

# BIOSYSTEMATICS OF THE CHEWING LICE OF POCKET GOPHERS

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## INTRODUCTION AND OVERVIEW

One of the greatest challenges in systematic and evolutionary biology concerns the taxonomy, coevolution, and biogeography of chewing lice of the genera *Geomydoecus* and *Thomomydoecus* (Mallophaga: Trichodectidae) and their vertebrate hosts, the more than 400 recognized species and subspecies of pocket gophers (Rodentia: Geomyidae). Pocket gophers are fossorial rodents restricted geographically to North and Central America. They are relatively sedentary, exhibit low vagility, and have male and female exclusive territories, low population densities, and patchy distributions. The tendency of groups of these mammals to occur in small local populations has resulted in the development of minor character differences that led to recognition of as many as 230 subspecies within a single species (14). In addition, researchers have long known that the relationships among many of these gopher taxa are poorly understood (1).

Fortunately, pocket gophers are common enough to be well represented in major vertebrate collections and have been the subject of exhaustive morpho-

logical, chromosomal, and genic investigations. The patterns of genetic variation in these and some other fossorial rodents have received more study than those in any other mammals except humans (49). Studies have shown that pocket gophers have a high degree of both intrapopulation and interpopulation divergence in genetic systems, including extreme variability in the number of chromosomes and chromosome arms (11, 12, 38, 39, 41–46). Such chromosomal reorganization often is associated with genetic incompatibility among populations and has resulted in reproductive isolation (76–79, 81). In some cases, however, chromosomal variation apparently is independent of reproductive isolation (39). Chromosome diversity may be accompanied by low levels of intrapopulation genic variability (37).

Pocket gopher lice and their hosts present a unique opportunity for the study of host-parasite relationships and cospeciation (6). No other arthropod-vertebrate association offers such a combination of great host diversity and availability coupled with the abundant and nearly universal presence of a diverse but related parasite fauna that has little or no impact on host survival. Chewing lice of the genera *Geomydoecus* and *Thomomydoecus* are the only lice found on pocket gophers. They are restricted to pocket gophers, abundant, and easily collected from hosts or prepared skins. In the 20 years that have elapsed since the last revision of *Geomydoecus* (53), more than 30 published papers have treated the systematics and associations of these lice with their mammalian hosts. Concurrently, but generally independently, mammalogists have continued investigations of geomyid rodents. Only recently, however, mammalogists and entomologists have collaborated in examining the relationships within and between the two groups of organisms. These studies have improved understanding of both the hosts and their parasites. We offer this review as a means of encouraging and furthering cooperative associations between entomologists and biologists working on associated host animals.

## TAXONOMIC HISTORY OF POCKET GOPHER LICE

### Methods

Researchers long have advocated studies of the relationships between ectoparasitic invertebrates, such as lice, and their hosts (33, 88). However, to accomplish these studies, large numbers of parasites must be collected from a broad spectrum of hosts. Studies of this kind require comprehensive collections of both host and parasite taxa from the entire geographic ranges of both groups of organisms. In addition, parasites must be well understood taxonomically, and both groups of organisms must be reliably identified. To be useful in considerations of host associations, the parasites must be subjected to a thorough taxonomic treatment that includes analyses of both

qualitative and quantitative characters and that employs statistical comparisons of populations and their phylogenetic relationships.

Large and intricate host taxonomic complexes, such as those among pocket gophers, present a quantity and complexity of data that can be adequately handled only with the aid of computers. In 1974, we began the development of a computerized pocket gopher-lice data management system. Identification, geographic distribution, and parasite-host association data for all pocket gopher lice that have been collected, with measurements and counts of their morphological characteristics, currently are stored as relational data bases on an IBM 370/3081 computer system at the University of Notre Dame (Table 1). A group of computer programs for host-parasite data storage, retrieval, and analysis called the BUG System (58) originally was developed for a Control Data Computer System at the University of Minnesota and subsequently was adapted for an IBM 370/3081 computer system at the University of Notre Dame. These programs are used to store and update louse, host, and locality information; define tentative taxonomic louse groups; retrieve louse data based on these groups; and analyze these data within a group or between groups. Automated techniques for examining Mallophaga populations for character heterogeneity and identifying potential taxonomic groups were developed from a variability model (Figure 1) based on estimations of variance components from a 5-level nested analysis of variance design. The investigators considered 55 quantitative morphological characters between lice from the same host, from different hosts at a single locality, from different localities within the same gopher taxon, and from different host taxa (18).

