

COPHYLOGENY BETWEEN POCKET GOPHERS AND CHEWING LICE

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Since first reported by Timm (1979, 1983), evidence of cophylogeny between pocket gophers (rodents of the family Geomyidae; Box 1) and chewing lice (insects of the order Phthiraptera; Box 2) has become so conclusive that the gopher-lice system is now perhaps the preeminent "text-book example" of cophylogeny (e.g., Noble et al., 1989; Esch and Fernández, 1993; Ridley, 1993; Brown and Lomolino, 1998; Page and Holmes, 1998). This pattern of cophylogeny between gophers and lice is now known to extend to the very deepest branches in the gopher tree (Hafner et al., 1994), suggesting that this host-parasite association has remained intact for several million years (based on known fossil dates for the gopher phylogeny; Russell, 1968). No other symbiotic association studied to date has shown such pervasive (in both space and time) and persuasive evidence of cophylogeny, which leads one to ask, "Why pocket gophers and chewing lice?"

Herein, we argue that pocket gophers and chewing lice represent an unusual—but probably not unique—symbiosis between creatures whose life histories are highly conducive to parallel speciation. We will review these life history attributes of gophers and lice, followed by a general discussion of major findings that have emerged from study of this unusual system. Finally, we will highlight several potential directions for future research on the gopher-lice assemblage, emphasizing how knowledge of this system has the potential to transcend gophers and lice to elucidate our general understanding of speciation, coevolution, rates of evolution, and host-parasite ecology.

Fossorial Mammals: A Potential Wellspring of Coevolution

Of the thousands of species of mammals that find shelter in subterranean burrow systems, only a few species spend most of their lives beneath the ground, where they tunnel through the soil in search of food. This highly specialized subterranean lifestyle is termed "fossorial" (*fossor* L. "digger"), and fossorial species share numerous adaptations for

subterranean life, including a fusiform body shape, enlarged incisors and claws for digging, and valvular ears and nostrils that can be closed to prevent the entry of soil. Fossoriality has evolved independently in multiple lineages of mammals, including marsupial moles of the family Notoryctidae (1 species), moles and golden moles of the insectivoran families Talpidae (42 species) and Chrysochloridae (19 species), and rodents (many species in several families). By far, the greatest diversity of fossorial mammals is seen in the Rodentia, which includes the African mole-rats of the family Bathyergidae (14 species), the South American tuco-tucos and octodonts of the families Ctenomyidae (48 species) and Octodontidae (1 fossorial species), the fossorial voles, blind mole-rats, and bamboo rats of the family Muridae (27 fossorial species), and pocket gophers of the New World family Geomyidae (40 species; data from Hall, 1981, and Nowak, 1999).

These fossorial mammals share more than superficial morphological similarities. For a number of reasons, the fossorial mode of existence usually involves a solitary lifestyle, with individuals often living in single-occupant burrow systems within small, isolated populations (Pearson, 1959; Patton, 1972; Nevo, 1979). This patchy distribution of populations usually reflects the patchy distribution of friable and flood-free soils, compounded by the often dispersed nature of suitable food resources. Within these isolated populations, individual subterranean mammals often live alone in burrow systems that are defended vigorously against intruders, including conspecifics. Presumably, the enormous energy invested in the excavation of a complex system of tunnels argues against sharing of burrows in most subterranean mammals. Notable exceptions include the highly social naked mole-rats (*Heterocephalus glaber*) of Africa (Jarvis and Bennett, 1991) and the colonial tuco-tuco (*Ctenomys sociabilis*) of South America (Lacey et al., 1997).

In the act of foraging through the soil, subterranean mammals create a cave environment that is ecologically very different from the typical surface environment of most mammals. Through evolutionary time, many creatures have invaded this cave environment (Fig. 1), and some of these cave occupants have evolved specialized adaptations unique to the unusual biotic and abiotic regime in which they live (Kim, 1985a, 1985b). Often, cave-specific adaptations, such as reduction of eyes and limbs, render the organism poorly adapted for life on the surface, meaning that subterranean mammals and many of the organisms that coexist with them may be locked into a long-term ecological association. If so, the likelihood of eventual biological interaction between these obligate cave dwellers is high—and biological interaction is, of course, the necessary precursor to coevolution (herein defined as reciprocal adaptation; Janzen, 1980). Clearly, the distribution of a species of subterranean mammal will influence (if not determine) the distribution of organisms that live in its burrow, which means that the latter creatures often will show the same patchy distribution characteristic of so many species of subterranean mammals.

In most species of fossorial mammals, the above factors work in concert to isolate individual mammals and their burrow cohabitants from conspecific individuals, from other subterranean organisms, and from surface-dwelling creatures, in general. Geographic isolation and small population sizes characteristic of subterranean organisms are powerful catalysts for evolutionary change and provide ample opportunity for the evolution of long-term symbioses between fossorial mammals and the many organisms that coexist with them. A recent review of subterranean rodents and their burrow associates (Hafner et al., in press) identified more than 200 associations that are likely to show some evidence of coevolution. Of these, only two host-parasite systems (ctenomyid rodents and their nematode parasites

[Gardner, 1991] and geomyid rodents and their chewing lice [Hafner et al., 1994]) have been investigated in any detail.

The Case for Cophylogeny between Fossorial Mammals and their Parasites

Perhaps the most conclusive evidence for coevolution comes from the study of host-parasite relationships (Stone and Hawksworth, 1986). In most cases, the parasite's dependence on the host for some or all of its required resources, and the resultant energetic drain on the host, combine to generate an evolutionary "arms race" as the host attempts to defend its energy resources and the parasite responds by countering the host's defenses. Although there are many well-studied host-parasite assemblages, few studies have examined the association from an historical perspective, and fewer yet are unequivocal examples of strict coevolution (defined here as reciprocal adaptation in the hosts and parasites; Janzen, 1980; Hafner et al., in press). Most studies document an adaptive response on the part of the parasite but fail to show a reciprocal response on the part of the host (Jermy, 1984). Those that show apparent evolutionary responses in both the host and parasite tend to lack evidence of a long-term relationship between the two, which leaves open the possibility of a recent association between the symbionts (termed "pseudo-coevolution"; Hafner et al., in press).

