

Phylogeny, taxonomy and distribution of the Neotropical lizard genus *Echinosaura* (Squamata: Gymnophthalmidae), with the recognition of two new genera in Cercosaurinae

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The family Gymnophthalmidae is a highly diverse Neotropical lizard clade. Although multiple phylogenetic and taxonomic studies have reshaped our understanding of gymnophthalmid systematics and diversity, many groups remain understudied. This is the case for the cercosaurine genus *Echinosaura*, which includes eight species of small riparian lizards distributed across lower Central America and northern South America. Here, we present a comprehensive phylogenetic analysis of *Echinosaura*, including DNA data for all species of the genus for the first time. To rigorously test the relationships of all *Echinosaura*, we have assembled the largest molecular dataset of cercosaurine lizards to date. Our analysis refutes the monophyly of *Echinosaura*, with *E. apodema* and *E. sulcarostrum* not closely related to the remaining species. To remedy the polyphyly of *Echinosaura*, we describe two new genera for *E. apodema* and *E. sulcarostrum*. Morphological distinctiveness and biogeography further support these taxonomic changes. In light of our phylogenetic results, we review the species-level taxonomy of the redefined *Echinosaura* based on morphological and genetic variation. We resurrect *E. centralis* and designate a neotype given the absence of type and topotypic material. In addition, we provide taxonomic accounts for each species and analyse their patterns of geographic distribution.

KEYWORDS: Lower Central America – Microteiid lizards – molecular phylogenetics – morphology – northern South America – Reptilia – species diversity – systematics.

INTRODUCTION

The family Gymnophthalmidae is one of the most diverse lizard clades in the Neotropical region. Knowledge on the relationships and systematics of gymnophthalmids has increased dramatically in the last two decades, as numerous studies have

presented phylogenetic hypotheses for many groups at different taxonomic levels, resulting in multiple taxonomic changes (e.g. Pellegrino *et al.*, 2001; Doan & Castoe, 2005; Goicoechea *et al.*, 2012; Kok, 2015; Goicoechea *et al.*, 2016; Torres-Carvajal *et al.*, 2016; Sánchez-Pacheco *et al.*, 2017; Moravec *et al.*, 2018). Nevertheless, despite much progress in understanding the diversity of gymnophthalmids, many groups remain understudied and need more attention. One of these poorly studied groups is the cercosaurine genus *Echinosaura* (Torres-Carvajal *et al.*, 2016).

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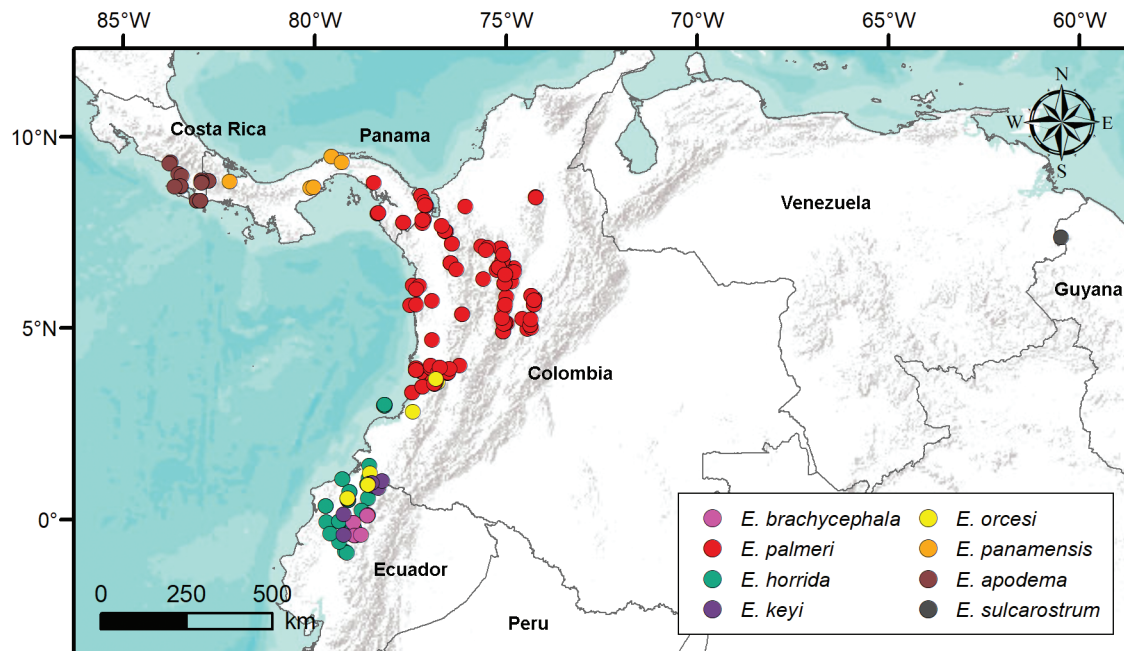


Figure 1. Current geographic distribution of the genus *Echinosauro* obtained from museum collection vouchers.

Echinosauro includes eight species of small riparian lizards (Uetz & Hošek, 2018). Seven species are trans-Andean, extending from eastern Costa Rica to north-western Ecuador (Fig. 1): *E. apodema* (Uzzell, 1966); *E. brachycephala* Köhler, Böhme & Schmitz, 2004; *E. horrida* Boulenger, 1890; *E. keyi* (Fritts & Smith, 1969); *E. orcesi* Fritts, Almendáriz & Samec, 2002; *E. palmeri* Boulenger, 1911; and *E. panamensis* Barbour, 1924. The remaining species, *E. sulcarostrum* Donnelly et al., 2006, is restricted to the Pantepui bioregion of the Guiana Shield (Fig. 1). These lizards are almost entirely confined to the immediate vicinity of streams (e.g. stream banks), and individuals are occasionally found submerged or swimming (Uzzell, 1965; Köhler et al., 2004; Donnelly et al., 2006; Ortega-Andrade, 2006). Like other riparian gymnophthalmids such as *Neusticurus* and *Potamites*, species of *Echinosauro* have some degree of vertical tail compression, which is a characteristic of several semi-aquatic tetrapods (Howell, 1930; Fish, 1982; Greene, 1997), including lizards (Leal et al., 2002; Bauer & Jackman, 2008). They also have enlarged tubercles and strongly keeled scales on body and tail, often forming crests. Such structures on the body and tail may enhance aquatic locomotion by increasing the propulsive surface (Marques-Souza et al., 2018). Similarly modified scales often form crests in other semi-aquatic lizards (e.g. the teiid *Dracaena guianensis* Daudin, 1802). These may be adaptations because riparian gymnophthalmids swim by undulating their bodies along with their laterally compressed tails (Uzzell, 1966; Donnelly & Myers, 1991; Vitt & Ávila-Pires, 1998).

Kok et al. (2012) and Kok (2015) were the first to include a species of *Echinosauro*, *E. sulcarostrum*, in phylogenetic analyses of gymnophthalmids using DNA sequence data. Initially (Kok et al., 2012), the position of *E. sulcarostrum* was unresolved in a clade also composed of *Cercosaura ocellata* Wagler, 1830, *Oreosaurus mediarmidi* Kok & Rivas, 2011, *Potamites ecleopus* (Cope, 1875) and *P. juruazensis* Ávila-Pires & Vitt, 1998. Later, Kok (2015) recovered a similar cercosaurine clade that included *Petracola* and *Proctoporus*, which were not sampled in the earlier study. That analysis resolved *Echinosauro* (*E. sulcarostrum*) as the sister-group of *Oreosaurus* (*O. mediarmidi*). Similar relationships were found by Goicoechea et al. (2016), although they also recovered *E. sulcarostrum* as the sister-species of *Macropholidus* + *Pholidobolus*. Sánchez-Pacheco et al. (2017) resolved *E. sulcarostrum* as sister to either *Petracola* or to a clade composed of *Oreosaurus*, *Potamites*, *Petracola*, *Cercosaura* and *Proctoporus*.

Torres-Carvajal et al. (2016) analysed a denser taxon sampling of cercosaurines, including additional members of *Echinosauro* (*E. brachycephala*, *E. horrida* – the type species of the genus – and *E. orcesi*) and the similarly riparian *Teuchocercus keyi*. Monotypic *Teuchocercus* nested within *Echinosauro*, and the species was transferred to that genus. *Echinosauro* was there recovered as the sister-group of the remaining cercosaurines, except for *Placosoma* + *Neusticurus*. *Echinosauro sulcarostrum* appeared either as the sister-taxon of *Proctoporus xestus* (Uzzell, 1969) or

as the sister-taxon of the remaining cercosaurines, except for *Placosoma*, *Neusticurus*, the remainder of *Echinosaura*, *Riama* and *Gelanesaurus*. [Moravec et al. \(2018\)](#) analysed an even denser taxon sampling of cercosaurines, in which *Echinosaura* and *Andinosaura* were found to be sister-groups and *E. sulcarostrum* was placed as the sister-species of *Euspondylus* (*E. excelsum* Chávez, Catenazzi & Venegas, 2017), corroborating the polyphyly of *Echinosaura*. Simultaneously, [Marques-Souza et al. \(2018\)](#) presented a hypothesis of relationships for riparian gymnophthalmids. Their study lacked rigorous taxon sampling of cercosaurines in general, and of *Echinosaura* in particular (e.g. they did not sample *Andinosaura* and *E. sulcarostrum*), but their main objectives were to investigate the relationships of *Neusticurus* and the position of the previously not-analysed *Potamites apodemus*, as well as to study the evolution of the riparian gymnophthalmids, rather than to resolve the phylogeny of *Echinosaura*. Nevertheless, they obtained *P. apodemus* as the sister-taxon of *Echinosaura* and transferred the species to that genus. *Echinosaura palmeri* and *E. panamensis* have not yet been included in phylogenetic analyses. Their inclusion in *Echinosaura* is based on their morphological resemblance to *E. horrida* ([Torres-Carvajal et al., 2016](#)).

The genus *Echinosaura* was erected by [Boulenger \(1890\)](#) for *E. horrida*. Later, [Boulenger \(1911\)](#), [Barbour \(1924\)](#) and [Dunn \(1944\)](#) added three more species (*E. palmeri*, *E. panamensis* and *E. centralis*, respectively). In his taxonomic revision of the genus, [Uzzell \(1965\)](#) relegated *E. horrida*, *E. palmeri* and *E. panamensis* to subspecies of *E. horrida*, resulting in the combinations *E. h. horrida*, *E. h. palmeri* and *E. h. panamensis*. Uzzell also placed *E. centralis* in the synonymy of *E. h. palmeri*. [Fritts et al. \(2002\)](#) described the new species *E. orcesi* and elevated the subspecies of *E. horrida* to species rank. Subsequently, [Köhler et al. \(2004\)](#) and [Donnelly et al. \(2006\)](#) described *E. brachycephala* and *E. sulcarostrum*, respectively. In their phylogenetic analysis of Cercosaurinae, [Torres-Carvajal et al. \(2016\)](#) transferred monotypic *Teuchocercus keyi* into *Echinosaura* (resulting in the combination *E. keyi*) and ‘excluded’ *E. sulcarostrum* from the genus. However, they did not propose a taxonomic change to accommodate the latter species. In a more recent study, [Marques-Souza et al. \(2018\)](#) transferred *Potamites apodemus* into *Echinosaura*, resulting in the combination *E. apodema*.

Although previous studies have advanced our understanding of the phylogeny and systematics of *Echinosaura*, several problems persist. First, the position of the genus (including that of *E. sulcarostrum*) among Cercosaurinae remains unclear due to differences in taxon sampling from competing hypotheses. Second, the incomplete taxon sampling of *Echinosaura*, which varies from one to five species per

analysis, has precluded a rigorous test of the monophyly of the genus. Third, compelling evidence for its non-monophyly is accumulating, and, although [Torres-Carvajal et al. \(2016\)](#) partially remedied this problem by transferring *T. keyi* to it, neither [Torres-Carvajal et al.](#) nor [Moravec et al. \(2018\)](#) proposed a taxonomic change to accommodate *E. sulcarostrum*, which still renders *Echinosaura* polyphyletic. Finally, species delimitation has not been tested within a phylogenetic context. Accordingly, we present a comprehensive phylogenetic analysis of *Echinosaura*, with the goals of (1) testing the monophyly of *Echinosaura*, including all its species, and (2) testing its phylogenetic position within Cercosaurinae. To this end, we assemble the largest molecular dataset of cercosaurines to date. We then propose a taxonomy, based on the resulting phylogenetic hypothesis, which is further supported by morphological distinctiveness and biogeography. We review the current species-level taxonomy of the redefined *Echinosaura* via an analysis of morphological and genetic variation, and analyse the patterns of geographic distribution of all its species.

MATERIAL AND METHODS

TAXON SAMPLING

Seventeen terminals representing all known species of *Echinosaura* are included in the phylogenetic analysis. If available, up to three samples for each species from different localities are included. Our ingroup sampling adds the previously not-analysed species *E. palmeri* and *E. panamensis*. Given that molecular evidence available for the critical taxon *E. sulcarostrum* is limited to 12S and 16S sequences from one terminal, we also add a newly sequenced specimen of that species in order to maximize intraspecific variation and loci coverage. To rigorously test the monophyly of *Echinosaura*, and due to the uncertain phylogenetic affinities of the genus, our outgroup sampling includes all species of Cercosaurinae for which DNA sequences are currently available. We also include representatives of all other major gymnophthalmid lineages and rooted the tree using two representatives of the family Alopoglossidae. In total, our dataset comprises 312 terminals, including 17 ingroup terminals representing eight species and 295 outgroup terminals.

CHARACTER SAMPLING

Mitochondrial DNA sequences used for the phylogenetic analysis include fragments of the rRNA subunits 12S and 16S, and the NADH dehydrogenase subunit IV (*ND4*) genes. The nuclear DNA sequences analysed include a fragment of the oocyte maturation factor (*C-mos*) gene. New sequences were deposited in

GenBank. We complement our new data with sequences available from GenBank. Voucher specimens and GenBank accession numbers are listed in Supporting Information, [Appendix SI](#).

DNA EXTRACTION, SEQUENCING AND EDITING

Total genomic DNA was extracted from frozen and ethanol-preserved tissues using either the GeneJET Genomic DNA Purification Kit (Thermo Fisher Scientific) or the DNeasy Kit (Qiagen), following the manufacturer's protocols. PCR amplification of partial sequences of 12S, 16S, *ND4* and *C-mos* was carried out in 25–30 µL reactions using the primers 12Sa–12Sb ([Harris et al., 1998](#)), 16Sa–16Sbr ([Palumbi et al., 1991](#)), 16SCL–16SDH ([Santos et al., 2003](#)), *ND4*–Leu ([Arevalo et al., 1994](#)) and G73–G74 ([Saint et al., 1998](#)), respectively. PCR conditions are those of [Santos et al. \(2003\)](#) and [Torres-Carvajal et al. \(2015\)](#). PCR products were purified using standard protocols and sequenced by the MacroGen sequencing facility (<http://www.macrogen.com>) and the molecular research lab at the Smithsonian Tropical Research Institute in Naos Marine Laboratories, Panama. Sequences were visualized, assembled and edited using GENEIOUS v.9.1.8 (<http://www.geneious.com>; [Kearse et al., 2012](#)).

