

CHECKLIST OF ENDO AND ECTOPARASITES FROM ANOLES (IGUANIDAE, DACTYLOINAE, ANOLIS) OF ECUADOR WITH NEW RECORDS

LISTA DE ENDO Y ECTOPARASITOS DE ANOLIS (IGUANIDAE, DACTYLOINAE, ANOLIS) DE ECUADOR CON NUEVOS REGISTROS

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Resumen.– Proporcionamos una lista de once taxones de endo y ectoparásitos asociados a nueve especies de anolis de Ecuador. Los parásitos identificados en laboratorio son: nemátodos de la familia Ascarididae en *Anolis dracula*, *A. trachyderma* y *A. scyphus*; larvas del género *Cochliomyia* spp. (Calliphoridae) en *Anolis parvauritus*, y larvas de ácaros de la familia Trombiculidae en *Anolis nemontea* y *A. gracilipes*.

Palabras claves.– Larvas, lagartijas, ácaros, parásitos.

Abstract.– We provide a list of eleven taxa of endo and ecto parasites associated with nine species of anoles from Ecuador. The parasites, identified in the laboratory, are: nematodes of the family Ascarididae in *Anolis dracula*, *A. trachyderma* and *A. scyphus*; larvae of the genus *Cochliomyia* spp. (Calliphoridae) in *Anolis parvauritus*, and mite larvae of the family Trombiculidae in *Anolis nemontea* and *A. gracilipes*.

Key words.– Larvae, lizards, mites, parasites.

INTRODUCTION

The anoles (Iguanidae, Dactyloinae) are a group of lizards with nearly 400 species naturally distributed from the United States of America through Central America and the Caribbean to Bolivia, with naturalized populations in Asia (Nicholson et al., 2012; Poe et al., 2017; de Queiroz et al., 2020). Forty-four anole species occur in Ecuador and to date there are few records of parasites (Torres-Carvajal et al., 2022). The knowledge of

parasitic fauna of more anole species may provide important information to better understand their diet, habitat use and biological interactions with other organisms (Marcogliese, 2004; Pereira et al., 2013). Parasites can influence competitive and predatory interactions between species by reducing the competitive strength of infected hosts against a non-host species (Hatcher et al., 2006). Helminths such as nematodes can

cause low food intake, reduce growth, and increase mortality of the hosts (Goater & Ward, 1992). In addition, helminth dominance patterns and anoles species composition show that habitat differences are determining factors for the infection of these parasites (Bundy et al., 1987). Arthropods can affect the behavior and the energy metabolism of lizards (Schall & Sarni, 1987), the outcome of interspecific competition among anoles (Schall, 1992) and decrease the survival of parasitized individuals (Irschick et al., 2006).

The present checklist summarizes the diversity of parasites in the anoles of Ecuador found in literature and in six species of anoles reviewed in the laboratory as a basis for providing a host-parasites list needed for future work and to understand their ecology.

MATERIALS AND METHODS

This checklist was prepared based on records of mites, dipterans and helminths from literature and was organized based on the taxonomic categories and the name of the authority who described each taxon and year, as well as new material examined in Ecuador. The taxonomy of the parasites follows the references in the literature, as well as nematodes (Ávila & Silva, 2010; Boada, 2015; Morand et al., 2015), platyhelminthes (Ávila & Silva, 2010), mites (Walter & Proctor, 2013); and dipterans (Florez & Wolff, 2009; Hall, 2013). Taxonomy of hosts is reviewed based on recent publications (de Queiroz et al., 2020; Torres-Carvajal et al., 2022; Uetz et al., 2022). Each record contains the phylum, class, order, family and species of the parasites. In addition to its host(s), site of infection and geographical record (state/province when available) are provided. Comments include specimens of literature reviewed and changes in the host taxonomy.

We examined six species of *Anolis* Daudin, 1802 from Ecuador deposited in the herpetology collection of the Zoology Museum of the Pontificia Universidad Católica del Ecuador (QCAZR): *Anolis dracula* Yáñez-Muñoz et al., 2018 (QCAZR 14888) from Goaltal, Carchi Province (0.82111° N, 78.13900° W, 1,542 m a.s.l.); *A. nemontae* Ayala-Varela et al., 2021 (QCAZR 14597) from Buenaventura Reserve, El Oro Province (3.65061° S, 79.78050° W, 372 m a.s.l.); *A. gracilipes* Boulenger, 1898 (QCAZR 10693) from Centro de Interpretación Ambiental Otongachi, Unión del Toachi, Pichincha Province (0.321389° S, 78.95150° W, 836 m a.s.l.); and *A. parvauritus* Williams, 1966 (QCAZR 12191) from Canandé Reserve, Esmeraldas Province (0.52069° N, 79.21438° W, 401 m. a. s. l.); *A. trachyderma* Cope, 1875 (QCAZR 11745) from Lorocachi, Pastaza Province (1.656694° S, 75.96980° W, 185 m a.s.l.); and *A. scyphus* Cope, 1864 (QCAZR 14789) from Saladero

Tabla 1. Lista de hospederos-parásitos de los anolis del Ecuador.

Table 1. List of host-parasites to anoles of Ecuador.

