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Review article

PATHOGENESIS AND BIOLOGY OF ANOPLOCEPHALINE CESTODES OF DOMESTIC ANIMALS

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Plan

Adult tapeworms parasitic in domestic herbivorous animals, exclusively belong to family Anoplocephalidae and are common in many countries. Yamaguti (1959) has recognized 23 species under seven genera in these hosts. This group has received good attention of helminthologists all over the world. Considerable literature has been accumulated since last few years and the need for a review article on the topic is felt necessary. In the present paper, literature on pathogenicity and biology of Anoplocephaline cestodes of domestic animals is reviewed and up-to-date bibliography available to the author is presented. Most of the Russian work was available only in the form of abstracts in English but original references are cited in the bibliography for the better use of readers.

Pathogenesis of Anoplocephaline cestodes

There is a wide divergence of opinion regarding the pathogenic effects of these tapeworms in cattle, sheep and goats. Hawkins (1946), Kates and Goldberg (1951) did not notice any observable injurious effects nor any significant retardation of growth in lambs heavily infected, experimentally with *Moniezia expansa*. Haematological studies by Deshpande *et al* (1980b) did not show any alteration in the values of haemoglobin, packed cell volumes and erythrocyte counts during prepatency of experimental monieziasis. But many of the Russian workers have noted high degree of pathogenicity, and adverse effects on weight gains and on yields of meat and wool. In lambs, Tableman (1946) recorded cases of convulsions and death and Hansen *et al* (1950) retarded weight gains and anaemia due to pure *Moniezia* infections.

Stampa (1967) found that in the lambs treated for *Moniezia sp* the weight gain was 109.8 g per day during first four weeks of age as against 69.4 g per day in untreated group. Afonina (1967) found weight gain of 10.2 kg in three months in treated lambs as against 4.2 kg in untreated ones.

Lyashenko and Teplov (1974) found that in sheep infected for three months, the wool yield per animal was less by 0.84 kg and meat yield by 4.11 kg as compared to uninfected sheep. They also recorded 43.5 % mortality in lambs due to monieziasis. Efner (1974) also found that the carcass yield in the infected Polish long wool sheep was less by 8.10 kg per carcass than in non-infected group.

In trials of anthelmintic treatment for monieziasis on several farms, Shakiev (1973) found that mortality rate was completely checked in treated farms while it remained at 3 and 0.8 % in lambs and ewes respectively of untreated farms. He further, noticed that wool yield was better and more lambs were born in treated farms.

In very extensive trials on 600 000 sheep, Vibe (1976) found that anthelmintic dosing against *Avitellina sp*, and *Moniezia sp*, brought down the mortality by 12.4 times. This also reduced mortality due to enterotoxaemia by 11.7 times thereby showing that high incidence of enterotoxaemia is associated with tapeworm infections in lambs.

The exact modes of pathogenicity in Anoplocephalines is still not fully known. The possibility of toxic effect of excretions and secretions of the parasite is indicated by Shakurova (1974) who showed that 50 to 150 mg of *M expansa* antigen injected intra-peritoneally into mice resulted in toxicity and death.

The injury caused to the intestinal mucosa also contributes to the pathogenicity as scolex of *M expansa* is burried deep into the mucosa (Casarosa 1964) and proliferative inflammation, nodulations, deeply inserted scolices, disquamation of epithelium and cellular infiltration in the jejunum is described in massive infections of *Stilesia globipunctata* (Bankov 1971, Amjadi 1971). Yet another explaination for the pathogenecity could be absorption of enormous amount of food by the parasite. Narsapur (1976c) found that during the period of 17 days (30th to 47th days) of prepatency in lambs *M expansa* grows from 2.2 to 195.0 cm in length and opined that for achieving such gigantic growth the parasite must be utilising enormous amount of food available in the intestine which otherwise would have been utilized by the host.

Soulsby (1982) concluded that light infections are of little importance and that as a rule only lambs, kids and calves under six months are substantially affected. However, from the evidence available it can reasonably be assumed that Anoplocephaline infections are of considerable economic importance for the animal industry.

Biology of Anoplocephaline cestodes

1.– *Developmental stages in oribatid hosts*

Moniezia expansa is known since 1810 as a common tapewormparasite of cattle, sheep and goats, but the knowledge regarding its life history and mode of transmission remained a mystery for a very long time. In 1890, Curtice, initiated serious studies in this direction and after a series of speculative experiments conducted by several research workers over a period of 47 years, the opinion had centered on the possibility of involvement of an intermediate host living on the pastures. The number of observations on epidemiology of *M expansa* made by Stoll (1935a, 1935b, 1936, 1937a, 1937b) contributed substantially to this belief although he himself did not appear to have been convinced then. It was Stunkard (1937a, 1937b) who made the epoch making discovery that an oribatid mite was the long searched intermediate host of *M expansa,* an anoplocephalid tapeworm.