PHYLOGENETIC ANALYSIS AND GENETIC DIVERGENCE

We performed a multiple alignment using MAFFT v.7.017 and the G-INS-i strategy for small-scale alignments ([Katoh & Standley, 2013](#)). PartitionFinder v.2.1.1 ([Lanfear et al., 2016](#)) was used to select the optimal partition scheme and substitution models for our dataset under the Akaike Information Criterion ([Akaike, 1974](#)). A maximum likelihood analysis was performed in IQ-TREE ([Nguyen et al., 2014](#)). Nodal support was estimated from 5000 ultrafast bootstrap pseudoreplicates. Ultrafast bootstrap is an alternative to the traditional bootstrap and uses the REL bootstrap and a tree likelihood threshold to accelerate nodal support estimation. Ultrafast bootstrap values above 95% indicate high support ([Minh et al., 2013](#)). Uncorrected pairwise distances for the 16S (552 bp) and *ND4* (621 bp) gene fragments were calculated in MEGA 7.0 ([Kumar et al., 2016](#)) and were employed to assess species limits. Previous studies of cercosaurines have also used pairwise comparisons to visualize species delimitation (e.g. [Sánchez-Pacheco et al., 2012](#)).

MORPHOLOGICAL DATA

One-hundred and seventy-four specimens were examined. Of these specimens, 62 were excluded

from morphometric analysis because 58 of them were not well-fixed or were in poor conditions, and the remaining four correspond to *Echinosaura sulcarostrum*, a taxon that represents a lineage that is not closely related to *Echinosaura s.s.* (see Results). Thus, we included a total of 112 specimens in our morphological analyses. Because numerous non-adult specimens were available in collections, we obtained linear measurements from all age classes. Specimens examined are listed in Supporting Information, [Appendix SII](#) and deposited in the reptile collections of: Museo de Herpetología Universidad de Antioquia, Medellín, Colombia (MHUA); Colección Zoológica de Prácticas de Docencia, Universidad del Valle, Cali, Colombia (CD); Colección de Herpetología Universidad del Valle, Cali, Colombia (UVC); Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia (ICN); Museo de La Salle, Universidad de La Salle, Bogotá, Colombia (MLS); Museo de Ciencias Naturales de La Salle, Medellín, Colombia (CSJ); Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Villa de Leyva, Colombia (IAvH); Colección del Círculo Herpetológico de Panamá, that now is the Collection of Herpetology (CH) deposited in the Smithsonian Tropical Research Institute, Panama; and Royal Ontario Museum, Toronto, Canada (ROM).

Linear measurements from 12 morphometric characters were obtained: snout–vent length (SVL), trunk length (TRL), tail length (TaL), snout length (SL), head length (HL), head width (HW), humerus length (HUM), forearm length (FAL), hand length (HND), femur length (FEM), tibia length (TIB) and foot length (FTL). SVL, TRL and TaL measurements were taken to ±1 mm with a piece of string and a ruler. The remaining measurements were taken with a digital calliper to ±0.01 mm. Each measurement was obtained in triplicate and then averaged. Sex was determined by noting the presence of hemipenes in males (if hemipenes were not everted, sex was determined by subcaudal incision) and/or secondary sex characters, such as the number of femoral pores. We also obtained nine meristic characters: frontal scale single or divided (F), number of large chin shields (CS), internasal scale single or divided (IS), number of supralabial (SLS) and infralabial (ILS) scales, number of femoral pores in males (FPM), number of subdigital lamellae on the fourth finger (S4F) and the fourth toe (S4T) and number of subcaudal scales (SCS). For bilateral characters, the amount of missing data on the right side was smaller than on the left side across the entire sample. Consequently, counts and linear measurements are reported from the right side. Terminology for cephalic scutellation follows [Fritts et al. \(2002\)](#).

MORPHOLOGICAL ANALYSES

Morphological variation among and within species was described and summarized using descriptive statistics and principal component analyses (PCAs). Due to the large number of specimens without tails and low interspecific variation in the number of large chin shields, we excluded TaL and CS from all numerical morphological analyses. We also excluded SVL from the multivariate analysis because we used it to size-correct our data, as described below. To determine if there was significant interspecific variation, two PCAs were performed separately using ten linear measurements and seven meristic variables, respectively. To avoid the effect of missing data in multivariate analyses, missing values in the dataset were inferred (Clavel *et al.*, 2014; Dray & Josse, 2014). For morphometric and meristic bilateral characters, missing data were completed with data taken from the left side (assuming negligible fluctuating asymmetry), while for meristic non-bilateral characters or meristic bilateral characters without left-side information, missing data were completed with the rounded mean for the species. Because our dataset included individuals of different age classes, all linear measurements were log-transformed and regressed against SVL in order to remove the size effect and to avoid excluding a significant number of samples (Reist, 1985; Klingenberg, 1996; Claude, 2008; Berner, 2011). Size correction was performed using a pooled regression including all species, under the assumption that growth is similar among species. Statistical analyses were conducted using RStudio 1.0.143 with R 3.4 and PAST 3 (Hammer *et al.*, 2001). Regression was conducted using the standardized major axis (SMA) with the R package *smatr* (Warton *et al.*, 2006; Warton *et al.*, 2012), and PCAs were performed using the R's native command *princomp*. Plots were generated using the *ggbiplot* package (Vu, 2011).

GEOGRAPHIC DISTRIBUTION

To assess patterns of distribution in *Echinosaura* and to describe the geographic ranges of all its species, we compiled 260 locality records from museum databases and literature. Described locality and geographic coordinates for each record were compared using Google Earth Pro v.7.3.2.5776 to ensure they were concordant. For records without georeference information (but having a locality description) and for records whose original coordinates were not at the described locality, new georeference data were assigned. When specific localities could not be found in the map, assignment of new georeference points was made by considering information from at least a second level of political administrative division or higher (according to each

country division), and using the nearest populated centre as reference. In both cases, we used the point method, trying to assign the most accurate possible location according to the available spatial information for each record (Wieczorek *et al.*, 2004). Many records used to delimitate species distributions without elevation data. Thus, to delimitate elevational ranges for each species, we obtained missing elevations using the NASA's digital elevation model SRTMGL1 V.3 (NASA JPL, 2013). Maps and the inference of the extent of occurrence (by convex hulls) were conducted in ArcMap 10.4.

RESULTS

PHYLOGENETIC RELATIONSHIPS

Sequence alignment results in a matrix of 2491 sites that correspond to 506 sites for 12S, 865 for 16S, 684 for ND4 and 436 for C-mos. The ML tree has a value of $-\ln L = 73123.085$ (Fig. 2; Supporting Information, Appendix SIII). As defined currently, *Echinosaura*, *Oreosaurus* and *Proctoporus* are non-monophyletic. *Echinosaura* is polyphyletic because *E. apodema* is sister to *Andinosaura* with high support (UFB 99%) and *E. sulcarostrum* is sister to a clade composed of *Anadia*, *Euspondylus*, *Macropholidus* and *Pholidobolus*, with high support (UFB 98%). The remaining *Echinosaura*, including the type species of the genus, form a clade with a support of 100%. This clade appears sister to *Andinosaura* + *E. apodema*. Accordingly, we propose a phylogenetic taxonomy that reflects historical relationships (see Discussion and Taxonomic accounts). Consequently, *E. apodema* and *E. sulcarostrum* will be treated hereafter as different entities. Within *Echinosaura s.s.*, our analysis identifies seven well-supported lineages: *E. brachycephala*, *E. horrida*, *E. keyi*, *E. orcesi*, *E. panamensis*, *E. palmeri* and a different lineage corresponding to individuals from the Magdalena Valley in Colombia. There is an available name for this latter lineage and we refer to it hereafter as *E. centralis* (see Discussion and Taxonomic accounts).

GENETIC DIVERGENCE

Uncorrected pairwise genetic distances among lineages within *Echinosaura s.s.* range between 5.6% (*E. centralis*/*E. palmeri*) and 12.6% (*E. horrida*/*E. panamensis*) for 16S, and 17.2% (*E. brachycephala*/*E. keyi*) and 25.4% (*E. keyi*/*E. centralis*) for the ND4 region (Table 1). The clade comprising the northern species (*E. centralis*, *E. palmeri* and *E. panamensis*) has lower interspecific genetic distances than the southern species (*E. brachycephala*, *E. horrida*, *E. keyi* and *E. orcesi*).

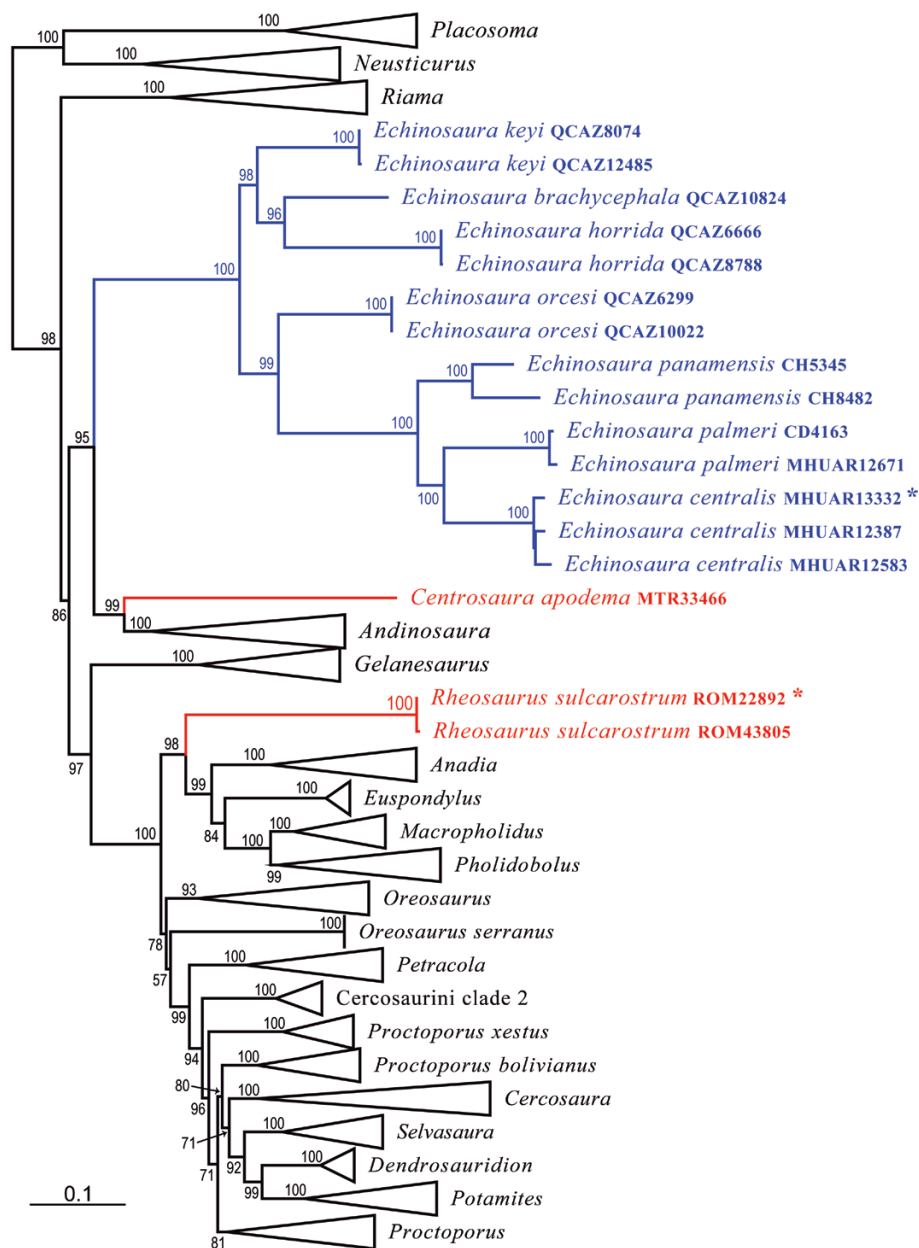


Figure 2. Maximum likelihood tree ($-\ln L = 73123.085$) depicting the phylogenetic relationships of *Echinosauroidea*, *Centrosaurinae* and *Rheosaurinae* within Cercosaurinae. The complete inferred tree is provided in Supporting Information, [Appendix SIII](#). Numbers above nodes represent ultrafast bootstrap support after 5000 pseudoreplicates. Neotype of *E. centralis* and paratype of *R. sulcarostrum* are marked with an asterisk.

