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Two new species of *Caecilia* (Gymnophiona: Caeciliidae) from the Ecuadorian humid Chocó

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Abstract. We describe two new caecilian species of the genus *Caecilia* (Gymnophiona: Caeciliidae) from the wet tropical Chocó Forest, north-western Ecuador. We applied an integrative taxonomic approach, taking into consideration external morphology, osteology from intensive ct-scanning, and molecular phylogenetic analyses. The two new species were compared to all other *Caecilia* species, known to occur west of the Ecuadorian and Colombian Andes. The new taxa can be distinguished by their external morphological characters, as well as by their osteology, genetic divergence, and phylogenetic relationships. The two new species, although morphologically quite different, were closely related. *Caecilia tesoro* sp. n. is a large-bodied, robust species with a unique colour pattern in larger individuals. In contrast, *Caecilia truncata* sp. n. is a smaller caeciliid and sister to medium-sized *C. volcani*, a species known from Panama. Morphologically, *C. truncata* sp. n. is best recognized by a very truncated snout shape. As know from many previously recognized neotropical caeciliids, both new species are likely endemic to small ranges, here the humid tropical lowland to mid-altitude forests of western Ecuador. Both new species seem to tolerate some degree of habitat degradation. Our new findings support to intensify research and conservation activities in one of South America's most diverse but severely endangered biomes. We also present, for the first time, some clues of the phylogenetic position of elongated *C. nigricans* and *C. leucocephala*. *Caecilia nigricans* was sister to a clade composed of one *Oscaecilia* and ten species of *Caecilia*. This topology rendered the genus *Caecilia* paraphyletic relative to *Oscaecilia*.

Key words. Amphibia, biodiversity, caecilians, integrative taxonomy, molecular genetics, morphology, osteology, rainforest.

Resumen. Describimos dos nuevas especies de cecilias del género *Caecilia* (Gymnophiona: Caeciliidae) del bosque lluvioso tropical del Chocó, en el noroeste de Ecuador. Aplicamos un enfoque taxonómico integrador, considerando la morfología externa, datos anatómicos de escaneo CT y análisis filogenéticos moleculares. Las dos nuevas especies fueron comparadas con todas las demás especies de *Caecilia* conocidas al oeste de los Andes ecuatorianos y colombianos. Las nuevas especies se distinguen por caracteres morfológicos externos, así como por osteología, divergencia genética y relaciones filogenéticas. Las dos nuevas especies, aunque morfológicamente muy diferentes, están estrechamente relacionadas. *Caecilia tesoro* sp. n. es una especie grande y robusta con un patrón de color único, al menos en individuos de mayor tamaño. *Caecilia truncata* sp. n. es más pequeña y es hermana de *C. volcani*, una especie de Panamá. Morfológicamente, *C. truncata* sp. n. se reconoce mejor por su hocico muy truncado. Ambas nuevas especies son endémicas de los bosques húmedos tropicales de tierras bajas hasta medias altitudes del oeste de Ecuador y parecen tolerar cierto grado de degradación del hábitat. Estos nuevos hallazgos son argumentos adicionales para intensificar las actividades de investigación y conservación en uno de los biomas más diversos, pero gravemente amenazados de América del Sur. También presentamos, por primera vez, la posición filogenética de *C. nigricans* y *C. leucocephala*. *Caecilia nigricans* es hermana de un clado compuesto por una *Oscaecilia* y diez especies de *Caecilia*. Esta topología hace que el género *Caecilia* sea parafilético en relación con *Oscaecilia*.

Palabras clave. Anfibios, biodiversidad, cecilias, taxonomía integrativa, genética molecular, morfología, osteología, selva tropical.

Introduction

Caecilians or Gymnophiona Müller, 1832 are the least species-rich of the three extant orders of amphibians with only 222 (3%) of the currently recognized 8752 amphibian species (Frost 2024). However, published studies on caecilians reported remarkable biological observations, for instance concerning their physiology and reproduction (e.g., Nussbaum & Wilkinson 1995, Kupfer et al. 2006, Gower et al. 2008, Wilkinson et al. 2013, Jared et al. 2018, Mailho-Fontana et al. 2024; summaries e.g. by Himstedt 1996, Jared et al. 1999, Exbrayat 2006, Gomes et al. 2012), but due to the predominately tropical distribution and fossorial life-style, still little is known concerning ecology and biology of most species (Wilkinson 2012). As recent species descriptions illustrate (Lalremsanga et al. 2021, Wilkinson et al. 2021, Malonza & Wasonga 2024; and see below), we are also still far from understanding the diversity of this cryptic group of subterranean vertebrates. As currently conceived, the Neotropical family Caeciliidae Rafinesque, 1814 comprises two genera (Wilkinson et al. 2011) with nine species of *Oscaecilia* Taylor, 1968, and 40 species of *Caecilia* Linnaeus, 1758 and is the second most species-rich of the ten currently recognized caecilian families (Wilkinson et al. 2011, Frost 2024). The two genera are just distinguished by a bone covering the eyes in *Oscaecilia* (Taylor 1968), whereas eyes are in an open orbit in *Caecilia*. However, Nussbaum & Wilkinson (1989) and Maciel & Hoogmoed (2011) report that the eyes of *Caecilia gracilis* Shaw, 1802 are sometimes covered by bone, challenging the validity of the generic distinction.

Seven new *Caecilia* species from Colombia have been described in recent years (Acosta-Galvis et al. 2019, Fernández-Roldán & Rueda-Almonacid 2022, Fernández-Roldán & Lynch 2023, Fernández-Roldán et al. 2023). It can be assumed that a similar unreported species richness exists in Ecuador, and although Taylor (1974) already listed two *Caecilia* spp., no new species from this genus has been described from the country during the past 50 years. Some 14–15 *Caecilia* species have been reported from Ecuador (e.g., Taylor 1974, AmphibiaWeb 2024, Frost 2024, Ortega-Andrade et al. 2021, Ron et al. 2024). Most of which are known from the Amazon or the eastern Andean slopes. Five species, *C. guntheri* Dunn, 1942, *C. leucocephala* Taylor, 1986, *C. nigricans* Boulenger, 1902, *C. pachynema* Günther, 1859, and *C. tenuissima* Taylor, 1973 have been recorded from the Pacific lowlands and the western Andean slopes and one species, *C. subterminalis* Taylor, 1968, is reported from Ecuador but lacks more precise information of its provenance. Two further species, *C. perdita* Taylor, 1968 and *C. wilkinsoni* Fernández-Roldán & Lynch, 2023 have been reported from the Pacific lowlands and western Andean slopes of adjacent regions in neighbouring Colombia. While studying Ecuadorian caecilians deposited in the collection of the Zoology Museum of the Pontificia Universidad Católica del Ecuador, and through ecological field work in the Ecuadorian Chocó, we discovered novel *Caecilia* specimens which could not be assigned to any of the known species.

By applying an integrative taxonomic approach (Padial et al. 2010), using morphological, computed-tomography derived anatomical, and molecular data, we confirmed these specimens represent two distinct species, formerly unnoticed and therefore, new to science. In the following we describe these two species from north-western Ecuador.

Material and methods

Selection of comparative materials

The tropical Andes are considered to be an impassable barrier for amphibians (e.g. Caminer & Ron 2020, Menéndez-Guerrero et al. 2024). Thus we restrict the morphological and osteological comparisons to *Caecilia* species from western Ecuador and south-western Colombia (Table 2) plus *C. subterminalis* and *C. volcani* Taylor, 1969 from Panama and Costa Rica (Taylor 1969a), the last of which is closely related to the herein described new taxa.

Sequenced individuals were selected from a preliminary unpublished phylogeny of *Caecilia* (Arroba 2017). We included individuals of the two new species described here, as well as sympatric *C. leucocephala* and *C. nigricans*, which are morphologically similar to the new species (Tables 1, 2; Appendix).

Morphology

Different morphological characters are commonly used in diagnosing *Caecilia* species, including dimensions, numbers, and disposition of annular grooves, presence of a terminal shield and anal papillae, as well as colour pattern and body shape. For the eleven species compared within this study we either assessed these data ourselves or extracted it from published sources (Tables 3, 4).

Examined specimens are deposited at the Zoology Museum, Pontificia Universidad Católica del Ecuador, Quito (QCAZ), Field Museum, Chicago (FMNH), Natural History Museum University of Kansas (KU), Museum of Zoology University of Michigan (UMMZ), and the Natural History Museum, London (BMNH); see type series, Appendix and Table 4. To avoid the possibility of species mischaracterization, we also examined the holotypes of relevant species: *C. guntheri* (BMNH 1946.9.5.12), *C. leucocephala* (KU 200985), *C. nigricans* (BMNH 1946.9.5.52), *C. pachynema* (BMNH 1946.9.6.83), *C. perdita* (UMMZ 121036), *C. subterminalis* (FMNH 189204), and *C. volcani* (KU 203035). We also examined the holotype of the *C. buckleyi* (BMNH 1946.9.5.15), a binomen currently considered junior synonym of *C. pachynema*. Newly collected vouchers were euthanized with 2.0% Roxicain (Box Dental, Ecuador). Prior to preservation, a piece of liver and/or muscle was extracted and stored in 96% ethanol without deterrents. Tissue samples were deposited at QCAZ (same accession num-

Table 1. GenBank accession numbers for DNA sequences used in the phylogenetic analyses (Fig. 1). Newly generated sequences for this study are shown in bold.

Species	Voucher/unique code	12S	16S	ND1
Caecilia gracilis	BMNH 2008.747	KF540147	KF540147	KF540147
Caecilia gracilis	MPEG 28603	KX757076	KX757086	–
Caecilia isthmica	ARA 5363	–	MN555719	–
Caecilia leucocephala	QCAZ-A 47071	**PP973086**	**PP973093**	–
Caecilia nigricans	QCAZ-A 37728	PP973087	PP973098	PQ382552
Caecilia pulchraserrana	0690-STB	–	MN555718	–
Caecilia pulchraserrana	0691-STB	–	MN555715	–
Caecilia sp.	MUSM31909	KX757075	–	–
Caecilia tentaculata	BMNH 2008.750	KF540146	KF540146	KF540146
Caecilia tentaculata	CHUFCA 6775 or CHUFCA 6543	KF745902	–	–
Caecilia tentaculata	ALPA 059	KX757077	KX757087	–
Caecilia tentaculata	MTR ALCX112P40	–	KU495167	–
Caecilia tentaculata	MTR ALCX112P41	–	KU495166	–
Caecilia tesoro sp. n.	QCAZ-A 7146	**–**	**PP973096**	–
Caecilia tesoro sp. n.	QCAZ-A 31448	**PP973088**	**PP973094**	–
Caecilia tesoro sp. n.	QCAZ-A 64560	**PP973089**	**PP973095**	–
Caecilia tesoro sp. n.	QCAZ-A 78501	PP973090	PP973099	PQ382553
Caecilia thompsoni	ARA 2623	–	MN555171	–
Caecilia truncata sp. n.	QCAZ-A 27774	**PP973091**	**PP973097**	–
Caecilia truncata sp. n.	QCAZ-A 40305	**PP973092**	**PP973100**	**PQ382554**
Caecilia volcani	MVZ 231242	GQ244466	GQ244466	GQ244466
Chthonerpeton indistinctum	MCP 3.814	KF540149	KF540149	KF540149
Oscaecilia ochrocephala	MVZ 222472	GQ244474	GQ244474	GQ244474
Typhlonectes natans		AF154051	AF154051	AF154051

Table 2. Data sets used for inter-specific comparisons between western Ecuadorian and south-western Columbian *Caecilia* species, plus *C. volcani* from Panama, which is genetically closest to the two new species; * = range unknown; source of morphology data, also compare Tables 3 to 7; source of molecular data (compare Table 1); ts = this study.

Caecilia species	morphology	osteology	molecular
C. guntheri	Taylor (1968); ts	ts	
C. leucocephala	Taylor (1968, 1973); ts	ts	ts
C. nigricans	Taylor (1968); ts	ts	ts
C. pachynema	Taylor (1968); ts	ts	
C. perdita	Taylor (1968, 1973); ts		
*C. subterminalis**	Taylor (1968); ts		
C. tenuissima	Taylor (1973); ts	ts	
C. tesoro sp. n.	ts	ts	ts
C. truncata sp. n.	ts	ts	ts
C. volcani	Taylor (1969a), Summers (2001), Summers & Wake (2001); ts	ts	ts
C. wilkinsoni	Fernández-Roldán & Lynch (2023)		

bers as the respective vouchers). Specimens were then fixed in 4–10% formalin and later transferred to 70–75% ethanol.

Measurements were taken by TEAL, SB, KNS, MW, and MOR with digital callipers Metav© (accuracy ± 0.1 mm) following Taylor (1968), Lynch (1999), or Maciel & Hoogmoed (2011) as well as more recent papers by Fernández-Roldán and colleagues (see references cited in introduction). Additional data were retrieved from published sources (see Table 3 for references). Counting of primary and secondary annular grooves, as well as measuring short distances was done under a dissecting microscope (Leica MZ12 and Olympus SZ61). Measures and assessed characters comprised the following: TL = total body length (from tip of the snout to tip of body terminus, tak-

Table 3. Main morphological data used to diagnose western Ecuadorian and south-western Colombian *Caecilia* species, plus *C. volcani* from Panama, which is genetically closest to the two new species. TL = Body length (maximum lengths, in mm); TL/BW = body length divided by body width (rounded); PA = number of primary annular grooves (range); SA = number of secondary annular grooves (range); SAc = number of continuous secondary annular grooves (range), * last two cm with complete grooves (Taylor 1969); TS = terminal shield (present/absent); AGP = anal papillae around cloaca (present/absent); CP = colour pattern; ts = this study (including data from the unpublished bachelor thesis of the second author and Ron et al. 2022). Numbers in parenthesis pertain to the holotypes.

Caecilia species	TL	TL/BW	PA	SA	SAc	TS	AGP	CP	source
C. guntheri	1010 (621)	33–63	108–133 (118)	0–22 (16)	0–14	no		Dorsum grey to coppery brown, ventrolateral pale brown, head bluish grey	Taylor (1968); Fernández-Roldán & Lynch (2023); ts
C. leucocephala	455 (177)	32–45	118–131 (126)	32–52 (34)	6–9	very small	no	Body dark-grey or dark brown; head lighter coloured, greyish cream or old ivory	Taylor (1968, 1973); ts
C. nigricans	1030 (594)	33–80	154–195 (176)	27–65 (54)	0–7	very small	yes	Uniform blueish-grey to black, only head slightly lighter coloured	Taylor (1968, 1973); ts
C. pachynema	852 (852)	49–108	150–208 (168)	0–11 (0)	0	yes	yes	Dorsum uniform dark-grey, head brownish; ventrolateraly brownish-cream band interrupted by grooves; ventral median light grey stripe	Taylor (1968, 1973); ts
C. perdita	521 (521)	34–56	133–152 (151)	64–83 (73)	10–16	very small	yes	Nearly uniform dark violet to violet-slate, head lighter or mottled grey	Taylor (1968, 1973); Fernández-Roldán & Lynch (2023)
*C. subterminalis**	436 (434)	34	170 (170)	16 (17)		yes		Dorsum dark lavender-slate; head greyish, snout tip, upper lip and lower jaw yellowish; lateral yellow stripe on head and body	Taylor (1968, 1974)
C. tenuissima	390	44–81	151–186	8–10	0–4	yes	yes	Purple-grey or dark brown with or without irregular whitish flecking, neck region with slightly lighter patches; top of head with whitish or yellowish	Taylor (1973); Fernández-Roldán & Lynch (2023); ts
C. tesoro sp. n.	790 (790)	35–40	117–121 (121)	14–18 (15)	0	no	no	Purple-grey head and tail and yellowish cream with irregular dark patterning in fully grown specimens; smaller individuals uniform dark grey or brown-purple with some clear spotting or light gray ventrolateral bands	ts
C. truncata sp. n.	482 (482)	25–31	123 (123)	7–8 (8)	0	yes	no	Almost uniform grey, but lighter on head and neck; two lighter grey lateral bands, interrupted by darker folds	ts
C. volcani	324 (329)	31	112–124 (124)	14–37 (35)	*, up to 3	no	yes	Uniformly grey, vaguely lighter on head and neck; venter greyish with dark mid region; lighter spots at eye, nostril, tentacle and vent openings	*Taylor (1969a); Summers (2001); Summers & Wake (2001); Fernández-Roldán & Lynch (2023); ts
C. wilkinsoni	650	66–75	190–195	51–71	6–7	no	yes	Almost uniform black; venter and head slightly lighter; upper and lower lips nostril and vent area creamish yellow	Fernández-Roldán & Lynch (2023)

Table 4. Measures (in mm) of *Caecilia* vouchers investigated for this study; holotypes printed in bold (compare Table 3). Given are species name; museum voucher number; TL = body length; BW = body width; PA = number of primary annular grooves; SA = number of secondary annular grooves; SAc = number of continuous secondary annular grooves; TS = terminal shield (present/absent); NV = number of vertebrae; HL = head length; HW= head width; IOD = interorbital distance; END = distance eye to nostril; TND = distance between tentacle and nostril; IND = internarial distance; ITD = distance between tentacles; AGP = anal papillae around cloaca; cf = indistinct or difficult to see; na = not accessed.

