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HELMINTHS OF MICROTINAE IN WESTERN MONTANA

by

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A.B. Bellarmine College, 1963

Presented in partial fulfillment of the requirements for the degree of

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1966

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INTRODUCTION

The parasites of native North American mice have been much neglected in the past despite the economic and ecological importance of these rodents. Much of the literature in this field consists of scattered lists of parasites from various heterogeneous collections of rodents and isolated descriptions of new species. In only a few instances has a particular group been selectively and comprehensively surveyed for parasites.

Members of the subfamily Microtinae are of particular interest because of their wide geographical distribution and interesting population behavior. The cyclic fluctuations of vole and lemming populations in relation to their effect on agriculture have long been observed. The classical work in North America in this field was done on Microtus pennsylvanicus by Hamilton (1937, 1941). The effect of these fluctuations on host-parasite relations and vice-versa is still poorly understood.

Of the genera of microtine rodents having a Holarctic distribution, the parasitic helminths of Dicrostonyx, Lemmus, Clethrionomys and some species of Microtus are relatively well-known. These helminths demonstrate a highly developed subfamily specificity, being restricted essentially to the Microtinae, but few show any host specificity at the specific or generic level (Rausch, 1957). The first extensive work on microtine helminths was reported by Rausch and Tiner in 1949. They examined over 600 voles of two species, Microtus pennsylvanicus and

M. ochrogaster, in the north central United States. For many helminths recovered they noted apparent seasonal fluctuations and host habitat correlations. Kuns and Rausch (1950) did a similar type of study on four species of voles from the Jackson Hole region in Wyoming. They examined a total of 103 specimens of M. pennsylvanicus, M. montanus, M. longicaudus, and M. richardsoni, described two new helminth species and related the presence of the parasites to host habitat, particularly with respect to altitude, moisture, and vegetation.

Rausch (1952b) surveyed the helminth fauna of voles and lemmings in Alaska, examining 2078 hosts representing 26 species and subspecies. Of the 26, only two (M. pennsylvanicus, M. longicaudus) are found to any large extent south of Canada. Relatively few specimens (35) of these two species were examined. His article offers a valuable summary of the taxonomic status of the species of helminths known up to that time in microtines.

The helminth parasites of members of the families Cricetidae and Zapodidae were surveyed in Quebec and Labrador by Schad (1954). Included in this study were 196 microtines of the genera Synaptomys, Dicrostonyx, Clethrionomys, and Microtus. The taxonomy of several parasites was considered. Murray (1964), in an unpublished Master's thesis, studied helminths of Cricetidae in Alberta, concentrating on the species Clethrionomys gapperi and C. rutilus in an attempt to clarify the evolutionary relationships of their parasites. No conclusive evolutionary evidence was found but several new host records were discovered. These few papers constitute the major work done on helminths of microtines in North America. The remainder of the distributional

records appear in numerous, less comprehensive reports.

In view of the extensive surveys by Rausch and others to the north and south of Montana, it seemed of interest to carry out a similar study here for purposes of comparison. Included in this study were Microtus pennsylvanicus, M. montanus, M. longicaudus, Clethrionomys gapperi, and Phenacomys intermedius. Two other voles, ecologically more limited in western Montana, M. richardsoni and Lagurus curtatus, were not examined. A summary of the scattered and fragmentary literature on helminths of the first five species is compiled in the Appendix. Of invaluable aid in this work was the catalogue of Doran (1954, 1955) on rodent parasites.

METHODS AND MATERIALS

Most of the 136 microtine hosts included in this study were collected between October 5, 1964, and December 10, 1965, from ten areas in western Montana. One adjacent Idaho collection was made and two additional specimens from Wyoming borrowed. In addition, comparative material was borrowed from the Rocky Mountain Laboratory in Hamilton, Montana, consisting of helminths collected by Miss Betty Locker from voles in 1951 and 1952 from Ravalli and Lake Counties. The locations of the collection areas follow:

Pattee Canyon (U. S. Forest Service Map Coordinates: R19W, T12N, Sec. 11); el. 4000 feet. This area included dense yellow pine-Douglas-fir forest and more open brush along two small tributaries of Pattee Creek.

Miller Creek (R20W, T12N, Sec. 13); el. 3000 feet. Although this area may be described generally as open, dry prairie, collections were made only from haystacks in dry hayfields at some distance from the creek bed.

Buckhouse Bridge (R20W, T12N, Sec. 13); el. 3000 feet. Trapping here was confined to an open wet meadow surrounding two small ponds.

Rattlesnake Creek (R18W, T14N, Sec. 19); el. 3500 feet. Trapping was done among shrubs and wet grass along a large swift-flowing stream.

O'Brien Creek (R20W, T13N, Sec. 34); el. 3000 feet. Voles were

obtained here in grass near the junction of the creek and the Bitterroot River.

Fort Missoula (R20W, T13N, Sec. 25); el. 3000 feet. The collection area was an open dry field near the State Forest Nursery.

Lubrecht Experimental Forest (R15W, T13N, Sec. 11); el. 3500 feet.

Trapping areas included dense, moist yellow pine-Douglas-fir forest and more open, dry forest in the same vicinity.

National Bison Range (R21W, T18N, Sec. 10); el. 3000 feet. Trapping was done in open, dry prairie. Two frozen specimens from the University of Montana Zoology Museum, trapped in the same area in April, 1963, were examined.

Lolo and Stevensville, upper Bitterroot Valley (R20W, T11N, Sec. 23) (R20W, T9N, Sec. 15); el. 3000 feet. These areas were very similar, consisting of wet marsh surrounding cat-tail ponds.

Horse Creek, Lemhi County, Idaho (R18E, T4S, Sec. 18); el. 7000 feet. Specimens were obtained in wet grass along the bank of the creek in a yellow pine-Douglas-fir forest.

Lolo Peak (R23W, T11N, Sec. 25); el. 9000 feet. One specimen, trapped along a mountain stream in a sub-alpine Douglas-fir forest, was borrowed from Ronald K. Plakke, University of Montana.

Beartooth Plateau, Park County, Wyoming (R104W, T58N, Sec. 31); el. 10,500 feet. Two specimens, trapped in a wet alpine meadow in June, 1964, were borrowed from Donald L. Pattie, Pacific Lutheran University.

Box-type live traps, constructed of $\frac{1}{4}$ " fiber board with aluminum pan and doors were used in all collections. Bait consisted simply of peanut butter. Non-absorbent cotton was added for nest material. Mortality in the traps during cold nights was diminished by the addition of commercial concentrated rat pellets. However, trap mortality averaged 35 per cent throughout the study.

In cases where mortality had occurred the animals were usually examined soon after return to the laboratory. If this was impossible, they were tagged and frozen. Live mice were placed in separate cages until such time as they could be sacrificed. At no time were they allowed to remain for more than a few days in the laboratory prior to examination in order to forestall possible loss of parasites.

Mice were killed by compressing the rib cage and the organs were placed in sodium chloride solution (0.9 per cent). The digestive tract was separated as follows: 1) esophagus and stomach, 2) small intestine, 3) cecum, and 4) large intestine. Other organs were examined in the following order: liver, lungs, heart, kidneys and bladder.

The digestive tract was opened first under the dissecting microscope and examined grossly for large cestodes. Then the wall was scraped and washed with saline and the contents examined closely. The other organs were teased apart with dissecting needles and examined under the microscope.

Cestodes and flukes, if alive, were placed in saline and relaxed by exposure to low temperatures in the refrigerator for periods of an hour or less. They were then transferred to cold alcohol-formalin-acetic acid fixative (AFA). Dead specimens were placed directly in the fixative.

Two methods were used for relaxing nematodes. Either they were dropped into hot 70 per cent alcohol or they were relaxed by exposure to cold and then fixed in 70 per cent alcohol. Both methods were suitable in most cases. However, two species of the genus Heligmosomum, spirally coiled in life, were never fully relaxed by either method.

Several methods were used in staining cestodes and flukes. Best results were obtained with Ehrlich's hematoxylin. Specimens were first hydrated from the fixative through a descending series of alcohols to water. They were then allowed to overstain in hematoxylin for 12 to 24 hours. After dehydration through an ascending series of alcohols, they were destained in 70 per cent acid alcohol to the desired clarity, then placed in alcohol containing an excess of sodium bicarbonate. Dehydration was completed through absolute alcohol and after a final dehydration in xylol-balsam, the specimens were mounted in Canada balsam.