The BUG system includes a geographic mapping module (20) that produces host-lice range maps from stored collection data. When localities are added to the system, the latitude and longitude of the closest town or other landmark are entered along with the angle and distance between the landmark and the specific collection site. The system adjusts the geographic coordinates to the specific locality using calculated lengths of degrees for the appropriate parallels and meridians. In producing range maps, the system determines the geographic limits of the locality data to be used, retrieves data defining political boundaries within the limits of the data to be plotted, and then plots the localities and political boundaries as a rectangular projection of the

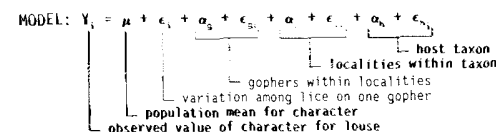


Figure 1 Model showing sources of variation for character traits in louse populations.

**Table 1** Louse/locality/host computerized data base summary

Type of information	Quantity	Percentage or average
Gopher taxa	403	90% of described taxa
Louse taxa	122	100% of described taxa
Localities	3,625	8.8/29.7 per gopher/louse taxon
Gophers with lice	6,614	1.8 per locality
Host-louse associations	8,657	1.3 louse taxa per host
Adult lice identified	83,976	12.7 specimens per host
Lice measured	14,641	17.4% of lice identified
Stored character data	403,860	25–30 observations per louse

appropriate portion of North and Central America. Latitude and longitude scales are independently calculated to best display the collection sites. The precision of the system is 0.01 degree (0.75 to 1.15 km).

A separate database containing host-parasite associations for the entire order Mallophaga, which includes all known associations between pocket gophers and their hosts, is being developed (R. D. Price, K. C. Emerson, & R. A. Helleenthal, unpublished information). This database and the programs for updating and retrieving it were developed for the dBASE III Plus™ data management package on IBM PC™ microcomputers and are maintained at the University of Notre Dame.

Because a substantial proportion of the accumulated pocket gopher louse character data is mensurative and subject to both large variation and significant intercharacter correlations, we have used mostly phenetic methods for our phylogenetic evaluations of these lice. Stepwise discriminant analysis was used to identify useful characters in taxonomic separations (86), and canonical correlation has been employed to document group separation and to reduce the effect of body size in establishing relative similarities among taxonomic groups.

### Systematics

In spite of the potential usefulness of studies of lice in both defining pocket gopher taxa and understanding relationships among them, intensive work on pocket gopher lice has been done only in the past 20 years. The five then-known species of pocket gopher lice had been placed in the genus *Trichodectes* until Ewing (8) described the genus *Geomydoecus*. Attempts to understand and explain louse-pocket gopher associations and relationships (50, 87) prior to a thorough taxonomic understanding of the lice have no relevance today. Before 1971, 10 species and one subspecies (*Geomydoecus chapini minor*) of lice had been recognized from all pocket gophers (89). These taxa were defined so poorly that they were essentially indistinguishable

except by their association with their known hosts. Price & Emerson (53) redescribed the taxa associated with the 11 previous names, elevated *G. chapini minor* to *G. minor*, and described 34 new species and subspecies, bringing the total recognized taxa to 45. This and subsequent work through 1989 increased the number of louse taxa for specimens previously assigned to the original 11 taxa to 81; all but one (*G. chapini*) of the original species represented an assemblage of from 2 to 26 taxa each. The louse fauna of pocket gophers now includes 122 species and subspecies. These are organized as 4 species and 22 complexes containing 2 or more closely related specific or subspecific taxa (Table 2); 3 of these cross host generic or subgeneric limits. The occurrence of such a diversity of recognizable taxa of lice on pocket gophers strengthens the potential use of the lice as indicators of host relationships.

*Geomydoecus* was subdivided into two subgenera (*Geomydoecus* and *Thomomydoecus*) (54); members of the subgenus *Thomomydoecus* include the more slender, tapered, and smaller lice that generally occur on the same host specimens with lice of the subgenus *Geomydoecus*. The subgenera subsequently were elevated to generic status (19). Lyal (30) theorized that both *Geomydoecus* and *Thomomydoecus* are paraphyletic and that *Thomomydoecus* might be polyphyletic as well. He concluded that recognition of these genera could not be reconciled with the cladistic methods used in his study. However, his methods have been challenged (10), and the recognition of these taxa as genera has been substantiated subsequently on both morphological and genetic grounds (36).

