Phylogeny and biogeography of a large radiation of Andean lizards (Iguania, *Stenocercus*)

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With 61 species occurring mostly in the Andes and adjacent lowland areas, *Stenocercus* lizards represent one of the most widespread and well-represented Andean vertebrate groups. Phylogenetic relationships among species of *Stenocercus* are inferred using different datasets based on mitochondrial DNA sequence data of 35 species and morphological data of 59 species. Among morphological data, polymorphic and meristic/morphometric characters are coded under the frequency parsimony and gap-weighting methods, respectively, and the accuracy of these methods is tested. When both types of characters are included, the resulting tree topology is more similar to the topologies obtained from analyses of DNA sequence data than those topologies obtained after exclusion of one or both types of characters. The phylogenetic hypotheses inferred including 59 species of *Stenocercus* (dataset 1) and excluding those species for which DNA data were not available (dataset 2) are generally congruent with each other, as well as with previously published hypotheses. The most parsimonious tree obtained from analysis of dataset 2 is used in a dispersal-vicariance analysis to infer ancestral areas and major biogeographical events. Species of *Stenocercus* are divided into two major clades. Clade A has diversified mostly in the central Andes, with a few species in the northern Andes and one species in the southern Andes. Clade B is more widespread, with species in the northern, central, and southern Andes, as well as in the Atlantic lowlands and Amazon basin. The most recent common ancestor of *Stenocercus* is inferred to have occurred in the eastern cordillera of the central Andes. Given morphological similarity and altitudinal distribution of some species nested in a northern-Andes clade, as well as the relatively recent uplift of this Andean region, it is possible that species in this clade have diverged as recently as the mid-Pliocene.

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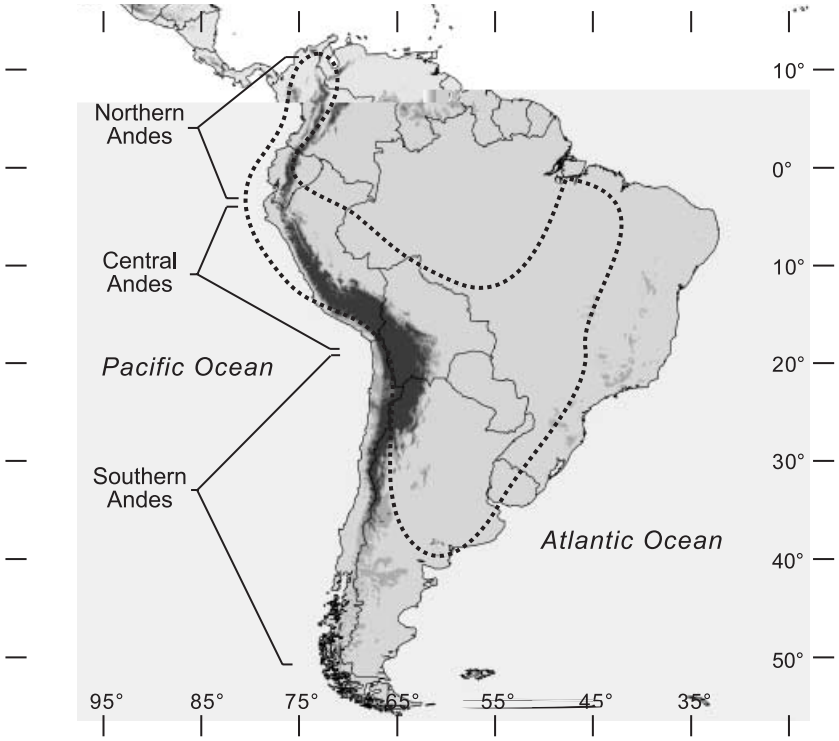
The Andes form a nearly continuous 8000-km-long mountain belt that extends along the western border of South America. Organisms inhabiting this exceptionally long mountain chain have attracted the attention of many biologists interested in explaining their evolution and distributions (e.g., Vuilleumier 1969; Duellman 1979; Remsen 1984; Hillis 1985; Vuilleumier & Monasterio 1986; Patton & Smith 1992; Bates & Zink 1994; Lynch & Duellman 1997; Patterson *et al*. 1998; Chesser 2000, 2004; Ezcurra 2002; Doan 2003; Graham *et al*. 2004; Sánchez-Baracaldo 2004). However, only a few biogeographical studies with a phylogenetic approach have been performed for speciose and widespread taxa. The iguanian lizard genus *Stenocercus* is one of the most widespread and well-represented vertebrate groups of the Andes. It includes 61 species, most of which occur at elevations between 0 and 4000 m in the Andes and adjacent lowland areas from northern Venezuela and Colombia to central Argentina, with only six species restricted to lowland areas away from the Andes (Fig. 1) — *S. azureus* (Uruguay and southern Brazil), *S. sinesaccus* (western-central Brazil), *S. tricristatus* (eastern-central Brazil), *S. dumerilii* (northern Amazonian Brazil), and the recently described *S. quinarius* (Cerrado, Brazil) and *S. squarrosus* (Caatinga and Cerrado, Brazil). This diversity and geographical range make *Stenocercus* lizards suitable organisms to study evolution and biogeography in the Andes.

More than three decades ago, Fritts (1974) published the first systematic study to include a phylogenetic analysis of species of *Stenocercus* including 19 species and 29 morphological characters. The resulting hypothesis indicated that *Stenocercus* was composed of three major clades. One clade included species from central Peru and Ecuador; the second major clade contained species with similar distribution to the



previous clade except that it also included species on the western slopes of the Andes in central and northern Peru; the third clade included species from the Amazonian slopes of Peru and Bolivia (Fritts 1974). Etheridge & de Queiroz (1988) proposed that *Stenocercus*, *Ophryoessoides* and *Proctotretus* form a monophyletic group, the *Stenocercus* Group, which they identified as the sister taxon of the *Tropidurus* Group. This sister taxon relationship has been recovered repeatedly in subsequent studies (e.g., Frost & Etheridge 1989; Frost 1992; Frost *et al*. 2001; Schulte *et al*. 2003). However, Etheridge & de Queiroz (1988) recognised that monophyly of the *Stenocercus* Group was supported only by the presence of a 'long' dentary bone. Furthermore, they mentioned that *Stenocercus* is likely paraphyletic because they found no single character or combination of characters to diagnose this genus relative to *Ophryoessoides* and *Proctotretus*. Frost & Etheridge (1989) found the *Stenocercus* Group to be weakly corroborated by secondary enlargement of the angular and extensive hemipenial sheath musculature. Their analysis inferred the monophyly of *Stenocercus* + *Tropidurus* Groups, which they named Tropidurinae. In a phylogenetic analysis of the *Tropidurus* Group, Frost (1992) proposed recognising the *Tropidurus* and *Stenocercus* Groups as the tribes Tropidurini and Stenocercini, respectively. Additionally, Frost (1992) synonymised *Ophryoessoides* and *Proctotretus* with *Stenocercus* based on morphological evidence suggesting that *Ophryoessoides* and *Proctotretus* are derived from *Stenocercus*.

