Two new and two redescribed species of *Anonchotaenia* (Cestoda: Paruterinidae) from South American birds

Anna J. Phillips¹, Boyko B. Georgiev², Andrea Waeschenbach³ and Jean Mariaux³,⁵

¹Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT, USA; ²Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, Sofia, Bulgaria; ³Department of Life Sciences, Natural History Museum, London, United Kingdom; ⁴Natural History Museum of Geneva, Geneva, Switzerland; ⁵Department of Genetics and Evolution, University of Geneva, Geneva, Switzerland

**Abstract:** Morphological examination of novel specimens of paruterinid cestodes from passerine birds from Brazil and Chile and from museum specimens from Paraguay revealed two new species: *Anonchotaenia prolixa* sp. n. from *Elaenia albiceps chilensis* Hellmayr from Chile, and *Anonchotaenia vaslata* sp. n. from *Tyrannus melancholicus* (Vieillot) (type host) and *Myiodynastes maculatus* (Statius Muller) from Paraguay. The generic diagnosis of *Anonchotaenia* Conn, 1900 is amended, prompted by the presence of the armed cirrus and the elongated cirrus sac of *A. prolixa*. Two species were redescribed: *Anonchotaenia brasiliensis* Fuhrmann, 1908 from *Tachyphonus coronatus* (Vieillot) and *Thraupis cyanoptera* (Vieillot) (new host records) from Brazil, and *Thraupis sayaca* (Linnaeus) and *Volatinia jacarina* (Linnaeus) from Paraguay (new host and geographic records); and *Anonchotaenia macrocephala* Fuhrmann, 1908 from *Tachycineta leucorrhoa* (Vieillot) (new host record) from Brazil, *Tachycineta meyenii* (Cabanis) from Chile (new host and geographic record) and *Stelgidopteryx ruficollis* (Vieillot) from Paraguay (new host and geographic record). Scanning electron microscopy of *A. brasiliensis* and *A. macrocephala* revealed less microthrix variation than has been reported for other cyclophyllidean taxa. Sequence data were generated for nuclear ssr- and lsr-DNA and mitochondrial rrnL and cox1 for *A. prolixa*, *A. brasiliensis*, and *A. macrocephala*. Maximum likelihood and Bayesian inference analyses supported each species as distinct, but revealed cryptic diversity among *A. brasiliensis* specimens from different host families. New host records of *A. brasiliensis* and *A. macrocephala* prompted a formal assessment of host specificity. *Anonchotaenia prolixa* was found to be oioxenous (HSₐ = 0), *A. vaslata* and *A. macrocephala* were found to be metastenoxenous (HSₐ = 3.000 and 3.302, respectively), whereas *A. brasiliensis* was found to be euryxenous (HSₐ = 5.876). *Anonchotaenia brasiliensis* has been found parasitising several species of different passerine families that participate in mixed-species foraging flocks in the Atlantic Forest. A diversity of species of other families join these flocks and are among the substantial number of South American passerine species yet to be examined for cestodes.

**Keywords:** *Anonchotaenia prolixa*, *Anonchotaenia vaslata*, *Anonchotaenia brasiliensis*, *Anonchotaenia macrocephala*, new species, new host record, Brazil, Chile, Paraguay, new geographical record

This article contains supporting information (Table S1, S2) online at http://folia.paru.cas.cz/suppl/2014-5-441.pdf

---

*Anonchotaenia* Cohn, 1900 is one of 22 genera of Paruterinididae that is characterised by an unarmed scolex, short, wide proglottides, vermiform oncospheres and a uterus without septa (Georgiev and Kornyushin 1994, Phillips et al. 2012). It contains 27 species that parasitise a wide diversity of passeriform hosts and has a cosmopolitan distribution (Voge and Davis 1953, Dollfus 1959, Singal 1963, Ulmer and James 1976, Olsen et al. 1978, Shinde 1984, Schmidt 1986, Sharma and Mathur 1987, Mariaux 1991). The latest contributions to the systematics of *Anonchotaenia* include erection of the subgenus *Anonchotaenia* (Paranonchotaenia) Mariaux, 1991 and the description of two new species from the Ivory Coast (Mariaux 1991). Most recently, sperm ultrastructure and spermiogenesis was characterised in *Anonchotaenia globata* (von Linstow, 1879) by Yoneva et al. (2010). Species delimitation within *Anonchotaenia* is challenging because the few available morphological characters are easily obscured or distorted in contracted material. Testis number per proglottis historically has been considered the most reliable character for delimiting species of *Anonchotaenia*, although this character is known to vary between conspecifics and even within an individual’s strobila (Mariaux 1991). The addition of molecular data to phylogenetic analyses has been...
suggested to clarify species boundaries within the genus (Mariaux 1991).

South American *Anonchotaenia* species are poorly known, with only six species in total reported from the continent and all but two of these species described with brief treatments prior to 1909 (Fuhrmann 1901, 1908). As part of the present study, fieldwork conducted near the Comau Fjord, Chile in 2008 and near São Paulo, Brazil in 2011 led to the collection of cestode specimens from a diversity of avian orders, but predominantly Passeriformes. Examination of this material combined with the study of museum specimens resulted in the description of two new species of *Anonchotaenia* as well as the redescriptions of *Anonchotaenia brasiliensis* Fuhrmann, 1908 and *Anonchotaenia macrocephala* Fuhrmann, 1908. *Anonchotaenia brasiliensis* and *A. macrocephala* are the first paruterinid taxa to be examined with scanning electron microscopy (SEM). Sequences from the newly collected specimens are some of the first molecular sequences of paruterinids and were the basis for phylogenetic analyses. Host specificity had not been previously measured for members of Paruterinidae prompting the first formal assessment of host specificity for the family to assess trends of host spectrum breadth, overlap of host spectrum and host specificity in comparison to other cestode groups.

**MATERIALS AND METHODS**

**Specimen sampling and abbreviations**

Cestodes studied included newly collected material from Brazil and Chile, which were obtained as part of a collaborative effort focused on a global assessment of cestode diversity funded by the National Science Foundation (NSF) Planetary Biodiversity Inventory (PBI) project ‘A Survey of the Tape-worms (Cestoda: Platyhelminthes) from Vertebrate Bowels of the Earth’ (NSF PBI award Nos. 0818696 and 0818823). In Brazil, birds were sampled at two localities. At Estação Biológica de Boracéia, São Paulo, Brazil, bird (23°38′S; 45°52′W, elevation 946 m) during 24–28 November 2011, 164 adult birds, including 46 passerine species and one species each from Columbiformes, Piciformes and Trogoniformes, were captured by shooting at Huinay Station, Comau Fjord, Los Lagos Region, Chile (42°22′47″S; 72°22′54″W, elevation 20 m). Avian no-

Museum abbreviations used here are: MHNG-PLAT – Natural History Museum of Geneva, Geneva, Switzerland; MZUSP – Museu de Zoologia Universidade de São Paulo, São Paulo, Brazil; MNRJ – Museu Nacional Rio de Janeiro, Brazil; UFRJ – Universidade Federal do Rio de Janeiro, Brazil; USNPC – United States National Parasite Collection, Smithsonian’s National Museum of Natural History, Washington, D.C.. Specimens collected through the PBI project are indicated by the number assigned specimens (PBI-) and are listed in the Global Cestode Database (tapewormdb.uconn.edu). Collectors’ authorities for specimens obtained during the Expédition du Muséum de Genève au Paraguay are given as EMGP.

**Specimen preparation and morphological examination**

Newly collected cestodes underwent different preparations: a subset of worms had the two to three most terminal proglottides removed and fixed in 95% ethanol for molecular work and the remaining complete worms and fragments were fixed in hot 5% formalin and subsequently transferred to 70% ethanol for storage. For light microscopy, a subset of worms were stained with hydrochloric carmine, dehydrated in an ascending ethanol series, cleared in methyl-salicylate, and mounted in Canada balsam for morphological examination.

Measurements were taken using an optical retical on a Nikon Eclipse 80i microscope. Measurements are given in micrometres (μm) unless otherwise stated. Measurements of the testes, cirrus sac, vitellarium and ovary were taken only from fully developed mature and early pregravid proglottides. Extent of the cirrus sac is reported as the percentage the cirrus sac that extends across the proglottis width. Metrical and meristic data are presented as the range, followed by the mean, standard deviation and the number of measurements or counts taken (n) in parentheses. Illustrations were made with the aid of a drawing tube and Adobe Illustrator® and Adobe Photoshop®. The terms used for the developmental stages of proglottides follow Geor-giev and Vaucher (2001).

Scoleces of worms from *Tachyphonus coronatus* (Vieillot), *Tachycineta leucorrhoa* (Vieillot), *Thraupis cyanoptera* (Vieillot) and *Annodramus humeralis* (Bosc) collected in Brazil in 2011 were prepared for SEM with the following procedure: they were hydrated in a graded filtered ethanol series, post-fixed in 1.5% osmium tetroxide overnight, washed in distilled water, dehydrated in a graded filtered ethanol series, transferred to hexamethyldisilazane (Ted Pella, Inc.), and allowed to air dry in a fume hood. The specimens were then mounted on aluminium stubs on double-sided adhesive carbon tabs (Ted Pella, Inc.). Specimens were sputter-coated with ca 35 nm of gold/palladium and examined with a LEO/Zeiss DSM982 (Zeiss, Oberkothen, Germany) digital field emission scanning electron microscope at the Electron Microscopy Laboratory at the University of Connecticut, Storrs, CT, USA. Scoleces examined with SEM were retained in the personal collection of Janine N. Cairns (University of Connecticut). During the present study, several specimens from passerine hosts in South America were determined to represent *Anoncho-taenia* but could not be definitively identified to species (Table S1). These specimens have been included here because they represent new host records and additional diversity of *Anonchotaenia*. 

