Ophiotaenia bonneti sp. n. (Eucestoda: Proteocephalidea), a parasite of *Rana vaillanti* (Anura: Ranidae) in Costa Rica

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Abstract. *Ophiotaenia bonneti* sp. n. is described from the intestine of the frog *Rana vaillanti* Brocchi, 1877 (Anura: Ranidae) from San Gerardo, Guanacaste, Costa Rica. The new species is characterized by the testes 100–177 in number, the genital pores situated anteriorly, the osmoregulatory canals overlapping the testis field, the cirrus pouch length as 15–24% of proglottis width, and the uterus with 18–32 ramified diverticula on each side. It differs from the 23 known species of the genus *Ophiotaenia* La Rue, 1911, parasitic in amphibians, by one to several morphological characters. It differs from *O. gracilis* Jones, Cheng et Gillespie, 1958, the most morphologically similar species, in the sucker diameter in % of scolex diameter and in the morphology of the eggs – funnel-like depression and embryophore closely investing the oncosphere in *O. gracilis*. We generally observe a very low mean prevalence of the Proteocephalidea in Neotropical amphibians (about 0.41%–3%), but in the case of some host species, the prevalence can reach up to 25%. We conclude that these cestodes exhibit a strict host specificity of the oioxene type. *Ophiotaenia junglensis* Srivastava et Capoor, 1980 is considered a *species inquirenda*. *Batrachotaenia hernandezi* (Flores-Barroeta, 1955) becomes *Ophiotaenia hernandezi* (Flores-Barroeta, 1955) comb. n., *B. tigrina* (Woodland, 1925) becomes *O. tigrina* (Woodland, 1925) comb. n. and *B. ceratophrys* (Parodi et Widakowich, 1916) becomes *O. ceratophrys* (Parodi et Widakowich, 1916) comb. n.

As a part of its mandate to develop and manage sustainably Costa Rica's biodiversity resources, the Area de Conservación Guanacaste (ACG) has approved a long-term project called "Inventory of the Eukaryotic Parasites of Vertebrates of the Area de Conservación Guanacaste". This is an effort to document all species of eukaryotic parasites inhabiting the estimated 940 species of vertebrates with populations living within the boundaries of the ACG.

In the framework of this project, 147 *Rana vaillanti* Brocchi, 1877 were examined for parasites between 1999 and 2002. Among them, 33 *Rana vaillanti* (22%) were found to harbour tapeworms belonging to the Proteocephalidea. In the Central American region, only one species of proteocephalidean, *Batrachotaenia hernandezi* (Flores-Barroeta, 1955), has previously been described from an amphibian, *Rana* sp., in Mexico (Flores-Barroeta 1955). The characteristics of the Costa Rican material led us to describe a new species of *Ophiotaenia* La Rue, 1911 in the present paper.

MATERIALS AND METHODS

The cestode specimens were fixed directly after dissection of the host's intestine in AFA solution and subsequently stored in 75% (v/v) ethanol. They were stained with Mayer's hydrochloric carmine solution or Weigert's haematoxylin, dehydrated in ethanol, cleared with Eugenol (clove oil) and mounted in Canada balsam. Pieces of strobila were embedded in paraffin wax, sectioned transversely at 12 µm, stained with

Weigert's haematoxylin and counterstained with 1% eosin B (acidified with five drops of pure acetic acid for 100 ml solution) following recently updated protocols (Scholz and Hanzelová 1998, de Chambrier 2001).

Three specimens were prepared for scanning electron microscopy (SEM) as follows: specimens were dehydrated in graded ethanol series, then transferred to graded amyl acetate series, critical point dried in CO₂, sputtered with gold and examined with a Zeiss DSM 940 A electron microscope at the Museum of Natural History, Geneva. Eggs were studied in distilled water. Microtrix terminology follows Thompson et al. (1980) and Hoberg et al. (1995). All measurements are given in micrometres unless otherwise indicated. Abbreviations used in descriptions are as follows: × – mean; n – number of measurements; OV – ovarian width as % of proglottis width; PP – position of genital pore as % of proglottis length from anterior end; PC – cirrus pouch length as % of proglottis width; CV – coefficient of variation. Museum abbreviations used are as follows: MHNG: Geneva Natural History Museum, Invertebrate Collection (INVE), Geneva, Switzerland; IPCAS: Institute of Parasitology, ASCR, České Budějovice, Czech Republic; USNPC: U.S. National Parasite Collection, Beltsville, USA. Names of amphibian hosts follow Frost 2004.