The developmental process of *M expansa* in oribatid hosts together with morphology of stages has first been described by Stunkard (1938) followed by many workers. A general account that emerges out from these studies indicates that the pattern of development and morphology of larval stages is similar in all the species of Anolanoplocephaline cestodes. Oncosphere which is found in body cavity of mites within 48 h after their exposure to tapeworm eggs, undergoes a continuous

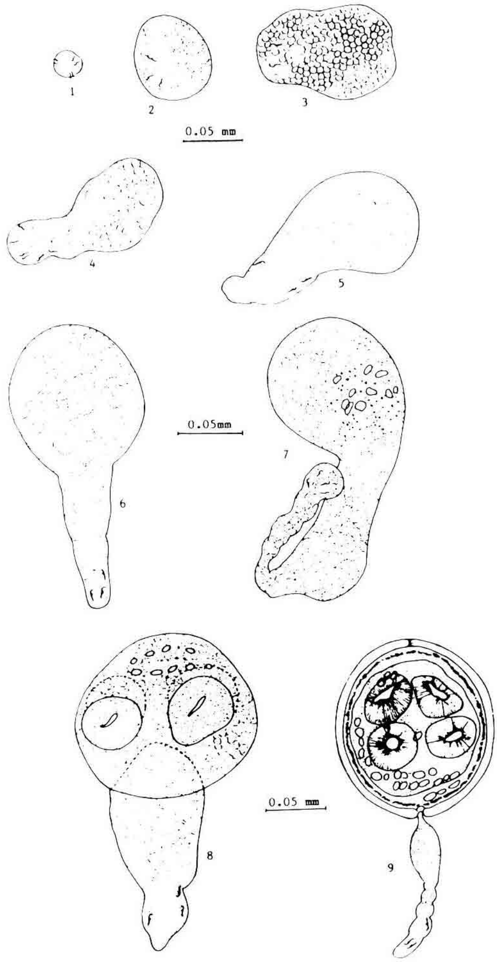

Fig 1. – Camera lucida drawings of developmental stages of *Moniezia expansa* in *Scheloribates laevigatus.*

1 : oncosphere
2, 3 : oblong stage
4, 5 : elongate stage
6 : stage with body and cermomere
7, 8 : stage with scolex, body and cercomere
9 : cysticercoid

process of development without any abrupt changes in their morphology demarcating different stages. However, following six morphological stages can be recognized before the infective stage (ie cysticercoid) is reached (Narsapur 1976c) (fig 1) :

1. Oncosphere : 22.9 μ × 21.3 μ in size with well arranged six embryonal hooks each 7.18 μ in length.

2. Oblong stage : 103 μ × 79.33 μ in size with embryonal hooks irregularly arranged.

3. Elongate stage : 158.3 μ in length, wider at (84.6 μ) one end and narrow at the other.

4. Stage with body and cercomere : body is subspherical, measures 134.6 μ × 100 μ and bears tail like cercomere 100 μ in length. Few embryonal hooks present on the tail.

5. Stage with scolex body and cercomere : the body it further devided by transverse constriction to anterior and middle parts with cercomere remaining as posterior part. At the anterior part there is accumulation of calcareous bodies and aggregation of cells indicating developing suckers. Few embryonal hooks may still be present on the tail.

6. Cysticercoid : the stage results by retraction of anterior part (scolex) into the middle part with sides closing on to from cyst wall. After slight shrinkage, the cyst wall becomes rigid. Cercomere persists as an appendage with few embryonal hooks still present. The scolex exhibits active movements.

The size of cysticercoid is subject to great variation depending upon the number of cysticercoids in the body cavity of the mite. Thus Narsapur (1976c) found smaller (110 × 100 μ) cysticercoids of *M expansa* in mites bearing many number and larger (175 × 140 μ) ones in mites bearing a single cysticercoid.

The position of embryonal hooks on different stages shows that there is a reversal of antero-posterior axis of the larvae as it transforms from oncosphere to cysticercoid (Stunkard 1938, 1941, Narsapur 1971).

Narsapur (1976c) further observed that *M expansa* oncospheres remained dormant in the body cavity of the mites up to 12 days after infection and the development then on started at a very uneven pace, so that during this phase larvae under various stages of development were present in the body cavity of the same mite. He cited that in a mite dissected after 57 days of the infection, all the stages from oncosphere to cysticercoid were found. Similar observations have been made earlier by Stunkard (1938, 1940, 1941), Anantaraman (1951) and Freeman (1952) with regard to different species of Anoplocephalines. Stunkard (1941) opined that this was due to influencing factors such as mite vector, number of larvae in haemocoel, age and development of larvae. Freeman (1952) stated that as most of the mites in experimental condition pick up the infection within 24 to 48 h, the above variations cannot be attributed to delayed pick up of the infection by mites.

