Research Article

Three new species of *Ophiotaenia* La Rue, 1911 (Cestoda: Proteocephalidae) from dipsadine snakes (Squamata: Colubridae) in Ecuador

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Abstract: The parasite fauna of Neotropical reptiles is poorly known, and the number of parasites described in these hosts does not seem to correspond to the actual species diversity in this zoogeographical region. This also applies to tapeworms such as proteocephalids, which are rarely found in reptiles and are strictly specific to their reptilian hosts. In the present paper, three new species of *Ophiotaenia* La Rue, 1911 are described from three dipsadine snake species (Squamata: Colubridae) in Ecuador, namely *O. jeanmarctouzeti* sp. n. from the Neotropical blunt-headed treesnake *Imantodes cenchoa* (Linnaeus), *O. barraganae* sp. n. from the beautiful calico snake *Oxyrhopus formosus* (Wied-Neuwied) and *O. velascoae* sp. n. from the forest flame snake *Oxyrhopus petolarius* (Linnaeus). The new species are characterised by type 1 uterine development, the number and distribution of testes, the size of the scolex and other metric features. As no molecular data are available on the specimens collected more than 35 years ago, the phylogenetic relationships of the individual taxa are not known.

Key words: Tapeworms, species diversity, taxonomy, morphology, South America, Ophidia, Dipsadinae

Proteocephalid tapeworms (Cestoda: Onchoproteo-cephalidea) are parasites of freshwater ray-finned fish (Actinopterygii) (more than 200 described species – Scholz and Kuchta 2022) and herptiles, especially frogs, lizards and snakes, with more than 130 described species (Freze 1965, Schmidt 1986, de Chambrier et al. 2017). Seventy proteocephalids from six genera have been reported from snakes (Ophidia), with 56 taxa from *Ophiotaenia* La Rue, 1911, including 18 species reported from colubrid snakes in the New World (Diard et al. 2022). However, the number of proteocephalids reported from Neotropical reptiles is apparently greatly underestimated, considering the high biodiversity of these hosts (Torres-Carvajal et al. 2019) and the little attention paid to their parasites (Gibson et al. 2005).

The parasite fauna of reptiles in Ecuador, one of the most reptile-rich countries in the world with 464 recognised species (Reyes-Puig et al. 2017), has not been intensively studied and very few data are available (see Gibson et al. 2005). Dyer and Carr (1990a) found the nematode *Atractis caballeroi* Brenes et Bravo-Hollis, 1960 (Cosmocercoidea: Atractidae) in the white-lipped mud turtle *Kinosternon leucostomum* (Duméril, Bibron et Duméril) and the large-nosed wood turtle *Rhinoclemmys nasuta* (Boulenger), as well as *Falcaustra tikasinghi* (Schoeneck-er, Schmidt et Everard, 1977) (Cosmocercoidea: Kathlaniidae) in *R. nasuta* and the Colombian wood turtle *Rhinoclemmys melanosterna* (Gray) in Ecuador. Bursey and Flanagan (2002) described *Atractis marquezi* Bursey et Flanagan, 2002 from the indefatigable island tortoise, *Geochelone nigrita* (Duméril et Bibron) (= *Chelonoidis niger* [Quoy et Gaimard]) in the Galápagos Islands. Ben Slimane and Durette-Desset (1996) described the nematode *Oswaldocruzia bainae* Ben Slimane et Durette-Desset, 1996 (Trichostrongyloidea: Molineidae) from the goldenscale anole *Anolis chrysolepis* Duméril et Bibron and the brown-eared anole *A. fuscoauratus* d'Orbigny in Ecuador.

Dyer and Carr (1990b) reported the following trematodes from *R. nasuta* in Ecuador: *Octangioides tlacotalpensis* Caballero, 1942 (Paramphistomatoidea: Microscaphidiidae), *Nematophila grandis* (Diesing, 1839), *Pseudallassostoma heteroxenus* (Cordero et Vogelsang, 1940) (= *Halltrema heteroxenum* [Cordero et Vogelsang, 1940]) and *Pseudocleptodiscus margaritae* Caballero, 1961 (Paramphistomatoidea: Cladorchiidae). Coquille and de Chambrier (2008) described two proteocephalid cestodes from lizards, *Cairaella henrii* Coquille et de Chambrier, 2008 in *Norops trachyderma* (Cope) (Polychrotidae) and *Ophiotaenia nicoleae* Coquille et de Chambrier, 2008 in *Thecadactylus rapicauda* (Houttuyn) (Gekkonidae).
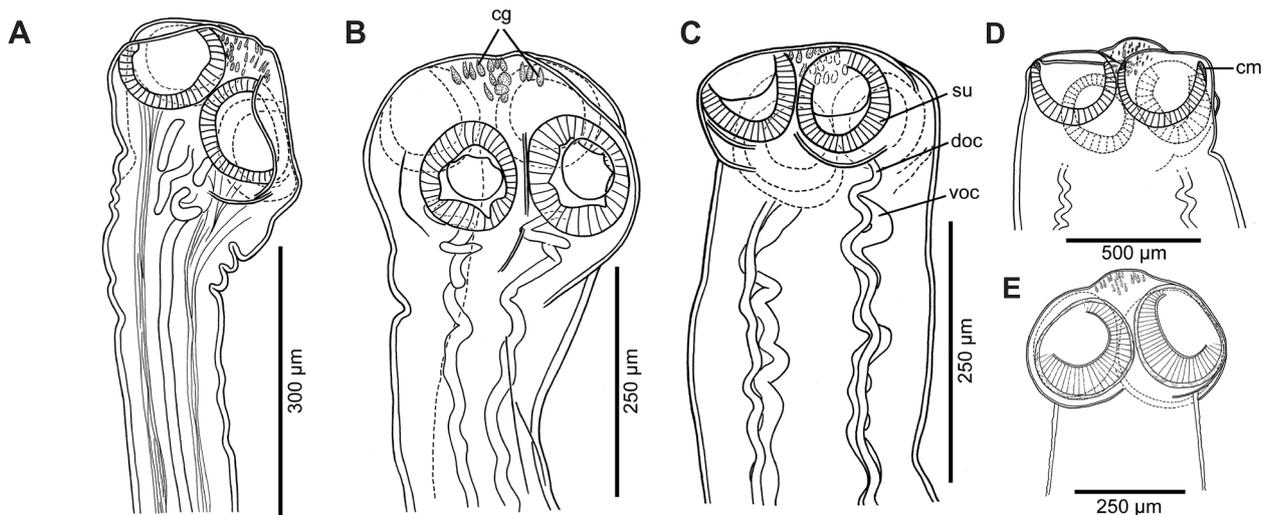
Fig. 1. Scoleces of *Ophiotaenia jeanmarctouzeti* sp. n. (A–C) and *Ophiotaenia* sp. (D, E) from *Imantodes cenchoa* (Linnaeus), Ecuador (A–D) and Costa Rica (E). **A** – holotype (MNHG-PLAT-0018666); **B** – paratype (MHNG-PLAT-0018669/IPCAS C-971); **C** – voucher (MHNG-PLAT-0018668); **D** – voucher (MHNG-PLAT-0018667); **E** – voucher (MHNG-PLAT-0061483). *Abbreviations*: cg – cells with finely granular cytoplasm; cm – circular musculature; doc – dorsal osmoregulatory canal; su – sucker; voc – ventral osmoregulatory canal.

However, only one cestode of snakes has been described from Ecuador, namely the proteocephalid *Vaucheriella bicheti* de Chambrier, 1987 from *Tropidophis* cf. *taczanowskyi* (Steindachner) (Serpentes: Tropidophiidae) from the province of Zamora-Chichipe (de Chambrier 1987). Three proteocephalid cestodes have been described in amphibians: *Ophiotaenia olseni* Dyer et Altig, 1977 and *O. ecuadorensis* Dyer, 1986 in the map tree frog *Boana geographica* (Spix) (Anura: Hylidae), and *Nomimoscolex touzeti* de Chambrier et Vaucher, 1992 from the Amazonian horned frog *Ceratophrys cornuta* (Linnaeus) (Anura: Ceratophryidae) (Dyer and Altig 1977, Dyer 1986, de Chambrier and Vaucher 1992).

In the late 1980s, Jean-Marc Touzet from France, founding member and former director of the Fundación Herpetológica Gustavo Orces, examined a large number of amphibians and reptiles for parasites and found many helminths, including tapeworms. Proteocephalid tapeworms of the genus *Ophiotaenia* La Rue, 1911 were found in three species of dipsadine snakes (Squamata: Colubridae). Their taxonomic examination revealed that they are new species, which are described in the present paper.

MATERIALS AND METHODS

The snakes were captured as part of a faunistic survey in Ecuador (collection export permit Ecuador No. 093, 21 April 1989, CITES permit Ecuador No. 018, 27 April 1989). They were euthanised by injection of Nembutal (phenobarbital) into the heart region. Immediately after the dissection of the snakes, the tapeworms were carefully isolated from the intestine of the host, rinsed in saline solution and fixed with a hot 4% formaldehyde solution. All tapeworms were collected by Jean-Marc Touzet who donated them to the Natural History Museum in Geneva.

In the laboratory, the worms were processed by the first author (AdC), i.e., stained with Mayer's hydrochloric carmine solution, dehydrated in an ethanol series, cleared with eugenol (clove oil) and mounted as permanent preparations in Canada balsam (Chervy 2024). For histological sections, pieces of the scolex and strobila were embedded in paraffin wax, sectioned (thickness 12–15 μm), stained with Weigert's hematoxylin and counterstained with 1% eosin B according to de Chambrier (2001). For scanning electron microscopic (SEM) observations, several scoleces of all species were prepared following the standard procedure (Chervy 2024) and observed using a JEOL JSM-740 1F scanning electron microscope at the Institute of Parasitology in České Budějovice. All measurements are given in micrometres unless otherwise stated. Abbreviations used in the descriptions: x = mean, n = number of measurements. Abbreviations for museum collections: IPCAS – Institute of Parasitology, Biology Centre of the Czech Academy of Sciences, České Budějovice, Czech Republic; MHNG-PLAT – Natural History Museum, Geneva, Switzerland.

