

# Variation of groove counts in *Caecilia thompsoni* (Gymnophiona: Caeciliidae) suggests gene flow between distant populations and calls for an updated diagnosis

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## Abstract

**Variation of groove counts in *Caecilia thompsoni* (Gymnophiona: Caeciliidae) suggests gene flow between distant populations and calls for an updated diagnosis.** *Caecilia thompsoni* is a Colombian endemic species known from the Magdalena Valley that reaches a large body size (1767 mm maximum total length). To clarify some taxonomic concerns, we studied variation of the primary grooves, secondary grooves, grooves interrupted by the vent, total length, body width at mid-body, and length/width. We examined 77 specimens from four populations within the Magdalena Valley and found significant variation in the east–west direction for the humid (north) and dry (south) populations. We provide a redescription for the species and comment on the taxonomic challenges that currently affect the genus *Caecilia*.

**Keywords:** Annuli, Caecilians, Intraspecific variation, Morphology, Neotropical.

## Resumen

**Variación en los conteos de surcos de *Caecilia thompsoni* (Gymnophiona: Caeciliidae) sugiere flujo genético entre poblaciones distantes y amerita una diagnosis actualizada.** *Caecilia thompsoni* es una especie endémica del Valle del Magdalena en Colombia y sobresale por alcanzar un gran tamaño corporal (1767 mm longitud total máxima). Con miras a resolver algunas dudas taxonómicas, estudiamos la variación de los surcos primarios, surcos secundarios, surcos interrumpidos por la cloaca, longitud del cuerpo, ancho a la mitad del cuerpo y largo/ancho. Examinamos 77 ejemplares provenientes de cuatro poblaciones dentro del Valle del Magdalena y encontramos que hay variación significativa en sentido occidente-oriente en las poblaciones húmedas (norte) y secas (sur). Por último hacemos una redescipción para la especie y discutimos sobre las dificultades taxonómicas que afectan actualmente al género *Caecilia*.

**Palabras clave:** Anillos, Cecílias, Morfología, Neotropical, Variación intraespecífica.

## Resumo

**Variação na contagem de sulcos em *Caecilia thompsoni* (Gymnophiona: Caeciliidae) sugere fluxo gênico entre populações distantes e exige uma diagnose atualizada.** *Caecilia thompsoni* é uma espécie endêmica da Colômbia conhecida do Vale do Magdalena que atinge um grande tamanho corporal (comprimento total máximo de 1767 mm). Para esclarecer alguns problemas taxonômicos,

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estudamos a variação dos sulcos primários, sulcos secundários, sulcos interrompidos pela cloaca, comprimento total, largura na metade do corpo e relação comprimento/largura. Examinamos 77 espécimes de quatro populações no Vale do Magdalena e encontramos variação significativa na direção leste-oeste para as populações úmidas (norte) e secas (sul). Fornecemos uma redescrição para a espécie e comentamos sobre os desafios taxonômicos que atualmente afetam o gênero *Caecilia*.

**Palavras-chave:** Anéis, Cecílias, Morfologia, Neotropical, Variação intraespecífica.

## Introduction

*Caecilia thompsoni* Boulenger, 1902 is the world's largest Gymnophiona, reaching a remarkable total length of 1767 mm. The species inhabits the Magdalena Valley lowlands as well as the neighboring foothills of the Cordillera Central and Cordillera Oriental of Colombia (79–1600 m a.s.l.). The type locality is Villeta, Cundinamarca. Over half a century ago, Edward H. Taylor provided the last meaningful taxonomic revision of *Caecilia thompsoni* (Taylor 1968), providing a detailed redescription of this taxon and offering valuable insights into its intraspecific variation. The closing remarks of his account said that he had examined two (of 10) specimens (MCZ 24552 and ILB 24 [now MLS 24]), which he doubted were conspecifics of *C. thompsoni*. Taylor (1968) considered the totality of the material to conform to two groups: the first had a lower count of primary grooves (187–207), and the second group had a higher count (220–243); he considered the latter group to attain a larger size than the former, but he was wary of the limitations imposed by the few specimens at his disposal. Moreover, Taylor (1968) claimed that the holotype of *C. thompsoni* (BMNH 1946.9.5.13) belonged to the first group. Dunn (1942) also examined 10 specimens of *C. thompsoni*, but he included two specimens that we consider dubious because their localities are unconfirmed (AMNH 49976 from ‘Bogotá?’) or out of the Magdalena Valley, (BMNH 1902.5.29, 179 from Río Caquetá). Acosta-Galvis (2012) reported an undescribed species (*Caecilia* sp.) from the Tatacoa Desert in Neiva, Huila. He claimed it was similar in color to *C. thompsoni* and that it differed from *C. thompsoni* by

presenting 181–203 (vs. 187–240) primary grooves and 11–32 (vs. 26–42) secondaries. We have examined the material from Tatacoa Desert (ICN 58393–58400 and 58409) and consider these specimens to be conspecifics of *C. thompsoni* because their measurements and meristics fall within the extent of variation that we now associate with this species. To assess the claims of an undescribed species by Taylor (1968) and Acosta-Galvis (2012) and to understand the variation of characters presented by these authors, we studied groove counts of 77 specimens that cover the full distribution range of the species in the Magdalena Valley of Colombia.