Host	Parasite
<i>Anolis dracula</i>	Ascarididae gen. sp.
<i>Anolis fuscoauratus</i>	<i>Cosmocerca vrcibradici</i>
<i>Anolis fuscoauratus</i>	<i>Strongyluris oscari</i>
<i>Anolis fuscoauratus</i>	<i>Rhabdias</i> sp.
<i>Anolis fuscoauratus</i>	<i>Oswaldocruzia bainae</i>
<i>Anolis fuscoauratus</i>	<i>Oswaldocruzia vitti</i>
<i>Anolis gracilipes</i>	Trombiculidae gen. sp.
<i>Anolis nemontae</i>	Trombiculidae gen. sp.
<i>Anolis parvauritus</i>	<i>Cochliomyia</i> sp.
<i>Anolis punctatus</i>	<i>Strongyluris oscari</i>
<i>Anolis punctatus</i>	<i>Rhabdias elegans</i>
<i>Anolis punctatus</i>	<i>Rhabdias</i> sp.
<i>Anolis punctatus</i>	<i>Oswaldocruzia vitti</i>
<i>Anolis purpurescens</i>	Nematoda
<i>Anolis scyphus</i>	Ascarididae gen. sp.
<i>Anolis trachyderma</i>	Ascarididae gen. sp.
<i>Anolis trachyderma</i>	<i>Cairaella henrii</i>

to 1.8 km N Río Yasuní, Yasuní National Park, Orellana Province (0.92100° S, 75.96358° W, 229 m a.s.l.).

The ectoparasites obtained from the lizards were extracted with forceps and the endoparasites were separated by dissection of the specimens. The parasites were deposited in the invertebrate collection (QCAZI) of the same institution. Taxonomic keys were used to identify the parasites (FAO, 1990; Hall, 2013; Florez & Wolff, 2009; Guimarães & Papavero, 1999; Serrano, 2010; Walter & Proctor, 2013; Morand et al., 2015). The parasites were identified to family and some to genus level because the larval stages have not yet matured their important characters to distinguish species.

Specimens were photographed with the Stereoscope ZEISS Stemi SV6 and inverted ZEISS TELAVAL 31 microscope. Measurements and digital analysis were performed with a Lumenera microscopy camera (model Infinity 1-M1, Canada) and Lumenera's Infinity Analyze and Capture software® (Lumenera Corporation, 2016). Reference specimens from the

Tabla 2. Parásitos de *Anolis* examinados en laboratorio, número de individuos, estadio y hábitat.**Table 2.** Parasites of *Anolis* examined in laboratory, number of individuals, stage and habitats.

Host	Parasites	No. Individuals	Habitat	Stage
<i>Anolis dracula</i>	Ascarididae	6	Thoracic cavity	Adult
<i>Anolis gracilipes</i>	Trombiculidae	3	Dewlap	Larvae
<i>Anolis nemontea</i>	Trombiculidae	1	Dewlap	Larvae
<i>Anolis parvauritus</i>	<i>Cochliomyia</i> sp.	8	Thoracic cavity, stomach, liver, pelvic cavity	Larvae second instar
<i>Anolis trachyderma</i>	Ascarididae	6	Thoracic cavity	Adult
<i>Anolis scypheus</i>	Ascarididae	1	Thoracic cavity	Adult

QCAZ Invertebrate Museum were also used to corroborate the information obtained from the identification of nematodes.

RESULTS

We compiled a list of 11 taxa of parasites and 9 species of host-anoles (Table 1) obtained from the literature and this study. In this study, we found three invertebrate families (Ascarididae, Trombiculidae and Calliphoridae) and 25 specimens of parasites (Table 2). The endoparasites recorded are nematodes of the family Ascarididae in anoles as *Anolis dracula*, *A. trachyderma* and *A. scypheus*. Among the recorded ectoparasites are larvae of the genus *Cochliomyia* Townsend, 1,915 of the family Calliphoridae in *Anolis parvauritus*; and mites of the family Trombiculidae in *Anolis nemontea* and *A. gracilipes*.

The specimens of the family Ascarididae (nematodes) are characterized by having a vermiform, cylindrical, non-segmented body, a slightly curved tail and three cephalic lips around the mouth, the average length of the individuals analyzed is 10 mm (10,000 μ m).

The specimens of the family Trombiculidae (mites) are characterized by having 6-legged, round-shaped larvae of small size 0.1 mm (100 μ m) not yet pigmented, poorly sclerotized with no external genitalia. The gnathosome is located in the middle of the first pair of legs, coxae I and II united; ventrally the idiosome shows very small setae while the legs, including the tarsi (final segments) show more defined setae.

The specimens of *Cochliomyia*, Calliphoridae (Diptera) belong to second-instar. On average they measured 6 mm in length (6,000 μ m \pm SD), presented a fusiform body (Fig. 1A), posterior margin of segment 11 without spines and not well developed and

sclerotized cephalopharyngeal skeleton (Fig. 1B), band of body spines with 2 tips, anterior spiracle from 9 to 11 gills, tracheal trunks with very light pigmentation in the 12th segment (Fig. 1C), posterior spiracle with incomplete peritreme lightly pigmented and imperceptible button (Fig. 1D).

LIST OF PARASITES

PHYLUM NEMATODA

Host: *Anolis purpurescens* Cope, 1899

Site of infection: Intestine.

Distribution: Pichincha.

