	66	293	50	186
[2]	161	404	0	313	424	524	419	680	998	675	308	413	207	338	111	454	589
[3]	152	91	313	0	111	212	106	368	685	363	5	100	106	25	202	141	277
[4]	263	20	424	111	0	101	5	257	574	252	116	11	217	86	313	30	166
[5]	364	121	524	212	101	0	106	156	474	151	217	112	318	187	414	71	65
[6]	258	15	419	106	5	106	0	262	579	257	111	6	212	81	308	35	171
[7]	519	277	680	368	257	156	262	0	318	5	373	268	474	343	569	227	91
[8]	837	594	998	685	574	474	579	318	0	323	690	585	791	660	887	544	409
[9]	514	272	675	363	252	151	257	5	323	0	368	263	469	338	564	222	86
[A]	147	96	308	5	116	217	111	373	690	368	0	105	101	30	197	146	282
[B]	252	9	413	100	11	112	6	268	585	263	105	0	206	75	302	41	177
[C]	46	197	207	106	217	318	212	474	791	469	101	206	0	131	96	247	383
[D]	177	66	338	25	86	187	81	343	660	338	30	75	131	0	227	116	252
[E]	50	293	111	202	313	414	308	569	887	564	197	302	96	227	0	343	479
[F]	293	50	454	141	30	71	35	227	544	222	146	41	247	116	343	0	136
[G]	429	186	589	277	166	65	171	91	409	86	282	177	383	252	479	136	0

;

USERTYPE char49 STEPMATRIX = 9

	0	1	2	3	4	5	6	7	8
[0]	.	185	444	555	592	666	777	888	999
[1]	185	.	259	370	407	481	592	703	814
[2]	444	259	.	111	148	222	333	444	555
[3]	555	370	111	.	37	111	222	333	444
[4]	592	407	148	37	.	74	185	296	407
[5]	666	481	222	111	74	.	111	222	333
[6]	777	592	333	222	185	111	.	111	222
[7]	888	703	444	333	296	222	111	.	111
[8]	999	814	555	444	407	333	222	111	.

;

USERTYPE char50 STEPMATRIX = 13

	0	1	2	3	4	5	6	7	8	9	A	B	C
[0]	.	56	71	75	283	339	368	374	518	565	594	678	999
[1]	56	.	15	19	227	283	312	318	462	509	538	622	943
[2]	71	15	.	4	212	268	297	303	447	494	523	607	928
[3]	75	19	4	.	208	264	293	299	443	490	519	603	924
[4]	283	227	212	208	.	56	85	91	235	282	311	395	716
[5]	339	283	268	264	56	.	29	35	179	226	255	339	660
[6]	368	312	297	293	85	29	.	6	150	197	226	310	631
[7]	374	318	303	299	91	35	6	.	144	191	220	304	625
[8]	518	462	447	443	235	179	150	144	.	47	76	160	481
[9]	565	509	494	490	282	226	197	191	47	.	29	113	434
[A]	594	538	523	519	311	255	226	220	76	29	.	84	405
[B]	678	622	607	603	395	339	310	304	160	113	84	.	321
[C]	999	943	928	924	716	660	631	625	481	434	405	321	.

;

```
USERTYPE char51 STEPMATRIX = 4
                0       1       2       3
[0]             .     500     625     999
[1]           500       .     125     499
[2]           625     125       .     374
[3]           999     499     374       .
;

USERTYPE char52 STEPMATRIX = 3
                0       1       2
[0]             .     667     999
[1]           667       .     332
[2]           999     332       .
;
```

