5-1998

Spatial Partitioning of Hosts (Thomomys bottae) by Parasitic Chewing Lice of the Genera Geomydoecus and Thomomydoecus

Melanie Ann Babin

Spatial Partitioning of Hosts (*Thomomys bottae*) by Parasitic Chewing Lice of the Genera *Geomydoecus* and *Thomomydoecus*

Honors Thesis
Louisiana State University
May, 1998

Melanie Babin

Abstract

Parasitic chewing lice of the genera *Geomydoecus* and *Thomomydoecus* are able to coexist on individual pocket gophers of the genus *Thomomys*. In this study, I investigate the spatial distribution of the two genera on their host and explore possible mechanisms of resource partitioning in chewing lice. Chewing lice appear to partition available host resources spatially, with *Geomydoecus* found primarily on anterior and dorsal regions of the host, and *Thomomydoecus* primarily on posterior and ventral regions of the gopher. Although spatial partitioning of the host habitat is evident, it does not appear to be influenced by hair diameter, which varies among body regions of the host. Instead, spatial partitioning of the host's body must be the result of some other factor, possibly temperature or humidity gradients of the host's body.

Introduction

Ectoparasitic chewing lice of the genera *Geomydoecus* and *Thomomydoecus* (Phthiraptera: Trichodectidae) live their entire lives exclusively on pocket gophers of the rodent family Geomyidae (Marshall, 1981; Hellenthal and Price, 1984). Because pocket gophers rarely interact with other species of gophers and because the lice are wingless, one species of louse often is confined to a single species of host (Nadler, 1990; Hafner, 1994). Because chewing lice depend on their host for food, shelter, warmth, and other resources, when a new species of gopher evolves, the lice must evolve as well (Nadler, 1990; Hafner, 1994). This process has led to the phenomenon known as "Fahrenholtz's rule," which states that hosts and their parasites tend to speciate concurrently (Eichler, 1948). Evidence of Fahrenholtz's rule has been documented in gophers and lice (Hafner, 1988; Page, 1993), but it does not explain how two different genera of lice, *Geomydoecus* and *Thomomydoecus*, can coexist on a single species of pocket gopher, *Thomomys bottae*.

Stable coexistence of two genera of lice on an individual host (i.e., without one genus outcompeting the other) requires that they partition the host's resources in some way. One possible mechanism for partitioning of host resources is hair diameter. A louse exists for the duration of its life cycle attached to the hair of its host by a head groove (Fig. 1). This attachment is necessary for the survival of the parasite because of the louse's absolute dependence on the host for all its resources. Therefore, it is mandatory that the head groove of the louse be of appropriate size and shape to grip tightly onto the hair of the host. Because chewing lice of the genera *Geomydoecus* and *Thomomydoecus* have different body shapes (Fig. 2), it is possible that their head grooves also are of different shape or size. This would permit the two genera to partition the host resources spatially by forcing each louse to find hairs of

suitable diameter for secure attachment. If hair diameter is different in different regions of the host (which I will examine in this study), then one would predict that lice of one genus might be able to grasp hairs in certain regions of the host better than hairs in other regions.

In this study, I investigate a potential mechanism for resource partitioning that may enable stable coexistence between these two genera of chewing lice on an individual pocket gopher. Specifically, I test the hypothesis that *Geomydoecus* and *Thomomydoecus* are partitioning the host's resources spatially. I begin by looking at different regions of the gopher to see which genus of louse is more abundant in each region. I then examine mean hair diameter in each region of the host to see if a relationship exists between hair diameter of the region and the particular genus of louse inhabiting that region.

Materials and Methods

Three specimens of *Thomomys bottae* (assigned numbers 3869, 3870, and 3871) were trapped on 17 March 1997 in Albuquerque, Bernalillo County, New Mexico. Two males (3869 and 3870) and one female (3871) were collected using Baker live traps (Baker and Williams, 1972). I used gophers collected on a single day to limit variance in louse population densities caused by weather patterns, reproductive condition of the host, and other extraneous factors.

Immediately upon collection, each gopher was chloroformed in a kill-jar lined with fresh paper towels. Once dead, the gopher was slit medially on its ventral side, and the entire skin was pinned to a piece of cardboard, fur side down. Unnecessary movement of the skin was avoided to reduce accidental displacement of the lice (which also were killed by the chloroform treatment). Once the body was removed, the skin was unpinned a section at a time on a block of dry ice to reduce shifting and curling of the skin. The skin was then pressed between two pieces of cardboard and frozen in an ultracold freezer (-75•C).

