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A REVISION OF AMERICAN BATS OF THE GENERA EUDERMA AND PLECOTUS

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Introduction

Confusion and damage to nomenclatural stability are consequences of taxonomic revisions that do not provide adequate explanations or justifications for proposed changes in nomenclature. They are ignored, accepted with reservation, or blindly followed by those who have occasion to use them. Confusion of this sort involves a widespread American bat, now referred to in literature either as *Corynorhinus* or *Plecotus*. The purpose of this paper is to clarify the status of this bat and its American and Eurasian relatives (particularly *Euderma*), to assay the evolution of the group, to map geographic distributions, and to bring together the literature on natural history of the group.

The genera *Euderma* and *Plecotus* are vespertilionid bats with exceptionally large ears. They are known colloquially as mule-eared bats, jack-rabbit bats, or, simply, big-eared bats, or long-eared bats. Some species are referred to as lump-nosed bats. *Plecotus*, as here understood, includes the American *Idionycteris* and *Corynorhinus* as subgenera.

Perhaps the earliest published reference to an American big-eared bat was that of Clayton (1694, p. 124) in his remarks on the "beasts of Virginia": "*Batts*, as I remember at least two sorts; one a large sort with long Ears, and particularly long stragling hairs. The other much like the *English*, something larger I think, very common."

There is now an extensive American literature on *Euderma* and *Plecotus*, but most reports contain little more than records of specimens. The only revisionary works have been those of H. Allen (1864, 1894), Miller (1897), and G. Allen (1916). Most of our knowledge of the anatomy and physiology of the group is included in the papers of Larsell and Dow (1935) and Pearson, Koford, and Pearson (1952). The few life history studies are generally superficial; those of Dalquest (1947), Pearson, et al. (1952), and Twente (1955) are notable exceptions. Much yet remains to be learned about *Euderma* and the American populations of *Plecotus*.

These bats occur in most temperate portions of the Northern Hemisphere. They are generally scarce. In America, *Euderma* is known by 16 specimens, the subgenus *Idionycteris* is known by less than a dozen specimens, all but two of them collected since 1955; and perhaps no other North American bat with such an extensive geographic range as the subgenus *Corynorhinus* has been collected so infrequently. Species of the latter subgenus are known to occur from the Atlantic to the Pacific and from Canada to the Isthmus of Tehuantepec in Mexico. This wide geographic range is deceptive, however, for these bats display narrow limits of tolerance in their choice of habitat. Within the bounds of their ranges are large areas in which they apparently do not occur, and others in which they occur only sparingly. There are few areas in which they are common.

MATERIALS

The scarcity of *Euderma* and *Plecotus* in America is evident from the small number of museum specimens listed in the early reviews. H. Allen's 1864 monograph included only 18 specimens, and his 1894 monograph only 19. For Miller's 1897 revision, 43 examples were available. G. Allen's 1916 review was based on a total of 126 specimens.

The material from which I have drawn my conclusions concerning these bats consists of four dry skins and skulls and a single specimen preserved in alcohol representing *Euderma;* three specimens of the subgenus *Idionycteris*, dry skins and skulls; 25 dry skins and skulls, two skeletons, and 32 specimens preserved in alcohol, representing at least five races of the subgenus *Plecotus;* and about 800 specimens (see species accounts for type of preservation) representing all the named forms of the subgenus *Corynorhinus*.

In the course of the study I have examined enough specimens to define *Euderma* and American *Plecotus*, but have not attempted to assemble all available specimens. Those examined are in the collections of the following:

American Museum of Natural History (AMNH)
Albert Schwartz (private collection) (AS)
California Institute of Technology (CIT)
Carlsbad Caverns National Park (CC)
Charleston (South Carolina) Museum (ChM)
Carnegie Museum (CM)
Chicago Natural History Museum (CNHM)
W. Gene Frum (private collection) (GF)
Instituto de Biología, Universidad Nacional Autónoma de México (IB)
Illinois Natural History Survey (INHS)
University of Kansas Museum of Natural History (KU)
Louisiana State University Museum of Zoology (LSU)
Harvard University Museum of Comparative Zoology (MCZ)
University of California Museum of Vertebrate Zoology (MVZ)
Oklahoma A. & M. College (OAM)
Ohio State Museum (OSM)
School of Tropical and Preventive Medicine, Loma Linda, Calif. (STPM)
Texas A. & M. College (Texas Cooperative Wildlife Collection) (TCWC)
Texas State Department of Health, Austin, Tex. (TSDH)
Texas Technological College (TT)
University of Arkansas Department of Zoology (UAZ)
University of Illinois Museum of Natural History (UI)
University of Kentucky Zoology Department (UK)
University of Michigan Museum of Zoology (UMMZ)
University of Oklahoma Museum of Zoology (UOMZ)
U.S. National Museum (including U.S. Fish and Wildlife Service's Biological Surveys collection) (USNM)
University of Utah Museum of Zoology (UU)

I express sincere thanks and appreciation to the owners of private collections and to the museum authorities who kindly loaned specimens for my study. To those at the American Museum of Natural History and at the Museum of Comparative Zoology, Harvard University, I am particularly grateful. I am indebted to Seth B. Benson, Museum of Vertebrate Zoology, University of California, and to Rollin H. Baker and E. Raymond Hall, Museum of Natural History, University of Kansas, for the loan of specimens set aside for their personal study. Special thanks are due to John A. Sealander, University of Arkansas, for allowing me to utilize specimens under his care in the description of a new subspecies, and for his kindness in depositing the type specimen in the U.S. National Museum; and to Aurelio Málaga Alba, Pan American Sanitary Bureau, for his cooperation in securing much needed Mexican specimens, one of which has served as the type of a new subspecies. The Fish and Wildlife Service, U.S. Department of the Interior, has generously allowed me to utilize from its files the unpublished field notes of its collectors.

The following individuals contributed information and other assistance for which I am grateful: R. W. Barbour, F. L. Burnett, W. W. Dalquest, W. G. Frum, A. F. Ganier, Helen Gaylord, B. P. Glass, Woodrow Goodpaster, R. M. Goslin, Iracy O. Handley, R. H. Hand-

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Methods

In tables 7–18 cranial and external measurements, in millimeters are given for *Euderma maculatum*, *Plecotus auritus*, *Plecotus phyllotis*, and for all the races of the subgenus *Corynorhinus*. Females are significantly larger than males in these bats. Accordingly, measurements for the two sexes are tabulated separately. Only adults, as determined by ossification of the finger joints and appearance of the skull, were measured.

Measurements of *Euderma* are from the following sources: Ashcraft (1932, p. 162), Durrant (1952, pp. 59, 66), Nicholson (1950, p. 197), Parker (1952, p. 480), Stager (1957, p. 260), and four specimens measured by me.

External measurements of *Plecotus*, except of the forearm, are those taken by the collectors. I measured the forearm (greatest length of radius-ulna including carpals) on the preserved specimens. All cranial measurements (fig. 1) were taken with dial calipers and the aid of a binocular microscope in the following manner:

Greatest length: Distance, on the diagonal, from the anteriormost border of the premaxilla to the posterior limit of the supraoccipital; incisors are excluded.

Zygomatic breadth: Greatest distance between the outer borders of the zygomatic arches.

Interorbital breadth: Least diameter of the interorbital constriction of the frontals.

Brain case breadth: Distance, measured above the auditory bullae, between the lateral limits of the parietals.

Brain case depth: Distance between the dorsal extreme of the skull and the ventral limit of the occipitosphenoid plate; auditory bullae are excluded. One bar of the calipers lies flat on the occipitosphenoid plate; the other is in contact with the top of the brain case.

Maxillary tooth row: Distance between the anterior edge of the canine and the posterior border of the third molar.

Postpalatal length: Distance from the anterior limit of the mesopterygoid fossa to the ventral lip of the foramen magnum.

Palatal breadth: Distance between the lateral extremes of M^3.

Presence or absence of a secondary cusp in I^1 was indexed according to the following scale (fig. 2):

0, Secondary cusp absent; no trace.
1, Secondary cusp incipient, in the form of a shoulder, not separated from primary cusp by a notch.
2, Secondary cusp present, separated from primary cusp by a notch.

Frequently, the degree of development of the secondary cusp of I^1 is not the same on both sides. When absent in one tooth and incipient in the other, it was indexed as 0.5; when absent in one and present in the other, as 1; when incipient in one and present in the other, as 1.5; etc.

The degree of development of the secondary cusp in each population was determined by averaging individual indexes. Thus, a population

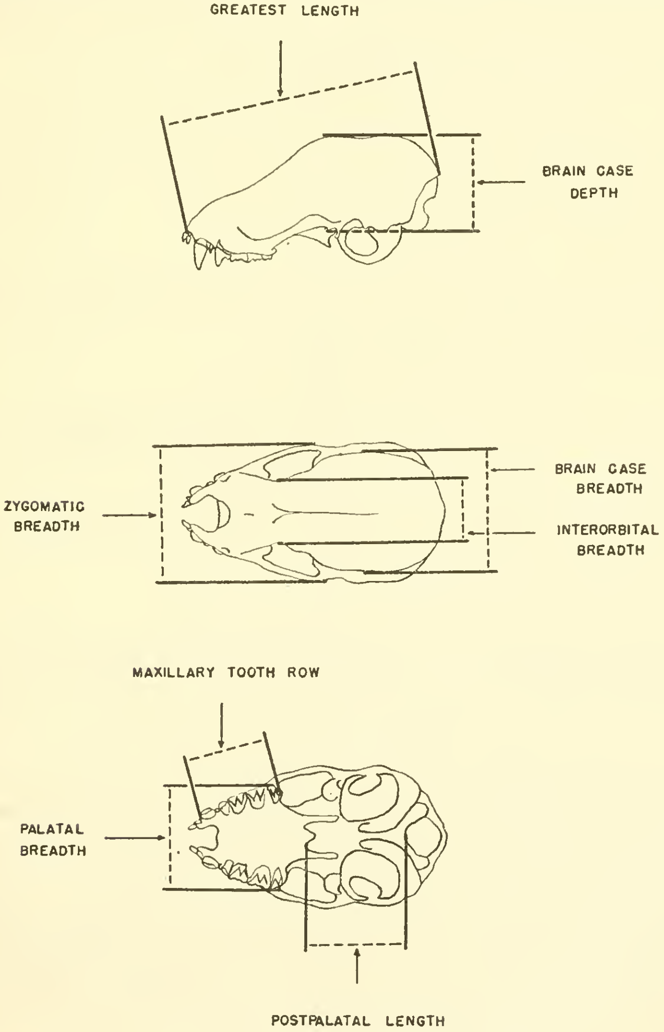


FIGURE 1.—Cranial measurements of *Euderma* and *Plecotus*.

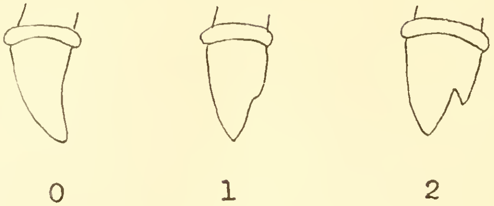


Figure 2.—Degrees of development of the secondary cusp in the first upper incisor (anterolateral view).

with an incisor cusp index of 0 lacks the secondary cusp. An index of 1 indicates some development of the secondary cusp, and so on.

Throughout the text, relative proportions are expressed as percentages of the greatest length of the skull.

Color was measured in diffused white fluorescent light, without direct natural light. Capitalized color terms in the text are from Ridgway (1912). There appears to be no sexual dichromatism or seasonal variation in coloration. If such exists, it is so slight that, except in cases of extremely worn pelage, it can be disregarded in comparisons.

The type of preservation of the specimens examined is indicated in the species accounts by the following abbreviations: a, alcoholic; b, bones (skeleton); and s, skin and skull.

Dental Nomenclature

The nomenclature of cusps and the numerical designation of teeth, as used in this paper, are outlined in figure 3. The naming of the individual teeth requires further explanation.

The complete primitive dentition of adult placental mammals is a set of 44 teeth:

$$I\,\frac{3-3}{3-3},\ C\,\frac{1-1}{1-1},\ P\,\frac{4-4}{4-4},\ M\,\frac{3-3}{3-3}.$$

The nearest approach to this in bats is a set of 38 teeth, lacking one upper incisor and one upper and one lower premolar in each jaw:

$$I\,\frac{2-2}{3-3},\ C\,\frac{1-1}{1-1},\ P\,\frac{3-3}{3-3},\ M\,\frac{3-3}{3-3}.$$

Incisors: Which of the incisors it is that is always missing in Chiroptera is a matter of controversy. Most authors have believed without much doubt that the consistently missing incisor is the first.

> According to Miller (1907, p. 27) this is indicated, as shown by Winge, by the correspondence of the two upper teeth with the two outer of the lower jaw when the maximum set is present, and also, even more strongly, by the general tendency throughout the group for the premaxillaries to become reduced, particularly along the inner edge. This would inevitably result in eliminating that part of the bone in which the first incisor grows.

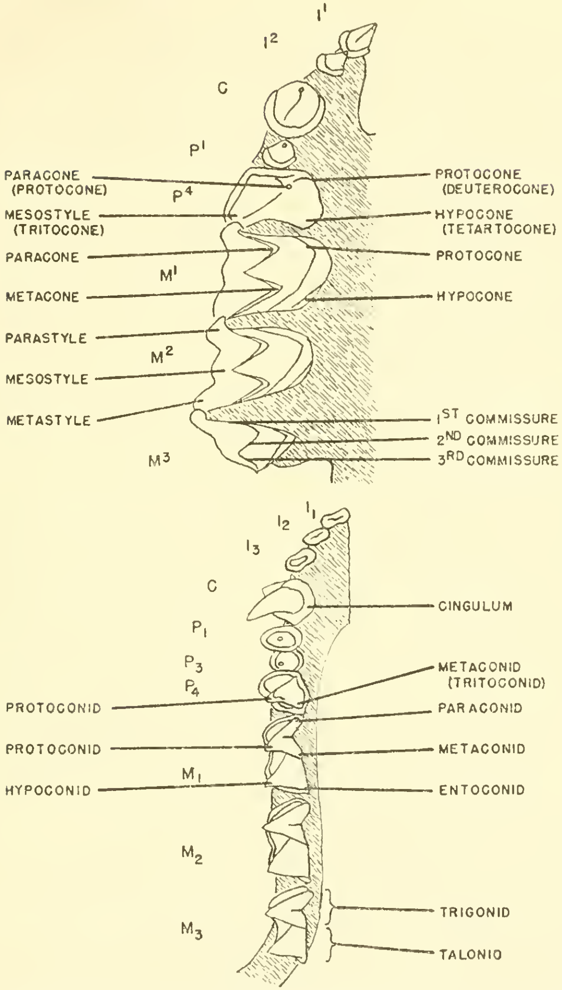


Figure 3.—Nomenclature of teeth of *Plecotus*. Right upper dentition (above) and left lower dentition (below).

There are many objections to the belief that the permanently missing incisor is I^1, and no really substantial evidence as to which, if either, of the others it may be. However, what evidence there is favors the theory that the missing tooth may be I^3.

The deciduous dentition does not contribute information on the lost tooth. No more than two upper incisors have been observed in any normal chiropteran deciduous dentition. For the Vespertilionidae, the formula is the same in all of the genera for which it is known:

$$\mathrm{di}\ \frac{2-2}{3-3},\ \mathrm{dc}\ \frac{1-1}{1-1},\ \mathrm{dp}\ \frac{2-2}{2-2}=22.$$

On the basis of an abnormal supernumerary deciduous incisor in *Myotis lucifugus*, Stegeman (1956, p. 60) postulated that the normally missing tooth may be I^2. G. Allen (1916, p. 335) described a specimen of *Plecotus townsendii* (USMN 150273) with three upper permanent incisors. The "extra" incisor was the outermost of the three and differed in form from the other two. Allen speculated that this might represent a long lost I^3.

The uniform absence of a tooth throughout a group as large and as varied as the Chiroptera compels the impression that the absence is a characteristic dating from the dawn of development of the group and subsequently shared by all derivatives. It is doubtful that deviations from such a deep-seated characteristic, such as the deviations reported by Allen and by Stegeman, can be assumed to represent a reversion to an even more primitive long lost characteristic.

An example of a clearly abnormal extra incisor may be seen in a specimen of *P. mexicanus* (KU 29858). In place of the right outer upper incisor there are two closely approximated twin teeth, neither of which resembles the normal outer incisor in the left premaxilla.

Investigation of the factors now operating to cause reduction and loss of the remaining incisors in Recent bats may give clues to the incisor missing throughout the order. As noted above, Miller, following Winge, supposed that reduction of the inner portion of the premaxillary bone left the innermost incisor without a place for its root. However, although all bats lack one upper incisor, not all bats have the tooth-bearing portions of the premaxillaries reduced. Therefore, if the same incisor is missing in all bats, then reduction of the premaxillaries can not always account for the loss.

Actually, several evolutionary trends may account for crowding and subsequent reduction and loss of incisors. In forms with an extensible tongue, the action of the tongue may be a responsible agent. In others, a narrowing of the rostrum and mandibles, an enlargement of the canines, or a reduction of the tooth-bearing portions of the premaxillaries may be a cause.

The result of these processes is always the same. It is not the reduction and loss of the innermost of the two remaining incisors, but a crowding of both toward the canine. A consequence of this crowding is conflict of the outermost incisor with the occluding lower canine. Further alternative consequences are reduction of the lower canine, diminution or obliteration of the outermost upper incisor, anterior or posterior displacement of the outermost incisor, rotation of the outermost incisor to a narrower axis, elevation of the rostrum, or depression of the mandible. All of these conditions may be observed in Recent bats. It is important to note that in all Chiroptera it is invariably the outer of the two remaining incisors that is reduced in size and apparently is the first to disappear. It is most reasonable to assume that these same factors may have operated to eliminate the missing incisor. The first to go then, at a very early stage of chiropteran development, was probably I^3. This is in agreement with Andersen's (1908, p. 205) and Thomas' (1908, p. 348) criticisms of Miller's conclusions.

PREMOLARS: Since the number of premolars in each maxilla and mandible in all known bats is at least one less than the primitive placental number, it is assumed that one has been lost from each jaw. Thomas (1908, p. 347) argued convincingly that the missing tooth is the second. Miller (1907, p. 28), without proof, arbitrarily assumed it to be the first. Evidence at hand possibly supports Miller's thesis. A specimen of *Plecotus townsendii* (USNM 81647) has four premolars in one mandible; the other ramus is normal. The extra tooth is on the lingual side of the tooth row, adjacent to the normal anterior premolar and forcing that tooth to the labial side of the row. Both teeth touch the canine. The extra tooth is smaller than the normal anterior premolar and rather like P_3 in size and shape. If it were to be assumed that this extra tooth reflects a primitive condition in which the normal mandible bore four premolars, then it would be necessary, because of its position, to assume that the extra tooth is P_1. However, the argument refuting similar evidence for the missing incisor can be applied with equal propriety here.

Besides lacking, as do all bats, P2 in maxilla and mandible, *Euderma* and *Plecotus* also lack another maxillary premolar. In this instance the missing tooth is probably P^3. An examination of *Myotis* in this connection proves instructive. This genus normally lacks only a single premolar, assumed to be the second, in each jaw. In some forms the remaining premolars normally are not even crowded (e.g., *M. lucifugus*). However, other forms (e.g., *M. occultus*) frequently lack two premolars in each jaw. The tooth that is variable in occurrence is the third premolar. In 15 specimens of *M. occultus* P^3 was present in 4, absent in 11; P_3 was present in 14, absent in 1. P^3 normally is absent in *Plecotus*, but occasionally is present (USNM 265387, 297711). In these specimens P^3 is present in only one maxilla, is similar to P^1 but is smaller, and is wedged between P^1 and P^4 (postero-internal to P^1, on the lingual border of the tooth row). The "extra" tooth in each instance is similar in form and position to P^3 of *Myotis occultus*. These teeth perhaps represent the normal third premolar and not merely abnormal accessory teeth. They thus may be authentic reversions to a primitive condition.

In addition, the third mandibular premolar normally is lacking in *Euderma*. In *Plecotus* it is present, but is smaller than either P_1 or P_4. In the subgenus *Corynorhinus* it is commonly squeezed between the larger teeth so that its cross-sectional outline is distorted. Frequently it is displaced to the lingual side of the tooth row.

DENTAL FORMULAE: Based on the foregoing conclusions, the dental formulae of the bats discussed in this paper may be written as follows:

$$\frac{\text{12–. 1. 1–34. 123}}{\text{123. 1. 1–34. 123}}=38\ \textit{Myotis}$$

$$\frac{\text{12–. 1. 1—4. 123}}{\text{123. 1. 1–34. 123}}=36\ \textit{Plecotus}$$

$$\frac{\text{12–. 1. 1—4. 123}}{\text{123. 1. 1—4. 123}}=34\ \textit{Euderma, Barbastella}$$

$$\frac{\text{12–. 1. ——4. 123}}{\text{123. 1. 1—4. 123}}=32\ \textit{Histiotus, Laephotis}$$

$$\frac{\text{1—. 1. ——4. 123}}{\text{123. 1. 1—4. 123}}=30\ \textit{Otonycteris, Nyctophilus, Pharotis}$$

$$\frac{\text{1—. 1. ——4. 123}}{\text{12–. 1. 1—4. 123}}=28\ \textit{Antrozous}$$

Supraspecific Nomenclature and Relationships

HISTORY OF NOMENCLATURE

SUPRAGENERIC NOMENCLATURE: Several genera of the family Vespertilionidae have exceptionally large ears: *Plecotus* (including *Corynorhinus* and *Idionycteris*, now regarded as subgenera), *Euderma*, *Histiotus*, *Laephotis*, *Otonycteris*, *Nyctophilus*, *Pharotis*, and *Antrozous*. The relationships of these genera have been variously interpreted. Typical of the opinion of his time, Dobson (1875, p. 348) included all known genera in his "Group Plecoti" which was the equivalent of a subfamily. As late as 1897 Miller (1897, p. 41) employed the name Plecotinae, of subfamily rank, to include the American big-eared vespertilionids *Plecotus* (subgenus *Corynorhinus*) and *Euderma*. For *Antrozous* he erected a separate subfamily, Antrozoinae. Later Miller (1907, p. 197) abandoned the subfamily Plecotinae and included its genera in the subfamily Vespertilioninae. At the same time he adopted the terminology of Peters (1865) and placed *Antrozous* in the subfamily Nyctophilinae.

The large ears and auditory bullae and strong zygomata—the principal characteristics common to the 10 genera and subgenera listed above—may not indicate kinship. The classification of Tate (1941, p. 590; 1942, p. 225), based on other characters, probably better expresses the natural relationships of these genera and subgenera:

Subfamily Vespertilioninae
    Group Myotini
        Genera: *Plecotus*
                Corynorhinus
                Idionycteris
                Euderma

Group Pipistrellini
    Genera: *Histiotus*
        Laephotis
Group Nycticeini
    Genus: *Otonycteris*
Subfamily Nyctophilinae
    Genera: *Nyctophilus*
        Pharotis
        Antrozous

Tate (1942, p. 229) supposed the assemblage of big-eared bats of the group Myotini to be simply a specialized derivative of the *Myotis* stock, presenting an odd combination of primitive and specialized characters, but not being sufficiently differentiated to warrant the erection of a special category.

GENERIC NOMENCLATURE: Initially confused with the exclusively South American genus *Histiotus* (J. Allen, 1891, p. 195), the bat *H. maculatum* was soon recognized as the representative of a distinct genus, *Euderma* (H. Allen, 1892, p. 467). Subsequently, the validity of *Euderma* has not been questioned.

The status of the names *Idionycteris, Plecotus,* and *Corynorhinus* has been less clear. *Idionycteris* has remained so little known since its description by Anthony in 1923 that there has been no speculation on its systematic position beyond Anthony's supposition that its nearest relative is *Plecotus auritus.* The nomenclatural history of the Eurasian *Plecotus* has been one of stability. Subsequent to the recognition of the genus in 1818 by E. Geoffroy Saint-Hilaire, the big-eared vespertilionines of Europe and temperate Asia have been recognized consistently by the name *Plecotus.*

No such stability characterizes the nomenclatural history of the bats to which the name *Corynorhinus* has been applied. Rafinesque used *Vespertilio* for the first named form in 1818. Later authors (Lesson, 1827; LeConte, 1831; Cooper, 1837) discerned a likeness between European and American big-eared bats and used the name *Plecotus* for both groups. Following this was a brief period of belief that the American big-eared bats and Eurasian barbastelles were related, and the name *Synotis* was used for both (Wagner, 1855; H. Allen, 1864). H. Allen gave the American big-eared vespertilionines independent generic status for the first time in 1865 with the name *Corynorhinus.* This position was confirmed by Miller (1897, 1907) and more recently by Tate (1942). In the 75 years following its conception, the name *Corynorhinus* has been in almost universal usage for the American forms exclusive of *Euderma.* A major exception was Dobson's (1878) conclusion that *Corynorhinus* is a synonym of *Plecotus.* Beginning with Simpson (1945), there has been a new trend away from the independent use of the name *Corynorhinus* and a tendency to synonymize it under the name *Plecotus*. However, there seems to have been no study of specimens to support the contention that *Corynorhinus* and *Plecotus* are congeneric, or to determine the relation of *Idionycteris* to them.

Classification of Big-Eared Bats

While agreeing with the basic outline of Tate's (1942, p. 225) classification of vespertilionid big-eared bats, I prefer a slightly modified version:

- Subfamily Vespertilioninae
  - Group Myotini
    - Genera: *Euderma*
    - *Plecotus*
      - Subgenera: *Idionycteris*
      - *Plecotus*
      - *Corynorhinus*
  - Group Pipistrellini
    - Genera: *Histiotus*
    - *Laephotis*
  - Group Nycticeini
    - Genus: *Otonycteris*

In my opinion, the degree of difference between the nominal genera *Idionycteris*, *Plecotus*, and *Corynorhinus* is of subgeneric or specific rather than generic grade. *Idionycteris* is a basal or relict form, whereas *Plecotus* and *Corynorhinus* represent more advanced or later evolutionary stages. *Corynorhinus* has evidently differentiated more rapidly than *Plecotus*, and has approached the point of generic distinction from its near relatives. Inasmuch as these forms represent different stages of evolution and since they form a disjunct series, at least one of the steps of which contains more than one species, it seems best to regard the degree of difference between the three forms of as subgeneric rather than specific magnitude. Evidence in support of this thesis is presented in the following pages.

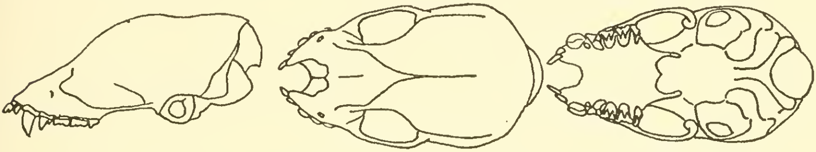
Characters and Comparisons

Cranial characters relating *Euderma* and *Plecotus* and distinguishing them from other big-eared bats (*Histiotus*, *Laephotis*, *Otonycteris*, *Nyctophilus*, *Pharotis*, and *Antrozous*) of the family Vespertilionidae are:

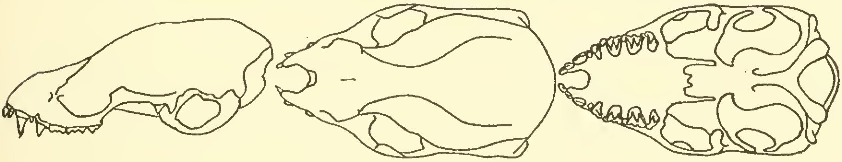
1. Rostrum relatively weak, narrow, and shallow.
2. Brain case elongated and vaulted in the frontal region.
3. Zygomata parallel (in dorsal view) and not bowed out posteriorly.
4. Dentition weak (teeth not robust).
5. Cusps of teeth high and sharp-pointed.
6. P_4 not so high as M_1.
7. Teeth reduced in number only slightly from the chiropteran maximum.

The bats of the genera *Euderma* and *Plecotus* form a close-knit unit, morphologically and, apparently, phyletically. *Euderma* and *Plecotus* appear to be more closely related to one another than either is to any other vespertilionid genus, yet the differences separating them are clearly of generic grade (table 1).

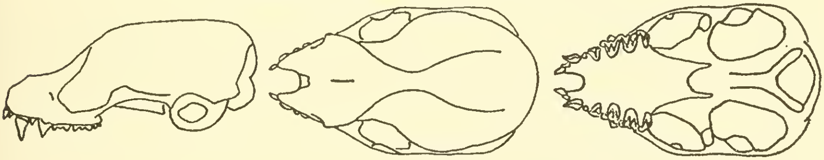
The nearest relative of *Euderma* and *Plecotus* appears to be *Barbastella* (p. 118). Also closely related are *Myotis* and *Pipistrellus* and their closest allies. Similarities most striking are the lack of



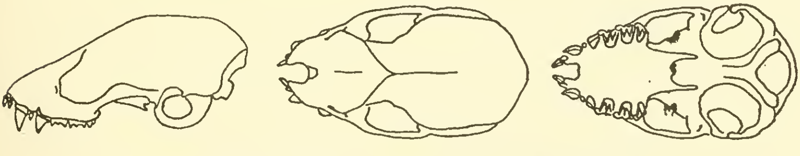
BARBASTELLA BARBASTELLUS USNM 142583 SWITZERLAND



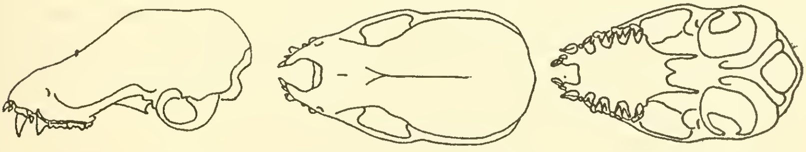
EUDERMA MACULATUM MCZ 42130 ARIZONA



PLECOTUS (IDIONYCTERIS) PHYLLOTIS AMNH 62260 TAMAULIPAS



PLECOTUS (PLECOTUS) AURITUS MCZ 36987 GERMANY



PLECOTUS (CORYNORHINUS) TOWNSENDII MCZ 40876 WASHINGTON

FIGURE 4.—Skulls of *Barbastella*, *Euderma*, and *Plecotus* (*Barbastella* about 4 times natural size, others about 3 times natural size). Traced from photographs.

shortening of the rostrum and lack of dental specialization (loss of teeth and cusps). In these features the resemblance of *Euderma* and *Plecotus* to *Myotis* is greater, to *Pipistrellus* less. This relation is further substantiated in the postcranial skeleton, where *Euderma* and *Plecotus* have some characters of *Myotis* (species compared: *lucifugus, thysanodes, yumanensis*), and some of *Pipistrellus* (species compared: *javanicus, subflavus*), but in most features they are more like *Myotis*. On the basis of dental, osteological, and external features, it appears that *Euderma* and *Plecotus* should stand between *Myotis* and *Pipistrellus* in the classification of Chiroptera.

GENUS EUDERMA: *Euderma maculatum* is more specialized than any species of *Plecotus*. It has carried auditory modification—the most spectacular character of the two genera—to the greatest extreme, and in dental characters it is unique. By elongation, in addition to enlargement, of the auditory bulla it has departed from the usual vespertilionid pattern. Externally too, *Euderma* has exceeded *Plecotus* and, indeed, all other vespertilionids in auditory specialization—in extreme enlargement of the auricle, in the simplification of the tragus by elimination of the posterior basal lobe, and in the attachment of the tragus to the posterior basal lobe of the auricle as well as to the anterior basal lobe so that the auricle forms a more perfect funnel to the auditory meatus.

Hall (1934) pointed out important differences between the body skeletons of *Euderma* and *Plecotus*. Notable are the unusual length and shape of the presternum and the shape and angle of the acromion process of the scapula in *Euderma*.

The anterior portions of the tooth rows show great specialization in *Euderma*. In the upper jaw I^1 and P^1 are reduced; in the lower the canine is reduced (though provided with a prominent accessory cusp), P_3 has been eliminated, and P_4 is single-rooted. The posterior portions of the tooth rows, on the other hand, are morphologically primitive in character: There is a trace of a hypocone cusp on M^1 and on M^2, the metacone of M^3 is well developed, and P_4 has a metaconid cusp. With the exception of the elongated brain case and bifid median postpalatal prominence, other features of the cranium are primitive as far as the genera *Euderma* and *Plecotus* are concerned: The rostrum is weak, the supraorbital region is sharply ridged, the temporal ridges do not coalesce, and the zygomata are strong and are provided medially with a large postorbital expansion.

The nostrils are unspecialized, retaining the primitive basic vespertilionid shape, as seen in *Myotis* and *Pipistrellus*.

The evolutionary significance of the bold black and white color pattern of the fur is not known. Such a pattern crops up sporadically in the orders of the class Mammalia, but is notably rare in Chiroptera.

Among the vespertilionids it is seen only in *Euderma maculatum* and in the rare African *Glauconycteris superba* (Hayman, 1939, 1946), which resembles *Euderma maculatum* in being black and white but has a more elaborate pattern. Hayman even suggested a similarity of the pattern of *Glauconycteris superba* to that of the spotted skunk, *Spilogale*. Some other species of *Glauconycteris* have a similar pattern but with subdued brown and buff tones rather than black and white. *Scotomanes ornatus* of southeastern Asia has a pattern of white spots and stripes on the pelage, but the ground color is bright reddish rather than black. In some other forms, *Kerivoula picta* and *Myotis formosus* for example, the flight membranes, rather than the fur, are patterned with contrasting colors (Wroughton, 1912, p. 1195, pl. A).

Despite numerous evidences of specialization, *Euderma* retains many primitive traits. It appears to occupy an evolutionary position below the more abundant and more progressive, although less specialized, *Plecotus*, with which it shares its geographic range. An early derivative of the *Euderma-Plecotus* stock, *Euderma maculatum* has traveled a road of independent specialization to the point where it is possibly overspecialized.

GENUS PLECOTUS: From the study of Recent and fossil material, I infer that the hypothetical ancestor from which the subgenera *Idionycteris*, *Plecotus*, and *Corynorhinus* were derived probably had the following characteristics: Tooth rows not crowded; I^1 bicuspidate; I^2 simple, about two-thirds the height of I^1; upper canine strong and exceeding P^4 in height; P^1 robust, considerably exceeding cingulum of canine in height; P^4 with full hypocone surface, a large anterior cingulum, and a protocone cusp; M^1 and M^2 without trace of a hypocone cusp; M^3 with prominent metacone and a fourth commissure; lower incisor series strongly imbricated and increasing in size from I_1 to I_3; lower canine equaling protoconid cusp of M_1 in height; P_1 much more robust than P_3; P_4 double-rooted; lower molars with internal cusps almost equaling external cusps in height. Rostrum narrow and arched; anterior nares not enlarged; supraorbital region sharply ridged; temporal ridges not forming a sagittal crest; zygoma strong and expanded in middle third; basial pits not developed; median postpalatal prominence absent. Nostril with full cornu and lacking posterior elongation; muzzle glands not enlarged; auricle large, with a simple, complete anterior basal lobe, a small accessory anterior basal lobe, and transverse ribs not reaching the posterior margin of the auricle.

From this generalized or primitive pattern, derivations, either in the form of reduction or simplification or in the form of elaboration, are to be regarded as traits of specialization or progressiveness. In no instance are these bats sufficiently well known to determine the teleological significance of these traits.

The differences distinguishing the subgenera *Idionycteris, Plecotus,* and *Corynorhinus* mainly concern the external configuration of the nostril, muzzle, and ears (table 2). Dental, cranial, and skeletal differences are numerous but slight (table 3). In the following discussion, *Plecotus townsendii* is given as a typical example of the subgenus *Corynorhinus.* Unless otherwise noted, statements regarding it apply equally to the other Recent species of the subgenus, *P. mexicanus* and *P. rafinesquii.* The subgenera *Plecotus* and *Idionycteris* are monotypic, represented respectively by the species *P. auritus* and *P. phyllotis.* Inasmuch as *P. phyllotis* is known to me only from three specimens, statements concerning it must be regarded as highly tentative.

The dental formula is the same in the three subgenera, and, as may be seen from the following comparisons, the individual teeth must be closely scrutinized in order to detect differences.

The secondary cusp of I^1 is absent or variable in *P. townsendii,* usually present in *P. mexicanus,* and always present in *P. rafinesquii, P. phyllotis,* and *P. auritus.* The space between I^2 and the canine is frequently, but not always, greater, and P^1 averages larger in *P. auritus* than in the other species. P^4 is consistently wider than long in *P. phyllotis* and *P. townsendii;* longer than wide in *P. auritus.* Because the metacone of M^3 is somewhat reduced in *P. auritus,* the third commissure of M^3 is equal to or shorter than the second in most individuals, whereas in *P. phyllotis* and *P. townsendii* the third commissure is normally equal to or longer than the second. P_1 is usually more robust in *P. auritus* and *P. phyllotis* than in *P. townsendii,* considerably exceeding P_3 in size. P_4 is double-rooted in *P. auritus;* single-rooted in *P. phyllotis* and *P. townsendii.* In *P. phyllotis* the internal cusps of the mandibular molars are almost as high as the external cusps; in the other species of *Plecotus* the internal cusps are lower.

An analysis of these observations on dentition reveals four features, which, because each is consistent in at least one of the subgenera, may be regarded as having primary taxonomic significance. These features are the simplification in I^1, M^3, and P_4 respectively, and the specialization in P^4. *P. phyllotis* exhibits the generalized (unsimplified and unspecialized) condition in three features, is specialized in one (P_4); whereas *P. auritus* is specialized in two (P^4 and M^3); and all of the species of the subgenus *Corynorhinus* are specialized in one (P_4) and one of the species in another (I^1). Three other features—crowding of the upper incisor series and diminution of the size of P^1 and P_1—are inconsistent, but may be of some significance. In these

Table 1.—*Morphological characters distinguishing* Euderma *from* Plecotus

Euderma	*Plecotus*
Median postpalatal process a bifid prominence.	Median postpalatal process absent or a simple spine.
Auditory bullae roughly elliptical in outline.	Auditory bullae roughly circular in outline.
Brain case relatively long: postpalatal length averages 40–41% of greatest length.	Brain case relatively short: postpalatal length averages 34–38% of greatest length.
Presternum longer than wide.	Presternum wider than long (unknown in *Plecotus phyllotis*).
Upper incisors stand in line with toothrow.	Upper incisors stand inside toothrow.
I^1 almost as small as I^2.	I^1 a third higher and twice as wide as I^2.
P^1 minute; not exceeding cingulum of canine in height.	P^1 larger; exceeding cingulum of canine in height.
Hypocone cusp barely indicated in M^1 and M^2.	Hypocone cusp not indicated in M^1 and M^2.
Lower canine small; not exceeding P_4 in height.	Lower canine large; much exceeding P_4 in height.
Anterointernal cusp of lower canine almost equal to primary cusp in height.	Anterointernal cusp of lower canine small and greatly exceeded by primary cusp.
P_3 absent.	P_3 present.
P_4 with well defined metaconid cusp.	P_4 lacking metaconid cusp.
Tragus lacking basal lobe.	Tragus with prominent basal lobe.
Tragus united with posterior basal lobe of auricle.	Tragus and posterior basal lobe of auricle not united.
Coloration black and white in bold pattern.	Coloration drab brownish, essentially without pattern.

TABLE 2.—*Comparison of external characters of the subgenera of* Plecotus (Idionycteris *most generalized*, Corynorhinus *most specialized*, Plecotus *intermediate*)

Idionycteris	*Plecotus*	*Corynorhinus*
Nostril unspecialized.	Nostril with posterior elongation; cornu reduced.	Nostril with posterior elongation; cornu absent.
Muzzle glands not enlarged (?).	Muzzle glands slightly enlarged.	Muzzle glands greatly enlarged.
Auricle with anterior basal lobe complete.	As in *Idionycteris*.	Auricle with anterior basal lobe reduced.
Accessory anterior basal lobe of auricle developed into a projecting lappet.	Accessory anterior basal lobe of auricle slightly developed.	Accessory anterior basal lobe of auricle absent.
Transverse ribs on auricle fade out before reaching posterior border.	Transverse ribs on auricle run without interruption to posterior border.	Transverse ribs on auricle interrupted by vertical rib near posterior border.
Second phalanx of third digit longer than first phalanx.	Second phalanx of third digit equal to or shorter than first phalanx.	As in *Idionycteris*.
Calcar keeled.	Calcar not keeled.	As in *Plecotus*.
Interfemoral membrane attached to tip of last caudal vertebra.	Interfemoral membrane attached to base of last caudal vertebra.	As in *Idionycteris*.

features *P. phyllotis* is generalized in one (P_1) and is dubiously specialized in the others; *P. auritus* is generalized in all; and *P. townsendii* is specialized in all.

Likewise, in cranial details specialization is greatest in *P. townsendii*, least in *P. phyllotis* (fig. 4). In the more primitive species, *P. phyllotis* and *P. auritus*, the supraorbital region is sharply ridged; in *P. townsendii* it is smoothly rounded [also in the Lower Pleistocene *P. crassidens;* faintly ridged in the Middle Pleistocene *P.* (*Corynorhinus*) *alleganiensis*]. The temporal ridges converge to form a median sagittal crest in *P. auritus* and *P. townsendii*, but remain apart in *P. phyllotis* and to a lesser degree in *P. alleganiensis*.

TABLE 3.—*Comparison of crania of the subgenera of* Plecotus (Idionycteris *most generalized,* Corynorhinus *most specialized,* Plecotus *intermediate*)

Idionycteris	*Plecotus*	*Corynorhinus*
Supraorbital region sharply ridged.	As in *Idionycteris.*	Supraorbital region smoothly rounded or faintly ridged.
Zygoma relatively thick and strong; postorbital expansion in middle third of arch.	As in *Idionycteris.*	Zygoma relatively thin and fragile; postorbital expansion in posterior third of arch.
Median postpalatal process absent.	Median postpalatal process a poorly developed spine.	Median postpalatal process a prominent spine.
Basial pits absent.	As in *Idionycteris.*	Basial pits prominent.
Brain case relatively shallow: averages 33% of greatest length.	Brain case relatively shallow: averages 32% of greatest length.	Brain case relatively deep: averages 35–38% of greatest length.
Brain case relatively broad: averages 53% of greatest length.	Brain case relatively narrow: averages 49% of greatest length.	Brain case relatively narrow: averages 48–50% of greatest length.
Rostrum flattened, with median concavity.	Rostrum arched, lacking median concavity.	As in *Idionycteris.*
P^4 wider than long.	P^4 longer than wide.	As in *Idionycteris.*
Metacone of M^3 not reduced; 3rd commissure equal to or longer than 2nd.	Metacone of M^3 reduced; 3rd commissure usually equal to or shorter than 2nd.	As in *Idionycteris.*
P_4 single-rooted.	P_4 double-rooted.	As in *Idionycteris.*

Broadening and anterior bulging of the brain case in *P. phyllotis* and increase in depth of the brain case in *P. townsendii* may be regarded as specializations. Shortening, broadening, and flattening of the rostrum together with enlargement of the anterior nares in *P. townsendii* are specializations that are somewhat paralleled in *P.*

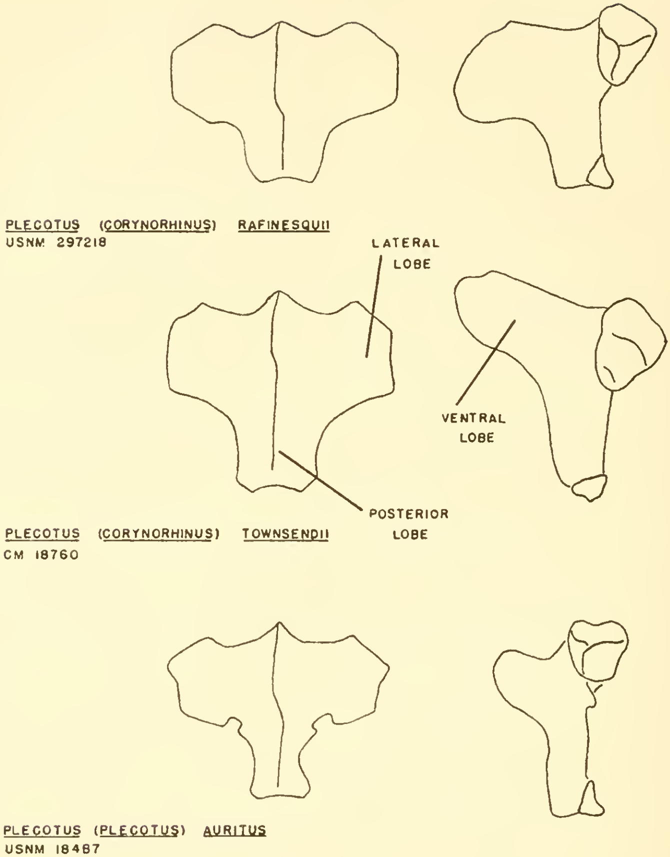


Figure 5.—Comparison of the presternum of three species of *Plecotus*. Ventral (left) and lateral (right) aspects. Camera lucida sketches.

phyllotis, although the anterior nares are not enlarged in the latter species.