OPTIONS DEFTYPE=unord PolyTcount=MINSTEPS ;
TYPESET * UNTITLED = unord: 53, ord: 1 4 8 10–11 15 21 23–25 31–32 48, char2: 2, char3: 3, char5: 5, char6: 6, char7: 7, char9: 9, char12: 12, char13: 13, char14: 14, char16: 16, char17: 17, char18: 18, char19: 19, char20: 20, char22: 22, char26: 26, char27: 27, char28: 28, char29: 29, char30: 30, char33: 33, char34: 34, char35: 35, char36: 36, char40: 40, char41: 41, char49: 49, char50: 50, char51: 51, char52: 52;
WTSET * BETWEENSTATE = 999.00: 1 4 8 10–11 15 21 23–25 31–32 37–39 42–48 53–56, 3.00: 2 6, 1.00: 3 9 12–14 16–20 27–30 33–35 36 40–41 51–52, 4.00: 5, 4.57: 7, 21.50: 22, 6.05: 26, 9.00: 49, 17.84: 50;
WTSET * BETWEENCHARACTER = 999: 1 4 8 10–11 15 21 23–25 31–32 37–39 42–48 53–56, 1: 2–3 5–7 9 12–14 16–20 22 26–30 33–35 36 40–41 49–52;
WTSET * MIXED = 999.00: 1 4 8 10–11 15 21 23–25 31–32 37–39 42–48 53–56, 3.00: 2 6, 1.00: 3 9 12–14 16–20 22 26–30 33–35 36 40–41 49–52, 4.00: 5, 4.57: 7;

ENDBLOCK;
BEGIN TREES;
TRANSLATE

1	Leiolepis,
2	Physignathus,
3	Pristidactylus,
4	Polychrus,
5	Brachylophus,
6	Ctenosaura,
7	Dipsosarus,
8	H.spinosus,
9	M.annularis,
10	M.groi,
11	E.cofanorum,
12	E.heterolepis,
13	E.laticeps,
14	E.microlepis,
15	E.oshaughness,
16	E.palpebralis,
17	E.praestabilis

;

TREE * UNTITLED = [andR] ((1,2),((6,7),5),(3,4),16,9,14,17,13,10,12,11,15,8);
ENDBLOCK;

Appendix V

Character Changes

Stems correspond to the trees in Figures 2–4. For a given character, the derived state that evolves at a given stem is placed after the decimal point; the number in parentheses indicates the cost of that change. Character lengths (costs) are much higher than those typically reported because of the use of step matrices (costs comparable to those reported in other studies can be obtained simply by dividing each value by 999). Furthermore, some meristic characters have weights >999 because of use of between-state scaling. For multistate and step matrix coded characters, states ranged in order from 0 to 9 followed by A to G. Most characters were coded with the smallest frequency or meristic trait value given the state 0, but states for the two morphometric characters are assigned based on their order in the order data matrix, not on character state values.

Between-state Scaling (Fig. 2)

Stem A.—ACCTRAN: 15.1 (999.0), 16.4 (999.0), 17.2 (999.0), 18.4 (999.0), 20.2 (999.0), 22.8 (2601.5), 23.1 (999.0), 24.1 (999.0), 29.2 (999.0), 30.2 (999.0), 34.3 (500.0), 35.7 (65.0), 41.9 (252.0), 44.1 (999.0), 50.4 (4049.7). DELTRAN: 16.4 (999.0), 17.2 (999.0), 18.4 (999.0), 20.2 (999.0), 22.8 (2601.5), 23.1 (999.0), 24.1 (999.0), 29.2 (999.0), 30.2 (999.0), 35.7 (65.0), 41.9 (252.0), 50.4 (4049.7).

Stem B.—ACCTRAN: 5.4 (980.0), 6.0 (1998.0), 7.9 (502.7), 21.1 (999.0), 22.7 (1526.5), 26.3 (1167.6), 35.G (130.0), 49.5 (999.0), 54.0 (999.0). DELTRAN: 5.7 (712.0), 7.9 (502.7), 22.7 (1526.5), 26.3 (1167.6), 49.5 (1998.0), 51.1 (500.0), 54.0 (999.0).