While still frozen, each gopher skin was cut into ten regions (Fig. 3): anterior ventral (ANVE), cheek (CHEK), dorsal head (DOHE), lateral nape (LANA), posterior dorsal (PODO), posterior ventral (POVE), rump (RUMP), and ventral head (VEHE). Each of the ten regions was placed in a separate plastic bag to avoid loss of lice and contamination by lice from other regions. Each of the ten regions was brushed vigorously and the lice collected in a 1.2 ml cryotube. Adult lice were then identified as either *Geomydoecus* or *Thomomydoecus* using light microscopy. Only adults were used in this analysis because identification of juvenile lice is problematic.

The number of lice of each of the two genera was recorded for each of the ten regions. For any given skin region, the null expectation was an equal

number of *Geomydoecus* and *Thomomydoecus* lice. I used Chi-square analyses to see if the observed population densities of the two louse genera differed significantly from the expected 1:1 ratio. I considered the two population densities significantly different only if the *p*-value was less than 0.05.

After the lice were brushed from the ten regions of each gopher, ten hairs were taken from each region. The hairs were mounted on microscope slides, and the diameter of each hair was measured (in μm) using a light microscope fitted with an ocular micrometer. Duncan grouping (SAS Institute, 1994) was used to detect significant differences in mean hair diameter among the ten regions. Duncan grouping assigns a letter to each data set (in this case, mean hair diameter). Data sets assigned the same letter are not significantly different, whereas, those assigned different letters are significantly different at, or below, the 0.05 confidence level. The more alphabetically distant two data sets are after letter assignment, the more significant their difference. These assigned Duncan groupings were examined qualitatively to see if there were significant differences in hair diameter between the regions used by *Geomydoecus* chewing lice compared to those used by *Thomomydoecus* lice.

Results

The number of lice collected in each of the ten regions of the gopher skin varied considerably (Table 1). The minimum number of lice collected in any one region was one louse in the cheek region of gopher 3869 and one louse in the dorsal-head region of gopher 3871. The maximum number of lice collected was 88 in the lateral region of gopher 3871 (Table 1).

The probability of one genus (either *Thomomydoecus* or *Geomydoecus*) being significantly more abundant than the other genus in a particular region on each of the three gophers is analyzed in Table 2. Overall, *Geomydoecus* was significantly more abundant than *Thomomydoecus* in the posterior-dorsal regions and slightly more common in the cheek and lateral-nape regions. In contrast, *Thomomydoecus* was more abundant in the anterior-ventral, lateral, posterior-ventral, and the rump regions, and only slightly more common than *Geomydoecus* in the nape region. There was no significant difference in occurrence of *Geomydoecus* and *Thomomydoecus* individuals in either the dorsal-head or ventral-head regions (Table 2).

When lice from all three gophers were pooled by region (rather than examining each gopher individually), stronger trends were evident (Table 3). Lice of the genus *Geomydoecus* were significantly more abundant in the cheek, dorsal-head, and posterior-dorsal regions, whereas individuals of the genus *Thomomydoecus* were significantly more abundant in the anterior-ventral, lateral, rump, and posterior-ventral regions. No significant difference was found between number of individuals of the two genera in the lateral-nape, nape, and ventral-head regions (Table 3).

The mean hair diameter per region varied from 33.609 μm in the rump region to 45.221 μm in the lateral-nape region (Table 4). Duncan groupings were used to investigate the possible relationship between hair diameter and louse

distribution. *Geomydoecus* lice were significantly more abundant than *Thomomydoecus* lice in the cheek region (mean hair diameter of 44.896 μm), but *Geomydoecus* also was most abundant in the posterior-dorsal region, which has a mean hair diameter (34.323 μm) that is significantly smaller than mean hair diameter in the cheek region (Table 5). Similarly, *Thomomydoecus* lice were found in regions with mean hair diameters that differed significantly.

Discussion

The data presented are consistent with the hypothesis that the two genera of chewing lice partition available gopher habitat spatially. Lice of the genus *Thomomydoecus* are significantly more abundant on the posterior and ventral surfaces of the gopher, whereas *Geomydoecus* lice are significantly more abundant on the anterior and dorsal surfaces of the gopher
(Figs. 4 and 5).

When the gophers were examined individually, *Geomydoecus* lice were significantly more abundant in the posterior-dorsal region and only slightly more abundant than *Thomomydoecus* in the cheek and lateral-nape regions. Similar trends were evident when results from all three gophers were pooled, except that the lateral-nape region no longer had significantly more *Geomydoecus* than *Thomomydoecus* individuals, whereas the dorsal-head region did. The lateral-nape region showed a significant difference in abundance of the two louse genera only in gopher 3869. This gopher, however, hosted considerably fewer lice overall than did the other two gophers (Table 1), and small sample sizes may have caused spurious results for this, and other, skin regions. Because louse population densities were low in all three dorsal regions (Table 1), the dorsal-head region showed a significant difference between louse genera only when lice from all three gophers were pooled (Table 3).

