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Review Article

Review of *Anoplocephaloides* species from African rodents, with the proposal of *Afrobaeria* n. g. (Cestoda: Anoplocephalidae)

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Summary

The anoplocephalid cestodes from African rodents previously assigned to *Anoplocephaloides* Baer, 1924 *sensu* Rausch (1976) represent a new genus. *Afrobaeria* n. g. differs from related genera in the morphology of the anterior strobila and scolex (neck absent), distribution of testes (dorsal), structure and position of the early uterus (tubular with lateral protuberances, positioned in the middle of the medulla, antero-posteriorly and dorso-ventrally) and alternation of the genital pores (irregularly and very frequently alternating). Two species of *Afrobaeria* are recognized, i.e. *Af. acanthocirrosa* (Baer, 1924) n. comb. (type species) and *Af. isomydis* (Setti, 1892) n. comb. It is shown that they can be differentiated from one another primarily by the structure of the cirrus sac and seminal receptacle. *Afrobaeria acanthocirrosa* parasitizes rodents of the genus *Otomys* (type host *O. irroratus*), and *Af. isomydis* has been found from *Arvicanthis abyssinicus* (type host), *Oenomys hypoxanthus* and, possibly, from *Otomys* spp. The systematic characters used for the classification of *Anoplocephaloides sensu* Rausch (1976) are discussed, and a redescription of *Af. acanthocirrosa* is provided.

Key words: *Afrobaeria* n. g.; *Anoplocephaloides*; Anoplocephalidae; Cestoda; rodents; Africa

Introduction

The genus *Anoplocephaloides* Baer, 1923 was erected for *Anoplocephala infrequens* Douthitt, 1915 and other related species with a single set of genitalia, unilateral genital pores, a tubular early uterus and antiporal testes (Baer, 1923). However, Baer (1927) synonymized *Anoplocephaloides* with *Paranoplocephala* Lühe, 1910. *Anoplocephaloides* was redefined and resurrected by Rausch (1976), who included in the genus a large and fairly heterogeneous assemblage of species from rodents, lagomorphs and perissodactyls. Rausch's view of the genus *Anoplocephaloides* was upheld in Beveridge's (1994) key to the Anoplocephalinae. However, as noted by Rausch (1976), the genus includes multiple morphologic types, each of which may warrant generic status (see also Genov & Georgiev, 1988 and Beveridge, 1994).

The splitting of *Anoplocephaloides sensu* Rausch (1976) was initiated by Genov *et al.* (1990), who proposed the genus *Leporidotaenia* Genov, Murai, Georgiev & Harris, 1990 for the small-sized cestodes from leporids (Lagomorpha). Later, Gulyaev (1996) erected *Paranoplocephaloides* Gulyaev, 1996 for two species from arvicoline rodents. Recently, *Anoplocephaloides variabilis* (Douthitt, 1915) and related forms from arvicoline rodents were assigned to a new genus, *Microcephaloides* Haukisalmi, Hardman, Hardman, Rausch & Henttonen, 2008, based on morphological and molecular evidence (Haukisalmi *et al.*, 2008). The *Anoplocephaloides*-like species from tapirs have also been assigned to a separate genus (i.e. *Flabelloskrjabinia* Spasskii, 1951) (see Spasskii, 1951; Rausch, 1976; Haukisalmi, 2005). In addition, molecular phylogenetics suggest that *Anoplocephaloides mamillana* (Mehlis, 1831), a cosmopolitan parasite of the horse, represents an ancestral clade separate from *Anoplocephaloides sensu stricto* and *Microcephaloides* (see Wickström *et al.*, 2005).

