READINGS IN MAMMALOGY

J. Knox Jones, Jr.
Sydney Anderson

Museum of Natural History
The University of Kansas
1970

Readings in Mammalogy

Selected from the original literature
and introduced with comments by

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PREFACE

This anthology is intended as an introduction to the study of mammals, principally for those who already have some biological background and who want to know the general scope of the field of mammalogy. The subdisciplines or specialties of mammalogy, its relationship to other biological fields, and specific examples of the type of work done by mammalogists are here introduced by means of a selection of complete papers in their original form. We hope that these will help college students looking forward to graduate work in biology obtain a realistic general view of mammalogy as a possible specialty. Also, beginning graduate students in related disciplines such as ornithology, mammalian physiology, or ecology, or undergraduate majors in wildlife management, may find their perspectives broadened by perusal of the present selection of papers and the introductory commentaries.

The published literature on the scientific study of mammals, which, broadly speaking, comprises the field of mammalogy, includes about 90,000 separate papers, and new papers are now being published at the rate of 5000 to 6000 each year, the actual number depending on where one draws the borders of the discipline. Precise borders do not exist. Mammalogy, like other scientific fields, draws from and contributes to various areas of human knowledge. Our selection of the 64 papers here reproduced was influenced by: (1) our concept of the scope of mammalogy and of a reasonable and representative balance of its parts at this time; (2) our desire to illustrate various ways in which a wide variety of information can be presented in published form; and (3) our awareness that most of our readers will be English-speaking Americans, which led us to use articles published in English and selected predominantly from American sources. Nevertheless, we judge that the broad sweep of concepts and methods portrayed is relevant to students of mammalogy in all parts of the world. We have selected short papers, in general less than 20 pages in length, in preference to either longer papers or excerpts therefrom—chiefly because of space, but also because we want the serious student, who may later contribute to the literature himself, to see each published work in its entirety as one tangible contribution to knowledge. He can then grasp its concept, its methodology, its organization, its presentation, its conclusions, and perhaps even its limitations. On the latter score we would note that, although we think the papers selected are worthy contributions and make the points we wish to emphasize, we do not pretend to have selected the finest papers ever published. We could have used a somewhat different selection to serve much the same purpose, and we are sure someone else would use a different selection to represent his views of mammalogy.

Although many college and university libraries have some or most of the journals and other sources from which papers were selected, we decided an anthology was warranted for those who want an overview of the field, who may not know where to find the relevant literature, or who want the convenience of a collection of separate papers. Many undergraduate students are largely unaware of the existence of, or the nature of, the technical literature of science, although their textbooks are replete with terminal citations. Hope-

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We have formulated our ideas for this anthology over the past three years and we are grateful for suggestions received from many persons in that time. We are grateful also to editors, publishers, and living authors for permission to include their works in READINGS IN MAMMALOGY.

J. KNOX JONES, JR.
SYDNEY ANDERSON

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READINGS IN MAMMALOGY

INTRODUCTION

The overall unity of the different fields of science and of other aspects of human experience, or at least their interdependence, is evident in both theory and practice. Nevertheless, this is an age of specialization. The sheer volume of information, the current rate of increase in knowledge, the changing and often elaborate techniques that must be learned, and human limitations all have contributed to the production of specialties.

A definition of the specialty of mammalogy as "all scientific study of mammals" is too broad, for that definition encompasses, for example, all parts of animal physiology in which any mammal, such as a white rat in the laboratory, may happen to be used. It also would include much of medical practice, because humans are mammals. Generally speaking, those scientists who call themselves mammalogists are interested in the mammal as an animal—as an organism—not just as a specific case of some more general phenomenon, be it the nature of life or the nature of the nerve impulse. For example, a physiologist who is interested in comparative studies between different mammals or in the function of a physiological process as an adaptive mechanism may regard himself as a mammalologist. A physiologist who studies one kind of laboratory animal and is interested in explaining a process in terms of progressively simpler mechanisms rarely will regard himself as a mammalogist. Both types of study, of course, contribute to biological knowledge.

Life is best comprehended in terms of four basic concepts: first, that biology, as all of science, is monistic, assuming one universe in which the same natural laws apply to living and non-living things; second, that life is a dynamic and self-perpetuating process; third, that the patterns of life change with time; finally, that these factors together have resulted in a diversity of living forms.

Different branches of biology tend to focus or concentrate on different concepts. Thus, the above four concepts are focal points, respectively, of (1) physiology and biochemistry, (2) ecology, (3) evolutionary biology, and (4) systematic biology. Mammalogy is the study of one systematic group or taxon, the Class Mammalia. Studies emphasizing different aspects of mammalian biology are evident in our section headings and in the specific papers reproduced. Biology as a whole and mammalogy specifically may be best likened to a woven fabric rather than to a series of compartments.

We feel that a unifying conceptual scheme for "mammalogy" lies in the realm of "systematic mammalogy." This scheme is unifying because it includes the basis for subsequent study and the only meaningful framework for the synthesis of existing knowledge of mammals. On this point, George Gaylord Simpson, in introducing his classic *The Principles of Classification and a Classification of Mammals* (1945) wrote (Simpson at that time used the term "taxonomy" as we use "systematics"):

> "Taxonomy is at the same time the most elementary and the most inclusive part of zoology, most elementary because animals cannot be discussed or treated in a scientific way until some taxonomy has been achieved, and most inclusive because taxonomy in its various guises and

> branches eventually gathers together, utilizes, summarizes, and implements everything that is known about animals, whether morphological, physiological, psychological, or ecological."

Knowledge of the identity of any animal studied is essential so that the results may be compared with other knowledge about the same kind of animal and with the same kind of knowledge about different animals.

We originally had hoped to develop the history of mammalogy along with our other objectives, but when the hard fact of page limitation was faced, some selections whose chief justification was historical were sacrificed. In the comments beginning each section, some historical information helps place the selections in an understandable framework. To attain variety we have included papers both of restricted and of general scope; for example, papers pertaining to local faunas and continental faunas, to higher classification and infraspecific variation, and to contemporary serum proteins and millions of years of evolution.

Every serious student of mammalogy, whether amateur or professional, researcher or compiler, writer or reviewer, artist or teacher, must learn to use the literature. One does not learn all about mammals because that is impossible. One learns what one can, where to look for further information, and, more important, how to evaluate what one finds.

Most of the literature on mammals is in technical journals, a few of which are devoted exclusively to mammalogy: Journal of Mammalogy (USA), Mammalia (France), Zeitschrift für Säugetierkunde (Germany), Säugetierkundliche Mitteilungen (Germany), Lutra (Benelux countries), Lynx (Czechoslovakia), Acta Theriologica (Poland), The Journal of the Mammalogical Society of Japan, Australian Mammal Society Bulletin, and Bulletin of the British Mammal Society. Also there are the specialized Folia Primatologica, an international journal of primatology, founded in 1963, and a number of serial publications such as Journal of Wildlife Management, Bulletin of the Wildlife Disease Association, and journals issued by various game departments and conservation agencies that may deal in large part, but not exclusively, with mammals. However, much of the published information on mammals, as on most aspects of biology, is widely scattered. About 40 journals include 50 per cent of the current literature, but to cover 70 per cent, at least 150 journals must be consulted. Articles in the Journal of Mammalogy (now more than 800 pages each year) comprise only about three per cent of all current titles on mammals, for example.

Some categories of literature other than journals are books, symposia, transactions of various meetings or groups such as the Transactions of the North American Wildlife and Natural Resources Conference (the 34th was issued in 1969), yearbooks such as the International Zoo Yearbook (the tenth was published in 1970), newsletters such as the Laboratory Primate Newsletter, Carnivore Genetics Newsletter, or Bat Research News, major revisions or compilations of special subjects, bibliographies, and abstracts. The chief bibliographic sources for mammalogists are the Journal of Mammalogy, through its lists of Recent Literature, Säugetierkundliche Mitteilungen, through its "Schriftenschau" section, the Zoological Record, published by the

Zoological Society of London, BIOLOGICAL ABSTRACTS (quite incomplete for some branches of mammalogy), and the quarterly WILDLIFE REVIEW that is issued by the U.S. Fish and Wildlife Service (along with the three collections of WILDLIFE ABSTRACTS—a misnomer because only citations are included—compiled therefrom and published in 1954, 1957, and 1964); one especially useful bibliography to older papers on North American mammals is that compiled by Gill and Coues (*in* Coues and Allen, 1877). Some individuals and institutions maintain records in the form of card files, or collections of separates, or both, over many years for special subjects, special geographic areas, or other more general purposes. It is important for the student to remember that large-scale faunal reports, catalogues, revisionary works, and the like often are valuable as bibliographic sources as well as sources of other information. Some of these reports are mentioned in the introductory remarks to several sections.

An individual who delves into the literature on a particular subject usually begins with one or more pertinent recent works and proceeds backward in time by looking up publications cited in the later works or found in other bibliographic sources.

An amazing amount of published information on a given subject frequently is available to the person willing to look for it. However, paradoxically, there is often no published record for what one might suppose to be nearly common knowledge. The questioning mind must return to nature when the literature holds no answer, exactly what the authors of papers reproduced in this anthology have done.

A few decades ago only a small number of American colleges and universities offered a formal course in mammalogy, and only since about 1950 have such courses been widely offered. It is not surprising, therefore, that only two textbooks, Cockrum's *Introduction to Mammalogy* (1962) and *Principles in Mammalogy* by Davis and Golley (1963) have been published in English. The former has a systematic orientation and the latter is predominantly ecological. Some instructors use general works like *Recent Mammals of the World, A Synopsis of Families* (edited by Anderson and Jones, 1967), *Mammals of the World*, a three-volume work by Walker *et al.* (1964), or Hamilton's (1939) *American Mammals* as texts or as references along with other suggested readings. Accounts of the mammals of certain states or regions also may be used as texts by persons in those places. Other general works of reference value are Bourlière's *Natural History of Mammals* (1954), Young's *The Life of Mammals* (1957), Crandall's *Management of Wild Mammals in Captivity* (1964), and the fascicles on mammals in the *Traité de Zoologie* (edited by Grassé, 1955 and later). Two classic general works less readily available are *An Introduction to the Study of Mammals, Living and Extinct* by Flower and Lydekker (1891) and *Mammalia* by Beddard (1902) in the Cambridge Natural History series.

Compact field guides to the mammals of a few parts of the world are available, such as those of Burt and Grossenheider (1964), Palmer (1954), and Anthony (1928) for parts of North America, and Van den Brink (1967) for Europe.

The dates in the two preceding paragraphs suggest the recent expansion in the volume of work in mammalogy. Another such measure is membership in The American Society of Mammalogists, which grew from 252 in 1919 to more than 3200 in 1969, and half of the growth occurred after 1957. Persons interested in mammalogy are invited to apply for membership in this society, members of which receive the JOURNAL OF MAMMALOGY.

Human medicine, veterinary medicine, animal husbandry, and animal physiology (including much work with a comparatively few species of mammals in the laboratory), all preceded mammalogy as separate disciplines dealing with mammals. Many of the first mammalogists (as defined here) trained themselves in one of these disciplines and some also practiced in fields other than mammalogy. C. Hart Merriam, who founded the U.S. Biological Survey, studied medicine, as did E. A. Mearns, who wrote on mammals of the Mexican boundary (1907). Harrison Allen wrote much of his first review of North American bats (1864) while on furloughs from duty as a surgeon in the Union army in the Civil War. Mammalogy continues to interact with the above-mentioned fields to their mutual benefit.

Another largely separate but partly overlapping field that flowered slightly later than mammalogy is genetics. We have included no papers on mammalian genetics as such, although the relevance of genetics is evident in some of our selections. A recent book on *Comparative Genetics of Coat Color in Mammals* by Searle (1968) contains about 800 references, including some fascinating works on species other than the oft-studied mouse *(Mus musculus)*.

Our six groupings of papers are somewhat arbitrary. Ecology is as closely allied to physiology or zoogeography as to behavior, and anatomy could as well have been placed with development as with physiology. The present arrangement as to the sequence of sections and the contents of sections seems to be about as convenient and useful as any other, and that is the extent of our expectations. We imply no hierarchy of subdisciplines.

In selecting works to be included here, we have, in addition to the considerations already noted, sought papers in which different kinds of mammals were compared, and in which different approaches, styles, and methods of presentation were used. Individual papers often pertain to more than one area of study. In fact, we favored papers that illustrated the relevance of different disciplines and methods of study to each other. Perhaps the reader will be able to appreciate our moments of anguish as the final selections were made for this anthology.

Our introduction for each section is brief. We hope that our comments aid the reader in considering (1) some historical aspects that make the papers more meaningful, (2) the major areas of study and some major concepts that the papers illustrate, (3) the existence of related literature, to which we can only call attention by citing a few examples, and (4) the continuous transfer of ideas, methods, and results from one worker to another, from one field of science to another, and between science and other fields of human endeavor.

SECTION 1—SYSTEMATICS

A sound classification provides the necessary framework upon which other knowledge about mammals can be built. In order to classify organisms, it first is necessary to know their similarities and differences; in other words, structures and their functions need to be observed, described, and compared, and taxa need to be recognized and named before a useful and meaningful classification can be constructed. The field of study relating to classification frequently is called "taxonomy," although the broader term "systematics" is also widely used and is preferred by us.

Prior to the first decade or so of the 20th century, the practice of mammalian taxonomy generally was based on a "hit-or-miss" typological approach, which, although it fostered considerable advancement in cataloguing the faunas of the world, was limited in perspective and potential. The development of evolutionary thought and the spectacular growth of genetics have led to the "new systematics," the biological species concept of today, as discussed in detail in such syntheses as Huxley (1943), Mayr *et al.* (1953), Simpson (1961), and Mayr (1963 and 1969), among others. Blackwelder's (1967) recent text in taxonomy also is deserving of mention here.

Technological advances in the means of collecting, preparing, and storing specimens resulted in the accumulation of series of individuals of the same species (the invention of the break-back mouse trap might be mentioned here along with the relatively recent widespread use of mist nets for capturing bats) and thus in turn allowed for assessment of variations within and between populations. Sophisticated studies of intergradation, hybridization, and the cenospecies concept in the past few decades are examples of results from technological and conceptual advances in this area.

To imply that all early taxonomic treatments of mammals were either inconsequential or poorly conceived would be a gross error. Pallas' (1778) revision of rodents, for example, was a monumental work far advanced for its day, as were many other outstanding contributions by 18th and 19th century mammalogists that could be mentioned. Nevertheless, one has only to compare the descriptions and accounts of Pallas with those found in papers reprinted here by Merriam, Handley, and Hoffmeister and de la Torre to appreciate the tremendous revolution in systematic practice. It is of interest to note that the 80-year-old paper by Merriam still is valid with reference to the specific status of grasshopper mice. The short contribution by J. A. Allen not only provides an example of a review, but deals in some detail with two substantial revisionary works published at the turn of the century. Among the larger modern revisionary studies that might be recommended to the student are those of Osgood (1909), Jackson (1928), Hooper (1952), Pearson (1958), Lidicker (1960), and Packard (1960). Ellerman's (1940, 1941, 1948) well organized review of living rodents and Hill's (1953 and subsequent volumes) somewhat more rambling and less critical coverage of the primates are also noteworthy as attempts to summarize selected bodies of knowledge of important groups of mammals.

The goal of scientific nomenclature is to assure that each kind of organism has a unique name, and only one name. The International Code of Zoological Nomenclature (latest edition, 1961) forms the legalistic framework for dealing with nomenclature, both past and present. The presently reprinted paper by Hershkovitz points up some of the kinds of nomenclatorial problems faced by the systematist. The Code is administered by the International Commission on Zoological Nomenclature but, as Blair (1968) pointed out, the Commission "has no way of enforcing its decisions, and the burden of holding names to conformity with the [Code] falls on the individual worker and on editors of scientific publications."

The emphasis in this section is mostly at the level of species and subspecies (for example, the papers by Benson and by Lidicker). Higher categories are dealt with primarily in Section 5. Attempts over the years by taxonomists to standardize techniques and definitions are illustrated by the papers of Thomas and Hall. The short essay by Grinnell also bears on this point.

The final four selections illustrate the application of new techniques and concepts to specific taxonomic problems, all of which were clarified in ways that might have been impossible otherwise. The treatment by Lawrence and Bossert of the problem of the relationships of the red wolf uses standard cranial measurements but analyzes them by discriminant analysis, a conceptually simple but computationally difficult statistical technique that has become generally applicable only with the development of digital computers. The karyological studies reported by Patton and Dingman treat some taxonomically interesting and previously confusing gophers in Arizona and enabled the authors to extend and refine the tentative conclusions based on other evidence; this paper also provides a good example of the careful integration of a new systematic approach with ecological and distributional considerations. Serological methods have been employed in taxonomic studies for many years, but new methods such as the serum protein electrophoresis used by Nadler and Hughes are increasing the useful means of approaching systematic problems at the biochemical or molecular level. Machado-Allison's contribution on host-parasite relationships illustrates the relevance of taxonomic data from one group, in this case ectoparasites, to the taxonomy of a different (host) group, bats.

Many papers in other sections of this anthology touch on systematics in one way or another, and the usefulness to the taxonomist of information from a variety of sources will be immediately evident to the reader. Two journals devoted to the concepts and practices of systematics and in which contributions in mammalogy regularly appear are SYSTEMATIC ZOOLOGY and ZEITSCHRIFT FÜR ZOOLOGISCHE SYSTEMATIK.

The Museum Conscience

THE scientific museum, the kind of museum with which my remarks here have chiefly to do, is a storehouse of facts, arranged accessibly and supported by the written records and labeled specimens to which they pertain. The purpose of a scientific museum is realized whenever some group of its contained facts is drawn upon for studies leading to publication. The investment of human energy in the formation and maintenance of a research museum is justified only in proportion to the amount of real knowledge which is derived from its materials and given to the world.

All this may seem to be innocuous platitude—but it is genuine gospel, never-the-less, worth pondering from time to time by each and every museum administrator. It serves now as a background for my further comments.

For worthy investigation based upon museum materials it is absolutely essential that such materials have been handled with careful regard for accuracy and order. To secure accuracy and order must, then, once the mere safe preservation of the collections of which he is in charge have been attended to, be the immediate aim of the curator.

Order is the key both to the accessibility of materials and to the appreciation of such facts and inferences as these materials afford. An arrangement according to some definite plan of grouping has to do with whole collections, with categories of specimens within each collection, with specimens within each general category, with the card indexes, and even with the placement of the data on the label attached to each specimen. Simplicity and clearness are fundamental to any scheme of arrangement adopted. Nothing can be more disheartening to a research student, except absolute chaos, than a complicated "system," in the invidious sense of the word, carried out to the absurd limits recommended by some so-called "efficiency expert." However, error in this direction is rare compared with the opposite extreme, namely, little or no order at all.

To secure a really practicable scheme of arrangement takes the best thought and much experimentation on the part of the keenest museum curator. Once he has selected or devised his scheme, his work is not *done*, moreover, until this scheme is in operation throughout all the materials in his charge. Any fact, specimen, or record left out of order is lost. It had, perhaps, better not exist, for it is taking space somewhere; and space is the chief cost initially and currently in any museum.

The second essential in the care of scientific materials is *accuracy*. Every item on the label of each specimen, every item of the general record in the accession catalog, must be precise as to fact. Many errors in published literature, now practically impossible to "head off," are traceable to mistakes on labels. Label-writing having to do with scientific materials is not a chore to be handed over casually to a "25-cent-an-hour" girl, or even to the ordinary clerk. To do this essential work correctly requires an exceptional genius plus training. The important habit of reading every item back to copy is a thing that has to be acquired through diligent attention to this very point. By no means *any* person that happens to be around is capable of doing such work with reliable results.

Now it happens that there is scarcely an institution in the country bearing the name museum, even though its main purpose be the quite distinct function of exhibition and popular education, that does not lay more or less claim to housing "scientific collections." Yet such a claim is false, *unless* an adequate effort has been expended both to label accurately and to arrange systematically all of the collections housed. Only when this has been done can the collections be called *in truth scientific*.

My appeal is, then, to every museum director and to every curator responsible for the proper use as well as the safe preservation of natural history specimens. Many species of vertebrate animals are disappearing; some are gone already. All that the investigator of the future will have, to indicate the nature of such then extinct species, will be the remains of these species preserved more or less faithfully, along with the data accompanying them, in the museums of the country.

I have definite grounds for presenting this appeal at this time and in this place. My visits to the various larger museums have left me with the unpleasant and very distinct conviction that a large portion of the vertebrate collections in this country, perhaps 90 per cent of them, are in far from satisfactory condition with respect to the matters here emphasized. It is admittedly somewhat difficult for the older museums to modify systems of installation adopted at an early period. But this is no valid argument against necessary modification, which should begin at once with all the means available—the need for which should, indeed, be emphasized above the making of new collections or the undertaking of new expeditions. The older materials are immensely valuable historically, often irreplaceable. Scientific interests at large demand special attention to these materials.

The urgent need, right now, in every museum, is for that special type of curator who has ingrained within him the instinct to devise and put into operation the best arrangement of his materials—who will be alert to see and to hunt out errors and instantly make corrections—who has the *museum conscience*.

March 29, 1921.

Vol. XVIII, pp. 191-196 September 2, 1905

PROCEEDINGS

OF THE

BIOLOGICAL SOCIETY OF WASHINGTON

SUGGESTIONS FOR THE NOMENCLATURE OF THE CRANIAL LENGTH MEASUREMENTS AND OF THE CHEEK-TEETH OF MAMMALS.

BY OLDFIELD THOMAS.

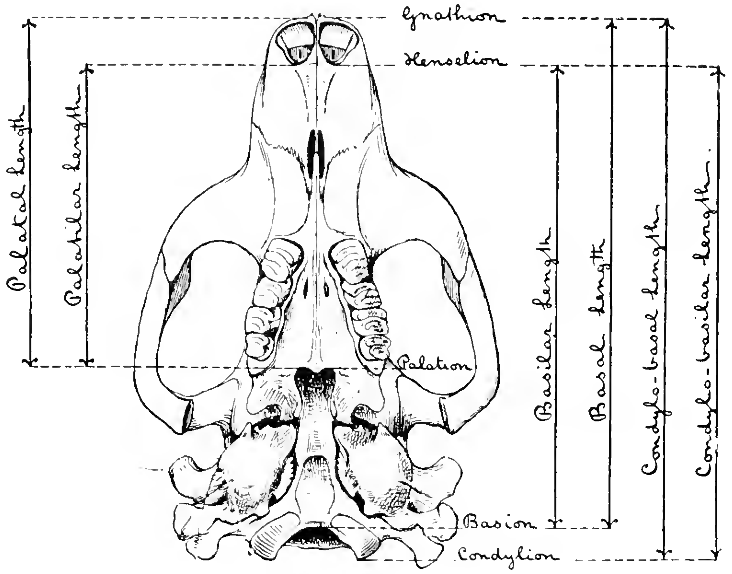
Although various reasons prevent the general success of such a wholesale revolution in scientific terms as is described in Wilder and Gage's Anatomical Technology (1882), where the many arguments in favor of accurate nomenclature are admirably put forth, yet in various corners of science improvements can be suggested which, if the workers are willing and in touch with each other, may be a real help in reducing the inconvenience of the loose or clumsy terminology commonly in vogue.

Two such suggestions, due largely to the instigation of Mr. Gerrit S. Miller, Jr., form the subject of the present paper.

I. Length Measurements of the Skull and Palate.

In giving the length measurement of the skull, not only do different authors at present use different measurements in describing the skulls of similar or related animals, but in doing so they designate these measurements by terms of which it is often difficult or impossible to make out the exact meaning. Such a name as " basal length " has I believe been used by one person or another for almost every one of the measurements to be hereafter defined, and readers are expected to know by heart everything that the user has ever written on the subject, footnotes and all, in order to understand what is meant by the particular term employed. Such a state of things has many inconveniences, and it is hoped the present communication, if it meets with the approval of other workers on the subject, may do a little toward putting an end to the existing confusion.

As long ago as 1894,* by agreeing with Dr. Nehring for the definition of the terms basal and basilar in our own future writings, I made a first step in this direction, and the present is an amplification of the principle then adopted.



All the difficulty has arisen from the fact that both at the anterior and the posterior ends of the skull there are two measurement points, so that there are four different ways in which the basal length of the skull may be taken, and under that name some authors have adopted nearly every one of them.

It is clear that if a definite name be given to each one of the four measurements, authors, by using these names, will be enabled to give the measurements they fancy without causing confusion in the minds of their readers as to their exact meaning.

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*Ann. & Mag. Nat. Hist., Ser. 6, XIII, p. 203.

The different points are:

Anteriorly: 1. The Gnathion, the most anterior point of the premaxillæ, on or near the middle line.

2. The Henselion, the back of the alveolus of either of the median incisors, the point used and defined by Prof. Hensel in his craniological work.

Posteriorly: 3. The Basion, a point in the middle line of the hinder edge of the basioccipital margin of the foramen magnum.

4. The Condylion, the most posterior point of the articular surface of either condyle.

A fifth measuring point to be referred to below is the Palation, the most anterior point of the hinder edge of the bony palate, whether in the middle line or on either side of a median spine.

Now using these words for the purposes of definition, I would propose, as shown in the diagram, the following names for the four measurements that may be taken between the points above defined:—

1. Basal length, the distance from Basion to Gnathion.
2. Basilar length, the distance from Basion to Henselion.
3. Condylo-basal length, the distance from Condylion to Gnathion.
4. Condylo-basilar length, the distance from Condylion to Henselion.

In addition there may be:

5. Greatest length, to be taken not further divergent from the middle line than either condylion. A long diagonal to a projecting bulla or paroccipital process would thus be barred. If however the words "between uprights" be added the measurement would be between two vertical planes pressed respectively against the anterior and posterior ends of the skull at right angles to its middle line.
6. Upper length, from tip of nasals to hinder edge of occipital ridge in middle line.

The difference between the words basal and basilar, which at first seemed trivial and indistinctive, is founded on the use of the English word basal by the older writers, such as Flower and others, who used the measurement from the gnathion; while basilar is an adaptation of the German of Hensel and his school, who used the "*basilar-länge*" from the henselion. These names again, combined with condylo-, readily express the points which are used by those who like to adopt the condylion as a posterior measuring point.

But further, the association of the ending "al" with a measurement from the gnathion, and "ilar" with one from the henselion, if once defined and fixed, may be utilized in a second case of similar character.

The length of the bony palate is a measurement given by all careful describers, but the anterior measuring point used is again either the gnathion or henselion, doubt as to which is being used often nullifying the value of the measurement altogether.* To avoid this doubt I would suggest, exactly as in the other case, that the name of the measurement from the gnathion should end in "al" and that from the henselion in "ilar." We should then have:

PALATAL LENGTH, the distance from gnathion to palation.

PALATILAR LENGTH, the distance from henselion to palation.

The indeterminate "palate length" would then be dropped altogether.

II. THE NAMES OF THE CHEEK-TEETH OF MAMMALS.

Although the cheek-teeth of mammals, the molars and premolars, have been studied and written about ever since the birth of zoology, no uniform system of naming them has been evolved and there is the greatest divergence between the usage of different workers on the subject. In old days all were called molars or grinders; then the premolars were distinguished from the true molars (although French zoologists, Winge in Denmark, and Ameghino in Argentina, continued to use a continuous notation for the two sets of teeth combined) and the usual habit among zoologists in general was to speak of them individually as "second premolar," "third molar," and so on. Even here, however, an important difference cropped up owing to Hensel

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* I may explain that in my own descriptions the palate of any given animal has always been measured from the same anterior point, gnathion or henselion, as the skull itself, this latter being indicated by the use of the words basal or basilar.

and his school in Germany numbering the premolars from behind forwards, while naturalists of other nations counted from before backwards, as with the incisors and molars, a difference often productive of fatal confusion.

Of late years, however, partly owing to an increasing concensus of opinion that the seven cheek-teeth of Placentals, four premolars and three molars, are serially and individually homologous with the seven of Marsupials, formerly reckoned as three premolars and four molars, many naturalists have again begun to think that a continuous numeration might be the best one.

But the difficulties in the way of its adoption are very great, largely owing to the absence of any convenient and suitable word in English less clumsy than "cheek-tooth," to express a tooth of the combined premolar and molar series. To speak of the "first cheek-tooth" or of the "predecessor to the fourth cheek-tooth" would be so retrogressive a step that I am sure no one would adopt it. But if instead of trying to find a word for the series combined with a numeral to show the position, we were to have a name for each tooth, we should get something of the immense convenience we have all realized in having definite names for the canine and the carnassial teeth, the latter name being found of value in spite of the fact that the upper and lower carnassials are not homologous with each other. Such names might be made from the positions of the teeth if their meanings were not so obtrusive as to confuse the minds of persons who do not readily understand how a tooth should be called "the second" or "secundus" when it is actually the most anterior of the series.

Now it fortunately happens that while the Latin terms "primus," "secundus," etc., express the serial positions too clearly for the convenience of weak minds, Latinized Greek terms have just about the right amount of unfamiliarity which would enable them to be used as names without their serial origin being too much insisted on. Moreover, their construction is similar to the process we all use in making generic names, and so far as I know they have never been previously utilized in zoology.

Then, after Latinizing the Greek ordinal terms πρωτος, etc. for the cheek-teeth of the upper jaw, the same modification as is already used in cusp nomenclature might be adopted for those of the mandible.

We should thus have, counting from before backwards:

	UPPER JAW.	LOWER JAW.
Cheek-tooth 1	Protus	Protid
" 2	Deuterus	Deuterid
" 3	Tritus	Tritid
" 4	Tetartus	Tetartid
" 5	Pemptus	Pemptid
" 6	Hectus	Hectid
" 7	Hebdomus	Hebdomid

To avoid any doubt, I would expressly allocate these names to the permanent teeth of placentals, leaving the names of the marsupial teeth to be settled in accordance with their placental homologies.

For the milk teeth a further modification would be available by prefixing the syllable Pro- to the names of the respective permanent teeth. We could thus for example in the case of a third lower milk premolar call it the protritid, and so use one word instead of four.

Of course I have no supposition that this system would ever be frequently or generally used, but I am convinced that in many special cases, and particularly in such descriptions and catalogues of isolated teeth as paleontologists often have to give, it might result in considerable convenience and saving of space.

CRITERIA FOR VERTEBRATE SUBSPECIES, SPECIES AND GENERA: THE MAMMALS

By

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Mr. Chairman, members of the American Society of Ichthyologists and Herpetologists, members of the American Society of Mammalogists, and guests: We had expected as a speaker at this time one of the senior mammalogists who now is unable to attend. I am glad to appear as a substitute because the subject under discussion is one in which I am especially interested. In these extemporaneous remarks I propose: (1) to indicate some steps which I think useful to take in classifying mammalian specimens as to subspecies; (2) to express my personal views as to criteria for subspecies, species, and genera of mammals; (3) to illustrate how some of these criteria for subspecies and species may be applied to closely related insular kinds of mammals; and (4) to suggest a way in which subspecies may disappear without becoming extinct.

When I undertake to classify mammalian specimens as to subspecies or species, or when I present a series to a beginning student for classification, I like to observe the following steps: (a) select for initial, intensive study a large series, 30 or more individuals, from one restricted locality; (b) segregate these by sex; (c) arrange specimens of each sex from oldest to youngest; (d) divide these into age-groups and within a given group, of one sex, from one locality, of what is judged to be one species, measure the amount of so-called individual variation; (e) with this measurement as a "yardstick," compare individuals, and if possible series, comparable as to sex and age (and seasons where characteristics of the pelage are involved) from this and other localities. The differences found are usually properly designated as geographic variations and form the basis for recognition of subspecies, which in turn comprise one of the tools used by some students of geographic variation.

As to criteria for the recognition of genera, species and subspecies of mammals, it seems to me that if crossbreeding occurs freely in nature where the geographic ranges of two kinds of mammals meet, the two kinds should be treated as subspecies of one species. If at this and all other places where the ranges of the two kinds meet or overlap, no crossbreeding occurs, then the two kinds are to be regarded as two distinct, full species. The concept of a species, therefore, is relatively clear-cut and precise; the species is a definite entity. Furthermore, if a zoologist knows the morphological characteristics diagnostic of the species, he has no difficulty in identifying a particular individual as of one species or another. In identification of subspecies, difficulty is frequently encountered, especially with individuals which originate in an area of intergradation.

The category next higher than the species, namely, the genus, is less definite and more subjective as regards its limits than is the species. As the species is the definite, clear-cut starting point for defining subspecies, the species is likewise the starting point for consideration of genera. Degree of difference is the criterion for a genus. The genus lies about midway between the species and the family. Because the limits of the family, like those of the genus, are subjective, it follows that the criterion for recognition of genera, although precise enough at the lower point of beginning, the species, is elastic at the upper end—namely, at the level of the family.

In summary, the criterion for subspecies is intergradation, that for species is lack of intergradation, and that for genera is degree of difference. These ideas agree in general with the ideas expressed by the previous speakers.

One of the situations in which it is difficult, or impossible, to apply these criteria to conditions actually existing in nature is comprised in some insular populations. Frequently the populations on two islands near each other differ enough to warrant subspecific or possibly specific distinction. A means of deciding on specific versus subspecific status for these populations is to find on the adjacent mainland a continuously distributed, related kind of mammal which there breaks up into subspecies. Ascertain the degree of difference between each pair of mainland subspecies which intergrade directly. If the maximum degree of difference between the insular kinds is greater than the difference between the two subspecies on the mainland, which intergrade directly, and greater than that between either insular kind and the related population on the nearby mainland, the two insular kinds may properly be treated as full species. If the maximum degree of difference between the insular kinds is no greater than, or less than, the difference found on the mainland between pairs of subspecies which intergrade directly, the insular kinds may properly be treated as subspecies of one species. In fine, the criterion is degree of difference with the limitation of geographic adjacency, rather than intergradation or lack of it.

Now to my fourth point, namely the suggestion that many subspecies disappear without becoming extinct. Permit me first to observe that although species and subspecies seem to have the same kinds of distinguishing characters, which appear to be inherited by means of essentially the same kinds of mechanisms in the germ plasm, there are two noteworthy differences between species and subspecies. One already implied is that, in a species which is continually distributed over a given area, its characters at the boundaries of its range are sharp, definite, and precise. Some of its characters comprised in size, shape and color, at any one place are either those of one species or instead unequivocally those of some other, whereas the characters of a subspecies, particularly at or near the place where two subspecies meet, more often than not are various combinations of those of the two subspecies and in many individual characters there is blending.

Second, through a given epoch of geological time while a species is in existence, one or more of its subspecies may disappear and one or several new subspecies may be formed. Subspecies, therefore, on the average are shorter-lived than species.

Now the disappearance of subspecies is to be expected on *a priori* grounds if we suppose that new subspecies are formed in every geological epoch. There is reason to believe that in the Pleistocene, the epoch of time immediately preceding the Recent, there were even more species of mammals than there are now. In each of several successively corresponding periods of Tertiary time before the Pleistocene, probably there were as many species as now. Probably too, these species then were about as productive of subspecies as species are now. Had even half of these subspecies persisted, either as subspecies unchanged or in considerable part by becoming full species, there would now be an array of species and subspecies many times as numerous as actually does exist. It is obvious therefore that many disappeared.

In accounting for this adjustment of numbers of kinds of mammals, I have spoken of the disappearance of subspecies rather than of their extinction because I can imagine how a species, say, the pocket gopher *Thomomys townsendii,* in the middle Pleistocene with three subspecies (geographic races) could have come down to the present by means of each of the three subspecies having gradually changed its characters into those of one of the three subspecies existing today in the area of northern Nevada that I have in mind. In this way, disappearance of subspecies living in the Pleistocene has been accomplished, without their having become extinct in the sense that the subspecies left no living descendants. Of course this has to be true for some of the subspecies of each successively preceding epoch if any animals at all persist, but what I wish to emphasize is the strong probability that many, perhaps more than 50 per cent, disappeared thus without actually becoming extinct, when, for example, two successive stages of the Pleistocene, south of the ice sheet, are considered. In this regard it is pertinent to recall that each of three Pleistocene kinds of pocket gophers, *Thomomys* (probably species *talpoides*) *gidleyi*, *Thomomys* (probably species *townsendii*) *vetus*, and *Thomomys* (probably species *bottae*) *scudderi*, from a short distance over the northern boundary of Nevada, differs from living representatives corresponding to it (several subspecies of one species) in greater width labially of the individual cheek teeth of the lower jaw. Significant for the thesis being defended is the point that each and all of these *Thomomys* in the Pleistocene differed, at least as regards the shape of the teeth, in the same way from the three living species which I feel confident are their descendants.

Let us suppose that three hypothetical subspecies of *Thomomys townsendii* in middle Pleistocene time each gradually changed into three different subspecies inhabiting about the same areas in upper Pleistocene time, and that these in turn were the ancestors of the three subspecies living in those same general areas today. A total of nine kinds is thus accounted for. At any one time there was geographical intergradation, which has reference to horizontal direction. Also there was intergradation up through time, which has reference for present purposes to a vertical direction. If I had before me all the material necessary to substantiate this or a similar case, I would be inclined to recognize nine subspecies of one species. This hypothetical case emphasizes the importance of intergradation, the criterion for subspecies.

In review: I have mentioned some preliminary steps useful for a person to take when he aims to analyze variation in mammals and to establish species and subspecies thereon; intergradation is the criterion for subspecies and degree of difference is the criterion for genera; degree of difference with the limitation of geographic adjacency may be used as the criterion for insular populations (the classification of which is doubtful as between subspecies and species); and, finally, I have sought to stress the importance of intergradation as a criterion for subspecies by showing how subspecies may disappear without becoming extinct.

The Nature of Subspecies Boundaries in a Desert Rodent and its Implications for Subspecies Taxonomy

WILLIAM Z. LIDICKER, JR.

IT SEEMS to me that the wide diversity of opinion which exists concerning the usefulness of trinomial nomenclature revolves in large measure on the more basic issue of whether or not it is possible to recognize infraspecific categories which reflect genetic relationships. As recently pointed out by Sneath (1961), taxonomic categories which are not based on relationships are thereby rankless and cannot logically be included in a taxonomic hierarchy. Thus if the subspecies category is used merely as an instrument for describing geographic variation in a few characters or as a device for cataloging geographic variants (as is done by many taxonomists), artificial classifications of convenience are characteristically produced. Such convenience classifications usually contain rankless groups (the "false taxa" of Sneath) which cannot be allocated in the taxonomic hierarchy. This is simply because categories based on a few arbitrary characters are themselves arbitrary, and lead to the objection of Brown and Wilson (1954) and others that trinomials based on one group of characters need not bear any relation to those based on different traits. Many of the same philosophical difficulties apply to systems such as that recently proposed by Edwards (1954) and Pimentel (1959) in which the subspecies would become a measure of isolation, by restricting its use to completely isolated and "obviously different" populations.

If on the other hand studies of infraspecific populations are focused on discovering evolutionary diversity or degrees of relationship between the various populations, I see no philosophical objection to the use of the trinomen. The question then reduces to one of the feasibility and/or desirability of searching for such relationships, and of deciding what level of dissimilarity if any justifies use of the formal trinomen. It is primarily these two subsidiary questions which are examined in this paper, with the frank hope that the subspecies can be rescued from the rankless limbo of the morph, ecotype, and form. If this rescue operation should prove successful, attention can then be directed to other problems of greater biological interest, such as whether or not determinations of genetic relationships within a species, which are based on phenotypes, can serve as a basis for speculations on phylogeny. Obviously geographic relations would have to be considered at this level, but, assuming that such information is taken into account, it would be highly informative to contrast phenetic and phylogenetic subspecies classifications. In any case, analyses of infraspecific relationships would very likely provide valuable clues concerning the environmental forces which have influenced the development of the existing evolutionary diversity.

In a previous paper (1960) I attempted to determine the genetic relationships among populations within a species of kangaroo rat (*Dipodomys merriami* Mearns, 1890) by a careful analysis of 20 morphological features. I concluded at that time that at least in well-known terrestrial species an attempt to recognize relative relationships within a species was at least possible. And, at the same time it was apparent that (besides the philosophical objections already pointed out) the subspecies category by itself was completely inadequate for describing the complex geographic variation occurring in that species. It is the raw data from this former investigation that I have used here to test further the reliability of those tentative conclusions.

The search for relationships among populations of the same species implies a search for total genetic differentiation (or at least its phenotypic manifestations), and hence of lineages with partially independent evolutionary origins such that they have some internal homogeneity and their own adaptive tendencies. To detect this kind of differentiation it seems important to analyze, among other things, the populations occurring at the boundaries between differentiating groups, just as in the analysis of species relationships it is the boundaries between them, or areas of sympatry, where the most significant information on relationships is to be found. This is not to say that information concerning the regions of greatest divergence or adaptive peaks (in this case peaklets) of infraspecific populations is not important, but only that such data should not be the only source material for taxonomic judgments. Thus it is the intent of this paper to focus attention on the previously all but ignored subspecies boundaries, and to examine the nature of these areas in *Dipodomys merriami* as I had previously and without the benefit of this analysis defined them (Lidicker, 1960). Because the determination of these intraspecific units was guided in this case by a desire to find populations of comparable evolutionary relationship, careful scrutiny of the intergrading zones between them and surrounding areas should be of particular interest. Comparisons will also be made with levels of differentiation in areas in which no subspecies boundary was recognized, as well as with one region in which species level differentiation was postulated to have been reached by an island isolate.

The second and related purpose of the paper is to describe a method which helps to accomplish the first objective by measuring total differentiation, or lack of similarity, in many diverse characters, and hence is proposed as a criterion of relationship. But at the same time the technique does not require the hard working taxonomist to have either access to a digital computer or facility with matrix algebra.

The Method

Most quantitative techniques available to the systematist, which concern themselves with determining relationships, and hence with similarities as well as differences, either involve the analysis of qualitative or discontinuous characters and thus are most useful at the species or genus level (e.g., Michener and Sokal, 1957; Lysenko and Sneath, 1959), or involve calculations sufficiently complex (e.g., Williams and Lance, 1958) that they are avoided by most practicing systematists. What seems to be needed is an additional technique which is sufficiently adaptable to handle continuously variable, as well as discontinuous, characters of diverse types (and so is useful in infraspecific studies), and which at the same time is sufficiently practical that it will be widely useful. To this end the following proposed method is dedicated. It is not intended as a substitute for discriminant function analysis (Fisher, 1936; Jolicoeur, 1959) and related methods which attempt to discriminate between previously conceptualized populations by using combinations of variables.

An analysis of relationship should ideally compare relative similarities and not differences. However, since the number of similarities between populations within a species is very large, it is much easier to measure their differences and consider that the reciprocal of the amount of difference represents a measure of similarity. Thus as the amount of difference approaches zero, the reciprocal approaches infinity. The problem then becomes one of summing the amount of difference in many diverse characters. To do this we must be able to express the differentiation for each trait by a pure number (no units). Cain and Harrison (1958), for example, accomplished this by dividing the differences which they observed between means by the maximum value recorded for each character. The resulting ratios, which they called "reduced values," express the observed differences in terms of a fraction of the maximum size of each character. Although this permits the comparison of diversity among traits of different absolute size, it does not take into account either the possibility that various characters may have different variabilities, or the statistical significance of the observed mean differences. Furthermore, maximum size would seem to be a statistic of dubious biological importance in continuously varying characters. On the other hand, all of these important variables, the variance of each trait, character magnitude, as well as a consideration of whether or not mean differences have a high probability of representing real differences, are taken into account by expressing differentiation as a proportion between the observed differences between samples and the maximum amount of difference expected on the basis of chance sampling variation. Only mean differences greater than that amount which may be due to chance would then be considered as real differences. For our purposes the maximum chance variation expected in any comparison can be equated to the minimum difference required for statistical significance (at any given confidence level). This minimum significant difference (*msd*) can be calculated in a number of ways. One possibility is to determine the standard error of the mean for each character for each sample. Then in comparing two samples for this character, $2\ \mathrm{SE}_{\bar{x}_1} + 2\mathrm{SE}_{\bar{x}_2} = msd$. This provides a conservative estimate of *msd* with confidence limits usually well in excess of 95%. For large studies, however, these calculations would be extremely laborious, as well as perhaps overly conservative, and a short-cut is suggested.

If we can assume that each quantitative character in a given species exhibits a characteristic variability throughout its range, then calculations would be tremendously reduced if we were able to determine the expected or pooled standard deviation (s_p) and standard error ($s_{p_{\bar{x}}}$) of samples for which say $n \geqq 20$. Very small samples would have to be grouped with adjacent samples whenever possible, or if necessary either ignored or have separate *msd*-values calculated for them. Under these conditions $4s_{p_{\bar{x}}}$ represents our best estimate of *msd*. Unfortunately confidence limits cannot be calculated for its reliability, although again it is generally a conservative estimate. The statistic s_p can be conveniently determined by averaging the weighted variances for several samples of adequate size (Hald, 1952: 395). Note that as the estimate of s_p improves it approaches the population standard deviation (σ), and hence is applicable to a wider range of sample sizes. Better estimates of s_p require knowledge of the total number of individuals in each of the populations sampled (see Cochran, 1959: 72), an obvious impossibility in this type of problem. In the examples given in this paper $4s_{p_{\bar{x}}}$ was estimated by using the standard deviation of one large sample collected near the center of the species' range, and by assuming $n = 20$. This expediency seemed justified because of the close similarity in values of s calculated for a given trait among several samples, and because of the likelihood that s approaches σ under these circumstances.

Still another method of deriving the statistic *msd*, but one not used in this report, involves a more laborious, but statistically more precise, procedure. The confidence limits for the difference between any pair of means can be calculated (see Dixon and Massey, 1957:128) whether or not we assume that we know the variance characteristic of each trait (s_p^2) or use only the pertinent sample variances (s_1^2 and s_2^2). For a large study, the calculations are very much reduced if one can estimate s_p (see above), and perhaps even use only samples in which $n \lesssim 20$. If these simplifications are possible, a pair of confidence limits can be computed which will be characteristic for each trait studied. In either case, one confidence limit gives us our *msd,* since mean differences greater than this can with a known probability be considered real. We need not be concerned with the possibility that the mean differences are even larger than those observed.

Consider then only those characters in which the differences in the mean values ($\bar{x}_1 - \bar{x}_2$) for a given pair of locations (samples) are greater than the minimum significant differences. Now, divide these significant differences in mean values by the minimum significant difference characteristic for that trait (or for that pair of samples). This procedure gives us our pure number which can be designated as d_1, d_2, ... d_n for successive characters, each representing a measure of differentiation in one character between one pair of samples. Having defined the amount of differentiation in each character in terms of a pure number, we can now add these to arrive at an estimate of total differentiation in the characters studied (Σd_i). In interpreting this statistic in any real situation, however, it seems apparent that the distance between the two samples compared should be taken into account. Obviously an amount of total differentiation exhibited between two samples which are close together geographically would be more significant than the same amount of differentiation between samples geographically distant. To compensate for this effect of distance, I have divided the total differentiation by the distance (in miles) between the two samples. The resulting figure, which I have called *D* or the Index of Differentiation,[1] represents the proportion of significant change that occurs between the two locations per mile. Then the reciprocal of *D* easily gives us our measure of similarity between populations. *D* need now only be further divided by the total number of characters studied, including those of course in which no differentiation occurred, to arrive at the mean character differentiation per mile (*MCD/mi.*).

The importance of considering distance between samples will depend in large measure on the specific problem under investigation. Obviously air-line distance between samples does not always accurately reflect the real magnitude of the distance or barriers between them. I feel that this is not a serious difficulty, however, since we are concerned with the abruptness of differentiation between adjacent populations and not with barriers *per se.* Moreover, in some ways *D* acts as a measure of restriction on gene flow, because, if distance is kept constant, *D* will tend to increase as gene flow is reduced. Another potential difficulty with the distance calculation is that it carries the assumption that if the two localities being compared were actually closer together, the amount of total differentiation shown would be less. This is not always true because not only are there sometimes large areas which exhibit very little geographic variation, but also there exist unavoidable gaps in specimen collections. For these reasons I felt that in the present analysis of *D. merriami* it was necessary to consider both Σd_i and *D* in assessing differentiation.

One further complication seems worth considering. This concerns variation in the direction of change between different characters. It seemed to me more significant if one or two characters were found to change significantly in a direction opposite to that of the other characters, than if they all changed in the same di-

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[1] Note that this is in no way similar to the "differentiation index" of Kurtén (1958) which compares growth gradients.

rection. Thus for each such direction change, I arbitrarily added one half the *d*-value for that specific character to Σd. This also serves to oppose any tendency to give too much weight to characters which may not be entirely independent in their variation, or to those varying allometrically. Otherwise no allowance has been made for differentially weighting characters which might be considered to have greater phylogenetic importance. Presumably this could be readily done, if there were some sound basis for making such judgments. Sneath (1961), however, points out some of the dangers inherent in attempts to do this, and argues for considering each character equally.

Table 1 summarizes the calculations for Σd, *D*, and *MCD/mi.* for one pair of localities in southeastern Arizona. Note that a value of 3.476 has been included in Σd for color changes. Ordinarily color characters should be quantified so that they can easily be added into this scheme. Unfortunately in my study, I did not quantify in numerical terms the six color features analyzed. This necessitated my determining when significant changes had occurred by reference to the color descriptions of each sample. Whenever important color changes were found between samples, I included in Σd for each such change a figure which represented the average *d*-value for all pairs of localities in the boundary region under study which exhibited the same number of color changes as the sample pair being calculated. For example, if two samples differed in three color features and if the average *d* for all pairs of samples in that region which also differed by three color features was 1.50, then 4.5 (3 x 1.50) would represent the combined value of *d* for the three color traits. Although this represents an unfortunate complication, it should not detract from the validity of the overall method being proposed.

Figures 1, 2, and 3 show the differentiation observed in 20 characters in *D. merriami* in selected portions of its large range. It is important to emphasize that these 20 characters were chosen in the original investigation (Lidicker, 1960) independently of the conclusions of other authors concerning what they considered important characters in distinguishing subspecies. The list thus includes not only most of the "taxonomically important" characters of other authors but numerous additional features as well. I chose for illustration regions which demonstrate various levels of differentiation

TABLE 1—CALCULATIONS FOR TOTAL DIFFERENTIATION, THE INDEX OF DIFFERENTIATION, AND THE MEAN CHARACTER DIFFERENTIATION PER MILE IN *Dipodomys merriami* FOR A PAIR OF LOCALITIES IN SOUTHEASTERN ARIZONA (VICINITIES OF THE HUACHUCA AND SANTA RITA MOUNTAINS 54 MILES APART).

CHARACTER *	$\bar{x}_1-\bar{x}_2$ (mm.)	msd	d_i
hind foot length	1.40	0.68	2.059
ear length	0.62	0.52	1.192
basal length of the skull	0.54	0.52	1.039
cranial length	0.78	0.48	1.625
rostral width	0.19	0.06	3.167
1 direction change (ear)	$(\frac{1}{2}d_2)$		0.596
2 color changes	($2\bar{x}_d$ for those pairs of localities with two color changes)		3.476
		Σd_i =	13.154
		D =	0.244
		MCD/mi. =	0.012 **

* See Lidicker (1960) for a description of these characters.

** Total of 20 characters studied.

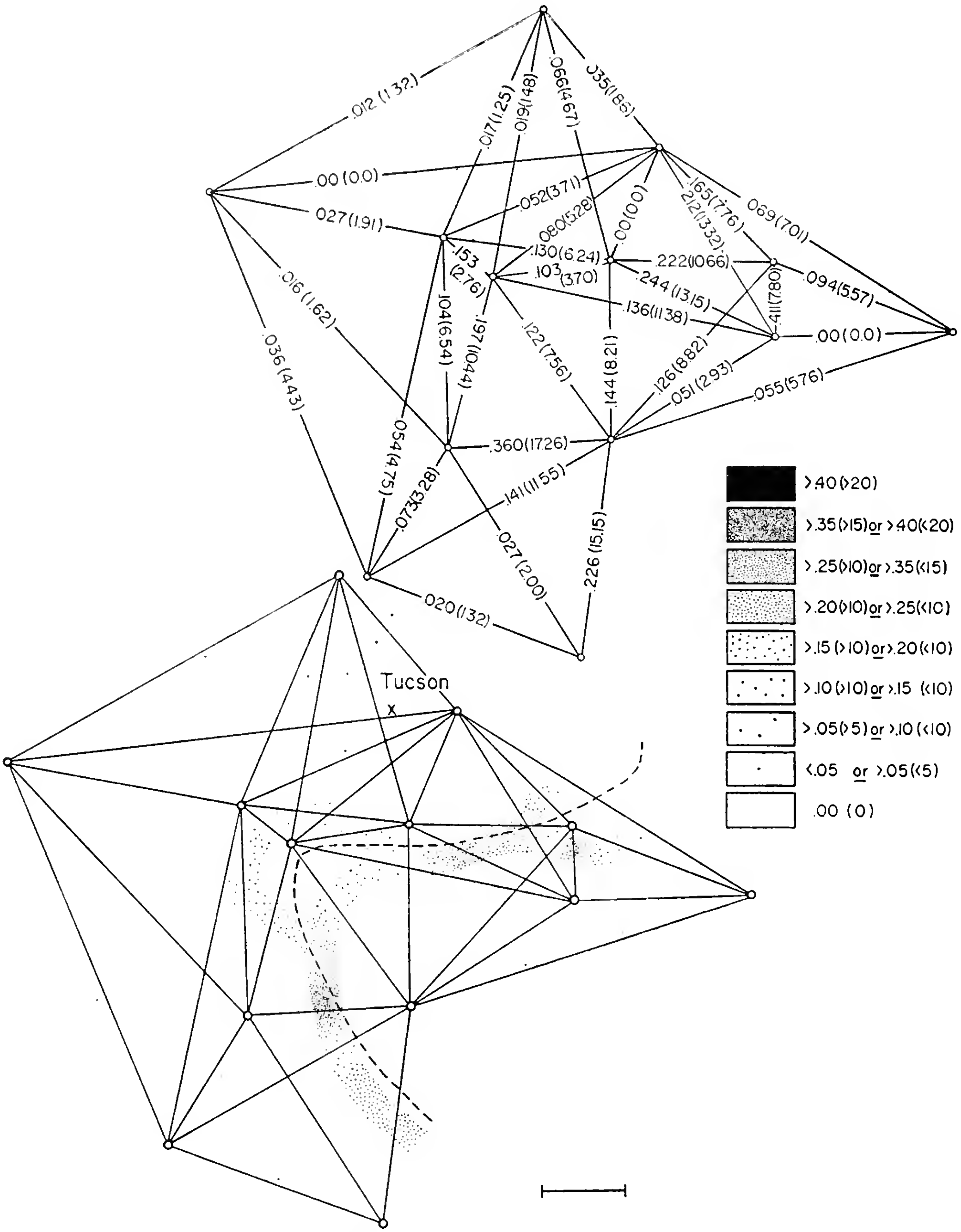

FIG. 1. Observed differentiation of *Dipodomys merriami* in southeastern Arizona and adjacent Mexico and New Mexico. Numbers on the lines connecting the various sample localities represent the calculated values for D and in parenthesis Σd_i. The key to the intensity of stippling is based on these same statistics. The scale associated with each map represents a distance of 25 miles. See also the text for a more complete explanation of the figures.

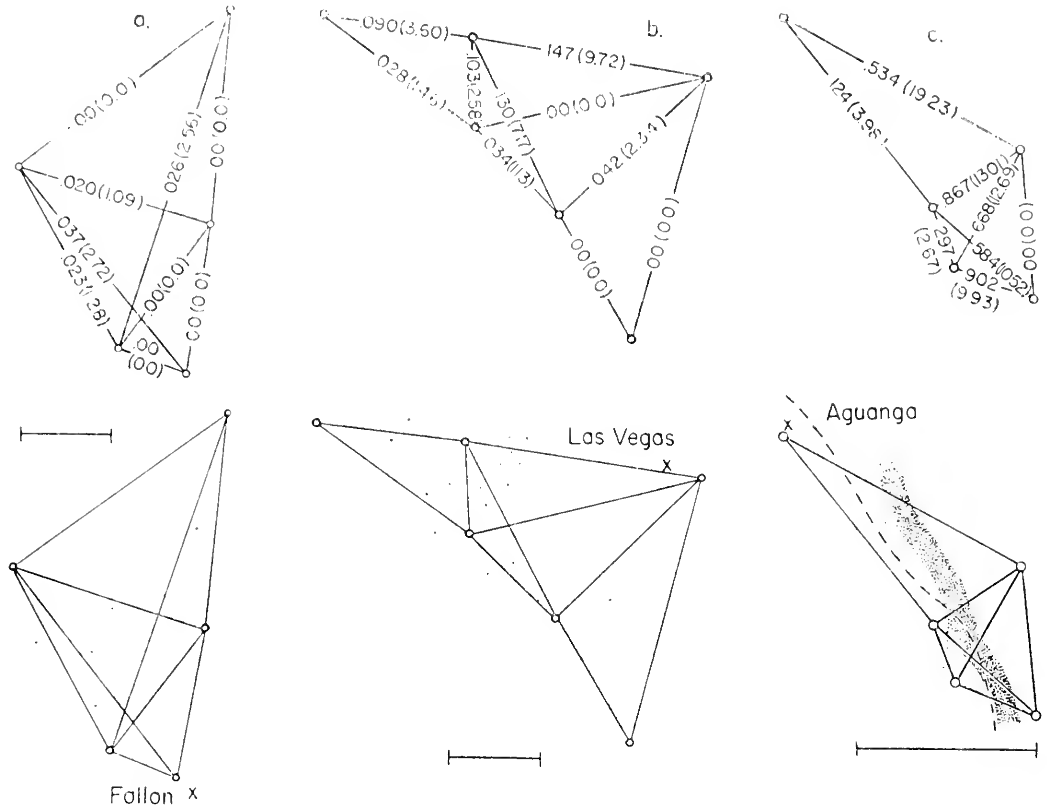

FIG. 2. Observed differentiation of *D. merriami* in a) northern Nevada, b) southern Nevada and adjacent Mojave desert of California, and c) small area in extreme southern California. For a more complete explanation of the figures and a key to stippling intensity, see the text and Figure 1.

ranging from essentially none to that judged to be at the species level. Figure 1 shows the boundary region between *D. merriami merriami* and *D. m. olivaceus* (nomenclature based on Lidicker, 1960) in southeastern Arizona and adjacent Mexico and New Mexico. Figure 2 illustrates areas in northern Nevada (a), southern Nevada and the adjacent eastern Mojave desert of California (b), and finally a small area in southern California at the boundary of *D. m. collinus* and *D. m. arenivagus* (c). Figure 3 represents the southern tip of the Baja California peninsula (a), and southern Sonora where the boundary between *D. m. merriami* and *D. m. mayensis* is found (b). The first of these (3a) is of particular interest as it shows the entire range of *D. m. melanurus* and the adjacent island populations of *D. m. margaritae* and the presumed allopatric species *D. insularis*. Notice that the key takes into account both *D* and Σd (but gives greatest weight to *D*) and is arranged so that increased intensity of stippling represents increased differentiation. Heavy dashed lines represent the locations of previously established subspecies boundaries, and double dashed lines previously established species boundaries (see Lidicker, 1960). Each drawing also indicates the location of one prominent town so that each chart can be placed geographically; all are oriented with north upward.

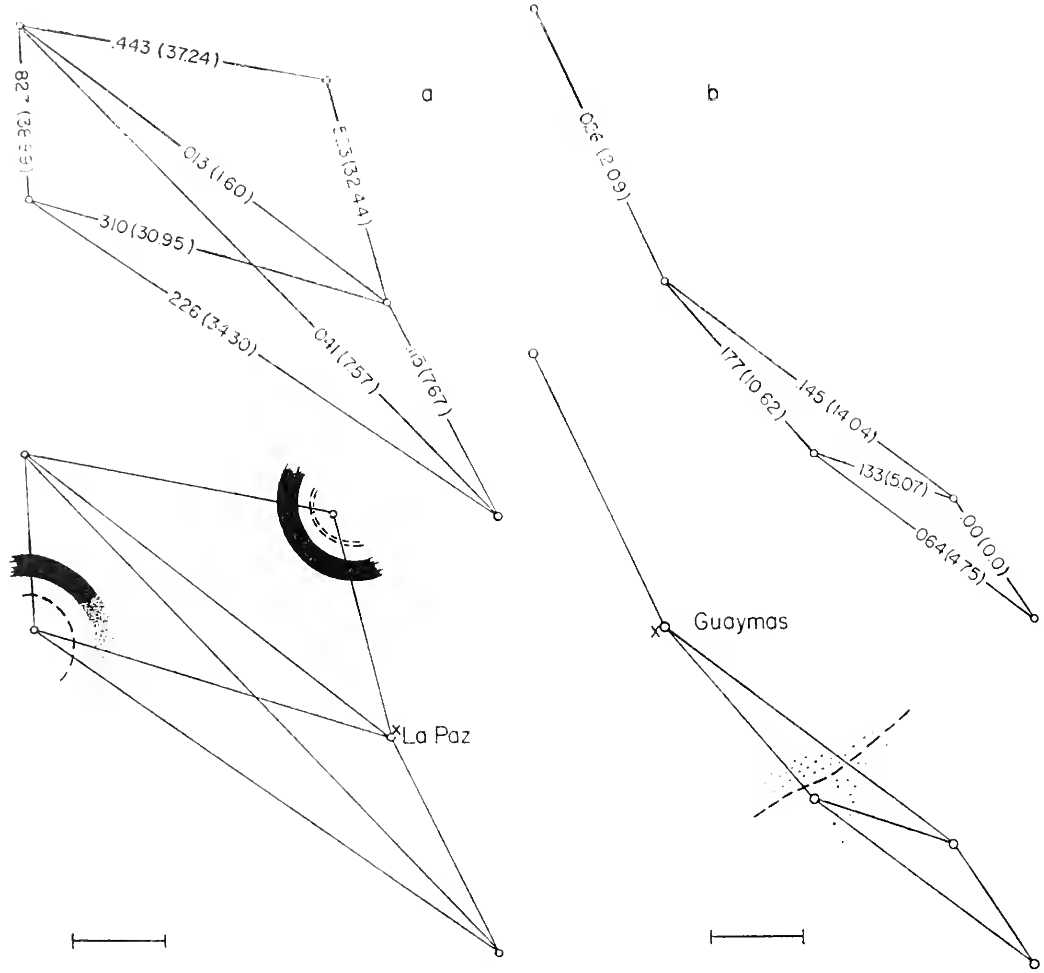

FIG. 3. Observed differentiation of *D. merriami* in a) southern Baja California, and b) southern Sonora. For a more complete explanation of the figures and a key to stippling intensity, see the text and Figure 1.

Discussion of the Method

The method described and its pictorial representation as shown in the figures gives us a geographically oriented summary of statistically significant differentiation in the characters studied. Its most important feature is that it takes into account the variability of each character as well as its magnitude, and concerns itself only with diversity which has a high probability of being real. Clearly, the more characters examined by the investigator, the greater will be his chance of discovering all of the existing differences between populations, and the better will be his estimate of genetic diversity. In the present case there is a remarkable correlation between the subspecies and species boundaries as previously described by the author and the bands of rapid character changes as defined by the Index of Differentiation.[2] It is clear that in this case subspecies boundaries uni-

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[2] No particular correlation is evident, however, with many of the taxonomic conclusions of previous authors.

formly appear as relatively narrow zones of high levels of differentiation or low levels of similarity, and, although it cannot be determined from the figures, these are usually, but not always, in areas of partial or complete isolation between populations. If the Index method truly describes genetic diversity, then our confidence is bolstered in the possibility of using the subspecies category for characterizing infraspecific lineages.

Besides the degree of differentiation, other suggested criteria for the recognition of such lineages include the following considerations: 1) the continuity of the zone of differentiation; 2) diversity of the two postulated adaptive peaks; 3) differences in the environments to which the adjacent populations are adapted, or consideration of the possibility that the two populations are adapted to the same environment in a different way; 4) geologic or paleontologic evidence of separate evolution. Moreover, it would seem to be a simple matter to devise modifications of the Index of Differentiation so as to incorporate discontinuous and qualitative characters. This would extend the usefulness of the method, not only to infraspecific populations which differ by such characters, but also to the species level. However, above the infraspecific level the problems of convergence, giving different weight to different characters (that is identifying primitive or generalized characters), and correlated characters (see especially discussions by Cain and Harrison, 1960) are aggravated. It might be added in passing, however, that these sources of error are not so great a problem as might be expected, because the proposed method emphasizes large numbers of characters and overall similarities. Under these circumstances a few convergent or pleiotropic traits would alter the results very little. Moreover, the problem of differentially weighting characters often leads into circular arguments as pointed out by Sneath (1961).

Although the proposed method incorporates a number of compromises with mathematical sophistication, I think that it is sufficiently accurate to be of considerable utility to the practicing taxonomist. Furthermore, several modifications are suggested for improving precision if this seems appropriate. The method will not of course make any decisions for the investigator, as it should not, but it will give him additional objective criteria on which to base his decisions. The fact that the conclusions suggested by the calculations and analysis of D's are similar if not identical to those proposed without the benefit of the method suggests that the method does not produce unreasonable results, and therefore must not suffer unduly from its lack of statistical elegance.

Discussion of Results

An obvious, but important, conclusion derived from a study of the figures is that statistically significant differences can be found between the vast majority of the population pairs. This serves to emphasize what is really intuitively obvious, namely that the ability to prove that two populations are statistically different in one or several characters is only a measure of the persistence and patience of the systematist. To base formal subspecific descriptions on this kind of evidence seems to me to be almost meaningless as well as a contribution to the degradation of the subspecies category to the extent of losing it as a legitimate member of the taxonomic hierarchy. Furthermore, this is precisely the philosophy which usually seems to nurture the widespread emphasis on naming with its often accompanying neglect of relationships, which has stimulated so much critical comment (see for example Wilson and Brown, 1953, and Gosline, 1954).

The description of differentiation provided in the figures carries the further implication that all levels of differentiation are found in *D. merriami*, and no obvious dividing line between subspecies and nonsubspecies, and species for that matter, is thereby indicated. The method thus gives us information regarding how different (or similar) populations are, but does not tell us which ones we should call subspecies. This finding is consistent with current concepts of intraspecific variation, and permits the systematist to decide what degree of relationship has phylogenetic significance for the particular organism involved, and finally what level, if any, he wants to recognize with formal subspecies descriptions. In the present example subspecific boundaries are found to be usually associated with continuous bands of differentiation characterized by *D*-values greater than 0.15.

The fact that this study has failed to reveal some biologically meaningful division marking the subspecies level does not mean of course that some such division will not be possible in the future. However, such a line of demarcation is obviously not a prerequisite to the success of the proposed method, which only concerns recognition of degrees of evolution. Nevertheless, one possible criterion for such a division which occurs to me is the relationship between the observed gene flow between two adjacent populations and that amount expected on the basis of the extent of physical contact existing between them. If the observed gene flow turned out to be less than that expected, or discriminating in terms of what genes were allowed to flow, this would serve as an indication that partially independent lineages were involved. This idea would not diminish in any way the obvious importance of geographical barriers in inhibiting gene flow, but merely suggests that some day it may be possible to ask the question—would a high level of differentiation persist between two geographically partially isolated populations if the barrier were reduced or eliminated? Or to put it in another way, how much reduction in the physical barrier between them can these two populations resist before gene flow becomes free flowing? This genetic concept of a subspecies argues that there are numerous infraspecific populations which by virtue of their past isolation (not necessarily complete) show some inhibition of gene flow between them and their neighbors, which would tend to slow down the dedifferentiation process. If the geographic isolation is current, the argument must be stated that such a reduction in gene flow would occur if they were not so isolated. This reasoning is merely a corollary of the fact that not all attempts by a species for isolation and differentiation result in species formation. There are a number of reasons why gene flow might be inhibited in such cases, and one of these is interdeme genetic homeostasis (Lerner, 1954). Other factors might be partial ecological or behavioral barriers to free interbreeding.

Although this suggestion for a biologically meaningful subspecies criterion is mainly speculative, it seems to me to be one possible direction that future developments in intraspecific analysis might take. The following definition of a subspecies is thus perhaps premature, but is offered because it is only a slight modification of widely used current definitions, but yet incorporates the concept outlined above; at the same time it does not commit one to any specific criteria for the recognition of subspecies. A subspecies is a relatively homogeneous and genetically distinct portion of a species which represents a separately evolving, or recently evolved, lineage with its own evolutionary tendencies, inhabits a definite geographical area, is usually at least partially isolated, and may intergrade gradually, although over a fairly narrow zone, with adjacent subspecies. This does not say that subspecies are "incipient species." It does say that subspecies are populations which have made initial steps in the direction of species formation, such that they might form species if suitable isolating conditions should develop, or they may be populations which have not reached the species level and are dedifferentiating. Obviously most subspecies will not become species, and likewise the process of dedifferentiation may become relatively stabilized through diverse selective pressures on either side of the intergrade zone.

It seems to me then that the Index of Differentiation or some similar device can give us an often needed additional criterion for judging relationship between populations. And it is these relative relationships that are of primary interest; and if used as guide lines to the recognition of subspecies will permit the legitimate retention of this category in the taxonomic hierarchy. Such an evolutionary philosophy applied to infraspecific analysis has a number of important advantages, not least of which is that it focuses attention on the speciation process and not on geographic variation *per se,* and thus emphasizes that the steps which can lead to species divergence must be initiated long before the process is actually completed. Other advantages not already alluded to include a consistency in applying the concept of relationship to all taxa and hence justifying to some extent the nomenclatorial equivalence of species and subspecies, provision of a more uniform goal for infraspecific systematists, and greater usefulness of subspecies to non-taxonomists because of the greater nomenclatorial stability and more reliable predictability of genetic differences in unstudied traits that would result.

There is little doubt that this approach will be considered impractical in some groups of organisms, but this seems of relatively little importance to the present discussion. Whereas a technique must be usable, no limits should be placed on the conceptualization of direction and significance of inquiry. I have confidence that systematists are not so unimaginative that appropriate procedures will not rapidly follow perception of important and necessary goals, as they have already done to some extent. Present day taxonomy is fraught with practicality, but is nevertheless shaken by criticism as to where it is all leading.

Summary

A growing dissatisfaction with much of what is now subspecies taxonomy and the associated indiscriminant use of the trinomen has caused many taxonomists to re-examine the basic tenets of intraspecific analysis. This "soul searching" has raised the important questions of whether or not it is possible or even desirable to use the subspecies category as a rankable taxon below the species level in the taxonomic hierarchy and at what level of dissimilarity, if any, formal trinomial nomenclature becomes appropriate. It is argued here that if the subspecies is to be preserved from degradation to the level of the rankless morphs, ecotypes, and forms, it must be based on degrees of relationship or evolutionary divergence. Moreover, the determinations of relative genetic relationships implies an emphasis on similarities between the various subpopulations comprising a species, as well as careful scrutiny of events occurring in the boundary regions between them. This paper is therefore concerned with characterizing some of these postulated boundary areas, as well as some areas of lesser and greater amounts of differentiation, in the kangaroo rat *Dipodomys merriami.*

To accomplish this, a method is outlined which serves to sum the observed statistically significant differentiation in many diverse characters between adjacent populations. In doing this, the method takes into account the variability and magnitude of each character. The estimate of total differentiation thus obtained can then be divided by the distance between the samples being compared to give the Index of Differentiation (*D*). The reciprocal of this statistic can also be taken as a measure of similarity. The Index of Differentiation can be further divided by the number of characters studied to give the mean character differentiation per mile (*MCD/mi.*). The system involves no complicated mathematical procedures, and yet contains only

minor compromises with statistical sophistication. Furthermore it is readily adapted to visual portrayal and analysis.

The results of this analysis demonstrate a very close agreement between levels of differentiation as determined by the Index of Differentiation and the taxonomic conclusions previously arrived at, when an attempt was made to base subspecies on the relative relationships among infraspecific populations. Under these conditions subspecies boundaries are uniformly characterized by a high level of differentiation which occurs over a relatively narrow zone, and is usually but not always associated with partial or complete isolation between populations. Moreover the analysis has emphasized the nearly ubiquitous occurrence of statistically significant differences between populations, and hence of the futility of basing formal subspecies on this kind of evidence. And finally a continuum of levels of differentiation was found, ranging from none at all to the species level.

It is concluded from this evidence that it is indeed possible to gather evidence on the relative relationships of the various portions of a species, and it is suggested that data of this sort should form the foundation for subspecific diagnosis. This approach tends to focus attention on the speciation process itself instead of on geographic variation *per se*. Various other advantages of this system are pointed out, and speculation is presented concerning the possible determination of a biologically meaningful division between subspecies and lesser categories.

Acknowledgments

I am greatly indebted to the following individuals who have critically read this manuscript, but who do not necessarily share the views which I have expressed: S. B. Benson, N. K. Johnson, O. P. Pearson, F. J. Sonleitner, and C. S. Thaeler. The figures were prepared by G. M. Christman of the Museum of Vertebrate Zoology.

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PROCEEDINGS
OF THE
BIOLOGICAL SOCIETY OF WASHINGTON

GENERIC NAMES OF THE FOUR-EYED POUCH OPOSSUM AND THE WOOLLY OPOSSUM (*Didelphidae*)

By Philip Hershkovitz

Published opinions on the status of *Philander* Tiedemann (Zoologie, vol. 1, p. 426, 1808) are not convincing for lack of evidence that the work cited had been carefully studied or even consulted. Tiedemann's system of classification is Linnaean with names for all hierarchies recognized (orders, families, genera, species) properly proposed and, for his time, adequately diagnosed. The following abstract from the "Zoologie" exposes the nature of the name *Philander.*

p. 426] Geschlecht 1.
Opossum. *Philander* (*Didelphys* L.)
(Sarigue)
[Generic description follows]

p. 427] [Description continued]
Es gibt gegen 10 bekannten Arten:
1) Das Virginische Opossum. P. virginianus (Did. opossum L.) (le sarique Buff. T. X. p. 279.)
Körper röthlich braun. Ueber jedem Auge ein gelblich weiser Flecken. Schwanz so lang als der Leib.
1 Fuss und 3 Zoll lang ohne den Schwanz.
In Virginien, Mexico, Peru u. s. w.
Schreb. tab. 146, A. B.
Edw. Tyson Carigueya seu marsupiale Americanum or the anatomy of an opossum. Philos. Transact. V. 1698. p. 105, V. 1704, p. 1576.
William Cowper an account of the anatomy of those parts of a male opossum that differ from the female. Ibid. V. 1704. p. 1576.
2) Das mausartige Opossum P. murinus (Did. murina L.) (la marmose Buff. T. X. p. 335.)

p. 428] [Specific description follows]
3) Das kurzgeschwänzte Opossum. P. brachyurus (Did. brachyuros Penn.) (le touan Cuvier Tabl. Element. d'hist. nat. p. 125.)

