A Review of the Geomydacecus subcalifornicus Complex (Mallophaga: Trichodectidae) from Thomomys Pocket Gophers (Rodentia: Geomyidae), with a Discussion of Quantitative Techniques and Automated Taxonomic Procedures

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ABSTRACT


Geomydacecus subcalifornicus is redescribed and illustrated, its known host range is 44 subspecies of Thomomys bottae and 3 of T. umbrinus from U.S.A. (Arizona, California, Nevada, Utah) and Mexico (Baja California, Sonora). New species, G. guadalupensis, is described from 5 subspecies of T. bottae (type-host T. b. guadalupensis) from U.S.A. (New Mexico, Texas) and Mexico (Coahuila). Quantitative characters of these lice, together with their host and locality data, were stored and evaluated by a computerized taxonomic analysis system. This was used to define and identify tentative taxonomic groups; evaluate these groups for homogeneity; make comparisons among groups; and produce preliminary descriptions, lists of material examined, and host geographic range maps. Distinctions among taxa are shown using qualitative and quantitative characters and principal components analysis of quantitative characters.

Price and Emerson (1971) described Geomydacecus subcalifornicus on the basis of 15 adult lice from 3 host localities in the U.S.A. (California) and Mexico (Sonora, Coahuila). Later, Price (1972) expanded the known distribution of this louse species to include 21 subspecies of the host Thomomys bottae (Eydoux and Gervais) and 1 subspecies of T. umbrinus (Richardson). Extensive collecting of lice from these pocket gopher hosts since that time has shown G. subcalifornicus to extend throughout a much larger geographic range than previously thought and to include an undescribed species.

In this study, we have made extensive use of computers for data handling and analyses. Our first use of computers for analyzing the quantitative morphological characteristics of Geomydacecus lice was in our review of G. expansus (Dages) from the pocket gopher Popo- pogomys castanops (Baird) (Price and Hellenthal 1975a). For this, we adapted several computer programs to summarize and compare our house taxa quantitatively. These programs were subsequently applied to re-examinations of house complexes associated with G. sceleri- tus (McGregor) (Price 1975), G. texanus Ewing (Price and Hellenthal 1975b), and G. copei Wernick (Price and Hellenthal 1976). By developing additional programs, we were able to examine house-host associations. This permitted us to use house relationships and distributions to consider postulated affinities among host P. castanops subspecies based on gopher morphology (Russell 1968) and chromosomes (Berry and Baker 1972). Our louse data strongly supported the latter (Hel- lenthal and Price 1976). In 1977, we began a review of the Geomydacecus lice from T. bottae and T. umbrinus. These species include approximately 225 described subspecies representing over half of all recognized gopher taxa and probably the largest taxonomic complex within the veebrates. We immediately realized that our operational procedures were wholly inadequate for a project of this size. Therefore, we greatly expanded our use of the computer, including the development of additional programs and the integration of these and our previous programs into an organized system for the taxonomic analysis of louse data. An outline of a preliminary version of this system is given by Price and Hellenthal (1979). However, before treating the taxonomy of the G. subcalifornicus complex, we believe that a more complete description of our completed analysis system is appropriate.

Quantitative Techniques and Automated Procedures

Quantitative character data for lice of the G. subcalifornicus complex combined with host and locality information form part of a computerized pocket gopher-louse data base which is maintained on a Control Data...
Our use of the BUG system for the taxonomic evaluation of Geomyodesus lice involves the following operations:

(1) Labelling of preliminary taxa

Initially lice are grouped into easily recognizable morphological complexes referred to as the Geomyodesus species given in Price and Emerson (1971) and Price (1972). Any tentative louse species we believe exist within a complex are further resolved by the BUG system into specific louse or host designation; numbers, collection localities, and host identification, in any order or combination. It is also possible to define separate species for each group of subtaxa resulting from the BUG system. Groups are defined as being distinct if they differ in any of the following characteristics of the data, we have automated our data handling and analyses and some portions of the taxonomic decision-making process.

All male and female lice were examined for qualitative morphological features than were measured and analyzed quantitatively. Taxonomic descriptions use both qualitative and quantitative characteristics and neither has taken precedence over the other in the taxonomic decision-making process.

Retrieval and analysis of stored louse data is performed with an integrated group of computer programs called the BUG system. These programs store and update louse, host, and location information, define tentative taxonomic louse groups, retrieve louse data, and store computer output shown above. Analyses of data are conducted with a mainframe computer, and the results are printed in tabular and graphical form.

