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Research Article


Filling the gaps in a highly diverse Neotropical lizard lineage: a new and endemic genus of Cercosaurinae (Squamata: Gymnophthalmidae) with the description of two new species from the Northern Andes of Colombia

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In the last decade, understanding of the Neotropical lizards family Gymnophthalmidae has changed dramatically with the recognition of several new genera, resolution of non-monophyly, definition of previously unknown lineages and refined biogeographic hypotheses. Recent field explorations on the northern Cordillera Central in Colombia uncovered two undescribed species that cannot be assigned to any currently recognized gymnophthalmid genus. Based on a molecular phylogenetic analysis combined with morphological and genetic distances, we describe a new genus and two new species from the northern Andes of Colombia. *Magdalenasaura* gen. nov. is restricted to the Magdalena biogeographic province and is sister to the cis-Andean genus *Gelanesaurus*. The new genus can be readily distinguished from all other Cercosaurinae genera by a combination of genetic and morphological characters. The new genus contains *Magdalenasaura leurosquama* sp. nov. and *M. adercum* sp. nov., both found in forested habitats near streams at altitudes ranging from 1300 to 1850 m on the eastern flank of the northern Cordillera Central in Colombia. We differentiate the Cercosaurinae genera from Colombia based on general scutellation. Filling the gaps of the tremendous diversity of gymnophthalmid lizards will improve taxonomic and biogeographic hypotheses to better understand the evolution of endemic lineages from the north-western corner of South America.

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Keywords: Cordillera Central, Magdalena biogeographic province, molecular phylogenetics, morphology, reptiles, South America, systematics

Introduction

During the last decade, the systematics of the Neotropical lizard family Gymnophthalmidae has been continuously changing due to new morphological and genetic evidence and the expansion of taxon sampling (Goicoechea et al., 2012; Goicoechea et al., 2016; Kok, 2009, 2015; Marques-Souza et al., 2018; Pellegrino et al., 2018; Peloso et al., 2011; Sánchez-Pacheco et al., 2018; Torres-Carvajal et al., 2015; Torres-Carvajal et al., 2016; Torres-Carvajal & Mafla-Endara, 2013; Vásquez-Restrepo et al., 2020). The most diverse lineage within this family is Cercosaurinae (*sensu* Pyron et al., 2013; Sánchez-Pacheco et al., 2018; Torres-Carvajal et al., 2016; Vásquez-Restrepo et al., 2020). Its

known diversity has been increasing in recent years with seven new genera proposed: *Andinosaura* Sánchez-Pacheco, Torres-Carvajal, Aguirre-Peñafiel, Nunes, Verrastro, Rivas, Rodrigues, Grant & Murphy, 2018; *Centrosaura* Vásquez-Restrepo, Ibáñez, Sánchez-Pacheco & Daza, 2020; *Dendrosauridion* Lehr, Moravec, Lundberg, Köhler, Catenazzi & Šmíd, 2019; *Gelanesaurus* Torres-Carvajal, Lobos, Venegas, Chávez, Aguirre-Peñafiel, Zurita & Echevarría, 2016; *Oreosaurus* Peters, 1862 (resurrected by Sánchez-Pacheco et al., 2018); *Rheosaurus* Vásquez-Restrepo, Ibáñez, Sánchez-Pacheco & Daza, 2020; and *Selvasaura* Moravec, Šmíd, Štundl & Lehr, 2018. Further studies are needed to solve either paraphyly of current genera (i.e., *Proctoporus*) or name recently uncovered lineages (i.e., Cercosaurini spp. *sensu* Torres-Carvajal et al., 2016).

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Recent field explorations in forested areas at mid elevations between 1200 and 2000 m asl. on the eastern flank of the northern Cordillera Central in the Magdalena river basin in Colombia, yielded a collection of several lizards that, based on preliminary genetic analysis, were assigned to Cercosaurinae but, based on external morphology, could not be assigned to any known genus within this clade. Here, to allocate these specimens we proposed a new genus that can be distinguished from the rest of the Cercosaurinae genera, infer its phylogenetic position within this clade, and describe two new species. We use morphological and genetic evidence to support the distinctiveness of the new genus and briefly discuss the systematics and biogeography of this enigmatic clade previously unknown from north-western South America.

Materials and methods

Specimen collection

We used 13 specimens collected during field explorations to the eastern flank of the northern Cordillera Central in Colombia between 2014 and 2019, as part of an ongoing inventory of amphibians and reptiles in this region. Specimens were euthanized with 2% lidocaine, fixed in 10% formalin solution for 2 days and then washed and stored in 70% ethanol. Before the formalin treatment, a tissue sample (muscle or leg) was obtained and preserved in 99% ethanol. All vouchers are deposited in the herpetological collection Museo de Herpetología Universidad de Antioquia (MHUA) in Medellín, Colombia.

Molecular laboratory procedures

Total genomic DNA was extracted from ethanol-preserved tissues using the GeneJET™ Genomic DNA Purification Kit (Thermo Fisher Scientific). For 13 specimens, we amplified and sequenced partial regions of three mitochondrial and one nuclear genes. We amplified partial sequences of the 12S ribosomal gene (primers 12Sa and 12Sb; Kocher *et al.*, 1989), the 16S ribosomal gene (primers 16SCL and 16SDH; Santos *et al.*, 2003), the protein-coding gene NADH dehydrogenase subunit 4 (primers ND4 and Leu; Arévalo *et al.*, 1994), and the nuclear protein-coding gene oocyte maturation factor MOS (primers G73 and G74; Saint *et al.*, 1998). PCR products were purified and sequenced using the forward amplification primer at the Macrogen Inc. facilities in Korea. Chromatograms were manually checked and edited using Geneious 9.1.8 (Kearse *et al.*, 2012). GenBank accession numbers for the new sequences are provided in Table S1).

Phylogenetic analysis

To infer the phylogenetic position of the new sequenced specimens, we included them in the largest assembled dataset of Cercosaurinae to date (Vásquez-Restrepo *et al.*, 2020). Each genomic region was aligned using MAFFT version 7 (Kato & Standley, 2013) and the G-INS-i algorithm. We inferred the optimal partition scheme using PartitionFinder 2.1.1 (Lanfear *et al.*, 2016) under the Bayesian Information Criterion (BIC). We implemented the greedy strategy to find the optimal partition scheme considering *a priori* partitions by gene in the ribosomal units and by codons in the coding regions *ND4* and *C-mos*. We inferred a Maximum likelihood tree and branch support using the program IQ-TREE (Nguyen *et al.*, 2015). As a successor of the IQPNNI program, IQ-TREE tree space search is based on the quartet puzzling algorithm and a likelihood optimization based on the fastNNI tree rearrangement (Vinh & von Haeseler, 2004). Branch support was estimated using the ultrafast bootstrap (UFB) method with 5000 pseudoreplicates. This method is an alternative to the traditional bootstrap and uses the RELL bootstrapping and a tree likelihood threshold to accelerate the branch support estimation (Minh *et al.*, 2013). We used two representatives of Alopoglossidae as outgroups to root the tree (Fig. S1).

To have an estimate of genetic divergence within/between species of the new specimens we calculated uncorrected genetic distances for 16S (753 bp) and ND4 (651 bp) using the program MEGA 7.0 (Kumar *et al.*, 2016).

