SYSTEMATICS

Taxonomic Importance of First-Instar Chewing Lice (Phthiraptera: Trichodeetidae) from Pocket Gophers (Rodentia: Geomyidae)

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Abstract

A study of 1st instar nymphs representing 119 of the 122 currently recognized taxa of pocket gopher lice of the genera Geomydocus and Thomomydocus resulted in the recognition of numerous valuable taxonomic features enabling reliable differentiation for a surprisingly large number of these lice. These characters are discussed primarily at the species complex level, with mention of specific differences where pertinent. A key is given for the identification of the currently recognized 28 complexes of pocket gopher lice.

Key Words: Geomydocus, Thomomydocus, taxonomy

During our taxonomic study of lice of pocket gophers, we amassed and slide-mounted an extremely large collection of immature lice representing virtually all nymphal instars of the 122 recognized taxa. At the time, we had no specific plans on what eventually would arise from this huge collection, but our hope was that they would provide an opportunity for someone to examine the significance of characters that might be peculiar to them. They might even, in the most optimistic sense, provide additional independently derived information on potential new phylogenetic relationships. To date, speculation on relationships of these lice has been based only on our completed study of the adults of the 122 taxa (Hellowthal and Price 1991, 1994).

It was with this in mind that we undertook the current study involving an exploration of morphological features associated with 1st-instar pocket gopher lice. There has been no significant treatise on the 1st instars of any chewing louse group, much less on one of this magnitude and complexity. Unfortunately, immature chewing lice generally have been viewed with disdain and have been, for the most part, relegated to the trash pile. We were pleased to find that the collection housed at the University of Minnesota contained 119 of the 122 total taxa from pocket gophers. Encouraged by this almost complete representation, we explored their characteristics to see if they showed anything of significance. Our preliminary feeling, based solely on intuition and not on any factual basis, was that these immature lice might have a few significant differences, grouping the 26 complexes into a smaller number of supercomplexes. Little did we suspect the considerable array of excellent features that would be demonstrated by these lice and the potential value they would provide for a further study of the phylogenies of this difficult group (Page et al. 1995).

The examination of morphological characters of these immature lice has impressed us in several regards. First, the chaetotaxy of these lice is extremely well organized and relatively simple, making comparison of all lice a feasible and meaningful project. Second, there has proven to be a vast array of excellent features dealing with distributions and lengths of setae, certain other structures, and dimensions. Third, a study of 1st-instar lice is much less complicated than that of adults because the differentiation into sexes and the associated secondary sexual characters is avoided.

Because some gopher taxa host \( > 1 \) louse taxon, the potential exists for associating 1st instars with the wrong species or subspecies. However, in all cases, individual gophers were found that hosted only a single louse species, enabling the identity of the 1st instar to be established with certainty. The most difficult situation, and the only real problem among all these lice, arose in associating the 1st instars of the mexicanus and the coronadai complexes, both of which invariably cooccurred on the same individual gophers. Fortunately, the cooccurrence of a species of the coronadai complex with 1 of the mexicanus complex, whose identity had been established previously, enabled us to assign this louse to the proper taxon and to clarify the identity of the other paired louse taxon.

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Discussion of Taxonomic Characters

To facilitate the presentation of descriptive features for the 1st-instar lice, we discuss each character, applying a figure number to each character and a letter to each state of that character (Table 1). The reader can refer to the single plate of figures containing illustrations of the character states for the 20 characters. The characters are organized more or less sequentially from anterior to posterior, and not in any order of importance. Reference to the generalized louse drawing in the upper, center portion of the plate will afford orientation for each character. Presentation of the data in this manner, although perhaps a bit awkward, results in a great saving of space and affords a relatively complete description of each complex. To do otherwise and to verbalize on each of the character states would involve a prohibitively large amount of space. All dimensions are in millimeters.

The only other useful feature, in addition to these 20 characters, is the templet width as measured across the broadest part of the posterior head region.