RESULTS

Ophiotaenia jeanmarctouzeti sp. nov.

Figs. 1A–C, 2A–C, 3, 4

ZooBank number for species:
urn:lsid:zoobank.org:act:8F151C4E-3919-443B-A0D2-BBA702DE8B62

Material examined (all from *Imantodes cenchoa* [Linnaeus]): One specimen on three slides from host Ec 2853, San Pablo de Kantesiya, Río Aguarico, Napo, Ecuador, collected on 25 December 1986 (MHNG-PLAT-0018666); two specimens on six slides and nine slides with cross-sections from host Ec 4203, San Pablo de Kantesiya, Río Aguarico, Napo, Ecuador, 12 February 1988 (IPCAS C-971; MHNG-PLAT-0018668); one specimen on three slides, four slides with cross-sections and scolex for scanning electron microscopy (SEM) from host Ec 4602, San Pablo de Kantesiya, Río Aguarico, Napo, Ecuador, 18 April 1988 (IPCAS C-971; MHNG-PLAT-0018669).
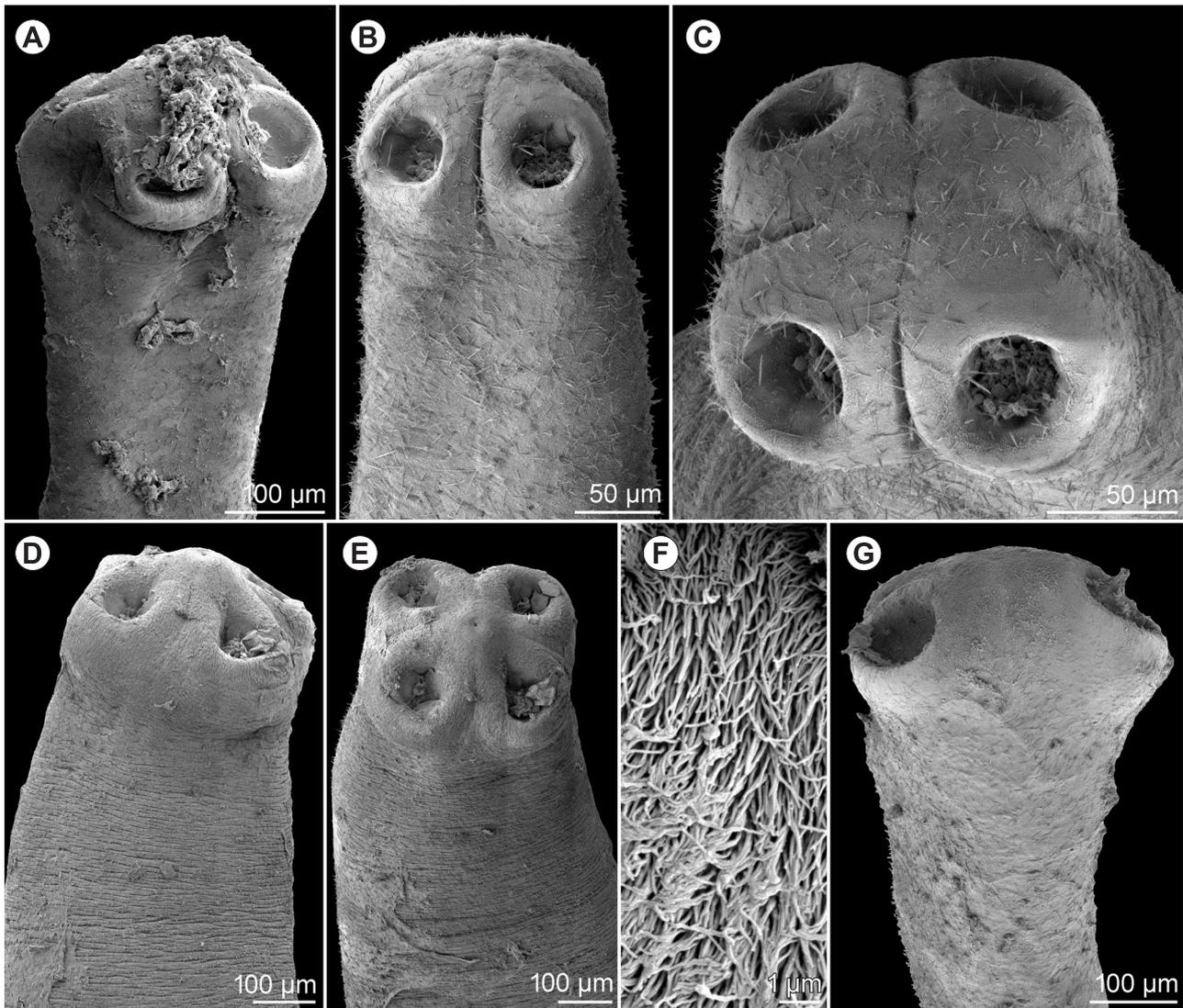
Fig. 2. Scanning electron micrographs of scoleces of *Ophiotaenia jeanmarctouzeti* sp. n. from *Imantodes cenchoa* (Linnaeus) (A – host Ec 2853, B, C – host Ec 4203), *Ophiotaenia barraganae* sp. n. from *Oxyrhopus formosus* (Wied-Neuwied) (D–F – host Ec 3260), and *Ophiotaenia velascoae* sp. n. from *Oxyrhopus petolarius* (Linnaeus) (G – host Ec 4623), all Ecuador. A, B, D – frontal view; C, E – subapical view; F – capilliform fillitriches on the scolex surface; G – lateral view. Note that the surface of the specimens that were collected more than 35 years ago is not sufficiently clean.

Description (based on two specimens of the hosts EC 2853 and 4602; measurements of the individual specimens examined in Table 1): Proteocephalidae. Large worms, up to 45 cm long and 2.0 mm wide, dorsoventrally flattened, with square to elongate proglottids, up to 1.75 mm long. Strobila acraspedote, anapolytic. Immature proglottids wider than long to square (length: width ratio 0.30–0.99); mature (length: width ratio 0.32–1.15), pregravid (length: width ratio 0.39–1.01) and gravid (length: width ratio 0.34–1.23) proglottids wider than long to longer than wide (Fig. 3A,B,D,E). Tegument thick, 20–25 in thickness.

Scolex spherical, aspinose (Figs. 1A–C, 2A–C), wider than neck, 250–275 long, 250–305 wide, with four uniloculate, spherical suckers 110–125 in diameter, directed anterolaterally (Figs. 1A,B, 2A–C); small cells of granular content present in scolex apex (Fig. 1A–C). Neck up to 185 wide; zone posterior to scolex to first recognisable proglottids long (up to 12 mm).

Inner longitudinal musculature formed by individual muscle fibres (Fig. 4C,D). Osmoregulatory canals median to vitelline follicles, scarcely crossing lateral margin of ovarian wings, overlapping testicular fields, without separating them (Fig. 3A,B,D). Ventral canals thin-walled, wide, 45–60 in diameter, may have secondary canals; dorsal canals sinuous, thick-walled, about 5–10 in diameter, situated at same level as ventral canals or slightly more median (Fig. 3A,B,D). Genital ducts run between osmoregulatory canals (Fig. 4D).

Testes oval to spherical, in one or two layers and in two fields between vitelline follicles, 100–123 in number, 45–70 long to 30–60 wide, each testicular field occupying 20–30% of proglottid width, not separated by osmoregulatory canals (Fig. 3A,B,D). Testes usually reach anterior margin of proglottids anteriorly but do not reach posterior margin of ovary posteriorly (Fig. 3A,D). Vas deferens strongly coiled, but never reaching mid-line

Table 1. Comparative measurements of new species of *Ophiotaenia* La Rue, 1911 (Cestoda: Proteocephalidae) from dipsadine snakes in Ecuador.