MORPHOLOGICAL ANALYSES

Within *Echinosauroidea* s.s., maximum sizes (SVL_{max}) of adults have slight variations among species (between 70 and 86 mm), with *E. horrida*, *E. keyi* and *E. orcesi* being the largest species (for further details see: [Table 2](#) and [3](#)). We found juveniles to be less than 50 mm SVL (based on the development of spine-like scales and body robustness). We also found that, within our sampling, *E. horrida* is the species with the shortest

snout and *E. orcesi* is the one with the largest snout ([Fig. 3](#)). Except for differences between sexes in the occurrence and number of femoral pores (with females having fewer femoral pores than males or lacking them), there is no evident sexual dimorphism because both males and females reach similar sizes, although HL/HW ratio suggests that males may have wider heads than females. Species of the northern clade (*E. centralis*, *E. palmeri* and *E. panamensis*) are

Table 1. Uncorrected pairwise genetic distances among species of *Echinosaura* s.s. Upper-right matrix shows genetic distances for 621 bp of the *ND4* gene. Lower-left matrix shows distances for 548 bp of the 16S fragment

	<i>E. brachycephala</i>	<i>E. horrida</i>	<i>E. keyi</i>	<i>E. orcesi</i>	<i>E. palmeri</i>	<i>E. panamensis</i>	<i>E. centralis</i>
<i>E. brachycephala</i>		0.188	0.172	0.192	0.213	0.221	0.225
<i>E. horrida</i>	0.065		0.182	0.192	0.212	0.217	0.235
<i>E. keyi</i>	0.067	0.082		0.174	0.231	0.222	0.254
<i>E. orcesi</i>	0.077	0.076	0.074		0.213	0.200	0.223
<i>E. palmeri</i>	0.116	0.120	0.113	0.099		0.178	0.179
<i>E. panamensis</i>	0.120	0.126	0.114	0.113	0.065		0.176
<i>E. centralis</i>	0.113	0.116	0.115	0.105	0.056	0.082	

Table 2. Summary of selected morphological characters in species of *Echinosaura* s.s. (northern group). Values of each variable come from either this study, literature or both. Femoral pores counts are per hind limb and only for males. Subcaudal scales are per caudal segment. For codification of tail patterns see species accounts

		<i>E. centralis</i> ^A	<i>E. palmeri</i> ^A	<i>E. panamensis</i> ^{A, B, C, E}
Max. SVL	♂	75 mm	80 mm	71 mm
	♀	77 mm	74 mm	74 mm
HL/HW	♂	1.35–1.82	1.32–1.90	1.41–1.98
	♀	1.59–2.15	1.62–1.95	1.61–1.90
Internasal		Usually divided longitudinally	Divided longitudinally	Divided longitudinally
Frontal		Single	Single	Divided transversely
Tail pattern		"="	Usually "·"	Usually "<"
Subcaudals		3	3	3
Supralabials		4–6	4–5	4–6
Infralabials		3–5	4–5	4–6
Femoral pores		4–9	6–10	3–9
Subdigital lamellae		12–18	12–17	13–16
on 4 th finger				
Subdigital lamellae		20–27	19–25	20–22
on 4 th toe				

A, this study; B, Barbour (1924); C, Uzzell (1965); D, Fritts *et al.* (2002); E, Köhler *et al.* (2004).

similar morphologically, but *E. panamensis* is easily distinguished from the other two by having a frontal scale transversely divided and usually five supra- and five infralabial scales, while *E. centralis* and *E. palmeri* share a single frontal scale and five supra- and four infralabials. In contrast, the southern species (*E. brachycephala*, *E. horrida*, *E. keyi* and *E. orcesi*) have marked interspecific differences in scutellation, including the condition of the internasal scale, number of supra- and infralabials, number of subcaudals and number of subdigital lamellae on the fourth finger and the fourth toe. Scutellation variation is summarized in Table 2 and 3 and Figure 4.

Multivariate analyses show that among species of *Echinosaura* s.s., differences related to linear measurements are shallower compared with those of meristic characters. The PCA analysis based on linear measurements shows a high overlap among species, in contrast to the PCA obtained from scale counts,

where several species can be easily distinguished in the multivariate space (Fig. 5). The four principal components retained for the PCA based on linear measurements explain 75.9% of the variation, while the same number of components for the meristic variables explain 92.4% of the total variation. Using linear measurements, PC1 is mostly correlated with the variables FAL, FEM, FTL, TIB and HUM, and PC2 with HL and HW. Using meristic variables, PC1 is mostly correlated with the variables S4T, SCS and S4F, and PC2 with F and ILS (Supporting Information, Appendix SIV).

We also noted differences in the arrangement of dorsal scalation among all species (Fig. 6; see taxonomic section for detailed descriptions). For example, we found previously undocumented variation in dorsal and lateral tail scutellation between *E. palmeri* and *E. centralis* (Fig. 7), which refutes the proposal of Uzzell (1965) that both species were morphologically

Table 3. Summary of selected morphological characters in species of *Echinosauro s.s.* (southern group). Values of each variable come from either this study, literature or both. Femoral pores counts are per hind limb and only for males. Subcaudal scales are per caudal segment. For codification of tail patterns see species accounts. ND = no data

		<i>E. brachycephala</i> ^E	<i>E. horrida</i> ^{A, C, E}	<i>E. keyi</i> ^{A, E}	<i>E. orcesi</i> ^{A, D, E}
Max. SVL	♂	72 mm	86 mm	80 mm	81 mm
	♀	78 mm	80 mm	64 mm	81 mm
HL/HW	♂	1.47–1.59	1.45–1.79	1.45–1.51	1.75–2.18
	♀	1.43–1.60	1.54–1.84	1.49–1.53	1.93
Internasal		Single	Single	Divided longitudinally	Single
Frontal		Single	Single	Usually single	Single
Tail pattern		"<"	"="	"^"	":"
Subcaudals		4	3	3	5–6
Supralabials		3–5	4–6	4	3–5
Infralabials		3	3–4	3–4	2–3
Femoral pores		7–9	7–10	8–11	9–16
Subdigital lamellae on 4 th finger		16–23	14–19	ND	20–22
Subdigital lamellae on 4 th toe		23–32	21–25	ND	30–36

A, this study; B, Barbour (1924); C, Uzzell (1965); D, Fritts *et al.* (2002); E, Köhler *et al.* (2004).

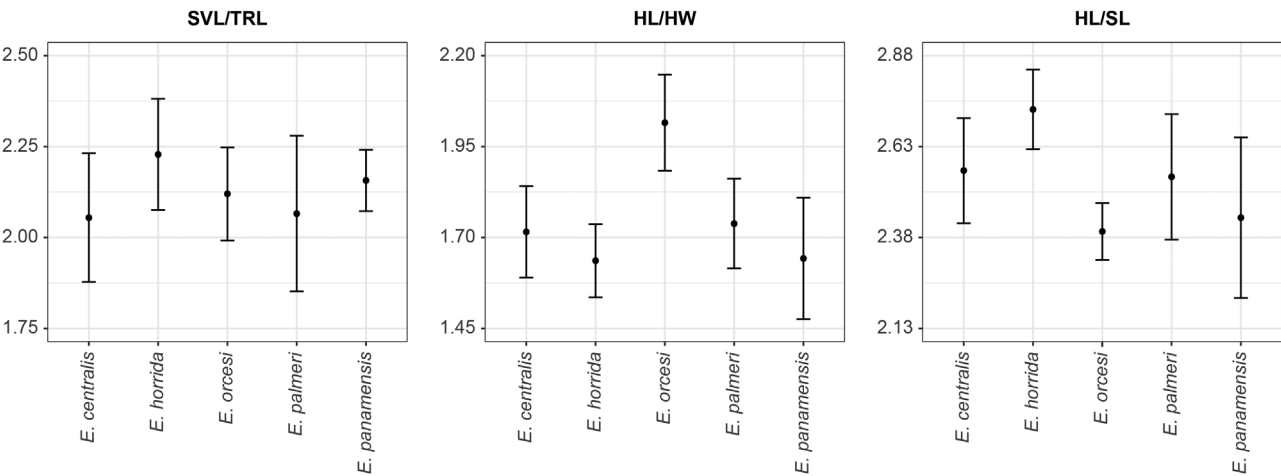


Figure 3. Morphological comparisons among species of *Echinosauro s.s.* using means and standard deviations of some linear measurements ratios.

indistinguishable. Additionally, we found that most individuals of *E. palmeri* have smooth ventral scales (82.4%), while most specimens of *E. centralis* have keeled ventral scales (76.5%). See Table 4.

GEOGRAPHIC DISTRIBUTION

We assigned coordinates to 78 records without them, corrected 16 erroneous localities and estimated missing elevations for 107 records. According to our results, all current lineages of *Echinosauro s.s.* are trans-Andean,

extending from lower Central America to north-western South America (Fig. 8A). Most records of *Echinosauro s.s.* are from lowlands (<1000 m a.s.l.), but their elevational range goes up to 2200 m a.s.l. (Fig. 8B). Species of the northern clade (*E. centralis*, *E. palmeri* and *E. panamensis*) have parapatric distributions. In contrast, southern species (*E. brachycephala*, *E. horrida*, *E. keyi* and *E. orcesi*) seem to be co-distributed, ranging from the Anchicayá region in Colombia southward to north-western Ecuador. Specific distribution notes for each species are given in the species accounts below.

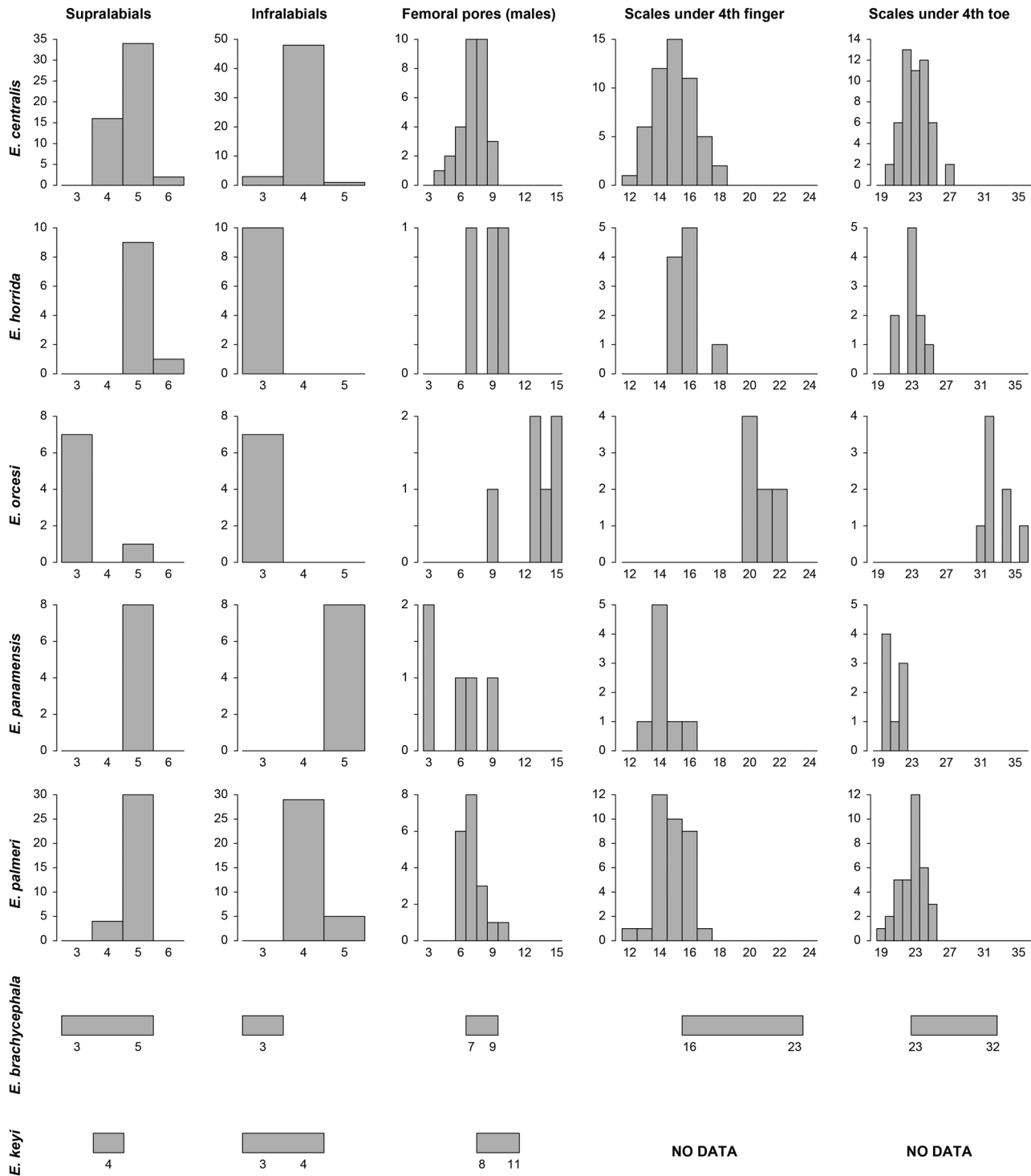


Figure 4. Morphological variation of meristic characters among species of *Echinosaura* s.s. Range values for *E. brachycephala* and *E. keyi* are based on Köhler *et al.* (2004).

According to the minimal convex hull, *E. palmeri* is the species with the largest extent of occurrence (c. 75,000 km²), while *E. brachycephala* has the smallest (c. 1400 km²). With respect to elevational ranges,

E. centralis is the species with the widest range (a span of 2154 m), while *E. panamensis* has the smallest (a span of 279 m). Following the biogeographic regionalization of Morrone (2014), all species of

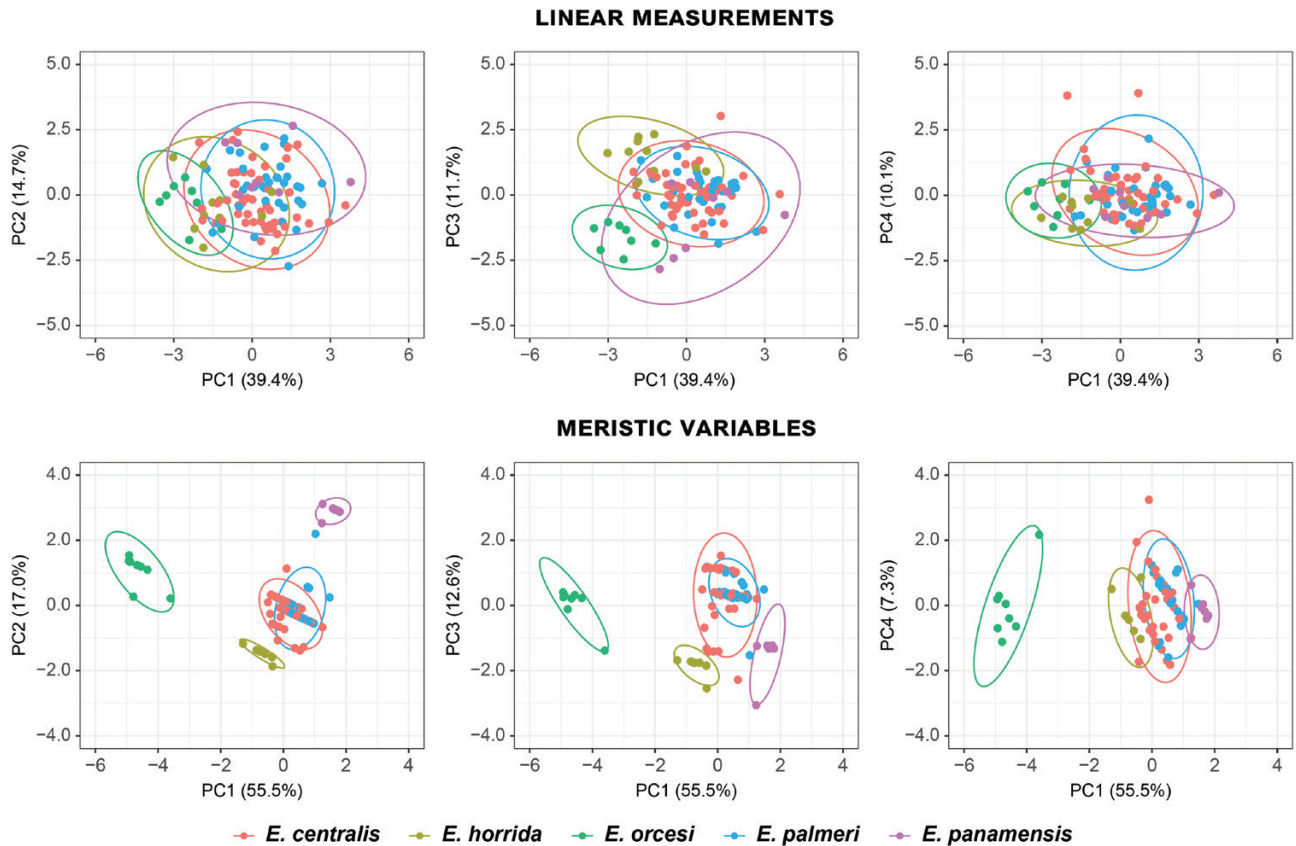


Figure 5. PCA results based on linear measurements and meristic variables among several species of *Echinosauro s.s.*

Echinosauro s.s. belong to the Pacific dominion as follows: *E. palmeri* to Chocó-Darién and Cauca provinces, *E. panamensis* to Puntarenas-Chiriquí and Guatuso-Talamanca provinces, *E. horrida* and *E. orcesi* to Chocó-Darién, western Ecuador and Cauca provinces, *E. brachycephala* and *E. keyi* to Cauca province and *E. centralis* to Magdalena province.

