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A review of color patterns in *Caecilia tentaculata* (Gymnophiona: Caeciliidae) reveals high frequency of partial leucism

Alice Maria Barbosa GUIMARÃES DIAS*, João Fabrício de Melo SARMENTO, Ana Lúcia da Costa PRUDENTE, Adriano Oliveira MACIEL

Museu Paraense Emílio Goeldi, Coordenação de Zoologia, Av. Perimetral, 1901, Terra Firme, 66077-830 Belém, Pará, Brazil

*Corresponding author: bio.alicedias@gmail.com

ABSTRACT

Caecilia tentaculata is an amphibian species of the order Gymnophiona, widely distributed throughout Amazonia. We reviewed the species' color pattern based on the analysis of collection specimens representing several populations across its geographic range. We identified two main color patterns determined by the pigmentation of the primary and secondary grooves, along with variations in the color of the head, lower jaw, gular and terminal regions of the body that occur independently of the two patterns. We observed a high frequency of partial leucism in the *C. tentaculata* populations studied. Considering that chromatic anomalies are rare in wild animals, the unexpected high frequency of partial leucism in this species is noteworthy. Our results underscore the importance of reassessing the color patterns of *Caecilia* species. Therefore, we recommend that color characters should be used with caution in *Caecilia* taxonomy since their variation is unknown for most species of the genus.

KEYWORDS: amphibians; coloration; chromatic anomalies; countershading; piebaldism

Revisão dos padrões de cor em *Caecilia tentaculata* (Gymnophiona: Caeciliidae) revela alta frequência de leucismo parcial

RESUMO

Caecilia tentaculata é uma espécie de anfíbio da ordem Gymnophiona amplamente distribuída na Amazônia. Revisamos o padrão de cor da espécie com base na análise de espécimes de coleção representando várias populações ao longo de sua distribuição geográfica. Encontramos dois principais padrões de cor determinados pela pigmentação dos sulcos primários e secundários, além de algumas variações de coloração da cabeça, mandíbula, região gular e terminal do corpo que independem dos dois padrões. Observamos uma alta frequência de leucismo parcial nas populações de *C. tentaculata* estudadas. Tendo em vista que anomalias cromáticas são raras em animais selvagens, a frequência inesperadamente alta de leucismo parcial encontrada na espécie é notável. Nossos resultados ressaltam a importância de reavaliar os padrões de cor das espécies de *Caecilia*. Portanto, recomendamos que os caracteres de coloração devem ser usados com cautela na taxonomia de *Caecilia*, uma vez que sua variação é desconhecida para a maioria das espécies do gênero.

PALAVRAS-CHAVE: anfíbios; coloração; anomalias cromáticas; coloração protetiva; piebaldismo

INTRODUCTION

Caecilians (Gymnophiona) are limbless, girdleless, snake-like amphibians that comprise the least numerous order of Lissamphibia (Duellman and Trueb 1994; Wilkinson and Nussbaum 2006). Currently, there are 222 recognized species distributed throughout the tropics and subtropics of the planet (Venu *et al*. 2021; Frost 2024). They are highly adapted for burrowing, although the Typhlonectidae members are aquatic or semiaquatic (Gower and Wilkinson 2005). Despite the fossorial habit of most caecilians, their coloration is relatively diverse, with blue and yellow being the most prevalent colors. Their color patterns often include longitudinal lateral stripes or distinct lines separating two colors, as well as stripes or serrated lateral color change following annuli and irregular blotches (Wollenberg and Measey 2009).

Coloration in amphibians is related to chromatophores, which are integumentary pigment-bearing cells of three different types: melanophores, containing eumelanin; iridophores, containing reflecting structures; and xanthophores, containing carotenoids and pteridines (Duellman and Trueb 1994; Stuckert *et al.* 2019). Thus, alterations involving those cells

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or the pigments within them may cause abnormal coloration phenotypes (Duellman and Trueb 1994; Brito-Zapata 2021).