Stem C.—ACCTRAN: 7.8 (635.2), 10.1 (999.0), 22.6 (731.0), 26.5 (326.7), 34.4 (71.0), 40.1 (333.0), 49.6 (999.0), 51.2 (125.0). DELTRAN: 7.8 (635.2), 10.1 (999.0), 22.6 (731.0), 26.4 (296.4), 34.2 (231.0), 44.1 (999.0), 49.6 (999.0).

Stem D.—ACCTRAN: 1.1 (999.0), 2.6 (1539.0), 3.3 (800.0), 6.2 (111.0), 7.5 (612.38), 8.1 (999.0), 9.4 (999.0), 17.0 (999.0), 18.2 (749.0), 19.1 (150.0), 20.1 (949.0), 21.0 (999.0), 22.3 (129.0), 24.0 (999.0), 27.1 (950.0), 29.0 (999.0), 33.0 (250.0), 41.G (86.0), 46.1 (999.0), 50.6 (1516.4). DELTRAN: 1.1 (999.0), 2.4 (1209.0), 3.1 (500.0), 5.5 (180.0), 7.7 (223.9), 8.1 (999.0), 9.4 (999.0), 15.1 (999.0), 17.0 (999.0), 18.3 (166.0), 19.1 (150.0), 20.1 (949.0), 22.4 (86.0), 24.0 (999.0), 29.0 (999.0), 35.C (117.0), 41.G (86.0), 50.6 (1516.4).

Stem E.—ACCTRAN: 19.3 (564.0), 20.0 (50.0), 26.7

(411.4), 34.2 (340.0), 40.0 (333.0), 41.A (282.0), 50.8 (2676.0). DELTRAN: 19.3 (564.0), 20.0 (50.0), 26.7 (441.6), 41.D (252.0), 50.8 (2676.0).

Stem F.—ACCTRAN: 3.4 (199.0), 5.3 (20.0), 7.3 (397.6), 18.3 (583.0), 19.4 (285.0), 26.8 (465.8), 27.2 (49.0), 35.D (33.0), 50.9 (838.5). DELTRAN: 2.6 (330.0), 3.2 (56.0), 6.1 (81.0), 7.6 (219.4), 26.8 (465.8), 27.2 (999.0), 50.9 (838.5).

Stem G.—ACCTRAN: 9.3 (285.0), 18.4 (166.0), 22.1 (881.5), 51.1 (125.0), 53.1 (999.0), 54.1 (999.0). DELTRAN: 3.4 (443.0), 7.3 (566.7), 18.4 (166.0), 19.4 (285.0), 22.1 (924.5), 53.1 (999.0).

Stem H.—ACCTRAN: 6.3 (138.0), 7.2 (100.5), 17.1 (857.0), 34.4 (340.0), 35.A (105.0), 40.2 (999.0), 43.1 (999.0), 46.0 (999.0). DELTRAN: 6.3 (168.0), 7.2 (22.0), 17.1 (857.0), 34.4 (340.0), 35.A (151.0), 40.2 (999.0), 43.1 (999.0).

Stem I.—ACCTRAN: 2.7 (18.0), 13.2 (167.0), 26.9 (471.9), 37.1 (999.0), 41.D (30.0), 50.A (517.4), 51.3 (374.0). DELTRAN: 2.7 (18.0), 6.2 (30.0), 13.2 (167.0), 26.9 (471.9), 37.1 (999.0), 50.A (517.4), 51.3 (499.0).

Between-character Scaling (Fig. 3)

Stem A.—ACCTRAN: 1.1 (999), 2.4 (403), 3.1 (500), 7.7 (298), 8.1 (999), 15.1 (999), 16.1 (167), 22.4 (230), 30.2 (999), 35.C (182), 44.1 (999), 49.6 (222), 50.8 (462). DELTRAN: 1.1 (999), 2.4 (403), 3.1 (500), 5.5 (223), 7.7 (298), 8.1 (999), 9.4 (999), 15.1 (999), 16.1 (167), 19.1 (150), 22.5 (228), 30.2 (999), 35.A (182), 44.1 (999), 49.5 (111), 50.6 (312), 54.0 (999).