More recently, in a phylogenetic analysis including 32 species of *Stenocercus* and 1641 bp of mitochondrial DNA, Torres-Carvajal *et al*. (2006) found strong statistical support for (i) monophyly of *Stenocercus* sensu Frost (1992), (ii) sister-taxon relationship between *Stenocercus* and the *Tropidurus* Group, (iii) non-monophyly of '*Ophryoessoides*' sensu Fritts (1974), and (iv) a basal split dividing species of *Stenocercus* into two major clades. Here, phylogenetic analyses of species of *Stenocercus* sensu Frost (1992) are performed using a larger dataset containing DNA sequence data of three species not included in Torres-Carvajal *et al*. (2006), as well as morphological data from all species except *S. quinarius* and *S. squarrosus*, which were described while this paper was in review (Nogueira & Rodrigues 2006). Step matrices are built to analyse polymorphic and meristic/morphometric characters using frequency parsimony and gap-weighting methods, respectively. The accuracy of these two methods is assessed with a congruence measurement. Finally, one of the resulting phylogenetic hypotheses is used in the inference of biogeographical events and ancestral areas.

Materials and methods

Taxon and character sampling

This study includes 59 species of *Stenocercus* and two outgroup taxa. Morphological data of *Microlophus occipitalis* and molecular data of *M. atacamensis* were combined into a single outgroup taxon in combined analyses; *Plica plica* was used as a second

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outgroup. Data on external morphology of all species was obtained upon examination of 2001 fluid-preserved specimens (listed in Torres-Carvajal 2005a) and from the literature (Cadle 1991, 1998, 2001; Avila-Pires 1995; Torres *et al.* 2000; Torres-Carvajal 2000, 2005b,c,d; Torres-Carvajal *et al.* 2005). Osteological data was obtained from 94 specimens representing 46 species of *Stenocercus* (Appendix 1). The morphological data matrix includes 90 discrete, 15 polymorphic (i.e., intraspecifically variable qualitative characters), 11 meristic and 6 morphometric characters (Appendix 2).

Torres-Carvajal *et al.* (2006) sampled a 1786-bp-long continuous fragment of mitochondrial DNA that extends from the protein-coding gene *ND1* (subunit one of NADH dehydrogenase) through the genes encoding *tRNA*$^{\text{Ile}}$, *tRNA*$^{\text{Gln}}$, *tRNA*$^{\text{Met}}$, *ND2* (subunit two of NADH dehydrogenase), *tRNA*$^{\text{Trp}}$, *tRNA*$^{\text{Ala}}$, *tRNA*$^{\text{Asn}}$, the origin of light-strand replication, *tRNA*$^{\text{Cys}}$, *tRNA*$^{\text{Tyr}}$, to the protein-coding gene *COI* (subunit I of cytochrome c oxidase). Following the same laboratory and alignment protocols (Torres-Carvajal *et al.* 2006), this fragment was sequenced for three additional species — *S. angulifer*, *S. chrysopygus* and *S. marmoratus* (GenBank accession numbers EF565141-EF565143). Thus, the molecular data matrix used in this study contains 35 species of *Stenocercus* and the outgroups.

Coding of intraspecifically variable morphological characters

To code intraspecific variation in qualitative morphological characters I used the MANOB method of frequency parsimony (Swofford & Berlocher 1987) with step matrices (Wiens 1995). In the MANOB method the optimality criterion corresponds to tree length in a Manhattan metric, under the constraint that only observed character state frequency arrays may be assigned to hypothetical ancestors (Swofford & Berlocher 1987). Although this frequency parsimony method was originally proposed for coding gene frequency data (Swofford & Berlocher 1987), it also applies to polymorphic morphological characters (Wiens 1995, 2000). In this method each taxon is assigned a unique character state in the data matrix. For a given character, the cost of transition between states is calculated and specified in a step matrix based on the Manhattan distances between the trait frequencies of each pair of species for that character (Swofford & Berlocher 1987; Wiens 1995). The Manhattan distance D between two taxa A and B is calculated with the formula

$$D(A,B) = \frac{1}{2}\sum_{j=1}^{N}\left| x_{Aj} - x_{Bj} \right|$$

where N is the total number of character states, and xA, xB are the frequencies of a given character state (j) in taxa A and B, respectively. Step matrices were built by (i) using the observed character state frequencies to create a FREQPARS file, and (ii) importing this FREQPARS file into PAUP*, which automatically calculates the step matrices. FREQPARS files and step matrices are available from the author upon request. Frequency parsimony was used to code all polymorphic characters except for presence/absence of pterygoid teeth (character 8) because sample size of osteological specimens was very small ($N = 2$) for most species. Since intraspecific variation in the presence or absence of pterygoid teeth in *Stenocercus* has been reported (Cadle 1991), character 8 was still treated as polymorphic and coded with the 'any instance' method (Campbell & Frost 1993). In addition, the 'modal' method was used to code the number of canthals (character 32) because the interspecific and intraspecific variation of this character is very small. The only possible states for this character are 'one' or 'two' canthals, and in most species two canthals were observed in all examined species.

Continuous characters were coded following Thiele's (1993) gap-weighting method using step matrices as proposed by Wiens (2001), with slight modifications as described below. Thiele (1993) proposed to account for differences in continuous trait values across species by giving small weights to small differences in trait means between taxa and large weights to large differences. For a given continuous character, this method involves (i) finding the mean value of the trait for each taxon included in the analysis, as well as the range of mean trait values across taxa, and (ii) dividing this range into smaller ranges equal to the maximum number of character states allowed by the phylogenetic software program (Thiele 1993). Because this method is limited by the maximum number of character states allowed in phylogenetic computer programs, Wiens (2001) proposed to weight the differences between mean taxa values with step matrices. For a given character, a unique character state is assigned to each taxon with a unique mean trait value. Changing from one state to another has a cost that is specified in a step matrix based on the difference in mean trait values between each pair of taxa (Wiens 2001). Given that the maximum cost between states in a step matrix is 1000 in PAUP*, Wiens (2001) proposed to convert the mean trait value (x) of each taxon to a score (X_s) between 0 and 1000 by modifying Thiele's (1993) formula as follows:

$$X_s = \frac{x - \min}{\max - \min} \times 1000$$

where 'min' and 'max' are the minimum and maximum mean taxa values of the trait across all taxa, respectively. The difference between these scores determines the costs of character state transformations in the step matrix. The above formula implies that if fixed characters also are included in the dataset, they need to be weighted by 1000. Here I modify the above formula by not multiplying the right term by 1000. Instead, the step matrices used in this study contain scores between 0 and 1, which does not require re-weighting fixed characters because the default weight in PAUP* is 1. These step matrices

were built by (i) using the calculated scores to create a FREQPARS file, and (ii) importing this FREQPARS file into PAUP*, which automatically calculates the step matrices. The FREQPARS file was constructed by creating 'dummy' alternative states (Y) for each score (i.e., X_s with no multiplier) as follows:

$$Y = 1 - X_s$$

The Manhattan distances calculated with these values (i.e., scores and corresponding 'dummy' alternative states) are equivalent to the differences between scores because there are never more than two states, and the second (Y) is always redundant with the first. All raw measurements were standardised with the transformation $\ln(x + 1)$ before computation of scores.