Endoparasites of fossorial mammals would seem to be ideal candidates for coevolutionary studies because of their unusually intimate symbiosis with their hosts. Although endoparasites have been reported from several groups of fossorial mammals (see references in Hafner et al., in press), only a few of these studies have explored the relationship from a coevolutionary perspective (e.g., Gardner, 1991). Our experience with pocket gophers suggests that they harbor many fewer metazoan parasites (especially helminth parasites) than do typical surface-dwelling rodents. Although more study is

needed, it is possible that the solitary existence of individuals of many species of fossorial mammals makes them unlikely candidates for acquisition and spread of endoparasites.

Ectoparasitic arthropods provide outstanding opportunities for study of coevolution in fossorial mammals because many ectoparasitic arthropods are restricted to a single host taxon, are geographically widespread, and show high prevalence and abundance on their hosts. For example, chewing lice (Phthiraptera) and sucking lice (Anoplura) have limited dispersal abilities and cannot survive for long periods of time off their host (Kellogg, 1913; Marshall, 1981). As a result, lice generally rely on host-to-host contact for dispersal, unlike other, more vagile, arthropods (Timm, 1983). Because host-to-host contact among fossorial mammals is almost exclusively intraspecific, there are few opportunities for lice to colonize new host species; hence we see a high degree of host specificity among lice (Hopkins, 1957; Marshall, 1981). High host specificity, in turn, makes lice ideal candidates for study of host-parasite coevolution. Although current taxonomy suggests that chewing lice are generally species-specific and sucking lice are only genus-specific, this difference may be more an artifact of taxonomy, rather than biological reality (Hopkins, 1957).

Host-parasite systems are intrinsically interesting to evolutionary biologists because they signal a long and intimate association between two or more groups of organisms that are distantly related and quite dissimilar biologically. This long history of association may lead to reciprocal adaptations in the hosts and their parasites (strict coevolution) as well as contemporaneous cladogenic events in the two lineages (variously termed “parallel cladogenesis,” “cospeciation,” or “cophylogeny”). The phenomenon of cophylogeny is of particular interest to comparative phylogeneticists because coincident branching points in the host and parasite trees represent temporal links that facilitate comparative studies of rates of evolution in the two groups. Evidence of cophylogeny also can be used to test hypotheses of

coadaptation in the hosts and parasites (see *Studies of Coadaptation*). Given the unusual natural history of many species of fossorial mammals—including their asocial behavior, patchy geographic distributions, and relative isolation from parasites of terrestrial animals—future studies of cophylogeny involving fossorial mammals and their parasites should prove unusually interesting and rewarding.

Study of Cophylogeny in Pocket Gophers and Chewing lice

Historical Perspective.—Recent advances in our knowledge of pocket gopher and chewing louse cophylogeny would not have been possible without the pioneering taxonomic studies of chewing lice by K. C. Emerson, R. A. Hellenthal, R. D. Price, and R. M. Timm (e.g., see Emerson and Price, 1981, and included references). In particular, Price and Hellenthal undertook an exhaustive survey of geographic variation in the two genera of chewing lice that parasitize pocket gophers (*Geomydoecus* and *Thomomydoecus*), which required examination of countless ectoparasites from many thousands of study skins contained in museum collections in the U.S. These critical studies identified major lineages within *Geomydoecus* and *Thomomydoecus* (e.g., Price and Hellenthal, 1981; Hellenthal and Price, 1984), and revealed the now well-established pattern of host-specificity among these lice and their hosts. In 1983, R. M. Timm, a former student of R. D. Price, was the first to propose an explicit hypothesis of cophylogeny between pocket gophers and chewing lice (Timm, 1983).

Studies of Gopher-Louse Cophylogeny based on Allozymes.—R. D. Price visited Hafner's laboratory in 1984 to brush ectoparasites from study skins of pocket gophers that Hafner and his colleagues had collected in Central America. Discussions between Price and Hafner concerning relationships among louse species stimulated Hafner (who was then using allozymes to investigate pocket gopher relationships) to attempt starch-gel electrophoresis of individual chewing lice to obtain independent, molecular-based phylogenies for the lice,

which he could then compare to the gopher phylogenies. Over the next few years, techniques for protein electrophoresis of chewing lice were developed in Hafner's lab by postdoctoral associate, S. A. Nadler. During this same time, C. H. C. Lyal (1985, 1986, 1987) published important empirical analyses and theoretical discussions of cophylogeny between chewing lice and their mammalian hosts based primarily on cladistic analyses of morphological data. Also during this time, the landmark book *Coevolution and Systematics* (Stone and Hawksworth, 1986) was published. In their review of the Stone and Hawksworth book, Futuyma and Kim (1987:441) offered this less-than-optimistic summary of the state of knowledge of cophylogeny:

"...the message nonetheless emerges that the phylogenies of hosts and parasites show little congruence at any taxonomic level. Cospeciation is far from universal, and host lineages seem often to have lost their parasites."

In 1988, the allozyme studies in Hafner's lab culminated in publication of the first molecular-based gopher and louse phylogenies (Hafner and Nadler, 1988). This study documented significant congruence between independently derived gopher and louse phylogenies (Fig. 2), thereby supporting Timm's (1983) hypothesis of cophylogeny in this host-parasite assemblage.

By late 1988, empirical studies of gopher and louse relationships were far ahead of available methods for comparative analysis of host and parasite trees. Although statistical methods for comparing trees were available (e.g., Nelson and Platnick, 1981; Simberloff, 1987), most were developed for use in biogeographical studies, and each had serious limitations for analysis of cophylogeny. Recognizing this need, R. D. M. Page (then a graduate student in New Zealand) contacted Hafner in 1989 to obtain the allozyme data sets for gophers and lice, which he used to develop his nascent program for comparative analysis

of trees (the forerunner of his program, *COMPONENT*; Page, 1993a). Thereafter, a synergistic relationship developed between the Hafner and Page laboratories because of Hafner's need for tools to analyze his gopher and louse phylogenies and Page's need for empirical data to develop his analytical tools for investigation of cophylogeny.

