# Review of oribatid mites as intermediate hosts of tapeworms of the Anoplocephalidae

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ABSTRACT

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A list of oribatid mites acting as intermediate hosts of tapeworms of the Anoplocephalidae is provided. To date, 127 species of oribatids included in 27 families, are implicated as intermediate hosts of the 14 genera and 27 species of anoplocephalid tapeworms. The most cited mites families are Oribatulidae with 35 species, Galumnidae with 22 species and Ceratozetidae with 15 species. *Scheloribates laevigatus* (Oribatulidae) is the species that demonstrated most susceptibility, both natural and experimental, to develop larval forms of anoplocephalid tapeworms. A theoretical–methodological model for parasitology based on the trophic characteristics of the intermediate and definitive mammalian hosts is reviewed.

INTRODUCTION

Stunkard (1937) defined the vector role of oribatid mites in the ontogeny of *Moniezia expansa* 55 years ago, after which following his approach, 127 species of oribatids included in 27 families were recorded as intermediate hosts of 14 genera and 27 species of tapeworms of the Anoplocephalidae (Balogh, 1972). The paradigm developed by Stunkard's investigation remained unquestioned until Kutznetsov (1962, 1966); Svadzhyan (1960, 1963) and Allen (1959, 1973) demonstrated that some genera of anoplocephalids (*Avitellina, Thysaniezia* and *Thysanosoma*) could be transmitted by psocids. Allen's work brought about an interesting discussion, both theoretical and methodological, in parasitology. In that, all his attempts to infest sheep with cysticercoids recovered from psocids were unsuccessful the suggested an ad-hoc hypothesis with two intermediate hosts of *Thysanosoma actinioides* indicated the need to determine criteria capable of explaining and forecasting in vector parasitology.

This review aims to provide a complete list of those species of oribatid mites acting as intermediate hosts for tapeworms of the Anoplocephalidae family to determine behaviour patterns of this association, and to reconsider the theoretical–methodological trophic proposal developed by Denegri (1991).

*Species of Oribatids reported as intermediate hosts of anoplocephalid tapeworms*

Table 1 presents, with citation, the genera and species of the anoplocephalids together with reported genera and species of the oribatid mites cited as intermediate hosts.

TABLE 1

Life cycle completion by 27 species of anoplocephalid cestodes through prior contact of the host with oribatid mites as cited from the literature.

| Anoplocephalid species | Intermediate hosts | Definitive hosts | Reference |
|---|---|---|---|
| *Anoplocephala magna* | *Scheloribates laevigatus, S. latipes* | *Equus caballus* | Bashkirova, 1941a |
| *Anoplocaphala perfoliata* | *Achipteria* spp., *Carabodes* spp., *Ceratozetes bulanovae, Eremaeus oblongus, Galumna dimofica, G. nervosus, G. obvius, Hermanniella granulata, Liacaruss* (spp.,) *Liebstadia similis, Parachipteria punctata, Platynothrus peltifer, Scheloribates laevigatus, S. latipes, Scheloribates* spp. *Trichoribates incisellus, Urubambates schachtachtinskoi, Zygoribatula microporosa.* | *Equus caballus* | Bashkirova, 1941a<br>Bashkirova, 1941b<br>Kuliev, 1963<br>Schuster, 1988<br>Romero *et al.*, 1989 |
| *Aprostatandrya cricetuli* | *Allogalumna longipluma, Scheloribates chauhani* | *Cricetus migratorius* | Lin *et al.*, 1984 |
| *Aprostatandrya macrocephala* | *Galumna curvum, Galumna* spp., *Oribatella quadricornuta, Platynothrus peltifer Scheloribates* spp. | *Microtus ochrogaster* | Gleason & Buckner, 1979 |
| *Avitellina centripunctata* | *Protoschelobates* spp., *Punctoribates punctum, Scheloribates laevigatus, S. laticeps, Trichoribates* spp., *T. incisellus.* | *Ovis aries* | Nadakal, 1960<br>Sengbusch, 1977<br>Zhaltsanova *et al.*, 1977 |
| *Avitellina lahorea* | *Scheloribates fimbriatus., S. laaevigatus* | *Ovis aries* | Narsapur, 1974 |
| *Bertiella mucronata* | *Dometorina suramericana, Scheloribates atahualpensis* | *Homo sapiens* | Denegri, 1985 |
| *Bertiella studeri* | *Achipteria coleoptrata, Galumna* spp., *Scutovertex minutus, Scheloribates laevigatus* | *Macacus rhesus* | Stunkard, 1940<br>Sengbusch, 1977 |