### HOST-PARASITE ASSOCIATIONS

The use of proper procedures for the collection and preparation of host material is crucial in studies of associations and relationships between ectoparasites and their hosts. Because of the amount of ectoparasite material available for study, we often could distinguish between legitimate associations of parasites with hosts and those that arise as a result of contamination or accidental transfer of parasites between hosts during collection, storage, or preparation of specimens. Measures that guard against potential transfer of lice in the collection, treatment, and preparation of hosts are particularly important in investigations of areas with host hybridization or where different host taxa occur in the same locality. For example, in examining the apparent transfer of lice among host taxa, we found that such exchanges occurred only when both host taxa were collected during the same day.

The practice of putting the carcasses of trapped hosts in a single pile prior to preparation of skins may destroy much of their value for considerations of parasitic associations. When collections of hosts and parasites are not large,

Table 2 Pocket gopher–lice associations

Host Genus (subgenus)	Gopher taxa <sup>a</sup>		Louse species or complex (# taxa)		Reference
	SP	SP+SSP	<i>Geomydoecus</i>	<i>Thomomydoecus</i>	
<i>Geomys</i>	8	38	<i>geomydis</i> (8)		86
			<i>scleritus</i> (2)		52, 69
			<i>texanus</i> (2)		56
			<i>truncatus</i> (2)		21
			<i>dalgleishi</i> (1)		85
			<i>quadridentatus</i> (1)		21
<i>Orthogeomys</i>					
( <i>Orthogeomys</i> )	2	17	<i>alleni</i> (2)		65
( <i>Heterogeomys</i> )	2	13	<i>chiapensis</i> (2)		65
( <i>Macrogeomys</i> )	6	12	<i>copei</i> (4)		57
			<i>panamensis</i> (6)		51, 68
<i>Pappogeomys</i>					
( <i>Pappogeomys</i> )	2	9	<i>bulleri</i> (5)		66
( <i>Cratogeomys</i> )	7	45	<i>mcgregori</i> (1)		67
			<i>coronadoi</i> (7)		67
			<i>mexicanus</i> (5)		67
			<i>texanus</i> (4)		56
			<i>mcgregori</i> (3)		67
			<i>expansus</i> (2)		55
			<i>telli</i> (1)		64
<i>Thomomys</i> <sup>b</sup>					
( <i>Thomomys</i> )	3	74	<i>thomomys</i> (8)	<i>wardi</i> (3)	22, 23
( <i>Megascapheus</i> )	4 <sup>c</sup>	231	<i>californicus</i> (16)	<i>minor</i> (9)	61, 63
			<i>umbrini</i> (8)	<i>neocopei</i> (7)	60, 62
			<i>subcalifornicus</i> (2)	<i>wardi</i> (1)	18, 19, 23
			<i>oregonus</i> (4)		59
			<i>tolucae</i> (5)		58
<i>Zygoeomys</i>	1	2	<i>trichopi</i> (1)		67
	35	441	(102)	(20)	

<sup>a</sup> Counts of pocket gopher species and subspecies generally follow Hall (14), except as noted.

<sup>b</sup> *Thomomys* subgenera from Thaler (80).

<sup>c</sup> *Thomomys* (*Megascapheus*) species from Patton et al (48).

this practice easily can lead to erroneous conclusions that can destroy much of the potential value of the work. We urge vertebrate field biologists to exercise great care to insure the integrity of the ectoparasite fauna on individual host specimens, even when all collected individuals appear to be a single taxon. Transfer of ectoparasites among prepared host specimens in museums appears to be a less serious problem, although common sense would suggest that

grooming skins over trays containing other specimens, for example, should be avoided.

Lice have been identified from all host genera and subgenera as well as from a majority of the host species and subspecies (Table 2). The most recently published host-parasite list of the Mallophaga on mammals (5) is incomplete for pocket gopher associations with their lice and should not be used with reference to those hosts. The associations between the lice and their hosts are summarized below.

### Geomys

The *Geomydoecus* taxa that occur on *Geomys* hosts show a high degree of host specificity with only a single louse taxon occurring on an individual host specimen. The eight species of the *geomydis* complex, which constitutes the largest of six complexes on *Geomys*, are restricted to the 21 taxa of *Geomys bursarius* sensu Hall (14) and are the only lice found on those gophers (86).

The only lice that occur on the eight taxa of the southeastern U.S. pocket gophers are the two species of the *scleritus* complex (52). These lice all are parthenogenetic; only several males have been collected along with nearly a thousand females.