Morphological analysis

We examined all individuals and obtained linear measurements from nine morphometric characters: (1) snout-vent length (SVL), distance from the tip of the snout to cloacal opening; (2) head length (HL), distance from the tip of the snout to the posterior margin of the ear opening; (3) head width (HW), measured at its widest point; (4) humerus length (Hu-L), distance from axilla to elbow; (5) radio-ulna length (RU-L), distance from elbow while flexed 90° to the inflection of the flexed wrist; (6) femur length (Fe-L), distance from the margin of the outer preanal scales to knee; (7) tibio-fibula length (TF-L), distance from the knee while flexed 90° to the base of the heel; (8) tail length (TL), distance from the cloacal opening to the tip of tail (in specimens with complete tail); (9) length of fingers and toes (measured only in holotypes). We also included 22 scale counts as meristic characters: (1) supralabials; (2) infralabials; (3) scales in palpebral disc; (4) superciliaries; (5) supraoculars; (6) suboculars; (7) postoculars; (8)

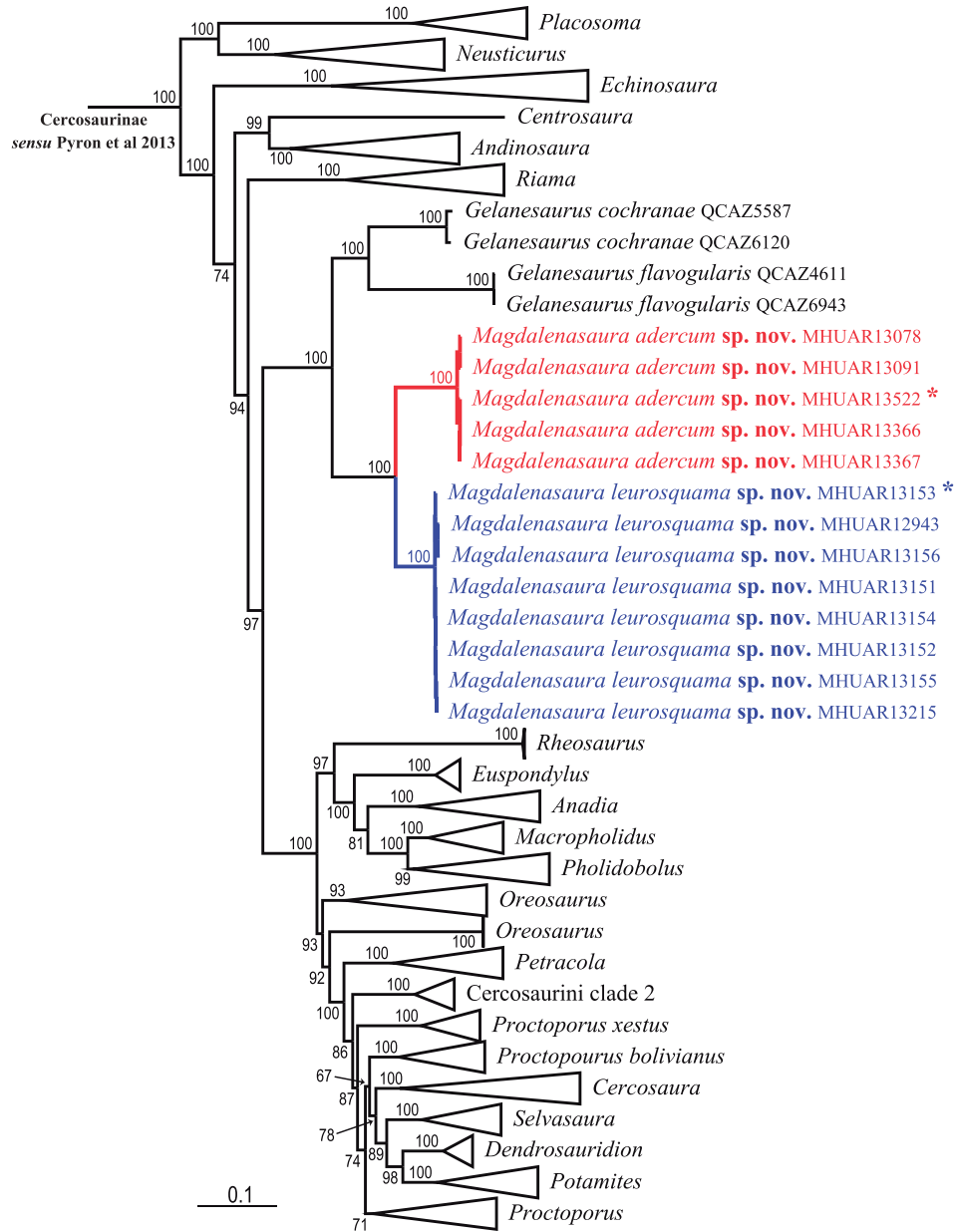


Fig. 1. Maximum likelihood tree ($-\ln L = 73477.133$) depicting the phylogenetic relationships within Cercosaurinae. Numbers above nodes represent ultrafast bootstrap support after 5000 pseudoreplicates. Asterisks indicate holotype specimens.

occipitals; (9) chin shields; (10) enlarged gulars (excluding collar scales); (11) collar scales; (12) transverse rows of dorsal scales, from the first scale row posterior to the occipitals to the level of the posterior edge of the cloaca; (13) longitudinal rows of ventral scales, at the level of the tenth transverse ventral scale row; (14) transverse rows of ventral scales, between collar fold and preanal scales; (15) lateral scales, at the level of the tenth transverse ventral scale row; (16) scales around midbody, at the level of the tenth transverse ventral scale row; (17) subdigital lamellae under finger IV

(ungual sheath omitted); (18) subdigital lamellae under toe IV (ungual sheath omitted); (19) scales in the anterior row of preanals; (20) scales in the posterior row of preanals; (21) femoral pores (per side); (22) segments of the tail, from the cloacal opening to the tip of tail (counted only in holotypes). Measurements were taken with a digital calliper (± 0.01 mm) and rounded to the nearest 0.1 mm. Variation between characters was recorded on both sides of the body and is denoted herein as left/right. Comparisons with other gymnophthalmids were made using the original descriptions

Table 1. Net uncorrected genetic distances in percentage among species of *Magdalenasaura* gen. nov. and *Gelanesaurus*. Lower diagonal indicates mean distances and upper diagonal indicates standard errors based on 1000 bootstraps; 753 sites for 16S and 651 sites for ND4 were used to calculate the distances.

	n	16S				ND4			
		<i>G. c.</i>	<i>G. f.</i>	<i>M. l.</i>	<i>M. a.</i>	<i>G. c.</i>	<i>G. f.</i>	<i>M. l.</i>	<i>M. a.</i>
<i>G. cochranae</i>	2	–	1.0	1.1	1.0	–	1.5	1.4	1.5
<i>G. flavogularis</i>	2	6.2	–	1.2	1.2	19.3	–	1.7	1.5
<i>M. leurosquama</i> sp. nov.	8	6.7	7.8	–	0.7	16.6	22.8	–	1.4
<i>M. adercum</i> sp. nov.	5	6.5	8.2	5.5	–	19.1	23.6	14.7	–

(Altamirano-Benavides *et al.*, 2013; Arredondo, 2013; Boulenger, 1911; C. E. Burt & Burt, 1931; Cope, 1868; O’Shaughnessy, 1879; Peters, 1862; Ruthven & Gaige, 1924). Description of colour in life was based on field notes and digital photos. Nomenclature of scales and diagnoses for the new species follows Uzzell (1966).

Results

Phylogenetic inference and genetic distances

Sequence alignment resulted in an aligned matrix of 325 terminals and 2234 sites and the best partition scheme included six partitions: 12S + 16S (GTR + G + I), ND4 1st codon (GTR + G + I), ND4 2nd codon (GTR + G + I), ND4 3rd codon (TIM + G), *C-mos* 1st codon + 2nd codon (SYM + G + I), and *C-mos* 3rd codon (K80 + G). The ML tree is shown in Fig. 1. Relationships among and within genera in Cercosaurinae agree with previous studies where *Placosoma* + *Neusticurus* is sister to the other Cercosaurinae (Goicoechea *et al.*, 2016; Pyron *et al.*, 2013; Sánchez *et al.*, 2018; Torres-Carvajal *et al.*, 2016; Vásquez-Restrepo *et al.*, 2020). Our tree differs from Vásquez-Restrepo *et al.* (2020) where *Echinosaura* was recovered as sister to *Andinosaura* + *Centrosaura*, but our alternative arrangement is not well-supported (74% UFB). The new specimens are recovered as sister to the genus *Gelanesaurus* with high support (100% UFB). Genetic divergence within and among lineages is shown in Table 1. The uncorrected genetic distance between our new specimens and the two species of *Gelanesaurus* ranged from 6.51 and 8.15% in 16S and 16.6 and 23.5% in ND4. We also found these new specimens forming two distant lineages with mean genetic distances of 5.56% in 16S and 13.9% in ND4. Together, mean genetic distances between the genus *Gelanesaurus* and the new clade was 7.4% in 16S and 21.1% in ND4. In comparison, genetic distances between well-supported sister genera in Cercosaurinae (see Fig. 1) are 5.9% (*Macropholidus/Pholidobolus*) and 7.5% (*Potamites/Proctoporus*) in 16S and 21.2% (*Macropholidus/*

Pholidobolus) and 17.7% (*Potamites/Proctoporus*) in ND4.

These results together with several morphological differences (see taxonomic accounts) provide strong evidence that the new specimens correspond to two new species belonging to a new genus within the subfamily Cercosaurinae.

Taxonomic account

Magdalenasaura gen. nov.

Type species. *Magdalenasaura leurosquama* sp. nov.

