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Systematics and biogeography of the widespread Neotropical gekkonid genus *Thecadactylus* (Squamata), with the description of a new cryptic species

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The systematics of the widespread neotropical gekkonid genus *Thecadactylus* is investigated using a combination of morphological, morphometric and mtDNA (cytochrome *b*) sequence data, forming a total evidence dataset. The analysis tackles the common yet complex problem of a widespread taxon consisting of one or more cryptic species that are difficult to diagnose using morphology alone. The data are analysed using both maximum parsimony and Bayesian inference. Virtually all analyses resolve a well-supported south-western Amazonian clade distinct from the remainder of the recognized *T. rapicauda*. The south-western Amazonian clade is not only robustly supported, but also exclusive, geographically coherent and sufficiently distinct to warrant specific recognition. The new species is diagnosable on the basis of molecular sequences that are 23.0–26.9% divergent from those of *T. rapicauda*, and morphological evidence. Bayesian inference analysis robustly resolves meaningful and repeatable patterns of relationship. The biogeography of *Thecadactylus* is interpreted in the context of its two constituent species, and difficulties of resolving systematic and biogeographical patterns in widespread, cosmopolitan taxa are discussed.

ADDITIONAL KEYWORDS: Bayesian inference – Gekkonidae – maximum parsimony – phylogenetics – total evidence.

INTRODUCTION

The Neotropics generally display a pattern of high taxonomic diversity, reflected in numbers of species of many higher taxonomic groups. Although groups as divergent as birds (Burns, 1997) and bivalves (Stehli, McAlester & Helsley, 1967) exhibit high diversity in the Neotropics, numerous herpetological examples are also evident. Anoles comprise well over 300 species, speciating prolifically enough to warrant recognition as a radiation (Guyer & Savage, 1986; Irschick *et al*., 1997; Schluter, 2000). Lizards of the genus *Liolaemus*, which are predominantly distributed around the Andes, are represented by about 160 species (Schulte *et al*., 2000). The Neotropics also represent the area of highest anuran diversity in the world (Duellman, 1988). For example, the Hylidae comprises 165 known species in Middle America (Duellman, 1970, 2001). The Neotropical frog genus *Eleutherodactylus* is exceedingly diverse, with approximately 130 species in the Caribbean alone (Hass & Hedges, 1991; Hedges, 1996b).

The Gekkota has a circumglobal distribution (Henkel & Schmidt, 1995), and high levels of diversity (Kluge, 1967; Russell, 1972; Bauer & Russell, 1989; Bauer, 1990a, b; Hass, 1991; Nussbaum & Raxworthy, 1998; Kluge, 2001). With over 1100 recognized species (Kluge, 2001; Han, Zhou & Bauer, 2004), it is one of the most diverse squamate lineages. For example, high intrageneric species richness is seen in the Caribbean genus *Sphaerodactylus*, with over 90 species on the Greater Antillean islands (Hass, 1991), and in *Phyllodatylus sensu antiquo* (Bauer, Good & Branch, 1997), *Bavayia* in New Caledonia (Bauer, Whitaker & Sadlier, 1998; Bauer, Jones & Sadlier, 2000) and

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Pachydactylus (Lamb & Bauer, 2002) in Africa. However, South American gekkotans are a notable exception comprising few species in a small number of disparate genera (Abdala & Moro, 1996; Russell & Bauer, 2002b), with independent evolutionary origins, distributions and histories (Vanzolini, 1968). Such low levels of gekkotan diversity stand in stark contrast to the diversity of other taxa in the same area (Ricklefs, 1993).

Relatively few studies have examined in detail cases where diversity is low over broad geographical areas (but see Klautau *et al*., 1999; Lessios *et al*., 1999). If the study of radiation is useful to the understanding of evolution (Schluter, 2000), then the study of the maintenance of low taxonomic diversity should be equally illuminating. The study of low diversity over wide geographical areas can be informative about mechanisms for its maintenance, such as extensive gene flow and ecological generalism.

Thecadactylus rapicauda Huouttuyn, the turnip-tailed gecko, is an example of a widespread taxon exhibiting low taxonomic diversity. It constitutes a monotypic genus belonging to the Gekkonidae *sensu stricto* (Russell, 1972; Kluge, 1983; Russell & Bauer, 2002b; Han *et al*., 2004). Since its discovery and description by Houttuyn (1782), the validity of *T. rapicauda* has been unchallenged (Avila-Pires, 1995; but see Burt & Myers, 1942). Few studies have focused exclusively on this taxon (see Dowling, Majupuria & Gibson, 1971; Vitt & Zani, 1997), although it has been included in several higher-level systematic analyses (Kluge, 1983, 1987; Russell & Bauer, 1988; Abdala & Moro, 1996; Abdala, 1996).

Thecadactylus rapicauda is one of the few nocturnal lizards occurring in the Amazonian region and is the only nocturnal, arboreal lizard over much of its range (Duellman, 1987; Duellman & Pianka, 1990; Morales & McDiarmid, 1996; Vitt & Zani, 1997, 1998). Furthermore, it is far larger than any other mainland Neotropical gekkonid, and rivaled only by *Aristelliger lar* and the recently extinct *Tarentola albertschwartzi* in the Caribbean (Vitt & Zani, 1998). It has been hypothesized that a high level of anuran diversity and endemism has constrained gekkonid diversity in the region because of competition for the same dietary and structural niches (Duellman & Pianka, 1990).

Under the assumption of monotypy, a number of descriptions of *Thecadactylus rapicauda* have been published (e.g. Daudin, 1802; Beebe, 1944; Vanzolini, 1968; Hoogmoed, 1973; Schwartz & Henderson, 1991; Avila-Pires, 1995; Breuil, 2002; Russell & Bauer, 2002a), many being very similar. The synopsis and species account of Russell & Bauer (2002a) comprehensively compiles the hundreds of literature sources mentioning *T. rapicauda*, and illustrates its high variability. Monophyly of *Thecadactylus* is firmly established on the basis of a combination of features that renders it readily diagnosable (Hoogmoed, 1973; Avila-Pires, 1995; Russell & Bauer, 2002a).

Thecadactylus rapicauda is extensively distributed in Central America, northern South America and the Lesser Antilles (Fig. 1; Russell & Bauer, 2002a: Map 1). In Brazil its southern extent is probably determined by the border between the Amazon and the drier Cerrado (Vanzolini, 1968; Hoogmoed, 1973). The attribution of embryonic material from Bahia, Brazil, to *Thecadactylus* appears doubtful because these embryos (deposited at the UMMZ) are gekkonid but lack interdigital webs (our pers. observ.) that are characteristic of *Thecadactylus*. Bahia also lies much further south than the otherwise recorded south-eastern extent of the distribution of the taxon (Fig. 1), and is located between the drier and more open Cerrado and Caatinga regions (Vanzolini, 1981: Map 1). Two further questionable localities have been recorded: Guadalajara, Jalisco, Mexico, which lies far north of the northern range limit in the Yucatán; and Cuba. The specimens associated with the latter locality belong to *Thecadactylus*, but are in very poor condition (P.J.B., pers. observ.). A complete listing of documented localities for *Thecadactylus* is presented in Russell & Bauer (2002a).

Approach

The question remains as to whether *Thecadactylus* represents a single species, a small number of closely related species or a more extensive species complex (Burt & Myers, 1942). Although recent phylogenetic analysis of the mitochondrial cytochrome *b* gene is suggestive that *T. rapicauda* actually comprises two species (Kronauer *et al*., 2005), potential morphological support for this segregation is an important consideration (Wiens & Penkrot, 2002). Assessment of the phylogeny of *Thecadactylus* represents an important first step in studying its apparently low level of diversity, biogeography, diverse ecology and behaviour.

To address these issues, we investigate the systematics of *T. rapicauda* using a total evidence approach (Kluge, 1989) and using Bayesian inference (BI) (Rannala & Yang, 1996; Mau & Newton, 1997; Huelsenbeck *et al*., 2001). These approaches allow us to combine morphological and morphometric datasets with DNA sequence data (Kronauer *et al*., 2005) and analyse them simultaneously. A BI framework allows us to analyse our combined data set using a maximum-likelihood model (Lewis, 2001a, b; see below), representing an alternative to maximum parsimony (MP). Agreement between data sets and analyses is perhaps the strongest phylogenetic evidence to supporting species recognition (Wiens & Penkrot, 2002).

Figure 1. Distribution of *Thecadactylus*, showing ranges of the two constituent species, *T. rapicauda* (diagonal lines) and *T. solimoensis* sp. nov. (cross hatching). Modified from Russell & Bauer (2002a).

MATERIAL AND METHODS

OUTGROUP SELECTION

Potential outgroups of *Thecadactylus* were initially chosen using statements in the literature (Underwood, 1954; Vanzolini, 1968; Russell, 1972; Kluge, 1983; Russell & Bauer, 1988; Abdala & Moro, 1996), and geographical proximity because the taxon is rarely included in phylogenetic analyses (Han *et al*., 2004). Taxa of close geographical proximity but not mentioned in the literature as being related to *Thecadactylus* were eliminated to avoid incorporating irrelevant taxa (Appendix 1). The choice of outgroups was confounded by a distinct lack of information about related taxa, forcing us to select from among gekkonine gekkonids with relatively wide basal toe pads. The outgroups retained in the morphological data set were *Bogertia lutzae* Loveridge, *Phyllopezus pollicaris* Spix, *Homopholis wahlbergi* Smith, *Homopholis fasciata* Boulenger, *Blaesodactylus boivini* Duméril and *Gekko gecko* L. However, owing to limited availability of outgroups for other data sets, only *H. wahlbergi* was included in the morphometric dataset, and only *B. boivini* was included in the molecular data set (Kronauer *et al*., 2005; see below). Despite the Afro-Malagasy distribution of *Homopholis* and *Blaesodactylus*, these taxa have been allied with *Thecadactylus* based on digital morphology (Russell, 1972). As the monophyly of *Thecadactylus* is well supported, and assumed in this analysis, in all analyses including multiple outgroups, outgroup taxa were designated, but their relationships were left unconstrained (Maddison, Donoghue & Maddison, 1984; Nixon & Carpenter, 1993).

SPECIMENS EXAMINED

A total of 439 specimens were examined. Morphometric and morphological characters were collected from subsets of these specimens (see below). Specimen information for all specimens included in the morphometric and morphological data sets, as well as those examined but not included, are listed in Appendix 1.

Due to time constraints associated with measuring specimens and obtaining statistically valid sample sizes, fewer specimens and localities are included in the morphometric data set – 157 specimens from 19 localities (see Appendix 2 for sample sizes), including the outgroup, *Homopholis wahlbergi*. Twelve operational taxonomic units (OTUs) represented localities strategically chosen to cover as much of the distribution of *Thecadactylus* as possible and had robust sample sizes ($N = 6$; generally $N > 10$). The remaining OTUs were deemed worthy of inclusion due to their interesting geographical location, but are supported by non-robust sample sizes ($N < 6$) (Fig. 2).

The morphological data set consisted of 366 specimens of *Thecadactylus*, in addition to 53 specimens from six outgroup taxa. The *Thecadactylus* specimens originated from 76 localities, distributed across 33 countries throughout the entire range, with any gaps in sampling resulting from a lack of specimen availability (Fig. 2, Appendix 2). Thirty-seven of these localities were combined into 13 composite localities based on close geographical proximity, absence of obvious intervening geographical barriers, and a high level of consistency of character states possessed by their specimens. Combined localities (Fig. 2) were subsequently treated as single OTUs, resulting in a total of 52 ingroup OTUs. The molecular data set consisted of 30 ingroup specimens from 18 localities across the range of *Thecadactylus*, with sample sizes of 1–4 (Fig. 2; Kronauer *et al*., 2005). One specimen of *Blaesodactylus boivini* was included as the outgroup.

CHARACTERS EXAMINED

Twenty-one external morphometric characters were included. All were measured three times, using Mitu-

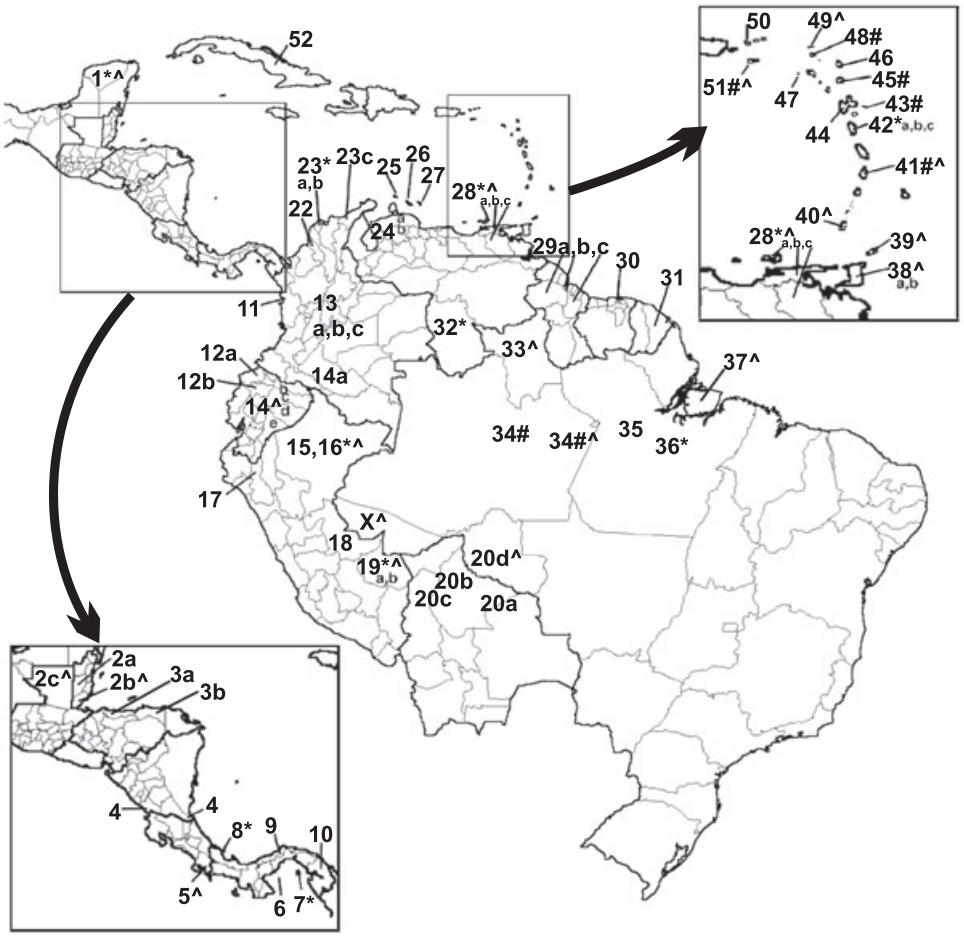

Figure 2. Distribution of localities sampled for the morphological, morphometric and molecular data sets. Localities denoted with * appear in the morphometric data set and have elevated sample sizes; those with # also appear in this data set, but have very low sample sizes; those with ^ are included in the molecular data set (also see Kronauer *et al*., 2005); those without a symbol are included in the morphological data set only. X^ denotes the localitiy of Acre, Brazil, which was only sampled for the molecular data set. Locality numbers correspond to those in Appendix 2.

toyo digital calipers, to the nearest 0.01 mm and averages were used in all subsequent analyses. Although recording of data to the nearest 0.01 mm represents pseudo-precision, it does not lead to different levels of significance or conclusions (Hayek, Heyer & Gascon, 2001; our pers. observ.). All morphometric variables included in the analysis and their abbreviations are presented in Appendix 3. All bilateral measurements and counts were taken from the right side, whenever possible.

