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Andryoides gen. n. and morphological key features in cestodes of the family Anoplocephalidae *sensu stricto* (Cyclophyllidea) in mammals

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Abstract: As presently defined, the tapeworm genus *Andrya* Railliet, 1895 (Cyclophyllidea: Anoplocephalidae *sensu stricto*) includes the type species *A. rhopalocephala* (Riehm, 1881) in hares of the genus *Lepus* Linnaeus (Leporidae) in western Eurasia and four species in cricetid (Neotominae, Sigmodontinae) and octodontid rodents in North and South America. The host range of *Andrya* is puzzling, because it is the only genus of anoplocephalid (*s. s.*) cestodes parasitising both rodents and lagomorphs. The present morphological analysis shows that the American species of *Andrya* share multiple consistent features, in which they differ from those of *A. rhopalocephala* and the morphologically related *Neandrya cuniculi* (Blanchard, 1891). The main differences concern the position of the uterus with respect to the longitudinal osmoregulatory canals and testes. Consequently, a new genus *Andryoides* gen. n. is proposed for the American species, resulting in the following combinations: *Andryoides neotomae* (Voge, 1946) comb. n. (type species), *Andryoides octodonensis* (Babero et Cattan, 1975) comb. n., *Andryoides vesicula* (Haverkost et Gardner, 2010) comb. n. and *Andryoides boliviensis* (Haverkost et Gardner, 2010) comb. n. However, *A. boliviensis* is regarded here as a junior synonym of *A. vesicula* (new synonymy). The present study also defines the morphological key features for all the valid genera of cestodes of the family Anoplocephalidae (*s. s.*), and discusses the phylogenetic affinities and historical biogeography of *Andryoides* and other endemic American anoplocephalid cestodes.

Keywords: new genus, *Andrya*, *Neandrya*, Cestoda, Rodentia, Cricetidae, Octodontidae

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The tapeworm genus *Andrya* Railliet, 1895 (Cyclophyllidea, Anoplocephalidae *sensu stricto*; hereafter "*s. s.*") was described for *Andrya rhopalocephala* (Riehm, 1881) (type species) in the mountain hare (*Lepus timidus* Linnaeus) and three additional species in hares and rabbits (Lagomorpha, Leporidae). As a nomenclatural note, the previously used authority ("Railliet, 1893") for the genera *Andrya*, *Ctenotaenia* Railliet, 1895 and *Stilesia* Railliet, 1895 is incorrect, because the book in which the descriptions appeared was published in 1895. Stiles (1896) confined *Andrya* to include only *A. rhopalocephala* and *Andrya cuniculi* (Blanchard, 1891), the latter from the European rabbit *Oryctolagus cuniculus* (Linnaeus). However, some of the subsequent authors applied a very wide and inconsistent view of *Andrya*, and ca. 30 species from lagomorphs and rodents were variously included in this genus (see the Global Cestode Database, hereafter "GCD"; Caira et al. 2022). Stiles's (1896) restricted view was later reinstated by F. Tenora and coauthors (Tenora and Murai 1978, Tenora et al. 1984, 1986).

Andrya rhopalocephala is a widespread but rare parasite of hares of the genus *Lepus* Linnaeus (*L. europaeus* Pallas and *L. timidus*) in Europe (e.g., Sugár et al. 1978, Tenora and Murai 1978, Chroust et al. 2012, Kornaś et al. 2014, Marinova 2020), but it has also been reported in *Lepus tibetanus* Waterhouse from Tadzhikistan (Gvozdev 1948) and, probably erroneously, in *O. cuniculus* from Algeria (Joyeux 1927).

The taxonomical history of *Andrya* and two morphologically related genera in rodents, *Paranoplocephala* Lühe, 1910 and *Aprostatandrya* Kirshenblat, 1938, has been complicated (Spasskii 1951, Rausch 1976, Tenora et al. 1985, Haukisalmi and Wickström 2005). Particularly, how to define the genera *Andrya* and *Paranoplocephala* and which species should be assigned to them, has been a major problem (Tenora et al. 1986, Genov et al. 1996).

In his redescription of *Andrya*, Stiles (1896) mentions a presence of a "pedunculated prostatic gland", which was later regarded as the main distinguishing feature of this genus (e.g., Douthitt 1915, Joyeux and Baer 1936, Spasskii 1951). However, Rausch (1976) showed that such a structure does not exist, the "prostatic gland" being actually a sac-like external seminal vesicle covered by a thick layer of (glandular) cells. Rausch (1976) therefore synonymised

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Aprostatandrya (lacking the "prostatic gland") with *Paranoplocephala*.

A wide-scale molecular phylogenetic analysis of anoplocephalid cestodes of rodents and lagomorphs (Wickström et al. 2005), including the type species *A. rhopalocephala* and *Paranoplocephala omphalodes* (Hermann, 1783), showed that *P. omphalodes* and related species in voles and lemmings (Cricetidae, Arvicolinae) comprise a monophyletic group, i.e. *Paranoplocephala* (*s. s.*), within the large "arvicoline clade" of cestodes (hereafter "ACC"). In addition, the status of *Aprostatandrya* as a junior synonym of *Paranoplocephala* was confirmed. *Andrya rhopalocephala*, *A. cuniculi* and *Ctenotaenia marmotae* (Frölich, 1802) from marmots (Sciuridae) grouped together and formed the sister group of the ACC (Wickström et al. 2005, Haukisalmi et al. 2010).

These phylogenetic patterns provided a framework for studying the morphological features that define and distinguish *Andrya*, *Paranoplocephala* and various genera within the ACC (Haukisalmi and Wickström 2005, Haukisalmi et al. 2014). The dorsoventral position and lateral extent of the uterus (tubular or reticular) with respect to the longitudinal osmoregulatory canals (hereafter "LOC") was found to be a synapomorphy for the ACC, in which the early uterus extends ventrally across the LOC's bilaterally, being positioned ventral to testes.