Etymology. *Magdalenasaura* (gender feminine) derives from the Spanish word *Magdalena* and the Greek word *saura* (lizard), in allusion to the Magdalena river basin where the two species have been found.

Diagnosis. Phenotypic synapomorphies are not known for this genus. *Magdalenasaura* gen. nov. can be distinguished from all other Cercosaurinae genera by the combination of the following character states: (1) head scales smooth and juxtaposed; (2) prefrontal, frontoparietal, and parietal scales paired; (3) frontonasal, frontal, and interparietal scales single; (4) large, paired, and symmetrical occipitals, in medial contact; (5) lower palpebral disc semitransparent and divided in several scales; (6) single nasal scale; (7) loreal scale present, in contact with supralabials; (8) tympanum slightly recessed; (9) three pairs of large chin shields, first and second pair in contact on midline; (10) enlarged posterior gular scales; (11) collar fold well developed; (12) dorsal scales smooth or keeled, not tuberculate, with heterogeneous size and shape, subimbricate, in transverse rows only, without forming longitudinal dorsal crests; (13) lateral fold absent; (14) lateral scales smaller than dorsal and ventral scales, irregularly shaped, juxtaposed; (15) ventral scales smooth, quadrangular, subimbricate, in transverse and longitudinal rows; (16) limbs pentadactyl, digits clawed; (17) tail slightly compressed laterally; (18) femoral pores present in both sexes (more in males); (19) lateral ocelli present in both sexes.

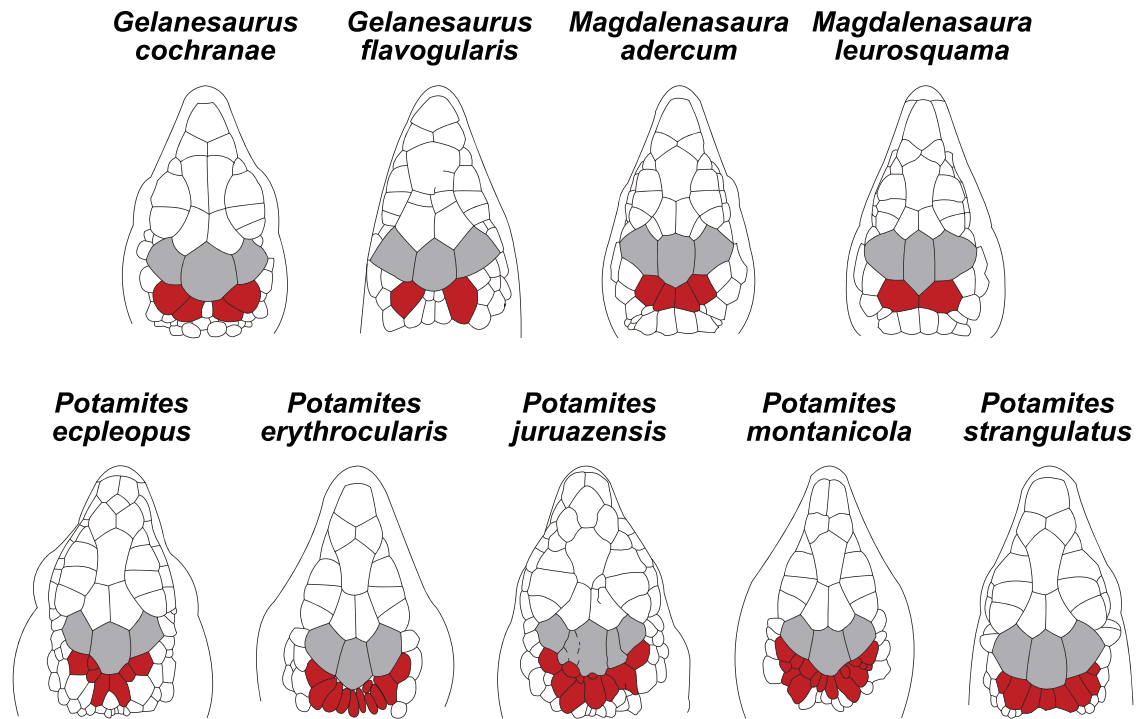


Fig. 2. Scheme showing head scutellation to differentiate *Magdalenasaura* gen. nov., *Gelanesaurus*, and *Potamites*. The interparietal and parietal scales are coloured in grey, and occipital scales in red (see discussion for a detailed description). Drawings are unscaled and based on MHUA-R 13522 (*M. adercum* sp. nov., holotype), MHUA-R 13153 (*M. leurosquama* sp. nov., holotype), QCAZ-R 12620 (*G. cochraeae*), DHMECN 4581 (*G. flavogularis*, holotype), MPEG 13030 (*P. ecleopus*), MUSM 28056 (*P. erythrocularis*, holotype), MPEG 17775 (*P. juruazensis*, holotype), CORBIDI 08322 (*P. montanicola*, holotype), and QCAZ-R 15470 (*P. strangulatus*). Drawings were based on photographs, or taken and adapted from original descriptions. See online [Supplemental Material](#) for details of the examined and referenced specimens.

Comparisons with related genera. *Magdalenasaura* gen. nov. can be readily distinguished from other genera of Cercosaurinae by the combination of the following characters (other genera in parentheses): dorsal scales heterogeneous in size and shape (homogeneous in *Anadia*, *Andinosaura*, *Cercosaura*, *Dendrosauridion*, *Euspondylus*, *Macropholidus*, *Oreosaurus*, *Petracola*, *Pholidobolus*, *Placosoma*, *Proctoporus*, *Riama*, and *Selvasaura*); dorsal scales smooth or weakly keeled, not tuberculate (strongly keeled and/or tuberculate, usually forming several longitudinal dorsal crests in *Centrosaura*, *Echinosaura*, *Gelanesaurus*, *Neusticurus*, *Potamites*, and *Rheosaurus*); prefrontal scales present (usually absent in *Andinosaura*, *Echinosaura*, *Oreosaurus*, *Petracola*, and *Riama*); large, paired and symmetrical occipitals in medial contact (usually the largest scales on the occipital region separated medially by smaller scales or slightly in contact in *Gelanesaurus*, and several small irregular or non-symmetrical scales in *Potamites*; see Fig. 2); and lower parpebral disc semi-transparent and divided (not divided in *Dendrosauridion*, *Macropholidus*, *Selvasaura*, and *Proctoporus*) (Betancourt, Reyes-Puig, Lobos, Yáñez-

Muñoz, & Torres-Carvajal, 2018; Borges-Nojosa et al., 2016; Chávez et al., 2017; Doan & Castoe, 2005; Echevarría & Venegas, 2015; Hurtado-Gómez et al., 2018; Kizirian et al., 2008; Kok et al., 2018; Lehr et al., 2019; Mamani et al., 2015; Moravec et al., 2018; Sánchez-Pacheco et al., 2018; Torres-Carvajal et al., 2016; Torres-Carvajal & Mafla-Endara, 2013; Vásquez-Restrepo et al., 2020; Venegas, Echevarría, Lobos, Nunes, & Torres-Carvajal, 2016). External characters of *Magdalenasaura* gen. nov. along with other gymnophthalmid lizards present in the northern Cordillera Central are shown in Fig. 3.

Geographic distribution. The genus is known from the eastern versant of the northern Cordillera Central in Colombia which is part of the Magdalena river basin, in elevations from 1300 to 1850 m asl.

Magdalenasaura adercum sp. nov.