The two species of the *truncatus* complex and both subspecies of the *Geomydoecus texanus* complex are found on *Geomys tropicalis* and on various subspecies of *Geomys personatus*, again with a high degree of specificity (21, 56). The host of *Geomydoecus truncatus* originally was thought to be *G. personatus personatus*. However, we have never collected this parasite from that host; the only host we have verified is *G. personatus fallax*. The host for *Geomydoecus neotruncatus* is *G. personatus streckeri*. One subspecies of *G. texanus* occurs on three subspecies of *G. personatus* and the other occurs on *G. tropicalis*. The remaining four members of the *texanus* complex occur on *Pappogeomys castanops*.

*Geomydoecus dalgleishi* is known only from *G. personatus fuscus* in southern Texas and is well isolated from all other populations of *Geomys*. Likewise, *Geomydoecus quadridentatus* occurs only on the two subspecies of *Geomys arenarius*, which are the westernmost *Geomys* and well removed from other members of this gopher genus.

*Geomys* subspecies with unknown louse associations are *G. bursarius ludemani*, *G. bursarius pratincola*, and *G. bursarius terricolus*.

### Orthogeomys (Orthogeomys)

The two species in each of the *alleni* and *chiapensis* complexes, which are among the largest *Geomydoecus*, occur only on *Orthogeomys grandis* (65). The two from the *alleni* complex live on five host subspecies in Mexico. Of the *chiapensis* complex, *Geomydoecus chiapensis* is found on two subspecies in Guatemala and *Geomydoecus pygacanthi* on one subspecies in El Salvador.

*Orthogeomys* (*Orthogeomys*) taxa with unknown louse associations are *O. cuniculus*, *O. grandis annexus*, *O. grandis carbo*, *O. grandis engelhardi*, *O. grandis guerrensis*, *O. grandis huixtlae*, *O. grandis pluto*, *O. grandis soconuscensis*, and *O. grandis vulcani*.

### *Orthogeomys* (*Heterogeomys*)

The four species of the *copei* complex are known from 10 subspecies of *Orthogeomys hispidus* in Mexico (57). The lice fall into two distinct groups; *Geomydoecus copei* is from four subspecies in the northern third of the host range and the other three species are from six host subspecies in the southern two-thirds (57). The only discrepancy these distributions show involves the occurrence of *G. copei* in the northern ranges of the hosts *O. hispidus hispidus* and *O. hispidus torridus* and of *Geomydoecus hoffmanni* in the southern ranges of these same host subspecies, which suggests either an illogical assemblage of gopher taxa or an improper indication of host phylogeny based on these lice.

*Orthogeomys* (*Heterogeomys*) taxa with unknown louse associations are *O. hispidus hondurensis*, *O. hispidus latirostris*, and *O. lanius*.

### *Orthogeomys* (*Macrogeomys*)

Of the six taxa of the *panamensis* complex (68), the two subspecies of *Geomydoecus panamensis* are southernmost in Costa Rica and Panama and found, respectively, on *Orthogeomys cavator* and *Orthogeomys dariensis*. *Geomydoecus costaricensis* has been taken only from the three subspecies of *Orthogeomys heterodus*. The remaining three species of this louse complex present a confused picture: *Geomydoecus setzeri* and *Geomydoecus davidhaffneri* are both known from *Orthogeomys cherriei* and *Orthogeomys underwoodi*, even occurring on the same host individuals. These two species are separable only on the basis of the male's morphology. *Geomydoecus cherriei* also occurs on *O. cherriei* as well as on *Orthogeomys matagalpae*. The significance of this situation is still the subject of study.

*Orthogeomys* (*Macrogeomys*) subspecies with unknown louse associations are *O. cavator nigrescens*, *O. cherriei cherriei*, and *O. cherriei carlosensis*.

### *Pappogeomys* (*Pappogeomys*)

The five taxa of the *bulleri* complex are associated with the eight subspecies of *Pappogeomys bulleri* (66). The most widespread of these, *Geomydoecus bulleri bulleri*, is recorded from five host subspecies, whereas the others are each associated with a single subspecies, and one of these is known only from an unidentified subspecies from Colima, Mexico. *Geomydoecus alcorni*, a member of the *mcgregori* complex whose other members occur on the other subgenus of *Pappogeomys*, is known only from *Pappogeomys alcorni*. This

represents one of only three instances reported here in which members of a louse complex are found on hosts in two genera or subgenera. This observation may be explained by the fact that both collection sites for *G. alcorni* are identical to those for a *Pappogeomys tylosinus* host of *Geomydoecus mcgregori*.