The character states for the 1st-instar nymphs for each of the 26 complexes of pocket gopher lice are given in Table 2. The character numbers and the letters for each character state are as listed above and are consistent with the labeling of the figures in the plate provided. Note that, in a number of places, a state is represented by multiple letters. This may be the result of one or more of the following 3 reasons: (1) the character is so variable within a group of species, especially in complexes with a large number of included taxa, that several states are present (this is especially true for measurement states in which the range overlaps several of the state limits); (2) there is individual variation in the expression of certain states (for example, state 2Bh, in the absence of the minute seta at the end of the row, becomes state 20c, and so on); (3) some complexes appear, on the basis of 1st-instar morphology, to be more heterogeneous than the study of adult lice suggested; this may require further study to determine the source of these differences. In the following portion, each complex is commented upon briefly, primarily to point out what appear to be significant differences among lice within the complex and, on occasion, to point out obvious similarities to other lice. No attempt has been made to diagnose the complex because that information is available in Table 2 and because the key differences among the complexes for identification purposes.

Complexes of Pocket Gopher Lice

Californicus Complex (Price and Hellenthal 1981b). This represents the 1st and largest of 22 complexes of lice in the nominate subgenus Geomygus Ewing, and is known from Thomomys bottae (Eyraux & Gervais) and T. montanus (Rich-
<table>
<thead>
<tr>
<th>Character</th>
<th>Character state</th>
<th>Character</th>
<th>Character state</th>
</tr>
</thead>
<tbody>
<tr>
<td>c. Medusa on II-V, very long on VI-VII</td>
<td>d. Shorter on V than on II-VI, very long on VI-VII</td>
<td>c. On II-VII, all minute to short</td>
<td>d. On II-VII, all long</td>
</tr>
<tr>
<td>e. Short on II-V, very long on VI-VII</td>
<td>f. Short on III-VI, very long on VII-VIII</td>
<td>g. On II-VII, all minute to short</td>
<td>h. On II-VII, all short</td>
</tr>
<tr>
<td>i. Short on II-VI, very long on VII-VIII</td>
<td>j. Short on III-VI, much shorter on VII</td>
<td>l. On II-VII, all minute</td>
<td>m. On II-VII, all minute</td>
</tr>
<tr>
<td>n. Short on II-VI, all long</td>
<td>o. On II-VII, all medium</td>
<td>p. On II-VII, all minute to short</td>
<td>q. On II-VII, all minute</td>
</tr>
<tr>
<td>r. Short on III-VI, much shorter on VII</td>
<td>s. On II-VII, all medium</td>
<td>t. On II-VII, all minute to short</td>
<td>u. On II-VII, all minute</td>
</tr>
<tr>
<td>15 Marginal setae on terminal segment</td>
<td>20 Medusal terminal abdominal setae</td>
<td>15 Marginal setae on terminal segment</td>
<td>20 Medusal terminal abdominal setae</td>
</tr>
<tr>
<td>a. None</td>
<td>b. With 2 short setae on each side</td>
<td>a. None</td>
<td>b. With 2 short setae on each side</td>
</tr>
<tr>
<td>c. With single very long setae on each side</td>
<td>d. On II-VII, all minute to short</td>
<td>c. On II-VII, all minute to short</td>
<td>d. On II-VII, all minute to short</td>
</tr>
<tr>
<td>e. On II-VII, all minute to short</td>
<td>f. On II-VII, all minute to short</td>
<td>g. On II-VII, all minute to short</td>
<td>h. On II-VII, all minute to short</td>
</tr>
<tr>
<td>i. On II-VII, all minute to short</td>
<td>j. On II-VII, all minute to short</td>
<td>k. On II-VII, all minute to short</td>
<td>l. On II-VII, all minute to short</td>
</tr>
<tr>
<td>m. On II-VII, all minute to short</td>
