

## *Afrojoyeuxia* gen. n. and *Hunkeleriella* gen. n., two new genera of cestodes (Cyclophyllidea: Anoplocephalidae) from African rodents

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**Abstract:** Based on the study of type material, two new genera of cestodes (Cyclophyllidea: Anoplocephalidae) are proposed for *Paranoplocephala* Lühe, 1910 *sensu lato* species from African rodents. *Afrojoyeuxia* gen. n., proposed for *A. gundii* (Joyeux, 1923) comb. n. from *Ctenodactylus gundi* (Rothmann) (Hystricomorpha: Ctenodactylidae), is characterized by a high length/width ratio of mature proglottids, longitudinally extensive testicular field positioned anterior to the female glands, an ovoid or subspherical cirrus-sac and a thick, conical cirrus. *Hunkeleriella* gen. n., proposed for *H. dasymidis* (Hunkeler, 1972) comb. n. from *Dasymys incommutus* (Sundevall) (Myomorpha: Muridae), differs from related genera mainly by its short (10–20 mm) and wide strobila and neck, unilateral genital pores (exceptionally with a few changes per strobila), the position of the genital pores (slightly anterior to the middle of proglottid margin) and initially tube-like early uterus (later reticulated). *Parandrya* Gulyaev et Chechulin, 1996, earlier suggested to be a junior synonym of *Paranoplocephala*, is considered to be a valid, independent genus. Evidence of non-monophyly and need for a taxonomic revision of *Paranoplocephala sensu lato*, as well as the phylogenetic position of *A. gundii* and *H. dasymidis* are discussed.

**Keywords:** Cestoda, *Paranoplocephala*, systematics, taxonomy, *Ctenodactylus*, *Dasymys*, Ethiopian region

*Paranoplocephala* Lühe, 1910 *sensu lato* (s.l.) (Cyclophyllidea: Anoplocephalidae) comprises a relatively diverse assemblage of cestodes (ca. 35 valid species) parasitizing mainly arvicoline rodents, i.e. voles and lemmings (Myomorpha: Cricetidae), in the Holarctic region (Tenora et al. 1986, Haukisalmi et al. 2002). Two species, i.e. *Paranoplocephala primordialis* (Douthitt, 1915) and *Paranoplocephala sciuri* (Rausch, 1947), appear, however, to be host-specific parasites of sciurid rodents (squirrels and flying squirrels, respectively), and one, *Paranoplocephala longivaginata* Chechulin et Gulyaev, 1998 from *Myodes rutilus* (Pallas), has been found sporadically also in squirrels (Douthitt 1915, Rausch 1947, Chechulin and Gulyaev 1998, Haukisalmi and Henttonen 2007, Haukisalmi and Rausch 2007). In addition, two species referable to *Paranoplocephala* s.l., i.e. *P. gundii* (Joyeux, 1923) and *P. dasymidis* Hunkeler, 1972, parasitize ctenodactylid (Hystricomorpha) and murid (Myomorpha) rodents, respectively, in Africa.

The allocation of species to *Paranoplocephala* and *Andrya* Railliet, 1893 has been controversial, but the morphological criteria proposed by Haukisalmi and Wickström (2005), based on the transverse and dorsoventral position of the early uterus with respect to the testes and longitudinal osmoregulatory canals, appear to provide

a straightforward, phylogenetically supported distinction between these genera. Thus, all *Paranoplocephala*-like species in arvicoline and sciurid rodents are assigned to *Paranoplocephala* s.l., because their reticulated early uterus is ventral to the testes and extends bilaterally (and ventrally) across the longitudinal canals. *Andrya* is confined to the type species *A. rhopalocephala* (Riehm, 1881) from leporids (Lagomorpha) and, possibly, to *A. octodontensis* (Babero et Cattani, 1975), *A. neotomae* (Vogel, 1946), *A. boliviensis* Haverkost et Gardner, 2010 and *A. vesicula* Haverkost et Gardner, 2010 from octodontid and neotomine rodents. The early reticulated uterus of *Andrya* is ventral to the testes, but does not extend laterally across the ventral longitudinal canals.

Several *Paranoplocephala*-like cestodes, including the two African species, have also been assigned to *Aprostotandrya* Kirshenblat, 1938. The type species of *Aprostotandrya*, *A. macrocephala* (Douthitt, 1915), is, however, morphologically and genetically closely related to *P. omphalodes* (Hermann, 1783), the type species of *Paranoplocephala*. Therefore, *Aprostotandrya* is a junior synonym of *Paranoplocephala* (see Rausch 1976, Haukisalmi and Henttonen 2003, Haukisalmi et al. 2004).

The position of the two African species within *Paranoplocephala* s.l. is intriguing because of their unusual hosts

and geographical distribution. Two species from African rodents, previously placed in *Anoplocephaloides* Baer, 1923, have recently assigned to a new genus *Afrobaeria* by Haukisalmi (2008).

