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DISTRIBUTIONAL ASSOCIATIONS AMONG *GEOMYDOECUS* AND *THOMOMYDOECUS* LICE (MALLOPHAGA: TRICHODECTIDAE) AND POCKET GOPHER HOSTS OF THE *THOMOMYS BOTTAE* GROUP (RODENTIA: GEOMYIDAE)[1]

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Abstract. A computerized taxonomic and geographic storage, retrieval, analysis, and distribution mapping system was used to evaluate 51,670 specimens of *Geomydoecus* and *Thomomydoecus* chewing lice collected from 226 species and subspecies of the pocket gophers *Thomomys bottae, T. umbrinus, T. townsendii,* and *T. bulbivorus.* These lice consisted of 52 species and subspecies in 8 complexes. Comparison of the geographic ranges of louse complexes with those of associated host taxa showed that, while most host taxa had a fairly uniform louse fauna, 70 subspecies possessed geographically separated localities with 2 or more louse taxa from the same genus. The distribution of louse complexes corresponded reasonably well to pocket gopher species but showed a somewhat different separation between *T. bottae* and *T. umbrinus* than that presently defined by gopher taxonomists. Comparison of geographically isolated host populations based on louse associations showed both similarities to and differences from that based on allozymal similarity among the hosts, with the louse-based groups geographically well defined. Individual hosts rarely harbored more than 1 louse species per genus, and in 1 case where this occurred the host was found to be an F_1 hybrid of parental taxa that were each associated with 1 of the louse species.

A major challenge in systematic and evolutionary biology concerns the taxonomy, evolution, and biogeography of chewing lice in the genera *Geomydoecus* Ewing and *Thomomydoecus* Price & Emerson (Mallophaga: Trichodectidae) and their vertebrate hosts, the pocket gophers (Rodentia: Geomyidae). These louse genera currently include 94 species, 7 of which are divided into 16 subspecies. Hall (1981) recognized 5 genera and 33 species of pocket gophers, 18 of which are divided into 425 subspecies, making this family one of the most taxonomically complicated vertebrate groups. According to Patton & Yang (1977), the patterns of genetic variation in pocket gophers and other fossorial rodents have received more study than any other mammals except man. These have shown that pocket gophers have a high degree of both intra- and interpopulational divergence in genetic systems, including extreme chromosomal variability involving both chromosome number and arm number changes. While this diversity is often associated with reproductive isolation and chromosomal reorganizations that have resulted in genetic incompatibility among populations, in some cases this chromosomal variation is apparently independent of reproductive isolation. In pocket gophers of the *Thomomys bottae* group, which consists of *T. bottae* (Eydoux & Gervais), *T. umbrinus* Richardson, *T. bulbivorus* (Richardson), and *T. townsendii* (Bachman), genetic and morphological variability have complicated interpretation of the relationships and specific and subspecific distinctions among taxa. This is evidenced by the lack of agreement among mammalogists about the validity of the species *T. bottae* as distinct from *T. umbrinus,* with Anderson (1966), Patton & Dingman (1968), and Patton (1973) supporting specific distinctions between these taxa, Hall (1981) regarding *T. bottae* as synonymous with both *T. umbrinus* and *T. townsendii,* and Hoffmeister (1969) indicating that the validity of these taxa is a matter of interpretation.

Whereas detailed studies of chromosomal and genic composition will undoubtedly yield much additional information on pocket gopher systematics and taxonomic relationships, the need for freshly collected specimens for preparations makes extensive studies difficult. Even though chromosomal characters have taken on an increasing importance in mammalian taxonomy, there is a continuing need to establish new taxonomic methods that are powerful and can use the tremendous resources represented by the preserved specimens maintained in the major museums. Furthermore, environmental studies often are concerned with the identification and former distribution of taxa that may have been eliminated from areas because of human disturbance. Unlike chromosome preparations, lice are easily collected from museum skins of hosts

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long dead, poorly prepared, or with skulls missing. They can, therefore, help answer questions of distributional changes through time and assist in solving problems of identification and relationships.

It is our purpose here to summarize the known biogeographical associations between *T. bottae*-group pocket gophers and their lice and to consider the potential for the use of these lice as indicators of host relationships.