TABLE 1 *(continued)*

| Anoplocephalid species | Intermediate hosts | Definitive hosts | Reference |
|---|---|---|---|
| *Cittotaenia ctenoides* | *Achipteria coleoptrata, Cepheus cepheiformis, Galumna nervosus, G. obvius, Liacarus coracinus, Liebstadia similis, Pelops acromius, P. tardus, Scutovertex minutus, Scheloribates* spp., *S. laevigatus Trichoribates incisellus, Xenillus tegeocranus* | *Oryctolagus cuniculus* | Stunkard, 1937**b** Stunkard, 1939**c** Stunkard, 1941 Sengbusch, 1977 |
| *Cittotaenia denticulata* | *Cepheus cepheiformis, Liacarus coracinus, Scutovertex minutus, Scheloribates laevigatus, Xenillus tegeocranus.* | *Oryctolagus cuniculus* | Stunkard, 1941 Sengbusch, 1977 |
| *Cittotaenia citelli* | *Galumna curvum, Scheloribates* spp. | *Citellus ungulatus and C. erythrogeny* | Lin & Linxian, 1986. |
| *Cittotaenia marmotae* | *Achipteria coleoptrata, Ceratoppia* spp. *Ceratozetes gracilis, Damaeus auritus, D. onustus, D. similis, Edwardzetes edwardsi, Euzetes globulus, Galumna* spp., *Hermannia gibba, Liacarus* spp., *L. globulus, Nothrus palustris, Parachipteria* spp., *Peloribates badensis, Scheloribates laevigatus, Trichoribates incisellus, T. trimaculatus, Xenillus* spp. | *Marmota marmota* | Ebermann, 1976 Sengbusch, 1977 |
| *Helictometra giardi* | *Zygoribatula elongata, Z. lata* | *Ovis aries* | Yannarella *et al.*, 1978 Denegri, 1983 Denegri, 1987 |
| *Moniezia benedeni* | *Achipteria* spp., *A. coleoptrata, Adorites coracinus, Ceratoppia bipilis, Ceratozetes* spp., *Galumna* spp., *G. elimata, G. fordi, G. hawaiiensis, G. obvia, G. obvius, Liacarus coracinus, Liebstadia* spp., *L. similis, Oribatula* spp., *O. minuta, Pergalumna nervosus, Platynothrus peltifer, Protoschelobates* spp. *Punctoribates hexagonus, P. punctum, Scheloribates* spp., *S. fimbriatus, S. laevigatus S. laticeps, S. latipes, S. madrescensis, S semidesertus, Spatiodamaeus subvertillipes Trichoribates* spp., *T. incisellus, T. novus,* | | Stunkard, 1937 Potemkina, 1941,1944, 1951 Anantaraman, 1948,1951 Roberts, 1953 Shaldibina, 1953,1964 Nadakal, 1960 Sokolova & Panin, 1960 Svadzhyan, 1962 |
| | *T. trimaculatus, Zygoribatula cognata, Z. frisiae Z. longiporosa, Z. skrjabini.* | *Ovis aries* and *Bos taurus* | Jurásek, 1962 Prokopic, 1962, 1967 |