The present study proposes two new genera, *Afrojoyeuxia* gen. n. and *Hunkeleriella* gen. n., for *Paranoplocephala gundii* and *Paranoplocephala dasymidis*, respectively.

## MATERIALS AND METHODS

The present study is based on the examination of the type material of *Paranoplocephala gundii* and *P. dasymidis* deposited in the Natural History Museum of Geneva (MHNG), Switzerland:

i) *Paranoplocephala gundii*: MHNG INVE 44562–44567 (syntypes) from *Ctenodactylus gundi* (Rothmann) from Gafsa, Tunisia;

ii) *Paranoplocephala dasymidis*: MHNG INVE 18583 (holotype) and 18584–18586 (paratypes) from *Dasymys incommutus* (Sundevall) from Tiegbé, Ivory Coast (collector P. Hunkeler, year of collection 1963).

## RESULTS

### *Afrojoyeuxia* gen. n.

Figs. 1–3

**Diagnosis:** Strobila long (up to 30 cm). Scolex merging gradually with neck. Neck long and narrower than scolex when relaxed. Suckers embedded within scolex, directed laterally or anterolaterally. Proglottids craspodote, as long as or longer than wide when relaxed.

Genital pores irregularly alternating, positioned near posterior margin of mature proglottid. Testes numerous (90–100), positioned as single group anterior to female glands and terminal genital ducts. Length of testicular field at least twice length of ovary in well-relaxed proglottids; few testes placed antiporal to ovary but not reaching posterior margin of proglottid. Several testes extend lateral to longitudinal ventral osmoregulatory canals on both sides; testes do not overlap ovary.

Cirrus-sac roughly as long as vagina, very wide, almost spherical in some proglottids, overlapping or extending across ventral longitudinal canals. Everted cirrus very wide, conical, covered with minute spines. External seminal vesicle present but inconspicuous, with poorly developed layer of glandular cells.

Ovary median, usually not reaching ventral longitudinal canals. Vagina curved, posterior to cirrus-sac, covered with thick, distally widened layer of glandular cells. Seminal receptacle large; spherical or ovoid. Genital ducts pass dorsal to longitudinal osmoregulatory canals. Vitellarium slightly poral with respect to ovary. Uterus not seen in type material. Eggs with pyriform apparatus.

In ctenodactylid rodents (*Ctenodactylus gundi*).

**Type and only species:** *Afrojoyeuxia gundii* (Joyeux, 1923) comb. n. [syns. *Andrya primordialis* var. *gundii* Joyeux, 1923; *Andrya gundii* (Joyeux, 1923) Spasskii, 1951; *Aprostataandrya gundii* (Joyeux, 1923) Quentin, 1979;

*Paranoplocephala gundii* (Joyeux, 1923) Tenora, Murai et Vaucher, 1984].

