NOTES ON SOME BRITISH COLUMBIAN FLEAS, WITH REMARKS ON THEIR RELATIONSHIP AND DISTRIBUTION*

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Any attempt to piece together the sequence of post-Pleistocene repopulations of life in the area now called British Columbia will require the concerted knowledge of the geologists, palaeontologists, botanists and zoologists, an impressive array of which are assembled here today. The contribution that a discussion of fleas will make to the theme of this symposium will be but small. However, I am pleased indeed to have this opportunity of presenting some generalities on these parasites, with some notes which I hope will be of interest, and have some bearing on the general discussion.

While, for centuries, the butterflies and other conspicuous forms have attracted the attention of amateur naturalists and professional investigators, the lowly and despised fleas have been woefully neglected. Only since the turn of the twentieth century has serious attention centred on these insects, over 90 per cent of the known species having been described since that time. This belated appreciation has stemmed partly from recognition of their role as disease vectors, and partly from the intensive studies of Rothschild and Jordan, and. to a lesser extent, Baker and Wagner. These men were not moved primarily by economic considerations, but loved the fleas for themselves alone! To the ardent siphonapterologist, no insect, however gaudy, can compare with a flea, under the microscope, especially when full justice has been done the specimen by proper preparation in mounting. As Dr. Karl Jordan is reported to have said "They are indeed the jolliest of all insects.

Now, although a succession of taxonomists has provided names by the hundreds for these jolly insects, and while their unsavoury association with such diseases as plague and murine typhus. has prompted exhaustive analyses of the bionomics of certain species, little has been published on the phylogeny of the order, its origin, and the history of its association with mammals and birds. Actually, only now is knowledge of the world fauna approaching the point where the data on which such research would be based could be considered representative.

My own studies of fleas, during the last few years, have related principally to their taxonomy and distribution in Canada. It became apparent at the commencement, of course, that an adequate understanding of the geographical distribution of these insects would not be achieved without serious attention being given the host animals. However, investigation soon revealed that the presence of preferred hosts was not necessarily the sole factor governing the range Thus, consideration of of flea species. geographical restriction by selective host requirements or circumstances independent of these has complicated the study of nearctic fleas, and drawn attention to numerous problems which await solution. The immediate need is for more material. An accurate understanding of the story these little parasites have to tell will require access to long series of specimens from representative localities, and from all hosts. This should be acompanied by biological studies of the species, with critical analysis of microclimatological conditions in the larval habitat. At the present time this ideal abundance of material and information is not available, although possible lines of investigation are suggested.

The fleas, or Siphonaptera are fundamentally mammalian ectoparasites, with a few forms now associated with some birds. Not all mammals have fleas. Apparently the prime criterion governing the suitability of a particular mammal as a potential flea host concerns the

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stability and type of its dwelling place. As a general rule, fleas are parasites of terrestrial mammals of nesting habits. There are exceptions, but in most instances mammals living in burrows, dens, or other confined quarters, tend to be more or less populated with these This is to be explained by the insects. fact that it is only the adult flea which is an animal parasite feeding upon the blood of the host, the larvae being legless, maggot-like creatures which live upon a variety of organic materials, including the faeces of adult fleas: such materials, in fact, as are to be found in greatest abundance in the hosts' permanent bedding. The presence of a nest then, or reasonable alternative, is a fundamental requirement, the larvae, normally, never occurring upon the host. Nearctic fleas are found in greatest number and variety on the Insectivora. Rodentia and Lagomorpha, nearly all of which are of nesting habits. Chiroptera, or bats, also have fleas, and while these flying mammals do not make nests in the accepted sense, they do tend to congregate in caves, attics or other places where suitable conditions (of humidity?) exist, and where the availability of organic substances for larval sustenance, and hosts for the freshly emerged adults assure opportunity for completing and repeating the life cycle.

Certain Carnivora such as bears (which live in "nests" at least during the winter) have their own fleas, but as a rule, true carnivore-fleas are rare.

The host specificity of fleas varies considerably. Some are very selective in this respect, and are rarely collected from any but a particular genus or species of host. Any occurrences recorded from other hosts are explainable by predation or other secondary or accidental association. Other species of fleas are able to exist upon a variety of hosts, and (presumably) to reproduce in their nests. Several genera of mouse-fleas appear to fall into this category, as they are collected equally commonly on various genera of Cricetidae and Zapodidae. Some of these exhibit interesting limitations in geographical range which apparently have nothing to do with the lack of availability of particular hosts. With these, it must be presumed that other ecological factors restrict the distribution of the flea, probably by affecting the larva.

