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A New Genus of Miniaturized and Pug-Nosed Gecko from South America (Sphaerodactylidae: Gekkota)

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Abstract

Sphaerodactyl geckos comprise five genera distributed across Central and South America and the Caribbean. We estimated phylogenetic relationships among sphaerodactyl genera using both separate and combined analyses of seven nuclear genes. Relationships among genera were incongruent at different loci and phylogenies were characterized by short, in some cases zero-length, internal branches and poor phylogenetic support at most nodes. We recovered a polyphyletic *Coleodactylus*, with *Coleodactylus amazonicus* being deeply divergent from the remaining *Coleodactylus* species sampled. The *C. amazonicus* lineage possessed unique codon deletions in the genes $PTPN_{12}$ and *RBMX* while the remaining *Coleodactylus* species had unique codon deletions in RAG_1. Topology tests could not reject a monophyletic *Coleodactylus*, but we show that short internal branch lengths decreased the accuracy of topology tests because there were not enough data along these short branches to support one phylogenetic hypothesis over another. Morphological data corroborated results of the molecular phylogeny, with *Coleodactylus* exhibiting substantial morphological heterogeneity. We identified a suite of unique craniofacial features that differentiate *C. amazonicus* not only from other *Coleodactylus* species, but also from all other geckos. We describe this novel sphaerodactyl lineage as a new genus, ***Chatogekko*** **gen. nov.** We present a detailed osteology of *Chatogekko*, characterizing osteological correlates of miniaturization that provide a framework for future studies in sphaerodactyl systematics and biology.

Keywords:

Amazon, Chatogekko gen. nov., Coleodactylus, lizard, morphology, osteology, phylogeny, polytomy, Squamata

INTRODUCTION

Sphaerodactyl geckos (Sphaerodactylini: Sphaerodactylidae) are a species-rich group of Neotropical lizards. They comprise more than 10% of gecko species with more than 150 described species in five genera: *Coleodactylus*, *Lepidoblepharis*, *Gonatodes*, *Pseudogonatodes*, and *Sphaerodactylus*(Kluge, 1995; 2001; Gamble *et al*., 2008a; Uetz, 2010). Sphaerodactyl geckos are distributed across Central and South America and the Caribbean, including several Pacific continental and oceanic islands, e.g. Gorgona, Cocos (Vanzolini, 1968a; Harris, 1982; Harris & Kluge, 1984; Kluge, 1995). Most sphaerodactyl gecko species are active during the day and the clade is thought to be secondarily diurnal, having evolved from a nocturnal ancestor (Werner, 1969; Underwood, 1970; Kluge, 1995; Röll & Henkel, 2002). They are generally small; some *Sphaerodactylus* species are among the smallest known amniotes, averaging only 16 mm snout–vent length (SVL) (Thomas, 1965; MacLean, 1985; Hedges & Thomas, 2001), and the largest forms do not exceed 65 mm SVL (Rivas & Schargel, 2008).

The genus *Coleodactylus* is distributed in north-eastern South America (Kluge, 1995) and consists of five described species: *C. amazonicus*(Andersson, 1918), *C. brachystoma*(Amaral, 1935), *C. meridionalis*(Boulenger, 1888), *C. natalensis*Freire, 1999, and *C. septentrionalis*Vanzolini, 1980. *Coleodactylus* has historically been defined by the structure of the ungual sheath, the scales covering the claw, being composed of five asymmetrical scales (Parker, 1926; Vanzolini, 1957; Kluge, 1995). *Coleodactylus amazonicus* differs from its congeners in having an ungual sheath possessing only four asymmetrical scales, a reduction caused by the loss of the medial-most dorsal scale (Andersson, 1918; Parker, 1926; Vanzolini, 1957; Avila-Pires, 1995). *Coleodactylus amazonicus* also has keeled dorsal scales, while all other members of the genus have smooth scales (Vanzolini, 1957; Avila-Pires, 1995). These morphological differences cast doubt on the diagnostic reliability of the ungual sheath and other characters for the genus and/or on the allocation of *C. amazonicus* to *Coleodactylus*.

Molecular data mirror the morphological differences among *Coleodactylus* species. Recent molecular phylogenies recovered two deeply divergent lineages in *Coleodactylus*, with one clade consisting of *C. amazonicus* and the other made up of the remaining *Coleodactylus* species, the '*C. meridionalis* group' (Geurgas, Rodrigues & Moritz, 2008; Geurgas & Rodrigues, 2010; Gamble *et al*., 2011). These results were not translated into a revised taxonomy however because of poor nodal support, e.g. bootstrap values and Bayesian posterior probabilities, for these relationships from the molecular data. Additionally, topology tests that constrained a monophyletic *Coleodactylus sensu lato*(*s.l.*) failed to reject the hypothesis that *C. amazonicus* forms a clade with the remaining *Coleodactylus* species (Geurgas *et al*., 2008; Gamble *et al*., 2011). Non-tree-based molecular evidence supports the distinction between *C. amazonicus* and the remaining *Coleodactylus* species. Two separate deletions of 18 and 6 bp in the *RAG_1* gene occur in species of the *C. meridionalis* group, but not in *C. amazonicus*(Gamble *et al*., 2008a, 2011; Geurgas & Rodrigues, 2010). Rare genomic events such as codon deletions and insertions (indels) are relatively homoplasy-free characters and can provide strong evidence of evolutionary history (van Dijk *et al*., 1999; Rokas & Holland, 2000; Simmons, Ochoterena & Carr, 2001).

The sum of available data calls into question the monophyly of *Coleodactylus. Coleodactylus amazonicus* is morphologically distinct from the remaining *Coleodactylus* species. Molecular data present a mixed picture of *Coleodactylus* relationships and sphaerodactyl phylogeny as a whole but, like the morphological data, cast doubt on *Coleodactylus* monophyly. We gathered new molecular and morphological data to address these issues. Our objectives were to: test the monophyly of *Coleodactylus* using a multigene molecular dataset and specifically address the failure of previous topology tests to support two distinct *Coleodactylus* lineages; review the morphology of *C. amazonicus* as a means to diagnose deeply divergent clades within *Coleodactylus s.l.*; and characterize osteological correlates of miniaturization in *Coleodactylus s.l.*

MATERIAL AND METHODS

TAXON SAMPLING AND MOLECULAR DATA

We assembled a nuclear gene dataset that included multiple species from each of the currently recognized genera of the New World Sphaerodactylini: *Coleodactylus* *s.l.*, *Gonatodes*, *Lepidoblepharis*, *Pseudogonatodes*, and *Sphaerodactylus*. We included several Old World members of Sphaerodactylidae as outgroups, including *Saurodactylus brosseti*, *Pristurus carteri*, and two species of *Teratoscincus*(i.e. *T. microlepis* and *T. przewalskii*). Phylogenies were rooted with the gekkonid *Hemidactylus platyurus*. Locality data and GenBank accession numbers for sampled taxa are listed in Table S2 of the Supporting Information.

We extracted genomic DNA from tissues using the DNeasy Blood and Tissue kit (Qiagen, Valencia, CA, USA) and used PCR to amplify gene fragments of seven nuclear loci for sequencing. Six loci were protein-coding regions: recombination-activating gene 1 (*RAG_1*); recombination-activating gene 2 (*RAG2*); oocyte-maturation factor MOS (*C-MOS*); acetylcholinergic receptor M4 (*ACM4* or *CHRM4*); phosducin (*PDC*); and protein tyrosine phosphatase, non-receptor type 12 (*$PTPN_{12}$*). The seventh locus included intron 8 (in *Gallus*) and flanking exon regions of RNA binding motif protein, X-linked (*RBMX*). Primers are listed in Table S1 of the Supporting Information. We purified PCR products using Exonuclease I and Shrimp Alkaline Phosphatase (Hanke & Wink, 1994). Big Dye sequencing was conducted at the BioMedical Genomics Center, University of Minnesota. Sequences were assembled and checked for accuracy using Sequencher 4.8 (Gene Codes, Ann Arbor, MI, USA). We translated protein-coding genes to amino acids using MacClade 4.08 (Maddison & Maddison, 1992) to confirm codon alignment and gap placement. We aligned *RBMX* sequences initially using T-Coffee (Notredame, Higgins & Heringa, 2000) and subsequently fine-tuned the alignment by hand.

Phylogenetic analyses

We conducted several phylogenetic analyses of the nuclear dataset. The seven loci were concatenated to conduct partitioned maximum likelihood (ML) analysis. We also analysed each locus separately. All ML analyses were conducted using RAxML 7.2.6 (Stamatakis, 2006). The concatenated ML analysis consisted of 19 partitions, with data partitioned by gene and by codon, except the intron *RBMX*, which consisted of a single partition. ML analyses of individual protein-coding loci also partitioned data by codon. All ML partitions utilized the GTR + Gamma model of sequence evolution and nodal support was estimated with 1000 bootstrap replicates (Felsenstein, 1985).

We conducted Bayesian analyses of the nuclear dataset using MrBayes 3.1.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003). All analyses used a neighbour-joining tree as a starting topology. Analyses of the individual genes involved two independent runs, each consisting of four parallel Markov chain Monte Carlo (MCMC) chains per run for five million generations and sampled every 1000 generations. Each Bayesian analysis of the individual genes utilized a model of molecular evolution as determined by Akaike's information criterion (AIC) in jModeltest (Posada, 2008). Analyses of the concatenated dataset partitioned data by codon with a separate partition for *RBMX*. Each partition utilized a model of molecular evolution as determined by AIC with model parameters estimated independently using the unlink option. The concatenated analysis involved two independent runs, each consisting of six parallel MCMC chains per run for ten million generations and sampled every 1000 generations. We assessed convergence and stationarity in all Bayesian analyses by plotting likelihood values in Tracer 1.5 (Rambaut & Drummond, 2007) as well as plotting split frequencies between independent runs using AWTY (Nylander *et al.*, 2008).

Poor phylogenetic resolution among sphaerodactyl genera in the concatenated analyses and incongruence among individual gene trees (see Results) motivated us to explore additional means of estimating phylogenetic relationships that could incorporate the sometimes diverse histories of individual genes. The probability of incomplete lineage sorting is increased when there are short internal branches (Maddison, 1997; Rosenberg & Tao, 2008), so we used two methods to estimate species trees that can accommodate individual gene genealogies. The first method, MDC (minimized deep coalescence), used individual gene trees to find a species tree that minimized the number of deep coalescent events across all loci (Maddison, 1997; Maddison & Knowles, 2006). The second method, BCA (Bayesian concordance analysis), estimated the species tree possessed by the plurality of clades recovered from individual loci, the concordance tree, and also estimated the proportion of loci that shared a specific clade with the concordance tree, the concordance factor (Ane *et al*., 2007; Baum, 2007).

We estimated the MDC tree using Mesquite 2.73 (Maddison & Maddison, 2008). This method required that 'species' be identified a priori and that individuals or taxa from the analyses of separate loci be assigned to each of these 'species'. Because we were interested in relationships among sphaerodactyl genera, we treated genera as 'species' in the MDC analysis. We accommodated phylogenetic uncertainty associated with the reconstruction of the individual gene trees using the Augist Mesquite module (Oliver, 2008). We estimated 1000 MDC trees with each search randomly sampling from the posterior distribution of trees from the Bayesian analyses of each of the nuclear loci. We used the subtree pruning and regrafting heuristic search algorithm with a maximum of 100 equally parsimonious trees saved at each search. Tree weights were stored for each search in the event multiple equally parsimonious MDC trees were found. The MDC species tree was calculated as a 50% majority-rule consensus tree with bipartition frequencies providing a measure of nodal support.

We estimated the BCA tree using BUCKy 1.4.0 (Ane *et al*., 2007). We conducted three separate analyses, each with a different a priori discordance level among gene trees, which was controlled by the variable α (Ane *et al*., 2007). Setting α = 0, for example, imposes a single species tree on all of the loci, while at the other extreme setting α = ∞ forces each locus to have its own independent history. We used an interactive web-based tool (http://www.stat.wisc.edu/~ane/bucky/prior.html) to calculate α values for our data. Each value for α placed a different prior on the number of possible species trees: α = 0.1 placed a high prior on one distinct tree; α = 1.0 placed a high prior on 2–3 species trees; and α = 10 placed a high prior on 5–6 species trees. All BUCKy analyses were run for 10 000 000 generations following a 10% burn-in.