In *A. rhopalocephala*, the early uterus is also ventral to testes, but it is confined within the ventral LOC's. However, in *A. cuniculi* the early uterus is positioned among testes dorsoventrally and extends across the LOC's dorsally. These patterns thus define unambiguously the genus *Andrya* with respect to the ACC, and also with respect to *A. cuniculi*, which was assigned to a new genus (*Neandrya* Haukisalmi et Wickström, 2005) as *Neandrya cuniculi* (Blanchard, 1891). The phylogenetic analyses also show that the structure of the early uterus (tubular vs. reticular) is not a main systematic determinant in the Anoplocephalidae (*s. s.*), which contrasts the earlier classification schemes and non-explicit evolutionary hypotheses for this family (Baer 1927, Spasskii 1951, Tenora 1976, Beveridge 1994).

In addition to the type species *A. rhopalocephala*, the latest redescription of the genus *Andrya* included two species from North and South American rodents, i.e. *Andrya neotomae* Voge, 1946 and *Andrya octodonensis* (Babero et Cattan, 1975), respectively (Haukisalmi and Wickström 2005). This action was based on the fact that in the latter species the uterus is ventral to the testes and mostly confined within the LOC's, although it was noted that the posterior appendices of the uterus overlap or extend across the canals dorsally.

Later, Haverkost and Gardner (2010) described two new species of *Andrya* from South American sigmodontine rodents (*Phyllotis* spp.). In addition, they redescribed *A. octodonensis* in the type host from the type region, and challenged the suggestion of Haukisalmi and Rausch (2006) that *A. octodonensis* is a junior synonym of *A. neotomae*.

The present view of the genus *Andrya* is puzzling, because its members parasitise lagomorphs in western Eurasia and indigenous rodents in the Americas, being thus the only genus of anoplocephalid cestodes occurring in both of these mammalian orders, and evidently having no relatives in the intervening regions or in other groups of rodents. The new materials of Haverkost and Gardner (2010) from Bolivia and Chile allow to evaluate more reliably the various morphological features of the American representatives of *Andrya* and to compare them with those of the type species *A. rhopalocephala* and other related taxa. Based on these comparisons, a new genus is proposed for the former set of species. Because the species composition in *Andrya* is altered, an updated generic diagnosis is provided for this genus. An amended diagnosis is also provided for the morphologically closely related genus *Neandrya*. In addition, this study defines the main morphological features for all valid genera of cestodes of the family Anoplocephalidae (*s. s.*) in mammals, and discusses the phylogenetic affinities and historical biogeography of the new genus and other endemic American anoplocephalid cestodes.

MATERIALS AND METHODS

The present taxonomical analysis of *Andrya* and *Neandrya* is based on information available in previous studies, primarily in those by Genov et al. (1996) and Haukisalmi and Wickström (2005) (*Andrya rhopalocephala*), Tenora et al. (2002) and Haukisalmi and Wickström (2005) (*Neandrya cuniculi*), and Haukisalmi and Rausch (2006) (*Andrya neotomae*, *Andrya octodonensis*). The data for the two new species from South America and additional data for *A. octodonensis* are extracted from Haverkost and Gardner (2010). New illustrations of the mature proglottid and uterus of *A. rhopalocephala* and *N. cuniculi* based on voucher specimens are presented.

The voucher and type specimens on which this study is based are/were deposited in the United States National Parasite Collection (USNM), National Museum of Natural History (USA, Smithsonian Institution; USNM), Harold W. Manter Laboratory of Parasitology (HWML), Finnish Museum of Natural History (FMNH), and Hungarian Natural History Museum (HNHM).

The voucher specimens of *A. rhopalocephala* (KN.34877, 34878) and *N. cuniculi* (KN.34879, 34880) examined and illustrated in the present study have been deposited in the FMNH. For other collection and/or GenBank numbers of *A. rhopalocephala*, *A. neotomae*, *A. octodonensis* and *N. cuniculi*, see Wickström et al. (2005), Haukisalmi and Rausch (2006) and Haukisalmi et al. (2010).

The main morphological features of the valid genera of anoplocephalid (*s. s.*) cestodes of mammals (Table 1) have been compiled from the original descriptions and redescriptions, available in the GCD. The family Anoplocephalidae (*s. l.*) in the GCD has been constructed and is maintained by the present author.

Four characters are used as morphological key features. The emphasis is on the uterine characters (three features), either because they differ between monophyletic groups of cestodes identified in molecular phylogenetic studies of the ACC and related genera (Wickström et al. 2005, Haukisalmi et al. 2010, 2014), and/or because they have been traditionally used in the classification of anoplocephalid cestodes (Beveridge 1994, Haukisalmi 2009). The fourth feature (distribution of testes), in the manner