It must not be presumed that one kind of animal harbours only one species of flea, although sometimes this is SO. Our pocket mice (Peroanathus parvus), groundhogs (Marmota flaviventris) and chipmunks (Eutamias spp.) for example, have but one species each, but the mountain beaver (Aplodontia rufa) has three, and white-footed mice (Peromyscus maniculatus) may have as many as eight species occurring upon a single individual! The coast squirrel (Tamiasciurus douglassii) has three, while the red squirrel (Tamiasciurus hudsonicus) has another three. belonging to the same genera, and a fourth occurring in the mountains and farther north. Some of these species are chiefly nest fleas, and are rarely collected upon the host, while others seem to enjoy touring the outside world as passengers.

In British Columbia, 88 species of fleas are known. Of these, 70 are regarded as monotypic, and 18 polytypic, with 23 subspecies represented, making a total of 93 forms recorded at present in the province (Holland, 1949:7-14). Five have been introduced within historic times, so that the total of indigenous species and subspecies of British Columbian fleas now stands at 88. seems likely that future studies will tend to equalize the present disparity between monotypic and polytypic species, partly through the reduction of some named species to subspecific rank, and partly through recognition of the advisability of splitting other species, which show consistent geographical variation. However, there are a number of species of very stable character, and sometimes of wide distribution, e.g., Monopsyllus vison (Baker), which occurs without apparent geographical variation over much of the range of red squirrels, Tamiasciurus hudsonicus, which will probably retain their monotypic status.

The 88 species and subspecies mentioned belong to 41 genera, only 5 of which remain monotypic. Among the others, sympatry may be demonstrated by species of a common genus, occurring on a single host (as various species of Megabothris which may be taken on, or collected from the nest of, a single Microtus) and species of a common genus occurring in the same geographical territory, but ecologically isolated by very selective host preferences (as Corupsulla ornata Fox which occurs on moles, Scapanus, and C. jordani Hubbard, a true parasite of shrew moles, Neurotrichus). Typical examples of allopatric species are the various species of Catallagia, parasites of white-footed mice, Peromyscus maniculatus, which replace each other geographically.

The indigenous flea fauna of British Columbia is at present most satisfactorilv classified into five families and about 12 subfamilies, although there is wide disagreement among siphonapterologists as to the definition and scope of these Because of the peculiar categories. structural modifications of fleas. resulting from a highly specialized parasitic existence, their phylogenetic .relationships with each other and with other orders of insects are difficult to interpret. Further, and for obvious reasons, the fossil record of fleas is so scanty as to be None-the-less. almost non-existent. there is ample evidence that the fleas are an ancient group, and that their association with mammals dates back to the early history of that Class. The prime evidence for this contention lies in the fact that today, divergent groups of host animals are usually infested by fleas of widely different character, suggesting that the fleas have evolved with the hosts. However, during the Cenozoic epochs, when certain groups of mammals evolved, flourished, declined and became extinct, leaving at least a fossil record, the fleas associated with them are almost completely unknown. Simpson (1945:34-35) points out that of the 32 recognized orders of mammals, 14 are now extinct; also that 54 per cent of the families and 67 per cent of the known genera of mammals are extinct. Thus the modern flea fauna, bereft of genera and families which must have depended upon these vanished mammals constitutes a number of tag ends of evolutionary lines, and leaves

but an irregular, disjointed picture of the story of the Order. To make matters even more difficult, inferences and analogies which might be drawn are fraught with pitfalls in the form of complications arising from habitat associations and transference of hosts, which have occurred at various times in the more recent past. Thus, although we may postulate that fleas evolved with the mammals so that, in general, modern primitive mammals are infested with relatively unspecialized fleas, and some of the higher mammals with fleas which may be regarded as more highly specialized, there are inter-relationships, resulting from contacts amicable or otherwise, between the ancestors of the host animals, which obscure the clarity of the picture. For example, there are at least two genera of fleas occurring on certain burrow-inhabiting sea birds which show obvious affinities with the rabbit-On the other hand, bats are infleas. fested by a special family of fleas (Ischnopsyllidae) no species of which is to be found on members of any other order of hosts. Thus, while it is, perhaps, reasonable to speculate that the Ischnopsyllidae are of ancient lineage, originating at the time when the bats themselves were splitting from the primitive mammalian trunk, the sea-bird fleas are almost certainly to be explained by the practice of some birds taking over the burrows of fossorial mammals for nesting purposes, with subsequent opportunity for transfer of ectoparasites. Evidently, some of the rabbit-fleas found the birds an adequate substitute for their normal hosts, and while the processes of evolution, perhaps accelerated by the new environment have brought about their present generic distinctions, the ancestral affinities remain obvious today. Other bird-fleas, including two genera known from British Columbia, are as obviously derived from rodent-fleas (Ceratophyllinae).