HYPOTHESIS TESTING

We tested the monophyly of *Coleodactylus s.l*. using two different methods. We implemented the likelihood-based Shimodaira–Hasegawa (SH) test (Shimodaira & Hasegawa, 1999), which compared the constrained topology, a monophyletic *Coleodactylus s.l.*, with the unconstrained ML tree. Per-site log likelihoods were estimated in RAxML 7.2.6 (Stamatakis, 2006) and *P*-values were calculated using CONSEL (Shimodaira & Hasegawa, 2001). We also tested alternative phylogenetic hypotheses in a Bayesian framework. We used the filter option in PAUP* 4.0b10 (Swofford, 2002) to calculate the posterior probability of a monophyletic *Coleodactylus s.l*. in the posterior distribution of trees from the MrBayes analyses. We tested the monophyly of *Coleodactylus s.l*. using the concatenated nuclear gene dataset and each locus separately.

Short internal branches connected the six sphaerodactyl genera in both the concatenated trees as well as individual gene trees (see Results). These short internal branches not only increased the likelihood of incomplete lineage sorting, as mentioned above, but the limited number of character changes along these extremely short branches could make it difficult to adequately compare alternative hypotheses using the SH test. Some of these internal branches were so short as to have effectively zero branch length. These phenomena could explain why previous attempts to test *Coleodactylus* monophyly failed to adequately distinguish among competing hypotheses (Geurgas *et al*., 2008; Gamble *et al*., 2011). We examined our ML trees for the presence of zero-length branches using a likelihood ratio test with the 'describe trees' function in PAUP* 4.0b10 (Swofford, 2002). Briefly, the likelihood of the best tree was compared with the likelihood of the same tree but with a single branch collapsed to zero using the likelihood ratio test. Each of the four branches connecting the six sphaerodactyl genera was sequentially tested in this manner. A significant result meant the branch length was significantly different from zero. Significance levels were Bonferroni-corrected for the number of intergeneric branches.

MORPHOLOGICAL DATA

We examined both internal and external morphological characters from specimens of several species of Sphaerodactylidae, including exemplars from each of the currently recognized sphaerodactyl genera, to assess the monophyly of *Coleodactylus s.l.*(see Supporting Information). We also examined *C. amazonicus* specimens from several localities across its distributional range. We viewed osteological characters using a variation of a common clearing and double staining technique (Hanken & Wassersug, 1981). This method is especially useful for small animals in which dry skeletal preparation techniques are not suitable due to the potential risk of damage by the insects used to prepare them or to distortion caused by the drying and shrinkage of unossified portions of the skeleton. We modified the protocol in that we did not remove the integument from specimens, and used KOH only as a clearing reagent, without exposing specimens to enzymatic solutions of trypsin or pancreatin. Specimens were observed under a Leica MS6 dissecting microscope. Illustrations were traced with Adobe Illustrator CS3 13.0.2 directly over a series of digital photographs taken with a Nikon Coolpix 995 camera (3.1 Megapixels, 3× Optical Zoom) at different magnifications. Images were complemented with drawings made with a camera lucida.

RESULTS

TAXON SAMPLING AND MOLECULAR DATA

The nuclear gene dataset consisted of 4116 aligned base pairs from seven loci for 33 gecko taxa (Table 1). Sequence alignment was unambiguous for protein-coding regions, but several insertion/deletions (indels) were detected in five of the genes (Table 1, Fig. 1). Indels in RAG_1, *C-MOS*, and *ACM4* have been commented on previously (Gamble *et al*., 2008a, c; Geurgas *et al*., 2008). Both *RBMX* and $PTPN_{12}$ had single codon deletions in *C. amazonicus* samples. The *RBMX* deletion occurred in the region analogous to exon 8 in chicken (*Gallus*).

Table 1 Details of the seven nuclear loci used in phylogenetic analyses, including the aligned length of sequences, the number of variable sites, and the number of parsimony-informative (PI) sites. The number of unique indels in protein-coding regions in each locus is indicated, as is the taxonomic distribution of each indel. Some indels occurred only in a subsample of the sampled species within a genus

Locus	Aligned length (bp)	Variable sites	PI sites	Number of indels in coding regions
ACM4	447	150	94	1: within *Gonatodes*
CMOS	384	157	97	2: within *Gonatodes* and within *Coleodactylus*
RBMX	632	202	119	1: *Chatogekko*
PDC	400	143	98	n/a
$PTPN_{12}$	1152	482	288	1: *Chatogekko*
RAG_1	1095	533	344	4: *Coleodactylus*(2), within *Coleodactylus*, and *Pristurus*
RAG2	366	166	108	n/a

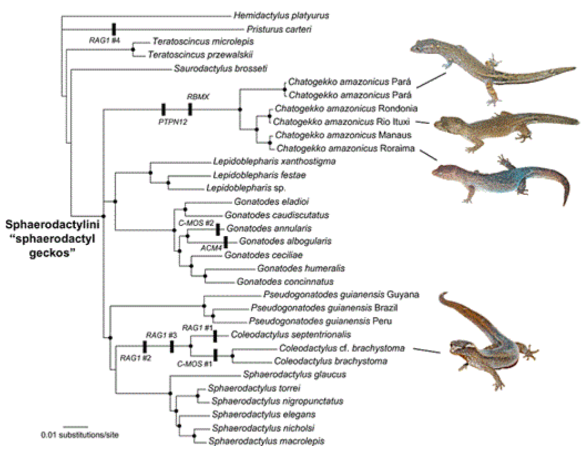

Figure 1 Bayesian phylogeny of sphaerodactyl genera from the concatenated nuclear gene data. Nodes with black circles possess posterior probabilities >0.95. Unique indels from protein-coding regions are indicated along with the gene name. Both *RAG_1* and *C-MOS* possessed multiple unique indels and each is numbered sequentially starting with the most 5′ indel and moving in the 3′ direction. Photos by L. J. Vitt, T. Gamble, and M. Hoogmoed.

PHYLOGENETIC ANALYSES

ML and Bayesian analyses of the concatenated nuclear gene dataset were largely congruent (Fig. 1). Relationships among the sphaerodactylid outgroups were inconsistent and generally poorly supported. Several clades received high levels of support in both analyses, including: a clade consisting of *Gonatodes*+ *Lepidoblepharis*; a clade consisting of *Coleodactylus sensu stricto*(*s.s.*) + *Pseudogonatodes*+*Sphaerodactylus*; and Sphaerodactylini. Generic-level sphaerodactyl clades were all well supported with the exception of *Coleodactylus s.l.*, which was polyphyletic with regards to other sphaerodactyl genera; for example, *C. amazonicus* did not form a clade with the remaining sampled *Coleodactylus* species. We recovered three clades within *C. amazonicus*:

one clade consisted of individuals from eastern Amazon (Pará); the second clade consisted of individuals from south-western Amazon (Rondônia and Rio Ituxi, Amazonas); and the third clade consisted of individuals from central and northern Amazon (near Manaus, Amazonas, and Roraima). ML branch lengths among these *C. amazonicus* clades were equivalent to species-level divergences within other sphaerodactyl genera and between the species *Teratoscincus microlepis* and *T. przewalskii*(Fig. 1).

Topologies among individual gene trees were largely incongruent (Fig. 2). The only well-supported nodes in all of the analyses were nodes subtending each of the sphaerodactyl genera, although, as with the concatenated analyses, *Coleodactylus s.l.* was polyphyletic in all loci with *C. amazonicus* samples forming their own clade distinct from other sampled *Coleodactylus* species.

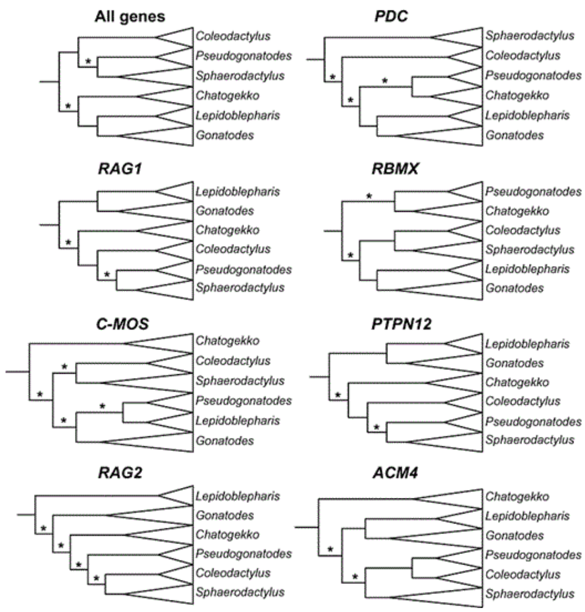

Figure 2 Cladograms for each nuclear locus and the concatenated nuclear gene dataset illustrating relationships among sphaerodactyl genera estimated using maximum likelihood. Branches with lengths not significantly different from zero are indicated with an asterisk.

The MDC consensus tree (Fig. 3) was largely congruent with the concatenated ML and Bayesian trees and recovered a well-supported Sphaerodactylini consisting of three lineages: a *Lepidoblepharis*+ *Gonatodes* clade; a *Coleodactylus s.s.*+ *Pseudogonatodes*+*Sphaerodactylus* clade; and a *C. amazonicus* clade. BCA with varying α levels produced identical concordance trees and concordance factors. The BCA tree (Fig. 3) was similar to the MDC consensus tree. Although it is difficult to assess what constitutes a significant concordance factor (Baum, 2007) the Sphaerodactylini clade and *Lepidoblepharis*+*Gonatodes* clade were the only relationships that received concordance factors exceeding 0.50.

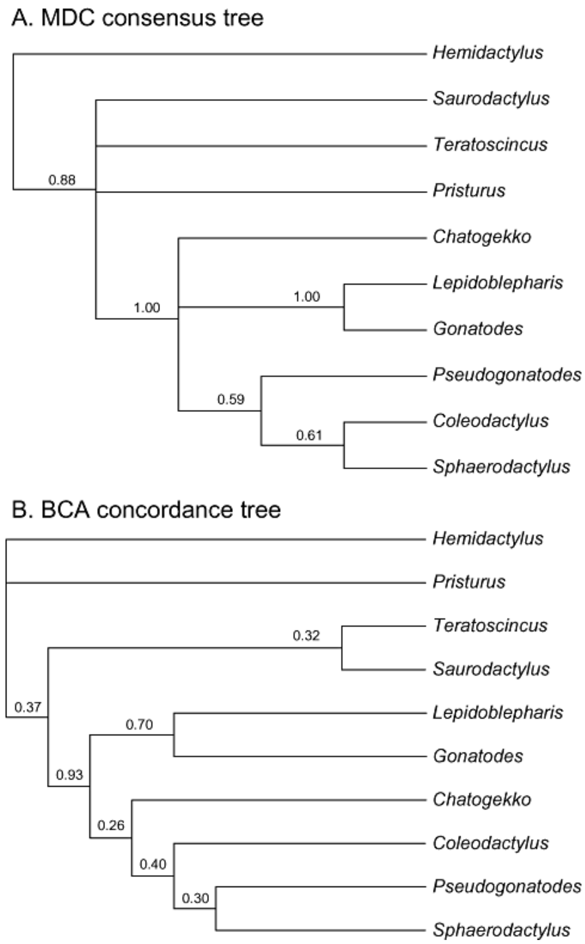

Figure 3 Phylogenetic relationships among sphaerodactyl genera estimated using (A) MDC (minimization of deep coalescence events) and (B) BCA (Bayesian concordance analysis). Node values on the MDC tree are bipartition frequencies from 1000 replicate analyses randomly sampled from the Bayesian posterior distributions of the individual gene trees. Node values on the BCA tree are posterior mean concordance factors.

HYPOTHESIS TESTING

Results of the SH tests that constrained *Coleodactylus s.l*. as monophyletic were not significant (Table 2). The Bayesian posterior probability of a monophyletic *Coleodactylus s.l*. was zero for the concatenated data and low, but not significant, for most of the individual gene analyses (Table 2).

Table 2 Results of topological constraint tests comparing a monophyletic *Coleodactylus s.l*. with the best phylogenetic estimates for seven nuclear genes analysed individually, as well as the combined analysis. Columns show the log likelihood (lnL) of the best tree, the likelihood of the tree with a monophyletic *Coleodactylus s.l*., the difference in likelihood values between the best tree and the constraint tree, and the *P*-value of the SH test. The last column shows posterior probabilities of a monophyletic *Coleodactylus s.l*. from the Bayesian analyses.