PREVIOUS INVESTIGATIONS OF LOUSE–POCKET GOPHER RELATIONSHIPS

It has long been postulated that 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 (Kellogg 1896, Rothschild & Clay 1952). However, to accomplish this, large numbers of parasites must be collected from a broad spectrum of hosts. They must then be subjected to a thorough taxonomic treatment that includes analyses of both qualitative and quantitative characters and that employs statistical comparisons of parasite populations and their phenetic relationships. Large or intricate host taxonomic complexes, such as the pocket gophers, present a quantity and complexity of data that can be adequately handled only by computers. This approach to the study of host relationships has been advocated by researchers such as Mayr (1957) and Wenzel & Tipton (1966).

Pocket gopher lice and their hosts present a unique opportunity for the study of host–parasite relationships. 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. Chewing lice of the genera *Geomydoecus* and *Thomomydoecus* are the only lice found on pocket gophers. They are restricted to pocket gophers and are abundant and easily collected from hosts or prepared skins. Pocket gophers are restricted geographically to North and Central America, are relatively sedentary, and are common enough to be well represented in major vertebrate collections. However, their tendency to occur in relatively small and isolated local populations has resulted in the development of minor character differences that have led recent workers to the recognition of 442 species or subspecies. In addition, relationships among these gopher taxa are poorly understood (Anderson 1966).

In spite of these factors and the potential that studies of lice may have for assisting in both the definition of pocket gopher taxa and in the understanding of relationships among them, it has only been in the past 12 years that any intensive work has been done on *Geomydoecus* and *Thomomydoecus* lice. Until 1971, only 11 louse species and subspecies were recognized from all pocket gophers (Werneck 1950). These were so poorly defined that they were essentially indistinguishable. Price & Emerson (1971), in a revision of *Geomydoecus*, redescribed the taxa associated with the 11 previous names and described 34 new species and subspecies, bringing the total recognized taxa to 45. Subsequent work through 1978 by Price, Hellenthal, and Emerson increased the number of defined taxa to 58. Recent publications by Timm & Price (1979, 1980) on the *Geomydoecus* of *Geomys* Rafinesque and by Hellenthal & Price (1980, 1984) and Price & Hellenthal (1979, 1980a,b,c, 1981a,b) on lice of the *Thomomys bottae* group have further increased the number of louse taxa to 103 species and subspecies, with those of the *bottae* group increasing from 11 to 52. The occurrence of such a diversity of recognizable louse taxa on these pocket gophers strengthens their potential as indicators of host relationships.

The procurement of large numbers of lice and the application of univariate and multivariate morphometric analyses in the past 8 years have resulted in a clearer delineation of previously known louse taxa, the description of a large number of additional louse species and subspecies, and an increased understanding of host relationships. Prior to our examination of lice on *T. bottae*-group gophers, 2 pocket gopher species had undergone intensive investigation of their host–parasite associations. These are summarized below.

Lice of the Yellow-faced Pocket Gopher, Pappogeomys castanops *(Baird)*

Based on application of conventional morphological criteria applied to limited material, Price & Emerson (1971) recognized 2 species of *Geomydoecus* from *P. castanops*. Yet, after studying over 5500 adult lice from 320 hosts representing all 25 *P. castanops* subspecies recognized by Russell (1968) and using multivariate morphometric analyses coupled with more conventional taxonomic methods, we found each of these louse species to represent a complex with 2 species in one (Price & Hellenthal 1975a) and 6 species and subspecies in the other (Price & Hellenthal 1975b). Study of the distribution of these *P. castanops* lice (Hellenthal & Price 1976) revealed groupings of gopher taxa with ma-

TABLE 1. Summary of computerized data base for *Geomydoecus* and *Thomomydoecus* lice obtained from *Thomomys bottae*-group gophers.

Gopher taxa sampled	226	97.4% of described taxa
Localities	2,136	9.5 per gopher taxon
Gophers with lice	3,834	1.8 per locality
Adult lice identified	51,670	13.5 per gopher
Lice measured	11,077	21.4% of identified lice
Stored character data	305,240	25–30 observations per louse

jor discrepancies from those proposed by Russell (1968) in the revision of pocket gophers of the genus *Pappogeomys* Merriam based on gopher morphology. The louse taxa did not conform to the subspecies groupings as defined by Russell (1968) but divided the hosts into northern and southern subspecies groups that corresponded with the findings of Berry & Baker (1972) that gophers north of the 25th parallel have a diploid chromosome number of 46 and those south of it have only 42.

