

A new phylogenetic classification for the gymnophthalmid genera *Cercosaura*, *Pantodactylus* and *Prionodactylus* (Reptilia: Squamata)

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Because of the poor state of knowledge of many of the gymnophthalmid genera, systematic revision is necessary to render the classification consistent with evolutionary history. To that end, I conducted a review of the species of three genera of the Cercosaurinae which appear to form a monophyletic group: *Cercosaura*, *Pantodactylus*, and *Prionodactylus*. Phylogenetic analysis of 61 morphological characters was conducted after specimens of all species were examined to evaluate the composition of each taxon. The phylogenetic reconstruction suggested that the genus *Prionodactylus* was paraphyletic. A new phylogenetic classification is proposed that synonymizes *Pantodactylus* and *Prionodactylus* with *Cercosaura*. *Cercosaura* is redefined to include 11 species and seven subspecies. A key is provided to distinguish among species. © 2003 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2003, 137, 101–115.

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INTRODUCTION

The family Gymnophthalmidae has endured an unstable taxonomic history. Many of the genera are inadequately characterized and the few published generic revisions usually have resulted in the authors noting that such allocations of species were ‘for convenience’ (e.g. Uzzell, 1973). Many others (Montanucci, 1973; Oftedal, 1974) have lamented the fragmentary state of knowledge of the relationships within the family. This is partly because of the dearth of specimens in collections due to the secretive habits of the species that occur in remote habitats, primarily in tropical America.

Phylogenetic relationships of the family have also been inadequately studied. Two morphological phylogenies have been published (Presch, 1980; Hoyos, 1998), but both were considered preliminary by the authors and clades within these phylogenies were poorly supported. It was not until the publication of the molecular phylogeny by Pellegrino *et al.* (2001)

that a more comprehensive attempt was made to examine the relationships of the genera by incorporating multiple species per genus. That phylogeny included 50 species (out of 178 total) representing 26 genera (out of 36 total), which allowed the authors to propose a phylogenetic classification of the higher order relationships within the family. They proposed four subfamilies (two novel and two resurrected), with two tribes each for two of the subfamilies. They left the generic and specific taxonomy unmodified.

One of the subfamilies resurrected by Pellegrino *et al.* (2001) was Cercosaurinae Gray. Two tribes were named in this subfamily, Eclepini Fitzinger and Cercosaurini Gray. Pellegrino *et al.* (2001) placed eight genera into the tribe Cercosaurini and mentioned that eight others that were not examined in their study probably belonged there as well. All of the Cercosaurini except for *Bachia* had been members of Boulenger’s (1885) Group II of the Teiidae. Group II (Boulenger, 1885) cannot now be considered a natural group because four members of Group II (*Arthrosaura*, *Ecleopus*, *Leposoma*, and probably *Amasaurus*) were placed in the tribe Eclepini, and *Alopoglossus* is now assigned to a separate subfamily, Alopoglossinae.

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During an ongoing revision of lizard species that formerly belonged to Group II (Boulenger, 1885), it came to my attention that some of the Cercosaurini species were in need of reallocation. *Cercosaura*, *Pantodactylus* and *Prionodactylus* were found to have relationships that did not coincide with current classification. These problems were suggested in the phylogeny of Pellegrino *et al.* (2001), but these investigators were hampered by relatively poor taxonomic sampling within the Cercosaurini, and chose not to make any taxonomic alterations at the generic level. The present paper addresses the taxonomy and relationships of these three genera of the Cercosaurini in an attempt to achieve a classification in agreement with phylogeny.

NOMENCLATURAL HISTORY

In 1830, Wagler described the monotypic genus *Cercosaura* for *C. ocellata*. Gray (1845) erected a new genus for *Emminia olivacea*, but that genus was later synonymized with *Cercosaura ocellata* by Peters (1862) and O'Shaughnessy (1881). The species *C. humilis* was proposed by Peters (1862) but later synonymized with *C. ocellata* by Boulenger (1885).

Gray (1838) erected the family Cercosauridae, which only contained the genus *Cercosaura*. His definition for the family was very general, consisting of 'body subcylindrical, sides rounder with scales like the back; back and upper part of the tail with rings of large keeled scales forming longitudinal series; throat, belly, and tail beneath, with flat square shields' (p. 391). His familial definition did not match with its content, which listed two species: *Cercosaura ocellata* and *C. schreibersii* Wiegmann. *Pantodactylus schreibersii* (as this species is currently classified) does not have dorsal scales in longitudinal series. O'Shaughnessy (1881) expanded the concept of the family by including species that are now placed in the genera *Cercosaura*, *Prionodactylus*, *Pantodactylus* and *Arthrosaura*. Cercosauridae has not received familial status since O'Shaughnessy (1881) and the species have since been placed in the Teiidae (Boulenger, 1885) and, more recently, the Gymnophthalmidae (Presch, 1983; Estes *et al.*, 1988). Pellegrino *et al.* (2001) recognized the subfamily Cercosaurinae within in family Gymnophthalmidae, in which they placed 22 genera.

O'Shaughnessy (1881) considered *Pantodactylus* Duméril and Bibron and *Prionodactylus* O'Shaughnessy (defined in that publication) to be subgenera of *Cercosaura*. *Pantodactylus* contained three species: *argulus* Peters, *reticulata* O'Shaughnessy and *schreibersii*, whereas *Prionodactylus* contained a single species, *manicata* O'Shaughnessy. Boulenger (1885) transferred *reticulata* to *Arthrosaura*, raised both subgenera to genera, and transferred *C. (Panto-*

dactylus) argulus Peters, *C. (Pantodactylus) quadrilineata* Boettger and *C. (Pantodactylus) vertebralis* O'Shaughnessy to *Prionodactylus*. Boulenger (1885) additionally distinguished and described *P. oshaughnessyi* from material previously thought to represent *P. argulus*. According to Boulenger's (1885) key, the principal difference between *Pantodactylus* and *Prionodactylus* was the arrangement of dorsal scales in either transverse and oblique rows (*Pantodactylus*) or transverse rows only (*Prionodactylus*).

Burt & Burt (1931) conducted a major revision of *Prionodactylus*, *Pantodactylus* and several other genera. They stated that they found no difference between *Prionodactylus* and *Euspondylus*, because the character that Boulenger (1885) had used to differentiate them (smooth or keeled dorsal scales) was not reliable and was prone to polymorphism within species (Burt & Burt, 1931). On that basis, and on their examination of many of the species, they constructed a key for *Euspondylus* (*sensu* Burt & Burt, 1931) that included members of the currently recognized genera *Euspondylus*, *Neusticurus*, *Pantodactylus*, *Pholidobolus*, *Placosoma*, *Prionodactylus*, *Ptychoglossus* and *Riolama*. They included *Pantodactylus quadrilineatus* in *Euspondylus* but treated the rest of *Pantodactylus* separately. According to Burt & Burt (1931, 1933), *Pantodactylus* contained four species, two of which they described as novel. They synonymized *Alopoglossus* and *Loxopholis* with *Pantodactylus*. None of the aforementioned changes made by Burt & Burt (1931) have been accepted by subsequent authors.

Ruibal (1952) is the only worker to have attempted a revision of the genera *Cercosaura* and *Pantodactylus*. He erected three subspecies within *C. ocellata*: *C. o. ocellata* from central and northern Brazil and Guyana, *C. o. petersi* from southern Brazil and Bolivia, and *C. o. bassleri* from Peru and Bolivia (Ruibal, 1952). Regarding *Pantodactylus*, he erected three subspecies of *P. schreibersii* (*schreibersii*, *albostrigatus* and *parkeri*) and transferred *Prionodactylus quadrilineatus* back to *Pantodactylus*. Ruibal (1952) and subsequent authors (e.g. Avila-Pires, 1995) remarked that *Pantodactylus* and *Prionodactylus* are virtually indistinguishable based on external morphology and may not represent distinct genera.