Thomomydoecus lice were significantly more abundant than *Geomydoecus* individuals in the anterior-ventral, lateral, posterior-ventral, and rump regions, regardless of whether lice from each gopher were considered independently, or pooled. Regions that showed no significant difference in the analysis of pooled data (e.g., lateral-nape, nape, and ventral-head) only showed significant differences in one of the three gophers
(Table 2).

Having demonstrated spatial partitioning of the host skin by the two genera of chewing lice, it is important to seek an explanation as to why this regional partitioning occurs. I have looked at hair diameter of the host as one possible mechanism of resource partitioning. This mechanism is a potential cause of partitioning because head groove size of *Geomydoecus* and *Thomomydoecus* lice may differ, given that body shape and size of the two genera differ (Fig. 2). Variation in head groove size, if present, could facilitate spatial partitioning of host resources.

Although I do not yet have data on head-groove size for the two genera of lice, evidence available thus far suggests that they are not selecting regions of the host based on hair diameter. Although hairs collected from the three gophers showed definite regional trends in terms of hair diameter (Table 4), there was no evidence that hair diameter had any bearing on which genus of louse was more abundant in that region. In fact, *Geomydoecus* individuals were most abundant in regions with both large hairs (44.896 μm) as well as small hairs (34.323 μm). Similarly, *Thomomydoecus* lice were found in the region with the smallest mean hair diameter (33.609 μm) and in the region with the third largest mean hair diameter (44.896 μm).

If lice are partitioning their host based on hair diameter, I would expect that all regions with significantly more *Geomydoecus* than *Thomomydoecus* should have the same (or, at least, similar) Duncan groupings (Table 5). In addition, these Duncan groupings should differ from the Duncan groupings assigned to regions with significantly more *Thomomydoecus* than *Geomydoecus*, as well as to regions showing no significant difference between the two genera. In the Duncan-group analysis (Table 5), the cheek region (with significantly more *Geomydoecus* than *Thomomydoecus*), the lateral-nape region (with no significant difference between the two louse genera), and the posterior-ventral region (with

significantly more *Thomomydoecus* than *Geomydoecus*) all were assigned the same Duncan group letter ("A" in Table 5), indicating that mean hair diameters of these regions were not significantly different.

These data show no relationship between mean hair diameter of the region and the genus of lice most abundant in that region. Thus, these data falsify the hypothesis that *Geomydoecus* and *Thomomydoecus* are partitioning the host resources spatially by cueing on hair diameter. It follows, then, that the lice must be partitioning their resources by means of a factor other than hair diameter. M. D. Murray (1957) suggested that certain species of ectoparasitic lice respond to temperature and humidity gradients of the host. It is possible that *Geomydoecus* and *Thomomydoecus* have different temperature and humidity tolerances that enable them to partition the pocket gopher according to these gradients. Further studies of live pocket gophers will be necessary to explore this potential mechanism in greater detail.

Literature Cited

Baker, R. J. and S. L. Williams. 1972. A live trap for pocket gophers, *Journal of Wildlife Management*, **36**: 1320-1322.

Eichler, W. 1948. Some rules in ectoparasitism. *Annals and Magazine of Natural History*, **12**: 588-598.

Hafner, M. S. and S. A. Nadler. 1988. Phylogenetic trees support the coevolution of parasites and their hosts. *Nature*, **332**: 258-259.

Hafner, M., P. D. Sudman, F. X. Villablanca, T. A. Spradling, J. W. Demastes, and S. A. Nadler. 1994. Disparate rates of molecular evolution in cospeciating hosts and parasites. *Science*, **265**: 1087-1090.

Hellenthal, R. A. and R. D. Price. 1984. Distributional associations among *Geomydoecus* and *Thomomydoecus* lice (Mallophaga: Trichodectidae) and pocket gopher hosts of the *Thomomys bottae* group (Rodentia: Geomyidae). *Journal of Medical Entomology*, **21**: 432-446.

Marshall, A. G. 1981. *The Ecology of Ectoparasitic Insects*. Academic Press, London.

Murray, M. D. 1957. The distribution of the eggs of mammalian lice on their hosts: II. Analysis of the oviposition behavior of *Damalinia ovis*. *Australian Journal of Zoology*. **8**: 19-29.

Nadler, S. A., M. S. Hafner, J. C. Hafner, and D. J. Hafner. 1990. Genetic differentiation among chewing louse populations (Mallophaga: Trichodectidae) in a pocket gopher contact zone. *Evolution*, **44**: 942-951.

Page, R. D. M. 1993. Parasites, phylogeny, and cospeciation. *International Journal of Parasitology*, **23**: 499.

SAS Institute. 1994. SAS/STAT User's Guide. Version 6, 4th ed.

Table 1. Number of specimens of each genus of louse collected from each of the ten skin regions of the three pocket gophers examined. Abbreviations for the skin regions as per text.