Holotype. MHUA-R 13522, an adult male from Colombia, department of Antioquia, municipality of San Rafael, vereda La Clara, Reserva Natural Manantiales

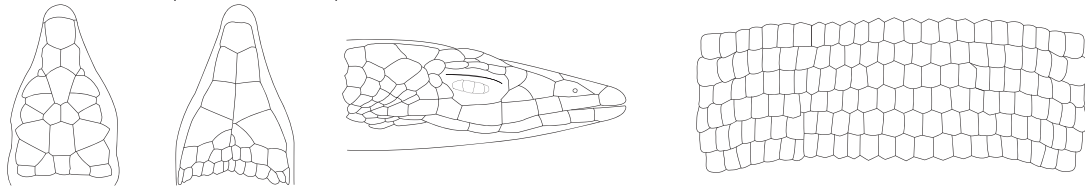
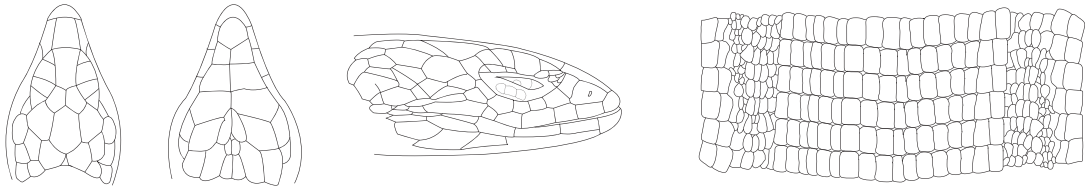
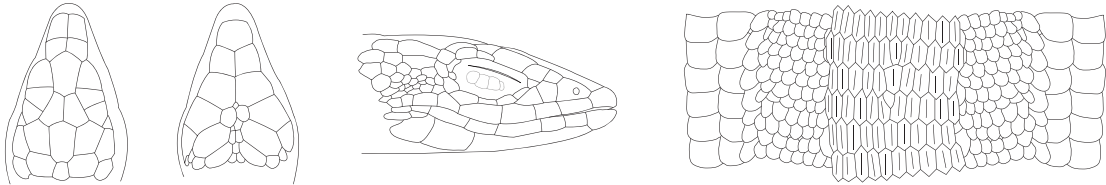
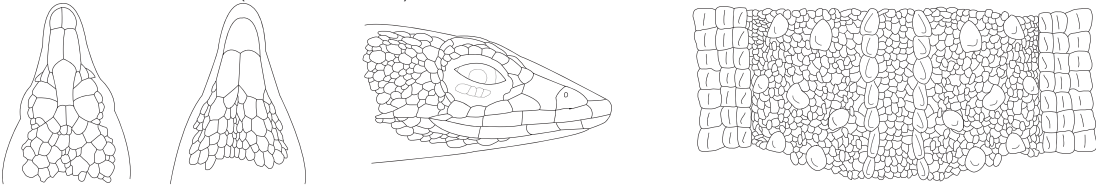
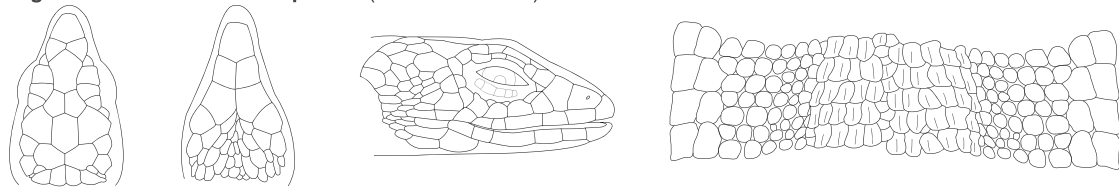
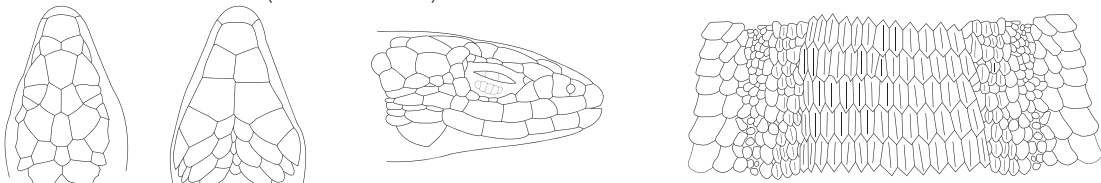
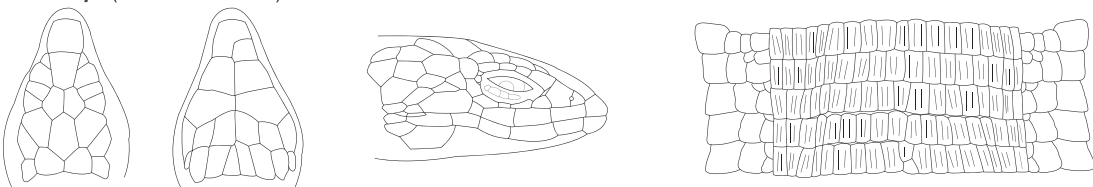
Anadia ocellata (MHUA-R 12694)***Andinosaura laevis*** (MHUA-R 11122)***Cercosaura argulus*** (MHUA-R 11250)***Echinosaura centralis*** (MHUA-R 13332)***Magdalenasaura adercum* sp. nov.** (MHUA-R 12694)***Pholidobolus vertebralis*** (MHUA-R 13280)***Riama* sp.** (MHUA-R 12748)

Fig. 3. Scheme showing morphological differences among several Cercosaurinae lizards from the Magdalena biogeographic province.



Fig. 4. Holotype of *Magdalenasaura adercum* sp. nov. in life (MHUA-R 13522). Photo by Juan M. Daza.

del Campo (6.252626 N, -75.103279 W, 1600 m asl), collected on 15 May 2019 by Juan M. Daza (Figs 4–5).

Paratypes. MHUA-R 13366 adult female, and 13367 adult male, from Colombia, department of Antioquia, municipality of San Rafael, vereda La Clara, Reserva Natural Manantiales del Campo (6.25274 N, -75.10194 W, 1585 m asl), collected on 20 June 2017 by Diego Rivera-Prieto. MHUA-R 13078 and 13091, adult females from Colombia, department of Antioquia, municipality of El Carmen de Viboral, vereda La Esperanza, near to Cocorná river (6.026747 N, -75.229359 W, 1835 m asl), collected on 10 November 2015 by Alejandro Montoya. See Fig. 6.

Etymology. The epithet *adercum* derives from the Greek word *aderkes* (unseen or unexpected), because after extensive sampling efforts in the region these lizards seem to be very rare, secretive and hard to see.

Diagnosis. *Magdalenasaura adercum* sp. nov. is assigned to the genus *Magdalenasaura* based on morphological characters and the molecular phylogenetic results. Phenotypic autapomorphies are not known for this species. *Magdalenasaura adercum* sp. nov. can be diagnosed by the combination of the following characters: (1) four supraoculars; (2) loreal scale in contact with the first and second supralabials; (3) 4–5 (usually 4) postoculars; (4) three suboculars; (5) five superciliaries; (6) lower palpebral disc semitransparent and divided in 5–6 enlarged scales; (7) 7–8 (usually 8) supralabials; (8) 6–7 (usually 7) infralabials; (9) 6–12 enlarged gulars; (10) 4–7 enlarged collar scales; (11) dorsal scales mostly weakly keeled; (12) 41–46 transverse rows of dorsal scales; (13) eight longitudinal rows of ventral scales; (14) 17–18 transverse rows of ventral scales; (15) 7–10 lateral scales; (16) 24–30 scales around midbody; (17) 12–13 (usually 13) subdigital lamellae under the finger IV, and 17–18 (usually 17) under the toe IV; (18) 12–15 femoral pores per side in male, 4–5 in females; (19) 1–2 (usually 2) scales in the anterior row of preanals, 3–5 (usually 5) in the posterior row; (20) dorsal

surface of head, body, tail and limbs are light olive-brown or dark brown, lateral surfaces of the body brown with ocelli present, ventral body colouration beige with light brown while ventral head colouration beige with brown blotches; (21) with one light yellow or cream oblique subocular stripe, crossing labials scales from posterior corner of the eyes to preangular scales.

Comparisons with related species. *Magdalenasaura adercum* sp. nov. can be distinguished from its congener *M. leurosquama* sp. nov. by the combination of the following characters (condition for *M. leurosquama* sp. nov. in parentheses): weakly keeled dorsal scales (smooth); 17–18 subdigital lamellae under IV toe (20–23); 17–18 transverse rows of ventral scales (19–21); eight longitudinal rows of ventral scales (10–12); 12–15 femoral pores on each side in males (17–18); and one yellow or cream oblique subocular stripe (more than one subocular stripe).

Magdalenasaura adercum sp. nov. is distinguished from the species of its sister genus *Gelanesaurus* by the combination of the following characters (condition for *G. cochranæ* and *G. flavogularis* in parentheses): weakly keeled dorsal scales, without forming longitudinal dorsal crests (strongly keeled and tuberculate dorsal scales, forming longitudinal dorsal crests); loreal scale in contact with supralabials (loreal scale separated from supralabials by the contact between the nasal and frenocular); large, paired and symmetrical occipitals in medial contact (usually the largest scales on the occipital region separated medially by smaller scales or in slight contact); homogeneous brown colouration around the nostril (a conspicuous black or brown spot surrounding nostril); and 24–30 scales around midbody (45–56 in *G. cochranæ* and 37–48 in *G. flavogularis*). See diagnostic characters for the species in Table 2, and variation of relevant meristic and morphological differences among *Gelanesaurus* and *Magdalenasaura* species in Figs 7–8.