Comments: Reported in Boada (2015).

CLASS CHROMADOREA

ORDER ASCARIDIDA

FAMILY ASCARIDIDAE gen. sp.

Host: *Anolis dracula* Yáñez-Muñoz et al., 2018 (QCAZR14888)

Site of infection: thoracic cavity.

Distribution: Carchi, Goaltal.

Comments: New material examined QCAZI261046.

Host: *Anolis trachyderma* Cope, 1875 (QCAZR11745)

Site of infection: cloaca.

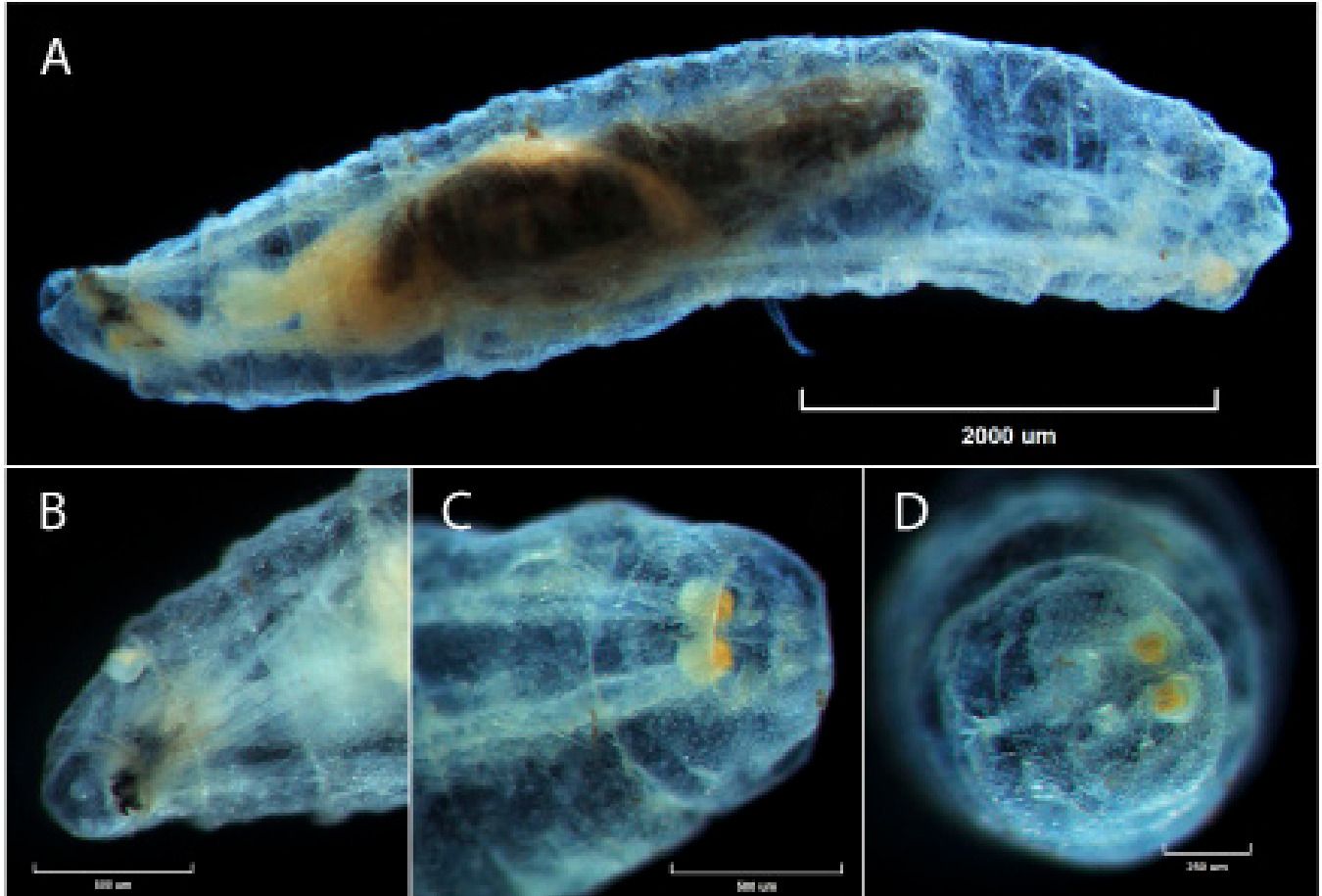


Figura 1. Calliphoridae, *Cochliomyia* sp., larvas, QCAZI261049: A) vista lateral, larva en segundo estadio; B) ganchos de boca; C) extremo caudal; D) espiráculo posterior. Fotos: Óscar Pérez. Barras de escala = 2.000 µm (A), 500 µm (B, C), 250 µm (D).

Figure 1. Calliphoridae, *Cochliomyia* sp., larvae, QCAZI261049: A) lateral view, second-instar larva; B) mouth hooks; C) caudal end; D) posterior spiracle. Photos: Oscar Pérez. Scale bars = 2.000 µm (A), 500 µm (B, C), 250 µm (D).

Distribution: Pastaza, Lorocachi.

Specimens deposited: QCAZI261050

Host: *Anolis scypheus* Cope, 1864 (QCAZR14789)

Site of infection: thoracic cavity.

Distribution: Orellana, Parque Nacional Yasuní, Río Yasuní.