Orchopeas sexdentatus (Baker) a packrat (Neotoma) flea frequently occurs on pikas (Ochotona) in talus slopes occupied by both mammals. Given sufficient time, it is possible that a form of Orchopeas peculiar to the pikas might evolve. Mice and insectivores, which frequently use each others' runways and burrows are regularly found to be temporary hosts to each others' fleas.

At the present time there are at least three species of fleas occurring on nearctic weasels or mink and which belong to genera most of the species of which occur on groups of animals forming the normal prey of these small carnivores. These fleas are Nearctopsylla brooksi (Rothschild) (the other species of Nearctopsulla occur on shrews), Ceratophyllus tundrensis Holland (the genus associated with birds) and Megabothris atrox (Jordan) (the genus ordinarily associated with the Microtinae). Thus far, none of these fleas has been recorded from the type of host that one would expect. This may be explained by the fact that collections are yet limited, but it is possible that these fleas, or their ancestral representatives, originating on the prey, have now transferred their entire attention to the genus Mustela. Future study should reveal the answer. An interesting fact is that all three species are larger and more deeply pigmented than others in their respective genera, and this may have some relation to conditions on the new host, conditions which have brought about this evolutionary modification in three unrelated genera.

Continuing with general discussion, it may be noted that fleas, like other parasitic forms, evolve more slowly than do their mammalian hosts. Local proof of this statement is provided by the known flea fauna of some islands off the coast. Although nearly all the small mammals of the Queen Charlotte and Vancouver Islands are regarded as racially or specifically distinct from corresponding forms on the adjacent mainland I have been able to detect no morphological difference in the small series of fleas (about 16 species from Vancouver Island; 3 from the Queen Charlotte Islands) available for study from these regions.

As Jellison points out (*in litt.*) fleas appear to be approximately one taxonomic category behind their hosts in evolution. Although zoological subspecies and species have a demonstrable

actuality in Nature, other taxonomic categories, while attempting to demonstrate natural groups, are in general only concepts, facilitating development of the classifications, sometimes rather arbitrary, by means of which we pigeon-hole animal life. Nevertheless, on the basis of classifications now existing, it appears that species of fleas are frequently associated with genera of mammals; genera of fleas with families of mammals: families with orders, and finally, the order Siphonaptera with the class Mammalia! For example, the fleas Monopsyllus vison (Baker) and Monopsyllus eumol-(Rothschild) infest the genera pi Tamiasciurus and Eutamias respectively. Thus, the genus Monopsyllus is associated with the family Sciuridae. The Ceratophyllidae, to which Monopsyllus belongs, includes many genera, mostly associated with the order Rodentia. In the same manner, the genus Corupsulla is associated with the Talpidae and the family Hystrichopsyllidae with the order Insectivora. Similarly Arctopsylla is a genus associated with Ursidae, and the Vermipsyllidae with Carnivora.

A survey of holarctic mammalian fauna reveals that many of the British Columbian forms have closely allied Asiatic counterparts. Many of these indeed, are regarded as congeneric. and are accepted as definite evidence of intercontinental migrations and countermigrations which have occurred across the intermittent Siberian-Alaskan land bridge from Miocene times to as recently as only a few thousands of years ago. As might be expected, many of the fleas infesting western Canadian and Alaskan mammals too have close Asiatic relatives, and occur on the corresponding hosts. Some of these fleas are regarded as only racially distinct, and are apparently attributable to late Pleistocene contacts.

Of the 41 genera of fleas recorded from British Columbia, 20 also occur in Asia (see Tables 1 and 2). These genera occur principally upon the shrews. bats, bears, marmots, groundsquirrels, tree-squirrels, meadow voles, red-backed mice, hares and pikas. which correspond closely in the New and Old Worlds. Two of the holarctic genera are restricted to birds, and some of the species of these fleas are circumpolar. Of the 21 genera not recorded from the Palaearctic region (Table 2), 6 at least are very closely allied to Old World forms, and only owe their present identity to recent generic splittings.