TABLE 1 *(continued)*

| Anoplocephalid species | Intermediate hosts | Definitive hosts | Reference |
|---|---|---|---|
| | | | Kuznetsov, 1966<br>Ilyasov, 1970<br>Nazarova, 1970<br>Al'kov, 1971, 1975<br>Krammoi, 1973**a,b**<br>Sengbusch, 1977<br>Zhaltsanova *et al.*, 1977<br>Prokopic & Narsapur, 1981<br>Cai & Jin, 1984<br>Barutski *et al*, 1986a,b<br>Durranii & Hameed, 1987 |
| *Moniezia expansa* | *Achipteria coleoptrata. A. punctata Adorites ovatus, Allogalumna longiplumus, Cepheus cepheiformis, Ceratopppia bipilis, Ceratozetes* spp., *C. gracilis. C. mediocris, C. minimus, Eremaeus hepaticus, Eupelops planicornis, Euzetes globulus, Furcoribula furcillata, Galumna* spp., *G. curvum, G. elimata, G. emarginata, G. longipluma, G. nervosus G. obvia, G. obvius, G. virginiensis, Hermanniella granulata, H. picea, Hypozetes* spp., *Liacarus* spp., *L. coracinus, Liebstadia* spp., *L. similis, Oribatella* spp., *Oribatula minuta, O. venusta, Parachipteria willmanni, Pelops planicornis, Peloribates badensis P. curtipilus, Pergalumna* spp., *P. formicarpus, P. nervosus, Pilogalumna t enuiclavus, Platynothrus peltifer, Protoribates lophotrichus, Protoschelobates* spp., *P. seghetti, Punctoribates* spp., *P.hexagonus, P. punctum, Scheloribates chauhani, S. fimbriatus, S. laevigatus, S. laticeps, S. latipes, S. madresensis, S. perforatus, S. semidesertus, S. zaherii, Scutovertex minutus, Spatiodamaeus subverticillipes, Trichoribates* spp., *T.incisellus, T. novus, T. trimaculatus, Unguizates reticulatus, Xenillus tegeocranus, Zygoribatula cognana, Z. elongata, Z. exarata, Z. lata., Z. longiporosa, Z. skrjabini Z. saayedi, Z. tadrosi.* | *Ovis aries* and *Bos taurus* | Stunkard, 1937a,b,c<br>Stoll, 1938<br>Stunkard, 1939a,b<br>Potemkina, 1941<br>Potemkina, 1944a,b<br>Stunkard, 1944<br>Potemkina, 1948, 1951<br>Anantaraman, 1948,1951<br>Shaldibina, 1953,1964<br>Nadakal, 1960<br>Sokolova & Panin, 1960<br>Jurásek, 1962<br>Rajski, 1959, 1961<br>Kassai & Mahunka, 1964, 1965<br>Prokopic, 1962,1967<br>Frank, 1953,1958<br>Frank & Zivkovitch, 1960<br>Krull, 1939,1940<br>Kates & Runkel, 1948<br>Kuznetsov, 1966,1970<br>Graber & Gruvel, 1969<br>Ilyasov, 1970 |

TABLE 1 *(continued)*

| Anoplocephalid species | Intermediate hosts | Definitive hosts | Reference |
|---|---|---|---|
| | | | Yannarella, 1971<br>Nazarova, 1970<br>Al'kov, 1971,1975<br>Lin *et al.*, 1975<br>Caley, 1976<br>Narsapur, 1976<br>Narsapur & Prokopic, 1979<br>Zarzará, 1973<br>Zhaltsanova *et al.*, 1977<br>Deshpande *et al.*, 1980<br>Denegri *et al.*, 1983<br>Skorski, 1984<br>Skorski *et al.*, 1984<br>Barutski *et al.*, 1986a<br>Barutski & Parwar, 1986<br>Hassanain *et al.*, 1987, 1989<br>Schuster, 1988, 1991<br>Schuster *et al.*, 1988<br>Denegri, 1989 |
| *Moniezia neumanni* | *Punctoribates punctun, Scheloribates laevigatus S. laticeps, Trichoribates incisellus* | *Ovis aries* | Zhaltsanova *et al.*, 1977 |
| *Moniezia* spp. | *Achipteria* spp., *Epilohmannia pallida, Furcoribula furcillata, Galumna obvia, Liacarus coracinus, Oppiella nova. Punctoribates puntum, Scheloribates* spp., *S. chauhani, S. laevigatus, S. laticeps, S. latipes S. semidesertus, Scutovertex minutus, Spatiodamaeus subverticillipes, Trichoribates incisellus, Xylobates souchriensis, Zygoribatula frisiae, Z. skrajabini* | *Ovis aries* and *Bos taurus* | Svadzhyan, 1960<br>Kassai & Mahunka, 1965<br>Nazarova, 1965, 1970<br>Prokopic, 1967<br>Alieva, 1970<br>Al'kov, 1971, 1975<br>Krammoi, 1973a<br>Doktorov, 1975<br>Akbaev, 1976<br>Hollands Barea, 1978<br>Orta & Boyackehyan, 1981 |