All morphometric variables recorded were standard (Appendix 3), except for those relating to the limbs. Although many studies use forelimb length and hindlimb length as morphometric characters (Kluge, 1967; Losos, 1990a, b; Powell & Russell, 1992; Couper, Covacevich & Moritz, 1993; Raxworthy & Nussbaum, 1993; Vitt & Zani, 1997; Kohlsdorf, Garland & Navas, 2001), we enhanced our data set by dividing the hindlimb into four segments (thigh, crus, metatarsus, digit IV), and the forelimb into two (brachium and lower limb) following Irschick & Jayne (1998) and Beuttell & Losos (1999). We also measured 1st pedal digit length and width because the first digit is often reduced or modified in gekkonid lizards (Russell, 1972; Russell & Bauer, 1990), and is thus of systematic and functional significance (Bergmann & Russell, 2003).

Of the 70 morphological characters included, 29 are meristic, 30 are binary and the remaining 11 are multistate, non-meristic characters (described in Appendix 3). Meristic characters are presented in Appendix 3 as the number of scales or other structures observed for each specimen. Prior to phylogenetic analysis, meristic characters were coded to range from zero up. Characters presented in Appendix 3 were coded to minimize both character interdependence and non-applicable characters (Maddison, 1993; Slowinski, 1993; Scotland, 1996; Nei & Kumar, 2000; Wiens, 2001). Non-applicable characters were coded as missing because this allows different subclades to influence one another. We argue that this is desirable when dealing with systematics at low taxonomic levels, as is the case here. The final morphological data set consisted of 60 characters for 58 OTUs (52 belonging to *Thecadactylus*).

Several included characters require clarification. The lamellae on a single digit are functionally divisible into scansors and basal lamellae (Russell, 1981; Bergmann & Russell, 2003). The number of total lamellae, scansors and basal lamellae are all valid systematic characters (Bergmann & Russell, 2003). The findings of Bergmann & Russell (2003) on lamellar correlational patterns were used to guide character selection in terms of which digits the counts were to be taken from.

All osteological characters were collected from radiographs, most of which were produced at the University of Calgary using a Hewlett-Packard Faxitron model 43805N radiology unit and Polaroid Type 55 black and white positive/negative film. Negatives were magnified on a Zeiss microfilm reader to facilitate data collection. A minority of radiographs were produced on mammography film plates at the ANSP, USNM, UMMZ and FMNH (all museum acronyms follow Leviton *et al*., 1985). Due to the low taxonomic level of this study, relatively few (14) osteological characters were included because they are far less variable than those of external scalation.

The molecular data set consisted of 584 base pairs of the mitochondrial cytochrome *b* (cyt *b*) gene, amplified using custom primers, the details of which are presented elsewhere (Kronauer *et al*., 2005). The amplified fragment corresponds to nucleotide positions 14 543–15 126 of the mitochondrial genome of the scincid lizard *Eumeces egregius* Baird (Kumazawa & Nishida, 1999). Details of analysis are presented in Kronauer *et al*. (2005), and these data are only included here in the total evidence analyses.

Data coding and multivariate analysis

The morphometric data set was log-transformed prior to statistical and phylogenetic analyses to normalize and linearize it (Pimentel, 1979; Sokal & Rohlf, 1995). All data transformations and general data handling were performed using Microsoft Excel XP.

The effects of ontogeny were removed statistically from the morphometric data set to avoid confounding the phylogenetic analysis with the inclusion of immature specimens (Rohlf & Bookstein, 1987). We removed size from the log-transformed data set using both reduced major axis (RMA) residuals (Ricker, 1984) and orthogonal projection (Burnaby, 1966; Rohlf & Bookstein, 1987), following the procedures of Beuttell & Losos (1999), but present only the former analysis because results were very similar.

Sexual dimorphism (e.g. Fitch, 1976, 1981) was evaluated to ensure that it did not confound the analysis (Pimentel, 1979; Beuttell & Losos, 1999; Bergmann & Russell, 2001). Factor scores for each principal component from a principal component analysis (PCA) were compared between the sexes using two-sample *t*-tests, or when any of the assumptions of the *t*-test were violated, the Mann–Whitney *U*-test. The assumption of normality was tested using the Kolmogorov–Smirnov test, and the assumption of homoscedasticity was tested using the F_{max} test.

PCA was conducted on RMA residual data following the methodology of Pimentel (1979) using SYSTAT 10.2 (Wilkinson, 2001), allowing for the evaluation of within- and between-taxon variability (Archie, 1985). Factor scores were calculated for the first eight PCs to obtain coordinates for each individual in eight-

dimensional space. Scatter plots were constructed for pairs of PCs to visualize patterns of clustering.

To evaluate whether samples of *Thecadactylus* from different localities could be systematically discriminated, multivariate analysis of variance (MANOVA) was run and the Wilks' λ statistic was calculated to test the null hypothesis of equality of group centroids (Pimentel, 1979; Parsons & Jones, 2000; Wilkinson, 2001). Upon rejection of this null hypothesis, a discriminant function analysis (DFA) was run on the RMA residual data set and the resulting jackknifed classification matrix was calculated to evaluate the success rate of assigning individuals to their correct locality (Wilkinson, 2001).

Multivariate analysis is sensitive to distinguishing between groups (Pimentel, 1979; Crochet, Geniez & Ineich, 2003), but does not lead to conclusions regarding hierarchical relationships (Archie, 1985), which is the phylogenetic agenda (Hennig, 1966; Wiley, 1981). Therefore, morphometric variables were also recoded for phylogenetic analysis (Chappill, 1989) using the gap-weighting approach of Thiele (1993) and analysed using PAUP* 4.0b10 (Swofford, 2002). The morphometric data set, coded using gap-weighting and 32 character states, is presented in Appendix 4. The step-matrix gap-weighting approach of Wiens (2001) recovered less phylogenetic signal than simple gap-weighting, so the results are not presented.

Coding of the morphological data set was done using a *laissez-faire* approach, in which characters were recoded as little as possible so as to avoid distortion of the data by reducing characters, especially meristic ones, to binary form. Meristic characters were treated as fully ordered and reversible (Slowinski, 1993). The basic morphological data set is presented in Appendix 5. Due to rampant polymorphism the majority coding method was used to code all binary characters, assigning the most commonly exhibited character state by individuals belonging to an OTU (Wiens, 1995; Wiens & Reeder, 1997). These characters were converted to ordered three-state characters when the same number of individuals had each of the two possible states. The mode method was used to assign character states to all multistate characters (Archie, 1985), as the frequency method of Wiens (1995) recovered less phylogenetic signal than the majority method.

Phylogenetic analyses

Phylogenetic analyses were conducted separately on the morphological and morphometric data sets. These two data sets were then combined with a molecular data set (cyt *b*), presented elsewhere (Kronauer *et al*., 2005) into a single data matrix and analysed simultaneously (see below for details). All of these analyses were conducted using both MP and BI.

Total evidence

Total evidence involves the analysis of an unpartitioned data set, and hence weights all characters equally, making few assumptions about the data (Kluge, 1989; Eernisse & Kluge, 1993; Jones, Kluge & Wolf, 1993). The application of the total evidence approach often leads to increased resolution of phylogenetic hypotheses (Hillis, 1987), and can yield unique hypotheses of relationships (Sorhannus, 2001).

The morphological and morphometric data were coded in the same form as when analysed independently, but morphometric characters were reduced to six character states each to allow analysis using not only PAUP*4.0b10 (Swofford, 2002), but also Mr Bayes 3.0b4 (Huelsenbeck & Ronquist, 2001). All molecular characters, which are in the form of aligned nucleotides, were maintained as unordered characters (Williams, 1996; Kronauer *et al*., 2005). All morphometric and molecular characters were coded as missing for OTUs included only in the morphological data set. For the six localities for which multiple individual cyt *b* sequences were obtained (Kronauer *et al*., 2005), a single sequence was selected arbitrarily as an exemplar of a locality represented by multiple sequences.

A number of localities were combined prior to analysis. In the morphometric data set, the OTUs of Demerara and Mazaruni-Potaro were averaged to make a Guyana OTU, equivalent to that in the morphological data set. In the morphological data set, the localities of Pará, Santárem and Belém, all in Brazil, were amalgamated into a single Santárem OTU, for which a nucleotide sequence was available. The Peruvian OTUs of Iquitos and Loreto, which were included in the morphological data set, were combined to coincide with the morphometric and molecular data sets. Acre in Brazil was added because a mtDNA sequence was available. The following cyt *b* sequences were chosen: Tra2 from Guatemala (belonging to the Belize/Guatemala OTU, following the morphological data set), AMB-7101 from Grenada, AMB-7111 from Guyana, AMB-7080 from St. Croix, AMB-7091 from St. Lucia and Trin-1 from Trinidad.

Due to a large amount of missing data in the total evidence data set, which can lead to decreased explanatory power, all analyses were conducted in duplicate: once with all OTUs included, and once with only OTUs with data present in two of the three constituent data sets, one of which was the molecular data set due to its high number of characters. The data set with missing data had 51 OTUs, while the reduced data set consisted of 19 OTUs, both including one outgroup. The total evidence data set comprised 664 characters: 60 morphological, 20 morphometric and 584 nucleotides. Because the morphometric data set included only a single outgroup, all outgroup OTUs were removed and replaced by a compiled hypothetical outgroup

(Sorhannus, 2001). Morphological and morphometric character states to this outgroup were contributed by *Homopholis wahlbergi*, while molecular character states were contributed by *Blaesodactylus boivini* (*Homopholis* and *Blaesodactylus* are sister taxa – Russell, 1978). The effects of using a composite outgroup are unknown (Sorhannus, 2001).

Parsimony analyses

All MP analyses were conducted in PAUP*4.0b10 (Swofford, 2002) on the morphological, morphometric and total evidence data sets and were carried out using the same search algorithms and options. Heuristic searches with the ACCTRAN setting, the tree bisection–reconnection (TBR) algorithm, a random taxon addition sequence and 10 000 replicates for each search were used (Nei & Kumar, 2000). The MULTREES option was disabled, as the most parsimonious trees found with it enabled were of the same length, suggesting that tree-searching ability was not impaired by its disabling (Swofford, 2002).

Two measures of phylogenetic signal and the quality of that signal were calculated. The g_1 or skewness statistic was calculated from a sample of one million randomly sampled trees (Hillis, 1991; for discussion of the difficulties with this approach see Källersjö *et al*., 1992; Wenzel & Siddall, 1999; Drovetski, 2002). Significance of g_1 was evaluated using tables in Hillis & Huelsenbeck (1992). The second measure, the consistency index (CI), measures the amount of agreement between the characters (Siebert, 1996; Nei & Kumar, 2000).

Clade support was calculated by bootstrapping, with 1000 bootstrap replicates (Felsenstein, 1985; Hedges, 1992). Each bootstrap replicate consisted of a heuristic search with all settings as described above, but with only 100 replicates. Bootstrap values are biased estimates of accuracy, and under most conditions a bootstrap value of 70% corresponds to a 95% probability of a clade being correct (Hillis & Bull, 1993; but see Felsenstein & Kishino, 1993; Efron, Halloran & Holmes, 1996; Soltis & Soltis, 2003; Taylor & Piel, 2004). Although bootstraps are not comparable between studies, or even analyses, they are still indicative of relative support of various clades on a tree (Hillis & Bull, 1993).

Bayesian inference

Markov (Mkv) models are a general class of models that can be modified to analyse discrete morphological data (Lewis, 2001a). Lewis (2001a) generated an Mkv model to account for the fact that morphological data sets do not include invariable characters (unlike sequence data) by calculating probabilities conditional on all characters being variable, resulting in branch lengths not being overestimated (Lewis, 2001a). The Mkv model is not equivalent to an MP analysis (Lewis, 2001a), and so is applied here to the morphological data set.

As Lewis's (2001a) Mkv model has been implemented only in the software Mr Bayes (Huelsenbeck & Ronquist, 2001; Altekar *et al*., 2004), BI analysis of the morphological *Thecadactylus* data set was carried out using Mr Bayes 3.0b4. The Mkv model was used (Lewis, 2001a), but modified by allowing the prior probability of character state frequencies to follow a uniform Dirichlet distribution, thereby allowing them to vary around the equal frequency value (P. O. Lewis, pers. comm.). This was deemed appropriate because character state frequencies were not equal.

In the analysis of the *Thecadactylus* morphological and morphometric and total evidence data sets, each Metropolis-coupled Markov-chain Monte Carlo (MCMCMC) analysis included four simultaneously running chains, heated at 0.20, and replicated four times to ensure that they all converged to the same result (Huelsenbeck & Ronquist, 2001; Huelsenbeck *et al*., 2001; Murphy *et al*., 2001). Each chain was run for one million generations, with a burnin of 100 000 (10%), sampling trees every 100 generations. All prior probabilities were uniform. As Mr Bayes 3.0b4 allows for the designation of only a single outgroup, *Bogertia* was defined as such, with all other outgroup OTUs unconstrained in the morphological analysis (Nixon & Carpenter, 1993).

Total evidence BI analyses were run by partitioning the data into the three respective data sets and applying the Mkv model to the morphological and morphometric partitions, and the GTR+G+I model (Kronauer *et al*., 2005) to the molecular partition. Substitution rate parameters were applied only to the molecular model, character state frequencies were linked between the morphological and morphometric partitions but unlinked with the molecular partition, and the topology parameter was linked between all partitions.

RESULTS

MORPHOLOGY

MP analysis of the morphological data set resulted in three equally most parsimonious trees of length 1361. Phylogenetic signal was low but significant ($g_1 = -0.3812$, $P < 0.05$) and characters were often inconsistent (CI = 0.2109). Clade support for the resulting cladograms was extremely low, with the highest ingroup bootstrap value being 49%, and hence they are not shown.

All four independent MCMCMC analyses gave consistent estimates of both the likelihood (mean = –2921.82, SD = 4.87) and the topology parameter (mean = 22.55, SD = 0.09), indicating convergence of the four analyses to the same maximum, suggesting its global nature. Plots of parameter values against generation time for each analysis (not shown) and low parameter estimate variances indicate a short burnin stage and a long, stable plateau. The 50% majority rule consensus tree arising from the BI analysis allies St. Lucia and Barbuda with a posterior probability (Pp) of 0.97. There is also some support (Pp = 0.87) for a south-western Amazonian clade consisting of Bolivia, Amazonian Ecuador and all Peruvian localities (Fig. 3). Other relationships are only modestly supported by posterior probabilities because of their less conservative nature than the bootstrap (Erixon *et al*., 2003).

MORPHOMETRICS

No sexual differences were evident in the first eight PCs from PCA of the residual data set (Table 1), indicating a lack of relative sexual dimorphism in the sample. Comparison of PC-1 from PCA on the non-size-removed data set indicated no sexual size dimorphism (Mann–Whitney *U*-test: $U = 3073$, d.f. = 1, $P = 0.9111$). Due to this, sexes were pooled in all subsequent analyses.

PC-1 for the residual data explains a slim minority of the variance (49.95%). This supports the notion that size-dependent variance, at least to some degree, swamps other variation when size effects are not removed (PC-1: 81.03% of variance), and shows the strength of using size-removed data for systematic purposes (Rohlf & Bookstein, 1987). Furthermore, in the size-removed data set even PC-8 still explains > 2% of the variance (Table 1).