Dataset	lnL of best tree	lnL of constraint tree	Difference in lnL	***P***	Posterior probability of alternative hypothesis

ACM4	−2 253.4118	−2 257.0046	3.59283	0.29	0.0566
CMOS	−2 034.1477	−2 034.1481	0.00038	0.15	0.0640
RBMX	−2 806.6269	−2 808.2078	1.58087	0.38	0.0501
PDC	−2 119.8431	−2 121.7696	1.92656	0.29	0.1280
$PTPN_{12}$	−4 385.4731	−4 389.2529	3.77983	0.16	0.0233
RAG_1	−6 532.1527	−6 535.0006	2.84790	0.22	0.0891
RAG2	−2 215.4702	−2 216.7298	1.25966	0.36	0.0425
Concatenated data	−22 871.9359	−22 883.5976	11.66164	0.06	0.0000

We used the likelihood ratio test to determine whether branch lengths of any of the four branches connecting sphaerodactyl genera were significantly different from zero (Fig. 2). The concatenated data, *RBMX*, $PTPN_{12}$, *ACM4*, and RAG_1, had two of four internal branches with lengths not significantly different from zero. *PDC* had three of four branches not significantly different from zero. *RAG2* and *C-MOS* had all four branches not significantly different from zero.

MORPHOLOGICAL DATA

We recovered several morphological traits to aid in the diagnosis and description of a new genus and provide a detailed osteology to guide future research in sphaerodactyl biology and evolution. Morphological descriptions and comparisons are explained in detail below, after we address taxonomic changes.

TAXONOMY

The combined morphological and molecular evidence suggested a new generic-level sphaerodactyl clade be described. We also redescribe *Coleodactylus s.s*. in light of our results.

REPTILIA: SQUAMATA: SPHAERODACTYLIDAE

CHATOGEKKO GAMBLE, DAZA, COLLI, VITT AND BAUER, GEN. NOV.

(Figs5, 6)

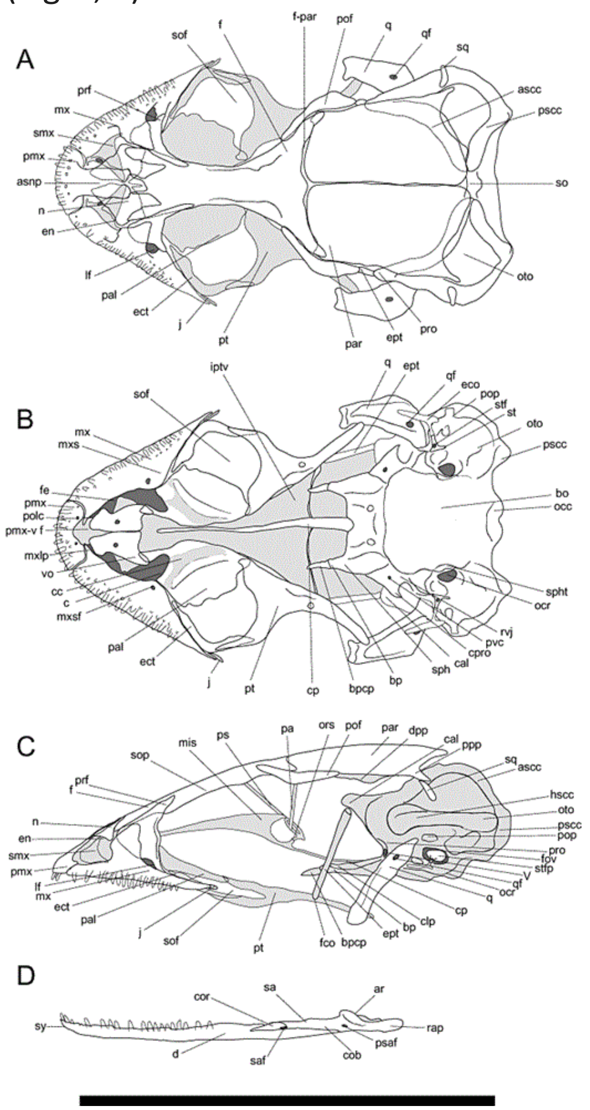

Figure 5 Skull of *Chatogekko amazonicus*(USNM 290904) from Pará, Brazil. A, dorsal; B, ventral; and C, lateral views of the cranium. D, labial view of the jaw. Abbreviations: ar, articular; ascc, anterior semicircular canal; asnp, ascending nasal process; bo, basioccipital; bp, basipterygoid process; bpcp, cartilaginous pad of the basipterygoid process; c, choana; cc, choanal canal; cal, crista alaris; clp, clinoid process; cob, compound bone; cor, coronoid; cp, cultriform process; cpro, crista prootica; d, dentary; dpp, decensus parietalis process; eco, extracollumella; ect, ectopterygoid; en, external nares; ept, epipterygoid; f, frontal; fco, fossa columellae; fe, fenestra exochoanalis; fov, fenestra ovalis; f-par, frontoparietal suture; hscc, horizontal semicircular canal; iptv, interpterygoid vacuity; j, jugal; lf, lacrimal foramen; mis, median interorbital septum; msy, mandibular symphysis; mx, maxilla; mxlp, maxillary lappet; mxs, maxillary shelf; mxsf, foramen of the maxillary shelf; n, nasal; occ, occipital condyle; ocr, occipital recess; ors, orbitosphenoid; oto, otooccipital; pa, pila accessoria; pal, palatine; par, parietal; pmx, premaxilla; pmx-v f, premaxillary-vomer fenestra; pof, postorbitofrontal; polc, posterior opening of the longitudinal canal; pop, paroccipital process; ppp, postparietal process; prf, prefrontal; pro, prootic; ps,

planum supraseptale; psaf, posterior surangular foramen; pscc, posterior semicircular canal; pt, pterygoid; pvc, posterior opening of vidian canal; q, quadrate; qf, quadrate foramen; rap, retroarticular process; rvj, recessus vena jugularis; saf, surangular foramen; sop, subolfactory process; spht, sphenooccipital tubercle; st, stapes; stf; stapedial foramen; stfp, stapedial footplate; sa, surangular; smx, septomaxilla; so, supraoccipital; sof, suborbital fenestra; sph, sphenoid; sq, squamosal; V, incisura prootica; vo, vomer. Scale bar = 5 mm.

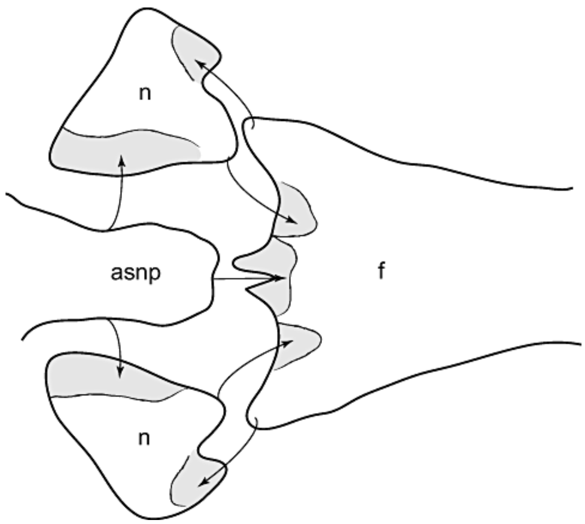

Figure 6 Inferred overlapping pattern among the medial bones of the snout in *Chatogekko amazonicus* specimen from Guyana (AMNH-R 132039). Grey indicates the overlap area; arrows indicate the place where each bone articulates. Abbreviations: asnp, ascending nasal process; n, nasal, f, frontal.

Type species: Sphaerodactylus amazonicus(Andersson, 1918)

Diagnosis and description: A miniaturized species complex of diurnal sphaerodactyl geckos. Mean SVL 21 ± 1.8 mm, *N*= 41. Snout shortened. Pupil round. Body cylindrical. Dorsal scales keeled. Claws enclosed in ungual sheath consisting of four scales. Posterior edge of premaxilla contacts medial process of frontal bone. Posterior edge of ascending nasal process bifurcated. Palatine longer than vomer. Postparietal process of parietal in contact with supraoccipital and otooccipital, but not squamosal. Reduced paroccipital process located dorsally to fenestra ovalis.

Chatogekko is distinguished from all gekkotans by the following unique combination of characters: (1) between two and four loreal scales (ls, Fig. 4A, also present in some *Sphaerodactylus*); (2) claws enclosed in an ungual sheath consisting of four scales (Parker, 1926; Vanzolini, 1957; Avila-Pires, 1995): inner supero-lateral (isl, Fig. 4B), outer supero-lateral (osl, Fig. 4B), inner infero-lateral (iil, Fig. 4C), and outer infero-lateral (oil, Fig. 4C) (ventrolaterals *sensu*Kluge, 1995); (3, Fig. 4D) keeled scales on dorsal body surface (Vanzolini, 1957; Avila-Pires, 1995), also present in some *Sphaerodactylus*; (4, Fig. 5A) bony external nares large and entering or approaching contact between prefrontal and nasals (as a consequence of extensive overlapping contact of maxilla and prefrontal); (5, Fig. 5A) posterior edge of premaxilla (i.e. the ascending nasal process) contacts medial process of frontal bone (Daza *et al*., 2008); (6, Fig. 5A) posterior edge of ascending nasal process bifurcated; (7, Fig. 5A) internasal contact absent; (8, Fig. 5A) jugal bone vestigial and limited to tip of maxilla; (9, Fig. 5A) postparietal process of parietal contacting supraoccipital and otooccipital, but not squamosal; (10, Fig. 5A) paroccipital process of otooccipital not visible in dorsal view; (11, Fig. 5B) paroccipital process very reduced and located dorsally to fenestra ovalis (instead of posterior as in other gekkotans) and not participating in quadrate articulation (paroccipital abutting); (12, Fig. 5B) palatine exceeds vomer substantially in length; (13, Fig. 10) duplicipalatinate condition; (14) a 3-bp deletion in coding region of exon 8 (in *Gallus*) of *RBMX*; and (15) a 3-bp deletion in coding region of exon 13 (in *Gallus*) of *$PTPN_{12}$*.

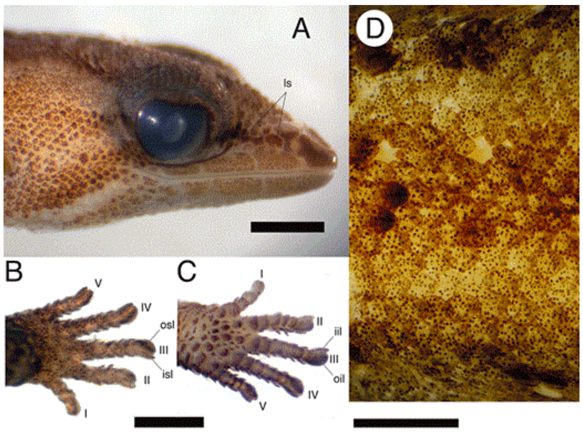

Figure 4 *Chatogekko amazonicus* specimens. A, lateral view of the head showing 2–4 loreal scales (ls); B, dorsal view of the left hand showing the inner supero-lateral and outer supero-lateral (isl and osl, Fig. 5B); C, ventral view of the left hand showing the inner infero-lateral and outer infero-lateral (iil and oil, Fig. 5C); and D, keeled scales along the dorsal surface of the body. A–C, USNM 288775; D, MZUSP 91394. Scale bar = 1mm.

Distribution: Central and eastern Amazonia, including the Brazilian states of Acre, Amazonas, Rondônia, Mato Grosso, Roraima, Pará, and Amapá; French Guiana; Guyana; Suriname; the Venezuelan state of Amazonas; and northern Bolivia (Gasc, 1990; Avila-Pires, 1995; Langstroth, 2005; Geurgas & Rodrigues, 2010).

Natural history: Chatogekko lives in the leaf litter in a variety of undisturbed lowland forested habitats (Vitt *et al*., 2005). These geckos are active throughout the day although they do not bask (Hoogmoed, 1973). Diet is made up of small insects including springtails, mites and ticks, termites, homopterans, and larval insects (Hoogmoed, 1973; Ramos, 1981; Vitt *et al*., 2005). Females lay one egg per clutch and can produce several clutches during the year (Hoogmoed, 1973; Gasc, 1990). *Chatogekko* can be locally very abundant but appears to be negatively affected by forest fragmentation (Carvalho *et al*., 2008).