Lice of the Plains Pocket Gopher,
Geomys bursarius (Shaw)

Price & Emerson (1971) had recognized 5 species and subspecies of *Geomydoecus* on this gopher species. A study by Timm & Price (1980) of over 20,000 adult lice representing 590 hosts from over 425 localities resulted in the description of 3 additional louse species and elevation of earlier subspecies to specific level, for a total of 8 species on *G. bursarius*. These louse taxa clustered in 2 distinct groups, a northern one with 5 species and a southern one with 3. While the lice did confirm to some extent the *G. bursarius* classification accepted at that time, they did not do so completely. However, a recent revision of this pocket gopher group (Heaney & Timm 1983) has indicated very close conformity of the louse and gopher taxonomies.

METHODS

Quantitative character data for lice included in this study, as well as associated host and locality information, are stored as a computerized data base, which is maintained on an IBM 370/168 computer system at the University of Notre Dame (Table 1). This data base is accessed by a storage, retrieval, and taxonomic analysis system, called the BUG System (Hellenthal & Price 1980), which performs taxonomic and geographical analyses and retrieves data required for host and louse distribution maps. The system also communicates with the NT-SYS Numerical Taxonomy System of Multivariate Statistical Programs (Rohlf et al. 1982), which is used for similarity and cluster analyses, and with the SAS Statistical Analysis System (SAS Institute 1983), which is used for the production of distribution plots.

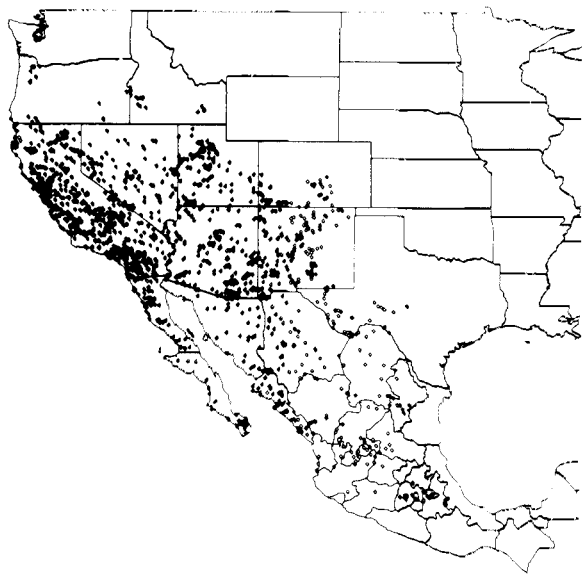

FIG. 1. Computer-generated distribution map (rectangular projection) of western United States and Mexico showing locations of host collection sites.

A host–parasite association data base, currently containing 5300 records for hosts collected from 2136 localities (Fig. 1), is used to keep track of the identified lice from each host and locality. Localities are identified by a 10-character code consisting of a 2-character country code, a 2-character state or province code, a 3-digit Federal Information Processing Standard (FIPS) county code (U.S. Department of Commerce 1973), and a 3-digit locality code. When localities are entered into the system, the latitude and longitude of the closest town or other landmark are entered with the bearing angle and distance between the landmark and the specific collection site. The system adjusts the geographic coordinates for the landmark to the specific locality using calculated lengths of degrees for the appropriate parallels and meridians.

The system can produce distribution maps by country, state, county, host identification, and by parasite genus, complex, or species. Selection of host or parasite data for mapping is performed interactively for data contained in up to 2400 host–parasite association records at a time. After the initial set of data is defined, the user may elect to

TABLE 2. Taxonomic history of *Geomydoecus* and *Thomomydoecus* lice from *Thomomys bottae*-group gophers.