Species/characters	Voucher#	TL	BW	PA	SA	SAc	TS	NV	HL	HW	IOD	END	TND	IND	ITD	AGP
***C. tesoro* sp. n.**	**QCAZ-A 78501**	790	19.6	121	15	0	no	126	23.6	14.8	12.2	10.2	3.4	6.9	10.0	no
C. tesoro sp. n.	QCAZ-A 64560	570	17.3	120	7	0	no	na	16.6	11.8	8.6	6.5	2.9	4.5	6.3	no
C. tesoro sp. n.	QCAZ-A 31448	154	4.4	117	14	0	no	124	8.5	5.3	3.1	2.0	0.9	1.6	2.0	no
C. tesoro sp. n.	QCAZ-A 7146	604	16.4	121	18	0	no	126	18.9	14.4	9.6	7.3	2.4	4.7	5.7	no
***C. truncata* sp. n.**	**QCAZ-A 27774**	482	13.2	123	8	0	yes	129	13.1	11.0	6.3	4.9	1.9	3.4	4.5	no
C. truncata sp. n.	QCAZ-A 40305	143.5	4.7	123	7	0	yes	128	6.2	3.9	3.5	1.9	1.1	1.5	2.2	no
C. truncata sp. n.	QCAZ-A 78979	387	9.0	119	5	0	yes	na	11.5	8.0	6.1	3.9	1.8	3.4	4.1	no
C. truncata sp. n.	QCAZ-A 79000	285	9.3	118	5	0	yes	na	9.5	7.3	4.9	3.3	1.9	2.8	3.7	no
C. truncata sp. n.	QCAZ-A 79001	133	5.7	107	6	0	yes	na	6.6	4.4	3.3	2.5	1.0	1.7	2.1	no
C. truncata sp. n.	QCAZ-A 79740	364	10.0	127	6	0	yes	na	11.0	5.2	5.1	3.8	1.0	2.2	na	no
C. leucocephala	QCAZ-A 47071	172	3.8	118	52	6	no	126	6.2	4.3	2.5	1.8	0.7	1.3	1.5	no
C. nigricans	QCAZ-A 37728	442	7.7	185	50	5	no	190	10.4	9.0	5.8	3.2	1.4	2.7	3.5	yes
C. pachynema	QCAZ-A 33235	701	5.9	208	0	0	yes	216	9.6	6.1	4.8	4.0	2.1	2.5	3.7	yes
C. pachynema	QCAZ-A 46983	473	12.8	201	0	0	yes	207	9.6	6.8	4.2	3.2	1.0	2.2	3.1	yes (cf.)
C. pachynema	QCAZ-A 31720	982	17.3	185	0	0	yes	na	20.2	13	10.8	7.8	2.3	5.5	7.7	yes
C. pachynema	QCAZ-A 46938	463	4.7	202	0	0	yes	188	9.7	5.9	4.5	4.8	1.8	2.6	3.3	no
C. tenuissima	QCAZ-A 23580	354	8.0	171	8	0	yes	178	7.2	6.0	3.2	2.1	0.7	1.7	2.5	yes
C. tenuissima	QCAZ-A 42637	332	4.7	151	10	2	yes	157	6.8	4.8	3.1	2.4	0.7	1.3	1.5	yes (cf)
C. guntheri	QCAZ-A 15568	686	17.9	133	15	0	0	133	18.2	14.2	9.7	7.1	2.9	4.6	6.7	no?

en from string laid alongside the caecilians' body); BW = body width (at widest point along all the body); PA = number of primary annular grooves; SA = number of secondary annular grooves; SAc = number of complete secondary annular grooves; TS = terminal shield (present/absent); NV = number of vertebrae (from ct-scans, see below); HL = head length; HW= head width (at corner of the mouth); IOD = interorbital distance; END = distance between eye to nostril; TND = distance between tentacular aperture and nostril; IND = distance between nares; ITD = distance between tentacular aperture; AGP = anal papillae around vent; number of denticulations in anterior and posterior edges of vent. Dentition data were collected from specimen examinations assisted by the Nussbaum technique (Wilkinson et al. 2013) or from ct-scans (see below). Measurements are presented in the species descriptions and are summarized in Table 4.

Sex was determined by direct examination of gonads through a longitudinal incision opening the coelom in the last third of the body; the length of the incision was variable, depending on reproductive condition. The presence and distribution of dermal scales along the body was assessed using the whole body ct-scans of the new taxa (Figs 3, 5). A few dermal scales were extracted from scale pockets. We used pointed forceps or an insect pin to break the epidermis covering the opening of the pocket on some of the 10 posterior-most annular grooves (following Taylor 1972), extracted the scales and preserved them in 75% ethanol. Some dermal scales were ct-scanned (see below), imaged, and measured. The description of colour pattern was based on the preserved specimens and, if available, photos of the live animals.

Osteology

For osteological comparisons, we investigated nine specimens belonging to eight *Caecilia* species: holotypes of *C. tesoro* sp. n. (QCAZ-A 78501), *C. truncata* sp. n. (QCAZ-A 27774), and *C. volcani* (KU 203035); plus specimens of *C. guntheri* (QCAZ-A 15568), *C. leucocephala* (QCAZ-A 47071), *C. nigricans* (QCAZ-A 37728), *C. pachynema* (QZAC-A 33235, QCAZ-A 37733), and *C. tenuissima* (QCAZ-A 23580). Apart from *C. volcani*, all voucher material was subjected to micro-tomographic analysis at the Museum für Naturkunde Berlin (SCR_022585) using a Phoenix nanotom X-ray|s (Waygate Technologies, Wunstorf, Germany; Equipment identification ID SCR_022582) and a Comet YXLON FF85 (Comet Yxlon GmbH, Hamburg, Germany; Equipment identification ID SCR_020917) at 90 kV and 100 kV or 90 µA, 100 µA, 500 µA, 549.99 µA, generating 1440, 2000, and 2500 projections with 400 ms (Comet YXLON FF85) and 750 ms (Phoenix nanotom X-ray|s) per scan. The different kV- and projection-settings were adjusted to respective specimens' size, which is also the reason for the differences in

the effective voxel size (4.5–14.12 µm). The cone beam reconstruction was performed using the datos|x 2.2 reconstruction software (Waygate Technologies, Wunstorf, Germany) or Nexus reconstruction software (Comet Yxlon GmbH, Hamburg, Germany), respectively. The bones were visualized and measured in Volume Graphics Studio Max 2023.4 (Volume Graphics GmbH, Heidelberg, Germany). Scanning of *C. volcani* was done by MW on a Nikon Metris X-Tek HMX ST 225 System with a molybdenum target set at 180kV and 200µA. Scan data were collected over 3142 projections, each with a single frame with 500 ms exposure (two frames per second), with a reconstructed voxel size of 9.11 µm.

Osteological terminology follows Wake (2003). Complete osteological descriptions are beyond the scope of our study. We used ct-scans to count vertebrae and assess selected skull characters that may be useful for species diagnosis. For symmetrical skull bones we took measurements on both sides of the head. We measured the length and widths of the entire skull (maximum length and widths), the frontals (f), parietals (p), nasopremaxillae (np), maxillopalatines (m), mesethmoid (me), Os basale (ob), squamosals (sq), the orbital openings (o), choanae (ch), external nostril openings (en), tentacular foramina (ta); and separately counted numbers of teeth in the premaxillary–maxillary, vomeropalatine, outer mandibular (dentary), and inner mandibular (splenial) series (left–right side; third values indicate azygous median teeth). Finally, we counted all foramina visible on the external surfaces of the skulls. Measures are given with 0.1 mm accuracy. Ct-scans have been archived at MorphoSource (www.morphosource.org) available at https://www.morphosource.org/projects/000669394.

Phylogenetic analyses

For the phylogenetic analyses, we obtained DNA sequences of the mitochondrial genes 12S rRNA, $tRNA^{Val}$,16S rRNA, $tRNA^{Leu}$, NADH dehydrogenase subunit 1 ND1, $tRNA^{Ile}$, $tRNA^{Gln}$, and $tRNA^{Met}$. We sequenced seven individuals of *Caecilia leucocephala*, *C. nigricans*, and the two new species. Tissues were obtained from the genome bank of the Zoology Museum, Pontificia Universidad Católica del Ecuador (QCAZ). DNA was extracted from liver or muscle tissue preserved in 95% ethanol or tissue storage buffer using guanidine thiocyanate protocol (M. Fujita, unpublished instructions) with some modifications. Primers used for 12S amplification were obtained from Pauly et al. (2004); for 16S from Pauly et al. (2004), San Mauro et al. (2004), and Heinicke et al. (2007); and for ND-1 from San Mauro et al. (2004). PCR amplification was performed under standard protocols and amplicons were sequenced by the Macrogen Sequencing Team (Macrogen Inc., Seoul, Korea). Sequences were assembled in Geneious R7.1 (Kearse et al. 2012).

We complemented our new sequences with all homologous sequences of *Caecilia* and *Oscaecilia* available from GenBank (http://www.ncbi.nlm.nih.gov/genbank) and those originally published by Zardoya & Meyer (2000), Zhan & Wake (2009), San Mauro et al. (2014), Borges-Nojosa et al. (2017), Maciel et al. (2017), and Acosta-Galvis et al. (2019). We also included GenBank sequences representative of the sister family of Caeciliidae, Typhlonectidae (Wilkinson et al. 2011), i.e., *Chthonerpeton indistinctum* (Reinhardt & Lütken, 1862), and *Typhlonectes natans* (Fischer, 1880) as outgroups. Vouchers and GenBank accession numbers for all analysed sequences, including newly generated, are shown in Table 1. Our final matrix consisted of sequences from 24 individuals and up to 3259 bp. Our ingroup had one species of *Oscaecilia* and 11 of *Caecilia*, including the undescribed taxa. The alignment of the sequences of each gene was performed with MAFFT under default settings (Katoh & Standley 2013). The aligned matrix is available at http://zenodo.org under DOI 10.5281/zenodo.10625957.

Phylogenetic relationships were inferred for all genes concatenated, but partitioned the matrix by gene and codon position for a total of five partitions (12S, 16S, and three codon positions for ND1). All partitions were analysed under the model GTR + G + R. Tree search used maximum likelihood as optimality criterion and was carried out with IQ-TREE multicore version 2.2.0.7 (Nguyen et al. 2015) under default settings. To assess branch support, we made 1000 ultrafast bootstrap searches (-bb 1000 command (Hoang et al. 2018) and 1000 replicates for the SH-like approximate likelihood ratio test (-alrt 1000 command; Guindon et al. 2010). We considered that branches with bootstrap values > 95 and SH-aLRT values > 80 had strong support.

Unfortunately, not all three data sets (morphology, osteology, molecular data) where fully available for all species. Table 2 provides an overview of what characters we could use in our inter-specific comparisons. A summary of species-specific characters is given in Tables 3 and 7. Identification of all specimens of the new species was corroborated with DNA sequences for the 16S rRNA gene (in part). The only exception was specimen QCAZ-A 79740 which is not part of the type series.

Nomenclatural acts

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature, and hence the new names contained herein are available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The LSID (Life Science Identifier) for this publication is: urn:lsid:zoobank.org:pub:2737830B-C27C-41E0-A763-03EA3D8D6C44. The electronic edition of this work was published in a journal with an ISSN and has been archived and is available from the following digital repositories: zenodo.org, salamandra-journal.com.

Results

Phylogenetic analyses

Our molecular phylogeny showed strong support for a distinct clade composed of the species from the Ecuadorian Chocó and Central America: *C. leucocephala*, *C. volcani*, *C. tesoro* sp. n., and *C. truncata* sp. n. (Fig. 1). Four individuals from four populations of *C. tesoro* sp. n. form a strongly supported clade, which is well supported as sister to a well-supported clade including *C. truncata* sp. n. + *C. volcani*. In our phylogeny *C. nigricans* is sister to a clade of the remaining species of the ingroup rendering *Caecilia* paraphyletic, although with weak support. Genetic distances for the 16S rRNA gene between *C. tesoro* sp. n. and *C. volcani* range from 4.4 to 5.5%; distances between *C. truncata* sp. n. and *C. volcani* range from 3.4 to 3.6%.

Morphology

The body size/length, known to date, in the eleven species studied herein ranged from smaller ones (290–450 mm), *C. volcani*, *C. truncata* sp. n., *C. tenuissima*, *C. subterminalis*, and *C. leucocephala*, over mid-sized species (500–650 mm), *C. perdita* and *C. wilkinsoni*, to large (730–790 mm), *C. pachynema* and *C. tesoro* sp. n., and very large (> 1000 mm) species, *C. guntheri* and *C. nigricans*. It should be kept in mind that for some species, only a few individuals are known. The data thus may not necessarily represent the species maximum size.

