FOLIA PARASITOLOGICA 45: 1-8, 1998

Anoplocephalid cestodes of veterinary and medical significance: a review

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Key words: Anoplocephalidae, veterinary importance, medical importance, biological cycle, review

Abstract. Cestodes of the family Anoplocephalidae Cholodkovsky, 1902, in their adult form, parasitize a variety of hosts, including reptiles, birds and mammals. To complete their life cycle, an intermediate host is required. This study gives a critical review of the life cycles of genera principally important to veterinary medicine (but sporadically infecting man): Anoplocephalinae (*Anoplocephala*, *Anoplocephaloides*, *Bertiella* and *Moniezia*) and Thysanosomatinae (*Avitellina*, *Stilesia*, *Thysaniezia* and *Thysanosoma*), using data reported by others and our own observations. The accepted paradigm on the biology of the anoplocephalid cestodes is that oribatid mites (Acarina) serve as intermediate hosts. However, as regards the genera *Avitellina*, *Thysaniezia* and *Thysanosoma*, it is still unclear whether oribatid mites are indeed the intermediate hosts, as larval forms (cysticercoids) have also been found in collembolans and psocids. Using the controversial biological cycle of *Thysanosoma actinioides* (Diesing, 1834), a theoretical methodological research proposal for parasitology was constructed which attempts to define a conceptional mark enabling us to predict and explain the parasite-hosts' related phenomenon. Aspects of this proposal are discussed using the biology of the cestodes of family Anoplocephalidae, as examples.

Cestodes of the family Anoplocephalidae Cholodkovky, 1902, are widely distributed parasites of a great variety of reptiles, birds and mammals. Most of them are found in mammals and present knowledge of their taxonomy, biology and evolution, therefore, is primarily derived from studies in mammalian host species. The potential for some of these anoplocephalid cestodes to infect economically important domestic ruminants (see e.g., Denegri 1987, 1990) makes them particularly significant.

The history of the family began when Blanchard (1891a) included the genera of the family Taeniidae, *Anoplocephala* Blanchard, 1849, *Bertia* Blanchard, 1891 and *Moniezia* Rudolphi, 1810 in the subfamily Anoplocephalinae (unarmed scolex). Subsequent authors, for example Cholodkowsky (1902), Fuhrmann (1907), Douthitt (1915) and Baer (1927), contributed to a greater understanding of the taxonomy of the group. Mola (1928) raised the subfamily Anoplocephalinae to the rank of family and created a new superfamily Anoplocephalioidea. Skrjabin (1933) introduced the suborder Anoplocephalata comprising two families, the Anoplocephalidae and the Stilesiidae. Further subdivision of these families resulting in the inclusion of a greater number of species arose from the work of Spasskii (1950, 1961), Baer and Fain (1951a,b) and Lopez-Neyra (1954, 1955). An important subsequent account of the family Anoplocephalidae (Stunkard 1961) suggested the inclusion, as subfamilies, of the four following distinct biological and bionomic groups: (i) Anoplocephalinae Blanchard, 1891, transmitted by oribatid mites, (ii) Catenotaeniinae Spasskii, 1950, transmitted by tyroglyphid mites, (iii) Linstowiinae Fuhrmann, 1907 transmitted by lepidopterous and coleopterous insects, and (iv) Thysanosomatinae Fuhrmann, 1907, transmitted by psocopterous insects. The suggestion of Stunkard (1961) with regard to the Catenotaeniinae Spasskii, 1950, was dismissed by Wardle et al. (1974). These authors created a new order Anoplocephalata, equivalent to Skrjabin's suborder Anoplocephalata, in which Stunkard's subfamilies are given full family status, i.e., Anoplocephalidae Blanchard, 1891, Linstowiidae Fuhrmann, 1932, and Thysanosomidae Fuhrmann, 1907. To these families they added Yamaguti's (1959) family Triplotaeniidae. Finally, Tenora (1976) using evolutionary criteria concluded that, based on the structure of the uterus, the family Anoplocephalidae should be subdivided into two subfamilies, Anoplocephalinae and Monieziinae. Most recently, Beveridge (1994) proposed four subfamilies based on four types of uterine development: Anoplocephalinae, Linstowiinae, Inermicapsiferinae and Thysanosomatinae.

