COSPECIATION OF POCKET GOPHERS (*GEOMYS*) AND THEIR CHEWING LICE (*GEOMYDOECUS*)

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Comparison of independently derived phylogenies for pocket gophers (*Geomys*) and their chewing lice (*Geomydoecus*) from Texas and Louisiana indicates a history of widespread cospeciation in this host-parasite assemblage. Inference of cospeciation is supported by statistical comparison of genetic-distance matrices for gophers and lice based on allozyme data. Although similar, host and parasite phylogenies are not identical; inconsistencies likely result from host-switching by the parasites, retention of ancestral taxa of parasites on recently evolved hosts, or poorly delineated taxonomic boundaries. The current disjunct distribution of *Geomydoecus ewingi* suggests that this chewing louse once parasitized the common ancestor of *Geomys breviceps* and *G. attwateri*. Combined protein and morphologic evidence suggests that the population of *Geomydoecus ewingi* hosted by *G. breviceps breviceps* in northeastern Louisiana may be a cryptic species of louse.

Key words: ***Geomys*, cospeciation, parasites, chewing lice**

The central concept of cospeciation is embodied in Fahrenholz's rule (Eichler, 1948), which states that phylogenies of parasites generally will correspond directly to those of their hosts. In practice, systematists have used Fahrenholz's rule as a rationale for classifying parasites by reference to host phylogenies (Brooks, 1977; Brooks and Overstreet, 1978) or classifying hosts by reference to parasite relationships (Hopkins, 1949; Timm, 1983; Wenzel et al., 1966). Clearly, cospeciation will occur in a host-parasite assemblage only if the parasite has shown a high degree of host specificity over a relatively long period of time. Host specificity usually is the result of the parasite's dependence on a particular species of host for one or more essential resources; thus, the parasite is unable to survive on potential hosts lacking those resources (Kethley and Johnston, 1975). However, high host specificity and hence, cospeciation, may occur simply because the parasite has low vagility and is unable to disperse to a new host. Importantly, these two factors (inability to survive on a new host and lack of opportunity to colonize a new host), although different biologically, yield identical patterns of cospeciation.

Pocket gophers (Rodentia: Geomyidae) and their chewing lice (Mallophaga: Trichodectidae) are an ideal system for the study of coevolutionary relationships between hosts and their parasites. Geomyid species seldom are found in sympatry, but often are parapatric and have long, narrow zones of contact (Patton and Yang, 1977). As a result, the majority of pocket gophers hosting one species of ectoparasite rarely, if ever, encounter pocket gophers hosting a different species of ectoparasite, such that few opportunities exist for chewing lice to colonize more than one species of pocket gopher. Although it is not known if chewing lice are restricted to a particular host species for physiological reasons, it is known that they are obligate ectoparasites that cannot survive off the host for a lengthy period of time (Askew, 1971; Marshall, 1981). This, coupled with the fact that geomyids are asocial and have low effective rates of dispersal (Daly and Patton, 1990), greatly restricts

dispersal of parasites. Thus, dispersal of chewing lice is thought to occur only during direct contact between host individuals, as in mating encounters or while rearing young (Hafner and Nadler, 1990).

Pocket gophers of the genus *Geomys* are distributed throughout Texas and much of Louisiana (Fig. 1a). Although systematic relationships among members of the genus in this region have been the subject of considerable study (Baird, 1854; Baker, 1950; Baker et al., 1989; Block and Zimmerman, 1991; Penney and Zimmerman, 1976), relationships among several species of *Geomys* have yet to be resolved in detail. Honeycutt and Schmidly (1979) studied geographic variation in *Geomys bursarius* in Texas and adjacent states, and found that three groups were distinguishable based on morphological and chromosomal criteria. Honeycutt and Schmidly (1979) referred to these groups as the *lutescens* group, which includes *G. bursarius knoxjonesi, G. bursarius major, G. bursarius llanensis,* and *G. bursarius texensis*; the *attwateri* group, which includes only *G. bursarius attwateri*; and the eastern or *breviceps* group, which includes *G. bursarius sagittalis* and *G. bursarius breviceps* (Fig. 1a). Tucker and Schmidly (1981) investigated a contact zone between *G. bursarius sagittalis* and *G. bursarius attwateri* in southeastern Texas and elevated *attwateri* to species status based on cytogenetic evidence. Similarly, Bohlin and Zimmerman (1982) elevated the *breviceps* group to species status after studying contact zones in Texas and Oklahoma involving *G. breviceps sagittalis* and *G. bursarius major*. *G. bursarius knoxjonesi* also was elevated to species status (Baker et al., 1989), but is not included in this study. More recently, Block and Zimmerman (1991) elevated *G. bursarius texensis* (plus *G. b. llanensis*) to species status (*G. texensis*) based on allozymic data corroborated by data on taxonomy of chewing lice.