Commenst: New material examined QCAZI261047 (Fig. 2).

FAMILY COSMOCERCIDAE

GENUS *Cosmocerca* DIESING, 1861

Cosmocerca vrcibradici BURSEY AND GOLDBERG, 2004

Host: *Anolis fuscoauratus* D'Orbigny, 1837

Site of infection: Intestine.

Distribution: Sucumbíos.

Comments: Reported in Ávila & Silva (2010).

CLASS SECERNENTEA

ORDER ASCARIDIDA

FAMILY HETERAKIDAE



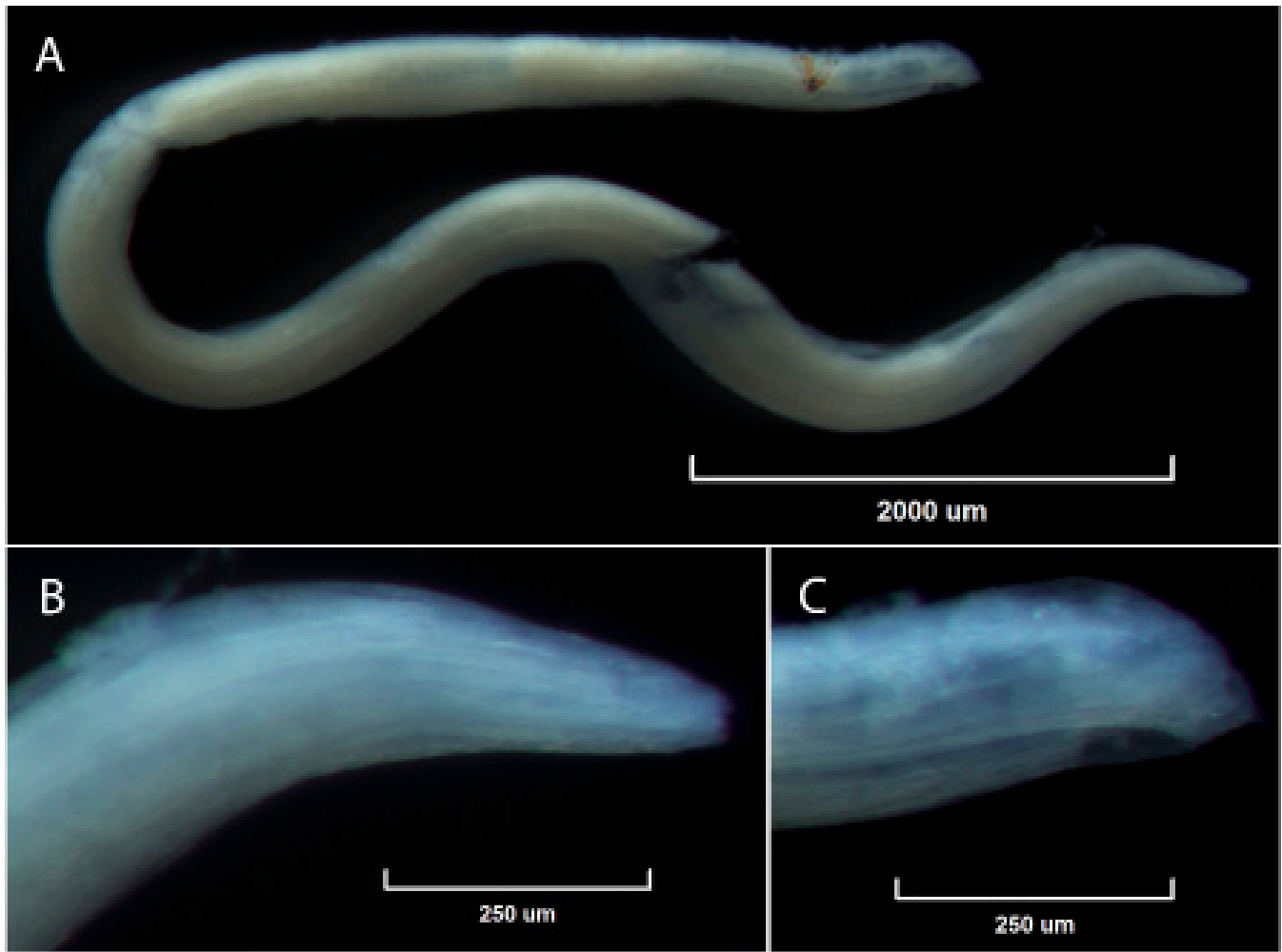


Figura 2. Ascarididae, QCAZI261046: A) vista dorso lateral; B) segmento anterior; C) segmento caudal. Foto: Óscar Pérez. Barras de escala = 2.000 µm (A), 250 µm (B, C).
Figure 2. Ascarididae, QCAZI261046: A) dorso lateral view; B) anterior segment; C) caudal segment. Photo: Oscar Pérez. Scale bars = 2.000 µm (A), 250 µm (B, C).

GENUS *Strongyluris* MUELLER, 1894

Strongyluris oscari TRAVASSOS, 1923

Host: *Anolis fuscoauratus*, *A. punctatus* Daudin, 1802, *A. transversalis* Duméril & Duméril, 1851.

Site of infection: Stomach, intestine.

Distribution: Sucumbíos and Pastaza.