442
Generation of nucleotide data

Sequence data for almost complete small subunit nuclear ribosomal RNA gene (ssrDNA) (= 18S rDNA), domains D1–D3 of large subunit nuclear ribosomal RNA gene (lsrDNA) (= 28S rDNA), partial large mitochondrial ribosomal RNA subunit (rrnL) (= 16S rDNA) and partial cytochrome c oxidase subunit 1 (cox1) were generated de novo for newly collected cestode specimens, i.e. two outgroup taxa and six Anonchotaenia representatives (GenBank accession numbers: KF685910–KF685939; Table S2). Tissue samples for DNA extraction consisted of two or three of the most terminal proglottides or a subset from the middle of the strobila of complete worms, while the scolex and remaining strobila of each worm were prepared as whole mounts as previously described. Voucher specimens were deposited in the MZUSP, MHNG and the USNPC. For details of genomic DNA extraction, PCR, sequencing, sequence editing and sequence identity verification, see Scholz et al. (2013).

Phylogenetic analyses

Outgroup selection consisted of Biuterina sp. (PBI-96 from host PBI-GAB-106 Andropadus latirostris Strickland from Franceville, Haut Ogooué, Gabon, 1°36’57”N; 13°34’55”E) and Dictyterina cholodkowskii (Skjærbø, 1914) (PBI-173 from host PBI-CHI-049 Laniaus tetraphonius (Vigors) from Yuzbong, Gansu, China, 35°46’33”N; 104°02’27”E), two species of paruterinid genera that are characterised by the possession of hooks and therefore easily distinguished morphologically from the taxa of interest in this study and formed part of the sister group to the ingroup in a wider analysis of Cyclophyllidea of currently unpublished data.

Sequences were aligned using MAFFT v. 6.611b (Katoh et al. 2005) with 1000 cycles of iterative refinement and the genafpair algorithm. The alignment was improved by eye using MacClade (Maddison and Maddison 2005). Positions that could not be unambiguously aligned were excluded from any subsequent analyses. Modeltest v. 3.7macX (Posada and Crandall 1998) was used to select models of evolution using the Akaike Information Criterion. Phylogenetic analyses were conducted using two approaches: Maximum likelihood (ML) and Bayesian inference (BI). Bayesian Inference trees were constructed using MrBayes v. 3.2.1 (Huelsenbeck and Ronquist 2001). Likelihood settings for ssrDNA and lsrDNA were set to nst = 6, rates = inv, and for rrnL and cox1 were set to nst = 6, rates = gamma, equivalent to the GTR+I and GTR+G models, respectively. Parameters were estimated separately for each partition. Four chains (heated chains temp = 0.2) were run for 5000000 generations and sampled every 1000 generations. A total of 500000 generations were discarded as burn-in, at which point the average standard deviation of split frequencies was < 0.01. The frequency with which a particular clade was present in the posterior distribution is represented by the clad’s posterior probability (pp).

Maximum likelihood analyses were performed in PAUP* v. 4b10 (Swofford 2003) using successive approximation: model parameters were estimated based on a starting tree determined by neighbour-joining. A heuristic search was performed implementing the estimated model parameters using nearest-neighbour-interchange branch swapping. Model parameters were estimated on the best tree and a heuristic search performed using subtree-pruning-regrafting branch swapping implementing the estimated model parameters. After estimating model parameters, heuristic searches using tree-bisection-reconnection branch swapping were performed until the topology remained unchanged. Un-corrected ‘p’ distances were calculated for rrnL and cox1 gene fragments using Geneious Pro v. 5.6.4 created by Biomaters and available at http://www.geneious.com.

Measurement of host specificity

Host specificity at the species level was assessed using the Index of Phylogenetic Host Specificity (Caira et al. 2003) and standardised terminology for categories of host specificity proposed by Caira et al. (2003) was followed.

RESULTS

Paruterinidae Fuhrmann, 1907

Genus Anonchotaenia Cohn, 1900

Anonchotaenia (Paranonchotaenia) prolixa sp. n.

Figs. 1A, 2

Description (based on one complete worm and one fragment of strobila): Body ribbon-like, up to 28 mm (n = 1). Maximum width 700 (n = 2), at level of early gravid proglottides (Fig. 1A). Mature proglottides acraspedate, 4 to 8 times wider than long; pregravid and gravid proglottides slightly craspedate, as wide as long. Scolex rounded, 565 (n = 1) in diameter, with 4 muscular suckers, 225–250 (240 ± 12, n = 4) in diameter (Fig. 3A). First proglottides appear 0.78 mm (n = 1) from posterior margin of suckers. Mature proglottides appear 3.74 mm (n = 1) posterior to appearance of first proglottides (Fig. 1A). Genital pores irregularly alternating in short series (e.g. 2, 1, 2, 2, 1, 1, 2, 1, 2, 2, 1, …), opening equatorial along lateral edge of proglottis. Genital atrium with infundibular orifice, pyriform, narrow, deep. Genital ducts pass between osmoregulatory canals. Osmoregulatory canals classically disposed; dorsal osmoregulatory canals 7.5–22 (12 ± 7, n = 4) in diameter; ventral osmoregulatory canals 20–50 (32 ± 13, n = 4) in diameter, with transverse anastomoses along posterior margin of each proglottis.

Testes spherical, slightly oval to oval in contracted proglottides, 4–6 [4 (14%), 5 (66%), 6 (20%)] (5 ± 0.6, n = 59) in number, 28–58 (47 ± 10, n = 10) long, 40–53 (48 ± 4, n = 10) wide; arranged in single transverse dor sal row, occasionally overlapping osmoregulatory canals (Fig. 2B), persist in pregravid proglottides. Cirrus sac very large, claviform, thick-walled, muscular (Fig. 2C); 172–225 (192 ± 14, n = 31) long and 38–60 (47 ± 6, n = 31) wide in mature proglottides, 245–270 (255 ± 12, n = 5) long and 55–62.5 (59 ± 3, n = 5) wide in postmature or early pregravid proglottides; crossing and surpassing osmoregulatory canals, reaching over one third of proglottis width, length extending 30–40% (36 ± 3%, n = 10) across width of proglottis. Cirrus cylindrical, finely and densely armed on its entire length with small spines approximately 3 in length, occasionally straight but usually with one or two loops at mid-length when invaginated (Fig. 2E). Internal vas deferens thin, making a few loops in proximal part of cirrus sac. External vas deferens coiled, ventral to cirrus sac.

Phillips et al.: Anonchotaenia spp. from South American birds
Ovary oval, medial, 65–95 (79 ± 9, n = 10) long, 58–103 (85 ± 13, n = 10). Vitellarium compact, round, 48–65 (57 ± 6, n = 10) long, 50–70 (59 ± 5, n = 10), aporal to ovary. Mehlis’ gland indistinct. Seminal receptacle fusiform, not clearly distinct from vagina. Vagina conspicuous, walls well-demarcated (Fig. 2C), opening posterior to male pore. Copulatory portion wide in mature proglottides (Fig. 2B), decreasing in width in pre gravid proglottides (Fig. 2D,F), tapering to conductive portion, passing posterior and parallel to cirrus sac, rarely crossing. Conductive portion making one or two very big loops along aporal end of cirrus sac.

Uterus circular to oval, sac-like, dorsal to ovary in post-mature and early pre gravid proglottides, expanding to fill median field, usually not overlapping cirrus sac in pre gravid proglottides (Fig. 2D,F). Uterine wall thickening as proglottis matures. Paruterine organ pyramidal, consisting of uniform fibrilar tissue, developing as thickening of anterior uterine wall, directed anteroporally to uterus, appearing approximately 150–163 proglottides posterior to first mature proglottides (Fig. 1A). Eggs initially spherical. Oncospheres and embryophore transform into vermiform shape in pre gravid proglottides approximately 40–42 proglottides posterior to appearance of paruterine organ (Fig. 1A), gradually filling uterus, eggs passing into paruterine cavity not observed (Fig. 2F). Embryonic hooks not observed.

**Type and only host:** *Elaenia albiceps chilensis* Hell, white-crested elaenia (Passeriformes: Tyrannidae).

**Type and only locality:** Huinay Station, Comau Fjord, Los Lagos Region, Chile (42°22’47’’S; 72°22’54’’W, 21 m).

**Site of infection:** Small intestine.

**Prevalence and intensity of infection:** 8.3% (1 host infected of 12 examined), 2 worms.

**Type specimens:** Holotype (MHNG-PLAT-64401); 1 paratype (MHNG-PLAT-64403).

**Etymology:** *prolixa* (Latin) = extended or elongated; referring to the unusually long cirrus sac.

**Remarks.** *Anonchotaenia* (*Paranonchotaenia*) *prolixa* sp. n. is unique from the other 27 species of *Anonchotaenia* (Table 1) in the possession of an armed cirrus and a cirrus sac that extends into the median field of the proglottis. The new species has genital ducts that pass between the osmoregulatory canals as in members of the subgenus *Anonchotaenia* (*Paranonchotaenia*), including *Anonchotaenia malaconoti* Mariaux, 1991, *Anonchotaenia prionopos* Mariaux, 1991 and *Anonchotaenia dendrocitta* (Woodland, 1929). *Anonchotaenia prolixa* sp. n. is unique from the *Anonchotaenia* species that possess fewer than 7 testes and for which the subgeneric position is unclear (Table 1): *Anonchotaenia prolixa* sp. n. possesses larger suckers (225–250 µm) than *Anonchotaenia mexicana* Voge et Davis, 1953 (121–198 µm), *Anonchotaenia ranae* (Ulmer et James, 1976) (138–175 µm) and *Anonchotaenia zonotrichicola* Dollfus, 1959 (170–200 µm), possesses a smaller scolex (565 µm in diameter) than *Anonchotaenia sbesteriometra* Joyeux et Baer, 1935 (740 µm), and a larger cirrus sac (172–225 × 38–60 µm) than *A. zonotrichicola* (46–54 × 22 µm) and *Anonchotaenia zanthopygiae* Yamaguti, 1956 (60–100 × 18–22 µm).
In light of the unique characters of *A. prolixa* sp. n., i.e. the possession of an armed cirrus and a cirrus sac that extends into the median field of the proglottis that differentiates this species from its congeners, the generic diagnosis proposed by Georgiev and Kornyushin (1994) was amended (as follows):

**Genus Anonchotaenia** Cohn, 1900

**Amended diagnosis:** Scolex without rostellum or rostellar hooks. Suckers muscular, deep. Mature proglottides considerably wider than long (seven to ten times or more), acraspedote; gravid proglottides with almost equal length and width, craspedote. Genital pores alternating. Genital ducts ventral to or between osmoregulatory canals. Testes occupying all median field. Cirrus sac may reach osmoregulatory canals or cross into median field. Cirrus unarmed or exceptionally armed. Vitellarium compact, round, slightly poral, median or slightly aporal. Ovary compact, oval, poral. Seminal receptacle round or slightly oval, near point where osmoregulatory canals and genital ducts cross. Uterus spherical or oval. Developing paruterine organ aporal and dorsal to uterus; paruterine organ anterior to uterus in last gravid proglottides. Eggs with vermiform oncospheres. In Passeriformes (different families), sometimes (probably accidentally) in Apodiformes (Apodidae, Trochilidae), Ciconiiformes (Threskiornithidae) and amphibians. Cosmopolitan.