The four species (including six subspecies) of *Geomys* investigated in this study (Fig. 1a) host four species of chewing lice (Timm and Price, 1980; Fig. 1b). *G. breviceps* hosts the louse species *Geomydoecus ewingi*, which also is found on westernmost populations of *G. attwateri*; all intervening populations of *G. attwateri* host the louse *Geomydoecus subgeomydis* (Fig. 1b). *G. bursarius major* hosts the widely distributed louse *Geomydoecus oklahomensis*. This chewing louse also occurs on *G. knoxjonesi* and two other subspecies of *G. b. bursarius*. *G. texensis texensis* and *G. t. llanensis* host the louse species *Geomydoecus heaneyi*.

Timm (1983) studied the morphology of the chewing lice hosted by *Geomys* and derived a phylogeny of lice primarily based on mean measurements of several morphologic attributes and the presence or absence of certain discrete characters, such as genital-sac spines in males. Timm (1983) compared this phylogeny of chewing lice with available phylogenies of pocket gophers, and concluded that cospeciation was likely in this host-parasite assemblage. Herein, we perform a quantitative test of cospeciation in the *Geomys-Geomydoecus* assemblage by comparing protein differentiation in the pocket gophers to that of their chewing lice.

Materials and Methods

Pocket gophers were collected at 10 localities in Texas and Louisiana (Fig. 1a). Carcasses of freshly captured specimens were exposed to chloroform for 3–5 min to facilitate collection of ectoparasites by brushing the pelage. Whole lice and tissue samples of pocket gophers immediately were frozen in liquid nitrogen. Homogenates of kidney and liver were prepared following the methods of Selander et al. (1971). Procedures for starch-gel electrophoresis followed Selander et al. (1971) and Harris and Hopkinson (1976), as modified by Patton and Yang (1977) for pocket gophers and Hafner and Nadler (1988) for chewing lice. *Thomomys bottae* and its chewing louse, *Geomydoecus centralis*, were used as outgroups in all analyses.

Whole individuals of chewing lice were crushed directly onto filter paper wicks saturated with a solution containing 6 g of sucrose and 10 mg each of dithiothreitol, β-NADP, and β-NAD in 100 ml of deionized water. Samples of lice were placed

