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Some Possible Effects of the Pleistocene on the Distributions of North American Scarabaeidae (Coleoptera)

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Abstract

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Factors, i.e., time, climate, and isolation, that have or may possibly have influenced the distribution and speciation of Scarabaeidae in North America are discussed. Specific examples of present distributional patterns in the genera *Phyllophaga, Serica, Diplotaxis, Onthophagus, Geotrupes* and *Trox* are mapped and described. A general comparison of the distributional patterns is made, and inferences are drawn concerning centers of dispersal and (or) areas of survival of the insect inhabitants of deserts and temperate forests during the various climatic changes of the Pleistocene.

Introduction

The interpretation of present distributional patterns of North American insects as indicators of past events is an involved and complicated subject. With the almost complete void in the fossil record of many insect groups, interpretation must depend on other evidence, often tenuous or incomplete, such as past climatic conditions, phylogeny based largely on morphology, isolating mechanisms, rates of dispersal, and other factors affecting speciation as we now see it.

In my present discussion, I will briefly mention some of the theories that may be useful in an interpretation of the distributional patterns, and then present selected examples of various types of distributions of North American Scarabaeidae.

The Time Factor

The further we retreat into the past histories of insect distributions the more tenuous our information becomes, particularly when we attempt to deduce the origin of insect faunas. Darlington (1957) has presented an exhaustive

Period	Epoch	Beginning of Epoch (in million year intervals)
Quaternary	Pleistocene	– 1 to 1½
Tertiary	Pliocene	– 13
	Miocene	– 25
	Oligocene	– 36
	Eocene	– 58
	Paleocene	– 63
CENOZOIC ERA		

Fig. 1. Time scale of the Cenozoic era.

analysis of the various invasions of the North American continent by vertebrates. The North American insect fauna seems to be derived from a series of similar invasions from the Old World, but this can only be documented to some extent by limited fossil evidence and by the presence of families, tribes, genera and species related to Old World groups. However, it is not the purpose of the present paper to discuss the possible Old World origin of the North American insect fauna. In general, at least in the Scarabaeidae, the North American elements were well established by Miocene times and most of our present genera or their *anlagen* were represented. The present day distributions of the North American species, and to a lesser extent, genera, were greatly influenced by the drastic climatic changes of the Pleistocene. The time scale for the Cenozoic era is presented in Fig. 1, but the events dealt with here occurred mainly during the Pleistocene epoch. I have presented arguments supporting my belief in the antiquity of some genera of Scarabaeidae in a previous paper (Howden 1963) in which I discussed the distributions of a number of flightless genera, their probable antiquity, and low dispersal powers. The distributional patterns of other scarabaeid genera (not flightless) coincide in many ways with those of the flightless groups, and seem to support my previous speculations, but in genera capable of flight, the speciation picture appears to be more strongly influenced by the events of the Pleistocene.

Climatic Effects

By the end of the Miocene, most of the major floral formations (i.e., deciduous and coniferous forests, deserts, and prairies) and their related faunas were present. The climate apparently was warmer than it is today, and this in all likelihood permitted many species, particularly subtropical forms, to have extensive ranges. As Darlington (1959) has pointed out, a large continental land mass having a fairly stable, mild climate, with sufficient moisture, can support a greater diversity of species than can areas with more variable climates or smaller habitable areas. I will discuss this more fully subsequently.

The events of the Pleistocene radically changed this, altering many of the more southern habitats by reducing, during glacial periods, the habitable portion of North America by approximately one-third. This climatic upheaval occurred not once but four times, with four great "ice ages," the Nebraskan, Kansan, Illinoian, and Wisconsin. Figure 2 shows the maximum extent of the last (Wisconsin) glaciation (after Dillon 1956). During the glacial periods the climate of the southern United States and Mexico was undoubtedly cooler and wetter (Dillon 1956). Sea levels were lowered, enlarging many coastal areas.

Fig. 2. Maximum extent of Pleistocene glaciation (after Dillon 1956).

Tree lines were depressed on mountain tops as far south as Mexico City (Flint 1957, p. 313), and temperate forest invaded many of the grassland areas of the semiarid Southwest. The effect in general was to compress the life zones southwards (Dillon 1956). The desert areas, although reduced in size, still existed, apparently serving as a barrier to the migration of many insects into possible refugia in Mexico (Howden 1963). During interglacial periods the reverse trend occurred, with invasion of northern areas and expansion of ranges. Some of the interglacial periods were milder and drier than the present, and probably many species (particularly xeric ones) had more extensive ranges than their counterparts today. There can be little doubt that the present assemblage of species arose because of distributional modifications caused by these changes, and, even today, minor trends toward cooler and wetter, or warmer and drier, cycles affect the distribution of some insect species.

Speciation

A number of the factors mentioned in this section are not directly applicable to the main theme of the present paper, but since they are the basis of many of our theories on speciation, I believe that their inclusion here is pertinent.