According to Rausch (1976), two to four species of *Anoplocephaloides* parasitize African murid rodents (Table 1). Various species and subspecies of African *Anoplocephaloides* have been suggested to represent two main taxa, i.e. those with and without an external seminal vesicle (Rausch, 1976). This organ has been described in *Anoplocephaloides isomydis* (Setti, 1892), but appears to be absent in *Anoplocephaloides acanthocirrosa* (Baer, 1924) and *Anoplocephaloides otomyos* (Collins, 1972). There may also be differences in the length of the cirrus sac and number of testes, but otherwise these taxa have not been adequately differentiated.

The present study attempts to define the morphological

differences and similarities among *Anoplocephaloides* spp. from African rodents, and their relationships with other *Anoplocephaloides* species *sensu* Rausch (1976).

Material and methods

The specimens examined, including the type material of *Anoplocephaloides acanthocirrosa* and *An. isomydis*, are listed in Table 1. The examined specimens originate from the Muséum d'histoire naturelle de la Ville de Genève (MHNG) and the United States National Parasite Collection (USNPC), Beltsville, Maryland. The material of *An. acanthocirrosa* includes three previously unstudied specimens from the type host (*Otomys irroratus*) from Kenya.

Table 1. Records of *Paranoplocephala* and *Anoplocephaloides* species of African rodents, and the cestode specimens examined in the present study.

Cestode species (original identifications)	Host species (original, synonymous names in parentheses)	Region	Source	Specimens examined
Paranoplocephala acanthocirrosa	*Otomys irroratus*	South Africa	Baer, 1924; Baer, 1926	MHNG* 41784, 41785 (syntypes)
P. acanthocirrosa	*Otomys irroratus*	Rhodesia	Baer, 1933	
P. acanthocirrosa kivuensis	*Otomys denti* (=*O. kempi*)	Congo	Baer, 1959	
Paranoplocephala omphalodes	*Otomys irroratus*, *O. unisulcatus*	South Africa	Collins, 1972	
Paranoplocephala otomyos	*Otomys irroratus*	South Africa	Collins, 1972	
Anoplocephaloides acanthocirrosa	*Otomys irroratus*	Kenya	Present study	USNPC# 54522, 54525, 54526
Paranoplocephala isomydis	*Arvicanthis abyssinicus* (=*Isomys a.*)	Eritrea	Setti, 1892; Baer, 1949	MHNG 41790 (holotype), 49187
P. isomydis	*Oenomys hypoxanthus*	Congo	Mahon, 1954	MHNG 41791
Anoplocephaloides isomydis	*Otomys tropicalis*	Kenya	Rausch, 1976	

* Muséum d'histoire naturelle de la Ville de Genève. # United States National Parasite Collection, Beltsville, Maryland.

Results

Afrobaeria n. g.

Diagnosis

Anoplocephalidae. Scolex not distinct from anterior strobila (neck absent). Suckers small, embedded within scolex, directed laterally or antero-laterally. Proglottides craspedote, much wider than long. Genitalia single. Genital pores irregularly and frequently alternating. Genital ducts cross osmoregulatory canals dorsally. External seminal vesicles present. Internal seminal vesicle small or absent. Testes dorsal, arranged antiporally, in single transverse group antiporal to female genitalia. Ovary and vitellarium poral. Vagina longer than cirrus sac. Early uterus transverse, tubiform with distinct lateral protuberances, positioned in middle of medulla antero-posteriorly and dorso-ventrally, does not overlap longitudinal osmoregulatory canals. Pregravid uterus with distinct anterior and posterior sacculations, may overlap longitudinal osmoregulatory canals dorsally; sacculations lost in fully gravid uterus. Pyriform apparatus present. Parasitic in African murid rodents. Type species: *Af. acanthocirrosa* (Baer, 1924) n. comb. Other species: *Af. isomydis* (Setti, 1892) n. comb.