Publication of the allozyme-based phylogenies for gophers and lice (Hafner and Nadler, 1988) stimulated a series of publications on methods and theory of cophylogeny analysis (e.g., Hafner and Nadler, 1990; Nadler et al., 1990, Page, 1990, 1993a, 1993b, 1993c, 1994; Demastes and Hafner, 1993). These contributions emphasized the need for increased rigor in phylogenetic studies, including the need for independent host and parasite phylogenies, improved statistical tests of tree similarity, and widespread (if not exhaustive) sampling of parasite taxa. These topics are developed further in Chapter 1.

Studies of Cophylogeny based on DNA sequences.— By the mid-1990s, cophylogeny of pocket gophers and their chewing lice had been investigated based on morphology (e.g., Timm, 1983; Page et al., 1995) and allozymes (e.g., Hafner and Nadler, 1988; Demastes and Hafner, 1993; Highland, 1996). Each of these studies reinforced previous evidence of cophylogeny in this host-parasite assemblage. In the first DNA-based study of the gopher-louse system, Hafner et al. (1994) obtained nucleotide sequences from a 379-bp (base pair) region of the cytochrome *c* oxidase subunit I (COI) gene from the mitochondria of 15 taxa of pocket gophers and 17 taxa of lice that parasitize these gophers. Hafner et al. (1994) used four tree-building methods to reconstruct gopher and louse relationships and showed that major portions of the phylogenies (Fig. 3) were recovered consistently regardless of the method of analysis.

Given robust and well-resolved phylogenies for gophers and lice, Hafner et al. (1994) employed a simple test to determine whether the structure of the parasite tree was

independent of that of its host. If so, one would expect the amount of cophylogeny observed between the hosts and parasites (i.e., the number of cospeciation events in the two phylogenies) to be no greater than that expected between the host tree and random parasite trees (Page, 1994). Applying this test to the phylogenies in Fig. 3 (using *COMPONENT*; Page, 1993a), Hafner et al. (1994) rejected the hypothesis that the louse phylogeny was independent of the gopher phylogeny ($p = 0.004$, computed using 1,000 random trees). Thus, the DNA sequence data corroborated earlier (morphological and allozyme) evidence for cophylogeny in the gopher-louse assemblage. An intensive DNA-based investigation of cophylogeny involving the gopher genera *Cratogeomys* and *Pappogeomys* and their lice is currently underway and nearing completion (Demastes, et al., in prep.). This study will be the first exhaustive (or nearly so) survey of multiple lineages of chewing lice collected from a geographically widespread host taxon.

Studies of Evolutionary rates.—Perhaps the most exciting aspect of cospeciation analysis has been its recent application to comparative studies of evolutionary rates (e.g., Hafner et al., 1994; Hafner and Page, 1995; Page, 1996; Page and Hafner, 1996). There are many ways to convert molecular data (including data from allozymes, restriction-fragment patterns, and protein and DNA sequences) into estimates of genetic divergence (Swofford and Olsen, 1990). Each method has inherent advantages and limitations, and each involves assumptions about the nature of evolutionary change at the molecular level. Most comparative studies of genetic differentiation in hosts and parasites have used either pairwise estimates of genetic distance (e.g., Hafner and Nadler, 1990; Page, 1990) or estimates of length of homologous branches in the host and parasite trees (e.g., Hafner et al., 1994; Page, 1996).

Hafner and Nadler (1990) proposed a theoretical framework for comparing host and parasite genetic divergence, whether measured as genetic distance or relative length of

branches on a phylogenetic tree. The regression of parasite divergence against host divergence (Fig. 4) allows us to describe simultaneously two aspects of host-parasite divergence. The slope of the line (Fig. 4a) is an estimate of the relative rate of genetic change in the two groups. The y-intercept of the line (Fig. 4b) measures genetic divergence in the parasites at the time of host speciation. For example, an intercept of zero indicates synchronous cospeciation, wherein hosts and parasites diverge simultaneously. A negative intercept suggests delayed cospeciation, in which case the parasites tend to diverge consistently after their hosts. Finally, a positive intercept signals preemptive cospeciation, in which case the parasites diverge prior to their hosts.

Although it is widely acknowledged that estimates of DNA sequence divergence should be adjusted for the effects of saturation (repeated nucleotide substitutions at a single site), there is no general consensus as to how this should be done. For example, Hafner et al. (1994) attempted to correct for transition bias in the gopher and louse COI data by using the largest observed pairwise transition bias in a maximum-likelihood phylogeny reconstruction. They reasoned that this value, which is usually measured between the most recently diverged taxa, is least likely to be affected by saturation and, therefore, is the most reasonable estimate of the actual transition bias for this gene region. In contrast, Page (1996) recommended use of the transition bias estimate that maximizes the likelihood of the phylogeny. Use of these different correction factors can have profound influence on estimates of branch length. For example, Hafner et al.'s analysis suggested that lice are evolving 10 to 11 times more rapidly than pocket gophers at selectively neutral sites. In contrast, Page's reanalysis of Hafner et al.'s data suggested that lice are evolving only two to three times as fast as gophers. Research into the effects of transitional saturation (and evolutionary models, in general) is now moving

at a rapid pace, and we expect that some degree of consensus will be reached in the near future.

Studies of Gopher-Louse Cophylogeny at Lower Taxonomic Levels.—The large-scale pattern of cophylogeny observed between genera of pocket gophers and their chewing lice (e.g., Hafner and Nadler, 1988; Hafner et al., 1994) must ultimately emanate from biological interactions at lower taxonomic levels and on smaller geographic scales. With this view in mind, Demastes and Hafner (1993) and Spradling (1997) investigated gopher-lice cophylogeny within a single genus of pocket gophers (*Geomys* and *Thomomys*, respectively) in the southwest U.S. Although the predicted pattern of cophylogeny was evident in both studies, there were numerous inconsistencies between the host and parasite trees that were variously attributed to host-switching by the parasites, retention of ancestral parasite taxa, and poorly delineated taxonomic boundaries in the hosts and parasites. Demastes and Hafner (1993) and Spradling (1997) concluded that studies of cophylogeny at lower taxonomic levels are likely to be confounded by population-level phenomena, including reticulate evolution of host taxa (i.e., merging of taxa previously thought to be distinct) and retention of ancestral parasite taxa on recently evolved host lineages. This topic is explored in greater detail in Chapter XY.