Many of the larger scarabaeid genera in North America have groups of closely related species or species apparently derived from a common ancestor. The majority of the species and some of the genera have almost certainly arisen within the confines of the North American continent. The question is when and how they arose, and this may be answered, at least in part, by an analysis of the present distributional patterns. It is generally agreed that some form of isolation (not necessarily geographical) is needed for differentiation of species. This may be by (1) colonization of a new habitat, isolated by distances or other factors, or (2) fragmentation of the widely dispersed population by intrusion of a physical or biotic barrier, a condition which may be temporary (e.g., warm-dry and cold-wet periods of the Pleistocene). Brown (1958) discusses some aspects of this in detail. A third possibility (an unlikely one, at least in Scarabaeidae) has been discussed by McAtee (1954) and others who postulate that population units may gradually evolve into separate species without intrusion of barriers, each population reacting differently to changes of the same environment.

Isolation is only one factor in the evolution (and possible subsequent fragmentation) of a species. Darlington (1959) hypothesized that in the tropics the diversity of species is probably affected by the large size of the land mass (particularly the Old World Tropics) and stability of a highly favorable climate. The population of any one species in the tropics tends to be small and scattered with only occasional interbreeding between different colonies. These factors would produce the opportunity for a maximum recombination-variability, one of the major necessities for possible future speciation. In temperate areas the conditions are less favorable (Fischer 1960) with large populations that tend to interbreed freely giving a relatively homogeneous gene pool, and consequently less variability. In Scarabaeidae, many North American species apparently have relatively low dispersal rates or are quite sedentary, for variation between colonies is evident in many widespread species. A good example of this is found in the genus *Eucanthus* (Howden 1964). It is this sedentary tendency, indicated by variation in local populations (in some ways similar to the conditions noted by Darlington, 1959, for tropical species), that has been one of the factors in the production of closely related species in the Scarabaeidae of Temperate North America.

Theories concerning the factors producing or affecting phenotypic variation are numerous and often difficult to apply. Some of these I have mentioned: size and stability of area, size of population, dispersal powers, and isolation. Others such as selection pressure or the effect of the number of generations per year are more tenuous and difficult to prove (Grant 1963, Chap. 18).

The genotypic effect within one species of a varying number of generations per year and how this affects variation is controversial and is usually dismissed as having little importance. However, since I believe that it may influence the development of variation in some Scarabaeidae, mention of it should be made.

In a hypothetical case, females of one species produce an average of 50 eggs per individual. The species averages one new mutation per 10,000 zygotes. In the northern portion of its range there is one generation per year and phenotypically the northern populations show little variation. In the southern portion of its range there are three generations per year and phenotypic variation is pronounced. Is the threefold increase in eggs produced per year (with the implied threefold possibility of mutations and recombinations) a factor affecting the increase in variation in the southern populations? I believe it can be.

Some species of *Phyllophaga* in Canada have only one generation every third (or possibly fourth) year, whereas in the Southeastern United States only two years are needed for development of the same species (Ritcher 1958). Here different developmental rates are apparently due largely to a temperature factor. *P. anxia* (LeC.) is one of these species, and variation in size and form of genitalia is most evident in southern populations. Some species of *Onthophagus* have successive generations every two months, as long as conditions (moisture and temperature) are favorable. *O. hopfneri* Har. (Fig. 17) ranges from Arizona to southern Mexico. In Arizona (with a 2-month rainy season) there is one generation per year, while in Veracruz (with a 6–8-month rainy season) there are two or more generations. Variations in color pattern, size, setal length and placement of punctures are most evident in specimens from Veracruz.

In the case of the *Phyllophaga*, temperature apparently is the major factor affecting the developmental rate while moisture is the main factor in the case of *O. hopfneri*. In both, variation is most evident in the area where development is most rapid (more generations per unit time) and, while this may not be the major factor, it should not be ignored just because it seems to be improbable and difficult to prove.

Taxonomy and Habits

The accuracy of interpretation of distributional patterns is, necessarily, based on our knowledge of the species under consideration. If our taxonomy is confused, our interpretations will also be confused. Hagmeier and Stults (1964) have seemingly done a thorough job of analyzing distributional patterns of the mammals of Canada and the United States, but when they tried to analyze the subspecies of the same mammals using the same methods, they admitted the results were inconclusive. This, in turn, seems to indicate that there is need for re-evaluation of mammalian taxonomy on the subspecific level. While admittedly our taxonomic knowledge of many of the insects is far behind the knowledge of vertebrates, some groups are becoming well-enough known so that important contributions to zoogeography are possible. The numerous contributions on insect distributions presented in the Proceedings of the Tenth International Congress of Entomology (1958, *Edited by* E. C. Becker) and those discussed by Munroe (1965) are an indication of this trend.

Often important in conjunction with taxonomy is a knowledge of the habits of the species. Many groups of insects have been reviewed taxonomically, yet virtually nothing is known of their life histories. Often, when biological data are lacking, it is nearly impossible to discuss intelligently the speciation and the possible isolating factors affecting it. Because of this, I have selected for illustration groups of Scarabaeidae that have been recently revised and whose general habits I know.

