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ECTOPARASITES OF NORTH AMERICAN AQUATIC RODENTS AND COMPARISON TO EUROPEAN FORMS

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ABSTRACT. The four species of large aquatic rodents of North America (*Castor canadensis*, *Ondatra zibethicus*, *Neofiber alleni*, and *Myocastor coypus*) have similar ectoparasite assemblages in that all are host to abundant, tiny hair-clasping listrophoroid mites that move up and down individual hairs, and 1 to 3 species of larger parasites. The American and Eurasian beavers each harbor large numbers of mites in the genus *Schizocarpus*. *Schizocarpus mingaudi* occurs on both species, whereas 16 and 32 additional species occur on the American and Eurasian beavers, respectively. The common (*O. zibethicus*) and the round-tailed (*N. alleni*) muskrats each harbor mites of the family Listrophoridae, 6 species of *Listrophorus* on *Ondatra*, and two species of *Listrophorus* and one of *Prolistrophorus* on *Neofiber*. Two species of *Listrophorus*, *L. kingstownensis* on *Ondatra* and *L. laynei* on *Neofiber*, are quite similar, consistent with the close phylogenetic relationship of the two muskrats. In addition, a tiny hypopial glycyphagid mite, *Zibethacarus ondatrae*, occurs on the American muskrat. The tiny mites of the other two rodent genera belong to different families; *Schizocarpus* (Chirodiscidae) on *Castor*, and *Myocastorobia myocastor* (Atopomelidae) on *Myocastor*. The 5 larger parasites consisted of a beetle (*Platypsyllus castoris*) on the beaver, *Laelaps multispinosa* on the common muskrat, *Laelaps evansi* and *Androlaelaps fahrenholzi* on the round-tailed muskrat, and a chewing louse, *Pitrufquenia coypus*, on the nutria. All of these are host specific except for *A. fahrenholzi* which occurs on numerous hosts. Across host taxa, parasite assemblages are similar in structure, probably because of ecologically similar aquatic habitats. However, the taxonomic affinities of the four mammal species are quite different, and therefore it is not surprising that likewise the parasite groups are diverse.

KEY WORDS: Aquatic Rodents, Ectoparasites, Beaver, Muskrat, Round-Tailed Muskrat, Nutria, *Castor, Ondatra, Neofiber, Myocastor*

INTRODUCTION

Four large aquatic rodent species occur in North America; the beaver, *Castor canadensis* Kuhl, 1820; the muskrat, *Ondatra zibethicus* (Linnaeus, 1766); the round-tailed muskrat, *Neofiber alleni* True, 1884; and the nutria (introduced from South America) *Myocastor coypus* (Molina, 1782). There is published information on the ectoparasite assemblages of the first three of these species, but relatively little on the nutria. Each of the three native species has an ectoparasite assemblage consisting of a complex of species of tiny hair-clasping mites in a single genus (2 genera in *Neofiber*), plus 1 or 2 larger ectoparasite species. Only one species of hair-clasping mite is known from the nutria (*Myocastorobia myocastor* Fain, 1970), but I suspected that it might harbor a complex of species, a situation similar to that found on the other three aquatic rodents.

The main objective of this paper is to compare and contrast the ectoparasite assemblages of these four large aquatic rodents, and to determine if adaptational themes have evolved in their ectoparasite assemblages. This included examination of nutrias from North America to determine if more than one species of tiny fusiform hair clasping mites of the genus *Myocastorobia* exists on this aquatic rodent as on the other host species.

MATERIALS AND METHODS

No data on mites of the nutria from North America have been published. Therefore I obtained two fresh nutria from Louisiana from James L. Wolfe (University of South Alabama, Mobile). They were examined visually using a 10 x 70 power binocular dissecting microscope. First the entire animal was examined for larger parasites. Second, ectoparasite samples were collected from 23 different sites (sites were about 8 square cm in area) on the animals and placed in separate vials of alcohol. They were later placed in a solution of alcohol with acid fuchsin stain, were mounted on slides in Hoyers Solution and ringed with Euparal. All other data presented here have been previously published (see accounts below).

