

# Helminths from fifteen species of frogs (Anura, Hylidae) from Costa Rica

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## Abstract

**Helminths from fifteen species of frogs (Anura, Hylidae) from Costa Rica.** Fifteen species of Costa Rican hylid frogs were examined for helminths: *Agalychnis annae*, *Agalychnis callidryas*, *Agalychnis spurrelli*, *Dendropsophus ebraccatus*, *Dendropsophus phlebodes*, *Duellmanohyla uranochroa*, *Hylomantis lemur*, *Hypsiboas rosenbergi*, *Isthmohyla pictipes*, *Isthmohyla rivularis*, *Isthmohyla tica*, *Scinax elaeochrous*, *Smilisca phaeota*, *Smilisca sordida*, *Tlalocohyla loquax*. The frogs were found to harbor twelve species of helminths including one species of Monogenea, (*Polystoma naevius*), two species of Digenea (*Gorgoderina diaster* and *Mesocoelium monas*), eight species of Nematoda (*Cosmocerca podicipinus*, *Falcaustra costaricensis*, *Ochoterenella digiticauda*, *Oswaldocruzia costaricensis*, *Oxyascaris mcdiarmidi*, *Rhabdias savagei*, *Physaloptera* sp. and *Acuariidae* gen. sp.) and one species of Acanthocephala (*Anuracanthorhynchus lutzii*). Mean number of helminth species per infected host species was  $2.7 \pm 0.3$  SE (range 1-5). Thirty-nine new host records are reported.

**Keywords:** Anura, Hylidae, helminths, Monogenea, Digenea, Nematoda, Acanthocephala, Costa Rica.

## Introduction

The helminth biodiversity of Neotropical vertebrates is virtually unknown (Salgado-Maldonado *et al.* 2000) and consequently little information is available on the helminths of Costa Rican hylid frogs. Helminths from seven anuran species from Costa Rica are listed in Rodrigues-Ortiz *et al.* (2003). Bursey and

Brooks (2004) described *Parapharyngodon duniae* from *Phrynohyas venulosa* (currently *Trachycephalus venulosus*). Brooks *et al.* (2006) listed platyhelminth parasites from 6 Costa Rican hylid species, *Isthmohyla lancasteri*, *Scinax boulengeri*, *Smilisca baudinii*, *Smilisca phaeota*, *Smilisca puma* and *Trachycephalus venulosus*. As part of an ongoing series of studies on this subject (Bursey and Goldberg 2005, 2006, 2007a,b, Bursey *et al.* 2001, Goldberg and Bursey 2008) reported helminths from an additional 18 anuran species from Costa Rica. Although some 133 anuran

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species are thought to occur in Costa Rica (Savage 2002), there are helminth records for only approximately one quarter of them. The purpose of this paper is to report helminths in 15 species of Costa Rican hylid frogs thereby increasing the database on helminths from tropical anurans.

## Materials and Methods

Two hundred individuals representing 15 species of hylid frogs collected 1959-1990 in Costa Rica and accessioned in the Natural History Museum of Los Angeles County (LACM), Los Angeles, California, were examined for helminths (descriptive statistics are given as means  $\pm$  one standard deviation unless otherwise noted): *Agalychnis annae* (N = 10) SVL = 54.7 mm  $\pm$  3.5, range: 47-58 mm; *Agalychnis callidryas* (N = 11) SVL = 45.9 mm  $\pm$  2.3, range: 42-50 mm; *Agalychnis spurrelli* (N = 10) SVL = 51.7 mm  $\pm$  8.8, range: 38-69 mm; *Dendropsophus ebraccatus* (N = 35) SVL = 24.9 mm  $\pm$  2.8, range: 22-33 mm; *Dendropsophus phlebodes* (N = 10) SVL = 22.7 mm  $\pm$  2.1, range: 19-26 mm; *Duellmanohyla uranochroa* (N = 5) SVL = 31.6 mm  $\pm$  1.5, range: 30-33 mm; *Hylomantis lemur* (N = 10) SVL = 32.2 mm  $\pm$  2.7, range: 30-39 mm; *Hypsiboas rosenbergi* (N = 3) SVL = 62.3 mm  $\pm$  2.1, range: 60-64 mm; *Isthmohyla pictipes* (N = 15) SVL = 34.3 mm  $\pm$  2.3, range: 32-39 mm; *Isthmohyla rivularis* (N = 15) SVL = 29.5 mm  $\pm$  1.6, range: 27-32 mm; *Isthmohyla tica* (N = 11) SVL = 32 mm  $\pm$  2.0, range: 30-37 mm; *Scinax elaeochrous* (N = 30) SVL = 30.9 mm  $\pm$  1.9, range: 28-33 mm; *Smilisca phaeota* (N = 10) SVL = 52.3 mm  $\pm$  8.2, range: 44-68 mm; *Smilisca sordida* (N = 10) SVL = 44.4 mm  $\pm$  8.9, range: 34-57 mm; *Tlalocohyla loquax* (N = 15) SVL = 40.7 mm  $\pm$  1.4, range: 38-43 mm (Appendix I).