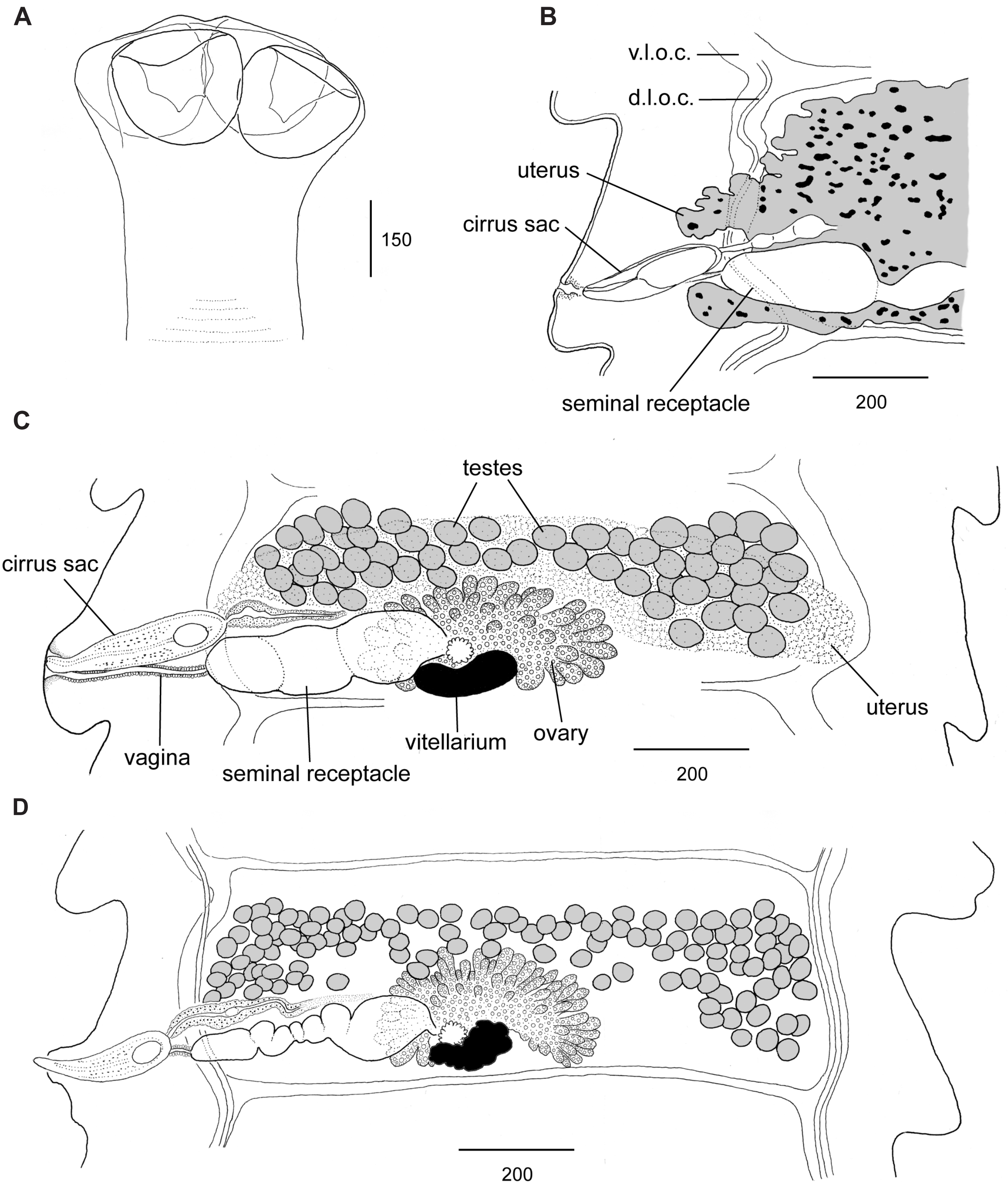

Fig. 1. *Andryoides* spp. **A**–**C** – *Andryoides neotomae* (Voge, 1946) comb. n. from *Neotoma* spp. A – scolex; B – poral region of pregravid proglottid (uterus dorsal to longitudinal canals); C – mature proglottid (early uterus ventral to testes and dorsal to longitudinal canals); D – *Andryoides octodonensis* (Babero et Cattan, 1975) comb. n. from *Octodon degus* (Molina) mature proglottid (type material). **A**–**D** – redrawn from Haukisalmi and Rausch (2006). Proglottids shown in dorsal view. Scale bars in micrometres. *Abbreviations*: v.l.o.c. – ventral longitudinal osmoregulatory canal; d.l.o.c. – dorsal longitudinal osmoregulatory canal

applied here (below), has not been used previously in systematic analyses of anoplocephalid cestodes.

The key features are: (1), the number of the genitalia per proglottid (single/double); (2), the structure of the early uterus (tubular/reticular); (3), the position of the early uterus with respect to the LOC's (strictly in the median field/extending across LOC's ventrally/extending across LOC's dorsally); (4), the distribution of testes (extensive/anterior/posterior). The extensive distribution of testes refers to a condition in which testes are scattered through the median field in the anteroposterior plane, either as a single aggregation of testes or more, rather than forming a group anterior or posterior to the female glands. This concept has the advantage of being applicable to both types of genitalia (single/double). For additional morphological characters used in the genus-level classification of anoplocephalids (*s. s.*), see Beveridge (1994), Haukisalmi (2009) and Haukisalmi et al. (2014).

RESULTS

Andryoides gen. n. Fig. 1

ZooBank number for species:
urn:lsid:zoobank.org:act:2885F483-ABE3-4EA7-A44A-F198079C2683

Type species: *Andryoides neotomae* (Voge, 1946) comb. n. Synonyms: *Andrya neotomae* Voge, 1946; *Aprostatandrya neotomae* (Voge, 1946) Rausch, 1948; *Paranoplocephala neotomae* (Voge, 1946) Tenora, Murai et Vaucher, 1984. Holotype: Originally, USNPC 45889; presently, USNM 1345176. Hosts: *Neotoma fuscipes* Baird (type host) and *N. cinerea* (Ord) (Cricetidae, Neotominae). See Voge (1946) and Haukisalmi and Rausch (2006).

Other species. *Andryoides octodonensis* (Babero et Cattan, 1975) comb. n. (Fig. 1). Synonyms: *Aprostatandrya octodonensis* Babero et Cattan, 1975; *Andrya octodonensis* (Babero et Cattan, 1975) Haukisalmi et Wickström, 2005; *Paranoplocephala octodonensis* (Babero et Cattan, 1975) Tenora, Murai et Vaucher, 1984. Holotype and paratype: Originally, USNPC 73439; presently, USNM 1369006. Type host: *Octodon degus* (Molina) (Octodontidae). See Babero and Cattan (1975), Haukisalmi and Rausch (2006), Haverkost and Gardner (2010).

Andryoides vesicula (Haverkost et Gardner, 2010) comb. n. Synonyms: *Andrya vesicula* Haverkost et Gardner, 2010; *Andrya boliviensis* Haverkost et Gardner, 2010 (new synonymy). The senior status of *A. vesicula* is determined by page precedence. Holotype and paratypes of *A. vesicula*: HWML 62731 (holotype HWML 62731 B). Holotype of *A. boliviensis*: HWML 62273. Hosts: *Phyllotis xanthopygus* (Waterhouse) (type host), *P. osilae* Allen (Cricetidae, Sigmodontinae). See Haverkost and Gardner (2010).