Nematodes were usually studied without the aid of stains. They were cleared by placing them in 70 per cent alcohol with 5 per cent glycerine and allowing the alcohol to evaporate over a period of days. Temporary mounts were then made in glycerine or glycerine jelly. Bursate nematodes were mounted in glycerine jelly, and the bursa was oriented before the jelly was allowed to harden. For better differentiation of the bursal rays, in some cases, an acid fuchsin stain was added to the clearing medium. Where more rapid clearing was desired, specimens were mounted directly in lactophenol (3 parts phenol, 1 part lactic acid, 2 parts glycerol, and 1 part water), which left them ready for examination within a few minutes.

MICROTINE HOSTS

In any consideration of parasitism, the influence of the habitat and food habits of the host are of interest. The biology of the hosts treated in this survey, although still incomplete in some cases, can be outlined as follows:

Phenacomys intermedius, often called the heather vole, and generally regarded as rather rare, is trapped infrequently. Isolated records indicate a wide adaptability to habitats, ranging from dry sagebrush prairie to wet, spruce-fir forest, and from low altitudes to the alpine (Negus, 1951). The few specimens obtained here ranged from the alpine (Beartooth Plateau) through riparian, pine-fir forest at 7000 feet (Horse Creek, Pattee Canyon) to a dry, pine-fir forest at about 3500 feet (Lubrecht Forest). Food habits of Phenacomys are more varied than are those of other voles, according to Foster (1961), and include willows, grass, bark, lichens, bearberry, various herbs and seeds, and possibly some insect matter.

Clethrionomys gapperi, the red-backed vole, has been most often recorded from moist, forested areas and is often the most common rodent in this habitat. Gunderson (1959) found the distribution of C. gapperi closely associated with the presence of stumps, rotting logs, and root systems in loose forest litter and sphagnum. In this study, no large populations of this vole were found, but those captured (Pattee Canyon, Lubrecht Forest) were confined to the type of habitat described above. In two areas in Pattee Canyon, C. gapperi was found in close association

with Microtus longicaudus. Food of this species includes the soft parts of many plants, seeds, nuts, bark, and immature stages of many insects.

Although the life history of M. longicaudus, the long-tailed vole, is not well-known, this species appears to be more adaptable in habitat requirements than other members of the genus. It has been recorded from alpine and sub-alpine meadows, brushy tangles along streams, and wet sphagnum swamps (Soper, 1964). In this study, M. longicaudus was trapped in riparian forest habitats (Pattee Canyon, Lolo Peak) and a haystack in a dry hayfield (Miller Creek), at altitudes ranging from 3000 to 9000 feet. Although populations of this vole are subject to great fluctuations, it is rare to find it in greater numbers in forest habitats than C. gapperi (R. S. Hoffmann, University of Montana, personal communication). Such a situation was noted in the fall of 1964 in Pattee Canyon, but the reverse was true in the fall of 1965. Food of M. longicaudus includes grasses, sedges and tender green shoots, as well as stems and leaves of various plants.

Several workers (Findley, 1951; Anderson, 1959) have shown that in areas such as western Montana, where the ranges of Microtus pennsylvanicus, the meadow vole, and M. montanus, the montane vole, overlap, the former species tends to be restricted to wet habitat and the latter to drier areas. In this study, M. montanus was trapped only from dry prairie (National Bison Range) and in haystacks (Miller Creek). M. pennsylvanicus was found in small numbers along streams in pine-fir forest (Pattee Canyon, Rattlesnake Creek) and in larger numbers in several locations (Upper Bitterroot, Buckhouse Bridge) on

the edge of cat-tail swamps and around ponds. The food habits of both species are similar, consisting mainly of plant material, such as leaves, seeds, roots, and most often, the fruiting heads of grasses and sedges.

OBSERVATIONS

Autopsies were performed on 136 microtine rodents. Table I records the number of each host species examined and the per cent of each species infected with one or more helminths.

TABLE I
PER CENT OF HOSTS INFECTED WITH ONE OR MORE HELMINTHS

Host	No. Autopsied	% Parasitized
<u>Phenacomys intermedius</u>	8	75
<u>Clethrionomys gapperi</u>	28	57
<u>Microtus longicaudus</u>	49	88
<u>Microtus montanus</u>	26	73
<u>Microtus pennsylvanicus</u>	25	88
Total	136	78

Tables II-VI comprise a record of all examinations and list the number of specimens of each helminth species recovered. One cestode and one nematode species were recovered from Phenacomys intermedius. Three cestodes and three nematodes occurred in Clethrionomys gapperi. Microtus longicaudus was the most heavily parasitized species, having three species of cestodes and six species of nematodes. Microtus montanus harbored only two cestodes and one nematode, while Microtus pennsylvanicus was infected with two trematodes, four cestodes, and two nematodes.

Table VII summarizes the new host and distributional records for the parasites recovered. Ten new host records for North America, 26 new host records for Montana, and two new host records for Idaho were found.

TABLE II
SUMMARY OF EXAMINATIONS OF PHENACOMYS INTERMEDIUS

Locality and Date	Number of Parasites per Host	
	<u>Andrya</u> <u>primordialis</u>	<u>Heligmosomum</u> <u>dubius</u>
Beartooth Plateau		
6-7-64	-	-
6-7-64	-	-
Lubrecht Forest		
4-24-64	-	50
Horse Creek		
7-10-65	3	-
7-11-65	4	3
7-11-65	1	3
7-11-65	-	6
Pattee Canyon		
7-25-65	-	6

TABLE III
SUMMARY OF EXAMINATIONS OF CLETHRIONOMYS GAPPERI

Locality and Date	Number of Parasites per Host					
	<u>Hymenolepis horrida</u>	<u>Taenia mustelae</u>	<u>Catenotaenia dendritica</u>	<u>Syphacia obvelata</u>	<u>Aspiculuris tetraptera</u>	<u>Pelodera sp.</u>
Pattee Canyon						
10-5-64	2	-	-	-	-	-
10-24-64	2	-	-	-	-	-
11-7-64	4	-	-	-	-	-
10-25-64	-	-	-	10	-	-
11-16-64	3	-	-	-	-	-
11-25-64	-	-	-	-	-	-
11-27-64	-	-	-	-	-	-
11-29-64	-	-	-	-	-	-
11-29-64	-	-	-	-	-	-
11-30-64	-	-	-	-	-	-
12-5-64	2	-	-	-	-	-
12-5-64	-	-	-	-	-	-
12-9-64	-	-	-	-	-	-
12-23-64	-	1	-	-	-	-
3-13-65	-	-	-	-	-	-
3-18-65	-	-	2	-	-	-
3-19-65	-	-	4	-	-	-
5-7-65	-	-	-	5	-	-
7-7-65	2	-	-	-	-	-
10-18-65	-	-	-	-	-	-
10-23-65	-	-	1	1	-	-
10-23-65	5	-	-	-	3	-
10-23-65	-	-	-	-	-	25
10-26-65	-	-	-	-	-	-
11-19-65	-	-	-	-	-	-
11-19-65	-	-	-	-	-	50
Lubrecht Forest						
4-27-65	-	-	-	-	-	-
4-28-65	2	-	-	-	-	-

TABLE IV

SUMMARY OF EXAMINATIONS OF MICROTUS LONGICAUDUS

Locality and Date	Number of Parasites per Host								
	<u>Paranoplocephala infrequens</u>	<u>Hymenolepis horrida</u>	<u>Taenia mustelae</u>	<u>Heligmosomum carolinensis</u>	<u>Heligmosomum costellatum</u>	<u>Syphacia obvelata</u>	<u>Aspiculuris tetraptera</u>	<u>Mastophorus sp.</u>	<u>Pelodera sp.</u>
Pattee Canyon									
10-8-64	-	3	-	4	-	-	-	-	-
10-24-64	-	4	-	8	-	3	-	-	-
10-29-64	-	9	-	8	-	-	-	-	-
10-31-64	-	1	-	-	-	1	-	-	-
11-6-64	-	-	-	10	-	-	-	-	-
11-7-64	-	-	-	6	-	-	-	-	-
11-8-64	-	-	-	-	-	-	-	-	-
11-11-64	-	-	-	-	-	1	3	1	-
11-14-64	-	3	-	-	-	1	-	-	-
11-15-64	1	3	-	-	-	3	-	-	-
11-18-64	-	-	-	3	-	-	-	-	-
11-19-64	-	3	-	3	-	-	-	-	-
11-21-64	1	2+*	-	4	-	-	-	-	-
11-22-64	-	1+	-	3	-	-	-	-	-
11-24-64	1+	-	-	3	-	-	3	-	-
11-24-64	1	-	-	-	-	-	-	-	-
11-25-64	-	1+	-	7	-	-	-	-	-
11-25-64	1	1+	-	1	-	-	-	-	-
11-26-64	-	-	-	5	-	-	-	-	-
11-27-64	-	3	-	20	-	-	-	-	-
12-1-64	2	-	-	1	-	-	-	-	-
12-2-64	1	-	-	-	-	-	-	-	-
12-9-64	-	1+	-	5	-	-	-	-	-
5-4-65	-	6	-	8	-	1	-	-	-
5-6-65	-	1	-	10	-	-	-	-	-
7-5-65	2	16	-	10	-	8	-	-	-
7-5-65	-	3	-	20	-	-	2	-	-
7-7-65	-	7	-	2	-	-	-	-	-