Frogs had been collected by hand, fixed in 10% buffered formalin and preserved in 70% ethanol. The body cavities were opened by a longitudinal incision from throat to vent and the

alimentary canals (esophagus to cloaca) were slit longitudinally and examined under a dissecting microscope. The lungs, body cavity and urinary bladder of each individual frog were also examined. All helminths were placed in vials of 70% ethanol for later examination at which time each helminth was placed on a glass slide in a drop of glycerol for study under a compound microscope. Nematodes and acanthocephalans were identified from these preparations, whereas trematodes were stained with hematoxylin and mounted in balsam for identification. Voucher helminths were deposited in the United States National Parasite Collection, USNPC, Beltsville, Maryland (Table 1). Frog taxonomy is in accordance with Frost *et al.* (2006) and parasite terminology is in accordance with Bush *et al.* (1997).

## Results

We found 12 helminth species in the frogs examined: one species of Monogenea, (Polystomatidae), *Polystoma naevius* Caballero and Cerecero, 1942, two species of Digenea, (Gorgoderidae), *Gorgoderina diaster* Lutz, 1926 and, (Brachycoeliidae), *Mesocoelium monas* (Rudolphi, 1819), eight species of Nematoda, (Cosmocercidae), *Cosmocerca podicipinus* Baker and Vaucher, 1984, (Kathlaniidae), *Falcaustra costaricensis* Bursey, Goldberg and Miller, 2004, (Onchocercidae), *Ochoterenella digiticauda* Caballero, 1944, (Molineidae), *Oswaldoocruzia costaricensis* Bursey and Goldberg, 2005, (Cosmocercidae), *Oxyascaris mcdiarmidi* Bursey and Goldberg, 2007, (Rhabdiasidae), *Rhabdias savagei* Bursey and Goldberg, 2005, (Physalopteridae), *Physaloptera* sp. (larvae) and (Acuariidae), Acuariidae gen. sp. (larvae in cysts), and one species of Acanthocephala, (Cavismidae), *Anuracanthorhynchus lutzi* (Hamman, 1891) (Table 1).

A total of 262 helminths was collected from 71 (36%) of the 200 frogs examined. Of these, 32 (12%) were larval forms not capable of reaching maturity in anurans. Of the infected

**Table 1 -** Site of infection, number of helminths, prevalence, mean intensity, range of infection and USNPC accession numbers for voucher specimens of helminths taken from 15 species of Costa Rican hylid frogs. \* = new host record.

Host Helminth	Site of infection	Number	Prevalence	Mean intensity ± SD	Range	USNPC Accession number
<i>Agalychnis annae</i>						
<i>Cosmocerca podicipinus</i> *	large intestine	7	2/10 20%	3.5 ± 0.7	3-4	98677
<i>Rhabdias savagei</i> *	lung	1	1/10 10%	1.0 ± 0.0	—	98678
<i>Agalychnis callidryas</i>						
<i>Cosmocerca podicipinus</i> *	large intestine	7	4/11 36%	1.8 ± 1.0	1-3	98679
<i>Oswaldocruzia costaricensis</i> *	small intestine	6	3/11 27%	2.0 ± 1.0	1-3	98680
<i>Physaloptera</i> sp. (larva)*	small intestine	2	2/11 18%	1.0 ± 0.0	—	98682
<i>Rhabdias savagei</i> *	lung	1	1/11 9%	1.0 ± 0.0	—	98681
<i>Agalychnis spurrelli</i>						
<i>Polystoma naevius</i> *	urinary bladder	2	2/10 20%	1.0 ± 0.0	—	98683, 98684
<i>Acuariidae</i> gen. sp. (larva)*	intestinal wall	9	3/10 30%	3.0 ± 2.7	1-6	98686
<i>Cosmocerca podicipinus</i> *	large intestine	3	2/10 20%	1.5 ± 0.7	1-2	98685
<i>Dendropsophus ebraccatus</i>						
<i>Cosmocerca podicipinus</i> *	large and small intestine	3	3/35 9%	1.0 ± 0.0	—	99648
<i>Falcaustra costaricæ</i> *	small intestine	1	1/35 3%	1.0 ± 0.0	—	99649
<i>Physaloptera</i> sp. (larva)*	stomach	2	2/35 6%	1.0 ± 0.0	—	99650
<i>Dendropsophus phlebodes</i>						
<i>Falcaustra costaricæ</i> *	small intestine	6	1/10 10%	6.0 ± 0.0	—	98749
<i>Duellmanohyla uranochroa</i>						
<i>Acuariidae</i> gen. sp. (larva)*	coelom	1	1/5 20%	1.0 ± 0.0	—	98688
<i>Anuracanthorhynchus lutzii</i> *	small intestine	4	1/5 20%	4.0 ± 0.0	—	98687
<i>Hylomantis lemur</i>						
<i>Rhabdias savagei</i> *	lung	3	3/10 30%	1.0 ± 0.0	—	99583
<i>Hypsiboas rosenbergi</i>						
<i>Falcaustra costaricæ</i> *	large intestine	3	1/3 33%	3.0 ± 0.0	—	99584
<i>Isthmohyla pictipes</i>						
<i>Gorgoderina diaster</i> *	urinary bladder	6	5/15 33%	1.2 ± 0.5	1-2	98750
<i>Cosmocerca podicipinus</i> *	large intestine	11	6/15 40%	1.8 ± 1.0	1-3	98751
<i>Oxyascaris mediamundi</i> *	large intestine	9	4/15 27%	2.3 ± 1.9	1-5	98752
<i>Anuracanthorhynchus lutzii</i> *	small intestine	5	5/15 33%	1.0 ± 0.0	—	98753
<i>Isthmohyla rivularis</i>						
<i>Cosmocerca podicipinus</i> *	large intestine	32	7/15 47%	4.6 ± 4.7	1-14	98754
<i>Anuracanthorhynchus lutzii</i> *	small intestine	1	1/15 7%	1.0 ± 0.0	—	98755
<i>Isthmohyla tica</i>						
<i>Cosmocerca podicipinus</i> *	large intestine	1	1/10 10%	1.0 ± 0.0	—	98756
<i>Rhabdias savagei</i> *	lung	3	1/10 10%	3.0 ± 0.0	—	98757