RESULTS

Ophiotaenia bonneti sp. n.

Figs. 1–14

Description (based on 7 specimens): Proteocephalidae, Proteocephalinae. Medium-sized to large worms 63–380 mm long (n = 4), up to 1.78 mm wide. Strobila

Figs. 1–6. *Ophiotaenia bonneti* sp. n. Scanning electron micrographs of the scolex, MHNG INVE 37251. **Fig. 1.** Scolex, apical view. **Fig. 2.** Scolex, lateral view. **Fig. 3.** Filiform and blade-like spiniform microtriches on the apex. **Fig. 4.** Detail of blade-like spiniform microtriches on the marginal surface of the suckers. **Fig. 5.** Blade-like spiniform microtriches on the surface of the suckers. **Fig. 6.** Blade-like spiniform microtriches on the surface of the neck. Figs. 1, 2: numbers 3–6 mark the areas shown at higher magnification in Figs. 3–6, respectively. Scale bars: Figs. 1, 2 = 50 μ m; Figs. 3, 5, 6 = 5 μ m; Fig. 4 = 2 μ m.

acraspedote. Scolex small, slightly wider than proliferation zone, 280–385 ($\times = 315$, $n = 4$, $CV = 15\%$) wide (Figs. 1, 2, 7), without apical organ, but with concentration of cells of granular content (glandular?) below apex and at level of suckers (Figs. 7, 8). Suckers uniloculate, circular, four in number, 130–180 ($\times = 154$, $n = 16$, $CV = 11\%$) in diameter. Sucker diameter 50–52% of scolex diameter. Tegument characterized by presence of filiform and small blade-like microtriches on apex (Fig. 3), slightly larger on marginal surface of suckers (Fig. 4), on internal surface of suckers (Fig. 5), and on anterior region of proliferation zone (Fig. 6).

Strobila consisting of 122–239 ($n = 4$) proglottides: 90–117 immature proglottides (up to appearance of spermatozoa in vas deferens), 4–12 mature proglottides (up to appearance of eggs in uterus), 11–42 pregravid proglottides (up to appearance of hooks in oncospheres) and 15–71 gravid proglottides.

Immature, mature and pregravid proglottides wider than long to longer than wide (length to width ratio 1:0.42–1.44) (Figs. 9, 10); gravid proglottides usually longer than wide (length to width ratio 1:0.91–2.48) (Fig. 11). Tegument thick. Internal longitudinal musculature developed, forming anastomosed bundles of muscles (Fig. 14). Sub-tegumental musculature developed. Ventral osmoregulatory canals 6–11 in diameter, dorsal osmoregulatory canals 4–9 in diameter, situated medially between 13–26% of lateral margin of proglottis, dorsal one often more medial than ventral (Figs. 9, 10).

Testes medullary, 100–177 ($\times = 134$, $n = 37$, $CV = 15\%$) in number, in two lateral fields, in one layer, longitudinally overlapped by osmoregulatory canals (Figs. 9, 10). Testes round to ovoid, 50–75 in diameter, usually reaching vitelline follicles in immature and mature proglottides, but not reaching posteriorly to ovary (Figs. 9, 10). Genital atrium present. Genital pores irregularly

Figs. 7, 8. *Ophiotaenia bonneti* sp. n. Line drawings of the scolex. **Fig. 7.** Holotype, dorsal view, MHNG INVE 37237, showing the osmoregulatory canals with numerous secondary canals directed towards the surface. **Fig. 8.** Paratype, frontal view, IPCAS C-400. Abbreviations: cg – cells with finely granular cytoplasm; cs – secondary canals ending beneath the tegument; do – dorsal osmoregulatory canal; vo – ventral osmoregulatory canal. Scale bars: Figs. 7, 8 = 100 μ m.

alternate, situated anteriorly, PP = 15–29% ($\times$ = 21%, n = 41, CV = 18%) (Figs. 9, 11).