A scatter plot of the first two PCs most clearly discriminates between localities, but still shows extremely high degrees of overlap in morphospace of 95% locality centroids (Fig. 4A). The plot does, however, suggest that specimens from Colombia (Atlantico), Venezuela (Amazonas) and St. Martin are somewhat morphometrically distinct from those from other localities. To evaluate the relative degree of within- and between-locality variation, pair-wise eight-dimensional distances were calculated between all 157 individuals from residual PCA factor scores. These were then plotted as a histogram (Fig. 4B). Good discriminatory power is dependent upon the distribution of within- and between-locality distances overlapping minimally (Peake *et al*., 1998; Rebbeck *et al*., 2001). Clearly, this is not the case here, in which the between-locality distribution is completely nested within the within-locality distribution and is demon-

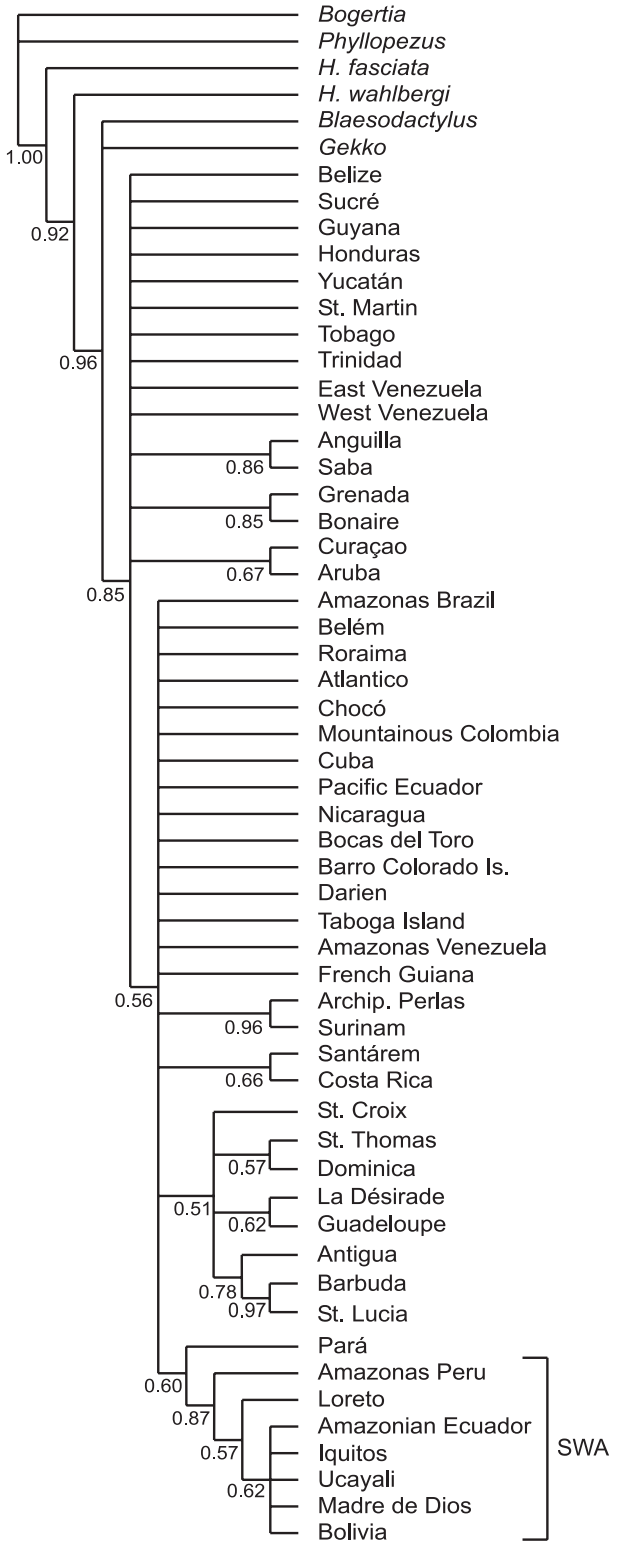

Figure 3. Majority rule consensus summary of trees sampled by the BI analysis of the morphological data set. Posterior probabilities are presented below branches. SWA indicates the south-western Amazonian clade, which is described herein as *T. solimoensis*.

Table 1. Evaluation of relative sexual dimorphism for *Thecadactylus* included in the morphometric data set (residual data). Percentage variation explained by each PC is presented, as well as the test used to compare PC factor scores between sexes, test statistics, degrees of freedom and probabilities

Variable	% Variation	Test	Statistic (*t*/*U*)	d.f.	*P*
PC-1	49.95	MWU	2957.000	1	0.7645
PC-2	12.68	*t*-test	–1.950	154	0.0530
PC-3	7.26	*t*-test	–0.010	154	0.9924
PC-4	5.56	*t*-test	1.832	154	0.0687
PC-5	4.21	*t*-test	0.210	154	0.8336
PC-6	3.33	*t*-test	0.773	154	0.4414
PC-7	2.87	*t*-test	0.279	154	0.7807
PC-8	2.47	*t*-test	–0.562	154	0.5749

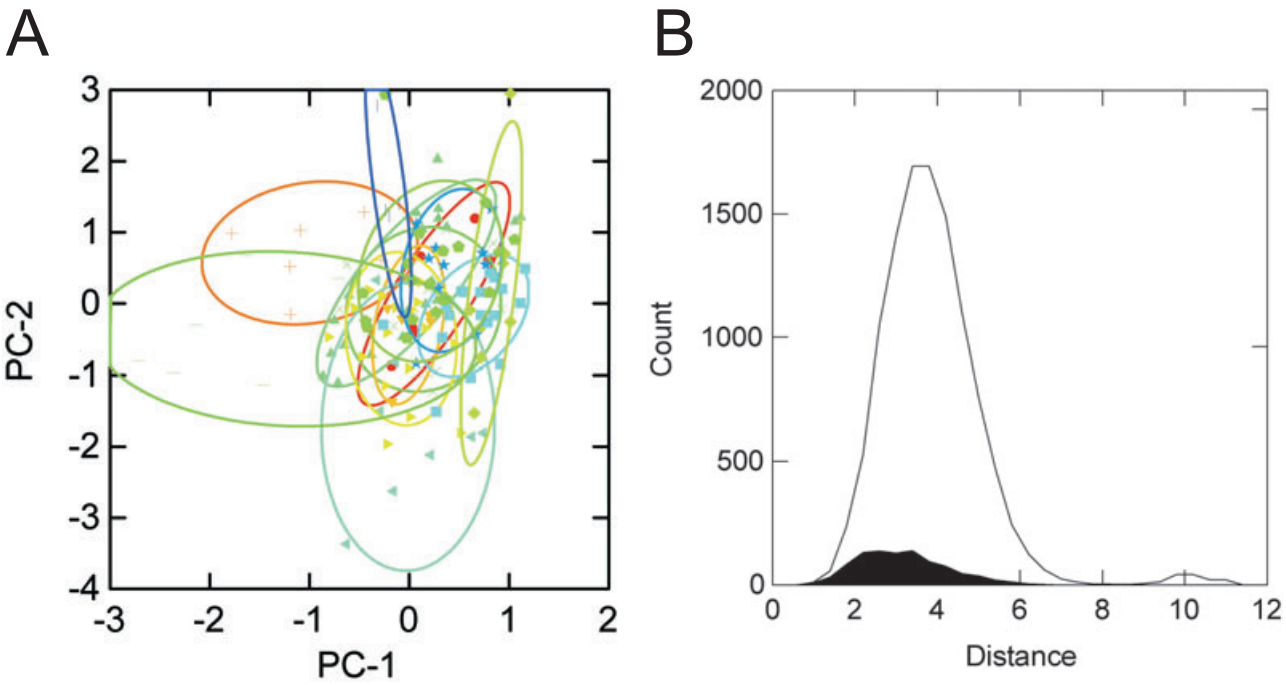

Figure 4. Summary of PCA results from analysis of the residual morphometric data set. A, plot of PC-1 and PC-2 with 95% locality centroids plotted. B, distribution of within- (unfilled) and between- (filled) clade (SWA and the remainder) Euclidean distances calculated based on the first eight PC factor scores.

strative of poor discriminatory power of the data with respect to geographical locality.

Wilks' λ and associated *f*-statistics from a MANOVA run of the residual data set indicate significant differences between locality centroids (Table 2), validating the use of DFA in further clarifying the situation. Tolerance values associated with the DFA ranged from 0.45 to 0.90 (mean 0.62), indicating that included variables each possessed considerable independent variation. *F*-statistics indicate that web breadth is the most useful discriminator, followed by internasal distance, eye to nostril distance and first pedal digital width, with other variables being less discriminatory

Table 2. MANOVA results comparing locality centroids for the morphometric data set (residual data). Wilks' λ is presented, along with associated degrees of freedom, the *F* approximation associated with Wilks' λ, degrees of freedom associated with *F*, and the probability

Statistic	Residual
Wilks' λ	0.0039
d.f. (λ)	19,12,133
F approx.	3.8099
d.f. (*f*)	228,1202
P	0.0000

between localities. The jackknifed classification matrix indicates that DFA correctly classifies individuals to their respective localities only 49% of the time, again demonstrating the poor discriminatory power of this data set.

Phylogenetically, the morphometric data set revealed very little. The characters did not agree with one another (CI = 0.3937), phylogenetic signal was very low ($g_1 = -0.2433$, $P < 0.05$) and the maximal bootstrap value on the most parsimonious tree (not shown) was 47%. Bayesian analysis was only marginally more successful, with all four independent runs of the MCMCMC algorithm converging to the same place in parameter space (likelihood: mean = –615.89, SD = 0.67; topology parameter: mean = 13.73, SD = 0.02). However, the consensus tree resulting from this analysis was particularly poorly resolved, indicating poor support for all clades, with the affinity of Colombia and St. Martin being best supported (Pp = 0.87).

TOTAL EVIDENCE

The MP analysis resulted in four disparate and equally most parsimonious cladograms (length 2012), yielding an extremely poorly resolved majority rule consensus tree (not shown). Both phylogenetic signal and consistency index were low ($g_1 = -0.6169$, $P < 0.05$; CI = 0.3524). Although this tree reveals little to elucidate the evolutionary history of *Thecadactylus*, part of the south-western Amazonian clade, consisting of Madre de Dios in Peru and Acre in Brazil, was supported by a robust bootstrap value (84%), resulting from the molecular data, which was the only source available from Acre.

When only OTUs with the majority of data available were considered, a single most parsimonious tree was obtained (length 1447) with improved phylogenetic signal ($g_1 = -0.7721$, $P < 0.05$; CI = 0.4686), and higher bootstrap values (Fig. 5). A clade consisting of Belize/Guatemala and Yucatan + Guyana, Tobago and Trinidad, respectively, is supported by a bootstrap value of 87% (Fig. 5). The sister group relationship of Belize/Guatemala and Yucatán is supported by a bootstrap value of 100%. A close affinity between the Brazilian OTUs of Santárem and Roraima is also well supported (bootstrap value of 85%). Finally, the south-western Amazonian clade, consisting of Bolivia, Amazonian Ecuador, Loreto, Brazilian Amazonas and Madre de Dios, is supported by a high bootstrap value of 95% (Fig. 5).

All independent runs of the total evidence BI analysis converged to similar likelihood and parameter values (Table 3). Estimates of molecular character state frequencies, gamma shape parameters and proportion of invariable sites were similar between analyses including all OTUs and those including only OTUs with few missing data, but rates of substitution between cytosine and thymine, and between adenine and guanine (both transitions) were estimated with poor precision (Table 3).

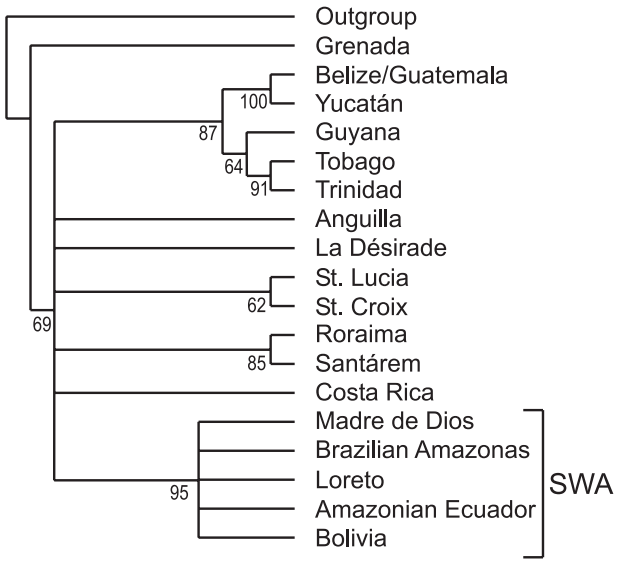

Figure 5. Majority rule bootstrap consensus tree of cladograms produced by MP analysis of the total evidence data set. Bootstrap values are presented below branches. SWA indicates the south-western Amazonian clade, which herein is described as *T. solimoensis*.

Table 3. Mean likelihood estimates, as well as mean topology, nucleotide frequency [$f(X)$], nucleotide rate substitution [$r(X)$], gamma shape distribution (alpha) and proportion invariable sites (Pinv) estimates for four independent iterations of BI analysis of the total evidence data set (see text for details). The r(GT) parameter is fixed at 1.0

Parameter	All OTUs	Robust OTUs
Likelihood	–7604.0400	–5914.4700
Topology	21.2527	9.9778
f(A)	0.3010	0.2988
f(C)	0.3871	0.3861
f(G)	0.1035	0.1044
f(T)	0.2084	0.2106
r(CT)	4.4540	3.9520
r(CG)	0.5730	0.4990
r(AT)	0.2400	0.2310
r(AG)	13.1710	11.0800
r(AC)	0.1900	0.2060
alpha	0.5628	0.6314
Pinv	0.3430	0.3499

Bayesian analysis of the complete data set of all OTUs was poorly resolved, but had high clade support for some groupings (Fig. 6A). Sister group relationships were recovered for Surinam and Archipelago de las Perlas (Pp = 0.99), and Bonaire and Grenada (0.92). A clade consisting of Yucatán, Belize/Guatemala, Honduras, Guyana, Trinidad and Tobago was well supported (Pp = 1.00), with high posterior probabilities of subgroupings of these OTUs (Fig. 6A). Finally, the south-western Amazonian clade was again recovered and well supported (Pp = 0.93; Fig. 6A).

Bayesian analysis including only OTUs with good character representation had somewhat improved resolution over other analyses and was highly congruent with the MP and BI analyses including all OTUs (Fig. 6B). Notably, both the south-western Amazonian and the northern Middle American + Guyana/Trinidad/Tobago clades were recovered (Pp = 1.00; Fig. 6B). The affinity of Costa Rica and La Désirade was strengthened (Pp = 1.00), as was that between St. Croix and St. Lucia (Pp = 0.97), relative to MP results. Within the south-western Amazonian clade, a sister group relationship was supported for Loreto and Brazilian Amazonas (Pp = 0.86), but other relationships within the clade were only poorly supported (Fig. 6B).

DISCUSSION

Support for the recognition of a south-western Amazonian species

Based upon our findings for the combined morphological, morphometric and molecular data, we propose that *Thecadactylus* comprises two distinct species, and that the south-western Amazonian clade represents a cryptic species, separable from the previously monotypic *T. rapicauda*. The strongest evidence for this relates to mtDNA sequence data, but there is also support from morphological and total evidence data.

It is unsurprising that the stongest evidence of a second species within this widespread and highly variable taxon arises from mtDNA sequence data. This type of evidence has long been used to detect cryptic species in such taxa (Avise *et al*., 1987; Hillis, 1987; Slade & Moritz, 1998; Wiens & Penkrot, 2002), and is useful in guiding their identification and separation (Seberg, 2004). Mitochondrial DNA has the advantages of being non-recombinant (Avise *et al*., 1987), leading to a smaller effective population size and faster coalescence, even when other, nuclear, characteristics are not yet fixed in a young species (Wiens & Penkrot, 2002).

