MISCELLANEOUS PUBLICATIONS
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 126

The Arid-Land Katydids of the North American Genus *Neobarrettia* (Orthoptera: Tettigoniidae): Their Systematics and a Reconstruction of their History

BY
THEODORE J. COHN
San Diego State College

ANN ARBOR
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN
FEBRUARY 10, 1965

MISCELLANEOUS PUBLICATIONS
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN

The publications of the Museum of Zoology, University of Michigan, consist of two series—the Occasional Papers and the Miscellaneous Publications. Both series were founded by Dr. Bryant Walker, Mr. Bradshaw H. Swales, and Dr. W. W. Newcomb.

The Occasional Papers, publication of which was begun in 1913, serve as a medium for original studies based principally upon the collections in the Museum. They are issued separately. When a sufficient number of pages has been printed to make a volume, a title page, table of contents, and an index are supplied to libraries and individuals on the mailing list for the series.

The Miscellaneous Publications, which include papers on field and museum techniques, monographic studies, and other contributions not within the scope of the Occasional Papers, are published separately. It is not intended that they be grouped into volumes. Each number has a title page and, when necessary, a table of contents.

A complete list of publications on Birds, Fishes, Insects, Mammals, Mollusks, and Reptiles and Amphibians is available. Address inquiries to the Director, Museum of Zoology, Ann Arbor, Michigan.

List of Miscellaneous Publications on Insects

No. 1.	Directions for collecting and preserving specimens of dragonflies for museum purposes. By E. B. Williamson. (1916) 15 pp., 3 figs.	$0.25
No. 2.	An annotated list of the Odonata of Indiana. By E. B. Williamson. (1917) 12 pp., 1 map	$0.25
No. 9.	Notes on American species of *Triacanthagyna* and *Gynacantha*. By E. B. Williamson. (1923) 67 pp., 7 pls.	$0.75
No. 11.	Notes on the genus *Erythemis* with a description of a new species (Odonata). By E. B. Williamson. The phylogeny and the distribution of the genus *Erythemis* (Odonata). By Clarence H. Kennedy. (1923) 21 pp., 1 pl.	out of print
No. 14.	The genus *Perilestes* (Odonata). By E. B. Williamson and J. H. Williamson. (1924) 36 pp., 1 pl.	$1.00
No. 21.	A revision of the libelluline genus *Perithemis* (Odonata). By F. Ris. (1930) 50 pp., 9 pls.	$0.75
No. 22.	The genus *Oligoclada* (Odonata). By Donald Borror. (1931) 42 pp., 7 pls.	$0.50
No. 23.	A revision of the Puer Group of the North American genus *Melanoplus*, with remarks on the taxonomic value of the concealed male genitalia in the Cyrtacanthacrinae (Orthoptera, Acrididae). By Theodore H. Hubbell. (1932) 64 pp., 3 pls., 1 fig., 1 map	$0.75
No. 36.	A review of the dragonflies of the genera *Neurocordulia* and *Platycordulia*. By Francis Byers. (1937) 36 pp., 8 pls., 4 maps	$0.50
No. 53.	The crane flies (Tipulidae) of the George Reserve, Michigan. By J. Speed Rogers. (1942) 128 pp., 8 pls., 1 map	$1.25
No. 54.	The ecology of the Orthoptera and Dermaptera of the George Reserve, Michigan. By Irving J. Cantrall. (1943) 182 pp., 10 pls. 2 maps	$1.50
No. 62.	Monograph of the family Mordellidae (Coleoptera) of North America, north of Mexico. By Emil Liljeblad. (1945) 229 pp., 7 pls.	$2.00

(Continued on back cover)

MISCELLANEOUS PUBLICATIONS
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 126

The Arid-Land Katydids of the North American Genus *Neobarrettia* (Orthoptera: Tettigoniidae): Their Systematics and a Reconstruction of their History

BY

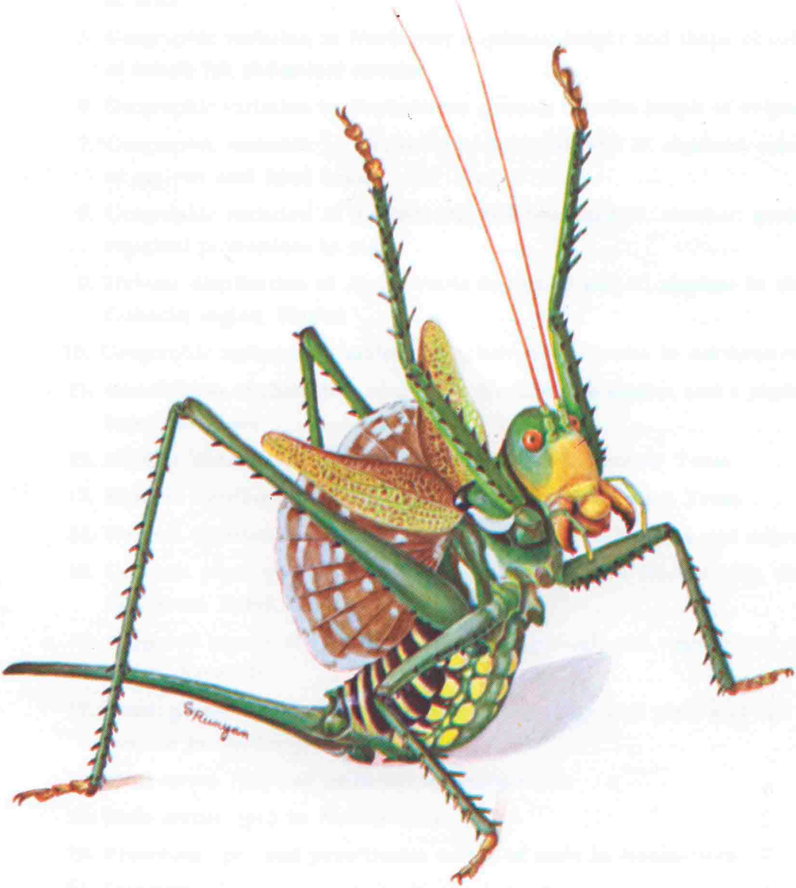
THEODORE J. COHN
San Diego State College

ANN ARBOR
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN
FEBRUARY 10, 1965

CONTENTS

ILLUSTRATIONS

FRONTISPIECE OPPOSITE PAGE 5



FRONTISPIECE

Female *Neobarrettia spinosa* in fighting pose. A watercolor by Suzanne Runyan based on specimens and photographs from the Big Bend region of Texas, eastern Chihuahua and eastern Durango.

THE ARID-LAND KATYDIDS OF THE NORTH AMERICAN GENUS *NEOBARRETTIA* (ORTHOPTERA: TETTIGONIIDAE): THEIR SYSTEMATICS AND A RECONSTRUCTION OF THEIR HISTORY

TO THE biologist who observes or collects over wide areas, a never ending source of fascination is the question of how organisms got to be what and where they are today. Two methods have been used in approaching the problem of the history of organisms which lack a fossil record. The first involves the study of the whole or a large part of the biota, the second, an intensive study of a small group of organisms. While the broad conclusions resulting from the first method are usually not possible with the second, the latter method has the advantage of dealing with a more intimate knowledge of the biology and distribution of the organisms. It thus yields more accurate information on cause and effect factors, and, in many cases, a more detailed knowledge of the nature of past environments.

This is an intensive study of a small group of katydids restricted to dry environments in northern México, Texas, and Oklahoma. The range of this genus of flightless or nearly flightless katydids is fragmented by the great mountain ranges and plateaus of México. It is to the problem of the origin of these disjunctions that this study is primarily directed, in the hope not merely of explaining the pattern of distribution and relationships in this genus, but of advancing our knowledge of the environmental history of the region and thus of the history of less well-known organisms which are found there.

A systematic analysis of the genus forms the basis of the study, for without an understanding of the relationships among the taxonomic units involved, no historical explanation is possible. I have attempted to bring to bear on this subject all possible facts about the biology of the katydids from both field and laboratory studies, and I have attempted to present the morphological characters in such a way as to facilitate independent assessment of my conclusions. Following this, a detailed analysis is made of the habitat tolerance of the species, and conclusions are drawn as to the probable tolerances of the ancestor of the modern species. Finally, the relationships and habitat tolerances are considered against the background of the general physiographic and environmental history of the region, and the evolutionary history of the katydids reconstructed. This analysis is also used to determine environmental conditions in certain areas more specifically than is possible by extrapolation from the as yet fragmentary geologic record in this region. I hope that the conclusions concerning environmental history presented here will stimulate other intensive studies of organisms with similar or complementary distributions and tolerances, studies which will test and confirm or modify these conclusions and thus lead to a rapid increase in our knowledge of the history of the region.

Several situations illustrative of evolutionary processes were discovered in the course of this investigation. One of these probably represents that fleeting stage of evolution when reproductive isolation is in the final phase of being perfected. Another involves striking clinal variation, which, because of its geography, allows for a historical reconstruction of its development. Based on this concrete example, the problem of the taxonomic treatment of subspecific variation has been analyzed from a genetic and historical point of view. Both examples are discussed in detail. The genus also provides an almost complete sequence of species interactions ranging from sympatry to apparent competitive replacement of one species by another. These situations are described although they were not specifically studied in detail in the field.

I consider this study to be entirely systematic since it is devoted to an interpretation and explanation of the relationships between the organisms studied. Because modern systematics has an evolutionary basis, it is in essence a historical science. The fundamental taxonomic unit, the species, is now generally considered to be a particular stage in evolutionary divergence, and classification is generally intended to reflect phylogeny. Owing to the practical necessity of producing descriptions and classifications, most taxonomic studies are only rarely concerned explicitly with history. But since the discrimination of taxonomic units and their classification are based at least implicitly on the consequences of historical processes, the explicit study of the historical factors which make relationships understandable should be within the realm of taxonomy as well as systematics. To some biologists this appears to be circular reasoning. In reality, it is nothing more than a matter of successive approximations in which the conclusions based on biological characteristics (usually only morphological) are tested by historical considerations, and *vice versa*. In most cases, moreover, different kinds of data are involved. Classification is usually based on the evolutionary probabilities of shared characteristics being the result of common descent or of convergent development, whereas historical analysis is most often based on the biological probability of the use of different paths of dispersal. When the two are combined, a complete picture is produced which serves to explain and interpret the patterns of similarities, differences, and distribution, a function which I consider to be the ultimate goal of systematics.

MATERIALS

Over 1900 specimens of *Neobarrettia* (and *Rehnia,* here synonymized) have been examined in the course of this study, and probably many more have been observed in the field. Most of the specimens were collected by myself, principally on two extensive trips made for this specific purpose, but also on several shorter ones in the course of general collection of Orthoptera. In all, more than one whole year has been spent in the field, in the course of which about 50,000 miles have been travelled in Texas and almost all the states of México.

Large series of *Neobarrettia* were studied in the collections of the Academy of Natural Sciences of Philadelphia (ANSP) and of the University of Michigan Museum of Zoology (UMMZ). Smaller amounts of material were borrowed from the following persons or institutions (abbreviations used in the lists of records are indicated in parentheses): E. R. Tinkham, Indio, California (TINK); C. Bolívar y Peltain, México, México (BOL); J. R. Hilliard, Abilene, Texas (HILL); American Museum of Natural History (AMNH); University of Arizona (ARIZ); Sul Ross State College (SRSC); Strecker Museum, Baylor University (SM); and Kansas State University (KSU). The types of all described species have been studied. The records at the end of the taxonomic treatment of each species are arranged geographically from north to south and from east to west. Specimens on which are based locality records not otherwise credited to an institution are in the collections of the University of Michigan Museum of Zoology, in which all of the material collected by myself has been deposited.

METHODS

Some comments are necessary here concerning certain of the concepts and methods employed in this study.

THE NATURE OF SUBSPECIFIC VARIATION AND ITS TAXONOMIC TREATMENT.—The problem of how to treat taxonomically the striking geographic variation seen in *Neobarrettia spinosa* has required a review of the whole problem of the nature of the subspecific category. Over the last ten years, a great many papers have been devoted to a discussion of the usefulness of the subspecies as a taxonomic unit. Almost every author has pointed out the inadequacy of the subspecies as a description of the geographic variation in the examples cited. I believe that these authors have confused the basic problem which is involved. Whatever its past use has been, the term subspecies refers to a taxonomic *unit* and not to a technique for describing variation. The real question is whether or not a unit exists below the level of the species which is predictive of the distribution of characteristics other than those used to delimit the unit. The problem cannot be solved merely by inspecting the patterns of geographic variation. The various combinations of genetic, environmental, and historical factors which are responsible for the patterns of variation must first be analyzed. Then the ways in which such situations can be handled taxonomically may be considered in terms of their biological implications and practical usefulness.

The case of a population which is completely isolated geographically from the rest of the species population requires little discussion. Because of its isolation it will be unaffected by events taking place elsewhere within the range of the species. In time, such a population is almost certain to become differentiated merely through the action of random mutation and slightly different selective pressures. It is thus pursuing a completely independent evolutionary course and qualified for the designation of subspecies (or species) under almost any definition. From a practical standpoint, nomenclatorial designation of these populations will be arbitrary at the lower levels of differentiation, while at the upper levels they may have already achieved specific status (the uncertainty at this upper limit is often indicated by the use of the term "superspecies"). For the very large range of differentiation between the two extremes, nomenclatorial designation is reasonable, predictive, and useful.

The case of widespread species whose populations are not entirely geographically isolated, poses a very different problem. Although any two populations may be slightly different, if only through randon mutation and a finite rate of gene flow, because they are connected geographically and reproductively the pattern of variation will not be as sharply defined as in the case discussed above. Most widespread species display some form of clinal variation, often in many characters. Clinal variation probably demonstrates only that there has been a cline in certain selective forces, or selection at one end of the character cline and reproductive continuity between the several populations involved. The delimitation of segments of a single cline must of necessity be biologically arbitrary. The methods generally used to analyze or present the data in such situations usually obscure the nature of the geographic variation and only rarely indicate the arbitrary nature of the boundaries of the subspecies established on these grounds. When several discordant clines are involved, as is usually the case, the units become even less meaningful.

Clines in character variation often show distinct steps, at which points the rate of change of the character is accelerated. Subspecies boundaries which coincide with these steps might make that category less arbitrary. A step in a character cline might be the result of one of the following three situations: first, a rapid shift in selection forces or in their intensity; second, a restriction of gene flow; or, third, the intergradation of two previously separated populations.

If the step in a cline is related only to a change in selective pressure without restriction of gene flow, then the naming of populations on either side would be merely descriptive of the distribution of the particular character studied, or of the forces which control its expression. Since it is unlikely that most of the variable characters in a species are controlled by the same selective forces, it is equally unlikely that steps in the clines of the different variable characters would occur in the same region. Except in areas of major environmental change, where presumably many selective factors are rapidly changing, clines are generally nonconcordant and the taxonomic units delimited by the steps in one or a few clines will not correspond with those based on the steps in other clines. Since no study of subspecific variation can hope to cover all of the variation inherent in the population, it is obvious that subspecies based on the study of a few stepped clines cannot be used to predict the distribution of other unstudied characters. Such subspecies would hardly be units with the predictable qualities required in taxonomy. It is equally difficult to see how the mathematical analysis of such clines as suggested by Womble (1951) would make the situation biologically more meaningful. Womble's method allows the objective determination of the area of greatest concordance in the steps in several nonconcordant clines, and thus enables one to draw subspecies boundaries with the greatest objectivity. It appears, however, that such a subspecies boundary corresponds to nothing biological and its usefulness is questionable. Furthermore, as the boundary determined by this method becomes biologically more realistic with greater concordance in clinal variation, visual inspection of the raw data will give increasingly accurate and objective determinations of the same boundary.

If the step in a character cline represents a restriction of gene flow, then other character gradients are likely to break in the same region. Character gradients which cross the area without showing any step may be those following an old and stabilized selection gradient established before gene flow was restricted. While this might confuse the situation, it would do so no more than where clines seem to cross the boundary of species with adjoining ranges. A case of this nature is discussed under *Neobarrettia hakippah*. However, it is difficult to envision a genetic mechanism which might produce such a restriction between populations which have been in broad and intimate contact for some period of time. Even under very strong selection, restriction of gene flow does not occur unless the populations are physically separated. In a case presented by Hooper (1941), genetic restriction is not developed even under the influence of strong selection until the populations become almost separated physically. Thus, black coat color is not developed in small rodents living on black lava beds when those beds are in broad physical contact with areas of light-colored rock. Only when the beds are completely or almost completely isolated do the mice living among them develop what must be a highly advantageous dark coat color. It thus appears that steps in clines do not normally represent intrinsic restriction in gene flow. The clines in characters not subject to the same selective pressures, therefore, would not be expected to show steps in the same areas, making the delimitation of subspecies based on steps in clines merely the reflection of the distribution of that particular character or set of characters.

The step in a character cline may be the result of the merging of two populations which were previously separated. If the two populations have diverged in isolation and some of the differences involve incipient isolating mechanisms, then they will rapidly become two species by the reinforcement of these isolating mechanisms as described by Dobzhansky (1951), Moore (1957), and Koopman (1950). If such differences have not developed, then interbreeding will take place more freely and a distinctive pattern of variation will develop. This pattern will be characterized by a narrow zone of intergradation involving all the divergent characters, and a high degree of variability and recombination of characters. In time, the two populations will merge and a situation very much like the first case, described above with regard to clines, will be developed.

Subspecies described on the basis of parts of clines (whether or not marked by steps), or of random samples of populations of species with relatively continuous distribution, would merely have descriptive value for the characters cited. Such a subspecies would not allow prediction of any other qualities of the population so designated and, in my estimation, would be no more worthy of formal nomenclatorial recognition than are distinctive mutants or the populations containing them. Conversely, in the case of populations which are now separated, or have been so until recently, prediction of the distribution of their characteristics is possible, extending to other features than the few characters used to distinguish them. Their history of physical reproductive isolation assures almost as much concordance of characters as would be found in species populations, and their designation as subspecies is consequently both practically useful and biologically meaningful.

TYPE DESCRIPTION AND DESIGNATION.—Because I am not following traditional entomological practice in the designation and description of the types of the new species some explanation is called for. The modern concept of species is not based on the holotype, but rather on the population from which the holotype has been selected in order to fix the name. The majority of persons using a paper such as this are presumably more interested in the identity of a species than in the verification of its name. To them, the range of variation within the species is of much greater importance than the detailed condition in the type. I have, therefore, described the population sample before me in preference to the type, but I have indicated the condition in the type of those characters which are variable within the species. An allotype has no more legal standing under the present rules of nomenclature than does any other paratype. I cannot foresee any use of the allotype in the fixation of the female characters in a species. This function is performed just as authoritatively and more completely by the description of the female series. Nor can I see any use of the allotype in the resolution of problems arising from the misassociation of sexes. In such a case, the allotype would have no legal function in the proper disposition of the name, and could hardly reflect more clearly the author's concept of the female of his species than would the series of female paratypes. Hence, I have not designated allotypes of the new species. Since paratypes serve to indicate the author's concept of the limits and variation of his species, I have designated the entire series of each new species as paratypes, excluding only very poorly preserved specimens and possible hybrids.

COLOR.—Despite the general opinion that color is not a reliable taxonomic character in Orthoptera, I have found that both color and color pattern are of considerable taxonomic value at the generic, specific, and subspecific levels in *Neobarrettia*. Certain of the body colors, however, fade or change after the death and preservation of the individual, and become more or less similar in the different species. For this reason, extensive color notes were made in the field. When a color character is based on the color in life, that fact is so indicated. In other cases I have interpreted the color of preserved specimens, based on my knowledge of the color of other species in life and after preservation. For the purposes of this study it has been found sufficient to describe color in broad general terms and no attempt has therefore been made to define colors precisely by reference, for example, to the Ridgeway color nomenclature system. Such precise definition may, in fact, obscure the similarities in general color that exist between the species.

WING VENATION.—The wing vein nomenclature of Ragge (1955) has been followed, although on some points, in particular the identity of the stridulatory vein, the interpretation of Zeuner (1939) may be the phylogene-

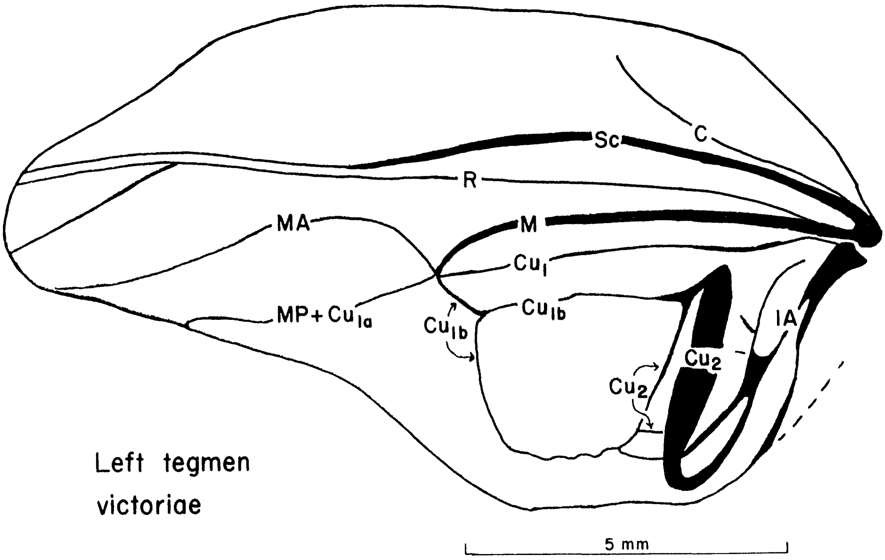
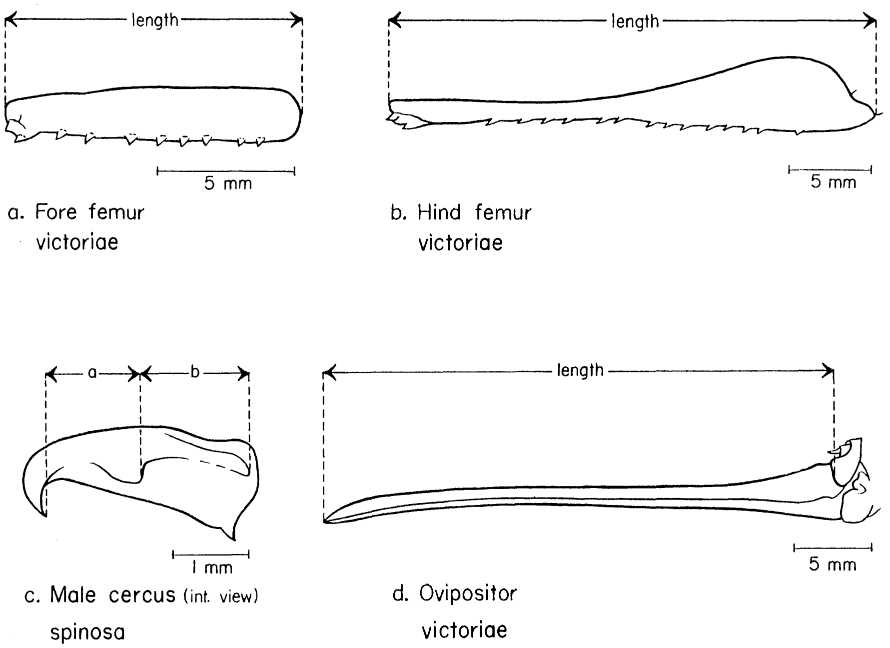


FIG. 1. Wing vein nomenclature in *Neobarrettia victoriae*. Left tegmen in male, 1.5 mi. NE Cd. Victoria, Tamps. Nomenclature after Ragge (1955).

tically correct one. Ragge's nomenclature, applied to the tegmen of *N. victoriae,* will be found in Figure 1. Description of tegminal venation, reticulation, and color are based on the condition of the left or uppermost tegmen.

MEASUREMENTS.—All measurements have been made either with vernier calipers, or with an ocular micrometer in a dissecting microscope at powers of 6 to 36×. The points on the organs between which various measurements were taken are indicated in Figure 2. The ratio of length of tegmen to length of fore femur is here considered to be a measure of the relative length of the tegmen. Comparison of the measurements of the femora, tegmen, pronotum and ovipositor indicates that the length of the fore femur is more closely related to body size than is any other measurement. In *N. spinosa* the ratio of the length of the internal ridge of the male cercus to the length of the apical tooth was taken to indicate the relative curvature of the apical tooth. In the graphic summary of the measurements of each species (Figs. 21 and 22), only ranges are given. These are intended only as very rough indices of absolute and relative size relationships among the species. Some geographic variation is probably present in most if not all of the measurements (strikingly so in those of *spinosa*), but no analysis of this variation has been made. My collecting has been concentrated in certain



a. Fore femur victoriae

b. Hind femur victoriae

c. Male cercus (int. view) spinosa

d. Ovipositor victoriae

FIG. 2. Dimensions in *Neobarrettia* species: a, *victoriae*, 1.5 mi. NE Cd. Victoria, Tamps., lateral view; b, same, lateral view; c, *spinosa*, 5 mi. S Pine Springs, Culberson Co., Tex., internal view (a = length of apical tooth, b = length of internal ridge); d, *victoriae*, 34 mi. NW Cd. Victoria, Tamps., lateral view.

regions, while others have been almost totally ignored. The resulting species samples are not random. Parametric descriptions (means and standard deviations) of the measurement data, therefore, would be misleading.

SONG RECORDS.—A general description of the song of each species was made in the field. In addition, living individuals were shipped to the University of Michigan Museum of Zoology, where their songs were recorded in the laboratory with a Magnacord or Magamite recorder, running at a tape speed of 15 inches per second, and equipped with an American D33A microphone. Audiospectrographs were made of selected songs with a Vibralizer.

FOOD HABITS.—Only a few observations of the feeding of *Neobarrettia* species were made in the field. In order to determine the diet of the genus, preserved crops and living individuals of all but one of the species were sent to S. K. Gangwere, a specialist in the food habits of Orthoptera. Gangwere examined the crop contents microscopically, and performed various experiments to test the food habits of the living individuals. His simple study technique for related Orthoptera have been described elsewhere (Gangwere, 1961).

ACKNOWLEDGMENTS

Many persons and institutions have aided me in this project, and to all I owe a large debt of gratitude.

The two major field trips could not have been undertaken without the generous financial assistance of the American Philosophical Society, the Society of the Sigma Xi, and the University of Michigan.

T. H. Hubbell accorded me full use of all the facilities of the University of Michigan Museum of Zoology where the laboratory work for this study was done. J. A. G. Rehn and H. J. Grant of the Academy of Natural Sciences of Philadelphia, and A. B. Gurney of the U. S. National Museum have been most helpful and hospitable when I visited their institutions.

I am indebted to the following persons who made loans of specimens from their personal collections or the collections under their care: E. R. Tinkham, C. Bolívar y Peltain, J. R. Hilliard, M. A. Cazier, W. L. Nutting, J. E. Gillaspie, B. C. Brown, and R. H. Painter. A. B. Gurney kindly examined and sketched the types of *Rehnia* under his care and searched the records of the U. S. National Museum at my request.

I. J. Cantrall, Roberto Sánchez, M. J. Erlewine, and J. Youngpeter accompanied me on field trips and provided welcome company and much assistance. Mrs. Nadine Miller and Simon Stopol extended to me the hospitality of their haciendas and provided various facilities and advice.

S. K. Gangwere and his students devoted much time and effort in observing the food habits of the living *Neobarrettia* which I shipped to Ann Arbor. I. J. Cantrall, R. D. Alexander, and T. E. Moore all have spent considerable time caring for the living materials, making notes, and recording the songs of the males.

The members of my Doctoral Committee at the University of Michigan, T. H. Hubbell, E. T. Hooper, R. McVaugh, and L. C. Stuart, and the members of the staff of the Museum of Zoology, have patiently listened to the development of my ideas concerning this problem and have offered advice, encouragement and criticism when most needed. They have been unstinting of their time in reading the original manuscript of this paper. I. J. Cantrall, W. H. Burt, and R. S. Storer read and criticized the final draft. I have profited greatly from discussions with J. Rzedowski and J. W. Hubbard concerning past and present vegetation of western North America, although they do not necessarily agree with my conclusions.

The illustrations are the work of the following persons: Figures 7, 8, and 17 to 20, Mrs. Elizabeth Anthony; Frontispiece and Figures 2, 11, 15, 16, 21, and 22, Miss Suzanne Runyan; Figures 1, 3 to 6, 9, 10, and 12 to 14, Mrs. Jean W. Cohn; Figure 24, Mrs. Stanlee Lonsdale; Figure 23, William Cristanelli.

Finally, the patience, tolerance, and encouragement of my wife, Jean W. Cohn, as well as her draftsmanship, are largely responsible for the completion of this work.

PART I. TAXONOMIC TREATMENT

In this part, the taxonomy of *Neobarrettia* is corrected and amplified, and the large amount of recently gathered information about the genus is summarized. This will provide the basis for the reconstruction of the history of the genus presented in Part III.

Generic Analysis

SUBFAMILIAL ASSIGNMENT

The genera *Neobarrettia* and *Rehnia* (here synonymized) were recently transferred to the subfamily Listroscelinae by Rehn (1957) and Cohn (1957) after having been classified among the Decticinae since their original description. The evidence for this transfer was fully discussed by Cohn (1957) and only the main argument and certain new data will be summarized here.

Although *Neobarrettia*, as here defined, possesses the two diagnostic features of the Decticinae (and the very closely related Tettigoniinae[1])—a free plantula on the hind tarsus and dorso-external spurs on the fore tibia—it does not possess any of the other features which are characteristic of that subfamily. Thus, the strongly compressed fastigium and short, semi-cylindrical, caudally upturned pronotum are very different from the broad fastigium and the caudally produced and often flat pronotum of the majority of the Decticinae. Conversely, the condition of these structures in *Neobarrettia* is typical of those found in the Listroscelinae. Similarly, in other features by which the two subfamilies differ, *Neobarrettia* is typically listrosceline and very different from the normal decticine: the fore legs of *Neobarrettia* are longer than the middle ones, in contrast to the reverse condition in the Decticinae; the pronotum is semi-cylindrical and in most of its length it is narrower than the head, in contrast to the broader and often carinate decticine pronotum; the pronotum does not possess a free ventral border, in contrast to the presence of this feature in most decticines; all the sternal spines are elongate, in contrast to the decticine condition in which at least the metasternal lobes are short. In most other characters, *Neobarrettia* resembles the Listroscelinae at least as closely as it does the Decticinae: the eyes of

---

[1] The headings "Decticinae (including Tettigoniinae)" and "Decticinae (S.L.)" in Cohn (1957) were not intended to indicate the synonymy of the Tettigoniinae under Decticinae, but were used merely as headings of convenience because of the few genera of Tettigoniinae involved and the close relationship of the two subfamilies.

Neobarrettia are considerably smaller and more protuberant than in most decticines (although similar to the tettigoniine *Tettigonia*), but not as small or as protuberant as in other listroscelines; the ventral armature of the tibia, femur, and coxa are much more strongly developed than in most decticines (although, again, the tibial spurs and femoral spines are similar to those of *Tettigonia*), but are generally smaller than in most of the listroscelines.

Neobarrettia resembles the Decticinae and Tettigoniinae more closely than the Listroscelinae in only three characters: the presence of a hind tarsal plantula; the straightness, depth, and lateral sulcation of the fore tibia; and the presence of fore tibial dorsoexternal spurs. The plantula, however, is not restricted to the Decticinae and Tettigoniinae, but is found in the Saginae (*Saga* and *Clonia*) and in at least one genus of the Conocephalinae (*Orchelimum*). Furthermore, the plantula in *Neobarrettia* is very short and apparently not highly sclerotized. It would require little more than a slight enlargement and sclerotization of the normal basal pulvillus in the Listrocelinae to produce the condition found in *Neobarrettia.* The above-mentioned tibial characters are also found in other subfamilies: straight tibiae are normal throughout the Tettigoniidae; deep, laterally sulcate tibiae are found in certain of the Copiphorinae (*Neoconocephalus*), and in the Saginae (*Saga, Clonia, Terpandrus,* and *Megatympanophon,* the latter genus transferred from the Tympanophorinae for reasons listed below); dorsal fore tibial spurs are found in the same position and form in the Phaneropterinae, Mecopodinae, Phyllophorinae and in one genus of the Saginae (*Terpandrus*). Moreover, the fore tibia of *Neobarrettia* resembles that of the sagines *Terpandrus* (with dorsal spurs) and *Megatympanophon* (without dorsal spurs) almost as closely as it does the tettigoniine *Tettigonia* and the decticine *Capnobotes.* Since the weight of critical morphological evidence favors a relationship with the Listroscelinae, the tibial and tarsal features of *Neobarrettia* probably represent the retention of primitive characters lost in the more derivative Listroscelinae, and thus do not necessarily indicate a direct relationship with the Decticinae and Tettigoniinae. This concept is further discussed in the next section.

POSITION WITHIN THE LISTROSCELINAE

Neobarrettia has no known close relatives. Neither immediate antecedents nor derivations of its more distinctive characteristics (see generic characterization) are found among the other genera of the subfamily. However, certain structural characteristics of the eye, pronotum, and tibia in *Neobarettia,* and the degree of development of the leg spines and spurs and of the sternal spines in this genus, appear to represent very primitive conditions of structures which are highly modified, presumably for active predation, in the majority of listrosceline genera.

Within the Listroscelinae, the feeding habits of only *Decolya* and *Phisis* have been recorded (Henry, 1932). Both are highly modified in the structures listed above, and both have been observed using their front legs in the capture of living insects for food. The crop contents of two other listrosceline genera, *Cerberodon* and *Hexacentrus*, have been examined by S. K. Gangwere and T. H. Hubbell (*in lit.*) and found to consist entirely of insect remains. *Cereberodon* is strongly modified in the above structures, *Hexacentrus* less so. From these observations, and from a general consideration of the requirements for carnivorous habits, it is reasonable to assume that the globose, strongly protruding eyes and the elongate fore legs provided with long ventral spurs and spines characteristic of listroscelines, represent specific adaptations for the capture of living prey. The strongly developed sternal and coxal spines of the listroscelines probably serve a similar function. Active predation requires increased activity and mobility of the fore legs and of the head, and is undoubtedly accompanied by an increase in the size of the leg and head muscles. The strongly impressed sulci of the pronotum of many listroscelines are probably the external manifestations of enlarged internal ridges for the attachment of these muscles, and the shallow lateral lobes of the pronotum may be associated with the greater mobility of the coxae. That all of these features are related to carnivorous habits is strongly suggested by their presence in the highly carnivorous subfamily Saginae. Furthermore, pronotal changes associated with foreleg modification are also seen in the Salomoninae. In several genera of that subfamily which have very large and heavy fore legs, the pronotum is deeply furrowed and the lateral lobes are very short. In other salomonine genera with fore legs which are less, or not at all enlarged, the pronotum is noticeably smoother and the lateral lobes are often quite deep. The fore tibiae of all the strongly modified listroscelines are shallow dorsoventrally, broadly rounded above, slightly curved, and without dorsal spurs. The very different structure of the fore tibiae in herbivorous tettigoniids suggests that the listrosceline condition is also associated with the raptorial function of the leg, although no specific function may be assigned to these tibial characteristics.

In each of the structures discussed above, the condition in *Neobarrettia* is considerably less modified than in the Listroscelinae. The eyes are less globose and much less protruding, and are similar to the eyes in certain Tettigoniinae and Decticinae. The short femoral teeth or spines, and the straight, deep fore tibiae with short ventral spurs are almost identical (except in their greater length) to those of several of the genera of the latter two subfamilies. The pronotum, although semicylindrical, is as smooth as that of the Phaneropterinae, Concephalinae, and Decticinae. The ventral coxal spines are not as well developed as those in many listrosceline genera. The meso- and metathoracic sternal spines, although longer than in other listroscelines, are less modified from a simple ventral elongation of a portion of the sternite and do not have the typical cylindrical listrosceline form.

Neobarrettia thus stands between the rest of the carnivorous Listroscelinae and omnivorous or herbivorous tettigoniid subfamilies in the degree of modification of these structures. The genus may be considered to represent either a primitive stage in the development of carnivorous adaptations, or an advanced stage in the conversion of a carnivore to an omnivore or herbivore. Since all observations and laboratory tests (see summary under the discussion of habitat) indicate that *Neobarrettia* is almost exclusively carnivorous, it must be considered a representative of a primitive stage in the development of carnivorous adaptations.

Further evidence of the primitive nature of *Neobarrettia* may be seen in its relationship with *Megatympanophon,* recently described from Brazil by de Toledo Piza (1958). Although originally placed in the Tympanophorinae, apparently solely on the basis of the absence of the dorso-internal distal spur of the hind tibia, this genus is probably a member of the subfamily Saginae. It resembles members of that subfamily in the enlarged tarsal pulvilli, the appressed antennal scrobae, and the serrulate ovipositor, and it specifically resembles *Saga* in the details of the fastigium, and *Terpandrus* in the general shape of the pronotum and details of the fore tibia. The absence of one of the dorsodistal spurs on the hind tibia is at least a tendency toward the condition characteristic of the Saginae in which both spurs are absent. *Neobarrettia* shows distinct resemblance to *Megatympanophon* in its smooth, deep pronotum, straight, deep, sulcate fore tibia with relatively short ventral spurs, prominently bispinose geniculae, long, tapering sternal spines, and carinate female subgenital plate. Except for the last, all of these structures are more strongly modified in other members of both subfamilies. It is thus probable that *Neobarrettia* is the modern representative of an extremely primitive listrosceline stock whose origin lay very close to the point of divergence of the Listroscelinae and Saginae. Under this interpretation, the presence of dorsal spurs on the fore tibia merely represents the retention of another character, which, because of its presence in other subfamilies, was probably present in ancestral listroscelines and lost at a more advanced stage of carnivorous adaptation.

Only one genus in the Listroscelinae bears more than a general relationship with *Neobarrettia.* This is the widespread Asiatic and African genus *Hexacentrus.* The coxal armature of this genus is less well developed than in *Neobarrettia,* the pronotum is at about the same level of primitiveness, the sternal spines are somewhat more modified (more cylindrical), and the eyes and fore legs are more highly modified and typically listrosceline. *Hexacentrus* evidently represents a higher level of carnivorous specialization.

No close relationship is seen between *Neobarrettia* and the other Asiatic genera. Most of the latter are highly specialized with small, elongate bodies, and very long fore legs provided with greatly elongate spurs and spines. Some of the South American genera, such as *Listroscelis, Macrometopon,* and their allies, bear superficial resemblance to *Neobarrettia,* but all have strongly modified pronota, legs, etc., and *Arachnoscelis* displays further specialization in the wings and the strikingly modified male genitalia. Most of these genera closely resemble *Neobarrettia* in the construction of the head, but none more closely than does *Hexacentrus.* The suggestions by Rehn (1957) and Cohn (1957) that *Neobarrettia* is more closely related to the known South American listroscelines than to any others, are not substantiated on morphological grounds.

Since the presence of dorsal spurs on the fore tibia of *Neobarrettia* is the only exception to the universal absence of these spurs in the Listroscelinae, a comment is appropriate here regarding their usefulness as a diagnostic character. Rehn (1957) states that limb spine characters are now known to be of less fundamental importance than long supposed for the separation of subfamilies of the Tettigoniidae. Judging from the example which he gives, the statement is based on the infraspecific variability of the character. However, the supporting data which he offers testify instead to the great stability of the character—the distal spur was present on the external margin of the fore tibia in 101 specimens of *Neobarrettia* and *Rehnia* which he examined, and in the remaining two specimens it was present but in an anomalous position! The fact that the spines are universally present in the Decticinae (and the closely related Tettigoniinae), and absent in all Listroscelinae except *Neobarrettia* makes this limb spine character extremely useful. Few if any characters are completely reliable at the subfamily level, and there is little reason to consider any character less fundamental because there are one or two exceptions to its universality. The data here presented suggest that the presence of the spines in *Neobarrettia* is not owing to convergent development, but rather represents the retention of a primitive condition. The implication of all the morphological data is that the *Neobarrettia* stock was differentiated so early in the development of the Listroscelinae that the modern *Neobarrettia* is morphologically not too distantly removed from the ancestor which also gave rise to the Decticinae, one of whose characters it shares. Although the dorsal tibial spine character, used alone, will not correctly place *Neobarrettia,* when used with other characters it serves the more important function of indicating the position of the genus within the subfamily.

NEOBARRETTIA REHN

Neobarrettia Rehn, 1901*a*, Ent. News 12:16.

1907. *Rehnia* Caudell, Proc. U. S. Natl. Mus. 32:35 (generotype, *Rehnia victoriae* Caudell, 1907, by original designation).

GENEROTYPE.—*Capnobotes imperfectus* Rehn, Trans. Amer. Ent. Soc. 27: 89, 1900, by original designation.

CHARACTERIZATION.—*Neobarrettia* possesses the following characteristics which are unique in the subfamily Listroscelinae:

Basic color pattern bright green, with ivory stripes on mes- and metepisternites and on caudal border of lateral lobe of pronotum, and with yellow longitudinal stripes or spots on venter of abdomen.

Wings brightly colored, black or dark brown, and white or yellow or both.

Fore tibia armed above with spurs.

Male cercus with a prominent but simple dorso-internal ridge on basal half, ending proximally in a prominent angulation (rounded in *hakippah*).

Seventh abdominal sternite of female with a tubercle or tuberculate ridge (except in *bambalio*).

Ovipositor as long as body and weakly decurved.

The following features found in *Neobarrettia* are also found occasionally in other listrosceline genera but never in combination:

Head moderately elongate; occiput prominent; fastigium of vertex short, strongly compressed; eye large and only moderately protuberant (in comparison with other listroscelines).

Fore tibia straight, relatively deep; ventral spurs relatively short, only slightly curved.

Pronotum with sulci barely visible and with deep lateral lobes.

Meso- and metathoracic sternites with long, tapering, broad-based spines.

Femoral teeth contrastingly colored.

Penultimate tergite of male short, shallowly notched caudally and with a semimembranous mediocaudal area.

Paraproct of male with a longitudinal ridge.

Subgenital plate of female with a median longitudinal ridge.
Habitat, dry environments—thorn forest to desert.

N. imperfecta, the generotype, may be readily derived from the stock heretofore known as *Rehnia,* and more specifically from one of the derivative species groups of that stock (see discussion of characters under *imperfecta* and in the character summary following the species treatment). The habitat and general biology of *imperfecta* are very similar to those of the other species of this assemblage, and it is found in the same geographical region as are those species. Since there are no supergeneric categories in the Listroscelinae it is impossible to indicate this special relationship if two genera are used; the purposes of classification are better served by considering all the species to be members of one genus. The relationships of *imperfecta* are thus made clear, while the distinctiveness of that species may be adequately indicated by the creation of a separate species group for it.

The probable reasons for the erection of the two genera are pertinent in this connection. *Imperfecta* was originally placed in the Decticinae by Rehn (1900) who erected the genus *Neobarrettia* for it one year later (1901*a*). When Caudell (1907) revised the North American Decticinae he described *victoriae* and *spinosa* and redescribed *imperfecta.* In order to determine the position of these species within the subfamily, he applied to them a criterion found to be useful in grouping decticine genera, namely, the number of ventroapical spurs of the hind tibia. In so doing, he found that *imperfecta* belonged in one section of the Decticinae and *victoriae* and *spinosa* in another. A new generic name was thus required for the latter two species and he proposed *Rehnia.* However, Caudell must have been impressed with the similarity among the three species for he commented as follows: "Superficially this genus [*Rehnia*] bears some resemblance to *Neobarrettia* Rehn, but structurally it is very different, . . . falling into a different section. . . . " The strong structural difference apparently was nothing more than the difference between two and four ventro-apical spurs. Had Rehn and Caudell originally placed these species in the subfamily Listroscelinae, this spur character probably would not have been given such weight, and similarities among the species might have made the description of *Rehnia* unnecessary.

GENERIC DESCRIPTION.—HEAD (Figs. 17a and 17b): moderately elongate (length about 1.4 to 1.6 times width); eye relatively large for subfamily (greatest diameter about .2 times length of head), weakly elliptical, moderately protruding[2], occiput higher than fastigium verticis, evenly rounded; fastigium verticis arising from occiput at an obtuse

---

[2] In laterocaudal view, eye is somewhat less than hemispheroidal in shape; in other listroscelines it is almost three-quarters spheroidal; in tettigoniines it is less than hemispheroidal; in most decticines it is one-quarter spheroidal or less.

angle, not projecting beyond antennal scrobae, narrow, strongly compressed, often sulcate above; frontal fastigium at most a weakly swollen area, sometimes not differentiated from frons; frons smooth, almost flat. THORAX: Pronotum (Figs. 17c and 17d) with cephalic three quarters (cephalic third in *imperfecta*) uniformly semicylindrical; caudal quarter or less (caudal third or more in *imperfecta*) sharply elevated, slightly produced (except in *imperfecta*), sometimes with a very low, broadly rounded median carina; lateral shoulders narrowly rounded (broadly rounded in *imperfecta*), not extending beyond upturned portion (extending to near middle of pronotum in *imperfecta*); cephalic margin weakly emarginate, weakly flared; caudal margin more or less truncate (sometimes weakly notched mesad in *imperfecta*); cephalic sulcus sinuate, slightly impressed; caudal sulcus barely indicated, V-shaped; lateral lobes of pronotum (Figs. 17c, 17d) deep (depth about .6 to .8 times length[3]), without a free ventral border; ventral portion of caudal margin forming an obtuse angle with horizontal, lobes thus without a distinct ventrocaudal angle (ventrocaudal angle present in *imperfecta*, see discription under that species); humeral sinus weak, sometimes absent; prothoracic stigma oblong, partially covered by lateral lobe of pronotum, without guard hairs. All sternites with paired, elongate, spiniform processes; those of prosternum thin, cylindrical; those of meso-and metasternum each tapering from broad base to acute apex. LEGS: fore leg longer than middle leg; all coxae below with a strong distal and mesal tooth, fore coxa with a spine above; middle trochanter with a ventrodistal tubercle; all femora below with short teeth or spines on both margins; genicular lobes briefly bispinose (unispinose in *imperfecta* and occasional individuals of other species); ventral armature of fore femur dentate (Fig. 2a), longest tooth on caudal margin less than .2 times mesal depth of femur (armature in *spinosa* is spinose, Fig. 17e, longest spine on caudal margin over .3 times mesal depth of femur); fore tibia straight (Fig. 17e), dorsoventrally deep for subfamily (depth about .8 to 1.1 times width at midlength), weakly sulcate laterally; auditory area weakly inflated, foramen slit-like; above usually with three to five spurs on caudal margin, a subapical caudal spur present; below with six pairs of spurs, longest about 1.5 to 2.3 times width of tibia at midlength; middle tibia above usually with three or four cephalic spurs, a subapical cephalic spur absent, and four to seven caudal spurs, a subapical caudal spur present; hind tibia above with spines on both margins and one pair of dorsoapical (subapical) spurs; below with spurs on both margins and with two pairs of ventroapical spurs (one pair in *imperfecta*); hind tarsus with a short free plantula about .3 to .5 times length of basitarsus. TEGMINA AND WINGS: macropterous to brachypterous; tegmina overlapping in both sexes (except in females of *imperfecta*); except in *imperfecta*, no or little sexual dimorphism in tegminal length (female tegmen longer than .7 times that of male), tegmina of male (Fig. 1) not inflated (dorsal width of folded tegmina about equal to or narrower than cephalic margin of pronotum); stridulating area more or less rectangular, length of stridulating vein equal to or less than length of mirror, costal margin of mirror (vein Cu_{1b}) more or less straight (corresponding conditions in *imperfecta* described under that species); wing as long as tegmen (several times shorter than tegmen in *imperfecta*). MALE TERMINALIA: Penultimate tergite (Figs. 20f to l and p to q) short (length about .3 to .4 times width), mediocaudal area depressed, semimembranous, less than .2 times width of plate; caudal margin broadly and usually only shallowly emarginate, lateral edges of emargination produced into short blunt lobes; cercus (Figs. 18a to e, 19a to e) with a prominent dorsointernal

---

[3] A rough measurement: depth measured from dorsum of pronotum to ventral margin; length, from middle of humeral sinus, or at about one-quarter the distance to ventral margin, to same level on cephalic margin.

ridge on proximal two-thirds to three-quarters, ridge generally broader proximally, terminating there in an acute angulation (rounded in *hakippah*), often terminating distad in a small tooth strongly bent downward and cephalad (tooth absent in *cremnobates* and *imperfecta* and greatly reduced in *bambalio*); apical tooth incurved and acute to acuminate; paraproct with a horizontal ridge; titillators in most species membranous with a small, rectangular, unarmed sclerite on ventral surface, length of sclerite about .2 times width of penultimate tergite (no sclerotizations in *imperfecta*) (in *sinaloae* and *hakippah*, titillators two finger-like projections, strongly sclerotized, armed distad with minute spines, Figs. 18f and g); subgenital plate simple, caudal margin with a wide V-shaped emargination; styles usually about two to four times as long as wide, length usually .1 to .3 times width of penultimate tergite. FEMALE TERMINALIA (Figs. 17f to n): subgenital plate with caudal margin triangularly produced to weakly emarginate; always with a sharp median carina of variable length, often with parallel or oblique carinae on either side of median one, often with a pit near lateral articulation of distal half of plate. Seventh abdominal sternite usually with a tubercle or tuberculate ridge on midline (absent in *bambalio*); ovipositor (Fig. 2d) about as long as body, weakly decurved, margins smooth, apex acuminate. BASIC COLOR PATTERN (Frontispiece): generally bright green; mes- and metepisternite and caudal border of lateral lobe of pronotum largely ivory, pronotal stripe extending dorsad at least to shoulder and usually reaching dorsum (restricted to ventral two-thirds of lobe in *imperfecta*); dorsum of abdomen usually transversely unicolorous, green, brown or black, sometimes darker mesally (*imperfecta* with a contrasting longitudinal chocolate stripe with white flecks, on either side); venter of abdomen usually with paired yellow longitudinal stripes or spots; most of tegminal venation green (sometimes yellowish in female *imperfecta*), membrane usually brownish or with black spots; wing brightly colored, spotted; black or brown on much or most of membranous areas, white or yellow (or a combination of both) on wing base, distal marginal band, and on cross veins; either dark or light colors forming spots; femoral armature entirely black or with black or dark brown tip.

SPECIES ANALYSIS

KEY TO THE SPECIES OF NEOBARRETTIA

The following key will serve to distinguish the species of the genus. Since keys are made primarily for the purposes of easy and rapid identification, external and readily visible characters have been used wherever possible; more reliable characters have been omitted where these require special mounting. The key is therefore artificial.

1. Caudal third or more of pronotum elevated and wider than cephalic portion; tegmina of male strongly inflated, stridulating area distinctly wider than long[4]; tegmina of female lobate and separated. . . . . *imperfecta*

   Caudal quarter or less of pronotum elevated and narrower than cephalic portion; tegmina of male not inflated, stridulating area longer than wide[4]; tegmina of female well developed, though usually short, and always overlapping 2

---

[4] Measured from the caudal edge of the pronotum to the distal end of the mirror, and from vein M to the caudal edge of the tegmen.

2. Tegmina with reticulation greatly reduced, the remaining veins forming readily visible cells; large discrete black spots within most cells; wings white with small black spots; titillators finger-like, dark brown, armed with minute spines (Fig. 18f and g)...... 3

   Tegmina densely reticulate over much of their surface; no black spots present although membrane may be dark; wings dark with light spots; titillators short tubercles, colorless, unarmed. 4

3. Pronotum margined cephalad with black or dark brown; occiput green or weakly infuscate; apical tooth of male cercus elongate, more than twice length of internal ridge. .... *sinaloae*

   Cephalic margin of pronotum green or light brown; middle of occiput usually with a large black marking; apical tooth of male cercus short, about 1.5 times length of internal ridge. .... *hakippah*

4. Cephalic margin of pronotum green or light brown (tegmina less than 1.6 times length of fore femur, costal margin green; femoral armature dentate, whitish, tipped with black or brown) 5

   Pronotum margined cephalad with black (*either* tegmina about twice length of fore femur, and femoral armature dentate, entirely black, *or* femoral armature spinose, entirely black, *or* costal margin of tegmina reddish)............................. 7

5. Pronotum elongate, length-width ratio in males rarely less than 1.41 (never less than 1.34), in females rarely less than 1.65 (never less than 1.53)[5]; *both* margin and spots of wing either yellow or white; spots usually few or absent in center of wing[5]; mandible with black color of molar and incisor areas sharply demarcated from white color of rest of cephalic surface .... *victoriae*

   Pronotum normal in form, length-width ratio in males rarely over 1.45 (never over 1.50), in females rarely over 1.60 (never over 1.65); margin of wing yellow, spots white and numerous; mandible with black color of molar and incisor areas merging gradually with yellowish white of cephalic surface 6

6. Median tooth of male cercus short but prominent; apical tooth bent only slightly below level of shaft (Fig. 19c); seventh adbominal sternite of female with a tubercle .... *pulchella*

   Median tooth of male cercus represented by a low swelling; apical tooth bent well below of shaft (Fig. 19d); seventh abdominal sternite of female smooth .... *bambalio*

7. Costal margin of tegmina with a broad reddish border; tegmina about as long as fore femur (never over 1.07 times as long); wing colors opaque, black and white; male cercus without a median tooth; femoral armature always dentate. .... *cremnobates*

   Costal margin of tegmina green; tegmina usually well over 1.10 times as long as fore femur (when less, femoral armature spinose); wing colors almost transparent, brown with white, greenish white or yellow spots; male cercus with a prominent median tooth; femoral armature spinose or dentate... 8

---

[5] Geographically variable; the shortest pronota and most heavily spotted wings are found in individuals south of Cd. Victoria, Tamps., México.

8. Tegmina as long as abdomen, about twice as long as fore femur; femoral armature dentate; venter of abdomen with longitudinal yellow bands. . . . . *vannifera*

Tegmina shorter than abdomen, less than 1.50 times as long as fore femur; femoral armature spinose; venter of abdomen with large, round, yellow spots. . . . . *spinosa*

THE SPINOSA GROUP

This group contains *N. spinosa* (Caudell) and the new species *N. vannifera,* which are found in northeastern México and Texas. They share the following distinctive characters, of which the first three are unique in *Neobarrettia*: wing colors light and almost transparent; cross veins of wing well developed; femoral armature largely or entirely black; cephalic and caudal borders of pronotum margined with black (as in *cremnobates, sinaloae,* and, in a restricted condition, in *imperfecta*); stridulating field of male tegmen more or less ringed with dark brown (as in *cremnobates*); caudal part of female tegmen dark brown (as in *cremnobates* and *victoriae*); fore femur with a number of minute teeth scattered among larger teeth or spines (a few such teeth are found in some individuals of various other species). The following combination of details of the structure of the male cercus is also distinctive: a median tooth present and strongly bent ventrad; apical tooth relatively long (at least one-half the length of the cercus); robust and evenly incurved. Although *spinosa* and *vannifera* are not very closely related, they appear to stand in direct sequential relationship to one another. Because of this, and because they share several characters unique to them and several others that are apparently primitive, they are placed in the same group.

The Spinosa Group is not very closely related to any other but it contains what I consider to be the most primitive member of the genus. It shares a few characters with the Cremnobates Group as indicated above, and it is similar to the Victoriae Group in the color of the female tegmen and in the general structure of the male cercus.

Neobarrettia vannifera[6] new species (Figs. 17f, 18a, 20o, 20p)

HOLOTYPE.—Male, 8 mi. SW Ciudad Victoria, Tamaulipas, México, 5 Oct. 1958 (T. J. Cohn, No. 166); University of Michigan Museum of Zoology.

COMPARISONS.—This is the only long-winged species in the genus. It may be distinguished from all the others by the following characteristics, which

---

[6] From the Latin, *vannus,* a fan + *fera,* bearing, in allusion to the long and delicately colored wings of this species.

are unique in *Neobarrettia*: caudal portion of pronotum sharply upturned and not at all recurved; tegmina and wings as long as abdomen; femoral armature dentate and almost wholly black (the combination is unique); abdomen with only one longitudinal yellow stripe on each side just ventrad of the tergites (members of the Pulchella Group also have only one stripe, but this is just lateral to the sternites). In addition, the penultimate tergite of the male shows the weakest emargination found in the genus (obsolete in *spinosa*) and the male cercus is distinctive in the following combination of characters: internal ridge short, apical tooth long (about twice the length of the internal ridge), robust and gently incurved (Fig. 18a); median tooth strongly bent ventrocephalad. These cercal characters are shared with only a few eastern individuals of *spinosa*.