### *Pappogeomys* (*Cratogeomys*)

A member of the *mexicanus* complex often occurs on the same host individual as one of the *coronadoi* complex (67). The host range for the five taxa of the *mexicanus* complex consists of five subspecies of *Pappogeomys merriami* and two of *Pappogeomys tylosinus*, evidencing a high degree of host specificity. The range for the seven taxa of the *coronadoi* complex is somewhat comparable. It includes the same five subspecies of *P. merriami* and two of *P. tylosinus*, but also includes *Pappogeomys zinseri*, a subspecies of *Pappogeomys gymnurus*, and two other subspecies of *P. tylosinus*. The two subspecies of the louse *Geomydoecus polydentatus* account for this expansion of host ranges.

The remaining three taxa of the *mcgregori* complex (67), excluding *G. alcorni* discussed above, are found on *Pappogeomys fumosus*, *Pappogeomys neglectus*, *P. zinseri*, the four subspecies of *P. gymnurus*, and the six subspecies of *P. tylosinus*. Both a member of the *mcgregori* complex and of the *coronadoi* complex often occur on the same host individual in six of these host taxa. To further complicate this picture, *Geomydoecus telli*, which is so unusual that it is placed in no other complex (64), occurs on two subspecies of *P. tylosinus* and one of *P. gymnurus*, and in all instances was collected along with a member of the *mcgregori* complex. This occurrence of two, and occasionally even three, species of *Geomydoecus* of these four complexes living together on the same host individual aggravates the problems of identification and defies an explanation on our part.

The remaining two *Geomydoecus* complexes found on *Pappogeomys* are limited to the 25 subspecies of *Pappogeomys castanops* extending from Colorado and Kansas southward into Mexico. A study of the host associations of the *expansus* and *texanus* complexes (17) revealed a northern and southern grouping of the lice. Individuals of these two complexes often occurred together on the same host specimen. Also, the single collection of *G. tamaulipensis* appears to be from a parthenogenetic population. The *texanus* complex represents the only case in which members are shared between two gopher genera; four taxa live on *P. castanops*, and the remaining two live on *G. personatus* collected primarily along the Gulf Coast of southern Texas and northern Mexico. This host-louse association remains an enigma.

The *Pappogeomys* (*Cratogeomys*) species with an unknown louse association is *P. merriami peraltus*.

## Thomomys (Thomomys)

The *Thomomys* subgenus of pocket gophers, composed of *Thomomys talpoides*, *Thomomys mazama*, and *Thomomys monticola*, contains a louse fauna distinct from those of all other gophers. Of the two louse complexes on this gopher group, the *Geomydoecus thomomys* complex is by far the largest and most widely distributed both geographically and with respect to hosts (22). The eight taxa in this louse complex extend throughout much of the range of the host taxa (22). An unusual situation was encountered for eight subspecies of *T. talpoides* in southwestern Canada and adjacent areas of the US in that no lice were obtained from about 435 gopher specimens that were brushed. While this absence could be ascribed to a variety of other reasons, some populations of pocket gophers may actually have no lice. Only females have been found for *Geomydoecus betleyae* and *Geomydoecus biagiae*, which indicates that these lice are likely parthenogenetic.

The other louse complex on these gophers, the *Thomomydoecus wardi* complex, apparently is restricted to the eastern half of the host range (23). Representatives of three taxa in this complex virtually always occur on the same host individual together with specimens of the *thomomys* complex. A fourth taxon of this complex, *Thomomydoecus byersi*, occurs on *Thomomys bottae* and is morphologically quite divergent from the other three taxa of the complex.

*Thomomys* (*Thomomys*) subspecies with unknown louse associations are *T. talpoides andersoni*, *T. talpoides cognatus*, *T. talpoides incensus*, *T. talpoides kelloggi*, *T. talpoides loringi*, *T. talpoides medius*, *T. talpoides relicinus*, *T. talpoides segregatus*, *T. talpoides shawi*, and *T. talpoides whitmani*.

## Thomomys (Megascapheus)

Most gopher groups contain relatively few taxa. The subgenus *Thomomys* discussed above is the largest thus far with 74 host taxa. In contrast, the *Thomomys bottae* group of gophers that constitutes the *Megascapheus* subgenus contains 231 species and subspecies, over half of all gopher taxa. These are distributed among four gopher species, *T. bottae*, *Thomomys umbrinus*, *Thomomys bulbivorus*, and *Thomomys townsendii*. Thirty-five taxa of *Geomydoecus* lice and 17 of *Thomomydoecus* are distributed among gophers of this group. This broad diversity of both hosts and lice results in a very complicated picture of distributional associations (20), a situation that cannot be dealt with here in detail.