The anoplocephalids are heteroxenous parasites and require both an intermediate and definitive host to complete their cycle. The experimental infection of

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intermediate host species, through the pioneering work of Stunkard (1937), has produced a paradigm in the subject. This author defined the role of oribatid mites in the ontogeny of *Moniezia expansa* (Rudolphi, 1810) of sheep by experimental infection with oncospheres of this parasite.

Oribatid mites are important components of the soil fauna and have a cosmopolitan distribution. Sengbusch (1977) analysed the relationship of oribatid and anoplocephalid species and produced a list of oribatid species that serve as intermediate hosts for several different anoplocephalid cestodes. Denegri (1993) demonstrated that 127 species of oribatid mites in 27 families served as intermediate hosts of 14 genera and 27 species of anoplocephalid tapeworms. A model based on the trophic characteristics of the intermediate and definitive hosts has been presented recently (Denegri 1991, 1996, 1997).

The aim of this study was to analyse the biological cycles of cestodes of the family Anoplocephalidae that are economically important or of public health concern. Additionally, the biological cycles of those species that still remain controversial are discussed.

Genera and species of the Anoplocephalidae with some significant agents of disease in humans and animals: biological cycle

Anoplocephalinae Blanchard, 1891

Anoplocephala Blanchard, 1849
(Syn. *Plagiotaenia* Peters, 1871)

This genus was created by Blanchard (1849) with the purpose of grouping all the tapeworms of horses. The two most important species found in horse are *Anoplocephala magna* (Abilgaard, 1789) and *A. perfoliata* (Goeze, 1782). These species are found rather frequently; light infections cause no clinical signs whereas high parasite burdens may cause disease. Bashkirova (1941) was the first to infect experimentally oribatid mites of the families Galumnidae Jacot, 1925 (*Galumna obvius* and *G. nervosus*), Oribatulidae Thor, 1929 (i.e., *Scheloribates laevigatus* and *S. latipis*) and Carabodidae Koch, 1837 (i.e., *Carabodes* spp.) with eggs of *A. perfoliata*. These experiments all led to the development of mature cysticercoids. Attemps to infect members of other families such as Achipteridae Thor, 1929 (*Achipteria* spp.) and Liacaridae Sellnick, 1929 (*Liacarus* spp.) failed to produce mature cysticercoids although in some larval development was observed. In these studies Bashkirova (1941) also obtained mature cysticercoids of *A. magna* from infected *S. laevigatus* and *S. latipes*. No other work on the biology of *A. magna* has been reported so far.

Subsequent authors (Kuliev 1963, Romero et al. 1989, Schuster 1991) incriminated other species (*Ceratozetes bulanovae*, *Eremaeus oblongus*, *Galumna dimorfica*, *Hermanniella granulata*, *Liebstadia similis*, *Scheloribates latipes*, *Scheloribates* sp., *Trichoribates incisellus*, *Urubambates schachtachtinskoi* and *Zygoribatula microspora*) as intermediate hosts of *A. perfoliata*.

Romero et al. (1989) discussed epidemiological aspects of horse anoplocephalosis in relation to other cestodes from the same family that are found in the domesticated herbivores of Argentina.

Anoplocephaloides Baer, 1923
(Syn. *Paranoplocephala* Lühe, 1910; *Aprostatandrya* Kirschenblatt, 1932)

The genus *Anoplocephaloides* was created by Baer in 1923 to include cestodes formerly assigned to the genus *Anoplocephala* Blanchard, 1848 (Rausch 1976). *Anoplocephaloides mamillana* (Mehlis, 1831) (syn. *Taenia mamillana* Mehlis, 1831; *Anoplocephala mamillana* Mehlis, 1831; *Paranoplocephala mamillana* Mehlis, 1831) occurs in the small intestine and sometimes in the stomach of horses. It is a small cestode and is characterized by having a narrow scolex with openings of the suckers that are slit-like. *A. mamillana* infections of horses very seldomly result in disease. Several species of oribatid mites may act as intermediate hosts. The most important ones include *Galumna obvia*, *G. eliminata*, *G. nervosus*, *Allogalumna longipluma*, *Achipteria* spp., *Ceratozetes* spp. and *Scheloribates* spp. (Bashkirova 1941, Spasskii 1961, Sengbusch 1977).