Closest relationship is shown with *spinosa* in the characters listed above for the group. In addition, the female subgenital plate is very similar to that found in individuals of *spinosa* that do not posses lateral ridges. Otherwise *vannifera* shows resemblance to *cremnobates* and *sinaloae* (and in a limited way to *imperfecta*) in the black pronotal margins, to *cremnobates* (and in a limited way to *victoriae*) in the dark caudal portion of the male and female tegmina, to *victoriae* in the color dimorphism of the wing, and to the Pulchella and Imperfecta Groups in the simplicity of the female subgenital plate.

I consider *vannifera* the most primitive member of the genus primarily on the basis of the long tegmina and wings, the well-developed cross veins of the wing, and the almost transparent wing colors (see further discussion in the section on species relationships). The following features may also be primitive, although this is considerably less certain: the simply elevated caudal portion of the pronotum, the strongly oblique ventral margin of the lateral lobe of the pronotum, and the absence of lateral carinae on the female subgenital plate. In addition, *vannifera* has a very simple call, and is restricted to what is probably the most humid environment occupied by a species of *Neobarrettia* (see discussion of habitat in part II).

SPECIES DESCRIPTION.—PRONOTUM (Fig. 20o): caudal portion turned up at a sharp angle, approximately 30–40°, not at all recurved; ventral margin of lateral lobe more strongly oblique than in other species, humeral sinus very weak. APPENDAGES: tegmina and wings long (1.87–2.19 times length of fore femur, 2.19 in holotype), reaching to end of abdomen (unique in *Neobarrettia*); reticulation dense; cross veins of wing well developed; caudal armature of fore femur with a variable number (rarely less than 3) of minute teeth scattered among large ones. MALE TERMINALIA: caudal margin of penultimate tergite (Fig. 20p) barely emarginate, margin on either side very weakly produced into broadly angulate, blunt-tipped lobes; caudolateral margins of semimembranous area almost rectangulate, angle subtuberculate; cercus (Fig. 18a) long (about .6 times width of penultimate tergite), apical tooth robust, elongate (about two times length of internal ridge), gently and evenly curved inward, apex acute to short-acuminate; internal ridge short (about one-half length of apical tooth); proximal tooth prominent, produced, acute, apex blunt; median tooth short, apex briefly acute, strongly bent ventrocephalad; distoventral portion of internal ridge joining shaft well below dorsum and continuing distad halfway to apex as a low longitudinal ridge. FEMALE TERMINALIA (Fig. 17f): subgenital plate with caudal half broadly and weakly triangular, strongly inflated, especially near midline, apex very briefly notched; median carina sharp, prominent, extending entire length of plate, median two-thirds raised, the whole distinctly sinuate in side view; no lateral carinae; a short oblique ridge near lateral articulation of caudal half of plate forming caudal border of a broad pit without demarcated cephalic border; basal transverse flange absent; tubercle of 7th abdominal sternite located on cephalic half of plate, very high, slender, curved caudad, apex acuminate. COLORATION: color of eyes in life unknown; cephalic margin of pronotum with a very narrow black line extending ventrad at least to ventrocephalic angle of lateral lobe and usually to a point just above coxa (to ventrocephalic angle in holotype); caudal margin with a narrow black or dark brown line extending just over shoulder; ivory stripe of lateral lobe margined cephalically by a narrow dark brown stripe (sometimes obsolete below shoulder) which becomes wider and darker on shoulder, and proceeds thence caudad on dorsal surface to form a usually complete but narrow dark posterior border; meso- and metanota marked caudad with black or very dark brown; venter of abdomen in preserved specimens with a yellow or whitish longitudinal stripe on each side just ventral to tergites, interrupted briefly at each intersegmental membrane (not visible in holotype); tegmen of both sexes green cephalad of vein Cu_1 on proximal half, distal half usually extensively sprinkled with fine brownish specks caudad of vein R (specks absent in holotype); male tegmen generally with membrane and all veins in stridulating area dark brown except reticulation in mirror; caudal border behind vein $MP + Cu_{1a}$ light or reddish brown (light brown in holotype), this color extending to apex; female tegmen with border of wing caudad of vein Cu_1 brown at base, becoming more reddish caudad of vein $MP + Cu_1$, this color extending to apex; in darkest female specimens area between veins Cu_1 and Cu_2 dark brown. Wing with background brown, spots and distal band either all white or all yellow (yellow in holotype), colors almost transparent; spots numerous, round to transversely elongate; distal band narrow and irregular; femoral teeth jet black except for small green basal portion; dorsal surface of all tibiae vinaceous or greenish yellow (latter color probably faded vinaceous, see discussion below) (green tinged with vinaceous in holotype). MEASUREMENTS (in mm.): Male Holotype: length of pronotum, 7.1; width of pronotum, 5.2; length of tegmen, 25.0; length of femora, fore, 11.8, middle, 11.4, hind, 29.4. Measurements of the series studied are summarized in Figures 21 and 22.

PARATYPES.—All specimens examined in this study, with the exception of very badly preserved ones, are designated as paratypes. Male and female paratypes are deposited in the University of Michigan Museum of Zoology, the Academy of Natural Science of Philadelphia, and the United States National Museum. A male paratype is deposited in the Tinkham Collection.

VARIATION.—The caudal margin of the pronotum in some individuals is broadly rounded, a departure from the more or less truncate condition which is normal in the genus. The central portion of the swollen area of the subgenital plate of some females is flattened, as if it had been membranous in life and had retracted slightly in drying. In this condition the plate has every appearance of being a morphological precursor of the condition found in *sinaloae,* which suggests a mode of origin of the lateral carinae in other species. The dorsal color of the tibiae in life is probably vinaceous; when green, it always has a yellowish cast, and often a very faint trace of vinaceous, suggesting a faded condition. The color of the wing spots is dimorphic, both types of wing spot colors being present in most populations. No geographic variation has been noted.

Distribution (Figs. 23 and 24).—This species has a restricted distribution on the northeastern coastal plain of México and at low elevations in the adjacent Sierra Madre Oriental. The limiting records, all in Tamaulipas, are as follows: northern, 10 mi. N Ciudad Victoria; eastern, 23 mi. SW Padilla; southern, 15 mi. SSW Llera; western, 8 mi. SW Cd. Victoria. Extensive sampling beyond these localities has been done, but no *vannifera* has been found. The western limits of the species in the Sierra Madra are known only on the Cd. Victoria-Jaumave Road. More intensive surveys at the base of the mountains farther north and south indicate that *vannifera* is absent along the roads between the following towns: Antiguo Morelos-Naranjo-Cd. del Maiz (Tamps. and S.L.P.); El Limón-Ocampo (Tamps.); 10 mi. N El Limón-Gómez Farías (Tamps.); and Linares-Galeana (N.L.). On all of these roads, as well as others to the east, *victoriae* has been found. That species apparently surrounds the range of *vannifera* on three sides. The ranges of the two species overlap north, northeast, and south of Cd. Victoria and near Llera.

Habitat.—*N. vannifera* has been found only in thorn forest or in the weeds and bushes at the edge, or in the openings, of thorn forest, through an altitudinal range of 800 to 2000 feet. A single nymph collected by H. R. Roberts at 16 mi. W Cd. Victoria, indicates that the species may penetrate into oak woodland. This is the only record of such occurrence and I have not verified it in the field. The upper altitudinal and habitat limits are not known with certainty.

Where the range of *vannifera* overlaps that of *victoriae,* north and northeast of Cd. Victoria, the former species is found in the thorn forest and the latter in disturbed habitats with lower bushes. The two species have been found together in the same habitat only at 7 mi. NE Cd. Victoria and at 13 mi. SE Llera (2 mi. SW La Clementina). The habitat at the first locality is a partially-thinned thorn forest, at the second, a bushy savanna on a mesa top surrounded by thorn forest.

Seasonal Occurrence.—The earliest record for adults of this species is 11 August and the latest, 9 October. On both dates adult males were common and singing vigorously. Two last instar nymphs collected on 5 October suggest that the species lives considerably longer into the fall than the latest collecting date indicates. No special search for this species has been made before or after these limiting dates.

Song.—*N. vannifera* sings commonly during the day and evening. The song consists of a simple, single phrase continuously repeated. Each syllable is about .05 seconds in duration (measured from audiospectrographs of recordings made in the laboratory at about 76°F). In the field, the note appears to be higher pitched than that of *victoriae,* with which this species occasionally occurs, owing apparently to the narrower range of frequencies in the call of *vannifera.*

Records.—Material examined: 28♂♂, 17♀♀, 10 nymphs, TAMAULIPAS: 10, 5 mi. N Cd. Victoria; 23 mi. SW Padilla (Río Corona); 4 mi. NE Cd. Victoria; 8 mi. SW Cd. Victoria (Jaumave Rd.); 16 mi. W [SW ?] Cd. Victoria (ANSP); 10 mi. SE Cd. Victoria; 15.4, 5, 2.5 mi. N Llera; 13 mi. SE Llera (2 mi. SW Hacienda La Clementina); 3 mi. S Llera; 5, 6, 15 mi. SSW Llera.

Neobarrettia spinosa (Caudell) (Frontispiece, Figs. 2c, 17e, 17g, 18b, 18c, 20h, 20m, 20n)

1907. *Rehnia spinosa* Caudell, Proc. U.S. Natl. Mus., 32:307, (♂ "Texas").

1920. *Rehnia cerberus* Rehn and Hebard, Trans. Amer. Ent. Soc., 46:234 [♂, ♀-Marathon, Brewster Co., Texas].

Holotype.—Male, "Texas?"; U.S. National Museum. The type locality of this species has been recorded as Texas by Caudell (1907:308), who stated that the information came from Bruner, the donor of the specimen to the U. S. National Museum. The only locality label on the type bears a pencilled "Texas?" which A. B. Gurney of that museum informs me probably did not originate with Bruner. Dr. Gurney could find no additional information in the files of the Museum. The shape and proportions of the cercus (ratio of length of internal ridge to length of apical tooth .51), the relatively gentle curvature of the caudal part of the pronotum, the narrow black margin and absence of other dark markings on the pronotum, fit the populations found in southeastern Texas and eastern México (Fig. 3).

Comparisons.—*N. spinosa* may be readily distinguished from all other species of *Neobarrettia* by the following features which are unique in the genus: eye color in life red (living eye color unknown in *vannifera*); femoral armature strongly spiniform; dorsal surface of all tibiae green; venter of abdomen with round yellow spots; median tooth of male cercus often truncate at apex; size very large.[7] In addition, the westernmost populations of this species possess the following unique characteristics: frons and clypeus yellowish or yellow-brown; caudal portion of pronotum sharply upturned at almost a 90° angle, then strongly and prominently recurved to horizontal (Fig. 20n); abdominal tergites black.

N. spinosa is most closely related to *vannifera,* as discussed above. It appears to be more specialized than *vannifera* in the spiniform nature of the femoral armature, the relatively smaller wings and tegmina, the presence of lateral carinae on the female subgenital plate (see discussion of these carinae under the section on species relationships), and the unique characteristics of the westernmost populations. *N. spinosa* shows similarities to other species but these are few and indicate only distant relationships: to *cremnobates* in the shape of the caudal part of the pronotum, the general nature of the carinae of the female subgenital plate, and the black pronotal margins; to *sinaloae* in the shape and carinae of the female subgenital plate and the black cephalic margin of the pronotum; and to *victoriae* in the structure of the carinae of the female subgenital plate.

The synonymous *cerberus* represents only the distinctive westernmost populations of this species. Every character in which these differ from the eastern Texas populations shows some form of clinal intergradation with those of the eastern populations. Because these clines are very discordant throughout most of central Texas, I do not consider it useful to designate the western populations as a subspecies. A detailed analysis of the variation in this species and its bearing on the subpecific category will be found below.

Species Description.—PRONOTUM (Figs. 29m, 20n): caudal portion turned up at an angle between 45° (rarely less) and almost 90°, weakly arched to very sharply and prominently recurved to below horizontal; weak, but definite, humeral sinus. APPENDAGES: tegmen medium in length (1.07 to 1.50 times length of fore femur), densely reticulate; cross veins of wing well developed; armature of fore femur strongly spiniform (Fig. 17e), spines long (length of longest spine about .35 times depth of femur) (both shape and length unique in *Neobarrettia*); often several to many minute teeth scattered among spines. MALE TERMINALIA: caudal margin of penultimate tergite (Fig. 20h) not at all to very weakly emarginate; caudolateral margin of semimembranous area rounded obtuse and subtuberculate (rare) to rectangular and tuberculate (normal); apical tooth of cercus (Figs. 18b, 18c) robust, varying from as long as internal ridge to a little over twice its length, moderately to strongly and evenly incurved, apex acute to short acuminate; internal ridge varying from one-half to same length as apical tooth; proximal tooth short, acute; median tooth prominent, bent strongly ventrad and projecting well below ventral margin of distal part of ridge, apex variable, briefly acute to acute, or trun-

---

[7] Length of fore femur of male, 11.5 to 18.8 mm.; of female, 12.5 to 19.2 mm. The length of the fore femur of the smallest individuals of this species overlaps only that of the largest individuals of several other species (Fig. 21).

cate, or truncate with a cephalic tooth, or briefly lobed, the cephalic portion often bent strongly cephaled; distal portion of internal ridge joining shaft of cercus as a deep dorsal ridge, sometimes with ventrodistal part joining shaft well below dorsum. FEMALE TERMINALIA (Fig. 17g): caudal margin of subgenital plate varying from truncate to shallowly and broadly emarginate, briefly notched mesally; caudal half of plate very strongly swollen; median carina low and narrow on cephalic third, prominent, broader and arcuate on median third, and either low and broad or obsolete on caudal third; lateral carinae sometimes obsolete, otherwise low, broad, oblique and converging distad, terminating cephalad in a prominence at edge of swollen area or appearing to converge rapidly there to form cephalic margin of swollen area; a short oblique ridge cephalad of lateral articulation of caudal half of plate partially overhanging a deep pit laterad of ridge, pit often shallow and wide; basal transverse flange absent; tubercle of 7th abdominal sternite conical, varying from low and rounded to very high and curved caudad with apex acuminate, base very broad and extending over cephalic two-thirds of plate, apex located over middle or caudal third plate. COLORATION (Frontispiece): eyes in life brick red; frons and clypeus varying from green through straw yellow to bright yellowish brown (the last two colors unique in *Neobarrettia*); cephalic margin of pronotum with a very thin black (or rarely brown) line or a narrow black stripe extending ventrad at least to ventrocephalic angle, more often to a point over coxa; caudal margin yellowish through variegated light and dark, to black extending to just over shoulder; ivory stripe of lateral lobe extending to dorsum in same or slightly decreased width, usually very prominent there and usually extending into middle third; black or brown on shoulder, varying from a few small indistinct spots to a large jet black spot completely interrupting ivory stripe, rarely extending to ventral margin as a thin cephalic border to ivory stripe, sometimes extending to dorsum as a thin dorsal border of ivory stripe and continuing as a caudal border of metazona; mesocaudal area of pronotum entirely green or with a small brown to large black spot, the latter often covering a third of width of pronotum; meso- and metanota green, or mesonotum marked mesad with light brown and metanotum with caudal portion brown to black; abdominal tergites entirely green, to black with a green or yellow caudal margin; venter of abdomen on each side with two yellow longitudinal stripes, one ventral to tergites and another broader one lateral to sternites, both interrupted at each segmental membrane, giving ventral stripe appearance of a series of conspicuous round yellow spots; tegmen in both sexes green cephalad of vein R, membrane darker caudad of vein R, with weakly defined small black spots between veins in distal portion; male tegmen with membrane immediately outside mirror (except proximad of it) dark brown, apex of stridulating vein black in darkest individuals; female tegmen caudad of veins Cu_1 and $MP + Cu_1$ brown, darkest between veins Cu_1 and Cu_2; wing colors almost transparent, background brown, spots greenish white, numerous, round to transversely elongate with rounded margins, marginal band narrow, irregular, greenish white; femoral spines entirely black; dorsum of all tibiae green. MEASUREMENTS: These are summarized in Figures 21 and 22.

VARIATION.—Almost every character described above shows marked individual or geographic variation, or both. The absence of lateral carinae on the female subgenital plate of some individuals is of particular significance. When compared with the normal condition, these variants suggest that the ridges are formed by the depression or retraction of the central part of the inflated region, rather than by the elevation of portions of the plate. The condition in these variants is very similar to that found in *vannifera*, and gives additional evidence of relationship between the two species.

The extreme conditions of the characters which vary geographically are presented in Table 1. These extremes are invariably found in the western and easternmost populations, although similar conditions often occur considerably farther east or west, respectively, of the areas where they predominate.

In the case of seven of the characters listed, the extreme condition found in the western populations represents a unique or highly divergent development among the species of *Neobarrettia*. These characters include the color of the face, the color of the cephalic and caudal portions of the pronotum, the extent of the ivory pronotal stripe, the structure of the caudal portion of the pronotum, and the color of the abdominal tergites. Only in wing color and body size are the conditions found in the eastern populations the most divergent from conditions general in the group. No such "general" condition can be determined for the other three characters because they vary widely in the genus. However, in two of these—the curvature of the apical tooth of the male cercus and the shape of the tubercle of the 7th abdominal sternite of the female—the condition found in the eastern populations is closer to that of *vannifera* (the nearest relative of *spinosa*) than is the condition in the western populations. In the case of the third character, the relative length of the ovipositor, the relationships are unclear. This evidence suggests that the western populations have diverged more from the ancestral *spinosa* than have the eastern ones. The taxonomic treatment of this situation is discussed in the section following the distributional records of this species.

It is interesting to note that all of the color characteristics of the westernmost populations tend to make the individuals appear more sharply variegated. This seems to be correlated with the strongly variegated colors of the desert environment in which these populations live. The eastern environments appear more uniformly green, the result of heavier bush growth and more complete herbaceous ground cover, and *spinosa* populations living there are also more uniformly green. It is likely, therefore, that the coloration of these katydids is in some degree protective, and that the marked geographic variation in coloration is the result of differential selection in differently colored environments.

The geographic distribution of selected characters is discussed and mapped in a section following the records.

DISTRIBUTION (Figs. 3 and 24).—*Neobarrettia spinosa* has a wide distribution over the southern part of the Great Plains Province in Texas and the northern portions of the eastern coastal plain and Northern Plateau

TABLE 1

COMPARISON OF EASTERN AND WESTERN POPULATIONS OF *Neobarrettia spinosa*

Character	Extreme Condition in Easternmost Populations	Extreme Condition in Westernmost Populations
Color of frons and clypeus	Green	Yellow-brown
Color of cephalic margin of pronotum	Very thin, black line not reaching coxa	Narrow black stripe reaching coxa as a black line
Color of caudal portion of pronotum	Green between dorsal edges of ivory stripes; indistinct brownish marks on shoulder	Wide black spot between dorsal edges of ivory stripes; black spot completely interrupting ivory stripe on shoulder
Ivory stripe on dorsum of pronotum	Narrow and reaching only to edge of median third	Wide, prominent and reaching to near midline
Shape of caudal portion of pronotum	Elevated close to a 45° angle and only gently arched (Fig. 20m)	Elevated at almost a 90° angle, strongly and prominently recurved to below horizontal (Fig. 20n)
Dark areas of tegmina	Lighter and least extensive	Darkest and most extensive
Wing colors	Lighter and less distinct	Darker and more contrasting
Color of abdominal tergites	Green	Black with yellow or green caudal border
Apical tooth of male cercus	Long and weakly incurved (Fig. 18b)	Short and strongly incurved (Fig. 18c)
Lateral carinae of female subgenital plate	Always present	Often absent
Tubercle of 7th abdominal sternite of the female	High, curved caudad, apex acuminate	Very low and blunt
Length of ovipositor relative to length of pronotum	Shortest (ratio of 3.5)	Longest (ratio of over 6)
Size	Largest (length of pronotum 11.7 mm.)	Smallest (length of pronotum 6.6 mm.)

of México. Limiting records are as follows: northwestern, 45 mi. E Roswell, Chaves Co., N.M.; northern, 2 mi. NE Holliday, Archer Co., Tex.; eastern, 3 mi. W Cuero, De Witt Co., Tex.; southeastern, 8 mi. SW Santa Teresa, Tamps., Mex.; southern, 10 mi. S Linares, N.L., Mex.; southwestern, 4 mi. SW Lerdo, Dgo., Mex. Most of the range of *spinosa* overlaps that of *victoriae*.

No intensive work has been done in the region of the northwestern and northern limits of this species. In western Texas, scattered observations, collecting records, and the results of one road survey indicate that the species occurs only in scattered colonies west of Marathon (Brewster Co.). At its known northernmost locality (Holliday), *spinosa* was common and is likely to occur north to the Oklahoma border. However, both Cohn and Hubbell have done general collecting in southwestern Oklahoma and have failed to find it there, although *victoriae* was collected at several localities. *Spinosa* may thus penetrate only slightly into Oklahoma if it is able to cross the Red River. The northeastern limits of the species have been carefully worked out in the vicinity of Austin (Tex.), the data for which are summarized on Figure 12 and discussed in Part II. Beyond the southeasternmost record, no *spinosa* has been found in the course of extensive sampling along the Pan-American Highway south of Cd. Victoria (Tamps.). To the west, it is apparently replaced by *pulchella* south of Saltillo (Coah.) at least along the highway to Matehuala (S.L.P.). No *Neobarrettia* has been heard on the Saltillo-Concepción del Oro (Zac.) road, nor southwest of the Lerdo colony on the Torreón (Coah.)-Durango highway which has been surveyed or sampled on several occasions. In Chihuahua, no *Neobarrettia* has been heard north of the Jiménez colony on the Jiménez-Cd. Juárez highway which has been surveyed or sampled, or in several areas to the west of the road. The results of the Jiménez-Cd. Juárez survey are shown on Figure 14 and discussed in Part II.

HABITAT (Figs. 12 and 14).—*N. spinosa* occurs in a variety of dry, bushy habitats through an altitudinal range of 50 to 5400 feet. It is found commonly in the Mesquite Savanna (vegetation regions in Texas are those of Tharp, 1952) of northern Texas, the Oak-Juniper rangeland of the Edwards Plateau of central Texas and the Tamaulipan Thorn Shrub (Muller's 1947 term) of southern Texas and northeastern México. It does not penetrate the Oak-Hickory woodland of eastern Texas or the thorn forest of Tamaulipas, and is apparently absent from the grasslands of eastern and western Texas. The southern limit of the species in Nuevo León corresponds with the northern limit of extensive areas of taller and more luxuriant thorn scrub vegetation.

This species extends far into the deserts of western Texas and Coahuila. Near Del Rio, Texas, where detailed observations have been made, *spinosa* usually occurs in the heavier vegetation of the washes and low ground and only rarely on the more barren desert flats. In the very dry desert east of Torreón, it appears to be restricted to the few scattered groves of tall, thick mesquite bushes. This habitat requirement (or preference) is particularly well illustrated by the colonies of *spinosa* in the Big Bend region of Texas along the road from Santa Elena Canyon to The Basin. At the lower elevation near the canyon, the vegetation is very sparse and low, and consists almost exclusively of small creosote bushes. As the road ascends, the bushes become more closely spaced, taller, more luxuriant and more varied. At the lower elevations, the colonies of *spinosa* are rare and are restricted to the washes, the only places where the bushes grow tall and thick. The colonies become more common at higher elevations, and near the upper altitudinal limit of the species they are found as commonly in the larger bushes on the flats as in the washes.

SEASONAL DISTRIBUTION.—The earliest record for adults in Texas is 9 June at Boquillas (Big Bend Natl. Pk.), Brewster Co., the latest 26 October in The Basin, Chisos Mts., Brewster Co. In México the earliest record is 7 June at Santa Teresa, Tamps.; the latest, 3 November at Jaral, Coah. No search specifically for *spinosa* has been made before or after these limiting dates.

SONG.—This species sings very commonly throughout the night, but rarely and very irregularly during the day. The song consists of a single very loud, resonant phrase repeated continuously at a rate of a little over one per second (early in the evening in northern Texas). Each phrase consists of several syllables delivered too rapidly to be heard individually, imparting a somewhat ragged quality to the phrase. Each syllable is about .05 sec. in duration, the last of a series usually considerably shorter and weaker. The interval between syllables is shorter than the syllable and usually marked by a few hardly audible tooth strikes. The entire phrase is about 0.2 sec. in duration. These details are taken from audiospectrographs of recordings of individuals of the eastern and westernmost populations made in the laboratory at about 75° F. No significant geographic variation in the song was noted. The song of *spinosa* is delivered at a rate about one-half as fast as that of *victoriae*, with which it commonly occurs, and each phrase is shorter and more homogeneous than that of the latter species.

RECORDS.—Material examined: 541 ♂♂, 64 ♀♀, 11 nymphs. TEXAS: Foard Co., Crowell (ANSP); Archer Co. (ANSP), 2 mi. NE Holliday; Baylor Co., Seymour; Jack Co., 3 mi. SE Jacksboro; Palo Pinto Co., 20 mi. SW Mineral Wells; Shackelford Co., Fort Griffin St. Pk. (14 mi. N Albany); Callahan Co., 15 mi. NW Cross Plains; Brown Co., 14 mi. S Cross Plains; Coleman Co., 5 mi. NW Coleman, 13 mi. S Santa Anna; Mills Co., 11 mi. SE Goldthwaite; Lampasas Co., 2–3 mi. SE Lometa; San Saba Co., 8 mi. E San Saba, San Saba (ANSP), 4 mi. S San Saba; Irion Co., 6 mi. S Mertzon; McCulloch Co., Brady (KSU); Burnet Co., 6 mi. E Burnet, 3 mi. W Burnet, 3 mi. N Burnet, 5–9 mi. SW Burnet, Inks Lake St. Pk. (13 mi. SW Burnet), 4 mi. NE Marble Falls, Longhorn Cavern (11 mi. SW Burnet), 5 mi. N Marble Falls, 1 mi. S Marble Falls, Buchanan (17 mi. E Llano, Llano Co.), 15.5 mi. E Llano, 4 mi. NE Kingsland; Llano Co., 20, 16, 2 mi. SE Llano, 16–17, 28 mi. NW Llano, 18 mi. S Llano; Gillespie Co., 18 mi. NW Fredericksburg; Fayette Co., 8–11 mi. S Smithville; Bastrop Co., 2 mi. SW Elgin, 12 mi. W Bastrop; Travis Co., 14, 17–18 mi. WNW Bastrop (Garfield), 5 mi. NE Austin P. O. (W. F. Blair's), McNeil (5 mi. SW Round Rock), Lake Travis (HILL), 5 mi. NW Oak Hill (13 mi. NE Dripping Springs), Cedar Valley (9 mi. E Dripping Springs); Blanco Co., 6 mi. S Johnson City, 3 mi. N Blanco, 8–10 mi. SE Blanco, 9 mi. S Blanco, 14 mi. W Dripping Springs; Hayes Co., 3 mi. E Dripping Springs, 3–8 mi. NW Kyle, 10–15 mi. W San Marcos; Comal Co., 6 mi. NW New Braunfels; Bexar Co., San Antonio, 6 mi. NW San Antonio (city limits), 1, 4 mi. NW Helotes, 6–8 mi. SW Boerne; Bandera Co., 13 mi. N Bandera, 7 mi. SW Bandera, 8 mi. NE Tarpley; Medina Co., 15 mi. NW Hondo, 5 mi. W Sabinal; Kimble Co., 5 mi. SW Junction; Real Co., 37 mi. N Leakey, 22 mi. ENE Rocksprings (Edwards Co.), 14 mi. ENE Rocksprings, 14 mi. NE Leakey, 10–14, 4 mi. NE Camp Wood; Edwards Co., 11 mi. ENE Rocksprings, 11–12 mi. NW Camp Wood, 13 mi. W Rocksprings, 12–21 mi. SW Rocksprings, 23 mi. N Brackettville; Uvalde Co., 5 mi. W Utopia, 32 mi. N Uvalde (Frio River, Garner St. Pk.), 30 mi. N Uvalde, 15 mi. N Uvalde, 15 mi. NW Uvalde, 2 mi. N Uvalde; Kinney Co., 13–20 mi. N Bracketville, 2 mi. S Brackettville; Sutton Co., 10 mi. S Sonora; Valverde Co., 45 mi. N Del Rio (Fawcett Ranch), 45 mi. N Del Rio (2.5 mi. N to 12 mi. NW Loma Alta), 32–37 mi. ENE Del Rio, 20–26, 16, 5, 1.5 mi. N Del Rio, Del Rio (UMMZ, ANSP), 4 mi. E Del Rio, 8 mi. SE Del Rio, 7, 11–13 mi. NW Del Rio, 12 mi. NW Del Rio (Steam Station), 16 mi. NW Del Rio, 6.5 mi. SE Comstock, 10.5 mi N Comstock, 3–4 mi. W Comstock; Pecos Co., 6 mi. W Ft. Stockton; Brewster Co., 16 mi. E Marathon, Marathon (UMMZ, ANSP), 4 mi. S Marathon, 12–13 mi. S Marathon (ANSP, TINK), Hills W Ord Mts. (ANSP), 8 mi. E Alpine (SRSC), Alpine (ARIZ), 46 mi. S Alpine, 2 mi. N Bone Spring (ANSP), Hackberry Creek (Boquillas Rd. ANSP), Persimmon Gap (44 mi. S Marathon, TINK) 5.6 mi. S Persimmon Gap, 3.6 mi. SE Panther Jct. (Big Bend Natl. Pk.), 13.5 mi SE Panther Jct., Boquillas (Big Bend Natl. Pk.), 1.1–2.7 mi. SSE Government Springs Jct. (Big Bend Natl. Pk.), Chisos Mts. (ANSP, SM), The Basin (Chisos Mts., UMMZ, AMNH, TINK, SM), 8.2 mi. NE Santa Elena Canyon (Big Bend Natl. Pk.); Presidio Co., Marfa (TINK), 10 mi. N Shafter (ARIZ), 4 mi. N Shafter (TINK), Shafter (ARIZ), 1 mi. S Shafter (TINK), Chinati Mts. (TINK, ANSP), Ruidosa (TINK), Haciendita (TINK), Presidio (ANSP, TINK); Culberson Co., Guadalupe Mts. (5 mi. S Pine Springs); Guadalupe Co., 4 mi. S Seguin; Gonzales Co., 2 mi. E Smiley; DeWitt Co., 3 mi. W Cuero; Goliad Co., Goliad; Live Oak Co., Three Rivers (ANSP); La Salle Co., 4 mi. NNE Encinal; Dimmit Co., Carrizo Springs (ANSP); Maverick Co., 5.3 mi. NE Eagle Pass; Webb Co., 14 mi SSW Encinal, Laredo (ANSP). NEW MEXICO: Chaves Co., Mescalero Sands (45 mi. E. Roswell, TINK). TAMAULIPAS: 8 mi. SW Santa Teresa. NUEVO LEÓN: 8 mi. SE Camarón, 13 mi. NE Sabinas Hidalgo, 34 mi. S Sabinas Hidalgo, Cola del Caballo Falls (nr. Villa Santiago), 6 mi. SE Villa Santiago, 25 mi. NW Montemorelos, 8 mi. SE Montemorelos, 10 mi. S Linares, 15 mi. W Monterrey (ANSP), 1.7, 3.4, 7.8, 10.3, 12.8, 17 mi. W Santa Catarina, 21 mi. NW Monterrey (TINK), 19 mi. NE Ramos Arizpe (Coahuila). COAHUILA: 34 mi. N Muzquiz, 11 mi. NW Muzquiz, 2 mi. SE Muzquiz, 5–7 mi. N Hermanas, 4 mi. N Hermanas, Rio Salado (1 mi. S Hermanas),

5 mi. S Hermanas, 26 mi. E Cuatro Ciénegas, 13 mi. E Cuatro Ciénegas, 5 mi. NW Cuatro Ciénegas, 3–4 mi. S Monclova, 4, 14, 15, 22, 25, 34, 38.8, 37–44 mi. S. Castaños, Plan de Guadalupe, 42 mi. NW Saltillo (TINK), Jaral (ANSP), 7–10 mi. NW Saltillo, 5 mi. NE Ramos Arizpe, 20 mi. W Saltillo (ANSP), 30–66 km. W Saltillo (ANSP), 4, 7 mi. N Parras, 83 mi. E Matamoros, Sierra de Tlahualilo (nr. Durango line), Sierra de Tlahualilo (3.5 mi. NE Ojo de Agua). DURANGO: 14 mi. E Mapimi, 4 mi. SW Lerdo, CHIHUAHUA: 1 mi. NW Jiménez, Salaices (AMNH).

THE TAXONOMIC TREATMENT OF GEOGRAPHIC VARIATION IN *N. spinosa*

The geographic variation of four characters in this species is mapped in Figures 3 to 6. Of the geographically variable characters in *spinosa* which were listed previously, these four represent the ones most easy to quantify. All of the categories used in the maps have been chosen arbitrarily.

The maps show that the populations found on the coastal plain of Texas and México are distinctly and uniformly different from those found in Trans-Pecos Texas and the region west of the Sierra Madre Oriental in México. The zone of intergradation between these eastern and western forms is very narrow in México and lies within the Sierra Madre. One population in this zone (at 34 mi. S Castaños) shows considerable variation in both male characters mapped (no females were collected at this locality). The narrowness of the zone of intergradation here and the variability of the characters within it, both suggest that the two forms have only recently come into contact with one another at this point. Farther north, however, the zone of intergradation is very wide and covers most of central Texas. In particular areas, the zone is restricted, as in the Del Rio region, and several characters change rapidly from the eastern condition to the western type. In other regions, as in much of north-central Texas, populations show a mixture of the characters of the two forms over wide areas, and in no one population is there much variation in these characters. Thus, in Texas, the two forms have evidently been in contact for a much longer period of time than in México.

The situation appears to be similar to the classic examples of subspecies rings. In this case, however, the two ends, although strongly differentiated, are not reproductively isolated. The ring was probably shaped like a horseshoe until recently, with the two ends occupying two very different habitats, one very dry, the other relatively humid. Because of the large extent of the two extreme habitats, and the great distance from one end of the range to the other, strong adaptive differences were able to develop in the two end populations. The genes controlling these characters have apparently been able to move freely and independently through the entire species population, subject only to selective forces.

It seems clear that the eastern and western populations of *spinosa* do

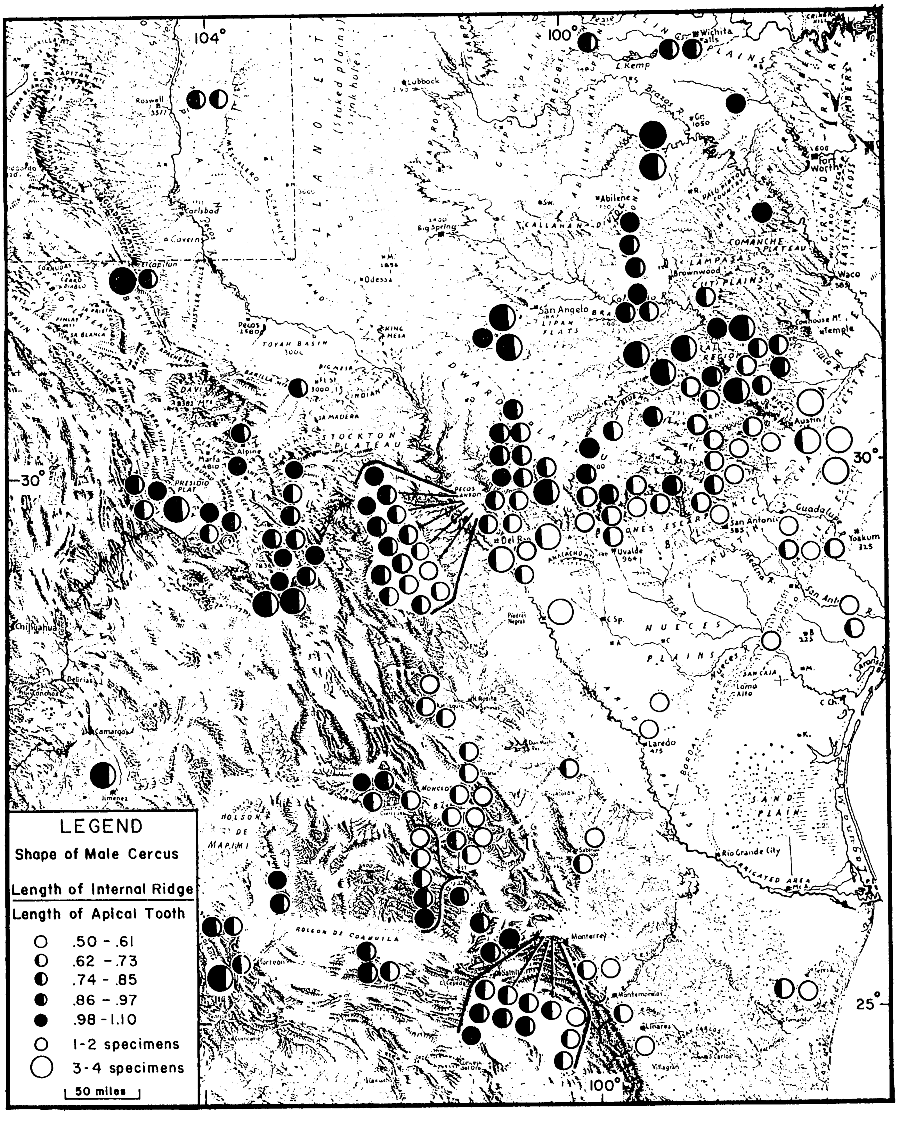


FIG. 3. Geographic variation in *Neobarrettia spinosa*; shape of male cercus.

not represent the distinct units which would qualify for designation as subspecies according to the principles presented earlier in the section on Methods. If the species consisted only of the Mexican populations, the eastern and western forms would be good examples of subspecies. Not only does their pattern of morphological variation indicate a history of

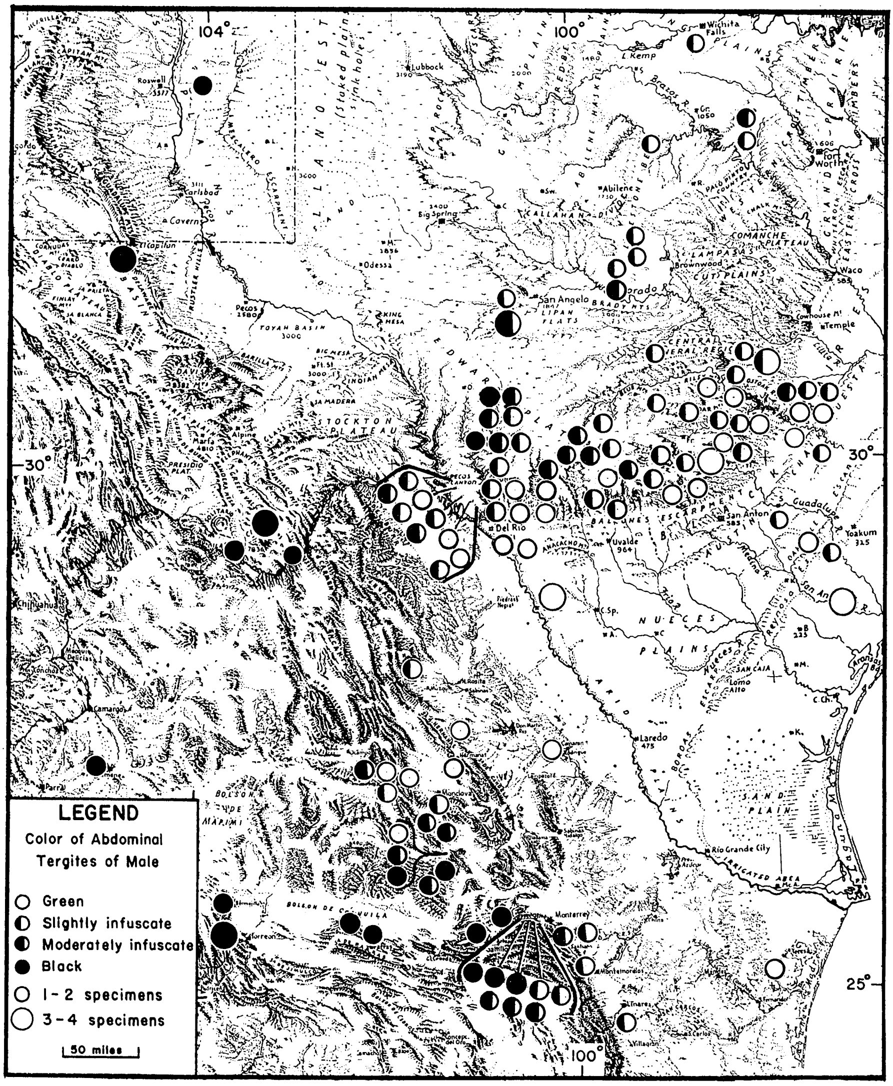


FIG. 4. Geographic variation in *Neobarrettia spinosa*; color of abdominal tergites of male.

relatively long separation and only recent contact, but entirely independent evidence, discussed in Part III, suggests that until recently there has been a formidable barrier between the two populations constituted by a more continuous and higher Sierra Madre Oriental. When the pattern of vari-

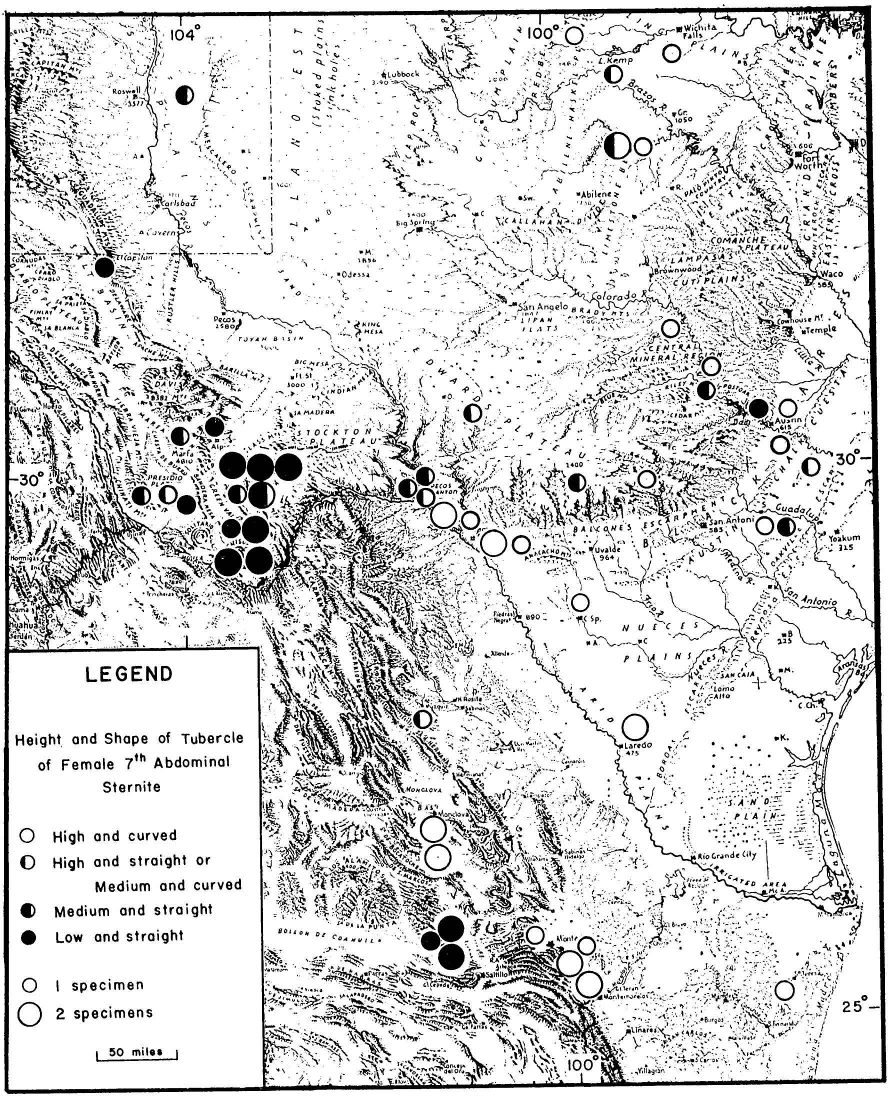


FIG. 5. Geographic variation in *Neobarrettia spinosa*; height and shape of tubercle of female 7th abdominal sternite.

ation of the species as a whole is considered, it is clear that these Mexican populations represent the ends of a series of clines. To designate the two ends as subspecies, defining their limits in Texas in terms of certain arbitrarily selected characters, and to call all of central Texas a zone of intergrada-

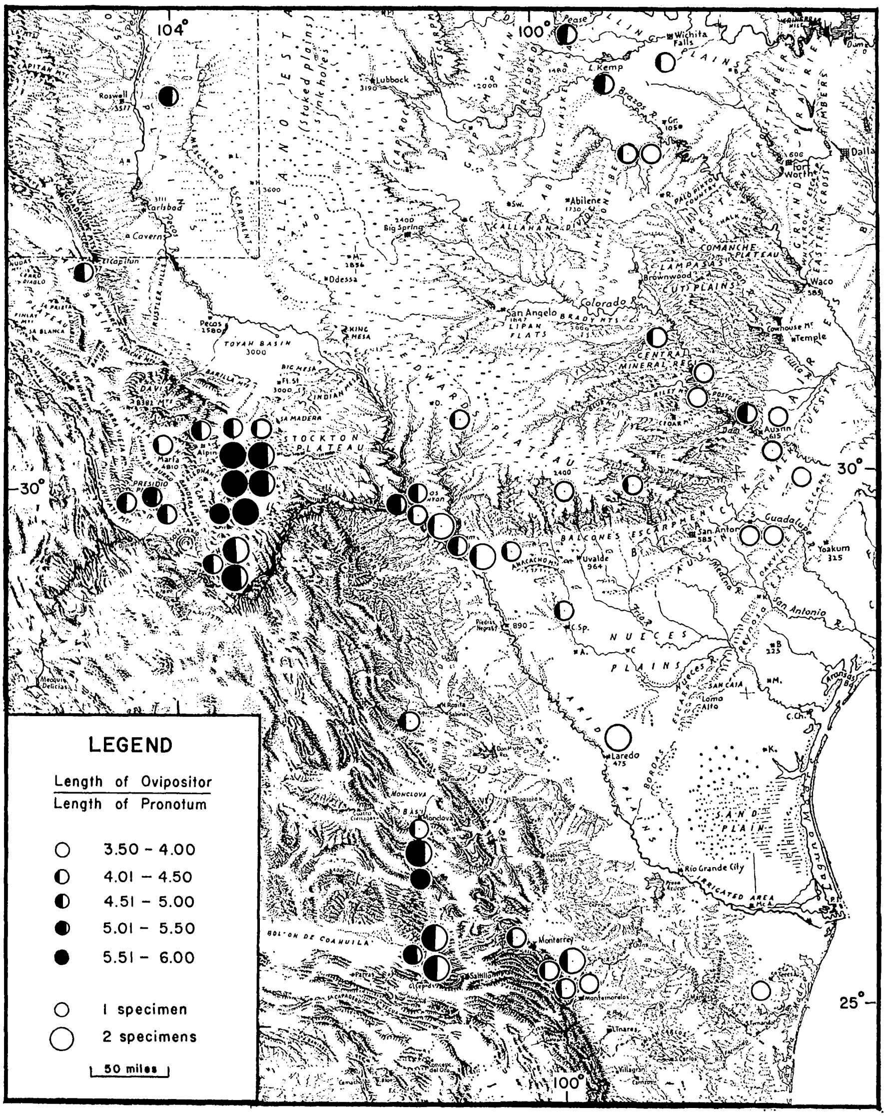


FIG. 6. Geographic variation in *Neobarrettia spinosa*; relative length of ovipositor.

tion, would in no way reflect the apparent biological situation, and would imply the existence of discrete units where in fact there are none. Under our present system of classification, the situation is best handled by description and illustration.

THE SINALOAE GROUP

This group contains *sinaloae* (Rehn and Hebard) and the new species *hakippah*, both of which occur on the northwestern coastal plain of México. They share the following characters which are unique in *Neobarrettia*: titillators well developed and armed with minute spines; cercus of male with a weak proximo-internal "angulation" (which is never acute or produced), a broad internal ridge, and a slender apical tooth which is acuminate at its apex; female subgenital plate with a prominent basal tranverse flange; femoral teeth greenish, briefly tipped with brown; tegmen with discrete black spots between veins (in *imperfecta* most of the membrane is dark and the veins green, giving the tegmen a superficially spotted appearance). The following characters are shared only with *imperfecta*: caudal portion of pronotum strongly turned up in male but only weakly so in female; tegmen of female somewhat shorter than that of male (but never as reduced as in females of *imperfecta*); tegminal reticulation reduced, cross veins more or less regularly spaced; wings white with black spots. In addition to these characters, the following two are distinctive: tegmina very short, in females .60 to .83 times length of fore femur (considerably longer than in *imperfecta*, but shorter than in any other species of the genus), in males .76 to 1.06 times length of fore femur (overlapping the tegminal measurements of *cremnobates*, *imperfecta*, and the smallest *victoriae*, but averaging distinctly less than any of the three; see measurement summary in Figs. 21 and 22); female subgenital plate broadly emarginate (as in some individuals of *spinosa*).

The Sinaloae Group shares several distinctive characters with *imperfecta* which are listed above. All of them may be the results of the manifold effects of the reduction of tegmen and wing size. The similarities may therefore be attributed to parallel development rather than to phylogenetic relationship. The matter is further discussed in terms of functional relationships under the taxonomic treatment of *imperfecta*.

The relationship of the Sinaloae Group to other species groups in the genus appears to be distant. The distribution of characters considered to be significant in determining relationships is shown in Table 2.

N. hakippah differs from *sinaloae* in four of the characters listed in Table 2. I believe these differences to be secondary intragroup developments in view of the apparent derivation of the former species from the latter, the evidence for which is given under *hakippah*. The data presented in Table 2 suggest a general relationship of the Sinaloae Group with the Cremnobates and Victoriae Groups, and a more distant relationship with the Spinosa Group. The characters of wing and spine color are shared by all but the Spinosa Group, and those of the color of the pronotal border and of the

TABLE 2

DISTRIBUTION OF CHARACTERS SUGGESTIVE OF RELATIONSHIPS BETWEEN THE SINALOAE AND OTHER GROUPS

Sinaloae Group	Cremnobates Group	Victoriae Group	Spinosa Group
Male tegmen with dark area in disto-cephalic portion of stridulating field	+	+	+
Female subgenital plate with median carina short and arcuate, lateral carinae present and oblique (except in *hakippah*)	± (median carina low)	+	+ (*spinosa*)
Wing colors opaque	+	+	–
Femoral teeth light colored but dark at apex	+	+	–
Cephalic border of pronotum with dark margin (except in *hakippah*)	+	–	+
Male cercus with median tooth visible from above	–	+	–
Male cercus elongate; internal ridge short, joining shaft very gradually (except in *hakippah*)	–	–	+ (*vannifera*)
Eyes bicolored	+	–	–
Tubercle of 7th abdominal sternite of female high, conical, apex acute and curved caudad, base broad (except in *hakippah*)	± (variable)	–	+ (eastern *spinosa*)

male tegmen may represent retentions of primitive characters in the Sinaloae Group.

Neobarrettia sinaloae (Rehn and Hebard) (Figs. 17j, 18d, 18f, 20b, 20g)

1920. *Rehnia sinaloae* Rehn and Hebard, Trans. Amer. Ent. Soc. 46:240–44, [♂, ♀-“Venvidio,” Sinaloa, México].

HOLOTYPE.—Male, “Venvidio,” Sinaloa, México, Aug. 14, 1918, J. A. Kusche; Hebard Coll. Type No. 534, Academy of Natural Sciences of Philadelphia. This town, “Venvidio,” the name of which appears under various spellings in other publications, is the type locality of a number of other insects collected by J. A. Kusche. Despite considerable search of maps and gazetteers by several interested taxonomists, the town has not hitherto been identified with assurance. Recently, Dr. I. J. Cantrall of the University of Michigan Museum of Zoology made a careful study of the problem. By an ingenious analysis of Kusche's correspondence, the dates of his various collections, the mode and speed of transportation available to him, and the possible phonetic variations of the name "Venvidio," which appears on no map and is unknown to residents of Sinaloa, Dr. Cantrall concluded that the locality must be the town of El Venadillo which is located four miles north of the Mazatlán Airport. In order to check this determination, several collections have been made by Dr. Cantrall and myself at various times in and near this town. Most of the Orthopteran species which have been recorded from "Venvidio," including *N. sinaloae,* were found at El Venadillo.

COMPARISONS.—The principal differences between this species and its closest relative, *hakippah,* are set forth in Table 3. In addition to these there appear to be less distinct differences in the color of the tegmen and the shape of the titillators. These characters have not been thoroughly studied because of their great infra-specific variability and the difficulty in quantifying them. The apex of the titillator is generally broader and more blunt, and has a larger number of smaller and more regularly-spaced spines in *sinaloae* than in *hakippah.* The stridulating field of the male tegmen in *sinaloae* is usually more or less concolorous with the rest of the tegmen and is often sprinkled with fine, obscure, black spots; that of *hakippah* is often a uniform yellowish, contrasting with the rest of the tegmen.

Despite the many differences between these two species, there are indications of limited interbreeding and backcrossing between them. The evidence and its bearing on the specific status of the two forms is discussed at length in a section following the treatment of *hakippah.*

Morphological data suggest that *sinaloae* has directly given rise to *hakippah.* In most of the characters by which the two species differ, the condition in *sinaloae* is most like that of other species of *Neobarrettia,* while that in *hakippah* is unique in the genus. In the remaining characters, the condition in *hakippah* may be readily derived from that in *sinaloae.* A detailed analysis is presented in the treatment of *hakippah.*

SPECIES DESCRIPTION.—PRONOTUM (Fig. 20b): caudal portion turned up at an angle between 30° and 45° in males, and less than 30° in females, and usually gently recurved to or near horizontal; humeral sinus usually absent, sometimes weakly indicated. APPENDAGES: tegmen very short (in males .76–.97, in females .60–.76 times length of fore femur); reticulation greatly reduced, cross veins more or less regularly arranged; cross veins of wing obsolete, barely visible with transmitted light; caudal armature of fore femur rarely with one or two minute teeth among larger ones. MALE

TABLE 3

COMPARISON OF *Neobarrettia sinaloae* AND *hakippah*

Character	*sinaloae*	*hakippah*
Color of cephalic border of pronotum	Margined with a narrow dark brown line	Yellow or yellowish brown
Cercus of male	Apical tooth long, .31–.47 times length of pronotum; basal tooth rectangulate; distal portion of internal ridge joining shaft gradually (Fig. 18d)	Apical tooth short, .18–.29 times length of pronotum; basal tooth broadly rounded; distal portion of internal ridge joining shaft abruptly (Fig. 18e)
Penultimate tergite of male	Mesal excision narrow, deep, angulate; distance between apices of lobes .20–.31 times length of pronotum (Fig. 20g)	Mesal excision broad, shallow, rounded; distance between apices of lobes .27–.41 times length of pronotum (Fig. 20f)
Subgenital plate of female	Median and lateral carinae about one-half length of plate; median carina arcuate; lateral carinae strongly curved; lateral pits nearer midline, partly concealed by a fold (Fig. 17j)	Median and lateral carinae about as long as plate; median carina not arcuate; lateral carinae almost straight; lateral pits more distant from midline, open (Fig. 17k)
Tubercle of 7th abdominal sternite of female	Located on median third of plate; conical, high (Fig. 17j)	Located at or very close to caudal margin of plate; rectangulate in side view, compressed, low (Fig. 17k)
Color of occiput	Generally green, some individuals in north with a dark suffusion over much of dorsum (Fig. 7)	Usually with a prominent black spot, becoming weak southward and often absent in southern populations (Fig. 7)
Color of cephalic face of hind femur	Uniformly green, without a black stripe (Fig. 7)	Green, with a black, longitudinal stripe; stripe becoming lighter southward, often absent in southern populations (Fig. 7)
Relative length of tegmen	Shorter, in males .76–.97, in females .60–.76 times length of fore femur (Fig. 22)	Longer, in males .85–1.06, in females .64–.83 times length of fore femur (Fig. 22)

TERMINALIA: caudal margin of penultimate tergite (Fig. 20g) with mesal excision distinctly but obtusely angulate, margin on either side produced into blunt-tipped rectangulate lobes; margin of semimembranous area usually smoothly continuous with that of lobes, sometimes with a weak distolateral angle, sometimes raised, never tuberculate; cercus (Fig. 18d) elongate (.7–.9 times width of penultimate tergite), apical tooth long, slender, very weakly curved inward, apex acuminate; internal ridge simple, shelf-like, short (no more than about .33 times length of entire cercus), broad and prominent, proximo-internal angulation rectangulate, sometimes briefly rounded, never produced; median tooth short, briefly acute to briefly acuminate, bent ventrad but visible from above; distal portion of internal ridge very gradually joining shaft of cercus; titillators (Fig. 18f) two, well developed, their length about .35 times width of penultimate tergite; bases separate, broad, membranous above, sclerotized below, tapering rapidly to completely sclerotized finger-shaped cylinders with blunt apices; armature on distal third variable, usually consisting of numerous small spines curved proximad on apex, sides and venter; spines often larger and less numerous than shown in Figure 18f. FEMALE TERMINALIA (Fig. 17j): caudal margin of subgenital plate usually with a broad and shallow, sometimes obtuse-angulate emargination; median carina strongly arcuate, obsolete on distal third of plate; lateral carinae not upraised, but forming edge of an oval depressed area on caudal two-thirds of plate; a deep transverse pit cephalad of, and partly concealed by, a low transverse ridge just mesad of lateral articulation of caudal portion of plate; a strong transverse flange forming cephalic margin of plate. Tubercle of 7th abdominal sternite prominent, often very weakly compressed, base broad, occupying cephalic two-thirds of plate, apex acuminate, directed caudad. COLORATION: eyes in life yellowish below, brownish above; occiput usually with a short transverse dark line on caudal margin, sometimes weakly infuscate, sometimes with entire dorsum suffused with brownish black; cephalic border of pronotum narrowly margined with dark brown or black which extends ventrad to near ventro-cephalic angle, rarely with a narrow, indistinct yellowish band just caudad of margin; caudal margin yellowish, sometimes dark brown; ivory stripe of lateral lobe margined cephalad with a narrow brown band (often very dark) which broadens and darkens on shoulder and proceeds thence caudad to form a narrow dorsocaudal brown border on metazona; dorsum of pronotum sometimes lightly infuscate; metanotum and mesal portion of mesonotum light brown; venter of abdomen on either side with a longitudinal yellow stripe ventral to tergites and another lateral to sternites, each often indistinct, broken and appearing to be double; tegmen in both sexes greenish brown; irregular but discrete black spots in most of cells cephalad of vein M, and scattered spots in cells caudad of M in females; male tegmen with stridulating area brownish green, usually no lighter than rest of tegmen, often with many small, indistinct spots; area between veins M and Cu_{1b} and the distocephalic portion of mirror sometimes with a dark brown wash; wing colors opaque, white with small irregular black spots between veins; femoral teeth greenish, briefly tipped with brown; dorsal surface of all tibiae light brown to chestnut brown. MEASUREMENTS: these of the series studied are summarized in Figures 21 and 22.