Parasite species	*O. jeanmarctouzeti* sp. n.	*O. jeanmarctouzeti* sp. n.	*O. jeanmarctouzeti* sp. n.	*Ophiotaenia* sp.	*O. barraganae* sp. n.	*O. velascoae* sp. n.	*O. velascoae* sp. n.
	Imantodes cenchoa	*Imantodes cenchoa*	*Imantodes cenchoa*	*Imantodes cenchoa*	*Oxyrhopus formosus*	*Oxyrhopus petolarius*	*Oxyrhopus petolarius*
Host code	Ec 2853	Ec 4602	Ec 4203	Ec 3864	Ec 3260	Ec 3920	Ec 2385
Collection No.	MHNG-PLAT-0018666	MHNG-PLAT-0018669	MHNG-PLAT-0018668	MHNG-PLAT-0018667	MHNG-PLAT-0018671	MHNG-PLAT-0018672	MHNG-PLAT-0018885
Locality	San Pablo de Kantesiya, Napo	San Pablo de Kantesiya, Napo	San Pablo de Kantesiya, Napo	Shushufindi, Pozo 4, Napo	San Pablo de Kantesiya, Napo	Shushufindi, Pozo 4, Napo	San Pablo de Kantesiya, Napo
Date of collecting	25 December 1986	18 April 1988	12 February 1988	16 April 1987	19 April 1987	19 September 1987	15 November 1986
Type material	holotype	paratype	voucher	voucher	holotype and paratype	holotype	paratype
Total length (mm)	450	172	180	35	39–43	89	38
Maximum width (mm)	1.6	2.0	1.5	1.8	1.5	1.0	0.8
Width of scolex (µm)	250	305	185–220	705	570–640	375	435–500
Diameter of suckers (µm)	115–125	110–125	80–95	310–360	200–240	135–155	160–200
Width of neck (µm)	135	185	215	820	615–630	380	350–415
Number of testes	100–119 (x = 112, n = 5)	111–123 (x = 116, n = 6)	72–117 (x = 92, n = 6)	100–141 (x = 114, n = 7)	92–123 (x = 107, n = 15)	45–63 (x = 55, n = 8)	49–64 (x = 56, n = 4)
PGP (%)	35–47% (x = 40%, n = 10)	41–46% (x = 43%, n = 6)	40–47% (x = 44%, n = 10)	37–45% (x = 40%, n = 12)	46–57% (x = 50%, n = 14)	31–40% (x = 35%, n = 7)	34–41% (x = 39%, n = 4)
RSCS (%)	20–25% (x = 24%, n = 11)	17–21% (x = 19%, n = 11)	19–25% (x = 22%, n = 11)	18–21% (x = 19%, n = 11)	17–23% (x = 19%, n = 15)	24–32% (x = 29%, n = 13)	26–31% (x = 29%, n = 7)
RSO (%)	5.7–6.1%	5.5%	3.8–5.2%	6.7–7.5%	3.0%	5.1%	6.1%
RWO (%)	65–74% (x = 68%, n = 10)	58–64% (x = 60%, n = 9)	64–69% (x = 67%, n = 10)	72–76% (x= 73%, n = 9)	56–60% (x = 58%, n = 14)	60–67% (x = 64%, n = 13)	67–71% (x = 69%, n = 4)
Position of vagina[*]	anterior-posterior	anterior-posterior	anterior-posterior	anterior-posterior	anterior-posterior	anterior-posterior	anterior-posterior
Vaginal sphincter	present	present	present	present	present	present	present
Aporal vitelline follicles – relative length	91–95%	88–94%	85–90%	88–97%	88–97%	70–87%	83–85%
Poral vitelline follicles – relative length	90–95%	89–94%	88–96%	91–96%	88–96%	78–87%	76–83%
Number of uterine diverticula[**]	17–21	17–22	21–42	17–20	32–49	15–21	15–18
Diameter of embryophore	25–26	24–26	24–26	18–21[***]	15–17[***]	21–22[***]	21–24[***]
Diameter of oncosphere	10–11	9–11	9–12	9–12[***]	9–10[***]	10–13[***]	10–13[***]
Type of uterine formation[#]	1	1	1	1	1	1	1

Abbreviations: PGP – position of the genital pore (percentage of the distance of the pore from the anterior margin of the proglottid in relation to the total length of the proglottid); RSCS – relative size of the cirrus sac (percentage of the length of the cirrus sac in relation to the width of the proglottid); RSO – relative size of the ovary (percentage of the ovarian size in relation to that of the entire proglottid – see p. 40 in de Chambrier et al. 2012 for methods of measuring); RWO – relative width of the ovary (percentage of the width of the ovary in relation to the width of the proglottid); * in relation to the cirrus sac; ** on one side; *** measurements in whole-mounts; # according to de Chambrier et al. (2004).

of proglottid, occupying oval, slightly elongate area (Fig. 3A,B,D,E). Cirrus sac elongate to pyriform, thin-walled, 275–330 long by 55–90 wide (Figs. 3A–D, 4A,B); length:width ratio 2.78–5.85. Cirrus sac width/proglottid width ratio 17–25%. Cirrus occupies 50–70% of length of cirrus sac (Fig. 4A,B). Genital atrium deep and narrow (Figs. 3A,B,D, 4A,B). Genital pores irregularly alternating, pre-equatorial, at 35–47% of proglottid length (Fig. 3A–E).

Ovary large, follicular, each wing triangular to oval-shaped, 880–1,125 wide, with long isthmus (Fig. 3A–E). Ovary width represents 58–74% of proglottid width; ovary length represents 13–17% of proglottid length. Relative ovarian size, i.e., ratio of ovary surface of ovary to surface of proglottid (see de Chambrier et al. 2012) 5.5–6.1%. Vagina anterior or posterior to cirrus sac, with vaginal sphincter 25–30 long (thick) and 45–60 in diameter, lined with thick layer of cells in its terminal (distal) part (Fig. 4A,B). Mehlis' gland 90–145 in diameter (Fig. 3A–C), representing 5.9–8.9% of proglottid width.

Vitelline follicles oval to elongate, arranged in two lateral, longitudinal bands on lateral sides of proglottid (Fig. 3A–E), occupying porally 88–96% and 85–94% aporally of proglottid length, interrupted dorsally on poral side at level of terminal genitalia (cirrus sac and vagina) with few vitelline follicles dorsal to cirrus sac, scarcely overlapped by lateral-most testes (Fig. 3A). Follicles closely approaching, but not reaching, anterior or posterior margin of proglottids (Fig. 3A–E).

Primordium of uterine stem ventral (Fig. 4C–E). Formation of uterus of type 1 of de Chambrier et al. (2004), with 17–22 lateral uterine diverticula on each side (21–42 diverticula in specimen from host Ec 4203 – Fig. 3C). Uterus reaching anterior part of proglottids anteriorly and ovarian isthmus posteriorly, never overpassing it (Fig. 3A–G). In terminal proglottids, uterine diverticula represent up to 75% of proglottid width. Eggs spherical, outer (hyaline) envelope up to 90 in diameter, bilayered embryophore 24–26 in diameter, oncospheres 9–11 in diameter with 3 pairs of hooks 5–6 long (Fig. 4G–I).

Taxonomic summary

Type and only host: *Imantodes cenchoa* (Linnaeus), Neotropical blunt-headed treesnake (or blunthead treesnake) (Colubridae: Dipsadinae).

Type locality: San Pablo de Kantesiya, Río Aguarico, Napo, Ecuador (-0.250, -76.433).

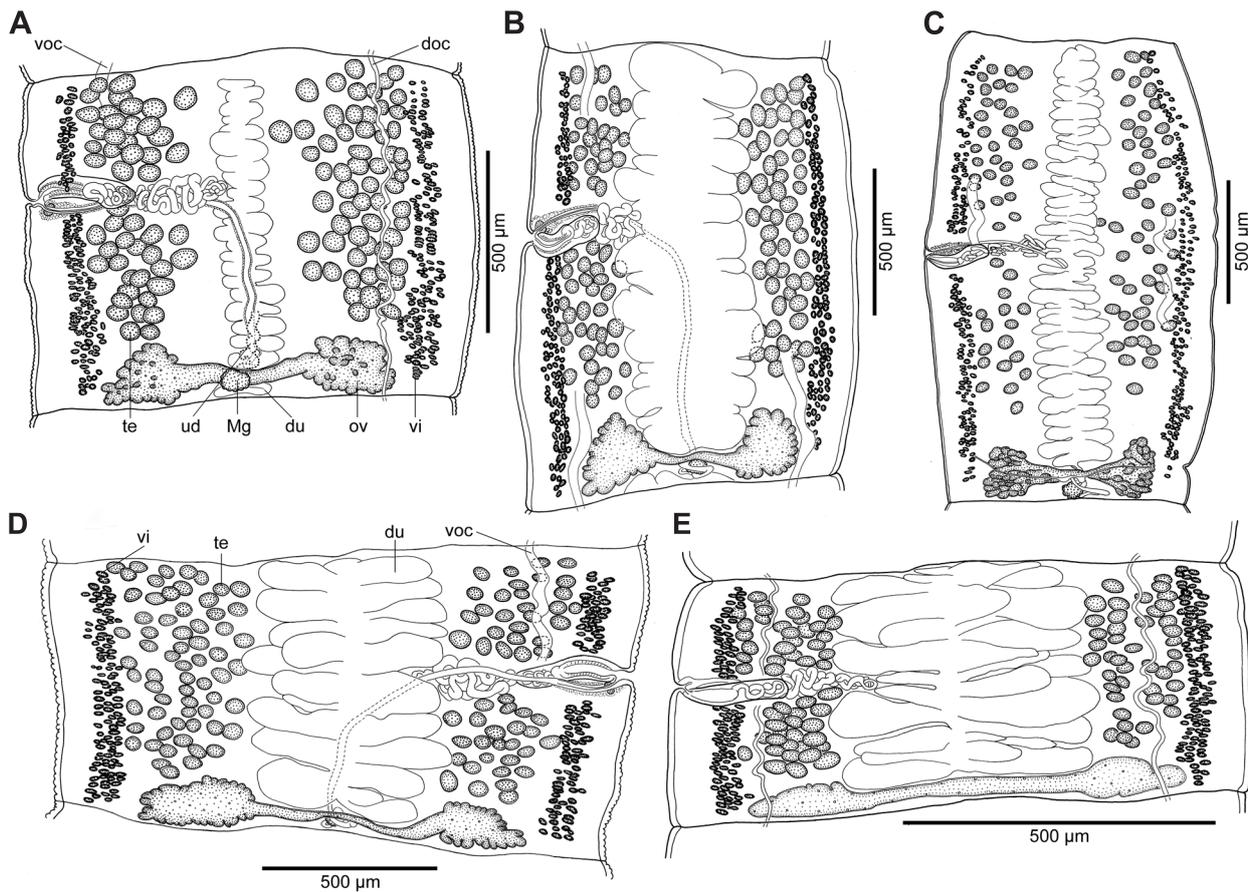Additional locality: Shushufindi, Pozo Shuara P4, Napo, Ecuador (-0.1871, -76.645).

