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OCCURRENCE AND DISTRIBUTION OF HYMENOLEPIDID CESTODES IN SHREWS

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A survey of the literature dealing with cestodes of shrews reveals the increasing interest of contemporary parasitologists in this poorly known group of symbionts. In the United States approximately 18 species have been described from shrews in the last 15 years. These reports deal almost exclusively with morphology of the cestodes; however, information on distribution, host specificity, rate and intensity of infection, is either fragmentary or not available in published form.

Examination of autopsy data from a relatively large number of shrews, collected primarily by Rausch, enabled us to obtain some information on the subjects listed above. During the study of our material, it also became desirable to compare some of the data from our shrews with those obtained from shrews elsewhere and to extend this comparison to other vertebrate groups, specifically with reference to infection with hymenolepidid cestodes.

The present study is based on an examination of 452 shrews belonging to 11 species collected during the last 10 years in the United States and in Alaska. Numbers and kinds of cestodes found in each shrew were recorded; all the material obtained from each host was preserved.

We are indebted to several workers for their help in the collection of the shrews: Mrs. Betty Locker Pope, 914 E. 61st St., Chicago 37, Illinois; Mr. Everett Schiller, U. S. Public Health Service, Anchorage, Alaska; and Dr. Oliver P. Pearson, Museum of Vertebrate Zoology, University of California, Berkeley.

HOST DISTRIBUTION OF THE SPECIES OF *HYMENOLEPIS* IN VERTEBRATES

At present, the genus *Hymenolepis* Weinland, 1858, contains approximately 400 species. The majority of these occur in birds and only a relatively small number parasitize mammals. Over 100 species have been reported from ANSERIFORMES, about 44 species from CHARADRIIFORMES, 36 from PASSERIFORMES, 18 from CICONIIFORMES, 16 each from GALLIFORMES and GRUIFORMES, 10 from COLUMBIFORMES, 8 from PELECANIFORMES and three or less from the remaining orders of birds (Hughes, 1940). Judging from the available host lists, host specificity of avian hymenolepidids is relatively low. *Hymenolepis coronula* (Dujardin, 1845) is known to parasitize 10 species of ducks, and *H. serpentulus* (Schränk, 1788) 25 species of passeriforms. Others may occur in hosts belonging to as many as three orders of birds. However, with the exception of *H. lanceolata* (Bloch, 1782), the species which parasitize birds have not been found in mammals.

The species of *Hymenolepis* in mammals differ considerably from those in birds

in their distributional pattern. Not only is the number of species reported from mammals much smaller (approximately 90, as compared to several hundred in birds), but there is also less overlap in occurrence among different orders of mammals. The only known ordinal overlap is that of *H. nana* (von Siebold, 1852) and *H. diminuta* (Rudolphi, 1819), which occur in both rodents and primates. Of the ninety or so species of *Hymenolepis* parasitizing mammals, 4 only have been reported from primates, about 25 from rodents, 8 from chiropterans, 1 from marsupials, 1 from carnivores, and about 50 from insectivores. None has been reported from lagomorphs, ungulates, or herbivores generally, or from the marine mammals. From the foregoing it is evident that in mammals the genus *Hymenolepis* has become adapted most successfully to species of INSECTIVORA: these are parasitized by a number of species larger than the combined total number found in all other mammalian groups. This relationship is even more obvious when one considers that the living genera of rodents (with 25 species of *Hymenolepis*) number 344, and the living genera of insectivores only 71 (Simpson, 1945). Furthermore, it is probable that rodents have been more thoroughly investigated than have insectivores, primarily because insectivores are more limited in distribution and caught with relative difficulty (Pearson, 1954). Also, because of their small size, many of the internal parasites of insectivores, including hymenolepidids, probably still await recognition and description.

Within the order INSECTIVORA, the shrews are hosts to more than 30 of the 50 or so hymenolepidids described to date. Sixteen of these, including 2 species of the genus *Protoprymella* Jones, and *Diorchis reynoldsi* Jones (see Schiller, 1953), were described from shrews in North America. Although no thorough comparative study has been made, the available evidence suggests that the North American species are distinct from European ones. From available North American and European data it is also apparent that the species which parasitize shrews are not found in families other than the SORICIDAE, although it will be seen that host specificity does not extend to the different soricid species.