(Continued)

Table IV (Continued)

Locality and Date	Number of Parasites per Host								
	<u>Paranoplocephala infrequens</u>	<u>Hymenolepis horrida</u>	<u>Taenia mustelae</u>	<u>Heligmosomum carolinensis</u>	<u>Heligmosomum costellatum</u>	<u>Syphacia obvelata</u>	<u>Aspiculuris tetraptera</u>	<u>Mastophorus sp.</u>	<u>Pelodera sp.</u>
Pattee Canyon (Cont.)									
7-8-65	-	18	-	7	-	-	-	-	-
7-25-65	-	10	-	-	-	-	-	-	-
7-28-65	-	2	-	18	-	-	-	-	-
10-18-65	-	7	-	8	-	-	3	-	-
12-10-65	3	4	-	6	-	40	1	-	50
Rattlesnake Creek									
11-29-64	7	-	1	-	-	-	-	-	-
12-7-64	9	-	-	-	-	-	-	-	-
12-14-64	-	-	-	-	-	6	-	-	-
1-18-64	6	-	-	-	-	1	-	-	-
Miller Creek									
1-30-65	-	-	-	-	-	-	-	-	-
2-6-65	-	-	-	-	-	1	-	-	-
2-7-65	-	-	-	-	-	-	-	-	-
2-10-65	-	-	-	-	-	25	-	-	-
2-10-65	-	-	-	-	-	7	-	-	-
2-11-65	-	-	-	-	-	10	-	-	-
2-13-65	-	-	-	-	-	80	-	-	-
2-14-65	-	-	-	-	-	33	-	-	-
2-20-65	-	-	-	-	-	-	-	-	-
2-20-65	-	-	-	-	-	-	-	-	-
2-27-65	-	-	-	-	-	-	-	-	-
Lolo Peak									
7-19-65	-	-	-	-	10	-	-	-	-

* (+) indicates number uncertain, scoleces not found.

TABLE V
SUMMARY OF EXAMINATIONS OF MICROTUS MONTANUS

Locality and Date	<u>Number of Parasites per Host</u>		
	<u>Paranoplocephala infrequens</u>	<u>Andrya macrocephala</u>	<u>Syphacia obvelata</u>
Miller Creek			
1-24-65	1	-	-
1-28-65	4	-	-
1-28-65	-	-	-
1-29-65	-	1	-
1-30-65	1	-	-
1-31-65	4	-	-
1-31-65	-	-	1
2-1-65	-	-	-
2-2-65	-	-	-
2-3-65	2	-	1
2-3-65	2	-	3
2-4-65	1	-	-
2-6-65	5	-	-
2-13-65	2	-	22
2-14-65	1	-	-
2-17-65	3	-	-
2-24-65	4	-	-
2-25-65	2	-	-
2-27-65	-	-	-
Bison Range			
4-6-63	6	-	1
4-6-63	3	-	1
5-29-65	-	-	-
5-29-65	3	-	-
5-30-65	-	-	-
5-30-65	-	-	-
5-30-65	-	-	2

TABLE VI
SUMMARY OF EXAMINATIONS OF MICROTUS PENNSYLVANICUS

Locality and Date	Number of Parasites per Host						
	<u>Q. quinqueserialis</u>	<u>Plagiorchis muris</u>	<u>Paranoplocephala infrequens</u>	<u>Paranoplocephala variabilis</u>	<u>Hymenolepis horrida</u>	<u>Taenia taeniaeformis</u>	<u>Heligmosomum carolinensis</u> <u>Syphacia obvelata</u>
Pattee Canyon							
10-31-64	-	-	-	-	1	-	2
11-23-64	-	-	-	-	-	-	6
Rattlesnake Creek							
11-28-64	-	-	-	-	-	-	-
O'Brien Creek							
2-17-65	7	-	-	-	-	-	-
2-17-65	1	-	-	-	-	-	2
2-24-65	4	2	-	-	-	-	7
Buckhouse Bridge							
3-7-65	-	-	-	-	-	-	5
3-13-65	-	-	1	-	-	-	-
3-20-65	-	-	3	-	-	-	-
3-26-65	-	-	-	1	-	-	-
4-6-65	2	-	-	-	-	-	70
4-15-65	1	-	-	1	-	-	-
11-27-65	-	-	5	-	-	-	60
Fort Missoula							
4-11-65	-	-	6	-	-	-	-
4-26-65	-	-	-	1	-	1	-
Upper Bitterroot							
4-22-65	26	1	-	-	-	-	-
5-11-65	-	-	4	-	-	-	-
5-14-65	-	-	-	1	-	-	95
5-15-65	-	-	-	1	-	1	-
6-13-65	5	-	-	-	-	-	-
6-13-65	-	-	-	-	-	-	-
6-19-65	26	-	-	-	-	-	-
6-28-65	10	-	-	-	-	-	-
7-7-65	-	-	-	-	-	-	-

TABLE VII
NEW HOST RECORDS

	<u>P.intermedius</u>	<u>C.gapperi</u>	<u>M.longicaudus</u>	<u>M.montanus</u>	<u>M.pennsylvanicus</u>
Trematoda:					
<u>Quinqueserialis quinqueserialis</u>					2
<u>Plagiorchis muris</u>					2
Cestoda:					
<u>Andrya macrocephala</u>				2	
<u>A. primordialis</u>	2,3				
<u>Paranoplocephala infrequens</u>			2	2	2
<u>P. variabilis</u>					2
<u>Hymenolepis horrida</u>		2	4		4
<u>Taenia mustelae</u>		2	1,2		
<u>T. taeniaeformis</u>					2
<u>Catenotaenia dendritica</u>		2			
Nematoda:					
<u>Heligmosomum costellatum</u>			1,2		
<u>H. carolinensis</u>			1,2		1,2
<u>H. dubius</u>	1,2,3				
<u>Syphacia obvelata</u>		2	2	2	2
<u>Aspiculuris tetraptera</u>		1,2	1,2		
<u>Mastophorus sp.</u>			1,2		
<u>Pelodera sp.</u>		1,2	1,2		

1. New host record for North America.
2. New host record for Montana.
3. New host record for Idaho.
4. Second record for Montana.

I. TREMATODA

Genus Quinqueserialis Skvortsov, 1934

Four species of the genus Quinqueserialis, all parasitic in microtine rodents, are listed by Yamaguti (1958): Q. quinqueserialis (Barker and Laughlin, 1911) Harwood, 1939; Q. hassalli (McIntosh and McIntosh, 1934) Harwood, 1939; Q. wolgaensis Skvortsov, 1934; and Q. floridensis Rausch, 1952.

The genus was reviewed by Harwood (1939) and more recently by Rausch (1952b), who described variation in important taxonomic characters in Q. quinqueserialis, these being: number of papillae in the ventral rows, form and distribution of the vitellaria, length of metratrem in relation to cirrus sac length, and egg size. Rausch compared his Q. quinqueserialis with Q. hassalli and Q. wolgaensis and demonstrated intergradation in these characters, indicating possible synonymy of the three species, but the absence of adequate material for comparative study indicated the need for further experimental work.

In a more recent study of the group, Smith (1954) also observed overlapping variations in the above characters, but suggested that the lateral extent of the uterine coils in Q. quinqueserialis and Q. hassalli was a distinct and constant taxonomic character. On this basis he placed Q. wolgaensis in synonymy with Q. hassalli and considered the status of Q. floridensis uncertain. He differentiated the three species as follows:

Key to the species of Quinqueserialis

1. Transverse loops of uterus not extending
laterally past intestinal cecae Q. quinqueserialis
Transverse loops of uterus extending
laterally past intestinal cecae 2
2. Vitellaria extend from testes anteriorly to
a point 2/3 or more the distance to the
cirrus sac Q. hassalli
Vitellaria almost wholly posterior to
uterine loops Q. floridensis

In this study, Q. quinqueserialis was found only in M. pennsylvanicus. Although M. pennsylvanicus was considered to be only an accidental host for Q. quinqueserialis by Schad (1954), with the muskrat (Ondatra zibethica) the more common host, specimens in this study were obtained in several areas where muskrats were not present. The average infection consisted of five worms. Two infections each consisting of 26 immature flukes were found.