---

**Fig. 2. Anonchotaenia prolixa** sp. n., holotype (MHNG-PLAT-64401), from *Elaenia albiceps chilensis*. A – scolex; B – mature proglottides; C – terminal genital ducts; D – early pre-gravid proglottides; E – everted armed cirrus; F – late pre-gravid proglottides.
Table 1. Key characters of *Anonchotaenia* spp. (Cestoda: Paruterinidae).

<table>
<thead>
<tr>
<th>Species</th>
<th>Authors</th>
<th>Locality</th>
<th>Host*</th>
<th>Scolex diameter</th>
<th>Sucker diameter</th>
<th>Position of GD**</th>
<th>Testis number</th>
<th>Cirrus sac extent</th>
<th>Cirrus sac length (MP)</th>
<th>Cirrus sac width (MP)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Anonchotaenia antirina</em></td>
<td>Singal (1963)</td>
<td>Delhi, India</td>
<td><em>Passer domesticus indicus</em> (Passeridae)</td>
<td>490</td>
<td>195</td>
<td>ventral</td>
<td>4-5 (5)</td>
<td>43-55</td>
<td>25-31</td>
<td></td>
</tr>
<tr>
<td><em>Anonchotaenia arhyncha</em></td>
<td>Fuhrmann (1918)</td>
<td>New Caledonia</td>
<td><em>Zosterops lateralis grisiconota</em> (Zosteropidae)</td>
<td>480</td>
<td>200-220</td>
<td>ventral</td>
<td>4-7</td>
<td>-</td>
<td>80-90</td>
<td>18</td>
</tr>
<tr>
<td><em>Anonchotaenia brasiliensis</em></td>
<td>Present study</td>
<td>São Paulo, Brazil</td>
<td><em>Tachyphonus coronatus</em> (Vieillot) (Thraupidae)</td>
<td>497-696 (628)</td>
<td>223-271 (247)</td>
<td>ventral</td>
<td>4-8 (6)</td>
<td>62.5-89 (73)</td>
<td>20-30 (25)</td>
<td></td>
</tr>
<tr>
<td><em>Anonchotaenia castellani</em></td>
<td>Fuhrmann and Baer (1943)</td>
<td>El Banno, Ethiopia</td>
<td><em>Eurocephalus rueppelli rueppeli</em> (Laniidae)</td>
<td>600-700</td>
<td>280-300</td>
<td>ventral</td>
<td>9-10</td>
<td>103-115</td>
<td>25-28</td>
<td></td>
</tr>
<tr>
<td><em>Anonchotaenia clelandi</em></td>
<td>Georgiev (1992)</td>
<td>Sydney, Australia</td>
<td><em>Zosterops carulescens</em> (Latham) (= <em>Zosterops lateralis carulescens</em>) (Zosteropidae)</td>
<td>424</td>
<td>172-185 (180)</td>
<td>ventral</td>
<td>3-7 (5)</td>
<td>52-58 (56)</td>
<td>25-30 (28)</td>
<td></td>
</tr>
<tr>
<td><em>Anonchotaenia dendrocitta</em></td>
<td>Southwell (1930)</td>
<td>India</td>
<td><em>Dendrocitta rufia</em> (Corvidae)</td>
<td>600-800</td>
<td>300</td>
<td>between</td>
<td>10-12</td>
<td>160</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Anonchotaenia gaungi</em></td>
<td>Singh (1952)</td>
<td>India</td>
<td><em>Turdoides striata somervillii</em> (Sykes) (Leothrichidae)</td>
<td>1250</td>
<td>330-360</td>
<td>-</td>
<td>12-13 (13)</td>
<td>129-155</td>
<td>39-45</td>
<td></td>
</tr>
<tr>
<td><em>Anonchotaenia globata</em></td>
<td>von Linstow (1879)</td>
<td>Kaliningrad, Russia (formerly Königsberg, Germany)</td>
<td><em>Parus major</em> (Paridae) (Oenanthe)</td>
<td>500-700</td>
<td>140-300</td>
<td>ventral</td>
<td>4-8, 4/5</td>
<td>60-128</td>
<td>18-36</td>
<td></td>
</tr>
<tr>
<td><em>Anonchotaenia indica</em></td>
<td>Singh (1964)</td>
<td>Mukukswar-Kumaun, India</td>
<td><em>Musciapa sundara</em> Hodgson (= <em>Nitava sundara</em>) (Musciicapidae)</td>
<td>890-997 (995)</td>
<td>312-401 (372)</td>
<td>ventral</td>
<td>4</td>
<td>110-150</td>
<td>26-36</td>
<td></td>
</tr>
<tr>
<td><em>Anonchotaenia jeandorsti</em></td>
<td>Dollfus (1959)</td>
<td>Bagua Grande, Amazon</td>
<td><em>Tyranus melancholicus melancholicus</em> (Tyrannidae)</td>
<td>810</td>
<td>380-395</td>
<td>ventral</td>
<td>5</td>
<td>-</td>
<td>110</td>
<td>28-30</td>
</tr>
<tr>
<td><em>Anonchotaenia longiovata</em></td>
<td>Fuhrmann (1908)</td>
<td>South America</td>
<td><em>Agelaius curvus</em> (Mohina) (= <em>Cunea curvus</em>) (Icteridae), <em>Loxops sp.</em> (Fringillidae), <em>Plegadis guarauna</em> (Vieillot) (= <em>Plegadis chilae</em>) (Threskiornithidae)</td>
<td>340-485</td>
<td>126-239</td>
<td>ventral</td>
<td>7-12 (8/9)</td>
<td>67-96 (82)</td>
<td>23-29 (26)</td>
<td></td>
</tr>
<tr>
<td><em>Anonchotaenia macrocephala</em></td>
<td>Present study</td>
<td>São Paulo, Brazil</td>
<td><em>Tachycineta leucorhoa</em> (Vieillot) (Hirundinidae)</td>
<td>994</td>
<td>412-428 (419)</td>
<td>ventral</td>
<td>4-8 (6)</td>
<td>104-178</td>
<td>25-34 (30)</td>
<td></td>
</tr>
</tbody>
</table>

(continued)
<table>
<thead>
<tr>
<th>Species</th>
<th>Authors</th>
<th>Locality</th>
<th>Host*</th>
<th>Scolex diameter</th>
<th>Sucker diameter</th>
<th>Position of GD**</th>
<th>Testis number1</th>
<th>Cirrus sac extent</th>
<th>Cirrus sac length (MP)</th>
<th>Cirrus sac width (MP)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anonchotaenia oriolina</td>
<td>Cholodkovsky (1906)</td>
<td>Russia</td>
<td>Oryzomys gallula (Linnaeus) (= O. oriolus) (Oriolidae)</td>
<td>600</td>
<td>-</td>
<td>-</td>
<td>15 or more</td>
<td>*</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>Anonchotaenia piriformis</td>
<td>Fuhrmann (1918)</td>
<td>Canala, New Caledonia</td>
<td>Pachycephala ‘moravienii’ (Pachycephalidae)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>12</td>
<td>*</td>
<td>90</td>
<td>16</td>
</tr>
<tr>
<td>Anonchotaenia prolixa</td>
<td>Present study</td>
<td>Comau Fjord, Chile</td>
<td>Elaenia abiceps chilensis Helmayr (Tyrannidae)</td>
<td>565</td>
<td>225–250 (240)</td>
<td>between</td>
<td>4–6 (5)</td>
<td>C</td>
<td>172–225 (192)</td>
<td>38–60 (47)</td>
</tr>
<tr>
<td>Anonchotaenia quiscali</td>
<td>Rausch and Morgan (1947)</td>
<td>Ohio, USA</td>
<td>Quiscalus versicolor Vieillot (‘Quiscalus quiscula versicolor’) (Icteridae)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>*</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Anonchotaenia ranae</td>
<td>Ulmer and James (1976)</td>
<td>Iowa, USA</td>
<td>Rana pipiens (Schreber) (= Lithobates pipiens) (Ranidae: Anura)</td>
<td>320–380 (353)</td>
<td>138–175 (155)</td>
<td>-</td>
<td>3–10 (8)</td>
<td>NR</td>
<td>50–62.5 (60)</td>
<td>17.5–20 (20)</td>
</tr>
<tr>
<td>Anonchotaenia sbesteriometra</td>
<td>Joyeux and Baer (1935)</td>
<td>Indochina</td>
<td>Motacilla cinerea caspica Gmelin (= Motacilla cinerea cinerea (caspica)) (Motacillidae)</td>
<td>740</td>
<td>240</td>
<td>-</td>
<td>4–6</td>
<td>*</td>
<td>108</td>
<td>18</td>
</tr>
<tr>
<td>Anonchotaenia trochili</td>
<td>Fuhrmann (1908)</td>
<td>Brazil</td>
<td>Eupetomena macrura (Gmelin) (= E. macroura) (Trochilidae)</td>
<td>250</td>
<td>100</td>
<td>-</td>
<td>14</td>
<td>*</td>
<td>60</td>
<td>*</td>
</tr>
<tr>
<td>Anonchotaenia vaslata</td>
<td>Present study</td>
<td>Jeju, San Pedro, Paraguay</td>
<td>Tyranus melanochilis Vieillot (Tyrannidae)</td>
<td>760–980 (878)</td>
<td>325–360 (346)</td>
<td>ventral</td>
<td>7–10 (8)</td>
<td>R</td>
<td>133–153 (141)</td>
<td>33–48 (42)</td>
</tr>
<tr>
<td>Anonchotaenia zandophygea</td>
<td>Yamaguti (1956)</td>
<td>Sinya, Aomori Prefecture, Japan</td>
<td>Zanthopogon narcissina narcissina (Temminck) (= Ficedula narcissina narcissina)</td>
<td>550–650</td>
<td>220–250</td>
<td>-</td>
<td>5–7 (6)</td>
<td>NR</td>
<td>60–100</td>
<td>18–22</td>
</tr>
</tbody>
</table>

* original host name followed by the current name if different in parentheses; ** in relation to osmoregulatory canals; MP – mature proglottides; GD – genital ducts; C – crossing and surpassing; R – reaching but not crossing; NR – not reaching; 1 – usually numbers are in parentheses.
Type species: Anonchotaenia clava Cohn, 1900, a junior synonym of A. globata (von Listow, 1879).