Studies of Gopher-Louse Cophylogeny on Small Geographic Scales.— Studies of cophylogeny that are restricted both taxonomically (e.g., to a single species of host) and geographically (to a small portion of the host's distribution) offer the greatest potential for elucidating fundamental host-parasite interactions that ultimately generate the pattern of cophylogeny. For example, Nadler et al. (1990) compared population structure in several populations of *Thomomys bottae* and their lice to determine if structuring of parasite populations on individual hosts (which likely is influenced by founder events as new hosts are colonized)

tends to accelerate parasite evolution relative to that of their hosts. Indeed, Nadler and his colleagues found significant levels of genetic differentiation among louse populations collected from hosts living only meters apart, reinforcing previous evidence that louse transfer among host individuals is severely restricted (Nadler and Hafner, 1989). Nadler et al. (1990) also showed that among-population differentiation in lice (i.e., lice from hosts collected at different geographic localities) was similar to that measured among the host populations themselves, suggesting a close association between gene flow in pocket gophers and gene flow in their lice.

Working at an even smaller geographic scale, Demastes (1996) examined gopher and louse genetics in a single alfalfa field in central New Mexico. Operating under the then widespread assumption that cophylogeny is the inevitable result of chewing lice being passed from mother to offspring within lineages of related hosts (see *Studies of Parasite Transmission*), Demastes used nuclear DNA fingerprint data to generate host pedigrees (“family trees”) in order to trace louse transmission patterns. Surprisingly, this microspatial genetic analysis revealed little or no relationship between genetic relatedness among gophers and the composition of their louse populations. Instead, Demastes showed that the genetic composition of louse populations on individual pocket gophers shows significant spatial autocorrelation at this locality, meaning that louse transmission depends more on spatial proximity of the hosts (i.e., the louse composition on nearest neighbors) than on host mating regimes. These nearest-neighbor effects have caused louse populations to be distributed in patches of related groups, generating a fractal-like distribution with self-similarity at multiple scales. Demastes (1996) concluded that simple models from complexity theory, including nearest-neighbor effects and basins of attraction might suffice to explain the overall distribution of chewing lice at this locality.

Studies of Contact Zones.— Studies of the distribution of chewing lice at zones of hybridization between gopher taxa have yielded important information about the history of the zone (e.g., Patton et al., 1984; Nadler et al., 1990; Hafner et al., 1998). If genetic introgression is present in both the hosts and parasites (as in the study by Nadler et al., 1990), then rate and pattern of introgression can be compared to reveal common demographic patterns. In other cases, parasites can be treated as "genes" of their hosts to serve as an independent measure of extent of host introgression (e.g., Bohlin and Zimmerman, 1982; Patton et al., 1984). Along these lines, Hafner et al. (1998) studied movement of a contact zone between two species of chewing lice in the Rio Grande Valley of New Mexico and showed that the midpoint of the contact zone had moved approximately 1 km during a five-year period (Fig. 5). This rate of zone movement, coupled with knowledge of the genetics of the hosts, had important implications, not only for rate of louse dispersal, but also for estimating the age of the contact zone—these new data suggested that the zone was only about 50 years old, rather than >10,000 years old, as previously hypothesized (Smith et al., 1983).

Studies of Parasite Transmission.—As mentioned earlier, researchers have long believed that chewing lice are transmitted primarily—if not exclusively—from a mother host to her offspring (e.g., Newson and Holmes, 1968; Rust, 1974), thereby generating the lineage-specific transmission pattern that, when viewed at large scales, is termed cophylogeny. A study by Demastes et al. (1998) tested this “maternal transmission hypothesis” using an indirect approach that compared the distribution of louse populations to the distribution of mitochondrial DNA (mtDNA) haplotypes in the pocket gophers (mtDNA haplotypes are known to be inherited maternally). Their study showed no significant relationship between louse distributions and mtDNA haplotypes for the gophers, thus falsifying the hypothesis

that chewing lice are transmitted exclusively from mother to offspring. These results were consistent with previous nuclear DNA fingerprint studies (Demastes, 1996) in showing little or no relationship between genetic relatedness among gophers and the composition of their louse fauna.

Given that there appear to be no intrinsic barriers to louse transmission within a population of pocket gophers, Reed and Hafner (1997) investigated whether or not such barriers may exist between host populations of varying degrees of relatedness. Laboratory transfer experiments were designed to test whether lice could establish successful colonies when transferred between two subspecies of the same host species, between two species of the same host genus, and between two genera of pocket gopher hosts. Although lice established successful colonies at each level, rate of colonization of new hosts (i.e., percentage of transfers that were successful) diminished with increasing phylogenetic distance from the natural host of each louse. Reed and Hafner (1997) concluded that the pattern of cophylogeny may result primarily from lack of opportunity for lice to colonize new hosts. However, in rare cases where lice disperse to new hosts, survival may be difficult on hosts that are not closely related to the natural host, which would reinforce the pattern of cophylogeny. Reed et al. (in press a) implicate hair diameter as an important factor that may determine suitability of new hosts for dispersing lice.

Studies of Coadaptation.—Component analysis (Page, 1993a) identifies pairs of equivalent nodes in host and parasite trees that reflect the same historical event. Hypotheses of coadaptation in the hosts and parasites can be tested using these nodes. For example, Harvey and Keymer (1991) used simplified phylogenies of gophers and lice taken from Hafner and Nadler (1988) to show that evolution of body size in lice and their hosts is highly correlated. Similarly, Morand et al. (in press) and Reed et al. (in press a) used independent

contrasts (which require knowledge of gopher and louse phylogenies) to investigate gopher and louse body size relationships and to analyze the relationship between louse body size and hair diameter of the host. Reed et al. (in press a) documented a significant, positive relationship between hair diameter in pocket gophers and rostral groove dimensions of their chewing lice (lice use the rostral groove to grasp the hair of their host; Fig. 6). Coupled with previous evidence of a strong allometric relationship between louse body size and rostral groove width (Morand et al., in press), this finding supports the contention that hair diameter of the host may be an important determinant of body size in chewing lice. Numerous other morphological, physiological, and ecological attributes of hosts and parasites can be compared using the cophylogeny framework.