It therefore appears, that more than anything else, larvae in the body cavity themselves exert a suppressive effect on each other, which triggers uneven development and it further accentuates as larvae in advanced stage exert more and more suppressive effect on less advanced larvae. Some of these suppressed larvae might reach cysticercoid stage belatedly and many of them die out as is shown in experimental infection with *M expansa* by Narsapur (1976c) that mites dissected on 30 th day revealed 0.2 to 0.3 cysticercoids per mite along with many earlier stages while the same batches dissected on 57th day revealed 2.2 to 7.0 cysticercoids per mite unaccompanied by earlier stages.

2. *Developmental conditions*

The developmental period in oribatid hosts varies greatly and this appears to be mainly, inversely influenced by temperature conditions, although, Stunkard (1938) mentions the mite species as an additional factor. The development of oncospheres in cysticercoids is performed in the best conditions at 25 °C. At this optimum the formation of infesting larvae is achieved in three months (Euzeby 1966). In warmer countries (between 27 and 33 °C) the development is accelerated, that is about from one to three months. In colder countries (between 18 and 20 °C) evolution in oribatids is slower and needs about from three to five months (refer tables 1a, 1b). However, the prepatent period in vertebrate hosts appears to be rather uniform as 45 ± 7 days in *Moniezia sp* is reported by many workers (Shorb 1939, Anantaraman 1951, Potemkina 1951, Mehra and Srivastava 1955 a b, Kuznetsov 1968, Davydov and Smirnov 1972, Alkov 1971, 1972, Gapon 1974, Worley *et al* 1974, Narsapur 1976c, Kramnoi 1980).

A patent period of 154 days (Kuznetsov 1968), 132 to 256 days (Davydov and Smirnov 1972) have been reported in case of *M expansa* but spontaneous expulsion of the infection due to acquisition of immunity (self-cure) takes place within two to three months of patency which explains why infection in lambs occur at two to five months and is rare after six months of age (Worley *et al* 1974, Gapon 1974, Lin *et al* 1975).

Oribatid intermediate hosts

1. *Species of oribatids as intermediate host*

There are many reports published from different

Tableau 1a – Summary of literature of relationship between temperature and developmental period of *Moniezia expansa*

Intermediate host Period of development (days)	Temperature (°C)	Reference
Scheloribates laevigatus		
27	28 a	Narsapur and Prokopic (1979)
45	20	Skorski *et al* (1984)
49-57	27-33	Narsapur (1976c)
75	27	Kuznetsov (1970)
97	18-20 a	Narsapur and Prokopic (1979)
150	18-20 b	Jurasek (1962)
Scheloribates latipes		
27	28 a	Narsapur and Prokopic (1979)
77-79	27	Nazarova (1970)
85-98	23	Nazarova (1970)
97	18-20 a	Narsapur and Prokopic (1979)
Scheloribates fimbriatus		
49-57	27-33	Narsapur (1976c)
Scheloribates semidesertus		
77-79	27	Nazarova (1970)
85-98	23	Nazarova (1970)
Galumna sp		
150	18-20 b	Jurasek (1962)
Pilogalumna tenuiclavus		
92	20	Skorski (1984)
Archipteria sp		
150	18-20 b	Jurasek (1962)
Platinothrus peltifer		
27	28 a	Narsapur and Prokopic (1979)
97	18-20 a	Narsapur and Prokopic (1979)
Liacarus sp		
150	18-20 b	Jurasek (1962)
Liacarus coracinus		
27	28 b	Narsapur and Prokopic (1979)
97	18-20 b	Narsapur and Prokopic (1979)
Leibstadia similis		
35	20	Skorski *et al* (1984)
65	27	Skorski *et al* (1984)

a: at 85 % of humidity
b: at 100 % of humidity

countries on the oribatid intermediate hosts of Anaplocephalids and the list is growing continuously. The present position is that 53 species of oribatids are listed as intermediate hosts of *M expansa* and 31 for *M benedeni*.