Two individual nutria is a rather small host sample size. However, all individuals of all the other three aquatic rodents had multiple species on each individual, and even on the 2 × 2″ fur samples. Therefore, if we had a complex as occurred in the other three rodent hosts, we expect that they would have been evident even in a sample of two nutria, and/or would have been present on the nutria examined by Fain (1970) from South America.

THE ECTOPARASITE ASSEMBLAGES

Beaver, *Castor canadensis*

Trouessart (1896) first described beaver mites, *Schizocarpus mingaudi*, and indicated they occurred on both Eurasian (*C. fiber*) and North American beavers (*C. canadensis*). For more than half a century, workers simply assigned beaver mites to this species. Dubinina (1964) examined mites from the Eurasian beaver from Russia, and found *S.*

Table 1
Ectoparasites of beaver and their habitat affinities — *Castor canadensis* of North America, *Castor fiber* of Eurasia

North American Beaver	
Small hair-clasping mites	
***mingaudi* group** — head and front legs	***virgulatus* group** — chest, abdomen, inside of front legs
S. mingaudi Trouessart, 1896	*S. virgulatus* Fain et al., 1984
S. paramingaudi Fain et Whitaker, 1988	*S. subvirgulatus* Fain et al., 1984
S. alaskensis Fain et Whitaker, 1988	*S. inversus* Fain et al., 1984
S. reductus Fain et Whitaker, 1988	*S. furcatus* Fain et al., 1984
***indianensis* group** — dorsum and sides	*S. protinus* Fain et Whitaker, 1988
S. indianensis Fain et al., 1984	*S. posticus* Fain et Whitaker, 1988
S. tetrapilus Fain et al., 1984	***spinifer* group** — rare, but not localized
S. postannulatus Fain et Whitaker, 1988	*S. spinifer* Fain et al., 1984
S. centralis Fain et Whitaker, 1988	
S. contrarius Fain et Whitaker, 1988	
S. distinctus Fain et Whitaker, 1988	
Eurasian Beaver	
Small hair-clasping mites	
S. mingaudi Trouessart, 1896	*S. hexapilis* Fain et Lukoschus, 1985
S. brachyurus Dubinina, 1964	*S. humilis* Fain et Lukoschus, 1985
S. brevicauda Dubinina, 1964	*S. insignis* Fain et Lukoschus, 1985
S. capitis Dubinina, 1964	*S. intercalatus* Fain et Lukoschus, 1985
S. fedjushini Dubinina, 1964	*S. modestus* Fain et Lukoschus, 1985
S. grandis Dubinina, 1964	*S. ornatus* Fain et Lukoschus, 1985
S. latus Dubinina, 1964	*S. parabrachyurus* Fain et Lukoschus, 1985
S. minor Dubinina, 1964	*S. parahexapilis* Fain et Lukoschus, 1985
S. numerosus Dubinina, 1964	*S. pusillus* Fain et Lukoschus, 1985
S. parvus Dubinina, 1964	*S. pygidialis* Fain et Lukoschus, 1985
S. subminor Dubinina, 1964	*S. radiatus* Fain et Lukoschus, 1985
S. subparvus Dubinina, 1964	*S. similis* Fain et Lukoschus, 1985
S. brevis Fain et Lukoschus, 1985	*S. subdiebzigensis* Fain et Lukoschus, 1985
S. curtus Fain et Lukoschus, 1985	*S. subhexapilis* Fain et Lukoschus, 1985
S. diebzigensis Fain et Lukoschus, 1985	*S. subornatus* Fain et Lukoschus, 1985
S. dubininae Fain et Lukoschus, 1985	*S. ventricosus* Fain et Lukoschus, 1985
S. exiguus Fain et Lukoschus, 1985	
Large Parasite	
Coleoptera, P*latypsylla castoris* Ritsema	

mingaudi plus 11 new species (Table 1). All of the species were described on the basis of variations in the male sucker plate. Dubinina believed that the species evolved in relation to differing hair habitats on different parts of the beaver. Since Dubinina described the 11 new species, I examined Indiana beavers for *Schizocarpus*. This led to the discovery of eight species, *S. mingaudi* and 7 additional new ones (Fain et al. 1984). Moreover, an additional 9 species of the genus were described from American beavers later from different localities (Alaska, Massachusetts, Maine; Fain and Whitaker 1988), bringing to 17 the number of *Schizocarpus* currently known from North American beavers.