Cirrus pouch pyriform, thin-walled, 119–323 long ($\times$ = 208, n = 44, CV = 30%) (Figs. 9, 11), PC = 15–24% ($\times$ = 19%, n = 44, CV = 12%) (Fig. 10). Cirrus occupying up to 65% of cirrus pouch length. Genital ducts passing between osmoregulatory canals. Ejaculatory duct coiled. Vas deferens coiled, occupying rounded field extending between proximal part of cirrus pouch and median part of uterus, not crossing midline of proglottis in mature and gravid proglottides (Figs. 9, 10), slightly anterior to base of cirrus pouch.

Vagina anterior (n = 375) to cirrus pouch, vaginal sphincter not observed (Figs. 9, 11). Ovary medullary, bilobed in dorso-ventral view and in cross-section, with some dorsal and ventral outgrowths in its marginal part (Figs. 9, 10), OV = 70–83% ($\times$ = 75%, n = 44, CV = 4%).

Vitelline follicles medullary, arranged in two lateral rows, slightly more numerous posteriorly, occupying 78% to 90% of proglottis length, somewhat interrupted at level of cirrus pouch, with 2–3 follicles dorsally and ventrally on each side (Figs. 9, 11).

Uterus medullary, visible in immature proglottides, with development of type 2 (see de Chambrier et al. 2004b) defined as follows: In immature proglottides, concentration of numerous intensely-staining cells, on either side of uterine stem, sometimes difficult to observe, occupying up to 30% of proglottis width. Lumen

present in uterine stem in last immature proglottides. In premature proglottides, uterine stem develops dense lateral elongated digitations, ramified or not. In mature proglottides, gradual appearance and extension of lumen from base to apex into each digitate diverticula; apex constituted by numerous chromophilic cells. Uterus growing in medullary parenchyma, transversally in diverticula, with lumen present in first mature proglottides. Gravid uterus with ramified diverticula on each side, comprising numerous chromophilic cells, occupying most of gravid proglottis width (Fig. 11). Uterus with 18–32 ramified lateral branches on each side occupying up to 93% of gravid proglottis width (Fig. 11). Eggs shed through a ventral longitudinal split along entire length of proglottis.

Eggs spherical, with hyaline outer envelope, about 50–70 in diameter; embryophore thick, 25–30 in diameter, consisting of two layers; outer layer thicker than inner nuclei-containing envelope; oncosphere spherical to oval, 11–14 in diameter, with 6 hooklets 6–7 long (Figs. 12, 13).

Type host: *Rana vaillanti* Brocchi, 1877 (Anura, Ranidae).

Type locality: San Gerardo, Guanacaste Province, Costa Rica, 22.05.2002, (10°52'50"N, 85° 25'31" W).

Site: Intestine.

Prevalence: 22% (33 of 147).

Type material: Holotype MHNG, INVE 37237: 02-PARA-472.02, San Gerardo, Guanacaste Province, Costa

Figs. 9, 10. *Ophiotaenia bonneti* sp. n. Line drawings of proglottides. Holotype, MHNG INVE 37237. **Fig. 9.** Dorsal view of an immature proglottis. **Fig. 10.** Dorsal view of a mature proglottis. Scale bars: Figs. 9, 10 = 500 µm.

Rica (10°52'50"N, 85°25'31"W), 22.05.2002; 1 paratype MHNG, INVE 37238: 02-PARA-467.01, Río Pizote between Brasilia and Dos Rios, Guanacaste Province, Costa Rica, (10°56'24"N, 85°24'46"W), 22.05.2002; 1 paratype MHNG, INVE 37239: cross-section series, remaining specimen whole-mounted, 01-PARA-367.03, Buenos Aires, Guanacaste Province, Costa Rica, 23.06.2001; 1 paratype IPCAS C-400: cross section series, remaining specimen whole-mounted), 01-PARA-368.03 A, Buenos Aires, Guanacaste Province, Costa Rica, 23.06.2001; 1 paratype (without scolex) USNPC 97297: 01-PARA-368.03 C, Buenos Aires, Guanacaste Province, Costa Rica, 23.06.2001; 1 paratype MHNG, INVE 37240 (SEM): whole-mount, 99-PARA-103, Río Pizote, Guanacaste Province, Costa Rica, 13.06.1999; 1 paratype MHNG, INVE 37241: whole-mount, 00-PARA-17, Río Pizote, Guanacaste Province, Costa Rica, 06.07.2000.