Description of the holotype. (Figs 4–5) Adult male (MHUA-R 13522); snout-vent length 67.1 mm; tail length 106.0 mm. Head scales smooth and juxtaposed. Rostral scale wider than high, dorsally in contact with the frontonasal and laterally touching the first supralabials and the nasals. Frontonasal single, pentagonal, longer than wide, in contact with the nasals, loreals and prefrontals. Prefrontals paired, pentagonal, wider laterally and narrower medially, in contact with each other, touching the first superciliary, the frontal, the anterior supraocular and the loreals. Frontal hexagonal, longer than wide, wider anteriorly, in contact with the prefrontals, the first to third supraoculars and the middle frontoparietals. Frontoparietals pentagonal, longer than wide, narrower anteriorly, contacting the third and fourth



Fig. 5. Holotype of *Magdalenasaura adercum* sp. nov. in preservative.

supraoculars laterally, and the parietals and interparietal posteriorly. Supraoculars four, second and third largest, contacting the superciliaries laterally and the parietal and uppermost postocular posteriorly. Interparietal hexagonal, longer than wide, narrower than the parietals and contacting laterally the parietals and posteriorly the occipitals. Parietals irregularly hexagonal, slightly longer than wide, shorter and wider than the interparietal, in contact with fourth supraocular and dorsalmost postocular anterolaterally, temporals posterolaterally, and occipitals posteriorly. Occipitals four, polygonal, smaller than parietals. Nasal single, sub-triangular, contacting the first supralabials and the loreal. Loreal pentagonal, in contact with first superciliary, frontonasal and prefrontals dorsally, first and second supralabial ventrally and frenocular posteriorly. Frenocular quadrilateral, touching the first infraocular and the second and third supralabial. Superciliaries five, the first larger than the others. Lower palpebral disc semitransparent and divided in five enlarged scales. Suboculars three, contacting supralabials three to five. Postoculars four. Temporals scales smooth and juxtaposed, with different shape and size. Supralabials seven, and infralabials six. Tympanum slightly recessed. Mental wider than long, contacting the first infralabial and postmental. Postmental single, pentagonal, contacting the first two infralabials and the anterior pair of chin shields. Three pairs of chin shields, all contacting infralabials, the first and second pair in contact on midline, second pair the largest and the third the smallest. Pregulars smooth, irregular, juxtaposed, increasing in size laterally. Gulars smooth, irregular,

smaller anteriorly, increasing in size posteriorly, with six enlarged scales, wider than long, in two median longitudinal rows. Collar fold distinct. Side of the neck with small and juxtaposed conic granules.

Dorsal scales mostly keeled (weakly), with heterogeneous sizes, the largest ones quadrangular to hexagonal, subimbricate, separated in the middorsal region by smaller, flat and irregular scales, which go dorsally from the posterior part of the head, to the anterior part of the tail. Transverse rows of dorsal scales 41. Lateral scales smaller than dorsals, juxtaposed, irregularly rounded, forming a band of eight/seven scales at midbody between dorsals and ventrals (the width of a dorsal transversal row at midbody about the width of two transversal rows of lateral scales), the lateral scales near ventral scales convex and enlarged. Scales around the midbody 26. Ventral scales quadrangular, smooth, subimbricate, in eight longitudinal rows and 17 transverse rows. Anterior row of preanal scales with two large scales, while the posterior row with five scales, the median and paramedian are largest and the outermost pair smaller. Tail scales arranged in 76 segments. Dorsal and dorsolateral scales of tail quadrangular with low keel, becoming rectangular and flat toward tip, with few small, flat and irregular scales only anteriorly and dorsally. Subcaudal scales smooth, quadrangular anteriorly becoming rectangular toward tip. Limbs pentadactyl with clawed fingers. Fore limbs with pentagonal to hexagonal, subimbricate, smooth and large scales, ventrals smaller than dorsals. Dorsal hand scales hexagonal, subimbricate, smooth and shorter than the dorsal lower arm



Fig. 6. Dorsal and ventral views of paratypes of *Magdalenasaura adercum* sp. nov. MHUA-R 13078 (female), MHUA-R 13091 (female), and MHUA-R 13367 (male).

scales. Palmar scales small, juxtaposed and granular. Finger length formula $IV > III > II > V > I$. Supradigital scales quadrangular, imbricate and smooth. Subdigital lamellae quadrangular, smooth, with 13/13 under the finger IV. Hind limbs with pentagonal to hexagonal, subimbricate, smooth and large scales, with granular scales on the posterior part of thigh and dorsal surface of shank (in the proximal and distal region). 12/13 developed femoral pores, three in preanal position. Dorsal foot scales polygonal, imbricate and smooth. Plantar scales small, juxtaposed and granular. Toe length formula $IV > III > V > II > I$. Supradigital scales quadrangular, subimbricate and wider than long. Subdigital lamellae quadrangular, with 18 under the toe IV (left side).

Colour of holotype in life (Fig. 4). Dorsal surface of the head light brown. Lateral surfaces of the head have the same colour as the dorsal surface, with one oblique clear stripe crossing labials scales from posterior corner of the eyes to preangular scales. Ventral surface of the head (infralabials, chin shields, preangular and gular scales) cream spotted with brown. Dorsal surface of the body has the same colour as the dorsal surface of the head, with paired cream spots extended from neck to the tail, becoming smaller towards the end of the tail. Lateral surfaces of the body light brown, with four white-centred and black-bordered ocelli on the left, and two on the right. Ventral surface of the body, tail and limbs cream with light brown, bearing some small dark spots. Anterior, posterior and dorsal surfaces of limbs darker than body.

Colour of holotype in preservative (Fig. 5). In 70% ethanol the dorsal and lateral surfaces of the head, body, tail, and limbs are light brown. Lateral ocelli and dorsal black spots visible. Subocular oblique posterior line cream. Ventral surfaces cream and light brown, with dark blotches on body and tail.

Measurements of the holotype (mm). Snout-vent length: 67.1; snout length: 7.3; head length: 19.7; head width: 11.5; humerus length: 8.8; radio-ulna length: 9.0; femur length: 12.32; tibio-fibula length: 11.4; tail length: 106.0.

Variation. Measurements and scale counts of the type series are presented in Table S2. *Magdalenasaura adercum* sp. nov. shows sexual dimorphism in number of femoral pores, with males having 13–15 pores per side, while females having 3–4 pores in preanal position and one additional pore at the distal end of each thigh. In the female MHUA-R 13366 pores are poorly developed. The belly colouration of the males tends to be beige with dark brown blotches, while in females the belly is immaculate (Fig. 6).

Distribution and natural history. *Magdalenasaura adercum* sp. nov. is known from two localities on the north-eastern Cordillera Central in the department of Antioquia, Colombia, between 1585 and 1835 m asl (Fig. 9). The region corresponds to Andean premontane forests, is highly fragmented and the dominant human activities are cattle grazing and agriculture.

The holotype (MHUA-R 13522) was collected during the night (around 20:00) sleeping on a leaf 30 cm above the ground and inside a forest about 40 m from the forest edge and 30 m to a stream. Specimens MHUA-R 13366 and 13367 were collected during the day in the same forest where MHUA-R 13366 was collected on a rock in the stream and MHUA-R 13367 on the ground about 20 metres from the stream. Specimens MHUA-R 13078 and MHUA-R 13091 were collected while they were asleep at night on bushes near the Cocorná river.

Magdalenasaura leurosquama sp. nov.

Holotype. MHUA-R 13153, an adult male from Colombia, department of Antioquia, municipality of

Table 2. Comparison of linear measurements and meristic characters between *Magdalenasaura* gen. nov. and *Gelanesaurus* given as range (mean \pm SD). Sex are coded M and F for males and females respectively. Data for *G. cochranae* and *G. flavogularis* were taken from Altamirano-Benavides *et al.* (2013).