Information on *Avitellina sp* is very scanty because many experimental infections have ended in failure due to peculiarities in the morphology of the uterus of this cestode (Matevosyan 1978). However, Kuznetsov (1965, 1966) experimentally infected adults and larvae of insects of the order *Psocoptera viz, Lachesilla pedicularia* and *L pedicularia* var *brevipenis* with *Avitellina sp* and obtained cysticercoids. Nadakal (1960a, 1960b) exposed thousands of Protoschelobates sp to infection of *Avitellina centripunctata* and obtained oncospheres in only five of them. Narsapur (1974b) successfully infected *Scheloribates laevigatus* and *S fimbriatus* to eggs of *Avitellina lahorea* and found cysticercoids, on 50th and 57th days. In *S laevigatus*, 3 of 91 mites and in *S fimbriatus* 3 of 158 mites showed larval development, with one cysticercoid per mite.

Tableau 1b – Summary of literature of relationship between temperature and developmental period of *Moniezia benedeni*

Intermediate host Period of development (days)	Temperature (°C)	Reference
Scheloribates laevigatus		
87	12-26	Kramnoi (1973)
150	18-20	Prokopic (1962a)
Scheloribates latipes		
34	28 a	Prokopic and Narsapur (1981)
77-79	27	Nazarova (1970)
85-98	23	Nazarova (1970)
87	12-26	Kramnoi (1973)
Scheloribates semidesertus		
77-79	27	Nazarova (1970)
85-98	23	Nazarova (1970)
Galumna eliminata		
150	18-20	Prokopic (1962a)
Trichoribates trimaculatus		
150	18-20	Prokopic (1962a)
Trichoribates novus		
34	28 a	Prokopic and Narsapur (1981)
Ceratozetes sp		
87	12-26	Kramnoi (1973)
Punctoribates punctum		
87	12-26	Kramnoi (1973)
Archipteria coleoptera		
150	18-20	Prokopic (1962b)
Zygoribatula skrjabini		
77-79	27	Nazarova (1970)
85-98	23	Nazarova (1970)
Patinothrus peltifer		
34	28 a	Narsapur and Prokopic (1981)
Oribatula sp		
162	17-20	Cai and Jin (1984)

a: at 85 % of humidity

Psocopteran insects are intermediate hosts also for *Thysaniezia sp* (Allen 1959, Kuznetsov 1965, 1966) in addition to seven species of oribatids, seven species of oribatid mites are reported intermediate hosts of *Stilesia globipuncta* two species of *Anoplocephala magna*, 18 of *A perfoliata*, 6 of *Paranoplocephala variabilis*, 4 of *P ryjikovi* and 2 of *P manilana*, in many of the papers the parasites and their hosts are mentioned only by generic name or by family name and these have not been included in the present list.

Apart from the adult stages of oribatids, the possibility of involvement of their juvenile stages in the transmission of tapeworms was investigated by Narsapur (1979). He found that the nymphal stage of oribatids pick up the tapeworm infection in the same way as adults and that the tapeworm larvae survive the moult in the body of juvenile oribatids reaching cysticercoid stage by the time juvenile become adult oribatids. This has significance in the epizootology since juvenile oribatids occur abundantly on pastures during prepeak seasons of oribatid mite populations.

2. *Oribatid host specificity*

In view of the growing list of oribatid species reported as intermediate hosts of anoplocephalids, two divergent views existed on the oribatid host

Table 2a – Summary of literature on *Scheloribates* as intermediate hosts of *Moniezia expansa* in different countries

Intermediate host Country	References
Scheloribates laevigatus	
USSR	Potemkina (1941)
USA	Kates and Runkel (1948)
Canada	Rao and Choquette (1951)
USSR	Orhekov (1960)
USSR	Sokolova ans Panin (1960)
Czekoslovakia	Prokopic (1962a)
Czekoslavakia	Jurasek (1962)
Bulgaria	Bankov (1965)
USSR	Alkov (1971)
China	Lin *et al* (1975)
India	Narsapur (1976c)
Czekoslovakia	Narsapur and Prokopic (1979)
GFR	Skorski *et al* (1984)
USSR	Kuznetsov (1970)
Scheloribates latipes	
USSR	Potemkina (1948)
USSR	Orekov (1960)
Czekoslovakia	Prokopic (1962)
USSR	Nazarova (1970)
USSR	Alkov (1971)
Czekoslovakia	Narsapur and Prokopic (1979)
Scherolibates pallidulus	
Bulgaria	Bankov (1965)
Scherolibates fimbriatus africanus	
Chad	Graber and Gruvel (1969)
Scheloribates fimbriatus	
India	Narsapur (1976c)
Scheloribates perforatus	
Chad	Graber and Gruvel (1969)
Scheloribates madrasensis	
India	Anantaraman (1951)
Scheloribates semidesertus	
USSR	Nazarova (1970)
Scheloribates chauhani	
China	Lin *et al* (1975)
Scheloribates sp	
Hungary	Kassai and Mahunka (1965)