## Materials and Methods

We examined a total of 77 specimens of *Caecilia thompsoni* (Appendix I) and recorded their counts of primary grooves, secondary grooves, grooves interrupted by the vent, total length, width at mid-body, and length divided by width to assess the variation of these morphological characters (Tables 1 and 2). Meristics and measurements of the holotype of *C. thompsoni* were taken from Taylor (1968), and the number of grooves interrupted by the vent was determined via photographs. All groove counts were performed under a stereoscope and repeated at least twice for each individual. Entomological pins were used to demark and differentiate primary and secondary grooves to avoid misrepresenting their individual counts. Careful incisions to the mouth's commissure were performed using a razor blade in order to fully open the mouth and access dentition, choanae, and tongue when necessary. A sharp

pin was used to open the pockets where the grooves concealed their dermal scales; once these were obtained, they were described in shape and size and put back in their respective positions so no material would be lost or damaged. Subdermal scales were sought by partial dissection of the annuli close to the mid-body point and removing a section of epidermis to expose the connective tissue and determine their presence or absence. Sex was determined through direct examination of gonads by performing a ventral longitudinal incision

posterior to the mid-body point and prior to the vent to look for testes in males and ovaries in females. If mature testes or ovaries were found, these individuals were considered adults. Specimens with weakly calcified teeth, incomplete dentition, undefined nuchal collars, and total length usually under 400 mm were considered juveniles. All measurements were performed under a stereoscope; these were taken to the nearest 0.1 mm using a Neiko digital caliper, and a metric measuring tape was used to determine total length.

**Table 1.** Variation of primary grooves, secondary grooves, grooves interrupted by the vent, total length, body width at mid-body point, and attenuation index (i.e., length divided by width), of adult males, adult females, and juveniles of *Caecilia thompsoni*. Measurements and meristic data are provided as mean ± SE (range).

Characters	Adult males (N = 33)	Adult females (N = 26)	Juveniles (N = 14)
Primary grooves	221.1 ± 3.7 (174–267),	221.6 ± 5.1 (174–276)	190.2 ± 3.6 (169–223)
Secondary grooves	37.4 ± 1.4 (25–58)	37.5 ± 0.9 (28–46)	35.7 ± 2.1 (13–45)
Grooves interrupted by vent	4.3 ± 0.1 (2–6)	4.0 ± 0.3 (3–6)	3.1 ± 0.2 (2–5)
Total length (mm)	866.67 ± 54.6 (440–1666)	645.6 ± 47.73 (370–1310)	283.21 ± 24.72 (165–470)
Body width (mm)	13.33 ± 0.19 (4.8–15.1)	8.66 ± 0.5 (4.5–15.2)	4.5 ± 0.18 (3.4–8.2)
Length/width (times)	99.71 ± 2.57 (52.8–156.2)	88.75 ± 2.27 (44.6–119.1)	47.75 ± 0.59 (40.7–69.1)

**Table 2.** Variation of primary grooves, secondary grooves, grooves interrupted by the vent, total length, body width at mid-body point, and attenuation index (i.e., length divided by width), in the humid and dry populations of *Caecilia thompsoni*. Measurements and meristic data are provided as mean ± SE (range).

Characters/ Populations	Dry east (N = 23)	Dry west (N = 16)	Humid east (N = 22)	Humid west (N = 16)
Primary grooves	197.2 ± 3.7 (169–225)	204.6 ± 4.1 (184–231)	230.4 ± 5.3 (192–276)	226.4 ± 4.9 (200–259)
Secondary grooves	36.3 ± 1.5 (13–45)	35.3 ± 2.6 (16–56)	35.8 ± 0.9 (26–43)	37.5 ± 2.0 (28–58)
Grooves interrupted by vent	3.8 ± 0.2 (2–6)	4.0 ± 0.2 (3–6)	5.1 ± 0.1 (5–6)	4.2 ± 0.3 (2–6)
Total length (mm)	575.2 ± 66.9 (220–1180)	749.4 ± 59.1 (340–1040)	698.2 ± 75.8 (370–1550)	736.3 ± 98.6 (165–1666)
Body width (mm)	8.8 ± 0.6 (4.7–14.3)	9.7 ± 0.8 (4.8–15.5)	8.1 ± 0.7 (4.5–20.7)	7.9 ± 0.6 (3.4–15.1)
Length/width (times)	61.1 ± 3.6 (40.7–97)	79.2 ± 5.5 (41.4–122)	86.9 ± 4.5 (53.1–128.4)	88.1 ± 6.9 (45–156.2)