DISCUSSION

PHYLOGENETIC SYSTEMATICS OF *ECHINOSAURA*

Phylogenetic studies over the last two decades have dramatically changed the systematics of gymnophthalmid lizards. Previous taxonomic arrangements were based entirely on external morphological similarity, and now it is clear that distantly related lineages have converged into similar lepidosis. In addition, a significantly better taxon sampling is shaping our understanding of the evolution and biogeography of the group. Our study, which is the first to include all known species of *Echinosauro*, strongly rejects the monophyly of this genus as currently defined, and corroborates the hypothesized composition presented by Torres-Carvajal et al. (2016).

We identify three lineages that are not closely related: *Echinosauro s.s.*, *E. apodema* and *E. sulcarostrum* (Fig. 2). Although our genetic dataset (the only evidence used to infer the phylogenetic hypothesis) is in conflict with previous morphological studies, these three lineages can be easily diagnosed using scutellation (see Taxonomic accounts below). Similar results of molecular phylogenetic hypotheses rejecting previous taxonomic proposals have been obtained for other cercosaurine genera such as *Anadia*, *Macropholidus*, *Potamites*, *Proctoporus*, *Pholidobolus* and *Riama* (Castoe et al., 2004; Goicoechea et al., 2012; Torres-Carvajal & Mafla-Endara, 2013; Torres-Carvajal et al., 2016; Sánchez-Pacheco et al., 2017).

Our analysis resolves *Echinosauro s.s.* (a clade of seven species) as the sister-group of *Andinosaura* + *E. apodema*. This finding partially agrees with the results of Moravec et al. (2018), whose study recovered *Echinosauro s.s.* as the sister-group of *Andinosaura*. However, they did not include *E. apodema* in their analyses. Using a less extensive sampling of cercosaurines, Torres-Carvajal et al. (2016) and Marques-Souza et al. (2018) found *Echinosauro s.s.* to be the sister of the remainder of cercosaurines, except for *Placosoma* + *Neusticurus*. Marques-Souza

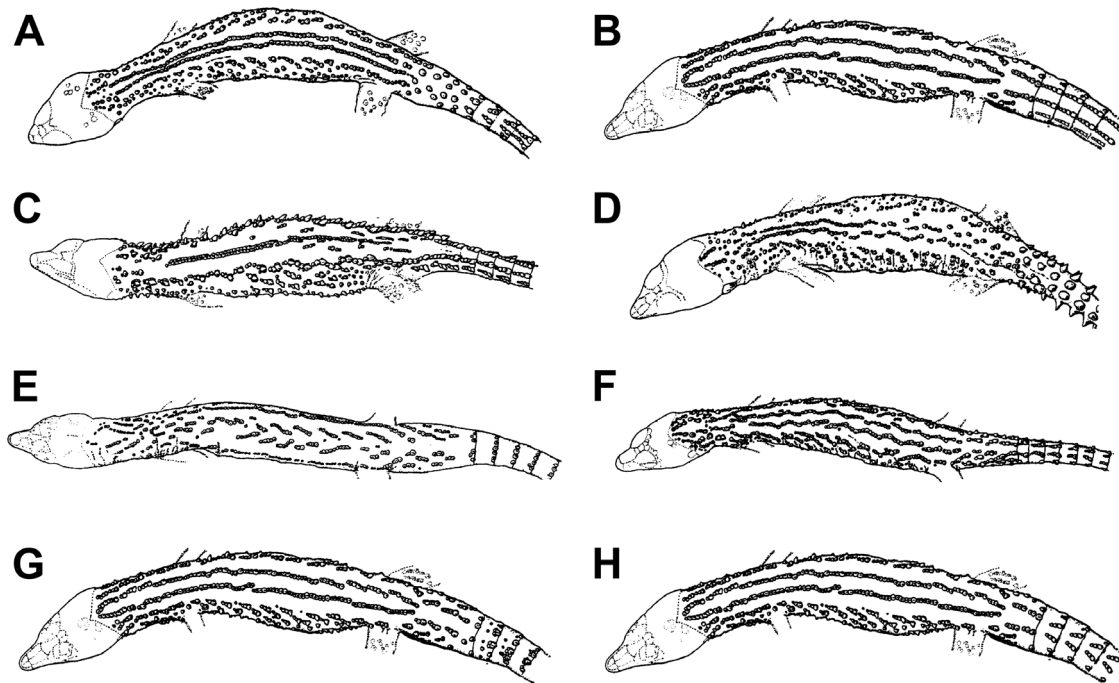


Figure 6. Arrangement of dorsal scalation in species of *EchinosaURA* s.s. *E. brachycephala* (A), *E. centralis* (B), *E. horrida* (C), *E. keyi* (D), *E. orcesi* (E), *E. panamensis* (F) and *E. palmeri* (G and H). Drawings adapted from Köhler *et al.* (2004). Illustrations of *E. centralis* and *E. palmeri* (H) were created using existent drawings as models but digitally modified to show tail variations.

et al. (2018) also included for the first time *Potamites apodemus* in a phylogenetic analysis. They found it to be sister to *EchinosaURA* and transferred the species to that genus. However, these two studies did not include the Andean clade *Andinosaura*. Thus, even though the placement of *E. apodema* in our analysis is different from Marques-Souza *et al.* (2018), this is not surprising given the limited taxon sampling in their analysis (Heath *et al.*, 2008; Wiens & Tiu, 2012).

Our results place *E. sulcarostrum* as sister to a clade composed of *Anadia*, *Euspondylus*, *Macropholidus* and *Pholidobolus*. While the placement of *E. sulcarostrum* outside *EchinosaURA* s.s. is consistent with recent findings (Torres-Carvajal *et al.*, 2016; Moravec *et al.*, 2018), its relationship to other cercosaurines has varied across studies, depending on the dataset and methods used. For example, Goicoechea *et al.* (2016) resolved *E. sulcarostrum* as sister to either *Macropholidus* + *Pholidobolus* (their TA + MP and SA + MP analyses) or to *Oreosaurus* (their SA + ML analysis). The latter relationship was also found by Kok (2015; MP, ML and BI analyses). The ML analysis of Torres-Carvajal *et al.* (2016) placed *E. sulcarostrum* and *Proctoporus xestus* as sister-species. However, their BI analysis recovered *E. sulcarostrum* as the sister-taxon of the remaining cercosaurines except for *Placosoma* + *Neusticurus*, the remainder of *EchinosaURA*, *Riama* and *Gelanesaurus*.

Sánchez-Pacheco *et al.* (2017) resolved the species as sister to either a clade including *Cercosaura*, *Oreosaurus*, *Potamites*, *Petracola* and *Proctoporus* (their MO + MP analysis) or to *Petracola* (their TE + MP analysis). More recently, Moravec *et al.* (2018; MP, ML and BI analyses) found it to be sister to *Euspondylus*. Despite the differences in the approach, and in the alignment and optimality criterion among (and within) these studies, the unstable position of *E. sulcarostrum* is most likely due to different taxon sampling and the low loci coverage for this species. These studies assembled different phylogenetic matrices of cercosaurines, and the only data available for *E. sulcarostrum* were partial regions of 12S and 16S from a single individual, while analyses have generally used sequences from four genetic markers (12S, 16S, *ND4* and *C-mos*). Thus, our inclusion of a newly sequenced terminal of *E. sulcarostrum* into the largest molecular dataset of cercosaurines assembled to date, increases the coverage of DNA sequences for this taxon by adding the previously not-analysed locus *ND4*, maximizes intraspecific variation of 12S and 16S sequences, and allows assessment of the placement of this species within a broader phylogenetic context. We find *E. sulcarostrum* to be sister to a clade including *Anadia*, *Euspondylus*, *Macropholidus* and *Pholidobolus* with high support, a hypothesis that can

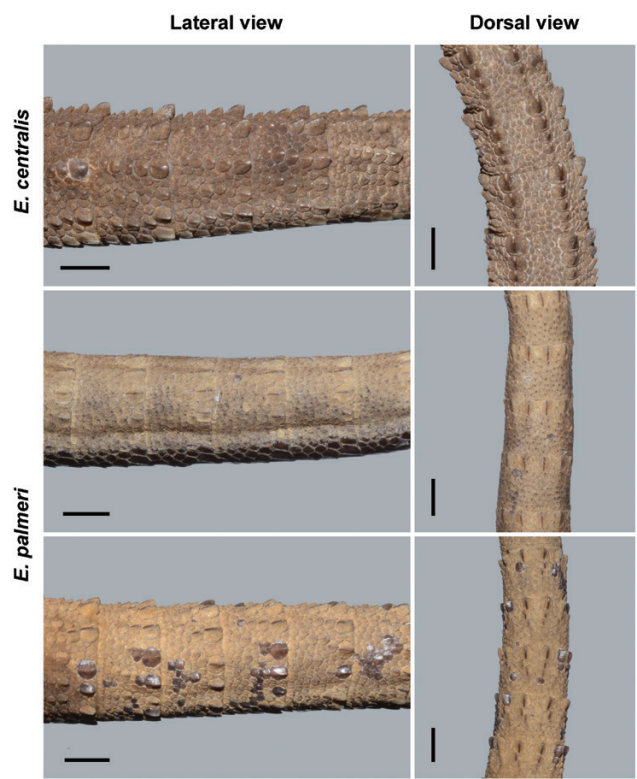


Figure 7. Dorsal and lateral view of scutellation tail patterns in *Echinosauro centralis* (MHUA-R 13212) and *E. palmeri* (MHUA-R 12293 and MHUA-R 12591). Bars = 2 mm.

Table 4. Tail pattern and ventral scale relief in *Echinosauro centralis* and *E. palmeri*. For codification of tail scutellation patterns see species accounts

	Tail scutellation patterns		
	:	<	=
<i>E. centralis</i> (N = 51)	0	0	51 (100%)
<i>E. palmeri</i> (N = 42)	16 (38.1%)	26 (61.9%)	0
Ventral scales			
	Smooth	Keeled	
<i>E. centralis</i> (N = 51)	12 (23.5%)	39 (76.5%)	
<i>E. palmeri</i> (N = 34)	28 (82.4%)	6 (17.6%)	

be tested by adding the locus that remains missing for this taxon (C-mos) and increasing taxon sampling.

Our analysis persists in corroborating the non-monophyly of *Echinosauro* not only due to the placement of *E. sulcarostrum* (Torres-Carvajal et al., 2016; Moravec et al., 2018), but also due to the position of *E. apodema*. Based on our results, and

given the morphological distinctiveness and disjunct distribution of both taxa with respect to their sister-groups and *Echinosauro s.s.*, and the lack of available generic names, we erect two new genera to contain them in order to remedy the polyphyly of *Echinosauro*. These taxonomic actions secure a monophyletic *Echinosauro*.

TAXONOMY AND DISTRIBUTION OF *ECHINOSAURO S.S.*

Morphometric analyses using linear and meristic characters are common in taxonomic studies of lizards. These analyses represent a quantitative way to determine not only the variation within species, but also the ‘morphological gap’ among them. However, often the differences expressed as ratios overlap, and conspicuous characters cannot be extracted for taxonomic diagnosis (except for the extreme values). Instead, individual key characters have proven to be sometimes more useful than multivariate and continuous traits. For example, as shown in Fig. 5, all species (except *E. orcesi*) overlap at some degree in the multivariate space, but individual key characters, such as number, condition or shape of scales, are more useful for species delimitation, and were consistent with the other examined evidence (geographic and genetic data). Thus, we advocate using individual traits to delimit species beyond its combination on statistical multivariate analyses.

In *Echinosauro s.s.* there are two geographic distribution patterns: parapatric distributions in the northern species (*E. centralis*, *E. panamensis* and *E. palmeri*) and co-distribution in the southern species (*E. brachycephala*, *E. horrida*, *E. keyi* and *E. orcesi*). We believe this is not just the effect of sampling effort, since we have the most complete dataset to date of these lizards, including morphological, genetic and geographic information. How this genus has evolved and how its species reached their current distributions is still unclear, but this study places *Echinosauro s.s.* as a good model to study how different evolutionary processes may act on closely related species.

Dunn (1944) described *Echinosauro centralis* from the central and eastern Andes of Colombia in the Magdalena Valley, but it was later synonymized with *E. palmeri* by Uzzell (1965). However, our genetic, morphological and geographic evidence supports the existence of two different species under the name *Echinosauro palmeri*. Accordingly, we resurrect the available name *E. centralis* from the synonymy of *E. palmeri* for the populations occurring in this region of the Andes and the Magdalena Valley. In the absence of type and topotypic material for this species, a neotype designation is needed, which was done below.