TABLE 1 *(continued)*

| Anoplocephalid species | Intermediate hosts | Definitive hosts | Reference |
|---|---|---|---|
| | | | Lin *et al.*, 1983<br>Hassanain *et al.*, 1989 |
| *Monocoecoestus americanus* | *Adorites poppei, Belba* spp., *Ceratoppia bipilis, Damaeus globifer, Eremaeus brevitarsus, Fuscozetes* spp., *Galumna emarginata, G. niger, Liacarus itascensis, Neoribates quadrisetosus, Scheloribates lanceoliger* | *Erethizon dorsatum* | Freeman, 1952<br>Sengbusch, 1977 |
| *Monoecocestus sigmodontis* | *Belba* spp., *Liacarus* spp., *Oribatella minuta. Protoschelobates seghetti* | *Erethizon dorsatum*<br>Sengbusch, 1977 | Freeman, 1952<br>Melvin, 1952 |
| *Monoecocestus variabilis* | *Cepheus corae, Ceratoppia bipilis, Galumna emarginata G. niger, Liacarus itascensis, Neoribates quadrisetosus* | *Erethizon dorsatum* | Freeman, 1952<br>Sengbusch, 1977 |
| *Monoecocestus* spp. | *Adorites poppei, Balzania microptera, Ceratoppia bipilis Eremaeus brevitarsus, Fuscozetes* spp., *Gulumna emarginata G. niger, Neoribates quadrisetosus, Scheloribates t Panceoliger, Zygoribatula curviseta* | *Erethizon dorsatum* | Freeman, 1952<br>Sengbusch, 1977 |
| *Mosgovoyia pectinata* | *Galumna curvum, Scheloribates* spp. | *Lepus oiostolus* | Lin & Linxian, 1986 |
| *Paranoplocephala mamillana* | *Achipteria* spp., *Allogalumna longipluma, Ceratozetes* spp.*Galumna obvius, G. eliminata, G. nervosus, Scheloribates* spp. | *Equus caballus* | Bashkirovai 1941a<br>Spasskii, 1951<br>Sengbusch, 1977 |
| *Paranoplocaphala ryjikovi* | *Galumna virginiensis, Parakalumma lydia, Scheloribates* spp., *S. chauhani* | *Marmota himalayana* | Lin *et al*, 1982a |
| *Paranoplocephala transversaria* | *Parakalumma lydia, Scheloribates* spp., *S. chauhani* | *Marmota himalayana* | Lin *et al.*, 1982b |
| *Paranoplocephala variabilis* | *Oribatella quadricornuta, Scheloribates laevigatus* | *Microtus ochrogaster* | Gleason & Bukner, 1979 |
| *Schizorchis altaica* | *Galumna* spp., *G. virginiensis, Scheloribates* spp., | *Ochotona curzoniae* | Jiazhen & Lin, 1990 |
| *Stilesia globipunciata* | *Africacarus calcaratus, Allogalumna pellucida Galumna baloghi, G. pellucida, Scheloribates conglobatus S. fimbriatus, S. perforatus, Zygoribatula conglobatus* | *Ovis aries* | Graber & Gruvel, 1964<br>Sengbusch, 1977 |
| *Thysaniezia giardi* | *Achipteria* spp., *Liebstadia similis, Punctoribates punctum, Scheloribates carvialatus, S. laevigatus* | | Potemkina, 1944a, 1951 |