Voucher material: 1 voucher MHNG, INVE 37251 (SEM): whole-mount, 01-PARA-368.03, Buenos Aires, Guanacaste Province, Costa Rica, 23.06.2001; 1 voucher MHNG, INVE 37247 (SEM): whole-mount, 02-PARA-450.3, Río Pizote, Guanacaste Province, Costa Rica, 21.05.2002.

Ophiotaenia sp., immature specimens: 1 voucher MHNG, INVE 37248: 99-PARA-104, San Gerardo, Guanacaste Province, Costa Rica, 13.09.1999; MHNG, INVE 37249: whole-mount, 02-438-2, Buenos Aires, Guanacaste Province, Costa Rica, 20.05.2002; MHNG, INVE 37250: in alcohol, 02-448-1, Río Pizote, Guanacaste Province, Costa Rica, 21.05.2002.

E t y m o l o g y : The species has been named after Nicolas Bonnet (Satigny, Geneva), famous Geneva winemaker, for his enthusiasm in sharing his outstanding knowledge in oenology.

DISCUSSION

The new species belongs to the genus *Ophiotaenia* because of the medullary distribution of gonads as well as the presence of four simple unilocular suckers and two testis fields (Freze 1965, Schmidt 1986). According to Brooks (1978a), Schmidt (1986) and Rego (1994), *Batrachotaenia* is considered as junior synonym of *Ophiotaenia*. Schmidt (1986) did not list three species which need to be transferred to *Ophiotaenia*: *Batrachotaenia ceratophryos* becomes *Ophiotaenia ceratophryos* (Parodi et Widakowich, 1916) comb. n., *B. tigrina* becomes *O. tigrina* (Woodland, 1925) comb. n., and *B. hernandezi* (Flores-Barroeta, 1955) becomes *O. hernandezi* (Flores-Barroeta, 1955) comb. n.

Of the approximately 74 species of *Ophiotaenia* currently recognized parasitizing reptiles and amphibians (Schmidt 1986), 23 species parasitize amphibians (Table 1): *Ophiotaenia alternans* Riser, 1942; *O. amphiumae* Zelif, 1932; *O. bonariensis* Szidat et Soria, 1954; *O. bufonis* Vigueras, 1942 (redescribed by Freze and Ryšavý, 1976, from *Bufo taladai*); *O. calamensis* Puga et Formas, 2005; *O. carpathica* (Sharpilo, Korniyushin et Lisitsina, 1979); *O. ceratophryos* (Parodi et Widakowich, 1916); *O. cryptobranchi* La Rue, 1914; *O. ecuadorensis* Dyer, 1986; *O. filaroides* (La Rue, 1909); *O. gracilis* Jones, Cheng et Gillespie, 1958; *O. hernandezi* (Flores-Barroeta, 1955); *O. junglensis* Srivastava et Capoor, 1980; *O. hylae* Johnston, 1912 (redescribed by de Chambrier 2004); *O. loennbergii* (Fuhrmann, 1895); *O. magna* Hannum, 1925; *O. noei* Wolffhügel, 1948; *O. olor* (Ingles, 1936); *O. olseni* Dyer et Altig, 1977; *O. ranae* Yamaguti, 1938; *O. saphena* Osler, 1931;

Figs. 11–14. *Ophiotaenia bonneti* sp. n. Line drawings. **Fig. 11.** Holotype, dorsal view of a gravid proglottis (diagrammatic), MHNG INVE 37237. **Fig. 12.** Holotype, egg in distilled water, MHNG INVE 37237. **Fig. 13.** Paratype, egg in distilled water, INVE 37238. **Fig. 14.** Paratype, cross-section of mature proglottis at the level of the ovary, MHNG INVE 37239. Abbreviations: em – embryophore; oe – outer envelope; om – oncospherical membrane; on – oncosphere. Scale bars: Figs. 11, 14 = 500 µm; Figs. 12, 13 = 50 µm.