In one area near Lolo, the opportunity was taken to compare specimens from the muskrat with specimens from Microtus. The observation by Rausch (1952b), that voles tend to have fewer but larger worms, was confirmed. Also, some slight irregularity in the lateral extent of the uterine coils, considered constant by Smith (1954) was observed. Different Q. quinqueserialis specimens from the same muskrat showed the uterine coils extending across the cecae or confined within the cecae. These findings indicate that the problem of synonymy in the genus should not be considered closed.

Genus Plagiorchis Lühe, 1899

Trematodes of the genus Plagiorchis are not common parasites of microtine rodents in North America. P. maculosus (Rudolphi, 1802) Braun,

1902, P. microcanthos Macy, 1931, P. proximus Barker, 1915, and P. muris Tanabe, 1922, have been recorded from the muskrat, O. zibethica. Of these, only P. muris has been recorded from voles.

Schultz and Skvortsov (1931) divided the genus Plagiorchis into two subgenera on the basis of the anterior extent of the vitellaria, meeting on the median line anterior to the acetabulum in Multiglandularis, and not meeting in Plagiorchis. Of the species above, only P. muris belongs to the subgenus Multiglandularis. Only two infections of P. muris were found in this study in 25 M. pennsylvanicus (4 per cent). A similar low incidence of infection, 3 per cent, was noted in 73 M. pennsylvanicus in Quebec by Schad (1954).

II. CESTODA

Genus Andrya Railliet, 1893

Only four North American cestodes of the genus Andrya from microtine rodents are now considered valid: Andrya primordialis Douthitt, 1915; A. macrocephala Douthitt, 1915; A. arctica Rausch, 1952; and A. bairdi Schad, 1954.

Douthitt (1915) described A. primordialis and A. communis as new species, pointing out that "differences in the two accounts are due probably to differences in the state of contraction in the material." In addition, he described A. macrocephala from Microtus pennsylvanicus. In a monograph on the Anoplocephalidae, Baer (1927) concluded that A. communis was a synonym of A. primordialis.

Considerably later, Hansen (1947) described A. microti from the prairie vole, M. ochrogaster, and Rausch (1948) described A. ondatrae from the muskrat, O. zibethica. Then, while reviewing variation in the genus, Rausch and Schiller (1949a) invalidated A. microti and A. ondatrae, considering both synonyms of A. macrocephala.

The genus Andrya was separated by Kirshenblatt (1938) into two subgenera, Andrya with a prostate gland and Aprostatatandrya without. Spasskii (1951) raised Aprostatatandrya to full generic standing. Some confusion based on this and other characters still exists. Douthitt (1915) described A. primordialis as having a prostate gland and unilateral genital pores. Rausch (1952b) was unable to find the gland in either Douthitt's material or in several hundred specimens of Andrya sp. in his own collections. In addition, he states: "Individuals

possessing unilateral genital pores have not been observed, although a condition approaching this has been noted in certain Rocky Mountain material." Rausch considered the elevation of Aprostata andrya invalid. This view is followed here.

In addition, Rausch (1952b) described A. arctica from lemmings on the basis of irregularly alternating genital pores, absence of a prostate gland, larger cirrus sac size, and larger egg size. Schad (1954) described a fourth species, A. bairdi, from the rock or yellow-nosed vole, M. chrotorrhinus, with unilateral genital pores, no prostate gland, and the testes not confined to the area between the longitudinal excretory ducts. Schad states, "It is probable that the North American Andrya possessing unilateral genital pores may be shown to be conspecific when an adequate series of specimens is examined. . . . Until the description of A. primordialis is modified . . . it is necessary to describe A. bairdi as a new species." The key given by Rausch (1948) cites A. primordialis as having testes overlapping the excretory canals. It appears that A. bairdi is distinguishable from A. primordialis only on the basis of the hypothetical prostate gland.

Several specimens of Andrya sp. were obtained from Phenacomys intermedius collected in Idaho. This material, although broken in several cases, shows completely unilateral genital pores. Careful examination reveals nothing which could be interpreted as a prostate gland, although slight irregularities in a few of the cirrus sacs could be misinterpreted as such. These specimens are assigned to Andrya primordialis. A specimen of Andrya, collected from Microtus montanus in Colorado by G. D. Schmidt, showed unilateral genital pores, with

the exception of two immature proglottids. This is apparently the condition which Rausch speaks of as "approaching" unilateral genital pores. No prostate glands were observed in this specimen either.

One specimen from Microtus montanus, showing a greater deviation toward alternate genital pores, and an average egg diameter of 35 microns is assigned to A. macrocephala.

Although Andrya spp. have been demonstrated to be widespread and common parasites of microtines in North America, only four infections were observed in this study. No reason is apparent for the low incidence of infections.

Genus Paranoplocephala Lühe, 1910

Only five species of the genus Paranoplocephala reported from North American microtines are now considered valid: P. omphalodes (Hermann, 1783); P. infrequens (Douthitt, 1915); P. variabilis (Douthitt, 1915); P. lemni (Rausch, 1952), and P. neofibrinus (Rausch, 1952).

The problem of synonymy in this genus has led to much confusion. Douthitt (1915), in a monograph on the family Anoplocephalidae, described two new species, Anoplocephala variabilis and A. infrequens. Baer (1927) reassigned these species to the genus Paranoplocephala and indicated that the two species were synonymous. Rausch (1946) described a new species, P. troeschi, from Microtus pennsylvanicus. In a review of the genus, Rausch and Schiller (1949b) studied Douthitt's original material and concluded that P. variabilis was morphologically distinct from P. infrequens. In addition, they raised Douthitt's subspecies P. variabilis borealis to full specific rank, P. borealis. P. troeschi was considered to be a synonym of P. infrequens. Rausch (1952a)

described P. neofibrinus from the round-tailed muskrat in Florida. Further taxonomic study by Rausch (1952b) showed that the species described by Voge (1948), P. kirbyi, was incorrectly assigned to this genus and was a synonym of Andrya macrocephala Douthitt, 1915. Examination of a larger series of material also revealed that P. borealis was only an immature form of P. variabilis. P. lemni from Lemmus trimucronatus was also described as a new species and the first record of P. omphalodes from North America was recorded. Finally, P. wigginsii was described from an Arctic ground squirrel, Citellus undulatus, by Rausch (1954). The following key to currently recognized species is derived from the species descriptions:

Key to the Species of Paranoplocephala

1. Genital pores irregularly alternate, strobila length 150-195 mm P. omphalodes
 Genital pores unilateral, strobila length greater than 100 mm P. wigginsii
 Genital pores unilateral, strobila length less than 100 mm 2
2. Gravid segments not filled by uterus beyond longitudinal excretory canals P. lemni
 Gravid segments completely filled by uterus 3
3. Testes do not extend beyond aporal longitudinal excretory canal, parasitic in cecum P. infrequens
 Testes extend beyond aporal canal, parasitic in small intestine 4
4. Strobila length 55-56 mm, segment number 180-190. P. neofibrinus
 Strobila length 15-41 mm, segment number 42-99. . P. variabilis

Paranoplocephala infrequens was the most common cestode occurring in this study, infecting three hosts, Microtus longicaudus, M. montanus, and M. pennsylvanicus. In those hosts sacrificed in the laboratory and examined immediately, these cestodes were invariably found with the scolex attached to the small intestine and the proglottids projecting

into the cecum. Cestodes in frozen hosts were usually found to have fallen into the cecum. An average of three worms per host occurred in M. longicaudus and M. montanus and two worms per host in M. pennsylvanicus.

Infections of Paranoplocephala variabilis were rare in this study, occurring only in Microtus pennsylvanicus. Where such infections did occur, only one specimen per host was found, usually attached to the uppermost portion of the duodenum. In one host, examined immediately upon sacrificing, a short length of proglottids was found free in the cecum, apparently in the process of being eliminated.

Genus Hymenolepis Weinland, 1858

The taxonomic history of this widely distributed genus is too extensive to review in this paper. Hughes (1940) listed 320 species and subspecies as valid and later (1941) presented a key for these species. Since that time extensive revision of various genera of the subfamily Hymenolepidinae has been undertaken by several authors, notably Spasskii (1954) and Yamaguti (1959). The concept of the genus Hymenolepis has been narrowed to include only those forms with unarmed suckers, rostellum absent or rudimentary and unarmed, and proglottids transversely elongated. Yamaguti (1959) lists only 13 valid species of the revised genus. Of these, only H. diminuta (Rudolphi, 1819) and H. horrida (von Linstow, 1901) have been recorded from North American rodents.