Table 1 - continued.

Host Helminth	Site of infection	Number	Prevalence	Mean intensity ± SD	Range	USNPC Accession number
<i>Scinax elaeochrous</i>						
<i>Cosmocerca podicipinus</i> *	large intestine	5	2/30 7%	2.5 ± 2.1	1-4	99651
<i>Oswaldocruzia costaricensis</i> *	small intestine	1	1/30 3%	1.0 ± 0.0	—	99652
Acuariidae gen. sp. (larva)*	stomach wall	18	1/30 3%	18.0 ± 0.0	—	99653
<i>Smilisca phaeota</i>						
<i>Polystoma naevius</i>	urinary bladder	1	1/10 10%	1.0 ± 0.0	—	98764
<i>Mesocoelium monas</i> *	small intestine	2	2/10 20%	1.0 ± 0.0	—	98763
<i>Cosmocerca podicipinus</i> *	large intestine	25	5/10 50%	5.0 ± 5.3	1-14	98765
<i>Oswaldocruzia costaricensis</i> *	small intestine	11	2/10 20%	5.5 ± 4.9	2-9	98766
<i>Rhabdias savagei</i> *	lung	1	1/10 10%	1.0 ± 0.0	—	98767
<i>Smilisca sordida</i>						
<i>Mesocoelium monas</i> *	small intestine	1	1/10 10%	1.0 ± 0.0	—	—
<i>Cosmocerca podicipinus</i> *	large intestine	7	2/10 20%	3.5 ± 0.7	3-4	98768
<i>Falcaustra costaricae</i> *	small intestine	17	4/10 40%	4.3 ± 2.5	1-7	98769
<i>Ochoterenella digiticauda</i> *	coelom	27	5/10 50%	5.4 ± 2.4	2-8	98770
<i>Tlalocohyla loquax</i>						
<i>Cosmocerca podicipinus</i> *	large intestine	3	2/15 13%	1.5 ± 0.7	1-2	98746
<i>Falcaustra costaricae</i> *	large intestine	5	2/15 13%	2.5 ± 2.1	1-4	98747
<i>Rhabdias savagei</i> *	lung	6	1/15 7%	6.0 ± 0.0	—	98748

frogs, 50 individuals (70%) harbored one species of helminth, 18 (25%) harbored two species and three (4%) harbored three species. There were  $1.39 \pm 0.07$  SE helminth species/infected frog and  $3.69 \pm 0.38$  SE (range 1-18) helminth individuals/infected frog. No host species harbored more than five helminth species: three (20%) frog species harbored one helminth species; four (27%) harbored two helminth species; four (27%) harbored three species; three (20%) harbored four species, and one (7%) harbored five species. There were  $2.67 \pm 0.32$  SE helminth species/host species.

*Cosmocerca podicipinus* was the most widely distributed helminth and occurred in 11 (73%) of the 15 frog species examined. *Rhabdias savagei* was the second most widely distributed species and was found in 6 (40%) of the 15 frog species sampled. Thirty-nine new host records are reported (Table 1).

## Discussion

*Polystoma naevius* was originally described from specimens taken from the urinary bladder of *Hyla* (currently *Smilisca*) *baudinii* collected in Veracruz, Mexico (Caballero and Cerecero 1941). It was redescribed from the type-host collected in Mexico by Lamothe-Argumedo (1976) and was first reported from Costa Rica by Brooks *et al.* (2006) in *Isthmohyla lancasteri*, *Scinax boulengeri*, *Smilisca phaeota* and *Trachycephalus venulosus*. It has also been reported from *Smilisca cyanosticta* from Mexico (Goldberg *et al.* 2002). Larvae of *P. naevius* infect tadpoles and become adults when the tadpoles metamorphose (Stunkard 1959).