VARIATION.—The armature and shape of the apices of the titillators are variable. One extreme condition is similar to the average in *hakippah* (see under Comparisons). The color of the stridulating field of the male tegmen is also variable, but the average condition is fairly distinct from that in *hakippah* (see under Comparisons). The suffused occiput is found only in the northern half of the range of this species and may be the result of introgression from *hakippah* (Fig. 7). The suffusion, however, is much more extensive and less circumscribed than that found in *hakippah.* It is also much more extensive than the average condition found in the southernmost populations of that species from which the character might have been derived. I am therefore not certain whether the dark suffusion is entirely homologous with that in *hakippah.* The variation in the male cercus, penultimate tergite, and length of tegmen is illustrated in Figure 8 and is discussed in the section following the treatment of *hakippah.*

Although *sinaloae* seems to be amply distinct from *hakippah,* the presence of three possible hybrids in the zone of contact between the two, and the geographic variation in the occipital color of both species and in the femoral color of *hakippah,* brings into question the specific status of the two forms. In contrast to the variation in these characters, the pattern of geographic variation of the cercus and penultimate tergite of the male, illustrated in Figure 8, strongly suggests a "reinforcement phenomenon"[8] between the two species. The problem is discussed in detail in the section following the treatment of *hakippah.*

DISTRIBUTION (Figs. 9 and 24).—The limiting records for this species are as follows: northern, 1 mi. S Caminajuato (14 mi. N Culiacán), Sin.; eastern, 4 mi. SW Santa Lucía, Sin.; southern, 15 mi. S Acaponeta, Nay. (song record). Considerable survey work done in the northern portion of the range of this species is summarized in Figure 9 and discussed in the section following the treatment of *hakippah.* In the vicinity of Culiacán, north of the Río Culiacán and west of the Río Humaya, only one individual of *sinaloae* has been found (1 mi. NW Río Culiacán at Culiacán) among the abundant *hakippah* near the banks of the rivers. Immediately south of the Río Culiacán, *sinaloae* is very common within Culiacán itself. Along the east side of the Río Humaya, colonies of *sinaloae* alternate with colonies of *hakippah,* while one-half mile inland, between Culiacán, Palos Blancos, and Tepuche, only colonies of *sinaloae* are found. A similar pattern was found between Tepuche and Caminajuato, although this area has not been as thoroughly surveyed as that farther south. East of the Río Humaya, no investigation has been made north of Caminajuato or farther than 4 mi. N Tepuche. Since *sinaloae* was present near the former locality and common at the latter, it probably extends farther north than the records indicate. The only transect across or into the Sierra Madre Occidental has been made on the Mazatlán-Durango Highway. The species was common from Concordia to 4 mi. SW Santa Lucía, Sin. in late October, 1958. In late

---

[8] A phenomenon in which selection against hybridization or competition between two closely related species results in greater differences between them where they are sympatric than where they are allopatric (see, for example, Moore, 1957).

August, 1961, the last colony was found at 8.6 mi. SW Santa Lucía, but it is possible that the species had not yet matured at higher elevations. The species has been heard commonly along the west coast highway as far south as 15 mi. S Acaponeta, Nay. No *sinaloae* have been heard between that point and Tepic, Nay., on several surveys along the main highway, or between Ruíz and the base of the Sierra Madre at Venado, Nay. None have been found in the Tepic region or in the barrancas east of Ixtlán del Río, Nay. and none have been heard along the main highway between Tepic and Guadalajara, Jal., on the several occasions when this route has been investigated.

HABITAT.—The range of *sinaloae* lies in a region mapped as thorn forest and tropical deciduous forest, but the species has been collected almost exclusively in roadside and ruderal habitats in this region. It occurs virtually continuously in all disturbed habitats except weeded fields. Investigation inside the thorn forest has been made at only a few localities. The species has been heard commonly deep within the thorn forest northeast and southwest of Tepuche. It has also been heard and collected within the thorn forest, but only a few hundred yards from the edge, at several other localities including the following: 39.9 mi. SE Culiacán, El Venadillo (4 mi. N. Mazatlán airport), 6.7 mi. NE Concordia, all in Sinaloa. Between Mazatlán and Durango the species was heard commonly between Concordia and 4 mi. SW Santa Lucía, the easternmost record. The Santa Lucía locality lies at an elevation of about 3500 feet and is just below the oak zone in which no *sinaloae* have been heard. According to Leopold's map (1951), the region around and below Santa Lucía is covered with tropical deciduous forest. Since all the records of *sinaloae* are from along the road, there is no certainty that the species occurs within that type of forest. Its abundance along the roadside suggests that in this area it occupies an environment more nearly like the drier thorn forest found at lower elevations. *N. sinaloae* is absent from the palmetto savannas south of Acaponeta, and from the heavy forest at the base of the Sierra at Venado, as well as from the forests along the road to Tepic. On the east bank of the Río Humaya north of Culiacán, *sinaloae* occurs only in the thorn forest when its close relative, *hakippah*, occupies the adjacent fields (Fig. 9). It appears that each species is restricted in its habitat occupancy here by the presence of the other species (see detailed discussion of this point following the treatment of *hakippah*).

SEASONAL OCCURRENCE.—The earliest record for this species is 11 August at El Venadillo and the latest is 21 November at 1 mi. W Acaponeta. It was heard fairly commonly along the west coast highway throughout its range in

Page 49 — Footnote 9, Insert חכפח, between "Hebrew," and "ha'kippah"

the middle of November. No collecting specifically for *Neobarrettia* has been done in this region before or after these limiting dates.

SONG.—*N. sinaloae* sings very commonly during all but the early hours of daylight and through the early hours of the evening. Later in the night, fewer individuals are heard and the song slows, becomes irregular, and eventually all but ceases in the predawn hours. On chilly evenings late in the season singing usually stops well before midnight. The call consists of a simple short syllable, delivered in bursts of two or more (except in very cold weather or late at night when the call may be reduced to one syllable). The interval between bursts is usually not much longer than the interval between syllables. The number of syllables per burst is quite variable. The call rate in the middle of a clear, hot afternoon in August was between two and five syllables per second at 83° F. On a hot evening (the next night) the call rate was five to ten syllables per second at 81° F. Each syllable is about .05 seconds in duration, the interval between syllables within a burst about 0.1 seconds (measured from audiospectrographs of recordings made in the laboratory at about 75° F. of individuals from Mazatlán and Culiacán). In the field the call rate of *sinaloae* is about double that of *hakippah* at the same temperature, and the number of syllables per burst always greater, usually over four.

RECORDS.—Material examined: 172 ♂♂, 55 ♀♀, 10 nymphs. Locality starred is north of the Río Culiacán and west of the Río Humaya. All other records in the Culiacán region are from east of the Río Humaya or south of the Río Culiacán. SINALOA: 1 mi. S Caminajuato (14 mi. N Culiacán); 0.5, 4 mi. N Tepuche; 4, 5 mi. SW Tepuche; 1, 2–3 mi. S Palos Blancos; 6.9, 6, 4 mi. N Culicán; 3 mi. NE Culiacán; 7 mi. E Culiacán; Culiacán; 1, 2, 3 mi. W Culiacán; *1.5 mi. NW Culiacán; 1.5, 6, 13, 17, 19.9, 37, 38, 39.9, 72 mi. SE Culiacán; 50, 40, 20 mi. NW Mazatlán Airport; El Venadillo (4.5 mi. NE Mazatlán Airport, UMMZ, ANSP); 4, 7.8 rd. mi. SW Santa Lucía; 3 mi. NE Concordia; 6.7 mi. SW Concordia; 26 mi. NW Escuinapa; 11 mi. SE Escuinapa. NAYARIT: 1 mi. W Acaponeta; 2 mi. S Acaponeta; 8.6 mi. SE Acaponeta; 15 mi. SE Acaponeta (song record, T. J. Cohn).

Hybrids between *sinaloae* and *hakippah*. SINALOA: 2♂♂, Palos Blancos; 1♀, 2–3 mi. S Palos Blancos.

Neobarrettia hakippah[9] new species (Figs. 17k, 18e, 18g, 20a, 20f)

HOLOTYPE.—Male, 42 mi. NW Culiacán, Sinaloa, México, 2 Sept. 1957 (T. J. Cohn and E. R. Tinkham, No. 98); University of Michigan Museum of Zoology.

COMPARISONS.—This species is most closely related to *sinaloae*, from which it may be distinguished by the characters given in Table 3. Of those

[9] From the Hebrew, ha'kippah, the traditional Jewish headgear, a skullcap, worn during worship; in allusion to the black spot on the occiput of this species.

eight characters, the condition of five in *hakippah* represent unique developments in *Neobarrettia*: the black spot on the occiput, the black stripe on the femur, the rounded proximo-internal "angulation" of the male cercus, the elongate lateral carinae of the female subgenital plate, and the caudal position of the tubercle of the 7th abdominal sternite of the female. By contrast, in *sinaloae* the condition of each of these features is similar to, or identical with that found in most of the other species of the genus. In addition, *sinaloae* closely resembles either *victoriae* or *vannifera* in three more characters by which it differs from *hakippah*: the elongate lobes of the male penultimate tergite and the strongly arcuate and caudal obsolescence of the median carina of the female subgenital plate, both as in *victoriae*; the general shape and proportions of the male cercus as in *vannifera*. While the condition of these three characters in *hakippah* cannot be considered unique, they show considerably less detailed similarity to any of the other species of the genus than do those in *sinaloae*. Only in its relatively longer tegmen does *hakippah* possess a condition more primitive than *sinaloae*. However, the difference between the two species is quite small and the individual variation great. There is no reason to believe that the tendency toward reduction of length of tegmen could not have been reversed to a slight degree in the ancestral *hakippah* population. *N. hakippah* is similar to other species in the genus in the following characters, all of which I consider to be superficial for the reasons cited: the median carina of the female subgenital plate is concave as in *cremnobates* (but in that species the carina is shorter and the plate very differently shaped); the compression and the rectangulate shape of the tubercle of the 7th abdominal sternite of the female are somewhat similar to individuals of *victoriae* and *pulchella* (but in other individuals of those two species the tubercle is differently shaped, and in all it is located near the middle or cephalic portion of the plate); the dark occiput suggests the condition found in the Pulchella and Imperfecta Groups (but the occiput is similarly darkly suffused in some individuals of *sinaloae*).

To summarize, in all but one of the characters by which *hakippah* and *sinaloae* differ, the condition found in *sinaloae* is similar to that in some or all of the other species of *Neobarrettia*, while the condition found in *hakippah* is unique in the genus or at least shows no detailed similarity to any other species. The single exception is tegmen length in which the difference between the species is too slight to be of any significance. There appears to be no morphological bar to the derivation of the characteristics of *hakippah* from conditions in *sinaloae*. The sum of the morphological evidence strongly suggests that *hakippah* was derived directly from *sinaloae*.

There are some indications that *hakippah* is interbreeding and backcrossing with *sinaloae*. These are analyzed in the section following the geographic distribution of *hakippah*, and the reasons for considering the two as distinct species are there discussed.

SPECIES DESCRIPTION.—PRONOTUM (Fig. 20a): caudal portion turned up at an angle between 30° and 45° in males and less than 30° in females, usually gently recurved to or near horizontal (in holotype, about 45° and weakly recurved); humeral sinus absent or weakly indicated (absent in holotype). APPENDAGES: tegmina very short (in males .85–1.06, in females .64–.83 times length of fore femur; .97 in holotype); reticulation greatly reduced, cross veins more or less regularly arranged; cross veins of wing obsolete, barey visible with transmitted light; caudal armature of fore femur sometimes with one or two minute teeth among larger ones (one in holotype). MALE TERMINALIA: caudal margin of penultimate tergite (Fig. 20f) with mesal excision broad, shallow, and rounded; margins on either side produced into short, blunt-tipped, more or less rectangulate lobes; semimembranous area obsolete, when visible, appearing as a small lighter area and rarely depressed; cercus (Fig. 18e) shorter than in *sinaloae* (its length .4–.6 times width of penultimate tergite), apical tooth shorter, slender, weakly to strongly incurved, apex acuminate; internal ridge simple, shelflike, about one-half length of entire cercus, very broad and prominent, proximo-internal region broadly rounded and not at all produced; median tooth more prominent than in *sinaloae*, apex subacuminate, bent gently ventrad and generally visible from above; distal portion of internal ridge broad, joining shaft of cercus much more abruptly than in *sinaloae*, but at a rounded angle; titillators (Fig. 18g) as in *sinaloae* except apex more acute and spines fewer, larger and less regularly arranged; sometimes entirely like those of *sinaloae* (holotype with former condition). FEMALE TERMINALIA (Fig. 17k): caudal margin of subgenital plate usually with a broad and shallow, sometimes obtuse-angulate emargination; median carina low, usually weakly concave, more or less obsolete on caudal quarter of plate and absent on cephalic eighth; lateral carinae extending almost entire length of plate, very broad, somewhat convergent distad, appearing to be formed as edge of a central longitudinal depression and by sharp dorsal flexure of lateral third of plate; a prominent, open, round pit proximad of lateral articulation of distal portion of plate, considerably more lateral than in *sinaloae*; a strong transverse flange forming cephalic margin of plate; tubercle of 7th abdominal sternite of medium height, lower than average condition in *sinaloae*, compressed; in side view nearly rectangulate, with a long cephalic and short caudal edge; base narrow, extending over caudal three-quarters of plate; apex acute, located over or very near caudal margin of plate. COLORATION: eyes in life brownish above, yellowish below; occiput with a mesal dark marking, varying in extent from a jet black band running from eye to eye, or a rounded black spot (a small dark spot in holotype), down to a small, dark suffusion, or sometimes absent (band and discrete dark spot unique in *Neobarrettia*); individuals with lightest or no spot always with a short, dark, transverse bar in center of caudal margin. Cephalic margin of pronotum yellowish or very light brown, usually succeeded by a narrow yellowish band; caudal margin yellowish; cephalic border of ivory stripe with a very narrow brown margin (sometimes black), which becomes broader and darker on shoulder, passing thence caudad to form a narrow caudal brown border on pronotum (dark brown in holotype); dorsum of pronotum sometimes lightly infuscate; mesal portion of mesonotum and often much of metanotum light brown (metanotum in holotype apparently green); venter of abdomen on either side with a longitudinal yellow stripe ventral to tergites and another lateral to sternites (stripes in life probably irregular as in *sinaloae*); tegmen yellow-green to light brownish green, with irregular but discrete black spots in most cells cephalad of vein M, spots more scattered caudad of vein M in females; stridulating area of male tegmen usually distinctly yellowish and lighter than rest of tegmen, area between veins M and Cu_{1b} often with blackish or brownish wash extending into mirror (in holotype, tegmen greenish yellow, wash present but light); wing colors opaque, white with small irregular black spots between veins; femoral teeth greenish, briefly tipped with brown; cephalic face of hind femur usually with a black longitudinal stripe, often light (very light in holotype), sometimes absent (stripe unique in *Neobarrettia*); dorsal surface of all tibiae dark to light brown (light brown in holotype). MEASUREMENTS (in mm.): Holotype male: length of pronotum, 6.6; width of pronotum, 5.0; length of tegmen, 11.1; length of femora: fore, 11.5, middle, 11.4, hind, 30.0. Measurements of the series studied are summarized in Figures 21 and 22.

PARATYPES.—All specimens examined in this study have been designated as paratypes, except for hybrids or badly damaged specimens. Male and female paratypes are deposited in the University of Michigan Museum of Zoology, the Academy of Natural Sciences of Philadelphia, the U. S. National Museum, and in the Tinkham Collection.

VARIATION.—Mention has been made under *sinaloae* and in the above description of the considerable individual variation in the shape and armature of the apices of the titillators and in the color of the tegmen in males of this species. Although there is wide overlap with *sinaloae* in the condition of these structures, there seem to be fairly pronounced average differences. Strong geographic variation is displayed by *hakippah* in the color of the occiput and the color of the cephalic face of the hind femur. Individuals with the darkest occiput and femur are found in the north, those with the lightest in the south. Less marked north-south variation is seen in the length of the apical tooth of the cercus, the width of the excision of the penultimate tergite, and the length of the tegmen of the male. The variation in all five characters is illustrated in Figures 7 and 8, and is discussed in the section below on the specific status of *sinaloae* and *hakippah*.

DISTRIBUTION (Figs. 9 and 24).—The limiting records for this species are as follows: northern, 39 mi. SSW Magdalena, Son.; eastern, Ures, Son. (song record, Tinkham), 8 mi. E Alamos, Son., and Badiraguato, Sin. (song record, Cohn); southern, Culiacán (S end RR bridge), Sin. Although no special survey has been made north of the Culiacán region, my recollection of the 1957 Cohn-Tinkham trip is that the species was almost continuously distributed throughout its known range along the west coast highway. Since the veteran Orthopterist, E. R .Tinkham, has collected intensively throughout southern Arizona without having found *hakippah,* it seems likely that the species does not occur much farther north of the northernmost record given above. The easternmost records represent the easternmost limits of my collecting; the species probably extends to the base of the mountains.

The southernmost part of the range of *hakippah* has been very intensively studied; the results are summarized in Figure 9. North of the Río Culiacán and east of the Río Humaya, only *hakippah* has been found, with the exception of a single individual of *sinaloae* at 1 mi. NW Río Culiacán at Culiacán. East of the Rio Humaya *hakippah* occurs in scattered colonies only along the river from Caminajuato (14 mi. N Culiacán) to 1.5 mi. N Culiacán. No investigation has been made north of Caminajuato. The species is not known south of the Río Culiacán, except at the south end of the railroad bridge which crosses the river; *sinaloae* is in exclusive occupancy of the city itself (in vacant lots) and to the south and east.

HABITAT.—Throughout its range, *hakippah,* like *sinaloae,* has been found commonly in the ruderal habitats along roads. In the northern desert country the species occurs at least in the roadside bushes, which are usually larger and more dense than those several yards away in the desert proper. In the south, where more intensive studies were conducted, the habitat of this species ranges from weedy fields (both in crops and fallow) through bushy second growth to thorn forest (Fig. 9). It has been heard deep in thorn forest between Jesús María and Agua Caliente, west of Tecorito, and west of Agua Caliente, all in Sinaloa. It has been heard also within the forest, but close to its edge, at 2.5 mi. N Culiacán and 42 mi. NW Culiacán, both in Sinaloa. East of the Río Humaya, *hakippah* is found only in the weedy fields next to the river. It is completely replaced by *sinaloae* in the adjacent thorn forest. In the fields at Palos Blancos and Tepuche, the colonies of *hakippah* are very large and dense. No investigation has been made in the foothills or at higher elevations in the Sierra Madre Occidental.

SONG.—*N. hakippah* sings during all but the early daylight hours and during most of the night. Late in the evening fewer individuals seem to be singing; the songs slow down and become very irregular, and usually cease entirely in the predawn hours. The song consists of a simple syllable delivered singly and continuously repeated, or delivered in bursts of two to four, with the interval between bursts slightly longer than that between syllables. Under an overcast sky in the late afternoon, the call rate was three or four syllables per second at an estimated temperature of 80° F. The length of each syllable was about .075 seconds duration in the song of males from Culiacán, Navajoa and Guasave, recorded at about 75° F. in the laboratory. The length of the syllable in the song of one male from either Hermosillo or Guasave was about .15 seconds, and the interval between syllables in a two-syllable phrase was about .12 seconds, as measured from an audiospectrograph of a recording made in the laboratory at 79° F. The song of this species is about one-half as fast as that of *sinaloae* at the same temperature, and contains fewer syllables per burst—usually only two, sometimes as many as four, but rarely if ever more.

RECORDS.—Material examined: 227 ♂♂, 37 ♀♀, 23 nymphs. Localities starred are east of the Río Humaya or south of the Río Culiacán. All other localities in the Culiacán region are west of the Río Humaya and north of the Río Culiacán. SONORA: 39 mi. SSW Magdelena, 49 mi. N Hermosillo, 40 mi. N Hermosillo (TINK), 45 mi. S Hermosillo, 33 mi. SE Guaymas, 25 mi. WNW Obregón, 10 mi. S Obregôn, 8 mi. E. Alamos (Río Cuchujaqui, TINK), 1 mi. NW Alamos, 5 mi. W Alamos (ARIZ), 4.7 mi. S Navajoa, 9 mi. S Navajoa (TINK), 50 mi. SSE Navajoa. SINALOA: 13 mi. N. Los Mochis (TINK); 19 mi. NW Guasave (UMMZ, TINK); 42, 19, 8 mi. NW Culiacán; *1 mi. S Caminajuato (14 mi. N Culiacán); Tecorito (13 mi. N Culiacán); *2 mi. E. Tecorito; *2 mi. SW Tepuche (11 mi. NE Culiacán); Agua Caliente (13 mi. N Culiacán); 2 mi. W Agua Caliente; *Palos Blancos (9 mi. N Culiacán): *1 mi. S Palos Blancos; *7.6 mi. N Culiacán (Hacienda Simón); El Barrio (7.5 mi. N Culiacán); 3 mi. N. Culiacán; *1.5 mi. N Culiacán; 1–2 mi. E Culiacancito; Santa Rosa (5 mi. E Culiacancito); 2.5, 2, 1 mi. NW Culiacán; N Bank Río Culiacán at Culiacán; *Culiacán (S end RR. bridge).

HYBRIDIZATION AND THE STATUS OF *N. sinaloae* AND *N. hakippah*

Although *sinaloae* and *hakippah* are as strongly differentiated as any of the other species of *Neobarrettia,* there are several indications that there may be gene flow between the two forms. First, several individuals in the zone of contact show either intermediacy in certain diagnostic characters, or a combination of the characters of the two forms. Second, two clines appear to pass across the boundary between the two. Finally, several characters show overlapping patterns of variation in the two forms. In order to determine whether interbreeding is taking place, and if so, what effect it is having, the variation in ten diagnostic characters has been carefully analyzed.

The geographic variation in the color of the occiput and of the hind femur is summarized in Figure 7. Color as well as geographic variation in both characters is continuous. Almost any other north-south groupings would show the same pattern. Samples from the Culiacán region (placed between the dashed lines in the graph) have been grouped in order to emphasize the possible influence of one form upon the other. Thus, the "W Side R. Humaya" grouping includes colonies of *hakippah* which are separated from the nearest *sinaloae* colonies by the width of the river and up to two miles of irrigated fields in which no *Neobarrettia* occurs. The "1 mi. NW Culiacán" groupings belongs here, but it is plotted separately because of the presence in the *hakippah* colony of a single individual of *sinaloae.* The "E Side R. Humaya" groupings include those colonies of both species which are in intimate contact with one another, *hakippah* being found in the fields and *sinaloae* in the surrounding forest. The species determinations are based on characters other than occipital and femoral coloration.

The north-south clinal nature of the variation in these two characters is clearly shown in the graph. In both characters there appears to be slightly greater influence of *sinaloae* in the *hakippah* colonies most intimately in contact with that species, than in *hakippah* colonies which are more widely separated from *sinaloae*. In the occipital color of the northern colonies of *sinaloae,* there also seems to be some influence of *hakippah,* whereas the dark femoral color is entirely restricted to the latter species. As will be shown, the interpretation of these clines is not as simple as might appear.

Three other characters, the width of the excision of the male penultimate tergite, the length of the apical tooth of the male cercus, and the length of the male tegmen, show much individual but only limited geographic variation, and therefore have been analyzed in a slightly different way. The variation in these characters in the geographically most widely separated colonies of both forms is compared in Figure 8 with the variation in the colonies within the zone of contact between the two. In order to make a valid comparison of the characters in individuals of different overall size, the genitalic measurements have been divided by the length of the pronotum, and the tegminal length by the length of the fore femur.

In the genitalic characters, the northernmost *hakippah* are more similar to the southernmost *sinaloae* than are the two forms in the zone contact. The marked difference between the two in the apical tooth of the cercus in the contact zone, however, is attributable entirely to the shift toward a longer tooth in the *sinaloae* colonies. The *hakippah* colonies in this area, on the other hand, show a distinct shift toward the *sinaloae* condition in both average and extremes. In the length of the tegmina, there seems to be no significant geographic variation in *sinaloae,* whereas the *hakippah* colonies in the zone of contact again show a shift toward the *sinaloae* condition in both average and extremes. Two individuals from the contact zone lie almost precisely between *sinaloae* and *hakippah* in both genitalic characters, and within the overlap zone between the forms in tegminal length.

The remaining characters which separate the two forms are difficult to quantify and no attempt has been made to do so. Five of them have been examined qualitatively: the length and shape of the carinae of the female subgenital plate; the shape and position of the tubercle of the 7th abdominal sternite of the female; the angulation of the basal "tooth" of the male cercus; the color of the cephalic margin of the pronotum; the call rate and the number of syllables per burst of the song. The first four characters show no obvious geographic variation. Very few data are available on the song. Recordings have been made in the laboratory of *sinaloae* from El Venadillo and Culiacán, and of *hakippah* from 7.6 mi. N Culiacán and 19 mi. NW Guasave to 33 mi. N Hermosillo. Careful, although not precise, observations were made in the field on the song of both species in the vicinity of Culiacán. No obvious geographic variation in song has been noted.

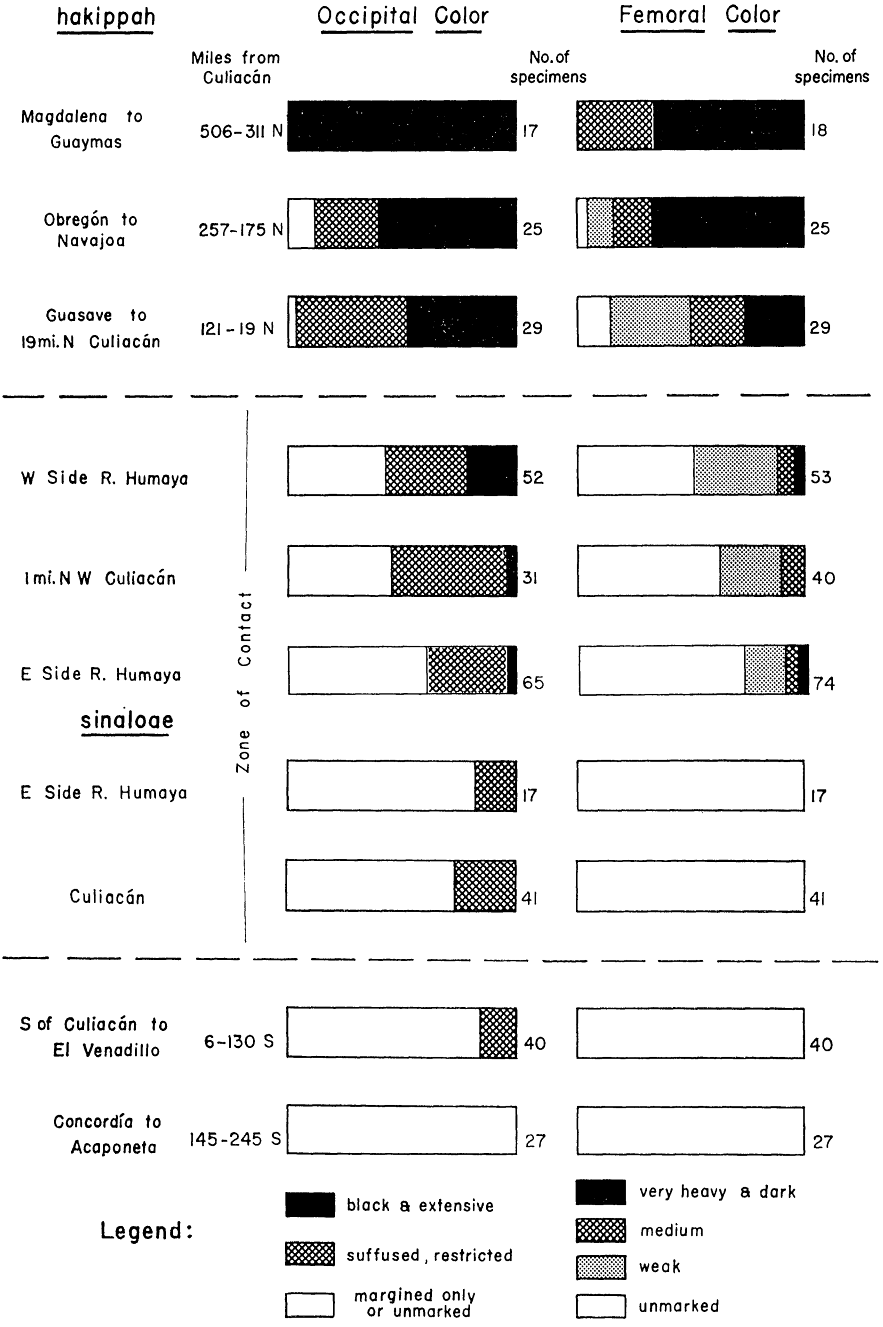
All five characters show the same distribution and are very closely correlated with the distribution of the genitalic characters previously discussed. Possible exceptions are as follows: six males from Palos Blancos with the basal tooth angulate or intermediate, otherwise with *hakippah* characters; one male from Palos Blancos with the basal tooth rounded, otherwise with *sinaloae* characters; one *hakippah* song heard in a chorus of *sinaloae* in the thorn forest between Palos Blancos and Tepuche; one *sinaloae* song heard in a chorus of *hakippah* in the thorn forest west of Tecorito; three possible hybrids from Palos Blancos (two males previously discussed, and one female).

At first glance, the geographic variation in occipital and femoral color seems to be clear evidence of intergradation between *sinaloae* and *hakippah*.

FIG. 7. Geographic variation in *Neobarrettia hakippah* and *N. sinaloae*; color of occiput and hind femur. The darkest occiput has a large central black spot or a wide black band between eyes; the darkest femur has a thick black longitudinal line on outer face. The lightest occiput and femur are entirely green, without black markings. Color categories are arbitrary. Geographic groupings are north-south segments of a linear distribution except in the zone of contact. The proportion of each symbol within the bar represents the proportion of individuals within the population having that color condition. Limiting localities of each grouped sample are as follows:

39 mi. SSW Magdalena to 33 mi. SE Guaymas
10 mi. S Obregón to 50 mi. SSE Navajoa
19 mi. NW Guasave to 19 mi. N Culiacán
W side R. Humaya—Tecorito to N bank Río Culiacán
  (not including Culiacancito localities or 2.5 mi. NW Culiacán)
E side R. Humaya (*hakippah*)—2 mi. E Tecorito
  to 1.5 mi. NW Culiacán
E side R. Humaya (*sinaloae*)—2 mi. N Tepuche to
  3 mi. NE Culiacán
Culiacán—1 mi. W Culiacán to 7 mi. E Culiacán
  and 1.5 mi. S Culiacán
6 mi. SE Culiacán to El Venadillo
3 mi. NE Concordia and 4 mi SW Santa Lucia to
  8.6 mi. SSE Acaponeta

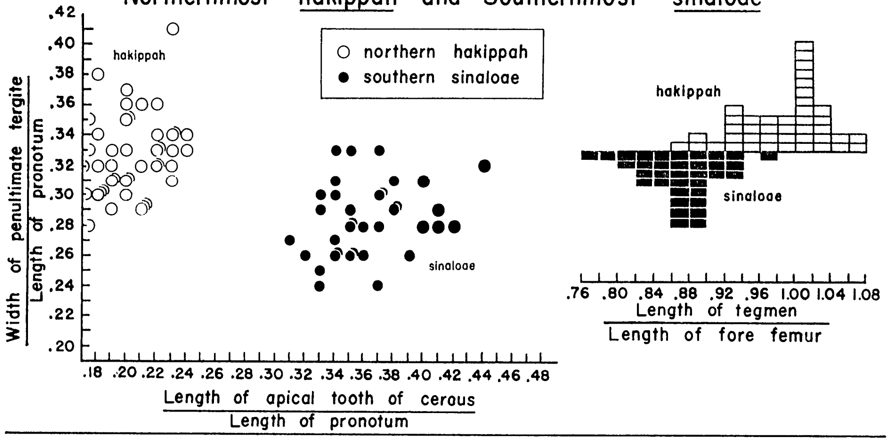
Included localities may be found in the list of records at the end of the treatment of each species, and in Figure 9.


hakippah
Occipital Color
Femoral Color
Miles from Culiacán
No. of specimens
No. of specimens
Magdalena to Guaymas
506-311 N
17
18
Obregón to Navajoa
257-175 N
25
25
Guasave to 19mi. N Culiacán
121-19 N
29
29
W Side R. Humaya
52
53
1 mi. N W Culiacán
31
40
E Side R. Humaya
65
74
Zone of Contact
sinaloae
E Side R. Humaya
17
17
Culiacán
41
41
S of Culiacán to El Venadillo
6-130 S
40
40
Concordía to Acaponeta
145-245 S
27
27
Legend:
black & extensive
suffused, restricted
margined only or unmarked
very heavy & dark
medium
weak
unmarked

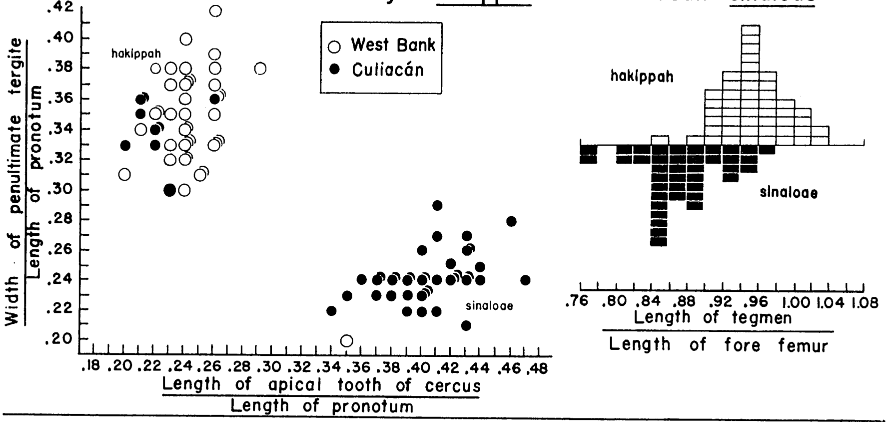
Further consideration reveals difficulties with this interpretation and suggests more probable explanations. One major difficulty lies in the geographically extensive penetration of characters of *sinaloae* into the range of *hakippah*. As indicated in Figure 7, both femoral and occipital characters typical of *sinaloae* are found throughout the southern half of the range of *hakippah*. This is an unexpected situation in view of the fact that the only other evidence of introgression lies within the contact zone. Although genetic factors for different characters need not move through a population at the same rate of speed, such gross differences in extent of introgression are unusual. It seems probable that the green occipital and femoral color in the *hakippah* colonies is not due to the influence of *sinaloae* at all. Green is the normal color for these structures in *Neobarrettia*. The black occipital spot and the black femoral stripe are unique developments (although some other species have a dark suffusion on the occiput) and almost certainly arose in a population in which these structures were green. The selective factors which allowed the black color to spread may have been clinal, strong for the black in the north and weak for the black in the south. Alternatively, the black color may have arisen in the north and have only recently spread south. In either case, the original green color would be expected to appear in a certain percentage of the individuals in the southern populations of *hakippah*, and there is no necessity to suppose its presence there is a result of introgression from *sinaloae*. A darkly suffused occiput is found in a small percentage of individuals in the northern colonies of *sinaloae*. As indicated previously, the appearance of this dark suffusion looks somewhat different from that in the southernmost colonies of *hakippah*—precisely those colonies most likely to have had an influence on *sinaloae*. There is reason to suspect, therefore, that the dark color in *sinaloae* may not be homologous with that in *hakippah*. Even if it is, there is an alternative to explaining its presence as a result of intro-

FIG. 8. Geographic variation in *Neobarrettia hakippah* and *N. sinaloae*; genitalic and tegminal proportions in males. Variation in the width of the excision of the penultimate tergite, the length of the apical tooth of the cercus, and the length of the tegmen is plotted; all measurements have been divided by the length of the pronotum or fore femur to allow comparison between individuals of different body size. Half-moon symbols in the upper scatter diagram indicate points which lie to the left of the ordinate; ordinate/abscissa values for these points are as follows: .35/.17, .33/.16, .32/15, .32/.15, .30/.13, and .28/.16. "Northernmost *hakippah*" includes all localities north of, and including, 19 mi. NW Guasave. "Southernmost *sinaloae*" includes all localities south of, and including, El Venadillo. Remaining geographic groupings include the localities as in Figure 7 in addition to the following: "West Bank" (Río Humaya) includes 2.5 and 1 mi. NW Río Culiacán; "Culiacán" includes S end RR. Bridge in Culiacán and 2 mi. W Culiacán. Other included localities may be found in the list of records at the end of the treatment of each species and in Figure 9.

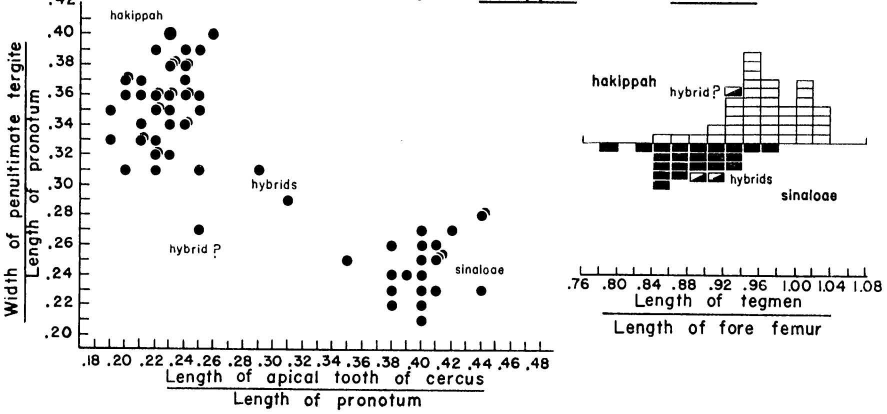
Northernmost *hakippah* and Southernmost *sinaloae*



West Side Río Humaya *hakippah* and Culiacán *sinaloae*



East Side Río Humaya *hakippah* and *sinaloae*



gression. It is at least equally reasonable to suppose that the dark occipital color arose before the two forms were separated, and that the same selective forces which (we may assume) are now responsible for the cline were also then operative, producing a similar cline. If the ancestral populations were subsequently fragmented into two colonies, both would have contained the genetic factors for green and for black occiput. With the re-establishment of a continuous linear distribution, the postulated continuance of the same selective forces might be expected to establish similar clines in the two forms. The environmental selection responsible for the high green-to-black ratio in the southernmost populations of *hakippah* must also be operating on the northernmost populations of *sinaloae*. Given similar genetic material in both forms, this selection might well produce similar phenotypic expression in the contact zone in each species (if that is what they are), and the old cline in selective factors would manifest itself by decreasing green-to-black ratio northward in *hakippah,* and an increasing green-to-black ratio southward in *sinaloae.*

In view of these alternatives, it is unnecessary to accept the interpretation that the clines in occipital and femoral color are the result of introgression, and other reasons why this explanation is unacceptable are brought out in the following.

That some hybridization is taking place in the area where the two forms are in the most intimate contact is evidenced by the presence of two males and one female there, whose characters are clearly of hybrid origin. The two males are almost precisely intermediate in the two genitalic characters graphed in Figure 8; in addition, the angulation of the basal "tooth" of the cercus is intermediate, the pronotal color is possibly intermediate (or closer to the *hakippah* condition); the occipital and femoral color, and tegminal length, fall in the overlap zone between the two forms. These two individuals probably had a *sinaloae* type call.[10] The female from 2–3 mi. S Palos Blancos has typical *sinaloae* type terminalia but almost a *hakippah* type of pronotal color. In the other characters, this female lies in the overlap zone of the two species. There can be little doubt that these three individuals are first generation hybrids.

Some backcrossing must also be taking place in the zone of contact between the two forms. The influence of *sinaloae* on the *hakippah* colonies in

---

[10] My field notes for the collection which included these specimens indicate that two individuals had faster songs than the rest and had consistently more syllables per burst. My recollection is that these calls were distinctively different from the others in the field. Unfortunately, these individuals were not kept separate from others collected, but since only two individuals in the entire lot from this locality show the series of intermediate characters listed above, there is no doubt in my mind that they are the ones that produced the *sinaloae* call.

this region is seen in the slight but distinct shift in both means and extremes in the length of the tegmina and the apical tooth of the cercus of *hakippah* toward the condition characteristic of *sinaloae*. On the other hand, the mean and lower extreme of the measurements of the penultimate tergite of *hakippah* show slight but definite shifts away from the *sinaloae* conditions. These same characters in the *sinaloae* colonies show no influence of backcrossing at all, and there is no significant change in tegminal length throughout the range of this form. In the zone of contact, the two genitalic characters in *sinaloae* show a strong shift away from the *hakippah* condition, suggesting a reinforcement phenomenon mentioned previously. The morphological evidence suggests that some hybridization is taking place, but that backcrossing is occurring only in the *hakippah* colonies, and then only to a very small degree.

An important clue to the explanation of this situation lies in the distribution pattern of the two forms in the zone of contact, illustrated in Figure 9. Each form occurs very commonly in the area; the symbols merely represent sampling stations and not the complete distribution of the forms. Outside the zone of contact along the Río Humaya, each form occurs abundantly in habitats ranging from heavy thorn forest through bushy second growth to weedy cultivated fields. East of the Río Humaya, *hakippah* is found in exclusive occupancy of certain weedy fields and open bushy pastures close to the river. It is usually abundant in those habitats, but is never found in the thorn forest. Immediately adjacent to the fields occupied by *hakippah, sinaloae* is found in exclusive occupancy of the thorn forest, where it is also often abundant. The two have never been found together except in one field near Caminajuato, and in one field northwest of Culiacán. South of Palos Blancos, *sinaloae* is found in exclusive possession of some bushy, weedy fields, and *hakippah* of others. West of the Río Humaya only *hakippah* has been found (except for a single individual of *sinaloae* taken northwest of Culiacán), and in that area *hakippah* occupies the full range of habitats normal for the species, including heavy thorn forest.

The sudden restriction in the habitat occupancy of both forms north of Culiacán is of critical significance. There are two possible explanations; first, ecological changes may occur in this vicinity which restrict the range of habitats occupied by each form; second, invasion by one form of the range of the other may be taking place, with the elimination of the second form through competition. Considering the first alternative, it is possible that the southern limit of *hakippah* and the northern limit of *sinaloae* occur in a region of general ecological change such that suitable habitats for each form are not available beyond these limits. There are no obvious changes, however, in topography, climate, soil or vegetation in this region, other than very gradual ones. If there were general changes, they likely would form a north-south gradient, but the shift in the habitat of the two forms does not show a regular change in this direction. On the contrary, *hakippah* occurs in thorn forest several miles south of the area where, just across the river, it is excluded from the thorn forest. Similarly, *sinaloae* is found in fields a few miles to the north of apparently similar fields in which *hakippah* is dominant (but where one individual of *sinaloae* was also found).

The fact that the restriction of habitat occupancy occurs only where the two forms are in contact, and the fact that they are very rarely found together, creates a strong presumption that competition exists between them. I have no direct evidence on the nature of the competition, nor on what kind of advantage might be possessed by *hakippah* in the fields and by *sinaloae* in the thorn forest. The food studies conducted by S. K. Gangwere on these and other species of *Neobarrettia* (further discussed in Part II) indicate that both forms are general carnivores with more or less similar tastes and capabilities. Under some circumstances they have been known to attack, kill and eat insects as large as themselves. Unless provided with adequate food they are quite cannibalistic in captivity. Competition may be direct, therefore, with one form attacking and killing the other. The pattern of distribution of the two forms on the east bank of the river suggests that *hakippah* may possess greater tolerance of some of the limiting physical factors of the field environment, and that it is consequently able to build up larger populations there, or to build them up faster. Under these circumstances, *hakippah* eventually would eliminate *sinaloae* in the fields even if the two were equally matched in combat. The reverse might be true in the thorn forest. It is also possible that *hakippah* hatches earlier than *sinaloae* in the fields and later than *sinaloae* in the thorn forest. The largest nymphs would undoubtedly be more successful in direct combat. Variation in hatching time and differential tolerance to environmental conditions might be variously combined.

The distribution of the two forms on the east bank of the Río Humaya is almost precisely what would be expected if *hakippah* were extending its range southward and had recently reached the partial barrier of the Río Humaya. It is in complete possession of the western bank and lives in all habitats there. Its distribution on the eastern bank has the appearance of a series of beachheads. If this species has a slight advantage over *sinaloae* in the fields, then these would be the only places where *hakippah* might make successful crossings to the east bank in the face of complete occupancy there of all habitats by *sinaloae*. The two forms have been found together

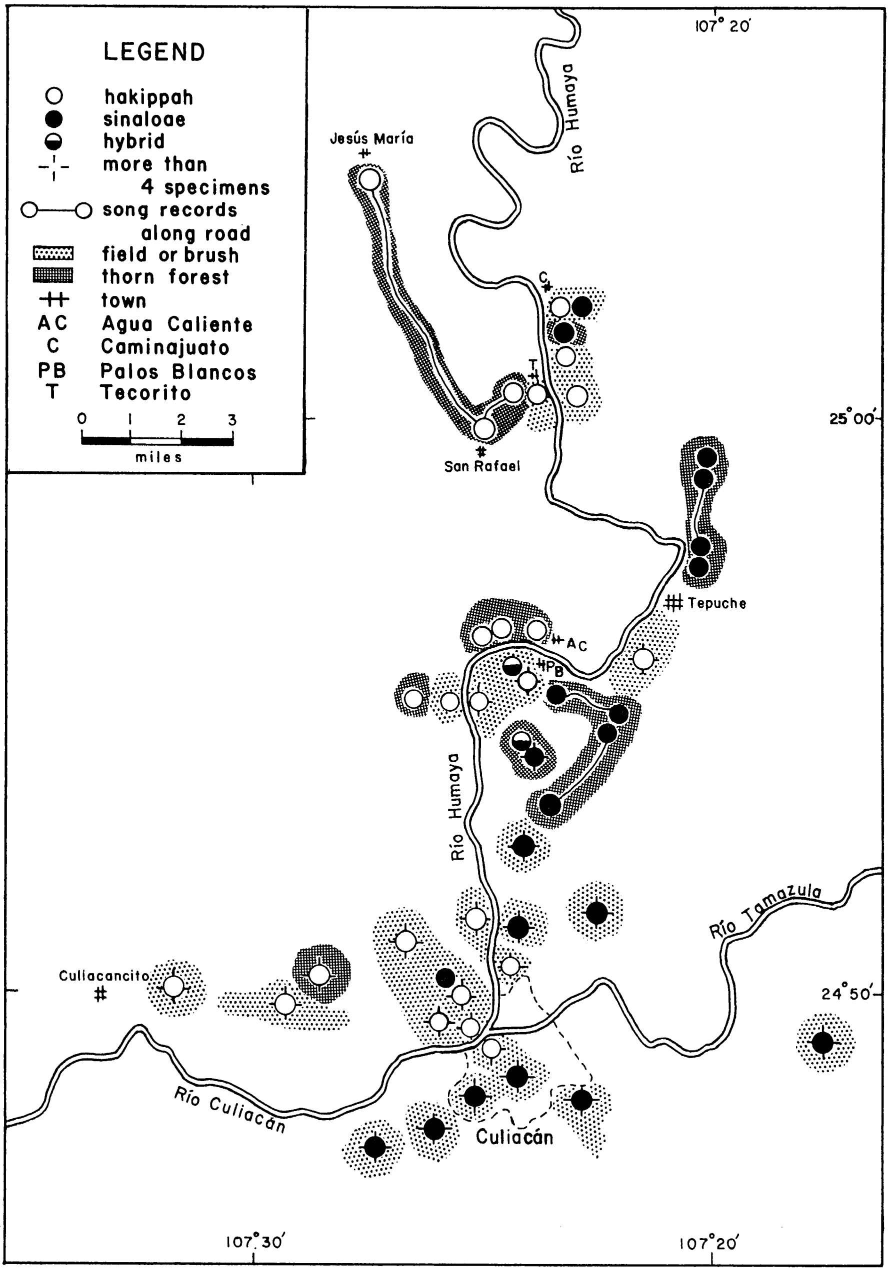


FIG. 9. Habitat distribution of *Neobarrettia hakippah* and *N. sinaloae* in the Culiacán region, Sinaloa. *N. sinaloae* also occurs in thorn forest localities south of region covered by the map.

at only three localities. In the two localities for which adequate data are available, *hakippah* was abundant, whereas *sinaloae* (or the hybrids between the two forms) were few. Again, this is what would be expected if *hakippah* were moving southward. Furthermore, *sinaloae* probably occupies a broad front in the thorn forest along the east bank of the Río Humaya, facing a similar habitat on the other side. If *sinaloae* were moving north, one would expect it to have crossed somewhere along the river, and to have invaded the thorn forest on the west side, since in that habitat it seems to have an advantage over *hakippah*. No *sinaloae* has been identified definitely in the thorn forest on the west bank of the river (with the exception of the single individual mentioned above).

The distributional and habitat evidence supports the hypothesis that *hakippah* is invading the range of *sinaloae* and eliminating that species. The nature of the interaction between the two forms is unknown, but several reasonable possibilities are available, as discussed above. The morphological data presented on preceding pages indicate that some hybridization and backcrossing is taking place but is not breaking down the differences between the two forms. With these two hypotheses, the pattern of variation in the two forms in the contact zone now becomes easy to explain.

If *hakippah* is invading the range of *sinaloae*, then it must be absorbing most of whatever backcrossing is taking place. The effects of this will persist in the variation pattern of *hakippah* long after the last *sinaloae* has been absorbed or eliminated. On the other hand, the *sinaloae* populations which might have absorbed some backcrossing would be the first to be eliminated by the continuing invasion by *hakippah*. This explains why only the *hakippah* colonies show evidence of backcrossing even where they are not in contact with *sinaloae*. Individuals of *sinaloae* are being eliminated either through competition or hybridization. Since the characters which are analyzed in Figure 8 do not appear to be related to any competitive advantage or disadvantage, the individuals which are eliminated would be expected to constitute a random sample of the variation in those characters. Thus, there appears to be no effect on the variation in tegminal length in *sinaloae* caused by the competition or hybridization. The differences between the two forms in both male genitalic characters graphed in Figure 8 are correlated with differences in the shape of subgenital plates in the respective females: the width of the excision of the male penultimate tergite closely corresponds to the width of the inflated portion of the female subgenital plate, and the length of the apical tooth of the male cercus closely corresponds to the position of the pits on the female subgenital plate into which the teeth fit (see discussion in section on Behavioral Details). The male *sinaloae* most successful in copulating with a female *hakippah* would probably be the one having genitalia most similar to those of *hakippah*. Since only these *sinaloae* individuals are being added, in essence, to the *hakippah* populations through the backcrossing of the hybrids, there is only a slight shift in the variation in the *hakippah* populations toward the conditions found in *sinaloae*. Since all of the *sinaloae* individuals are at the same time being eliminated from their parental populations, there is a more marked shift in the variation of these *sinaloae* populations away from the *hakippah* condition. But why this effect should also be seen in those *sinaloae* populations that are far from localities where the two forms are in intimate contact is difficult to understand. Perhaps the selection against male *sinaloae* with characters similar to those of *hakippah* has been so strong (as is suggested by the large difference in the pattern of variation between the upper and lower diagram in Figure 8) that normal gene flow has been able to strongly affect the more distant populations.

The fact that the southernmost populations of *hakippah* are barely affected by introgression, and then in only two visible characters, suggests that either most of the genetic material of *sinaloae* is incompatible with that of *hakippah* or that extremely little interbreeding is taking place despite the close contact between the two forms. The variation in the genitalic characters in *sinaloae* strongly suggests a "reinforcement phenomenon," as does the variation in the penultimate tergite character in *hakippah*. This further implies the existence of some sort of incompatibility between the two genomes (which might be manifested by reduced viability, less successful competition among the offspring, or some other adverse affect of hybridization).

In the interaction between these two forms, we are probably witnessing the last stages in the achievement of reproductive isolation. *N. hakippah* and *sinaloae* may be considered, therefore, to have just reached specific status.

THE CREMNOBATES GROUP

This group contains only the new species, *cremnobates*, found in the western portion of the Mexican Trans-Volcanic Belt. It is characterized by the vinaceous costal border of the tegmen in both sexes and the distinctive male cercus, which possesses a weblike structure extending from the internal ridge to the apical tooth (Fig. 19b), and which does not have a median tooth. In addition to these features, which are unique in *Neobarrettia*, *cremnobates* possesses the following characters which are found in several other species but never in this combination: cephalic and caudal borders of the pronotum margined with black; tegmen short (.97–1.07 times the length of the fore femur); tegmen of the female with the caudal portion largely dark, of the male with dark markings around the stridulating area; wing colors opaque, white and black, the two colors of about equal extent; femoral teeth white with brown apices.

N. cremnobates shows strong similarities to *vannifera.* Both species possess the following characteristics: cephalic and caudal margins of the pronotum black, the black of the same extent in the two species; caudal area of the female tegmen dark and the stridulating area of the male tegmen bordered by dark markings; wing spots often transversely elongate; sternal abdominal tubercle of the female high, acute and often compressed, and cephalic in position on the sternite. The following features found in *cremnobates* closely approach the conditions found in *victoriae*: female tegmen with the caudal area dark, that of the male with a dark spot on vein Cu_{1b}; wing colors opaque; femoral teeth white, tipped with brown; subgenital plate of the female with short lateral carinae, a restricted median carina, and shallow lateral pits; tubercle of 7th abdominal sternite of the female variable (in one individual it is similar to the condition in eastern populations of *spinosa,* in the other two, it is similar to *vannifera* and *victoriae* in shape and intermediate between the two in height). Morphologically, *cremnobates* stands between *vannifera* and *victoriae*; it can be easily derived from *vannifera,* while *victoriae* may be derived with equal ease from an ancestral *cremnobates* which lacks only the two unique characters of the modern species. *N. cremnobates* also resembles *sinaloae* in a number of characters, summarized in Table 3, most of which are shared as well with other species; none of the similarities, with the possible exception of the eye color pattern, are as detailed as those shared with *vannifera* and *victoriae. N. cremnobates* resembles *imperfecta* in the following four characters: shoulders of the pronotum with a longitudinal brown band; cephalic and caudal margins of pronotum black; cercus of male without a median tooth, and with a very short apical one. The difference between *cremnobates* and *imperfecta* in the details of all of these characters leads me to believe that they represent independent parallel developments in the two species, especially in view of the greater detailed similarity between *imperfecta* and the members of the Pulchella Group (see discussion under *imperfecta*).

