

## Oribatid mites as vectors of invasive diseases

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**ABSTRACT** — Research on mites as intermediate hosts of the tapeworms of the Anoplocephalidae family was encouraged by Stunkard (1937), who discovered that mites are intermediate hosts and vectors for *Moniezia expansa* tapeworms. This discovery stimulated other researchers to look for other mite hosts. In his review written in 1993, Denegri gathered data available up to 1991 associated with mites acting as intermediate hosts. We extended his list by adding information concerning Oribatida, which participate in the life-cycle of tapeworms of the Anoplocephalidae and Mesocestoididae families. We gathered the Oribatida species that were found to be intermediate hosts by Denegri after 1991 and those that were available but not found in his review. This may be due to the difficulty in obtaining certain articles at that time. We gathered data concerning factors that influence the distribution of oribatid mites, development of cysticercoids in their bodies, and factors that limit the Oribatida species as intermediate hosts.

**KEYWORDS** — Oribatida; intermediate host; Anoplocephalidae; Mesocestoididae; Cestodes; equines; ruminants; cysticercoid

### INTRODUCTION

Oribatid mites (Oribatida) are widespread throughout the world and constitute one of the largest mites orders. They play an important role in the ecosystem as decomposers of plant detritus. Moreover, some of them may be of epidemiological and medical significance because they act as intermediate hosts in the life-cycle of tapeworms of the Anoplocephalidae and Mesocestoididae families. At present, there are about 10,000 species of the described oribatid mites. They are widely distributed: 3620 oribatid species are known from the Palaearctic region (Macaronesia, North Africa, Europe, Caucasus, Asia/Palaearctic, China/Palaearctic, Japan), 1900 from Oriental regions (Oriental West, Oriental East, China/Oriental), 1450 from the Ethiopian

regions (Africa/Ethiopian, Madagascar), 1120 from the Nearctic, 1850 from the Neotropical (Central America, South America), 1245 from the Australian/Pacific region (New Guinea, Australia, New Zealand, Pacific Islands, Hawaii), and 118 from the Subantarctic/Antarctic (Subantarctic, Antarctic) (Schatz 2004) and there are still new ones being discovered (Bayartogtokh 2012; Seniczak *et al.* 2013; Bayartogtokh and Akrami 2014; Bayartogtokh and Ermilov 2015; Ermilov and Minor 2015).

### RESULTS

#### The occurrence of Oribatida

Oribatid mites are the most abundant soil-living microarthropods reaching densities of up to a hun-

dred thousand individuals per square meter in temperate forest soil (Skubała 2002). There are reports showing forest biota with absolute numbers of moss mites reaching more than one million individuals per one square meter (Rajski 1961). There are between several hundred and several thousand oribatid mites per square meter in meadows, while the least numerous oribatid mites are found in agricultural soils. This amounts from a few to several thousand individuals per square meter since agriculture has a negative impact upon wildlife (Niedbała 1980). Oribatid mites live wherever dead organic matter occurs, and their habitat includes soil, mosses, lichens, trees, wood or even nests of birds and other animal species (Niedbała 1980; Schatz and Behan-Pelletier 2008). They are saprophagous as they feed on dead organic matter, lichens, fungi (Erdmann *et al.* 2007) as well as dead or living animals (Heidemann *et al.* 2011). They are normally found on land, however they might be present in fresh and salty water (Niedbała 1980; Pfingstl 2013). Noti *et al.* (2003) analyzed the African fauna soil and studied in three ecosystems of a regressive sere: forest, woodland and savanna. They showed that overall savanna is the richest ecosystem (149 adult oribatid mite species), but forests show densities with a wider range than that of woodland and savanna. Maraun and Scheu (2000) analyzed 20 habitats in order to increase the density of oribatid mites. Most of the data are from Germany but also from USA, Austria, Canada and Finland. The studies were selected to cover a wide range of habitats including mor, moder and mull forests, broad-leaf and coniferous forests, pastures, meadows, arable fields and fallows of different ages. The fewest oribatid mites (up to 20,000 ind./m<sup>2</sup>) occurred in old fallow, arable land, pasture grazed by sheep, in base rich mull soils - all places in Germany and in riverine forest in the central Alps of Austria. Density of oribatid mites in the range between 20,000 and 60,000 ind./m<sup>2</sup> recorded in mixed oak forest (USA), old beech stand and old beech forests from Germany. The humus form at these sites is intermediate between moder and mull, but mull dominated. A density ranging from 60,000 to 180,000 ind./m<sup>2</sup> was recorded in an old beech forest, beech and spruce forests, acidic forests with the humus