Remarks

Afrobaeria n. g. differs from the type species of *Anoplocephaloides* [i. e. *Anoplocephaloides infrequens* (Douthitt, 1915)] and related species (*Anoplocephaloides sensu stricto*) in the morphology of the anterior strobila and scolex, the dorso-ventral distribution of testes, the structure and position of the early uterus and alternation of the genital pores. In *Afrobaeria*, the suckers are small and the scolex is not distinct from the anterior strobila even in well-relaxed specimens. In *Anoplocephaloides sensu stricto*, the scolex is large, provided with prominent suckers and is separated from the anterior strobila by a distinct constriction. In addition, the testes of *Afrobaeria* are dorsal, whereas those in *Anoplocephaloides sensu stricto* fill the whole medulla dorso-ventrally. The early uterus of *Afrobaeria* is positioned in the middle of the proglottis, both antero-posteriorly and dorso-ventrally; it has distinct lateral protuberances and does not overlap the ventral longitudinal canals. The early uterus of *Anoplocephaloides sensu stricto* is ventral and anterior, uniformly tubular (no protuberances) and extends across the ventral longitudinal canals.

Afrobaeria is similarly differentiated from *Paranoplocephaloides* and *Microcephaloides*, although the scolex and suckers are rather small is the latter genera. In *Leporidotaenia* and *Flabelloskrjabinia*, the early tubular uterus does not overlap the ventral longitudinal canals, but the uteri in these genera lack the lateral protuberances of the early uterus, and they have a distinct neck and unilateral genital pores. The dorso-ventral position of the early uterus and testes in the type species of the latter genera have not been defined.

Afrobaeria acanthocirrosa (Baer, 1924) n. comb.

Syns. *Paranoplocephala acanthocirrosa* Baer, 1924, *Anoplocephaloides acanthocirrosa* (Baer, 1924) Rausch,

1976, *Paranoplocephala omphalodes* (Hermann, 1783) *sensu* Collins (1972), *Paranoplocephala otomyos* Collins, 1972.

Redescription (Fig. 1, Table 2).

Redescription is based on the sectioned syntype specimens from *Otomys irroratus* from South Africa and three whole-mount specimens from the same host species from Kenya. Measurements refer to the Kenyan specimens; those of Baer (1926) are in square brackets. All measurements are in mm.

Genital pores irregularly and very frequently alternating, on average with 69 changes per 100 proglottides or 1.4 proglottides in each unilateral set, opening in middle of proglottis margin. Genital atrium capable of forming prominent genital papilla.

Longitudinal muscles forming two layers; external layer consisting of elongate, equally-spaced bundles with several fibres; internal layer consisting of less elongate and less equally spaced bundles with fewer fibres.

Longitudinal ventral osmoregulatory canals relatively wide (up to 0.15), connected by slightly narrower transverse canals (up to 0.12). Longitudinal dorsal canals narrow,

