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Host-ectoparasite relationships among North American chipmunks

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A review of the fleas and lice of the Nearctic chipmunks indicates that North American chipmunks, *Neotamias* and *Tamias,* have had separate histories; and that one has not been derived directly from the other. The western chipmunks (*Neotamias*) have in common a species assemblage of sucking lice and fleas, and the single eastern species, *Tamias striatus* (Linnaeus, 1758), has distinctive species of fleas which do not generally occur on other small mammals; none of the lice or fleas on *T. striatus* occcurs on the western chipmunks. This dichotomy of distribution of external parasites on these chipmunks indicates a very long separation of the hosts, and could not occur if one group had been directly derived from the other. Chipmunks in western North America, on the basis of the molecular evidence and distribution of sucking lice and fleas, are most logically placed in the genus *Neotamias*. Such an arrangement is consistent with the morphological, molecular, and parasitological evidence, and suggests a plausible history and relationship of the three groups of chipmunks.

The fossil distribution of North American chipmunks indicates an early movement from Asia in the Oligocene, and a scarcity or absence of chipmunks from the middle Miocene until the Pleistocene. Both *Tamias striatus* and species of *Neotamias* are probably a product of two Pleistocene movements across the Bering connection.

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Introduction

The generic and subgeneric assignment of chipmunks has been a topic of discussion for the past two decades. Although morphometric, immunological and electrophoretic studies all confirm that there are three distinct groups of species, generally considered to be genera or subgenera, disagreements arise from opinions regarding the interpretation of the published data.

The geographic origin of American chipmunks is presumed to have been from Asia, via a Bering crossing. The chipmunk of eastern North America, *Tamias striatus* (Linnaeus, 1758), typically lacks a peglike upper premolar (p^3), and is thus easily separated from the other groups. *Eutamias sibiricus* (Laxmann, 1769) and chipmunks of western North America, *Neotamias*, both possess p^3, which is characteristic of most sciurids (Korth 1994).

The first thorough revision of American chipmunks was that of Howell (1929). Although Howell placed the single Old World species and those of western North America together in the genus *Eutamias*, he emphasized the similarities of *Eutamias sibiricus* and *Tamias striatus*. These two species resemble each other in (1) shape of antorbital foremen and (2) postorbital process; (3) breadth of interorbital region; (4) upper molariform tooth rows converging posteriorly; and (5) shape of ear pinna. In these features *E. sibiricus* differs from *Neotamias* chipmunks of western North America. *E. sibiricus* resembles the *Neotamias* in (1) shape of rostrum, (2) flattening of temporal region, (3) striations on upper incisors, and (4) presence of p^3.

On the basis of immunological data, Ellis and Maxson (1979) confirmed that chipmunks could be divided into three lineages. They suggested a single crossing of the Bering land bridge, and proposed divergence of the western chipmunks, *Neotamias*, from *Tamias* of eastern North America in the late Miocene. They postulated that orogeny in western North America, which created a major rainshadow with arid and semiarid regions over much of western North America, accounted for the separation of the eastern chipmunk (*Tamias*) from the western species (*Neotamias*). They recognized two genera: *Tamias*, containing the single species *striatus*, and *Eutamias*, with two subgenera: *Eutamias* for the single Asiatic species, *sibiricus*, and *Neotamias* for the species of western North America. This taxonomy had been followed for many years.

Levenson *et al.* (1985), in a meticulous electrophoretic and morphometric study, also placed the chipmunks into the three same groups, and confirmed Howell's opinion that the species *T. sibiricus* and *T. striatus* are closer to each other than either is to the species in western North America. They suggested that *T. sibiricus* and *T. striatus* are sister groups, and together constitute a sister group of the remaining *Neotamias* species in western North America. They felt that all living chipmunks should be placed in the genus *Tamias*.

All three studies confirmed that there are three distinct groups of chipmunks. The disagreement concerning the generic placement of these species stems not from the two sets of data, but rather from interpretation of the data. Generic boundaries are concepts; and, as such, tend to be flexible. The data are objective, and lead to similar though not identical relationships of species, but the final conclusions tend to be subjective. Records of sucking lice and fleas on Nearctic chipmunks confirm the relationships suggested by Howell (1929) and Levenson *et al.* (1985). The fossil record of chipmunks suggests a history different from that previously proposed.

Ectoparasitic record

Parasites generally speciate more slowly than do their hosts, and this pattern is apparent in the records given below. Characteristic parasites of hosts are useful in indicating relationships among a group of host species. I have examined the

occurrence of sucking lice (Anoplura) and fleas (Siphonaptera) of North American chipmunks in order to reveal possible history of these taxa. Because the entire life cycle of sucking lice is spent on the host, and the transfer of lice from one individual to another individual is almost always within the same host species, lice develop a high degree of specificity to their host (Durden and Musser 1994a). Although adult fleas usually do not attach permanently to their hosts, it is quite common for a given host mammal to have one or several characteristic species of fleas, which may or may not occur on other small mammals in their habitat. Fleas are far more mobile than are lice, and host-parasite distributions of fleas are influenced by environmental features. Nevertheless, host-parasite affinities are well known for many species of fleas occurring on sciurid rodents.