HYMENOLEPIDID CESTODES IN SHREWS

Before attempting to analyze the hymenolepidid cestodes of shrews in greater detail, it should be mentioned that the cestode fauna of these mammals is with few exceptions limited to members of the HYMENOLEPIDIDAE. The only non-hymenolepidid cestodes described from North American shrews are the dilepidid, *Liga soricis* Neiland, and the linstowiid, *Oochoristica pennsylvanica* Chandler. *Choanotaenia* sp. has been found in shrews in Alaska. The only non-hymenolepidid cestodes described from European shrews are two species of the dilepidid genus *Choanotaenia*. Recently (Soltys, 1953) a species of *Dicranotaenia* (syn. *Hymenolepis*) was described from shrews in Poland. This lack of variety in cestode parasites is somewhat surprising and is reminiscent of the situation in ruminants and horses, in which the adult cestode fauna is essentially limited to different anoplocephaline genera.

Among the hymenolepidid cestodes of shrews, one observes certain indications of trends in morphological patterns and specializations. The most obvious one is very small body-size, which, in a general way, can be correlated with the small size of the hosts. The mature strobila in some of the species is less than one-half millimeter long. In the largest species, the strobila attains a length of 100 mm. (*H.*

anthocephalus Van Gundy). In 11 European species, strobilar length is not more than 10 mm. The longest European specimen known to us (Rausch, unpublished) measures over 50 mm. Most of the hymenolepidids described from non-sorcid insectivores (moles, hedgehogs) are considerably larger. This does not mean that small tapeworms, or specifically small hymenolepidids, always occur in relatively small hosts, nor is it to be understood that relatively large tapeworms never occur in small host species. It is desirable, however, to emphasize that shrews as a group are the smallest mammals and that they harbor a relatively large number of the smallest tapeworms described.

The shape of the strobila is distinctive and even diagnostic for some of the very small hymenolepidids (Plate 1). Terminal gravid proglottids may differ markedly in size and shape from preceding proglottids, so that the transition between gravid and other parts of the strobila may be very abrupt. In addition, the relatively small number of proglottids as well as the structure of the cirrus or vagina, may contribute to distinctiveness in shape of the strobila in different species. In *H. virilis* Voge, for example, the cirrus is proportionately very large and bears relatively few, but unusually long and slender spines. In *H. sphenomorphus* Locker and Rausch, the terminal portion of the cirrus is enlarged, giving it a club-shaped appearance; in *H. intricatus* Locker and Rausch, the terminal portion of the vagina is highly modi-

TABLE I.—Incidence of tapeworm infection in shrews in California

Host species	Number examined	Number infected	Number uninfected
<i>Sorex bendirei</i>	4	4	0
<i>S. pacificus</i>	15	10	5
<i>S. vagrans</i>	19	13	6
<i>S. ornatus</i>	2	2	0
<i>S. trowbridgei</i>	5	5	0
<i>S. palustris</i>	2	2	0

fied. With the exception of the scolex of *Protogynella*, the scolices in American shrew hymenolepidids do not have any unusual features.

Examination of North American data on incidence, intensity of infection and multiple infection with hymenolepidid cestodes, shows that shrews are frequently, as well as heavily, parasitized animals. Of 138 *Blarina brevicauda* examined by one of us (Rausch) from 1943–1948 in Ohio, Michigan and Wisconsin, 52 (or 37%) were infected with tapeworms which, with one single exception, belong to the HYMENOLEPIDIDAE. Similarly, of 190 *Sorex cinereus* examined during 1947–1948 in Wisconsin, 91 (or 48%) were infected with hymenolepidids. No other tapeworms were found in this host. Of 47 shrews from California examined by Voge, 36 (or 77%) were infected with tapeworms. Only two of these hosts (*Sorex bendirei*) were infected with cestodes other than hymenolepidids (Table 1).

Of 50 *Sorex vagrans* collected by Betty Locker Pope in Oregon and Washington and examined by Rausch, 47 or 94% were infected with cestodes. Except for unidentified specimens from 7 of these hosts, all cestodes were hymenolepidids (*Hymenolepis* and *Protogynella*).