Fig. 3. Proglottids of *Ophiotaenia jeanmarctouzeti* sp. n. (A–D) and *Ophiotaenia* sp. (E) from *Imantodes cenchoa* (Linnaeus), Ecuador. **A, B** – holotype (MNHG-PLAT-0018666); **C** – voucher (MHNG-PLAT-0018668); **D** – paratype (MHNG-PLAT-0018669/IPCAS C-971); **E** – voucher (MHNG-PLAT-0018667). A – mature proglottid, dorsally; B–D – pregravid proglottids, ventrally; note numerous uterine diverticula in C; E – gravid proglottid, ventrally. *Abbreviations*: doc – dorsal osmoregulatory canal; du – diverticula of uterus; Mg – Mehlis' glands; ov – ovary; te – testes; ud – uteroduct; vi – vitelline follicles; voc – ventral osmoregulatory canal.

Site of infection: Intestine.

Infection rate: Infected 5 snakes of 74 examined (prevalence 7%).

Type material: Holotype: complete specimen on three slides from host Ec 2853 (MHNG-PLAT-0018666); paratype: one specimen on three slides and two slides with cross-sections from host Ec 4602 (IPCAS C-971) and two slides with cross-sections (MHNG-PLAT-0018669).

Etymology: The species was named in honour of Jean-Marc Touzet from France, founding member and former director of the Fundación Herpetológica Gustavo Orces during ten years, who collected all specimens in the living area of Siona Secoya people in Ecuador from 1983 to 1989.

Representative DNA sequences and phylogenetic relationships: No molecular data are available.

Differential diagnosis (Tables 1 and 2)

Ophiotaenia jeanmarctouzeti sp. n. differs from all but four species of *Ophiotaenia* parasitising colubrid snakes in the New World, *O. racemosa* (Rudolphi, 1819), *O. nattereri* (Parona, 1901), *O. sanbernardinensis* Rudin, 1917 and *O. currani* de Chambrier, Kudlai, McAllister et Scholz, 2023, by the number of testes (Table 1). The new species differs from *O. racemosa* by the width of the scolex (185–305 μm

compared to 540–650 μm) and by the number of uterine diverticula (usually 17–22 compared to 40–50), and from *O. currani* and *O. nattereri* by a much lower ratio between the length of the cirrus sac and the width of the proglottids (17–25% compared to 35–50%) and a more posterior position of the genital pore (35–47% of the proglottid length compared to 23–32%) (Table 1). *Ophiotaenia jeanmarctouzeti* differs from *O. sanbernardinensis* by the type of uterine development (Type 1 versus Type 2) and by the number of uterine diverticula (17–22 versus 27–33).

Remarks. The tapeworms of the new species from different host specimens resemble each other in most morphological features, but some exceptions are noteworthy. One specimen (voucher) from host Ec 4203 (Figs. 1C, 3C) has more elongated proglottids, a higher number of uterine diverticula than other specimens (up to 42) and fewer testes (72–117), but the specimen otherwise closely resembles the holotype and paratype of *O. jeanmarctouzeti* and is considered tentatively as conspecific. In the absence of molecular data on individual tapeworms of *I. cenchoa*, the above differences are not considered to justify the description of another new species and are regarded as intraspe-

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Table 2. Tapeworms (Cestoda: Proteocephalidae) from colubrid snakes in the New World.

Species	Type host	Country	Total length (mm)	Width of scolex (μm)	Testis number	Relative cirrus sac length[1]	Genital pore position[2]	Position of vagina	Vaginal sphincter	No. uterine diverticula	Apical organ	Ovary surface[3]	Diameter of embryophore	Uterine development[4]
O. arandasi (dos Santos et Tayt-son Rolas, 1973)	Erythrolamprus miliaris	Brazil	70–90	315–480	41–90	35–45%	27–39%	ant-post	absent	N/A	absent	4.7–5.5%	N/A	type 1
O. barbouri Vigueras, 1934	Tretanorhinus variabilis	Cuba	16–18	730	46–58	N/A	33%	posterior	N/A	18–22	absent	2.9%	26–28	N/A
O. currani de Chambrier, Kudlai, McAllister et Scholz, 2023	Nerodia fasciata confluens	USA	86	185–200	89–118	35–50%	23–32%	ant-post	absent	24–36	absent	6%	25–32	type 2
O. elongata Fuhrmann, 1927	"a small snake"	Brazil	30–40	N/A	26–44	N/A	50% (?)	N/A	N/A	13–16	N/A	2.5%	19	N/A
O. faranciae (MacCallum, 1921)	Farancia abacura	USA	>180	500	390–420	25% (?)	16–25%	posterior	N/A	30–50	present	2.1%	N/A	N/A
O. flava Rudin, 1917	"Coluber sp."	Brazil	50–60	500–600	45–60	50%	20–40%	ant-post	absent	N/A	absent	3.6%	28–30	N/A
O. gilberti Ammann et de Chambrier, 2008	Thamnodynastes pallidus	Paraguay	60–120	140–145	57–91	15–23%	42–50%	ant-post	present	28–41	present	3.7%	27–28	type 1
O. habanensis Freze et Rysavy, 1976	Tropidophis pardalis	Cuba	57–67	360	31–51	>50%	~60%	N/A	present	26–32	absent	2.7%	22–28	type 1 (?)
O. hyalina Rudin, 1917	"Coluber sp."	Brazil	120	680–800	50–55	50%	33% (?)	ant-post	present	N/A	absent	5.5%	N/A	N/A
O. karipuna Trindade, Rebêlo et Melo, 2024	Erythrolamprus miliaris	Brazil	6–9	533–619	57–59	36–44%	48–50%	ant-post	absent	19–30	present	4.6–5.5%	20–21	type 1
O. joanae de Chambrier et Paulino, 1997	Xenodon neuwiedii	Brazil	140–250	480–790	147–210	14–25%	28–56%	ant-post	present	26–49	present	3.1%	26–30	type 2
O. laruei de Chambrier, Kudlai, McAllister et Scholz, 2023	Nerodia rhombifer	USA	176	280–340	275–314	13–15%	28–38%	ant-post	present	30–45	absent	5.2%	N/A	type 2
O. nattereri (Parona, 1901)	"Coluber sp."	Brazil	75–250	250	80–100	28–33%	<50%	ant-post	present	15–30	absent	N/A	22–26	N/A
O. paraguayensis Rudin, 1917	Hydrodynastes gigas	Paraguay	550–600	240	238–344	12–19%	27–39%	ant-post	present	20–36	absent	3.3%	21–24	type 2
O. perspicua La Rue, 1911 (type species)	Nerodia rhombifer	USA	360	255–410	150–215	25–33%	33–50%	anterior	present	20–30	present	2.3%	40–43	type 2
O. racemosa (Rudolphi, 1819)	"Coluber sp."	Brazil	160	540–650	80–120	~33%	~33%	ant-post	present	40–50	N/A	4.3%	24	N/A
O. sanbernardinensis Rudin, 1917	Helicops leopardinus	Paraguay	100–120	230–250	70–102	N/A	20–40%	ant-post	present	27–33	absent	5.0%	22–23	type 2
O. tkachi de Chambrier, Kudlai, McAllister et Scholz, 2023	Nerodia fasciata confluens	USA	71–97	190–230	153–261	19–27%	21–33%	mainly post	absent	24–38	absent	5.3–8.5%	18–22	type 2
O. jeanmarctouzeti sp. n.	Imantodes cenchoa	Ecuador	172–450	185–305	100–123	17–25%	35–46%	ant-post	present	17–22	absent	5.5–6.1%	24–26	type 1
Ophiotaenia sp. (Ec 3864)	Imantodes cenchoa	Ecuador	35	705	100–141	18–21%	37–45%	ant-post	present	17–20	absent	3.8–6.1%	18–21	type 1
Ophiotaenia barraganae sp. n.	Oxyrhopus formosus	Ecuador	39–43	570–640	92–123	17–23%	46–57%	ant-post	present	32–49	present	3.0%	15–17	type 1
Ophiotaenia veluscoae sp. n.	Oxyrhopus petolarius	Ecuador	38–89	375–500	45–64	24–32%	31–41%	ant-post	present	15–21	present	5.1–6.1%	21–24	type 1