A well-known parasite of Eurasian voles, H. horrida was first recorded from North America by Kuns and Rausch (1950). Additional records by Rausch (1952b), Schad (1954), and Murray (1964) have shown

it to be a common and widespread parasite of Clethrionomys and Microtus species on this continent. Schiller (1952b) discovered considerable morphological variation within this species, necessitating a redescription. The identification of much of the material in this study was greatly aided by comparison with the original Montana material collected by the Rocky Mountain Laboratory and identified by Schiller. Three species were infected with this cestode, C. gapperi, M. longicaudus, and M. pennsylvanicus. An average number of mature worms per infected host is probably four; several larger infections of up to 18 contained no mature worms.

Genus Taenia Linnaeus, 1758

Larval stages of the genus Taenia have been recorded as common parasites in many North American rodents. The most widespread of these in microtines has frequently been recorded as T. tenuicollis Rudolphi, 1819. Host records for both the larval stage in rodents and the adult cestode in mustelid carnivores were summarized by Locker (1955). Freeman (1956) reviewed the taxonomy of this species and proposed T. mustelae Gmelin, 1790, as the valid name. He also suggested that the cysticerci identified by Rausch and Tiner (1949) from Microtus pennsylvanicus as Cladotaenia sp. were probably T. mustelae. According to Freeman, this species is unusual in that both uniscolax and multiscolax larval forms commonly occur. The larvae are readily identified on the basis of the rostellar hooks, which have the typical taeniid shape but are extremely small, having an average length of 16 microns. Freeman was unable to correlate larval forms with intermediate host species or age or intensity of infection. The same strain

apparently was capable of producing either larval type, both sometimes occurring in the same host.

Two infections of T. mustelae were observed in this study, a single cycticercus in the liver of Clethrionomys gapperi, and a coenurus in the liver of Microtus longicaudus. The latter constitutes a new host record. This single coenurus contained ten scolices. Coenuri containing up to 120 scolices were recorded by Locker (1955) in the muskrat.

A distinctive strobilocercus larval stage was used as the basis of the distinction of the taeniid genus Hydatigera by Wardle and McLeod (1952). In a critical study of the morphology of H. taeniaeformis Batsch, 1786, Esch and Self (1965) were of the opinion that this distinction was invalid and listed the genus as a synonym of Taenia.

Only two infections of T. taeniaeformis were noted in this study, each consisting of a single cyst in the liver of M. pennsylvanicus. These were readily identified on the basis of the length of the strobila (both over 150 mm) and number of hooks (30). In addition, the hooks were dissected out, mounted, and compared with specimens collected in 1952 at the National Bison Range by Miss Betty Locker of the Rocky Mountain Laboratory. The hooks were similar both in shape and size, the average length of the large hooks being 390 microns and the small, 242 microns.

Genus Catenotaenia Janicki, 1904

Prior to 1950 the genus Catenotaenia had been placed by different authors in three families, Taeniidae, Dilepididae, Anoplocephalidae. Spasskii (1950) placed the genus in a separate family, Catenotaeniidae.

Wardle and McLeod (1952) independently erected the same family. In a comprehensive review of the taxonomy of the genus, Wolfgang (1956) considered the family invalid and listed *Catenotaeniinae* Spasskii, 1949, as a subfamily of Anoplocephalidae. He lists the following North American species as valid: *C. pusilla* (Goeze, 1782), *C. californica* Dowell, 1953, *C. dendritica* (Goeze, 1782), and *C. reggiae* Rausch, 1951.

C. dendritica, the only species recorded from microtine rodents, has a complicated synonymy. Smith (1954) and Schad (1954) both listed *C. linsdalei* McIntosh, 1941, as a synonym of *C. dendritica*. Wolfgang (1956) added *C. peromysci* Smith, 1954, and *C. laguri* Smith, 1954, as synonyms. The host range was thereby widened to include such diverse rodents as Kangaroo rats, ground squirrels, deer mice, and sagebrush voles.

Of the voles covered in this study, only *C. gapperi* was found to harbor *C. dendritica*. Three of 26 *C. gapperi* (11.5 per cent) were infected. Murray (1964) found only 2 per cent of 168 *C. gapperi* infected with this worm in Alberta.

III. NEMATODA

Genus Heligmosomum Railliet et Henry, 1909

The genus Heligmosomum was established by Railliet and Henry in 1909 on the basis of the greatly reduced dorsal ray of the bursa. Misinterpretation of this character has led to the creation of several invalid genera which are now considered synonyms of Heligmosomum. These include Heligmosomoides Hall, 1916, Nematospira Walton, 1923, and Sincosta Roe, 1929. Species of Heligmosomum may be conveniently divided into those having symmetrical lateral lobes of the bursa and those having asymmetrical lobes. The latter are often recorded in the genus Nematospiroides Baylis, 1926, which was included as a synonym of Heligmosomum by Skrjabin et al. (1954). Species recorded from North America having symmetrical bursae are H. costellatum (Dujardin, 1845), H. hudsoni Cameron, 1937, H. polygyrum (Dujardin, 1845), and H. turgidum (Walton, 1923) Skrjabin et al., 1954. Those with asymmetrical bursae are H. dubius (Baylis, 1926) Tenora, 1958 (syn. Sincosta aberrans Roe, 1929), H. carolinensis (Dikmans, 1940) Skrjabin et al., 1954, H. longispiculatus (Dikmans, 1940) Skrjabin et al., 1954, and H. microti (Kuns and Rausch, 1950).

H. costellatum, a common European parasite of voles, was first reported from North America in Microtus montanus and M. richardsoni by Kuns and Rausch (1950). Later Rausch (1952b) listed this species as ". . . a widely distributed parasite of various species of voles in Alaska," but failed to name the host species. In a personal communication (1965), Rausch mentioned M. oeconomus as one of these hosts, and

excluded M. longicaudus. The report here of an infection in M. longicaudus is, therefore, a new host record.

H. dubius was found only in Phenacomys intermedius and constitutes a new host record for this species. Although only a few specimens of this vole were obtained, infections of this nematode were recorded from two locations in Montana and one in Idaho, indicating that it may be a common parasite of Phenacomys. Although H. dubius has been commonly recorded from North America in feral Mus musculus and Peromyscus spp., only one other record is known in microtines, from Microtus chrotorrhinus in Canada (Schad, 1954).

A high rate of infection in M. longicaudus of a nematode similar in morphology to H. carolinensis (Dikmans, 1940) and H. microti (Kuns and Rausch, 1950) prompted a re-examination of the status of these two species. H. carolinensis was described from C. gapperi by Dikmans (1940) on the basis of limited material. H. microti was described from M. montanus and M. richardsoni by Kuns and Rausch (1950). Later, Schad (1954) presented additional morphological data on H. carolinensis from C. gapperi in Canada. A comparison of these descriptions with my material is presented in Table VIII. All measurements relating to my material were taken from 25 specimens with the exception of length of females. Because the coiled nature of these nematodes greatly limits accuracy in the measurement of length, only maximum lengths for several females are given and no means are computed.

It is apparent from Table VIII that considerable morphological variation occurs in the series collected in Montana. Only one measurement previously reported for either species lies outside the range of

TABLE VIII

COMPARISON OF HELIGMOSOMUM CAROLINENSIS AND H. MICROTI
(All measurements in millimeters)

	<u>H. carolinensis</u>						<u>H. microti</u>		
	Dikmans, 1940		Schad, 1954		This paper*			Kuns and Rausch, 1950	
	Min.	Max.	Min.	Max.	Min.	Max.	Mean	Min.	Max.
<u>Male</u>									
Length		4.0	6.42	6.50	3.8	7.2	5.5	5.8	6.0
Width		---	.12	.15	.09	.13	.11	.08	.10
Esophagus length		---	.47	.54	.51	.68	.59	.59	.60
Spicule	1.8	1.9	---		2.14	2.43	2.28	2.08	2.20
Spicule type	filiform		simple, filiform		simple, filiform			simple, filiform	
Shape of dorsal ray	long external branches		longer internal branches		longer internal branches			4 slender points	
<u>Female</u>									
Length		---	10.40	11.79	7.6	13.2	---	8.0	10.5
Width		---	.12	.19	.10	.16	.13	.12	.13
Esophagus length		---	.52	.56	.52	.80	.62	.68	.69
Eggs - length	.060	.065	.050	.060	.053	.082	.067	.070	.078
width	.040	.045	.030	.040	.030	.043	.036	.040	.043
Tail spike	.015		.010		.010	.017	.012	.010	.012
Tail length	.06	.07	.04	.06	.050	.063	.057	.058	.064
Ovejector	.175		.14	.20	---	---	---	.16	.19

* Based on 25 specimens.

variation found, namely, the length of the spicules as recorded by Dikmans (1940). Since this description was based on only one complete immature male, the discrepancy appears to be of little significance. Rausch and Tiner (1949) described specimens of Nematospiroides sp. which did not agree with any of the described species but appeared to be nearest to N. carolinensis Dikmans, 1940. The lengths of spicules were reported to be 1.9 to 2.4 mm in males which were 5.1 to 7.4 mm in length, measurements which overlap both H. carolinensis and the later described H. microti.