Comments: Reported in Goldberg et al. (2006), McAllister et al. (2010), and Ávila & Silva (2010).

ORDER RHABDITIDA

FAMILY RHABDIASIDAE

GENUS *Rhabdias* STILES AND HASSALL, 1905

Rhabdias elegans GUTIERREZ, 1945

Host: *Anolis punctatus*

Site of infection: Lungs.

Distribution: Pastaza.

Comments: Reported in McAllister et al. (2010).

Rhabdias sp.

Host: *Anolis fuscoauratus*, *A. punctatus*.

Site of infection: Lungs, stomach.

Distribution: Sucumbíos.

Comments: Reported in Goldberg et al. (2006) and Ávila & Silva (2010).

ORDER STRONGYLIDA

FAMILY MOLINEIDAE

GENUS *Oswaldocruzia* TRAVASSOS, 1917

Oswaldocruzia bainaie BEN-SLIMANE AND DURETTE-DESSET, 1996

Host: *Anolis fuscoauratus*, *A. scyphus*.

Site of infection: Intestine.

Distribution: Sucumbíos.

Comments: Reported in Ávila & Silva (2010).

Oswaldocruzia vittii BURSEY AND GOLDBERG, 2004

Host: *Anolis fuscoauratus*, *A. punctatus*.

Site of infection: Intestine.

Distribution: Sucumbíos.

Comments: Reported in Goldberg et al. (2006) and Ávila & Silva (2010).

PHYLUM PLATYHELMINTHES

CLASS CESTODA

ORDER ONCHOPROTEOCEPHALIDEA

FAMILY PROTEOCEPHALIDAE

GENUS *Cairaella* COQUILLE AND DE CHAMBRIER, 2008

Cairaella henrii COQUILLE AND DE CHAMBRIER, 2008

Host: *Anolis trachyderma* Cope, 1876

Site of infection: Intestine.

Distribution: Sucumbíos.

Comments: Reported in Avila & Silva (2010).

PHYLUM ARTHROPODA

CLASS EUHELICERATA

ORDER TROMBIDIFORMES

FAMILY TROMBICULIDAE gen. sp.

Host: *Anolis nemoteae* (QCAZR14597)

Site of infection: dewlap.

Distribution: El Oro, Reserva Buenaventura.

Comments: New material examined QCAZI261048.

Host: *Anolis gracilipes* Boulenger, 1898 (QCAZR10693):

Site of infection: dewlap.

Distribution: Pichincha, Centro de Interpretación Ambiental Otongachi.

Comments: New material examined QCAZI261051 (Fig. 3).

CLASS INSECTA

ORDER DIPTERA

FAMILY CALLIPHORIDAE

GENUS *Cochliomyia* sp.

Host: *Anolis parvauritus* Williams, 1966 (QCAZR12191)

Site of infection: internal damage in abdominal and pelvic region.

Distribution: Esmeraldas, Reserva Canandé.

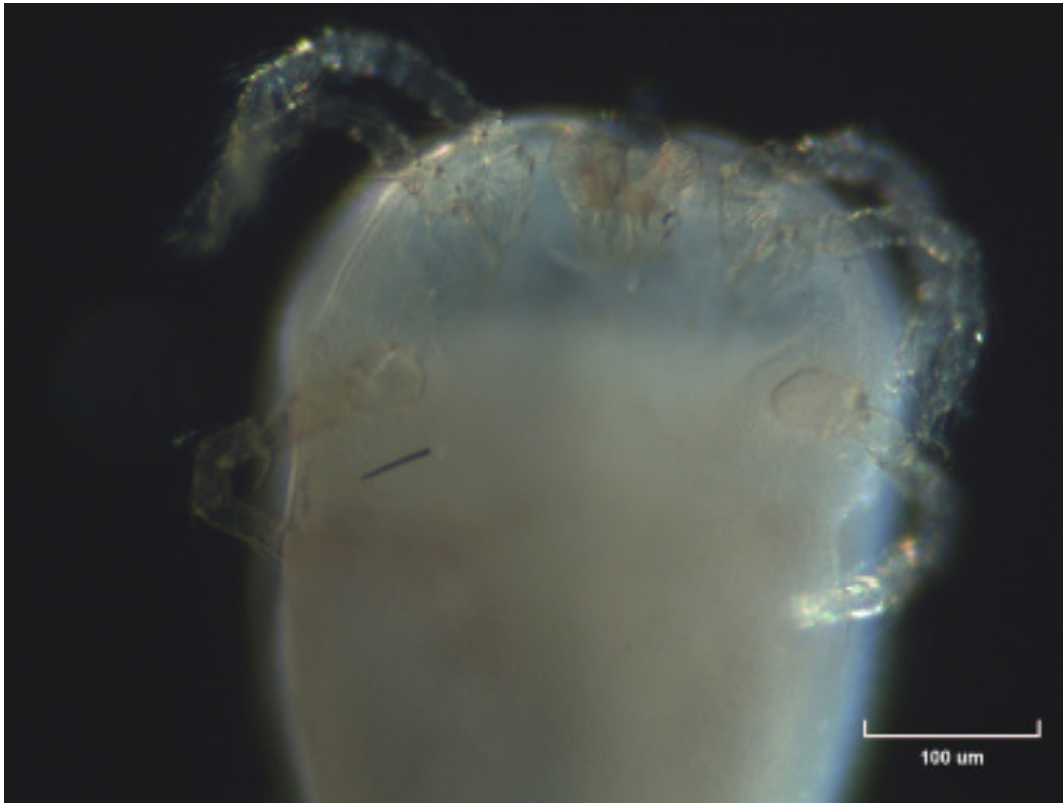


Figura 3. Trombiculidae, larvas QCAZI261051. Foto: Óscar Pérez. Barras de escala = 100 μ m.