form moder (places in Germany and Canada) and pine forests with raw humus (Finland) (Maraun and Scheu 2000). Erdmann *et al.* (2012) indicated that the most important factor for the incidence of the oribatid mites is the presence of a litter layer. He investigated the effect of four forest types at large geographic ranges in Central Europe: the highest density of oribatid mites occurred in coniferous forests (120,000 ind./m<sup>2</sup>), lower in the 30 years old (60,000 ind./m<sup>2</sup>) and 70 year-old (50,000 ind./m<sup>2</sup>) beech forests and lowest in the natural beech forests (30,000 ind./m<sup>2</sup>) (Erdmann *et al.* 2012). The type of forest impacts the thickness of its litter layer, so in a coniferous forest it is the thickest, and in old-growth, natural beech forests the layer is of minimum thickness (Erdmann *et al.* 2012). Oribatid mites are more commonly associated with soil and litter (Wallwork 1983; Lindo and Winchester 2006), but they are often the dominant mite group collected from forest canopies. Nadkarni and Longino (1990), Paoletti *et al.* (1991) and Behan-Pelletier *et al.* (1993) found mites to be the numerically dominant arthropods in cloud forest canopy in tropical forests and the same showed Schowalter (1989) and Winchester *et al.* (1999) in temperate forests. Lindo and Winchester (2006) found that oribatid and prostigmatid mites in suspended soils were not significantly different from an average abundance on the forest floor, but communities thriving in the canopy are more heterogeneous in species composition than in the forest floor.

#### Conditions affecting oribatid mites distribution

Critical environmental factors affecting oribatid mites distribution are: temperature, soil moisture, solar radiation, and food availability. One must also take into account soil depth (Mitchell 1979; Van Nieuwenhuizen *et al.* 1994). Oribatid mites are exothermic so they rely on the ambient temperature directly for many of their physiological processes, such as respiration, ingestion, growth and their survival (Mitchell 1979). Noti *et al.* (2003) claim that organic matter, C/N ratio, and total nitrogen content appear to be other key factors controlling the species richness. In André *et al.* 1997 study, mite population densities are significantly

correlated with cations  $K^+$  and  $Na^+$  as well as with the C/N ratio. Additional drivers such as atmospheric nitrogen deposition that influence soil fungal communities could have indirect effects on oribatid communities (Gan *et al.* 2013). In Gan *et al.* (2013), it is demonstrated that chronic N deposition has a detrimental effect on soil detritus food web and that the negative effect may feed back to influence litter decay and ecosystem functioning. Research by Graczyk *et al.* (2008) also showed the impact of cattle liquid manure on oribatid mites. The dose of 40m<sup>3</sup> cattle liquid manure per ha increased the number of mites, compared with the control surface. Doses of 60 and 80m<sup>3</sup> per ha had the opposite effect on the incidence of mites. A fungicidal and bactericidal agent combined with a medium and high dose of fertilizer significantly decreased the density of Oribatida, Gamasida and Actinedida in comparison with a small dose of fertilizer combined with this agent (Graczyk *et al.* 2008). High doses of nitrogen fertilizer disturb the relationship between organisms living in the soil and the physical and chemical structure of the soil. In their experiment, Trojanowski and Baluk (1992), found the smallest number of Acarina in a field fertilized with 270kg N/ha, while fertilization using a dose of 90kg N/ha stimulated Acarina and Collembola.