Uzzell (1973) conducted the only review of the genus *Prionodactylus*. He reallocated all of the species included in Burt & Burt's (1931) key and separated the species of *Euspondylus* from those of *Prionodactylus* and other genera based on dorsal scale shape (Uzzell, 1973). He also erected a new genus, *Riolama*, for *Prionodactylus leucostictus* Boulenger, and described a new species, *Prionodactylus dicrus*. He discussed the taxonomy of *Prionodactylus* and its relationship to *Euspondylus*, a genus with which *Prionodactylus* has often been associated. Additionally,

Uzzell (1973) synonymized *P. palmeri* Boulenger and *Euspondylus ampuedai* Lancini with *P. vertebralis*, *P. okendeni* Boulenger with *P. manicatus bolivianus*, and *P. oshaughnessyi*, *P. holmgreni* Andersson and *P. columbiensis* Werner with *P. argulus*.

Avila-Pires (1995) resurrected *P. oshaughnessyi* from within *P. argulus*, presenting new data based on Brazilian specimens supporting their distinctiveness. La Marca & García-Pérez (1990) resurrected *P. ampuedai* from synonymy with *P. vertebralis*, mentioning a few characters that suggested its specific status. Gorzula & Señaris (1998) described a new species from Venezuela, *P. nigroventris*, transferred another Venezuelan species from *Euspondylus*, *P. phelporum* (Lancini), to *Prionodactylus*, and synonymized *Euspondylus goeleti* Myers & Donnelly with *P. phelporum*. Later, Myers & Donnelly (2001) resurrected *E. goeleti* from *P. phelporum*, but accepted its transfer to *Prionodactylus* as *P. goeleti*.

MATERIALS AND METHODS

Construction of a classification that is congruent with evolutionary history required two steps. (1) It was first necessary to establish the terminal taxa for phylogenetic analysis. This was critical because of the great amount of taxonomic confusion that has surrounded the species in these genera. (2) A phylogenetic analysis was performed using the operational taxonomic units (OTUs) established in step 1 and the resulting topology was examined for congruence with current classification of this group.

Preserved specimens of all species of the three genera were examined from museum collections. Museum abbreviations follow Leviton *et al.* (1985) except for Museo de Historia Natural, Universidad Nacional de San Antonio Abad de Cusco, Peru (UNSAAC). Material examined is listed in Appendix 1. For taxonomic and phylogenetic comparisons, 61 external morphological characters were examined. The list and definition of characters appears in Appendix 2.

Statistical tests (correlation, multiple regression, principal components analysis) were performed with Statistica version 4.5 (StatSoft, 1993) and cluster analyses were performed by using UPGMA as implemented in PAUP* version 4.0b8 (Swofford, 2001). For phylogenetic analyses, the maximum parsimony criterion was implemented with PAUP* version 4.0b8 (Swofford, 2001). I found that nearly all characters (60 of 61) displayed some degree of intraspecific polymorphism. Because of this high level of polymorphism, and its potentially informative nature (Campbell & Frost, 1993; Wiens, 1995, 1998, 2000; Smith & Gutberlet, 2001), polymorphism was utilized to aid in phylogeny reconstruction wherever possible. Several authors have shown that the frequency method is

most appropriate for analysing polymorphic data (Wiens, 1995, 1998; Kornet & Turner, 1999; Smith & Gutberlet, 2001). Frequencies were calculated using the Generalized Frequency Coding (GFC) method (Smith & Gutberlet, 2001; implemented by Bonett, 2002). Strict frequencies were used for characters that could not be validly ordered a priori. Cumulative frequencies were used for characters with obvious order as dictated by the GFC methodology (Smith & Gutberlet, 2001). The subcharacters calculated by GFC were input into PAUP* and used as characters in the phylogenetic analysis with unequal subcharacter weighting. In this way, all polymorphism data were utilized and no information was discarded (as is often the case with polymorphic characters; see Wiens, 2000). Branch and bound searches were performed and support for nodes was assessed by using 100 non-parametric branch and bound bootstrap replicates (Felsenstein, 1985) implemented with PAUP*.

Outgroup selection was problematic, given the poorly known relationships among gymnophthalmid genera. Initially, outgroups were selected based on the topology of Pellegrino *et al.* (2001) to allow direct comparison of resultant phylogenies. However, it is more likely that taxa that were left out of the Pellegrino *et al.* (2001) analysis were more closely related to the target group (as suggested by previous morphological studies; e.g. Uzzell, 1973; Presch, 1980) and therefore were more appropriate outgroups (Griffiths, 1983). On that basis, two outgroups were utilized: *Opipeteu xestus* Uzzell was the designated outgroup in the parsimony analysis, whereas *Euspondylus spinalis* (Boulenger) was treated as part of the ingroup and its position allowed to float with respect to the other ingroup taxa.

In addition to simply searching for the shortest tree, three comparisons were made to test the null hypotheses established by the Pellegrino *et al.* (2001) topology. These comparisons were performed by constraining the topology of the shortest tree derived in this study. The first constraint was to force *Pantodactylus quadrilineatus* to be basal to the rest of the clade containing *Cercosaura*, the remaining *Pantodactylus* species, and *Prionodactylus* (i.e. the position of *P. quadrilineatus* in the Pellegrino *et al.*, 2001, topology). The second constraint was to force the monophyly of the genus *Prionodactylus* to assess this genus' phylogenetic validity. The third constraint was to use the Pellegrino *et al.* (2001) topology as a 'backbone constraint' (Swofford, 1993), allowing the taxa that were not included by Pellegrino *et al.* (2001) to form clades based on that topology backbone. The difference in length between the constraint trees and the shortest tree without constraints was examined using the a Wilcoxon signed ranks test (Templeton, 1983) implemented with PAUP*.

DETERMINATION OF TERMINAL TAXA

At present, a maximum of 18 terminal taxa (species or subspecies) are currently recognized under *Cercosaura*, *Pantodactylus* and *Prionodactylus* (Ruibal, 1952; Uzzell, 1973; La Marca & García-Pérez, 1990; Myers & Donnelly, 2001; Table 1). The status of some of these taxa has been disputed by various authors, making it necessary to discuss the most recent evidence to determine which taxa should be operationally used in the phylogenetic reconstruction. Below, I provide a justification for the disputed OTUs that I use in the phylogeny reconstruction. Taxa not discussed below are those that have not been disputed recently and, for that reason, are not examined here. Table 1 contains a list of all potential taxa with their OTU allocations for this study.

CERCOSAURA OCELLATA WAGLER

Cercosaura ocellata Wagler, 1830: 158.
Emminia olivacea Gray, 1945: 24.
Cercosaura humilis Peters, 1862: 180.
Euspondylus simonsii Burt & Burt, 1931: 337.
Cercosaura ocellata ocellata Ruibal, 1952: 494.
Cercosaura ocellata petersi Ruibal, 1952: 497.
Cercosaura ocellata bassleri Ruibal, 1952: 499.

The subspecies of *Cercosaura ocellata* that were diagnosed by Ruibal (1952) have not been disputed by other authors. For the purposes of this study all subspecies were treated together. Specimens of *C. o. petersi* were not available for examination; therefore, *C. o. ocellata* and *C. o. bassleri* were included.