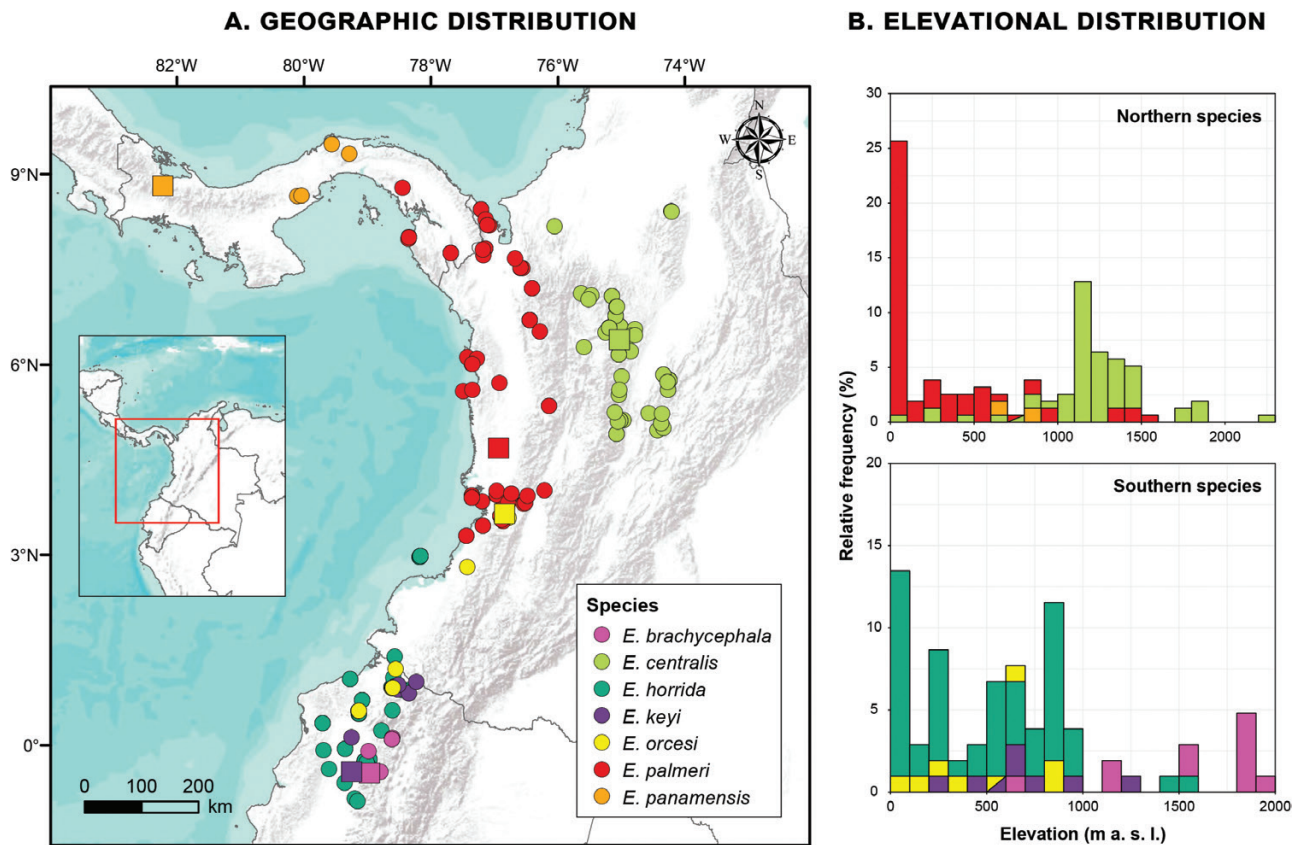


Figure 8. Distribution map of all known species of *Echinosauroidea* s.s. (A) and their elevational distributions (B). Circles represent museum records and squares type localities. Elevational histograms are split into two groups (northern and southern species; see text for definition of groups) to allow a better visualization of the information, since many of the elevational ranges overlap partially among species. Frequencies are relative by groups (156 individuals for northern species and 104 for southern species).

TAXONOMIC ACCOUNTS

CENTROSAURA VÁSQUEZ-RESTREPO ET AL., GEN. NOV.

Type species: Neusticurus apodemus Uzzell, 1966.

LSID: urn:lsid:zoobank.org:act:39D45340-0068-49FD-8209-90B7E6B20A0D

Content: One species: *Centrosaura apodema* (Uzzell, 1966) comb. nov. [previously *Neusticurus apodemus* Uzzell, 1966; *Potamites apodemus* (Doan & Castoe, 2005); *Echinosauroidea apodema* (Marques-Souza et al., 2018)].

Diagnosis: Phenotypic characteristics of *Centrosaura* include: (1) dorsal scales heterogeneous, with large or polygonal, longitudinally keeled scales intermixed with small irregular scales; (2) dorsal surface of the head with small, asymmetrical and non-paired scales anteriorly, and with large regular scales posteriorly;

(3) several scales on internasal and frontonasal region; (4) prefrontals paired; (5) frontal divided; (6) frontoparietals small, paired; (7) interparietal well defined; (8) parietals paired; (9) postmental single, large; (10) large chin shields in three pairs; (11) lower eyelid developed, with a palpebral disc divided into several, unpigmented scales; (12) ventral scales squared, not imbricated; (13) limbs pentadactyl, digits clawed; (14) femoral pores in both sexes, with males having more femoral pores than females.

Centrosaura differs from other cercosaurine genera except *Echinosauroidea* s.s., *Gelanesaurus*, *Neusticurus*, *Potamites* and *Rheosaurus* in having heterogeneous dorsal scalation. It differs from *Echinosauroidea* in having large, longitudinally keeled dorsal scales intermixed with small irregular scales (vs. small or granular, irregular dorsal scales intermixed with tubercular or spine-like scales), a well-defined interparietal (vs. irregular scales on parietal region) and irregular and asymmetrical scales on prefrontal–nasal region with paired prefrontals (vs. symmetrical scales on

prefrontal–nasal region and prefrontals usually absent); from *Gelanesaurus* in lacking a black ring around the nostril (vs. black ring around the nostril present); from *Neusticurus* in having a slightly compressed tail (vs. strongly compressed tail) and calcareous spinules on flounces of hemipenes (vs. no calcareous spinules on hemipenes); from *Potamites* in having irregular scales on prefrontal–nasal region (vs. a single frontonasal) and from the new genus *Rheosaurus* in having internasal irregularly divided (vs. internasal symmetrically divided), several irregular scales in frontonasal region (vs. three frontonasals) and frontal divided (vs. frontal single). *Centrosaura* differs from *Andinosaura*, its sister-clade, in having heterogeneous dorsal scalation (vs. homogenous dorsal scalation) and irregular scales on prefrontal–nasal region with prefrontals present (vs. a single frontonasal and prefrontals usually absent). For comparisons among related or similar genera see [Figure 9](#) and [Table 5](#).

Etymology: *Centrosaura* (gender feminine) is derived from the Latin *centrum* (centre or middle) and the Greek *σαύρα*, *saura* (lizard), in reference to its geographic distribution in Central America.

Geographic distribution: *Centrosaura* is distributed along the Pacific drainage of eastern Costa Rica and western Panama ([Lotzkat et al., 2018](#)). Its elevational range goes from 30 to 1200 m a.s.l. ([Savage, 2002](#); [Sasa et al., 2010](#); [Lotzkat et al., 2018](#)).

Remarks: The sister-clade to *Centrosaura* is *Andinosaura*, an exclusively Andean radiation of 11 species ([Sánchez-Pacheco et al., 2017](#)).

RHEOSAURUS VÁSQUEZ-RESTREPO ET AL., GEN. NOV.

Type species: *Echinosaura sulcarostrum* [Donnelly et al., 2006](#).

LSID: urn:lsid:zoobank.org:act:A7C758C4-CD77-4CCF-BF4B-79C1D1A1C854

Content: One species: *Rheosaurus sulcarostrum* ([Donnelly et al., 2006](#)) comb. nov.

Diagnosis: Phenotypic characteristics of *Rheosaurus* include: (1) dorsal scales heterogeneous, with large or polygonal, longitudinally keeled scales intermixed with small irregular scales; (2) dorsal surface of the head with large, symmetrical scales; (3) internasal divided; (4) frontonasals three; (5) prefrontals paired; (6) frontal single; (7) frontoparietals paired; (8) interparietal well defined; (9) parietals paired;

(10) rostral and mental striated; (11) three rows of scales between rostral and frontal scales; (12) postmental absent; (13) large chin shields in three pairs; (14) lower eyelid developed, with a palpebral disc divided into several, unpigmented scales; (15) ventral scales squared, not imbricated; (16) limbs pentadactyl, digits clawed; (17) femoral pores present in males (weakly developed) and absent in females.

Rheosaurus differs from all other cercosaurines, including *Echinosaura* s.s. and its sister-group, in having striated rostral and mental scales and three rows of scales between rostral and frontal scales, and in lacking a postmental scale. It also differs from other cercosaurines, except *Centrosaura*, *Echinosaura* s.s., *Gelanesaurus*, *Neusticurus* and *Potamites*, in having heterogeneous dorsal scalation. For comparisons among related or similar genera see [Figure 9](#) and [Table 5](#).

Etymology: *Rheosaurus* (gender masculine) is derived from the Greek *ῥέω*, *rheo* (flow or stream) and *σαύρα*, *saura* (lizard), in reference to the riparian habit of this lizard.

Geographic distribution: Pantepui bioregion of the Guiana Shield, from the vicinity of the Baramita area in north-western Guyana (100 m a.s.l.) to the Wokomung massif in west-central Guyana ([Donnelly et al., 2006](#); [Cole et al., 2013](#)).

Remarks: [Donnelly et al. \(2006\)](#) tentatively allocated *sulcarostrum* to *Echinosaura* and emphasized that this generic assignment reflected convenience rather than an understanding of the phylogenetic relationships of this species. They also anticipated that its disjunct distribution with respect to other *Echinosaura* and the differences in external head morphology, may reflect an independent phylogenetic history.

ECHINOSAURA BOULENGER, 1890

Type species: *Echinosaura horrida* [Boulenger, 1890](#) (by original designation).

Content: Seven species: *Echinosaura brachycephala* [Köhler et al., 2004](#); *E. centralis* [Dunn, 1944](#); *E. horrida* [Boulenger, 1890](#); *E. keyi* ([Fritts & Smith, 1969](#)); *E. orcesi* [Fritts, Almendáriz & Samec, 2002](#); *E. palmeri* [Boulenger, 1911](#); *E. panamensis* [Barbour, 1924](#).

Diagnosis: Phenotypic characteristics of *Echinosaura* include: (1) dorsal scales heterogeneous, with small or granular, irregular scales intermixed with tubercular

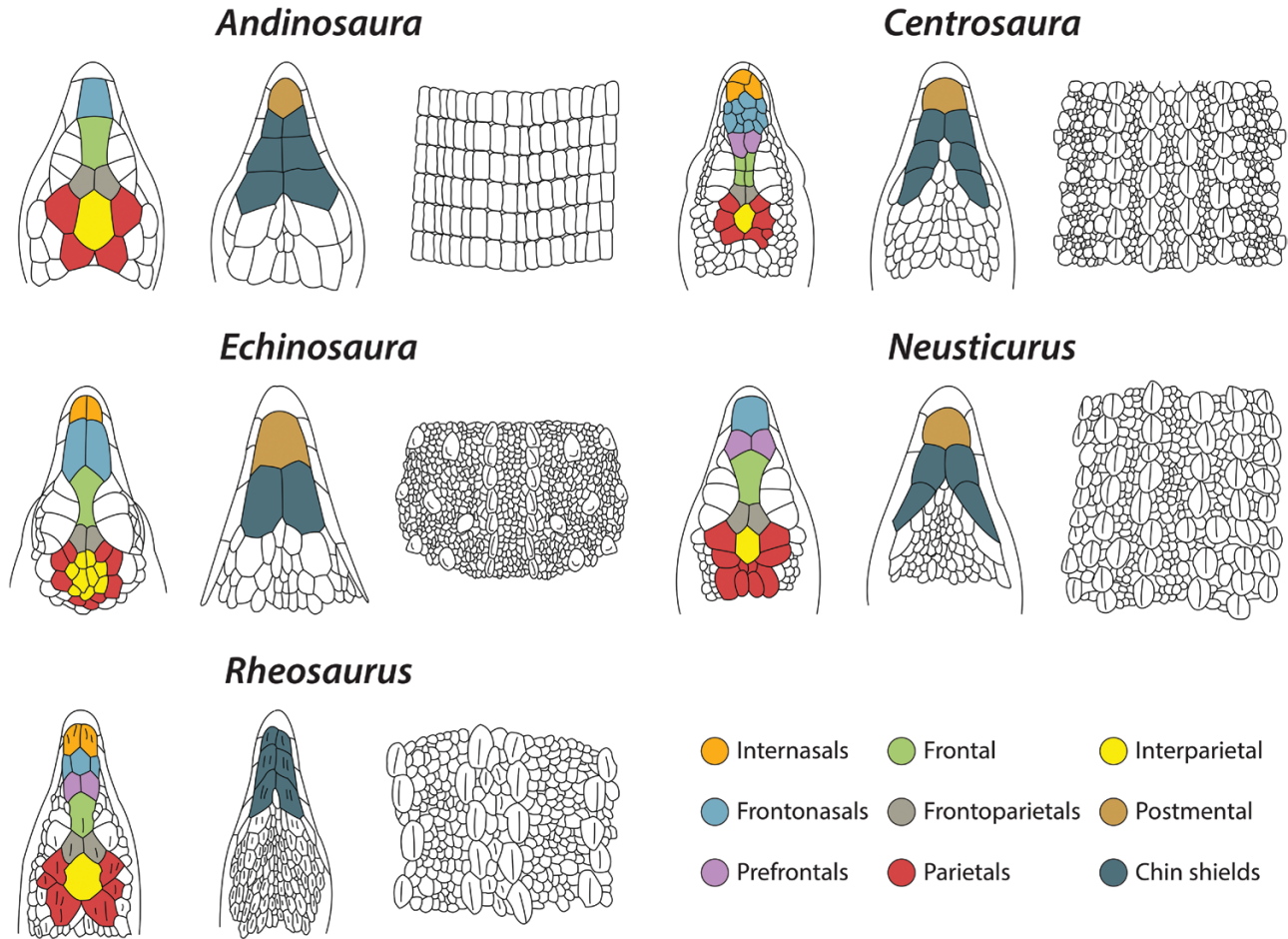


Figure 9. Variation in scutellation among several genera of Cercosaurinae. Drawings are based on MHUA-R 11122 (*Andinosaura laevis* from Caldas, Colombia), KU 67375 (*Centrosaura apodema* from San José, Costa Rica), MHUA-R 12250 (*Echinosauro centralis* from Antioquia, Colombia), ROM 22893 (*Rheosaurus sulcarostrum* from Baramita, Guyana) and IRSNB 2687 (*Neusticurus arekuna* from Bolívar, Venezuela). Illustrations of *R. sulcarostrum* and *N. arekuna* were based on drawings or photographs from Donnelly *et al.* (2006) and Kok *et al.* (2018), respectively.

or spine-like scales; (2) dorsal surface of the head with large, symmetrical and paired scales anteriorly, and with irregular small scales posteriorly; (3) internasal single or divided; (4) frontonasals paired; (5) prefrontals usually absent; (6) frontal scale single or divided; (7) frontoparietals small, paired; (8) interparietal and postparietal scales not well defined (Fig. 10); (9) postmental large, single (reduced or absent in *E. brachycephala*); (10) chin shields usually large, in one pair (smaller in *E. horrida*, not differentiated in *E. brachycephala*) (Fig. 10); (11) lower eyelid developed, with a palpebral disc divided into several, unpigmented scales; (12) ventral scales squared (or rounded squares), not imbricated; (13) limbs pentadactyl, digits clawed; (14) males with well-developed femoral pores, females usually lacking them or having fewer femoral pores than males (if

present, weakly developed or barely distinguishable). Morphological variation among species of *Echinosauro* is summarized in Table 2 and 3.