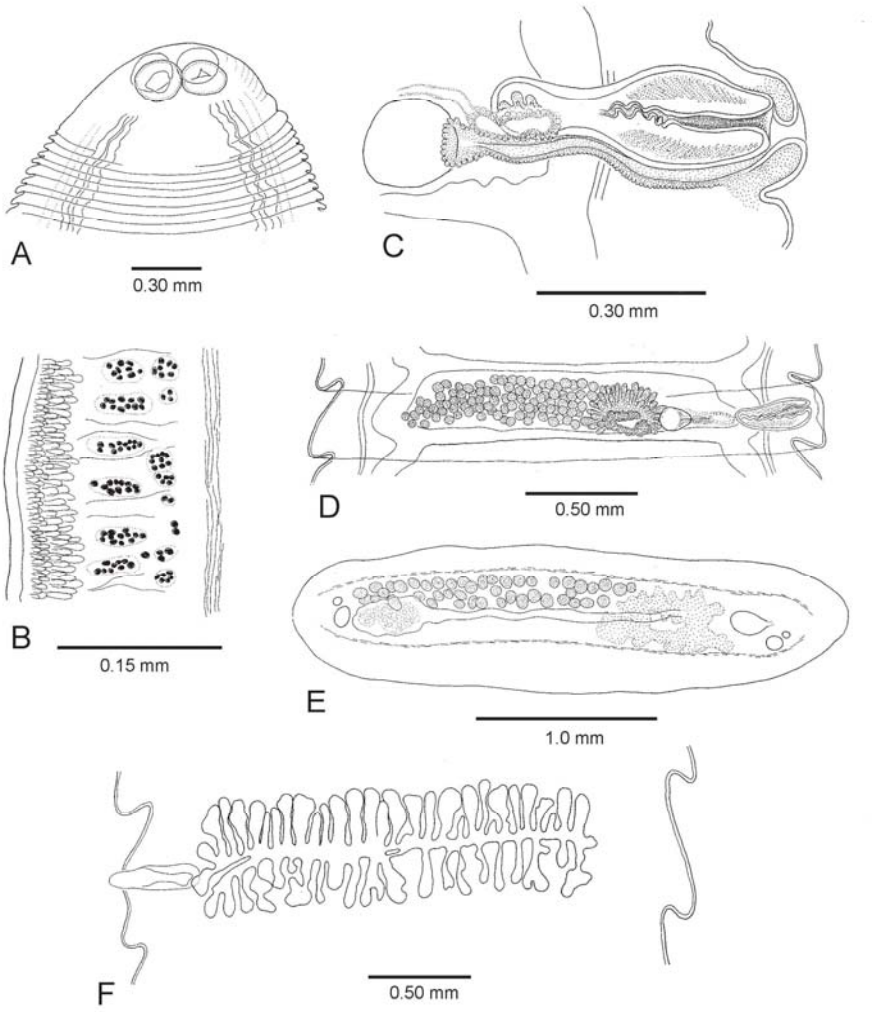

Fig. 1. *Afrobaeria acanthocirrosa* from *Otomys irroratus*. A - anterior strobila (Kenya). B - transverse section of muscle layers (South Africa, type material). C - terminal genital ducts (Kenya). D - mature proglottis (Kenya). E - transverse section of a mature proglottis (South Africa, type material). F - pregravid uterus (Kenya).

Body 70 [45 – 60] long, relatively wide (5.0) [5]. In contracted state scolex not distinct from anterior strobila; in relaxed state scolex more elongate, but neck absent (see Baer, 1926). Suckers small, 0.14 – 0.20 [0.20], positioned close to each other, directed antero-laterally. Proglottides much wider than long, with distinct, serrated velum.

overlapping or positioned lateral to ventral canals. Genital ducts pass dorsally across longitudinal canals.

Number of testes ca. 110 [40 – 50], distributed dorsally in single group from antiporal ventral canal to level of antiporal margin or middle of vitellarium; antiporal testes may be separated from antiporal canal by distinct gap. Cirrus

sac 0.34 – 0.55 long [0.8], 0.11 – 0.19 wide, muscular with distal half thicker than proximal half, increasing significantly in size in postmature and pregravid proglottides, extending markedly across longitudinal ventral canal. Ductus cirri distally wide, armed with short spines, proximally convoluted; small internal seminal vesicle visible in some proglottides, in others replaced by looped duct. Extruded cirrus thick and short. Vas deferens forming distinct but relatively narrow and short external seminal vesicle covered by thick cell layer; in syntype sections, external seminal vesicle looped and long.

Table 2. Main morphometric features of *Afrobaeria acanthocirrosa* and *Af. isomydis*. See Table 1 for the original identifications, host species and regions.