Museum abbreviations are as follows: Colección de Anfibios, Museo de Historia Natural, Universidad de Los Andes, Bogotá, D.C. (ANDES-A), Colección de Anfibios, Colecciones Zoológicas, Universidad del Tolima, Ibagué, Tolima (CZUT-A), Colección de Anfibios, Instituto Alexander von Humboldt, Villa de Leyva, Boyacá (IAvH-Am), Colección de Anfibios, Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, D.C. (ICN), Museo de Herpetología, Colección de Anfibios, Museo La Salle, Bogotá, D.C. (MLS), Museo de Herpetología, Universidad de Antioquia, Medellín, Antioquia (MHUA), Colección de Herpetología, Museo de Historia Natural, Universidad del Cauca, Popayán (MHUC), Colección de Anfibios, Pontificia Universidad Javeriana, Bogotá, D.C. (MUJ), Colección de Herpetología, Colección de Anfibios, Universidad Industrial de Santander, Bucaramanga (UIS-A), Universidad del Valle, Cali, Valle del Cauca (UVC), Natural History Museum in London, U.K (BMNH) and Museum of Comparative Zoology, Harvard College, Cambridge, Massachusetts, U.S.A. (MCZ).

#### *Sampling Geographic Area*

The Magdalena Valley of Colombia is a heterogeneous region located between the eastern slopes of the Cordillera Central and the western slopes of the Cordillera Oriental of Colombia; its northernmost extension reaches the Caribbean coast, while the Huila Department marks its southern limit. The Magdalena Valley is often subdivided into three basins: The Upper Magdalena Valley (southern Cundinamarca, southern Tolima, and Huila) to the south, the Middle Magdalena Valley (Antioquia, Boyacá, Caldas, northern Cundinamarca, and Santander), and the Lower Magdalena Valley to the north (Atlántico, Bolívar, Cesar, and Magdalena). The Lower and Middle Magdalena Valley differ notably from the Upper Magdalena Valley because these areas are predominantly humid lowland forest, while the Upper Magdalena

Valley comprises dry tropical forests and the Tatacoa Desert (Acosta-Galvis 2012) (Figure 1). For the purposes of this study, we use environmental heterogeneity to subdivide the Magdalena Valley into northern (humid) and southern (dry) sections, marked roughly by 4.5°N in Tolima and Cundinamarca, as well as east and west of the Magdalena River (Figure 1).