The sucking lice of the western chipmunks are confined to species of *Neotamias*, and do not parasitize other mammals. Known hosts to *Hoplopleura arboricola* (Hoplopleuridae) are *Neotamias alpinus, N. amoenus, N. dorsalis, N. merriami, N. minimus, N. ochrogenys, N. quadrivittatus, N. sonomae, N. speciosus,* and *N. townsendii*. Another species, *Neohaematopinus pacificus* (Polyplacidae), also occurs on *Neotamias alpinus, N. amoenus, N. dorsalis, N. merriami, N. quadrivittatus, N. sonomae, N. speciosus,* and *N. townsendii* (Durden and Musser 1994b). The same authors record *Hoplopleura erratica* as the only louse known from *Tamias striatus*. The host distribution of the above species of lice indicates (1) that species of *Neotamias* are very closely related and would seem to have radiated relatively recently, and (2) the species of *Neotamias* have had a history quite separate from that of *Tamias striatus*.

The host distribution of fleas on chipmunks is similarly disparate. Species of *Neotamias* are hosts to A*monopsyllus ciliatus* (Ceratophyllidae), which has been recorded from *N. amoenus, N. minimus, N. quadrimaculatus, N. ruficaudus, N. speciosus, N. merriami* and *N. townsendii,* as well as from their predators and also the red squirrel (*Tamiasciurus* spp.). Species of *Neotamias* are also typical or usual hosts to another flea, *Eumolpianus eumolpi* (Ceratophyllidae), as well as six other species, which are probably only well marked subspecies of *E. eumolpi* (Traub *et al.* 1983). These two fleas and their subspecies do not regularly occur on hosts other than chipmunks, except occasionally on mammals that are chipmunk predators.

Tamias striatus is host to two species of fleas which do not regularly parasitize other small mammals. *Megabothris acerbus* (Ceratophyllidae) is a common parasite, and only sporadically occurs on other hosts. The second flea characteristic of the eastern chipmunk is *Tamiophila grandis* (Hystrichopsyllidae), a monotypic genus, which very rarely parasitizes other small mammals in its habitat. The nearest relatives of *T. grandis* are species of *Neopsylla*, a large genus of eastern Asia, the species of which parasitize small mammals (Hopkins and Rothschild 1962). In North America there is only one species, *Neopsylla inopina* Rothschild, and it occurs on *Spermophilus* spp. Because the nearest relatives of *Tamiophila grandis* are preponderately in eastern Asia (including India) (Hopkins and

Rothschild 1962), it is most likely that the ancestor of *T. striatus* crossed the Bering connection from Asia into North America. It is interesting that the fleas *T. grandis* and *M. acerbus* parasitize *T. striatus* only in the northern part of its range (L. A. Durden, pers. comm.).

Inasmuch as environmental factors, in addition to hosts, affect the occurrence of fleas, their host distributions alone only suggest long isolation of the two groups of chipmunks. The dichotomy of species of lice, however, with no species shared by *Neotamias* and *Tamias*, is very strong evidence that these two stocks made separate entries into North America, and that one group could not have been derived from the other.

Unfortunately the external parasites of the Asiatic chipmunk (*Tamias sibiricus*) are not closely allied to those on Nearctic chipmunks, and do not indicate the affinities of *T. sibiricus* to other chipmunks. *Tamias sibiricus* is host to a single species of louse, *Enderleinellus tamiasis* (Enderleinellidae). Species of *Enderleinellus* are exclusively parasites of squirrels, and are known from many species of sciurids in both Eurasia and North America (Durden and Musser 1994a).

The host distributions of external parasites are not generally employed to indicate phylogenetic relationships, and it is useful to compare external parasites of other pairs of mammalian genera to emphasize the great historical distance of the western North American chipmunks (*Neotamias*) from *Tamias striatus*. Species of *Chaetodipus* and *Perognathus* (Heteromyidae), for example, are hosts to the same species of lice: species of both genera are parasitized by *Fahrenholzia reducta* and *F. pinnata*; and *F. pinnata* occurs also on species of kangaroo rats (*Dipodomys* spp.) and kangaroo mice (*Microdipodops* spp.). Similarly, within the Muridae, some species of *Peromyscus* are hosts to *Hoplopleura hesperomydis* which also parasitizes the golden mouse (*Ochrotomys nuttalli*) (Durden and Musser 1994a). I do not imply that genera of sciurids, heteromyids, and murids are necessarily comparable, but a commonality of sucking lice does generally indicate a phylogenetic relationship of the hosts.