	<i>M. adercum</i> sp. nov. (n = 5)	<i>M. leurosquama</i> sp. nov. (n = 8)	<i>G. cochranae</i> (n = 6)	<i>G. flavogularis</i> (n = 8)
SVL (mm)	67.1–76.6 (72.32 \pm 4.02)	44.8– 88.1 (70.48 \pm 15.84)	45–91 (71.83 \pm 16.44)	35–75 (63.1 \pm 14.2)
Dorsal scale relief	Keeled (weakly)	Smooth	Keeled	Keeled
Dorsal crests	Absent	Absent	Present	Present
Longitudinal rows of ventral scales	8 (8 \pm 0)	10–12 (10.3 \pm 0.7)	–	–
Transverse rows of ventral scales	17–18 (17.4 \pm 0.5)	19–21 (19.9 \pm 0.6)	15–18 (16.8 \pm 1.1)	15–19 (17.3 \pm 1.3)
Scales around midbody	24–30 (26.0 \pm 2.3)	19–28 (23.8 \pm 2.7)	45–56 (51.8 \pm 4.3)	37–48 (41.8 \pm 3.5)
Subdigital lamellae under finger IV	12–13 (12.8 \pm 0.4)	14–15 (14.9 \pm 0.4)	13–16 (14.6 \pm 1.0)	13–16 (13.5 \pm 1.0)
Subdigital lamellae under toe IV	17–18 (17.4 \pm 0.5)	20–23 (21.4 \pm 1.3)	18–21 (19.6 \pm 1.0)	15–18 (16.7 \pm 1.0)
Number of femoral pores (per side)	M (n = 2): 12–15 (13.5 \pm 2.1) F (n = 3): 4–5 (4.3 \pm 0.6)	M (n = 3): 17–18 (17.3 \pm 0.6) F (n = 5): 4–6 (4.4 \pm 0.9)	M (n = 4): 22–25 (23.8 \pm 1.3)	M (n = 3): 19–21 (20.3 \pm 1.1)
Tail/SVL	1.4–1.6 (1.53 \pm 0.12) n = 3	1.1–1.8 (1.59 \pm 0.25)	1.22–1.58 (1.43 \pm 0.15) n = 4	1.31–1.41 (1.37 \pm 0.03) n = 4

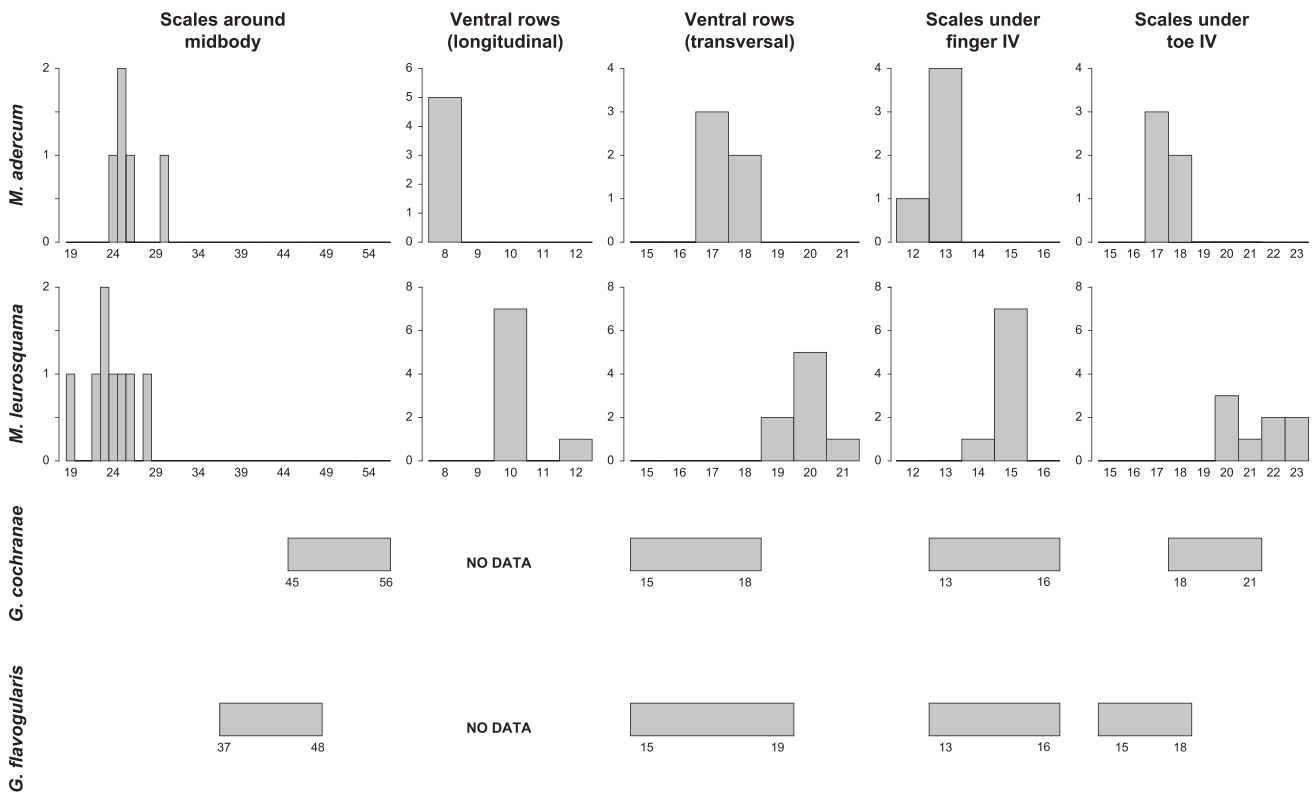


Fig. 7. Selected quantitative morphological characters showing differences in scutellation among *Magdalenasaura* gen. nov. and *Gelanesaurus* species. Ranges are shown for *G. cochranae* and *G. flavogularis* based on available data from literature (Altamirano-Benavides *et al.*, 2013).

Alejandría, vereda El Cerro, El Edén forest (6.36701 N, –75.02718 W, 1348 m asl), collected on 20 August 2016 by Carlos M. Marín (Figs 10–11).

Paratypes. MHUA-R 12943 adult female, Colombia, department of Antioquia, municipality of Alejandría, vereda El Cerro, El Edén forest (6.36725 N,

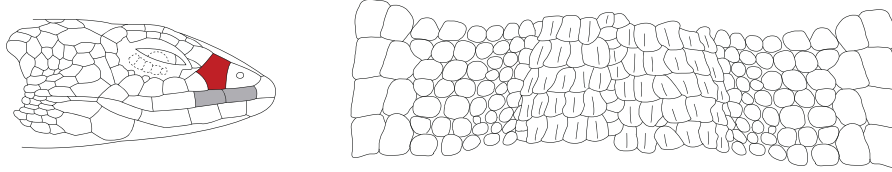
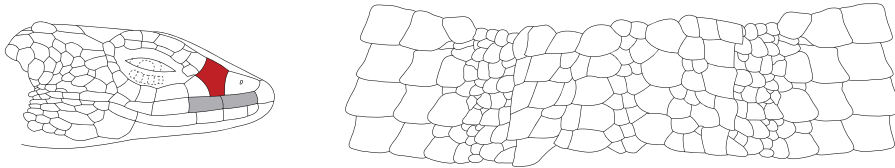
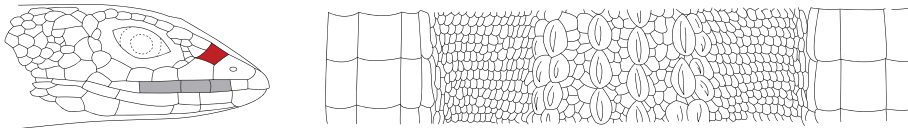
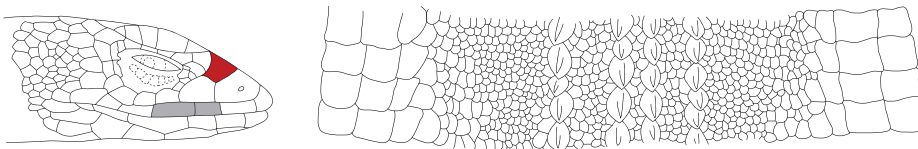
Magdalenasaura adercum (MHUA-R 13522)*Magdalenasaura leurosquama* (MHUA-R 13153)*Gelanesaurus cochraeanae* (QCAZ-R 12620)*Gelanesaurus flavogularis* (DHMECN 4581)

Fig. 8. Scheme showing differences among *Magdalenasaura* gen. nov. and *Gelanesaurus* species. Drawings for *G. cochraeanae* and *G. flavogularis* were adapted from C. E. Burt and Burt (1931) and Altamirano-Benavides et al. (2013).

–75.02723 W, 1309 m asl), collected on 26 August 2015 by Claudia M. Molina. MHUA-R 13151 adult male, MHUA-R 13152 juvenile male, MHUA-R 13154 adult female, MHUA-R 13155 juvenile female, and MHUA-R 13156 adult female, collected along with the holotype. MHUA-R 13215 adult female, Colombia, department of Antioquia, municipality of Alejandría, vereda El Cerro, El Edén forest (6.3672 N, –75.02728 W, 1304 m asl), collected on 7 February 2017 by Carlos M. Marín. See Fig. 12.