The remaining 15 genera are somewhat more remote, and, not surprisingly, are associated principally with strictly nearctic genera of mammals. Notes on a few of these follow.

Corypsylla is associated with western nearctic moles, Scapanus and Neurotrichus, and the related Corypsylloides and Nearctopsylla are found on New World Sorex. At present no palaearctic equivalents of these fleas are known, so it may be that the group originated on some nearctic Talpidae, subsequently spreading to the ubiquitous Sorex. Sorex also has fleas of the genus Corrodopsylla, common in Asia and North America.

Most of the species of Opisocrostis are associated with the mammalian genus Citellus. As Opisocrostis is not known from palaearctic ground-squirrels, it may be (as Jellison suggests, 1947:65) that the genus originated on prairie dogs (Cynomys), a group of nearctic fossorial rodents which also harbour two species of Opisocrostis, the fleas spreading to Citellus in the New World in comparatively recent times. However, a representative of Opiscrostis tuberculatus (Baker) has recently been collected from Citellus parryi (a relict species, and not now in contact with more southerly populations of Citellus or with Cynomus). A similar situation occurs with the genera Orchopeas and Opisodasys, also apparently strictly nearctic and with no close palaearctic relatives. Most of the species of Orchopeas occur on arboreal squirrels, Sciurus and Tamaisciurus, which have close relatives in the Old However, the two remaining World. species, Orchopeas leucopus (Baker) and O. sexdentatus (Baker) are true parasites of the nearctic mammalian genera Peromyscus and Neotoma, and it appears likely that the genus Orchopeas originated on nearctic Cricetinae, spreading subsequently to the squirrels. It should be noted that northern New World tree-squirrels also have the fleas Monopsyllus vison (Baker) and Tarsopsylla coloradensis (Baker) which show obvious affinities with the palaearctic squirrel fleas, Monopsyllus sciurorum (Schrank) and Tarsopsylla octodecimdentatus (Kolenati).

The genus *Megabothris* is associated primarily with the Microtinae, and a sequence of the described species, arranged to show the progressive evolution of the spiniform setae on the male clasper processes shuttles us back and forth between the Old and New Worlds in a manner that suggests a succession of contacts and dispersals.

Anomiopsyllus, Callistopsyllus, Stenistomera and Megarthroglossus belong to a group of primitive nest-fleas, all the genera of which appear to be entirely Nearctic. Again the prime association seems to be with white-footed mice and pack rats, with some species of Megarthroglossus having spread to tree-squirrels.

The nearctic genus Meringis is entirely restricted to pocket mice (Perognathus) and pocket rats (Dipodomys). The related Phalacropsylla occurs on pack rats (Neotoma).

Trichopsylloides and Dolichopsyllus (both monotypic genera) are found only on the "mountain beaver" (Aplodontia) and like their host, are without close relatives.

Foxella and Dactylopsylla, blind ceratophylline fleas, are restricted to pocket gophers (Thomomys and Geomys).

Some of the fleas of certain northern Microtinae (Microtus, Clethrionomys, and presumably Lemmus and Dicrostonyx, although from the lemmings, but little material is available as yet) show closer affinities with the Asiatic fauna than they do with the fleas of temperate North America. Malaraeus penicilliger dissimilis Jordan and Amphipsylla sibirica pollionis (Rothschild) are considered only as nearctic races of palaearctic species. Recently, nearctic representatives of Megabothris calcarifer (Wagner) and Catallagia dacenkoi Ioff have been collected from microtines in Alaska and the Mackenzie delta of Canada.

A further note of interest concerns

the New World representatives of Malaraeus penicilliger (Grube) which occur on red-backed mice, Clethrionomys, and other microtines. across sub-Arctic North America from Alaska to Labra-Although Clethrionomys ranges dor. well to the south and may be found in woodland habitats at low altitude as well as high, there is a representative of this flea which (apparently) is restricted to that part of the mouse's range which occurs in alpland and subalpine forest. Records are available from Maligne Lake in the Rockies and Tenquille Lake, and Anahim Lake, in the Coast Range. It is not known as yet if the species is of continuous distribution from the Arctic to the southern mountain ridges or whether the northern and southern populations are separated. In any case, it illustrates the general situation, that the fleas of Arctic and sub-Arctic Alaska and Yukon show closest affinity with the modern flea fauna of northeastern Asia, and are followed next by those of the mountains and then the great Boreal Forest of British Columbia. However, many of the fleas of the bottomlands and valleys of the southern part of the province, even on holarctic genera of hosts, represent strictly nearctic genera, and are obvious intrusions from the south. A single example may suffice. Oropsylla idahoensis (Baker) is the dominant flea of Citellus columbianus. but only in the northern part of its range, and in localities at high altitude in the southern part. In the low valleys of the Okanagan and the Kootenays, where Columbian ground-squirrels also occur, the dominant flea is Thrassis petiolatus (Baker), belonging to a purely New World genus, which has its greatest centres of abundance and variety on marmots and ground-squirrels in the Western United States. In areas where Thrassis petiolatus occurs, Oropsylla idahoensis is rare to absent, and vice versa.