Stem B.—ACCTRAN: 2.7 (116), 3.2 (56), 5.4 (22), 7.5 (85), 13.1 (77), 16.4 (832), 18.2 (250), 20.1 (50), 23.1 (999), 34.4 (571), 35.G (13). DELTRAN: 13.1 (77), 16.4 (832), 18.2 (250), 23.1 (999), 34.2 (231).

Stem C.—ACCTRAN: 2.8 (77), 3.3 (244), 6.4 (80), 22.2 (34), 40.1 (333), 48.2 (999), 51.1 (125). DELTRAN: 2.6 (110), 3.3 (300), 6.3 (83), 7.6 (48), 22.3 (4), 27.1 (950), 35.G (13), 40.1 (333), 48.2 (999), 49.6 (111).

Stem D.—ACCTRAN: 3.4 (199), 19.4 (666), 20.0 (50), 26.8 (77), 27.2 (49), 34.2 (340), 35.D (33), 40.2 (666), 41.D (75), 50.9 (47). DELTRAN: 3.4 (199), 19.4 (849), 26.8 (77), 27.2 (49), 41.D (66), 50.9 (197).

Stem E.—ACCTRAN: 2.6 (83), 5.3 (5), 6.3 (34), 7.3 (87), 9.3 (285), 13.0 (77), 18.4 (749), 22.1 (9), 41.A (30), 53.1 (999), 54.1 (999). DELTRAN: 7.3 (124), 18.4 (749), 22.1 (41), 53.1 (999).

Stem F.—ACCTRAN: 7.2 (22), 17.1 (857), 34.4 (340), 35.A (105), 43.1 (999), 46.0 (999), 48.1 (999). DELTRAN: 7.2 (22), 17.1 (857), 34.4 (340), 35.A (138), 43.1 (999), 48.1 (999).

Stem G.—ACCTRAN: 13.2 (90), 17.2 (999), 18.3 (583), 20.2 (949), 21.1 (999), 22.5 (2), 29.1 (231), 32.1 (999), 49.5 (111), 51.3 (374). DELTRAN: 17.2 (999), 18.3 (583), 20.2 (999), 21.1 (999), 29.1 (231), 32.1 (999), 34.3 (269), 41.B (9).

Stem H.—ACCTRAN: 1.0 (999), 2.2 (519), 3.0 (556), 5.7 (67), 6.0 (37), 7.8 (134), 8.0 (999), 9.0 (999), 11.0 (999), 12.2 (999), 18.4 (166), 19.0 (333), 22.6 (2), 24.1 (999), 26.5 (68), 27.0 (950), 29.2 (768), 33.1 (250), 35.7 (130), 41.7 (268), 46.0 (999), 50.4 (235). DELTRAN: 1.0 (999), 2.2 (403), 3.0 (500), 7.8 (49), 8.0 (999), 9.0 (999), 18.4 (166), 19.0 (150), 22.6 (2), 24.1 (999), 26.5 (68), 29.2 (768), 33.1 (250), 41.9 (263).

Stem I.—ACCTRAN: 7.9 (139), 10.0 (999), 22.7 (34), 26.3 (54), 34.3 (71), 51.1 (499). DELTRAN: 7.9 (139), 10.0 (999), 22.7 (34), 26.3 (54), 51.1 (125).

Mixed Scaling (Fig. 4)

Stem A.—ACCTRAN: 7.9 (110.0), 12.2 (999.0), 15.1 (999.0),16.4 (999.0), 18.2 (250.0), 22.7 (192.0), 23.1 (999.0), 30.2 (999.0), 34.3 (500.0), 35.7 (65.0), 44.1 (999.0), 49.5 (111.00), 50.7 (318.0). DELTRAN: 16.1 (167.0), 22.8 (121.0), 30.2 (999.0), 35.7 (65.0), 44.1 (999.0), 50.4 (227.0).