Echinosauro differs from other cercosaurines, except *Centrosaura*, *Gelanesaurus*, *Neusticurus*, *Potamites* and *Rheosaurus*, in having heterogeneous dorsal scalation. It differs from the other genera with heterogeneous dorsal scalation in having small or granular, irregular dorsal scales intermixed with tubercular or spine-like scales (vs. small irregular or granular dorsal scales intermixed with large or polygonal keeled scales), several irregular scales on the parietal region (vs. regular scales on parietal region) and usually one pair of large chin shields (vs. usually more than one pair of large chin shields). A comparison of *Echinosauro* and closely related and morphologically similar genera is given in Table 5 and Figure 9.

Table 5. Comparison of *Echinosaura* s.s. and morphologically similar and closely related genera

Genus	Dorsum	Internasal	Frontonasals	Prefrontals	Interparietal	Parietals	Postmental	Chin shields
<i>Andinosaura</i>	Homogenous rectangular scales	Absent	Present (single)	Absent	Well defined (single)	Well defined (paired)	Present	Two or three pairs
<i>Centrosaura</i>	Heterogenous scales; irregular small scales intermixed with tubercular and large, flat, longitudinally keeled scales	Present (several irregular scales)	Present (several irregular scales)	Present (paired)	Well defined (single)	Well defined (paired)	Present	Three pairs
<i>Echinosaura</i>	Heterogenous scales; irregular small scales intermixed with tubercular and spine-like scales	Present (single or divided)	Present (paired)	Absent	Not well defined (several irregular scales)	Not well defined (several irregular scales)	Usually present (absent or reduced in <i>E. brachycephala</i>)	Usually one pair (not differentiated in <i>E. brachycephala</i>)
<i>Neusticurus</i>	Heterogenous scales; irregular small scales intermixed with large flat or polygonal, longitudinally keeled scales	Absent	Present (single or paired)	Present (paired)	Well defined (single)	Well defined (paired)	Present	Several pairs
<i>Potamites</i>	Heterogenous scales; irregular small scales intermixed with tubercular and flat, longitudinally keeled scales	Absent	Present (single or paired)	Present (paired)	Well defined (single)	Well defined (paired)	Present	Several pairs
<i>Rheosaurus</i>	Heterogenous scales; irregular small scales intermixed with large flat or polygonal, longitudinally keeled scales	Present (divided)	Present (three)	Present (paired)	Well defined (single)	Well defined (paired)	Absent	Three pairs

Etymology: Although not explicitly stated by [Boulenger \(1890\)](#), the name *Echinosaura* (gender feminine) is presumably formed from the Ancient Greek ἐχῖνος, *echinos* (hedgehog or urchin) and σαύρα, *saura* (lizard) – a spiny lizard.

Geographic distribution: All species of *Echinosaura* are trans-Andean, extending from western Panama to north-western Ecuador. Most species occur in lowlands, but some reach as high as c. 2200 m a.s.l.

Remarks: Our phylogenetic analysis corroborated the inclusion of the previously not-analysed species *E. palmeri* and *E. panamensis* in *Echinosaura* s.s., as recently hypothesized by [Torres-Carvajal et al. \(2016\)](#).

ECHINOSAURA BRACHYCEPHALA KÖHLER ET AL., 2004

(FIGS 6A, 10A)

Echinosaura brachycephala [Köhler et al., 2004](#): 52–60 (original description). **Holotype:** Male (MHNG 2359.77) from ‘Las Pampas (=San Francisco de las Pampas, 0° 25′ 60″ S, 78° 25′ 00″ W, 1275 m elevation), Provincia Cotopaxi, Ecuador’.

Diagnosis: The following data are based on the original description and high-quality photographs of specimens deposited at QCAZ (Museo de Zoología, Pontificia Universidad Católica del Ecuador; photographs are available online through www.bioweb.bio). *Echinosaura brachycephala* possesses the following characteristics: (1) snout relatively short and rounded; (2) internasal single; (3) frontonasals paired [rarely with 1–4 small irregular scales between the frontonasals and the frontal (‘prefrontals’)]; (4) frontal single (rarely divided); (5) frontoparietals paired; (6) supraoculars three (third supraocular smaller than first and second); (7) supralabials 3–5 (usually four); (8) infralabials three; (9) postmental reduced or absent; (10) chin shields not differentiated; (11) two paravertebral rows of tubercles or spine-like scales, slightly undulating, separated from each other by 4–6 small, irregular scales; (12) tubercular scales forming oblique lines on lateral surface of body; (13) ventral scales keeled, squared (or are rounded squares); (14) subdigital lamellae on the fourth finger 16–23; (15) subdigital lamellae on the fourth toe 23–32; (16) femoral pores per hind limb in males 7–9, in females 1–2; (17) dorsal and lateral surface of tail with small tubercles scattered along each caudal segment (coded as ‘< pattern’); (18) subcaudals per caudal segment four (when tail is not regenerated); (19) dorsum brown or dark brown, relatively uniform, with some clear

spots more or less visible; ventral surface of head and neck light brown with several scales bearing white spots, except on the edges near the mouth where there is a darker ground colour with some transverse cream blotches which extend to labial scales; ventral surface of body (including limbs and tail) mainly light brown spotted with dark brown and cream.

Combination of these characteristics distinguishes *Echinosaura brachycephala* from its congeners. In addition, the distinctiveness of *E. brachycephala* and its sister-species, *E. horrida* ([Fig. 2](#)), is further corroborated by uncorrected pairwise distances of 18.8% in ND4 and 6.5% in 16S ([Table 1](#)).

Geographic distribution: *Echinosaura brachycephala* is endemic to Ecuador. It occurs in the west versant of the Andes in Pichincha and Cotopaxi provinces at elevations between 690 and 1915 m a.s.l. ([Fig. 8](#)).

Remarks: Most paratypes (42 specimens) were collected at the type locality (paratopotypes), whereas the remaining eight paratypes are from Tandapi, Pichincha province, Ecuador ([Köhler et al., 2004](#)). Although the distributions of *Echinosaura brachycephala* and *E. horrida* partially overlap, *E. brachycephala* seems to be more common above 1200 m a.s.l.

ECHINOSAURA CENTRALIS DUNN, 1944

(FIGS 6B, 7, 10B, 11, 12)

Echinosaura centralis [Dunn, 1944](#): 397–398 (original description). Types destroyed or lost (see below), from ‘Muzo (Humbo) [Boyacá department, Colombia]’ and ‘Robledo (near Medellín) [Antioquia department, Colombia]’, exact localities are unknown.

Echinosaura horrida palmeri ([Boulenger, 1911](#)) – [Uzzell, 1965](#): 85 (for ILS 216–218 from ‘Muzo’ and CNHM 63813 from ‘4 km northeast of Bellavista, on the Río Porce, in Antioquia’).

Designation of neotype: [Dunn \(1944\)](#) described *Echinosaura centralis* based on eight specimens, seven of which were collected in Muzo, department of Boyacá, Colombia and deposited in the collection of Museo de La Salle (Bogotá, Colombia, MLS). The remaining specimen was collected in Robledo, Medellín, department of Antioquia, Colombia and deposited in the collection of Colegio San José (Medellín, Colombia, now Museo de Ciencias Naturales de La Salle, CSJ). However, Dunn did not provide an individual identification for each specimen beyond mentioning that the holotype was the largest

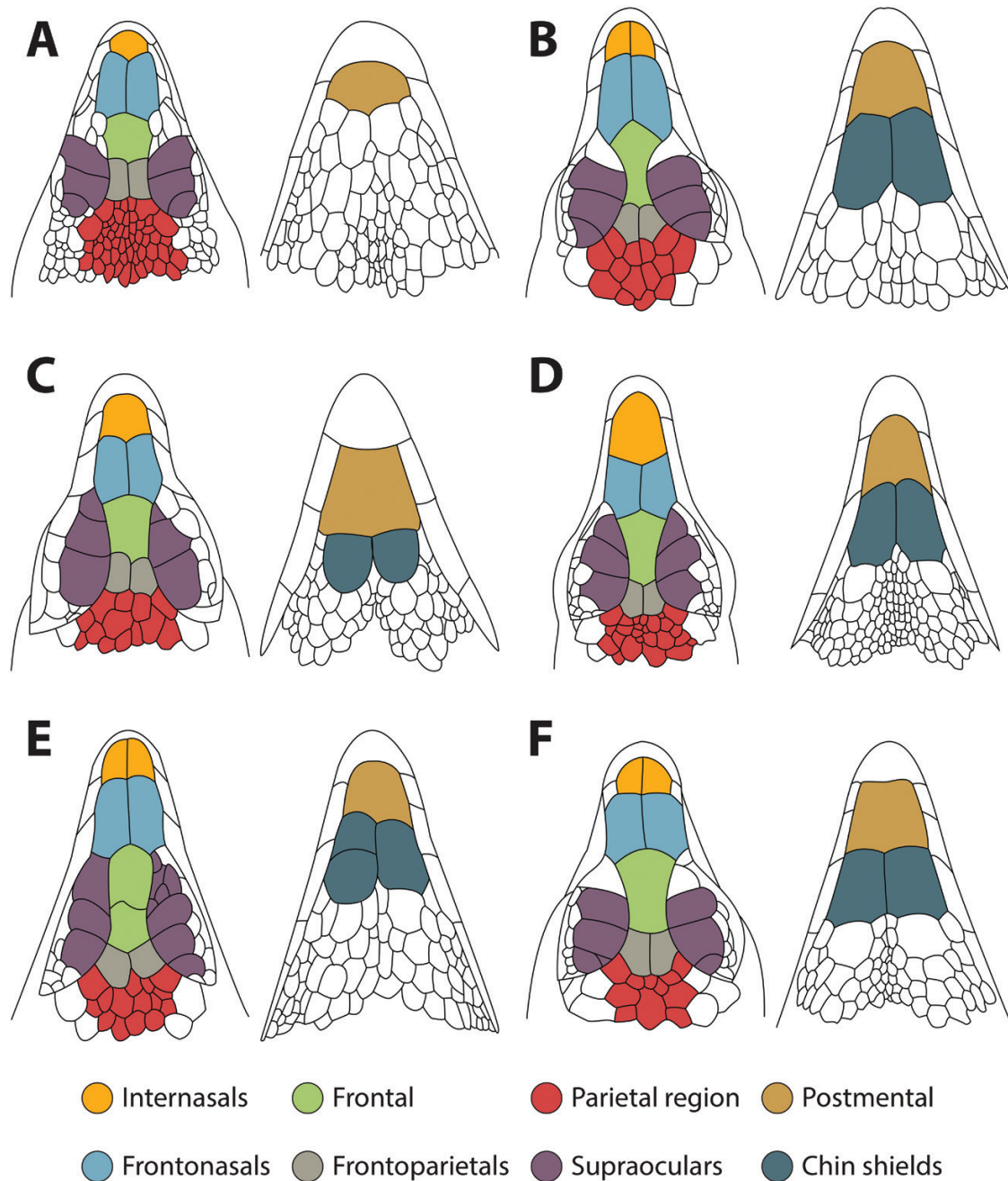


Figure 10. Variation in dorsal and ventral head scutellation among species of *Echinosauroidea* s.s. *E. brachycephala* (A), *E. centralis* (B), *E. horrida* (C), *E. orcesi* (D), *E. panamensis* (E) and *E. palmeri* (F). Drawings are not scaled as are for scutellation comparisons only. Drawings based on: MHNG 2359.77 (*E. brachycephala*), MHUA-R 12250 (dorsal) and MHUA-R 13158 (ventral) (*E. centralis*), MHUA-R 10214 (*E. horrida*), CD 3778 (dorsal) and CD 2420 (ventral) (*E. orcesi*), MCZ 17746 (*E. panamensis*), MHUA-R 10069 and MHUA-R 10344 (*E. palmeri*).

specimen from Muzo. According to Uzzell (1965: 85), Hno. Nicéforo María informed him 'the specimens in the Instituto de La Salle, including the holotype and 6 of the 7 paratypes, have been destroyed'. Details were not given, but those specimens were probably destroyed during the fire of the institute (MLS) in

1948. Therefore, Uzzell based the synonymization of *E. centralis* with *E. h. palmeri* (currently *E. palmeri*) on examination of three topotypic specimens from Muzo [ILS (=MLS) 216–218] and one specimen from '4 km northeast of Bella Vista, on the Río Porce, in Antioquia' (CNHM 63813), and according to him



Figure 11. Neotype of *Echinosaura centralis* in life (MHUA-R 13332).

near the ‘type-localities’. We visited both Museo de La Salle (Bogotá) and Museo de Ciencias Naturales de La Salle (Medellín), but had no success in locating the remaining type specimen and no record in the museum database suggests its existence. We also noticed that ‘topotypic’ specimens from Muzo municipality mentioned by Uzzell (1965), are actually from Otanche municipality (based on the original specimen tags). Given the absence of type material of *E. centralis*, and in accordance with the ICZN (1999) Art. 75, we designate a neotype for this species. We considered this specimen the best candidate because: (1) there is enough evidence to identify it as the same entity described by Dunn (1944), (2) it is an adult male in excellent preservation condition, (3) there is a photograph in life and (4) it could be included in our phylogeny. A description of the neotype is given below.

Neotype (designated here): MHUA-R 13332, an adult male (Figs 11, 12). Colombia, department of Antioquia, municipality of San Rafael, embalse Jaguas, Caño Girón (6° 23' 54.672' N, 75° 01' 37.092' W, 1275 m a.s.l.). Collected on 23 August 2017 by Juan D. Vásquez-Restrepo.