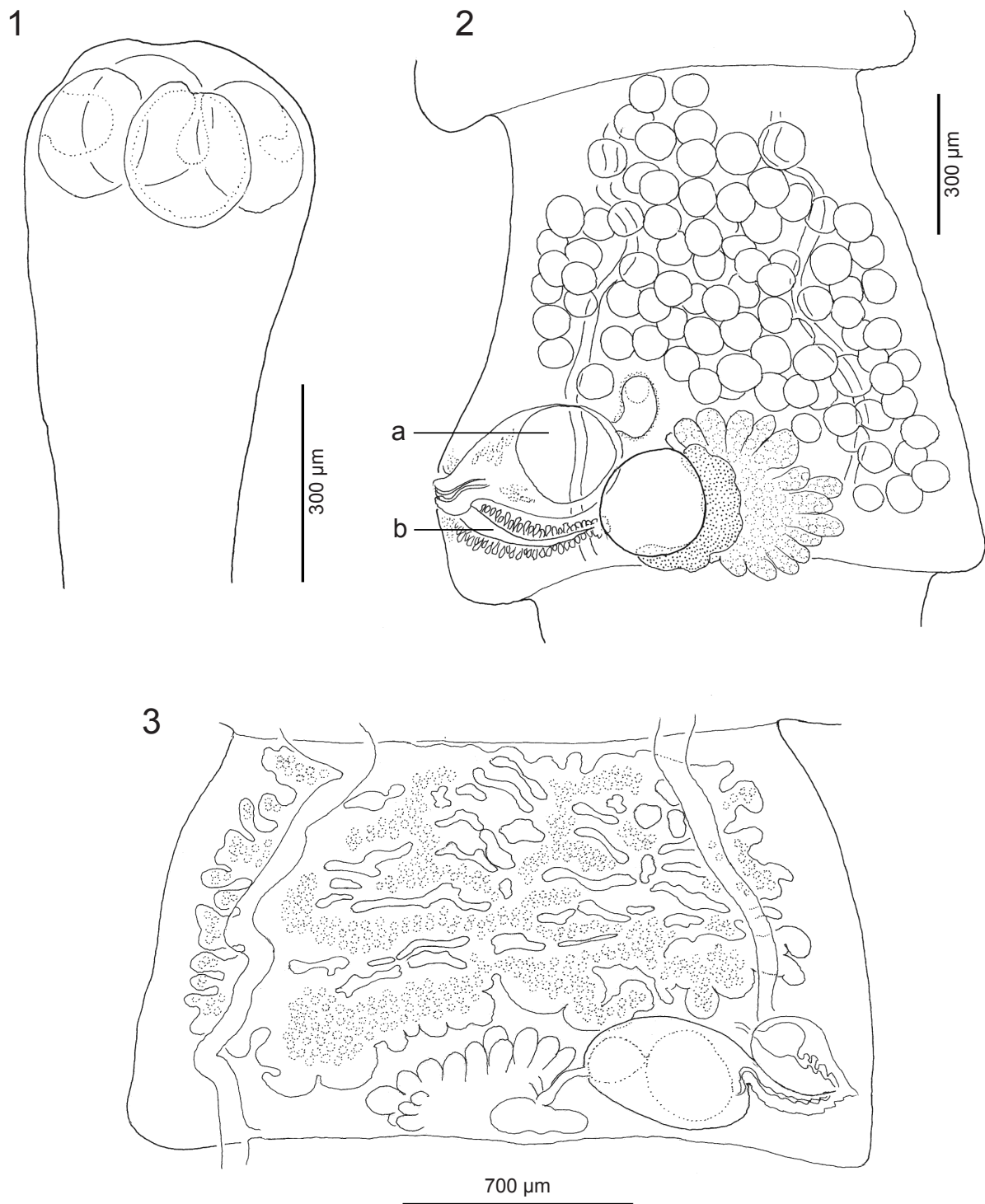
**Etymology:** The name of the new genus refers to Africa and the eminent cestodologist Charles Joyeux (1881–1966), the author of *Andrya primordialis* var. *gundii*.

**Remarks.** Joyeux (1923) gave a very brief account of *Andrya primordialis* var. *gundii* stating that it resembles *Andrya primordialis* Douthitt, 1915 (a parasite of North-American sciurids), except that the testes are more numerous and pass more extensively across the ‘canals’ in var. *gundii*. Spasskii (1951) raised var. *gundii* to a species level within the genus *Andrya*, but did not provide additional morphological data. Quentin (1979) provided a detailed redescription of *A. gundii* based on new material from the type locality, which fully confirmed the status of *A. gundii* as a valid species. However, Quentin (1979) assigned *A. gundii* to the genus *Aprostataandrya* because of the absence of a distinct ‘prostatic gland’. Finally, Tenora et al. (1984) moved *A. gundii* to the genus *Paranoplocephala*, thereby following the emended diagnosis of the latter genus by Rausch (1976).

The structure of the early uterus was not visible in the type material, but according to the redescription of Quentin (1979), the early uterus is reticulate, developing into complex sacculated and fenestrated organ in pregravid proglottids, covering most of the medulla and extending ventrally across longitudinal ventral canals on both sides. If we adopt the criteria of Haukisalmi and Wickström (2005) concerning the extent and position of early uterus, *A. gundii* belongs to *Paranoplocephala*. However, *A. gundii* can be differentiated unambiguously from all species representing *Paranoplocephala* s.l. based on the shape of mature proglottids, the distribution of testes, and the shape of the cirrus-sac and cirrus.

The well-relaxed mature proglottids of *A. gundii* are as long as wide, or even longer than wide according to the illustration of Tenora et al. (1986) based on the type material. Among *Paranoplocephala* s.l., the relatively longest mature proglottids are found in *P. arctica* (Rausch, 1952) and *P. fellmani* Haukisalmi et Henttonen, 2001, even they do not exceed 75% and 60% of the proglottid width, respectively, when fully relaxed (Haukisalmi and Henttonen 2001, Haukisalmi et al. 2001). In most of the species of *Paranoplocephala* the length of the mature proglottids is less than 30% of the proglottid width.