Chromatic anomalies in amphibians are well registered in scientific literature (e.g., Neff *et al*. 2015; Thomas and Follum 2016; Lunghi *et al*. 2017; Tavares-Pinheiro *et al*. 2020), although reports of those in caecilians are quite scarce (Table 1) and sometimes may even be misinterpreted as chromatic intraspecific variation. Albinism and leucism are the most common forms (Jablonski *et al*. 2014). Nevertheless, such terminologies are still not a consensus among researchers (Allain *et al*. 2023). In general, both conditions are characterized by the lack of integumentary pigmentation in the body, but while albinos also lack pigments in their eyes, which become red or pink, leucistic individuals retain normal eye coloration (Dyrkacz 1981). Additionally, some authors use terms such as partial leucism and piebaldism as synonyms to define abnormal coloration in amphibians that displayed partial depigmentation of the body with pigmented eyes (Thomas and Follum 2016; Brito-Zapata 2021).

Caecilia tentaculata Linnaeus, 1758 is a South American species that inhabits the Amazonian wet forests of Brazil (states of Acre, Amapá, Amazonas, Maranhão, Mato Grosso and Pará), Colombia, Ecuador, French Guiana, Guyana, Peru, Suriname and Venezuela (Frost 2024). Also in Brazil, the species is known to occur in the state of Ceará in two isolated sites of relict mountain forests (Brejos de altitude) that have been considered an ancient connection between the coastal Atlantic forest and Amazonian forests (Borges-Nojosa *et al*. 2017).

As noted by Maciel and Hoogmoed (2011), both in life and in preservation, the species' color varies between shades of gray or blue, with the dorsum slightly darker than the venter and flanks of the specimens. The primary grooves of most individuals maintain the dark color of the dorsum along their ventrolateral extension. According to Maciel and Hoogmoed (2011), two distinct ventral color patterns occur in populations from Brazil and Suriname: one in which the venter is whitish with dark blotches nearly the same color of the dorsum, and another in which the venter is slightly paler than the dorsum and lacks blotches.

However, in a recent ongoing study of external characters used in the taxonomy of *Caecilia,* we observed that the first pattern, previously interpreted by Maciel and Hoogmoed (2011) as intraspecific variation in *C. tentaculata* rather represents a gradient of partial leucism. Therefore, we revised the species' color pattern and evaluated the frequency of partial leucism among some populations across its known distribution. Considering that *Caecilia* is a genus that harbors numerous morphologically similar species, it is important to accurately characterize the coloration of its members.

MATERIAL AND METHODS

Specimens analyzed

We examined 90 specimens (Supplementary Material, Appendix S1) of *C. tentaculata in situ* in the following collections: herpetological collection of Museu Paraense Emílio Goeldi (MPEG), herpetological collection of Universidade Federal do Ceará (UFC), and zoological collection of Universidade Federal do Acre (UFAC). Additionally, one individual (CHUFC A6773) was analyzed through photos published in Borjes-Nojosa *et al.* (2017).

Color pattern revision

We assessed the variation in color shades among the dorsum, flanks and venter, and compared the color shade of the head, lower jaw, gular region and terminal region close to the vent with the shade of the dorsum and venter. We then examined whether the color of the primary and secondary grooves diverges from the color of the dorsum. In some specimens it was not possible to evaluate all these features due to their state of preservation. We analyzed the presence of partial leucism and its frequency of occurrence throughout the distribution range of the species. Following Thomas and Follum (2016) and Brito-Zapata (2021), we considered as partially leucistic all individuals displaying normal eye color and partial depigmentation along the body, ranging from a few spots or blotches to extensive areas. For those affected by partial leucism, we also determined whether their condition extended to the anterior region (gular and lower jaw) and the terminal region close to the vent.

Table 1. Reports in the literature of chromatic anomalies in Gymnophiona.

Chromatic anomaly	Species	Reference
Albinism	*Chthonerpeton indistinctum* (Reinhardt and Lütken, 1862) *Gegeneophis mhadeiensis* Bhatta, Dinesh, Prashanth, and Kulkarni, 2007 *Ichthyophis beddomei* Peters, 1880	Cacivio and Cespedez 1998 Bhatta *et al.* 2007 Venu *et al.* 2022
Partial leucism (requires confirmation)	*Caecilia volcani* Taylor, 1969	Kubicki and Arias 2017
Leucism	*Ichthyophis kodaguensis* Wilkinson, Gower, Venu, and Venkatachalaiah, 2007 *Gymnopis multiplicata* Peters, 1874	Venu *et al.* 2021 Villagra and Escalante 2023
Partial melanism	*Uraeotyphlus narayani* Seshachar, 1939	Venu *et al.* 2022
Hypermelanism	*Ichthyophis beddomei*	Venu *et al.* 2022
Blue-colored	*Uraeotyphlus narayani* *Gegeneophis ramaswamii* Taylor, 1964	Venu *et al.* 2022 Villagra and Escalante 2023
Piebaldism	*Siphonops annulatus* (Mikan, 1822) *Siphonops paulensis* Boettger,1892	Almeida *et al.* 2024