In experiments conducted by Graczyk *et al.* (2008), Domek-Chruścicka and Seniczak (2005), Sokołowska and Seniczak (2005), oribatid mites lived mostly on the lower part of plants and their density distinctly decreased with soil depth. The soil depth influences the temperature, moisture, organic matter quality, and pore space. Smaller-sized oribatid mites species are more likely to predominate in deeper soils (Mitchell 1979). Noti *et al.* (2003) noted that soil moisture is a key factor influencing the density of Oribatida. Tomczuk (2012) showed that prevalence and intensity of the invasion of *Anoplocephala perfoliata* tapeworms were the highest in horses that preferred wet pasture and low-lying soils in the vicinity of reservoirs. Pastures of low humidity and at high altitudes were characterized by the lowest extensiveness. Possibly, this issue is associated with the presence of various species of mites which are intermediate hosts for

*A. perfoliata* tapeworms (Gundlach *et al.* 2003, Tomczuk 2012, Tomczuk *et al.* 2015). This is in line with Mitchell (1977), who claims that oribatid larvae die when humidity is low and appear in large numbers when the amount of moisture in the environment increases (Mitchell 1977). Denegri and Alzuet (1992) state that this environmental influence may be key to controlling the intermediate host.

According to Taylor and Wolters (2005) water content affects the oribatids in an indirect way by limiting food. Drought has a limiting effect on fungi and micro-organisms that serve as food for Oribatida which in dry periods decrease in quantity. Oribatid mites are saprophagous, coprophagous and mycophagous. They can be also phytophagous, feeding on live plant tissues (Mitchell 1979; Schuster 1956). As most oribatid species and Collembola rely at least partially on fungal hyphae as a food resource, oribatid mites and Collembola may compete for food resources (Gan 2013). Since oribatid mites have many different feeding habits and they live not only in soil but also in the lower sections of grasses, the possibility of tapeworm egg ingestion varies greatly among potential intermediate hosts (Pinto *et al.* 1998).

Also a huge impact on soil mesofauna has the effect of different tillage systems. Twardowski *et al.* (2004) conducted research on three different tillage systems in a winter wheat field: reduced tillage, zero-tillage and conventional ploughing. The most species were found in zero-tillage system (no post-harvest cultivation; before sowing - a total herbicide treatment using Roundup®; sowing with no-till seeder) and in reduced tillage (a disc harrow ploughing 10 cm deep after the harvest; a disc harrow 10 cm with a roller prior to sowing; sowing with a disc seeder). The least amount of species occurred with conventional ploughing (skimming at 10 cm plus harrowing; before sowing medium plough 18 cm; conventional sowing). In the case of Oribatida they found four more arthropods in soil samples from the zero-tillage system compared to other methods of cultivation. Destruction of soil structure using a deep plough (18 cm) or a disc harrow (10 cm) strongly influenced negatively on the numbers of arthropods compared with the cultiva-