From three Eurasian beavers, *Castor fiber*, Fain and Lukoschus (1985) found an additional 21 species of *Schizocarpus*, bringing the number of *Schizocarpus* from the Eurasian beaver to 33. There is much variation in mite assemblages among different parts of the beaver's body, with species groups occurring on particular regions of the beaver. The only large parasite of the beaver I found was a platypsyllid beetle, *Platypsyllus castoris* Ritsema, 1869, and it occurs on both beaver species (S.B. Peck, unpubl.). However, there is another beetle, *Leptinillus validus* Horn, 1872, which I did not find. It has a less intimate association with beavers and occurs only in the northern half of the range of the beaver and not in Eurasia (Stewart Peck, pers. comm.).

The species of *Schizocarpus* of the Eurasian beavers are distinct from those of the North American beavers, with the exception of the earliest described species, *S. mingaudi* Trouessart (1896). In light of the species richness of *Schizocarpus* infesting beaver, it is incredible that the one species described by Trouessart (1896) is unique among the 48 new species in that it occurs on both Eurasian and American hosts. We (Fain et al. 1984) disagree with Dubinina's (1964) suggestion that the species have evolved in relation to differing hair habitats. If that were the case it seemed that all stages of the mites would have evolved to fit the various habitats. The females and male juveniles did not. The female juveniles have sucker plates corresponding with those of the males and they remain attached to the males during their nymphal life. However, adult females and juvenile males are free living and do not have sucker plates, and to date nobody is able to separate the juvenile males and adult females to species because they are all so similar. We believe (Fain et al. 1984) that the differences between the sucker plates of the species have evolved as a means of species identification for the mites, i.e., allowing them to avoid hybridization as is the case among closely related birds (e.g., wood warblers and dabbling ducks). We have found multiple individuals of most of the species. We have also found a very few individuals that appear to be hybrids, further supporting this idea. It is of course possible that the individuals we called "hybrids" are actually aberrant individuals or yet additional new species. We tentatively called them hybrids because they were so few in number, and they were intermediate between other described species.

The tiny hair clasping mites of the beaver consist of *Schizocarpus mingaudi* on American and Eurasian beavers, at least 16 additional species on North American beavers, and at least 32 additional species on Eurasian beavers. From these data, it appears that only S. *mingaudi* was present when the American and Eurasian beavers diverged, and that speciation within *Schizocarpus* rapidly occurred. Speciation appears to be independent on each of the beaver species, and appears to be driven by geographic isolation. The species of *Schizocarpus* appear to be very closely related and recognize each other by the characteristic male and juvenile female sucker plates. This process of producing many species of one genus on a host has been called multiple speciation (Fain & Lukoschus 1985).

Finally, Dubinina et al. (1993) reported on 12 species of *Schizocarpus* from 14 *C. canadensis*, kept at the experimental beaver farm in the Voronezh, Russia). One was new, *S. anomalus* Bochkov, 1993 (Dubinina et al. 1993), and 4 (*S. paramingaudi* Fain et Whitaker, 1988; *S. spinifer* Fain, Whitaker et Smith, 1984; *S. centralis* Fain et Whitaker, 1988; and *S. inversus* Fain, Whitaker et Smith, 1984) were species from the North American beaver. Seven were parasites of Eurasian beavers [*S. grandis* (Dubinina, 1964); *S. latus* (Dubinina, 1964); *S. numerosus* (Dubinina, 1964); *S. parvus* (Dubinina, 1964); *S. subparvus* (Dubinina, 1964); *S. minor* (Dubinina, 1964); and *S. subhexapilis* Fain et Lukoschus, 1985]. Dubinina et al. (1993) indicated that "sustaining of beavers of both species in the same fur farm and impoverishment of ectoparasite fauna on the Canadian beaver under conditions unusual for it apparently favoured a transfer of mites from the European to Canadian beaver." This indicates how easily *Schizocarpus* mites can move from one beaver to another.