The first important line of molecular evidence supporting two species of *Thecadactylus* is sequence divergence. Sequence divergences within the south-western Amazonian clade range from 0.2 to 9.8%, and those within the remaining clade range from 0 to 23.6% (Kronauer *et al*., 2005). Sequence divergences between these two clades range from 23.0 to 26.9%, so are almost always greater than within clade divergences. Little overlap between ranges of within- and between-sequence divergences further supports the distinction of these two clades (Kronauer *et al*., 2005). The strength of the sequence divergence evidence is best evaluated comparatively to determine the degree of divergence used by other authors to delimit species. In almost all situations, sequence divergences documented between the two species of *Thecadactylus* are much greater than those separating related species in many other taxa (Kronauer *et al*., 2005, and references therein).

High sequence divergences between OTUs in the non-south-western Amazonian clade are the result of the presence of a number of molecularly distinctive OTUs, including Costa Rica, Grenada and St. Lucia. The inclusion of sequences from Roraima and Santarem also resulted in high divergences. However, unlike the south-western Amazonian clade, these OTUs do not associate closely with any others, nor do they form geographically coherent clades (Wiens & Penkrot, 2002). With more detailed study, some of these OTUs may also be found to represent distinctive species of *Thecadactylus*.

Phylogenetic evidence from the molecular data set supports the existence of two species of *Thecadactylus* equally strongly. Two basal lineages were identified (south-western Amazonia, and the remainder), and the monophyly of these has high clade support (Kronauer *et al*., 2005). Strong clade support, exclusivity and geographical concordance are advocated as being strongly supportive of multiple species (Wiens & Penkrot, 2002; Morando, Avila & Sites, 2003). The first of these is clearly met in the current situation. The second refers to a requirement for mtDNA haplotypes to not be shared between hypothesized species (Wiens & Penkrot, 2002). Sharing of haplotypes, or non-exclusivity, is indicative of gene flow between clades (Morando *et al*., 2003). The exclusivity criterion is also met for the two *Thecadactylus* clades, and is further supported by high divergences (Kronauer *et al*., 2005). More intensive locality sampling for the molecular data set will enable further testing of this exclusivity. Finally, it is clear that both clades are geographically concordant in that the south-west Amazonian clade is restricted to that region and it does not subdivide the remaining clade into discrete geographical units.

Supporting evidence for the two species of *Thecadactylus* is derived from morphological and total evidence analyses. The great majority of analyses including either morphological or all data recovered the south-western Amazonian clade. Clade support was lower than for the molecular data alone, with the

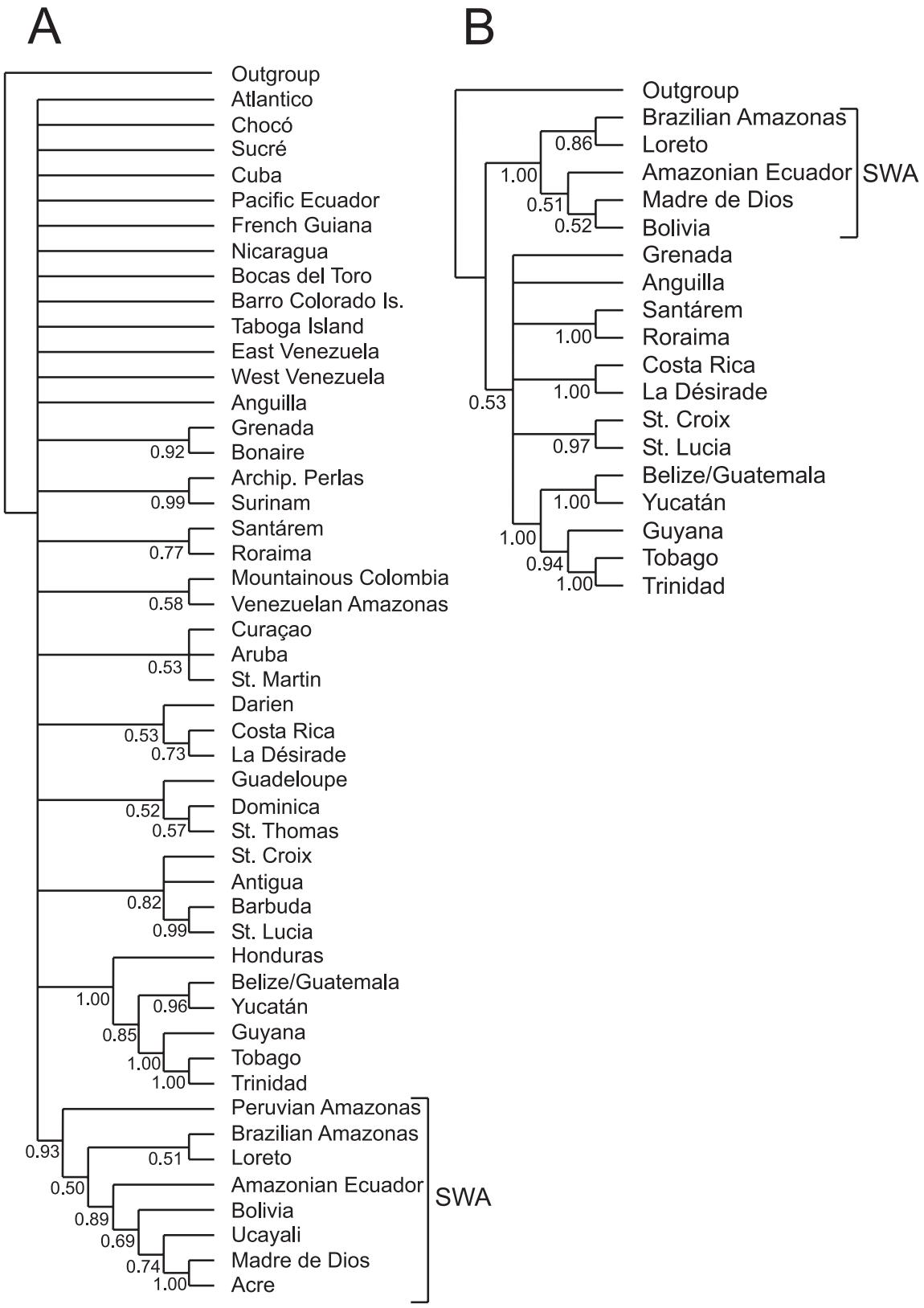

Figure 6. Majority rule consensus summary of trees sampled by the BI analysis of the total evidence data set including all OTUs (A) and including only those OTUs for which a majority of the data was available (B). Posterior probabilities are presented below the branches. SWA indicates the south-western Amazonian clade, which herein is described as *T. solimoensis*.

most robust figures arising from Bayesian analysis. This provides evidence of congruence between analyses of different sources of data (Wiens & Penkrot, 2002; Morando *et al*., 2003). Robust support for exlusive, geographically coherent, basal lineages has been suggested as supportive of different species when morphological or molecular data are considered (Wiens & Penkrot, 2002). The south-western Amazonian clade is exclusive in all analyses.

Diagnostic morphological characters that are fixed and non-overlapping with those of other species do support the recognition of separate species (Puorto *et al*., 2001; Wiens & Penkrot, 2002), but the difficulties of meeting this criterion for cryptic species are formidable. For example, two of the five species of *Sceloporus* recognized by Wiens & Penkrot (2002) lacked fixed diagnostic features. No fixed and non-overlapping morphological features are identifable for the south-western Amazonian clade, but the diagnostic features listed in the species description below do characterize the great majority of individuals examined, and further support the validity the species.

Choice of species concept does not typically affect phylogenetic analysis, but it can influence species recognition and delimitation (Hillis, 1987). From the numerous available species concepts (reviewed by Ridley, 1996; de Queiroz, 1998; Wheeler & Meier, 2000), we adopt the general lineage concept of species (GLSC) of de Queiroz (1998), which views a species as a segment of a population-level evolutionary lineage. Under the GLSC all traditional species concepts are simply considered species definitions that emphasize different species criteria (de Queiroz, 1998) and we evaluate each criterion for the south-western Amazonian clade with the evidence available.

Phylogenetic (Cracraft, 1983; Donoghue, 1985; Mishler, 1985; Panchen, 1992; Mishler & Theriot, 2000) and evolutionary (Wiley, 1981) criteria for defining species are all met by the south-western Amazonian clade, which forms a separate clade from the rest of *Thecadactylus*, and is at least partially diagnosable using morphological characters. Evolutionarily, sequence divergences indicate pronounced differences between the two *Thecadactylus* clades, suggesting a long history of isolation and separate identity (Kronauer *et al*., 2005). These observations further serve to satisfy the phenetic species definition (Sokal & Crovello, 1970), and the genotypic cluster definition (Mallet, 1995). Although this study does not directly address the biological (Mayr, 1942), isolation/recognition (Paterson, 1985), ecological (Van Valen, 1976) or cohesion (Templeton, 2001) species definitions, allopatry, exclusivity and lack of interdigitation of haplotypes between clades indirectly suggests an absence of interbreeding (Wilson & Brown, 1953; Wiens & Penkrot, 2002; Morando *et al*., 2003). Under the cohesion species definition, the null hypothesis that the taxon being studied represents a single evolutionary lineage (Templeton, 2001) is tested here and rejected for *Thecadactylus*. However, the null hypothesis that the two species are genetically and/or ecologically interchangeable (Templeton, 2001) is beyond the scope of this study (see Morando *et al*., 2003).

Under the species definitions considered above, and under the general framework of the GLSC, the validity of the south-western Amazonian clade as a species is justified. Under many of these definitions (phylogenetic, and evolutionary), evidence for two species is strong. Although all species criteria are important, often not all are met when closely related species are considered (de Queiroz, 1998).

DESCRIPTION OF *THECADACTYLUS SOLIMOENSIS* SP. NOV.

Synonymy: See Russell & Bauer (2002a) for complete list.

Material examined: Holotype: QCAZ-6691 (= OMNH-36431). Male, collected by L. J. Vitt in 1994 from the type locality of Reserva Faunistica Cuyabeno (Estacion Biologia da Universidad Catolica), Sucumbios, Ecuador. Description (Fig. 7A): 116 mm SVL, 76 mm TL, 29 mm HL, 24 mm HW, 6 mm IND; regenerated tail broader than more proximal stump and relatively unpatterned; 4 nasal granules, dorsalmost enlarged; internasals with reduced contact medially; 11 supralabials, 6 anterior to the eye; 10 infralabials; rostral partly divided; 11 spinose supraciliaries; postmetals stubby; 3 post-postmetals, medial one enlarged; 9 post-infralabials; dorsal forearm and ventral neck scales granular; hindlimb web and tail base scales imbricate; 1 single-apexed, pointy cloacal spur; cloacal sacs present; total manual lamellae on digits I, IV and V, 15, 21 and 19, respectively; total pedal lamellae on digits I, IV and V, 18, 22, 20, respectively; scansors on manual and pedal digits IV, 12 and 13, respectively; subdigital sulcus divides all lamellae on manual digit II, but only some on digit I; lateral stripe absent; dorsal colour and pattern light, unmottled, consisting of 5 diamonds; 7 paravertebral pairs of spots, of varying definition, some interconnected across the midline; nuchal spot absent; postocular stripes project posterodorsally, but do not connect middorsally; dark caudal blotches present; 13 teeth occluded by rostral; anterolateral process of parietal swept back; otic capsule anterolateral to occipital complex; 26 presacral vertebrae, 3 cervical vertebrae without ribs; 22 ribs, 2 anterior to medial level of clavicles, 6 shortened; cloacal bones absent; paraphalanges not visible in radiographs.

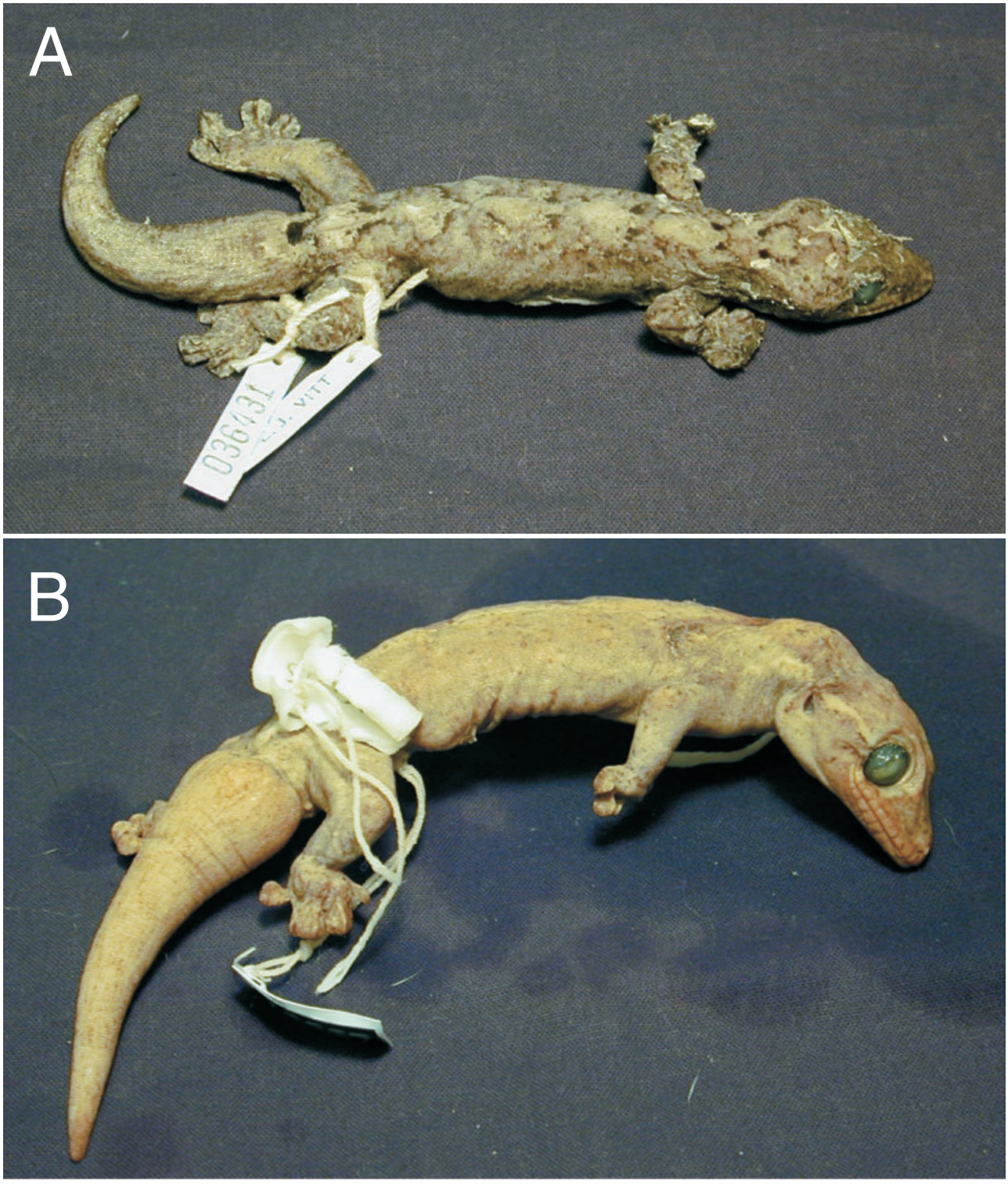

Figure 7. Photographs of the holotype of *Thecadactylus solimoensis* [QCAZ-6691 (= OMNH-36431)] (A), and the neotype of *T. rapicauda* (RMNH-16267) (B).

Paratypes: All paratypes were collected by L. J. Vitt in 1994 from the type locality, but from Neotropic Turis, instead of Estacion Biologia. Five paratypes are defined: OMNH-36427: male, original tail; OMNH-36428: female, original tail; OMNH-36429: male, regenerated tail; OMNH-36430: male, regenerated tail; and OMNH-36433: female, regenerated tail.