[Specific description follows]

The above three species are all that were included in the genus *Philander.* It is perfectly clear from the description and the references to Buffon, Linnaeus and Schreber, that the first species *P. virginianus* is merely a new name for the four-eyed pouch opossum, *Didelphis opossum* Linnaeus. The second species is a *Marmosa,* the third a *Monodelphis.* As *P. virginianus* is virtually tautonymic, it is here designated genotype of *Philander* Tiedemann. Designation of the woolly opossum, *Didelphis philander* Linnaeus, as genotype by Thomas (Catalogue of the Marsupialia and Monotremata in the collection of the British Museum, p. 336, 1888) is untenable. In reality, the *Philander* of Thomas and subsequent authors is the homonym *Philander* Burmeister 1856, with type *Didelphis philander* Linnaeus.

Arguments presented by Allen (Bull. Amer. Mus. Nat. Hist., vol .13, pp. 188-189, 1900) against usage of *Philander* Tiedemann stem from a misunderstanding of the original composition of the genus and are not relevant. Nevertheless, Allen's substitution of his own *Caluromys* (*D. philander* Linnaeus type) for *Philander* authors (not Tiedemann), is accidentally valid. Tate's (*Ibid.*, vol. 76, p. 164, 1939) rejection of *Philander* Tiedemann is based primarily on the misidentification of *P. virginianus* as a *Didelphis*, and secondarily on the ''homonymity'' with *Philander* Brisson, 1762. This last in spite of the fact that Tate (*op. cit.* p. 161) listed *Philander* Brisson as an unavailable synonym of *Metachirops* Matschie! With all due respect for Tate's doubtful endorsement, Brisson's system of classification is non-Linnaean and merits no consideration. Furthermore, it already has been shown by Hopwood (Proc. Zool. Soc. London, vol. 117, p. 533, 1947), that Brisson's generic names are pre-Linnaean and unavailable in any case. Hopwood (*op. cit.* p. 535) erred, however, in naming ''*Didelphys philander* Linnaeus'' the genotype of *Philander* Tiedemann. In addition, he disinterred *Philander* Gronovius, 1763, with the same genotype designated. Names by Gronovius are no better than those of Brisson and need not be revived at this late date (*cf.* Opinion 89, International Commission on Zoological Nomenclature).

To avoid the possibility of future confusion, disposition must be made of two other and unused generic names each with several species including those under discussion. Genotype of *Gamba* Liais (Climats, geol. faune et geogr. bot. Bresil, p. 329, 1872) is here designated *Gamba palmata* Liais (= *Chironectes minimus* Zimmermann); genotype of *Cuica* Liais (*loc. cit.*) is here designated *Cuica murina* Liais (= *Marmosa murina* Linnaeus).

Pertinent data presented are summarized in the following synonymies,

Genus *Philander* Tiedemann (Four-eyed pouch opossums).

Philander Tiedemann, Zoologie, vol. 1, p. 426, 1808 (genotype, *P[hilander] virginianus* Tiedemann = *Didelphis opossum* Linnaeus).

Metachirops Matschie, Sitz-ber. Gessellsch. naturforsch. Fr. Berlin, p. 268, 1916 (genotype, *Didelphis opossum* Linnaeus).

Holothylax Cabrera, Genera Mammalium, (Monotremata, Marsupialia), Mus. Nac. Cien. Nat., Madrid, p. 47, 1919 (genotype, *Didelphis opossum* Linnaeus).

Genus *Caluromys* Allen (Woolly opossums).

Philander Burmeister, Erläuterungen Fauna Brasiliens, p. 74, Berlin 1856 (genotype, *Philander cayopollin* Burmeister = *Didelphis philander* Linnaeus; homonym of *Philander* Tiedemann, 1808).

Caluromys Allen, Bull. Amer. Mus. Nat. Hist., vol. 13, p. 189, 1900 (genotype, *Didelphis philander* Linnaeus).

Micoureus Matschie, Sitz-ber. Gesellsch. naturforsch. Fr. Berlin, pp. 259, 269 (genotype, *Didelphis laniger* Desmarest = *D. lanata* Olfers; homonym of *Micoureus* Lesson, 1842).

Mallodelphys Thomas, Ann. Mag. Nat. Hist., ser. 9, vol. 5, p. 195, 1920 (substitute name for *Micoureus* Matschie).

REVIEWS OF RECENT LITERATURE.

ZOÖLOGY.

Two Important Papers on North-American Mammals. — The literature relating to recent work on North-American mammals is so scattered, and the results have been the outcome of investigations by such a number of different workers, and based on such varying amounts of material, that it is a great gain when a competent authority on any given group can go over it and coördinate the efforts of his predecessors in the light of, practically, all of their material, combined with a vast amount in addition. In other words, the monographic revision of any of the larger genera of North-American mammals by an expert is a distinct advance, for which all mammalogists may well feel grateful. It is with pleasure, therefore, that we call attention to two recent contributions of this character — Mr. Vernon Bailey's "Revision of American Voles of the Genus Microtus," and Mr. W. H. Osgood's "Revision of the Pocket Mice of the Genus Perognathus."

Mr. Bailey's revision[1] of the American voles, or meadow mice, is "based on a study of between five thousand and six thousand specimens from more than eight hundred localities, including types or topotypes of every recognized species with a known type locality, and also types or topotypes of most of the species placed in synonymy." With such material at command, and with a wide experience with the animals in life, and personal knowledge of the actual conditions of environment over a large part of the range of the group, Mr. Bailey has had peculiar advantages for his work, and his results are subject to revision only at points where material is still deficient, or from some other point of view. This revision, while obviously not final, presents a new starting point for future workers, and is likely to be a standard for many long years to come.

The little animals here treated are the short-tailed field mice,

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[1] Revision of American Voles of the Genus Microtus. By Vernon Bailey, Chief Field Naturalist, Division of Biological Survey, U. S. Department of Agriculture. Prepared under the direction of Dr. C. Hart Merriam, Chief of the Division. *North American Fauna*, No. 17, pp. 1–88, with 5 plates and 17 text-figures. Issued June 6, 1900.

familiarly typified by our common "meadow mice" of the Eastern States. The group is divisible into several well-marked subgenera, formerly generally known under the generic term "Arvicola," which has had to give way to the less known but older term "Microtus." The group is especially distinctive of the northern hemisphere north of the tropics, and is found throughout North America from the mountains of Guatemala and southern Mexico northward, increasing numerically, both in species and individuals, from the south northward till it reaches its greatest abundance in the middle and colder temperate zones, again declining thence northward to the Arctic coast. They are vegetable feeders, and often do considerable damage to trees and crops; they are active in the winter, forming long burrows or tunnels under the snow; they are also very prolific, breeding several times a year, young being found throughout the warmer months.

The seventy species and subspecies recognized by Mr. Bailey are arranged in nine subgenera; between the extreme forms the differences are strongly marked, but the intermediate forms present gradual stages of intergradation. The subgenus Neofiber, of Florida, embracing the round-tailed muskrat, and the subgenus Lagurus, of the semi-arid districts of the northwestern United States, present the most striking contrast, not only in size but in many other features. The former is perhaps the largest known vole, while the latter group includes the smallest.

Mr. Bailey's paper, being a synopsis rather than a monograph, leaves much to be desired in point of detail, but is admirable in its way, and covers the ground with as much fullness as his prescribed limits would permit. Of the twenty-six synonyms cited, it is noticeable that thirteen relate to our common eastern meadow mouse, and date from the early authors, while two other eastern species furnish three others, also of early date. Only six of the remaining ten are of recent date, showing that of some fifty-five forms described within the last ten years, by nine different authors, forty-eight meet with Mr. Bailey's approval. Four of the remaining seven are identified with earlier names which for many years have been considered indeterminable, but which Mr. Bailey claims to have established on the basis of topotypes.

While he may be correct in these determinations, it would have been of interest to his fellow-specialists if he had stated the basis of his determination of certain type localities, notably those of Richardson's species, described as from the "Rocky Mountains," or similarly vague localities. If he has some "inside history" to fall back upon, it is only fair that the secret should be made public.

It may be said further, in the way of gentle criticism, that it is hardly fair wholly to ignore such knotty points as the allocation of a few names which he omits, since they form part of the literature of the subject, as, for example, *Hypudæus ochrogaster* Wagner, *Arvicola noveboracensis* Richardson, and some of Rafinesque's names. Mr. Bailey describes as new two species and one subspecies.

Mr. Osgood's "Revision of the Pocket Mice"[1] is an equally welcome contribution, and has been prepared upon much the same lines, with equal advantages in the way of material and field experience. The pocket mice of the genus Perognathus are confined to a limited portion of North America, being found only west of the Mississippi, and ranging from the southern border of British Columbia south to the valley of Mexico. They are strictly nocturnal and live in burrows, are partial to arid regions and seem to thrive even in the most barren deserts. Their habits are hence not well known, as they are very shy and even difficult to trap. They are mouse-like in form, but only distantly related to the true rats and mice. Their most obvious character is the possession of cheek pouches which open externally.

The pocket mice vary greatly in size, form, and in the nature of their pelage, which may be either soft or hispid; but between the wide extremes there are so many closely connecting links that it is difficult to find any sharp lines of division, although two subgenera are fairly recognizable. The whole number of forms here recognized is 52 — 31 species and 21 additional subspecies, about equally divided between the subgenera Perognathus and Chætodipus. Of these, thirteen are here for the first time described. Out of a total of 61 specific and subspecific names applied to forms of this group, 9 are relegated to synonymy. Of these 61 names, it is interesting to note that 52 date from 1889 or later, and that of these, eight prove to be synonyms, three of them having become so through the identification of older names thought ten years ago to be indeterminable, but since reëstablished on the basis of topotypes.

A previous revision of this group was made in 1889 by Dr. C. Hart Merriam, on the basis of less than two hundred specimens —

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[1] Revision of the Pocket Mice of the Genus Perognathus. By Wilfred H. Osgood, Assistant Biologist, Biological Survey, U. S. Department of Agriculture. Prepared under the direction of Dr. C. Hart Merriam, Chief of Division of Biological Survey. *North American Fauna*, No. 18, pp. 1–72, Pls. I–IV, and 15 text-cuts. Issued Sept. 20, 1900.

all of the material then available — when the number of currently recognized forms was raised from six to twenty-one. Dr. Merriam's work, however, cleared the way for a better conception of the group, rectifying important errors of nomenclature and making known many new forms. Mr. Osgood, with fifteen times this amount of material, seems to have settled all of the remaining doubts regarding the application of certain early names, and, besides coördinating the work of his predecessors, has immensely extended our knowledge of the group. The paper is admirable from every point of view and does great credit to its author.

J. A. A.

No. 2. NORTH AMERICAN FAUNA. October, 1889.

DESCRIPTIONS OF TWO NEW SPECIES AND ONE NEW SUBSPECIES OF GRASSHOPPER MOUSE,

WITH A DIAGNOSIS OF THE GENUS ONYCHOMYS, AND A SYNOPSIS OF THE SPECIES AND SUBSPECIES.

By C. Hart Merriam, M. D.

A. DESCRIPTIONS OF NEW SPECIES AND SUBSPECIES.

ONYCHOMYS LONGIPES sp. nov.

(Texas Grasshopper Mouse.)

Type $\frac{3207}{3839}$ ♀ ad. Merriam Collection. Concho County, Texas, March 11, 1887. Collected by William Lloyd.

Measurements (taken in the flesh by collector).—Total length, 190^{mm}; tail, 48 [this measurement seems to be too short]; hind foot, 25; ear from crown, 13 (measured from dry skin).

General characters.—Size larger than that of the other known representatives of the genus, with larger and broader ears, and much longer hind feet. Ears less hairy than in *O. leucogaster*, with the lanuginous tuft at base less apparent; tail longer and more slender.

Color.—Above, mouse gray, sparingly mixed with black-tipped hairs, and with a narrow fulvous stripe along each side between the gray of the back and white of the belly, extending from the fore-legs to the root of the tail; under parts white.

Cranial characters.—Skull longer and narrower than that of *O. leucogaster* (particularly the rostral portion), with much longer nasals, and a distinct supraorbital "bead" running the full length of the frontals and there terminating abruptly. The nasals overreach the nasal branch of the premaxillaries about as far as in *leucogaster*. The incisive foramina, as in *O. leucogaster*, barely reach the anterior cusp of the first molar. The roof of the palate extends further behind the last molar than in *leucogaster*, and gives off a median blunt spine projecting into the pterygoid fossa. The palatal bones end anteriorly exactly on a line with the interspace between the first and second molars. The presphenoid is excavated laterally to such a degree that the middle portion is reduced to a narrow bar less than one-third the width of its base. The condylar ramus is lower and more nearly horizontal than in *leucogaster*, and the angular notch is deeper. The coronoid process resembles that of *leucogaster*.

ONYCHOMYS LONGICAUDUS sp. nov.

(LONG-TAILED GRASSHOPPER MOUSE.)

Type $\frac{5201}{5896}$ ♂ ad. St. George, Utah, January 4, 1889. Collected by Vernon Bailey.

Measurements (taken in the flesh by the collector).—Total length, 145; tail, 55; hind foot, 20; ear from crown, 10 (measured from dry skin).

General characters.—Similar to *O. leucogaster*, but smaller, with longer and slenderer tail. Pelage longer, but not so dense. General color above, cinnamon-fawn, well mixed with black-tipped hairs.

Cranial characters.—Skull smaller and narrower than that of *O. leucogaster;* zygomatic arches less spreading; nasals less projecting behind nasal branch of premaxillaries. The coronoid and condylar processes of the mandible are shorter, and the coronoid notch is not so deep as in *leucogaster*. The presphenoid shows little or no lateral excavation. The incisive foramina do not quite reach the plane of the anterior cusp of the first molar. The shelf of the palate projects posteriorly considerably beyond the molars, and terminates in a nearly straight line without trace of a median spine.

ONYCHOMYS LEUCOGASTER MELANOPHRYS subsp. nov.

(BLACK-EYED GRASSHOPPER MOUSE.)

Type, $\frac{5199}{5894}$ ♂ ad. Kanab, Utah, December 22, 1888. Collected by Vernon Bailey.

Measurements (taken in the flesh by collector).—Total length, 154; tail, 41; hind foot, 21. Ear from crown 10 (measured from the dry skin).

Size of *O. leucogaster*. Ear a little smaller. Hind foot densely furred to base of toes. Color above, rich tawny cinnamon, well mixed with black-tipped hairs on the back, and brightest on the sides; a distinct black ring round the eye, broadest above. This ring is considerably broader and more conspicuous than the very narrow ring of *leucogaster*.

Cranial characters.—Skull large and broad; very similar to *O. leucogaster* in size and proportions, but with zygomatic arches less spreading posteriorly, interparietal narrower, nasals not reaching quite so far beyond the nasal branch of premaxillaries, and antorbital slit narrower. Presphenoid moderately excavated, as in *leucogaster*. The incisive foramina reach past the plane of the first cusp of the anterior molar. The condylar ramus is longer and directed more obliquely upward than in *leucogaster*, with the coronoid and infra-condylar notches deeper.

NOTE.—In order to render the preceding diagnoses of new forms more useful, the following brief descriptions of the skulls of the two revious ly known species are appended for comparison, together with figures of the skull of the type of the genus (*O. leucogaster*):

Onychomys leucogaster Max.—Skull large and broad, with zygomatic arches spreading posteriorly. Antorbital slit larger than in the other known species. Palate hort, ending posteriorly in a short median spine (see figure).

Onychomys torridus Coues.—Skull small, narrow, with zygomatic arches not spreading, and vault of cranium more rounded than in any other member of the genus. Interparietal relatively large. Nasals projecting far beyond nasal branch of premaxillary. Incisive foramina very long, extending back to second cusp of first molar. Shelf of palate produced posteriorly nearly as far as in *longicaudus*, and truncated. Presphenoid slightly excavated laterally. Mandible much as in *longicaudus*, but with coronoid process more depressed and condylar ramus more slender.

B. DIAGNOSIS OF THE GENUS ONYCHOMYS.

The striking external differences which distinguish the Missouri Grasshopper Mouse from the other White-footed Mice of America (*Hesperomys* auct.) led its discoverer, Maximilian, to place it in the genus *Hypudæus* (=*Evotomys*, Coues), and led Baird to erect for its reception a separate section or subgenus, which he named *Onychomys*. Coues, the only recent monographer of the American Mice, treats *Onychomys* as a subgenus, and gives a lengthy description of its characters. Since, however, some of the statements contained in this description are erroneous, and the conclusions absurd,* and since the most important taxonomic characters are overlooked, it becomes necessary to redefine the type. A somewhat critical study of the cranial and dental characters of *Onychomys* in comparison with the other North American White-footed Mice has compelled me to raise it to full generic rank. It may be known by the following diagnosis:

Genus ONYCHOMYS Baird, 1857.

Baird, Mammals of North America, 1857, p. 457 (*subgenus*).

Type, *Hypudæus leucogaster*, Max. Wied, Reise in das innere Nord Amerika, II, 1841, 99–101 (from Fort Clark, Dakota).

Hesperomys auct.

First and second upper molars large and broad; third less than half the size of the second. First upper molar with two internal and three external cusps, the anterior cusp a trefoil when young, narrow, and on a line with the outside of the tooth, leaving a distinct step on the inside. Second upper molar with two internal and two external cusps, and a narrow antero-external fold. Last upper molar subcircular in outline, smaller than in *Hesperomys*, and less indented by the lateral notches.

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* Coues says: "Although unmistakably a true Murine, as shown by the cranial and other fundamental characters, it nevertheless deviates much from *Mus* and *Hesperomys*, and approaches the Arvicolines. Its affinities with *Evotomys* are really close." (Monographs of North American Rodentia, 1877, p. 106.) As a matter of fact, *Onychomys* has no affinities whatever with *Evotomys*, or any other member of the Arvicoline series, its departure from *Hesperomys* being in a widely different direction.

Lower molar series much broader than in *Hesperomys*. First lower molar with an anterior, two internal, and two external cusps, and a postero-internal loop. In *Hesperomys* the anterior cusp is divided, so that there are three distinct cusps on each side. Second lower molar with two internal and two external cusps, an antero-external and a postero-internal fold. Third lower molar scarcely longer than broad, subcircular in outline, with the large posterior lobe of *Hesperomys* reduced to a slight fold of enamel, which disappears with wear.

Coronoid process of mandible well developed, rising high above the condylar ramus and directed backward in the form of a large hook (see accompanying cut). Nasals wedge-shaped, terminating posteriorly considerably behind the end of the nasal branch of the premaxillaries.

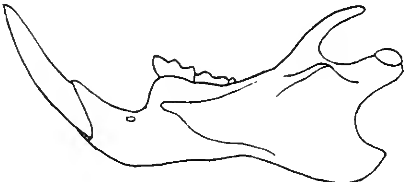

FIG. 1.

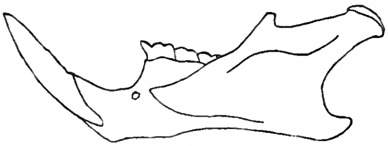

FIG. 2.

1. Lower jaw of *Onychomys leucogaster*. 2. Lower jaw of *Hesperomys leucopus*.

Body much stouter and heavier than in *Hesperomys*. Tail short, thick, and tapering to an obtuse point.

Fore feet larger than in *Hesperomys*; five-tuberculate, as usual in the Murine series. Hind feet four-tuberculate, and densely furred from heel to tubercles. Tubercles phalangeal, corresponding to the four anterior tubercles of *Hesperomys*, that is to say, the first is situated at the base of the first digit, the second at the base of the second digit, the third over the bases of the third and fourth digits together, the fourth at the base of the fifth digit. The fifth and sixth (or metatarsal) tubercles of *Hesperomys* are altogether wanting.

C. SYNOPSIS OF SPECIES AND SUBSPECIES.

(1) BY EXTERNAL CHARACTERS.

Length, about 150$^{\rm mm}$; tail, about 40; hind foot, about 21; ear from crown, 10. Color above, mouse-gray; black ring around eye inconspicuous .... *O. leucogaster.*

Size of *O. leucogaster*. Color above, rich tawny cinnamon, brightest on the sides; black ring round eye conspicuous .... *O. leucogaster melanophrys.*

Length, about 145$^{\rm mm}$; tail, about 55; hind foot, 20; ear from crown, 10. Color above, cinnamon fawn .... *O. longicaudus.*

Length, about 190$^{\rm mm}$; tail, about 50; hind foot, 25; ear from crown, 13. Color above, mouse-gray, with a narrow fulvous stripe along the sides...... *O. longipes.*

Length, about 135$^{\rm mm}$; tail, about 45; hind foot, 20; ear from crown, 10. Color above, uniform dull tawny cinnamon; no black ring around the eye. Tail thick with a dark stripe above reaching three-fourths its length; rest of tail white. *O. torridus.*

(2) By Cranial Characters.

- Palate ending posteriorly
  - with a blunt median spine
    - a distinct supraorbital bead .... *longipes.*
    - no distinct supraorbital bead .... *leucogaster.*
  - with straight or slightly convex edge
    - skull large and broad .... *melanophrys.*
    - skull smaller and narrower
      - incisive foramina barely reach plane of first molar .... *longicaudus.*
      - incisive foramina reach second cusp of first molar .... *torridus.*

Cranial measurements of the known forms of the genus Onychomys.

	O. leucogaster, Fort Buford, Dakota.		Melanophrys, Kanab, Utah.		Longipes, Concho County, Texas,
	4418 ♀	4419 ♂	5893 ♂	5894 ♂	3839 ♀
Basilar length of Hensel (from foramen magnum to incisor).	22	22	22.3	21.6	23.3
Zygomatic breadth	15	15.2	15.4	15.5	15.5
Greatest parietal breadth	12.9	12.7	12.8	12.5	12.2
Interorbital constriction	4.5	4.5	5.2	4.8	4.4
Length of nasals	10.8	11.6	10.7	10.7	12.5
Incisor to post-palatal notch	12	12	11.7	11.5	12.4
Foramen magnum to incisive foramina	14.7	14.6	15	14.5	15.7
Foramen magnum to palate	9.7	10	10.2	9.9	10.6
Length of upper molar series (on alveolæ)	4.5	4.2	4.6	4.8	4.4
Length of incisive foramina	5	5.7	5	5	5.3
Length of mandible	15.5	15.8	15.7	15.3	16
Height of coronoid process from angle	6.5	7.3	6.8	6.8	7.2
Ratios to basilar length:					
Zygomatic breadth	68.1	69	69	71.7	66.6
Parietal breadth	58.9	57.7	57.3	57	52
Nasals	49	52.7	47.9	49.5	52.3
Molar series (on alveolæ)	20.4	19	20.6	22	20
Incisive foramina	22.7	25.9	22.4	23.1	22.7
Foramen magnum to incisive foramen	66	66.3	67.3	67	67.3
Foramen magnum to palate	44	45.4	45.7	45.8	45.4

	Longicaudus, St. George, Utah.			Torridus, Grant County, N. Mex.
	5895 ♀	5896 ♂	5897 ♂	2839 ♂
Basilar length of Hensel (from foramen magnum to incisor)	19.3	19.3	19.4	18.5
Zygomatic breadth	13	13	13.1	12.5
Greatest parietal breadth	11.2	11.5	11.2	11.4
Interorbital constriction	4.7	4.7	4.8	4.2
Length of nasals	10	9.5	9.7	9.6
Incisor to post-palatal notch	10.5	10.5	10.4	10
Foramen magnum to incisive foramina	13.5	13.4	13.3	12.5
Foramen magnum to palate	8.8	8.7	8.7	8.5
Length of upper molar series (on alveolæ)	3.8	3.8	3.8	3.5
Length of incisive foramina	4.3	4.3	4.4	5
Length of mandible	13.4	13.5	13.2	13.2
Height of coronoid process from angle	6.2	6.3	6.2	5.8
Ratios to basilar length:				
Zygomatic breadth	67.3	67.3	68	67.5
Parietal breadth	58	59.5	57.7	61.6
Nasals	51.8	49.2	50	51.8
Molar series (on alveolæ)	19.6	19.6	19.5	18.9
Incisive foramina	22.2	22.2	22.6	27
Foramen magnum to incisive foramen	68.3	69.4	68.5	67.5
Foramen magnum to palate	45.5	45	44.8	45.8

PLATE I.

Figs. 1, 2, 3, 4, and 5, *Onychomys leucogaster*, ♂ young. (Skull No. 4422.) Fort Buford, Dakota.

1. Skull from above, and left under jaw from outside (× 2).
2. Crowns of left upper molars from below (× 10).
3. Crowns of left lower molars from above (× 10).
4. Crowns of right upper molars from the side (× 10).
5. Crowns of right lower molars from the side (× 10).

Figs. 6 and 7, *Onychomys leucogaster*, ♀ ad. (No. 5012). Valentine, Nebraska.

6. Crowns of left upper molars from below (× 10).
7. Crowns of left lower molars from above (× 10).

Figs. 8 and 9, *Onychomys longicaudus*, ♂ ad. (No. 5896). St. George, Utah.

8. Crowns of left upper molars from below (× 10).
9. Crowns of left lower molars from above (× 10).

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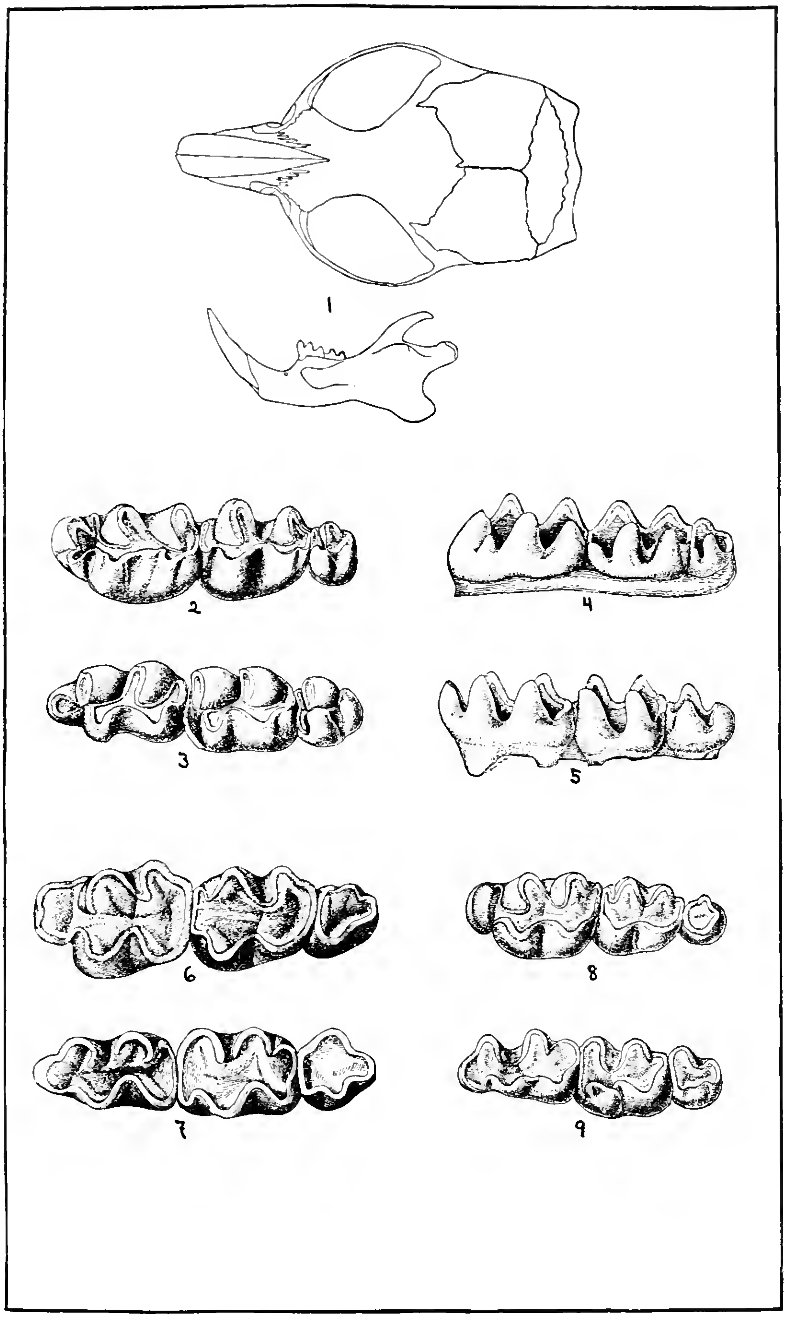

1-5. *Onychomys leucogaster*, ♂ young.
6, 7. *Onychomys leucogaster*, ♀ adult.
8, 9. *Onychomys longicaudus*, ♂ adult.

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PROCEEDINGS
OF THE
BIOLOGICAL SOCIETY OF WASHINGTON

DESCRIPTIONS OF NEW BATS (*CHOERONISCUS* AND *RHINOPHYLLA*) FROM COLOMBIA

BY CHARLES O. HANDLEY, JR.
U. S. National Museum, Washington, D. C.

An imperfectly known endemic mammalian fauna is found on the Pacific coast and Andean foothills of northwestern Ecuador and Colombia and northward into Panama, where it crosses to the Caribbean slope and continues into Costa Rica and Nicaragua and in some instances even into Mexico. The relatives of its endemic species are mostly South American, but some are Mexican. Species characteristic of this fauna, such as *Carollia castanea, Vampyressa nymphaea, Heteromys australis, Oryzomys bombycinus,* and *Hoplomys gymnurus,* were among the mammals collected in the course of virological studies of the Rockefeller Foundation on the Pacific coast of Colombia in 1962 and 1963. In addition there were striking new species of *Choeroniscus* and *Rhinophylla.*

I am grateful to Wilmot A. Thornton, Center for Zoonoses Research, University of Illinois, Urbana (formerly at Universidad del Valle, Cali, Colombia) for the opportunity to study the Colombian material here reported. Richard G. Van Gelder, American Museum of Natural History (AMNH); Philip Hershkovitz and J. C. Moore, Chicago Natural History Museum (CNHM); Bernardo Villa-R, Instituto de Biología, Mexico (IB); Barbara Lawrence, Museum of Comparative Zoology, Harvard University (MCZ); J. Knox Jones, Jr., Museum of Natural History, University of Kansas (KU); William H. Burt, Museum of Zoology, University of Michigan (UMMZ); A. Musso, Sociedad de Ciencias Naturales La Salle (LS); and Juhani Ojasti, Universidad Central de Venezuela (UCV) kindly permitted me to study comparative material. Specimens in the U. S. National Museum are designated by the abbreviation (USNM). Studies which led to the following descriptions were supported in part by National Science Foundation Grant G–19415.

All measurements are in millimeters. For definition of cranial measurements see Handley (1959: 98–99). Capitalized color terms are From Ridgway (1912).

CHOERONISCUS

There are few specimens of the poorly known glossophagine genus *Choeroniscus* in collections. The limits of variation in the genus are incompletely known (Sanborn, 1954), and until now its separation from *Choeronycteris* has been questionable. A specimen of a new species of *Choeroniscus* from the west coast of Colombia greatly extends knowledge of the genus and strengthens its stature as a genus distinct from *Choeronycteris.*

Choeroniscus periosus, new species

Holotype: USNM no. 344918, adult female, alcoholic and skull, collected 1 February 1963, by Wilmot A. Thornton, at the Río Raposo, near sea level, 27 km south of Buenaventura, Departamento de Valle, Colombia, original number 592.

Etymology: Greek *periosus*, immense.

Distribution: Known only from the type-locality.

Description: Body size large (forearm 41.2; greatest length of skull 30.3). Dorsal mass effect coloration (after three month's submersion in formalin) rich blackish-brown; basal three-fourths orange-brown in dorsal hairs; underparts but slightly paler than dorsum. Vibrissae abundant and conspicuous on snout and chin. Ears, chin, noseleaf, lips, membranes, legs, feet, and fingers blackish. Lancet of noseleaf relatively narrow, with three notches on each side near tip, and with prominent vertical median ridge on anterior face. Membranous "tongue-channel" on chin unusually well developed, protruding 1.5 mm forward and 2.0 mm up from lower lip; dorsal and anterior edges scalloped. Ear short, tip rounded, antitragus well defined; tragus spatulate, 3.8 mm long, with margins entire (except for prominent posterior notch opposite anterior base), and with anterior edge and posterior basal lobe thickened. Interfemoral membrane broad, naked. Hind legs naked. Calcar shorter than foot, not lobed.

Rostrum longer than braincase; cranium little elevated from basicranial plane; profiles of rostrum and cranium evenly tapered, without sharp angle in between; no orbital ridges or processes; zygoma absent; lambdoidal crest low; sagittal crest absent; maxillary toothrows subparallel; palate relatively broad anteriorly and narrow posteriorly; posterolateral margin of palate not notched; postpalatal extension parallel-sided, tubular, reaching posterior to level of mandibular fossae; mesopterygoid fossa reduced to a straight-sided, V-shaped notch; hamular processes greatly inflated and approaching, but not quite touching, auditory bullae; basial pits prominent, separated by broad median ridge.

Dentition weak. Dental formula $\frac{2}{0}, \frac{1}{1}, \frac{2}{3}, \frac{3}{3} = 30$. Upper incisors small, unicuspid; inner upper incisors (I^1) separated by a space three to four times the width of the teeth; larger, outer upper incisor (I^2) separated by somewhat less than its own width from I^1 and from canine.

Upper canine with small posterobasal cusp. Upper premolars very narrow; median cusp, particularly of anterior premolar, very little higher than well-defined anterior and posterior cusps. Upper molars with cusps greatly reduced; M^1 and M^2 similar in size and shape, M^3 slightly shorter and broader. Upper premolars widely spaced; molars closer together, but not touching. Lower premolars narrow, with well-defined, subequal anterior, posterior, and median cusps. Metaconid cusps of lower molars enlarged and protoconid cusps reduced; paraconid cusps in line with protoconids, not inflected. Anterior lower premolar close behind, but not touching, canine; spaces between premolars great, but spaces between P_4 and M_1 and between other molars, much less.

Measurements (All external dimensions taken from specimen in alcohol): Total length 62, tail vertebrae 10, hind foot 12, ear from notch 15, forearm 41.2, tibia 13.3, calcar 7.9.

Greatest length of skull 30.3, zygomatic breadth 11.0, postorbital breadth 4.7, braincase breadth 9.9, braincase depth 7.4, maxillary tooth row length 10.8, postpalatal length 7.0, palatal breadth at M^3 5.2, palatal breadth at canines 4.6.

Comparisons: *C. periosus* can be distinguished from all other species of *Choeroniscus* by its longer (longer than braincase), more robust rostrum; more inflated hamular process; and larger size (*e.g.*, forearm 41.2 *vs.* 32.4–36.9; greatest length of skull 30.3 *vs.* 19.3–24.4; maxillary tooth row 10.8 *vs.* 6.5–9.2). It is allied with the Amazonian species *C. minor*, *C. intermedius*, and *C. inca*, and distinguished from the Central American and northern South American *C. godmani*, in having the posterolateral margin of the palate unnotched and the cranium not so markedly elevated from the basicranial plane.

Remarks: With the addition of *C. periosus*, the genus *Choeroniscus* includes five nominal species. *C. periosus* is much the largest species; *C. inca* Thomas, *C. intermedius* Allen and Chapman, and *C. minor* Peters are intermediate in size; and *C. godmani* Thomas is smallest.

Choeroniscus is the most specialized of a group of nominal glossophagine genera which may be characterized briefly as follows:

Teeth nearly normal	pterygoids normal	*Lichonycteris*
Teeth slightly reduced	pterygoids?	*Scleronycteris*
Teeth reduced; PM high	pterygoids slightly specialized	*Hylonycteris*
Teeth reduced; PM high	pterygoids specialized	*Choeronycteris*
Teeth greatly reduced; PM low	pterygoids greatly specialized	*Choeroniscus*

Lichonycteris has 26 teeth and the other genera have 30.

As here understood, the genus *Choeronycteris* includes *Musonycteris harrisoni* Schaldach and McLaughlin, which is distinguished from *Choeronycteris mexicana* Tschudi principally by its strikingly elongated rostrum and associated modifications in proportions. The disparity in rostral proportions is much greater, however, between *Choeroniscus godmani* and *Choeroniscus periosus* than between *Choeronycteris mexicana* and *Choeronycteris harrisoni*. Thus, to distinguish *C. harrisoni* as representative of a separate genus tends to obscure relationships in this segment of the Glossophaginae. *Musonycteris* should be regarded as a synonym of *Choeronycteris*.

Specimens examined: *Choeroniscus godmani*. COLOMBIA: META: Restrepo, 1 (MCZ). COSTA RICA: Vicinity of San José, 3000 ft, 5 (AMNH). HONDURAS: Cantoral, 1 (AMNH); La Flor Archaga, 2 (AMNH). MEXICO: CHIAPAS: Pijijiapan, 50 m, 1 (UMMZ); GUERRERO: 1 mi. SE San Andrés de la Cruz, 700 m, 1 (UMMZ); OAXACA: 16 km ENE Piedra Blanca, 1 (IB); SINALOA: San Ignacio, 700 ft, 1 (KU). NICARAGUA: El Realejo, 1 (KU), 2 (USNM). VENEZUELA: BOLIVAR: 38 km S El Dorado, 1 (UCV); DISTRITO FEDERAL: Caracas (Santa Monica), 900 m, 1 (LS); Chichiriviche, 1 (UCV). *Choeroniscus inca*. BRITISH GUIANA: Kamakusa, 1 (AMNH); Kartabo, 1 (AMNH). ECUADOR: Los Pozos, 2 (AMNH). VENEZUELA: BOLIVAR: Chimantá-tepuí, 1300 ft, 9 (CNHM). *Choeroniscus intermedius*: TRINIDAD: Irois Forest, 1 (AMNH); Maracas, 1 (AMNH), Princestown, 1 (holotype of *C. intermedius*, AMNH); Sangre Grande, 1 (AMNH). *Choeroniscus minor*. BRAZIL: PARÁ: Belém, 3 (USNM). PERU: PASCO, San Juan, 900 ft, 1 (USNM); Puerto Melendez, above Marañon, 1 (AMNH). *Choeroniscus periosus*. COLOMBIA: VALLE: Río Raposo, 1 (holotype of *C. periosus*, USNM). Also, numerous specimens of *Lichonycteris*, *Hylonycteris*, and *Choeronycteris* (including *C. harrisoni*).

RHINOPHYLLA

The carolliinine genus *Rhinophylla* has until now been known only from the basin of the Rio Amazonas and the lowlands of northeastern South America (Husson, 1962: 152–153). The sole representative of the genus, *R. pumilio* Peters, has been regarded as closely related to, but more specialized than, the species of the abundant and widespread genus *Carollia* (Miller, 1907: 147). It is thus rather surprising to find in the collection of W. A. Thornton from the west coast of Colombia a number of specimens of a striking new species of *Rhinophylla* that is even more strongly differentiated from *Carollia* than is *R. pumilio*.

Rhinophylla alethina, new species

Holotype: USNM no. 324988, adult male, skin and skull, collected 13 July 1962, by Wilmot A. Thornton, at the Río Raposo, near sea level, 27 km south of Buenaventura, Departamento de Valle, Colombia, original number 172.

Etymology: Greek, *alethinos*, genuine.

Distribution: Known only from the type-locality.

Description: Size large for genus (forearm 34.9–37.2 mm). Coloration blackish, darkest anteriorly, paler posteriorly. In holotype, head and nape black, shading to Fuscous-Black on rump; underparts varying from black on chin to Fuscous-Black on chest and to Natal Brown on abdomen. Another specimen (Univ. del Valle 220) slightly paler: Fuscous-Black anteriorly and Natal Brown posteriorly on dorsum, and correspondingly paler on underparts. Hairs of dorsum and abdomen sharply tricolor: at mid-dorsum Slate-Black basally, with broad Benzo Brown median band; on sides, neck, and shoulders median band pales almost to Ecru-Drab and shows through to surface rather prominently. Noseleaf, lips, ears, tragis, fingers, forearms, legs, feet, and all membranes blackish. Fur soft, woolly; legs, feet, interfemoral membranes, and basal two-thirds of forearm hairy; interfemoral membrane fringed. Interfemoral membrane narrow (about 5 mm at base); calcar short (less than length of metatarsals); tibia and forearm stout; pinna with anterior margin convex, posterior margin concave, tip blunt, antitragus triangular; tragus usually blunt, with upper posterior margin entire or notched; lancet of noseleaf longer than broad, upper margins slightly concave; horseshoe of noseleaf with median half of base bound to lip; chin ornament composed of four parts—a central triangular element (apex down), a pair of narrow, elongated lateral elements converging ventrally but not meeting (their outer margin more or less scalloped), and a small, circular median ventral element.

Skull like that of *Rhinophylla pumilio* but rostrum slightly heavier (broader and deeper anteriorly), and a distinct low sagittal crest present.

Dentition, with the exception of inner incisors, extremely weak and reduced; formula $\frac{2}{2}-\frac{1}{1}-\frac{2}{2}-\frac{3}{3}=32$. Inner upper incisor ($I^1$) large, adz-shaped, with cutting edge entire; outer upper incisor (I^2) small, featureless. Canine simple, without cingulum or subsidiary cusps. Anterior upper premolar (P^1) small and featureless; posterior upper premolar (P^4) almost rectangular, longer than broad, with large median cusp and tiny posterior cusp. M^1 short and M^2 shorter, almost triangular in occlusal shape, each with a single prominent internal cusp (the metacone); protocone obliterated; paracone barely indicated in M^1, obliterated in M^2; parastyle and metastyle, particularly the latter, low and weakly developed; M^3 reduced to a tiny featureless spicule.

Inner lower incisors (I_1) large, trilobed (occasionally bilobed); I_2 small, unicuspid. Canine simple, without accessory cusps. Premolars simple, unicuspid; anterior premolar wider than any succeeding tooth. Molars very narrow, tricuspid; anterior and posterior cusps low on M_1 and M_2 and more or less obliterated on M_3.

Measurements (Extremes in parentheses, preceded by means and followed by number of individuals (only adults included). Measurements of the total length, ear, and weight were made by the collector in the field. All other measurements were made by me in the laboratory.): Total length ♂ 55, 58; hind foot ♀ 11 (11–11) 4, ♂ 11 (10–11) 6; ear from notch ♂ 15, 16; forearm ♀ 36.4 (35.5–37.2) 4, ♂ 35.7 (34.9–36.6) 4; tibia ♀ 12.3 (11.2–12.9) 4, ♂ 12.0 (11.5–12.5) 4; calcar ♀ 3.1 (3.0–3.5) 4, ♂ 3.4 (3.3–3.5) 5. Weight ♂ 12 gm, 16 gm.

Cranial measurements of male holotype: Greatest length of skull 19.5, zygomatic breadth 10.7+; postorbital breadth 5.3, braincase breadth 8.9, braincase depth 7.5, maxillary tooth row length 4.9, postpalatal length 7.2, palatal breadth at M^2 6.4, palatal breadth at canines 5.1.

Comparisons: Specimens of *R. alethina* are slightly larger than specimens of *R. pumilio* from the valley of the Rio Amazonas; have the interfemoral membrane narrower; calcar shorter; hind legs stouter; legs, feet, and interfemoral membrane (including posterior margin) more hairy; fur more woolly in texture; and coloration, including that of lips, ears, and membranes, darker, more blackish. As noted in the description, the skulls of the two species are very similar. However, except for the inner incisors, the teeth of *R. alethina* are smaller and weaker, and the tooth rows are shorter than in *R. pumilio*. *R. alethina* has cutting edges of I^1 and I_2 entire rather than notched; P^4 shorter; cusps of upper molars more reduced; and I_2, P^1, M^3, and lower molars notably smaller.

Aside from its relative *R. pumilio, R. alethina* is likely to be confused only with the Glossophaginae and with *Carollia castanea.* Its non-extensible tongue and lack of rostral elongation are sufficient to distinguish it from the Glossophaginae. From *Carollia castanea* it can be distinguished easily by its blacker coloration, narrow, fringed interfemoral membrane, hairy legs, simple chin ornament, and smaller, simplified teeth. In most of these characteristics *R. alethina* differs more from the species of *Carollia* than *R. pumilio* does.

Specimens examined: *Rhinophylla alethina.* COLOMBIA: VALLE Río Raposo, 11 (including the holotype, USNM), 1 (Univ. del Valle). *Rhinophylla pumilio.* BRAZIL: PARÁ: Belém, 52 (USNM). ECUADOR: Boca de Río Curaray, 2 (USNM). PERU: PASCO: San Juan, 900 ft, 4 (USNM).

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THE STATUS OF REITHRODONTOMYS MONTANUS (BAIRD)

By Seth B. Benson

The status and relationships of *Reithrodontomys montanus* have been uncertain ever since this harvest mouse was named and described by Baird in 1855. Study of the type specimen, and of specimens collected in the type locality of *R. montanus*, has revealed that all the specimens, except the type itself, are examples of the species *Reithrodontomys megalotis* (Baird). Confusion has arisen because these specimens have been mistakenly referred to *R. montanus*.

The nomenclatural history is as follows. Baird (1855, p. 355) described *Reithrodon montanus* on the basis of a single specimen collected by a Mr. Kreutzfeldt [= J. Creutzfeldt, botanist of Gunnison's expedition] at "Rocky Mountains, Lat. 38°." Later, Baird (1857, p. 450) gave the locality as "Rocky Mountains, 39°." Coues (1874, p. 186) listed *Ochetodon montanus* as a questionable species. This he also did later (1877, p. 130), stating "The single specimen is too imperfect to permit of final characterization, or to enable us to come to any positive conclusion; but if the size and coloration it presents are really permanent, we should judge it entitled to recognition as a valid species. At present, however, we regard it with suspicion and are unwilling to endorse its validity."

This remained the status of the name until Allen (1893, p. 80), after examining the type specimen, stated "I have therefore no hesitation in recognizing *Reithrodontomys montanus* (Baird) as a well-marked, valid species, which will probably be found to range from the eastern base of the Rocky Mountains eastward to middle Kansas."

When Allen (1895) revised the harvest mice the type of *montanus* was still unique. In his treatment of the species (pp. 123–125) he determined the type locality to be the upper part of the San Luis Valley in Colorado. He stated that "Until this region has been thoroughly explored for 'topotypes' of *R. montanus*, it would be obviously improper to reject this species as unidentifiable or to give the name precedence over *R. megalotis* for the form here recognized under that name."

At this time the species currently recognized as *albescens* was not known, although Allen actually had specimens which he confused with the form now known as *R. megalotis dychei* (see Howell, 1914, p. 31). Subsequently Cary (1903, p. 53) described *Reithrodontomys albescens* from Nebraska, stating that the species required "no close comparison with any described *Reithrodontomys*." Bailey (1905, p. 106) described *Reithrodontomys griseus* from Texas, and remarked that it probably graded into *albescens*.

In 1907 Cary visited Medano Springs Ranch in search of topotypes of *R. montanus*. He collected twenty specimens, most of them immature, which he identified as *montanus*. Cary (1911, pp. 108–110), following a manuscript of A. H. Howell, regarded *R. montanus* as a species related to *R. albescens* and *R. griseus*. He placed *albescens* as a subspecies of *montanus*.

When Howell (1914) revised the harvest mice, the specimens from the type locality of *montanus* consisted of the type specimen and the specimens collected by Cary at Medano Springs Ranch. In this revision Howell altered his earlier opinions concerning the relationships of *montanus*. He wrote (p. 26) "The species, although combining in a remarkable degree the characters of the *megalotis* and *albescens* groups, seems not to be directly connected with either of them. It is perhaps best placed in the *megalotis* group, but seems not to intergrade with any member of it." He pointed out that the relationships of the species were yet not clear, since the type specimen did not agree with any of the "topotypes" collected by Cary, but instead resembled specimens of *R. a. griseus* from Texas. Because the color of the "topotypes" agreed with the original description of *montanus*, he decided to "consider the type skull aberrant, and to continue to use the name for the form represented by the modern series." It might be mentioned here that no specimens of the *albescens* group have as yet been taken near the type locality of *montanus*.

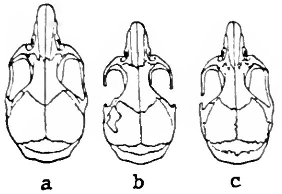

Fig. 1. Drawings Made from Photographs of Skulls of Harvest Mice. Natural Size

a. Reithrodontomys megalotis subsp., no. 61120, Mus. Vert. Zool., from Medano Ranch, 15 miles northeast of Mosca, Alamosa County, Colorado.

b. Reithrodontomys montanus montanus, type specimen, no. 1036/441, U. S. Nat. Mus., from upper end of San Luis Valley, Colorado.

c. Reithrodontomys montanus griseus, no. 58737, Mus. Vert. Zool., from 3 miles north of Socorro, Socorro County, New Mexico.

In 1933, Miss Annie M. Alexander and Miss Louise Kellogg collected harvest mice from several localities in Colorado and New Mexico including the type localities of *R. megalotis aztecus* and *R. montanus*. Two of the three specimens from the Medano Ranch, 15 miles northeast of Mosca, Alamosa County, Colorado, were adults similar to adult topotypes of *aztecus*. The third, a young individual, was so much smaller that at first I judged it was of a different species. I suspected then that Howell's treatment of *montanus* was the result of confusing two distinct species, one a small form like *albescens*, the other a larger one like *megalotis*. The occurrence of two species at this locality seemed possible, since *albescens* occurs with *dychei* in Nebraska, *griseus* is known to occur with *dychei* in Kansas, and in 1933 I collected *megalotis* and *griseus* together in the bottom-land of the Rio Grande, three miles north of Socorro, New Mexico, which is in the same drainage system as San Luis Valley.

At my request the Bureau of Biological Survey loaned me 16 of the specimens collected by Cary at Medano Ranch. Only one of these was fully adult (the one whose skull is figured as *montanus* in Howell's revision). Among the younger specimens were some which matched the smallest of the three specimens collected by Miss Alexander and Miss Kellogg, and the rest formed a series approaching the largest specimens. The adult specimen collected by Cary is smaller than the other two adults, yet is similar to them in most characters. It was obvious that all belonged to a single species. I concluded that all the Medano Ranch specimens I had examined were of the species currently known as *megalotis*. It was also obvious that if the type of *montanus* were conspecific with the other San Luis Valley specimens, *megalotis* would become a synonym of *montanus*, since *montanus* has priority.

Through the courtesy of Dr. Remington Kellogg and others in charge of the collection of mammals in the United States National Museum, I was granted the loan of the type specimens of *R. megalotis* and *R. montanus*. After studying these specimens I reached the following conclusions: (1) The Medano Ranch specimens are conspecific with the type of *megalotis*; (2) the type specimen of *montanus* is specifically distinct from *megalotis*, and is conspecific with *albescens* and *griseus*. Some characters in which the type of *montanus* and specimens of *griseus* (MVZ no. 41192, from Hemphill Co., Texas; no. 56220, from 44 miles northwest of Roswell, N. M.; and no. 58737, from 3 miles north of Socorro, N. M.) differ from *megalotis* are: smaller size; shorter, more depressed rostrum; narrower interorbital space; relatively shorter brain case.

As a result, *megalotis* is not a synonym of *montanus*, and *montanus* becomes the specific name for the species currently known as *albescens*. Until additional specimens of *montanus* from San Luis Valley are available to allow a more thorough appraisal of its characters, it seems best to regard *albescens* and *griseus* as valid races of *montanus*, although it is quite likely that *griseus* may become a synonym of *montanus*. The three races here recognized are:

Reithrodontomys montanus montanus (Baird)
Reithrodontomys montanus albescens Cary
Reithrodontomys montanus griseus Bailey.

It may be well to remark here that all the available information indicates that the species *R. montanus* is rarely abundant and that it prefers more arid, sandier ground than does its relative *R. megalotis*, although both species may be found together.

The racial identity of the San Luis Valley *megalotis* has also presented some problems. At first I referred them to the race *aztecus* because some of them fell within the range of variation present in specimens from within the distributional area assigned to *aztecus* in Howell's revision. In addition, there was so much variation in size in the few adults available to me that I felt it was possible they did not truly represent the population, and so could not serve as a satisfactory basis for the description of a new race. However, Mr. Howell, who has restudied the problem with the aid of a greater amount of material than was available to me, has concluded that the San Luis Valley *megalotis* represent an unnamed race. He will describe this race in another article.

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A REVISION OF THE WOOD RAT *NEOTOMA STEPHENSI*

By Donald F. Hoffmeister and Luis de la Torre

Within the last few years, some field guides to mammals of the United States have appeared which do not include the wood rat *Neotoma stephensi.* The implication is that *Neotoma stephensi* is not a valid species. Some specific characters of *Neotoma stephensi* were enumerated in the original description by Goldman in 1905, and its specific distinctness (from *Neotoma lepida*) was reaffirmed by Goldman in 1932. Because of the previous confusion of *Neotoma stephensi* with *Neotoma lepida,* and even the subsequent confusion of the two species following Goldman's review (Jour. Mamm., 13: 59–67, 1932), it is somewhat understandable that some authors might question the validity of *stephensi.* Even the recently published work by Hall and Kelson (The Mammals of North America, 2: 690, 1959) fails to show the coexistence of *N. lepida* and *N. stephensi* in parts of their range, a fact which lends additional evidence for the distinctness of the two species. With more adequate material, and using Goldman's work as a starting point, we have attempted to define more clearly the species *N. stephensi.*

Many persons have made available, for study, specimens of *Neotoma stephensi* in their collections. We should especially like to thank Richard G. Van Gelder, Stanley P. Young, Viola Schantz, Laurence Huey, Seth B. Benson, William Z. Lidicker, and William H. Burt. Specimens from the following collections have been examined (the abbreviations in parentheses are used under *Specimens examined*): American Museum of Natural History (AM); United States Biological Survey (BS); Grand Canyon National Park Museum (GC); San Diego Society of Natural History (SD); University of California, Museum of Vertebrate Zoology (UC); University of Illinois, Museum of Natural History (UI); University of Michigan, Museum of Zoology (UM). Capitalized color terms are from Ridgway (Color Standards and Color Nomenclature, 1912). All measurements are in millimeters. Under *Additional records* we have included localities from which the species is known but from which we have not examined specimens. The Graduate College of the University of Illinois has financially aided us in this study. Illustrations were prepared by Alice A. Boatright and Harry C. Henriksen of the University of Illinois.

GENERAL CHARACTERS OF THE SPECIES

Obvious characters of *Neotoma stephensi,* which in part are diagnostic, are the presence of a semi-bushy tail (bushier than in all species except *N. cinerea*) in a medium- to small-sized *Neotoma*; dusky coloration extending down the top of the foot one-fourth to one-third the distance below the ankle; skull resembling *N. lepida.* A closer study indicates the following characters are diagnostic:

Baculum.—Exclamation-mark-shaped or wedge-shaped (Fig. 1); small, being one-fifth or less than the length of the baculum in *N. lepida*; smaller than in any species of *Neotoma* found in the United States; similar in size and shape to that of *Neotoma phenax,* except not indented along sides and thus not "violin-shaped." When everted from the prepuce, the distinctively small size of the baculum in *N. stephensi* is clearly noticeable, and in contrast to the condition in *Neotoma lepida, N. albigula,* and *N. mexicana.* In one specimen of *N. s. relicta,* the baculum is identical to that in *N. s. stephensi.*

Skull.—Teeth: The pattern of M^3 together with features of M^1 serves to distinguish *N. stephensi* in most cases. In M^1, the antero-medial fold is usually absent or, if present, is shallow, approaching *albigula,* never deeply re-entrant as in *mexicana.* In M^3, the postero-labial fold (Fig. 1) is directed postero-medially and "terminates" posterior to the lingual fold. In *N. lepida,* the postero-labial fold (Fig. 1) is directed medially and less posteriorly, nearly meeting the lingual fold. In M^3 of *stephensi,* the second loph is usually long and narrow, extending diagonally across the tooth (Fig. 1). In this regard, it is similar to *N. mexicana* and *N. albigula,* but differs from *N. lepida* in which the second loph is usually broad labially and nearly at right angles to the long axis of the toothrow (Fig. 2).

In *N. stephensi,* the lingual fold of M_3 is as deep as or deeper than the labial fold (Fig. 2), whereas in *N. lepida* and *N. albigula,* the lingual fold is shorter than the labial fold. In *N. mexicana,* both conditions seem to occur.

Rostrum: The rostrum is narrower than in any other species within the range of *N. stephensi* (Fig. 3). Generally, the nasals in *stephensi* are truncate posteriorly, rarely sharply pointed as is common in *lepida* and *albigula* (Fig. 3). The posterior extensions of the premaxillaries seldom expand posteriorly as in *albigula,* but are more as in *mexicana* except that they are longer.

Interorbital region: The region between the orbits is broader and less depressed than in either *lepida, albigula,* or *mexicana.* In some instances, it is difficult to distinguish between *stephensi* and *lepida* on the basis of this character. The supraorbital ridges in *stephensi* tend to remain lateral as they continue forward toward the rostrum, whereas in the other species these ridges approach the midline, ending almost in line with the posterior extensions of the premaxillaries (Fig. 3).

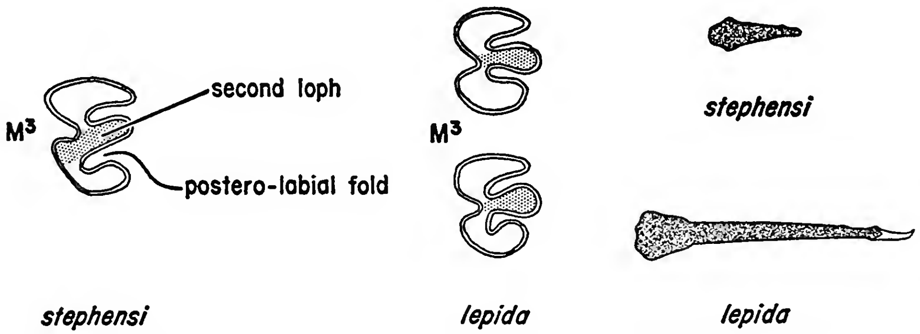

Fig. 1.—Third upper molar (×6.5) and baculum (×2.4) of *Neotoma stephensi* and *Neotoma lepida.*

Of perhaps lesser diagnostic significance when compared with *N. lepida* are the following skull characters: upper incisors strongly recurved; tubercle on outer face of mandible at base of lower incisor hardly noticeable, whereas more nearly knoblike in *lepida*.

External features.—The bushiness of the tail, particularly the terminal third, approaches that of *Neotoma cinerea.* The tail is far more bushy than in any other species within the range of *stephensi,* and probably exceeds that of any wood rat except *cinerea.* In young *stephensi,* only a few weeks old, the tail already is bushy, and specific recognition is possible on this character.

On the hind foot, a wedge of dusky-colored hair may extend onto the dorsal surface as much as one-third the distance to the base of the toes. In most specimens of *N. lepida,* particularly in those races which are not melanistic, the dorsal surface of the foot is whitish, with the dusky color stopping at the tarsal region.

The underparts are suffused with an ochraceous or buffy wash in nearly all specimens. In *N. stephensi stephensi* the throat region also shows this same wash, but the region between the forelegs is whitish. In *N. stephensi relicta,* the wash does not extend onto the throat and thus it is usually white. The coloration of the underparts in *N. s. stephensi* is similar to that in most specimens of the dark races of *N. lepida,* such as *monstrabilis* and *harteri,* and is thus noticeably different than in the light-colored races of the latter species. Where *N. lepida* occurs within the range of *N. stephensi,* nearly all specimens of *lepida* have light-colored underparts and thus this character aids in distinguishing the two.

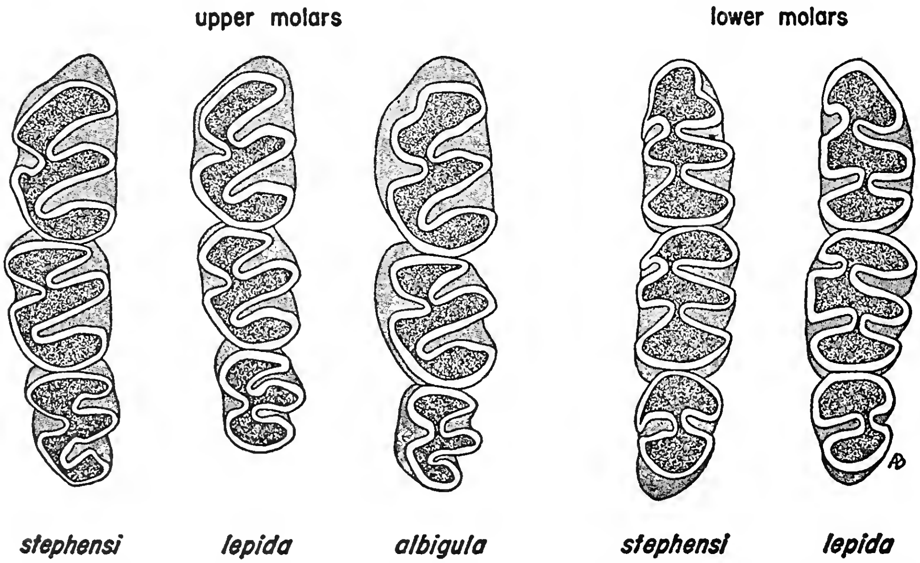

FIG. 2.—Occlusal view of right upper molars of *Neotoma stephensi, N. lepida, N. albigula,* and left lower molars of *N. stephensi* and *N. lepida* (×6.5).

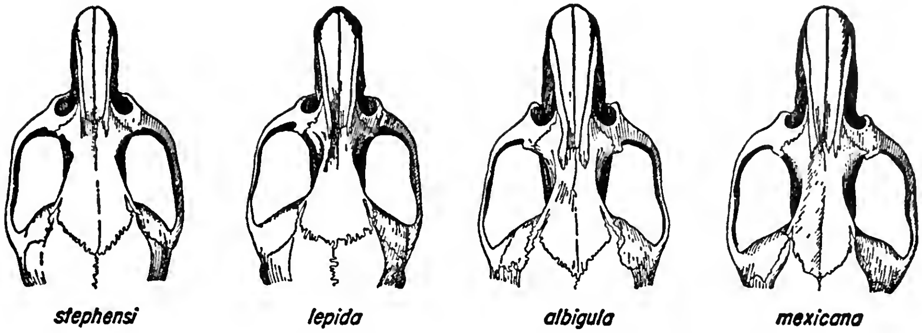

FIG. 3.—Dorsal view of anterior part of skull of *Neotoma stephensi, N. lepida, N. albigula,* and *N. mexicana* (×1).

VARIATION

Age.—In *N. stephensi,* we can recognize four groups which include young animals, old animals, and two categories between these extremes. These groups are based on the degree of eruption and wear of the upper molar teeth. We attempted to corroborate this grouping by the use of other characters, such as closure of sutures, size and proportion of various parts of the skull, and molt, but these proved to be of little help. Further discussion of the younger groups is given under *Growth and Reproduction.*

GROUP 1. Immatures; M^3 not erupted or in the process of erupting and occlusal surface of posterior loph isolated from that of more anterior lophs.

GROUP 2. Young adults; females, at least, sexually mature. Folds of M^1, as seen laterally, continuing down below alveolus; M^3 fully erupted and occlusal pattern usually complete with posterior loph rarely isolated.

GROUP 3. Adults; folds of M^1 not extending to alveolus, but to or below an arbitrary midpoint between alveolus and occlusal surface.

GROUP 4. Old adults; folds of M^1 very short and not reaching midpoint between occlusal surface and alveolus. Folds may be entirely absent.

Sexual.—Although there is a size difference between males and females, it is less marked in certain age groups. From our sample, we find that in Groups 1 and 2, the sexual difference is slight. In Group 3, males usually average larger than females in most measurements. For example, in specimens from the Hualpai Mountains (6♂♂, 10♀♀), the Grand Canyon (4♂♂, 4♀♀), and Wupatki (4♂♂, 4♀♀), the males are larger than the females by percentages ranging from 1 to 13 in *most* measurements. In all three localities, however, the females average larger than the males in length of maxillary toothrow as follows: Hualpai Mountains, 2.3; Grand Canyon, 1.2; Wupatki, 1.2 per cent. The larger average size of the toothrow in females is also indicated in specimens from other localities. Group 4 is represented by too few individuals to determine sexual differences. Aside from the quantitative differences pointed out, the skull of adult females is characteristically short and broad, in contrast to the long and narrower skull of the males.

No sexual difference in color was apparent.

Color.—The color of an "average" specimen consists of a light buff wash extending from the chest to the inguinal region. The chest is white, with the throat a buffy color with the hair plumbeous basally and buffy-tipped. The white of the chest may extend anteriorly to the chin as a median narrow stripe. The inguinal area is whitish.

The coloration of the underparts, including the buffy wash, throat, and chest color, in any one population, may be highly variable. For example, near Montezuma Well, Yavapai County, Arizona, one specimen has 98 per cent of the underparts heavily washed with a dark buff, one has little or no buff, and one has no white on the chest and throat. Still other specimens from here show varying stages of intermediacy. In other populations, individuals can be found that have the throat entirely white, with the basal portions of the hairs not plumbeous or gray-colored. The whitish throat is "typical" of another, unrelated species—*albigula.* Such occurrences of "white-throatedness" are widely scattered throughout the range of the species, being found in populations from the Hualpai Mountains in the northwest to the Burro Mountains in the southeast.

The extreme of this white-throatedness is found in *N. stephensi relicta.* In this race, nearly all individuals, and probably every adult, have white throats. Within the race *stephensi,* certain populations have most of the adults with white throats. This is true for the populations at Hilltop, west end of Grand Canyon National Park, but is not true for other populations within the Park or for most specimens from the Hualpais. The population from the Burro Mountains, New Mexico, has all of the specimens white-throated. In general, specimens with the entire throat region white have the buffy wash over the abdominal region greatly reduced or entirely lacking. Thus most specimens of *relicta* and specimens of *stephensi* from Hilltop and the Burro Mountains lack the buffy wash.

Variation of the dorsal coloration within a population is less easily observed. The geographical variation of this color, within subspecies, is discussed beyond and illustrated in Plate I.

GROWTH AND REPRODUCTION

In the absence of growth data for *N. stephensi,* we have been guided by previous work in other species of *Neotoma,* especially in *N. albigula* from Arizona (Richardson, Jour. Mamm., 24: 134, 1943). Although two species may well differ markedly in their rate of growth and reproductive patterns due to different heredity and different environmental conditions, we have used the *N. albigula* information to put forth tentative conclusions, leaving it to future work to prove or disprove the validity of our interpretations. We have, thus, assumed that the progress of growth is essentially the same in *N. albigula* from Arizona as it is in *N. stephensi* from that area, and that the gestation period in *N. stephensi* is, as in other species, approximately 30 days in length. From the growth curve of head and body size in *N. albigula* (Richardson, *op. cit.*), approximate ages and thus dates of birth were calculated for our sample of immature specimens (Group 1) of *N. stephensi.* Table 1 indicates the chronological distribution of Group 1 and Group 2 specimens studied, and the dates of capture of pregnant and lactating females.

The near disappearance of Group 1 individuals following the middle of August, and the clear increase of Group 2 animals from this time on, strongly suggest that Group 2 is a composite group. Group 2 specimens taken in June, July and August most likely are young born late in the preceding year, that is, in August, September and October. Specimens taken in September and October, however, probably represent young of the year, born in the early months following the earliest breeding period.

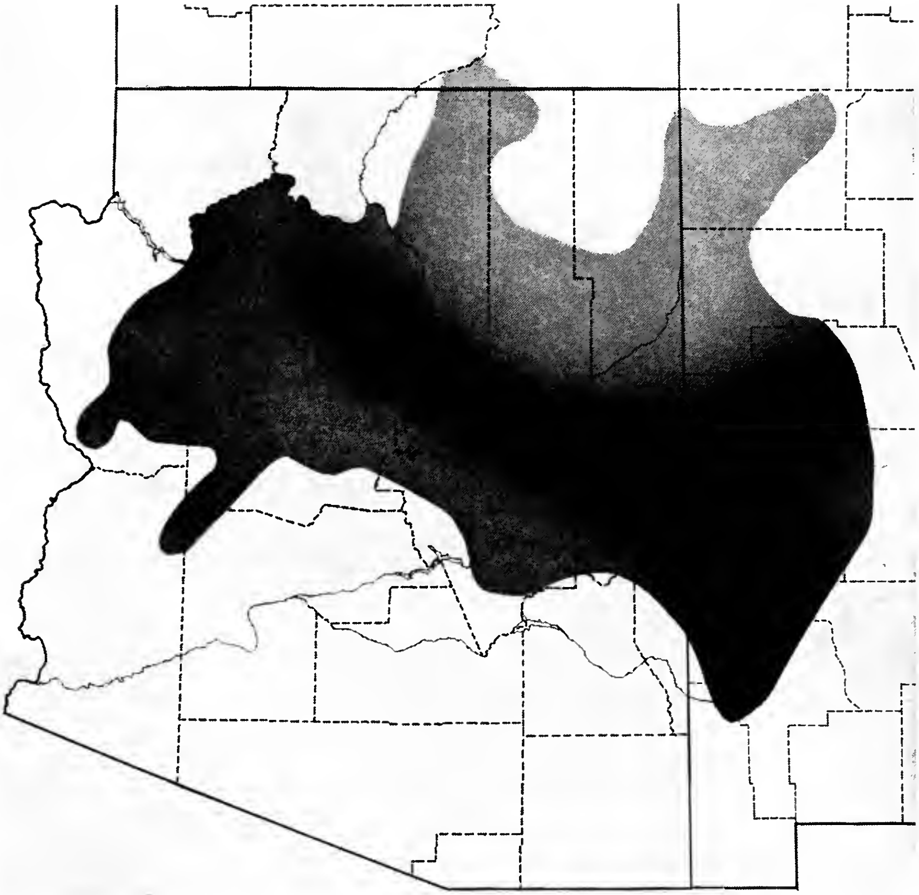

PLATE I

Variation in the intensity of the over-all color in *Neotoma stephensi.* The darkest-colored populations are represented by the darkest area; the lightest, by the lightest area.

TABLE 1.—*Bimonthly distribution of Group 1 and Group 2 individuals, with dates of capture and age of pregnant and lactating females*

Date of Capture		Group 1	Group 2	Pregnant ♀♀	Lactating ♀♀
April	16–30			Apr. 30 (Group 4)	
May	1–15	1	1		
	16–31	1			
June	1–15	3			
	16–30	5	1	June 18 (Group 3)	June 26 (Group 3)
July	1–15	6	8	July 13 (Group 2)	July 15 (Group 2)
	16–31	6	1		
Aug.	1–15	6	5		
	16–30		3		Aug. 22 (Group 4)
Sept.	1–15	1	4		
	16–30	1	11	Late Sept.	
Oct.	1–15		11		

Using the growth rate of *N. albigula* as a guide, the dates of birth of Group 1 individuals begin in early March, and thus mating must begin early in February. The dates of birth appear to form two groups—one including March and April, and the other from the middle of May to the middle of July. This suggests two litters but, if a litter can follow another in a period of 15 days, as has been reported for *N. albigula*, it is quite possible that *N. stephensi* may have more than two litters. The usual litter seems to consist of two young, as indicated by four cases of pregnant females containing two embryos each. It is of interest that one of the pregnant animals taken on 13 July, and a lactating female taken 15 July, were clearly of Group 2. The date of capture, in addition to the age group of these animals, certainly seems to indicate that females reach sexual maturity the second season after birth. These females must have been born in the spring or summer of the preceding year.

HABITAT

Neotoma stephensi occupies an ecological niche quite distinctive from that of *Neotoma lepida*. In our collecting experience, *N. stephensi* is found in rocky situations, usually where the rocks are in piles, and usually where there are piñons and junipers. *Neotoma stephensi* is not a cliff dweller, although it may be found in the general vicinity of cliffs, but is found where the rocks have rolled down and become stacked. However, even though suitable rocks may be present, *N. stephensi* most likely will not be found if piñons and junipers are absent. This wood rat is frequently found associated with the piñon mouse, *Peromyscus truei*, the brush mouse, *Peromyscus boylii*, or the cactus mouse, *Peromyscus eremicus*.

Within Grand Canyon National Park, *Neotoma stephensi* is to be found in several ecological situations. In the majority of places, *N. stephensi* was found in rocky situations where there were piñon, juniper, scrub oak and cliffrose. In these situations, it was usually associated with *Neotoma mexicana*, but in a few cases, with *N. albigula.* In Long Jim Canyon, *N. stephensi* was in a rocky place within the yellow pine forest. At Cedar Mountain, the species was at the lowest edge of the piñon-juniper belt. Here, on the rocky, desert slopes, there were many cacti and agave plants and only a few straggling piñons or junipers. *N. stephensi* widely overlapped the range of *N. albigula* here. At Hilltop, near the western boundary of the Park, *N. stephensi* was in rocky places decidedly below the piñon-juniper zone and in an area where there were sagebrush, Indian paintbrush and grasses. Here, *Perognathus intermedius, Neotoma albigula, Eutamias dorsalis,* and even *Peromyscus truei* and *P. boylii* were present.

In the vicinity of Rimrock and Montezuma Well in eastern Yavapai County, Arizona, *N. stephensi* was found along the fractured limestone outcrop extending horizontally near the top of the low mesas. This outcrop was 5 to 8 feet in height and was fractured along its length into large blocks. *N. stephensi* occurred in the crevices among these blocks, along with many *Peromyscus eremicus.* Rat houses and piles of droppings were evident all through the outcrop. About 40 feet below the limestone stratum there occurred a short dark lava outcrop which was much more finely fractured. *Neotoma albigula* was found here as well as on the valley floor where it lived among the cacti. No *N. albigula* was taken among the blocks of limestone where *N. stephensi* occurred. These field observations made by John S. Hall suggest an important difference in the habitat preference of *N. stephensi* and *N. albigula,* even in areas where these two species are very near to each other.