Bertiella Stiles et Hassall, 1902
(Syn. *Bertia* Blanchard, 1891; *Parabertiella* Nybelin, 1917; *Indotaenia* Singh, 1962; *Prototaenia* Baer, 1927; *Beveridgia* Spasskii, 1988)

The genus *Bertia* was first described by Blanchard (1891b) in the chimpanzee (*Troglodytes niger*) with *Bertia satyri* and *B. studeri* in the orang-utan (*Simia satyri*). The name *Bertia* was later changed to *Bertiella* by Stiles and Hassall (1902).

Cestodes of the genus *Bertiella* are common parasites in primates, rodents, dermopterans, Australian marsupials and are the only anoplocephalids occurring in man. Two species, *B. studeri* and *B. mucronata*, each with a different geographic distribution, parasitize human beings.

The majority of human cases involve *B. studeri*, although some cases of *B. mucronata* infections have also been reported (Feldman et al. 1983, Denegri and Perez-Serrano 1997). A comparative study (Denegri 1985a) established the differences between a human *B. mucronata* isolate and a monkey (*Alouatta caraya*) *B.*

mucronata isolate as well as with *B. studeri*, thereby elaborating on the geographic distribution of both species. In this study the author also discussed the epidemiological aspects concerning the acquired potentiality of this parasite to infect man.

In attempting the completion of its biological cycle, Stunkard (1940) experimentally infected two species of oribatid mites, *Scheloribates laevigatus* and *Galumna* sp., with eggs of *B. studeri* derived from a non-human primate *Macacus rhesus* originating from India. Although cysticercoids were produced in these mites, no adult cestodes were obtained when these cysticercoids were fed to *M. cynomolgus*. Denegri (1985b) reported the experimental infection of two species of the family Oribatulidae, *Dometorina suramericana* and *Scheloribates atahualpensis,* with eggs of human *B. mucronata*. Furthermore, this study determined the epidemiological chain of this parasitosis and, based on ecological considerations, has formulated the concept of its potential biotope.

Moniezia Blanchard, 1891
(Syn. *Fuhrmannella* Baer, 1925, *Baeriezia* Skryabin et Schulz, 1937; *Blanchardiezia* Skryabin et Schulz, 1937; *Eranuides* Semenova, 1972)

The first account of the genus *Moniezia* by Blanchard (1891a) included 11 species. Moniez (1891) broadened the concept of this genus by the addition of *Taenia ovilla* Rivolta, 1878, as well as *Thysanosoma actiniodes* Diesing, 1834. Stiles and Hassal (1893) reduced the number of species to 8 and divided them into three groups based on the presence or absence of interproglottidal glands: (i) *plannissima* group with interproglottidal glands arranged in a linear manner, (ii) *expansa* group with "sac-like" interproglottidal glands, and (iii) *denticulata* group without interproglottidal glands. A later study (Douthitt 1915) grouped the species into two groups: (i) *carrinoi* group and (ii) *expansa* group. Further generic subdivision was provided by the taxonomic studies of Theiler (1924) and Meggitt (1927). A monographic study of the genus *Moniezia* conducted by Baer (1927) included six species, *M. benedeni* (Moniez, 1879), *M. denticulata* (Rudolphi, 1810), *M. expansa* (Rudolphi, 1810), *M. pallida* Möning, 1926, *M. rugosa* (Diesing, 1850) and *M. trigonophora* Stiles et Hassall, 1893. However, the generic subdivision and the key provided by Lopez-Neyra (1954, 1955) are the best so far. *Moniezia* has attracted most attention because of its cosmopolitan distribution and economic losses due to infections of domestic ruminants.