Neobarrettia cremnobates[11] new species (Figs. 17h, 19b, 20e, 201)

Holotype.—Male, 20 mi. E Ixtlán del Río (Nayarit), Jalisco, México, 2 Sept. 1961 (I. J. Cantrall and T. J. Cohn, No. 71); University of Michigan Museum of Zoology.

Comparisons.—See preceding discussion.

Species Description.—PRONOTUM (Fig. 20e): caudal portion turned up at a sharp angle, usually greater than 45° (about 45° in holotype), then recurved to horizontal (or occasionally directed slightly downward; horizontal in holotype); humeral sinus represented by a very weak sinuation in margin of pronotum. APPENDAGES: tegmen short (.97–1.07 times length of fore femur; 1.06 in holotype), reticulation dense; cross veins of wing weak; caudal armature of fore femur without minute teeth among larger ones. MALE TERMINALIA: caudal margin of penultimate tergite (Fig. 201) moderately excised mesally, margin on either side produced into an obtuse-angulate lobe, blunt at apex; caudolateral margins of semimembranous area raised, and obtuse-angulate; cercus (Fig. 19b) very short (about .4 times width of penultimate tergite), apical tooth very short, sharply bent inward, apex acute; internal ridge very broad at base, terminating there in a very prominent acute tooth, ridge narrowing rapidly to middle where dorsal portion smoothly joins shaft of cercus and ventral portion extends to apex of cercus as a weblike structure across angle formed by apical tooth; median tooth absent. FEMALE TERMINALIA (Fig. 17h): caudal half of subgenital plate triangular, inflated, apex entire; median carina low and weak, very weakly concave, absent from proximal third and obsolete on apical eighth of plate; lateral carinae weak, broadly rounded, converging caudad, restricted to caudal third of plate; a weak depression cephalad of a short, strong ridge near lateral point of articulation of caudal half of plate; basal transverse flange absent; tubercle of 7th abdominal sternite located on cephalic half of plate, high, compressed to conical, slightly curved caudad, apex acute to narrowly blunt. COLORATION: eyes in life dull purple above, yellowish white below; cephalic margin of pronotum with a very narrow black line extending ventrad to a point just over coxa; caudal margin with a narrow black line extending just over shoulder; an irregular, light brown, horizontal stripe on shoulder, extending length of pronotum in living individuals (indistinct in dried specimens); ivory stripe of lateral lobe margined cephalically on ventral two-thirds by a narrow light chestnut stripe which becomes darker and broader dorsad, capping ivory stripe on shoulder; mesonotum marked mesally with light reddish brown, metanotum mesally with dark brown (almost black); venter of abdomen (in life) on each side with a longitudinal yellow stripe lateral to sternites and another narrow whitish stripe ventral to tergites; tegmen in both sexes vinaceous in area cephalad of vein C, this color extending to apex of tegmen; area between veins C and Cu_1 green; male tegmen with area between veins Cu_1 and Cu_{1b} and including part of Cu_{1b} (cephalic margin of mirror) black to dark brown, the color sometimes extending a short distance into mirror as a suffusion (in holotype black and mirror slightly suffused); apex of vein Cu_2 (stridulating vein) and veins immediately adjacent in margin, dark brown to black; caudal border of tegmen outside mirror brownish vinaceous; female tegmen with area between veins Cu_1 and Cu_2 dark brown (almost black) in basal third; area caudad of Cu_2 light yellow brown in basal third or quarter; caudal border vinaceous; wing colors black and white, opaque; base

---

[11] From the Greek, κρημνοβατης, one who lives among cliffs, in allusion to the habitat of this katydid, which presents a cliff-climbing challenge to the collector.

of wing with a pink suffusion; white spotting slightly greater in extent than black (markedly so in holotype), spots often and irregularly fused (markedly so in holotype), their margins more or less rounded, never angulate; unfused spots usually transversely elongate; femoral teeth whitish, very briefly tipped with brown; dorsum of fore and middle tibiae dark vinaceous, that of hind tibia light brownish red in life, fading to brown in dried specimens. MEASUREMENTS (in mm.): length of pronotum, 6.2; width of pronotum, 4.7; length of tegmen, 11.4; length of femora: fore, 10.8; middle, 10.2; hind, 28.3. Measurements of the material studied are summarized in Figures 21 and 22.

PARATYPES.—All specimens examined in this study are designated as paratypes with the exception of several poorly preserved individuals. Male and female paratypes are deposited in the University of Michigan Museum of Zoology, and male paratypes in the Academy of Natural Science of Philadelphia and the United States National Museum.

VARIATION.—No variation considered to be significant was observed in the present series. Minor variation is indicated in the above description.

DISTRIBUTION (Fig. 24).—*N. cremnobates* is known only from the great barranca system, in westernmost Jalisco, formed by the tributaries of the Río Grande de Santiago. It has been collected or heard almost continuously between the western and eastern edges of the barranca east of Ixtlán del Río, across which the Tepic-Guadalajara Highway passes. No individuals were heard on the plateau within a few miles of either edge of this barranca during the same day and evening on which the series was collected within the barranca in 1961. None have been heard between Mazatlán and Tepic (day and night collecting) along a route which crosses the Río Santiago near its mouth; none have been heard in the Tepic region (day and night), along the Tepic-Guadalajara Highway (day), except for the Ixtlán colony, or in the Barranca de Oblatos (late afternoon and early evening), which is formed by a tributary of the Río Santiago north of Guadalajara. The other barranca systems between Tepic and Tequila, where extensions of the Ixtlán colony might be present, have not been investigated.

HABITAT.—The barrancas in which this species occurs possess a good cover of bushes, in contrast to the grassy plateau to the east and west. The vegetation includes both spiny shrubs—*Acacia cymbispina*, *Eysenhardtia*, and others—and also low trees, tall columnar cacti and small areas of fairly heavy weedy growth; in places the vegetation is thick enough to resemble Sinaloan thorn forest. *N. cremnobates*, which ranges from the bottom of the barranca at about 2700 feet to the top at around 3900 feet, has been found in several kinds of bushes. It does not occur to the west, where there is an abrupt shift to a grassy plateau on which are scattered trees and small patches of bushes, nor to the east, where there is a zone of transition to similar grasslands. This zone is marked by somewhat hilly and broken terrain which is covered by a heavier growth of bushes and trees than that found on the western side of the barranca. On the plateau the spiny bushes seem to be fewer in numbers and kind than in the barranca.

SEASONAL OCCURRENCE.—This species has been collected on only two dates, 2 September and 2 October; it was common at both times. The region in which the species occurs has not been surveyed for it at other times.

SONG.—This species was singing commonly during the chilly evening hours on both the above-mentioned dates, and was singing vigorously in the early afternoon in bright sunshine on the first mentioned date. The call consists of a simple short syllable of about .07 seconds duration (measured from an audiospectrograph of a recording made in the laboratory at 79° F.), continuously but somewhat irregularly repeated at the approximate rate of one syllable per second. The song of this species is similar to that of a species of *Microcentrum* with which it occurs, but the short "dzip" of *cremnobates* is slightly longer and more resonant than that of the *Microcentrum*.

RECORDS.—Material examined: 11 ♂♂, 3♀♀. JALISCO: 10, 12, 14, 20 mi. E Ixtlán del Río (Nayarit).

The Victoriae Group

This group contains only *victoriae* (Caudell), which occurs on the northeastern coastal plain of México and extends through Texas and western Oklahoma into southern Kansas. The species possesses the following unique characteristics: color of the mandibles black and white, sharply contrasted; length of pronotum in all but the southernmost populations more than 1.5 times width; caudal portion of pronotum elevated at approximately a 30° angle or less, caudal margin often broadly rounded; central portion of wing usually without cross veins (except in southern and westernmost populations in México), this area jet black surrounded by a broad ring of white or yellow. The species may also be distinguished by the following combination of characters: eyes in life whitish, cephalic margin of pronotum green; caudal portion of female tegmina brown; wings black, and either white or yellow; penultimate tergite of male strongly incised and strongly lobate; internal tooth of male cercus well developed, acute to blunt, apical tooth elongate, sharply bent mesad and usually projecting well beyond the internal ridge (Fig. 19a); female subgenital plate with strong lateral ridges; 7th abdominal sternite of female with a usually slender, acute tubercle.

N. victoriae stands morphologically intermediate between the Spinosa and Pulchella Groups. It shares with the Spinosa Group the following characteristics: wing colors dimorphic (as in *vannifera*); caudal area of female tegmen brown; fore femur with numerous minute teeth between large ones in some individuals; subgenital plate of female swollen in distal half and with well-developed lateral carinae (as in *spinosa*); 7th abdominal sternite of the female with the tubercle usually narrow and elongate (but not high), and located on the cephalic third of the plate (as in *vannifera*). *N. victoriae* shares the following characteristics with the Pulchella Group: eye color in life whitish (eye color unknown in *vannifera*); cephalic margin of pronotum green; pronotum sometimes without dorsal or lateral dark markings; meso- and metanota black in some individuals; wing colors bright and almost opaque; femoral teeth white with brown tips; internal tooth of the male cercus often blunt. Several of these characters are not restricted to the two groups, but elsewhere they never occur in this combination. Certain variant conditions of the female subgenital plate, and of the tubercle of the 7th abdominal sternite of the female closely resemble the conditions characteristic of *vannifera*. Other variant conditions of the tubercle closely approach the condition characteristic of *pulchella*.

These morphological data suggest that *victoriae* was derived from a *vannifera*-like ancestor, and that the Pulchella Group was derived from the *victoriae* stock. In addition, *victoriae* shows peripheral relationships with the Cremnobates and Sinaloae Groups, the details of which are discussed under those groups.

Neobarrettia victoriae (Caudell) (Figs. 1, 2a, 2b, 2d, 17a, 17c, 17i, 19a, 20q)

1907. *Rehnia victoriae* Caudell, Proc. U.S. Natl. Mus. 32: 306–07, [♂-Victoria, "Guerrero," México].

HOLOTYPE.—Male, Victoria, "Guerrero," México, O. W. Barrett; U. S. National Museum.

Caudell (1907:307) is the authority for the designation of the state from which the type came. *N. victoriae* has not been found in Guerrero in the course of intensive collecting specifically for *Neobarrettia*, and careful collecting farther north indicates that the southern limits of the species lie in eastern San Luis Potosí. I, therefore, believe that the type locality as recorded by Caudell is incorrect. The second locality label on the type bears the word "Victoria" followed by a handwitten word which appears to both Dr. Gurney and myself most like "Grun," and this followed in turn by "No. 234." Although Barrett did collect in Guerrero, he also collected material of at least two species of grasshoppers later recorded as coming from Victoria in Tamaulipas: *Rhomalea* [=*Chromacris*] *colorata* Serv. recorded by Rehn (1900:97), and *Calotettix bicoloripes* Bruner [=*Phaulotettix compressus* Sc.] described by Bruner (1908:310–11). The first species has been found both north and south of Ciudad Victoria, Tamps.; the second has been found commonly on the coastal plain near that city, and is not known south of the state of San Luis Potosí. Since *victoriae* has been found almost within the city limits of Ciudad Victoria in Tamaulipas, it seems almost certain that this city is the type locality and that Caudell erred in recording the state as Guerrero.

COMPARISONS.—See preceding discussion of group characteristics and relationships.

SPECIES DESCRIPTION.—PRONOTUM (Fig. 17c): elongate, caudal portion narrow, dorsal length usually greater than 1.5 times caudal width (less than this figure only in southernmost populations, see Fig. 10) (unique in *Neobarrettia);* caudal portion turned up at an angle less than 30° (unique among males), and usually gently and weakly recurved as in *vannifera*; caudal margin often broadly rounded; humeral sinus well marked to obsolete. APPENDAGES: tegmen medium in length (1.03 to 1.48 times length of fore femur), reticulation dense; cross veins of wing weak, usually very few or absent in center of wing (unique), more numerous (up to 10 in center) in southern and westernmost populations in México; caudal armature of fore femur usually with a few (rarely numerous) minute teeth among larger ones. MALE TERMINALIA: caudal margin of penultimate tergite (Fig. 20q) deeply excised mesally, margin on either side produced into distinctly angulate, blunt-tipped lobes; caudolateral margins of semimembranous area usually widely obtuse-angulate, raised, usually subtuberculate; cercus (Fig. 19a) medium in length (about .55 times width of penultimate tergite); apical tooth elongate, robust, strongly incurved with one or two weak angles, often rectangulate, usually with apical portion projecting mesad far beyond internal ridge, apex acute to acuminate; internal ridge only slightly broader proximad than distad, proximal angulation usually not produced, angulate but blunt-tipped; median tooth bent ventrad, but usually visible from above, often bent somewhat cephalad, apex narrow, briefly acute, often blunt; distal portion of internal ridge usually a simple dorsal shelf, sometimes deep, abruptly joining shaft of cercus immediately distad of median tooth so that ridge has a prominent disto-internal angle. FEMALE TERMINALIA (Fig. 17i): subgenital plate with caudal half truncate to weakly triangulate, strongly inflated mesally, margin weakly and narrowly notched mesally; median carina prominent, sharp, obsolete on caudal quarter or third, gently to strongly arcuate; lateral carinae prominent, usually straight, oblique, converging distad, often fusing just short of distal margin, absent from proximal third of plate; a short oblique ridge at lateral articulation of free caudal portion of plate forming caudomesal border of a broad, usually shallow pit. Basal transverse flange absent; tubercle of 7th abdominal sternite located on cephalic third of plate, almost always slender, acute agulate, compressed, sometimes very short, rarely blunt and almost rectangulate, apex often slightly produced, usually slightly offset caudad. COLORATION: eyes in life whitish; mandible with molar and incisor areas jet black, sharply demarcated from white color of rest of cephalic face, no transitional brownish area as in all other species of *Neobarrettia*; cephalic margin of pronotum green, caudal margin yellowish to brown; caudal portion of pronotum green or with a light brownish suffusion, sometimes dark brown to black, when dark the color extending ventrad as a thin cephalic margination of ivory stripe, usually very light or absent along ventral half of stripe; caudal portion of metanotum sometimes jet black, the rest lighter in color, brown or green; mesonotum green to dark brown, or caudal portion black; dorsum of abdomen sometimes infuscate; venter of abdomen on each side with a longitudinal yellow stripe just lateral to sternites and another just ventral to tergites, the latter usually narrowly interrupted on each intersegmental membrane; most of tegmen green in both sexes; male tegmen caudad of vein Cu_1 and $MP + Cu_1$ yellowish to light brown; a darker brown spot between veins M and Cu_{1b} and including part of vein Cu_{1b} often extending into distocaudal corner of mirror; female tegmen yellow-brown caudad of vein Cu_1 and $MP + Cu_1$; wing colors almost opaque, bright; center of wing jet black (unique); spots, base, and distal band either yellow or white; several spots cephalad of vein M, usually only a few scattered ones caudad of this vein (unique), rarely as many as 10 and this only in southern and westernmost populations in México; spots more or less round, distal marginal band usually broad and regular, basal white area usually broad; femoral teeth whitish, briefly tipped with brown; dorsal surface of all tibiae light vinaceous, occasionally yellowish or yellowish green (then possibly faded, see discussion under *vannifera*). MEASUREMENTS: these of the series studied are summarized in Figures 21 and 22.

VARIATION.—Two structures in this species display variation of particular morphological interest. The variation in wing spotting is associated with variation in number and position of cross veins. Spots are invariably centered on cross veins, and the wings with the least number of spots in the central portion have the least number of cross veins there. The broad disto-marginal band is apparently formed by the coalescence of white spots on the very numerous marginal cross veins. The prominent lateral ridges of the female subgenital plate are greatly reduced in occasional specimens. Comparison of this condition with the normal plate suggests that the ridges are probably formed as remnants of the original swollen portion when the central area is depressed.

N. victoriae displays geographic variation in four characters: wing spotting, length-width ratio of the pronotum, relative length of the tegmina (Fig. 10), and the darkness of the meso- and metanota. Heavily spotted wings are found only in the southernmost colonies (from 25 mi. S Llera, Tamps. to Valles, S.L.P.) and in the westernmost colonies in México (26 mi. E Cuatro Ciénegas, 15 to 34.8 mi. S Castaños, Coah., and 17 mi. W Santa Catarina, N.L.). All individuals in those colonies possess wings more heavily spotted than elsewhere in the range of the species. There appears to be no transition between the areas where strongly and weakly spotted wings occur, although there is considerable individual variation in both types. North-south clinal variation occurs in the three remaining characters. The southernmost colonies possess the shortest and broadest pronota, the longest wings, and the darkest meso- and metanota. These conditions change through northern México to the condition found in Texas, Oklahoma, and Kansas. In each of the four characters, the condition found in the southernmost populations is more nearly like the condition normal for the rest of the genus or for the Pulchella Group, suggesting that these populations have retained more of the characteristics of the immediate ancestor of *victoriae* than have the colonies farther north.

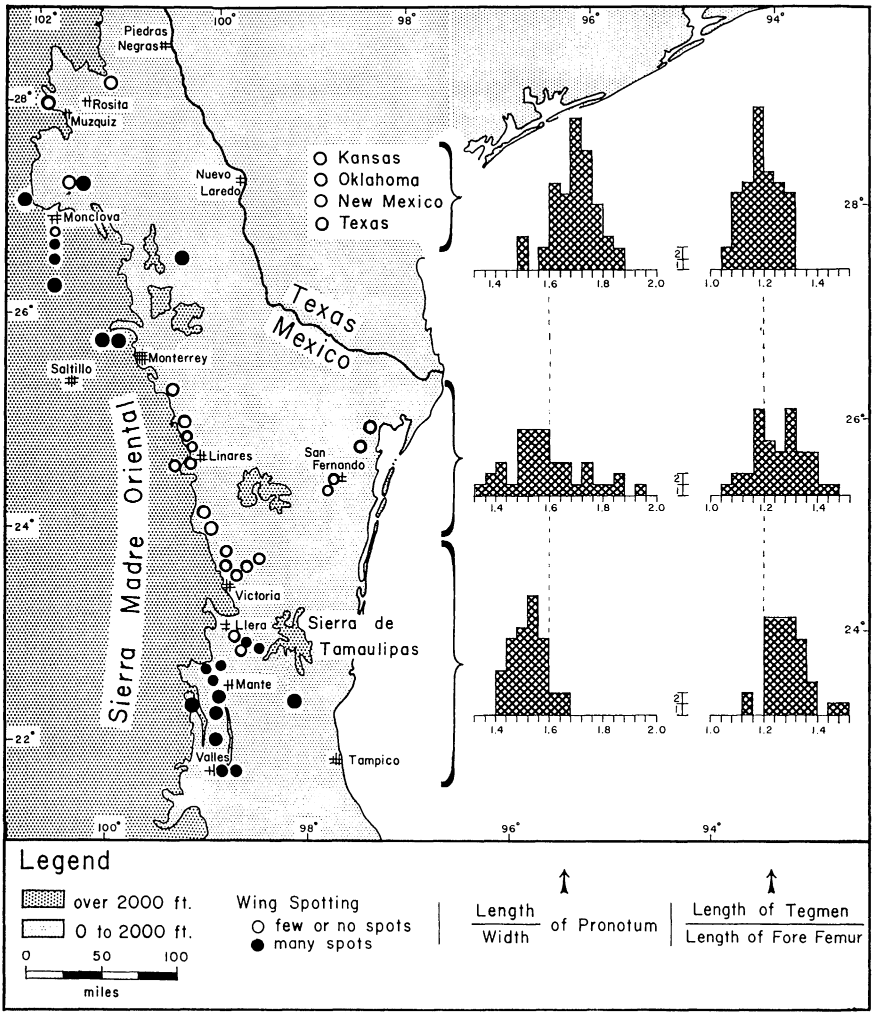


FIG. 10. Geographic variation in males of *Neobarrettia victoriae* in northeastern México. The entire distribution of the species south of the international border is shown. Difference in size of the circles is unintentional. Middle histogram includes all Mexican records north of 16 mi. NW Ciudad Victoria.

DISTRIBUTION (Figs. 10, 13, 23, 24).—This species has the widest distribution of any of the members of the genus. Limital records are as follows: northwestern, 11 mi. S Hobbs, Lea Co., N. M.; northern, Seward and Meade cos., Kans.; eastern, Karnes City, Karnes Co., Tex.; southern, 1.5 mi. E Valles, S.L.P.

No detailed work has been done in the region of the northwestern and northern portions of the range of *victoriae,* but enough general collecting has been done there to suggest that the species does not occur much beyond the limital records. The species appears to be absent from all of the Llano Estacado except the southern tip, which is covered with scrub oak and bushes. In east-central Texas, the distribution pattern is irregular and complex. Some careful sampling work has been done there, and the pattern as indicated, Figure 13, is probably an accurate representation of the distribution of *victoriae* in that area. The irregularity is almost certainly owing both to ecological and historical factors, as discussed below. The region south of Valles has not been closely examined, but judging from the ecological distribution of the species in the Sierra Madre a short distance to the north and west of that city, it seems unlikely that *victoriae* occurs much farther south. Many of the roads leading through or into the Sierra Madre Oriental have been carefully sampled or surveyed. The following represent the western or southwesternmost records along these roads: 4 mi. SE Salto del Agua, S.L.P.; 5 mi. SE Gómez Farías, Tamps.; 5.7 mi. E Iturbide, N.L.; 17.2 mi. W Santa Catarina, N.L.; 34.8 mi. S Castaños, Coah. *N. victoriae* has not been found on the Northern Plateau between Saltillo and Torreón, Coah., or between Saltillo and Ciudad del Maíz, S.L.P. It does occur in the dissected edge of this Plateau near Santa Catarina and Castaños (records cited above) and 26 mi. E Cuatro Ciénegas, Coah., but no farther.

HABITAT (Fig. 13).—Throughout its range in the United States, *victoriae* lives in bushy habitats in which mesquite is either a dominant or a conspicuous element, except in Kansas and northern Oklahoma. In Kansas, the species occurs in an area where mesquite is almost nonexistent, but where *Acacia,* sagebrush, and other bushes are common (from conversation with C. W. Hibbard). In northern Oklahoma, where mesquite may also be rare, the species has been found in sagebrush in bushy habitats. In southern Oklahoma, all but one of the habitats in which *victoriae* has been found contain mesquite, or are in areas where mesquite is common (from field notes of T. H. Hubbell, and conversation with T. E. Moore). The single exception is the Caddo County record, which lies in an area mapped as oak woodland (Game Type Map of Oklahoma, Game and Fish Dept., State of Okla., 1943), but which undoubtedly includes fields invaded by mesquite, if my recollection of the area is correct. In all of Texas, the species has been found outside a mesquite habitat in only two localities. At the first of these, in Montague County, the habitat is open oak woodland, but only a few miles to the west lies the beginning of the Mesquite Savanna (vegetation regions in Texas are from Tharp, 1952). At the second, in Edwards County, the habitat is juniper rangeland, but again mesquite habitats lie a short distance to the west. One other record, in Parker County, lies within the area mapped by Tharp (1952) as Blackland Prairie. This prairie almost certainly includes areas of invading mesquite, which are probably connected with the Mesquite Savanna through the Cross-Timbers to the west. *N. victoriae* has not been found in the Oak-Hickory region of east Texas or in the Oak-Juniper region of the Edwards Plateau, with the exception of the Edwards County record discussed above (Fig. 13). The species apparently never occurs in pure grasslands. The single record from the Llano Estacado (11 mi. S Hobbs, Lea Co., N. M.), a region which is generally grass covered, is represented by a small series taken on sand dunes in an area which is probably characterized by pygmy oak, catclaw, mesquite and sagebrush (an extrapolation of about five miles from the map and description of Tharp, 1952).

On the northeastern coastal plain of México, the species occurs widely through the Tamaulipan Thorn Shrub (Muller's 1947 term). In the southern part of its range, *victoriae* penetrates beyond this formation into regions mapped as Tropical Deciduous Forest (Martin 1958*a*; Leopold, 1951), but only in more open and disturbed habitats. It has not been found within undisturbed Tropical Deciduous Forest or in the oak woodland of the Sierra Madre Oriental. Farther north and west, in the drier regions of Nuevo León and Coahuila, only the records south of Castaños, Coah., seem to be clearly within the Chihuahuan Desert Shrub (Muller's 1947 term), and here the records are only a few miles from the boundary between this formation and the Tamaulipan Thorn Shrub. All other western records in this area lie within the western edge of the Thorn Shrub region. In adjacent parts of Texas, however, *victoriae* penetrates deeply into the Chihuahuan Desert Shrub northwest of Eagle Pass.

N. victoriae is found with *spinosa* throughout much of the range of the latter. In the area of overlapping distribution the two species occupy the same habitat and are occasionally found in the same bush; *victoriae* also occurs along the edge of the range of *vannifera* (Fig. 23). Where these two species overlap, they are usually found in slightly different but adjacent habitats, *victoriae* in disturbed and more open situations, *vannifera* in less disturbed thorn forest. The details of this overlap are discussed under *vannifera*. *N. victoriae* has also been found together with members of the coastal plain colony of *pulchella* at 9 mi. NNE Antiguo Morelos, Tamps. (Fig. 23).

SEASONAL OCCURRENCE.—The earliest record for adults of this species is 7 June at 8 mi. SW Santa Teresa, Tamps., México; the latest is 1 January at 20 mi. SE Montemorelos, N. L., Méx. In Texas, the earliest record is

23 June at 3 mi. E Windthorst, Clay Co., and the latest, 3 October at Monohans, Ward Co. In the course of intensive collecting by Hubbell in Harmon County in southwestern Oklahoma between 16 and 21 June, only fourth instar or younger nymphs were found, indicating that in the northern part of its range *victoriae* probably does not mature until late June. No collecting specifically for *Neobarrettia* has been done in the late winter or spring months, and it is probable that the species lives somewhat beyond the last dates given above.

SONG.—*N. victoriae* often sings during the day, but most commonly at night. The song consists of a pulsating phrase, repeated at the approximate rate of two phrases per second in northern Texas. Each phrase consists of four or five syllables delivered too rapidly to be counted, which impart a pulsating or ragged quality to the phrase. Each syllable is between .03 and .05 seconds in duration, the interval between syllables between .02 and .03 seconds, and a four syllable phrase between .2 and .25 seconds (measured from audiospectrographs of recordings made at 73° F.). The song of this species can be readily distinguished from that of *spinosa*, with which it commonly occurs. The phrases of the song of *victoriae* are longer and the intervals between them shorter than in the song of *spinosa*, and the phrases are delivered at a rate about twice as fast as that of *spinosa* (from field notes made in northern Texas).

RECORDS.—Material examined: 295 ♂♂, 77 ♀♀, 27 numphs. KANSAS: Meade Co. (UMMZ, ANSP); Seward Co. (UMMZ, ANSP). OKLAHOMA: Alfalfa Co., Cherokee (ANSP), Ingersoll (7 mi. NE, 2 N); Woods Co. (UMMZ, ANSP), Alva (ANSP); Harper Co., 20 mi. SE Buffalo, 4.5 mi. N Laverne; Dewey Co., 8 mi. S Taloga; Caddo Co., Cement; Kiowa Co., Quartz Mt. St. Pk.; Jackson Co., Altus (ANSP), Red River S Olustee; Harmon Co., 9.6 mi. NW Hollis, 7 mi. SW Hollis. TEXAS: Hemphill Co., 10 mi. N Canadian, Canadian (ANSP); Wheeler Co., Shamrock; Wichita Co., Iowa Park; Wilbarger Co. (ANSP); Montague Co., Bonita; Clay Co., 4 mi. E Henrietta, Henrietta, 10, 3 mi. E Windthorst; Archer Co., 2 mi. NE Holliday; Baylor Co., Seymour (ANSP); Jack Co., 3 mi. SE Jacksboro; Parker Co., 8 mi. NE Cresson; Palo Pinto Co., 8 mi. S Perrin; Shackelford Co., Ft. Griffin St. Pk., Albany; Callahan Co., 15 mi. NW Cross Plains; Taylor Co., Abilene (HILL), Abilene St. Pk.; Coleman Co., 5 mi. NW Coleman, 16 mi. SSW Coleman, Shields; Mitchell Co., 1 mi. W Colorado City; Howard Co., Coahoma; Irion Co., 6 mi. S. Mertzon; Midland Co., Midland (ANSP); Crane Co., 14 mi. S Penwell (Ector Co.; TINK); Ward Co., Monohans (TINK, UMMZ); Pecos Co., 6 mi. W Ft. Stockton; Jeff Davis Co., 10 mi. S Balmorhea (ARIZ); Llano Co., 20 mi. ESE Llano, 2 mi. SE Llano, 3 mi. W Llano; Gillespie Co., 1 mi. NW Cherry Springs; Sutton Co. (ANSP), 19 mi. ESE Sonora; Medina Co., Dunlay, 15 mi. NW Hondo; Real Co., 2 mi. NE Camp Wood; Edwards Co., 2, 13 mi. W Rocksprings, 12, 16 mi. SW Rocksprings; Uvalde Co., 20, 15, 4, 2, mi. N Uvalde, Uvalde; Maverick Co., 5.3 mi. NE Eagle Pass, 1.8 mi. E Eagle Pass, Eagle Pass (UMMZ, TINK); Kinney Co., 2 mi. S Brackettville; Val Verde Co., 45 air mi. N Del Rio, 21, 20, 16, 5 mi. N Del Rio, 8 mi. SE Del Rio, 4 mi. E Del Rio, Del Rio, 7, 11, 13 mi. NW Del Rio; Terrell Co., Sanderson; Brewster Co., 6 mi. S Marathon, 12 mi. S Marathon (ANSP), 20 mi. N Chisos Mts. (ANSP);

Karnes Co., 6 mi. NW Karnes City; Bee Co., Beeville (ANSP); San Patricio Co., Gregory (ANSP, KSU); La Salle Co., 15 mi. NNE Cotulla, Cotulla (ANSP); Webb Co., 1, 14, 15 mi. SSW Encinal, between Cactus & Encinal (ANSP), 4.5 mi. NE Laredo, Laredo (ARIZ, TINK, ANSP); Duval Co., Benavides (ANSP); Brooks Co., 3 mi. NE Falfurrias; Jim Hogg Co., 26 mi. S Hebbronville; Cameron Co., Lyford (ANSP). NEW MEXICO: Lea Co., 11 mi. S Hobbs (TINK). NUEVO LEON: 4 mi. NE Sabinas Hidalgo; Mamulique Pass (ANSP); 17, 17.2 mi. W Santa Catarina; 6 mi. SE Villa Santiago; 8, 15, 20.6 mi. SE Montemorelos; 17 mi. NW Linares; 5.7, 10 mi. E Iturbide. COAHUILA: 19 mi. NE Nueva Rosita; 11 mi. NW Múzquiz; 5–7 mi. N Hermanas; 2 mi. NW Hermanas; 26 mi. E Cuatro Ciénegas; 4 mi. S Monclova; 4, 15, 34.5–.8 mi. S Castaños. TAMAULIPAS: 12 mi. S Nuevo Laredo (ANSP); 37 mi. S Linares; 37, 16 mi. NW Victoria; 6 mi. N Victoria; 8 mi. SW Santa Teresa; 22 mi. NNE San Fernando; 3, 6 mi. SW San Fernando; 30 mi. NE Padilla; 11, 21 mi. SW Padilla; 15 mi. N Llera; 2 mi. SE Hacienda Clementina (13 mi. E Llera); Zaragoza (21 mi. ESE Llera); 7 mi. SE Llera; 25 mi. S Llera; 47 mi. E Mante; 5 mi. SE Gómez Farías; 7 mi. SE Ocampo; 8 mi. E Ocampo; 9, 4 mi. NE Antiguo Morelos. SAN LUIS POTOSI: 4 mi. SE Salto del Agua (17 mi. WNW Antiguo Morelos); 18 mi. S. Antiguo Morelos; 1.5 mi. E Valles; Valles (BOL); 5–9 mi. W Tamuín.

THE PULCHELLA GROUP

This group contains *pulchella* Tinkham and the new species *bambalio*, both of which are found on the northern portion of the Central Plateau of México. The two are extremely closely related and can be distinguished only by song and by small morphological differences. They share the following distinctive features, of which the first four are unique in *Neobarrettia*: tegmina entirely green; wings thickly sprinkled with opaque spots which are white in the center of the wing and yellow on the distal margin (the color combination is unique); abdomen with only one stripe on each side just lateral to the sternites (*vannifera* also has one stripe, but it is just ventrad of the tergites); median tooth of male cercus usually reduced and rounded at apex; eye color in life whitish (as in *victoriae*; eye color unknown in *vannifera*); cephalic margin of pronotum green (as in *victoriae*); meso- and metanota jet black or shining dark brown (as in *imperfecta, vannifera,* and some individuals of *victoriae*); caudal half of female subgenital plate triangular and without lateral carinae (as in *imperfecta* and *vannifera*).

Within the genus, this group is most closely related to the monotypic Victoriae Group. The two groups share the following characteristics: eye color in life whitish; cephalic margin of pronotum green; lateral lobes of pronotum generally without dark markings; tegmen of same relative size and with a similar degree of reticulation; wings with bright opaque colors; femoral teeth whitish tipped with brown; dorsal surface of tibiae reddish or vinaceous. Although only the first three of these characters are restricted to the two groups (eye color is unknown in *vannifera*), the constant association of all of them in the species of both groups indicates a close relationship. The subgenital plate of the species of the Pulchella Group is similar to that of *vannifera,* but the lack of other common characters (except for those shared with other species) suggests that there is no close relationship to the latter species.

N. imperfecta shares a number of characters with this group and is believed to have been derived directly from it. The relationship is discussed in detail in the taxonomic treatment of *imperfecta.*

Neobarrettia bambalio[12] new species (Figs. 17m, 19d, 20c, 20i)

HOLOTYPE.—Male, 12 mi. NW Ciudad del Maíz, San Luis Potosí, México, 22 Aug. 1959 (I. J. Cantrall and T. J. Cohn, No. 18); University of Michigan Museum of Zoology.

COMPARISONS.—This species may be distinguished from its closest relative, *pulchella* Tink., by the following characteristics of the male sex: median tooth of cercus represented by a low swelling; internal ridge of cercus simple and shelf-like throughout its length; apical tooth of the cercus bent well below the axis of the shaft; call a stutter, each phrase consisting of several very rapidly delivered syllables. In the female of this species there is no tubercle on the 7th abdominal sternite (unique in *Neobarrettia*) and no lateral pits and ridges on the subgenital plate. In addition, the following *bambalio* features are more variable and overlap with the condition found in *pulchella*: apical tooth of male cercus always relatively long and slender, never as short or as thick as in many individuals of *pulchella* (compare Figs. 19c and 19d); penultimate tergite of male with distal margin generally less deeply excised and at most weakly raised, never tuberculate; relative length of tegmina averaging less (Fig. 22); wings generally less heavily spotted than the average condition in *pulchella.* The structure of the internal ridge of the male cercus closely resembles that in *imperfecta,* but differs in the presence of a swollen area representing the median tooth; the female subgenital plates in the two species are almost identical, differing only in the more weakly triangulate shape in *bambalio.* The angulation of the apical tooth of the male cercus is very similar to that in *sinaloae* and *victoriae.*

Of the differences between *bambalio* and *pulchella,* only the three involving the median tooth of the male cercus, the lateral ridges and pits of the female subgenital plate, and the tubercle of the 7th abdominal sternite of the female represent anything more significant than slight

---

[12] From the Latin, *bambalio,* a stutterer, in allusion to the call of this species.

changes in shape or proportion. In these three characters, the condition in *bambalio* represents a strong reduction in size, or absence of structures found in all or most of the other species in the genus. It is therefore very easy to derive *bambalio* directly from *pulchella,* if the assumption is made that the simple conditions in *bambalio* do *not* represent the primitive condition in the genus. The reasons for making this assumption are discussed in detail in the section on species relationships.

Species Description.—PRONOTUM (Fig. 20c): caudal portion turned up at an angle usually somewhat less than 45°, occasionally 45° or slightly more (in holotype, less than 45°), and either generally and weakly recurved, or briefly and strongly recurved caudally; distinct but weak humeral sinus. APPENDAGES: tegmen medium in length (1.08–1.39 times length of fore femur); reticulation dense. Cross veins of wing weak. Caudal armature of fore femur occasionally with one or two minute teeth among large ones (none in holotype). MALE TERMINALIA: caudal margin of penultimate tergite (Fig. 20i) weakly emarginate, margin on either side weakly produced into a broadly rounded lobe; caudolateral margins of semimembranous area flat, bluntly obtuse-angulate; cercus (Fig. 19d) short (about .5 times width of penultimate tergite); apical tooth short, gently curved inward with two weak obtuse angles, depressed considerably below axis of shaft (degree of depression unique in *Neobarrettia*); proximo-internal angle of internal ridge usually prominent, acute angulate, sometimes only moderately produced and blunt; median tooth a weak broad swelling (unique); distal portion of internal ridge joining shaft dorsally as a simple shelf. FEMALE TERMINALIA (Fig. 17m): subgenital plate with caudal half broadly and weakly triangular, weakly inflated, apex very briefly and narrowly notched; median carina sharp, very weakly and broadly arcuate, extending almost entire length of plate, very briefly obsolete on caudal tenth of plate; no lateral carinae, lateral pits and ridges, or basal transverse flange; seventh abdominal sternite without a tubercle (unique). COLORATION: eyes in life whitish or with a faint yellowish or reddish tinge; occiput and dorsum of pronotum often with a brownish suffusion (very light in holotype); cephalic and caudal margins of pronotum green; brown markings rare, when present, a light to moderate brown suffusion on upturned portion, extending ventrad as a weakly-defined narrow cephalic margin of ivory stripe (holotype without brown markings); meso- and metanota jet black and very dark shining brown; venter of abdomen with one longitudinal yellow stripe on each side lateral to sternites; tegmina green in both sexes; wing colors opaque, background black, central spots white, some distal spots wholly or partially yellow, distal marginal band yellow, spots numerous, irregular, infrequently fused, generally angulate; femoral teeth whitish, briefly tipped with brown. Dorsum of all tibiae vinaceous. MEASUREMENTS (in mm.): male holotype: length of pronotum, 5.5; width of pronotum, 4.5; length of tegmen, 20.9; length of femora: fore, 8.8; middle, 8.5; hind, 21.0. Measurements of the material studied are summarized in Figures 21 and 22.

Paratypes.—All specimens studied are designated as paratypes[13] with the exception of a few badly damaged ones. Male and female paratypes are deposited in the University of Michigan Museum of Zoology, the Academy

---

[13] Only a part of the series of this species at the Academy of Natural Sciences of Philadelphia was borrowed and studied with care; the remainder which were merely identified and measured, are not designated as paratypes.

of Natural Sciences of Philadelphia, and the U. S. National Museum. A male paratype is deposited in the Tinkham Collection.

VARIATION.—The degree to which the caudal portion of the pronotum is turned up and recurved is quite variable. In general, this portion is less sharply upturned and recurved than in *cremnobates* and *spinosa,* more recurved than in *vannifera,* and never as weakly upturned as in *victoriae.* The number, size and distribution of the wing spots is also variable; in general the black color appears to be more extensive than the white. The spots are usually more or less rectangular or six-sided, very rarely rounded or oblong; some spots occasionally are fused with the distal band. The antennae are most often green, and it is possible that the yellowish or brownish color seen in some specimens results from poor preservation. I have been informed by J. W. Cohn that the green antennae of living individuals of this species are in sharp contrast to the brown antennae of living *pulchella.*

DISTRIBUTION (Figs. 23, 24).—This species occurs in two areas in southern San Luis Potosí, apparently widely separated from each other by the southern colonies of *pulchella.* The species has been found only along the Ciudad del Maíz-San Luis Potosí Highway. It occurs almost continuously from 1.2 mi. NE Cd. del Maíz to 4 mi. SE El Tepeyac, and from Núñez (20.5 mi. NE Villa Hidalgo) to 2.7 mi. SW Villa Hidalgo, with a gap between 5 mi. W Núñez and Villa Hidalgo. *N. pulchella* occupies almost the entire area between El Tepeyac and Núñez. There is a gap of 14 miles between the last *bambalio* southeast of El Tepeyac and the first *pulchella* northwest of that town. In the Núñez area, the two species overlap for about 0.5 miles. This overlap zone may be moving slowly eastward at the present time. In 1958 both species were found in the town itself, and mixed colonies were heard as far as 0.5 miles east of Núñez, whereas in 1961, pure *bambalio* colonies were found as far as 0.3 miles east of town, mixed colonies between 0.5 and 0.8 miles east, and pure *pulchella* colonies starting 1.0 miles east of Núñez. Each species was very common and singing vigorously on the three occasions when the Núñez area was investigated and they were found virtually continuously through that part of the area surveyed. Investigations immediately beyond the range of this species are discussed under the distribution of *pulchella.*

HABITAT.—*N. bambalio* occurs in the southern portion of the Chihuahuan desert, through an altitudinal range of 3400 to 5700 feet. The desert in which it is found is characterized by a very rich growth of bushes and cacti, including the following: abundant creosote bush, mesquite (usually small trees), salt bush, *Koeberlina,* and several types of tree cactus.

The gap between this species and *pulchella* in the El Tepeyac area corresponds to an area of lower and sparser vegetation in the deepest portion of a desert basin; the last *bambalio* was found on a small hillock of thick vegetation at the very edge of the zone of sparse vegetation. The gap between the Núñez and Villa Hidalgo colonies also corresponds to the flat floor of a desert basin. Some of the vegetation in the northeastern end of this basin is heavier and richer, and a few scattered *bambalio* have been found here. The western limit of this species lies within a mile or two of the beginning of a savanna in which bushes and cacti are common. The eastern limit coincides with the beginning of the oak forests of the Sierra Madre Oriental. The last colony of *bambalio* was heard in a bushy and weedy field within a hundred yards of the first wooded ridge of the Sierra Madre. The species was not found in the patches of bushy grassland within the mountains, nor in the bushes on exposed rocky slopes there.

SEASONAL OCCURRENCE.—*N. bambalio* has been found as early as 20 August and as late as 25 December; on both dates the species was abundant and calling vigorously. No survey has been made specifically for *Neobarrettia* in this region between January and August.

SONG.—This species apparently rarely sings during the daylight hours, but begins singing immediately after dusk and continues through the early hours of the morning. On the one occasion when *bambalio* was heard during the day, many individuals in a colony were singing vigorously and very rapidly on a warm, bright sunny afternoon in mid-November. The song consists of a stuttering phrase, continuously repeated at a rate of several phrases per second early in the evening, becoming very much slower and less regular in the cold early morning hours. Each syllable in the phrase is about .04 seconds or less in duration, and a three-pulse phrase is about .13 seconds in duration (measured from audiospectrographs of recordings made in the laboratory at about 76° F.). The individual syllables of the "stutter" usually can be barely distinguished. In the western colony, however, the syllables are often slow enough to be counted. Very late on a cold misty night in November in this area, each "stutter" was reduced to one or two syllables, and the interval between "stutters" was very long and irregular.

RECORDS.—Material examined: 75 ♂♂, 13 ♀♀, 3 nymphs. SAN LUIS POTOSI: 1.2 mi. NE Cd. del Maíz; 5 mi. NW Cd. del Maíz; 6 mi. W Cd. del Maíz (ANSP); 12 mi. NW Cd. del Maíz; 4 mi. SE El Tepeyac (24 mi. NW Cd. del Maíz); vic. Núñez (20.5 mi. NE Villa Hidalgo), 5 mi. SW Núñez; 17 mi. NE Villa Hidalgo; Km. 60–75 E San Luis Potosí (ANSP); 2–2.7 mi. SW Villa Hidalgo.

Neobarrettia pulchella (Tinkham) (Figs. 17l, 19c, 20d, 20j)

1944. *Rehnia pulchellus* [*sic*] Tinkham, Amer. Midland Nat., 31:284–86, Fig. 12, [♂, ♀–4 mi. N Escondida, SW Nuevo León, México].

Holotype.—Male, 4 mi. N Escondida, SW Nuevo León, México, 26 Aug. 1940 (E. R. Tinkham); Tinkham Collection.

Comparisons.—This species may be distinguished from its very close relative, *N. bambalio*, n. sp., by details of the male cercus, female subgenital plate and 7th abdominal sternite (all described below), and by the simple call of the male which consists of a single syllable continuously repeated. *N. pulchella* resembles *imperfecta* in the tubercle of the 7th abdominal sternite of the female which is low and blunt, arises from the cephalic half of the plate, and has its apex near the middle of the plate, in addition to characters also shared with *bambalio* (see group characters).

Species Description.—Similar to *bambalio* in all features except the following: MALE TERMINALIA: distal margin of penultimate tergite (Fig. 20j) often more excised mesally, caudolateral margins of semimembranous area usually raised, angle sometimes weakly tuberculate; cercus (Fig. 19c) with apical tooth usually shorter, thicker, the apex more blunt and bent only slightly below axis of shaft; median tooth a distinct projection, rounded at apex, bent ventrad; distal portion of internal ridge bent ventrad, ventral part joining shaft of cercus well below dorsum and continuing to near apex as a low longitudinal ridge. FEMALE TERMINALIA (Fig. 17l): subgenital plate with caudal half more triangular, slightly more inflated; median carina higher, sharper; a shallow pit present just laterad of a short oblique ridge near lateral point of articulation of free caudal half of plate; tubercle of 7th abdominal sternite located on cephalic half of plate, low, weakly compressed, apex usually acute, often rounded, centered over cephalic third of plate. COLORATION: caudal portion of pronotum often with a chestnut suffusion, which extends ventrad as a narrow border along ivory stripe on lateral lobe; wing spots generally larger. MEASUREMENTS: these of the series studied are summarized in Figures 21 and 22.

Variation.—As indicated above, this species shows considerable individual and some geographic variation. Although the apical tooth of the cercus is usually short and thick, as indicated in Figure 19c, it is sometimes as long and as narrow as in *bambalio*, and in one specimen is even longer and narrower. The median tooth and the internal ridge are widely different from those of *bambalio*, and the apical tooth is always less depressed. The relative size of the white spots is very hard to quantify and no attempt has been made to do so; the largest white spots appear to occur in *pulchella* and there seem to be more individuals with large spots in this species. The northern and eastern specimens have the smallest spots. The specimens from the coastal plain all have very long tegmina (those of the females are the longest in the series) and the wing spots are very small and rounded.

Distribution (Figs. 23, 24).—This species has an extensive distribution on the Central Plateau of México in the states of San Luis Potosí and Nuevo León. Limital records are as follows: northern, 29 mi. SE Arteaga (Coah.), N.L.; eastern, 22 mi. SW Cd. Victoria, Tamps.; southern, 10 mi. NW Río Verde, S.L.P.; western, Núñez (20.5 mi. NE Villa Hidalgo), S.L.P. In addition, an isolated colony occurs on the coastal plain between Mante and 9 mi. NNE Antiguo Morelos, Tamps. Most of the regions surrounding the range of this species have been surveyed or sampled, except for the region between Núñez and Concepción del Oro.

Very careful surveys have been made for both *pulchella* and *bambalio* along the main highway from Antiguo Morelos to San Luis Potosí. Between Antiguo Morelos and the foothills of the Sierra Madre near El Naranjo only *victoriae* has been heard. No *Neobarrettia* has been heard in the forests of the Sierra Madre. *N. bambalio* is found in the desert immediately to the west of the last forested ridge of the Sierra and continues to near El Tepeyac. There is a gap of 14 miles between the last *bambalio* southeast of that town and the first *pulchella* at 10 mi. NW El Tepeyac. From this point, *pulchella* occurs virtually continuously to Núñez where it is replaced by *bambalio*. The overlap zone is discussed under *bambalio*. That species is then found from Núñez to 2.8 mi. W Villa Hidalgo, beyond which no *Neobarrettia* has been heard. A similar survey has been made between San Luis Potosí and Río Verde. *N. pulchella* was first heard at 6 mi. W Santa Catarina, then continued sporadically to the last colony at 10 mi. NW Río Verde. Only sampling work has been done around the coastal plain colony which appears to be surrounded by scattered colonies of *victoriae*.

HABITAT.—Throughout most of its range, *pulchella* is found in the rich Chihuahuan desert in a habitat generally similar to that described for *bambalio*. It occurs through an altitudinal range from approximately 600 to 6050 feet. On the northern, eastern and southern periphery of its range, the species extends into several different vegetational zones. The northernmost individuals were found in the lower edge of the pine zone, where pines are mixed with a rich variety of desert bushes on rocky slopes. Several individuals at this locality were heard singing high in pine trees, but none were heard in pure stands of pine at nearby localities at higher elevations. Surprisingly, no individuals were heard on the bush-covered rocky slopes nearby, or in the pure creosote desert a few miles to the south at lower elevations. Survey in this region was not possible, and it is likely that the sampling was insufficient. In the eastern part of its range, *pulchella* penetrates deeply into the Sierra Madre Oriental near Jaumave. The road through the Sierra Madre here rarely ascends into pure oak or pine woodland, and *pulchella* was found in desert vegetation. Only on the westernmost ridge was a colony found in an almost pure stand of juniper, but even here the individuals were found on a plant which occurs commonly in the desert. In the southern part of its range west of Río Verde this species was heard or collected throughout the thorn forest zone (the "matorral submontano" of Rzedowski and Rzedowski, 1957). It does not extend into agricultural land in the lowlands near Río Verde, and it does not extend into the oak zone in the mountains to the west, where it has been heard only one mile away from the first oaks. The habitat of the coastal plain colony is not known with certainty. One specimen was collected in roadside weeds next to farm land but with thorn or tropical deciduous forest a few hundred yards away. Another specimen was collected on a ridge with "very interesting and rich tropical growth" (from field notes of H. R. Roberts).

Seasonal Distribution.—The earliest records for *pulchella* are 19 July at 10 mi. S Mante, and 30 July at La Maroma. The latest record is 25 December at Núñez. No collecting specifically for *Neobarrettia* within the range of *pulchella* has been done before or after these limiting dates.

Song.—*N. pulchella* normally sings throughout the night and only rarely during the daylight hours. On one occasion, however, individuals were singing over a wide area near Tula on a hot, bright afternoon in mid-August. The song consists of a simple, single syllable (occasionally quickly repeated to give a double syllable phrase), continuously repeated at a rate of probably several phrases per second early in the evening, slowing down to one phrase per second or less in the cold early morning hours. Each syllable is .05 to almost 0.1 seconds in duration (measured from audiospectrographs of recordings made in the laboratory at about 78° F.).

Records.—Material examined: 69 ♂♂, 17 ♀♀. COAHUILA: 27, 29 rd. mi. SE Arteaga. NUEVO LEON: 4, 6 mi. N Escondida (TINK). TAMAULIPAS: 22 mi. SW Cd. Victoria; La Maroma (N of Jaumave, ANSP); 1, 5, 28 mi. SW Jaumave; 4 mi. N Tula; 10 mi. S Villa Juárez [Mante] (ANSP); bet. Villa Juárez & 35 mi. S (ANSP); 9 mi. NNE Antiguo Morelos. SAN LUIS POTOSI: 7 mi. E Matehuala (TINK); 10 mi. NW Tepeyac (37 mi. NW Cd. del Maíz); 10 mi. SE Presa de Guadalupe (40 mi. NW Cd. del Maíz); Km. 100–110 E San Luis Potosí (ANSP); 38, 25 mi. NE Villa Hidalgo; 2 mi. NE Núñez; vic. Núñez (20.5 mi. NE Villa Hidalgo); 10 mi NW Río Verde; 5.5 mi. W Santa Catarina.

THE IMPERFECTA GROUP

This group contains only *N. imperfecta* (Rehn), the generotype, which occurs in the basin of the Río Balsas, between Taxco, Arcelia and Chilpancingo. *N. imperfecta* differs in many characters from the other species of the genus as listed in Table 4, but may be most readily distinguished in both sexes by the chocolate, white-flecked lateral stripe on either side

TABLE 4

COMPARISON OF THE UNIQUE CHARACTERISTICS OF *N. imperfecta* WITH THE CORRESPONDING CONDITIONS IN THE OTHER SPECIES OF *Neobarrettia*

Condition in *imperfecta*	Condition in other species of *Neobarrettia*
1. Brachypterous, tegmen of female lobate	Macropterous to brachypterous, tegmen never lobate
2. Wing stublike, several times shorter than tegmen; wing veins apparently absent	Wing as long, or almost as long, as tegmen; wing veins present but sometimes weak
3. Sclerotized titillators absent	Sclerotized titillators present, but in most species only partly sclerotized
4. Hind tibia with one pair of ventroapical spurs	Hind tibia with two pairs of ventroapical spurs
5. Male tegmina inflated	Male tegmina not inflated
6. Lateral lobe of pronotum with a broadly rounded ventrocaudal angle near dorsum, without humeral sinus	Lateral lobe without a ventrocaudal angle, often with a weak humeral sinus
7. Subcosta and radius of male tegmen generally yellowish white	Subcosta and radius green, except when whole wing fades to yellowish
8. Lateral edges of abdominal tergites with a longitudinal brown stripe with whitish flecks, sharply contrasting with dorsal color	Abdominal tergites without longitudinal stripe, tergites transversely concolorous or shading gradually from dark to light
9. Geniculae with one (dorsal) spine	Geniculae with two spines
10. Caudal third or more of pronotum elevated and wider than cephalic margin; shoulders broadly rounded	Caudal quarter or less of pronotum elevated and narrower than cephalic margin; shoulders narrowly rounded
11. Ivory stripe of lateral lobe of pronotum restricted to ventral two-thirds or less of lobe	Ivory stripe of lateral lobe reaching dorsum (rarely only reaching shoulder)
12. Cephalic and caudal borders of pronotum with black margin on mesal third only	Cephalic and caudal borders of pronotum green, or with black or brown margin across entire dorsal width
13. Mirror of male left tegmen roughly triangular, costal margin (vein Cu_{1b}) curved, stridulatory vein long	Mirror of male left tegmen roughly rectangular, costal margin straight, stridulatory vein short

of the abdominal tergites, in the female by the lobate, nonattingent tegmina and in the male by the inflated tegmina which are wider than the cephalic margin of the pronotum, and the consequently greater length and angle of the upturned portion of the pronotum (one-third of the pronotum turned up at an angle greater than 45° as opposed to one quarter of the pronotum turned up at an angle less than 45° and usually recurved).

The imposing list in Table 4 might be considered to indicate a generic level of difference between *imperfecta* and its congeners, and *imperfecta* has been treated as a separate genus since the description of the other members of the genus. However, closer examination of these characters, as well as those which *imperfecta* shares with certain other species of the genus to be discussed below, indicates a special relationship which would be, and indeed has been, obscured by generic separation.

Most of the *imperfecta* characteristics in the table may be easily derived from conditions in the remaining species of *Neobarrettia*. In the first five characters, the condition in *imperfecta* is either unique or very rare among related genera and subfamilies, whereas the condition in the other species of *Neobarrettia* is widespread among other genera, and thus presumably primitive. The same is probably true of characters 6 to 8, although their variability in other genera makes this conclusion less certain. The *imperfecta* condition in character 9 is foreshadowed in other species by individual variants which do not possess the ventral spine. The remaining characters are either special developments restricted to *Neobarrettia* (10, 11, and 12) or are too variable in other genera for a reasonable determination of primitive or derivative conditions (character 13). Thus, five of the unique characters in *imperfecta* were probably derived from the primitive condition common to the other species of the genus, and four more characteristics could have been similarly derived. The remaining four are relatively simple, and there seems to be no morphological reason to bar their derivation from conditions found in the other species. Since *imperfecta* certainly belongs to the same stock as do the remaining species of *Neobarrettia* (see previous discussion of distinctive generic characters), it is reasonable to conclude on the basis of the above morphological data that *imperfecta* was derived from within the genus. This conclusion is further strengthened by the detailed similarity which *imperfecta* bears specifically to one of the other *Neobarrettia* species groups as discussed below.

The distribution of characters suggestive of relationships between *imperfecta* and other species is indicated in Table 5. *N. imperfecta* also bears some resemblance to other species, but in fewer and less specific characters.