The *Geomydoecus californicus* complex contains 16 louse taxa and is the most widespread of all pocket gopher louse complexes, having been collected from 144 *T. bottae* and 14 *T. umbrinus* subspecies. It is generally absent from *T. bottae* subspecies of southern Oregon and California north of San Francisco Bay and is not found on *T. bulbivorus* or *T. townsendii*, except in a small hybrid zone in northeastern California. The eight taxa of the *umbrinus* complex

are known only from 22 subspecies of Mexican *T. umbrinus*. The two species of the *subcalifornicus* complex are distributed widely throughout the southwestern US and northern Mexico and have been collected from 43 subspecies of *T. bottae* and three of *T. umbrinus*. The lice of these three complexes form a closely knit group morphologically, and provide further support for the louse-based separation of *T. bottae* and *T. umbrinus*.

The four species of the *oregonus* complex are restricted to 21 subspecies of *T. bottae* in northern California and spottily distributed in southern California, as well as on *T. bulbivorus* and all seven subspecies of *T. townsendii*. The distribution of this complex suggests a difference between *T. bottae* taxa from these areas and those found elsewhere, with a possible affinity between the former and *T. bulbivorus* and *T. townsendii*. The five taxa of the *tolucae* complex, which have been collected from eight Mexican *T. umbrinus* subspecies and two isolated populations of *T. bottae* subspecies in Arizona, are morphologically closest to those of the *oregonus* complex.

The *Thomomydoecus* taxa nearly always occur on individual gophers that also are carrying *Geomydoecus* lice. However, *Geomydoecus* often occurs in the absence of *Thomomydoecus*. The *minor* complex is the largest of the *Thomomydoecus* complexes; its nine species were collected from 75 *T. bottae* subspecies and 18 *T. umbrinus*. The seven species of the *neocopei* complex occur on 10 subspecies of *T. umbrinus* in Mexico and southwestern New Mexico. Each louse taxon of this complex has a very restricted distribution, which may reflect the limited distribution of the hosts. The members of the *wardi* complex are principally found on *T. talpoides* group gophers, but one species occurs on two subspecies of *T. bottae* in New Mexico and southern Colorado.

*Thomomys* (*Megascapheus*) subspecies with unknown louse associations are *T. bottae aureiventris*, *T. bottae magdalenae*, *T. bottae powelli*, *T. bottae pusillus*, *T. bottae spatiosus*, *T. bottae subsimilis*, *T. bottae varus*, *T. mazama couchi*, *T. mazama melanops*, and *T. mazama premaxillaris*.

## Zygogeomys

The genus *Zygogeomys* consists of only a single species and it is the host for the louse *Geomydoecus trichopi* (67). While the distribution of this pocket gopher is close to those carrying lice of the *coronadoi* and *mcgregori* complexes, *G. trichopi* is sufficiently distinct to merit standing apart from lice of the other complexes.

## DISTRIBUTIONAL SIMILARITIES AND INCONGRUITIES

The procurement of large numbers of lice and the application of both univariate and multivariate morphometric analyses during the past 15 years resulted in a clearer delineation of previously known taxa of lice and the description of

a large number of additional louse species and subspecies and an increased understanding of host relationships. In many cases, the lice have distributions that closely approximate those of the species and subspecies of their hosts.

This is particularly true for *Orthogeomys* and *Pappogeomys* pocket gophers inhabiting central Mexico and ranging south through Panama, where gophers occur in geographically isolated populations. While louse species in this region also have restricted ranges, often two or even three species of *Geomydoecus* occur on a single host taxon, and, for some host taxa, on the same individual. By contrast, louse distributions from *Zygoeomys* and *Geomys* typically have only one *Geomydoecus* louse taxon on a single host taxon or individual, and *Thomomydoecus* lice have never been found on these same hosts. On many *Thomomys*, a species of *Thomomydoecus* nearly always occurs with a species of *Geomydoecus* on the same gopher. However, *Geomydoecus* species often occur on hosts without *Thomomydoecus*.