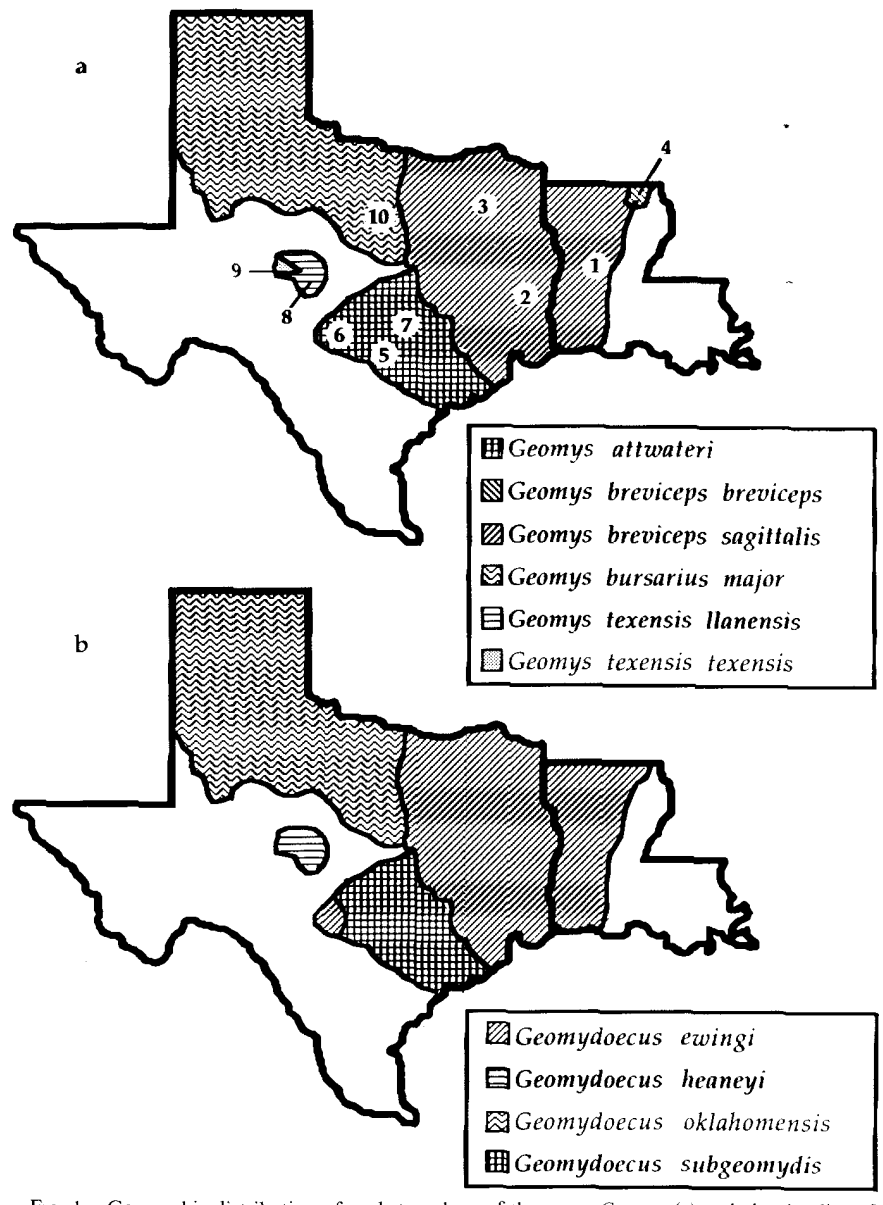

FIG. 1.—Geographic distribution of pocket gophers of the genus *Geomys* (a) and chewing lice of the genus *Geomydoecus* (b) in Texas and Louisiana. Numbers indicate collecting localities as listed in Materials and Methods.

next to host samples on the gels to insure that putative proteins of lice were not, in fact, host proteins contained in the louse's gut.

Twenty-six presumptive gene loci were surveyed in pocket gophers; 4-methyl-umbelliferyl acetate esterase (EST-D, Enzyme Commission number 3.1.1.1), fumerate hydratase (FUM, 4.2.1.2), superoxide dismutase (SOD-1, SOD-2, 1.15.1.1), 6-phosphogluconate dehydrogenase (6-PGD, 1.1.1.44), isocitrate dehydrogenase (IDH-1, IDH-2, 1.1.1.42), lactate dehydrogenase (LDH-1, LDH-2, 1.1.1.27), malate dehydrogenase (MDH, 1.1.1.37), peptidase (PEP-A, valyl-leucine; PEP-B, leucyl-glycyl-glycine; PEP-C, leucyl-alanine; PEP-S, leucyl-alanine, 3.4.11; PEP-D, 3.4.13.9), creatine kinase (CK-1, CK-2, 2.7.3.2), adenylate kinase (AK, 2.7.4.3), aconitase (ACON, 4.2.1.3), hexokinase (HK, 2.7.1.1), nucleoside phosphorylase (NP, 2.4.2.1), mannose phosphate isomerase (MPI, 5.3.1.8), alpha-glycerophosphate dehydrogenase (α-GPD, 1.1.1.8), xanthine dehydrogenase (XDH), hemoglobin (Hb), and prealbumin (PALB). Fourteen loci were surveyed in individual chewing lice; malate dehydrogenase (MDH, 1.1.1.37), malic enzyme (ME, 1.1.1.40), isocitrate dehydrogenase (IDH, 1.1.1.42), superoxide dismutase (SOD-1, SOD-2, 1.15.1.1), arginine kinase (ARK, 2.7.3.3), 4-methyl-umbelliferyl acetate esterase (EST-D, 3.1.1.1), alpha-naphthyl acetate esterase (EST, 3.1.1.1), peptidase (PEP-A, valyl-leucine; PEP-C, leucyl-alanine, 3.4.11), adenosine deaminase (ADA, 3.5.4.4), fumerate hydratase (FUM, 4.2.1.2), glucose phosphate isomerase (PGI, 5.3.1.9), and xanthine dehydrogenase (XDH).