The BUG system also allows for direct access to the database, allowing users to search for specific lice or taxa definitions.

(2) Heterogeneity analyses, character comparisons, and evaluation of taxa in reduced character space

The next step is the evaluation of each taxonomic unit for character heterogeneity. The BUG system does this by subdividing low taxa data into subgroups and then comparing each of the characters among subgroups. The results are displayed in tabular form.

Additionally, the BUG system allows for the analysis of character combinations, providing insights into the relationships among different taxa.

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Highly significant but trivial distinctions among subgroups for many characters. Where comparisons among subgroups failed to confirm significant differences for all characters, homogeneity was assumed. A 0.01 significance level was used in tests to reduce the likelihood of character significance given the large number of comparisons.

Our other heterogeneity criteria were developed from a comprehensive study of pock-socket louse variation and morphometrics. We have used these criteria to select samples of both sexes of G. martini Price and Hellenthal and G. expansus, variation of quantitative characters was partitioned for individual lice, host, gophers, localities, and louse taxa using a 5.0 level of significance. ANOVA. Observer errors were estimated using a 2-way ANOVA for measurements made by different persons and a second ANOVA using the same persons. The coefficient of intraclass correlation is used in heterogeneity evaluations because it is largely independent of sample size and the number of subgroups being compared. The critical R value of 0.60 was derived empirically, based on the results of numerous comparisons among various Geomyodesus taxa. It corresponds roughly to a 20% probability of single character misidentification for 2 group comparisons.

The heterogeneity criterion, based on the relative size of estimated variance component for among groups, is used to select taxa which are less than would be expected among different observers. Remaining taxa are divided into 4 groups. These criteria allow for the division of taxa into subgroups for further analysis.

(3) Evaluation of geographic ranges of taxa

Our operation routinely performed is a check of the geographic distribution of species for each taxonomic unit. When host location data are entered into the BUG system, the latitude and longitude of an identifiable town are recorded. If the collection site is located at a known angle and distance from the principal locality, the system determines the coordinates of the specific collection site using calculated lengths of degrees for latitude and longitude. These values are used as coordinates for scaled range maps.

(4) Production of preliminary species descriptions and diagnostic analyses

Following the principal components analysis and geographic range comparisons, the preliminary louse taxon is assigned formal taxonomic status. In general, taxa which show both qualitative and quantitative morphological differences are regarded as species, whereas those based on qualitative characters are designated as subspecies. The BUG system produces tabular quantitative preliminary species descriptions and qualitative material examined for the taxon within a complex. These descriptions are based on the examination of manuscripts. Diagnostic and key characters are identified by an examination of the results of group comparison and these are used to determine qualitative morphological characteristics and host associations. When
making comparisons of preliminary taxa, the system calculates the discriminating value of each character assuming normality and equal variance and ignoring the probability of collection. When no single character is capable of discriminating among taxa with a probability of misidentification of less than 5%, discriminant functions are calculated using all combinations of the best 4 discriminating characters. These discriminant functions are included in descriptions when they offer substantial improvement over single characters.

**Evaluation of the G. subcalifornicus Complex**

Quantitatively examined material for the *G. subcalifornicus* complex consisted of 806 female lice from 333 host pocket gophers and 855 males from 334 hosts. Two taxa were believed to exist within the complex, based on qualitative differences in host morphology. The first group was defined by the BUG system as lice collected on hosts identified as *T. b. guadalupensis* Goldman (BUG system retrieval code: 101090), *T. b. posterioris* Goldman (101156), and *T. b. sturgisi* Goldman (101202), plus those collected at Van Horn (USTX15001) or Diablo Mountains (USTX11502), Hudspeth County, Texas, plus those collected on a gopher with Texas A&M University accession number 1624 (1624). The second group was defined as all lice of this complex from other gopher taxa, localities, and individuals (BUG system retrieval code: A11). The line within these groups was labelled GU and SA, respectively.