In *Geomys*, northern *Pappogeomys*, and *Thomomys*, distributional associations between lice and their hosts may be much more complicated and suggest independent distributions. These host taxa, while generally allopatric, have distributions that often are contiguous, offering a greater opportunity for transfer of parasite species between host species. Thus, the interpretation of host-parasite associations in these groups rests on whether transfer of parasites among host taxa is possible or likely. While there is no intrinsic reason to believe that transfer cannot occur, an increasing body of evidence suggests that it is exceedingly rare. For example, the *T. bottae* group consists of 231 named taxa that represent over half of all of the taxa recognized in the pocket gophers. Most of the distinctions between these taxa are based on variation in adaptive pelage color and body size (14). However, the *T. bottae* group exhibits a greater degree of chromosomal variability than any other known mammalian species (39). While most of the host taxa from which lice were obtained showed a fairly uniform louse fauna, each of 70 subspecies possessed geographically separated localities with 2 or more related louse taxa. In many of these cases, the distribution of louse taxa appeared to divide the host taxa into two or more parts, indicating that some refinement of the host distributions might be appropriate. In other cases, host-lice incongruities appeared in peripheral areas of the host ranges and might indicate misidentification of the host taxa. While this observation could be cited as an example of transfer of parasites among host taxa, recent treatments of the *T. bottae* of California (47, 73) resulted in a two-thirds reduction in the number of defined taxa. These newer definitions show close conformity to the distributions of *T. bottae*-associated lice (3).

A similar but less complicated case of host-parasite distributional incongruity appears with *P. castanops*. Study of the distribution of *P. castanops* lice (17) revealed groupings of gopher taxa with major discrepancies from those

proposed by Russell (72) in the revision of the genus *Pappogeomys* based on morphology. While the distribution of louse taxa conformed reasonably well to that of their hosts as given by Hall & Kelson (15), it departed substantially from the subspecies groupings defined by Russell (72) and subsequently adopted by Hall (14). Instead, the louse groupings divided hosts into northern and southern subspecies groups. This corresponded perfectly with the findings of Berry & Baker (2) that gophers north of the 25th parallel have a diploid chromosome number of 46 and those south of it have only 42. Thus, the louse associations, rather than presenting an example of host-parasite incongruity, support a classification of hosts based on genetics rather than morphology and suggest the need for additional study of this gopher group by mammalogists.

Comparison of louse distributional relationships with *G. bursarius* also showed discrepancies with the existing host classification (86). However, subsequent morphological, genetic, and biochemical work on this pocket gopher genus (16, 74) indicated a very close conformity of the louse and gopher taxonomies. As an example, the distributions of *Geomydoecus nebrathkensis* and *Geomydoecus oklahomensis* lice in Nebraska had not corresponded with the distribution of what was then recognized as *G. bursarius lutescens*. Subsequently, this host taxon was divided into two subspecies in exact agreement with the louse distributions.

One of few examples of apparent crossover and successful establishment of lice from one major host taxon to another appears among the lice on *T. talpoides levis* in Utah. Here we have seen collections from seven gophers in six localities associated with specimens of *Thomomydoecus zacatecae*, a normal inhabitant of *T. bottae*, along with the usual lice of the *thomomys* complex. This part of Utah is an interface area between the two *Thomomys* gopher subgenera and exchanges of lice would be possible. With the exception of those occurring in hybrid zones (48), this crossover is the only one we can document even when different host species or genera occur in the same locality. For example, *Geomys* and *Thomomys* occur together in a field northwest of Las Cruces, New Mexico. C. S. Thaler, Jr. (personal communication) has collected gophers of both genera from the same burrow system, and we have collected and examined lice from these and other hosts in this area. We can find no evidence for transfer of lice between host taxa in this or other areas where opportunities for exchange of parasites exist.

The extent to which louse movement between pocket gopher taxa may occur in areas of host hybridization has been considered (48). Genetic similarity and ectoparasite associations were compared for *T. bottae* × *T. townsendii* hybrids from Gold Run Creek in California. While both F<sub>1</sub> hybrid and presumptive backcross pocket gophers were apparent, no genetic introgression was evident, based on five diagnostic allozyme loci present in parental

populations of either taxon within a mile of the hybrid zone. Similarly, louse species unique to each parental gopher did not penetrate beyond the geographic limits of the genetic hybrid zone into the range of the opposite gopher species. Thus, a narrow zone of hybridization was defined concordantly by genetic, morphologic, and ectoparasitic parameters. On the basis of this study, these two gopher taxa were determined to be genetically, if not reproductively, isolated and should be considered separate biological species. To our knowledge, that paper (48) is the first to combine mammalian cytogenetics with parasite associations in evaluating the validity of mammalian species. Other examples of louse crossover restricted to zones of host hybridization have been documented for *T. bottae canus*  $\times$  *T. townsendii relictus* hybrids (75) in the Garnier Ranch area in California and for *T. bottae modicus*  $\times$  *T. umbrinus intermedius* hybrids (40) at Sycamore Canyon in Arizona.