The origin of *Schizocarpus* on beavers is not clear. *Schizocarpus* is a chirodiscid mite, and most chirodiscids parasitize bats. However, there are a few chirodiscids on other species of mammals, including one on African otters (*Lutrilichus schoutedeni* Fain, 1970; Fain, 1972) which seems from the literature to be more similar to this species than others of which I am aware. Neither does *Platypsyllus* have any near relatives that might help determine its origin or the origin of beavers. Contributing to the high species richness of mites on beaver may be the three levels of isolation, i.e., between different geographic localities, between different host individuals, and between microhabitats on an individual host.

Muskrat, *Ondatra zibethicus*

The North American muskrat, *O. zibethicus*, has seven principal species, all mites (Table 2; Indiana hosts): five species of the genus *Listrophorus*; a glycyphagid hypopus, *Zibethacarus ondatrae* (Rupes et Whitaker, 1968); and a laelapid mite, *Laelaps multispinosa* (Banks, 1910) (Bauer and Whitaker 1981). We were surprised not to find *Myocoptes ondatrae* Lukoschus et Rouwet, 1968 and *Radfordia zibethicalis* (Radford, 1936) on muskrats from Indiana. Both have been found on this host in Michigan (OConnor, pers. comm.). An additional species of *Listrophorus*, *L. kingstownensis* Fain et Hyland, 1973, is known from New York and Rhode Island (Fain and Hyland 1974),

Table 2
Parasites of muskrat, round-tailed muskrat, and nutria

Common muskrat, *Ondatra zibethicus* (n = 40)	
North America	**Europe**
Small hair-clasping mites	
Listrophorus americanus Radford, 1944	*L. americanus*
Listrophorus dozieri Radford, 1944	*L. dozieri*
Listrophorus faini Dubinina, 1972	*L. faini* (as *validus*)
Listrophorus validus Banks, 1909	*L. validus* (as *grandior*)
Listrophorus ondatrae Fain et al., 1970	
Listrophorus kingstownensis Fain et Hyland, 1973	
Zibethacarus ondatrae (Rupes et Whitaker, 1968)	
Large parasites	
Laelaps multispinosa (Banks, 1910)	
Round-tailed muskrat, *Neofiber alleni* (Listrophoridae)	
Small hair-clasping mites	
Listrophorus laynei Fain et al., 1986	
L. caudatus Fain et al., 1986	
Prolistrophorus birkenholzi Fain et al., 1986	
Large parasites	
Laelaps evansi Tipton, 1960	
Nutria, *Myocastor coypus* (Atopomelidae)	
Small hair-clasping mites	
Myocastorobia myocastor Fain, 1970	
Large parasites	
Pitrufquenia coypus Marelli, 1932	

and three of the species of *Listrophorus* from muskrats are known from Alaska (Fain and Whitaker 1988), *L. faini* Dubinina, 1972, *L. americanus* Radford, 1944, and *L. dozieri* Radford, 1944. Four species of *Listrophorus* occur on Russian muskrats, *L. faini* (Dubinina called it *validus*), *L. americanus*, *L. dozieri*, and *L. validus* (Dubinina described it as *L. grandior*) (Dubinina 1967). Although the abundance of the various species of *Listrophorus* varies greatly across different parts of the muskrat, there is far more spatial overlap of species on this host than on the beaver. Hypopial mites are common on many species of small mammals. *Zibethacarus ondatrae* presumably evolved from a rodent parasite, probably a species of the genus *Glycyphagus*. Bauer and Whitaker (1981) regularly recovered two laelapid mites from muskrats — the host-specific species *Laelaps multispinosa* and *Androlaelaps fahrenholzi* (Berlese, 1911). The latter is widespread geographically and has been found on over 100 North American host species, showing its great adaptability, although it may constitute a complex of species. It is the only regularly occurring non-host specific parasite we found on any of the four species of rodents.