TABLE 1 *(continued)*

| Anoplocephalid species | Intermediate hosts | Definitive hosts | Reference |
|---|---|---|---|
| | *S. laticepts, S. latipes, Trichoribates incisellus, eliminate, Zygoribatula cognata, Z. skrjabini* | *Ovis aries* | Ilyasov, 1970<br>Sengbusch, 1977<br>Zhaltsanova *et al.*, 1977<br>Maglini & Boli, 1990 |
| *Thysaniezia ovilla* | *Punctoribates* spp. | *Ovis aries* | Potemkina, 1951<br>Sengbusch, 1977 |
| *Sub-Orden Anoplocephalata* | *Punctoribates monodactylus, Scheloribates laevigatus Zygoribatula skrjabini* | *Ovis aries* | Nazarova, 1975 |

We conclude from the analysis of the literature in Table 1 that numbers of the mite family Oribatulidae are quantitatively the most significant as intermediate hosts–with 35 species. The Galumnidae with 22 species and Ceratozetidae with 15 species are of secondary and tertiary importance respectively.

*Scheloribates laevigatus* (Oribatulidae) is the most frequent species acting as intermediate host of 14 species of anoplocephalids (*Anoplocephala magna, A. perfoliata, Avitellina centripunctata, A. lohorea, Bertiella studeri, Cittotaenia ctenoides, C. denticulata, Ctenotaenia marmotae, Moniezia autummalis, M. benedeni, M. expansa, Moniezia* spp., *Paranoplocephala variabilis* and *Thysaniezia giardi*). Moreover, it is the species most frequently found with natural cysticercoid infestation of *Moniezia* (*M. benedeni, M. expansa* and *Moniezia* spp.). Therefore, it is the genus (plus species) that showed the greatest susceptibility, both natural and experimental, to develop larval forms of anoplocephalid tapeworms. The other oribatid families found with minor frequency were: Liacaridae and Achipteriidae each with six species; Damaeidae with five species; Haplozetidae, Mycobatidae and Pelopidae with four species; Eremaeidae with three species; Hermanniellidae, Cepheidae, Xenillidae, Metrioppiidae, Oribatellidae and Parakalummidae with two species; Epilohmanniidae, Belbidae, Astegistidae, Carabodidae, Oppiidae, Scutoverticidae, Euzetidae, Mochlozetidae, Nothridae, Camisiidae and Hermanniidae with one species. Most of the species of oribatids cited as intermediate hosts of anoplocephalids were the product of experimental infections in the laboratory. Only 42 out of the 127 species found were natural cysticercoid carriers. Again, and coinciding with the studies of experimental infestations, the families most naturally infested were Oribatulidae (with 12 species); Ceratozetidae and Galumnidae (with seven species each).

*Analysis of theoretical–methodological proposals in parasitology*

Denegri (1991) defined a theoretical–methodological proposal in parasitology from an analysis of a biological cycle of *Thysanosoma actinioides*. He took the methodology developed by Lakatos (1978), known as Scientific Research Programmes, as a reference mark; it consists of three parts: (i) hard core; (ii) protector belt of the auxiliary hypotheses and (iii) initial conditions.

The 'hard core' in parasitology (especially with regard to endoparasites) is: the characteristic trophic behaviour of the hosts (intermediate and definitive) explains and forecasts the parasitic fauna which they harbour.

The auxiliary hypotheses of the protector belt were:

(a) hypothesis of the biological cycles;

(b) hypothesis of the development of parasite communities;

(c) hypothesis of the potential biotope.

The habitat of the host would act as the initial condition. This habitat may be aquatic, terrestrial, aerial, arboreal or subterranean.

In this paper, I discuss this proposal taking, as examples, the oribatids as intermediate hosts of tapeworms.