	Af. acanthocirrosa					*Af. isomydis*	
	Baer, 1926	Baer, 1959	Collins, 1972	Collins, 1972	Present study	Baer, 1949	Mahon, 1954
Body, length	45 – 60	50	61 – 74	73.5	70	15 – 20	max. 35
Body, max. width	5	5	5.0 – 7.0	6.0	5.0	5	7
Scolex, width	0.5 – 1.0	0.59	0.76 – 0.80	0.58	-	0.29	0.50
Suckers, width	0.2	0.19	0.20 – 0.24	0.20	0.14 – 0.20	0.13	0.20
Cirrus sac, length	0.8	0.37 – 0.69	0.44 – 0.70	0.14 – 0.28*	0.34 – 0.55	0.16 – 0.25	0.30 – 0.36
Testes, number	40 – 50	40 – 60	90 – 120	75 – 95	ca. 110	40 – 50	75 – 100
Egg, length	0.05	0.045	-	0.040 – 0.044	ca. 0.040	0.039	0.041 – 0.043

* - cirrus sac contracted

Ovary relatively small, 0.35 – 0.63 wide, compact, densely lobed, positioned in poral half of proglottis, separated by distinct gap from poral ventral longitudinal canal. Vitellarium 0.21 – 0.37 wide, asymmetrically bilobed, positioned in middle of ovary. When fully extended, vagina very long, 0.58 – 0.66, almost twice length of cirrus sac, of uniform width, 0.04 – 0.05, running ventrally or postero-ventrally to cirrus sac. Seminal receptacle small, 0.17 – 0.26 x 0.10 – 0.19, spherical or ovoid. Early uterus tubular with distinct lateral protuberances, positioned in middle of medulla antero-posteriorly and dorso-ventrally. Early uterus does not reach ventral longitudinal canals; with further development, it may overlap but not extend across ventral canals, usually dorsally. In pregravid proglottides, uterus consists of numerous, distinct anterior and posterior sacculations. Sacculations lost in fully gravid proglottides. Eggs ca. 0.040 [0.05] long, with pyriform apparatus.

Remarks

Afrobaeria acanthocirrosa was briefly described from the vlei rat, *Otomys irroratus,* from South Africa (Baer, 1924), and redescribed in more detail from the type material (Baer, 1926). The whole-mount specimens from Kenya agree well with the syntypes and original description, with the exception of the number of testes, which was stated to be 40 – 60 in the type material (Baer, 1926; Baer, 1959), but was ca. 110 in the Kenyan specimens (Table 2). This discrepancy is not considered significant, because Collins (1972) reported 90 – 120 testes in "*P. omphalodes*" (Hermann, 1783) from *Otomys* spp. from South Africa; her material included a paratype of *P. acanthocirrosa*. Collins' (1972) description agrees well with the present redescription, and *P. omphalodes sensu* Collins (1972) thus becomes a synonym of *Af. acanthocirrosa*. Collins (1972) also described *Paranoplocephala otomyos* Collins, 1972 from *O. irroratus* from South Africa, which was differentiated from other congeners by the "structure of the cirrus pouch", evidently referring to the thick muscle layers in the proximal cirrus sac. Collins' (1972) illustrations show a short and much contracted cirrus sac within a prominent genital papilla, but otherwise no significant differences compared with various specimens assigned here to *Af. acanthocirrosa* (Table 2). *Paranoplocephala otomyos* is therefore regarded as a junior synonym of *Af. acanthocirrosa*.

Baer (1959) described a new subspecies of *P. acanthocirrosa*, i.e. *P. a. kivuensis*, from *Otomys denti* from Congo. According to Baer (1959), *P. a. kivuensis* differs from the nominal subspecies by its shorter cirrus sac (0.22 – 0.37 vs. 0.37 – 0.80) and more numerous testes (60 – 65 vs. 40 – 60). Rausch (1976) suggested that these differences may indicate a presence two species, but considering the high variability in the length of the cirrus sac and number of testes in *Af. acanthocirrosa*, specific and subspecific distinctions do not appear to be valid. The short cirrus sac and well-developed internal seminal vesicle in *P. a. kivuensis* suggest that it may in fact belong to *Af. isomydis* (below), but the brief description of Baer (1959) does not allow a definitive judgment.