PANTODACTYLUS SCHREIBERSII (WIEGMANN)

Cercosaura schreibersii Wiegmann, 1834: 10.
Pantodactylus dorbignyi Duméril & Bibron, 1839: 431.
Cercosaura (Pantodactylus) schreibersii: Peters, 1862: 182.
Pantodactylus bivittatus Cope, 1863: 103.
Pantodactylus schreibersii: Boulenger, 1885: 388.
Pantodactylus borelli Peracca, 1894: 176.
Prionodactylus albostrigatus Griffin, 1917: 314.
Euspondylus quadrilineatus: Burt & Burt, 1931: 335.
Pantodactylus schreibersii albostrigatus: Parker, 1931: 286.
Pantodactylus schreibersii schreibersii: Ruibal, 1952: 515.
Pantodactylus schreibersii: Tedesco & Cei, 1999: 314 (exclusive of *P. s. parkeri*).

Ruibal (1952) recognized three subspecies of *Pantodactylus schreibersii* corresponding with geographical groups of forms that had been considered to be different species (*P. albostrigatus*, *parkeri* and *schreibersii*). I was not able to examine *P. s. albostrigatus*. Ruibal (1952) had considerable difficulty with this subspecies because he was only able to examine females of *Prionodactylus albostrigatus* and the original description was also restricted to females (Griffin, 1917). Burt & Burt (1931) had synonymized *Pr. albostrigatus* with *Pa. quadrilineatus* and, because Ruibal (1952) only examined female *Pr. albostrigatus* specimens and male *Pa. quadrilineatus* specimens, he expressed concern that there was a possibility that they could be conspecific (in agreement with Burt & Burt, 1931).

Table 1. Potential and operational taxonomic units applied in this study

Species/subspecies name	Author	Operational taxonomic unit in this study
<i>Cercosaura ocellata bassleri</i>	Ruibal	<i>Cercosaura ocellata</i>
<i>Cercosaura ocellata ocellata</i>	Wagler	<i>Cercosaura ocellata</i>
<i>Cercosaura ocellata petersi</i>	Ruibal	<i>Cercosaura ocellata</i>
<i>Pantodactylus quadrilineatus</i>	Boettger	<i>Pantodactylus quadrilineatus</i>
<i>Pantodactylus parkeri</i>	Ruibal	<i>Pantodactylus parkeri</i>
<i>Pantodactylus schreibersii albostrigatus</i>	(Griffin)	<i>Pantodactylus schreibersii albostrigatus</i>
<i>Pantodactylus schreibersii schreibersii</i>	(Wiegmann)	<i>Pantodactylus schreibersii schreibersii</i>
<i>Prionodactylus ampuedai</i>	(Lancini)	<i>Prionodactylus vertebralis</i>
<i>Prionodactylus argulus</i>	(Peters)	<i>Prionodactylus argulus</i>
<i>Prionodactylus dicrus</i>	Uzzell	<i>Prionodactylus dicrus</i>
<i>Prionodactylus eigenmanni</i>	Griffin	<i>Prionodactylus eigenmanni</i>
<i>Prionodactylus goeleti</i>	(Myers and Donnelly)	<i>Prionodactylus phelporum</i>
<i>Prionodactylus manicatus bolivianus</i>	Uzzell	<i>Prionodactylus manicatus</i>
<i>Prionodactylus manicatus manicatus</i>	O'Shaughnessy	<i>Prionodactylus manicatus</i>
<i>Prionodactylus oshaughnessyi</i>	Boulenger	<i>Prionodactylus argulus</i>
<i>Prionodactylus nigroventris</i>	Gorzula and Señaris	<i>Prionodactylus nigroventris</i>
<i>Prionodactylus phelporum</i>	(Lancini)	<i>Prionodactylus phelporum</i>
<i>Prionodactylus vertebralis</i>	(O'Shaughnessy)	<i>Prionodactylus vertebralis</i>

Table 2. A comparison of *Pantodactylus quadrilineatus*, *P. parkeri* and *P. schreibersii* based on specimens examined in this study and the descriptions of *P. schreibersii albostrigatus* by Griffin (1917) and Ruibal (1952)

Character	<i>P. schreibersii albostrigatus</i>	<i>P. schreibersii schreibersii</i>	<i>P. parkeri</i>	<i>P. quadrilineatus</i>
Number examined	0	14	10	6
Dorsal transverse rows	28–32	27–35	28–36	28–34
Lateral scales	smaller than dorsals	same size as dorsals	same size as dorsals	same size as dorsals
Longitudinal ventral rows	6	6	6	4
Transverse ventral rows	17–20	19–24	20–22	21–23
Postocular scales	2*	2	3	3
Posterior cloacal plate scales	2	2–4	2–3	3–6
Femoral pores in males	not available	3–5	2–6	8
Femoral pores in females	0–1	2–3	1–3	1–3

*Ruibal (1952) noted that scalation of *P. s. albostrigatus* was similar to *P. s. schreibersii* except where noted. He did not mention the postoculars.

However, Ruibal (1952) supported the distinctness of the two forms based on his limited data.

Although I was not able to examine *P. s. albostrigatus*, most of the *P. quadrilineatus* that I examined were females, in contrast to the sex of those specimens examined by Ruibal (1952). I was therefore able to compare the original description of *Prionodactylus albostrigatus* and the comments of Ruibal (1952) concerning his female specimens with the mostly female specimens of *P. quadrilineatus* that I examined; many differences were found (Table 2). The differences are great enough to convince me that *P. s. albostrigatus* is closely related to *P. schreibersii* and only distantly related to *P. quadrilineatus*. This conclusion is supported by the molecular analysis of Pellegrino *et al.* (2001) in which *P. s. albostrigatus* and *P. s. schreibersii* were sister taxa, whereas *P. quadrilineatus* did not form a clade with either species.

Ruibal (1952) treated *P. s. parkeri* as a subspecies comprising the western populations of *P. schreibersii* from Peru, Bolivia and extreme western Brazil. The known range was later extended to north-west Argentina (Viñas & Daneri, 1991). A recent study by Tedesco & Cei (1999) utilized osteological characters to determine if the two Argentinean forms, *P. s. parkeri* and *P. s. schreibersii*, merited species status. Their study revealed several osteological characters that distinguished the two forms. Therefore, Tedesco & Cei (1999) raised both *P. s. schreibersii* and *P. s. parkeri* to species status. Tedesco & Cei (1999) did not examine any specimens of *P. s. albostrigatus*, nor did they mention what status that subspecies might have. From the available data (based on the 61 characters that I examined and published information), *P. s. albostrigatus* appears to be quite similar to *P. s. schreibersii* and less similar to *P. s. parkeri*. Therefore, I tentatively consider *P. s.*

albostrigatus to be a subspecies of *P. schreibersii*, whereas *P. parkeri* should retain the specific status granted by Tedesco & Cei (1999).

PANTODACTYLUS PARKERI RUIBAL

Pantodactylus schreibersii albostrigatus: Parker (part), 1931: 286.

Euspondylus champsonatus: Burt & Burt (part), 1931: 335.

Pantodactylus schreibersii parkeri Ruibal, 1952: 518.

Pantodactylus parkeri: Tedesco & Cei, 1999: 314.

To assess the assertion of Tedesco & Cei (1999) about the specific status of *P. parkeri*, I examined 61 morphological characters to determine if a notable difference between this species and *P. schreibersii* existed. Although I found colour and pattern differences and overlapping meristic variation in several characters, the differences between the species for external morphology were few (Table 2). No external morphological character differences appeared to be fixed; however, based on the significant, presumably fixed osteological differences discovered by Tedesco & Cei (1999), I continue to recognize this taxon as a distinct species.