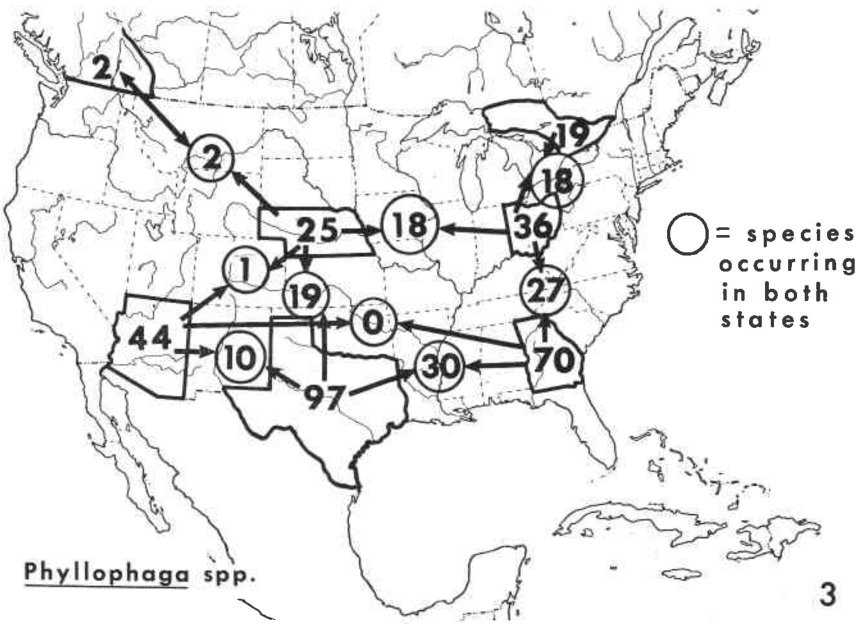
Distributions

North–south zonations in North America of both flora and fauna are well documented. Recently, Simpson (1964) illustrated the increase in the number of species of mammals from north to south and also discussed some of the differences in east–west change of fauna. Hagmeier and Stults (1964) developed this further and, by analysis of the mammalian species, produced a map indicating areas of faunistic change. If similar maps were drawn using certain groups of insects (i.e., Scarabaeidae), there would be many similarities.

In the phytophagous genus *Phyllophaga* (Fig. 3) there is an obvious decline in numbers of species from Georgia to southern Ontario and from Texas or Arizona to Nebraska. The number of species common to two states is placed in a circle, and serves to indicate the amount of relationship between the states selected. The Arizonian species are most distinct and if some areas of western Texas were included with Arizona and New Mexico, the eastern and western faunas would show almost no overlap. While the Mexican species are so poorly known that they cannot be included at present, it can safely be said that many of the Arizonian species, at least in the southern part of the State, represent the northern limits of Mexican species. On the basis of our present knowledge, we can state that the majority of North American species of *Phyllophaga* are seemingly derived from two Pleistocene refugia, one in the southeastern United States and one in Mexico.

The genus *Serica*, with habits that roughly parallel those of *Phyllophaga*, shows some distinct difference in distribution probably because the genus has a greater host selectivity. *Serica* adults usually feed on the leaves of broad-leaved, deciduous trees, species of oaks (*Quercus*) being the major group of hosts. Figure 4 illustrates the distribution of the species by states or provinces. The most striking feature is the absence of the genus in Mexico (although there are supposedly four species occurring in Central and South America), even though suitable habitats and hosts are numerous. In addition there is almost no overlap between the eastern and western species, the 100th meridian representing roughly the eastern and western divisions. To explain this type of pattern, the following assumptions may be made: (1) Speciation in North American *Serica* (the genus occurs also in the Oriental and African regions) took place mainly after the development of the southwestern desert regions, which fragmented forest habitats as early as the Miocene. (2) During pluvial periods in the Pleistocene there was some rejoining of forested areas, but the oak forests of Mexico did not merge with forested areas to the north; seemingly the desert area continued to act as a barrier to the southward dispersal of *Serica*. (3) The presence of 43 species of *Serica* (34 endemic) in California probably indicates both fragmentation and fusion of different forested areas within the state during the Pleistocene and also indicates the presence of refugia in southern California and Baja California. (4) Eastern species survived the glaciations in refugia in the southeastern United States, but because of greater uniformity of habitats, did not speciate to the degree evident in California. However, isolation of habitats, particularly on the coastal plain, did occur (Hubbell 1961; Howden 1963) and undoubtedly contributed to the formation of the endemic elements found in some numbers in Georgia, Florida, and Alabama. Figures 5–8 illustrate some of the typical distributional patterns of widespread eastern North American *Serica*, while Figs. 9 and 10 illustrate typically western patterns. Records are lacking for a few of the states within the range of some of the species. This, almost certainly, indicates poor collecting and illustrates why it is so often difficult to plot accurate distributional patterns of insects.

A third phytophagous genus, *Diplotaxis*, occurs only in the New World, the lack of Old World relatives being perhaps indicative of a longer isolation than in the case of *Serica*. As seen in Fig. 11, the genus is centered in Mexico. Numbers in parentheses show the number of endemic species within a country or area. Although some species of *Diplotaxis* have feeding habits similar to those of *Serica*, many others feed on conifers, desert shrubs, or herbaceous vegetation. Arid areas support large numbers of species, and since 56 species are common to the United States and Mexico, the desert areas have not served as a barrier to the spread of the genus. The large number of endemic species in Mexico and the United States seems to indicate a long history of development in both countries. Survival during the various glaciations probably occurred in a number of forest and desert areas. Figure 12 illustrates the relatively restricted distributions of two species (*tarsalis* Schf. and *hirsuta* Vaurie). These are common patterns for southwestern United States and Mexican species. The ranges of *D. tristis* Kby.