Several species were distinct by showing particularly large numbers of primary and secondary annular grooves, *C. pachynema* (primary 150–208/secondary: 0–11), *C. tenuissima* (151–168/8–10), *C. nigricans* (154–195/27–65),

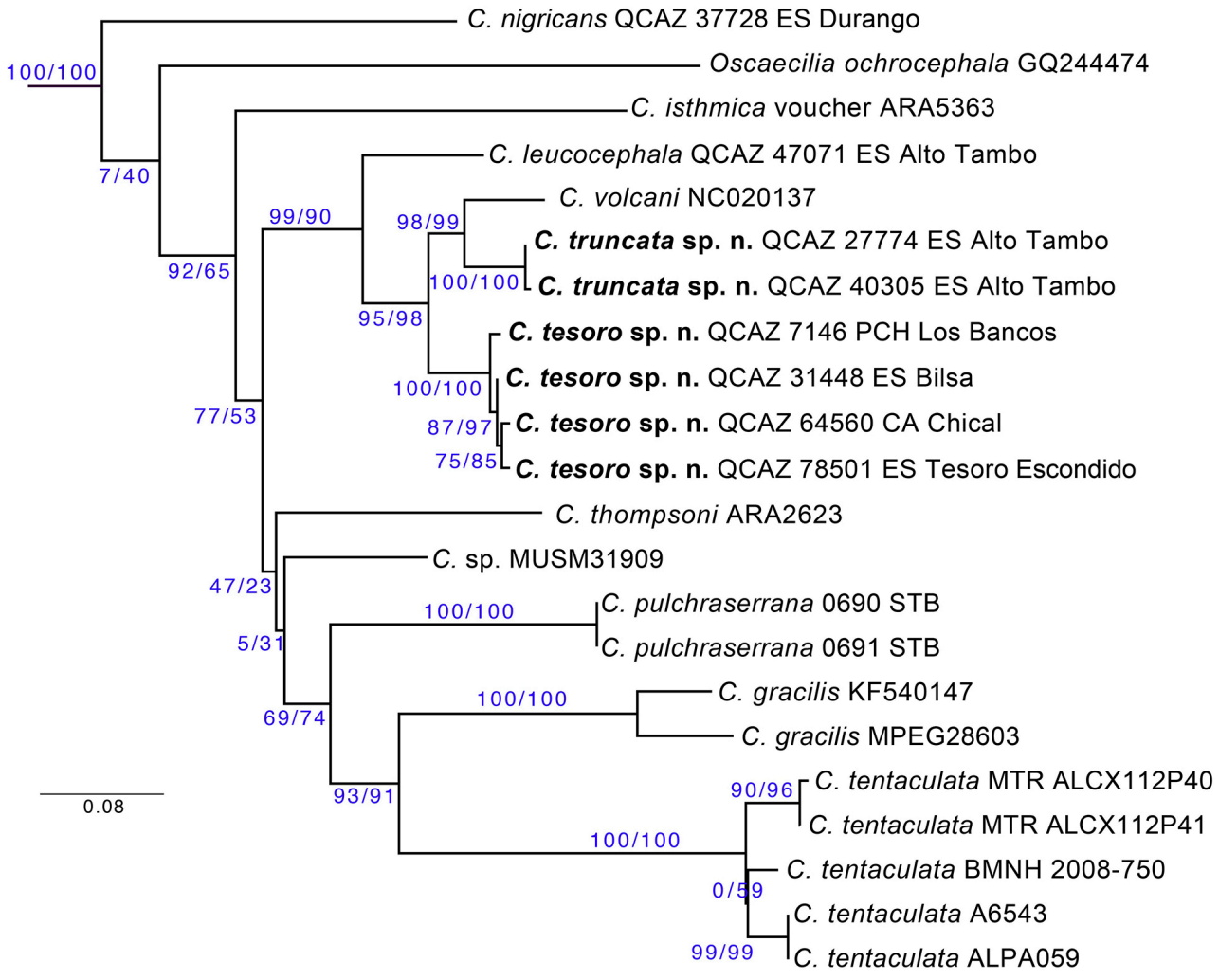

Figure 1. Maximum likelihood tree inferred from a partitioned analysis of 12S rRNA, $tRNA^{Val}$ 16S rRNA, $tRNA^{Leu}$, ND1, $tRNA^{Ile}$ and $tRNA^{Gln}$ showing phylogenetic relationships of *Caecilia* species. SH-aLRT support (before slash) and ultrafast approximation bootstrap support (after slash) are shown as percentages on branches. The outgroups are not shown. The species name is followed by the voucher collection number; if voucher number was not available, we give the GenBank accession for one of the genes. For the two new species, we also provide geographic information. Abbreviations: CA = Provincia Carchi, ES = Provincia Esmeraldas, PCH = Provincia Pichincha.

Table 5. Ct-derived measures of species of *Caecilia* skull bones and openings. Measurements are in mm. Bone length of right/left body side in upper row, widths of right/left body side in lower row. *Ctr* = *C. truncata* sp. n. (QCAZ-A 27774), *Cte* = *C. tesoro* sp. n. (QCAZ-A 78501), *Cl* = *C. leucocephala* (QCAZ-A 47071), *Cn* = *C. nigricans* (QCAZ-A 37728), *Ct* = *C. tenuissima* (QCAZ-A 23580), *Cg* = *C. guntheri* (QCAZ-A 15568), *Cp*1 = *C. pachynema* (QZAC-A 33235), *Cp*2 = *C. pachynema* (QCAZ-A 37733), *Cv* = *C. volcani* (KU 203035); ch = choanae; en = external naris; f = frontal; m = maxillopalatine; me = mesethmoid; np = nasopremaxillae; o = orbital opening; ob = os basale; p = parietal; sq = squamosal; ta = tentacular foramina; s = skull.

	Ctr	*Cte*	*Cl*	*Cn*	*Ct*	*Cg*	*Cp*1	*Cp*2	*Cv*
ch	1.12/1.11	1.76/1.8	0.46/0.47	0.9/0.91	0.77/0.73	1.46/1.48	0.97/0.96	1.14/1.1	0.77/0.72
	1.08/1.1	1.27/1.26	0.4/0.42	0.69/0.73	0.61/0.62	1.26/1.36	0.7/0.62	0.91/1.01	0.72/0.65
en	1.09/1.13	1.65/1.6	0.51/0.49	0.75/0.73	0.64/0.68	1.33/1.39	0.76/0.7	0.73/0.83	0.5/0.5
	1.19/1.18	1.47/1.49	0.49/0.48	0.76/0.83	0.66/0.59	1.49/0.88	0.62/0.6	0.94/0.9	0.47/0.48
f	3.99/4.01	7.39/7.45	1.5/1.47	4/3.8	2.28/2.11	5.82/6.29	2.58/3.1	3.78/4.18	2.71/2.63
	2.45/2.46	3.77/3.73	1.0/1.07	1.92/2.01	1.49/1.57	2.58/2.73	1.38/1.35	2.03/2.1	1.7/1.65
m	5.27/5.31	8.33/8.25	1.46/1.58	3.3/3.04	2.39/2.4	6.73/6.78	2.81/2.8	4.00/4.00	2.74/2.86
	1.98/1.91	2.45/2.39	0.49/0.5	1.05/0.95	1.26/1.27	2.39/2.32	1.41/1.24	2.12/2.3	1.54/1.58
me	4.19	4.72	0.88	2.2	1.99	4.53	1.99	2.2	2.18
	1.16	1.65	0.19	0.52	0.33	0.69	0.3	2.29	0.81
np	4.42/4.61	7.64/7.55	1.83/1.9	3.66/3.71	2.45/2.44	6.06/5.75	2.61/2.56	3.91/4.02	2.47/2.45
	2.71/2.57	4.27/4.03	0.8/0.87	1.67/1.74	1.25/1.27	2.9/2.89	1.43/1.42	1.95/1.89	1.65/1.52
ob	8.61	14.4	3.97	6.66	5.23	9.31	6.1	7.7	4.48
	5.76	10.59	2.25	4.17	2.97	7.61	3.48	4.73	3.61
o	0.76/0.79	1.17/1.11	0.21/0.22	0.48/0.51	0.55/0.47	1.21/1.23	0.66/0.73	0.72/0.74	0.62/0.66
	0.79/0.71	1.03/0.94	0.16/0.21	0.35/0.37	0.42/0.38	0.96/0.99	0.53/0.59	0.69/0.68	0.57/0.52
p	4.34/4.42	7.09/6.64	2.04/2.23	3.29/3.34	2.51/2.34	4.43/4.26	3.6/3.57	4.05/4.03	3.05/2.97
	2.46/2.5	4.41/4-39	1.32/1.38	1.92/1.98	1.45/1.5	3.04/2.97	1.54/1.58	2.19/2.16	1.91/1.89
sq	3.67/3.65	3.27/3.23	1.36/1.3	2.99/3.03	2.13/2.2	4.91/4.76	2.71/2.78	3.55/3.55	2.4/1.18
	2.27/2.3	7.62/7.54	0.51/0.57	1.38/1.37	1.41/1.52	3.85/3.97	1.42/1.32	2.62/2.64	1.86/1.89
ta	0.6/0.62	0.88/0.93	0.23/0.29	0.38/0.34	0.37/0.42	0.79/0.8	0.57/0.44	0.54/0.58	0.36/0.4
	0.54/0.60	1.1/1.16	0.21/0.39	0.39/0.30	0.3/0.26	0.9/0.83	0.40/0.48	0.57/0.61	0.29/0.26
s	13.12	24.11	5.68	10.66	7.66	17.8	9.13	12.78	9.05
	8.83	14.65	3.28	6.33	4.45	11.57	5.09	8.1	5.25

C. subterminalis (170/16), and *C. wilkinsoni* (190–195/51–71), or an elevated number of primary annular grooves and an unusually large number of secondary annular grooves, *C. perdita* (133–152/64–83). All remaining five species, including the two new species, have relatively few primary (107–133) annular grooves. Between these five species, *C. leucocephala* stands out by their large number of secondary annular grooves (32–52; Table 3).

Obvious differences in body shape were observed between several species. *Caecilia tenuissima* (range of body length/body width: 81), *C. guntheri* (33–63), *C. nigricans* (33–80), and *C. wilkinsoni* (66–75) are relatively slender species. *Caecilia perdita* (34–56) shows a very slender head and a considerably widened terminal end. *Caecilia subterminalis* (34), *C. volcani* (30–37), *C. leucocephala* (32–45), *C. tesoro* sp. n. (35–40), and *C. truncata* sp. n. (23–43) are moderately robust to robust species (see Table 3 for summary). Adult *C. truncata* sp. n. exhibits a particularly truncated snout shape, whereas all other species show more or less rounded snouts (Fig. 14). Regarding the relative size of head and body, *C. tenuissima* stands out by a very slender appearance. *Caecilia pachynema* in contrast is most often very robust shaped (49–108). However, the huge range in body size ratio may be attributable to sex, age, or body condition differences, but also could indicate the existence of more than one species being involved. It seems likely that the body shape of *C. pachynema* may change with age. Juveniles are very slender (e.g., QCAZ-A 46938) but show the same colour pattern as adults (see below). In QCAZ-A 33235 the colour pattern was less distinct.

Although in several *Caecilia* species colouration in life is not documented and colour pattern may have faded in preservation, we observed few, but distinct differences in colour between some species. Most species are more or less uniformly dark grey, brown or black, often with slightly lighter heads and ventral surfaces, the latter then sometimes with a darker median region (Table 3). In life, the grey or black skin of preserved species has been usually reported as blueish grey or dark purple (e.g. Taylor 1968, 1974; own observations). Other lighter, whitish, or yellowish areas are often observed bordering the lips, as well as the region around eyes, nostrils, tentacular aperture, and the vent. A distinct colour pattern has been documented for *C. subterminalis*, showing continuous yellow or cream colouration with lateral stripes on head and body (Taylor 1968, 1974). *Caecilia tenuissima* is almost uniform dark grey. *Caecilia pachynema* possess a unique colour-

ation. They are uniform light grey on back and venter, clearly demarcated by straight and broad yellowish ventrolateral bands. The borders of annular grooves have dark grey markings (colour as on back and venter). In QCAZ-A 33235 this pattern was less distinct. The specimen is very long and slender, and at first glance seems uniform grey. Only when it starts to dry do the light ventrolateral bands became visible. *Caecilia truncata* sp. n. is mostly grey but shows lighter lateral bands. Large individuals of *C. tesoro* sp. n., exhibit a purple-grey head and yellowish cream body with irregular dark patterning, resembling some *Epicrionops* species more closely than other *Caecilia* (compare figures in Fernández-Roldán et al. 2022, Ron et al. 2024).

Osteology

All scanned *Caecilia* skulls were robust and heavily ossified; stegokrotaphic (temporal foramen closed) (Figs 2, 4, 6); orbit open; mouth subterminal with large backward curved, pointed monocuspid teeth, arranged in four series. Teeth numbers were similar between species and showed slight intra-specific variation (Table 7). Remarkably different from other species, however, were the high number of vomeropalatine teeth in *C. tesoro* sp. n., the high number of outer mandibular teeth in *C. truncata* sp. n.; the high number of inner mandibular teeth in *C. occidentalis* and *C. subterminalis*, and the low number of outer mandibular teeth in *C. wilkinsoni* (Table 7).

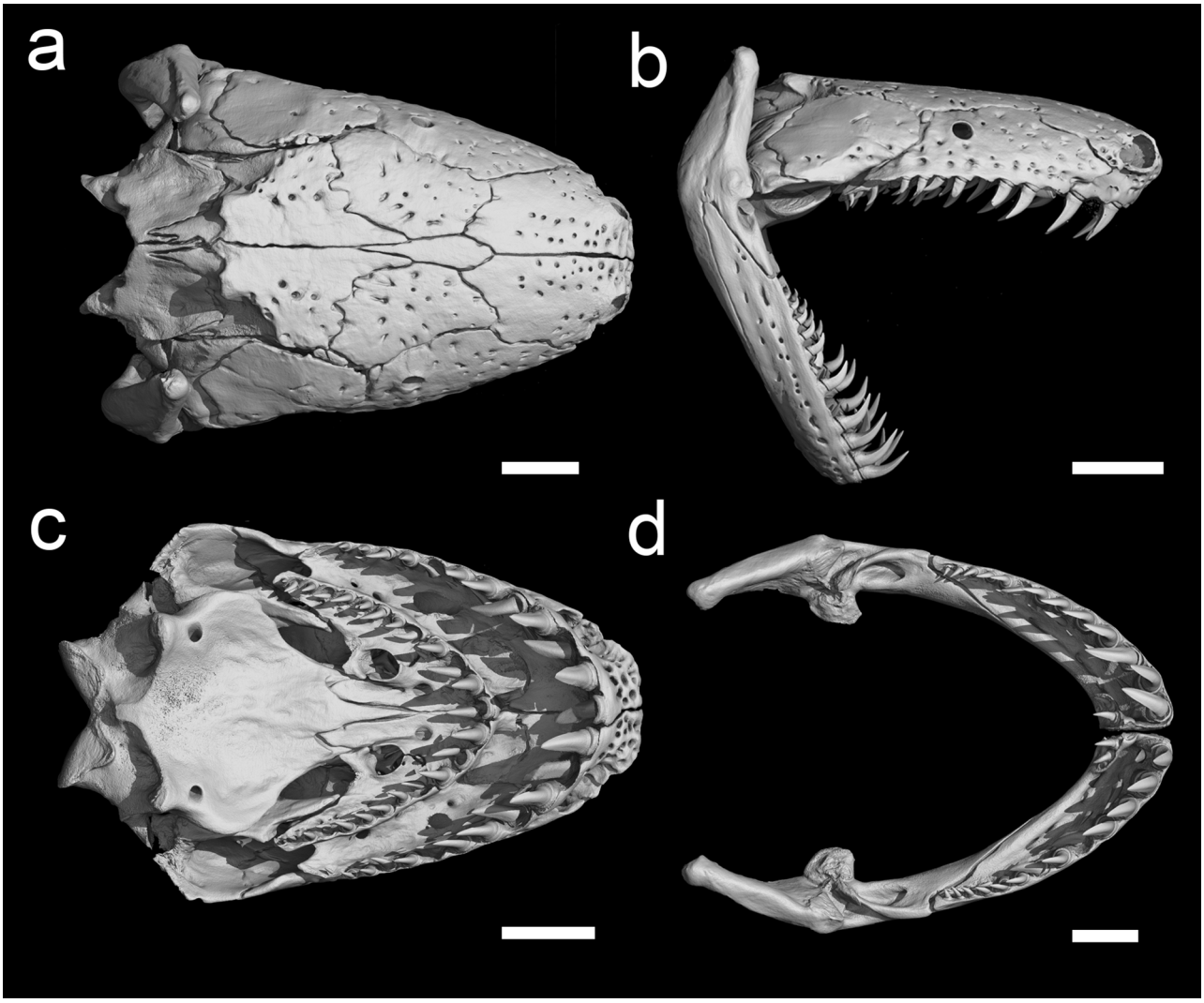

Figure 2. Ct-scan of the head of the *Caecilia tesoro* sp. n. holotype (QCAZ-A 78501). Shown are head in dorsal (a), and lateral view (b), upper mandible and roof of mouth in ventral (c), and lower mandible in dorsal view (d); scale for different sub-figures: a = 3 mm, b = 4.5 mm, c = 4 mm, d = 3 mm.