PRIONODACTYLUS ARGULUS (PETERS)

Cercosaura (Pantodactylus) argulus Peters, 1862: 184.

Prionodactylus argulus: Boulenger, 1885: 391.

Prionodactylus oshaughnessyi Boulenger, 1885: 392.

Prionodactylus holmgreni Andersson, 1914: 9.

Prionodactylus columbiensis Werner, 1916: 306.

When Uzzell (1973) synonymized *P. oshaughnessyi* with *P. argulus*, he did so because he did not find sufficient differences between the two species based on

the four specimens of *P. oshaughnessyi* that he examined. Avila-Pires (1995) examined 90 individuals that she considered to be *P. oshaughnessyi* and presented evidence for its recognition as a distinct species. She provided a table of seven characters that differed between the species and also used two other characters as supporting evidence (numbers of transverse rows of ventral scales and transverse rows of dorsal scales). In many cases the meristic characters had overlapping ranges that made interpretation difficult. I examined 39 individuals for seven of her nine characters and 50 other external morphological characters to determine if a significant difference was in fact apparent.

Upon examination of specimens for this study I could not distinguish between the species using the characters designated by Avila-Pires (1995) because the defining characters did not appear to be correlated with each other. Therefore, I chose one of those characters, lateral scale size, to name individuals. Avila-Pires (1995) states that *P. argulus* has lateral scales that are moderately smaller than the dorsals, whereas *P. oshaughnessyi* has lateral scales that are distinctly smaller than the dorsals. Although this character could appear to be subjective, it was actually obvious as to which lateral scale condition the specimen possessed. Therefore, in all subsequent analyses I grouped the specimens based on this character.

Of the nine characters of Avila-Pires (1995), seven were examined in this study: lateral scale size, number of femoral pores in males and females, presence of preanal pores, number of scales in a transverse ventral row between pores, transverse rows of ventrals, and transverse rows of dorsals. Of the other two characters, scales around midbody is too variable to be reliable (because an exact scale position for counting was not stated) and tail/snout-vent length ratio was not possible due to the fact that most specimens did not have complete, original tails. To determine if Avila-Pires's (1995) characters in fact may be used to differentiate between species, I constructed a correlation matrix of five of the Avila-Pires characters for which I

had data for 23 individuals (Table 3). If these characters serve to diagnose the two species, each of the characters should correlate strongly with one another. This was not the case – only number of ventral scale rows and presence of preanal pores were moderately negatively correlated with each other ($R = -0.65235$). None of the other characters displayed high correlation with any other.

To simultaneously examine multiple characters, a principal components analysis (PCA) was performed. The analysis utilized 49 characters, including seven of those used by Avila-Pires (1995), to determine if distinct groups were obvious from the data. As can be seen in Fig. 1, no real structure is apparent and there appears to be intergradation between the two putative species. A cluster analysis of 55 characters showed the same pattern of no separation of species based on morphology (Fig. 2). Specimens did not convincingly cluster by species or by geographical location. Thus, each analysis suggests that *P. argulus* represents only one species, with *P. oshaughnessyi* being a junior synonym (in agreement with Uzzell, 1973).

Although specimens did not cluster by species, the cluster analysis suggested a possible geographical trend (Fig. 2), potentially representing clinal variation within the species. In order to examine this, I conducted a multiple regression of the five Avila-Pires (1995) characters on latitude. This type of analysis is possible because the specimens represented here occur almost in a linear distribution, following the eastern Andean foothills in a north–south direction. The regression was significant ($R = 0.87616$; $F = 9.2511$; $P = 0.00046$). This implies significant clinal variation in the five characters, which further refutes the recognition of two separate taxa (Endler, 1977). Even though specimens from the entire geographical range of the species were not examined, the specimens examined for this study did cover the entire range of character variation as those examined by Avila-Pires (1995). Thus, the variation found by Avila-Pires (1995) appears to have been clinal in nature and not due to distinct species.

Table 3. Correlation matrix of the five characters used by Avila-Pires (1995) to distinguish *Prionodactylus oshaughnessyi* from *P. argulus*

	Preanal pores	Interpreanals	Dorsals	Ventrals	Laterals
Preanal Pores	1				
Interpreanals	0.28916	1			
Dorsals	0.33918	0.38509	1		
Ventrals	-0.65235	0.09748	0.28824	1	
Laterals	-0.32441	0.08619	-0.23204	0.34940	1

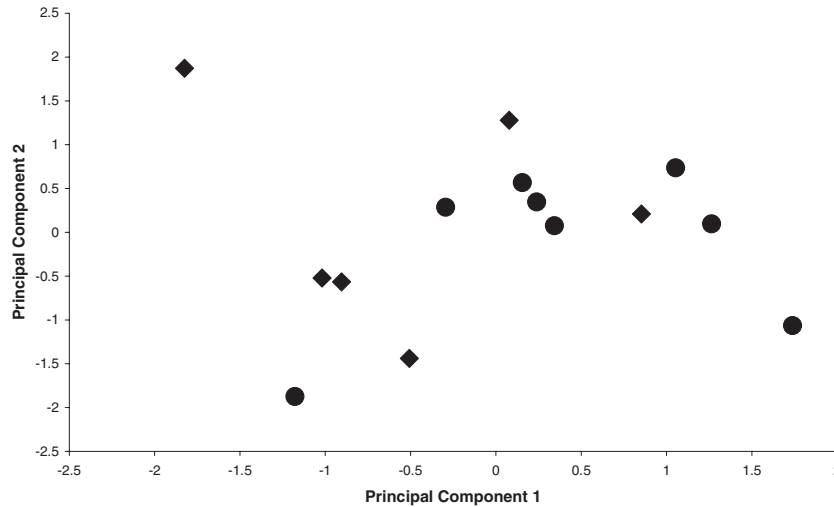


Figure 1. Principal components analyses of *Prionodactylus argulus* based on 49 variables. Diamonds represent '*Prionodactylus oshaughnessyi*' individuals; circles represent *P. argulus* (*sensu stricto*) individuals.

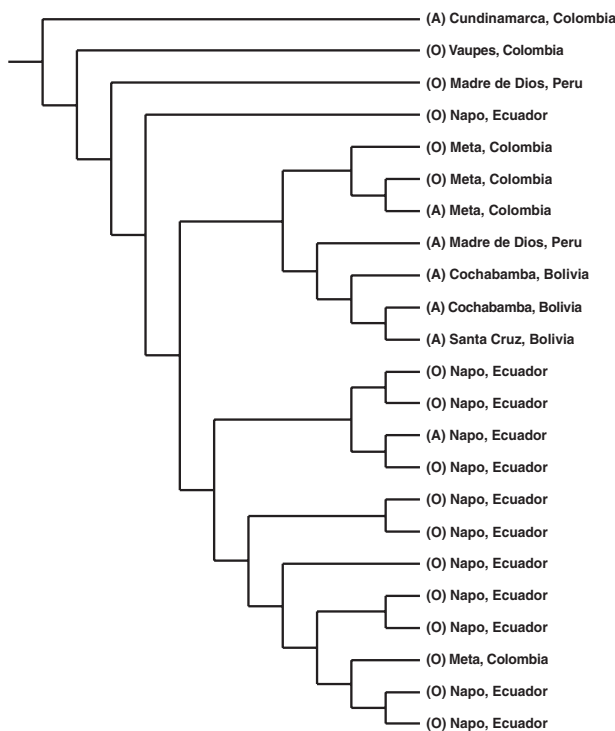


Figure 2. Cluster analysis of 23 specimens of *Prionodactylus argulus* for 55 characters. Specimens are listed by the department or province in which their locality lies and the country. (A) indicates that the specimen was classed as *P. argulus* (*sensu stricto*) and (O) indicates that the specimen was classed as *P. oshaughnessyi*. Species classifications were based on lateral scale size (see text).