Etymology. *Andryoides* is derived from *Andrya*, which refers to the Frenchman Nicolas Andry (1658–1742), a physician and writer, who played a significant role in the early history of parasitology (Andry 1700 and later editions, Dupouy-Camet 2019).

Diagnosis. Strobila of medium size. Suckers slightly protruding and directed anteriorly (type species) or embedded within scolex and directed anterolaterally (other species). Neck short and relatively wide (ca. 60% of scolex width). Proglottids craspedote, significantly wider than long. Genitalia single. Genital atrium capable of forming genital papilla. Genital pores opening in posterior third of proglottid margin; pores irregularly alternating in very short series (on average two proglottids in each unilateral set). Two pairs of longitudinal osmoregulatory canals present, narrower dorsal canal overlapping ventral one. Genital ducts pass osmoregulatory canals dorsally.

Cirrus sac slender, with distinct muscle layers; ductus cirri armed densely with minute spines. Distinct internal seminal vesicle present; external seminal vesicle either inconspicuous, elongate and slightly convoluted or very large and sacculate; covered by loose, continuous layer of (glandular) cells. Testes confined between longitudinal ventral canals, forming two anteriorly connected groups poral and antiporal to ovary.

Vagina thin, of uniform width, as long as cirrus sac or slightly shorter; runs and opens ventral or posteroventral to cirrus sac and male pore. Seminal receptacle long; massive and sacculate when fully developed. Female glands median or slightly poral. Ovary flabelliform, deeply lobulate. Vitellarium arched, asymmetrically bilobed, positioned in middle of ovary in transverse plane.

Early uterus finely reticulate, ventral to testes, distributed mainly in spaces occupied by testes, significantly overlapping or extending slightly across ventral longitudinal osmoregulatory canals dorsally; posterolateral fringes of pregravid and gravid uterus extend significantly across longitudinal canals, either posterior or posterior and anterior to terminal genital ducts. Pregravid uterus saccate with irregular diverticula and complex internal structure. Fully gravid uterus sparsely lobed. Eggs with pyriform apparatus. In cricetid (Sigmodontinae, Neotominae) and octodontid rodents in South and North America.

Andrya Railliet, 1895 Fig. 2

Type and only species: *Andrya rhopalocephala* (Riehm, 1881) Railliet, 1895. Synonyms: *Taenia rhopalocephala* Riehm, 1881; *Anoplocephala rhopalocephala* (Riehm, 1881) Blanchard, 1891.

Diagnosis. Strobila long. Suckers directed anterolaterally, embedded within scolex. Proglottids craspedote, significantly wider than long. Genitalia single. Genital pores positioned in posterior half of proglottid margin; unilateral or irregularly alternating in large series. Genital atrium prominent, but evidently not capable of forming genital papilla. Two pairs of longitudinal osmoregulatory canals present, narrower dorsal canal running lateral to ventral canal. Genital ducts pass osmoregulatory canals dorsally. Cirrus sac large, with distinct muscle layers, pyriform when fully withdrawn. Ductus cirri armed with minute spines. Distinct internal and external seminal vesicles present; latter usually saccate or pedunculated, covered by dense layer of intensively staining (glandular) cells. Testes mainly antiporal, with small number anterior to ovary; testes confined by ventral longitudinal canals.

Vagina short and thick, with wide lumen; runs and opens posterior or postero-ventral to cirrus sac and male pore. Seminal receptacle sacculate when fully developed. Female glands poral. Ovary flabelliform, deeply lobulate. Vitellarium arched, asymmetrically bilobed, positioned slightly porally with respect to midline of ovary.

Early uterus finely reticulate, relatively narrow transverse band ventral to testes, confined by ventral longitudinal canals. Pregravid uterus saccate with irregular diverticula and complex internal structure; individual lateral diverticula of expanding uterus occasionally overlap slightly ventral longitudinal canal, usually anterior to genital ducts. Eggs with pyriform apparatus. In *Lepus* spp. (Leporidae, Lagomorpha) in western Eurasia.

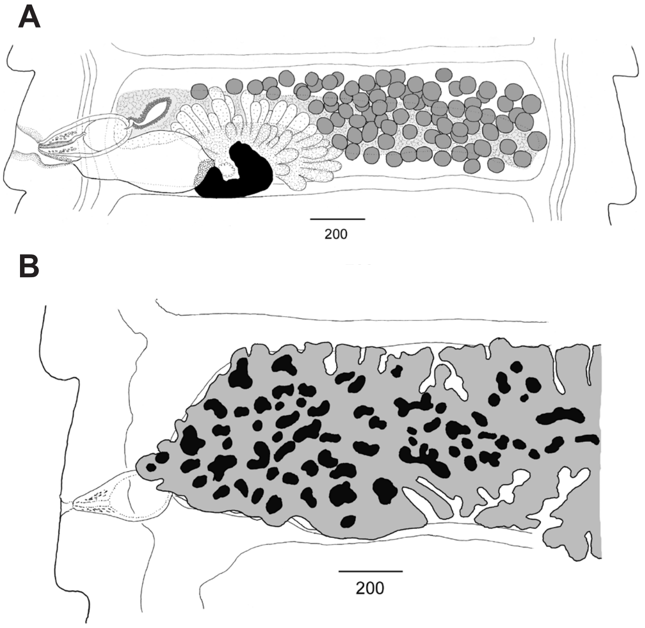

Fig. 2. *Andrya rhopalocephala* (Riehm, 1881) from *Lepus europaeus* Pallas. **A** – mature proglottid (early uterus ventral to testes, dorsoventral position with respect to ovary undefined); redrawn from Genov et al. (1996); **B** – poral region of pregravid proglottid; original (KN.34878). Proglottids shown in dorsal view. Scale bars in micrometres.