Molecular sequencing

We sequenced a very thin specimen (MPEG 40347) exhibiting the most extreme partially leucistic pattern observed, to confirm its specific identity. This specimen was collected by P. S. Medeiros and J. F. M. Sarmento in March 2017, during the rainy season, in Floresta Nacional de Carajás (FLONA Carajás) (6º4'14.9"S; 50º4'6.8"W), municipality of Canaã dos Carajás, state of Pará, Brazil. Total DNA was extracted from a piece of muscle using the DNeasy Blood and Tissue Kit (Qiagen). The 16S RNA ribosomal gene was amplified by polymerase chain reaction (PCR) using primers 16Sar-L and 16Sbr-H as described by Palumbi *et al.* (1991). The sequences (forward and reverse) were generated on a SeqStudio genetic analyzer (ThermoFisher Scientific) and the edition and generation of the consensus sequence were performed using BioEdit (Hall 1999). The final sequence consists of 342 base pairs and has been deposited in the Genbank database under accession number PP915736.

Geographical distribution map

We produced a distribution map of *C. tentaculata* using the QGIS program (version 3.32 Lima) based on location points from our analyzed specimens, literature sources (McDiarmid and Paolillo 1988; Barrio-Amorós 1998; Maciel and Hoogmoed 2011; Borges-Nojosa *et al.* 2017; Rojas-Runjaic *et al.* 2018; Barrio-Amorós *et al.* 2019) and the Global Biodiversity Information Facility (GBIF 2023) plugin for QGIS, with results filtered by preserved specimens only. We marked Andean localities as questionable because further taxonomic evaluation is required to confirm the specific identity of those specimens. To assign specimens to populations, we used the geographical concept of Silva *et al.* (2019, see Figure 1 therein) based on endemism areas traditionally recognized for multiple vertebrate groups. Specimens from "Brejos de altitude" in the state of Ceará, Brazil (Borges-Nojosa *et al.* 2017) were included as a single population.

Statistical analysis

We conducted a Pearson's chi-squared test using the rstatix package in R to relate sex with the occurrence frequency of partial leucism in *C. tentaculata*. For this analysis, we used 48 specimens (19 females and 29 males) of the overall sample of 91, which could be sexed. The sex of the individuals was determined through direct observation of the gonads via a ventral longitudinal incision.

RESULTS

Description of the color pattern

In a dorsal view, the color was homogeneously distributed from the head to the posterior end of the body, with the head being slightly lighter colored in some specimens. In all individuals, the color of the dorsum was visibly darker than that of the venter, which was darker than the flanks. Still, in 15 specimens, the difference in color intensity among the dorsum, venter and flanks was very subtle. In 32 specimens, the color of the gular region and lower jaw was somewhat similar to that of the dorsum (i.e., darker than the rest of the venter), while in 51 specimens, the terminal region close to the vent was slightly darker than the rest of the venter, resembling the color of the dorsum. In all analyzed specimens, the color of the primary and secondary grooves extended laterally and ventrally, gradually becoming more complete posteriorly. Fifty-five specimens displayed grooves with the same color of the dorsum (Figure 1a), while 36 specimens had primary and secondary grooves markedly darker than the dorsum (Figure 1b).

Thus, we identified two main patterns of color in *C. tentaculata* based on the color of the grooves: 1) dorsum of the same color of the annular grooves, darker than the flanks and venter; 2) dorsum lighter than the annular grooves, but darker than the flanks and venter. When present, the dark color of the gular region, lower jaw and terminal region close to the vent occurred independently of the color pattern displayed by the specimens.