Diamanus presents an interesting example of a flea genus which, in times prior to the last ice inundation probably was represented in Canada. The genus is quite distinct, and associated with ground-squirrels of the genus Citellus. Two species are known today. One.

Diamanus montanus (Baker) is recorded from California, Oregon, Nevada, Utah, Arizona and Mexico, where it occurs most commonly on Citellus beecheyi ssp. and C. variegatus ssp. The other. Diamanus mandarinus (Jordan and Rothschild) is known only from China, where it occurs on Citellus dauricus mongolicus. Diamanus is not known from any of the ground-squirrels now occurring in Canada, and we must presume that while Western Canada has become populated by Citellus since the ice retreated, certain factors now preclude the re-establishment of Diamanus. The nature of these cannot be stated with certainty at this time, but ecological factors of a climatic nature, the time element and perhaps some aspect of species competition all may have had contributory effect. The element of competition in fleas is one concerning which virtually no information is available. Little or nothing is known of the interrelationships between the flea species themselves, and the manner or means whereby certain species might be crowded out either as larvae or adults.

The genus Geusibia provides another example. G. torosa Jordan, the genotype, was described from China where it was collected on pikas, Ochotona cansa. Another species, Geusibia ashcrafti Augustson has now been described from California and Colorado from Ochotona schisticeps. Although pikas are common in the British Columbian mountains, the genus Geusibia has not come to light, and it may be that it no longer occurs there. The Rocky Mountain pika, O. princeps does carry characteristic fleas of two genera, Amphalius and Ctenophyllus, both of which are found in Eastern Asia today.

Of interest too, among the fleas which apparently do not occur in British Columbia are representatives of Ctenophthalmus, Stenoponia, Saphiopsylla, Odontopsyllus and Doratopsylla, genera associated with various mice, rabbits and insectivores. These five genera occur also in the Palaearctic region, and are undoubted evidence of former faunal contacts. In Canada, they are restricted to the southern part of the Eastern Provinces with the exception of two

which range westward into Alberta. If one subscribes to theories of recent Atlantic continental connections, the present distribution of these genera, perhaps, constitutes no particular problem. If, however, as seems probable, the ancient avenue whereby the ancestors of these fleas were exchanged (either way) was the Alaska-Siberian land bridge, then we must deduce that the fleas. with their hosts, were exterminated across most of "Canada." with a residual fauna remaining in the southeast, and the Middle and Eastern "United States" and that (as with Diamanus and Geusibia) they have been unable to re-establish themselves over their entire former Certainly these genera appear range. now to be completely lacking from the whole of British Columbia and most of the rest of Canada.

According to Jellison and Kohls (1939:2022) and Jellison (1945-96) Alaskan specimens of the Parry groundsquirrel, Citellus parryi, were infested with Oropsylla idahoensis (Baker), which, in typical form is common on our Citellus columbianus. However. the Alaskan fleas they ascribe to this species were stated to be somewhat larger, darker and with slight differences of vestiture, characters indeed which might well be considered of subspecific value.* If Citellus parryi and C. columbianus have a common ancestry, or a history of former contiguity such similarity in their fleas might readily be ex-There is no contact between plained. these rodents today, but in the past, it seems there must have been. Another

example showing that the progenitors of the mammals now separated into the northern and southern alplands of Munro and Cowan (1947) had a point of contact prior to the last glaciations is Amphalius necopinus (Jordan), a flea recorded by Hubbard (1947:172)from the northern collared pika. Ochotona collaris and well known from the Rocky Mountain pika, O. princeps. Munro and Cowan (1947:32) explain their definition of northern and southern alpland biotic areas on the basis of repopulations of the two areas from northern and southern residual faunae. subsequent to the melting of the Pleistocene ice cap. The mammals, and others, in the time that has elapsed since, have evolved good specific distinctions, but the relative recentness of their contact is suggesed by the possession of common species of fleas.