Description of neotype: Adult male (Figs 11, 12), SVL = 60 mm, TRL = 27 mm, SL = 5.7 mm; HL = 15.2 mm, HW = 9.1 mm, TaL = 10.2 mm. Rostral scale single. Internasals two, longer than wide, with three longitudinal stretch marks, in contact with rostral anteriorly, nasals laterally, frontonasals posteriorly. Nasals subtriangular, in contact with internasals and first supralabials. Frontonasals about three times longer than wide, rectangular, with the posterior edges forming an obtuse angle and a depressed area in the middle part of each scale. Frontal single, wider anteriorly and thinner posteriorly, with a series of longitudinal, barely visible longitudinal ridges. Supraoculars three, first supraocular in contact with frontal and frontonasals, smaller than second and

third; third supraocular in contact with three small, keeled ciliaries. Lower eyelid with a palpebral disc divided into three large, unpigmented scales. A large polygonal scale in loreal region not in contact with the supralabials, except on the right side where it is fused with the first large subocular scale. Loreal in contact with preciliary, frontonasal and nasal. Suboculars in four small rows, in contact with a fifth row formed by five large scales on the left side and four on the right side (fifth scale fused with loreal), which are in contact with second to fifth supralabials. Frontoparietals paired, small, well defined. Parietal region covered with small irregular scales. Five upper and four lower labials on both sides. Mental posteriorly in contact with postmental. Postmental trapezoidal, in contact with first infralabial and anterior half of second infralabial. Chin shields large, in one pair, about three times longer than wide, in contact with posterior half of the second and anterior half of the third infralabials, separated from infralabials by three rows of small, hexagonal scales arranged longitudinally, larger than adjacent. Gular region with small, semicircular and tubercular scales, becoming spine-like scales that extend to posterior part of head in dorsal view in four longitudinal rows. Two of these lines are continuous and parallel, extending on paravertebral region and separated from each other by 6–7 irregular, small scales. The remaining two rows extend on upper coastal region, also formed by spine-like scales, but forming a discontinuous longitudinal and sinuous line. On the sides, there is a series of spine-like scales forming oblique lines. Spine-like scales on dorsum separated from each other by small, irregular or tubercular scales. Limbs pentadactyl, digits clawed. Subdigital lamellae on the fourth finger 15/14 (second one on left side divided); subdigital lamellae on the fourth toe 21. Scales on pectoral region flat, rounded, becoming six rows of squared and keeled scales on the belly. Tail with two parallel ridges dorsally, formed by a series of increasing in size scales from the anterior margin of each caudal segment, with more-developed scales forming longitudinal ridges laterally. Tail complete, with three subcaudal scales per caudal segment.

Dorsum light brown, with some dark-brown scales on head, barely yellowish blotches on body and limbs, and two cream spots at the base of the tail. Scales of ventral surface of head dark brown (almost black), most of them with a cream spot on the centre. Mental and labials with whitish colouration on the posterior edges. Suture between postmental and chin shields with a white transverse stripe. Scales on belly with an irregular pattern of chessboard (black and cream scales). Ventral surface of tail dark brown (almost black) from the basis, except by a few whitish scales on the anterior and posterior part.

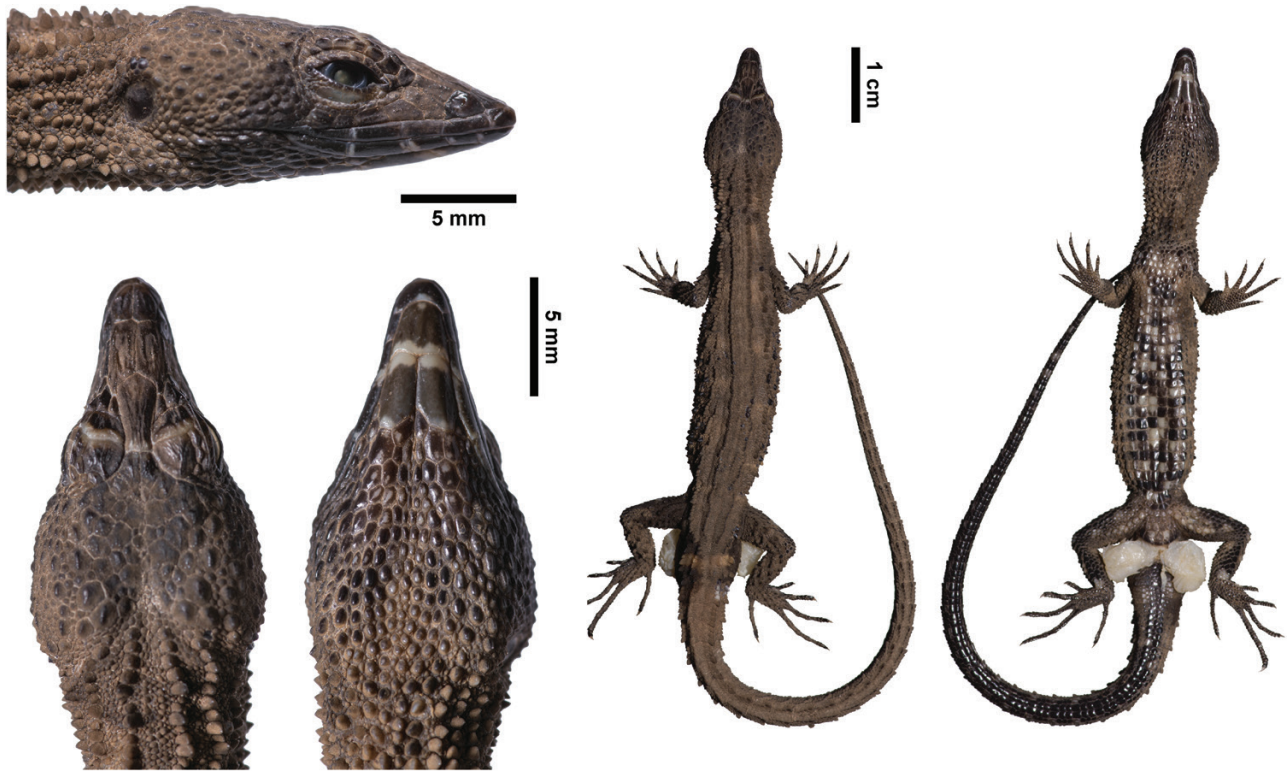


Figure 12. Neotype of *Echinosauro centralis* in preservative (MHUA-R 13332).

Diagnosis: The following data are based on 70 examined specimens (referred material listed in Supporting Information, [Appendix SII](#)). *Echinosauro centralis* possesses the following characteristics: (1) snout pointed; (2) internasal divided longitudinally (rarely single); (3) frontonasals paired; (4) frontal single and long (it extends up to the middle of the eyes); (5) frontoparietals paired; (6) supraoculars two or three, large; (7) supralabials 4–6 (usually five); (8) infralabials 3–5 (usually four); (9) postmental single; (10) large chin shields in one pair; (11) two paravertebral ridges, separated from each other by usually five or more small, irregular scales; (12) spine-like scales forming oblique lines on lateral surface of body; (13) ventral scales squared, usually keeled; (14) subdigital lamellae on the fourth finger 12–18; (15) subdigital lamellae on the fourth toe 20–27; (16) femoral pores per hind limb in males 4–9; (17) dorsal surface of tail with two parallel ridges, formed by a series of increasing in size scales from the anterior margin of each caudal segment; lateral surface of tail with more-developed scales forming longitudinal ridges (coded as ‘= pattern’); (18) subcaudals per caudal segment three (when tail is not regenerated); (19) dorsum brown or dark brown, relatively uniform, sometimes with yellowish marks and/or two spots more or less distinguishable

at the base of tail; ventral surface of head and neck mainly light brown, except on the anterior part where there is a darker ground colour with some transverse cream blotches, extending to labial scales; ventral surface of body (including limbs) mainly light brown spotted with dark brown or cream, while that of tail almost completely dark. Colouration in preservative is darker in some specimens.

Combination of these characteristics distinguishes *Echinosauro centralis* from its congeners. In addition, the distinctiveness of *E. centralis* and its sister-species *E. palmeri* ([Fig. 2](#)) is corroborated by uncorrected pairwise distances of 17.6% in *ND4* and 5.6% in *16S* ([Table 1](#)).

Geographic distribution: *Echinosauro centralis* is endemic to Colombia. It occurs in the Cordillera Central from Tolima to Bolívar departments, the adjacent Magdalena Valley and the west versant of the Cordillera Oriental in Cundinamarca and Boyacá departments. Most records are above 1000 m a.s.l., but its elevation ranges from 50 to 2200 m a.s.l. ([Fig. 8](#)).

Natural history: We have observed individuals of *Echinosauro centralis* diving into the streams and swimming short distances after being disturbed.

Variation: The referred specimens are similar to the neotype with the following noteworthy exception: internasal scale single (an unusual condition) in MHUA-R 10132, 11245, 11440, 12111, 12273 and 13212.

ECHINOSAURA HORRIDA BOULENGER, 1890

(Fig 6C, 10C)

Echinosauro horrida Boulenger, 1890: 83 (original description). **Syntypes:** Two specimens (BMNH 1946.8.31.60–61) (see below) from ‘Ecuador’, exact locality unknown.

Echinosauro horrida horrida (Boulenger, 1890) – Uzzell, 1965: 83.

Type material: Boulenger (1890: 83) described *Echinosauro horrida* based on two specimens deposited in the lizard collection of the British Museum (BMNH), a female and a young, neither of which was referenced with a specific collection number. Boulenger also did not designate a holotype. However, according to the data portal of the BMNH (<http://data.nhm.ac.uk>) and Torres-Carvajal (2001), there are two type specimens (syntypes following the Art. 73.2 of the ICZN) of *E. horrida* (BMNH 1946.8.31.60 and 1946.8.31.61) whose information matches the original description.

Diagnosis: The following data are based on 13 examined specimens (referred material listed in Supporting Information, Appendix SII) and data taken from the literature (Uzzell, 1965; Köhler *et al.*, 2004). *Echinosauro horrida* possesses the following characteristics: (1) snout pointed, relatively short; (2) internasal single; (3) frontonasals paired; (4) frontal single, short; (5) frontoparietals paired; (6) supraoculars two or three, large; (7) supralabials usually five or six; (8) infralabials three (some specimens from Ecuador have four supralabials and/or infralabials); (9) postmental single; (10) chin shields short, rounded and in one pair; (11) two longitudinal, parallel and juxtaposed paravertebral ridges; (12) series of spine-like scales forming oblique lines on lateral surface of body; (13) ventral scales squared, keeled; (14) subdigital lamellae on the fourth finger 14–19; (15) subdigital lamellae on the fourth toe 21–25; (16) femoral pores per hind limb in males usually 7–10; (17) dorsal surface of tail with two parallel ridges, formed by a series of scales increasing in size from the anterior margin of each caudal segment; lateral surface of tail with more-developed scales forming longitudinal ridges (coded as ‘= pattern’); (18) subcaudals per caudal segment three (when tail is not regenerated); (19) dorsum brown, sometimes with faint

yellowish spots; ventral surface of head and neck mostly light brown, except on the anterior part where there is a darker ground colour, with some transverse cream blotches extending to labial scales; ventral surface of body (including limbs) mainly light brown spotted with dark brown and cream, while that of tail has blotches or dark transverse marks. Colouration in preservative similar to that in life.

Combination of these characteristics distinguishes *Echinosauro horrida* from its congeners. In addition, the distinctiveness of *E. horrida* and its sister-species *E. brachycephala* (Fig. 2) is further corroborated by uncorrected pairwise distances of 18.8% in ND4 and 6.5% in 16S (Table 1).

Geographic distribution: *Echinosauro horrida* occurs on the Pacific versant of Ecuador and Colombia, from central-west Ecuador in the western part of Cotopaxi province to Isla Gorgona in Colombia and the adjacent mainland. This is mainly a lowland species, but its elevation ranges from 10 to c. 1546 m a.s.l. (Fig. 8).

Remarks: *Echinosauro horrida* occurs in sympatry with *E. keyi* in Ecuador, in the vicinity of Mataje and in El Placer, Esmeraldas province and in La Florida, Pichincha province (Fritts *et al.*, 2002).

ECHINOSAURA KEYI (FRITTS & SMITH, 1969)

(Fig. 6D)

Teuchocercus keyi Fritts & Smith, 1969: 54–59 (original description). Holotype: Male (UIMNH 80451) from ‘4 km E Río Baba bridge, 24 km S Santo Domingo de los Colorados, 600 m, Pichincha, Ecuador’.

Echinosauro keyi (Fritts & Smith, 1969) – Torres-Carvajal *et al.*, 2016: 69 (first use of that combination).

Diagnosis: The following data are based on the original description, literature (Köhler *et al.*, 2004) and high-quality photographs of specimens deposited at QCAZ (available online through www.bioweb.bio). *Echinosauro keyi* possesses the following characteristics: (1) snout relatively short; (2) internasal longitudinally divided; (3) frontonasals paired; (4) frontal extending up to the middle of the eyes, usually single but could be divided transversely; (5) frontoparietals paired; (6) supraoculars three (third supraocular smaller than first and second); (7) supralabials four; (8) infralabials 3–4; (9) tympanum covered with small, granular scales; (10) postmental single, short; (11) large chin shields in one pair; (12)

two longitudinal paravertebral ridges formed by spine-like scales, discontinuous on posterior portion of body; (13) series of conical scales of different sizes forming oblique lines on lateral surface of body; (14) ventral scales squared, smooth; (15) femoral pores per hind limb in males usually 8–11; (16) tail with six longitudinal rows of enlarged conical scales on the posterior part of each caudal segment (coded as ‘^ pattern’); (17) subcaudals per caudal segment three (when tail is not regenerated); (18) dorsum dark brown or almost black, with some yellow or cream reticulate spots; ventral surface of head and neck mainly cream with some dark spots; ventral surface of body (including limbs) mainly cream or light brown spotted with dark brown, while that of tail spotted with light and dark brown.

Combination of these characteristics distinguishes *E. keyi* from its congeners. In addition, the distinctiveness of *E. keyi* and its congeners is corroborated by a minimal uncorrected pairwise distances of 17.2% in ND4 and 6.7% in 16S (Table 1).

Geographic distribution: *Echinosauro keyi* is endemic to Ecuador. Its known distribution is restricted to the Pacific versant of north-western Ecuador, including Santo Domingo, Pichincha, Esmeraldas, Imbabura and Carchi provinces. Its elevational range is from 200 to 1235 m a.s.l. (Fig. 8).

Remarks: *Echinosauro keyi* occurs in sympatry with *E. horrida* in the vicinity of Mataje and in El Placer, Esmeraldas province and in La Florida, Pichincha province (Fritts *et al.*, 2002). It is possible that this species extends into southern Colombia.

ECHINOSAURA ORCESI FRITTS ET AL., 2002

(FIGS 6E, 10D)

Echinosauro orcesi Fritts *et al.*, 2002: 349–355 (original description). Holotype: Male (AMNH 109822) from ‘Colombia: Valle [Valle del Cauca]: approximately 13 km west of Dagua, Rio Anchicaya drainage, 820 m’.