	Gopher 3869		Gopher 3870		Gopher 3871	
Region	*Thomomydoecus*	*Geomydoecus*	*Thomomydoecus*	*Geomydoecus*	*Thomomydoecus*	*Geomydoecus*
ANVE	10	2	31	7	39	2
CHEK	0	1	1	7	1	4
DOHE	0	3	0	2	0	1
LANA	0	9	13	10	8	10
LATE	11	5	37	13	80	8
NAPE	1	3	4	10	11	1
PODO	4	16	8	14	16	32
POVE	15	8	18	0	38	4
RUMP	9	1	63	1	81	2
VEHE	1	4	7	2	9	3

Table 2. Genus of louse most abundant in each of the ten skin regions of the three pocket gophers. T=*Thomomydoecus;* G=*Geomydoecus;* G>T= *Geomydoecus* is more abundant than *Thomomydoecus* in the particular region; T>G= *Thomomydoecus* is more abundant than *Geomydoecus* in the particular region.

Region	Gopher 3869	Gopher 3870	Gopher 3871
ANVE	* T>G	**** T>G	**** T>G
CHEK	ns	* G>T	ns
DOHE	ns	ns	ns
LANA	** G>T	ns	ns
LATE	ns	*** T>G	****T>G
NAPE	ns	ns	** T>G
PODO	** G>T	ns	* G>T
POVE	ns	**** T>G	**** T>G
RUMP	* T>G	**** T>G	**** T>G
VEHE	ns	ns	ns

ns = No significant difference in number of individuals of the two genera
* = $P<0.05$
** = $P<0.01$
*** = $P<0.001$
**** = $P<0.0001$

Table 3. Genus of louse most abundant in each region when lice from all three pocket gophers are pooled by region. T=*Thomomydoecus*; G=*Geomydoecus*; G>T= *Geomydoecus* is more abundant than *Thomomydoecus* in the particular region; T>G= *Thomomydoecus* is more abundant than *Geomydoecus* in the particular region.

Region	All Gophers
ANVE	****T>G
CHEK	** G>T
DOHE	* G>T
LANA	ns
LATE	**** T>G
NAPE	ns
PODO	*** G>T
POVE	**** T>G
RUMP	**** T>G
VEHE	ns

ns = No significant difference in the number of individuals of the two genera
* = $P<0.05$
** = $P<0.01$
*** = $P<0.001$
**** = $P<0.0001$

Table 4. Mean hair diameter ± SE in each of the ten skin regions (Fig. 3) of *Thomomys bottae*.

Region	Mean Hair Diameter + SE (μm)
LANA	45.221 ± 8.397
CHEK	44.896 ± 9.624
POVE	42.658 ± 6.890
ANVE	41.396 ± 8.614
LATE	39.528 ± 10.038
VEHE	38.715 ± 8.274
DOHE	38.308 ± 8.431
NAPE	35.227 ± 8.394
PODO	34.323 ± 9.151
RUMP	33.609 ± 9.734

Table 5. Relationship between mean hair diameter and significantly most-abundant genus of chewing louse. Means with the same Duncan grouping letter are not significantly different.

Region	Mean Hair Diameter (μm)	Duncan Grouping	Genus Most Abundant
LANA	45.221	A	N/A
CHEK	44.896	A	*Geomydoecus*
POVE	42.658	A B	*Thomomydoecus*
ANVE	41.396	A B	*Thomomydoecus*
LATE	39.528	B	*Thomomydoecus*
VEHE	38.715	B C	N/A
DOHE	38.308	B C D	*Geomydoecus*
NAPE	35.227	C D E	N/A
PODO	34.323	D E	*Geomydoecus*
RUMP	33.609	E	*Thomomydoecus*