For heterogeneity evaluation, our 2 preliminary taxa were subdivided by host taxa. Our measured specimens were collected from 47 host sub-species for SA and 44 for GU. Analysis of the character data among subgroups gave no evidence of heterogeneity within either preliminary taxa. For SA, the female character indicating the greatest heterogeneity among subgroups was the number of genital sac loops (P = 0.00, R = 0.46, CVa = 0.11, CVb = 0.12) and the corresponding male character was head width (P = 0.00, R = 0.45, CVa = 0.02, CVb = 0.02). With both sexes, the greatest R value was well below the required 0.60. For GU, the female character indicating the greatest heterogeneity was head width (P = 0.00, R = 0.62, CVa = 0.03, CVb = 0.02) and the corresponding male character was head length (P = 0.00, R = 0.60, CVa = 0.03, CVb = 0.03). In this case, while both R values were at or slightly above our criteria for heterogeneity, the values for CVa were less than the required 0.05. Results similar to these were obtained for our analyses among host localities. We, therefore, concluded that these preliminary taxa should not be subdivided.

Comparisons between our preliminary taxa gave markedly different results. For females, 2 characters were flagged by the BUG system as indicating heterogeneity. These were the genital sac loop length (P = 0.00, R = 0.85, CVa = 0.22, CVb = 0.09) and the number of genital sac loops (P = 0.00, R = 0.81, CVa = 0.22, CVb = 0.16). No characters passed our heterogeneity criteria for males, although 2 characters (scope length and scope distance) had R values of 0.57 and CVa which exceeded 0.05.

Although our preliminary taxa demonstrated sufficient quantitative and qualitative differences to enable their separation, even the best quantitative character showed some overlap. However, this is not unexpected given the individual variability and large sample size.

Principal components analysis of pooled quantitative data offered added support for our separations. Using the centered R-technique (Orrick 1967) for 9 characters for females and 10 characters for males, the first 3 components accounted for 68% of the female variation and 74% of the male variation. Scattergrams with coordinates representing the 1st, 2nd, and 3rd principal axes in reduced character space for each sex all generally supported our separation of taxa. The best separations were achieved by graphing the 1st and 2nd axes for both sexes (Fig. 13). A plot of the distributions of the host gophers for these taxa shows them to be allopatric (Fig. 13).

In the following descriptions, counted or measured characters are followed by the minimal and maximal observed values, and, in parentheses, sample size, mean, and standard deviation. All measurements are in millimeters. Illustrations are for material from the type-host. In evaluating character usefulness for specific discrimination, critical values for each character were calculated as the point where the likelihood of single character misidentification of the 2 compared taxa was equal, given normality and equal variance, and ignoring the probability of collection. For characters offering moderately good discriminating ability, these critical values and the corresponding probabilities of misidentification are given. In the "Material Examined" section, a number in parentheses following a locality represents the total number of gophers from which the sample was taken. Original locality data expressed in miles are followed parenthetically by the metric equivalent to 0.1 km. The English figure, rather than the metric, expresses the precision of the location estimate.

**Geomydaceus subcalifornicus Price and Emerson, 1957**

Type-host: *Thomomys bottae* subsp., Colorado Desert, California [= *T. b. riparius* Grinnell and Hill].

Female. -- As in Fig. 1. Temple width (TW) 0.385–0.475 (764: 0.429 ± 0.0148); head length (HL) 0.246–0.349 (763: 0.292 ± 0.0136); sub-epimeral and inner marginal temple setae (STS, MTS: Fig. 2) 0.060–0.115 (601: 0.090 ± 0.0070) and 0.035–0.060 (757: 0.064 ± 0.0067); legs, respectively, with STS latero-teraterme and inner MTS. Prothorax width (PW) 0.270–0.370 (769: 0.315 ± 0.0147). Tergal setae: 1, 11–23 (769: 17.2 ± 1.64); 11–17 (769: 23.8 ± 1.97); IV, 19–33 (770: 26.1 ± 3.34); V, 17–31 (769: 23.7 ± 2.32); VI, 15–30 (773: 22.4 ± 2.33). Tergal and pleural setae on VII, 26–43 (772: 33.9 ± 2.57). Longest setae of medial 10 on tergite VI, 0.070–0.115 (772: 0.094 ± 0.0069); on tergite VII, 0.075–0.125 (770: 0.099 ± 0.0076), with 0.7 (770: 0.67 ± 1.31) of these longer than 0.100. Longest of medial pair of setae on tergite VIII, 0.045–0.100 (772: 0.070 ± 0.0091). Last tergite with 3 lateral setae (LS: 5–7) close together on each side; outer seta generally shorter, 0.040–0.085 (640).
Aegyptodacus guadalupensis, n. sp. (Fig. 11)

Type-host: Thomomyia botorri guadalupensis Goldman.