Diagnosis: The following data are based on nine examined specimens (referred material listed in Supporting Information, Appendix SII) and the original description. *Echinosauro orcesi* possesses the following characteristics: (1) snout pointed, long; (2) internasal single; (3) frontonasals paired; (4) frontal long, single; (5) frontoparietals paired; (6) supraoculars large, usually two or three; (7) supralabials 3–5 (usually three); (8) infralabials 2–3 (usually three); (9) postmental single; (10) large chin shields in one pair;

(11) dorsally two discontinuous sinuous or S-shaped ridges formed by spine-like scales; (12) alternate tubercular scales on lateral surface of body; (13) ventral scales smooth, squared (or are rounded squares); (14) subdigital lamellae on the fourth finger 20–22; (15) subdigital lamellae on the fourth toe 30–36; (16) femoral pores per hind limb in males usually 9–16; (17) each caudal segment without crests, with a pair of more-developed scales or tubercles on the distal region forming transverse rings (coded as ‘: pattern’); (18) subcaudals per caudal segment five or six (when tail is not regenerated); (19) dorsum brown with transverse alternate darker bands, and with lateral ocelli more or less visible; ventral surface of head and neck cream or clear brown, except on the anterior part where there are some transverse dark brown blotches that extend to labial scales; ventral surface of body (including limbs and tail) mainly cream or reddish light brown spotted with dark (in some cases dark spotted with cream). Colouration in preservative darker.

Combination of these characteristics distinguishes *E. orcesi* from its congeners. In addition, the distinctiveness of *E. orcesi* and its congeners is corroborated by a minimal uncorrected pairwise distances of 17.4% in ND4 and 7.4% in 16S (Table 1).

Geographic distribution: *Echinosauro orcesi* occurs on the western versant of the Cordillera Occidental and in the Pacific region of Colombia, from Anchicayá region in Valle del Cauca department to north-western Ecuador in Esmeraldas and Carchi provinces. Its elevational range extends from 50 to c. 866 m a.s.l. (Fig. 8).

Remarks: *Echinosauro orcesi* occurs in sympatry with *E. palmeri* on the Anchicayá drainage in the Valle del Cauca department, south-western Colombia. In Ecuador, near the border with Colombia in Esmeraldas and Carchi provinces, *E. orcesi* overlaps in its distribution range with *E. horrida* and *E. keyi*. Köhler *et al.* (2004) also reported that these three species occur sympatrically in Paramba, Imbabura province.

ECHINOSAURA PALMERI BOULENGER, 1911

(FIGS 6G, 6H, 7, 10F)

Echinosauro palmeri Boulenger, 1911: 23 (original description). Holotype: Male (BMNH 1946.8.31.24) (see below) from ‘Noananoá [=Noanamá, Uzzell (1965)], Río San Juan, Choco, S.W. Colombia, 100 feet [~ 30 m a.s.l.]’.

Echinosauro horrida palmeri (Boulenger, 1911) – Uzzell, 1965: 84.

Type material: Boulenger (1911) described *Echinosaura palmeri* based on a single male deposited in the lizard collection of the British Museum, which he did not designate explicitly as the holotype. However, according to Art. 73.1.2 of the ICZN (1999), this specimen is assumed to be the holotype. Boulenger also did not provide a museum number for it. However, according to the data portal of the BMNH (<http://data.nhm.ac.uk>), there is a type specimen of *E. palmeri* (BMNH 1946.8.31.24) whose information matches the original description. Thus, following the Art. 72.4.1.1 of the ICZN, we consider this specimen as the holotype of *E. palmeri*.

Diagnosis: The following data are based on 70 examined specimens (referred material listed in Supporting Information, Appendix SII). *Echinosaura palmeri* possesses the following characteristics: (1) snout pointed; (2) internasal divided longitudinally; (3) frontonasals paired; (4) frontal long, single, extending up to the middle of the eyes; (5) frontoparietals paired; (6) supraculars usually two or three; (7) supralabials 4–5 (usually five); (8) infralabials 4–5 (usually four); (9) postmental single; (10) large chin shields in one pair; (11) two longitudinal, parallel paravertebral ridges, separated from each other by 3–8 (usually five) small irregular scales; (12) series of spine-like scales forming oblique lines on lateral surface of body; (13) ventral scales squared, usually smooth (rarely weakly keeled); (14) subdigital lamellae on the fourth finger 13–16; (15) subdigital lamellae on the fourth toe 19–25; (16) femoral pores per hind limb in males usually 7–8; (17) each caudal segment usually without crests, with a more-developed scales or tubercles on the distal region forming transverse rings (coded as ‘: pattern’), but in some cases dorsally with some small scales oblique forming a V shape (coded as ‘< pattern’); laterally without more-developed scales forming longitudinal ridges; (18) subcaudals per caudal segment three (when tail is not regenerated); (19) dorsum brown or dark brown relatively uniform, sometimes with yellowish marks and/or two spots more or less distinguishable at the base of the tail; ventral surface of head and neck mainly light brown, except in the anterior part where there are some transverse dark brown blotches that extend to labial scales; ventral surface of body (including limbs) mainly cream or light brown spotted with dark brown, while that of tail almost completely dark. Colouration in preservative could be darker.

Combination of these characteristics distinguishes *Echinosaura palmeri* from its congeners. In addition, the distinctiveness of *E. palmeri* and its sister-species, *E. centralis* (Fig. 2), is further corroborated by uncorrected pairwise distances of 17.9% in *ND4* and 5.6% in 16S (Table 1).

Geographic distribution: *Echinosaura palmeri* occurs in the southern part of Valle del Cauca department in Colombia, through the Pacific and adjacent Cordillera Occidental, to the Darien region in Panama. This is mainly a lowland species (Uzzell, 1965; Köhler *et al.*, 2004), but its range extends from 2 to c. 1520 m a.s.l. (Fig. 8; Jaramillo *et al.*, 2010).

Remarks: *Echinosaura palmeri* occurs in sympatry with *E. orcesi* in the Anchicayá region in Colombia, near the southern distribution limit of *E. palmeri* and the northern one of *E. orcesi*.

ECHINOSAURA PANAMENSIS BARBOUR, 1924

(FIGS 6F, 10E)

Echinosaura panamensis Barbour, 1924: 7–10 (original description). Holotype: Male (MCZ 17746) from ‘La Loma in the mountains of Bocas del Toro Province, western Panama [according to Uzzell (1965) on the Atlantic slope along the trail from Chiriquí Grande to Boquete, Bocas del Toro, about 600 m (but see Geographic distribution below)]’.

Echinosaura horrida panamensis (Barbour, 1924) – Uzzell, 1965: 86.

Type material: Barbour (1924) described *Echinosaura panamensis* based on a single specimen (MCZ 17746), although he mentioned a series of ‘no less than five [specimens]’. However, Barbour did not provide museum numbers for the remaining specimens (paratypes according to the Art. 74.4.5 of the ICZN). Later, Uzzell (1965) mentioned the existence only of three paratypes (MCZ 18857–59), but according to the written museum catalogue (available online), there is a fourth specimen (MCZ 18860). Additionally, in the MCZ data portal (<http://mczbase.mcz.harvard.edu>, accessed July 30 of 2019) this last specimen, also flagged as paratype, was sent to Chicago in 2015. Its current location is unknown. Although the existence of a fourth paratype is not in conflict with the original description (i.e. at least five), we consider as paratypes only those revised by Uzzell (1965), until physical evidence of the existence of MCZ 18860 is given. The above follows Art. 72.4.1.1 of the ICZN.

Diagnosis: The following data are based on the original description, eight examined specimens (referred material listed in Supporting Information, Appendix SII) and data taken from the literature (Uzzell, 1965; Köhler *et al.*, 2004). *Echinosaura panamensis* possesses

the following characteristics: (1) snout pointed; (2) internasal divided longitudinally; (3) frontonasals paired; (4) frontal divided transversely, the anterior being larger than the posterior; (5) frontoparietals paired; (6) supraoculars large, usually three; (7) supralabials 4–6 (usually five); (8) infralabials 4–6 (usually five); (9) postmental single; (10) large chin shields in one pair; (11) two longitudinal paravertebral ridges formed by tubercular scales arranged in zig-zag or sinuous pattern; (12) series of tubercular scales forming oblique lines on lateral surface of body; (13)

ventral scales squared, smooth; (14) subdigital lamellae on the fourth finger 13–16; (15) subdigital lamellae on the fourth toe 20–22; (16) femoral pores per hind limb in males usually 3–9; (17) each caudal autotomic segment dorsally with two small crests, oblique or V-shaped (coded as ‘< pattern’) and sometimes almost straight; laterally, last scales of each caudal segment forming transverse rings, and without more-developed scales forming longitudinal ridges; (18) subcaudals per caudal segment three (when tail is not regenerated); (19) dorsum brown, sometimes with yellowish marks

KEY TO THE SPECIES OF THE GENUS *ECHINOSAURA*

1. More than three transverse rows of subcaudal scales per autotomic caudal segment (counted in segments of the first half of the tail where it is thicker but avoiding the first segments near the base; Fig. 13B, C) . 2
 - Three transverse rows of subcaudal scales per autotomic tail segment (counted in segments of the first half of the tail where it is thicker but avoiding the first segments near the base; Fig. 13A) 3
2. Four subcaudal scales per caudal segment (Fig. 13B); postmental scale reduced or absent; chin shields not differentiated (Fig. 10A); snout relatively short and rounded; paravertebral rows parallel (Fig. 6A).....*E. brachycephala*
 - 5–6 subcaudal scales per caudal segment; postmental scale long; large chin shields in one pair (Fig. 10D); snout long and pointed; paravertebral rows discontinuous, sinuous or S-shaped (Fig. 6E).....*E. orcesi*
3. Internasal scale undivided (Fig. 10C); two longitudinal, parallel and juxtaposed paravertebral ridges (Fig. 6C)*E. horrida*
 - Internasal scale longitudinally divided; two paravertebral ridges not juxtaposed and separated from each other by small irregular scales 4
4. Frontal scale transversely divided (Fig. 10E); paravertebral ridges in zig-zag (Fig. 6F); usually five infralabials.....*E. panamensis*
 - Frontal scale undivided; paravertebral ridges almost straight, or straight on the anterior part but discontinuous on the back; usually less than five infralabials 5
5. Tympanum covered with small irregular scales; paravertebral ridges straight on the anterior part but discontinuous on the back (Fig. 6D); tail with enlarged conical scales forming rings on each caudal segment; postmental scale small*E. keyi*
 - Tympanum not covered with small irregular scales; tail without enlarged conical scales forming rings on each caudal segment; postmental scale large 6
6. Ventral scales usually keeled; each caudal segment dorsally with two parallel crests, formed by a series of scales increasing in size, and laterally with more-developed scales forming longitudinal ridges (Fig. 7 upper).....*E. centralis*
 - Ventral scales usually smooth or weakly keeled; each caudal segment usually without crests, with more-developed scales or tubercles on the distal region forming transverse rings, but in some cases dorsally with some small scales oblique forming a V shape (Fig. 7 lower)*E. palmeri*

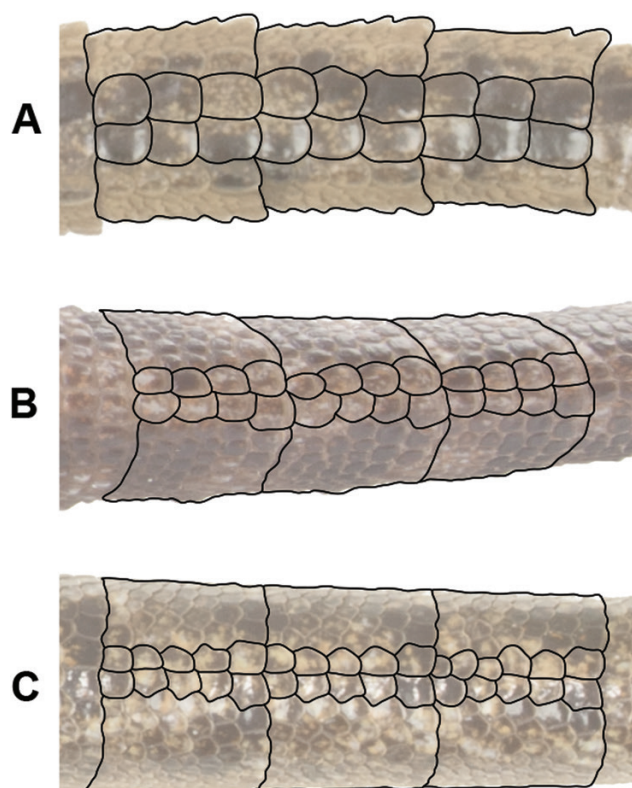


Figure 13. Scheme showing the differences in number of transverse rows of subcaudal scales per autotomic caudal segment in *Echinosaura*. Three rows (A), four rows (B) and five to six rows (C). Photographs and drawings correspond to: *E. horrida* (QCAZR 15030), *E. brachycephala* (QCAZR 10824) and *E. orcesi* (QCAZR 15026). Photographs were taken from the online database of QCAZ herpetology museum at www.bioweb.bio (under a BY-NC-ND 4.0 international Creative Commons license).

more or less distinguishable and with two yellow or cream spots on the base of the tail; ventral surface of head and neck mainly light brown, except on the anterior part where there are some transverse dark brown blotches that extend to labial scales; ventral surface of body (including limbs) mainly cream or light brown spotted with dark brown, while that of tail has blotches or dark transverse marks. Colouration in preservative darker.

Combination of these characteristics distinguishes *E. panamensis* from its congeners. In addition, the distinctiveness of *E. panamensis* and its congeners is corroborated by a minimal uncorrected pairwise distances of 17.8% in *ND4* and 6.5% in 16S (Table 1).

Geographic distribution: *Echinosaura panamensis* is endemic to Panama. It occurs throughout western

to central-eastern Panama, from La Loma (currently in the Comarca Ngäbe-Buglé) to Cerro Brewster in the Panama province. This is a lowland species with most of its records between 60 and 900 m a.s.l. (Fig. 8; Jaramillo *et al.*, 2010). La Loma, also known as Buena Vista, is located 15 km south-west of Chiriquí Grande; various incorrect elevations in the literature have been ascribed to this locality, but it is approximately at 300 m a.s.l. (Myers & Duellman, 1982).

Remarks: Uzzell (1965) commented in error that *Echinosaura panamensis* is known from elevations up to 8400 m a.s.l.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

Appendix SI. Genbank accession numbers used in this study.

Appendix SII. List of examined specimens. Specimens measured are marked with an asterisk. Museum acronyms follow the provided in the methodology.

Appendix SIII. Maximum likelihood tree ($-\ln L=73123.085$) depicting the phylogenetic relationships of Cercosaurinae. Numbers next to nodes represent ultrafast bootstrap support after 5000 pseudoreplicates.

Appendix SIV. Loading values for PCA analysis.