Other species: See Table 1 for the list and key measurements of valid Anonchotaenia spp.

Anonchotaenia (Anonchotaenia) vaslata sp. n.
Figs. 1B and 3

Description (based on five complete worms and one detached scolex from Tyrannus melancholicus (Vieillot)):
Body ribbon-like, up to 31 mm (n = 5) long, maximum width 810–900 (853 ± 35, n = 5) at level of pregravid proglottides (Fig. 1B). Formation of primordial genital organs appearing before external segmentation, which becomes distinct at level of late pre-mature proglottides. Proglottides slightly craspedote, wider than long when mature (Fig. 3C); craspedote when pregravid and gravid, wider than long, only most terminal gravid proglottides as long as wide (Fig. 3E). Scolex rounded, 760–980 (878 ± 80, n = 6) in diameter, with 4 round, muscular suckers, 325–360 (346 ± 10, n = 24) in diameter (Fig. 3A). First proglottides appear 0.37–1.01 mm (0.8 ± 0.3, n = 5) from posterior margin of suckers. Mature proglottides appear 2.14 mm (n = 1) posterior to appearance of first proglottides (Fig. 1B). Genital pores irregularly alternating (e.g. 3, 2, 1, 1, 1, 1, 1, 2, 1 …), opening in anterior third of lateral margin of mature proglottides and equatorial along lateral edge of post-mature and gravid proglottides. Genital atrium with infundibular orifice, narrow, deep

Fig. 3. Anonchotaenia vaslata sp. n., holotype (MHNG-PLAT 37770), from Tyrannus melancholicus. A – scolex; B – terminal genital ducts; C – mature proglottides; D – pre-gravid proglottides; E – gravid proglottides with eggs passing into the paruterine organ.
Table 2. Key measurements of specimens of *Anonchotaenia vaslata* sp. n. from various hosts from Paraguay.

<table>
<thead>
<tr>
<th>Catalog number</th>
<th>Host species</th>
<th>Locality</th>
<th>Scolex diameter</th>
<th>Sucker diameter</th>
<th>Testes number</th>
<th>CS length MP</th>
<th>CS width MP</th>
<th>CS length PP</th>
<th>CS width PP</th>
</tr>
</thead>
<tbody>
<tr>
<td>MHNG-PLAT 37966</td>
<td><em>Tyrannus melancholicus</em></td>
<td>Paraguay</td>
<td>1 075</td>
<td>405–425</td>
<td>7–10*</td>
<td>135–150</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>(Viellot) (Tyrannidae)</td>
<td></td>
<td>n = 1</td>
<td>n = 4</td>
<td>(4 ± 3)</td>
<td>(43 ± 6)</td>
<td>n = 5</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>MHNG-PLAT 39505</td>
<td><em>Myiodynastes maculatus</em></td>
<td>Paraguay</td>
<td>1 075</td>
<td>390–420</td>
<td>7–10* (8 ± 1)</td>
<td>135–150</td>
<td>50</td>
<td>40–45</td>
<td>163–9</td>
</tr>
<tr>
<td></td>
<td>(Status Muller) (Tyrannidae)</td>
<td></td>
<td>n = 1</td>
<td>n = 4</td>
<td>(9 ± 7%)</td>
<td>(14 ± 7%)</td>
<td>n = 4</td>
<td>(64 ± 3)</td>
<td>n = 4</td>
</tr>
</tbody>
</table>

CS – cirrus sac; MP – mature proglottides; PP – pregravid proglottides; * n = 14 from 1 worm.

extended tubular middle part, flat base. Genital ducts pass ventrally to osmoregulatory canals. Osmoregulatory canals classically disposed; dorsal osmoregulatory canals 14–18 (15 ± 2, n = 4) in diameter; ventral osmoregulatory canals 35–43 (40 ± 4, n = 4) in diameter, with transverse anastomoses along posterior margin of each proglottis.

Testes spherical, slightly oval to oval in contracted proglottides, 45–55 (49 ± 4, n = 10) by 40–55 (49 ± 4, n = 10), arranged in single transverse dorsal row, occasionally overlapping osmoregulatory canals; 7–10 [7 (33%), 8 (44%), 9 (9%), 10 (14%)] (8 ± 1 n = 36) in number (Fig. 3C). Cirrus sac pyriform, tapering orally, rounded aporally, muscular, thick-walled (Fig. 3B), 133–153 (141 ± 6, n = 10) by 33–48 (42 ± 4, n = 10) in mature proglottides (Fig. 3C), 118–170 (143 ± 19, n = 8) by 38–45 (41 ± 2, n = 8) in early pre gravid proglottides, reaching but not crossing osmoregulatory canals; length extending 16–18% (16 ± 1%, n = 10) across width of proglottis. Cirrus unarmed, cylindrical, 10–13 (12 ± 1, n = 10) in diameter. Internal vas deferens forming several coils in aporal portion of cirrus sac. External vas deferens large, wide, prominent, forming coiled mass occupying poral field of proglottis.

Ovary oval, medial, 50–73 (64 ± 6, n = 10) by 113–130 (120 ± 5, n = 10). Vitellarium compact, circular to oval, 38–60 (49 ± 6, n = 10) by 45–75 (62 ± 9, n = 10), aporal to ovary. Mehlis’ gland indistinct. Seminal receptacle tubular to fusiform. Vagina conspicuous, walls well-demarcated, thick, opening posterior to male pore, separated into copulatory and conductive parts, passing posterior and ventral to cirrus sac and external vas deferens, lumen of copulatory canal crenulated (Fig. 3B).

Uterus in post-mature and early pre gravid proglottides circular to oval, sac-like, occupying center of median field, dorsal to vitellarium, expanding to occupy posterior median field in gravid and gravid proglottides. Uterine wall thickening as proglottis matures. Paruterine organ developing from anterior wall of uterus, conical, consisting of uniform fibrilar tissue, appearing 94 proglottides posterior to first mature proglottides (Fig. 1B); initially directed anteriorly or antero-laterally, curving dorsally in pre gravid and gravid proglottides (Fig. 3D,E), curving 63 proglottides posterior to appearance (Fig. 1B). Eggs passing into paruterine cavity observed in terminal proglottis of one worm (Fig. 3E). Gravid proglottides with all eggs completely within paruterine organ not observed. Eggs initially spherical. Oncospheres and embryophore transform into veriform shape in late pre gravid proglottides, appearing approximately 69 proglottides posterior to first appearance of paruterine organ, passing into paruterine cavity in veriform state. Embryonic hooks present in central portion of veriform oncospheres.

**Type host:** *Tyrannus melancholicus* (Viellot), tropical kingbird (Passeriformes: Tyrannidae).

**Type locality:** Jejui, San Pedro, Paraguay (24°06’S; 56°27’W, elevation 96 m).

**Site of infection:** Small intestine.

**Type specimens:** MHNG-PLAT 37770: Holotype (in black brackets) and 1 paratype on the same slide, 4 paratypes (3 complete worms and 1 detached scolex) on a separate slide.

**Additional material examined:** 1 complete worm (MHNG-PLAT 37966) from *T. melancholicus* from Arroyo Tapiacuari, San Pedro, Paraguay (24°36’S; 56°45’W); 1 complete worm in 4 fragments (MHNG-PLAT 39505) from *Myiodynastes maculatus* (Status Muller), streaked flycatcher (Passeriformes: Tyrannidae) from Carapegua, Paraguari, Paraguay (25°44’S; 57°14’W).

**Etymology:** *Vas* (Latin) – vessel or duct + *lata* (Latin) – broad or wide; referring to the wide external vas deferens observed in this species.

**Remarks.** The new species presents a combination of characters unique from the other 28 species of *Anonchotaenia* (Table 1): wide, prominent external vas deferens rather than thin, coiled external vas deferens embedded within dense tissue, a paruterine organ that is conical but curves dorsally (even in relaxed proglottides) rather than thin, coiled external vas deferens embedded within dense tissue, a paruterine organ that is conical but curves dorsally (even in relaxed proglottides) rather than between the canals as in the four species of *Anonchotaenia* (*Paranonchotaenia*: *A. dendroicta*, *A. malaconoti*, *A. prionapos* and *A. prolica*). *Anonchotaenia vaslata* belongs to a group of 15 *Anonchotaenia* species that have fewer than 11 but more than 6 testes per proglottis (Table 1). *Anonchotaenia vaslata* usually possesses 7–8 testes per proglottis unlike *Anonchotaenia cas-
Anonchotaenia vaslata possesses a longer cirrus sac (133–153 µm) than Anonchotaenia arhyncha Fuhrmann, 1918 (80–90 µm); this further differentiates the new species from A. brasiliensis (62.5–89 µm), Anonchotaenia longiovata Fuhrmann, 1901 (67–96 µm), A. ranae (50–62.5 µm), A. yadavi (19–110 µm), A. castellani (103–115 µm), A. zanthopygiae (60–100 µm), and A. clelandi (52–58 µm). The cirrus sac of A. vaslata reaches the osmoregulatory canals unlike Anonchotaenia antirina Singal, 1964, A. brasiliensis, A. indica Singh, 1964, A. longiovata, A. ranae, and A. zanthopygiae and is further differentiated from A. globata in this respect.