The zygomatic arches show progressive reduction and weakening through the series from relatively heavy and strong in *P. phyllotis* and *P. auritus* to relatively light and weak in *P. townsendii*. Also, in the latter species there is a shift of the postorbital expansion of the zygoma from its primitive median position to a posterior location.

The median postpalatal process, absent in *P. phyllotis*, is slightly developed in *P. auritus*, and is a prominent spine in *P. mexicanus* and in some forms of *P. townsendii*. The lateral grooves ("basial pits") commencing in the basioccipital and ending abruptly in the basisphenoid are prominent in *P. townsendii;* they are ill-defined or absent in the more primitive *P. phyllotis* and *P. auritus*. Slight elongation of the auditory bullae is a specialization peculiar to *P. phyllotis*. The typical vespertilionid bullar shape, as seen in *P. auritus* and *P. townsendii,* is roughly circular.

The postcranial skeleton is unknown in *P. phyllotis* and differences in this respect between *P. auritus* and *P. townsendii* are few. In the latter species the proximal articular surface of the radius is expanded, and the presternum has the ventral lobe enlarged and the posterior lobe laterally expanded (fig. 5). *P. auritus* has departed from the usual phalangeal pattern of *Plecotus* and *Euderma,* in which the second phalanx of the third digit is longer than the first (by a slight elongation of the first phalanx and a considerable shortening of the second), rendering not only the proportion different but the combined length less (fig. 6). The calcaral keel, present in *P. phyllotis,* is lacking in the other species of *Plecotus.*

Hamilton (1949, p. 100) pointed out distinctions between the bacula of *P. rafinesquii* and *P. auritus* (as described and figured by Matthews, 1937, p. 222). However, intrageneric discrepancies of similar magnitude seem also to exist among the several species of *Myotis, Pipistrellus,* and *Lasiurus* as described and figured by these same authors. Krutzsch and Vaughan (1955, p. 99) described the

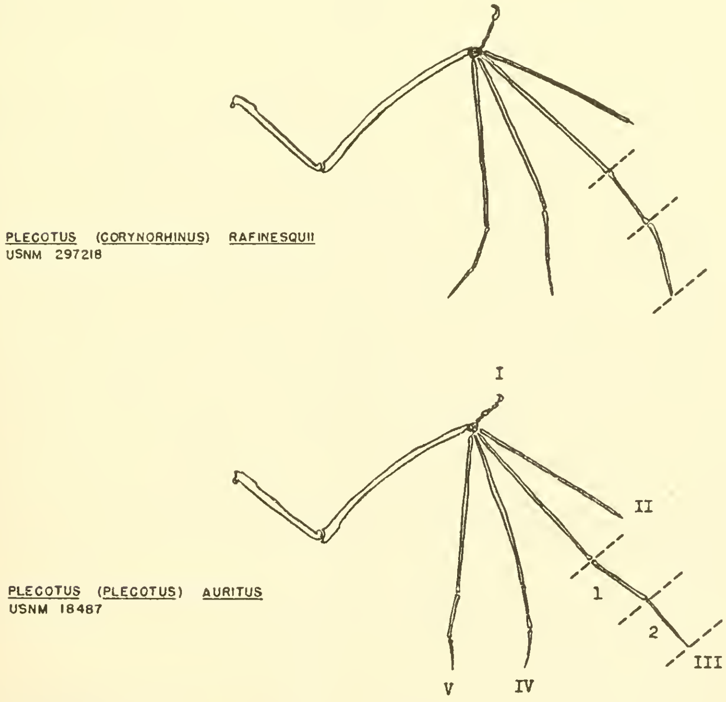


Figure 6.—Pectoral appendages of *Plecotus,* showing relative proportions of first and second phalanges of third digit.

baculum of *P. townsendii* as being similar to that of *P. rafinesquii*. Pearson, Koford, and Pearson (1952, p. 281) noted that the subgenera *Plecotus* and *Corynorhinus* "possess in common two pairs of Cowper's glands, a feature not found in other vespertilionids. Likewise, seminal vesicles apparently are lacking in both of these genera [subgenera]."

Of all the morphological features distinguishing the species of *Plecotus*, those of the muzzle and external ears have been supposed to be of the greatest taxonomic significance.

Enlarged muzzle glands in *P. townsendii* protrude as grotesque lumps two to three millimeters high on either side of the muzzle (fig. 7). There are similar glandular areas on the muzzle of *P. auritus*, but they do not project as in *P. townsendii*. They may not be conspicuous in *P. phyllotis;* there is no external trace of them on three dry study skins. Dalquest and Werner (1954, p. 156) have observed that the facial glands of *P. rafinesquii* are histologically similar to those of other vespertilionids, particularly *Myotis* and *Pipistrellus*. The prominent muzzle glands (or "nose lumps") are solid masses of skin covered sebaceous glandular tissue. There are in addition, in the facial area, nests of sebaceous glandular cells, sudoriferous glands, and a sublingual gland of the mucous type. The submaxillary gland apparently has been forced out of the facial area by the extensive development of the other glandular tissues.

A peculiar posterior elongation of the nostril in *P. auritus* gives the nostril a crescentic shape (fig. 8). The cornu surrounding the narial opening is slightly reduced from the primitive vespertilionid condition, as seen in *Myotis* and *Pipistrellus*, and there is a conspicuous shallow basin extending posteriad from the posterolateral corner of the opening and separated from it by a septum. A similar posterior elongation of the nostril in *P. townsendii* is partially concealed by the overlapping muzzle glands. In this species the cornu is reduced to the point of obliteration, and the narial opening is squarish in outline and is bordered by smooth pale-colored skin resembling the lining of the nostril. As in *P. auritus*, the narial opening proper and the posterior elongation are separated by a septum. In the available specimens of *P. phyllotis* the nostrils appear to approximate the primitive vespertilionid type, with full cornua and without posterior elongations.

The snout is truncate in *P. auritus* and *P. townsendii* rather than acute as in *Euderma maculatum* and most other vespertilionines (possibly acute in *P. phyllotis*).

A lappet projecting over the forehead from the anterior base of the auricle is the chief characteristic of *P. phyllotis*. This appendage is an enlargement of the accessory anterior basal lobe of the auricle (fig.

9), a lobe that is present, although small and inconspicuous, in *P. auritus* but absent in *P. townsendii.* Modification also occurs in the primary anterior basal lobe, where variation ranges from reduction in *P. townsendii* to no modification in *P. phyllotis* and enlargement in *P. auritus* (fig. 9).

Thus, with regard to the dental, osteological, and external characteristics of these bats, it appears that *P.* (*Idionycteris*) *phyllotis* is the most generalized and primitive member of the group; *P.* (*Corynorhinus*) *townsendii* is most specialized and progressive; and *P.* (*Plecotus*) *auritus* is intermediate (but nearer *P. townsendii*).

Comparison of *Plecotus* with other vespertilionine genera confirms the observation that the differences among its species are, at most, of no more than subgeneric magnitude. *Myotis*, *Pipistrellus*, and

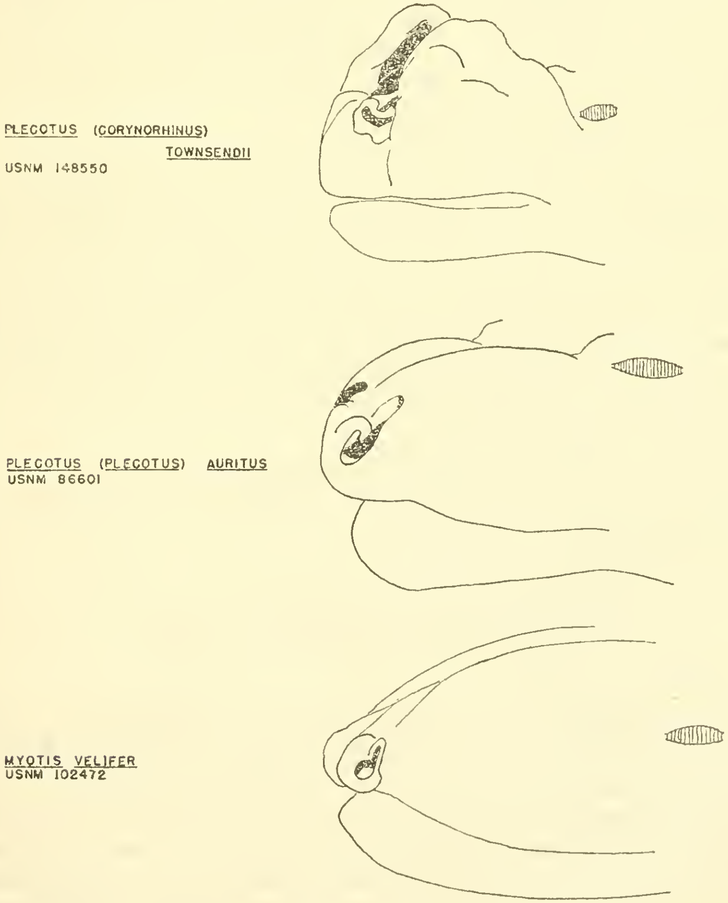


FIGURE 7.—Muzzles of *Plecotus*, compared in anterolateral aspect with the muzzle of *Myotis*, a generalized vespertilionid. Camera lucida sketches.

Eptesicus are not suitable for such a comparison because of the probability that they are polyphyletic aggregations, and not natural groups. Most of the other vespertilionine genera are either monotypic, consist of slightly differentiated species, are of disputed validity, or are not sufficiently well known. The American genus *Lasiurus* is a notable exception, being well known, widely distributed, and containing several well-differentiated species. Included in the genus are the red bats (*L. borealis*, etc.), hoary bats (*L. cinereus*, etc.), and yellow bats (*L. ega*, etc.). The magnitude of the differences distinguishing these species equals or exceeds the magnitude of the differences distinguishing the species *Plecotus phyllotis*, *P. auritus*, and P. *townsendii* (compare tables 2, 3, and 4).

STATUS OF GENUS BARBASTELLA: Miller (1907, p. 224) pointed out the likeness of *Barbastella* to *Euderma* and *Plecotus*, whereas Tate (1942, p. 230) tried to show that any relationship between *Barbastella* and these genera is remote. Tate believed that *Euderma* and *Plecotus* are derivatives of the *Myotis* stem, and he supposed that *Barbastella* came from the *Pipistrellus* stem.

The strongest resemblances of *Barbastella* to *Pipistrellus* are in tooth formula, and in the posterior shortening of the palate, which extends only a short distance past M^3. Like *Pipistrellus*, but also like *Myotis* as well, *Barbastella* has small, relatively simple auditory bullae; fragile, much-reduced zygomata without postorbital expansions; and a short angular process of the mandible. The few resemblances of *Barbastella* to *Pipistrellus* and its relatives seem to lose much of their significance, however, in view of the many similarities of *Barbastella* to *Euderma* and *Plecotus:*

1. Rostrum relatively narrow and weak.
2. Brain case elongated and vaulted in frontal region.
3. Zygomata (in dorsal aspect) parallel and not bowed out posteriorly.
4. Coronoid process of mandible high.
5. Dentition weak.
6. Cusps of teeth high and sharp.
7. Lower incisors graduated in size (I_3 large to I_1 small).
8. I_3 with prominent extra internal cusp (total of 4 cusps).
9. Lower canine with prominent anterointernal basal cusp.
10. P_4 not so high as M_1.

The resemblance of the teeth in *Barbastella*, *Euderma*, and *Plecotus* is particularly striking. In shape and proportions, the teeth of these genera are almost identical. The facts that one of the upper premolars (P^1) has been crowded out of the tooth row and that one of the lower premolars (P_3) has been eliminated in *Barbastella* are not sufficient in themselves to indicate that *Barbastella* is closely related to *Pipistrellus*. (Note that *Euderma* also has the same dental formula as *Pipistrellus*.)

TABLE 4.—*Morphological characteristics of bats of the genus* Lasiurus

red bats (*L. borealis*, etc.)	hoary bats (*L. cinereus*, etc.)	yellow bats (*L. ega*, etc.)
Size small (forearm 37–44 mm.)	Size large (forearm 46–57 mm.)	Size large (forearm 44–57 mm.)
Lateral wings of presternum equal to body of presternum in width.	Lateral wings of presternum equal to body of presternum in width.	Lateral wings of presternum considerably broader than body of presternum.
Presternum about as long as wide.	Presternum much longer than wide.	Presternum about as long as wide.
Auditory bullae not enlarged.	Auditory bullae slightly enlarged.	Auditory bullae not enlarged.
Rostrum relatively short.	Rostrum medium.	Rostrum relatively long.
Sagittal crest very weak.	Sagittal crest weak.	Sagittal crest strong.
Coronoid process medium height.	Coronoid process low.	Coronoid process high.
P^1 usually present.	P^1 usually present.	P^1 always absent.
Hypocone slightly reduced on M^1 & M^2.	Hypocone much reduced on M^1 & M^2.	Hypocone slightly reduced on M^1 & M^2.
M^3 very reduced.	M^3 reduced.	M^3 slightly reduced.
P_4 double-rooted.	P_4 single-rooted.	P_4 double-rooted.
M_3 talonid reduced.	M_3 talonid only slightly reduced.	M_3 talonid much reduced.

Barbastella is unique in the degree of posterior extension of the anterior nares, which reach so far back that the vomer is exposed as a median spine. Its muzzle glands are almost as large as those in the subgenus *Corynorhinus*. A pair of deep grooves extend from the nostrils to the upper lip. The auricles are peculiarly short and broad and are connected across the forehead. In each there is a conspicuous subapical lobe on the posterior border, and the posterior basal lobe is attached nearer the angle of the mouth than in *Euderma* or *Plecotus*.

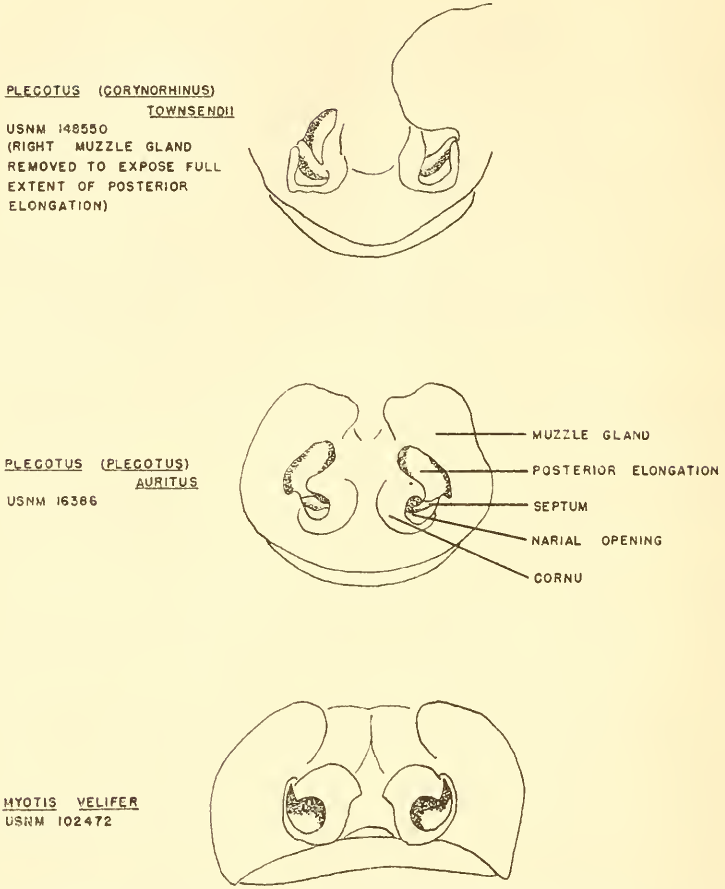


Figure 8.—Muzzles of *Plecotus*, compared in anterodorsal aspect with the muzzle of *Myotis*, a generalized vespertilionid. Camera lucida sketches.

The tragus is relatively long, is broad at the base, and tapers abruptly to a pointed tip.

Barbastella is a relative of *Euderma* and *Plecotus* that lacks the extreme auditory specialization characterizing these genera. In this respect, *Barbastella* must be more primitive than *Euderma* and *Plecotus*. On the other hand, in most cranial details *Barbastella* is similar to *Euderma* and *Plecotus*, and in some features such as fragile zygomata, large anterior nares, posterior nares lying far forward, and short tooth rows it has surpassed them in degree of specialization.

If the assumption is correct that *Barbastella* is closely related to *Euderma* and *Plecotus*, then it follows that most of the cranial characters shared by the three genera must have been established before auditory specialization occurred. Further, the *Barbastella* stock must

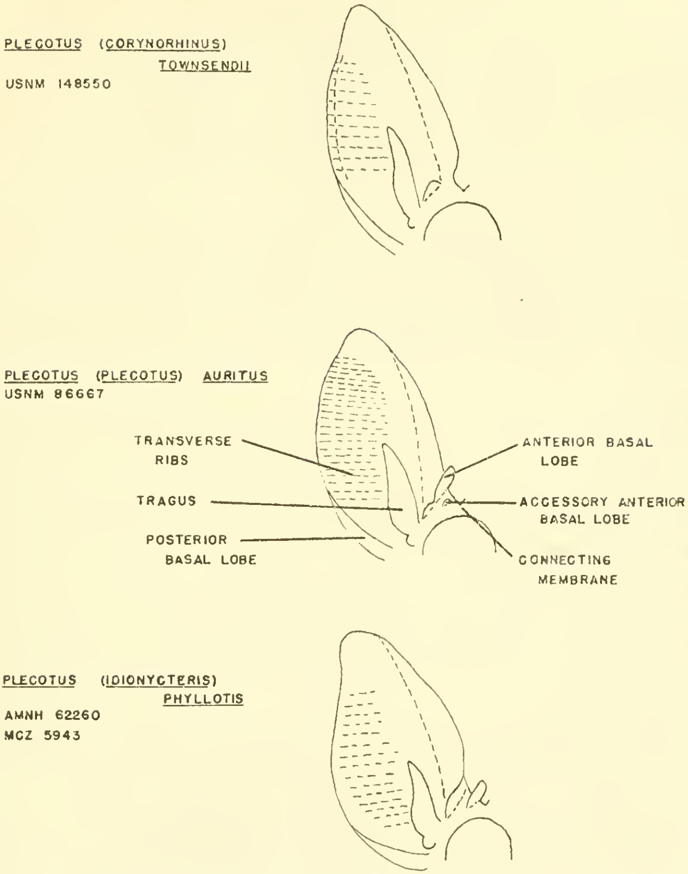


FIGURE 9.—Variation in the auricle and its appendages in *Plecotus*. Free-hand sketches.

have been derived very early and had a long subsequent period of independent development and specialization.

Systematic Treatment

Key to the genera *Euderma* and *Plecotus*

Posterior basal lobe of auricle attached to base of tragus; auditory bulla elongated (elliptical in outline); I^1 almost as small as I^2; hypocone cusp indicated on M^1 and M^2; lower canine small, but its anterointernal cusp greatly enlarged; P$_3$ absent; P$_4$ with well defined metaconid cusp; coloration black and white in bold pattern . . . . **Euderma** (p. 122)

Posterior basal lobe of auricle separated from tragus by a notch; auditory bulla not elongated (circular in outline); I^1 a third higher and twice as wide as I^2; hypocone cusp not indicated on M^1 and M^2; lower canine large, but its anterointernal cusp small; P$_3$ present; P$_4$ lacking metaconid cusp; coloration drab brownish, essentially without pattern . . . . **Plecotus** (p. 127)

Genus *Euderma* H. Allen

Histiotus J. A. Allen, 1891, p. 195. (Part.)
Euderma H. Allen, 1892, p. 467.

Type species: *Histiotus maculatus* J. A. Allen.

Distribution: Southwestern United States and probably northwestern Mexico.

Description: Supraorbital region sharply ridged (fig. 4); temporal ridges not coalescing posteriorly to form a sagittal crest; brain case exceptionally elongated; zygoma relatively heavy, with postorbital expansion in middle third of arch; median postpalatal process a bifid prominence; auditory bulla roughly elliptical in outline; presternum longer than wide.

Upper incisors in line with tooth row; I^1 simple, without accessory cusps (fig. 2), except occasionally near cingulum, and small, only slightly larger than I^2; I^2 close to or touching upper canine; P^1 minute; hypocone cusp barely indicated on M^1 and M^2; third commissure longer than second and metacone relatively well developed in M^3; lower canine reduced in thickness, not exceeding P_4 in height, and possessing a prominent anterointernal secondary cusp almost equaling primary cusp in height; P_1 about one-half the size of P_4, and not crowded; P_3 absent; P_4 single-rooted and possessing a well defined metaconid cusp.

No large glandular masses on muzzle (fig. 7); nostril opening small, of primitive vespertilionid type (fig. 8), provided with a cornu, and not extended posteriorly or opening upward; auricle and tragus very large (fig. 9); tragus not provided with a basal lobe, but united with posterior basal lobe of auricle; anterior basal lobe of auricle complete; transverse ribs on auricle extend to posterior border of auricle; second phalanx of third digit longer than first phalanx (fig. 6); calcar not keeled; interfemoral membrane attached to base of last caudal vertebra; coloration black and white in bold pattern; membranes and ears grayish.

Euderma maculatum J. A. Allen

Histiotus maculatus J. A. Allen, 1891, p. 195.
Euderma maculata H. Allen, 1894, p. 61.

Holotype: AMNH 3920/2991; young adult skin (skull lost subsequent to original description); "caught on a fence" in March 1890, by Thomas Shooter; near Piru, Ventura County, Calif. [probably mouth of Castac Creek, Santa Clara Valley, 8 miles east of Piru, Los Angeles County, Calif. (Miller, 1897, p. 49)].

Distribution: Southwestern United States and probably northwestern Mexico (fig. 10). West to Washoe County, Nev.; Mariposa, Kern, and Los Angeles Counties, Calif. South to Riverside County, Calif.; Yuma County, Ariz.; (?Magdalena, Sonora?); Dona Ana County, N. Mex. East to Dona Ana County, N. Mex.; San Juan and Salt Lake Counties, Utah; Yellowstone County, Mont. North to Yellowstone County, Mont.; Canyon County, Idaho; Washoe County, Nev. Zonal range: Lower Austral to Transition. Altitudinal range: 189 feet below sea level in Riverside County, Calif., to 4,045 feet in Mariposa County, Calif. Only 16 specimens are known to be preserved in museums.

Description: As indicated above. Adult coloration: Upper parts blackish with large, roughly circular, white spots on the shoulders

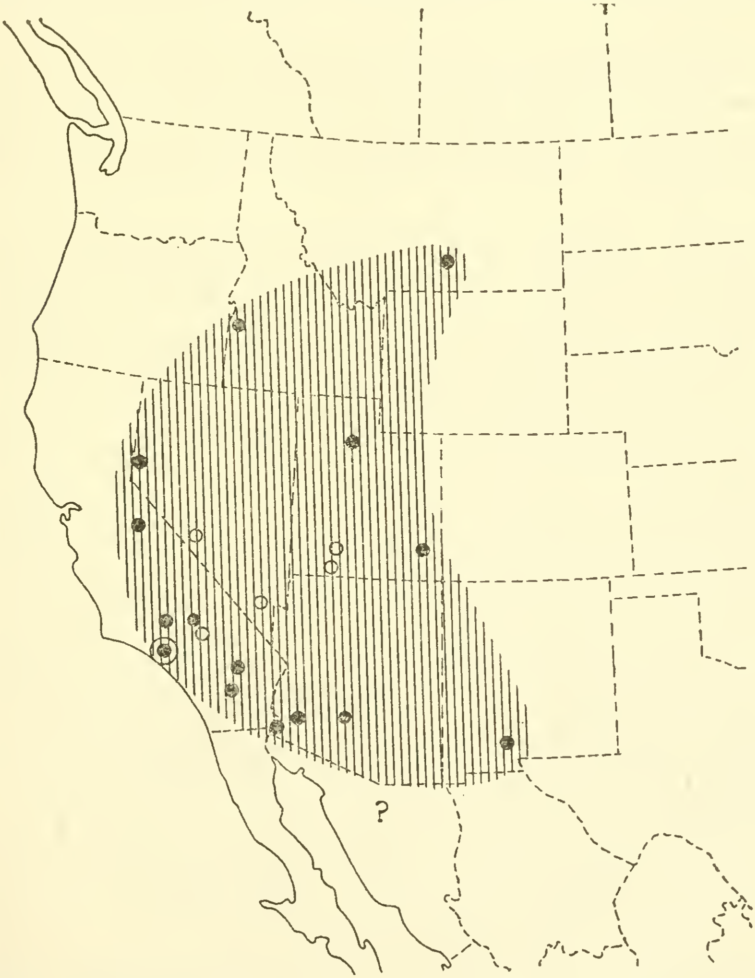


Figure 10.—Distribution of *Euderma maculatum* J. A. Allen. Solid symbols, specimens in museums; open symbols, other records; encircled solid symbol, type locality.

and at the base of the tail, and patches of cottony white hair at the posterior base of each auricle; all hairs black at base, except those at posterior bases of auricles. Underparts with hairs white tipped, the white incompletely concealing the black bases. Membranes pale grayish brown, auricles and tragi yellowish brown.

Measurements: See tables 7, 13.

Remarks: USNM 269842, not reported previously, was captured 9 miles east of Roll, Yuma County, Ariz., on 5 August 1940, and was submitted to the National Museum by Mrs. W. A. Jones, Box 3, Roll, Ariz. It is an adult, probably a male, mummified, with the skull still inside the skin. In Mrs. Jones' words, the details of its capture were as follows:

> Dear Sirs. Am sending a bat of a kind I haven't seen before. . . . The bat was captured the fifth of August, here at my home. It was a very hot day, and the bat kept coming and lighting on the screened porch. My son [Weldon Allen, Jr.], nine years old, caught it and brought it in the house. We gave it water. It was very thirsty. It lived about three hours after catching it. . . . I wish you could have seen the bat when it was alive. It was a pretty thing in an odd way.

Habitat: *Euderma* has seldom been collected or observed alive by a mammalogist, despite the fact that it inhabits one of the most intensively collected areas of the world. At least five of the records for it can be attributed to small boys, and many of the other records stem from persons neither scientists nor naturalists. Use of mist nets and other trapping devices has failed to produce specimens.

Euderma appears to be an inhabitant primarily of open or scrub country. There is only one record of occurrence in a forest, in Yosemite Valley, Calif. (Parker, 1952, p. 480); however, Vorhies (1935, p. 225) quoted Herbert Brown as stating that Arizona Indians assured him it was a forest dweller. Usually it has been found in or on houses—in biological laboratory (Miller, 1903, p. 165; Hall, 1935, p. 148); in residence (Nicholson, 1950, p. 197); on porch (Hardy, 1941, p. 293; Mrs. W. A. Jones, 1940, in litt.; Benson, 1954, p. 117); under eaves of house (Durrant, 1935, p. 226; Ashcraft, 1932, p. 162); clinging to side of brush house (Vorhies, 1935, p. 225); in driveway near house (Tucker, 1957, p. 406). Less frequently it has been observed in caves or cave-like structures—in moist cave (Hardy, 1941, p. 293); in springhouse dug into hillside (Parker, 1952, p. 481); in mine tunnel (Vorhies, 1935, p. 225); in root cellar (Hall, 1946, p. 158). One that was being attacked by yellow jackets when found perhaps had tried to creep into a crevice or tree hole where these insects nested (Parker, 1952, p. 480). Several specimens have been in or near water—floating in puddle, the overflow from a railway water tank (J. Grinnell, 1910, p. 317); floating in shallow reservoir (Benson, 1954, p. 117);

damp and bedraggled, one foot from river's edge (Parker, 1952, p. 480); hanging from rock projection in closed springhouse (Parker, 1952, p. 481); hibernating above large pool of water in cave (Hardy, 1941, p. 293). One was found hanging [impaled?] on a fence (J. A. Allen, 1891, p. 195) and one with injured wing was found clinging to the lower side of a rock at the base of a cliff (Hall, 1939, p. 103).

Five of the specimens were dead, two were obviously injured, and all but one of the remainder died within a few hours after capture. Several that were obtained alive showed great thirst for water, and at least 10 of the live individuals were exposed to daylight where found. Of the 22 recorded occurrences, 13 were about houses. Six of the 13 were clinging to the outside of the structures.

The normal habitat of this species is unknown. The foregoing facts suggest departures from its normal habitat in response to stimuli of rather frequent occurrence. A narrow tolerance in habitat selection by the spotted bat could explain the lack of natural collections and the frequency of abnormal ones. Suppose that the bat's habitat were very restricted and were such that it might frequently change to the bat's disadvantage. Suppose for instance that *Euderma maculatum* requires absolute privacy from other bats and requires moist places for roosting in its normally arid surroundings. This might restrict it largely to moist crevices, which because of their limited extent might occasionally dry up and force the bat out, to alight, thirsty and dying from desiccation, on porches, sides of houses, in driveways, etc.

The spotted bat fits very well Amadon's description (1953, p. 464), of relict species:

> Relicts are species that tend to become more and more restricted both geographically and ecologically, because they are unable to compete successfully with other species . . . . On continents, relicts often survive by becoming more and more specialized, through a process of natural selection, to a narrow ecological niche where they do manage to retain a competitive advantage.

BEHAVIOR: Most recorded individuals appear to have been solitary wanderers. Although *Euderma maculatum* has been observed at all seasons, seven of the 17 occurrences for which the date is recorded are for the months of August, September, and October, the period of postbreeding season wandering characteristic of many bats. Only at Yosemite Valley, Calif., where two specimens were collected 20 years apart, has more than one specimen been secured, although Hardy (1941, p. 293) was told that four had been found hibernating in a Utah cave. C. Hart Merriam was told by ranchers in the Vegas Valley, Nev., that "a very large bat 'with ears like a jackass and a white stripe on each shoulder' is abundant in that place in the summer" (Miller, 1897, p. 49).

Two reports suggest possible association of *Euderma* with other species of bats. Vorhies (1935, p. 225) quoted Mexican informants as saying "there were many bats in the drifts [side shafts of a mine] and among them was the one spotted one." Hardy (1941, p. 293) observed *Myotis subulatus* and *Plecotus townsendii* in a Utah cave in which *Euderma* had been reported.

Apparently *Euderma* rests suspended by the feet with head down (Parker, 1952, p. 480); an informant of Hardy (1941, p. 293) reported hibernating individuals suspended by the thumbs, with head up. Parker (1952, p. 480) recorded that a captive specimen walked with wrists and feet, and could thus travel over horizontal surfaces with considerable facility. Durrant (1935, p. 226) was told that a captive moved about its cage in pursuit of flies held with forceps.

When the bat is alert the normal carriage of the ear is erect, directed slightly forward, with tip bent slightly back. When disturbed, the bat folds ears, but not the tragus, down against the side of the neck, much in the fashion of *Plecotus townsendii* (Parker, 1952, p. 480).

Some individuals were docile, with little inclination to resist handling (Parker, 1952, p. 481), but one was said to have "had plenty of fight" when molested (Hall, 1939, p. 103). One was being attacked by one or more "yellow jackets," and had sustained injury to the humeral areas of both wings when it was found. It was attempting to fend off the insects with its feet (Parker, 1952, p. 480).

The voice of this bat has been described as a "soft, extremely high-pitched, metallic squeak" (Parker, 1952, p. 481); a hissing noise and rat-like squeak (Hall, 1939, p. 103); and a typical bat chirp (Durrant, 1935, p. 226). Also, it clicks its teeth together (Hall, 1939, p. 103) and makes "a queer grinding noise by gnashing its teeth" (Ashcraft, 1932, p. 162).

The report of an individual that flew through an open door or window into a house at about 11 p.m. (Nicholson, 1950, p. 197) indicates that *Euderma*, like *Plecotus auritus*, may be nocturnal rather than crepuscular.

FOOD: Although several captive individuals eagerly accepted water to drink, few showed interest in various types of food. One ate cottage cheese (Parker, 1952, p. 481). Another, force-fed at first, later readily took flies offered with forceps. It accepted five flies at each of two daily feeding periods. When flies were offered it wrinkled up its nose, chirped, and advanced as rapidly as possible to seize the fly. It also eagerly pursued empty forceps. This individual lived for three weeks in captivity. Its death was accidental (Durrant, 1935, p. 226). Food habits under natural conditions are not known.

Data on migration, hibernation, reproduction, and molt are lacking for this species.

LOCAL NAMES: "Spotted" bat is the name in most general usage, although Hardy (1941, p. 293) referred to the use of the name "pinto" bat in Utah, and Vorhies (1935, p. 225) reported that Mexicans knew it as "pinto" bat in Sonora. Nevadan ranchers likened its ears to those of a jackass (Miller, 1897, p. 49) and Grinnell (1910, p. 318) likened its dorsal color pattern to a "death's-head." Two boys who discovered one on the side of a brush house mistook it, at first glance, for a young rabbit (Vorhies, 1935, p. 225), while a boy who saw one crawling on the ground first thought it was a tarantula spider (Parker, 1952, p. 480). People who saw one with its ears folded back thought it was "some sort of horned beast" (Parker, 1952, p. 480).

Specimens examined: Five, from the following U.S. localities:

New Mexico: *Dona Ana County:* Mesilla Park, 1a (USNM). Arizona: *Yuma County:* 9 miles east of Roll, 1s (USNM); 4 miles south of Yuma, 1s (MCZ). California: *Los Angeles County:* Mouth of Castac Creek, 8 miles east of Piru, 1s (AMNH). Utah: *Salt Lake County:* Salt Lake City, 1s (UU).

Additional records (asterisk indicates specimen preserved in a museum):

MEXICO: Sonora: Near Magdalena (Vorhies, 1935, p. 225).

UNITED STATES: Arizona: *Maricopa County*: Tempe* (Stager, 1957, p. 260). California: *Kern County*: Red Rock Canyon*, 30–40 miles north of Mohave (Hall, 1939, p. 103). *Mariposa County:* Yosemite National Park*, Yosemite Valley, 4,045 feet, 2 specimens (Ashcraft, 1932, p. 162; Parker, 1952, p. 480). *Riverside County:* Mecca*, 189 feet below sea level (J. Grinnell, 1910, p. 317). *San Bernardino County:* China Lake*, 4 miles south of Inyo County line (Stager, 1957, p. 260); Granite Wells, near Pilot Knob, Barstow area (Parker, 1952, p. 481); Twentynine Palms* (Benson, 1954, p. 117). Nevada: *Clark County:* Vegas Ranch, Vegas Valley (Miller, 1897, p. 49). *Esmeralda County:* Fish Lake Valley (Hall, 1946, p. 158). *Washoe County:* Reno* (Hall, 1935, p. 148). Utah: *Garfield County:* Hatch (Hardy, 1941, p. 293). *Kane County:* Crocodile Cave, 4 miles north of Kanab (Hardy, 1941, p. 293). *San Juan County:* 5 miles northwest of Monticello* (Benson, 1954, p. 117). Idaho: *Canyon County:* 15 miles southwest of Caldwell* (Tucker, 1957, p. 406). Montana: *Yellowstone County:* Billings* (Nicholson, 1950, p. 197).

Genus *Plecotus* E. Geoffroy Saint-Hilaire

The synonymy is given under the subgenera.

Type species: *Vespertilio auritus* Linnaeus.

Distribution: Temperate parts of North America, Eurasia, and northern Africa (Palaearctic and Nearctic regions) (fig. 11).

Description: Supraorbital region sharply ridged or smoothly rounded (fig. 4); temporal ridges remain apart or coalesce to form sagittal crest; brain case relatively short; zygoma relatively heavy or light, with postorbital expansion in middle or posterior third of arch; median postpalatal process absent or a spine-like prominence; auditory bulla roughly circular in outline; presternum wider than long.

Figure 11.—Distribution of *Plecotus*, showing coincidence with the North Temperate Zone (here defined as a region having an average annual temperature between 35° and 70° F.).

Upper incisors not in line with remainder of tooth row (lingual); I^1 simple or bifid (fig. 2), much larger than I^2; I^2 not touching canine; P^1 small; hypocone absent and protocone reduced posteriorly in M^1 and M^2; size of third commissure and metacone variable in M^3; lower canine much exceeding P_4 in height, and possessing a well defined, although small, anterointernal basal cusp; P_1 and P_3 small and crowded or not; P_4 single-rooted or double-rooted and lacking a well defined metaconid cusp.

Muzzle provided with dorsolateral glandular masses which in some forms rise above the muzzle as peculiar lumps (fig. 7); nostril openings small and of primitive vespertilionid type or large, opening upward, and peculiarly extended posteriorly (fig. 8); auricle and tragus large (fig. 9); tragus provided with a prominent basal lobe, and not united with posterior basal lobe of auricle; anterior basal lobe of auricle normal, expanded, or reduced; transverse ribs on auricle variable in posterior extension; second phalanx of third digit longer or shorter than third phalanx (fig. 6); calcar keeled or not; interfemoral membrane attached to base or tip of last caudal vertebra; coloration brown, without pattern, except for ventral pallor; membranes and ears brownish.

Key to subgenera of *Plecotus*

1. Nostril unspecialized; accessory basal lobe of auricle developed into a projecting lappet; calcar keeled; brain case broad (53 percent of greatest length). Subgenus **Idionycteris** (p. 129)

Nostril with posterior elongation and reduction of cornu; accessory basal lobe of auricle absent or only slightly developed; calcar not keeled; brain case narrow (averaging 48–50 percent of greatest length) 2

2. Supraorbital region sharply ridged; postorbital expansion of zygoma in middle third of arch; basial pits absent; P^4 longer than wide; 3d commissure of M^3 equal to or shorter than 2d; P_4 double-rooted; muzzle glands slightly enlarged; anterior basal lobe of auricle complete; 2d phalanx of 3d digit shorter than 1st phalanx . . . . Subgenus **Plecotus** (p. 132)

   Supraorbital region smoothly rounded or faintly ridged; post orbital expansion of zygoma in posterior third of arch; basial pits prominent; P^4 wider than long; 3d commissure of M^3 equal to or longer than 2d; P_4 single-rooted; muzzle glands greatly enlarged; anterior basal lobe of auricle reduced; 2d phalanx of 3d digit longer than 1st phalanx.
   Subgenus **Corynorhinus** (p. 136)

Subgenus *Idionycteris* Anthony

Plecotus J. A. Allen, 1881, p. 184. (Part.)
Corynorhinus G. M. Allen, 1916, p. 352. (Part.)
Idionycteris Anthony, 1923, p. 1.

TYPE SPECIES: *Idionycteris mexicanus* Anthony.

DISTRIBUTION: Northeastern Mexico and southwestern United States (fig. 12).

DESCRIPTION: Supraorbital region sharply ridged (fig. 4); temporal ridges do not coalesce to form a sagittal crest; rostrum broad for a *Plecotus*, flattened, and with pronounced middorsal concavity; brain case relatively broad and shallow; zygoma relatively thick and strong in appearance, with postorbital expansion in middle third of arch; median postpalatal process absent; basial pits absent; auditory bulla slightly elongated in outline.

I^1 with accessory cusp (fig. 2), near base of tooth; P^1 small, barely exceeding cingulum of canine in height; P^4 wider than long; space between posterointernal edge of P^4 and anterior edge of M^1 only about one-third the lingual length of P^4; third commissure of M^3 equal to or longer than second commissure (fourth commissure may be barely indicated); metacone of M^3 fairly prominent; P_1 much larger than P_3; P_4 single-rooted.

Glandular masses on muzzle not noticeably enlarged (fig. 7); nostril of primitive vespertilionid type, with well-defined cornu (fig. 8); auricle with anterior basal lobe complete, but not prolonged beyond anterior edge of auricle (fig. 9); accessory anterior basal lobe enlarged and produced beyond edge of auricle as a "lappet"; transverse ribs on auricle may or may not extend to posterior edge of auricle;[1] tragus relatively broad and short; second phalanx of third digit longer than first phalanx (fig. 6); forearm averages relatively short; calcar keeled; interfemoral membrane with 12 to 13 transverse ribs and attached to tip of last caudal vertebra.

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[1] In the type of *mexicanus* the ribs fade out indeterminently near the posterior border, leaving this area of membrane clear; in the type of *phyllotis* the ribs apparently end about 3 mm. from the posterior border, at which point they break into a multiplicity of wrinkles which extend to the border; in USNM 302900, from Arizona, the ribs definitely extend to the posterior border of the auricle.

Plecotus phyllotis G. M. Allen

Plecotus auritus J. A. Allen, 1881, p. 184.
Corynorhinus phyllotis G. M. Allen, 1916, p. 352.
Idionycteris mexicanus Anthony, 1923,[2] p. 1.
Plecotus phyllotis Dalquest, 1953, p. 63.
Idionycteris phyllotis Handley, 1956, p. 53.

Holotype: MCZ 5943; adult female, skin and skull; collected 24 March 1878 by Edward Palmer; San Luis Potosí, [probably near the city of San Luis Potosí or near Río Verde (J. A. Allen, 1881, p. 193)], Mexico.

Distribution: Known only from San Luis Potosí, Tamaulipas, and Arizona (fig. 12). Further collecting may show this species to have a geographic range similar to that of *Plecotus* (*Corynorhinus*) *mexicanus* (fig. 15).

Description: As in subgeneric description. Adult coloration: Mass effect of upperparts between Warm Buff and Cinnamon-Buff; hair bases Bone Brown, sharply distinguished from hair tips; a conspicuous cottony tuft of whitish hairs surrounds the posterior base of each auricle. Tips of hair of underparts between Pale Ochraceous-Buff and Light Buff, sharply distinguished from the Bone Brown to Fuscous-Black hair bases. Face covered with short hairs; anterior external border of auricle with many long, curly hairs; hairs long, lax, and dense on remainder of body. Size large for genus; tragus appearing shorter than in other species of *Plecotus* and almost as broad as in *Plecotus auritus*.

Measurements: See tables 7, 13.

Remarks: Until Cockrum's capture of a specimen in southeastern Arizona in 1955 (Cockrum, 1956b, p. 546), this species had been known only by two Mexican specimens which had served individually as types for *Corynorhinus phyllotis* G. M. Allen and *Idionycteris mexicanus* Anthony. These names have been shown to be synonymous (Handley, 1956, p. 53). The two Mexican specimens are almost identical. Compared with them, the example from Arizona is larger, its tragus is more broadly rounded (more blunt) distally, and the bat is more pallid throughout. Dorsally its fur is more buffy, less yellowish brown, and its ears and membranes are more grayish, less brownish. These differences may represent geographic variation, but it hardly seems worthwhile to apply a new subspecific name until additional specimens, now available, are studied.