Etymology: A composite word from the Spanish and Portuguese ‘Chato’, derived from the Greek ‘Platus’, meaning ‘flat’ and referring to its pug-nosed snout; and gekko from the Malay ‘gekoq’, onomatopoeic of the call of the species *Gekko gecko* and the common name to all limbed gekkotans. A Sri Lankan origin for the word gekko, derived from the Sinhalese word ‘gego’, is also possible (de Silva & Bauer, 2008). The name is masculine.

Species composition: Chatogekko amazonicus(Andersson, 1918). In addition, the names *C. zernyi*(Wettstein, 1928) and *C. guimaraesi*(Vanzolini, 1957) are available for populations from eastern Amazonia and south-west Amazon, respectively. See Discussion for details.

Coleodactylus Parker, 1926

Type species: Sphaerodactylus meridionalis(Boulenger, 1888).

Diagnosis and description: A miniaturized species complex of diurnal sphaerodactyl geckos. SVL 20–28 mm (Vanzolini, 1968b; Avila-Pires, 1995). Snout elongate. Pupil round. Body cylindrical. Dorsal scales smooth or imbricate. Claws enclosed in an ungual sheath consisting of five scales.

Coleodactylus is a miniaturized species complex of diurnal sphaerodactyl geckos that can be differentiated from all other gekkotans by the following unique combination of characters: (1) claws enclosed in ungual sheath consisting of five scales (Parker, 1926; Vanzolini, 1957; Avila-Pires, 1995); (2) smooth or imbricate scales on dorsal body surface (Vanzolini, 1957; Avila-Pires, 1995), present in most other gekkotans; (3) ascending nasal process separates nasals approximately one-quarter their length, one of the shortest among sphaerodactyl geckos (Daza *et al*., 2008); (4) proximal portion of metatarsal IV not very expanded; and (5) two separate deletions of 18 and 6 bp in exon 1 (in *Gallus*) of RAG_1.

Distribution: Northern and eastern Brazil including states of Alagoas, Bahia, Ceará, Goiás, Maranhão, Mato Grosso, Mato Grosso do Sul, Pará, Paraíba, Pernambuco, Piauí, Rio Grande do Norte, Roraima, Sergipe, and Tocantins; Guyana; Suriname; the Venezuelan states of Monagas, Delta Amacuro and possibly Bolívar (Vanzolini, 1980; Hoogmoed, 1985; Avila-Pires, 1995; Freire, 1999; Rivas & Molina R., 2001).

Species composition: Coleodactylus brachystoma(Amaral, 1935); *C. meridionalis*(Boulenger, 1888); *C. natalensis*Freire, 1999; and *C. septentrionalis*Vanzolini, 1980.

Osteology

Because most characters that differentiate *Chatogekko* from other sphaerodactyl geckos come from osteology, a detailed description of its skeleton would be convenient for future taxonomic differentiation of sphaerodactyl taxa. Additionally, a detailed osteology provides a baseline for future morphological research aimed at diagnosing the putative *Chatogekko* species. We present the osteological data in a framework that highlights the extremely small size of these lizards. It has been stated that is impossible to present a unifying model of miniaturization encompassing all lizards (Rieppel, 1984a). Even so, many anatomical similarities of the cranial structure of *Chatogekko* are present in other miniaturized gekkotans, especially closely related sphaerodactyl genera. Because the cranial anatomy of *Sphaerodactylus roosevelti* has been described in detail (Daza *et al*., 2008), we only highlight those structures that show differences in this new genus. We do this in the context of a descriptive approach and do not intend to imply any particular character polarity. Additionally, we review the postcranium, which has been described previously (Noble, 1921), but not in great detail.

SKULL

The skull of *Chatogekko* is wedge shaped with a maximum width at the level of the otic capsules. It has a rounded outline in lateral view as there is a continuous curvature from the tip of the snout to the skull table. It has the shortest muzzle unit among sphaerodactylids (Fig. 5). This is especially evident in the anterorbital region, where a high degree of overlap occurs between the bones. The premaxilla has a very elongated ascending nasal process (asnp, Fig. 5A), with lateral margins that do not converge posteriorly. The last three-quarters of this process are reduced in width to a narrower projection that contacts the medial process of the frontal. In *Sphaerodactylus*, this process may reach the level of the frontal bone, but never contacts it directly because the nasal bones lie between them (Daza *et al*., 2008). The ascending nasal process is much shorter and does not reach the level of the frontal bone in *Coleodactylus brachystoma*. The posterior projection of the ascending nasal process varies among the specimens of *Chatogekko* examined and may be bifurcated or assume an almost transverse orientation.

The dorsal process of the maxilla is very narrow and exhibits an extensive overlap with the prefrontal bone. Proportionally, the bony external nares of *Chatogekko* are larger, and the prefrontal is closer to the posterior edge of this opening than in other sphaerodactyls. In *Chatogekko*, the approximation of the prefrontal to the external nares is mainly the result of the reduction of the nasal process of the maxilla instead of being the consequence of the posterior extension of the external nares, as in varanid lizards (Lee, 1997; Conrad, 2008; Conrad, Rieppel & Grande, 2008).

The orbit in *Chatogekko* occupies about 32% of the skull length, which is slightly more than in other sphaerodactyls (Daza *et al*., 2008). As in most limbed geckos, the orbit is bounded by the postorbitofrontal, frontal, prefrontal, maxilla, and jugal (Evans, 2008; Daza & Bauer, 2010); the jugal is reduced or vestigial and contacts the tip of the posterior portion of the maxilla on the medial side. The floor of the orbit is pierced by a very large, D-shaped suborbital fenestra, which is present in all sphaerodactyls as well as the more distantly related sphaerodactylids *Pristurus* and *Saurodactylus*(Daza *et al*., 2008) and *Euleptes*(J.D.D., pers. observ.).

The rear portion of the skull is typical of miniaturized lizards (Rieppel, 1984a), which indicates how size reduction directly affects cranial structure. The basicranium is massive, being the widest part of the skull at the level of the otic capsules. The skull table is comparatively small, given that the parietals leave exposed a larger area of the basicranium. The outer margin of the basicranium (prootic, ottoccipital, and supraoccipital), as a consequence, is completely visible in dorsal view. The otooccipital area is so prominent and the horizontal semicircular canal bulges to the extent that the paroccipital process, normally seen in sphaerodactyls, is totally hidden. This paroccipital process is rudimentary and plays little or no function at all in the streptostylic quadrate articulation as in other lizards (Versluys, 1912; Frazzetta, 1962; Rieppel, 1978). The quadrate is very lightly built and articulates with the basicranium in a very anterior position, just in front of the fenestra ovalis. A quadrate foramen is present but its location is more proximal than in *Sphaerodactylus*. The squamosal bone is minuscule, and lost in some populations of *Chatogekko*. When this bone is present, it barely contacts the postparietal process of the parietal and lies against the basicranium, without contacting the quadrate or wrapping around it. Another consequence of this massive basicranium is the shape of the pterygoids, which have an almost straight medial margin (i.e. not curved or sigmoidal), and create a very wide interpterygoid vacuity posteriorly. The basipterygoid process and the cartilaginous pad that covers it are very narrow in *Chatogekko*.

In the palate the premaxillary–vomerine fenestra is very large and irregularly shaped, and partially invaded by the maxillary lappets. The vomer is reduced in size relative to the other palatal bones, leaving a very large fenestra exochoanalis and is partially overlapped by the septomaxilla.

JAW

The jaw of *Chatogekko* is typically sphaerodactyl, very straight with an elongated dentary that extends posteriorly almost to the level of the articular surface of the craniomandibular articulation. The coronoid is low and very small, without projecting above the contour of the mandible. In lingual view, the splenial seems to be fused with the coronoid, a character that unites *Pristurus* with the sphaerodactyls.

HYOID APPARATUS

There are no major differences between the hyoid structure of *Chatogekko*(Fig. 7) and that of *Sphaerodactylus macrolepis*(Noble, 1921). In these two genera, medial or lateral projections of the hypohyal (hyoid cornu) do not exist. Among sphaerodactyls these are only present in *Gonatodes*. The second ceratobranchial (2 cb, Fig. 7) is comparatively shorter than in *Sphaerodactylus* and is oriented posteromedially. The second epibranchial (2 eb, Fig. 7) is not joined to the second ceratobranchial as in *Sphaerodactylus*.

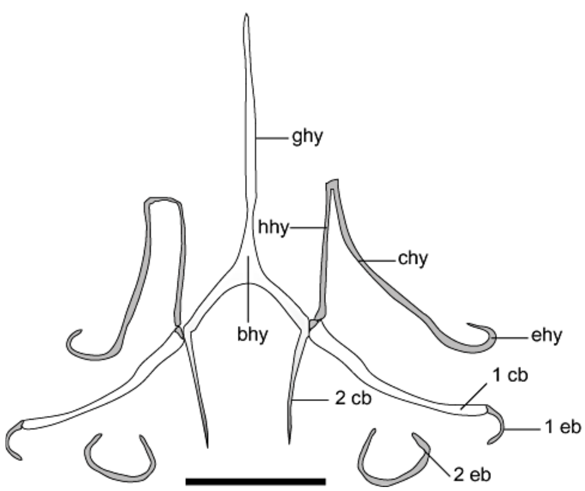

Figure 7 Hyoid apparatus of *Chatogekko amazonicus* specimen from Serra do Navio, Amapá, Brazil (AMNH R-138726). Abbreviations: 1 cb, first ceratobranchial; 1 eb, first epibranchial; 2 cb, second ceratobranchial; 2 eb, second epibranchial; bhy, basihyal; chy, ceratohyal; ehy, epihyal; ghy, glossohyal; hhy, hypohyal. Different shades of grey indicate the ossification of each element: grey, cartilaginous; white, ossified. Scale bar = 1 mm.

POSTCRANIUM

The postcranium of *Chatogekko* comprises 85% of the entire body length; the body and tail sections are subequal (Fig. 8). The vertebral column is composed of 47 vertebrae: 26 presacrals, two sacrals and 19 caudals. The presacral region comprises eight cervical, 17 thoracic and one lumbar. In the cervical region only the atlas and the axis are ribless and the remaining six cervicals bear ribs that increase in length gradually. The atlas is fused dorsally as in all sphaerodactyls except *Gonatodes*, which has paired elements. The 3rd and 4th cervicals have short ribs that are widened and bifurcated distally. The ribs of cervicals 5–7 are set closer to the suprascapula. The rib of the 8th cervical approaches but does not contact the sternum. The sternal ribs of the first four thoracic vertebrae are attached to the sternum directly. The 5th thoracic may be attached to the xiphisternum in specimens in which this structure is branched. The remaining thoracic vertebrae have short postxiphisternal inscriptional ribs that reduce their size gradually until becoming only a small nubbin.

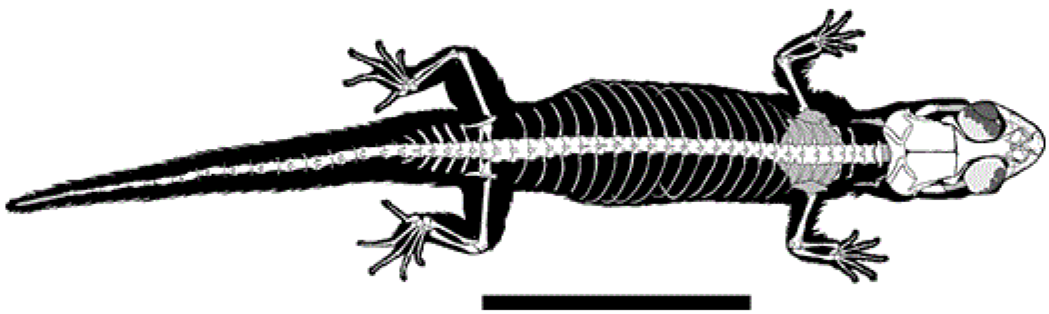

Figure 8 Articulated skeleton of *Chatogekko* sp. Specimen (USNM 289061) from Reserva Biologica Rio Trombetas, Pará, Brazil. Scale bar = 10 mm.