Figure 3. Trombiculidae, larvae QCAZI261051. Photo: Oscar Pérez. Scale bars = 100 μ m.

Comments: Larvae report in Narváez et al. (2019) like *Chrysomya* sp. Robineau-Desvoidy, 1830 (Calliphoridae), QCAZI261049 (Fig. 1).

DISCUSSION

We report for the first time, mites and nematodes found in three species of *Anolis* of the western slopes of Ecuador (*A. dracula*, *A. gracilipes* and *A. nemonteae*). Most reports of parasites in Ecuador are for Amazonian host species (*A. fuscoauratus*, *A. punctatus*, *A. scypheus*, and *A. trachyderma*). We also report a new family of Nematoda for *A. trachyderma*. which indicates the importance of characterizing taxonomically the parasites of all species of anoles.

Reptiles are hosts to a wide variety of nematodes, many of which inhabit the digestive tract or lungs (Jacobson, 2007). Nematodes of the family Ascarididae have high prevalence rates in lizards of the genus *Anolis* and exhibit the greatest diversity in relation to the specificity with these lizards. Therefore, there is a great opportunity to test hypotheses about the diversification of parasites in these lizards (Morand et al., 2015).

Mites of the family Trombiculidae were not identified to genus or species because they lack further development of their characters. These mites are the only ones parasitizing vertebrate hosts during their larval instar (Walter & Proctor, 2013).

Larvae of the family Calliphoridae cause cutaneous myiasis (FAO, 1990). We reviewed the larvae reported by Narvaez et al. (2019) that were identified as belonging to the genus *Crysomya*. However, taxonomic re-identification showed that they belonged to the genus *Cochliomyia* as Carrillo (2015) points out that the presence of bands of small spines with 1 to 2 tips in the body of members of *Cochliomyia* is a diagnostic trait of the genus, while Florez & Wolff (2009) mention the presence of up to 3 tips in the body spines of *Chrysomya*.

The peritreme is slightly pigmented in *Cochliomyia* while *Chrysomya* shows a marked pigmentation. In addition, Carrillo (2015) states that in the late larval stages of *Cochliomyia* presents two tracheal trunks that can be pigmented from the 9th to 12th segment, even if pigmentation can be found only up to 1/3 of the 12th segment.

On the other hand, in early larval stages this pigmentation is very light. In addition, Guimarães & Papavero (1999) indicate that the genus *Cochliomyia* does not have spines on the posterior margin of segment 11 while the genus *Chrysomya* does have spines on this body segment.

The larvae of the family Calliphoridae were not found in an external wound in the lizards of the genus *Anolis*, because wounds are scarce in natural conditions, the female *Cochliomyia* must lay her eggs at the edge of the natural orifices of favorably exposed vertebrates (Forero et al., 2008).

Because knowledge of the immature stages of Calliphoridae species in South America is poor, it is important to rear the larvae to adults for effective species identification following the FAO (1990) manual.

Parasites compete with their hosts for resources, causing damage in many ways (Price, 1980). However, parasitism has an important role in ecosystems, regulating the abundance or density of host populations, stabilizing food chains and structuring animal communities (Zaman et al., 2014).

Zaman et al. (2014) considers that host parasite interaction causes a co-evolution where parasites force their hosts to become more complex to avoid extinction. Therefore, parasites are important promoters and protectors of biological diversity because antagonistic interactions and natural selection together increased complexity and evolvability.

We think that comparative studies among different anole populations are necessary to determine the most important factors that establish the composition and structural distribution of the parasites in these lizards, and to understand the infection levels and the effects of the parasites on their ecology and survival.

The present work is an important contribution to the knowledge of parasites in *Anolis*. It is necessary to study the parasitology associated with *Anolis*, since the current situation demands not only the knowledge of its taxonomy but also monitoring studies that allow understanding the ecological impacts on the populations of this host genus.

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MA, 003-15- IC-FAU-DNB/MA and 002-16-IC-FAU-DNB/MA of the Ministerio del Ambiente, Ecuador.