Schuster (1956) published an early paper on feeding habits of oribatid mites. Anderson (1975) stated that, despite the generalized feeding habits of the mites, there was evidence of trophic separation of cryptostigmate species according to their body size. The largest mites (1.00mm.) usually fed on leaf litter and there was an increase in the proportion of fungal material ingested when the size of the mites decreased. This may provide an explanation for the extant species which were exclusively mycophagous.

Behan and Hill (1983) considered that an understanding of oribatid feeding habits was essential to understanding their influence of soil fertility. Oribatids may be classified into six feeding groups: (i) macrophytophages: feeding on higher plant material; (ii) microphytophages: feeding on microflora; (iii) panphytophages: unspecialised plant feeders; (iv) zoophages: feeding on living animal material; (v) necrophages: feeding on carrion and (vi) coprophages: feeding on faecal material.

Kaneko (1988) analysed the relationship between feeding habits and size of chelicerae. Species of the same family tend to have similar feeding habits. Kaneko found that macrophytophages and panphytophages had larger chelicerae in comparison with those of microphytophages and fragment feeders. The size and shape of the chelicerae should be one of the factors which determine the food items used by each of the oribatid mites. The variation in feeding habitat of oribatid mites should partially contribute to increase species diversity by means of specialization of the food resources as well as the microhabit used.

For tapeworm infestations in ruminants, the vertical migration of oribatids, studied by numerous research workers (Soldatova, 1950; Shaldibina, 1953; Kuznetsov, 1959; Frank and Zivkovitch, 1960; Wallwork and Rodriguez, 1961; Nazarova, 1963 and Denegri and Alzuet, 1992) appears to be of great importance. The most significant factors inducing vertical migration are temperature and soil moisture.

Kassai and Muhunka (1965) defined criteria of the mites suitability as vectors for the anoplocephalids and identified: (a) morphological factors: body size, structure and dimension of mouth parts; (b) biological factors: hygrophily, xerophily, feeding habits, *etc.* For these authors, the lower limit of the vector size might be somewhere between 300 and 400 μm. In the intermediary host research, species smaller than 300 μm were disregarded, but those varying in length between 300 and 400 μm were examined for the presence of cysticercoids (Denegri, 1989). In my opinion, it is wrong to consider a potential oribatid intermediate host as a coprophage. The ingestion of eggs is not necessarily associated with this feeding habit as a slight rainfall may wash away eggs from proglotids localized on the surface of dry pellets and carry them far from the faeces on the ground and vegetation or even into the soil. Moreover, the oncospheres in soil have a different survival time in their infective capability, ranging from a few days to four months (Yannarella, *et al.* 1981).

The parasite eggs enter the mite organism at random during food ingestion. This apparent uncertainty is governed by the trophic characteristics of the oribatids. The eggs are simply too large to be ingested by accident. Clearly the mite must interpret the eggs as potential, if not preferential, food. In fact, the most cited species as intermediate hosts for the anoplocephalid tapeworms were panphytophages and zoophages (*Scheloribates laevigatus, S. latipes, Galumna obvius*).

The trophic proposal not only helps us to explain and forecast the intermediate hosts, but also the definitive hosts. Freeman (1952) studied the biology and life history of *Monoecocestus* from *Erethizon dorsatum.* The problem of scientific interest was to determine whether for the porcupine cestode, was eliminate the life cycle like those already investigated for this family, or did the arboreal habitat of the porcupine required major modifications in the established pattern for anoplocephaline life cycles. This paper helps to ratify it and reveals new facts on feeding behaviour of porcupines since I demonstrated that oribatid mites acted as intermediate hosts of *Monoecocestus* spp. The *Monoecocestus* has a life cycle remarkably adapted to that of the porcupine. This was demonstrated by the high percentage of the latter found infected in nature.

Freeman's paper as well as others by Denegri (1991) show that the trophism of intermediate and definitive hosts help to explain and forecast the parasitic fauna that these hosts harbour, whereas the knowledge of the parasitic fauna of a host explains and forecasts its trophic behaviour.

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