Overall, there was no geographical variation in color pattern throughout the Amazon, i.e, both color patterns were present in all populations sampled throughout the species' Amazonian distribution range. In the small "Brejos de altitude" sample, only the second pattern was identified.

Partial leucism

We observed 54 specimens exhibiting partial leucism to varying degrees, with the condition primarily affecting the lateral or ventrolateral surfaces of the body. The extent of

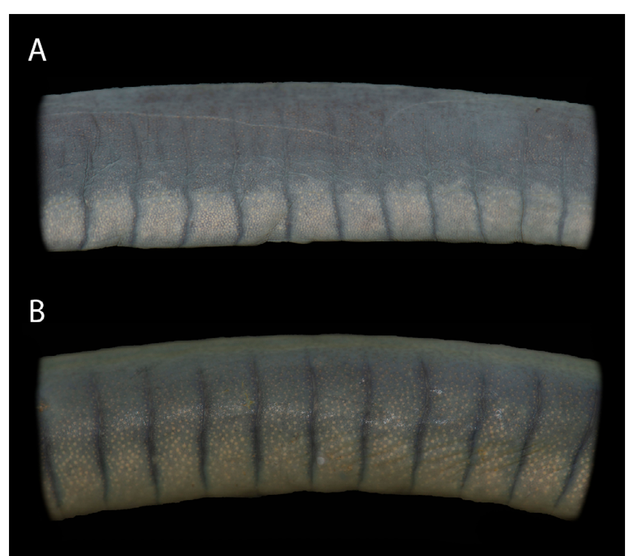

Figure 1. Color patterns of *Caecilia tentaculata*. A – Lateral view of MPEG 16757, in which the dark color of the dorsum extends to the grooves; B – Lateral view of MPEG 40932, in which the color of the dorsum is lighter than of the grooves.

depigmentation ranged from a few scattered spots along the venter to large areas (Figure 2). In the latter case, incomplete depigmentation of the body resulted in blotches of pigmentation in some specimens. Partial leucism reached the gular region and lower jaw in four specimens but did not extend to the terminal region close to the vent in any specimen analyzed. Furthermore, partial leucism affected individuals from both color patterns described here (33 and 21, respectively).

One specimen, MPEG 40347, displayed an extreme partial leucism condition, being the only one we examined in which the depigmentation affected not only the venter and flanks but also the dorsum, resulting in a marbled color pattern (Figure 3). Its head was almost entirely unpigmented, with just a few dark blue pigmented spots. The body was predominantly dark blue with large unpigmented areas, especially concentrated on the anterior half, the venter, and the flanks. Due to these depigmented areas, a few dark blue blotches formed throughout the body. Although the right eye was covered by a thin epidermis, the left eye underneath the skin remained darkly pigmented. Despite MPEG 40347 having an extremely thin body, different from a typical *C. tentaculata*, its meristic data (primary annuli: 119; secondary grooves: 28) fitted the species' diagnosis. The genetic sequence we obtained for the specimen was identical to that of a *C. tentaculata* from Marabá (state of Pará, Brazil) (GenBank: KX757087), collected 120 km northwest of the MPEG 40347 specimen. Moreover, it showed a low level of differentiation (2%) from a specimen from Guyana (DQ283406), near Suriname, the type locality of the species.

The frequency of partial leucism among the populations revealed a surprisingly high interpopulational incidence of this chromatic anomaly (Figure 4): 41.6% (N = 12) in the Belém endemism area; 73.9% (N = 23) in the Xingu endemism area; 58.6% (N = 29) in the Tapajós endemism area; and 75% (N = 20) in the Guiana endemism area. No cases of partial leucism were identified in the Inambari endemism area and in Brejos de altitude (N = 4 and N = 3, respectively). We found no significant difference in the frequency of partial leucism between sexes (X^2 = 2.8499e-^{31}, df = 1, p = 1).