Table 6. Indices of length versus width relation of *Caecilia* skull bones and openings, give are species names and values: right/left for paired bones and openings. *Ctr* = *C. truncata* sp. n. (QCAZ-A 27774), *Cte* = *C. tesoro* sp. n. (QCAZ-A 78501), *Cl* = *C. leucocephala* (QCAZ-A 47071), *Cn* = *C. nigricans* (QCAZ-A 37728), *Ct* = *C. tenuissima* (QCAZ-A 23580), *Cg* = *C. guntheri* (QCAZ-A 15568), *Cp*1 = *C. pachynema* (QZAC-A 33235), *Cp*2 = *C. pachynema* (QCAZ-A 37733), *Cv* = *C. volcani* (KU 203035); ch = choanae; en = external naris; f = frontal; m = maxillopalatine; me = mesethmoid; np = nasopremaxillae; o = orbital opening; ob = os basale; p = parietal; sq = squamosal; ta = tentacular foramina; skull (length).

	ch	en	f	m	me	np	ob	o	p	sq	ta	skull
Ctr	1.04/1	0.92/0.96	1.63/1.63	2.66/2.78	3.61	1.63/1.74	1.49	0.96/1.11	1.76/1.77	1.62/1.59	1.11/1.03	1.49
Cte	1.39/1.43	1.12/1.07	1.96/2	3.4/3.45	2.86	1.79/1.87	1.36	1.14/1.18	1.61/1.51	0.43/0.43	0.8/0.8	1.65
Cl	1.13/1.12	1.04/1.02	1.43/1.37	2.98/3.16	4.63	2.08/2.18	1.76	1.31/1.05	1.55/1.62	2.67/2.28	1.10/0.74	1.73
Cn	1.3/1.25	0.99/0.88	2.08/1.89	3.14/3.20	4.23	2.19/2.13	1.60	1.37/1.38	1.71/1.69	2.17/2.21	0.97/1.13	1.68
Ct	1.26/1.18	0.97/1.15	1.53/1.34	1.9/1.89	6.03	1.96/1.92	1.76	1.31/1.24	1.73/1.56	1.51/1.45	1.23/1.62	1.72
Cg	1.16/1.09	0.89/1.58	2.26/2.19	2.82/2.92	6.57	2.09/1.99	1.22	1.26/1.24	1.46/1.43	1.28/1.20	0.88/0.96	1.54
*Cp*1	1.39/1.55	1.23/1.17	1.87/2.3	1.99/2.26	6.63	1.83/1.8	1.75	0.9/1.24	2.34/2.26	1.91/2.11	1.19/0.92	1.79
*Cp*2	1.25/1.09	0.78/0.92	1.86/1.99	1.89/1.74	7.86	2.01/2.13	1.63	1.04/1.09	1.85/1.87	1.35/1.34	0.95/0.95	1.58
Cv	1.07/1.11	1.06/1.06	1.59/1.59	1.78/1.81	3.05	1.5/1.61	1.24	1.09/1.27	1.6/1.57	1.29/1.15	1.24/1.54	1.72

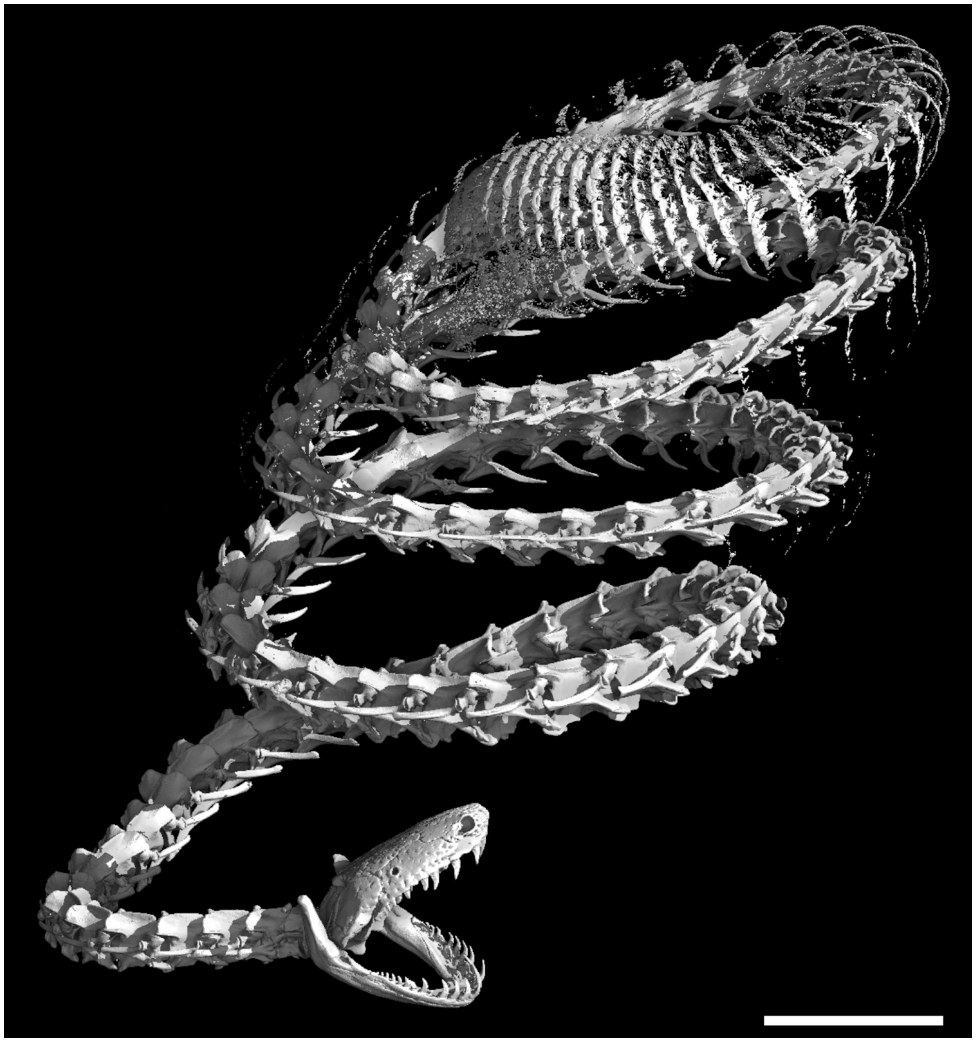

Figure 3. Ct-scan of the entire *Caecilia tesoro* sp. n. holotype (QCAZ-A 78501). The 'foggy' voxels around the animal, in particular around its caudal end, indicate the distribution and density of dermal scales. Scale = 20 mm.

Table 7. Teeth numbers of *Caecilia* species. Values from left and right body side; third values indicate azygous median teeth. Counts from Taylor (1968) are maximum values and partly include not fully erupted teeth; ts = this study, counted from ct-scans. Collection numbers of museum vouchers shown in parenthesis.

Caecilia species	Premaxillary & maxillary	Vomero–palatine	Outer mandibular (dentary)	Inner mandibular (splenial)	Source
C. guntheri	12–1–12; 11–1–11	11–1–11; 12–10	11–11	2–2; 4–3	Taylor (1968), ts (QCAZ-A 15568)
C. leucocephala	8–1–8; 9–1–8	10–1–10; 12–11	11–1–11; 10–10	2–2	Taylor (1968), ts (QCAZ-A 47071)
C. nigricans	12–1–12; 10–1–10	12–1–12; 10–9	12–12; 10–11	3–3; 2–2	Taylor (1968), ts (QCAZ-A 37728)
C. pachynema	10–1–10; 8–1–9 / 8–1–8	10–1–11; 11–11 / 10–10	11–11; 10–10 / 10–9	3–3; 2–2 / 3–3	Taylor (1968), ts (QZAC-A 33235, QCAZ-A 37733)
C. perdita	9–1–9	10–10	10–10	2–2	Taylor (1968)
C. subterminalis	9–1–9	10–1–10	11–11	4–4	Taylor (1968)
C. tesoro sp. n.	12–1–11	13–13	13–13	2–2	ts (QCAZ-A 78501)
C. tenuissima	11–?; 10–1–11	11–7; 12–11	9–?; 12–12	2–2; 2–3	Taylor (1973), ts (QCAZ-A 23580)
C. truncata sp. n.	11–1–11	11–12	15–15	2–2	ts (QCAZ-A 27774)
C. wilkinsoni	7–1–8; 6–6	10–1–8; 6–7	8–8; 7–8	2–2	Fernández-Roldán & Lynch (2023)
C. volcani	12–1–12; 9–1–9; 10–1–10; 8–8; 9–10	10–1–10; 9–1–9; 8–1–8; 7–7; 11–10	11–11; 10–10; 9–9; 9–8; 8–8	2–2; 1–1	Taylor (1969a), Summers & Wake (2001), ts (KU 203035)

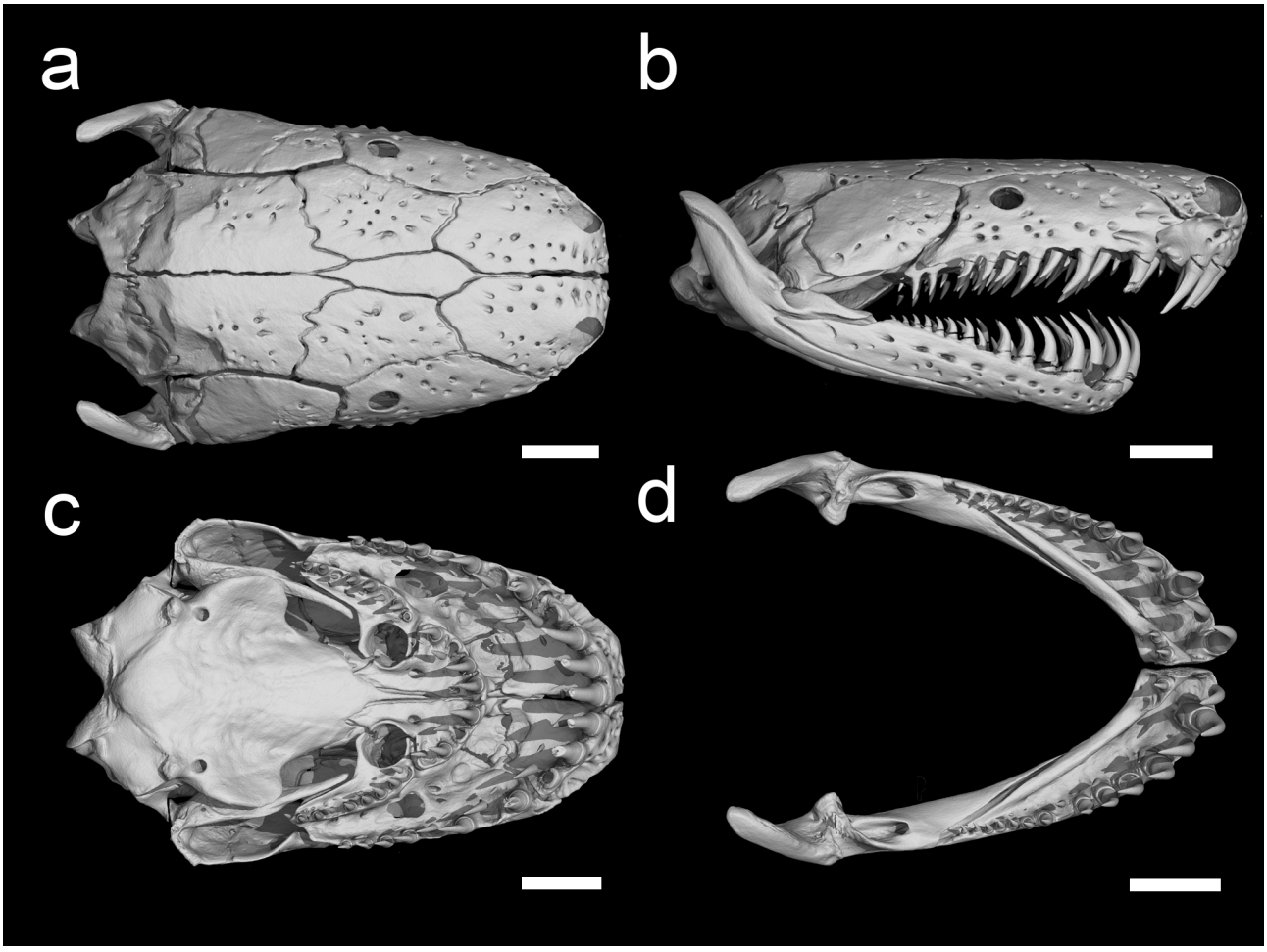

Figure 4. Ct-scan of the head of the *Caecilia truncata* sp. n. holotype (QCAZ-A 27774). Shown are head in dorsal (a), and lateral view (b), upper mandible and roof of mouth in ventral (c) and lower mandible in dorsal view (d); scale = 2 mm.

The skulls of the scanned species differed most notably in size and shape of the mesethmoid, and in the relative size of some other bone pairs (Figs 2, 4, 6 and Tables 5, 6). The skull of *C. tesoro* sp. n. is broader, more massive and slightly V-shaped, compared to *C. nigricans*, *C. leucocephala,* and *C. volcani* (Figs. 2, 6). In *C. tesoro* sp. n. the mesethmoid is long, narrow, and kite-shaped (length/width: 2.86; Fig. 6, Table 6). It extends anteriorly, with the broadly rounded end, to about ¼ between nasopraemaxillaries; posteriorly, the pointed end reaches for about ⅓ of its length in-between the parietals (Fig. 2). It therewith resembles the state in *C. volcani* (3.05; Fig. 21 in Taylor 1969b), *C. guntheri,* and *C. pachynema* (Fig. 6). In the latter two species the mesethmoid is however, much narrower (6.57 and 6.63, 7.86, respectively). In *C. truncata* sp. n. the mesethmoid is also kite-shaped but broader (3.61), and the posterior end extends less deep in-between the parietals (Fig. 4), which have less pronounced anterior processes, compared to *C. tesoro* sp. n. In *C. nigricans* (4.23), *C. leucocephala* (4.63) and *C. tenuissima* (6.03) the mesethmoid is shorter and narrower compared to the new species, of almost parallel shape, and not (*C. leucocephala*) or only slightly (*C. nigricans, C. tenuissima*) extending in-between the parietals in others (Fig. 6; and *C. nigricans* Fig. 17 in Taylor 1969b). Compared to *C. nigricans, C. leucocephala* and *C. tenuissima*, the skull shape of *C. truncata* sp. n. is the most straight and parallel, almost rectangular, the tip clearly truncated. In contrast, *C. tesoro* sp. n. shows the most triangular shaped skull, with a particularly broad posterior end (Figs 2, 4, 6). Further skull measures were also taken (summarized in Tables 5 and 6).