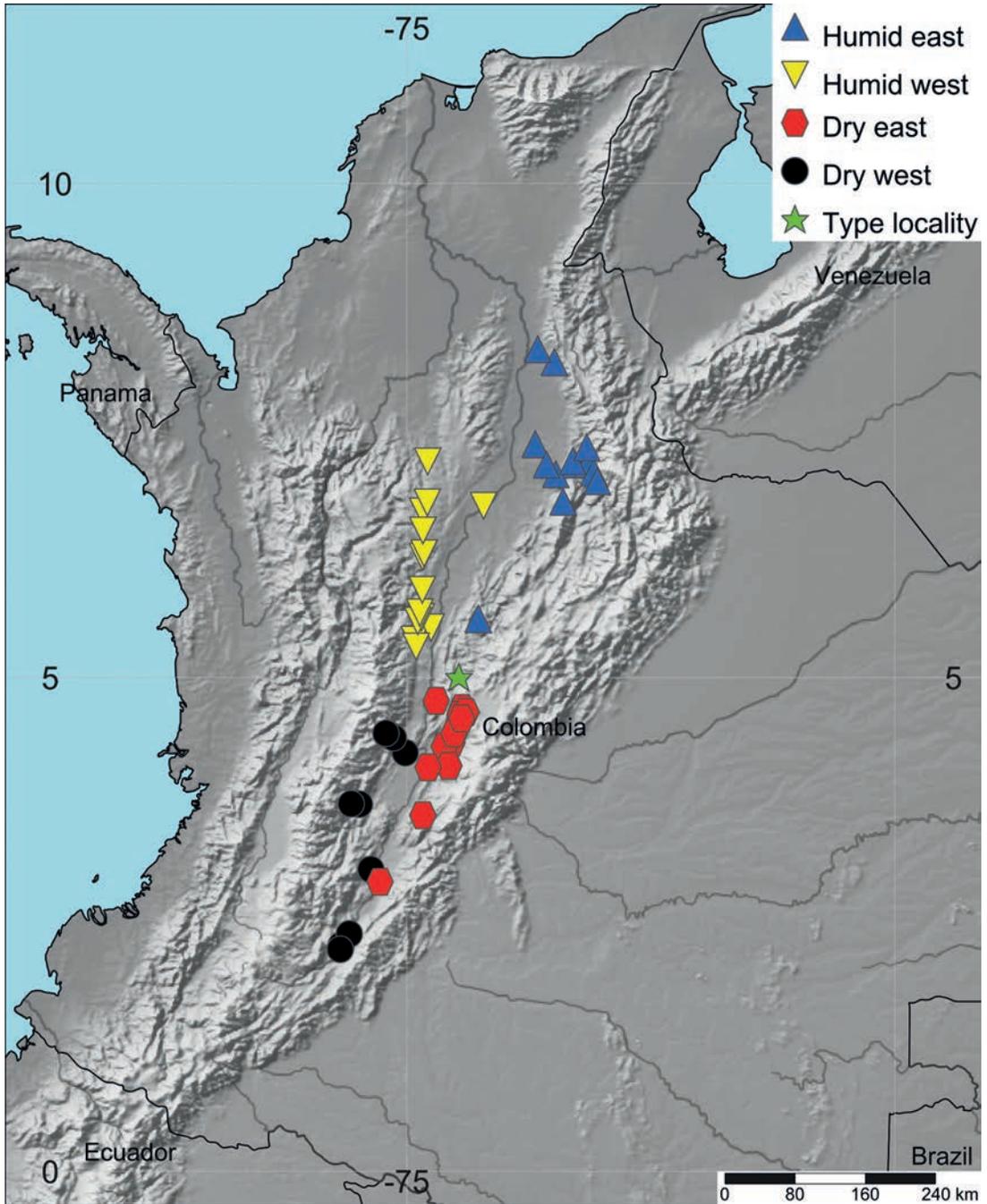
## Results

Our results, based on qualitative and quantitative analyses of external morphology of the specimens fail to support the Taylor (1968) and Acosta-Galvis (2012) hypothesis of an undescribed species allied to *C. thompsoni* in Magdalena Valley. Herein we provide a redescription for the species based on variation of the morphological characters studied in our sample.

#### *Diagnosis*

Adults 400–1767 mm total length (Arredondo Salgar 2007), body width at mid-body point 4.5–20.7 mm, attenuation index (length divided by width) 45–156.2 times, sexual dimorphism not evident in any characters studied (meristics and measurements summarized in Table 1). Snout rounded in profile, projected anteriorly in some specimens, interorbital distance smaller than distance from tip of snout to eye level, margins of upper lips concave and downturned from the commissure of the mouth to the level of the tentacular opening, eye barely visible or hidden under translucent epidermis, tentacular openings oval in outline, elevated above skin, positioned below and slightly anterior to nostril, closer to margin of mouth than to nostril, not visible in dorsal view but clearly visible in ventral and lateral view, head narrower than body.

First nuchal collar smaller than second, with faint transverse nuchal grooves dorsally, missing medially but notable and deep ventrally, the second nuchal collar wider and more evident than the first, bearing a faint nuchal groove



**Figure 1.** Map showing the geographic distribution of *Caecilia thompsoni* in the Magdalena Valley of Colombia. The humid east populations are represented by blue triangles, the humid west populations by yellow inverted triangles, the dry east populations by red rhombus, and the dry west populations by black circles. The type locality (Villeta, Cundinamarca) is indicated by a green star.

dorsally and slightly to flanks but absent ventrally; third nuchal groove incomplete ventrally. Body width increases considerably past nuchal collars, then gradually tapers toward mid-body point, where width remains mostly constant until last portion proceeding terminus which tapers abruptly, only to regain considerable width at end of body, i.e., terminus is wider than collars. Primary grooves 174–276, secondary grooves 25–58; last 4–9 primary grooves fully encircle posterior end of body, vent small, transverse, light gray in coloration, situated in a slight depression (concave), with 4–5 anterior denticulations and 5–6 posterior ones, anal glands white and small. No terminal shield, terminus segmented throughout. Dermal scales present throughout the body, those obtained posterior to collars are subcircular in shape, dermal scales present toward the terminus quite large, thick, and subrectangular, i.e., curved at anterior end of scale but almost straight at posterior end of scale (fitting Taylor's 1972, Fig. 76 description of dermal scales); those found toward flanks are overall rounded and less thick. Subdermal scales scattered along the connective tissue of skin.