Accuracy of frequency parsimony and gap-weighting methods

Accuracy is the ability of a method to estimate the 'true' phylogeny. Given that the 'true' phylogeny is usually never available, accuracy can be better defined as the ability of a method to estimate what we think is *the best* phylogeny. For the purposes of this study, accuracy of the frequency parsimony and gap-weighting methods was evaluated by comparing the tree topologies resulting from analyses of several morphological datasets under these methods with *the best* tree topology based on analyses of non-morphological (i.e., molecular) data. The measurement of tree similarity used in each case was the consensus fork index (Colless 1980, 1981), which quantifies the amount of resolution of a consensus tree by calculating the proportion of nodes in common between the trees being compared.

Morphological datasets. Four morphological datasets were analysed in PAUP* 4.0b10 (Swofford 2003) under the parsimony criterion — (i) fixed characters only, (ii) fixed and polymorphic, (iii) fixed, meristic and morphometric, and (iv) all characters combined. Because these analyses were used to test the accuracy of frequency parsimony and gap-weighting methods, only those species of *Stenocercus* with available DNA sequence data were included. For each dataset, a heuristic search with 1000 random addition sequence replicates and tree bisection and reconnection (TBR) branch swapping was performed. The complete morphological data matrix (i.e., all characters included) is available in TREEBASE (Study S1783; Matrix M3257).

Molecular dataset. The molecular dataset used in the accuracy tests was analysed under parsimony, maximum likelihood and Bayesian approaches, and is available in TREEBASE (Study S1783; Matrix M3256). Of the 1786 bp sequenced, 145 bp were excluded from each analysis due to ambiguity of inferred homology among aligned DNA sequence sites. The parsimony analysis was performed in PAUP* 4.0b10 using a heuristic search with 100 000 random addition sequence replicates and TBR branch swapping. Models of evolution for the likelihood and Bayesian analyses were selected under the Akaike information criterion in MODELTEST 3.06 (Posada & Crandall 1998). The maximum likelihood tree was obtained by selecting the best tree from 10 runs performed in GARLI 0.95 (Zwickl 2006) using default settings. These runs resulted in similar trees with similar log-likelihood scores indicating that additional runs were not necessary.

Bayesian inference was used to estimate posterior probabilities of bipartitions. Data were divided into four partitions — (i) first, (ii) second, (iii) third codon positions for the protein coding genes *ND1*, *ND2* and *COI*, and (iv) *tRNA* genes. Four independent analyses were performed in MRBAYES 3.1.2 (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003), each consisting of 5×10^6 generations and four Markov-chains with default heating values. Parameter values were estimated from the data and initiated with flat priors except for branch lengths, for which an exponential prior was used. Trees were sampled every 100 generations resulting in 50 000 trees saved per run, of which 5000 were discarded as 'burn-in'. Remaining trees were used to calculate posterior probabilities of bipartitions by constructing a 50% majority-rule consensus tree. Stationarity was assessed by plotting the log-likelihood scores per generation in TRACER 1.2 (Rambaut & Drummond 2003). Additionally, the standard deviation of the partition frequencies and the potential scale reduction factor (Gelman & Rubin 1992) were used as convergence diagnostics for the posterior probabilities of bipartitions and branch lengths, respectively. These diagnostics were obtained by summarising all runs (Table 1).

Phylogenetic analyses of combined datasets

Two combined datasets were analysed, one containing all 59 species of *Stenocercus* (dataset 1) and another one excluding

Table 1 Bayesian convergence diagnostics for posterior probabilities of bipartitions and branch lengths in four datasets. Ranges of standard deviation of the partition frequencies (SD) and potential scale reduction factor values (PSRF) are given for each dataset. SD is expected to approach 0 and PSRF is expected to approach 1 as runs converge onto the posterior probability distribution. Bipartitions were sampled by all runs in each case.

Dataset	Model	SD	PSRF
Molecular	GTR + *I* + Γ	0.000–0.019	1.000–1.003
Morphological (Dataset 2)	Mkv	0.000–0.017	1.000–1.004
Morphological (Dataset 2)	Mkv + Γ	0.000–0.019	1.000–1.003
Combined	GTR + *I* + Γ (molecular) Mkv + Γ (morphological)	0.000–0.012	1.000–1.005

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those species for which DNA sequence data were not available (dataset 2). Polymorphic, meristic and morphometric characters were recoded for each dataset using the methods described above for intraspecifically variable morphological characters. Character state data and aligned DNA sequences are available in TreeBASE (Study S1783; Matrices M3259 and M3258, respectively). Dataset 1 contained 61 taxa (59 species of *Stenocercus*, two outgroups) and 1763 characters; for those species with no DNA sequence data, molecular characters were coded as missing data. Dataset 2 included 35 species of *Stenocercus*, one outgroup, and the same number of characters as dataset 1. These datasets were each analysed in PAUP* under parsimony using a heuristic search with 1000 random addition replicates and TBR branch swapping. Support for individual nodes was assessed with non-parametric bootstrap resampling using 1000 bootstrap replicates with five random addition sequence replicates each.

Additionally, combined dataset 2 was analysed in a Bayesian framework using the GTR + I + Γ model for molecular data and two variants of the maximum likelihood model for discrete morphological character data (Markov *kv* or Mkv; Lewis 2001) implemented in MrBayes 3.1.2. Within the morphological partition, only variable characters were allowed to be sampled. The first variant of the Markov *kv* model assumed equal rates of change among characters (Mkv), whereas the second variant incorporated unequal rates among characters using the gamma distribution (Mkv + Γ). Because MrBayes does not allow for use of step matrices, polymorphic and continuous data could not be coded using the methods described above. Instead, I followed Wiens *et al.* (2005) in coding polymorphic characters using the majority approach (i.e., < 50% = 0 and > 50% = 1), which is expected to produce similar results as the frequency parsimony method (Wiens 1995, 1999). There were no species with trait frequencies of 50%. In addition, the continuous characters were ordered and recoded to have a maximum of six states, which is the maximum number of ordered states allowed in MrBayes. All three analyses (i.e., morphological dataset under Mkv and Mkv + Γ models, and combined dataset 2 with selected model for morphological partition) consisted of four runs of 5×10^6 generations and four Markov chains each, with default heating values and priors. Trees were sampled every 100 generations resulting in 50 000 saved trees per run, of which 5000 were discarded as 'burn-in'. Stationarity was confirmed as described above (Table 1). In each analysis, the resultant 180 000 trees were used to calculate posterior probabilities for each branch in a 50% majority-rule consensus tree. Using harmonic means to estimate the marginal likelihood of each model, the Mkv + Γ was selected over the Mkv model with an estimated Bayes factor value of 300. Molecular data were partitioned and assigned a model as described for the molecular dataset above.