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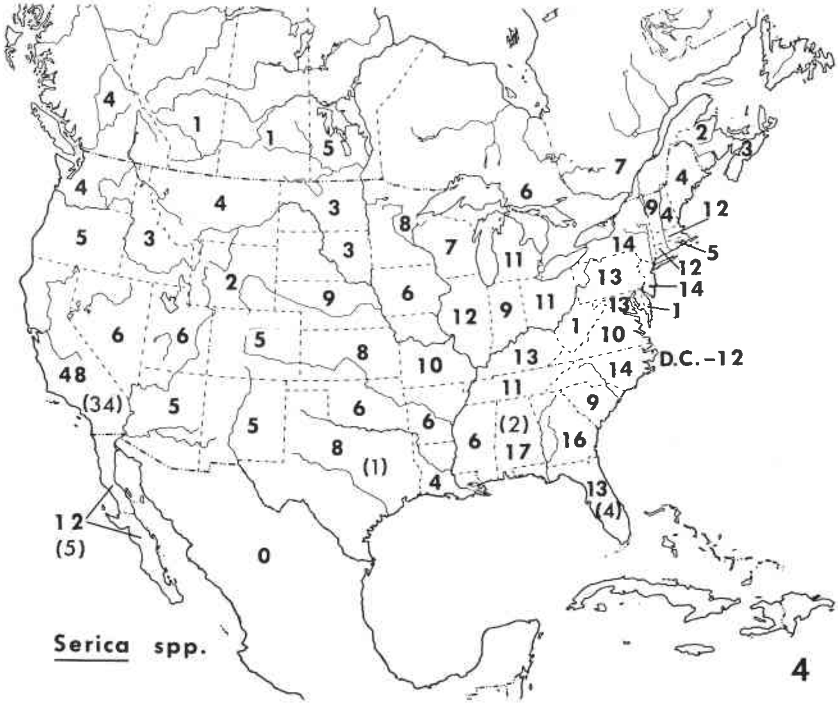

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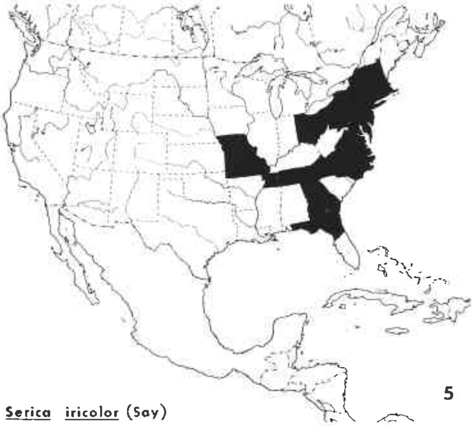
Fig. 3. Number of species of *Phyllophaga* occurring in Georgia, Texas, Arizona, Nebraska, Ohio, southern Ontario, and British Columbia.

Fig. 4. Number of species of *Serica* in a state or province. Numbers in parentheses indicate endemics.


Serica iricolor (Say)

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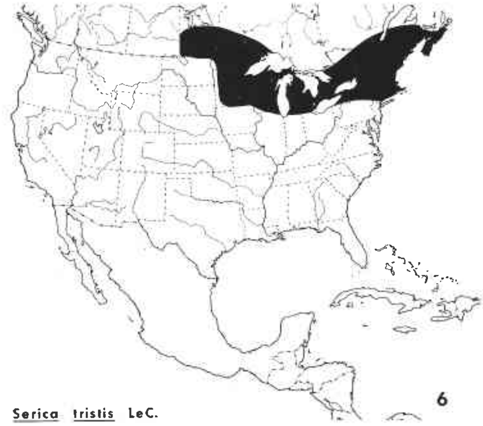
Serica tristis LeC.

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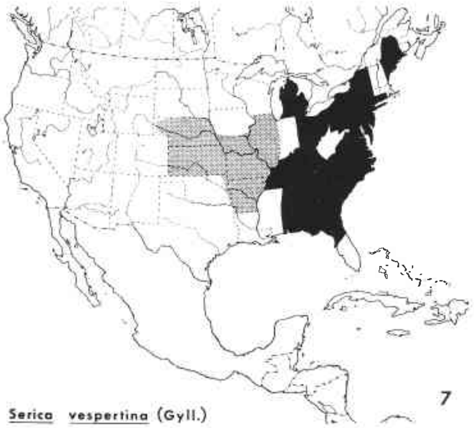
Serica vespertina (Gyll.)

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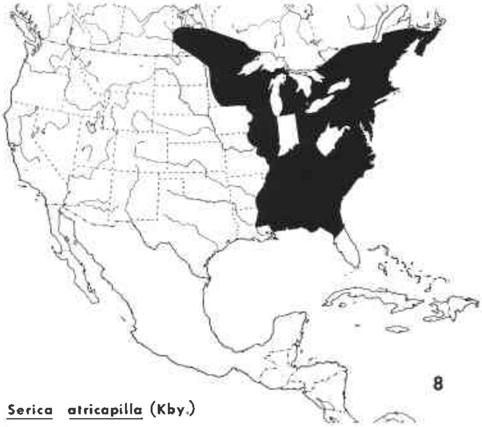
Serica atricapilla (Kby.)