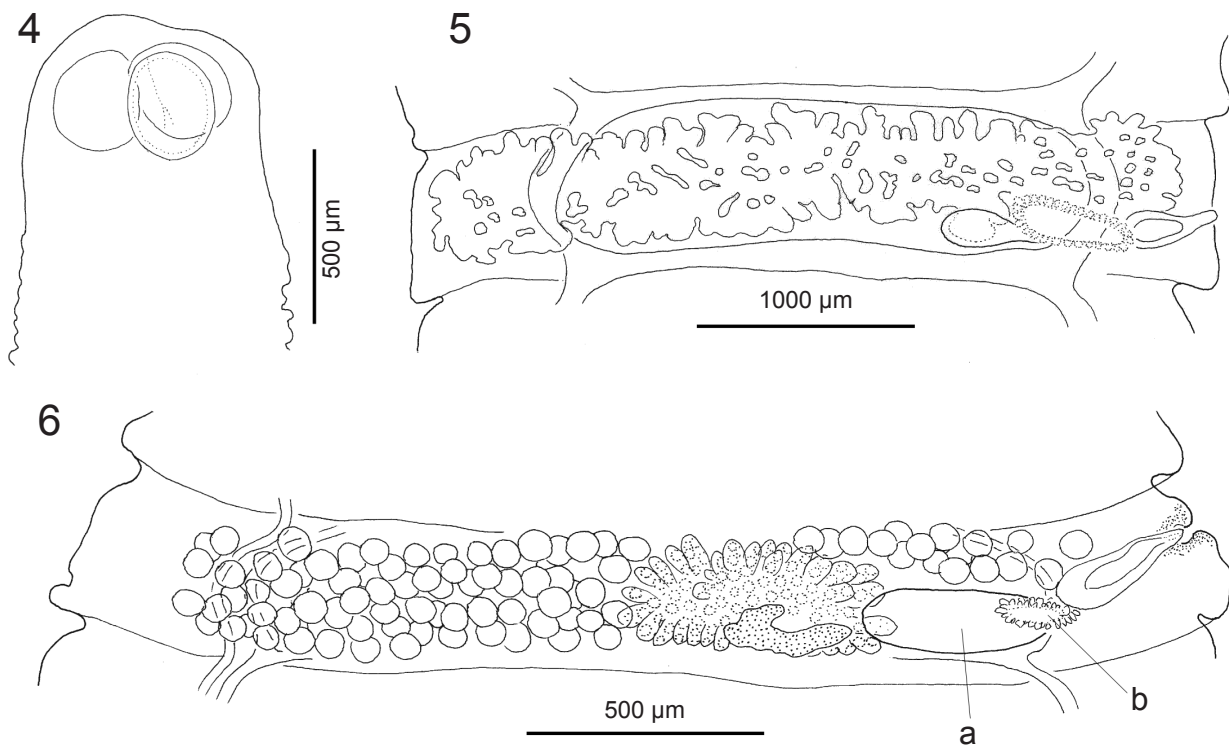
The testicular field of *A. gundii* is very long, covering more than half of the proglottid length, and most of the testes are positioned anterior to the female glands and genital ducts. These features do not occur in other species of *Paranoplocephala* s.l. There are, however, species of *Paranoplocephala* in which some of the testes are positioned anterior to the female glands and genital ducts, but the number and longitudinal extent of these testes are low, and most of the testes are always found antiporal to the ovary.



**Figs. 1–3.** *Afrojoyeuxia gundii* (Joyeux, 1923) comb. n. from *Ctenodactylus gundi*. **Fig. 1.** Scolex and neck (syntype). **Fig. 2.** Mature proglottid (syntype). **Fig. 3.** Pre gravid proglottid (redrawn from Quentin 1979). *Abbreviations:* a – cirrus sac; b – vagina.

The ovoid or subspherical shape of the cirrus-sac of *A. gundii* is unique among *Paranoplocephala* spp. (s.l.), other species having a distinctly elongated cirrus-sac. *Afrojoyeuxia gundii* has also a very thick, conical cirrus (when extruded), whereas the cirrus of *Paranoplocephala* species is slender, usually tapering distally.

*Afrojoyeuxia gundii* also significantly differs from *Paranoplocephala omphalodes* and related species representing the monophyletic *Paranoplocephala* s.s. (see Haukisalmi et al. 2004) in the morphology of the scolex and suckers (see Discussion).



**Figs. 4–6.** *Hunkeleriella dasymidis* (Hunkeler, 1972) comb. n. from *Dasymys incomtus*. **Fig. 4.** Scolex and neck (paratype). **Fig. 5.** Pregravid proglottid (holotype). **Fig. 6.** Mature proglottid (holotype). *Abbreviations:* a – seminal receptacle; b – external seminal vesicle.

***Hunkeleriella* gen. n.**

Figs. 4–6

**Diagnosis:** Strobila short (10–20 mm), but relatively wide (up to 4 mm). Scolex prominent, not separate from neck. Neck very short and usually as wide as scolex. Suckers embedded within scolex. Proglottids craspedote, transversely elongated. Genital pores unilateral, exceptionally irregularly alternating, positioned slightly anterior to middle of lateral margin of mature proglottids.

Testes numerous (120–130), mostly antiporal to ovary; smaller group of testes positioned poral to ovary and anterior to genital ducts. Few testes extending across longitudinal osmoregulatory canals on both sides; testes do not overlap ovary. Cirrus-sac elongate, short, barely extending to ventral longitudinal canal. External seminal vesicle prominent, covered with thick layer of glandular cells, expanding markedly in postmature and pregravid segments.