The new species possesses a larger scolex (760–980 µm) than A. quiscali (580 µm), A. mexicana (522–612 µm), A. zanthopygiae (550–650 µm) and A. globata (500–700 µm), further differentiating the new species from these taxa. The new species differs from Anonchotaenia lambi (Voge et Davis, 1953) in the possession of a smaller scolex (760–980 µm rather than 1120 µm) and a shorter cirrus sac (102–118 µm rather than 133–153 µm). Anonchotaenia vaslata possesses larger suckers (325–360 µm) than A. mexicana (121–198 µm) as well as a wider cirrus sac (33–48 µm rather than 19–27 µm in A. mexicana).

Material included here from T. melancholicus (MHNG-PLAT-37966) and M. maculatus (MHNG-PLAT 39505) is morphologically consistent with the type specimens (Table 2); M. maculatus represents an additional host record for A. vaslata.

Additional specimens examined in this study were found not to be conspecific with A. vaslata (Table S2). Specimens from Paraguay (MHNG-PLAT 37807 and MHNG-PLAT 39512) resemble A. vaslata in the form of the external vas deferens, paruterine organ, and genital atrium but differ in the possession of a smaller scolex (410–530 µm rather than 760–1075 µm), smaller suckers (170–195 µm rather than 325–425 µm) and a shorter cirrus sac (92.5–110 µm rather than 133–153 µm). Specimens from Bolivia (MHNG-PLAT 83085) resemble A. vaslata in the form of the external vas deferens, paruterine organ and genital atrium, but differ in the possession of a higher number of testes per proglottis (8–12, usually 10 rather than 7–10, usually 7 or 8). For these reasons, this material has not been included in the type series of the new species.

**Anonchotaenia (Anonchotaenia) brasiliensis** Fuhrmann, 1908

**Redescription** (based on eight complete worms and one scolex prepared for SEM from T. coronatus from Bra-
zil): Body ribbon-like, 31–47 (38 ± 6 mm, n = 6) in length, 
maximum width 593–696 (636 ± 33, n = 6), at level of pre-
gravid proglottides (Fig. 4A). External segmentation lack-
ing at level of developed mature proglottides (Fig. 5C).
Mature, post-mature and early pregravid proglottides 
slightly craspedote, wider than long (Fig. 5C); late pre-
gravid proglottides slightly craspedote, as wide as long 
(Fig. 5E). Scolex rounded, 497–696 (628 ± 70, n = 7) 
in diameter, with 4 round, muscular suckers, 222–271  
(247 ± 13, n = 28) in diameter (Figs. 5A, 6A). Sucker 
proximal and distal surfaces covered by acicular filitrich-
es (Fig. 6B,C). First proglottides appear 1.0–1.4 mm 
(1.2 ± 1, n = 7) from posterior margin of suckers. Mature 
proglottides appearing approximately 3.56 mm (n = 1) 
from posterior margin of suckers (Fig. 4A). Genital pores 
irregularly alternating in short series (e.g. 2, 1, 1, 2, 1, 3, 
1, 2, 1, 1, 1, 1, 1 …); opening equatorial along lat-
eral edge of proglottis. Genital atrium with infundibular
orifice, tubular. Genital ducts pass ventral to osmoregulatory canals. Osmoregulatory canals classically disposed; dorsal osmoregulatory canals 8–18 (11 ± 2, n = 23) in diameter; ventral osmoregulatory canals 17–25 (21 ± 2, n = 18) in diameter; transverse anastomoses along posterior margin of each proglottis.

Testes spherical, circular to oval in contracted proglottides, 4–8 [4 (2%), 5 (30%), 6 (45%), 7 (19%), 8 (4%)] (6 ± 2, n = 112) in number; arranged irregularly across proglottis in single plane, sometimes overlapping; 29–51 (43 ± 6, n = 38) by 24–46 (37 ± 6, n = 38), occasionally overlapping margins of ventral osmoregulatory canal (Fig. 5C). Cirrus sac pyriform, tapering slightly porally and aporally, muscular, thick-walled (Fig. 5B), 62.5–89 (73 ± 7, n = 25) by 20–30 (25 ± 2, n = 25) in mature proglottides (Fig. 5C), 65–89 (76 ± 5, n = 25) by 20–35 (28 ± 4, n = 25) in early pregravid proglottides, not reaching osmoregulatory canals, length extending 11–20% (14 ± 2%, n = 40) across width of proglottis. Cirrus unarm ed, cylindrical. Internal vas deferens forming several coils in aporal portion of cirrus sac. External vas deferens forming coiled mass, occupying anterior poral portion of median field of proglottis.

Ovary round to oval, poral, 36–62 (50 ± 7, n = 28) by 45–94 (67 ± 10, n = 28). Vitellarium compact, circular, 31–48 (38 ± 4, n = 28) by 34–53 (45 ± 5, n = 28), medial. Mehlis’ gland not distinct. Seminal receptacle fusiform. Vagina tubular, opening posterior to male pore, not clearly separated into copulatory and conductive parts, passing posteriorly to cirrus sac, sometimes overlapping slightly, intertwining with external vas deferens (Fig. 5B). Uterus coiled mass, occupying anterior poral portion of median field of proglottis.

Testes spherical, circular to oval in contracted proglottides, 4–8 [4 (2%), 5 (30%), 6 (45%), 7 (19%), 8 (4%)] (6 ± 2, n = 112) in number; arranged irregularly across proglottis in single plane, sometimes overlapping; 29–51 (43 ± 6, n = 38) by 24–46 (37 ± 6, n = 38), occasionally overlapping margins of ventral osmoregulatory canal (Fig. 5C). Cirrus sac pyriform, tapering slightly porally and aporally, muscular, thick-walled (Fig. 5B), 62.5–89 (73 ± 7, n = 25) by 20–30 (25 ± 2, n = 25) in mature proglottides (Fig. 5C), 65–89 (76 ± 5, n = 25) by 20–35 (28 ± 4, n = 25) in early pregravid proglottides, not reaching osmoregulatory canals, length extending 11–20% (14 ± 2%, n = 40) across width of proglottis. Cirrus unarm ed, cylindrical. Internal vas deferens forming several coils in aporal portion of cirrus sac. External vas deferens forming coiled mass, occupying anterior poral portion of median field of proglottis.

Ovary round to oval, poral, 36–62 (50 ± 7, n = 28) by 45–94 (67 ± 10, n = 28). Vitellarium compact, circular, 31–48 (38 ± 4, n = 28) by 34–53 (45 ± 5, n = 28), medial. Mehlis’ gland not distinct. Seminal receptacle fusiform. Vagina tubular, opening posterior to male pore, not clearly separated into copulatory and conductive parts, passing posteriorly to cirrus sac, sometimes overlapping slightly, intertwining with external vas deferens (Fig. 5B). Uterus coiled mass, occupying anterior poral portion of median field of proglottis.

Ovary round to oval, poral, 36–62 (50 ± 7, n = 28) by 45–94 (67 ± 10, n = 28). Vitellarium compact, circular, 31–48 (38 ± 4, n = 28) by 34–53 (45 ± 5, n = 28), medial. Mehlis’ gland not distinct. Seminal receptacle fusiform. Vagina tubular, opening posterior to male pore, not clearly separated into copulatory and conductive parts, passing posteriorly to cirrus sac, sometimes overlapping slightly, intertwining with external vas deferens (Fig. 5B). Uterus coiled mass, occupying anterior poral portion of median field of proglottis.
Table 3. Key measurements of type material and specimens of *Anonchotaenia brasiliensis* from various localities and host species and *A. cf. brasiliensis* from Brazil.

<table>
<thead>
<tr>
<th>Catalog number</th>
<th>Host species</th>
<th>Locality</th>
<th>Scolex diameter</th>
<th>Sucker diameter</th>
<th>Testes number</th>
<th>CS extent</th>
<th>CS length</th>
<th>CS width</th>
</tr>
</thead>
<tbody>
<tr>
<td>MHNG-PLAT 40213 (type material)</td>
<td><em>Cacicus haemorrhous</em> (Linnæus) (Icteridae)</td>
<td>Brazil</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>8–11% (10 ± 1%)</td>
<td>53–75 (65 ± 8)</td>
<td>33–40 (36 ± 3)</td>
</tr>
<tr>
<td>MZUSP 7191, MZUSP 7192, MZUSP 7193</td>
<td><em>Thraupis cyanoptera</em> (Vieillot) (Thraupidae)</td>
<td>Brazil</td>
<td>536–559</td>
<td>202–241</td>
<td>n = 2</td>
<td>5–8* (7 ± 0.8)</td>
<td>69–95 (79 ± 8)</td>
<td>25–35 (28 ± 3)</td>
</tr>
<tr>
<td>MHNG-PLAT 39494, MHNG-PLAT 82656</td>
<td><em>Ammomimus hernalis</em> (Bosc) (Empididae)</td>
<td>Brazil</td>
<td>335–440</td>
<td>154–183</td>
<td>n = 6</td>
<td>9–13%</td>
<td>64–81 (72 ± 5)</td>
<td>25–33 (29 ± 2.5)</td>
</tr>
</tbody>
</table>

CS – cirrus sac; MP – mature proglottides; PP – pregravid proglottides; * n = 50 from 3 worms; ** n = 200 from 4 worms.

**Material examined:** From *Tachyphonus coronatus* (Vieillot), ruby-crowned tanager (PBI BRE-094) (Passeriformes: Thraupidae); 8 complete worms and 1 scolex prepared for SEM (MZUSP 7213, 7214) from Boracéia Biological Station, Salesópolis, São Paulo, Brazil (23°38'S; 45°52'W, elevation 946 m).