Allozyme data were analyzed using phenetic and phylogenetic approaches. Matrices of Rogers' (1972) genetic distance (D) were generated for pocket gophers and chewing lice using the BIOSYS-1 program of Swofford and Selander (1981). Genetic distances were clustered using the unweighted pair-group method (UPGMA—Sneath and Sokal, 1973). A basic assumption of this method is that evolutionary rates are approximately equal in all taxa analyzed (Nei, 1975). Page (1990, 1991) documented that rates of protein change in pocket gophers and chewing lice (including the genera studied herein) are consistent with predictions of a molecular clock. Hence, UPGMA clustering is an appropriate technique for tree estimation in this study. This observed lack of a significant departure from rate uniformity for allozymes in these pocket gophers and chewing lice is important if all allozyme characters (both plesiomorphies and apomorphies) are to be used to estimate evolutionary history in a phenetic analysis.

Parsimony analyses were performed using the programs FREQPARS (Swofford and Berlocher, 1987) and PAUP (Swofford, 1990). Use of FREQPARS avoids the problem of lost information resulting from the coding of alleles as presence-absence data (Page, 1990), and it assigns each internal node a realistic allele frequency (Swofford and Berlocher, 1987). However, FREQPARS does not perform branch-and-bound searches to assure that the most parsimonious tree (or trees) is found (Hendy and Penny, 1982). In contrast, PAUP performs branch-and-bound searches, but does not accept allele-frequency data. Accordingly, we followed the method of Page (1990) and generated minimal-length and near-minimal-length trees using the branch-and-bound procedure in PAUP, then we input these trees into FREQPARS as user trees. In the PAUP analysis, alleles were coded as unordered independent characters (Mickevich and Mitter, 1983). This coding method preserves more of the phylogenetic information present in the original data than does the more conservative method (i.e., alleles as character states; Page, 1990).

Host and parasite distance matrices were tested for significant association using Mantel's (1967) test. This procedure tests the hypothesis that the pattern of distances in one matrix is independent of the pattern of distances in the second matrix by generating a matrix of t-values (Schnell et al., 1985). This test can falsify the hypothesis of cospeciation by showing that there is no significant association between the host and parasite distance matrices (Hafner and Nadler, 1990). Distance data also provide a means to compare the relative timing of cladogenic events of the hosts and their parasites (Hafner and Nadler, 1990).

The population genetics and systematics of the species of *Geomys* included in this study are reasonably well understood (Baker et al., 1989; Block and Zimmerman, 1991; Penney and Zimmerman, 1976). Thus, collecting localities in the present study (Fig. 1) were chosen to maximize information about genetics and phylogeny of lice ($n \geq 15$ lice per locality). Although the number of pocket gophers sampled per locality was small, each pocket gopher represents an entire population of lice. Archie et al. (1989) cautioned that small samples may decrease the stability of dendrograms calculated from allele-frequency data; however, they emphasized that certain datasets (those with low heterozygosities, allele frequencies generally near zero or one, and patterns of fixed or nearly fixed alleles unique to certain groups) were less prone to this potential source of error. Because the *Geomys* dataset (Table 1) shows all of these characteristics (also see Block and Zimmerman, 1991; Penney and Zimmerman, 1976), a dendrogram generated from these