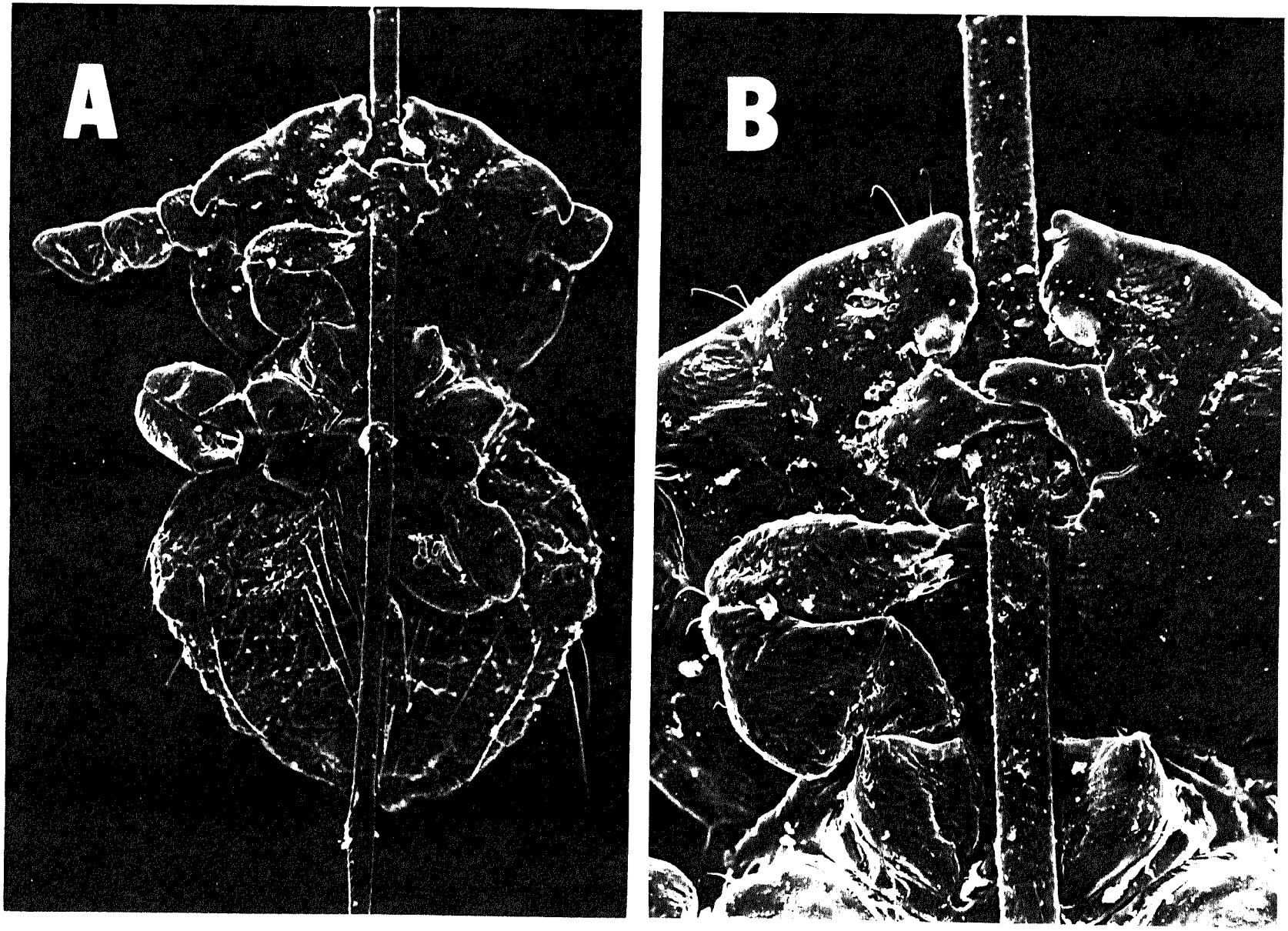

Figure 1. A) Attachment of chewing louse to host hair. B) Ventral view of louse head groove.