Habitat: Very little is known of the natural history of this species. The Arizona specimen was taken at 1:00 a.m. on 30 May 1955 in a mist net stretched across an artificial swimming pool on the lawn of

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[2] Holotype: AMNH 62260; adult female, skin and skull; collected 17 June 1922 by W. W. Brown; Miquihauna [=Miquihuana?], Tamaulipas; collector's No. 2. This locality is on the eastern flank of the Sierra Madre Oriental, at about 5,000 feet elevation, near the upper edge of the Lower Austral Zone (Goldman, 1951, p. 263).

Figure 12.—Distribution of *Plecotus phyllotis* G. M. Allen. Solid symbols, specimens examined; encircled solid symbol, type locality.

the Southwestern Research Station of the American Museum of Natural History (Cockrum, 1956b, p. 546). This is a riparian community in a region where the oak-juniper association dominates.

Subsequently, additional specimens of *P. phyllotis* have been netted in the same area, but data on them have not been published.

Specimens examined: Three, from the following localities:

MEXICO: San Luis Potosí: 1s (MCZ). Tamaulipas: Miquihauna [=Miquihuana?], 1s (AMNH).

UNITED STATES: Arizona: *Cochise County:* Southwestern Research Station, 5 miles west-southwest of Portal, 5,400 feet, 1s (USNM).

Subgenus *Plecotus* E. Geoffroy Saint-Hilaire

Vespertilio Linnaeus, 1758, p. 32. (Part.)
Macrotus Leach, 1816, p. 5. (Nomen nudum.)
Plecotus E. Geoffroy Saint-Hilaire, 1818, pp. 112, 118.
Plecautus F. Cuvier, 1829, p. 415.

Type Species: *Vespertilio auritus* Linnaeus.

Distribution: Temperate parts of Eurasia and northern Africa. Norway, Great Britain, Ireland, Portugal, and Canary Islands east to Kamchatka, and Japan; north to Kola Peninsula, lat. 60–62°N. in Siberia, Sakhalin, and Kamchatka; south to Canary Islands, French Morocco, Tunisia, Sudan, Israel, northern Iran, northern Pakistan, Nepal, Sinkiang, Szechwan, Hopeh, Korea, and Japan (fig. 13). Altitudinal range, sea level to 10,500 feet.

Description: Supraorbital region sharply ridged (fig. 4); temporal ridges coalesce to form a sagittal crest; rostrum narrow compared with other subgenera of *Plecotus*, arched, and without mid-dorsal concavity; brain case relatively narrow and shallow; zygoma relatively thick and strong in appearance, with postorbital expansion in middle third of arch; median postpalatal process a poorly developed spine; basial pits absent; auditory bulla circular in outline.

I^1 with accessory cusp (fig. 2); P^1 relatively large, considerably exceeding cingulum of canine in height; P^4 longer than wide; space between posterointernal edge of P^4 and anterior edge of M^1 almost equals lingual length of P^4; third commissure of M^3 equal to or shorter than second commissure; metacone of M^3 not prominent (reduced to

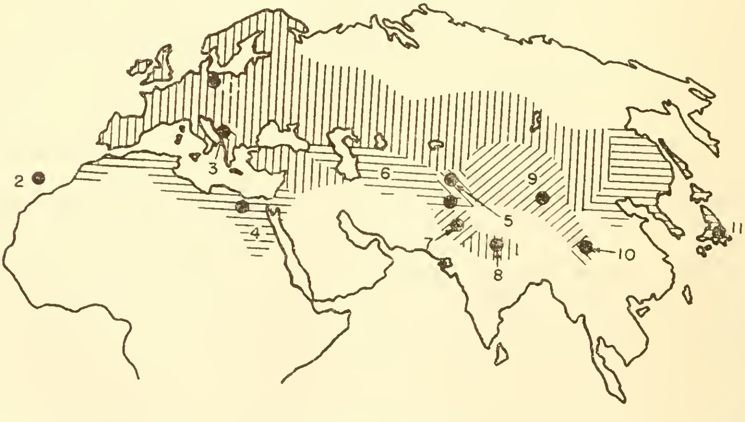

Figure 13.—Distribution of *Plecotus auritus* Linnaeus. Solid symbols, type localities. 1, *P. a. auritus* Linnaeus; 2, *P. a. teneriffae* Barrett-Hamilton; 3, *P. a. meridionalis* Martino; 4, *P. a. christiei* Gray; 5, *P. a. mordax* Thomas; 6, *P. a. wardi* Thomas; 7, *P. a. puck* Barrett-Hamilton; 8, *P. a. homochrous* Hodgson; 9, *P. a. kozlovi* Bobrinskii; 10, *P. a. ariel* Thomas; 11, *P. a. sacrimontis* G. M. Allen.

vanishing point in some specimens); P_1 much larger than P_3; P_4 double-rooted, almost as long in anteroposterior diameter at the cingulum as the tooth is high.

Glandular masses on muzzle slightly enlarged (fig. 7); nostril with slightly reduced cornu and with posterior elongation (fig. 8); auricle with anterior basal lobe complete and projected noticeably beyond anterior edge of auricle (fig. 9); accessory anterior basal lobe small and not projected beyond edge of auricle; transverse ribs on auricle extend without interruption to posterior border of auricle; tragus relatively broad and long; second phalanx of third digit equal to or shorter than first phalanx (fig. 6); forearm averages relatively short; calcar not keeled; interfemoral membrane attached to base of last caudal vertebra.

MEASUREMENTS: See tables 7, 13.

REMARKS: According to Ellerman and Morrison-Scott (1951, p. 181), the subgenus includes only one species, *P. auritus*. They list 11 geographic races (fig. 13).

Literature on the natural history of *Plecotus auritus* is extensive. The following data were gleaned from English sources, mostly from Alcock and Moffat (1901), Barrett-Hamilton (1910–1911), Matthews (1952), and Millais (1904). For reference to the excellent studies in Germany, see Eisentraut (1937).

HABITAT: *Plecotus auritus* is distinctly arboreal, characteristically hunting in the foliage of large trees. Ash trees seem to be particularly favored, but oaks and other deciduous species also may be frequented. However, it is not unusual to see *P. auritus* hawking around the upper shoots of hedgerows and willows, and sometimes it descends to forage among the lower shrubs and flowers in gardens. Rarely it hunts low over meadows, and has been observed to alight on cow dung to devour the insects attracted there.

P. auritus commonly hangs up by day in the summertime in old boathouses, cowsheds, church attics, and similar places; behind window shutters and under eaves of old houses; in tree holes; and even on trunks of trees, sheltered only by the roughness of the bark. This species may utilize separate sites as daytime sleeping places and night-time dining-halls or lounges. Barns and outbuildings are favored for the latter, but tree-trunks are also used. Accumulations of insect remains in such places betray the nightly visits of the bats.

Winter roosts are principally in caves, where crevices as well as open chambers may be utilized. Attics of old houses and occasionally hollow trees are also used.

BEHAVIOR: In some parts of its range, as in Britain, *P. auritus* may be one of the commonest and most widely distributed bats, yet its habits render it less conspicuous than many of the others. It is nocturnal and not crepuscular, beginning to forage 30 to 40 minutes after sunset. Then it moves in such a delicate, mothlike fashion in and out of foliage that it is not easily detected. It has been suggested that to see this species the observer should station himself at dusk under a tree whose foliage is not too dense to be seen through (e.g., an ash) and watch closely for the bats to appear among the branches overhead. Close attention is necessary, for the movements of the long-ear may be so stealthy that the presence of even five or six individuals hunting simultaneously in a single tree may be overlooked. Furthermore, the observer should choose fine weather for his vigil inasmuch as *P. auritus* seems to be much affected by atmospheric conditions.

Undoubtedly this species catches some flying insects, but much of its prey is picked from foliage. It hovers somewhat like a hummingbird to pick insects from leaves or flowers, or it plunges into the middle of a spray and remains for several seconds clinging to the twigs. It has been observed climbing among branches, on tree trunks, and on walls, presumably in search of food.

Flight from tree to tree or roost takes a special form. When the destination is near at hand the bat darts through the air with a swift, direct flight. When the destination is more distant, the bat makes a plunging descent to within a few inches of the ground and makes off in a jerking zig-zag fashion. So sudden and irregular are its movements that its course is difficult to follow.

In direct flight the ears appear to be held erect, but when the bat threads its way among foliage in search of insects they are thrown forward so as to resemble a "proboscis" or are curled downward and forward so as to suggest "cheek pouches." In sleep the ears are bent backwards until they lie close along the body, partially covered by the wings, or they are curled down and forward almost like the horns of a ram. In the former position the tragus always points forward, in the latter it may be reflexed. The ears may be folded or unfurled slowly, or snapped up suddenly. The action of the two ears can be synchronized or independent.

P. auritus alights in an upright position, clinging first to an object with its thumbs. It soon reverses its position and hangs head downward. In climbing or walking, the limbs are moved alternately, the head bobs to and fro, and the bat advances in a curious jerky fashion but with surprising speed. Preparing to fly, the bat raises its head, pricks forward its ears, and looks about with a seemingly intelligent air. When forced to do so, *P. auritus* swims rather well.

The long-ear has a variety of call notes. The commonest are a high-pitched chirping squeak used in ordinary communication and in quarrels, and a shrill, long-drawn, querulous, childlike note uttered when the bat is disturbed or surprised. There are also buzzing sounds, and a short, melodious, trilling, birdlike sound used for communication, both in flight and at rest.

Moffat (1922, p. 107) observed mating both before and after hibernation. The single young is born in June or July. Females commonly form nursery colonies of up to 50 or 100 or more individuals during spring and summer. Large winter aggregations are infrequent. Solitary hibernating individuals are often found. The long-ear is ordinarily rather quarrelsome in disposition, attacking and biting bats of other species that venture too near its roosting spot. It has been observed to attack and drive away the pipistrelle from its feeding area. Occasionally mixed colonies of *P. auritus* and *Pipistrellus pipistrellus* and various species of *Myotis* have been encountered.

Ryberg (1947, p. 71) tested the homing ability of the long-ear. Two of nine banded individuals returned 32 miles from the point of release to their home territory.

P. auritus is easily maintained in captivity. It tames quickly, eats readily, and remains in good health for some time. It is clean in its habits, grooming itself carefully after feeding. It seems more intelligent than other bats and is playful, alert, and lively, even in daytime.

Flower (1931, p. 161) recorded the survival of a *P. auritus* in captivity for 1 year, 2 months, and 2 days. The maximum recorded ages of banded, wild individuals are 5 years, 4 months (Ryberg, 1947, p. 78) and 5 years, 6 months (Verschuren, 1956, p. 5).

PARASITES: Stiles and Nolan (1931, p. 713) listed 27 genera of parasites known to have infested *P. auritus*.

FOOD: The long-eared bat is primarily a moth-eater. Gould (1955, p. 400) reported Lepidoptera of 22 species in its diet. These varied in wing spread from 30 to 67 millimeters (average 45). Remains of several species of Coleoptera and Diptera have been found in its droppings. In captivity it seems to prefer mealworms, but will also accept flies and raw meat.

HIBERNATION: In the British Isles the hibernating season for *P. auritus* extends from about the middle of October to early April. This species is a light sleeper, and if disturbed will generally wake, chatter, and attempt to bite if touched. It sometimes emerges in winter from its hibernating quarters when the weather is mild, and it commonly shifts during the winter from spot to spot within its place of hibernation without venturing out into the open.

Subgenus *Corynorhinus* H. Allen

Vespertilio Rafinesque, 1818, p. 446. (Part.)
Plecotus Lesson, 1827, p. 96. (Part.)
Synotus Wagner, 1855, p. 720. (Part.)
Corynorhinus H. Allen, 1865, p. 173.
Corynorhynchus Peters, 1865, p. 524. (Nomen nudum.)
Corinorhinus Dobson, 1875, p. 348.

TYPE SPECIES: *Plecotus macrotis* LeConte.

DISTRIBUTION: Temperate North America in Lower Austral and Lower Sonoran to Canadian life zones from Virginia, Ohio, Illinois, Kansas, South Dakota, Idaho, and British Columbia south to the Gulf of California and the Gulf of Mexico and through the Mexican Highlands to the Isthmus of Tehuantepec (fig. 27).

DESCRIPTION: Supraorbital region smoothly rounded or faintly ridged (fig. 4); temporal ridges remain apart or coalesce to form a sagittal crest; rostrum broad compared with other subgenera of *Plecotus*, flattened, and with slight middorsal concavity; brain case relatively narrow and deep; zygoma relatively thin and fragile in appearance, with postorbital expansion in posterior third of arch; median postpalatal process a prominent spine; basal pits prominent; auditory bulla circular in outline.

I^1 with or without accessory cusp (fig. 2); P^1 small, barely exceeding cingulum of canine in height; P^4 wider than long; space between posterointernal edge of P^4 and anterior edge of M^1 only about one-third lingual length of P^4; third commissure of M^3 equal to or longer than second commissure; metacone of M^3 fairly prominent; P_1 only slightly larger than P_3; P_4 single-rooted, much shorter in anteroposterior diameter at the cingulum than the tooth is high.

Glandular masses resembling thumbless mittens, rise from sides of muzzle (fig. 7); nostril without cornu and with posterior elongation (fig. 8); auricle with anterior basal lobe reduced to a small lap of membrane near tragus (fig. 9); accessory anterior basal lobe absent; transverse ribs on auricle interrupted by vertical rib near posterior border of auricle; tragus relatively narrow and long; second phalanx of third digit longer than first phalanx (fig. 6); forearm averages relatively long; calcar not keeled; interfemoral membrane attached to tip of last caudal vertebra.

Key to species of the subgenus *Corynorhinus*

1. M^3 with 4th commissure almost as long as 3rd (Pleistocene species).
P. tetralophodon (p. 140)
M^3 with 4th commissure barely indicated or absent 2
2. Supraorbital region faintly ridged, those ridges continuous with the temporal ridges, which do not coalesce to form a sagittal crest (Pleistocene species).
P. alleganiensis (p. 137)

Supraorbital region not ridged; extension of temporal ridges into the interorbital region variable; temporal ridges normally coalesce to form a sagittal crest (Recent species) 3

3. Tips of ventral hairs white or whitish, sharply contrasted with blackish bases; median postpalatal process triangular in shape, with a broad base; rostrum weak and much depressed; I^1 with prominent secondary cusp; anterointernal cusp of cingulum of P^4 usually present (Southeastern United States). **P. rafinesquii** (p. 151)

Tips of ventral hairs brownish or buff, often not sharply contrasted with slate, gray, or brownish bases; median postpalatal process usually styliform, with a narrow base (occasionally triangular); rostrum strong and not depressed (east of Great Plains and in Pacific Northwest), or variable; I^1 with or without secondary cusp; anterointernal cusp of cingulum of P^4 absent (east of Great Plains), or variable 4

4. Coloration of dorsum dark sooty-brown, with scant contrast between bases and tips of hairs; greatest length of skull usually less than 15.7 mm. (♀) or 15.5 mm. (♂); maxillary tooth row usually less than 4.9 mm.; I^1 usually with secondary cusp; tragus usually less than 13 mm. long; interfemoral cross-ribs usually less than 9 (Mexico) . . . . . **P. mexicanus** (p. 141)

Coloration of dorsum (in Mexico) yellow-brown, with sharp contrast between bases and tips of hairs; greatest length of skull usually more than 15.7 mm. (♀), or 15.5 mm. (♂); maxillary tooth row usually more than 4.9 mm.; I^1 usually simple; tragus usually more than 13 mm. long; interfemoral cross-ribs usually more than 9 (Appalachians, Ozarks, western United States, southwestern Canada, Mexico) . . . . **P. townsendii** (p. 165)

PLEISTOCENE SPECIES

Plecotus alleganiensis Gidley and Gazin

Corynorhinus alleganiensis Gidley and Gazin, 1933, p. 345.

Holotype: USNM (Vert. Paleont.) 12412; skull with incomplete dentition and lacking auditory bullae, zygomatic arches, and mandibles; collected 1912–1915, by J. W. Gidley; Cumberland Cave, Allegany County, Md.

Distribution: Known only from the Pleistocene fauna of Cumberland Cave, Md. (fig. 14).

Description: Skull similar in size and proportions to those of the Recent species *P. rafinesquii* and *P. townsendii*, but brain case possibly shallower and wider; supraorbital region slightly ridged; temporal ridges strongly marked, continuous with supraorbital ridges, and converging posteriorly, but not coalescing to form a sagittal crest; dorsal profile of rostrum almost straight; upper dentition (P^1—M^3 known) appears to be identical to that of Recent material; lower dentition (I_1—M_3 known) similar to that of Recent species, but teeth average slightly more robust.

Measurements: Holotype, in millimeters: Greatest length, 15.9+; interorbital breadth, 3.9; brain case breadth, 8.5; brain case depth, 5.5; maxillary tooth row, 4.9±; postpalatal length, 5.9±; palatal breadth, 5.9.

Figure 14.—Type localities of the Pleistocene species: 1, *Plecotus alleganiensis* Gidley and Gazin; 2, *Plecotus tetralophodon* Handley.

Comparisons: When Gidley and Gazin described *Plecotus alleganiensis* from the Pleistocene deposits of Cumberland Cave, Md., they had little comparative material of Recent species from nearby areas. I have compared the type and other cranial fragments of *Plecotus alleganiensis* with the now abundant material of *P. townsendii* from West Virginia and of *P. rafinesquii* from the southeastern United States. While some of the characters ascribed to *P. alleganiensis* by Gidley and Gazin are not as distinctive as they supposed, still there are sufficient differences to warrant separation of *P. alleganiensis* from *P. townsendii* and *P. rafinesquii*.

The faint supraorbital ridges and the prominent, independent, temporal ridges distinguish *P. alleganiensis* from the Recent species. In both specimens of *P. alleganiensis* that have the middorsal portion of the skull intact, the supraorbital and temporal ridges are continuous, and the temporal ridges converge posteriorly to within about 0.75 mm. of each other, but do not merge to form a sagittal crest. In Recent species of the subgenus *Corynorhinus* the temporal ridges sometimes extend into the interorbital region, but there is no supraorbital ridge. A sagittal crest usually is present in Recent species (exceptions noted are a specimen of *P. mexicanus* (KU 29911) from

Mexico and specimens of *P. townsendii* (AMNH 142023, USNM 297710) from West Virginia; in these the temporal ridges are contiguous but not coalesced).

The presence of supraorbital ridges is interpreted as a primitive characteristic. They are present in *Euderma maculatum*, *Plecotus auritus*, and *P. phyllotis*. They are absent in *P. mexicanus*, *P. rafinesquii*, and *P. townsendii*. Separate temporal ridges, also considered to be a primitive characteristic, are observed in *Euderma maculatum* and in *Plecotus phyllotis*; they unite to a common crest in the other Recent species of the genus *Plecotus*.

Other cranial characters relate *P. alleganiensis* closely to the Recent species *P. rafinesquii* and *P. townsendii*. The rostrum is relatively broad and flattened; the anterior nares are enlarged; the rostral profile is almost straight (normally, though not invariably, concave in *P. townsendii virginianus*, and normally almost straight in *P. rafinesquii*). The palate and basicranium are similar to those of Recent species of the subgenus *Corynorhinus*; basial pits are prominent.

General proportions of the skull of *P. alleganiensis* are the same as in *P. t. virginianus*; the brain case may be a trifle shallower. Depth of the brain case is difficult to assess in the only specimen in which it is intact, however, for the posterior part of the skull has been compressed (the occipital condyles are in the plane of the basioccipital-basisphenoid plate, the foramen magnum is in almost the same plane, and the supraoccipital, rather than being almost vertical to the main axis of the skull, has its lower margin tilted forward about 30°).

The upper dentitions of Recent *P. t. virginianus* and fossil *P. alleganiensis* are indistinguishable. None of the 27 mandibular fragments of *P. alleganiensis* is complete, but all parts of the lower jaw are represented. Differences between the mandibles of *P. alleganiensis*, *P. townsendii*, and *P. rafinesquii* are slight. The masseteric (coronoid) fossa is usually deeper and better defined in the fossil, and the mandibular foramen lies more posteriorly and lower, nearer the base of the angular process; the canine averages larger in diameter at the cingulum; P_1 averages slightly larger; and the molars average slightly broader—in essence, the dentition of *P. alleganiensis* is slightly more robust.

P. alleganiensis differs markedly from the other Pleistocene species, *P. tetralophodon*, in having the skull apparently broader, the supraorbital region ridged, the temporal ridges farther apart, and the fourth commissure of M^3 barely indicated.

Relationships: *P. alleganiensis* shares many morphological features with the two Recent species of the genus that now inhabit the eastern United States. It could have been directly ancestral to either or both of these species. Relationship of *P. alleganiensis* to the

Mexican Pleistocene species, *P. tetralophodon,* appears to be more remote.

Specimens examined: Four cranial fragments and 27 fragments of mandibles from Cumberland Cave, Md.

***Plecotus tetralophodon* Handley**

Corynorhinus tetralophodon Handley, 1955b, p. 48.

Holotype: CIT (Vert. Paleont.) 192/2989; well preserved skull with worn teeth (lacking mandibles, auditory bullae, hamular processes, all incisors, right canine, and the minute premolar, P^1, from each maxilla); collected by Chester Stock in Pleistocene deposits of San Josecito Cave, near the town of Aramberri, southern Nuevo León, Mexico, elevation 7,400 feet.

Distribution: Known only from the Pleistocene fauna of San Josecito Cave, Nuevo León, Mexico (fig. 14).

Description: Similar to Recent species of the subgenus *Corynorhinus* in most cranial details. Anterior nares relatively small and rounded in outline (dorsal view); brain case relatively shallow; supraorbital ridges lacking; temporal ridges prominent and converging posteriorly, so that they meet but do not completely merge; intermaxillary notch relatively small; extension of palate posterior to M^3 relatively short; median postpalatal process styliform; basial pits deep and well defined. Tooth rows crowded; teeth relatively fragile (not robust); canine with small internal cingular cusp; anterointernal cingular cusp of P^4 only slightly indicated; M^3 with well developed fourth commissure, almost equaling third commissure in length.

Measurements: Holotype, in millimeters: Greatest length, 15.6; zygomatic breadth, 8.2; interorbital breadth, 3.4; brain case breadth, 7.7; brain case depth, 5.3; maxillary tooth row, 5.0; postpalatal length, 5.9; palatal breadth, 5.7.

Comparisons: A well developed fourth commissure of M^3 distinguishes *P. tetralophodon* from related species. This commissure is barely indicated in other New World species of *Plecotus* and in *Euderma maculatum*; there is no trace of it in the Old World *Plecotus auritus,* in which even the third commissure of M^3 is reduced.

The degree of shallowness in the cranium of *P. tetralophodon* (brain case depth equals 34 percent of greatest length) is rarely equaled in Recent specimens of the subgenus *Corynorhinus.* It is observed in less degree in *Euderma maculatum, Plecotus auritus, P. phyllotis,* and possibly in *P. alleganiensis.*

Absence of a sagittal crest is a character shared with *Euderma maculatum, Plecotus alleganiensis,* and *P. phyllotis.* The temporal ridges usually are even farther apart in those forms, however. A few specimens of *P. mexicanus* and *P. townsendii* resemble *P. tetralophodon* in this respect.

Relationships: *Plecotus mexicanus* and *P. townsendii* now inhabit the region where the fossil *P. tetralophodon* was found. *P. tetralophodon* must have been closely related to these species, for the general conformity of the skull is similar in all three; probably all came from a common stock. I do not believe that *P. tetralophodon* is directly ancestral to either of these Recent species, however. It is less like *P. rafinesquii* and *P. alleganiensis.*

Specimen examined: The holotype.

RECENT SPECIES

Plecotus mexicanus G. M. Allen

Corynorhinus macrotis pallescens Miller, 1897, p. 52. (Part.)
Corynorhinus megalotis mexicanus G. M. Allen, 1916, p. 347.
Corynorhinus rafinesquii mexicanus Miller, 1924, p. 83. (Part.)
Plecotus rafinesquii mexicanus Dalquest, 1953, p. 64. (Part.)
Corynorhinus mexicanus Handley, 1955c, p. 148.

Holotype: USNM (Biol. Surv. Coll.) 98285; adult female, skin and skull; collected 25 August 1899, by E. W. Nelson and E. A. Goldman; near Pacheco [Sierra de Breña, 8,000 feet], Chihuahua, Mexico; collector's No. 13955.

Distribution: The higher and more humid parts of the Sierra Madre Occidental, the transverse volcanic belt of central Mexico, and the Sierra Madre Oriental (fig. 15). North to El Tigre Mountains, Sonora; near Pacheco, Chihuahua; and 22 miles south-southeast of Monterrey, Nuevo León. South to Pátzcuaro, Michoacán; Monte Río Frío, 28 miles east-southeast of Ciudad México; and Jico, Veracruz. Zonal Distribution: Mostly Transition and Upper Austral. Altitudinal range from 4,800 feet to 10,500 feet; usually above 6,000 feet.

Description: Adult coloration: Tips of hairs of upperparts vary from Verona Brown to Fuscous, bases from Bone Brown to Fuscous-Black; degree of differentiation between tips and bases of hairs slight; burnishing of hair tips absent or only slightly evident in most specimens; hairs at posterior base of auricle paler than remainder of dorsum. Bases of hairs of underparts vary from Benzo Brown to Fuscous, tips are about Pale Pinkish Cinnamon. Immature coloration: Dorsum smoky brown, similar to coloration of some adults.

Size small for subgenus; lobes of presternum slightly expanded; forearm averages relatively long; brain case averages relatively wide and deep, sloping up abruptly above the short, depressed rostrum; anterior nares, viewed from above, usually relatively small and angular in posterior outline; median postpalatal process varies from styliform to triangular; auditory bulla averages relatively small. First upper incisor usually with a prominent accessory cusp and always

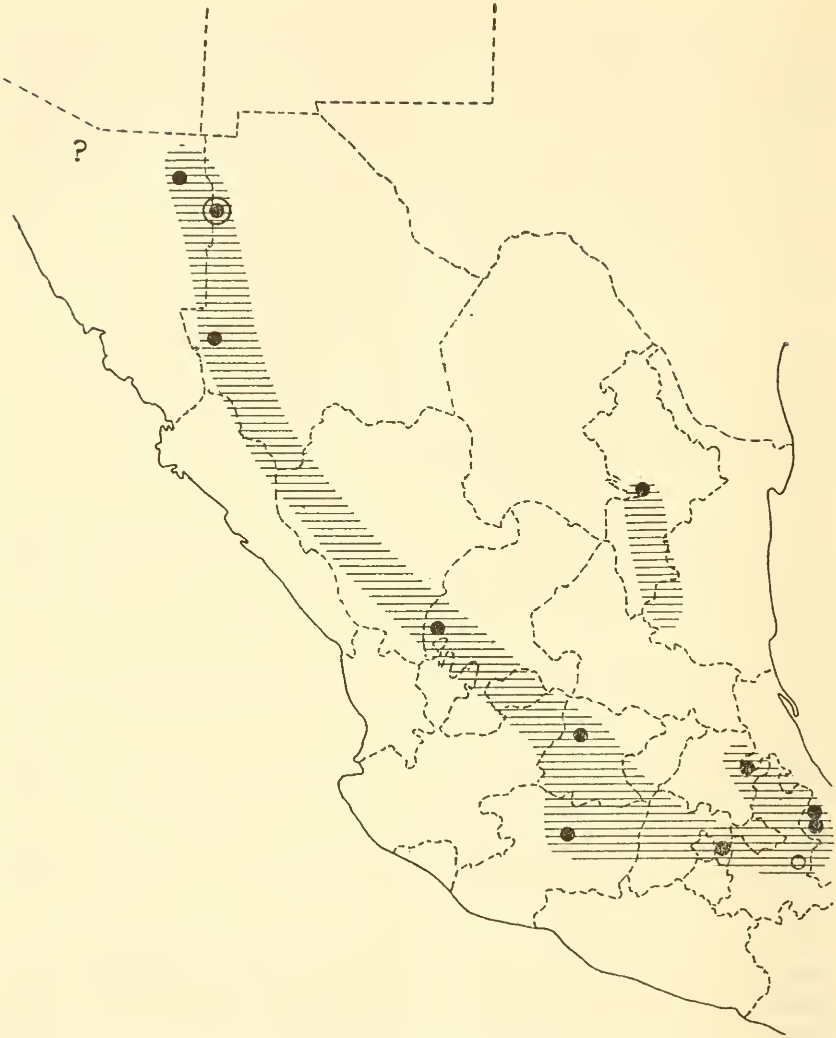

Figure 15.—Distribution of *Plecotus mexicanus* G. M. Allen. Solid symbols, specimens examined; open symbols, other records; encircled solid symbol, type locality.

with at least a trace of such a cusp; upper canine somewhat reduced in size; P^4 usually with a small anterointernal cingular cusp. Tragus (possibly also auricle) averages relatively short; cross-ribs on interfemoral membrane average eight.

Measurements: See tables 8, 14.

Comparisons: Compared with *Plecotus townsendii australis* and *P. t. pallescens*, *P. mexicanus* is darker, with less contrast between bases and tips of dorsal hairs; usually fewer cross-ribs on the interfemoral membrane; smaller tragus on the average; smaller skull;

deeper brain case; shorter, weaker, and more depressed rostrum; smaller auditory bullae; actually and relatively shorter maxillary tooth row; and more consistently bilobed first upper incisor. There is at least an indication of an accessory cusp on I^1 in all specimens of *P. mexicanus* that I have examined; few specimens of *P. t. australis* or *P. t. pallescens* have even a trace of it.

Relationships: There is a strong resemblance between *P. mexicanus* and *P. rafinesquii*. Similarities include short, weak, depressed rostrum; deep brain case; bilobate first upper incisor; and possession of a small anterointernal cingular cusp on P^4.

P. mexicanus differs from *P. townsendii* in somewhat the same manner as does *P. rafinesquii*. This parallel may not be purely coincidental. Perhaps both *P. mexicanus* and *P. rafinesquii* were isolated from a common stock (of which *P. townsendii* is the Recent descendant) at about the same time. However, *P. mexicanus* is not differentiated from *P. townsendii* quite as well as is *P. rafinesquii*. This may indicate more complete or longer isolation for *P. rafinesquii*, or partially parallel evolution between *P. mexicanus* and *P. townsendii*.

In coloration *P. mexicanus* resembles typical *P. t. townsendii* of the Pacific Northwest. Apparently this parallel can be traced to similar environmental stimulae. *P. t. townsendii* inhabits cool, humid, coastal lowlands, and *P. mexicanus* inhabits cool, relatively drier highlands.

Remarks: Since 1890 it has been known that bats of the subgenus *Corynorhinus* inhabit Mexico. The first specimen was referred by J. A. Allen (1890) to *Plecotus townsendii*, then thought to be monotypic. Miller (1897) referred all Mexican specimens to a new race, *P. macrotis pallescens*, restricting the name *townsendii* to populations in the Pacific Northwest. Later, G. M. Allen (1916) referred all Mexican material to a new race, *P. megalotis mexicanus*, restricting *pallescens* to the relatively arid portions of the western United States. Subsequent authors, with the exception of Burt (1938) for bats of northern Sonora, have applied the name *P. rafinesquii mexicanus* to all Mexican populations of the subgenus *Corynorhinus*. Present evidence, however, indicates that there are in Mexico two species to which the names *P. townsendii* and *P. mexicanus* apply.

Evidence that these are distinct species has been overlooked, although examples of each have been in museum collections for more than 60 years. Reasons for this oversight are several:

1. Populations of *P. townsendii* just north of the range of *P. mexicanus* in Arizona converge toward *P. mexicanus* in size and in coloration, giving an illusion of geographic intergradation between the two species.
2. The two species are not strikingly different, although they are more distinct than some species in other genera of bats, such as of *Myotis*.

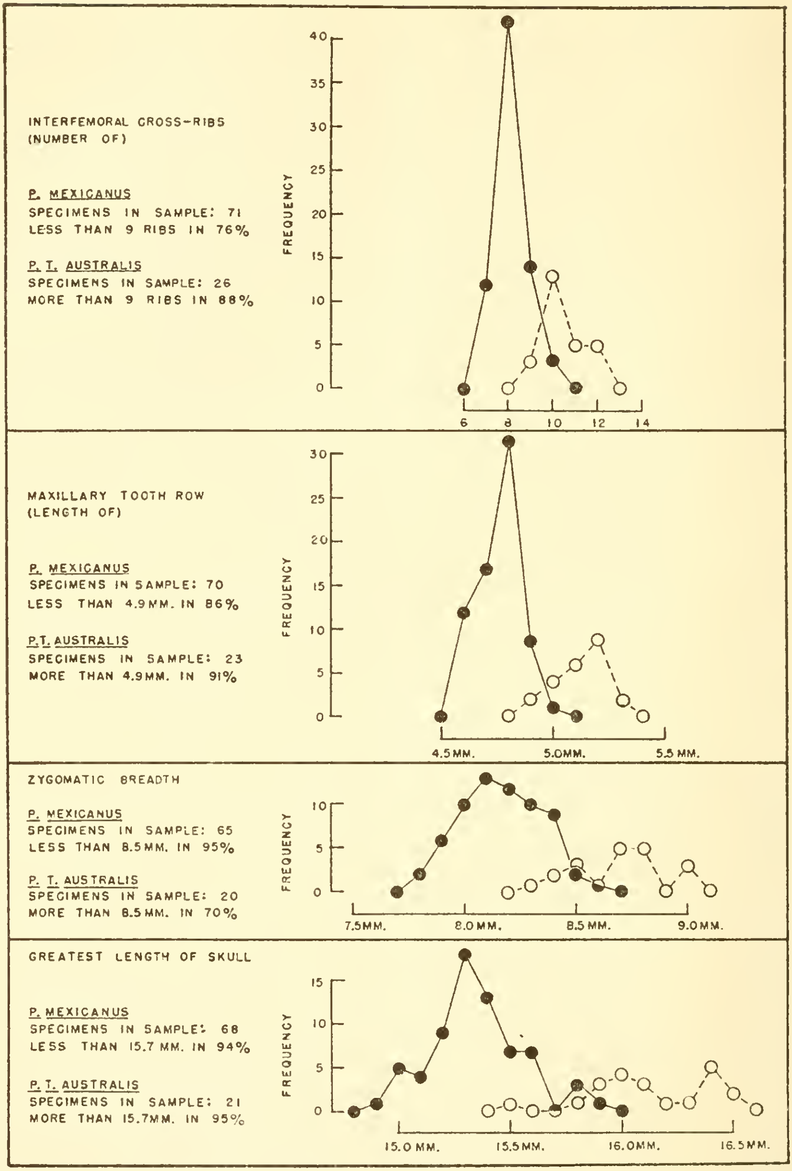

Figure 16.—Comparison of frequency of occurrence of certain measurements in adult female *P. mexicanus* (solid symbols) and *P. t. australis* (open symbols), including all measurable individuals studied.

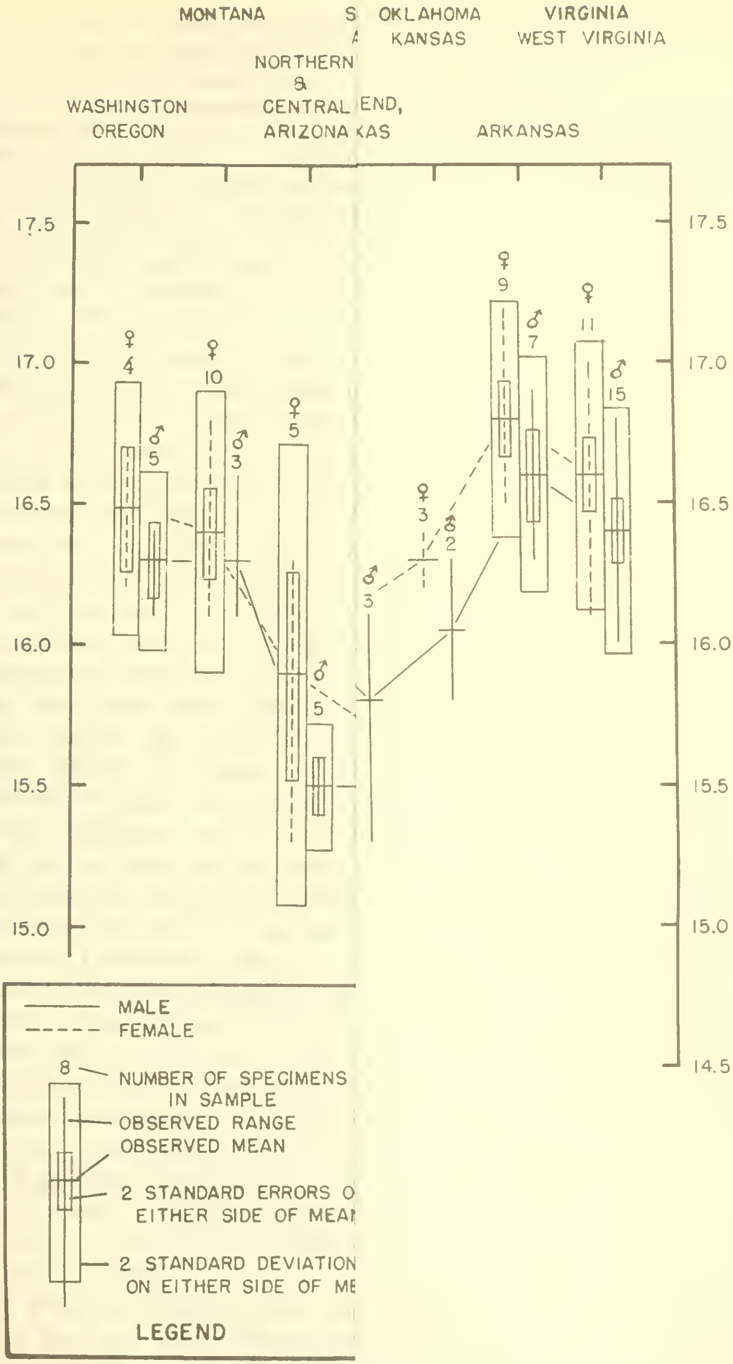

Figure 17.—G*llecotus mexicanus*

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497256 O - 59 (Face p. 144)

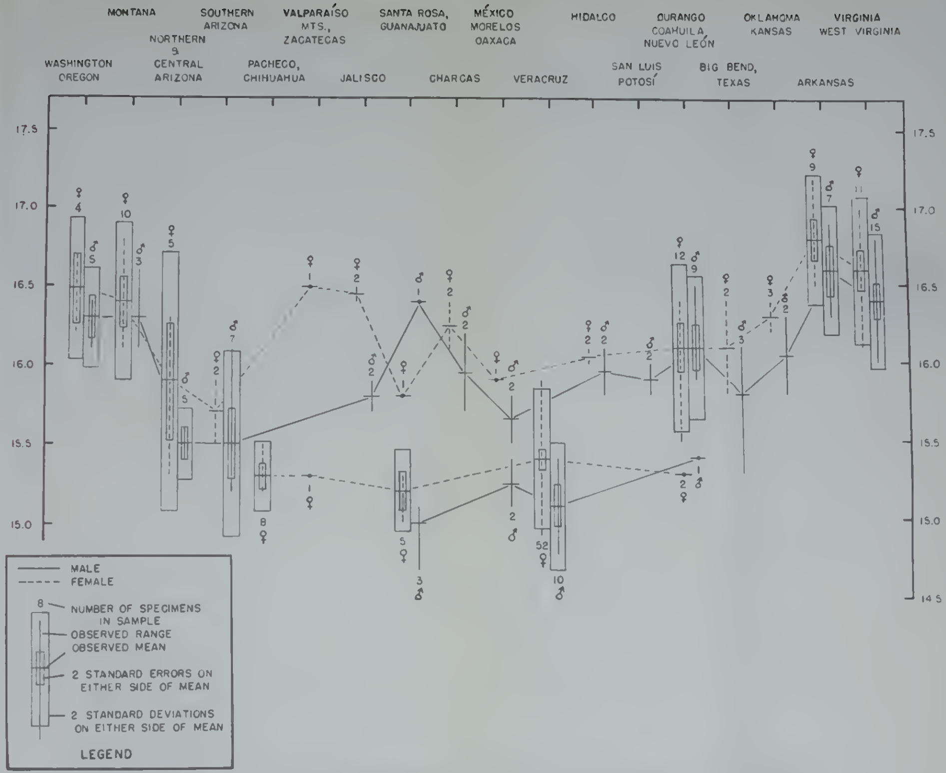

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FIGURE 17.—Greatest length (in mm.) of skulls of specimens of *Plecotus townsendii* (upper set of figures) and *Plecotus mexicanus* (lower set of figures), arranged in geographic sequence from northwest to south, thence to northeast.

3. No other two species of the subgenus were known to be sympatric.
4. Relatively few specimens have been available for study. Until recently, both species were represented only in the U.S. National Museum. The Texas Cooperative Wildlife Research Unit has had an example of each species since 1942; the Museum of Zoology, University of Michigan, has had both since 1946 (skins and skulls of *P. townsendii; P. mexicanus* in alcohol); and the Museum of Natural History, University of Kansas, has had both since 1948.
5. With the exception of the type series of *P. mexicanus* (preserved as dry skins and skulls), all early collections of Mexican big-eared bats in the National Museum were preserved in alcohol, and in a random selection of specimens for removal of skulls, only *P. mexicanus* happened to be chosen. The presence of *P. townsendii*, thus, was not detected.

When Mexican material was assembled from several museums for this study, variation was found to be slight in some series, great in others. The entire sample segregated into two groups (figs. 16, 17), each of which included both sexes and various ages. The amount of variation far exceeded that observed in samples from other parts of the range of the subgenus *Corynorhinus* (fig. 17). With one exception, all specimens could be referred without hesitation to one group or the other on the basis of a dozen diagnostic characters. Each specimen had most of the characters of its group, i.e., any specimen with dark coloration also had small tragi and few cross-ribs on the interfemoral membrane, etc. (fig. 16).

The two forms have distinct although broadly overlapping geographic ranges (fig. 18). The range of *P. mexicanus*—the cooler, moister, higher elevations of the Sierra Madre Occidental, the transverse volcanic belt of central Mexico, and the Sierra Madre Oriental (Goldman and Moore, 1946)—is strikingly similar to the ranges of the dark colored races of the harvest mouse, *Reithrodontomys megalotis*, outlined by Hooper (1952, p. 51) and to that of the white-footed mouse, *Peromyscus difficilis* (Osgood, 1909, p. 179). The range of the other form, *P. townsendii*, is in part complementary. It inhabits the lower elevations of the arid plateau and desert ranges of north-central Mexico north of the transverse volcanic belt, and the arid valleys of Jalisco, Morelos, and Oaxaca south of the transverse volcanic belt. In addition, it occurs together with *P. mexicanus* in the southern extremity of the Sierra Madre Occidental (Sierra de Valparaíso, 8,200 feet) and in the transverse volcanic belt (Santa Rosa, 9,500 feet, Convento de Acolman, and Lago Texcoco, 7,500 feet. However, it should be noted that the latter localities are relatively arid, despite their high elevation (Davis, 1944, p. 371; Goldman, 1951, p. 146).

This pattern of distribution might exist without intergradation between the two forms if they were: (1) Subspecies with seasonal migrations; (2) ecologically isolated subspecies; or (3) distinct, partially sympatric, species.

