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DISTRIBUTION AND SPECIFICITY OF HELMINTHS IN MICROTINE RODENTS: EVOLUTIONARY IMPLICATIONS

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Among those genera of microtine rodents having holarctic distribution, the parasitic helminths of North American representatives of *Dicrostonyx*, *Lemmus*, *Clethrionomys*, and *Microtus* are relatively well known. These helminths demonstrate a highly developed phylogenetic specificity, being restricted essentially to the Microtinae, but few show any evidence of host-specificity at the generic level. Both nematodes and cestodes are prevalent endoparasites of these rodents in boreal North America. For the purposes of the present work, emphasis is placed upon the cestodes, most of which are members of the subfamily Anoplocephalinae. Some of the latter are unusually interesting in that they occur in a variety of host-species over extensive geographic ranges. With the exception of *Paranoplocephala omphalodes* (Hermann, 1783), it has not been determined whether these cestodes are holarctic. It is evident, however, that some described from microtine rodents in Eurasia correspond morphologically to species in North America.

It appears in Alaska that significant relationships between the distribution of certain cestodes and the distribution of their hosts may be recognized. Any attempt to evaluate these apparent relationships is contingent upon determining whether or not these cestodes are holarctic. The study of this problem has now been undertaken in light of work published recently by Eurasian helminthologists and the acquisition of additional comparative material. This paper contains a review of the taxonomic status of anoplocephaline cestodes from microtine rodents and a discussion of some of the

evolutionary and zoogeographic implications of distribution and host-occurrence of these and other helminths.

I. *The genus Andrya*. Five species of *Andrya* parasitic in microtine rodents may be considered valid at the present time.

1. *Andrya macrocephala* Douthitt, 1915, is the most common cestode observed in species of *Microtus* in North America. Its unusually wide range of normal morphological variation (Rausch and Schiller, 1949a; Rausch, 1952) has led to the description of some of its variants as distinct species. *A. macrocephala* has been well characterized from North American material. Two species closely resembling *A. macrocephala* have been described in Eurasia; however, their validity is questionable. One of these, *A. bialowizensis* Soltys, 1949, has been reported only from Poland. *A. caucasica* Kirshenblat, 1938, was described from Transcaucasia.

It was suggested by Rausch and Schiller (1949a) that *A. caucasica* might be conspecific with *A. macrocephala*. This possibility was not considered by Spasskii (1951), in his monograph of anoplocephalid cestodes. Later, Spasskii, Romanova, and Naidenova (1951) made a survey of the helminth parasites of muskrats (an introduced species) in Russia, and from this host collected specimens of *Andrya* in the Kurgansk and Archangel'sk Oblasti. They also had cestodes of this genus from voles in Pribaikal'. These workers noted the lack of significant morphological differences between these specimens and the description of *A. macrocephala*. It was also observed that the cestodes from the voles of Pribaikal' did not differ in any essential way from *A. caucasica* and *A.*

bialowizensis. They concluded that the latter two species are either conspecific with *A. macrocephala* or that a distinct palearctic species exists which is morphologically indistinguishable from the latter. In this event, it was believed that *A. bialowizensis* would be a synonym of *A. caucasica*. However, since other criteria are lacking, the taxonomy of these cestodes can only be based upon their morphology. More recently, Żarnowski (1955) studied specimens of *Andrya* from voles from the environs of Puławy, Poland. He observed the usual wide range of morphological variation in this material, and concluded that *A. caucasica* is conspecific with *A. macrocephala*. Although Żarnowski did not consider the status of *A. bialowizensis*, it is morphologically identical with *A. macrocephala* and cannot justifiably be regarded as distinct. Consequently, *A. caucasica* Kirshenblat, 1938, and *A. bialowizensis* Sołtys, 1949, may be added to the list of synonyms of *A. macrocephala*.

2. *Andrya primordialis* Douthitt, 1915, was described from a squirrel, *Tamiasciurus*, in North America. At the same time, *A. communis* Douthitt, 1915, was described from a red-backed vole, but it was regarded as a synonym of the former by Baer (1927). According to Douthitt (1915), *A. primordialis* differs from *A. macrocephala* in having a prostate gland and unilateral genital pores. Satisfactory material for comparative study has not been available, and the status of this cestode remains indefinite (Rausch, 1952; Schad, 1954).