**Additional material examined:** From *Cacicus haemorrhous* (Linnæus), red-rumped cacique (Passeriformes: Icteridae): 2 syntypes and 3 slides of longitudinal sections (MHNG-PLAT 40213) from ‘San Paulo’, Brazil (GPS data not specified); from *Thraupis cyanoptera* (Vieillot), azure-shouldered tanager (PBI BRE-070) (Passeriformes: Thraupidae): 3 contracted worms (MZUSP 7191–7193) and 1 detached scolex prepared for SEM from Boracéia Biological Station, Salesópolis, São Paulo, Brazil (23°38'S; 45°52'W, elevation 946 m); from *Volatinia sayaca* (Linnæus), sayaca tanager (Passeriformes: Thraupidae): 2 worms with contracted strobila (MHNG-PLAT 39504) from Carapegua, Paraguari, Paraguay (25°44'S; 57°15'W, elevation 92 m); 1 complete worm, 5 worms with incomplete strobila, 14 fragments of strobila, 1 detached scolex (MHNG-PLAT 39531) from San Lorenzo, Central, Paraguay (23°18'S; 57°30'W, elevation 146 m); from *Volatinia jaca rina* (Linnæus), blue-black grassquit (Passeriformes: Thraupidae): 3 worms with incomplete strobila and 2 fragments of strobila (MHNG-PLAT 39494) from Carapa, Canendiyu, Paraguay (24°08'24"S; 55°40'12"W, elevation 143 m); 3 complete worms and 3 fragments of strobila (MHNG-PLAT 82656) from Bahia Asunción, Distrito de la Capital, Paraguay (27°16'22"S; 57°37'37"W, elevation ca 61 m).

**Prevalence and intensity of infection:** From pregravid proglottides posterior to appearance of paruterine organ (Fig. 4A). Oncospheres pass into paruterine organ in coiled state (Fig. 5D). Embryonic hooks not observed.

![Fig. 7. Anonchotaenia brasiliensis, syntype: MHNG-PLAT 40213 from Cacicus haemorrhous. A – pregravid proglottides; B – terminal genital ducts.](image)
**T. coronatus**, 14% (1 host infected of 7 examined), 25 worms; from *T. cyanoptera*, 25% (1 host infected of 4 examined), 7 worms.

**Remarks.** The original description of *A. brasiliensis* by Fuhrmann (1908) was very brief and included measurements and information about few, yet essential, characters without illustrations. The present redescription expands the range and provides information on additional morphological features with illustrations and scanning electron micrographs (see Figs. 5 and 6A–C for the morphology of newly collected specimens and Fig. 7A,B for syntype morphology). *Anonchotaenia brasiliensis* is now characterised by its possession of five to eight, but usually six, testes per proglottis, a scolex 497–696 µm in diameter, suckers 223–271 µm in diameter, a cirrus sac 62–89 µm in length in mature proglottides, and a conical paruterine organ.

Prior to this study, *A. brasiliensis* had only been reported from *C. haemorrhous* and *Hemignathus virens* (Gmelin) (see Fuhrmann 1908, van Riper 1991). Material included here from *T. coronatus, T. cyanoptera, T. sayaca* and *V. jacarina* is morphologically consistent with...
specimens from the type host, *C. haemorrhous* (Table 3). These species represent new host genus records and Thraupidae is a new host family record for *A. brasiliensis*. Specimens from the MHNG extend the geographic range of the species beyond Brazil to include areas in Paraguay.

Specimens from *Ammodramus humeralis* (Bosc), grassland sparrow (Passeriformes: Emberizidae) (MZUSP 7284) from Boracéia Biological Station, Salesópolis, São Paulo, Brazil (23°38'S; 45°52'W, elevation 946 m) are morphologically indistinguishable from *A. brasiliensis*, but the results of molecular analyses suggest they represent a species distinct from *A. brasiliensis*. As a result, these specimens were not included in the redescription based on the results of the molecular phylogeny and are referred to as *A. cf. brasiliensis* PBI-228.

*Anonchotaenia* (*Anonchotaenia*) *macrocephala*
Fuhrmann, 1908  
**Redescription** (one complete worm, two fragments of strobila and one scolex prepared for SEM from *T. leucorhoia* from Brazil): Body ribbon-like, up to 59 mm long (*n* = 1), maximum width 878–1011 (963 ± 59, *n* = 3), at level of pregravid proglottides (Fig. 4B). Proglottides acraspedote, wider than long in mature, post-mature and young pregravid (Fig. 8D,E); slightly craspedote, as wide as long or longer than wide in late pregravid and gravid proglottides (Fig. 8C,F). Scolex rounded, massive, 994 (n = 1) in diameter with 4 round, muscular suckers, 412–428 (419 ± 7, *n* = 4) in diameter (Figs. 6D, 8A). Sucker proximal and distal surfaces covered by acicular filitriches (Fig. 6E,F). First proglottides appear 1.9 mm (n = 1) from posterior margin of suckers. Mature proglottides appear approximately 3 mm (n = 1) from posterior margin of suckers (Fig. 2B). Genital pores irregularly alternating in short series (e.g. 3, 2, 1, 1, 1, 1, 1, 1, 2, 1, 2, 1, 2, 1, 2), opening equatorial along lateral edge of proglottis. Genital atrium with infundibular orifice, pyridiform. Genital ducts pass ventrally to osmoregulatory canals. Osmoregulatory canals classically disposed; dorsal osmoregulatory canals 6–12 (9 ± 2, *n* = 12) in diameter; ventral osmoregulatory canals 22–57 (31 ± 10, *n* = 12) in diameter; transverse anastomoses along posterior margin of each proglottis.

Testes spherical, slightly oval to oval in contracted proglottides; 4–8 [4 (4%), 5 (17%), 6 (36%), 7 (32%), 8 (11%)] (6 ± 1, *n* = 95) in number, arranged in single dorsal transverse row, 29–55 (43 ± 7, *n* = 37) by 31–57 (44 ± 7, *n* = 37), not overlapping marginal osmoregulatory canals (Fig. 8D), persist in pregravid proglottides. Cirrus sac pyriform, tapering porally, rounded aporally, muscular, thick-walled (Fig. 8B), 104–178 (137 ± 19, *n* = 24) by 25–34 (30 ± 3, *n* = 24) in mature proglottides, 93–125 (113 ± 9, *n* = 24) by 23–31 (28 ± 2, *n* = 24) in early pregravid proglottides, not reaching osmoregulatory canals; length extending 10–17% (13 ± 1%, *n* = 28) across width of proglottides (Fig. 8D,E). Cirrus unarmed, cylindrical. Internal vas deferens forming several coils in aporal portion of cirrus sac. External vas deferens appearing as bulbous mass in mature proglottides, developing into coiled, tubular mass in pregravid proglottides, occupying poral portion of median field.

Ovary round to oval, poral, 44–65 (54 ± 7, *n* = 17) by 57–105 (89 ± 13, *n* = 17). Vitellarium compact, circular, medial, 30–50 (39 ± 6, *n* = 17) by 35–55 (43 ± 6, *n* = 17). Mehlis’ gland not distinct. Seminal receptacle fusiform. Vagina narrow, opening posterior to male pore, not clearly separated into copulatory and conductive parts, passing posteriorly to cirrus sac (Fig. 8B). Uterus circular to slightly oval, sac-like, occupying median field in post-mature and early pregravid proglottides. Paruterine organ consisting of uniform fibrilar tissue, developing as thickening of anterior uterine wall, initially conical, directed anteriorly (Fig. 8E), appearing approximately 150 proglottides posterior to first mature proglottides.
(Fig. 4B). In pregravid proglottides pressing posteriorly into anterior uterine wall to form conical pocket inside uterine margins, but not invading uterus (Fig. 8C), approximately 105 proglottides posterior to appearance of paruterine organ (Fig. 4B). Eggs passing into paruterine cavity observed in terminal proglottis (Fig. 8F). Gravid proglottides with all eggs completely within paruterine cavity not observed. Eggs initially spherical. In pregravid proglottides oncospheres and embryophore transform into vermiform shape approximately 112 proglottides posterior to appearance of paruterine organ (Fig. 4B), pass into paruterine cavity in vermiform state (Fig. 8F). Embryonic hooks not observed.

Material examined: From Tachycineta leucorrhoa (Vieillot), white-rumped swallow (PBI BRE-211) (Passeriformes: Hirundinidae): 1 complete worm, 2 fragments of strobila, and 1 scolex prepared for SEM (MZUSP 7313, MZUSP 7314) from Boracéia Biological Station, Salesópolis, São Paulo, Brazil (23°38’S; 45°52’W, elevation 946 m).

Additional material examined:

From Progne purpurea [sic] (most likely Progne subis (Linnaeus), purple martin) (Passeriformes: Hirundinidae): 2 syntypes (MHNG-PLAT 40225) from Brazil (exact locality is unknown); from Progne tapera (Linnaeus), brown-chested martin (Passeriformes: Hirundinidae): 1 syntype (MHNG-PLAT-40266) from Brazil (exact locality is unknown); from Progne chalybea (Gmelin), grey-breasted martin (Passeriformes: Hirundinidae): 3 syntypes (MHNG-PLAT 40227) from Brazil (exact locality is unknown); 4 complete worms and 4 fragments of strobila (MHNG-PLAT 37772) from Jejui, San Pedro, Paraguay (24°06’S; 56°27’W, elevation 96 m); 4 complete worms and 2 fragments of strobila (MHNG-PLAT 39528) from Caicisa, Itapua, Paraguay (26°19’12”S; 55°13’11”W, elevation 324 m); 2 worms with contracted strobila and 1 fragment of strobila (MHNG-PLAT 39529) from Caicisa, Itapua, Paraguay (26°19’12”S; 55°13’11”W, elevation 324 m); 1 complete worm (MHNG-PLAT 39519) from Santa Maria, Itapua, Paraguay (26°53’59”S; 55°49’12”W, elevation 206 m); from Hirundo sp. (Passeriformes: Hirundinidae): 1 syntype (MHNG-PLAT 40229) from Brazil (exact locality is unknown); from Hirondella sp. [sic] (Passeriformes: Hirundinidae): 2 syntypes (MHNG-PLAT-40577) from Brazil (exact locality is unknown); from Tachycineta meyeni (Cabanis), Chilean swallow (PBI-CHI-043): 5 worms (MHNG-PLAT 83087) from Huinay Station, Comau Fjord, Los Lagos Region, Chile (42°22’47”S; 72°24’54”W, elevation 22 m); from Stelgidopteryx ruficollis (Vieillot), southern rough-winged swallow: 3 complete worms and 7 fragments of strobila (MHNG-PLAT 39521), 3 complete worms and 4 fragments of strobila (MHNG-PLAT 39522), and 2 worms with incomplete strobila and 2 fragments of strobila (MHNG-PLAT-39523), all from San Benito (Pastoreo), Itapua, Paraguay (26°48’35”S; 55°43’11”W, elevation 207 m).