Etymology. The epithet *leurosquama* derives from the Greek word *leuros* (smooth), and the Latin word *squama* (scale), in allusion to the smooth dorsal scales of this species.

Diagnosis. *Magdalenasaura leurosquama* sp. nov. is assigned to the genus *Magdalenasaura* based on morphological characters and the molecular phylogenetic results. Phenotypic autapomorphies are not known for this species. *Magdalenasaura leurosquama* sp. nov. can be diagnosed by the combination of the following characters: (1) 3–4 (usually 4) supraoculars; (2) loreal scale in contact with the second or the first and second supralabials; (3) 4–5

postoculars; (4) 3–4 (usually 4) suboculars; (5) 5–6 (usually 5) superciliaries; (6) lower palpebral disc semitransparent and divided in 4–6 enlarged scales; (7) 8–9 (usually 8) supralabials; (8) 6–8 infralabials; (9) 8–11 enlarged gulars; (10) 5–6 (usually 6) enlarged collar scales; (11) dorsal scales smooth; (12) 41–46 transverse rows of dorsal scales; (13) 10–12 (usually 10) longitudinal rows of ventral scales; (14) 19–21 transverse rows of ventral scales; (15) 4–9 lateral scales; (16) 19–28 scales around midbody; (17) 14–15 (usually 15) subdigital lamellae under finger IV, and 20–23 under toe IV; (18) 17–18 femoral pores per side in males, 4–6 in females; (19) 1–2 scales in the anterior row of preanals, 5 in the posterior row; (20) dorsal surface of head, body, tail and limbs are light olive-brown or dark brown, lateral surfaces of the body light brown with ocelli present, ventral body colouration beige with brown and ventral head colouration beige with brown blotches; (21) with several light yellow or cream subocular stripes, the posterior oblique and crossing labials scales from posterior corner of the eyes to preangular scales.

Description of the holotype. Adult male (MHUA-R 13153); snout-vent length 78.7 mm; tail length 132.3 mm. Head scales smooth and juxtaposed. Rostral

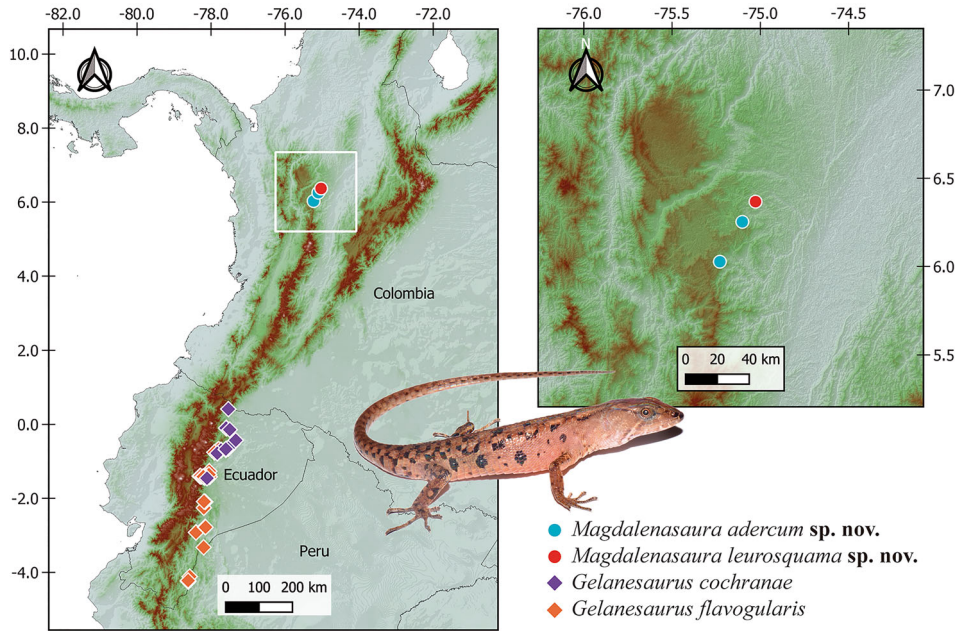


Fig. 9. Geographic distribution of *Magdalenasaura* gen. nov. and *Gelanesaurus* in north-western South America.



Fig. 10. Holotype of *Magdalenasaura leurosquama* sp. nov. in life (MHUA-R 13153). Photo by Estefany Cano.

scale wider than high, dorsally in contact with the frontonasal and laterally touching the first supralabials and the nasals. Frontonasal single, pentagonal, longer than wide, in contact with the nasals, loreals and prefrontals. Prefrontals paired, pentagonal, wider laterally and narrower medially, in contact with each other, touching the first superciliary, the frontal, the anterior supraocular and the loreal on each side. Frontal hexagonal, longer than wide, wider anteriorly, in contact with the prefrontals, the first to third supraoculars and the frontoparietals. Frontoparietals pentagonal, longer than wide, narrower anteriorly, contacting the third and fourth supraoculars laterally, and the parietals and interparietal posteriorly. Supraoculars four, second the largest, contacting the superciliaries laterally and the parietal and uppermost postocular posteriorly. Interparietal hexagonal, longer than wide, narrower than the parietals and contacting laterally the parietals and posteriorly the

occipitals. Parietals irregularly hexagonal, slightly longer than wide, shorter and wider than the interparietal, in contact with fourth supraocular and dorsalmost postocular anterolaterally, temporals posterolaterally, and occipitals posteriorly. Occipitals two, polygonal, smaller than parietals. Nasal single, sub-triangular, contacting the first supralabials and the loreal. Loreal pentagonal, in contact with first superciliary, frontonasal and prefrontals dorsally, first and second supralabial ventrally and frenocular posteriorly. Frenocular quadrilateral, touching the first infraocular and the second supralabial. Superciliaries five, the first and second larger than the others. Palpebral disc semitransparent and divided in five/six enlarged scales. Suboculars three, contacting supralabials three to five. Postoculars four/five. Temporals scales smooth, with different shape and size, juxtaposed. Supralabials eight and infralabials seven/eight. Tympanum slightly recessed. Mental wider than long, contacting the first infralabial and postmental. Postmental single, pentagonal, contacting the first two infralabials and the anterior pair of chin shields. Three pairs of large chin shields, all contacting infralabials, the first and second pair in contact on midline, second pair the largest and the third the smallest. Pregulars smooth, irregular, juxtaposed, increasing in size laterally. Gulars smooth, irregular, smaller anteriorly, increasing in size posteriorly, with 11 enlarged scales, wider than long, in two median longitudinal rows. Collar scales six, decreasing in size laterally. Collar fold distinct. Side of the neck with small and juxtaposed conic granules.

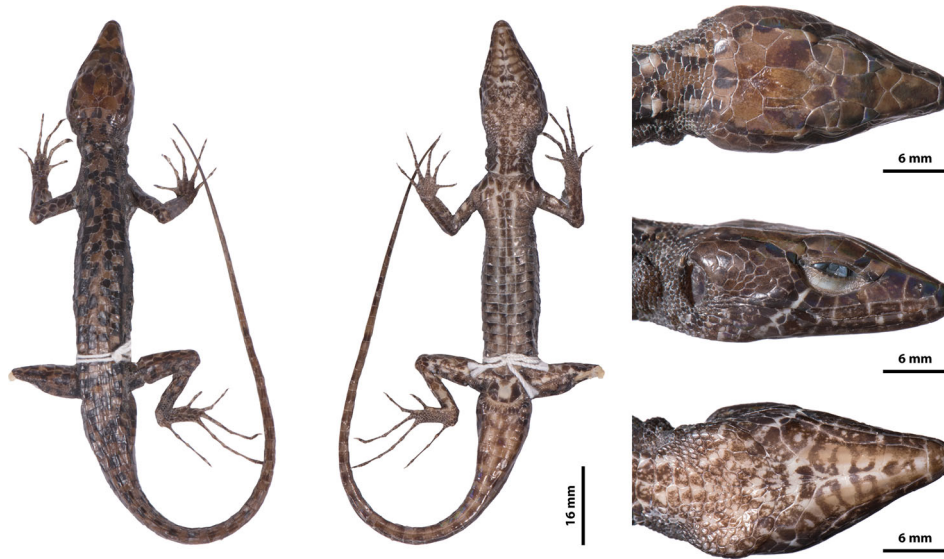


Fig. 11. Holotype of *Magdalenasaura leurosquama* sp. nov. in preservative.