The hair-clasping mites of North American muskrats consist of six species of *Listrophorus* (Listrophoridae), and *Zibethacarus ondatrae*, a glycyphagid hypopus (non-feeding, transport stage). Adult glycyphagids are presumably in the muskrat nests. The muskrat was introduced into Eurasia in 1905, and at least four of the species of *Listrophorus* are on muskrats there. It appears that the muskrat mites have now stabilized (i.e., there is little evidence of recent speciation).

Round-tailed (or Florida) Muskrat, *Neofiber alleni*

The ectoparasite assemblage of *Neofiber* consists of three species of listrophorid mites — 2 of *Listrophorus*, and 1 of *Prolistrophorus* (Fain et al. 1986). *Listrophorus laynei* Fain, Smith et Whitaker, 1988 of *Neofiber* is quite similar to *L. kingstownensis* of *Ondatra*. The occurrence of listrophorids in general as the hair-clasping mites of both species, and the occurrence of the similar *L. kingstownensis* and *L. laynei* on the two species of muskrats indicate their close relationship, and that something near *L. kingstownensis* is probably the progenitor of *Listrophorus* on the muskrat species.

Prolistrophorus is found on *Sigmodon* and *Oryzomys* in the southeastern US. Its occurrence on *Neofiber* may represent a host switching event. The large parasites of *Neofiber* are *Laelaps evansi* Tipton, 1960 and *Androlaelaps fahrenholzi*. This latter species is the only non-host-specific regularly occurring ectoparasite of the large aquatic rodents. Smith et al. (1988) also reported an undescribed *Radfordia* near *R. zibethicalis*.

Ondatra and *Neofiber* harbor listrophorid mites of the genera *Listrophorus* (both muskrats) and *Prolistrophorus* (*Neofiber*), and these mites support the close relationship of the two muskrats, probably through a progenitor near *L. kingstownensis*.

Nutria, *Myocastor coypus*

The nutria is native to southern South America but has become widely established in the southeastern United States (Whitaker and Hamilton 1998). Fain (1970) described an atopomelid mite, *Myocastorobia myocastor* (Fain, 1970), from the nutria from South America. To our knowledge, there are no published records of this species from the nutria from North America (Whitaker and Wilson 1974; Whitaker, Wilson, and Ritzi, unpubl.), although G. W. Krantz may have a specimen from a nutria from Oregon (B. OConnor, pers. comm.). Fain indicates that this species attaches to the hairs in the anterior and posterior region of the host's body. *Myocastorobia* is an atopomelid mite, and atopomelids are common on many South American hystricomorph rodents, thus this host relationship is logical. Why this species has not undergone multispeciation we do not know. However, atopomelids do not generally undergo localization on the host, nor do they normally have several species per host, although rats of the genus *Maxomys* (Muridae) can have up to 5 species of *Listrophoroides* on a host (Bochkov and OConnor 2005). It was felt that this host would be especially interesting to examine for ectoparasites since the other 3 large aquatic rodents harbor multiple species of tiny hair-clasping mites, yet only one species had been found on this host.

A chewing louse (Mallophaga, Gyropidae, *Pitrufquenia coypus*) was described from the nutria from South America by Marelli (1932), and was also reported from that host from Louisiana (Miller 1956) and from Great Britain (Newson and Holmes 1968). The latter authors also reported four species of ticks from Great Britain, *Ixodes arvicolae* Warburton 1926 (n=39), *Ixodes ricinus* Linnaeus, 1758 (n=34), *I. trianguliceps* Birula, 1895 (n=2), and *I. hexagonus* Leach**,** 1815 (n=1). Harman et al. (1984) found 464 American dog ticks, *Dermacentor variabilis* (Say, 1821), on 66 nutria of 537 examined from Maryland.