The similarities between *imperfecta* and *cremnobates* appear to be

TABLE 5

Distribution of Characters Suggestive of Relationships Between *Neobarrettia imperfecta* and Other Species

imperfecta	*cremnobates*	*sinaloae*	*pulchella* and *bambalio*
Male cercus without median tooth and with short apical tooth	+	—	±[1] (*bambalio*)
Female subgenital plate with caudal half triangular, with median carina elongate, and without lateral carinae or pits	—	—	+ (*bambalio*)
Metanotum entirely black or dark brown	—	—	+
Sternal tubercle of female abdomen low, blunt, compressed	±[2]	—	+ (*pulchella*)
Femoral teeth white and brown	+	—	+
Mesal portion of cephalic and caudal margins of pronotum black	±[3]	±[4]	—
Irregular longitudinal brown stripe on shoulders of pronotum	+	±[5]	±[5]
Occiput often brown	—	±[5]	±[5]
Wings white with black spots	—	+	—
Tegminal reticulation greatly reduced	—	+	—
Tegmen of female shorter than that of male	—	±	—
Caudal portion of pronotum in male strongly upturned, in female barely elevated	—	±	—

[1] Median tooth represented by a low swelling, apical tooth longer.
[2] Variable, sometimes high and acute.
[3] Both margins completely black.
[4] Cephalic margin completely, caudal margin sometimes black or dark brown.
[5] Dorsum of pronotum and occiput sometimes suffused, suffusion extending to shoulder.

superficial. Although the apical tooth of the male cercus is short and the median tooth absent in both species, the distal webbing and very strong basal tooth in *cremnobates* gives its cercus a very different appearance from that of *imperfecta* (compare Fig. 19b with 19e). On the other hand, the cercus of *imperfecta* resembles the *bambalio* cercus in all details except for the lack of the low swelling which represents the median tooth in *bambalio.* Of the other three characters which *imperfecta* shares with *cremnobates,* only the lateral pronotal stripes are restricted to the two species, and even this character may be represented by the lateral edges of the dorsal suffusion in *pulchella, bambalio,* and *sinaloae.*

The characteristics shared by *sinaloae* and *imperfecta* are more detailed, but most of them may be attributed only to the manifold effects of wing reduction. The wings of *Neobarrettia* apparently function primarily for display (see discussion in a later section on Behavioral Details). Once they have been reduced beyond the point where they can perform this function effectively, they may be readily and rapidly reduced even further. The tegmina in the females of the brachypterous species probably serve only as protection for the wings. Thus when the wings in this sex are reduced, the tegmina would be reduced to the same extent. In the male sex, the tegmina also serve the more important function of sound production, and therefore cannot be reduced below the minimal size effective for singing if this function is to be retained. The size and shape of the upturned portion of the pronotum in *Neobarrettia* seem to be closely associated with the size and shape of the base of the tegmina. It is greatly enlarged and very sharply upturned in male *imperfecta* in association with the marked inflation of the stridulating area of the tegmina. In females of other species, the tegminal base is more or less the same size as that of the male, and the size and shape of the caudal portion of the pronotum is similar to that of the male. Where the tegmina of the female have been reduced further than those of the male, one might expect sexual dimorphism in size and shape of the pronotum. This is the case, but only to a slight extent, in *sinaloae,* where the tegmina show slight sexual dimorphism in length, and it is strikingly so in *imperfecta* where the tegmina are markedly dimorphic in length. Wing reduction may also account for the difference in the color pattern of the wing between *imperfecta, sinaloae,* and *hakippah* (dark spots on a light background) and the other species of *Neobarrettia* (light spots on a dark background). The light color in all species of the genus is centered over the cross veins, while the dark occurs in the intervening membranous areas. If the presence of a vein ensures a certain minimum of light color, then the crowding of veins as the wing is reduced might cause the encroachment of light color on areas of dark. This might result eventually in the coalescence of the light color areas and the consequent restriction of the dark color to spots between the veins. There is also some reason to believe that tegminal reduction might result in the reduction of the amount of reticulation merely because of reduced function and space. There is thus good reason to believe that a parallel reduction in wings might lead to similarities among species otherwise not closely related, in sexual dimorphism of tegminal and pronotal size and shape, in tegminal reticulation, and in wing color pattern. Since the only other characters shared by *imperfecta* and *sinaloae* are also shared with other species (Table 5), and in view of the apparent tendency toward wing reduction in the genus, there is little reason to believe that *imperfecta* and *sinaloae* are closely related.

The similarities between *imperfecta* and the Pulchella Group are not numerous, but they are detailed and cannot be ascribed to simple parallel development. The most detailed resemblances are found in the male cercus and the female subgenital plate. The cercus of *imperfecta* is similar to that of *bambalio* in the shape and length of the apical and basal teeth and in the shape of the internal ridge, and differs only in the complete absence of the median tooth. The female subgenital plates of both species are closely similar in the shape of the caudal portion, the length and shape of the median carina, and the absence of lateral carinae, ridges and pits. A functional relation exists between the pits of the female subgenital plate and the median tooth of the male cercus (see discussion in the section on Behavioral Details), and there is a parallel sequence of reduction of both structures among *pulchella, bambalio,* and *imperfecta.* A relatively well-developed median cercal tooth, as well as lateral pits and ridges on the subgenital plate are present in *pulchella,* the cercal tooth is very weak and the pits and ridges are absent in *bambalio,* and all three structures are absent in *imperfecta.* In these genitalic characteristics, *imperfecta* shows no closer similarity to any other species. As indicated in Table 5, *imperfecta* also shares with the Pulchella Group a completely dark metanotum otherwise found only in *vannifera* and southern populations of the related *victoriae,* as well as three more general characteristics found also in several other species. Thus, *imperfecta* shares with this group a number of characteristics, some of them very detailed, and even one by which it differs (the absence of the cercal tooth) seems to represent the culmination of a trend within the Pulchella Group. Since almost all the unique characteristics of *imperfecta* tabulated previously can be derived from conditions found within the Pulchella Group, it is evident that *imperfecta* was derived from a recent ancestor of that group. Only two characteristics are not readily derivable from the Pulchella Group: (1) the black pronotal margins which may represent a retention of a primitive character, in keeping with the above conclusion (see discussion under *imperfecta* in Part III), and (2) the chocolate abdominal stripes which must be considered to represent merely a unique development in the species.

Neobarrettia imperfecta (Rehn) (Figs. 17b, 17d, 17n, 19e, 20k)

1900. *Capnobotes imperfectus* Rehn, Trans. Amer. Ent. Soc. 27:89–90 [3 ♂ ♂–Río Cocula, Guerrero, México].

Types.—Three males, Río Cocula, Guerrero, México, December, 1898 (Otis W. Barrett); Academy of Natural Sciences of Philadelphia.

Comparisons.—See preceding discussion.

Species Description.—PRONOTUM (Fig. 17d): cephalic third uniformly semicylindrical; caudal third elevated at a very slight angle in female, at an angle greater than 45°, often approaching 90°, in male, with a very low, broadly rounded median carina; caudal margin sometimes weakly notched, not at all produced; lateral shoulders broadly rounded, extending obliquely forward to near middle of pronotum. Lateral lobe with ventral portion of caudal margin forming an acute angle with horizontal, dorsal portion almost perpendicular, margin thus having a distinct, broadly rounded ventrocaudal angle (unique in *Neobarrettia*); humeral sinus absent. APPENDAGES: tegmina in male short (.71 to 1.12 times length of fore femur); in female, extremely short (less than .2 times length of fore femur), lobate, nonattingent (unique); reticulation greatly reduced, remaining veins forming distinct cells; male tegmina strongly inflated (dorsal width of folded tegmina 1.2 to 1.3 times width of cephalic margin of pronotum), stridulating area more or less triangular, length of stridulating vein greater than length of mirror, costal margin of mirror (vein Cu_{1b}) strongly curved (all unique); wing stublike in male, several times shorter than tegmen, hardly developed in female; veins apparently absent (all unique); caudal armature of fore femur without minute teeth among larger ones; all geniculae unispinose; hind tibia with one pair of ventro-apical spurs (unique). MALE TERMINALIA: caudal margin of penultimate tergite (Fig. 20k) broadly and shallowly emarginate, margin on either side weakly produced into very short, broadly rounded lobes; caudolateral edges of semimembranous area flat, broadly rounded or weakly obtuse-angulate. Cercus (Fig. 19e) short (about .4 to .5 times width of penultimate tergite); apical tooth very short, strongly curved inward with two weak obtuse angles in same plane as shaft of cercus in internal view, apex briefly acute; proximo-internal angle of internal ridge moderately produced, bluntangulate; no median tooth; distal portion of internal ridge joining shaft dorsally as a simple shelf; no sclerotized titillators (unique). FEMALE TERMINALIA (Fig. 17n): caudal half of subgenital plate strongly triangular, very weakly inflated, apex briefly but strongly notched; median carina prominent, very weakly and broadly arcuate, extending entire length of plate; no lateral carinae, folds and pits, or basal transverse flange; tubercle of 7th abdominal sternite low, rounded, somewhat elongate or compressed, located on cephalic quarter of plate. COLORATION: eyes in life grayish, brown, olive or tan (late December individuals); occiput and dorsum of pronotum and abdomen often light to dark brown; cephalic and caudal borders of pronotum above with narrow black margins on mesal third (unique), caudal margin sometimes black between shoulder and ivory stripe; muscle scars dark brown (unique); ivory stripe of lateral lobe restricted to ventral two-thirds of lobe (unique), margined cephalically with a broad brown or black stripe on lower quarter or less, sometimes entire cephalic margin with a very narrow brown or black stripe; shoulder of pronotum with an irregular light (sometimes dark) brown longitudinal stripe, extending length of pronotum. Meso- and metanota entirely jet black or very dark brown, sometimes metanotum lighter caudad and laterad; dorsum of abdomen green to brownish, a longitudinal chocolate brown stripe with whitish flecks along lateral edges of tergites (unique), stripe often broken, with dark color and flecks restricted to laterocaudal edges of tergites; venter of abdomen variable (late December individuals), greenish, reddish, yellow, or green cephalad becoming bright yellow caudad, sometimes with a narrow longitudinal yellow stripe lateral to sternites and another ventral to tergites. Tegmen of male with veins Sc and R yellowish white (unique), remaining veins bright green, membrane generally dark brown; veins of female tegmen yellowish or green (dried specimens); femoral teeth white, briefly tipped with brown; dorsum of all tibiae brown to chestnut. Wing whitish with small, irregular, black spots. MEASUREMENTS: these of the series studied are summarized in Figures 21 and 22.

VARIATION.—Individual variation is included in the above description. No obvious geographic variation has been noted in this species, with the possible exception of the small size of individuals of the southernmost populations. The six males taken south of Petaquillas fall in the lowermost range of the species in all of their measurements. This might be considered an indication of the rigor of the environment at the edge of the species range, although individuals collected at the same time six miles to the north and at a similar elevation, are considerably larger and vary around the mean size for the species.

DISTRIBUTION (Fig. 24).—As presently known, *imperfecta* is restricted to the central part of the basin of the Río Balsas in Guerrero and Morelos. Limital records are as follows: southern, 2.2 mi. S Petaquillas; western, Arcelia; northwestern, 4.7 mi. SE Mogote (song record only); northeastern, 9.3 mi. SW Amacuzac (song record only). The species was not found in apparently suitable habitats in the following areas which more or less surround this region: the Apatzingán area, Michoacán; the Izúcar de Matamoros-Petlacingo area, Puebla; the Cuernavaca-Amacuzac area, Morelos; and the area along the main highway between the road summit at 4 mi. S Petaquillas and Acapulco, Guerrero. The failure to locate *imperfecta* in these areas is unlikely to have been a collecting error, since they were carefully investigated within a few days of the time when the species was found common and actively singing elsewhere.

HABITAT.—This species has been found very commonly in weedy and bushy vegetation, usually associated with spiny leguminous bushes, and especially in disturbed roadside habitats. It has also been encountered in green cornfields with only weeds and no bushes nearby, and in dry, cutover cornfields with sparse weedy growth. Although it has been found in close proximity to tropical deciduous forest in the Taxco region, its characteristic stridulation has never been heard within the forest, but no close search was made to determine whether or not it was present there. No individuals were heard in the heavy woodland of the canyon southeast of Petaquillas, although the species was singing in the more open vegetation at either end of the canyon during the same evening. *N. imperfecta* has an altitudinal range from 1550 ft. near Mexcala, Guerrero, to approximately 4000 ft. south of Amacuzac, Morelos.

SEASONAL OCCURRENCE.—The earliest record for adults of this species is August at Río Cocula (ANSP), the latest, 25 December, northeast of Taxco (UMMZ). One last instar nymphal male was collected on 8 August near Chilpancingo (ANSP). Singing males were common on 16 September and 25 December northeast of Taxco. No search specifically for *imperfecta* has been made before or after the above limiting dates in areas where it is known to occur. It is therefore likely that the species matures earlier and lives longer than these dates indicate.

SONG.—The males of *imperfecta* sing vigorously and commonly during the day (contrary to the first report of this species by O. W. Barrett, see Rehn, 1901*b*), and less vigorously at night. The song consists of a single, simple, long syllable usually delivered in groups of three during the day at a rate of about three syllables per second, the phrase rapidly repeated. At night, the singing slows down, and very late on cold nights the song consists of only a single syllable repeated very slowly and irregularly. In the laboratory, this species has been recorded producing as many as seven syllables per phrase at 70° F. Each syllable is about .15 seconds in duration, the interval about 0.1 second (measured from audiospectrographs of recordings made in the laboratory at 70° F.). The song has a high-pitched, tinny quality, quite different from that of other *Neobarrettia* species, the songs of which are much more noisy in quality. This results from the much narrower range of frequencies and the higher tooth strike rate in the song of *imperfecta* than in those of the other species of *Neobarrettia*.

RECORDS.—Material examined, 78 ♂♂, 24 ♀♀, 18 nymphs. MORELOS: 10 mi. SW Coatlán de Río; Km. 93 between Cuernavaca and Taxco (ANSP) (see Part II for a discussion of this record). GUERRERO: 4.7 mi. SE Mogote (song record, T. J. Cohn); 16 mi. NE Taxco; 1 mi. S Taxco; toll road between Iguala and 9.3 mi. SW Amacuzac (song records, T. J. Cohn); 6 mi. W Iguala; 1.6 mi. NE Cocula; Río Cocula (ANSP); 12 mi. NW Iguala; 22, 6 mi. NE Arcelia; Arcelia; 6, 11 mi. S. Iguala; Km. 215 between Iguala and Río Balsas (ANSP); Mexcala (ANSP); 33 mi. N Chilpancingo; 36 mi. S Iguala; 28 mi. N Chilpancingo; Cañón de Zopilote (ANSP); 4 mi. N Chilpancingo (ANSP); Gorge, S Chilpancingo (ANSP); 4 mi. SE Chilpancingo; 1.7, 2.2 mi. S Petaquillas; 4.3 mi. E Petaquillas.

BEHAVIORAL DETAILS

DISPLAY.—One of the interesting features of the behavior of *Neobarrettia* is the striking display posture assumed by individuals of both sexes when "provoked." Thus treated, a *Neobarrettia* will often open its mandibles, raise its fore legs high over its head, "rear back" on its middle and hind legs exposing the cephalic part of the abdominal venter, and spread its tegmina and wings (Frontispiece). Individuals display in the field and the laboratory, but it is not known whether this is a normal reaction to a predator or other large animals. All species have been observed to display readily except *sinaloae, hakippah,* and *imperfecta.* A few active individuals of *sinaloae* tested in the field in early September reacted by partially spreading their wings. Several active individuals of *imperfecta,* collected in late December and similarly tested in the field, failed to react in any manner suggesting the display of other species.

The colored hind wings of *Neobarrettia* are prominent during the display and it is interesting to note the relation between size, coloration and degree of display. *N. vannifera* and *spinosa* have the largest wings (Fig. 21), weak coloration, and an active display. *N. cremnobates, victoriae, pulchella,* and *bambalio* have considerably smaller wings which are more brightly colored than those of *vannifera* and *spinosa,* and have an active display. *N. sinaloae* and *hakippah* have the smallest wings and the greatest sexual dimorphism in wing length (Fig. 22), the least conspicuous coloration (to the human eye at least), and a weak display. The wings of *sinaloae* and *hakippah* may have reached or passed the minimum effective size and conspicuousness for display. The tegmen and wings may now be in the process of rapid reduction accompanied by increased sexual dimorphism in tegmen size. The final stage in this sequence may be represented analogously by *imperfecta* in which the wing has been almost lost and the tegmen of the female greatly reduced. These functional relationships have been discussed in greater detail in the species treatment of *imperfecta.*

Mating Behavior.—The only copulation which has been observed in *Neobarrettia* took place on 6 October 1957 in the laboratory at the University of Michigan between a male *hakippah* from 33 mi. N Hermosillo or 19 mi. NW Guasave and a female of the same species from 42 mi. NW Culiacán, both collected between 31 August and 2 September 1957. No notes were taken on the initial stages of courting. During the active copulation, the male was situated upside down below the female, facing to the rear and clinging to her ovipositor with his fore and middle legs. The tips of his cerci were inserted at the points of articulation of the free caudal end with the fixed base of her subgenital plate. With the apical tooth of the cercus in this position, the median tooth was so situated as to fit into the lateral pit of the female subgenital plate, possibly providing leverage for any attempt to pull down the plate. During the half hour preceding the formation of the spermatophore, the male extruded and retracted his phallus at approximately five-second intervals. At maximum extrusion, the titillators pointed dorso-cephalad and appeared to scratch along the lateral edges of the free portion of the female subgenital plate. Whether the female plate was pulled down to expose the genital orifice during this time was not noted. The spermatophore was formed in less than five minutes and apparently attached early in the process because the male pulled slightly away before completion of that structure.

RELATIONSHIPS AMONG THE SPECIES OF *Neobarrettia*

The distribution of characters among the species of the genus is summarized in Table 6 and the dendrogram (Fig. 11) based on it. These are intended as summaries of characters and as aids to the independent assessment of the relationships among the species as suggested in the text.

All characters used in this study except those noted below are tabulated and portrayed graphically. Among the characters which are restricted to one species, only those for which primitive and derivative conditions are objectively determinable have been included; others contribute nothing to an understanding of relationship. A few characters mentioned in the text have been omitted because of the difficulty of applying to them the system of notation employed here, or because of their occurrence as individual variants in several species. Song characteristics have also been excluded for reasons discussed later in this section.

The characters listed in Table 6 are divided into three groups. The first group includes characters A to I for which primitive or derivative conditions may be determined with some degree of objectivity. The condition which is similar to that found in most of the Listroscelinae and other tettigoniid subfamilies is considered to be primitive, and that which is unique or which occurs very rarely among tettigoniids is considered derivative. In general, the primitive condition of these characters is sufficiently complex to render it unlikely that each could have been redeveloped with all of the normal details from the condition here designated as derivative. The remaining characters are either restricted to *Neobarrettia* in all of their conditions, or are judged to be too simple or labile for objective determination of their primitive and derivative conditions. Nevertheless, for characters J to W the conditions in each may be reasonably derived one from another. Those conditions which are found in *vannifera*, objectively judged to be primitive on the basis of the previously mentioned characters, are inferred to be primitive, and the alternative conditions derivative. The remaining characters (AA to GG) form the third group in which no morphological sequences are obvious, and no determination of primitive and advanced conditions is possible.

The notation system here employed is as follows. The primitive conditions for characters A to I are indicated by small case letters, the derivative conditions by capital letters, and the most advanced conditions by a single or double prime ('). Characters J to W are indicated by capital letters with superscripts, the condition found in *vannifera* designated as superscript "^{1}" (except in character P). The different conditions in characters AA to GG are indicated by symbols. For characters which are being scored for variable properties rather than presence or absence, the term "indeterminate" and the notation superscript "^{0}" indicates the absence or strong modification of the structure and thus a condition which is not comparable with that in other species.

The data in the table are organized into a dendrogram portrayed in Figure 11. Within the limitations of its two dimensional form and of the notation system employed, it represents a preliminary phylogeny which will be modified later when geographic, geologic, and other morphologic considerations are taken into account.

This dendrogram has been constructed in a manner similar to that used by Wagner (1961) in his divergence indices, and is based on maximum correlation of characters, minimum convergence, and the successive change of primitive to derivative conditions. Species with the greatest number of similarities are joined by lines to the notation of the characteristics they share. These groups are then joined with others showing the next lower order of similarity, and so on. Species with the most primitive characteristics in both numbers and condition are placed at the bottom of the dendrogram; those with the most derivative nearest the top. At the base are listed the most primitive conditions of all characters for which such conditions may be reasonably inferred. The underlined characters represent those for which primitive and derivative conditions may be objectively determined as discussed previously; above the base, only derivative changes in these characters are indicated by underlined capitals. Following the underlined letters listed at the base, are capital letters indicating conditions of characters J to W inferred to be primitive by their association with the objectively primitive ones in *vannifera,* with the exception of P (judging from the distribution of all other characters, P^2 in *vannifera* may represent an independent development of this condition). The appropriate notation is placed at the point beyond which all species share the derivative characteristic (or a more derivative condition). The only exception is W^1 in *victoriae,* which may represent another convergence. Because the primitive or advanced conditions of characters AA to GG cannot be determined, they are not listed at the base of the dendrogram. In general these characters are too variable and their distribution among the species forms too much of a mosaic to indicate any *sequential* relationships. Nevertheless they distinguish groups of species and are useful in determining general relationships, and their conditions are indicated for each species or group in the dendrogram.

The data on which are based the derivations of *bambalio* from *pulchella*, and *hakippah* from *sinaloae*, as shown in the dendrogram, are not indicated because of the exclusion of unique characters from the table and the difficulties of the notation system. These data were discussed under the species analyses.

On the basis of characters A to I, *imperfecta* is objectively judged to be the most derivative species, and *vannifera* the most primitive species of the genus. Because of the similarity of *pulchella* and *bambalio* to *imperfecta* in other characters in addition to their possession of several derivative characters, those species are considered to be the next most derivative. This arrangement is the exact reverse of that suggested by independent consideration of genitalic and color characters. The unicolorous pronotum and tegmen (characters L, M, and N) of *pulchella* and *bambalio* are the rule among listroscelines, whereas the dark markings on the pronotum and tegmen of *vannifera* and other *Neobarrettia* species are unique in the subfamily. More significantly, the median tooth of the male cercus and the lateral carinae and pits of the female subgenital plate (characters S and GG), found in *vannifera* and other *Neobarrettia* species, are unique among the less strikingly modified listroscelines (*Hexacentrus*, and *Listroscelis* and its allies). On the other hand, the cercus and subgenital plate of *imperfecta* (and to a lesser extent of *pulchella* and *bambalio*) which lack these details, resemble the very simple cercus and subgenital plate of the aforementioned listroscelines.

There appear to be three ways of explaining this apparent parodox. The first assumes that the *pulchella-bambalio-imperfecta* characteristics mentioned above are indeed primitive and that this line was derived from the ancestral *Neobarrettia* stock earlier than any of the other species groups. This explanation presents the difficulty of requiring the independent development of three objectively derivative characteristics (shortened tegmen, A, weak cross veins, C, and opaque wing colors, I) and one probably derivative character (black-tipped white femoral teeth, Q^{2B}) on at least two occasions.

The second explanation also assumes that the color and genitalic characteristics of *imperfecta* and its allies are primitive, but that the line merely retained these characteristics although it was the last to differentiate. This explanation presents the greater difficulty of requiring the independent development of the alternative conditions of all of these characters (L, M, N, S, U, and GG) in several different lines.

The third explanation assumes that the *pulchella-bambalio-imperfecta* color and genitalic characteristics represent derivative conditions due to simplification. This explanation has the advantage of eliminating the necessity of convergent development of all of the characteristics mentioned above, of allowing the objectively primitive *vannifera* to be derived earlier than any other species except *spinosa* (a close relative), and of allowing a more reasonable placement of *victoriae* (see discussion of that species below).

Closer inspection of the problematical characteristics of *imperfecta* and its allies, and the alternative conditions in other species, reveals morphological sequences between the two extremes in each character. Considered independently, these sequences may be read in either direction, from *imperfecta* and its allies as primitive to *vannifera-spinosa,* or from the latter species as primitive to *imperfecta* and its allies. While this does not add to the argument for considering the *pulchella-bambalio-imperfecta* characteristics derivative, it does eliminate a possible source of objection. Thus, the pronotal margin is often dark brown in *sinaloae,* and the black margin is retained mesally in *imperfecta.* The dark color on the tegmen of both sexes is variously developed in different species, being darkest in *vannifera* and lightest and least extensive in *victoriae.* The cercal tooth is absent in *cremnobates,* and a sequence in reduction of the tooth is found within the *pulchella-bambalio-imperfecta* group itself. A functionally related sequence involving the reduction of the lateral ridges and pits of the female subgenital plate is also found within the group. Finally, the lateral carinae of the female subgenital plate are weak in *sinaloae* and *cremnobates,* and individual variants in *vannifera* and *spinosa* offer clues to the manner in which they may have been produced or reduced. In some individuals of *vannifera,* a partial retraction of the swollen mediocaudal part of the plate has produced low lateral ridges. Conversely, this portion of the plate in some individuals of *spinosa* is more swollen than usual and the lateral carinae are obliterated. Thus, the normal plate in *vannifera* may represent either the antecedent of the carinated plate or the result of the loss of the carinae. If the first interpretation is correct, then the carinae need have been lost only in the *pulchella-bambalio-imperfecta* line. If the second interpretation is correct, then the carinae must have been lost twice, but a simple mechanism for such loss is seen in the *spinosa* case. Because of the difficulty of choosing between two alternatives, and of differentiating between the subgenital plates of *pulchella* and *vannifera* in this character, the presence or absence of lateral carinae has been included in the group of characters for which primitive and derivative conditions cannot be determined in Table 6. Thus, on the dendrogram in Figure 11, it appears that lateral carinae have arisen four times, although this is almost certainly not the case.

The position of *victoriae* in the dendrogram is somewhat anomalous since it apparently shares no more characteristics with the *imperfecta-pulchella-bambalio* group than it does with *cremnobates.* However, geographical considerations to be discussed in Part III make it probable that characteristics L^3 and BB^+, which are represented as convergences between *victoriae* and *pulchella-bambalio,* are homologous in the three species. Furthermore, there is reason to believe that characteristic P^2 was the ancestral condition in *victoriae,* thus joining it to the *imperfecta-pulchella-bambalio* stem in a third character. Characteristic P^1 is probably a secondarily developed geographic variant in *victoriae*; this matter is also discussed in Part III. While the morphological data indicate a closer relationship with this group than with any other, *victoriae* shares too few characters with any one species of the group to have been derived from within it. This together with the presumably primitive characteristics which it shares with other species (J^1, M^1, N^1, and characteristics of the subgenital plate discussed below) make it probable that *victoriae* represents a somewhat modified derivative of the ancestral stock which gave rise to *imperfecta, pulchella,* and *bambalio.* Geographic reasons for the retention of primitive characters in *victoriae* are discussed in Part III. *N. victoriae* shares with *sinaloae* and *spinosa* a relatively complex female subgenital plate which is very similar in several of its details in all three species (short, lateral carinae, and a short, arcuate, median carina, characters U, FF, and GG), and which is basically similar to that in *cremnobates* and *hakippah.* While it would appear from the above discussion of the subgenital plate that the *victoriae* type is probably primitive, the uncertainty of the significance of the *vannifera* type and the difficulties of the notation system make it impossible to indicate this on the dendrogram.

The position of *cremnobates* in relation to the *sinaloae* group cannot be determined with assurance. Its position on the dendrogram is consistent with the distribution of characters Q and F. In the most reasonable developmental sequence of color combinations of the femoral armature found in *Neobarrettia,* starting with the entirely black tooth (Q^1) of *vannifera* and *spinosa,* the *sinaloae* type (Q^{2A}) would form the next stage in which the black was restricted to the tip and replaced at the base with green which was readily available as the basic color of the leg. The final stage would be the replacement of the green with white (Q^{2B}), an entirely new leg color. The arrangement of species on the dendrogram follows this sequence. If the positions of *cremnobates* and the *sinaloae* group were reversed, then the

TABLE 6

DISTRIBUTION OF CHARACTERS AMONG THE SPECIES OF *Neobarrettia*

Characters for which primitive and advanced conditions may be determined objectively	*vannifera*	*spinosa*	*sinaloae*	*hakippah*	*cremnobates*	*victoriae*	*pulchella*	*bambalio*	*imperfecta*
A. Length of tegmen: long (normal)—a; medium—A; short—A′; lobate—A″	a	A	A′	A′	A′	A	A	A	A′–A″
B. Length of wing: as long as tegmen (normal)—b; shorter than tegmen—B	b	b	b	b	b	b	b	b	B
C. Cross veins of wing: well developed (normal)—c; weak—C; very weak—C′; apparently absent—C″	c	c	C′	C′	C	C	C	C	C″
D. Distribution of cross veins of wing: evenly distributed (normal)—d; absent in center—D; indeterminate—D^{o}	d	d	d	d	d	D	d	d	D^{o}
E. Tegminal reticulation: dense (normal)—e; open—E	e	e	E	E	e	e	e	e	E
F. Titillators: well developed (normal)—f; reduced—F; absent—F′	F	F	f	f	F	F	F	F	F′
G. Width of stridulatory area of male tegmen: narrow (normal)—g; inflated—G	g	g	g	g	g	g	g	g	G
H. Ventroapical spurs of hind tibia: two pair (normal)—h; one pair—H	h	h	h	h	h	h	h	h	H
I. Transparency of wing colors: transparent—i; opaque—I	i	i	I	I	I	I	I	I	I
Characters for which primitive and advanced conditions may be determined by inference									
J. Color of light portion of wing: white or yellow—J^1; white and yellow—J^2	J^1	J^1	J^1	J^1	J^1	J^1	J^2	J^2	J^1
K. Wing color pattern: background dark, spots light—K^1; background light, spots dark—K^2	K^1	K^1	K^2	K^2	K^1	K^1	K^1	K^1	K^2

TABLE 6 (continued)

DISTRIBUTION OF CHARACTERS AMONG THE SPECIES OF *Neobarrettia*

Characters for which primitive and advanced conditions may be determined by inference (continued).	*vannifera*	*spinosa*	*sinaloae*	*hakippah*	*cremnobates*	*victoriae*	*pulchella*	*bambalio*	*imperfecta*
L. Color of cephalic margin of pronotum: black or dark brown—L^1; black mesally—L^2; green or yellowish—L^3	L^1	L^1	L^1	L^3	L^1	L^3	L^3	L^3	L^2
M. Color of stridulatory area of male tegmen: ringed or suffused with black or brown—M^1; green—M^2; indeterminate—M^0	M^1	M^1	M^1	M^1	M^1	M^1	M^2	M^2	M^0
N. Color of caudal portion of female tegmen: dark—N^1; green—N^2; indeterminate—N^0	N^1	N^1	N^0	N^0	N^1	N^1	N^2	N^2	N^0
O. Tegminal spotting: no or minute spots—O^1; large discrete dark spots—O^2	O^1	O^1	O^2	O^2	O^1	O^1	O^1	O^1	O^1?
P. Color of metanotum: green to partly infuscate—P^1; entirely black—P^2	P^2	P^1	P^1	P^1	P^1	P^{1-2}	P^2	P^2	P^2
Q. Color of femoral teeth: entirely black—Q^1; bicolored green and black—Q^{2A}; bicolored white and black—Q^{2B}	Q^1	Q^1	Q^{2A}	Q^{2A}	Q^{2B}	Q^{2B}	Q^{2B}	Q^{2B}	Q^{2B}
R. Color of occiput: green—R^1; suffused or with black spot—R^2	R^1	R^1	R^{1-2}	R^2	R^1	R^1	R^{1-2}	R^{1-2}	R^{1-2}
S. Median tooth of male cercus: well developed—S^1; weak—S^{2A}; absent—S^{2B}	S^1	S^1	S^1	S^1	S^{2B}	S^1	S^{2A}	S^{2A}	S^{2B}
T. Shape of caudal portion of female subgenital plate: triangular to truncate—T^1; emarginate—T^2	T^1	T^1	T^2	T^2	T^1	T^1	T^1	T^1	T^1
U. Shape of median carina of female subgenital plate: briefly arcuate or sinuate—U^1; broadly and weakly arcuate—U^2; concave—U^3	U^1	U^1	U^1	U^3	U^3	U^1	U^2	U^2	U^2

TABLE 6 (continued)

DISTRIBUTION OF CHARACTERS AMONG THE SPECIES OF *Neobarrettia*

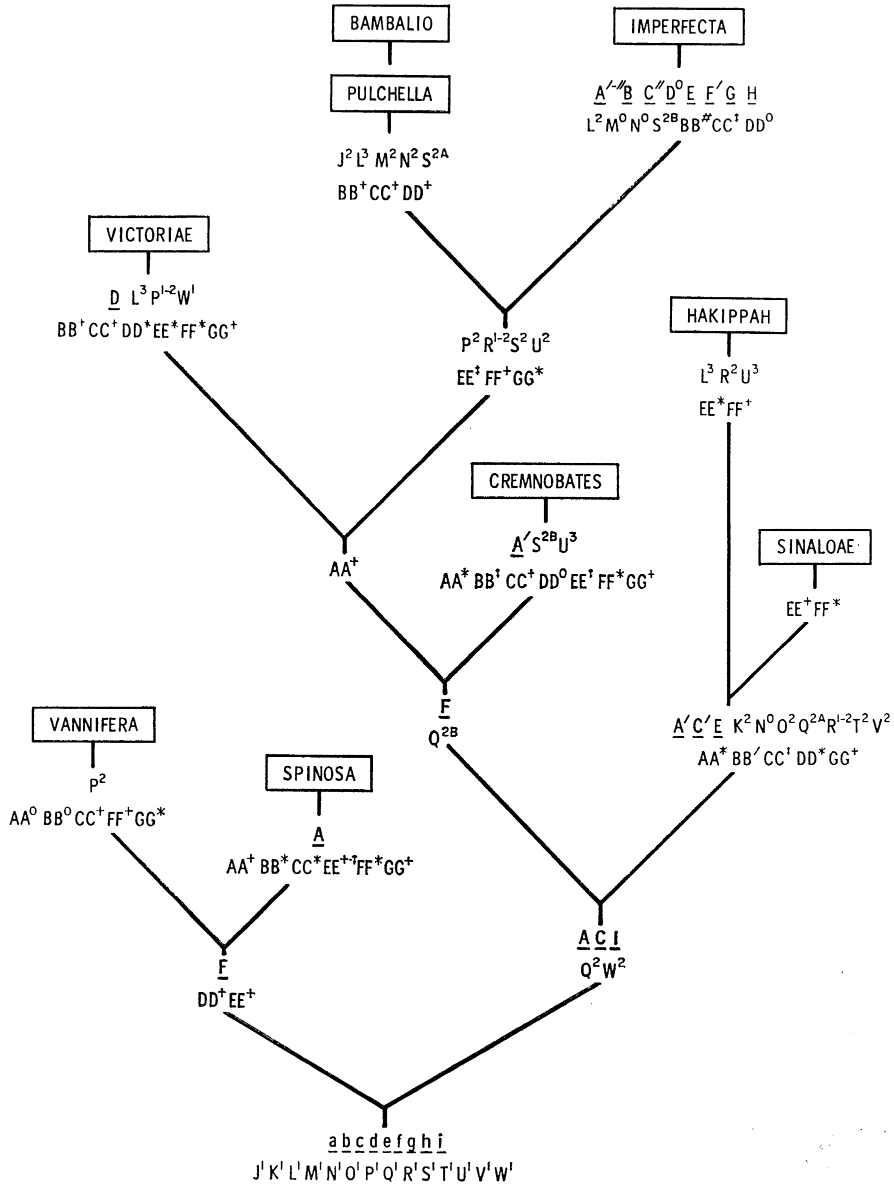
Characters for which primitive and advanced conditions may be determined by inference (continued)	*vannifera*	*spinosa*	*sinaloae*	*hakippah*	*cremnobates*	*victoriae*	*pulchella*	*bambalio*	*imperfecta*
V. Proximal flange of female subgenital plate: absent—V^1; present—V^2	V^1	V^1	V^2	V^2	V^1	V^1	V^1	V^1	V^1
W. Minute teeth among larger teeth of fore femur: present—W^1; absent or rare—W^2	W^1	W^1	W^2	W^2	W^2	W^1	W^2	W^2	W^2
Characters for which primitive and advanced conditions cannot be determined									
AA. Eye color pattern: uniform—AA†; bicolored—AA*; indeterminate—AA○	AA○	AA†	AA*	AA*	AA*	AA†	AA†	AA†	AA†
BB. Color of eye: red—BB*; white—BB†; purple and yellow—BB‡; brown and yellow—BB′; brownish—BB♯; indeterminate—BB○	BB○	BB*	BB′	BB′	BB‡	BB†	BB†	BB†	BB♯
CC. Color of dorsum of fore tibia: vinaceous—CC†; green—CC*; brown—CC‡	CC†	CC*	CC‡	CC‡	CC†	CC†	CC†	CC†	CC‡
DD. Visibility of median tooth of male cercus: invisible from above—DD†; visible from above—DD*; indeterminate—DD○	DD†	DD†	DD*	DD*	DD○	DD*	DD†	DD†	DD○
EE. General shape of male cercus: apical tooth long, internal ridge short—EE†; tooth long, ridge long—EE*; tooth short, ridge long—EE‡	EE†	EE†-‡	EE†	EE*	EE‡	EE*	EE‡	EE‡	EE‡
FF. Length of median carina of female subgenital plate: long—FF†; short—FF*	FF†	FF*	FF*	FF†	FF*	FF*	FF†	FF†	FF†
GG. Lateral carinae of female subgenital plate: absent—GG*; present—GG†	GG*	GG†	GG†	GG†	GG†	GG†	GG*	GG*	GG*

white femoral tooth base would have had to be developed twice and the titillators independently reduced a third time. Although this position would place *cremnobates* near *spinosa* and *vannifera,* with which species *cremnobates* shares several characters (L^1, M^1, N^1), all of these characters are found in other species higher in the dendrogram and thus are presumably primitive. While this position is not impossible, since the reduction of titillators is probably not an uncommon phenomenon and the independent development of a white tooth base apparently not intrinsically difficult, it produces a more complex situation than does the position shown on the dendrogram.

At first glance, the position of the *sinaloae-hakippah* group on the dendrogram does not accord with the evidence from the variation of the titillators within the genus. These structures are well developed in this group and are almost certainly primitive in comparison with their greatly reduced nature in other species. Furthermore, the titillators in the *vannifera-spinosa* group, here considered to be the most primitive in the genus, are reduced to the same extent as those in all the remaining species except *imperfecta,* where they are absent. This suggests that the *vannifera-spinosa* group had a common ancestry with all the species above the point of derivation of the *sinaloae-hakippah* group. However, such an arrangement would require that opaque wing colors and bicolored teeth be independently developed on two occasions (unless bicolored teeth are assumed to be primitive and the all black teeth of the *vannifera-spinosa* group derivative). While this is not impossible, the alternative seems to be simpler. Reduction or loss of titillators in various groups of tettigoniids is apparently a common phenomenon. It therefore seems to be more reasonable to assume that the titillators were independently reduced in the ancester of the *vannifera-spinosa* group and again in the stem which gave rise to the remaining species above the point of derivation of the *sinaloae-hakippah* group, and that the opaque wing and bicolored tooth developed only once.

The songs of the species of *Neobarrettia* have been intentionally excluded from consideration in determining their relationships. From the available data, it appears that each species has only one kind of song, and that the differences between species are in syllable and phrase rate. These

FIG. 11. Distribution of characters among the *Neobarrettia* species and a phylogeny based on them. Different characters are indicated by different single or double letters, and the condition of each by capital or lower case and primes for the underlined characters, or by superscript numbers and symbols for all the rest. Characters and their conditions are listed in Table 6, and explained and discussed in the preceding text. Species for which characters are not indicated possess the condition found in the next listing of that character below on the same phyletic line. Symbol + represented by † in Table 6.


BAMBALIO
IMPERFECTA
PULCHELLA
$\underline{A}^{\prime-\prime\prime}\underline{B}\ \underline{C}^{\prime\prime}\underline{D}^{0}\underline{E}\ \underline{F}^{\prime}\underline{G}\ \underline{H}$
$L^2 M^0 N^0 S^{2B} BB^{\#} CC^{\ddagger} DD^0$
$J^2 L^3 M^2 N^2 S^{2A}$
$BB^+ CC^+ DD^+$
VICTORIAE
$\underline{D}\ L^3 P^{1-2} W^1$
$BB^+ CC^+ DD^+ EE^* FF^* GG^+$
$P^2 R^{1-2} S^2 U^2$
$EE^{\ddagger} FF^+ GG^*$
HAKIPPAH
$L^3 R^2 U^3$
$EE^* FF^+$
CREMNOBATES
$\underline{A}^{\prime} S^{2B} U^3$
$AA^* BB^{\ddagger} CC^+ DD^0 EE^{\ddagger} FF^* GG^+$
AA^+
SINALOAE
$EE^+ FF^*$
$\underline{F}$
Q^{2B}
$\underline{A}^{\prime}\underline{C}^{\prime}\underline{E}\ K^2 N^0 O^2 Q^{2A} R^{1-2} T^2 V^2$
$AA^* BB^{\prime} CC^{\ddagger} DD^* GG^+$
VANNIFERA
P^2
$AA^0 BB^0 CC^+ FF^+ GG^*$
SPINOSA
$\underline{A}$
$AA^+ BB^* CC^* EE^{+-\ddagger} FF^* GG^+$
$\underline{F}$
$DD^+ EE^+$
$\underline{A}\,\underline{C}\,\underline{I}$
$Q^2 W^2$
$\underline{a}\,\underline{b}\,\underline{c}\,\underline{d}\,\underline{e}\,\underline{f}\,\underline{g}\,\underline{h}\,\underline{i}$
$J^1 K^1 L^1 M^1 N^1 O^1 P^1 Q^1 R^1 S^1 T^1 U^1 V^1 W^1$

differences are of considerable value in identifying species in the field. However, the high probability that closely related, sympatric species will develop markedly different songs, and the likelihood that distantly related species which have always been allopatric will retain similar songs, make this character unreliable and often misleading in the determination of relationships among forms having simple songs. Such unreliability may be seen in the strongly different songs of *pulchella* and *bambalio,* species barely distinguishable morphologically and sympatric over part of their ranges, as compared with the almost identical songs of *vannifera* and *sinaloae,* species differing markedly in many morphological characters and separated by the entire width of northern México, probably since the Miocene.

PART II. HABITAT AND HABITAT HISTORY

ANALYSIS OF HABITAT TOLERANCES OF *Neobarrettia*

The basic facts about the biology of the species of *Neobarrettia* have been presented in the preceding part. Here certain of the distributional and habitat data will be examined more closely in order to assess those aspects of their habitat tolerance which may be useful in tracing their history.

The preferred and limiting habitats of each species have been characterized in terms of vegetation types. This is not meant to imply that the vegetation itself is necessarily the factor which determines whether or not a particular habitat is suitable. Since the vegetation so accurately reflects differences in many environmental conditions, it is reasonable to assume that whatever does determine the suitability of the habitat for these katydids will be correlated with much the same type of vegetation in different areas. There are very few clues to the specific factors which determine the distribution of *Neobarrettia,* and it would not have been practicable to try to measure even the basic environmental parameters throughout the study area in the time available.

Only one possible limiting factor has been analyzed. A detailed study of food habits was made to determine whether these katydids were restricted to specific habitats by their dependence upon particular food plants. Living material of all but one species was sent to S. K. Gangwere at Ann Arbor, Michigan. His work with the living katydids showed that they are active carnivores capable of capturing and eating living prey as large as themselves. With very few exceptions, they ignored all vegetable food except lettuce, and it is not unlikely that the lettuce was accepted only because of its high water content. Some individuals ate fruit or flowers sparingly, and one ate pine needles. The crops of a few specimens of all the species were also examined by Dr. Gangwere. He found that the crops of both adults and nymphs (second to fifth instars) contained insect remains exclusively, except for a very small amount of unidentifiable material in one crop. Only a few individuals were observed feeding in the field: one *victoriae,* eating a grasshopper almost as large as itself; a male *spinosa,* feeding on a female of the same species; a female *spinosa,* devouring a cicada; and one *hakippah,* eating a carabid beetle. It seems evident that so far as their food requirements are concerned, species of *Neobarrettia* are not directly dependent on vegetation.

The only information about the oviposition of these katydids comes from observation of caged individuals, which laid eggs freely in sand or soil. This is probably their normal habit, and it may be reasonably concluded that they do not require the presence of specific plants for this function.

METHODS AND DEFINITIONS

A primary objective of this study was to determine as precisely as possible the distributional limits of the species, and to analyze the environmental changes in the vicinity of those limits. The tolerances and preferences of the species are inferred from the data obtained. The reliability of these inferences depend on the reliability and precision of the distributional data, which was obtained by much careful field work devoted specifically to this purpose. Fortunately, it is considerably easier to make an accurate survey of the distribution of *Neobarrettia* than it would be for most other Orthoptera for two reasons. First, the distribution of individuals in suitable habitats throughout the range of the species is almost uninterrupted. Second, the loud, continuous singing of the males makes them very easy to detect and identify. The song is audible for at least one hundred yards and can be readily heard from a moving car. Not only is the song distinctive for the genus, but most of the species may be identified on the basis of the song alone. In clear weather most of the males in an area apparently sing continuously through at least the first half of the night. When colonies were resurveyed after an interval of one week, very little change in numbers or positions of individuals was noted, and no significant change in the location of specific colonies has been observed over a period of several years.

Considerable effort was made to determine the location of the peripheral colonies of each species; more time was probably devoted to this than to collecting. Species were traced to the limits of their range along roads, and the position of the last colonies was noted. The surveys were continued many miles beyond these points to confirm the limits. During such an extralimital survey, every effort was made to conclude the night's work at the site of a known colony in order to determine whether the weather conditions were still favorable for singing. If the males of the check colony were singing, then the absence of songs elsewhere could be reliably taken as indicating the absence of the species. The same route was generally covered during the day and vegetational conditions were recorded, especially in the places where gaps in range or distributional limits had been observed.

The terminology here used for vegetation types is generally that of the most recent paper treating the area under consideration, as cited in the text. A correlation of the names used by different authors may be found in Rzedowski (1961). Since none of the species of *Neobarrettia* appear to be restricted to specific microhabitats, the terms used for the vegetation types are not intended to carry very precise definitions. In areas where special vegetational studies were not available, I have used terms with the following broad definitions:

Desert: Woody vegetation usually under eight feet high, usually providing less than fifty per cent ground cover and often very much less. Sometimes with scattered trees or tall yuccas. Little or no grass.

Grassland: Grass cover conspicuous. Bushes, trees, or yuccas rare or in patches only.

Savanna: Grass cover conspicuous. Cactus, bushes, or trees of regular occurrence, providing a ground cover of no more than twenty-five per cent.

Thorn forest: Woody vegetation providing almost complete ground cover. Canopy between ten and thirty feet high. Many of the species thorny and microphyllous.

Thorn scrub: Woody vegetation providing over fifty per cent ground cover, usually consisting of bushes between four and eight feet high. Many thorny species. No oaks.

Tropical deciduous forest: Trees providing a complete ground cover, canopy between twenty and fifty feet high. Few thorny species.

For convenience in reference in the preceding and succeeding discussion, I have used the term "humid tropical forest" to cover tropical deciduous, evergreen, and rain forest; "bushland" to cover desert vegetation, thorn, and arid tropical scrub; and "oak woodland" to cover all types of vegetation which contain arboreal oaks as a conspicuous element.

In Figure 15, I have similarly used terms for vegetation types in a broader sense than is usual in order to facilitate mapping. "Tropical humid forest" includes tropical deciduous forest which is often considered to be a sub- or semihumid formation. "Temperate humid forest" includes dry oak woodland at low elevations on mountains. Woodland and grassland have been combined in this figure because of the difficulty of clearly differentiating the two in the fossil record. Woodland, as used in this category, includes dry open oak woodland, oak scrub, or the woody vegetation in savannas.

The following discussion is centered around evidence concerning the tolerances of the species of *Neobarrettia* to oak woodland, grassland, humid tropical forest, and desert.

OAK WOODLAND.—Six species of *Neobarrettia* are found at some point in their range at the edge of oak woodland or what may have formerly been oak woodland. Only one species has been found within such woodland.

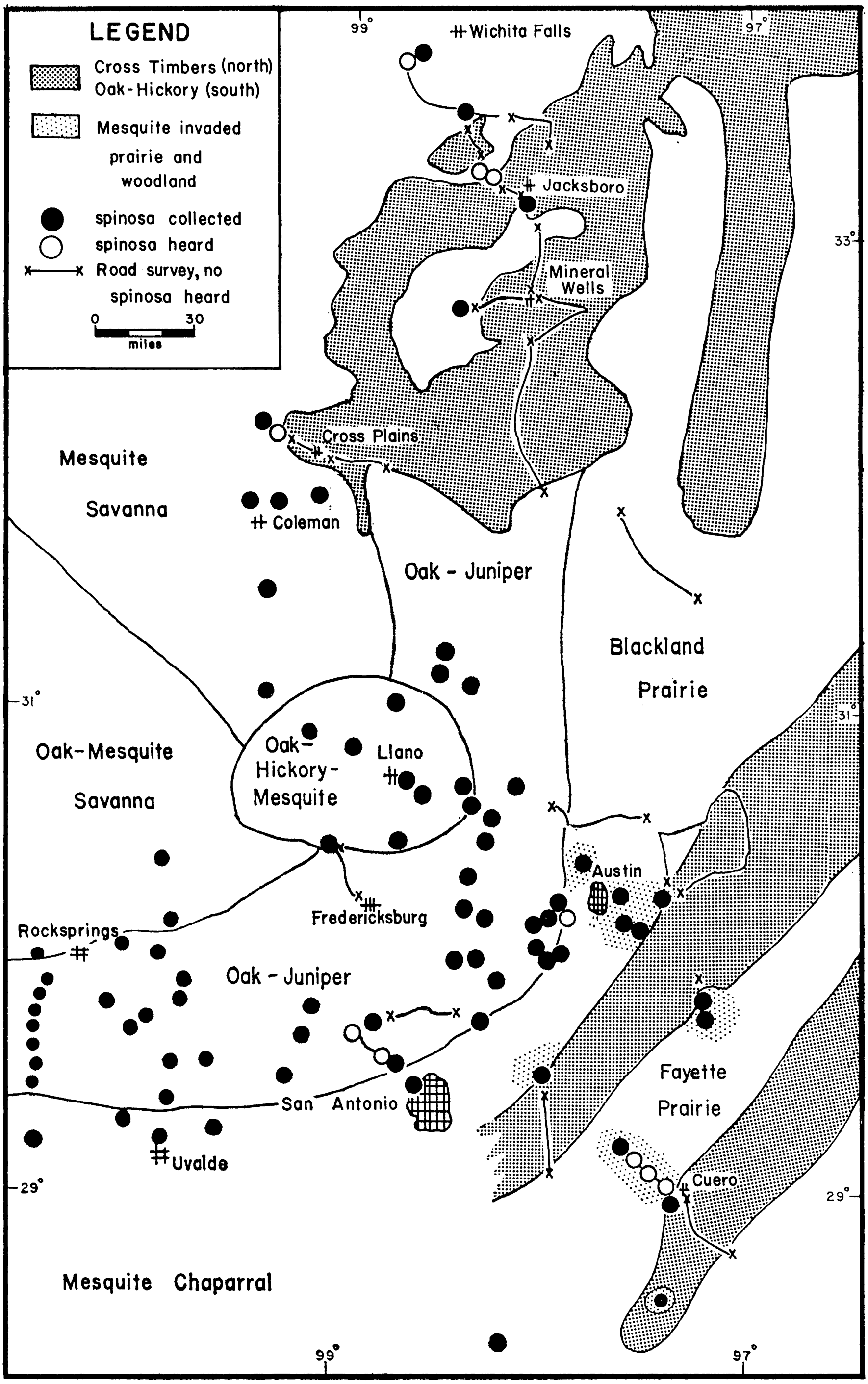
N. spinosa has an extensive range in the Oak-Juniper woodlands of the Edwards Plateau of Texas (Fig. 12) (terms for vegetation types in Texas are from Tharp, 1952). These are usually open and often have many bushes among the trees. The colonies of *spinosa* are generally small and scattered in this habitat whereas the adjacent areas of mesquite often support larger and more abundant colonies, such as those near Inks Lake and southeast of Llano. The species is apparently absent from large areas of this woodland, such as the region north of Fredericksburg, and in the region east and west of Boerne.

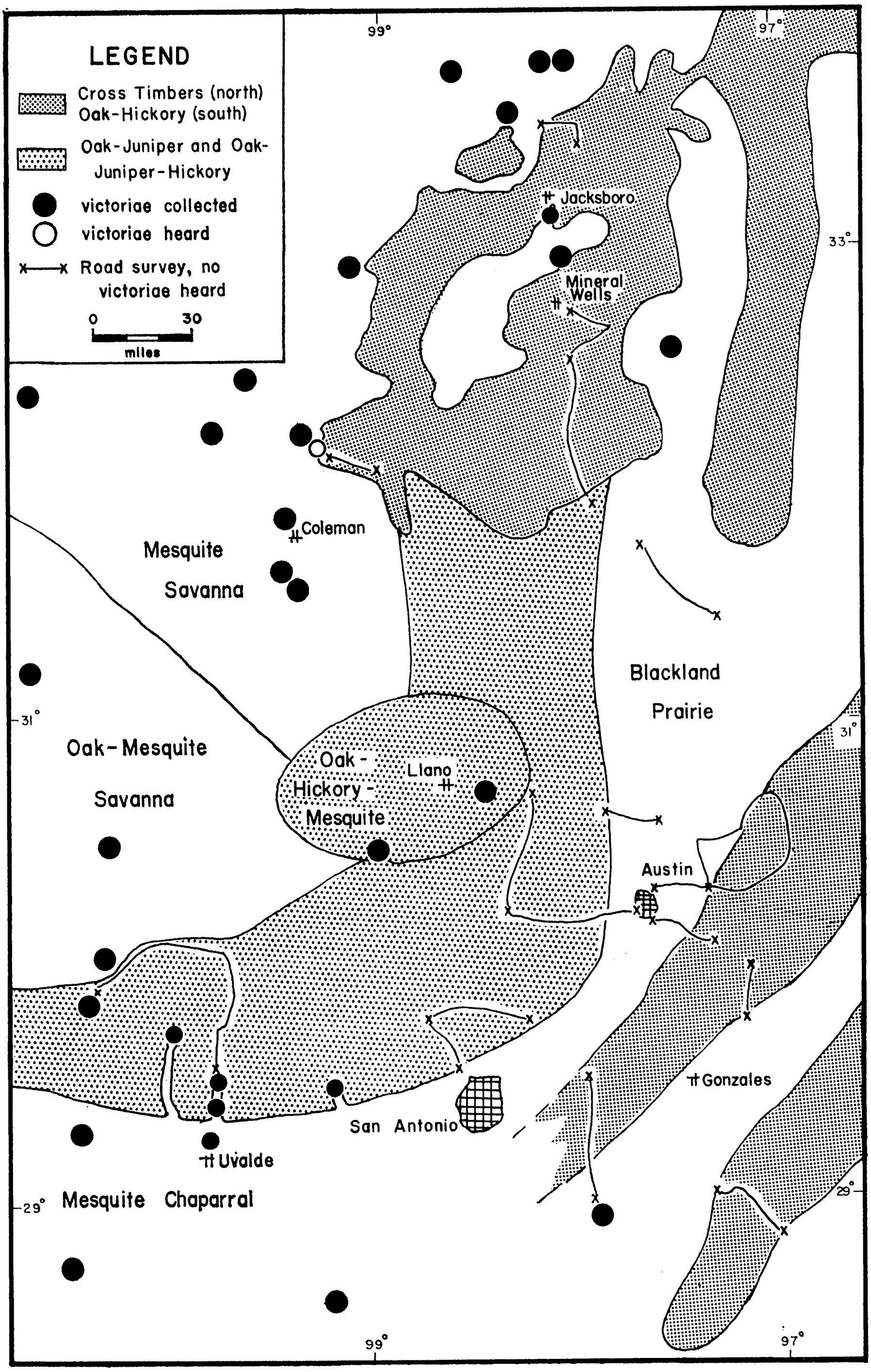
N. spinosa is completely absent from the oak woodlands of the Western Cross Timbers in northcentral Texas, as well as from the Oak-Hickory region to the southeast. Intensive surveys were made in the Jacksboro, Brownwood, and Austin regions to determine the location of the easternmost colonies of this species in relation to those woodlands (Fig. 12). In northern Texas, colonies of *spinosa* were scattered but common in the Mesquite Savanna from near Wichita Falls to the western edge of the Cross Timbers about 20 miles northwest of Jacksboro. Within the edge of the Cross Timbers region northwest of that town, oak woodland alternates with mesquite patches. Calling males of *spinosa* were absent from the oaks and were heard only in the mesquite. The southeasternmost males of this species were heard just south of Jacksboro in bushy fields with scattered trees adjoining areas overgrown with mesquite. Mesquite is present, south of this point, only in small, young stands, and gives way to oak woods or cleared fields north of Mineral Wells. South and east of that city, the main roads pass through oak woodland with little or no mesquite. No *spinosa* were heard in this region during several nights of survey in two different years. Farther south, in the vicinity of Cross Plains, the boundary between the Mesquite Savanna and the Cross Timbers is very sharp. *Spinosa* is common in the former habitat, occurs sparingly in the narrow oak-mesquite ecotone, and is completely absent from the woodlands.