PRIONODACTYLUS VERTEBRALIS (O'SHAUGHNESSY)
Cercosaura (*Pantodactylus*) *vertebralis* O'Shaughnessy, 1879: 298.
Prionodactylus vertebralis: Boulenger, 1885: 394.
Prionodactylus palmeri Boulenger, 1908: 518.
Prionodactylus marianus Ruthven, 1921: 1.
Euspondylus ampuedae Lancini, 1968: 4.
Prionodactylus ampuedai: La Marca & García-Pérez, 1990: 111.

When Uzzell (1973) synonymized *Euspondylus ampuedae* with *Prionodactylus vertebralis*, he did so without examining any specimens of *E. ampuedae*. There were few specimens known at that time. La Marca & García-Pérez (1990) reported additional specimens and resurrected the species as *Prionodactylus ampuedai* (correcting the latinized name ending). They based their conclusion on five differences, three of which are based on colour pattern. Similar to Uzzell (1973), I have not been able to examine any of the specimens designated as *P. ampuedai* (most of which are held in private collections), but I tend to follow Uzzell (1973) because the differences presented in the La Marca & García-Pérez (1990) table are poorly delineated and not convincing (i.e. shape of pale lip line and overlapping femoral pore counts). Until more definitive evidence is presented, the status and relationships of *P. ampuedai* will not be assessed.

PRIONODACTYLUS PHELPSORUM (LANCINI)
Euspondylus phelpsi Lancini, 1968: 2.
Euspondylus phelpsorum: Myers & Donnelly, 1996: 23.

Euspondylus goeleti Myers & Donnelly, 1996: 23.

Prionodactylus phelpsorum: Gorzula & Señaris, 1998: 139.

Prionodactylus goeleti Myers & Donnelly, 2001: 60.

It seemed questionable that this taxon belongs to *Prionodactylus* because of the condition of its gular scales. Uzzell (1973) re-diagnosed the genus *Prionodactylus* as having a double widened row of gular scales, at least posteriorly. He was not able to examine *Euspondylus phelpsi* but, because Lancini (1968) did not mention the gular scales, he retained *E. phelpsi* as *Euspondylus*. Gorzula & Señaris (1998) also did not mention the gulars, but decided without explanation that the taxon should be included in *Prionodactylus*. I found the gular character to be variable in the three individuals I examined (see Appendix 1), with one individual possessing a complete double row, one individual without any differentiation in size from the ventrolateral gular scales, and one individual with the double widened row only posteriorly. The photographs of *P. goeleti* in Myers & Donnelly (1996, 2001) also display variation in the gular character. I would be hesitant to decide on its generic status except for its obviously close relationship with *P. nigroventris* (see below), a species that possesses all the diagnostic characters of *Prionodactylus*. Based on these similarities, I retain this species in *Prionodactylus*.

The status of *P. goeleti* remains in question with alternating publications of Myers & Donnelly (1996, 2001) and Gorzula & Señaris (1998). I was unable to examine specimens assigned to *P. goeleti* and only consider *P. phelpsorum* for this study.

PHYLOGENETIC RELATIONSHIPS OF THE SPECIES

The phylogenetic reconstruction based on 61 morphological characters (60 of which were variable within the ingroup) is depicted in Fig. 3. A single most parsimonious tree was found and the resulting topology required 3 389 574 weighted steps. Of the 469 GFC subcharacters, 331 were parsimony informative. To accompany that tree, a partial topology reconstructed under maximum likelihood criterion of the same group of species from the Pellegrino *et al.* (2001) combined data set of five genes is shown in Fig. 4. Although this study included many more taxa from this group of gymnophthalmids than did Pellegrino *et al.* (2001), comparison of Figs 3 and 4 shows that, although there are conflicts between the two reconstructions, similar results regarding current classification are evident. In both cases, *Prionodactylus* is paraphyletic with respect to *Cercosaura* and *Pantodactylus schreibersii*. The position of *Pantodactylus quadrilineatus* is not congruent between the two trees. The morphological phylogeny places all three *Pantodactylus* species in a

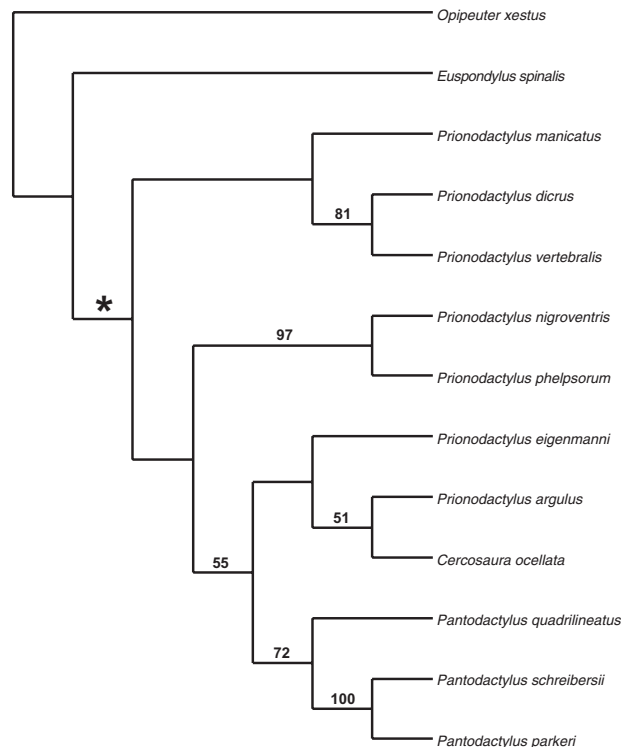


Figure 3. Phylogenetic reconstruction of all known *Cercosaura*, *Pantodactylus* and *Prionodactylus* species based on maximum parsimony analysis of 61 morphological characters. Numbers above branches are bootstrap values above 50%. The * indicates the content of the phylogenetic genus *Cercosaura*.

monophyletic group, which renders *Prionodactylus* paraphyletic, but the molecular phylogeny depicts *Pantodactylus* as non-monophyletic with respect to *Prionodactylus* and *Cercosaura*. Support for the exact placement of the *Pantodactylus* species is low and more characters will be needed to adequately resolve their phylogenetic positions.

The three constraint analyses demonstrated that, in each case, the shortest tree derived by the current analysis was significantly better than the alternatives. The constraint in which *Pantodactylus quadrilineatus* was forced to be basal to all other ingroup taxa resulted in a tree of 3 431 857 steps, which was significantly different than the tree without constraints ($n = 28$, $T = 116$, $Z = -2.2678$, $P = 0.0233$). The constraint forcing monophyly of *Prionodactylus* required 3 490 856 steps and was also significantly different from the unconstrained tree ($n = 165$, $T = 3962.5$, $Z = -4.6947$, $P < 0.0001$). Likewise, the backbone constraint forcing the Pellegrino *et al.* (2001) topology required 3 454 731 steps and differed significantly from the unconstrained tree ($n = 183$, $T = 6089$, $Z = -3.2457$, $P = 0.0012$). These results indi-

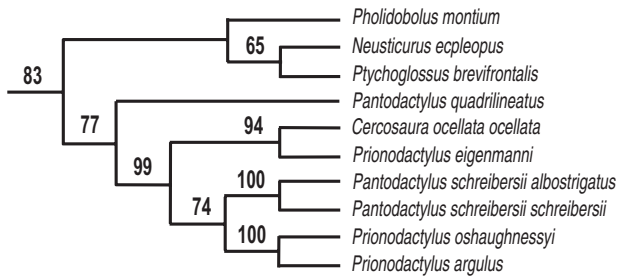


Figure 4. Partial phylogenetic reconstruction from Pellegrino *et al.* (2001) showing a portion of their maximum likelihood tree. Numbers above branches are bootstrap values above 50%.

cate that there is significant conflict between the morphological tree of this study and the molecular tree of Pellegrino *et al.* (2001).