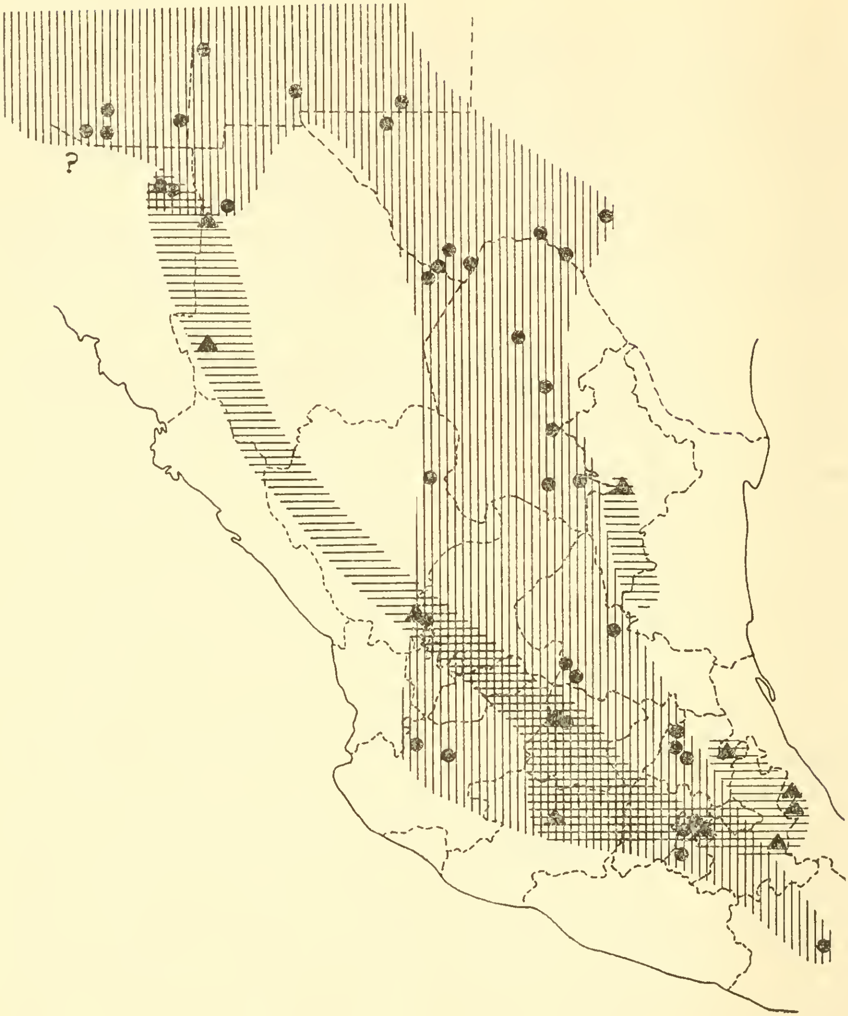

Figure 18.—Sympatry of *Plecotus mexicanus* (triangular symbols) and *Plecotus townsendii* (circular symbols) in Mexico.

Seasonal movement is not apparent in available samples (table 5). *P. mexicanus* is found in northern and southern parts of its range in both winter and summer. *P. townsendii* has been taken at high elevations in the transverse volcanic belt (in the range of *P. mexicanus*) in both summer and winter, has been found south of the belt in spring, late summer, and fall, and north of the belt at all seasons.

The theory of conspecificity becomes less tenable when seasonal movement of one or the other of the subspecies cannot be demonstrated. The phenomenon of overlapping ends of a chain of sub-

TABLE 5.—*Seasonal distribution of* P. mexicanus *and* P. townsendii *in Mexico, as determined from specimens for which collection date is known*

P. mexicanus			
North of transverse volcanic belt		In transverse volcanic belt	
February:	Mojarachic	January:	Las Vigas
February:	Monterrey	June:	"Morelos"
August:	El Tigre Mts.	July:	Jico
August:	Pacheco	July:	Monte Río Frío
December:	Sierra de Valparaíso	July:	Pátzcuaro
		November:	Santa Rosa
		November:	Zacualpilla

P. townsendii			
North of transverse volcanic belt		In or south of transverse volcanic belt	
January:	Yoltepec	April:	San Andrés
February:	San Juan	July:	Convento de Acolman
April:	Gen. Cepeda	August:	Oaxaca
April:	Sta. Helena	September:	Guadalajara
June:	San Buenaventura	September:	Cuernavaca
July:	Zimapán	November:	Charcas
September:	Bella Unión	November:	Santa Rosa
October:	Presa de Guadalupe		
November:	Bledos		
November:	Muralla		
December:	Sierra de Valparaíso		

species, reacting to one another as species rather than as related subspecies, however, occurs with some frequency in mammals, although it is more conspicuous in birds. It might apply in this instance if it could be proved that both *P. mexicanus* and the Mexican populations of *P. townsendii* (*P. t. australis*) intergrade to the northward with other populations of *P. townsendii* (*P. t. pallescens*). Then it could be assumed that the extremely arid environment of eastern Chihuahua and western Coahuila, where big-eared bats are not known to occur, has served as a barrier, sufficiently isolating related populations to the east and west of it so that they reacted to each other as species when both segments invaded areas to the south of the deserts.

Mexican populations of *P. townsendii* intergrade northward with other populations of *P. townsendii.* The zone of intergradation is broad, extending from northern Coahuila, through the Texas Panhandle. There is no evidence in existing samples of intergradation between *mexicanus* and *townsendii.*

The geographic ranges of the two forms overlap in northern Sonora; a sample from El Tigre Mountains contains typical individuals of both forms, and Burt (1938, p. 26) may have had both species in material from Sáric. It is true that populations of *P. townsendii* become smaller in body size and darker in color toward the Mexican border, but there is no accompanying increase in the frequency of the accessory cusp of I^1, reduction in the number of interfemoral cross-ribs, reduction in contrast between bases and tips of dorsal hairs, disproportionate decrease in the size of the auditory bullae, the auricles and tragi, or the average length of the maxillary tooth row, increase in the average depth of the brain case, or depression of the rostrum. In other words, populations of *P. townsendii*, neighboring *P. mexicanus* on the north, show a convergence of some morphological characters toward *P. mexicanus*, perhaps in response to similar environmental stimulae. Lack of convergence in other characters, however, indicates a different genetic structure in the two forms.

Dice (1940) used a concept of ecological subspecies to explain the discontinuous distribution of dark-colored subspecies on isolated mountain peaks surrounded by lowlands inhabitied by pale-colored subspecies. Dice supposed that the several isolated dark-colored populations might have originated in situ as independent derivations from the pale-colored stock, presumably in response to similar environmental conditions. According to this hypothesis, some subspecies may be ecological units, rather than units of similar heredity.

Were it not for the mixed samples (Sierra de Valparaíso and Santa Rosa) and absence of intergradation between the two forms, the concept of ecological subspecies could be an adequate explanation for the distribution of the Mexican bats of the subgenus *Corynorhinus.* It could be assumed that the alternative forms developed wherever certain ecological conditions prevailed. Under this hypothesis, independent development of the "*mexicanus*"-type might be expected wherever relatively cool, moist conditions of environment occur, and the "*australis*"-type would be expected under conditions of greater warmth and aridity. The distribution of both forms then would be largely independent of geography and would be related primarily to ecology. The mixed samples could be accounted for as chance mingling of the two forms during the nonbreeding season as a consequence of the interfingering of humid and arid environments. Existing samples appear to be too numerous and too well distributed, however, to have failed to show evidence of intergradation, if such exists.

It thus appears that the hypothesis of conspecificity is in no wise applicable to the Mexican populations of the subgenus *Corynorhinus.*

Provided that the data from available samples have not been misinterpreted, the two forms in consequence must be considered distinct but partially sympatric species.

A few specimens—such as KU 44759 from near Hacienda La Mariposa, Coahuila, which has the coloration, size, large auricle, and shallow brain case of *P. townsendii*, but the short tooth row, short tragus, and few interfemoral cross-ribs of *P. mexicanus*—may be hybrids. In view of the probable close relationship between the two species, it is surprising that such specimens appear to be so infrequent.

Geographic variation in cranial characters in *P. mexicanus* seems insignificant; even individual variation in these characters is of small magnitude. Geographic and individual variation in color is slight. The average mass effect of the dorsum in the fine series from Las Vigas is smoky, blackish brown, with the hair tips so dark as to be hardly distinguishable from the dark hair bases. The dark extreme appears almost black to the casual glance, while the pale extreme is brownish, with sooty tones less pronounced, and with the hair tips slightly paler than the hair bases. Specimens from the northwestern extremity of the range of the species are somewhat paler than those from the southeast; dark extremes are similar in the two regions.

The fur is usually rather short and woolly, but specimens from 10,500 feet in Estado de México (TCWC 2823), 8,200 feet in Zacatecas (USNM 91931), and west-central Chihuahua (USNM 265660) have long, lax fur. This does not appear to be a seasonal phenomenon, for short-haired individuals have been taken in January, February, August, November, and December. The long-haired specimens were taken in February, July, and December. These differences in pelage are not obviously related to age or sex.

HABITAT: Apparently this species is partial to forested mountainous regions, where it roosts in caves, mine tunnels, and buildings. Warmer, less humid, and more desert-like districts in the same general area are inhabited by *P. townsendii*. *P. mexicanus* has been reported in the following habitats:

Summer: Flying about rain pool in opening in pine-fir forest on Monte Río Frío (Davis, 1944, p. 380); in ranch house on lower border of oak forest (5,500 feet) above Jico (E. W. Nelson, field notes); hanging from roof of small, damp, north-facing grotto in vicinity of mixed forest of pine, oak, and madroño near Pátzcuaro (E. W. Nelson, field notes; Goldman, 1951, p. 195).

Winter: In old mine near Santa Rosa, near summit of Sierra de Guanajuato, upper slopes of which are characterized by light rainfall and second-growth forest of oak, alder, madroño, *Crataegus*, and wild cherry (E. A. Goldman, field notes; Goldman, 1951, p. 146). Hibernating at 8,200 feet in Sierra de Valparaíso in cold, damp cavern through which strong currents of air passed from one entrance to another; upper slopes of sierra forested with pine, juniper, cypress, oak, madroño, and manzanita, frequently interrupted by wet, grassy meadows (E. A. Goldman, field notes; Goldman, 1951, p. 290). In shallow cave in region of oak and pine near Mojarachic (Knobloch, 1942, p. 297).

Behavior: Information on behavior is scant. E. W. Nelson (field notes) remarked of a Pátzcuaro specimen that:

> When first taken in hand its long ears were bent spirally back and downward close against the sides of the head exactly like a pair of little recurved horns. While examining the animal with surprised curiosity these horns suddenly extended and became a pair of huge upright ears. While examining these ears at first I noted a fine regular waviness to the inner margin of the coiled ear which disappeared when the ear was extended.

The field notes of E. A. Goldman tell of a group of big-eared bats found in the Sierra de Valparaíso in December, 1897:

> I found eight specimens of this species hibernating in a cave at 8,200 feet altitude. Six of them in formalin were unfortunately lost along with my tank by my hunter while descending to the town of Valparaíso. They were hanging as usual by their feet, from the roof of the cave and at considerable distances from each other—6 to 10 or 12 feet. Their eyes were closed and their bodies cold and stiff. Their wings were hanging very close to the sides of their bodies. Their long ears had the margins rolled inwards and they were curled over backward and downward somewhat like the horns of a sheep and were pressed close to the sides of the head. When first taken from the cave the only signs of life that I noticed in them was a very slight moving of the feet, and they would hook them to my finger. I tied them all up together in a [handkerchief?] and carried them to camp. Their blood soon began to circulate, their bodies became warm and they revived sufficiently to be able to chatter and bite at each other and my fingers. Six hours after they were taken from the cave they could crawl about but although uninjured none of them were able to fly or at least made no effort to do so. The cave was cold and damp and a strong current of air passed in at one entrance and out at another.

Food: Not known.

Migration: Like other species of *Plecotus*, *P. mexicanus* is not known to make extensive migrations (see table 5 and p. 146).

Hibernation: According to Goldman's 1897 field notes (above), this species may become very lethargic under certain conditions.

Reproduction: Dalquest noted on specimen labels that no embryos were found among a large group of females collected at Las Vigas in January. Adult males (10) and adult females (53) were together in this colony. Adults of both sexes (3 males, 10 females) likewise were found together at Santa Rosa in November. A group of nine females, accompanied by five immatures, almost fully grown, but with finger joints not completely ossified, were collected near Pacheco on 25 August. Solitary immature individuals of slightly younger age were found on 14 July at Jico and at Pátzcuaro.

Molt: Two of nine adult females collected near Pacheco on 25 August were beginning to molt on chest and shoulders (new hairs still short and prostrate). Two of five immatures collected with this group were beginning to molt on the belly.

Specimens examined: A total of 104 from the following localities in Mexico:

Chihuahua: Near Pacheco [Sierra de Breña, 8,000 feet], 14s (USNM); Mojarachic [=Mafuarachic?], Rayon District, 1s (USNM). Guanajuato: Santa Rosa [9,500 feet], 13a (USNM). México: Monte Río Frío, 10,500 feet, 28 miles east-southeast of Ciudad México, 1s (TCWC). Michoacán: 2 miles north of Pátzcuaro, 7,100 feet, 1a (USNM). Morelos: No exact locality, 1a (USNM). Nuevo León: 22 miles south-southeast of Monterrey, 4as (MCZ). Sonora: Santa María Mine, El Tigre Mts., 1a (UMMZ). Veracruz: Jico [5,500 feet], 1a (USNM); 2.5 miles east of Las Vigas, 8,500 feet, 59bs (KU), 4s (GF); 6 miles west-southwest of Zacualpilla, 6,500 feet, 3s (KU). Zacatecas: Sierra de Valparaíso [13 miles west of Valparaíso, 8,200 feet], 1s (USNM).

Additional records: The following records from Mexico probably refer to this form:

Puebla: Hacienda de Miguel Sesma, 2 miles northwest of Esperanza (Schwartz, 1954, in litt.). Sonora: Sáric (Burt, 1938, p. 26).

Plecotus rafinesquii Lesson

Synonymy is given under the subspecies.

Distribution: Southeastern United States (fig. 19).

Description: Adult coloration: Hairs of upperparts blackish at base and yellowish brown to reddish brown distally, the two areas sharply demarked; hairs at posterior bases of ears usually not different from those of remainder of dorsum. Mass effect darkens with wear. Hairs of chest and belly black or blackish at base, white or whitish at tip, the division between the two colors sharp; hairs of chin and throat like remainder of underparts or with buffy wash encroaching from sides of neck; hairs bordering membranes whitish throughout. Immature like adult, except much darker throughout, the Avellaneous tips of the dorsal hairs and the whitish tips of the ventral hairs failing to conceal the blackish hair bases.

Size medium for the subgenus; presternum with all lobes, but especially the ventral lobe (almost as wide at tip as lateral lobe), somewhat expanded. Rostrum weak and much depressed, rendering facial profile relatively straight; anterior nares relatively small, and posterior border with somewhat angular shape; intermaxillary notch of palate relatively narrow posteriorly; median postpalatal process triangular in shape, with broad base; brain case averages relatively deep for subgenus. I^1 with prominent secondary cusp; P^4 normally has small anterointernal cingular cusp.

Comparisons: *Plecotus rafinesquii* may be distinguished from geographically contiguous races of *Plecotus townsendii* by numerous characters. When all populations of *P. townsendii* are considered, however, the separation is not so striking. Apparently, only coloration will distinguish all the individuals of the two species, all populations considered. *P. rafinesquii* always has the bases of the ventral hairs

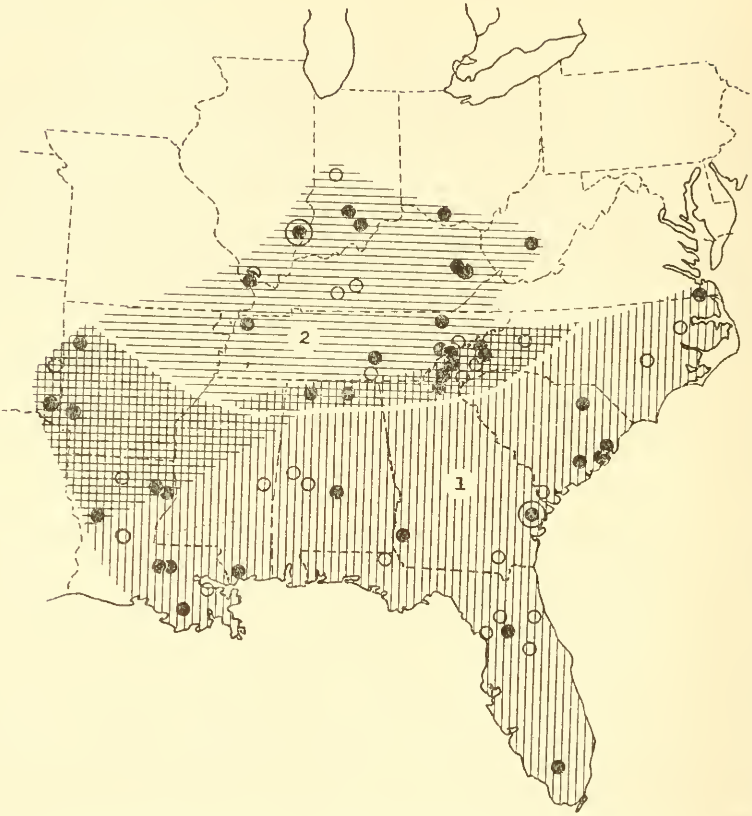

Figure 19.—Distribution of *Plecotus rafinesquii* Lesson: 1, *P. r. macrotis;* 2, *P. r. rafinesquii.* Solid symbols, specimens examined; open symbols, other records; encircled solid symbols, type localities. Cross-hatching indicates known areas of intergradation between subspecies.

black or blackish and the tips white or whitish, with the two colors sharply contrasted, whereas *P. townsendii*, on the other hand, always has the bases of the ventral hairs slate, gray, or brownish and the tips brown or buff, with the two colors often not sharply contrasted.

A secondary cusp on the inner upper incisor is present in all specimens of *P. rafinesquii.* It is absent (or represented only by a slight shoulder) in all specimens of the geographically adjacent *P. t. virginianus.* It is absent in most but not all examples of the geographically more remote *P. t. australis*, *P. t. pallescens*, and *P. t. townsendii.* It is usually present in geographically adjoining *P. t. ingens.* The secondary cusp is present in all specimens of *P. mexicanus.*

In *P. rafinesquii* there is usually, though not always, a small anterointernal cingular cusp on P^4. This cusp was not observed in specimens of *P. t. ingens* or *P. t. virginianus*, but is usually present in *P. t. town-*

sendii and *P. mexicanus* and sometimes occurs in *P. t. australis* and *P. t. pallescens.*

The median postpalatal process is triangular in shape, with a broad base, in *P. rafinesquii.* It is normally narrower at the base and more styliform in *P. townsendii.* In some examples of *P. t. australis* and *P. mexicanus* the process is almost needle-like. The broad-based form is encountered in some individuals of all races of *P. townsendii,* however.

The intermaxillary notch of the palate is narrower posteriorly in *P. rafinesquii* than in most individuals of *P. townsendii.* Likewise, the anterior nares are relatively small in *P. rafinesquii* and have the posterior border angular in outline. Geographically adjacent races of *P. townsendii* have the nares larger and the posterior border rounded in outline. The nares in the more remote *P. t. townsendii* and *P. t. australis* are generally large and rounded, but in *P. mexicanus* and *P. t. pallescens* they are relatively small and angular as in *P. rafinesquii.*

Another characteristic of *P. rafinesquii* that is geographically variable in *P. townsendii* is the appearance of the rostrum. In *P. rafinesquii* the rostrum is typically weak and much depressed. On the other hand, adjacent races of *P. townsendii, P. t. ingens* and *P. t. virginianus,* as well as *P. t. townsendii,* have the rostrum strong and not depressed. The rostrum usually is not so weak or depressed in *P. t. australis* and *P. t. pallescens* as in *P. rafinesquii.* *P. mexicanus,* showing these characters in the extreme, is similar to *P. rafinesquii.*

Skeletons are not available for all of the races of either species, but it appears that the presternum may have taxonomic worth. In specimens examined, all lobes, but particularly the ventral lobe, were more expanded in *P. rafinesquii* than in *P. townsendii* (fig. 5). The presternum of *P. mexicanus* is intermediate between these extremes.

Relationships: *Plecotus rafinesquii* is the most primitive living member of the subgenus *Corynorhinus.* It is similar in many respects *P. mexicanus* (see p. 143). It is more distinct from geographically contiguous races of *P. townsendii* (*ingens* and *virginianus*) than it is from some of the geographically more remote races (*pallescens* and *townsendii*) of that species. This indicates a considerable period of isolation for *P. rafinesquii* and a subsequent extension of range to bring the more progressive *P. townsendii* into geographical contact with *P. rafinesquii.* Isolation for *P. rafinesquii* is further confirmed by the fact that primitive traits (e.g., secondary cusp on I^1, anterointernal cingular cusp on P^4, triangular shape of median postpalatal process, small anterior nares and intermaxillary notch) which are constant or nearly so in *P. rafinesquii* are normally variable in *P. townsendii.* The coloration of *P. rafinesquii,* the only character separating all individuals of the Recent species of the subgenus *Corynorhinus,* most resembles the coloration of the more primitive subgenera *Idionycteris* and *Plecotus*.

Remarks: Referring to a visit to the "lower parts of the Ohio, the Wabash, Green River, Barrens, Prairies, and the States of Indiana, Illinois, etc.," Rafinesque (1818, p. 446) described nine species of bats, ten mice and shrews, and a number of snakes and fish. Four of the nine species of bats and a number of the mice and shrews cannot be related to species known to occur in the lower Ohio Valley. The description of one of the bats, *Vespertilio megalotis*, suggests what we now know as *Plecotus: "Vespertilio megalotis*. R. (Big-eared bat.) Tail three-eighths of total length, body dark gray above, pale gray beneath, ears very large, duplicated, auricles nearly as long. Length 4 inches, breadth 12 inches." Most of Rafinesque's contemporaries thought his *V. megalotis* was related to Eurasian *Plecotus*. Lesson (1827, p. 96) paraphrased Rafinesque's description of *V. megalotis* and renamed it *Plecotus rafinesquii*. He stated that it was "perhaps only a variety of our long-eared bat [European *Plecotus*]."

After a brief period of use, *V. megalotis* and *P. rafinesquii* fell into obscurity, and *Plecotus macrotis* of LeConte (1831, p. 431) came into universal usage as the name for the big-eared bat of the eastern United States.

A. H. Howell's (1909, p. 68) collection of a second species of big-eared bat at Burkes Garden in the Allegheny Mountains of Virginia in 1908 led to G. M. Allen's resurrection of the name *V. megalotis*. In his revision of the genus (now subgenus) *Corynorhinus*, Allen (1916, p. 339) wrote:

> The discovery of a Corynorhinus (*sic*) distinct from *C. macrotis*, from extreme western Virginia, westward, in the eastern United States was wholly unexpected. It is the eastern representative of the desert-colored *pallescens* of west-central United States, from which it chiefly differs in its somewhat darker, more drab, coloration.

On the basis of specimens from Virginia, Kansas, and Colorado, Allen supposed that this *Plecotus*, distinct from *P. macrotis*, had a range continuous across the Ohio and upper Mississippi valleys from Virginia to Kansas and Colorado. His Kansas and Colorado specimens were somewhat paler than those from Virginia, indicating, Allen thought, intergradation with the western *pallescens*. He presumed that specimens from Kentucky and Indiana, recorded in literature as *P. macrotis*, had been misidentified, and were actually representatives of the newly discovered second species. With the range that he envisioned for the second species, Allen's choice of Rafinesque's old name, *Vespertilio megalotis* (type locality, lower Ohio River), as the name for it was a logical step. In the absence of material from the type region, Allen considered specimens from Burkes Garden, Va., to be typical.

That *Vespertilio megalotis* Rafinesque is a junior homonym of *Vespertilio megalotis* Bechstein (1800, p. 622) escaped Allen's notice. Bechstein's *V. megalotis* is based on Le Vaillant's (1796, p. 279) description of a bat that came into his tent while he was one or two day's journey north of the Orange River in Great Namaqualand, South-West Africa (about lat. 28° S.). There is little doubt that Bechstein's *Vespertilio megalotis* is a member of the megadermatid genus *Lavia*. The description, except for the measurements, is an accurate one for that genus. No specimen of this family has been reported subsequently south of lat. 15° S.

Thomas (1916, p. 127) pointed out the unavailability of the name *V. megalotis* for an American bat and proposed the substitution of *P. rafinesquii* Lesson in its place. Subsequently the two eastern American species of *Plecotus* have been known as *P. macrotis* (Southeastern States) and *P. rafinesquii* (North-Central States). Collections of *Plecotus* from north of the Ohio River have never been critically examined (e.g., Lyon, 1936, p. 86).

Numerous specimens of big-eared bats are now available from the type region of Lesson's *P. rafinesquii:* the Ohio Valley and upper Mississippi Valley States of Tennessee, Kentucky, Illinois, Indiana, Ohio, and West Virginia. All of those specimens are the "*C. macrotis*" of G. M. Allen. Big-eared bats from a small portion of the Appalachian Highlands in western Virginia, eastern West Virginia, and eastern Kentucky are the "*C. rafinesquii*" of G. M. Allen. Likewise, specimens from the Ozark Highlands of northwestern Arkansas, and from the gypsum cave area of south-central Kansas, Oklahoma, and northern Texas are the "*C. rafinesquii*" of G. M. Allen. Instead of having a continuous distribution from Virginia to Kansas as Allen supposed, his "*C. rafinesquii*" apparently is isolated in the central Appalachians, and reappears again to the westward only in the Ozark Highlands and beyond.

Further, Lesson's description of *P. rafinesquii*, "Pelage dark gray above, and pale gray below . . . ." comes closer to the yellowish brown above, grayish white below of Allen's "*C. macrotis*" than it does to Allen's "*C. rafinesquii*" which is reddish brown above, buffy below. In this connection, Neill's observation (1953, p. 383) on the appearance of a live example of *P. macrotis* is pertinent:

> In life, the dorsal hairs were dark, grayish-black with light, horn-colored tips. These light tips were very inconspicuous, however, and to casual inspection the upper surfaces were grayish-black. The ventral hairs were dark gray with whitish tips which were more evident posteriorly.

My own observations of living specimens of the mid-Appalachian big-eared bat ("*C. rafinesquii*" of G. M. Allen) show it to be as brown in appearance when living as when made up as a study skin. It could not be described as "dark gray above" under any circumstances.

Thus, as first pointed out by G. M. Allen (1916, p. 339), there are two species of *Plecotus* in the eastern United States. Current application of names and delineation of geographic distributions for the two species are incorrect, however. One species inhabits the southeastern and central United States. The names *P. rafinesquii* Lesson (=*V. megalotis* Rafinesque) (type locality, "Lower Ohio Valley") and *P. macrotis* LeConte (type locality, "Georgia") are available for it. The earlier name is *P. rafinesquii* Lesson. The second species inhabits the central Appalachian Highlands, the Ozark Highlands, and the western United States, southwestern Canada, and Mexico. The earliest name for this species is *P. townsendii* Cooper (type locality, "Columbia River") (Handley, 1955c, p. 147).

Although the geographic ranges of *P. rafinesquii* and *P. townsendii* overlap in the Appalachian Highlands and are at least contiguous in the Ozark Highlands, the two forms have never been taken at the same locality. Frum (1948, p. 418) secured specimens of typical *P. rafinesquii* near the region inhabited by *P. townsendii* in West Virginia. Barbour (1957, p. 141) collected typical *P. townsendii* within the range of *P. rafinesquii* in Powell County, Ky. Welter and Sollberger (1939, p. 79) reported *P. townsendii* from nearby Rowan County, Ky. However, this identification is questionable since no specimen was preserved (Barbour, 1957, p. 141). Typical *P. rafinesquii* (MCZ 6062) has been collected on the Osage River in Arkansas. This locality cannot be pinpointed but may be within the range of *P. townsendii*. A skeleton (KU 5645) of *P. rafinesquii* from Crawford County, Ark. (Black, 1936, p. 30), was secured near collecting stations of *P. townsendii*, but at a lower elevation, in the Lower Austral zone.

P. rafinesquii is polytypic. One geographic race inhabits the Atlantic and Gulf Coast regions, the other the area west of the Appalachians and north of Alabama, Mississippi, and Louisiana. Lesson's name *P. rafinesquii* can be used for the interior race, and LeConte's *P. macrotis* for the coastal race.

HABITAT: *Plecotus rafinesquii* occurs in a forested region largely devoid of natural caves. It has been observed most frequently in buildings. Natural roosting places are hollow trees, crevices behind loose bark, and similar arboreal retreats. Lowery (1943, p. 224) found it in hollow trees (as well as in buildings) in Louisiana; a specimen in the U.S. National Museum was collected in a hollow cypress in the Dismal Swamp of Virginia; and Harper (1927, p. 280) was told of one that had been found under dry leaves in a cypress swamp in Georgia.

In some regions where natural caves occur, *P. rafinesquii* has been found in buildings but not in caves, despite diligent search. Thus, the only specimen from Florida Caverns State Park was taken in a building (Sherman, 1945, p. 201). Hibbard (1954, in litt.) found the species only in the attic of an old house at Mammoth Cave, Ky.

Where *P. rafinesquii* occurs with some frequency in caves, it usually has been found in small caves, or near the entrances of larger caverns. P. M. Smith (1954, in litt.) found an individual 25 feet from the entrance of a small cave in Indiana and another 50 feet from the entrance of a small limestone cave in Ohio. Ganier (1954, in litt.) found numerous individuals 30 to 100 feet from the entrance of a small cave on a wooded mountainside, 400 feet above a valley floor in Tennessee. Hahn (1908, p. 145) observed this species in Indiana only in dim light near cave entrances and believed (1909, p. 619) that it is not truly a cave dweller. However, all records from the northern fringe of the range of this species are from caves or subterranean excavations and, it should be noted, all are for the cooler months of the year (October to May), indicating, possibly, a choice of some other roosting place during the warmer months.

P. rafinesquii also inhabits other cave substitutes. Neill (1953, p. 282) reported one that was found clinging to the wall of an artificial limestone grotto, built for ornamental purposes and overgrown with ferns and mosses so as to resemble natural limestone caverns which are numerous around Silver Springs, Fla. Moore (1949a, p. 60) recorded finding big-eared bats on two occasions in a concrete culvert (6×6×75 feet) at the bottom of a ravine, some 40 feet deep, which probably had water running through it the year around (Florida). Goodpaster and Hoffmeister (1952, p. 365) found big-eared bats on several occasions in western Tennessee in an open cistern, 20 feet deep, built in the shape of a bottle, with open top about 2½ feet in diameter extending about 3 feet above the ground, and containing about an inch of water at the bottom. In warm weather the bats hung near the top; in cold weather near the bottom. Harper (1927, p. 280) noted that a *Plecotus* had been found in a turpentine still in the Okefenokee Swamp.

P. rafinesquii roosts both in occupied and abandoned buildings. In the Great Smoky Mountains, Stupka (1954, in litt.) found this species to be a regular inhabitant of a house that had been abandoned for about 15 years. Two or three rooms and the attic were utilized by the bats. He reported others that had been found in a schoolhouse (in summer) and in a Civilian Conservation Corps camp building. In the same region, the Komareks (1938, p. 148) found *Plecotus* in the attic of an abandoned schoolhouse and on the chimney, above the hearth, in an occupied cabin. Barbour (1957, p. 141) located a colony in the attic and storerooms of a large log building in a recreation camp. In North Carolina, Brimley (1945(?), p. [10]) reported it in an "old house," and Odum (1949, p. 188) had a specimen from an occupied dwelling. Some South Carolina specimens have come from a barn (Schwartz, 1954, in litt.) and from a closet in an occupied dwelling (ChM specimen labels). Harper (1927, pp. 279–281) recorded that residents of the Okefenokee Swamp had observed *Plecotus* most frequently in buildings—on several occasions during services in a meeting-house, in occupied dwelling houses (on wall near ceiling, and on chimney), in a shanty, in a commissary, and beneath the flooring of a railway telephone booth. In Florida big-eared bats have been discovered in the headquarters building of an Indian reservation (E. V. Komarek, 1954, in litt.) and in the basement of an occupied dwelling in an urban area (Moore, 1949b, p. 50). Alabama records cite the ceiling of a small round gatehouse and the garret of an old abandoned grist mill (A. H. Howell, 1921, p. 28). In Louisiana, Vernon Bailey (field notes) found it in the attic of a large plantation house, and Louisiana State University specimen labels record it from occupied farm houses.

BEHAVIOR: *P. rafinesquii* seems to be rather unsociable. Solitary individuals are more commonly encountered than clusters of individuals. Summer colonies have been recorded as follows: 5 gravid females, Houma, La., 12 May (Vernon Bailey, field notes); 20 or 25 (3 collected were gravid females) in small cave in Warren County, Tenn., 31 May (Ganier, 1954, in litt.); breeding colony (females and young) in Breathitt County, Ky., 14 June (Barbour, 1957, p. 141); 3 females and 1 small young collected near Baton Rouge, La., 17 June (LSU specimen labels). Five of unspecified sex were taken at Taylorsville, N.C., on 25 August (Brimley, 1945(?), p. [10]); and a group of seven, of both sexes, were collected at Cades Cove, Tenn., on 15 July (Stupka, 1954, in litt.).

Winter aggregations (usually consisting of both sexes) are more numerous, but even at this season solitary individuals are frequently encountered. Stupka (1954, in litt.) collected 11 in a house near Gatlinburg, Tenn., on 17 November, but the bats were scattered in two or three rooms and the attic; seven were collected in Georgetown County, S.C., on 18 December (ChM specimen labels); Ganier (1954, in litt.) has reported small groups in caves of Warren County, Tenn., on 19 March and in early September; and in western Tennessee Goodpaster and Hoffmeister (1952, p. 365) found several big-eared bats hanging in a clump in an open cistern on 2 September (15 were collected) and on 13 March found numerous *Plecotus* in the same cistern, hanging individually and in two or three small clumps (25 specimens taken).

Many references to *P. rafinesquii* specify that no other species of bats were found in the same building or cave. Stupka (1954, in litt.) mentioned that the abandoned house near Gatlinburg, Tenn., in which he found big-eared bats for several years, was shared with wood rats (*Neotoma*). *Pipistrellus* was found on four occasions and *Plecotus* twice in a Florida culvert, but not on the same dates (Moore, 1949a, p. 60).

The sleeping *P. rafinesquii* hangs head downward with its ears curved backward and flattened against the sides of its neck. In this position the anterior edge of the ear is uppermost and forms a half ellipse. The posterior portion of the ear folds along its transverse ribs like an accordion. When the bat wakes the ears are usually straightened slowly (Hahn, 1909, p. 619).

Residents of the Okefenokee Swamp told Harper (1927, p. 280) of a peculiar motion of the ears of these bats. One was discovered on the wall of a commissary when it attracted attention by "waving" its ears. Another that was seen several times in a railway telephone booth "wagged" its ears alternately. Several other informants also mentioned "ear-wagging."

P. rafinesquii must be strictly nocturnal, for it has never been observed in twilight flight.

Hahn, (1908, p. 177) experimented with the ability of bats to avoid obstacles. His subjects were mostly *Myotis* and *Pipistrellus* but included one *Plecotus rafinesquii.* The big-eared bat struck vertical wires 52 out of 102 chances, while in contrast *Myotis* and *Pipistrellus* struck on 24 to 25 percent of the chances and *Eptesicus* on 67 percent. In these experiments there may have been a relationship between wingspread of bat and success of avoidance. Hahn noted that the flight of captive *Plecotus* was swift and steady and that both *Myotis* and *Plecotus* in attempting to escape from a captivity room repeatedly flew against window panes and screens with great force.

Several references to *P. rafinesquii* indicate a variable agility in avoiding capture. One that began flying about during a service (17 July) in the meeting-house on Billy's Island in the Okefenokee Swamp was caught by hand by a member of the congregation (Harper, 1927, p. 280). Goodpaster and Hoffmeister (1952, p. 365) found (25 May) a *Plecotus* hanging in the upper part of a cistern that had an opening at the top 2½ feet in diameter. When disturbed the bat first flew to the bottom of the cistern and there circled until forced to attempt to escape through the top. It was then captured by hand. Hahn (1909, p. 619) saw two of these bats on 22 February in a cave at Mitchell, Ind. They avoided capture and flew out of the cave into the cold winter air. A solitary individual in a mine tunnel in Illinois (5 October) avoided three persons and escaped out of the tunnel (Elder, 1946, p. 434). An immature that Hamilton (1930, p. 308) found injured on a Kentucky roadway may have struck a vehicle.

On the authority of a local informant Harper (1927, p. 280) reported the voice of *P. rafinesquii* as a "fizzling noise."

FOOD: The food habits of *Plecotus rafinesquii* appear to be unrecorded. Specimens that Hahn (1909, p. 619) kept in captivity refused food and soon died.

MIGRATION: There is no evidence of migration by this species. It has been found at all seasons throughout its range except in the extreme northern part, where it has been discovered only in winter (October to May).

HIBERNATION: Whether *Plecotus rafinesquii* becomes lethargic in the winter in all parts of its range is not certain. At least under some circumstances it does truly hibernate. Goodpaster and Hoffmeister (1952, p. 365) found (13 March) big-eared bats hibernating near the bottom of an open cistern. The bats were cold and sluggish and made no attempt to escape when placed in a cage. A February observation in the Okefenokee Swamp reported by Harper (1927, p. 280) suggests injury or hibernation. On the other hand, specimens found in November in a culvert near Satsuma, Fla., had to be captured with a net (Moore, 1949a, p. 60). One that Elder (1946, p. 433) found in a mine in southern Illinois on 5 October was very alert and escaped out of the mine when it was approached. Two that Hahn (1909, p. 619) saw on 22 February in a Mitchell, Ind., cave escaped capture and flew out into the cold air.

REPRODUCTION: The season of mating and length of gestation are not known in this species. The young usually are born in late May or early June, shed their milk dentition by mid-July, and reach full size and assume the adult pelage in August or early September.

With regard to a female captured near Satsuma, Fla., on 5 November, Moore (1949a, p. 60) reported that her "vulva was perforate, reddish, and swollen. Her teats were dry and her uterus was empty." Schwartz noted on specimen labels that testes were prominent in all males captured near Andrews, N.C., on 19 and 20 January. Goodpaster and Hoffmeister (1952, p. 365) observed that bats taken in hibernation in Obion County, Tenn., on 13 March began mating after warm surroundings had overcome their lethargy.

Vernon Bailey (field notes) collected females containing single well-developed embryos in the attic of a large plantation house near Houma, La., on 12 May. On 31 May, in a Tennessee cave, Ganier (1954, in litt.) found females with pregnancy so advanced that birth of the one young of each seemed imminent. Barbour (1957, p. 141) reported a nursery colony in Kentucky in which the young averaged 66 mm. in total length on 22 June.

A specimen (LSU 1846) with milk teeth still in place, M^2 and M^3 not fully erupted, no trace of postjuvenile molt, and total length of 71 mm., was collected near Baton Rouge, La., on 17 June. AMNH 70517 with some milk teeth still in place, M^3 not fully erupted, no trace of postjuvenile molt, and total length of 84 mm. was collected near Quicksand, Ky., on 8 July. LSU 1397, collected on 28 June in Nachitoches Parish, La., has mature dentition, no trace of postjuvenile molt, and total length of 88 mm. Individuals almost full-grown (total length 93, 98, 99, and 100 mm.), and molting to a postjuvenile pelage, have been collected in South Carolina and Alabama on 24 July, 17 August, and 22 August. However, UI 853, collected on 2 September in Tennessee, although almost full-grown (total length 101 mm.), shows no trace of the postjuvenile molt.

MOLT: Molt is evident on the head, neck, and underparts, but not on the back of ChM 33.188.3 (24 July); on head, neck, underparts, and rump of ChM 33.218.3 (17 August); on neck and upper back, and almost completed on the belly of ChM 33.218.2 (17 August); and on all parts of the body of USNM 180198 (22 August).

Molting in adults has been noted only in two specimens, both of which show molt on all parts of the body: USNM 201714, male, Alabama, 4 July; and ChM 33.218.4, female, South Carolina, 17 August.

Plecotus rafinesquii macrotis LeConte

Plec[otus] macrotis LeConte, 1831, p. 431.
Plecotus lecontii Cooper, 1837, p. 72, pl. 3, fig. 5. (Substitute name for *macrotis*.)
Vesp[ertilio] macrotis Lesson, 1842, p. 23. (Not *Vespertilio macrotis* Temminck, 1840, p. 218=*Pipistrellus imbricatus* Horsfield.)
S[ynotus] Lecontii Wagner, 1855, p. 720.
Synotus macrotis H. Allen, 1864, p. 63. (Not *Synotus macrotis* Wagner, 1855, p. 719=*Pipistrellus imbricatus* Horsfield.)
C[orynorhinus] macrotis H. Allen, 1865, p. 174.
Corynorhinus rafinesquii Handley, 1955c, p. 147.

HOLOTYPE: None designated. Type locality subsequently fixed (Miller, 1897, p. 51) near the LeConte plantation, 5 miles south of Riceboro, Liberty County, Ga., (see p. 162.)

DISTRIBUTION: Southeastern United States (fig. 19). Northeastward to Dismal Swamp, Va. Southwestward to Terrebonne, West Baton Rouge, and Natchitoches Parishes, La.; and McCurtain and LeFlore Counties, Okla. Inland to Dismal Swamp, Va.; Bertie and Wayne Counties, N. C.; Darlington County, S. C.; Autauga and Green Counties, Ala.; Kemper County, Miss., and Crawford County, Ark. Zonal distribution, Lower Austral. Altitudinal distribution, sea level to about 500 feet.

Description: As for the species. In adults, hairs of upper parts blackish basally; tips between Sayal Brown and Snuff Brown. Hairs of underparts blackish basally, with a slight reddish tinge; tips whitish with a yellowish buff cast.

Measurements: See tables 9, 15.

Comparisons: Compared with *P. r. rafinesquii*, *P. r. macrotis* has coloration darker, more brownish dorsally; mass effect of the under parts less clear white, more yellowish; and mesopterygoid fossa and postdentary part of palate averaging narrower.

Remarks: Body size averages small in populations in southern Alabama, Mississippi, and Louisiana (tables 9, 15). Specimens from other parts of the range of *P. r. macrotis* (Atlantic coast and Arkansas, Oklahoma, and northern Louisiana average larger in body size, and resemble *P. r. rafinesquii* in this respect. There is no corresponding variation in coloration. Morphologically large and morphologically small populations of *P. r. macrotis* are similarly colored and are equally distinct from *P. r. rafinesquii.*

Intergradation between *P. r. macrotis* and *P. r. rafinesquii* is shown in numerous specimens. Some from Sevier County, N.C., dorsally are like typical *P. r. rafinesquii*, but some show traces of the yellowish ventral coloration characteristic of *P. r. macrotis*. Individuals from Marshall and Weaverville, N.C., and Huntsville, Ala., are more perfectly intermediate in all details of coloration, but are nearer *P. r. rafinesquii.* A specimen from Leighton, Ala., approaches Gulf Coast populations of *P. r. macrotis* in size, but is like *P. r. rafinesquii* in coloration. Specimens from central and northern Louisiana are unaccountably variable in coloration but average nearer *P. r. macrotis.* Characters of *P. r. macrotis* apparently are most accentuated in coastal plain populations. Those of *P. r. rafinesquii* are found west of the Appalachians, from Tennessee northward.

