



Integrative taxonomy of the lizards *Cercosaura ocellata* species complex (Reptilia: Gymnophthalmidae)



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ABSTRACT

Cercosaura ocellata has for long been considered a polytypic species. A recent molecular study elevated one of the recognized subspecies as full species, but based on limited sampling. For species delimitation a more extensive study is warranted, both in terms of number of specimens and geographical coverage. We conduct an integrative taxonomic study of *C. ocellata* complex, based on external morphology and genomic data (RAD-seq), considering its entire geographic distribution. Our results support the recognition of four species, three of which are restricted to Amazonia: *Cercosaura ocellata* from the Guianan region, north of the Amazon river, and east of the Tapajós river, in Pará, Brazil; *Cercosaura bassleri* from western Amazonia, eastward limited by the Negro (north of the Amazon) and the Madeira (south of it) rivers; and an undescribed species partially in sympatry with the former two, distributed between the Purus and Xingu rivers. *Cercosaura olivacea*, the fourth species, occurs in the Cerrado, Atlantic forest, Pantanal and Pampas. *Cercosaura ocellata petersi* and *Cercosaura humilis* are junior synonyms of *C. olivacea*. The new species is recovered as sister to *C. bassleri* (*C. ocellata*–*C. olivacea*).

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1. Introduction

Widely distributed species often turn out to be species complexes, as shown in recent studies of South American lizards (D'Angiolella et al., 2011; Domingos et al., 2014; Gamble et al., 2012; Nunes et al., 2012; Recoder et al., 2014; Sturaro and Avila-Pires, 2011). However, few of these studies address the taxonomy and morphological limits between the putative species. Proper recognition of species, reflecting the existence of evolutionarily independent lineages, is important both for a better comprehension of the group and its evolution, as well as for improving conservation policies.

Of the 14 species of *Cercosaura* presently recognized (Doan and Cusi, 2014; Doan and Lamar, 2012; Echevarría et al., 2015;

Sturaro et al., 2017; Torres-Carvajal et al., 2015), the *C. ocellata* complex has the widest distribution, occurring in large part of cis-Andean South America, including Amazonia, Cerrado, Atlantic Forest, Pantanal and Pampas (Avila-Pires, 1995; Nogueira et al., 2011; Ruibal, 1952). *Cercosaura ocellata* was described by Wagler in 1830 based on a specimen (referred to, in a footnote, as *Leptus ocellatus*, a *nomen nudum*) with dubious locality (Asia?), probably from northeastern South America (Suriname?), according to Ruibal (1952). Gray (1845) described a monotypic *Emminia*, for *E. olivacea*, based on a single specimen from Pernambuco, Brazil. Peters (1863) synonymized *Emminia* with *Cercosaura* and considered *Pantodactylus Duméril and Bibron, 1839* a subgenus of *Cercosaura*. In the subgenus *Cercosaura*, besides *Cercosaura ocellata* and *Cercosaura olivacea*, he described *Cercosaura humilis* (type-locality “Brasilien”). O'Shaughnessy (1881) considered *Cercosaura olivacea* a junior synonym of *C. ocellata* and proposed a third subgenus to allocate *Cercosaura (Prionodactylus) manicata*, described in his study. Boulenger (1885), examining the holotype of *Emminia*

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olivacea and a specimen from Pará state, Brazil, synonymized *C. olivacea* and *C. humilis* with *C. ocellata*.

The first taxonomic arrangement of *C. ocellata* was proposed by [Ruibal \(1952\)](#), who recognized three subspecies, two of which he described as new: *C. ocellata ocellata* (from Guyana and Brazil, in the states of Pará and Bahia), having as junior synonyms *Emminia olivacea* and *Cercosaura humilis*; *C. ocellata petersi* (type-locality Santa Maria, Rio Grande do Sul state, Brazil, but also in São Paulo state, Brazil, and Sara Province, Departamento de Santa Cruz, Bolivia); and *C. ocellata bassleri* (type-locality Rio Perené, Perené District, Peru, also in eastern Peru and northwestern Bolivia).

[Peters and Donoso-Barros \(1970\)](#) followed [Ruibal \(1952\)](#) arrangement for *Cercosaura*. [Avila-Pires \(1995\)](#) recognized *C. ocellata ocellata* and *C. ocellata bassleri* as occurring in Brazilian Amazonia and discussed their differences and distribution. [Doan \(2003\)](#) examined specimens of these two subspecies for phylogenetic inference (using morphological data), but treated them as a single taxon. Among faunistic studies that included *C. ocellata*, several ([Avila-Pires et al., 2010](#); [Borges-Nojosa and Caramaschi, 2003](#); [Couto-Ferreira et al., 2011](#); [Loebmann and Haddad, 2010](#); [Oliveira and Moura, 2013](#); [Recoder et al., 2011](#); [Recoder and Nogueira, 2007](#); [Sales et al., 2014](#); [Sousa et al., 2010](#); [Uetanabaro et al., 2007](#); [Valdujo et al., 2009](#)) did not identify the subspecies. At least in part, especially outside Amazonia, this was probably due to uncertainties regarding such identification.

[Torres-Carvajal et al. \(2015\)](#), in a molecular phylogeny of *Cercosaura*, elevated *C. ocellata bassleri* to species, based on genetic distances between five specimens from Peru and a single specimen of *C. ocellata ocellata*. They did not include samples of *C. ocellata petersi* in the study neither make any reference to this subspecies. [Sturaro et al. \(2017\)](#), in a molecular phylogeny of *C. ocellata*, corroborated its monophyly and the existence of genetic structure, recovering several clades within the species complex. However, for species delimitation a more extensive study was necessary to define the species boundaries, characterize them, and establish their distribution, which we present here.