The situation is very similar in the Austin region in southcentral Texas, where *spinosa,* which occurs sparingly in the woodlands of the Edwards Plateau to the west, is abundant in the extensive areas of mesquite just east of Austin. The latter areas immediately adjoin the Oak-Hickory Forest belt which extends in a northeast-southwest direction, about 20 miles east of that city. Again, *spinosa* occurs in the patches of mesquite that alternate with oak woodlands just west of the main woodland, and in tongues of mesquite that penetrate the woodland near Bastrop. Careful surveys were made east of Elgin and Bastrop, but no *Neobarrettia* were heard. The oak woodlands east of those two towns are typically eastern in appearance, with an almost closed canopy, thin underbrush and considerable leaf litter. Some mesquite is found in cleared areas, but the patches are usually few, scattered, and small. *N. spinosa* is very common south of Smithville, where the woodland is interrupted by extensive stands of mesquite. These mesquite stands probably represent intrusions in the ecotone between the Fayette Prairie to the south and the main woodland to the north. Much of the Prairie has probably been invaded by mesquite from the Mesquite-Chaparral region not far to the south; *spinosa* is common in the latter region and may have invaded the Oak-Hickory woodlands from the south rather than have passed through the woodland to the northwest.

The Western Cross Timbers and the Oak-Hickory woodland are very similar. They share the same dominant oaks and agree closely in general appearance; *spinosa* does not occur in either one. The Oak-Juniper woodland differs in tree composition and general appearance from those two woodlands, and *spinosa* occurs extensively in it. The reasons why the species is absent from the first two woodlands and is present in the last are not obvious. It seems improbable that oaks themselves constitute a barrier, in view of the exclusively carnivorous habits of the katydids and the fact that farther west the animals occur in the oaks of the Oak-Juniper woodland. Macroclimatic differences between the regions occupied by the contrasted woodlands can be eliminated as a cause on the basis of the checkerboard occurrence of colonies near or within the oak woodlands in regions where the only topographic variation is produced by slightly rolling hills. Soil cannot be directly limiting, for typically both the Cross Timbers and the Oak-Hickory woodland are developed on sandy soil (Dyksterhuis, 1948; Carter, 1931; Tharp, 1926), and yet colonies of *spinosa* have been found on almost pure sand at Roswell, New Mexico. There remains the

FIG. 12. Habitat distribution of *Neobarrettia spinosa* in central Texas. Concentration of collections in the Oak-Juniper region is an artifact of collecting since less time was spent in other regions. Colonies were generally smaller and fewer here than in the savanna or chaparral. Vegetation regions are from Tharp (1952) and Dyksterhuis (1948).


LEGEND
Cross Timbers (north) Oak-Hickory (south)
Mesquite invaded prairie and woodland
spinosa collected
spinosa heard
Road survey, no spinosa heard
0 30
miles
99°
97°
Wichita Falls
Jacksboro
33°
Mineral Wells
Cross Plains
Mesquite Savanna
Coleman
Oak - Juniper
Blackland Prairie
31°
Oak-Mesquite Savanna
Oak-Hickory-Mesquite
Llano
Fredericksburg
Austin
Rocksprings
Oak - Juniper
Fayette Prairie
San Antonio
Uvalde
Cuero
29°
Mesquite Chaparral
99°
97°


LEGEND
Cross Timbers (north) Oak-Hickory (south)
Oak-Juniper and Oak-Juniper-Hickory
victoriae collected
victoriae heard
Road survey, no victoriae heard
0
30
miles
99°
97°
33°
31°
29°
Jacksboro
Mineral Wells
Coleman
Mesquite Savanna
Blackland Prairie
Oak-Mesquite Savanna
Oak-Hickory-Mesquite
Llano
Austin
Gonzales
San Antonio
Uvalde
Mesquite Chaparral

miscellany of factors which result from the denseness of the growth within the woodlands: considerable shade, lack of heavy undergrowth, relatively deep leaf litter, and so forth. Somewhere in this complex, acting individually or jointly and directly or indirectly, probably lie the effective controls. Among these may well be the radical differences, both as to species and abundance, in the nature of the available prey in the occupied and unoccupied habitats.

The distribution of *victoriae* in Texas (Fig. 13) indicates that it is even less tolerant of oak formation than is *spinosa.* Only three records for this species fall within areas mapped as oak zones, and all three lie at the very edge of these zones. The first, from Caddo County in south-central Oklahoma, is based on a specimen that almost surely came from a mesquite-invaded field. The second, from Montague County in north-central Texas, rests on material collected in a weedy-bushy area, with no oaks in the immediate vicinity, although the locality is ten miles within the edge of the oak woodlands. The third record, from Edwards County in south-central Texas, is of specimens that came from an area dominated by low scrubby juniper and various bushes, again with no oaks in the vicinity. Areas of mesquite may occur only a few miles to the west of this place, where scrub vegetation ascends the stream valleys in the southwestern edge of the Edwards Plateau. The two easternmost records of *victoriae* in central Texas (Gillespie and Llano counties) are both from mesquite areas that probably have broad connections with the Mesquite Savanna to the northwest.

At the western edge of the Cross Timbers in north-central Texas, the distribution pattern of *victoriae* is very similar to that of *spinosa.* Thus, near Windthorst, the easternmost colony was found in a large mesquite stand within a few miles of pure oak woodland. North of Mineral Wells, the last colony was found in a pasture invaded by mesquite, just west of where oak woodlands enclose the road. West of Cross Plains, the species was common in the Mesquite Savanna, and the last colony was heard in the oak-mesquite ecotone. *N. victoriae* is completely absent from the Oak-Juniper woodlands which cover the southern and eastern edges of the Edwards Plateau. It is common, however, in the Mesquite-Chaparral region just to the south, and is found within the dissected edge of the Plateau wherever mesquite and leguminous bushes from the Mesquite-Chaparral region have followed up the streams that cut into the Balcones Escarpment. Near Hondo, the northernmost colony was found in the last grove of

FIG. 13. Habitat distribution of *Neobarrettia victoriae* in central Texas. Vegetation regions are from Tharp (1952) and Dyksterhuis (1948).

mesquite along the road before the oaks take over. North of Uvalde, *victoriae* was traced to the last stand of roadside leguminous bushes, within a few hundred yards of the point where the oaks and junipers descend from the hills to form a continuous stand from there northward, unbroken by mesquite. West of Rocksprings, the Oak-Juniper woodland becomes mixed with mesquite and finally gives way to the desert vegetation characteristic of the region around Del Rio. *N. victoriae* becomes common almost with the first rich stand of mesquite west of Rocksprings and is abundant in the Del Rio area.

The absence of *victoriae* from apparently suitable habitats in the Austin region (such as those occupied by *spinosa* there) can now be understood in terms of the barrier habitats which surround the area. The species is blocked from entering the area from the south by the presence of the Blackland Prairie and the Oak-Hickory woodlands. It is found in abundance in mesquite fields at Karnes City, but is completely absent from the woodlands which start just north of that city. The species is also blocked from entering the area from the west or northwest (where it is abundant in the Mesquite Savanna) by the Oak-Juniper woodlands of the Edwards Plateau. In contrast, *spinosa* has probably been able to enter the Austin area because of its ability to penetrate this Oak-Juniper belt.

The distribution of *bambalio* is also clearly limited by oak woodlands. The easternmost colony of this species has been found in a weedy, bushy field within a few hundred yards of the first oak woodland of the Sierra Madre. The transition between these woodlands and the desert brush in which *bambalio* occurs in abundance, is exceptionally sharp. Even the open areas within the edge of the woods have a very different vegetation cover from that just outside. No *bambalio* has ever been found in the oak woodland here on the several occasions when the area was carefully surveyed at times when the species was singing vigorously in the nearby desert.

The limiting records of several other species lie near oak woodlands, but the barrier effect of these formations on them is not as clear as in the instances discussed above. In the mountains west of the city of Río Verde, *pulchella* occurs commonly in a thorn forest formation (the "matorral submontano" of Rzedowski and Rzedowski, 1957) at low elevations. It extends to the upper limits of this formation, and the last colony is found within two miles of the first oaks. None were heard in the oak woodlands, and none in the desert below the oak zone on the west slopes of the mountains. Farther north, *pulchella* is found commonly within the Sierra Madre Oriental near Jaumave, Tamaulipas. Although it is present in the desert vegetation just west of the last pass leading to the coastal plain, it apparently does not penetrate the oak woodlands within that pass, since it is absent from the east slope of the mountains beyond. That it is well able to exist in the more humid environment of the east slope is indicated by its presence on the coastal plain south of Mante, Tamaulipas.

In the Ciudad Victoria region of Tamaulipas, *vannifera* has a distribution complementary to that of *pulchella.* The species *vannifera,* which is found on the east slope of the Sierra Madre, apparently does not extend through the pass into the desert vegetation on the other side. In this case, however, it is possible that it is stopped more by the aridity of the environment to the west side than by the oak woodland within the pass. The field notes for a single nymph of *vannifera,* collected in this area by H. R. Roberts, indicate that it came from an area of oaks. Whether this was well within the oak zone or at its edge is not known.

The southern limits of *imperfecta* are found just below an area of scrub oak and grassland in the hills near Petaquillas, Guerrero. Individuals are very scattered in this region, although the species is common only a few miles to the north. The hills on either side are covered in large part with scrub oak, and the presence of a small grove of oak trees just below the last colony of *imperfecta* suggests that the entire area may have been covered once by oaks and then formed a continuous barrier to the species. *N. imperfecta* does not occur in apparently suitable bushy habitats only a few miles to the south and at lower elevations.

GRASSLANDS.—No species of *Neobarrettia* occurs today in grasslands, although the ranges of a number of them extend very close to present day grassland or open savanna formations, or what might have been grasslands in the recent past.

N. spinosa has been found in the valley of the Pecos River near Roswell, New Mexico, where is occurs amid low scrub oaks and bushy vegetation. It has not been recorded from the nearby pure grassland of the Llano Estacado to the east nor on the grassland of the rolling piedmont to the west. The bushy vegetation of the Pecos Valley at Roswell is probably continuous with the desert vegetation of Trans-Pecos Texas, in the southern part of which *spinosa* is common.

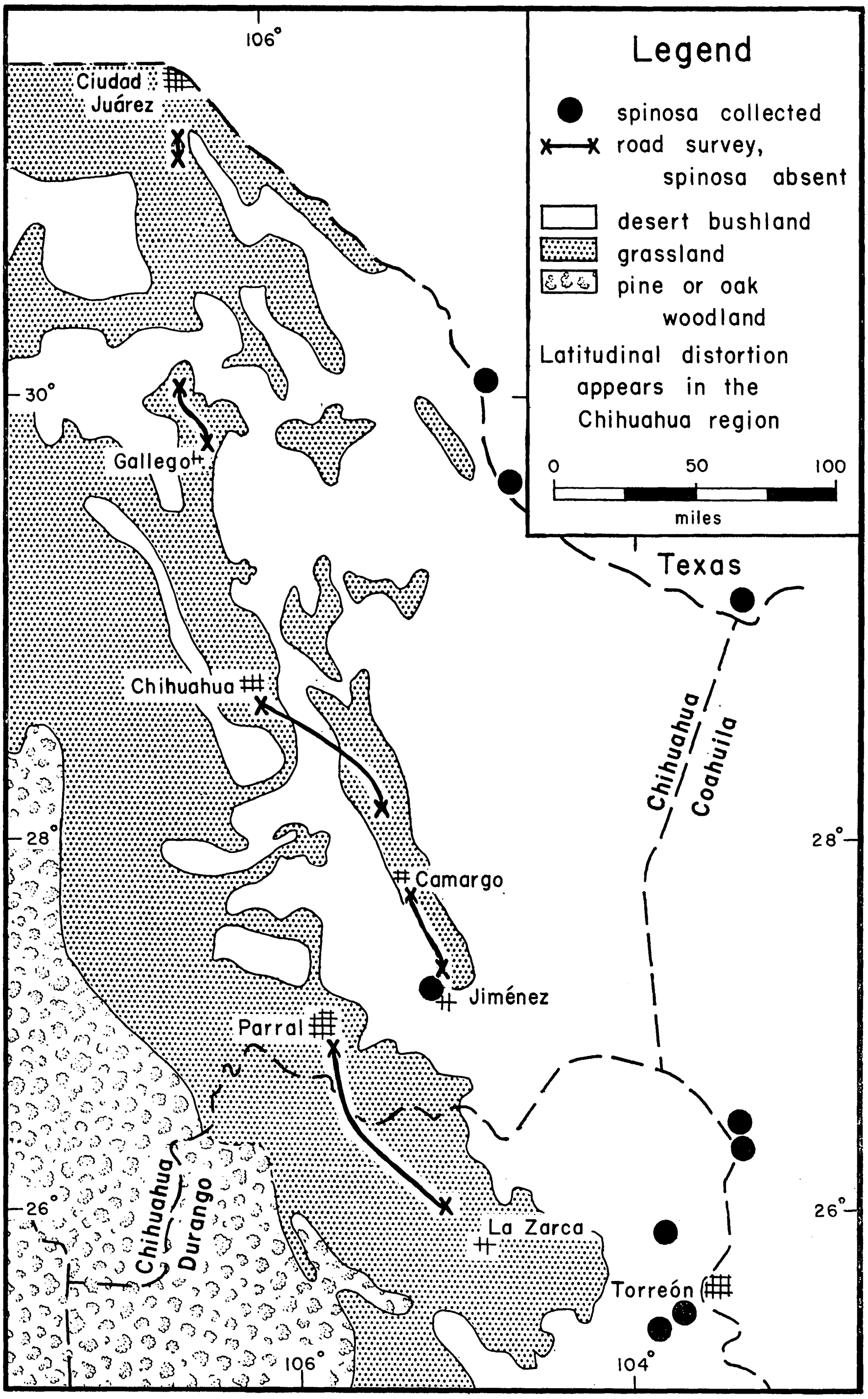
N. spinosa is apparently absent from the route of the main highway between El Paso, Texas, and Jiménez, Chihuahua, where careful survey or sampling work was done (Fig. 14). At Jiménez it suddenly appears in numbers, but it is absent again between Parral, Chihuahua, and La Zarca, Durango. Although much of the route of this highway north of Jiménez passes through what appear to be creosote flats, almost all of it lies in areas mapped as grassland by Hernández and González (1959) and by Le Sueur (1945). Both maps indicate that the grassland is replaced by bushland just north of Jiménez. South of Parral, the road again passes through an area mapped as "navajito" grassland by Hernández and González, in which scattered trees and shrubs occur.

Although *victoriae* is found in the southern portion of the Great plains it is apparently never found in pure grasslands there. It is common in the mesquite savanna of north-central Texas and extends westward almost to the edge of the Llano Estacado. The westernmost colony of *victoriae* in this region (Hemphill County) was found, however, in the valley of the Canadian River in a bushy habitat normal for the species (from field notes of T. H. Hubbell). All records in Oklahoma for which field notes are available are from dissected country with abundant bushes, or from bush-covered plains. The two counties in southwestern Kansas, in which the northernmost colonies of this species have been found, contain large areas of bushland characterized by abundant sage, wild plum, shrub hackberry, aromatic sumac, and *Acacia* (the last sometimes common according to C. W. Hibbard). This would seem to be a bushy habitat not very different from those commonly occupied by the species farther south. Significantly, these two counties in Kansas lie immediately south of the plains grassland country which extends to the north and west.

The westernmost limits of *bambalio* coincide almost exactly with the beginning of the grassland savannas in western San Luis Potosí. Southwest of Villa Hidalgo, this species was abundant in an area of low desert bushes on rocky or gravel soil. Within one mile to the southwest, where the soil becomes a clayey sand and the vegetation grassy, only an occasional individual was heard. West of this point, no *bambalio* was ever heard on several surveys made in different years. Notes taken during the day indicate that within one mile southwest of the abundant colony in desert bushes, the vegetation changes to a bush or cactus savanna and that three miles farther southwest are extensive grasslands. The country becomes flat just west of the *bambalio* colony and continues that way to the city of San Luis Potosí. Although much of this plain is now covered with patches of bushes, many of these may be the result of recent overgrazing of what was probably very extensive grasslands.

In the northernmost part of its range, *pulchella* is found near the zone of grassland which occurs at moderate elevations in the mountains south of Saltillo. It was absent from grassland about seven miles north of the northernmost record for the species. This grassland was carefully examined at one locality on the same evening when *pulchella* was heard and collected farther south.

FIG. 14. Habitat distribution of *Neobarrettia spinosa* in Chihuahua and adjacent states. Vegetation regions are from Hernández and González (1959) for Chihuahua, and from Gentry (1957) for Durango.


Legend
● spinosa collected
road survey, spinosa absent
desert bushland
grassland
pine or oak woodland
Latitudinal distortion appears in the Chihuahua region
0
50
100
miles
106°
30°
28°
26°
104°
Ciudad Juárez
Gallego
Chihuahua
Camargo
Jiménez
Parral
La Zarca
Torreón
Texas
Chihuahua
Coahuila
Durango

N. cremnobates is common in the "thorn forest" vegetation of the barrancas west of Ixtlán del Río. It extends up to the very lip of the barranca, but is apparently absent from the plains to the west where the vegetation becomes a savanna with large patches of woodland and bushland. The species has not been found beyond the eastern edge of the barranca. Here the country is more broken and is more often bush-covered. However, my impression of this bush cover is that it is quite different from what is found in the barranca, and that much of it may be the result of overgrazing.

The southern limits of *sinaloae* lie in the northern edge of a wet savanna area in northern Nayarit. The precise location of colonies of this species in relation to the vegetation is unknown, but none have been found in the savanna itself.

The northern limits of *hakippah* are not known with certainty. The northernmost record is within 50 miles of the beginning of the grasslands of northwestern Sonora and southwestern Arizona. It seems certain that the species does not occur in the latter region, since E. R. Tinkham has collected Orthoptera extensively there and has never found a *Neobarrettia.*

N. imperfecta reaches its northeastern limits in an area which I believe was once covered by grassland or savanna. Since this area is mapped as arid tropical scrub by Leopold (1951), the evidence on which my concept is based is presented below.

Topography: Northeast of Taxco, Guerrero, the very rugged mountainous terrain changes abruptly to rolling hills, then to plains which extend to Cuernavaca, Morelos, and Izúcar de Matamoros, Puebla. At the base of the mountains northeast of Taxco, the country has the appearance of a rim of a gently sloping basin, now mostly dissected away. From this rim the country dips down toward Puente de Ixtla, Morelos, then gradually ascends toward Cuernavaca and Izúcar. Northwest of this region, and separated from it by about ten miles, is a very extensive flat plain south of Ixtapan de la Sal, México. This seems to be the surface of a lava flow into which is cut the great Barranca de Malinaltenango.

Rainfall and present vegetation: Rainfall at Taxco is 1455 mm. annually (Contreras Arias, 1942), and is probably sufficient to support tropical deciduous forest there as it does farther north (Rzedowski, 1961). Most of the forest cover of the mountains has been cut and is now replaced with a rich scrub, but patches of the original cover are still visible on some of the less accessible slopes. Rainfall over the lower, flatter region to the northeast is 900 to 1000 mm. annually (data for Puente de Ixtla, Cuernavaca, and Cuautla, Morelos, in Contreras Arias, 1942). Such a rainfall regimen might be expected to favor sod formation in flat or rolling country.

Near the base of the mountains the hilly country east of Axixintla is not intensively farmed and supports an *Acacia* savanna. The country around Coatlán del Río, Morelos, supports a rich grassland. The plains around Puente de Ixtla were described by Goldman (1951) as "open and grassy, with woody vegetation limited in extent." To the northwest, extensive agriculture and grazing have obscured the nature of the original vegetation. Nevertheless, some patches of short dry grassland are present, bushland is restricted and there is little woodland except on the ridges or in rough country. West of Chietla, Puebla, the great plains stretching away to the north are covered with short grass, apparently heavily grazed, and have very few bushes. The lava plain south of Ixtapan de la Sal likewise supports short grass with very few bushes.

Arid tropical scrub: The rainfall in this region, which I suggest was once grassland, seems to be too low to support tropical deciduous forest, but is entirely adequate for arid tropical scrub. If the region was once covered by such vegetation it is difficult to see why there is so little of it left now, and why the areas not under cultivation support grassland instead. Most agricultural and grazing practices favor the increase of bushland over grassland. The only exception is burning, which is commonly practiced in México and would, if done regularly for a number of years, completely eliminate the bushes. Such burning as has been done in the past, however, has not eliminated all bushes, and has had little visible effect on the trees of the nearby forests. It thus seems unlikely that burning has been extensively practiced in this region.

From these observations, I conclude that the region between Taxco and Izúcar de Matamoros was once largely grassland. The location of the northern and northeasternmost colonies of *imperfecta* corresponds very closely to the limits of this suggested grassland region. North of Iguala on the Cuernavaca toll road, *imperfecta* extends to the beginning of the descent into the lowlands nine miles north of Amacuzac, Morelos, which town lies well within the plains area. East of Axixintla, Guerrero, the last colonies of *imperfecta* are found only two miles within the savanna edge. From the scrub of the nearby mountains, *imperfecta* extends to within four miles of the grasslands around Coatlán del Río, with some woodland intervening between the last colony and the grassland. To the northwest, the last *imperfecta* was heard in open and scrubby woods within three miles of the edge of the grassland of the lava plain, again with woodland intervening. Within the suggested grassland area, from Axixintla to Chietla, various areas were sampled and roads surveyed, but no *imperfecta* was seen or heard. One specimen in the collection of the Academy of Natural Sciences of Philadelphia comes from a locality in the middle of the suggested grassland region. Since I have carefully surveyed this area, as well as that to the north and southwest on a night when *imperfecta* was singing elsewhere, I believe the locality to be in error.

The distribution of the last colonies of *imperfecta* north and northeast of Taxco thus corresponds very closely to the boundary of the area which, according to this evidence, was until recently covered with grassland. Therefore, it is reasonable to assume that this formation acts as a barrier to *imperfecta* in the same way as it does to most other species of *Neobarrettia*. At the risk of circular reasoning, I would also point out that it is impossible to explain the distributional limits of *imperfecta* under the assumption that until the agricultural practices of man modified the original cover, the region northeast of Taxco was covered with either tropical deciduous forest or arid tropical scrub. *N. imperfecta* has very successfully occupied the scrubby, cutover patches of forest near Taxco, and could as easily have done the same in an adjacent area to the northeast. Similarly, in what was once undoubtedly arid tropical scrub country south of Iguala, *imperfecta* is very common in the spiny roadside bushes next to cornfields, and has even been found far within the cornfields. It also occurs in weedy cornfields near Axixintla, within the edge of the suggested grassland region. If this latter region was formerly covered with arid tropical scrub, it is hard to understand why *imperfecta* is absent from the scattered patches of scrub that exist within the region today.

HUMID TROPICAL FOREST.—Under this term are included tropical deciduous forest, evergreen forest, and rain forest. The possible limiting effect of these types of vegetation is harder to assess than that of the types previously discussed. Fewer species are found in or near these forests, and the areas in which they occur are harder to survey.

The ranges of five species extend into or very near tropical deciduous forest. On the eastern coast of México, *vannifera* is found within the edge of tropical deciduous forest between Llera and Mante, Tamaulipas, as mapped by Martin (1958*a*). Since the species occurs in thorn forest farther north, and does not occur in the heavier tropical deciduous forest just southeast of its southernmost colonies (in the Gómez Farías and Ocampo areas in Tamaulipas), it is likely that the species has only penetrated the edge of this humid forest where it is relatively dry and mixed with thorn forest species.

N. victoriae and *pulchella* also occur in this region, although both have a more extensive distribution in drier areas. The two are found well within the region mapped by Leopold (1951) as tropical deciduous or evergreen forest, but occur only in the more open habitats representing drier environments. Thus, between Mante and Tampico, Tamaulipas, *victoriae* was found only in an *Acacia* savanna and not in the low woodlands which cover much of the area. Similarly, the species was found in a bushy, disturbed area near Ocampo. East of this town, it has penetrated the forest on a low ridge of the Sierra Madre, but only for a mile, and then probably only along the road. South of Mante the species is common in weedy and bushy fields and was encountered in the same sort of habitat north of Antiguo Morelos, Tamaulipas. Only near El Salto, San Luis Potosí, does the species occur in woodland, but here again it was found along a road where the woodland has been thinned. *N. pulchella* is known from two localities between Mante and Antiguo Morelos. At one locality the species was found in a colony of *victoriae* in roadside weeds (and probably bushes) next to cultivated fields. The habitat at the other locality was described by H. R. Roberts as a ridge with rich tropical vegetation, but whether the specimens were collected in the woodland or along the roadside is not known.

N. imperfecta occurs near Taxco within a region originally covered by tropical deciduous forest. There it has been found only in the scrubby cut-over areas which resemble the disturbed habitats in drier regions farther south where it is abundant.

On the west coast of México, the range of *sinaloae* extends into the northern edge of the wet savanna country in northern Nayarit. In this area, thorn forest is replaced by more humid formations. This species has not been found in the humid forests (possibly tropical evergreen forest) at the base of the mountains about 25 miles south of the last colony at the edge of the savanna.

The remaining four species are prevented from reaching humid forests by other factors. Two are blocked by grassland, savanna, or oak woodland (*bambalio, cremnobates*), one by heavy thorn scrub and thorn forest (*spinosa*) and the last (*hakippah*) by the presence of another species (*sinaloae*).

The following areas of humid tropical forests beyond the known ranges of the species of *Neobarrettia* have been investigated: the area between Tepic and Tuxpan, Nayarit; the Colima-Manzanillo area, Colima; the Tierra Colorada-Acapulco area, Guerrero; and several areas in the states of Veracruz, Tabasco, and Campeche.

DESERT.—Five of the nine species of *Neobarrettia* occur in deserts, but of these, only *bambalio* is restricted to that environment. It inhabits the desert on the Central Plateau in the state of San Luis Potosí. Its very close relative, *pulchella*, has an extensive range in the same desert, but is also common in the thorn forest ("matorral submontano" of Rzedowski and Rzedowski, 1957) east of the city of San Luis Potosí, and also occurs in what is probably an equivalent habitat in disturbed tropical deciduous forest on the coastal plain between Mante and Antiguo Morelos. *N. spinosa* occurs extensively in the deserts of Coahuila and western Texas, but almost one-half of its range lies in more humid habitats in southern Texas and northeastern México. *N. hakippah* is found in the southern part of the Sonoran Desert, but has a more extensive distribution in the thorn forests of Sinaloa. It has not been found in the drier portions of the Sonoran Desert in southern Arizona, where the veteran Orthopterist, E. R. Tinkham, has collected for many years. The fifth species which occurs in deserts, *victoriae,* has a very wide range on the coastal plain of México and in Texas, and it penetrates the desert only in western Texas.

On morphological grounds two of the five species which occur in deserts, as well as the desert populations of a third, are clearly more modified than their next of kin (see discussion under the taxonomic treatment of each species). *N. bambalio* is only slightly differentiated from its nearest relative, *pulchella*; its three distinctive characters probably represent the loss or reduction of structures found (with one exception) throughout the genus. Similarly, most of the characters that differentiate *hakippah* from *sinaloae* represent unique developments in the genus. Of the highly distinctive characteristics which distinguish the desert populations of *spinosa* from those which occur on the coastal plain, the majority also represent unique developments in the genus.

In summary, of the five species of *Neobarrettia* which are found in deserts, all but one also occur in more humid environments. Three of these species (or populations), including the one restricted to the desert, are almost certainly derivative. One of the remaining two makes only a relatively limited penetration into the desert from an extensive distribution in more humid habitats. The conclusion to which these observations lead is that adaptation to desert conditions is a secondary and probably a relatively recent development in *Neobarrettia.*

SUMMARY OF THE HABITAT TOLERANCES OF THE MODERN SPECIES AND THE HABITAT OF THEIR ANCESTOR

The habitat distribution of each of the species of *Neobarrettia* is summarized in Table 7. The letters P and D following the species names indicate, respectively, the most primitive and the most clearly derivative species. Question marks indicate occurrence of a species in what is probably the type of vegetation indicated, but the precise vegetational nature of that habitat has not been determined. Adaptation to the driest of these vegetation types appears to have been a relatively recent development. Grassland, oak woodland and humid tropical forest act as barriers to all but one of

TABLE 7

HABITAT DISTRIBUTION OF THE SPECIES OF *Neobarrettia*

Species	Desert	Thorn Scrub (or Arid Tropical Scrub)	Thorn Forest	Disturbed Areas in Tropical Deciduous Forest
vannifera (P)	..	..	X	..
spinosa	X	X	..	..
sinaloae	..	..	X	?
hakippah (D)	X	?	X	..
cremnobates	..	?	X?	?
victoriae	X	X	?	X
pulchella	X	..	X	X
bambalio (D)	X	..	..	..
imperfecta (D)	..	X	..	X

the species which come into contact with them. The exception is *spinosa* which is able to live in the drier type of oak woodland in Texas. However, that habitat appears to be less favorable than the adjacent thorn scrub. Three species are able to penetrate humid tropical forests, but only in open, drier, and disturbed situations.

In view of the wide separation of the modern species in these dry environments (Figs. 15, 24), it seems likely that the common ancestor of all the species was adapted to a thorn forest-thorn scrub habitat, and that grassland, oak woodland and humid tropical forest formed barriers to its dispersal. It follows that the development of both the preferred and barrier habitats through geological time should provide the temporal and geographical framework within which the evolution of *Neobarrettia* has taken place.

THE HISTORY OF DRY ENVIRONMENTS IN NORTH AMERICA

The thorn forest-thorn scrub environment preferred by *Neobarrettia* is primarily the result of warm, dry climate. On the basis of climatic theory a zone of such climate would be expected to develop in the middle latitudes of a generalized, uniformly low continent; in North America, it would extend in an arc from the northern half of the west coast of México to the region of the plains states. With the exception of major topographic changes, the global features responsible for this zone of dry climate have undoubtedly remained throughout the Cenozoic. The uplift of mountain ranges and plateaus would be expected to fragment or expand the dry climate of this region—expand it by a rain shadow effect into regions normally having higher rainfall, and fragment it by the development of bands of greater rainfall on the windward side of mountains and plateaus, or by the greater effectiveness of the same low rainfall at higher elevations and consequently lower temperatures.

Most of the western United States and México was covered by the sea during part of the Upper Cretaceous (Kellum, 1944; P. B. King, 1959). Not until after this vast area had been uplifted at the end of the Cretaceous could the modern distribution of *Neobarrettia* have been initiated. Recently gathered evidence along several lines, or recent analyses of older evidence (summarized by King, 1958) now indicate that during the early Cenozoic the western United States must have been quite low, with no mountains high enough to constitute barriers to the dispersal of plants and animals, or to create rain shadows. Since this situation was apparently true for the entire region north of the Mexican boundary, I think it reasonable to assume that it was also true for most of México, although there is as yet no evidence which might demonstrate the case. It was not until mid-Miocene that any of the great North American mountains or plateaus arose. Garfias and Chapin (1949) indicate a Miocene rejuvenation (or topographic mountain building according to the concept described above) of the Sierra Madre Occidental, the Northern and Central Plateaus, the Trans-Volcanic Belt and the Sierra Madre del Sur. Cook (1961) summarized the evidence for the Miocene uplift of the Rocky Mts.; Chaney (1940) indicated the same age for the Cascade Range as did Hunt (1956) for the Colorado Plateau. Uplifted later were the Sierra Madre Oriental in the Pliocene (Garfias and Chapin, 1949; Segerstrom, 1962), the isolated ranges of western Texas and central and southern New Mexico in the late Pliocene or early Pleistocene (King, 1948), the Sierra Nevada in the earliest Pleistocene (Axelrod and Ting, 1960), the Coast Ranges of California (and possibly also the Peninsular Ranges of southern California and Baja California) in the mid-Pleistocene (King, 1959), and at least portions of Jalisco also in mid-Pleistocene (Clements, 1963). Most or all of the mountains which had been uplifted earlier were further elevated in the Pleistocene.

According to this geologic evidence, dry climate could not have extended beyond the boundaries of the zone predicted by climatic theory before the mid-Miocene. Another line of evidence suggests that during the early Cenozoic the climate within this zone must have been more humid than it is today. Two independent studies of fossil marine organisms (Emiliani, 1954 and Durham, 1950) indicate that the Pacific Ocean was considerably warmer in the early Cenozoic and has gradually cooled to its present temperature. Air masses over a warmer ocean would pick up more moisture and would thus be able to provide more rain on land.

The above data can indicate only where relatively drier or wetter climates were located in the past. The actual climatic conditions must be determined from the nature of the fossil floras and faunas. Unfortunately, even the best fossil record (for example, that of plants of California for the Cenozoic) is fragmentary, and a usable record is almost completely absent from México. To draw any general picture of past environmental conditions in western North America, considerable extrapolation from the data is necessary. Such extrapolation can be done only within the guidelines set by climatic theory and paleophysiography.

The early Cenozoic paleofloras of the western United States were generally characteristic of much warmer and more humid conditions than exist there now. Succeeding floras testify to a continuous trend (somewhat deranged in the Pleistocene and Quaternary) toward drier and colder conditions. During the Paleocene and Eocene, tropical and subtropical vegetation covered the southern portion of the Southwest and extended as far north as southern Alaska. A few small floras of this epoch located within, or not far to the north of, the "theoretical" dry zone all have a relatively humid tropical aspect, suggesting that the entire zone was covered by humid tropical forests or savannas with scattered small areas of semi-arid vegetation in the interior (Axelrod, 1950, 1958). Since there were probably no extensive highland areas in México at this time, it seems reasonable to assume that the northeastern part and the southern two-thirds (or more) of México was covered by humid tropical forests. The interior of the western United States was dominated by temperate forests which extended north to the Arctic Circle (Chaney, 1947; Axelrod, 1950, 1958; MacGinitie, 1958). Following the Eocene, these temperate forests moved south, largely eliminating the tropical and subtropical forests of Washington, Oregon, northern California, and Colorado by Miocene times (Chaney, 1940; MacGinitie, 1958). Elements of humid subtropical forests persisted in diminishing importance into the Pliocene in the Pacific Northwest (Axelrod, 1956).

In the interior, the temperate forests contacted subhumid vegetation which had been developing and expanding farther south. This dry vegetation is first recorded as a major formation in the Lower Oligocene Florissant of Central Colorado (MacGinitie, 1953). By Mio-Pliocene time, the dry woodland, chaparral, and thorn forest elements of this formation dominated southern Nevada and southern California, and dry woodland extended into southern Idaho (Axelrod, 1956, 1957). By extrapolation, thorn forest and tropical deciduous forest probably covered much of the Sonoran and Chihuahuan desert regions in México (Axelrod, 1950). The Pliocene saw the reduction or disappearance of mesic temperate forests in northern Nevada. Dry woodland and chaparral expanded in the region but were later reduced and apparently largely replaced with grassland, suggesting a climatic trend toward increasing aridity accompanied by decreasing temperatures. In the interior to the south, dry woodland, chaparral, and thorn forest were slowly replaced by semiarid shrubby vegetation or by grasslands which are inferred to have been widespread on the more level ground. To the west in California, dry woodland and chaparral persisted in modified form. True desert plant associations are not found in the fossil record, and are believed by Axelrod to have been Pleistocene developments (Axelrod, 1950, 1956).

In the Great Plains, grasslands probably developed in the Miocene, at which time fossil grass seeds appear in the record. Prairie floras, including both grassland and arboreal streamside formations, were widespread in the Pliocene (Elias, 1942; Chaney and Elias, 1936). It has recently been suggested that these formations may have been savannas, with grasslands being a post-Pleistocene development (MacGinitie, 1962).

The extent of climatic and vegetational changes during Pleistocene and post-Pleistocene times, especially at low latitudes, is still the subject of controversy. Evidence of moister and probably colder conditions in the southwestern United States and the Great Plains has been presented by Axelrod and Ting (1961), Martin, Sabels and Shutler (1961), Hafsten (1961), Graham and Heimsch (1960), Hibbard (1960), and a summary has been given by Martin (1958*b*).

The little direct evidence of Pleistocene changes for México and Central America has been summarized by Martin (1958*b*), and additional evidence presented by Martin (1958*a*). Indirect evidence is afforded by biogeography. The presence of a rich and distinctive desert biota in northern México suggests that these dry areas persisted throughout the Pleistocene. Similarly, the absence of a major biotic element common to the temperate regions of México (especially in the Sierra Madre Oriental) and the ecologically similar eastern United States (including eastern Texas) testifies to the persistence of the subhumid vegetation belt in southern Texas and northeastern México (Martin and Harrell, 1957). Conversely, the absence of more than a few desert and thorn scrub-thorn forest restricted elements (at least among the Orthoptera) common to the Sonoran and Chihuahuan deserts, or to the northeastern and northwestern coastal areas, and the absence of a northern desert element in dry areas in southern México, indicate a minimum of Pleistocene expansion of the present Mexican desert and subdesert areas. The Martin and Harrell theory (1957) that glacial periods, in middle México at least, were characterized by cool-dry conditions and interglacials by warm-moist conditions, implies that while dry bushland may have expanded and contracted somewhat during the Pleistocene, it was limited then by the same more humid vegetation as today, and that it probably occupied the same general position during the Pleistocene that it does now. In the region of the Central Plateau and Trans-Volcanic Belt, however, bushland was probably replaced by grassland and oak-pine woodland during the Pleistocene uplift of that region.

In summary, semiarid environments suitable for *Neobarrettia* probably developed in northwestern México in the Oligocene and expanded northward. Miocene uplift of the Sierra Madre Occidental and the Mexican Plateaus probably allowed the southeastward expansion of this environment. Starting in the Oligocene, temperate forests migrated southward into northern and central California and Nevada where they met the dry woodlands migrating northward. Following this junction, grasslands or savannas developed in Nevada (and possibly also in the Mohave and Sonoran desert regions) in the Pliocene, eliminating habitats suitable for *Neobarrettia* in the western United States. Deserts have probably only recently developed there. Grassland also developed in the Great Plains during the Miocene and probably extended south and west in the Pliocene. Uplift of the Sierra Madre Oriental in the Pliocene and uplift of the Central Plateau and Trans-Volcanic Belt in the Pleistocene restricted or fragmented bushland areas by the development of grassland and oak woodland at the higher elevations. Pleistocene climatic changes are not believed to have disrupted the general vegetational pattern as seen today in México, except for some expansion and contraction of various of the vegetational formations.

PART III. A RECONSTRUCTION OF THE HISTORY OF *NEOBARRETTIA*

Direct evidence of the history of *Neobarrettia* is lost in the imperfection of the fossil record. To the best of my knowledge, no fossils of this genus or other members of the subfamily Listroscelinae have been found. Even without fossil documentation, I believe that a reliable reconstruction of its history can be made by indirect means. Some indication of the time of origin of these katydids may be obtained from the fossil record of the more primitive katydid groups and of the tettigoniid subfamilies of approximately the same level of advancement as the Listroscelinae. The temporal and geographical outlines of their subsequent history may be deduced from their present distribution and ecology, considered in relation to the development in geologic time of the preferred and the limiting habitats of *Neobarrettia* and of its relatives.

THE AGE OF THE SUBFAMILY

Although the fossil record is meager, the available evidence suggests that the modern tettigoniid subfamilies, probably including the Listroscelinae, did not begin to differentiate until late Jurassic. Fossil representatives of the Prophalangopsidae, the primitive family from which the Tettigoniidae are believed to have been directly derived (Zeuner, 1939), appear in the Triassic and are comparatively common in the Jurassic. The earliest true tettigoniid appears in the Upper Jurassic. This katydid was only slightly advanced over the Prophalangopsidae, and is the only tettigoniid known from the Jurassic. Cretaceous deposits have yielded no determinable katydid remains. By Eocene time prophalangopsids and primitive tettigoniids seem to have been replaced[14] by representatives of the modern tettigoniid subfamilies (Zeuner, 1939), which therefore must have differentiated in the Cretaceous, although their presence as a very minor element of the orthopteran fauna of the Jurassic cannot be excluded as a possibility. Because well-differentiated genera of two subfamilies related to the Listroscelinae are known from the Oligocene,[15] it is likely that the Listroscelinae and possibly some of its modern genera were in existence by that time.

THE TIME OF ISOLATION OF THE NORTH AMERICAN LISTROSCELINES

The subfamily Listroscelinae is essentially pantropical in distribution. In the Eastern Hemisphere, only two species of the widespread genus *Hexacentrus* extend any distance into the north temperate zone; one occurs as far north as the Tokyo region in Japan, the other as far north as the central part of Korea.[16] Neither species appears to be a relict of previously widespread cold-adapted forms. The other Old World genera are found in the humid tropical portions of Asia and Africa. In South and Central America, where the distribution of these katydids is poorly known, most of the genera and species occur in humid, tropical regions. Individuals of only one genus, *Cerberodon*, are found south of the Tropic of Capricorn,[17] but these occur

---

[14] Doubtless a replacement only in terms of abundance and variety, since the Prophalangopsidae are still represented by two genera with very restricted distributions.

[15] *Eomortoniellus* and *Lipotactes*, Tympanophorinae, Lower Oligocene, and *Orchelimum* (*s.l.*), Conocephalinae, "Miocene: Florissant." An exhaustive review of the Florissant flora by MacGinitie (1953) indicates that the deposits are of Lower Oligocene age.

[16] *H. unicolor* Serville, known as far north as Tokyo, Japan, and widely spread farther south; *H. japonicus* Karny, known as far north as Yokohama, Japan, Shantung Province, China, and central Korea.

[17] Another genus, *Dasylistroscelis*, described as a listrosceline by Mello-Leitão (1940) from Rio Grande do Sul, Brasil, is reported by T. H. Hubbell (*in litt.*), who has examined the type, to be a member of the Gryllacrididae.

within the limits of subtropical climates[18] close to the coast in Brasil. Several nominal genera are found in relatively dry areas in the interior of Brasil,[19] but there is reason to believe that they inhabit the patches of more humid forest there.

Only *Neobarrettia* shows strong adaptation to subhumid environments. The species of this genus seem to be unable to enter forests of either northern or humid tropical derivation except where these have been modified by man (see Part II). Two species penetrate into colder regions,[20] but even here they are not associated with vegetation of northern derivation, but rather with northward extensions of semiarid bushland.

At the present time, passage between North America and Eurasia by listroscelines would be blocked by temperate and boreal climatic and vegetational conditions in the Alaska-Siberia region if the katydids were able to reach that area. Passage to North America would be blocked for the South and Central American listroscelines by the arid zone in México if they were able to extend their range that far north, and *Neobarrettia* would be barred from entry into Central and South America by the humid forests of southern México. To account for the present pantropical distribution of the subfamily, it must be supposed either that some of the genera formerly had very different habitat tolerances or that the continental environments must have been markedly different in the past. As indicated above, there is no evidence that any listroscelines except *Neobarrettia* have ever become adapted to dry or cold conditions. However, there is ample proof that major environmental changes have occurred in the past, some of which might have allowed wide dispersal of humid tropical forms and others of which might have stimulated adaptation of listroscelines to subhumid conditions in the American southwest.

The Pacific Northwest has been covered by temperate forests throughout most of the Cenozoic and during the Upper Cretaceous as well. The paleobotanical record, however, reveals that in Eocene time there was a great expansion of tropical and subtropical floras, bringing habitats suitable for listroscelines far to the north of the present subtropical zone. The recorded culmination of this movement took place in the Upper Eocene when floras of the northwestern United States were of a tropical or subtropical nature, and when elements of such floras occurred as far north as Kupreanof Island

---

[18] This term is used loosely but corresponds more or less to Köppen's "C" climates. Temperature and precipitation in the regions where the southernmost individuals of *Cerberodon* are found are well above the minimum for this type of climate.

[19] *Carliella, Macrometopon,* and *Isocarliella,* all of which are probably congeneric. Material of one of these genera in the collections of the University of Michigan Museum of Zoology comes from the rain forest of the Rio Xingu, Pará, Brasil.

[20] *N. victoriae* reaches southern Kansas, and *spinosa* northern Texas.

in southern Alaska. To bring a subtropical forest from that point to the latitude of the continental shelf in the Bering Sea region would require a northward shift of the recorded vegetation zones of from 4 to 12 degrees of latitude, or 500 to 1000 miles.[21]

The land bridge which would have afforded the easiest passage to migrants between Asia and North America may have been responsible for creating an even warmer and more humid climate in the northern Pacific than the few known fossil floras record. Such a bridge across the Bering Sea would have barred the cold Arctic waters from flowing into the Pacific. Uncontaminated by them, the Japan Current, larger in volume because none of it could flow northward into the Arctic Ocean, would have bathed the southern shore of the bridge as well as the coast of the Pacific Northwest with warmer water, thus producing warmer climates (probably by increased minimum rather than increased maximum temperatures) and, indirectly, more abundant precipitation. These climatic conditions would have permitted the development of vegetation requiring warmer and more humid conditions than would normally have existed in the region, and therefore would have produced a habitat on and near the bridge suitable for the migration of listroscelines.

There is no direct evidence that subtropical vegetation ever existed in the region of the Bering Sea. There is evidnce, however, that the temperature of the waters off the Pacific Northwest coast was higher in the Eocene than in the Upper Cretaceous, and two independent sources (Durham, 1950, and Emiliani, 1954) indicate that the Pacific has been cooling since the end of the Eocene. That a land bridge did exist in the Eocene is attested by the well-documented exchange of mammalian faunas between Asia and North America during this epoch (Simpson, 1947). The few known northern floras of the Upper Eocene, a period of time spanning several millions of years, can do little more than indicate general vegetation conditions; there was ample time for the northward migration of subtropical vegetation to have reached a Bering land bridge without a record of this culmination having been preserved in the fossil floras so far discovered.

The increasingly abundant fossil floras of succeeding epochs record the replacement of the subtropical forests of the Pacific Northwest by temperate forests moving down from the north. This was presumably in response to the cooling of climates indicated both by the paleobotanical data and by the independent evidence of cooling Pacific and Arctic waters mentioned

---

[21] The northern limit of Eocene subtropical floras probably lay between the Puget Sound area in Washington, where the tropical or subtropical element was dominant, and Kupreanof I., where some subtropical elements were present in an essentially temperate forest. The figures above represent distances from these two areas to latitude 61° N, the approximate southern limit of the continental shelf in the Bering Sea.

above. The record of mammalian migration between Asia and North America offers particularly convincing evidence that the climate of the Bering Straits area has been cool to cold temperate since the mid-Tertiary. From the Miocene to the present, virtually all the migrants have been members of cold-climate groups, or of cold-adapted offshoots from warm-climate groups. Conversely, the nonmigrants have all been warm climate animals which failed of passage even though they were widespread and abundant in the tropics and subtropics. Prior to the Miocene, the climatic adaptations of the migrants cannot be determined with certainty, but there is reason to believe that the derivation of the migrants and nonmigrants followed the same pattern as later (Simpson, 1947).

Thus, a large amount of circumstantial evidence indicates that conditions during the late Eocene were suitable for the migration of subtropical listroscelines between Asia and North America. More direct evidence indicates that such intercontinental connections must have been broken in the Oligocene, and that they were never again re-established.

Nothing certain is known of climatic or vegetational conditions in México during the early Cenozoic. However, a number of peripheral fossil floras provide sufficient data to allow a reasonable extrapolation to cover much of northern México. Late Cretaceous floras of the Mississippi Embayment region contained numerous representatives of Holarctic temperate forest species, but in the succeeding Eocene floras there this Holarctic element was absent, and instead they were characterized by having many warm temperate and tropical genera (Braun, 1947). It is estimated that sixty per cent of the Lower Eocene Wilcox flora entered the Gulf Coast area from equatorial America. The Middle and Upper Eocene floras of eastern Texas record progressively warmer climates. A small Venezuelan Eocene florule contains "several types identical even to species" with the Upper Eocene floras of the Mississippi Embayment (Berry, 1937), a statement which assumes considerable significance in the light of Chaney's (1947) opinion that Berry has overmultiplied the species of the Wilcox flora. Thus the available evidence strongly suggests that during the Eocene, and especially in the Upper Eocene, there was relatively free migration of humid tropical vegetation between northern South America and the Mississippi Embayment through northern México, an area which, on theoretical grounds, would be the first to show signs of the subhumid climates which were to develop later in the Cenozoic. This conclusion is supported by a small humid tropical Eocene flora known from the Big Bend region of Texas, which lies in the middle of the same zone which theoretically has always had the driest climate on the continent. Athough some plants adapted to semiarid climates do appear in Eocene floras, they are considered to have existed under special local xeric conditions, both on account of the nature of the floras and sediments in which they were found, and the generally humid aspect of other Eocene floras in the region from Texas to California. In that region, and presumably in northern México as well, no subhumid barrier seems to have existed in Eocene time, and listroscelines that required warm humid conditions could then have passed between North and South America.

Shortly thereafter, the Mexican route was closed to animals having such requirements by the development of subhumid climates in the South and Middle West. The occurrence of a substantial semiarid element in the Colorado Florissant flora of the Lower Oligocene is evidence that semiarid climate had become established over the southwestern interior by mid-Oligocene time. By mid-Miocene, a pure semiarid (Madro-Tertiary) flora dominated the Mohave Desert region in southern California, and at the same time, prairie grasslands were developing in the High Plains. All subsequent floras from both regions indicate maintenance or intensification of semiarid to arid conditions. This subhumid barrier stretching from California through the High Plains probably became established in the Oligocene, for Oligocene Arcto-Tertiary species were unable to penetrate into México or the eastern United States (MacGinitie, 1958). As the climate in the interior of the United States became more continental, the increasing monsoonal deflection of the trade winds robbed northeastern México of much of its rainfall and probably extended the subhumid barrier to the Gulf Coast in Miocene times.

Wherever the ancestral listroscelines arose, whether in Asia or in the New World, their distribution must have been affected by the climatic changes outlined above at times and in ways that, as has been shown, permit the dating of certain events in their history. If the highly probable assumption is made that the ancestral forms were adapted to warm, humid environments, then the distributional and paleoecological data support the following conclusions: (1) the Eocene is the most recent time in which distribution of this group could have been continuous between Asia and South America; (2) the *Neobarrettia* stock has been isolated from its relatives in Asia at least since the Oligocene, and from those in South America perhaps as long as, and certainly since, the Miocene.

Morphology furnishes additional data pertinent to the time of origin of the *Neobarrettia* stock. Its descendant now possesses the most primitive characters found in the subfamily These characters are judged to be primitive on one of the following grounds: with respect to a given structure, either its condition is less modified in a direction associated with carnivorous habits than other listroscelines,[22] or its condition is one that is com-

---

[22] For example, the lesser protuberance of the eyes and the relative shortness of the ventral tribal spurs of the foreleg. See discussion under the section on generic relationships.

mon to many other subfamilies in the Tettigoniidae.[23] If the estimates thus based are correct, then *Neobarrettia* cannot be derived from any of the other modern listrosceline genera or their recent ancestors. Many of the Asiatic and South American listroscelines share a derivative condition[24] of characters which in *Neobarrettia* are primitive. It seems unlikely that the assemblage of derivative characters common to the Asian and South American genera resulted from parallel modifications occurring independently in the two regions; a monophyletic origin therefore is assumed for them. On this assumption, the *Neobarrettia* stock must already have been separated from the stock that produced the other genera prior to the origin of the advanced characteristics, and that origin must have preceded the isolation of the South American from the Asiatic listroscelines. From the evidence already cited, this isolation occurred in the Oligocene, which would mean that the *Neobarrettia* stock became differentiated during the Eocene or earlier. Indirect support for assuming so ancient an origin is found in the absence of closely related listroscelines in either South America or Asia. The genus which is morphologically closest to *Neobarrettia* is the Asiatic *Hexacentrus*. This genus shows considerably more specialization, and the relationship is not especially close.

In summary, morphological, distributional, and paleoecological evidence strongly suggest that the *Neobarrettia* stock has had a separate existence since the Eocene or earlier, and that it has been in North America at least since that epoch. Furthermore, it seems probable that its adaptation to arid and semiarid environments, unique in the subfamily, was acquired in North America (see discussion below).

Rehn (1957, 1958) cited no evidence in support of his assertion that *Neobarrettia* (and the synonymous *Rehnia*) represents a development from a listrosceline line derived from South America.[25] The present study lends support neither to this opinion nor to Cohn's (1957) tentative placement of

---

[23] For example, the straightness, lateral sulcation, and dorsal spur armature of the fore tibiae and the smoothness of the pronotum, all of which are conditions found in many other tettigoniid subfamilies. See discussion under the section on generic relationships.

[24] Especially the curvature of the fore tibiae and the greatly increased length of their ventral spurs, but also other details of the tibiae, pronotum and head, and of the armature of the femora, coxae, trochanters, and sternites. See discussion under generic relationships.

[25] Apparently Rehn (1957) did not compare the two genera with any Asiatic listroscelines other than *Xiphidiopsis*. That genus belongs to the closely related Meconeminae, although it has occasionally been placed in the Listroscelinae to form a distinctive group with such genera as the South American and Asiatic *Phlugis*. I assume that Rehn's statement that *Rehnia* and *Neobarrettia* are closer to some of the Neotropical genera such as *Arachnoscelis* than to lines represented by *Phlugis* and *Xiphidiopsis*, was meant as a general comparison, and not intended to exclude a closer relationship with such Asiatic genera as *Hexacentrus*, which apparently was not studied in this connection.

the two genera close to the South American *Carliella* and its allies. Until some definite evidence pointing to another origin is discovered, it is probably best to consider *Neobarrettia* as an autochthonous North American development. The central geographic position and primitive morphology of the genus in relation to that of the rest of the subfamily suggest (but by no means prove) that North America may have been the region of origin of the subfamily. There is little in the morphology or distribution of the other listrosceline genera, other than their greater diversity in Asia, which definitely precludes this as a possibility.

THE "SEMIARID ADAPTATION" OF THE *Neobarrettia* STOCK

The adaptation and restriction to semiarid environments is a basic characteristic of *Neobarrettia.* It is found in all of the species, and to much the same degree in each. It must have been characteristic of the common ancestor of the modern species since several of these are widely separated from the others by unoccupied humid environments. It seems hardly likely that the adaptation to semiarid conditions was developed independently in each of the several lines, and that all evidence of the original "humid adaptation" has disappeared in each line. If the reconstruction of the history of the genus offered below is correct, then the "semiarid adaptation" must have been achieved by the ancestral *Neobarrettia* prior to the initial separation of the species groups in mid-Miocene.

Adaptation to semiarid conditions could either have been developed by the early listroscelines in North America, or have been brought to North America by listrosceline immigrants from Asia or South America. Consideration of the habitats occupied by the other modern listrosceline genera makes the second hypothesis unlikely. All of these other genera occur in humid environments, or in regions where humid climates predominate. Even if forms adapted to semiarid conditions were present on other continents in past times, it is unlikely that they could have migrated into North America. The Pacific Northwest was covered with humid forests or savannas during the only time in the Cenozoic when the Bering Straits area could have had a subtropical climate suitable for listrosceline migration. It is less easy to demonstrate that a semiarid or arid corridor did not exist between North and South America, but there are indications that no such route was open. There are, it is true, some striking instances of disjunct bicontinental genera and species of desert plants, and of some deserticolous plant families restricted to one continent except for a few disjunct species in the other. There seem to be too few of these cases to indicate the former existence of a major arid corridor, especially in view of the apparent absence of similar disjunct distributions among desert animals. Furthermore, our present knowledge of the geology, paleogeography and paleoclimatology of Middle America is all adverse to the hypothesis that such a corridor could have existed. In the western United States and México there was no well-developed belt of *arid* climate prior to the mid-Miocene orogenies which account for the isolation of at least one of the species groups of *Neobarrettia*. The fossil floras of the middle and western United States indicate considerably greater rainfall in Lower and Middle Tertiary times than at present, a condition which almost certainly extended much farther south. Although these same floras also indicate that higher temperatures existed in regions farther from the equator, recent analysis of Miocene floras from northern South America suggest that temperatures in the tropical zone may have been slightly lower than they are today (Miranda, 1960), which would have made rainfall more effective. The paleobotanical evidence is supported by that from physical geology. Until mid-Miocene, there were no greatly elevated regions in México (and probably none in Central America) to produce rain-shadow belts and dry interior basins, and it is currently believed that Central and South America were not connected by a continuous land mass until late Cenozoic time.