TABLE 1: Factors affecting oribatid mite distribution

| Factors affecting oribatid mite distribution | Optimal influence/ the highest number of oribatida                                   | literature   |
|--|--|--|
| Temperature air                              | 13,2 – 16,7 C (day temperature)  | Van Nieuwenhuizen <i>et al.</i> 1994; Mitchel 1979; Gan 2013;  |
| Time of day (morning, afternoon, evening)    | morning  | Van Nieuwenhuizen <i>et al.</i> 1994   |
| Rainfall                                     | during summer when the rainfall was high 0 - 5,8mm                                   | Van Nieuwenhuizen <i>et al.</i> 1994   |
| Relative humidity                            | 70,5 – 90,6%   | Van Nieuwenhuizen <i>et al.</i> 1994   |
| Soil moisture                                | 27,9 – 32% wet mass  | Van Nieuwenhuizen <i>et al.</i> 1994; Mitchel 1979; Noti <i>et al.</i> 2003  |
| Radiation                                    | 125 – 361 Wm <sup>2</sup>  | Van Nieuwenhuizen <i>et al.</i> 1994   |
| Illumination                                 | 11,4 – 31,0 Klux   | Van Nieuwenhuizen <i>et al.</i> 1994   |
| Type of soil                                 | sandy soil, containing humus and vegetation  | Schalk 1968; Maraun and Scheu 2000; Erdmann <i>et al.</i> 2012; Wallwork 1983; Lindo and Winchester 2006; Noti <i>et al.</i> 2003; André <i>et al.</i> 1997; Noti <i>et al.</i> 2003; Maraun and Scheu 2000; Erdmann <i>et al.</i> 2012; |
| Type of vegetation                           | forest, savanna  | Van Nieuwenhuizen <i>et al.</i> 1994;  |
| pH of the soil                               | low pH   | Loots and Ryke 1967;   |
| Food availability                            | saprophages, dead organic material, lichens, fungi                                   | Schuster 1956; Mitchel 1979; Pinto <i>et al.</i> 1998; Erdmann <i>et al.</i> 2007; Heidemann <i>et al.</i> 2011; Gan 2013; Taylor and Wolters 2005;  |
| Soil depth                                   | oribatid mites lived mostly on the lower part of plants and in the upper soil layers | Graczyk <i>et al.</i> 2008; Domek-Chruścicka and Seniczak 2005; Sokołowska and Seniczak 2005;  |
| Impact of cattle liquid manure               | 40m <sup>3</sup> cattle liquid manure/ ha  | Graczyk <i>et al.</i> 2008   |
| Nitrogen fertilizer                          | 90 kg N / ha   | Trojanowski and Baluk 1992   |
| Total nitrogen                               | 0,04-0,14 %  | Noti <i>et al.</i> 2003; André <i>et al.</i> 1997; Gan <i>et al.</i> 2013;   |
| C/N ratio                                    | 1,6 – 7,8  | Noti <i>et al.</i> 2003; André <i>et al.</i> 1997; Gan 2013  |
| Cation concentration                         |  | Noti <i>et al.</i> 2003; André <i>et al.</i> 1997  |
| K  | 0,64 – 1,5 meq./100g soil  |  |
| Na   | 0,31 – 0,65 meq./100g soil   |  |
| Tillage system                               | zero-tillage system  | Twardowski <i>et al.</i> 2004  |

tion pattern without the use of tillage tools (Twardowski *et al.* 2004).

The type of soil may affect mites. Schalk (1968), Maraun and Scheu (2000), Erdmann *et al.* (2012), Wallwork (1983), Lindo and Winchester (2006), Noti *et al.* (2003), André *et al.* (1997) recorded that sandy soils with a litter layer and vegetation are ideal for oribatid mites. This may explain a lower prevalence of equine tapeworms in the southeastern USA with typically dry, sandy pastures (Proudman *et al.* 1998). Oribatid mites prefer soils rich in organic matter with lower pH (Loots and Ryke 1967). This may explain the presence of a lower variety of species of mites on pasture where pH was 7.6 (Van Nieuwenhuizen *et al.* 1994).

All parameters (Table 1) related to the microclimate and seasons. Depending on the climate, different key factors seem to determinate the soil meso-fauna richness.

### Oribatida - Biological and morphological requirements for vectors

The efficiency of mites as vectors (alternate hosts of tapeworms) is limited by several factors. They are regarded to be morphological and biological factors (Shaldybina 1953; Kassai and Mahunka 1965). The biological ones are feeding habits, hygrophily, xe-