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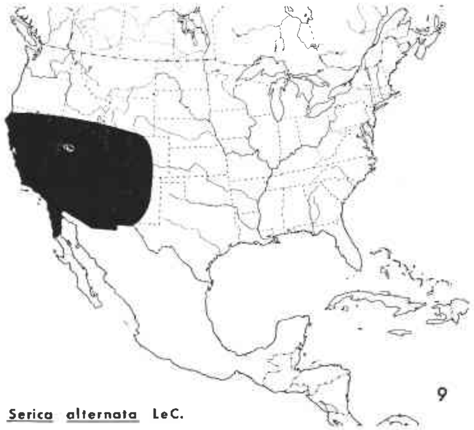
Serica alternata LeC.

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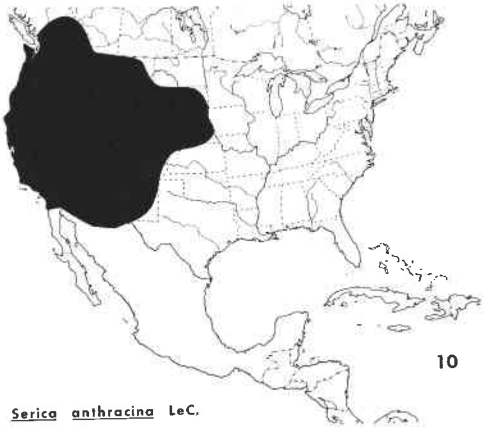

Serica anthracina LeC.

10

Fig. 5. Approximate distribution, by state, of *Serica iricolor* (Say).

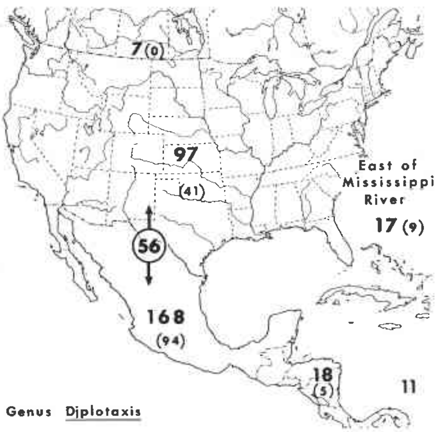
Fig. 6. Distribution of *Serica tristes* LeC.

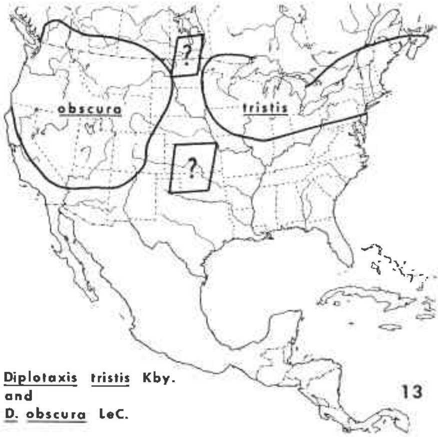
Fig. 7. Approximate distribution, by state, of *Serica vespertina* (Gyll.). Stippled area represents distribution of the subspecies *accola* Dawson.

Fig. 8. Approximate distribution, by state, of *Serica atricapilla* (Kby.).

Fig. 9. Distribution of *Serica alternata* LeC. This species occurs largely in forested localities.

Fig. 10. Distribution of *Serica anthracina* LeC. This species occurs largely in forested localities.





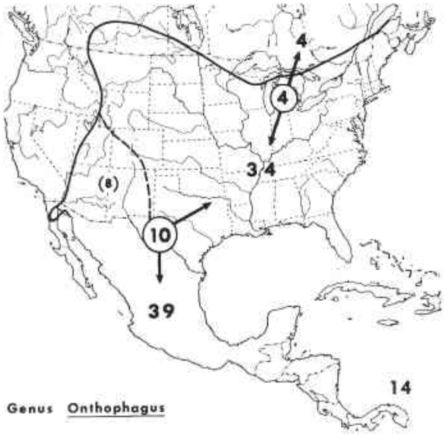


Fig. 11. Number of species of *Diplotaxis* in Central America, Mexico, the United States, and Canada. Numbers in parentheses indicate endemics. Circled numbers represent species common to two areas.

Fig. 12. Distribution of two species of *Diplotaxis*.

Fig. 13. Distribution of two closely allied species of *Diplotaxis*.

Fig. 14. Number of species of *Onthophagus* occurring in Mexico, the United States, and Canada. Circled numbers represent species occurring in two countries. The number in parentheses indicates endemics found west of the dotted line.

Fig. 15. Distribution of two species of *Onthophagus*.

Fig. 16. Distribution of two species of *Onthophagus*.

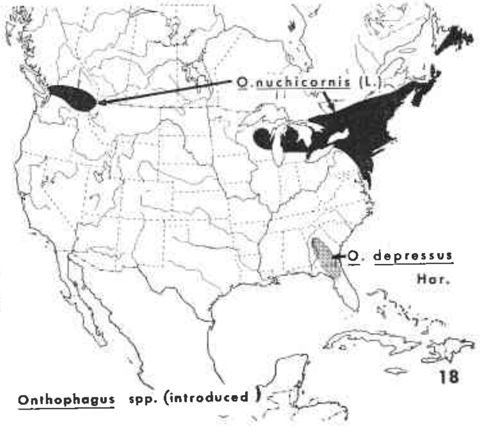


Fig. 17. Distribution of two species of *Onthophagus.*

Fig. 18. Distribution of Old World species of *Onthophagus* established in North America.

and *D. obscura* LeC. (Fig. 13) overlap in the areas indicated by "?". These two so-called species are very closely related; they are distinguishable mainly by slight differences in pronotal shape and by the length of the setae along the elytral margins. In Manitoba there appears to be secondary intergradation of characters. Further collecting may indicate that only one species, with an east–west cline in certain characters, is represented. In this and in many other cases, plotting the range of closely allied species is extremely useful as an adjunct to interpreting difficult taxonomic complexes.