Fossil record

The earliest record of chipmunks in North America is from the Arikareean (late Oligocene or earliest Miocene), and are referred to the primitive genus, *Nototamias* (Pratt and Morgan 1989, Korth 1992). *Nototamias* is distinctive in having lower molars with only two roots in contrast to modern chipmunks, which have lower molars with four roots (Pratt and Morgan 1989). In the absence of upper cheek teeth of that and other fossils, the presence or absence of p^3 is unknown, and it cannot be definitely placed in either *Tamias* or *Eutamias*. Black (1963) reported "*Tamias*" from the early Miocene of South Dakota and Colorado. Hall (1930) assigned a fossil from Nevada (Barstovian or Clarendonian- middle Miocene) to *Eutamias* on the basis of size, but the presence of p^3 could not be determined. Shotwell (1968 and 1970) reported *Eutamias* from the Clarendonian (middle

Miocene) of southeastern Oregon. Shotwell made a strong case, on morphological grounds, for the retention of two subgenera (*Eutamias* and *Neotamias*) for Recent chipmunks, which, he suggested, had been derived from the same ancestral stock, and a subsequent movement of *Neotamias* into North America. Ray (1965) described a large species of *Tamias* from Pleistocene deposits from Georgia, and reviewed Pleistocene records of *Tamias striatus* from Hamilton, Ontario south to Georgia and west to Arkansas and Missouri.

Chipmunks have a long history in Asia; *Eutamias* is reported also from the late Miocene of Pakistan (Munthe 1980); and *E. eviensis* is described from the lower Miocene of Greece (de Bruijn *et al.* 1980). *Eutamias sihongensis*is described from the early Miocene of Xiacaowan, Jiangsu, China (Qui 1996) and *Eutamias ertemtensis* was described from isolated teeth from the middle Miocene of inner Mongolia (Qui 1991). In each case the generic assignment is questionable, because the descriptions are based mostly on isolated teeth, and the presence or absence of p^3 is unknown.

There is an apparent absence of chipmunks from the middle Miocene until the Pleistocene, an hiatus of from 4 to 9 million years, in both Eurasias and North America. This is a period from which are known many fossils of small mammals, and the absence of fossil chipmunks, although negative evidence, suggests a scarcity or absence of chipmunks during the late Tertiary. The scarcity of late Cenozoic chipmunk fossils could have been climate related, for this was a period of major climatic change, with a longterm trend of cooling and expanding aridity (Janis 1993). This indicates the possibility of two widely separated movements across the Bering connection, one in the Oligocene and another (one or two) much later, in the Plio-Pleistocene.

Discussion

There were many (perhaps seven or more) Tertiary Bering connections when the climate was temperate (Janis 1993). Shotwell (1970), on the basis of fossil evidence, stated that the separation of the subgenera *Neotamias* and *Eutamias* apparently occurred in eastern Asia and not in North America. The first Nearctic chipmunks, known from Oligocene and Miocene fossils, may have disappeared by the middle Miocene, or they may have survived to produce *Tamias striatus*. The movement of one (or more) species of chipmunks into North America was probably Pleistocene; and such a movement may have occurred more than once. If the Oligocene and Miocene chipmunks did not survive in the Nearctic Region, *Tamias striatus* (or its ancestor) crossed a Bering connection in the Pleistocene, and the second invasion involved one or more species of *Neotamias*.

This leaves open the question of a possible ancestor of the species of *Neotamias*. It is most logical to assume that, as suggested by Shotwell (1970), *Neotamias* and *Eutamias* had a common ancestor in Asia. Shotwell's suggestion is supported by the fact that the occurrence of sucking lice and fleas indicate that species of *Neotamias*

have not been derived from *T. striatus*. Because there is no apparent ancestor of the species of *Neotamias* in Asia today, it is logical to assume that the Old World ancestor of the chipmunks of western North America became extinct, perhaps in the Pleistocene. Pleistocene extinctions were not limited to the "megafauna", but included many small mammals as well (Hibbard *et al.* 1965, and Kowalski 1967).

Alternatively, if *Tamias striatus* and *Eutamias sibiricus* are sister species, and that pair is in turn sister to *Neotamias* sp., then the first divergence could have occurred in Asia fairly early, giving rise to the ancestor of *Tamias/Eutamias*, and the ancestor of *Neotamias*. The latter then could have crossed the Bering connection in the Miocene/Pliocene, and radiated in North America, while the former remained in Asia, to divide into *sibiricus* and *striatus*, the second crossing into North America at a later time.

The complete dichotomy of host occurrence of both lice and fleas on chipmunks, together with the morphological and molecular data, confirms the separate history of *Tamias striatus* from the species of *Neotamias,* and justifies their being placed in separate genera, *Tamias* and *Neotamias*. The fossil record of Oligocene and Miocene chipmunks in North America and the subsequent absence of chipmunk fossils until the Pleistocene suggests that the early taxa in the New World may not have been ancestral to Recent Nearctic species. *T. striatus* has lost p^3, present in *T. sibiricus,* but, because of the morphological, immunological, and molecular similarity of *T. sibiricus* and *T. striatus*, it is apparent that they are closer to each other than either is to species of *Neotamias*. Most logically the Asiatic chipmunk should be called *Eutamias sibiricus*, the eastern Nearctic species remains *Tamias striatus*, and the species in western North America then fall into the genus *Neotamias*. Allocation of these species to three genera best reflects the relationships and apparent history of chipmunks.

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