All teeth monocuspid, recurved backwards and well-spaced from one another. Four series present, premaxillary–maxillary series bears maximum of 10–1–10 teeth, thick, though not very sharp, small, and decreasing in size posteriorly; vomeropalatine series has maximum of 12–12 teeth, thin, long, and sharp; dentary series has maximum of 10–12 teeth; inner mandibular teeth 3–3, small, pointed and partly concealed by gums. Teeth replacement signs evident in gums. Choanae deep, subcircular in shape and widening medially, distance separating them slightly greater than diameter of one choana; protruding narial plugs same color as tongue.

Coloration in life mostly dark gray dorsally, lighter gray toward flanks and slightly lighter on ventral surfaces (Figure 2). In preservative the main body coloration light gray, somewhat darker on the dorsal surfaces and slightly lighter

on the ventral surfaces; in contrast, the mouth, tentacle, nostril and vent have a light cream coloration. Grooves appear to attain slightly blue tonality in preservation. No apparent ventrolateral stripe (Figure 3).

#### *Morphological Remarks*

Taylor (1968) provided a good diagnosis and redescription of the species, but we found a few errors on his behalf. He included material from a locality outside the Magdalena Valley, a misidentified specimen of *Caecilia nigricans* Boulenger, 1902 from Valle del Cauca in the Pacific region of Colombia (Thornton collection no. 154). He included two photographs supposedly of *C. thompsoni* but his drawings and a radiograph are in fact of *C. nigricans* (another elongated congener from the Pacific region of Colombia, Ecuador, and Panama). Taylor (1968) also claimed that anal glands were found only in females (i.e., sexually dimorphic), but we have found them in both sexes, independent of body size or geography. All material of *C. thompsoni* examined by Taylor during his visit to MLS, Bogotá during the mid-1960's are adult males (i.e., MLS 21–24). Two specimens examined (ICN 60332–60333) are peculiar because they lack inner mandibular teeth. The other specimens have 1–1 to 3–3 inner mandibular teeth. Regarding variation in total length, we are aware of an (expected) overlap in juveniles and adults at around 400 mm total length (Table 1) and emphasize that TL should not be the only character used to determine the age of specimens. The best way to determine sex and age is direct examination of gonads (Serrano-Pérez and Ramírez-Pinilla 2020).

#### *Distribution*

*Caecilia thompsoni* has been regarded as a lowland species that ascends to moderate elevations in the foothills of the Cordillera Central and Cordillera Oriental (Lynch 2000); however, this geographic view must be



**Figure 2.** Chromatic variation of *Caecilia thompsoni*. (A) ICN 60332, from corregimiento Jerusalen, Sonsón, Antioquia (humid west); (B) ICN 60333, from Aguachica, Cesar (humid east); (C) ICN 58389, from El Agrado, Huila (dry west); (D) uncatalogued individual from Purificación, Tolima (dry east). Photographs by Giovanni Chaves-Portilla (A–B), Guido Fabian Medina-Rangel (C), and Francisco José López-López (D).