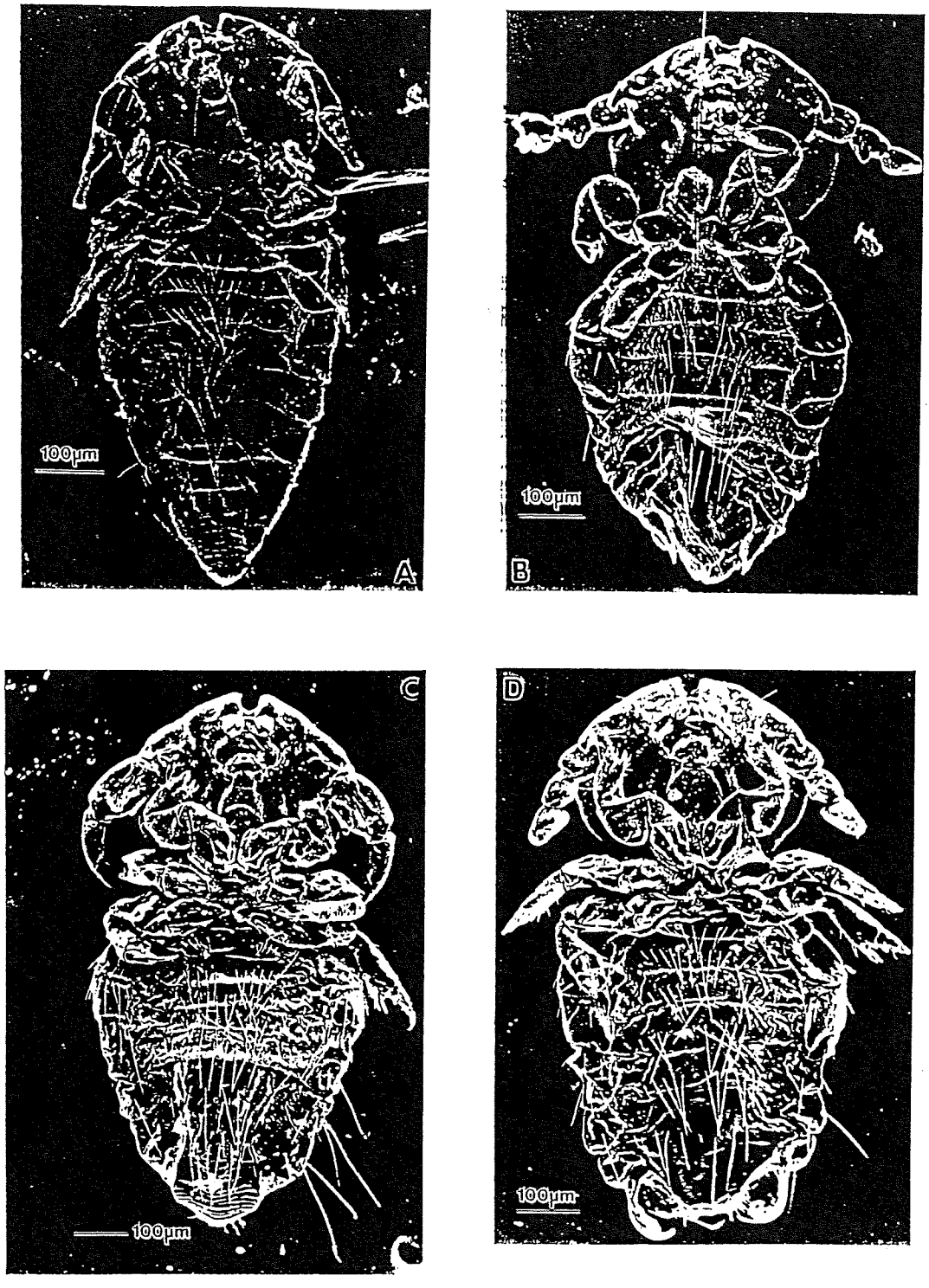

Figure 2. Ventral views of chewing lice (Mallophaga). A) *Thomomydoecus* male; B) *Thomomydoecus* female; C) *Geomydoecus* male; and D) *Geomydoecus* female