At the western edge of the range of *Neotoma stephensi,* in the Hualpai Mountains, it may also occur above the piñon-juniper zone in the scrub oak and yellow pine. However, it was taken in rocky situations and in association with *Peromyscus boylii.*

Occasionally, *N. stephensi* will desert its preferred rocky habitat and move into or under man-made structures. At Pasture Wash, a female with half-grown young was living among bales of hay in the loft of an unused barn. Near McMillen Mine, individuals had homes under large sheets of building material which had been on the ground for a long period of time.

In New Mexico, according to Bailey (N. Amer. Fauna 53: 188, 1931), *N. stephensi* in the Burro Mountains live in "stick nests placed about logs or brush, and in places their burrows entered the ground about the bases of rocks with many sticks piled about the entrances." Bailey stated that they occupy the juniper-piñon plateau region, frequenting rocky places and even cliffs.

Neotoma stephensi Goldman

Range.—Central Arizona, from Hualpai Mountains on the west to western New Mexico on the east, and from McMillenville on the south to extreme south-central Utah (Navajo Mountain) on the north (Fig. 4).

Diagnosis.—A medium-sized species of *Neotoma* with a bushy tail (bushier than in any other species except *N. cinerea*); dusky coloration on dorsal surface of foot extending from ankle nearly one-third distance to base of toes; small baculum, exclamation-mark-shaped (Fig. 1); upper molariform teeth with following combination of characters: M^1 with antero-medial fold absent or poorly developed, and M^3 with postero-labial fold and second loph directed obliquely (Figs. 1, 2); last lower molar with deep lingual fold as deep or deeper than labial fold (Fig. 2); skull broad and flat interorbitally; rostrum narrow; nasals truncate posteriorly (Fig. 3).

Neotoma stephensi stephensi Goldman

Neotoma stephensi Goldman, 1905, Proc. Biol. Soc. Wash., 18: 32, 2 Feb.
Neotoma lepida stephensi, Goldman, 1910, N. Amer. Fauna 31: 80, 19 Oct.
Neotoma stephensi stephensi, Goldman, 1932, Jour. Mamm., 13: 66, 9 Feb.

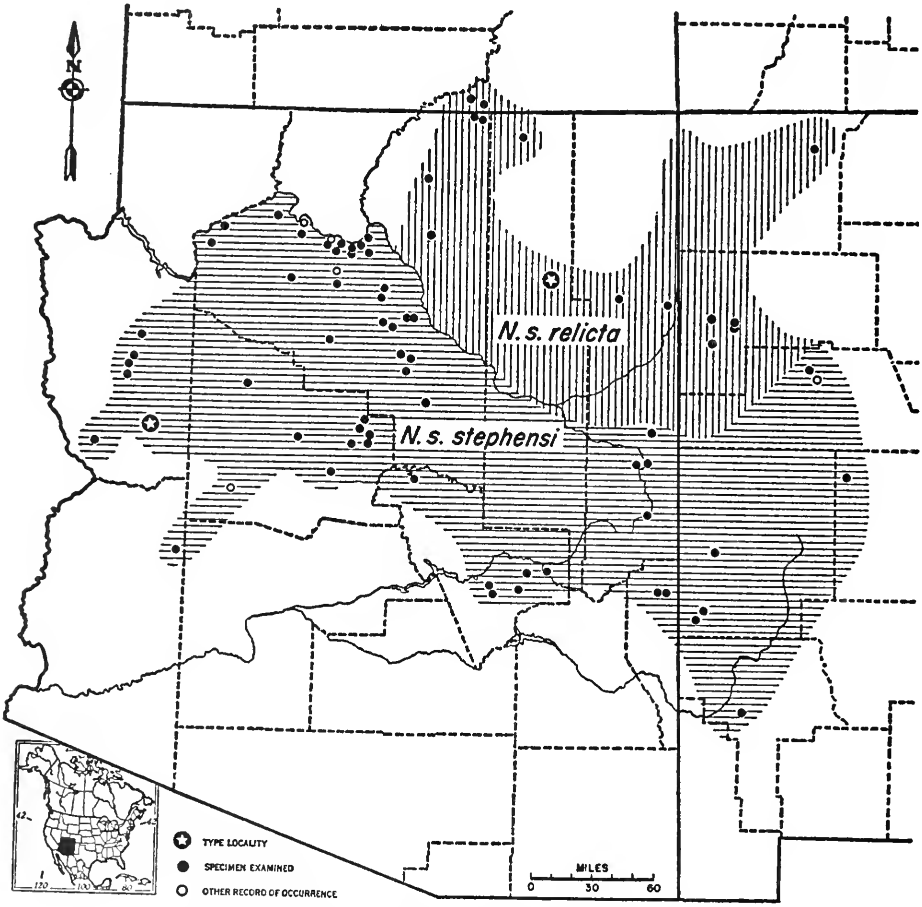

FIG. 4.—Distribution of the subspecies of *Neotoma stephensi.*

Type.—Adult female, U.S. National Museum (Biol. Surv.), No. 117466, from Hualpai Mountains, 6,300 ft., actually at Horse Tank (see *Remarks*), Mohave County, Arizona, collected on 1 July 1902 by Frank Stephens; original no. 4192.

Range.—From the Hualpai, Chemehuevis, and Harquahala mountains in western Arizona east along the Mogollon Plateau to the Burro and Gallinas mountains in southwestern New Mexico (see map, Fig. 4).

Diagnosis.—A race showing considerable variation throughout its range but possessing the following characteristics: color of dorsum dark, being darkest in central Arizona and southwestern New Mexico (Plate I); sides above lateral line with narrow fulvous band near Pinkish Buff; nose, forehead and cheeks grayish or plumbeous; hair of throat usually plumbeous basally; top of tail appears dark, almost black, because more black hairs and few or no white hairs interspersed or show through; size large, as indicated by weight in adult males of usually more than 180 grams; skull large, usually averaging more in greatest length than 41.2 mm. in adult males; upper toothrow long, usually 8.4 mm. or more; skull with supraorbital ridges frequently beaded and heavy.

Comparisons.—Since there is considerable variation within the subspecies *stephensi*, groups of populations of this race have been compared with the relatively homogeneous "population" of *relicta.*

From *relicta*, the race *stephensi* from the Hualpai Mountains, Hackberry, Harquahala Mountains, and Grand Canyon National Park differs as follows: darker coloration (but less different than in other populations of *stephensi*); more grayish nose, forehead and cheeks; not "white-throated" except for specimens from Hilltop; markedly heavier in weight; broader skull, both actually and relatively to its length (especially marked in specimens from the Hualpai Mountains); longer toothrow and broader interorbitally (especially in specimens from the Hualpais).

Central Arizona populations (for discussion, see under *Remarks*) differ from *N. s. relicta* as follows: color markedly darker, both on the dorsum and sides; dorsal tail stripe more blackish, less gray; body-weight, length of toothrow, and interorbital width greater, but not so pronounced as in topotypes of *stephensi* from the Hualpai Mountains; differ from *relicta* in other features the same way as do topotypes of *stephensi.*

Populations from eastern Arizona and southwestern New Mexico differ from *N. s. relicta* as follows (for discussion, see under *Remarks*): color darker, including facial region, sides and tail; throat tending to be partially or entirely white (in the latter case showing similarity to *relicta*); externally larger and heavier; skull with nasals broad, tending to be bell-shaped anteriorly, but constricted posteriorly; ascending arms of premaxillaries broader; differ from *relicta* in other features as do topotypes of *stephensi.*

Measurements.—See Tables 2 and 3.

Remarks.—As mentioned under *Comparisons*, there is considerable varia-

TABLE 2.—*External and cranial measurements of "Group 3" male specimens of Neotoma stephensi stephensi. Grouped localities are as follows: Western Arizona (Hackberry, Hualpai Mts., Lucky Star Mine); Northern Arizona (Grand Canyon); Central Arizona (Red Lake, Wupatki area); Southeastern Arizona (McMillenville area, Nantanes Plateau, Black River); Western New Mexico (Burley, Burro Mts., Glenwood)*

	Western Arizona	Northern Arizona	Central Arizona	Southeastern Arizona	Western New Mexico
Number	8	4	6	3	4
Total length	301.2	311.2	314.0^{4}	308.3	298.3^{3}
	283.0–334.0	305.0–320.0	303.0–320.0	302.0–313.0	290.0–310.0
Head and body	173.6	175.8	183.2^{4}	174.0	169.5^{3}
	161.0–201.0	172.0–178.0	171.0–203.0	165.0–182.0	165.0–177.0
Tail	127.6	135.0	132.7^{4}	134.3	127.3^{3}
	120.0–135.0	127.0–144.0	125.0–138.0	131.0–137.0	120.0–133.0
Hind foot	32.3	31.5	32.7	31.7	31.6
	31.0–34.0	29.0–34.0	32.0–34.0	31.0–32.0	30.0–33.0
Condylobasal length	39.5^{7}	39.7	40.0	38.6	37.3
	37.6–41.5	39.3–40.1	37.7–42.5	37.7–39.3	36.5–39.2
Zygomatic breadth	22.1^{7}	21.2	21.3^{5}		20.4^{3}
	21.0–23.0	20.6–21.8	20.6–21.9	21.0^{1}	20.2–20.8
Interorbital	5.7	5.4	5.5	5.5	5.3
	5.6–6.0	5.1–5.7	5.3–6.0	5.4–5.6	5.0–5.6
Breadth of rostrum	6.5	6.4	6.1	6.5	6.1
	5.9–6.9	6.3–6.5	5.9–6.4	6.2–7.0	5.6–6.5
Depth of rostrum	6.8	6.9	6.8	6.7	6.3
	6.5–7.0	6.8–7.1	6.5–7.1	6.4–7.1	6.1–6.5
Nasal	15.5	16.0	16.3	16.0	15.1
	15.0–16.2	15.4–16.8	15.7–17.5	15.8–16.3	14.1–16.8
Incisive foramen	9.1	9.0	9.5	8.7	8.4
	8.8–9.5	8.8–9.4	9.0–10.2	8.2–9.2	8.0–9.0
Palatal bridge	7.6	7.5	7.5	8.1	7.7
	7.4–7.9	7.3–7.6	7.0–7.7	7.9–8.4	7.5–7.9
Maxillary toothrow	8.7	8.3	8.5	8.9	8.6
	8.3–9.3	8.1–8.6	7.9–9.0	8.7–9.2	8.4–8.8

tion within the subspecies *N. s. stephensi* as here delimited. This variation can be discussed by grouping the populations into three segments, from (1) the Hualpai Mountains, including others from western Arizona and the Grand Canyon region, (2) central Arizona, and (3) eastern Arizona and western New Mexico. We prefer to describe these three "variants" but not to give them names.

The first group of populations in western Arizona possesses the following characteristics: light color (see Plate I); long toothrow, broad across zygomatic arches, broad interorbitally, yet skull is only of average length; large foot, average length of body, and short tail. Within this group of populations, those specimens from the type locality (Hualpai Mountains) have certain unique features such as relatively short but broad skulls, long toothrows, broad interorbital regions, greater weight, and slightly paler than "average" coloration for the subspecies. If only topotypes are used for comparison with other populations of *N. stephensi*, the impression may be gained that the population is quite distinct. However, when the range of variation in all characters from throughout the geographic range of *stephensi* is taken into consideration, the differences are less impressive and not as significant. In many features, topotypes of *stephensi* are not "typical" or "average" for the race.

In central Arizona, there is a series of populations of *N. stephensi* which possesses characteristics of an average difference distinguishing it from neighboring populations. This series, depicted by the dark area in Plate I, comprises populations from Black Tank to the north, south through Deadman's Flat, Wupatki Monument, Winona, Walnut, Verde Valley, and west to Red Lake and Fort Whipple. Specimens from as far south as McMillenville and the Natanes Plateau in Gila County are not included. This complex of populations possesses the following features, many of which are of an average sort: color dark; dorsal tail stripe often black; sides with the ochraceous color along the lateral line greatly restricted; body long, as long or longer, on the average, than in any population; body weight intermediate between that of *relicta* and

TABLE 3.—*External aand cranial measurements of "Group 3" female specimens of Neotoma stephensi stephensi. Grouped localities are as in Table 2*

	Western Arizona	Northern Arizona	Central Arizona	Southeastern Arizona
Number	12	5	5	3
Total length	274.2	298.3^{6}	309.8^{4}	
	264.0–329.0	279.0–323.0	293.0–322.0	304.0^{1}
Head and body	170.1	168.3^{6}	175.0^{4}	
	148.0–195.0	160.0–180.0	173.0–179.0	164.0^{1}
Tail	129.0	130.0^{6}	134.8^{4}	
	106.0–141.0	119.0–143.0	118.0–148.0	140.0^{1}
Hind foot	32.0	31.3^{6}	33.3^{4}	
	30.0–34.0	30.0–32.0	33.0–34.0	32.5^{1}
Condylobasal length	38.8^{11}	36.6	38.6	38.8^{2}
	36.8–40.7	35.9–37.5	38.0–39.7	38.2,39.3
Zygomatic breadth	21.8^{8}	20.7	20.7	21.6
	21.1–23.2	20.4–20.9	20.5–20.9	21.2–22.0
Interorbital	5.4	5.4	5.4	5.7
	4.7–5.8	5.2–5.7	5.0–5.7	5.3–6.0
Rostrum breadth	6.3	5.9	6.3	6.4^{2}
	6.0–6.6	5.6–6.0	6.1–6.5	6.3,6.5
Rostrum depth	6.6	6.1	6.5	6.7^{2}
	6.2–7.0	5.5–6.2	6.4–6.7	6.5,6.8
Nasal	15.3	14.3	15.7	15.5^{2}
	13.9–16.6	13.7–14.6	15.3–16.3	14.9,16.1
Incisive foramen	8.5	8.4	9.1	8.7^{2}
	7.9–8.8	8.1–8.8	8.5–9.5	8.5,8.9
Palatal bridge	7.6	7.2	7.2	7.8
	6.9–8.5	6.9–7.9	6.5–7.5	7.5–8.5
Maxillary toothrow	8.9	8.4	8.6	9.0
	8.4–9.5	8.1–8.8	8.5–8.8	8.6–9.3

specimens from the Hualpai Mountains; skull long and narrow, with the percentage of zygomatic breadth to greatest length in adult males being between 48.4 and 50.4; for the Hualpais, 51.7 to 53.6; for the Grand Canyon, 49.7 to 51.4; similar percentages for adult females from the respective localities are between 49.2 and 53.8; 50.8 to 54.8; 51.6 to 53.5. The length of the upper toothrow and width of the interorbital region are intermediate between *relicta* and specimens from the Hualpai Mountains.

Although this complex of populations may possess some average differences of color and size, we feel that it has not reached the subspecific stage of differentiation.

In western New Mexico and eastern Arizona, there is a group of populations that has certain characters in common, and differs in an average way from *N. s. stephensi* in western Arizona. This group includes localities from 25 mi. N Springerville and from Springerville in Arizona southeast to the Burro Mountains, New Mexico, and northeast to Grants. Some features of this group, many of which are not diagnostic, include: nasals broad, almost bell-shaped anteriorly; posterior arms (ascending branches) of premaxillae on dorsum of skull broad; nasals, posteriorly, constricted more by premaxillae than in most other populations; color dark, as dark as that in central Arizona populations except for specimens from Burley. For remarks about the white-throatedness of specimens from the Burro Mountains, see page 480. One specimen from Grants, Catron County, New Mexico, in many ways exemplifies the extreme of these characters listed: nasals bell-shaped anteriorly, constricted posteriorly; posterior, ascending arms of premaxillae broad; interorbital region broad; color dark, with the addition of a heavy, rich fulvous wash over the entire underparts. This specimen lacks 90 per cent of the tail, and our first reaction was that this specimen was not a bushy-tailed *Neotoma stephensi.* The heavy wash of fulvous on the underparts is duplicated in one of three specimens of *Neotoma mexicana* from 5 mi. SE Grants. However, careful analysis, particularly of cranial features, indicates that the specimen is *N. stephensi,* not *N. mexicana.* This individual is either aberrant or reflects the extreme characters of this group of populations we have described above. We prefer the latter interpretation. The fulvous wash on the underparts may reflect the "influence" of the black lava near Grants. We do not think this fulvous wash represents a "dichromatic condition" that Goldman (N. Amer. Fauna 31: 81, 1910) alluded to, although more specimens may indicate that such is the case. A specimen from 4 mi. W McCartys, which is near Grants, is a very young animal and shows none of the features of the Grants' specimen.

According to Laurence Huey, the type locality should be regarded as Horse Tank at the southern end of the Hualpai Mountains. Mr. Huey informs us that Frank Stephens provided him with this information.

Specimens examined.—Total number, 163, from the following localities: ARIZONA—*Mohave County:* Hackberry, 7 (BS); Democrat Mine, 13 mi. ESE Kingman, Hualpai Mts., 1 (UI); Hualpai Mtn. Park, Hualpai Mts., 1 (UI); 1 mi. N Hualpai Peak, Hualpai Mtn.

Park, 7,000 ft., 1 (UI); Pine Lake, Hualpai Mtn. Park, 6,000 ft., 1 (UI); Hualpai Mts., 5,600 ft., 7,000 ft., 6 (BS), 1 (UI); Horse Tank, 5 (SD); Lucky Star Mine, Chemehuevis Mts., 3 (SD); *Yuma County:* Harquahala Mts., 5,000 ft., 3 (BS); *Coconino County:* Hilltop, S side GCNP [= Grand Canyon Nat. Park], 4 (UI); Lower end Prospect Valley, 5,200 ft., 2 (BS); Pasture Wash Ranger Station, 6,300 ft., GCNP, 3 (UI); Pasture Wash, Jct. rds. W9A & W9, GCNP, 1 (UI); 8 mi. N Pine Spg., Hualpai Indian Reservation, 3 (BS); E side Cedar Mt., 6,400 ft., GCNP, 2 (UI); Yaki Burn, S rim Grand Canyon, 2 (GC); Yavapai Point Station, S rim Grand Canyon, 3 (GC); Grand Canyon Village, S rim Grand Canyon, 1 (GC); S rim Grand Canyon, 1 (GC); S boundary GCNP, nr. Rowes Well, GCNP, 1 (UI); School athletic grounds, Village, GCNP, 7 (UI); Shoshone Point, GCNP, 2 (UI); Wayside Museum, S rim Grand Canyon, 1 (GC); 1 mi. E, ½ mi. S Desert View Pt., GCNP, 1 (UI); Grandview Pt., GCNP, 1 (UI); Long Jim Canyon, 3 (UI); W side Zuni Pt., 7,200 ft., GCNP, 6 (UI); Rt. 64, SE Boundary GCNP, 1 (UI); Cataract Canyon, 12 mi. WSW Anita, 2 (BS); Red Butte, 2 (BS); Black Tank Lava Beds, 6,100 ft., 3 (UC); Lava Field, 12 mi. N Deadman's Flat, NE San Francisco Mt., 1 (UC); 2.6 mi. W Wupatki Ruins, 8 (UC); Wupatki Indian Ruins, 35 mi. NE Flagstaff, 5,100 ft., 1 (BS), 6 (UC); Deadman's Flat, NE San Francisco Mt., 6,400 ft., 2 (UC); 4 mi. NE Deadman Ranger Station, San Francisco Mt., 6,600 ft., 1 (BS); Red Lake, 5 (BS); 3 mi. NW Winona, 6,200 ft., 6,400 ft., 2 (BS); Aztec Tank, 5,800 ft., 2 (BS); Winona, 6,400 ft., 2 (UC); Walnut, 1 (BS); Walnut Canyon, 5 mi. S Mt. Elden, 6,500 ft., 1 (BS); Anderson Mesa, Anderson Canyon, 30 mi. SE Flagstaff, 6,500 ft., 1 (BS); *Yavapai County:* Pine Flat, Juniper Mts., 20 mi. NW Simmons, 3 (BS); 5 mi. S, 1 mi. W Sedona, 1 (UI); 2 mi. N Montezuma Well, 3 (UI); 2 mi. N Rimrock, 1 (UI); Montezuma Well, 3,500 ft., 2 (BS); 3 mi. N Ft. Whipple, 1 (BS); 6 mi. NW Camp Verde, 1 (UI); Mayer, 1 (BS); *Gila County:* 7 mi. N Payson, 4,500 ft., 1 (BS); Black River, 5 mi. above mouth White River, 4,600 ft., 1 (BS); nr. sawmill, 25 mi. NE Rice [now San Carlos], Natanes Plateau, 5,800 ft., 3 (BS); McMillen Mine, 5 mi. E, 12½ mi. N Globe, 4 (UI); Cazador Spring, S base Natanes Plateau, San Carlos Indian Reservation, 4,000 ft., 1 (BS); McMillenville, 4,300 ft., 3 (BS); *Apache County:* Zuni River, 3 (BS); 8 mi. S St. Johns, 5,800 ft., 4 (BS); 25 mi. N Springerville, 2 (BS); Springerville, 7,000 ft., 1 (BS); *Greenlee County:* 3 mi. W Cosper Ranch, 6,000 ft., 1 (BS); Cosper Ranch, Blue River, 5,000 ft., 2 (BS); NEW MEXICO—*Valencia County:* Grants, 1 (BS); 4 mi. W McCartys, 1 (UM); *Socorro County:* Burley [22 mi. N Augustine], 3 (BS); *Catron County*: Largo Canyon, 1 (UC); Whitewater Canyon, 5 mi. NE Glenwood, 5,450 ft., 1 (AM); Glenwood, San Francisco Valley, 5,000 ft., 1 (BS); *Grant County:* Burro Mts., 8 (BS).

Additional records.—ARIZONA—*Coconino County:* S side Bass Camp, 8 mi. NW Grand Canyon (BS); 1 mi. N Bass Camp, 5,200 ft., (BS); 3 mi. S Bass Camp, 5,400 ft., (BS); Bass Camp (BS); nr. Bright Angel Trail, Grand Canyon, (BS); S Yaki Point, in yellow pine, Grand Canyon (BS); top of rim nr. Village, Grand Canyon, 6,800 ft., (BS); Grand View Point, Grand Canyon, (BS); Trash Tank, S rim Grand Canyon, (GC); Trash Wash, S rim Grand Canyon, (GC); N Red Butte, Main Road, Grand Canyon, (BS); Red Butte, Museum of Northern Arizona; Wupatki Nat'l Monument, 5,100 ft., Museum of Northern Arizona; Wupatki Indian Ruins, 35 mi. NE Flagstaff, 5,100 ft., (BS); *Yavapai County:* Fools Gulch, Weaver Mts., (BS).

Neotoma stephensi relicta Goldman

Neotoma stephensi relicta Goldman, 1932, Jour. Mamm., 13: 66, 9 Feb.

Type.—Adult female, U.S. National Museum (Biol. Surv.), No. 67780, from Keams Canyon, Navajo County, Arizona, collected on 22 July 1894 by A. K. Fisher; original no. 1649.

TABLE 4.—*External and cranial measurements of "Group 3" specimens of Neotoma stephensi relicta. Localities represented are as follows: Utah—Navajo Mt., Rainbow Bridge; Arizona—Rainbow Lodge, Cedar Ridge, Keams Canyon; New Mexico—Wingate area, Long Canyon, Blanco*

	Females	Males
Number	10	10
Total length	296.7^{9}	304.7^{9}
	273.0–320.0	283.0–333.0
Head and body	163.0^{9}	172.0^{9}
	153.0–175.0	159.0–187.0
Tail	133.7^{9}	130.9
	120.0–145.0	123.0–144.0
Hind foot	30.4^{9}	31.2
	28.0–33.5	29.0–33.0
Condylobasal length	36.3^{8}	37.8^{8}
	33.7–38.0	36.8–38.6
Zygomatic breadth	20.0^{8}	20.5^{9}
	18.4–20.2	20.0–21.1
Interorbital	5.2	5.3^{9}
	4.8–5.7	5.2–5.4
Breadth of rostrum	5.9	6.0^{9}
	5.5–6.3	5.5–6.4
Depth of rostrum	6.2	6.6
	5.8–6.5	6.4–7.0
Nasal	14.7^{7}	15.4
	13.5–15.8	14.9–16.0
Incisive foramen	8.4	8.8
	7.8–9.0	8.5–9.4
Palatal bridge	7.2	7.4
	6.7–7.8	7.1–7.9
Maxillary toothrow	8.1	8.2
	7.7–8.3	7.9–8.4

Range.—East of the Colorado River, from Navajo Mountain in extreme south-central Utah, south to the Little Colorado River, and eastward in New Mexico to the San Juan Basin at the north and the Zuni Mountains at the south (see map, Fig. 4).

Diagnosis.—A race of *Neotoma stephensi* characterized by markedly pale buffy color, with much less blackish and brownish than in other populations of species; sides, above lateral line, with large extent of buffy color, which varies between Pinkish Buff and Light Ochraceous-Salmon; nose, forehead and cheeks buffy, less plumbeous than other subspecies; hairs on throat usually white throughout (base not plumbeous); top of tail appears grayish because few dark hairs present; underparts usually without fulvous wash; size small, being best indicated by light weight (adult males less than 117 gms.); skull small, greatest length averaging less than 41.2 mm. in adult males; upper toothrow short, usually less than 8.4 mm.; skull narrow, with interorbital width usually 5.3 mm. or less and narrow across zygomata, with males usually averaging less than 21.0 mm.; skull delicate for the species, with supraorbital ridges not heavily beaded.

Comparisons.—For a comparison with *N. stephensi stephensi,* and the geographic variants within that subspecies, see the account of *N. s. stephensi.*

Measurements.—See Table 4.

Remarks.—*N. s. relicta* is a pale race inhabiting the mountainous areas of the elevated, short grass region of northeastern Arizona. The race does extend into New Mexico and Utah, but its principal center of distribution is in Arizona.

N. s. relicta is quite distinctive from many populations of *N. s. stephensi* adjacent to its range. It is less distinctive from some other populations farther removed. However, with a combination of characters (principally on the basis of color), *relicta* and *stephensi* can be distinguished. As here delimited, *relicta* shows less morphological variation geographically than does *stephensi.* Specimens from the eastern part of Grand Canyon National Park, referred to *stephensi,* show considerable approach toward specimens from Cedar Ridge, referred to *relicta.* These two localities are less than 45 miles apart. The intermediacy is in color and, to some extent, size of the skull. Specimens from Wingate and Gallup are of a color intermediate between that of *relicta* and *stephensi,* but the skulls of the adult specimens seem more as in *relicta,* to which subspecies they are referred.

Specimens examined.—Total number, 62, from the following localities: UTAH—*San Juan County:* Rainbow Bridge, 4,000 ft., 1 (UC); nr. War God Spring, 8,500 ft., Navajo Mt., 1 (AM); Navajo Mt. Trading Post, SE side Navajo Mt., 1 (UC); ARIZONA—*Coconino County:* Rainbow Lodge, Navajo Mts., 6,400 ft., 2 (BS); 5 mi. S summit, Navajo Mt., 1 (UC); Cedar Ridge, 30 mi. N Tuba, 3 (BS); Cedar Ridge, 6,000 ft., 10 (UC); Tuba, 1 (BS); *Navajo County:* Long Canyon, 6,450 ft., 1 (AM); Keams Canyon, 80 mi. N Holbrook, 20 (BS); Keams Canyon, 6,200 ft., 6 (UC); *Apache County:* Ganado, 6,500 ft., 5 (BS); St. Michaels, 7,000 ft., 2 (BS); NEW MEXICO—*San Juan County:* Blanco, 1 (BS); *McKinley County:* Gallup, 1 (BS); Wingate, 2 (BS); Fort Wingate, 3 (BS); 12 mi. S Gallup, 1 (BS).

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Multiple Character Analysis of *Canis lupus, latrans,* and *familiaris,* With a Discussion of the Relationships of *Canis niger*

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Synopsis. A multiple character analysis was undertaken of a broadly representative sample of three species: *Canis lupus* (wolf), *C. latrans* (coyote), and *C. familiaris* (dog). These species are clearly and significantly distinguished by the technique of linear discrimination. The analysis provides a basis for the identification of skulls not obviously distinguishable by size or other diagnostic characters.

Early populations of *Canis n. niger* and *C. n. gregoryi* (red wolf) are compared with the three species above and are found to form a cluster with *lupus* and to be sharply distinct from the other two species. Additional comparisons show that while *lupus lycaon* and *niger* both overlap with *lupus,* they are distinct from each other. This entire cluster is quite distinct from *latrans,* with *niger* being the farthest removed. A sample population of *C. n. gregoryi,* from the edge of the extending range of *C. latrans,* was examined and found to show too great a range of variation to be attributed to a single species.

With the advent of white man in North America and his consequent modification of the environment by lumbering and clearing for farming, coyotes have been extending their range (Young and Jackson, 1951). As they have extended their range, on the fringes of their newly acquired territories, animals which are difficult to identify have frequently been captured. In the South, as often as not, these are called red wolves, in the Northeast, coydogs. In both parts of the country these animals occur where coyotes have moved into areas that formerly were inhabited by small races of wolf. Coincident also with these shifts in distribution has been an upward revision in the reported weights for coyotes. Young and Jackson (1951), eliminating a few outsized individuals, give a range of 18-30 pounds for typical western coyotes, while Burt (1946) gives a range of 23-50 pounds for Michigan coyotes. The latter overlaps with weights of a long series of wolves from Algonquin Provincial Park (unpublished data from the Ontario Department of Lands and Forests) and, as a result, size alone becomes a less useful criterion in distinguishing between wolves and coyotes.

In the following discussion, since *Canis lupus,* the wolf, and *Canis latrans,* the coyote, are both composite species, these names as used in the text refer to each species as a unit. When a particular subspecies is referred to, a trinomial is used, as *Canis lupus lycaon. Canis niger,* the red wolf, is usually considered to include three subspecies. Their status is uncertain, and *Canis niger* as used in the present work refers to the typical form, *C. n. niger,* and to those southeastern populations, presently called *C. n. gregoryi,* which show no evidence of hybridization and which were collected from well outside the range of *latrans. Canis familiaris,* the dog, presents no problem because, in spite of its variability, it is monotypic.

The present study was undertaken because attempts to identify skulls of the northeastern population of rather large-sized members of the genus *Canis* bogged down in a mass of overlapping characters. It was then decided that before such fringe populations could be identified we needed to know what, if any, combinations of characters reliably separated known *Canis lupus, latrans,* and *familiaris,* particularly if size were eliminated as a character. This part of the work will be described in detail in section I.

While these three species are unquestionably distinct, the red wolf, currently called *Canis niger,* is a more problematical entity and will be discussed in section II in the light of our findings in section I.

SECTION I

The purpose of this part of the study was to determine what, if any, combinations of characters separate the three species, *C. lupus, C. latrans,* and *C. familiaris,* and how widely they are separated. To do this, we have used a biased random selection of 20 adult members, including males and females, of each species. In *latrans,* wide geographic distribution within the original range of the species was an important factor in choice of specimens. In *lupus,* only North American races were used and large individuals were avoided. In *familiaris,* the selection was deliberately biased to include the most wolf-like and coyote-like animals.

Characters to be used were not randomly selected but chosen because of their known value in distinguishing the species involved. Forty-two different measurements (see appendix) were taken on as many as 225 skulls. The measurements of 125 of these were then variously plotted to estimate regression lines. Based on these, 24 possibly significant characters were selected, 13 dealing with skull shape and 11 with tooth form, to test for diagnostic value. Since we wished to ascertain whether or not, regardless of size, skulls of each of the species had certain unique characters or combinations of characters, size was eliminated as a factor by relating all measurements to total length of skull. The mean and standard deviation of these 24 characters, as a fraction of total length, were computed for each of the selected series. The value of each character in distinguishing a pair of species was tested by computing single character distances for the pair, dividing the difference in means for the two populations by the average standard deviation.

From this analysis, nine cranial and six tooth measurements were found to be most diagnostic, although no single character was found without overlap between a pair of species. These were the measurements used in our linear discrimination.

In the following non-numerical description of differences between the species considered, the numbers of the measurements, which are expressions of these differences, and which were used in our linear discrimination, are given in parentheses. For descriptions of the measurements see Appendix A.

When *lupus* and *latrans* are compared, it is found that the most significant differences are in the relative development of the rostrum and of the brain case. Wolves have a relatively small brain case and massive rostrum. The latter is presumably a reflection of the large size of the animals on which they prey. Breadth of palate (7, 19), large teeth (11, 12, 13, 15, 20), and heavy maxilla (8), all contribute to the formation of powerful jaws. The position of the anterior root to the zygomatic arch and its massiveness help to buttress the teeth and strengthen the crushing action of the jaws. In the intermediate region of the skull, the strength of the masticatory apparatus shows in the depth of the jugal bone (18) and in the size of the temporal fossa. The one provides attachment for the masseter muscle, the other space for the temporal muscle. This space is difficult to measure, but the relation between the broadly spreading zygomatic arches (4) and the narrow brain case (6) expresses it well. Size of the temporal muscle is also shown by the development of a large sagittal crest.

Coyotes, preying as they do on small species, have opposite skull proportions and small, narrow teeth. Compared with the brain case, the rostrum is slender, the maxilla and the anterior root of the zygomatic arch less massive, the temporal fossa smaller, and the jugal narrower. All of this gives the skull a rather long slender appearance as compared with that of a wolf. This overall distinction is a good one and has often been used as diagnostic in separating wolf and coyote skulls, but it can be confusing. Ratios of total length to zygomatic breadth in long, narrow, wolf skulls may overlap with these ratios for short, broad, coyote skulls. If width of the brain case, width across molars, and width between premolars anteriorly are also taken into account, the characteristic, relatively-small brain case of a typical wolf skull is immediately apparent.

Dogs present a different problem. Essentially they are small wolves, distinguishable from coyotes by many of the wolf-like proportions of rostrum and brain case. However, their great variability means that no single set of characters is equally diagnostic for all kinds. Key characters for separating *lupus* and *latrans* are based on a certain intraspecific homogeneity which is not too difficult to describe or to see. *C. familiaris* lacks this homogeneity and often superficially resembles either of the other two more than it does other *familiaris.* This means that the best combinations of characters to be used for purposes of identification vary depending on whether the animal in question is large and wolf-like or smaller and coyote-like. Certain of the highly modified breeds are, of course, easily identified by the disproportionate development of brain case or rostrum. Other less modified forms may be distinguished by the inflation of the frontal sinuses and resultant steep angle of the forehead. They may also be recognized by a bend in the mid-region of the skull so that rostrum and brain case meet at more of an angle than is usual in wild canids.

Turning to the less modified kinds, and these include many mongrels, the large dogs differ from wolves in having relatively small teeth, and having the skull elongated in the interorbital region so that the distance between the tooth row and the bulla (2) is long compared with the length of the tooth row (10). The palate also is elongated so that its posterior margin lies well posterior to m^{2}. The brain case often looks atypically heavily ossified. The sagittal crest is usually drawn out less far beyond the occiput; when it is strongly developed and projecting, the dorsal margin usually curves strongly down at the tip. Briefly, big dogs look rather as if they had outgrown themselves and were never meant to be that size.

For the most part, wolf-like proportions of brain case and rostrum distinguish most dogs from coyotes. Long, narrow-skulled dogs may approach coyotes in some of their length-breadth proportions, but not in all of them, and a coyote-like elongation of the tooth row is not usually accompanied by coyote-like proportions of the teeth.

Disparate proportions of the teeth which show as differences in certain of them also help to distinguish dogs and coyotes. The relatively greater size of the canine (13) in dogs may be a reflection of their relationship with wolves. The greater width across the incisors (15) is partly an expression of larger tooth size; however, it also expresses the greater premaxillary width of dogs. In contrast, the last upper molar is small (14). This tooth, as frequently happens with the anteriormost or posteriormost of the cheek teeth, is the most variable tooth in the upper jaw. Nevertheless, its average smaller size in dogs than in wolves and coyotes is a good diagnostic feature and may be one of the results of domestication. The last character to be considered is characteristic of most coyotes and is one of the best expressions of the general narrowing of the premolars and carnassials in this form. The posterior part of p_{4} (22) is relatively long compared both to the length of the tooth (20) and to its maximum width. Because of this lengthening, a second accessory cusp behind the main cusp is usually present in coyotes and has often been used as diagnostic (Gidley, 1913).

We have applied the technique of linear discrimination as described by Kendall (1946). Jolicoeur (1959), who has used linear discrimination to somewhat different ends, gives an excellent graphical explanation of the technique. The computations were done on an IBM 7094 computer using the BIMD 05 program developed by the University of California at Los Angeles Medical School. In short, the technique finds the weighted sum of a number of characters which is most different for two populations, that is, the weighted sum of characters which best separates the populations. The sum itself is called the discriminant function, and the weights, determined by the computations, are called the discriminant coefficients. The mean value of the discriminant function for each of the populations can be obtained by multiply-ing the mean value of each character over the population by the discriminant coefficient for the character and then summing. If an individual is known to belong to one of a pair of populations, he can be identified by evaluating the discriminant function separating the pair for his values of the characters (that is, summing the weighted measurements for the specimen) and assigning him to the population having the closest mean value of the function. The accuracy of the identification will depend, of course, on the degree to which the populations are separated by the discriminant function. A useful measure of the multiple character difference between two populations is the D^2 statistic of Mahalonobis (see Rao, 1952). This is a general extension of the distance comparisons for single characters mentioned earlier.

For this study the discriminant coefficients and the D^2 statistic for each pair of the selected populations of *C. latrans, lupus,* and *familiaris* were computed using the fifteen characters discussed above. The discriminant coefficients are given in Table 1 along with the mean values of the discriminant functions for the populations, D^2 and D. The last value is roughly the difference in standard deviations between the mean values of the function for the two populations. We see that *latrans* differs by eight and nearly 11 standard deviations from *lupus* and *familiaris,* respectively, while *lupus* and *familiaris* differ by only a little more than five.

A clear view of the degree of separation of the populations achieved by the discriminant functions results from the *a posteriori* identification of the original individual specimens using the functions. For each of the pairwise discriminations the specimens were assigned to one species tentatively. A final identification was then made by assigning the specimen to that species for which two tentative assignments had been made. For example, if between *latrans* and *lupus* the specimen was assigned to *lupus,* between *latrans* and *familiaris* to *latrans,* and between *lupus* and *familiaris* to *lupus,* then the specimen was identified as *lupus.* In this way all sixty of the specimens were unambiguously and correctly identified; there was no overlap in the values of the various discriminant functions for the populations on which they were based. Figure 1 gives a plot of the populations using the *latrans-lupus* and *latrans-familiaris* discriminant functions as

TABLE 1. *Results of pairwise discriminant analysis for* C. latrans, lupus, *and* familiaris.

	Discriminant coefficient		
Measurements*	*lupus vs. latrans*	*latrans vs. familiaris*	*lupus vs. familiaris*
2	3.389	—16.876	— 6.900
4	— 7.107	14.670	8.494
6	14.971	—11.182	— 6.760
7	— 0.495	—11.246	— 5.124
8	— 7.313	—33.699	— 7.849
10	9.889	—24.989	—10.108
11	14.984	66.749	26.784
12	—12.510	—25.968	— 1.089
13	—24.891	—77.655	— 4.088
20	—32.167	5.155	22.738
22	87.360	35.272	—33.076
14	3.652	63.729	0.606
15	— 8.932	—28.702	— 3.531
18	3.299	31.510	0.784
19	1.230	—15.404	—10.638
Average discriminant function value for *latrans*	4.79	—14.6	
for *lupus*	3.10		— 4.73
for *familiaris*		—17.8	— 5.44
D^2 (D)	64.1 (8.0)	119.9 (10.9)	27.2 (5.2)

* Measurements are numbered as in Appendix. Each must be divided by total length of skull, measurement 1.

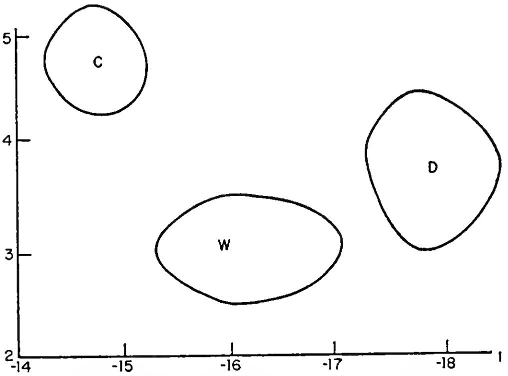

FIG. 1. Linear discrimination of *C. latrans* (C), *C. lupus* (W), and *C. familiaris* (D). The contours indicate the extreme range of individuals in the populations used. The *latrans-familiaris* discriminant function is used as the abscissa and the *latrans-lupus* discriminant function is used as ordinate.

coordinate axes. This figure shows the relative separations of the populations as well as the lack of overlap.

SECTION II

As stated earlier, in North America, in addition to *C. lupus* and *C. latrans,* a third species of wild *Canis, C. niger,* the red wolf, is currently recognized. Young and Goldman (1944) describe it as a wolf which is somewhat intermediate between *lupus* and *latrans,* with a distribution limited to the south-eastern part of the United States. This is a unique situation since all other wolves in both Eurasia (Pocock, 1935) and North America are races of *C. lupus.* Ranges as plotted for *lupus* and *niger* by Young and Goldman (1944) show an overlapping of *lupus* with *niger* in the southeastern part of the former's range. Even more surprising is the overlapping of all three species of *Canis* at the western edge of the range of *niger* and the eastern edge of that of *latrans* (Young and Jackson, 1951; Young and Goldman, 1944). Such an occurrence together of three closely related members of the genus *Canis* is without parallel elsewhere in the world. The situation is obviously peculiar, and various authors have attempted to explain it. It is not pertinent here to review these discussions; suffice it to say that for the most part they have concentrated on the relationship between *niger* and *latrans.* The most recent effort to unravel the problem is a paper by McCarley which includes an interesting discussion of the possibility of hybridization and population replacement (1962) where *latrans* is encroaching on the range of *niger.*

Implicit in McCarley's interpretation of his data, though not explicitly stated, is the fact that, while closely related species usually differ most from each other where their ranges meet or overlap, the opposite is true of these forms in the south-central states. Here, at the western edge of the range of *niger,* the small *C. n. rufus* Audubon and Bachman 1851 is often difficult to tell from *C. latrans frustror* Woodhouse 1851, while at the eastern end of its range, the larger *C. n. niger* Bartram 1791 is said to resemble *C. lupus lycaon* Schreber 1775 (Young and Goldman, 1944). Essentially, as presently defined, *niger* appears as a population intermediate in characters between a large western *latrans* and a small eastern *lupus.*

Efforts to determine the true status of *niger* will be helped if we first understand some of its taxonomic history. Because of the complications of priority, *Canis rufus* from Texas with three subspecies of increasing size from west to east now figures in the literature as *Canis niger* of Florida with three subspecies of decreasing size from east to west. The three related forms are the same in each case, but depending on which end of the range one starts from, the reasons for the primary distinction of the species are different. *Canis rufus* as a Texas phenomenon had a quite different reason for being set apart than did *Canis niger* as a Florida phenomenon. The earliest descriptions of a small wolf in the south-central states are based on the occurrence of a medium-sized non-coyote in eastern Texas. Animals were found which resembled coyotes in size but not in cranial characters, and the difference in size between these animals and the big plains wolves was so great that the two were scarcely compared. Typical coyotes were also found to occur in the same area. The fact that two distinct kinds of *Canis* were recognized is more important than the reasons why the name *rufus* was selected for the one and *frustror* for the other (Young and Goldman, 1944; Young and Jackson, 1951). Once *rufus* was set apart as a distinct species of wolf, efforts were made to determine the eastern limits of its range. A reasonable number of specimens was available from Louisiana, but progressing towards Florida the number of available specimens diminishes rapidly. There are very few from that part of the range where *niger* and *lupus lycaon* supposedly meet. Since, in addition to this, there are almost no extant specimens of *C. lupus lycaon* from the southeastern states, it is easy to see why the relationship between the eastern red wolf, *C. n. niger,* and *C. lupus lycaon* has not been more thoroughly analyzed.

If the study of the small wolves in the southern states had begun with *niger* in Florida and been based on adequate series, it is highly unlikely that *niger* ever would have been separated as a species from *lupus*. The biologically difficult problem of reconciling the existence of two similarly-sized forms of wolf in one continuous habitat would never have arisen and the area of systematic uncertainty would have been more properly limited to the eastern edge of the coyote's extending range.

The purpose of this part of the present work has been to establish whether or not two distinct species of wolf occur in the southeastern United States. The following discussion presents our evidence for considering that the wolves of this area all belong to the species *lupus* and that *niger* is not a distinct species. Unequivocal establishment of the status of *niger* has seemed a necessary preliminary to understanding and identifying the widely varying populations from west of the Mississippi presently identified as *n. gregoryi* Goldman 1937 and *n. rufus*.

In order to be as certain as possible that we were excluding *latrans* from our sample population, the series selected for a linear discrimination was limited to all available specimens of *C. n. niger* and *C. n. gregoryi* collected before 1920 from Louisiana, Alabama, and Florida; in addition, a Florida skull previously identified as *C. lupus lycaon* was included. In the following discussion this series is referred to as *C. niger*. The type of *floridanus* Miller 1912 (= *niger*), though it could not be included because the skull is too broken, falls within the range of variation of the rest of the series.

In our linear discrimination, comparison was made with the broadly representative series of the three species, *lupus, latrans,* and *familiaris,* used in the first section. It was also made with a series of ten males and ten females, all adult, of *Canis lupus lycaon*, the race whose range has been presumed to overlap with that of *niger* in the Southeast. The individuals were randomly selected from 71 specimens from Algonquin Provincial Park in Canada and weighed from 48-81 pounds (average 58). It was necessary to use a northern population because adequate series from farther south were not preserved before wolves were exterminated.

To the eye, the specimens of *niger* studied appear *lupus*-like and this is borne out by the numerical analysis. As a first step in the analysis, all of the individual specimens in the *niger* and *lycaon* populations were identified using the discriminant functions presented in the previous section. All were assigned to the *lupus* category; they were on the whole both less coyote-like and less dog-like than the original *lupus* population. In itself this provides little information about the relationships of *lupus* to these populations, of course, since the identification tacitly assumes the individuals to be from the *latrans, lupus,* or *familiaris* groups. The study was continued, therefore, by computing the discriminant function coefficients and D^2 values for all pairs of the five populations. The values of D^2 are given in Table 2. Using these with the cluster grouping technique discussed by Rao (1952), the *lycaon* and *niger* populations form a cluster with the selected *lupus* population. The average D^2 within this cluster is 28.8, while the average D^2 of its members to populations outside the cluster is 71.8. Although the *lycaon* and *niger* populations are fairly distinct, they are even more distant from the *latrans* and *familiaris* species groups, and have a common similarity to the *lupus* population. These relationships are shown fairly well in Figure 2, the plot of the populations using the *latrans-lycaon* and *lycaon-niger* discriminant functions as coordinate axes. The latter axis provides maximum separation of the wolf populations. Notice that the *lu-*

TABLE 2. *The generalized distance, D^2, between populations described in the text.*

	C.latrans	*C.lupus*	*C.familiaris*	*C.lupus lycaon*
C. lupus	64.1			
C. familiaris	119.9	27.2		
C. lupus lycaon	69.5	10.0	66.6	
C. niger	116.0	20.3	87.6	56.0

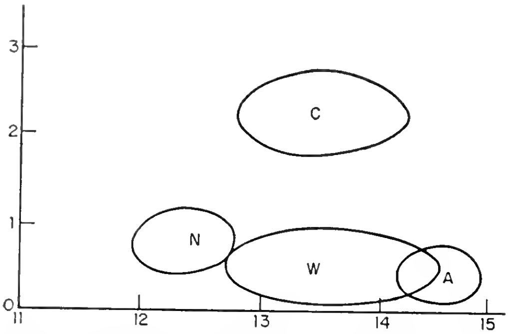

FIG. 2. Linear discrimination of *C. latrans* (C), *C. lupus* (W), *C. lupus lycaon* (A), and *C. niger* (N). The *lycaon-niger* discriminant function is used as the abscissa and the *latrans-lycaon* discriminant function is used as ordinate.

pus population falls intermediate to, and completely bridges, the gap between *lycaon* and *niger*.

Although we did not include recently collected specimens of red wolf from Louisiana in our linear discrimination, the relative position of each individual specimen was computed and, while found to be clearly wolf, the specimens were spread somewhat over the range from *niger* to *lycaon*.

It now appears that the early populations described as *Canis niger* and *n. gregoryi* from the southeastern wooded regions, east of the range of *Canis latrans*, are a local form of *Canis lupus*, not a distinct species of wolf. The situation in the areas where these small wolves and the large coyote, *C. l. frustror*, meet is much more confused. The present study has not attempted to go beyond McCarley's conclusions (1962). We have, however, tested our methods on a small series from Fallsville, Newton County, Arkansas. The specimens, collected in 1921 and identified as *Canis niger gregoryi* (Young and Goldman, 1944), span the whole range of variation from coyote to wolf. Figure 3 shows this variation of the individuals using the *latrans-lycaon* and *lycaon-niger* discriminant function as coordinate axes, as in Figure 2.

DISCUSSION

To date most efforts to measure differences between wolf, coyote, and dog skulls

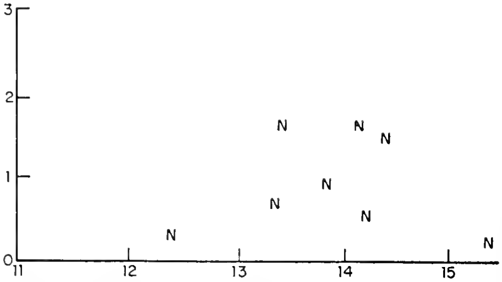

FIG. 3. Evaluation of discriminant functions for the series of *C. niger gregoryi* from Fallsville, Arkansas. The coordinate axes are identical to those of Figure 2.

have used a few specific measurements such as width between the premolar teeth anteriorly, or have relied on standard length-breadth comparisons of the whole skull as, for instance, relation of zygomatic width to total length. Such data are useful but show too much overlap to separate reliably the species involved. They are also inadequate as an expression of the basic differences between the skulls. These basic differences center around the differential development of different segments of the skull which, in their extreme form, are easily seen. Brain case, rostral, and interorbital shape of a typical coyote are quite different from those of a typical wolf. The significance of cranial measurements in expressing these differences in proportion depends on the multiple relationships of each measurement with a number of others, when size has been eliminated as a factor. The technique of linear discrimination has allowed us to make use of these multiple relationships in comparing skulls. The results of these comparisons showed that all three species are sharply distinct, with *lupus* and *familiaris* resembling each other more than either does *latrans*.

Since size has been eliminated as a character, the numerical values of the discriminant function may show two skulls to be most closely related which on the basis of size alone would be easy to tell apart. The same may be true of other unmeasurable but diagnostic characters.

Often, of course, there is little difficulty in distinguishing between the three species without resort to the kind of analysis described above. In addition to differences already discussed in the text, certain spot differences are often highly diagnostic: flattened, rugose bullae characterize dogs. Coyotes have the dorso-posterior part of the brain case well inflated, with the maximum width of brain case in the region of the parieto-temporal suture, the frontal shield not tilted up, and the postorbital constriction close to the postorbital processes. In wolves and dogs, the maximum width of the brain case is usually at the roots of the zygoma; the frontal shield tilts up, and the postorbital region is elongated, so that the constriction at the anterior part of the brain case and that behind the postorbital processes are well separated and the area between inflated. Further accentuating the different appearance of this region is the fact that the dorsal surface of the brain case in wolves and dogs is lower relative to the postorbital processes than in coyotes. The orbit in coyotes tends to be large; this shows both in vertical dimensions and in its length as compared to that of the zygomatic arch. In coyotes also, as distinct from dogs and wolves, there is a round protuberance of the occiput, often thin-walled, over the vermis of the cerebellum; certain differences in the teeth, though not precisely measurable, are also rather diagnostic. These are well reviewed in Young and Jackson (1951) and will not be repeated here. In addition, the present authors have found useful the fact that in coyotes $\mathrm{M}^{\underline{1}}$ measured lateromedially has the distance from the outer border of the tooth to the base of the paracone less than the distance from this point to the inner margin of the tooth, while the reverse is true in wolves and dogs. Wear makes this a difficult measurement to take precisely, but the difference, expressing as it does the plumper para- and metacones of wolves and dogs, is a significant one. None of these characters is completely reliable, just as is none of those described earlier. Used in combination, and with total size included, they are adequate to identify most canids.

The significance of the present study lies in the fact that linear discrimination, based on characters tested for their diagnostic value, can separate similarly-sized individuals of each of the three species considered. A corollary of this is the fact that a small wolf does not assume the characters of a large coyote, nor is the reverse true. Criteria have been observed and tested which distinguish the two species and these may be used to separate individuals which approach each other in size. This has made possible a re-examination of the specific status of the red wolf, long a biologically-puzzling phenomenon. From the evidence at hand, it appears that from central Louisiana east to Florida the large canids hitherto called *C. niger* and *niger gregoryi* are no more than subspecifically distinct from *Canis lupus*. Preliminary study of a small sample from the western part of the red wolf's range shows typical *lupus* and typical *latrans* both present, with the possibility of hybridization as McCarley has suggested. In investigating this possibility, we can now assume that we are considering only two species of wild canid, not three as has been previously supposed, and that we have overlapping and possible hybridization of these two distinct species, not an intergrading from coyote to wolf across the southern states as has sometimes been postulated. Our test analysis of the Fallsville specimens has also confirmed what has been apparent for a long time, that cranial variation in localized series currently called *C. niger gregoryi* or *C. niger rufus* is atypically wide for a race of North American *Canis*. Not only is it greater than the range for a local population of a given subspecies of either *lupus* or *latrans*, but it is also wider than the range for either species taken as a whole. Either this means sympatry of locally similar forms which have the same chromosome number and essentially similar karyograms (Benirschke and Low, 1965; Hungerford and Snyder, 1966), or it means hybridization. Before this can be decided, both the morphological and the behavioral characteristics of these populations need to be studied in more detail.

APPENDIX A

Following are listed the 42 measurements taken on the entire series. In the first paragraph are given the 24 tested for diagnostic value. The 16 of these used in our linear discrimination are italicized. In the second paragraph is a briefer listing of the remaining 18 characters, which were found to be not taxonomically reliable.

Skull. 1. *Total length from sagittal crest to alveoli of* I^1; 2. *Minimum distance from alveolus of* M^2 *to depression in front of bulla at base of styloid process*; 3. Minimum length of rostrum from orbital margin to alveolus of I^1; 4. *Zygomatic width*; 5. Breadth across postorbital processes; 6. *Maximum breadth of brain case at parieto-temporal suture*; 7. *Maximum crown width across upper cheek teeth*; 8. *Minimum distance taken at right angles from alveolar margin of molars to orbit*; 9. Maximum diameter of orbit, parallel to medial edge and starting at most ventral point; 10. *Crown length of upper cheek teeth from* C - M^2; 11. *Crown length of* P^4 *externally*; 12. *Minimum crown width of* P^4 *taken between roots*; 13. *Maximum antero-posterior width of upper canine taken at base of enamel*; 14. *Crown width of* M^2; 15. *Crown width across upper incisors*; 16. Height of brain case vertical to basi-sphenoid and not including sagittal crest; 17. Maximum width across occipital condyles; 18. *Minimum height of jugal at right angles to axis of bone*; 19. *Minimum width between alveoli of* P^1. Lower jaw. 20. *Crown length of* P_4; 21. Maximum crown width of P_4; 22. *Length of posterior cusps of* P_4*, along line parallel to base from back of tooth to point below notch posterior to main cusp*; 23. Crown length of M_1 parallel to main axis; 24. Maximum crown width of M_1 at right angles to main axis.

Skull. Condylo-basal length; palatal length; length of brain case; interorbital width; width of rostrum; width of nasals; height of nasal aperture; alveolar length of upper cheek teeth; alveolar length of P^4; maximum width of P^4 anteriorly; antero-posterior diameter of I^3; height of bullae; height of posterior bony nares. Lower jaw. Total length; distance from back of tooth row to condyle; alveolar length P_1 - M_3; alveolar length C - M_3; crown length C - M_3.

ACKNOWLEDGMENTS

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CHROMOSOME STUDIES OF POCKET GOPHERS, GENUS *THOMOMYS*. I. THE SPECIFIC STATUS OF *THOMOMYS UMBRINUS* (RICHARDSON) IN ARIZONA

James L. Patton and Ross E. Dingman

Abstract.—The complexities of morphology and, hence, taxonomy of pocket gophers (genus *Thomomys*) in southern Arizona are reflected by extreme interpopulation chromosomal variation in both *T. bottae* ($2n = 76$) and *T. umbrinus* ($2n = 78$). The variation consists of differing numbers of morphological types of chromosomes for nearly each population karyotype. The known range of variation in either species is less than the amount of difference between the two. A somewhat strict ecological separation exists between *T. bottae* and *T. umbrinus* in areas of sympatry or near sympatry, with the former preferring the more friable soils of the valley floors and mountain tops and the latter confined to the indurate soils of the oak zones at intermediate elevations. Chromosomal and ecological concordance support the interpretation that *T. bottae* and *T. umbrinus* are distinct species. Limited hybridization between the two species at one locality of sympatric contact, however, is known.

The taxonomy of *Thomomys umbrinus* (Richardson) has been the subject of considerable confusion in recent years. This problem centers primarily around isolated gopher populations inhabiting montane woodlands in southeastern Arizona. These gophers have been allocated to three subspecies of *T. umbrinus* by Goldman (1947) and to two subspecies by Cockrum (1960). Lange (1959) also recognized only two subspecies but used a different combination of names than did Cockrum (1960). We follow this latter interpretation and recognize *T. u. intermedius* Mearns as occurring in the Santa Rita, Patagonia, and Huachuca mountains, and *T. u. quercinus* Burt and Campbell as occurring in the Pajarito Mountains.

Hoffmeister and Goodpaster (1954:95) felt that ". . . perhaps in all of southern Arizona, gophers regarded as *T. umbrinus* by Goldman (1947) are best referred to *T. bottae*." This was finalized with their arrangement of *T. burti proximus* Burt and Campbell (= *T. umbrinus proximus* auct.) as a synonym of *T. bottae hueyi* Goldman. On the basis of this interpretation, Hall and Kelson (1959) regarded all populations of *T. umbrinus* and *T. bottae* as conspecific. Subsequently, Lange (1959) and Anderson (1966) have recorded sympatry or near sympatry for some populations of *T. bottae* and *T. umbrinus*, and Hoffmeister (1963) has revised his opinion of 1954 and implied that the populations of *T. umbrinus* in the Huachuca, Patagonia, and Pajarito mountains of southern Arizona are not conspecific with *T. bottae*.

As recognized here, *T. umbrinus* (*sensu stricto*) is essentially limited to the Mexican Plateau (see Anderson, 1966) whereas *T. bottae* has a more northern and western distribution including most of the southwestern United States and northwestern Mexico. The two species are sympatric, or nearly so, in at least six localities, all in the extreme northwestern part of the range of *T. umbrinus* (*i.e.*, the Pajarito, Patagonia, Santa Rita, and Huachuca mountains of Arizona, the Animas Mountains of New Mexico, and the Sierra de la Breña of northwestern Chihuahua). In the first five of these areas, *T. umbrinus* occurs as "insular" populations, surrounded by intervening populations of *T. bottae*.

The systematic status of the Arizona populations has been a difficult problem to approach by use of conventional characters, and it still remains the subject of considerable debate. Many authors (Baker, 1953; Hoffmeister and Goodpaster, 1954; Lange, 1957; and Anderson, 1966) have pointed out the lack of a single, definable character that can be used consistently to separate *T. umbrinus* from *T. bottae* throughout the areas of sympatry or near sympatry. The karyotypic analysis reported herein may supply such a "diagnostic character," for in studies thus far conducted consistent differences exist between *T. umbrinus* and *T. bottae* in Arizona.

Chromosomal characters in the future will aid in the "purification" of samples so that other characters, including standard morphological ones, may be better evaluated, and the ecologic, geographic, and genetic limits of gopher populations more clearly ascertained. At present, and until such "purified" collections are available, analysis of this type is difficult.

MATERIALS AND METHODS

The animals studied ($N = 65$) were trapped alive using traps designed by Howard (1952). Specimens were initially assigned to species on the basis of pelage characters (see Goldman, 1947; Lange, 1957; Hoffmeister and Goodpaster, 1954). Such initial identification was later substantiated by the karotypes. Allocations of specimens to subspecies were based primarily on geography and gross morphology (Goldman, 1947; Hall and Kelson, 1959; Cockrum, 1960; Lane, 1965). Conventional museum skins and skulls were saved of all animals examined and these are deposited in the collection of mammals of the Department of Biological Sciences (Zoology), University of Arizona, Tucson. See the list of specimens examined below for museum catalogue numbers and localities.

Karyotype analysis.—Metaphase chromosomes of bone marrow cells were analyzed using the *in vivo* colchicine-hypotonic citrate sequence described elsewhere (Patton, 1967). For the present analysis, the preparation of karyotypes from photomicrographs was based on the number of biarmed (metacentric, submetacentric, and subtelocentric) and uniarmed (acrocentric or telocentric) autosomes present in the complement, and on the morphology of the X-chromosome.

Sampling procedure.—Interpopulation variation was analyzed by comparing 16 populations of gophers in Arizona, 13 of *T. bottae* and three of *T. umbrinus* (see Fig. 1). Intrapopulation variation was assessed by examining at least two individuals from all but one population sampled. The largest samples from a single population of both species

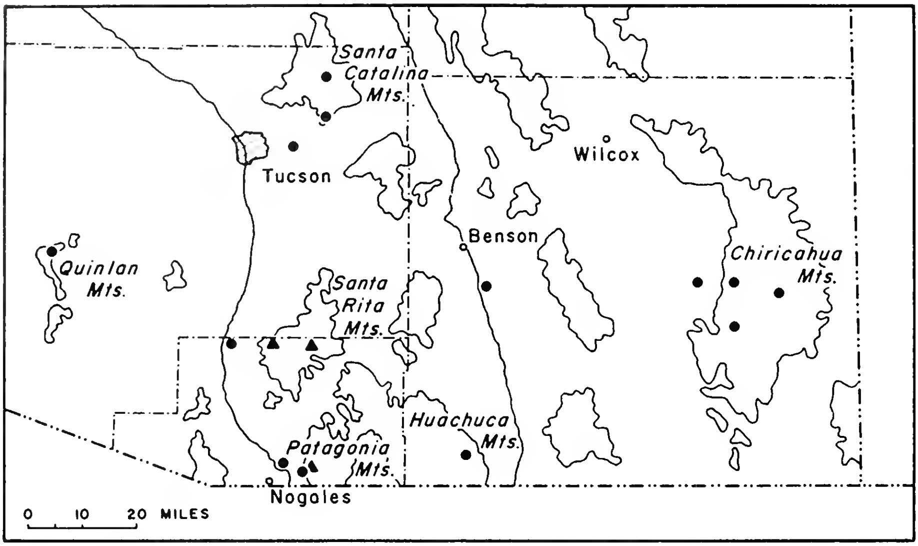

FIG. 1.—Map of southeastern Arizona showing localities of gophers analyzed (solid circles = *T. bottae;* solid triangles = *T. umbrinus*); 5000-ft contour line shown.

were 16 *T. umbrinus* and 11 *T. bottae,* both from the Patagonia Mountains. These represent the most critical samples in the present analysis. Although the samples are relatively small, they do indicate no chromosomal variation within any single population.

RESULTS

Extensive variation in the chromosomal complements between populations of *T. bottae* (*i.e.,* subspecies or demes) and slight variation between populations of *T. umbrinus* was found. No intrapopulation variation was found in either species.

FIG. 2.—Karyotype of *Thomomys bottae modicus* Goldman (♀, UA 14992). Yerba Buena Ranch, Santa Cruz Co., Arizona.

TABLE 1.—*Summary of karyotypic variation in populations of* Thomomys bottae *in southern Arizona.*

Subspecies	♂	♀	Locality	Number of acrocentrics	Morphology of X-chromosome*
T. b. alienus	–	1	St. David, San Pedro River, Cochise County	9 pairs	ST**
T. b. collinus	2	4	Turkey Creek and Rucker canyons, Chiricahua Mts., Cochise County	8 pairs	M
T. b. collinus	1	1	Rustlers Park, Chiricahua Mts., Cochise County	6 pairs	M**
T. b. extenuatus	1	1	Sulfur Springs Valley, Cochise County	8 pairs	M
T. b. proximus	1	3	Carr Canyon, Huachuca Mts., Cochise County	4 pairs	SM**
T. b. catalinae	2	3	Mt. Lemmon, Santa Catalina Mts. Pima County	1 pair	SM
T. b. modicus	3	2	vic. Tucson, Pima County	2 pairs	ST
T. b. modicus	4	7	Patagonia Mts., Santa Cruz County	0 pairs	SM
T. b. pusillus	1	1	Kit Peak, Quinlan Mts., Pima County	0 pairs	SM**

* M = metacentric; SM = submetacentric; ST = subtelocentric.
**Indicates probable designation of X-chromosomes.

Thomomys bottae.—Although all *T. bottae* studied to date have a diploid number of 76 and a low number of acrocentric autosomes, seven different population karyotypes have been discovered. These populations differ in the number of acrocentric chromosomes and in the morphology of the X-chromosome (see Table 1). Samples of *T. bottae modicus* Goldman (Fig. 2), with no acrocentric elements present, and of *T. bottae alienus* Goldman (Fig. 3), with nine pairs of acrocentrics, represent the extremes of interpopulation chromosomal variation known for the species. This great variation contrasts to chromosomal variation known for other mammals, but it does parallel (and perhaps correlates with) the great variation in other morphological characters of this species (see Goldman, 1947; Durrant, 1946; Hall and Davis, 1935). Indeed, the populations sampled represent seven different subspecies to some workers (see Hall and Kelson, 1959).

Thomomys umbrinus.—Populations of only one of the two subspecies recognized in Arizona by Lange (1959) have been sampled. This subspecies,

TABLE 2.—*Summary of karyotypic variation in populations of* Thomomys umbrinus intermedius *from the Santa Rita and Patagonia mountains, Arizona.*

Population	♀	♂	M and SM*	ST*	A*	Minute chromosomes	Morphology of X-chromosome
Madera Canyon, Santa Rita Mts.	1	3	10	12	54	6	ST
Gardner Canyon, Santa Rita Mts.	2	–	8	12	56	6	ST
Sycamore and Italian canyons, Patagonia Mts.	6	10	10	10	56	6	ST

* M = metacentric; SM = submetacentric; ST = subtelocentric; A = acrocentric.

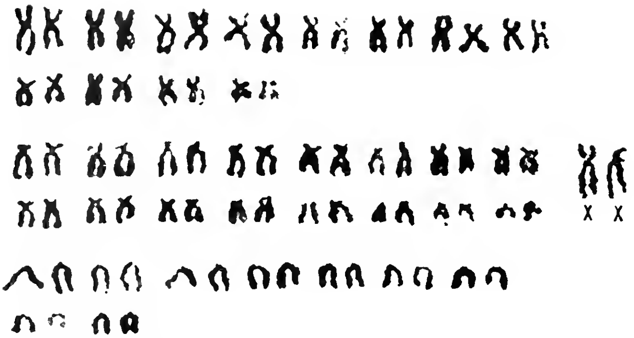

FIG. 3.—Karyotype of *Thomomys bottae alienus* Goldman (♀, UA 14989). About 4.5 mi S St. David, San Pedro River Valley, Cochise Co., Arizona.

T. u. intermedius Mearns, is represented by three sampled populations that are characterized by a diploid number of 78, a high number of acrocentrics in the autosomal complement, and the presence of three pairs of minute acrocentrics (these latter elements are absent in all karyotypes of *T. bottae*). Slightly different karyotypes were found for each of these samples (see Table 2 and Figs. 4, 5, and 6). Again, the samples differ in the number of acrocentrics and in the relative number of each type of biarmed chromosomes. Unlike *T. bottae*, the X-chromosomes of all *T. umbrinus* are subtelocentric and do not vary in morphology.

The various population karyotypes of *T. bottae* have little similarity with those of *T. umbrinus*. These two species differ noticeably in the number of biarmed and uniarmed chromosomes present in their respective complements (see Table 3). From Table 3 it is also apparent that the total known range of variation within each species is less than the difference between them.

T. bottae × *T. umbrinus hybrids.*—The number of differences between the karyotypes of the two species facilitates the determination of any gene flow between them, since hybrids can be readily detected by the number of acrocentric chromosomes present in their complements. In the sample of both species from the sympatric locality in the Patagonia Mountains, a

TABLE 3.—*Chromosome features of populations of* Thomomys bottae *and* Thomomys umbrinus *in southern Arizona, including total known range of variation for each species.*

Feature	*T. bottae*	*T. umbrinus*
Diploid number	76	78
Number of metacentrics and submetacentrics	22–32	8–10
Number of subtelocentrics	32–46	10–12
Number of acrocentrics	0–18	54–56
Number of minute chromosomes	0	6

TABLE 4.—*Summary of chromosome features between sampled populations of* Thomomys bottae modicus *and* T. umbrinus intermedius *from the Patagonia Mountains, Santa Cruz Co., Arizona, and of the four proposed hybrids.*

		F_1 hybrids	Backcross hybrids			
Feature	*T. bottae*	(UA15158)	UA14991	UA15424	UA15935	*T. umbrinus*
Diploid number	76	77	76	76	77	78
Number of metacentrics and submetacentrics	32	21	31	33	16	10
Number of subtelocentrics	42	26	40	40	13	10
Number of acrocentrics	0	28	3	1	48	56
Number of minute chromosomes	0	3	0	0	4	6
Morphology of X-chromosome*	SM	SM/ST	?	?	?	ST

* SM = submetacentric; ST = subtelocentric.

single individual examined (UA 15158) possessed a diploid number of 77, and in all aspects of the karyotype it was intermediate between the two species (see Fig. 7 and Table 4). Such total intermediacy when compared to both species karyotypes from this locality (see Figs. 2, 6, and 7) leaves little doubt but that the specimen represents a first generation hybrid between *T. bottae* and *T. umbrinus*. The animal was a pregnant adult female with three nearly full-term and apparently normal embryos. The hybrid is thus judged to be fertile, and backcrossing to either parental species presumably occurs, at least to a limited degree.

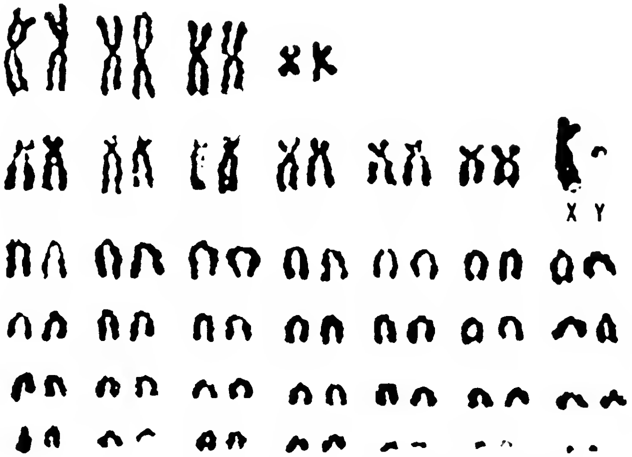

FIG. 4.—Karyotype of *Thomomys umbrinus intermedius* Mearns (♂, UA 14987). Gardner Canyon, Santa Rita Mts., Santa Cruz Co., Arizona.

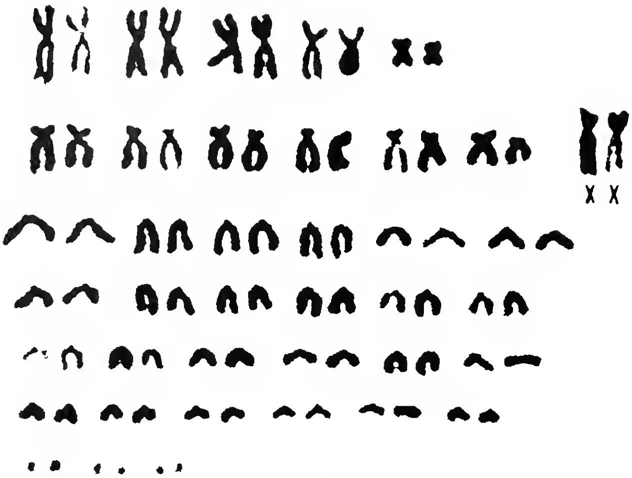

FIG. 5.—Karyotype of *Thomomys umbrinus intermedius* Mearns (♀, UA 15343). Madera Canyon, Santa Rita Mts., Santa Cruz Co., Arizona.

Three additional specimens examined from this population are judged to be backcross hybrids on the basis of the number of acrocentric elements in their respective karyotypes (Table 4). Two of these (UA 14991, ♀, and UA 15424, ♂) are the probable results of backcrossing to parental *T. bottae*, and one (UA 15935, ♀) the result of backcrossing to parental *T. umbrinus*. A more detailed analysis of this hybridization is presently under investigation and will be presented in the future.

DISCUSSION

Ecological considerations.—Correlated with the karyotypic distinctness of the two species of *Thomomys* is a somewhat marked ecological separation in areas where the two are found in sympatry or near sympatry. *Thomomys umbrinus* was found only in the oak woodland through oak-pine woodland in the intermediate elevations of the Santa Rita and Patagonia mountains. These are two of the four mountain ranges in Arizona where presumed specimens of *T. umbrinus* were reported by Cockrum (1960). The other two populations allocated to *T. umbrinus* inhabit equivalent habitats in the Pajarito and Huachuca mountains. We have not yet sampled these populations for karyotypic analyses, but have examined specimens from these areas.

In the Huachuca Mountains, specimens obtained from what could be considered typical habitat for *T. umbrinus* (*i.e.*, oak woodland) in Carr Canyon were found to be *T. bottae*, referable to the subspecies *T. b. proximus* Burt and Campbell. These specimens lack the somewhat distinctive dark, purplish-hued dorsum characteristic of *T. umbrinus*, and even without karyotypes they would not be confused with that species. Hoffmeister and Goodpaster (1954) correctly allocated all of the specimens they examined from

FIG. 6.—Karyotype of *Thomomys umbrinus intermedius* Mearns (♂, UA 14990). Sycamore Canyon, Patagonia Mts., Santa Cruz Co., Arizona.

the Huachuca Mountains to *T. bottae.* However, they incorrectly identified the material from Carr Peak as *T. umbrinus intermedius* Mearns, and on this basis, in part, assumed that only *T. bottae* occurred in the mountain range. Lange (1959) examined the type of *T. u. intermedius* and considered this name as valid and specifically distinct from the Carr Peak material examined by Hoffmeister and Goodpaster. Moreover, both Lange (1959) and Cockrum (1960) consider specimens from Brown Canyon and the vicinity of Panama Mine (near the west gate of Fort Huachuca) as *T. umbrinus.* Specimens examined by one of us (JLP) through the courtesy of Dr. Seth B. Benson from the Peterson Ranch, Sunnyside Canyon, definitely are referable to this species. *Thomomys umbrinus* is unquestionably present in the Huachuca Mountains, therefore, but additional specimens must be collected and karyotyped to enable assessment of their ecological as well as genetical relationships to *T. bottae* in this same mountain range.