3. *Andrya montana* Kirshenblat, 1941, is known from voles from Georgia and Armenia (see Spasskii, 1951, p. 397). From Spasskii's description, it is apparent that this cestode resembles *A. primordialis* in having a prostate gland and unilateral genital pores.

4. *Andrya arctica* Rausch, 1952, is widely distributed in arctic North America, where it has been recorded from *Dicrostonyx*, *Lemmus*, *Clethrionomys rutilus*, and species of *Microtus*. A poorly

preserved cestode from *Lemmus lemmus*, collected at Enontekis, Finland, has been tentatively referred to this species (Rausch, 1952). This cestode may be holarctic in distribution.

5. *Andrya bairdi* Schad, 1954, is a unique form, known only from *Microtus chrotorrhinus* from the type locality (Quebec, Canada). It is characterized by unilateral genital pores and the absence of a prostate gland.

II. *The genus Paranoplocephala*. Six species of *Paranoplocephala* occurring in microtine rodents are recognized here:

1 and 2. *Paranoplocephala omphalodes* (Hermann, 1783) has been reported frequently from western Europe. Farther east in Poland, it was collected by Pojmańska (1956) from voles near Poznań, and by Sołtys (1949) from voles in the Białowieża Forest. Spasskii (1951) listed its occurrence in the following localities in Russia: Voronezh Oblast', Volga delta, Armenia, Georgia, West Siberia, and Chita Oblast'. In North America, it is known only from Alaska.

P. omphalodes as defined by Baer (1927) is a well characterized species. Its status is confused, however, by the fact that *P. blanchardi* (Moniez, 1891) is currently regarded by most workers as being synonymous with it. *P. blanchardi* was considered distinct by Baer (1927), in his monograph of the Anoplocephalidae. He later (1932) concluded that a single, variable species exists which, according to his definition, would be dimorphic. In support of his conclusion, he stated (p. 5), "En effet, la seule différence entre ces deux Cestodes réside dans le fait que chez *P. omphalodes*, les pores génitaux alternent irrégulièrement, tandis qu'ils sont unilatéraux chez *P. blanchardi*. D'autre part, *P. omphalodes* est beaucoup plus grand que *P. blanchardi*. Leurs anatomies sont identiques, tous deux ont 50 testicules par segment, une poche du cirrhe longue de 0,2 mm à 0,4 mm et des oeufs de 40 μ à 60 μ de diamètre. Or nous trouvons dans notre matériel un Ver long de 50 mm et large de 2 mm (*P.*

blanchardi), mais avec des pores génitaux alternants. D'autre part, nous trouvons des Vers longs de 80 mm et larges de 5 mm (*P. omphalodes*), mais avec les pores génitaux unilatéraux. Il n'existe donc pas de caractère spécifique valable permettant de séparer ces deux espèces l'une de l'autre. *P. omphalodes* ayant priorité sur *P. blanchardi*, ce dernier nom doit tomber en synonymie avec le premier." Cameron and Parnell (1933, p. 148) reached the same conclusion regarding the two species: "We found several specimens of this tapeworm in the small intestine of a vole from Caithness. In one, the genital pores were completely unilateral; in another they were irregularly alternating, about half a dozen to a dozen opening on one side to be succeeded by a similar number opening on the other. We have seen a similar phenomenon in specimens of *Hymenolepis diminuta* from the rat, and we are in agreement with Baer that *P. blanchardi* cannot be differentiated from *P. omphalodes* on this point and that the former name is a synonym of the latter."

Joyeux and Baer (1936, p. 44) stated that *P. omphalodes* may have either a length of 20 to 40 mm and unilateral genital pores, or a length of 100 to 215 mm with irregularly alternating pores. This view was reiterated by Baer (1949, p. 43).

Spasskii (1951, p. 307) reviewed this problem, after having studied cestodes from the Novosibirsk Oblast' which corresponded in some details with the description of *P. blanchardi*. He regarded the published accounts of the status of *P. blanchardi* as being "contradictory and incomplete" and gave a detailed description of the Novosibirsk specimens.