Studies of Parasite Ecology.—In efforts to understand the fundamental biological basis of cophylogeny between pocket gophers and chewing lice, our research has moved progressively from the study of large-scale patterns (e.g., studies at the genus level in hosts and parasites) to microgeographic studies at the level of the host and parasite population. These latter studies have laid to rest the intuitively appealing—but, apparently, incorrect— notion that the pattern of cophylogeny emanates solely from mother-to-offspring transfer of chewing lice by pocket gophers (Demastes et al., 1998). Although maternal transmission of chewing lice is known to occur (Rust, 1974) and certainly contributes to the emergent pattern of cophylogeny (Timm, 1983), it alone cannot explain the pattern. Reed and Hafner (1997) have suggested that cophylogeny may result from a combination of factors, including patchy distribution of hosts, low dispersal abilities of the parasites, and ecological constraints on the part of the parasites that reduce their abilities to establish successful colonies on new host taxa. Reed et al. (in press a) showed that one of these constraints may relate to the louse's ecological requirement for host hairs of a certain diameter or range of diameters.

Another ecological factor that may constrain or prevent louse colonization of new host taxa is simple competition between the dispersing louse and the louse population already in residence on the new host. It is reasonably well documented that two congeneric species of lice (whether of the genus *Geomydoecus* or *Thomomydoecus*) do not—and probably cannot—coexist for any meaningful period of time on a single host individual (Timm, 1983; Demastes, 1996; Hafner et al., 1998). This suggests that any louse that manages to disperse to a new host taxon (an event that, itself, will be rare, given the patchy distribution of host taxa and the poor dispersal abilities of lice) will find it difficult to establish a successful colony on the new host in the face of competition from the more numerous resident lice. The exact nature of this louse competition is presently unknown, but ongoing and planned studies in the Hafner laboratory using high-resolution videomicroscopy should reveal whether or not species of lice engage in direct (interference) competition—such as fighting or destroying the eggs of the competitor—when experimentally introduced onto a single host individual.

Although congeneric species of chewing lice appear unable to coexist on a single host individual, several species of pocket gopher are known to host mixed louse populations consisting of one species of *Geomydoecus* and one species of *Thomomydoecus*. These lice coexist in what appears to be stable, long-term equilibrium on single individual hosts. Reed et al. (in press *b*) explored the nature of this coexistence and discovered that the chewing lice appear to partition available host resources spatially, with the *Geomydoecus* species living primarily on the lateral and dorsal regions of the host, and the *Thomomydoecus* species living primarily on the lateral and ventral regions (Fig. 7). This dorsoventral habitat partitioning does not appear to be explained by hair diameter, which means that the lice may be responding to some other factor that varies dorsoventrally, such as temperature or humidity gradients of the host's body (Reed et al., in press *b*).

Development of Evolutionary Models.—The remarkable level of cophylogeny documented for gophers and lice, and the size and scope of the gopher-lice DNA data set (Hafner et al., 1994; Hafner and Page, 1995) have made this system especially useful for development and testing of models in the areas of phylogenetics and molecular evolution. Studies using the gopher-lice data have focused on use of differential equations for modeling in biology (e.g., Taubes, in press), testing of similarity between evolutionary trees (e.g., Page, 1993a; Huelsenbeck et al., 1997), measurement of evolutionary rate differences in hosts and parasites (e.g., Hafner et al., 1994; Page, 1996), and development of likelihood-ratio tests to address a wide range of biological questions, including models of DNA substitution (Huelsenbeck and Rannala, 1997). There is every reason to believe that future DNA-based studies of the gopher-lice system will continue to contribute, both directly and indirectly, to development of evolutionary models in phylogenetics, molecular evolution, and related fields. Studies that involve exhaustive sampling of host and parasite taxa within a large and diverse assemblage (discussed below) offer special promise in this area.

Conclusions and Future Directions for Research

This overview of our knowledge of the gopher-lice system reveals three major gaps in our understanding of the evolution of this unusual symbiotic relationship. First, we do not yet know the root cause of host-specificity in this system, nor do we have a clear understanding of how louse species interact ecologically on an individual host. Second, all studies of the gopher-lice system published thus far have suffered from sparse taxonomic sampling, and we have yet to explore the potentially confounding effects of inadequate phylogenetic sampling on studies of cophylogeny. Finally, although we have produced clear and convincing evidence of cophylogeny between gophers and lice, we have yet to

investigate whether other participants in this system (e.g., other parasites of the gophers or parasites of the lice) also show cophylogeny with their symbionts.

Our ongoing and future studies of the gopher-louse system will explore these major gaps in our knowledge and will necessarily require studies on three very different evolutionary and geographic scales. The first of these will employ controlled laboratory and field transfer experiments and videomicroscopy techniques to further our understanding of the intimate ecological relationship between gophers and lice and between coexisting louse species. Our working hypothesis is that these ecological factors reinforce the overall pattern of cophylogeny, which is determined ultimately by the patchy distribution of the hosts and the low dispersal ability of the lice.

Our second line of inquiry will focus on completion of the first exhaustive taxonomic survey of a single lineage of gophers and their lice. For years, researchers have stressed the critical importance of thorough phylogenetic sampling in evolutionary studies (e.g., Moore et al., 1976; Fitch and Bruschi, 1987; Sanderson, 1990), and Page (1996) has documented the adverse effects of incomplete phylogenetic sampling on host-parasite studies. We are currently completing an exhaustive survey of pocket gophers of the sister taxa *Cratogeomys* and *Pappogeomys* and their chewing lice. This has involved several months of fieldwork in Mexico and the U.S. and will result in a complete systematic revision of the host genera. This data set promises to have multiple applications that transcend the basic question of cophylogeny between these particular hosts and parasites, including development of models for testing similarity between phylogenetic trees, detection of multiple parasite lineages, identification of host-switching events, and study of rates of molecular evolution.