Ovary poral, but not reaching poral ventral canal. Vagina short (about half of cirrus-sac length), narrow, of uniform width, covered with layer of glandular cells, positioned ventral or postero-ventral to cirrus-sac. Seminal receptacle with narrow distal region and elongate, expanded proximal region. Genital ducts pass dorsal to longitudinal osmoregulatory canals. Vitellarium asymmetrically bilobed, slightly poral with respect to ovary.

Uterus initially tube-like, developing into complex sacculated and fenestrated organ in pregravid proglottids, covering most of medulla and extending ventrally across

longitudinal ventral canals on both sides. Eggs with pyriform apparatus.

In murid rodents (*Dasymys incomtus*).

Type and only species: *Hunkeleriella dasymidis* (Hunkeler, 1972) comb. n. [syns. *Andrya dasymidis* Hunkeler, 1972; *Aprostotandrya dasymidis* (Hunkeler, 1972) Hunkeler 1973; *Paranoplocephala dasymidis* (Hunkeler, 1972) Tenora, Murai et Vaucher, 1984].

**Etymology:** The name of the new genus refers to the cestodologist Pierre Hunkeler (Switzerland), the author of *Andrya dasymidis*.

**Remarks.** Based on the structure (below), dorso-ventral position and transverse extent of the early uterus, the type and only species of *Hunkeleriella*, *H. dasymidis*, unambiguously belongs to *Paranoplocephala* (s.l.). However, *H. dasymidis* is characterized by a very short (10–20 mm) and relatively wide strobila compared with other *Paranoplocephala* spp. (s.l.). The shortest species within the latter group (*P. janickii* Tenora, Murai et Vaucher, 1985) is on average 50 mm long (see Tenora et al. 1985) and most of the other species exceed 100 mm.

The neck of *H. dasymidis* is very short and wide, usually as wide as the scolex, although the anterior region of the holotype specimen is contracted. Within *Paranoplocephala* (s.l.), most species have a long and slender neck (<< 50% of scolex width), with a group of species having a wider neck (60–80% of the scolex width),

namely *P. blanchardi* (Moniez, 1891) *sensu* Tenora et al. (1985), *P. etholeni* Haukisalmi, Henttonen, Niemimaa et Rausch, 2002, *P. feodorovi* Gulyaev et Chechulin, 1996, *P. oeconomi* Gubányi et Murai, 2002, and *P. yoccozi* Haukisalmi et Henttonen, 2005 (Haukisalmi et al. 2002). However, *H. dasymidis* differs from the latter species in the position of the genital pores (see below) and distribution of the testes (in *H. dasymidis* the testes are poral and antiporal to the ovary, whereas in the other ‘wide-necked’ species there are no testes poral to the ovary).

The genital pores of *H. dasymidis* are unilateral (exceptionally with a few changes per strobila), in which it differs from the species of *Paranoplocephala sensu stricto* (s.s.) and most of the species within *Paranoplocephala* s.l., which have irregularly alternating genital pores. In addition, the genital pores of *H. dasymidis* are usually positioned slightly anterior to the middle of proglottid margin in mature proglottids. In most of the *Paranoplocephala* species (s.l.), the genital pores are positioned posterior to the middle of mature proglottid margin (rarely in the middle of the margin) and never anterior to the middle of the margin.

This may seem as a minor difference, but morphological and molecular data within the ‘arvicoline clade’ of cestodes (Wickström et al. 2005) suggest that this feature may be phylogenetically and systematically informative. In *Paranoplocephala*, *Microcephaloides* Haukisalmi, Hardman, Hardman, Rausch et Henttonen, 2008 and *Diandrya* Darrah, 1930, the genital pores are usually (slightly) posterior to the middle of proglottid margin (rarely median), whereas the pores of *Anoplocephaloides* are slightly, but consistently anterior to the middle of margin (Haukisalmi 2009).

Tenora et al. (1986) suggested that *P. dasymidis* can be separated from other species of *Paranoplocephala* by its unique distribution of testes (without further specifying the feature). The testes of *H. dasymidis* are widely distributed, extending across the longitudinal canals on both sides, with a tendency to form two separate fields. This feature is rare in species of *Paranoplocephala* (s.l.), but a similar distribution is seen in *P. sciuri* (Rausch, 1947), *P. aquatica* Genov, Vasileva et Georgiev, 1996 and *P. freemani* Haukisalmi, Henttonen et Hardman, 2006.

Of these, *P. aquatica* and *P. freemani* also have a tendency for the testes to occur in two separate groups. Moreover, *P. freemani* has a short vagina and a distally narrow seminal receptacle, features that also characterize *H. dasymidis*. However, these three species of *Paranoplocephala* differ markedly from *H. dasymidis* in having a much longer and more slender strobila and neck, more posteriorly positioned genital pores and, perhaps, a different type of early uterus.