The two most important species are *M. benedeni*, principally infecting cattle, and *M. expansa*, principally infecting sheep. Seventy three species of oribatid mites have been incriminated as intermediate hosts for *M. expansa* and 43 species for *M. benedeni* (see Denegri 1993). Earlier studies performed by Stunkard (1937, 1939) defined the role of oribatid mites in the biology of *M. expansa* while many investigators have searched for species of naturally infected oribatid mites, or have attemp their experimental infection. Thus, various studies were initiated with the purpose of elucidating epidemiological aspects of ovine and bovine monieziosis due to infections with the genus *Moniezia* (Kates and Runkel 1948, Soldatova 1950, Shaldibina 1953, Kuznetsov 1959, 1966b, 1970, Rajski 1961, Nazarova 1963, Kassai and Mahunka 1965, Alkov 1971, Lin and Sung 1975, Narsapur and Prokopič 1979, Barutski et al. 1986, Denegri and Alzuet 1992, Xiao and Herd 1992).

Thysanosomatinae Skryabin, 1933

Avitellina Gough, 1911
(Syn. *Hexastichorchis* Blei, 1921; *Anootypus* Woodland, 1928; *Ascotaenia* Baer, 1927).

The genus *Avitellina* includes four species of veterinary importance, *Avitellina chalmersi* Woodland, 1927, *A. centripunctata* (Rivolta, 1874), *A. goughi* Woodland, 1927 and *A. tatia* Bahlerao, 1936. Members of this genus occur in the small intestine of sheep and other domestic ruminants in Europe, Asia, Africa and North America. The parasite may reach a length of more than 3 metres. The genital organs are single and the genital pores alternate irregularly. The uterus transverses the central region of the proglottids. The eggs, after being formed, pass into a thick-walled paruterine organ.

In studying the biological cycle of *A. centripunctata* of sheep and goats, it was demonstrated (Nadakal 1960) that oribatid mites serve as intermediate hosts of the parasite.

Svadzhyan (1960) tried to infect oribatid mites with eggs of *A. centripunctata* and *Thysaniezia giardi* but failed to do so. Kuznetsov (1962) reported the development of larval stages of *Avitellina* sp. and *T. giardi* in psocids but failed to induce the development of adults in sheep that were fed with mature cysticercoids. In a subsequent paper Kuznetsov (1966a) reviewed his previous work and that of Svadzhyan (1960) concluding that insects of the order Corrodentia may serve as intermediate hosts. Kuznetsov (1966a), nevertheless, suggested that psocids were merely facultative hosts of *A. centripunctata* and that the real intermediate hosts were either, other species of psocids or groups of insects phylogenetically related to psocids.

A report from India (Narsapur 1974) described the infection of two species of oribatid mites of the genus *Scheloribates* (*S. fimbriatus* and *S. laevigatus*) using eggs of *Avitellina lahorea*, a species parasitic in sheep. The involvement of oribatid mites in the life cycle of *A. centripunctata* was also mentioned in the review article of Sengbusch (1977), as well as in the report of Zhaltsanova et al. (1977).

A report by Tverdokhlebov et al. (1988) claimed to have completed the life cycle of *A. centripunctata* under laboratory conditions. In this study, infection of collembolans of the genus *Entomobrya* resulted in the production of cysticercoids 22 days later. When sheep were fed with these collembolans, immature cestodes were found in their intestines 40 days later. Tishchenko (1991) investigated the epidemiology of *Avitellina* infections in sheep. After analysing soil collembolans for seasonal variations in natural infections, and lambs for the presence of adult tapeworms, he suggested optimal periods for anthelmintic treatments.

Stilesia Railliet, 1893
(Syn. *Aliezia* Shinde, 1969)

This genus includes two species infecting domestic ruminants: *Stilesia hepatica* Wolffhügel, 1903 and *S. globipunctata* Rivolta, 1874. *S. hepatica* occurs in the biliary ducts of sheep, cattle, goats and wild ruminant species in Sudan, Kenya, Tanzania, Angola, Zambia, Malawi and South Africa. In some countries of Africa it affects 90-100% of sheep. Adults are between 20 and 50 cm long; the proglottids contain single genital organs with irregularly alternating genital pores. The eggs may be found in two paruterine organs each containing approximately 30 eggs. The biological cycle of *S. hepatica* is not known. It is probable that oribatid mites function as intermediate hosts.

S. globipunctata occurs in the small intestine of domestic and wild ruminants in Europe, Africa and Asia. It is 40 to 60 cm long and localises at the duodenal-jejunal junction. Heavy infection with this parasite may cause the death of the host animal. The following species of oribatid mites have been shown to be intermediate hosts: *Africacarus calcaratus*, *Allogalumna pellucida*, *Galumna baloghi*, *G. pellucida*, *Scheloribates conglobatus*, *S. fimbriatus*, *S. perforatus* and *Zygoribatula conglobatus* (Graber and Gruvel 1964, 1967, Sengbusch 1977).