Biogeographic analysis

Locality data were obtained from the literature (Fritts 1972, 1974; Castro & Ayala 1982; Corredor 1983; Cei 1986, 1993; Cadle 1991, 1998, 2001; Castro & Granados 1993; Avila-Pires 1995; Cardinale & Vignolo 1996; Cruz *et al.* 1996; Avila 1999; Torres *et al.* 2000; Torres-Carvajal 2000, 2005b,c,d; Andrade *et al.* 2003; Harvey *et al.* 2004) and from museum collections after confirmation of species identification. A total of 582 localities were geo-referenced mostly using Global Gazetteer Version 2.1 (Falling Rain Genomics, Inc.).

Andean regions. The Andes are composed of three main segments of distinct orientation separated by two major bends (Jaillard *et al.* 2000); each segment can be divided into subregions as follows (Fig. 1):

1 The northern Andes (12°N–5°S) are 2000 km long, have a NNE–SSW orientation, and extend from easternmost Venezuela to northernmost Peru. Here, I recognise the following subregions proposed by previous authors (Duellman 1979, 1999; Jaillard *et al.* 2000): eastern, central and western cordilleras in Colombia; Nudo de Pasto (*c.* 100 000 km^2 of highlands in southern Colombia and northern Ecuador); inter-Andean basins and eastern and western cordilleras in Ecuador.

2 The central Andes (5°S–18°S) also are about 2000 km long, have a NW–SE orientation, and extend from northern Peru to Bolivia and northern Chile; they are separated from the northern Andes by the Huancabamba Depression (Mégard 1987; Aleman & Ramos 2000; Jaillard *et al.* 2000). Eastern and western cordilleras are recognised herein as major subregions within the central Andes (Jaillard *et al.* 2000).

3 The southern Andes (18°S–56°S) are 4000 km long and have a N–S orientation. They are separated from the central Andes by the Arica bend (Jaillard *et al.* 2000). Species of *Stenocercus* occur only on the north-eastern slopes of the southern Andes. This portion of the Andes was formed much earlier than the central and northern Andes, possibly prior to the Tertiary (Simpson 1979). The central Andes were next, followed by the northern Andes, which did not reach their current high elevations before the mid-Pliocene (Simpson 1979; Aleman & Ramos 2000).

Ancestral areas. To infer ancestral distributions of *Stenocercus*, I used dispersal-vicariance (DIVA) 1.1 (Ronquist 1996) to perform a dispersal-vicariance analysis as proposed by Ronquist (1996, 1997). This is a character optimisation method that allows reconstruction of ancestral distributions by maximising vicariance events and minimising dispersal and extinction events. The analysis is based on a three-dimensional cost matrix derived from a simple biogeographical model in which vicariance events have a cost of zero and dispersal or extinction events have a cost of one. I used the

most parsimonious tree obtained from the analysis of combined dataset 2 to optimise the known distributions of species of *Stenocercus*. Each species was coded as absent or present in 11 geographical subregions within the Andes and adjacent lowland areas — (i) western; and (ii) eastern cordilleras in the northern Andes; (iii) inter-Andean basins in the northern Andes; (iv) Nudo de Pasto; (v) Huancabamba Depression; (vi) western; and (vii) eastern cordilleras in the central Andes; (viii) eastern cordillera in the southern Andes; (ix) Pacific coast lowlands; (x) Atlantic coast lowlands; and (xi) Amazon Basin. An exact search was performed in DIVA 1.1 with a maximum of 2 unit areas for ancestral distributions (MAXAREAS = 2) and the maximum upper bound to tree length of the optimal reconstruction allowed by the program (BOUND = 250).

Results

Accuracy of frequency parsimony and gap-weighting methods

The proportion of nodes in common between molecular and morphological phylogenetic trees ranged between 0.059 and 0.265. Overall, the molecular tree obtained under parsimony is more similar to the morphological trees than the molecular trees supported by maximum likelihood or Bayesian approaches (Fig. 2). Regardless of the method used to analyse molecular characters, however, the phylogenetic tree obtained from analysis of fixed morphological characters is less similar to the molecular trees than those phylogenetic trees obtained after adding polymorphic or meristic/morphometric characters. Moreover, the largest proportion of nodes in common between molecular and morphological trees results when polymorphic, meristic and morphometric characters are included (Fig. 2). For this reason, fixed, polymorphic, meristic, and morphometric characters were included in the combined datasets (i.e., morphological and molecular data), where polymorphic and meristic/morphometric morphological characters were analysed under frequency parsimony and gap-weighting methods, respectively.

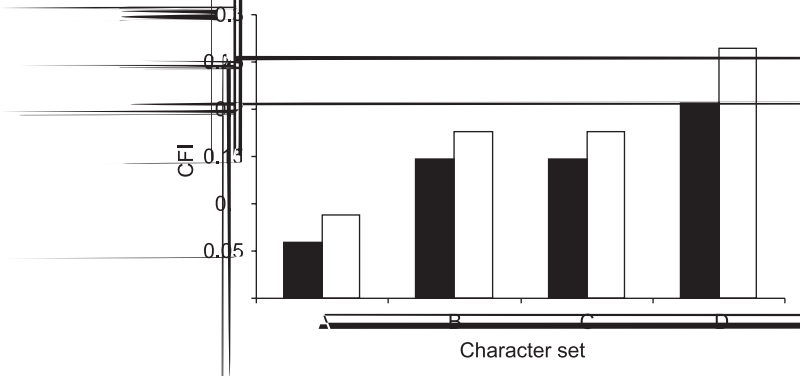

Fig. 2 Accuracy of methods for coding intraspecifically variable characters as measured by the consistency fork index (CFI). Parsimony trees obtained from four different morphological datasets are compared with molecular trees. Black bars correspond to comparisons with molecular trees obtained under maximum likelihood and Bayesian approaches, whereas white bars correspond to comparisons with the most parsimonious molecular tree. A, fixed characters only; B, fixed, meristic and morphometric; C, fixed and polymorphic; D, fixed, meristic, morphometric and polymorphic.

Phylogeny of Stenocercus

The maximum parsimony analysis of the combined dataset including 59 species of *Stenocercus* (dataset 1) yielded a single most parsimonious tree of 5619.892 steps, with consistency index 0.299 and retention index 0.443 (Fig. 3). Of the 1763 characters included in this analysis, 1067 are variable and 876 are parsimony informative. Even though most branches have low bootstrap support values, the resulting tree follows the same general topology as the phylogenetic trees supported by maximum likelihood and Bayesian analyses of molecular data (Torres-Carvajal *et al*. 2006). Low bootstrap support values are not surprising given the large amount of missing DNA data. Species of *Stenocercus* are split between two major clades congruent with the two major clades obtained from analyses of molecular data. These clades contain 27 and 32 species and for purposes of this study I will refer to them as clades A and B, respectively (Fig. 3). Following the classification proposed by Torres-Carvajal *et al*. (2006), clade A corresponds to clade *Scelotrema*. Within this clade, *S. chrysopygus*, *S. modestus* and *S. ivitus* are contained in subclade *Saccodeira*, and *S. praeornatus* is part of clade *Microphractoides*, which is nested within clade *Microphractus*. Within clade B, *S. fimbriatus* and *S. nigromaculatus* are contained in clade *Anatomegalepis*, and *S. limitaris*, *S. ornatus*, *S. percultus*, *S. lache*, *S. trachycephalus*, *S. santander*, *S. erythrogaster*, *S. huancabambae*, *S. aculeatus* and *S. angulifer* are nested within clade *Boreomegalepis*.