Other interesting examples of flea distribution and relationship might be cited, but time does not permit. Ĭn closing, I should like to stress the desirability of saving fleas in the course of mammalogical studies. Careful collections from territories recognized as the sites of Pleistocene refugia may readily bring to light fleas of great importance as phylogenetic missing links. Although many of the known fleas are of wide distribution, there are others that are extremely local, and a search over the vast northern part of this continent (practically virgin territory insofar as fleas are concerned) and especially from isolated species of mammals such as the Vancouver Island marmot, Marmota vancouverensis and the Sitka white-faced mouse, Peromyscus sitkensis, which may themselves be pre-Pleistocene relicts, should bring to light valuable material.

^{*} Study of this situation might indicate the advisability of reinstating bertholfi Fox 1927 (synonymized by Jordan 1933;74), described from Citellus plesius nebulicola, Nagai Island, Alaska, as a subspecies of idahoensis.

TABLE 1

A List of Holarctic Genera of Fleas

(Genera known from B. C. marked with an asterisk*)

FAMILY	GENUS	PREFERRED HOST
PULICIDAE	* Pulex	Man? Artiodactyla?
VERMIPSYLLIDAE	* Hoplopsyllus * Arctopsylla * Chaetopsylla	Hares (Lepus) Bears (Ursus) Carnivora (Euarctos, Lynx, Felis, Canis, Gulo, Procyon)
HYSTRICHOPSYLLIDAE	* Hystrichopsylla Saphiopsylla Stenoponia * Catallagia * Neopsylla * Rectofrontia Ctenophthalmus Doratopsylla * Corrodopsylla dontopsyllus Geusibia * Ctenophyllus * Amphalius * Ceratophyllus * Dasypsyllus Mioctenopsylla * Monopsyllus	Procyon) Insectivora, Mice Insectivora, Mice Insectivora, Mice Mice Ground-Squirrels (Citellus) Small Rodentia Insectivora, Mice Shrews (Sorex, Blarina) Shrews (Sorex, Blarina) Shrews (Sorex) Microtinae (Microtus, Clethrionomys) Rabbits (Sylvilagus, Oryctolagus) Pikas (Ochotona) Pikas (Ochotona) Pikas (Ochotona) Pikas (Ochotona) Many birds Many birds Many birds Rodentia (Sciurus, Tamiasciurus, Eutamias, Peromyscus)
	*Megabothris	Microtinae (Microtus, Clethrionomys, Lemmus, Dicrostonux)
	*Malaraeus	Cricetidae (Microtus, Clethrionomys, Peromys- cus, Apodemus, Lemmus)
	* Tarsopsylla Diamanus * Oropsylla * Peromyscopsylla	Sciuridae (Sciurus, Tamiasciurus, Glaucomys) Ground-Squirrels (Citellus) Sciuridae (Marmota, Citellus) Cricetidae (Microtus, Clethrionomys, Peromys-
ISCHNOPSYLLIDAE	* Myodopsylla	cus, Neotoma, Apodemus) Bats (Chiroptera)

TABLE 2

A List of Purely Nearctic Genera of Fleas Occurring in B.C.

FAMILY	GENUS	PREFERRED HOST
HYSTRICHOPSYLLIDAE	Atyphloceras Delotelis Epitedia Phalacropsylla Meringis Micropsylla Trichopsylloides Callistopsyllus Megarthroglossus Corypsylla	Cricetidae (Peromyscus, Microtus) Cricetidae (Peromyscus, Microtus) Small rodents and insectivores Woodrats (Neotoma) Pocket mice (Perognathus) White-footed mice (Peromyscus) Mountain beaver (Aplodontia) White-footed mice (Peromyscus) Neotoma and Tamiasciurus Moles (Scapanus and Neurotrichus)
CERATOPHYLLIDAE	Corypsylla Corypsylla Dolichopsylla Thrassis Opisocrostis Foxella Dactylopsylla Opisodasys Orchopeas	Shrews (Sorex) Shrews (Sorex) Mountain beaver (Aplodontia) Sciuridae (Citellus and Marmota) Ground-squirrels (Citellus) Pocket gophers (Thomomys) Pocket gophers (Thomomys) Mice (Peromyscus); squirrels (Glaucomys) Sciuridae and Cricetidae (Tamiasciurus, Neo-
ISCHNOPSYLLIDAE	Eptescopsylla Myodopsylloides	toma and Peromyscus) Bats (Lasionycteris) Bats (Eptesicus)