*Gorgoderina diaster* was originally described from a microhylid frog, *Pseudis paradoxa*, collected in Venezuela (Lutz 1926), and recently redescribed from specimens taken

from *Rana* (currently *Lithobates*) *vaillanti* and *Rana* (currently *Lithobates*) cf. *forreri* collected in Costa Rica (Mata-López *et al.* 2005). *Gorgoderina diaster* is also known from *Bufo* (currently *Rhinella marina*) *marinus*, and *Rana* (currently *Lithobates*) *palmipes* (Fernandes 1958, Brooks 1976). Frogs acquire such parasites by ingesting infected mollusks or arthropods (Odlaug 1937).

The genus *Mesocoelium* was established by Odhner (1911) with *Mesocoelium sociale* (Lühe, 1901) as the type species. Freitas (1958) reassigned *Distoma monas* Rudolphi, 1819 to *Mesocoelium* and later revised the genus recognizing seven valid species with *M. monas* (= *M. sociale*) as the type species (Freitas 1963). The first report of *M. monas* in Costa Rica was by Caballero and Brenes (1959). It is cosmopolitan in distribution and has been reported in bony fishes, amphibians, and reptiles; records are summarized in Bursey *et al.* (2007). *Bufo* (currently *Ollotis*) *luetkenii*, *Eleutherodactylus diastema*, *Eleutherodactylus* (currently *Craugastor*) *fitzingeri*, *Leptodactylus poecilochilus*, *Rana* (currently *Lithobates*) *brownorum*, *Rana* (currently *Lithobates*) cf. *forreri*, and *Smilisca puma* (see Brooks *et al.* 2006), as well as *Craugastor crassidigitus* and *Craugastor taurus* (Goldberg and Bursey 2008) should be added to that summary. Terrestrial molluscs are presumably the first intermediate hosts (Prudhoe and Bray 1982).

*Cosmocerca podicipinus*, a monoxenous (i.e. has a direct life cycle) and generalist nematode, was originally described from a leptodactylid frog, *Leptodactylus podicipinus* from Paraguay (Baker and Vaucher 1984). It is widespread and known from aromobatid, bufonid, hylid, leptodactylid and ranid frogs from Mexico and Central and South America (Cabrera-Guzmán *et al.* 2007). It was first reported from Costa Rica in ranid frogs by Bursey and Goldberg (2005) and also occurs in eight species of brachycephalid frogs from that country (Goldberg and Bursey 2008). Hosts become infected by direct (i.e. without

participation of intermediate hosts) ingestion of immature stages or via active skin penetration by larvae (Anderson 2000).

*Falcaustra costaricæ* was described from specimens taken from a polychrotid lizard, *Anolis* (= *Norops*) *tropidolepis*, collected in Costa Rica (Bursey *et al.* 2004), and has also been reported from three Costa Rican frog species: the ranid *Lithobates vibicaria* and the brachycephalids, *Craugastor ranooides* and *Craugastor taurus* (Bursey and Goldberg 2006, Goldberg and Bursey 2008). *Falcaustra* is a member of the family Kathaniidae for which the mode of transmission is unknown; however, invertebrates are suspected to act as paratenic hosts for such nematodes (Anderson 2000).

*Ochoterenella digiticauda* was originally described from *Bufo marinus* (currently *Rhinella marina*) collected in Mexico (Caballero 1944) and later redescribed by Esslinger (1986) based on the type specimens. This species was first reported from Costa Rica by Brenes and Bravo-Hollis (1959) and subsequently reported from *Craugastor ranooides* and *Craugastor taurus* collected in that country (Goldberg and Bursey 2008). It has also been reported from *Rana* (currently *Lithobates*) *dunni* and *Rana* (currently *Lithobates*) *vaillanti* from Mexico (Pulido-Flores 1994, Goldberg *et al.* 2002). Wong and Bundy (1985) suggested that a haematophagous arthropod vector is required for infection by *O. digiticauda*.

*Oswaldocruzia costaricensis* was described from *Rana* (currently *Lithobates*) *forreri* from Costa Rica by Bursey and Goldberg (2005). It also occurs in the brachycephalid frogs, *Craugastor fitzingeri*, *Craugastor gollmeri*, *Craugastor ranooides* and *Craugastor taurus* from Costa Rica (Goldberg and Bursey 2008). Although development is monoxenous, there are conflicting reports regarding the mode of infection for species of *Oswaldocruzia*. Hendrikx (1983) successfully infected toads orally with third-stage larvae of *O. filiformis* and Baker (1978) reported cutaneous transmission for *O. pipiens*.