DISCUSSION

Our analysis of color patterns in *Caecilia tentaculata* mostly agrees with the description provided for the species by Maciel and Hoogmoed (2011). However, we have refined our understanding of the intraspecific variation in color distribution along the body, thereby expanding the range of coloration characters to be included in the species' description. We identified a slight intraspecific variation in the pigmentation between the annular grooves and the dorsum of the specimens, allowing us to define two main patterns of color distribution based on a comprehensive analysis of body parts,

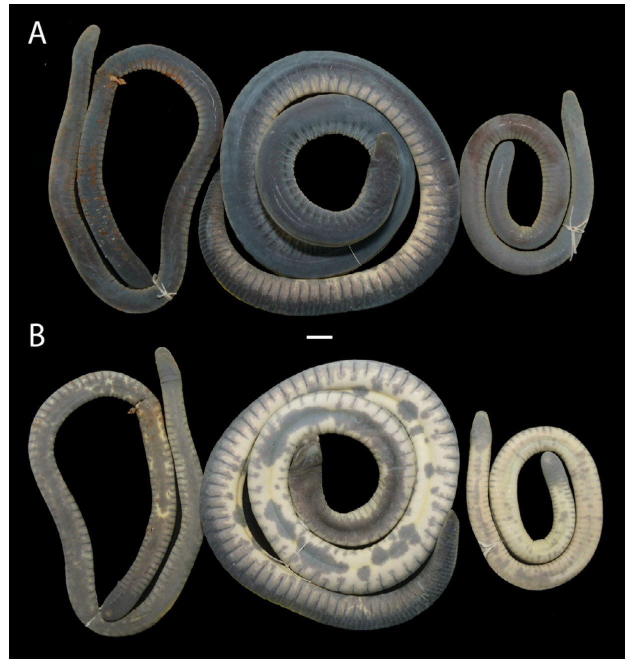

Figure 2. Degrees of partial leucism in *Caecilia tentaculata* (specimens MPEG 29091, MPEG 40270 and MPEG 38391, from left to right). A – Dorsal body view; B – Ventral body view. Scale bar = 1 cm.

Figure 3. Specimen MPEG 40347 of *Caecilia tentaculata*, which presented the most extreme partially leucistic phenotype in a sample of 91 specimens. A – Dorsal, lateral and ventral view of anterior region; B – Dorsal, lateral and ventral view of posterior region; C – Dorsal body view; D – Ventral body view. Scale bars = 1 cm.