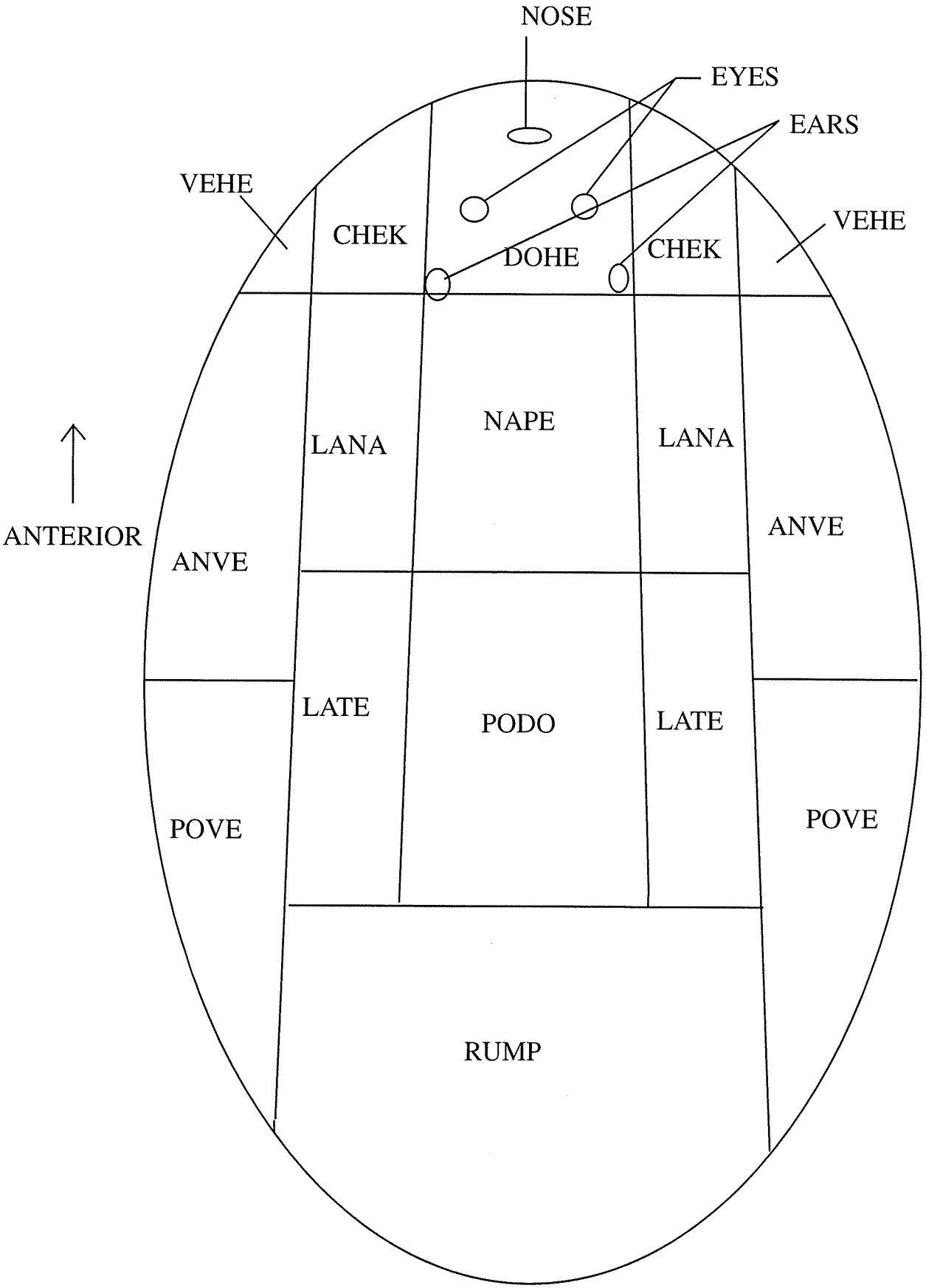

Figure 3. Diagrammatic view of the regional divisions of the skin of a specimen of *Thomomys bottae* (dorsal view). Abbreviations as per text. Corresponding regions on the left and right side were pooled in the analysis.