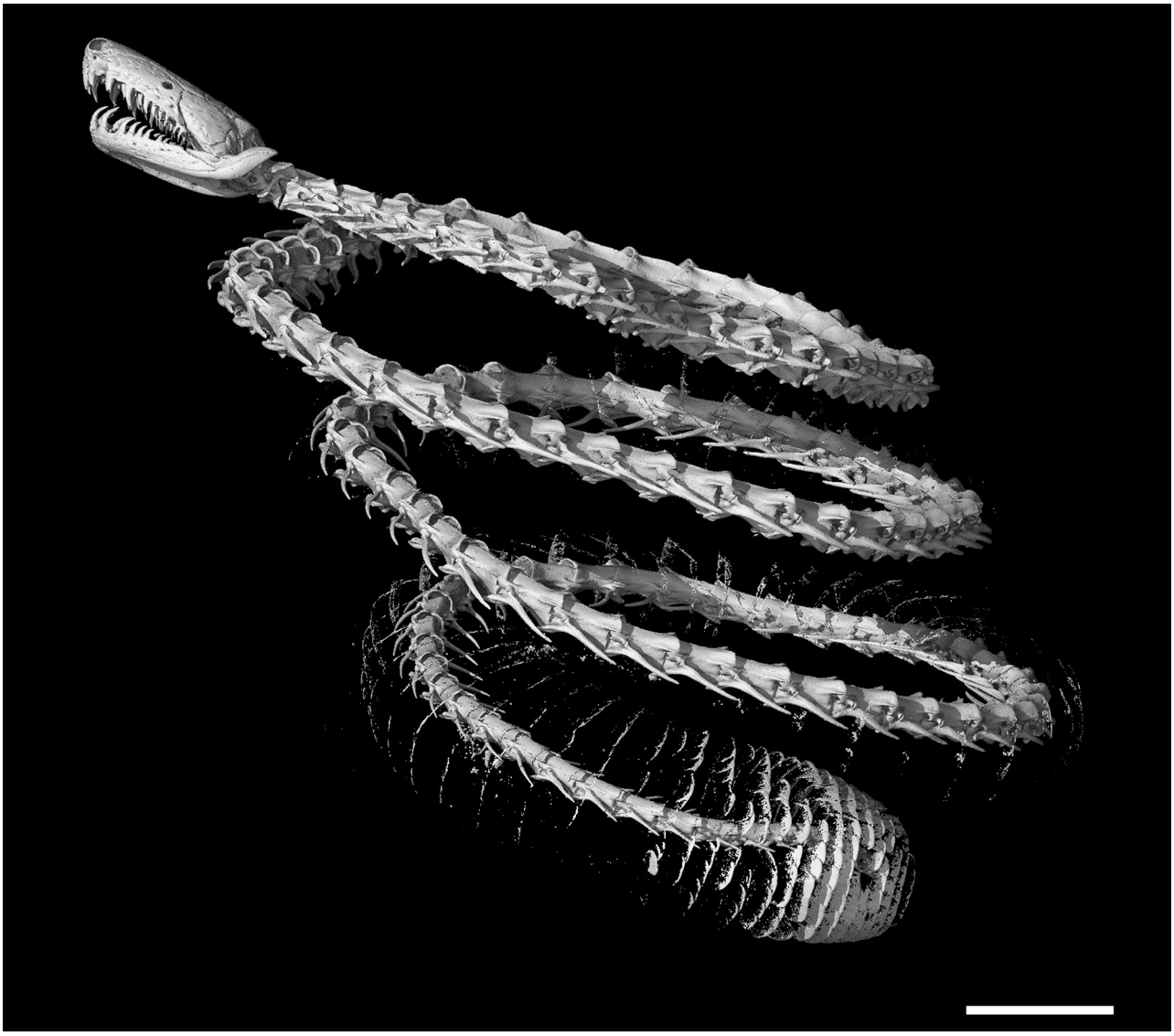

Figure 5. Ct-scan of the entire holotype *Caecilia truncata* sp. n. holotype (QCAZ-A 27774). The 'foggy' voxels around the animal, in particular around its caudal end, indicates the distribution and density of dermal scales. Scale = 9 mm.

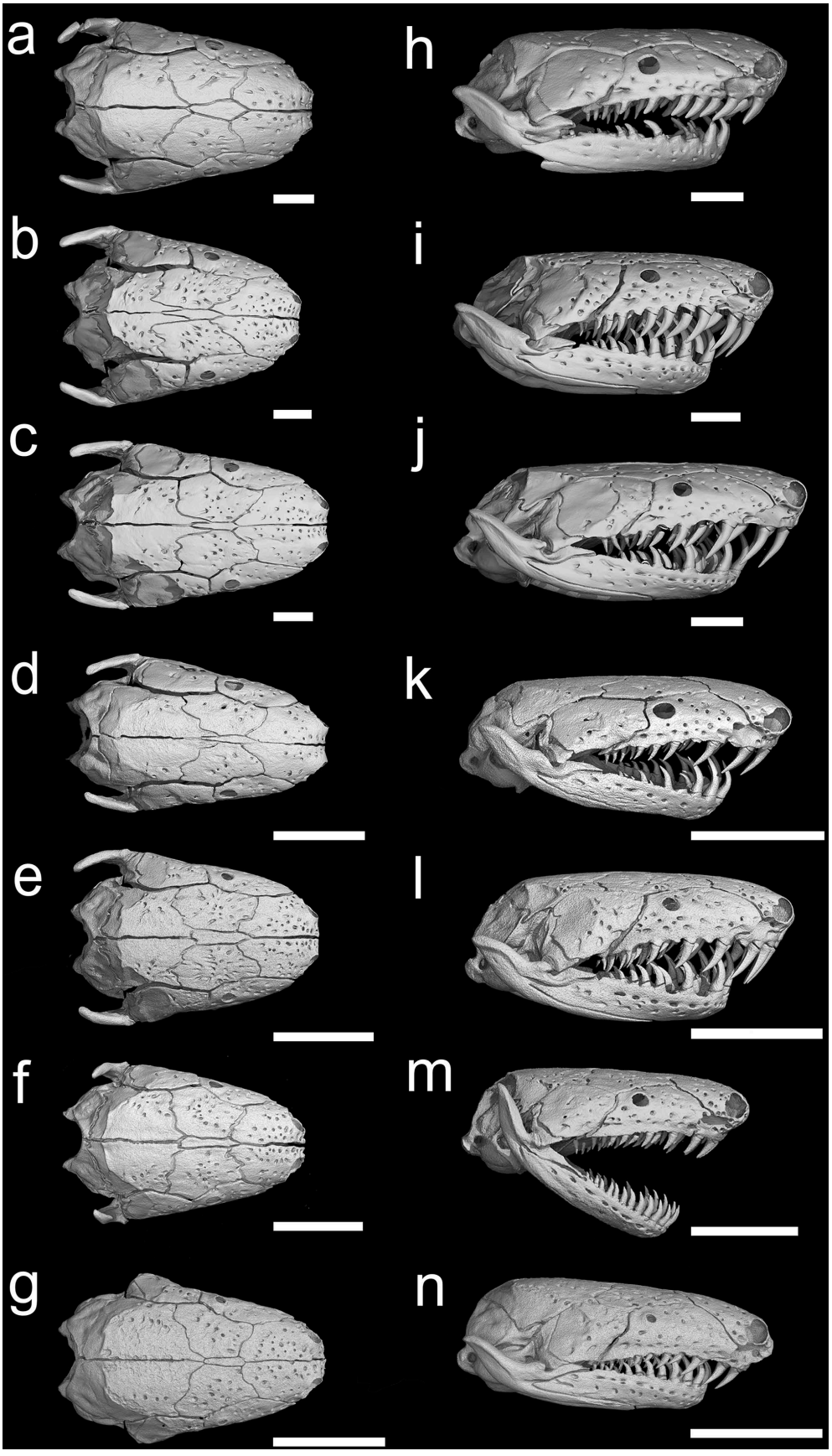

Figure 6. Ct-scans of the heads of western Ecuadorian *Caecilia* species and *C. volcani* (Central America) in dorsal (left) and lateral (right) views; (a, h) *C. volcani* (holotype; KU 203035); (b, i) *C. guntheri* (QCAZ-A 15568); (c, j) *C. pachynema* (QCAZ-A 37733) and (d, k) *C. pachynema* (QZAC-A 33235); (e, l) *C. nigricans* (QCAZ-A 37728); (f, m) *C. tenuissima* (QCAZ-A 23580); (g, n) *C. leucocephala* (QCAZ 47071); for comparison with *C. tesoro* sp. n. (holotype; QCAZ-A 78501), and *C. truncata* sp. n. (holotype; QCAZ-A 27774) see Figures 2 and 4. Scale bars for sub-figures: a, b = 1.5 mm; c, d, l, m = 3 mm; e, f = 2 mm; g, n = 2.5 mm, h = 3.5 mm, i = 4 mm; j, k = 4.5 mm.

Another apparent interspecific difference in skull anatomy was the number of the usually symmetrically arranged skull openings (foramina) on the external surface. In the *C. tesoro* sp. n. and *C. truncata* sp. n. holotypes we counted 286 and 213 openings, respectively. Respective numbers were 145 in *C. volcani* (KU 203035), 188 (QCAZ-A 37733) and 242 (QZAC-A 33235) in *C. pachynema*, 242 in *C. leucocephala* (QCAZ-A 47071), 272 in *C. tenuissima* (QCAZ-A 23580), 255 in *C. nigricans* (QCAZ-A 37728), and 348 in *C. guntheri* (QCAZ-A 15568).

The two new species (*C. tesoro* sp. n.: 124–126; *C. truncata* sp. n.: 128) and *C. leucocephala* (126) had a similar, relatively low number of vertebrae (Figs 3, 5), significantly differing from vertebrae numbers in *C. nigricans* (188), *C. occidentalis* (225), *C. pachynema* (168–215; lower numbers in specimens labelled *C. buckleyi,* e.g. QCAZ-A 37733), *C. perdita* (155), and *C. tenuissima* (157–191) (Taylor 1968, 1974; Table 4). In *C. guntheri* (QCAZ-A 15568) we counted 133 vertebrae (Table 4).

In summary and although many character values overlapped in range interspecifically, our integrative taxonomic approach of combining molecular, morphological, and osteological data, confirmed the specific distinctiveness of the two proposed new species, which are formally described in the following section.

Taxonomy

Caecilia tesoro sp. n.

ZooBank LSID: urn:lsid:zoobank.org:act:8B2430B2-9302-493E-87FA-A17FD49F9642
(Figs 2, 3, 7–11)

Holotype: QCAZ-A 78501, an adult female from Ecuador, Provincia Esmeraldas, Tesoro Escondido Reserve, N 0.54033, W 79.14432, 328 m a.s.l., 22 April 2023, at 5:30 pm (with sunlight, before dusk), moving on the ground of a regenerating former cacao plantation, after heavy rain, coll. H. L. Velez Giler and S. Bock.

Paratypes: All specimens are from Ecuador. QCAZ-A 31448, juvenile, Provincia Esmeraldas, Bilsa, N 0.34367, W 79.71618, 510 m a.s.l., 28 January 2006, at 10:00 pm, coll. W. Chun; QCAZ-A 7146 an adult female, Provincia Pichincha, 5 km from Los Bancos, Quito-Los Bancos road, N 0.02199, W 78.85099, 1200 m a.s.l., 5 February 1995, coll. E. Patzel; QCAZ-A 64560 an adult female, Provincia Carchi, Chical–Guanchal road, N 0.92470, W 78.19889, 1420 m a.s.l., 8 August 2016, coll. D. Nuñez, D. Almeida, K. Nusirquia, S. Guamán and K. Hinojosa.

Diagnosis: Member of the family Caeciliidae based on its phylogenetic position and the anatomical definition by Wilkinson et al. (2011), i.e., stapes imperforate, inner mandibular teeth present, eyes surrounded or covered by maxillopalatine, all teeth monocuspid, as well as by molecular data. Member of the genus *Caecilia* based on the definition by Wilkinson et al. (2011) i.e., eyes visible externally, not covered by bone.

Robust, large *Caecilia* characterized by the combination of the following characters: (1) body length up to 790 mm, (2) larger specimens with unique colour pattern with grey head and posterior part of body, remaining body yellowish-cream to caramel with irregular darker markings (presumably scars), smaller individuals almost uniformly dark grey with or without light spotting or ventrolateral light gray bands, (3) absence of terminal shield, (4) visible eye, not covered by bone, (5) 117–121 primary folds (CV = 1.58), (6) 14–18 secondary folds (CV = 34.5), (7) lack of complete secondary folds, (8) 124–126 vertebrae.

Caecilia tesoro differs from other western Ecuadorian and south-western Colombian *Caecilia* species as follows (compare Table 3): adults larger (> 570 mm) than *C. leucocephala, C. perdita, C. subterminalis, C. tenuissima, C. truncata* sp. n., and *C. volcani* (all < 505 mm); body more slender (TL/BW: 35–40) than (most) *C. truncata* sp. n. and *C. volcani* (all in-between 22–43); body more robust (smaller TL/BW ratio) than *C. nigricans* (most), *C. pachynema*, *C. perdita* (some), *C. tenuissima*, and *C. wilkinsoni* (> 44); less primary annular

Figure 7. Holotype of *Caecilia tesoro* sp. n. (QCAZ-A 78501) in life (TL = 790 mm), illustrating head shape and the very unusual colouration for a *Caecilia* species (compare Figs 10, 11, 15).

grooves (117–121) than *C. nigricans, C. pachynema, C. perdita, C. subterminalis, C. tenuissima*, and *C. wilkinsoni* (all > 133); more secondary annular groves (14–18) than *C. pachynema, C. tenuissima,* and *C. truncata* sp. n. (all < 11); less secondary annular groves than *C. leucocephala, C. nigricans, C. perdita, C. volcani* (most), and *C. wilkinsoni* (> 27); the absence of complete secondary annular grooves, these are present in at least some or most: *C. guntheri, C. leucocephala, C. nigricans, C. perdita, C. tenuissima, C. volcani,* and *C. wilkinsoni*; the absence of a terminal shield distinguishes *C. tesoro* from *C. leucocephala, C. nigricans, C. pachynema, C. perdita, C. subterminalis*, and *C. tenuissima*. Finally, large *C. tesoro* have a unique colour pattern, not shared by any other described *Caecilia* species (see above).

Description of the holotype: Large adult female with a TL of 790 mm; TL/BW ratio is 40.3; robust body almost round in cross-section; HL/HW ratio 1.6; head narrower than body; snout rounded in lateral and dorsal view, slightly truncated in dorsal view; lower jaw widely rounded in ventral view; snout tip projects 4.5 mm ahead of anterior end of lower jaw; eyes very small, diameter 1.6 mm, difficult to

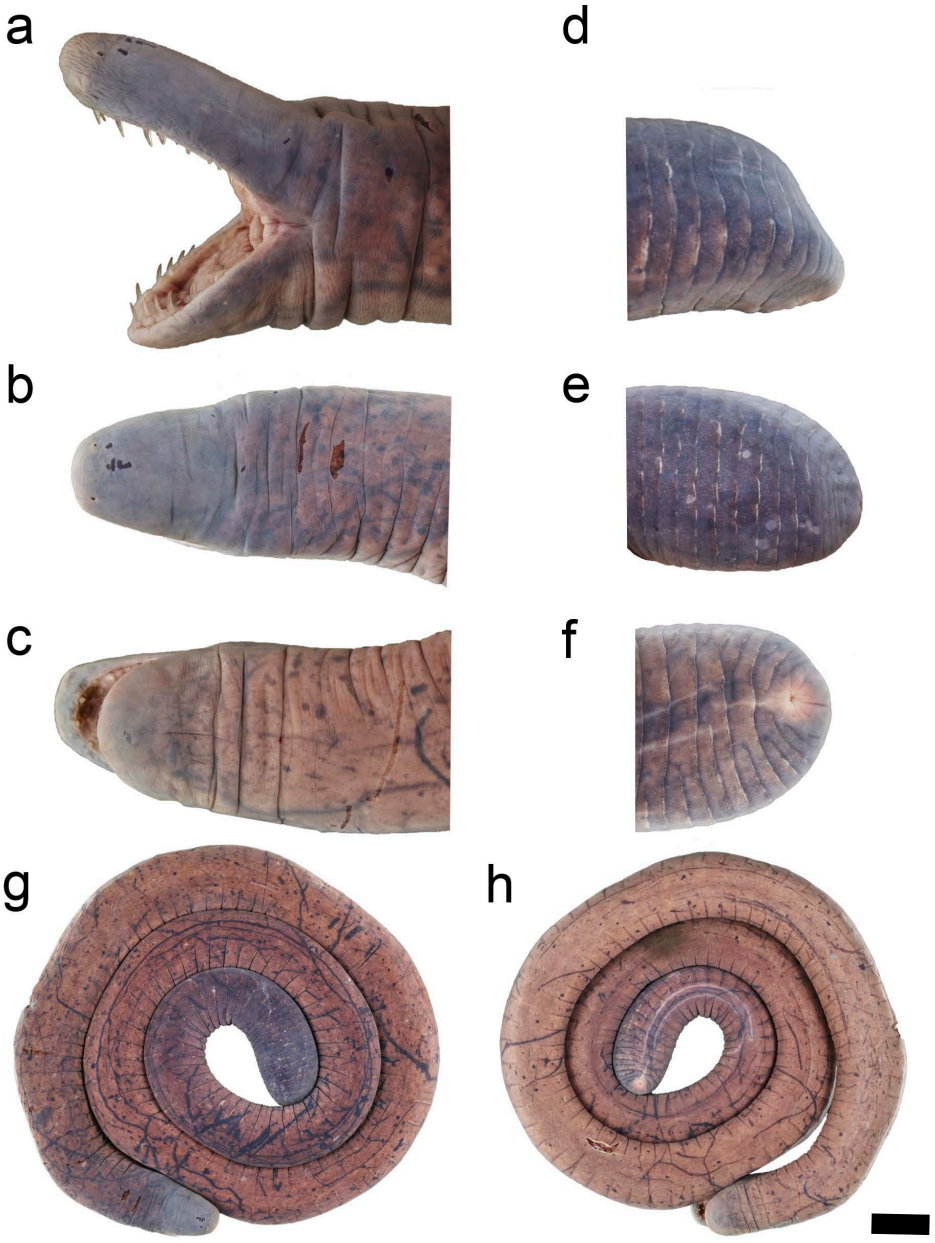

Figure 8. Preserved holotype of *Caecilia tesoro* sp. n. (QCAZ-A 78501); head in lateral (a), dorsal (b), and ventral (c) views; tail in lateral (d), dorsal (e), and ventral (f) views; and entire animal in dorsal (g) and ventral (h) views; scale bar for g, h = 1 cm.

see in preserved animal (distinct in life), positioned dorsolaterally in an open orbit, not covered by bone, visible externally in dorsal and lateral view; IOD slightly narrower than HW, HW/IOD 1.2; nares small, 0.6 mm and circular, positioned dorsally near anterior end of rostrum, visible in dorsal and lateral view; HW/IND ratio 2.1; tentacular aperture circular, positioned anteroventrally to nares, much closer to nares (3.4 mm) than to eye (10.9 mm), slightly elevated, not visible in dorsal view; ITD larger than IND, ITD/IND 1.4; tongue broad and fleshy.