Thomomys bottae is not known from the higher elevations of the Patagonia and Santa Rita mountains, although the latter supports well-developed pine forests similar to those occupied by *T. bottae* on more northern mountains in Arizona as well as the adjacent Huachuca Mountains.

Gophers occurring in oak woodland habitats in other mountain ranges in southern Arizona, namely the Santa Catalina, Quinlan, and Chiricahua mountains, have karyotypes identical or similar to those of nearby populations of *T. bottae.* These animals have been considered to be *T. bottae* and not *T. umbrinus* by most authors.

The ecological separation of the two species is quite apparent in Sycamore and Italian canyons of the Patagonia Mountains. Generally, samples of *T. bottae* were obtained only at lower elevations in desert grassland or riparian

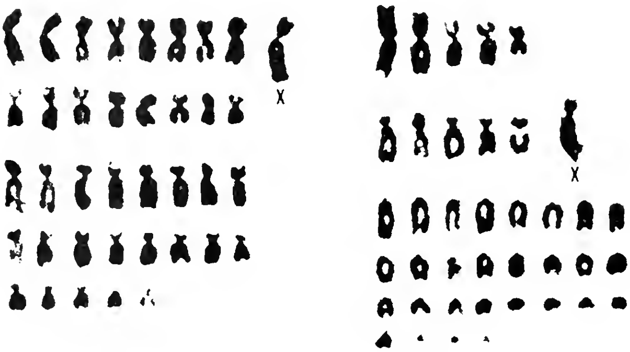

FIG. 7.—Karyotype of F_1 hybrid between *T. bottae modicus* and *T. umbrinus intermedius* (♀, UA 15158). The proposed parental genomes are separated, with that of *T. bottae* on the left and that of *T. umbrinus* on the right.

habitats (3600–4800 ft), while *T. umbrinus* was found in open oak or juniper-oak woodlands (4500–6000 ft). Unlike the spatial separation of *T. bottae* and *T. umbrinus* at two localities in northwestern Chihuahua (Anderson, 1966), the two species are sympatric along a narrow zone in the flat ground bordering the stream beds of Sycamore and Italian canyons (*ca.* 4400–4850 ft; see Fig. 8). The floors of the canyons in this area consist of a mesquite-desert willow-grassland association with a few riparian elements (*e.g.*, cottonwoods and sycamores) in Sycamore Canyon and a narrow desert riparian woodland community in Italian Canyon. Although both species were trapped on the canyon floors in such communities, *T. umbrinus* appears more limited to the open, rockier hillsides where Emory and Mexican blue oaks (*Quercus emoryi* and *Q. oblongifolia*) predominate.

Hybridization.—At present, little more than speculative remarks can be made concerning the natural hybridization between *T. bottae* and *T. umbrinus* in Sycamore and Italian canyons of the Patagonia Mountains. The single F_1 hybrid and the three individuals considered by their karyotypes to be backcross hybrids all were trapped within the narrow zone of sympatry (see Fig. 8, note localities of hybrids), an indication that the main populations of both species are not affected to a great extent by the hybridization. Although the F_1 hybrid was fertile and backcrossing to both parental species is, therefore, judged to occur, lack of extensive introgression coupled with the narrowness of the hybrid zone indicates restricted gene flow between *T. bottae* and *T. umbrinus* at this single locality.

Historical considerations.—The present distributions of many species in the inland Southwest have been explained in part by the shifting climatic and vegetational events of the late Pleistocene (summarized by Martin and Mehringer, 1965). Some populations that were continuous during late glacial to post-glacial times became disjunct, and interconnections were formed between other previously disjunct populations. This is apparent in the cases

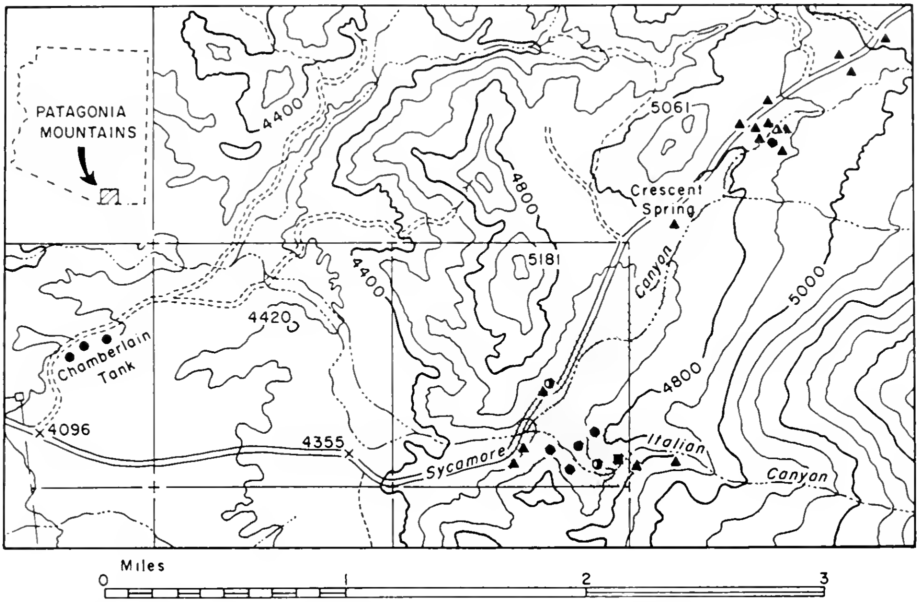

FIG. 8.—Map of Sycamore and Italian canyons, Patagonia Mountains, Santa Cruz Co., Arizona, showing area of sympatric contact between *T. bottae* and *T. umbrinus* (shaded area) and localities where gophers were trapped in relation to zone of contact. Solid circles = *T. bottae;* solid triangles = *T. umbrinus;* solid square = F_I hybrid; half-filled circles = hybrids backcrossed to *T. bottae;* half-filled triangle = hybrid backcrossed to *T. umbrinus.* (Additional specimens of *T. bottae* were trapped from outside the area indicated on map.)

of *T. bottae* and *T. umbrinus.* Their present distributional pattern with "islands" of *T. umbrinus* in a "sea" of *T. bottae,* and the increased contact between the two species in Recent times, have been accompanied by reproductive isolating mechanisms that were inadequate to prevent limited hybridization between the two species in the restricted area of the Patagonia Mountains. Presumably this occurred as the two species came into contact following changes in the vegetation in the present area of sympatry. Present hybridization between other groups of vertebrates (for example, *Cnemidophorus*—Zweifel, 1962; Lowe and Wright, 1966) and plants (for example, oaks—Tucker, 1963) in the same general area has been attributed to these factors also.

Much of the current vegetation between the Santa Rita, Huachuca, and Patagonia mountains is desert grassland with scattered oaks and mesquites. A more well-developed oak woodland is present between the Patagonia and Pajarito mountains, following elevational contours into and out of Sonora. If the oak woodland were lowered 400 m during the late Pleistocene (Wisconsin glaciation), as suggested by Martin and Mehringer (1965), all of these ranges would have been connected by well-developed oak woodland. Such habitats appear ideal for *T. umbrinus* in these mountain ranges today.

Thomomys umbrinus is presently widespread on the Mexican Plateau, and was once undoubtedly more widely spread in southern Arizona. The area that *T. umbrinus* now inhabits is known to contain the greatest degree of Mexican floral influence anywhere in Arizona (Marshall, 1957; Martin, 1963; Lowe, 1964); this applies especially to the vegetation at the lower and intermediate elevations. The two main factors contributing to the presently isolated state of *T. umbrinus* populations in Arizona were, then, the withdrawal of the extensive woodlands of the late glacial period to their present positions during the past 10,000 years (Martin and Mehringer, 1965), and the spread of *T. bottae* through the lower elevations in recently invaded desert scrub and desert grassland communities.

In areas where *T. bottae* is present in the higher pine forests and the lower valley floors (for example, in the Huachuca Mountains), *T. umbrinus*, so far as is known, is restricted to the intermediate elevations in the oak zones. However, in mountain ranges where no *T. bottae* are found in upper elevations (for example, in the Santa Rita Mountains), *T. umbrinus* inhabits both the oak woodland and the pine forests. It is apparent, therefore, that the present restriction of *T. umbrinus* to the oak zone is due in part to displacement through inability to compete with *T. bottae*. In all cases where *T. bottae* and *T. umbrinus* approach or meet in Arizona, the former occupies the more friable soils of the valley floors and mountain tops, whereas *T. umbrinus* is restricted more to the harder soils of the somewhat steeply inclined middle elevations. *Thomomys bottae* probably does not compete with *T. umbrinus* for these somewhat marginal habitats, for even in mountain ranges where *T. umbrinus* is absent, *T. bottae* populations are scarce in the indurate soils of the oak zones. The ability of *T. umbrinus* to survive in these habitats appears to have resulted in the present spatial and ecological relationships of the two species of gophers in southern Arizona.

Taxonomic conclusions.—A basic problem to systematics has arisen from the above discussion—that is, whether to consider *T. bottae* and *T. umbrinus* in Arizona as distinct species that infrequently hybridize, or to consider them subspecies that intergrade. At the present time, it would appear more important not to overshadow the biological findings with nomenclatorial problems. In this respect, we judge that consideration of the two forms as distinct species is in greater accord with the biological inferences. This interpretation allows for a greater appreciation and understanding of the past historical events, present distributional and ecological discordance, and great chromosomal distinction between *T. bottae* and *T. umbrinus*.

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SPECIMENS EXAMINED

Specimens prefixed by UA refer to those catalogued in the mammal collection, Department of Biological Sciences (Zoology), University of Arizona, Tucson. Other numbers refer to the personal field catalogue of one of us (JLP).

Thomomys bottae catalinae (2♂, 3♀).—ARIZONA. *Pima Co.*: Snow Bowl, Mt. Lemmon, Santa Catalina Mts. (JLP 737); Bear Wallow, Santa Catalina Mts. (UA 15411-14).

Thomomys bottae modicus (8♂, 9♀).—ARIZONA. *Pima Co.*: Tucson (UA 15149-50, JLP 688); Molino Basin, Santa Catalina Mts. (UA 15415-16). *Santa Cruz Co.*: 1.1 mi E Amado (UA 15410); Yerba Buena Ranch (UA 14992, UA 15144, UA 15154); mouth of Italian Canyon, Patagonia Mts. (UA 14988, UA 15409, UA 15943-44); Chamberlain Tank, Patagonia Mts. (UA 14993, UA 14906-07); Sycamore Canyon, Patagonia Mts., 9.3 mi E Jct Arizona 82 and Washington Camp Road (UA 15942).

Thomomys bottae extenuatus (1♂, 1♀).—ARIZONA. *Cochise Co.*: 0.2 mi E Jct Arizona 181 and Turkey Creek Canyon Road, Sulfur Springs Valley (UA 15145); 3.9 mi E Jct Arizona 181 and Turkey Creek Canyon Road, Sulfur Springs Valley (UA 15151).

Thomomys bottae collinus (3♂, 5♀).—ARIZONA. *Cochise Co.*: El Coronado Ranch, West Turkey Creek Canyon, Chiricahua Mts. (UA 15154, UA 15147); 1.7 mi E El Coronado Ranch, West Turkey Creek Canyon, Chiricahua Mts. (UA 15152, UA 15148); Rucker Canyon, Chiricahua Mts., *ca.* 5600 ft (UA 15146, UA 15153); 1 mi below Rustlers Park, Chiricahua Mts. (UA 15406-07).

Thomomys bottae proximus (1♂, 3♀).—ARIZONA. *Cochise Co.*: Carr Canyon Ranch, Huachuca Mts. (UA 15404-05); 0.5 mi N Clark Spring, Carr Canyon, Huachuca Mts. (UA 15417-18).

Thomomys bottae alienus (1♀).—ARIZONA. *Cochise Co.*: *ca.* 4.5 mi S St. David on US 80 (UA 14989).

Thomomys bottae pusillus (1♂, 1♀).—ARIZONA. *Pima Co.*: *ca.* 1.5 mi below Kit Peak National Observatory, Quinlan Mts. (UA 15419-20).

Thomomys umbrinus intermedius (10♂, 12♀).—ARIZONA. *Santa Cruz Co.*: Madera Canyon, Santa Rita Mts. (UA 15343, UA 15163, UA 15403, UA 15001); Gardner Canyon, Santa Rita Mts. (UA 14986-87); Sycamore Canyon, Patagonia Mts., *ca.* 9.9 mi E Jct Arizona 82 and Washington Camp Road (UA 14985) and *ca.* 9.3 mi E Jct Arizona 82 and Washington Camp Road (UA 15937-41); *ca.* 1.2 mi E Crescent Spring (UA 15156, UA 15012); *ca.* 0.4 mi E Crescent Spring (UA 15160); *ca.* 0.6 mi E Crescent Spring (UA 14990); Crescent Spring (UA 15159); *ca.* 8.7 mi E Jct Arizona 82 and Washington Camp Road (UA 15408); mouth of Italian Canyon, Patagonia Mts. (UA 15157, UA 14983); Italian Canyon, Patagonia Mts. (UA 14984, UA 15936).

Thomomys bottae × *Thomomys umbrinus* hybrids (1♂, 3♀).—ARIZONA. *Santa Cruz Co.*: Italian Canyon, Patagonia Mts. (UA 15158, UA 15424); Sycamore Canyon, Patagonia Mts., *ca.* 8.7 mi E Jct Arizona 82 and Washington Camp Road (UA 14991) and *ca.* 9.3 mi E Jct Arizona 82 and Washington Camp Road (UA 15935).

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SERUM PROTEIN ELECTROPHORESIS IN THE TAXONOMY OF SOME SPECIES OF THE GROUND SQUIRREL SUBGENUS *SPERMOPHILUS**

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Abstract—1. Serum protein patterns of *Spermophilus undulatus, Spermophilus columbianus* and *Spermophilus beldingi* were analyzed by two-dimensional starch-gel electrophoresis.

2. The patterns, although generally similar, exhibited variation in nine fractions or groups of fractions and these fractions had taxonomic significance at the level of population, subspecies or species. Intraspecific variability of two unidentified protein fractions was observed in *S. undulatus kennicotti* and *S. beldingi* and a third protein polymorphism involving transferrin was also observed in *S. undulatus kennicotti.* Intraspecific divergence between Arctic and sub-Arctic subspecies of *S. undulatus* was found and proteins from the latter show a closer resemblance to *S. columbianus.*

3. The protein characters support present taxonomic concepts of the species of *Spermophilus* that indicate a close relationship between all three species and a closer relationship between *S. undulatus* and *S. columbianus.*

4. Protein characters, as observed in the genus *Spermophilus,* appear to offer great promise as a method for systematic investigation at intraspecific levels where gross morphologic characters are least definitive.

INTRODUCTION

The concept that protein synthesis is dependent on rigid genetic control and is therefore a reflection of the genotype has provided a sound theoretical basis for utilizing physico-chemical characteristics of proteins in taxonomic studies. Among the simpler and more reliable techniques for study of serum protein fractions are paper electrophoresis and starch-gel electrophoresis. The more recent use of starch-gel electrophoresis provides an increased resolving power that results in patterns containing as many as thirty protein fractions in some human sera (Smithies, 1959), in comparison to the usual five fractions observed with paper electrophoresis.

Many different vertebrates including primates (Goodman, 1963) and Rodentia (Blumberg *et al.*, 1960) of the class Mammalia, Reptilia and Amphibia (Dessauer *et al.*, 1962) and fishes (Sanders, 1964) have been investigated with electrophoretic techniques and the data applied to the taxonomy of groups within the respective

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classes. In their excellent review, Dessauer and Fox (1964) concluded that starch-gel electrophoresis showed greatest taxonomic promise at infraspecific and specific levels where the probability was high that proteins of identical mobility had identical structure. Certain proteins have been demonstrated to be polymorphic within a species and under genetic control. In the case of transferrin, which binds serum iron, gene frequencies can be calculated and successfully used to evaluate species and population relationships (Goodman *et al.*, 1965).

In the present investigation the serum proteins of *Spermophilus undulatus*, *Spermophilus columbianus* and *Spermophilus beldingi* were analyzed by two-dimensional starch-gel electrophoresis (Poulik & Smithies, 1958). These species constitute three of the eight species presently classified in the ground squirrel subgenus *Spermophilus* (Hall & Kelson, 1959) and they are of taxonomic interest for several reasons. First, *Spermophilus* is considered the most specialized of the ground squirrel subgenera (Bryant, 1945) and most recently evolved (Black, 1963) yet there is a paucity of gross morphological characters for convincing definition of interspecific relationships. Second, other lines of evidence have been applied to the latter problems that have yielded differing conclusions; zoogeographic evidence (Rand, 1954; MacPherson, 1965) and host–parasite observations (Holland, 1958) indicate a close affinity between *S. undulatus* and *S. columbianus* whereas chromosomal evidence (Nadler, 1963, 1966) suggests an equal degree of divergence between *S. undulatus*, *S. columbianus* and *S. beldingi*. Because introducing evidence from additional characters might resolve these interspecific problems, the present study was undertaken with the following aims:

(1) to determine whether the number and mobilities of fractions comprising the total serum protein pattern can be analyzed to yield reliable taxonomic characters; (2) to determine the appropriate taxonomic level at which the protein characters are applicable; and (3) to test the validity of these characters by correlating and comparing them with known systematic data of *Spermophilus*.

MATERIALS AND METHODS

Serum was obtained from the following animals:

Spermophilus undulatus kennicotti (Ross). Alaska: 30 miles E. of Anaktuvuk Pass, 9 males and 5 females; 6 miles E. of Anaktuvuk Pass, 15 males and 7 females.

Spermophilus undulatus kodiacensis (Allen). Alaska: Kodiak Island, 1 male and 2 females.

Spermophilus beldingi crebrus (Hall). Idaho: Twin Falls Co.; 10 miles N.W. of Buhl, 3 males and 3 females.

Spermophilus beldingi oregonus (Merriam). Oregon: Harney Co.; Malheur Valley, 2 males and 1 female; Burns, 6 males and 4 females.

Spermophilus columbianus columbianus (Ord). Idaho: Adams Co.; Brundage Mountain, 4 males and 10 females.

Blood was drawn from the heart using sterile equipment and the serum was stored at 4°C. Serum proteins were analyzed using a technique for horizontal, two-dimensional, starch-gel electrophoresis (Poulik & Smithies, 1958) combined with a tris-discontinuous buffer system (Poulik, 1957). The procedure was modified as reported by Goodman (1963). Starch blocks were bisected, stained with Nigrosin for 2–5 min (1 g Nigrosin, 30 cc acetic acid, 135 cc methyl alcohol and 135 cc distilled water) and decolorized for 24 hr using the same solution without the dye. Two to three separations of each serum specimen were performed on different days and all runs were carefully compared before recording the protein pattern of an individual animal as a scale indian ink drawing. Fractions with staining density equal to albumin or transferrin were recorded in black, those with faint staining reaction were drawn with open lines and fractions of intermediate intensity were stippled. When question arose regarding the presence or absence of a given fraction, additional runs were made to clarify the problem.

The densely staining fraction with fastest mobility on paper and starch is tentatively labeled albumin and the fraction with slowest migration rate is labeled gamma globulin. Transferrins (*Tf*) were identified in several animals of each species by Fe^{59} radioautography (Smithies, 1959). Transferrin was investigated at the interspecific level by simultaneously running serum samples from each species in one-dimensional starch-gel separations.

RESULTS

The serum protein patterns of *S. undulatus*, *S. columbianus* and *S. beldingi* show an overall similarity in the number of protein fractions and their respective mobilities (Figs. 2–8). However, a careful comparison shows nine major differences, illustrated in Fig. 1, that are exhibited in one or more species or populations and

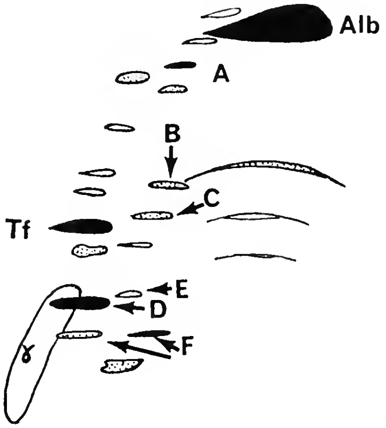

FIG. 1. A hypothetical separation of ground squirrel serum proteins illustrating fractions with taxonomic significance. The inital separation on paper results in a horizontal separation from left to right, followed by starch-gel electrophoresis which produces a vertical separation. The labeled fractions correspond with the following characters: Albumin (Character I), Fraction Group A (II), Fraction B (IV), Fraction C (V), Transferrin or *Tf* (III), Fraction D (VI), Fraction E (VII) and Fraction F (VIII). The number of arc-like fractions constitute Character IX. Gamma globulin, γ, has the slowest mobility on both paper and starch.

they may be evaluated as possible taxonomic characters. Other differences in the protein patterns were observed in some of the figures, but were inconsistent or difficult to evaluate because of faint staining properties. Because fractions other than transferrin were not characterized with regard to chemical structure or function, they are given a letter designation from A through F. It is recognized that similarity in mobility and configuration, as determined by a single technique, does not necessarily indicate identical chemical structure and it should be emphasized that no individual studied contained all nine characters.

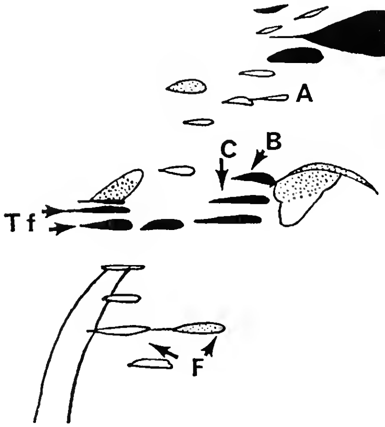

Fig. 2. A protein pattern from *S. undulatus kennicotti* (30 mile population). The albumin is homogeneous. Fraction Group A contains four fractions; Fractions B and C are both present; two transferrins are present; Fractions D and E are absent; and Fraction Group F is not separated. One arc fraction is observed.

For clarity, the nine protein characters observed in *S. undulatus*, *S. columbianus* and *S. beldingi* will be described individually and later comparisons made between taxa. The same data are presented in tabular form for each species in Table 1.

Character I. This character consists of the presence or absence of a homogeneous serum albumin fraction. *S. undulatus* (Figs. 2–6) and *S. beldingi* (Fig. 8) have a homogeneous serum albumin while *S. columbianus* (Fig. 7) showed an indication of two fractions migrating with nearly identical mobilities on starch.

Character II. This character, designated Fraction Group A, is composed of three to four fractions that migrate slightly slower than albumin (Fig. 1). Both populations of *S. undulatus kennicotti* are characterized by Fraction A containing four individual fractions having an identical group configuration (Figs. 2, 3, 4, 5). In contrast, *S. undulatus kodiacensis* has only three fractions and these assumed a different configuration (Fig. 6). This pattern seen in *S. undulatus kodiacensis* is found to be identical to Fraction Group A in *S. columbianus* (Fig. 7). Fraction Group A of *S. beldingi* (Fig. 8) contains three fractions that exhibit a configuration different from the other taxa. Therefore, Character II shows both interspecific and intraspecific variability without individual variation.

TABLE 1—COMPARISON OF PROTEIN CHARACTERS OF *S. undulatus*, *S. columbianus* AND *S. beldingi*

Character	*S. undulatus kennicotti*		*S. u. kodiacensis*	*S. beldingi*	*S. columbianus*
	30 mile pop.	6 mile pop.			
I Homogeneous albumin	+	+	+	+	0
II Fraction Group A	4 fractions	4 fractions	3 fractions, same as *S. columbianus*	3 fractions	3 fractions, same as *S. u. kodiacensis*
III Number of transferrins	8/14 have 2*Tf*	1	1	1	1
Transferrin mobility	Slow	Slow	Slow	Fast	Fast
IV Presence of Fraction B	4/14	0/22	3/3	1/10,* 1/3,† 6/6‡	10/10
V Presence of Fraction C	8/14	15/22	3/3	19/19	10/10
VI Presence of Fraction D	0	0	+	+	+
VII Presence of Fraction E	0	0	0	+	+
VIII Separation of two fractions comprising Fraction F	No	No	Yes	Yes	Yes
IX Number of arc fractions	1	1	1	1	3

* = *S. beldingi* from Burns, Oregon; † = *S. beldingi* from Malheur Valley, Oregon; ‡ = *S. beldingi* from Buhl, Idaho.

Character III consists of the number of transferrin fractions and their mobilities (Fig. 1). The population of *S. undulatus kennicotti* from 30 miles E. of Anaktuvuk Pass is polymorphic with respect to transferrin because 8 of 14 animals have two darkly staining bands with nearly identical mobility (Figs. 2, 3), both of which bind Fe^{59}. At present, the slower fraction is designated as a second molecular form of transferrin. The population of *S. undulatus kennicotti* from 6 miles E. of Anaktuvuk Pass is homogeneous with respect to transferrin, and only one fraction, migrating with a mobility identical to the faster fraction from the 30 mile population,

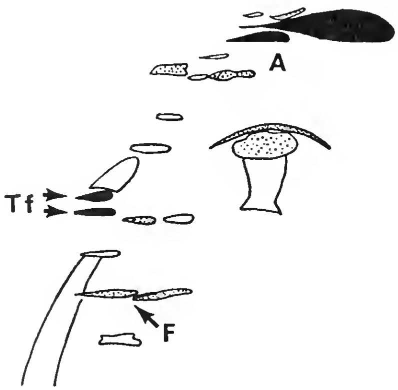

Fig. 3. A protein pattern from *S. undulatus kennicotti* (30 mile population). This animal differs from the animal in Fig. 2 by an absence of Fractions B and C. Two transferrins are present. Fraction Group F is continuous.

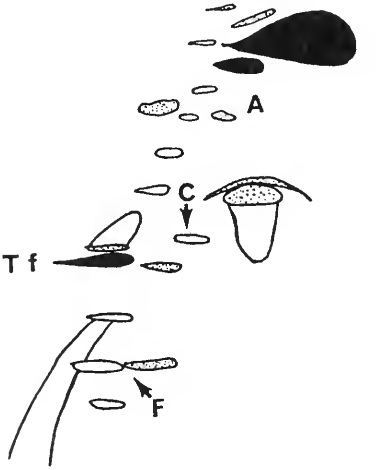

Fig. 4. A protein pattern from *S. undulatus kennicotti* (30 mile population). This specimen lacks Fraction B, but Fraction C is present and only one transferrin (*Tf*) is observed. Note the absence of a separation within Fraction Group F.

is observed in each of the 22 animals (Fig. 5). On the basis of the transferrin polymorphism it is possible, when the populations are considered as a whole, to differentiate the two by this character.

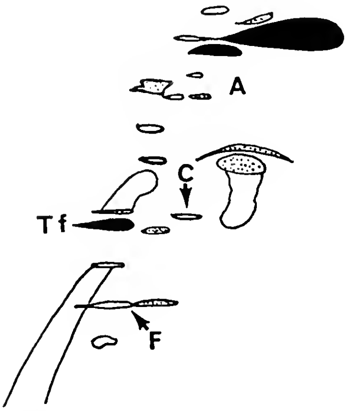

FIG. 5. A protein pattern from *S. undulatus kennicotti* (6 mile population). Fraction B is absent which is characteristic of all specimens from the 6 mile population. A single transferrin (*Tf*) is present. Fraction F is continuous.

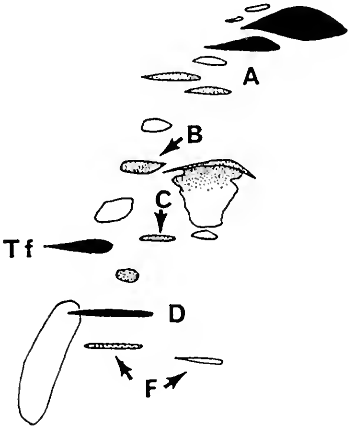

FIG. 6. A protein pattern from *S. undulatus kodiacensis*. Fraction Group A contains three fractions with a configuration similar to *S. columbianus* (Fig. 7). Fractions B and C are present and a single transferrin (*Tf*) with a mobility identical to the faster fraction of *S. undulatus kennicotti* is observed. A darkly staining Fraction D is present whereas Fraction E is absent. The two fractions comprising F are separated.

All 3 specimens of *S. undulatus kodiacensis* (Fig. 6) have a single transferrin fraction that migrates at the same rate as the faster transferrin of both population samples of *S. undulatus kennicotti*, which suggests a common relationship between the three populations studied.

S. columbianus (Fig. 7) and *S. beldingi* (Fig. 8) each have a single transferrin fraction and the transferrins of both species have an identical mobility that is faster than the mobility of *S. undulatus* transferrin.

Character IV consists of a single fraction that migrates slightly more slowly, on both paper and starch-gel, than the fastest arc-like fraction, and it is designated Fraction B (Fig. 1). It stains with moderate or strong intensity. Fraction B was present in 4 of the 14 specimens of *S. undulatus kennicotti* (Fig. 2) from the 30 mile population and absent in all animals from the 6 mile population (Fig. 5).

Fraction B was present in all 3 specimens of *S. undulatus kodiacensis* (Fig. 6), 8 of 19 specimens of *S. beldingi* (Fig. 8) and all 10 specimens of *S. columbianus* (Fig. 7).

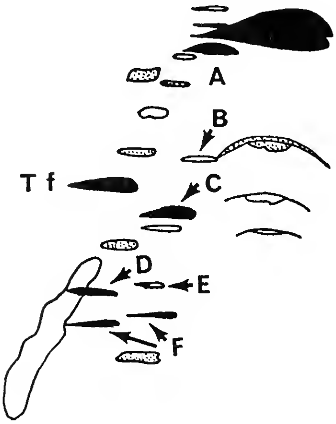

FIG. 7. A protein pattern from *S. columbianus columbianus*. The albumin is notched, indicating a heterogeneous fraction. Three fractions comprise Fraction Group A and their configuration resembles *S. undulatus kodiacensis* (Fig. 6). Both Fractions B and C are present and a single transferrin (*Tf*) migrates more rapidly than Fraction C and the *Tf* of *S. undulatus* (Figs. 2–6). Fractions D and E are present and Fraction Group F is separated. Three arc fractions are observed, a characteristic feature of the species.

Character V. Fraction C constitutes Character V. It migrates faster than transferrin, slower than Fraction B and is located diagonally between the two fractions on the two-dimensional separation (Fig. 1). Staining intensity varies between individual specimens from moderate to strong.

Among specimens of *S. undulatus kennicotti*, from the 30 mile population Fraction C was observed in 8 of 14 specimens (Fig. 2, 4) and 15 of 22 specimens from the 6 mile population (Fig. 5). All specimens of *S. undulatus kodiacensis* (Fig. 6), *S. columbianus* (Fig. 7) and *S. beldingi* (Fig. 8) had patterns containing Fraction C, and no geographic variation was seen.

Character VI is a strongly staining fraction, designated Fraction D, that migrates faster than gamma globulin on paper but slower in starch (Fig. 1). Fraction D is absent in both populations of *S. undulatus kennicotti* (Figs. 2, 3, 4 and 5) and present in *S. undulatus kodiacensis* (Fig. 6), *S. columbianus* (Fig. 7) and *S. beldingi* (Fig. 8). There is no intrapopulational variation.

Character VII consists of a small lightly or moderately staining fraction, Fraction E, that migrates slightly faster than Fraction D on both paper and starch-gel (Fig. 1). Fraction D is absent in both populations of *S. undulatus kennicotti* (Figs. 2–5) and in *S. undulatus kodiacensis* (Fig. 6). It is present in *S. columbianus* (Fig. 7) and *S. beldingi* (Fig. 8).

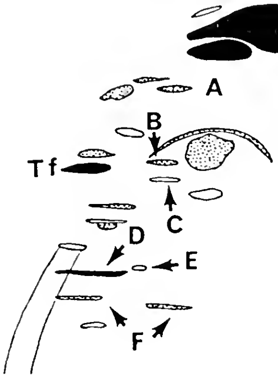

FIG. 8. A protein pattern from *S. beldingi crebrus*. Fraction Group A contains three fractions with different configuration from *S. undulatus* and *S. columbianus*. Fractions B, C, D and E are present. A single transferrin (*Tf*) with mobility more rapid than Fraction C and similar to *Tf* of *S. columbianus* is present. Fraction Group F is separated.

Character VIII consists of two fractions that migrate more slowly than Fraction E on starch but at the same or faster rate on paper, and they are designated Fraction Group F (Fig. 1). The two fractions are separated by a gap in *S. undulatus kodiacensis* (Fig. 6), *S. columbianus* (Fig. 7) and *S. beldingi* (Fig. 8) that is produced by more rapid migration of one fraction during the initial paper run. Conversely, Fraction Group F is not separated by a gap in either population of *S. undulatus kennicotti* (Figs. 2, 3, 4, 5).

Character IX. The number of arc-like fractions observed in the protein pattern varies. *S. undulatus kennicotti*, *S. undulatus kodiacensis* and *S. beldingi* patterns are characterized by one arc fraction whereas *S. columbianus* patterns (Fig. 7) contain three arc fractions.

DISCUSSION

The present study demonstrates that serum protein patterns from three related ground squirrel species can be analyzed to provide nine potential taxonomic characters. The theoretical basis for the valid use of proteins as characters rests upon the assumption that they are under genetic control and differences in genotype will be reflected by an alteration in chemical structure and behavior. However, before accepting these characters as reliable indicators of taxonomic relationships, it is important to attempt to exclude protein differences influenced by the stage of development or physiologic state of the animal (Dessauer & Fox, 1964). In this study, no juvenile or pregnant animals were studied and no differences in pattern could be attributed to the sex of the animal. With respect to seasonal influences, *S. undulatus kodiacensis* specimens were obtained in late April 1965, *S. beldingi* specimens were collected from 27 May–25 June 1965, and *S. columbianus* specimens were collected on 19 August 1965. The two populations of *S. undulatus kennicotti* that showed the greatest intraspecific variation in proteins were collected between 20–30 August 1965. Animals were not examined just before or after hibernation. These observations, we believe, indicate that the proposed protein characters are not due to non-genetic variation.

Protein characters appear definitive at the species level where Characters I, II, III, VI, VII, VIII and IX may be used alone or in combination (Table 1) to distinguish individual species, and these characters appear fully as diagnostic as such gross morphological characters as pelage color, size, etc. (Howell, 1938). Two taxonomic conclusions at the species level are suggested by the protein characters derived from this investigation. First, *S. undulatus*, *S. beldingi* and *S. columbianus* all show a certain general similarity in their protein patterns that suggests a common ancestral relationship, although each exhibits a number of characteristic features. *S. beldingi* is unique in its manifestation of Character II, by a combination of Characters I and IX it can be distinguished from *S. columbianus*, and utilizing Characters III and VII it can be distinguished from *S. undulatus*. *S. columbianus* has two unique characters, I and IX, yet it exhibits a similarity and presumably close relationship to *S. beldingi* with respect to Characters III, VI, VII and VIII.

Second, it is pertinent that *S. undulatus kennicotti* and *S. undulatus kodiacensis*, which share a number of characters that distinguish them from the other species (Table I), also differ with respect to Characters II, VI and VIII. In fact, these latter characters suggest a close relationship between *S. undulatus kodiacensis* and *S. columbianus* whereas *S. undulatus kennicotti* might be considered more divergent. The validity of these seemingly paradoxical observations receives support from zoogeographic and ectoparasite studies. Rand (1954) suggests that *S. undulatus* and *S. columbianus* originated from the same stock which became separated by continental glaciation. One part survived in the Beringia refugium during the Wisconsin phase of the Pleistocene and differentiated during the separation to become *undulatus* and the other survived in a refugium south of the ice and became what is now *columbianus*. Holland (1958) compared samples of fleas from *S. undulatus* of Western Alaska and Northern British Columbia with samples from *S. columbianus* and regarded the fleas only weakly differentiated at the subspecies level. These observations suggested the ranges of the two ground squirrels were at one time contiguous (Holland, 1963) and the possibility that they evolved from a single ancestral stock is also strongly suggested by protein data from the present study. MacPherson (1965) also accepts the thesis offered by Rand (1954) and supported by Holland (1958). Therefore, among the three species we have examined, the *kodiacensis* population of *S. undulatus* exhibits a closer degree of relationship to *S. columbianus* than that found between any other two species.

Analysis of mitotic chromosomes from species of the genus *Spermophilus* has provided evidence for an equal degree of karyotypic divergence between *S. beldingi* with diploid number ($2n$) of 30, *S. columbianus* $2n = 32$ and *S. undulatus* with $2n = 34$ (Nadler, 1966). Comparison of their chromosomes did not suggest a particularly close relationship between *S. undulatus* and *S. columbianus* because several relatively uncommon types of rearrangements had to be postulated as the mechanisms responsible for their karyotypic divergence. The chromosome data might be interpreted to indicate that the two species diverged less recently than other lines of evidence suggest, but it is generally recognized that no one line of evidence invariably provides unequivocal evidence for satisfying taxonomic decisions.

The subspecific divergence between *S. undulatus kennicotti* and *S. undulatus kodiacensis*, which is suggested by protein Characters II, VI and VIII, correlates with Holland's (1958, 1963) observations that Arctic and sub-Arctic populations of *S. undulatus* are parasitized by different species of fleas. He postulated a possible intraspecific divergence within these ground squirrels, although it was recognized that the differences could be explained by a dependence of the fleas upon ecologic factors other than the host. Perhaps these three lines of evidence, mammalian morphology, Siphonapteran morphology and protein analysis, may be interpreted as indicating differing rates of evolutionary divergence from what must have once been a common ancestral gene pool. The Arctic subspecies of *S. undulatus* may have diverged farther from the ancestral genotype than sub-Arctic subspecies which appear to share a greater number of common characteristics with *S. columbianus*. It should, of course, be emphasized that the several evidences of divergence manifested by *S. undulatus* are of a low degree of magnitude and do not imply achievement of species status, although they do suggest the probability of incipient speciation within *S. undulatus*.

The two subspecies of *S. beldingi* that were studied could not be differentiated by trenchant protein characters. However, the frequency of Fraction B in two populations of *S. beldingi oregonus* was 1/10 and 1/3 and in *S. beldingi crebrus*, it was 6/6. This fraction, constituting Character IV, appears to be a genetically controlled protein that exists in a polymorphic state similar to, but distinct from, transferrin and haptoglobin. As such, its gene frequency might be determined in larger samples from additional populations and thereby serve as a means for distinguishing these two subspecies of *S. beldingi*.

Differences in protein pattern between populations of *S. undulatus kennicotti* are quite striking and they involve two apparently unrelated fractions (Table 1). First, 8 of 14 specimens of *kennicotti* from the 30 mile population exhibit two transferrin fractions as judged by the ability of both to bind Fe^{59}. In contrast, sera from the 22 animals obtained 6 miles from Anaktuvuk Pass contain only one transferrin. Thus, the two populations can be differentiated on the basis of the frequency of one versus two transferrins; similar observations have been reported in primates (Goodman *et al.*, 1965) and reptiles (Dessauer *et al.*, 1962). A second population difference consists of the presence of a low frequency of Fraction B (4/14) in the 30 mile *kennicotti* population and a complete absence in the 6 mile population (0/22). The chemical identity and function of this fraction are not known: it exists in a polymorphic state in both *S. undulatus kennicotti* and *S. beldingi*, whereas it is present in all samples of *S. undulatus kodiacensis* and *S. columbianus*. As mentioned in the discussion of this fraction in *S. beldingi*, calculation of its frequency in larger population samples might provide an additional reliable indicator of population composition that could be employed with transferrin in the study of *kennicotti* populations. A third protein, Fraction C, exhibits a nearly equal degree of variation in the two *kennicotti* populations and therefore this fraction does not aid in their differentiation, although the fact that all three specimens of *S. undulatus kodiacensis* manifested this fraction suggests that Character V might be applicable at the subspecies level if larger samples were studied.

Because of the differences shown to exist between the proteins of ground squirrels from the 30 and 6 mile localities, it is necessary here to consider the taxonomic status of specimens from the Anaktuvuk Pass region and the geographic distribtuion of animals examined in the present study. Concerning taxonomic status, Bee & Hall (1956) examined a large sample of *S. undulatus* from the entire Arctic slope of Alaska, including specimens from Anaktuvuk Pass and Tulugak Lake located 12 miles N. of Anaktuvuk Pass, and concluded that all were referable to a single subspecies, *kennicotti*. Specimens analyzed in the present study were taken from a locality on the Anaktuvuk River (Arctic slope Brooks Range) 6 miles E. of Anaktuvuk Pass and are probably also referable to *kennicotti*. The second population we studied, however, was taken 30 miles E. of Anaktuvuk Pass on Ernie Creek, which is a tributary of the Koyukuk–Yukon River Drainage (south slope Brooks Range). Since animals from the south slope of the Brooks Range have not yet been studied in detail, our sample from the 30 mile population can be only tentatively regarded as *kennicotti* and the possibility that they are referable to a different subspecies, perhaps *osgoodi*, is open to consideration.

There are no obvious physical barriers at the divide that might separate the two populations of *S. undulatus* we studied, although we did observe that the terrain even in mid-August was wet and poorly drained for about 2 miles on either side and that area may be unsuitable for burrow construction. Future studies might be profitably directed toward analysis of proteins from larger samples and examination of additional north and south slope colonies in an attempt to further characterize and explain the mechanisms responsible for the divergence we observed within *S. undulatus kennicotti*.

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THE SYSTEMATIC POSITION OF THE BATS *DESMODUS* AND *CHILONYCTERIS*, BASED ON HOST-PARASITE RELATIONSHIPS (MAMMALIA: CHIROPTERA)[1]

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Patterson (1956) has pointed out that the fossils and ectoparasites of bats provide very little evidence which can be used in clarifying the problems of phylogeny in the order Chiroptera. Indeed, chiropteran fossils are scarce, and the majority of chiropteran ectoparasites belong to groups that, having a life history stage off the body of the host, do not show notable specificity. Another factor detracting from the use of ectoparasites is the intimate ecological association existing between bats of different groups, particularly those found in caves, holes in trees, etc., where, occasionally, several species roost together. This behavior favors, without doubt, polyhaematophagy, and there are striking cases of this such as the presence of fleas of the family Ischnopsyllidae on bats of the distantly related families Molossidae (*Tadarida* Rafinesque) and Noctilionidae (*Noctilio* Linnaeus). However, host-parasite relationships may yet prove to be of value in shedding new light on phylogenetic problems in Chiroptera. It must be realized that we still know little about such relationships in the majority of bats and that only in the last few years have careful, well-documented collections of the ectoparasites been made.

In view of these facts, it becomes particularly important to study a group of ectoparasites, such as the Spinturnicidae (Acarina, Mesostigmata) which apparently show great host

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specificity (Rudnick, 1960; Machado-Allison, 1965a), and also show peculiar modifications in their life cycle (Baer, 1952; Rudnick, *op. cit.*), for instance, ovoviviparity and reduction in number of nymphal stages.

In the past few years I have been studying the taxonomy of the Neotropical Spinturnicidae, especially of the genus *Periglischrus* Kolenati (Machado-Allison, 1965b), which is intimately related to the bats of the family Phyllostomidae. Comparing the arrangement of the genera and subfamilies of Phyllostomidae, based on the work of Miller (1907) and Simpson (1945), now accepted by most mammalogists, with certain data offered by the relationships of Spinturnicidae and the bats, I find some significant disagreements which I want to point out.

According to Simpson (*op. cit.*), the superfamily Phyllostomoidea includes the families Phyllostomidae and Desmodidae. Simpson divided the family Phyllostomidae into seven subfamilies: Chilonycterinae, Phyllostominae, Glossophaginae, Carolliinae, Sturnirinae, Stenodermatinae, and Phyllonycterinae. Among these subfamilies, only one, Phyllonycterinae, is not known to be parasitized by the Spinturnicidae (there are no published data on the Carolliinae, but I have recently found a new spinturnicid on *Rhinophylla pumilio* Peters).

The Chilonycterinae occupy a special position in the Phyllostomidae. The absence of a noseleaf and the lack of articulation of the trochiter with the scapula clearly differentiate these bats from those of the other subfamilies. These features led Winge (1923) to associate the Chilonycterinae with the Noctilionidae in a section of the Phyllostomidae that he called "Mormopini." Novick (1963) found the orientation sounds and associated anatomical features of the Chilonycterinae to differ sharply from those of other phyllostomids.

Spinturnicidae have not been found on the Noctilionidae, and the only South American form that I have found on *Chilonycteris* Gray presents morphological characteristics so peculiar that I have considered it to belong to a genus *Cameronieta* Machado-Allison, distinct from *Periglischrus* (Machado-Allison, 1965a). The other subfamilies of Phyllostomidae are

TABLE 1. Host-parasite relationships of Phyllostomidae with Spinturnicidae.

Spinturnicid species	Chiropteran genera	Present subfamilial assignment
Cameronieta thomasi	*Chilonycteris*	Chilonycterinae
Periglischrus acutisternus	*Phyllostomus*	
Periglischrus torrealbai	*Phyllostomus*	Phyllostominae
Periglischrus parvus	*Micronycteris*	
Periglischrus setosus	*Glossophaga*	
Periglischrus squamosus	*Anoura*	Glossophaginae
Periglischrus hopkinsi	*Lionycteris*	
Periglischrus ojastii	*Sturnira*	Sturnirinae
Periglischrus iheringi	*Artibeus*, *Vampyrops*, etc.	Stenodermatinae
Periglischrus sp.	*Rhinophylla*	Carolliinae
Periglischrus herrerai	*Desmodus*	Desmodidae

parasited by species of *Periglischrus* (three species on Glossophaginae, three on Phyllostominae, one on Carolliinae, one on Sturnirinae, and one on Stenodermatinae; see Table 1).

Desmodus rotundus E. Geoffroy, family Desmodidae, is the host of the species *Periglischrus herrerai* Machado-Allison, which clearly belongs to the genus *Periglischrus.* In orientation behavior *Desmodus* resembles phyllostomid genera (Novick, *op. cit.*).

The evidence presented here indicates that a reappraisal of the familial relationships of the Chilonycterinae and the Desmodidae is in order. I would suggest that rather than being a subfamily of the Phyllostomidae, the chilonycterines may form a distinct family. The desmodids, on the other hand, may be no more than a subfamily of the Phyllostomidae.

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SECTION 2—ANATOMY AND PHYSIOLOGY

Form and function are intimately related. It is difficult to consider one for long or at all thoroughly without considering the other.

In comments elsewhere we apply a concept of organizational levels. In taxonomy, classification begins with individuals and proceeds through local aggregates or populations, geographic variants, subspecies, and species, and on to groupings at the level of higher categories. In ecology, the individual organism is the basic unit, then progressively more inclusive and more complex levels are local populations of single species, local communities of many species, larger ecosystems, and finally the entire biosphere of life-supporting parts of the surface of the Earth. Similarly in anatomy and physiology there are organizational levels. However, in these fields the individual is the largest unit instead of the smallest, except as we may speak of the anatomical characters of a species or other taxon. Form or function may be studied at the biochemical or molecular level, or at progressively higher levels through more complex molecules, mixtures and solutions, organelles, cells, tissues, organs, systems, and finally to the organism in its entirety.

The study of anatomy began at the gross level and only after the invention of the microscope and development of special techniques of preparing materials did histological and cytological studies become possible. The recent development of the electron microscope has added several orders of magnitude to the possibilities of studying fine structure. Physiology developed later than gross anatomy and in many ways paralleled chemistry and physics.

Our selection of examples is a modest one, drawn from a rich field, and we will have to be content with the above mention of the broad scope of anatomy and physiology, inasmuch as none of our selections has electron photomicrographs or histochemical analyses. The selections do, nevertheless, serve to illustrate some fundamental biological concepts.

The concept of homeostasis was conceived and broadly applied in physiology. The concept is relevant, at least by analogy, in ecology under the guise of the "balance of nature," recently expanded to include a sizable vocabulary of terms such as "feedback regulatory mechanism" and "damped cycles." We judge that homeostasis or the tendency of an organism to maintain internal conditions at a dynamic equilibrium is the most general concept of physiology, and that homology is the most general concept of anatomy.

The short paper by Hill that begins this section presents one simple anatomical problem, and at the same time presents the concept of homology and the problems of interpreting it.

The subsequent contributions by Hooper, Hughes, and Mossman are comparative studies within one family (Cricetidae), one order (Marsupialia), and one class (Mammalia), respectively. Each author studied a different part of the animals concerned and attempted to relate his observations to existing knowledge within the systematic framework.

The next paper, by Noback, treats hair, one of the unique features of the Class Mammalia, and theorizes about its adaptive and phylogenetic implications. This article is from a symposium that contains other interesting papers on hair.

The two reprinted papers by Vaughan and Rabb treat form and function together, the former at the level of a taxonomic family, the latter in terms of one set of glands in one species.

Among the classic works in mammalian anatomy is Weber's *Die Säugetiere* (1927, 1928). English mammalogists dating back to Richard Owen and earlier have published many comparative papers on mammalian anatomy (see for example Pocock's *The External Characters of the Pangolins*, 1924). One of the most productive American mammalian anatomists was A. B. Howell, whose *Anatomy of the Wood Rat* (1926) and *Aquatic Mammals* (1930) both have much to offer. Four good recent works of a comparative nature are Rinker's (1954) study of four cricetine genera, Vaughan's (1959) paper on three kinds of bats, Klingener's (1964) treatment of dipodoid rodents, and D. Dwight Davis' major work (1964) on the greater panda. Hildebrand's (1959) paper on locomotion in the cheetah and the horse should be consulted by any student interested in functional anatomy or locomotion. The ANATOMICAL RECORD and JOURNAL OF MORPHOLOGY are two of the more important serial publications containing papers on anatomy.

Among the environmental influences that are important to organisms, and whose effects within the organism must be mitigated, are water, oxygen and other gases, energy sources (food), ions, temperature, and radiation. Most of these factors are touched upon in one or more of the last four papers in this selection in ways that help clarify the adaptive nature of internal, behavioral, and ecological responses. In addition to these aspects of physiology, some areas of special mammalogical interest are hibernation, estivation, thermoregulation, and sensory physiology. Examples appear in Section 4 (Ecology and Behavior) as well as in this section.

A recent paper by Brown (1968), too long to include among our selections, is an excellent example of how physiological adaptations, related in this case to environmental temperature, can be studied comparatively. Other important contributions in mammalian physiology can be found in such journals as COMPARATIVE BIOCHEMISTRY AND PHYSIOLOGY, JOURNAL OF APPLIED PHYSIOLOGY, JOURNAL OF CELL AND COMPARATIVE PHYSIOLOGY, and PHYSIOLOGICAL ZOÖLOGY.

THE HOMOLOGY OF THE PRESEMIMEMBRANOSUS MUSCLE IN SOME RODENTS

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ONE FIGURE

Appleton ('28) has distinguished between the caudofemoralis muscle and the presemimembranosus muscle (of Leche, 1883) on the basis of their respective relations to the 'nerve to the hamstring muscles.' At the same time he has emphasized the importance of considering topographical relations in any discussion of the homologies of muscles. The caudofemoralis, according to this author, crosses over the nerve to the hamstring muscles, dorsal and lateral to this, while the presemimembranosus is medial to the nerve.

In many rodents (Parsons, 1894, 1896) the caudofemoralis arises from the caudal vertebrae and inserts on the medial epicondyle of the femur and the caudal surface of this bone. This is the condition in the white rat (Rattus norvegicus) where I found the muscle dorsal to the nerve. In this rodent, and in the others mentioned below, the caudofemoralis is supplied by the most cephalic branch of the nerve to the hamstring muscles. In the pocket gophers (Thomomys bulbivorus and Geomys bursarius), in the kangaroo rat (Dipodomys spectabilis), and in a specimen of the wood rat (Neotoma fuscipes), I found that the caudofemoralis arises from the ischial tuberosity and inserts on the medial epicondyle. Howell ('26) found that, in some specimens of the wood rat, the muscle originates from the caudal vertebrae, and in all these cases the caudofemoralis is dorsal (that is superficial) to the nerve to the hamstring muscles; so there is no doubt of its identity. In Dipodomys a few fibers of the muscle were medial to the nerve.

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However, in two specimens of a ground squirrel (Citellus richardsonii) and in a mountain beaver (Aplodontia rufa) I found a muscle which originated from the ischium medial (that is deep) to the nerve to the hamstrings, but which otherwise presented the same topographical relations as the caudofemoralis in the other rodents. Like the latter muscle in these other forms, it was supplied by the most cephalic branch of the nerve to the hamstrings. According to the views of Appleton ('28) and Leche (1883), however, this muscle would be a presemimembranosus and not a caudofemoralis.

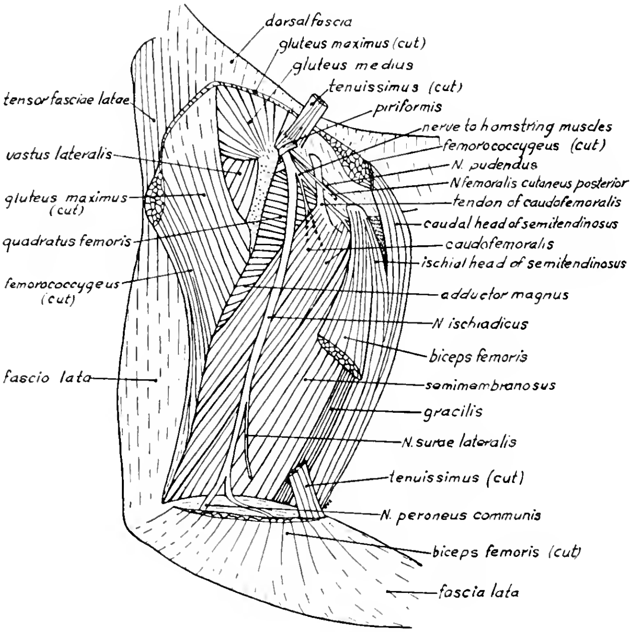

Fig. 1 The muscles of the thigh of Sciurus griseus showing the relations of the caudofemoralis (presemimembranosus).

The condition of this muscle in the gray squirrel (Sciurus griseus) suggests a solution to the problem of its homology, in rodents at least. In the specimen dissected, the muscle arose by tendinous and fleshy fibers from the ischial bone and, by a slender tendon (fig. 1), from the transverse process of the first caudal vertebra. The tendon crossed superficial to the nerve to the hamstring muscles, while the part of the muscle arising from the ischium lay medial and deep to the nerve. Alezais ('00) described the muscle in Sciurus vulgaris as the 'ischio-condylien.' In this animal it is apparently identical with the muscle described above in Sciurus griseus, but that author did not perceive the significance of the peculiar relation between the muscle and the nerve to the hamstrings. This relation may be considered a stage intermediate between the typical position of the caudofemoralis and that of the so-called presemimembranosus.

It may be concluded that muscles do, in rare instances, change their topographical relations to nerves; and that the caudofemoralis and the presemimembranosus are homologous muscles. Consequently, when the muscle in question is continuous with the semimembranosus, the condition should not be considered primitive or undifferentiated, but rather as a secondary fusion of the caudofemoralis and the semimembranosus. Also, since it is generally accepted by workers in comparative myology (Alezias, '00; Parsons, 1892; Leche, '00) that the presimimembranosus forms part of the great adductor in man, the identification of the former muscle as a modified caudofemoralis seems to fill a gap between the known morphological history of the sciatic part of the adductor magnus and the phylogeny of the caudofemoralis as traced by Appleton ('28).

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THE GLANS PENIS IN *SIGMODON, SIGMOMYS,* AND *REITHRODON* (RODENTIA, CRICETINAE)

By EMMET T. HOOPER

COTTON rats (*Sigmodon* and *Sigmomys*), marsh rats, (*Holochilus*), coney rats (*Reithrodon*), and red-nosed rats (*Neotomys*) compose an assemblage which Hershkovitz (1955) considers to be natural and which he designates as the "sigmodont group." This group contrasts with oryzomyine, ichthyomyine, phyllotine, akodont, and other supraspecific assemblages which various authors (e.g., Thomas, 1917; Gyldenstolpe, 1932; Hershkovitz, 1944, 1948, 1955, 1960; and Vorontsov, 1959) have recognized in analyzing the large cricetine fauna of South America. While all of these groups are tentative, at least in regard to total complement of species in each, nevertheless some are strongly characterized and probably natural; and all, whether natural or not, are useful in that they constitute conveniently assessable segments of an unwieldly large South American cricetine fauna, now disposed in approximately 40 nominal genera. New information regarding three of those genera is provided below. It is derived from fluid-preserved and partially cleared glandes (procedures described by Hooper, 1959) as follows:

Reithrodon cuniculoides: Argentina, Tierra del Fuego, 1 adult. *Sigmodon alleni*: Michoacán, Dos Aguas, 3 adults. *S. hispidus*: Arizona, Pima Co., 1 subadult. Florida, Alachua and Osceola counties, 3 adults. Michoacán, Lombardia, 2 adults. *S. minimus*: New Mexico, Hidalgo Co., 1 juvenile. *S. ochrognathus*: Texas, Brewster Co., 1 subadult. *Sigmomys alstoni*: Venezuela, Aragua, 1 subadult.

I am indebted to Elio Massoia for the specimen of *Reithrodon* and to Charles O. Handley, Jr., for the example of *Sigmomys*. Figures 1 and 2 were rendered by Suzanne Runyan, staff artist of the Museum of Zoology. The National Science Foundation provided financial aid.

Listed below in sequence are representative measurements (in mm.)

of *Sigmodon hispidus* (averages of five adults), *Sigmomys alstoni* (one subadult), and *Reithrodon cuniculoides* (one adult). Length of hind foot: 34, 30, 33; greatest lengths of glans, 7.6, 6.6, 7.8; greatest diameter of glans, 6.2, 4.0, 5.0; length of main bone of baculum, 5.5, 4.9, 4.1: length of medial distal segment of baculum, 2.8, 2.0, 2.7; total length of baculum, 8.3, 6.9, 6.8.

DESCRIPTION OF GLANDES

Sigmodon hispidus.—In *Sigmodon hispidus* the glans is a spinous, stubby, contorted cylinder (Fig. 1), its length one-fourth to one-fifth that of the hind foot and its greatest diameter approximately three-fourths its length (see measurements). The spines which densely stud almost all of the epidermis, except that of the terminal crater, are short and thick-set; each is recessed in a rhombic or hexagonal pit. The glans is somewhat swayback and potbellied, yet in its basal one-half or two-thirds it is essentially plain and cylindrical, without lobes or folds other than a short midventral frenum which, as an indistinct raphe, continues distad to the rim of the crater. The distal third or half of the glans is conspicuously hexalobate, the six lobes separated from each other by longitudinal troughs or grooves which increase in depth distad. The lobes are unequal in size and shape; the ventral pair is largest and the least convex, the lateral pair smallest, and the dorsal pair the most convex; the latter is a key item in the swayback appearance of the glans. These lobes converge distally, and their crescentic lips form the scalloped, overhanging rim of the terminal crater.

The largest structure in the crater is the mound which houses the medial distal segment of the baculum. Nestled between the lips of the ventral lobes, it projects outside the crater approximately to the limits of the dorsal lobes. The two smaller lateral mounds, housing the lateral processes of the baculum, are closely appressed to the medial mound, and the tip of each is distinctly pointed, rather than gently rounded like the medial mound. Immediately ventral to the medial mound is the meatus urinarius which is guarded ventrally by a urethral process. This process consists of a pair of rather thick arms each of which is out-curved and tapers to an obtuse tip (Fig. 1); in one specimen the ventral face of the process is studded with spines. Dorsal to the medial mound is the dorsal papilla, which is a single distensible cone of soft tissue dotted with spines both dorsally and laterally. Two additional pairs of crater conules, here termed "dorsolateral and lateral papillae," are particularly noteworthy because, insofar as known

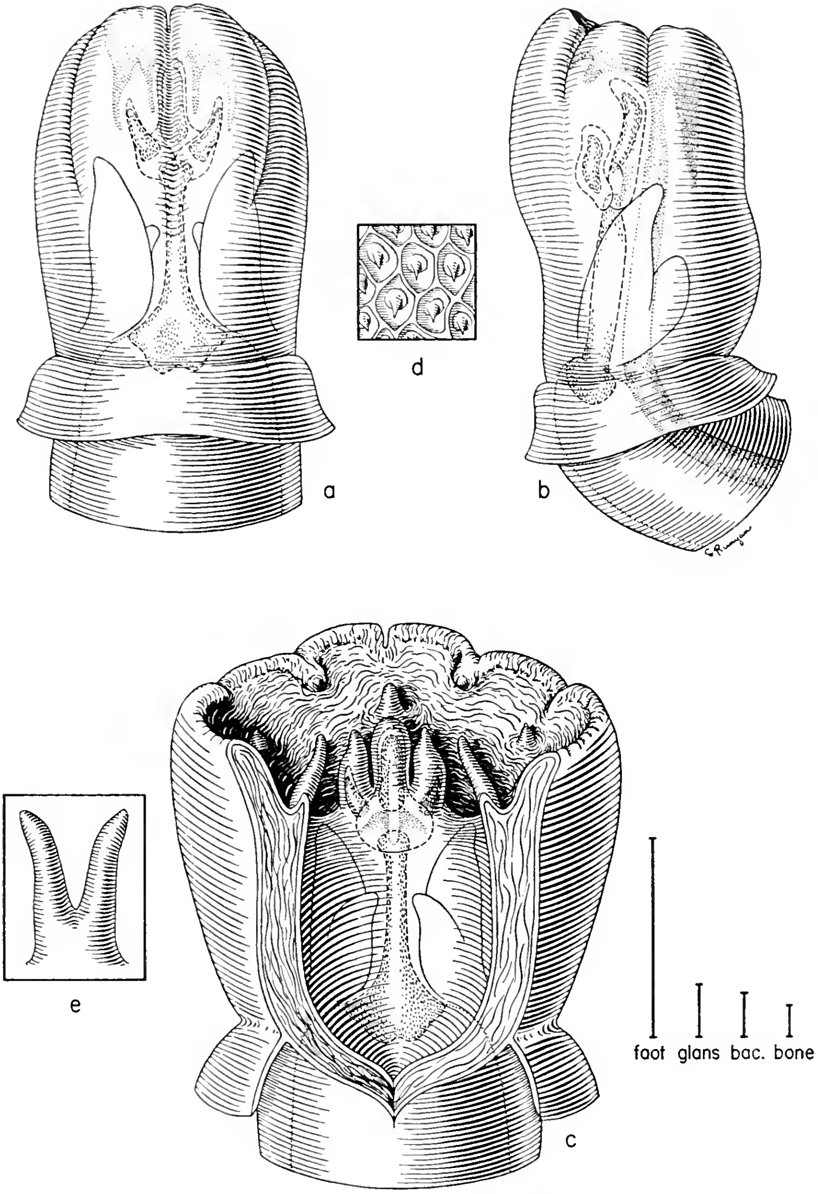

FIG. 1. Views of glans penis of *Sigmodon hispidus*: *a,* dorsal; *b,* lateral; *c,* incised midventrally exposing urethra; *d,* epidermal spines, enlarged; *e,* urethral process, enlarged, ventral aspect; UMMZ 97270, Florida.

in the New World cricetids studied to date, they are peculiar to *Sigmodon* and *Sigmomys*. All four of these are spine-studded, stubby, and smoothly rounded terminally. Each dorsolateral papilla is situated just below the crater rim at the junction of the dorsal and lateral lobes. Each lateral papilla is partly recessed in a pocket on the lower flank of the crater wall alongside a lateral bacular mound.

There is no ventral shield (a large mass of tissue between the urethral process and the ventral lip of the crater) as seen in most microtines, and the bacular mounds are relatively free within the crater, there being no partitions connecting the lateral mounds with the crater walls; the urethra empties onto the crater floor, not into a partition-encircled secondary crater within the larger crater, an arrangement seen in some rodent species.

Below the crater floor is a right and left pair of bilobed sacs (Fig. 1), each ovoid ventral lobe about 1.5 mm. in length, and each attenuate dorsal lobe approximately a millimeter longer, its tip extending distad almost to the limits of the main bone of the baculum. These sacs or sinuses emerge from tissues situated beside the corpora cavernosa penis and they extend alongside the baculum and the corpus cavernosum urethra, but they apparently are not parts of either of those structures. Composed entirely of soft tissues and engorged with blood in some specimens, they appear to be continuous with the deep dorsal vein and, thus, they seem to be part of the vascular system. Similar sacs, as illustrated in *Phyllotis* by Pearson (1958:424) for example, occur in all of those New World cricetids studied to date that have a four-part baculum; they have not been observed in *Peromyscus, Neotoma,* or other cricetid groups which are characterized by a simple baculum and glans.

The four-part baculum is at least as long as the glans and is one-fourth the hind foot in length (see measurements). The main bone, one-sixth the length of the hind foot, is angular and gross. The dorsal face of its wide and angular base is deeply concave between prominent lateral and proximal condyles to which the corpora cavernosa attach, while the ventral surface is almost flat except for a midventral keel of either cartilage or bone which, spanning approximately four-fifths the length of the bone, terminates at the cartilage of the digital junction. The shaft is oval in cross-section, the dorsoventral diameter exceeding the transverse one; as viewed laterally it is slightly bent and is constricted terminally, while in ventral view it is gently tapered distad before expanding to form a distinct terminal head.

The three distal segments of the baculum are subequal in length, the lateral pair slightly shorter than the medial one. They differ considerably in shape and amount of ossification. In one breeding adult they are entirely cartilaginous, while in four other adults they contain various amounts of osseous tissue in addition to cartilage; probably in very old animals they are entirely osseous. The medial segment, attached to the ventral sector of the main bone, projects distad and slightly ventrad, then it bends abruptly dorsad before terminating in a rounded tip. It is approximately oval in cross section in its distal three-fourths, but in its proximal fourth it is much wider than deep and is keeled ventrally; moreover, at the digital junction it bears a pair of lateral processes and a medial flange, the continuation of the midventral keel, which extends over the ventral face of the head of the main bone. In all specimens at hand these three processes are cartilaginous; furthermore, the osseous tissue of the three distal segments is restricted to, or concentrated in, the distal parts of each segment, indicating that ossification apparently proceeds from the tip proximad in *S. hispidus*.

The lateral segments, situated dorsolateral to the medial unit, attach onto the dorsal and lateral parts of the head of the main bone—dorsal to the flanges of the medial segment. Each is pointed and blade-shaped, the dorsoventral diameter exceeding the transverse one; and as viewed ventrally each curves gently distad and slightly laterad. Whether cartilaginous or osseous, they are situated in the lateral parts of each bacular mound, while the medial and distalmost parts of each mound consist entirely of soft tissue, a large part of which is vascular and appears to be instrumental in distention of the mounds. In some examples, the basal parts of the three distal segments of the baculum are more or less coalesced; this is particularly true of the two lateral units, and the two have been interpreted as a single horn-shaped structure (Hamilton, 1946). However, as indicated by Burt (1960) they are separate units (Fig. 1); their individual limits are clear in specimens at hand.

Sigmodon minimus, S. ochrognathus, and *S. alleni.*—I recognize no interspecific differences in the specimens of *minimus* and *ochrognathus,* both examples of which are young and rather unsatisfactory. Each closely resembles specimens of *hispidus* of like age in external size and shape, and in conformation of the six exterior lobes, dorsal papilla, dorsolateral papillae, lateral papillae, urethral process, crater mounds, and baculum. If there are interspecific differences, they are not clearly evident in the materal at hand.

The three adults from Dos Aguas, Michoacán, which are labeled *S.*

alleni, are also like adults of *hispidus.* The two series differ slightly in regard to size of glans and shape of baculum, but these are small differences and doubtfully interspecific.

A few remarks regarding the identification of the specimens from Dos Aguas are needed. Until variation in *Sigmodon* is better understood, *S. alleni* seems to be the most appropriate name to apply to these specimens and, as well, to others like them from the vicinity of Autlán, Jalisco, and Angahuan and Uruapan, Michoacán. Cranially and externally distinguishable from specimens of *S. hispidus* and *S. melanotis* from nearby localities in the same states, they appear to represent a species other than either *hispidus* or *melanotis.* They agree well with the description of *alleni,* but they have not been compared directly with the type specimen of that form.

Sigmomys alstoni.—The specimen of *Sigmomys alstoni* resembles examples of *Sigmodon* of comparable age in length (relative to hind foot), in external configuration (hexalobate, swaybacked and potbellied in lateral view, and covered with proximally directed, thickset, sharp, entrenched spines), shape of dorsal papilla (single, spine-studded cone), appearance of urethral process (two outcurved arms with a longitudinal row of spines on the ventral face of each), shape of the bacular mounds (the medial one large and rounded, each lateral one smaller and rounded laterally but acute medially), position of digits of baculum with respect to the main bone, presence of ventral keel and lateral arms on the medial digit, and occurrence of a midventral keel on the main bone. The specimen differs from examples of *Sigmodon* in characters as follows: glans smaller in diameter (diameter-length ratio approximately 60 per cent, compared with 70–88 per cent in *Sigmodon*); the six external lobes, particularly the dorsal pair, less prominent; dorsolateral papillae smaller, scarcely more than the spine-studded infolding of the dorsal and lateral lobes; crater more extensively spinous (spines studding most of inner wall of each lateral lobe); medial digit of baculum projecting principally distad, its tip not sharply flexed dorsad; and the osseous proximal segment flatter and wider for a larger fraction of its length.

The lateral papillae and baculum warrant additional comment. It is uncertain whether lateral papillae are present in the specimen. Two papillose vascular cores occur at sites where papillae are to be expected, but in the present damaged specimen the overlying crater floor is not correspondingly papillose, although it is strongly spinous; the spiny area occupies most of the inner face of the lateral lobe and of the adjoining crater floor. On the left side of the specimen this roughly circular spiny area is plate-like, while on the right side it is buckled distad and, thus, resembles a large papilla. If, in undamaged specimens, these areas are papillose, then the lateral papillae in *S. alstoni* are relatively larger than any yet seen in *Sigmodon*.

In ventral view, the main bone of the baculum is shaped roughly like an isosceles triangle—wide basally and tapered rather evenly distad (without pronounced incurve) almost to the slight constriction which subtends the small, round, terminal head. Its wide basal part is concave dorsally (between low lateral condyles) and almost flat ventrally; but farther distad the bone is deeper than wide and, somewhat triangular in cross section, it bears a slight midventral ridge to which a cartilaginous keel is attached. The distal segments are entirely cartilaginous. The medial one is deeper than wide in its distal half and blunt terminally; basally it bears a medial process and two lateral flanges. Each lateral segment, also deeper than wide and blunt terminally, is situated dorsolateral to the medial unit.

Reithrodon cuniculoides.—The glans of *R. cuniculoides* (Fig. 2) is stubby (diameter-length ratio 64 per cent), subcylindrical, and indistinctly lobate, the lobes defined by four, shallow, longitudinal troughs. Two of these depressions, one situated middorsally and the other midventrally, extend approximately the full length of the glans and thereby divide the surface of the glans into right and left halves; the distal limit of each is a notch in the crater rim. The shorter third pair of troughs is situated dorsolaterally in the distal half of the glans, but each terminates short of the rim. All of the epidermis as far distad as the crenate, membranous, overhanging rim of the crater is densely studded with small, conical, recessed tubercles.

The three bacular mounds, together with the underlying baculum, resemble a fleur-de-lis in ventral aspect (Fig. 2); the erect medial part extends beyond the crater, while each of the truncate lateral pair sends off an attenuate lateral segment which curves laterad and then distad before terminating in an acute tip. These lateral processes contain no cartilage or bone; they consist entirely of soft tissues, a large part of which is vascular and apparently erectile. The spine-tipped dorsal papilla is unusually small and slender; it is a single cone, but a slight cleft near its tip suggests that the papilla may consist of two conules in other specimens. The urethral process is a bilobed flap with two attenuate and erect (not outcurved) arms; it bears two longitudinal rows, each of eight tubercles, on its ventral face. There are no lateral or dorsolateral papillae, and the crater walls and floor are smooth and non-spinous.

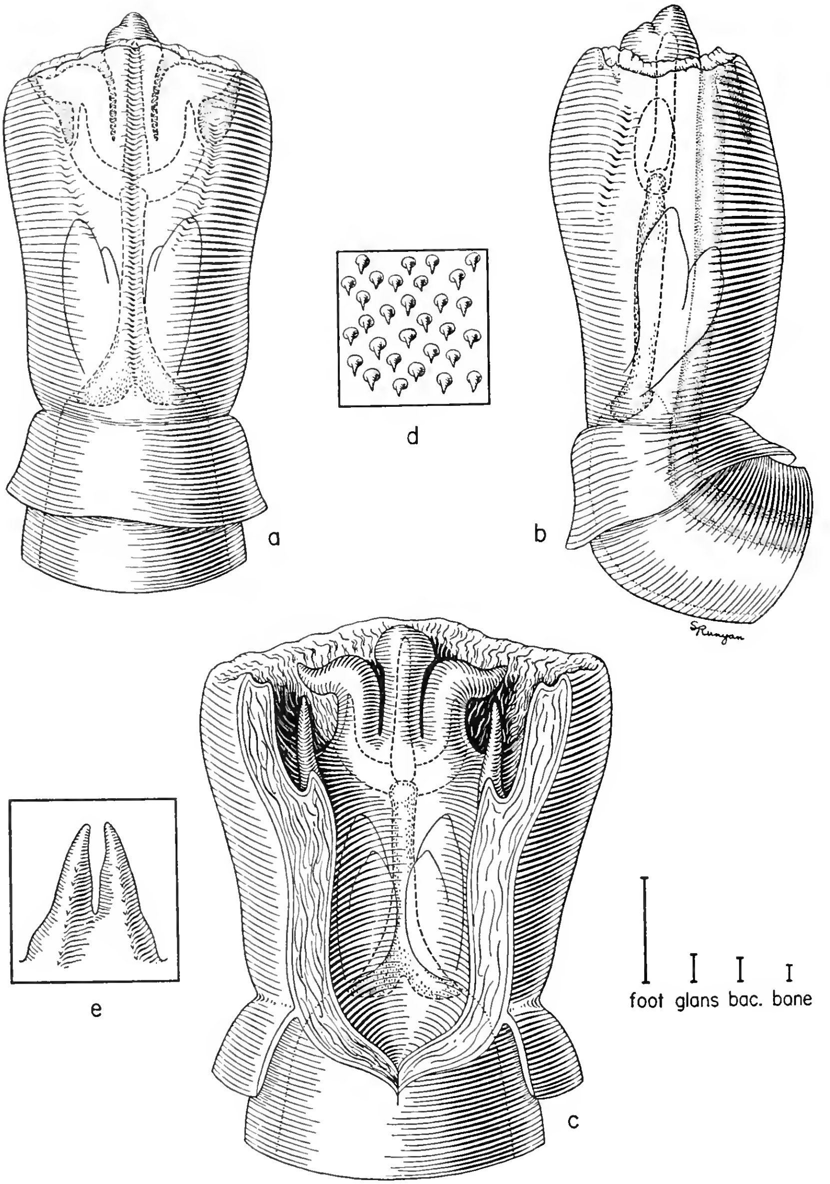

Fig. 2. Views of glans penis of *Reithrodon cuniculoides*; UMMZ 109233, Argentina. For explanation see Fig. 1 and text.