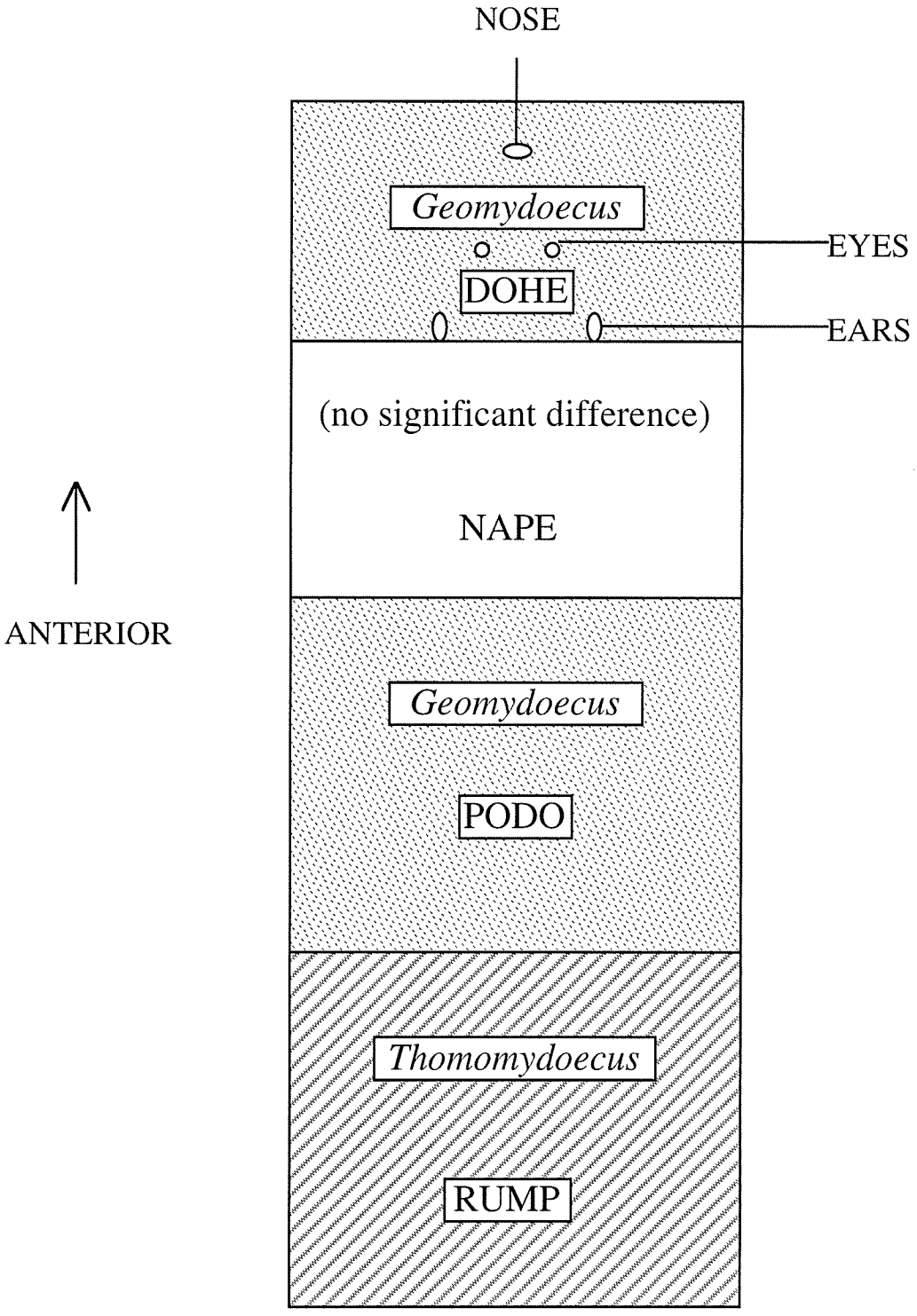

Figure 4. Dorsal regions of the *Thomomys bottae* skin indicating the genus of louse significantly most abundant ($p<0.05$) in each region. Abbreviations as per text.

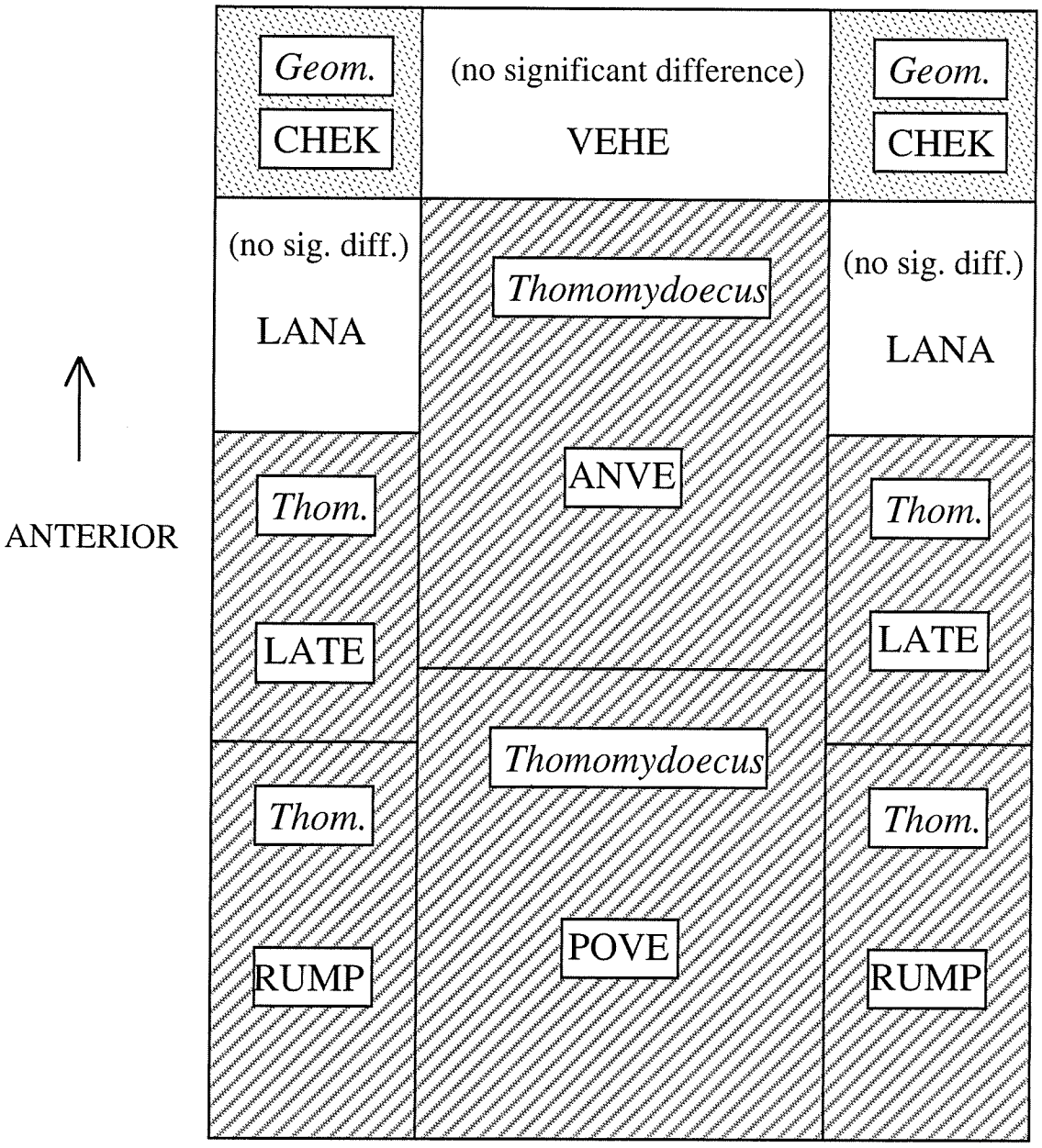

Figure 5. Ventral regions of the *Thomomys bottae* skin indicating the genus of louse significantly most abundant ($p<0.05$) in each region. Abbreviations as per text.