**Table 2 -** Helminths of Costa Rican hylid frogs. Legend: 1. This paper; 2. Brooks *et al.* 2006; 3. Bursey and Goldberg 2007a; 4. Bursey and Brooks 2004.

Helminth	Host																			
	<i>Agalychnis annae</i>	<i>Agalychnis callidryas</i>	<i>Agalychnis spurrelli</i>	<i>Dendropsophus ebraccatus</i>	<i>Dendropsophus phlebodes</i>	<i>Duellmanohyla uranochroa</i>	<i>Hylomantis lemur</i>	<i>Hypsiboas rosenbergi</i>	<i>Isthmohyla lancasteri</i>	<i>Isthmohyla pictipes</i>	<i>Isthmohyla rivularis</i>	<i>Isthmohyla tica</i>	<i>Scinax boulengeri</i>	<i>Scinax elaeochrous</i>	<i>Smilisca baudinii</i>	<i>Smilisca phaeota</i>	<i>Smilisca puma</i>	<i>Smilisca sordida</i>	<i>Tlalocohyla loquax</i>	<i>Trachycephalus venulosus</i>
<i>Polystoma naevius</i>	-	-	1	-	-	-	-	-	2	-	-	-	2	-	2	1,2	-	-	-	2
<i>Gorgodinera diaster</i>	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
<i>Mesocoelium monas</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2	1	-	-	-
<i>Cosmocerca podicipinus</i>	1	1	1	1	-	-	-	-	1	1	1	-	1	-	1	-	1	1	-	-
<i>Falcaustra costaricæ</i>	-	-	-	1	1	-	-	1	-	-	-	-	-	-	-	1	1	-	-	-
<i>Ochoterenella digiticauda</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
<i>Oswaldocruzia costaricensis</i>	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-
<i>Oxyascaris mediarmidi</i>	-	-	-	-	-	3	-	-	1	-	-	-	-	-	-	-	-	-	-	-
<i>Rhabdias savagei</i>	1	1	-	-	-	-	1	-	-	-	1	-	-	-	1	-	-	1	-	-
<i>Parapharyngodon duniae</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4
<i>Physaloptera</i> sp. (larva)	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Acuariidae</i> gen. sp. (larva)	-	-	1	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-
<i>Anuracanathorhynchus lutzi</i>	-	-	-	-	-	1	-	-	1	1	-	-	-	-	-	-	-	-	-	-

*Oxyascaris mediarmidi* was described from *Duellmanohyla uranochroa* from Costa Rica by Bursey and Goldberg (2007a). It also occurs in a brachycephalid frog, *Craugastor ranooides* from Costa Rica (Goldberg and Bursey 2008). *Isthmohyla pictipes* is the second host reported to harbor this helminth. The method of transmission for *Oxyascaris* is unknown but may involve an invertebrate paratenic host (Anderson 2000).

*Rhabdias savagei* was described from *Lithobates forreri* from Costa Rica by Bursey and Goldberg (2005). It has also been reported from six species of brachycephalid frogs from Costa Rica (Goldberg and Bursey 2008). Adult nematodes in the family

Rhabdiasidae are common lung parasites of amphibians and reptiles and infection in amphibians is thought to occur by skin penetration (Anderson 2000).

Larvae of *Physaloptera* (but not adults) are common in anurans; their occurrences were summarized in Goldberg *et al.* (1993). Their occurrence in *Agalychnis callidryas* likely resulted from ingestion of an infected insect (see Anderson 2000). Larvae of *Physaloptera* sp. have previously been reported in neotropical anurans from Brazil and Peru (Boquimpani-Freitas *et al.* 2001, Bursey *et al.* 2001) and the brachycephalid frogs, *Craugastor ranooides* and *Craugastor taurus* from Costa Rica (Goldberg and Bursey 2008).

Species of the Acuariidea are mainly parasites of the upper alimentary tract of birds and require an arthropod intermediate host to infect the final host; they are usually unable to complete their development when acquired by reptilian or amphibian hosts (Anderson 2000).

*Anuracanthorhynchus lutzi* was originally described as *Echinorhynchus lutzi* from *Rhinella marina* (as *Bufo agua*) from Brazil by Hamman (1891). It was transferred to *Acanthocephalus* by Meyer (1931), but later reassigned to *Anuracanthorhynchus* by Bursey and Goldberg (2007b) based upon specimens taken from *Lithobates warszewitschii* collected in Costa Rica. It has also been found in the brachycephalid *Craugastor melanostictus* from Costa Rica (Goldberg and Bursey 2008). Acanthocephalans require at least two hosts during their life cycle; arthropods are the usual intermediate hosts in which the infective stage, the cystacanth, develops and when eaten by an appropriate final host develops to maturity (Kennedy 2006).

Helminth lists for Costa Rican hylid frogs are presented in Table 2. Costa Rican hylid frogs are infected by generalist helminth species (i.e. species capable of infecting two or more host species). The questions that remain to be answered are why differential rates of infection occur within these hosts and are they related to the small sample of hosts examined or are ecological and/or physiological factors at work?