***Neandrya* Haukisalmi et Wickström, 2005** Fig. 3

Type and only species: *N. cuniculi* (Blanchard, 1891) Haukisalmi et Wickström, 2005. Synonyms: *Taenia rhopaliocephala* Riehm, 1881; *Anoplocephala cuniculi* Blanchard, 1891; *Andrya cuniculi* (Blanchard, 1891) Railliet, 1895.

Diagnosis. Strobila of medium length. Suckers directed anterolaterally, embedded within scolex or slightly protruding. Proglottids craspedote, wider than long. Genitalia single. Genital atrium capable of forming genital papilla. Genital pores opening in posterior half of proglottid margin; pores irregularly alternating in large series. Two pairs of longitudinal osmoregulatory canals present; ventral canal wide, narrower dorsal canal running lateral to ventral one. Genital ducts pass osmoregulatory canals dorsally.

Cirrus sac with prominent muscle layers, pyriform when fully withdrawn; ductus cirri armed with minute spines. Distinct internal and external seminal vesicles present; latter usually saccate or pedunculated, covered by dense layer of intensively stained (glandular) cells. Testes occupying spaces antiporal and anterior to ovary and terminal genital ducts, confined between longitudinal ventral canals.

Vagina short and relatively thin, of uniform width; runs and opens posterior or postero-ventral to cirrus sac and male pore. Seminal receptacle long; massive and sacculate when fully developed. Female glands slightly poral. Ovary flabelliform, deeply lobulate. Vitellarium arched, asymmetrically bilobed, positioned in middle of ovary in transverse plane.

Early uterus finely reticulate, extensive, occupying spaces anterior and lateral to ovary and genital ducts and extending dorsally across longitudinal osmoregulatory canals; positioned among and dorsal to testes and dorsal to ovary. Pregravid uterus saccate with irregular diverticula and complex internal structure; extends significantly across longitudinal canals, but does not occupy spaces posterior to terminal genital ducts. Eggs with pyriform apparatus. In leporids (Lagomorpha) in Europe.

Remarks. In addition to *Andryoides*, there is just one genus (*Neandrya*) characterised by a single set of genitalia per proglottid and a reticular early uterus that crosses LOC's dorsally (Table 1). However, because *Andryoides* spp. were previously assigned to the genus *Andrya*, the morphological features separating these two genera are also described.

Andryoides* vs. *Andrya Table 2

The main morphological features differentiating *Andryoides* from *Andrya* concern the position and extent of the uterus. The uterus of *Andryoides* has distinct posterolateral fringes significantly overlapping or extending across the ventral LOC's dorsally; this feature is constant and present in all *Andryoides* species. In *Andrya*, the early uterus is confined in the median field, not overlapping the ventral LOC's. Additional consistent differences concern the body size, frequency of the alternation of genital pores, position of the dorsal LOC's, distribution of testes, shape of the cirrus sac, structure of the external seminal vesicle and length of the vagina with respect to the cirrus sac.

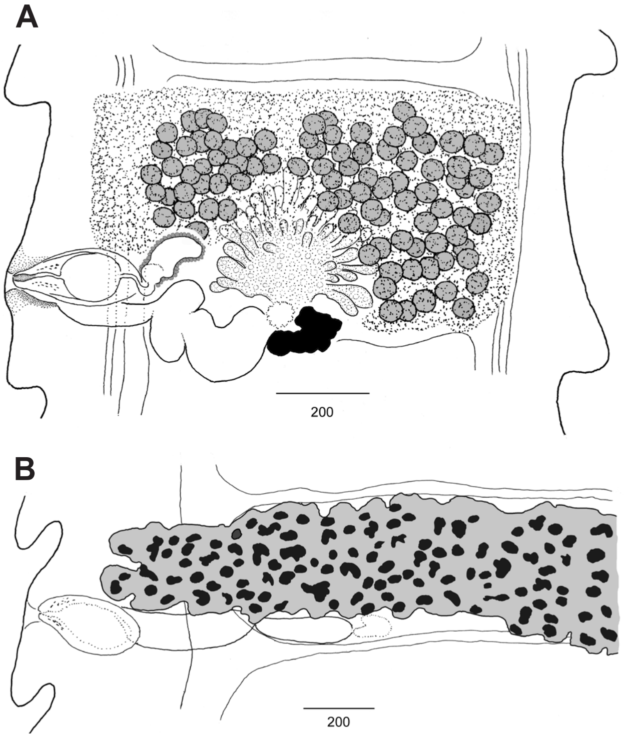

Fig. 3. *Neandrya cuniculi* (Blanchard, 1891) from *Oryctolagus cuniculus* (Linnaeus). **A** – mature proglottid (early uterus among and dorsal to testes, and dorsal to ovary and longitudinal canals); original (KN.34879). **B** – poral region of pregravid proglottid (uterus dorsal to longitudinal canals); original (KN.34880). Proglottids shown in dorsal view. Scale bars in micrometres.

Table 1. Morphological key features for the valid genera of cestodes of the family Anoplocephalidae (*sensu stricto*) in mammals, with background information. See the Global Cestode Database (Caira et al. 2022) for descriptions and redescriptions and other taxonomical information. Character states corresponding to those of *Andryoides* gen. n. are shown in bold. See the Materials and methods for the extensive distribution of testes.