Intensity of infection varies considerably in different host individuals and seems to be correlated with general body-size of the tapeworm species involved. From our data, it appears that relatively large tapeworm species occur in smaller numbers and very small species in larger numbers, per host individual. Intensity of infection with *Hymenolepis anthocephalus* Van Gundy, and *Hymenolepis falculata* Rausch and Kuns is illustrated in Tables II and III.

TABLE II.—*Hymenolepis anthocephalus* in *Blarina brevicauda*

Number of worms	1	2	3	4	5	6	10	11	15	17*	21*	48*
Number of hosts	9	5	4	1	6	2	1	1	1	1	1	1

* Immature worms.

It is obvious that 1–5 specimens per host individual occur much more frequently than larger numbers of worms. It should be pointed out that no other cestodes were present in the hosts listed in Tables II and III. A similar numerical relationship was observed for *Hymenolepis horrida* (von Linstow) in the mouse *Peromyscus californicus* (see Voge, 1952). However, species of smaller body size tend to occur more frequently in large numbers. This is seen in Table IV which illustrates the distribution of *Hymenolepis parva* Rausch and Kuns, in *Sorex cinereus*.

Strobilar length in *H. parva* is about 5 mm. Strobilar lengths of *H. falculata* and *H. anthocephalus* are about 40 mm. and 100 mm., respectively. The few data available on intensity of infection with very small hymenolepidids measuring 2 mm. or less, indicate a tendency toward even higher numbers of specimens present in individual hosts. Specimen numbers for *Protogynella* in *Sorex cinereus* are as follows: 13, 87, 95, 245 (Rausch); in *Sorex vagrans*: 1, 1, 1, 3, 3, 4, 5, 5, 6, 7, 8, 10, 15, 30, 30, 35, 40, 50, although in this series, the majority of the hosts were infected

TABLE III.—*Hymenolepis falculata* in *Sorex cinereus*

Number of worms	1	2	3	4	5	6	9	13*
Number of hosts	10	7	4	2	2	1	1	1

* Immature worms.

with one or more species of *Hymenolepis* in addition to *Protogynella*; in *Blarina brevicauda*: 29, 260 (Oswald, 1955); in *Sorex trowbridgei*: 13, 39 (Voge).

Multiple infections with hymenolepidids, although relatively infrequent in the shrews examined from the Middle West, are commonly seen in shrews on the Pacific Coast. Of 21 shrews examined in California (Voge), 6 were infected with one hymenolepidid species, 9 with 2 species, 4 with 3 species and 2 with 4 species, so that 15 of the 21 shrews contained more than one species of hymenolepidids. Neiland (1953) reported 7 different cestode species from one *Sorex bendirei* in Oregon. Of 40 *Sorex vagrans* examined by Pope from various localities in Oregon and Washington, 11 were infected with one hymenolepidid species, 16 with 2 species, 12 with 3 species, and 1 with 4 species, giving a total of 29 of 40 host individuals infected with more than 1 species of hymenolepidids. This high incidence of multiple infections may be in part attributable to the fact that most of the North American species described from shrews do occur on the Pacific Coast. However, for many of the Eastern and Midwestern shrews no parasitological information is available at present.

Our records indicate a complete lack of host specificity of hymenolepidids in different species of shrews. *Hymenolepis parva* has been found in 7 species of

TABLE IV.—*Hymenolepis parva* in *Sorex cinereus*

Number of worms	1	2	3	4	5	7	9	10	11	12	15	18	20	25	30	39	50
Number of hosts	7	3	1	1	3	1	1	1	1	3	2	1	2	2	1	1	2

shrews, *H. falcata* in 5 species, *H. kenki* and *H. macyi* each in 4 species. With regard to geographic distribution, the available data indicate that some of these hymenolepidids occur in California, Oregon and Alaska (*H. sphenomorphus*), others (*H. parva*) in the Eastern and Western United States as well as in Alaska. New host records from Alaska are presented in Table V.