Cestodes from Alaska identified as *P. omphalodes* correspond to Baer's (1927) characterization in their relatively large size, in having irregularly alternating genital pores, in size of egg, number and distribution of testes, and size of the cirrus sac. They also were morphologically identical with specimens in the writer's possession from *Microtus* from

Belgium. In a series of more than 50 cestodes with gravid segments, most of which were collected from *Microtus* on St. Matthew Island, Alaska, nothing approaching the smaller form with unilateral genital pores was seen. It is difficult to believe that the range of normal variation in *P. omphalodes* would be so great as to account for the form designated as *P. blanchardi*. Arrangement of the genital pores (whether unilateral or irregularly alternating) provides an important differential character in the anoplocephaline cestodes; other than the findings of the European workers regarding *P. omphalodes-blanchardi*, there is no evidence that this character is subject to variation within a given species. The relatively wide range of morphological variation in *A. macrocephala*, for example, was never observed to include any deviation from the irregularly alternate arrangement of the genital pores (Rausch and Schiller, 1949a). The study of a large series of specimens from Europe should show a gradation in size if a single species were involved, rather than two non-intergrading size-groups. Apparently specimens of the larger size have never been observed to possess unilateral pores. It appears that *P. blanchardi* is a distinct species.

No cestodes conforming to the description of *P. blanchardi* have been found in North America. It may be that this form is the Eurasian counterpart of the nearctic *P. variabilis* (Douthitt, 1915). The latter and *P. neofibrinus* Rausch, 1952, resemble *P. blanchardi*, but in number of testes, size of cirrus sac, and size of egg are dissimilar. Further study of Eurasian material is needed.

3. *Paranoplocephala infrequens* (Douthitt, 1915) is a very common parasite of *Microtus* spp. in North America. It is distributed over much of the continent and is also morphologically variable (Rausch, 1952).

A cestode designated as *P. brevis* Kirshenblat, 1938, is recognized in Eurasia. Since first collected from voles in Georgia (Kirshenblat, 1938), it has been

recorded from several localities, and appears to be a relatively common cestode. Spasskii (1951) recorded *P. brevis* from Armenia and the Barbinskoi Steppe (Novosibirsk Oblast'). Żarnowski (1955) collected it in the environs of Puławy, and Pojmańska (1956) found it in voles from the vicinity of Poznań. Heretofore, *P. brevis* has not been reported west of Poland. It was suggested by Rausch and Schiller (1949b) that *P. brevis* may be conspecific with *P. infrequens*, since there appear to be no morphological differences. Spasskii (1951) stated (p. 312) in reference to *P. brevis*: "In its anatomomorphology and ecology (habitat in the large intestine of the vole) is an indication this species is identical with *P. troeschi* Rausch, 1946, described from a vole in North America." *P. troeschi* is a synonym of *P. infrequens* (Rausch and Schiller, 1949b). Morphological variation in *P. brevis* was observed by both Spasskii (1951), who published descriptions of specimens from Siberia and from the Transcaucasus, and by Żarnowski (1955). The writer has from Belgian voles specimens which are clearly referable to *P. infrequens* and indistinguishable from *P. brevis*. Since these cestodes are obviously identical, *P. brevis* becomes a synonym of *P. infrequens*.

4. *Paranoplocephala variabilis* (Douthitt, 1915) is distributed over much of North America, including Alaska, but is unknown from Eurasia. It is of interest, however, that the cestodes described by Spasskii (1951, p. 308) from the Novosibirsk Oblast' resemble *P. variabilis* in some of the more important diagnostic characters. *P. variabilis* is most often found in *Microtus* spp.

5. *Paranoplocephala lemmi* Rausch, 1952, is known only from boreal North America, where it occurs in *Lemmus*. This species, both morphologically and in its habitat requirement (cecum of the host), is similar to *P. infrequens*. *P. lemmi* may eventually be found to represent an extreme variant of *P. infrequens*.

6. *Paranoplocephala neofibrinus* Rausch, 1952, has been reported but once, from *Neofiber* in Florida. It certainly is not a part of the boreal fauna, and may be restricted to the one species of rodent. Additional work is needed to determine this.