<td>n. On II-VII, all minute to short</td>
<td>o. On II-VII, all minute to short</td>
<td>p. On II-VII, all minute to short</td>
</tr>
<tr>
<td>q. On II-VII, all minute to short</td>
<td>r. On II-VII, all minute to short</td>
<td>s. On II-VII, all minute to short</td>
<td>t. On II-VII, all minute to short</td>
</tr>
<tr>
<td>u. On II-VII, all minute to short</td>
<td>v. On II-VII, all minute to short</td>
<td>w. On II-VII, all minute to short</td>
<td>x. On II-VII, all minute to short</td>
</tr>
<tr>
<td>16 Intermediate terminal abdominal setae</td>
<td>17 Submedian terminal abdominal setae (on II-VII)</td>
<td>16 Intermediate terminal abdominal setae</td>
<td>17 Submedian terminal abdominal setae (on II-VII)</td>
</tr>
<tr>
<td>a. Minute on II-VII, all minute to short</td>
<td>b. On II-VII, all short</td>
<td>a. Minute on II-VII, all minute to short</td>
<td>b. On II-VII, all short</td>
</tr>
<tr>
<td>c. On II-VII, all minute to short</td>
<td>d. On II-VII, all minute to short</td>
<td>g. On II-VII, all minute to short</td>
<td>h. On II-VII, all minute to short</td>
</tr>
<tr>
<td>e. On II-VII, all minute to short</td>
<td>f. On II-VII, all minute to short</td>
<td>i. On II-VII, all minute to short</td>
<td>j. On II-VII, all minute to short</td>
</tr>
<tr>
<td>18 Median terminal abdominal setae</td>
<td>19 Intermediate terminal abdominal setae</td>
<td>18 Median terminal abdominal setae</td>
<td>19 Intermediate terminal abdominal setae</td>
</tr>
<tr>
<td>c. On II-VIII, much shorter on VII</td>
<td>d. On II-VIII, all minute</td>
<td>c. On II-VIII, much shorter on VII</td>
<td>d. On II-VIII, all minute</td>
</tr>
<tr>
<td>e. On II-VIII, much shorter on VII</td>
<td>f. On II-VIII, all minute</td>
<td>e. On II-VIII, much shorter on VII</td>
<td>f. On II-VIII, all minute</td>
</tr>
<tr>
<td>g. On II-VIII, all minute</td>
<td>h. On II-VIII, all minute</td>
<td>g. On II-VIII, all minute</td>
<td>h. On II-VIII, all minute</td>
</tr>
<tr>
<td>i. On II-VIII, all minute to short</td>
<td>j. On II-VIII, all minute to short</td>
<td>i. On II-VIII, all minute to short</td>
<td>j. On II-VIII, all minute to short</td>
</tr>
<tr>
<td>k. On II-VIII, all minute to short</td>
<td>l. On II-VIII, all minute to short</td>
<td>k. On II-VIII, all minute to short</td>
<td>l. On II-VIII, all minute to short</td>
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<tr>
<td>m. On II-VIII, all minute to short</td>
<td>n. On II-VIII, all minute to short</td>
<td>m. On II-VIII, all minute to short</td>
<td>n. On II-VIII, all minute to short</td>
</tr>
<tr>
<td>o. On II-VIII, all minute to short</td>
<td>p. On II-VIII, all minute to short</td>
<td>o. On II-VIII, all minute to short</td>
<td>p. On II-VIII, all minute to short</td>
</tr>
<tr>
<td>q. On II-VIII, all minute to short</td>
<td>r. On II-VIII, all minute to short</td>
<td>q. On II-VIII, all minute to short</td>
<td>r. On II-VIII, all minute to short</td>
</tr>
<tr>
<td>s. On II-VIII, all minute to short</td>
<td>t. On II-VIII, all minute to short</td>
<td>s. On II-VIII, all minute to short</td>
<td>t. On II-VIII, all minute to short</td>
</tr>
<tr>
<td>u. On II-VIII, all minute to short</td>
<td>v. On II-VIII, all minute to short</td>
<td>u. On II-VIII, all minute to short</td>
<td>v. On II-VIII, all minute to short</td>
</tr>
<tr>
<td>w. On II-VIII, all minute to short</td>
<td>x. On II-VIII, all minute to short</td>
<td>w. On II-VIII, all minute to short</td>
<td>x. On II-VIII, all minute to short</td>
</tr>
<tr>
<td>y. On II-VIII, all minute to short</td>
<td>z. On II-VIII, all minute to short</td>
<td>y. On II-VIII, all minute to short</td>
<td>z. On II-VIII, all minute to short</td>
</tr>
</tbody>
</table>