The layer of glandular cells surrounding the external seminal vesicle is prominent in *H. dasymidis*, which aids in its distinction from most of the species of *Paranoplocephala* (s.l.).

The structure of early uterus in *H. dasymidis* was not clearly visible in the specimens studied, but Quentin (1979) stated that the uterus first has the form of a transverse tube, which then becomes lobed and reticulated and extends significantly across the osmoregulatory canals. If the early uterus is initially tubiform, that would separate *H. dasymidis* from *Paranoplocephala* (s.l.), which always have an initially reticulated early uterus, although the median part may appear cordiform, especially in *Paranoplocephala* s.s.

In addition to the features discussed above, *Hunkeleriella* differs unambiguously from *Paranoplocephala* s.s. in the morphology of the scolex, suckers and neck. The species of *Paranoplocephala* s.s. have a large scolex with prominent, crateriform suckers directed anteriorly (Haukisalmi et al. 2004), whereas *H. dasymidis* has a relatively small scolex with rather inconspicuous suckers that are more or less embedded within scolex and directed laterally/anterolaterally.

*Hunkeleriella* shows affinity with *Anoplocephaloides* s.s., since species of both genera have a short, wide strobila, unilateral genital pores that are positioned anterior to the middle of proglottid margin and an initially tubular uterus. However, *H. dasymidis* differs conspicuously from *Anoplocephaloides* due to the pronounced differences in the size and morphology of the scolex (larger and distinctly separate from the neck in *Anoplocephaloides*), length/width ratio of proglottids (lower in *Anoplocephaloides*) and structure of the fully developed (pregravid) uterus (saccate, not reticulated in *Anoplocephaloides*).

## DISCUSSION

Although the molecular phylogenetic resolution of the ‘arvicoline clade’ of cestodes (see Introduction) is low (Wickström et al. 2005), there is evidence suggesting that *Paranoplocephala* s.l. is a non-monophyletic assemblage. Specifically, the combined use of two independent molecular markers (*cox1*, 28S rDNA) showed that *Paranoplocephala oeconomi* Gubányi et Murai, 2002 and *Paranoplocephala nordenskioeldi* Haukisalmi, Wickström, Hantula et Henttonen, 2001 are more closely related to *Microcephaloides* spp. and *Diandrya composita* Darrah, 1930, respectively, than they are to other species of *Paranoplocephala* (Wickström et al. 2005, Haukisalmi et al. 2009). More comprehensive data based on sequences of two mitochondrial genes (*cox1*, *nad1*) corroborate these relationships and suggest additional relationships supporting the non-monophyly of *Paranoplocephala* s.l. (V. Haukisalmi, L.M. Hardman, E.P. Hoberg, H. Henttonen – unpublished data).

*Paranoplocephala* s.s. forms a monophyletic, morphologically well-defined assemblage of species within the genus *Paranoplocephala* (s.l.) (Haukisalmi et al. 2004, Wickström et al. 2005). The type species *Paranoplocephala omphalodes* and related species are characterized

by a large scolex with protruding, crateriform suckers directed anteriorly. In other species within *Paranoplocephala* (s.l.), the scolex is smaller, the suckers are less prominent, more or less embedded within scolex and directed laterally or anterolaterally.

Considering the above facts and the high morphological variability among *Paranoplocephala* spp. (s.l.), a taxonomic revision is clearly needed for this diverse assemblage. Attempts to reorganize the genus *Paranoplocephala* (s.l.) have been few. As mentioned above, the proposal of *Aprostotandrya* for a set of species earlier assigned to *Paranoplocephala* and *Andrya* (see Kirshenblat 1938, Spasskii 1951) is refuted by molecular and morphological evidence (Haukisalmi and Henttonen 2003, Haukisalmi et al. 2004).

Since then, a single new genus has been proposed for *Paranoplocephala*-like species, i.e. *Parandrya* Gulyaev et Chechulin, 1996 for *P. feodorovi*, but the genus was synonymized with *Paranoplocephala* by Haukisalmi and Henttonen (2000). However, a subsequent molecular phylogenetic analysis of Haukisalmi et al. (2009b) showed that, contrary to the suggestion of Haukisalmi and Henttonen (2000), *P. feodorovi* does not belong within *Paranoplocephala* s.s., and *Parandrya* should therefore be considered a valid, independent genus.

Although there are no molecular data for *Afrojoyeuxia* or *Hunkeleriella*, their approximate phylogenetic position may be predicted from certain morphological features. There are two suggested synapomorphies for species in the 'arvicoline clade' of anoplocephalid cestodes (including *Paranoplocephala* s.l., *Anoplocephaloides*, *Microcephaloides*, *Parandrya* and *Diandrya*), i.e. a slightly developed genital atrium (incapable of forming a genital papilla) and an anterior (or anterior and median) early uterus (tubular or reticulate) that extends across the ventral longitudinal canals ventrally (Haukisalmi 2009).