Based on the previous and present descriptions, the morphological similarity of *Af. acanthocirrosa* and *Af. isomydis* is obvious (Table 2; Figs 1 and 2). For example, they share a similar scolex and anterior strobila, frequently alternating genital pores, a very long vagina, a similar structure and position of the early uterus, and similar transverse and dorso-ventral distributions of the testes (see also the above diagnosis of *Afrobaeria*). The only consistent qualitative differences seem to be the size and shape of the cirrus sac and seminal receptacle. In *Af. acanthocirrosa*, the cirrus sac is large and muscular and extends across

the longitudinal canals, at least in post-mature proglottides. The cirrus sac of *Af. isomydis* is smaller with poorly developed muscle layers and apparently does not overlap the ventral longitudinal canal. In addition, the seminal receptacle of *Af. acanthocirrosa* is small and ovoid/spherical, whereas in *Af. isomydis* it is elongate and tortuous (Fig. 2). There may also be differences in the size of the internal and external seminal vesicles (more voluminous in *Af. isomydis*), but these organs seem to be subject to considerable intraspecific variation.

Afrobaeria isomydis was originally described from the Abyssinian grass rat, *Arvicanthis abyssinicus,* from Eritrea, and Mahon (1954) later described it from the rufous-nosed rat, *Oenomys hypoxanthus,* from Congo. Mahon (1954) did not compare her specimens with *Paranoplocephala acanthocirrosa*, but the short, non-muscular cirrus sac, well-developed internal seminal vesicle and tortuous, narrow seminal receptacle suggest that Mahon's specimens belong to *Af. isomydis* rather than *Af. acanthocirrosa* (Fig. 2).

Rausch (1976) reported the finding of two specimens of *Anoplocephaloides isomydis* from *Otomys tropicalis* imported from Kenya. These specimens "were in good agreement with the descriptions of *P. isomydis* by Baer (1949) and Mahon (1954)", but no details were given. If confirmed, this observation would represent the first finding of *Af. isomydis* in rodents of the genus *Otomys*.

Systematic characters in *Anoplocephaloides sensu* Rausch (1976)

The distinction of genera of the Anoplocephalinae has been based primarily on a few key characters. These are the number of genitalia per proglottis (1 vs. 2), type of the early uterus (tubular vs. reticulate/fenestrate), distribution of testes with respect to other organs and the opening of vagina with respect to the cirrus sac (anterior vs. posterior). Cestodes of the genus *Anoplocephaloides sensu* Rausch (1976) are characterized by a single set of genitalia, tubular