The baculum is shorter than the glans (see measurements). Its proximal, osseous segment consists of a wide basal part and a slender shaft. The basal part, which bears large, proximally directed condyles (these separated medially by a deep notch), is broadly concave ventrally and narrowly and shallowly concave dorsally. The relatively straight shaft is slightly deeper (dorsoventrally) than wide and it bears a slight ventral keel; its terminal portion is slightly expanded laterad and slightly constricted dorsoventrally (Fig. 2). The three distal segments are cartilaginous. The long medial one (its length two-thirds that of the bone) is rod-like for much of its length, but it is enlarged basally and is tapered distally to a pointed tip. The lateral units are disc-shaped in cross section, the dorsoventral diameter of each much greater than the transverse one. From its attachment on the head of the bone (the attachment dorsal and lateral to that of the medial unit) each lateral segment curves gently laterad and distad before it terminates at the base of the laterally projecting process of its lateral mound.

DISCUSSION

To judge from specimens at hand, the glandes of *Sigmodon alleni, S. hispidus, S. minimus,* and *S. ochrognathus* are fundamentally alike, although they may differ interspecifically in details which can not be appraised in present samples. In each species the stubby, swayback, tubercle-invested glans bears six prominent exterior lobes which surround the terminal crater and divide its rim into six corresponding parts. Within the crater there are five spine-studded papillae consisting of dorsolateral and lateral pairs in addition to a single cone middorsally. The urethral process bears two attenuate, outcurved arms. The bacular mounds are truncate except for a small, acute medial crest on each lateral mound, and the medial distal segment of the four-part baculum bears a medial keel and a pair of lateral processes on its base, while its tip is flexed sharply dorsad. These characters, together with others, distinguish *Sigmodon* from the other New World cricetid genera which have been studied to date, with the possible exception of *Sigmomys. Sigmomys alstoni,* the only species of *Sigmomys* about which there is information on the glans, appears to be closely similar to species of *Sigmodon,* but its characters are not yet adequately known.

In contrast to the phalli of *Sigmodon* and *Sigmomys,* the glans of *Reithrodon cuniculoides* is comparatively slim and simple. There are only four exterior lobes, and these are less prominent than the lobes of *Sigmodon or Sigmomys.* The membranous, crenate, and non-spiny crater rim is not divided into six distinct lobes. The crater, also smooth and spineless, has no dorsolateral or lateral papillae. The slender dorsal papilla bears spines only at its tip. Each lateral mound has an attenuate lateral process, and the entire configuration of the three crater mounds as well as of the underlying baculum is distinctive. The three, long, erect distal segments of the baculum, all cartilaginous insofar as known, are essentially rod-like in form, without prominent keels or processes. These and other contrasting characters indicate that the glans of *R. cuniculoides* is morphologically quite different from that seen in *Sigmodon* and *Sigmomys*. Preliminary comparisons suggest that it may be more similar to glandes of phyllotine or other species which are not now included in the sigmodont group of rodents.

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COMPARATIVE MORPHOLOGY OF SPERMATOZOA FROM FIVE MARSUPIAL FAMILIES

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Summary

The spermatozoa of 18 marsupial species derived from five families have been examined and of these only the spermatozoon of the bandicoot *Perameles nasuta* has previously been described adequately.

The spermatozoon morphology within the families Macropodidae, Dasyuridae, Phascolarctidae, and Peramelidae was relatively homogeneous. A distinctive morphology occured between these families. Within the family Phalangeridae spermatozoa were morphologically diverse, however, as a group they were relatively separate from those of the other families studied.

The spermatozoa of the Phascolarctidae (koala, *Phascolarctos cinereus*, and wombat, *Phascolomis mitchelli*) have a unique, somewhat rat-like morphology which clearly separates them from those of the other marsupial sperm studied. This finding is of considerable taxonomic interest as most authorities consider the koala to be more closely related to the phalangerid marsupials than to the wombat.

I. Introduction

Previous descriptions of marsupial spermatozoon morphology cover six of the major marsupial groups. A considerable proportion of these accounts is devoted to a study of the spermatozoon morphology of three species, each belonging to separate marsupial families. (1) Family Didelphidae: *Didelphis* [Selenka (1887), Fürst (1887), Waldeyer (1902), Korff (1902), Retzius (1909), Jordan (1911), Duesberg (1920), Wilson (1928), McCrady (1938), Biggers and Creed (1962)]; (2) family Phalangeridae: *Phalangista vulpina* (= *Trichosurus vulpecula*) [Korff (1902), Benda (1897, 1906), Retzius (1906), Bishop and Walton (1960)]; (3) family Peramelidae: *Perameles nasuta* [Benda (1906), Cleland (1955, 1956, 1964), Cleland and Rothschild (1959), Bishop and Austin (1957), Bishop and Walton (1960)].

The spermatozoon morphology of two Dasyuridae, *Phascogale albipes* (= *Sminthopsis murina*) and *Dasyurops maculatus*, was studied by Fürst (1887), Bishop and Austin (1957), and Bishop and Walton (1960).

Benda's (1906) description of an epididymal sperm from the koala, *Phascolarctos* (family Phascolarctidae), is, as he admits, inadequate.

Spermatozoon morphology studies on members of the family Macropodidae include those of an unknown *Macropus* sp. (Benda 1906), *Macropus billardierii* (= *Thylogale billardierii*), *Petrogale penicillata*, *Onychogale lunata* (= *Onychogalea lunata*), *Bettongia cuniculus* (Retzius 1906), *Macropus giganteus* (= *Macropus canguru*) (Binder 1927), and *Potorous tridactylus* (Hughes 1964).

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The spermatozoa examined in the present study were obtained from members of the five Australasian marsupial families: Phalangeridae, Peramelidae, Dasyuridae, Phascolarctidae, and Macropodidae. The present series of observations has been viewed with reference to those of earlier workers and this has permitted at least an elementary discussion of the comparative aspects of spermatozoon morphology between the marsupial families examined.

II. Material and Methods

The testes together with the attached epididymis were removed from the scrotum soon after death and fixed in 10% neutral formalin or, more rarely, Bouin's fluid or Carnoy fixative.

(i) *Method for Adhering Spermatozoa to Microscope Slides*

The slides were labelled at one end with a diamond pencil and a 15-mm square was marked out at the opposite end. The entire surface of the slide was liberally smeared with Mayer's albumen. A small piece of epididymal tissue was placed in a drop of 10% neutral buffered formalin within the marked square and extensively teased with dissecting needles. Filter paper circles of 5·5 cm diam. were saturated with 10% formalin, drained, and placed over the specimen by a rolling action. Air bubbles were punctured with a needle. The filter paper was kept moist with 10% formalin for at least 30 min and then permitted to dry until free fluid between the slide and the filter paper had disappeared. The filter paper was then removed by a rolling action, excess tissue was removed with fine forceps, and the preparations rinsed and stored in water for staining.

(ii) *Staining of Spermatozoa*

(1) *Heidenhain's Iron Haematoxylin*.—Slides containing adhering spermatozoa were transferred from water to a 5% solution of iron alum and kept in a warm place for 2–3 days. They were then stained with Heidenhain's haematoxylin for a similar period. The area not containing the specimen was thoroughly cleaned with paper tissues during a 10–15 min rinsing period in running tap water. The preparations were then differentiated in 5% iron alum under a staining microscope at 30 sec intervals. The preparation was washed in water and re-examined after each differentiation interval. Differentiation times of between 30 sec and 5 min proved satisfactory to show the desired range of structures. The preparations were upgraded to absolute ethyl alcohol, placed in two changes of xylol, and mounted in euparal.

(2) *Periodic Acid–Schiff* (*with saliva controls*).—Slides containing the mounted spermatozoa were removed from water and placed horizontally in two groups on a flat tray. One group was flooded with water and the other with saliva for 1 hr at a temperature of 37°C. The slides were then thoroughly rinsed in distilled water and stained by a method described by Carleton and Drury (1957, p. 143). The Schiff's reagent used was de Tomasi (for preparation see Pearse 1961, p. 822). The preparations were mounted in euparal.

(3) *Feulgen* (*with and without fast green counterstain*).—Slides containing the adhering spermatozoa were removed from water and stained by a method described

by Pearse (1961, p. 823). The Schiff's solution used was de Tomasi. Half the Feulgen preparations were stained with fast green counterstain (0·5% solution in 70% ethyl alcohol) for 15–20 min. Both Feulgen and Feulgen–fast green preparations were quickly passed through three changes of 90% alcohol (dips only) to absolute ethyl alcohol and then cleared in xylol and mounted in euparal.

Slides were stored until dry in an oven at a temperature of 37°C after mounting in euparal. Preparations were not permitted to dry out during any of the earlier stages in preparation.

The drawings of spermatozoa shown in Figure 1 are based on camera lucida outlines using a ×12 eyepiece in conjunction with a ×100 oil-immersion objective.

The spermatozoon dimensions shown in Table 1 are means of 25 observations and were obtained with a special Leitz ×12·5 screw micrometer eyepiece and a ×100 oil-immersion objective. The preparations used were fixed in 10% neutral formalin or, more rarely, Bouin's fluid or Carnoy and were stained with Heidenhain's iron haematoxylin.

During the course of the observations on sperm it became apparent that the efferent ducts connecting the testis and epididymis were either multiple or single within each marsupial family. This was investigated further from frozen transverse sections stained with haematoxylin and eosin. The sections were prepared from the efferent duct or ducts at the point of their emergence from the testis and also approximately midway between the testis and epididymis.

The author follows Cleland and Rothschild (1959) in considering for the purpose of description that the flagellum is inserted into the ventral surface of the sperm head and the opposite surface is taken as dorsal.

III. RESULTS

The mature epididymal spermatozoa of 18 marsupial species have been examined. The dimensions of 13 of these spermatozoa are shown in Table 1. The gross morphology of 14 of the spermatozoa is shown in Figure 1.

Spermatozoa of each of the five marsupial families studied (Macropodidae, Phalangeridae, Dasyuridae, Peramelidae, Phascolarctidae*) exhibited sufficient homogeneity in morphology and dimensions of the head, flagellum, and fine structure to be of taxonomic value.

The heads of all marsupial spermatozoa examined showed some dorsoventral flattening. This was most marked in the Dasyuridae and Peramelidae. It was least evident in the Phascolarctidae and the genus *Pseudocheirus* of the Phalangeridae. Macropod and the other phalangerid spermatozoa exhibited an intermediate condition. The distal extremity of the head of all species when viewed dorsally was relatively rounded while the shape of the lateral margins and proximal tip varied considerably. In the Dasyuridae the spermatozoon heads of up to 12·7 μ in length in *Dasyuroides byrnei* are among the longest known for mammals (Table 1). The

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* The author follows Sonntag (1923) in grouping the wombat and koala in the family Phascolarctidae.

lateral head margins of dasyurid sperm are slightly convex in dorsal view and taper gradually to a proximal point. Macropod sperm heads are considerably shorter than those of the Dasyuridae and in dorsal outline are elongated ovoids bluntly pointed proximally. The sperm head of the macropod *Megaleia rufa* (Figs. 1*g* and 1*h*) is rapidly tapering, a condition typically found in the Phalangeridae. Phalangerid sperm, when viewed dorsally, exhibit considerable variability in the convexity of the lateral head margins. The proximal region of the head is typically semicircular, although sometimes bluntly pointed as in *Pseudocheirus cupreus* (Figs. 1*n* and 1*o*).

TABLE 1

MARSUPIAL SPERMATOZOON DIMENSIONS

Family and Species	Mean ±SD (μ)				
	Head		Middle-piece		Flagellum
	Length	Width	Length	Diameter	Length
Macropodidae					
Macropus canguru	7·3±0·16	2·2±0·11	10·7±0·24	1·5±0·14	111·6± 3·60
*Megaleia rufa**	5·1±0·21	2·4±0·09	7·9±0·25	1·4±0·12	104·0± 4·74
Protemnodon rufogrisea	8·5±0·22	2·3±0·18	11·7±0·34	1·6±0·14	115·4± 8·85
Protemnodon agilis†	7·1±0·38	1·8±0·12	11·0±0·28	1·4±0·13	— —
*Thylogale stigmatica**	7·2±0·09	2·2±0·11	10·9±0·22	1·5±0·12	103·1± 4·43
Dasyuridae					
Dasyuroides byrnei	12·7±0·41	2·5±0·15	40·7±1·26	3·1±0·19	242·1± 6·77
Sarcophilus harrisii	11·1±0·45	2·2±0·17	34·4±0·84	2·6±0·13	207·4±12·02
Phalangeridae					
Petaurus breviceps‡	5·9±0·19	2·5±0·18	8·3±0·27	1·4±0·11	101·3± 4·96
Pseudocheirus cupreus‡	5·4±0·16	2·6±0·11	6·2±0·16	1·5±0·17	84·7± 2·47
Pseudocheirus peregrinus	5·9±0·38	3·8±0·18	6·9±0·21	2·1±0·22	106·9± 5·31
Phascolarctidae					
Phascolomis mitchelli	5·7±0·33	1·7±0·09	18·0±1·56	0·9±0·10	87·9± 8·23
Peramelidae					
Perameles nasuta	5·7±0·15	3·0±0·13	14·0±0·32	2·0±0·11	194·1± 5·25
Isoodon macrourus	6·0±0·13	3·3±0·18	10·7±0·19	1·8±0·14	165·1± 3·64

* Fixed in Bouin's fluid; † Carnoy fixative; ‡ from New Guinea.

Peramelid spermatozoon heads have concave lateral margins when seen in dorsal view and are relatively square proximally with a median cap. In phascolarctid sperm the proximal portion of the spermatozoon head of both the wombat *Phascolomis mitchelli*, and the koala, *Phascolarctos cinereus*, bears a strongly recurved hook.

In all sperm, a positive Feulgen reaction for nuclear material (DNA) was given by almost the entire head mass. The DNA-negative areas that took up a fast green counterstain in Feulgen preparations were the acrosome (Fig. 1; *AC*) and basal granule complex which is located at the proximal tip of the flagellum. The acrosome

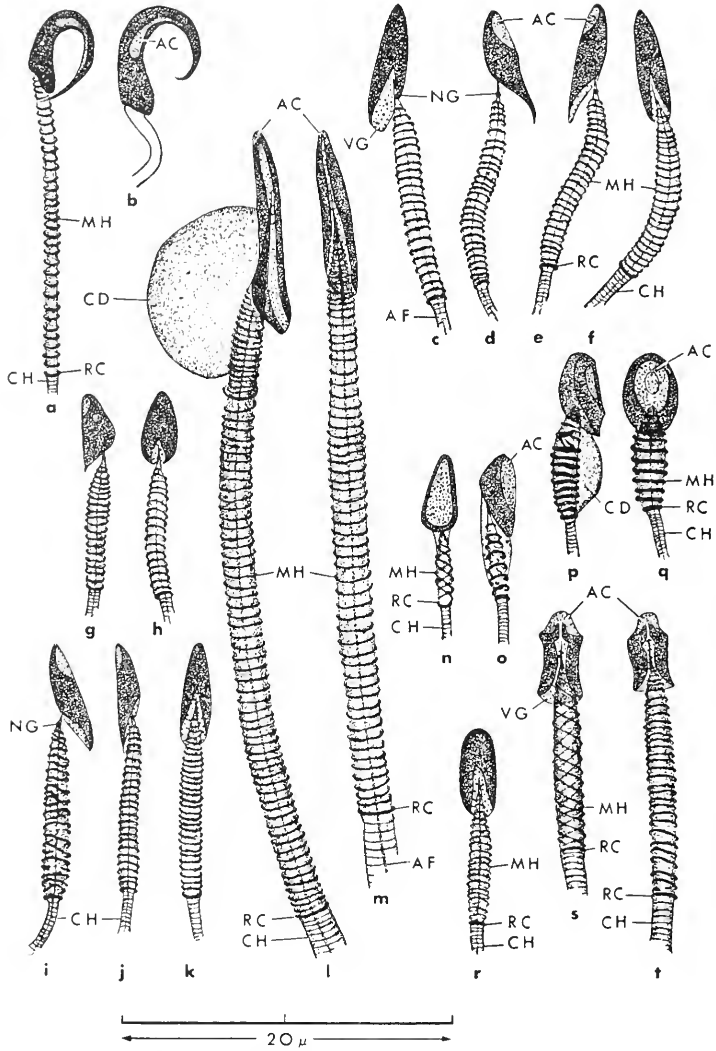

Fig. 1.—Marsupial epididymal spermatozoa: the drawings are all at the same scale and are based on camera lucida outlines of formalin-fixed Heidenhain's iron haematoxylin preparations. A ×12 eyepiece was used in conjunction with a ×100 oil-immersion lens. Fam. Phascolarctidae: *Phascolomis mitchelli*, (*a*) lateral view; *Phascolarctos cinereus*, (*b*) lateral view of spermatozoon head with flagellum outline. Fam. Macropodidae: *Protemnodon rufogrisea*, (*c*) ventral view, (*d*) lateral view; *Protemnodon agilis**, (*e*) lateral view, (*f*) ventral view; *Megaleia rufa*†, (*g*) lateral view, (*h*) ventral view; *Macropus canguru*, (*i*) lateral view; *Thylogale stigmatica*†, (*j*) lateral view; (*k*) ventral view. Fam. Dasyurinae: *Dasyuroides byrnei*, (*l*) dorsolateral view; *Sarcophilius harrisii*, (*m*) ventral view. Fam. Phalangeridae: *Pseudocheirus cupreus*, (*n*) dorsal view, (*o*) lateral view; *Pseudocheirus peregrinus*, (*p*) lateral view, (*q*) dorsal view; *Petaurus breviceps*, (*r*) ventral view. Fam. Peramelidae: *Isoodon macrourus*, (*s*) ventral view; *Perameles nasuta*, (*t*) ventral view. Key: *AC*, acrosome; *AF*, axial filament; *CD*, cytoplasmic droplet (middle-piece bead); *CH*, cortical helix of main-piece sheath; *MH*, mitochondrial helix of middle-piece; *NG*, neck granule; *RC*, ring centriole; *VG*, ventral groove.

* Fixed in Carnoy fixative. † Fixed in Bouin's fluid.

was also variably positive to periodic acid–Schiff (P.A.S.) between species and the basal granule complex was invariably strongly P.A.S.-positive. Neither acrosome nor basal granule complex exhibited any reduction in P.A.S. activity in saliva controls. A faint tinge of green over the entire head surface in Feulgen–fast green preparations presumably represents a limiting membrane.

A "nuclear rarefaction" of vacuole-like appearance results from a minute superficial nuclear indentation. The nuclear rarefaction was most conspicuous in the Dasyuridae and Peramelidae and least evident in the Macropodidae. This structure is located on the mid-median aspect of the ventral nuclear surface of all sperm with the exception of those of the Phascolarctidae, where its occurrence is also ventral and median but distal.

In most of the marsupial sperm examined acrosomal material (Fig. 1; *AC*) was apparently confined to a relatively small surface area of the head. In the Macropodidae the acrosome is relatively small and is a discrete ovoid structure embedded superficially in the extreme proximal portion of the dorsal head surface. In some of the Phalangeridae it has a definite structure as in *Pseudocheirus* (Figs. 1*n*–1*q*) where it occupies all but a marginal annular zone of the dorsal head surface and is rather deeply embedded. In other phalangerids, such as *Petaurus breviceps* (Fig. 1*r*), the dorsal head surface in Feulgen–fast green preparations gives a diffuse acrosomal reaction and bears a shallow depression which extends to all but the margins. A similar diffuse acrosomal reaction of at least the proximal half of the dorsal head surface occurred in the Dasyuridae. The proximal dorsal tip of the dasyurid sperm has a concentration of acrosomal material situated in a minute groove. The acrosomal material in the Peramelidae was found in a small distally flanged proximal cap which covered a minute nuclear protuberance. In the Phascolarctidae the acrosome is a small "comma-shaped" structure. The body of the acrosomal "comma" is embedded superficially in about the middle of the dorsal head surface and the tail of the comma extends throughout the greater portion of the inner curvature of the head hook.

In marsupial sperm the ventral surface of the head (by convention that bearing the flagellum) is typically grooved (Fig. 1; *VG*) or bears a shallow distal notch as in the case of the Phascolarctidae. At the distal extremity of the head the groove is broad and deep so that the head is here relatively broad and has the form of an extremely thin curved plate. The groove becomes shallow and narrow towards its proximal extremity; in the Macropodidae and Phalangeridae it terminates at about the mid-median portion of the ventral head surface. The groove is most extensive in the Peramelidae involving the whole of the ventral aspect of the nucleus, only the proximal acrosomal head cap is excepted. In the Dasyuridae it extends throughout the distal four-fifths of the head.

Spermatozoa are immature when they enter the head of the epididymis and were characterized by the orientation of the long axis of the head at 90° to the flagellum which was directed towards the nuclear rarefaction. The ventral surface of the spermatozoon head was supported by a somewhat cone-shaped cytoplasmic droplet (Fig. 1; *CD*) of characteristic morphology for each species. Phascolarctid sperm from the head region of the epididymis differed from the other marsupial species examined in that the flagellum was most frequently observed not to meet the head at right angles and cytoplasmic droplets were small and often absent. On entering the epididymis the head hook of the phascolarctid spermatozoa were only slightly recurved or of an irregular spiral configuration. During the passage of spermatozoa through the epididymis the head hook became simple (without spiral) and more tightly recurved.

Maturation of spermatozoa is completed during their passage through the epididymis and is accompanied by shedding of the cytoplasmic droplet and rotation of the long axis of the head parallel to that of the flagellum. The neck of the flagellum of mature epididymal sperm in all species was inserted in the vicinity of the nuclear rarefaction. In the Dasyuridae the neck was inserted rather deeply into the proximal margin of the nuclear rarefaction. In the Peramelidae the proximal tip of the flagellum was also deeply inserted and extended from the proximal margin of the nuclear rarefaction to a point about midway between the anterior rim of the nuclear rarefaction and the most proximal extremity of the nucleus.

The flagellum is traversed throughout its entirety by an axial filament (Fig. 3; *AF*). The size of the flagellum varies from species to species. The smallest flagellum was that of *Phascolomis mitchelli* with a maximum diameter of 0·9 μ and a minimum length of 87·9 μ (Table 1). The giant flagella of dasyurid sperm are among the largest known for mammals. *Dasyuroides byrnei* has a minimum flagellum length of 242·1 μ and a maximum flagellum thickness of 3·1 μ. In an old museum specimen of the testes of the now possibly extinct dasyurid *Thylacinus cynocephalus* (Tasmanian wolf or tiger) the flagellum of epididymal sperm in wax sections had a maximum diameter of 3·0 μ and comparable morphology to that of other dasyurids; the sperm heads, although degenerate, were in the form of a long narrow plate, dorso-ventrally flattened and with the flagellum inserted at about the mid-median ventral aspect. Peramelid sperm flagellae were also relatively large, having a maximum diameter of as much as 2 μ and a minimum length of up to about 200 μ (Table 1). Macropod and phalangerid sperm flagellae were of intermediate dimensions rarely varying from a maximum diameter of 1·5 μ and a minimum length of a little over 100 μ.

The basal granule complex located at the proximal end of the flagellum consists of at least fused proximal and distal components in the Dasyuridae and Peramelidae.

The neck region of the flagellum is a slender proximally pointed cone with a smooth contour, and a small neck granule (Fig. 1; *NG*) is situated at approximately half its length. It was only possible to identify the neck granule with certainty in the Peramelidae, Dasyuridae, and Macropodidae. In the Peramelidae and Dasyuridae it seemed to be a more deeply stained, modified portion of the ground substance of the neck rather than the discrete granule found in the Macropodidae. The sperm of the dasyurids *Dasyuroides byrnei*, *Sarcophilus harrisii*, and *Thylacinus cynocephalus* had a neck length of about 3·5 μ in comparison with 2·7 μ for the peramelids *Isoodon macrourus* and *Perameles nasuta*. Macropod sperm necks ranged in length from 1·8 μ in *Thylogale stigmatica* to 2·6 μ in *Protemnodon rufogrisea*. The neck lengths of the Phalangeridae and Phascolarctidae were somewhat reduced in comparison to those of other marsupial families.

The proximal portion of the middle-piece in all species examined tapered gradually to the diameter of the neck and was particularly firmly clasped by the lateral margins of the sperm head in the Peramelidae and Dasyuridae. The remainder of the middle-piece was relatively cylindrical. A mitochondrial helix (Fig. 1; *MH*) of spiral configuration gave the entire surface of the middle-piece sheath a slightly uneven contour. The mitochondrial helix is a relatively fine structure in the Dasyuridae and Peramelidae, of moderate thickness in the Macropodidae and Phascolarctidae and *Petaurus breviceps* of the Phalangeridae. It was quite thick and granular with relatively few gyres in the genus *Pseudocheirus* of the Phalangeridae. The middle-piece is terminated distally by a ring centriole (Fig. 1; *RC*).

The flagellum undergoes an abrupt reduction in diameter on the main-piece side of the ring centriole in both the *Pseudocheirus* species and to a moderate degree in *Petaurus breviceps* and the Macropodidae, but not to any appreciable extent in the Dasyuridae, Peramelidae, and Phascolarctidae.

The main-piece of the flagellum tapers distally and in twisted specimens appears not to be circular in cross section in *Pseudocheirus peregrinus*, Peramelidae, Dasyuridae, and Macropodidae. Striations of the sheath of the main piece in all sperm indicate the presence of a fine spiral cortical helix (Fig. 1; *CH*). The tail sheath also gave a strong impression of two lateral thickenings in transverse axis in *Macropus canguru*, *Protemnodon rufogrisea*, *Pseudocheirus peregrinus*, *Perameles nasuta*, and *Isoodon macrourus*.

The axial filament protruded beyond the terminal portion of the sheath of the main-piece in apparently complete sperm of all species but this cannot be positively taken to represent a true end-piece for in all preparations terminal breakage of the main-piece was prevalent.

IV. Discussion

Spermatozoa from three other Peramelidae, *Perameles gunnii*, *Isoodon obesulus*, and *Echymipera rufescens* have also been examined superficially and it can be stated that they are comparable in morphology to other peramelid sperm. The spermatozoa of marsupial mice, *Antechinus flavipes flavipes*, *A. f. leucogaster*, *A. swainsonii*, *A. stuartii*, and *Sminthopsis crassicaudata*, have a morphology typical of other dasyurids (Woolley, personal communication). This similarity in morphology also extends to two other dasyurids, *Phascogale albipes* (= *Sminthopsis murina*) (Fürst 1887) and *Dasyurops maculatus* (Bishop and Austin 1957; Bishop and Walton 1960). The spermatozoon morphology of the macropod species examined in the present study varies in only minor details from that of six other macropods previously described by Benda (1906), Retzius (1906), and Hughes (1964).

The phenomenon of conjugate spermatozoa (pairing of relatively numerous epididymal spermatozoa) redescribed and reviewed by Biggers and Creed (1962) for the American opossum, *Didelphis*, has not been observed in any of the sperm preparations from Australian marsupials; however, fresh unfixed material has been examined only for *Potorous tridactylus* (Hughes 1964) and *Phascolomis mitchelli*.

Another feature worth mentioning is that the head of the epididymis was not fused with the testis in any marsupial examined, including *Thylacinus cynocephalus* and *Dendrolagus lumholtzi*. In the Dasyuridae and Peramelidae a relatively long single efferent duct together with associated blood vessels links the epididymis to one pole of the testis long axis by way of an extensive membrane, the mesorchium. A tract of relatively long multiple efferent ducts serves the same function in the Phalangeridae, Phascolarctidae, and Macropodidae. A ligament was inserted by way of the mesorchium into the opposite pole of the testis.

In both the wombat and the koala the morphology of the sperm, particularly the head, differs strikingly from that of any marsupial sperm previously described. In both species the proximal portion of the spermatozoon head bears a strongly recurved hook not described for other marsupial sperm, and the flagellum is inserted into a notch on one side of the distal portion of the head (Plate 1, Fig. 1; and Figs. 1*a* and 1*b*). These features, although somewhat resembling those of certain murid sperm, are not strictly comparable (Plate 1, Fig. 2) (Friend 1936). The hook in the wombat sperm resembles that of *Microtus hirtus*, *Lemmus lemmus*, and several other members of the murid subfamily Microtinae in that the hook contains no supporting "rod" and its tip like that of *Lemmus lemmus* is typically extremely reflected so that it lies against the distal portion of the head (Friend 1936). The position of the hook in *Phascolomis* is not an artefact of fixation for it was observed in living spermatozoa from the epididymis of several specimens. In sperm from the head of the epididymis the curvature of the hook frequently approximated to that of rats and mice. It can be seen from Plate 1, Figure 1, and Figures 1*a* and 1*b* that the insertion notch of the flagellum of the wombat and koala sperm is located on the opposite side of the head to the hook, whereas in the hooked types of murid sperm both structures occur on the same side of the head (Plate 1, Fig. 2). A head hook is absent in at least the murine, *Micromys minutus* and in the microtine *Ondatra zibethica* (Friend 1936). In Heidenhain's iron haematoxylin preparations the head length of the wombat sperm measured from the distal extremity to the most proximal point of the curvature of the hook (i.e. excluding the recurved portion of the hook) is about 5·7 μ in contrast to 8·0 μ and 11·7 μ for mouse and rat, respectively (Friend 1936). Feulgen preparations (with or without fast green counterstain) of wombat and koala sperm have shown that nuclear material (DNA) extends to the tip of the hook and occupies all but a small comma-shaped acrosomal portion of the head. Herein lies the greatest departure of wombat sperm from the hooked varieties of murid sperm. In several microtine species the hook is formed entirely from a proximal extension of the nuclear cap (acrosome). In murine sperm a hooked portion of the nucleus bearing a rod extends into the hooked nuclear cap and follows its contour almost to its proximal extremity (Friend 1936).

On the basis of skeletal and dental structure most workers consider the koala to be more closely related to the ringtail possums of the genus *Pseudocheirus* than the wombat (Wood Jones 1924; Simpson 1945). Comparisons of sperm morphology on which selection pressure would presumably be lower than that for external characters of an animal such as skeletal or dental characters, is therefore of considerable interest as a possible basis for taxonomic classification.

It can be seen from the previous descriptions that the spermatozoon of *Pseudocheirus peregrinus* is not intermediate in structure between the more typical marsupial types (Macropodidae and Dasyuridae) and those of the highly divergent wombat and koala. On the contrary, it deviates in quite a different manner from the typical marsupial patterns. The head is broad (3·8 μ) in comparison to its length (5·9 μ), the anterior end lacks a hook and is semi-circular in dorsal view (Plate 1, Figs. 3 and 4). Other distinguishing features are the shape and position of the acrosome previously mentioned and a relatively short middle-piece (6·9 μ). The view that the koala is more closely related to the ringtail possum than the wombat is not supported by comparisons of sperm morphology. On the contrary, the findings reported here support the observations of Sonntag (1923) and Troughton (1957) who considered that the koala shares sufficient characters with the wombat for its classification along with the phalangers to be rejected.

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Explanation of Plate 1

Figures 1 and 2 are photographs of Heidenhain's iron-haematoxylin preparations from formalin-fixed epididymal material

Fig. 1.—*Phascolomis mitchelli*, mature epididymal spermatozoon, lateral view.

Fig. 2.—*Rattus norvegicus*, mature epididymal spermatozoon, lateral view.

Fig. 3.—*Pseudocheirus peregrinus*, spermatozoon head, showing centrally placed acrosomal pit, dorsal view.

Fig. 4.—*Pseudocheirus peregrinus*, epididymal spermatozoon, lateral view.

MORPHOLOGY OF SPERMATOZOA

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THE GENITAL SYSTEM AND THE FETAL MEMBRANES AS CRITERIA FOR MAMMALIAN PHYLOGENY AND TAXONOMY

By H. W. Mossman

All systems of classification of natural phenomena are admittedly imperfect because these phenomena differ from one another in such infinitely variable degrees that it is impossible to divide them into a system of groupings which do not frequently overlap or intergrade. It is also absolutely impossible consistently to select morphological criteria for a scheme of classification that will lend themselves to the assignment of a series of ranks such as species, genera, and families, in one group that will be of parallel value to a similar series assigned to another related group. Yet in spite of these obviously insurmountable barriers to perfection, convenience and orderliness in science demand that classifications be made, and that their categories be of as nearly parallel value as possible.

Most biologists believe that the best basis for classification is phylogeny, that is, the evolutionary or genetic relationships within and of the group. This is so widely accepted that practically all other forms of classification are considered "artificial." Although artificial classification is often temporarily necessary, as in tentatively fitting a poorly understood entity into a general scheme, still a natural or phylogenetic classification should always be the ultimate aim.

Criteria for classification of any group should therefore be characters of phylogenetic significance. Furthermore there should be some way to evaluate the relative significance of one set of criteria in relation to another set; for instance, dentition as compared to skull proportions; or pelage as compared to baculum. There should also be some method for determining whether a given set of characters is suitable for separating the lower categories such as species and genera, or the higher categories such as families and orders.

The more conservative characters obviously will be of greater value in characterizing the higher categories, while the less conservative will only be of use in the lower categories. The presence of the fetal membranes (amnion, chorion, yolk sac, and allantois) is a highly conservative character appearing in all Amniota. Yet certain aspects of the finer morphology of the placenta, such as whether it is villous, trabecular, or labyrinthine, are of use only in characterizing the families within a suborder, for example the Anthropoidea. This is true because parallel transitions in placental morphology are known to occur independently in other orders not closely related to the Anthropoidea or to one another. These same aspects of finer morphology are, however, too conservative to be of much use in separating genera or species, there being very slight or no differences in this character within single families or genera.

The relative conservatism of biological characters is based on two entirely distinct and independent things. The first is the human factor, or simply the question of generality versus particularity of concept. The greater the breadth or inclusiveness of a character concept the more conservative it is within its particular field. For example, the character "bony skeleton" is much broader and therefore much more conservative than the character "cranium", while the latter is in turn much broader and more conservative than "zygoma." We can and do quite properly select the generalized and broader characters as criteria for separating the higher categories, and the more narrow and particular ones for the lower subdivisions.

Superimposed on this, much more complex, and equally as important, is the second or biological factor in determining conservatism. This may be expressed as the degree to which a character has been subjected to natural selection.

Assuming equal, intrinsic genetic factors, it is certainly true that the more intimately a character is related to the environment the more rapid and extensive will be its environmental adaptations during the course of evolution. The main thesis of this discussion rests on this assumption. It is maintained that the structural characters of the reproductive tracts and fetal membranes of mammals, because they have been largely independent of environmental selection, show relatively little evolutionary divergence as compared to most other organ systems. This is not the place to discuss, statistically, results to be expected in the evolution of a genetically variable system subjected to environmental selection in contrast to one subjected to very little and indirect environmental action. However, it can be readily understood that without the selective effects of *differing environments*, variations would tend to be submerged because of continuous selection for *one constant set of environmental conditions.* A race under these conditions would become more and more stabilized and specialized, but no new divergent races would arise from it. But this is not the situation in regard to a genetically variable system, such as the fetal membranes that are practically *isolated from any direct selective effects of external environment.* In such a system, in this case the fetal membranes, evolution is free to proceed along almost any line so long as it meets certain vital requirements: (1) the supplying of a means of maintaining an embryo within the mother's uterus until mature enough to be born; (2) structural conditions which will allow the uterus to resume a normal nonpregnant state after delivery, so that another pregnancy may ensue.

Certainly these fundamental requirements are far from simple in either a structural or physiological sense; they involve extremely complex mechanisms. But the point is that not only is the intrauterine environment relatively constant in mammals generally, but so are the requirements for maintenance of an embryo and for restorability of the uterus to the condition for beginning another pregnancy.

What then should one expect of the evolution of an organ system, such as the fetal membranes, largely isolated from the external environment and charged with a highly complex job to do, but one which is fundamentally the same in all members of the group, in this case the Subclass Eutheria? It seems that, regardless of rate of genetic variation of the system, divergence would be relatively slow and narrow, and that intergradation would be the rule, there being slight environmental selection, and little race isolation due directly to adaptive variations in this system itself. But while this type of evolution would be taking place in an environmentally independent organ system, the group of organisms in which the organ system existed could nevertheless be undergoing the usual evolutionary course in its other organ systems: diverging widely in adaptation to environmental niches old or new; losing species or whole major groups by extinction; in short, becoming the widely divergent, often aberrant or isolated groups that are characteristic of mammals at the present time.

Such an environmentally isolated system must then be very conservative in its characters as compared to those organ systems related closely to the environment and therefore subject to intense, adaptive evolution. The characteristics of such a system should vary relatively little between major groups, and almost none between closely related minor categories. This lack of divergence should make it possible to detect common characteristics among groups widely separated from one another in other characteristics, whether this be due to adaptations to divergent environments, or to extinction of intergrading groups. Conversely, dissimilarity in characters of a conservative organ system should be good evidence of lack of close phylogenetic relationship.

It is generally conceded that similarity of more conservative characters between two forms is better evidence of close relationship than similarity of less conservative characters. Whether lack of conservatism is due to more intensive environmental selection or to a combination of this with such things as more intensive sexual selection, or greater innate potential of genetic variability, there is more chance that similarities in less conservative characteristics are due to evolutionary parallelism or convergence. In estimating phylogenetic relationship it is therefore extremely important to know which are the more conservative organ systems and to give their characters the greater weight. It is also important to evaluate the various characters of such an organ system to determine which are the more conservative within the system. The more conservative will serve to characterize the higher categories, the less only the lower ones.

The foregoing discussion largely reiterates generally recognized principles which have been used for years by students of evolution and taxonomy. However it seemed best to restate them here since the chief purpose of this paper is to point out that the reproductive tracts and fetal membranes of mammals are conservative systems which have never been adequately used in phylogenetic and taxonomic studies of this group. It will be shown that the relative conservatism of the various features of these organ systems can be estimated and the characters used as criteria in proper relation to their significance. It is now best to proceed to specific examples. The first concerns the male genital tract of the Sciuridae.

In 1923, Pocock pointed out the marked difference between the male external genitalia of *Tamiasciurus* and *Sciurus* and separated the two genera on this basis. In 1932, Mossman, Lawlah, and Bradley published a more detailed study of the tracts of *Sciurus carolinensis*, *S. niger*, *Tamias striatus*, *Citellus tridecemlineatus*, *Glaucomys volans*, and *Tamiasciurus hudsonicus*. They showed that the typical sciurid male tract as seen in all these genera (except *Tamiasciurus*), and as also described by Krölling (1921) in *Sciurus vulgaris*, is characterized by a unique arrangement of the ducts of the bulbo-urethral glands. Tullberg (1899) gave enough information on several other genera to indicate the probability that they also have this same character, and Oudemans (1892) made it fairly clear that *Petaurista petaurista* is essentially like *Sciurus*. So, with the exception of *Tamiasciurus*, other sciurids so far as known have a pair of large bulbo-urethral glands drained by a pair of voluminous ducts which, upon entering the sheath of the corpus cavernosum urethrae in the bulb region, become highly modified to form another accessory organ, the bulbar gland. This whole complex is then drained by a single long glandular duct, the penile duct, which lies ventral to the urethra throughout almost the entire length of the corpus cavernosum urethrae, finally entering the urethra at approximately the base of the glans. The author has examined some other genera, including *Marmota* and *Heliosciurus* and has found them also fundamentally like this.

At the same time we showed that *Tamiasciurus*, the red squirrel or chickaree, possesses an entirely different type of bulbo-urethral gland and duct. It has no bulbar gland and no penile duct. It does have a urethral sinus in the bulb much like that of some Muridae. Later it was shown that the female tract of the chickarees is also unique, the vagina being extremely long and coiled while that of all other Sciuridae studied is short and broad (Mossman, 1940). Other peculiar features of the male tract of the chickarees, such as the long filiform penis and the absence of a baculum, were also pointed out at that time. (Layne (1952) has shown that *Tamiasciurus* does possess a minute baculum averaging only .26 mm. in length in adults. Pocock and the author both failed to note this structure.)

A recent, and as yet unpublished manuscript by Mr. M. R. N. Prasad of Central College, Bangalore, India entitled, "Male genital tract of two genera of Indian squirrels," presents excellent descriptions of the palm squirrel, *Funambulus palmarum palmarum* Linn., and of the giant Malabar squirrel, *Ratufa indica maxima* Schreb. *Ratufa* has the typical sciurid tract, but *F. palmarum* is like *Tamiasciurus* in having minute Cowper's glands and no bulbar gland or penile duct. Obviously this indicates close relationship between this species and the Tamiasciurinae, and poses a number of interesting questions in regard to sciurid phylogeny and geographic distribution, to say nothing of the doubt it throws on the present taxonomy of the whole group.

Although the nature of the reproductive tracts of most of the genera of squirrels is still unknown, enough knowledge is available to make it seem very probable that instead of a wide range of types within the family, there are at least two fundamentally different types. This seems probable as it is definitely known that at least one genus of three of the six tribes that Simpson (1945) includes under the subfamily Sciurinae has the typical male sciurid tract; and that two genera of his second subfamily, Petauristinae, also are typical. One can raise the question then as to the logic in placing the chickarees and Funambulini as tribes of the subfamily Sciurinae when the reproductive tracts of *Tamiasciurus* and *F. p. palmarum* are so different from others of this group. Also, in view of Prasad's work, *F. p. palmarum* and *Ratufa* should not be in the same tribe with one another. Furthermore, it is illogical to place the chickarees and *Funambulus* in these subgroups and at the same time to put *Petaurista* and *Glaucomys* in a separate subfamily, although their genital tracts are almost identical to that of Sciurus. Obviously the flying squirrels (Petauristinae) have been separated on the basis of petagial characters; but these must be highly subject to environmental selection, hence nonconservative. Very similar petagial characters have been developed in certain marsupials (*Acrobates* and *Petaurus*), and in other Eutheria, namely in the Dermoptera, and in the Anomaluroidea among the rodents. Of course one could ask if similar reproductive tract characters may not also have developed in widely unrelated groups. There is no evidence that this is true, but it must be admitted that the data are insufficient. This in itself should be a challenge, to those who ask the question, to make an effort to gather the information.

There may be those who will still fall back on the fundamental question of whether the genital tract characters are more conservative than others in the Sciuridae. If they will allow the ruling out of the genus *Tamiasciurus* and the species *Funambulus p. palmarum* as members of the family, then one can cite the fact that the genital tracts of *Sciurus*, *Tamias*, *Citellus*, *Marmota*, *Ratufa*, and *Glaucomys* are the same in fundamentals, and indeed very similar even in details, while there is great divergence between these various genera in body form, pelage, feet, ears, skeleton, skull, and teeth. If one is not willing to allow the ruling out of the chickaree group, and *F. p. palmarum*, then in the face of the apparent aberrance of these he is bound to withhold judgment until someone can show whether or not there are intergrading forms, so far as male genitals are concerned, between them and the typical sciurids. If there are, then perhaps the genitals are not as conservative as they now seem.

There are a few minor characters of male genital tracts that are variable enough in some groups to be of use in separating species of a single genus. Howell (1938) published a plate showing the bacula of several species each from the genera *Eutamias*, *Citellus*, and *Sciurus*. There are fairly obvious intrageneric differences between these bones within each of the three genera, although occasionally in two species they are practically identical (*Sciurus carolinensis* and *niger*). It is probable that there are other features of the male genitals which would show intrageneric differences: certainly differences in the glans penis correlated with those of the bacula would be expected. However, appreciable intrageneric, species differences in the *internal* genitalia of either the male or female have never been noted by the author in the sciurids or other groups, but intergeneric differences are the rule, and are often rather extensive; for example between *Tamias*, *Citellus*, and *Sciurus* (Mossman, Lawlah and Bradley, 1932).

To the author's knowledge, no attempt has ever been made to compare the reproductive tract at the level of the higher categories. It seems doubtful that such clearcut indications of relationship would be found as occur in the case of the fetal membranes, where, for example, considerable affinity is shown between the Artiodactyla, Perissodactyla, and Cetacea; and between the Fissipedia and Pinnipedia. Before such a study would be sound, a thorough investigation of the various genera and families of several well-defined orders should be made, in order to evaluate the conservativeness of the various genital tract features.

The female genital tract characters are probably about as equally conservative as those of the male, but those of the female are in general more difficult to observe and define. A good example of this is the os clitoridis or baculum, which in recent years has been demonstrated in females of several species, leading one to expect that, where present in the male, it probably also occurs in the female. This female element may show intrageneric differences like its male homolog, but the fact that it is usually so small and so obviously rudimentary argues against its value as a character for taxonomic purposes. The other characters of the female external genitalia are also relatively indefinite and difficult to observe. Female internal genitalia show a few very definite features which could be of considerable use, but they are almost always too conservative for intrageneric taxonomy, in fact in most cases they are of use only in separating groups higher than genera. For instance, the form of the uterus, oviduct, and ovary is almost identical in the Cervidae and Bovidae. The Mustelidae, Procyonidae, and Ursidae have a peculiar configuration of the oviduct in relation to the ovary and ovarian bursa that is highly characteristic and differs very little between the three families. The Heteromyidae and Geomyidae likewise have a characteristic oviduct pattern which is practically identical in the two groups. By and large then, it may be said that the characters of the female internal genitalia are very conservative, but usually rather obscure and difficult to observe.

Comparative studies of the microscopic anatomy of the ovaries have revealed no case where obvious intrageneric differences exist, except those due to differences in body size of the species. However some intergeneric differences in microscopic structure do occur: for example; ovaries of mature females of *Sylvilagus* and *Lepus* are rather easily distinguished from one another, but those of *Lepus* and *Oryctolagus* would be difficult; *Citellus* and *Sciurus* are separable, but *Sciurus* and *Tamias* are alike, except for size. When one reaches the higher categories such as families and orders, then microscopic features become characteristic for each group. All the mustelids examined have a very similar and typical interstitial cell pattern: this includes *Martes americana*, *Taxidea taxus*, *Mephitis mephitis*, *Spilogale interrupta*, and *Mustela vison*, *cicognani*, *frenata*, and *putorius*. There are even examples of striking similarity in microscopic structure between related families, at least so far as the few genera of each studied are an indication. Examples of this are Ursidae and Procyonidae, Cervidae and Bovidae, and Erethizontidae and Dasyproctidae.

Let us now turn our attention briefly to the fetal membrane characters of the Sciuridae (Mossman, 1937; Mossman and Weisfeldt, 1939). It is not necessary to enter into a detailed description of the sciurid membranes and placentation, as the main point to be made is that these are even more conservative characters than the male genital system of the group. So it is not surprising that in all the genera studied, *including Tamiasciurus*, the fetal membranes are practically the same, differing only in minor details. These include all the genera mentioned in connection with the male genitals, except *Heliosciurus* and *Petaurista*, and two others in addition, *Cynomys*, *Xerus* (Rau, 1925). In fact the membranes and placenta of *Aplodontia* are distinctly sciuroid, although the male genitals lack the bulbar gland and penile duct.

It appears then that the criteria of the male and female reproductive tracts and the fetal membranes could be applied to advantage in determining the phylogenetic relations of the Sciuridae, and consequently in establishing a more logical taxonomy of this group. The fetal membrane characters are even more conservative criteria than those of the male or female genital tracts.

The application of the genital tract and fetal membrane criteria in the phylogeny and taxonomy of the Sciuridae has been discussed first, since it is the only group in which the author has made reasonably comprehensive studies of both systems. Little has been said thus far of the evaluation of specific criteria, as the studies of the male tract in such a small group do not lend themselves to adequate analysis. The author has however made extensive comparative studies of mammalian fetal membranes and believes, that for them, the basis is broad enough to enable clearly reliable estimates to be made of the relative value of the different characters involved. Since this subject was presented fully in his 1937 monograph, it is not necessary to repeat the details here. Suffice it to point out that all the descriptions of the fetal membranes of specific species which have appeared in the literature since then, and all of the numerous additional observations of the author, bear out the thesis proposed at that time. The facts derived from these studies can be stated very simply.

1. In every group of mammals, high or low in category, in which the members can be clearly related to one another on the basis of total anatomical similarity, their fetal membranes are fundamentally similar, showing far less divergence than do other characters. These groups are perhaps best illustrated by the orders Lagomorpha, Rodentia, Carnivora, and Artiodactyla; by the suborders Microchiroptera, Lemuroidea, and Anthropoidea; by the families Tenrecidae, Soricidae, Talpidae, Cebidae, Cercopithecidae, Pongidae, Dasypodidae, Sciuridae, Heteromyidae, Geomyidae, Muridae, Canidae, Mustelidae, Felidae, Cervidae, and Bovidae; and by numerous genera in these and some other families. All these groups consist of anatomically closely related forms and all have even closer fetal-membrane affinities. They are used as illustrations because enough is known about the fetal membranes of enough members of each group to make

it reasonably certain that the above statement is true. There are other anatomically homogeneous groups such as the Megachiroptera, Cetacea, and Perissodactyla where the limited data available points in the same direction. This is particularly true of the data on the species of numerous genera of the groups already mentioned.

2. In many groups of mammals made up of subgroups widely divergent or of uncertain affinities there are fundamental differences in the fetal membranes. This is true of the Insectivora; the Chiroptera, where there is wide divergence between the membranes of the two suborders (Microchiroptera and Megachiroptera); the Primates, where the membranes of Lemuroidea and Tarsoidea differ widely from one another and from the Anthropoidea; and the Edentata, where the Bradipodidae and Myrmecophagidae are probably much alike, but differ markedly from the Dasypodidae. The Pholidota, often included in the order Edentata, differ fundamentally from all others of this order.

3. The membranes of certain groups commonly separated on anatomical grounds, but known to be somewhat related, are often so similar that the wideness of separation does not seem justified. This is true of the Pongidae and Hominidae, the Lagomorpha and Rodentia, and of the Perissodactyla and Artiodactyla.

4. There are fundamental similarities between certain aberrant groups and other groups to which they have not been supposed to be clearly related. Striking examples of this are the strong resemblances between the membranes of the Bradypodidae and the Anthropoidea; between the Lemuroidea, Pholidota, Cetacea, and Sirenia and those of the Perissodactyla and Artiodactyla; and between the Dasypodidae, Rodentia, Microchiroptera and Soricoidea.

More data than are at present available are certainly necessary to warrant drawing more than very tentative conclusions as to the significance or nonsignificance of these facts, but it is interesting to note that there are many points of anatomical resemblance between lemurs and the hoofed animals, and between the sloths and anthropoids. Certainly taxonomists should not close their minds to the possibility that lemurs are an arboreal line derived from stock ancestral to the hoofed animals, and that their relatively slight resemblance to anthropoids is due to retention of primitive characters in both lines, and to convergence and parallelism effected by adaptation of both to an arboreal habitat. Nor should one close his mind to the possibility that the sloths represent highly specialized edentulous forms derived from the same ancestral stock as the anthropoids.

Now that the general method of application of the reproductive tract and fetal membrane criteria to the taxonomy and phylogeny of mammals has been described and illustrated, one must clear up the important point of the evaluation of the criteria used. The basis for this is the observation described as number 1 above; namely, that in every group of mammals in which the members can be clearly related to one another on the basis of total anatomical similarity their fetal membranes are fundamentally similar, showing far less divergence than do other characters. This makes it possible to compare the variability of different features of the membranes within the group as a whole and within its various lesser taxonomic categories, as was done by the author some years ago (Mossman, 1937). Those characters which are consistently constant throughout all the subgroups of a major category certainly are the more conservative ones of that group. If the same characters are also constant, but not necessarily alike, throughout several well established orders, then they are certainly characters conservative enough to be used for establishing phylogenetic relationships between orders. If they are constant within single families, but vary between different families of an order, then they are only conservative enough to establish relationship between families. This general principle can be applied to all categories. Obviously one must choose test groups in which the taxonomy is quite clear and definite, and must compare parallel, major groups in which the minor categories are also reasonably parallel in value. This is obviously arguing in a circle, and thus a dangerous practice if not tempered with good judgment and a reasonable scientific conservatism on the part of the person using it. However it is the best method available, and far superior to making no attempt at evaluation.

One further argument in favor of the fetal membranes as criteria for phylogeny must be stated. This point seems even more important than that of their conservatism. In fact, coupled with their conservatism, it makes them the most ideal of all anatomical criteria for recent forms. This is the fact that the history of the development of the fetal membranes of a species is the history of a complete, complex, and, structurally, highly independent organ system, from its inception during cleavage to its complete functional maturity, old age, and death at the time of birth of the young. We are therefore dealing with the complete life history of an organ system carried out in the relatively constant environment of the uterus, thus almost completely isolated from adaptational demands of the varying external environment. Other criteria commonly used do not offer this overall picture of the individual. The fetal membranes and their development are complicated, but far less so than the total history of all the organ systems ordinarily used as criteria. Their conservatism, and the total developmental picture that they give, render them the most ideal of all organ systems for phylogenetic and taxonomic studies of recent mammals.

SUMMARY

When compared with the organ systems ordinarily employed as criteria for taxonomic and phylogenetic studies of mammals, the characters of the male and the female reproductive systems and of the fetal membranes are the more conservative. This is apparently due to the relatively minor role that adaptation to external environment has played in the evolution of these systems.

Little effort has ever been made to apply male and female genital tract characters to such studies of mammals, but a limited consideration of them by the author indicates that they are less conservative than the fetal membranes. They furnish characters that are of use in the study of the interrelationships of genera and families, and, in some cases, even of species. Whether or not they would be

reliable in showing affinities between higher categories, such as orders and suborders, is unknown.

On the contrary, the fetal membranes are so conservative that clear-cut interspecific or even intergeneric differences seldom exist. Furthermore interorder and interfamily fetal-membrane similarities often demonstrate relationships between these major groups. This conservatism, plus the fact that the complete life cycle of the fetal membranes takes place during embryonic development and is therefore much more easily studied than that of any other organ-system ontogeny, makes this system the most ideal of all criteria for the study of phylogenetic interrelationships of recent mammals.

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MORPHOLOGY AND PHYLOGENY OF HAIR

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Hair is a structure found exclusively in mammals. With this in mind, Oken named the Mammalia, Trichozoa (hair animals), and Bonnet (1892) named them Pilifera (hair bearers).

Of the many aspects of morphology and phylogeny of hair, only four will be discussed. These include (1) the principle of the arrangement of hairs in group patterns, (2) the types of hair and their relation to the principle of the group pattern, (3) a brief analysis of the structural elements of hair and their relation to the types of hair, and (4) the phylogeny of hair, with some remarks on (*a*) the relation of hair to the epidermal derivatives of other vertebrate classes and (*b*) aspects of the phylogeny of the hair and wool of sheep to illustrate that marked differences in hair coats exist between closely related animals.

Hair is the subject of a voluminous literature. Toldt (1910, 1912, 1914, and 1935), Danforth (1925a), Pinkus (1927), Pax and Arndt (1929–1938), Trotter (1932), Lochte (1938), Smith and Glaister (1939), and Stoves (1943a) discuss the problem of mammalian hair in general. Wildman (1940), von Bergen and Krause (1942), and the American Society for Testing Materials (1948) discuss the problem of fiber identification as applied to textiles.

Principle of the Group Pattern of Hairs

In the only extensive survey of the grouping of hair in mammals, DeMeijere (1894) documented the concept of the group pattern of hair (FIGURES 1–6). Unfortunately, the few studies on this phase of the problem since that time have not fully exploited the implications of this concept. DeMeijere concluded that hairs are mainly arranged in groups with the pattern of 3 hairs—with the largest hair in the middle—as the basic pattern. The concept of the basic trio as the primitive condition is accepted as an adequate working hypothesis by Wildman (1932), Galpin (1935), Höfer (1914), Gibbs (1938), Hardy (1946), and others. DeMeijere described 8 patterns: (1) 3 or less hairs behind each scale of the tail (as in the opossum, *Didelphis marsupialis*), (2) more than 3 hairs behind each scale of the tail (as in the rodent, *Loncheres* [Echimys] *cristata*), (3) 3 hairs (as in the back of the marmoset, *Midas rosalia*), (4) more than 3 hairs arranged in a regular pattern with some of greater diameter than others (as in the back hairs of *Loncheres* [Echimys] *cristata* in FIGURE 3), (5) several hairs composed of a number of fine hairs and one coarse hair (as in the back of the dog, *Canis familiaris*, in FIGURE 5D), (6) several hairs composed of a number of fine hairs and one isolated coarse hair (as in the back hairs of the mouse, *Mus decumanus*, in FIGURE 6D), (7) scatterings of fine hairs with no apparent

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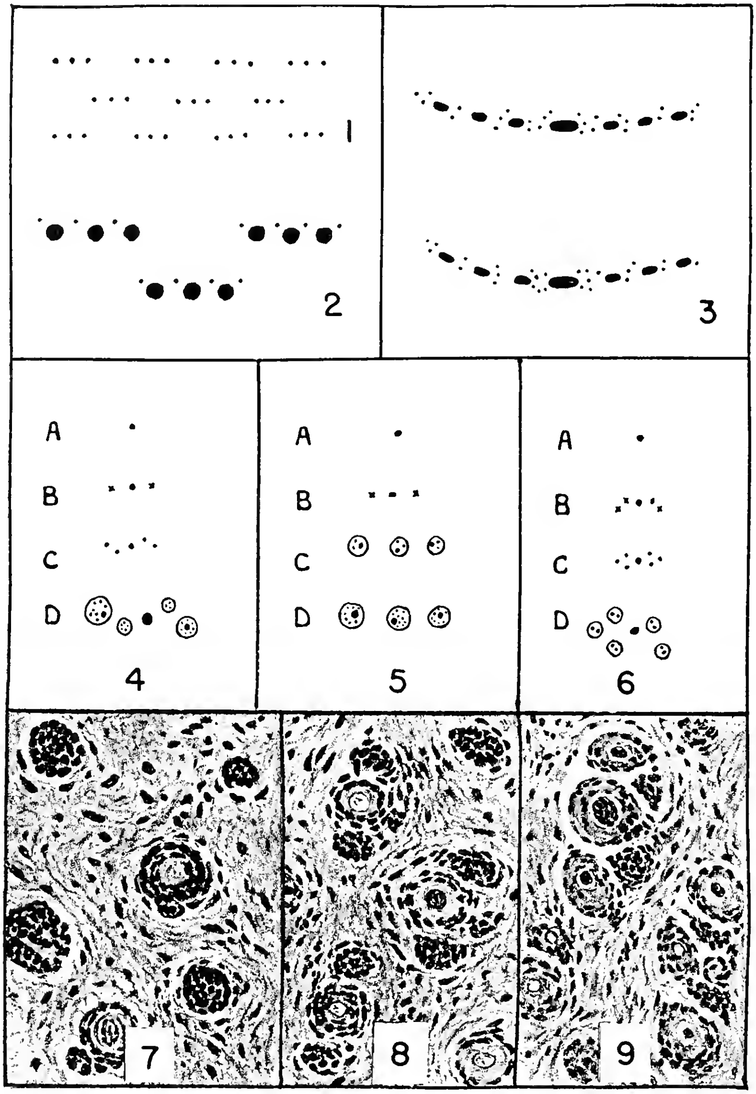
arrangement and a few intermingled coarse hairs (as in the back hairs of the cat, *Felis domesticus* in FIGURE 4D), and (8) hairs in irregularly scattered groups (as in the back hair of the raccoon, *Procyon cancrivorus*).

Dawson (1930) does not completely agree with DeMeijere's pattern in the guinea pig. She found variations in the pattern and no correlation between the size of hair and the arrangement of the hairs in each group. Histological study frequently shows follicle grouping which was not apparent to DeMeijere when he was examining only the skin surface, *e.g.*, in *Felis domesticus* (see Höfer, 1914). This indicates that analyses of the group pattern of hairs are needed in both common laboratory mammals and mammals in general.

In addition, DeMeijere analyzed the formation of the patterns by examining the skins of animals during their development (FIGURES 4–6). This phase of the problem has been extended to include a study of the ontogeny of the arrangement of hair follicles in sheep (Wildman, 1932, Galpin, 1935, and Duerden, 1939), in the cat (Höfer, 1914), in marsupials (Gibbs, 1938, Stoves, 1944b, and Hardy, 1946), in the mouse (Calef, 1900, Dry, 1926, and Gibbs, 1941) in the rat (Frazer, 1928), and in a number of mammals (Duerden, 1939). The terminology used by these authors in this problem is summarized in TABLE 1 (adapted from Wildman and Carter, 1939 and Carter, 1943).

Utilizing the terminology of Wildman and Carter, 1939, the following is a brief statement of the relation of the fiber generations. The first follicles to differentiate are the central trio follicles (FIGURE 7). If these follicles appear at two different times as in the opossum (Gibbs, 1938), then the follicles are called "primary X" and "primary Y." The essential point is that each of these primary follicles will be the central follicle of different hair groups. Later in development, other follicles of the hair group differentiate in relation to these central trio follicles. The trio is formed when two follicles are differentiated lateral to the primary follicles (FIGURE 8). The lateral follicles associated with primary X and primary Y are called respectively "primary x" and "primary y." If only one lateral follicle is formed adjacent to a primary follicle (X or Y), then a couplet follicle is formed. If no lateral follicles differentiate, a primary follicle (X or Y) is called a "solitary follicle." Later, another generation of follicles is differentiated—the secondary follicles. In the opossum (FIGURE 9), these secondary follicles are located between the central trio follicle and the lateral trio follicles. The ontogenetic studies of follicle arrangement have added confirmatory evidence to DeMeijere's basic concept that in mammals there is a universal and regular grouping of hair follicles (Hardy, 1946).

In general, the early differentiating follicles (central trio follicles) form the coarse overhair, while the late differentiating follicles (lateral trio follicles and secondary follicles) form the fine underhair. Lateral trio follicles sometimes at least produce overhair like that of the central follicles (*e.g.* in sheep) or intermediate types such as awns, which are classified by Danforth (1925a) as overhair. In *Ornithorhynchus anatinus* (Spencer and Sweet, 1899) and many marsupials (Gibbs, 1938, Bolliger and Hardy, 1945, Hardy, 1946), however, the lateral trio fibers are indistinguishable from those of secondary follicles, so it is difficult to place them in either the "overhair" or the "underhair" category.



Figures 1-9 (*see facing page*).

Spencer and Sweet (1899) claimed that, in monotremes, each group of follicles was differentiated by budding from the central follicle. This has not been described in marsupials or in eutherians, in which the follicles arise independently as epidermal downgrowths. Monotremes and marsupials have in common the fact that a follicle group typically contains a large central follicle with a sudoriferous gland, and two or more clusters of smaller lateral follicles (Spencer and Sweet, 1899, Gibbs, 1938, Hardy, 1946). This arrangement is also found in some eutherians, such as the cat (Höfer, 1914) and dog (Claushen, 1933). In the cat and a few other eutherians, the first-formed lateral follicles (primary x and y of the classification of Wildman and Carter, 1939) produce hairs intermediate in type between those of the central and the other lateral follicles. There are other eutherians in which the lateral primary x and y fibers are still more like the central primary X and Y fibers, as in the pig (Höfliger, 1931) and the sheep (Carter, 1943). Except in the rodents, there is always a sudoriferous gland opening into the central primary X or Y follicle (Hardy, unpublished data). Many animals, such as the pig and sheep, also have a sudoriferous gland opening into each primary x and y follicle, but others do not (Duerden, 1939). Some of the eutherians have only primary follicles in their skin, each with a sudoriferous gland. Findlay and Yang (1948) showed that this is the arrangement in cattle, and the same is probably true in horses and in human head hair (Hardy, unpublished observations).

Types of Hair

DeMeijere's analysis leads to the classification of hair types by Toldt (1910 and 1935) and by Danforth (1925a). Many details of the hair types in many species of animals and the variations of the structure of these types are described, illustrated, and bibliographically annotated by Toldt (1935) and Lochte (1938).

Types of Mammalian Hair
(after Danforth, 1925*a*)

1. Hairs with specialized follicles containing erectile tissue. Large, stiff hairs that are preeminently sensory. They have been variously designated as feelers, whiskers,

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Figures 1–9 (*see opposite page*).

Figure 1. The trio hair group pattern on the back and tail of the marmoset, *Midas rosalia* (after DeMeijere, 1896). All hairs have similar diameters.

Figure 2. The hair group pattern of more than 3 hairs with some fibers of greater diameter than other fibers on the back of the paca, *Coelogenys paca* (after DeMeijere, 1896).

Figure 3. The hair group pattern of more than 3 hairs with some fibers of greater diameter than other fibers on the back of the rodent, *Loncheres* (Echimys) *cristata* (after DeMeijere, 1896).

Figure 4. Ontogeny of a hair group on the back of the cat, *Felis domesticus*. A, from a newborn animal; B and C, from an older animal; and D, from an adult animal (after DeMeijere, 1896).

Figure 5. Ontogeny of a hair group on the back of the dog, *Canis familiaris*. A, from an embryo dog; B, from a newborn animal; C, from a young dog; and D, from an adult animal (after DeMeijere, 1896).

Figure 6. Ontogeny of a hair group on the back of the mouse, *Mus decumanus*. A, from a 7 cm. long animal; B, from a 9 cm. long animal; C, from a 12.5 cm. long animal; and D, from an adult animal.

(Figures 4, 5, and 6 illustrate that the follicle of the first hair to erupt (A) will be the follicle of the coarsest hair of the hair group in the adult. The type of hair group pattern in the adult (D) in each figure is noted in the text. The X in the diagrams marks the location of erupting follicles.)

Figure 7. The primary follicles X (the more differentiated follicles) and the primary follicles Y (the less differentiated follicles) in the transverse section of skin of a 12.5 cm. Australian opossum embryo (*Trichosurus vulpecula*). Follicles are scattered irregularly. (After Gibbs, 1938.)

Figure 8. Two new follicles (primary x or primary y) have become grouped with each previously differentiated follicle (primary X or primary Y) to form the typical trio arrangement. The trio would be either primary x, primary X, primary x or primary y, primary Y, primary y. Transverse section of skin of a 15.0 cm. Australian opossum embryo (*Trichosurus vulpecula*). (After Gibbs, 1938.)

Figure 9. Two secondary follicles have added to each trio group to form a 5 follicle group. The secondary follicles differentiate between the primary X (or Y) follicle and the primary x (or y) follicles. The five group would be either primary x, secondary follicle, primary X, secondary follicle, primary x or primary y, secondary follicle, primary Y, secondary follicle, primary y. Transverse section of skin from 20.0 cm. Australian opossum embryo (*Trichosurus vulpecula*). Note presence of a dermal capsule surrounding each 5 follicle group. (After Gibbs, 1938.)

(In figures 7, 8, and 9, the terminology of Wildman and Carter (1939), noted in the text, is used.)

TABLE 1
FIBER-FOLLICLE TERMINOLOGY IN THE MAMMALIA*

Wildman and Carter (1939)		*Duerden (1939) (sheep)*	*Hardy (1946) (marsupials)*	*Gibbs (1938) (opossum)*	*Galpin (1935) (sheep)*	*Wildman (1932) (sheep)*	*Toldt (1911) (various animals) and Höfer (1914) (cat)*
Primary follicles		trio follicles					
(a) Central trio follicles	primary X primary Y	central trio follicles	central follicle	primary follicles secondary follicles	X follicle Y follicle	primary follicle secondary follicle	Mittelhaar follicle
(b) Lateral trio follicles	primary x primary y	lateral trio follicles	large lateral follicle	tertiary follicles	x follicle y follicle	lateral trio follicle	Stammhaar follicles
(c) Couplet follicles	primary X + x primary Y + y						
(d) Solitary follicles	primary X or primary Y						
Secondary follicles		post-trio follicles	lateral follicles	quaternary follicles			Beihaar follicles

* Adopted from Wildman and Carter (1939).

sensory hairs, sinus hairs, tactile hairs, vibrissae, *etc.* They occur in all mammals except man, and are grouped by Botezat (1914) (Pocock, 1914) essentially as follows:
   (1). Active tactile hairs—under voluntary control.
   (2) Passive tactile hairs—not under voluntary control.
      (*a*) Follicles characterized by a circular sinus.
      (*b*) Follicles without a circular sinus.

2. Hairs with follicles not containing erectile tissue. The remaining types of hair, most of which are more or less defensive or protective in function. In many cases, the follicles have a good nerve supply, endowing the hair with a passive sensory function as well. These hairs are grouped here according to their size and rigidity.
   (1). Coarser, more or less stiffened "overhair," guard hair, top hair.
      (*a*) Spines. Greatly enlarged and often modified defensive hairs, quills.
      (*b*) Bristles. Firm, usually subulate, deeply pigmented, and generally scattered hairs. "Transitional hairs" (Botezat, 1914), "Leithaare" (Toldt, 1910), "protective hair," "primary hair," "overhair." This group also includes mane hairs.
      (*c*) Awns. Hairs with a firm, generally mucronate tip but weaker and softer near the base. "Grannenhaare" (Toldt, 1910), "overhair," "protective hair."
   (2). Fine, uniformly soft "underhair," "ground hair," "underwool."
      (*a*) Wool. Long, soft, usually curly hair.
      (*b*) Fur. Thick, fine, relatively short hair—"underhair," "wool hair."
      (*c*) Vellus. Finest and shortest hair—"down," "wool," "fuzz," "lanugo." (Danforth, 1939).

The following comments supplement the above classification. The guard hairs are listed in a series from greater to lesser rigidity (in order: spines, bristles, and awns). There are many intergrade hairs between the typical bristle and the typical awn and between the typical awn and the typical fur hair (FIGURES 10, 11, and 12).

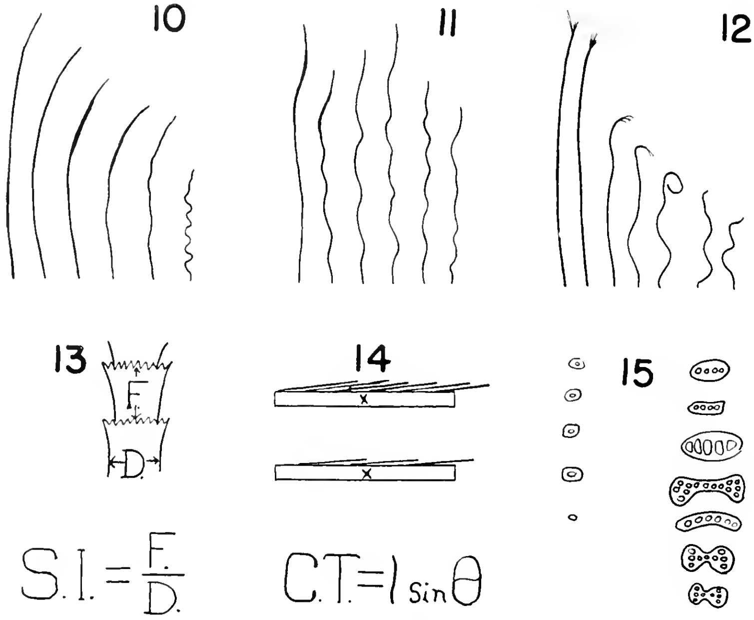
The tactile hairs have a rich nerve supply, while the roots of some are encircled by large circular sinuses containing erectile tissue. When the pressure in the circular sinus is increased the hair becomes a more efficient pressure receptor. The overhairs have a definite nerve supply, while the underhairs have no direct nerve supply. As a general but not absolute rule, the coarser hairs appear ontogenetically earlier than the finer hairs (Gibbs, 1938, Danforth, 1925*a*, Duerden, 1937 (reported by Wildman, 1937), Höfer, 1914, and Spencer and Sweet, 1899).

The contour, diameter, and shape of a hair fiber changes from its root to its tip (Note awns, FIGURES 16–18). The cross-sectional outline of hairs may vary from the thick rounded porcupine quill to the eccentric flattened hairs of seals. The former serves a protective function, while the latter is adapted to hug to the skin so as not to hinder aquatic locomotion. Many details of the anatomy of hair form are noted by Stoves (1942 and 1944a), Toldt (1935), and Lochte (1938).

It is possible for a hair follicle to differentiate one type of hair at one stage and another type at another stage. The follicle of a bristle (kemp) of the Merino lamb may become the follicle of wool in the adult sheep (Duerden, 1937, reported by Wildman, 1937). A fine lanugo hair of the human fetus is associated with a follicle which will later be the follicle of a coarser hair.

The theories of hair curling are reviewed by Herre and Wigger (1939). The curling of hair in primitive sheep is independent of the arrangement of hair, existence of hair whorls, or the cross section of the hair (Pfeifer, 1929).

Wildman (1932) suggests that the shape of the follicle, especially the curve in its basal portion, is a possible factor in hair curling. Reversal of the spiral in some wool fibers may be explained according to Wildman as due to a shift in the growing point of the follicle and inner root sheath. Spiral reversal occurs in human hair (Danforth, 1926). Pfeifer (1929) doubts that curling is determined by a curve of the follicle alone and suggests that Tänzer's (1926) contention that the follicle must be saber-shaped is important. Waving of all compact wools is due at least in part to the flattening of the primary spiral and to the unequal lateral growth of the fiber (Duerden, 1927). The curling of hair in karakul sheep fetuses may be associated with the differences in the rates of growth in the various skin layers (Herre and Wigger, 1939).