[1] Ratio of the cirrus sac length to the proglottid width (in%);
[2] Ratio of the genital pore position to the proglottid length (in %);
[3] Ratio of the ovary surface to the proglottid surface (in %; see de Chambrier et al. 2012);
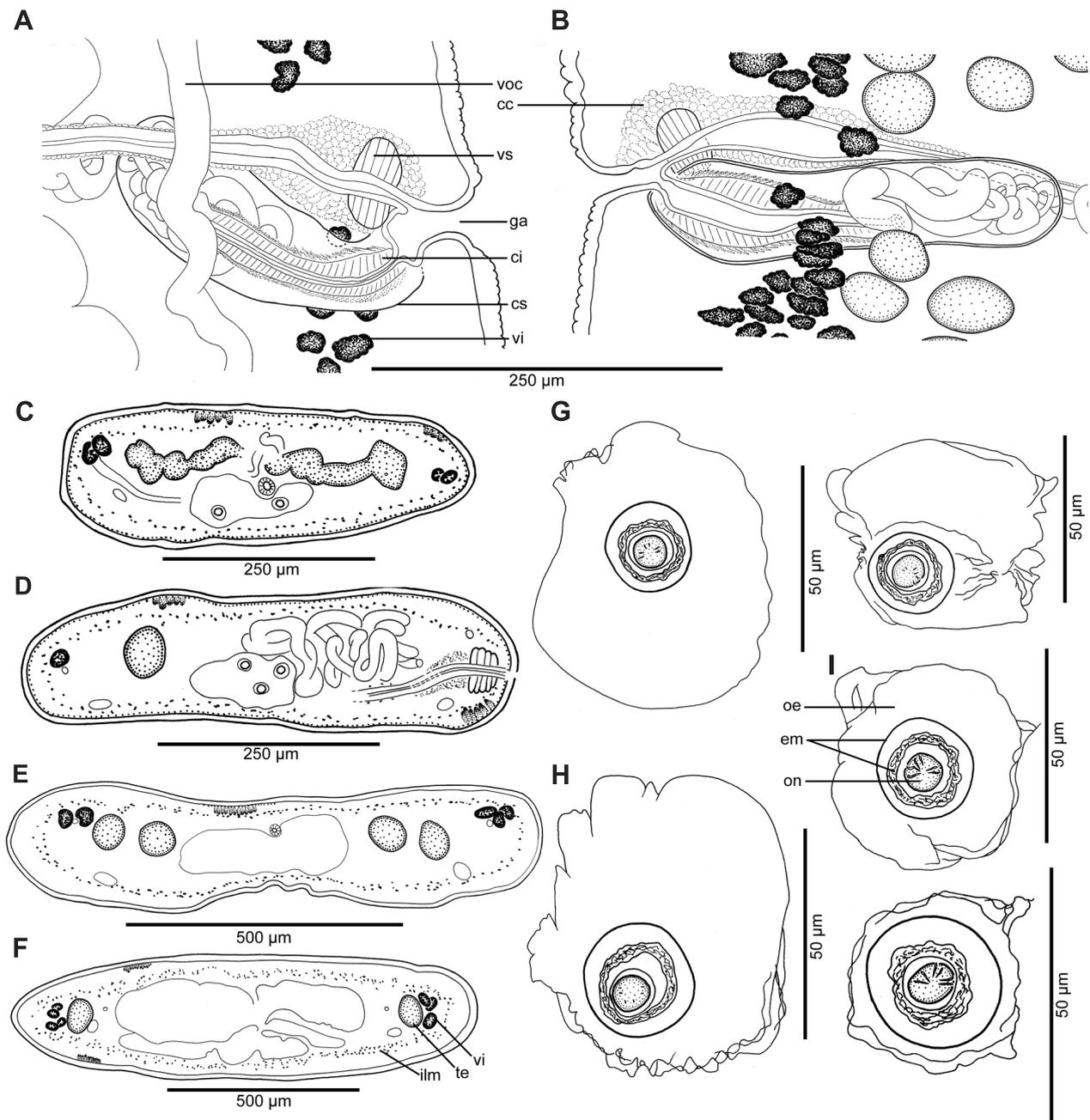[4] Type of development of the uterus according to de Chambrier et al. (2004)

Fig. 4. *Ophiotaenia jeanmarctouzeti* sp. n. from *Imantodes cenchoa* (Linnaeus), Ecuador. A, B – terminal genitalia of holotype, ventrally (MHNG-PLAT-0018666) and voucher, dorsally (MHNG-PLAT-0018668); C–F – cross-sections at the level of the ovary (C), terminal part of the vagina with a sphincter (D – both holotype, MHNG-PLAT-0018666), testes and uterus (E – MHNG-PLAT-0018668) and uterus with lateral diverticula on ventral and dorsal sides (F – MHNG-PLAT-0018667); G–I – eggs in water (G – holotype; H – paratype; I – voucher Ec 4203). *Abbreviations*: cc – chromophilic cells; ci – cirrus; cs – cirrus sac; em – bi-layered embryophore; ga – genital atrium; ilm – inner longitudinal musculature; oe – outer envelope; on – oncosphere; te – testes; vi – vitelline follicles; voc – ventral osmoregulatory canal; vs – vaginal sphincter.

cific variability, as all tapeworms are similar in other morphological and biometric characters (Figs. 1–3; Table 1).

Imantodes is a genus of colubrid snakes commonly referred to as blunt-headed vine snakes or blunt-headed tree snakes. *Imantodes cenchoa* is native to southern Mexico, Central America and South America (up to northern Argentina) (Uetz et al. 2024).

Ophiotaenia barraganae sp. n.   Figs. 2D–F, 5

ZooBank number for species:
urn:lsid:zoobank.org:act:B7C62E8C-9779-45B4-BB72-7BB4283CD312

Material studied: Two slides with two specimens, 12 slides with cross-sections and scolex for SEM from *Oxyrhopus formosus* (Wied-Neuwied) Ec 3260, San Pablo
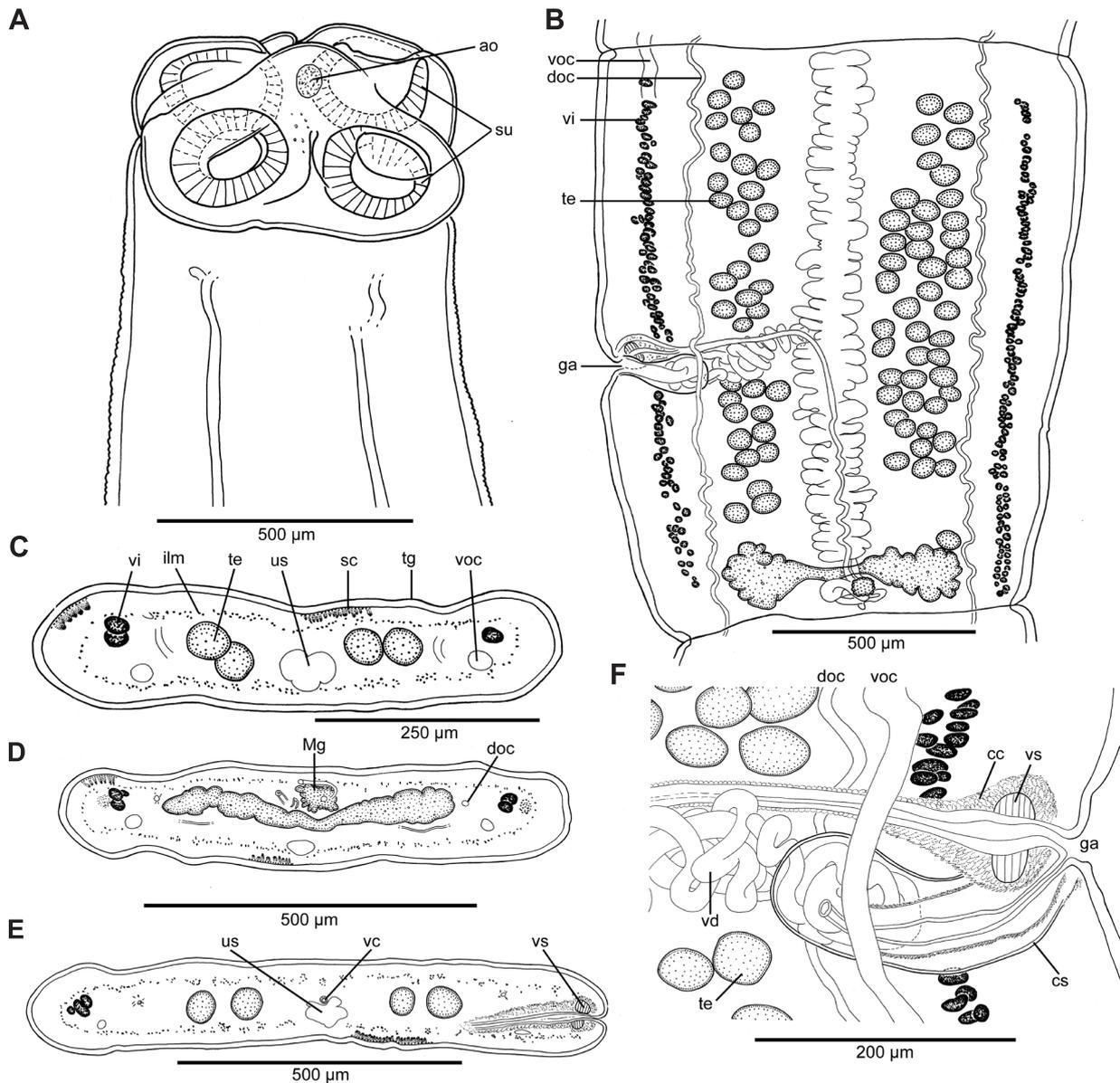
Fig. 5. *Ophiotaenia barraganae* sp. n. from *Oxyrhopus formosus* (Wied-Neuwied) (host Ec 3260), Ecuador. **A** – scolex; **B** – pre-gravid proglottid, dorsally; **C–E** – cross-sections at the level of testes (C), ovary (D) and distal vagina (E; note a ring-like vaginal sphincter and terminal part of the vagina lined with numerous cells); **F** – terminal genitalia, ventrally. **A, C, D, F** – paratype (MHNG-PLAT-0159497); B, E – holotype (MHNG-PLAT-0018671). *Abbreviations*: ao – apical organ; cc – chromophilic cells; cs – cirrus sac; doc – dorsal osmoregulatory canal; ga – genital atrium; ilm – inner longitudinal musculature; Mg – Mehlis gland; sc – sub-tegumental cells; su – suckers; te – testes; tg – tegument; us – uterine stem; vc – vaginal canal; vd – vas deferens; vi – vitelline follicles; voc – ventral osmoregulatory canal; vs – vaginal sphincter.

de Kantesiya, Río Aguarico Napo, Ecuador, collected by J.-M. Touzet on 19 April 1987 (IPCAS C-972; MHNG-PLAT-0018671).

Description (based on holotype and paratype; measurements in Table 1): Proteocephalidae. Small worms, 39 and 43 mm long, up to 1.5 mm wide, flattened dorsoventrally, with proglottids square to elongated, up to 1,410 long. Strobila acraspedote, anapolytic. Immature proglottids wider than long (length: width ratio 0.07–0.64); mature (length: width ratio 0.51–1.80), pregravid (length: width ratio 0.72–1.59) and gravid (length: width ratio 1.24–3.27) proglottids wider than long to longer than wide (Fig. 5B). Tegument thick, 17–22 in thickness.