Although there is no assurance that the specimens upon which LeConte based his description of *Plecotus macrotis* came from his plantation near Riceboro, it is reasonably certain that they came from Georgia. The original description stated the range simply as the "United States," but in a later note on *macrotis*, LeConte (1855, p. 437) specified that it "inhabits Georgia." There are two LeConte specimens of *Plecotus* in the U.S. National Museum, perhaps the very specimens upon which the description of *macrotis* was based. Both are skulls only, labeled simply "United States." Both could very well have come from the same coastal locality, possibly from the LeConte Plantation. Since coastal Georgia is an area probably typical of the coastal race of *P. rafinesquii*, and lacking evidence that LeConte's description was based on specimens from elsewhere, I follow Miller (1897, p. 51) in designating the vicinity of the LeConte Plantation, 5 miles south of Riceboro, Liberty County, Ga., as the type locality of *P. r. macrotis.*

SPECIMENS EXAMINED: A total of 56 from the following U.S. localities:

VIRGINIA: *Nansemond County* or *Norfolk County:* Lake Drummond, Dismal Swamp, 1s (USNM). SOUTH CAROLINA: *Charleston County:* Hampton Plantation, Santee, 4s (ChM). *Darlington County:* Society Hill, 2s (USNM). *Dorchester County* (?): Summerville, 1s (ChM). *Georgetown County:* Darlington Plantation, 9s (ChM). *No exact locality,* 2s (USNM). GEORGIA: *Early County:* Kesler, 1a (MCZ). "*United States*" [=*Liberty County*: 5 miles south of Riceboro?], 2s (USNM). FLORIDA: *Hendry County:* Big Cypress Seminole Indian Reservation Headquarters, 27 miles east-southeast of Immokalee, 1s (USNM). *Marion County:* Silver Springs, 1a (USNM). ALABAMA: *Autauga County:* Autaugaville, 2a (USNM). MISSISSIPPI: *Hancock County:* Bay St. Louis, 1a (USNM). Westville, 1s (USNM). LOUISIANA: *East Baton Rouge Parish:* Baton Rouge, and 3 miles south of Baton Rouge, 7s (LSU), 1s (USNM). *Madison Parish:* Tallulah, 2a (USNM); Waverly, 1s (LSU). *Natchitoches Parish:* Kisatchie, 3s (LSU). *Terrebonne Parish:* 9 miles southeast of Houma, 3s (USNM). *West Baton Rouge Parish:* Lobdell, 1s (USNM). ARKANSAS: *Crawford County:* Mulberry, 1b (KU). *Sevier County:* Near Horatio, 1s (OAM). *County uncertain:* "Osage River," 1a (MCZ). OKLAHOMA: *McCurtain County*: 2.5 miles west of Smithville, 5s(UOMZ).

ADDITIONAL RECORDS: The following records probably refer to this form:

NORTH CAROLINA: *Bertie County:* No exact locality (Brimley, 1905, p. 22). *Wayne County:* Goldsboro (Brimley, 1905, p. 22). SOUTH CAROLINA: *Beaufort County:* Hardeeville (Miller, 1897, p. 52). GEORGIA: *Charlton County:* Okefenokee Swamp (Harper, 1927, p. 279). *Ware County:* Okefenokee Swamp (Harper, 1927, p. 280). FLORIDA: *Alachua County:* Micanopy (H. Allen, 1864, p. 65). *Jackson County:* Florida Caverns State Park, near Marianna (Sherman, 1945, p. 201). *Levy County:* Gulf Hammock (Pearson, 1954, p. 474). *Orange County:* Zellwood (Moore, 1949b, p. 50). *Putnam County:* 1.6 miles north of Satsuma (Moore, 1949a, p. 60). ALABAMA: *Greene County:* Eutaw (H. Allen, 1864, p. 65). *Hale County:* Greensboro (Miller, 1897, p. 52). MISSISSIPPI: *Kemper County:* No exact locality (H. Allen, 1864, p. 65). LOUISIANA: *Lincoln Parish:* Ruston (Lowery, 1943, p. 224). *Orleans Parish:* New Orleans (Lowery, 1936, p. 18). *Rapides Parish:* Alexandria (Dalquest & Werner, 1954, p. 156). OKLAHOMA: *Le Flore County:* Houston (Blair, 1939, p. 102).

Plecotus rafinesquii rafinesquii Lesson

Vespertilio megalotis Rafinesque, 1818, p. 446. (Not *Vespertilio megalotis* Bechstein, 1800.)
Plecotus rafinesquii Lesson, 1827, p. 96.
Plecotus macrotis Garman, 1894, p. 58.
Corynorhinus macrotis Butler, 1895, p. 86.
Corynorhinus rafinesquii Handley, 1955c, p. 147.

HOLOTYPE: None designated. Type locality: ". . . lower parts of the Ohio, the Wabash, Green River, Barrens, Prairies, and the states of Indiana, Illinois, etc." (Rafinesque, 1818, p. 446). Herein restricted to Mount Carmel, Wabash County, Ill. (see p. 164).

Distribution: East-central United States (fig. 19). North to Nicholas County, W. Va.; Adams County, Ohio; Putnam County, Ind.; Wabash and Alexander Counties, Ill. West to Putnam County, Ind.; Alexander County, Ill.; and Obion County, Tenn. South to Obion County, Tenn.; Colbert and Madison Counties, Ala.; Towns County, Ga.; and Macon, Transylvania, and Alexander Counties, N.C. East to Alexander County, N.C. and Nicholas County, W. Va. Zonal distribution: Upper Austral and lower portions of Transition. Altitudinal distribution: From 400 feet above sea level in western Tennessee to 3,850 feet in western North Carolina.

Description: As for the species. In adults, hairs of upperparts blackish basally; tips between Sepia and Buffy Brown. Hairs of underparts black at base, almost pure white at tip.

Measurements: See tables 9, 15.

Comparisons: For comparison with *P. r. macrotis*, see page 162.

Remarks: Rafinesque's specimens, which led to the description of *P. rafinesquii* by Lesson, are not known to be still in existence. This material is said to have been secured on the ". . . lower parts of the Ohio, the Wabash, Green River, Barrens, Prairies, and the states of Indiana, Illinois, etc." (Rafinesque, 1818, p. 446). The big-eared bat is not known to occur as far north as the Green River, and it has not been taken on the barrens or prairies of Illinois, Indiana, or Kentucky. Neither has it been taken on the banks of the Ohio River, although it undoubtedly occurs there. However, there are specimens in the U.S. National Museum secured in 1896 and 1903 at Mount Carmel on the Wabash River in Illinois, a region specifically mentioned by Rafinesque. In addition, the species is also known to have occurred at other localities in Illinois and Indiana. Consequently, I propose that the type locality of *Plecotus rafinesquii rafinesquii* Lesson be restricted to Mount Carmel, Wabash County, Ill.

Plecotus rafinesquii seems to be rare near the northern limits of its range. Despite repeated investigations, the caves and mines of Illinois have produced but two recent records (Elder, 1946, p. 433; and Smith and Parmalee, 1954, p. 204); Indiana, two (P. M. Smith, 1953, specimen submitted to U.S. Nat. Mus.; and R. E. Mumford, 1954, in litt.); Ohio, one (Goslin, 1954, p. 430); West Virginia, one (Frum, 1948, p. 418); and Kentucky, two (Barbour, 1957, p. 141; and Hibbard, 1954, in litt.).

Plecotus may have occurred in Pennsylvania within historic times, but it has not been found there by recent investigators (Mohr, 1954, p. 21). Harrison Allen (1864, p. 64) stated that "I am informed by Prof. Baird that specimens of a *Synotus*, probably of this species [*Synotus macrotis*], were received some years ago by the Smithsonian Institution, from Meadville, Pa., but that they have become in some way misplaced and are not now to be found." I have checked the early catalogs of the U.S. National Museum and have failed to find any record of big-eared bats from Pennsylvania. In 1857 and again on two occasions in 1861 specimens were received from J. T. Thuckston of Meadville, Pa. These were *Condylura*, *Myotis*, *Tamiasciurus*, *Peromyscus*, and *Microtus*. If big-eared bats were received from the same source they apparently were never cataloged.

SPECIMENS EXAMINED: A total of 50 from the following U.S. localities:

NORTH CAROLINA: *Buncombe County:* Weaverville, 1s (USNM). *Cherokee County:* 4 miles east-southeast of Andrews, 1s (AS). *Madison County:* Marshall, 1s (MCZ). *Swain County:* 14 miles northeast of Andrews, 5s (AS); Forney Creek, 2,400 feet, 9 miles northwest of Bryson City, 1s (USNM). GEORGIA: *Towns County:* Young Harris, 1s (USNM). ALABAMA: *Colbert County:* Forster's Mill on Town Creek, 5 miles east of Leighton, 1s (USNM). *Madison County:* Monte Sano, 1,600 feet, southeast of Huntsville, 1s (USNM). TENNESSEE: *Blount County:* Cades Cove, 1,750 feet, 1s (USNM). *Campbell County:* Well Springs, Powell Valley, 1s (OSM). *Obion County:* 10 miles northeast of Tiptonville, 6s (UI). *Sevier County:* Sugarlands area, 1,900 feet, 3 miles south of Gatlinburg, 13ab (USNM). *Warren County:* McMinnville, 1s (CNMH). KENTUCKY: *Breathitt County:* Noble, 5s (UK); Quicksand, 1s (AMNH). ILLINOIS: *Alexander County:* One-half mile north of Olive Branch, 1s (INHS). *Wabash County:* Mount Carmel, 2a (USNM). INDIANA: *Lawrence County:* Mitchell, Upper Twin Cave, 1s (UI), 1s (USNM). *Washington County:* Near Salem, 1s (OSM). OHIO: *Adams County:* Waggoner Ripple Cave, Green Township, 1s (OSM). WEST VIRGINIA: *Nicholas County:* Collison Cave, near Mt. Lookout, 1s (CM), 2s (GF).

ADDITIONAL RECORDS: The following records probably refer to this form:

NORTH CAROLINA: *Alexander County:* 10 miles northwest of Taylorsville (G. M. Allen, 1916, p. 351). *Macon County:* Highlands, 3,850 feet (Odum, 1949, p. 188). *Transylvania County:* Pink Beds, head of South Fork of Mills River, 3,300 feet, Pisgah National Forest (Oberholser, 1905, p. 9). TENNESSEE: *Franklin County:* "Southeast portion" (Ganier, 1954, in litt.). *Sevier County:* Greenbrier Cove (Komarek and Komarek, 1938, p. 148). *Warren County:* Near Hubbard's or Bat Cave, 8 miles north of Beersheba Springs (Ganier, 1954, in litt.). KENTUCKY: *Edmonson County:* Mammoth Cave (Hibbard, 1954, in litt.). *Warren County:* Bowling Green (Garman, 1894, p. 58). ILLINOIS: *Alexander County:* Elco (Elder, 1946, p. 433). INDIANA: *Putnam County:* 5 miles southwest of Greencastle (Butler, 1895, p. 86). *Washington County:* Near Saltillo (Mumford, 1954, in litt.).

Plecotus townsendii Cooper

Synonymy is given under the subspecies.

DISTRIBUTION: Central Appalachian Highlands, Ozark Highlands, western United States, southwestern Canada, and Mexico south to the Isthmus of Tehuantepec (figs. 22–24).

DESCRIPTION: Adult coloration: Hairs of upperparts gray or slate at base; color of tip varying from pale cinnamon brown to blackish brown; division between colors of tip and base often not sharp; hairs at posterior bases of ears frequently paler than those of other parts of dorsum. Mass effect darkens with wear. Hairs of chest and belly slate, gray, or brownish at base, brownish or buff at tip, the division between the colors often not sharp; hairs of chin and throat like remainder of underparts or with darker colored tips; hairs bordering membranes with bases colored like tips. Immature like adult, except darker or duller throughout.

Size varies from medium to large for the subgenus; forearm varies from medium, relative to skull length, to long; presternum with lobes not expanded (ventral lobe narrower at tip than lateral lobe) (fig. 5). Rostrum varies from weak and depressed to strong and not depressed; anterior nares relatively small to relatively large, and posterior border rounded, or with angular shape; intermaxillary notch usually relatively broad; median postpalatal process usually styliform, with narrow base (sometimes triangular); auditory bulla averages relatively large; brain case averages relatively shallow for subgenus. I^1 with secondary cusp varying from prominent to absent (fig. 2); P^4 with small anterointernal cingular cusp varying from present to absent. Tragus (possibly also auricle) averages relatively long; cross-ribs on interfemoral membrane average 10 or more.

Comparisons: See pages 138, 140, 142, and 151.

Relationships: Of the three Recent species of the subgenus *Corynorhinus*, *P. townsendii* has the largest geographic range and the greatest environmental tolerance. Its geographic range almost spans the continent from east to west and extends through 35 degrees of latitude. It inhabits broadleaf deciduous forests, coniferous forests, prairies, and desert scrub; cool, humid, rain forests and hot, arid, deserts; coastal lowlands and high mountains; areas with great annual temperature variation and areas with slight annual temperature variations.

The other species of the subgenus are much more restricted: *P. mexicanus* to the cool, humid, highlands of northern and central Mexico; *P. rafinesquii* to the warm, humid, lowlands of the southeastern United States.

P. mexicanus and *P. rafinesquii* appear to be genetically stable and only slightly variable, whereas *P. townsendii* is so variable that several geographic races are recognized. *P. townsendii* appears to be the most plastic, progressive species of the genus *Plecotus*.

Remarks: *Plecotus townsendii* was long known only by the Columbia River specimens upon which Cooper based his 1837 description. Beginning with Harrison Allen in 1864, *P. townsendii* was confused by all authors with *P. rafinesquii* (=*P. macrotis*) until the two species were recognized as distinct by G. M. Allen in 1916. Allen continued the confusion of names, however, believing *P. rafinesquii* and *P. macrotis* to be the names applicable to the two species. It is now evident (p. 156) that both of these names apply to a single species of the southeastern United States, and that *P. townsendii* is the name to be used for the wide-ranging species inhabiting parts of Canada, the United States, and Mexico.

HABITAT: In a species so widely distributed as *P. townsendii*, the formulation of a generalized description of its habitat preferences is a difficult matter. For the brief description of such a distributional pattern, the life zones of Merriam are the most useful of the numerous ecological unit concepts that have been proposed. Such units as the biotic provinces, faunal areas, biotic areas, and biotic districts of American authors (Cockrum, 1952, pp. 9–15) are useful in small scale, as in describing the distribution of an animal in a county or a state, but they are not adapted to definition of a range continental in scope.

P. townsendii is an inhabitant chiefly of the Upper Sonoran and Transition life zones, ranging in some places into the cooler Canadian zone and in others into the warmer Lower Sonoran zone. Eastern populations occupy parts of the humid subdivisions of the Upper Sonoran (Upper Austral) and Transition zones.

This species appears to be absent or generally uncommon in prairie and extreme desert habitats but may be relatively common in a variety of others. Dalquest (1947, pp. 21–24) provided excellent notes on habitats of the species in California (west of the Great Valley). Typical are: Cultivated valleys bordered by broad-leafed trees and dense thickets of brush; nearby hills with extensive grassy slopes, groves of oaks, areas of chaparral, and forests of coniferous trees and madroña. Oak-covered hills just below the juniper and piñon belt. Coastal lowland supporting dense, ocean-side vegetation, such as brush and lush annuals.

Johnson, et al. (1948, p. 343) in the Providence Mountains of the Mohave Desert found this bat in caves and tunnels near the boundary between the yucca belt of the lower slopes and the piñon-juniper belt of the upper slopes of the mountains. In the Pocatello region of Idaho, Whitlow and Hall (1933, p. 243) observed *Plecotus* in mine tunnels in the juniper belt lying between the Douglas fir-aspen zone of the mountain tops and the sagebrush zone of the valleys.

Most Mexican records for *P. townsendii* are from arid regions. Thus, Hooper (1955, p. 5) found this species at San Andrés where the hills were grass covered and the nearby mountains were arid, mostly grassy, but with pines and deciduous oaks scattered over the upper slopes, and forming thickets and forest on the canyon floors. However, Goldman (field notes) collected *P. townsendii* together with *P. mexicanus* at more humid localities in Guanajuato and Zacatecas where oak, pine, juniper, cypress, madroña, and mansanita were prominent.

Bailey (1936, p. 387) noted big-eared bats in the pine-fir-hemlock-broadleaf deciduous forest of western Oregon. Findley and Negus (1953, p. 237) reported a specimen captured at the edge of a spruce-fir forest in Colorado.

In Kansas, Oklahoma, and Texas, *Plecotus* occurs in gypsum caves in the zone of meeting of tall-grass and short-grass prairies. Ozark and Appalachian populations inhabit caves mostly in oak-hickory forests. Originally, there were few natural openings in these forests, and even today cultivated areas are mostly restricted to narrow bands along valley bottoms. Some Appalachian caves frequented by big-eared bats are situated in unbroken forest several miles from meadow and farmland.

Roosting sites: *P. townsendii* apparently is a true cave bat, for unlike *P. rafinesquii* it has not been known to roost in trees. Many populations of the western United States and Mexico have found to their liking such man-made structures as abandoned mine tunnels and pits, wineries, missions, stage stations, etc., and less frequently, occupied human dwellings. East of the Rocky Mountains, *P. townsendii* has been recorded only in caves; never in houses. In some areas *P. townsendii* has been quick to appropriate man-made structures as roosting places. For example, Townsend (1839, p. 325) observed that it was already a rather common inhabitant of the Hudson's Bay Company fur storehouses of the Columbia River district, not long after the construction of the first buildings in that region.

Pearson, et al. (1952, p. 317) theorized that since natural caves are few in California, and since most known colonies of *Plecotus* in that area inhabit man-made structures, it must have been rare in California before the advent of civilization. However, beyond a certain point, increasing the number of roosts does not seem to increase the population. Large numbers of mine tunnels dug in the western foothills of the Sierra Nevada in the last half of the nineteenth century were subsequently abandoned. Despite the prevalence of apparently suitable roosts, *P. townsendii* does not seem to be more numerous in that part of California than elsewhere.

Roosts may be classified according to the use made of them by the bats. For *P. townsendii* there are at least four categories: Winter hibernating roosts, occupied by both sexes; summer nursery roosts, utilized by females and young; ordinary summer roosts, inhabited mostly by males; and summer night-time roosts, used probably by both sexes. With regard to the latter, Dalquest (1947, p. 26) has noted that *P. townsendii*, in common with several other species of bats, retires to a convenient cave or building to hang up and rest after feeding flights at night. By taking advantage of this habit, a collector may utilize the night-time roost as an effective trap. Two small buildings at Lebec, Calif., served as bat traps for Dalquest on 4 June 1945. At midnight the traps held a *Plecotus townsendii*, 6 *Myotis yumanensis*, and 2 *Myotis volans*. Earlier in the night these same traps caught 11 *Myotis yumanensis*, 3 *Myotis volans*, 1 *Myotis californicus*, and 4 *Antrozous pallidus*. Three *Myotis thysanodes* were taken later in the traps. Often the night-time retreats are uninhabited by bats during daylight hours.

There is much variation in the selection of specific microhabitats within the roosting structures chosen by various kinds of bats. Many authors have noted the preference of *P. townsendii* for an open ceiling, wall, or beam rather than a crack or crevice as a roosting site. Apparently this species seldom crawls away from the spot where it first lands, and thus normally is found hanging in places open enough to be reached by flying. In Kansas caverns Twente (1955b, p. 721) observed that this bat characteristically roosted on very rough walls. Wind currents and consequently temperature fluctuations were often great in such places. However, the bats usually rested in slight concavities or behind projections on the rough walls. In these pockets, air movement was slight and the temperature relatively constant in contrast to the gross conditions prevailing a few inches away.

The intensity of light in roosting sites of *P. townsendii* varies from the total darkness of deep caverns or tunnels, to semidarkness in houses, small caves, and near the entrances of deeper structures. With regard to Californian populations, Dalquest (1947, p. 24) reported that all retreats of *Plecotus* that he had examined were dark or but dimly lighted. In the best lighted roosts the bats could be seen without the use of a flashlight once the observer's eyes had become accustomed to the darkness. Lights were necessary for observation in the other retreats.

Likewise, humidity seems to be usually of secondary importance in roost-site selection. Twente (1955b, p. 716) noted an apparent indifference of the big-eared bat to varying degrees of humidity (90 to 21 per cent in hibernating sites). Beer and Richards (1956, p. 34) reported a similar variation (100 to 38 per cent) in the relative humidity of *Eptesicus* hibernating sites.

Temperature appears to be the critical factor. Twente (1955b, p. 706) observed that bats must rest in habitats whose temperatures are suited to their metabolic needs. Thus, there may be variation in choice of roost according to season, time of day, weather, sex of bat, etc. For example, hibernating bats must roost in cool places to keep metabolism low so that energy reserves will be conserved. During the feeding season warm roosting sites permit digestion and assimilation of food to proceed. In general, *P. townsendii* roosts in warm places after having eaten and in cool places when food is scarce. In addition, it has been postulated that warm sites may be required for the satisfactory progress of some reproductive processes (pp. 171, 182).

The bat's perception of the microclimate of its roosting site does not seem to be especially good. Twente (1955b, p. 714) determined that *P. townsendii* apparently locates a suitable roosting spot by a trial and error system. If the spot first selected is unsuitable the bat awakens and moves to another place. Eventually optimum conditions may be located. The social tendency of the bats to seek their own species increases the probability of most of the individuals finding suitable sites.

SOCIABILITY: *P. townsendii* seems as a rule not to associate in its daytime and hibernation roosts with other species of bats, although scattered individuals of other normally colonial species occasionally may be present. Often such joint habitation does not actually bring the bats into close contact, for they may occupy different parts of the roosting structure or may occupy the same part at different times.

Goldman (field notes) found *P. townsendii* hibernating with *P. mexicanus* in a cave and in an abandoned mine shaft. At one time or another Dalquest (1947, pp. 21–23) noted *P. townsendii* in the same retreats as *Antrozous pallidus*, *Myotis californicus*, *M. evotis*, *M. thysanodes*, *M. volans*, *M. yumanensis*, and *Tadarida mexicana*. Stager (1939, p. 226) observed large numbers of *P. townsendii*, *Myotis velifer*, and *Macrotus californicus*, together with smaller numbers of four other species of bats, in an abandoned mine shaft. In addition to the species already noted, Pearson, et al. (1952, p. 275) found *Myotis lucifugus*, *M. subulatus*, and *Eptesicus fuscus* roosting with *P. townsendii*. Two *M. subulatus* were actually in a cluster of hibernating *Plecotus*. I have found numerous scattered dormant individuals of *Myotis lucifugus*, *M. sodalis*, and *Pipistrellus subflavus* only a few inches from hibernating clusters of *Plecotus townsendii* in a West Virginia cave.

Intraspecific sociability in *P. townsendii* is seasonally variable. Nursery colonies of females and young are common in summer, but solitary pregnant females are frequently encountered. Males at this season are usually, but not always, solitary. Both sexes have been found together in summer roosts, though usually not clustering together. Winter aggregations may include a random assortment of both sexes, or, according to the physical aspect and atmospheric condition of the roost, males and females alike may tend to be solitary. If there is an average seasonal divergence in roost-site selection by the sexes, probably the female prefers cooler winter roosts and warmer spring and summer sites than the male.

Dalquest (1947, p. 22) noted females with newborn young gathered so closely together that the edges of the cluster appeared to be a solid line. The bats normally pack so tightly in the cluster that their number is usually considerably underestimated in a casual observation. As shown by Twente (1955b, pp. 707, 714, 723) the function of the cluster is seasonally variable.

Contrary to the opinion of many authors, the winter cluster functions to protect the bats from heat rather than from cold. The body temperatures of the clustered bats approach the temperature of the substrate upon which they are resting, whereas the body temperature of the solitary bat is more affected by the surrounding air temperature. Low body temperatures and consequent low metabolic rates are imperative to insure conservation of fat reserves through the hibernating season. Beer and Richards (1956, p. 39) have demonstrated for *Eptesicus* that in some circumstances there may be a delicate balance between length of fasting (hibernating) season and quantity of stored fat in the bat. Unusually high metabolism in the bat or abnormally protracted cold weather result in starvation of the bat.

Since temperatures within spring and summer clusters may exceed the environmental temperatures, heat conservation seems to be the primary function of the cluster at these seasons. The higher temperatures presumably would aid digestion and assimilation of food. Twente found that *Myotis* moved to the cooler parts of caves and assumed deeper torpidity, as in winter hibernation, when stormy weather prevented their normal summer foraging flights. Warmer sites were chosen and higher cluster temperatures prevailed after the bats had eaten. Pearson, et al. (1952, pp. 303, 311) suggested that gestation, lactation, and other reproductive processes also might be facilitated by the elevated temperatures maintained in clusters. Clustered young, their metabolism possibly accelerated by the higher temperatures, may grow more rapidly than solitary young.

According to the observations of Pearson, et al. (1952, p. 275) in central California and Twente (1955b, p. 724) in Oklahoma and Kansas, nursery colonies of pregnant females begin to form early in April and increase gradually well into May. The colonies may consist of individuals from diverse hibernating sites. Varying from a few to 200 individuals, these colonies remain more or less intact until after the young are weaned in late summer. The bats ordinarily return to the same sites—buildings, mine tunnels, or caves—year after year.

Population: By studying and banding nursery colonies, Pearson, et al. (1952, p. 314) were able to calculate probable survival rates in *P. townsendii*. Although differences in habits of males and females render it difficult or impossible to determine the sex ratio in the adult population, the ratio is about 50 : 50 in the young. Only 5.5 per cent of 470 females examined in nursery colonies were neither pregnant nor lactating (reproductive failure is more common in young females than in adults). Basing their figures on these facts and on recovery of banded individuals, Pearson, et al., reasoned that a colony of 100 females should produce about 45 young females in a season. Of this number, 20 would survive to join the colony as breeding adults the following season. Assuming an average survival of 80 per cent of these bats each year after their first and an equal rate of mortality for adults of all ages, the colony would, as they found through three years of observations, remain static at about 100 breeding females each season. Age composition of such a colony would be as in table 6, with the median age 3.1 and the average age 5.0 years. Figures beyond the 3-year-old age class are theoretical.

TABLE 6.—*Theoretical age composition of a nursery colony of 100 female* Plecotus townsendii. (*Modified from Pearson,* et al., 1952, p. 315.)

Age in years	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Number of individuals	20	16	13	10	8	7	5	4	3	3	2	2	1	1	1	1	1	1	1

Pearson, et al. (1952, p. 316) estimated a population density of one *P. townsendii* per 310 acres on 62,000-acre Santa Cruz Island off the coast of California. The island was shared with at least an equal number of *Antrozous pallidus* and an undetermined number of *Myotis californicus*. Basing their estimate on the spacing of known colonies, these authors supposed that on the mainland of California the population density might be as small as one *Plecotus* per 419 acres, but supposed that in actuality each *Plecotus* probably had available considerably less than 419 acres. This would be especially true if unknown food habits restrict the hunting of *P. townsendii*. By doubling the estimated total of individuals in nursery colonies, Twente (1955a, p. 387) determined that there might be 300 to 500 *P. townsendii* in the gypsum caves of extreme northern Oklahoma and adjacent parts of Kansas. For the same area he estimated 25,000 to 50,000 *Tadarida brasiliensis*, 15,000 to 20,000 *Myotis velifer*, and 200 to 400 *Antrozous pallidus*. No estimate was made for *Eptesicus fuscus* and *Pipistrellus subflavus* which were present in smaller numbers.

How populations of *P. townsendii* are limited is not clear. Probably the same factors do not operate throughout the bat's range. Twente (1955a, p. 388) calculated that the yearly mortality could not exceed 33.3 per cent in animals with a reproductive potential of only one young per year if the population was to maintain a constant level. On this basis the daily population decrease could not be more than 1.1 per thousand. Twente suggested that in Kansas and Oklahoma the observed predation on bats by rat snakes, raccoons, hawks, owls, and other animals might account for such a loss and thus would be the primary limiting factor. Rice (1957, p. 30) postulated that predation by rat and corn snakes, opossums, owls, and cockroaches was the most important mortality factor among populations of *Myotis austroriparius* in Florida.

The possibility of antisocial tendencies and consequent need of some degree of privacy from other species of bats might be a limiting factor for *P. townsendii* where roosting places are not abundant. Pearson, et al. (1952, p. 317) believed it most likely that the population level of this species in California depended upon the number of suitable winter roosting sites and the number of summer roosting sites surrounded by adequate feeding territory. Their data indicated that disease, predation, and amount of food and water probably did not limit the Californian populations. They observed that colonies remained static in size, year after year, and believed that a species population increase might depend on establishment of new nursery colonies.

How new nursery colonies become established is not known. Pearson, et al. (1952, p. 317) determined that when a satisfactory nursery site becomes available near an already-established colony, the colony does not divide to make use of both sites, but uses either one or the other, or alternates between the two. Consequently, they thought, for a new nursery colony to become established, some females either through chance, faulty navigation, or some inner drive must find a suitable roosting place outside of the range of an existing colony. Furthermore, they believed it necessary for several females to arrive at this place almost simultaneously if gestation were to proceed normally, since females are gregarious and may depend upon clustering to keep their body temperatures high.

These hypotheses might serve to explain the evident slowness of *Plecotus* in reoccupying apparently suitable territory to the north of their present geographic range since the retreat of the Wisconsin glaciers.

PARASITES AND DISEASE: No ticks, lice, fleas, or bedbugs have been reported on *P. townsendii*, and this bat is not particularly noted for heavy infestations of other ectoparasites.

Winged parasitic flies of the family Streblidae (*Trichobius corynorhini* Cockerell and *Trichobius quadrisetosus* Kessel) appear to be encountered most often. I have noted flies of this family on specimens of *Plecotus* from Veracruz and West Virginia. Others have reported them as follows: Sprague (1938, p. 500) an infestation in Oklahoma, Wilson (1946, p. 86) in West Virginia, Dalquest (1947, p. 30) no more than one per bat in California, Krutzsch (1955, p. 458) up to three or four per bat on fur and membranes of specimens from "western

North America," and Smith (1934, p. 63) up to eight or ten per bat, mostly in the ears, on specimens from Kansas and Oklahoma.

Wingless parasitic flies of the family Nycteribiidae (*Basilia antrozoi* Townsend and *Basilia corynorhini* Ferris) (Stiles and Nolan, 1931, p. 715) seem to be generally less common on *P. townsendii*, although Dalquest (1947, p. 30) found up to five per bat in California and Krutzsch (1955, p. 458) up to two or three per bat in "western North America."

Sprague (1938, p. 500) reported mites on specimens from Oklahoma, and Krutzsch (1955, p. 458) found up to eight or nine mites of the genus *Ichoronyssus* per bat on the membranes of specimens from "western North America."

One of four California specimens of *P. townsendii* examined by Mitchell (1956, p. 444) was infected with *Trypanosoma vespertilionis*.

Twente (1955a, p. 387) discovered a possibly diseased specimen of *P. townsendii* in a cavern in Kansas on 31 October. It was a fat male, and although it had a rectal temperature of 93.9° F. it was very feeble and was unable to fly. A week later it was found dead.

Food: Apparently no one has observed *P. townsendii* engaged in its normal feeding activity. Little is known of its food habits. Hamilton (1943, p. 104) reported that all specimens that he had examined contained only the remains of Lepidoptera. Pearson, et al. (1952, p. 317) believed that *P. townsendii* eats moths and other insects (probably mostly flying insects). In stomachs of *P. townsendii* and *Myotis velifer* hibernating together in an Oklahoma cave, Sprague (1938, p. 500) found remains of insects and hairs of both species of bats. Inasmuch as the bats were heavily parasitized with bat flies (Streblidae), Sprague supposed that the bats might be feeding on the parasites. Twente (1955b, p. 713) observed no evidence of feeding among hibernating populations that he studied in Oklahoma and Kansas.

Pearson, et al. (1952, p. 274) found it difficult to induce captive big-eared bats to feed themselves. The bats were offered mealworms, supplemented occasionally by percomorph oil. Most could be taught in a day or so to accept decapitated mealworms forced into their mouths. Self-feeding was encouraged by stringing mealworms on wires along the sides of the cage. Some individuals eventually learned to eat worms from a dish, although many had to be hand fed throughout their captivity. As many as 40 mealworms might be taken daily. The most successful captives were ones that had learned to feed themselves and were kept in a cage large enough to permit flight. However, pregnant individuals, even though eating well, aborted or resorbed their embryos. The maximum period of survival in captivity was about six months. Some individuals survived without food when kept at a temperature of 45° F. in almost-covered aquaria stocked with drinking water.

Movements: Cockrum (1956a, p. 51) classified the movements of bats in three major categories: Diurnal movements (routine daily movements in quest of food and water), local migrations (irregular movements from one roost to another without regard for season), and seasonal migrations (seasonal movement from one roost to another, perhaps as little as ten miles or less apart). These categories overlap and are not clearcut. Consequently, some movements are difficult to classify.

Diurnal movements: H. H. T. Jackson (field notes) encountered *P. townsendii* in the month of August in a cave at the east side of Montezuma Well, Arizona. During the day the bats occupied the dark interior parts of the cave, but late in the afternoon they were to be found in the partially lighted section near the entrance. At this time they were unusually wild and the slightest noise or shadow caused them to retire to the deeper parts of the cave. Twente (1955b, p. 727) described a similar light-sampling behavior of *P. townsendii* in a cavern in Kansas. Toward evening the bats moved from the depths of the cavern to lateral depressions near the entrance. From these stations they made periodic sorties to the entrance until nightfall allowed their departure from the cavern.

Many authors have noted that *P. townsendii* leaves its daytime retreat only after darkness has fallen. Dalquest (1947, p. 24) believed that the species had never been observed in its hunting flight. Pearson, et al. (1952, p. 274) stated that it is a relatively late-flying species, emerging from its roosting structure after dark and not returning until almost dawn.

On the other hand, Vernon Bailey (field notes) reported that in the Sundance region of Wyoming:

> These are the earliest bats seen flying in the evening, and they seem to come from various parts or openings in the canyon walls. When they first come out it is light enough to see their long ears as they fly about. Their flight is rather slow and they would be easy to shoot . . . .

Bailey (1930, p. 181) again saw big-eared bats in early evening flight at Yellowstone National Park, and shot two (1936, p. 387) one evening at McKenzie Bridge, Oregon, when they circled about at the edge of the forest. Krutzsch and Heppenstall (1955, p. 127) shot a *P. townsendii* in Utah as the bat foraged in the early twilight. Hamilton (1943, p. 102) watched big-eared bats leave a West Virginia cave during the late dusk. The cave opening was well above the valley floor, and the emerging bats first flew yet higher, soaring and circling at a height of several hundred feet until it was too dark for successful shooting. Then they descended to within a few feet of the ground.

During the hibernating season there is considerable movement of bats within the roost. Apparently the selection of a suitable spot for hibernation is a hit or miss proposition. Thus the bats repeatedly awaken from dormancy and move to other spots until a favorable site is located. Consequently, a few flying bats are likely to be found in the roost at any time, although the majority of individuals may be lethargic (p. 179). To illustrate this, Pearson, et al. (1952, p. 278) in midwinter marked with chalk the locations of 56 torpid bats in a California cave. Temperature within the cave was 34° F. Particular effort was made to avoid disturbing the bats. The following day there were as before 56 torpid bats in the chamber, but at least 17 had moved to new locations. Records indicate that males are more active in winter than females.

Local migrations: At all seasons individuals or populations of *P. townsendii* may normally alternate between two or more roosts, or may irregularly seek new roosts. These facts have been emphasized by the banding of hibernating populations and by the observation of nursery colonies. Banding operations in West Virginia (504 *Plecotus*, Mohr, 1952, p. 7), Kansas (155 *Plecotus*, Twente, 1955a, p. 380), and California (1500 *Plecotus*, Pearson, et al., 1952, p. 274) all indicate movement of *P. townsendii* from cave to cave during even the coldest weather. Much of this movement undoubtedly was precipitated by the disturbance to the bats when they were banded, or when the band numbers were read. Twente (1955a, p. 380) found that when thus disturbed the bats invariably awakened and left the cavern, not to be seen there again for several days or months, if ever. The banding data indicated in addition that there was considerable movement from cave to cave by bats that had not been disturbed by banding. Apparently these individuals were seeking circumstances more favorable for hibernation.

Pearson, et al. (1952, p. 276) described the effect of disturbance on a nursery colony. One evening, after the adult bats had left the roost, their 75 young were banded. The adults returned, picked up their young, and by morning all were settled in an alternate roost 1.3 miles away. How the colony quickly agreed to move and arrived intact at a distant new roosting place is an intriguing mystery.

Seasonal migrations: There is no evidence of long migrations by *P. townsendii*. Among the 1500 banded in California by Pearson, et al. (1952, p. 275) most that were recaptured were recovered at the original banding site or not more than 1.5 miles from it. A young male found dead 20 miles from his birthplace was the most distant recovery. Twenty-four percent of 504 individuals banded in West Virginia were recovered in a subsequent season, all near their banding sites. For information on dates of movements to and from nursery and hibernating roosts, see pp. 171, 180, and 183.

Homing: Only Cockrum (1956a, p. 49) has reported homing experiments with *P. townsendii*. He secured 54 individuals from a cave in Arizona in May. These were released at a point 28 miles away. Three of the bats were recovered at the home cave two days later and a fourth two months later.

Flight: After spending several hours swinging a butterfly net in a nearly futile attempt to capture *P. townsendii* confined in a room, Dalquest (1947, p. 24) concluded that this bat sees well, is a swift flier, an agile dodger, and possesses an excellent sense for danger. Hundreds, if not thousands, of sweeps netted but one bat in free flight.

Not only is *P. townsendii* adroit at avoiding hand-operated nets, but some characteristic keeps it from becoming entangled in mist nets as well. Although these nets are very effective for capturing many species of bats, those that do not forage near the ground and those whose flight is slow, cautious, and butterfly-like are seldom taken. Also, perhaps those with an unusually well developed echo location apparatus can detect and avoid the nets more readily. Only Baker (1956, p. 187) has reported taking *P. townsendii* in a mist net.

The flight of captive big-eared bats has been described in detail by Grinnell (1918, p. 344) and Dalquest (1947, p. 25). In the confinement of a room, the flight pattern most often was a figure eight, varied with ovals and circles, extending from floor level to the beamed recesses of the ceiling. Flight character varied from hovering like a hummingbird to slow and butterfly-like to swift and swallow-like. Wing-beats, deep and smooth, often alternated with short glides. In average flight the head was bent ventrally so that the body formed a smooth curve from chin to tip of tail. The ears, pointed forward and held almost parallel to the horizontal plane of the body, were, surprisingly, scarcely noticeable. The legs were spread apart so that the interfemoral membrane was expanded. I have noted that in slow flight the head is not so depressed and the ears are more conspicuous, as they are held more nearly perpendicular to the horizontal plane of the body. On some occasions the flight of *P. townsendii* may be silent, with no squeaking, swishing, or fluttering. At other times it is relatively noisy.

When it alights on a wall or ceiling, *P. townsendii* swoops up from below, its wings close, and with great agility it flips over so that its feet become foremost and almost simultaneously grasp a foothold.

Resting posture: In ordinary sleep the big-eared bat normally hangs free, suspended only by the feet (see Dalquest, 1947, p. 25, for a detailed description). Many observers have noted its peculiarity of frequently hanging suspended by only one foot, and Dalquest (1947, p. 29) has pointed out that the truly lethargic bat clings with both feet and thumbs and presses its body tightly to the surface of its roost-site. Among big-eared bats hibernating in the gypsum caverns of Oklahoma and Kansas, Twente (1955b, p. 721) observed a different posture. The ears were folded back along the neck, the fingers were spread so that the wings effectively covered the ventral surface of the body, the tail and interfemoral membrane were bent down to cover the venter and hind parts of the wings, and the long body hairs stood out perpendicularly. In this position the bat was practically enveloped with a layer of dead air, effectively insulating it from the surrounding warm air of the cavern, and helping it to assume a body temperature similar to that of the substrate from which it was suspended. Grinnell and Swarth (1913, p. 380) noted a similar posture in lethargic big-eared bats in California.

The normal position of the ear in the undisturbed resting bat appears to be coiled back and down tightly against the side of the neck like a ram's horn. The posterior portion of the ear is wrinkled, rather accordion-like, and there is lateral contraction in accomplishing the spiral shape. The ears can be coiled independently, and sometimes an individual is seen with one ear erect while the other is coiled. Apparently the tragus always remains erect, regardless of the position of the ear. Upon superficial examination, when the ear is coiled, the erect tragus may be mistaken for the ear.

Possibly *P. townsendii* sometimes adopts the common ear posture of the resting *P. auritus*, that is, with the ear folded back against the side of the neck and chest and partially concealed beneath the folded wing, rather than coiled against the side of the head and neck (Grinnell and Swarth, 1913, p. 380; Howell, 1920, p. 174; Alcorn, 1944, p. 309).

When the bat is not lethargic, the ears are unfurled at the slightest alarm, and move with increasing vigor as the observer approaches. The sight of a tightly packed cluster of bats with long ears quivering, waving, and in constant motion is a memorable one.

Hamilton (1943, p. 102) and Mohr (1933, p. 50) noted that big-eared bats lapsed into disoriented flight or fell stunned when guns were discharged near them in caves. These authors presumed that the auditory apparatus of *P. townsendii* is more sensitive than that of bats with smaller ears.

Voice: The voice of *P. townsendii* is difficult to describe. A high pitched twittering is commonly heard both in roosts and in captivity. H. W. Grinnell (1918, p. 344) noted that an individual "protested in shrill cicada-like notes" when handled. Grinnell and Swarth (1913, p. 380) described the voice as a "grating squeak," and Dalquest (1947,

p. 29) stated that semi-lethargic individuals were able to "hiss" when disturbed. Mohr (1933, p. 50) reported that E. L. Poole made the following observations on the call of an individual less than a week old: "It has a ventriloquial hollow *cuc-cuc-cuc*, like a yellow-billed cuckoo; close at hand a high thin *tse-tse-tse*, like the song of a blackpoll warbler, which could be heard synchronized with the other sound."

HIBERNATION: Hibernation in an animal is a state of lethargy in which body temperature is depressed in correspondence with a low environmental temperature and in which physiological activity is proportionally curtailed. Hibernation may be of long or short duration. Among bats there appears to be no clear distinction between sleep and hibernation. When the bat rests its temperature approaches that of its environment. Thus, without regard for season, if the air temperature of its roosting place is low enough, the bat assumes a lethargic condition.

However, Twente (1955b, p. 713) found that the body temperature of bats difficult to awaken and bats easy to awaken may be the same. He postulated that the degree of lethargy is dependent upon how high or how low the bat's body temperature has been during the period of lethargy. This factor would determine the amount of stored food that had been catabolized during the period of inactivity. The primary wastes of this process are carbon dioxide, nitrogenous byproducts, and water. The observation that *Myotis* nearly always urinates when awakened suggested to Twente that a possible factor causing awakening is the amount of urine in the bladder and the nervous consequences of bladder distension. He proposed that it would be more appropriate to refer to the bat's lethargic state in degrees of irritability rather than in degrees of lethargy. Thus, bats hibernating in places that are warm or have fluctuating low temperatures are usually more irritable than those that have been hibernating in places that have relatively constant low temperatures. Similarly, bats at the edges of clusters tend to be more irritable than those in the center, for they have been members of the cluster the shortest time and have higher temperatures and a higher rate of metabolism. If the place that the bat has selected for hibernation is unsuitable, the animal awakens, probably because a high metabolic rate has made it irritable, and moves to another place. The bat always awakens and moves when the temperature of its environment approaches 32° F.

Twente (loc. cit.) found that once the awakening process is initiated, the bat's body temperature rises at a constant and rapid rate (about 1.8° F. per minute for *P. townsendii*) until flight becomes possible for the animal. Reeder and Cowles (1951, p. 395) determined the threshold of flight to be at a rectal temperature of 73.9° F. in *P. townsendii*. Twente's specimens of this species flew at a rectal temperature of

75.2° F. but did not fly agily until a temperature of 82° to 86° F. was reached.