The maximum parsimony analysis of the combined dataset including only species of *Stenocercus* for which both morphological and DNA sequence data were available (dataset 2) yielded a single most parsimonious tree of 5252.378 steps, with consistency index 0.310 and retention index 0.412 (Fig. 4). Of the 1763 characters included in this analysis, 1040 are variable and 825 are parsimony informative. As in tree topologies discussed above, this tree supports a basal split in the phylogeny of *Stenocercus* with no species switching between the two major clades. Moreover, all branches with likelihood bootstrap support values above 90 and Bayesian posterior probabilities of 1.00 (Torres-Carvajal *et al*. 2006) are inferred in the parsimony analysis of dataset 2.

Bayesian analysis of combined dataset 2 supported a tree topology similar to the one obtained under parsimony. If we compare those bipartitions with posterior probabilities of 0.95 or higher, the main differences are that (i) *S. crassicaudatus* and *S. torquatus* form a clade sister to *S. humeralis*, and (ii)

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Table 2 Distribution and endemism of *Stenocercus* in South America. Number of species and percentage of endemics (in parentheses) by Andean region and country are given. Andean regions are defined in text.

Distribution	Clade A	Clade B	Total
Andean regions			
Northern Andes	6 (100%)	14 (93%)	20 (95%)
Western cordillera and/or Adjacent Pacific lowlands	4 (75%)	9 (11%)	13 (31%)
Central cordillera	1 (100%)	0	1 (100%)
Eastern cordillera	0	5 (80%)	5 (80%)
Inter-Andean basins	2 (50%)	5 (0%)	7 (14%)
Nudo de Pasto	0	1 (100%)	1 (100%)
Caribbean lowlands	0	1 (0%)	1 (0%)
Central Andes	21 (95%)	13 (54%)	34 (79%)
Western cordillera and/or Adjacent Pacific lowlands	12 (92%)	3 (33%)	15 (80%)
Eastern cordillera	10 (80%)	9 (67%)	19 (74%)
Southern Andes	1 (0%)	3 (0%)	4 (0%)
Other regions			
Atlantic lowlands	0	5 (60%)	6 (67%)
Amazon basin	0	3 (33%)	3 (33%)
Cerrado/Caatinga	0	3 (100%)	3 (100%)
Countries			
Argentina	1 (0%)	5 (40%)	6 (33%)
Bolivia	1 (0%)	3 (0%)	4 (0%)
Brazil	0	9 (56%)	9 (56%)
Colombia	1 (100%)	6 (67%)	7 (71%)
Ecuador	5 (100%)	10 (60%)	15 (73%)
Paraguay	0	1 (0%)	1 (0%)
Peru	20 (100%)	13 (62%)	33 (85%)
Uruguay	0	1 (0%)	1 (0%)

S. iridescens, *S. pectinatus*) and nearly 4000 m (*S. guentheri*, *S. lache*, *S. trachycephalus*). Unlike species in clade A, only 35% and 17% of the species in clade B are restricted to areas above 1500 and 2000 m, respectively.

Origin and radiation of Stenocercus

DIVA analysis was performed on the most parsimonious tree resulting from analysis of dataset 2, which is the most complete dataset available. The DIVA analysis resulted in a single optimal reconstruction of ancestral distributions requiring 28 dispersal events. According to this analysis, the most recent common ancestor of *Stenocercus* occurred in the eastern cordillera of the central Andes (Fig. 4). This area is still occupied by species belonging to both major clades (A and B) within *Stenocercus* (Figs 3 and 4). However, there are major differences in the geographical areas that have been occupied by each clade.

Clade A includes ancestral lineages that have dispersed and subsequently diversified mostly into the western cordilleras of the central and northern Andes, as well as inter-Andean basins in the northern Andes (Figs 3 and 4). This clade is composed of two main subclades with different biogeographical histories. The subclade containing *S. latebrosus* and *S. stigmosus* (i.e., clade *Saccodeira*) is unique in that it has diversified almost exclusively along the western cordillera of the central Andes in Peru. Two other species of *Stenocercus* (*S. ivitus*, *S. modestus*), not included in the DIVA analysis but also restricted to the western side of the central Andes, are contained in clade *Saccodeira* when dataset 1 is analysed (Fig. 3). In contrast, the second main subclade within Clade A includes lineages that have diversified on a larger geographical area including the eastern and western (northern part) cordilleras in the central Andes, and western cordillera and inter-Andean basins in the northern Andes. Furthermore, one species (*S. marmoratus*) extends its distribution into the eastern cordillera of the southern Andes in Argentina.

Clade B includes two sets of lineages that have dispersed and diversified in different directions. About one half of species in Clade B have resulted from one set of ancestral lineages that have spread and speciated along the northern Andes and adjacent Pacific lowland areas (and Caribbean coast if we include *S. erythrogaster* in this clade; Fig. 3). The second group of lineages within Clade B has dispersed and diversified along the eastern slopes of the central Andes, north-eastern slopes of the southern Andes, and Brazilian Cerrado, as well as Atlantic lowlands of northern Argentina, Uruguay, and Brazil.

Discussion

Stenocercus *phylogeny*

This is the first attempt to infer phylogenetic relationships among all recognised species of *Stenocercus* except for two recently described species from Brazil (Nogueira & Rodrigues 2006). Most previous molecular phylogenies include no more than four species of *Stenocercus* (e.g., Frost 1992; Schulte *et al.* 1998, 2003; Harvey & Gutberlet 2000; Frost *et al.* 2001), and the only other analysis based on morphological data included 19 out of 29 species known at that time (Fritts 1974). Torres-Carvajal *et al.* (2006) presented a robust hypothesis of phylogenetic relationships among 32 species of *Stenocercus* based on analyses of mitochondrial DNA data. This hypothesis indicated a basal split in the phylogeny of *Stenocercus*, which is supported by all analyses presented in this study. Other similarities between these two studies are that (i) former genera *Ophryoessoides* and *Proctotretus* are included within *Stenocercus* (Clade B) as suggested by Frost (1992), and (ii) monophyly of *Ophryoessoides* as defined by Fritts (1974) is not supported. These similarities are very important since it has been demonstrated with simulations that agreement among phylogenies estimated using different methods can be an index of the reliability of the resultant phylogenies (Kim 1993).