The genus *Onthophagus* is nearly world-wide. In North America (Fig. 14) the species are largely dung feeders, particularly in the larval stages. Some are rather indiscriminate feeders whereas others are selective. Examples of the latter are *O. browni* H. & C. and *O. brevifrons* Horn, which live only in pack rat (*Neotoma*) nests. The species of the United States and Mexico are very distinctive, with only 10 species occurring in both countries; the distributions of seven of these are illustrated in Figs. 15–17. All 10 species common to both countries are of Mexican origin and, in the United States, all are restricted to the arid southwest. The result is that there are two distinct assemblages of species apparently developed from separate centers, one in the southeastern United States and one in Mexico. Occasional atypical patterns are produced by introduced species. Figure 18 illustrates eastern and western introductions of *O. nuchicornis* L. (from Europe) and *O. depressus* Har. (from Africa).

The distribution of the genus *Geotrupes* (Fig. 19) illustrates clearly the separation between the fauna of the southeastern forest habitat and that of the temperate forested areas of Mexico. The genus is holarctic, has its ancestral stock reported (although the relationship is vague) as a fossil in the lower Cretaceous deposits of China (Crowson 1955, p. 42), and today the antiquity of the group is indicated by a number of small, relict populations. The Mexican species are very distinctly separated morphologically from the United States species, and in a number of cases they show closer relationship to Asian or European species (Howden 1964) than to those in the southeastern United States. The distributional patterns coupled with the morphological differences clearly indicate a long separation and support the hypothesis that the desert barrier was well established before the Pleistocene and remained, at least to a great degree, as a barrier during that time.

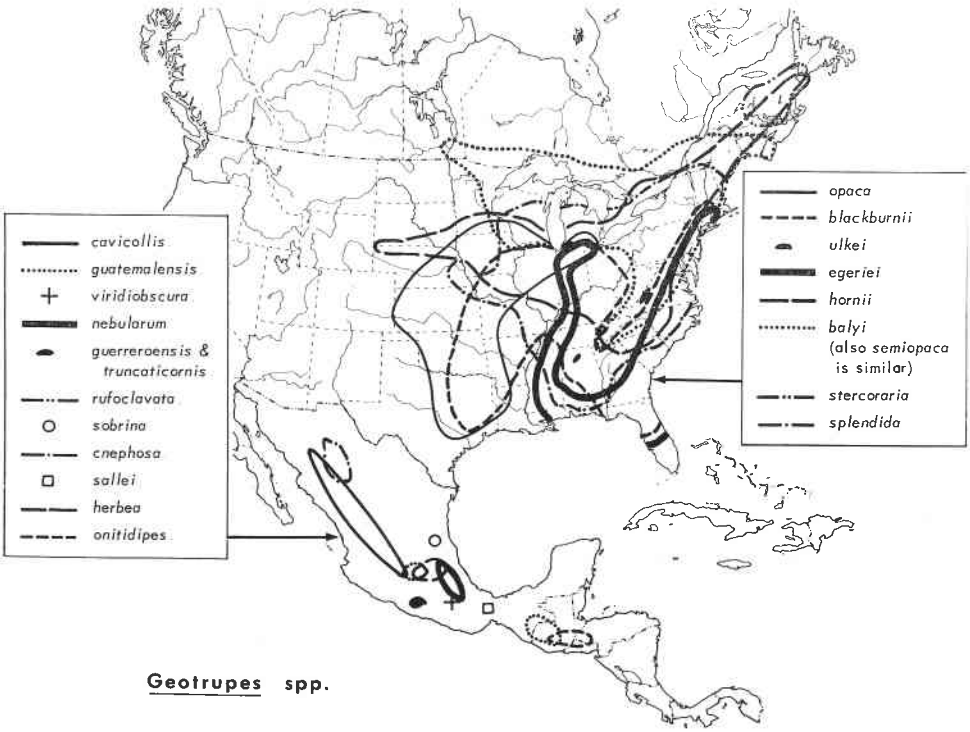
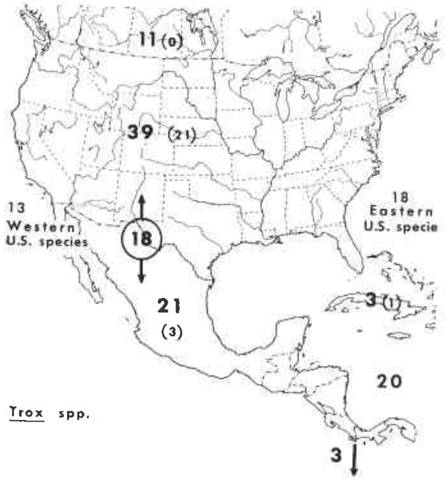