Parasites of Nutria from Louisiana

An estimated total of about 4700 mites occurred on the two nutria examined, of which about 750 were collected and superficially examined. They were relatively uniformly distributed over the animal's bodies. A total of 391 individuals were mounted on slides and examined, usually 20 per sampling area if that many were present. Of the total examined, 233 were adult males, 104 were adult females, and 54 were nymphs. Fairly large numbers of mites (150–400 per site) were found in 17 of the sampling sites. Numbers in the other six sites varied from 3 to about 75 mites. Males predominated in 15 of the 17 sites with large numbers of mites. Females and nymphs predominated in the other two sites, and also in 5 of the 6 sites with low numbers of mites. All 337 adult mites were examined, and all appeared to be of the one species, *Myocastorobia myocastor* (Fain 1970). A beaver or either of the muskrats would have yielded at least 3 species of listrophoroid mites with that many examined. Fain (1970) also found numerous individuals of *M. myocastor* on nutria from South America.

It is remarkable that only a single parasite species was found, which is very unusual for a host of this size. Second, the other three aquatic rodents examined all had several species of tiny fusiform hair-clasping mites present, and also one large parasite as well. This thus raises two questions: why are there no more than one hair clasping mite species on nutria, and why are there no other kinds of parasites? Both answers could relate to the small sample size of two host individuals. Perhaps more species would be recovered if larger numbers were examined. It is also interesting that no lice were found, since lice have been found on this species in South America (Marelli 1932), Louisiana (Miller 1956), and England (Newsome and Holmes 1968). Most likely lice would be found if more individuals were examined; the numbers of nutria with lice in Britain ranged from 43.3% to 77% (Newsome and Holmes 1968). Also Newsome and Holmes found a total of 76 ticks on 2578 nutrias examined, thus ticks were not very abundant on nutria from Britain. Unlike the other large aquatic rodents, this host had only 1 species of tiny hair clasping mite, *Myocastorobia myocastor*, and one larger parasite, a chewing louse, *Pitrufquenia coypus*.

Thus, three of the four species of aquatic hosts examined harbored a species complex of listrophoroid mites, whereas the nutria did not. This may suggest that multiple speciation (or multispeciation) is not a phenomenon particularly related to aquatic rodents, since it does not occur on all the aquatic rodents but does occur on several unrelated hosts. It may be a random phenomenon and not related to aquatic life.

DISCUSSION

Evolution within the assemblage

There has been much difference in evolution of the small mites within the parasite assemblage across the four host species (Table 3). The listrophoroid mites on all host species herein are tiny fusiform hair-clasping species that occur in very large numbers. At least one and often several species occur on each individual host, and in fact often at each location examined on a host. Besides the large numbers of tiny mites with multiple species, each host has 1 or 2 larger parasitic forms.

Table 3

Numbers of major species of tiny and of larger ectoparasites on larger aquatic rodents

Species	Tiny	Large
Castor canadensis	17	1
C. fiber	33	1
Ondatra zibethicus (N.America)	6	2
Neofiber alleni	3	1
Myocastor coypus	1	1

These four hosts have interesting and unique ectoparasitic assemblages with nearly all forms being host specific. Also, except for the nutria, each has several species of tiny hair-clasping mites, all in the same or related genera, and with several species occurring on each host individual. Few mammalian hosts have this sort of ectoparasite assemblage with large numbers of tiny mites including several species. Similar complexes are known from the potoroo, *Potorous tridactylus* (Kerr, 1792), a kangaroo (Macropodidae) from the Australian region (Fain & Domrow 1974). The potoroo is host to 21 species of the genus *Cystostethum* Domrow (Atopomelidae). Moreover, a central African rat, *Malacomys longipes* Milne-Edwards, 1877 hosts six species of the genus *Listrophoroides* subgenus *Afrolistrophoroides*; all six species are known occur on a single host (Fain 1972 a,b). The situation with *Listrophoroides* on *Maxomys surifer* and *M. rajah* in Southeast Asia is similar to that of *Potorous*, with many species on these hosts, but most have relatively small geographical ranges (see Bochkov and OConnor 2005).