This is the 1st of 6 complexes that have members with a conspicuous extensive patch of dark "bumps" on the ventral surface. Within this complex, there is a marked tendency for 6 western taxa—*G. californica* (Chapman), *G. centrata* Price & Hellowthal, *G. altata* Price & Hellowthal, *G. anguinalis* Price & Hellowthal, *G. japonica* Price & Hellowthal, and *G. djohorica* Price & Hellowthal—to have longer or more abundant chaotaxy than the other taxa (Table 7, 7a, 7b, 7c, 7d, 7e, 7f, 7g, 7h, 7i, 7j, 7k, 7l, 7m, 7n, 7o, 7p, 7q, 7r, 7s, 7t, 7u, 7v, 7w, 7x, 7y, 7z).
involving, having unique states 3a and 20 versus 38c and 29g.

geometric Complex (Timm and Price 1980). Within this complex of 8 species from Geomys inauratus (Shaw), 2—G. subunguis Price & Emerson and G. m. inauratus Emerson are monotypic, and apart from the other 6 by having unique states 7ab, 17a, 18f, and 20g versus 49d, 17b, 18e, and 20e.

truncus Complex (Helleluff and Price 1918). The 2 taxa from Geomys personatus True are essentially inseparable, with the only suggestion of difference being G. personatus with 2c versus G. neustrumcris Helleluff & Price with 3c.

dolichocephus Complex (Timm and Price 1979). The single species of this complex, G. dolichocephus Timm and Price, appears closest to the taxa of the geomys complex, differing only by having state 17c versus 17b.

selecutus Complex (Price 1975). There are no differences shown between the 2 species found on the Geomys taxa in the southeastern United States.

tenax Complex (Price and Helleluff 1975b). Pronounced differences in abdominal chaetotaxy of the 2 taxa—G. tenax tenax Ewing and G. tenax tigrina Price & Helleluff—from Geomys seem to be due to the taxa from Papagoeyus, these involving states 13a, 16a, 18e, and 19e versus 13f, 16b, 18f, and 19e, respectively. Of the 1 species, G. subulatus Price & Helleluff and G. savani Helleluff group is unique among the taxa by having a very long pair of setae on the last segment (15e), similar to the state for the single species in the trichopoli Complex (Price and Helleluff 1985b). The single species of this complex from Papagoeyus trichopoli Merrick shares the unique chaetotaxy of the last segment with G. subulatus of the tenax complex.

orgeus Complex (Price and Helleluff 1980a). A marked heterogeneity is shown among the 4 species of this complex, Two of them—G. orgeus Price & Emerson and G. infulatus Price & Emerson—from Thamoseus hildachonis (Richardson) and T. concinnus (Bachman) have states 8a, 12b, 18e, 14a, 16a, 17c, and 19e versus 8c, 12d, 13d, 14c, 16b, 17c, and 18e for the other 2 taxa—G. concinnus Price & Helleluff and G. harrisi Price & Helleluff—from T. hildachonis.

tobane Complex (Price and Helleluff 1979). There is no discernible pattern of differentiation among the 5 taxa in this complex from T. undulatus.

velli Complex (Price and Helleluff 1988a). Details of abdominal chaetotaxy set the single species of this complex from Pygmygongyus gynagnostikus (Russell) apart from closely related taxa.

panasus Complex (Price et al. 1985). The 5 taxa of this complex from Papagoeyus, with adult size relationships, the 1st instar of G. panasus Price & Emerson is smaller than that of G. panasus Price & Emerson with juvenile states 13d, state 14 with 0.410 ± 0.455 versus 0.465 ± 0.49. This complex, together with the alenii complex, is among the largest of the 1st instars, and also among the largest as adults.