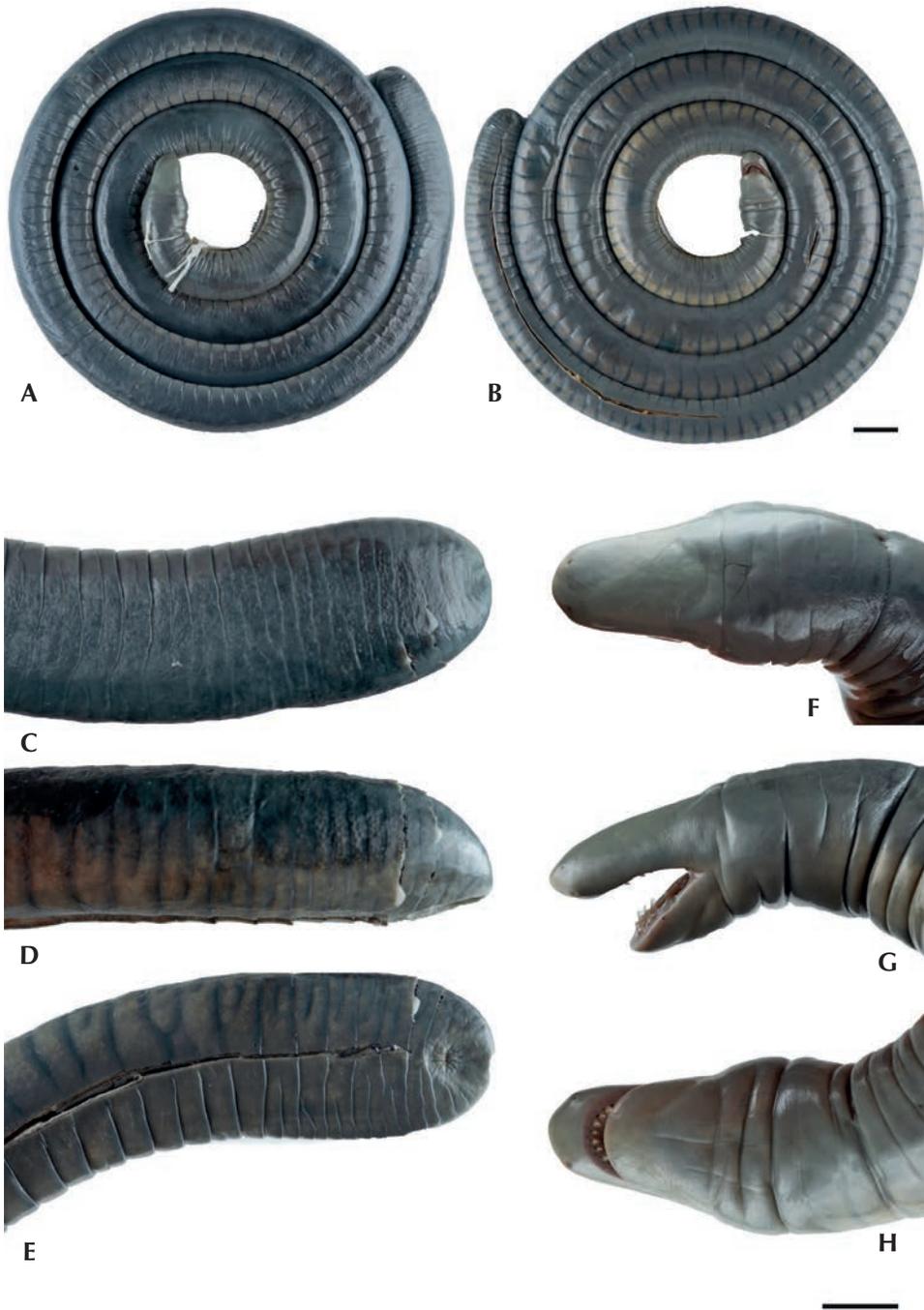
reevaluated because the bulk of the collections of *C. thompsoni* come from moderate elevations (400–1600 m a.s.l.) on the eastern slopes of the Cordillera Central and the western slopes of the Cordillera Oriental. Very few records occur between 79–150 m a.s.l., i.e., from the true lowlands of the Middle Magdalena Valley.

Perhaps this species is more common or prefers the ecological conditions presented by the foothills of the Cordilleras Central and Oriental rather than those offered by the lowlands of the Magdalena Valley (Figure 1). However, one should not discard field work effort biases among the foothills of the Cordilleras (more explored) and the Magdalena Valley lowlands.

## Discussion

### *On the Status of Caecilia thompsoni*

Taxonomically, we were unable to find morphological evidence to support the Taylor (1968) and Acosta-Galvis (2012) hypothesis of two species concealed under the name *Caecilia thompsoni*. Our results indicate that there are slight differences between the four populations defined, such as the highest counts of primary grooves and largest body sizes in both the humid east and humid west populations of *C. thompsoni* (Tables 1 and 2), but we interpret this as individual variation and not as support for the



**Figure 3.** *Caecilia thompsoni* from El Agrado, Huila (dry west) (ICN 58389). (A–B) dorsal and ventral view of the body; (C–E) dorsal, lateral, and ventral view of the terminus; (F–H) dorsal, lateral, and ventral view of the head and collars. Upper scale bar equals 12 mm; lower scale bar equals 6 mm.

description of a new species, at least not until further evidence is presented. The fact that groove counts have such a wide range of variation suggests that more emphasis should be put on finding new diagnostic and informative characters for caeciliid taxonomy (Tables 1–2). Wilson and Brown (1953) had already contemplated a scenario where intraspecific geographic variation—either concordant or discordant—could be better analyzed, described, and named (either as subspecies or geographic variants) depending on the number of diagnostic characters employed by taxonomists in their studies. The fact that no meaningful diagnostic characters were found in the cephalic, terminal, genital, dental, and scale morphology to divide *C. thompsoni* indicates that the species should be regarded as valid.

#### *Geographic Variation*

At present, only three of the 77 records (3.8%) of *C. thompsoni* come from the Magdalena Valley lowlands (79–106 m a.s.l.) in municipios Aguachica (Cesar), and Barrancabermeja and Puerto Wilches (Santander), thus ruling out the possibility of thoroughly discussing variation of the lowland populations (Table 2). Therefore, we decided to limit our remarks to the populations of *C. thompsoni* on the east and west side of the Magdalena Valley and for both humid and dry populations (i.e., north and south). In this zone (Andean foothills), there is a significant difference in the east–west (latitudinal) orientation that is discordant in groove counts with the wet–dry (north–south) orientation (Table 2).