Both of these features characterize *Afrojoyeuxia* and *Hunkeleriella*, and it may thus be predicted that they are positioned within the arvicoline clade, the crown clade of mammalian anoplocephaline cestodes. In addition, *A. gundii* and *H. dasymidis* are both characterized by the

presence of testes lateral to the ventral longitudinal canals, a feature that occurs in many species in the arvicoline clade of cestodes (particularly in *Paranoplocephala* s.l. and *Microcephaloides*), but is very rare in other anoplocephaline cestodes (Spasskii 1951, Beveridge 1994, Haukisalmi 2009).

If *A. gundii* and *H. dasymidis* are truly positioned within the arvicoline clade of cestodes, they would be first species in this clade known to occur in regions where there are practically no arvicoline rodents (voles and lemmings). This would be unexpected, since it appears that this cestode clade has primarily radiated in arvicoline rodents in the Holarctic region and secondarily colonized other rodents (Wickström et al. 2005).

However, it is possible that arvicoline rodents and endemic African rodents have had historically overlapping distributions in northern Africa, providing possibilities for host shifts, although there are evidently no records of (sub)fossils of arvicoline rodents in that region (Repenning et al. 1990). At present, there is a small, isolated population of *Microtus guentheri* (Danford et Alston) in northern Libya (Amr et al. 2008), which may overlap with *Ctenodactylus gundi*, the host of *A. gundii*.

Alternatively, the arvicoline clade of cestodes has its origin in African rodents, but the main radiation has taken place later in arvicoline rodents in the Holarctic region. The latter scenario would imply historical range shifts of hosts and subsequent colonization of arvicoline rodents by cestodes of murid rodents. To test this scenario, molecular phylogenetic data would be needed for *Afrojoyeuxia*, *Hunkeleriella* and other anoplocephaline cestodes parasitizing murid rodents in Africa (*Afrobaeria* Haukisalmi, 2008) and elsewhere (*Gallegoides* Tenora et Mas-Coma, 1978 and *Hokkaidocephala* Tenora, Gulyaev et Kamiya, 1999).

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## REFERENCES

- AMR Z., SHENBROT G., HUTTERER R., AMORI G., KRYŠTUFEK B., YIGIT N., MITSAIN G., PALOMO L.J. 2008: *Microtus guentheri*. IUCN 2012. The IUCN Red List of Threatened Species. Version 2012.2, www.iucnredlist.org/details/23179, 6/2013.
- BEVERIDGE I. 1994: Family Anoplocephalidae Cholodkovsky, 1902. In: L.F. Khalil, A. Jones and R.A. Bray (Eds.), Keys to the Cestode Parasites of Vertebrates, Commonwealth Agricultural Bureaux International, Wallingford, Oxfordshire, pp. 315–366.
- CHECHULIN A.I., GULYAEV V.D. 1998: [*Paranoplocephala longivaginata* sp. n. (Cyclophyllidea: Anoplocephalidae) - a new cestode of rodents from East Siberia.] Parazitologiya 32: 352–356. (In Russian.)
- DOUTHITT H. 1915: Studies on the cestode family Anoplocephalidae. Illi. Biol. Monogr. 1: 1–96.
- HAUKISALMI V. 2008: Review of *Anoplocephaloides* species from African rodents, with the proposal of *Afrobaeria* n. g. (Cestoda: Anoplocephalidae). Helminthologia 45: 57–63.
- HAUKISALMI V. 2009: A taxonomic revision of the genus *Anoplocephaloides* Baer, 1923 sensu Rausch (1976), with the description of four new genera (Cestoda: Anoplocephalidae). Zootaxa 2057: 1–31.
- HAUKISALMI V., HENTTONEN H. 2000: Description and morphometric variability of *Paranoplocephala serrata* n. sp. (Cestoda: Anoplocephalidae) in collared lemmings (*Dicrostonyx* spp.,