Biogeography

Phylogenetic studies of Andean taxa have allowed formulation of hypotheses to explain evolutionary patterns and processes

for Andean organisms (e.g., Lynch 1986; Patton & Smith 1992; Bates & Zink 1994; Lynch & Duellman 1997; Chesser 2000, 2004; Ezcurra 2002; Graham *et al*. 2004). In this study, I have used DIVA analysis to infer the distribution of ancestral lineages within *Stenocercus* and hypothesize how this group of lizards has diversified along the Andes and adjacent lowland areas. The results presented here suggest that *Stenocercus* originated in the eastern cordillera of the central Andes and not in the southern Andes as proposed by Duellman (1979). This ancestor diverged into one lineage that diversified primarily within the central Andes (Clade A), and another more widespread lineage that diversified along the northern, central and southern Andes, as well as Atlantic and Pacific lowlands, Amazon Basin and Cerrado (Clade B). Currently, species in Clade A are basically absent from the southern Andes and have highly restricted distribution ranges, which are reflected in the high levels of endemism by country or Andean region (Fig. 3, Table 2). Furthermore, no species in this clade occurs both in the northern and central Andes; rather, most species (74%) in Clade A are endemic to the central Andes in Peru. In contrast, Clade B appears to have been more 'successful' in expanding its range, and presently includes species in all three main Andean regions (Fig. 3, Table 2) — northern (44%), central (41%) and southern (9%), as well as the Atlantic lowlands (16%) of south-eastern South America, Amazon Basin (9%) and Cerrado (3%). Moreover, two species probably related to *S. dumerilli* and *S. tricristatus* (Clade B) were recently described from the Cerrado and Caatinga biomes in Brazil (Nogueira & Rodrigues 2006). Major differences in distribution patterns between Clades A and B are: (i) the western cordillera south of 7°S in Peru (central Andes) appears to have been colonised only by species in Clade A; (ii) unlike Clade A, Clade B includes some species with large latitudinal ranges, such as *S. caducus*, *S. guentheri*, *S. iridescens* and *S. roseiventris*; (iii) Clade A includes more species occurring at high elevations (67% > 1500 m, 52% > 2000 m) than clade B (35% > 1500 m, 17% > 2000 m).

A south-to-north speciation hypothesis (SNSH) congruent with the south-to-north uplift of the Andes (Simpson 1979; Aleman & Ramos 2000) has been proposed for Andean lizards '*Proctoporus*' (Doan 2003), with basal species occurring in Bolivia and southern Peru and more derived species in Venezuela. However, a fine-scale evaluation of the SNSH in '*Proctoporus*' was not possible because of poor resolution of the phylogenetic tree (Doan 2003). Furthermore, Castoe *et al*. (2004) demonstrated that '*Proctoporus*' as conceived by Doan (2003) was not monophyletic, and the name *Proctoporus* was suggested for a clade restricted to the Andes of central and southern Peru and Bolivia (Doan & Castoe 2003, 2005; Doan *et al*. 2005). In *Stenocercus*, a south-to-north speciation pattern cannot be explained with the phylogenetic hypotheses inferred in this study. Only the clade stemming from the most recent common ancestor of *S. rhodomelas* and *S. guentheri* in the parsimony tree used in the DIVA analysis suggests a perfect south-to-north speciation sequence except for the position of *S. chota* (northern Ecuador) as basal to *S. festae* (southern Ecuador); however, this exception does not contradict the SNSH. A fine-scale south-to-north speciation sequence is not a prediction of the SNSH, and such a sequence is not necessarily expected because of (i) the complexity of Andean orogeny, and (ii) the possible repeated events of expansion and compression of species distributions caused by Pleistocene glaciations. Regardless of a geographical speciation sequence, it is likely that species of *Stenocercus* inhabiting the northern Andes have diverged recently because of the relatively recent geological uplift of this part of the Andes (i.e., mid-Pliocene; Simpson 1979; Aleman & Ramos 2000) to elevations at which these species live, and because of morphological similarity among some of these species.

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Appendix 1

Specimens examined for osteological characters. Museum abbreviations follow Frost (2006).

Microlophus occipitalis: KU 142714, 142721. *Stenocercus angel*: QCAZ 1354 (paratype). *S. angulifer*: KU 121093, MCZ 8061. *S. apurimacus*: KU 134278, 134284 (paratypes). *S. azureus*: MCZ 17640. *S. boettgeri*: MCZ 45843, KU 134014. *S. bolivarensis*: ICN 4206 (paratype). *S. caducus*: AMNH 37907, 143053, MCZ 24883, 29022. *S. carrioni*: AMNH 22157, MCZ 93589. *S. chota*: QCAZ 2654 (paratype). *S. chrysopygus*: KU 133895, 133906. *S. crassicaudatus*: KU 133959, 163602. *S. cupreus*: KU 133974, MCZ 43789. *S. doellojuradoi*: FML 503, 3521. *S. dumerilii*: MCZ 160242. *S. empetrus*: KU 134401, 134403–4, 134421. *S. erythrogaster*: ICN 9096. *S. eunetopsis*: FMNH 232539, 232555, 232589 (paratypes). *S. festae*: AMNH 23418, KU 134595, 134603. *S. fimbriatus*: AMNH 56792. *S. formosus*: KU 134110, MCZ 11295. *S. frittsi*: KU 134198, 134213 (paratypes). *S. guentheri*: KU 147319, 147326. *S. huancabambae*: AMNH 28636, MCZ 18785 (paratypes). *S. humeralis*: KU 134001, 134004. *S. imitator*: FMNH 232584–8, 232590 (paratypes). *S. iridescens*: AMNH 21993, 112989–90, KU 142695. *S. lache*: ICN 9262. *S. latebrosus*: KU 134351, 134360. *S. limitaris*: AMNH 22119 (paratype). *S. melanopygus*: KU 134058. *S. nigromaculatus*: KU 134089, 134092, MCZ 18767 (paratype). *S. ochoai*: KU 133878, 133884 (paratypes). *S. orientalis*: KU 134452, 134460 (paratypes). *S. ornatus*: KU 121128, KU 134128. *S. pectinatus*: KU 187794, 187798, MCZ 17634. *S. percultus*: FMNH 232530–33 (paratypes). *S. praeornatus*: KU 134229 (paratype). *S. puyango*: QCAZ 6720 (paratype). *S. rhodomelas*: KU 152184, 152186. *S. roseiventris*: KU 172196. *S. santander*: MCZ 36877. *S. scapularis*: AMNH 56770, 56777. *S. torquatus*: AMNH 23132. *S. trachycephalus*: AMNH 91749, 131223, 131227. *S. variabilis*: USNM 299613. *S. varius*: KU 121135, 134563, 142704.

Appendix 2

Morphological characters used in phylogenetic analyses. Range of means of meristic and morphometric characters are for all species of *Stenocercus* included in this study and the outgroups *Microlophus* and *Plica*.

Osteology

1 Nasal process of premaxilla (Frost 1992) (0) significantly narrower (i.e., < 50%) than dentigerous portion; (1) as wide as, or broader than dentigerous portion, at least ventrally. Fixed.

2 Anterolateral processes of frontal (Etheridge 1964) (0) exposed; (1) completely covered by nasals and/or prefrontals. Fixed.

3 Frontal-postorbital contact (Wiens & Reeder 1997) (0) absent; (1) present. Fixed.

4 Anterodorsal postorbital process (Torres-Carvajal 2003) (0) absent; (1) present. Fixed.

5 Posterior end of squamosal (Wiens & Reeder 1997) (0) articulates on or adjacent to dorsal crest of supratemporal process of parietal; (1) articulation more ventral (articulating with supratemporal). Fixed.

6 Squamosal shape and skull width (Frost 1992) (0) squamosal relatively straight, posterior apex of supratemporal fossa forms an acute angle; (1) squamosal bone curved around posterior end of supratemporal fossa — posterior apex of supratemporal fossa forms smooth curve. Fixed.