Referred specimens: All those listed in Appendix 1 that originate from Bolivia, Peru and Ecuador. Also, those from the Brazilian states of Amazonas and Rondonia. Tentatively, the single specimen from the southern Colombian state of Caqueta is also referred.

Variation: Presented only for characters that do not span the entire range for *Thecadactylus*. 2–5 nasal granules; 8–14 supralabials, 4–7 anterior to the eye; 8–12 infralabials; rostral never fully divided; up to 12 spinose supraciliaries; 2–7 post-postmentals; 4–11 post-infralabials; 1–3 cloacal spurs; total manual lamellae on digits I, IV and V, 13–20, 17–25, 16–24, respectively; total pedal lamellae on digits I, IV and V, 14–21, 19–25, 18–23, respectively; scansors on manual and pedal digits IV, 9–14 and 10–14, respectively; 0–7 dorsal diamonds; 0–8 paravertebral spots; 0–5 dark caudal blotches; 0–10 caudal bands; 11–15 teeth occluded by rostral; 26–27 presacral vertebrae, 2–3 cervicals without ribs; 21–24 pairs of ribs, 0–3 anterior to medial level of clavicles, 5–6 shortened.

Although both species of *Thecadacytlus* are highly variable in general, *T. solimoensis* displays less variability than does *T. rapicauda*. This is especially true in terms of maximal SVL (*T. solimoensis* specimens are relatively large) and in terms of pattern (*T. solimoensis* specimens tend to have a dorsally directed postocular stripe and a dorsal diamond pattern, see below).

Diagnosis: *Thecadactylus solimoensis* invariably possesses strongly dilated subdigital pads, well-developed subdigital sulci that house the claws and divide the lamellae into two series, and interdigital webs, uniting it with *T. rapicauda* within the genus. *T. solimoensis* also possesses morphological, morphometric and molecular autapomorphies that distinguish it from *T. rapicauda*. Morphological and morphometric divergence is less pronounced than molecular divergence, which includes sequence divergences of 23.0–26.9% between the two species (Kronauer *et al*., 2005).

Morphological characters that diagnose *T. solimoensis* are never fixed, but are possessed by the majority of specimens. This is unsurprising for a cryptic species, and similar characters have been used as diagnostic by other authors (Branch, Bauer & Good, 1996; Wiens & Penkrot, 2002). Four morphological characters are here denoted as diagnostic. The strongest of these is that 78% of specimens examined have a dorsally directed postocular stripe, compared with < 0.01% of specimens of *T. rapicauda*. Seventy-seven per cent of those specimens examined have a dorsal diamond pattern (39% of *T. rapicauda*), and 69% possess stubby postmental scales (53% of *T. rapicauda*). Finally, 65% of specimens assigned to *T. solimoensis* have granular scales on the gular region (25% in *T. rapicauda*).

All morphometric characters examined have a high degree of range overlap between *T. solimoensis* and *T. rapicauda*. However, significant differences occur in some, when size-removed (residual data set) species means are compared using two-sample *t*-tests or Mann–Whitney *U*-tests, as appropriate (Table 4). Mean values for *T. solimoensis* are significantly greater for internasal distance, interorbital distance, ear–eye distance, axilla–groin distance, metatarsus length, fourth toe width and first toe length than for *T. rapicauda*. Means are significantly less for eye–naris distance, orbital diameter, upper arm length and crus length than for *T. rapicauda* (Table 4).

Cytochrome *b* sequences between the two species are highly distinct (Kronauer *et al*., 2005; see above). As molecular evidence provides very strong support for the recognition of a second species (Seberg, 2004) and broad geographical samplings of numerous specimens for each species were included, diagnostic

Table 4. Tests of equality of means for residual morphometric variables between *Thecadactylus rapicauda* and *T. solimoensis*. Included are the test used, the test statistic, associated degrees of freedom and probability. Significant probabilities are in bold type

Variable	Test	d.f.	*t*/*U*	*P*
LHL	*t*	154	0.9533	0.3419
LHW	*U*	1	2319	0.7506
LHD	*t*	154	1.0321	0.3036
LIND	*t*	153	–3.7487	**0.0003**
LEND	*t*	154	2.9907	**0.0032**
LIOD	*t*	154	–2.7614	**0.0065**
LOD	*U*	1	2756	**0.0338**
LEED	*t*	154	–2.6042	**0.0101**
LAGD	*U*	1	1458	**0.0012**
LFLL1	*t*	154	2.5851	**0.0107**
LFLL2	*t*	154	1.2533	0.2120
LHLL1	*U*	1	2624	0.1148
LHLL2	*t*	154	3.2435	**0.0014**
LHLL3A	*t*	154	–3.4762	**0.0007**
L4TL	*U*	1	2239	0.9901
L4TW	*U*	1	1597	**0.0077**
L1TL	*U*	1	1564	**0.0051**
L1TW	*t*	154	–1.1509	0.2516
LWB	*U*	1	1904	0.1629

Table 5. Nucleotide autapomorphies for *Thecadactylus solimoensis*, including position in the sequenced fragment (Kronauer *et al*., 2005), position relative to the mitochondrial genome of *Eumeces egregius* (Scincidae) (Kumazawa & Nishida, 1999), character state at that position and homologous character state for *T. rapicauda*. Asterisks denote characters that are not fully exclusive to *T. solimoensis* (see text)

Fragment position	Genome position	NTP *T. s.*	NTP *T. r.*	Fragment position	Genome position	NTP *T. s.*	NTP *T. r.*
31	14 574	A	C	481	15 024	AG*	CT
63	14 606	C*	AG	489	15 032	T	C
95	14 638	G*	T	490	15 033	A	CT
97	14 640	T	AG	493	15 036	A	CT
160	14 703	C	AG	494	15 037	T*	C
223	14 766	C	AGT	499	15 042	T*	AC
235	14 778	A	C	500	15 043	A	C
283	14 826	T*	AC	509	15 052	C	A
311	14 854	T	C	517	15 060	C	AG
314	14 857	T	C	520	15 063	CG	AT
327	14 870	A	C	523	15 066	C	AG
328	14 871	C*	A	529	15 072	A	CT
334	14 877	A	CT	532	15 075	AG	CT
364	14 907	A	CT	550	15 093	AG	CT
415	14 958	A*	CGT	559	15 102	C	AG
454	14 997	CT	AG	570	15 113	C	G
457	15 000	AG*	CT	574	15 117	A	CT
475	15 018	G	A				

molecular characters are detailed (Table 5). A smaller cyt *b* sample size would tend to inflate these differences and negate the use of this approach. Of 584 bp sequenced, 26 are fixed and exclusive to *T. solimoensis*. A further 9 bp are fixed and almost exclusive to *T. solimoensis* in that only a single specimen sequenced of *T. rapicauda* shares the same nucleotide. Within the sequenced fragment, a highly diagnostic region, located between nucleotide positions 489 and 532, contains 12 of the 35 fixed sites, ten of which are exclusive (Table 5).

Distribution: *T. solimoensis* occurs throughout Ecuador, Peru and Bolivia, only east of the Andes, in Brazilian Amazonas and Rondonia, and in southern Colombia (Fig. 1). The western and southern extent of its range is absolutely delimited by the edge of the range of *Thecadactylus*, with the western edge bounded by the Andes, and the south-eastern extent of the range defined by the edge of mesic Amazonia. The northern extent of the range is difficult to determine with current specimen availability, but may be defined by the Colombian Cordillera Oriental. The eastern range boundary tentatively approximates the political boundary between the Brazilian states of Amazonas and Pará, as inferred from molecular sampling (Kronauer *et al*., 2005). More intensive sampling is required to determine the northern and eastern boundaries more definitively.

Etymology: The specific epithet, *solimoensis*, is a locative adjective referring to the drainage of the Solimões River, representing the headwaters of the Amazon River, and draining much of the area in which *Thecadactylus solimoensis* occurs.

Redefinition of *T. rapicauda* (Houttuyn)

The loss of the original holotype of *Thecadactylus rapicauda* (Hoogmoed, 1973) and the current description of *T. solimoensis*, rendering the genus polytypic, necessitates the designation of a new type series for *T. rapicauda* (ICZN, 1999: article 75), based on specimens from the likely original type locality (Hoogmoed, 1973). It is undisputed that the lost holotype of *T. rapicauda* originated from outside of the range of *T. solimoensis* (Hoogmoed, 1973; Avila-Pires, 1995). Published descriptions of *T. rapicauda* (Daudin, 1802; Beebe, 1944; Vanzolini, 1968; Hoogmoed, 1973; Schwartz & Henderson, 1991; Avila-Pires, 1995; Breuil, 2002; Russell & Bauer, 2002a) remain valid. Although individuals of this species may possess a postocular stripe, this is virtually never directed dorsally (see above). The distribution of *T. rapicauda* is also reduced in light of the description of a second species (see below).

Material examined: Neotype: RMNH-16267. Male, collected 4.xii.1955 by D. C. Geijskes from Republeik,

Surinam. Description: (Fig. 7B) 119 mm SVL, 73 mm TL, 37 mm HL, 24 mm HW, 4 mm IND; regenerated tail, only slightly broader than more proximal stump and regularly streaked; 4 nasal granules, dorsalmost enlarged; internasals with broad contact medially; 14 supralabials, 7 anterior to the eye; 13 infralabials; rostral partly divided; 10 spinose supraciliaries; postmentals elongate; 6 post-postmentals, medial one enlarged; 10 post-infralabials; dorsal forearm, tail base and ventral neck scales granular; hind limb web scales imbricate; 1 single-apexed, tuberculate cloacal spur; cloacal sacs absent; total manual lamellae on digits I, IV and V, 17, 23 and 19, respectively; total pedal lamellae on digits I, IV and V, 15, 24, 21, respectively; scansors on manual and pedal digits IV, 11 and 12, respectively; subdigital sulcus divides all lamellae on manual digit II, but only some on digit I; lateral stripe absent; dorsal colour and pattern light, mottled, with no diamonds; paravertebral spots absent; nuchal spot absent; postocular stripes project posterolaterally, but do not continue as a series of spots; 12 teeth occluded by rostral; 26 presacral, 2 cervical vertebrae without ribs; 23 ribs, 3 anterior to medial level of clavicles, 5 shortened; cloacal bones absent; paraphalanges visible in radiographs. Characters not included here, but included for the description of the holotype of *T. solimoensis*, represent data that could not be obtained from any *T. rapicauda* specimens.

Neoparatypes: RMNH-5651: male with regenerated tail from Paramaribo, Surinam; RMNH-16259: male with regenerated tail from Paramaribo, Surinam; RMNH-16279: female with regenerated tail from Republeik, Surinam: RMNH-16280: male with original tail from Republeik, Surinam; RMNH-26478: female with autotomized tail from Paramaribo, Surinam.

Referred specimens: All those listed in Appendix 1 and not assigned to *T. solimoensis*.

Distribution: The distribution of *Thecadactylus* to the exclusion of areas inhabited by *T. solimoensis*: Yucatan in Mexico, south to southern Colombia on both sides of the Andes, extending east in Venezuela, Guyana, Surinam, French Guyana, Brazilian Roraima, Brazilian Pará, and all of the Lesser Antilles to the exclusion of the Puerto Rican bank (but including Necker Island) and Barbados.

Dataset and analysis performance

The morphological data set represents the most extensive sampling of OTUs (localities) of the three sets considered. Hence, it held the greatest promise for revealing a detailed picture of which locality samples belonged to which clades. However, although 60 characters were included, a considerable number for an intraspecific morphological data set (for comparison see Zamudio & Greene, 1997; Puorto *et al*., 2001; Hall & Harvey, 2002), there is an almost equal number of OTUs. This low character-to-OTU ratio negatively impacted cladogram resolution (Hillis *et al*., 2003), translating to poor clade support. High levels of homoplasy further limited the utility of the morphological data set, probably due to local adaptation of a wide-ranging species to its surroundings (Schluter, 2000), suggesting a correlation between morphology and environmental context rather than with cladogenetic evolutionary history.

The morphometric data set was limited by both the number of OTUs and the characters included. Morphometrics have been considered useful for the identification of cryptic species (Puorto *et al*., 2001), but this was not the case here. OTU centroid overlap in morphospace defined by PCA was extensive (Fig. 4A). Consideration of pairwise distances within and between OTUs reinforced this point (Fig. 4B). Homoplasy was again high, limiting clade support and resolution. The morphometric data set appears to be reflective of highly conserved body proportions, which may be characteristic of geckos (Zaaf & Van Damme, 2001).

The molecular data set consisted of sequences for a fragment of the mitochondrial gene cyt *b*, sampled from a limited number of localities, but consisting of 584 characters, 270 of which were parsimony informative (Kronauer *et al*., 2005). As a result, this data set also represented the most robust data for the elucidation of well-supported clades. The non-recombinant and rapidly fixing nature of mtDNA (Avise *et al*., 1987; Hillis, 1987; Wiens & Penkrot, 2002) makes it particularly useful for detecting cryptic species that are poorly differentiated morphologically (Slade & Moritz, 1998). Congruence between molecular and morphological data sets suggests that the gene tree (Nichols, 2001) is reflective of the species tree. Both resolution and clade support were greatest for analyses of the molecular data set (Kronauer *et al*., 2005), which yielded the most robust hypotheses of relationships and were highly independent of the other two data sets (Kluge, 1989).

Combined, or total evidence, analysis is often hailed as an objective approach which places fewer assumptions on the data and tends to result in higher resolution of the resulting phylogenetic hypothesis (Kluge, 1989; Eernisse & Kluge, 1993; Kaiser, 1996; Murphy & Collier, 1996; Sorhannus, 2001). This, however, was not observed for *Thecadactylus*. Phylogenetic signal consistency index revealed a situation comparable with that evident in the molecular data set (Kronauer *et al*., 2005). However, both MP and BI analyses

resulted in cladograms with poor resolution, due to extensive amounts of missing data associated with disparate levels of OTU sampling for each source data set, as both resolution and clade support improved when only OTUs with the greatest amount of data present were included in the analysis (Fig. 6B). Total evidence and independent analyses were highly congruent, indicating the uncovering of a common historical pattern (Hillis, 1987). However, little added insight resulted from the total evidence approach, something also observed by Wiens & Penkrot (2002), but *contra* Sorhannus (2001).

Although the use of Bayesian inference in phylogeny reconstruction is not a new approach (Rannala & Yang, 1996) and is increasingly applied, the analysis of morphological data in such a way has only recently been suggested (Lewis, 2001a), and has only infrequently been applied (e.g. Snively, Russell & Powell, 2004; Vieira, Colli & Bao, 2005). Others who have applied the Markov model of Lewis (2001a) to morphological and total evidence data have, in general, noted the robustness of this approach. Cabrero-Sanudo & Zardoya (2004) found that Bayesian analysis of their total evidence data set resulted in a better resolved phylogeny than either data set individually. Nylander *et al*. (2004) noted that morphological characters tend to influence tree topology even when accounting for only 5% of the total data, when analysis is implemented using BI. Furthermore, BI topologies tend to be congruent with MP topologies when morphological data are analysed (Glenner *et al*., 2004; Vieira *et al*., 2005). These observations seem to validate the analysis of morphological characters using BI and the Markov model (Lewis, 2001a), and are in accordance with our observations. Because of the novelty of this approach, it seems prudent to continue to compare its results with those of tranditional MP analysis (Engstrom, Shaffer & McCord, 2004).

Systematics and biogeography of *Thecadactylus*

One of the basic questions addressed here is whether there are any consistently identifiable clades within *Thecadactylus*. A number of groupings were identified repeatedly throughout the analyses presented. Yucatán and the Belize/Guatemala OTU were clustered by all data sets except the morphometric, which did not include the latter locality. Morphological, molecular, and total evidence data sets also clustered Guyana with Yucatán + Belize/Guatemala, which clearly represents a geographically incoherent grouping.