Stem B.—ACCTRAN: 1.1 (999.0), 2.4 (1209.0), 3.1 (500.0), 5.5 (180.0), 7.7 (859.2), 8.1 (999.0), 9.4 (999.0), 19.3 (714.0), 22.4 (38.0), 26.7 (122.0), 35.C (117.0), 41.D (86.0), 49.6 (111.0), 50.8 (144.0). DELTRAN: 1.1 (999.0), 2.4 (1209.0), 3.1 (500.0), 5.5 (928.0), 7.7 (1361.9), 8.1 (999.0), 9.4 (999.0), 19.2 (333.0), 22.4 (109.0), 26.7 (122.0), 35.C (117.0), 49.6 (222.0), 50.8 (235.0), 54.1 (999.0).

Stem C.—ACCTRAN: 2.7 (348.0), 3.3 (300.0), 5.4 (88.0), 7 .5 (388.4), 12.0 (999.0), 13.1 (77.0), 22.3 (2.0), 26.8 (77.0), 27.2 (999.0), 34.4 (71.0), 35.D (46.0), 50.9 (47.0). DELTRAN: 2.6 (330.0), 3.2 (56.0), 6.2 (111.0), 7.6 (219.4), 16.4 (832.0), 18.1 (214.0), 23.1 (999.0), 27.1 (950.0), 34.2 (231.0), 35.G (13.0).

Stem D.—ACCTRAN: 5.3 (20.0), 7.2 (498.1), 17.1 (857.0), 18.3 (583.0), 35.A (105.0), 47.1 (999.0). DELTRAN: 5.3 (108.0), 7.3 (566.7), 18.3 (619.0), 26.8 (77.0), 27.2 (49.0), 50.9 (47.0).

Stem E.—ACCTRAN: 2.6 (18.0), 3.4 (199.0), 9.3 (285.0), 13.0 (77.0), 18.4 (166.0), 19.4 (285.0), 22.1 (41.0), 41.A (30.0), 51.1 (125.0), 53.1 (999.0), 54.1 (999.0). DELTRAN: 3.4 (443.0), 18.4 (166.0), 19.4 (666.0), 22.1 (43.0), 53.1 (999.0).

Stem F.—ACCTRAN: 6.3 (138.0), 40.2 (999.0), 43.1 (999.0), 46.0 (999.0), 47.0 (999.0). DELTRAN: 6.3 (138.0), 7.2 (100.5), 17.1 (857.0), 34.4 (340.0), 35.A (138.0), 40.2 (999.0), 43.1 (999.0).

Stem G.—ACCTRAN: 2.8 (231.0), 6.4 (240.0), 40.1 (333.0), 48.2 (999.0). DELTRAN: 2.8 (249.0), .3.3 (244.0), 6.4 (240.0), 13.1 (77.0), 22.3 (2.0), 40.1 (333.0), 48.2 (999.0).

Stem H.—ACCTRAN: 9.0 (500.0), 10.0 (999.0), 11.0 (999.0), 17.2 (999.0), 18.4 (749.0), 20.2 (999.0), 24.1 (999.0), 29.2 (999.0), 32.1 (999.0), 33.1 (250.0), 41.7 (257.0), 51.1 (125.0.) DELTRAN: 16.4 (832.0), 17.2 (999.0), 18.4 (999.0), 20.2 (999.0), 23.1 (999.0), 24.1 (999.0), 33.1 (250.0), 41.7 (272.0).

Stem I.—ACCTRAN: 6.0 (111.0), 21.1 (999.0), 33.2 (749.0), 46.0 (999.0), 50.4 (91.0). DELTRAN: 5.7 (712.0), 7.9 (502.7), 21.1 (999.0), 22.7 (71.0), 46.0 (999.0), 49.5 (111.0), 54.0 (999.0).