specificity since long time. Kates and Runkel (1948), Potemkina (1951) considered that susceptibility of different species of mites varied greatly but Kassai and Mahunka (1964, 1965) believed that there was no high degree of host specificity in different oribatids and that any species larger than 300 to 400 microns in length had the ability of acting as intermediate host. However, the scanning of world literature (table 2a, 2b, 2c, 3a, 3b, 3c) shows that *Scheloribates sp* followed by *Galumna sp* have been more often incriminated as intermediate hosts of *M expansa* and *M benedeni* in several countries and by this fact alone they could be more specific intermediate hosts of the two tapeworms than other species of oribatid mites. Intermediate hosts of *Avitellina sp, Stilesia globipunctata* and *Thysaniezia* reported in several countries have been summarised in tables 4 and 5.

Intermediate hosts of *Anoplocephala perfoliata*, observed in USSR, are : *Galumna obvius, Galumna nervosus, Scheloribates laevigatus, Scheloribates latipes, Carbodidae, Archipteria sp, Liacaridae, Platinothrus pelfiter, Hermaniella granulata, Eremaeus oblongus, Parachipteria punctata, Ceratozetes bulanovae, Trichoribates incisellus, Galumna diforma, Urubambates schachtachtiaskoi, Zygoribatula*

Table 2b – Summary of literature on *Protoschelobates* and *Galumna* as intermediate hosts of *Moniezia expansa* in different countries

Intermediate host Country	References
Protoschelobates sp	
India	Nadakal (1960)
Protoschelobates seghettii	
USA	Runkel and Kates (1947)
Protoschelobates curtilipes	
USA	Runkel and Kates (1947)
Galumna sp	
USA	Stoll (1938)
USA	Stunkard (1937, 1938)
India	Anantaraman (1951)
Czekoslovakia	Jurasek (1962)
Bulgaria	Bankov (1965)
USSR	Alkov (1971)
Galumna elimata	
Czekoslovakia	Prokopic (1962a)
Galumna nigra	
USA	Stoll (1938)
Galumna obvia	
USSR	Potemkina (1941)
USSR	Alkov (1971)
Galumna longipluma	
China	Lin *et al* (1975)
Galumna virginiensis	
USA	Kates and Runkel (1948)
USA	Edney and Kelly (1953)
China	Lin *et al* (1975)
Galumna curvum	
China	Lin *et al* (1975)
Galumna emarginata	
USA	Krull (1939)
USA	Kates and Runkel (1948)
Galumna flagellata	
USSR	Orekhov (1960)
Galumna type minor	
USSR	Orekhov (1960)

tenicola, Zygoribatula microporosa, Leibstadia similis, and four unspecified oribatid mites (Bashkirova 1941, Kuliev 1963, Urmanbetova 1979).

Intermediate hosts of *Anoplocephala magna,* observed in USSR, are : *Scheloribates laevigatus, Scheloribates latipes* and four unspecified oribatid mites (Bashkirova 1941, Urmanbetova 1979).

Intermediate hosts of *Paranoplocephala mamillana,* observed in URSS, are : *Galumna obvius* and *Allogalumna longipluma* (Bashkirova 1941).

Intermediate hosts of *Paranoplocephala variabilis* are : *Galumna sp, Galumna curvum, Galumna virginiensis, Scheloribates laevigatus, Oribatella quadricarnata* and *Platynothrus peltifer* (Gleason and Buckner 1979).

Intermediate hosts of *Paranoplocephala ryjikovi,* observed in China, are : *Scheloribates chauhani, Galumna virginiensis, Scheloribates sp* and *Parakalumna lydia* (Lin *et al* 1982).

Two criteria viz percentage of mites infected and

Table 2c – Summary of literature on *Pergalumna, Pilogalumna, Scutovetex, Oribatula, Ceratozetes, Trichoribates, Punctoribates* and *Protoribates* as intermediate hosts of *Moniezia expansa* in different countries.

Intermediate host Country	References
Pergalumna nervosa	
Bulgaria	Bankov (1961)
Pergalumna sp	
Hungary	Kassai and Mahunka (1965)
Pilogalumna tenuiclavus	
GFR	Skorski (1984)
Scutovetex minutus	
UK UK	Morgan (1947) Rayski (1947)
Oribatula minuta	
USA	Kates and Runkel (1948)
Ceratozetes mediocris	
Hungary	Kassai and Mahunka (1965)
Trichoribates trimaculatus	
Czekoslovakia USSR	Prokopic (1962) Alkov (1971)
Trichoribates novus	
Bulgaria	Bankov (1965)
Trichoribates incisellus	
USSR	Alkov (1971)
Punctoribates sp	
USSR	Potemkina (1951)
Punctoribates punctum	
Bulgaria USSR	Bankov (1965) Alkov (1971)
Punctoribates hexagonus	
USSR	Sokolova and Panin (1960)
Protoribates lophotrichus	
USSR	Rukarina *et al* (1960)

average number of cysticercoids per mite could be applied to either naturally infected mites or to the experimentally exposed ones to determine relative host specificity. Narsapur (1976a) compared the performances of *S laevigatus* and *S fimbriatus* by these criteria after exposing them to uniform suspension of the eggs of *M expansa* and *M benedeni* and found that for *M expansa, S laevigatus* was more specific intermediate host than *S fimbriatus* and for *M benedeni* it was reverse.