DISCUSSION

The present work is concerned with the helminths occurring in microtine rodents of the genera *Dicrostonyx*, *Lemmus*, *Clethrionomys*, and *Microtus*. These mammals are closely related phylogenetically, and their digestive tracts have become similarly adapted to a diet of relatively coarse, fibrous vegetation. They appear to fulfill more or less uniformly the habitat requirements of several species of helminths, although there are a few which demonstrate a definite host-specificity.

Dicrostonyx and *Lemmus* are relatively quite restricted in their distribution, and rodents representing the four genera coexist only in high-boreal regions. Also, in these animals several species of helminths are present only at high latitudes. Of the latter, a few range widely over the North American continent but most of these are holarctic species with apparently limited distribution in North America. The relationships of the helminths in microtine rodents as observed in Alaska are summarized in table 1. These are discussed below only in reference to genus of the host, since, with the exception of *Microtus*, each genus is represented in Alaska by only one species, and besides, we cannot yet define any differences existing at the species level.

Since *Dicrostonyx* is not always isolated ecologically from *Lemmus* and *Microtus*, it would seem that frequent exposure to infection by a variety of helminths would be unavoidable. It may be seen from the table that *Dicrostonyx* has few helminths in common with the other genera, *Andrya arctica* and *Hymenolepis horrida* being the only cestodes showing little development of host-specificity. *Paranoplocephala variabilis* was reported

TABLE 1. Occurrence of the more common parasitic helminths in 4 genera of microtine rodents in Alaska

Parasites	Hosts			
	<i>Dicrostonyx</i>	<i>Lemmus</i>	<i>Clethrionomys</i>	<i>Microtus</i>
Cestoda:				
* <i>Andrya macrocephala</i> Douthitt, 1915				X
<i>A. arctica</i> Rausch, 1952	X	X	X	X
* <i>Paranoplocephala omphalodes</i> (Hermann, 1783)				X
* <i>P. infrequens</i> (Douthitt, 1915)				X
<i>P. variabilis</i> (Douthitt, 1915)				X
<i>P. lemmi</i> Rausch, 1952		X		
* <i>Hymenolepis horrida</i> (von Linstow, 1901)	X	X	X	X
* <i>Catenotaenia dendritica</i> (Goeze, 1782)			X	
* <i>Echinococcus multilocularis</i> Leuckart, 1863		X	X	X
* <i>Taenia mustelae</i> Gmelin, 1790		X	X	X
* <i>T. crassiceps</i> Rudolphi, 1810		X		X
* <i>T. polyacantha</i> Leuckart, 1856		X		X
Nematoda:				
<i>Nematospiroides</i> spp.		X	X	X
<i>Heligmosomum hudsonius</i> Cameron, 1937	X			
* <i>H. costellatum</i> (Dujardin, 1845)				X
* <i>Mastophorus muris</i> (Gmelin, 1790)			X	
<i>Syphacia arctica</i> Tiner and Rausch, 1950	X			
* <i>S. obvelata</i> (Rudolphi, 1802)			X	X
Trematoda:				
<i>Quinqueserialis</i> spp.				X

* Species known to be holarctic.

in *Dicrostonyx* in eastern Canada (Schad, 1954), and, of the larval cestodes, only those of *Taenia crassiceps* have been found in the collared lemming, and these in northern Canada (Rausch, 1952). In localities where *Lemmus* and *Dicrostonyx* occur together, a high proportion of the former may be found infected with the larval cestode, *Taenia mustelae*, the latter never. The definitive hosts of this cestode are *Mustela erminea* and *M. rixosa*, both frequently coexisting with the brown and collared lemmings. It would again seem that exposure to infection would be inescapable for *Dicrostonyx*. Further, larvae of *Echinococcus multilocularis* in experimentally-induced infections developed abnormally in *Dicrostonyx* as compared to *Lemmus* and *Microtus* (Rausch and Schiller, 1956). Two species of nematodes, however, are known only from *Dicrostonyx*; both, *Syphacia arctica* and *Heligmosomum hudsonius*, are found in

the cecum, the latter coiled around the cecal villi.

The helminth fauna of *Lemmus* is much like that of *Microtus*. Only one cestode appears to be specific to *Lemmus*, *Paranoplocephala lemmi*, which is presently regarded as distinct from *P. infrequens*, although they are alike morphologically and ecologically; both are found in the cecum of the host. *Lemmus* can serve equally well with *Clethrionomys* and *Microtus* as an intermediate host for *E. multilocularis*.