In summary, it seems unlikely that a listrosceline adapted to arid conditions could have reached México from South America, and even more unlikely that such a form arrived there from Asia. It is highly probable that the "semiarid adaptation" arose in western North America as semiarid environments developed and spread in post-Eocene times.

The geography of the early stages in the development of subhumid vegetation in western North America suggests a simple mechanism by which some of the early North American listroscelines might have achieved adaptation to semiarid habitats. These early forms were probably inhabitants of the humid subtropical or tropical forests and savannas which covered most of the southwestern and western portions of North America during the Eocene. The known and inferred geographical conditions of this epoch were conducive to humid climates in these regions, and from the paleobotanical evidence it appears that even the "theoretical" zone of dry climates (a zone based on climatic theory; see Part II) was covered with mesic vegetation. Pockets of subhumid conditions were doubtless present during the Eocene, but they must have been small, local, and not very dry. A secular trend toward drier and colder climates was initiated in the Oligocene. A Colorado flora of Lower Oligocene age is considered by Axelrod (1950) to indicate the general occurrence of semiarid climate over the southwestern interior. At about the same time, subtropical forests are recorded from the Pacific Northwest. Thus, as would be predicted from general climatological principles, the trend toward drier climates was felt most intensively and probably earliest in the "theoretical" continental dry zone. Since the site of the Lower Oligocene Colorado flora lies near the edge of this zone, it is reasonable to assume that semiarid vegetation extended throughout the zone in that epoch. By this early climatic development, a large pocket of vegetation requiring warm humid conditions was isolated in the western United States from similar vegetation in México. The cooling of climates and the spread of temperate forests from the north isolated this warm humid pocket from contact with similar vegetation in Asia. Compressed between the temperate forests moving south and the semiarid vegetation moving northwest, the warm humid pocket was gradually reduced in area during the Oligocene and Miocene, and mostly eliminated by the end of the latter epoch (Fig. 15).

For plants and animals living in this humid pocket, these events must have placed great selective advantage on adaptation to the encroaching drier conditions. It is reasonable to suppose that some of the early "humid-adapted" listroscelines were among the forms thus trapped, and that one stock survived because it succeeded in developing the "semiarid adaptation" seen today in all the species of *Neobarrettia.* Although this suggestion of entrapment is entirely hypothetical, it fits well with the distribution of semiarid- and humid-adapted listroscelines in North and Central America. It is also compatible with the probable time of development of adaptation to semiarid environments, determined on other grounds as having occurred after the Eocene migrations between Asia and North and South America, and before the mid-Miocene isolation of the *Neobarrettia* species groups. No other hypothesis agrees so well with the facts of existing distribution, or with current interpretations of past climatic, physiographic, and ecologic changes. Furthermore, no other offers so convincing a cause and so specific a time and place for the evolutionary change to the new environmental adaptation.

After the ancestral *Neobarrettia* stock attained its adaptation to semiarid conditions, its members were probably able to spread widely in northern México and the southern portions of the southwestern United States before the great mid-Miocene orogenies. Since a thorn forest or thorn scrub flora is recorded from the Miocene in southeastern California, just north of the "theoretical" zone of subhumid climates, it is reasonable to assume that much of that zone (which included the northern interior and northwestern coastal regions of México) was covered during the early Miocene by these or similar formations, and could then have provided a suitable habitat for an ancestral *Neobarrettia.* This thorn forest or thorn scrub habitat probably extended eastward through Arizona into Texas, where it merged with the developing grasslands (or savannas) of the Great Plains. These grasslands were evidently well developed by the end of the Miocene and would have formed a northeastern barrier to the dispersal of the ancestral *Neobarrettia.* To the north, it was probably limited by a belt of oak woodland and temperate forest stretching from California and Nevada (where such forests are recorded in late Miocene deposits) to the Great Plains. Southward, the land was relatively low during the early Miocene, and the southern half of México was probably covered by humid tropical forests which would have constituted a southern barrier to the dry-adapted *Neobarrettia* stock. These forests probably encroached on the southern portion of the "theoretical" dry zone and may have extended through much of Sinaloa and thence eastward. Today, some form of humid tropical forest and savanna formations occur in the lowlands of Nayarit (between Acaponeta and Tepic) and extrapolation of climatic data lead to the conclusion that these formations were more extensive during the Miocene. Oceans are known to have been warmer off the entire Pacific Coast of the United States at this time (Durham, 1950); the Miocene floras of southern California indicate greater rainfall; and a Miocene flora from the Isthmus of Tehuantepec (Berry, 1923) indicates that the climate there was at least as warm and as humid as it is today.

THE MODERN DISTRIBUTION: GEOLOGICAL AND VEGETATIONAL FACTORS

The modern distribution pattern of *Neobarrettia* (Fig. 24) is best explained in terms of the great mid-Miocene orogenies which elevated most of the mountains and plateaus of México, and the Pliocene orogeny which elevated the Sierra Madre Oriental. The uplift of the mountain chains created suitable climatic conditions at high elevations for the development of oak and pine forests, which act as barriers to the species of the genus. At the same time the mountains produced rain shadows in the interior of the country which were responsible for the expansion of the dry environments in which are found the preferred habitats of the species. The uplift of the plateaus similarly expanded the drier environments of the interior, also by a rain shadow effect. Their eastern edges forced air masses from the Gulf of México to rise and cool, and thus lose some of their moisture before reaching the surface of the plateaus. Later, the Sierra Madre Oriental was elevated, creating a more effective rain shadow.

As the higher portions of the Central and Northern Plateaus approached their present elevations, however, their lowered temperatures were responsible for greater and more effective rainfall. This created climatic conditions in the southern and western interior of México suitable for the development of grasslands (or savannas), which act as barriers to the species of *Neo-*

barrettia. Before the mid-Miocene orogenies, most of the southeastern portion of the Northern Plateau and all of the Central Plateau were probably covered with humid (or semi-humid) forests, both inhospitable to *Neobarrettia.* As the plateaus rose, the humid forests probably retreated southeastward, and were replaced by thorn forest. As aridity increased, the thorn forest was in turn replaced by thorn scrub, and the latter eventually by desert. At higher elevations, desert vegetation or thorn scrub was replaced by grassland and savanna, and in the still higher portions of the Trans-Volcanic Belt, grassland gave way to oak and coniferous forests which are even more effective barriers to *Neobarrettia* dispersal.

These geologic and vegetational events and their effect on the distribution of *Neobarrettia* are summarized in Figures 15 and 16. These figures are intended to accompany the more detailed discussion below of the distributional history of the *Neobarrettia* species.

THE SINALOAE GROUP.—Isolation of ancestral *sinaloae* on the northwest coastal plain of México is the first event in the shaping of the modern distribution of *Neobarrettia* which can be dated with some degree of assurance. This was a result of the mid-Miocene rise of the Sierra Madre Occidental to heights suitable for the establishment of an unbroken zone of oak-pine woodland and forest. Such a zone would have effectively split a population of *Neobarrettia* which initially ranged across the site of the mountains. Oak-pine woodlands are now found below 4000 feet east of Mazatlán, Sinaloa, but are probably not continuous except at somewhat higher elevations. Under the warmer and more humid conditions of the Miocene, the oak zone may not have extended below 5000 feet. Although the present height of the Sierra Madre Occidental is apparently the result of renewed uplift in the Pliocene and Pleistocene, it is reasonable to assume that the initial orogeny raised the mountains at least 5000 feet, which is about one-half of their present height.

Ancestral *sinaloae* was prevented from reaching the southern end of the mountains by the humid and semi-humid forests and savannas in northern Nayarit, which probably extended far into Sinaloa under the climatic conditions of the late Miocene. To the north, the species may have extended through southwestern Arizona into southeastern California, where thorn forest is well represented in Miocene and early Pliocene floras.

As aridity increased in the Mohave and Sonoran Desert regions during the Pliocene, ancestral *sinaloae* was probably eliminated from the northern portions of its Miocene range. Even *hakippah,* of the two species the more tolerant of arid conditions, is now absent from the drier portions of the Sonoran Desert. Sometime during this retreat to the south, a pocket of thorn forest with its ancestral *sinaloae* inhabitants may have been isolated in a sheltered situation. Inflow of genes from the parental population that was adapted only to a semiarid thorn forest environment would have been cut off by the intervening desert. As the thorn forest pocket was slowly restricted and eventually eliminated, genes producing tolerance to drier conditions would have been strongly and quickly selected in the isolated population. Isolation would also have allowed the rapid development of other new characters. With the final achievement of adaptation to desert conditions concomitant with the elimination of the thorn forest pocket, this population would have been able to invade the region from which the parental population had been eliminated by increasing aridity. In this manner, *hakippah* could have developed. However, there is no proof that this was the actual course of events. The hypothesis nevertheless accords well with the distributional facts, with the apparent differences in ecological requirements and tolerances of the two species, and with the inferred climatic changes that occurred in the region. Furthermore, it obviates the need for a major topographic barrier to fragment the ancestral *sinaloae* range, for the existence of which there is no evidence at all. The newly differentiated *hakippah* overtook the retreating sinaloae and displaced it from the more arid habitats to which *hakippah* was, by hypothesis, better adapted. Open fields probably represent the more arid habitats in thorn forest country, and the agricultural activities of man, therefore, have undoubtedly aided the spread of *hakippah.* In the fields, *hakippah* was probably able to build up very large populations. With such a reservoir to draw from, it was able to replace *sinaloae* in the thorn forest by sheer force of numbers, despite an apparent initial competitive disadvantage in that habitat.

Continuing invasion of the range of *sinaloae* by *hakippah* can be seen taking place at the present time in the vicinity of Culiacán, Sinaloa. North of the Río Culiacán and west of the Río Humaya, *hakippah* has just completed the elimination of *sinaloae,* if my interpretation of the pattern of variation in *hakippah* and of the presence there of a single individual of *sinaloae* (in 1958) is correct (see discussion under the taxonomic treatment of *hakippah*). On the east side of the Río Humaya, *hakippah* is making its initial invasion, and so far has been able to obtain a foothold only in the fields along the river. In these fields, however, *hakippah* apparently has an advantage over *sinaloae* for reasons already discussed, and when the field populations build up to a sufficiently high level in the near future, *hakippah* may be expected to invade the adjacent thorn forest and to replace *sinaloae* there.

The Sierra Madre Occidental, which for a long distance forms a continuous barrier to the eastward dispersal of this species group, breaks

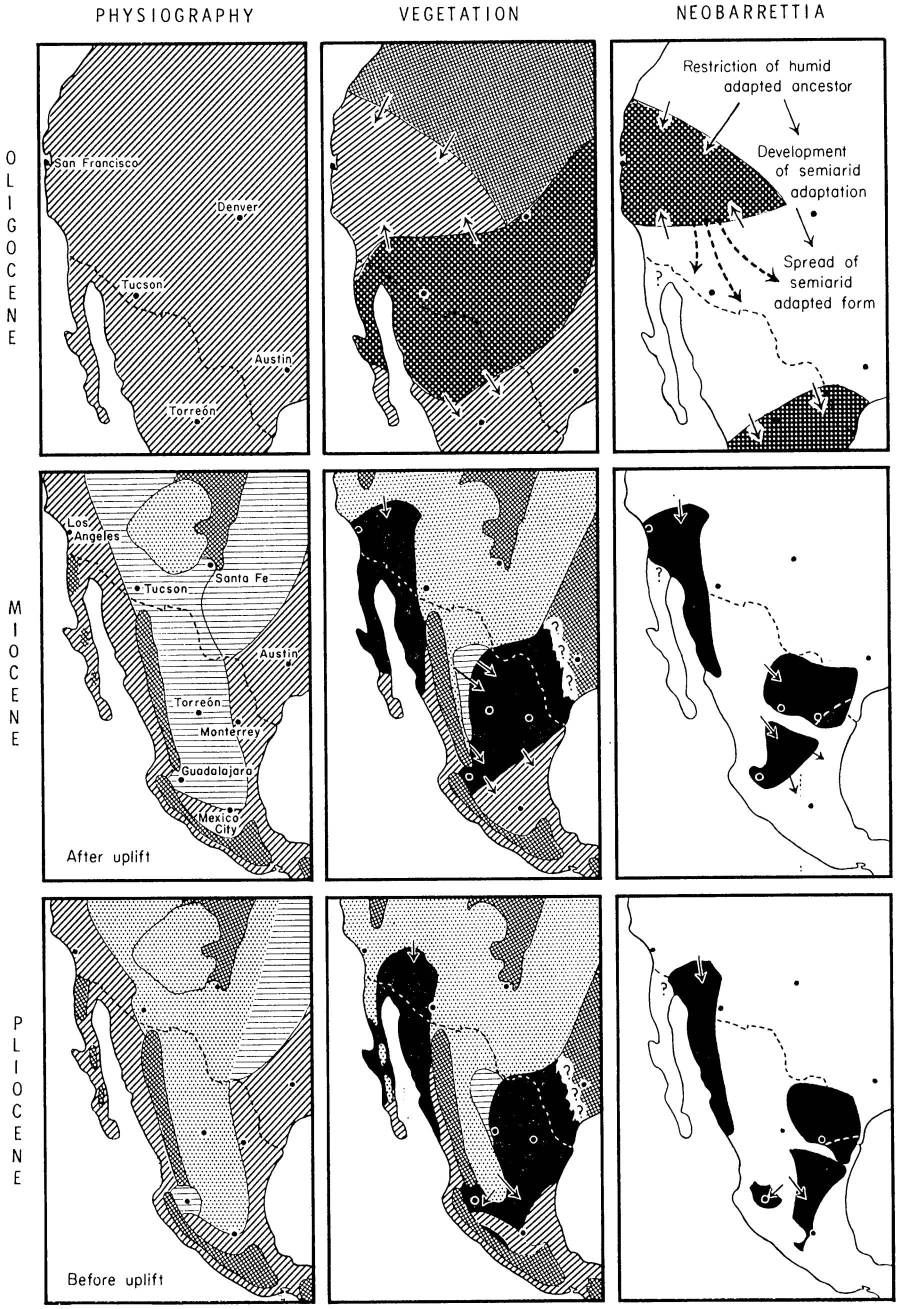


FIG. 15a. See page 139 for legend.

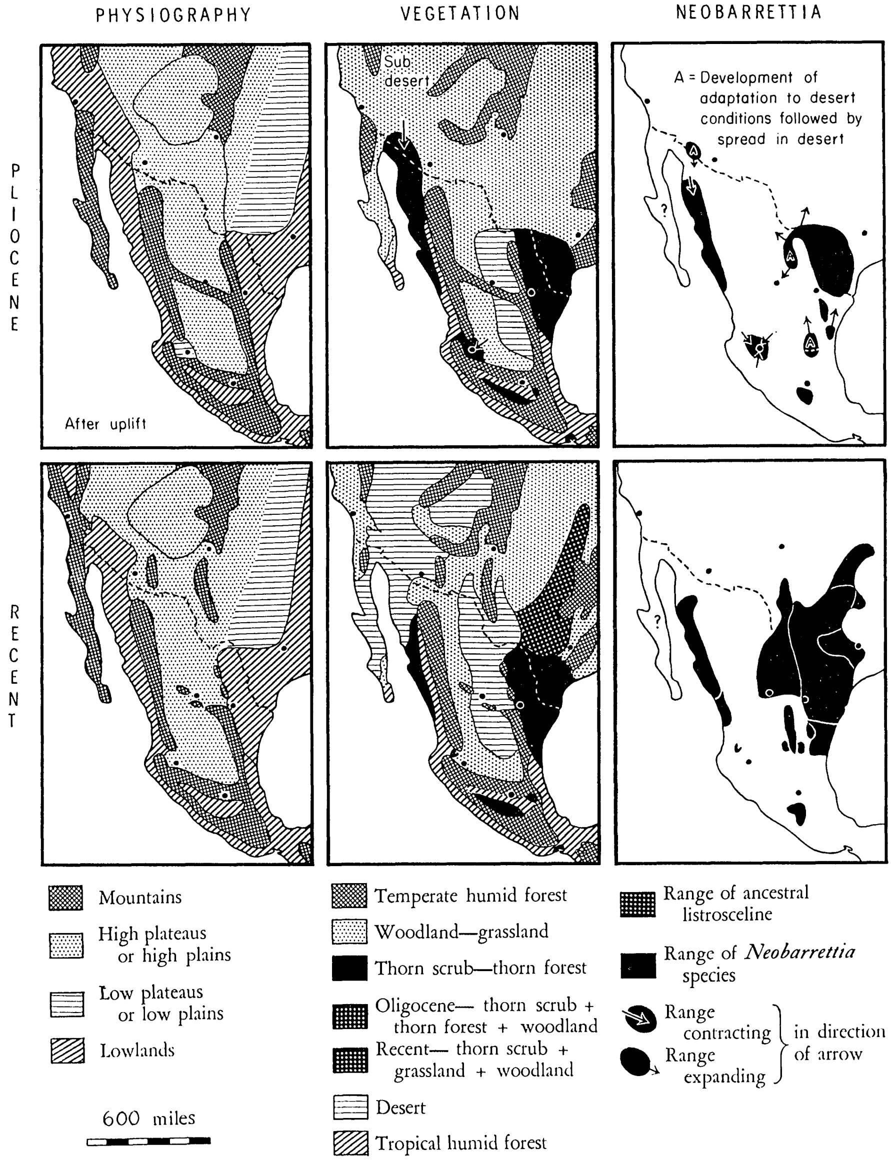


FIG. 15b. Cenozoic physiography, vegetation and hypothetical *Neobarrettia* distribution in western North America. Physiography and vegetation are based on sources cited in the text and on extrapolation from them. Modern Mexican vegetation is modified from Leopold (1951); Mexican vegetation for other epochs is based entirely on extrapolation. Terms for vegetation types are here used in a broader sense than usual; see Part II of text for definitions. Changing continental shoreline is not shown. Filled circles (●) represent location of modern cities which are identified for the Oligocene maps on the Oligocene physiographic map, and for all other maps on the Miocene physiographic map.

up in northwestern Sonora. The lowest gaps between the isolated mountains in this region lie at slightly less than 5000 feet and are now covered with grassland or oak savannas (Marshall, 1957), both of which are barriers to *Neobarrettia.* It might be supposed that under a different climatic regime at some time in the past, these gaps were covered with vegetation which might have allowed the migration of *Neobarrettia* through them. There are several reasons for believing this to be improbable. First, it is not the species closest to the gaps (*hakippah*) which shows the closest relationship to the eastern species of *Neobarrettia,* but rather the one more distant from the gaps (*sinaloae,* see Figure 24). This indicates that any migration which might have occurred must antedate the divergence of *hakippah,* which probably took place well before the middle Pleistocene. Second, there is no evidence that there were climatic changes during the Pleistocene (and probably the late Pliocene as well) sufficient to bring either thorn forest or desert vegetation (both suitable for *Neobarrettia*) into the gaps. The nearest thorn forest lies 250 miles to the south and 3000 feet lower than the present elevation of the gaps (Gentry, 1942). Desert vegetation is now found a short distance to the west, but lies 1500 feet lower than the gaps (Shreve, 1951). Furthermore, these gaps were undoubtedly higher in the past, so that even greater climatic changes would have been required to produce conditions for thorn forest or desert vegetation than would now be necessary. Third, there is reason to believe that during the late Miocene and the Pliocene, the region was covered with grassland rather than thorn forest. In the High Plains states well-developed prairie grassland floras are recorded from the Pliocene, and close relatives of prairie grasses are known from the Miocene. Axelrod (1950) suggests that plains grasslands occupied the low-lying parts of southeastern California during the Lower and Middle Pliocene. If it is assumed that northeastern Sonora was uplifted during the mid-Miocene, at the same time as were the mountains and plateaus to the south, north, and northeast, then it is highly probable that this region stood considerably higher than southeastern California during the late Miocene and the Pliocene. There is also good reason to believe that northeastern Sonora stood higher than the High Plains during this period. The general level of the region even today is much higher, and the gaps seem to be the result of stream erosion, much of which must have taken place during the Pleistocene. With grasslands known or inferred at lower elevations to the north, it is probable that grassland or woodland covered the higher plains in northeastern Sonora during the Pliocene. Although thorn forest is recorded in the Miocene and Pliocene floras in southeastern California, it was greatly diminished during the latter epoch, presumably because of lowered temperatures and reduction in summer rainfall. Colder conditions at the higher elevations of the northeastern Sonora region probably prevented thorn forest from developing there during the Pliocene, and possibly during the late Miocene as well. Finally, among those Orthoptera which are *restricted* to desert or thorn scrub-thorn forest habitats, there are very few species or genera in common between the Sonoran and Chihuahuan deserts, and none (except *Neobarrettia*) between the thorn scrub-thorn forest regions of the east and west coasts of México. This striking differentiation testifies to the long existence of grassland or woodland barriers north of the Sierra Madre Occidental.

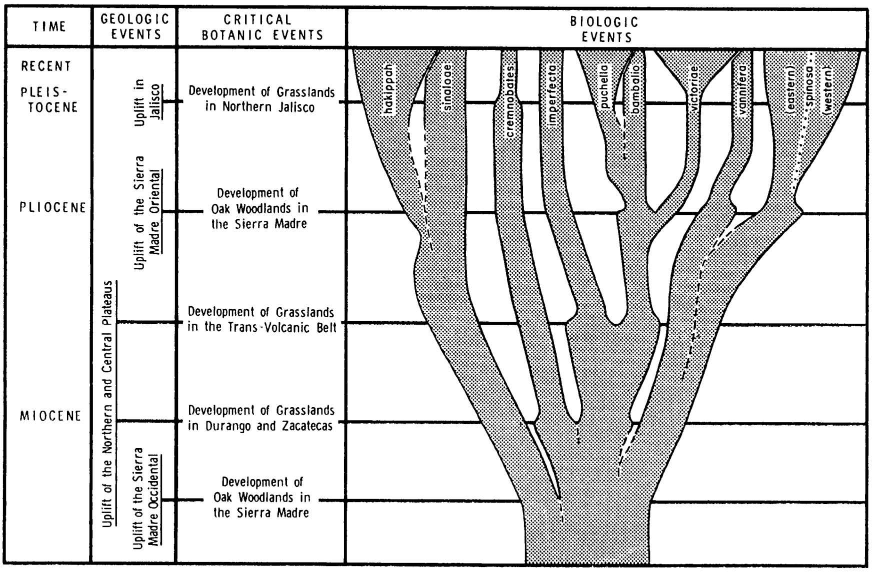


FIG. 16. Suggested history of *Neobarrettia*, and the geologic and vegetational events which shaped it. Dashed lines represent uncertain time of divergence; dotted line, subspecific differentiation. Changing width of areas represent contraction or expansion of range. Contiguous ranges are indicated by contiguous lines; replacement of species is represented by restriction of area of one and expansion of area of the other species.

It seems reasonable to conclude, therefore, that the Sinaloae Group has been isolated on the west coast of México since the uplift of the Sierra Madre Occidental in the Mid-Miocene.

THE CREMNOBATES GROUP.—The same geologic events which isolated ancestral *sinaloae* were also responsible for the expansion of dry environments in the interior of México. Populations of *Neobarrettia* followed the retreating humid forests down the east side of the Sierra Madre Occidental. Before the western portions of the Northern and Central Plateaus reached their present elevations, there must have been a broad thorn forest or thorn scrub corridor across Durango and Zacatecas which provided an easy path of migration for *Neobarrettia* into Jalisco. Continued uplift in western Durango and Zacatecas was responsible for the development of extensive grasslands and savannas, isolating the *Neobarrettia* populations which had reached Jalisco earlier, and allowing them to differentiate as *cremnobates*. Apparently, much of Jalisco remained low until the mid-Pleistocene (Clements, 1963) and if so, thorn forest or scrub and its *Neobarrettia* inhabitants must have been widespread in the state. When uplift was renewed in this region, the vegetation over at least the central part of the state was converted into grasslands or modified scrub. The antecedent vegetation was preserved in the great barrancas of the Río Grande de Santiago, which was probably cut at this time. The ancestral *cremnobates* populations on the surface of the plateau were eliminated by the new environmental conditions, but were preserved in the barrancas along with the remnants of the earlier vegetation cover. Unfortunately, very little information is available concerning two points critical to this hypothesis. First, the vegetation of the barrancas *appears* to be what might have covered the whole region when the elevation was lower, but this cannot be demonstrated. One may assume, however, that the present climates of the barrancas are more like those that existed on that surface when it was less elevated. If this be so, one would expect the relicts of the vegetation that covered the lower surface to be restricted now to the barrancas. Second, nothing is known of the extent of the range of *cremnobates* in the barrancas, or whether it occurs beyond the barrancas in other areas. I have assumed that its distribution in the one barranca where it was studied is typical of its occurrence throughout its range. More information on these points would go far to verify or disprove the above hypothesis.

N. cremnobates is now separated from *sinaloae* by an area only 120 miles across and without continuous mountain barriers. This suggests the possibility that *cremnobates* could have been derived from *sinaloae* and could have arrived in Jalisco from the west. Morphological evidence rules out both this possibility and its converse. Neither species shares any of the characteristics of the other, with the possible exception of bicolored eyes (in which, however, the colors are somewhat different). Any relationship must therefore antedate the differentiation of the two forms. On the other hand, *cremnobates* shares with *victoriae* a few characteristics different from those of *sinaloae*. This indicates that *cremnobates* and *victoriae*, despite their present wide geographic separation, did not differentiate until after *sinaloae* was isolated, and that the former two species arose from a stock which occupied a region east of the Sierra Madre Occidental.

THE PULCHELLA GROUP.—At the same time that the ancestral *cremnobates* stock was following the retreating humid forests southward, another stock, which was to give rise to the Pulchella, Imperfecta and Victoriae groups followed the forests southeastward across the rising Northern and Central Plateaus. These stocks probably dispersed from the Chihuahua-Durango region. This would have been the driest warm region on the continent east of the Sierra Madre Occidental. Prior to the uplift of that mountain chain, the region was probably covered by thorn forest or thorn scrub, as suggested by the fossil floras farther north. True desert vegetation was apparently not yet in existence. Following the uplift of the Sierra Madre, arid conditions must have developed east of the mountains and eliminated the *Neobarrettia* populations in that area. As arid vegetation expanded in the interior, however, the humid forests to the south and southeast, which had previously acted as barriers to *Neobarrettia* dispersal, were replaced by thorn forest and this later by thorn scrub. Thus, as the ancestral *Neobarrettia* populations were being eliminated in their old center, they were able to expand into the newly developing semiarid habitats to the south and southeast.

Before the Central Plateau reached an elevation suitable for the development of grasslands, the *pulchella-victoriae-imperfecta* stock may have reached as far south as the latitude of México City. From this point, a colony was able to cross the band of tropical deciduous forest and to enter the arid tropical scrub of the basin of the Río Balsas, there to differentiate as *imperfecta*. The colony was isolated by the continued uplift of the Central Plateau and the Trans-Volcanic Belt. The vegetational changes which resulted from this uplift—scrub to grassland and, in the higher portions, later to oak and coniferous forests—eliminated all *Neobarrettia* populations south of San Luis Potosí. Early in the expansion of the *pulchella-victoriae-imperfecta* stock, colonies reached the coastal plain, there to be isolated by the rise of the Sierra Madre Oriental, and to develop into *victoriae*.

Prior to the uplift of the Sierra Madre Oriental, the southern part of the state of San Luis Potosí was probably covered by semiarid thorn forest rather than the present desert vegetation. Even now, where the Sierra Madre is broken or low, as betwen Valles and Ciudad del Maíz, thorn forest is able to develop on the east-facing slopes of the inland mountains. To the north, conditions were drier, and desert vegetation may have been well developed in Coahuila early in the Pliocene. Data have been presented already (see Part II) suggesting that the adaptation to desert conditions in *Neobarrettia* is a secondary and relatively recent development. The ancestral *pulchella* stock was thus probably adapted to conditions no more than semiarid, and must have been restricted to the less arid southern portion of

San Luis Potosí. The presence of *pulchella* colonies on the coastal plain and in the thorn forest east of the city of San Luis Potosí (Fig. 23) may represent instances of the retention of the ancestral "semiarid adaptation." The uplift of the Sierra Madre Oriental must have produced arid conditions in the interior and at the same time barred the retreat of the *Neobarrettia* populations to less arid environments on the coastal plain. The colonies trapped on the plateau either became adapted to their now desert environment or were eliminated. In consequence, it was only after the uplift of the Sierra Madre that ancestral *pulchella* was able to spread northward through the deserts of northern San Luis Potosí and western Nuevo León. Now, however, the western spur of the Sierra Madre barred further dispersal into the Coahuila deserts. This hypothesis explains why the Pulchella Group, the members of which are now well adapted to desert conditions, failed to spread into the Coahuila deserts which lie adjacent to the probable center of origin of the group in the Durango-Chihuahua region.

N. bambalio is almost certainly a development from a *pulchella*-like ancestor. The only distinctive morphological characteristics of *bambalio* (the small size of the median tooth of the male cercus, the absence of a tubercle on the 7th abdominal sternite of the female, and the absence of lateral pits and ridges on the female subgenital plate) could easily have resulted from reduction or loss of structures found both in *pulchella* and, with one exception, in the other species of the genus. *N. bambalio* most probably arose after desert conditions were established on the Plateau and after the "desert-adaptation" was attained, as described above. Unfortunately, the events involved in the differentiation of *bambalio* cannot be reconstructed from the evidence at hand. The presence of the coastal plain colony of *pulchella* suggests that the Sierra Madre may have fragmented the ancestral population, leading to the differentiation of *bambalio* on the Plateau and *pulchella* on the coastal plain. There are two objections to this hypothesis. The first involves the difficulty which *pulchella* would then have encountered in penetrating the mountains and establishing itself in the deserts of the Plateau. This invasion must have taken place some time ago in view of the wide distribution of *pulchella* on the Plateau, although the Sierra Madre must have been an even more formidable barrier in an earlier stage of the erosional cycle. More serious, *pulchella* would have had to enter an entirely new habitat to which it had no prior adaptation, in the face of occupancy by a well-adapted relative. The second objection centers on the origin of *victoriae*. This species probably differentiated in the southern part of its present range as a coastal plain isolate of the ancestral *pulchella-victoriae-imperfecta* stock (as discussed below under *victoriae*). But it is difficult to see how *pulchella* and *victoriae* could both have differentiated in the same part of the coastal plain at the same time. It seems much more reasonable to assume that the coastal plain population of *pulchella* represents a recent invasion *from* the Plateau. At least one colony of *pulchella* now occurs in the valley of the Río Guayelejo, halfway through the Sierra Madre toward the coastal plain. There is no reason why a similar route closer to the present coastal plain population could not have been used in the recent past. The absence of any major morphological differences between this population and those on the plateau points to the recent derivation of one from the other.

A better clue to the cause of differentiation of *bambalio* seems to lie in the barrier effect of old lake basins. *N. bambalio* and *pulchella* are now separated by a dry lake basin west of Ciudad del Maíz, and there is a conspicuous gap in the distribution of *bambalio* west of Núñez, corresponding to another dry lake basin (Fig. 23). Such basins must have constituted even more effective barriers during the Pleistocene pluvial periods when they were filled with water. An extensive lake could easily have fragmented a *Neobarrettia* population, and could have kept the colonies isolated for some length of time. Pleistocene isolation also accords well with the very slight differentiation between the two species. Suggestive as this clue may be, it does not indicate where the barrier might have been to produce the present distribution pattern. Further studies of the detailed distribution of both species in the southern portion of their ranges (south of the Ciudad del Maíz-San Luis Potosí highway) should help to clarify the problem.

THE IMPERFECTA GROUP.—The single species of this group is now isolated far to the south of its nearest relatives by a wide area of high plateaus and mountains. The habitat in which it occurs in the basin of the Río Balsas is typical of that of its relatives—thorn scrub and forest (here called arid tropical scrub) and the scrubby cut-over portions of the adjacent tropical deciduous forest. Not far to the east of the present range of *imperfecta* lie areas of apparently similar vegetation near Tehuacán and Acatlán in the state of Puebla. The absence of *Neobarrettia* from these areas suggests that the "semiarid-adapted" ancestor of the genus was not present here early in its history. Prior to the mid-Miocene, much of México was uniformly low, and the distribution of climates probably closely followed the theoretical distribution on a uniformly low continent, as discussed earlier. Before mountain building, the climate of the region south and east of the Colima-Brownsville axis was probably warm and wet, and occupied by humid tropical forests unsuitable as a habitat for "semiarid-adapted" listroscelines (Fig. 15). Thus, the ancestral *imperfecta* must have arrived in the Balsas region from the north only after the uplift of the mountains and plateaus caused the widespread development of dry environments in central and southern México.

N. imperfecta displays similarities to the Sinaloae and Pulchella Groups. If *imperfecta* were derived from the Sinaloae Group, it must have come from the northwest coast and either crossed the Central Plateau through suitable habitats such as those now occupied by *cremnobates*, or migrated along the coast through Colima where there are habitats apparently very similar to those occupied by *sinaloae* to the north. The absence of relict populations in either of these regions suggests that the range of ancestral *sinaloae* never extended that far to the south or east. Furthermore, for southward migration to have taken place, much drier conditions must have existed in the region of the present humid barriers in northern Nayarit, and in southern Nayarit and western Jalisco (Duellman, 1961:43). It is unlikely that such arid conditions existed in the past, if the climatic inferences based on other evidence are correct and may be extrapolated to this region. Thus, in southern California, greater rainfall during the Miocene and the Lower and Middle Pliocene is indicated by the fossil floras. During the Pleistocene, drier conditions would have been accompanied by lower temperatures in México (suggested by Martin and Harrell, 1957, see previous discussion), which would have favored the lowering of the oak zone rather than the expansion of thorn forest or thorn scrub. A critical appraisal of the similarities between *imperfecta* and the Sinaloae Group indicates that most of them may be interpreted as consequences of a parallel reduction in tegminal length in the two stocks. This is further discussed in the taxonomic treatment of *imperfecta*.

On the other hand, *imperfecta* shares a number of detailed, as well as general similarities with the Pulchella Group. Even one of the characteristics which differentiate *imperfecta* from the members of that group appears to be the culmination of a trend manifested within the group (see discussion under *imperfecta*). The morphological evidence argues strongly for a relationship of *imperfecta* to the Pulchella Group rather than to the Sinaloae Group. An attempt to derive *imperfecta* from an ancestor of the Pulchella Group, however, must resolve a curious temporal paradox. The morphology of *imperfecta, pulchella* (and *bambalio*), and *victoriae* indicates a common ancestry. If *imperfecta* was isolated from the ancestral population before the differentiation of *pulchella* and *victoriae*, then it should not possess the presumably derivative characters which it shares with *pulchella* but not with *victoriae*. These characters must have developed after the separation of *victoriae*. On the other hand, if *imperfecta* was isolated from the ancestral stock *after* the differentiation of *victoriae*, then the presumably derivative characters shared by *victoriae* and *pulchella* should also be present in *imperfecta,* but they are not. These characters must have developed before the separation of *victoriae* and *pulchella,* and therefore also before the separation of *imperfecta* (see listing of characters in Table 6). Various of the similarities may be explained as parallelisms, and the dissimilarities by subsequent modifications, but these explanations are merely *possible* alternatives and are not directly supported by independent evidence. The paradox may be resolved if it is assumed that particular characters arose in different parts of the range of the common ancestor of the three species and spread slowly across the elongate range suggested for this population prior to the isolation of *imperfecta.* This type of assumption is almost an axiom in evolutionary thought. On this basis, the characteristics which are shared only by *pulchella* and *victoriae* may have arisen in the north and spread early to the coastal plain colonies (or the reverse) before the uplift of the Sierra Madre isolated ancestral *victoriae.* But these characters did not reach the southernmost colonies until *imperfecta* was isolated. Conversely, the characteristics which are shared only by *pulchella* and *imperfecta* may have arisen in the south before the isolation of *imperfecta* and not have reached the northern colonies until after the isolation of *victoriae.*

This hypothesis may also explain why the pronotal margins are black in *imperfecta* but green in both the Pulchella and Victoriae Groups—a major difficulty in deriving *imperfecta* from the Pulchella Group. A black margin is probably a primitive character, as suggested by its presence in the primitive *vannifera* and in several other widely-separated species (*sinaloae, cremnobates,* and *spinosa*). A green margin may be merely the result of loss of the original black pigment. The ancestral form which gave rise to *pulchella, victoriae,* and *imperfecta* may have possessed originally black pronotal margins. Following this hypothesis, the black pigment was probably lost early in the northern colonies, but the modification did not spread southward in time to have affected *imperfecta* before that species was isolated.

The ancestral *pulchella* stock which I believe gave rise to *imperfecta* could easily have extended as far south as the latitude of México City in the late Miocene or early Pliocene, under the climatic and vegetational circumstances attending the slow uplift of the Central Plateau. No unusual climatic conditions would have been required. Much of the Central Plateau is now covered with grasslands or scrub savanna. At lower elevations, the vegetation cover would have been thorn scrub, or, at still lower elevations, thorn forest, either of which would have provided an easy path for *Neobarrettia* migration. South of México City, however, the same band of tropical deciduous forest which is now found below the oak zone has probably been in existence since the elimination of the more humid lowland tropical forests there. On climatological grounds there is no reason to believe that a semiarid corridor ever existed across this forest zone. The absence in the Balsas basin of all but a few of the "arid-adapted" grasshoppers characteristic of the northern deserts would suggest that the access route taken by *imperfecta* must have existed only a short time and was probably discontinuous. The distance between México City and the present northern limits of the range of *imperfecta* is less than 70 miles, and not all of the intervening region may have been covered with deciduous forest. Ancestral *imperfecta* may have crossed it by taking advantage of isolated patches of scrub, the existence of which depends upon local edaphic and climatic conditions. The species is found in patches of scrub within this zone today (as for example, at Taxco), and could as easily have existed in such areas in the past.

The reasons for the absence of *imperfecta* from the arid or semiarid regions that lie east of its present range can only be surmised. It may be that its rate of spread is slow, and that there has not been enough time for it to reach the limits of the available territory. This could have happened if the now dry regions to the east remained humid until the uplift of the mountains and volcanoes to the east completed the rain shadow in eastern Puebla, or if *imperfecta* entered the Balsas basin so far to the west that it has taken a long time to reach its present eastern limits. Or it may be that eastward spread was blocked until relatively recently by the existence of a topographic barrier that has since been eroded away by the Balsas and its tributaries. In view of the postulated time of origin of *imperfecta,* and the probability that these active insects are capable of fairly rapid spread, none of these explanations appears adequate.

THE VICTORIAE GROUP.—The morphology of *victoriae,* the sole member of this group, indicates a common ancestry with the Pulchella Group. The two groups share several characters which occur only sporadically or are poorly developed elsewhere, in addition to other features more commonly found in the genus. The stock which gave rise to the Victoriae and Pulchella Groups was probably widely distributed in San Luis Potosí and southern Tamaulipas after the elimination of the humid forests in that region (see discussion under the Pulchella Group). The uplift of the Sierra Madre Oriental fragmented the stock; the segment isolated on the coastal plain subsequently differentiated as *victoriae.*

I have postulated below that the ancestral *victoriae* was originally isolated in what is now the southern portion of the range of the modern species. There is little reason to believe that this region has changed very much since the time when the isolation was accomplished, presumably in the Pliocene. The climate might have been somewhat wetter, but was probably never much drier. Even if drier conditions did occur, a *Neobarrettia* population could have ascended the adjacent mountains to maintain itself in a suitable habitat. In contrast, the interior region occupied by *pulchella* and *bambalio,* the closest relatives of *victoriae,* has altered drastically since the Pliocene uplift of the Sierra Madre Oriental. For those species there was no possibility of a retreat to regions in which the old habitat remained unaltered. This difference in the history of the environment of the two groups perhaps partly accounts for the fact that *victoriae* has retained the presumably primitive condition of several characters (color of the tegmen and details of the male cercus and female subgenital plate) which became modified in the Pulchella Group.

Both the geographic variation and the distribution pattern of *victoriae* (Fig. 10) suggest that the species originated in the southernmost part of its present range, the southern Tamaulipas-eastern San Luis Potosí region. The morphological evidence is seen in the four characters which display the most marked geographic variation in the species: the relative length of the tegmen, the narrowness and elongation of the pronotum, the color of the metanotum, and the spotting of the wing. In each of these, the condition which most resembles that typical of the Pulchella Group occurs in this region. Narrow and elongate pronota and unspotted wings, characteristics which are unique in the genus and probably derivative, are found outside this region, while the primitive condition, almost like that in the Pulchella Group, occurs here.

It is possible that early in its history the species spread over much of its present range and was generally similar morphologically to the present southernmost populations. The features now characterizing the northern populations may have arisen somewhere north of Ciudad Victoria and have replaced the primitive features everywhere but in the south. If this were the case one would expect to find considerable variability in the northern characteristics as well as pockets of relicts similar to the southern populations. Since neither is found, this explanation is unlikely. A second possibility is that the characteristics of the southern populations result from introgression from *pulchella.* In view of the limited geographic extent of these characteristics the introgression should be of recent occurrence and the most likely source would be the coastal plain colony of *pulchella.* But not only does this small colony, which has been in existence for at least 20 years, show no sign of *victoriae* influence, but even the *victoriae* colony in which a *pulchella* individual was found shows no greater similarity to that species than do the other southern *victoriae* colonies. The most reasonable explanation of this pattern of variability is that the southern region was the original home and as the species spread northward into drier environments the new northern characteristics developed, while the primitive features were preserved in the original, unchanged habitat in the south.

The distribution pattern of *victoriae* (Fig. 10) suggests that it has only recently occupied the greater part of its present range—all that north of Monterrey, an area which lies north of the northernmost limits of its closest relative, *pulchella*. The Sierra Madre Oriental forms the western limit of the range of *victoriae* in México. South of Monterrey these mountains are almost continuous and form a complete barrier to *victoriae*. North of that city, the Sierra Madre becomes broken and would not appear to constitute a major barrier. Nevertheless, *victoriae* extends only a short distance through the several gaps. West of Monterrey and east of Cuatro Ciénegas, the species is found within passes leading to the desert; south of Castaños, it occurs just beyond a pass and in the desert itself. It is interesting to note that in each of these three cases, the westernmost (or southwesternmost) colony of *victoriae* occurs within, or very close to, the narrow zone of intergradation between the desert and coastal plain forms of *spinosa*. This suggests that the same barriers which have kept the two forms of *spinosa* separated until recently (as the abruptness of their intergradation indicates) have also prevented *victoriae* from passing through the gaps until recently. In the succeeding discussion of the Spinosa Group reasons are given for believing that the gaps in the Sierra Madre are relatively recent developments, and that even after their development they may have been covered for a time with oak woodland or grassland which would have blocked the passage of either species through them. Thus, in México, a topographic or vegetational barrier has probably prevented *victoriae* from invading the Coahuila deserts.

The same explanation cannot be used to account for the failure of *victoriae* to enter Coahuila through the eastern portion of the Big Bend region of Texas. Here the continuous ridges of the Sierra Madre end just north of the border. The other mountains in the area are topographically and geologically isolated and the broad gaps between them have probably always afforded easy passage into Coahuila. Nor is it likely that this region was once covered with grassland, as apparently was western Texas (see discussion under *spinosa*). The general elevation of the eastern part of the Big Bend region is lower than that farther west. The highland areas seem to be mostly outwash from the mountains and are likely to have been lower at an earlier stage in the erosion cycle. There are few grassland areas in the region today, and those few are restricted to the base of the mountains and to the higher basins. If grasslands did cover the region in the Pleistocene or more recently, then they also should have blanketed the deserts to the south, which lie at nearly the same elevation and have a similar climate. It is hardly likely for the rich and distinctive desert biota in this region to have developed after the elimination of the grasslands in post-Pleistocene times. It seems much more likely that a desert or thorn scrub corridor has long existed between the coastal plain and the interior deserts through the Big Bend region.

Nor does it seem likely that *victoriae* has been barred from the Coahuila deserts because it is ill-adapted to arid environments. Although in México the western limits of the species coincide with the boundary between thorn scrub and desert, as drawn by Muller (1947), the westernmost colonies in Texas lie well within the area mapped by Muller as desert. Furthermore, this species has a broad distribution in western Texas, extending from near Penwell, New Mexico, to Marathon, Texas. Not all the vegetation of this area is like that characteristic of the Coahuila deserts, but it is all dry and scrubby.

If, as it appears, no obstacle exists now, or for a long time has existed, to the passage of *victoriae* through the Big Bend region into the Coahuila deserts, why has it not done so? The only explanation appears to be that it has only recently arrived in the Big Bend region and has not yet had time to spread farther southwest. This interpretation of the distribution pattern agrees with the entirely independent conclusion drawn from the geographic pattern of morphological variation in the species. It follows that *victoriae* must have been isolated until relatively recent times somewhere in the southern portion of its range.

A very likely barrier to northward movement in this region is found in the Sierra de Tamaulipas, located southeast of Ciudad Victoria. This mountain mass extends almost across the entire width of the coastal plain and lies directly north of the colonies in which the most primitive characters in the species are found (Fig. 10). Although there is a gap between the Sierra de Tamaulipas and the Sierra Madre Oriental, the broken ground between them is much higher than the general level of the coastal plain, and was doubtless considerably higher and more continuous in the recent past. At least part of the southern face of this highland now supports a heavy thorn forest in which *vannifera* is found, but not *victoriae*. In addition, part of the southern foot of the mountain mass is now covered by savanna (Martin, 1958*a*), another barrier formation which may have been much more extensive prior to the advent of domestic animals and overgrazing.

Once past this barrier, *victoriae* probably spread rapidly to the north and northwest in the absence of further topographic barriers. In east-central Texas its progress was impeded by the Coastal and Fayette prairies, and by

Oak-Hickory and Oak-Juniper woodlands, which have prevented it from extending much farther north than the latitude of San Antonio (Fig. 13). The path of its migration into central and north-central Texas lay farther west, through the brush and mesquite country northeast of Del Rio. From this region it has been able to extend far to the east, but only in the mesquite country just north and west of the zone of Oak-Juniper woodland covering the southern and eastern edges of the Edwards Plateau, or in valleys within the Oak-Juniper zone which are filled with mesquite and have broad connections with the mesquite country to the west (the case of the two records near Llano, in Figure 13). If *victoriae* had arrived in north-central Texas earlier than was suggested in the above discussion, it may not then have been able to establish itself in the region of the present Mesquite Savanna in Texas, or farther north in Oklahoma and Kansas. What is now the Mesquite Savanna was probably grassland until recent erosion and overgrazing resulted in a great expansion of the bush habitat. Since the streams and rivers in this region all flow eastward or southeastward, a *Neobarrettia* would not have been able to spread northward and take advantage of the bush habitats in the stream valleys until overgrazing permitted an extensive invasion of bushes onto the divides between the streams. The species has probably already reached the limits of suitable habitat under the present vegetational conditions of the Great Plains.

THE SPINOSA GROUP.—The two species comprising this group, *vannifera* and *spinosa*, stand apart from all other species of *Neobarrettia* in respect to three characters, the condition of which in these two species is demonstrably, or at least possibly, more primitive than the conditions shown by the other species. These characters are: (1) the well-developed cross veins of the wing, certainly primitive; (2) the light and transparent wing colors, probably primitive; and (3) the black femoral teeth, possibly primitive. All other species have weak cross veins (or apparently none in *imperfecta*), bright opaque wing colors, and bicolored teeth—the condition of the first character certainly, of the second probably, and of the third possibly derived.

On these morphologic grounds and for other reasons to be discussed, the Spinosa Group is believed to be the oldest one of the assemblage. Probably because it is the oldest, clues to its past history are few and obscure. Nevertheless, we may deduce the minimum age of its separation from the stock that produced the remaining species by extrapolating from the demonstrable age of the latter. That stock, which gave rise to the remaining groups of *Neobarrettia*, and which must have possessed the alternative condition of the characters which set off the Spinosa Group, was apparently already in existence in the mid-Miocene. The evidence for this lies in the probability, already discussed, that one of the species of that stock, *sinaloae,* arose as the result of isolation that occurred at that time. Since *vannifera* and *spinosa* do not show the derivative condition of the three abovementioned characters found in *sinaloae* and all other species, it follows that the separation of the two main lines of development—the Spinosa stock and the other—must have antedated the isolation of *sinaloae,* and have occurred in Oligocene or early Miocene times.

Regardless of the validity of the above reasoning, the origin of the Spinosa Group certainly antedates the Pliocene elevation of the Sierra Madre Oriental, which played a part in the infraspecific differentiation of one of its two species. Judging from the modern distribution of *vannifera* and *spinosa,* the ancestral stock may have been initially isolated to the east or northeast of the deserts which were developing during the Miocene in the northwestern interior of México. The populations which became *vannifera,* the more primitive of the two, probably withdrew coastward with the retreating thorn forests, and became restricted to the eastern face of the Sierra Madre Oriental when the Pliocene uplift of that range converted the northeastern part of the region behind it into desert. Southward ancestral *vannifera* must have reached its limit at the edge of the humid lowland forest; today it barely penetrates the northern edge of the tropical deciduous forest near Llera, Tamaulipas. On the north and east it doubtless extended to the edge of the thorn scrub (another formation into which the species barely penetrates today), and its range must have been restricted by the southward spread of that environment. At higher elevations it was the margin of the dry pine-oak woodland that formed the limiting barrier. Not far to the north of the present range of *vannifera* coastal plain thorn scrub merges into pine-oak woodland without an interposed zone of thorn forest, and here, as would be expected, the species is absent. Thus, the present geographical and ecological distribution of the species is exactly what would be expected of a primitive *Neobarrettia* originally adapted to thorn forest, whose ecological requirements have remained unaltered while the thorn forest environment has dwindled in size as the thorn scrub and desert environments grew.

The other member of the group, *spinosa,* represents a stock which early acquired an adaptation to the drier environments—thorn scrub and eventually desert. This may have happened as was suggested for ***hakippah***—isolation in a pocket of thorn forest that was surrounded and eventually eliminated by thorn scrub. Just where and when this is likely to have happened cannot be postulated with assurance. The fact that *spinosa* does not occur in thorn forest (or even in denser stands of thorn scrub) suggests that the same events that resulted in the adaptive changes also isolated the ancestral *spinosa* stock from all contact with the *vannifera* populations, and that this isolation has been of long duration. For reasons which will appear, it seems likely to have occurred before the Pliocene uplift of the Sierra Madre Oriental, at a time when thorn scrub occupied a wide expanse both on the northern coastal plain and in the interior. Once the "thorn scrub adaptation" had been attained, the *spinosa* stock would have spread to the limits of this formation, regardless of just where it originated.

The next stage in the evolution of the *spinosa* stock was the acquisition of the more extreme "desert adaptation" characteristic of the present populations occupying the region west of the northern spur of the Sierra Madre Oriental. This probably occurred subsequent to the Pliocene orogeny that produced the range (including its northern and western spurs) and increased the aridity in its lee. If the adaptation had occurred earlier, *spinosa* should now be found south of the western spur of the Sierra Madre (south of Saltillo and Torreón). It seems likely that there was a repetition of the process assumed to have brought about the earlier "thorn-scrub adaptation" —the gradual elimination of pockets of thorn scrub west of the rising mountains by the encroachment of the desert environment, and the adaptive modification of one or more of the isolated *spinosa* populations trapped in them. Once the "desert adaptation" had been achieved, *spinosa* was able to spread widely in the interior, but was prevented from penetrating southward into the San Luis Potosí deserts by the presence of the western spur of the Sierra Madre which was uplifted at the same time as was the northern spur which was responsible for the "desert adaptation." *N. spinosa* is just now apparently in the process of penetrating the gaps in this western spur southeast of Torreón.

In the relatively recent past, the western spur probably formed a strong barrier to the southward migration of desert animals, despite its present-day broken aspect. The topography and surface geology of the region suggest that the range was once continuous and joined the Durango highlands to the west. Most, if not all, the gaps have been produced by stream erosion, much of which was doubtless accomplished during the pluvial periods of the Pleistocene and in post-Pleistocene time. Earlier in the erosion cycle the gaps must have been considerably higher, and therefore might have been covered with grassland or oak woodland, either of which acts as a barrier to *spinosa*. The higher rainfall during pluvial periods would have allowed the growth of oaks and grass at much lower elevations than at present, and even during the drier Pleistocene periods the gaps may have been covered with oak forest or grassland if, as Martin and Harrell (1957) have suggested, these periods were characterized by colder conditions than now exist at this latitude.

Evidence from various sources supports the view that the western spur of the Sierra Madre did, in fact, constitute a continuous barrier separating the northern from the southern deserts. The presence of elephant and grass remains in Pleistocene deposits near Parrás, discussed by Martin (1958*a*), indicates the existence of conditions moist enough to support savannas and marshes in a region now very dry desert. That author also points to biogeographic evidence suggesting that a continuous woodland corridor must at some recent time have connected the Sierra Madre Oriental and Occidental. Woodland animals cannot now pass between the two ranges, yet there are numerous instances in which the same or closely related subspecies or species occur in both. Many of these distribution patterns cannot be explained as the result of spread across the continuous woodland route afforded by the mountains of the Trans-Volcanic Belt because of the presence there of related forms, or the complete absence of the species-group in question. The best explanation of the occurrence of such forms in the eastern and western Sierra Madre is that dispersal occurred by way of a woodland corridor along the western spur of the Sierra Madre Oriental at a time when that spur was higher, less interrupted, and better watered than it is now. That time must have been recent, considering the small amount of differentiation that has occurred between the isolated eastern and western populations. The existence of such a corridor would have barred *spinosa* from the deserts south of the mountains, and the gaps in it must have developed very recently, since *spinosa* seems to be only now spreading through them.

The northern spur of the Sierra Madre Oriental has probably played a similar role as a barrier to *spinosa*. Here, however, populations of *spinosa* were probably isolated on both sides of the barrier, as discussed above. This mountain range earlier in its history may have been continuous to the Texas border. It does not extend far across the border, however, and most of the mountains in the Big Bend region of Texas are both topographically and geologically isolated from one another, and are probably younger than the Sierra Madre. Contact therefore was probably maintained in this region between *spinosa* populations which farther south were completely isolated. This situation permitted the southern populations on either side of the Sierra Madre to become strongly differentiated, and accounts for the very discordant clinal variation of the populations occurring in Texas.

South of the Texas border, isolation of the coastal plain and interior populations is nearly complete, but contacts occur in a few places. Between Monterrey and Saltillo the two have met in a canyon and have intergraded over a very narrow zone, suggesting that the encounter has been quite recent. The canyon sides are at least partially covered with oaks, and one attenuated finger of oak woodland reaches the canyon floor. Not very long ago the canyon may have been less deep, and its floor may have been covered with oak woodland. Since in this part of its range *spinosa* does not occur in oak forest, so far as can be determined, this would have kept the two populations apart. This conclusion is not invalidated by the fact that in Texas *spinosa* does sometimes occur in oak woodland. Even there, woodland is not an optimum environment, as is shown by the fact that colonies found in that habitat are much smaller and more localized than those in adjacent bushland. Furthermore, the Texas oak woodlands in which the species has been found may be secondary, and thus not strictly comparable with those near Saltillo.

Farther north in México another area of contact has been studied in the Castaños region. North of that town the coastal plain form of *spinosa* has made a deep penetration into the Monclova basin, through the low and very broken mountains that bound it to the northeast. South of Castaños, however, where a much higher ridge forms the south end of the basin, there is a rather abrupt change from the coastal plain to the desert form. The gap north of Monclova appears to be geologically much older than that south of Castaños.

The populations occurring west of Saltillo and east of Monterrey are quite uniform and distinctly different from one another (Figs. 3 to 6). Intergradation, as indicated above, takes place over short distances, usually in less than twenty miles. In Texas, on the other hand, populations of *spinosa* show various mixtures of the characteristics of the coastal plain and desert forms over a wide area in the central part of the state. Most of the characters vary clinally, but the geographical position of the steps in the clines differs widely in the clines of different characters. This situation suggests that the desert and coastal plain forms have been in broad contact with one another in this region for a long time—a suggestion supported by the general lack of topographic barriers north of the Sierra Madre Oriental.