alenii Complex (Price and Helleluff 1988a). Again, as with the previous complex, the 2 included taxa are separable primarily on size differences, with G. alenii Price & Emerson having a trend width of 0.420 ± 0.445 versus 0.475 ± 0.490 for G. geoffrey Price & Emerson. This size relationship holds true for the adults.

thomosus Complex (Helleluff and Price 1986a). The species of this complex, the various subgroups of the Geomys subgenus Thamoseus Helleluff & Price, are quite homogeneous, with only 3 of 20 characters showing differences of states and these are of a very minor nature.

megeregri and minitaur Complexes (Price and Helleluff 1986c). These 2 complexes constitute the nominate subgenus of the Thamoseus Price & Emerson. The homogeneity of only 1 of the 6 members of the former complex [uniform of T. perplexus (Price & Helleluff) is not available] and the 9 of the latter is close, with the differences expressed being much variation between adjacent character states. The most apparent difference involves T. perplexus (Price & Helleluff) with 13f, 14d, and 19b, the remaining showing 13c, 14e, and 20c.

helleluff and Price 1984, 1986). The species of this complex (we lack T. perplexus Helleluff & Price, the 4th member of the complex), the only members of the Thamoseus Price & Emerson, are quite homogeneous for the 1st instars, with no differences noted for any of them.

Key to Complexes of First-Instar Lice from Pocket Gophers

1. Latral seta relatively short on abdominal segments V-VII (Fig. 14g) 2
   Lateral seta very long on abdominal segments VII-V and V, or VII-V (Fig. 14a) 3

2(1). Median tergal abdominal setae all marginal (Fig. 20a); submarginal temple seta #4 present (Fig. 1a), with 2 pairs of short marginal setae on last abdominal segment (Fig. 13b) 1
   Median tergal abdominal setae all long, short complex conchopa (Fig. 20a), submarginal temple seta #4 absent (Fig. 1b), without marginal setae on last abdominal segment (Fig. 13a) 3

3(1). Small terminal width, not >0.355; 2 pairs of short marginal setae on last abdominal segment (Fig. 15b) 4
   Larger terminal width, at least 0.270, without short marginal setae on last abdominal segment (Fig. 21a) 5
   Without conspicuous patch of dark "bumps" on ventral temple (Fig. 15e) 6
   With conspicuous patch of dark "bumps" on ventral temple (Fig. 15c) 7

4(3). Submedian terminal seta on abdominal segments II and III very long, much longer than corresponding setae on IV and V (Fig. 17g) 8
   Submedian terminal setae on abdominal segments II-IV of similar length... 8

5(6). Temple width >0.410... alenii Complex. Temple width <0.410... megregei Complex

6(10). Submedian sternal abdominal setae in 13a, intermediate sternal abdominal setae in 14a, intermediate sternal abdominal setae in 14c, and intermediate sternal abdominal setae in 15c... megregei complex

7(9). All median terminal abdominal setae minute, difficult to discern (Fig. 20b) at least some median terminal abdominal setae longer, conspicuous... 13

8(5). Lateral seta on abdominal segment II longest (Fig. 18b) lateral seta on abdominal segment IV longest (Fig. 18d) 9
   Lateral seta on abdominal segment VI longest (Fig. 18f) lateral seta on abdominal segment VII (Fig. 18c) 10

9(8). Temple width >0.400, outer mid-dorsal head seta >0.085... chalaicus Complex. Temple width <0.370, outer mid-dorsal head seta <0.069... 11

10(11). Medial sternal abdominal setae medium... anteriorly, minute postmorn (Fig. 18b), temple width <0.400... 12
   Medial sternal abdominal setae of similar length (Fig. 18f), temple width >0.400... 12

11(12). Outer metanal seta very long... 13(13) outer metanal seta medium... 14(14)
   Outer metanal seta very short... 13(13)