2. Material and methods

2.1. Morphological data and analyses

We examined 729 specimens of *Cercosaura* (type material in Results section, others in SI 1). We use the museum acronyms of [Sabaj Perez \(2014\)](#). Holotypes of *Cercosaura ocellata* (ZSM 643/0), *Emminia olivacea* (BMNH 1946.8.2.6), and *Cercosaura humilis* (ZMB 899) were examined by photos.

Measurements and scale counts were taken under a stereomicroscope when necessary (SI 2–4). Measurements were taken with a digital caliper (to the nearest 0.1 mm), on the right side of specimens whenever possible, as follows: **SVL** (snout–vent length, from tip of snout to cloacal opening); **TL** (tail length, from cloacal opening to tip of tail); **HL** (head length, from tip of snout to anterior margin of ear-opening); **HW** (head width, on the widest part of head); **HD** (head depth, on the highest part of head); **NL** (neck length, from anterior margin of ear opening to anterior margin of forearm insertion); **LAL** (lower arm length, from tip of elbow to wrist); **HaL** (hand length, from wrist to tip of longest finger); **LLL** (lower leg length, from knee to ankle); **FoL** (foot length, from ankle to tip of longest toe); **DBL** (distance between limbs, from axilla to groin); **RD** (rostral scale depth, between upper and lower margins at midline); **RW** (rostral scale width, between lateral corners); **FL** (frontal scale length, between anterior and posterior corners); **AFW** (frontal scale anterior width, between latero-anterior corners); **PFW** (frontal scale posterior width, between latero-posterior corners); **IPL** (interparietal scale

length, between anterior and posterior corners); **AIPW** (interparietal scale anterior width, between latero-anterior corners); **PIPW** (interparietal scale posterior width, between latero-posterior corners); **ML** (mental scale length, between anterior and posterior margins at midline); **MW** (mental scale width, between lateral corners); **PML** (postmental scale length, between anterior margin at midline and posterior corner); **APMW** (postmental scale anterior width, between latero-anterior corners); **PPMW** (postmental scale posterior width, between latero-posterior corners).

Scales were counted as follows: **SAM** (scales around midbody, midway between fore- and hind limbs); **DLR** (dorsals in a longitudinal row, along a middorsal line, from occipitals to anterior margin of hind limbs); **DTR** (dorsals in a transverse row, midway between fore- and hind limbs, not including laterals, which are distinctly smaller); **LTS** (lateral scales, in a vertical row midway between fore- and hind limbs); **VLR** (ventrals in a longitudinal row, along a midventral line, from anterior margin of forelimbs to anterior margin of hind limbs); **VTR** (ventrals in a transverse row, midway between fore- and hind limbs); **FN** (frontonasals); **FR** (frenoculars); **LO** (loreal); **OC** (occipitals); **SL** (supralabials, distinctly enlarged scales reaching the posterior margin of orbit); **PSL** (post-supralabials, between posterior supralabial and commissure of the mouth); **IL** (infralabials, distinctly enlarged scales reaching the posterior margin of orbit); **PIL** (post-infralabials, between posterior infralabial and commissure of the mouth); **SO** (supraoculars); **PRO** (preoculars, on anterior margin of orbit, not in touch with supralabials); **SBO** (suboculars, on ventral side of orbit, in touch with supralabials); **PO** (post-oculars, on posterior margin of orbit, not in touch with supralabials); **PS** (palpebrals, enlarged scales that form the translucent disc of the lower eyelid); **CI** (supraciliaries, on the dorsal margin of the orbit); **SPAL** (suprapalpebrals, along the margin of the upper eyelid); **IPAL** (infrapalpebrals, along the margin of the lower eyelid); **ST** (supratemporals, in a longitudinal row following dorsalmost postocular, in touch with parietal and lateral occipital); **TEV** (temporals in a vertical row bordering postoculars, between supralabial and parietal); **CS** (pairs of chinshields); **GL** (gulars in a longitudinal row, including collar scales); **PG** (paired enlarged gulars in the medial region of the throat); **CO** (collars); **NS** (scales on side of neck, between the fourth gular, counted from collar, and the lateralmost dorsal scale on nape); **FP** (number of femoral pores, on one side of specimen); **L1F, L2F, L3F, L4F and L5F** (lamellae under respectively first to fifth fingers, from base of finger to unguis scale); **L1T, L2T, L3T, L4T and L5T** (lamellae under respectively first to fifth toes, from base of toe to unguis scale). Sex was determined by the presence of hemipenis (males), eggs (females) or shape of preloacal plate (see more details on variation section).

We performed two discriminant function analyses (DFA), one for 23 measurements (all but tail length) and other for 14 scale counts (NS, DTR, SAM, VTR, LA1F, LA2F, LA3F, LA4F, LA5F, LA1T, LA2T, LA3T, LA4T and LA5T), to test if groups defined *a priori* could be differentiated by a combination of these morphological characters ([Tabachnick and Fidell, 2007](#)). For these analyses, we (1) removed all juveniles (SVL > 38 mm, based on smaller adult females observed) and specimens with missing scale counts and morphometric values; (2) log-transformed (base 10) measurements and scale counts, and removed all multivariate outliers with the R package “mvoutlier” ([Filzmoser and Gschwandtner, 2015](#)); (3) tested the multivariate normality of both datasets with the R package “mvnormtest” ([Jarek, 2015](#)) – although neither dataset was normally distributed, we performed the discriminant analyses, because this kind of analysis is robust to failures of normality if the outliers are removed ([Tabachnick and Fidell, 2007](#)); and (4) removed size effect from measurements, regressing each variable separately on the first principal component of a Principal Component Analysis and utilizing the residuals of these regression in the DFA, as proposed by [Strauss \(1985\)](#) and [Reis et al. \(1990\)](#).

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