The longest rib is present on the 11th thoracic vertebra, after which ribs start to decrease in size until lost on the lumbar. A single lumbar vertebra does not differ in size from the posterior thoracic vertebrae. The two sacral vertebrae differ in structure. The first has expanded transverse processes that articulate with the pelvic girdle (illum) and posteriorly it is fused to the transverse processes of the second sacral, whereas the second has a short transverse process which are oriented anterolaterally. The tail is formed by 19 caudals. The pygial vertebrae have been described as those anterior caudals devoid of fracture planes (Holder, 1960).
In *Chatogekko*, autotomy planes are visible after the 6th caudal vertebrae, but only the first three lack hemal arches. The transverse processes are elongated and oriented posteriorly on the first five caudals; these processes gradually reduce in length distally. Beyond the 6th caudal vertebrae, centrum length increases, almost doubling the length of the presacral vertebrae.

The pectoral girdle comprises suprascapulae, scapulocoracoids, epicoracoids, clavicles, interclavicle, and sternum. The suprascapula is expanded and cartilaginous. The scapular portion of the scapulocoracoid is elongated and narrow. The scapulocoracoid fenestra is closed by a projection of the cartilaginous scapular epicoracoid bar. The anterior coracoid fenestra (i.e. anterior primary coracoid emargination) is present, but the posterior one is absent. The clavicles are expanded medially and more or less rotated forward. They lack the clavicular fenestra, as do *Lepidoblepharis*(Noble, 1921; Parker, 1926) and *Gonatodes*. Parker (1926) also described *Coleodactylus* and *Pseudogonatodes* with no clavicular fenestra, although we found specimens of *Coleodactylus* and *Pseudogonatodes* with clavicular fenestrae, which indicates that this character is variable or polymorphic for these two genera; in *Sphaerodactylus*, the clavicle is invariably perforated (Noble, 1921), which we were able to corroborate in all species reviewed (see Supporting Information). The interclavicle in *Chatogekko* has lateral arms, but these are very broad and almost indistinct. The sternum is shield-like and well ossified.

The pelvic girdle is formed by the fusion of the ilium, ischium, and pubis. The ischium and pubis are in close contact with their fellows, but not fused. The ischiopubic fenestra is large and compressed anteroposteriorly. In *Chatogekko* the ilium is constricted dorsal to the acetabulum and extends dorsally as a rod-like process. The ischium is wider than the pubis, and the metischial processes are widely separated. The hypoischium is absent. The pubic symphysis is slender and capped by a small epipubic cartilage. In all sphaerodactyls, the pectineal process is large and ventrally directed. This is a highly diagnostic feature, mentioned by Noble (1921) as a difference between the African '*Gonatodes dickersoni*' (now *Cnemaspis dickersoni*) and the Neotropical sphaerodactyls. The rounded obturator foramen for the course of nerves lies at the boundary between the ischium and pubis. This foramen is present in all limbed gekkotans and lost in pygopodids.

The limbs are short and stout, but most typical elements of the gecko appendicular skeleton (Russell, 1972; Fabrezi, Abdala & Oliveri, 2007; Russell & Bauer, 2008) are present. One variation that occurs in sphaerodactyls is the increase in number of sesamoids on the proximal epiphyseal end of the radius with respect to other lizards. These elements have been described for a few lizards, for instance *Sphaerodactylus klauberi* and the xantusiid *Lepidophyma gaigeae*(Jerez, Mangione & Abdala, 2010). In *Chatogekko* and *Coleodactylus* there are three of these elements between the radius and the humerus (Fig. 8). This number is variable among other sphaerodactyls; for example, *Pseudogonatodes* and *Sphaerodactylus* have two, and *Lepidoblepharis* and *Gonatodes* only one. *Pseudogonatodes*, *Coleodactylus*, and *Chatogekko* also have sesamoids dorsal to the metacarpal–carpal and metatarsal–tarsal articulations (Figs 5, 7). These ossifications appear sporadically in *Lepidoblepharis*, but not in *Gonatodes*.

The phalangeal formulae of the manus and pes of sphaerodactyls are typically 2-3-4-5-3 and 2-3-4-5-4 (Table 3), respectively, which are primitive for squamates (Greer, 1992). One phalanx in the fourth manual digit of *Pseudogonatodes*, *Coleodactylus*, and *Chatogekko* and the fourth pedal digit of *Pseudogonatodes* are lost (Table 3, Fig. 9) The identity of the phalanx lost is hard to determine without developmental series, but it is likely that it is either the ultimate or penultimate phalanx.

Table 3 Summary of digital characteristics for each genus of sphaerodactyl gecko

	Phalangeal formula (manus)	Phalangeal formula (pes)	Increasing order of digit length (manus)	Increasing order of digit length (pes)	Dorsal metacarpophalangeal sesamoids	Dorsal metatarsophalangeal sesamoids
Gonatodes	2-3-4-5-3	2-3-4-5-4	1-2-5-3-4	1-2-3-5-4	No	No

Lepidoblepharis	2-3-4-5-3	2-3-4-5-4	1-5-2-3-4	1-2-3-5-4	No	Yes
Sphaerodactylus	2-3-4-5-3	2-3-4-5-4	1-5-2-4-3	1-2-5-3-4	No	No
Pseudogonatodes	2-3-4-4-3	2-3-4-4-4	1-5-2-4-3	1-2-5-3-4	Yes	Yes
Coleodactylus	2-3-4-4-3	2-3-4-5-4	1-5-2-4-3	1-2-5-3-4	Yes	Yes
Chatogekko	2-3-4-4-3	2-3-4-5-4	1-2-5-4-3	1-2-5-3-4	Yes	Yes

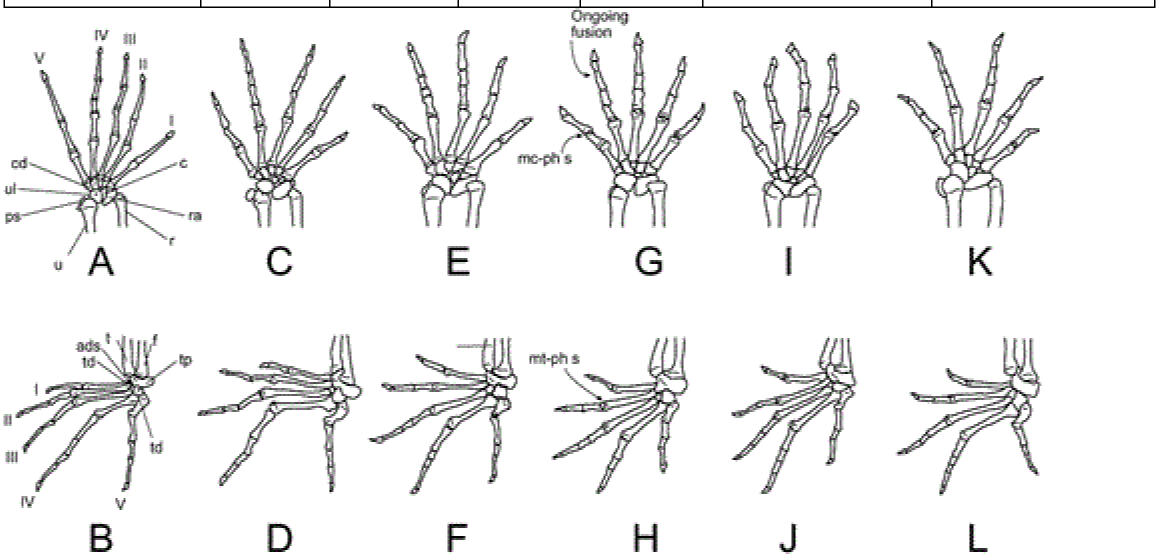

Figure 9 Left manus and pes of sphaerodactyl geckos. A, B, *Gonatodes albogularis*(UIS-R-2079); C, D, *Lepidoblepharis xantostigma*(USNM 313791); E, F, *Sphaerodactylus klauberi*(UPRRP 006416); G, H, *Pseudogonatodes guianensis*(MZUSP 94826); I, J, *Coleodactylus brachystoma*(MZUSP uncatalogued); K, L, *Chatogekko amazonicus*(USNM 289061). Drawings not to the same scale. Abbreviations: I–V, digits; ads, anterior distal sesamoid; c, centrale; cd, distal carpal; f, fibula; mc-ph s, sesamoid dorsal to the metacarpal–phalange articulation; mt-ph s, sesamoid dorsal to the metatarsal–phalange articulation; ps, pisiform; r, radius; ra, radiale; t, tibia; td, distal tarsal; tp, proximal tarsal, u, ulna, ul, ulnare.

DISCUSSION

PHYLOGENY

Phylogenetic analyses of the combined nuclear gene data, using both a concatenation approach and a gene tree approach, recovered three lineages of sphaerodactyl genera: *Chatogekko*; a *Lepidoblepharis*+*Gonatodes* clade; and a *Pseudogonatodes*+*Sphaerodactylus*+ *Coleodactylus* clade. Other published molecular phylogenies have consistently recovered the *Lepidoblepharis*+ *Gonatodes* clade, but have failed to recover the other clades with strong support (Gamble *et al*., 2008a, 2011; Geurgas *et al*., 2008). The difficulty in recovering these clades is probably due to the short internal branches linking genera at the base of the sphaerodactyl clade. Short internal branches are a signature of rapid cladogenesis, indicating that divergences among sphaerodactyl genera occurred in a relatively short time frame (Gamble *et al*., 2008a, 2011). Short internal branches can also hamper phylogenetic reconstruction (Jackman, Larson, de Queiroz & Losos, 1999; Slowinski, 2001; Poe & Chubb, 2004). Indeed, our failure to reject the hypothesis that several of those internal branches had lengths not significantly different from zero suggests hard polytomies in the molecular data (Maddison, 1989; Slowinski, 2001). One possible cause of zero-length branches is insufficient data (Poe & Chubb, 2004). This may play some role in our results as our three loci with the least amount of data, namely *RAG2*, *C-MOS*, and *PDC*, had either three or four of the four branches connecting sphaerodactyl genera with branch lengths not significantly different from zero. The remaining loci had more data, sometimes substantially so, and possessed only two of four branches with lengths not significantly different from zero. This was also the case with the concatenated dataset. Close examination of which branches were statistically indistinguishable from zero shows some similarities among the loci with more data (*ACM4*, RAG_1, $PTPN_{12}$, and *RBMX*) and the concatenated dataset (Fig. 2). The branch leading to the *Gonatodes*+ *Lepidoblepharis* clade, for example, was always significantly different from zero, while the branch connecting *Chatogekko* with its sister taxon (which was not consistent and changed from tree to tree) was always not significantly different from zero. These similarities among the longer single-gene datasets and their concordance with the concatenated dataset indicate we had enough data for those loci. It is therefore likely that two of the four branches connecting sphaerodactyl genera actually possessed zero branch lengths. These were, in the concatenated nuclear gene dataset, the branch connecting *Chatogekko* to its sister taxon and the branch connecting *Coleodactylus* to the *Pseudogonatodes*+*Sphaerodactylus* clade. The presence of a hard polytomy in the data has serious implications for our hypothesis testing. Our topology tests were probably unable to distinguish among alternative phylogenetic hypotheses because there were very little data or, in the cases of branches with zero lengths, no data supporting any one phylogenetic hypothesis over the other. This is a difficult situation for testing phylogenetic hypotheses because the lack of data means that essentially any alternative hypotheses involving these short, zero-length branches will not be rejected. The only way of evaluating alternative hypotheses when this occurs is to look to other sources of data. In our case, we had indels and morphological data providing strong evidence that *Chatogekko* is distinct from *Coleodactylus s.s*.

Polytomies in gene trees do not automatically translate to hard polytomies in the underlying species trees (Slowinski, 2001; Poe & Chubb, 2004) and the recovery of a bifurcating sphaerodactyl phylogeny is not an impossible task. We show here that rare genomic events such as indels can be used to provide diagnostic characters for sphaerodactyl clades at multiple hierarchical levels. Deletions unique to *Chatogekko* in *RBMX* and $PTPN_{12}$ and unique RAG_1 deletions in *Coleodactylus* provide strong evidence that they are two separate lineages. Indels are considered relatively homoplasy-free characters and have proven useful in diagnosing numerous vertebrate clades (van Dijk *et al*., 1999; Ericson, Johansson & Parsons, 2000; de Jong *et al*., 2003; Townsend *et al*., 2004; Gamble *et al*., 2008b). Decreasing costs for high-throughput sequencing will make the identification and collection of this sort of data, e.g. indels or LINE/SINE insertions, easier and could prove useful in further untangling the phylogenetic relationships among sphaerodactyl geckos.