TABLE V.—Records of hymenolepis from shrews in Alaska

Sorex	Hymenolepis	Locality
<i>S. obscurus</i>	<i>H. parva</i>	Anaktuvuk Pass
	<i>H. falcata</i>	2 mi. S. Anchorage
	<i>H. sphenomorphus</i>	8 mi. S. Anchorage
	<i>H. intricatus</i>	6 mi. N. Anchorage
<i>S. cinereus</i>	<i>H. parva</i>	Nunivak Island
	<i>H. falcata</i>	2 mi. S. Anchorage
	<i>H. schilleri</i>	Katmai National Monument
	<i>H. sphenomorphus</i>	8 mi. S. Anchorage
<i>S. palustris</i>	<i>H. parva</i>	20 mi. NE. Anchorage

Additional records of hymenolepidids in Alaskan shrews were reported by Johnson and Clanton (1954) and Voge (1955). Thus it appears that the distribution of these cestodes is by no means restricted to small areas, and that their occurrence is probably limited only by the distribution of the definitive hosts and their intermediate hosts, although nothing definite is known about the latter. None of the hymenolepidids from shrews has been reported from hosts other than shrews.

DISCUSSION

In his classification of mammals, Simpson (1945, p. 175) made the following statement: "It is probable that the most characteristic insectivores, such as the erinaceoids and the soricoids, do belong to an order of unified origin." With this idea in mind, it is of interest to review the data of our parasitological investigations of these groups of insectivores. We have stated that the family SORICIDAE, in contrast to the TALPIDAE and ERINACEIDAE, harbors a morphologically distinct cestode fauna which is apparently restricted to the SORICIDAE. The TALPIDAE and ERINACEIDAE, on the contrary, harbor forms which, morphologically at least, conform to a common pattern, observed in non-soricid insectivores as well as in other mammals. One may infer from this observation that physiologically and ecologically at least, the SORICIDAE have diverged and specialized much more than have the TALPIDAE and ERINACEIDAE.

Such specializations would have to provide suitable ecological and physiological environments for the successful completion of life cycles of the cestode parasites in order to permit speciation within this group. It is apparent from the data presented in this study, that extensive speciation has occurred within the hymenolepidids of shrews. Therefore, a discussion of pertinent characteristics of the shrew hosts may be of interest. The first characteristic to be considered is food habits. It is known that many hymenolepidid cestodes of terrestrial vertebrates require an insect or other invertebrate intermediate host. Of the European hymenolepidids from shrews, *H. furcata* (Stieda, 1862) uses a beetle, and *H. pistillum* (Dujardin, 1843) a millipede (Joyeux and Baer, 1936). Analyses of contents of shrew stomachs (Johnson and Clanton, 1954) revealed a large number of insects belonging to several different orders, as well as spiders.

However, the insectivorous habit alone does not explain the high incidence of

infection, the frequent multiple infections, nor the relatively large number of species present in shrews generally. An explanation of some of these facts can probably be found in the extreme voraciousness of shrews (Pearson, 1954). The hazards involved in the successful completion of a cestode life cycle (viability and survival of eggs, availability and ingestion of infected intermediate hosts, infectivity of larval stages, etc.) are many and the loss of eggs and larval stages is bound to be extensive. A high infection rate as well as frequent multiple infection of the definitive host must reflect a relatively high infection rate of the intermediate hosts which are eaten in large numbers. The voraciousness of shrews may well be an important factor determining the high incidence of infection with hymenolepidids. The frequency of multiple infections with hymenolepidids may be in part explained by the variety of insects and other invertebrates consumed and by a minimal or non-existing cross immunity of the definitive host.

The most controversial question is that of speciation, particularly the external factors predisposing to speciation within the HYMENOLEPIDIDAE. As stated previously, among the mammals the INSECTIVORA and the shrews in particular harbor the largest number of species, while among the birds, the ANSERIFORMES harbor the largest number. The assumption that extensive speciation of the host group might be followed by extensive speciation of their parasitic fauna is possibly a reasonable one. However for a relatively homogeneous group such as the HYMENOLEPIDIDAE, this does not hold. Every group of parasites has specific requirements which are intimately associated with the ecology of their definitive as well as their intermediate hosts. A vertebrate group, no matter how numerous (in terms of genera and/or species) is a suitable host for any given type of parasite only if it has the ecological and physiological specializations essential for the completion of the life cycle of the parasite. One example is that of anseriform and falconiform birds with approximately 64 and 89 genera respectively. While there are over 100 species of *Hymenolepis* described from ANSERIFORMES, only two have been reported from FALCONIFORMES, one of these two species being a frequent parasite of passeriform birds, *H. passeris* (Gmelin, 1790), and probably accidentally ingested by the hawk (*Accipiter nisus*). As far as known, the intermediate hosts of *Hymenolepis* spp. in anseriforms are various crustaceans, *H. collaris* (Batsch, 1786), *H. coronula* (Dujardin, 1845), and molluscs, *H. microsoma* (Creplin, 1829). Adaptation to the food habits of this group of birds is obvious.