Scolex spherical, aspinose (Figs. 2D–F, 5A), wider than neck, 385–420 long, 570–640 width, with four uniloculate, spherical suckers 200–240 in diameter, directed anterolaterally (Figs. 2D–F, 5A); small apical organ present under the apex, 60–72 long and 50–55 wide (Fig. 5A). Neck up to 630 wide; unsegmented zone posterior to scolex to first recognisable proglottids long (up to 3.2 mm).

Inner longitudinal musculature formed by individual muscle fibres, often close together, but not forming bundles (Fig. 5C–E). Osmoregulatory canals median to vitelline follicles, crossing lateral margin of ovarian wings, not overlapping testicular fields (Fig. 5B). Ventral canals thin-walled, 20–25 in diameter, sinuous, overlapping ventrally vitelline follicles
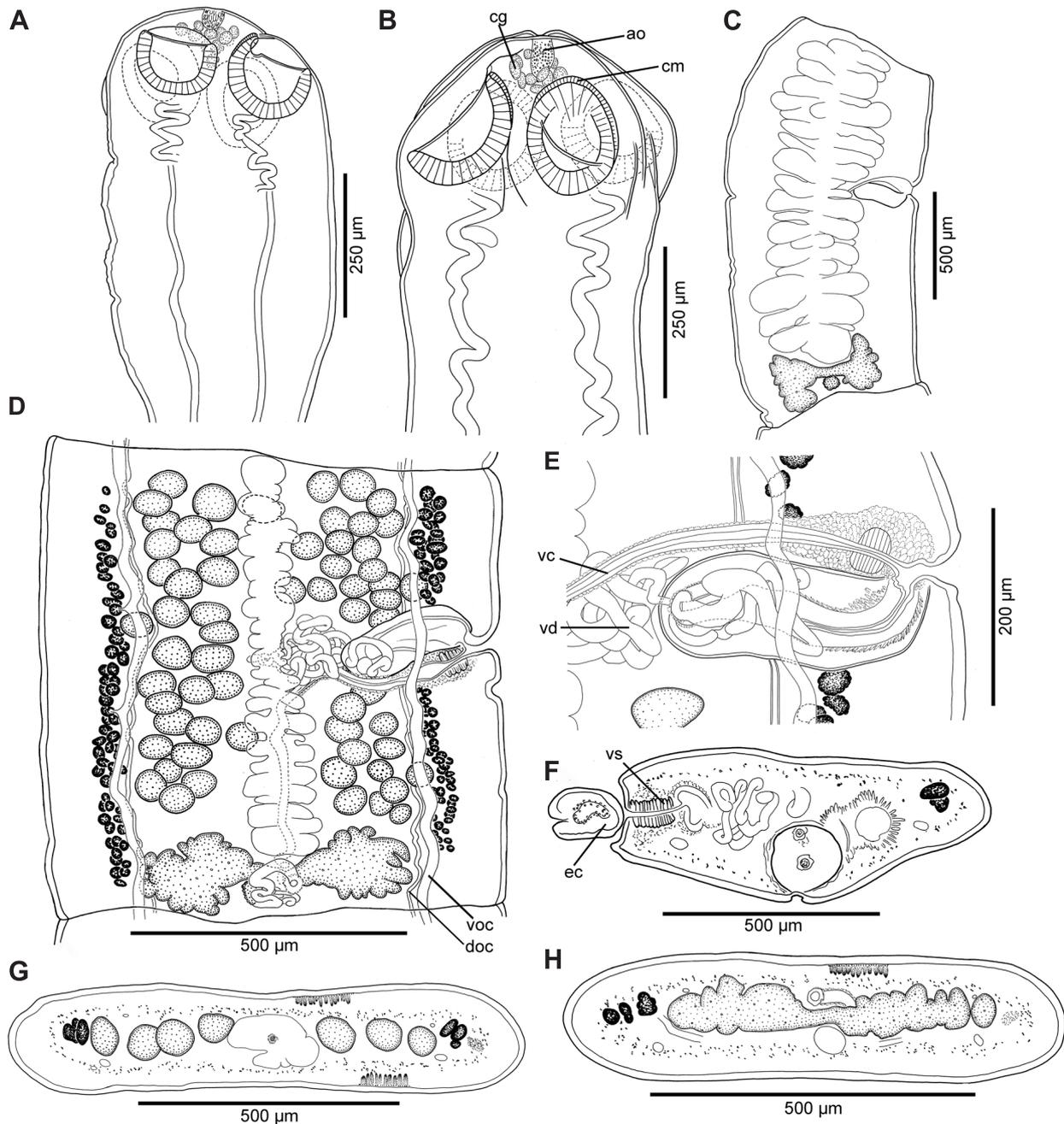
Fig. 6. *Ophiotaenia velascoae* sp. n. from *Oxyrhopus petolarius* (Linnaeus), Ecuador. **A**, **B** – scolex; **C** – sketch of gravid proglottid, ventrally; **D** – pregravid proglottid, ventrally; **E** – terminal genitalia, ventrally; **F–H** – cross-sections at the level of the uterus and vaginal sphincter F), testes (G) and ovary (H). A, C–H – holotype (MHNG-PLAT-0018672); B – paratype (MHNG-PLAT-0018885). *Abbreviations*: ao – apical organ; cg – cells with finely granular cytoplasm; cm – circular musculature; doc – dorsal osmoregulatory canal; ec – evaginated cirrus: vc – vaginal canal; vd – vas deferens; voc – ventral osmoregulatory canal; vs – vaginal sphincter.

(Fig. 5B,D); dorsal canals sinuous, thick-walled, about 8–10 in diameter, median to ventral canals (Fig. 5B–D), situated 16–19% of proglottid width from lateral margins. Genital ducts run between osmoregulatory canals (Fig. 5D).

Testes oval to elongated, in one or two layers and in two fields between vitelline follicles, in more or less compact bands, 92–123 in number, 45–70 long to 30–55 wide; each testicular field situated at 20–24% of proglottid width from lateral margin, never separated by osmoregulatory canals (Fig. 5B). Testes do not reach anterior margin of proglottids anteriorly and do very scarcely reach posterior margin of

ovary posteriorly (Fig. 5B). Testes degenerate progressively with maturation of pregravid and gravid proglottids. Vas deferens strongly coiled distally, becoming thinner when approaching median side of proglottid, never reaching midline of proglottid (Fig. 5B). Cirrus sac pear-shaped to elongate, thick-walled, 215–270 long by 60–85 wide (Fig. 5F); length: width ratio 2.65–4.07. Cirrus sac length/proglottid width ratio 17–23%. Cirrus occupies 62–70% of length of cirrus sac (Fig. 5F). Genital atrium shallow. Genital pores irregularly alternating, slightly pre-equatorial to slightly post equatorial, at 46–57% of proglottid length (Fig. 5B).

Ovary large, slightly lobed, lateral wings elongate-oval, 530–755 wide, with narrow and long isthmus (Fig. 5B). Ovary width represents 56–60% of proglottid width; ovary length represents 9–13% of proglottid length. Relative ovarian size, i.e., ratio of ovary surface of ovary to surface of proglottid (see de Chambrier et al. 2012) 3.0%. Vagina thick, anterior or posterior to cirrus sac, with large vaginal sphincter 75–95 thick (long) and 80–85 in diameter, lined with a thick layer of chromophil cells in its terminal (distal) part (Fig. 5E,F). Mehlis' gland 55–80 in diameter, representing 4.8–6.5% of proglottid width.

Vitelline follicles arranged in two longitudinal bands on lateral sides of proglottid (Fig. 5B), occupying 88–96% and 88–97% of proglottid length on poral and aporal sides, respectively, interrupted ventrally on poral side at level of terminal genitalia (cirrus sac and vagina) with few vitelline follicles dorsal to cirrus sac. Follicles approaching, but not reaching, anterior or posterior margin of proglottids (Fig. 5B).

Primordium of uterine stem ventral (Fig. 5B–E). Formation of uterus of type 1 of de Chambrier et al. (2004). Uterus with about 32–49 uterine diverticula. Uterus length occupies about 91–94% of proglottid length. Eggs spherical, embryophore 15–17 and oncosphere 9–10 in diameter (measured in whole mounts).

Taxonomic summary

T y p e   a n d   o n l y   h o s t : Beautiful calico snake or false coral snake *Oxyrhopus formosus* (Colubridae: Dipsadinae).

T y p e   a n d   o n l y   l o c a l i t y : San Pablo de Kantesiya, Río Aguarico Napo, Ecuador (-0.250, -76.433).

S i t e   o f   i n f e c t i o n : Intestine.

I n f e c t i o n   r a t e : Infected one snake of two examined.

T y p e   m a t e r i a l : Holotype: one specimen on two slides and two slides with cross-sections from host Ec 3260 (MHNG-PLAT-0018671); paratype: one specimen on one slide and seven slides with cross-sections from the same host specimen (IPCAS C-972).

E t y m o l o g y : This species is dedicated to María Elena Barragan, director of the Fundación Herpetológica Gustavo Orces, who has contributed significantly to the current knowledge and protection of the reptiles and amphibians of Ecuador.

R e p r e s e n t a t i v e   D N A   s e q u e n c e s   a n d   p h y l o g e n e t i c   r e l a t i o n s h i p s : No molecular data are available.

Differential diagnosis (Tables 1 and 2)

The most typical feature of *O. barraganae* sp. n. is the position of the testes, which are arranged on both sides of the proglottids at a distance from the vitelline follicles and always median to the osmoregulatory canals (Fig. 5B). A somewhat similar arrangement of testes exists only in *Ophiotaenia jarara* Fuhrmann, 1927, a parasite of *Bothrops alternatus* Duméril, Bibron et Duméril in Brazil (Fuhrmann 1927, de Chambrier et al. 1991), but this species differs from *O. barraganae* sp. n. in having a larger scolex (1.1–1.2 mm versus 570–640 µm), the vagina anterior to the cirrus sac and the absence of a vaginal sphincter.