Female.—As for G. subcaudalis, except as follows. Temporal width 0.395–0.450 (0.415 ± 0.0126). Prothorax width 0.290–0.330 (0.302 ± 0.0111). Tergal setae: II, 14–18 (31: 16 ± 1.222); III, 19–25 (31: 22.3 ± 1.636); IV, 21–29 (31: 24.3 ± 1.599); V, 18–26 (30: 22.4 ± 0.025); and raptoral and pleural setae on VII, 31–43 (31: 36.1 ± 0.024). Longest seta of medial 10 on tergite VI, 0.075–0.100 (0.090 ± 0.0006). on tergite VIII, 0.085–0.105 (30: 0.095 ± 0.0037). Longest seta of medial pair on tergite VIII, 0.060–0.090 (29: 0.076 ± 0.0083). Sternal setae: III, 12–18 (31: 15.2 ± 1.492); IV, 12–18 (31: 14.5 ± 1.236); V, 8–18 (31: 11.5 ± 1.297). Subgenital plate with 15–22 (31: 19.2 ± 1.853) setae. Genital sac as in Fig. 11, length 0.170–0.230 (31: 0.198 ± 0.0167), with 4–11 (31: 7.8 ± 1.68) loops, posteriormost loop situated 0.065–0.140 (31: 0.068 ± 0.0176) back from anterior margin.

Male.—As for G. subcaudalis, except as follows. Temporal width 0.395–0.450 (0.376 ± 0.0081); head length 0.270–0.305 (0.291 ± 0.0108); inner marginal tergal seta 0.025–0.030 (0: 0.026 ± 0.0024) long. Antennal scape length 0.166–0.195 (0.183 ± 0.0044); scape width medial 0.095–0.110 (0.103 ± 0.0047), scape distal width 0.115–0.140 (0.128 ± 0.0057). Prothorax width 0.255–0.310 (38: 0.285 ± 0.0115). Tergal setae: II, 10–16 (38: 13.1 ± 1.35); III, 14–24 (38: 19.3 ± 1.72); IV, 18–25 (37: 21.7 ± 1.73); V, 15–23 (38: 19.8 ± 1.95); VI, 12–17 (38: 14.6 ± 1.37); tergal and pleural setae on VII, 18–24 (37: 21.4 ± 1.106); Sternal setae: II, 11–17 (38: 13.8 ± 1.30); IV, 12–17 (38: 14.3 ± 1.23); V, 9–15 (38: 10.6 ± 1.45); VI, 7–12 (36: 9.7 ± 1.21); VII, 3–10 (38: 8.0 ± 1.00); VIII, 5–7 (37: 6.1 ± 0.33). Total length 1.095–1.335 (36: 1.234 ± 0.0513). Genitalia essentially as in Fig. 7; parameral arch width 0.140–0.170 (37: 0.151 ± 0.0088); endophalome width 0.085–0.090 (37: 0.075 ± 0.0037), length 0.065–0.080 (36: 0.075 ± 0.0038).

Remarks.—The principal feature for separating G. guadalupensis from G. subcaudalis involved the configuration of the lines to the being present in the former having fewer significantly of these lines and with not extending so deeply into the sac. Quantitatively, this was best represented by the statistical value for discriminant variable and probability of misidentification for the distance of the posteriormost loop from the anterior sac margin being 0.120 (0.044) and the number of loops in the genital sac being 10 (0.073). While the males of these species do not show any good qualitative separations, the best quantitative features with their critical values and probabilities of misidentification were the scape distal width 0.135 (0.207), the scape length 0.159 (0.090), and the head width 0.386 (0.032). The long submarginal setae possessed by both sexes of G. guadalupensis afforded good means of separating this species from G. quadriplagiatus found on Oryctes ornatus.


Acknowledgment

We would like to thank the following for allowing us to brush lice from pocket gopher skins or for otherwise assisting in this paper: Dr. E. Lendell Cockrum, University of Arizona; Dr. Robert E. Elbel, University of Utah; Dr. R. C. Emerson, U.S. National Museum of Natural History; Dr. Robert S. Hoffmann, University of Kansas; Dr. Robert T. Orr, California Academy of Sciences; Dr. R. S. Paton, University of California, Berkeley; Dr. Amadeo R. Rea, San Diego Natural History Museum; Dr. David J. Schmidt, Texas A&M University; and Dr. Fred S. Truax, Los Angeles County Museum of Natural History. We also thank the staff of the University of Minnesota University Computer Center for the use of its facilities and Dr. Frank B. Martin, Director of the University of Minnesota Statistical Center, for his advice throughout our study.

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