First two nuchal collars, 7.8 and 8.4 mm, respectively, are longer than subsequent grooves (ca. 5.4 mm); body width slightly increases after 2nd nuchal collar and decreases towards the broadly rounded tail tip. Body with 121 complete primary annular grooves, and 15 secondary grooves, none of which is complete; secondary grooves all in posterior third of body; terminal shield absent; anal papillae absent; circular cloacal aperture (vent) surrounded by 13 denticulations, seven anterior and six posterior; cloaca opening round, slightly recessed, interrupting 5 annular grooves. Small opening (tissue extracted) ventrally between primary annular grooves 47–50. A summary of measurements is provided in Table 4.

Dermal scales in scale pockets, in single rows, starting at the 84th primary annular groove and extending to last primary groove (Fig. 3); very numerous and dense in last 5th of body; dermal scales taken towards tail tip small and rectangular to oval. Dermal scale surfaces measured from extracted scales were 2.64–3.59 mm and 2.97–3.04 mm (length and width); ranging from 0.036 to 0.024 mm in height (Fig. 9a, b). Small, subspherical, subdermal scales present, but rare and irregularly distributed along midbody.

Skull robust and heavily ossified (Fig. 2), almost triangular in dorsal view, broad posteriorly and broadly rounded, slightly truncated snout tip; total skull length 24.1 mm, maximum width 14.7 mm, with 286 foraminae; orbit open; mouth subterminal with large backward curved, pointed monocuspid teeth, arranged in four dental series, premaxillary and maxillary: 12-1-11, vomeropalatine: 13-13, outer mandibular: 13-13, inner mandibular row: 2-2; choanae oval, maximum diameter 1.2 mm; less than half the greatest distance between them, 2.8 mm.

Nasopremaxillae trapezoidal in shape, in dorsal view, almost twice as long as wide, with large external nares (1.65 mm) and tentacular foramina (0.88 mm); posterior

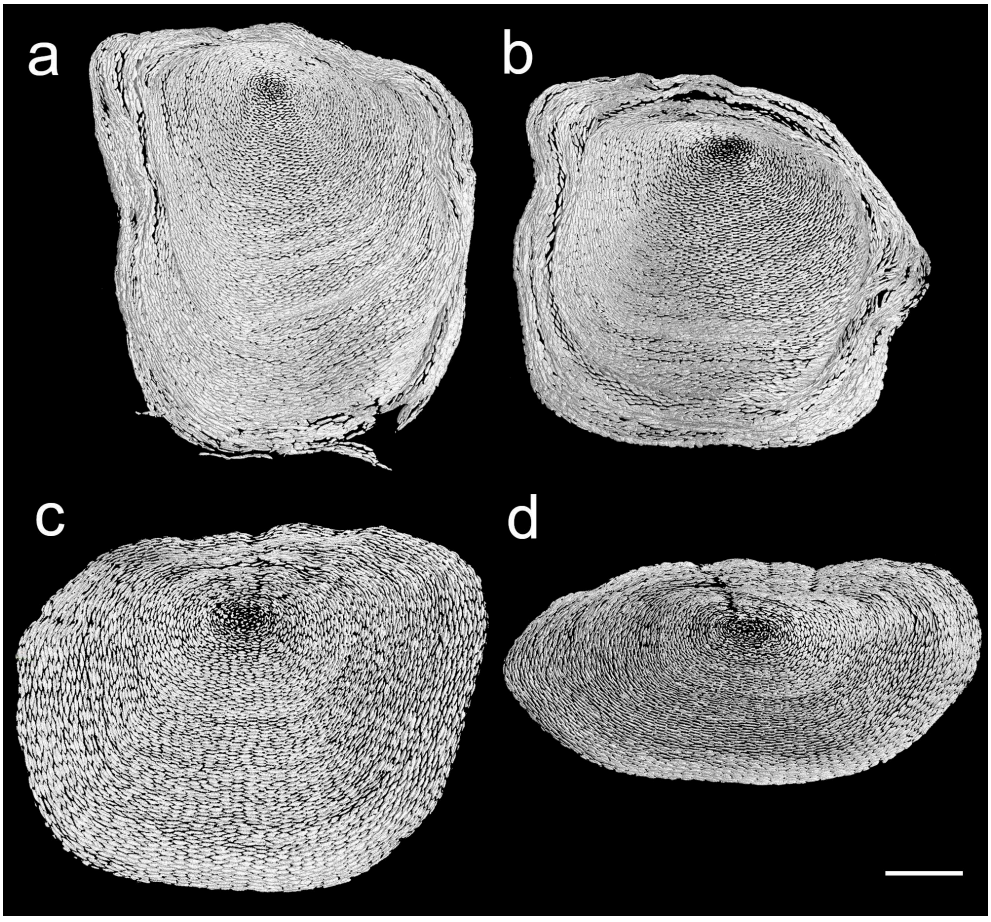

Figure 9. Ct-scans of dermal scales from the new *Caecilia* species; (a, b) *C. tesoro* sp. n. (holotype; QCAZ-A 78501); (c, d) *C. truncata* sp. n. (holotype; QCAZ-A 27774). Scale bars for subfigures: a = 0.65 mm, b = 0.45 mm, c, d = 0.35 mm.

Figure 10. Paratypes of *Caecilia tesoro* sp. n. in live (a; QCAZ-A 64560) and preservative (b; QCAZ-A 31448), illustrating variation in colour pattern (compare Figs 7 and 11, as well as Supplementary Videos 1 + 2).

part of nasopremaxillae separated mid-dorsally by broadly rounded end of longish (47 mm), narrow (17 mm), kite-shaped mesethomid, bordered by posteriorly diverging frontals, posteriorly separating for about ⅓ of lengths the anterior part of parietals; frontals slightly smaller than nasopremaxillae, about twice as long as wide; parietals slightly shorter, almost triangular shaped; 126 vertebrae (Tables 5–6).

In life, anterior of head violet-grey, body terminus dark grey with lighter marbling; body colour changes abruptly posterior to corners of mouth to yellowish-caramel with irregular dark grey to black stripes and spots; disc cream coloured (Fig. 7). In preservative, after 6 months in 75% ethanol, the violet-grey colouration is faded to grey (head and posterior body), and the yellowish-caramel has become light brown with dark patterning (rest of the body; Fig. 8).

Variation: All paratypes were smaller than the holotype, but have similar body proportions, number of vertebrae (124–126), primary (117–121) annular grooves, secondary (14–18) annular grooves. The available information suggests that there is ontogenetic or geographic variation in colouration. In preservative, the smallest individual (QCAZ-A 31448) is dark-brown to brown-purple with some clear spotting (Fig. 10b). Colour in life of the only paratype for which this data is available (QCAZ-A 64560) is notably different from that of the holotype. It shows a bicolour pattern consisting of dark grey dorsum and light grey ventrolateral bands with a sharp colour transition along mid-flank. In preservative, it has a uniform dark grey back and medium venter, and a light-yellow disk, ventrolaterally it is slightly lighter coloured with dark annular grooves, resembling a faded *C. pachynema*.

Thus, all paratypes are distinctly darker than the holotype, which is the largest specimen. Photos and videos of other, presumably conspecific, large individuals are similar in colour to the holotype (Ortega-Andrade et al. 2010; www.instagram.com/p/BjiaupcFts9/; www.instagram.com/p/B4izjPiAP-4/; www.instagram.com/reel/CsVBMjxNAl5/?igshid=MzRlODBiNWFlZA==; Instagram accounts checked on 9 February 2024). In the Tesoro Escondido (N 0.5552, W 79.1728) and Canandé Reserves (N 0.5263, W 79.2130) we also observed two large, non-vouchered, non-sexed individuals with that colour pattern (see below, Fig. 11 and Supplementary Materials). We thus are confident that the colouration of the holotype is characteristic for its size and/or sex and darker colouration may be characteristic of juvenile and subadult individuals.

Figure 11. Living *Caecilia tesoro* sp. n. (specimen not collected) from old growth forest in the Canandé forest reserve; see also Video 1 in Supplementary Materials. Photo extracted from video provided by D. V. Loor Bermeo.

In the paratype QCAZ-A 64560, the vent is surrounded by 14 denticulations, 7 anterior and 7 posterior. Snout shape in dorsal view broadly rounded, tentacles below nostrils, nostrils slightly slit-shaped, minute eyes on level with nares, positioned laterally, difficult to see from dorsal view, tentacle bases elevated, slightly triangular, dermal scales discernible at about 7–8 groove when animal slightly dry, denser after about first third of body (skin

then looks almost granular with roundish knobs). The remaining paratype (QCAZ-A 7146) is more or less uniform dark grey.

Habitat and ecology: The available data indicates that the species occurs in habitats ranging from old growth forest to artificial open areas. Habitat data are available for the holotype, one paratype, and five non-vouchered individuals from the Tesoro Escondido and Canandé Reserves. The holotype was detected moving in the late afternoon on a steep slope on muddy ground of a regenerating cacao plantation, after a heavy rain. This former plantation is in proximity of degraded (direct vicinity) as well as old growth forest (< 200 m distance). It is thus not clear if the species lives in forest and only travelled through the degraded area or can resist some habitat degradation. The large size of the species suggests a life in soil which is not as compact and stony as the loamy muddy soil of the plantation (Fig. 12).

Figure 12. Habitats of *Caecilia tesoro* sp. n. and *C. truncata* sp. n. (a) type locality of *Caecilia tesoro* sp. n. an active cacao plantation; (b) old growth rainforest in the Tesoro Escondido Reserve, close (< 500 m) to the type locality, on this forest ridge another adult *C. tesoro* sp. n. has been observed (Supplementary Video 2); (c, d) old growth rainforest on ridges where *C. truncata* sp. n. (see Fig. 15) have been collected in the Tesoro Escondido (c; QCAZ-A 79740) and the Canandé (d; QCAZ-A 78979, 79000, 79001, paratypes) Reserves, Esmeraldas Province, Ecuador.

An observation from late afternoon, 4:40 pm, 23 June 2023, shows that the species occurs in the nearby forest. On that day one of us (VM) observed a large specimen (app. 800 mm TL) moving in the leaf-litter in the nearby primary forest (ca. 1 km from the type locality; no GPS reading available) on a montane ridge (see video in Supplementary Materials). In the Tesoro Escondido Reserve VM also observed two further individuals (not collected, approximately 800 mm TL) in primary forest during the day (11:30 and 17:00 h), after heavy rains. Paratype QCAZ-A 64560 was collected next to a road, within a human populated area. Photos which show non-vouchered specimens of *C. tesoro* published in literature (Fig. 11A and Appendix 3 in Ortega-Andrade et al. 2010) and Instagram (see above; posts from 2018 and 2019, no locality data given) were taken in forest habitats. We received a video of an animal, presumably slightly smaller but coloured like the holotype, from the Canandé Reserve (N 0.4846°, W 79.2139°, 355 m elevation), moving in the leaf litter of an old growth forest (Fig. 11 and Supplementary Materials).

Elevation ranges from about 300 m to slightly more than 1400 m, thus comprising lowlands to lower montane altitudes (Ortega-Andrade et al. 2010, this study). Three specimens of the type series were collected during the core rainy season in January, February, and April. Two observations by VM took place in June and November and one

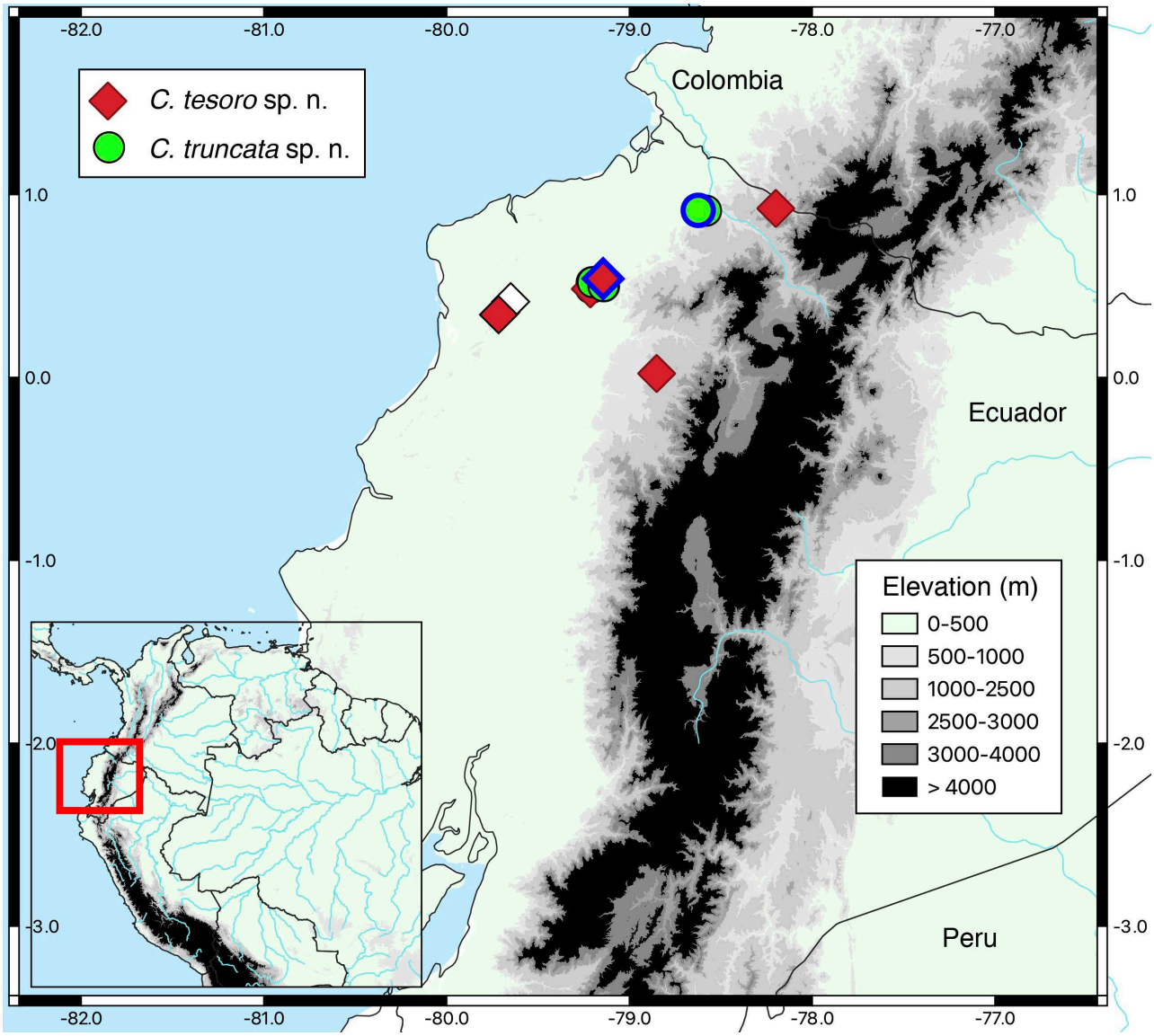

Figure 13. Map showing the distribution of *Caecilia tesoro* sp. n. (red rhombuses) and *C. truncata* sp. n. (green circles) in western Ecuador. Type localities are shown with blue border. The white symbols refer to records from the literature and social media which we assume belong to the new species. Other records are based on the type material and non-collected individuals observed by the authors. See text for details.

paratype was collected in August, during a drier season. It is possible that animals are always active on the surface after heavy rains. Annual precipitation in the type locality is between 4000 to 6000 mm (unpubl. data of the Reassembly project; www.reassembly.de). More ecological and biological data for this enigmatic species are highly desirable. The natural regions at known localities are Chocoan Humid Tropical Forest and Western Foothill Forest (as defined by Ron et al. 2024).