TAXONOMY

We used molecular phylogenetic analyses to identify *Chatogekko* as a distinct lineage of sphaerodactyl gecko and, with a thorough examination of morphology, provided a suite of diagnostic characters for that lineage. Although some of the characters used to diagnose *Chatogekko* have been known for a long time, e.g. *Coleodactylus* has smooth dorsal scales and an ungual sheath composed of five scales while *Chatogekko* has keeled dorsal scales and an ungual sheath composed of four scales (Vanzolini, 1957, 1968a, b), most of our synapomorphies are new.

The discovery of generic polyphyly resulting from well-sampled phylogenetic analyses is relatively common (Lanyon, 1994; Campbell *et al*., 2005; Amaral *et al*., 2006). This problem has been particularly pervasive in geckos where digital morphology, a character suite prone to homoplasy, has played an historically important role in defining genera (Bauer, Good & Branch, 1997; Russell & Bauer, 2002). The classification of sphaerodactyl genera has been similarly dependent on digital morphology (Vanzolini, 1957; Kluge, 1995) and the historical clustering of *Chatogekko* with *Coleodactylus s.s*. was done primarily because of superficial similarities in the ungual sheath (Vanzolini, 1957). By looking beyond the digits, we were able to uncover many morphological characters unique to *Chatogekko*, strengthening the argument for a taxonomic change.

We recovered three deeply divergent lineages within *Chatogekko*. These results are consistent with Geurgas & Rodrigues (2010) and Geurgas *et al*. (2008), who also recovered multiple species-level lineages within *C*. *amazonicus*. The geographical distribution of the three *Chatogekko* lineages corresponds to three described *Chatogekko* species, two of which are currently synonymized with *C*. *amazonicus*. Specimens from Manaus and Roraima correspond to *C. amazonicus s.s*., with a type locality in the central Amazon near Manaus, Amazonas, Brazil (Andersson, 1918). Specimens from Pará probably correspond to *C*. *zernyi*, with a type locality from Taperinha, Pará, Brazil, in the eastern Amazon near Santarém (Wettstein, 1928). Specimens from Rondônia and Rio Ituxi probably correspond to *C*. *guimaraesi*, with a type locality in Porto Velho, Rondônia, Brazil, in the south-western Amazon (Vanzolini, 1957). Although our limited sampling is insufficient to resurrect *C*. *zernyi* and *C*. *guimaraesi*, the existence of available names for those clades makes such a decision reasonable and the eventual resurrection of these taxa seems inevitable. It should be noted that Geurgas & Rodrigues (2010) also recovered significant phylogenetic structure within *Chatogekko amazonicus s.s and C*. cf. *zernyi*. It is possible that splitting each species into two or more species-level lineages may be warranted although additional data would be needed to confirm this.

Coleodactylus and *Chatogekko* appear to be morphologically conservative and the identification of species-level lineages in both genera using morphology has historically been difficult (Moretti, 2009). Our examination of *Chatogekko* osteology bears this out. Even though we examined specimens from three putative *Chatogekko* species we could not identify morphological synapomorphies for these lineages with our data. Our results mirror other morphological analyses of *Chatogekko*(Vanzolini, 1968b; Avila-Pires, 1995), raising the possibility that species of *Chatogekko* may be morphologically cryptic. A lineage-based species concept requires that species be diagnosable and genetic evidence and the molecular synapomorphies that support each of the species-level clades within *Chatogekko* are sufficient to satisfy the need for diagnosability (Zink & McKitrick, 1995; de Queiroz, 1998, 2007; Sites & Marshall, 2004). That said, a thorough examination of morphological characters with a larger sample of specimens in light of the molecular phylogenetic hypothesis could be productive. Other means of identifying species, such as ecological niche modelling, cytogenetics, or multivariate morphometrics, may also prove useful (Raxworthy *et al*., 2007; Colli *et al*., 2009; Leaché*et al*., 2009; Oliver *et al*., 2009).

MORPHOLOGY

The skull of *Chatogekko* exhibits interesting modifications associated with miniaturization. The extensive overlapping pattern of the premaxilla is not typical of miniaturized gekkotans (except perhaps in the pygopodid *Pletholax*), although a similar pattern is found in other miniaturized lepidosaurs. The uniqueness of the *Chatogekko* skull compared with other small gekkotans is not surprising, given the association between morphological novelty and miniaturization in vertebrates (Hanken, 1984). The repeated evolution of this overlapping pattern in independent lineages is simply one of several possible solutions to the problems associated with extreme size reduction and highlights the novelty often found in miniaturized taxa.

Miniaturization is often associated with paedomorphosis, the retention of juvenile traits in adult organisms (Gould, 1966; Alberch *et al*., 1979; Rieppel, 1996). Gekkotans possess several paedomorphic skeletal characters such as amphicoelous vertebrae (Camp, 1923; Kluge, 1967; Werner, 1971) and paired premaxilla or parietal bones (Stephenson, 1960; Kluge, 1967, 1987; Daza, 2008) although none of these skeletal changes are found exclusively in miniaturized forms. In fact, miniaturized species present a fused premaxilla and braincase bones more frequently than larger gekkotans (Daza, 2008). One character that might reflect paedomorphosis in *Chatogekko* is the slightly larger eyes proportional to the head (Daza *et al*., 2008), but this would have to be corroborated with a developmental series of different sized sphaerodactyl species.

Another interesting feature of the *Chatogekko* skull is the development of an incomplete secondary palate. A secondary palate is frequently listed as a very distinct structure in mammals, but is also present in some reptiles. A secondary palate is present in many fossil reptiles (Romer, 1956; Carroll, 1988; Benton, 2005), but among extant groups, this structure appears only in crocodilians, some turtles, and some lizards (Iordansky, 1973; Presch, 1976; Greer, 1977; Gaffney, 1979; Meylan *et al*., 2000). It has long been thought that no true secondary palate was present in lizards and the tongue was used for closing the naso-pharyngeal passages during respiration (Camp, 1923). The secondary palate in sphaerodactyls resembles that of pygopodids (Conrad, 2008) and xantusiids (Malan, 1946; Savage, 1963). In sphaerodactyls, especially in *Chatogekko*, the secondary palate is distinctive in that the paleochoanate condition is present, but the palatine is extremely duplicipalatinate, where this bone develops a deep choanal canal formed by the vomerine process and a ventral crest of the palatine. These two structures tend to converge ventrally creating a structure that in cross-section has the shape of a ‘C’; in this sense, the palatines roof over most of the length of the choanal tubes and the ectochoanal cartilage floors the ventral surface, and extends well posteriorly so the nasal passageway opens on the posteromedial side of the palatine (ce, Fig. 10).

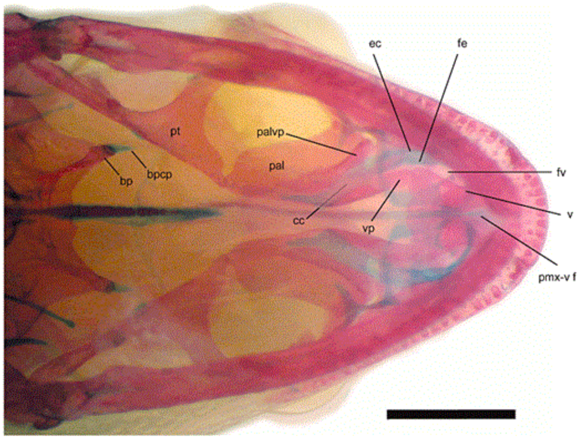

Figure 10 Palatal view of cleared and stained *Chatogekko amazonicus* specimen from Guyana (AMNH-R 132039) showing the secondary palate formed on the palatine. Abbreviations: bp, basipterygoid; bpcp, cartilaginous pad of the basipterygoid process; cc, choanal canal; ec, ectochoanal cartilage; fe, fenestra exochoanalis; pal, palatine; palvp, ventral process of the palatine; pmx-v f, premaxillary–vomer fenestra; pt, pterygoid; sof, suborbital fenestra; v, vomer; vp, vomerine process of palatine. Scale bar = 1 mm.

The amount of overlap of the premaxilla with the nasal bones, and the contact of nasals have been used as phylogenetic characters (Kluge, 1976), but it has been suggested that they should be treated as independent characters because in certain forms nasal separation can be an artefact of premaxillary overlap, even if the nasals remain in contact with one another (Daza *et al*., 2008). This seems to be the case in all sphaerodactyls, except in *Chatogekko* where there is both overlap and complete separation of the nasal bones (i.e. there is no internasal contact). A similar arrangement is present in: the pygopodid *Pletholax gracilis*(Rieppel, 1984b); the chameleon *Rhampholeon spectrum*(Evans, 2008); the xantusiid *Cricosaura typica*(Savage, 1963); some miniaturized gymnophthalmids such as *Bachia bicolor*(Tarazona, Fabrezi & Ramirez-Pinilla, 2008), *Gymnophthalmus speciosus*(MacLean, 1974), *Vanzosaura rubricauda*(Guerra & Montero, 2009), *Calyptommatus nicterus*, *Scriptosaura catimbau*, and *Nothobachia ablephara*(Roscito & Rodrigues, 2011); many amphisbaenians (Montero & Gans, 2008); and to some extent in the colubrid *Scaphiophis albopunctatus*(Cundall & Irish, 2008). The loss of the internasal results in some substantial changes to snout configuration and to the distribution of forces; the medial laminar contact between these bones is replaced by an exclusive dorsoventral butt–lap suture with the ascending nasal process of the premaxilla. Open contact sutures are thought to work as shock absorbers or assist to allow micro-movements to dissipate forces acting between bones on the skull (Pritchard, Scott & Girgis, 1956; Jaslow, 1989), behaving in an analogous manner to the flexible material used between the slabs of concrete pavement. The loss of contact, together with the separation of nasals (dashed line in Fig. 5A), combined with the loss of a butt–lap joint with the maxilla (a suture present in other sphaerodactyls) suggest that the nasal bones will tend to be less stable and more inclined to move sideways. It has been demonstrated with three-dimensional finite element models that sutures relieve strain locally, but only at the expense of elevated strain in other regions (Moazen *et al*., 2009). Using this reasoning, a hypothesized reduction in the medial strain on the nasals would have played an important part in the development of a posterior interlocking suture with the frontal (Fig. 6). This is purely conjectural, but is derived from the observed elaborated type of suture and comparison with a similar interlocking suture between nasals and frontal in some amphisbaenians (R. Montero, pers. comm.). The nasofrontal suture of *Chatogekko* is reciprocally overlapping; the nasal develops a narrow posterior process that overlaps the frontal bone, and the anterolateral process of the frontal overlaps the posterolateral surface of the nasal.

Characters from the postcranium were not diagnostic for *Chatogekko*; nonetheless it is worthwhile commenting on the occurrence of perforated clavicles among sphaerodactyl geckos. The perforation was described as variable within the gekkonid genus *Cnemaspis* and considered as the final stage in the thinning process of the bone, with no phylogenetic significance (Smith, 1933). This statement is not entirely true for sphaerodactyls, where similar sized species with comparable clavicles might have unperforated (e.g. *Lepidoblepharis* and *Gonatodes*) or perforated clavicles (e.g. *Sphaerodactylus*). In the latter, perforated clavicles are present in both small and medium-sized species, indicating that this character might be diagnostic for the genus and have a phylogenetic significance at that level.

Another variable trait from the postcranium is the phalangeal formula. These characters were used in previous intergeneric cladistic analyses of sphaerodactyl geckos (Kluge, 1995). The absence of the fourth phalangeal element in the fourth finger was one of the characters that supported the sister relationship of *Coleodactylus s.l* and *Pseudogonatodes*; likewise, *Pseudogonatodes* was differentiated from *Coleodactylus s.l*. by the loss of the fourth phalangeal element in the fourth toe. A re-examination of Kluge's (1995) dataset showed that he scored the fourth phalangeal element in the fourth toe (character 12) as absent in *Coleodactylus*, but not in *Pseudogonatodes*, which is incorrect. Reanalysis of the corrected dataset does not produce any change in the topology (J.D.D., unpubl. data).