Thus, in the epidemiological consideration of Anoplocephaline infections, it is necessary to recognize the variations in the host specificity of oribatid mites and determine the predominant and highly host specific oribatid species occuring in the area. In general, it may be said that wherever, *Scheloribates sp* and *Galumna sp* predominate in the soil, the area is vulnerable for outbreaks of Anoplocephaline infections.

3. *Alternative intermediate hosts*

Since the discovery of life cycle of *Moniezia expansa* by Stunkard in 1937a, a large number of papers have been published on the biology of Anoplocephalid tapeworms from which two generalizations can be made viz

Table 2d – Summary of literature on *Archipteria, Adoristus, Platynothrus, Eremaeus, Ceratoppia, Liacarus, Peloptulus, Unguizetes, Zygoribatula, Leibstadia, Hypozetes* and *Spatiodaemaeus* as intermediate hosts of *Moniezia expansa* in different countries

Intermediate host Country	References
Archipteria sp	
USSR	Potemkina (1951)
Czekoslovakia	Jurasek (1962)
Archipteria coleoptera	
Czekoslovakia	Prokopic (1962b)
Adoristus ovatus	
USSR	Potemkina (1951)
Platynothrus peltifer	
USSR	Shaldibina (1953)
Czekoslovakia	Narsapur and Prokopic (1979)
Eremaeus hepaticus	
USSR	Shaldibina (1953)
Ceratoppia bipitis	
USSR	Shaldibina (1953)
Liacarus sp	
Czekoslovakia	Jurasek (1962)
Liacarus coracinus	
Czekoslovakia	Prokopic (1967)
Czekoslovakia	Nasarpur and Prokopic (1979)
Peloptulus phaenotus	
Bulgaria	Bankov (1965)
Unguizetes reticularis	
Chad	Graber and Gruvel (1969)
Zygoribatula exarata	
Hungary	Kassai and Mahunka (1965)
Zygoribatula lata	
Argentina	Yanavella (1971)
Zygoribatula skrjabini	
USSR	Ilyasov (1970)
USSR	Nazarova (1970)
Leibstadia similis	
GFR	Skorski *et al* (1984)
Hypozetes sp	
India	Deshpande *et al* (1980)
Spatiodaemaeus subverticulipes	
USSR	Alkov (1972)

Table 3a – Summary of literature on *Scheloribates* and *Protoschelobates sp* as intermediate hosts of *Moniezia benedeni* in different countries

Intermediate host country	References
Scheloribates laevigatus	
USSR	Potemkina (1944a)
Czekoslovakia	Prokopic (1962a)
Bulgaria	Bankov (1965)
USSR	Kuznetsov (1970)
USSR	Alkov (1971)
USSR	Kramnoi (1973)
India	Narsapur (1976b)
Czekoslovakia	Prokopic and Narsapur (1978)
Scheloribates latipes	
USSR	Potemkina (1951)
Czekoslovakia	Prokopic (1962a)
USSR	Nazarova (1970)
USSR	Alkov (1971)
USSR	Kramnoi (1973)
USSR	Abkev (1976)
Czekoslovakia	Prokopic and Narsapur (1978)
Scheloribates semidesertus	
USSR	Nazarova (1970)
Scheloribates fimbriatus	
USSR	Nazarova (1970)
India	Narsapur (1976b)
Scheloribates madrasensis	
India	Anantaraman (1951)
Scheloribates sp	
China	Cai and Jin (1984)
Protoschelobates	
India	Nadakal (1960)

(1) oribatid mites are the intermediate hosts of only Anoplocephalids and

(2) Anoplocephalids are almost exclusively transmitted by oribatid mites.

However, certain exceptions are reported for both. Prokopic (1962b) showed that *Rodentolepis straminea* (Hymenolepidoidea) can also develop in *Achipteria coleoptera*, an oribatid mite.