LOUSE GENUS AND COMPLEX	PRICE & EMERSON (1971)*	PRICE & EMERSON (1972)	NO. CURRENT TAXA
Geomydoecus			
Californicus	*californicus*	*californicus*	16
Umbrini	*umbrini*	*umbrini*	8
Subcalifornicus	*subcalifornicus*	*subcalifornicus*	2
Oregonus	*oregonus*	*oregonus*	1
	idahoensis	*idahoensis*	3
Tolucae	*tolucae*	*tolucae*	5
Thomomydoecus			
Minor	*minor*	*minor*	4
		dickermani	5
Neocopei	*neocopei*	*neocopei*	1
		genowaysi	3
		jamesbeeri	3
Wardi	none	none	1
Total	8	11	52

* Only *G. californicus* and *T. minor* were described prior to Price & Emerson (1971).

group these data by host or parasite identification so that each taxon is uniquely identified on the map. The output of this program is a file containing the latitude and longitude of selected localities with state and county information, which will be used to retrieve political boundary data for the map, and an additional value used to identify groups. The map is produced by the SAS procedure GMAP using unprojected data bases containing U.S. state and county map outlines obtained from the U.S. Department of Commerce.

For Mexico, a similar unprojected state map data base was constructed with eastern, western, and southern border data obtained from the SAS world map data base (Langston 1981), the northern border data extracted from adjoining U.S. states, and Mexican state boundaries obtained using a digitizer from a rectangular projection of the country.

Since the SAS GMAP procedure does not permit the placement of points on maps, data for each locality to be included on a map are converted to a small area that is merged with the map data as if it were an additional state or county. Thus, maps may contain both political boundaries and symbols indicating specific collection sites (e.g., Fig. 1).

Similarity analyses of the parasite composition of hosts and host localities used the Jaccard Coefficient of Association (Sneath 1957), a matching procedure for binary data that excludes negative matches. Thus in our analyses, common absence of a parasite taxon is not considered in the determination of similarity. Cluster analyses of similarity matrices were performed by the unweighted pair-group method using arithmetic means (UPGMA; Sneath & Sokal 1973).

HOST–LOUSE ASSOCIATIONS OF *T. bottae*-GROUP GOPHERS

Most gopher complexes, including the 2 examples cited previously, contain relatively few taxa; however, the *Thomomys bottae* group contains 4 species divided into 231 subspecies and represents over ½ of the recognized taxa in the pocket gophers (Fig. 2). *Thomomys bulbivorus* occurs in northwestern Oregon (no subspecies described), and *T. townsendii* in northern Nevada, southern Idaho, southeastern Oregon, and northeastern California with 7 recognized subspecies. *Thomomys bottae* includes 189 subspecies extending from southwestern Oregon, southern Nevada, Utah, and southern Colorado south into northern Mexico, and *T. umbrinus*, with 35 subspecies, extends from extreme southeastern Arizona and southwestern New Mexico south through central Mexico. Most of the distinctions between these are based on variation in adaptive pelage color and body size (Hall 1981); however, the *bottae* group exhibits more chromosomal variability than any other known mammalian species (Patton 1972).

Our studies have resulted in the recognition of 47 species, 3 of these divided into 8 subspecies, in the genera *Geomydoecus* and *Thomomydoecus*, almost a 5-fold increase in the number of taxa (Table 2). All but 2 of the 11 louse taxa considered by Price & Emerson (1971, 1972) from *Thomomys bottae*-group gophers were later shown to represent species

complexes. The remaining 9 taxa have been divided into 49 species and subspecies. The lice of the *bottae* group of pocket gophers are divisible into 2 genera, with 35 taxa in the genus *Geomydoecus* and the remaining 17 taxa of smaller, more slender and tapered lice in the genus *Thomomydoecus* (see Price & Emerson 1972, Hellenthal & Price 1984). A list of pocket gopher taxa and their associated louse fauna is given in Emerson & Price (1981). The genus *Thomomydoecus* includes 1 additional species that shows its closest affinities to a complex of lice that otherwise occurs only on *T. talpoides* (Richardson) pocket gophers (Hellenthal & Price 1984).

Below is a summary of the results of our taxonomic findings for the lice from the *T. bottae* group.