Kuns and Rausch (1950) state that H. microti is readily distinguished from other members of the genus by the elongate lateral and externo-dorsal rays of the male. An examination of Kuns and Rausch's type specimens from the U. S. National Museum Helminthological Collection showed that the rays were comparable in length to my material. In addition, a comparison of the original drawings of these rays in the two species, when converted to the same scale, reveals no marked difference in length.

One point remains to distinguish these two species. Although Dikmans (1940) did not describe the dorsal ray, his diagrammatic figure shows it to have four branches, with the outer branches longer than the inner. Schad (1954) mentions that his specimens differ in having the inner branches longer. Kuns and Rausch (1950) state that the dorsal ray of H. microti branches to end in four slender points, but they do not mention the relative lengths of the branches. In an examination of the type specimen of H. microti, the dorsal ray could not be seen because of the position of the mount. My own material clearly shows

the inner branches of the dorsal ray to be longer than the outer. Since no additional material was available from either Rausch or Schad to clarify this point, the question of the validity of H. microti must be deferred, pending the availability of comparative material of that species. It seems unlikely, however, that this single character is sufficient to warrant the retention of H. microti. Because of the shape of the dorsal ray, my material is assigned to H. carolinensis. M. longicaudus and M. pennsylvanicus are recorded as new hosts for this species. The absence of H. carolinensis from the type host, C. gapperi, in the same area is unexplainable.

Genus Syphacia Seurat, 1916

Only two nematodes of the genus Syphacia have been recorded from microtine rodents, S. obvelata (Rudolphi, 1802) and S. arctica Tiner and Rausch, 1950. S. obvelata is a cosmopolitan parasite of mice, rats, monkeys, and man, while S. arctica has only been recorded from the collared lemming, Dicrostonyx groenlandicus in Alaska. Tiner (1948) summarized the taxonomy of the genus and offered a key to the species described at that time.

S. obvelata was the most common helminth recorded in this study, found in every species, with the exception of Phenacomys intermedius. Since the life cycle of this worm was shown to be direct by Lawler (1939) and because of the known wide range of hosts, its absence in P. intermedius is perhaps due to the small sample size rather than host specificity. Infections were found only in the cecum and, in a few heavy infections, the large intestine of the host. Of the 136 voles collected, 26 per cent were infected with this parasite, with a

maximum number of 95 worms in a single host. Male worms were rarely found in this study, a condition noted by other workers (Rausch and Tiner, 1949). In one infection of 95 worms, only four were males. Although the males are of extremely small size (1.3 mm) and could be easily missed, errors in technique probably do not account for the disparity noted. A shorter life span for males was suggested by Rausch and Tiner as the reason for their absence. Chan (1958) states that males of S. obvelata pass out of the host after six days.

Genus Aspiculuris Schultz, 1924

No nematodes of the genus Aspiculuris have previously been recorded from microtine rodents in North America. A. tetraptera (Nitzsch 1821) is a common Eurasian parasite of murid rodents and has been collected in North America from introduced mice and rats. Other North American species are A. americana, described by Erickson (1938a) from Peromyscus maniculatus ssp. in Minnesota, and A. ackerti, described from Neotoma spp. in Arizona by Kruidenier and Mehra (1959).

Consequently, the records of A. tetraptera in this study from C. gapperi and M. longicaudus constitute the first records from microtine rodents in North America. Infections found in freshly-killed animals were extremely localized, found only in the short, tightly-coiled colic spiral of the large intestine. Infection levels were low, the largest being three worms per host. One mixed infection of three A. tetraptera and 40 S. obvelata was noted. Because of the superficial resemblance of this worm to S. obvelata, it is possible that infections have been missed by other workers. More probable, perhaps, is the possibility that the worm has only recently become established in North American

microtines from introduced populations of Mus musculus or other murids.

Genus Mastophorus Diesing, 1853

The only species of this genus recorded from North American microtine rodents is Mastophorus muris (Gmelin, 1790) Diesing, 1853. An uncommon parasite of voles, M. muris was found in 2 per cent of 345 M. pennsylvanicus in Michigan by Rausch and Tiner (1949), and in 1 per cent of 168 C. gapperi in Alberta by Murray (1964). Rausch (1952b) found this nematode locally distributed in red-backed voles in Alaska. A single, large male nematode was collected from the stomach of one M. longicaudus in this study. The worm was readily assigned to Mastophorus sp., but further identification on the basis of this single male was impossible. This, however, constitutes the first record of this genus from M. longicaudus.

Genus Pelodera (Schneider)

The presence of an unidentified nematode in the orbits of lemmings was first reported by Rausch (1952b) in Alaska. Poinar (1965) described the life history of Pelodera strongyloides (Schneider) in the lacrimal fluid of the bank vole, Clethrionomys glareolus in England. A normally free-living soil nematode, P. strongyloides was found to form infective, third-stage "dauer" larvae during dry periods. After transferral to the orbits of the mouse, possibly during grooming, the larvae developed in the lacrimal fluid for 2-3 weeks and then returned to the soil to molt to the adult stage. The only North American record listed by Poinar is from Microtus californicus in California. Additional murid and microtine hosts in Europe were listed by Osche

(1963) and Trapido (1966).

In this study, several infections of larval nematodes were found in the lacrimal fluid of C. gapperi and M. longicaudus collected from Pattee Canyon. Since no orbital parasites have been recorded from these species, these infections constitute new host records. Orbital examinations were not done in this study prior to March, 1965. Consequently, the overall incidence of infection is not known. However, continuing examinations of recently collected material indicate that this nematode may be a common parasite in this area. These larvae agree completely with the description of P. strongyloides given by Poinar (1965), but positive identification is deferred until sexually mature specimens can be obtained by culture.

DISCUSSION

Habitat and Seasonal Variation in Helminth Infections

The distributional patterns of some of the parasites encountered appear to be more understandable when their life cycles are taken into consideration. In particular, infections of trematodes in voles seem to be most closely related to the habitat of the intermediate host. The life cycle of Q. quinqueserialis, as described by Herber (1942), involves ingestion of the eggs by an aquatic snail, Gyraulus parvus, and encystment of the cercariae on vegetation. Infection in voles is probably limited to areas in which water is only seasonally present, since these animals do not commonly feed on aquatic plants. Rausch and Tiner (1949), while studying Q. hassalli, found heavy infections in winter months, including immature trematodes, indicating that infective stages were available to some degree during this season. A decrease of infections was noted in late spring. A similar pattern was found with Q. quinqueserialis in this study with infections first noted in February and extending through July. Three animals examined in November from a previously infected area were not infected. More extensive sampling of infection foci is now under way to verify this point. Both Q. quinqueserialis and Q. hassalli have been recorded as common parasites of M. pennsylvanicus, the most common vole in this type of habitat. Q. hassalli has been more rarely recorded from M. montanus, which invades this habitat only in the absence of M. pennsylvanicus (Koplin, 1962).

The life cycle of Plagiorchis muris, as described by McMullen (1937), can proceed by a precocious encysting of cercariae within the snail host, Lymnaea emarginata, or encysting of cercariae in second intermediate hosts, such as chironomid or mosquito larvae. Although none of these invertebrates are considered as usual food items for herbivorous voles, the incidence of P. muris infections indicates that perhaps they are occasionally ingested. Only two North American records exist for Plagiorchis in voles. Rausch (1952b) reported Plagiorchis sp. from Clethrionomys rutilus in Alaska and Schad (1954) reported P. muris from M. pennsylvanicus and Plagiorchis sp. from C. gapperi in Canada. The ecology of the cycle in voles is perhaps similar to that postulated above for Q. quinqueserialis and directly related to seasonal fluctuations in water level and abundance of intermediate hosts.