rophily (these factors are discussed in **Conditions affecting Oribatida distribution**). The morphological factors are body size, the size of the mouth opening and the structure of the mouth parts. The lower limit of this vector's size varies between 300 and 400 µm (Kassai and Mahunka 1965; Graber and Gruvel 1969; Denegri 1989). The representative genus *Scheloribates* usually has a minimum length of 500 µm, so they are often used in studies of Oribatida as intermediate hosts in tapeworms. This finding was confirmed by the research undertaken by Akrami *et al.* (2007). The species of 400 and 465 µm in size (*Scheloribates fimbriatus* and *Galumna iranensis*, respectively) contained only 1 cysticeroid in their bodies while the species of a larger size (540 – 567 µm *Galumna karajica*) contained up to 7 cysticeroids (Akrami *et al.* 2007). Those mites that have less chitin cuticle and a more flexible body, they are capable of swallowing tough food. In such creatures, pollen of similar size to the one of a parasite egg was observed (Żbikowska-Zdun and Koczara 2013). Schuster *et al.* (2000) observed that oncosphere in larger mites (in their research *Galumna racilis*, *Kilimabates* sp.) are not developed in such a degree as in the smaller ones (*Scheloribates fusifer*, *Ceratozetoidea immatures*, *Muliercula ngoyensis*, *Zygoribatula undulata*). This may be due to the fact that in larger species ingested

eggs pass through the alimentary tract before the oncosphere have hatched (Ebermann 1976). Trowe (1997) reported that the size of tapeworm larvae decreases with a rising burden of cysticercoids. It is due to the presence of a hard exoskeleton in oribatid mites, preventing a body cavity from expanding. This has been described for cysticercoids of four anoplocephalid cestodes: *M. expansa*, *M. benedeni*, *A. perfoliata*, *A. mamillana* that were experimentally grown in both *Scheloribates laevigatus* and *S. latipes* (Trowe 1997). The calculated average volume for cysticercoids of *A. perfoliata* and *A. mamillana* were the largest ( $1.97$  and  $2.27 \times 10^6 \mu\text{m}^3$ ) for single cysticercoids, less ( $1.63$  and  $1.61 \times 10^6 \mu\text{m}^3$ ) for two cysticercoids and the least for three cysticercoids per a mite ( $1.47$  and  $1.35 \times 10^6 \mu\text{m}^3$ ) (Trowe 1997). Schuster and Coetzee (2012) in their experiments used *Scheloribates pallidulus* as an intermediate host for *A. magna* and achieved  $1.23 \times 10^6 \mu\text{m}^3$  for the volume of one cysticercoid per a mite and  $0.872 \times 10^6 \mu\text{m}^3$  for two and  $0.684 \times 10^6 \mu\text{m}^3$  of three cysticercoids per a mite. The smaller dimensions of cysticercoids are due to the smaller size of *S. pallidulus*.

#### Cysticercoid development in the body of Oribatida

As decomposers of plant detritus in the ecosystem, they are convenient vectors of the larval form of tapeworms. Mites are transmitted to ruminants per os, while grazing (Boczek and Błaszak 2005). The parasite eggs enter mite's body at random during food ingestion. Caley (1975) indicates that mites become infected when they mechanically destroy the outer shell of tapeworm eggs. In this case, the oncosphere moves from the alimentary tract and develops as a cysticercoid larva in the oribatid body cavity (Murai 1989; Xiao and Herd 1992; Schuster *et al.* 2000; Akrami *et al.* 2007). Ebermann (1976) reports that larger mites are able to swallow whole eggs of tapeworms. The oncosphere is not able to hatch and the egg passes through the alimentary tract of the mite (Ebermann 1976).

Stunkard (1937) described the morphological transformation of a tapeworm embryo. An oncosphere develops from the egg, and the shell will be

left only in the intermediate host. The next stage of development are larval cysts, which distinguished by four developmental forms, formed in the following manner: after 48 hours, an egg swallowed by an oribatid mite finds itself in the body of the mite. The oncosphere initially expands and takes the form of a large ball. Later, it expands transversely and is divided into three parts to form a segmented larva. At the front and before the division, suckers are formed. The front part of the embryo becomes invaginated and the posterior segment of the body forms a kind of tail (cercomer). This results in an invasive larval cyst called cercocyst composed of two parts: a spherical body (of 140 to 180 microns in diameter) and cercomer (50 microns in diameter). Finally, in the final host a mature tapeworm develops from a cercocyst. The development of all tapeworms of this group is very similar (Stunkard 1937; Potjomkina 1948; Rajski 1959).