The four rodent species studied here are aquatic in habitat, and thus it may not be surprising that they exhibit similarities in their respective ectoparasite assemblages. The major ectoparasite species, by number of individuals, consist of tiny fusiform hair clasping mites that crawl up and down individual hairs and feed by dipping their mouthparts into fluids of the hair follicles. This morphology and behavior is probably beneficial to these mites by either allowing them to remain attached through the frequent immersion in water, or more likely, to avoid being immersed in water by remaining in the dry underfur of the host.

Although the general structure of aquatic rodent ectoparasite assemblages is quite similar, the taxonomic constituents are quite different. This may have resulted from convergent evolution. Each of the four hosts have listrophoroid mites in 3 different families, Chirodiscidae on beavers, Atopomelidae on the nutria, and Listrophoridae on the two muskrats, *Ondatra* and *Neofiber*. The two muskrats are thought to be quite closely related (Anderson 1985). That both have listrophorids further supports Anderson. In addition, *Listrophorus kingstownensis* of *Ondatra* and *L. laynei* of *Neofiber* are closely related, supporting the relationship of the two hosts and suggesting *L. kingstownensis* and *L. laynei* as being near the progenitor species for the muskrat listrophorids.

The beaver, muskrat, and round-tailed muskrat have few parasites other than the listrophoroids. The beaver has only the beetles, the muskrat has a hypopial glycyphagid (another hair clasping mite) and a laelapid, and the round-tailed muskrat has two laelapid mites. The host's affinities to aquatic habitats may explain the occurrence of few parasites in addition to the fur-clasping listrophoroids. One of the species on the Florida muskrat is *Androlaelaps fahrenholzi*, an exceedingly non-host specific form. It is known from more than a hundred North American hosts (Whitaker and Wilson 1974). Otherwise, all major species involved are host specific.

It would appear that the numerous tiny hair-clasping mites on these hosts with one (or two in *Neofiber*) genera of hair-clasping mites is because of the unique habitat. Probably few forms manage to survive there, but the ones that do survive adapt to this environment and form large populations that often give rise to other sister species.

Larger species are perhaps more at risk especially at the invasive stage, as again, they may be washed off. Therefore there are few of these either. The Florida muskrat appears to have more larger species including the widespread and non-adapted *A. fahrenholzi*, and more incidental forms, perhaps because this host is less aquatic than the other species.

It would appear that the muskrat, round-tailed muskrat and beaver each had one species of chirodiscid or listrophorid progenitor mite and that the host populations were later split by primary isolating mechanisms, i.e., that the different parasite species evolved in different geographic areas. This may be the most likely hypothesis to explain large number of species in the complexes on these two hosts.

As mentioned above, Dubinina (1964) thought that multispeciation occurred through adaptation to various hair habitats, whereas we (Fain et al. 1984) felt that the sucker plates evolved primarily for species recognition. On the other hand, 3 of the species groups (*mingaudi*, *indianensis*, and *verticillatus*) are roughly restricted to different parts of the body of the beaver. This habitat restriction may have been caused by selection based on mite mate-finding likelihood. However, it does lend an additional "microgeographic" source of primary isolating mechanism in addition to geographic ones which separate the species. These two levels of isolating mechanisms have probably radically increased the opportunities for speciation to occur leading to the high numbers of species. That the host animals are large in body size, and that they have large disjunct distributions, have probably increased the tendency for speciation among their parasitic mites.

An alternative hypothesis is that the various species of *Schizocarpus* and/or listrophorids respectively arose sympatrically within populations of the hosts. This is much less tenable as it is very difficult to imagine any primary isolating mechanism which could separate them on individual hosts such that secondary isolating mechanisms could evolve. On the contrary, if sympatric speciation did occur on the beaver, round-tailed muskrat and muskrat, it would seem likely that it would also occur on the nutria, since similar ecological factors would seem to be in effect. If the first hypothesis is correct, then the nutria might lack such a complex of species because South American nutria populations were more compact (i.e., not split into isolates) such that gene flow between hosts and parasites could generally occur more freely throughout the range of this host.