Thysaniezia Skrjabin, 1926
(Syn. *Helictometra* Baer, 1927)

Thysaniezia ovilla Rivolta, 1878 occurs in the small intestine of domestic ruminants in Europe, former USSR, Asia, Africa and America. *Thysaniezia* was once considered a genus distinct from the other genera of the family Anoplocephalidae. Wardle et al. (1974) dismissed this contention, proposing instead to consider *Thysaniezia* and *Helictometra* as synonyms. Following this proposal, Soulsby's (1982) account of the genus *Thysaniezia* included all species previously allocated to a separate genus *Helictometra*. The latter are economically important parasites in America (Denegri 1987).

Oribatid mites have been incriminated as experimental intermediate hosts. The species capable of producing the larval stage of the parasite included: *Achipteria* spp., *Liebstadia similis*, *Punctoribates punctum*, *Scheloribates carvialatus*, *S. laevigatus*, *S. laticeps*, *S. latipes*, *Trichoribates incisellus*, *Zygoribatula cognata* and *Z. skrjabini* (Potemkina 1944, Sengbusch 1977, Zhaltasanova et al. 1977, Migliani and Bali 1990). In contrast, Svadzhyan (1960, 1963) failed to experimentally infect oribatid mites with eggs of *T. giardi*. Conversely, Kuznetsov (1962, 1966a) having recovered larval stages of this parasite from psocids, failed to produce its strobilar form.

In South America (and in Argentina, in particular) the intermediate hosts of *H. giardi* (now *T. ovilla*) are oribatid mites of the family Oribatulidae, *Zygoribatula lata* and *Z. elongata* (Yannarella et al. 1978, Denegri et al. 1983).

Thysanosoma Diesing, 1835

Thysanosoma actinioides (Diesing, 1834), the "fringed tapeworm", occurs in the biliary and pancreatic ducts and the anterior parts of the duodenum mainly of sheep, and to a lesser extent cattle and goats, especially in the western parts of the USA (Allen 1973) and also in South America (Yannarella et al. 1978, Denegri 1987, 1990). It has a high prevalence in Argentina's Patagonian region. In San Carlos de Bariloche (a zone of the province Rio Negro) 100% of sheep were found to be heavily infected, the mean worm burden being 35.5 specimens per individual (Led et al. 1979, 1980). High parasite burdens do not produce clinical signs, although the parasites may produce distention of the biliary ducts, generally accompanied by marked fibrosis (Allen 1973). Inflammation (catarrhal) of the duodenum and the biliary tract and multiple petechiae in the duodenum (probably) attributable to scolex implantations (Denegri 1987) have been reported.

T. actinioides measures less than 30 cm. Each segment contains two sets of genital organs. The posterior border of each segment is markedly fringed which explains the common name "fringed tapeworm". This parasite, in common with those of the genera *Avitellina*, *Stilesia* and *Thysaniezia*, has paruterine organs, evaginations of the uterine wall where the eggs are formed. Following maturation, the sac-like structures detach from the uterus, form a thick covering around several oncospheres and then transform into egg capsules. These structures have several advantages: (i) the thick wall of the capsule protects the enclosed eggs, (ii) a number of eggs packed together in such protective covers facilitates better scattering, and (iii) the larger size renders them more conspicuous to the intermediate hosts (Spasskii 1961).

Controversy exists concerning the biological cycle of *T. actinioides*. Studies carried out by Allen (1959) demonstrated unequivocally that larval stages of this cestode could develop in insects of the order Psocoptera. However, as he was unable to infect sheep fed cysticercoids from infected psocids, he postulated that two intermediate hosts were required.

Studies of the soil fauna carried out in Argentina's Patagonia region (a highly endemic zone for thysanosomosis) revealed the presence in this region of 'an abundance' of oribatid species. Experimental infections of oribatid mite species with eggs of *T. actinioides* produced larval stages that were not completely developed (Denegri, unpubl. data).