The south-western Amazonian clade was consistenly recovered by analyses of all data sets. In the morphological data set this clade included Bolivia, Madre de Dios, Ucayali, Loreto, Iquitos, Peruvian Amazonas and Amazonian Ecuador (including Caqueta, Colombia). The molecular data set did not sample Ucayali, Iquitos or Peruvian Amazonas, but added Brazilian Amazonas and Brazilian Acre to the cluster (Kronauer *et al*., 2005). The total evidence data set included all of these OTUs in this clade (Figs 5, 6). Therefore, the evidence supports two identifiable evolutionary lineages: a south-western Amazonian lineage, recognized as *T. solimoensis*, and a cluster consisting of the remainder of *Thecadactylus*, recognized as *T. rapicauda*.

Relationships between the OTUs within these clades are poorly resolved. Although one explanation for this might be an inadequate data set that includes inappropriate characters, obscuring patterns of clustering, we posit that this is not the case. A wide geographical distribution and extensive morphological polytypy make phylogenetic reconstruction and species delimitation difficult (Morando *et al*., 2003). Wilson & Brown (1953) noted that widely distributed, highly variable species are difficult to subdivide because genetically independent morphological characters often exhibit geographically independent patterns of variation, character states recur multiple times in different portions of the range, and microgeographical races are often present. Systematic hypotheses in these situations are primarily dependent upon the characters that are considered, and are obscured as more characters are added (Wilson & Brown, 1953). All of these problems were observed with *Thecadactylus*. For example, specimens from St. Martin often have a highly unusual spotted pattern, while those from St. Lucia, Grenada and Guyana tend to be very small, with minimal patterning (our pers. observ.). Lack of resolution and poor clade support can be used as supportive evidence of a single species. Wiens & Penkrot (2002) noted that one would expect hierarchical patterns of relationships within a species to be obscured, poorly supported, and geographically discordant due to gene flow and character recombination between populations. This is exactly what is observed with *Thecadactylus*, with the exception of the two identified clades.

Despite poor phylogenetic resolution it is reasonable to argue that *Thecadactylus* arrived on the Lesser Antilles through dispersal. As a result of the volcanic (Rosen, 1976), Eocene (Hedges, Hass & Maxson, 1992) origin of these islands, it is universally accepted that they represent a separate biogeographical unit from the Greater Antilles (Rosen, 1976; Breuil & Masson, 1991) and that their fauna arose through dispersal, primarily from South America via ocean currents (Pregill & Olson, 1981; Hedges, 1996a,b,c). It is likely that *Thecadactylus* dispersed to these islands during the Quaternary (Hedges, 1996b). Late Pleistocene fos-

sils of *Thecadactylus* found in caves on Barbuda (Etheridge, 1964) are consistent with this hypothesis. A South American dispersal origin to the Lesser Antilles has also been advocated for the yellow warbler, *Denroica petechia* L. (Klein & Brown, 1994), *Sphaerodacytlus* geckos (King, 1962; Hass, 1991) and *Eleutherodactylus* frogs (Kaiser, Green & Schmid, 1994; Kaiser, 1996).

When identifiable distinct clades of *Thecadactylus* are considered, several other biogeographical scenarios enter into consideration. The northern Middle American clade, consisting of Yucatán and Belize/Guatemala, is also repeatedly identified, but its southern boundaries are not identifiable because of current sampling incompleteness. *Thecadactylus* belongs to the humid herpetofaunal assemblage in Middle America, and so may be limited to more mesic areas in the region (Wilson & McCranie, 1998). Also in this region, our data suggest continuity in the range of *T. rapicauda* between Yucatán localities and those further south (Russell & Bauer, 2002a), consistent with new locality data of Luja & Calderon-Mandujano (2005).

Mountains play a vicariant role in the distribution of *Thecadactylus solimoensis* and are a significant barrier to gene flow. The boundaries of this species are the Andes Mountains to the west, and the Colombian Cordillera Oriental to the north-west. The Andes as a barrier to gene flow is supported by the exclusion of the Pacific Ecuador OTU from *T. solimoensis* and its inclusion in *T. rapicauda*. Comparatively, the Andes have been implicated as a major vicariant agency for the viper *Lachesis muta* L. (Zamudio & Greene, 1997), the toad *Bufo marinus* L. (Slade & Moritz, 1998), lizards of the genus *Liolaemus* (Schulte *et al*., 2000), and a number of marsupial and rodent clades (da Silva & Patton, 1998).

The southern extent of *Thecadactylus solimoensis* is in Bolivia and Rondônia, at the southern extreme of the range of the genus (Fig. 1; Russell & Bauer, 2002a), correlating well with the area outside of the 'north-west arc' identified by Vanzolini (1968). By contrast, the eastern boundary of *T. solimoensis* is very uncertain. This is in part due to inadequate sampling within the central Amazon basin, and in part due to conflicting evidence from phylogenetic analyses. Morphological phylogenetic analyses did not group the Brazilian Amazonas OTU with *T. solimoensis*, restricting its range to extreme western Amazonia. By contrast, molecular analyses placed the Brazilian Amazonian locality within *T. solimoensis*, extending its eastern boundary as far east as the western border of Pará (Fig. 1). More credence is lent to the conclusions drawn from the molecular analyses because these were supported by more characters and by extremely robust clade support values (bootstrap values up to 100%, Pp up to 1.00). A similar western Amazonian area was identified for anurans (Ron, 2000) and lizards (Avila-Pires, 1995). Both of these areas correlate very closely with the range of *Thecadactylus solimoensis*. Furthermore, Avila-Pires's (1995) eastern boundary of this area was also at the Pará–Amazonas border. A western Amazonian area similar to the range of *T. solimoensis* has also been identified for primates (da Silva & Oren, 1996), but its western boundary is slightly further to the east, defined by the Rios Trombetas and Tapajós.

From the findings presented here, *Thecadacytlus* represents a widespread and highly variable taxon that exhibits low taxonomic diversity, but that consists of two species. This is similar to the situation seen in the pantropical sea urchin (Lessios *et al*., 1999), which also consists of relatively few species. However, unlike the urchin, *Thecadactylus* is much more variable, but this variation, although geographically correlated, is continuous across the landscape and has few discrete breaks. This is the situation described by Wilson & Brown (1953) as characteristic of widespread species.

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APPENDIX 1

Following is a list of all specimens examined (whether included in a data set or simply inspected) organized by locality and museum. Use of specimen is noted in parentheses: M – included in morphometric data set, L – included in morphological data set, S – examined, but not included in a data set. All abbreviations (museum acronyms) follow Leviton *et al*. (1985), except OMNH (Oklahoma Museum of Natural History). AMB refers to field collection number, specimens collected by the authors. Specimens included in the molecular data set are listed and detailed in Kronauer *et al*. (2005).

Anguilla: *Corito Bay:* CM-115506 (L); *North Hill Village:* CM-114761 (L); *Rendezvous Bay:* CM-114690 (S), CM-114691 (S); *Shoal Bay:* CM-122417 (S), CM-122416 (L), CM-122430 (L); *Sile Bay:* CM-115529 (S), CM-115530 (S); *South Hill Village:* USNM-236265 (L), USNM-236266 (L); *Other:* CM-115486 (S), MCZ-R-6065 (S).

Antigua: *The Farrington:* CM-115476 (S), CM-114747 (L), CM-115475 (L); *Mill Reef:* MCZ-R-75383 (L); *St. John's:* MCZ-R-28569 (L); *Other:* AMB-7090 (M,L), CAS-85167 (S), MCZ-R-15714 (S);.

Aruba: *Baranca Alto:* UMMZ-57173 (S); *Bubali:* ANSP-27758 (L), ANSP-27759 (L), ANSP-27760 (L), ANSP-27761 (L), ANSP-27762 (L), ANSP-27764 (L); *Perlieten Poseh:* UMMZ-57139 (L); *Rooi Hundoe:* UMMZ-57140 (S), UMMZ-57138 (L); *Santa Cruz:* MVZ-181626 (S); *W Punt:* UMMZ-57141 (S); *Other:* MVZ-181676 (S), MVZ-181677 (S).

Barbuda: MCZ-R-32234 (S), MCZ-R-13323 (L).

Belize: *Cayo:* CM-91010 (L), CM-91011 (L); *Toledo:* AMNH-R-125716 (L), USNM-319789 (L).

Bolivia: *Beni:* AMNH-R-101442 (M,L), USNM-280235 (M,L), USNM-280236 (M,L), USNM-280237 (M,L), USNM-280238 (M,L), USNM-280963 (M,L); *La Paz:* AMNH-R-22461 (L), AMNH-R-22505 (L); *Pando:* CAS-49888 (S); *Ribualti:* UMMZ-57701 (L).

Bonaire: *Antriol Village:* UMMZ-179308 (S); *Between Tanki Maraka and Porta Spaho:* UMMZ-57301 (S), UMMZ-57303 (S), UMMZ-57302 (L); *Fontein:* MVZ-181725 (S), MVZ-181750 (S); *Kralendijk:* CM-66336 (L), CM-66337 (L), CM-66338 (L), CM-66339 (L), CM-66340 (L), CM-66341 (L); *Santa Barbara:* UMMZ-57142 (L).

Brazil: *Amazonas:* AMNH-R-101935 (M,L), AMNH-R-101936 (M,L), MCZ-R-4744 (M,L), OMNH-37635 (S), OMNH-37636 (S); *Bahia:* UMMZ-143090 (S); *Pará:* KU-130197 (M,L), OMNH-36758 (S), OMNH-36751 (M,L), OMNH-36752 (M), OMNH-36753 (M,L), OMNH-36754 (M,L), OMNH-36755 (M,L), OMNH-36756 (M,L), OMNH-36757 (M,L), OMNH-36759 (M,L), OMNH-36760 (M,L), USNM-288852 (M,L), USNM-288853 (M,L), USNM-303476 (M,L); *Rondonia:* AMNH-R-130236 (L), AMNH-R-130237 (L), OMNH-37332 (L), OMNH-37333 (L), OMNH-37334 (L), OMNH-37335 (L), OMNH-37336 (L); *Roraima:* OMNH-36310 (L).

Colombia: *Atlantico:* AMNH-R-32660 (M,L), AMNH-R-32661 (L), AMNH-R-32664 (M,L), AMNH-R-32665 (M), USNM-117463 (M); USNM-117465 (M), USNM-117480 (M,L); *Boyaca:* MCZ-R-46444 (L); *Caqueta:* FMNH-69667 (L); *Choco:* AMNH-R-18303 (L), ANSP-25562 (L), FMNH-63819 (L); *Cundinamarca:* AMNH-R-140088 (L), AMNH-R-140089 (L), AMNH-R-140090 (L), AMNH-R-140091 (L), AMNH-R-140092 (L), USNM-154006 (L); *Guajira:* AMNH-R-109917 (S), AMNH-R-109914 (L), AMNH-R-109915 (L), AMNH-R-109916 (L); *Huila:* MVZ-42007 (S), MVZ-42008 (S); *New Grenada:* AMNH-R-17645 (L), AMNH-R-17646 (L), AMNH-R-17648 (L); *Sucre:* FMNH-165815 (S), FMNH-165170 (L), FMNH-165171 (L), FMNH-165172 (L), FMNH-165173 (L), FMNH-165174 (L), FMNH-165175 (L); *Tolima:* MCZ-R-19212 (L).

Costa Rica: *Puntarenas:* UMMZ-137540 (L), USNM-219546 (L).

Cuba: USNM-81921 (S), USNM-83456 (L).

Curacao: *Landhuis Knip:* UMMZ-57136 (L), UMMZ-57137 (L); *Willemstad:* CM-66345 (S), CM-66363 (S), CM-66342 (L), CM-66343 (L), CM-66344 (L), CM-66364 (L), CM-66365 (L), CM-66366 (L).

Dominica: *Cabrits:* MCZ-R-60816 (M,L), MCZ-R-60817 (M), MCZ-R-60818 (M,L), MCZ-R-60819 (M,L), USNM-154534 (M), USNM-154535 (M); *South central:* UMMZ-83324.1 (M,L), UMMZ-83324.2 (M,L), UMMZ-83324.3 (M), UMMZ-83324.4 (M,L), UMMZ-83324.5 (M,L), UMMZ-83325.1 (M,L), UMMZ-83325.2 (M,L), UMMZ-83325.3 (M,L), UMMZ-83325.4 (M,L), UMMZ-83325.5 (M,L); *St. George:* KU-229881 (M,L), KU-229882 (M,L), KU-229883 (M,L), KU-229884 (M,L), KU-229885 (M,L), KU-229886 (M,L).

Ecuador: *Esmeraldas:* MCZ-R-147200 (L), USNM-204292 (L), USNM-204293 (L); *Morona-Santiago:* AMNH-R-113678 (L), AMNH-R-113679 (L), AMNH-R-113680 (L), AMNH-R-113681 (L), AMNH-R-113682 (L); *Napo: Limoncocha:* MCZ-R-96053 (L), MCZ-R-96054 (L), MCZ-R-96055 (L), MCZ-R-156854 (L); *Napo-Pastaza:* CAS-15816 (S), CAS-15817 (S); *Pastaza:* USNM-204278 (S), USNM-204279 (S), USNM-204282 (S), USNM-234576 (S), USNM-204280 (L), USNM-204281 (L), USNM-204283 (L), USNM-204284 (L), USNM-204285 (L); *Pichincha:* CAS-13263 (S), USNM-204294 (L), USNM-285442 (L), USNM-285443 (L), USNM-285807 (L), USNM-285808 (L); *Sucumbios:* OMNH-36429 (S), OMNH-36432 (S), OMNH-36434 (S), OMNH-36435 (S), OMNH-36436 (S), OMNH-36437 (S), OMNH-36427 (L), OMNH-36428 (L), OMNH-36430 (L), OMNH-36433 (L), QCAZ-6691 (= OMNH-36431) (L).

French Guiana: *Cayenne:* USNM-287757 (S); *Inini:* MCZ-R-149502 (L), MCZ-R-149503 (L).

Grenada: *Bcausejour:* MCZ-R-86682 (L); *Green Island:* MCZ-R-79745 (L); *Point Saline:* MCZ-R-86683 (L), MCZ-R-86684 (L); *St. Andrew Parish:* USNM-67216 (L); *St. George:* MCZ-R-8101 (S), MCZ-R-8099 (L), MCZ-R-8100 (L); *Other:* MCZ-R-4512 (S).

Grenadines: *Carriacou Island:* USNM-79132 (L).

Guadeloupe: *La Desirade:* MNHN 1997.6135 (M,L), MNHN 1997.6136 (M,L); *Other:* MCZ-R-10365 (S), MCZ-R-10366 (S), MCZ-R-10367 (S), MCZ-R-10370 (S), MCZ-R-10371 (S), MCZ-R-10374 (S), MCZ-R-2166 (L), MCZ-R-10364 (L), MCZ-R-10368 (L), MCZ-R-10369 (L), MCZ-R-10372 (L), MCZ-R-10373 (L), USNM-11250 (S), USNM-11182.1 (L), USNM-11182.2 (L).

Guatemala: *Peten:* AMNH-R-140264 (L), FMNH-22212 (S), MCZ-R-24501 (L), MCZ-R-38663 (L), UMMZ-117872 (L), USNM-113035 (S), USNM-71411 (L), USNM-71412 (L), USNM-113036 (L), USNM-113037 (L).