N. spinosa has not been found west of the Guadalupe Mountains in Texas, although large areas apparently suitable for the species exist in westernmost Texas, southern New Mexico, and western Chihuahua. The reasons for this are not obvious since elsewhere the species has been found farther north, at higher elevations, and under drier conditions. It is here suggested that the reason for its absence from those regions may be found in the former distribution of grasslands.

The evidence that grasslands constitute a barrier to *spinosa* is meager but apparently reliable. In Chihuahua, the species is entirely absent from the grassland areas between Ciudad Juárez and Jiménez, but is abundant in the rich bushland around Jiménez. *N. spinosa* again is absent from the highland region southwest of Jiménez, most of which is covered with savanna-type vegetation. In New Mexico, *spinosa* occurs in the scrub vegetation of the Pecos Valley east of Roswell, but is apparently wholly absent from the extensive grasslands to the east and west. To these observations must be added the fact that none of the other species of *Neobarrettia* has been found in grassland formations, with the exception of mesquite savanna, which is more bushland than grassland.

Various lines of evidence point to a former more widespread occurrence of grassland. All of western Texas and most of southern New Mexico are extensions of the Northern Plateau of México, uplifted in mid-Miocene. The mountains of this region, for which the time of uplift can be determined, are relatively recent, probably no older than late Pliocene. The major agents of erosion here—the Rio Grande, the Río Conchos, and the Pecos River—are demonstrably no older than latest Pliocene (King, 1935, 1948; Ruhe, 1960). The absence of the rivers during Pliocene times may be taken as indicating that the mountains which are the present sources of the streams were either absent or of low elevation during that epoch (King, 1935). Thus, it appears that prior to the orogeny and consequent stream erosion of the late Pliocene and Pleistocene the entire region was probably a rolling plateau, topographically well suited for the development of grasslands.

Grassland floras were well developed in the Great Plains region during the Pliocene, if not somewhat earlier. They were therefore available for expansion onto the more southern plains when climatic conditions permitted. Greater rainfall in the Pliocene and in Pleistocene pluvial periods probably allowed grasslands to cover much of southeastern New Mexico, western Texas and western Chihuahua except for the mountains, when these arose. Dry, cold periods, the conditions suggested by Martin and Harrel (1957) for glacial periods in slightly lower latitudes, would also have favored the occurrence of grasslands rather than thorn scrub in these areas. It would appear, then, that in the past, grasslands would have been more extensive and more continuous in this region than they are today.

Large areas of the Southwest are still covered by some form of grassland, generally the "desert grassland" of Humphrey (1958)—much of the plains of southern New Mexico, the Marathon region and Marfa Plains of Texas, and most of the highlands of Chihuahua east of the Sierra Madre Occidental. These are probably relicts of much more extensive areas of more pure and richer grasslands, as indicated by the reports of the early explorers of the American Southwest (carefully analyzed in relation to this problem by Gardner, 1951, and Humphrey, 1958). The successional features of the extensive invasion of the grasslands by desert shrubs in Chihuahua are discussed by LeSueur (1945). Overgrazing and the control of grassland fires have probably been the major factors in the reduction of the grasslands in historic times according to these authors. Stream erosion has been at work for a longer time (though intensified more recently by overgrazing), cutting into grassland plains and providing eroded surfaces suitable for the development of bushland. Uplift of the mountains created more streams to erode the surrounding grasslands, while the mountain slopes themselves provided suitable environments for bushland.

All of these factors have come into operation quite recently—uplift of the mountains in the late Pliocene, formation of the Rio Grande and its tributaries in the early or middle Pleistocene, and control of fires, overgrazing, and rapid gullying in historic times. Thus, habitats suitable for *spinosa* have been expanding westward only since the beginning of the Pleistocene, and large areas in western Texas, southern New Mexico, and western Chihuahua may have become available only in historic times. The species is probably a recent arrival in this region of former grasslands, and its absence farther west may be owing only to the slowness of its spread.

The northern parts of its range also may have been occupied by *spinosa* only recently. The Mesquite Savanna, in which the northernmost colonies of the species now occur, was probably pure grassland during the Pleistocene, and perhaps even more recently. There is a strong possibility that overgrazing in the last century has permitted so great an increase of mesquite on these plains as to have turned what was formerly a barrier into a favored habitat for the species.

No such problems surround the question of the eastern limits of *spinosa*. These limits are set by the Oak-Hickory woodlands and the blackland prairies, into neither of which does the species penetrate, although it may be found on their very edges. These plant formations, or more humid environments, either have occupied their present positions or were located farther west ever since Oligocene times. They have probably always limited the eastward spread of *Neobarrettia*.

SUMMARY

The genus *Neobarrettia* (including the species of *Rehnia* here synonymized) is a member of the subfamily Listroscelinae in which it has no close relatives. It is considerably less modified in typically listrosceline characters which are presumably associated with carnivorous habits, and is similar in

certain respects to the Decticinae and Saginae. *Neobarrettia* may thus represent a very primitive listrosceline which was derived shortly after that subfamily diverged from the other two.

Rehnia is synonymized under *Neobarrettia* because the species of the two lack any distinctive biological differences, and because of the special derivational relationship between the single species of the latter genus with one of the advanced species groups previously included in the former, a relationship which would be, and has been, obscured by generic separation. Four species are described as new, the remaining five are redescribed, and the distribution, habitat, seasonal occurrence and song of each is recorded. The species range from Chilpancingo in México to southern Kansas, and from the northwestern to the northeastern coastal plain of México, but are absent from the intervening mountains and from the highest parts of the plateaus.

Detailed studies of the distribution of each species at the edge of its range indicate that oak woodland, grassland, and humid tropical forest generally act as barriers to their dispersal. The preferred habitat is thorn scrub-thorn forest, while adaptation to the desert environment is probably a secondary and recent development.

Evidence from the habitat requirements of *Neobarrettia* and other listrosceline genera, and consideration of the probable changes in the vegetation of North America during the Cenozoic Era, suggest that the ancestral stock of *Neobarrettia* has been isolated from its Asiatic relatives since the Eocene Epoch, and from its South American relatives possibly since that time, but certainly since the middle of the Miocene. Morphological evidence suggests that this ancestral stock was in existence as an entity separate from the ancestor of the other Listroscelinae since the Oligocene. It is likely that the *Neobarrettia* adaptation to semiarid environments, unique in the subfamily, was developed in the Oligocene or Miocene. The geographic origin of the *Neobarrettia* stock is as yet unclear, and until more precise data are available it is best to consider the genus a North American autochthone.

The evolutionary history of the species of *Neobarrettia* is summarized in Figures 15 and 16. Indicated therein are the geological events and the inferred vegetational changes which accompanied them, and which are considered to have caused the isolation of the several species and species groups. The Sinaloae Group was isolated on the northwest coast of México by the uplift of the Sierra Madre Occidental in the mid-Miocene. *N. hakippah* arose from a *sinaloae*-like ancestor at a later time, possibly as a result of entrapment in a pocket of thorn forest which was eventually eliminated by surrounding desert or subdesert conditions. It is now invading the range of *sinaloae* and possibly eliminating it through direct competition. The two forms are hybridizing to a limited extent. The very small amount of backcrossing suggests that the two forms are in the final stages of the achievement of reproductive isolation. Ancestral *cremnobates* migrated southward from the ancestral home of the genus, in the Chihuahua-Durango region, as the uplift of the Sierra Madre Occidental and the Northern and Central Plateaus caused the expansion of dry environments in the northern interior of México. *N. cremnobates* was isolated in Jalisco by the continued uplift of the Central Plateau and was restricted to the barrancas of the Río Grande de Santiago by later uplift in Jalisco, possibly in the mid-Pleistocene. The *pulchella-victoriae-imperfecta* stock migrated southeastward from the ancestral generic home and possibly reached as far south as the latitude of México City. From that point a colony reached the basin of the Río Balsas where it was isolated by continued uplift of the Trans-Volcanic Belt and developed into *imperfecta.* The populations of the *pulchella-victoriae* stock were restricted northward by the continued uplift of the Central Plateau. The Pliocene uplift of the Sierra Madre Oriental isolated the populations on the Plateau from those on the coastal plain. This uplift created rain-shadow deserts in the lee of the range and caused the *pulchella* stock to become adapted to arid conditions, enabling *pulchella* to spread as far north as the western spur of the Sierra Madre. *N. bambalio* arose from a *pulchella*-like ancestor, possibly as a result of isolation by a pluvial lake in the Pleistocene. The ancestral home of *victoriae,* isolated on the coastal plain by the uplift of the Sierra Madre, was probably in the southern part of its present range, south of the Sierra de Tamaulipas. *N. victoriae* has only recently occupied the greater part of its present range, and has not yet had time to invade the deserts in Coahuila. The origin of the Spinosa Group antedates the mid-Miocene uplift of the Sierra Madre Occidental. It probably dispersed eastward as a result of the increasing aridity in its ancestral home in the Chihuahua-Durango region. *N. vannifera,* a member of this group and the most primitive species in the genus, was probably restricted to the east face of the Sierra Madre Oriental when the uplift of that range created inhospitable rain-shadow deserts in the interior. It now occupies a habitat almost exactly like that predicted for the ancestral *Neobarrettia. N. spinosa* probably acquired adaptation to semi-arid conditions at the same time that it was isolated from ancestral *vannifera.* Its adaptation to desert conditions was developed after the uplift of the Sierra Madre since it is now absent south of the western spur of that range. Until recently the northern spur of the Sierra Madre completely isolated the Mexican populations of this species that occur on the Northern Plateau from those that live on the coastal plain, and allowed strong differences to develop in the very different habitats in which these two forms are found. Despite evidence of recent contact between them in México, it is considered neither useful nor biologically meaningful to designate the two forms as subspecies in view of the discordant pattern of variation of the species in much of Texas.

The following conclusions may be drawn from the evidence from the biology and distribution of the species of *Neobarrettia* regarding specific environmental conditions in México and the southwestern United States in times past, within the framework of the general physiographic and vegetational conditions indicated by the geological record. (1) Since the uplift of the Sierra Madre Occidental to heights suitable for the development of grassland, woodland, or forest, there has been a continuous belt of grassland or woodland across the low region between that range and the Colorado Plateau to the north. (2) A humid formation (either tropical savanna or forest) has existed in coastal Nayarit (and possibly in Colima and Jalisco as well) since the uplift of the Sierra Madre Occidental. (3) Desert environment developed in the northern lee of the Sierra Madre Occidental shortly after its uplift, but the desert was of small extent until after the uplift of the Sierra Madre Oriental. (4) The western spur of the Sierra Madre Oriental until recently formed a continuous range between the main masses of the Sierra Madre Oriental and Occidental, and was covered with grassland, woodland, or forest. (5) The northern spur of the Sierra Madre Oriental was similarly more continuous in the recent past, and also covered then with grassland, woodland, or forest. Its uplift created desert conditions in its lee. (6) The bushland of much of western Texas and New Mexico, exclusive of the desert in the river bottoms, is of very recent origin (possibly since the Pleistocene) and has probably replaced what was originally grassland there. (7) The Sierra de Tamaulipas once formed a continuous barrier across the coastal plain, the lowest points being covered with grassland or humid tropical forest. The region immediately to the south was relatively dry and covered with thorn scrub or thorn forest at least since the time of uplift of the Sierra Madre Oriental. (8) The Central Plateau and northern portions of the Trans-Volcanic Belt were covered with thorn scrub-thorn forest at an intermediate stage in their uplift.

LITERATURE CITED

AXELROD, DANIEL I.

1950 Studies in Late Tertiary paleobotany. Carnegie Inst. Washington, Publ. 590:1–323, Pls. 1–19, Figs. 1–4.

1956 Mio-Pliocene floras from west-central Nevada. Univ. Calif. Publs. in Geol. Sci., 33:1–322, Pls. 1–32, Figs. 1–18.

1957 Late Tertiary floras and the Sierra Nevadan uplift. Bull. Geol. Soc. Amer., 68:19–45, Pl. 1, Figs. 1–7.

1958 Evolution of the Madro-Tertiary geoflora. Bot. Rev., 24:433–509, Figs. 1–10.

AXELROD, DANIEL I., AND WILLIAM S. TING

1960 Late Pliocene floras east of the Sierra Nevada. Univ. Calif. Publs. in Geol. Sci., 39:1–118, Pls. 1–24, Figs. 1–10.

1961 Early Pleistocene floras from the Chagoopa surface, southern Sierra Nevada. *Ibid.* 39:119–94, Pls. 25–37, Figs. 1–7.

BERRY, EDWARD W.

1923 Miocene plants from southern Mexico. Proc. U. S. Natl. Mus., 62:1–27, Pls. 1–7, Fig. 1.

1937 Tertiary floras of eastern North America. Bot. Rev., 3:31–46.

BRAUN, E. LUCY

1947 Development of the deciduous forests of eastern North America. (In a symposium on Origin and development of natural floristic areas with special reference to North America.) Ecol. Monog., 17:211–19.

BRUNER, LAWRENCE

1900–1909 Biologia Centrali–Americana. Insecta. Orthoptera. Vol. II. The Acrididae. London: Taylor & Francis, 412 pp., 8 pls.

CARTER, W. T.

1931 The soils of Texas. Tex. Agric. Exp. Sta. Bull., No. 431:1–189, Figs. 1–90.

CAUDELL, ANDREW NELSON

1907 The Decticinae (a group of Orthoptera) of North America. Proc. U. S. Natl. Mus., 32:285–410, Figs. 1–94.

CHANEY, RALPH W.

1940 Tertiary forests and continental history. Bull. Geol. Soc. Amer., 51:469–88, Pls. 1–2, Figs. 1–3.

1947 Tertiary centers and migration routes. Ecol. Monog., 17:140–48.

CHANEY, RALPH W., AND MAXIM K. ELIAS

1936 Late Tertiary floras from the High Plains. Carnegie Inst. Washington, Publ. No. 476:1–72, Pls. 1–7, Figs. 1–10.

CLEMENTS, THOMAS

1963 Pleistocene history of Lake Chapala, Jalisco, Mexico. In: Clements, T. (ed.). Essays in Marine Geology in Honor of K. O. Emery. Los Angeles: Univ. So. Calif. Press, Pp. 35–49, Figs 1–5.

COHN, THEODORE J.

1957 The relationships of the North American genera *Rehnia* Caudell and *Neobarrettia* Rehn (Orthoptera, Tettigoniidae). Occ. Papers Mus. Zool. Univ. Mich., No. 588:1–16.

CONTRERAS ARIAS, ALFONSO
1942 Mapa de las provincias climatológicas de la República Mexicana. Instituto Geográfico, Dirección de Geografía, Meteorología e Hidrología, Secretaría de Agricultura y Fomento: X–XXVII, 1–54, 2 maps.

COOK, HAROLD J.
1961 New concepts of Late Tertiary major crustal deformation in the Rocky Mountain region of North America. Rept. 21st Session, Internatl. Geol. Congr., Copenhagan. Pt. XII, Proc. of Sect. 12:198–212.

DOBZHANSKY, THEODOSIUS
1951 Genetics and the origin of species. New York: Columbia Univ. Press. 364 pp., 23 figs.

DUELLMAN, WILLIAM E.
1961 The amphibians and reptiles of Michoacan, Mexico. Univ. Kans. Publ., Mus. Nat. Hist., 15:1–148, Pls. 1–6, Figs. 1–11.

DURHAM, J. W.
1950 Cenozoic marine climates of the Pacific coast. Bull. Geol. Soc. Amer., 61:1243–64, Figs. 1–3.

DYKSTERHUIS, E. J.
1948 The vegetation of the western cross timbers. Ecol. Monogr., 18:325–76, Figs. 1–35.

ELIAS, MAXIM K.
1942 Tertiary prairie grasses and other herbs from the high plains. Geol. Soc. Amer. Special Paper No. 41:1–176, Pls. 1–17.

EMILIANI, CESARE
1954 Temperatures of Pacific bottom waters during the Tertiary. Science, 119:853–55.

GANGWERE, S. K.
1961 A monograph on food selection in Orthoptera. Trans. Amer. Ent. Soc., 87:67–230.

GARDNER, J. L.
1951 Vegetation of the creosotebush area of the Rio Grande valley in New Mexico. Ecol. Monog. 21:379–403, Figs. 1–7.

GARFIAS, VALENTÍN R., AND THEODORE C. CHAPIN
1949 Geología de México. México: Editorial Jus., 202 pp., 6 figs.

GENTRY, HOWARD SCOTT
1942 Rio Mayo Plants. Carnegie Inst. Washington Publ. 527:1–328, Pls. 1–29, Figs. 1–5, 1 map.
1957 Los pastizales de Durango. México, D. F.: Ediciones del Inst. Mex. Rec. Nat. Ren., A. C.: 361 pp., 30 figs., 1 map.

GOLDMAN, EDWARD ALPHONSO
1951 Biological investigations in México. Smithsonian Misc. Coll., 115:1–476, Pls. 1–70, 1 folded map, frontis.

GRAHAM, ALAN, AND CHARLES HEIMSCH

1960 Pollen studies of some Texas peat deposits. Ecology, 41:751–63, Figs. 1–5.

HAFSTEN, ULF

1961 Pleistocene development of vegetation and climate in the southern High Plains as evidenced by pollen analysis. Fort Burgwin Res. Center Publ. No. 1:59–91, Figs. 19–34.

HENRY, G. M.

1932 Notes on Ceylon Tettigoniidae, with descriptions of new species. Part 1. Ceylon Jour. Sci., Sect. B, 16:229–56, Pls. 43–50, Figs. 1–4.

HERNÁNDEZ XOLOCOTZI, EFRAÍM, AND MARTÍN H. GONZÁLEZ

1959 Los pastizales de Chihuahua. Secr. Agric. y Ganadería, Circular la Campaña No. 3:1–48, Figs. 1–45, frontis.

HIBBARD, CLAUDE W.

1960 The president's address: An interpretation of Pliocene and Pleistocene climates in North America. Mich. Acad. Sci., Arts and Letters, 62nd Ann. Rept. Pp. 5–30, Pl. I, Figs. 1–2.

HOOPER, EMMET T.

1941 Mammals of the lava fields and adjoining areas in Valencia County, New Mexico. Misc. Publ. Mus. Zool. Univ. Mich., No. 51:7–47, Pls. 1–3, 1 map.

HUMPHREY, ROBERT R.

1958 The desert grassland. Bull. Ariz. Agric. Exp. Sta. 299:1–62, 4 figs.

HUNT, CHARLES B.

1956 Cenozoic geology of the Colorado Plateau. U. S. Geol. Surv. Prof. Paper 279:1–99, Figs. 1–62.

KELLUM, LEWIS B.

1944 Geologic history of northern Mexico and its bearing on petroleum exploration. Bull. Amer. Assoc. Petr. Geologists, 28:301–25, Figs. 1–10.

KING, PHILIP B.

1935 Outline of structural development of Trans-Pecos Texas. Bull. Amer. Assoc. Petr. Geologists, 19:221–61, Figs. 1–7.

1948 Geology of the southern Guadalupe Mountains in Texas. U. S. Geol. Surv. Prof. Paper 215, Pp. 1–183, Pls. 1–19, Figs. 1–24.

1958 Evolution of modern surface features of western North America. *In*: Hubbs, C. L. (ed.). Zoogeography. Washington: Amer. Assoc. Adv. Sci. Publ. 51:3–60, Figs. 1–11.

1959 The evolution of North America. Princeton, N. J.: Princeton Univ. Press. 189 pp., 96 figs., 1 map.

KOOPMAN, KARL F.

1950 Natural selection for reproductive isolation between *Drosophila pseudoobscura* and *Drosophila persimilis*. Evolution, 4:135–48, Figs. 1–3.

LEOPOLD, A. STARKER

1951 [A revision of a map appearing in Leopold, 1950, Ecol., 31:508].

LeSueur, Harde

1945 The ecology of the vegetation of Chihuahua, Mexico, north of parallel twenty-eight. Univ. Tex. Publ. No. 4521:1–92, Figs. 1–28, Maps 1–4.

MacGinitie, Harry D.

1953 Fossil plants of the Florissant Beds, Colorado. Carnegie Inst. Washington, Publ. 599:1–198, Pls. 1–75, Fig. 1.

1958 Climate since the Late Cretaceous. *In*: Hubbs, C. L. (ed.). Zoogeography. Washington: Amer. Assoc. Adv. Sci. Publ. 51:61–79.

1962 The Kilgore flora. A Late Miocene flora from northern Nebraska. Univ. Calif. Publs. Geol. Sci., 35:67–158, Pls. 1–16, Figs. 1–2.

Marshall, Joe T., Jr.

1957 Birds of pine-oak woodland in southern Arizona and adjacent Mexico. Pacific Coast Avifauna No. 32:1–125, Figs. 1–25, frontis.

Martin, Paul S.

1958*a* A biography of reptiles and amphibians in the Gomez Farias region, Tamaulipas, Mexico. Misc. Publ. Mus. Zool., Univ. Mich. No. 101:iv + 5–102, Pls. I–VII, Figs. 1–6, Maps 1–4.

1958*b* Pleistocene ecology and biogeography of North America. *In*: Hubbs, C. L. (ed.). Zoogeography. Washington: Amer. Assoc. Adv. Sci. Publ. 51:375–420, Figs. 1–6.

Martin, Paul S., and Byron E. Harrell

1957 The Pleistocene history of temperate biotas in Mexico and eastern United States. Ecology, 38:468–80, Figs. 1–15.

Martin, Paul S., Bruno E. Sabels, and Dick Shutler, Jr.

1961 Rampart cave coprolite and ecology of the Shasta ground sloth. Amer. Jour. Sci., 259:102–27, Figs. 1–8.

Mello-Leitao, C. de

1940 Quatro novos tetigonioides do Brasil (Orthoptera). Rev. Ent., 11:150–58, Figs. 1–12.

Miranda, F.

1960 Posible significación del porcentaje de generos bicontinentales en América tropial. An. Inst. Biol., 30:117–150.

Moore, John A.

1957 An embryologist's view of the species concept. *In*: Mayr, Ernst (ed.). The species problem. Amer. Assoc. Adv. Sci. Publ. 50:325–338.

Muller, Cornelius H.

1947 Vegetation and climate of Coahuila, Mexico. Madroño 9:33–57, Pls. 3–7, Fig. 1.

Ragge, D. R.

1955 The wing-venation of the Orthoptera Saltatoria. London: Brit. Mus. (Nat. Hist.), 159 pp., 106 figs.

Rehn, James A. G.

1900 Notes on Mexican Orthoptera, with descriptions of new species. Trans. Amer. Ent. Soc., 27:85–99.

1901*a* A new genus of Decticinae. Ent. News, 12:16.

1901*b* Remarks on some Mexican Orthoptera, with descriptions of new species. Trans. Amer. Ent. Soc., 27:218–29.

1957 On the removal of certain new world genera from the Decticinae to the Listroscelinae (Orthoptera; Tettigoniidae). Ent. News, 68:175–77.

1958 The origin and affinities of the Dermaptera and Orthoptera of western North America. *In*: Hubbs, C. L. (ed.). Zoogeography. Washington: Amer. Assoc. Adv. Sci. Publ. 51:253–97.

REHN, JAMES A. G., AND MORGAN HEBARD

1920 Descriptions of new genera and species of North American Decticinae (Orthoptera, Tettigoniidae). Trans. Amer. Ent. Soc., 46:225–65, Pls. 8–11.

RUHE, R. V.

1960 Age of the Rio Grande Valley in southern New Mexico. Bull. Geol. Soc. Amer., 71:1962–63.

RZEDOWSKI, JERZY

1961 Vegetación del Estado de San Luis Potosí. Mexico: Univ. Nac. Aut. Mex., Fac. Sci., Tesis Doctoral, iv + 228 pp., 1 folded map, 35 figs.

RZEDOWSKI, J., AND GRACIELA C. DE RZEDOWSKI

1957 Notas sobre la flora y la vegetación del estado de San Luis Potosí. V. La vegetación a lo largo de la carretera San Luis Potosí-Río Verde. Acta Cientifica Potosina, 1:7–68, Figs. 1–13.

SEGERSTROM, KENNETH

1962 Geologic investigations in Mexico. Chapter C. Geology of south-central Hidalgo and northeastern Mexico, Mexico. U. S. Geol. Surv. Bull. 1104–C:87–162, Pl. 3 (folded map), Figs. 35–72.

SHREVE, FORREST

1951 Vegetation of the Sonoran Desert. Carnegie Inst. Washington, Publ. 591:1–192, Pls. 1–37, Maps 1–27.

SIMPSON, GEORGE GAYLORD

1947 Holarctic mammalian faunas and continental relationships during the Cenozoic. Bull. Geol. Soc. Amer., 58:613–87, Figs. 1–6.

THARP, BENJAMIN CARROLL

1926 The structure of Texas vegetation east of the 98th meridian. Univ. Tex. Bull. No. 2606:1–97, Pls. 1, 1a, 2–29.

1952 Texas range grasses. Austin: Univ. Tex. Press, Pp. xiv + 125, 30 figs.

TINKHAM, ERNEST R.

1944 Biological, taxonomic and faunistic studies on the shield-back katydids of the North American deserts. Amer. Midland Nat., 31:257–338, Figs. 1–28.

TOLEDO PIZA, S. DE, JR.

1958 A primeira especie neotropical da familia "Tympanophoridae" (Orthoptera, Tettigonioidea). Rev. Brasil. Biol. 18:237–41, Figs. 1–3.

WAGNER, W. H., JR.

1961 Problems in the classification of ferns. *In*: Bailey, D. L. (ed.). Recent Advances in Botany I. Toronto: Univ. Toronto Press, Pp. 841–44.

WOMBLE, WILLIAM H.

1951 Differential systematics. Science, 114:315–22, Figs. 1–8.

ZEUNER, FREDERICK EBERHARD

1939 Fossil Orthoptera Ensifera. Text. London: Brit. Mus. (Nat. Hist.), 321 pp.

Accepted for publication March 30, 1964

Fig. 17. Head, pronotum (pt.), fore leg, and female subgenital plate and 7th abdominal sternite in *Neobarrettia*. Length of 1 mm. is shown beneath each figure:

a, *victoriae*, topotype, Victoria, Tamaulipas; laterocephalic view of head and insert showing fastigial region in same view
b, *imperfecta*, 11 mi. S Iguala, Guerrero; same views
c, *victoriae*, male, topotype, Victoria, Tamaulipas; lateral view of pronotum, cephalic end toward right
d, *imperfecta*, male, 11 mi. S Iguala, Guerrero; same view as in c
e, *spinosa*, 5 mi. S Pine Springs, Culberson Co., Texas; lateral view of fore femur and tibia

f to n, ventrolateral view of female subgenital plate and 7th abdominal sternite, caudal end uppermost

f, *vannifera*, paratopotype, 8 mi. SW Cd. Victoria, Tamaulipas
g, *spinosa*, 12 mi. W Bastrop, Bastrop Co., Texas
h, *cremnobates*, paratopotype, 19.9 mi. E Ixtlán del Río (Nayarit), Jalisco
i, *victoriae*, 34 mi. NW Cd. Victoria, Tamaulipas
j, *sinaloae*, topotype, El Venadillo, Sinaloa
k, *hakippah*, 19 mi. NW Guasave, Sinaloa
l, *pulchella*, 28 mi. SW Jaumave, Tamaulipas
m, *bambalio*, paratopotype, 12 mi. NW Cd. del Maíz, San Luis Potosí
n, *imperfecta*, 11 mi. S Iguala, Guerrero

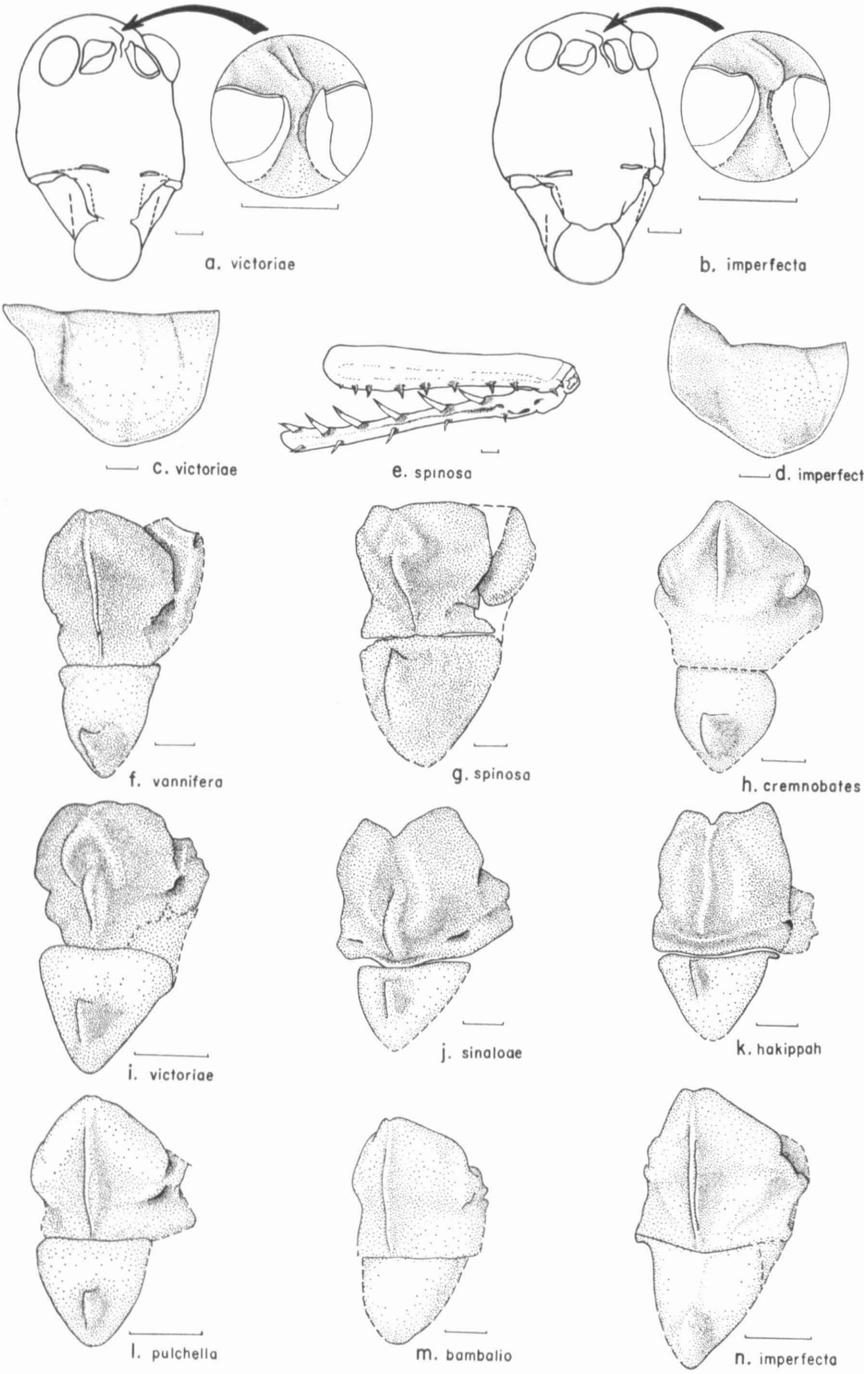

a. victoriae
b. imperfecta
c. victoriae
e. spinosa
d. imperfecta
f. vannifera
g. spinosa
h. cremnobates
i. victoriae
j. sinaloae
k. hakippah
l. pulchella
m. bambalio
n. imperfecta

FIG. 18. Male cercus (pt.) and titillators in *Neobarrettia*. Length of 1 mm. is shown beneath each figure:

a to e, male cercus; dorsal view shown in left column, internal view in right column

a, *vannifera,* type, 8 mi. SW Cd. Victoria, Tamaulipas
b, *spinosa* (eastern form), Goliad, Goliad Co., Texas
c, *spinosa* (western form), 5 mi. S Pine Springs, Culberson Co., Texas
d, *sinaloae,* topotype, El Venadillo, Sinaloa
e, *hakippah,* type, 42 mi. NW Culiacán, Sinaloa

f and g, dorsal views of male titillators, lined areas are membranous, dashed line indicates limit of sclerotization on ventral surface

f, *sinaloae,* topotype, El Venadillo, Sinaloa
g, *hakippah,* paratopotype, 42 mi. NW Culiacán, Sinaloa

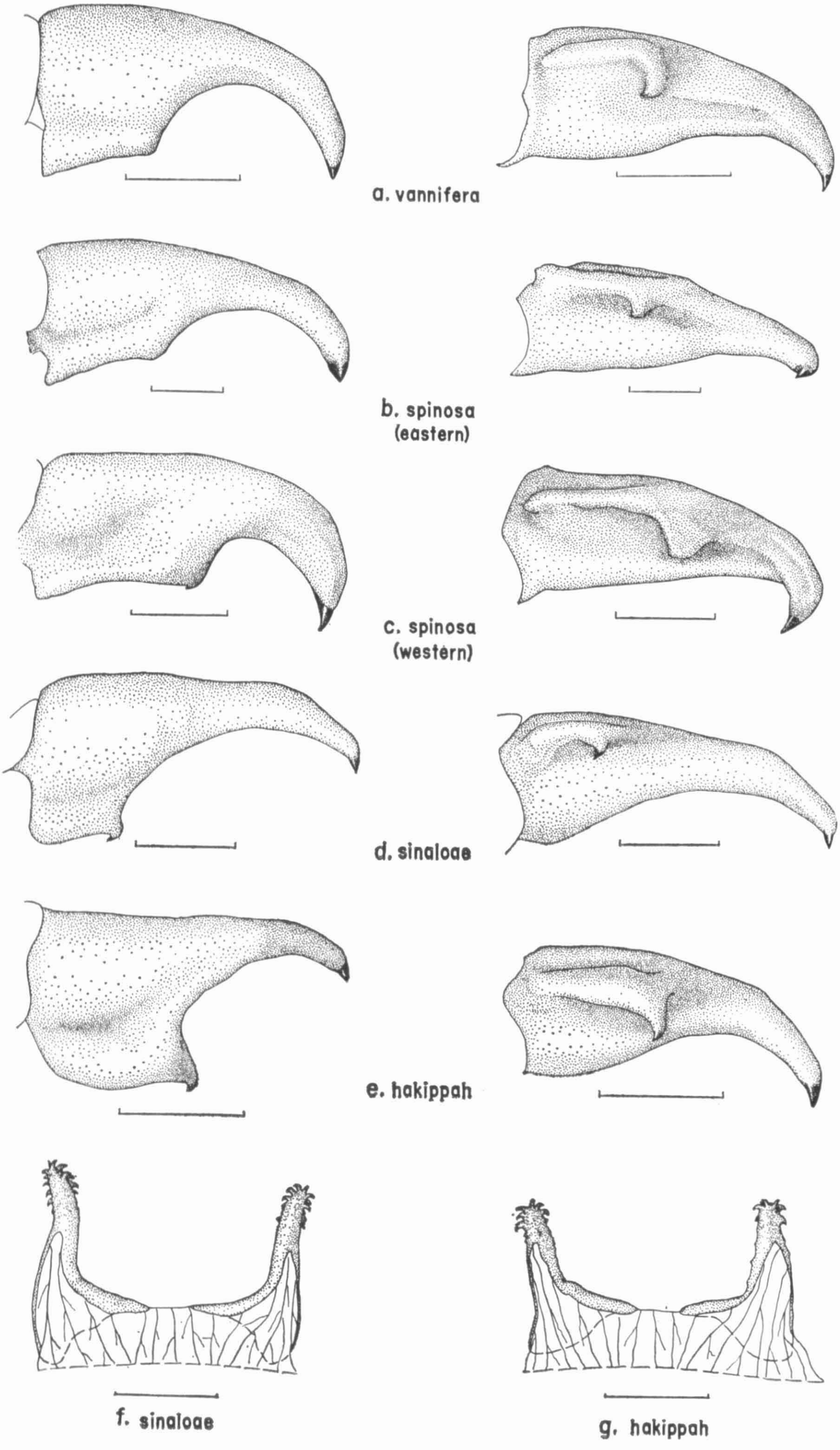

a. vannifera
b. spinosa (eastern)
c. spinosa (western)
d. sinaloae
e. hakippah
f. sinaloae
g. hakippah

FIG. 19. Male cercus (pt.) in *Neobarrettia*. Length of 1 mm. is shown beneath each figure; dorsal view shown in left column, internal view in right:

a, *victoriae,* topotype, Victoria, Tamaulipas
b, *cremnobates,* 14.4 mi. E Ixtlán del Río (Nayarit), Jalisco
c, *pulchella,* paratopotype, 4 mi. N Escondida, Nuevo, León
d, *bambalio,* type, 12 mi. NW Cd. del Maíz, San Luis Potosí
e, *imperfecta,* 11 mi. S Iguala, Guerrero

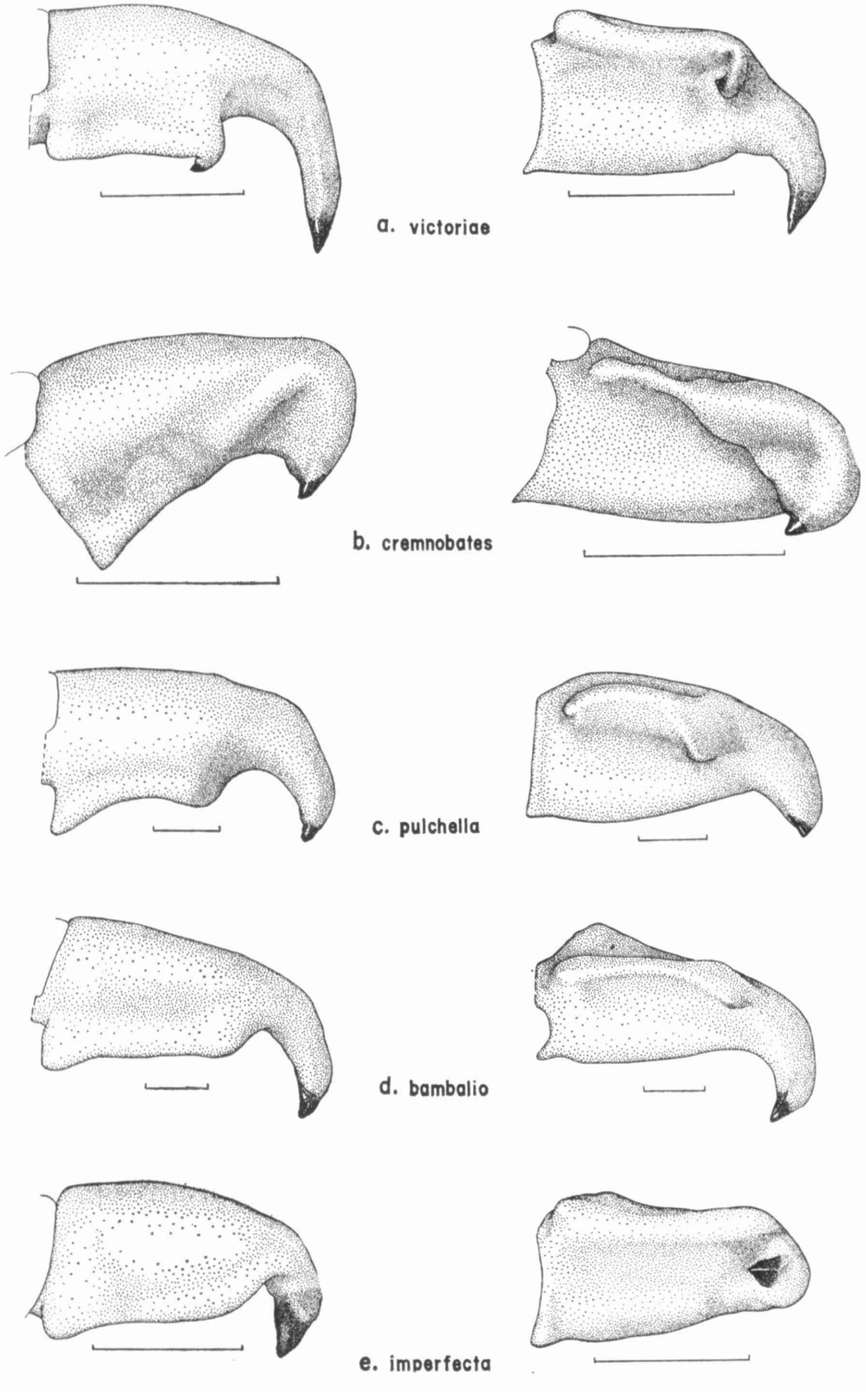
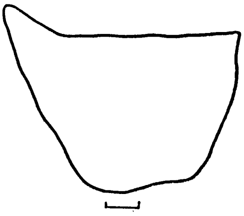

a. victoriae
b. cremnobates
c. pulchella
d. bambalio
e. imperfecta

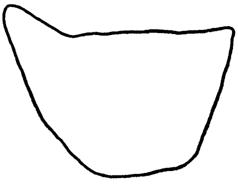
FIG. 20. Pronotum (pt.) and penultimate tergite of male in *Neobarrettia*. Length of 1 mm. is shown below each figure:

a to e and m to o, lateral outline of male pronotum, cephalic end toward the right
f to l and p and q, dorsal view of male penultimate tergite, caudal end uppermost

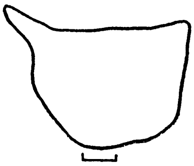
a, *hakippah,* type, 42 mi. NW Culiacán, Sinaloa
b, *sinaloae,* topotype, El Venadillo, Sinaloa
c, *bambalio,* type, 12 mi. NW Cd. del Maíz, San Luis Potosí
d, *pulchella,* topotype, 4 mi. N Escondida, Nuevo León
e, *cremnobates,* 14.4 mi. E Ixtlán del Río (Nayarit), Jalisco
f, *hakippah,* type, 42 mi. NW Culiacán, Sinaloa
g, *sinaloae,* topotype, El Venadillo, Sinaloa
h, *spinosa,* Goliad, Goliad Co., Texas
i, *bambalio,* type, 12 mi. NW Cd. del Maíz, San Luis Potosí
j, *pulchella,* topotype, 4 mi. N Escondida, Nuevo León
k, *imperfecta,* 6 mi. W Iguala, Guerrero
l, *cremnobates,* 14.4 mi. E Ixtlán del Río (Nayarit), Jalisco
m, *spinosa* (eastern form), Goliad, Goliad Co., Texas
n, *spinosa* (western form), 5 mi. S Pine Springs, Culberson Co., Texas
o, *vannifera,* type, 8 mi. SW Cd. Victoria, Tamaulipas
p, same as o
q, *victoriae,* topotype, Cd. Victoria, Tamaulipas



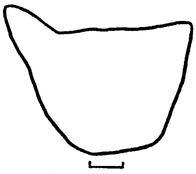
a. hakippah



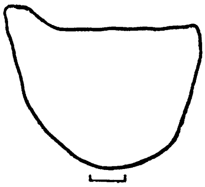
b. sinaloae



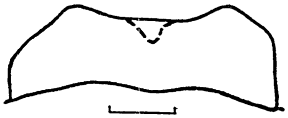
c. bambalio



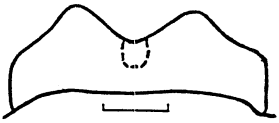
d. pulchella



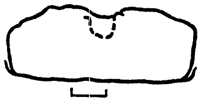
e. cremnobates



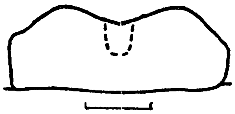
f. hakippah



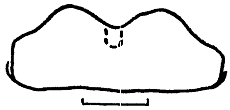
g. sinaloae



h. spinosa

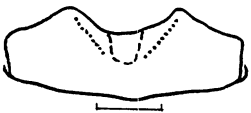


i. bambalio

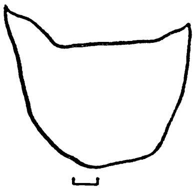


j. pulchella

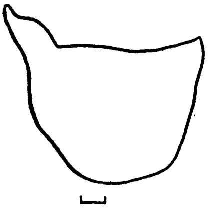
k. imperfecta



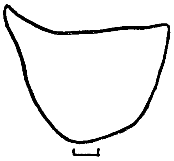
l. cremnobates



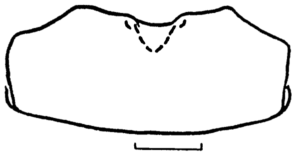
m. spinosa



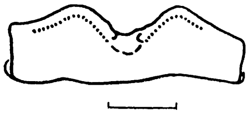
n. spinosa



o. vannifera



p. vannifera



q. victoriae

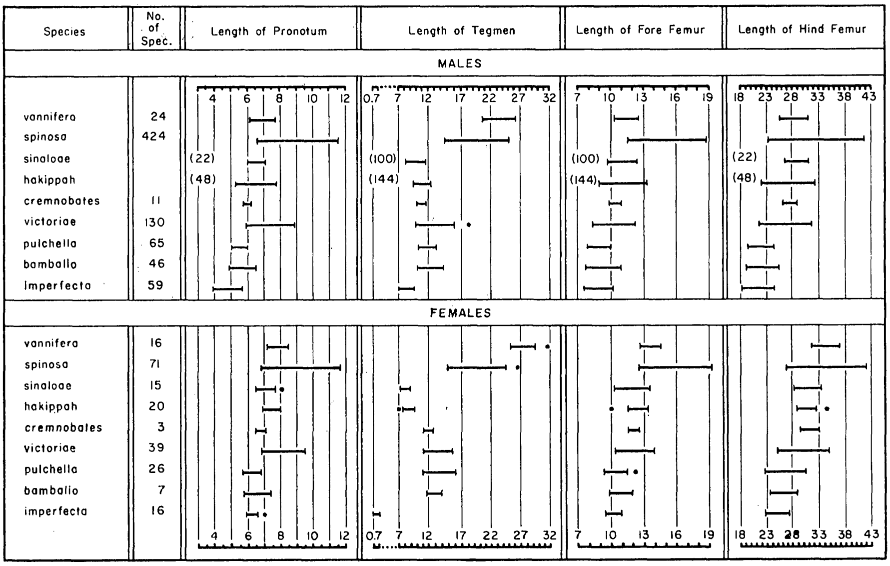


FIG. 21. Summary of measurements in *Neobarrettia* I. Ranges of measurements of males (above) and females (below). Points outside the range bars represent single measurements which are separated by more than 20 per cent of the total range from the next nearest measurement in samples of over 15 specimens.

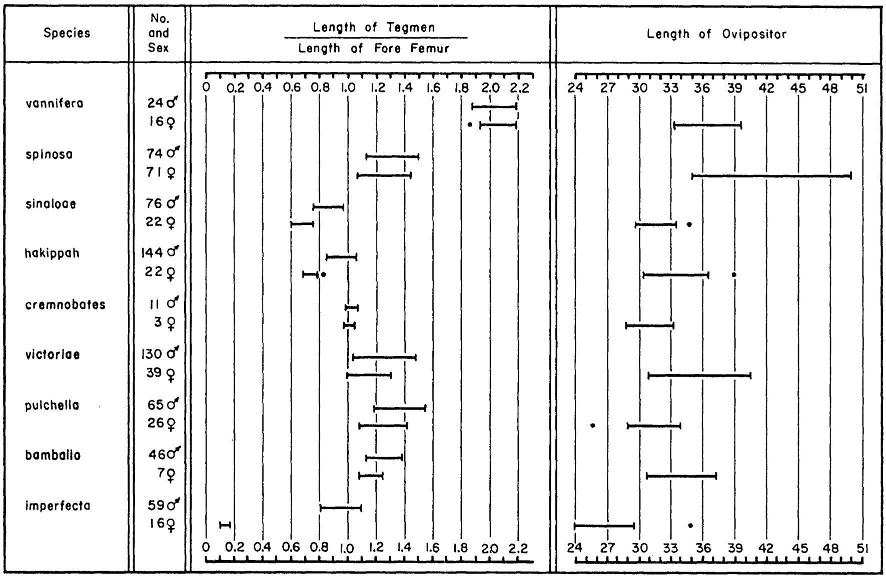


FIG. 22. Summary of measurements in *Neobarrettia* II. Ranges of ratios and measurements in both sexes. Points outside the range bars represent single measurements which are separated by more than 20 per cent of the total range from the next nearest measurement in samples of over 15 specimens.

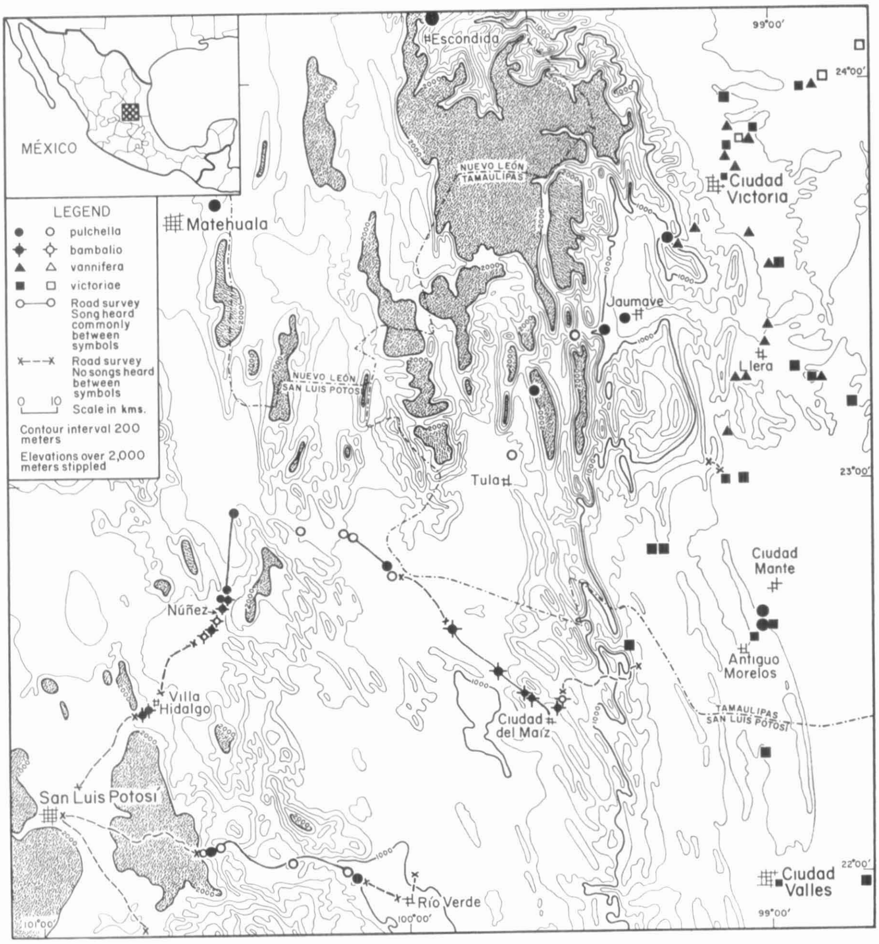


FIG. 23. Distribution of *Neobarrettia vannifera, victoriae, pulchella,* and *bambalio* in northeastern México. All records for *vannifera* and *bambalio* are shown. Northernmost records for *pulchella* (south of Arteaga) and northern and eastern records for *victoriae* fall beyond the limits of the map. Open symbols represent song records only. Closed symbols, specimens collected.

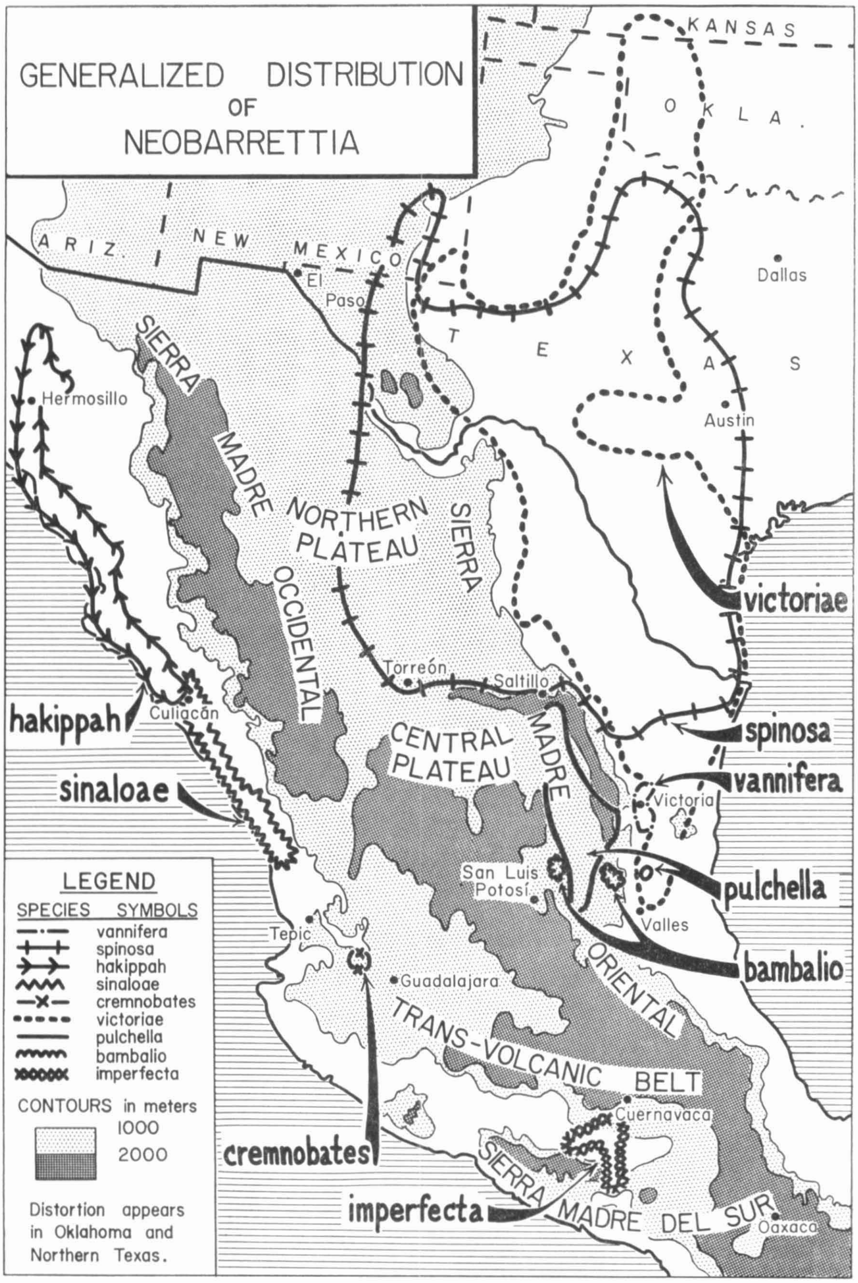


FIG. 24. Generalized distribution of the species of *Neobarrettia*.

No. 84.	The burrowing beetles of the genus *Mycotrupes* (Coleoptera: Scarabaeidae: Geotrupinae). By Ada L. Olson, T. H. Hubbell, and H. F. Howden. (1954) 59 pp., 8 pls., 3 figs.	$0.60
No. 88.	An annotated list of the moths of Michigan exclusive of Tineoidea (Lepidoptera). By Sherman Moore. (1955) 87 pp.	$0.90
No. 90.	The crane flies of Alaska and the Canadian northwest (Tipulidae, Diptera). The genus *Erioptera* Meigen. By C. P. Alexander. (1955) 33 pp., 38 figs.	$0.50
No. 98.	A synopsis of the Tabanidae (Diptera) of Michigan. By Kirby L. Hays. (1956) 79 pp., 3 pls.	$1.15
No. 104.	Catalogue of the Odonata of Michigan. By Edward J. Kormondy. (1958) 43 pp., 1 map	$0.65
No. 107.	The systematics of *Tetragoneuria,* based on ecological, life history, and morphological evidence (Odonata: Corduliidae). By Edward J. Kormondy. (1959) 79 pp., 4 pls., 4 maps	$1.20
No. 116.	The sibling species of the Alutacea Group of the bird-locust genus *Schistocerca* (Orthoptera, Acrididae, Cyrtacanthacridinae). By Theodore H. Hubbell. (1960) 136 pp., 23 pls., 9 figs.	$3.00
No. 121.	The evolutionary relationships of 17-year and 13-year cicadas, and three new species (Homoptera, Cicadidae, *Magicicada*). By Richard D. Alexander and Thomas E. Moore. (1962) 59 pp. frontis., 10 figs.	$1.50
No. 126.	The arid-land katydids of the North American genus *Neobarrettia* (Orthoptera: Tettigoniidae): their systematics and a reconstruction of their history. By Theodore J. Cohn. (1965) 179 pp., frontis., 24 figs.	$3.00