Fig. 19. Distribution of New World species of *Geotrupes.*

The genus *Trox* (Fig. 20) was selected because of the rather peculiar and widespread range of some of its species. The genus is nearly world-wide in distribution, but with a distinct assemblage of species in North America (Vaurie 1955). Twenty-one species are endemic to the United States, with only three endemic to Mexico. Members of the genus feed largely on fur, skin, or feathers. Some species are general carrion feeders, with distributions similar to those of some general dung feeders, whereas others are closely associated with certain species of birds. *Trox tytus* Rob. (Fig. 21) for example has been recorded from a number of widely scattered localities that do not fall into any usual pattern. However, the species has been associated only with barn owl nests and when the breeding range of the barn owl is delimited, the scattered distribution of *T. tytus* does not seem so odd. Figure 22 depicts the ranges of three subspecies of *T. spinulosus* Rob. (after Vaurie 1955). The isolation of the subspecies *simi* Rob. may indicate lack of collecting, or if actual, *simi* perhaps should be treated as a distinct species. Figures 23–25 are examples of the types of distributions of the more generalized carrion feeding *Trox.* Since many species occur in arid areas, and others are associated with mammals or birds, any interpretation of distributional patterns should be done only after the habits of most of the species are well known.

Conclusions

The scarabaeid fauna of North America was well developed before the Pleistocene. Except for a few species in *Aphodius* and *Aegialia,* all of the North American scarabaeids survived the glaciations of the Pleistocene in refugia (or areas) in the southern United States or in Mexico. Our present genera or species groups associated with the coniferous and deciduous forest formations have



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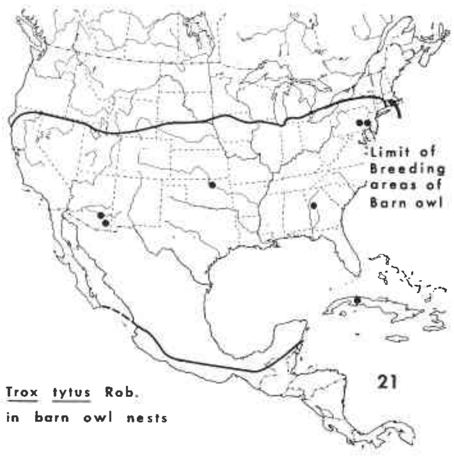
Trox spp.



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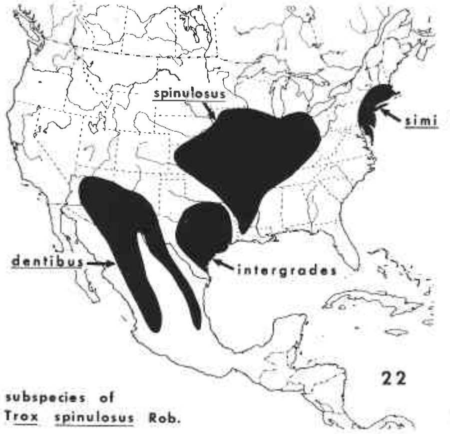
Trox tytus Rob. in barn owl nests



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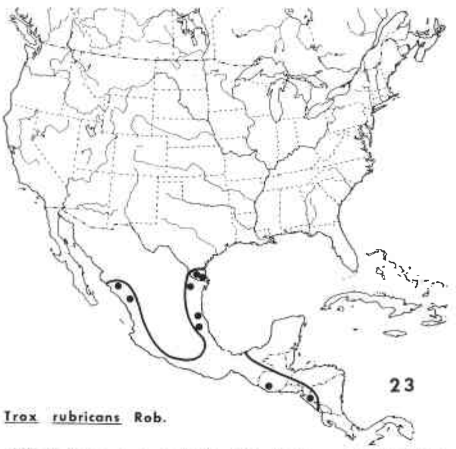
subspecies of *Trox spinulosus* Rob.



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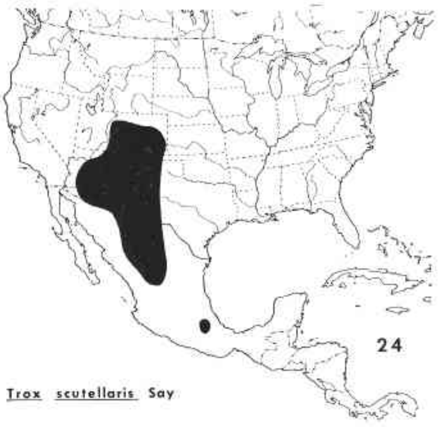
Trox rubricans Rob.



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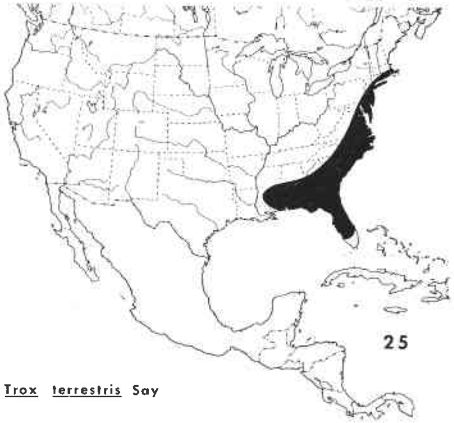
Trox scutellaris Say



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Trox terrestris Say

Fig. 20. Number of species of *Trox* in Central America, Cuba, Mexico, the United States, and Canada. Numbers in parentheses indicate endemics. Circled numbers represent species occurring in two countries.