The development of cestode larval stages in immature mites has been described by some researchers. In 1978 Narsapur noted the presence of *Moniezia* larval stages only in immature mites of *Platynothrus pelifer*. Schuster *et al.* (2000) demonstrated a much higher cysticercoid prevalence in immature stages of Ceratozetoidea than in adult stages. In general, the cysticercoid development within the body cavities of oribatid mites is influenced by the species of mite, the intensity of infection and the ambient temperature (Narsapur 1988).

Formation of cysticercoids in the body cavity as a space demanding process might influence on the reproductive ability of the mites. Natural and experimental infection with *M. expansa* and *M. benedeni* cause sterility in female oribatids, regardless of the number of cysticercoids. This fact has been noted by many researches: (Fritz 1995; Schuster 1995; Akrami *et al.* 2007). Schuster *et al.* (2000) also reported that the infected mites did not contain any mite eggs, while low numbers of mite eggs were found in only one third of the adult mites which were negative for cysticercoids.

#### Oribatida as intermediate hosts of tapeworms

Interest in oribatid mites acting as intermediate hosts began to rise with the Stunkard study (1934;

1937), who discovered that they are intermediate hosts and vectors of the tapeworm *Moniezia expansa*. Since then other researchers have shown that oribatid mites are also hosts for other tapeworms of the Anoplocephalidae family. A comprehensive list of anoplocephalids and their intermediate and definitive hosts was compiled by Denegri (1993). He listed 127 mites species which belong to 27 families. He assigned them to 27 tapeworms species belonging to the family Anoplocephalidae. There are several scientists who are involved in exploring oribatids in respect of their role as intermediate hosts (Xiao and Herd 1992; Schuster *et al.* 2000; Denegri *et al.* 2002; McAloon 2004; Akrami *et al.* 2007; ElMehlawy 2009; Schuster and Coetzee 2012; Ire *et al.* 2013; Żbikowska-Zdun and Koczara 2013). There was an attempt at studying the growth of oncosphere in mites (Xiao and Herd 1992; Schuster *et al.* 2000; Denegri *et al.* 2002; Akrami *et al.* 2007; Schuster and Coetzee 2012). Furthermore, a number of new species of oribatids that participate in life cycles of tapeworms were described (Haq *et al.* 1999; Schuster *et al.* 2000; Denegri *et al.* 2002; McAloon 2004; Shimano 2004; Akrami *et al.* 2007; Schuster and Coetzee 2012). The list created by Denegri (1993) might be extended by additional items with respect of oribatids participating in the life cycle of tapeworms of the Anoplocephalidae family. In his review, Denegri (1993) considered the state of research until 1991. The Table 2 presents Oribatida species examined by scientists after 1991 and those that were not found in Denegri's review.

Scientists have also undertaken to find oribatid mites acting as intermediate hosts for other cestodes. *Thysanosoma actinoides* (Cestoda: Anoplocephalidae) parasitizes domestic and wild herbivores. Allen (1973) confirmed that *T. actinoides* requires two intermediate hosts. In his investigation he tried to infect sheep and goats directly by supplying egg capsules. Egg capsules were usually obtained from the intestinal contents of infected sheep or from rectal fecal samples. Allen (1973) discovered that some egg capsules were resistant to artificial gastric juice and would probably pass through the gastrointestinal tracts of mammals without releasing the oncospheres. Some of these were fed in-

tact while others were fed after having been mashed to release all or part of the oncospheres. Tapeworms did not appear in the final host so he collected invertebrates on range known or suspected to be infectious. These were: psocopterous insects, beetles, ants, grasshoppers, tyroglyphid mites, oribatid mites, also foot lice, sheep keds and biting lice. Previously he fed the egg capsules to invertebrates and ectoparasites. Although the eggs of the cestodes were ingested, no larval stages developed in those hosts. *T. actinoides* larvae developed and supported development of the larval stages only in psocid body cavities. Cysticercoids from psocids have the appearance of stages infective to a definitive host. Then he fed of these forms directly to tapeworm-free lambs. No tapeworm infections were produced in any of lambs (Allen 1959, 1973). Allen (1973) postulated that psocids in which they found the cestode larvae are the first intermediate hosts and that the obligate hosts are either other species of psocids or other groups of insects closely related phylogenetically to them.