## EVOLUTION AND COSPECIATION

Studies of ectoparasites such as chewing lice, because of their conservative rates of evolution with respect to their hosts, may aid in recognition of host relationships (26, 71). While researchers generally believe that arthropod ectoparasites have a high degree of host specificity and that parasite phylogeny reflects host phylogeny (i.e. Fahrenholz's Rule or *host tracking*), Kethley & Johnston (27), drawing from their experience with quill mites but citing other examples, concluded that noncongruent host-parasite relationships, indicative of resource tracking, are much more common than previously realized. This idea is supported for the chewing lice of birds by Eveleigh & Amano (7) in their study of the lice of alcids. However, other workers continue to find evidence supporting instances of host tracking (9, 28, 29, 35, 70).

The controversy over this question extends to pocket gophers and their lice. Timm (82, 83) found evidence for host tracking among the lice of *G. bursarius*. Lyal (31, 32) claimed that these data are consistent with a resource-tracking hypothesis. Problems with underlying assumptions of Fahrenholz's Rule also are discussed by Mitter & Brooks (34) and Humphries & Seberg (24). Hafner & Nadler (13) tested Fahrenholz's Rule by constructing phylogenetic trees for both pocket gophers and their lice using protein electrophoretic data. They found a high degree of concordance in the branching patterns of trees, which suggests that a history of cospeciation exists in this host-parasite assemblage. In several cases in which the branching patterns were identical in the host and parasite phylogenies, the branch lengths also were similar. Given the assumptions of molecular clock theory, this similarity suggests that the speciation of these hosts and ectoparasites was roughly contemporaneous and causally related.

While we believe that resource tracking may have contributed to host-parasite associations in other groups of Mallophaga, evidence of genetically based associations between trichodectid lice and pocket gopher hosts is sufficient to justify a host-tracking model of cospeciation for these organisms. Pocket gopher lice already have been employed effectively to provide definitions of host taxa independent of those determined through the morphological and genetic study of host populations. They also have been successfully used as indicators of gene flow between host populations and as a means of evaluating the validity of and relationships among currently defined host taxa.

The evolutionary relationships between ectoparasitic chewing lice and their geomyid hosts appear to fit the cospeciation model described by Brooks (4) and Janzen (25). While chewing lice appear to have evolved some close, parallel behavioral traits in response to their hosts (83), pocket gophers appear to have undergone little, if any, evolutionary change in response to chewing lice. The chewing lice of pocket gophers apparently feed only on dead tissue and are not known to transmit diseases or other parasites to their hosts. Therefore, the only potential cost to the host for harboring these parasites would be increased time spent in grooming. However, this increased grooming has not been observed, and, since both grooming and feeding occur away from potential predators in enclosed tunnel systems and host populations appear to be nearly universally infested with lice, louse infestation is probably not a significant factor in host fitness or fecundity (84). Furthermore, the host as a chewing louse resource differs little within many of the large pocket gopher subspecies complexes that contain diverse allopatric louse species. Lyal (30) investigated evolutionary relationships in the Trichodectidae, but omitted analysis of the cladistic relationships among most pocket gopher lice. These relationships have been examined phenetically for lice of *T. bottae* in California (3) and a cladistic examination of the *Geomydoecus* and *Thomomydoecus* lice is ongoing.

## CONCLUSION

Although detailed studies of chromosomal and genic composition undoubtedly will yield much additional information on pocket gopher systematics and taxonomic relationships, the requirement of freshly collected specimens for preparations makes extensive studies difficult. Even though chromosomal characters have taken on an increasing importance in mammalian taxonomy, the need for taxonomic methods that are powerful and can utilize the tremendous resources contained in the preserved specimens maintained in the major museums continues. Furthermore, environmental studies often are concerned with the identification and previous distribution of taxa that may have been eliminated from areas because of human disturbance. Lice are easily collected from museum skins of hosts long dead, poorly prepared, or



even from those with skulls missing. The lice may, therefore, help answer questions of distributional changes through time and assist in solving problems of host identification as well as of relationships.

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