Although the helminths of *Synaptomys* are poorly known, its affinities in this connection appear to be with *Microtus*. From the few specimens examined in Alaska, the writer has collected *Paranoplocephala infrequens* and the larval *Taenia mustelae*. *P. variabilis* has also been recorded from *Synaptomys* (Rausch, 1952), and in eastern Canada, Schad (1954) collected *P. infrequens* and *T. tenuicollis* (= *T. mustelae*).

Besides *Dicrostonyx*, the tribe Lemmini contains the genera *Lemmus*, *Synaptomys*, and *Myopus* (Simpson, 1945). According to Hinton (1926, p. 35), "*Dicrostonyx* is fundamentally the most primitive of the lemmings, and is by its structure one of the most isolated genera of the subfamily." The intestine of *Dicrostonyx* is modified to a degree not seen in the other genera considered here, in that the cecum possesses strongly developed villi (see Voge and Bern, 1955). In *Lemmus* and the nearctic *Synaptomys*, the cecum lacks villi and the intestinal tract more closely resembles that of *Microtus*. The writer has no information on the anatomy of the palearctic *Myopus*, whose helminths apparently have not been investigated.

In the writer's opinion, the host-parasite relationships discussed above clearly support Hinton's view that *Dicrostonyx* occupies an isolated position in the Microtinae. Excepting *Myopus*, for which little information is available, it might be said that *Dicrostonyx* differs more from the other genera of the tribe in important details of its structure and in its helminth fauna than the latter do from some members of the Microtini (e.g., *Microtus*).

The genera *Clethrionomys* and *Microtus* are included in the tribe Microtini. *Clethrionomys* is distributed over most of Alaska, where it is commonly found in the boreal forests, but it also occurs beyond the forest limits and may coexist at times with *Dicrostonyx*, *Lemmus*, and species of *Microtus*. In addition to those listed in Table 1, *Andrya macrocephala* has been reported from *Clethrionomys* in eastern Canada (Schad, 1954), and a questionable record of *Paranoplocephala infrequens* was given for Minnesota (Rausch and Tiner, 1949). The identity of the *Syphacia* in the red-backed vole has not been certainly defined, but excluding the possibility that it is host-specific, the only helminth of red-backed voles not known in other microtine rodents is the cestode, *Catenotaenia dendritica*. The latter has been collected from animals taken in forested regions,

so it is possible that its occurrence is more dependent upon the habitat of the host than upon host-specificity. The same possibility of an ecological specificity exists in the case of *Mastophorus muris* (Rausch, 1952; Schad, 1954). This nematode parasitizes *Microtus* in central North America.

The species of *Microtus* comprise a particularly homogeneous group, and the study of their helminths in North America has shown few differences in host-occurrence which cannot be explained as an effect of extrinsic factors (e.g., dissimilarities in the habitats of the hosts; restricted geographical distribution of certain species of helminths) (Rausch and Tiner, 1949; Rausch, 1952). But for *P. lemni*, *P. neofibrinus*, and *A. primordialis*, all the species of anoplocephaline cestodes in North American microtine rodents have been reported from species of *Microtus*. *Andrya bairdi*, however, is known only from *M. chrotorrhinus*. Structurally, this vole is "... quite unique in the subgenus *Microtus*" (Bailey, 1900, p. 58), and has a relatively limited range in eastern North America. Further investigation may prove that *A. bairdi* is specific for *M. chrotorrhinus*.