DISCUSSION

In the cestode literature, oribatid mites are attributed an essential role in the biology of the family Anoplocephalidae, as the intermediate hosts. However, there is also undeniable experimental evidence indicating that some genera of the family (*Avitellina*, *Thysaniezia* and *Thysanosoma*) utilize other hosts.

In his account of the family Anoplocephalidae, Stunkard (1961) divided it into subfamilies on the basis of the group of invertebrates acting as intermediate hosts. Thus the subfamily Thysanosomatinae Skrjabin, 1933, was erected with the genus *Thysanosoma* as the type. The subfamily which also includes the genera *Avitellina* and *Thysaniezia* may be differentiated from the subfamily Anoplocephalinae by the structure of its uterus. The controversial and, as yet, unresolved biological cycle of *Thysanosoma actiniodes* prompted Denegri (1991, 1996, 1997) to carry out some theoretical-methodological analytical studies resulting in the construction of a program for research in parasitology. The program is based on the methodology proposed in "Programmes for Scientific Research" by the epistemologist Lakatos (1978).

Using the approach by Denegri (1991, 1996, 1997) for studying parasitic cestodes of the family Anoplocephalidae, the following might be deduced:

(a) The more herbivorous the higher the density of infecting anoplocephalids and the species diversity. For example in sheep the following genera and species are found: *Avitellina* (*centripunctata*); *Moniezia* (*benedeni*, *expansa*); *Stilesia* (*hepatica*, *globipunctata*); *Thysaniezia* (*ovilla*) and *Thysanosoma* (*actinioides*).

(b) The less herbivorous the host, the less the intensity and (species) density of the infecting anoplocephalids. In non-human primates, for example, *Bertiella* and *Moniezia* are found.

(c) In omnivorous hosts, occasionally anoplocephalids at very low density and species diversity occur. In humans some sporadic cases of infections with the genus *Bertiella* have been reported.

(d) In carnivorous hosts, except one report describing the genus *Bertiella* in a dog (Africa and Garcia 1935), no cestodes of the family Anoplocephalidae have been found. Regarding the above *Bertiella* infection in dogs, Denegri (1991) explains this finding on the basis of the "hard core" in parasitology he proposes. In this concept the occurrence of an anoplocephalid cestode in the dog is due to the trophic variations the dog has been subjected to during its domestication by man. Thus the dog has come to be a potential host for anoplocephalids, this being dependent on the frequency of contacts with soil oribatid mites.

The relevance to the theory for inferred parasitism through trophic behaviour we are defending here is not the finding (thus far advocated) of larval stages (cysticercoids) in collembols, oribatid mites and/or psocids. This condition solely signals the potential of such organisms to act as intermediate hosts for anoplocephalid cestodes. For our program of investigation in parasitology though, what is of fundamental importance, is demonstrating that collembols, oribatid mites and/or psocids are important components of the fauna ingested with food by the definitive hosts. Thus, nonconstituents of the habitual diet of the definitive hosts, despite being potential intermediate hosts (i.e. having the capacity to produce cysticercoids), have no probability of being regular intermediate hosts for the parasitic cestode studied.

The theory on trophism enables us to explain why domestic ruminants harbour only adult parasitic cestodes of the family Anoplocephalidae. With respect to the intermediate hosts, we can reject the *ad hoc* hypothesis of two intermediate hosts for *T. actinioides* as proposed by Allen (1973) and maintain the notion that oribatid mites remain the most probable true intermediate hosts. We support the suggestions of Kuznetsov (1966a) stating that insects of the order Psocoptera are mainly facultative hosts or carriers of parasites pertaining to the genera *Avitellina* and *Thysaniezia*. To these two genera we add also the genus *Thysanosoma*. The recent work of Tverdokhlebov et al. (1988) and Tishchenko (1991) demonstrated that experimental development of larval stages of *A. centripunctata* in Collembola and the adult stage in sheep put some questionmarks on the mode of transmission of the subfamily Thysanosomatinae. Notwithstanding the behavioural characteristics of collembols, we believe that their role as intermediate hosts for anoplocephalids is improbable.

Acknowledgments. We would like to thank anonymous referees and Dr. T. Scholz for suggestions.

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Received 19 August 1996

Accepted 14 May 1997