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## References

- Anderson, R. C. 2000. *Nematode Parasites of Vertebrates: Their Development and Transmission*, 2<sup>nd</sup> ed. CAB International, Wallingford, Oxon, U.K. 650 pp.
- Baker, M. R. 1978. Development and transmission of *Oswaldocruzia pipiens* Walton, 1929 (Nematoda: Trichostrongylidae) in amphibians. *Canadian Journal of Zoology* 56: 1026–1031.
- Baker, M. R. and C. Vaucher. 1984. Parasitic helminths from Paraguay VI: *Cosmocerca Diesing, 1861* (Nematoda: Cosmocercoidea) from frogs. *Revue Suisse de Zoologie* 91: 925–934.
- Boquimpani-Freitas, L., D. Vrcibradic, J. J. Vicente, C. R. Bursey, C. F. D. Rocha, and M. Van Sluys. 2001. Helminths of the horned leaf frog, *Proceratophrys appendiculata*, from southeastern Brazil. *Journal of Helminthology* 75: 233–236.
- Brenes, R. R. and M. Bravo-Hollis. 1959. Helmintos de la República de Costa Rica VIII. Nematoda 2. Algunos nemátodos de *Bufo marinus marinus* (L.) y algunas consideraciones sobre los géneros *Oxysomatium* y *Aplectana*. *Revista de Biología Tropical* 7: 35–55.
- Brooks, D. R. 1976. Five species of platyhelminths from *Bufo marinus* L. (Anura: Bufonidae) in Colombia with descriptions of *Creptotrema lynchii* sp. n. (Digenea: Allocreadiidae) and *Glyptelmins robustus* sp. n. (Digenea: Macroderoididae). *Journal of Parasitology* 62: 429–433.
- Brooks, D. R., V. León-Règagnon, D. A. McLennan, and D. Zelmer. 2006. Ecological fitting as a determinant of the community structure of platyhelminth parasites of anurans. *Ecology* 87 (suppl.): S76–S85.
- Bursey, C. R. and D. R. Brooks. 2004. *Parapharyngodon duniae* n. sp. (Nematoda: Pharyngodenidae) in *Phrynohyas venulosa* (Anura: Hylidae) from the Área de Conservación Guanacaste, Guanacaste, Costa Rica. *Journal of Parasitology* 90: 137–139.
- Bursey, C. R. and S. R. Goldberg. 2005. New species of *Oswaldocruzia* (Nematoda: Molineoidae), new species of *Rhabdias* (Nematoda: Rhabdiasidae), and other helminths in *Rana cf. forreri* (Anura; Ranidae) from Costa Rica. *Journal of Parasitology* 91: 600–605.
- Bursey, C. R. and S. R. Goldberg. 2006. New species of *Raillietnema* (Nematoda: Cosmocercidae) and other helminths in *Rana vibicaria* (Ranidae) from Costa Rica. *Comparative Parasitology* 73: 193–200.
- Bursey, C. R. and S. R. Goldberg. 2007a. A new species of *Oxyascaris* (Nematoda, Cosmocercidae) in the Costa Rica brook frog, *Duellmanohyla uranochroa* (Anura, Hylidae). *Acta Parasitologica*. 52: 58–61.
- Bursey, C. R. and S. R. Goldberg. 2007b. New species of *Hedruris* (Nematoda: Hedruridae), *Anuracanthorhynchus lutzi* (Hammann, 1891) n. comb. and other