Pearson, et al. (1952, p. 276) found most *P. townsendii* lethargic at air temperatures below 62° F. and recorded temperature as low as 28.5° F. near hibernating individuals. Twente (1955b, p. 715) observed an air temperature range of 37.4° to 69.8° F. where lethargic big-eared bats were resting. When Dalquest (1947, p. 29) placed active specimens of *P. townsendii* in a refrigerator at a temperature of 40° F. all became lethargic within 20 minutes.

Pearson, et al. (1952, p. 277) observed in their studies of *P. townsendii* in California that the bats began to arrive in their hibernating quarters in late October, reached peak numbers in January, and departed by April. Females arrived earlier and stayed later than males. Females were usually lethargic both day and night during the coldest periods, whereas males tended to awaken at night the year around, even in midwinter. During spring, summer, and fall both sexes were usually alert day and night and lethargic individuals were uncommon, especially in September when the males were coming into breeding condition.

In central California, Pearson, et al. (1952, p. 280) found that some male *P. townsendii* apparently did not hibernate. Individuals came to night roosting places throughout the winter in outside air temperatures ranging from 37° to 57° F. Winter records of females at night roosts were more irregular but indicated activity on nights when the outside air temperature ranged between 47° and 57° F. Pearson, et al., did not determine what food sustained this winter activity. Although flying insects were probably scarce at this season, these authors captured adult male bats that lacked stored fat. Elsewhere, males that they weighed averaged 8.36 grams on 3 February and had dropped 0.64 grams to 7.72 grams by 2 April. This loss probably represented the amount of stored fat required to sustain the bats for this period (temperatures 37° to 50° F.) without intake of additional food.

For further data on roosts, sociability, and movement during hibernation, see pp. 168, 170, and 176.

Reproduction: Unless otherwise noted, all of the following information on reproduction in *P. townsendii* is taken from Pearson, et al. (1952, pp. 281–314).

Insemination.—The mating season extends from early October to late February. Copulatory activity is greatest in the winter roosts, but some, perhaps most, females have mated at least once before they arrive at the wintering places. Unmated females may be found throughout September, but spermatozoa are to be found in all after about the third week of October. Young females (as little as 3 or 4 months old) mate as early as do adult females, but because they produce few sperms and because their sex accessories are small, young males (4 to 9 months old) are almost certainly sterile in their first breeding season.

At times the males, more or less active throughout the winter, approach and probably achieve intromission with lethargic females. The passive state of the females and the absence of a vaginal plug would permit each female to be mated many times in the course of the winter. Since all females in the hibernating quarters contain spermatozoa by late October, subsequent copulatory activity on the part of the males must be directed toward females already inseminated.

It is not known how the male circumvents the female's interfemoral membrane, which during lethargy is usually curled tightly over the abdomen. The only copulation that Pearson, et al., observed took place on a cave ceiling too high to allow observation of detail. However, the male embraced the female from behind in the usual manner of copulating mammals.

Precopulatory activity was observed among captive bats. The female hung by her feet and was approached from the front by a male. Twittering, the male proceeded to embrace the female with his wings, then vigorously rubbed his snout, perhaps making use of his muzzle glands, over the foreparts and ventral surface of the female. A strong bat odor was noted.

Sperm storage.—Spermatozoa of bats are viable for surprisingly long periods. In male *P. townsendii* they retain their motility for six or more months after they reach the epididymis. However, it is not known whether motile spring spermatozoa are capable of fertilizing. Spermatozoa remained abundant in the uteri of females kept isolated in cool temperatures for as long as 108 days. Probably in *P. townsendii*, as in other vespertilionid bats, spermatozoa stored over winter in the female reproductive tract are capable of fertilizing in the spring. After ovulation, spermatozoa disappear quickly from the uterus.

Ovulation.—In *P. townsendii* ovulation occurs from February to April. Maturation of the ovarian follicle and its subsequent ovulation may depend upon the stimulation of copulation, and this stimulus may be effective even though administered several months before ovulation. It appears that there is an autumnal and early winter period during which ovulation normally will not occur. Neither females that are active in winter nor those that are lethargic in winter ovulate before spring, and those that are removed from hibernation and kept at warm temperatures do not ovulate readily. The possibilities of sperm storage in the female and insemination of unreceptive females while they are lethargic may have permitted the advanced copulatory period to evolve.

Gestation.—The duration of gestation may depend upon the body temperature of the bat and upon whether or not it was lethargic during a portion of the period. Variation in environmental conditions in hibernating quarters and nursery roosts thus may have a profound effect on gestation. The gestation period varied from 56 to 100 days in the California populations of *P. townsendii* studied by Pearson, et al.

Parturition.—The birth process was observed in a captive female. She hung from the wire top of her cage by widespread hind feet and thumbs. Her tail was curled upward so that it completed the "inverted umbrella" effect and made it quite unlikely that the young could fall. In fact, not even a drop of blood or fluid reached the cage floor. This position was maintained all during parturition and for half an hour afterward. The birth was a breech presentation. Within minutes the fluids and afterbirth were consumed by the mother, and while she licked her membranes and offspring, the young moved forward, secured a nipple, and attached its feet to the top of the cage.

A single young is the rule in this species, and 49 out of 50 embryos were found in the right horn of the uterus. After parturition this horn never returns to its original small size, but remains larger than the left, about 1.5 to 2 mm. in diameter. This disparity in size may lead to presumably erroneous reports of fall pregnancies as that of Bailey (1936, p. 390).

The average date of parturition of a colony varies from year to year, and there seems to be a considerable variation in the spread of birth dates in different colonies (19 to 35 days). It is probable that birth dates extend over a long period in a colony whose females roosted in diverse places with a variety of environmental temperatures before they congregated at the nursery colony. There is evidence also that young females tend to join the nursery colony later in the spring than do adults, and that they bear their young later in the season than do adults.

Pearson, et al., estimated birth dates for several hundred western American *P. townsendii* from specimens, field notes, and literature by reference to graphs relating embryo size and forearm length to age (figs. 20, 21). The earliest calculated birth date was 19 April in California, and the latest was 22 July in Arizona. Records for the Appalachian population indicate a similar breeding season.

Growth of young.—Pearson, et al., described the newborn *P. townsendii* as a grotesque creature, its large ears flopping over its unopened eyes and the disproportionately large size of its thumbs and hind feet giving it a spider-like appearance. The following chronology of growth was set forth:

The average weight of newborn young was 2.4 grams, and the forearm length averaged 16.6 mm. (there is no significant size varia-

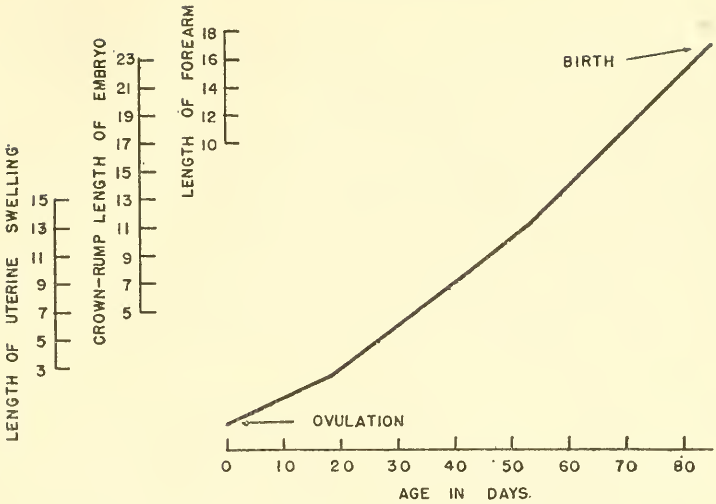

FIGURE 20.—Average growth-rate of embryo in *Plecotus townsendii pallescens*. Measurements in millimeters. (Modified from Pearson, et al., 1952, p. 302.)

tion between sexes until late in development when smaller size of male becomes apparent). Within a few hours the young one is able to utter a characteristic sharp, metallic "chirp." The dried umbilical cord may remain attached for a day or two. Before five days of age the naked pink body becomes covered with short gray hair. At seven days the young bat can make the "squaking" noise of the disturbed adult, and the ears assume the erect position of the adult. A few days later the eyes open. Up to the age of 16 days (forearm less than 35 mm.), while the growth curve is approximately linear, the forearm lengthens 1.2 mm. per day. Forearm length is a reliable indicator of age up to about three weeks. At four weeks the forearm is so close to adult length that it can no longer be relied upon. The young fly at about two and a half to three weeks of age, and at six weeks some young fly out at night as do the adults. The summer colonies start to break up in August when the older young are just over three months old.

Lactation.—In *Plecotus* there is a single pair of pectoral mammae, lateral in position. Tiny nipples (less than 0.6 mm. long in fresh specimens) are characteristic of young and nonparous females, and once a female has borne young the nipples do not return again to the tiny category, although they frequently become small again. The nipples of the young remain tiny through the summer, fall, and winter of their first year, and begin to enlarge at about the time of implantation of the embryo. The nipples reach full size (up to about 3 mm. in length) at the end of pregnancy or shortly thereafter.

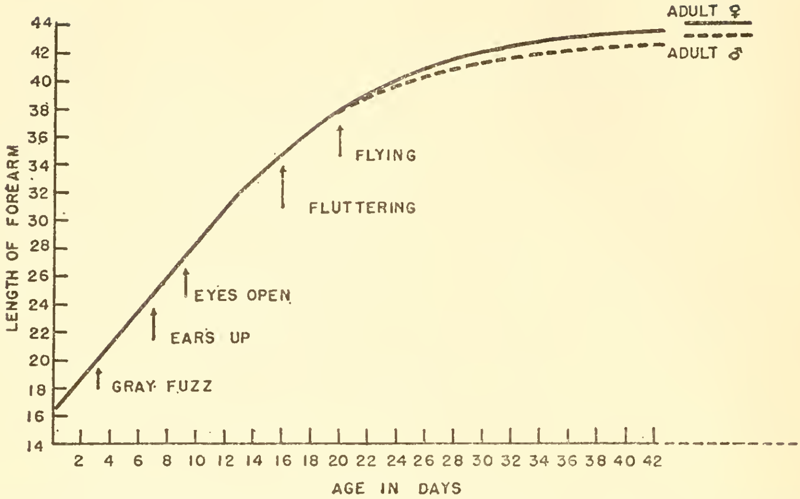

Figure 21.—Average growth-rate of forearm in *Plecotus townsendii pallescens.* Measurements in millimeters. (Modified from Pearson, et al., 1952, p. 313.)

The young probably nurse with their heads hanging down, and most nursing must occur during the day, for from the time that they are born or within a day or two of their birth, the young bats are left in the roost at night while the adults go out to feed. Banding has proved that each female bat unerringly selects her own young from amongst the many in the cluster when she returns to the nursery from her foraging flight.

The young bats cling to anything that comes into their grasp, and it is difficult to remove them from their mother. A disturbed mother may sometimes be seen flying with a young-one dangling from a nipple, but usually the young bat clings to its mother's fur with well-clawed thumbs and feet, as well as to the nipple with its mouth. Adults may fly with attached volant young weighing as much as six grams—about two-thirds of the adult's weight.

It is difficult to tell when lactation ceases, but it appears that females nurse their young for about two months. By that time the young are as large as their mothers and are skillful fliers.

Molt: The young big-eared bat molts from its juvenile pelage to adult pelage at about the time that it reaches adult body size, between the ages of one and two months. One collected on 7 August at Burkes Garden, Va. (USNM 157075), was beginning the molt on chest and belly. Three collected on Sand Creek, Wyo. (USNM), on 24 August, had barely begun to molt.

Adults have a single complete molt annually, most commonly in August. Possibly the molt normally occurs earlier in males than in females. New hairs usually appear at almost the same time on all parts of the body. Short, prostrate, new hairs are found on some individuals as early as June (MVZ 103184, ♂, San Luis Obispo County, Calif., 24 June) or July (USNM 250084, ♂, Fallon, Nev., 7 July). Specimens from Evergreen, Calif. (MVZ 71619, ♂, 2 August), Huachuca Mountains, Ariz. (UI 4674, ♂, 7 August, and UI 1425, ♀, 15 August), and Vidal, Calif. (LSU 1121, ♀, 29 August) were molting when captured. Six of seven females (USNM) taken on 24 August along Sand Creek, Wyo., were molting. Of five specimens (USNM) collected on 24 August at Las Cruces, N. Mex., one male had completed the molt; one female had completed the molt on the dorsum, but was still molting on the belly; two females were molting on all parts of the body; and one male apparently had not begun to molt.

Some of the summer specimens from New Mexico and southern California have a peculiar, short, woolly, relatively sparse pelage, possibly due to early shedding of guard hairs. The same condition has been observed in some specimens of *P. mexicanus*.

Plecotus townsendii australis Handley

Plecotus (*Corinorhinus*) *townsendi* J. A. Allen, 1890, p. 176.
Corynorhinus macrotis pallescens Miller, 1897, p. 52. (Part.)
Corynorhinus megalotis mexicanus G. M. Allen, 1916, p. 347. (Part.)
Corynorhinus rafinesquii mexicanus Miller, 1924, p. 83. (Part.)
Plecotus rafinesquii mexicanus Dalquest, 1953, p. 64. (Part.)
Corynorhinus townsendii australis Handley, 1955c, p. 147.

Holotype: USNM 297265; adult female in alcohol, skull removed; collected 20 December 1952 by Aurelio Málaga Alba; 2 miles west of Jacala, 5,500 feet, Hidalgo, Mexico; collector's No. 1053.

Distribution: Arid interior mountain ranges of central and northern Mexico (fig. 24). North to San Juan, Durango, and near Hacienda La Mariposa, Coahuila. East to near Hacienda La Mariposa and near Bella Unión, Coahuila; Presa de Guadalupe, San Luis Potosí; near Jacala and near Yoltepec, Hidalgo; Lago Texcoco, México; and Oaxaca, Oaxaca. South to Oaxaca, Oaxaca; Cuernavaca, Morelos; and San Andrés, Jalisco. West to San Andrés, Jalisco; Sierra de Valparaíso, Zacatecas; and San Juan, Durango. Zonal distribution: Upper Sonoran and upper portion of Lower Sonoran. Altitudinal distribution: 1,800 to 9,500 feet. Most collecting stations are between 4,000 and 7,000 feet.

Description: Adult coloration: Hair of upperparts between Benzo Brown and Fuscous at base; tips brighter brown, burnished with dark brown; mass effect between Russet and Cinnamon-Brown; hair bases sharply differentiated from tips. Hair of underparts Natal Brown at base; tips about Light Pinkish Cinnamon on belly, somewhat darker on throat.

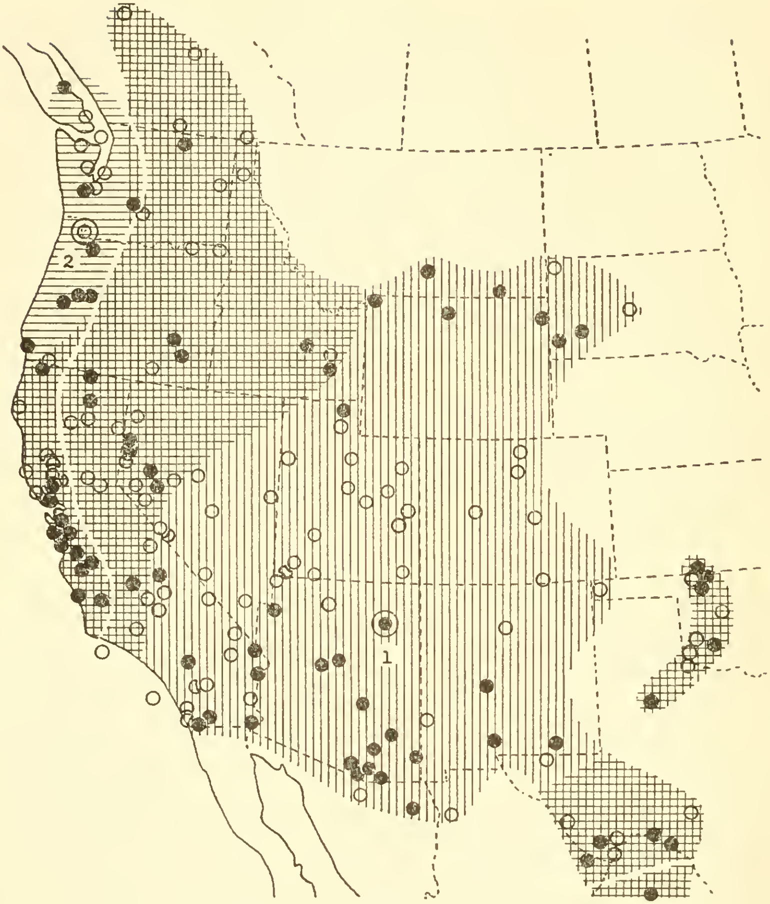

Figure 22.—Distribution of *Plecotus townsendii* Cooper (western section): 1, *P. t. pallescens;* 2, *P. t. townsendii.* Solid symbols, specimens examined; open symbols, other records; encircled symbols, type localities. Cross-hatching indicates known areas of intergradation between subspecies (between *pallescens* and *townsendii* in California, Nevada, Idaho, Oregon, Washington, and British Columbia; between *pallescens* and *ingens* in northern Texas, Oklahoma, and Kansas; and between *pallescens* and *australis* in western Texas, Chihuahua, and Coahuila).

Size averages medium for the subgenus; forearm averages relatively long. Rostrum averages relatively long, dorsolaterally inflated, and usually not particularly depressed; anterior nares relatively large and usually rounded posteriorly (dorsal view). First upper incisor normally without secondary cusp; upper canine averages less robust than in northern populations; anterointernal cingular cusp of P^4 frequently present.

Measurements: See tables 10, 16.

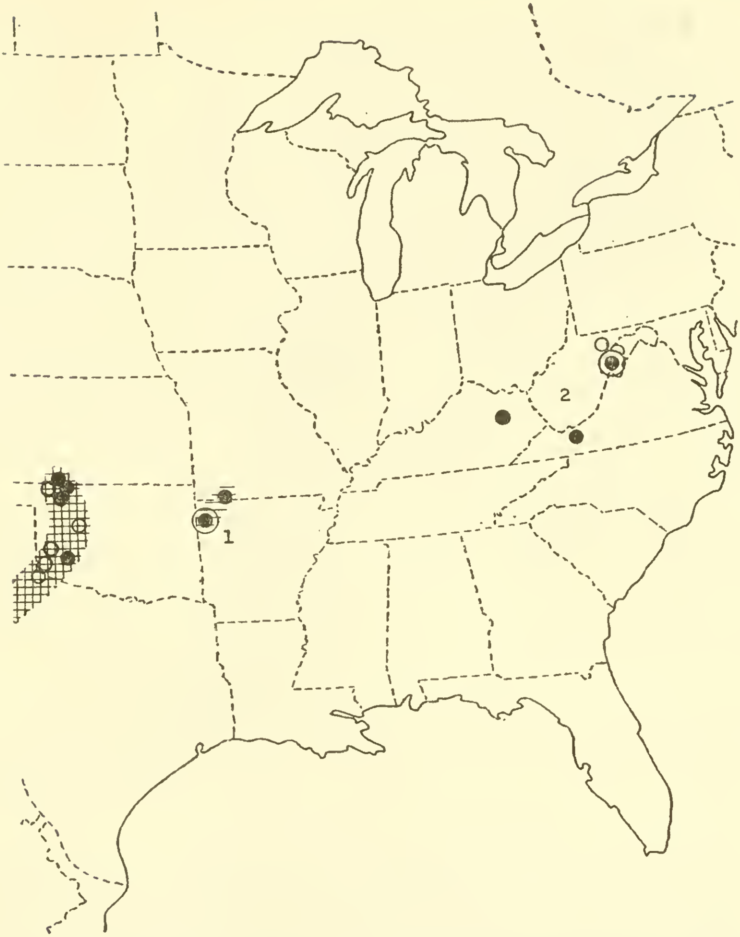

Figure 23.—Distribution of *Plecotus townsendii* Cooper (eastern section): 1, *P. t. ingens;* 2, *P. t. virginianus.* Solid symbols, specimens examined; open symbols, other records; encircled symbols, type localities. Cross-hatching indicates known areas of intergradation between subspecies *ingens* and *pallescens.*

Comparisons: *P. t. australis* is most similar to *P. t. pallescens,* but averages darker, browner, and less cinnamon dorsally. *P. t. australis* averages larger in most cranial dimensions than Arizonan *P. t. pallescens,* but can be scarcely distinguished cranially from other populations of *P. t. pallescens.*

For comparison with *P. mexicanus,* see account of that species.

Remarks: Mexican populations of *P. townsendii* are relatively uniform in coloration and cranial characters despite the wide range of latitude and elevation inhabited. The greatest divergence noted is in specimens from San Andrés, Jalisco, in which the rostrum is unusually

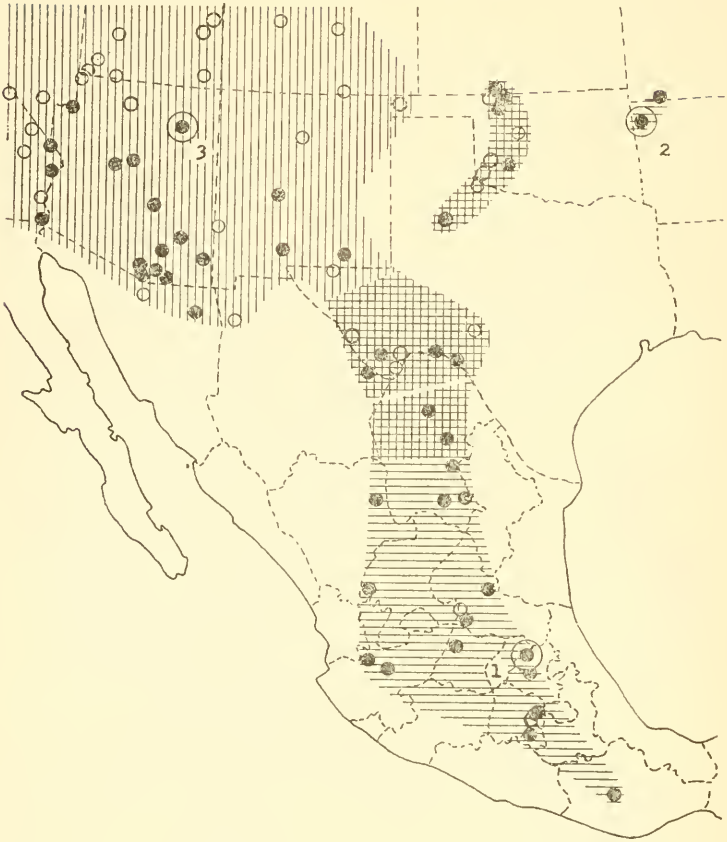

FIGURE 24.—Distribution of *Plecotus townsendii* Cooper (southern section): 1, *P. t. australis;* 2, *P. t. ingens;* 3, *P. t. pallescens.* Solid symbols, specimens examined; open symbols, other records; encircled symbols, type localities. Cross-hatching indicates known areas of intergradation between subspecies (between *pallescens* and *ingens* in northern Texas, Oklahoma, and Kansas; between *pallescens* and *australis in* western Texas, Chihuahua, and Coahuila).

broad and inflated. Indeed, the whole skull is broad (reflected in zygomatic breadth, breadth of brain case, etc.) in those specimens.

P. t. australis intergrades with *P. t. pallescens.* Samples from southern Coahuila have the coloration of *P. t. australis.* Two specimens from near San Buenaventura in central Coahuila resemble *P. t. pallescens,* whereas one from the Chisos Mountains, Texas, is very similar to *P. t. australis.* Other specimens from the Big Bend region of Texas and Chihuahua are, on the average, sufficiently similar to *P. t. pallescens* to be identified as that subspecies, and central and southeastern New Mexican specimens are essentially identical with samples of typical *P. t. pallescens* (northern and central Arizona). Apparently intergradation between these two races of *P. townsendii* occurs in northern Coahuila and western Texas.

Specimens examined.—A total of 58 from the following localities:

MEXICO: Coahuila: 1 mile south and 4 miles west of Bella Unión, 7,000 feet, 3s (KU); 4 miles west of Hacienda La Mariposa, 2,300 feet, 1s (KU); one-half mile north of Muralla, 4,500 feet, 19bs (KU); 9 miles west and 4 miles south of San Buenaventura, 2,000 feet, 3s (KU); Sierra Guadalupe, 7,800 feet, 10 miles south and 5 miles west of General Cepeda, 1s (KU). Durango: San Juan, 3,800 feet, 12 miles west of Lerdo, 2s (UMMZ). Guanajuato: Santa Rosa [9,500 feet], 7a (USNM). Guanajuato?: Charcas, 5a (USNM). Hidalgo: Grutas Xoxafi, 6.6 miles southeast of Yoltepec [=Yolotepec?, 6,600 feet], 1s (KU); 2 miles west of Jacala, 5,500 feet, 3a (USNM); Río Tasquillo (Río de Tula), 5,200 feet, 16 miles east [=12 miles south-southeast?] of Zimapán, 1s (TCWC). Jalisco: San Andrés [4,900 feet], 10 miles west of Magdalena, 3s (UMMZ); San Pedro, Guadalajara, 1s (AMNH). México: Convento de Acolman, 9 miles north of México, Distrito Federal, 1s (IB); Lago Texcoco, 7,500 feet, 1a (USNM). Morelos: Cuernavaca [4,900 feet], la (USNM). Oaxaca: Oaxaca [Motne Albán, 6,500 feet, 3 miles southwest of Oaxaca], la (USNM). San Luis Potosí: Bledos [6,200 feet], ls (LSU)1; Presa de Guadalupe [4,000 feet] ls (LSU). Zacatecas: Sierra de Valparaíso [13 miles west of Valparaíso, 8,200 feet], 1s (USNM). "Mexico": No exact locality, 1b (USNM).

Additional records: The following records probably refer to this form:

MEXICO: Distrito Federal: Desierto de los Leones [measurements taken by Villa in 1958, according to my instructions, agree fairly well with those of *P. t. australis*] (Villa R., 1953, p. 340). San Luis Potosí; Hacienda La Parada [6,000 feet] (Miller, 1897, p. 53).

Plecotus townsendii ingens Handley

Corynorhinus rafinesquei rafinesquei Sealander, 1951, p. 465.
Corynorhinus townsendii ingens Handley, 1955c, p. 148.

Holotype: USNM 296767; adult male, skin and skull; collected 4 December 1950 by John A. Sealander; Hewlitt Cave, 12 miles west of Fayetteville, Washington County, Ark; collector's No. 50–14.

Distribution: Ozark Highlands in northwestern Arkansas and southwestern Missouri (fig. 23); possibly also extreme eastern Oklahoma. North to Stone County, Missouri. South to Washington County, Ark. Zonal distribution, Upper Austral. Altitudinal distribution, approximately 1,000 to 1,500 feet.

Description: Adult coloration: Mass effect of upperparts between Hazel and Mars Brown; hair bases Fuscous. Hair of underparts between Light Vinaceous-Cinnamon and Light Pinkish Cinnamon distally, the bases, except those bordering membranes, Fuscous; bases of border hairs same as tips. Distinction between bases and tips of hairs fairly sharp, on both dorsum and underparts.

Size averages large; forearm averages relatively long; skull of heavy construction; rostrum relatively long, inflated, and not depressed; anterior nares average relatively large and rounded in posterior outline (dorsal view). First upper incisor usually with at least a trace of a secondary cusp; anterointernal cingular cusp of P^4 absent; molariform teeth robust.

MEASUREMENTS: See tables 10, 16.

COMPARISONS: Bats of the race *P. t. ingens* are the most reddish and the largest of *P. townsendii*. From *P. t. pallescens*, the only geographically adjacent race of this species, *ingens* is distinguished by darker, more orange or reddish coloration, average larger size, relatively larger auditory bullae, more inflated rostrum, relatively more robust molariform teeth, and more frequent development of a secondary cusp on the first upper incisor.

For comparison with *P. t. virginianus* see account of that subspecies (p. 202).

REMARKS: The Ozark form is similar to both *P. t. virginianus* to the eastward and *P. t. pallescens* to the westward. Specimens of *P. t. pallescens* from western Oklahoma and south-central Kansas approach *P. t. ingens* in size and coloration, although they are more like typical *P. t. pallescens*.

SPECIMENS EXAMINED: A total of 18 from the following U.S. localities:

ARKANSAS: *Washington County:* Basset Cave, near Hicks, 1s (UAZ); Devil's Icebox, Devil's Den State Park, 25 miles southwest of Fayetteville, 2s (CNHM), 9s (UAZ), 1s (USNM), 1s (GF); Hewlitt Cave, 12 miles west of Fayetteville, 2s (UAZ), 1s (USNM). MISSOURI: *Stone County:* No exact locality, 1a (AMNH).

Plecotus townsendii pallescens Miller

Synotus macrotis H. Allen, 1864, p. 63. (Part.)
Synotus townsendi H. Allen, 1864, p. 65.
C[orynorhinus] macrotis H. Allen, 1865, p. 174. (Part.)
C[orynorhinus] townsendi H. Allen, 1865, p. 175.
Corynorhinus macrotis pallescens Miller, 1897, p. 52.
Corynorhinus macrotis intermedius H. W. Grinnell, 1914, p. 320. (Part.)
Corynorhinus megalotis megalotis G. M. Allen, 1916, p. 338. (Part.)
Corynorhinus megalotis pallescens G. M. Allen, 1916, p. 341.
Corynorhinus rafinesquii pallescens H. W. Grinnell, 1918, p. 340.
Plecotus rafinesquii pallescens Blair, 1952, p. 96.
Corynorhinus t[ownsendii] pallescens Handley, 1955c, p. 147.

HOLOTYPE: USNM (Biol. Surv. Coll.) 66534; adult female, skin and skull (crushed); collected 3 August 1894 by A. K. Fisher; Keam Canyon, Navajo County, Ariz.; collector's No. 1715.

DISTRIBUTION: Western United States, northwestern Mexico, and southwestern Canada, including parts of the Great Plains, Rocky

Mountains, Great Basin, Mohave and Colorado Deserts, etc., but excluding the northwestern coast region (fig. 22). North to Stanley and Harding Counties, S. Dak.; Powder River and Yellowstone Counties, Mont.; Yellowstone National Park, Wyo.; Riske Creek and Williams River, British Columbia. West to Riske Creek and Williams River, British Columbia; Okanogan and Yakima Counties, Wash.; Harney County, Oreg.; Siskiyou, Tehama, Placer, Tulare, and Kern Counties, Calif., and the coast and Channel Islands of California south of Point Conception. South to San Diego and Imperial Counties, Calif.; northern Baja California, northern Sonora, and northern Chihuahua, Mexico; Dona Ana County, N. Mex.; Culberson, Presidio, Brewster, Val Verde, and Edwards Counties, Tex. East to Val Verde and Edwards Counties, Tex.; Eddy County, N. Mex.; Cimarron County, Okla.; El Paso, Boulder, and Larimer Counties, Colo.; Custer and Stanley Counties, S. Dak. An apparently isolated population inhabits the gypsum cave region in south-central Kansas, central Oklahoma, and north-central Texas (specimens from Barber and Comanche Counties, Kans., south to Garza County, Tex. Zonal distribution: Most numerous in Upper Sonoran and Transition zones, but also occurs at the upper edge of the Lower Sonoran and the lower edge of the Canadian. Altitudinal distribution: Sea level (possibly below sea level in southern California) to 9,600 feet.

DESCRIPTION: Adult coloration: Mass effect of upperparts averages between Sayal Brown and Cinnamon; hair bases Light Cinnamon-Drab to Benzo Brown. Hair bases of underparts average between Fawn Color and Benzo Brown; tips between Light Pinkish Cinnamon and Pinkish Buff. Distinction between bases and tips of hairs usually everywhere slight. Immature coloration: Mass effect of upperparts between Drab and Cinnamon-Drab; hair bases slightly grayer. Hair tips of underparts "dirty" white; bases Benzo Brown to Light Mouse Gray.

Size averages medium for the subgenus; forearm averages relatively long; skull relatively light in construction; rostrum averages relatively long, not particularly depressed, and not inflated; anterior nares average relatively small and angular in posterior outline (dorsal view). Canine relatively strong; secondary cusp on I^1 usually absent; anterointernal cingular cusp of P^4 frequent.

MEASUREMENTS: See tables 11, 17.

COMPARISONS: In coloration of fur, membranes, and ears *P. t. pallescens* is the palest and most yellowish known population of the species.

For comparison with related subspecies see accounts of *P. t. australis* (p. 187), *P. t. ingens* (p. 190), and *P. t. townsendii* (p. 198).

Remarks: There are four centers of saturate coloration in *P. townsendii:* (1) the central Appalachians; (2) the Ozark Plateau; (3) the Pacific Northwest; and (4) to a lesser degree, north-central Mexico. Between the three latter centers is a pale-colored population (*P. t. pallescens*) which exhibits maximum pallor and yellowness in the area extending from southeastern California and central Arizona northeastward to Wyoming, southeastern Montana and southwestern South Dakota. The extreme in pallor is found in the northeastern and southwestern parts of this belt. The very palest specimens that I have seen come from southeastern California. Southward, eastward, and westward from the pallid belt there is a gradual and progressive darkening of pelage toward the saturate centers (fig. 22).

Populations inhabiting the northern flanks of the Sierra Madre Occidental in northern Sonora and adjacent parts of Arizona are somewhat darker than populations of central and northern Arizona, but are much paler than *P. mexicanus* which is at the northwestern limit of its range in the same region. New Mexican specimens are but slightly darker and less yellow than the typical coloration of *pallescens*. Specimens from Oklahoma and Kansas are clearly intermediate between *pallescens* and the Ozark form, there being considerable variation in color. The series as a whole, however, is nearer *pallescens*. Most Texas (Big Bend) specimens, while not appreciably darker, are much less yellowish than typical *pallescens*. One specimen is darker and resembles more southerly populations called *P. t. australis*.

Proceeding westward from the pallid belt, increasing darkness of coloration is encountered as the range of the dark-colored northwestern coast population of *P. townsendii* is approached. The zone of intergradation between pale-colored and dark-colored populations is broad and includes the coast region of northern and central California; much of the remainder of California east of the Coast Range, but excepting the southern deserts; northwestern Nevada; Idaho; eastern Oregon; eastern Washington; and south-central British Columbia.

Within this zone there is considerable individual variation in dorsal coloration, shades of yellowish brown and grayish brown being most common, but reddish brown individuals also occurring. Tone is very variable throughout the zone, the range in some samples almost bridging the gap between the pale and dark extremes of the northwestern coast and the pallid belt.

Various authors (among them, H. Grinnell, 1914, p. 320; Whitlow and Hall, 1933, p. 245; Hall, 1946, p. 160; and Dalquest, 1947, p. 20) have regarded the populations of this region as being subspecifically distinct from *townsendii* and *pallescens*. The appropriate name, "*intermedius*" H. W. Grinnell, is available for this population.

Dalquest (1947, p. 20) suggested that this intergrading population probably developed intermediate characters in response to the nature of its environment—intermediate between the humid, forested coast and the arid, treeless deserts, and further postulated that genetic intergradation was not necessarily implied. If this were not an intergrading population I would expect to find constant adaptive characters developed in some portion of its geographic range. However, in examining specimens from all portions of the range assigned to "*intermedius*," I have failed to find such a condition.

A series of 25 specimens from Mission San Jose, Alameda County, Calif., when arranged in order from pale to dark, quite effectively bridges the color gap between *pallescens* and *townsendii;* the average is nearest *townsendii.* Among 14 specimens from Tulare County, Calif., are three as pale as *pallescens,* two as dark as *townsendii* (although more reddish), and nine that are intermediate; the average is nearest *pallescens.* In a series of 16 specimens from Pyramid Lake, Nev., the palest individuals are indistinguishable from typical *pallescens,* while the darkest, without reservation, could be called *townsendii;* the average is nearest *pallescens.* Six of seven from Malheur County, Oreg., are indistinguishable from typical *pallescens,* while one is intermediate but nearer *pallescens.* In a series of three specimens from Boulder Cave, Kittitas County, Wash., one is as dark as typical *townsendii,* while the others are somewhat paler, but nevertheless nearer *townsendii.* Whitlow and Hall (1933, p. 246) regarded a large series from the Pocatello Region of Idaho as intermediate.

Similarly, there is intergradation between pale-colored and dark-colored populations in cranial characteristics. This is best seen in the relative stoutness of the rostrum (normally stout in dark-colored northwestern coast populations, normally less stout in pale-colored interior populations). Within the zone of intergradation, stoutness of the rostrum can not be correlated with coloration: Some pale-colored individuals have the rostrum very stout; some dark-colored individuals have the rostrum rather frail.

From the specimens and information available to me, it does not appear that there is a population with constant morphological characters that could justifiably bear the name "*intermedius*." The fact that intergradation between *P. t. townsendii* and *P. t. pallescens* occurs over an extensive geographic area does not make the application of the name "*intermedius*" to the intermediate population more valid. The ideal in mammalian systematics is to avoid application of special names to geographically and genetically intermediate populations. The use of the name "*intermedius*" is clearly in violation of this principle, and the name is best relegated to synonymy.

SPECIMENS EXAMINED: A total of 313, from the following localities:

MEXICO: CHIHUAHUA: Tinaja de Ponce, 2,600 feet, Sierra de Ponce, 12 miles southwest of Santa Helena, 16as (USNM). SONORA: Santa María Mine, El Tigre Mts., 3a (UMMZ); Pilares, 1a (UMMZ).

UNITED STATES: CALIFORNIA: *Imperial County:* Potholes, 1a (USNM); 6 miles north of Potholes, 1a (MCZ). *Inyo County:* Lone Pine, Alabama Hills, 4as (MCZ); Owen's Lake, 1a (USNM); Owen's Valley, 1a (USNM). *Riverside County:* 2 miles west of Red Mountain Lookout, 2s (STPM), 2s (USNM); Riverside Mts., 2s (LSU). *San Bernardino County:* "Manvel" or "Marvel," 1a (USNM); Eagle Pass, 12 miles southwest of Needles, 1s (LSU); Oro Grande, 2s (USNM); Vidal (Alice Mine), 4a (USNM); 6 miles south of Vidal, 1s (LSU). *San Diego County:* Dulzura, 1a (USNM); El Monte Oaks Park, 1a (CNHM); Pine Valley, 1a (USNM); Vallecito Stage Station, 1s (CNHM). *Shasta County:* Fort Creek, 1a (USNM). *Siskiyou County:* Lava Cave, 5 miles southwest of Tule Lake, 1s (USNM). *Tulare County:* 4 miles southeast of Porterville, 550 feet, 10s (AMNH); 10 miles east of Porterville, 1s (AMNH); 4 miles east-southeast of White River, 1,700 feet, 3s (AMNH). OREGON: *Malheur County:* 15 miles south-southwest of Carol, 17as (USNM); Malheur Cave, 20 miles east of Malheur Lake, 1s (USNM). WASHINGTON: *Okanogan County:* Okanogan Highlands, 15 miles east of Tonasket, 1s (MCZ). IDAHO: *Bannock County:* Portneuf River, 3 miles northwest of Inkom, 1bs (USNM); Chinks Peak, 1.5 miles southeast of Pocatello, 1bs (USNM). *Butte County:* Craters of the Moon National Monument, 1s (USNM). NEVADA: *Churchill County:* Fallon, 1s (USNM). *Mineral County:* 1 mile northwest of Rawhide, 1s (UI). *Washoe County:* Sutcliffe, 3,700 feet, 1s (AMNH); The Needles (The Pinnacles), 3,900 feet, north end of Pyramid Lake, 35as (USNM). UTAH: *Cache County:* Logan Canyon, 15 miles above Logan, 1a (MCZ), 6a (USNM). *No exact locality:* 1a (USNM). ARIZONA: *Cochise County:* Chiricahua Mts., 1a (USNM); Fort Huachuca, 3a (USNM); 8 miles west of Fort Huachuca, 2s (UI); 11 miles south of Fort Huachuca, 1s (UI); Ash Canyon, 19 miles south of Fort Huachuca, 1s (UI); Carr Canyon, 7,200 feet, Huachuca Mts., 4a (MCZ), 3s (UI); Miller Canyon, Huachuca Mts., 3a (MCZ); Montezuma Canyon, 5,300 feet, Huachuca Mts., 4a (MCZ); Ramsey Canyon, Huachuca Mts., 2a (MCZ); Huachuca Mts., 1s (MCZ). *Graham County:* Ash Creek, 4,200 feet, Graham Mts. (Pinalino Mts.), 1s (USNM). *Maricopa County:* Roosevelt [Bumblebee Creek, below Roosevelt Dam], 2,300 feet, 1s (USNM); Christmas Mine, 3,000 feet, 5 miles southwest of Roosevelt, 1s (USNM). *Mohave County:* Oatman, 6as (MCZ); Rampart Cave, 2 miles southeast of Pierce's Ferry, Hoover Dam National Recreational Area, 1s (USNM). *Navajo County:* Keam Canyon, 1s (USNM). *Pima County:* 2 miles northeast of Arivaca, 4,000 feet, 11s (AMNH); Las Guijas Mts., north slope, 7 miles north-northwest of Arivaca, 5s (AMNH); Las Guijas, about 10 miles north-northwest of Arivaca, 1a (USNM); Santa Catalina Mts., 3a (AMNH); Colossal Cave, 28 miles southeast of Tucson, 2s (USNM). *Pinal County:* No exact locality, 1s (AMNH). *Santa Cruz County:* Oro Blanco Mts., 4,600 feet, 12a (MCZ); Patagonia Mts., 3a (MCZ); McCleary's Ranch, Santa Rita Mts., 1s (USNM). *Yavapai County:* Camp Verde, 3,200 feet, 1s (USNM), 1s (AMNH); Montezuma Well, 3,500 feet, 6as (USNM); Prescott, 1s (AMNH); Turkey Creek [east slope of Bradshaw Mts., 7 miles northeast of Crown King], 3,400 feet, 1s (USNM). NEW MEXICO: *Dona Ana County:* San Andreas Mts., 5,600 feet, 35 miles northeast of Las Cruces, 5s (USNM). *Eddy County:* Carlsbad, 1s (USNM); McKitterick Cave, 20 miles west of Carlsbad, 1s (USNM); Carlsbad Caverns, 4s (CC). *Socorro County:* Socorro, 1s (USNM). TEXAS: *Brewster County:* West slope of Emory Peak, 7,100 feet, Chisos Mts., 4s

(UMMZ); Kibbe Spring, 5,700 feet, Chisos Mts., 1s (CNHM); Pine Canyon, 4,700 feet, Chisos Mts., 1s (UMMZ); Johnson Ranch, 1a (USNM); Viviani Mines, Mariscal Mts., 1s (TSDH). *Garza County:* Post, 1s (TT). *Val Verde County:* East Painted Cave, northwest of Del Rio, 1a (USNM); Langtry, 1a (USNM). OKLAHOMA: *Comanche County:* Wichita Mountains National Wildlife Refuge, 3s (USNM). *Woods County:* Alva, 1a (USNM); no exact locality, 2b (MCZ). *Woodward County:* Alabaster Cave, 2s (CNHM); 6 miles southwest of Freedom, 1a (USNM). KANSAS: *Barber County:* Sun City, 2s (USNM). WYOMING: *Big Horn County:* 25 miles northeast of Greybull, 3a (AMNH). *Crook County:* Sand Creek, 3,750 feet, Black Hills, 10s (USNM). *Yellowstone National Park:* Devil's Kitchen, Mammoth Hot Springs, 6as (USNM). MONTANA: *Powder River County:* Moorhead, 24s (USNM). *Yellowstone County:* 5 miles west of Billings, 1a (CNHM). SOUTH DAKOTA: *Custer County:* Hell Canyon, 13 miles west of Custer, 7s (USNM); 18 miles southwest of Custer, 1s (USNM). *Pennington County:* Mouth of Spring Creek, Cheyenne River, 3s (AMNH). *County uncertain:* Crowfeet [=Crow Peak, Lawrence County?], Black Hills, 7a (AMNH).