Dorsal scales smooth, with heterogeneous sizes, the largest ones quadrangular to hexagonal, subimbricate, separated in the middorsal region by smaller, flat and irregular scales, which go dorsally from the posterior part of the head, to the anterior part of the tail. Transverse rows of dorsal scales 46. Laterals scales smaller than dorsal, juxtaposed, irregularly shaped, forming a band of seven/six scales at midbody between dorsals and ventrals (the width of a dorsal transversal row at midbody about the width of two transversal rows of lateral scales), the lateral scales near ventral scales convex and enlarged. Scales around the midbody 24. Ventral scales quadrangular, smooth, subimbricate, in 10 longitudinal rows and 20 transverse rows. Anterior preanal row with a single large median scale, while posterior preanal row with five scales, two paramedian which are a little larger than the median, and two very small lateral scales. Tail scales arranged in 82 segments, dorsal and lateral scales smooth, quadrangular anteriorly becoming rectangular toward tip, with few small, flat and irregular scales only anteriorly and dorsally. Subcaudal scales smooth, quadrangular anteriorly, becoming rectangular toward tip, with one row of lateral scales per one ventral tail scale. Limbs pentadactyl with clawed fingers. Fore limbs with pentagonal to hexagonal, subimbricate, smooth and large scales, ventrals smaller than dorsals. Dorsal hand scales hexagonal, subimbricate, smooth, and smaller than the dorsal lower arm scales. Palmar scales small, juxtaposed and granular. Finger length formula $IV > III > II > V > I$. Supradigital scales quadrangular, imbricate and smooth. Subdigital lamellae quadrangular, smooth, with 15/15 under finger IV. Hind limbs with pentagonal to

hexagonal, subimbricate, smooth and large scales, with granular scales on the posterior part of thigh and dorsal surface of shank (in the proximal and distal region). 17 femoral pores on each side (2 of these in preanal position). Dorsal foot scales polygonal, subimbricate and smooth. Plantar scales small, juxtaposed and granular. Toe length formula $IV > III > V > II > I$. Supradigital scales quadrangular, subimbricate, smooth and wider than long. Subdigital lamellae quadrangular, smooth with 23 under toe IV (right side).

Colour of the holotype in life (Fig. 10). Dorsal surface of head light olive brown with dark brown. Lateral surfaces of the head have the same colour as the dorsal surface, with some bright yellow stripes between subocular scales and ventral surface of the head, the posterior being the largest one, which crossing labial scales from posterior corner of the eyes to preangular scales. The ventral surface of the head (infralabials, chin shields, preangular, and gular scales) brown with irregular beige spots. Dorsal surface of the body has the same colour as the dorsal surface of the head, with paired yellowish spots extending from neck to the tail, becoming smaller towards the tip of the tail. Lateral surfaces of body light brown with eight yellow-centred, black-bordered ocelli along the side behind the ear opening to near the insertion of hind limbs. Ventral surface of the body, tail and limbs yellowish orange with light brown. Anterior, posterior and dorsal surfaces of the limbs light olive brown with dark brown. Femoral pores yellow.

Colour of the holotype in preservative (Fig. 11). In 70% ethanol the dorsal and lateral surfaces of the head, body, tail, limbs light and dark brown. Lateral stripes of



Fig. 12. Dorsal and ventral views of three paratypes of *Magdalenasaura leurosquama* sp. nov. MHUA-R 12943 (female), MHUA-R 13151 (male) and MHUA-R 13215 (female).

the head and dorsal spots of body cream. Lateral ocelli imperceptible. Ventral surfaces of the head, body, limbs and tail cream with light brown. Femoral pores cream.

Measurements of the holotype (mm). Snout-vent length: 78.7; snout length: 8.3; head length: 23.7; head width: 13.5; humerus length: 12.1; radio-ulna length: 12.8; femur length: 16.9; tibio-fibula length: 15.8; tail length: 132.3.

Variation. Measurements and scale counts of the type series are presented in Table S2. *Magdalenasaura leurosquama* sp. nov. shows sexual dimorphism in number of femoral pores, with males having 17–18 pores on each side, while females have 2–4 pores in preanal position and 1–2 additional pores at the distal end of each thigh. In two females (MHUA-R 12943 and MHUA-R 13215) pores are poorly developed. The belly colouration in *M. leurosquama* sp. nov. is variable, in males MHUA-R 13151 and MHUA-R 13153 is yellowish orange with conspicuous brown blotches, but light yellow with diffuse brown in the male MHUA-R 13152. In females the belly is beige without conspicuous blotches (Fig. 12).

Distribution and natural history. *Magdalenasaura leurosquama* sp. nov. is known only from the type locality in the department of Antioquia, Colombia (Fig. 9). All collected specimens were found inside a mature forest and were observed active during the day within rocky caves with an internal water stream, commonly known in Spanish as 'organales'.

Discussion

We provide multiple lines of evidence to support the recognition of a distinct evolutionary lineage as a new genus within the highly diverse lineage Cercosaurinae. Thus, with the recognition of the genus

Magdalenasaura gen. nov., the number of genera within the subfamily increases to 20. In the last decade, another seven genera have been proposed with the aim to solve some taxonomic problems or describe previously unknown or unnamed species: *Andinosaura*, *Centrosaura*, *Dendrosauridion*, *Gelanesaurus*, *Oreosaurus*, *Rheosaurus*, and *Selvasaura*. With the recent revision of *Echinosaura* (Vásquez-Restrepo *et al.*, 2020), the major outstanding issues in Cercosaurinae systematics are the need for rearrangement of *Proctoporus* to eliminate its rampant polyphyly, and the description and naming of Cercosaurini clade 2 *sensu* Torres-Carvajal *et al.* (2016).

Gymnophthalmidae is a highly morphologically diverse lizard lineage with a complex taxonomic history due, in part, to the differential use and interpretation of phenotypic characters. Morphological studies in these lizards have been based on traits related to osteology, general scutellation of head, body, tail and limbs, and hemipenial morphology (Betancourt *et al.*, 2018; Doan, 2003; Doan & Castoe, 2005; Hoogmoed & Avila-Pires, 1992; Kizirian, 1996; Köhler & Lehr, 2004; Kok, 2009; Marques-Souza *et al.*, 2018; Peloso *et al.*, 2011; Presch, 1980; Rivas *et al.*, 2012; Rodrigues *et al.*, 2005; Rodrigues *et al.*, 2009; Sánchez-Pacheco *et al.*, 2018; Uzzell, 1958, 1966). Although these types of characters are widely used in reptile taxonomy, recent molecular phylogenies are challenging the systematics of Cercosaurinae, and a better interpretation of phenotypic traits in an evolutionary framework is needed. For instance, many molecular phylogenetic studies have focused on resolving systematics problems (Castoe, Doan, & Parkinson, 2004; Goicoechea *et al.*, 2016; Pellegrino, Rodrigues, Yonenaga-Yassuda, & Sites, 2001), without careful examination of morphology as an important additional element for differentiating evolutionary lineages (e.g., *Gelanesaurus*, *Magdalenasaura* gen. nov., and *Potamites*; see Fig. 2). As we show in

Fig. 3, there are morphological differences between genera of Cercosaurinae, but also convergent characters. More sampling and more complete molecular phylogenies will aid the identification of phenotypic synapomorphies and previously unconsidered diagnostic characters, and the attempt to elucidate convergence phenomena within this complex clade.

The Magdalena biogeographic province (Morrone, 2001) harbours 10 genera of Gymnophthalmidae with the highest diversity centred in Cercosaurinae (Uetz, 2019). Six genera within this subfamily are currently distributed in this region ranging from the lowland rainforest ~100 m asl to paramo ecosystems at 3500 m asl. Despite this diversity, no endemic lineages at the genus level exist as all its representatives are shared with contiguous biogeographic provinces (i.e., Chocó, Caribe, and the Andes). With *Magdalenasaura* gen. nov., the number of genera increases to seven and this new genus becomes an endemic lineage for the Magdalena province. *Gelanesaurus*, its sister taxon is distributed in the Amazon piedmont of southern Colombia and eastern Ecuador, and although no explicit biogeographic hypothesis is proposed, it is likely that the orogeny of the Cordillera Oriental in Colombia promoted the divergence between these two lineages.

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Supplemental data

Supplemental data for this article can be accessed here <https://dx.doi.org/10.1080/14772000.2020.1783714>.

Disclosure statement

No potential conflict of interest was reported by the authors.

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