TABLE 1.—*Allelic variation at 24 polymorphic loci in 10 populations of* Geomys *and the outgroup,* Thomomys bottae. *Numbers below taxon names refer to collecting localities (Fig. 1). Letters refer to allelic alternatives, and parenthetical values represent allele frequencies other than 100%.*

	Species and locality										
	breviceps				*attwateri*			*texensis*		*bursarius*	*Thomomys*
Locus	1	2	3	4	5	6	7	8	9	10	
ACON	b	b	b	b	b	b	a (0.75) d (0.25)	b	b	b	c
AK	a	a	a	a	a	a (0.75) b (0.25)	a	a	a	a	a
α-GPD	a	b	a	a	a	a	a	a	a	a	a
CK-1	c	c	c	c	c	c	c	c	a	c	b
CK-2	c	c	b (0.25) c (0.75)	c	c	c	c	c	c	c	a
EST-D	d (0.67) c (0.33)	d	d (0.75) c (0.25)	d	b	b	b	d	d	d	b (0.86) a (0.14)
FUM	b	b	b	b	b	b	b	b	b	b	a
Hb	b	b	b	b	b	b	b	b	b	b	a
HK	c	c	c	c	c	c	c	a	a	a	b
IDH-1	a	a	a	a	a	a	a	a	a	b	c (0.14) a (0.86)
IDH-2	a	a	a	a	c	c	c	a	a	a	b
LDH-1	a	a	a	a	a	a	a	b	a	a	c (0.29) d (0.14) e (0.57)
MDH-1	b	b	b	b	b	b	b	b	b	b	a
MPI	c (0.5) e (0.5)	c (0.5) b (0.5)	c	c	c	c (0.5) d (0.5)	c	f	f	c	g (0.71) a (0.29)
NP	b	b	b	b	b	b	b	b	b	b	a
PALB	a	a	a	a	c	c	c	a	a	a	b (0.57) d (0.43)
PEP-A	b	b	b	b	b	b	b	b	b	a	c (0.86) d (0.14)
PEP-B	b	b	b	b	b	b	b	c	c	a	b
PEP-C	a (0.83) b (0.17)	a	a	a	a	a	a	a	a	a	c
PEP-D	c (0.67) b (0.33)	c	c	c	a	a	a	a	a	a	b
PEP-S	c	c	c (0.5) d (0.5)	c	c	c	c	c	c	c	a (0.86) b (0.14)
PGD	b	b	b	c	b	b	b	b	b	b	a
SOD-1	a	a	a	a	a	a	a	a	a	a	a (0.86) b (0.14)
XDH	b	b	b	b	b	b	b	e	b	a	c (0.71) d (0.29)

TABLE 2.—*Allelic variation at seven polymorphic loci in the chewing louse* Geomydoecus. *Numbers below taxon names indicate corresponding host populations (Fig. 1 and Table 1). Letters refer to allelic alternatives and parenthetical values represent allele frequencies other than 100%.*

	Geomydoecus						
Locus	*ewingi* (1–3, 6)	*ewingi* (4)	*subgeomydis* (5, 7)	*heaneyi* (8)	*heaneyi* (9)	*oklahomensis* (10)	*centralis*
EST	a (0.5) b (0.5)	a (0.5) b (0.5)	a (0.5) b (0.5)	a (0.5) b (0.5)	a (0.5) b (0.5)	a (0.5) b (0.5)	c (0.63) d (0.37)
FUM	a	a	a	a	a	a	b
IDH	a	a	a (0.9) b (0.1)	a (0.8) c (0.2)	a (0.8) c (0.2)	a	a
ME	b	b	b	b	b	a	b
PEP-C	b	d	b	a	c	c	e
PGI	a	a	a	a	a	a	b
XDH	a	a	a	a	a	a	b

data likely would resemble a dendrogram generated from a larger dataset.