Prevalence and intensity of infection: T. leucorrhoa infected of 1 examined, 2 worms; from T. meyeni, 16.7% (1 host infected of 6 examined), 2 worms.

Remarks. The original description of A. macrocephala is brief and included measurements and descriptions of few, yet essential, characters. Fuhrmann (1908) described A. macrocephala as possessing 10–13 testes per proglottis, but examination of the type material showed the syntypes to actually possess 6–10 testes per proglottis (Table 4, Fig. 9). This redescription shifts the range of testes per proglottis from 10–13 to 6–10 and contributes information about additional morphological features with illustrations and scanning electron micrographs (see Figs. 6D–F, 8 for morphology of newly collected specimens and Figs. 9A,B, 10A–C for syntype morphology). Fuhrmann (1908) does not mention the change of paruterine organ shape we observed in pregravid proglottides, although the description included an illustration of a proglottis with a conical paruterine organ projecting anteriorly from the uterus. This illustration resembles the shape of the paruterine organ we observed in post-mature proglottides of newly collected material and the unique shape of the paruterine organ was observed in pregravid proglottides of the type material (Fig. 10C). Anonchotaenia macrocephala is
Table 4. Key measurements of specimens of Anonchotaenia macrocephala from various localities and host species.

<table>
<thead>
<tr>
<th>Catalog number</th>
<th>Host species</th>
<th>Locality</th>
<th>Scolex diameter</th>
<th>Sucker diameter</th>
<th>Testes number</th>
<th>CS extent</th>
<th>CS length MP</th>
<th>CS width MP</th>
<th>CS length PP</th>
<th>CS width PP</th>
</tr>
</thead>
<tbody>
<tr>
<td>MHNG-PLAT 40266</td>
<td>Progne tapera (Linnaeus)</td>
<td>Brazil</td>
<td>710</td>
<td>310–330 (320 ± 9)</td>
<td>n = 4</td>
<td>15–16%</td>
<td>95–108 (102 ± 6)</td>
<td>28–33 (31 ± 3)</td>
<td>90–108 (99 ± 8)</td>
<td>28–30 (29 ± 1)</td>
</tr>
<tr>
<td>MHNG-PLAT 40229</td>
<td>Hirondella sp.</td>
<td>Brazil</td>
<td>660–790 (765)</td>
<td>240–415 (319 ± 83)</td>
<td>n = 4</td>
<td>11–19%</td>
<td>60–93 (79 ± 11)</td>
<td>20–28 (26 ± 3)</td>
<td>78–88 (82 ± 4)</td>
<td>28–30 (29 ± 1)</td>
</tr>
<tr>
<td>MHNG-PLAT 40577</td>
<td>Hirondella sp.</td>
<td>Brazil</td>
<td>700–720 (780)</td>
<td>255–310 (293 ± 18)</td>
<td>n = 8</td>
<td>7–10** (9 ± 1)</td>
<td>13–16%</td>
<td>-</td>
<td>68–73 (70 ± 2)</td>
<td>18–23 (22 ± 3)</td>
</tr>
<tr>
<td>MHNG-PLAT 40227</td>
<td>Progne chalybea (Cabanis)</td>
<td>Paraguay</td>
<td>760–975 (858 ± 73)</td>
<td>290–360 (326 ± 17)</td>
<td>n = 34</td>
<td>5–8*** (7 ± 1)</td>
<td>-</td>
<td>-</td>
<td>72–125 (102 ± 6)</td>
<td>21–30 (27 ± 3)</td>
</tr>
<tr>
<td>MHNG-PLAT 39528</td>
<td>Progne chalybea (Cabanis)</td>
<td>Paraguay</td>
<td>840–1000 (900 ± 47)</td>
<td>305–460 (361 ± 43)</td>
<td>n = 36</td>
<td>5–7* (6 ± 1)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>MHNG-PLAT 39523</td>
<td>Stelgidopteryx ruficollis (Vieillot)</td>
<td>Paraguay</td>
<td>670–900 (748 ± 97)</td>
<td>305–410 (357 ± 32)</td>
<td>n = 12</td>
<td>5–7* (6 ± 1)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

CS – cirrus sac; MP – mature proglottides; PP – pregravid proglottides; * n = 37; ** n = 14; *** n = 54; * n = 10; i n = 3.

characterised by a scolex 650–994 µm in diameter, a cirrus sac 60–178 µm in length in mature proglottides, and a paruterine organ that turns inward and expands towards the uterus rather than protruding from it.

Anonchotaenia macrocephala was originally described from Progne ‘purpurea’, P. tapera, P. chalybea, Hirundo sp., and Hirundella sp. Of the syntypes available at the MHNG, the most intact specimens are from Progne ‘purpurea’ (MHNG-PLAT-40226); this host species name seems to be the latinisation of the common name purple martin (Progne subis). Voucher material from the MHNG, the most intact specimens are from Paraguay and Chile.

Molecular analysis

The combined molecular dataset included a total of 6328 aligned characters (ssrDNA: 2692 characters, lsrDNA: 2119 characters, rrl: 917 characters, cox1: 600 characters).

Pairwise uncorrected p-distances between the cox1 gene fragments were as follows: between specimens of A. prolixa (PBI-147) and those identified as A. brasiliensis (PBI-204+212) averaged 14.3% ± 0.6%; between A. brasiliensis (PBI-204+212) and A. macrocephala (PBI-156+235) averaged 13.5% ± 0.4%; and between A. brasiliensis (PBI-204+212) and A. cf. brasiliensis (PBI-228) averaged 11.7%. The pairwise distances between the rrl gene fragments were as follows: between specimens identified as A. brasiliensis (PBI-204+212) and A. prolixa (PBI-147) averaged 21.6% ± 0.7%.

cephala (PBI-156+235) and A. prolixa (PBI-147) averaged 22.2%; between A. brasiliensis (PBI-204+212) and A. macrocephala (PBI-156+235) averaged 18.9% ± 0.8%; and between A. brasiliensis (PBI-204+212) and A. cf. brasiliensis (PBI-228) averaged 15.6% (Table 5).

The log-likelihood of the topology produced by the ML analysis of the combined dataset was -14462.43. The harmonic means of estimated marginal likelihood values from the two BI runs were -14107.63 and -14113.62. The topologies of the BI and ML analyses were identical, thus the results of the determinations of relative host specificity for each species are provided in Table 6.

The host data for each paruterinid used in the assessment of host specificity was derived from type and voucher specimens. The HS values calculated for each cestode species and the results of the determinations of relative host specificity for each species are provided in Table 6. The four species of paruterinids examined in this study exhibit host specificity index values ranging from HS = 0 (A. prolixa) to HS = 5.876 (A. brasiliensis).
**Table 5. Uncorrected pairwise distances of cox1 and rrl gene fragments**

<table>
<thead>
<tr>
<th>Cestode species</th>
<th>cox1</th>
<th>rrl</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. A. brasiliensis (PBI-204)</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>2. A. brasiliensis (PBI-212)</td>
<td>0.009</td>
<td>0.008</td>
</tr>
<tr>
<td>3. A. cf. brasiliensis (PBI-228)</td>
<td>0.118 0.116</td>
<td>0.160 0.152</td>
</tr>
<tr>
<td>4. A. macrocephala (PBI-156)</td>
<td>0.139 0.138 0.129</td>
<td>0.196 0.185 0.187 0.01</td>
</tr>
<tr>
<td>5. A. macrocephala (PBI-235)</td>
<td>0.133 0.131 0.128 0.011</td>
<td>0.211 0.21 0.226 0.22</td>
</tr>
<tr>
<td>6. A. prolixa sp. n. (PBI-147)</td>
<td>0.148 0.148 0.134 0.141 0.139</td>
<td>0.239 0.239 0.257 0.263 0.264 0.275</td>
</tr>
<tr>
<td>7. Biuterina sp. (PBI-96) outgroup</td>
<td>0.154 0.151 0.158 0.143 0.138 0.136</td>
<td>0.212 0.255 0.278 0.288 0.289 0.193 0.243</td>
</tr>
</tbody>
</table>

**Table 6. Host specificity data for Anonchotaenia spp. from South America.**

<table>
<thead>
<tr>
<th>Cestode species</th>
<th>No. host species</th>
<th>No. host genera</th>
<th>No. host families</th>
<th>No. host orders</th>
<th>No. host classes</th>
<th>Rank</th>
<th>HS Index Value</th>
<th>Host specificity category (Caira et al. 2003)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anonchotaenia prolixa sp. n.</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>oioxenous</td>
</tr>
<tr>
<td>Anonchotaenia vaslata sp. n.</td>
<td>2</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1,001</td>
<td>3.000</td>
<td>metastenoxenous</td>
</tr>
<tr>
<td>Anonchotaenia macrocephala</td>
<td>6</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>2,003</td>
<td>3.302</td>
<td>metastenoxenous</td>
</tr>
<tr>
<td>Anonchotaenia brasiliensis</td>
<td>6</td>
<td>5</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td>75,1497</td>
<td>5.876</td>
<td>euryxenous</td>
</tr>
</tbody>
</table>

**DISCUSSION**

**Morphology**

Morphological distinction amongst *Anonchotaenia* species can be challenging due to the scarcity of morphological characters and their tendency to become easily obscured or distorted in contracted material. In this study, we complement the set of historically useful characters for species delimitation with some previously disregarded additional characters. Paruterine organ shape is easily distorted by contraction in short proglottides and has not been considered reliable for species delimitation within *Anonchotaenia* (Fuhrmann 1908, Joyeux and Baer 1935, Rausch and Morgan 1947), although this character has been informative of species boundaries for other paruterinid genera (Georgiev and Kornyushin 1994).