GENUS *Geomydoecus*

G. californicus complex

Price & Hellenthal (1981a) showed that *G. californicus* (Chapman) actually includes 16 species and subspecies of lice. It is the most widespread of all gopher–louse complexes, having been collected from 144 *T. bottae* and 14 *T. umbrinus* subspecies (Fig. 3). The complex is generally absent from the *T. bottae* subspecies of southern Oregon and California north of San Francisco Bay except for the southern ½ of *T. b. minor* Bailey along the northern California coast. It is also absent from *T. bulbivorus* and *T. townsendii* except for a small hybrid zone between *T. t. relictus* Grinnell and *T. b. canus* Bailey in northeastern California (Thaeler 1968). It has not been collected from 20 subspecies of *T. umbrinus* at the southern end of its host range in central Mexico nor from 27 subspecies of *T. bottae* in the range of *G. subcalifornicus* Price & Emerson from northwestern Mexico and southern Arizona.

The complex is divided into 4 subcomplexes of 2 to 6 louse taxa each. The *bajaiensis* subcomplex (Fig. 3: stars) has the most limited distribution, with 2 louse species occurring on 18 subspecies of *T. bottae* from Baja California. No other *Geomydoecus* or *Thomomydoecus* louse taxa have been collected from any of these host taxa except for *T. b. martirensis* Allen in northern Baja California, from which we obtained *G. bajaiensis* Price & Hellenthal in 2 localities and louse taxa belonging to other groups in 4 other localities.

The *aurei* subcomplex (Fig. 3: squares) contains 6 louse taxa distributed in the eastern ½ of the complex east of the California and Nevada borders and throughout northern Mexico. While members of the subcomplex have been collected from 32 subspecies of *T. bottae* and 13 of *T. umbrinus*, 5 of the louse taxa are essentially restricted to *T. bottae* subspecies. *Geomydoecus warmanae* Price & Hellenthal is restricted to 11 subspecies of *T. umbrinus*, 2 of which have some collections with *G. warmanae* and additional collections with other louse subspecies within the *aurei* subcomplex.

The *californicus* subcomplex (Fig. 3: circles) contains 4 louse taxa and is the most broadly distributed of the subcomplexes, occurring on 82 subspecies of *T. bottae* and on *T. u. emotus* Goldman, which is found in the northern extreme of the *T. umbrinus* range in the southwestern corner of New Mexico and a small area of adjacent Mexico. *Thomomys u. emotus* is bordered on all sides by subspecies of *T. bottae*.

The *limitaris* subcomplex (Fig. 3: triangles) contains 4 louse taxa that occur on 21 subspecies of *T. bottae* and on *T. u. intermedius* Mearns, which is found in southern Arizona just north of the Mexican border. *Thomomys u. intermedius* is another subspecies bordered mostly by *T. bottae* subspecies on the north, east, south, and northwest, and by *T. u. quercinus* Burt & Campbell on the southwest. We also obtained specimens of *G. warmanae* of the *aurei* subcomplex from host gophers identified to these subspecies occurring within the normal range of the host taxa. The distributions of lice on these host taxa suggest a possible affinity of these hosts with *T. bottae*.

G. umbrini complex

Price & Hellenthal (1981b) found *G. umbrini* Price & Emerson to consist of 8 species and subspecies of lice occurring on 22 subspecies of Mexican *T. umbrinus* gophers (Fig. 4). The taxa of this louse complex are morphologically closest to those of the *californicus* complex but are restricted in their distributions to subspecies of *T. umbrinus*. We have not collected any members of this complex from *T. u. emotus*, *T. u. intermedius*, or *T. u. quercinus*, all of which occur in the northern part of the *T. umbrinus* range and are generally bordered by *T. bottae* subspecies. Thus, members of both the *G. umbrini* and *G. californicus* complexes appear to show a different *T. bottae* and *T. umbrinus* separation than that defined by gopher taxonomists.

G. subcalifornicus complex

Hellenthal & Price (1980) found this complex to consist of 2 louse species that are widely distributed throughout the southwestern U.S. and northern Mexico (Fig. 5). Lice belonging to this complex

have been collected from 43 subspecies of *T. bottae* and from the *T. umbrinus* subspecies *T. u. emotus*, *T. u. intermedius*, and *T. u. sonoriensis* Nelson & Goldman. Members of this louse complex share many morphological features with the 2 preceding complexes and appear to provide further support for the louse-based separation of *T. bottae* and *T. umbrinus* suggested by the distributions of the *californicus* and *umbrini* louse complexes.