Specimens examined.—Locality numbers (in parentheses) refer to the map (Fig. 1a). *Geomys breviceps sagittalis*: (1) Louisiana: Vernon Parish, Fort Polk National Forest, 0.5 mile N Ranger Station (n = 3); (2) Texas: Jasper Co., 0.9 mile S Kirbyville (n = 1); (3) Texas: Smith Co., 2.6 miles N Lindale (n = 2). *Geomys breviceps breviceps*: (4) Louisiana: Morehouse Parish, 3.1 miles E Bastrop (n = 2). *Geomys attwateri*: (5) Texas: Gonzales Co., 0.8 mile S Ottine (n = 2); (6) Texas: Medina Co., 1 mile SE Natalia (n = 2); (7) Texas: Bastrop Co., 4.9 miles SE Bastrop (n = 2). *Geomys bursarius llanensis*: (8) Texas: Gillespie Co., 9 miles E Fredericksburg (n = 2). *Geomys bursarius texensis*: (9) Texas: Mason Co., 2 miles W Mason (n = 1). *Geomys bursarius major*: (10) Texas: Hood Co., 7.5 miles N Granbury (n = 1). *Thomomys bottae*: New Mexico: Socorro Co., San Acacia (n = 7). Subsamples of lice from each locality were identified based on morphologic characters by R. D. Price without his prior knowledge of collecting locality or host species. Voucher specimens of lice are deposited in the Entomology Collection of the University of Minnesota. Specimens of pocket gophers are housed in the Museum of Natural Science, Louisiana State University.

RESULTS AND DISCUSSION

Allozyme analysis.—Twenty-four of 26 loci surveyed in *Geomys* were polymorphic (Table 1), and 7 of 14 loci were polymorphic in the chewing lice (Table 2). All individuals of *G. bursarius* and *G. texensis* share a unique allele at the HK locus, and individuals of both subspecies of *G. texensis* share unique alleles at two loci (PEP-B and MPI). Individuals of *G. attwateri* are linked by shared-unique alleles at the PALB and IDH-2 loci, and the two subspecies of *G. breviceps* are linked by a unique allele at the PEP-D locus. *G. b. breviceps* (the isolated subspecies in northeastern Louisiana; locality 4 in Fig. 1a) has an autapomorphic allele at the PGD locus. These data indicate that this subspecies is genetically and morphologically differentiated from other populations of *Geomys*, corroborating previous suggestions (Honeycutt and Schmidly, 1979; Lowery, 1974) that gene flow is reduced or absent between *G. b. breviceps* and other populations of *Geomys*.

The population of *Geomydoecus ewingi* hosted by *G. b. breviceps* (locality 4 in Fig. 1a) has a unique allele at the PEP-C locus (Table 2). This evidence, combined with the morphologic findings of Timm and Price (1980), suggests that those populations of *Geomydoecus ewingi* hosted by *G. b. breviceps* may represent a cryptic species. *Geomydoecus subgeomydis* has a rare allele at the IDH locus that is not found in *Geomydoecus ewingi*. *Geomydoecus oklahomensis* has an autapomorphic allele at the ME locus and a synapomorphic allele at the PEP-C locus that links this species with *Geomydoecus heaneyi* from locality 9 (Fig. 1a).

Comparison of distance matrices.—Statistical comparison of the pocket gopher and chewing louse distance matrices by Mantel's test (Mantel, 1967) yielded a t-value of 3.5, which indicates that the probability of random association between these two independent matrices is remote ($P < 0.005$). This is direct statistical evidence for widespread cospeciation in this assemblage (Hafner and Nadler, 1990). When the matrices are compared graphically (Fig. 2), the array of points suggests a line with a negative y-intercept. A negative y-intercept is expected to occur in cases of "delayed cospeciation" (Hafner and Nadler, 1990:194), wherein speciation events in the parasites occur subsequent to speciation events in their hosts.

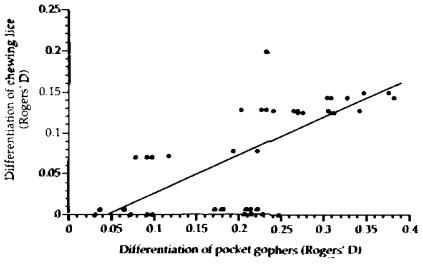

FIG. 2.—Genetic distances for hosts and their corresponding parasites. No statistical significance can be assigned to the least-squares line because of the lack of independence among the data points (Hafner and Nadler, 1990).