Extensive speciation of hymenolepidids in shrews must be in part related to food habits, both qualitative and quantitative; assuming that the amount of insects consumed is proportional to the infection rate and survival of the hymenolepidid population, there may be a greater opportunity for the survival of mutants when the infection rate is high. It is likely that a relatively dense and stable host population which maintains a constantly high infection rate over long periods of time is an important condition for speciation of the parasitic fauna of this host population.

The paucity of cestodes other than hymenolepidids in shrews cannot be explained satisfactorily on the basis of food habits. One might expect better representation of davaineids, linstowiids and dilepidids, members of which are known to employ insect or other invertebrate intermediate hosts.

The frequency of numbers by which certain species are represented in their hosts, deserves comment. Li and Hsü (1951) reported that "the most frequent

numbers of worms in their naturally infected hosts are the lowest numbers, especially of one or two worms." Their findings are in accord with the data on shrew hymenolepidids presented in this study, at least with respect to species of relatively large body-size. The species of very small body-size, however, are more often represented by larger numbers. This phenomenon may well be related to the total amount of usable intestinal space which is available to a given tapeworm species, and which provides the necessary physiological niches as well as sufficient food for the individuals of this tapeworm species. Thus the amount of living adult tapeworm tissue in any vertebrate host is limited by the intestinal environment provided by the host; in any given situation, more living space is probably available for large numbers of small individuals than for large numbers of large individuals, as illustrated to some extent by experiments on the "crowding effect" (Read, 1951). Unfortunately, little is known about differences in specific environmental requirements of different species of hymenolepidid tapeworms.

SUMMARY AND CONCLUSION

From the evidence presented in this report, certain conclusions may be reached. Among the mammals, hymenolepidid cestodes have attained their greatest development in the soricid insectivores which harbor more species than any other group of mammals. The cestode fauna of soricid insectivores is, with few exceptions, limited to the family HYMENOLEPIDIDAE.

The hymenolepidid species in shrews are morphologically distinct from hymenolepidids in non-soricid insectivores or in other mammals. They seem to be much more host-group specific than are other hymenolepidids. The species occurring in shrews have not been found in non-soricid hosts. Conversely, hymenolepidids described from non-soricid mammals have not been reported from shrews. From the evidence available, it may be concluded that host specificity of hymenolepidids of insectivores and particularly of shrews is much more pronounced than that of other hymenolepidids.

Hymenolepidid species described from North American shrews do not occur in Europe, and the European species do not occur in America. However, several of the hymenolepidid species from North American shrews have a wide distribution which includes various areas of the United States and Alaska (see new host records presented above).

The high infection rate as well as the high incidence of multiple infections with hymenolepidid cestodes in shrews is largely a reflection of the food habits of the hosts. The nature of the food as well as the quantity consumed play an important role in the rate as well as the intensity of infection. From the high incidence of multiple infections it may be concluded that cross immunity of the shrew host is relatively low and that the different hymenolepidid species have achieved a high level of physiological compatibility.

Hymenolepidid species of relatively large body size occur most frequently in low numbers in individual shrew hosts; species of very small body size are frequently present in large numbers.

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EXPLANATION OF FIGURES

All drawings made with the aid of a camera lucida.

- FIG. 1. *Hymenolepis virilis* Voge, 1955.
- FIG. 2. *H. sphenomorphus* Locker and Rausch, 1952.
- FIG. 3. *H. parvissima* Voge, 1953.
- FIG. 4. *H. macyi* Locker and Rausch, 1952.
- FIG. 5. *H. intricatus* Locker and Rausch, 1952.

PLATE I