If the geographic isolation hypothesis is correct for beaver and muskrats, then different populations of the hosts should have different combinations of parasites, since populations have presumably been exposed to one another differently through time. We have examined beaver and muskrats, from Oregon, Alaska, and elsewhere. There is much difference in the *Schizocarpus* assemblage from beavers at different places. There is more similarity among the muskrat ectoparasite assemblages, but one of the muskrat listrophorids, *L. kingstownensis*, has not been taken in Indiana. The round-tailed muskrat, *Neofiber alleni*, has a much smaller range (mostly in Florida), yet there may still have been geographic isolation present between populations of this host.

Where the nutria has been introduced into the southern United States it co-occurs and competes with the muskrat, having partially replaced the muskrat in some areas. Both mammals are highly aquatic, eat similar foods, and use similar burrows; the nutria sometimes appropriates muskrat houses (Lowery 1974). Thus, it would seem that there would be ample opportunity for the movement and establishment of ectoparasites from one to the other. However, we have seen no evidence of this.

CONCLUSIONS

1. The unique and arguably harsh aquatic host environment has allowed relatively few arthropod species to exist in the hair of larger North American aquatic rodents. That assemblage generally consists of numerous individuals of several to many species of tiny hair clasping mites, usually belonging to one genus but in one case two genera, and one to three species of larger parasites. I suspect that establishment is generally unlikely, as arthropods are washed off; those that have become established are adapted to the dry underfur.

2. Nearly all the species are highly host specific because those that have managed to survive have become highly adapted to their habitat. Species of the same genus, *Listrophorus* (Listrophoridae), occur on both muskrat species. This may indicate their presence on the muskrats before divergence of the two muskrat genera. The progenitor species was probably near *L. kingstownensis* or *L. laynei*.

3. The groups of parasites are taxonomically different because of chance availability; that is, there were different, but suitable forms available on their progenitor mammal host, and these survived and evolved with the respective aquatic rodents. They are morphologically similar because the tiny,

hair-clasping habit is well adapted to the unique environment.

4. The occurrence of listrophorids on both muskrats is consistent with the fact that members of these mite genera are found on many arvicoline species. Similarly, that atopomelids are found on nutria is consistent with their occurrence on other, related South American rodents. However, beaver have no close sister mammal group, and beaver mites are not close to any other known mites. Most chirodiscids are found on bats but a few are found on other species. *Lutrilichus schoutedeni* Fain 1970 of an African otter is the most similar chirodiscid that I am aware of.

Needs for further work on *Schizocarpus*

These questions are well suited for DNA analysis. My hypotheses are that rapid active speciation is in progress, that the species are very closely related, that species selection is based on the sucker plates of the adult males and juvenile females fitting together, and that a few hybrids might be formed, thus reinforcing the system. DNA sequence data would allow more rigorous testing of these hypotheses, expose other information on the complex, and allow us to identify adult female and juvenile males. DNA analysis could perhaps also help to determine:

a. Are *S. mingaudi* on Eurasian and American beavers one and the same species?
b. Are all of the described species actually good species?
c. How closely related are these species?
d. How long have the various species been in existence?
e. Is hybridization occurring and if so, how often?
f. Are there species complexes among the 32 Eurasian species?
g. Are any of the 32 similar to any of the North American species, other than *S. mingaudi*?
h. Can we determine how to identify immature males and adult females of the various species?
i. Ecological studies could be done — how many species occur on one part of the body and what is the relationship between the various species on the body?

Problems that would make DNA work difficult are that adult males are needed in order to make identifications, that the mites are laterally compressed, yet have to be mounted dorsoventrally, and that multiple species normally occur in a single collection (i.e., from one portion of the host), which makes it more difficult to get correctly identified material to work with.

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