12(11). Meine sternal abdominal setae very long, sternal abdominal setae, sternal abdominal setae... 13
   Medial sternal abdominal setae very long, sternal abdominal setae... 14
   Meine sternal abdominal setae... 13

13(12). Lateral seta on abdominal segments II and III with pair of very long unguinal setae (Fig. 13c) 15
   Lateral seta on abdominal segments II and III without unguinal setae (Fig. 13a) 15

14(13). Lateral seta on abdominal segments with pair of very long unguinal setae (Fig. 13c) 16
   Lateral seta on abdominal segments without pair of very long unguinal setae (Fig. 13a) 16

15(14). Meine abdominal segment with pair of long unguinal setae (Fig. 13b) 17
   Meine abdominal segment without pair of long unguinal setae (Fig. 13a) 17
15(14). Majority of median sternal abdominal setae minute, difficult to see (Fig. 18h) ........................................... truncatus complex
Majority of median sternal abdominal setae short to medium, easily visible .............................. 

16(15). Median sternal abdominal setae present on IX (Fig. 18d) ......................................................... 17
16(16). Median sternal abdominal setae absent on IX ................................................................. 19

17(16). Median tergal abdominal setae present on VII (Fig. 20h) .............................................. tuberculatus complex
Median tergal abdominal setae absent on VIII (Fig. 20c) ...................................................... 18

18(17). Dorsal antenal pedicel seta < 0.045 (Fig. 5c) .............................................. gromylis complex
(only G. nebrotherensis) .......................... 19
Dorsal antenal pedicel seta > 0.045 (Fig. 5b) .................................................. origanus complex

19(16). Dorsal antenal pedicel seta < 0.085 (Fig. 5a) .................................................. mexicanus complex (remainder)
Dorsal antenal pedicel seta < 0.080; subtergal abdominal setae on II-VI generally much shorter than median terminal setae .............................. 20

20(19). Each side of at least abdominal sterna II and III with several setae lateral to median setae (Fig. 16f); short dorsal antenal pedicel setae, not < 0.0100 .................................................. 21
Each side of at least abdominal sterna II-VI with only single seta lateral to median setae; variable antenal setae .............................. 22

21(20). Subtergal lateral abdominal setae short on II-VI, very long on VII and VIII (Fig. 17c); cora III spine as in Fig. 12d; quadridensatus complex Subtergal lateral abdominal setae otherwise (Fig. 17f); cora III spine as in Fig. 12c; californcius, umbrius, and subtergalis complexes With pair of median sternal abdominal setae on IX (Fig. 18d) .................................................. 23

22(21). No median sternal abdominal setae on IX ................................................................. 23

23(22). Abdominal segment VI with minute to small lateral setae (Fig. 14f) ........................................... salbachi complex
Abdominal segment VI with very long lateral setae, similar to those on VII and VIII .............................. 24

24(23). Median tergal abdominal setae on I-VI (Fig. 20c); some to all of median length .............. 35

25(24). Subtergal setae longer than 0.040, very long on II-VII (Fig. 17b) .............................................. dalgleishii complex
Subtergal lateral abdominal setae longer on II-VII (Fig. 17d) .............................................. gromylis complex (remainder)

26(24). Abdomen with long to very long subtergal setae on II-VII (Fig. 17c) ................... expansus complex
Abdomen with minute to short subtergal setae on II-VI, often also on VII (Fig. 17e) ........... coronatus complex

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References Cited


Price, R. D. 1975. The Geomydinae (Mammalia, Cladechidae) of the southwestern USA pocket go-


1979. A review of the Geomyopus todiace complex (Mallopha: Trichodectidae) from Thomomys (Rodentia: Geomyidae), based on qualitative and quantita-


1980b. The Geomyopus incoceri complex (Mallopha-


1988a. A new species of Geomyopus (Mallopha: Trichodectidae) from Pappoagymys (Rodentia: Geomyidae) pocket gophers in Jalisco, Mexico. J. Ento-


1989a. Geomyopus belloni complex (Mallopha: Trichodectidae) from Belloni's pocket gopher, Pappo-


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