G. oregonus complex

Price & Hellenthal (1980a) reported 4 louse species in this complex. They are restricted to 21 subspecies of *T. bottae* gophers in California and Oregon as well as to *T. bulbivorus* and all 7 subspecies of *T. townsendii* (Fig. 6). These lice differ in a number of morphological details from those of the preceding 3 complexes. They appear to be the principal louse on *T. bottae* subspecies in California north of San Francisco Bay and have a rather spotty distribution on the *T. bottae* of southern California. Unlike the previously discussed louse complexes, the louse genus *Thomomydoecus* apparently does not co-occur on hosts with members of the *oregonus* complex. The distribution of this complex appears to suggest a difference between the *T. bottae* taxa in this area and those elsewhere, with a possible affinity between them and *T. bulbivorus* and *T. townsendii*.

G. tolucae complex

The 5 species and subspecies of lice in this complex, described by Price & Hellenthal (1979), are morphologically closest to those of the *oregonus* complex and quite different from those of the other *Geomydoecus* louse complexes. They have been collected on 8 Mexican *T. umbrinus* gopher subspecies and on 2 isolated populations of *T. bottae* subspecies in Arizona (Fig. 7).

GENUS *Thomomydoecus*

These taxa nearly always occur on individual gophers that also have *Geomydoecus* lice. However, *Geomydoecus* often occurs in the absence of *Thomomydoecus*.

T. minor complex

The lice of this complex, reviewed by Price & Hellenthal (1980c), have been divided into 2 subcomplexes that are widely distributed on both *T. bottae* and *T. umbrinus* gopher subspecies (Fig. 8). The *minor* subcomplex consists of 4 species and is distributed on over 75 *T. bottae* subspecies covering much of the *bottae* group range, and on 12 subspecies of *T. umbrinus*. The *minor* subcomplex appears to be further subdivided by *T. timmi* (Price & Hellenthal), which occurs in the western ½ of the range, and by *T. minor* (Werneck), which occurs in the eastern ½. Together these species occur on 68 subspecies of *T. bottae*. The *dickermani* subcomplex consists of 5 species that are distributed on 6 subspecies of *T. umbrinus* gophers in the extreme southern portion of the host range.

T. neocopei complex

Price & Hellenthal (1980b) found this complex, which originally included 3 species of lice, to consist of 7 species occurring on 10 subspecies of *T. umbrinus* in Mexico and southwestern New Mexico (Fig. 9). Each louse species has a very restricted distribution, which may reflect the limited distribution of the hosts.

T. wardi complex

Originally known only from *T. talpoides*, this complex was found by Hellenthal & Price (1984) to also include a single species occurring on 2 *T. bottae* subspecies in an area where the geographic distributions of these 2 host species are in close proximity (Fig. 10). *Thomomydoecus wardi* complex lice occurring on *T. talpoides* have not been subjected to taxonomic analysis, and their distributional associations are not well documented.

HOST–LOUSE DISTRIBUTIONAL CONFLICTS

While a high percentage of the host taxa from which lice were obtained showed a uniform louse fauna, 70 host subspecies possessed geographically separated localities with 2 or more taxa of the same louse genus (Fig. 11). In many of these cases, the distribution of louse taxa appears to divide the host taxa into 2 or more parts. This could indicate that some refinement of the host distributions may be appropriate. In other cases, host–louse incongruities appear in peripheral areas of the host ranges. These may indicate misidentification of some host taxa or, in a few cases, contamination by parasites from other hosts collected or stored together. Also, large geographical areas with numerous gopher taxa having a uniform louse content may suggest that those gophers are taxonomically closer to each other than to members of other groupings. For example, the lice occurring on *T. b. bottae* and *T. b. minor* (Fig. 12, 13) appear to subdivide the distributions of these gopher taxa. The distribution of *G. angularis* Price & Hellenthal may indicate

dectidae) from the *Geomys bursarius* complex (Rodentia: Geomyidae). *J. Med. Entomol.* **17:** 126–45.

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