O. schultzei (Hungerbühler, 1910); *O. tigrina* (Woodland, 1925) (redescribed by Gupta and Arora 1979).

Ophiotaenia bonneti is compared to the 23 species of the *Ophiotaenia* recorded from amphibians (Fuhrmann 1895, La Rue 1909, 1914a, b, Hungerbühler 1910, Parodi and Widakowich 1916, Hannum 1925, Woodland 1925, Osler 1931, Zelif 1932, Ingles 1936, Yamaguti 1938, Riser 1942, Vigueras 1942, Wolffhügel 1948, Szidat and Soria 1954, Flores-Barroeta 1955, Jones et al. 1958, Dyer and Altig 1977, Gupta and Arora 1979, Sharpilo et al. 1979, Srivastava and Capoor 1980, Dyer 1986, Puga and Formas 2005). All these species differ

from *O. bonneti* by one or several characters: *O. bonariensis*, *O. ecuadorensis*, *O. filaroides*, *O. hylae*, *O. saphena* and *O. tigrina* possess an apical organ, while an apical organ is absent in *O. bonneti*; *O. cryptobranchi* has a posterior position of the vagina; *O. loennbergii* possesses anterior and posterior position of the vagina, while the position of the vagina in *O. bonneti* is anterior; *O. calamensis*, *O. ceratophryos* and *O. olseni* possess a greater PC than *O. bonneti*; *O. alternans* shows the presence of a vestigial fifth sucker and the tapered shape of the egg's outer envelope, while *O. bonneti* does not show these features; *O. bonneti* has fewer uter-

ine diverticula than *O. amphiumae*; the sucker diameter in % of scolex diameter in *O. bonneti* is 50–52%, while it is 26–32% in *O. ceratophrys*, 30–32% in *O. gracilis* and 66% in *O. loennbergii*; eggs of *O. gracilis* have a funnel-like depression and embryophore closely investing the oncosphere, while *O. bonneti* does not show these features; *O. magna* and *O. olor* possess a lateral position of the osmoregulatory canals, while the osmoregulatory canals overlap the testis field in *O. bonneti*; *O. bonneti* differs from *O. noei* by a lower number of testes and from *O. hernandezi* and *O. schultzei* by a greater number of testes; *O. bonneti* differs in the more anterior position of the genital pore (15–29%) from *O. bufonis* (50%), *O. carpathica* (54–55%), *O. ceratophrys* (39%), *O. ecuadorensis* (42–44%), *O. hylae* (44–55%), *O. noei* (39%), *O. olseni* (59%) and *O. schultzei* (48%). Finally, *O. ranae* differs in the paramuscular position of vitelline follicles (see definition in de Chambrier 1990), while *O. bonneti* possesses vitelline follicles entirely medullary. *Ophiotaenia junglensis* (Srivastava et Capoor, 1980) is considered a *species inquirenda*, complying with Art. 67.2.5. of the International Code of Zoological Nomenclature (1999), as the characters that purported to differentiate the taxon were doubtfully defined.

Rudin (1917) erected the genus *Batrachotaenia* to accommodate four species of proteocephalideans inhabiting anurans. Freze (1965) followed the opinion of Rudin (1917), confirmed the validity of the genus, and transferred 13 species to *Batrachotaenia*, stressing the following morphological features: (i) scolex and neck always without spines; (ii) mature (and even gravid) proglottides subquadrate or slightly longer than broad; (iii) internal musculature layer extremely weak or absent; (iv) Mehlis' gland large. Brooks (1978a) argued that the subdivision of *Ophiotaenia* proposed by Freze (1965), which was based on definitive host type, did not constitute natural groups. He also pointed out that Freze's diagnosis of *Batrachotaenia*, *Testudotaenia* Freze, 1965 and *Ophiotaenia*, did not fit all the species Freze placed in these genera (Freze 1965). Brooks (1978a) considered *Batrachotaenia* and *Testudotaenia* as junior synonyms of *Ophiotaenia*. He also discussed the status of *Ophiotaenia*, which, according to Freze (1965), differs from *Proteocephalus* in having a preformed uterus and parasitism in reptiles, and considered *Ophiotaenia* as a junior synonym of *Proteocephalus*. However, in a phylogenetic analyses of the order Proteocephalidea, de Chambrier et al. (2004) evaluated the structure of the clade *Proteocephalus* and showed that *Proteocephalus* species are fundamentally parasites of Palaearctic fishes. Pending a complete revision of the group, they defined an aggregate (see Article 6B of the International Code of Zoological Nomenclature 1999) for the Palaearctic *Proteocephalus*, while the affinities of the remaining eight Nearctic and Neotropical *Proteocephalus* species remained unsatisfactorily resolved (see