ADDITIONAL RECORDS: The following records probably refer to this form:

MEXICO: BAJA CALIFORNIA: No exact locality (Pearson, et al., 1952, p. 273). CHIHUAHUA: Casas Grandes (Málaga, 1953, in litt.). SONORA: Sáric (Burt, 1938, p. 26).

UNITED STATES: CALIFORNIA: *El Dorado County:* No exact locality (Taylor, 1919, p. 86). *Imperial County:* Palo Verde (H. W. Grinnell, 1918, p. 343). *Inyo County:* Mountain Springs Canyon, 5,500 feet, Argus Mts. (Dalquest, 1947, p. 19); 4.5 miles southwest of Bishop, 5,200 feet, and 4 miles south-southeast of Bishop, 4,700 feet (Dalquest, 1947, p. 19). *Kern County:* Old Fort Tejon, near Lebec (Dalquest and Ramage, 1946, p. 62); Red Rock Canyon (Dalquest, 1947, p. 19); Weldon (Dalquest, 1947, p. 20). *Lassen County:* Near Wendel (Dalquest, 1947, p. 20). *Los Angeles County:* Johnson's Harbor, Santa Catalina Island (H. W. Grinnell, 1914, p. 320). *Placer County:* Auburn, 1,300 feet (H. W. Grinnell, 1914, p. 320); Pioneer Cave (H. W. Grinnell, 1914, p. 320). *Riverside County:* Hemet Peak, 6,500 feet, San Jacinto Mts., 2 miles northeast of Kenworthy (Grinnell and Swarth, 1913, p. 379); near Whitewater (H. W. Grinnell, 1918, p. 343). *San Bernardino County:* 5 miles southwest of Ivanpah, 4,500 feet (Dalquest, 1947, p. 19); Horse Spring, 2,700 feet, Kingston Range (Dalquest, 1947, p. 19); Mitchell's (Johnson, et al., 1948, p. 343). *San Diego County:* One-half mile west of Banner (Frum, 1954, in litt.); Excondido (Dalquest, 1947, p. 19); Julian (H. W. Grinnell, 1918, p. 343); Oak Grove (Frum, 1954, in litt.); San Diego (Stephens, 1906, p. 265); Suncrest (Mitchell, 1956, p. 444); Vallecito (H. W. Grinnell, 1918, p. 343); 1.5 miles northwest of Vallecito (Dalquest, 1947, p. 19). *Santa Barbara County:* Santa Cruz Island (Pearson, 1951, p. 366). *Shasta County:* Old Station, 4,300 feet (Pearson, et al., 1952, p. 277). *Siskiyou County:* Lava Beds National Monument, 4,800 feet (Pearson, et al., 1952, p. 278). *Tehama County:* Mouth of Battle Creek, near Bloody Island, 350 feet (Dalquest, 1947, p. 20). OREGON: *Harney County:* Roaring Springs Cave, 80 miles south of Burns (Cressman and Reed, 1938, p. 248). *Umatilla County:* 5 miles east of Milton (Booth, 1945, p. 26). *Wallowa County:* Grande Ronde Canyon, [12 miles northeast of] Paradise (Bailey, 1936, p. 388). WASHINGTON: *Spokane County:* 10 miles north of Spokane (Svihla, 1938, p. 18). *Yakima County:* Selah (Dalquest, 1948, p. 164). IDAHO: *Bannock County:* 3–4 miles east of Pocatello, 5,000 feet (Whitlow and Hall, 1933, p. 243); Schutt's Mine, 6,300 feet, 9 miles east of Pocatello (Whitlow and Hall, 1933, p. 243); 1 mile east of Portneuf, 4,500 feet (Whitlow and Hall, 1933, p. 243). *Bingham*

County: Blackfoot, 4,500 feet (Whitlow and Hall, 1933, p. 246). *Bonner County:* Deer Island, Lake Pend Oreille, and near Lakeview (Jones, 1948, p. 416). NEVADA: *Churchill County:* 9 miles north of Eastgate (Alcorn, 1944, p. 309); 10 miles southeast of Fallon (Hall, 1946, p. 159); 10 miles south and 5 miles west of Fallon, 4,300 feet (Hall, 1946, p. 162); 4.5 miles east of Stillwater, 4,000 feet (Hall, 1946, p. 160). *Clark County:* 7 miles east of Las Vegas (Burt, 1934, p. 397). *Esmeralda County:* Chiatovich Ranch, 4,850–4,900 feet (Hall, 1946, p. 162); 1 mile southeast of Dyer Ranch, 5,300 feet (Hall, 1946, p. 160). *Lander County:* one-quarter mile west-northwest of Austin (Alcorn, 1944, p. 309). *Lyon County:* 2 miles southwest of Pine Grove, 7,250 feet (Hall, 1946, p. 160); near Ramsey (Alcorn, 1944, p. 309); Muriel Bee Mine, 5,800 feet, 4 miles west of Wichman (Hall, 1946, p. 159); 9 miles east and 2 miles north of Yerington, 4,700 feet (Hall, 1946, p. 159); Bluestone Mine, 5,200 feet, 3.5 miles southwest of Yerington (Hall, 1946, p. 159). *Mineral County:* Fletcher, 6,100 feet (Frum, 1954, in litt.); Stanmoore Mine, about 7,000 feet, Lapon Canyon, Mount Grant (Hall, 1946, p. 159). *Nye County:* Amargosa River, 3,400–3,500 feet, 3.5 miles northeast of Beatty (Hall, 1946, p. 162); Hot Creek Range, 1 mile west of Hot Creek (Hall, 1946, p. 162); Springdale, north end of Oasis Valley (Davis, 1939, p. 124). *Washoe County:* 10 miles north-northwest of Deep Hole, 5,150 feet (Hall, 1946, p. 161); near Olinghouse (Alcorn, 1944, p. 309); Horse Canyon, 5,800 feet, Pahrum Peak (Hall, 1946, p. 161); 1 mile southwest of Pyramid Lake (Hall, 1946, p. 162); Smoke Creek, 9 miles east of California boundary, 3,900 feet (Hall, 1946, p. 162); 2 miles north of Sparks (Alcorn, 1944, p. 309). *White Pine County:* Lehman Cave, 7,200 feet (Hall, 1946, p. 162). UTAH: *Beaver County:* Fort Beaver, 5,900 feet (Long, 1940, p. 172). *Carbon County:* Range Creek (Hardy, 1941, p. 293); Sunnyside (Hardy, 1941, p. 293). *Emery County:* Horse Creek Canyon (Hardy, 1941, p. 293). *Grand County:* 4 miles north of Thompsons (Krutzsch and Heppenstall, 1955, p. 127); Post Canyon, Book Cliffs, 8,200 feet, 75 miles south of Ouray (Krutzsch and Heppenstall, 1955, p. 127). *Kane County:* 4 miles north of Kanab (Hardy, 1941, p. 293). *San Juan County:* Bluff, 3,300 feet (Hardy, 1941, p. 293). *Sanpete County:* Pete Canyon, 5,800 feet, west of Wales (Hardy, 1941, p. 293). *Tooele County:* Goldhill (Durrant, et al., 1955, p. 72). *Uintah County:* 1 mile southeast of Ouray, 4,700 feet (Durrant, 1952, p. 59). *Utah County:* Rock Canyon, near Provo (Biol. Surv. files); east of Springville (Hardy, 1941, p. 293). *Washington County:* Apex Mine (Hardy, 1941, p. 293); Bloomington Cavern (Hardy, 1941, p. 293); Mineral Mountain (Hardy, 1941, p. 293); Zion National Park (Hardy, 1941, p. 293). *Weber County:* South fork of Ogden River (Durrant, et al., 1955, p. 72). ARIZONA: *Cochise County:* Portal (Cahalane, 1939, p. 422). *Coconino County:* Grand Canyon National Park (Hearst Ranch, Grandview, and Pasture Wash Ranger Station) (Hoffmeister, 1955, p. 5). *Mohave County:* Virgin Narrows, northeast of Littlefield (Hardy, 1949, p. 434). *Santa Cruz County:* Peña Blanca Spring (Campbell, 1934, p. 242). *Yavapai County:* Martinez Creek, 7 miles southwest of Yarnell (Hatfield, 1942, p. 148). NEW MEXICO: *Grant County:* Mule Creek (Bailey, 1931, p. 381). *Santa Fe County:* Santa Fe (H. Allen, 1864, p. 65). TEXAS: *Brewster County:* Maravillas Canyon, east of Black Gap (Tamsitt, 1954, p. 46); southeast slope of Mariscal Mountain, 2,800 feet (Borell and Bryant, 1942, p. 10). *Culberson County:* Bell Creek, 5,300 feet, 7 miles north of Pine Springs (Davis and Robertson, 1944, p. 262); Upper Sloth Cave, west slope of Guadalupe Mts., 7,000 feet (Davis, 1940, p. 74). *Edwards County:* Devil's Sinkhole, 6.5 miles northeast of Rocksprings, 2,300 feet (White, 1948, p. 6). *Hardeman County:* Acme (Dalquest, 1954, in litt.); 3 miles southeast of Lazare (Dalquest, 1954, in litt.); Panther Cave, 10 miles southeast of Quanah (Blair, 1954, p. 242). *Presidio County:* Sierra Vieja (Blair and Miller, 1949, p. 76). *Val Verde County:*

Mouth of Pecos River (Blair, 1952, p. 96). Oklahoma: *Blaine County:* Salt Creek Canyon (Blair, 1939, p. 102); 3 miles southeast of Southard (Blair, 1939, p. 102). *Cimarron County:* Tesequite Canyon [1.7 miles southeast of Kenton] (Glass, 1951, p. 26). *Greer County:* 3.5 miles north of Jester (Glass, 1955, p. 128). *Harmon County:* 3 miles west and 1 mile south of Reed (Glass, 1955, p. 128). *Woods County:* 2 miles west of Edith (Blair, 1939, p. 102); 6 miles northeast of Freedom (Blair, 1939, p. 102); Marehew Cave, one-half mile south of Oklahoma-Kansas boundary (Hibbard, 1934, p. 237). *Woodward County:* 10 miles south of Freedom (Blair, 1939, p. 102). Kansas: *Barber County:* Several caves 3 to 5 miles southwest of Aetna (Cockrum, 1952, p. 79; Frum, 1954, in litt.; Twente, 1955a, p. 379); several caves 2 to 18 miles south of Sun City (Cockrum, 1952, p. 79; Hibbard, 1933, p. 233; Twente, 1955a, p. 379). *Comanche County:* Several caves 4 to 6 miles west and northwest of Aetna (Cockrum, 1952, p. 79; Hibbard, 1934, p. 237; Twente, 1955a, p. 379). Colorado: *Boulder County:* Boulder Canyon, 7,700 feet (Young, 1908, p. 407); Fourmile Canyon, 7,000 feet, near Crisman (Cary, 1911, p. 204); 12 miles south of Lyons (G. Allen, 1916, p. 341). *El Paso County:* 1 mile north of Glen Eyrie (near Colorado Springs) (Warren, 1942, p. 30). *Gunnison County:* Gothic, 9,600 feet (Findley and Negus, 1953, p. 237). *Larimer County:* Fort Collins (Cary, 1911, p. 204); no exact locality (Miller, 1897, p. 53). *Las Animas County:* Trinidad (Warren, 1906, p. 267). South Dakota: *Custer County:* Jewel Cave National Monument (National Park Service Collection, Washington, D.C.). *Harding County:* Ludlow Cave Hills (Biol. Surv. files). *Stanley County:* White River (Biol. Surv. files).

CANADA: British Columbia: Adam's River, northwest of Shuswap Lake (Anderson, 1946, p. 32); Creston, Kootenay River (Anderson, 1946, p. 32); Keremeos, Similkameen Valley (Anderson, 1946, p. 32); Riske Creek and Williams River (Cowan and Guiguet, 1956, p. 67).

Plecotus townsendii townsendii Cooper

Plecotus townsendii Cooper, 1837, p. 73, pl. 3, fig. 6.
S[ynotus] townsendii Wagner, 1855, p. 720.
Corinorhinus townsendi Dobson, 1875, p. 356.
Plecotus (Corinorhinus) macrotis Dobson, 1878, p. 180. (Part.)
Corynorhinus macrotis townsendii Miller, 1897, p. 53.
Corynorhinus macrotis intermedius H. W. Grinnell,[3] 1914, p. 320.
Corynorhinus megalotis townsendii G. M. Allen, 1916, p. 344.
Corynorhinus rafinesquii townsendii H. W. Grinnell, 1918, p. 345.
Corynorhinus townsendii townsendii Handley, 1955c, p. 147.

Holotype: Not known to be in existence. Type locality: "Columbia River," herein restricted to Fort Vancouver, Clark County, Wash.

Distribution: Coast region of the northwestern United States and southwestern Canada (fig. 22). North to Comox, Vancouver Island, British Columbia. South to Santa Barbara County, Calif. Inland to eastern flanks of Coast Range in south; to eastern flanks of Cascade Range in north. Zonal distribution: Transition and Upper Sonoran.

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[3] Holotype: MVZ No. 7753; adult female, skin and skull; collected 31 July 1909, by J. C. Hawver; Auburn, Placer County, Calif.; original No. 2387.

Description: Adult coloration: Mass effect of upperparts in darkest individuals between Natal Brown and Bone Brown, with little distinction between bases and tips of hairs; mass effect in palest individuals between Vandyke Brown and Verona Brown, with hair bases considerably paler than the tips, about Benzo Brown. Hair of underparts Fuscous at base; darkest individuals have hair tips of throat and breast between Snuff Brown and Bister, those of the belly Light Pinkish Cinnamon; palest individuals have hair tips of entire underparts Light Pinkish Cinnamon. Immature coloration: Similar to the darkest adults or slightly darker.

Size averages medium for subgenus; forearm averages relatively short. Construction of skull heavy; rostrum relatively long, inflated, and not depressed; anterior nares, viewed from above, usually rounded in posterior outline. Canine strong; first upper incisor frequently with trace of secondary cusp; P^4 usually with anterointernal cingular cusp.

Measurements: See tables 12, 18.

Comparisons: *P. t. townsendii* is the darkest colored and shortest winged population of the species *P. townsendii*. Compared with *P. t. pallescens*, into which it grades to the east and south, *P. t. townsendii* is darker, averages slightly larger, and has a more robust skull, heavier rostrum, and anterior nares that average relatively larger and more rounded in posterior outline.

Remarks: The type locality of this form is not "Columbia River, Oregon" as has been assumed by many authors (e.g., Miller, 1897, p. 53; G. M. Allen, 1916, p. 344; Anderson, 1946, p. 33; Miller and Kellogg, 1955, p. 110). Bailey (1936, p. 387) and Dalquest (1948, p. 163) were correct in naming "Fort Vancouver, Washington" as the type locality.

Cooper's description (1837, p. 73) of *Plecotus townsendii* was based on three specimens which he stated had been obtained by J. K. Townsend on the Columbia River. In the appendix to the narrative of his journey to the Columbia, Townsend (1839, pp. 324, 325) mentioned the species as follows:

> [*Plecotus Townsendii* is the] So-capual of the Chinook Indians . . . . Inhabits the Columbia river district, rather common. Frequents the store houses attached to the forts, seldom emerging from them even at night. This, and a species of *Vespertilio*, (*V. subulatus*), which is even more numerous, are protected by the gentlemen of the Hudson's Bay Company, for their services in destroying the *dermestes* which abound in their fur establishments.—Towns.

In these sentences from Townsend's narrative there are many clues to the whereabouts of the type locality of *P. townsendii*. First is the fact that the bat "Inhabits the Columbia river district." Next, "Frequents the store houses attached to the forts." According to his narrative, Townsend visited four Columbia River forts: Fort Walla-Walla, near the present site of Wallula, Washington, half a mile above the mouth of the Walla Walla River; Fort Vancouver, 6 miles above the mouth of the Willamette River, Clark County, Wash.; Fort William, on the southwest side of Sauvie Island, Multnomah County, Oreg.; and Fort George at Astoria, Clatsop County, Oreg. Fort William can be eliminated immediately, for it was an American establishment, built during Townsend's visit. There the bats could not have been "protected by the gentlemen of the Hudson's Bay Company." Townsend's citation of a Chinook Indian name for the bat, "So-capual of the Chinook Indians," eliminates Fort Walla-Walla, because the Chinooks normally did not occur above the cascades of the Columbia (Townsend, 1839, p. 220), although Townsend's party did encounter a band at The Dalles (1839, p. 159). Furthermore, Cooper's description agrees with the dark, coastal race of the bat, whereas a pallid form occurs in the vicinity of Fort Walla-Walla. Finally, Townsend's description of Fort George (1839, p. 182) eliminates it as a possibility:

> We anchored off *Fort George*, as it is called, although perhaps it scarcely deserves the name of a fort, being composed of but one principal house of hewn boards, and a number of small Indian huts surrounding it, presenting the appearance, from a distance, of an ordinary small farm house with its appropriate outbuildings.

Compare with this the statement, "Frequents the store houses attached to the forts." Townsend described Fort Vancouver, where he had residence during his months on the Columbia, as follows (1839, pp. 170–172):

> The space comprised within the stoccade is an oblong square, of about one hundred, by two hundred and fifty feet. The houses built of logs and frame-work, to the number of ten or twelve, are ranged around in a quadrangular form . . . in the vicinity of the fort, are thirty or forty log huts . . . placed in rows, with broad lanes or streets between them, and the whole looks like a very neat and beautiful village.

Fort Vancouver appears to be the logical choice for the restricted type locality of *Plecotus townsendii* Cooper.

P. t. townsendii intergrades with the very differently colored *P. t. pallescens* over a wide area in central and northern California and northward between the Cascades and the Rockies. Allocation of specimens, especially in inadequate series, from much of this area to one race or the other is largely a matter of personal opinion. As a result, various authors have disagreed on just where the artificial boundary between the ranges of *townsendii* and *pallescens* should be set. Other authors have chosen to solve the problem by applying a subspecific name, *intermedius*, to populations of the intergrading area. For a discussion of this problem, see the remarks under *P. t. pallescens* (p. 192).

Dark-colored populations, resembling those at the type locality probably occur only in the Coast Ranges and humid lowlands west of the Cascade Range from northern California northward to Vancouver Island. Progressive increase in pallor apparently takes place even as the western slopes of the Cascades are approached. Thus, in the Willamette Valley in Oregon, specimens from Carver and Vida, at lower elevations, are darker than those from McKenzie Bridge a little further up-stream. On the eastern slopes of the Cascades, as at Boulder Cave, Wash., specimens average even paler, but are, nevertheless, nearer *townsendii* than *pallescens*. A single specimen from Happy Camp, Siskiyou County, Calif., is paler than most other specimens identified as *townsendii*, but it is from an area where *townsendii* theoretically should occur, and on the supposition that a larger series would show the average to be nearer *townsendii*, it has been identified as that form.

Samples from collecting stations in the lowlands and Coast Range south of San Francisco Bay are variable, showing intergradation with *P. t. pallescens*. From Santa Barbara County northward the samples average nearer *P. t. townsendii* in morphological characters.

Plecotus appears to be absent from most parts of the Great Valley of California.

SPECIMENS EXAMINED: A total of 83, from the following localities:

UNITED STATES: CALIFORNIA: *Alameda County:* Mission San Jose, 25s (MVZ). *Fresno County:* New Jaria [=New Idria?], 1b (USNM). *Marin County:* Nicasio, 1s (USNM). *Monterey County:* Stonewall Creek, 1,300 feet, 6.3 miles northeast of Soledad, 2s (MVZ). *Napa County:* Mount Veeder [1,950 feet], 1s (USNM). *San Benito County:* Bear Valley [The Pinnacles, near Cook, 2,000 feet], 2s (USNM); 4 miles west-northwest of Panoche, 1s (MVZ). *San Luis Obispo County:* 5 miles south-southwest of Adelaida, 2,200 feet, 1s (MVZ); San Simeon, 1s (MVZ); 6.5 miles southeast of Shandon, 1s (MVZ). *San Mateo County:* 2.0 to 2.5 miles east of Pescadero, 2s (MVZ). *Santa Clara County:* Evergreen, 2s (MVZ); 2.25 miles northwest of San Felipe, 2s (MVZ). *Santa Cruz County:* 2 miles southwest of Brookdale, 1s (MVZ); Mouth of Meder Creek, 2s (MVZ); 2 to 3 miles east of Santa Cruz, 2s (MVZ). *Siskiyou County:* Happy Camp, 1s (USNM). OREGON: *Clackamas County*: Carver, 4s (CNHM), 3s (USNM). *Curry County:* Gold Beach, 5s (CNHM), 1s (MCZ), 1a (USNM). *Lane County:* Creswell, 1a (USNM); McKenzie Bridge, 3s (USNM); Vida, 1s (USNM). WASHINGTON: *Kittitas County:* Boulder Cave, Naches River, 43 miles northwest of Yakima, 14as (USNM). *Thurston County:* Olympia, 1s (USNM).

CANADA: BRITISH COLUMBIA: *Vancouver Island:* Comox, 1s (USNM).

ADDITIONAL RECORDS: The following records probably refer to this form:

UNITED STATES: CALIFORNIA: *Alameda County:* 4 miles east-southeast of Mission San Jose (Dalquest, 1947, p. 20). *Colusa County:* 2.25 miles south-southeast of Wilbur Springs, 1,800 feet (Frum, 1954, in litt.). *Humboldt County:* Carlotta (Dickey, 1922, p. 116). *Lake County:* Long Valley (Dalquest,1947, p. 20); Lucerne (Frum, 1954, in litt.); 4 miles east of Upper Lake (Dalquest, 1947, p. 20). *Marin County:* Inverness (Pearson, et al., 1952, p. 275); 1.3 miles southeast of Inverness (Frum, 1954, in litt.). *Mendocino County:* 1.5 miles north of Gualala (Dalquest, 1947, p. 20). *Napa County:* Aetna Springs (Pearson, et al., 1952, p. 275); one-half mile south of Angwin, 1,600 feet, and 1 mile south of Angwin, 1,500 feet (Dalquest, 1947, p. 20); 4 miles south of Calistoga (Dalquest, 1947, p. 20); near Knoxville, 2,000 feet (Pearson, et al., 1952, p. 279); Pope Creek, 8 miles northwest of Monticello (Dalquest, 1947, p. 20). *San Benito County:* Hernandez (H. W. Grinnell, 1914, p. 320). *Sonoma County:* 10 miles east of Stewart's Point (Dalquest, 1947, p. 20). OREGON: *Clackamas County:* Clackamas (V. Bailey, field notes). *Josephine County:* Siskiyou Mts., Oregon Caves National Monument (Roest, 1951, p. 346). *Lane County:* Eugene (Bailey, 1936, p. 387). *Multnomah County:* Portland (Bailey, 1936, p. 387). WASHINGTON: *Clallam County:* Elwha River (Johnson and Johnson, 1952, p. 33). *Clark County:* Fort Vancouver (Bailey, 1936, p. 386). *King County:* Seattle (Dalquest, 1948, p. 163). *Mason County:* Lake Cushman (Dice, 1932, p. 48). *Pierce County:* Puyallup (Dalquest, 1938, p. 213). *San Juan County:* Blakeley Island (Dalquest, 1948, p. 162); Friday Harbor (Dalquest, 1948, p. 161). *County uncertain:* Hood's Canal (Johnson and Johnson, 1952, p. 33).

CANADA: BRITISH COLUMBIA: Nanaimo Bay, Vancouver Island (Anderson, 1946, p. 33); Newcastle Island (Anderson, 1946, p. 33).

Plecotus townsendii virginianus **Handley**

Corynorhinus macrotis A. H. Howell, 1909, p. 68. (Part.)
Corynorhinus megalotis megalotis G. M. Allen, 1916, p. 338. (Part.)
Corynorhinus rafinesquii Thomas, 1916, p. 127. (Part.)
Corynorhinus townsendii virginianus Handley, 1955c, p. 148.

HOLOTYPE: USNM 269163; adult male, skin and skull; collected 12 November 1939, by W. J. Stephenson; Schoolhouse Cave, 4.4 miles northeast of Riverton, 2,205 feet, Pendleton County, W. Va.; no collector's number.

DISTRIBUTION: Central part of Appalachian Highlands in eastern Kentucky, western Virginia, and eastern West Virginia (fig. 23). North to Hardy, Grant, and Preston Counties, W. Va. West to Preston, Tucker, and Randolph Counties, W. Va. South to Randolph and Pendleton Counties, W. Va. East to Pendleton and Hardy Counties, W. Va. Apparently isolated populations further south and west, in Tazewell County, Va., and Powell County, Ky. Zonal distribution, Transition. Altitudinal distribution, 1,700 to 3,500 feet.

DESCRIPTION: Adult coloration: Hair of upperparts about Benzo Brown at base; subterminal band orange-brown, tip dark brown; mass effect between Prout's Brown and Bister. Hair of underparts between Light Vinaceous-Cinnamon and Light Pinkish Cinnamon distally, occasionally somewhat darker on throat and chin; bases, except of those hairs bordering membranes, Fuscous; border hairs monocolored. Distinction between tip and base of hair sharp on underparts, poor on dorsum. Immature coloration: Hair of upperparts between Natal Brown and Benzo Brown distally; bases slightly grayer, hardly distinguished from tips. Hair of underparts Mouse Gray at base, pale buff at tip; distinction between base and tip slight.

Size averages medium for subgenus; forearm averages relatively long. Rostrum relatively long and not depressed; anterior nares (viewed from above) wide and rounded in posterior outline. First upper incisor usually without trace of secondary cusp.

MEASUREMENTS: See tables 12, 18.

COMPARISONS: Compared with *P. t. ingens*, *P. t. virginianus* is more sooty dorsally and averages slightly smaller in all dimensions; the first upper incisor rarely has a trace of a secondary cusp; and the rostrum is less heavy and inflated.

REMARKS: The Appalachian populations (*P. t. virginianus*) appear to be isolated by no less than 600 miles from the nearest closely related populations (*P. t. ingens*) in the Ozark Highlands. Despite this separation, the two forms are not strikingly different, and although there is no possibility of demonstrating intergradation between them, they may be treated best as being conspecific. On the other hand, the Appalachian populations of *P. townsendii* are specifically distinct from *P. rafinesquii*, whose geographic range they overlap. This peculiar pattern of distribution, perhaps related to Pleistocene disturbances, is discussed in the section on history (p. 215).

There is no obvious explanation for the limited and apparently discontinuous distribution of the populations within the bounds of the Appalachian Highlands. The species is relatively numerous, even the most abundant bat in some caves, in two adjacent drainage systems in northeastern West Virginia. It has been found in at least 15 caves at the head of the Potomac River and in four caves at the head of the Cheat River. All of these caves are in limestone, in an area 30 miles wide and 40 miles long. Three other populations have been discovered away from this main body: One a few miles to the north in Preston County, W. Va. (Kellogg, 1937, p. 450), another 150 miles to the south-southwest in a limestone cavern in Tazewell County, Va. (Howell, 1909, p. 68; Mohr, 1933, p. 49), and the third in a cave 200 miles to the west-southwest in Powell County, Ky. (Barbour, 1957, p. 141). The intervening extensive limestone caverns, mostly well explored, in Pocahontas, Greenbrier, and Monroe Counties, W. Va., and in the Valley of Virginia do not seem to be occupied by the species.

Isolation such as apparently exists among the Kentucky, Virginia, and West Virginia populations of this species favors differentiation. It is not surprising then that differentiation is evident. Virginia and Kentucky specimens average smaller than those from West Virginia. Kentucky and West Virginia specimens are similar in color to Virginia specimens obtained in 1908. However, specimens collected in Virginia in 1957 average considerably darker, more sooty, both dorsally and ventrally, than those collected recently in Kentucky and West Virginia or in the same Virginia cave fifty years earlier. They resemble typical *P. t. townsendii* in coloration.

SPECIMENS EXAMINED: A total of 100, from the following U.S. localities:

KENTUCKY: *Powell County:* Natural Bridge State Park, 2s (UK). VIRGINIA: *Tazewell County:* Burkes Garden, 3,200 feet, 9as (USNM). WEST VIRGINIA: *Grant County:* 10 miles south of Petersburg, 3s (CM). *Pendleton County:* Cave Mountain Cave, 2,450 feet, 1.4 miles west of Brushy Run, 11as (USNM); Hellhole, 2,200 feet, 3.6 miles northeast of Riverton, 5a (USNM); Hoffman School Cave, 2,175 feet, 4.9 miles south-southwest of Franklin, 2s (USNM); Schoolhouse Cave, 2,205 feet, 4.4 miles northeast of Riverton, 31as (USNM); "Smokehole" [=Smokehole Cave, 1,730 feet, 1.9 miles west-northwest of Brushy Run?], 29abs (AMNH); "Cave Rock Cave, Smokehole" [=Cave Mountain Cave, 2,450 feet, 1.4 miles west of Brushy Run?], 8s (AMNH).

ADDITIONAL RECORDS: The following records probably refer to this form:

KENTUCKY: *Rowan County:* Carter Caves (Welter and Sollberger, 1939, p. 79). WEST VIRGINIA: *Grant County:* Klines Gap Cave, 1,700 feet, 4 miles southwest of Maysville (Frum, 1954, in litt.); Peacock Cave, 1,755 feet, 7.6 miles southwest of Petersburg (Fowler, 1941a, p. 35); Petersburg (McKeever, 1952, p. 47). *Hardy County:* Baker's Cave, near Durgon [apparently not the "Baker Cave" of Davies, 1949, p. 139] (Wilson, 1946, p. 86). *Pendleton County:* Mill Run Cave, 1,800 feet, one-half mile southeast of Kline (Frum, 1954, in litt.); Seneca Caverns, 2,200 feet, 3 miles northeast of Riverton (Reese, 1934, p. 47); Sinnit Cave, 2,250 feet, one-quarter mile northwest of Moyers (Frum, 1954, in litt.); Thompson Cave, 2,350 feet, 1.5 miles east-southeast of Riverton (Frum, 1954, in litt.) [=5.6 miles north-northeast of Circleville, 2,350 feet (McKeever, 1952, p. 47)?]; Torys Cave, 2,000 feet, 5 miles southwest of Franklin (Frum, 1954, in litt.) [=Tory's Cave, 10 miles south of Franklin (Barbour, 1951b, p. 369)?]; Trout Cave, 5 miles southwest of Franklin (Fowler, 1941b, p. 47). *Preston County:* No exact locality (Kellogg, 1937, p. 450; Barbour, 1951a, p. 50). *Randolph County:* 6.7 miles east-northeast of Glady, 3,500 feet (McKeever, 1952, p. 47); The Sinks, Cave No. 1, 3,500 feet, one-half mile west of Osceola (Reese, 1934, p. 47). *Tucker County:* Arbegast Cave, 2,600 feet, 6 miles southeast of Hendricks (Frum, 1954, in litt.); Cave Hollow Cave, 2,400 feet, 5 miles southeast of Hendricks (Frum, 1954, in litt.).

INCERTAE SEDIS

***Vespertilio maugei* Desmarest**

Vespertilio maugei Desmarest, 1819, p. 480.
Plecotus Maugei Lesson, 1827, p. 96.
Vespertilio (Plecotus) Maugei Cooper, 1837, p. 71.
Synotus Maugei Wagner, 1855, p. 719.
Vespertilio maugei H. E. Anthony, 1916, p. 360.

HOLOTYPE: From Puerto Rico. Collected by Maugé. The present disposition of the holotype is unknown. Some of Desmarest's types are in the Paris Museum, but Rode (1941) did not list *Vespertilio maugei* in his catalog of the type specimens of Chiroptera in the Paris Museum.

DISTRIBUTION: "Puerto Rico."

DESCRIPTION: Following is my translation of Desmarest's (1819, p. 480) description:

> *Vespertilio maugei*, new species.
>
> This bat, brought back from Puerto Rico by the late Maugé, is of medium size and approaches, in its physiognomy, the barbastelle, notably by the distinguishing character of the union of the ears at their internal bases.
>
> Its pelage is long, silky, of a blackish brown above, lighter beneath, particularly in the region near the interfemoral membrane, where it becomes almost white; its tail is nearly as long as the body; its membranes are of a dark gray.
>
> Its mouth is provided with four upper incisors of which the two inner are the largest, separated from one another and bifurcate, the exterior being simple; the six lower incisors overlap one another and have three lobes, and medium-sized canines are very closely followed by the molars.
>
> The muzzle is short, slender, pointed, and forms, with the ears, a right angle; the nose is rather broad, that is to say, that the nostrils are separated by a cartilage in the form of a plate, which resembles somewhat a lyre; the ears are large, their extremity is rounded, their exterior border notched, with a longitudinal fold provided with very dense and very noticeable hairs; the tragi are pointed and do not reach half the height of the ears; the eyes are small and placed at the base of the latter.

Desmarest (1820, p. 145) modified this description slightly the following year. My translation of the most significant portions of the new description is as follows:

> Ears very large, united, notched exteriorly near the tip . . . Dimensions, a little larger than the barbastelle. . . ."

REMARKS: For the early 19th century these are surprisingly detailed descriptions. However, the bat described is quite unlike any bat known to occur in the West Indies. *Eptesicus* is the only vespertilionid that has subsequently been collected on Puerto Rico, and *Myotis*, *Nycticeius*, and *Lasiurus* are the only other vespertilionid genera recorded from the West Indies.

Vespertilio maugei has been overlooked or ignored by most authors. Those who have considered it (see synonymy, p. 203) have thought it to be a species of *Plecotus*. *Plecotus* has not been collected subsequently in the West Indies, however, and no skeletal remains of *Plecotus* have been recognized in the sub-Recent bone deposits that are abundant in West Indian caves.

Anthony (1918, p. 360) suggested that Maugé's specimen actually was a *Plecotus* which had been obtained in the United States and was attributed to Puerto Rico by mistake. It is true that Desmarest's descriptions agree in some details with *Plecotus*, but there are many discrepancies: Coloration of the underparts is wrong, the canines are not "very closely followed by the molars," the nostrils are not separated by a lyre-shaped plate, and the auricles are not notched on their exterior borders.

There is a possibility that the description of *V. maugei* is a composite. The dental characters could apply to *Eptesicus.* Externally, the West Indian phyllostomid *Macrotus waterhousii* agrees fairly well with Desmarest's description. Although its tail is a trifle short, and its nose leaf can hardly be said to be "lyre-shaped," it nevertheless has unusually large ears, connected at their internal bases, and its coloration exactly matches Desmarest's description. On the other hand, with regard to its dentition, *Macrotus* bears no resemblance whatsoever to the description of "*V. maugei.*"

It seems probable that the bat Desmarest described was the Eurasian *Barbastella,* with which his descriptions agree in all details. In all probability the specimen did not originate in Puerto Rico or elsewhere in the Western Hemisphere. Consequently, the name *Vespertilio maugei* should be placed in the synonymy of *Barbastella* and should be disassociated from *Plecotus* and the American fauna.

History

PALEONTOLOGICAL RECORD

Chiroptera

The paleontological record is so fragmentary for bats that few conclusions can be drawn from it. Crania and upper dentitions are disappointingly rare in fossil bat material. The commonest remains are mandibles or long bones, neither of which, when isolated and fragmentary, are very satisfactory for studies of evolution and relationships or even for taxonomic classification. Paradoxically, the oldest known chiropteran remains—those of *Archaeonycteris, Palaeochiropteryx,* and *Cecilionycteris* of the Middle Eocene—are also the best preserved. Complete dentitions and skeletons are intact, and even the outlines of the wing membranes can be traced (G. Allen, 1939, p. 177).

Most of the work on fossil Chiroptera has been done in Europe. A majority of the named forms and a preponderance of the literature on the subject are from that region. Investigations conducted elsewhere, principally in China and in the United States are insignificant by comparison. Preglacial fissure and cave microfaunas have been virtually untouched outside of Europe.

The European record indicates that the extinct families Archaeonycteridae and Palaeochiropterygidae occurred with some variety in Middle Eocene time. Rhinolophidae were numerous and predominant in Upper Eocene and Oligocene deposits. Species of Megadermatidae and Emballonuridae were somewhat less numerous during the same period. The Vespertilionidae became abundant somewhat later.

FAMILY VESPERTILIONIDAE

According to Revilliod (1919, p. 94), the genus *Stehlinia* [=*Nycterobius* Revilliod and *Revilliodia* Simpson (Handley, 1955a, p. 128)] of the Quercy fauna of the Upper Eocene or Lower Oligocene of Europe is the most ancient known vespertilionid. It has cranial characters of the Vespertilionidae, but is distinguished from modern genera by several primitive characters, including very elongated rostrum, relatively very long premolar series, and 2-rooted P^1. It most closely resembles some of the small species of *Myotis*, which is generally conceded to be the most primitive living genus of the family.

True *Myotis* appears for the first time in the Stampien and Aquitanien faunas of the Middle and Upper Oligocene of Europe [*Myotis salodorensis* Revilliod (1919, p. 94) and *Myotis insignis* von Meyer (Revilliod, 1922, p. 166)]. Other *Myotis* have been described from the Middle Miocene of Europe [*Myotis antiquus* Gaillard (1899, p. 8) and *Myotis sancti-albani* Viret (1951, p. 19)], and *Myotis*-like remains occur in Lower Miocene beds in Florida (Lawrence, 1943, p. 364). Some of the Recent species of *Myotis* (*M. bechsteinii, M. mystacinus*, and *M. oxygnathus*) were possibly derived by Pliocene or Lower Pleistocene time (e.g., see Heller, 1930, p. 154; Kormos, 1937, p. 33; and Kowalski, 1956, p. 331), although most late Tertiary and Quaternary material has been described as now extinct species (e.g., see Heller, 1936, p. 113; Kormos, 1934, p. 306; Kowalski, 1956, p. 331; Sickenburg, 1939, p. 8; and Wettstein, 1923, p. 40).

Another primitive vespertilionid genus, *Miniopterus*, is thought to have been recognizable as far back as the Miocene epoch (*M. fossilis*, Zapfe, 1950, p. 60). The Lower Pliocene *Mystipterus* (Hall, 1930, p. 319) from Nevada, first supposed to be related to *Miniopterus*, subsequently has been shown to be an insectivore (Patterson and McGrew, 1937, p. 256).

The oldest *Eptesicus*-like remains are from Lower Miocene beds of Florida (Lawrence, 1943, p. 367). Other *Eptesicus*-like genera, *Samonycteris* (Revilliod, 1919, p. 95) and *Pareptesicus* (Zapfe, 1950, p. 58), have been described from the Miocene of Europe. From the Upper Pliocene of Arizona comes *Simonycteris* (Stirton, 1931, p. 27), also possibly a relative of *Eptesicus*. The most ancient remains attributed to true *Eptescius* are those discovered in the Pliocene or Lower Pleistocene of Hungary (Kormos, 1930a, p. 41). Brown (1908, p. 174) regarded Middle Pleistocene material from the Conard Fissure of Arkansas as being only subspecifically distinct from the Recent *Eptesicus fuscus*. Gidley and Gazin (1938, p. 11), with more abundant

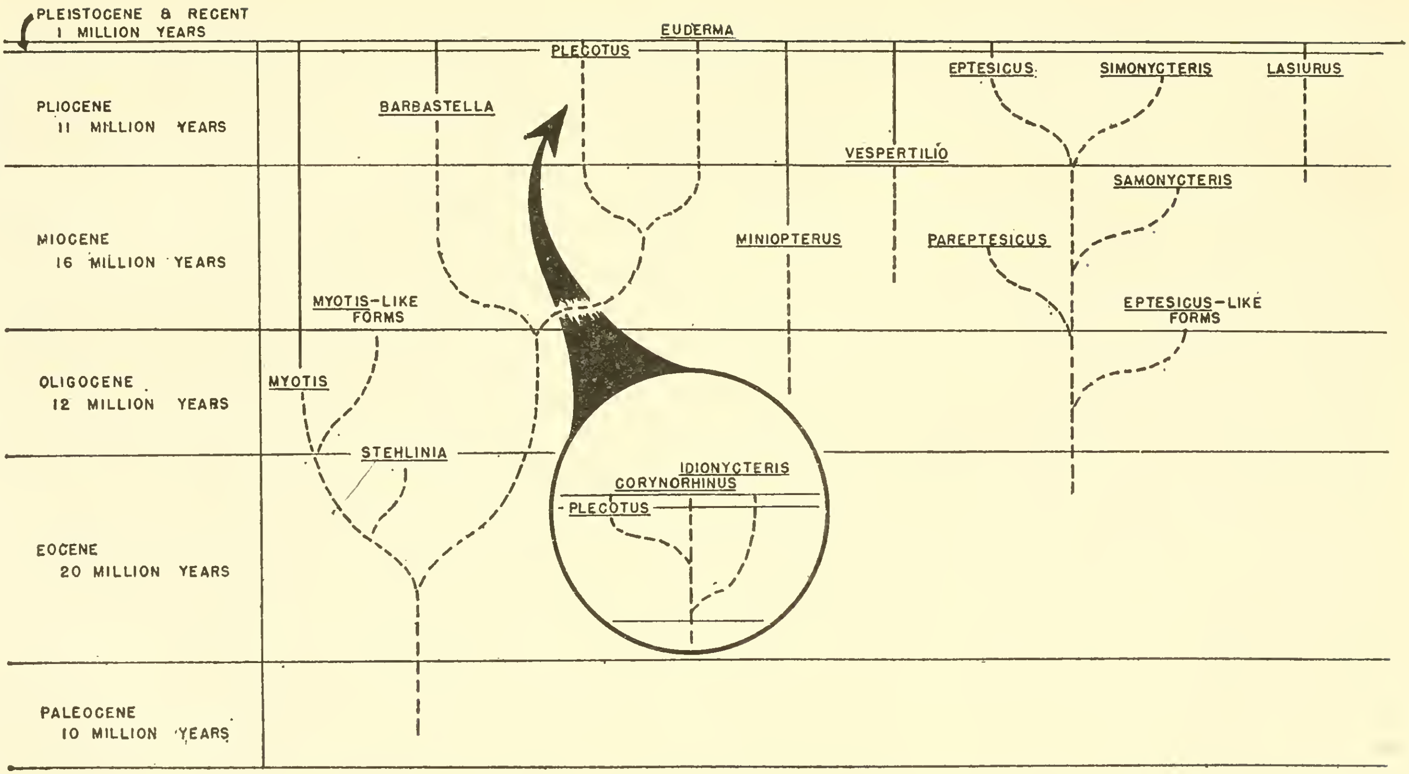

FIGURE 25.—Estimate of chronological distribution of some vespertilionid genera, with inset showing subgenera of *Plecotus*. Geological time scale from Richards (1953, p. 2).

material from the Pleistocene of Cumberland Cave, Md., agreed that the relationship of *grandis* to the Recent species is close but believed it to be sufficiently different to warrant specific separation.

Records for *Barbastella* (Wettstein, 1931 p. 780), *Lasiurus* (Hibbard, 1950, p. 134), and *Vespertilio* (Kormos, 1934, p. 312) extend back at least to the Pliocene. Numerous other Recent vespertilionid genera have been identified in Pleistocene deposits.

To recapitulate: The oldest recognizable vespertilionid was of Upper Eocene or Lower Oligocene age. The morphologically more primitive Recent genera emerged in the Oligocene and Miocene. Recent species of these genera were in some instances perhaps derived as early as the Pliocene, although fossil species of the same genera persisted into the Pleistocene (fig. 25).