The morphological phylogeny (Fig. 3) resolved the internal *Prionodactylus* relationships because it included all taxa. *Prionodactylus vertebralis* and *P. dicrus* are sister taxa, as was predicted by Uzzell (1973), with *P. manicatus* the sister to that clade. *Prionodactylus nigroventris* and *P. phelporum* are also sister taxa, as was suggested by Gorzula & Señaris (1998). The two reconstructions differ in which taxon is the closest relative of *Cercosaura*. In the molecular phylogeny (Fig. 4) *Prionodactylus eigenmanni* is the sister but in the morphological phylogeny (Fig. 3) *P. argulus* is the sister, with *P. eigenmanni* as sister to the clade containing *Cercosaura* and *P. argulus*. The lack of congruence between the two data sets on the placement of those three species renders confidence about those relationships uncertain.

A NEW PHYLOGENETIC CLASSIFICATION

Because of the lack of monophyly of the genus *Prionodactylus*, as demonstrated by Pellegrino *et al.* (2001), the reconstruction presented in the current study, and the Templeton test demonstrating that a monophyletic *Prionodactylus* was significantly less parsimonious, a taxonomic rearrangement is warranted. *Prionodactylus* is paraphyletic with respect to *Cercosaura* and at least *Pantodactylus schreibersii*, whereas *Pantodactylus* may be paraphyletic with respect to *Cercosaura* and some species of *Prionodactylus* (Fig. 4; based on the molecular tree of Pellegrino *et al.*, 2001). Because of the lack of congruence in some aspects of the molecular (Pellegrino *et al.*, 2001) and morphological phylogenies, I choose a conservative approach that utilizes data congruent between data sets. In order to have a classification that contains only monophyletic groupings, *Pantodactylus* and *Prionodactylus* are con-

sidered junior synonyms of *Cercosaura* and a redefinition of *Cercosaura* is necessary. Therefore, the genus *Cercosaura* now includes all species of the three genera and its content is indicated by an asterisk on the branch leading to the *Cercosaura* node on Fig. 3.

GENUS *CERCOSAURA* WAGLER

Cercosaura Wagler, 1830: 158.

Pantodactylus Duméril & Bibron, 1839: 428. **Syn. n.**

Emminia Gray, 1845: 24.

Prionodactylus O'Shaughnessy, 1881: 231. **Syn. n.**

Definition. Tongue at least anteriorly covered by imbricate scale-like papillae. Head scales smooth and consist of the following: frontonasal divided or undivided; single frontal and interparietal; paired prefrontals and parietals; usually a median and two paramedian occipitals; nostril pierced in a single or divided nasal; loreal and frenocular present; supraoculars two to four; superciliary series usually complete, first expanded dorsally or not; palpebrals one to four; suboculars three to seven; single postmental followed by one to three pairs of genials and one to two pairs of chin shields that do not contact at midline; gular scales flat, rectangular, median two rows of scales usually forming a double widened row of scales, at least posteriorly. Collar fold weak to well developed. Limbs pentadactyl, digits clawed. Dorsal scales imbricate, quadrangular or hexagonal, keeled, homogeneous; forming transverse rows, forming longitudinal or oblique rows occasionally. Ventral scales as wide or wider than dorsals, smooth, quadrangular, in longitudinal and transverse rows. Preanal scales in two rows. Femoral pores present in males, occasionally absent in females. Preanal pores may or may not be present in either sex. Tail round or cyclotetragonal; caudal scales like dorsals but smaller; subcaudals like ventrals, two medial rows widest.

Diagnosis. *Cercosaura* differs from other genera of the Cercosaurini (*sensu* Pellegrino *et al.*, 2001) in the following characters (condition for *Cercosaura* in parentheses): *Anadia* and *Opipeuter*: smooth dorsal scales (keeled); *Bachia*: diminutive limbs (fully developed); *Echinosaura*, *Neusticurus*, and *Teuchocercus*: dorsal scalation heterogeneous (homogeneous); *Euspondylus*: postorbital bone expanded into supratemporal fenestra (no expansion); *Macropholidus*: medial two dorsal scale rows greatly enlarged (not enlarged); *Pholidobolus*: tympanum deeply recessed (slightly recessed); *Placosoma*: femoral pores in a continuous series from one thigh to another (distinct femoral and preanal pores, if present); *Proctoporus*: prefrontal scales absent (present); *Ptychoglossus* and *Riolama*: lingual papillae plicate anteriorly (scale-like anteriorly).

Table 4. Content of the redefined genus *Cercosaura*

Species/subspecies name	Author	Year	Comments
<i>Cercosaura argulus</i>	Peters	1862	
<i>Cercosaura dicra</i>	(Uzzell)	1973	comb. nov.
<i>Cercosaura eigenmanni</i>	(Griffin)	1917	comb. nov.
<i>Cercosaura manicata boliviana</i>	Werner	1899	comb. nov.
<i>Cercosaura manicata manicata</i>	O'Shaughnessy	1881	
<i>Cercosaura nigroventris</i>	(Gorzula and Señaris)	1998	comb. nov.
<i>Cercosaura ocellata bassleri</i>	Ruibal	1952	
<i>Cercosaura ocellata ocellata</i>	Wagler	1830	
<i>Cercosaura ocellata petersi</i>	Ruibal	1952	
<i>Cercosaura phelpsorum</i>	(Lancini)	1968	comb. nov.
<i>Cercosaura quadrilineata</i>	Boettger	1876	
<i>Cercosaura parkeri</i>	(Ruibal)	1952	comb. nov.
<i>Cercosaura schreibersii albostrigata</i>	(Griffin)	1917	comb. nov.
<i>Cercosaura schreibersii schreibersii</i>	Wiegmann	1834	
<i>Cercosaura vertebralis</i>	O'Shaughnessy	1879	comb. nov.

KEY TO THE SPECIES OF *CERCOSAURA*

- 1a. Dorsal scales quadrangular *C. ocellata*
 1b. Dorsal scales hexagonal 2
 2a. Dorsal scales arranged in transverse and oblique series 3
 2b. Dorsal scales arranged in transverse series only 5
 3a. Ventral scales in 4 longitudinal rows *C. quadrilineata*
 3b. Ventral scales in 6 or more longitudinal rows 4
 4a. Postoculars 3 *C. parkeri*
 4b. Postoculars 2 *C. schreibersii*
 5a. Supradigital lamellae of the fifth toe 4 or less *C. eigenmanni*
 5b. Supradigital lamellae of the fifth toe 5 or more 6
 6a. Subdigital lamellae not tuberculate for entire length of toes 7
 6b. Subdigital lamellae tuberculate for entire length of toes 8
 7a. Posterior cloacal plate of males composed of 2 scales *C. argulus*
 7b. Posterior cloacal plate of males composed of more than 2 scales *C. dicra*
 8a. Palpebral disc divided into 5–8 scales *C. vertebralis*
 8b. Palpebral disc undivided or divided into 2–4 scales 9
 9a. Venter light in colour, being yellow and/or white *C. manicata*
 9b. Venter dark in colour, being brown and/or black 10
 10a. Medial region of ventral surface of tail beige *C. nigroventris*
 10b. Medial region of ventral surface of tail dark brown or black *C. phelpsorum*

Content. The genus *Cercosaura*, as currently recognized, contains 11 species and seven subspecies (see Table 4).