A study in seasonal variation of infections of Paranoplocephala troeschi (= P. infrequens) in voles by Rausch and Tiner (1949) showed that heaviest infection rates occurred in the winter months. No specimens were collected before October or after May and it was concluded that infections in the warmer months must be rare. In general, their observation is confirmed in this study, although the first infections were not noted until mid-November and several infections were noted later than May, one as late as July 5. Whether the restricted seasonal presence of the cestode is related to the ecology of the intermediate host or to some seasonal variation in microtine behavior or physiology is unknown. Most anoplocephalids utilize mites as intermediate hosts, but no cycles have been determined as yet for members of the genus Paranoplocephala. No habitat specificity was observed here

in either P. infrequens or P. variabilis, since infected voles of three species were trapped in forests, dry brush, and in haystacks.

An interesting field note on P. infrequens concerns two populations of Microtus sampled from haystacks in winter. Two haystacks about two hundred yards apart contained separate populations of M. longicaudus and M. montanus. The sample of M. longicaudus (12 hosts) had no infections with this worm, while the sample of M. montanus (19 hosts) was two-thirds infected. Reasons for this sharp demarcation could be that the intermediate host was not present in one haystack, or the population moving into this haystack was not infected. Studies of such concentrated populations in small areas could be fruitful in clarifying the role of parasites in cyclic outbreaks of rodents.

The larval cestodes found in this study presumably reflect the presence of appropriate definitive hosts. The most commonly recorded hosts for Taenia mustelae are the short-tailed weasel, Mustela erminea, and the mink, Mustela vison, both of which could have been present in the infected habitats. The house cat is the common definitive host for T. taeniaeformis, although the bobcat has been reported as a host in Minnesota (Rollings, 1945). Both infections in this study occurred in areas readily accessible to house cats. The infections noted on the Bison Range by Miss Locker were probably also from house cats, since the bobcat is said to have been eliminated from that area.

Infections of eight worms in this study (H. horrida, C. dendritica, H. carolinensis, H. costellatum, H. dubius, A. tetraptera, Mastophorus sp., Pelodera sp.) were found only in forest habitats. Rausch (1952b) considered H. horrida to be a boreal forest and sub-

alpine species in Alaska. Murray (1964) also found host habitat to be a limiting factor in the presence of this worm. Infections of M. pennsylvanicus in his study were found only in the same traplines as infected C. gapperi, a fact also noted in this study. Apparently no records outside of boreal forest have yet been recorded.

C. dendritica infections in voles seem to be limited to Clethrionomys spp. Since the non-microtine host range of this worm is so wide, it is probable that infections are limited by the food habits of the host or by the habitat of the intermediate hosts, rather than by the habitat of the definitive host.

Infections of Mastophorus muris were noted by both Rausch (1952b) and Schad (1954) to be confined to spruce forest habitats. The single infection here occurred in similar terrain.

Kuns and Rausch (1950) concluded that the distribution of infections of Heligmosomum spp. was influenced by moisture conditions rather than habitat. According to Rausch (1952b), infections of H. costellatum in North America have been recorded only from wet, sub-alpine habitats, as was the single infection in this study. Rausch and Tiner (1949) found infections of Nematospiroides sp. (= Heligmosomum) in wet marsh habitats, but never in any animals trapped within forest areas. The restriction here of H. carolinensis and H. dubius to wet forest areas perhaps strengthens the conclusion that the limiting factor is moisture, not habitat.

Multiple Infections

In this study, 35 per cent of all hosts and 44 per cent of infected hosts harbored two or more helminth species. Of the M.

longicaudus populations trapped in forest habitats, 73 per cent had multiple infections, several of three or four species and one with six.

In both multiple and single infections the parasites encountered within the digestive tract demonstrated a striking microhabitat specificity. Table IX gives a qualitative summary of the distribution of the parasites within the tract. Only M. muris was found in the stomach. P. variabilis, C. dendritica, and Heligmosomum spp. were confined in light infections to the duodenum. H. horrida, Andrya spp., and F. muris occurred throughout the small intestine. P. infrequens was the most restricted and was always found attached to the terminal end of the small intestine, with proglottids projecting into the cecum. Q. quinqueserialis was usually restricted to the terminal portion of the cecum, while S. obvelata was found throughout the cecum and, in heavy infections, in the cecum and large intestine. A. tetraptera was found to be narrowly restricted to the colic loops of the large intestine.

The possibility of interspecific competition between parasites, which could be important as a factor in their distribution and abundance, has received some attention. Holmes (1961), in a study of concurrent infections of an acanthocephalan, Moniliformis dubius, and Hymenolepis diminuta, found that these two worms were displaced anteriorly and posteriorly, respectively, from their normal intra-intestinal infection sites. In mixed infections, each parasite species was found to have a lower average weight:length ratio than in single infections. Schad (1963), in a study of niche diversification in turtle nematodes, found strong differences in radial distribution. Some species were restricted to the mucosal surface of the gut while others were found

TABLE IX
INTRA-INTESTINAL DISTRIBUTION OF HELMINTHS

	Stomach	Duodenum	Lower Small Intestine	Cecum	Colic Loops	Large Intestine
<u>Q. quinqueserialis</u>				X		
<u>P. muris</u>			X			
<u>A. macrocephala</u>			X			
<u>A. primordialis</u>			X			
<u>P. infrequens</u>				X		
<u>P. variabilis</u>		X				
<u>H. horrida</u>			X			
<u>C. dendritica</u>		X				
<u>H. carolinensis</u>		X	X*			
<u>H. costellatum</u>		X				
<u>H. dubius</u>		X				
<u>S. obvelata</u>				X	X*	X*
<u>A. tetraptera</u>					X	
<u>Mastophorus</u> sp.	X					

* Only in heavy infections.

throughout the lumen. In the present study, although mixed infections were common, two species were rarely found in the same area of the intestine. In one infection of five species in M. longicaudus, no two overlapped. Chubb et al. (1964) emphasized that infections of helminths should be considered to be in dynamic equilibrium, reflecting a continuous gain and loss of worms from the host. It may be through such dynamic gain and loss that stratification is achieved rather than through a process of intra-intestinal migration.

In several cases of heavy infection with H. horrida of up to 18 worms, and with P. infrequens of up to 9 worms, only immature worms were present. The largest mature infections of these two species were four and five, respectively, possibly indicating some degree of intra-specific competition in the case of these two species.

Pathology

No pathological effects of the parasites on the hosts were noted, with the exception of the liver cysts of Taenia mustelae and T. taeniaeformis. In the four infections of these species, cysts were confined to one per host and probably exerted little influence on the overall condition of the animal. In a study of 570 voles in the North Central States, Rausch and Tiner (1949) noted pathology by helminths only in the case of infections of liver fluke, Mediogonimus ovilacus.

SUMMARY

1. A total of 136 microtine rodents of five species, Phenacomys intermedius, Clethrionomys gapperi, Microtus longicaudus, M. montanus, M. pennsylvanicus, were examined for helminths in western Montana from October 5, 1964, to December 10, 1965.

2. Seventeen species of helminths were recorded, including two trematodes, Quinqueserialis quinqueserialis, Plagiorchis muris; eight cestodes, Andrya macrocephala, A. primordialis, Paranoplocephala infrequens, P. variabilis, Hymenolepis horrida, Taenia mustelae, T. taeniaeformis, Catenotaenia dendritica; and seven nematodes, Heligmosomum costellatum, H. carolinensis, H. dubius, Syphacia obvelata, Aspicularis tetraptera, Mastophorus sp., and Pelodera sp.

3. Ten new host records were found: H. dubius in P. intermedius; A. tetraptera and Pelodera sp. in C. gapperi; T. mustelae, H. costellatum, H. carolinensis, A. tetraptera, Mastophorus sp., and Pelodera sp. in M. longicaudus; and H. carolinensis in M. pennsylvanicus. Twenty-six new host records for Montana and two for Idaho were found.

4. Comparison of specimens of Q. quinqueserialis from M. pennsylvanicus and Ondatra zibethica demonstrates enough morphological variation to re-open the question of its possible synonymy with Q. hassalli. Seasonal variation in infections of Q. quinqueserialis indicates a possible correlation with movement of voles in and out of infected areas due to fluctuations of water level. Further work is under way to verify this pattern.

5. The taxonomic status of Andrya primordialis is reviewed. The absence of a prostate gland in several specimens with unilateral genital pores is not deemed sufficient to exclude them from this species.