Figs. 21–25. Distribution of *Trox* spp.: 21, *tytus* Rob.; 22, *spinulosus* Rob.; 23, *rubricans* Rob.; 24, *scutellaris* Say; 25, *terrestris* Say.

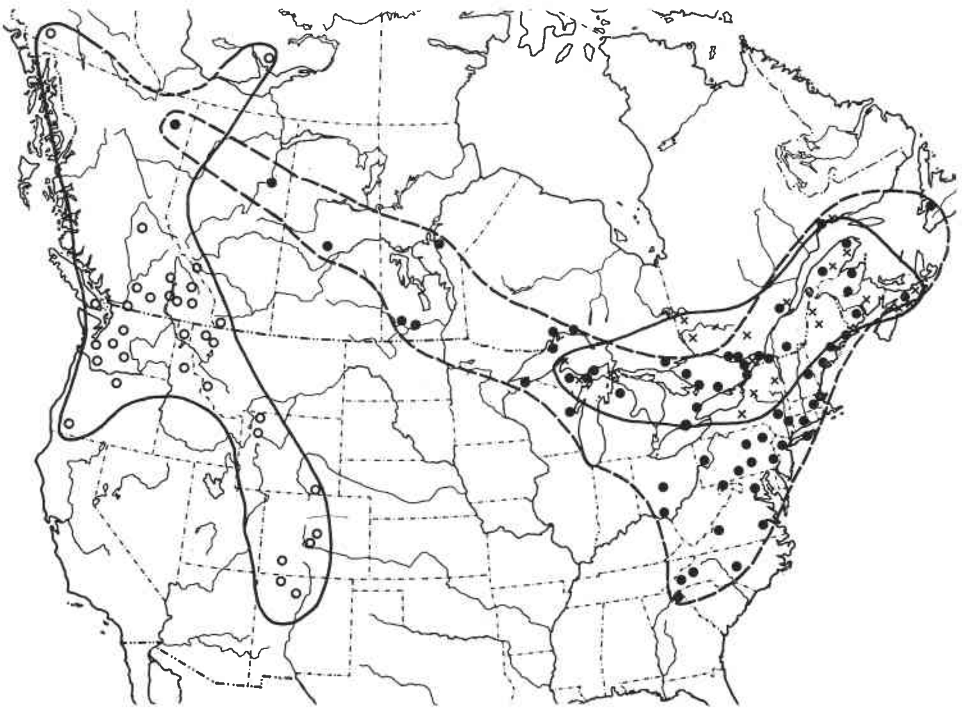

Fig. 26. Distribution of *Anoplodera mutabilis* (Newman) [●], *A. aspera* (LeConte) [○], and *A. brevifrons* Howden [×].

speciated in and dispersed from three major regions, one in the southeastern United States, a second centered in southern and central California, and a third that includes most of the high mountain regions of Mexico. The fauna of these three regions is quite distinct. Desert barriers probably separated these areas even in Miocene times, and there is considerable evidence to indicate that the deserts remained a barrier to insect migrations along the Mexican – United States border during the pluvial periods of the Pleistocene. The fluctuations of moisture and temperature and the corresponding expansion or contraction (combination and isolation) of habitats undoubtedly played a major role in the formation of many of today's groups of related species. The distributional patterns of genera with large groups of species adapted to arid environments differ greatly from those of the forest-inhabiting groups, and different factors seemingly affected their dispersal. These factors can often be understood only after a careful study of the habits of the species under consideration. The complexity and diversity shown by the desert-inhabiting scarabaeids indicate a long evolutionary history and support the supposition that the North American deserts of the southwestern United States and Mexico, although probably reduced in size, still represented sizable habits, even during the maximum periods of glaciation. If they had been reduced to small "islands" of desert, it is doubtful that they could have supported enough species to give rise to the complex fauna existing today.

In utilizing the distributional pictures of insects in any zoogeographical studies, the examples used must be carefully selected. None of the genera and few of the species mentioned here show any of the common types of northern distributions, one of which is illustrated in Fig. 26. This figure depicts the distributions of three closely related species of Cerambycidae, and shows a fairly typical trans-Canadian type as well as a northwestern mountain form. Other good examples of northern distributions are discussed by Ball (1963). Because of the great diversity of habits and methods of dispersal, general statements on "regions" or "life zones" of insects in North America usually have little meaning, except in northern regions. Van Dyke (1939) divided North America into a series of "zones" using the distribution of Coleoptera as his criterion. I am not sure what groups he utilized as the criteria for his zones, but if the Scarabaeidae were used as a basis for such a map, the zones would differ greatly. Hagmeier and Stults (1964) compiled a similar map based on mammal distributions. The differences seen between this map and Van Dyke's are no greater than if two different families of Coleoptera with different habits and dispersal powers had been chosen. If one compares Van Dyke's "Neotropical Zone" in Mexico with Halffter's work (1964) on the "biotic provinces" of Mexico and with some of the scarabaeid distributions depicted in this paper, it becomes evident that the only concordance in distributions is of a very general nature. Until our knowledge of the insect fauna is further advanced than it is today, distributional studies, based on specialized groups that are relatively well known, seem to be one of the more fruitful methods of contributing to our knowledge of insect zoogeography.

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