Distribution. The genus *Cercosaura* occurs in 12 of 13 countries in South America (absent from Chile) and in one Central American country (Panama), ranging from temperate Argentina, Paraguay and Uruguay in the south, through Amazonian Bolivia, Peru, Brazil, Ecuador and Colombia, the western slope of the Andes in northern Peru and Ecuador, the Chocó region of

Colombia and Panama, and in the Guianan Shield region of Venezuela, Guyana, Suriname, French Guiana, and north-central Brazil (Ruibal, 1952; Uzzell, 1973; Avila-Pires, 1995). The elevational distribution of the genus is known to extend from 100 m to at least 2500 m (Ruibal, 1952; Uzzell, 1973).

CONCLUSIONS

Since the publication of the phylogenetic analysis of Pellegrino *et al.* (2001), Boulenger's (1885) Group's II,

III and IV of the Teiidae can no longer be accepted as natural groupings. Group II, of which all of the species treated in the current study were members, has species placed in two different subfamilies (*sensu* Pellegrino *et al.*, 2001), with *Aloglossus* in its own subfamily and the rest of the former Group II in the Cercosaurinae. In addition, the tribe Cercosaurini now contains a genus of Boulenger's Group III, *Bachia*. It is clear that external morphology alone is not sufficient to define the natural groups of the Gymnophthalmidae. The analysis of morphological and molecular (Pellegrino *et al.*, 2001) data allows for phylogenetic reconstruction and taxonomic rearrangement that appear to better reflect the evolutionary history of this group of lizards.

However, further study of the Cercosaurinae is clearly warranted. Although Pellegrino *et al.* (2001) had relatively good taxon sampling of the Gymnophthalminae, taxon sampling was poor for the Cercosaurinae (they sampled approximately 11% of the 140 known species). Speciose genera such as *Proctoporus*, *Anadia* and *Euspondylus* were omitted completely from the analysis, as well as less diverse genera including *Opipeuter*, *Riolama*, *Amapasaurus*, *Teuchocercus*, *Macropholidus* and *Echinosaura*. Although the Pellegrino *et al.* (2001) phylogenetic study was an excellent beginning, additional analyses including more genera and species are essential to understand adequately this complex group of lizards. Additional studies that consider both morphological and molecular data are necessary to continue to derive a classification for the Cercosaurinae that is congruent with the evolutionary history of these organisms.

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APPENDIX 1

SPECIMENS EXAMINED

Specimen localities are given according to museum catalogue information. Cataloged localities and spellings were used as is, without correction of errors.

Cercosaura argulus: BOLIVIA: *Cochabamba* (UMMZ 68087); *Santa Cruz*: Buena Vista (UMMZ 60600, 68088); COLOMBIA: *Cundinamarca*: Fusagasuga (UMMZ 131680); *Meta*: Serranía de la Macarena: Caño Sardinata, 30 km WSW of Vista Hermosa (UTA R-3480); Sabana de San Juan de Arama Camp, Upper Río Guejar (UMMZ 131679); Northern Park Caño Guapaya Tributary of Río Guejar Forest (UMMZ 131682); Caño Los Micos, near Cabaña Los Micos, 16 km S San Jurvi de Arama (UTA R-3329); *Vaupés*: Upper Río Apaporis, Comisaría Vaupés, Tributary of Río Caqueta (UMMZ 131681); EQUADOR: unknown province: San Francisco, Río Napo [UMMZ 84746 (two specimens), 84747 (seven specimens)]; *Napo*: near Tena Napo (UMMZ 84745); 2.5 km S Ongota, between Latas and Napo (UMMZ 123893); Napo-Pastaza: near Mera, Alpa Yacú (UMMZ 90771); PERU: *Madre de Dios*: Manu: Estación Biológica Cocha Cashu (UNSAAC BA701); Tambopata: no locality given (UNSAAC PT483); Cusco Amazónico (UNSAAC PT335-PT337, PT1019, PT1043, PT1046); EcoAmazónica (UNSAAC PT233, PT1033, PT1047); Explorer's Inn (UNSAAC PT1050); Sachavacayoc Centre [UNSAAC PT370, PT482, PT1005 (two specimens), PT1013]; Tambopata Research Center (UNSAAC PT1057).

Cercosaura dicra: ECUADOR: unknown province: Baños, Abi Taqua [AMNH R-24144 (paratype)]; Baños [FMNH 28043, 28049 (paratypes)]; *Napo*: between Baños and Puyo [USNM 194383 (paratype)]; *Tungurahua*: Baños [USNM 193592 (paratype)].

Cercosaura eigenmanni: BOLIVIA: *Beni*: Rurrenabaque (AMNH R-22537, R-33538); *Santa Cruz*: Buena Vista (MCZ R-24887, UMMZ 101150); Velasco, top of meseta, Parque Nacional Noel Kempff Mercado (UTA R-38059); Velasco, Estancia El Refugio (UTA R-48040); BRAZIL: *Acre*: Centro Experimental da Universidade do Acre, Km 29 on Río Branco-Pto Acre Road, 2–3 km from Humaita (AMNH R-139996); *Parana*: Curutiba, Jardim de las Americas (UTA R-35951); *Rodônia*: Santa Barbara (AMNH R-131881-131883); PERU: *Madre de Dios*: Cusco Amazónico (KU 214989-214995); Cocha Cashu, Parque Nacional de Manu (MCZ R-145049-145050).

Cercosaura manicata: ECUADOR: *Pastaza*?: Canelos to Mariana River (MCZ R-37261); *Zamora-Chichipe*: Santiago, Zamora Province (MCZ R-45779); PERU: *Huánuco*: 1 km W Amaybamba (MCZ R-182064); Divisoria (FMNH 55986-55988); *Pasco*: Oxapampa (FMNH 134398); *Puno*: Oconeque, Río Quitun (FMNH 40424); Santo Domingo (FMNH 39368, 40420-40423, 40425); *Cercosaura nigroventris*: VENEZUELA: *Bolívar*: Cerro Guanay, alto, Río Paragua, [MHNLS 10720 (paratype)].

Cercosaura ocellata bassleri: BOLIVIA: *La Paz*: Tumupasa (AMNH R-22530); PERU: unknown

department: Bombo, Río Tapiche Valley (AMNH R-56271, R-56287, R-56301); Chanchamayo (AMNH R-56391); Pampa Hermosa, Río cayali Valley, near mouth Río Cushabatay (AMNH R-56275, R-56290); Lower Río Cushabatay, Río Ucayali (AMNH R-56300); Uchpayacu, upper Río Curshabatay, Río Ucayali (AMNH R-56489).

Cercosaura ocellata ocellata: GUYANA: Dunoon, Demerara River (UMMZ 46771-46772, 53896); Marudi (AMNH R-61385); Mazaruni-Potaro, Kartabo, 6 21' N, 58 41' W (AMNH 21264); SURINAME: *Brokopondo*: Brokopondo (AMNH R-119406); 65 km airline SSE Paramaribo on Afobaka Road (AMNH R-108787).