6. Wide morphological variation in H. carolinensis prompted an examination of the species H. microti, which it closely resembles. Although the range of variation observed overlapped the descriptions of both species, the question of synonymy is deferred in the absence of comparative material of H. microti.

7. A distinct seasonal pattern of infections of P. infrequens was noted, beginning in mid-November and extending through July. Infection foci of this worm were found in a wide range of habitats.

8. Infections of H. horrida, C. dendritica, Heligmosomum spp., A. tetraptera, Pelodera sp., and Mastophorus sp. were restricted to moist forest habitats.

9. A distinct stratification of helminths within the digestive tract was proposed as one possible reason for the high frequency of successful mixed infections in voles.

10. No pathology was noted with the exception of encystment of taeniid larvae within the liver. In all instances worm loads were moderate and had no obvious detrimental effect on the host.

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APPENDIX

APPENDIX

HOST CATALOGUE OF HELMINTHS OF MICROTINES

(Numbers in parentheses refer to the references cited)

Phenacomys intermedius

Cestoda

Andrya macrocephala Douthitt, 1915 - (47).

Andrya primordialis Douthitt, 1915 - (44) (60) (63) (this paper).

Paranoplocephala variabilis (Douthitt, 1915) Baer, 1927 - (44).

Nematoda

Heligmosomum polygyrum (Dujardin, 1845) Railliet et Henry, 1909
- (44).

Heligmosomum dubius (Baylis, 1926) Tenora, 1958 - (this paper).

Clethrionomys gapperi

Trematoda

Plagiorchis sp. - (68).

Cestoda

Andrya macrocephala Douthitt, 1915 - (44) (47) (68).

Andrya primordialis Douthitt, 1915 - (13) (26) (44).

Andrya sp. - (68).

Paranoplocephala sp. - ? - (15) (66).

Hymenolepis horrida (von Linstow, 1900) - (44) (47) (68) (this
paper).

Catenotaenia dendritica (Goeze, 1782) Janicki, 1904 - (41) (44)
(47) (60) (68) (this paper).

C. gapperi

Cestoda

Taenia mustelae Gmelin, 1790 - larvae - (44) (68) (this paper).

Taenia rileyi Loewen, 1929 - (47).

Cladotaenia mirsoevi Skrjabin and Popov, 1924 - larvae (?) - (44).

Cladotaenia globifera (Batsch, 1786) Cohn, 1901 - larvae - (23).

Paruterina candelabraria (Goeze, 1782) - larvae (exp.) - (22).

Nematoda

Capillaria hepatica (Bancroft, 1893) Travassos, 1915 - eggs in
liver - (19).

Heligmosomum carolinensis (Dikmans, 1940) Skrjabin et al., 1954
- (8) (68).

Syphacia obvelata (Rudolphi, 1802) Saurat, 1916 - (27) (47)
(this paper).

Aspiculuris tetraptera (Nitzsch, 1821) Schultz, 1924 - (this
paper).

Mastophorus muris (Gmelin, 1790) Diesing, 1853 - (47) (68).

Reticularia microti McPherson and Tiner, 1952 - (47).

Pelodera sp. - (this paper).

Microtus longicaudus

Cestoda

Andrya primordialis Douthitt, 1915 - (41) (55).

Paranoplocephala infrequens (Douthitt, 1915) Baer, 1927 - (39)
(this paper).

Hymenolepis diminuta (Rudolphi, 1819) Weinland, 1858 - (55).

Hymenolepis horrida (von Linstow, 1900) - (71) (this paper).

M. longicaudus

Cestoda

Taenia mustelae Gmelin, 1790 - larvae - (this paper).

Nematoda

Heligmosomum carolinensis (Dikmans, 1940) Skrjabin et al., 1954
- (this paper).

Heligmosomum costellatum (Dujardin, 1845) Railliet et Henry, 1909
- (this paper).

Heligmosomum longispiculatus (Dikmans, 1940) Skrjabin et al.,
1954 - (60).

Syphacia obvelata (Rudolphi, 1802) Seurat, 1916 - (39) (41) (55)
(this paper).

Aspiculuris tetraptera (Nitzsch, 1821) Schultz, 1924 - (this
paper).

Mastophorus sp. - (this paper).

Reticularia coloradensis Hall, 1916 - (55).

Pelodera sp. - (this paper).

Microtus montanus

Trematoda

Quinqueserialis hassalli (McIntosh and McIntosh, 1934) Harwood,
1939 - (39) (74).

Cestoda

Andrya macrocephala Douthitt, 1915 - (39) (this paper).

Andrya primordialis Douthitt, 1915 - (39) (41) (55) (63).

Paranoplocephala infrequens (Douthitt, 1915) Baer, 1927 - (39)
(this paper).

M. montanus

Cestoda

Paranoplocephala variabilis (Douthitt, 1915) Baer, 1927 - (39).

Hymenolepis horrida (von Linstow, 1900) - (39) (71).

Nematoda

Heligmosomum costellatum (Dujardin, 1845) Railliet et Henry,
1909 - (39).

Heligmosomum microti (Kuns and Rausch, 1950) n. comb. - (39).

Syphacia obvelata (Rudolphi, 1802) Seurat, 1916 - (39) (41) (42)
(55) (this paper).

Microtus pennsylvanicus

Trematoda

Plagiorchis muris Tanabe, 1922 - (68) (this paper).

Mediogonimus ovilacus Woodhead and Malewitz, 1936 - (66) (87).

Brachylaema sp. - (60).

Entosiphonus thompsoni Sinitzin, 1931 - (66).

Quinqueserialis quinqueserialis (Barker and Laughlin, 1911)

Skvortsov, 1934 - (14) (31) (50) (60) (68) (this paper).

Quinqueserialis hassalli (McIntosh and McIntosh, 1934) Harwood,
1939 - (31) (39) (45) (66) (74).

Monostoma sp. - (79).

Nudacotyle novicia Barker, 1916 - (1) (2).

Schistosomatium douthitti (Cort, 1915) Tanabe, 1923 - (53).

Schistosomatium sp. - (51).

Alaria mustelae Bosma, 1931 - larvae (exp.) - (15).

M. pennsylvanicus

Cestoda

Andrya macrocephala Douthitt, 1915 - (25) (39) (44) (57) (63)
(66) (68).

Andrya primordialis Douthitt, 1915 - (13) (26) (39) (41) (44).

Andrya sp. - (15) (66).

Paranoplocephala infrequens (Douthitt, 1915) Baer, 1927 - (25)
(39) (44) (56) (60) (66) (68) (this paper).

Paranoplocephala variabilis (Douthitt, 1915) Baer, 1927 - (44)
(60) (68) (this paper).

Hymenolepis horrida (von Linstow, 1900) - (44) (71) (this paper).

Hymenolepis sp. (?) - (25).

Rodentolepis evaginata (Barker and Andrews, 1915) Spasskii, 1954
(14) (66).

Rodentolepis johnsoni (Schiller, 1952) Yamaguti, 1959 - (60) (70).

Vampirolepis fraterna (Stiles, 1906) Spasskii, 1954 - (66).

Echinococcus multilocularis Leuckart, 1863 (exp.) - larvae - (65).

Echinococcus sp. (exp.) - larvae - (60).

Taenia mustelae Gmelin, 1790 - larvae - (43) (44) (68).

Taenia taeniefornis Batsch, 1786 - larvae - (15) (66) (this paper).

Taenia sp. - larvae - (66).

Cladotaenia sp. - larvae - (66) (= T. mustelae Gmelin, 1790 -
(21) (60)).

Nematoda

Trichuris opaca Barker and Noyes, 1915 - (66) (81).

Trichuris sp. - (25)

M. pennsylvanicus

Nematoda

Heligmosomum carolinensis (Dikmans, 1940) Skrjabin et al., 1954
- (this paper).

Heligmosomum longispiculatus (Dikmans, 1940) Skrjabin et al.,
1954 - (8).

Heligmosomum turgidum (Walton, 1923) Skrjabin et al., 1954 -
(84).

Heligmosomum sp. - (25) (66).

Longistriata dalrymplei Dikmans, 1935 - (7) (66).

Dictylocaulus viviparus (Bloch, 1782) Railliet et Henry, 1907 -
(66).

Syphacia obvelata (Rudolphi, 1802) Seurat, 1916 - (15) (16) (25)
(39) (41) (66) (68) (this paper).

Oxyuris sp. - (79).

Reticularia coloradensis Hall, 1916 - (44).

Mastophorus muris (Gmelin, 1790) Diesing, 1853 - (66).

Capillaria murissylvatici (Diesing, 1851) - (66).