Involvement of insects of the order Psocoptera in the life cycle of an anoplocephalid tapeworm viz *Thysaniezia actinoides* was reported for the first time by Allen (1959) which was later confirmed in respect of *Thysaniezia sp* and *Avitellina sp* by Kuznetsov (1963, 1965, 1966)).

In case of *Oochoristica osheroffi*, an anoplocephalid tapeworm of rattle snakes, flour beetles (*Tribolium confusum*) migratory grass hoppers (*Conozoa wallula*), and two striped grass hoppers (*Melonoplus bivittatus*) have been shown to be intermediate hosts (Widmer and Oken 1967).

Recently Fritz (1985) again went into the question of alternative intermediate hosts of *M expansa* and reported an interesting finding that larvae of fire ants *Solenopsis invicta* readily fed on eggs of *M expansa* and showed oncospheres in the gut. It therefore appears that although the above made generalizations hold good in much part, the question of alternative intermediate hosts of Anoplocephalines in different biotopes is still open for curious investigations.

Biological phenomena in nature

Some interesting observations have been made regarding mode of infection of mites in nature. According to Krull (1939), mites cannot ingest the tapeworm eggs entirely but make hole in the shell and suck the contents during which hexacanth embryo is taken in.

Stunkard (1938) considered that mites feed on tapeworm eggs purely incidentally or accidentally. The eggs of *Moniezia* survive only for few hours (4 to 12) on pasture and few (nine) days in sheep faeces as noted by Kuznetsov (1959) in Volga

Table 3b – Summary of literature on *Galumna, Trichoribates, Ceratozetes, Punctoribates* and *Archipteria* as intermediate hosts of *Moniezia benedeni* in different countries

Intermediate host Country	References
Galumna sp	
India	Anantaraman (1951)
USSR	Alkov (1971)
Galumna elimata	
Czekoslovakia	Prokopic (1962a)
Galumna obvia	
USSR	Potemkina (1944)
USSR	Alkov (1971)
Galumna nervosus	
USSR	Potemkina (1951)
Trichoribates sp	
USSR	Potemkina (1951)
Trichoribates trimaculatus	
Czekoslovakia	Prokopic (1962a)
USSR	Alkov (1971)
Trichoribates incisellus	
USSR	Alkov (1971)
Trichoribates novus	
Cezkoslovakia	Prokopic and Narsapur (1981)
Ceratozetes mediocris	
Hungary	Kassai and Mahunka (1965)
Ceratozetes sp	
USSR	Kramnoi (1973)
Punctoribates sp	
USSR	Potemkina (1951)
Punctoribates punctum	
USSR	Alkov (1971)
USSR	Kramnoi (1973)
Archipteria sp	
USSR	Potemkina (1951)
USSR	Akbev (1976)
Archipteria coleoptera	
Czekoslovakia	Prokopic (1962b)

region of USSR. This period might be still shorter in tropics.

Kozlov and Tikhomirova (1979) state that oribatid mites in fact avoid fresh cattle faeces for 1.5 to 2 weeks which is best time for infection with Anoplocephalines. However, they explain, coprophagous beetles invade fresh faeces almost immediately and proceed to bury it. The infective material is taken into the ground where it is protected from rapid dessication and where it is brought in contact with oribatid host. The observations by Fritz (1985) indicate that fire ants *Solenopisis invicta* also help in disseminating and preserving the tapeworm eggs in the soil.

Under natural conditions, on heavily contaminated pasture the mites are exposed to heavy concentration of tapeworm eggs, but the percentage of infected mites in nature as reported by different

Table 3c – Summary of literature on *Adoristus, Liacarus, Spatiodaemeus, Platynothrus, Oribatula* and *Zygoribatula* as intermediate hosts of *Moniezia benedeni* in different countries

Intermediate host Country	References
Adoristus ovatus	
USSR	Potemkina (1951)
Liacarus coracinus	
Czechoslovakia	Prokopic (1967)
Spatiodaemeus subverticillipes	
USSR	Alkov (1971)
Platinothrus peltifer	
USSR	Alkov (1971)
Czekoslovakia	Prokopic and Narsapur (1981)
Oribatula sp	
China	Cai and Jin (1984)
Zygoribatula longiporosa	
Australia	Roberts (1953)
USSR	Sokolova and Panin (1960)
Zygoribatula frisiae	
USSR	Sokolova (1958)
USSR	Sokolova and Panin (1960)
Zygoribatula cognata	
USSR	Sokolova and Panin (1960)
Zygoribatula exarata	
Hungary	Kassai and Mahunka (1965)
Zygoribatula skrjabini	
USSR	Ilyasov (1970)
USSR	Nazarova (1970)

workers is between 0.05 % to 2.0 % and rarely up to 5 % (Prokopic 1962a, Lin *et al* 1975, 1983). This might be due to heavy mortality in mites resulting from infection of tapeworm eggs as noted by Potemkina (1944a) and Prokopic (1962a). Interestingly enought the hexacanth embryos arrest the reproduction of mites and make them sterile (Kramnoi 1978). Thus, to some extent, tapeworm infection in grazing animals paradoxically limits the oribatid mite population on the pastures.