Genus	Host order	Distribution	Genitalia single/double	Structure of early uterus	Transverse and dorsoventral position of uterus	Distribution of testes
***Andryoides* gen. n.**	**Rodentia**	**South and North America**	**single**	**reticular**	**across canals dorsally**	**extensive**
"Arvicoline clade" (18 genera; see Haukisalmi et al. 2014)	Rodentia	Holarctic	**single** or double	**reticular** or tubular	across canals ventrally	**extensive**
Afrobaeria Haukisalmi, 2008	Rodentia	Africa	**single**	tubular	median field	**extensive**
Afrojoyeuxia Haukisalmi, 2013	Rodentia	Africa	single	**reticular**	across canals ventrally	**extensive**
Andrya Railliet, 1895	Lagomorpha	Eurasia	**single**	**reticular**	median field	**extensive**
Anoplocephala Blanchard, 1848	Hyracoidea, Perissodactyla, Primates, Proboscidea	Cosmopolitan	**single**	tubular	median field	**extensive**
Bertiella Stiles et Hassall, 1902	Diprotodontia, Rodentia, Primates, Dermoptera	Australasia, Southeast Asia, Japan, Africa, South America	**single**	tubular	**across canals dorsally**	anterior
Cittotaenia Riehm, 1881	Lagomorpha	Europe	double	tubular (slightly reticular)	median field	**extensive**
Crossotaenia Mahon, 1954	Artiodactyla	Africa	**single**	spherical	median field	posterior
Ctenotaenia Railliet, 1893	Rodentia	Eurasia	double	tubular	median field	**extensive**
Diuterinotaenia Gvozdev, 1961	Lagomorpha	Eurasia	double	tubular (longitudinal)	median field	posterior
Ectopocephalium Rausch et Ohbayashi, 1974	Lagomorpha	Eurasia	**single**	tubular	median field	posterior
Equinia Haukisalmi, 2009	Perissodactyla	Cosmopolitan	**single**	tubular	median field	**extensive**
Flabelloskrjabinia Spasskii, 1951	Perissodactyla	East Asia	**single**	tubular	median field	**extensive**
Genovia Haukisalmi, 2009	Lagomorpha	Central America, Spain	**single**	tubular	mainly median field	**extensive**
Hokkaidocephala Tenora, Gulyaev et Kamiya, 1999	Rodentia	Japan	**single**	tubular	mainly median field	**extensive**
Hunkeleriella Haukisalmi, 2013	Rodentia	Africa	**single**	**reticular**	across canals ventrally	**extensive**
Leporidotaenia Genov, Murai, Georgiev et Harris, 1990	Lagomorpha	Mexico	**single**	tubular	median field	**extensive**
Marmotocephala Gvozdev, Zhigileva et Gulyaev, 2004	Rodentia	Holarctic	**single**	tubular	median field	**extensive**
Moniezia Blanchard, 1891	Artiodactyla	Cosmopolitan	double	**reticular**	**across canals dorsally**	**extensive**
Monoecocestus Beddard, 1914	Rodentia, Artiodactyla, Rheiformes (Aves)	South, Central and North America, Cuba	**single**	**reticular**	median field	posterior
Mosgovoyia Spasskii, 1951	Lagomorpha	Eurasia, North America, Africa	double	tubular	median field	posterior
Neandrya Haukisalmi et Wickström, 2005	Lagomorpha	Europe	**single**	**reticular**	**across canals dorsall**y	**extensive**
Neoctenotaenia Tenora, 1976	Lagomorpha	Europe, Africa	double	tubular	**across canals dorsally**	posterior
Parasciurotaenia Haukisalmi, 2009	Rodentia	Central Asia	**single**	tubular	median field	**extensive**
Phascolocestus Beveridge, 2014	Diprotodontia	Australia	double	tubular	median field	**extensive**
Phascolotaenia Beveridge, 1976	Diprotodontia	Australia	double	tubular	median field	**extensive**
Progamotaenia Nybelin, 1917	Diprotodontia	Australasia, Indonesia	double	tubular	median field	anterior
Pseudocittotaenia Tenora, 1976	Rodentia	North America	double	tubular	across canals ventrally	**extensive**
Schizorchis Hansen, 1948	Lagomorpha	Holarctic	**single**	tubular	median field	posterior
Triplotaenia Boas, 1902[1]	Diprotodontia	Australia	-	saccate	-	-
Viscachataenia Denegri, Dophic, Elissondo et Beveridge, 2003	Rodentia	South America	double	reticular	median field	median
Wallabicestus Schmidt, 1975	Diprotodontia	Australasia	double	tubular	median field	**extensive**

[1] *Triplotaenia* is morphologically very divergent.

Andryoides vs. *Neandrya* and other related genera

Tables 1, 2

In *Neandrya*, the lateral margins of the reticulated early uterus are extensive in anteroposterior plane and extend significantly across the LOC's dorsally, thus differing from the early uterus of *Andryoides* described above (see also Tenora et al. 2002 for the morphology of *N. cuniculi*). In addition, the pregravid uterus of *Neandrya* does not extend posterior to the terminal genital ducts, as it does in *Andryoides*. The dorsoventral position is also different: the early uterus of the new genus is positioned ventral to testes (the general pattern in anoplocephalids with a reticulated early uterus, including *Andrya*), whereas the early uterus of *Neandrya* runs among and dorsal to testes (Haukisalmi and Wickström 2005). Notice that the original diagnosis of *Neandrya* (Haukisalmi and Wickström 2005) erroneously states that the uterus is "medullary", although it was shown in the text and illustrations that the uterus extends dorsally across the LOCS's.

The alternation of genital pores has not been quantified for *Neandrya*, but it is significantly less frequent than in

Table 2. Morphological features separating the genera *Andryoides* gen. n., *Andrya* Railliet, 1895 and *Neandrya* Haukisalmi et Wickström, 2005.

Genus	***Andryoides* gen. n.**	***Andrya***	***Neandrya***
Strobila, size	intermediate	long	intermediate
Genital pores, alternation	irregularly alternating in short series	unilateral or rarely irregularly alternating in large series	irregularly alternating in large series
Dorsal osmoregulatory canals, position	overlapping ventral canals	lateral to ventral canals	lateral to ventral canals
Testes, distribution	two anteriorly connected lateral groups	mainly antiporal to female glands	antiporal, anterior and poral to females glands
Cirrus sac, shape	slender	pyriform	pyriform
External seminal vesicle, shape	slender	saccate/pedunculated	saccate/pedunculated
External seminal vesicle, covering	loose, poorly stained	dense and thick, intensely stained	dense and thick, intensely stained
Female glands, position	median or slightly poral	poral	median or slightly poral
Vagina, length and width	long, thin	short, thick	short, thin
Early uterus, position with respect to ventral canals	extending across dorsally (posterior fringes)	not overlapping	extending across dorsally
Early uterus, dorsoventral position	ventral to testes	ventral to testes	among and dorsal to testes
Pregravid uterus, anteroposterior position with respect to terminal genital ducts	posterior or anterior and posterior to ducts	overlapping and/or anterior to ducts	anterior to ducts

Andryoides (see Tenora et al. 2002). In addition, the dorsal LOC's overlap the ventral LOC's in *Andryoides*, but run lateral to them in *Neandrya*, the cirrus sac is long and slender in *Andryoides* and pyriform in *Neandrya*, and the vagina is long (with respect to the cirrus sac) in *Andryoides* and short in *Neandrya*. The structure of the external seminal vesicle is also different in these genera.