Guyana: *Demerara:* AMB-7110 (S), AMB-7102 (M,L), AMB-7103 (M,L), AMB-7104 (M,L), AMB-7106 (M,L), AMB-7107 (L), USNM-561449 (L), USNM-561450 (M,L), USNM-561451 (L), USNM-561452 (M,L); *Dubulay Ranch:* AMNH-R-140956 (L), AMNH-R-140957 (L), AMNH-R-140958 (L); *Mazaruni-Potaro:* AMNH-R-137414 (M,L), AMNH-R-137415 (M,L), AMNH-R-137416 (M,L), AMNH-R-14110 (M,L), AMNH-R-21303 (M,L), AMNH-R-21304 (M,L), MCZ-R-81220 (M,L), MCZ-R-171650 (M,L).

Honduras: *Atlantida:* AMNH-R-70447 (L), FMNH-13005 (L); *Colon: Balfate:* AMNH-R-58618 (S), AMNH-R-58619 (S), AMNH-R-58666 (S), AMNH-R-58667 (S), AMNH-R-58616 (L), AMNH-R-58617 (L), AMNH-R-58620 (L), AMNH-R-58622 (L), AMNH-R-58623 (L).

Martinique: MNHN 2001.701 (S).

Mexico: *Jalisco: Guadelajara:* USNM-24916 (S), USNM-24917 (S); *Quintana Roo:* MVZ-148834 (S), MVZ-148835 (S); *Yucatan: Chichen Itza:* FMNH-49109 (M,L), FMNH-49110 (M,L), FMNH-49111 (M,L), FMNH-49112 (M,L), FMNH-49114 (M,L), FMNH-49115 (M,L), FMNH-49116 (M,L), FMNH-49117 (M,L), UMMZ-80810 (M), UMMZ-80811 (M,L), UMMZ-80812 (M,L), UMMZ-80813 (M,L), UMMZ-83282.1 (M), UMMZ-83282.2 (M,L), UMMZ-83283 (M), UMMZ-83284 (L), UMMZ-83927.1 (M,L), UMMZ-83927.2 (M).

Nicaragua: *Bonanza:* AMNH-R-75435 (S); *Rivas:* USNM-14821.1 (L); *San Juan del Norte:* USNM-15645 (L).

Panama: *Archipelago de las Perlas: Isla San Jose:* AMNH-R-115895 (M,L), USNM-120418 (M), USNM-120419 (M), USNM-120420 (M), USNM-120421 (M), USNM-120422 (M), USNM-120423 (M), USNM-120424 (M,L), USNM-120425 (M), USNM-120426 (M,L), USNM-120427 (M,L), USNM-120428 (M,L), USNM-120455 (M), USNM-120456 (M,L), USNM-120457 (M), USNM-120458 (M,L), USNM-120459 (M), USNM-120460 (M,L); *Barro Colorado Island:* AMNH-R-89871 (L), FMNH-123784 (L), FMNH-177232 (L), MCZ-R-18903 (L), MCZ-R-28197 (L), MCZ-R-31581 (L), UMMZ-64456 (L), USNM-203829 (L), USNM-203830 (L); *Bocas del Toro:* AMNH-R-119019 (M,L), FMNH-154461 (M), FMNH-154464 (M), KU-96489 (M,L), KU-96490 (M,L), USNM-148258 (M,L), USNM-150003 (M,L), USNM-338684 (M,L); *Darien:* AMNH-R-65480 (S), AMNH-R-37570 (L), FMNH-170083 (L), FMNH-170084 (L), FMNH-170121 (L), FMNH-170159 (L), UMMZ-124883 (L), UMMZ-124884 (L), USNM-141788 (S), USNM-140632 (L), USNM-140644 (L); *Taboga Island:* CAS-39517 (S), CAS-39518 (S), MCZ-R-9901 (S), MCZ-R-9903 (S), MCZ-R-9899 (L), MCZ-R-9900 (L), MCZ-R-9902 (L), MCZ-R-9904 (L), MCZ-R-9905 (L), UMMZ-181423 (L).

Peru: *Amazonas:* MVZ-163045 (S), MVZ-163046 (S), USNM-316689 (S), USNM-316688 (L), USNM-316690 (L), USNM-316691 (L); *Loreto:* AMNH-R-56412 (M,L), AMNH-R-57096 (M,L), AMNH-R-57104 (M,L), AMNH-R-57119 (M,L), AMNH-R-57125 (M,L), AMNH-R-77073 (M), CAS-7546 (S), CAS-7558 (S), CAS-8335 (S), CAS-8735 (S), FMNH-45449 (M,L), FMNH-109825 (M,L), KU-220485 (M,L), KU-222360 (M,L); *Madre de Dios:* FMNH-168128 (M,L), FMNH-228257 (M,L), KU-194933 (M,L), KU-204963 (M,L), KU-204964 (M,L), KU-204965 (M,L), KU-207765 (M,L), KU-209196 (M), KU-215009 (M,L), KU-220185 (M,L), KU-220186 (M,L), MVZ-173751 (S), MVZ-197119 (S), USNM-

222324 (M), USNM-247451 (M,L), USNM-269006 (M,L), USNM-333019 (M), USNM-342679 (M), USNM-342680 (M), USNM-345303 (M), USNM-345304 (M); *Ucayali:* CAS-93247 (S), CAS-95145 (S), FMNH-56102 (S), FMNH-45094 (L), FMNH-45095 (L), FMNH-45447 (L), FMNH-56101 (L), FMNH-56103 (L), FMNH-56104 (L), FMNH-56105 (L), FMNH-56106 (L), FMNH-56107 (L).

Saba: USNM-103981 (L), USNM-103982 (L), USNM-103983 (L).

Saint Barts: MNHN 1997.6092 (S), MNHN 1997.6093 (S).

Saint Lucia: *Maria Major:* USNM-561448 (M,L).

Saint Martin: MNHN 1997.6069 (M,L), MNHN 1997.6070 (M,L), MNHN 1997.6137 (M,L), MNHN 1997.6154 (M,L).

St. Croix: *Bethlehem:* AMNH-R-90488 (L); *Christiansted:* UMMZ-80572 (L), UMMZ-80573 (L); *Estate Mary's Fancy:* AMNH-R-99505 (L); *Fredericksted:* CM-1090 (S); *Mt. Victory Estate:* UMMZ-80781 (L); *Santa Cruz:* ANSP-7513 (S), ANSP-7514 (S), ANSP-7512 (L); *Sugar Central:* MCZ-R-42372 (L); *Other:* USNM-561446 (M,L), USNM-561447 (M,L), CAS-8767 (S), CM-18822 (L), CM-18823 (L), CM-18824 (L), CM-18825 (L); CM-18826 (L), CM-18827 (L), MCZ-R-74360 (L).

St. Thomas: ANSP-7515 (L).

Surinam: *Paramaribo:* AMNH-R-73844 (L), RMNH-5651, RMNH-16259, RMNH-26478; *Republeik:* RMNH-16267, RMNH-16279, RMNH-16280.

Tobago: *St. John:* USNM-227899 (S), USNM-227903 (S), USNM-227904 (S), USNM-227905 (S), USNM-227906 (S), USNM-192770 (L), USNM-195138 (L), USNM-227898 (L), USNM-227900 (L), USNM-227901 (L), USNM-227902 (L).

Trinidad: *Arima Valley:* AMNH-R-75824 (S), AMNH-R-85312 (S), UMMZ-155756 (L), UMMZ-155762 (L), UMMZ-155763 (L), UMMZ-155773 (L), UMMZ-155779 (L), USNM-166672 (L), USNM-166673 (L); *Caroni Parish:* MVZ-83760 (S); *St. George:* AMNH-R-137601 (S), AMNH-R-137602 (S), AMNH-R-137613 (S), CM-4848 (S), CM-6502 (S), CM-6538 (S), CM-4972 (L), CM-6492 (L), CM-6510 (L), CM-6523 (L), CM-6563 (L), CM-6590 (L).

Venezuela: *Amazonas:* AMNH-R-129246 (M,L), AMNH-R-133642 (M,L), USNM-162708 (M,L), USNM-162709 (M,L), USNM-162710 (M), USNM-162711 (M), USNM-216892 (M,L), USNM-216893 (M,L), USNM-216894 (M,L); *Falcon:* MCZ-R-48722 (L), MCZ-R-48900 (L), MCZ-R-49034 (L), USNM-216898 (L), USNM-216899 (L), USNM-216900 (L), USNM-216901 (L), USNM-216902 (L); *Margarita Island:* MCZ-R-8274 (L), MCZ-R-8275 (L), MCZ-R-8276 (L); *Miranda:* CAS-94657 (S), CAS-139916 (S); *Monagas:* AMNH-R-57350 (L), USNM-217263 (S); *Sucre:* CM-7926 (S), CM-7940 (S), CM-7877 (L), CM-7878 (L), CM-7879 (L), MCZ-R-50201 (L), MCZ-R-81219 (L), USNM-216903 (L), USNM-216904 (L); *Urama:* MVZ-110736 (S), USNM-162712 (L), USNM-162713 (L), USNM-162714 (L), USNM-162715 (L), USNM-162716 (L).

Outgroup specimens included

Aristelliger praesignis **(Jamaica): UMMZ:** 145847, 174683, 85878.1, 85879.1, 85879.2, 85880.1, 85880.2, 85880.3, 85880.4, 85880.5, 85880.6, 85880.7.

Blaesodactylus boivini **(Madagascar): FMNH:** 73067; **UMMZ:** 201502, 201503, 201505, 149852, 218648.

Bogertia lutzae **(Brazil): AMNH-R**: 65381, 74480; **MCZ-R:** 46190, 46191; **UMMZ:** 115644; USNM: 200658.

Gekko gecko **(Asia??): ANSP:** 27529, 27530, 27534, 27535, 27541, 27559, 27560; **(Philippines): CM:** 2422, 2429, 2432.

Hemidactylus mabouia **(Anguilla): CM:** 114694, 114695, 114697, 114698, 115496, 115510, 117926, 117927, 117932, 117945, 119265; **(Brazil):** 64468, 64469; **(Namibia):** 130239, 130242, 130243.

Homopholis fasciata **(Africa?): MCZ-R:** 93593, 96969, 96972.

Homopholis wahlbergi **(Africa?): FMNH:** 209457, 209458; **MCZ-R:** 12581, 14239, 41830, 41832, 41833, 67793; **UMMZ:** 227208, 227209; **USNM:** 159100; one specimen from the personal collection of PJB.

Phyllopezus pollicaris **(Bolivia): AMNH-R:** 141623, 141630, 141632, 141633, 141635, 141636; **(Brazil): UMMZ:** 103038, 103040, 209948; **(Paraguay): USNM:** 342013, 342014, 342015; **(South America?): MCZ-R:** 128448, 128449, 128450, 28632.

Pseudothecadactylus australis **(Australia): MCZ-R:** 35162; **UMMZ:** 127150.

Tarentola americana **(Cuba): MCZ-R:** 11871, 11873, 11875, 56373, 56376, 56377, 59320, 67917.

APPENDIX 2

Listing of all localities, sample sizes associated with each, and locality numbers, corresponding to those in Figure 2. Numbers in parentheses indicate sample sizes for the morphometric data set.

Locality	Code	*N*	Locality	Code	*N*	Locality	Code	*N*
Anguilla	49	8	Dominica	42	(22)	Peru		
Antigua	45	3 (1)	Cabrits	42a	3	Amazonas	17	3
						Loreto	15 + 16	(10)
Aruba	25	8	St. George	42b	6	Loreto: Iquitos	15	3
Barbuda	46	1	South Central	42c	9	Loreto: Other	16	6
Belize			Ecuador			Madre de Dios:	19	19
Cayo	2a	2	Esmeraldas	12a	3	Cuzco Amazonico	19a	7
Toledo	2b	2	Morona-Santiago	14e	5	Madre de Dios: Other	19b	5
Bolivia			Napo: Limoncocha	14b	4	Ucayali: Yarinacocha	18	9
Beni	20a	6 (6)	Pastaza	14d	5	Saba	47	3
Paz	20b	2	Pichincha	12b	5	St. Croix	51	16 (2)
Ribualti	20c	1	Sucumbios	14c	5	St. Lucia	41	1 (1)
Bonaire	27	8	French Guiana	31	2	St. Martin	48	4 (4)
Brazil			Grenada	40	8	St. Thomas	50	1
Amazonas	34	3 (3)	Guadeloupe			Surinam	30	1
Pará: Belém	37	1	La Désirade	43	2 (2)	Tobago		
Pará: Santárem	36	8 (13)	Other	44	8	St. John	39	6
Pará: Other	35	3	Guatemala			Trinidad		
Rondônia	20d	7	Peten	2c	8	Arima Valley	38a	7
Roraima	33	1	Guyana			St. George	38b	6
Colombia			Demerara	29b	9 (6)	Venezuela		
Atlantico: Caracolito	23b	1	Dubulay Ranch	29c	3	Amazonas	32	7 (9)
Atlantico: Sabanalarda	23a	3 (6)	Mazaruni Potaro	29a	8 (8)	Falcon	24a	8
Boyaca	13a	1	Honduras			Margarita Island	28a	3
Caqueta	14a	1	Atlantida	3a	2	Monagas	28c	1
Chocó	11	3	Colon: Belfate	3b	5	Sucre	28b	7
Cundinamarca	13b	6	Mexico			Urama	24b	5
Guajira: Merochon	23c	3	Yucatan: Chichen Itza	1	14 (18)			
Nueva Grenada	21	3	Nicaragua	4	2			
Sucré	22	6	Panamá					
Tolima	13c	1	Archip. de las Perlas	7	8 (18)			
Costa Rica			Bocas del Toro	8	6 (8)			
Puntarenas	5	2	Barro Colorado Island	9	9			
Cuba	52	1	Darien	10	9			
Curaçao	26	8	Taboga Island	6	6			

APPENDIX 3

List and descriptions for all morphometric and morphological characters included. All numbered characters were included in phylogenetic analyses.

1. Head length (HL): from the tip of the snout to the posterior margin of the occiput.
2. Head width (HW): measured as the widest point of the head in dorsal view, typically just anterior to the level of the ears.
3. Head depth (HD): measured as the distance from the ventral to the dorsal surface of the head at mid-eye level, as denoted by the pupil. Reliability of this measurement is increased by tightening the calipers in order to use the ventral edge of the mandible and the parietal to buttress the landmarks used.
4. Internasal distance (IND): measured anterodorsally by inserting the blades of the calipers into the left and right external nares to record the distance between them.
5. Eye to nostril distance (END): measured from the right dorsolateral aspect as the distance from the external naris to the anterior margin of the eye (not including the ocular flap of skin) as defined by the bone of the socket.
6. Interorbital distance (IOD): measured dorsally as the narrowest distance between the supraorbital ocular skin flaps, inclusive.

7. Orbital diameter (OD): measured from the right side as the maximal longitudinal length of the eyeball, as visible externally and exclusive of the ocular skin flaps. Ocular skin flaps are displaced during this measurement.
8. Ear to eye distance (EED): measured from the right side as the distance from the posterior margin of the eye (including ocular skin flap) to the anterior margin of the ear opening.

Two further cephalic morphometric characters have been calculated and reported in descriptions of *Thecadactylus* (Hoogmoed, 1973; Avila-Pires, 1995; Russell & Bauer, 2002a) and are included herein for their utility in making comparisons to these published sources. The first is the ratio of HL to HW, and the second the ratio of HW to HD. Both measures allow an evaluation of the relative gracility or robustness of the head. Although both are discussed in this review, they are not numbered as they are not included in subsequent analysis, because they are secondary characters and because of the unfavourable qualities of ratios from a statistical standpoint (Pimentel, 1979; Sokal & Rohlf, 1995).