We reviewed phalangeal formulae in the specimens available and encountered a problem of homology. In all sphaerodactyls, there is a minimum of four phalanges in the fourth digits of the manus and pes. Is the element lost in *Coleodactylus*, *Pseudogonatodes*, and *Chatogekko* the fourth (penultimate) phalanx and the remaining element the fifth (ungual)? Or is the terminal element lost and the fourth phalanx modified to develop an ungual morphology? The third phalanx of digit 4 seems to show a fusion of the third and fourth phalanges in the manus of *Pseudogonatodes*, resulting in only four phalanges in this digit. This process is symmetrical, but in the pes there is no sign of an ongoing fusion process. If a phalanx was lost, we would expect to have a shorter digit, although alternative processes such as nonossification, fusion, and reabsorption have been discussed (Shapiro, Shubin & Downs, 2007). To evaluate this, we measured the length of each digit; these measurements were converted to equivalent proportions by dividing each by the length of the shortest digit (i.e. first digit, Fig. 11). With these values, we estimated the increased order of digit length in both manus and pes (Table 3). The manus in *Sphaerodactylus*, *Pseudogonatodes*, and *Coleodactylus* presented an increase order of digit length of 1-5-2-4-3. In *Lepidoblepharis* and *Gonatodes*, the longest digit was the fourth and in *Chatogekko* the fourth digit was almost equal to the third. The situation in *Lepidoblepharis* is expected because this genus exhibits no reduction of any kind in the fourth digit (Fig. 9A). *Sphaerodactylus* exhibits similar proportions to those of *Pseudogonatodes* and *Coleodactylus*(where one phalanx is lost or fused to another) because the second phalanx of digit 4 is very reduced. The second digit in *Gonatodes* and *Chatogekko* is short in comparison with the other sphaerodactyls. In *Chatogekko*, digital proportions differ from all other sphaerodactyls, as digits 2 and 5 and digits 3 and 4 become sub-equal, but the latter are proportionally longer (Fig. 11). The pes shows a more stable pattern; in *Lepidoblepharis*, the order of increase of digit length is 1-2-3-5-4, while in the rest of the sphaerodactyls it is 1-2-5-3-4. The only taxon that showed element loss in the fourth finger was *Pseudogonatodes*, a process that is clearly demonstrated by the measurements, as the third and fourth digits become sub-equal. Developmental data would be necessary to corroborate fusion or loss of phalanges in the fourth digit of the manus in *Pseudogonatodes*, *Coleodactylus*, and *Chatogekko*.

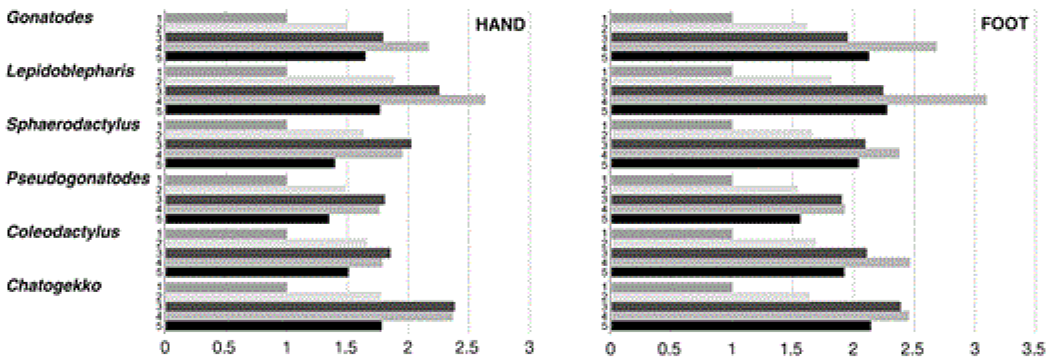

Figure 11 Relative length of hand and foot digits with respect to digit 1 in representative species from each sphaerodactyl genus. *Gonatodes albogularis*(UIS-R-2079), *Lepidoblepharis xantostigma*(USNM 313791), *Sphaerodactylus klauberi*(UPRRP 006416), *Pseudogonatodes guianensis*(MZUSP 94826), *Coleodactylus brachystoma*(MZUSP uncatalogued), *Chatogekko amazonicus*(USNM 289061).

CONCLUSIONS

Small size and cryptic habits have made sphaerodactyl geckos among the most poorly studied lizard groups. Our combined use of morphological and molecular data led to the recognition and description of a new genus-level lineage of sphaerodactyl gecko, *Chatogekko*. Previously considered part of the genus *Coleodactylus*, *Chatogekko* possesses a unique suite of morphological and molecular characters that distinguish it from *Coleodactylus s.s*. Further work with additional sampling will be necessary to uncover morphological synapomorphies for three putative *Chatogekko* species and other potentially undescribed taxa in the genus. Our detailed osteological data will provide a framework to move forward with that research, as well as assist more generally with the systematic research of other sphaerodactyl clades. There are certainly many more sphaerodactyl species to be formally recognized and the use of multiple sources of data, including molecular data and morphology as done here, will be necessary to reveal the true diversity of this fascinating group of lizards.

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Supplementary data

Appendix S1. Specimens used in the morphological analyses. Abbreviations used follow (Leviton, Gibbs, Heal & Dawson, 1985) and the following unlisted collections: RT, Collection of Richard Thomas, University of Puerto Rico (San Juan, Puerto Rico).

Aristelliger barbouri: AMNH R–45811; *Aristelliger expectatus*: AMNH R–63015; *Aristelliger georgeensis*: CAS 176485; *Aristelliger lar*: AMNH R–46019, AMNH R–50272; *Aristelliger praesignis*: BMNH 1964.1812, BMNH 86.4.15.4; *Aristelliger praesignis nelsoni*: AMNH R–146747–146748; *Aristelliger praesignis praesignis*: AMNH R–71593, 71595, AMNH R–75976; *Aristelliger sp.*: RT 4921; *Chatogekko amazonicus:* OMNH 36262, OMNH 37616, USNM 302283–302284; OMNH 37110, OMNH 37274; OMNH 36712, AMNH–R 138670, AMNH R–138726; AMNH R–132039, AMNH R–132052, USNM 124173, USNM 200660–200666, USNM 288763–

288788, USNM 289061–289066, USNM 290881–290882, USNM 290904, USNM 290944–290945, USNM 303472–303473, USNM 570538, USNM 304122–304123; *Coleodactylus brachystoma*: MZUSP Uncataloged, MZUSP Uncataloged; *Coleodactylus septentrionalis*: MZSP 66554, USNM 302285–302287, USNM 302337–302361; USNM 531620–531622, USNM 566300; *Euleptes europaea*: AMNH R–144404; *Gonatodes albogularis*: FMNH 55929, FMNH 209439, FMNH 209440, UV–C Uncataloged; *Gonatodes antillensis*: AMNH R–72642; *Gonatodes atricucullaris*: AMNH R–144391–144393; *Gonatodes humeralis*: RT 01198; *Gonatodes taniae*: UPRRP 006045; *Lepidoblepharis peraccae*: UV–C 8999; *Lepidoblepharis xanthostigma*: AMNH R–144541, RT 1875, USNM 313758, USNM 313834; *Pristurus carteri*: CAS 225349, BMNH 1971.44, JFBM 15821; *Pristurus insignis*: BMNH 1953.1.7.73; *Pristurus sp*.: AMNH R–20032, AMNH R–20056, AMNH R–20071; *Pseudogonatodes barbouri*: AMNH R–144395, AMNH R–146746, AMNH R–146752–146757; *Pseudogonatodes* cf. *guianensis*: MZUSP 94826; *Quedenfeldtia trachyblephara*: FMNH 197682; *Saurodactylus mauritanicus*: BMNH 87.10.6.1.6, FMNH 197462; *Sphaerodactylus argus*: Uncataloged; *Sphaerodactylus armstrongi*: RT 5255; *Sphaerodactylus cinereus*: AMNH R–49566; *Sphaerodactylus copei*: RT 10576; *Sphaerodactylus corticola*: USNM 220548–220552; *Sphaerodactylus gaigeae*: UPRRP 6428–6432, UPRRP 6434–6436; *Sphaerodactylus klauberi*: UPRRP 6409–6421, UPRRP 6423–6427; *Sphaerodactylus levinsi*: Uncataloged, RT 8283–8284; *Sphaerodactylus lineatus*: UPRRP 3172; *Sphaerodactylus macrolepis*: AMNH R–144331, UPRRP 6437–6445; *Sphaerodactylus millepunctatus*: AMNH R–16284; *Sphaerodactylus monensis*: UPRRP 6454; *Sphaerodactylus nicholsi*:, Uncataloged,UPRRP 6383–6386, 6388; *Sphaerodactylus nigropunctatus decoratus*: AMNH R–73470; *Sphaerodactylus parkeri*: Uncataloged; *Sphaerodactylus richardsonii*: BMNH 1964.1801–2; *Sphaerodactylus roosevelti*: UPRRP 6376–6378, 6380–6381, UPRRP 6488,; *Sphaerodactylus townsendi*: UPRRP 6389–6400, 6402–6407; *Teratoscincus microlepis*: AMNH R–88524, BMNH 1934.10.9.14; *Teratoscincus przewalskii*: CAS 171013, JFBM 15826; *Teratoscincus roborowskii*: JFBM 15828; *Teratoscincus scincus*: BMNH 92.11.28.1.

Table S1. Primers used in the molecular analyses.

Primer name	Primer sequence (5' to 3')	Source
RAG1		
R13	TCTGAATGGAAATTCAAGCTGTT	(Groth & Barrowclough, 1999)
R18	GATGCTGCCTCGGTCGGCCACCTTT	(Groth & Barrowclough, 1999)
F700	GGAGACATGGACACAATCCATCCTAC	(Bauer, De Silva, Greenbaum & Jackman, 2007)
R700	TTTGTACTGAGATGGATCTTTTTGCA	(Bauer et al., 2007)
693R	TGRATCTTTTTGCAGTTGGTAAT	This study
R1tgR	CTCCACCTTCTTCTTTCTCAGCA	This study
RAG2		
EM1-F	TGGAACAGAGTGATYGACTGCAT	(Gamble, Bauer, Greenbaum & Jackman, 2008)
EM1-R	ATTTCCCATATCAYTCCCAAACC	(Gamble et al., 2008)
PY1-F	CCCTGAGTTTGGATGCTGTACTT	(Gamble et al., 2008)
PY1-R	AACTGCCTRTTGTCCCCTGGTAT	(Gamble et al., 2008)
C-MOS		
G73	GCGGTAAAGCAGGTGAAGAAA	(Saint, Austin, Donnellan & Hutchinson, 1998)
G74	TGAGCATCCAAAGTCTCCAATC	(Saint et al., 1998)
FU-F	TTTGGTTCKGTCTACAAGGCTAC	(Gamble et al., 2008)
FU-R	AGGGAACATCCAAAGTCTCCAAT	(Gamble et al., 2008)
ACM4		
tg-F	CAAGCCTGAGAGCAARAAGG	(Gamble et al., 2008)
tg-R	ACYTGACTCCTGGCAATGCT	(Gamble et al., 2008)
PDC		
PHOF2	AGATGAGCATGCAGGAGTATGA	(Bauer et al., 2007)
PHOR1	TCCACATCCACAGCAAAAAACTCCT	(Bauer et al., 2007)
PTPN12		
F1	AGTTGCCTTGTWGAAGGRGATGC	(Townsend, Alegre, Kelley, Wiens & Reeder, 2008)

R6	CTRGCAATKGACATYGGYAATAC	(Townsend et al., 2008)
ColeoF	CGGCAGATGTGAATGAAAACTAC	This study
RBMX		
HNRNP1F	CCACGAGATTATGCCTACCG	This study
HNRNP1R	CATCATAKCGACTGCTTCCA	This study
RBMX-F1	TCCTCTTACAGTGAYCGTGATG	This study
RBMX-R1	TCCCGTAATCATCATAGCGACT	This study

Table S2. Specimens used in the molecular analyses. We used the following abbreviations: AMCC, Ambrose Monell Cryo Collection, American Museum of Natural History; CHUNB, Coleção Herpetológica da Universidade de Brasília; FLMNH, Florida Museum of Natural History; JAC, Jonathan Campbell; JB, Jon Boone; JFBM, James Ford Bell Museum of Natural History; KU, University of Kansas Museum of Natural History; LSUMZ, Louisiana State University Museum of Zoology; MF, Mike Forstner; MVZ, Museum of Vertebrate Zoology, Berkeley; MZUSP, Universidade de São Paulo, Museu de Zoologia; ROM, Royal Ontario Museum; TG, Tony Gamble; YPM, Yale Peabody Museum.