In addition, the new species has a type 1 uterine development and differs from species with the same uterine

development except *O. nattereri*, *O. racemosa* and *O. jeanmarctouzeti* sp. n. by the number of testes (92–123 vs. < 91 or > 140). *Ophiotaenia nattereri* differs from the new species by the width of the scolex (250 µm versus 570–640 µm), by the ratio of the length of the cirrus sac to the length of the proglottids (28–33% vs. 17–23%) and by the absence of an apical organ (Table 1). *Ophiotaenia racemosa* differs from *O. barraganae* sp.n. by the relative size of the cirrus sac (33% of proglottid width versus 17–23%), and by the position of the genital pore position (33% vs. 46–57%). *Ophiotaenia jeanmarctouzeti* sp. n. differs from *O. barraganae* sp. n. by the width of the scolex (185–305 µm vs. 570–640 µm), by the position of the genital pore (35–47%, i.e., pre-equatorial, vs. 46–57%, i.e., more or less equatorial) and by the number of uterine diverticula (Table 1).

Remarks. Only two specimens of the new species were found in a specimen of *Oxyrhopus formosus*, but these specimens are clearly distinct from other *Ophiotaenia* species, including *O. jeanmarctouzeti* sp. n., which was described from another dipsadine snake at the same locality in Ecuador (see above). *Ophiotaenia barraganae* sp. n. is almost unique among *Ophiotaenia* species because of the arrangement of the testes, which form well-separated longitudinal fields at some distance from the vitelline follicles.

The arrangement of the testes in two compact bands on the sides of the proglottids at some distance from the vitelline follicles is very unusual in the Proteocephalidae. In most *Ophiotaenia* species, the testicular fields are arranged more laterally and touch vitelline follicles, often being divided into two unequal groups of testes by osmoregulatory ducts. Only *O. jarara* has a similar arrangement of testes to the new species (see de Chambrier et al. 1991). *Ophiotaenia echidis* de Chambrier, Alves, Schuster et Scholz, 2021 from the saw-scaled viper, *Echis carinatus sochureki* Stemmler (Ophidia: Viperidae), in the United Arab Emirates also has testicular fields spaced from the vitelline follicles, but the testes are arranged in a single longitudinal line on each side of proglottids (de Chambrier et al. 2021).

The type and only host of the new species, *O. formosus*, was described from Bahia (Brazil) and has also been reported from Argentina, Colombia, French Guiana, Peru, Suriname and Venezuela (Uetz et al. 2024). However, the distribution range of this snake is not fully known due to imprecise identification and confusion with other *Oxyrhopus* species (Uetz et al. 2024).

Ophiotaenia velascoae sp. n.　　　　　　　Figs. 2G, 6

ZooBank number for species:
urn:lsid:zoobank.org:act:DC0D4714-D3AF-4CAE-A401-FF44E34E374B

Material studied: One slide with a few gravid proglottids from *Oxyrhopus petolarius* (Linnaeus) (Ec 229), San Pablo de Kantesiya, Río Aguarico, Napo, Ecuador, collected on 21 February 1985 (MHNG-PLAT-0018670); two slides with three immature specimens on one slide and another slide with almost complete specimen, four slides with cross-sections and scolex for SEM from host Ec 2385,

San Pablo de Kantesiya, Río Aguarico, Napo, Ecuador, 15 November 1986 (IPCAS C-973; MHNG-PLAT-0018885); two slides with one scolex and fragments of one gravid specimen and four slides with cross-sections from host Ec 3920, Shushufindi, Pozo Shuara P4, Napo, Ecuador, 19 September 1987 (MHNG-PLAT-0018672); two slides with longitudinal sections of the scolex, 12 slides with cross-sections and scolex for SEM from host Ec 4623, San Pablo de Kantesiya, Río Aguarico, Napo, Ecuador, 19 June 1988 (IPCAS C-973; MHNG-PLAT-0018699), all specimens collected by J.-M. Touzet.

Description (based on four specimens from hosts Ec 2385 and Ec 3920; measurements of individual specimens in Table 1): Proteocephalidae. Medium-sized worms, up to 89 mm long and 1.0 mm wide, flattened dorsoventrally, with proglottids square to elongate, up to 1.7 mm long. Strobila acraspedote, anapolytic. Immature proglottids wider than long to longer than wide (length: width ratio 0.63–1.32); mature proglottids wider than long to longer than wide (length: width ratio 0.79–1.60), pregravid proglottids almost square to longer than wide (length: width ratio 1.04–1.41) and gravid proglottids slightly wider than long to much longer than wide (length: width ratio 0.94–2.39) (Fig. 6C,D). Tegument thick, 15–18 in thickness.

Scolex spherical, aspinose (Figs. 2G, 6A,B), wider than neck, 265–310 long, 375–500 width, with four uniloculate, spherical suckers 135–200 in diameter, directed anterolaterally (Figs. 2G, 6A,B); Anterior margin of suckers with circular muscles (Fig. 6A,B). Apical organ 40–65 long and 35–50 wide; large cells (8–20 × 15–30) of granular content in scolex apex, surrounding apical organ posteriorly (Fig. 6A,B). Neck up to 350–415 wide; unsegmented zone posterior to scolex to first recognisable proglottids long (up to 7 mm).

Inner longitudinal musculature developed, consisting of isolated muscle fibres (Fig. 6F–H). Osmoregulatory canals median to vitelline follicles or overlapping them, crossing or not lateral margin of ovarian wings, rarely overlapping testicular fields. Ventral canals thin-walled, wide, 10–20 in diameter, showing some secondary canals; dorsal canals sligthly sinuous, thick-walled, about 3–5 in diameter, situated at same level as ventral canals or slightly more median (Fig. 6D–F). Genital ducts run between osmoregulatory canals (Fig. 6D,E).

Testes oval to spherical, in one or two layers and in two fields between vitelline follicles, 45–63 in number; testes very scarcely overlapped by osmoregulatory canals (Fig. 6D). Testes reach anterior margin of proglottids anteriorly but do not reach anterior margin of ovary posteriorly (Fig. 6D), disappear progressively when proglottids become gravid. Vas deferens strongly coiled, reaching mid-line of proglottid and sometimes overlapping it, occupying widely oval area (Fig. 6D). Cirrus sac pyriform, thin-walled, 220–295 long by 65–115 wide (Fig. 6E); length: width ratio 1.97–3.30. Cirrus sac width/proglottid width ratio 24–32%. Cirrus occupies up to 90% of length of cirrus sac (Fig. 6E). Genital atrium shallow and narrow. Genital pores irregularly alternating, pre-equatorial, at 31–41% of proglottid length (Fig. 6D).

Ovary large, folliculate, bilobed, 320–720 wide, with a short isthmus (Fig. 6D). Ovary width represents 60–71% of proglottid width; ovary length represents 11–19% of proglottid length. Relative ovarian size, i.e., ratio of ovary surface of ovary to surface of proglottid (see de Chambrier et al. 2012) 5.1–6.1%. Vagina anterior or posterior to cirrus sac, with well-developed vaginal sphincter 40–70 thick (long) and 40–50 in diameter, lined with thick layer of chromophil cells in its terminal (distal) part (Fig. 6D–F). Mehlis' gland 60–90 in diameter, representing 7.6–14.0% of proglottid width.

Vitelline follicles oval, arranged in two lateral, longitudinal bands on lateral sides of proglottid (Fig. 6D), occupying porally 76–87% and aporally 70–87% of proglottid length, interrupted ventrally on poral side at level of terminal genitalia (cirrus sac and vagina; Fig. 6E), with few vitelline follicles dorsal to cirrus sac, scarcely overlapped by lateral-most testes. Follicles not reaching anterior or posterior margin of proglottids (Fig. 6D).

Primordium of uterine stem ventral (Fig. 6D,F,H). Formation of uterus of type 1 of de Chambrier et al. (2004). Uterus with 15–21 lateral diverticula on each side. In terminal proglottids, uterine diverticula represent up to 74% of proglottid width. Eggs spherical, embryophore 21–24 and oncosphere 10–13 in diameter (measured in whole mounted slides).

Taxonomic summary

Type and only host: Forest flame snake *Oxyrhopus petolarius* (Colubridae: Dipsadinae).

Type locality: Shushufindi, Pozo Shuara P4, Napo, Ecuador (-0.1871, -76.645).

Additional locality: San Pablo de Kantesiya, Río Aguarico Napo, Ecuador (-0.250, -76.433).

Site of infection: Intestine.

Infection rate: Infected four of 26 snakes examined (prevalence 15%).

Type material: Holotype: one adult specimen on two slides and four slides with cross-sections from host Ec 3920 (MHNG-PLAT-0018672); paratype: one slide with almost complete specimen and two slides with cross-sections from host Ec2385 (MHNG-PLAT-0018865) and two slides with cross-sections (IPCAS C-973).

Etymology: This species is named in honour of Ana María Velasco, co-founder and former director of the Fundación Herpetológica Gustavo Orces, who played an essential role in the education of many young Ecuadorian scientists.

Representative DNA sequences and phylogenetic relationships: No molecular data are available.