Tree estimation.—The PAUP analysis generated two minimum-length trees for the pocket gophers, each with 83 steps and a consistency index (*CI*) of 0.697 (excluding uninformative characters). There were 22 trees with one additional step, and 51 trees with two additional steps. The PAUP tree that was topologically identical to the UPGMA tree (Fig. 3a) had a length of 85 steps and a *CI* of 0.657. When input as user trees in a FREQPARS analysis, the two shortest PAUP trees had lengths of 71.50 steps, whereas the UPGMA tree (Fig. 3a) contained 71.22 steps. Thus, the UPGMA tree is at least as parsimonious as either of the two shortest PAUP trees when analyzed by FREQPARS. The single shortest tree generated by FREQPARS (using its own tree-building algorithm) contained 71.72 steps. Hence, the combined use of PAUP and FREQPARS (Page, 1990) yields shorter trees than does FREQPARS alone, and is less time consuming than the manual-rearrangement method suggested by Swofford and Berlocher (1987).

The topology of the UPGMA tree for pocket gophers (Fig. 3a) agrees with that of the parsimony tree described by Block and Zimmerman (1991), which was based on larger samples. Phenetically, *G. breviceps* is most similar to *G. attwateri*, with an average Rogers' (1972) genetic distance of 0.206 between the two taxa. The *bursarius* cluster is an average distance of 0.290 from the other surveyed populations of *Geomys*. The three major clusters in the UPGMA tree correspond to species groups identified in previous systematic studies. For example, each of the three chromosomal and morphological races identified by Honeycutt and Schmidly (1979), and subsequently elevated to species status by Bohlin and Zimmerman (1982) and Tucker and Schmidly (1981), appear to be monophyletic. Also consistent with previous studies, the *attwateri* and *breviceps* groups appear to be sister lineages (Block and Zimmerman, 1991; Honeycutt and Schmidly, 1979).

PAUP analysis of the chewing louse data yielded four trees with a minimum length of 20 steps and a *CI* of 0.750 (excluding uninformative characters). One of these trees was topologically identical to the tree generated in the UPGMA analysis (Fig. 3b). The PAUP analysis generated 21 trees with one additional step, and 63 trees with two additional steps. When the four shortest PAUP trees were input as user trees in a FREQPARS analysis, two were found to

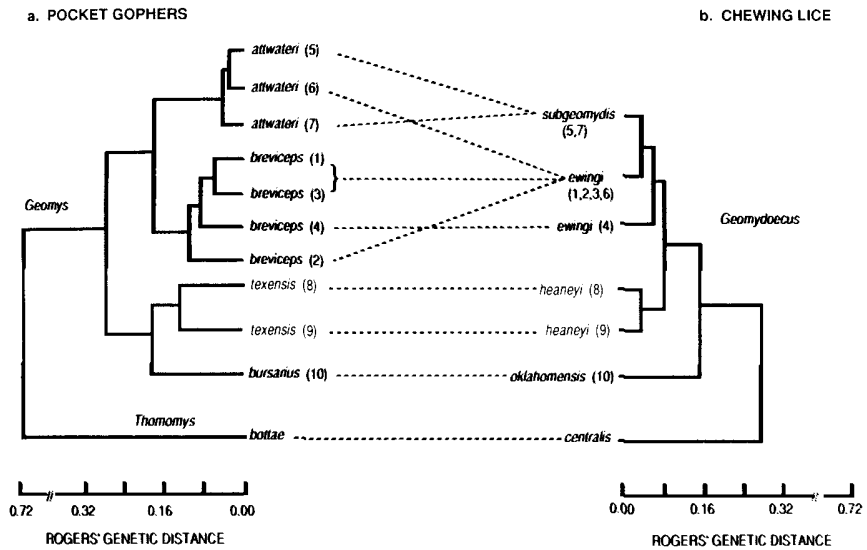

FIG. 3.—Comparison of UPGMA trees for pocket gophers (a) and their chewing lice (b). Numbers following taxon names refer to the map (Fig. 1), and dotted lines indicate host-parasite associations. The cophenetic correlation coefficient is 0.986 for the pocket gopher tree and 0.978 for the chewing louse tree.

contain 18.6 steps and two contained 19.0 steps. The PAUP tree that was topologically identical to the UPGMA tree (Fig. 3b) was one of the two shorter trees (18.6 steps). The single shortest tree generated by FREQPARS (using its own tree-building algorithm) contained 19.0 steps.