Genus *Plecotus*

Vespertilio (Plecotus) grivensis Depéret

Remains undoubtedly referable to *Plecotus* have been found only in Upper Pliocene (possibly actually Lower Pleistocene) and Pleistocene deposits. Records of greater antiquity are erroneous or questionable. The controversial *Vespertilio* (*Plecotus*) *grivensis* of Depéret (1892, p. 11, pl. 2) from the Vindobonien (Middle Miocene) fauna of Grive Saint-Alban, France, is a case in point. Depéret's material consisted of two fragmentary mandibles. Gaillard (1899, p. 7) later reported a total of four mandible fragments from Grive Saint-Alban in the Museum of Lyon. All apparenty agreed with *V. grivensis*, but did not elucidate the unknown portions of the mandible.

Depéret (loc. cit.) believed that the remains most closely resembled *Plecotus*, and to this opinion Wettstein (1931, p. 779) agreed. On the other hand, Gaillard (loc. cit.) preferred to leave the generic designation questionable. When Revilliod (1922, p. 172) reviewed all the Tertiary Chiroptera, his conclusion was that *Vespertilio grivensis* was in actuality a *Myotis*.

More recently, Viret (1951, p. 21) redescribed and figured the specimens (now totaling five fragments) of *Vespertilio grivensis* which were initially reported by Depéret and Gaillard. Viret argued convincingly that the type and one additional fragment should be regarded as *Rhinolophus grivensis*, while the third fragment proved to be *Myotis sancti-albani*, the fourth *Sorex pusillus*, and the fifth indeterminate.

Plecotus crassidens Kormos

Next in geologic age is the Pliocene or Lower Pleistocene *Plecotus crassidens* of Kormos (1930b, p. 238) from Hungary and Poland. Kormos did not figure the fragmentary mandible upon which he based the name, and there was nothing positive about his description.

Subsequently, however, Kowalski (1956, p. 359, pl. 3) figured and described in detail ten maxillary and cranial frgaments which he had compared directly with Kormos' type of *P. crassidens.* He characterized *P. crassidens* as follows: ROSTRUM BROAD (much more so than in *P. auritus*), FLATTENED, AND WITH A MEDIAN DEPRESSION; intermaxillary notch broad and cordate; palate extends one molar breadth posterior to toothrows; LACHRYMAL [AND SUPRAORBITAL] REGIONS NOT RIDGED; P^4 labially broader and less obliquely placed than in *P. auritus;* molars larger and more massive than in *P. auritus;* coronoid process of mandible distinctly pointed; angular process broad and blunt and deflected outward; P_3 smaller than P_1; P_4 2-rooted, subquadrate in basal cross-section, provided with strong cingulum, and not so high as M_1; M_3 talonid narrower than trigonid. Also apparent from Kowalski's figures, although not stated in his description are the facts that the braincase bulges dorsally in the parietal region, and THE ZYGOMATIC ARCH IS NOT EXPANDED IN ITS MIDDLE THIRD (posterior third missing). The characters in larger type relate *P. crassidens* to the subgenus *Corynorhinus,* while the shape and 2-rooted condition of P_4 show an affinity to the subgenus *Plecotus.*

On the basis of these specimens Kowalski (1956, p. 340) supposed that the North American *Corynorhinus* might be a relict of the Tegelien Interglacial of Europe (possibly equivalent to the Aftonian Interglacial of North America), analogous to the several species of the Tegelien flora, now extinct in Europe but persisting in North America.

Plecotus abeli Wettstein

Wettstein (1923, p. 39; 1931, p. 779) described abundant Pleistocene remains from the Drachenhöhle in Austria as belonging to a distinct species, *Plecotus abeli,* averaging slightly smaller than the Recent form and having the cusps of the lower molars not so high and sharp. Kowalski (1956, p. 361), judging from Wettstein's descriptions, ventured the opinion that *P. abeli* was no more than subspecifically distinct from *P. auritus.*

Plecotus auritus Linnaeus

Most of the undoubted remains of *Plecotus* that have turned up in the Pleistocene and dubiously Upper Pliocene fissure and cave deposits of Europe have been identified as *Plecotus auritus,* the Recent species now inhabiting Europe (e.g., see Heller, 1930, p. 154; 1936, p. 112; Kowalski, 1956, p. 361; and Sickenburg, 1939, p. 9).

Corynorhinus alleganiensis Gidley and Gazin

Corynorhinus alleganiensis from Cumberland Cave, Md. (Gidley, 1913, p. 96; Gidley and Gazin, 1933, p. 345; 1938, p. 12), is the best known North American fossil *Plecotus.* The geologic age of this species cannot be determined stratigraphically, since the material upon which it is based is from a fissure type deposit. However, the, fauna associated with the bat remains is certainly Pleistocene in age and Gazin (in Gidley and Gazin, 1938, p. 7) concluded from the number of extinct forms present and from the difficulty encountered in identifying others as Recent that the Cumberland Cave fauna can hardly be considered Upper Pleistocene, and is more likely Middle Pleistocene in age. There is no reason to suppose that the bat remains were not deposited at the same time as the remainder of the Cumberland Cave fauna.

P. alleganiensis was similar in many respects to (and possibly directly ancestral to) *P. townsendii*, the *Plecotus* occurring nearer than any other to Cumberland Cave today. It possessed the primitive characteristics of supraorbital ridge and lack of a sagittal crest. See pages 137–139 for a full description of *P. alleganiensis.*

Corynorhinus tetralophodon Handley

The other American Pleistocene species, *C. tetralophodon*, from San Josecito Cave, Nuevo León, Mexico, is known from a single skull. It was found in a cave deposit of indeterminable age, but judging from its similarity to Recent forms and from the associated fauna, it is probably Upper Pleistocene (Wisconsin) in age and younger than *Plecotus alleganiensis.* It differs from Recent forms in possession of a fourth commissure on M^3 and in failure of the temporal ridges to coalesce completely. Probably it was related most closely to *P. townsendii*, but possibly was not a direct ancestor of that species. See page 140 for a full description of *P. tetralophodon.*

ORIGIN AND DISPERSAL OF EUDERMA AND PLECOTUS

The paleontological record is so incomplete that a discussion of the origin and dispersal of *Euderma* and *Plecotus* necessarily must rely heavily upon speculation. However, with the historical record of other vespertilionid groups in mind, and with the evidence of present day geographic distribution of taxonomic characters in *Euderma* and *Plecotus* as a factual foundation, there is ground for speculation on the evolution of these genera. In the systematic section and in the preceding paragraphs of this section the facts have been presented. The remainder of this section is devoted to an interpretation of them.

Several factors govern the dispersal of bats. Of paramount importance are food supply and shelter. For insectivorous forms, such as *Euderma* and *Plecotus*, the vegetation controlling the distribution of the bat's insect prey and the climate controlling the distribution of the vegetation are the ultimate critical factors in the bat's dispersal as far as food supply is concerned. For antisocial, nonmigratory, cool climate inhabitants, such as some *Plecotus* are, not only is the presence of caves suitable for hibernation essential, but the caves must be sufficiently abundant to allow a degree of privacy and isolation from other species of bats. Unfortunately, it is not possible to index all of these factors through time. Otherwise, a more satisfactory picture of the differentiation and dispersal of these bats might be drawn with less recourse to speculation.

The present distribution of *Euderma* and *Plecotus* and their relative, *Barbastella,* coincides rather closely with the North Temperate zone. Thus, it may be assumed that tropical and boreal climates have served as barriers to their dispersal. The center of origin for the group may have been either Nearctic or Palearctic. Since distantly related primitive forms and closely related progressive forms occur in both regions, a hypothesis of multiple invasion is required to explain present distributions regardless of which region may have served as the center of origin. No paleontological record is available for the more primitive forms, so paleontology gives no hint of origin or ancestry. If it be assumed that the area of most active differentiation and greatest elaboration of forms indicates the center of origin of a group of animals, and that the most advanced, most progressive, and most specialized form is to be found about the center of origin, while the most primitive, most conservative, and least progressive is to be found on the peripheries (Matthew, 1939, p. 32), then it must be reckoned that this group of bats originated in the Nearctic.

Ancestral Forms

It is probable that the ancestral forms were derived early in the Cenozoic, since the related living genus *Myotis* is recognizable at least as far back as Middle Oligocene. During the Eocene and Oligocene epochs, low relief of the northern continents and lack of climatic barriers permitted a moist temperate forest to extend from Greenland across northern America to Alaska, Siberia, northern Europe, and Spitzbergen. A land bridge at Bering Strait intermittently connected North America and Eurasia [indicated by strong Lower Eocene, Upper Eocene, and Lower Oligocene migrations of mammals (Simpson, 1947, p. 625)]. The temperate forest of this region was characterized by redwood (*Sequoia*), and included such other trees and shrubs as alder (*Alnus*), dogwood (*Cornus*), maple (*Acer*), oak (*Quercus*), ash (*Fraximus*), madrone (*Arbutus*), beech (*Fragus*), and elm (*Ulmus*) (Cain, 1944, p. 107). During this period the ancestors of *Euderma* and *Plecotus* possibly could have had a Holarctic distribution.

Continental uplift, beginning in the Oligocene epoch and continuing to the present time, led to a gradual southward spread of the temperate forests, so that in the Miocene they became discontinuous, with segments in North America and Eurasia (Cain, 1944, p. 107). Presumably, the distribution of the ancestors of *Euderma* and *Plecotus* may have become discontinuous at the same time, providing isolation for major evolution within the group.

The Eurasian segment developed into an evolutionary dead end, *Barbastella*, which, though greatly modified in form, represents the ancestral stock. *Barbastella* has a geographic range most remote from the postulated Nearctic center of origin of the group.

Genus *Euderma*

Meanwhile, in the North American segment, evolution was rapid and spectacular, directed toward auditory specialization. *Euderma* is a derivative of the early stages of this evolution. It is the most specialized, and, in many respects, the most primitive of the big-eared forms. It must have had a long period of evolution along its own line, distinct from that of the other members of the group. Whereas *Euderma* has developed characters of its own, such as the connection of the posterior basal lobe of the auricle with the tragus, unique coloration, reduction of dentition, and specialization of the canines, among the other big-eared forms (genus *Plecotus*) there have been only minor variations of features common to all. The nature of the isolating mechanism that allowed the divergence of the *Plecotus* and *Euderma* stems is not apparent. Possibly *Euderma* was southern and widespread during Pliocene and had its range restricted and displaced by the more northern *Plecotus* during the Pleistocene glaciations.

Genus *Plecotus*

Subgenus *Idionycteris*

The species of *Plecotus* seem to represent evolutionary stages. *P. phyllotis* is most primitive and conservative, and most like *Euderma; P. auritus* is somewhat more progressive; and *P. mexicanus*, *P. rafinesquii*, and *P. townsendii* are most progressive. *P. phyllotis* presumably diverged from the main stem while it still bore much resemblance to the earlier derived *Euderma*. *P. phyllotis* failed to match the specializations of the later derived forms, and if abundance and area of distribution be taken as measures of success, it definitely occupies a position inferior to them. It seems to be extremely rare, and inhabits a restricted area on the fringe of the ranges of *P. mexicanus* and *P. townsendii*. On the other hand, the more progressive *P. auritus* and *P. townsendii* are widely distributed, with ranges trans-continental in scope, and are relatively abundant. *P. auritus* is even the most abundant bat in some parts of its range.

Subgenus *Plecotus*

Invasion of Eurasia by way of the Bering Strait area by the *P. auritus* stock probably occurred during the Pliocene [much migration in Middle and Upper Pliocene (Simpson, 1947, p. 625)]. This would have required a more northern distribution than any species of *Plecotus* has today. Changes in habits or habitat could have allowed a more northern range.

Species of *Plecotus* now range into the warmer portions of the Canadian life zone (and its Eurasian equivalent). The cooler portions of this zone lie within 1,000 miles of Bering Strait. Only a slight amelioration of today's climate would be required to provide similar floral conditions to Bering Strait. The present wide distribution of cool climates seems to be an exception in geological history. Even during the Pleistocene "Ice Age" warm climates and their associated faunas extended farther north during the interglacial periods than they do today. Presumably, during the Pliocene, warmer climates may have extended even farther north.

If the pre-Pliocene *Plecotus*-like bats were not cave inhabitants, then a change in habit to include cave roosting would have allowed a more northern dispersal, provided suitable food supplies and adequate caves were available. Resort to caves for hibernation permits habitation of areas with colder winters. It also provides refuge in eras of changing climate, for modification of the climate within the cave may be negligible in comparison with the change on the surface. *Barbastella* and *Plecotus auritus* frequently roost during the summer under loose bark on tree trunks, in cavities in trees and under the eaves of houses, but usually hibernate in caves or in attics of houses. The most primitive living species of the subgenus *Corynorhinus*, *P. rafinesquii*, appears to be primarily a tree rooster, whereas the progressive species *P. townsendii* seems to roost only in caves and houses.

The ancestors of *Plecotus auritus* spread through most of the temperate portions of Eurasia, but were blocked from southward expansion into Maylasia and Africa by the hot climates of the equatorial regions. They came eventually to overlap broadly and perhaps partially displace the range of their relative, *Barbastella*, a rather rare bat whose continent-spanning range averages somewhat more southern than the range of *P. auritus*.

The *Plecotus* that now inhabits Eurasia and northern Africa is probably not very different in appearance from the pre-Pleistocene migrant. This may be inferred from its similarity to the primitive New World species *P. phyllotis* and Pleistocene *P. alleganiensis* and *P. crassidens*. If a common origin for these forms and *P. auritus* be envisioned, and if a pre-Pleistocene dispersal of *Plecotus* into Eurasia

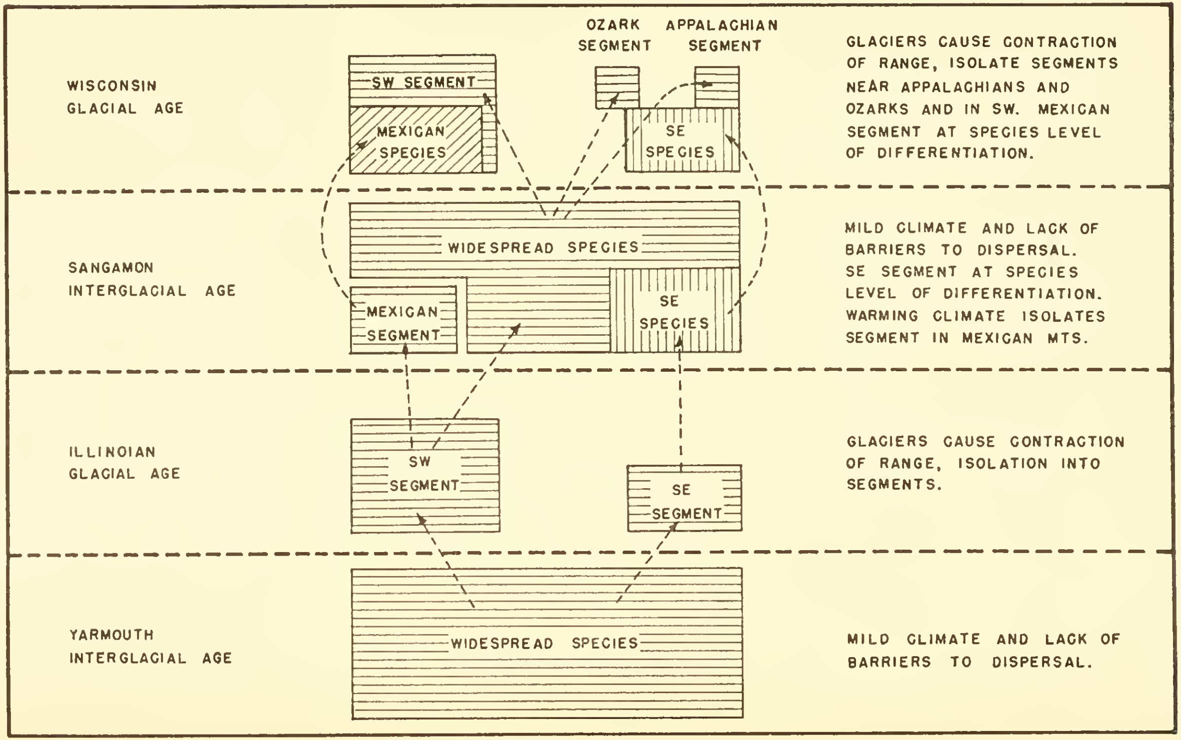

Figure 26.—Theoretical distribution of the subgenus *Corynorhinus* in relation to later phases of Pleistocene glaciation.

be accepted, then the morphological similarities between Old and New World *Plecotus* must be characters that were shared before dispersal occurred.

The primitive *Corynorhinus*-like *Plecotus crassidens* may have reached Eurasia in a secondary Pliocene invasion, bringing it into contact with the already widespread and firmly established *P. auritus*. Apparently it did not persist beyond the early Pleistocene and left no derivatives.

Subgenus *Corynorhinus*

The group of species that form the American subgenus *Corynorhinus* seem to represent the stem of the evolutionary line that has developed *Barbastella*, *Euderma*, and *Plecotus*. The present center of differentiation of this division appears to be in the arid southwestern portion of the United States. This area is presently inhabited by *Plecotus townsendii*, a form that is actively differentiating today. It is the most abundant and widespread member of the subgenus, there is much regional variation within its large geographic range, and its range is fringed with derivatives from it or from its immediate ancestors.

The evolution and present distribution of the Recent species of the subgenus *Corynorhinus* can possibly be related to glacial disturbances during the Pleistocene (fig. 26). The picture presented in this figure reduces the problem to its barest essentials and is almost certainly oversimplified. Forms that occurred earlier in the Pleistocene (Nebraskan, Aftonian, and Kansan ages) cannot be accounted for, and it is very likely that other, now extinct, species existed within the time represented in this diagram. For example, *Plecotus tetralophodon* lived perhaps as recently as late Wisconsin glacial age. It was closely related to *P. townsendii* but probably was not ancestral to it. *P. alleganiensis* probably lived as recently as the Sangamon interglacial age. It was closely related to *P. townsendii* and *P. rafinesquii* and may have been a direct ancestor of either of these Recent species.

The Pleistocene epoch was characterized by an alternation of periods of warmth and cold. During the warm interglacial ages, forms such as the species of *Plecotus* conceivably could have been distributed across the continent from coast to coast, provided trees or caves were present. During glacial times distribution patterns were shifted southward, contracted, and may have been split into isolated segments as icecaps moved southward toward the Gulf of Mexico and through the Rocky Mountain range. The most southerly advance of the ice brought it within 500 miles of the present Gulf Coast. Adjacent to the ice front was a belt of treeless tundra of unknown width. Faunas and floras were compressed southward

Figure 27.—Relationship of the present distribution of the subgenus *Corynorhinus* and the maximum southward extension of Wisconsin glaciation. *Plecotus townsendii*, horizontal shading; *P. mexicanus* and *P. rafinesquii*, vertical shading; southern limit of glaciers, heavy line.

before the advance of the ice. Probably temperate climate inhabitants found conditions least severe in the southwest and in the extreme southeast, in the region of the Carolinas and Florida which was protected by the Appalachian Highlands from the winds that blew off the icecaps during some phases of the glacial cycle. The Gulf Coastal pathway south of the ice may have been less hospitable for these forms inasmuch as it was unprotected from the ice chilled winds and had rivers of meltwater flowing across it. Furthermore, competition for its limited niches may have been acute.

Under these conditions, a population of *Plecotus* that may have had a transcontinental distribution in the Yarmouth interglacial age, might have been isolated into southeastern and southwestern segments during the ensuing Illinoian glacial age. The southwestern segment included the mountains of northern and central Mexico in its range.

With the retreat of the Illinoian icecap and the warming during Sangamon time, *Plecotus* could have expanded its range again from coast to coast and perhaps northward into Canada and Alaska if caves were available. By this time the southwestern and southeastern segments had differentiated to the species level and remained genetically distinct when their expanding ranges came into contact. In the meantime, northward advance of warm climate floras and faunas isolated the *Plecotus* of the Mexican mountains from the remainder of the southwestern segment.

Southward advance of the Wisconsin icecaps and cooling climates once again contracted the range of *Plecotus* and broke its wide, continuous distribution into several isolated segments, remnants of which now occur in the southeastern lowlands, in the Appalachians, in the Ozarks, and in southwestern North America. Contact was reestablished between the southwestern segment and the Mexican segment which had by this time diverged to the species level.

Withdrawal of the Wisconsin icesheets and amelioration of climate, still proceeding, make it possible once more for the ranges of *Plecotus* to expand. Plotting the present distribution of American *Plecotus* on a map (fig. 27) showing the maximum southward extension of Wisconsin glaciation lends emphasis to the probability that range expansion has progressed slowly. The present distribution of *Plecotus* probably bears considerable resemblance to its distribution in the Wisconsin age. It is significant that, in the several thousand years since the last glacial retreat, bats of several genera have moved northward, far into the glaciated area, but *Plecotus* has barely penetrated it. No sharp biotic division marks the drift border, and there is no lack of caves north of the present range of *Plecotus* (caves in Wisconsin, Pennsylvania, New England, and Ontario, for example) to prevent its northward spread. To assume a relatively slow rate of dispersal for *Plecotus* could explain its present pattern of distribution, and furnish an important mechanism for speciation.

TABLE 7.—*Skull measurements of* Euderma maculatum, Plecotus phyllotis, *and* P. auritus

	Greatest length	Zygomatic breadth	Interorbital breadth	Brain case		Maxillary tooth row length	Postpalatal length	Palatal breadth	I^1 cusp index
				breadth	depth				
Female:									
E. maculatum									
(Western U.S.)									
Average	18.9	10.5	4.3	9.4	5.7	6.0	7.7	6.8	0.0
Extremes	18.8–19.0	10.2–10.9	4.2–4.3					6.7–7.0	
No. individuals	2	3	2	1	1	1	1	2	1
P. phyllotis									
(Mexico)									
Average	17.0	9.6	4.3	9.0	5.6	5.6	6.1	6.3	2.0
Extremes	16.7–17.2	9.4–9.8	4.2–4.4	8.8–9.2	5.6–5.6	5.5–5.7	6.0–6.1	6.2–6.3	2–2
No. individuals	2	2	2	2	2	2	2	2	2
P. auritus									
(China, Hopeh Prov.)									
Average	17.0	9.0	3.5	8.3	5.4	5.7	5.8	6.5	2.0
Extremes	16.9–17.2	8.7–9.2	3.4–3.7	8.1–8.4	5.3–5.6	5.5–5.7	5.6–6.0	6.3–6.6	2–2
No. individuals	4	4	4	4	4	4	4	4	4
Male:									
E. maculatum									
(Western U.S.)									
Average	18.7	10.0	4.0	9.5	5.7	6.0	7.5	6.5	0.0
Extremes	18.4–18.9	9.9–10.1	3.9–4.0	9.3–9.7	5.5–5.9	5.8–6.1	7.3–7.7	6.4–6.5	0–0
No. individuals	2	2	2	2	2	2	2	2	2
P. phyllotis									
(Arizona)									
Average	17.4	9.6	3.9	9.0	5.4	5.7	6.2	6.3	2.0
Extremes									
No. individuals	1	1	1	1	1	1	1	1	1
P. auritus									
(China, Hopeh Prov.)									
Average	16.8	8.9	3.5	8.2	5.4	5.6	5.8	6.4	2.0
Extremes	16.0–17.1	8.5–9.2	3.5–3.6	7.7–8.5	5.2–5.6	5.5–5.7	5.6–5.9	6.3–6.6	2–2
No. individuals	4	4	4	4	4	4	4	4	4

TABLE 8.—*Skull measurements of* Plecotus mexicanus

	Greatest length	Zygomatic breadth	Interorbital breadth	Brain case		Maxillary tooth row length	Postpalatal length	Palatal breadth	I^1 cusp index
				breadth	depth				
Female:									
(Chihuahua)									
Average	15.3	8.0	3.3	7.6	5.6	4.8	5.8	5.7	2.0
Extremes	15.2–15.5	7.8–8.3	3.2–3.4	7.5–8.1	5.4–5.7	4.7–4.8	5.6–5.9	5.6–5.8	2–2
No. individuals	8	6	9	8	8	9	8	9	9
(Guanajuato)									
Average	15.2	8.2	3.4	7.6	5.6	4.7	5.6	5.6	1.9
Extremes	15.0–15.3	8.0–8.5	3.2–3.5	7.5–7.7	5.5–5.7	4.6–4.8	5.6–5.8	5.4–5.7	1–2
No. individuals	5	5	5	5	5	5	5	5	9
(Veracruz)									
Average	15.4	8.2	3.4	7.6	5.6	4.8	5.8	5.7	1.9
Extremes	14.9–15.9	7.8–8.6	3.2–3.6	7.3–7.8	5.4–6.0	4.6–5.0	5.5–6.2	5.4–6.0	1–2
No. individuals	52	52	52	52	52	52	52	52	51
(Localities [except those above] in all parts of range)									
Average	15.3	8.0	3.4	7.7	5.5	4.7	5.8	5.7	1.5
Extremes	15.3–15.3	7.9–8.1	3.4–3.4	7.5–7.8	5.4–5.7	4.6–4.8	5.7–5.8	5.6–5.8	1–2
No. individuals	3	3	4	4	4	4	4	4	6
Male:									
(Localities in all parts of range)									
Average	15.1	8.0	3.3	7.5	5.6	4.7	5.8	5.5	1.8
Extremes	14.7–15.4	7.6–8.2	3.2–3.4	7.3–7.8	5.4–5.7	4.7–4.8	5.5–5.9	5.5–5.7	1–2
No. individuals	16	15	16	16	16	16	15	16	19

TABLE 9.—*Skull measurements of* Plecotus rafinesquii

	Greatest length	Zygomatic breadth	Interorbital breadth	Brain case		Maxillary tooth row length	Postpalatal length	Palatal breadth	I^1 cusp index
				breadth	depth				
Female:									
P. r. macrotis									
(Atlantic coastal lowlands)									
Average	16.2	8.8	3.6	7.9	5.9	5.3	5.8	6.1	2.0
Extremes	15.8–16.5	8.6–9.2	3.5–3.8	7.7–8.0	5.7–6.0	5.2–5.4	5.6–5.9	6.0–6.3	2–2
No. individuals	8	7	8	7	8	10	7	9	10
P. r. macrotis									
(Gulf coastal lowlands)									
Average	15.8	8.7	3.6	7.7	5.9	5.2	5.8	5.9	2.0
Extremes	15.3–16.2	8.2–9.0	3.4–3.8	7.4–8.0	5.7–6.0	5.0–5.3	5.6–6.0	5.6–6.2	2–2
No. individuals	11	9	11	11	11	12	10	11	14
P. r. rafinesquii									
(Localities in all parts of range)									
Average	16.3	8.9	3.7	7.9	5.9	5.3	6.0	6.1	2.0
Extremes	16.0–16.7	8.5–9.2	3.4–4.0	7.6–8.2	5.7–6.1	5.2–5.6	5.7–6.2	6.0–6.4	2–2
No. individuals	14	11	14	14	14	14	13	14	24
Male:									
P. r. macrotis									
(Atlantic coastal lowlands)									
Average	15.8	8.9	3.5	7.8	5.9	5.2	5.7	6.1	2.0
Extremes	15.6–16.1	8.6–9.1	3.5–3.6	7.7–7.9	5.8–6.0	5.2–5.3	5.7–5.8	6.0–6.3	2–2
No. individuals	5	5	6	6	6	6	6	6	11
P. r. rafinesquii									
(Localities in all parts of range)									
Average	16.1	8.8	3.6	7.8	5.8	5.3	5.9	6.0	2.0
Extremes	15.8–16.6	8.6–9.0	3.5–3.8	7.6–8.0	5.7–6.0	5.2–5.5	5.7–6.2	5.9–6.2	2–2
No. individuals	10	9	11	10	10	11	10	11	15

TABLE 10.—*Skull measurements of* Plecotus townsendii australis *and* P. t. ingens

	Greatest length	Zygomatic breadth	Interorbital breadth	Brain case		Maxillary tooth row length	Postpalatal length	Palatal breadth	I^1 cusp index
				breadth	depth				
Female:									
P. t. australis									
(Coahuila)									
Average	16.1	8.6	3.5	7.8	5.7	5.1	6.0	5.9	0.2
Extremes	15.5–16.4	8.4–8.8	3.2–3.7	7.7–8.0	5.6–6.0	4.9–5.2	5.9–6.1	5.6–6.1	0–1
No. individuals	11	11	11	11	11	11	11	11	11
P. t. australis									
(Localities in parts of range other than Coahuila)									
Average	16.2	8.7	3.6	8.0	5.7	5.2	6.0	5.9	0.1
Extremes	15.8–16.5	8.3–9.0	3.4–3.7	7.6–8.3	5.5–5.9	5.0–5.3	5.8–6.3	5.7–6.1	0–1
No. individuals	10	9	11	10	10	12	11	10	15
P. t. ingens									
(Arkansas)									
Average	16.8	9.2	3.9	8.1	5.9	5.5	6.3	6.4	0.6
Extremes	16.5–17.2	9.0–9.6	3.7–4.0	7.9–8.4	5.7–6.1	5.4–5.6	6.1–6.6	6.2–6.5	0–2
No. individuals	11	10	11	11	11	11	11	11	11
Male:									
P. t. australis									
(Coahuila)									
Average	16.1	8.6	3.6	7.8	5.7	5.1	6.0	5.7	0.3
Extremes	15.9–16.5	8.3–9.0	3.4–3.7	7.6–7.9	5.6–5.9	4.8–5.2	5.9–6.2	5.6–5.8	0–1
No. individuals	8	7	8	8	8	8	7	8	8
P. t. australis									
(Localities in parts of range other than Coahuila)									
Average	15.9	8.5	3.6	7.8	5.6	5.1	5.9	5.8	0.4
Extremes	15.5–16.4	8.2–8.8	3.4–3.7	7.5–8.1	5.4–5.9	4.9–5.3	5.6–6.1	5.4–5.9	0–2
No. individuals	13	13	14	13	13	14	12	14	13
P. t. ingens									
(Arkansas and Missouri)									
Average	16.6	9.1	3.8	8.2	5.8	5.4	6.2	6.3	1.0
Extremes	16.3–16.9	9.0–9.1	3.8–3.9	8.0–8.3	5.7–5.9	5.3–5.6	5.8–6.4	6.0–6.4	0–2
No. individuals	7	4	7	7	7	7	7	7	6

TABLE 11.—*Skull measurements of* Plecotus townsendii pallescens

	Greatest length	Zygomatic breadth	Interorbital breadth	Brain case		Maxillary tooth row length	Postpalatal length	Palatal breadth	I^1 cusp index
				breadth	depth				
Female:									
(Southern Arizona)									
Average	15.7	8.6	3.6	7.8	5.5	5.1	6.0	5.7	0.5
Extremes	15.5–15.9	8.3–8.8	3.5–3.7	7.6–7.9	5.4–5.7	5.0–5.1	----------	5.5–6.0	0–1
No. individuals	2	2	3	3	3	3	1	3	4
(Central & northern Arizona)									
Average	15.9	8.5	3.5	7.7	5.6	5.1	6.0	5.6	0.3
Extremes	15.3–16.3	8.3–8.7	3.5–3.6	7.5–7.9	5.5–5.7	4.9–5.3	5.9–6.1	5.5–5.6	0–1
No. individuals	5	3	5	5	5	6	3	2	6
(Montana)									
Average	16.4	8.8	3.6	8.0	5.8	5.3	6.2	6.0	0.1
Extremes	16.1–16.8	8.6–9.3	3.4–3.8	7.8–8.2	5.5–6.0	5.1–5.3	6.0–6.4	5.9–6.2	0–1
No. individuals	10	10	10	10	10	10	10	10	10
Male:									
(Southern Arizona)									
Average	15.5	8.5	3.5	7.6	5.5	5.0	5.8	5.6	0.2
Extremes	15.2–16.1	8.4–8.6	3.3–3.6	7.4–8.0	5.4–5.8	4.8–5.1	5.6–6.1	5.4–5.7	0–1
No. individuals	7	7	7	7	7	8	7	7	8
(Central and northern Arizona)									
Average	15.5	8.5	3.4	7.7	5.6	4.9	5.8	5.8	0.2
Extremes	15.4–15.6	8.4–8.7	3.3–3.6	7.6–7.8	5.5–5.7	4.8–5.0	5.7–6.0	5.6–5.9	0–2
No. individuals	5	5	5	5	5	5	5	5	6
(Montana)									
Average	16.3	8.7	3.5	7.9	5.6	5.3	6.1	6.0	0.2
Extremes	16.1–16.6	8.6–8.9	3.4–3.6	7.7–8.2	5.4–5.8	5.1–5.3	6.0–6.1	5.9–6.0	0–1
No. individuals	3	3	5	4	4	5	3	4	5

TABLE 12.—*Skull measurements of* Plecotus townsendii townsendii *and* P. t. virginianus

	Greatest length	Zygomatic breadth	Interorbital breadth	Brain case		Maxillary tooth row length	Postpalatal length	Palatal breadth	I^1 cusp index
				breadth	depth				
Female:									
P. t. townsendii									
(Western Oregon & Washington)									
Average	16.6	9.0	3.7	8.0	5.8	5.3	6.3	6.1	0.4
Extremes	16.2–16.9	8.8–9.2	3.5–3.8	7.8–8.2	5.5–5.9	5.1–5.3	6.1–6.4	6.0–6.3	0–1
No. individuals	6	6	8	8	7	8	7	8	8
P. t. virginianus									
(West Virginia)									
Average	16.6	9.0	3.8	8.1	5.8	5.3	6.2	6.1	0.1
Extremes	16.1–17.0	8.8–9.1	3.6–3.9	7.7–8.4	5.5–6.0	5.2–5.4	6.0–6.4	6.0–6.3	0–1
No. individuals	11	8	11	11	11	10	11	11	20
P. t. virginianus									
(Virginia)									
Average	16.4	8.8	3.9	7.9	5.7	5.3	6.1	6.0	0.3
Extremes									0–1
No. individuals	1	1	1	1	1	1	1	1	3
Male:									
P. t. townsendii									
(Western Oregon)									
Average	16.2	8.7	3.7	7.9	5.7	5.2	6.1	6.0	0.6
Extremes	16.1–16.4	8.6–8.9	3.6–3.9	7.7–8.2	5.6–5.9	5.1–5.3	5.8–6.2	5.7–6.2	0–2
No. individuals	7	6	7	7	7	7	7	7	7
P. t. virginianus									
(West Virginia)									
Average	16.5	8.8	3.7	8.0	5.8	5.3	6.1	6.0	0.0
Extremes	16.2–16.8	8.6–9.0	3.6–3.9	7.7–8.3	5.6–5.9	5.2–5.4	6.0–6.3	5.9–6.2	0–1
No. individuals	13	13	13	13	13	13	13	13	42
P. t. virginianus									
(Virginia)									
Average	16.1	8.7	3.8	7.8	5.8	5.3	6.0	6.1	0.3
Extremes	15.8–16.3	8.5–8.8	3.7–3.9	7.6–8.0	5.7–5.9	5.1–5.3	6.0–6.1	5.7–6.3	0–1
No. individuals	6	6	6	6	6	6	6	6	6

Table 13.—*External measurements of* Euderma maculatum, Plecotus phyllotis, *and* P. auritus

	Total length	Tail vertebrae	Hind foot	Ear from notch	Tragus length	Forearm length	Wing expanse
Female:							
E. maculatum							
(Western U.S.)							
Average	111	49	11	42	15	50	----
Extremes	107–115	47–50	10–12	37–47	13–17	48–51	----
No. individuals	3	3	4	2	2	4	----
P. phyllotis							
(Mexico)							
Average	110	50	10	[33]	[13]	44. 2	285
Extremes	----	----	10–10	----	----	44. 0–44. 4	----
No. individuals	1	1	2	1	1	2	1
P. auritus							
(China, Hopeh Prov.)							
Average	105	52	----	37	17	41. 9	----
Extremes	103–106	50–53	----	36–39	16–17	41. 5–42. 4	----
No. individuals	4	4	----	4	4	4	----
Male:							
E. maculatum							
(Western U.S.)							
Average	110	47	10	41	14	49	346
Extremes	107–114	46–48	9–10	39–43	13–16	48–50	----
No. individuals	5	5	2	5	3	6	1

P. phyllotis (Arizona)							
Average	118	52	11	40	16	46. 5	
Extremes							
No. individuals	1	1	1	1	1	1	
P. auritus (China, Hopeh Prov.)							
Average	100	49		37	17	41. 3	
Extremes	97–103	46–51		35–38	16–17	40. 2–41. 8	
No. individuals	4	4		4	4	4	

Table 14.—*External measurements of* Plecotus mexicanus

	Total length	Tail vertebrae	Hind foot	Ear from notch	Tragus length	Forearm length	Wing expanse
Female:							
(Chihuahua)							
Average	99	48	12	----	----	42. 0	----
Extremes	92–103	46–51	12–13	----	----	39. 3–43. 5	----
No. individuals	9	9	9	----	----	9	----
(Guanajuato)							
Average	----	----	----	[32]	[12]	42. 3	----
Extremes	----	----	----	[30]–[33]	[11]–[13]	40. 7–43. 3	----
No. individuals	----	----	----	10	10	10	----
(Veracruz)							
Average	98	48	10	33	11	42. 4	----
Extremes	90–102	42–51	10–10	31–34	11–12	40. 4–44. 3	----
No. individuals	43	42	43	43	43	43	----
(Localities [except those above] in all parts of range)							
Average	95	45	11	34	13	42. 4	----
Extremes	92–99	41–50	9–13	33–36	----	40. 7–45. 2	----
No. individuals	5	5	5	4	1	6	----
Male:							
(Localities in all parts of range)							
Average	96	46	10	32	12	41. 0	----
Extremes	92–100	43–50	9–11	29–35	11–15	39. 7–43. 1	----
No. individuals	13	13	13	18	17	18	----

TABLE 15.—*External measurements of* Plecotus rafinesquii

	Total length	Tail vertebrae	Hind foot	Ear from notch	Tragus length	Forearm length	Wing expanse
Female:							
P. r. macrotis							
(Atlantic coastal lowlands)							
Average	100	47	10	----------	12	43.0	275
Extremes	99–103	42–51	8–11	----------	----------	41.9–44.8	270–280
No. individuals	3	3	2	----------	1	10	2
P. r. macrotis							
(Gulf coastal lowlands)							
Average	97	50	11	34	15	41.9	----------
Extremes	93–101	48–51	11–12	33–35	----------	40.4–42.8	----------
No. individuals	4	4	4	4	1	10	----------
P. r. rafinesquii							
(Localities in all parts of range)							
Average	99	48	11	34	14	43.8	281
Extremes	92–106	43–54	10–12	32–36	12–16	42.1–45.8	270–292
No. individuals	9	9	10	9	6	21	11
Male:							
P. r. macrotis							
(Atlantic coastal lowlands)							
Average	98	48	11	----------	----------	42.3	280
Extremes	97–98	45–51	10–11	----------	----------	41.1–45.3	----------
No. individuals	2	2	2	----------	----------	8	1
P. r. rafinesquii							
(Localities in all parts of range)							
Average	99	46	12	33	14	43.0	273
Extremes	91–106	41–50	11–12	32–34	13–14	41.1–44.8	265–277
No. individuals	12	11	10	10	8	16	4

Table 16.—*External measurements of* Plecotus townsendii australis *and* P. t. ingens

	Total length	Tail vertebrae	Hind foot	Ear from notch	Tragus length	Forearm length	Wing expanse
Female:							
P. t. australis							
(Coahuila)							
Average	101	48	10	33	----------	42. 8	----------
Extremes	98–107	45–52	9–12	31–35	----------	39. 2–44. 4	----------
No. individuals	11	10	11	11	----------	11	----------
P. t. australis							
(Localities in parts of range other than Coahuila)							
Average	98	52	11	34	15	43. 6	----------
Extremes	93–101	48–54	10–13	33–36	14–15	42. 0–45. 1	----------
No. individuals	4	4	4	13	14	15	----------
P. t. ingens							
(Arkansas)							
Average	98	46	10	35	15	46. 5	325
Extremes	95–103	43–49	8–12	34–37	14–16	45. 1–47. 6	----------
No. individuals	10	10	10	10	10	10	1
Male:							
P. t. australis							
(Coahuila)							
Average	96	46	10	34	----------	42. 4	----------
Extremes	92–100	41–53	9–11	32–36	----------	40. 8–43. 8	----------
No. individuals	7	7	7	7	----------	8	----------

P. t. australis (Localities in parts of range other than Coahuila)							
Average	97	48	10	35	15	42. 5	297
Extremes	91–101	45–50	9–10	33–38	13–17	39. 4–44. 5	----------
No. individuals	7	6	6	13	14	13	1
P. t. ingens (Arkansas and Missouri)							
Average	95	42	10	35	14	45. 2	----------
Extremes	90–102	35–46	9–10	34–36	13–15	44. 1–46. 2	----------
No. individuals	6	6	6	6	6	7	----------

Table 17.—*External measurements of* Plecotus townsendii pallescens

	Total length	Tail vertebrae	Hind foot	Ear from notch	Tragus length	Forearm length	Wing expanse
Female:							
(Southern Arizona)							
Average	97	46	10	32		43. 1	
Extremes	90–103	43–51	10–11			42. 5–43. 6	
No. individuals	3	3	3	1		2	
(Central & Northern Arizona)							
Average	100	48	10			42. 7	306
Extremes	93–105	45–50	9–11			40. 9–43. 8	302–310
No. individuals	5	5	3			7	2
(Montana)							
Average	107	51	11			44. 6	309
Extremes	103–110	47–53	10–12			42. 7–45. 8	298–320
No. individuals	10	10	10			10	10
Male:							
(Southern Arizona)							
Average	95	48	10	34	15	41. 6	300
Extremes	90–102	45–52	9–11	32–36	12–17	40. 1–43. 2	
No. individuals	7	7	8	7	5	8	1

(Central & northern Arizona)							
Average	98	46	10			41. 8	
Extremes	95–101	41–50	9–11			41. 3–42. 3	
No. individuals	5	5	5			5	
(Montana)							
Average	108	51	10			44. 1	307
Extremes	105–110	47–54	9–11			43. 5–44. 6	305–311
No. individuals	5	5	5			2	5

TABLE 18.—*External measurements of* Plecotus townsendii townsendii *and* P. t. virginianus

	Total length	Tail vertebrae	Hind foot	Ear from notch	Tragus length	Forearm length	Wing expanse
Female:							
P. t. townsendii							
(Western Oregon & Washington)							
Average	107	48	12	33		43. 8	
Extremes	100–112	46–53	11–12	30–36		43. 3–44. 7	
No. individuals	10	10	5	2		5	
P. t. virginianus							
(West Virginia)							
Average	103	49	12	35	15	45. 8	316
Extremes	99–112	46–54	11–13	34–39		44. 6–47. 4	310–321
No. individuals	10	10	10	9	1	14	3
P. t. virginianus							
(Virginia)							
Average	103	45	11	38		46. 3	
Extremes						46. 3–46. 3	
No. individuals	1	1	1	1		2	
Male:							
P. t. townsendii							
(Western Oregon)							
Average	100	46	11	30		41. 9	
Extremes	96–103	44–51	10–11			41. 2–42. 5	
No. individuals	7	8	5	1		4	

P. t. virginianus (West Virginia)							
Average	101	50	11	34	14	44. 6	307
Extremes	98–103	48–52	10–12	31–38	11–15	43. 1–46. 4	300–314
No. individuals	21	20	22	22	3	38	2
P. t. virginianus (Virginia)							
Average	99	48	11	37	----------	43. 6	313
Extremes	97–101	40–52	11–12	37–38	----------	42. 6–44. 3	313–313
No. individuals	4	6	6	4	----------	6	2

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