Our third major research effort involves expansion of our ongoing studies of gopher and louse cophylogeny to include selected lineages of endosymbiotic bacteria hosted by the

chewing lice. We are currently collaborating with systematic microbiologists F. A. Rainey and N. L. Ward-Rainey to investigate phylogenetic patterns in this three-tiered system. To date, we have amplified, cloned and sequenced between 500 and 1500 base-pairs of the 16S rRNA ribosomal RNA gene for over 500 clones from 11 distinct bacterial lineages associated with the gopher-louse system.

Preliminary phylogenetic analysis of sequence data for the first of the 11 bacterial lineages (*Staphylococcus*) has revealed significant phylogenetic structure. Although the tree is still preliminary and many additional taxa have yet to be added, the basic structure suggests some level of cophylogeny between the bacteria and their hosts. However, the preliminary analysis also suggests the possibility of multiple lineages of *Staphylococcus*-like bacteria in chewing lice, which may reflect multiple, independent invasions. This possibility will be tested by examination of additional clones, and it is conceivable that cophylogeny may have occurred subsequent to each independent bacterial invasion. More sophisticated phylogenetic analyses using complex maximum-likelihood models may reveal relationships heretofore unresolved in our preliminary analyses.

Although, at present, there are few published studies of cophylogeny explored from a molecular perspective (e.g., Moran et al., 1993, 1995; Hafner et al. 1994; Page et al., 1998; see also Chapters X and Y) we anticipate rapid growth in this research area as molecular tools become more widely available and the advantages of this approach better known. We believe that fossorial mammals and their parasites, especially the gopher-louse assemblage, will continue to play a prominent role in cophylogeny research, largely because of the unusual life history characteristics of subterranean mammals, which are particularly conducive to parallel speciation. Unfortunately, many host-parasite systems will show little or no evidence of cophylogeny (e.g., Baverstock et al., 1985), which will preclude comparative

studies of higher-order phenomena, such as evolutionary rates. However, in those systems with appreciable cospeciation, the researcher will have the unparalleled opportunity to compare evolution in the same genes, and over the same period of time, in distantly related organisms. Within this framework, the potential is great for discovery of large-scale evolutionary patterns that apply to diverse groups of organisms.

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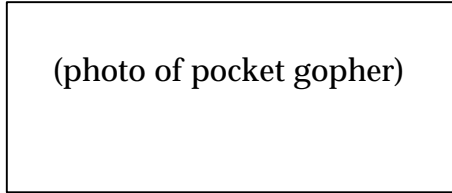
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Box 1



Pocket gophers (family Geomyidae) are herbivorous rodents that spend nearly their entire lives in subterranean tunnels which they dig while foraging through the earth for food. Most specialists recognize six genera and approximately 40 species of pocket gophers. The family Geomyidae (G. "earth mice") is exclusively New World, with a geographic distribution ranging from southwestern Canada to northwestern Colombia.

Box 2

(photo of chewing louse)

Chewing lice of the genera *Geomydoecus* and *Thomomydoecus* (family Trichodectidae) are wingless insects that are found exclusively on pocket gophers (see Box 1). The louse's entire life cycle takes place on its host, and lice cannot live for extended periods of time off their host. Unlike sucking lice, chewing lice do not pierce the skin of their host, but rather feed on sloughed skin and hair detritus. To date, more than 120 species of chewing lice have been described from pocket gophers.

Figure Legends

Figure 1.—A diagrammatic depiction of the burrow ecosystem of a pocket gopher and its many burrow associates. Arrows indicate trophic relationships (modified from Hubbell and Goff, 1940). Each of the organisms that coexists with a fossorial mammal is a promising candidate for study of coevolution and cophylogeny.

Figure 2.—Phenogram of pocket gopher and chewing louse relationships inferred by Hafner and Nadler (1988) from protein electrophoretic data. Data were clustered using UPGMA analysis (Sneath and Sokal, 1973) of Rogers' genetic distance values (Rogers, 1972). This was the first molecular-based study of gopher-louse cophylogeny, and the first to document a significant level of branching similarity between the gopher and louse trees. Rates of protein evolution in gophers and lice could not be compared using these data because different suites of proteins were examined in the two groups (Hafner and Nadler, 1988).

Figure 3.—Phylogenies of pocket gophers and their chewing lice based on nucleotide sequence data analyzed by Hafner et al. (1994). Shown are composite trees based on multiple methods of phylogenetic analysis. Branch lengths are proportional to inferred amounts of genetic change. Pocket gopher genera are *Orthogeomys*, *Zygogeomys*, *Pappogeomys*, *Cratogeomys*, *Geomys*, and *Thomomys*. *Geomys bursarius* is represented by two subspecies (a = *G. b. halli*; b = *G. b. majusculus*). Chewing louse genera are *Geomydoecus* and *Thomomydoecus*. The program COMPONENT (Page, 1993a) was used to document significant similarity in branching structure between these trees. Because the host and parasite trees were based on DNA sequences from the same gene (cytochrome *c* oxidase subunit I), rates of DNA evolution could be compared in the two groups. Based on these data, Hafner et al. (1994) estimated that chewing lice were evolving approximately 10-

times faster than pocket gophers in this gene region. Page (1996) reanalyzed these same data using a different estimate of transition bias and reported only a 2-fold rate difference between gophers and lice.

Figure 4.—Graphical method developed by Hafner and Nadler (1990) to investigate relative rates of evolution and timing of divergence events in cospeciating hosts and their parasites. Both panels represent bivariate plots of the relationship between genetic divergence in a hypothetical groups of hosts and their parasites. The slope of the relationship (panel A) indicates relative rates of evolution in the two groups. The trees (inset in panel A) are drawn with branch lengths proportional to amount of genetic change in the hosts (H) and parasites (P). The y-intercept (panel B) indicates the relative timing of divergence events in the two groups. A positive y-intercept is evidence of “preemptive cospeciation,” in which case the parasites are assumed to have diverged in advance of their hosts. A negative y-intercept signals “delayed cospeciation” (hosts diverge in advance of their parasites), and a y-intercept of zero is evidence of “synchronous cospeciation” in the two groups. The inset figures in panel B illustrate relative timing of divergence events in the hosts (outer portion of figure) and their parasites (thin line within each figure). Modified from Hafner & Nadler (1990; figure 2) and Hafner and Page (1995; figure 4).