de Chambrier et al. 2004, p. 162, fig. 1). They suggested that those *Proteocephalus* species should be formally removed from the genus after their evolutionary relationships are better known. With such a redefinition of the genus *Proteocephalus*, it would only cause more confusion if we place our new species in this genus, even provisionally.

A similar situation prevails in the structure of the clade *Ophiotaenia* (see de Chambrier et al. 2004, fig. 1): a monophyletic group of species harbouring the uterus of the type 1 is found in the Elapidae and Viperidae whereas others species with the uterus of the type 2 (see de Chambrier et al. 2004 for definition) are dispersed in different clades. No *Ophiotaenia* species parasitizing amphibians was included in that study, however, we know that both types of uterine development occur in *Ophiotaenia* from amphibians, i.e. the type 1 in *O. bufonis* (Freze and Ryšavý 1976, p. 103, fig. 6), *O. bonariensis* (Szidat and Soria 1954, fig. 9b, c); the type 2 in *O. filaroides* (La Rue 1909, figs. 30, 31) and *O. bonneti* (Fig. 9, present paper). This may be an indication that proteocephalideans of amphibians are not monophyletic. Until more information is available, we conservatively choose to keep all of them in *Ophiotaenia*, regardless of definitive host type.

The prevalence of the Proteocephalidea is usually very low in amphibians, at least in the Neotropical region (Table 2). In Ecuador, only 9 (all anurans) of 2,200 (0.41%) amphibians representing 91 species (90 anurans and 1 caudatan) studied between 1983 and 1990 were infected with proteocephalidean cestodes: four *Hyla geographica* Spix, 1824, two *Hyla boans* (Linnaeus, 1758), one *Osteocephalus taurinus* Steindachner, 1862, one *Leptodactylus labrosus* Jiménez de la Espada, 1875 and one *Ceratophrys cornuta* (Linnaeus, 1758) – host of *Nomimoscolex touzeti* de Chambrier et Vaucher, 1992, (Zygobothriinae) (unpublished results, MHNG data base). In Paraguay, only 7 (all anurans) of 1,510 amphibians representing 64 species (all anurans) studied between 1979 and 2002 (0.46%) were infected with proteocephalideans: one *Hyla raniceps* (Cope, 1862), one *H. sanborni* Schmidt, 1944, two *Pseudis paradoxa* (Linnaeus, 1758), two *Physalaemus nattereri* (Steindachner, 1863) and one *Lepidobatrachus* sp. (unpublished results, MHNG data base). Similarly, participants in a project coordinated by one of the authors (D. Brooks) have examined 1,008 amphibians representing 47 species (46 anurans and 1 caudatan) in the ACG and have found proteocephalideans only in 33 individuals (3%). It is important to note, however, that all adult proteocephalideans occurred in *Rana vaillanti*. Thus, the prevalence of *O. bonneti* is 22% (33/147 *R. vaillanti* examined). We globally observe a very low mean prevalence of the Proteocephalidea in Neotropical amphibians (about 0.41%–3%), but in the case of some host species, the prevalence can reach up to 25%. We do not consider the prevalence of the two host species,

Table 1. *Ophiotaenia* species (currently accepted taxons only) previously known as parasite of amphibian hosts.