Contrary to expectation, paruterine organ shape was distinguishable and remarkably consistent within each of the four *Anonchotaenia* spp. examined here (Figs. 3D,E, 4D,E, 5D–F, 7A, 8C,E,F, 10B,C). *Anonchotaenia brasiliensis* and *A. prolixa* had paruterine organs with a similar shape, a conical paruterine organ that maintained this shape in pregravid proglottides. *Anonchotaenia macrocephala* had a paruterine organ that was initially conical but in pregravid proglottides pressed posteriorly towards the anterior uterine wall forming a conical pocket inside the anterior margin of the uterus although not invading it. *Anonchotaenia vaslata* had a paruterine organ that was initially conical but curved dorsally in pregravid proglottides. These differences were present in contracted and relaxed proglottides, suggesting that these differences were not an artefact of proglottis contraction, but rather represent species-level variation.

Among the species of *Anonchotaenia* examined here, landmarks of maturation of proglottides along the length of the strobila were observed and compared. The development of mature proglottides, the appearance of the paruterine organ, and the appearance of vermiform oncospheres occurred at a similar distance or number of proglottides posterior to the scolex with the number of proglottides between landmarks increasing with the length of the worm (Figs. 1, 4). Previous reports have suggested that the proglottides of some *Anonchotaenia* species mature earlier in the strobila than other paruterinid genera (Fuhrmann 1908, Rausch and Morgan 1947, Saxena and Baugh 1978), but few studies have reported variation in proglottis maturation along the length of the strobila among paruterinids. Future examination across the other 21 paruterinid genera will determine the variability of the location of these landmarks in comparison to *Anonchotaenia*.

Scanning electron microscopy is a standard tool used in species descriptions across a wide array of cestode taxa (see Chervy 2009) and until now has not been used to view
This is considerably less variation than has been reported for other cyclophyllidean taxa. It will be interesting to compare microthrix patterns across a broader spectrum of taxa that bear a rostellar. We will focus on members of Paruterinidae. Within Cyclophyllidea, SEM has been used mostly to view scolex microthrix patterns of taxa that bear a rostellar, such as species of Dilepididae, Davaineidae, Hymenolepididae, Taeniidae and Anoplocephalidae (e.g. Mariaux and Vaucher 1990, Casado et al. 1994, Cielecka et al. 1994, Bâte et al. 1995). Our examination of scolec, ex of *Anonchotaenia brasiliensis* and *A. macrocephala* showed a consistent pattern of acicular filitriches across all scolex surfaces of each of the two species (Fig. 6). This is considerably less variation than has been reported for other cyclophyllidean taxa. It will be interesting to compare microthrix patterns across a broader spectrum of paruterinid taxa including both those with and without a rostellar to determine its utility as a taxonomic character among paruterinids.

**Molecular analysis**

This study provides the first published DNA sequence data of paruterinid beyond *ssrDNA* sequences of *Lyuterina nigropunctata* (Spasskaya et Spasskii, 1971) (AJ555173, AJ555174, Foronda et al. 2004) and a single translated *cox1* sequence of *A. globata* (JX310719) by presenting a four-gene phylogenetic analysis of six newly sampled paruterinid species (Fig. 11). Within the clade of *Anonchotaenia* representatives, specimens of *A. macrocephala* form a clade distinct from those identified as *A. brasiliensis* and *A. cf. brasiliensis*. The distinction of these species is further supported by the greater average genetic distance between these morphologically distinct species (on average 13.5% ± 0.4%; Table 5) than the genetic distances between conspecifics (0.9% in *A. brasiliensis* and 0.11% in *A. macrocephala*; Table 5).

Of the specimens identified as *A. brasiliensis*, those found in tanagers (PBI-204 and PBI-212) are each other’s closest relatives showing little genetic divergence (0.8—0.9%; Table 5), whereas *A. cf. brasiliensis* (PBI-228) from an American sparrow represents a distinct lineage to the former (Fig. 11) despite being morphologically indistinguishable. The pairwise distances between *A. brasiliensis* (PBI-204 + PBI-212) and *A. cf. brasiliensis* (PBI-228) are 13 times (*cox1*) and 19 times (*rrnL*) as large as the distance between *A. brasiliensis* conspecifics (Table 5) indicating that *A. cf. brasiliensis* (PBI-228) may represent a distinct species. More specimens of *A. cf. brasiliensis* are necessary to determine if these specimens represent a cryptic species of *Anonchotaenia*.

Our analyses did not contradict the erection of *A. proliza* as a new species. Interspecific genetic distances between previously described *Anonchotaenia* species (*A. brasiliensis* and *A. macrocephala*) were similar to those between these species and *A. proliza* (Table 5). The inclusion of additional sequences of the other 26 *Anonchotaenia* spp. is needed to determine their relationship to *A. proliza*.

**Host associations**

Members of Tyrannidae (tyrant flycatchers) are interesting hosts for *Anonchotaenia* species not only in terms of the diversity of tyrannids, but also because multiple *Anonchotaenia* species can parasitise a single tyrannid species. In this study, we found species of Tyrannidae host a diversity of morphologically distinct forms of *Anonchotaenia* and at least one tyrannid species is host to more than one *Anonchotaenia* species; *T. melancholicus*...
has been reported to host both Anonchotaenia jeandorsti Dollfus, 1959 and A. vaslata. Tyriinidae is the most diverse avian family in the Western Hemisphere and contains approximately 100 genera and 430 species (Rheindt et al. 2008). This study includes cestode specimens from only three species of three tyrannid genera, a minute proportion of the described diversity within the family of which most species have yet to be examined for cestodes. Concentrating efforts on examining the diversity of tyrannids for cestodes and tracking cestode presence and absence among that diversity will contribute towards understanding the breadth of tyrannid species that host Anonchotaenia, but also the frequency by which the host spectrum of different Anonchotaenia species overlaps.

Even though patterns of paruterinid host associations are poorly understood, these associations appear to be closely tied to host diet. Intermediate hosts are unknown for most paruterinid species, but are suspected to be terrestrial insects in most cases. Anonchotaenia brasiliensis has been reported from three unrelated host families (Icteridae, Fringillidae and Thraupidae) whose members consume insects in addition to fruits and seeds, and frequently participate in mixed-species foraging flocks in the South American Atlantic forest (Develey and Peres 2000). These foraging flocks are composed predominately of omnivores and insectivores (Dario and De Vincenzo 2011) and members of these flocks exhibit common behaviours that increase foraging efficiency, such as prey flushing (Sridhar et al. 2009), which may explain the broad spectrum of host associations exhibited by A. brasiliensis.

Anonchotaenia species have been reported from a variety of passerine families (see Table S2) and exhibit a wide spectrum of host specificity (Table 6). Anonchotaenia prolixia was found in a single host species and by definition is oioxenous (HS$_s$ = 0), although this could be an artefact of low sampling. Anonchotaenia vaslata and A. macrocephala both have been reported in multiple genera of a single host family and were metastenoxenous (HS$_g$ = 3.000 and HS$_s$ = 3.302, respectively). Anonchotaenia macrocephala has been found in more genera than A. vaslata and thus had a higher index value. Anonchotaenia brasiliensis was the least host specific species evaluated here. It has been reported from multiple host families and was euryxenous (HS$_s$ = 5.876). Host specificity of cestodes has been most thoroughly evaluated for species that parasitise elasmobranchs, partially because of the strict host specificity exhibited by most elasmobranch cestodes (Caira and Jensen 2001, Caira et al. 2003). Host specificity has not been formally assessed for most cyclophyllideans, which comprise over half of cestode diversity (> 3 500 species). In the present study, the HS$_s$ values of the non-oioxenous species ranged from 3.000–5.876 (Table 6). These taxa exhibit a more relaxed pattern of host specificity than exhibited by the cestode taxa most often evaluated in formal assessments of host specificity (i.e. elasmobranch cestodes). It is possible that additional paruterinid species parasitise multiple avian host species and genera and, in some cases, multiple host families.

**Acknowledgements.** We thank Fernando Marques for his help in organising fieldwork and permits for our work in Brazil and Natalia Da Mata Luchetti (both from Laboratorie Helminologia Evolutiva – Universidade de São Paulo) for her effort in organising our fieldwork and for being a valuable member of our team. We are thankful for the ornithological expertise of Luis Fabio Silveira, Luciano Moreira Lima, Deborah Oliveira, Rafael Sobral Marcondes (all MZUSP), Guilherme Renzo Rocha Brito, Marco Aurélio Crozariol and Daniel Honorato Firme (all Museu Nacional, UFRJ). Fieldwork in Chile was possible with the support of the staff of the Huinay Scientific Field Station (HSFS), especially Günter Föstera and Vreni Häusserman. We thank the staff of the sequencing facility at the Natural History Museum in London for their sequencing expertise. We are thankful to Janine Caira (University of Connecticut) for her thoughtful comments and insights that greatly improved this manuscript, and to Kent Holsinger (University of Connecticut) for his assistance with the analyses of host specificity. Elizabeth Barbeau (University of Connecticut) and Freya Goetz (Smithsonian’s National Museum of Natural History) provided valuable advice and assistance with the figures. This work was funded by the National Science Foundation, PBI grants 0818696 and 0818823. This paper is publication number 87 of the HSFS.

**REFERENCES**