Figure 5.—Transects (sampled in 1991 and 1996) through the zone of overlap between two species of lice that meet in the Rio Grande Valley of central New Mexico. For each 200-meter interval along the transect, Hafner et al. (1998) calculated the percentage of pocket gophers that hosted the “northern” (*Geomydoecus aurei*) versus “southern” (*G. centralis*) louse species (n = number of pocket gophers surveyed at each interval along the transect). The midpoint of each zone (calculated as one-half of the distance between the northernmost

occurrence of a southern louse and the southernmost occurrence of a northern louse) moved approximately 700 m southward between 1991 and 1996. This discovery had important implications for rate of louse dispersal (estimated from these data to be approximately 150 meters/year) and age of this contact zone (estimated to be approximately 50 years old). Hafner and his colleagues will return to the contact zone in 2001 to determine if zone movement continues in the predicted direction (southward) and at the predicted rate (150 meters/year).

Figure 6.—Linear regression of chewing louse groove width and pocket gopher hair diameter from Reed et al. (in press *a*). Chewing lice use the head groove to grasp the hair of their host (inset). This significant relationship suggests that hair diameter of the host is an important element of the louse's physical environment and may be an important determinant of whether or not a louse is able to colonize a new species of host.

Figure 7.—Reed et al. (in press *b*) studied the point-in-time distribution of two species of chewing lice that coexist on individual pocket gophers of the genus *Thomomys*. This is a diagrammatic view of the external surface of a pocket gopher (the skin is incised mid-ventrally then laid flat) showing the simultaneous distributions of *Geomydoecus aurei* and *Thomomydoecus minor*. Distributions were analyzed on three host individuals, and pooled results are presented here. Darkly shaded regions contained more lice than expected in all three pocket gopher specimens examined. Stippled regions contained more lice than expected in two of the three hosts examined. Unshaded regions contained fewer lice than expected on at least two of the hosts examined. These results suggest that the two species of lice tend to partition their habitat dorsoventrally.

Figure 1

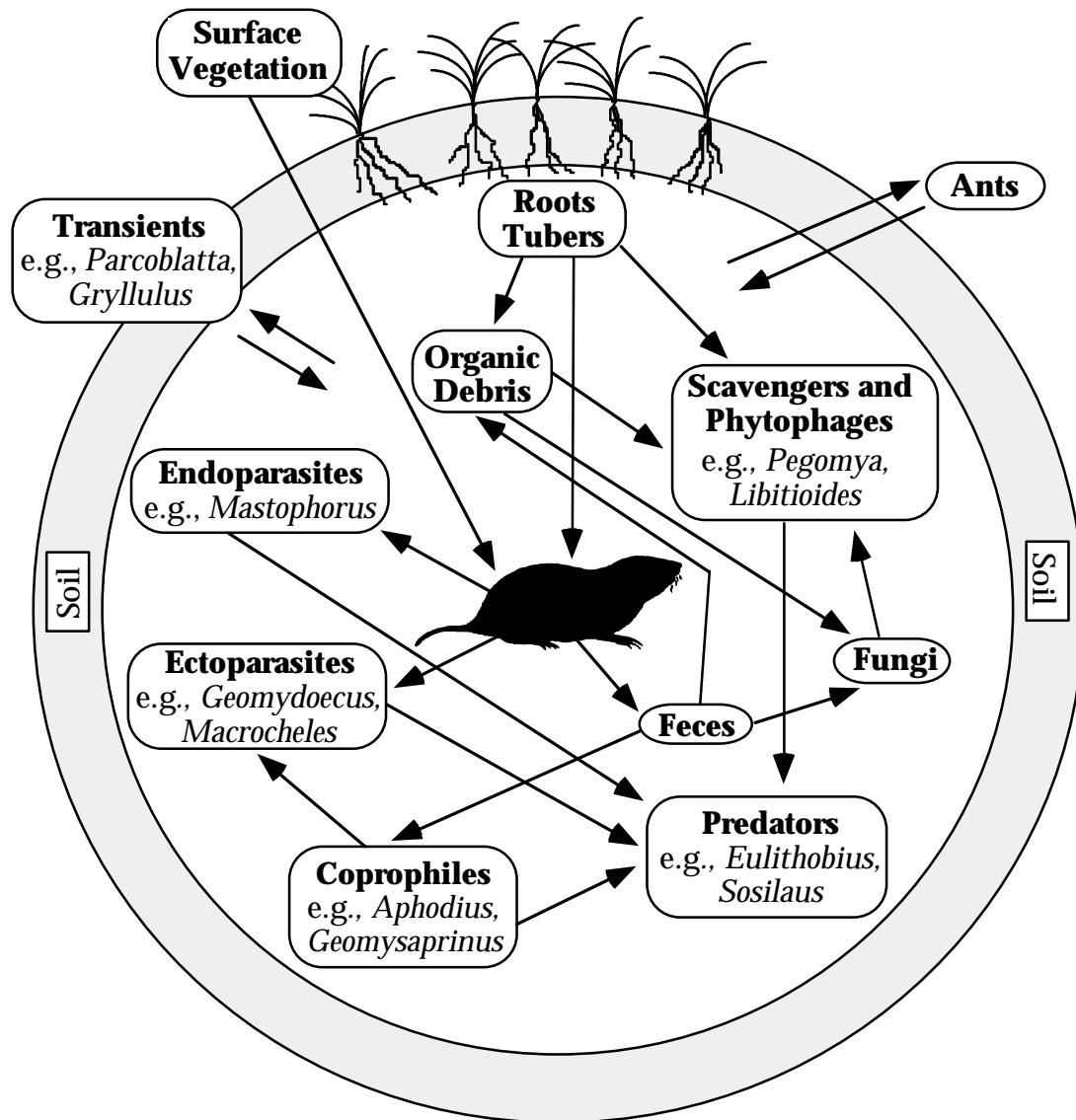


Figure 2

(modified NATURE figure)