In addition to *Neandrya* and *Andryoides*, there are three genera with a uterus that extends dorsally across the LOC's (Table 1). Of these, *Moniezia* Blanchard, 1891 has double genitalia (and a reticular early uterus), and *Bertiella* Stiles et Hassall, 1902 and *Neoctenotaenia* Tenora, 1976 have a tubular early uterus (and single and double genitalia, respectively), which separates them from *Andryoides*.

Synonymies

Andrya octodonensis was regarded as a junior synonym of *A. neotomae* by Haukisalmi and Rausch (2006), because no major morphological differences were detected. Haverkost and Gardner (2010) collected new material of *A. octodonensis* from the type host *Octodon degus*, and based on additional, relatively minor morphometric differences suggested that it is a valid species, separate from *A. neotomae* and the two new South American species from sigmodontines. Because the species in the genus *Andryoides* seem to be morphologically uniform, the action of Haverkost and Gardner (2010) is accepted here.

According to Haverkost and Gardner (2010), *A. vesicula* can be separated from the other *Andrya* species by its very large, sacculated external seminal vesicle. However, the same authors described another species of *Andrya* (*A. boliviensis*), with a somewhat smaller vesicle, in the same host genus (*Phyllotis* Waterhouse) from the same locality. Because the description of *A. boliviensis* is based on a single specimen and because the main feature proposed to separate the two species from *Phyllotis* spp. (the size of the external seminal vesicle) is highly variable in *A. vesicula*, it cannot be excluded that the apparent interspecific difference simply reflects intraspecific variation. Therefore, *A. boliviensis* is regarded here as a junior synonym of *A. vesicula* (new synonymy).

DISCUSSION

In the present analysis, three species in the genus *Andryoides* (*A. neotomae, A. octodonensis, A. vesicula*) are considered valid. However, the morphological differences between *Andryoides* spp. are very limited, and the true number of species in this genus may probably be determined only by applying molecular phylogenetic methods.

Host and geographical distribution

The three acknowledged species are each primarily parasites of a single genus of hosts, i.e., *Neotoma* Say et Ord, *Phyllotis* and *Octodon* Bennett, respectively. However, *A. octodonensis* was reported by Landaeta-Aqueveque et al. (2018) in *Phyllotis darwini* (Waterhouse) from Chile and by Haverkost and Gardner (2010) in *P. xanthopygus* from Argentina, but no descriptions were provided. The host range of *Andryoides* is somewhat puzzling, being represented by two genera of myomorph rodents belonging to different subfamilies (Neotominae and Sigmodontidae, Cricetidae) and a genus of hystricomorph rodents (Octodontidae).

The genus *Andryoides* has a wide, but probably a disjunct geographical distribution, spanning from Alberta (Canada) in the North (*A. neotomae*) to Central Chile in the South (*A. octodonensis*) (see Lubinsky 1957, Babero and Cattan 1975). *Andryoides neotomae* has also been reported from California, Idaho and Oregon in the USA (Voge 1946, Miller and Schmidt 1982, Haukisalmi and Rausch 2006). Based on an extensive (but not an exhaustive) literature search on helminths of sigmodontines and octodontids in South America, no reports of *Andrya*-like species other than those presented here were found. Thus, *Andryoides* spp. seem to absent in the southern and south eastern parts of North America, Central America and northern and eastern parts of South America, including Brazil, where the helminths of indigenous rodents have been studied rather extensively. However, this could naturally be partly due to the sporadic nature of helminthological surveys of rodents,