The UPGMA tree for the chewing lice (Fig. 3b) is consistent with the morphology-based phenogram presented by Timm and Price (1980), with the exception of the placement of the *Geomydoecus ewingi* population from locality 4. Whereas most populations of *Geomydoecus ewingi* (localities 1, 2, 3, and 6) are genetically similar to *Geomydoecus subgeomydis*, the *ewingi* population from locality 4 lies outside this group (Fig. 3b). Timm and Price (1980) also found *Geomydoecus ewingi* to be most similar to *Geomydoecus subgeomydis*, and they determined that *heaneyi* is more similar morphologically to lice in the *ewingi-subgeomydis* group than *heaneyi* is to *Geomydoecus oklahomensis* (Fig. 3b). Recognition of the *ewingi* population of lice from locality 4 as a distinct species (which is supported by protein data [this study] and suggested by morphologic evidence [Timm and Price, 1980]) would remove the apparent paraphyly of *Geomydoecus ewingi* evident in Fig. 3b.

Tree comparison.—The host and parasite trees (Fig. 3) are similar, but not identical. In one case, *Geomydoecus ewingi* (locality 6) appears to have switched from its original host (*G. breviceps*) to a new host (*G. attwateri*). Alternatively, presence of *Geomydoecus ewingi* may be a shared-primitive feature of *G. breviceps* and population 6 of *G. attwateri*. One of Manter's (1955) rules of parasitism states that if the same or two closely related species of host exhibit a disjunct distribution and possess similar parasite faunas, the areas in which the hosts occur must have been contiguous at some time in the past. Using this reasoning, we postulate that the common ancestor of *G. attwateri* and *G. breviceps* once was widely distributed throughout the study area, hosting only one species of louse. When the *G. attwateri* and *G. breviceps* lineages split, *Geomydoecus ewingi* persisted on most populations of *G. breviceps* and on certain populations of *G. attwateri* in southcentral Texas (Fig. 1b). The louse *subgeomydis* evolved subsequent to the divergence of *G. breviceps* from *G. attwateri*, and is now locally extinct in population 6 of *attwateri* (or was unsampled in this and previous studies of *Geomys* lice). The *ewingi* population from locality 4 is most likely specifically distinct from other *ewingi* populations (based on protein and morphologic evidence) and would appear to represent a relict lineage of lice unique to the population of *G. breviceps* isolated in northeastern Louisiana.

The high degree of topological similarity between the pocket gopher and chewing louse trees (Fig. 3), together with the nonrandom association of the two genetic-distance matrices, documents a history of widespread cospeciation in this host-parasite assemblage. Regions of discordance in the trees can be explained by host-switching by the parasites, retention of ancestral parasite taxa on recently evolved host taxa, or poorly delineated taxonomic boundaries. A similar study restricted to host species of the genus *Thomomys* found little evidence of cospeciation (S. A. Nadler, pers. comm.). However, in another study focused at higher taxonomic levels, Hafner and Nadler (1988) reported considerable concordance between phylogenies of pocket gophers and chewing lice. Together, these findings suggest that studies of cospeciation focused at lower taxonomic levels (generally below the level of the species) are likely to encounter problems associated with reticulate evolution of host taxa (hence, mixing of parasite lineages) and retention of ancestral ("plesiomorphic") parasite taxa on recently evolved host lineages. In contrast, studies focused at higher taxonomic levels (generally above the species level) are more likely to find evidence of cospeciation because host lineages have been isolated genetically (often, geographically) for long periods of time and, given time, chance extinction of parasite lineages will lead inevitably to reciprocal monophyly of parasite lineages on sister taxa of hosts (analogous to "lineage sorting" of mitochondrial DNA haplotypes—Avise et al., 1984).

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