FIGURES 10–15.

FIGURE 10. The hair of the fox, *Canis vulpes* (after Toldt, 1935), illustrating intergrade hairs. From the left to the right, Toldt named the fibers Leithaar (bristles), Leit-Grannenhaar, thick Grannenhaar (awns), thin Grannenhaar, Grannen-Wollhaar, and Wollhaar (fur).

FIGURE 11. The hair of the chinchilla, *Chinchilla laniger* (after Toldt, 1935) illustrating an animal hair coat with hairs of approximately the same length. The 2 hairs on the left are awns, and the rest, either intergrade hairs or fur hairs.

FIGURE 12. The hair of the wild pig, *Sus scrofa* (after Toldt, 1935) illustrating bristles on the left and underhair on the right with some intergrade hairs between them. Note the brushlike distal ends of the bristles.

FIGURE 13. The scale index (S. I.), according to Hausman (1930), is equal to the ratio of the free proximodistal length of a scale (F) to the diameter of the hair shaft (D).

FIGURE 14. The thickness of the cuticle (C. T.), according to Rudall (1941), is equal to the length of a cuticular scale (1) times the sine of angle (sin Θ) the scale makes with the cortex (X).

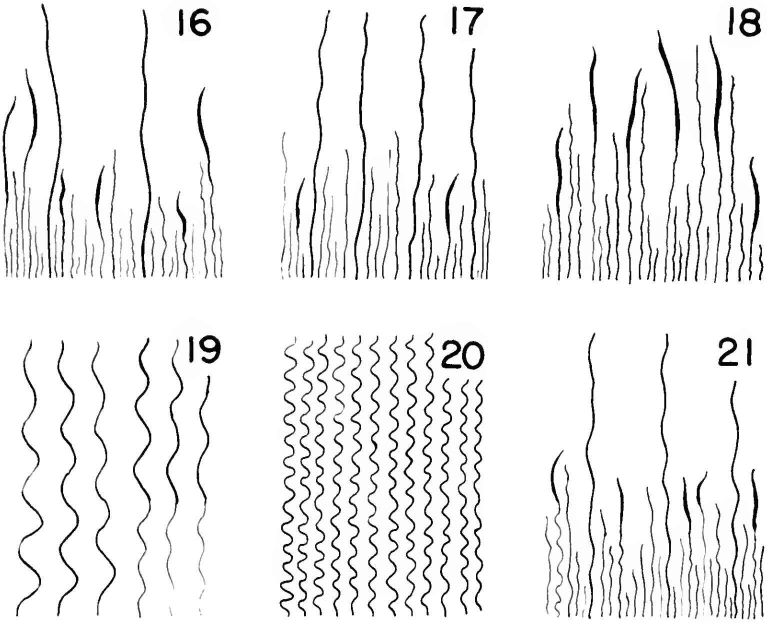
FIGURE 15. Cross sections of several regions of a fur hair (left) and an awn (right) of the rabbit (after Toldt, 1935). The sections, at the top of the figure, are from the base of the hair and, at the bottom of the figure, from the tip of the hair. Illustrates general uniformity of the diameters of the fur hair and differences in diameters and contour of awn hairs throughout their lengths.

The factors responsible for curling and crimping of hair are as yet not completely known.

Structural Components of Hair

The cuticle, cortex, and medulla are the three structural components in hair. They will be discussed in order.

Cuticle. The cuticle consists of thin, unpigmented, transparent overlapping scales, whose free margins are oriented toward the tip of the hair (FIGURE 22). Within the follicle, the free margins of the hair cuticular scales interlock with the inner root sheath cuticular scales, which are oriented in the opposite direction toward the papilla. This interlocking of scales helps to secure the hair in place (Danforth, 1925*a*). The cuticle functions as a capsule containing the longitudinally splitable cortex (Rudall, 1941). This explains why the cortex of a hair frays at its severed end. In addition, the cuticle, with its oily layer, prevents the transfer of water (Rudall, 1941).



FIGURES 16–21.

FIGURE 16. Diagram of the fiber components of coat of a generalized non-wooled animal (after Duerden, 1929). Note presence of bristles (coarse fibers), awns (fibers with fine basal segments and coarse distal segments) and fur fibers (fine fibers).

FIGURE 17. Diagram of the fibers of the wild sheep (after Duerden, 1929). Note the presence of bristles (kemp), awns (heterotypes), and wool.

FIGURE 18. Diagram of the fibers of British mountain breeds (after Duerden, 1929). The fibers are mainly awns and wool. Few bristles are present.

FIGURE 19. Diagram of the fibers of the British luster breeds (after Duerden, 1929). Fibers on the left are wool fibers which are coarser than the wool fibers of wild sheep. The fibers on the right are modified awns with fine proximal segments and slightly coarse distal segments. All fibers are elongated and spiraled.

FIGURE 20. Diagram of fibers of adult Merino sheep (after Duerden, 1929). All fibers are wool. Note uniformity of all fibers as to size, length, and waviness. These wool fibers are coarser than wool fibers from wild sheep. Unlike the fibers of other breeds, the fibers of the adult Merino sheep grow from persistent germs and do not shed.

FIGURE 21. Diagram of the fibers of the Merino lamb. Note the presence of bristles (kemp), awns (heterotypes), and wool. During later development, the bristles are shed and the distal coarse segments of the awns are lost. The adult coat is formed by the persistent growth of the wool fibers of the lamb, by the replacement of wool in the follicles of the shed kemp, and by the persistence of the growth of the proximal segments of the awns.

The cuticular scales vary in thickness from 0.5 to 3 micra (Frölich, Spötel, and Tänzer, 1929). Since the scales overlap, the number of overlapping scales at any point on the hair surface determines the thickness of the cuticle. The cuticular thickness may be expressed as being equal to the length of the scales times the sine of the angle the scale makes with the cortical surface (FIGURE 14, Rudall, 1941).

The cuticular scales may be classified into two types: coronal scales and imbricate scales (Hausman, 1930). A coronal scale completely encircles the hair shaft. They are subdivided according to the contour of the free margins as: simple, serrate, or dentate (FIGURE 23). Müller (1939) contends that a coronal scale is in reality several scales whose lateral edges are fused. For example, a dentate coronal scale with 5 processes in its free border is the fused product of 5 elongated pointed scales.

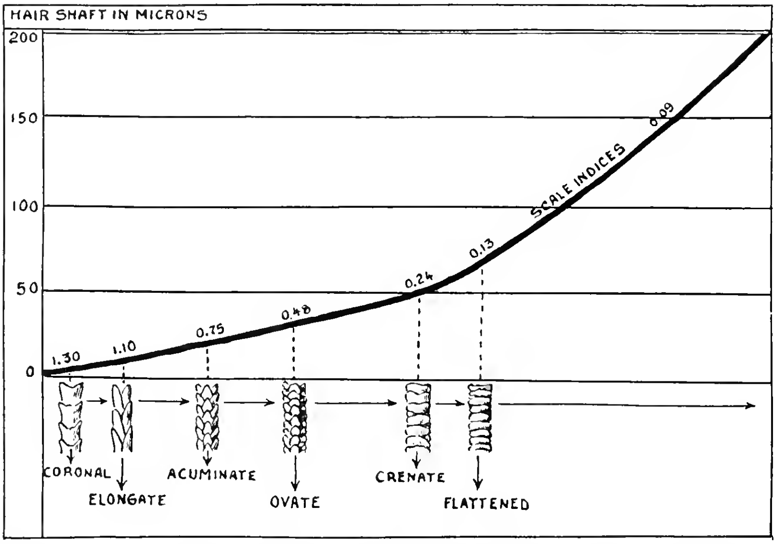


FIGURE 22. Graph illustrating the relation of the diameter of the hair to the types of cuticular scales. The finest hairs (with small diameters) have a high-scale index and coronal scales. The coarsest hairs (with large diameters) have a low-scale index and flattened scales. Diameters of hair shafts are plotted on the ordinate. General regions of the occurrence of scale forms are shown along the abscissa, the average scale indices along the curve. The figures of the scale types beneath the graph are not drawn to scale. (After Hausman, 1930.)

An imbricate scale does not completely surround the hair shaft. They are classified as ovate, acuminate, elongate, crenate, and flattened (FIGURE 22, Hausman, 1930).

Hausman (1930) devised a scale index to express the relation between the diameter of the hair shaft and the free proximo-distal dimension of the scales (FIGURE 13). The free proximo-distal dimension is actually a means of expressing the type of scale. For example, coronal scales have a large proximo-distal dimension, while crenate scales have a small dimension (FIGURE 22). An analysis of the scale indices indicates that a relation exists between the types of scales and the shaft diameters. In general, the finest hairs have large scale indices and coronal scales, while the coarsest hairs have small scale indices and crenate or flattened scales. On the basis of the above, it is concluded that the types of cuticular scales present on hair are related not to the taxonomic status of the animal possessing the hair but rather to the diameter of the hair shaft (Hausman, 1930). In hairs with both thick and thin segments, the thick segments have the scale types of large diameter hairs while the thin segments have the scale types of small diameter hairs.

A coarse guard hair has scales with free lips that are closely applied to the cortex and are scarcely raised. As a result, these hairs have a high luster (due to unbroken reflection of light from the hair surface) and do not interlock with other hairs. A fine underhair has scales with lips that have raised margins. As a result, these hairs are dull (due to broken reflection of light) and interlock with other fine hairs. Thus, mohair has a high luster but makes poor felt, while wool is dull but makes good textiles.

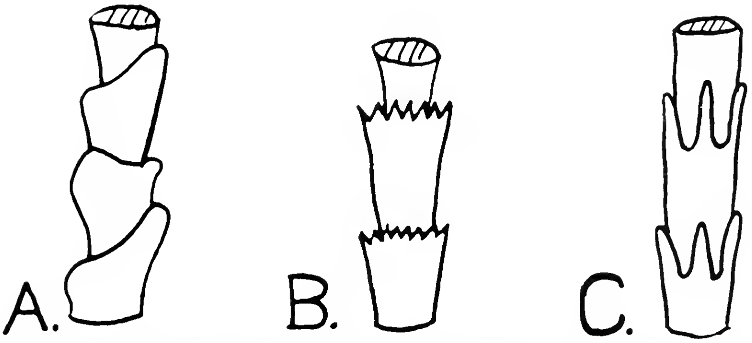


FIGURE 23. Figures illustrating the types of coronal cuticular scales. A. simple scales, B. serrate scales, C. dentate scales, (after Hausman, 1930). Note raised margins on the free lips of scales.

Many details of the cuticle in many species of animals are presented and illustrated by Lochte (1938).

Cortex. The cortex usually forms the main bulk of a hair. It is a column of fusiform keratinized cells which are coalesced into a rigid, almost homogeneous, hyaline mass (Hausman, 1932). Damaged hairs tend to split lengthwise because the elongated cortical cells are oriented longitudinally. The cortex has such a low refractive index—due to the degree of cornification—that, in the absence of pigment, it is translucent. Since cortical scales have not been analyzed in such detail as cuticular scales, no statement can be made of a relation between cortical scale morphology and hair size. The form and distribution of the pigment in the cortex and the medulla is noted by Lochte (1938), Toldt (1935), and Hausman (1930).

Hausman (1932 and 1944) analyzed the cortical air spaces known as cortical fusi—cortical in location and fusiform in shape—air vacuoles, air chambers, air vesicles, or vacuoles. As the irregular-shaped cortical cells located in the bulb rise to the follicular mouth, they carry between them cavities filled with tissue fluid. As the hair shaft dries out, the cavities lose the fluid, and air may fill the resulting spaces—the fusi. The shape of the fusi vary. They are largest, most numerous, and most prominent near the base of the hair, and they are filiform and thin or lost in the distal segments of the hair. Seldom do they persist to the tip of a hair. As a rule, they are visible only under a microscope. Hausman implies that there is a relation between fusi and hair size. Presumably, the coarser a hair segment is, the more numerous the fusi.

Ringed hair results when the fusi appear in masses at regular intervals in the shaft. Fractured fusi result when hairs are damaged sufficiently to separate the cortical cells enough to allow air to collect between them. Fusi can be distinguished from pigment granules, for they are fusiform, whereas pigment granules have blunt ends.

The presence of a thin membrane located between the cuticle and the cortex has been assumed by Lehmann (1944). Observations of pigment granules, cell nuclei, and submicroscopic fibrils are presented by Mercer (1942), Hausman (1930), and others.

Medulla. The medulla (pith), when present, is composed of shrunken and variably shaped cornified remnants of epithelial cells connected by a filamentous network. In contrast to the cortex, the medulla is less dense and has fewer and larger cells, which are more loosely held together. In the medulla are air cells or chambers, which are filled by a gas, probably air. These air cells may be intracellular (deer) or intercellular (dog, weasel, and rat) (Lochte, 1938). The intercellular air cells are classifiable according to their coarseness and arrangement (Lochte, 1934 and 1938).

Medullas are classified by Hausman (1930) as follows: absence of medulla, discontinuous medulla (air cells separate), intermediate medulla (several separate air cells of the discontinuous type arranged into regular groups), continuous medulla (air cells arranged to form a column), and fragmental medulla (air cells arranged into irregular groups). These types are illustrated in FIGURE 24 and are arranged in the order of the sizes of hairs in which they are located. In the finest hairs (underfur), the medulla is either absent or of the discontinuous type. In the coarsest hairs, the medulla is either of the continuous or the fragmental type (FIGURE 24). If a hair varies in thickness, its medulla will vary. For example, in the awns of sheep, the distal thickened segment has a medulla, while the fine proximal segment may have no medulla. The arrangement of the medullary air cells is related not to the taxonomic group of the animal possessing the hair nor the age of the hair, but rather to the diameter of the hair shaft (FIGURE 24) (Hausman, 1930; Wynkoop, 1929; and Smith, 1933). The sheens and colors of hairs are largely determined by the light reflected from the medulla (Hausman, 1944).

Although the cortex forms the bulk of the shaft in most hairs, the medulla assumes large proportions in some hairs. In rabbit hair (FIGURE 15), the medulla is composed of large air cells separated by little more than a framework of cortex (Stoves, 1944*a*).

The significance of the cuticle, cortex, and medulla in the commercial aspects of fur is presented by Bachrach (1946). Although many of the details of the structural elements of hair cannot be definitely utilized to identify an animal species (Hausman, 1944), it is possible that some morphological features of hair can be used (Williams, 1938).

Some chemical and physical aspects of the morphological elements of hair have been analyzed. Not only do the cuticle, cortex, and medulla exhibit different chemical and physical properties, but various segments of these structural elements may have different chemical and physical properties (Rudall, 1944; Stoves, 1943*b*, 1945; Lustig, Kondritzer, and Moore, 1945; Leblond, 1951; and Giroud and Leblond, 1951).

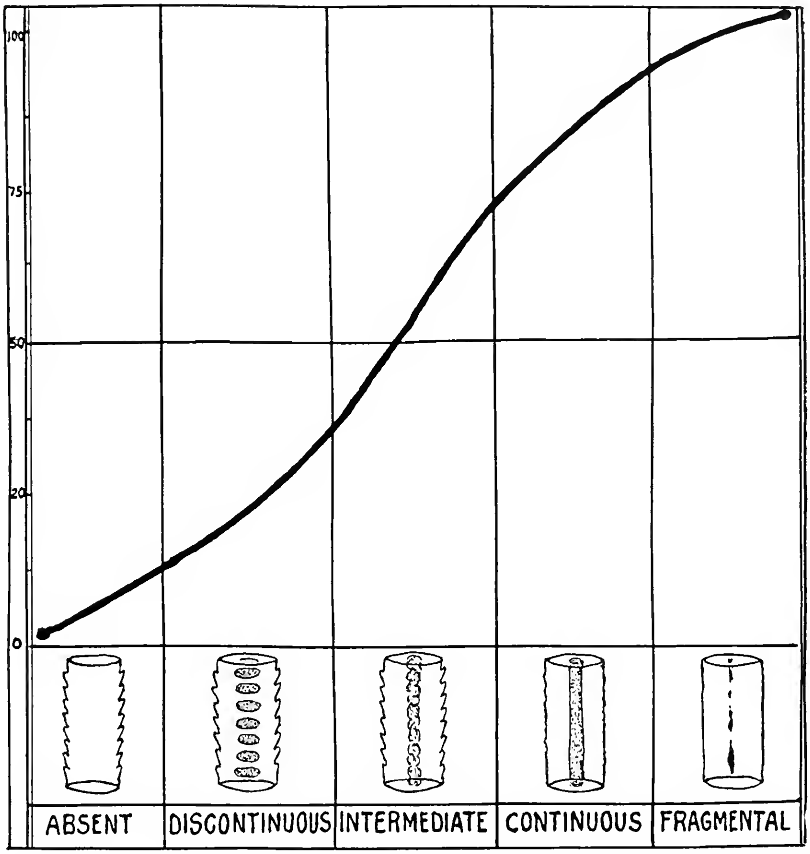


FIGURE 24. Graph illustrating the relation of the diameter of the hair to the types of medullas. The finest hairs have no medulla, and the coarsest hairs have a fragmental medulla. Diameters in micra of the hair shafts are plotted on the ordinate. The figures of the types of medullas beneath the graph are not drawn to scale. (After Hausman, 1930.)

Some Phylogenetic Aspects of Hair

The relation of hair to the epidermal structures in non-mammalian animals has been discussed by many authors and has been summarized by

Botezat (1913 and 1914), Danforth (1925b), and Matkeiev (1932). No direct relation between hair and non-mammalian epidermal elements has been established. Hair is most probably an analog to these structures. Danforth (1925b) and others conclude that hair is probably a *de novo* morphological entity in mammals.

Broili (1927) reports that he identified hair and hair follicles in a fossil aquatic reptile, *Rhamphorynchus*. This animal is a specialized reptile, removed from those reptiles in the evolutionary line to mammals. If established, this observation would alter the concept that only mammals produce hair.

The phylogeny of hair in related groups of animals has not been analyzed extensively. Because of the economic importance of wool, several studies of the hair types in the coat of a number of breeds of sheep have been made. One significant aspect of these studies is that they illustrate how the hair coat may vary in closely related forms.

This statement is adapted primarily from Duerden (1927 and 1929). The generalized wild animal hair coat consists of an overcoat of bristles and awns and an undercoat of fur (FIGURE 16). In the wild sheep and the black-headed Persian sheep, the hair coat is similar to that of the wild animal. These sheep have an overcoat of bristles (called kemp) and awns (called heterotypes) and an undercoat of wool (FIGURE 17). The British mountain breeds have a hair coat consisting of awns and wool (FIGURE 18). In these breeds, kemp formation is negligible. The coat of the British luster breeds have evolved in another direction. The awns retain their fine proximal segments. Their distal segments are still thicker than the proximal segments, but are thinner than the distal segments of the awns of primitive sheep. The wool undercoat fibers have thickened. Both fiber types are elongated and spiraled (FIGURE 19). The adult Merino sheep, the most efficient wool-producing sheep, has a coat consisting of elongated, regularly crimped fibers of uniform diameters and lengths (FIGURE 20). An analysis of the coat of the Merino lamb is essential for the identification of the types of fibers that form the coat of the adult sheep. The Merino lamb coat has bristle, awn, and wool fibers (FIGURE 21). During ontogeny, the bristles are shed and then replaced by wool fibers. The awn fibers lose their distal thickened segments, but the thin proximal segments persist. The wool fibers are retained, but are coarser than the wool of primitive sheep. Hence, the adult Merino sheep coat consists of wool fibers differentiating from follicles which produced kemp in the lamb, of awns deprived of their distal segments, and of wool fibers differentiating from follicles which produced wool in the lamb. A major difference between the Merino sheep and other sheep is in the nature of the hair follicles. Whereas the coat of other breeds is shed periodically and then new hairs differentiate from the follicles, the fibers of the adult Merino sheep grow from persistent germs and are not shed.

In the evolution of the sheep coat from primitive wild sheep to the various domestic breeds, several changes have occurred. As summarized by Duerden (1927), the domestic wooled sheep has evolved in the direction of the loss of the protective coat both of bristles (kemp) and awns (heterotypes), the increase in length, density, and uniformity of the fibers, and the tendency of the retained bristles to become finer but still capable of being shed. In addition, the Merino sheep has developed persistently growing hair follicles.

Important implications of the evolution of the sheep coat are that the types of hair in the hair coat may differ (1) in closely related animals and (2) at various stages of ontogeny with the same animal. Hence, data derived from a study of the coat of one animal species may not always apply to another animal species.

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Discussion of the Paper

DOCTOR M. H. HARDY (*McMaster Laboratory, Glebe, N. S. W., Australia*): I am glad Dr. Noback mentioned sheep, because the study of the arrangement of follicles in groups on these animals has disclosed some important principles. Terentjeva,[1] Duerden,[2] and Carter[3] showed that de Meijere's trio group is the basic unit in the follicle population of sheep. The trio (primary) follicles develop first and have accessory structures (sudoriferous gland, arrector pili muscle) which are absent from the later developing (secondary) follicles of the group.[3] In the young lamb, it is the primary follicles which produce the coarse, and frequently medullated, kemp fibers and the secondary follicles which produce the fine and usually non-medullated wool fibers. These correspond respectively to the 'overhair' and 'underhair' in Danforth's classification. The primary follicles may produce kemp in the lamb and wool in the adult sheep, as Dr. Noback has mentioned.

The size of the follicle groups, *i.e.*, the number of secondary follicles to each trio of primary follicles, varies greatly between breeds[4] and individuals[5] and also between body regions.[6] The breeds and, to some extent, individuals with the largest group size have also the greatest number of fibers to the square inch and the greatest uniformity of fiber thickness and length.[5] In the midside region, at least, the potential group size (including secondary follicle rudiments in the young lamb) is strongly inherited, but the actual group size (number of active follicles) in the mature animal varies according to the food intake in the first year of life.[7] Thus, it is possible to alter the group size experimentally. Varying the food intake in the second and third year of life had no marked effect on group size.[8,9]

It seems that many properties of the coat of the sheep depend on the inherited follicle group pattern and the modifications of this superimposed by the environment. Perhaps the same principles apply to other mammals.

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MORPHOLOGY AND FLIGHT CHARACTERISTICS OF MOLOSSID BATS

BY TERRY A. VAUGHAN

ABSTRACT: Selected aspects of the morphology of bats of the family Molossidae are described and the functional significance of these features are discussed. The structure and proportions of the ears and the wings are considered to reflect primarily the rapid enduring flight typical of molossids. Comparisons of some characteristics of the wings of three molossids and of four bats of the family Vespertilionidae were made, and several aerodynamic relationships were applied to a consideration of the styles and speeds of flight of these bats. Molossid bats in general seem adapted to fast flight in open areas, whereas the vespertilionids studied are apparently suited to slower flight fairly low to the ground, near vegetation and other obstacles.

Bats of the family Molossidae form a distinctive and anatomically peripheral group, and their flight probably surpasses that of all other bats in speed and endurance. Repeated mention in the literature has been made of the mode of flight of these bats (H. W. Grinnell, 1918; A. B. Howell, 1920; Orr, 1954; Vaughan, 1959; Hall and Dalquest, 1963); and Miller (1907), Vaughan (1959) and Struhsaker (1961) have described selected aspects of the postcranial morphology of molossids.

MATERIALS AND METHODS

Specimens in alcohol representing the following species and families were examined for this study: *Macrotus californicus* (Phyllostomidae); *Myotis lucifugus, M. yumanensis, M. velifer, M. evotis, Lasiurus borealis, L. cinereus, Plecotus townsendii, Antrozous pallidus* (Vespertilionidae); *Tadarida brasiliensis, T. molossa, Eumops perotis* (Molossidae). The specimens are in the collection of the author.

Measurements of areas and proportions of wings were made from tracings of wing outlines. Although care was taken to pin each wing in the same fully spread position, the wing measurements of preserved specimens probably differ from those of fresh animals.

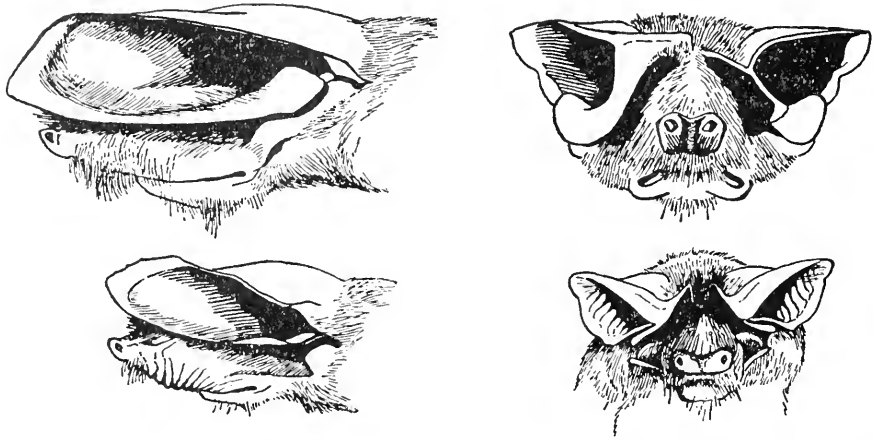

FIG. 1.—Front and side views of the heads of *Eumops perotis* (above) and *Tadarida molossa* (below). In the front view of *Eumops* the anterior part of the left ear is removed to show the structure of the ear.

All wing measurements were taken as follows from fully outstretched wings: the length of the distal segment of the wing (chiropatagium) was measured from the base of the thumb to the wing tip; the length of the proximal segment of the wing (plagiopatagium) was measured from the middle of the base of the wing where it joins the body to the middle of the fifth digit; the width of the wing was measured across the flattened airfoil from the base of the thumb to the tip of the fifth digit; the length of the wing was measured from the center of the base of the wing to the wing tip. Wing areas were measured as if the wings were continuous through the interfemoral membrane (uropatagium) and the body. Ear lengths were measured from the crown, and ear widths were measured across the base of the pinna where it joins the head, or, as in the case of molossids, from the posterior base of the pinna to where the anterior base joins the fold of tissue connecting the anterior edges of the pinnae.

RESULTS AND DISCUSSION

Head.—The heads of all molossid bats are similar in basic design: the braincase and rostrum are broad and the muzzle is truncate; the lips are thick and frequently wrinkled; the ears are usually broader than long, have thickened and reinforced borders, and face more nearly downward or to the side than forward (Fig. 1). The design and position of the ears is of considerable aerodynamic importance in a bat with rapid, sustained flight, and with this in mind the ears of molossid bats merit close attention.

The shape and proportions of the ears of molossids are distinctive and fairly uniform. The ears are characteristically very broad, relative to their length, and have squared-off tips. In *Eumops perotis* and *Tadarida molossa* the ears are 1.6 times as wide as high. The corresponding figure for *T. brasiliensis* is 1.2. The ears of most vespertilionid bats, in contrast, are longer than wide. In the vespertilionid bats listed in Table 1, for example, the ratio of ear width to ear length is from 0.39 to 0.70.

In molossid bats the anterior and ventral borders of the pinnae are generally

TABLE 1.—*Sizes of heads of bats and birds and proportions of the ears of bats. All figures are averages; the numbers of specimens measured are given in parentheses*

Species		Weight of head / Total weight	Ear width / Ear length
Sturnus vulgaris	(9)	0.11	–
Turdus migratorius	(13)	0.11	–
Myotis yumanensis	(10)	0.15	0.58
M. velifer	(10)	0.17	0.70
Plecotus townsendii	(10)	0.16	0.39
Tadarida brasiliensis	(10)	0.16	1.15
T. molossa	(3)	0.20	1.56
Eumops perotis	(5)	0.23	1.61

strongly braced by connective tissue. Viewed from the side, the pinna arches dorsad and resembles a crude airfoil of high camber (Fig. 1). The base of the leading edge of the pinna is almost directly anterior to the base of the trailing edge, thus furthering the resemblance of the ears to short, broad wings. During flight the thickened ventral borders of the ears lie against the side of the head and cover the eyes in some molossids. Short, broad ears which lie against the head and do not directly face the airstream during flight are found also in *Lasiurus*. Here, as in the molossids, this type of ear is associated with rapid flight.

In both birds and bats there has been a trend toward the concentration of weight near the center of gravity. The heads of most birds are light; they carry no teeth and generally have only light jaw musculature. In a series of 13 robins (*Turdus migratorius*) and 9 starlings (*Sturnus vulgaris*) from Colorado the head comprised on the average 10.9% and 11.2% of the total weight, respectively. Relative to total body weight, bats have heavier heads than those of birds. In the bats studied the weight of the head comprised from approximately 15 to 23% of the total weight (Table 1). The heads of two of the molossid bats are relatively considerably heavier than the heads of the vespertilionid bats. When in flight most bats carry the occipital portion of the head against the interscapular depression, thus compensating for the weight of the head by bringing it fairly close to the center of gravity.

The unique design of the ears of molossid bats probably developed in response to fast, sustained flight, and serves to minimize drag and to brace the ears against the force of the airstream. In addition, the ears probably develop some lift during flight, allowing the heavy head to be supported as least in part by the airstream. During long flights this could result in an important conservation of energy which would otherwise be expended in supporting the head.

A further characteristic of the molossid head which has probably been developed in response to rapid flight is the loose or wrinkled lips. It remains for high-speed photography to demonstrate the operation of the lips in catching insects, but it seems probable that when the mouth is wide open during flight

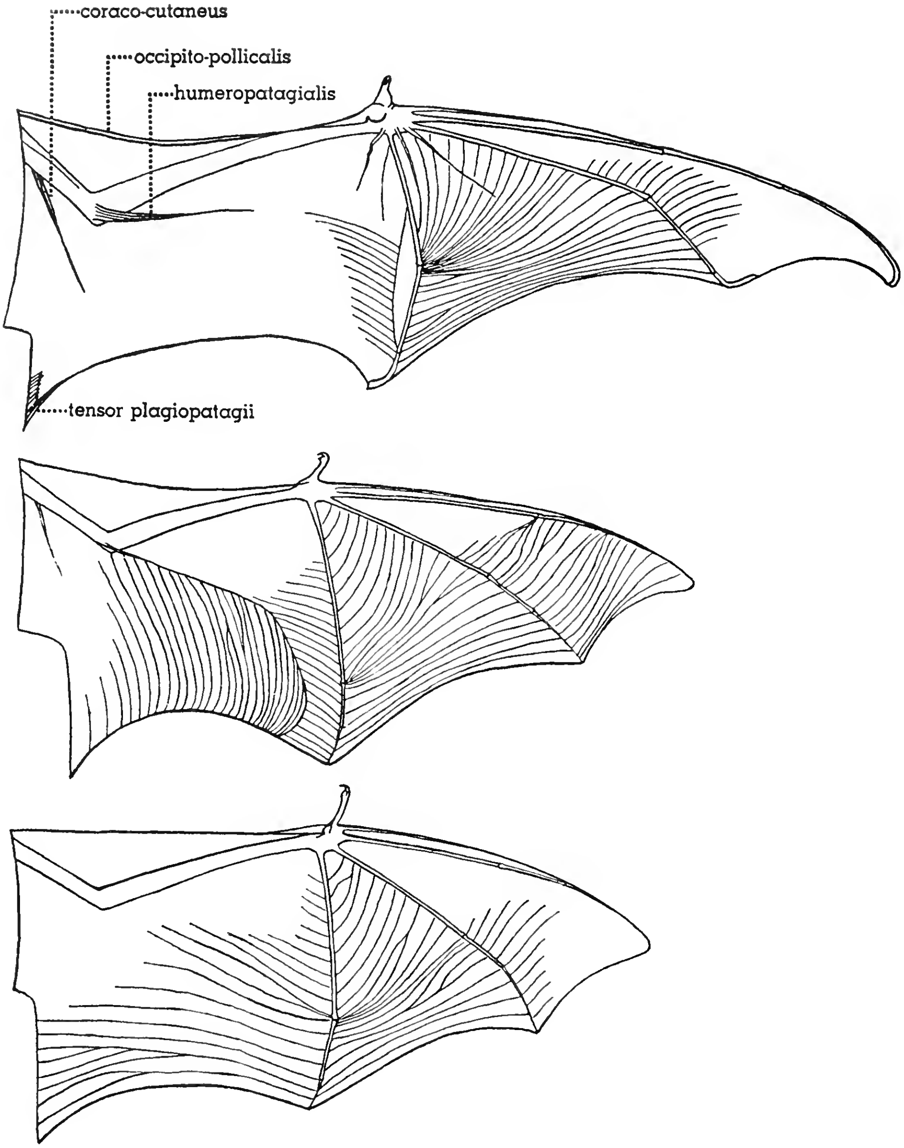

FIG. 2.—The wings of *Eumops perotis* (top), *Lasiurus borealis* (middle), and *Myotis evotis* (bottom), showing the muscles and networks of elastic fibers that tighten and brace the wing membranes.

the lips spread outward, away from the teeth, thus increasing the area of the mouth. The wrinkled or loose lips of molossids seem functionally homologous to the rictal bristles around the bills of caprimulgiform birds; in both groups the increase in the effective area of the mouth may partially compensate for the sacrifice of maneuverability attending rapid flight.

Wings.—Molossids possess many advanced chiropteran characteristics associated with efficient flight, such as the well-developed humeroscapular locking device (Vaughan, 1959: 54); but in addition they are obviously highly specialized for fast flight, with a resulting sacrifice in maneuverability and lifting power. Davis and Cockrum (1964) have shown by experimentally attaching weights to bats that, although the animals are roughly equal in weight, *Macrotus californicus* (Phyllostomidae) can take flight with approximately five times the additional load lifted by *Tadarida brasiliensis* (Molossidae). Differences in the ability to take off with extra loads reflect, in part, differences in wing design.

The long, narrow wings of molossid bats are unique in several ways. The fifth digit is unusually short, making the plagiopatagium narrow. The first phalanges of the third and fourth digits flex posteriorly instead of ventrally as in most other bats. This allows the long part of the wing distal to the third and fourth metacarpals to be folded compactly against the posterior surfaces of these bones when the wing is at rest or is used in terrestrial locomotion. In molossid bats the third metacarpal, the longest bone in the hand, is almost exactly the same length as the radius. Consequently, because of the pattern of flexion of the third and fourth digits, the long chiropatagium folds into a bundle no longer than the radius.

In considering the form and function of wings, the amount of camber (anteroposterior curvature) is of basic importance. The amount of camber is a major factor in determining the ability of a wing to develop lift. Airfoils with high camber develop high lift at low speeds, but create considerable drag. Relative to airfoils of high camber, those of low camber are effective at producing lift at higher speeds and produce little drag. The airfoils of most bats are of high camber, whereas those of molossids are of relatively low camber. In terms of function, the latter design creates relatively little drag but forces molossid bats to fly fairly rapidly to enable the airfoils to produce sufficient lift to maintain flight. An aerodynamic refinement occurring in bats but not in birds is the ability to vary the camber of the wing. Flexion of the phalanges of the fifth digit and lowering the hind limbs increases the camber of the wing by curving the trailing edge of the plagiopatagium downward and causing it to function like a flap on an airplane. Such a flap enables either bats or aircraft to increase the camber of an airfoil for higher lift at low speeds and to flatten the airfoil and reduce the drag at higher speeds. Thus, a wing with flaps can operate effectively under a greater range of speeds than that within which the same wing could function if it had a fixed airfoil. The ability to change the amount of camber of the wings is probably important in enabling small, broad-winged bats such as *Myotis evotis* and *Plecotus townsendii* to fly at a great variety of speeds. The camber of the narrow molossid wing seems less variable than that of broad-winged vesperitilionids.

The flight membranes of molossids are leathery and elastic and seem much stronger than those of other bats. In molossids the wing membranes are braced

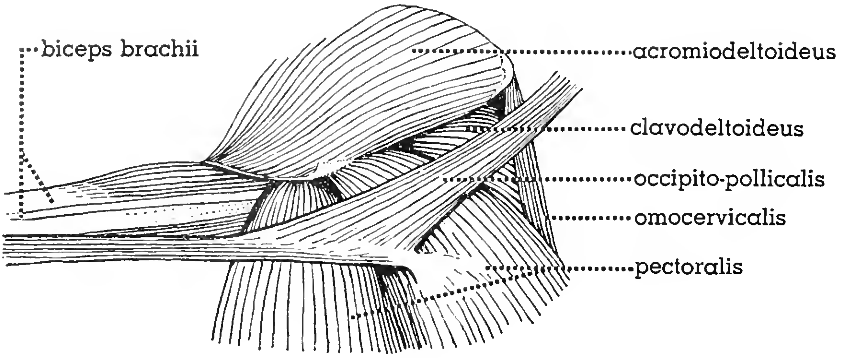

FIG. 3.—Front view of the right shoulder of *Eumops perotis* showing the attachment of the occipito–pollicalis muscle to the pectoralis muscle.

by cartilaginous extensions of the distal ends of the third, fourth and fifth phalanges and by complex meshworks of connective tissue in the plagiopatagium and in the interdigital membranes (Fig. 2). The elasticity of the wing membranes may be of considerable aerodynamic importance. When the wings are partially flexed, as they are during dives or in rapid level flight, the tension on the plagiopatagium is partially relaxed and this membrane narrows sharply, reducing its area and the drag it creates. This narrowing is probably caused by both the elastic network and by the humeropatagialis muscle. The high-speed dives made by *Eumops perotis,* and sometimes made by *Tadarida brasiliensis,* when approaching a roosting place in a cliff (see Vaughan, 1959: 20) may be made possible partly by the narrowing of the plagiopatagium when the wing is partly flexed.

In all bats the wing membranes are strengthened by muscles not present in other mammals, but in molossids there has been a greater development of these muscles than in any other group of bats. The occipito–pollicalis muscle in most bats originates on the lambdoidal crest, extends along the leading edge of the propatagium (the membrane anterior to the humerus and radius), and inserts along the anterior surface of the second metacarpal. This muscle keeps the propatagium taut during flight, pulls this membrane slightly ventrad, and thereby helps give camber to the plagiopatagium. This improves the effectiveness of this segment of the wing as an airfoil. This narrow muscle is attached by fascia to the front of the shoulder in most bats. In molossids, however, the muscle is relatively large and is more complex: it is divided into a proximal and a distal part, and the junction of these parts is attached strongly by a tendon-like fascial bundle to the pectoralis muscle (Fig. 3). The coraco–cutaneous muscle, which occurs in all bats, originates on the humerus and passes into the proximal part of the plagiopatagium. This muscle helps maintain the tautness of the axillary portion of the plagiopatagium. Two additional muscles, serving to tense the plagiopatagium, are present only in molossid bats and are probably adaptations to fast flight. The first, the tensor plagiopatagii, originates on the tibia and tarsus and inserts into the part of the plagiopatagium adjoining the shank and into the connective tissue that reinforces the trailing edge of the plagiopatagium. This muscle not only tenses this part of the wing but is of importance in strengthening the attachment of the plagiopatagium to the shank and tarsus. The second muscle, the humeropatagialis, originates on the distal end of the humerus and inserts into the elastic fibers in the distal part of the plagiopatagium (Fig. 2). The most important function of the muscles and connective tissue which reinforce and tense the plagiopatagium is to maintain this proximal segment of the wing as an efficient airfoil during flight and to keep the membrane from being distorted by the force of the airstream. In fast-flying bats considerable distortion could occur and this would reduce sharply the effectiveness of the plagiopatagium as a lifting surface. Because the plagiopatagium supplies the major share of lift during flight, this is of critical importance. An additional function of the plagiopatagialis may be to narrow the plagiopatagium during dives or when the wings are partially flexed during rapid flight.

The morphology of the scapula varies considerably within the order Chiroptera and reflects, in part, degrees of specialization for various modes of flight. One variable structure is the long coracoid process, which, because it extends ventral to the plane of the scapula, allows the biceps brachii and coracobrachialis muscles to serve as adductors of the wing. In most bats the coracoid curves laterad (toward the wing), whereas in all molossids the coracoid is directed sharply mediad (Fig. 4). This "molossid" type of coracoid is found also in *Miniopterus* (Miller, 1907), and to a lesser degree in *Lasiurus*. Attending this difference are differences between the brachial musculature of molossid bats and most other bats. In the latter the coracobrachialis and the biceps brachii muscles are the important members of the flexor group of the arm. The glenoid head of the biceps originates on the lateral base of the coracoid process and is the larger division of the biceps. The smaller coracoid head originates along the distal part of the coracoid process. Both divisions insert into a slit in the anteromedial surface of the radius just distal to its head. Molossids, in contrast, have lost the coracobrachialis muscle; and the coracoid head of the biceps, rather than the glenoid head, is the largest division of this muscle (Fig. 4). Because of the medial curvature of the coracoid process in molossids, during the lower part of the downstroke of the wing the coracoid head of the biceps can act as a far more effective adductor than can this muscle in most nonmolossid bats (Vaughan, 1959: 90). In molossids, due partly to the modifications of the scapula and biceps mentioned above, occurs the most perfect development of the basic chiropteran trend toward dividing the labor of the downstroke of the wing between a number of muscles. This division of labor was probably developed in response to the demands of the enduring flight typical of most molossids.

The shapes and aerodynamic characteristics of the wings considered in this

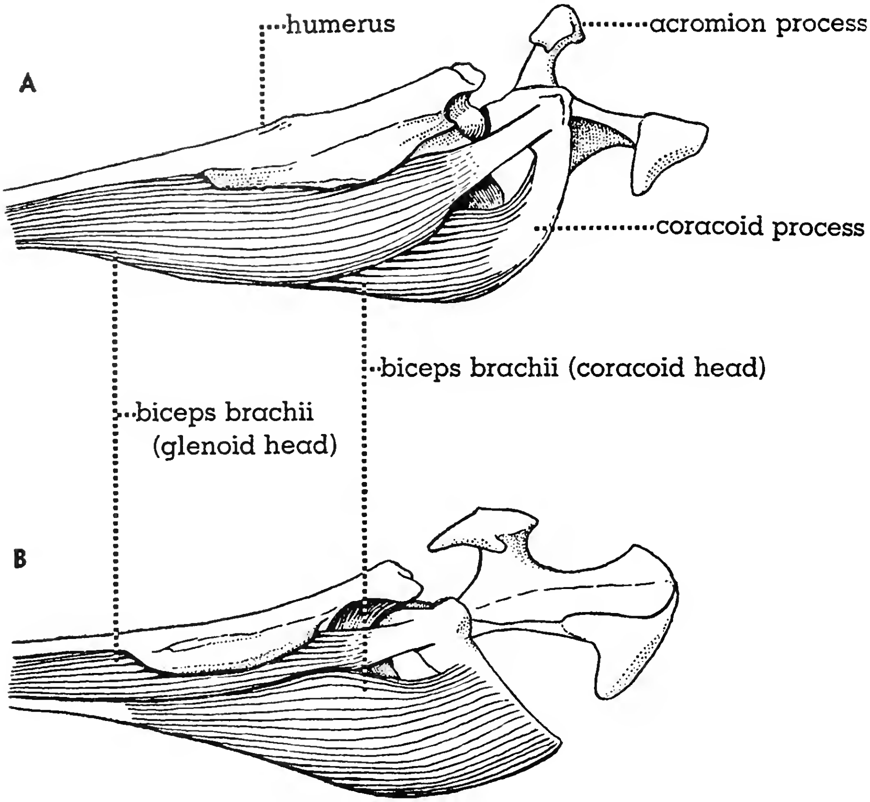

FIG. 4.—Front views of the right shoulders of *Antrozous pallidus* (above), showing the lateral curvature of the coracoid process of the scapula typical of most vespertilionid bats, and of *Eumops perotis* (below), showing the medial curvature of the coracoid process typical of molossid bats.

study differed widely (Fig. 2, Table 2), but certain differences between the molossid and vespertilionid wings are readily apparent and are indicative of functional contrasts. The ratios based on wing proportions illustrate that, compared to the vespertilionid wing, the molossid wing is narrow, has a long distal segment, a high aspect ratio (the ratio of length to width of a wing; for irregularly shaped wings it is considered to be the ratio of the wing span^2/wing area), and a high wing loading (weight in pounds/wing area in feet^2).

For the molossid bats considered here the length of the chiropatagium averaged 154.1% of the length of the plagiopatagium, and the width of the wings averaged 36.8% of the length. In the vespertilionids measured the corresponding figures were 138.5% and 48.7%. The aspect ratios reflect these differences and are higher for the molossids (8.60–9.98) than for the vespertilionids (5.99–6.74). In general, the higher the aspect ratio the more efficient the wing because of the reduction of drag at the wing tip. The wing

TABLE 2.—*Proportions of wings of bats. All figures are averages; the numbers of specimens measured are given in parentheses*

Species		Area of chiropatagium / Area of plagiopatagium	Length of chiropatagium / Length of plagiopatagium	Greatest width of wing / Length of wing	Aspect ratio: Wing span^2 / Area of wings
Myotis yumanensis	(5)	0.95	1.32	0.47	6.74
M. evotis	(5)	0.80	1.35	0.51	6.48
M. lucifugus	(5)	0.69	1.41	0.48	6.47
Plecotus townsendii	(5)	0.86	1.46	0.50	5.99
Tadarida brasiliensis	(5)	0.93	1.58	0.38	8.60
T. molossa	(3)	0.86	1.47	0.36	9.71
Eumops perotis	(5)	0.83	1.58	0.36	9.98

loadings of the molossid bats (0.325–0.546) are considerably higher than those of the vespertilionids (0.157–0.202). As a rule, the higher the wing loading the greater the speed necessary to produce adequate lift for sustained flight. Usually the smaller the bat the lower the wing loading because in small bats the ratio of mass to surface is small (the volume and mass vary as the cube of the linear dimensions whereas the surface area varies as the square).

Instructive comparisons can be made between habitat and wing form in both bats and birds and between the characteristics of the wings of certain bats and those of the wings of birds with well-known modes of flight. The plan form of the wing of *Myotis evotis* (Fig. 2) is similar to that of many small passerine birds. This roughly elliptical wing is fairly efficient for low speed flight, and occurs in birds adapted to flight through brush or woods, or where numerous obstacles make long wings unmanageable (Savile, 1957). The short, broad wing of *Myotis evotis* is seemingly well suited to flight near the ground in the wooded or brushy areas the bat inhabits. A markedly different adaptation is illustrated by the wings of molossid bats which are similar to the “high-speed” wings of many birds known to be strong enduring fliers or to feed on the wing (falcons, plovers, sandpipers, swifts and swallows). Such birds characteristically fly in open places with few obstructions, a situation “allowing” the development of long, aerodynamically efficient wings. The wings of these birds have the following characteristics according to Savile (1957): low camber; high aspect ratio; taper to a slender, elliptical tip; pronounced sweepback of the leading edge; and wing root fairing. These same features describe well the molossid wing. Thus, in wing design and foraging habits the molossids appear to be chiropteran counterparts of the swifts and swallows, whereas the smaller vespertilionids seem to most nearly resemble the smaller flycatchers in wing design, but differ from the latter in flying continuously while feeding.

TABLE 3.—*Sizes, aerodynamic characteristics and computed minimum flight speeds of seven species of bats. All figures are averages; the numbers of specimens measured are given in parentheses*

Species		Weight (g)	Wing span (cm)	Wing area (cm^2)	Wing loading		Minimum flight speed (mph)
					lbs/ft^2	g/cm^2	
Myotis yumanensis	(5)	5.2	20.26	60.95	0.173	0.084	8.3
M. evotis	(5)	6.2	22.80	80.20	0.157	0.077	7.9
M. lucifugus	(5)	8.1	23.30	83.41	0.202	0.099	8.8
Plecotus townsendii	(5)	9.1	24.52	100.41	0.184	0.090	8.5
Tadarida brasiliensis	(5)	12.2	25.08	73.14	0.339	0.165	11.6
T. molossa	(3)	16.2	31.33	101.12	0.325	0.159	11.7
Eumops perotis	(5)	53.5	44.58	199.22	0.546	0.266	14.7

From the weight of a bat and the area of its wing surfaces the speed it must fly to sustain level flight can be approximated by the equation

$$V^2 = \frac{2g_cW}{AC_L\surd}$$

(von Mises, 1945) where V is velocity (in feet per second); 2 g_c is a unit-conversion constant; W is the total weight; A is the area of the wings; C_L is the coefficient of lift; and $\surd$ is the density of air in pounds per cubic foot. The coefficient of lift is derived from the size, camber, aspect ratio, angle of attack and other characteristics of the wing, and for the present study was assumed to be 1.0, which probably approximates the actual values closely enough to cause little error. These calculations are based on the further assumption that each bat has its wings fully and rigidly outstretched. Although the calculated speeds may not correspond closely to the actual flight speeds of the bats, they probably reflect accurately the relative flight speeds. Except for the molossids, flight speeds arrived at by the above equation (Table 3) are fairly close to those found experimentally by Hayward and Davis (1964). As these authors mention, the speeds shown for the molossids in their study are probably too low because the bats could not fly normally under their experimental conditions.

The speeds calculated on the basis of the figures for total weight and wing area shown in Table 3 suggest that in order to maintain level flight the molossids must fly faster than do the vespertilionids. The speed for *Myotis evotis* (7.9 mph), for example, is roughly half that of *Eumops perotis* (14.7 mph). The calculated speeds probably approximate the relative speeds of the bats under study in level flight, but all of these bats seem to be capable of a wide range of flight speeds. Judging from my own observations, *M. evotis* can hover briefly and can fly at very low speeds; at the other extreme, some molossids are capable of rapid dives and of level flights at speeds far greater than those listed here. A complicating factor, but one of critical importance when considering the flight capabilities of a bat, is the animal's ability to vary the camber, angle of attack and the areas of the membranes. A further complexity is the fact that the wings are in nearly constant movement during flight, and supply both the lift and the thrust necessary for flight.

Various aerodynamic relationships are pertinent to the problem of relative flight speeds and differences in morphology in bats. For example, because drag increases in proportion to surface area and as the square of the speed, *E. perotis* is probably subject to about three times the drag faced by *M. evotis*. This explains why features which tend to minimize drag, such as low camber of the wing and short ears which present their most streamlined aspect to the airstream, are of vastly greater importance in the large *E. perotis*, and in most molossid bats, than in smaller, relatively slow-flying bats. Even the short, velvety fur of molossids may be an adaptation to reduce drag caused by the body during flight.

Miscellaneous considerations.—The family Molossidae is unique in having developed the most rapid, enduring flight occurring in bats while retaining (or developing) the most accomplished terrestrial locomotion. Consequently, molossids offer many trenchant examples of a single morphological character serving diverse functional ends.

One such character is the posterior flexion of the first phalanges of digits three and four. Because of this modification the long tip of the narrow wing is manageable when the bats are not flying, an important feature in a group including many species which take daytime refuge in narrow crevices. This unusual pattern of flexion may have developed prior to the lengthening of the wing tip and may have "allowed" the evolution of this typically molossid character. The part of the wing distal to the carpus folds into a bundle no longer than the radius, facilitating a lateral action of the forelimb during quadripedal locomotion which enables molossids to move remarkably rapidly and easily within the confines of narrow crevices. Thus, the pattern of phalangeal flexion in molossids has probably played a role in both terrestrial and aerial locomotion.

The small uropatagium of these bats slips forward along the tail freeing the hind limbs to move in a wide arc when the animals run. Also, the reduced drag during flight resulting from the small size of the uropatagium is probably aerodynamically important in furthering the cause of fast flight. The well-braced flight membranes of molossids may also serve two ends, for in addition to resisting effectively the force of the airstream during rapid flight, they are better able than are the delicate membranes of most bats to withstand the occasional rough treatment resulting from crawling between the irregular and abrasive surfaces of rock crevices.

Perhaps the strong adductors and flexors of the hind limbs represent the best example of a dual-purpose molossid character. These limbs are remarkably robust and strongly muscled and account in large part for the accomplished terrestrial locomotion typical of the group. Of equal importance, however, is their function in serving as a rigid anchor for the posterior portion of the plagiopatagium. This function requires strong flexors and adductors of the shank to resist the powerful lateral and dorsal pull exerted by the flight membranes during the downstroke of the wing, and is of basic importance in maintaining the proper angle of attack and camber of the plagiopatagium.

Considering the evolution of the family Molossidae, the sturdiness of the hind limb and the complete fibula suggest that the basal molossid stock may have diverged early from the rest of the Chiroptera, before the hind limbs had been greatly modified from their primitive structure and proportions. By contrast, in many members of the family Phyllostomidae the hind limbs have become so highly specialized that they no longer function effectively in quadripedal locomotion. But in molossids, probably because the primitive hind limbs suited the demands of both terrestrial and aerial locomotion, the hind limbs have remained basically primitive through a period of time that saw the evolution of the highly specialized molossid wing of today.

Some vespertilionid bats and one rhinolophid bat have been shown to use the flight membranes in capturing insects (Webster and Griffin, 1962). In these species most modifications tending to reduce the dexterity of the phalanges were probably disadvantageous, and the evolution of the hand was probably influenced by its use in capturing insects, as well as by the demands of aerial and terrestrial locomotion.

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Toxic Salivary Glands in the Primitive Insectivore *Solenodon*

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In 1942 O. P. Pearson demonstrated the toxic property of the saliva of *Blarina brevicauda,* a common shrew of the eastern United States, and identified its principal source as the submaxillary gland. Comparative studies at that time and subsequently revealed that similar poisonous factors were not present in the salivary glands of other soricid and talpid insectivores (Pearson, 1942, 1950, 1956). I had an unexpected opportunity to make a crude check on the salivary glands of *Solenodon paradoxus,* a remote relative of the shrews, when three of these animals died at the Chicago Zoological Park within two months after their arrival in 1958 from the Dominican Republic.

Parts of the submaxillary and parotid glands of one animal that had died one to two hours beforehand were ground separately with sand, diluted to 10 per cent by weight solutions with 0.9 per cent NaCl solution, and filtered, following the procedure of Pearson (1942). These solutions were injected into a small series of male white mice that ranged in weight from 29 to 44 grams.

All of the mice injected with extract from submaxillary gland showed some reaction — at least urination and irregular or rapid breathing for several minutes. Five that received intravenous doses of extract of .09 to .38 mg. submaxillary gland per gram of body weight did little more than this and recovered within 30 minutes. Five that received intravenous doses of .38 to .55 mg. per gram additionally exhibited protruding eyes, gasping, and convulsions before dying within two to six minutes. Two animals that had intraperitoneal injections of extract of .56 and .66 mg. per gram died in about 12 hours, and one injected at the level of 1.02 mg. per gram died in 13 minutes. Urination, cyanosis, and depression were observed in these animals. Three "control" mice injected intravenously with extract of 1.02, 1.68, and 1.87

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*Chicago Zoological Park, Brookfield, Illinois mg. of parotid gland per gram of body weight showed no distress except for initially very rapid breathing in the last case.

In general these results are very like those described for *Blarina* extracts. It may be noted that the twentyfold lesser potency evident here of *Solenodon* extract as compared to that of *Blarina* may be due to postmortem inactivation of the toxic principle as reported by Ellis and Krayer (1955) for fresh *Blarina* material. Further tests with the refined techniques of these authors using acetone treated glands will be necessary for a fairer assessment of the potency of *Solenodon* toxin.

Sections were made of the submaxillary glands and stained with hematoxylin and eosin and also with a modification of Mallory's triple stain. These sections showed some large cells with coarse acidophilic granules and small nuclei in the secretory ducts. Pearson (1950) suspected that such cells in *Blarina* might be concerned in the production of the saliva's toxic principle, although somewhat similar cells are found in other soricids.

The submaxillary glands of *Solenodon* are rather enormous and conspicuous structures (see fig. 47 in Mohr, 1938). Each gland weighs three to four grams in adult animals. According to Allen (1910), the duct of the submaxillary gland ends at the base of the large deeply channeled second incisor tooth of the lower jaw (see fig. 19D in McDowell, 1958). Presumably toxic saliva would be conducted thereby into a wound. I could not induce *Solenodon* to bite live mice and therefore have no direct evidence on this point. However, in 1877 Gundlach reported inflammatory effects of bites by Cuban *Solenodon* to himself and a mountaineer (although he dismissed the possibility of venomous action on the basis of authority!). Of his hand bite he said: ". . . I was bitten by the tame individual, which gave me four wounds corresponding to the [large] incisors: those from the two upper incisors healed well, but those from the lower ones inflamed."

Moreover, there are indications that *Solenodon* is not immune to its own venom. Autopsy of the third animal disclosed multiple bite wounds on the feet and no obvious internal evidence of other causes of death. Sections of the liver show considerable congestion in that organ. The snout, lips, limbs, and tail were very pale the afternoon preceding death. Mohr (1937, 1938) gave accounts of several cases in which death was the outcome of fighting with cage mates although only slight foot wounds were inflicted. Pearson (1950) reported that *Blarina* was relatively immune to its own venom, although the single test animal died and the interpretation was problematical. The utility of the venom for

Solenodon in its natural environment is unknown and is certainly not indicated by its insectivorous habits. The explanation may be phylogenetic and historical rather than one of present-day function.

I wish to acknowledge the help of the park's veterinarian, W. M. Williamson, and medical technician, Ruth M. Getty.

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SOME ASPECTS OF THE WATER ECONOMICS OF TWO SPECIES OF CHIPMUNKS

The water economics of chipmunks have not received much attention from physiological ecologists. Allen (New York State Mus. Bull., 314: 1–122, 1938) wrote of *Tamias striatus*: "Unlike many of the western ground squirrels, the Eastern chipmunk requires a great deal of water to drink." Panuska and Wade (J. Mamm., 38: 192–196, 1957) found that water consumption of captive *T. striatus* decreased from 33.4 ml per day just after capture to 29.2 ml per day after the animals had been confined for a time. Davis (Murrelet, 15: 20–22, 1934) wrote that water was not a factor in determining the distribution of the cliff chipmunk, *Eutamias dorsalis*, in Nevada. Seton (Lives of game animals, 4: 184–215, 1929) observed that west and south of Manitoba the least chipmunk, *E. minimus*, is found in desert environments far from permanent water. Manville (Misc. Publ. Mus. Zool., Univ. Michigan, 73: 1–83, 1949) thought water to be of little importance in the distribution of *E. minimus* in the Huron Mountains of Michigan.

In the Itasca region of Minnesota the ranges of the gray eastern chipmunk, *T. striatus griseus*, and the least chipmunk, *E. minimus neglectus*, overlap. Since *striatus* and *minimus* apparently have markedly different water economics in the extremes of their ranges, I wondered if the two species, in the mesic, forested Itascan habitats, would differ from each other in their gross and weight-relative water consumption and in their responses to water deprivation.

These studies were conducted in August and September 1963. Chipmunks of both species were captured in National Live Traps, 5½ × 5½ × 16 inches, set within 3 miles of Itasca State Park, Hubbard and Clearwater counties, Minnesota. The chipmunks were transferred to an animal room in the zoology building at the University of Minnesota, Minneapolis. There were no provisions for regulating light, temperature, or humidity in the room.

Nine *striatus* and nine *minimus* were confined individually in cages 18 × 18 × 12 inches with wood shavings provided for litter, and were fed only sunflower seeds. The seeds contained water amounting to about 12% of their weight. Tap water was provided *ad libidum* in 30 cc or 100 cc graduated drinking tubes. One tube of each size, hung on the rack of cages, permitted assessment of evaporative water loss from the tubes. For 36 days, daily records were kept of the change of water level in each tube. On 18 days, at least one of the *striatus* spilled water, indicated by wet litter below the tube. Least chipmunks were not known to spill water. Records of water consumption for the 18 days on which no spillage was noted were used to calculate each animal's gross water consumption. Each animal's mean daily water consumption was calculated by dividing gross water consumption by 18. Each animal's water consumption per g of body weight was estimated by dividing gross water consumption by the mean value of the animal's body weight as recorded on the first and thirty-sixth days. The arithmetic mean, standard deviation, standard error of the mean, and coefficient of variation (V) were computed for each of the foregoing variables for each species.

Following the studies of water consumption, seven individuals of each species were deprived of water for five consecutive days. Two individuals of each species served as controls and were allowed unrestricted access to drinking water. The chipmunks were weighed daily during the five days of water deprivation and for seven days after *ad libidum* access to water was restored. Each animal's daily weight was recorded as a percentage of its body weight at the outset of the experiment. Mean daily percentages were calculated for each species.

Statistical procedures followed were those of Simpson, Roe, and Lewontin (Quantitative zoology, 1960). The level of significance used for tests of hypotheses was 95%.

Data on water consumption are summarized in Table 1. Although the gross water requirement of *minimus* was about one-third that of *striatus*, there was no significant difference in the weight-relative water consumptions of the two species. The coefficients

TABLE 1.—*Summary of data on water consumption of confined chipmunks.*

Variable	*T. striatus* Mean Range	*T. striatus* SE	*T. striatus* V	*E. minimus* Mean Range	*E. minimus* SE	*E. minimus* V
Weights of animals (g)	115.0 102.8–132.8	3.4	8.9	46.2 42.0–50.2	0.8	5.1
Total H_2O consumed (ml)	296.1 208–471	26.5	26.8	97.8 76–150	7.6	23.2
Mean H_2O consumed per day (ml)	16.4 11.6–26.2	1.5	—	5.4 4.2–8.3	0.4	—
Mean H_2O consumed per g body weight	2.52 1.98–3.60	0.18	20.8	2.16 1.62–2.96	0.17	23.6

of variation show that individual variation in water consumption was very large. There are individual and specific differences in the adjustments of the animals to captivity. As a group, eastern chipmunks were more sedentary in their cages than were least chipmunks, but activity among individual *striatus* was quite variable.

The two species did not differ significantly from each other in their abilities to resist weight loss during water deprivation or to regain weight once access to water was restored (Table 2). When experimental animals were deprived of water, they first became more active than usual. Their activity decreased markedly during the last three days of water deprivation. Normally, a lively chase ensued before an animal could be caught by hand for weighing, but by the fifth day of water deprivation one could easily pick up a dehydrated chipmunk from its cage. Control animals remained quick and alert. Their weights varied only a few grams on either side of their pre-experimental weights during this study. The mean weights of rehydrating *striatus* are distorted by the weights of one individual that continued to lose weight even after access to water was restored. Ultimately,

TABLE 2.—*Percentages of pre-experimental weights of experimental chipmunks during dehydration and rehydration.*

Day number	*T. striatus* n	*T. striatus* Range	*T. striatus* Mean	*T. striatus* SD	*E. minimus* n	*E. minimus* Range	*E. minimus* Mean	*E. minimus* SD
1	7	89.9–95.5	93.0	1.8	7	89.5–95.4	93.4	1.8
2	7	85.5–91.6	88.2	2.2	7	85.6–91.6	88.6	1.9
3	7	80.0–86.7	83.6	2.6	7	79.2–85.2	82.9	2.2
4	7	74.6–82.5	78.6	3.4	7	74.8–83.7	78.8	3.1
5	7	70.4–79.4	75.7	4.0	7	69.4–79.2	74.9	3.7
Access to water restored								
6	7	76.6–85.4	82.5	2.9	7	80.7–92.0	84.7	4.5
7	6*	67.8–85.5	81.1	6.6	7	77.3–95.0	84.9	6.2
8	6	63.6–92.8	83.3	10.1	6*	79.1–96.5	88.1	6.3
9	6	62.8–94.3	85.7	11.6	6	80.7–100.0	89.1	7.0
10	6	59.4–97.4	87.0	14.1	6	79.9–100.0	89.1	7.1
12	6	57.9–100.0	89.1	16.3	6	82.7–100.0	90.6	6.0

* One experimental animal found dead.

this animal lost half of its pre-experimental weight, but the pre-experimental weight was eventually regained and surpassed.

The literature suggests that *striatus* is somewhat more dependent upon a plentiful supply of drinking water than are *minimus* and its relatives. The present experimental evidence suggests that this is so. The gross water requirements of *minimus* are small. With some insects and fruit of high water content, and a morning supply of dew, Itascan *minimus* can probably keep themselves in good condition with no permanent source of drinking water. When raspberries (*Rubus minnesotanus*) are in fruit at Itasca, *minimus* is found in greatest abundance around raspberry thickets. Often, several chipmunks at a time can be seen eating the fruit, the seeds of which the animals carry away in their cheek pouches. While such a diet would supplement a marginal water supply, I think the chipmunks take the fruit as much for the seeds as for the moist, pulpy parts.

It was surprising to me that *minimus*—a small, active species with high metabolic and breathing rates—did not require more water per g of body weight than did the larger, seemingly less active *striatus* whose metabolic and breathing rates are lower. Nor did comparison of rates of dehydration and rehydration suggest any significant difference between the water economics of the two species. At Itasca, as in other parts of its range, *minimus* is most common in exposed habitats such as the margins of slash piles and gravel pits. Exposure to wind and solar radiation is maximal in such situations; daytime temperatures, consequently, are often high and relative humidity is often low. In contrast, *striatus* remains beneath tree and shrub cover where, since insolation and wind are reduced, daytime temperatures are lower and relative humidity is higher than in open habitats. In view of the morphologic, physiologic, and behavioral differences between the two species, the similarities found in their water economics may represent the existence of physiologic adaptations in *minimus* to its somewhat more xeric Itascan microhabitats.

A thorough analysis of the water economics of these and other chipmunks could, in addition to testing these results, provide information relevant to habitat preferences among the many species of *Eutamias*. In addition, Nadler (Amer. Midland Nat., 72: 298–312, 1964) has suggested that physiologic and ecologic study may shed light on phylogenetic problems involving *Eutamias*. I have found chipmunks to be difficult subjects for experiments of this sort. They are active and often hard to catch for weighing. Some individuals invariably shake water out of their drinking tubes; others are inclined to pack litter into the tubes, but use of cedar tow as litter reduces this. Control of temperature, light, and humidity, and selection of experimental animals of about the same size and age, should reduce the variability in performance.

Part of this work was done while I held an NSF Summer Fellowship for Teaching Assistants, awarded through the University of Minnesota.—RICHARD B. FORBES, *Department of Biology, Portland State College, Portland, Oregon 97207.* *Accepted 30 January 1967.*

THE OXYGEN CONSUMPTION AND BIOENERGETICS OF HARVEST MICE

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RATES of metabolism or of oxygen consumption have been reported for many species of small mammals, but little effort has been made to relate such measurements to the energy economy of small mammals in the wild. Such effort has been avoided because the rate of metabolism varies so much with changes of the ambient temperature and with activity of the animal. I believe, however, that these variables can be handled with sufficient accuracy so that one can make meaningful estimates of the 24-hour metabolic budget of free-living mice in the wild. In this study I have measured the oxygen consumption of captive harvest mice under different conditions, and from these measurements I have estimated the daily metabolic exchange of wild harvest mice living in Orinda, Contra Costa County, California.

The harvest mice used in the study (*Reithrodontomys megalotis*) are nocturnal, seed-eating rodents living in grassy, weedy, and brushy places in the western half of the United States and in Mexico. In Orinda they encounter cool wet winters (nighttime temperatures frequently slightly below 0° C.) and warm dry summers (daytime temperatures sometimes above 35° C., but nights always cool). They do not hibernate.

MATERIAL AND METHODS

Five adult harvest mice were caught on January 29 and 30, 1959, and were kept in two cages in an unheated room with open windows so that the air temperature would remain close to that outside the building. They were fed a mixture of seeds known as "wild bird seed." Metabolic rates were tested between January 29 and April 1 in a closed-circuit oxygen consumption apparatus similar to the one described by Morrison (1947) but without the automatic recording and refilling features. All tests except the 24-hour runs were made during the daytime and without food. Since harvest mice are strongly nocturnal, several hours had usually elapsed between their last meal and the measuring of their oxygen consumption. When placed in the apparatus, the mice usually explored the metabolic chamber and groomed their fur for about half an hour and then went to sleep on the wire mesh floor of the chamber. One hour or more was allowed for the animals to become quiet and for the system to come to temperature equilibrium. The animals usually were left in the chamber until from five to ten determinations of oxygen consumption had been made, during which they had remained asleep or at least had made no gross movements. Each determination lasted between 9 and 24 minutes. The mice were weighed when they were removed from the apparatus. Oxygen consumptions are reported as volume of dry gas at 0° C. per gram of mouse.

RESULTS

SIZE × RATE OF METABOLISM

Adult harvest mice weigh between 7 and 14 grams. Larger individuals consume oxygen at a lower rate per gram of body weight (Fig. 1). For example, at 12° C. a 12-gram mouse would use only 1.17 times as much oxygen per hour as an 8-gram mouse, although it is 1.5 times as heavy. The various points in the regression of body weight against rate of oxygen consumption can be fitted adequately with a straight line, and from the slopes of such lines illustrating the regression at different ambient temperatures it may be seen (Fig. 1) that at cold temperatures a variation of 1 gram in body weight causes a greater change in metabolic rate than at 30° C. At 1°, 12°, and 24° a change of 1 gram in weight is associated with a change in oxygen consumption of 0.98, 0.48, and 0.35 cc/g/hr, respectively.

At warm and moderate temperatures there was little variation in the measurements of each mouse during any one run (Fig. 1), but at 1° C. the variation was sometimes enormous. Since each measurement was made over a period while the mouse was inactive, the variation must stem from a real difference in the resting metabolism of each mouse at different times. I believe that lability of body temperature is the cause. Harvest mice exposed to cold and hunger in box traps sometimes are found to be torpid and with a cold body temperature. If they are tagged and released, they can be recaptured in good health at subsequent trappings, demonstrating that harvest mice have a labile body temperature and can recover from profound hypothermia. During the metabolic tests at 1° C., especially those with the mouse in a nest, there was a tendency for most of the measurements to lie at one level; but there would be a few very low readings and a few intermediate readings, presumably as the animal entered and emerged from the low-metabolic condition (best shown by the 11½-gram mouse in Fig. 1). In response to cold coupled with restful surroundings, as in a nest, the animals probably relaxed their temperature control temporarily. This explanation seems plausible in view of the known lability of the body temperature of some rodents such as *Peromyscus* (Morrison and Ryser, 1959), *Dipodomys* (Dawson, 1955), and *Perognathus* (Bartholomew and Cade, 1957) under similar circumstances. Birds permit their body temperature to drop about 2° C. when they sleep at night, and this is accompanied by a drop of as much as 27 per cent in rate of metabolism (De Bont, 1945). The 40 per cent drop shown by some of the mice may have been accompanied by a drop in body temperature of several degrees.

RESTING METABOLISM AT DIFFERENT TEMPERATURES

Since the weights of adult harvest mice vary so much, it is desirable to eliminate the size variable by adjusting all rates of metabolism to a single average size (9 grams). This has been done by using the series of regression lines in Figure 1. Where each of these lines crosses the 9-gram ordinate, that value is taken as the appropriate rate for a "standard" 9-gram harvest mouse and is used in Figure 2.

The middle curve in Figure 2 shows that the minimum rate of oxygen consumption of harvest mice (2.5 cc/g/hr for a 9-gram mouse) is reached at the relatively high ambient temperature of 33° or 34° C. and that there is almost no zone of thermal neutrality. Rate of metabolism almost certainly begins to increase before 36° C. is reached so that the zone of minimum metabolism could not include more than 3°. The critical temperature (33–34°) is remarkably close to the upper lethal temperature. The single animal tested at 37° died after two hours at this temperature but provided several good measurements before entering the

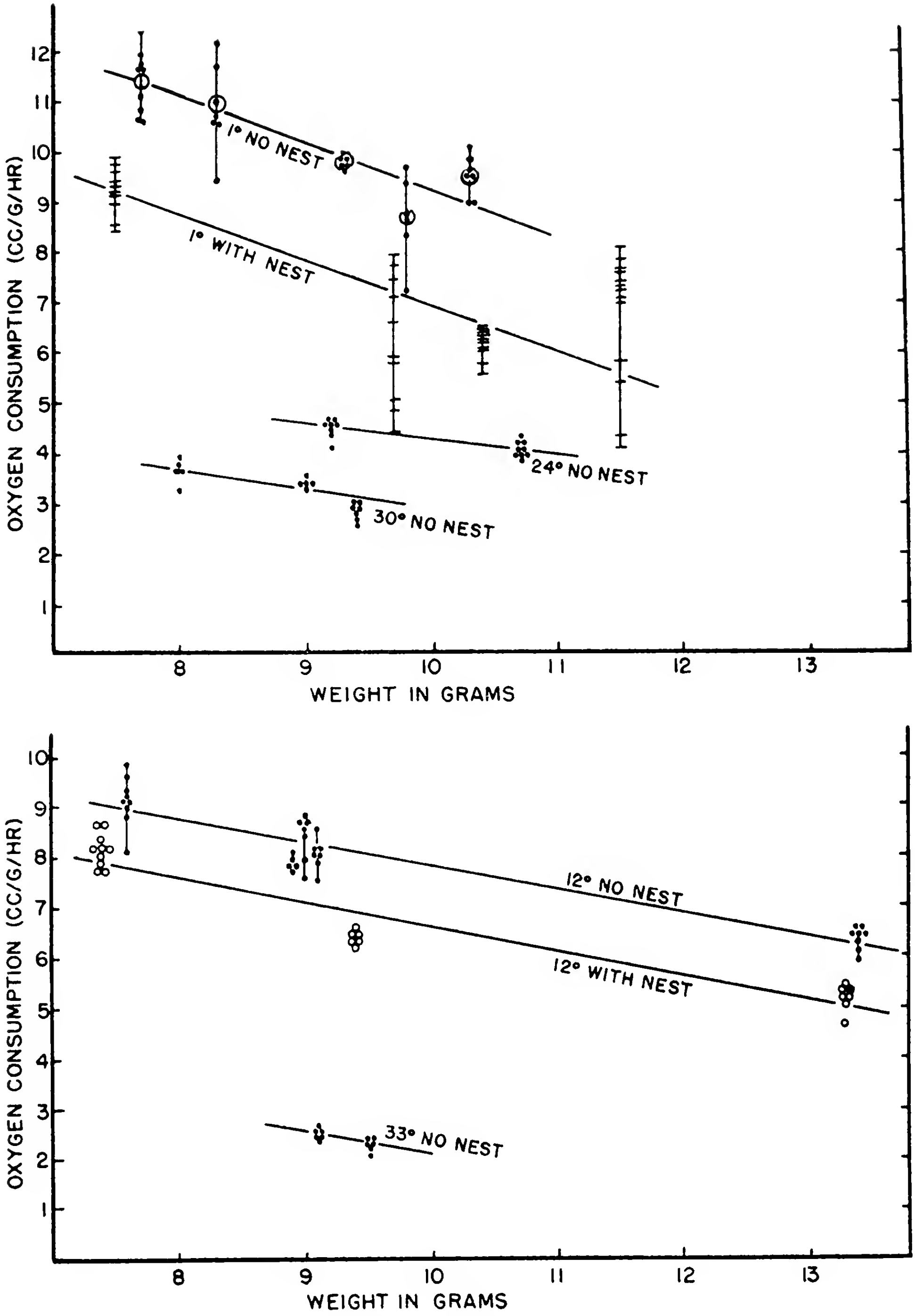

Fig. 1.—The relation between body weight and rate of oxygen consumption under different conditions, showing also the variation in individual measurements. Each cluster or vertical array of points represents a series of values obtained from a single individual.

final coma. Because of the large exposed surface of calcium chloride and soda lime in the metabolic chamber, relative humidity was probably low; heat death would probably occur at an even lower temperature under humid conditions in which cooling by evaporation would be limited.