- helminths in *Lithobates warszewitschii* (Anura: Ranidae) from Costa Rica. *Caribbean Journal of Science* 43: 1–10.
- Bursey, C. R., S. R. Goldberg and C. L. Miller. 2004. Two new species of *Falcaustra* and comments on helminths of *Norops tropidolepis* (Sauria: Polychrotidae) from Costa Rica. *Journal of Parasitology* 90: 598–603.
- Bursey, C. R., S. R. Goldberg and J. R. Parmelee. 2001. Gastrointestinal helminths of 51 species of anurans from Reserva Cuzco Amazónico, Peru. *Comparative Parasitology* 68: 21–35.
- Bursey, C. R., S. R. Goldberg and Sam R. Telford, Jr. 2007. Gastrointestinal helminths of 14 species of lizards from Panama with descriptions of five new species. *Comparative Parasitology* 74: 108–140.
- Bush, A. O., K. D. Lafferty, J. M. Lotz, and A. W. Shostak. 1997. Parasitology meets ecology on its own terms: Margolis *et al.* revisited. *Journal of Parasitology* 83: 575–583.
- Caballero, E. 1944. Estudios helmintológicos de la región oncocercosa de México y de la República de Guatemala. Nematoda: la. parte. Filarioidea. I. *Anales del Instituto de Biología de la Universidad Nacional Autónoma de México* 15: 87–109.
- Caballero, E. and R. R. Brenes. 1959. Helmintos de la República de Costa Rica. VII. Tremátodos de algunos vertebrados salvajes, con descripción de una nueva especie de *Acanthostomum* Looss, 1899. *Anales del Instituto de Biología de la Universidad Nacional Autónoma de México* 29: 165–179.
- Caballero, E. and C. Cerecero. 1941. Una nueva especie de *Polystoma* (Trematoda: Polystomatidae) parásito de la vejiga urinaria de *Hyla baudinii* (Dum. y Bibr.). *Anales del Instituto de Biología de la Universidad Nacional Autónoma de México* 12: 615–621.
- Cabrera-Guzmán, E., V. León-Règagnon and L. García-Prieto. 2007. Helminth parasites of the leopard frog *Rana cf. forreri* (Amphibia: Ranidae) in Acapulco, Guerrero, Mexico. *Comparative Parasitology* 74: 96–107.
- Esslinger, J. H. 1986. Redescription of *Ochoterenella digitorqua* Caballero. 1944 (Nematoda: Filarioidea) from the toad, *Bufo marinus*, with a redefinition of the genus *Ochoterenella* Caballero, 1944. *Proceedings of the Helminthological Society of Washington* 53: 210–217.
- Fernandes, J. C. 1958. Notas sobre algumas espécies do gênero *Gorgoderina* Looss, 1902 (Trematoda: Gorgoderidae). *Memórias do Instituto Oswaldo Cruz* 56: 1–15.
- Freitas, J. F. T. 1958. Breve nota sobre o *Distoma monas* Rudolphi, 1819 (Trematoda). *Revista Brasileira de Biologia* 18: 171–174.
- Freitas, J. F. T. 1963. Revisão da família Mesocoeliidae Dollfus, 1933 (Trematoda). *Memórias do Instituto Oswaldo Cruz* 61: 177–311.
- Frost, D. R., T. Grant, J. Faivovich, R. H. Bain, A. Haas, C. F. B. Haddad, R. O. de Sá, A. Channing, M. Wilkinson, S. C. Donnellan, C. J. Raxworthy, J. A. Campbell, B. L. Blotto, P. Moler, R. C. Drewes, R. A. Nussbaum, J. D. Lynch, D. M. Green, and W. C. Wheeler. 2006. The amphibian tree of life. *Bulletin of the American Museum of Natural History* 297: 1–370.
- Goldberg, S. R. and C. R. Bursey. 2008. Helminths from 10 species of brachycephalid frogs (Anura: Brachycephalidae) from Costa Rica. *Comparative Parasitology* 75: 255–262.
- Goldberg, S. R., C. R. Bursey, G. Salgado-Maldonado, R. Báez, and C. Cañeda. 2002. Helminth parasites of six species of anurans from Los Tuxtlas and Catemaco Lake, Veracruz, Mexico. *Southwestern Naturalist* 47: 293–299.
- Goldberg, S. R., C. R. Bursey and R. Tawil. 1993. Gastrointestinal helminths of the western brush lizard, *Urosaurus graciosus graciosus* (Phrynosomatidae). *Bulletin of the Southern California Academy of Sciences* 92: 43–51.
- Hamman, O. 1891. Monographie der Acanthocephalan (Echinorhynchen). Ihre entwicklungsgeschichte, histogenie u. anatomie. *Jenaische Zeitschrift für Naturwissenschaft* 25: 113–231.
- Hendrikx, W. M. L. 1983. Observations on the routes of infection of *Oswaldoecozia filiformis* (Nematoda: Trichostrongylidae) in Amphibia. *Zeitschrift für Parasitenkund* 69: 119–126.
- Kennedy, C.R. 2006. *Ecology of the Acanthocephala*. Cambridge. Cambridge University Press. 249 pp.
- Lamothe-Argumedo, R. 1976. Monogéneos de los anfibios de México VI. Redescripción de *Polystoma naevius* Caballero y Cerecero, 1941. *Anales del Instituto de Biología de la Universidad Nacional Autónoma de México* 47: 1–8.
- Lutz, A. 1926. Trématodes et oligochètes observés dans les canaux excréteurs du rein des batraciens de l'Amérique méridionale. *Comptes Rendus des Séances et Mémoires de la Société de Biologie* 95: 1503–1504.
- Mata-López, R., V. León-Règagnon and D. R. Brooks. 2005. Species of *Gorgoderina* (Digenea: Gorgoderidae) in *Rana vallanti* and *Rana cf. forreri* (Anura: Ranidae) from Guanacaste, Costa Rica, including a description of a new species. *Journal of Parasitology* 91: 403–410.
- Meyer, A. 1931. Neue Acanthocephalen aus dem Berliner Museum, Begründung eines neuen Acanthocephalensystems auf Grund einer Untersuchung der Berliner. *Sammlung Zoologischer Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere* 62: 53–108.
- Odhner, T. 1911. *Nordostafrikanische Trematoden, grösstenteils von Weissen Nil. I. Fascioliden (von der*