Distribution and conservation status: The type series originates from sites in three western Ecuadorian provinces, Esmeraldas, Pichincha, an Carchi, and covers an elevational range from 300 to 1420 m a.s.l. (Fig. 13). Known sites comprise at least three privately protected areas, namely the Tesoro Escondido and Canandé Reserves (this study), as well as the Bilsa Biological Station (Ortega-Andrade et al. 2010). The type material and additional records from literature, social media (see above), and our own observations and videos (Supplementary Materials and Fig. 11), indicate a range of lowland habitats from pristine rainforests to active plantations and other open areas. Given the scant known records, we recommend assigning the new species to the Data Deficient category.

Etymology: The name *tesoro* means 'treasure' in Spanish, thereby referring to the rich biodiversity of the Chocó lowland forests, and the name of the reserve with the type locality of the species, and thus honouring the Ecuadorian NGO Tesoro Escondido (www.tesororeserve.org), which protects this outstanding forest. The specific epithet is a genderless noun in apposition. As English common name, we suggest Tesoro's Caecilia, in Spanish this should be Cecilia Tesoro.

Caecilia truncata sp. n.

ZooBank LSID: urn:lsid:zoobank.org:act:02FAAD1A-C353-46C0-ADB7-905DB2436A57
(Figs 4, 5, 9, 14, 15)

Holotype: QCAZ-A 27774, adult male from Ecuador, Provincia Esmeraldas, Cantón San Lorenzo, Alto Tambo, El Placer, Río Carolina, N 0.7045, W 78.2011, 500 m a.s.l., 2 November 2005, coll. Í. Tapia.

Paratypes: All from Ecuador, Provincia Esmeraldas. QCAZ-A 40305, juvenile male, from Cantón San Lorenzo, 4 km W from Alto Tambo, along the train track, N 0.9124, W 78.5809, 700 m a.s.l., next to a stream, near a road, 14 March 2009, coll. by D. Almeida, A. Manzano, S. R. Ron and Í. Tapia; QCAZ-A 78979, from Cantón Eloy Alfaro, Parroquia Malimpia, Reserva Río Canandé, N 0.5203, W 79.2063, 513 m a.s.l., on rainforest trail, shortly after heavy rain, 02 December 2023, coll. by M. A. Guerra, M. Vélez-Cárdenas, M. Wiedebusch, I. Moreira, and M.-O. Rödel; QCAZ-A 79000, same locality as QCAZ-A 78979, N 0.5114, W 79.1913, 486 m a.s.l., on rainforest trail, 05 December 2023, coll. by M. Wiedebusch, I. Moreira, and M. Baluarte; QCAZ-A 79001, juvenile, same locality as QCAZ-A 78979, N 0.4893, W 79.2212, 529 m a.s.l., degraded rainforest, 11 December 2023, coll. M. Wiedebusch, I. Moreira, M. Baluarte, and L. de la Cruz.

Referred specimen: QCAZ-A 79740, from Ecuador, Provincia Esmeraldas, Cantón Eloy Alfaro, Parroquia Telembí, Reserva Tesoro Escondido, Casa Guayacán, N 0.5148, W 79.1464, 512 m a.s.l., primary rainforest, during very heavy rainfall, 20 March 2024, coll. by V. Moreira, N. Fuchs, M. Schönleitner, and M.-O. Rödel.

Diagnosis: Member of the family Caeciliidae based on its phylogenetic position and the anatomical definition by Wilkinson et al. (2011). Relatively small but robust *Caecilia* species characterized by the combination of the following characters: (1) smaller *Caecilia* with short snout, truncated in dorsal view, (2) eye visible, not covered by bone, (3) 107–123 primary folds (CV = 5.79), (4) 5–8 incomplete secondary folds (CV = 19.0), (5) presence of terminal shield, (6) 128–129 vertebrae, (7) dark grey dorsum and venter, lighter grey flanks, head, and neck, lighter areas not always evident. Of available sequences, *C. truncata* is most closely related to *C. volcani*, an endemic species of Panama.

From other western Ecuadorian and south-western Colombian *Caecilia* species, *C. truncata* differs as follows (compare Table 3): *C. truncata* has a more truncated head shape than all other species (Fig. 14); it is smaller (< 500 mm) than *C. guntheri, C. nigricans*, *C. pachynema, C. tesoro*, and *C. wilkinsoni* (> 650 mm); it has a more robust body shape (BL/BW: 23–43) than *C. pachynema, C. tenuissima,* and *C. wilkinsoni* (all > 44, up to 108); it has less primary annular grooves (107–123) than *C. nigricans, C. pachynema, C. perdita, C. subterminalis, C. tenuissima*, and *C. wilkinsoni* (> 133); it has less secondary annular grooves (5–8) than *C. leucocephala, C. nigricans, C. perdita, C. subterminalis, C. tesoro, C. volcani*, and *C. wilkinsoni*; it has a terminal shield in contrast to *C. guntheri, C. tesoro, C. volcani,* and *C. wilkinsoni*; it shows an almost uniform greyish-blue colour pattern, as typical for most *Caecilia*, but very different to *C. pachynema* and large *C. tesoro* (compare above and Table 3).

Description of the holotype: Adult male with a TL of 482 mm and 129 vertebrae; TL/BW ratio is 36.5; body slightly dorsoventrally compressed; the ventral surface is slightly flattened due to preservation; HL/HW ratio 1.2; snout rounded in lateral as well as in dorsal view, it projects 2.5 mm ahead of the anterior end of the lower jaw; snout tip truncated in dorsal view; eyes located dorsolaterally, visible externally in an orbit not covered by bone; nares positioned dorsally near anterior end of rostrum, HW/IND ratio 3.2; tentacular aperture positioned posteroventrally to nares, much closer to nares than to eyes, not visible in dorsal view; ITD/IND 1.3; narial plugs present.

Nuchal region approximately same width as HW, with two well-defined nuchal collars; first nuchal collar length is 3.0 mm; second nuchal collar length is 5.3 mm, partially joined to the first primary annulus because third nuchal groove is incomplete medioventrally; both collars with short transverse groove dorsally; body with 123 complete primary annular grooves, and 8 secondary annular grooves, none of which is complete; terminal shield present, 2.1 mm long, interrupting four dorsal primary annular grooves; anal papillae absent; vent surrounded by eight denticulations, three anterior, five posterior to vent (Table 4).

Single rows of dermal scales sitting in scale pockets (Fig. 5), starting at the 107th primary annular groove and extending to last primary groove; very numerous and dense in posterior 5th of body; dermal scales collected from towards tail tip are regular and broad to narrow and oval. Extracted dermal scales with surface of 1.41–1.93 mm to 2.43–2.77 mm (length and width), height = 0.02 mm (Figs 9c, d). Small subcircular subdermal scales are present but rare and irregularly distributed along midbody.

Skull robust and heavily ossified, with broad truncated snout (Fig. 4), total length 13.1 mm, maximum widths

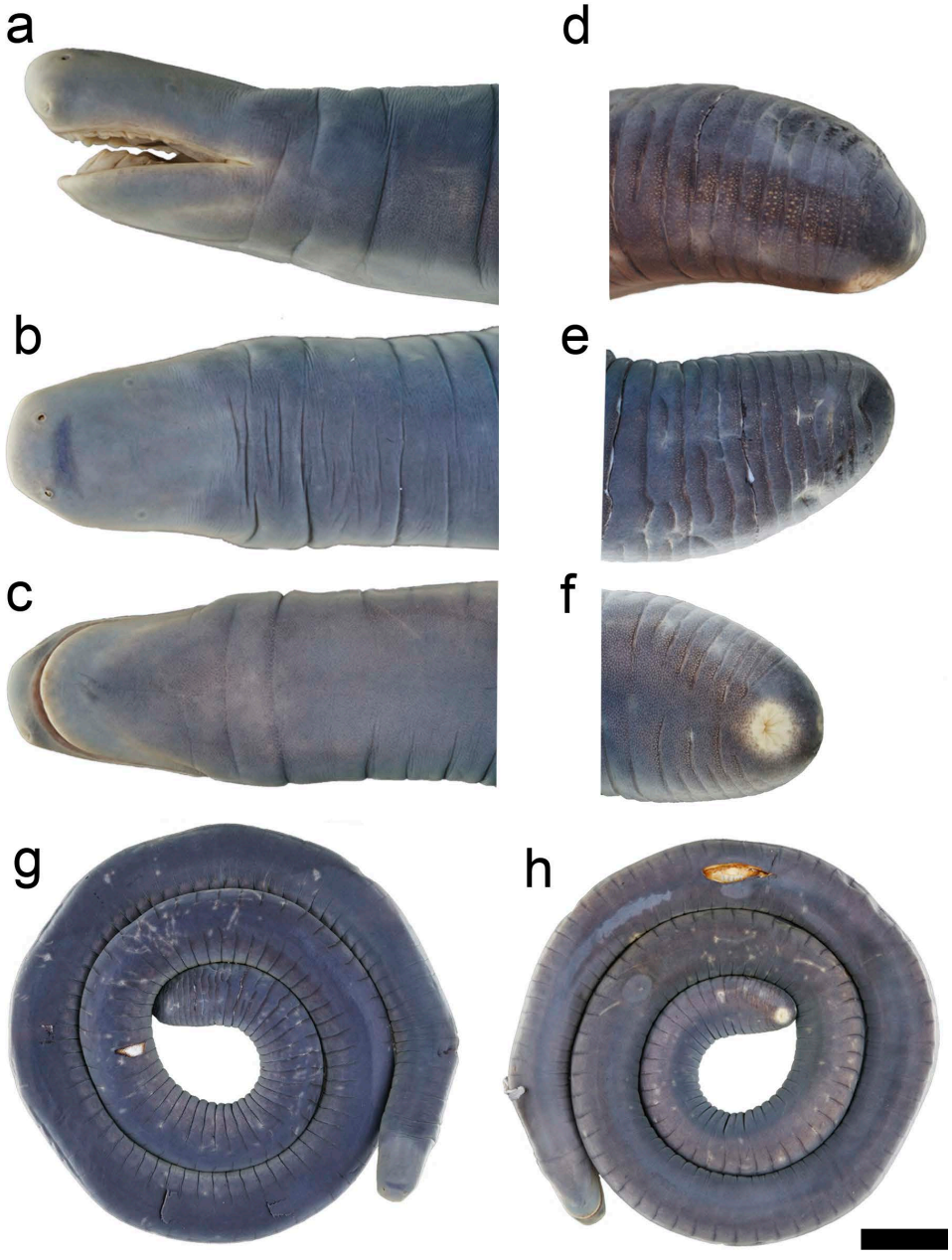

Figure 14. Preserved holotype of *Caecilia truncata* sp. n. (QCAZ-A 27774); head in lateral (a), dorsal (b), and ventral (c) view; tail in lateral (d), dorsal (e), and ventral (f) views; and entire animal in dorsal (g), and ventral (h) views; scale bar for g, h = 1 cm.

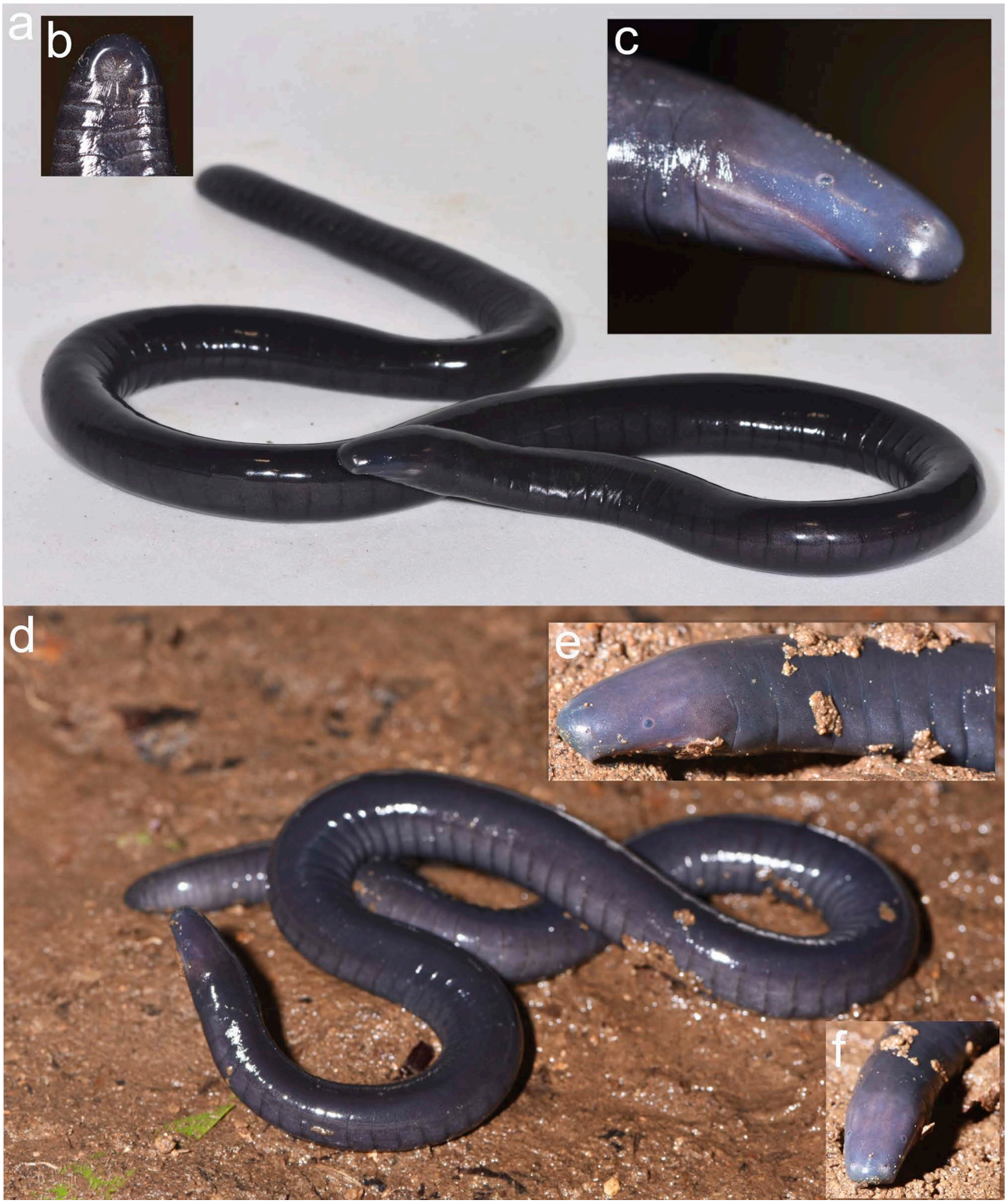

Figure 15. *Caecilia truncata* sp. n. in life, illustrating body shape and colour, as well as head shape and cloacal details. (a–c) QCAZ-A 78979 from Canandé Reserve (paratype); (d–f) QCAZ-A 79740 from Tesoro Escondido Reserve.