7 Squamosal and superior fossa of quadrate (modified from Frost 1992) (0) squamosal not penetrating fossa; (1) a process of the squamosal fitting into the fossa. Fixed.

8 Pterygoid teeth (0) absent; (1) present. Polymorphic.

9 Lingual coronoid process of dentary (Frost 1992) (0) overlapping anterior lingual process of coronoid; (1) not overlapping anterior lingual process of coronoid. Fixed.

10 Second ceratobranchials (Wiens & Reeder 1997) (0) parallel through most of their length; (1) divergent through most of their length. Fixed.

11 Posterior process of interclavicle (Frost 1992) (0) 'free' part of process short, < 25% of total length of sternum; (1) 'free' part of process long, > 25% of total length of sternum. Fixed.

12 Interclavicle median process (Etheridge 1964) (0) not extending posteriorly beyond lateral corners of sternum; (1) extending posteriorly well beyond the lateral corners of the sternum. Fixed.
13 Scapular fenestra (Lécuru 1968) (0) present; (1) absent. Fixed.
14 Sternal fontanelle (0) small, only slightly wider than the posterior process of the interclavicle; (1) large, much wider than the posterior process of the interclavicle. Fixed.
15 Postxiphisternal inscriptional ribs (Etheridge 1965; Torres-Carvajal 2004) (0) not in contact medially; (1) articulating medially. Fixed.
16 Medial centrale: (0) present; (1) absent. Fixed.
17 Number of phalanges in Finger IV (0) five; (1) four. Fixed.
18 Number of distal tarsals (0) three; (1) two. Fixed.
19 Haemal spines in adult males (0) not expanded; (1) expanded in the proximo-distal plane. Fixed.
20 Caudal fracture planes (Frost 1992) (0) present; (1) absent. Fixed.

Squamation
21 Scales on fronto-nasal, parietal, postparietal, and occipital regions (0) smooth or granular; (1) slightly keeled, wrinkled, or raised into small ridges; (2) strongly keeled. Fixed.
22 Posterior dorsal head scales (0) small, occipitals, parietals, and postparietals broken into many scales; (1) large, distinct parietals, postparietals, and occipitals. Fixed.
23 Interparietal (Frost 1992) (0) enlarged, larger than interorbital distance; (1) not enlarged, smaller than interorbital distance or absent. Fixed.
24 Interparietal cornea (0) absent; (1) present. I propose this term instead of the traditional and misleading terms parietal eye, 'third eye', or pineal organ to refer to that region of the interparietal scale that lies dorsal to the parietal eye and has been modified to form a cornea (Quay 1979). Polymorphic.
25 Temporal scales between postoculars and ear opening (0) imbricate; (1) juxtaposed or granular. Fixed.
26 Temporal scales between postoculars and ear opening (0) keeled; (1) smooth. Fixed.
27 Enlarged angulate temporal (0) absent; (1) present, not projected; (2) present, dorsally projected. Fixed.
28 Posterior supraciliary (0) not enlarged or projected; (1) enlarged, projected. Fixed.
29 Supraciliary scales (0) not or only weakly projected laterally; (1) projected laterally to form a lateral crest. Fixed.
30 Row of enlarged supraoculars (0) absent; (1) present. Fixed.
31 Maximum number of supraoculars between supraciliaries and frontals. Meristic. Range of mean species values = 3.54–8.50.
32 Number of canthals (0) one; (1) two. Fixed.
33 Subnasal-postrostral contact (Wiens & Reeder 1997) (0) absent; (1) present. Polymorphic.
34 Number of postrostrals. Meristic. Range of mean species values = 4.00–7.50.
35 Rostral-nasal contact (Wiens & Reeder 1997) (0) absent; (1) present. Polymorphic.
36 Nostril position (0) medial to canthus; (1) lateral to canthus. Fixed.
37 Nasal (0) about as broad as high; (1) elongated, about twice as broad as high. Fixed.
38 Number of internasals. Meristic. Range of mean species values = 2.11–9.00.
39 Minimum number of lorilabial scale rows (Wiens & Reeder 1997) (0) one row; (1) two rows. Fixed.
40 Maximum number of longitudinal scale rows between suboculars and supralabials (modified from Frost 1992) (0) one; (1) two. Fixed.
41 Number of supralabials. Meristic. Range of mean species values = 3.94–6.00.
42 Number of loreals. Meristic. Range of mean species values = 1.93–4.59.
43 Loreals and/or loreolabials (0) smooth; (1) keeled. Fixed.
44 Mental scale (Frost 1992) (0) reduced, not extending posteriorly well beyond level of adjacent infralabials; (1) enlarged, extending posteriorly well beyond level of adjacent infralabials. Fixed.
45 Mental-infralabials relationship (Wiens & Reeder 1997) (0) mental not indented by infralabials; (1) mental deeply indented by infralabials. Fixed.
46 Mental groove (0) absent; (1) present. Fixed.
47 Mental-sublabial contact (Wiens & Reeder 1997) (0) absent; (1) present. Fixed.
48 Third sublabial-second infralabial contact (0) absent; (1) present. Polymorphic.
49 Infralabials and sublabials (0) smooth; (1) keeled. Fixed.
50 Postmental series (Frost 1992) (0) well defined, very distinct from anterior gulars; (1) poorly defined, not distinguishable from adjacent gulars except for first pair. Fixed.
51 Postmentals (0) smooth; (1) keeled. Fixed.
52 First pair of postmentals (0) separated by gulars; (1) in contact. Polymorphic.
53 Anteriormost gulars between anterior chin shields (Wiens & Reeder 1997) (0) paired; (1) single. Polymorphic.
54 Lateral gular scales (Frost 1992) (0) imbricate laterally; (1) imbricate posteriorly. Fixed.
55 Gulars (0) cycloid, smooth, slightly imbricate; (1) rhomboidal, smooth or slightly keeled, imbricate; (2) projected posteriorly, strongly keeled, strongly imbricate. Fixed.
56 Apical pits in gulars (0) absent; (1) present. Fixed.
57 Posterior gulars (0) all unnotched; (1) some or all notched. Fixed.