- Arvicolinae) from Arctic Siberia and North America. *Syst. Parasitol.* 45: 219–231.
- HAUKISALMI V., HENTTONEN H. 2001: Biogeography of helminth parasitism in *Lemmus* Link (Arvicolinae), with the description of *Paranoplocephala fellmani* n. sp. (Cestoda: Anoplocephalidae) from the Norwegian lemming *L. lemmus* (Linnaeus). *Syst. Parasitol.* 49: 7–22.
- HAUKISALMI V., HENTTONEN H. 2003: What is *Paranoplocephala macrocephala* (Douthitt, 1915) (Cestoda: Anoplocephalidae)? *Syst. Parasitol.* 54: 53–69.
- HAUKISALMI V., HENTTONEN H. 2007: A taxonomic revision of the *Paranoplocephala primordialis* (Douthitt) complex (Cestoda: Anoplocephalidae) in voles and squirrels. *Zootaxa* 1548: 51–68.
- HAUKISALMI V., HENTTONEN H., HARDMAN L.M., HARDMAN M., LAAKKONEN J., MURUEVA G., NIEMIMAA J., SHULUNOV S., VAPALAHTI O. 2009: Review of tapeworms of rodents in the Republic of Buryatia, with emphasis on anoplocephalid cestodes. *ZooKeys* 8: 1–18.
- HAUKISALMI V., HENTTONEN H., NIEMIMAA J., RAUSCH R.L. 2002: Description of *Paranoplocephala etholeni* n. sp. (Cestoda: Anoplocephalidae) in the meadow vole *Microtus pennsylvanicus*, with a synopsis of *Paranoplocephala* s.l. in Holarctic rodents. *Parasite* 9: 305–314.
- HAUKISALMI V., RAUSCH R.L. 2007: *Paranoplocephala sciuri* (Rausch, 1947) (Cestoda: Anoplocephalidae), a parasite of the northern flying squirrel (*Glaucomys sabrinus*), with a discussion of its systematic status. *Comp. Parasitol.* 74: 1–8.
- HAUKISALMI V., WICKSTRÖM L.M. 2005: Morphological characterisation of *Andrya* Railliet, 1893, *Neandrya* n. g. and *Paranoplocephala* Lühe, 1910 (Cestoda: Anoplocephalidae) in rodents and lagomorphs. *Syst. Parasitol.* 62: 209–219.
- HAUKISALMI V., WICKSTRÖM L.M., HANTULA J., HENTTONEN H. 2001: Taxonomy, genetic differentiation and Holarctic biogeography of *Paranoplocephala* spp. (Cestoda: Anoplocephalidae) in collared lemmings (*Dicrostonyx*; Arvicolinae). *Biol. J. Linn. Soc.* 74: 171–196.
- HAUKISALMI V., WICKSTRÖM L.M., HENTTONEN H., HANTULA J., GUBÁNYI A. 2004: Molecular and morphological evidence for multiple species within *Paranoplocephala omphalodes* (Cestoda, Anoplocephalidae) in *Microtus voles* (Arvicolinae). *Zool. Scr.* 33: 277–290.
- JOYEUX C. 1923: Recherches sur la faune helminthologique Africaine. *Arch. Inst. Pasteur Tunis* 12: 119–167.
- KIRSHENBLAT Y.D. 1938: [Generalities in the Dynamics of the Parasite Fauna of Mouse-like Rodents.] *Izdanie Leningradskogo Gosudarstvenogo Universiteta*, 92 pp. (In Russian.)
- QUENTIN J.-C. 1979: Anatomie et taxonomie d'*Aprostotandrya gundi* (Joyeux, 1923), cestode parasite du rongeur *Ctenodactylus gundi* (Rothman). *Bull. Mus. Nat. Hist. Nat. A* 1: 251–256.
- RAUSCH R. 1947: *Andrya sciuri* n. sp., a cestode from the northern flying squirrel. *J. Parasitol.* 33: 316–318.
- RAUSCH R.L. 1976: The genera *Paranoplocephala* Lühe, 1910 and *Anoplocephaloides* Baer, 1923 (Cestoda: Anoplocephalidae), with particular reference to species in rodents. *Ann. Parasitol. Hum. Comp.* 51: 513–562.
- REPENNING C.A., FEJFAR O., HEINRICH W.D. 1990: Arvicolid rodent biochronology of the Northern Hemisphere. In: O. Fejfar and W.D. Heinrich (Eds.), *International Symposium on Evolution, Phylogeny, and Biostratigraphy of Arvicolids (Rodentia, Mammalia)*, Pfeil-Verlag, Prague, pp. 385–418.
- SPASSKII A.A. 1951: [Anoplocephalate tapeworms of domestic and wild animals.] *The Academy of Sciences of the USSR, Moscow*, 783 pp. (In Russian.)
- TENORA F., MURAI E., VAUCHER C. 1984: On Anoplocephalidae (Cestoda), parasitizing Rodentia and Lagomorpha in Europe. *Parasitol. Hung.* 17: 51–57.
- TENORA F., MURAI É., VAUCHER C. 1985: On some *Paranoplocephala* species (Cestoda: Anoplocephalidae) parasitizing rodents (Rodentia) in Europe. *Parasitol. Hung.* 18: 29–48.
- TENORA F., MURAI É., VAUCHER C. 1986: On *Andrya* Railliet, 1893 and *Paranoplocephala* Lühe, 1910 (Cestoda, Monieziinae). *Parasitol. Hung.* 19: 43–75.
- WICKSTRÖM L.M., HAUKISALMI V., VARIS S., HANTULA J., HENTTONEN H. 2005: Molecular phylogeny and systematics of anoplocephaline cestodes in rodents and lagomorphs. *Syst. Parasitol.* 62: 83–99.

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