The total count of primary grooves, total body length, and attenuation indexes (length/width) differ between the humid and dry populations of *C. thompsoni*, given that the humid populations attain higher counts of primary grooves and are overall longer and more slender than their counterparts from dry populations. The dry populations are stouter, shorter, and attain lower counts of primary grooves (Table 2). Moreover, variation of

secondary grooves, body width at mid-body point, and grooves interrupted by the vent does not vary geographically and is rather consistent between the humid and dry populations (Table 2). We recognize differences in the total counts of primary grooves, total length, and attenuation indexes as morphological tendencies (i.e., individual variation) of the populations studied (Wilson and Brown, 1953).

We also recognize slight variations in the main body coloration of *C. thompsoni* because some individuals from the dry populations, namely El Agrado, (Huila) (ICN 58389), Carmen de Apicalá (ICN 58509), and Purificación, (Tolima) (uncatalogued), appear to be darker (almost black), while most specimens from the humid populations are lighter gray or purple instead (Figure 2). Some individuals of *C. thompsoni* (Figures 2B and 2D) have a more pronounced bicolored pattern (similar to that of *Caecilia goweri* Fernández-Roldán and Lynch, 2021 and *C. pachynema* Günther, 1859), where the ventral surfaces of the body, and to some extent the flanks, have a light cream or white pigmentation subdivided by the primary and secondary grooves while the dorsal surfaces are notably darker-colored. This ‘‘bicolored pattern’’ is less common than the ‘‘unicolored pattern’’ (i.e., almost the same coloration on the dorsal and ventral surfaces), seen in most specimens such as those in Figures 2A and 2C. Nonetheless, we emphasize that we do not attribute diagnostic value to these color variants.

#### *On the Taxonomic Challenges of the Genus Caecilia*

Caecilian taxonomy has historically relied on groove counts to diagnose and describe new species, primarily because these are easy to count and to use in dichotomous keys, but also (and perhaps more importantly) because posterior to the nuchal collars, most primary grooves have a ‘one to one’ relation to each vertebra. This arrangement means that the number of primary grooves is almost always equivalent to or very

similar to the number of vertebrae (Nussbaum and Wilkinson 1989). Secondary grooves, on the other hand, are seemingly more variable, to the extent that some species have individuals with and without secondary grooves [i.e., *Caecilia abitaguae* Dunn, 1942, *C. guntheri* Dunn, 1942, *C. subdermalis* Taylor, 1968, *C. occidentalis* Taylor, 1968, *C. orientalis* Taylor, 1968, and *C. pachynema*, while others consistently lack them (*C. atelolepis* Fernández-Roldán, Lynch, and Medina-Rangel, 2023, *C. caribea* Dunn, 1942, *C. corpulenta* Taylor, 1968, *C. degenerata* Dunn, 1942, *C. pulchraserrana* Acosta-Galvis, Torres, and Pulido-Santacruz, 2019, *C. macrodonta* Fernández-Roldán, Lynch, and Medina-Rangel, 2023, and various undescribed taxa)]. However, we have demonstrated that their intraspecific variation—at least within *C. thompsoni*—is more limited than that of the primary grooves (Table 2).

Perhaps the strong point of the present study is the large sample of specimens of *Caecilia thompsoni* that allowed a more detailed examination of intraspecific variation, which, as expected, is considerably greater than what Dunn (1942), Taylor (1968), and Lynch (2000) had previously reported (but see Taylor's 1968: 311 account of *Chthonerpeton viviparum* Parker and Wettstein, 1929, a Brazilian typhlonectid with a wide range of primary grooves and vertebrae). This study has made us question if perhaps most caecilian species that are poorly circumscribed are prone to have a wider range of variation with regard to groove counts than what was previously reported in the literature. We consider that (caeciliid) groove-based taxonomy has been stable for the most part because of the paucity at which new caecilian specimens are obtained and the slow rate at which taxonomic revisions are published.

We determined that six characters (primary grooves, secondary grooves, the number of grooves interrupted by the vent, total length, body width, and attenuation index (length divided by width)), might serve to confront the suggestion of Taylor (1968) and the implication (without arguments or data) of Acosta-Galvis (2012) that

there could be an undescribed species under the name *C. thompsoni* (the data for our specimens is summarized in Tables 1 and 2). These data illustrate that no significant difference is available to separate dry and humid subdivisions of the Magdalena Valley and, furthermore, that variation is individual and discordant for the six characters. In the future, a study that includes multiple samples from the entire distribution range of the species would provide insight into the population dynamics of *C. thompsoni*. For now, following Wilson and Brown (1953), we infer genetic flow throughout the distribution of *C. thompsoni* and recognize no taxonomic subdivisions.