Species	Specimen ID	Locality	*RAG1*	*RAG2*	*C-MOS*	*ACM4*	*PDC*	*PTPN12*	*RBMX*
Chatogekko amazonicus	LSUMZ-H12416	East of Rio Ajarani, Roraima, Brazil	JF416911	JF416915	JF416921	JF416918	JF416924	JF416845	JF416878
Chatogekko amazonicus	LSUMZ-H16400	Manaus, Amazonas, Brazil	HQ426268	HQ426441	HQ426525	HQ426348	HQ426179	JF416848	JF416881
Chatogekko amazonicus	LSUMZ-H14192	Southeast of Santarém, Pará, Brazil	JF416912	JF416916	JF416922	JF416919	JF416925	JF416846	JF416879
Chatogekko amazonicus	LSUMZ-H14233	Southeast of Santarém, Pará, Brazil	HQ426267	HQ426440	HQ426524	HQ426347	HQ426178	JF416847	JF416880
Chatogekko amazonicus	LSUMZ-H14050	Rio Ituxi, Amazonas, Brazil	HQ426269	HQ426442	HQ426526	HQ426349	HQ426180	JF416849	JF416882
Chatogekko amazonicus	LSUMZ-H17771	Parque Estadual Guajara-Mirim, Rondonia, Brazil	JF416913	JF416917	JF416923	JF416920	JF416926	JF416850	JF416883
Coleodactylus brachystoma	MZUSP92569	Piauí, Brazil	EF534792	EF534959	EF534917	EF534874	EF534833	JF416851	JF416884
Coleodactylus cf. *brachystoma*	CHUNB43901	São Domingos, Goiás, Brazil	HQ426270	HQ426443	HQ426527	HQ426350	HQ426181	JF416852	JF416885
Coleodactylus septentrionalis	LSUMZ-H12351	East of Rio Ajarani, Roraima, Brazil	EF534791	EF534958	EF534916	EF534873	EF534832	JF416853	JF416886
Gonatodes albogularis	MVZ 204073	Limon, Costa Rica	EF534797	–	–	–	EF534839	–	–
Gonatodes albogularis	KU 289808	San Salvador, El Salvador	–	EF534965	EF534923	EF534880	–	JF416854	JF416887
Gonatodes annularis	ROM 22961	Guyana	–	EF534961	EF534919	EF534876	–	JF416855	JF416888

Gonatodes annularis	No ID	French Guiana	EF534794	–	–	–	EF534835	–	–
Gonatodes caudiscutatus	KU218359	Limon, Ecuador	EF534795	EF534962	EF534920	EF534877	EF534836	JF416856	JF416889
Gonatodes ceciliae	TG00039	Trinidad	JF416914	EF564114	EF564088	EF564062	HQ426193	JF416857	JF416890
Gonatodes concinnatus	LSUMZ-H12688	Sucumbios, Ecuador	HQ426282	EF564096	EF564070	EF564044	HQ426194	JF416858	JF416891
Gonatodes eladioi	CHUNB40097	Pará, Brazil	HQ426283	EF564107	EF564081	EF564055	HQ426195	JF416859	JF416892
Gonatodes humeralis	MF19492	Tiputini Biodiversity Station, Orellana, Ecuador	EF534796	EF534964	EF534922	EF534879	EF534838	JF416860	JF416893
Lepidoblepharis sp.	KU218367	Manabi, Ecuador	EF534789	EF534956	EF534914	EF534871	EF534830	JF416861	JF416894
Lepidoblepharis festae	LSUMZ-H12704	Sucumbios, Ecuador	HQ426297	EF564094	EF564068	EF564042	HQ426208	JF416862	JF416895
Lepidoblepharis xanthostigma	MVZ171438	Limon, Costa Rica	EF534790	EF534957	EF534915	EF534872	EF534831	JF416863	JF416896
Pseudogonatodes guianensis	AMCC106916	Berbice River, Guyana	HQ426316	HQ426490	HQ426571	HQ426399	HQ426228	JF416864	JF416897
Pseudogonatodes guianensis	KU222142	Loreto, Peru	EF534784	EF534950	EF534908	EF534865	EF534824	JF416865	JF416898
Pseudogonatodes guianensis	LSUMZ-H13583	Rio Jurura, Acre, Brazil	HQ426317	HQ426491	HQ426572	HQ426400	HQ426229	JF416866	JF416899
Saurodactylus brosseti	TG00082	Morocco	EF534802	EF534970	EF534928	EF534885	EF534844	JF416867	JF416900
Sphaerodactylus elegans	YPM 14795	Monroe County, Florida, USA	EF534787	EF534954	EF534912	EF534869	EF534828	JF416868	JF416901
Sphaerodactylus glaucus	JAC24229	Oaxaca, Mexico	HQ426325	HQ426498	HQ426579	HQ426408	HQ426237	JF416869	JF416902
Sphaerodactylus macrolepis	TG00099	Puerto Rico	HQ426326	HQ426499	HQ426580	HQ426409	HQ426238	JF416870	JF416903

Sphaerodactylus nicholsi	TG00211	Puerto Rico	HQ426328	HQ426501	HQ426582	HQ426411	HQ426240	JF416871	JF416904
Sphaerodactylus nigropunctatus	FLMNH144010	Long Island, Bahamas	HQ426329	EF534953	EF534911	EF534868	EF534827	JF416872	JF416905
Sphaerodactylus torrei	JB34	Cuba	EF534788	EF534955	EF534913	EF534870	EF534829	JF416873	JF416906
Pristurus carteri	TG00083	Yemen	EF534803	EF534971	EF534929	EF534886	EF534845	JF416874	JF416907
Teratoscincus przewalskii	TG00253	China	HQ426335	HQ426507	HQ426588	HQ426417	HQ426246	JF416875	JF416908
Teratoscincus microlepis	TG00074	Pakistan	EF534800	EF534968	EF534926	EF534883	EF534842	JF416876	JF416909
Hemidactylus platyurus	JFBM15815	unknown	HQ426273	HQ426446	HQ426530	HQ426353	HQ426184	JF416877	JF416910

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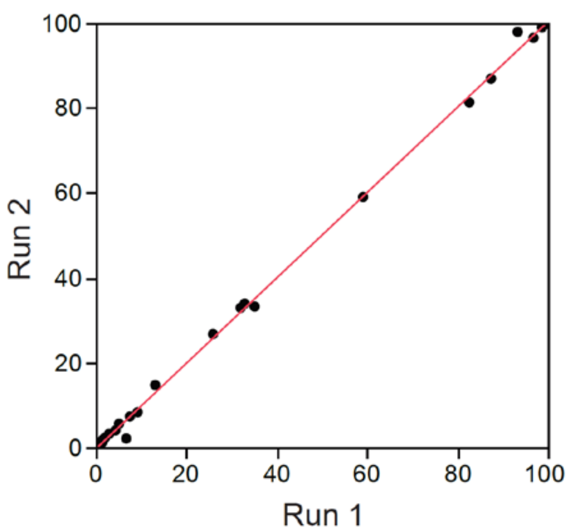
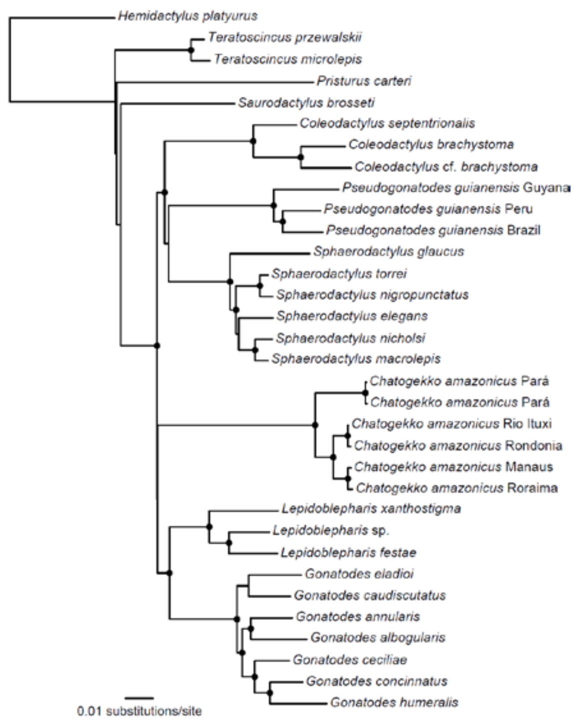
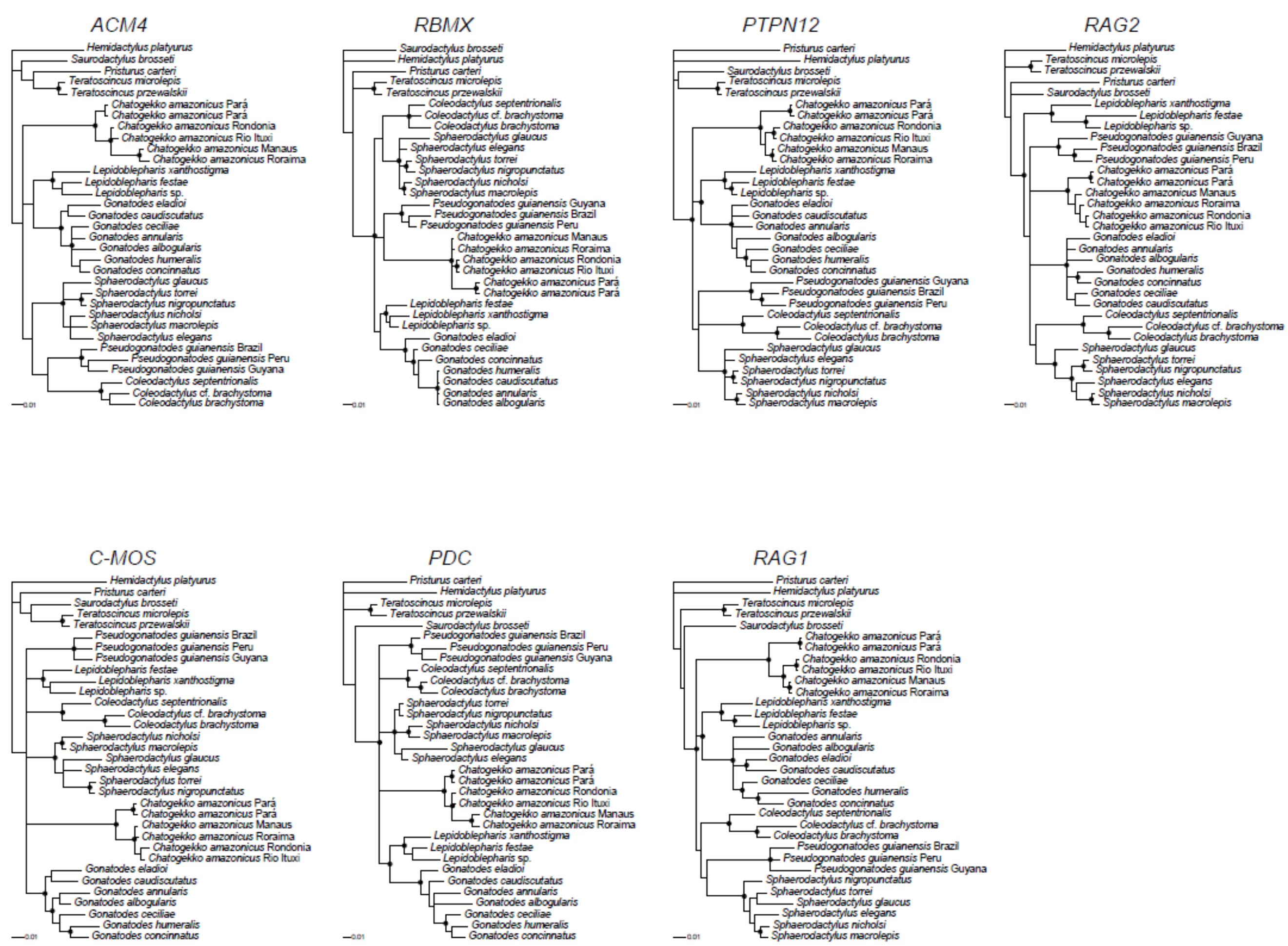
Supplementary Figures



Supplementary Figure 1. Split frequencies in run1 vs. run2 for the concatenated Bayesian analysis of the nuclear gene data.



Supplementary Figure 2. Partitioned Maximum Likelihood phylogeny estimated from the nuclear gene dataset. Black circles indicate nodes with bootstrap values > 70.



Supplementary Figure 3. Bayesian phylogenies for each of the individual loci from the nuclear gene data. Black circles indicate nodes with posterior probabilities > 0.95.