- Schweidischen Zoologischen Expedition gesammelt). Results of the Swedish Zoological Expedition to Egypt and the White Nile 1901 under the direction of L. A. Jagerskiöld. No. 23A. Uppsala, Sweden, 170 p.
- Odlaug, T. O. 1937. Notes on the development of *Gorgodera amplicava* in the final host. *Biological Bulletin* 72: 80-87.
- Prudhoe, S. and R.A. Bray. 1982. *Platyhelminth Parasites of the Amphibia*. British Museum (Natural History), London. Oxford University Press. 217 pp + 4 microfiche.
- Pulido-Flores, G. 1994. Helmintos de *Rana dunnii* especie endémica del lago de Pátzcuaro, Michoacán, México. *Anales del Instituto de Biología de la Universidad Nacional Autónoma de México* 65: 205-207.
- Rodríguez-Ortíz, B., L. García-Prieto and G. Pérez-Ponce de León. 2003. Checklist of the helminth parasites of vertebrates in Costa Rica. *Revista de Biología Tropical* 51: 1-41.
- Salgado-Maldonado, G., A. N. García Aldrete and V. M. Vidal-Martínez (eds.). 2000. *Metazoan Parasites in the Neotropics: A Systematic and Ecological Perspective*. Instituto de Biología, Universidad Nacional Autónoma de México, México, D.F., 310 pp.
- Savage, J. M. 2002. *The Amphibians and Reptiles of Costa Rica - A Herpetofauna Between Two Continents, Between Two Seas*. Chicago. The University of Chicago Press. 934 pp.
- Stunkard, H. W. 1959. Induced gametogenesis in a monogenetic trematode, *Polystoma stellai* Vigueras, 1955. *Journal of Parasitology* 45: 389-394.
- Wong, M. S. and D. A. P. Bundy. 1985. Population distribution of *Ochoterenella digiticauda* (Nematoda: Onchocercidae) and *Mesocoelium monas* (Digenea: Brachycoeliidae) in naturally infected *Bufo marinus* (Amphibia: Bufonidae) from Jamaica. *Parasitology* 90: 457-461.

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**Appendix I - Hylid frogs from Costa Rica examined by province from the herpetology collection of the Natural History Museum of Los Angeles County**

*Agalychnis annae* Puntarenas: 157132, 157133, 157135, Cartago: 157137, 157139, 157144, Limón: 157140, 157142, San José: 157141, 157145; *Agalychnis callidryas* Guanacaste: 158250, 158251, 158254, 158256, 158258, 158260-158263, 158265, 158266; *Agalychnis spurrelli* Puntarenas: 156867-156869, 156872-156878; *Dendropsophus ebraccatus* Cartago: 158645, 158646, 158648, 158651, 158652, 158659, 158661, 158682, 158688, 158692, Heredia: 158644, 158727, Guanacaste: 158549, 158563, 158622, 158637, Puntarenas: 158523, 158680, 158693, 158696, 158700, 158702, 158703, 158706, 158708-158710, 158712-158714, 158716, 158718, 158721, 158722, 158724; *Dendropsophus phlebodes* Cartago: 150252, 150262, 150273, Guanacaste: 150259, 150260, 150269-150272, 150275; *Duellmanohyla uranochroa* Puntarenas: 149831, 149859, 149869, 149881, Cartago 149868; *Hylomantis lemur* San José 156161-156163, 156165, 156168-156171, 156190, 156197; *Hypsiboas rosenbergi* Puntarenas: 156477, 156481, 156490; *Isthmohyla pictipes* San José: 150172, 150179, Heredia: 150178, 150180, 150182, 150195, 150200, 150201, 150203, 150205, 150207-150209, 150211, 150212; *Isthmohyla rivularis* Alajuela: 155744, Heredia 155700, 155745, 155755, 155775, Puntarenas: 155713, 155715, 155731, 155738, 155740, 155760, 155777, San José: 155727, 155743, 155762; *Isthmohyla tica* Alajuela: 156028; Cartago: 156001, 156019, 56020, Heredia: 156004, Puntarenas: 156010, 156016, San José: 156015, 156021, 156027; *Scinax elaeochrous* Cartago: 161327, 161334-161336, 161338, 161339, 161342, 161343, 161351-161353, 161357, 161364, 161368, 161372, 161374, 161425, 161489, 161560, 161594, 161597, Guanacaste: 161363, Heredia: 161392, 161568, Limón: 161333, 161407, 161497, 161513, 161598, 161603; *Smilisca phaeota* Cartago: 149726, 149733, 149735, 149741, Guanacaste: 149731, Limón: 149720, 149728, 149748, Puntarenas: 149719, San José: 149740; *Smilisca sordida*: San José: 157528, Puntarenas: 157560-157562, 157565, 157566, 157569-157572; *Tlalocohyla loquax* Cartago: 150054, 15055, 150057, 150062, 150067, 150071, 150074, 15077, 150079, 150086, 150114, Heredia: 150093, Guanacaste: 150102, 150108, 150113.