Denegri *et al.* (2002) analyzed the role of oribatid mites as intermediate hosts of *T. actinoides*. They experimentally infected *Zygoribatula striassima* (Family: Oribatulidae) and *Oribatella spp.* (Family: Oribatellidae) with larval stages of *T. actinoides*. The percent of infected mites ranged from 1.3 to 7.3%. Cysticercoids found in oribatid mites were not completely developed and not infective due to the lack of primordial suckers (Denegri *et al.* 2002).

Oribatid mites are also the first intermediate host of Mesocestoididae family tapeworms. Cysticercoids, which are produced in oribatid mites, are ingested by the second intermediate host (small mammals, birds, reptiles, amphibians), where tetrathyridia are formed in the body cavity (Zaleśny and Hildebrand 2012; Cho *et al.* 2013; Tokiwa *et al.* 2014). Soldatova (1944) claimed to have successfully infected oribatid mites with tapeworm eggs of *Mesocestoides lineatus*, but did not have enough cysticercoids to complete the life cycle experimentally. Later Webster (1948), James (1968), Kugi (1983) tried to infect oribatid mites and other invertebrates with eggs of Mesocestoides. They attempted to determine the existence of the first intermediate host of

TABLE 2: List of the oribatid mites – intermediate host of tapeworm

| Cestoda species  | Intermediate host                             | Definite host           | reference                       |
|--|---|-------------------------|---------------------------------|
| <i>Anoplocephala manubriata</i><br>(Cestoda: Anoplocephalidae) | <i>Galumna flabellifera orientalis</i>        | elephants               | McAloon 2004                    |
|  | <i>Scheloribates latipes</i>                  |                         |                                 |
|  | <i>Scheloribates praecincisus</i>             |                         |                                 |
|  | <i>Protoribates seminudus</i>                 |                         |                                 |
|  | <i>Protoribates triangularis</i>              |                         |                                 |
| <i>Anoplocephala magna</i>                                     | <i>Scheloribates pallidulus</i>               | zebra                   | Schuster and Coetzee 2012       |
| <i>Anoplocephala perfoliata</i>                                | <i>Scheloribates</i> spp.                     | horses                  | Trowe 1997                      |
|  | <i>Scheloribates laevigatus</i>               |                         | Isoda <i>et al.</i> 1966        |
|  | <i>Scheloribates latipes</i>                  |                         | Schuster 1991                   |
| <i>Moniezia</i> spp.   | <i>Galumna flabellifera orientalis</i>        | domestic ruminants      | Haq 1981                        |
|  | <i>Scheloribates latipes</i> ,                |                         | Ismailov 1988                   |
|  | <i>Scheloribates laevigatus</i> ,             |                         |                                 |
|  | <i>Zygoribatula terricola</i> ,               |                         |                                 |
|  | <i>Zygoribatula cognate</i> ,                 |                         |                                 |
|  | <i>Pergalumna obvia</i>                       |                         |                                 |
|  | <i>Scheloribates praecincisus interruptus</i> |                         | Haq 1999                        |
|  | <i>Proxenillus pressulus</i>                  |                         | Watanabe <i>et al.</i> 1955     |
| <i>Moniezia benedeni</i>                                       | <i>Scheloribates laevigatus</i>               | cattle                  | Xiao and Herd 1992              |
|  | <i>Exoribatula</i> sp. Cf. <i>biundatus</i>   |                         |                                 |
|  | <i>Xylobates (Protoribates) capucinus</i>     |                         |                                 |
|  | <i>Zygoribatula undulata</i>                  |                         |                                 |
|  | <i>Galumna ithacensis</i>                     |                         |                                 |
|  | <i>Scheloribates lanceoliger</i>              |                         |                                 |
|  | <i>Oribatula sakamorii</i>                    |                         | Irie <i>et al.</i> 2013         |
|  | <i>Scheloribates</i> spp.                     |                         | Trowe 1997                      |
| <i>Moniezia expansa</i>  | <i>Scheloribates laevigatus</i>               | sheep                   | Xiao and Herd 1992              |