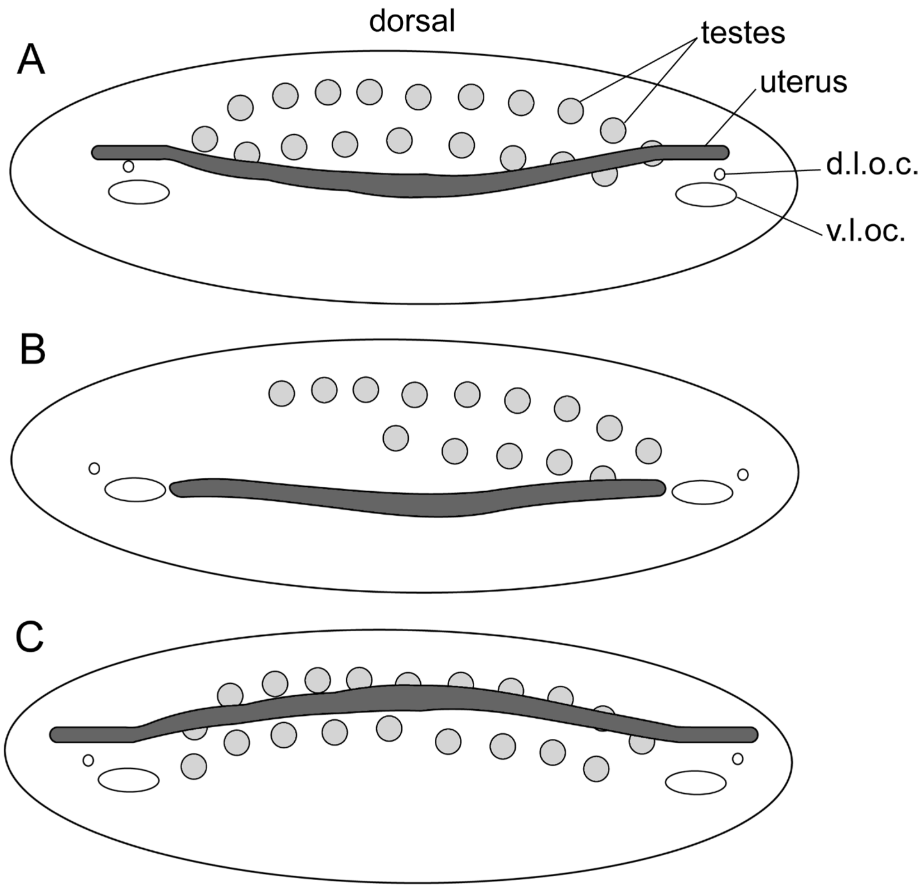

Fig. 4. Diagrammatic transverse views of mature proglottids showing the position of the early uterus with respect to testes and longitudinal osmoregulatory canals in *Andryoides* spp. (A), *Andrya rhopalocephala* (Riehm, 1881); (B) and *Neandrya cuniculi* (Blanchard, 1891) (C). Other relationships are arbitrary. *Abbreviations*: v.l.o.c. – ventral longitudinal osmoregulatory canal; d.l.o.c. – dorsal longitudinal osmoregulatory canal.

particularly the highly diverse sigmodontines of South America. *Andrya*-like cestodes are not known to occur in North American sigmodontines (*Sigmodon* Say et Ord, *Oryzomys* Baird).

Phylogenetic affinities

Because of their pronounced morphological uniformity, *Andryoides* spp. as a group are almost certainly monophyletic. *Andryoides* is probably not phylogenetically associated with the ACC, because it lacks their unambiguous synapomorphy (uterus extending ventrally across the LOC's). The ACC is also the only lineage of anoplocephalid (*s. s.*) cestodes in which testes overlap or extend across ventral canals unilaterally or bilaterally (with a few species with testes strictly in the median field; see the GCD).

The ''*Andrya*-clade'', the sister group of the ACC, consists of three species with variable morphology with respect to the number of genitalia and structure and position of the uterus. These species have either a single (*A. rhopalocephala, N. cuniculi*) or double genitalia (*Ctenotaenia marmotae*), a reticulate (*A. rhopalocephala, N. cuniculi*) or tubular early uterus (*C. marmotae*) and a uterus that is either confined in the median field (*A. rhopalocephala, C. marmotae*) or extends dorsally across longitudinal canals (*N. cuniculi*). The morphology of the species in the *Andrya*-clade does not seem to provide any obvious synapomorphies, and the possible phylogenetic affinity of *Andryoides* with this clade and also with other non-ACC lineages remains obscure.

Historical biogeography

The fossil record suggests that the highly diverse rodent family Cricetidae (Myomorpha) originates in Eurasia (Emry 2007). The Cricetidae was initially split in two major lineages approximately 15 mya (Middle Miocene): (i) the Palearctic subfamily Cricetinae plus the Holarctic Arvicolinae, and (ii) the Nearctic/Neotropical subfamilies Sigmodontinae + Tylomyinae and Neotominae (Steppan and Schenk 2017). Sigmodontines invaded South America from the North probably prior to the main event of the Great American Biotic Interchange in Late Miocene, resulting in immense radiation in the former region (Leite et al. 2014). The genus *Phyllotis* represents a derived lineage within the South American sigmodontines (Leite et al. 2014). The neotomines have remained a largely North American lineage; only two species are known to occur in the northernmost part of South America (Voss 2014).

Compared with sigmodontines and neotomines, *Octodon degus* and other octodontids (Hystricomorpha) have a different origin and much longer history in South America; the ancestral hystricomorph rodents probably arrived there via a trans-Atlantic dispersal event 40–50 Ma (Middle Eocene) (Rowe et al. 2010).

Because of its geographical and host distribution, it is most parsimonius to assume that *Andryoides* appeared in America, rather than being present in the early cricetids in Eurasia. A North American origin for *Andryoides* is more probable than a South American one, because the recolonisation of North America by sigmodontines from the South (*Oryzomys*-lineage) has been limited. *Oryzomys* spp. are presently restricted to the southern North America and are not known to harbour anoplocephalid cestodes (Kinsella 1988 and references therein).

Whether *Andryoides* appeared early in the (precursor of the) American cricetid clade or later in sigmodontines or neotomines with a subsequent parasite shift between these lineages remains speculative. However, *Andryoides* probably colonised South America in sigmodontines, which suggests that it may have been part of the Great American Biotic Interchange. The fact that *Phyllotis* spp. are evidently the only hosts of *Andryoides* among the highly diverse South American sigmodontines suggests that these cestodes were once more widespread or that they still exist in some of the (basal) sigmodontine lineages in South America. The presence of *A. octodonensis* in unrelated octodontid rodents is most plausibly explained by a host shift from sigmodontines to octodontids in South America. *Octodon* and *Phyllotis* still coexist in Chile.

The origin and later biogeographical history of *Andryoides* and *Monoecocestus* Beddard, 1914 *sensu* Beveridge (1994) may have been parallel, because both are American endemics, occur on both continents and parasitise partly the same groups of rodents (particularly sigmodontines and hystricomorphs). *Monoecocestus* is among the most basal lineages within the Anoplocephalidae (*s. s.*), and in some analyses appears as the sister lineage of other anoplocephalids (Wickström 2004, Wickström et al. 2005 and V. Haukisalmi et al. – unpubl. data). This suggests that the endemic anoplocephalids of indigenous American rodents have a long evolutionary history and may represent a divergence event off the earliest anoplocephalid stock (excluding the poorly known species from birds). The phylogenetic relationships and historical biogeography of species in the genus *Monoecocestus* have not been studied. To examine how and when *Andryoides* and *Monoecocestus* originated and expanded, it would be crucial to obtain DNA sequence data for both lineages in South and North America, and analyse them in the context of wide-scale phylogeny of the Anoplocephalidae (*s. s.*).

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