The occurrence of certain cestodes in *Microtus* spp. on islands in the Bering Sea suggests that they had differentiated before the end of the Pleistocene period, and prior to considerable evolutionary divergence in their hosts. *Paranoplocephala omphalodes* and *P. infrequens*, for example, are found in *M. abbreviatus* on St. Matthew Island. The St. Matthew group of islands is regarded as having been isolated since some time prior to the last Pleistocene glaciation, when the last land-bridge between North America and Eurasia was present (Walters, 1955). Although some controversy exists as to whether *M. abbreviatus* is more closely related to *M. oeconomus* or to voles of the subgenus *Stenocranius* (represented by *M. gregalis* in Siberia, and by *M. miurus* in boreal North America), it is nevertheless specifically distinct. This

suggests that the precursor of *M. abbreviatus* reached the St. Matthew Islands long before certain other species of microtine rodents invaded North America, probably via the last land-bridge (cf. Gilmore, 1942). Some of the latter, such as the holarctic *Microtus oeconomus* and *Clethrionomys rutilus*, have diverged little in continental North America. That the cestodes *P. omphalodes* and *P. infrequens* could have been introduced to St. Matthew Island in more recent times is possible; infected mites conceivably might have been carried in by birds or in floating debris, but this seems most improbable.

The cestodes have not been investigated on the Pribilof Islands; since the latter are also in deeper water they would appear to have been isolated at least as long as the St. Matthew Islands. Here, the one species of microtine rodent present (*Lemmus*) is conspecific with that occurring on the North American continent. This fact, however, does not necessarily invalidate the hypothesis that the degree of divergence shown by *M. abbreviatus* is indicative of long isolation. On St. Lawrence Island, not isolated during the last Pleistocene glaciation, are found well differentiated subspecies of *M. oeconomus* and *C. rutilus*, both characterized by large size. *Andrya macrocephala* and *P. infrequens* have been collected here from *M. oeconomus*.

It appears, therefore, that anoplocephaline cestodes such as *Paranoplocephala omphalodes*, *P. infrequens*, and *Andrya macrocephala* existed in their present form prior to the invasion of North America by some of the species of microtine rodents now holarctic in their distribution. Relatively minor morphological changes have taken place in some of these rodents during and since the Pleistocene period, but there probably has been little or no change in their dietary habits, and none in their alimentary canals. Consequently, with little change in the habitats of the cestodes, it is probable that they have long been genetically stabilized.

Since some of these cestodes are now

widely distributed over two continents, it is impossible to determine whether their origin was Eurasian or North American. However, it seems significant that the known North American range of *P. omphalodes* on the continent corresponds approximately to that of two holarctic species of voles, *Microtus oeconomus* and *Clethrionomys rutilus*, considered to be palearctic in origin (Gilmore, 1942; Zimmermann, 1942).

SUMMARY

The taxonomic status of anoplocephaline cestodes of microtine rodents has been reviewed. Of the genus *Andrya* Railliet, 1883, five species are considered valid: *A. macrocephala* Douthitt, 1915; *A. primordialis* Douthitt, 1915; *A. montana* Kirshenblat, 1941; *A. arctica* Rausch, 1952; *A. bairdi* Schad, 1954. Of the genus *Paranoplocephala* Luehe, 1910, six species are regarded as valid: *P. omphalodes* (Hermann, 1783); *P. blanchardi* (Moniez, 1891); *P. infrequens* (Douthitt, 1915); *P. variabilis* (Douthitt, 1915); *P. lemmi* Rausch, 1952; *P. neofibrinus* Rausch, 1952. *Andrya caucasica* Kirshenblat, 1938, and *A. bialowizensis* Sołtys, 1949, are regarded as synonyms of *A. macrocephala*. *Paranoplocephala brevis* Kirshenblat, 1938, is regarded as a synonym of *P. infrequens*. Three species, *A. macrocephala*, *P. omphalodes*, and *P. infrequens*, are holarctic in distribution, occurring mainly in species of *Microtus*.

The uniformity of microtine rodents as hosts for various helminths has been discussed. It is concluded that *Dicrostonyx* is the most isolated genus from this standpoint, having two nematodes which have not been recorded from members of other genera, and harboring few helminths in common with others. This agrees with Hinton's conclusions, based on morphological characters of *Dicrostonyx*.

From the present concept of Pleistocene glaciations, it is concluded that *P. omphalodes* and *P. infrequens* reached the St. Matthew Islands, in Bering Sea, as parasites of a vole from which *Microtus ab-*

breviatus has evolved. It appears that this vole arrived on these islands before North America was invaded, in the late Pleistocene, by the palearctic *M. oeconomus* and *Clethrionomys rutilus*. The present known distribution of *P. omphalodes* in North America corresponds about to that of *M. oeconomus* on the continent.

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