Figure 3

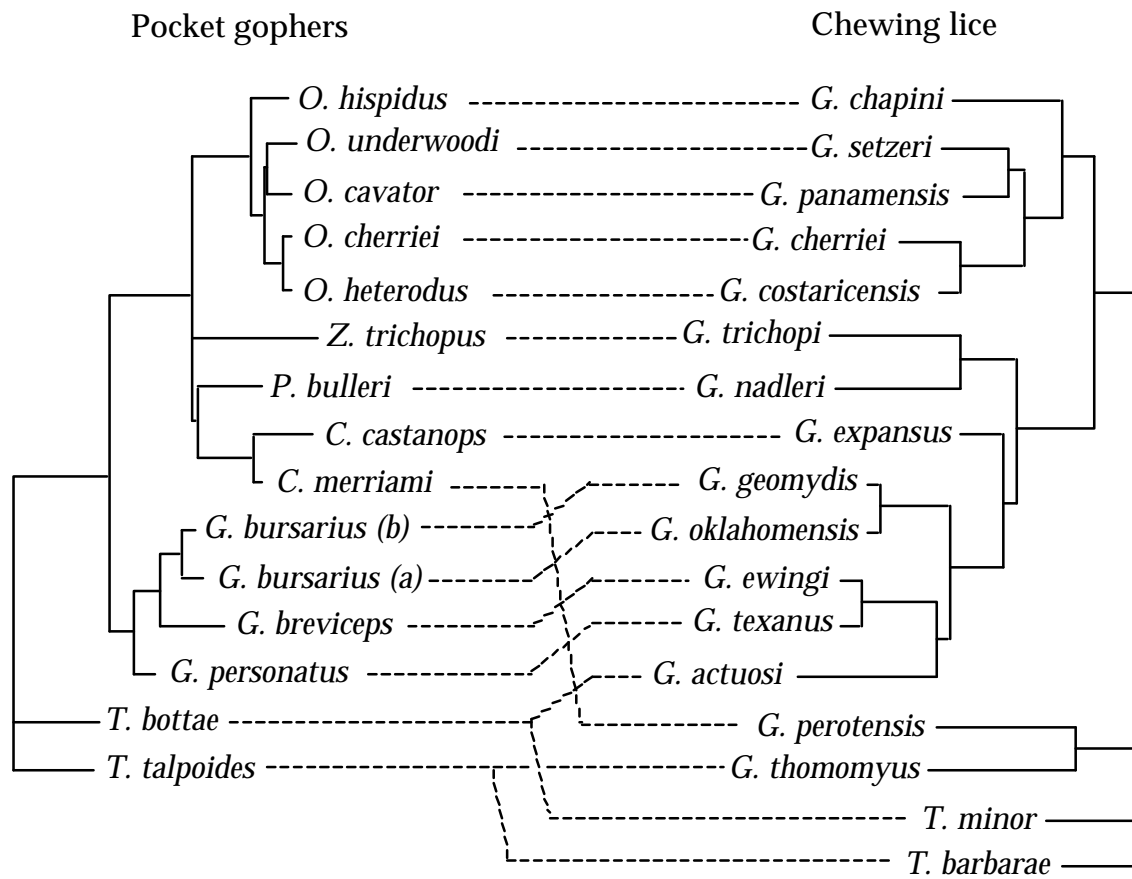


Figure 4

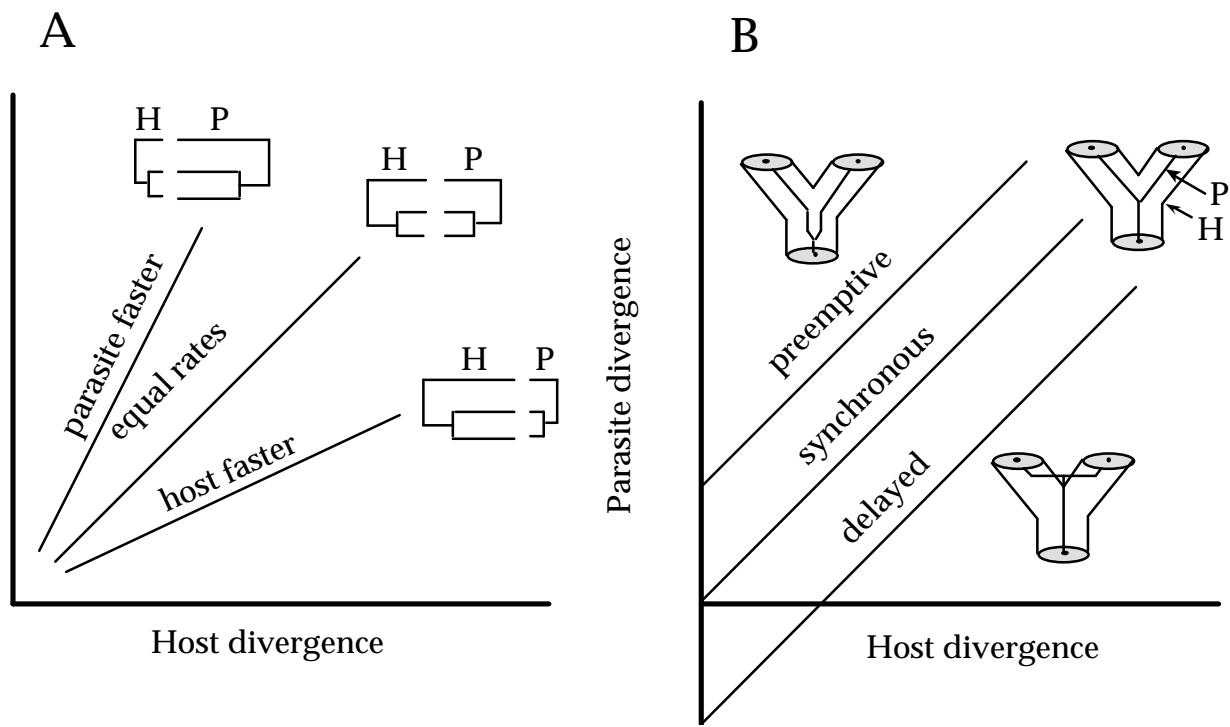


Figure 5

(figure from the zone-movement paper)

Figure 6

Use Fig. 3 from Reed et al (bivariate plot of gopher hair and rostral groove)

Figure 7

(fig. 2 from Reed et al. b—gopher “pelts”)