Parasite species	Host species	Locality
<i>Ophiotaenia alternans</i>	<i>Amphiuma tridactylum</i> Cuvier, 1827	USA
<i>O. amphiumae</i>	<i>Amphiuma tridactylum</i> Cuvier, 1827	USA
<i>O. bonariensis</i>	<i>Leptodactylus ocellatus</i> (Linnaeus, 1758)	Argentina
<i>O. bufonis</i>	<i>Bufo peltacephalus</i> Schwartz, 1960	Cuba
<i>O. calamensis</i>	<i>Telmatobius dankoi</i> Formas, Northland, Capetillo, Nuñez, Cuevas et Brieve, 1999	Chile
<i>O. carpathica</i>	<i>Triturus cristatus</i> (Laurenti, 1768)	Ukraine
<i>O. ceratophrys</i>	<i>Ceratophrys ornata</i> (Bell, 1843)	Argentina
<i>O. cryptobranchi</i>	<i>Cryptobranchus alleganiensis</i> (Daudin, 1803)	USA
<i>O. ecuadorensis</i>	<i>Hyla geographica</i> Spix, 1824	Ecuador
<i>O. filaroides</i>	<i>Amblystoma tigrinum</i> Green, 1825	USA
<i>O. gracilis</i>	<i>Rana catesbeiana</i> Shaw, 1802	USA
<i>O. hernandezi</i>	<i>Rana</i> sp.	Mexico
<i>O. junglensis</i>	<i>Hoplobatrachus tigerinus</i> (Daudin, 1802)	India
<i>O. hylae</i>	<i>Litoria aurea</i> (Lesson, 1829)	Australia
<i>O. loennbergii</i>	<i>Necturus maculosus</i> (Rafinesque, 1818)	USA
<i>O. magna</i>	<i>Rana catesbeiana</i> Shaw, 1802	USA
<i>O. noei</i>	<i>Caudiverbera caudiverbera</i> (Linnaeus, 1758)	Chile
<i>O. olor</i>	<i>Rana aurora</i> Baird et Girard, 1852	USA
<i>O. olseni</i>	<i>Hyla geographica</i> Spix, 1824	Ecuador
<i>O. ranae</i>	<i>Rana nigromaculata</i> Hallowell, 1861	Japan
<i>O. saphena</i>	<i>Rana clamitans</i> Latreille in Sonnini de Manoncourt and Latreille 1801	USA
<i>O. schultzei</i>	<i>Pyxicephalus adspersus</i> Tschudi, 1938	South Africa
<i>O. tigrina</i>	<i>Hoplobatrachus tigerinus</i> (Daudin, 1802)	India

Table 2. Proteocephalidean tapeworms collected from amphibian hosts in South American and Central American countries.

Country/Parasite species	Host	No. hosts examined	No. hosts infected	Prevalence (%)
Ecuador	91 species	2,200	9	0.41
<i>Ophiotaenia olseni</i>	<i>Hyla geographica</i>	30	1	3.3
<i>Ophiotaenia</i> sp. 1	<i>Hyla geographica</i>	30	3	10
<i>Ophiotaenia</i> sp. 2	<i>Hyla boans</i>	9	2	22
<i>Ophiotaenia</i> sp. 3	<i>Osteocephalus taurinus</i>	46	1	2.2
<i>Ophiotaenia</i> sp. 4	<i>Leptodactylus labrosus</i>	4	1	25
<i>Nomimoscolex touzeti</i> de Ch. et Vaucher, 1992	<i>Ceratophrys cornuta</i>	1	1	100
Paraguay	64 species	1,510	7	0.45
<i>Ophiotaenia</i> sp. 5	<i>Hyla raniceps</i>	100	1	1
<i>Ophiotaenia</i> sp. 6	<i>Hyla sanborni</i>	15	1	6.6
<i>Ophiotaenia</i> sp. 7	<i>Pseudis paradoxa</i>	38	2	5.2
<i>Ophiotaenia</i> sp. 8	<i>Physalaemus nattereri</i>	45	2	4.4
<i>Ophiotaenia</i> sp. 9	<i>Lepidobatrachus</i> sp.	1	1	100
Costa Rica	47 species	1,008	33	3.3
<i>O. bonneti</i>	<i>Rana vaillanti</i>	147	33	22

Ceratophrys cornuta and *Lepidobatrachus* sp., collected in only one individual (Table 2). We have to point out that all the *Ophiotaenia* sp. listed in Table 2 are considered as new species, study of which is in progress. These preliminary studies indicate that each amphibian species listed above (Table 2) hosts a different species of proteocephalidean; therefore, these proteocephalideans all appear to be oixenous (sensu Euzet and Combes 1980).

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