CITED LITERATURE

- Ávila, R.W. & R.J. Silva 2010. Checklist of helminths of lizards and amphisbaenians (Reptilia, Squamata) of South America. The Journal of Venomous Animals and Toxins including Tropical Diseases 4:543-572.
- Ayala-Varela, F., S.Valverde, S. Poe, A. Narváez, M. Yáñez-Muñoz & O. Torres-Carvajal. 2021. A new giant anole (Squamata: Iguanidae: Dactyloinae) from southwestern Ecuador. *Zootaxa* 4991:295-317.
- Ben-Slimane, B. & M.C. Durette-Desset. 1996. Four new species of *Oswaldocruzia* (Nematoda: Trichostrongylina, Molineoidea) parasitizing amphibians and lizards from Ecuador. *Memórias do Instituto Oswaldo Cruz* 3:317-328.
- Boada, E. 2015. Ecología de una comunidad de lagartijas del género *Anolis* (Iguanidae: Dactyloinae) de un bosque piemontano del Ecuador Occidental. Tesis de Licenciatura, Pontificia Universidad Católica del Ecuador.
- Boulenger, G.A. 1898. An account of the reptiles and batrachians collected by Mr. W. F. H. Rosenberg in western Ecuador. *Proceedings of the Zoological Society of London* 1898:107-126.
- Bundy, D., P.Vogel & E. Harris. 1987. Helminth parasites of Jamaican anoles (Reptilia: Iguanidae): a comparison of the helminth fauna of 6 *Anolis* species. *Journal of Helminthology* 61:77-83.
- Burse, C. & S.R. Goldberg. 2004. *Cosmocerca vrcibradici* n. sp. (Ascaridida: Cosmocercidae), *Oswaldocruzia vitti* n. sp. (Strongylida: Molineoidea), and other helminths from *Prionodactylus eigenmanni* and *Prionodactylus oshaughnessyi* (Sauria: Gymnophthalmidae) from Brazil and Ecuador. *Journal of Parasitology* 1:140-5.
- Carrillo, J. 2015. Identificación morfológica y molecular de *Cochliomyia* spp. de la Colección Científica del Centro Internacional de Zoonosis. Tesis en Medicina Veterinaria, Universidad Central del Ecuador.
- Cope, E. 1864. Contributions to the herpetology of tropical America. *Proceedings of the Academy of Natural Sciences of Philadelphia* 16:166-181.

- Cope, E. 1875. Report on the reptiles brought by Professor James Orton from the middle and upper amazon and western Peru. Proceedings of the Academy of Natural Sciences of Philadelphia 8:159-183.
- Cope, E. 1899. Contributions to the herpetology of New Granada and Argentina, with descriptions of new forms. Philadelphia Museum of Sciences Bulletin 1:1-19.
- Coquille, S.C. & A. de Chambrier. 2008. *Cairaella henrii* gen. n., sp. n., a parasite of *Norops trachyderma* (Polychrotidae), and *Ophiotaenia nicoleae* sp. n. (Eucestoda: Proteocephalidea), a parasite of *Thecadactylus rapicauda* (Gekkonidae), in Ecuador. Folia Parasitologica 55:97-206.
- Daudin, F.M. 1802. Histoire Naturelle, Générale et Particulière des Reptiles. Vol. 4. F. Dufart, Paris.
- de Queiroz, K., O. Torres-Carvajal & J.A. Schulte. 2020. "Iguania" in Phylonyms: A Companion to the PhyloCode. Pp. 1149–1154, in de Queiroz K., Cantino P.D., Gauthier J.A. (Eds.), Phylonyms. CRC Press, Boca Raton, USA
- Diesing, C.M. 1861. Revision der Nematoden. Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaften Classe 28:595-736.
- D'Orbigny, A. 1837. *Anolis fuscoauratus*. In Duméril A.M.C., Bibron G. Erpétologie générale ou histoire naturelle complète des reptiles. Vol. 4. Librairie Encyclopédique de Roret, Paris.
- Duméril, A.M.C. & A.H.A. Duméril. 1851. Catalogue méthodique de la collection des reptiles. Gide et Baudry, Libraires-Éditeurs, Museum d'Histoire Naturelle de Paris.
- Florez, E. & M. Wolff. 2009. Descripción y clave de los estadios inmaduros de las principales especies de Calliphoridae (Diptera) de importancia forense en Colombia. Neotropical Entomology 3:418-429.
- Food and agriculture organization of the United Nations (FAO). 1990. Manual for the Control of the Screwworm Fly, *Cochliomyia hominivorax* (Coquerel). Rome.
- Forero, E., J. Cortés & L. Villamil. 2008. Problemática del gusano barrenador del ganado, *Cochliomyia hominivorax* (Coquerel, 1858) en Colombia. Revista MVZ Córdoba 2:1400-1414.
- Goater, C.P. & P.I. Ward. 1992. Negative effects of *Rhabdias bufonis* (Nematoda) on the growth and survival of toads (*Bufo bufo*). *Oecologia* 2:161-165.
- Goldberg, S.R., C.R. Bursey & L.J. Vitt. 2006. Parasites of two lizard species, *Anolis punctatus* and *Anolis transversalis* (Squamata: Polychrotidae) from Brazil and Ecuador. *Amphibia-Reptilia* 27:575-579.
- Guimarães, J.H. & N. Papavero. 1999. Myiasis in man and animals in the Neotropical region: Bibliographic database. Pleiade/FAPESP, São Paulo, Brasil.
- Gutierrez, R.O. 1945. Contribución al conocimiento de los Nematodos parásitos de Anfibios Argentinos. Tesis Doctoral, Universidad Nacional de La Plata, Argentina
- Hall, M.J. 2013. New World Screwworm (*Cochliomyia hominivorax*) and Old World Screwworm (*Chrysomya bezziana*). Pp. 1-9, in OIE Biological Standards Commission (Eds.), Manual of Diagnostic Tests and Vaccines for Terrestrial Animals. OIE, Paris, Francia
- Hatcher, M.J., J.T.A. Dick & A.M. Dunn. 2006. How parasites affect interactions between competitors and predators. *Ecology Letters* 9:1253-1271.
- Irschick, D.J., G. Gentry, A. Herrel & B. Vanhooydonck. 2006. Effects of Sarcophagid fly infestations on green anole lizards (*Anolis carolinensis*): An analysis across seasons and age/sex classes. *Journal of Herpetology* 1:107-112.
- Jacobson, R.E. 2007. Infectious Diseases and Pathology of Reptiles: color atlas and text. CRC Press, Boca Raton, USA.
- Lumenera Corporation. 2016. Infinity Analyze and Capture for Windows. Version 6.5.6. Available from: <https://www.lumenera.com/infinity-analyze-and-capture-for-windows.html>
- McAllister, C.T., C.R. Bursey & P.S. Freed. 2010. Helminth parasites of selected amphibians and reptiles from the Republic of Ecuador. *Comparative Parasitology* 77:52-66.
- Marcogliese, D.J. 2004. Parasites: Small players with crucial roles in the ecological theater. *EcoHealth* 2:151-164.
- Morand, S., B. Krasnov & T. LittleWood. 2015. The evolutionary history of parasite diversity. Pp. 91–334, in Morand S., Krasnov B., LittleWood T. (Eds.), Parasite Diversity and Diversification:



- Evolutionary Ecology and Meets Phylogenetics. Cambridge University Press, Cambridge, England
- Müller, A. 1894. Helminthologische Beobachtungen an Bekannten und Unbekannten Entozoen. Archiv für Naturgeschichte 60:113-129.
- Narváez, A. & A. Marmol & A. Argoti. 2019. Blow fly infestation on *Anolis parvauritus*: Notes of the effects of myiasis on lizard's behaviour. Herpetology Notes 12:847-852.
- Nicholson, K.E., B. I. Crother, C. Guyer & J. M. Savage. 2012. It is time for a new classification of anoles (Squamata: Dactyloidae). Zootaxa 3477:1-108.
- Pereira, H.M., S. Ferrier, M. Walters & G. Geller. 2013. Essential biodiversity variables. Science 6117:277-278.
- Poe, S., A. Nieto-Montes de Oca, O. Torres-Carvajal, K. de Queiroz, J.A. Velasco, B. Truett, L. N. Gray, M. J. Ryan, G. Köhler, F. Ayala-Varela & I. Latella. 2017. A phylogenetic, biogeographic, and taxonomic study of all extant species of *Anolis* (Squamata; Iguanidae). Systematic Biology 2017:1-35.
- Price, P.W. (1980). Evolutionary Biology of Parasites. Princeton University Press, Princeton, USA
- Robineau-Desvoidy, André J.B. 1830. Essai sur les Myodaires. Mémoires Présentés par Divers Savans á l' Académie Royale des Sciences de l' Institut de France. <https://www.biodiversitylibrary.org/item/35324#page/20/mode/thumb> [Accessed in October 2022]
- Schall, J.J. & G.A. Sarni. 1987. Malarial parasitism and the behavior of the lizard, *Sceloporus occidentalis*. Copeia 1987:84-93.
- Schall, J.J. 1992. Parasite mediated competition in *Anolis* lizards. Oecologia 1:58-64.
- Serrano, F. 2010. Manual práctico de parasitología veterinaria. Servicio de Publicaciones, Extremadura, España
- Stiles, Ch.W. & A. Hassall. 1905. Determination of generic types, and a list of roundworm genera, with their original and type species. U.S. Department of Agriculture Bureau of Animal Industry Bulletin 79:1-150.
- Torres-Carvajal, O., G. Pazmiño-Otamendi, F. Ayala-Varela & D. Salazar-Valenzuela (Eds.). 2022. Reptiles del Ecuador. Version 2022.1. Available from: <https://bioweb.bio/faunaweb/reptiliaweb>. [Accessed in October 2022]
- Travassos, L. 1917. Nematodeos parasitos de roedores. Brazil-Medico 3:35.
- Travassos, L. 1923. Informacoes sobre a fauna helminthological de Matto Grosso (II nota). Folha Medica 2:12.
- Townsend, C.H.T. 1915. A new generic name for the screwworm fly. Journal of the Washington Academy of Sciences 20:644-646.
- Uetz, P., P. Freed & J. Hošek (Eds.). 2022. The reptile database. Available from: <http://www.reptile-database.org/>. [Accessed in October 2022]
- Walter, D. & H. Proctor. 2013. Mites: Ecology, Evolution & Behaviour. Springer Science Business Media, Berlin, Germany
- Williams, E.E. 1966. South American anoles: *Anolis biporcatus* and *Anolis fraseri* (Sauria: Iguanidae) compared. Breviora 239:1-14.
- Yáñez-Muñoz, M., C. Reyes-Puig, J. Reyes-Puig, J. Velasco, F. Ayala-Varela & O. Torres-Carvajal. 2018. A new cryptic species of *Anolis* lizard from northwestern South America (Iguanidae, Dactyloinae). ZooKeys 794:135-163.
- Zaman, L., J. R. Meyer, S. Devangam, D.M. Bryson, R. E. Lenski & C. Ofria. 2014. Coevolution drives the emergence of complex traits and promotes evolvability. PLoS Biol12:e1002023.