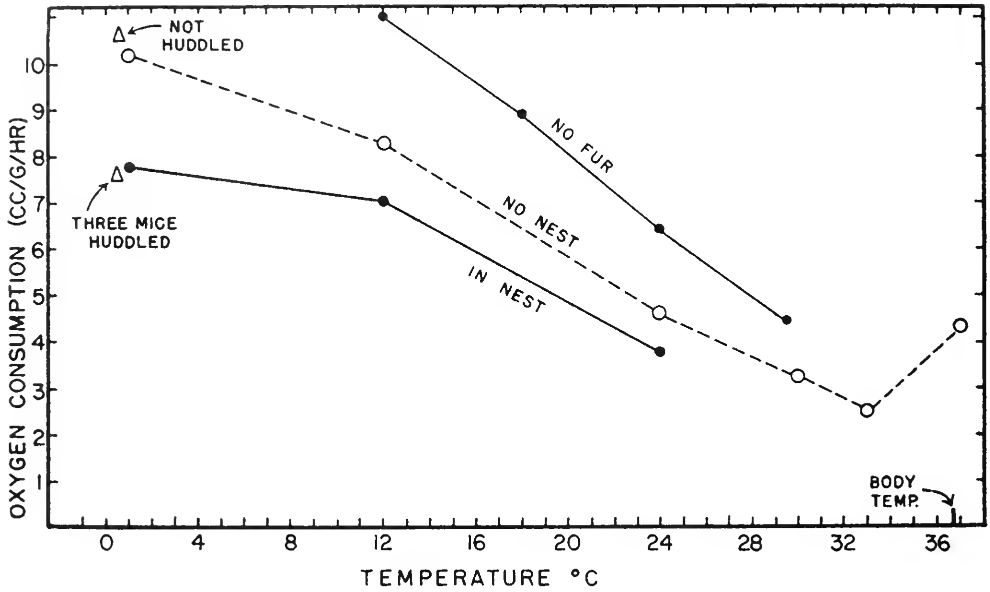

Fig. 2.—The rate of oxygen consumption of resting harvest mice at different temperatures in a nest, without nest, and without fur. All three curves have been adjusted, on the basis of the regression lines shown in Fig. 1, to represent a 9-gram mouse. Triangles indicate rate of oxygen consumption of three mice huddled together without a nest compared with the expected rate for the same three mice singly (average weight 8.5 grams). I am grateful to Martin Murie for supplying the value for deep body temperature, which was the average of many determinations made during the day and night at ambient temperatures between 14° and 27° C.

The increase in rate of metabolism at cool temperatures is almost linear between 33° and 12°; each drop of 1° C. causes an increase in the rate of oxygen consumption of 0.27 cc/g/hr. This rate of change, possibly because of the small size of harvest mice, is greater than that of any of the rodents listed by Morrison and Ryser (1951) and by Dawson (1955). The averages used for the two points at 1° C. include several low values obtained while the animals probably had a slightly lowered body temperature. Inclusion of these low values causes the apparent decrease of the slope of the two curves between 12° and 1°. No body temperatures, however, dropped to the torpid level. *Reithrodontomys megalotis* is able to maintain its temperature well above the torpid level even when sleeping in cold surroundings. In this respect it differs from the pocket mouse (*Perognathus longimembris*), a mouse with which it should be compared because of its similarly small size. When pocket mice are caged at cold temperatures with adequate food, they either drop into torpor or are continually awake and active. They may even be *unable* to maintain a high body temperature during a prolonged period of sleep at cool temperatures (Bartholomew and Cade, 1957).

The only other report on the rate of oxygen consumption of harvest mice lists a rate of 3.8 cc/g/hr at 24° C. for mice with an average weight of 9.6 grams (Pearson, 1948*a*). This rate is almost 10 per cent lower than the comparable rate obtained from Figure 1 and is below the range of variation obtained at this temperature. The difference may be accounted for by the fact that the mice used in the earlier study were acclimated to a warmer temperature (for discussion of the effect of acclimatization on metabolism see Hart, 1957).

INSULATING EFFECTIVENESS OF FUR

Figure 2 shows also the metabolic effect of removing all the fur (277 mg. in the single 8.8-gram specimen used) with an electric clipper. When calculating the points for the curve in Figure 2, 0.28 grams was added to the naked weight and then this rate was adjusted to that for a 9-gram animal on the basis of the regression lines shown in Figure 1. The rate of metabolism of the naked mouse was about 35 per cent higher at each of the temperatures used, and the rate increased 0.38 cc/g/hr for each 1° C. drop in air temperature.

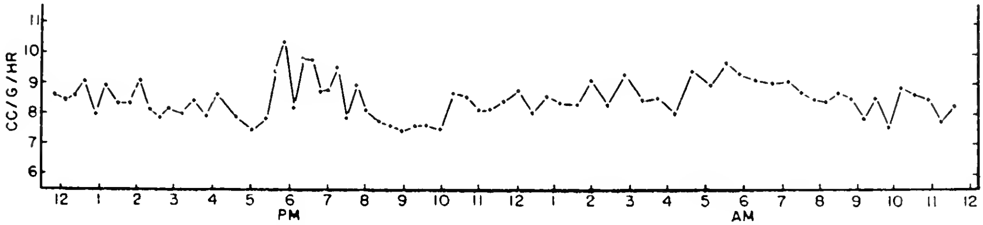

FIG. 3.—Rate of oxygen consumption of a 9-gram harvest mouse for 24 hours at 12° C.

INSULATING EFFECTIVENESS OF NESTS

When normal, fully furred mice were given an opportunity to increase their insulation by constructing nests, their metabolic rates were lowered about 17 per cent at intermediate temperatures and 24 per cent at 1° C. (lowest curve in Fig. 2). To obtain these measurements, individual mice placed in the metabolic chamber were provided with a harvest mouse nest collected from the wild (shredded grass and down from Compositae), and this the mouse quickly rebuilt into an almost-complete hollow sphere about three inches in diameter. Metabolic rates were counted only when a mouse was resting quietly deep in the nest.

THERMAL ECONOMY OF HUDDLING

The metabolic economy of huddling was measured on one occasion with three mice at an environmental temperature of 1° C. without nesting material. The rate of metabolism per gram of huddled mice was 28 per cent less than it would have been for a single one of the mice (Fig. 2). The metabolic saving would probably be greater when more mice were huddled together and less when only two mice were huddled, as is true for feral *Mus* (Pearson, 1947) and laboratory mice (Prychodko, 1958).

24-HOUR OXYGEN CONSUMPTION IN CAPTIVITY

Figure 3 illustrates the rate of oxygen consumption of a mouse kept in the apparatus at 12° C. without nesting material but with food and water for 24 hours. The mouse consumed 1,831 cc. of oxygen to give an average rate of 8.48 cc/g/hr. This is equal to a heat production of about 8.8 Calories per day. In agreement with the fact that activity of harvest mice in the wild is greatest shortly after dusk (Pearson, 1960), the oxygen consumption was greatest at that time. The prolonged low period lasting from about 8:30 to 10:00 P.M. was unexpected in this nocturnal animal.

Pearson (1947) used as an indicator of the nocturnality of different species the ratio of the total amount of oxygen consumed at night (6:00 P.M. to 6:00 A.M.) to that consumed in the daytime. For the harvest mouse described in Figure 3, the ratio is low—1.02—but it should be pointed out that the record was made at 12° C., which is colder than the temperature used for the species in the earlier report. Temperature affects the night/day ratio of oxygen consumption because the difference in amount of oxygen consumed during rest and during activity is proportionately great at warm temperatures and small at cold temperatures.

EFFECT OF ACTIVITY ON METABOLISM

An athlete is able, for short periods, to raise his rate of metabolism to a level 15 to 20 times his basal rate, but small mammals do not match this effort. The peak metabolic effort of mice running in a wheel is only 6 to 8 times their basal rate (Hart, 1950). At 0° C. lemmings running in a wheel at a speed of 15 cm/sec increase their oxygen consumption less than 35 per cent above the level of resting lemmings (Hart and Heroux, 1955). At cool ambient temperatures, such as this, small mammals expend so much energy at rest that a considerable amount of activity causes only a proportionately small increase in oxygen consumption;

TABLE 1

THE 24 HOUR OXYGEN CONSUMPTION (IN CC.) OF A 9-GRAM HARVEST MOUSE DURING DECEMBER AND JUNE AT ORINDA, CALIFORNIA

		DECEMBER			JUNE	
		Without Nest	With Underground Nest		Without Nest	With Underground Nest
Nocturnal habit	4 hr. above ground at 1° C.*	367	367	4 hr. above ground at 12° C.†	297	297
	20 hr. under ground at 10° C.‡	1,548	1,296	20 hr. under ground at 18° C.§	1,152	954
	Activity correction‖	+119	+119	Activity correction‖	+119	+119
		2,034	1,782 cc. (8.55 Cal.)#		1,568	1,370 cc. (6.58 Cal.)#
Diurnal habit	20 hr. under ground at 10° C.‡	1,548	1,296	20 hr. under ground at 18° C.§	1,152	954
	4 hr. above ground at 6° C.**	333	333	4 hr. above ground at 25° C.††	155	155
	Activity correction‖	+119	+119	Activity correction‖	+119	+119
		2,000	1,748 cc. (8.39 Cal.)#		1,426	1,228 cc. (5.89 Cal.)#

* Mean temperature in runways at time of passage of harvest mice in December.
† Mean temperature in runways at time of passage of harvest mice in June.
‡ Underground temperature in December.
§ Underground temperature in June.
‖ Add 40 per cent of the oxygen consumption on the surface at a temperature of 12° C.
\# Assumed 4.8 Cal. per liter of oxygen.
** Mean half-hourly temperature in runways between 6 A.M. and 6 P.M. in December.
†† Mean half-hourly temperature in runways between 6 A.M. and 6 P.M. in June.

and at cold temperatures the metabolic cost of keeping warm may be so high as to leave little or no capacity for exercise (Hart, 1953). During measurement of the resting metabolism of harvest mice, numerous measuring periods had to be discarded because the mouse was moving around in the metabolism chamber. Such activity rarely raised the oxygen consumption more than 40 per cent above the level of a resting animal at the same temperature. During the 24-hour run at 12° C., the highest metabolic rate occurred during an 11-minute period when the average oxygen consumption was 10.36 cc/g/hr. This is only 40 per cent greater than the lowest rate recorded for that mouse during any one measuring period. The maximum metabolic effort recorded for any harvest mouse was that of an 8.6-gram mouse at 1° C. This animal persisted in gnawing, exploring, and trying to escape from the chamber for more than two hours. During one 10-minute period its oxygen consumption averaged 15.8 cc/g/hr, which is 50 per cent higher than the rate of a resting mouse at the same air temperature and six times the minimum value for the species at thermal neutrality. This is probably not far from the peak metabolic effort of the species.

On several occasions I have watched undisturbed harvest mice carrying on their normal activities in the wild, and I have been impressed by their leisurely approach to life. Hard physical labor and strenuous exercise must occur quite infrequently. Most normal activities of harvest mice are probably accomplished without a rise in metabolic rate more than 50 per cent above what it would be in a resting animal at the same air temperature.

24-HOUR METABOLISM IN THE FIELD

The preceding observations indicate that ambient temperature is a much more important variable than activity in the 24-hour energy budget of harvest mice in the wild. By use of automatic devices that record the temperature in mouse runways whenever a mouse passes by, the temperature encountered by harvest mice during their nightly periods of activity are known (Pearson, 1960). I have also recorded throughout the year the temperature five inches below the surface of the ground. This gives an approximation of the temperature encountered by the mice while they are in their retreats during the daytime. Some of these surface and underground temperature measurements have been used in the calculations summarized in Table 1.

To complete the calculations in Table 1, it has been necessary to estimate how many hours of each 24 the mouse spends on the surface of the ground and how many below the surface. No good data exist, so I have made an estimate based on the behavior of captive animals and on automatic recordings made at the exit of an underground nest box being used by wild harvest mice. Admittedly this estimate (4 hours on the surface each night) could be wrong by 50 per cent or more, but it should be noted that an error of two hours in this estimate would only alter the answer (the total 24-hour metabolism) by about 25 per cent. Assuming that the rate of oxygen consumption during above-ground activity is 40 per cent higher than the rate of a mouse resting at 12° C. (see above), the activity correction used in Table 1 can be calculated.

In 24 hours in December a harvest mouse uses 8.55 Calories, and in June, 6.58 Calories (Table 1), assuming that the mouse has the benefit of a nest. A nest reduces his daily energy budget by about 12 per cent. These estimates of daily metabolic demands seem reasonable when compared with the values actually obtained by measuring the 24-hour oxygen consumption of captive animals, as reported above. The average metabolic impact, or daily degradation of energy, by a single harvest mouse should be somewhere between that in December and that in June, perhaps 7.6 Calories. This is about the same as that of a hummingbird in the wild (Pearson, 1954)—less than half that of a much heavier English sparrow (Davis, 1955).

BIOENERGETICS

In seasons when harvest mice are abundant, there may be twelve of them per acre (Brant, 1953). At that population density, the species would be dissipating at the rate of 91 Calories per acre per day the solar energy captured by photosynthesis, or something like ½ of 1 per cent of the energy stored each day by the plants in good harvest-mouse habitat in the Orinda area. This percentage was calculated using a net productivity of 20,000 Cal/acre/day, which was estimated by assuming 4 Calories per gram of dry vegetation (based on data in Brody, 1945, pp. 35, 788) and an annual crop of 1,800 kg. of dry vegetation per acre (based on Bentley and Talbot, 1951). The harvest mice on this hypothetical acre are causing about the same caloric drain on the environment as all the small mammals in the acre of forest described by Pearson (1948*b*).

By using caloric units, direct comparison can be made of the metabolic impact of different species, as in the example above. Similarly, the metabolic cost of different activities and different habits can be compared (Pearson, 1954). For example, harvest mice are strongly nocturnal (Pearson, 1960), in spite of the fact that air temperatures are much colder at night and force mice to consume more oxygen and more food than if they were diurnal. Since evolution has permitted nocturnality to persist, it seems logical to assume that the value of nocturnality to harvest mice is greater than the metabolic cost. I estimate that during a 24-hour period in December a 9-gram harvest mouse uses 0.16 more Calories by being nocturnal than it would if it were diurnal (Table 1). In summer, the difference is even greater, 0.69 Calories. The average is 0.42 Calories, or about 3½ grains of wheat. This is a rough estimate of the price each harvest mouse pays for nocturnality. Some environmental pressure makes harvest mice remain nocturnal, and this pressure must be more than 0.42 Calories per mouse per day. If harvest-mouse nocturnality evolved for one reason only—to avoid predation by hawks—then we would have discovered a minimum estimate of the predation pressure of hawks on harvest mice. Surely the situation is not this simple; nevertheless, it is interesting to measure the pressure that makes harvest mice nocturnal even if the cause of the pressure is not known.

SUMMARY

Oxygen consumption of harvest mice reaches a minimum of 2.5 cc/g/hr at an ambient temperature of 33° C., and the zone of thermal neutrality is not more than 3°. Each drop of 1° in ambient temperature causes an increase in the rate of metabolism of 0.27 cc/g/hr. Removing the fur raises the rate of metabolism about 35 per cent, and use of a nest lowers it 17 to 24 per cent. Huddling by three mice at 1° reduces the rate 28 per cent.

Exercise at cool temperatures causes a relatively small increase in the rate of metabolism, whereas change of ambient temperature has a great effect. Making use of the temperatures that harvest mice are known to encounter in the wild, the 24-hour oxygen consumption of a wild harvest mouse was calculated to be 1,782 cc. in December and 1,370 cc. in June. The average (1,576 cc.) is equivalent to about 7.6 Calories per day. A dense population of harvest mice would dissipate about 91 Calories per day per acre, which is about $\frac{1}{2}$ of 1 per cent of the energy stored by the plants each day.

By being nocturnal, harvest mice encounter cooler temperatures, and this habit increases the daily energy budget of each mouse by 0.42 Calories, or about $3\frac{1}{2}$ grains of wheat.

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OXYGEN CONSUMPTION, ESTIVATION, AND HIBERNATION IN THE KANGAROO MOUSE, MICRODIPODOPS PALLIDUS[1]

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THE pallid kangaroo mouse occurs only in the desert parts of western Nevada and extreme eastern California. Its habitat is restricted to areas of fine sand which support some plant growth. Like its relatives, the kangaroo rats (*Dipodomys*) and the pocket mice (*Perognathus*), it is nocturnal, fossorial, and gramnivorous and can under some circumstances live indefinitely on a dry diet without drinking water. The general life history (Hall and Linsdale, 1929) of this kangaroo mouse and the details of its distribution (Hall, 1946) are known, but virtually no quantitative data on its physiology are available.

The present study was undertaken to compare the thermoregulation of *Microdipodops* with that of the better-known genera, *Dipodomys* and *Perognathus*. These three genera belong to the family Heteromyidae, which has been more successful in occupying the arid parts of western North America than any other group of mammals.

MATERIAL AND METHODS

Experimental animals.—The twenty-three kangaroo mice used were trapped in sand dunes four miles south of Arlemont Ranch, Esmeralda County, Nevada, in April, 1959, and May, 1960. They were housed individually in small terraria partly filled with fine sand, kept in a windowless room on a photoperiod of 12 hours, and fed on a diet of mixed bird seed supplemented occasionally with small pieces of cabbage. Survival was excellent, and some of the animals were kept for over ten months.

Body temperatures.—All temperatures were measured with 30-gauge copper-constantan thermocouples connected to a recording potentiometer. All body temperatures were taken orally by inserting a thermocouple to a depth of at least 2 cm.

Ambient temperatures.—The ambient temperatures were monitored with thermocouples and controlled by insulated chambers equipped with automatic heating and cooling units, blowers, and lights.

Oxygen consumption.—Oxygen con-

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[1] This study was aided in part by a contract between the Office of Naval Research, Department of the Navy, and the University of California (Nonr 266[31]).

sumption was measured by placing a mouse in an air-tight 500-cc. glass container equipped with a thermocouple and ports for the introduction and removal of air. The bottom of the container was covered to a depth of about 1 cm. with fine dry sand. The glass container with animal inside was placed in a temperature-control chamber, and dry air was metered through the container at a rate of 250 cc/min and then delivered to a Beckman paramagnetic oxygen analyzer which, used in conjunction with a recording potentiometer, gave a continuous record of oxygen consumption. All data used were from post-absorptive animals.

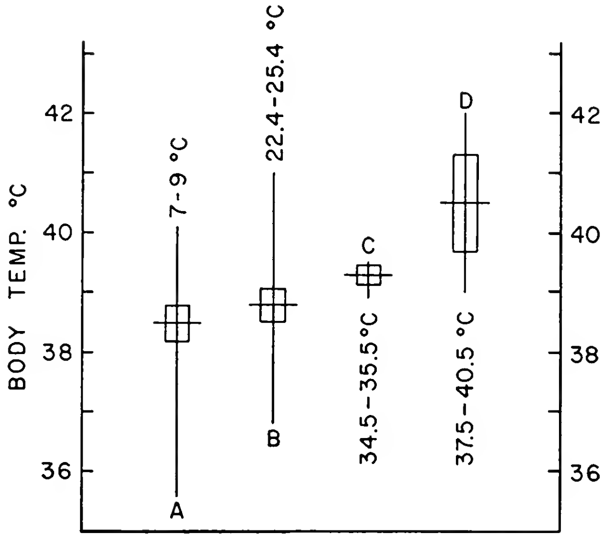

FIG. 1.—Body temperatures of *M. pallidus* at various ambient temperatures. *A*, 47 measurements on twelve animals; *B*, 38 measurements on thirteen animals; *C*, 7 measurements on four animals; *D*, 9 measurements on four animals (three other animals tested at this temperature died). The horizontal lines indicate the means (*M*). The rectangles inclose $M \pm \sigma_M$. The vertical lines indicate the range.

RESULTS

Body temperature during normal activity.—Normally active animals kept at room temperature (22.4°–25.4° C.) had body temperatures ranging from slightly less than 37° to as high as 41° C., with a mean of 38.8° C. (Fig. 1). To determine the response of body temperature (T_B) to moderately low ambient temperatures (T_A), kangaroo mice were placed at T_A of 7°–9° C. for five days starting May 11, 1959, with food available in excess; measurements of T_B were made at 24-hour intervals. There were no apparent changes in T_B during the test period, nor was the mean T_B significantly different from that of animals maintained at room temperature. The animals appeared normally active and unaffected by the change in environmental temperature.

Animals were maintained at T_A of 37.5°–40.5° C. for 24 hours to test their response to moderately high environmental temperatures. They showed a conspicuous elevation in T_B with a mean almost 2° C. higher than that of animals at room temperature. Animals maintained at T_A close to 35° C. also became hyperthermic and showed a mean T_B intermediate between that of animals held at room temperatures and those held at 39° C. There was no mortality in animals held at 35° C., but exposure to 39° C. for more than a few hours killed three out of the seven animals tested. At a high T_A the kangaroo mice did not salivate or pant; they merely sprawled out flat on the sand with legs extended and lower jaw and neck prone on the substrate. This prone posture alternated with brief bursts of intense activity characterized by repeated shifts in position and much digging and moving of sand.

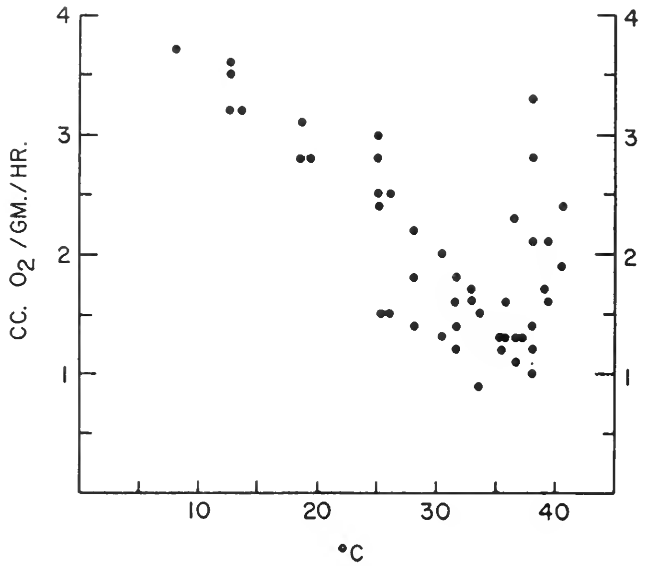

FIG. 2.—The relation of oxygen consumption to ambient temperature. Data obtained from ten animals. Each point represents the minimum level of oxygen consumption maintained by an animal for half an hour. Oxygen volumes are corrected to 0° C. and 760 mm. (Hg.) pressure.

Oxygen consumption.—The relation of oxygen consumption to T_A is summarized in Figure 2. There is no clearly defined zone of thermal neutrality, but oxygen consumption is minimal at about 35° C. The increase in oxygen consumption at temperatures above 35° C. is relatively more rapid than is the increase below this point of thermal neutrality. No differences in oxygen consumption were apparent between males and females.

The calculated metabolism of *Microdipodops pallidus* (mean weight, 15.2 gm.) is 1.8 cc O_2/gm/hr when the formula $M = 3.8W^{-0.27}$ is used (see Brody, 1945, and Morrison, Ryser, and Dawe, 1959). The observed basal metabolism of our kangaroo mice (mean, 1.3 ± 0.2 cc O_2/gm/hr) was about three-fourths of the predicted value. This relatively low figure is consistent with the observation on some other heteromyids (Dawson, 1955).

The only comparative data on the energy metabolism of *Microdipodops* is that of Pearson (1948) on *M. megacephalus*. Pearson's data, obtained at temperatures near 24° C. from animals that were not post-absorptive, gave oxygen consumptions of 3.4–3.7 cc O_2/gm/hr. Pearson's measurements, as might be expected from the fact that he was not using post-absorptive animals, are higher than our determinations of 2.7 cc O_2/gm/hr at 25° C.

Hibernation and estivation.—No information on hibernation or estivation is available for *Microdipodops*. Hall (1946, p. 386) pointed out that kangaroo mice are often active above ground in temperatures many degrees below freezing, and Ingles (1954, p. 214) suggested that kangaroo mice probably do not hibernate.

Under laboratory conditions we found that kangaroo mice at any time of year will spontaneously become dormant at ambient temperatures ranging at least from 5° to 26° C. and can readily be induced to hibernate (or estivate) over this range of temperatures by reduction of food for 24 hours or less.

Body temperature and behavior during entry into torpor were not recorded, but the animals apparently entered torpor in the crouching posture normally used in sleeping. Dormant animals had body temperatures 1°–2° C. above ambient. Judging from the course of body temperature during arousal from torpor, there are no conspicuous physiological differences between arousal from spontaneous dormancy and that from induced dormancy.

Animals dormant at room temperatures (estivating) started to arouse immediately upon being handled. The rate of increase in T_B varied but usually fell between 0.5° and 0.8° C. per minute. Usually within 20 minutes of the onset of arousal the animals attained their normal operating temperature, and within as little as 12–15 minutes from the start of arousal they appeared to behave normally, even though T_B approximated 30° C. Arousal from low temperatures was essentially the same as arousal from high temperatures (Fig. 3). However, animals arousing from low temperatures attained maximal body temperatures about 1° C. higher than did those arousing from room temperature.

Incidental to the measurement of T_B the relations of various types of behavior

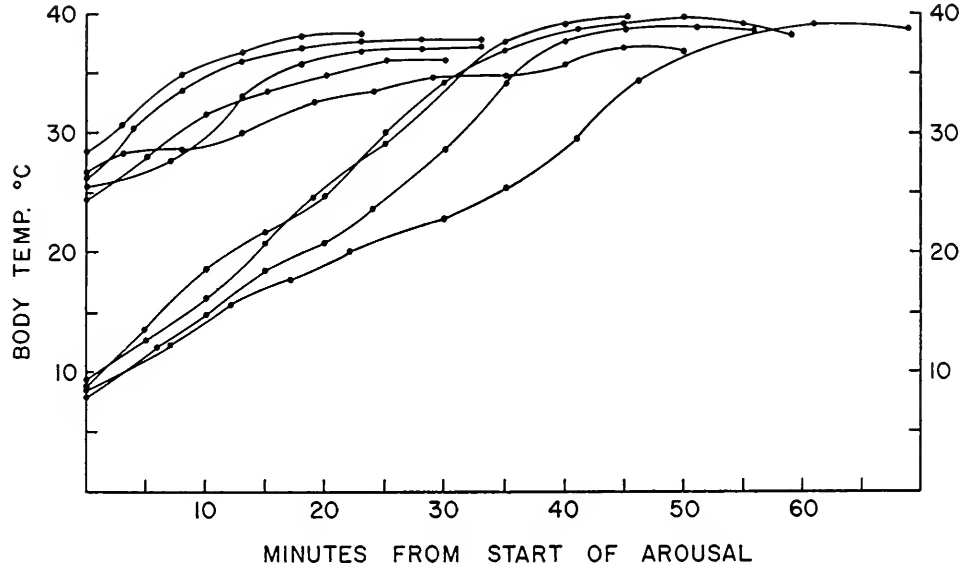

Fig. 3.—Increases in oral temperatures in nine kangaroo mice during arousal from torpor. All arousals took place in ambient temperatures between 23° and 26° C. Temperatures taken manually with thermocouples. The five upper animals were dormant at room temperature (22°–25° C.); the four lower animals were dormant at 5°–8° C.

to body temperature were noted during nine arousals. Mice unsuccessfully attempted to right themselves when turned over at T_B between 16.1° and 18.2° C. and successfully righted themselves at T_B between 19.0° and 22.0° C. The first vocalizations were given at T_B between 24.7° and 28.6° C. Grain was available to the animals during arousal, and seven of the nine animals ate during arousal. The lowest T_B for eating was 25.5° C., and three animals ate at temperatures between 25° and 29.4° C. The mean T_B for onset of visible shivering for seven animals was 25.5° C. Two of the nine animals observed did not visibly shiver during arousal. Shivering usually stopped at a T_B of 34°–35° C.

DISCUSSION

The general features of thermoregulation in *Microdipodops pallidus* are similar to those of the related genus *Perognathus* in that both show well-developed patterns of hibernation and estivation, essentially normal behavior at T_B below 35° C., obligate hyperthermia at T_A above 35° C., and no apparent salivary response to elevated body temperature. *Microdipodops* differs from the related genus *Dipodomys* in that the latter does not readily become dormant at either high or low temperatures and does use salivation as an emergency thermoregulatory response (Schmidt-Nielsen and Schmidt-Nielsen, 1952).

In kangaroo mice, as in *Perognathus longimembris* (Bartholomew and Cade, 1957) and *Citellus mohavensis* (Bartholomew and Hudson, 1960), there appears to be no sharp physiological differentiation between hibernation and estivation. This underscores the point that the facultative hypothermia shown by mammals should not be thought of only as an adaptive response to low environmental temperatures; at least for small desert mammals the ability to become dormant and to decrease body temperature and metabolic activity may be more useful in the summer than in the winter, and it may be as important for water conservation as for energy conservation.

Kangaroo mice are unique among heteromyids in having conspicuous deposits of adipose tissue in the proximal third of the tail, which is considerably larger than either its base or its distal half. Hall (1946, p. 379) suggests that the fleshiness of the tail permits it to function in balancing. However, since these mice hibernate but do not show conspicuous seasonal deposits of subcutaneous fat over the body as a whole, it seems reasonable to suggest that the fat tail serves as a reserve of energy for use during periods of torpor. In the laboratory with food available in excess, many of the kangaroo mice showed a marked increase in tail diameter.

Our data (Fig. 1) show almost no indication of a discrete zone of thermal neutrality for the kangaroo mouse. Its critical temperature is unusually high for an animal living in an area characterized by cold winters. For months on end kangaroo mice can be active only at temperatures below thermal neutrality. Presumably, their energetic and thermal problems are reduced in cold weather by periodic episodes of torpor. It is of interest that we captured our animals on nights when environmental temperatures went below −10° C., and Hall (1946, p. 396) reports that these animals are often "active on nights when the temperature is so low as to freeze to a state of stiffness the bodies of mice caught in traps." Thus, although they can hibernate, they are also commonly active during subfreezing weather.

This species has remarkably shallow burrows, often no deeper than 4 inches (Hall, 1946, p. 396). Consequently, when high daytime temperatures occur, at least some members of the population may be exposed to temperatures near 35° C. It is possible, therefore, that the high point of thermal neutrality of this species allows a significant metabolic economy and a significant reduction in pulmocutaneous water loss during the severely hot desert summers.

Extrapolation of the plot of metabolism against ambient temperature below thermal neutrality does not intersect the abscissa within the usual range of body temperature (38°–39°C.) of kangaroo mice (Fig. 2). This means that, unlike some of the species considered by Scholander *et al.* (1950), and unlike the masked shrew, *Sorex cinereus* (Morrison, Ryser, and Dawe, 1959), the kangaroo mouse does not follow Newton's empirical law of cooling in a simple and direct manner. The failure to follow the pattern predicted by Newton's law of cooling may be related to the fact that kangaroo mice start to become hyperthermic as they approach their critical temperature (Fig. 1), and it suggests that the relation between skin and ambient temperature in this species differs from the usual pattern. It is of interest that Pearson's data (1960) for *Reithrodontomys* show a situation similar to that reported here for *Microdipodops*, that is, almost no zone of thermal neutrality, a high critical temperature, and a failure of the curve of metabolism against ambient temperature to intersect the abscissa at the usual body temperature. Although Pearson does not comment on this point, it appears that in *Reithrodontomys* as in *Microdipodops* the curve of metabolism against ambient temperature intersects the abscissa at a point above the lethal temperature for the species.

The apparent absence of a marked increase in salivation at high temperatures in *Microdipodops* correlates nicely with its strong tendency toward hyperthermia at high ambient temperatures. For animals living in a desert environment where water is usually in short supply, hyperthermia is a more advantageous response to heat than is evaporative cooling.

SUMMARY

Microdipodops pallidus occurs only on sparsely vegetated sand dunes in the desert parts of western Nevada and eastern California. In the absence of temperature stress body temperature, T_B, averages 38.8°C. There is no diminution of T_B with decreasing ambient temperature, T_A, at least to 8° C. However, hyperthermia is apparent at a T_A of 35° C. and at 39° C. T_B averages 40.5° C. Exposure for more than a few hours to 39° C. is often lethal. At high ambient temperatures kangaroo mice neither pant nor drool. They have no clearly defined zone of thermal neutrality; oxygen consumption is minimal at 35° C. and increases more rapidly at temperatures above this point than below it. Basal metabolism is 25 per cent less than that predicted on the basis of body size. Kangaroo mice are capable of both estivation and hibernation. In the laboratory they often become dormant at ambient temperatures ranging at least from 5° to 26° C. The rate of temperature increase during arousal at room temperature is 0.5°–0.8° C. per minute. Terminal body temperatures after arousal from low temperatures averaged about 1° C. higher than after arousal from room temperature. By the time the T_B of arousing animals reaches 30° C., their behavior appears normal. The thermoregulatory responses of kangaroo mice are compared with those of other desert heteromyids, and the ecological significance of their physiological capacities is discussed.

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Counter-Current Vascular Heat Exchange in the Fins of Whales[1]

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IT MAY BE a source of wonder that whales swimming about in the icy waters of the polar seas can maintain a normal mammalian body temperature. What prevents them from being chilled to death from heat loss through their large thin fins?[2] These are well enough vascularized to justify the question (fig. 1). One may conjecture that a whale may be so well insulated by its blubber that it needs such large surfaces to dissipate its heat. On the other hand, if heat conservation is at a premium, there must be some mechanism whereby the fins can be circulated without losing much heat to the water. One may point to two circulatory factors which would reduce the heat loss from the fin: *a*) slow rate of blood flow and, *b*) precooling of the arterial blood by veins before it enters the fin.

Bazett and his coworkers (1) found that in man the brachial artery could lose as much as 3°C/decimeter to the two *venae comitantes*. This simple counter-current exchange system is a mere rudiment compared to the multichannelled arteriovenous blood vascular bundles which we find at the base of the extremities in a variety of aquatic and terrestrial mammals and birds. These long recognized structures have most recently been studied by Wislocki (2), Wislocki and Straus (3) and Fawcett (4).

The function of these bundles has long been a mystery. No matter what else they do, they must exchange heat between the arteries and veins, and it has been pointed out that they very likely play an important role in the preservation and regulation of the body heat of many mammals and birds (5).

In the present study we describe a conspicuous arteriovenous counter-current system in the fins and flukes of whales, which we interpret as organs for heat preservation.

MATERIAL

Two species of porpoises have been studied: *Lagenorhynchus acutus:* dorsal fin, tail-fluke, and flipper of an adult female collected 50 miles east of Cape Cod; *Tursiops truncatus:* dorsal fin and tail-fluke of a 4-month-old calf from Florida, supplied through the courtesy of the Marineland Research Laboratory.

Lagenorhynchus is a genus of fairly high latitudes, the southern limit of *L. acutus* being about latitude 41°N. on the New England coast and about 55°N. in the British Isles. It has been caught at least as far north as latitude 64°N. in west Greenland and Norwegian waters. *Tursiops* is found in lower latitudes, *T. truncatus* overlapping slightly with *L. acutus* and occurring south into the tropics.

DESCRIPTION

Figure 2 illustrates the vascular supply at the base of the dorsal, pectoral and caudal fins. It may be seen that all major arteries are located centrally within a trabeculate venous channel. This results in two concentric conduits, with the warm one inside. In addition to the circumarterial venous channels there are separate superficial veins, as seen in figure 2. The circumarterial venous channels are conspicuously thin walled compared to the simple veins, as may be seen in figure 3. When an artery was perfused with saline, the solution returned through both of these venous systems.

INTERPRETATION

Based on the anatomical findings and on the perfusion experiments, we interpret the artery-within-vein arrangement as a heat-conserving counter-current system, as schematically presented in fig. 4. In such an arrangement the warm arterial blood is cooled by the venous blood which has been chilled in the fin. The result is a steep proximodistal temperature drop from the body into the appendage. The heat of the arterial blood does not reach the fin, but is short-circuited back into the body in the venous system. Body heat is therefore conserved at the expense of keeping the appendage cold. There is reason to believe that the analogous blood vascular bundle in the proxi-

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[1] Contribution Number 807 from the Woods Hole Oceanographic Institution.

[2] In 'fin' we include the structures more specifically called flippers (pectoral fins), flukes (caudal fins) and dorsal fin.

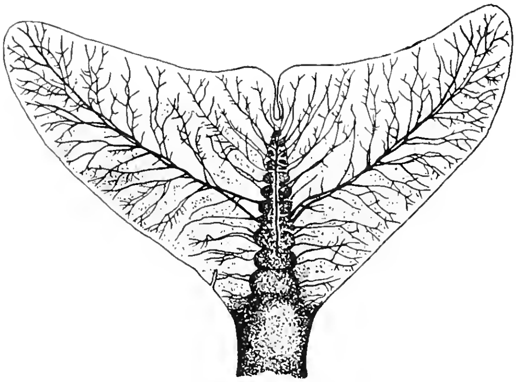

FIG. 1. Arterial supply to the flukes in the common porpoise (*Phocoena phocoena*), drawn from an x-ray picture by Braun (6).

mal part of the extremities of sloths serves a similar function, inasmuch as these animals can barely keep warm even in their warm environment (5). Cold extremities have been described in many arctic mammals and birds as important factors for conservation of body heat (7), but to what extent arteriovenous counter-current structures are present in these animals is not known.

The efficiency of heat exchange in a system like that diagrammed in figure 4 is related to the blood flow. The slower the flow, the more nearly identical will be the arterial and venous temperatures along the system, and the more efficient will be the heat conservation. At high rates of flow, warm blood will reach the periphery and cool venous blood will penetrate into the body.[3]

It was shown by perfusion experiments on the detached fins that the arterial blood may return via the concentric veins, and/or through the separate superficial veins. As pointed out above, the concentric vein channels are very thin walled and weak compared to the thick-walled superficial veins (fig. 3). One may interpret these anatomical facts in the following way. If the animal needs maximal heat conservation, blood circulation through the fins should be slow, and the venous return should preferentially take place through the counter-current veins. But a slow rate of blood flow would need only weak venous walls, as actually found. If, on the other hand, the animal needed maximal cooling, as during exercise in relatively warm water, this would be most effectively accomplished by a high rate of blood flow through the fins, with venous return through the superficial veins and the least possible flow through the concentric veins. This would require the strong and thick walls of the superficial veins. One may even see the likelihood of a semiautomatic regulatory function in the concentric system, for when the artery is swelled by increased blood flow, the concentric veins will be more or less obliterated,

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[3] The theory for a multichannel counter-current system has been elaborated in connection with the swimbladder in deep sea fishes (8).

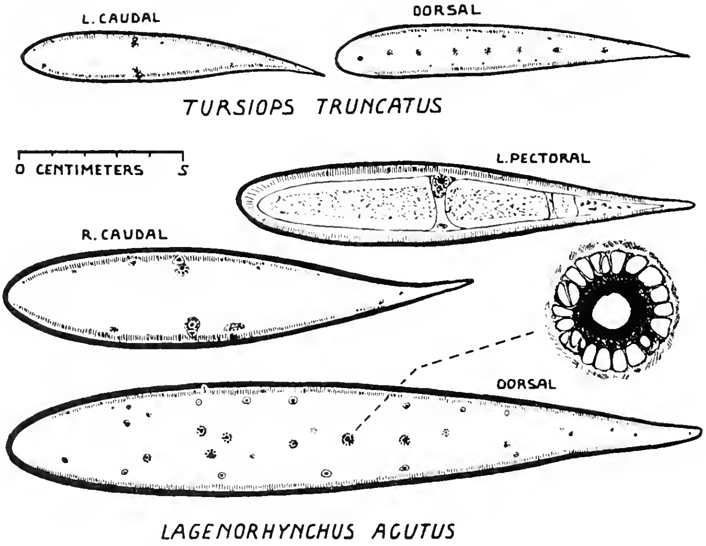

FIG. 2. Sections near base of fins and flukes of two species of porpoises. Each artery is surrounded by a multiple venous channel. Simple veins are near the skin (only the larger ones are indicated).

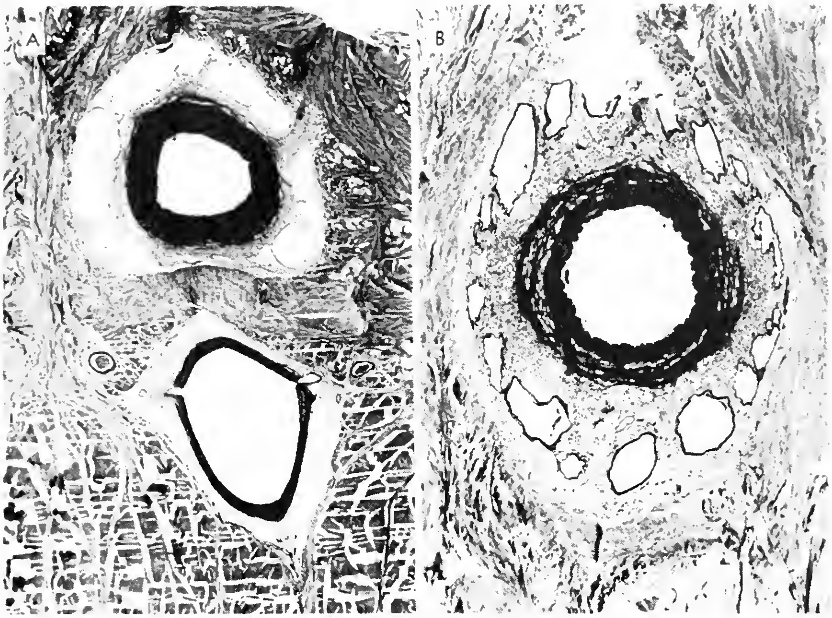

FIG. 3. Sections from *Tursiops truncatus*. (Courtesy of the Department of Anatomy, Harvard Medical School.) *A*. From tail-fluke. Upper: artery surrounded by thin-walled venous channels. Lower: superficial single thick-walled vein in the hypodermis. (× 9) *B*. From dorsal fin. Artery surrounded by thin-walled venous channels (× 12)

but will remain open when the diameter of the artery is reduced during decreased blood flow. Thus the anatomical findings fit logically into the simplest possible scheme of heat regulation in the fins.

There are a few observations available indicative of heat regulation in the fins of porpoises. Tomilin (9) made some observations on an east Siberian 'white-sided dolphin' on deck, and found that the fins could vary between 25° and 33.5°C, while the body varied only 0.5°. Schevill observed that the flukes in a Florida *Tursiops* out of water became about 10° warmer than the body surface itself. In both of these cases the animals were probably resisting overheating. On the other hand, Scholander (5) has recorded cold flippers in water-borne common porpoises (*Phocoena*).

The concentric counter-current system of an artery within a vein appears to be a peculiarly cetacean arrangement, and we have seen it only in the fins, flippers and flukes of these animals.[4] This is an impressive example of bioengineering, which, together with other factors, adapts these homeotherms for a successful existence in a heat-hungry environment.

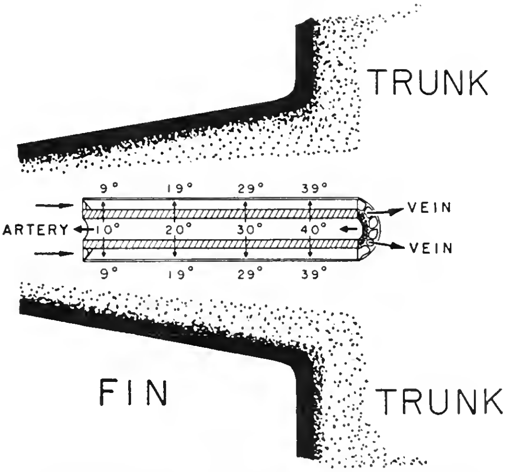

FIG. 4. Schematic diagram of hypothetical temperature gradients in a concentric counter-current system.

SUMMARY

The vascular supply to the fins and flukes of two species of porpoises, *Lagenorhynchus acutus* and *Tursiops truncatus*, is described. All major arteries entering the fins and flukes

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[4] The present material is from odontocetes, but these structures have also been noted by Scholander in the tail flukes of a mysticete (fin whale).

are surrounded by a trabeculate venous channel. The arteries drain into these, but also into superficial simple veins. The artery within the venous channel is interpreted as a heat-conserving counter-current exchange system. The heat regulatory aspects of the two venous systems are discussed.

We wish to express our appreciation to Dr. F. G. Wood, Jr., and the Marineland Research Laboratory, Marineland, Fla., for providing the material of *Tursiops truncatus*, and to Dr. G. B. Wislocki of the Dept. of Anatomy, Harvard Medical School, Boston, Mass., for providing the histological sections and photographs.

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SECTION 3—REPRODUCTION AND DEVELOPMENT

Just as animal structures must be adaptive, so must reproductive and developmental patterns. In other words, the organism must be a functioning unit in its particular environment at all times. In our selections, Spencer and Steinhoff discuss the possible functional significance of geographic variation in litter size, and Sharman points out the adaptive value of some peculiarities of kangaroo reproduction. The interrelationships of reproductive and developmental patterns in the fisher are evident in the account by Wright and Coulter. Superfetation (or the fertilization of new ova during gestation, known in kangaroos, rabbits, and some rodents), delayed implantation (which occurs in some mustelids), and delayed fertilization (through sperm storage, known in some bats) all are interesting variations of the reproductive theme, and all are adaptive in certain circumstances. A recent study of reproductive adaptations of the red tree mouse by Hamilton (1962, not reprinted here) related small litters, long gestation, delayed implantation during lactation, and slow development of young with the limited amount of energy available in the food sources of the mice. The study here reproduced by Jones on the evening bat relates development to function, in this case flight, and also nicely illustrates some quantitative refinements that adequate data provide.

The student of any field is well advised to learn what compilations, summaries, or collected works are available. Sometimes a summary is short, as is the paper by Hamilton included herein on reproductive rates of some small mammals. In the field of mammalian reproduction, the classic summary by Asdell (as revised in 1964), and recent collections of contributions edited by Enders (1963) on delayed implantation and by Rowlands (1966) on comparative biology of mammalian reproduction will repay study.

Two classic books in the field of development in which relative growth rates were considered at length are *On Growth and Form* by D'Arcy Wentworth Thompson (1942) and *Problems of Relative Growth* by Julian Huxley (1932). A comparative study of two related species (Butterworth on *Dipodomys*) is included here. A recent and detailed account (too long to include here) of one species in terms of relative growth and in comparison to several other species is the study by Lyne and Verhagen (1957) on *Trichosurus vulpecula,* an Australian brush-tailed possum.

A number of studies of single species may be found in the literature. Allen's paper (reprinted here) is of interest because it is one of the earliest to give serious consideration to variation as such and to possible relevance of variation to systematic and other problems. Hall (1926) described at greater length than could be included here and in detail uncommon at that time the changes during growth of the skull in the California ground squirrel. Two among the many good recent studies of development of single species are by Layne (1960, 1966) on *Ochrotomys nuttalli* and *Peromyscus floridanus.*

Although we have not included examples of methods of determining age other than the report of Wright and Coulter on the fisher, we must comment that age determination is important in many practical problems of wildlife management as well as in studies of population composition or of growth as such. Managers of deer herds, for example, can examine the teeth of hunter-killed animals using standards developed by Severinghaus (1949) and later workers. The formation of annuli in dental cement in various kinds of mammals provides another method for determining age—see Adams and Watkins (1967) on its application to ground squirrels. Epiphyseal growth as observed in X-ray photographs and the use of lens weights are other means (see Wight and Conaway, 1962, on aging cottontails).

A short paper on maturational and seasonal molt in the golden mouse concludes our selection for this section. Studies of molt in furbearers are, of course, of special economic import, and knowledge of pelage differences related to age, sex, or season are of obvious use in most studies of mammalian populations.

THE REPRODUCTIVE RATES OF SOME SMALL MAMMALS

By W. J. Hamilton, Jr.

Students of cyclic mammal populations realize the necessity of properly evaluating the breeding rate. A proper assessment of the reproductive rate is frequently essential for a correct interpretation of population levels. Without a satisfactory estimate of breeding rate, conclusions regarding cyclic populations may be invalid. Unfortunately, it is difficult to secure accurate data on the breeding rate in feral species; analogous observations on captive species may not give a true picture of the breeding behavior in wild species. Many field investigators believe that small mammals have successive litters, one following another in rapid succession during the height of the breeding season. On the other hand, there are those who argue that a post-partus oestrus in wild species seldom occurs. They insist that mating during the lactation period is rare under natural conditions; captive individuals alone exhibit this phenomenon due to crowding or other factors imposed by laboratory conditions. Since the subject is an important one in population studies, I present such data as are available to demonstrate that certain shrews, mice, and other small mammals are not only capable, but do mate successfully following partus. Actively lactating species are upon occasion gravid.

In an important paper on discontinuous development in mammals, Hamlett (1935) remarks that in a fairly extensive series of mice of various kinds, including free living house mice, Norway rats, and wild species of deer mice and field mice, pregnant suckling females were never found. He concludes that copulation immediately after parturition in mice is a response to domestication, and is rare or lacking in free living races. Pearson (1944) examined early pregnant females of *Blarina* in which placental scars were visible and the mammary glands greatly developed, indicating that these individuals had been nursing young recently. He suggests the possibility that the young may have been lost or destroyed a short time before, and that mating took place after the loss of the young. Pearson believes that shrews with advanced mammary development merely indicate that it is possible for *Blarina* to produce more than one litter, but his data do not prove that there is a true post-partum oestrus. He concludes that true post-partum mating and pregnancy during lactation rarely, if ever, occur in *Blarina*; remating depends upon the loss of a litter.

Several investigators have demonstrated a post-partum oestrus in captive cricetid rodents. Bailey (1924) observed that captive meadow voles, *Microtus p. pennsylvanicus*, mated immediately following parturition, one female producing seventeen litters in a year. The gestation of this species is twenty-one days; lactation does not lengthen the period. Svihla (1932) reports several species of captive *Peromyscus* mating shortly after parturition. Practically all females of the European wild rabbit (*Oryctolagus cuniculus*) under natural conditions become pregnant again at each post-partum oestrus during the height of the breeding season (Brambell, 1943). Elsewhere (Hamilton, 1940), I have shown that the cottontail, *Sylvilagus floridanus mearnsii*, presumably has a post-partus oestrus, for actively nursing females have contained embryos, suggesting that mating occurs shortly following parturition. Vorhies and Taylor (1940), in their study of the white-throated wood rat, *Neotoma albigula*, suggest that it is highly probable that this species produces successive litters with only very short intervals. In one den they found a female with two newly born young hanging to the teats, with three half-grown young in the same den. This presumptive evidence of rapid succession in litters is nevertheless suggestive.

Obviously with the species discussed above there is a post-partum oestrus at which time the female is receptive to the male. It appears unlikely that the imposition of captivity would modify the reproductive cycle in a short time. The absolute proof of such should be studied under natural conditions, though positive data are rather difficult to secure.

A feral Norway rat will cease lactating within forty-eight hours after the loss of a litter. Gentle traction on the teats fails to produce milk following this period. Meadow voles usually cease to lactate a day after the young are removed. The short-tailed shrew, *Blarina brevicauda*, will not produce a flow of milk in a similar length of time if the nursing young be destroyed. Since such is known of these three species, we may adduce the probability of pregnant females nursing a litter if a flow of milk is possible. The mammary glands and teats swell noticeably in many mammals shortly before parturition. Interpretation of data may be faulty if such evidence is not considered with care. A colustral flow is evident in several cricetid rodents and some insectivores shortly before parturition. Inexperienced observers may mistake this secretion for milk and draw faulty conclusions. The following data lend support to the assumption that some small mammals, under natural conditions, successfully mate shortly after parturition and produce successive litters in rapid succession during part of the breeding season. Unless otherwise stated, the observations below relate to those of small mammals under conditions in the vicinity of Ithaca, New York.

Blarina brevicauda. Short-tailed shrew.—On July 23, 1947, E. W. Jameson, Jr. collected a nursing shrew. Under gentle pressure, milk could be drawn from the posterior teats. This shrew had four embryos, the uterine swellings measured 10 mm. in greatest width, suggestive of at least half-time pregnancy. A week later I trapped a nursing *Blarina* with five 11-mm. embryos. The teats, on traction, produced milk. A *Blarina* with six 9-mm. embryos was taken on August 10, 1948. The teats were drawn out and produced milk under gentle traction. In my field notes from 1926 to 1941 I have recorded data on many hundreds of these shrews, and noted on numerous occasions the occurrence of lactating gravid females. I have always considered this condition a perfectly natural one in shrews.

Sorex f. fumeus. Smoky shrew.—Mating may follow parturition in this species (Hamilton, 1940). Actively nursing females have been taken which contained well-developed embryos. Specimens of pregnant *Sorex cinereus* have likewise been collected with prominent mammary glands containing an abundance of milk.

Peromyscus leucopus noveboracensis. White-footed mouse.—Many hundreds of adult females have been examined during the breeding season over a twenty-year period. Many of these were actively nursing and contained embryos of various sizes. Pregnant nursing individuals appear more frequently in May and June collections. It is possible that more lactating individuals were gravid than my notes indicate, since early pregnancy cannot be determined by macroscopic examination.

Oryzomys palustris. Rice rat.—This is a prolific species. Field data obtained in Virginia demonstrates that actively nursing females are occasionally pregnant; there is evidence that a high fertility, resulting in vigorous females actually producing nine litters in a breeding season, is quite possible. The females are capable of breeding when seven weeks old.

Clethrionomys gapperi. Red-backed vole.—On October 10, 1941, I took a 35-gram nursing female with four 3-mm. embryos and recent placental scars. The mammary glands, when dissected out, weighed 2.5 grams. On May 29, 1940, a nursing individual contained five 6-mm. embryos. Such data are admittedly fragmentary, but do suggest the rapidity of breeding in this species. Apparently many parous animals of the bank vole, *Clethrionomys glareolus*, are pregnant and lactating simultaneously. In such, pregnancies are prolonged by lactation causing a delay in implantation. This delay results in the blastocysts remaining in a resting state in the uterine lumen for a considerable period (Brambell and Rowlands, 1936).

Microtus pennsylvanicus. Meadow vole.—The reproductive behavior of this species in the wild is similar to that of captives. Adult females give birth to one litter after another in rapid succession. Data on this high fecundity are readily obtainable by live trapping. Females approaching full term are readily recognized; repeated captures of specific individuals indicate that in some instances young are produced at three-week intervals over a period of several successive months. The capture of numerous wild pregnant females with nest-young is indubitable proof that post-parous mating occurs normally from early spring to fall. I have obtained many records of such.

Ondatra zibethica. Muskrat.—Arthur C. Cook of the New York Conservation Department informs me (personal letter) that on June 20, 1941, he dug out a muskrat den at Howlands' Island, Cayuga County, New York. From the den he recovered a pregnant muskrat with two litters of different size. In captivity, this gravid female suckled the smaller litter. This is presumptive evidence that the muskrat may mate following partus.

Some polyoestrous rodents, in which two litters a year are the rule, have the litters widely spaced. Mating normally occurs in the late winter and midsummer. No post-partum oestrus occurs. Deanesly and Parkes (1933) indicate that there is no oestrus immediately after parturition or during lactation in the gray squirrel, *Sciurus carolinensis*. A similar condition obtains with *Tamiasciurus*, *Tamias*, and *Eutamias*.

Where populations of small mammals are sufficiently large, it appears probable that fruitful matings often occur following partus, at least during the height of the breeding season. If such a condition be generally true, it enables one to compute, in a measure, the probable reproductive rate. One may thus visualize the annual natural increment in a population during the breeding season. Such data are most useful to students of populations and animal behavior.

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Cornell University, Ithaca, New York. Received October 4, 1948.

AN EXPLANATION OF GEOGRAPHIC VARIATION IN LITTER SIZE

Albert W. Spencer and Harold W. Steinhoff

Abstract.—Our explanation of the latitudinal and altitudinal variation in litter sizes of small mammals invokes the effect of length of season and parental mortality related to reproduction. It may be assumed that a portion of the maternal mortality rate varies directly as the size of litter produced. Short seasons limit the maximum number of times a female can reproduce in her lifetime and give an advantage to phenotypes producing large litters. Long seasons favor producers of small litters. The contribution to the total rate of increase of the litters produced in the additional time afforded by long seasons is greater for producers of small litters because a larger proportion of parents of small litters survive to produce throughout the periods. The increment provided is sufficient to overcome the initial advantage of parents producing large numbers of young in their first litters.

Variation in mean litter size related to latitude and altitude has been reported for several species of small mammals. Lord (1960) analyzed data on several species and concluded there was a regression of litter size on latitude in small nonhibernating prey species. Dunmire (1960) added the dimension of altitude when he reported an increase with elevation of mean litter sizes of deer mice from the White Mountains in California. Mean litter sizes in all cases were larger at northern locations and high elevations than at more southern or lower localities.

Several explanations have been proposed to account for the observed variation. Lord (1960) reviewed and rejected several hypotheses before proposing his own theory that higher mortality rates during northern winters required an increase in reproductive rate. We cannot accept this explanation because it contradicts established principles of population dynamics.

The problem is part of the larger question of regulation of fecundity in all animals. Lack (1948, 1954) has explained the regulation of clutch size and litter size in terms of natural selection. The modal number in his view represents the most consistently successful clutch or litter. Williams (1967) has presented a mathematical refinement of Lack's Principle. According to his concept, an allocation of parental energy between present and residual reproductive values that will maximize the total reproductive value is selectively advantageous. The cost of rearing a large or better nourished brood now is reduction of future reproduction. The litter size prevalent in a particular population represents the best investment possible for the particular situation of the population.

Although Williams did not specifically consider intraspecific latitudinal variation in litter size, our own explanation, developed independently, substantially parallels his general treatment. We believe the shorter seasons of more northern latitudes or higher altitudes limit the number of times an animal resident in those areas is able to reproduce in its lifetime compared to its relatives in lower or more southern regions. It therefore becomes advantageous for an animal to invest its energies in a few, large, early litters even though doing so reduces its life expectancy and total reproductive contribution below the maximum achievable by many small litters. This is so because short seasons make it impossible for the animal to realize the returns from the conservative approach within its life-span. The most productive strategy is the production of large litters. This idea is developed and illustrated below.

Results and Discussion

Our interest in the problem began with the observations recorded in Table 1. *Peromyscus maniculatus* had been collected at several sites in Colorado along a transect extending from the plains of central Weld County to timberline in western Larimer County. The increase in mean potential litter size parallels the experience of Dunmire (1960) in the White Mountains of California. The regression of mean litter size on elevation is of the same order of magnitude as that on latitude as determined by Lord (1960). The data thus illustrate the general nature of the variation.

The major factors influencing the potential rate of increase of a species are the number of female young per female per parturition and the length of the period from birth to first reproduction. However in realistically appraising the number of young per female per litter it is necessary to consider the actual contribution to the next generation represented by that litter (Lack, 1948, 1954). If survival to maturity were a linear function of litter size and decreased 10% for each additional young, then only 2.5 (1.25 females) in a litter of five and only 2.4 (1.2 females) in a litter of six would effectively be contributed on the average to the next generation. If these were the only factors influencing the rate of increase and time to maturation were uniform in the species, then a phenotype producing the greatest effective number (5) would have the highest potential rate of increase and thus the selective advantage.

Reproductive longevity and subsequent reproduction, however, also play a role in determining the rate of increase. Each successive litter contributes an increment to the total reproductive value. The value of each increment declines the later its production occurs in life, but the collective importance of the increments in influencing the rate of increase grows as the margin of difference between the effective numbers of different litter sizes diminish and as the length of the maturational period lengthens (Fisher, 1930; Birch, 1948). This portion of the reproductive value is the major element involved in the phenomenon of latitudinal and altitudinal variations in litter size.

The magnitude of the contribution to the rate of increase by successive litters depends in part on the survival of the parents (Birch, 1948). Bearing and rearing young constitutes a risk for the parent. The presence of the young reduces concealment of parents from, and adds to their vulnerability to, predators. Increased foraging activity also exposes the parents to greater dangers of predation. Physiological stresses such as nutritional deficiencies

TABLE 1.—*Frequency distribution of embryo counts in* Peromyscus maniculatus *from different elevations.*

Site	Number of females	1	2	3	4	5	6	7	8	9	Mean litter size	Mean body length
Plains (5100–5300 ft)												
Coal Creek	10		1	5	3	1						
Pierce	17	1	1	2	9	4						
Cobb Lake	29			2	17	9	1					
Subtotal	56	1	2	9	29	14	1				4.0	95.5 –0.7
Foothills (5500–6500 ft)												
Rist Canyon	22		1	2	8	6	2	3				
Sultzer Gulch	15		1	2	10	2						
Subtotal	37		2	4	18	8	2	3			4.4	95.9 –0.9
Mountains (8000–11,000 ft)												
Buckhorn R. S.	7			1	3	1	1		1			
Pennock Creek	4			1	3							
Cirques	3						1	1	1			
Subtotal	14			2	6	1	2	1	2		5.0	94.2 –2.2
Pingree Park	33	1		1	6	6	11	5	2	1	5.6	
Mountain subtotal	47	1		3	12	7	13	6	4	1	5.4	

and post partum difficulties impair the survival of the parents and damage their capabilities for reproduction in the future. It is reasonable to assume that the effects are proportional to the number of young produced (Lack, 1954, 1948). Such risk is incurred at each successive reproductive event. The greater the risk and the more times repeated, the more the survival rate is lowered and reproduction in later life is curtailed. Less drastic effects than actual death of the parents are probable and perhaps even more important. However the end result is the same and we feel justified in regarding these lesser effects as a form of mortality.

The natural longevity (maximum physical reproductive longevity) of the organism and extrinsic factors such as climate impose an upper limit on the maximum number of opportunities for reproduction (hereafter designated MOR). For example if the season permitted four litters annually and the maximum reproductive longevity of the species were 2 years the MOR would be eight. Only a fraction of any age class would attain the maximum limit MOR. The actual proportion of the population that achieved the maximum would depend upon the mortality rates discussed above, and would be inversely proportional to litter size. It follows, then, that any reduction in the MOR would have a relatively greater effect on the rate of increase of phenotypes producing smaller number of young per litter and having higher survival rate than on phenotypes producing large litters.

This is the line of reasoning that led to our conception of the connection between length of season and variation in litter size. Thus far we have approached the problem strictly from the theoretical aspect by constructing models of the growth of idealized populations. We then studied the consequences for the potential intrinsic rate of increase of reducing the MOR and changing the length of the period of maturation. For simplicity, the relationships of survival of the young to maturity and survival of parents was assumed to be an inverse linear function of litter size. Consideration of available data on guinea pigs (Lack, 1948), *Peromyscus* (McCabe and Blanchard, 1950) and birds and lizards (Lack, 1954) indicated that these may be acceptable approximations. All effects of fecundity on future parental reproduction were combined under the heading of parental mortality. All mortality not related to litter size was ignored. Litter size was assumed to be a constant characteristic throughout the population and independent of age. Only female births were considered. The unit of time was taken to be the minimum interval between successive parturitions and each mature female was assumed to reproduce at each interval. Net reproductive ratios and rates of increase were evaluated by a combination of numerical integration and graphic methods. Lotka (1925), Fisher (1930), and particularly Birch (1948) were the main sources of inspiration and methods used in the computations.

Fig. 1 summarizes the findings of our study. Observe that the size of the litter with the greatest potential rate of increase declines as the MOR increases. The shift reflects the relatively greater increase in the total reproductive value of producers of small litters as the number of late reproductions is allowed to increase. Note also that the shift is rather abrupt and little affected by further increase in MOR. The range of the shift increases as the period of maturation lengthens. Changes in the parameters of survival of parents and young also affect the locus and magnitude of the shift but these effects have not yet been thoroughly explored. Approximations of the variation shown in Table 1 were achieved by substitution into the calculations for curve C (Fig. 1) of the following coefficients. The coefficient of regression for survival of young to maturity on litter size used was –.10 and of survival of parents on litter size was –.016. It of course would be possible to obtain the same approximation by an almost limitless number of combinations, but the important point is that the magnitude of the coefficients required is of plausible order.

The analysis offers an explanation of the observed distribution of latitudinal variation in litter size among mammals considered by Lord (1960). The fossorial and hibernating species investigated (*Spermophilus* and *Thomomys*) usually have one litter annually. Their period of development from birth to first reproduction is about 1 year or 6 months when two litters are produced (Asdell, 1964). The effect of shortening the annual season would thus have little effect on the reproductive opportunities of these organisms. Their patterns of reproduction are approximated by that shown in curve A in Fig. 1.

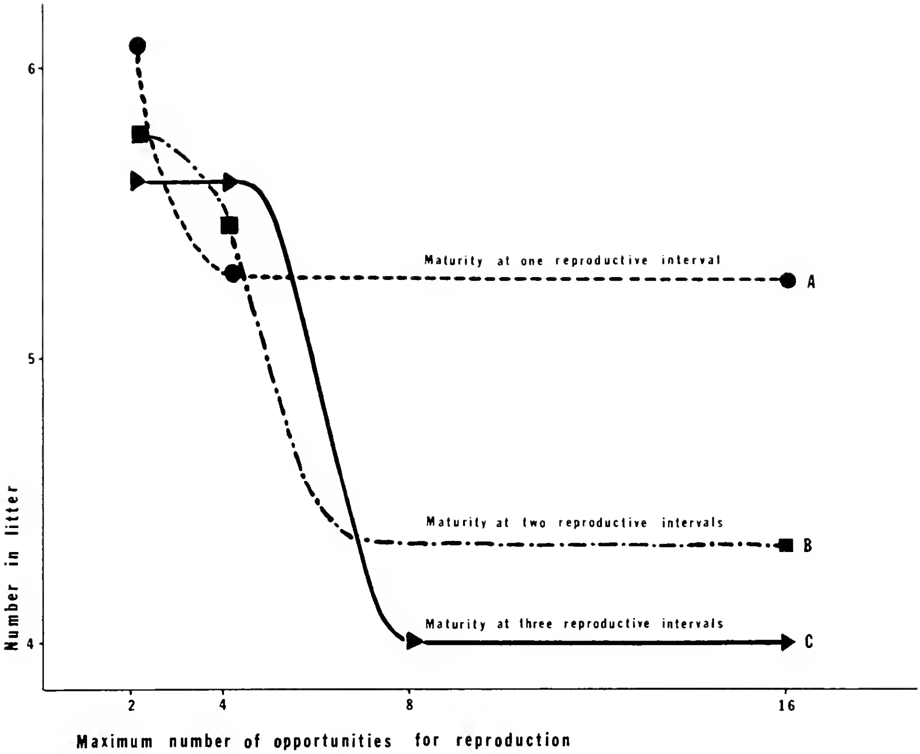

FIG. 1.—Change in the fitness of litter sizes as the maximum number of opportunities for reproduction is increased. The lines connect the litter sizes having the greatest potential rate of increase under the limitations imposed.

Only drastic differences in length of season would produce noticeable effects. Even then the magnitude of variation would be relatively small. On the other hand, the species of mice and shrews that display latitudinal variation can produce several (up to 12) litters annually and yet have a period of development from birth to first reproduction equal to several reproductive intervals. Many shrews begin reproducing at the age of 1 year. The reproductive patterns of these animals correspond to curve C. Effects of significant magnitude could be produced with relatively small changes in the length of the season. In the Colorado data, for example, the growing seasons on the plains (5000 ft) and in subalpine areas (8000–10,000 ft) differ by almost a factor of two.

An interesting aspect of the analysis is that the relative superiority of the favored phenotype is reduced directly as the MOR. Therefore, the genetic variance in the population would be correspondingly reduced. Attainment of maximum fitness in the population should be a long process; in two populations, the one occupying the environment with the shorter season should have the greater variability in litter size after a given period. This would be particularly true if gene flow between them were occurring. This condition is seen in Table 1.

Intraspecific variation may originate in many ways. There is, however, only one agency, natural selection, regularly producing the directed sort of variation we are considering. Lord (1960) has suggested that the increased size of litters may be a compensating response to mortality among the small mammals during winter. However, if a population of a species were able to increase its reproductive potential in this manner, the ability would be just as adaptive in any environment. Variation would quickly disappear. If the variation is to be described in terms of fitness then the particular phenotypes characteristic of each locality must have the greatest fitness in that situation. Our explanation offers an hypothesis explaining how the differential in fitness may originate.

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The effects of suckling on normal and delayed cycles of reproduction in the Red Kangaroo

By G. B. Sharman

Eingang des Ms. 23. 12. 1963

Introduction

In non-lactating female marsupials the occurrence of fertilization, followed by immediate gestation of the embryo, does not delay the onset of the following oestrus. In those marsupials in which the gestation period is considerably shorter than the length of one oestrous cycle, such as *Didelphis virginiana* (Hartman, 1923) and *Trichosurus vulpecula* (Pilton and Sharman, 1962), oestrus recurs at the expected time if the young are removed at birth. In several species of Macropodidae, such as *Setonix brachyurus* (Sharman, 1955), *Potorous tridactylus* (Hughes, 1962) and the Red Kangaroo (Sharman and Calaby, 1964), the gestation period occupies almost the length of one oestrous cycle and oestrus is imminent at the time of parturition. Oestrus thus recurs just after the young reach the pouch (post-partum oestrus) presumably because pro-oestrus changes are initiated before the onset of the suckling stimulus. In all marsupials suckling of young in the pouch is accompanied by a lengthy period during which oestrus does not occur. This period is called the quiescent phase of lactation or, simply, the quiescent phase. It differs from seasonal anoestrus in that the ovaries and other reproductive organs respond to the removal of the suckling stimulus by resuming cyclic functions. Those marsupials in which post-partum oestrus occurs exhibit discontinuous embryonic development analogous to the delayed implantation which occurs in some eutherian mammals. If fertilization takes place at post-partum oestrus the resulting embryo assumes a dormant phase, at the blastocyst stage, and is retained as a dormant blastocyst during the quiescent phase. In these marsupials pregnancy (the interval between copulation at post-partum oestrus and parturition) is long and gestation of the embryo is interrupted by the dormant phase.

In the Red Kangaroo, *Megaleia rufa* (Desm.), the oestrous cycle averages 34 to 35 days and the gestation period is 33 days in length (Sharman and Calaby, 1964). Post-partum oestrus occurs, usually less than 2 days after the newborn young reaches the pouch, and a dormant blastocyst is found in the uterus of females, fertilized at post-partum oestrus, which are suckling young less than 200 days old in the pouch (Sharman, 1963). If the young is removed from the pouch suckling ceases and the dormant blastocyst resumes development: the young derived from it being born about 32 days after removal of the pouch young (RPY). This birth is followed by another post-partum oestrus or, if the female was not carrying a blastocyst, by a normal oestrus. Oestrus recurs at the same number of days after RPY irrespective of whether a delayed blastocyst was carried or not. The sequence of events from RPY to the next oestrus is called the delayed cycle of reproduction[1] to distinguish it from the normal reproductive cycle which follows oestrus. The delayed reproductive cycle may be divided into delayed gestation and delayed oestrus cycle according to whether a dor-

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[1] The term "delayed cycle of reproduction" or "delayed (reproductive) cycle", was introduced by Tyndale-Biscoe (1963) to describe the resumption of ovarian activity, and the features associated with it, following removal of pouch young (RPY).

mant blastocyst does or does not complete development. If the young is retained in the pouch until it leaves in the normal course of events the delayed reproductive cycle occurs coincident with the latter stages of pouch life. The dormant phase of the blastocyst gives way to renewed development when the pouch young is a little over 200 days old and subsequent vacation of the pouch, at an average age of 235 days, is immediately followed by birth of another young (SHARMAN and CALABY, 1964). The young is suckled for another 130 days, that is until it is about a year old, after it leaves the pouch. During this period the normal reproductive cycle occurs if the pouch is not occupied. It is thus evident that, although the delayed reproductive cycle occurs after RPY and cessation af lactation, some factor other than the actual production of milk must be implicated for both delayed and normal cycles may also occur during lactation.

The aim of the experiments reported below was to determine the effect of the suckling stimulus on both normal and delayed reproductive cycles. Additional suckling stimulus was provided by fostering an extra young on to females already suckling a young-at-foot. The experimental approach was suggested by chance observations on a female Red Kangaroo which, while suckling her own young-at-foot, alternately fed the young of another female kept in the same enclosure. There are four teats in the pouch but the teat to which the young attaches after birth alone produces milk and its underlying mammary gland produces all the milk for the young from birth to weaning. The female's own young and the foster-young thus shared the products of a single mammary gland and used the same teat alternately. Some initial results, in so far as they were relevant to the theme of delayed implantation, were reported earlier in a review of that subject (SHARMAN, 1963).

Methods

The results presented consist of observations on a minimum of five reproductive cycles in the female Red Kangaroo in each of the following categories:

1. Normal cycle of reproduction, suckling one young-at-foot.
2. Normal cycle of reproduction, suckling two young-at-foot.
3. Delayed cycle of reproduction, suckling one young-at-foot.
4. Delayed cycle of reproduction, suckling two young-at-foot.

The results are compared with data on the normal and delayed cycles of reproduction in non-lactating females most of which have been published elsewhere (SHARMAN, 1963; SHARMAN and CALABY, 1964; SHARMAN and PILTON, 1964). In most cases the experimental females were pregnant or carrying dormant blastocysts so that cycles of normal or delayed gestation with subsequent post-partum oestrus were studied. The gestation periods and cycles were regarded as having been significantly lengthened when they occupied a time greater by the length of two, or more, standard deviations than similar cycles in control, non-lactating, females

Some difficulty was experienced in getting females to accept foster-young and only six females readily did so. The experiments were therefore done serially one female being used in two and two females in three experiments.