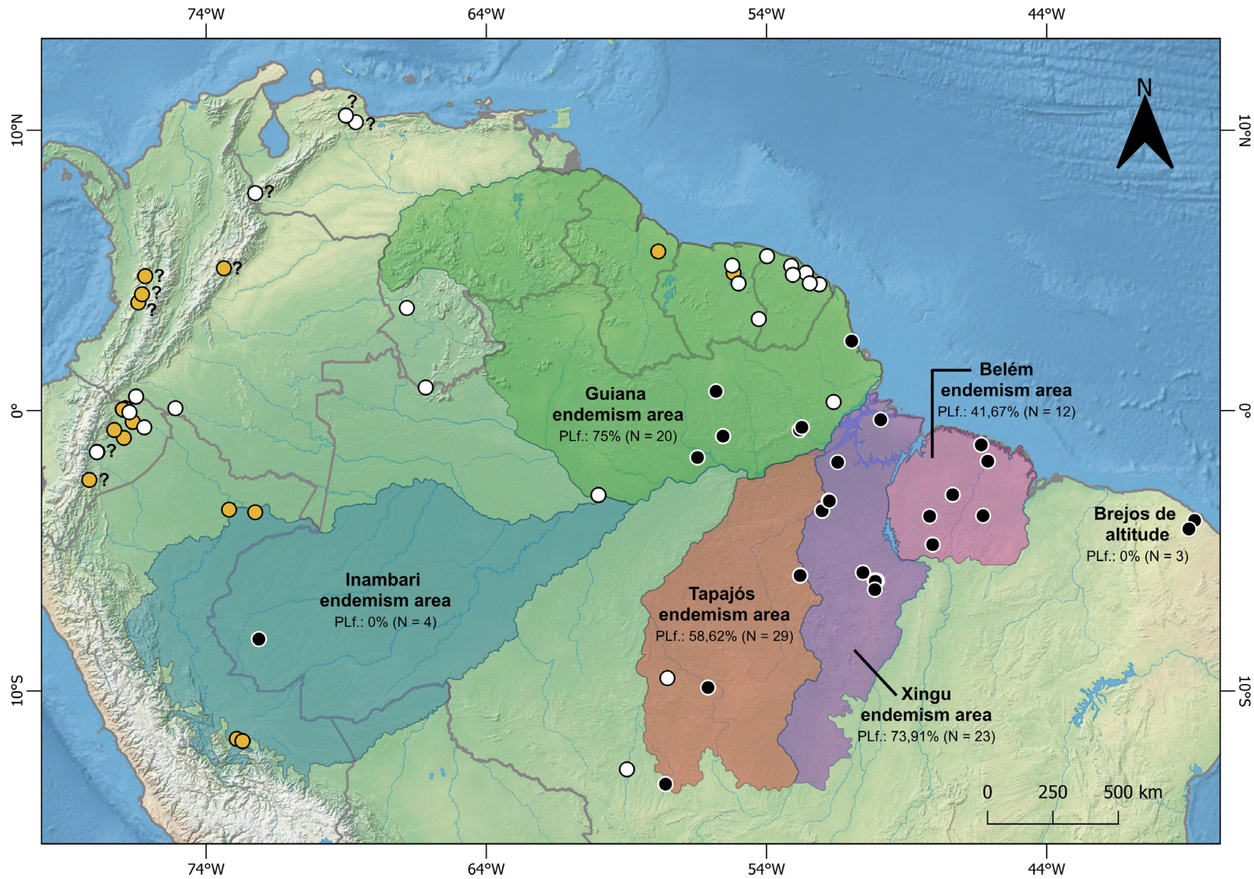

Figure 4. Distribution map of *Caecilia tentaculata* within Amazonian areas of endemism. PLf = partial leucism frequency; N = total sample size per endemism area. White dots are locations from literature sources; black dots are locations from examined collection material; orange dots are locations from the GBIF 2023 plug in. Only interfluves for which we had specimens examined *in situ* are shown. Trans-andean records are marked with a question mark, as they need confirmation of taxonomic identity.

rather than relying solely on the ventral coloration pattern. We identified no geographical variation in those color patterns among the Amazonian populations studied by us. The records of *C. tentaculata* in Ceará are from isolated relict mountain forests surrounded by dry Caatinga scrubland (Borges-Nojosa *et al*. 2017). Although only one of the two patterns described by us was identified in this disjunct area, the small smaple size does not allow us to discard the occurrence of the other color pattern and/or partial leucism in this population.

Despite being distinguishable, the difference between the two patterns observed by us is very subtle, and both are consistent with a countershading color pattern. Countershading, i.e., dark dorsum and light venter, is widespread among vertebrates because it is a highly effective crypsis strategy (Mills and Patterson 2009) and is displayed by most caecilians (Wollenberg and Measey 2009). Chromatic anomalies may compromise the effectiveness of countershading because they negatively interfere with camouflage, making the animal more visible to predators (Sazima and Di-Bernardo 1991). The possible effect on the animal's fitness that may be caused by such color aberrations makes them uncommon in wildlife. In this context, the consistently high frequencies of partial leucism in *C. tentaculata* populations is unexpected.

Our results suggest that the chromatic anomaly observed in *C. tentaculata* does not affect crypsis in this species and may be selectively neutral. In an adult male specimen of the aposematic and cryptic anuran *Anomaloglossus stepheni* (Martins, 1989), leucism was concentrated in the ventrolateral region of its body, where it does not interfere with the camouflage function of the dorsum, allowing the animal to reach maturity (Moraes and Kaefer 2015). This seems to be the case of *C. tentaculata*, as in almost all the partially leucistic specimens the condition is restricted to the ventrolateral surface of the body. Consequently, the dark pigmented dorsum is retained, while the ventral depigmented areas remain hidden most of the time and do not interfere with the countershading effect.

The fact that *C. tentaculata* is a fossorial species and lives below ground most of the time is also likely to play a role in the fixation of partial leucism in several populations. The animals probably rarely emerge to the surface, usually being collected when heavy rain floods its subterranean galleries (pers. obs.), thus are not frequently exposed to visually oriented predators. Our results also show that leucism affects conspecifics regardless of sex, suggesting that the partially leucistic phenotype is unlikely to be produced by sexual selection, probably due to the limited functionality of the eyes in caecilians (Wollenberg and Measey 2009). Further studies will be necessary to determine the cause of the high frequency of partial leucism in *C. tentaculata*.