8.8 mm; with 213 foraminae openings, stegokrotaphic; orbit open; mouth subterminal with large, monocuspid teeth, backward curved, and pointed; arranged in four dental series: premaxillary–maxillary with 11-1-11 teeth, vomeropalatine 12-11, outer mandibular 15-15, inner mandibular: 2-2; choanae oval, diameter 1.2 mm.

Nasopremaxillae square shaped, almost twice as long as wide, with opening for nostril and tentacle; nostril opening 0.6 mm, tentacular foramina 0.6 mm; posterior part of nasopremaxillae separated by broadly rounded end of elongated (41.9 mm), broad (11.6 mm), kite-shaped mesethomid; bordered by posteriorly diverging frontals and posteriorly extending for about ⅕ of length between anterior parts of parietals; frontals slightly smaller than nasopremaxillae, about twice as long as wide; parietals slightly shorter, almost triangular shaped; 128 vertebrae (Tables 5, 6).

Life colouration of the holotype is unknown. After 18 years in 75% ethanol, the holotype is uniformly grey, slightly lighter on the head and neck, and has two lighter grey lateral bands, interrupted by dark grey folds. The area around the snout, tentacles, and nostrils are yellowish cream (Fig. 14).

Variation: Two paratypes were juveniles (QCAZ-A 40305, 79001) with 133 and 143.5 mm TL; the holotype is the largest known specimen. There is little variation in the number of primary (107–123) and secondary (5–8) annular grooves. The terminal shield is present and interrupts 3–4 primary grooves. Paratypes are more slender or stockier than holotype, TL/BW ratio varies from 23–43; smaller individuals are more slender than larger ones. Morphology and morphometry of head are similar to the holotype; the snout in the smallest individuals is however, more rounded in lateral and dorsal view. The holotype has the longest head (HL/HW ratio = 1.2; paratypes: 1.3–2.1; the smallest individual has the shortest head) and the most dorsally positioned eyes (HW/IOD ratio = 1.7; paratypes: 1.0–1.5; eyes positioned more laterally in smaller individuals). Tentacular aperture of specimens from Canandé and Tesoro Escondido Reserves were positioned below or even slightly anteroventrally to nares.

In life, dark grey to almost black; body shows not much patterning. The flanks are lighter than the dorsum (Fig. 15); paler lateral bands along the body are not visible; cream colouration is evident in the areas surrounding the snout, tentacles, and nostrils. Similar colouration has been observed in QCAZ-A 79740 and six non-collected specimens from Tesoro Escondido and Canandé Reserves. The entire lower mandible of the smallest individual, QCAZ-A 79001 is uniform, yellow creamish. After 14 years in preservative (70% ethanol), the lateral bands of QCAZ-A 40305 are barely visible.

The TL of six non-collected animals ranged from 280 to 382 mm (each individual measured twice), thus being smaller than the holotype. One animal of 382 mm TL had a BW of 8 mm, a BH of 7.5 mm, and weighed 30 g (taken with a Pesola balance).

Habitat and ecology: The species occurs in old growth and secondary forest. QCAZ-A 40305 was found above ground, near a stream of about 5 m width, next to a road. QCAZ-A 27774 was deposited without any ecological information. In the Tesoro Escondido and Canandé Reserves we observed a total of eleven animals, all during the night and during very heavy rain, moving on the muddy ground of paths through good standing forest. One was collected at about midnight in the Canandé Reserve (QCAZ-A 78979) on 2 December 2023 (Fig. 12d). Very close to this locality, a further individual was observed on 8 April 2024 at 19:43; temperature: 22.4 °C. Five animals have been seen on two consecutive nights in the Tesoro Escondido Reserve, one on 20 March 2023 (QCAZ-A 79740), the other four on 21 March 2023. Vouchered and non-vouchered specimens have been traced along an elevation range from 500–701 m a.s.l. The natural region for all known localities were Western Foothill Forest (as defined in Ron et al. 2024). These forests are characterized by humid and moderately warm conditions. Canopy reaches 30 m and there is a high abundance of palms and trees dominated by the families Mimosaceae, Fabaceae, and Burseraceae. Trees are covered by mosses, orchids, ferns, and bromeliads (Ron et al. 2024).

Distribution and conservation status: *Caecilia truncata* is known from its type locality, Alto Tambo and one nearby site, as well as from the Canandé and Tesoro Escondido Reserves, all in the western Ecuadorian province of Esmeraldas. We recommend classifying this new species as Data Deficient due to the low number of known specimens and sites. The available habitat information suggests tolerance of anthropogenic habitat modification, however, with larger abundances in mid-altitude primary rainforest.

Etymology: The species name is the Latin adjective *truncata* referring to the blunt shape of the snout. As English common name, we suggest Truncated Caecilia, in Spanish Cecilia Truncada.

Discussion

We provide morphological, osteological, and molecular evidence documenting two new species of *Caecilia* from the Ecuadorian Chocó. They are the first Caeciliidae described from Ecuador in 50 years. Both new taxa exhibit unique morphological features distinguishing them from described *Caecilia*, i.e. *C. tesoro* is very large, although by far not the largest *Caecilia* (see Arredondo-Salgar 2007: *C. thompsoni* achieving a total length of 1767 mm), and adults have a unique colour pattern; *C. truncata* exhibits a very unusual, truncated head shape for a *Caecilia*. However, the new species are not only morphologically, but genetically distinct from other species form the Chocó region and suggest that the use of molecular evidence can significantly improve our understanding of the species content of this enigmatic family.

Remarkably, prior to our study, only a single Caeciliidae species, *Caecilia pulchraserrana*, had been described using genetic data (Acosta-Galvis et al. 2019). This contrasts starkly with Neotropical anurans on which the use of genetic evidence in species descriptions has become the norm (e.g., Catenazzi & Lehr 2018, Rivera-Correa et al. 2017, Moravec et al. 2020, Carvalho et al. 2021, Reyes-Puig et al. 2022). Unlike other vertebrate orders, systematics of Neotropical Gymnophiona have been largely unchanged by the technological advances that have facilitated the generation of genetic data (but see Maciel et al. 2018, 2019, Acosta et al. 2019 for exceptions). The reasons for this peculiarity are unknown, but may have to do with (1) scarcity of caecilian specimens in general, and (2) consequently the rarity of genetic samples of Gymnophiona in the Neotropics. The nearly complete absence of genetic data in alpha-systematics of Caeciliidae is a serious challenge for caecilian taxonomyand conservation.

For instance, although our own (unpublished) results suggest that there are many caecilian species waiting to be described, most of them are morphologically cryptic. So far caecilians have been mainly diagnosed based on morphological differences (see e.g. references in Introduction). The lack of distinct morphological differences may thus hinder the recognition of valid species, and therewith also negatively impact other biological fields as specific distinctiveness cannot be recognized and considered, e.g. in biogeographic or ecological analyses (Gotelli 2004, Bevilacqua et al. 2021); and thus finally also hampers conservation (Mace 2004, Wandeler et al. 2007). However, our study also shows that morphological disparity may not necessarily mean specific distinctiveness. Smaller and larger *C. tesoro* exhibit strikingly different colour patterns, a character that traditionally might have resulted in the description of two new species (but see Maciel & Hoogmoed 2011, 2018 for examples of highly colour-polymorphic species). Our genetic data in contrast suggests that the species undergoes a striking and so far non-documented ontogenetic change in colour. Similarly, we observed that in *C. pachynema*, the overall colour pattern remains with age, but body shape seems to change. While adults were heavy built robust animals, juveniles are very slender (see the 'Morphology' section). Sex and age-related morphological differences in caecilians have been so far only very rarely reported (Kupfer et al. 2004), however, including one *Caecilia* species from Colombia, *C. epicrionopsoides*. In this species the number and position of annular grooves seem to vary with age, sex and/or geographic occurrence (Fernández-Roldán et al. 2023). The biological and ecological, maybe even behavioural, reasons of these colour and morphological differences are so far unknown but promise exciting research questions.

Some further morphological characters, traditionally used in caecilian taxonomy, are also not easy to interpret. For instance, there should be caution interpreting the published numbers of complete secondary grooves and the reported presence versus absence of a terminal shield. Both new species have in common the absence of complete secondary grooves, unlike *C. pachynema*. In other species these grooves have been reported from some individuals, but not from others. The numbers range from 0–14 in *C. guntheri*, 0–7 in *C. nigricans*, and 0–4 in *C. tenuissima*. *Caecilia volcani* seems to have a very low number of complete secondary grooves (up to 3). Anal papillae have not been found in *C. leucocephala, C. tesoro*, and *C. truncata* (Fig. 14, Table 3).

The addition of genetic evidence therefore has not only the potential of a dramatic increase of described species of Caeciliidae during the next decade, it also will help to discover and answer other biological questions. In general, genetic evidence is particularly useful in taxa on which morphological variation is poorly understood, such as the Caeciliidae. We therefore urge all colleagues to publish genetic sequences of new and known species, even when only limited comparative material is available.

In addition to the description of the two new species, we report, for the first time, the phylogenetic position of *C. nigricans* and *C. leucocephala*. The new inclusion of four species in the phylogeny of Caeciliidae increases by ~ 60% the species sampling for the family. Nevertheless, our phylogeny only includes one fifth of the described species. Acosta-Galvis et al. (2019) and San Mauro et al. (2014) revealed that *Oscaecilia* is the sister group of *Caecilia*, thus seemingly confirming Taylor (1968). Our improved species sampling altered the topology, especially for the position of *C. nigricans*, which however, has low support in our phylogeny. For that reason, the paraphyly of *Caecilia* relative to *Oscaecilia,* shown in our tree, should be considered tentative. However, Wilkinson et al. (2011) already discussed the monophyly of *Caecilia* and their generic distinctiveness from *Oscaecilia.*

Our phylogenetic data also confirmed a well-known biogeographic relationship. Both new taxa are closely related to the Central American *C. volcani*. A close relationship of Chocó taxa with Central American species has been reported, amongst many other taxa, for instance for caecilians of the Pacific lowlands from Colombia (Fernández-Roldán & Lynch 2023), well-known toads (Menéndez-Guerrero et al. 2024), and tree vipers (Arteaga et al. 2024).

Nevertheless, all these publications underlined the biogeographic distinctiveness of the Chocó region, and our new descriptions add to the long list of species endemic to the Chocó. This ecoregion is unique, but unfortunately also considered a global biodiversity hotspot (Myers et al. 2000, López et al. 2010). This definition means that globally it is one of the most biodiverse areas, including high species richness and endemism, but as well that this biodiversity is highly threatened (Myers et al. 2000). Indeed, the Chocó faces significant threats from human activities, and the Chocó amphibians comprise a large number of endemic but threatened species (Ortega-Andrade et al. 2021). Deforestation rate is one of the highest in the World (Gonzalez-Jaramillo et al. 2016), and mainly driven by agricultural encroachment, ranging from small

subsistence farming, small scale cash crops (i.e. cocoa), and cattle ranching, to the establishment of industrial-like plantations (mostly oil palms), logging, and the development of infrastructure development and land-use change (Fagua & Ramsey 2019, Fagua et al. 2019, Kleemann et al. 2022).

Globally, 31 of the 40 *Caecilia* species have been assessed for their threat status (IUCN 2024), 16 are listed as of Least Concern, one as Near Threatened, one being Endangered and 13 Data Deficient. The conservation status of all 14 Ecuadorian *Caecilia* has also been assessed nationally, three taxa each are considered of Least Concern and Vulnerable, four taxa each are defined as Endangered and Data Deficient. From the five western Ecuadorian caecilian species only one was classified as Least Concern, all other were placed in different threat categories (Ortega-Andrade et al. 2021). Fortunately, our data of the range and habitat preferences of the two new species seem to indicate that both can deal at least with some extend of habitat degradation, and both occur in some protected reserves. Nevertheless, more data on their distribution, population sizes, habitat requirements, and biology would be highly desirable.

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Appendix

Comparative *Caecilia* specimens studied for morphology and/or osteology

C. guntheri: BMNH 1946.9.5.12 (holotype), western Ecuador; QCAZ-A 15568, Ecuador, Provincia Cotopaxi, Las Pampas Otonga, Lat. -0.4178, Long. -78.9880, 1882 m a.s.l.

C. leucocephala: KU 200985 (holotype), Colombia, Virology Field Station, Río Raposo, Valle del Cauca, south of Buenaventura; QCAZ-A 47071, Ecuador, Provincia Esmeraldas, 4 km W at Alto Tambo, along train tracks, Lat. 0.9124, Long. -78.58092.

C. nigricans: BMNH 1946.9.5.52 (holotype), north-western Ecuador, the Rio Lita, 3000 feet; QCAZ-A 37728, Ecuador, Provincia Esmeraldas, 2.1 km de Durango vía al Rio San Francisco, Lat. 1.04704, Long. -78.61821, 104 m a.s.l.

C. pachynema: BMNH 1946.9.6.83 (holotype), western Ecuador; QZAC-A 31720, Ecuador, Provincia Azuay, San Antonio de Chaucha, Lat. -2.9079, Long -79.41347, 1841 m a.s.l.; QZAC-A 33235, Ecuador, Provincia Azuay, Reserva Yunguilla (Fundación Jocotoco), El Unión, cerca a Santa Isabel, Lat. -3.2260, Long. -79.27690, 1887 m a.s.l.; QZAC-A 46938, Ecuador, Provincia Azuay, Sector Río Chipla, Lat. -2.7457, Long. -79.4089, 2500 m a.s.l.; QZAC-A 46983, Ecuador, Provincia Azuay, Río Chipla desde Molleturo hacia la Costa por la carretera pequeña no la principal, Lat. -2.7457, Long. -79.4089, 2500 m a.s.l.; QCAZ-A 37733, Ecuador, Provincia Cotopaxi, Naranjito, Bosque Integral Otonga (BIO), Lat. -0.426279, Long. -79.01537, 2175 m a.s.l. (labelled as *C. buckleyi*, regarded as synonym of *C. pachynema*, see Frost 2024).

C. perdita: UMMZ 121036 (holotype), Colombia, Andagoya, Condoto, Choco.

C. subterminalis: FMNH 189204 (holotype), Ecuador.

C. tenuissima: QCAZ-A 23580, Ecuador, Provincia Guayas, al rededores Estación Cerro Masvale, Lat. -2.3986, Long. -79.6335; QCAZ-A 42637, Ecuador, Provincia El Oro, Universidad Técnica de Machala, Lat. -3.28, Long. -79.91899.

C. volcani: KU 203035 (holotype), Panamá, El Valle de Antón, Coclé, 550 m a.s.l.

Supplementary data

The following data are available online:

Supplementary Video 1. *Caecilia tesoro* sp. n. (not collected) from old growth forest in the Canandé Reserve (N 0.4846°, W 79.2139°, 355 m elevation). Video provided by D. V. Loor Bermeo.

Supplementary Video 2. *Caecilia tesoro* sp. n. (not collected) from old growth forest in the Tesoro Escondido Reserve. The animal was observed near the type locality at 4:40 pm on 23 June 2023. Video recorded by V. Moreira.