Differential diagnosis (Tables 1 and 2)

Ophiotaenia velascoae sp. n. has a type 1 uterine development and differs from species with the same uterine development, i.e., *O. faranciae* (MacCallum, 1921), *O. nattereri*, *O. racemosa* and *O. jeanmarctouzeti* sp. n., by the number of testes (see Table 2). The new species differs from *O. elongata* Fuhrmann, 1927, *O. gilberti* Ammann et de Chambrier, 2008, *O. habanensis* Freze et Rysavy, 1976, *O. hyalina* Rudin, 1917 and *O. karipuna* Trindade, Rebêlo

et Melo, 2024 by the position of the genital pore and from *O. arandasi* (dos Santos et Tayt-son Rolas, 1973), *O. flava* Rudin, 1917 and *O. karipuna* by the presence of a vaginal sphincter (Table 2). *Ophiotaenia velascoae* sp. n. differs from *O. barbouri* Vigueras, 1934 in the position of the vagina (posterior in *O. barbouri* vs. anterior and posterior in *O. velascoae* sp. n.) and from *O. barraganae* sp. n. by fewer testes (92–123 vs. 45–64) and uterine diverticula (15–21 vs. 32–49) and position of the gonopore (31–41 % of the proglottid length vs. 46–57%).

Remarks. Two new species of *Ophiotaenia* are described from congeneric hosts, namely *Oxyrhopus formosus* and *O. petolarius*, from the same locality. Although no molecular data are available on these species, they are morphologically so different (see Figs. 5 and 6 and data in Table 1) that there is no doubt about their validity. Both species are most likely strictly specific (oioxenous, i.e., occurring in a single host species), similar to other proteocephalids of reptiles in the Neotropics (Ammann and de Chambrier 2008, de Chambrier et al. 2017). In contrast, some species of *Ophiotaenia* from Nearctic watersnakes (Colubridae), such as *O. tkachi* de Chambrier, Kudlai, McAllister et Scholz, 2023, are not as strictly specific and occur in up to four species of *Nerodia* Baird et Girard (Colubridae) and in the cottonmouth *Agkistrodon piscivorus* (Lacépède) (Viperidae) (de Chambrier et al. 2023).

The presence of an apical organ surrounded by large cells with granular contents is not common in *Ophiotaenia* species. Only *O. bungari* de Chambrier, Binh et Scholz, 2012 and *O. gilberti* have the same morphology of the apical region as *O. velascoae* sp. n. (see Ammann and de Chambrier 2008, de Chambrier et al. 2012). Suckers surrounded anteriorly by circular musculature have already been described for some proteocephalid cestodes from freshwater siluriforms (e.g., Woodland 1925, Jones et al. 1954, Pavanelli and Rego 1992, Rego 1994, de Chambrier and Rego 1995). In the proteocephalids of reptiles, this structure has only been observed in a few parasites of snakes, e.g., *Ophiotaenia jarara* and *O. catzeflisi* de (Chambrier, Vaucher et Renaud, 1992) by de Chambrier et al. (1991, 1992).

The type and only host of the new species, *O. petolarius*, occurs in southeastern Mexico, Central America and South America as far as Argentina (Uetz et al. 2024).

Ophiotaenia sp.   Figs. 1D, 3E, 4F

Material examined: One specimen on one slide and two slides with cross-sections from *Imantodes cenchoa* (Linnaeus) Ec 3864, Shushufindi, Pozo Shuara P4, Napo, Ecuador, 16 September 1987 (MHNG-PLAT-0018667).

Remarks. The dimensions of this highly contracted tapeworm are shown in Table 1. Although it resembles *O. jeanmarctouzeti* sp. n. and was found in the same host, it is referred to as *Ophiotaenia* sp. It is much shorter and wider compared to *O. jeanmarctouzeti* (scolex width 705 µm – Fig. 1D), possibly due to the strong contraction that seems to have affected the dimensions of the worm (Table 1). It is probably another new species, differing from

O. jeanmarctouzeti sp. n. by a larger scolex with suckers with circular muscles on the margin (Fig. 1D).

The presence of more than one species of *Ophiotaenia* in *I. cenchoa* is likely because another tapeworm with a similar scolex morphology (width of scolex 435 µm), including the presence of circular muscles on the outer edge of the suckers (Fig. 1E), was found in *I. cenchoa* from Costa Rica collected by Daniel R. Brooks on 6 March 2003 (MHNG-PLAT-0061483). Unfortunately, neither of these specimens is good enough for a reliable description of a new species.

DISCUSSION

Most proteocephalid tapeworms in amphibians and reptiles have been classified in the most species-rich genus *Ophiotaenia*, with around 100 nominal species (de Chambrier et al. 2017, Caira et al. 2024). However, this genus is an artificial, non-monophyletic assemblage of not closely related groups of tapeworms that parasitise different groups of amphibian and reptilian hosts worldwide (de Chambrier et al. 2015). Recently, de Chambrier et al. (2023) genetically and morphologically characterised *O. perspicua* La Rue, 1911, the type species of the genus described from the northern diamondback watersnake, *Nerodia rhombifer* (Hallowell) (Colubridae: Natricinae), in North America. The authors show that tapeworms of watersnakes (Colubridae) in the Nearctic and Palaearctic belong to the 'true' *Ophiotaenia* (= *Ophiotaenia* sensu stricto).

In contrast, large tapeworms that have been reported from venomous snakes in the tropics, including Australia (clade K of de Chambrier et al. 2015), *O. paraguayensis* Rudin, 1917 from the false water cobra *Hydrodynastes gigas* (Duméril, Bibron et Duméril) in Paraguay and *O. sanbernardinensis* from the leopard keelback *Helicops leopardinus* (Schlegel) (both Colubridae: Dipsadinae) in Paraguay (clade N of de Chambrier et al. 2015), *O. filaroides* (La Rue, 1909) from the tiger salamander *Ambystoma tigrinum* (Green) (Urodela: Ambystomatidae), *O. marenzelleri* (Barrois, 1898) from the northern cottonmouth *Agkistrodon piscivorus*, and *O. saphena* Osler, 1931 from true frogs (Urodela: Ranidae), all in North America, should not really be classified in *Ophiotaenia* (de Chambrier et al. 2015, 2018, 2023, Scholz et al. 2023a,b).

In the absence of molecular data for the three new species, it is not clear whether they are closely related to *O. paraguayensis* and *O. sanbernardinensis*, which have also been described from dipsadine snakes from the Neotropical region (Paraguay). Although these species are morphologically similar, they differ significantly in the development of the uterus: the new species have a type 1 uterine development, while *O. paraguayensis* and *O. sanbernardinensis* have a type 2 uterine development. The similarity in other features does not necessarily mean that they are closely related, as the *Ophiotaenia* species of reptiles are very uniform and morphological features are homoplastic (de Chambrier et al. 2015).

The Dipsadinae are a large subfamily of colubrid snakes with more than 700 species (Pyron et al. 2013, Zheng and Wiens 2016, Uetz et al. 2024), sometimes previously re-

ferred to as a family (Dipsadidae) (Vidal et al. 2010). They are found in most parts of the Americas, including the West Indies, and are most diverse in South America (Grazziotin et al. 2012). Dipsadine snakes are an ecologically and morphologically diverse group of mostly small to medium-sized snakes (typically with a total length less than 80 cm). Some are arboreal, others live in water or on land and can even burrow. Most are oviparous (Vitt and Caldwell 2014). Many eat frogs or lizards, some also eat mammals and birds. Snakes of several genera specialise on sticky and slimy prey such as frog eggs, earthworms, snails and slugs (Ray et al. 2012). Almost all species are completely harmless to humans, although some genera have caused painful bites with localised, non-life-threatening symptoms (Weinstein et al. 2011).

The life cycles of a few *Ophiotaenia* species are at least partially known but nothing is known about the development and transmission of the Neotropical taxa. It can be assumed that planktonic crustaceans (copepods) serve as first intermediate hosts and amphibians (tadpoles?) and small fish may serve as second intermediate or paratenic hosts, based on the analogy with the taxa from temperate zones such as *O. perspicua* and *O. europaea* Odening, 1963 from watersnakes in North America and Europe (Thomas 1934a, 1941, Biserkov and Genov 1988), and *O. saphena* Osler, 1931 and *O. ranae* Yamaguti, 1938 from ranid frogs in North America and Japan (La Rue 1909, Thomas 1931, 1934b, Yamaguti 1943, Buhler 1970).

The parasite fauna of *Imantodes cenchoa* and *Oxyrhopus* spp. snakes is poorly known, and only the following helminths were found by Goldberg and Bursey (2009), McAllister et al. (2010) in *I. cenchoa* from Costa Rica and Peru: cystacanths of one acanthocephalan (Oligacanthorhynchidae), tetrathyridia of the cestode *Mesocestoides* sp. (Mesocestoididae) and the nematodes *Strongylurus*

oscari Travassos, 1923 (Heterakidae) and *Physalopteroides venancioni* (Lent, Freitas et Proenca, 1946) (Physalopteridae). In addition, Peichoto et al. (2016) found the ascaridid nematode *Hexametra boddaertii* (Baird, 1860) in *Oxyrhopus guibei* Hoge et Romano collected in Iguazu National Park (Argentina).

However, further studies will certainly reveal new taxa of proteocephalids and other helminth parasites in Neotropical reptiles, provided that it will be possible to screen these potential hosts for parasites. Given the current decline in faunal surveys, the limited number of specialists able to properly work on helminth parasites, and the limitations in terms of accessibility of herptiles for parasitological studies, it is uncertain whether the current diversity of parasites of these hosts will be sufficiently known in the near future. In contrast, there is a risk that many herptiles will become extinct before their parasite fauna is uncovered and adequately characterised.

Contribution of the authors. Two reviewers provided helpful suggestions. Alain de Chambrier stained and sectioned all tapeworms for the following study. Alain de Chambrier and Tomáš Scholz performed the morphological analysis. Roman Kuchta carried out the SEM observations. Tomáš Scholz wrote the original draft of the manuscript. All authors read and corrected the manuscript. Tomáš Scholz received financial support.

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Cite this article as: de Chambrier A., Kuchta R., Scholz T. 2024: Three new species of *Ophiotaenia* La Rue, 1911 (Cestoda: Proteocephalidae) from dipsadine snakes (Squamata: Colubridae) in Ecuador. Folia Parasitol. 71: 020.