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**Appendix I.** *Specimens examined. Countries appear in bold caps, departments written in italic type, localities given in plain text. F = adult females, M = adult males and J = juveniles, U = undetermined sex.*

*Caecilia thompsoni* (N = 77) (33 males and 26 females). **COLOMBIA:** *Antioquia:* San Carlos, Juanes, Puente Roto (1500 m a.s.l.): MHUA 7115 (F), Quebrada El Jordán (900 m a.s.l.): MHUA 7192 (F), San Roque, Estación Piscícola Universidad de Antioquia (1450 m a.s.l.): MHUA 5157 (F), Segovia, vereda Calavera (210 m a.s.l.): ICN 59586 (M), Sonsón, corregimiento Jerusalén, camino al Reserve Río Claro (385 m a.s.l.): ICN 60332 (M), Vegachi, vereda San Rafael (970 m a.s.l.): ICN 59664 (M)–65 (F), Yolombó, vereda vereda Santa Ana (977 m a.s.l.): ICN 58438 (J), Yondó, El Silencio (106 m a.s.l.): ICN 58437 (M). *Boyacá:* Humbo, Estación de Policía de Humbo (1035 m a.s.l.): MLS 21–22 (M). *Caldas:* Norcasia, Río Manso (400 m a.s.l.): ANDES-A 4458 (J) and MUJ 7368 (M), La Miel (735 m a.s.l.): IavH 9688 (M), Samaná (500 m a.s.l.): ICN 41233 (J), La Victoria (510 m a.s.l.): ICN 43668 (M), MHUA 4432 (M) and 4247 (M). *Cesar:* Aguachica (79 m a.s.l.): ICN 60333 (M), Río de Oro, quebrada Peralonso (215 m a.s.l.): ICN 58392 (F). *Cundinamarca:* Beltrán, vereda El Tabór (375 m a.s.l.): ICN 58441 (M), Mesitas del Colegio (1260 m a.s.l.): ANDES-A 1904 (F), Nilo (330 m a.s.l.): ICN 47997 (M), La Esperanza (1240 m a.s.l.): ICN 21431 (M), Nilo: Pueblo Nuevo, hacienda La Isla (816 m a.s.l.): ICN 11763 (M), Tena, La Gran Vía, finca Tacarcuna (1100 m a.s.l.): MUJ 3402 (M) and 3713 (M), La Mesa (1270 m a.s.l.): MLS 24 (M), Viotá, finca El Danubio (1100 m a.s.l.): MUJ 8933 (M), Villeta (1000 m a.s.l.): BMNH 1946.9.5.13. (F). *Huila:* El Agrado (770 m a.s.l.): ICN 58389 (M), MHUC 1131–32 (U), Neiva, Desierto de La Tatacoa (400 m a.s.l.): ICN 58393–58400 and 58409 (J), El Quimbo (936 m a.s.l.): ICN 58439 (F), Neiva, ecoserva La Tribuna (515 m a.s.l.): IavH 16719 (M). *Santander:* Barrancabermeja (115 m a.s.l.): IavH 17819 (U), Lebríja (717 m a.s.l.): UIS-A 5189 (M), vereda Portugal, Finca La Armenia (1090 m a.s.l.): UIS-A 20 (F), Puerto Wilches (105 m a.s.l.): IavH 17017 (U), Rionegro (700 m a.s.l.): UIS-A 4938–40 and 4943–46 (F), Floridablanca, barrio Bucarica (912 m a.s.l.): UIS-A 5190 (F), San Vicente de Chucurí, vereda La Colorada (1543 m a.s.l.): UIS-A 5378 (M) and 6865 (F), Betulia, vereda Aguamieluda (185 m a.s.l.): UIS-A 5753 (F), Rionegro, hotel campestre El Portal (793 m a.s.l.): UIS-A 6201 (F), Piedecuesta, vereda Monterredondo (1000 m a.s.l.): UIS-A 6427 (F). *Tolima:* Carmen de Apicalá, vereda Cuatro Esquinas (335 m a.s.l.): ANDES-A 4462 (M) and ICN 58509 (F), Chaparral, casco urbano, sector La Marina (1089 m a.s.l.): MHUA 6611 (M) and MLS 23 (M), Dolores, San Andrés: CZUT 1620 (M), Ibagué, casco urbano (1100 m a.s.l.): CZUT 277 (F)–78 (M), 1621 (F), 1622 (M), 1623 (M), 1625 (F), 2013 (J), MLS 34 (M), UVC 15666 (F), Icononzo, vereda Cafreñas (1320 m a.s.l.): ANDES-A 4448–49 (M), San Luis, hacienda Los Pijaos: CZUT 1624 (J) (465 m a.s.l.).