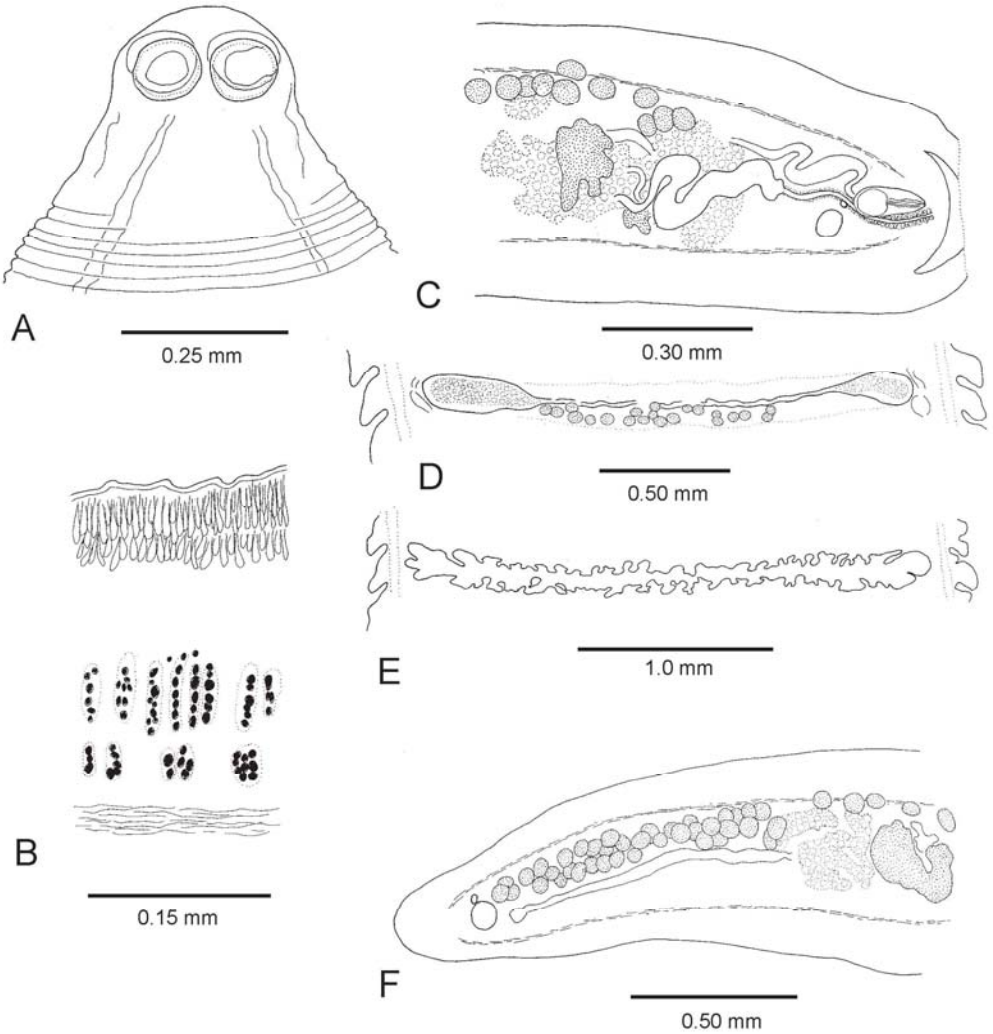

Fig. 2. *Afrobaeria isomydis* from *Arvicanthis abyssinicus*, Eritrea (type material). A - anterior strobila. B - transverse section of muscle layers. C - transverse section of terminal genital ducts. D - longitudinal section of early uterus. E - longitudinal section of pregravid uterus. F - transverse section of a mature proglottis.

early uterus, antiporal distribution of testes and a vagina opening posterior (or postero-ventral) to cirrus sac. Thus, new characters are needed to distinguish genera within this morphologically heterogeneous assemblage.

The size and form of the strobila separate *Anoplocephaloides* spp. into several categories, such as those with a short and wide (”wedge-shaped”) strobila, long and slender strobila and strobila of intermediate form (Rausch, 1976; Genov & Georgiev, 1988). The recent molecular phylogenetic analyses of anoplocephaline cestodes (Wickström *et al.*, 2005; Haukisalmi *et al.*, 2008) show that at least two of these categories represent monophyletic groups, i.e. the wedge-shaped *Anoplocephaloides sensu stricto* and *Microcephaloides*, the latter with a strobila of intermediate form. This suggests that body size and form are generally reliable systematic characters in *Anoplocephaloides sensu* Rausch (1976), thus also supporting the independent status of the miniature *Leporidotaenia* spp. from leporids (Lagomorpha), classified within *Anoplocephaloides* by Rausch (1976) and Beveridge (1994). It is also probable that the three long-bodied *Anoplocephaloides* spp. from marmots are monophyletic and separate from the other *Anoplocephaloides* spp. (Rausch, 1976), although this has not been studied rigorously. Both *Afrobaeria* species both have a wide body, but appear to differ slightly in the length of the strobila.

The monophyletic genera *Anoplocephaloides sensu stricto* and *Microcephaloides* also differ markedly from each other with respect to the size and shape of the scolex and anterior strobila, as well as the orientation of the suckers. Both species of *Afrobaeria* have basically a similar anterior strobila, i.e. lacking a distinct neck , which separates them from all other species of *Anoplocephaloides sensu* Rausch (1976). This also supports the status of *Paranoplocephaloides*, which has a distinct (though fairly small) scolex with anteriorly directed suckers.