In the final host, only a few number (3 to 4 %) of the ingested cysticercoids reach the adult stage (Narsapur 1976c). Thus, it is likely that heavy tapeworm infections encountered in animals are the result not of a single heavy exposure but of continuous pick up over a longer period. In the latter process the percentage of cysticercoids developing to adult parasite in final host is likely to be still low as immunological responses of the host are coming into play. It therefore stands to reason that, heavy infections with Anoplocephaline cestodes occur only in certain circumstances viz (1) in the seasons when oribatid mite population, particularly of *Scheloribates sp* and *Galumna sp* is high in nature and (2) over crowding of the pastures with infected animals in this season. Hence, anthelminthic treatment of the herd or flock at the time corresponding to the beginning of prepaek periods of oribatid mite population would therefore be a suitable strategy to control Anoplocephaline tapeworm infections as postulated by Narsapur (1977).

Conclusions

Anoplocephaline cestodes have been conclusively shown to adversly affect the growth, production and resistance of the animals. Since 1938, very extensive literature has appeared on the biology of these tapeworms. The larval development in the

Table 4 – Summary of literature on intermediate hosts of *Avitellina* and *Stilesia* in different countries

Intermidiate host Country	References
Avitellina sp	
Lachisella pedicularia (Psocoptera : Insecta)	
USSR	Kuznetsov (1965, 1966)
Lachisella pedicularia var *brevipenis* (Psocoptera : Insecta)	
USSR	Kuznetsov (1965, 1966)
Scheloribates laevigatus	
India	Narsapur (1976)
Scheloribates fimbriatus	
India	Narsapur (1976)
Stilesia globipunctata	
Scheloribates indica	
India	Tandon (1963)
Scheloribates perforatus	
Chad	Graber and Gruvel (1967)
Scheloribates conglobatus	
Chad	Graber and Gruvel (1967)
Scherolibates fimbriatus africanus	
Chad	Graber and Gruvel (1967)
Galumna pellucida	
Chad	Graber and Gruvel (1967)
Africacarus calcaratus	
Chad	Graber and Gruvel (1967)
Erythraeus sp	
India	Tandon (1963)

body cavities of oribatid mite hosts is influenced by the species of the mite, intensity of infection and the environmental temperature.

All over the world, 53 species of oribatid mites have been shown to be intermediate hosts of *Moniezia expansa*, 31 of *M benedeni*, 2 of *Avitellina sp*, 7 of *Thysaniezia sp*, 7 of *Stilesia globipunctata*, 2 of *Anoplocephala magna*, 4 of *P ryjukovi* and 2 of *P mamillana*.

A degree of host specificity has been demonstrated between the species of mites and tapeworms. *Scheloribates sp* and *Galumna sp* have been more often incriminated in several countries as intermediate hosts of common Anoplocephalines and hence can be considered highly specific intermediate hosts.

Nymphal stages of oribatids can also be infected and the tapeworm larvae survive moults in their body cavities which adds to the dimensions of tapeworm epidemiology.

The question of alternate intermediate hosts is still fascinating as it is known that in case of some species, intermediate hosts other than oribatid mites are involved. The direct or indirect role of other creatures like beetles, ants, grasshoppers, etc... in the spread of Anoplocephalines has once again drawn the attention of researchers.

The immune expulsion phenomenon is another area that needs more elucidation and strategic treatment for control, more field trials.

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Table 5 – Summary of literature on intermediate hosts of *Thysaniezia* in different countries

Intermediate host Country	References
	Thysaniezia sp
Lachisella pedicularia (Psocoptera : Insecta	
USSR	Kuznetsov (1965, 1966)
Lachisella Pedicularia var brevipenis	
USSR	Kuznetsov (1965, 1966)
	Thysaniezia giardi
Zygoribatula Skrjabini	
USSR	Iliasov (1970)
	Thysaniezia ovilla
Scheloribates laevigatus	
USSR	Potemkina (1944b, 1951)
Scheloribates latipes	
USSR	Potemkina (1944b, 1951)
Trichoribates sp	
USSR	Potemkina (1944b, 1951)
Galumna obvious	
USSR	Potemkina (1944b, 1951)
Adoristus ovatus	
USSR	Potemkina (1944b, 1951)
Phthiracarus	
USSR	Potemkina (1944b, 1951)

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