|  | <i>Scheloribates latipes</i>                  |                         | Schuster <i>et al.</i> 2000     |
|  | <i>Galumna racilis</i>                        |                         | Schuster 1995                   |
|  | <i>Kilimabates pilosus</i>                    |                         |                                 |
|  | <i>Kilimabates</i> sp.                        |                         |                                 |
|  | <i>Scheloribates fusifer</i>                  |                         |                                 |
|  | <i>Muliercula ngoyensis</i>                   |                         |                                 |
|  | <i>Zygoribatula undulata</i>                  |                         | Akrami <i>et al.</i> 2007       |
|  | <i>Ceratozetoidea</i> Immatures               |                         | Polec and Moskwa 1994           |
|  | <i>Scheloribates fimbriatus</i>               |                         | Trowe 1997                      |
|  | <i>Pergalumna nervosa</i>                     |                         | Denegri and Alzuet 1992         |
|  | <i>Ceratozetes</i> sp                         |                         | Denegri <i>et al.</i> 1983      |
|  | <i>Scheloribates</i> spp.                     |                         | Mazyad and El Garhy 2004        |
|  | <i>Zygoribatula lata</i>                      |                         |                                 |
|  | <i>Zygoribatula elongata</i>                  |                         |                                 |
|  | <i>Scheloribates zaherii</i>                  |                         |                                 |
|  | <i>Zygoribatula tadrosi</i>                   |                         |                                 |
|  | <i>Zygoribatula sayedi</i>                    |                         |                                 |
|  | <i>Oppiella nova</i>                          |                         |                                 |
|  | <i>Xylobates souchiensis</i>                  |                         |                                 |
| <i>Epilohmannia pallida aegyptiaca</i>                         |   |                         |                                 |
| <i>Moniezia sichuanensis</i>                                   | <i>Galumnoid</i> sp.                          | musk deer               | Yang <i>et al.</i> 2002         |
| <i>Moniezia</i> sp.  | <i>Scheloribates</i> sp.                      | sheep, cattle           | Lin <i>et al.</i> 1992          |
|  | <i>Scheloribates latipes</i>                  |                         |                                 |
| <i>Thysanezia giardii (Helicometra giardia)</i>                | <i>Zygoribatula lata</i>                      | sheep                   | Denegri and Alzuet 1992         |
|  | <i>Zygoribatula elongata</i>                  |                         | Denegri <i>et al.</i> 1983      |
| <i>Paranoplocephala mamillana</i>                              | <i>Scheloribates</i> spp.                     | small intestine, horses | Trowe 1997                      |
| <i>Vampirolepis asymmetrica</i> Cestoda:<br>Hymenolepididae    | <i>Ceratozetes garcilis</i>                   | voles                   | Murai 1989                      |
|  | <i>Achipteria coleoprata</i>                  |                         | Prokopič 1970, 1972             |
|  | <i>Scheloribates laevigatus</i>               |                         | Prokopič and Mauer 1969,        |
| Tapeworms of Anoplocephalide species                           | <i>Mixacarus exilis</i>                       |                         | Shimano and Kamimura 2005       |
|  | <i>Scheloribates laevigatus</i>               |                         |                                 |
|  | <i>Scheloribates zaheri</i>                   |                         | ElMehlawy 2009                  |
|  | <i>Zygoribatula undulate</i>                  |                         |                                 |
|  | <i>Zygoribatula niliaca</i>                   |                         | Žbikowska-Zdun and Koczara 2013 |
|  | <i>Galumna flabellifera</i>                   |                         |                                 |
|  | <i>Xylobates lophotricus</i>                  |                         |                                 |
|  | <i>Liebstadia similis</i>                     |                         |                                 |
|  | <i>Achipteria coleoprata</i>                  |                         |                                 |

Mesocestoides. Unfortunately, all studies were not successful.

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