Cercosaura parkeri: BOLIVIA: *Beni*: Vacadiez, Guayaramerin (USNM 280965); *La Paz*: 15 km before Chulumani, Km 100 post (USNM 207050-207051); Yanacachi (USNM 207046-207048); *Santa Cruz*: Chiquitos, Cantón-El Cerro, Finca Dos Milanos (UTA R-38058); Florida, El Chape (UTA R-34760); Florida, Paredones, Río Paredones (UTA R-347590); Hwy 4 from Comarapa to Samaipata, 123 km from Comarapa (UTA R-34758).

Cercosaura phelpsorum: VENEZUELA: *Amazonas*: Cerro Yaví (MHNLS 11141-11142); Serranía de Yutaje (MHNLS 11387).

Cercosaura quadrilineata: BRAZIL: *Rio de Janeiro*: Rio de Janeiro (MCZ R-4326); *Sao Paulo*: Rio Pinheiros (MCZ R-154219-154223).

Cercosaura schreibersii schreibersii: ARGENTINA: *Cordoba*: 40 mi W of Cordoba, 5 km W of Salsipuedes (USNM 196174); BRAZIL: *Rio Grande do Sul*: Viamao, Vila 5 Irmaos (UTA R-43955, R-43957); PARAGUAY: *Alto Paraguay*: Parque Nacional Defensores del Chaco, 15 km N of Tribu Nueva, Cerro Leon (USNM 347912); *no state given*: Florida (USNM 139286); *Central*: Villeta (USNM 341988-341989); URUGUAY: *no locality data* (USNM 70486); *Montevideo*: Cerro de Montevideo (UTA R-7615-7616); Montevideo (USNM 68034, 73915); Punta Carretas, near Montevideo (USNM 38112-38113).

Cercosaura vertebralis: COLOMBIA: San Pedro (AMNH R-32737-32744); Sonson (AMNH R-32725-32736).

Euspondylus spinalis: PERU: *Piura*: Huancabamba [UMMZ 51280, 58918 (three specimens), 89489, 89490 (three specimens)].

Opipeteur xestus: BOLIVIA: *Cochabamba*: Carrasco, Khara Huasi (UTA R-34592); Carrasco, road from Khara Huasi to El Empalme at Km 10 (UTA R-34593); *Chuquisaca*: Sud Cinti, Cerro Bufete (UTA R-39117, R-39119-39120); Sud Cinti, near Rinconada Bufete base camp (UTA R-39121-39122, R-39124-39125); Sud Cinti, Cerro Mojón (UTA R-39126).

APPENDIX 2

CHARACTERS FOR PHYLOGENETIC ANALYSIS

Some characters were ordered (O) and others were considered unordered (U). Some of the character states listed here may not be found in any of the taxa examined in this study. A larger study of Cercosaurini relationships utilizes all of these states (Doan, unpublished).

Character 1 (O): frontonasal condition: undivided 0, divided 1.

Character 2 (O): frontonasal length: shorter than frontal 0, same length as frontal 1, longer than frontal 2.

Character 3 (U): prefrontal suture: no suture because of lack of prefrontal scales 0, entire length of prefrontal scales 1, short (i.e. less than entire length of prefrontal scales) 2, point suture 3, suture absent 4.

Character 4 (U): frontoparietal contact with which supraoculars: one/two 0, one/two/three 1, two 2, two/three 3, two/three/four 4, three 5, three/four 6, four 7, four/five 8.

Character 5 (O): relative interorbital/eye-snout distance: expressed as an approximate decimal multiplied by 10. For example, if the interorbital distance were seven tenths that of the eye to snout distance a 7 would be recorded.

Character 6 (O): relative eye-snout/crus length: expressed as a decimal, as in Character 5.

Character 7 (O): number of supraoculars.

Character 8 (O): relative interparietal width: anteriormost suture thinner than posteriormost suture of frontal 0, equal to frontal 1, wider than frontal 2.

Character 9 (O): number of occipitals.

Character 10 (O): nasal condition: undivided 0 (i.e. nasal and loreal fused), incompletely divided 1, divided into separate nasal and loreal scales 2.

Character 11 (O): loreal contact with supralabial: no 0, yes 1.

Character 12 (O): number of supraciliaries.

Character 13 (O): number of eye palpebral scales of the main row.

Character 14 (O): number of reduced lower orbital scales on the ventralmost margin.

Character 15 (O): number of suboculars.

Character 16 (O): number of postoculars.

Character 17 (O): number of first anterior row of temporals.

Character 18 (O): number of supratympanic temporals.

Character 19 (O): number of reduced scales surrounding tympanum.

Character 20 (U): tympanum shape: half circle 0, round 1, oblong 2.

Character 21 (O): number of supralabials.

Character 22 (O): number of scales in a row from supralabials to tympanum.

Character 23 (O): number of infralabials.

Character 24 (O): approximate number of scale organs on first supralabial, recoded as: five 0, 10 1, 15 2, 20 3, 25 4, 30 5, 35 6, 40 7, 45 8.

Character 25 (O): scale organs on first infralabial: identical to Character 24.

Character 26 (O): number of genials.

Character 27 (O): number of scales in posterior transverse pregular row.

Character 28 (O): number of scales in medial pregular row (often not a complete row but all scales counted on the midline).

Character 29 (O): number of scales in first transverse gular row.

Character 30 (O): number of transverse gular rows (not including reduced scales folded into the collar).

Character 31 (O): number of ventral scales in the first transverse row between forelimbs.

Character 32 (O): number of longitudinal ventral rows at midbody.

Character 33 (O): number of transverse ventral rows.

Character 34 (O): number of scales in posteriormost transverse ventral row.

Character 35 (O): number of interpreanal scales.

Character 36 (O): number of cloacal plate rows (1 or 2).

Character 37 (O): number of posterior cloacal plate scales in males.

Character 38 (O): number of posterior cloacal plate scales in females.

Character 39 (O): number of scales around base of tail.

Character 40 (O): number of femoral pores on one leg in males.

Character 41 (O): number of femoral pores on one leg in females.

Character 42 (O): number of total preanal pores of males.

Character 43 (O): number of longitudinal dorsal rows at midbody.

Character 44 (O): number of transverse dorsal rows.

Character 45 (U): dorsal scale shape: quadrangular 0, hexagonal 1, rhomboid 2, rounded rectangle 3, pyramidal 4.

Character 46: not used in this study.

Character 47 (O): number of lateral scale rows at midbody.

Character 48 (O): lateral scale size: much smaller than dorsals 0, approximately half the size of dorsals 1, same size as dorsals 2, no differentiated lateral scales 3.

Character 49 (O): number of scales in a row along the dorsal surface of forelimb from insertion to manus.

Character 50 (O): number of supradigital lamellae of fifth finger.

Character 51 (O): number of subdigital lamellae of fourth finger.

Character 52 (U): femoral scale relief: smooth 0, keeled 1, striate/rugose 2, tuberculate 3.

Character 53 (O): number of supradigital lamellae of fifth toe.

Character 54 (O): number of subdigital lamellae of fourth toe.

Character 55 (O): tubercles on subdigital lamellae of fourth toe: double 0, single 1.

Character 56 (O): relative toe length of fifth and third toes: expressed as a decimal as in Characters 5 and 6.

Character 57 (O): relative brachial/crus length: expressed as a decimal as in Characters 5, 6, and 56.

Character 58 (O): barred lip: no 0, yes 1.

Character 59 (O): number of longitudinal dorsal stripes.

Character 60 (O): number of lateral ocelli in the main row.

Character 61 (O): ventral scale pigmentation: none 0, lateral only 1, less than 50% of each ventral scale covered by dark pigment 2, more than 50% covered by pigment 3.

Character 62 (O): number of total preanal pores in females.