There are other species of *Caecilia* that exhibit whitish regions on the body, but none of them have been identified as being affected by a chromatic anomaly. For example, some specimens of *C. marcusi* Wake, 1985 (Maciel and Hoogmoed 2011) and the holotype of *C. museugoeldi* Maciel and Hoogmoed, 2018 (Maciel and Hoogmoed 2018) display a pattern of whitish venter with dark blotches similar to that described for *C. tentaculata*, which could be indicative of partial leucism. Also, *C. pachynema* Günther, 1859, *C. occidentalis* Taylor, 1968 and *C. goweri* Fernández-Roldán and Lynch, 2021 exhibit a very similar color pattern characterized by a broad white ventrolateral stripe along the body, which has been interpreted as light-colored ventrolateral rectangles delimited by the primary grooves (Fernández-Roldán and Lynch 2021). Considering that many species of *Caecilia* are morphologically very similar (e.g., Maciel and Hoogmoed 2018; Acosta-Galvis et al. 2019; Fernández-Roldán et al. 2023), further studies will be necessary to analyze whether these coloration patterns are consistent with partial leucism and how frequent and widespread they are throughout the distribution range of each species.

The knowledge on the intra and interpopulational variation in most morphological characters used in the taxonomy of *Caecilia* is very limited. It is common to use diagnostic coloration characters based on few specimens that occur in proximity to each other (e.g., Maciel and Hoogmoed 2018; Fernández-Roldán and Lynch 2021; Fernández-Roldán *et al*. 2023). Therefore, the range of variation and frequency of occurrence of coloration characters, thus their diagnostic validity in discriminating among species, is not known. Studies like ours are important to advance the knowledge on the phenotypic diversity and its evolutionary implications within the genus.

CONCLUSIONS

To the best of our knowledge, this is the first report of partial leucism in *C. tentaculata*. Our review of the intraspecific variation in color patterns in *C. tentaculata* provides a greater level of detail to the description made by Maciel and Hoogmoed (2011) and enhances the understanding of individual coloration diversity and geographic distribution within the species. This is particularly crucial in *Caecilia* to prevent specific misidentification, given the presence of several morphologically similar species within the genus. We hope our work contributes to the scientific knowledge of caecilians by highlighting the importance of studying variations in coloration characters used in the taxonomy of the group.

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SUPPLEMENTARY MATERIAL

Guimarães Dias *et al*. A review of color patterns in *Caecilia tentaculata* (Gymnophiona: Caeciliidae) reveals high frequency of partial leucism

Appendix S1. Material examined (90 specimens) for variation in coloration of *Caecilia tentaculata* (Gymnophiona: Caeciliidae). UFACF - zoological collection of Universidade Federal do Acre; MPEG - herpetological collection of Museu Paraense Emílio Goeldi; UFC - herpetological collection of Universidade Federal do Ceará.

Caecilia tentaculata. BRAZIL: ACRE: Resex Riozinho da Liberdade (UFACF 680, 688, 692, 697); AMAPÁ: Calçoene (MPEG 934); CEARÁ: (UFC 002601), Maranguape (UFC A6773), Pacoti (UFC A6477); MARANHÃO: Nova Vida (MPEG 7340-7342), Bom Jardim (MPEG 36614); MATO GROSSO: Campo Novo dos Parecis (MPEG 16756-16766), Alta Floresta (no voucher number); PARÁ: Almeirim (MPEG 18159-18160, 23542-23547), Canaã dos Carajás (MPEG 40347), Chaves (MPEG 37125), Marabá (MPEG 29089-29091, 40242, 40268), Óbidos (MPEG 26468-26475), Oriximiná (MPEG 09758, 20165-20166), Paragominas (MPEG 26467, 40270, 42131), Parauapebas (MPEG 22068-22073, 22811, 40319-40320), Portel, MPEG 22700), Rondon do Pará (MPEG 41003-41004), São Félix do Xingu (MPEG 40925-40938), Senador José Porfírio (MPEG 38390-38395), Viseu (MPEG 1359, 1362, 7344), Vitória do Xingu (MPEG 39111-39113).