9. Snout–vent length (SVL): measured from ventral aspect as the distance from the tip of the snout to the cloacal opening.
10. Axilla–groin length (AGL): measured ventrally, on the right side, as the distance from the axilla to the point at which the anterior margin of the hindlimb begins to protrude from the body. This represents a measure of body size that is independent of HL and the appendicular girdles, which can all confound body size due to sexual selection and locomotor demands, respectively (Moody, 1984; Powell & Russell, 1992).
11. Tail length (TL): measured ventrally as the distance from the cloacal opening to the tip of the tail. Only useful systematically when original tails are considered.
12. Upper arm length (FLL1): measured dorsolaterally as the distance from the ventral margin of the glenoid fossa to the proximal tip of the ulna (elbow). The ventral rim of the glenoid can be palpated in the shoulder as a pointy, osseous projection. The proximal tip of the ulna is also palpable as a sharp bony projection.
13. Forearm and manus length (FLL2): measured dorally with the fourth digit stretched straight between the examiner's fingers. The distance from the proximal tip of the ulna to the tip of the fourth digit.
14. Thigh length (HLL1): measured ventrally as the distance from the point at which the anterior margin of the leg begins to protrude from the body wall to the knee. The knee is the midpoint of the broad, hard articulation between the femur and tibia.
15. Crus length (HLL2): measured ventrally as the distance from the knee to the distal end of the astragalocalcanaeum at the distal end of the tibia and fibula (Romer, 1956: fig. 190E; Russell, 1975: fig. 1). The proximal margin of the zeugopodium is palpable and is characterized by a bony shelf proximal to the origin of the first digit.
16. Metatarsal length (HLL3a): calculated as pes length (HLL3) minus the length of the fourth digit (4TL – see below). HLL3 is measured ventrally as the distance from the distal end of the astragalocalcanaeum to the tip of the fourth digit. This calculation allows for the division of the hindlimb into four functional segments (Bergmann & Russell, 2002), and eliminates the redundancy of including HLL3 and 4TL.
17. Fourth hind toe length (4TL): measured ventrally as the distance from the point at which subdigital scales begin to enlarge transversely, to form lamellae, to the tip of the fourth digit, exclusive of the claw.
18. Fourth hind toe width (4TW): measured ventrally at the widest part of the subdigital adhesive pad.
19. First hind toe length (1TL): measured ventrally as the distance from the point at which subdigital scales begin to enlarge transversely, to form the lamellae, to the tip of the first digit, exclusive of the claw.
20. First hind toe width (1TW): measured ventrally at the widest part of the subdigital adhesive pad.
21. Web breadth (WB): measured ventrally, between the third and fourth digits, from the edge of the interdigital web to the point at which the web begins to thicken, becoming continuous with the main part of the pes.

All scale descriptions and nomenclature follow Peters (1964), unless otherwise noted.

22. Number of nasal granules (range: 2–6). The number of small, granular scales bordering the external naris. These form a curved line along the posterodorsal margin of the naris, from the first or second supralabial scale to the internasal scale.
23. Dorsal-most nasal granule small (approximately same size as others) (0); or greatly enlarged, at least twice the area of the other nasal granules (1).
24. Internasal scales medially abuttting squarely and in broad contact (0); abutting medially with a bevelled posteromedial corner and in reduced contact (1); or not touching and with granules between them (2).
25. Number of supralabial scales (7–14).

26. Number of supralabial scales anterior to anterior edge of orbit (3–9). Although not independent of character 25, the number of these scales is less variable than the total number of supralabials.
27. Number of infralabial scales (8–13).
28. Rostral scale completely undivided (0); partly divided, with a cleft always occurring at its posterior margin (1); or fully divided, forming two discrete scales (2).
29. Number of spinose supraciliaries (0–13).
30. Postmental scales elongate, clearly twice as long as wide (0); or relatively short, less than twice as long as wide (1).
31. Number of post-postmental scales (1–9).
32. Medial post-postmental scale enlarged relative to the scales posterior to it and the other post-postmentals (0); or of the same size (1).
33. Number of post-infralabial scales (4–11). This row of scales is medial to the infralabials.
34. Dorsal forearm scales, at the proximal end of the antebrachium, imbricate (0); or granular (1).
35. Dorsal hindlimb web scales, lining the dorsal surface of the interdigital web between digits III and IV on the hindlimb, imbricate (0); or granular (1).
36. Dorsal original tail scales, located mid-dorsally at the very base of the tail, present even after autotomy, imbricate (0); or granular (1).
37. Medial ventral neck scales in the gular region at the level of the jowls imbricate (0); or granular (1).
38. Number of cloacal spurs (0–3).
39. Cloacal spurs pointed and conical (0); or tuberculate, round and dome-shaped (1).
40. Cloacal spurs all with a single apex (0); or some/all of the cloacal spurs with a double apex (1).
41. Cloacal sacs present (0); or absent (1). Although in some species they are thought to be sexually dimorphic (absent in females), this is not the case in *Thecadactylus*, where they are variable in both sexes (Hoogmoed, 1973; our pers. observ.).
42. Base of the regenerated tail much broader, laterally, than more proximal original stump (0); only slightly broader (1); or not swollen at all and of equal diameter to the more proximal tail (2).
43. Lamellae on digit I of the manus (11–20).
44. Lamellae on digit IV of the manus (14–25).
45. Scansors on digit IV of the manus (9–14).
46. Basal lamellae on digit IV of the manus (5–12).
47. Lamellae on digit V of the manus (11–24).
48. Lamellae on digit I of the pes (10–22).
49. Lamellae on digit IV of the pes (15–26).
50. Scansors on digit IV of the pes (9–14).
51. Basal lamellae on digit IV of the pes (5–13).
52. Lamellae on V of the pes (12–24).
53. All (0); or some (1) of the lamellae on digit I of the manus divided (Fig. 2.4.b).
54. All (0); or some (1) of the lamellae on digit II of the manus divided.
55. Dorsum background colour light (0); or dark (1).
56. A thin, dark stripe running longitudinally along the lateral aspect of the body, from the axilla almost to the groin present (0); or absent (1).
57. Dorsal pattern mottled (0) or not (1).
58. Number of dorsal diamonds (0–6).
59. Number of paravertebral spots (0–6).
60. Distinct vertebral spot at the nape of neck absent (0); discrete (1); or forming a 'V' with paired spots anterior to it (2).
61. Postocular stripe dorsal and connecting mid-dorsally (0), dorsal but unconnecting (1), lateral (2), or absent (3). Due to close similarity of states 0 and 1, relative to the other states, transition between these states was assigned a cost of one, while all other transitions were assigned a cost of two. Although the institution of such a differential cost to state transitions was suggested by Maddison (1993), such an approach might still be viewed as somewhat arbitrary. Very few OTUs in this analysis had dorsally connecting postocular stripes, so the influence of this form of differential weighting would have minimal affect on the outcome of the analysis.
62. Number of caudal blotches (0–6).
63. Caudal blotches well defined (0), or reduced (1).
64. Caudal blotches diamond/triangular (0), pentagonal (1), or irregular (2).
65. Number of caudal bands (3–14), counting both darker and lighter bands on tail.
66. A light band at the tip of the original tail present (0), or absent (1).
67. Regenerated tail relatively unpatterned (0); irregularly banded with streaks (1); regularly streaked (2); or banded, looking much like an original (3).
68. Number of teeth subtended by the rostral scale (9–16).
69. Frontal bone single (0); or paired (1).
70. Anterolateral process of parietal bone swept back (0); or directed sharply anteriorly (1).
71. Centre of otic capsules project anterior to the occipital complex (0), or remain lateral to it (1).
72. Number of presacral vertebrae, including atlas and axis (24–27).
73. Number of vertebrae in cervical region without ribs (2–3).
74. Number of caudal vertebrae (25–34).
75. Total number of ribs (20–24).
76. Number of ribs anterior to or at the level of the medial end of the clavicles (0–3).
77. Number of short posterior ribs (5–7). The posterior-most ribs are more robust, shorter, less

curved, and lack the distal costal cartilage of the more anterior ribs.

78. Cloacal bones present (0); or absent (1) in males.
79. Cloacal bones present (0); or absent (1) in females. Cloacal bones are paired free-floating ossified elements of the tail base, whose presence is often sexually dimorphic, and are variable in the Gekkonidae (Peters, 1964: 271; Russell, 1977; Kluge, 1982).
80. Paraphalangeal elements visible in radiographs (0); or not (1) on any digit of the manus.
81. Paraphalangeal elements visible in radiographs (0); or not (1) on any digit of the pes. Paraphalangeal elements are paired cartilages (calcified or not) associated with intephalangeal joints (Wellborn, 1933) located on either side of the phalanges and are associated with the adhesive mechanism in many gekkonids (Russell & Bauer, 1988).

APPENDIX 4

Gap-weighted residual morphometric data set. Tail length (11) is excluded from the matrix because it was not included in phylogenetic analyses.

	1				5					10		13		15						21
AFR	0	G	V	0	0	0	0	J	K	S	6	U	R	L	B	V	0	4	0	0
ANT	8	V	G	6	O	A	1	0	R	V	4	F	A	E	0	P	M	L	G	S
BOL	A	A	6	H	P	K	4	G	N	C	C	D	A	C	G	C	N	I	M	U
BRA_A	C	A	8	D	V	A	8	V	I	I	6	6	m	6	B	8	I	B	J	U
BRA_P	F	5	3	F	M	I	J	4	K	L	E	B	L	E	C	E	O	D	O	T
COL	L	H	E	9	U	C	E	D	H	E	R	Q	U	P	E	J	I	K	I	Q
DOM	E	C	A	P	T	G	8	J	V	C	C	7	I	8	G	D	M	J	M	T
GUA	T	2	G	H	V	9	U	B	E	B	L	0	0	E	6	L	5	0	B	S
GUY_D	B	9	1	G	M	J	7	1	2	N	3	8	O	8	C	A	J	C	K	T
GUY_M	A	0	0	3	Q	A	5	5	5	D	8	7	5	A	0	9	C	B	E	T
MEX	D	F	E	8	O	B	A	C	B	D	L	F	J	O	D	6	G	7	F	T
PAN_A	9	4	4	5	J	B	K	0	I	G	N	I	I	J	H	C	Q	D	M	V
PAN_B	B	A	2	G	N	F	8	D	L	B	R	U	D	C	I	Q	M	H	N	V
PER_L	L	A	C	O	N	I	A	G	M	K	D	H	D	A	K	E	U	K	I	U
PER_M	6	8	2	L	F	K	9	D	S	M	A	8	H	4	L	D	O	I	N	T
SCR	A	V	J	J	L	R	D	A	T	O	1	9	J	0	E	S	E	G	R	T
SLU	3	L	B	O	J	V	I	B	0	m	0	E	V	F	V	L	V	V	Q	T
SMA	V	P	P	V	M	U	V	D	9	0	V	V	K	V	G	G	R	J	V	S
VEN	7	0	3	B	R	9	C	6	9	G	N	8	L	K	9	0	F	B	D	P
END																				

APPENDIX 5

Majority and mode coded morphological data set.

```
                          22      30          40          50          60          70          80
ANG                       220211072624000220021985 47b85382002000020XX02060002 2?2120?20
ANT                       300322152524000222001ba73bga75b2002200030XX?2?620220?3200?00
ARU                       301312150313220010021985 38aa6272002200030XX02040002212122200
BAR                       200110172301000222022ab65bga73c2002200030XX0?29??????????XX??
BELGUT                    200412172213200010000775279862720022700 20XX72160012 2?2310000
BOL                       101212160104200220000b9649ea63b200225X01401a1060002212100220
PERMD                     111212182203100220020a9449ea74a200025421501920601021222002 22
BON                       101102160204200012022853278752621022000?0XX?2062002 0?210?2?2
BRAMZ                     300312150304200212020ba64agb66b20022?00?41?40160012212222?212
BRAPAB                    200442260323202012220b954bfc66b200200002?01??2600222?2220?00
BRAPAO                    220322172325200010000b963bec75b0002207023006 2?60022202101222
BRPAS                     220423160426200010020ba65cfd76c2022260022025016 0002202110200
BRROR                     200312150005200010020aa64bec849200227002?????170000 2?0102?00
COLCHO                    2014221b210200001022?cc76ddd76d2022200020XX90?6???2212?0?220
COLNGR                    301524192404022010000ab65adb6592002200030XX0207??????????XX??
COLSUC                    101212052223010011222985 38d9638200220002?02b206??022?20???20
COLA                      201413142104020010020785 39d8548200206002022021 40?12202012211
COLM                      220322161203000010020a954beb73a0002270020XX6216????????????
COSPUN                    120422160325200010020 9b65adc75b10121?00?0XX5??5202222?2210211
CUB                       100421170205000010 20?aa64aaa6482002250020XX80???????????XX??
CUR                       201111050203222220010886 37c96382002200030XX0207000 22?2222?20
DOMI                      220213172205102112001db659hd76a2002000020XX92270002242120222
ECUA                      2022221?2114200210000a964aeb75a200025001401000600002212112200
ECUP                      211422192204100010021ca64bed76d200226002022020602222?2200?20
FGU                       201321160214200111 01?99548bb65a210200?0231?80?6??????????XX??
GRE                       000223160203000012001664269752620020000 20XX??16??????????XX??
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GUA                       210322180325000012001cb66bec66b2022200020XX022702222?2122?22
GUYA                      200323162215200110000875 28b86382002200020XX00060002212220200
HOND                      200422152224000020000975 28ba6492002270 02?????16????????????
MEXYUC                    200322052106220030000875 37a963720022660 20XX71060022202120100
NIC                       200424180202000021 11?bb65acc75d21022?0020XX80?6??????????XX??
PANAPS                    200321192105222102 21ba649cb65b2002100020XX90150002232211222
PANBDT                    200412170223200111020cc65cdd76b200220522?2280?60022282221200
PANCZB                    200222162323000010 2218a649eb64b2002270020XX92160012202211201
PANDAR                    200322180223000010221bb64aec75a2002200020XX0?1620222?2200?00
PANTAB                    220311171123000011020aa52ac96492002000020XX70?7?0?22?2102??2
PERAMZ                    102313192326200020000aa64bda64a2002200005010206??????????XX??
PERLOI                    201312162105000220000a9639fb65b2000260?1001??060?032?3120222
PERLOO                    102312162203000210001aa639da64b20002000?40??2060122212201220
PERUCY                    201214162003000220001996 49da64a000224410501?2060002 2?212?200
SAB                       220213162303000032021b9638a97382002000020XX0?06??????????XX??
SCR                       220213172423000012001bb65afc85b2002200020XX91?600222?2100200
SLU                       100210152302200212001994 57c9637200220003?????0620222?3220?00
SMA                       220002152425220010220a9549c96392002200030XX?2060?12232121?11
STO                       220215082306000012001ba55bfc66a2002200030XX??2602220?2220?22
SUR                       2005220d01052222102 00a9547ca64a200226012?????16??????????XX??
TOB                       200322170223222010000685 29a86380002200020XX0?16??????????XX??
TRIN                      200313162323000010001785 38a96480002200020XX?0?60?2220222?222
VENAMZ                    221323172204200012020995 5beb74b2002260020XX72060002212201210
VENE                      201212170423202010120985 38aa6382002260 02?22a206????????????
VENW                      200322160324000010221985 38b96380000000020XXe2060012 2?222??2
PHYLLOP                   0211101921020X00300020100021101220220002 0XX02040222?2121222
HWAHL                     1024220523130X00300026403394133220220003 0XXc2020014 2?3221222
HFASC                     0023210021200X22300024303365052222220003 0XX9201????????????
BBOIV                     3025330604230X004100278357a62362202000030XX02021002 2?2122222
GEKKO                     2225351421030X2220002a9268db36822020000 30XXh2010222292102222
BOGERTIA                  0012110722050X010XX023001100100220200002 0XX0?0002022?2221?22
END
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