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58 Number of gulars on an imaginary transverse line between ventral margins of ear openings. Meristic. Range of mean species values = 13.00–56.00.
59 Preauricular fringe (modified from Frost 1992) (0) absent or inconspicuous; (1) formed by projected granular scales; (2) formed by projected non-granular scales that partially or completely cover the ear opening. Fixed.
60 Lateral nuchals (Fritts 1974) (0) same size as dorsal nuchals; (1) less than half the size of dorsal nuchals. Fixed.
61 Lateral nuchals (0) granular; (1) smooth and imbricate; (2) keeled and imbricate. Fixed.
62 Dorsal nuchals (0) granular; (1) keeled and imbricate. Fixed.
63 Laterals (Fritts 1974) (0) same size as dorsals; (1) less than half the size of dorsals. Fixed.
64 Lateral body scales (Frost 1992) (0) granular, weakly imbricate in some cases; (1) smooth or slightly keeled (i.e., very sharp keel, sometimes occupying less than 50% the length of the scale), imbricate; (2) strongly keeled, imbricate, keels not projected; (3) strongly keeled, imbricate, keels projected posteriorly. Fixed.
65 Paravertebrals (i.e., 3–5 rows next to vertebral row on each side) (0) granular, weakly imbricate in some cases; (1) smooth or slightly keeled (i.e., very sharp keel, sometimes occupying less than 50% the length of the scale), imbricate; (2) strongly keeled, imbricate, keels not projected; (3) strongly keeled, imbricate, keels projected posteriorly. Fixed.
66 Vertebral scales (Etheridge & de Queiroz 1988) (0) same size as adjacent paravertebral scales; (1) larger than adjacent paravertebral scales forming a distinct, longitudinal middorsal row or crest. Fixed.
67 Dorsolateral crest (0) absent; (1) present. Fixed.
68 Number of scales around midbody. Meristic. Range of mean species values = 32.50–135.50.
69 Number of vertebrals (middorsal scales between occipitals and level of posterior edge of thigh extended perpendicular to the body). Meristic. Range of mean species values = 22.00–98.86.
70 Number of paravertebrals (scales adjacent to vertebrals between occipitals and level of posterior edge of thigh extended perpendicular to the body). Meristic. Range of mean species values = 28.00–128.23.
71 Ventral scales in adult specimens (modified from Frost 1992) (0) smooth and imbricate; (1) smooth or slightly keeled, imbricate, not mucronate; (2) strongly keeled, mucronate. Fixed.
72 Caudal notch on ventrals (Harvey & Gutberlet 2000) (0) absent; (1) present. Fixed.
73 Preanals (0) not projected; (1) moderately projected posteriorly; (2) strongly projected posteriorly forming denticulate border. Fixed.
74 Inguinal groove (0) absent; (1) present. Fixed.
75 Distal margin of palmars (0) uniform, without projections; (1) tridentate. Fixed.
76 Number of subdigital lamellae on manual digit IV (ventral scales from point of convergence of manual digits III and IV to terminus of digit IV). Meristic. Range of mean species values = 9.39–29.43.
77 Distal margin of plantars (0) uniform, without projections; (1) tridentate. Fixed.
78 Number of subdigital lamellae on pedal digit IV (ventral scales from point of convergence of digits III and IV to terminus of digit IV). Meristic. Range of mean species values = 19.00–37.02.
79 Posterior thigh scales (Fritts 1974) (0) not imbricate; (1) imbricate. Fixed.
80 Posterior thigh scales (Fritts 1974) (0) granular; (1) imbricate. Fixed.
81 Posterior thigh scales (0) same size as dorsal thigh scales; (1) less than half the size of dorsal thigh scales. Fixed.
82 Row of enlarged, projected scales on posterodorsal aspect of thigh (Avila-Pires 1995) (0) absent; (1) present. Fixed.
83 Caudal whorls per autotomic segment (0) none; (1) two; (2) three; (3) four; (4) five or more. Fixed.
84 Caudal scales (modified from Frost 1992) (0) without posterodorsally projected mucrons; (1) with moderate to strongly posterodorsally projected mucrons. Fixed.
85 Cross-section shape of tail in adult males (0) rounded or elliptical (i.e., weakly compressed); (1) strongly compressed laterally. Fixed.

Dermal folds and mite pockets

86 Antehumeral fold (0) absent; (1) present. Fixed.
87 Gular fold (0) absent; (1) present. Fixed.
88 Supra-auricular fold (Frost 1992) (0) absent or poorly developed; (1) present. Fixed.
89 Oblique neck fold (0) absent; (1) present. Fixed.
90 Antegular fold (modified from Frost 1992) (0) absent; (1) present, incomplete medially; (2) present, complete medially. Fixed.
91 Longitudinal neck fold (0) absent; (1) present. Fixed.
92 Postauricular fold (0) absent; (1) present. Fixed.
93 Ventrolateral fold (0) absent; (1) present. Fixed.
94 Inguinal granular pocket (Frost 1992) (0) absent; (1) present. Fixed.
95 Posthumeral or axillary pocket (Frost 1992) (0) absent; (1) one or more vertical folds; (2) shallow semicircular depression with wide opening; (3) deep depression with wide or narrow opening. Fixed.
96 Axillary flap (Cadle 2001) (0) absent; (1) present. Fixed.
97 Postfemoral mite pocket (0) absent; (1) one or more vertical folds; (2) distinct pocket with vertical or posteroventrally orientated slit-like opening. Fixed.

98 Nuchal mite pocket under oblique neck fold (0) absent; (1) present, deep. Fixed.

Colouration

99 Dark gular patch in adult females (0) absent; (1) present, covering most or all of gular region. Polymorphic.
100 Dark gular patch in adult males (0) absent; (1) present, covering most or all of gular region. Polymorphic.
101 Black patch on neck in adult males (0) absent; (1) present. Polymorphic.
102 Dark midventral stripe in adult males (0) absent; (1) present as faint, narrow line, or wide stripe sometimes covering most of the ventral surface of body. Polymorphic.
103 Dark patches extensively covering ventral surface of thighs in adult males (modified from Frost 1992) (0) absent; (1) present. Fixed.
104 Black patch on shoulder in adult males (0) absent; (1) present. Fixed.
105 Light vertical stripe on shoulder (0) absent; (1) present. Fixed.
106 Black collar in adult males (0) absent; (1) present. Fixed.
107 White or cream horizontal stripe on posterior surface of thigh (0) absent; (1) present. Fixed.
108 Oblique dark stripe on eye (0) absent; (1) present. Fixed.
109 Light stripe from below eye to shoulder (0) absent; (1) present. Polymorphic.
110 Light stripe between ventral margin of tympanum and forelimb insertion (0) absent; (1) present. Polymorphic.
111 Dark interorbital bar (0) absent; (1) present. Polymorphic.
112 Dark lips contrasting with rest of head (0) absent; (1) present. Polymorphic.
113 Dark mark on tympanic region in adult females (0) absent; (1) present. Polymorphic.

Hemipenes

114 Hemipenial lobes (Frost 1992) (0) long; (1) short. Fixed.
115 Transvs. penis muscle (Arnold 1984; hemipenial sheath musculature of Frost 1992) (0) not extensive; (1) extending almost entirely around hemipenial sheath. Fixed.
116 Hemipenial dorsal accessory muscle (Arnold 1984) (0) present; (1) absent. Fixed.

Morphometric characters

117 Head length (distance between anterior margin of tympanum and snout)/SVL ratio (modified from Frost 1992). Range of mean species values = 0.22–0.30.
118 Maximum head height/head length ratio (modified from Frost 1992). Range of mean species values = 0.56–0.72.
119 Tail length/total length ratio in adult males. Range of mean species values = 0.52–0.73.
120 Tail length/total length ratio in adult females. Range of mean species values = 0.49–0.72.
121 Hind limb length (distance between limb insertion and tip of Toe IV)/SVL ratio. Range of mean species values = 0.60–1.04.
122 Forelimb length (distance between limb insertion and tip of Finger IV)/SVL ratio. Range of mean species values = 0.38–0.58.

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