There are basically two types of genital pore alternation in *Anoplocephaloides sensu* Rausch (1976), i.e. unilateral and irregularly alternating. Unilaterality is the prevalent form in *Anoplocephaloides sensu* Rausch (1976), with some significant exceptions. Irregular alternation seems to be a shared character within *Paranoplocephaloides* and *Afrobaeria*. However, alternation is very frequent in *Afrobaeria*, compared with *Paranoplocephaloides*, *Anoplocephaloides ryjikovi* (Spasskii, 1950) and *Anoplocephaloides wigginsi* (Rausch, 1954), which also have irregularly alternating pores. Genital pore alternation should not, however, be given too much weight, because in some other anoplocephalines, unilateral and alternating pores may occur in the same species (Haukisalmi & Henttonen, 2000; Haukisalmi *et al.*, 2005).

All species of *Anoplocephaloides sensu* Rausch (1976) have a basically similar distribution of testes, extending from the ventral antiporal osmoregulatory canal to female glands and filling the whole medulla antero-posteriorly. However, in *Anoplocephaloides sensu stricto* and *Microcephaloides*, testes also fill the medulla dorso-ventrally, but in *Afrobaeria* they are exclusively dorsal. The dorso-ventral distribution of testes has not been examined in other species of *Anoplocephaloides sensu* Rausch (1976), except that in *An. ryjikovi* they appear to be dorsal (Spasskii, 1951).

The structure of the early uterus and its subsequent development have played a significant role in attempts to classify anoplocephaline cestodes. The idea that the structure of the early uterus should be a major systematic determinant in the Anoplocephalinae has, however, been refuted (Wickström *et al.*, 2005). Phylogenetic results show that tubular uterus has given rise to reticulate uteri on multiple, independent occasions. For example, *Anoplocephaloides sensu stricto* and *Microcephaloides* are phylogenetically more closely related to *Paranoplocephala* Lühe, 1910 (with reticular uteri) than to *An. mamillana* (with a tubular uterus).

However, it seems that the position and extent of the early tubular uterus can be used in the generic classification of the Anoplocephalinae. The ”arvicoline clade”, a crown clade within the Anoplocephalinae consisting of *Anoplocephaloides sensu stricto*, *Microcephaloides*, *Paranoplocephala* spp. and *Diandrya composita* Darrah, 1930, is characterized by an early uterus (either tubular or reticular) that is positioned ventrally and extends ventrally the across longitudinal canals. In the species with a tubular uterus, it is positioned in the anterior part of the proglottis. In other, ancestral taxa (*Anoplocephaloides mamillana*, *Anoplocephala* Blanchard, 1848, *Mosgovoyia* Spasskii, 1951, *Schizorchis* Hansen, 1948), the tubular early uterus is usually confined between longitudinal canals and is positioned in the middle of the medulla antero-posteriorly. The dorso-ventral position of the early uterus in these taxa has not been adequately defined. Thus, the position and extent of the early tubular uterus reflect the phylogenetic position of species, and are potential diagnostic features at the generic level. This also gives further support to the idea that *Afrobaeria* does not belong in the arvicoline clade with *Anoplocephaloides sensu stricto* and *Microcephaloides*, and should represent an independent genus. It is also predicted that other taxa (not included in phylogenetic analyses) with a tubular uterus positioned in the middle of medulla are ancestral to and separate from the arvicoline clade of cestodes. It should be mentioned that the transverse extent and dorso-ventral position of the reticular early uterus now forms the basis of the generic differentiation of *Andrya* Railliet, 1893, *Neandrya* Haukisalmi & Wickström, 2005 and *Paranoplocephala* (see Haukisalmi & Wickström, 2005).

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