The animals were watched from a hide overlooking the enclosures and observed with binoculars. An initial watch was always done to find whether females accepted their potential foster-young. Thereafter prolonged watches were kept on some females to determine the amount of time spent suckling the young-at-foot.

Vaginal smears for the detection of oestrus and copulation were taken as reported previously (SHARMAN and CALABY, 1964).

Results

Effects of suckling on the normal cycle of reproduction

In thirteen non-lactating female Red Kangaroos forty-two intervals from oestrus to the succeeding oestrus averaged 34.64 days with a standard deviation of 2.22 days (34.64 ± 2.22 days). Twenty gestation periods in fourteen females lasted 33.00 ± 0.32 days (Fig. 1A). In five females, each observed for a single reproductive cycle while suckling one young-at-foot, the intervals between two successive oestrous periods were not different from those in non-lactating females (Fig. 1B). In another female (K32a) the gestation period was not significantly different from that of control females but oestrus did not occur until 5 days post-partum. This was the longest interval between parturition and post-partum oestrus recorded but it is not regarded as significant. Two cycles in female K31, one lasting 41 days and one 47 days, were abnormally long. The 41-day cycle is of special significance since the interval between copulation and birth was 40 days. This differs so much from the gestation period in the control, non-lactating, females that it must be assumed that suckling of the single young-at-foot induced a short quiescent phase in the uterus accompanied by a dormant phase of about 7 days in the embryo. The 47-day cycle was over 12 days longer than the mean normal cycle length and 7 days longer than the maximum cycle length. The female copulated at oestrus but did not give birth so it is presumed that fertilization did not occur.

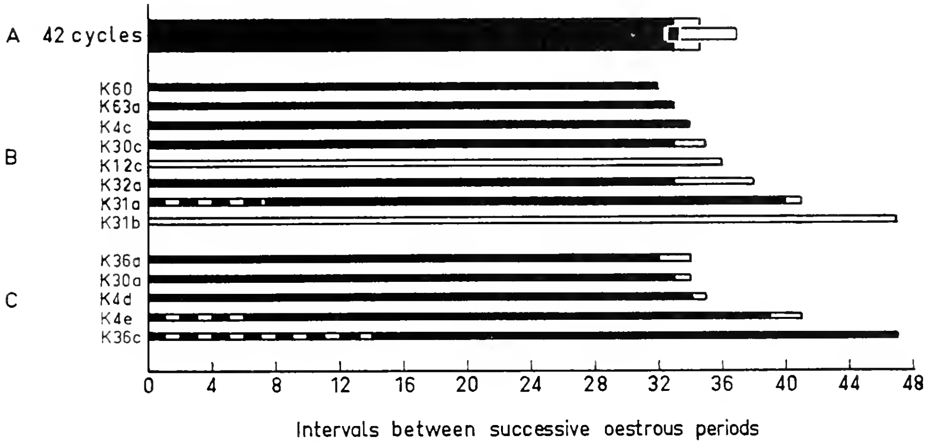

Fig. 1. Intervals between successive oestrous periods in nonlactating (control) female Red Kangaroos (A), females suckling one young-at-foot (B) and females suckling two young-at-foot (C). Black lines — continuous embryonic development, broken lines — approximate periods of dormant phase in embryo induced and maintained by suckling young-at-foot, open lines — no embryos present, bars inserted in A — standard deviations either side of mean.

In three females already suckling one young-at-foot, which had another young-at-foot fostered on to them at about the time of fertilization, the lengths of the reproductive cycles were not significantly different from those in control females. Two females had significantly longer cycles than in control females. One of these (K36) was used in three successive experiments while suckling the same two young-at-foot. In the first of these (K36a) the extra suckling stimulus had no significant effect on the length of the reproductive cycle. The second experiment concerned the delayed reproductive cycle and is reported below. During the third experiment (K36c) the young were being weaned but a highly significant result was obtained. The interval from copulation to birth showed conclusively that a dormant phase had been induced and maintained in the embryo for about 14 days of the 47-day pregnancy. In the other female in which the cycle was prolonged (K4e) the embryo presumably had a dormant phase of about 6 days.

Effects of suckling on the delayed cycle of reproduction

In ten non-lactating females thirteen intervals from RPY to the succeeding oestrus were 34.46 ± 1.92 days. In seven of these females the delayed gestation period was 31.64 ± 0.65 days (Fig. 2A). There was no evidence that suckling one young-at-foot had any effect on the length of the delayed reproductive cycle (Fig. 2B). In one female (K12a) the interval from RPY to the following oestrus was 38 days but this falls short of the minimum interval accepted as significantly different.

All six females suckling two young-at-foot (Fig. 2C) were carrying a dormant blastocyst in the uterus when the pouch young were removed. In five of these the interval RPY to birth was significantly longer than in control females (Fig. 2C). The interval RPY to the next oestrus was longer than the mean for control non-lactating females in all six experimental females and in three of them (K4b, K30b, K36b) the difference from controls was highly significant. It must be concluded that the blastocysts of five of the above experimental females remained in the dormant phase for between 3 and 22 days longer after RPY than did those of control non-lactating females and females suckling one young-at-foot.

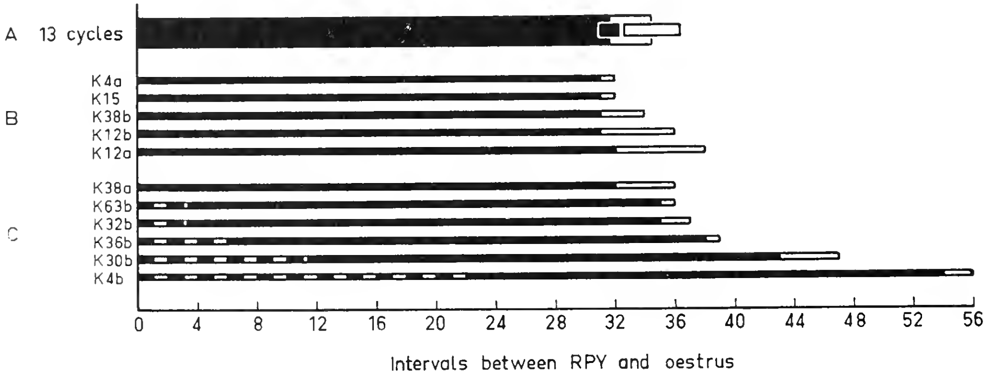

Fig. 2. Intervals between removal of pouch young (RPY) and the next oestrus in non-lactating (control) female Red Kangaroos (A), females suckling one young-at-foot (B) and females suckling two young-at-foot (C). Black lines — continuous embryonic development, broken lines — approximate periods of continued dormant phase of embryo maintained by suckling young-at-foot, bars inserted in A — standard deviations either side of mean.

The amount suckling in relation to occurrence of parturition and return to oestrus

Observations on the habits of the pouch young suggested that the stimulus causing withholding of the mother's reproductive cycles might be tactile and received via the teat. The young during the early stages of pouch life, when reproductive cycles were withheld, were suckled continuously and could not regain the teat if removed before the age of 6 weeks. Later young were able to take the teat back into their mouths but were seldom found free of the teat before the age of about 5 months. On the other

Table 1

Effects of suckling one and two young-at-foot on subsequent parturition and oestrus in Red Kangaroos

No. of female	Ages of joung (days)		No. of hours observed	Minutes of suckling			Type of cycle	Effects of suckling on subsequent parturition and oestrus	
	Own young	Foster-young		Own young	Foster-young	Per day		Occurrence of parturition	Occurrence of oestrus
K 60	255	—	13,5	44	—	78	normal	when expected	when expected
K 31 (a)	255	—	15,5	31	—	48	normal	late	late
K 31 (b)	269	—	96	203	—	51	normal	no young born	late
K 30 (c)	288	—	13,5	38	—	68	normal	when expected	when expected
All females suckling 1 young			138,5	316	—	53			
K 4 (e)	259	245	22,5	86	55	150	normal	late	late
K 63 (b)	309	309	15.5	27	31	90	delayed	late	when expected
K 36 (b)	322	315	78	192	83	85	delayed	late	late
All females suckling 2 young			116	305	169	98			

hand the pouch young present when the delayed reproductive cycle occurred apparently frequently released the teat as they were seen protruding their heads from the pouch to feed from the ground or leaving the pouch entirely (Sharman and Calaby, 1964).

Theoretically it was to be expected that if reproductive cycles resumed in response to a lowered suckling stimulus, as they did during the terminal stages of pouch feeding, then the cycles which occurred as soon as the young left the pouch should have been of normal length. Six of the eight cycles shown in Fig. 1 B were the first which occurred after termination of pouch feeding. Four were of normal length but two cycles in one female (K 31 a, b) were lengthened by a significant amount. Observations on the habits of the young, just after they left the pouch permanently, showed that they frequently attempted to regain the pouch but were restrained from doing so by their mothers (Sharman and Calaby, 1964). In these cases they spent long periods with their heads in the pouch during which time they may have grasped the teat. It is also possible that the young, subjected permanently for the first time to the cooler environment outside the pouch, fed more frequently than they did during the terminal stages of pouch life. This would result in a greater suckling stimulus being exerted: at least during the initial stages of life outside the pouch.

A number of females suckling one or two young-at-foot were watched continuously for varying periods and the amounts of time spent suckling were recorded (Table 1). It was at once apparent that females feeding two young-at-foot spent nearly twice as much time suckling as did females with a single young-at-foot. The relationship between amount of suckling and interruption or resumption of the reproductive cycle is, however, not so obvious. Thus, in female K31, 48 and 51 minutes of suckling per day were associated with lengthening of the interval between successive oestrous periods and 48 minutes per day with inducing and maintaining a short dormant phase in the embryo. In two other females (K60, K30c) a greater amount of suckling apparently had no effect on the length of the cycle or on pregnancy. However, although the watches were done during the relevant cycles, they were not necessarily done at the critical period of the cycle when the suckling stimulus exerted its effect. This period could not be ascertained since no evidence of its occurrence was available until the females gave birth or returned to oestrus. The figures in Table 1 are thus to be regarded as no more than a guide to the amount of suckling which occurred at the critical period.

The most conclusive evidence about the effect of the suckling stimulus on the reproductive cycle came from the females from which pouch young were removed while they were suckling two young-at-foot (Fig. 2C). In one of these females (K38a) the suckling of two young-at-foot was without effect on the delayed reproductive cycle; in three (K32b, K36b, K63b) the delayed cycle began while two young were being suckled but in two others (K4b, K30b) the delayed cycle was only initiated when one of the suckling young-at-foot was removed. The interval from removal of the young-at-foot to completion of the delayed cycle was approximately the same (31—32 days) as from RPY to the completion of the cycle in the control females.

The two intervals between successive oestrous periods with intervening pregnancies which were observed in the same female (K36a, c) while suckling the same two young-at-foot call for some comment. Parturition and return to oestrus occurred when expected in the first cycle but were delayed significantly in a subsequent cycle when the young were much older and were being weaned (Fig. 1C). During this, latter, cycle one of the young frequently grasped the teat for periods of 10 minutes or more but when the female's pouch was examined it was found that no milk could be expressed from the teat and that the mammary gland was regressing. This was in contrast to the condition in other females suckling young-at-foot in which milk could usually be readily expressed. No watch was done to observe the amount of time the young spent sucking the dry teat as the significance of the observation was only realised after completion of the cycle. This cycle is, however, of particular significance because it appears likely that the suckling stimulus, in the absence of lactation, induced a quiescent phase in the uterus lasting some 14 days and a corresponding period of dormancy in the blastocyst.

Discussion

Delayed implantation in the Red Kangaroo is of the type usually referred to as lactation controlled delayed implantation. This description is adequate in so far as the delayed cycle of reproduction is initiated following removal of the pouch young and cessation of lactation. However, the delayed cycle also occurs during the seventh and eighth months of the 12-month lactation period. It therefore follows that, in these cases, the delayed cycle does not begin in response to the cessation of lactation or to the imminent cessation of lactation. The quiescent phase of lactation with associated arrested development of the embryo is initiated during the early part of lactation while a small young is suckled continuously in the pouch but the normal reproductive cycle may, as has been shown above, occur during the latter part of lactation. It is thus much more likely that the amount of suckling stimulus which the female receives at various phases of the lactation period is of paramount importance in determining whether the normal reproductive cycle shall be interrupted or whether the delayed cycle shall be initiated. The experiments reported above have shown that in some females the normal cycle is interrupted and a quiescent phase of lactation, with associated dormant phase of the embryo is induced by increasing the suckling stimulus. It has also been shown that the stimulus of suckling of young, outside the pouch, is capable of prolonging the quiescent phase of lactation and dormant phase of the embryo.

Two other factors could be of importance in determining the time of onset of the delayed cycle of reproduction: 1. Temporary or permanent vacation of the pouch. 2. Fall in milk yield. Temporary emergence from the pouch first occurs when the young are less than 190 days old and permanent emergence at the average age of 235 days — that is a few days before the completion of the delayed cycle (SHARMAN and CALABY, 1964) but the delayed cycle apparently begins when the young are a little over 200 days old. Precise data on this point are difficult to obtain but assuming that the delayed cycle, once initiated, proceeds at the same rate in lactating females as it does in females from which the pouch young are removed then it must begin about 30 days before the young leaves the pouch. This is in agreement with the massive amount of data obtained from Red Kangaroos taken in the field. The onset of the delayed cycle can hardly occur in response to a fall in milk yield since it takes place when the young is actively growing and when it is increasing rapidly in weight. From the age of 200 days to the age of 220 days, during which period the delayed cycle is resumed, the pouch young increase from about 2.5 to 3.5 kg in weight which is not the expected result of a fall in milk yield. Furthermore removal of young from the pouches of females which were suckling two young-at-foot must have been accompanied by a fall in milk yield yet under these circumstances the quiescent phase of lactation with associated dormant blastocyst continued in five of six females (Fig. 2C).

The importance of the suckling stimulus in marsupial reproduction was demonstrated by SHARMAN (1962) and SHARMAN and CALABY (1964) who transferred newborn young *Trichosurus vulpecula* and *Megaleia rufa* to the pouches or teats of non-lactating, non-mated or virgin females of each of these species at the appropriate number of days after oestrus. The suckling stimulus exerted by the young induced the onset of lactation without the prior occurrence of pregnancy and oestrous cycles were withheld while the foster-young were suckled in the pouch. SHARMAN and CALABY (1964) were unable to demonstrate any behavioural differences between pregnant and non-mated female Red Kangaroos at the same number of days after oestrus except that pregnant females repeatedly cleaned their pouches just before giving birth. Other authors (HILL and O'DONOGHUE, 1913; HARTMAN, 1923; SHARMAN, 1955; PILTON and SHARMAN, 1962) have drawn attention to the remarkable resemblances of post-oestrous changes in pregnant females to those of non-mated females in various species of marsupials. It is apparent, that whereas in polyoestrous eutherian mammals hormones produced by the embryonic membranes modify the reproductive cycle and prevent the recurrence of oestrus during pregnancy, no such mechanism has yet been demonstrated in any marsupial. In those marsupials which do not have a seasonal anoestrous period, such as the Red Kangaroo, the reproductive cycle is continuous except when interrupted by the quiescent phase of lactation.

OWEN (1839—47) determined the gestation period (interval from mating to birth) of a lactating female Great Grey Kangaroo as 38—39 days. Hediger (1958) stated that K. H. Winkelsträter and E. Cristen in Zurich Zoo found gestation periods of 30 and 46 days in the same species and later, in the same paper, stated that a young was born on the forty-sixth day after mating in a lactating female Great Grey Kangaroo. However the dates quoted by Hediger show that the „gestation period" was actually 57 days. In non-lactating Great Grey Kangaroos Miss Phyllis Pilton (pers. comm.) found the gestation period was about 30 days and in the C.S.I.R.O. Division of Wildlife Research four gestation periods in three non-lactating females were 33 days 6 hours to 34 days 6 hours, 33 days 18 hours to 34 days 10 hours, 34 days to 34 days 17 hours and 34 days to 34 days 20 hours. It is apparent that, although the Great Grey Kangaroo does not have the same type of lactation controlled delayed implantation as occurs in the Red Kangaroo and other marsupials (Sharman, 1963), intervals between mating and birth in lactating females may be an unreliable guide to the gestation period. Hediger (1958) stated that exact gestation periods in kangaroos and other marsupials are difficult to determine because ovulation occurs several days after mating and spermatozoa can remain active in the oviduct for long periods. This may be true of the marsupial *Dasyurus viverrinus*, but Hill and O'Donoghue's (1913) work on this species has not been repeated and confirmed. Delayed ovulation and storage of spermatozoa do not occur in *Didelphis* (Hartman, 1923), *Setonix* (Sharman, 1955) or *Trichosurus* (Pilton and Sharman, 1962) and gestation periods in non-lactating females of these species can be determined with considerable accuracy. In the Red Kangaroo the intervals between mating and birth in some lactating females (Table 2) are not true gestation periods since they include a period of arrested development of the embryo. However, in thirteen non-lactating female Red Kangaroos one gestation period was 32 days, one was 34 days and eighteen were 33 days in length (Sharman and Calaby, 1964). The true gestation period, as in the species above, can therefore be determined with precision.

Table 2

Intervals from mating to birth and intervals from removal of pouch young (RPY) to birth in seven female Red Kangaroos subjected to different levels of suckling stimulus

No. of female	K 4	K 30	K 31	K 32	K 36	K 38	K 63
	Intervals from mating to birth						
Non-suckling	33	—	—	33	—	—	33
Suckling 1 young	34	33	40	33	—	—	33
Suckling 2 young	34,39	33	—	—	32,47	—	—
	Intervals from RPY to birth						
Non-suckling	32	32	—	—	—	32	—
Suckling 1 young	31	—	—	—	—	31	—
Suckling 2 young	54	43	—	35	38	32	35

Perhaps failure to recognise the importance of the suckling stimulus accounts for the inaccuracy of some of the marsupial gestation periods given in International Zoo Year Book Vol. 1 (Jarvis and Morris, 1959). The list is incomplete and at least half of the figures given are wrong.

The occurrence of lactation controlled delayed implantation in marsupials was reported in 1954 (Sharman, 1954) and numerous papers have since appeared indicating that it is of widespread occurrence among kangaroo-like marsupials. Records of birth in captive female marsupials after long isolation from males, such as those reported by Carson (1912) in the Red Kangaroo and, recently, by Hediger (1958) in Bennett's Wallaby, are readily explained in terms of the occurrence of delayed implantation.

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Summary

In non-lactating female Red Kangaroos the oestrous cycle lasted about 35 days and the gestation period was about 33 days. Gestation did not interrupt the oestrous cycle. Postpartum oestrus, at which copulation and fertilization took place if the female was with a male, occurred just after parturition. Recurring reproductive cycles were replaced by the quiescent phase of lactation for up to about 200 days while the young were suckled in the pouch. If fertilization occurred at postpartum oestrus a dormant blastocyst was carried in the uterus during the quiescent phase of lactation. The delayed cycle of reproduction during which the hitherto dormant blastocyst, if present, completed development occurred following removal of young less than 200 days old from the pouch. If the young were retained in the pouch until they emerged in the normal course of events the delayed cycle of reproduction occurred coincident with the last month of pouch life and was completed a day or two after the young permanently left the pouch. Suckling of the young occupied one year: they were suckled for about 235 days in the pouch and for a further 130 days after leaving the pouch. The delayed cycle of reproduction could thus occur during, and long before the cessation of, lactation. Normal cycles of reproduction occurred during lactation if the pouch was not occupied.

The lengths of normal and delayed cycles of reproduction in females suckling one and two young-at-foot were compared with those in control, non-lactating, females. The results were as follows:

Normal cycle of reproduction

Females suckling one young-at-foot. Six cycles not significantly different from those of controls; two cycles significantly longer than in controls in one of which a dormant phase of about 7 days occurred in the embryo. Total: 8 cycles.

Females suckling two young-at-foot. Three cycles not significantly different from those of control females: two cycles significantly longer than in control females which included dormant periods of 6 and 14 days in the embryos. Total: 5 cycles.

Delayed cycle of reproduction

Females suckling one young-at-foot. No effect of suckling. Total: 5 cycles.

Females suckling two young-at-foot. One cycle not significantly different from those of control females. Five cycles longer than those of control females in which the dormant periods of the blastocysts were extended by 3, 3, 6, 11 and 22 days. In the two latter cycles resumption of development of the dormant blastocysts did not occur until removal of one of the suckling young-at-foot. Total: 6 cycles.

Observations showed that females with two young-at-foot suckled their young for about twice the length of time that females suckled a single young-at-foot. It was concluded that the suckling stimulus exerted by one or two young-at-foot could induce and maintain the quiescent phase of lactation and the associated dormant phase in the embryo. Available evidence suggested that the stimulus causing onset of the quiescent phase was tactile and received via the teat and that the delayed cycle of reproduction occurred, or the interrupted normal cycle was resumed, when the suckling stimulus was lessened.

It is suggested that some published gestation periods of marsupials owe their error to the failure of observers to appreciate the significance of concurrent suckling. Reported cases of female marsupials giving birth after long isolation from males can readily be explained as due to the occurrence of the delayed cycle of reproduction.

Zusammenfassung

Bei nichtsäugenden ♀♀ des Roten Riesenkänguruhs dauert der Oestrus-Cyclus rund 35 Tage, die Trächtigkeit rund 33 Tage. Trächtigkeit unterbricht den Cyclus nicht. Postpartum-Oestrus, bei dem Begattung und Befruchtung stattfanden, erfolgten unmittelbar nach der Geburt. Wiederkehr des Oestrus wurde durch eine Latenz während der Laktation bis zu 200 Tagen verhindert, während welcher das Junge im Beutel gesäugt wurde. Wenn beim Postpartum-Oestrus Befruchtung erfolgt war, enthält der Uterus während dieser Latenzperiode eine ruhende Blastocyste. Der verzögerte Cyclus der Fortpflanzung, während der die bisher ruhende Blastocyste (wenn sie vorhanden ist) ihre Entwicklung vollendet, tritt auf, wenn das Junge früher als 200 Tage nach der Geburt aus dem Beutel entfernt wird. Wenn die Jungen jedoch so lange im Beutel bleiben, bis sie ihn normalerweise verlassen hätten, fällt der verzögerte Cyclus der Fortpflanzung mit dem letzten Monat des Beutellebens zusammen und ist vollendet ein oder zwei Tage nachdem die Jungen den Beutel endgültig verlassen haben. Das Säugen dauert ein volles Jahr: die Jungen werden rund 235 Tage lang im Beutel und noch weitere 130 Tage bei Fuß gesäugt.

Der verzögerte Cyclus der Fortpflanzung kann also während und auch lange vor Beendigung der Laktation auftreten. Normaler Cyclus der Fortpflanzung tritt auf, wenn kein Junges im Beutel ist. Die Länge von normalen und verzögerten Cyclen der Fortpflanzung bei säugenden ♀♀ mit einem bzw. zwei Jungen bei Fuß wurde mit solchen bei nicht säugenden Kontroll-♀♀ verglichen. Die Ergebnisse waren:

Normaler Cyclus der Fortpflanzung

bei ♀♀, die 1 Junges bei Fuß säugten: 6 Cyclen waren nicht besonders verschieden von den Kontroll-♀♀. Zwei Cyclen waren bedeutend länger; bei einem davon machte der Embryo eine Ruhepause von etwa 7 Tagen durch. Im ganzen 8 Cyclen.

Bei ♀♀, die 2 Junge bei Fuß säugten: 3 Cyclen nicht besonders verschieden von den Kontroll-♀♀; 2 Cyclen bedeutend länger als bei den Kontroll-♀♀ mit Ruheperioden des Embryos von 6 und 14 Tagen. Im ganzen 5 Cyclen.

Verzögerter Cyclus der Fortpflanzung

bei ♀♀, die ein Junges bei Fuß säugten, ergab sich kein Einfluß des Säugens. Im ganzen 5 Cyclen.

Bei ♀♀, die 2 Junge bei Fuß säugten, war 1 Cyclus nicht sehr verschieden von den Kontroll-♀♀. 5 Cyclen waren länger als bei den Kontroll-♀♀, bei denen die Ruhezeit der Blastocyste resp. 3, 3, 6, 11 und 22 Tage betrug. In letzteren beiden setzte die Weiterentwicklung nicht ein, bevor nicht eines der Jungen weggenommen wurde. Im ganzen 6 Cyclen.

Die Beobachtungen zeigten, daß ♀♀ mit 2 Jungen bei Fuß ihre Jungen doppelt so lange säugen, wie sie ein einziges gesäugt haben würden. Daraus wurde geschlossen, daß der Sauge-Stimulus, von einem oder zwei Jungen bei Fuß ausgelöst, sowohl die Ruhephase während der Laktation, als auch die damit gleichlaufende Ruhephase des Embryos einleitet und erhält. Die bisherige Erfahrung läßt annehmen, daß der Stimulus, der den Beginn der Ruhephase bewirkt, tactil ist und über die Zitze empfangen wird, und daß der verzögerte Cyclus der Fortpflanzung auftritt, oder der unterbrochene normale Cyclus wieder aufgenommen wird, wenn der Saugereiz sich vermindert.

Einige von anderer Seite veröffentlichte Daten über Trächtigkeitsdauern von Beuteltieren enthalten offenbar Fehler, da die betreffenden Autoren die Bedeutung gleichlaufenden Säugens nicht beachteten. Mitgeteilte Fälle, daß ♀ Beuteltiere auch nach langer Isolierung vom ♂ warfen, kann ohne weiteres durch das Auftreten des verzögerten Fortpflanzungs-Cyclus erklärt werden.

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REPRODUCTION AND GROWTH IN MAINE FISHERS[1]

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Abstract: New data concerning reproduction, aging techniques, and growth of fishers (*Martes pennanti*) were obtained from 204 specimens taken from October to April during 1950–64. All female fishers more than 1 year old were pregnant. The immature class consisted of juveniles in their first year. The period of delayed implantation lasted from early spring until mid- or late winter. Nine adult females taken in January, February, or March showed implanted embryos. Fishers in active pregnancy had corpora lutea 7 times the volume of those in the period of delay. Most litters are born in March, but some as early as late February and some in early April. Counts of corpora lutea of 54 animals taken during the period of delay and during active pregnancy averaged 3.35 per female. The number of embryos, either unimplanted or implanted, corresponded exactly with the number of corpora lutea in 18 of 21 animals. Two recently impregnated 1-year-old females, recognizable from cranial characters, had tubal morulae, confirming that females breed for the first time when 1 year old. Also confirmed are previous findings of Eadie and Hamilton that juvenile females can be distinguished from adults by open sutures in the skull throughout their first year. Juvenile males can be recognized in early fall by open sutures in the skull, absence of sagittal crest, immature appearance and lighter weight of bacula, unfused epiphyses in the long bones, and small body size. The sagittal crest begins to develop in December and often is well developed by March. The baculum grows slowly during the early winter, but by February there was some overlap with weights of adult bacula. Male fishers showed active spermatogenesis at 1 year. Open sutures were found in juvenile male skulls throughout the first year. Pelvic girdles of juveniles were distinguished by an open pubo-ischiac symphysis; adults of both sexes showed the two innominates fused into a single bone resulting from at least a partial obliteration of the symphysis. Mean body weights of animals weighed whole in the laboratory were as follows: adult males, 10 lb 12 oz; juvenile males, 8 lb 7½ oz; adult females 5 lb 8 oz; juvenile females, 4 lb 11 oz.

After reaching an all-time low during the early part of the century, the fisher has made a remarkable recovery during the past 25 or 30 years in Maine (Coulter 1960) and in New York State (Hamilton and Cook 1955). The increase in abundance of this high quality furbearer in New York to the point that it could be legally trapped allowed Hamilton and Cook (1955) and later Eadie and Hamilton (1958) to discover significant facts from studying carcasses obtained from trappers.

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In Maine, the season was reopened in 1950, permitting collection of data and material from fishers trapped there. The purpose of the present paper is to present new information about reproduction, age determination, and growth of fishers, derived from study of Maine animals obtained between 1950 and 1964.

More than a dozen biologists and many wardens of the Maine Department of Inland Fisheries and Game collected material from trappers. Special thanks are due to Myron Smart, Biology Aide, who assisted in numerous ways throughout the entire study, and to Maynard Marsh, Chief Warden, who made arrangements for confiscated specimens to be processed at the Maine Unit. Numerous graduate assistants at the Maine Unit helped with processing carcasses and the preparation of skulls and bacula. We are indebted to Howard L. Mendall for editorial assistance and to Virginia Vincent and Alden Wright who made the statistical calculations. Margaret H. Wright did the microtechnique work. Elsie H. Froeschner made the drawings. Some of these findings were summarized in an unpublished Ph.D. dissertation presented by Coulter at the State University College of Forestry at Syracuse University.

FINDINGS OF PREVIOUS WORKERS

Hall (1942:147) published data from fur farmers in British Columbia showing that the gestation period in captive fishers ranges from 338 to 358 days and that copulation normally takes place about a week after the young are born. Enders and Pearson (1943) described the blastocyst of the fisher from sectioned uteri of trapper-caught animals and showed that the long gestation period is due to delayed implantation. It was assumed that the blastocysts remain inactive from spring until sometime during winter. De Vos (1952) studied fishers in Ontario and made preliminary attempts to establish an aging method based upon skulls of males and females and the bacula of males. Hamilton and Cook (1955) published information about the current status of fishers in New York State and described a technique for recovering the unimplanted blastocysts from fresh reproductive tracts by flushing them out with a syringe. Eadie and Hamilton (1958) provided additional data on the numbers of blastocysts in pregnant tracts and described cranial differences between adult and immature females.

MATERIALS AND METHODS

Coulter collected material in Maine from trapped fishers, starting in 1950 when the season was first reopened. The intensity of the collection varied over the years depending upon the legal regulations in effect. Data are available from 204 animals.

In addition to animals legally taken during the trapping season, Coulter obtained a number of animals both before and after the season, taken by trappers who were trapping other species, primarily bears and bobcats. Trappers who caught fishers accidentally were required to turn them over to the Department of Inland Fisheries and Game which in turn brought or sent them to the Maine Unit at Orono where they were autopsied by Coulter. Unskinned fishers as well as skinned carcasses were submitted to the laboratory. Whenever possible, weights were taken immediately before and after skinning to obtain an index for converting the weights of carcasses received from trappers to whole weights. During the trapping season carcasses were collected at trappers' homes. Usually the material was submitted in fresh condition; often it was frozen or thoroughly chilled when received at the laboratory. Because of the interest of the cooperators, most of the material was accompanied by collection dates, method of capture, locality, and other notes. These data together with measurements, weights, observations about the condition and completeness of the specimens, and a record of material saved for future study were entered on individual cards for each animal.

A special effort was made from the fall of 1955 to the spring of 1958 to obtain complete skeletons, and 59 such specimens were obtained. Coulter trapped a series of especially needed animals in late March and early April, 1957. Because of excellent cooperation by State Game Wardens and Regional Biologists, a good sample of specimens was available for study over a 6-month period from October to April.

This series of fishers is an unusually valuable one for discerning important aspects of the growth and the reproductive cycle of this mustelid. For example, nine females in active pregnancy were obtained, as well as several adult males in full spermatogenesis. Furthermore, the juvenile fishers were growing and maturing rapidly during the collecting period, and this fairly large collection has allowed us to reach significant conclusions concerning the onset of sexual maturity and the distinction between the age classes with more assurance than de Vos (1952) was able to do with more limited material.

The reproductive tracts of female fishers were removed in the laboratory and preserved in 10-percent formalin, in AFA, or in special cases, Bouin's fluid. The bacula of all the males were air-dried, as were the skulls of both sexes. Testes from a few representative males were fixed in formalin also. Coulter solicited the cooperation of Wright in 1955 and all of the material then available was shipped to him for further analysis and for histological work. Most of the skeletal material was cleaned by dermestid beetles in Montana.

This study was carried out without the aid of known-age specimens. Since the study was completed, three known-age animals have become available: an 18-month-old female in Maine which was in captivity for 1 year, and two females captured in central British Columbia, released in western Montana, and recaptured 6 years later. Study of these three animals in no way affects the findings presented in this paper. Evidence is presented to indicate that young-of-the-year animals can be distinguished from adults by studying either their skulls and skeletons or their reproductive tracts. Animals judged by these criteria to be less than 1 year old are, for convenience, referred to as juveniles even though in a few cases they may be almost 1 year old. Except for one criterion for distinguishing yearling females from older adult females, described by Eadie and Hamilton (1958:79–81) and confirmed here, no method of determining the relative ages of adults was discovered.

Wherever appropriate, standard deviations and standard errors have been calculated, but generally such figures are not presented here. When it is stated that a significant or highly significant difference exists, it is based upon the use of the *t* test.

FINDINGS

Female Reproductive Tracts

The reproductive tract of the female fisher is similar to that of other mustelids. The ovaries are completely encapsulated with only a small ostium through which a small portion of the fimbria extends. The ovary must be cut free from the bursa under a dissecting scope with a pair of fine scissors. The oviduct encircles the ovary as in other mustelids. The oviducts were not highly enlarged in any animals studied, since no estrous stages were seen. The uterus has a common corpus uteri which allows embryos developing in one horn to migrate to the other horn. The uterine horns are 40–60 mm long in adult females in inactive pregnancy, and 2½–4 mm in diameter. Immature fishers show smaller uteri with horns about 30–40 mm long and 1½–2½ mm in diameter. No search was made for an os clitoridis.

The ovaries from each preserved tract were dissected from the fixed reproductive tract, blotted, and weighed. Each ovary from animals taken in fall or early winter was sliced macroscopically and the number of corpora lutea present determined by the use of a dissecting microscope. Of the 77 tracts handled in this way, 44 animals showed corpora and were thus judged to be adults. Thirty-three animals were without corpora and were judged to be immature. The average combined weights of the ovaries was 134.4 mg for adults and 76.5 mg for immatures. The average weight of the left ovaries (I—40.3 mg, A—70.0 mg) was greater than that of the right ovaries (I—36.2 mg, A—64.4 mg) in both immatures and adults, but no special significance is ascribed to this matter. The average number of corpora lutea from this series of 44 adult females was 1.68 in the right ovaries and 1.60 in the left; the average was 3.28 per adult female. Eadie and Hamilton (1958) reported that the mean number of corpora lutea in 23 adult New York fishers was 2.72. The difference in the average number of corpora lutea between the Maine and New York samples is highly significant. The distribution of the corpora lutea from all of the Maine, pregnant animals is shown in Table 1.

Table 1. Distribution of corpora lutea in ovaries of pregnant Maine fishers.

NO. OF CORPORA IN SINGLE OVARIES	NO. OF CASES	NO. OF CORPORA IN BOTH OVARIES OF INDIVIDUAL FEMALES	NO. OF FEMALES
4	2	5	1
3	14	4	21
2	42	3	30
1	43	2	2
0	8		—
	—		54
Total	109*		

* One case in which only one ovary available.

To determine the relationship between the number of corpora lutea in the ovaries and the number of blastocysts in the uteri, 11 tracts of adult females were studied in detail. After the ovaries were removed and sectioned by hand, uteri were selected that appeared to be the best preserved. These entire uteri were dehydrated and cleared in wintergreen oil. Study of the entire cleared tract under a dissecting scope using transmitted light often revealed the location of blastocysts. Serial sections of each of these tracts were made to locate the blastocysts. As soon as all of the expected blastocysts were found, no further sectioning of that tract was done. In some cases the entire uterus was sectioned before all the blastocysts could be located, and in 2 of the 11 tracts, 1 potential blastocyst was not found. This represents a loss of only 6 percent, as there were 35 corpora in the ovaries of the 11 animals and 33 blastocysts were located. The technique of Hamilton and Cook (1955:30–31) of flushing the uteri for the blastocysts was not followed here since the tracts had been fixed in formalin.

The sectioned blastocysts were similar to those described by Enders and Pearson (1943:286). The extremely thick zona pellucida, 14.4 μ according to these authors, makes it possible to find the blastocysts in very poorly preserved material. None of the blastocysts studied was in better condition than those seen by Enders and Pearson, and the relative numbers of nuclei in the trophoblast and the inner cell mass for this species is still not known. In order to ob-

Table 2. Findings in nine reproductive tracts of female fishers in active pregnancy.

Date Killed	Weight of Ovaries (mg)		Distribution of Corpora Lutea		State of Uterus
	Right	Left	Right	Left	
January, 1965	—	—	–	–	3 embryos, 18 mm CR (Crown–Rump)
February 2, 1961	118	77	3	1	4 embryos, 2R, 2L, 17-mm swellings, embryo 8 mm CR
February 7, 1956	182	98	3	0	3 embryos, 1R, 2L, embryo 13 mm CR
February 21, 1964	110	73	2	1	3 embryos, 2R, 1L, embryo 18 mm CR
Late February, 1959	98	108	1	3	4 embryos, 2R, 2L, embryo 8 mm CR
March 3, 1959	179	138	3	1	4 fetuses, 2R, 2L, 2 males, 2 females, fetuses 53, 54, 55, 57 mm CR
March 11, 1965	—	—	2	1	3 fetuses, 2R, 1L, 3 males, fetuses 69, 71, 74 mm CR
March 13, 1956	92	92	2	1	3 early embryos, 2R, 1L, 7-mm swellings
March 20, 1957	121	137	1	2	3 fetuses, 2R, 1L, 3 females, fetuses 74, 80, 83 mm CR

tain such material, adult tracts would have to be preserved in a matter of minutes after the animal was killed.

Tracts of nine adult fishers in which there were implanted embryos were studied (Table 2). Studies of the marten and a weasel are of some value in estimating the times of parturition in these tracts. Jonkel and Weckwerth (1963:96–97) made a series of laparotomies on late-winter adult female marten (*Martes americana*) and determined that the interval between implantation and parturition was less than 28 days. In the long-tailed weasel (*Mustela frenata*), Wright (1948) showed that the postimplantation period lasted about 23 or 24 days. In estimating the parturition dates from the pregnant fisher tracts it is assumed that the period of active pregnancy is about 30 days. This seems reasonable on the basis of the larger size of the fisher in comparison with the marten and the weasel.

The female fisher with the largest fetuses, taken on March 20, would probably have borne young before April 1. The one with the earliest stages was taken on March 13, and it is estimated that her litter would not have been born until after April 1. The one with the 13-mm (crown-rump) embryos, taken on February 7, would have borne her young before the end of February. Two recently captured females produced litters on March 2 and on March 20 at the Maine Unit. The evidence indicates that the majority of Maine fishers produce their litters during the month of March, but some do so as early as mid-February, and some as late as early April.

The ovaries of female fishers with implanted embryos were all serially sectioned. The ovaries are much larger than those in inactive pregnancy, the average combined weight being 231.9 mg as compared with 134.4 mg for the inactive group. The corpora lutea are markedly enlarged in active pregnancy as is generally known in mustelids with long periods of delayed implantation (Wright 1963:87). The corpora of three of these animals averaged 2,380, 2,917, and 3,057 μ in diameter, whereas corpora from two animals with unimplanted blastocysts averaged 1,387 and 1,219 μ. Although these corpora in animals with implanted embryos are more than seven times the volume of those with unimplanted embryos, the increased size of the ovaries is not due solely to the increase in corpus size.

In no case is the histological preservation of high quality, but the corpora lutea were readily seen and counted in all ovaries.

There is a great deal of interstitial tissue in all of these ovaries, and in this they differ from weasel ovaries (Deanesly 1935:484) in which the interstitial tissue is most active in late summer but by implantation time shows considerable degeneration. There are also numerous small and medium-sized follicles in these fisher ovaries. In all cases the cells of the corpora lutea are highly vacuolated. Vacuolated cells in corpora are common in many mustelids during the period of inactive pregnancy. Eadie and Hamilton (1958:78) noted that their fisher corpora in ovaries in inactive pregnancy were highly vacuolated. Wright and Rausch (1955:348–350) describe vacuolated corpora in the wolverine (*Gulo gulo*) in inactive pregnancy, but during active pregnancy the vacuolation had disappeared. It appears then that vacuolated corpora lutea during active pregnancy is a condition not commonly seen in this group. We suppose that the corpora lutea of active pregnancy are secreting progesterone, whereas during the inactive period there may be no active secretion of progesterone. This is suggested by the urine analysis conducted in various stages of pregnancy by Ruffie et al. (1961) on the European badger (*Meles meles*) which has a similar reproductive cycle.

The number of embryos or fetuses in these eight animals averaged 3.38 and in each case the number of corpora lutea corresponded to the number of embryos; that is, there was seen here no loss of potential embryos that may have occurred during either the preimplantation period or the postimplantation period.

There was evidence of migration of embryos from one uterine horn to the other in five of the eight animals. Migration of embryos is well known in other mustelids. It apparently occurs largely during the process of spacing just before implantation. Only one example of migration was seen in all 11 tracts which were preserved during inactive pregnancy and which were sectioned to locate all of the blastocysts.

On a few occasions at the time of autopsy, Coulter observed darkened areas in the uteri which were apparently placental scars. After being fixed and cleared, most of these areas were no longer visible. Wright (1966:29) found that in the badger (*Taxidea taxus*) placental scars can readily be found in cleared tracts of parous females, provided the uteri were preserved at once after death. Placental scars are difficult to find, even in lactating badgers, in material that is not freshly preserved. It seems likely that the general level of preservation in these fisher tracts was not good enough to preserve placental scars.

Breeding Season

Earlier workers, Hall (1942:147), for example, indicate that the female fisher breeds soon after her litter is born; thus the gestation period may be as long as 51 weeks. Since no recently postparturient tracts were available for study, this particular point could not be confirmed from wild-caught animals. However, among specimens collected in late March and early April, 1957, two recently bred nulliparous females were obtained and the tracts preserved fresh. These two tracts are the best preserved in the entire series, and tubal embryos were found in each by serially sectioning the oviducts. Each animal had three corpora lutea, 2 R, and 1 L, and 3 morulae were found in one and 2 in the other. In the one taken on March 28, one morula had about 228 nuclei (Fig. 1A); the other embryos were of comparable development, but it was not possible to count the nuclei.

The animal taken on April 4 showed 2 morulae with 12 and 20 nuclei (Fig. 1B). No evidence was found of the expected

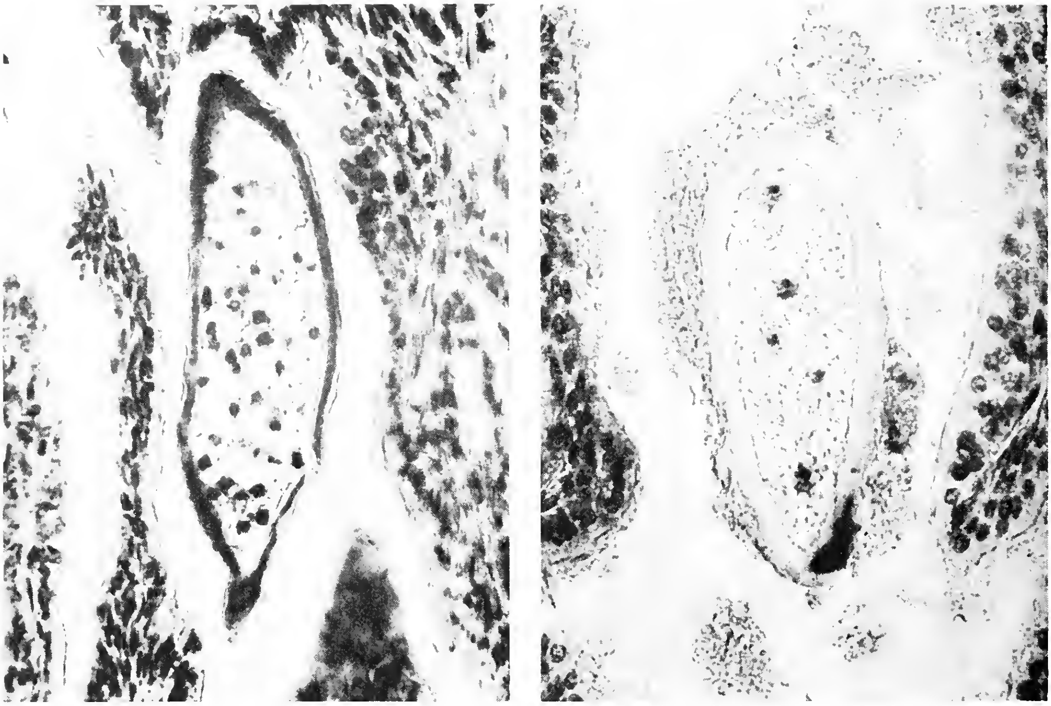


Fig. 1. Photomicrographs of tubal morulae from recently impregnated female fishers. (Left) Embryo of about 225 nuclei, from 1-year-old female taken on March 28. (Right) Embryo of about 12 nuclei from oviduct of 1-year-old female taken on April 4.

third embryo. The only mustelid possessing a long period of delay in implantation in which the rate of cleavage is known is the long-tailed weasel (Wright 1948). If the fisher has a comparable slow rate of cleavage, the March 28 animal was impregnated about March 18, and the April 4 specimen was impregnated about March 27. This is probably about the same time as recently parturient females would be impregnated. The young developing from these tubal embryos would normally have been born about 1 year later.

The ovaries of these nulliparous animals were largely masses of interstitial tissue, apparently of cortical origin. There were no graafian follicles of medium or large size. The small, almost fully formed corpora lutea with organized connective tissue centers also suggested that ovulation had occurred some 8 or 10 days earlier. The luteal cells were not vacuolated. The medulla of these ovaries was discernible only as a small area adjacent to the mesovarium.

Both of these recently bred females, even though nulliparous, showed slight mammary development. In weasels, Wright (Unpublished data) has never seen mammary development associated with the summer breeding season. The nipples become conspicuous for the first time about the time of implantation.

Both of the fishers in question were judged to be 1 year old, on the basis of the development of both their skulls and skeletons. Another nulliparous female taken at the same time, March 27, was also judged to be 1 year old, but showed no sign of reaching estrus. This animal might have attained estrus within 2 or 3 weeks.

Table 3. Findings in tracts of male fishers taken in late winter and early spring.

DATE (1957)	WEIGHT OF COMBINED TESTES AND EPIDIDYMIDES (G)	PAIRED TESTIS WEIGHT (G)	PAIRED EPIDIDYMIS WEIGHT (G)	STATUS OF SPERM IN TESTES	STATUS OF SPERM IN EPIDIDYMIDES	BACULUM WEIGHT (MG)	ESTIMATED AGE OF ANIMAL	BODY WEIGHT
January 5	2.7	1.8	0.4	None	None	1262	Juv.	7 lb 3 oz
February 26	7.4	5.6	1.4	Active spermatogenesis	None	?	?	?
February or early March	6.3	4.8	1.1	None	None	1725	Juv.	10 lb 7 oz
March 1	6.3	4.8	1.0	Active spermatogenesis	Few	1252	Juv.	8 lb 5 oz
March 1	8.6	6.9	1.3	Abundant	Abundant	1550	Juv.	9 lb 12 oz
March 1–15	10.3	7.6	1.9	Abundant	Abundant	1562	Adult	—
March 17	11.3	8.6	1.9	Abundant	Abundant	1522	Adult	11 lb 5 oz
March 27	7.4	5.8	1.2	Abundant	Abundant	1921	Adult	8 lb 3 oz
March 27	13.0	9.8	2.2	Abundant	Abundant	2053	Adult	14 lb 6 oz
April 4	9.0	7.0	1.7	Abundant	Abundant	1800	Adult	9 lb 5 oz

Coulter has often noticed a definite change in travel pattern beginning in March and suspects that it is associated with breeding activities. Earlier, the animals are fairly solitary and travel in long routes in more or less direct fashion. But during March there are numerous cases of animals traveling together. The incidence of scent posts is much higher than in early or midwinter. At this season, reports are received of "dozens of fisher" in a given locality. Closer study shows that only two or three animals may be responsible for an unbelievable maze of tracks in a small area.

In the European badger, which may also have a gestation period of almost a full year, both Neal and Harrison (1958:115–116) and Canivenc and Bonnin-Laffargue (1963:121–122) present evidence for sterile matings occurring outside of the usual breeding season and ovulation in animals already in inactive pregnancy. Although no fishers were obtained during the period extending from early April until October, it is clear from the material at hand that ovulation occurs only during the breeding season, and there is no evidence of sterile matings.

Male Tracts

Since testes were generally inactive during the trapping season, they were not routinely saved from trapper-caught specimens. With a breeding season in March and April, it was obvious that late-winter animals would show transitional stages from the inactive early-winter condition to the active state in the breeding season. An effort was made, therefore, in the late winter of 1957 to preserve testes from available males. The results of the observations are included in Table 3.

The weights of the combined testes and epididymides were obtained after first stripping free the tunica vaginalis. Then the testes were further separated from the epididymides and both were weighed again. Thus, the total of the separated weights does not equal the combined weights because additional connective tissue and fat had been removed. Representative sections of testes from each animal and from the

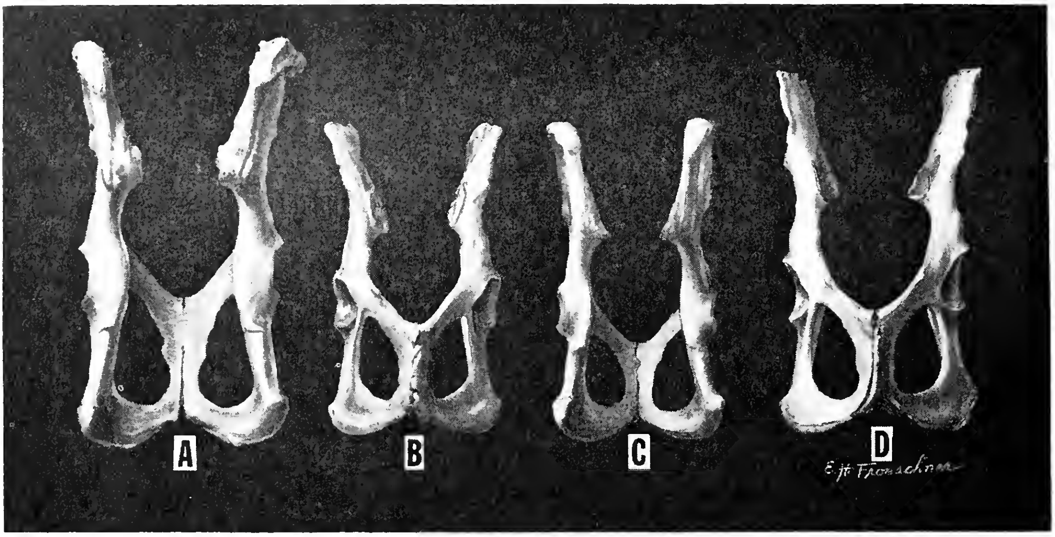


Fig. 2. Dorsal and ventral views of adult and juvenile fisher pelvic girdles. (A) Dorsal view of adult ♂ showing complete disappearance of the symphysis in a portion of the anterior half of pubo-ischiac junction. (B) Ventral view of adult ♀ showing almost complete disappearance of pubo-ischiac symphysis. There are conspicuous rugosities projecting from each side of the symphyseal line. (C) Dorsal view of juvenile ♀ showing complete separation of the innominates by symphyseal cartilage. (D) Ventral view of juvenile ♂ in which the two innominates are completely separated by a substantial symphyseal cartilage.

tail of the epididymis were prepared and stained.

The juvenile male taken on January 5 was aspermatic. By late February and early March three juveniles showed somewhat enlarged testes, but only one of these animals was in breeding condition. All of the adults taken from early March into early April were fully developed with abundant sperm in the tails of the epididymides. It would have been desirable to have tracts from additional males taken earlier in the winter. The results indicate, however, that adult males are fully active sexually during the breeding season; and the young males, now just 1 year old, are also apparently in breeding condition.

Skeletal Development

The series of 59 skeletons was studied with respect to the fusion of the epiphyses in each of the long bones and representative vertebrae. Sixteen specific sites were studied in addition to the status of fusion of the pubo-ischiac symphysis and certain sutures in the skulls.

Examination of the November and December skeletons showed striking differences between two groups, apparently juveniles and adults, in both sexes. All of the sutures studied were open in November and December males judged to be juveniles; and most of the sutures were only partly closed in comparable females thought to be juveniles. The obviously juvenile animals were smaller and showed many open sutures in the skulls. The bacula of the males in this group were small and weighed less than 1,000 mg, compared to an average of more than 2,000 mg for those with closed sutures. The ovaries of females regarded by skeletal criteria as juveniles were all without corpora lutea; the ovaries of all those classed as adults possessed corpora lutea.

The pubo-ischiac symphysis clearly remains open longer than most of the sutures.

It was completely open in all animals that were regarded as less than 1 year old taken throughout the fall, winter, and early spring. It was at least partially obliterated, when viewed either dorsally or ventrally, in all animals regarded as more than 1 year of age (Fig. 2). The findings of striking differences in the fusion of this symphysis parallel those of Taber (1956), who described differences in this symphysis extending over several years in deer (*Odocoileus hemionus* and *O. virginianus*). The pubo-ischiac symphysis should be studied in other mammals in which aging criteria are needed.

Baculum

Weights of bacula are shown in Fig. 3, and drawings of representative types are shown in Fig. 4. The bacula of adults are more than 100 mm long, and they commonly weigh 2,000 mg or more. The fully mature baculum shows an elevated ridge near the proximal end that completely encircles the bone in a diagonal line when viewed from the side. The bacula of juveniles taken in the fall and early winter are much smaller. Although they show the typical splayed tip at the distal end, which is universally perforated by a small, round, or oval foramen, they do not show the enlarged proximal end typical of the adults. The series of bacula in Fig. 3 shows that those of the juveniles are growing rapidly during the winter months. By February some of them weigh as much as 1,600 mg (one 2,099 mg) and thus overlap the weight of those of adults. Two such bacula are shown in Fig. 4, F and G. Since the testes of juveniles in February were becoming active, it seems reasonable to assume that such animals were secreting androgen at high levels.

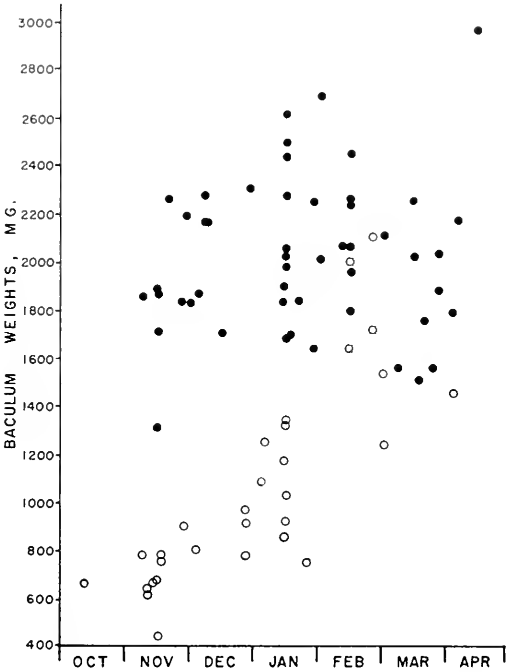
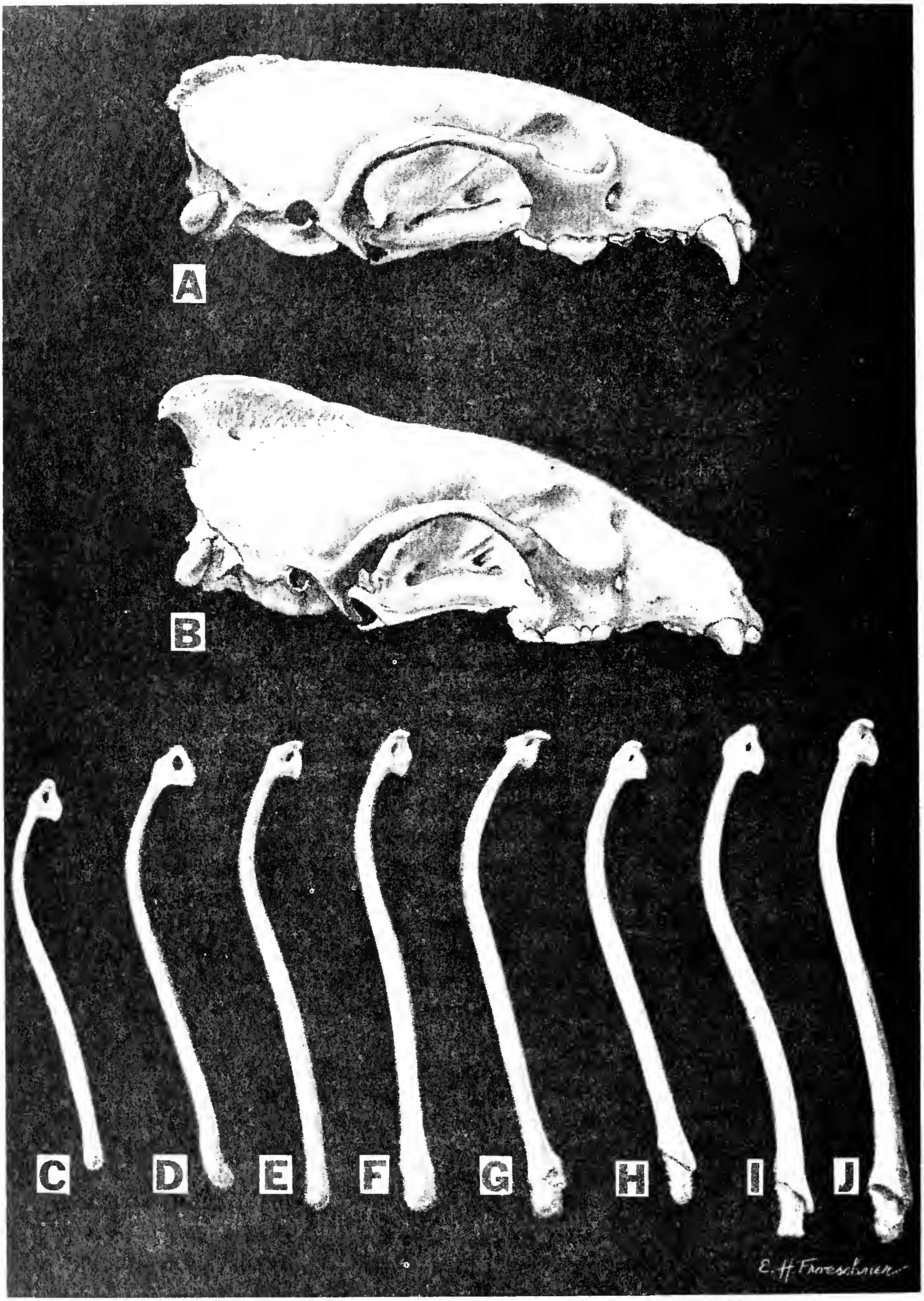


Fig. 3. Baculum weights. Adults are shown in solid dots, juveniles with open circles. The continued growth of the juvenile baculum during the winter months is clearly shown as is the overlap in weights of February, March, and April juveniles and adults.

The fully adult baculum undoubtedly develops under the influence of androgen, as it probably does in all mustelids. This was demonstrated (Wright 1950) to be the case in the long-tailed weasel. Probably the fully adult type of baculum would develop by late spring in these year-old males, since Deanesly (1935:469) concluded that the adult baculum of the European stoat (*Mustela erminea*) develops to adult type within 1 month after the testes become active for the first time. Although Elder (1951:44) showed that bacula may continue to develop in succeeding years in sexually mature mink (*Mustela vison*), the lack of known-age fishers in this series does not make such conclusions possible here. The tentative conclusion reached by de Vos (1952), that bacula were not of value in distinguishing adult from juvenile fishers, resulted from failure to recognize changes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in the rapidly maturing skulls of juvenile male fishers during the late winter. This will be discussed further in a later section.

Skulls

The specimens were placed in four groups (adult males, juvenile males, adult females, and juvenile females) on the basis of reproductive condition and skeletal analysis, and 12 measurements were taken of each skull (see Wright 1953:78–79). Means, standard errors, and coefficients of variation were calculated for each group. It is clear from study of these statistics that the skulls of the juvenile animals in both sexes have not reached maximum growth. In many cases the differences between the means is statistically significant, but, because of overlap between the measurements in adults and juveniles, it is not possible to develop aging criteria based on measurement of a single skull parameter, with one exception to be discussed later.

The differences between the means of these measurements was generally much greater among males than among females. For example, the mean weight of adult male skulls was 70.6 g, whereas in juvenile males it was 53.9 g, a difference of some 20 percent. In female skulls, however, the adults average 32.1 g and the juveniles 31.1 g, a difference of only 3 percent.

The postorbital constriction becomes somewhat smaller with increased age in both sexes of fishers, as it does in other mustelids. Another striking difference between adult and juvenile skulls was seen in males where the zygomatic breadth averages 77.4 mm in adults and only 64.8 mm in juveniles. In spite of this 18 percent smaller measurement in juveniles, there is overlap. It is not possible to classify a male fisher as juvenile or adult solely on the basis of this measurement. The difference in zygomatic breadth would, in most cases, produce a broader appearing face on adult males than on juvenile males.

The sutures in the skulls of fishers, like those of all other mustelids, tend to disappear at a relatively young age (Marshall 1951:278, Greer 1957:322–323) as compared to the Ursidae, for example, where they persist for many years (Rausch 1961: 86, Marks and Erickson 1966:398). Juvenile male fishers taken in early fall (Fig. 5A) show almost all of the sutures unfused, but on specimens during March or April (Fig. 5C) almost all have completely disappeared. Eadie and Hamilton (1958:77) showed, in New York fishers from which they had reproductive tracts, that "All breeding females showed at least partial fusion of the temporal ridges . . . to form a sagittal crest, and [that] the maxillary-palatine sutures were completely fused. Non-breeding females showed the temporal ridges in various degrees of separation and had the maxillary-palatine sutures at least partly open. It is concluded that female fisher normally breed at the age of one year in the wild, and that these criteria will separate young-of-the-year from adults."

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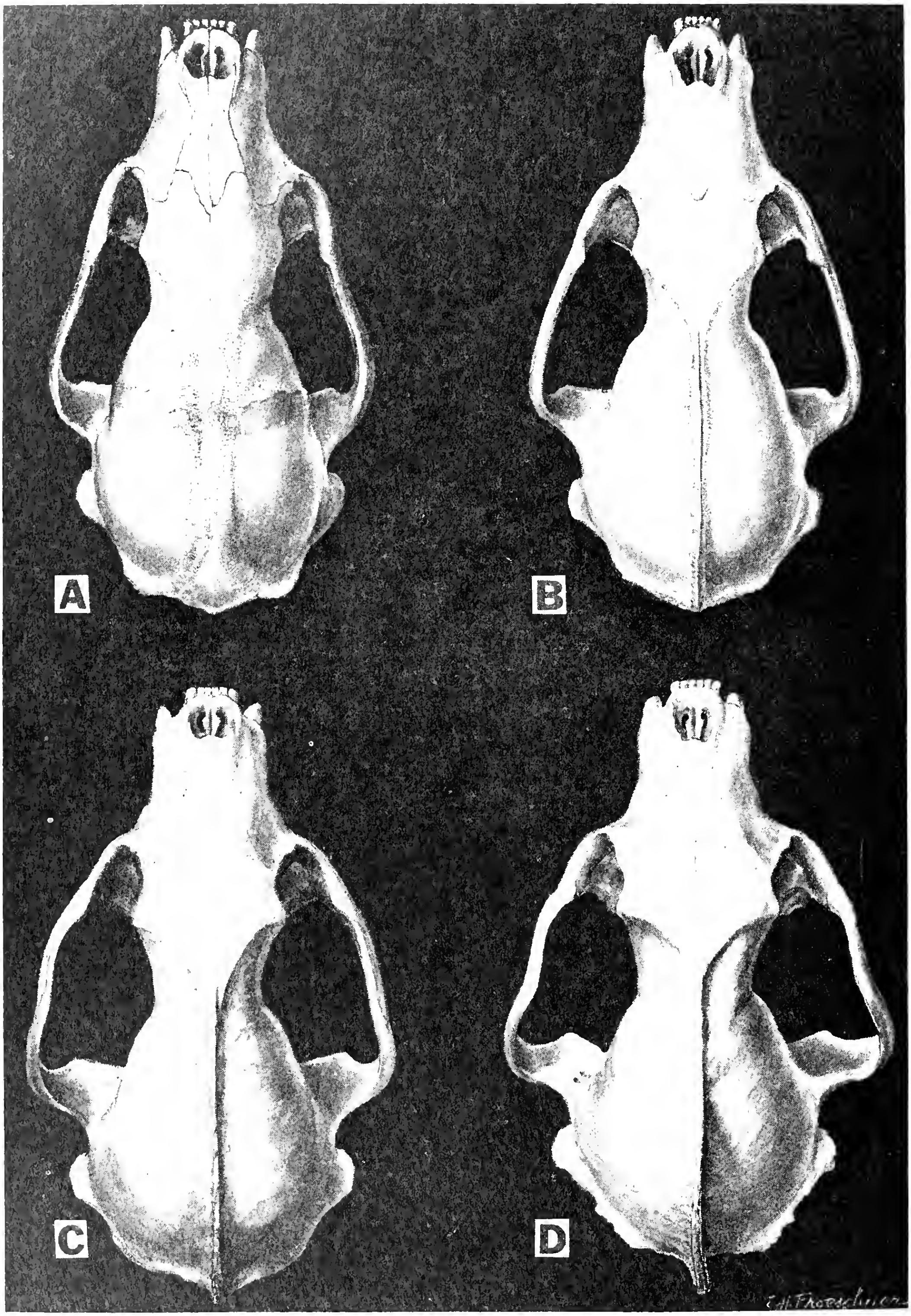
Fig. 4. (A) Lateral view of skull of winter juvenile male, February, showing well developed sagittal crest and open zygomatic–maxillary suture. (B) Lateral view of skull of fully adult male showing typical tremendously developed sagittal crest and disappearance of zygomatic–temporal suture. The heavily worn teeth shown are not necessarily characteristic of adult fishers. (C to J) Baculo of male fishers showing progressive changes with age, distal end to the top, the youngest to the left and oldest to the right. C, D, and E are from juveniles, C taken October 12, D taken December 3, E taken January 5. F and G are from late winter juveniles showing progressive changes toward the adult type with increased deposition of bone at the basal end. Both F and G were taken in February or early March. H, I, and J are selected adult bacula showing the characteristic oblique ridge near the basal end and generally more massive appearance. H is from a smaller-than-average male (body weight, 9 lb, 5 oz), I and J from larger-than-average males (I, carcass weight 10 lb; J, body weight, 14 lb 6 oz).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Our findings from study of 66 female fishers from Maine, from which comparable data were available, confirm in detail the findings of Eadie and Hamilton (1958). It is also clear that the maxillary-palatine suture is among the last, if not the last, to disappear.

These authors also describe a frequency distribution in the length of the sagittal crests in adult females, and reference to their Fig. 3 shows that there are two peaks of sagittal crest lengths which they tentatively regarded as representing a group of 1½-year-old females and another group of older females. When we plotted our data in comparable fashion, the line exactly paralleled theirs; and there is thus further evidence that such separation into young adults and older adults is possible. The distribution of the lengths of the sagittal crests of the adult Maine female fishers, plotted in the same fashion as did Eadie and Hamilton, is as follows: 0–10, 1; 11–20, 11; 21–30, 3; 31–40, 8; 41–50, 19; 51–60, 1.

The findings in the skulls and skeletons of the two recently bred nulliparous females, whose reproductive tracts were described in an earlier section, also provide significant evidence that the onset of breeding in female fishers occurs when they are 1 year old. In each case there was no sagittal crest, and the maxillary-palatine suture was partially open. Eadie and Hamilton (1958:79) found this suture closed in all New York fishers judged to be adults. In their collection, adult fishers, taken entirely in fall and winter, would have been at least 20 months old, whereas our two animals were almost exactly 1 year of age. One of these animals shows the pubo-ischiac symphysis still open; the other shows it partly closed. Further, the fact that during the fall and winter there is only one type of skull to be found in fishers that have not bred makes it virtually certain that wild Maine fishers are regularly impregnated at the age of 1 year and thus produce their first litters at the age of 2 years.

The sagittal crests of adult male fishers are extremely well developed as was mentioned by Coues (1877:65), and the degree of sexual dimorphism in skulls of fishers is greater than in any other American mustelid. All adult females develop sagittal crests, but even the most highly developed crests in females are almost vestigial compared with those of adult males. It is natural to suspect that with this tremendous development in mature males the crest might begin to develop earlier in juvenile males than in females. This is exactly the case, and sagittal crests were first seen in one of two juvenile males taken in December (Fig. 5B). By February, March, and April the crests of the juvenile class, now almost 1 year old, are well developed (Fig. 5C), as much so as they ever become in adult females.

In the female fishers it is clear that the sagittal crest develops first at the posterior end of the skull and grows progressively

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Fig. 5. Dorsal view of male fisher skulls showing characteristic changes associated with development. (A) Juvenile male, October 12, showing narrow zygomatic breadth, all sutures in nasal region clearly open; the fronto-parietal sutures are partly fused. The poorly developed temporal lines are wide apart and thus there is no sagittal crest. (B) Juvenile male, December 3, showing disappearance of fronto-parietal suture, less conspicuous sutures in nasal region, and characteristic early development of sagittal crest running throughout the middle and posterior portions of the cranium. (C) Juvenile male in late winter, February, in which these naso-maxillary and maxillary-frontal sutures are barely visible, but the zygomatic-temporal sutures are still very distinct and the sagittal crest is better developed. (Same skull as shown in Fig. 4A). (D) Skull of adult male in which the entire dorsal skull is ankylosed into a single unit; no suture visible except for faint remains of posterior internasal suture. The characteristic highly developed keel-like sagittal crest of all adult males is clearly shown. (Same skull as shown in Fig. 4B).

forward over a period of months or probably years. In the male fisher the temporal lines move rapidly together during the winter months; and as soon as the crest is formed, it runs essentially the entire length of the dorsal region from the postorbital constriction to the inion, a distance of 50–60 mm. The sagittal crest continues to develop in adult males, and they have the crest developed to the extent of forming a "thin, laminar ridge" (Coues 1877:65). It is difficult to measure the extent of this ridge objectively; but since it extends posteriorly in fully adult males, one can use the method employed by Wright and Rausch (1955) on wolverines to subtract the condylobasal length from the greatest length of the skull. This is one accurate method of showing the posterior extension of this crest. This indirect measurement shows no overlap whatever between males classed as adults and those classed as juveniles. The mean for the former group is 11.9 mm and for the latter, 3.9 mm (see Fig. 4, A and B). Thus in male skulls if the difference between the greatest length of the skull and the condylobasal length is 6 or more mm (may be as much as 15 mm), the animal is an adult; if it is less than 6 mm, the animal is a juvenile.

Another reason for assuming that skulls of males with immature bacula, but with sagittal crests, are still in their first year of life is provided by data on the closure of sutures in the skull. The last sutures to close in males are the zygomatic-temporal, the naso-maxillary, the internasal, and the naso-frontal. In all of the skulls classed as adult, all of these sutures were closed, but in every male skull classed as juvenile, all four of these sutures were still open (Figs. 4 and 5).

On the basis of this evidence, it seems clear to us that males classed by de Vos (1952) as "adults" were in effect juveniles as well as his "juvenile" class, and that only the animals he called "old adults" were adult males over 1 year of age.

It is concluded, therefore, that during the early winter, adult males can be separated from juvenile males by the occurrence of a well developed sagittal crest on adults; but by mid- or late winter only those males with all of the skull sutures closed are adults.

Body Weights

Both de Vos (1952) and Hamilton and Cook (1955) have provided body weights of wild-caught fishers, and both studies show that males often weigh twice as much as females. The latter indicate an average weight for males of 3,707 g (8 lb 3 oz) and 2,057 g (4 lb 9 oz) for females. De Vos's figures are roughly comparable. In both studies many of the body weights were estimated from carcass weights by applying a correction factor to skinned carcasses. (Most fisher specimens coming to biologists are likely to be carcasses skinned by trappers.) Hamilton and Cook (1955:21–22) state that the fresh carcasses average 80 percent of the unskinned weight. In the present study many fishers were confiscated and were available intact. Thus, it was possible to obtain a sample of weights taken directly from the entire unskinned carcasses, allowing consideration of differences between adult and juvenile classes in both sexes.

Data obtained from those fishers which were weighed entire in the laboratory are shown in Table 4. The differences between the juveniles and adults in both sexes is highly significant although there is some overlap in each case. Furthermore, juvenile males are significantly heavier than the adult females. The available mean weights of adults are probably more satisfactory than those of the juveniles. Presumably, the adults were no longer growing, but the juveniles were growing throughout the collection period from October to April. The sample is not large enough to allow a breakdown within the juvenile classes by month, but the smallest juveniles were taken in the fall.

The fact that weights of the juvenile males are 21 percent less than those of the adult males, while the weights of juvenile females are only 15 percent less than those of the adult females, further indicates that juvenile female fishers are more nearly full grown during the first winter of life than are the juvenile males.

In many cases, the fishers that were weighed whole were also weighed after skinning. This allowed determination of a correction factor. Thirty-nine animals were weighed both before and after skinning: 14 adult males, 5 juvenile males, 8 adult females, and 12 juvenile females. The carcasses averaged 81.9 percent of the whole weight; or, stated conversely, one could multiply the carcass weight by 1.22 to obtain an estimate of the entire adult weight. This latter conversion factor was applied to those animals that were weighed only after being skinned. Estimated entire body weights obtained in this fashion were comparable for both adult and juvenile males, but weights of females were significantly below the weights of those females weighed entire. For this reason, it was obvious that in the interval between skinning and weighing, many of the female carcasses had lost significant weight. It was therefore necessary to abandon any attempt to use the more numerous carcass weights for interpretation of possible growth rates in the juveniles or other weight changes that might exist between months.

Table 4. Body weights of Maine fishers weighed whole.

CLASS	NO. OF ANIMALS	MEAN BODY WEIGHT (OUNCES)	SE IN OZ	MAX.	MIN.
Adult ♂	23	172.1 (10 lb 12 oz)	±6.30	14- 6	7- 4
Juv. ♂	10	135.5 (8-7½)	±7.08	10- 8	6- 8
Adult ♀	13	88.2 (5-8)	±3.61	7-11	4- 8
Juv. ♀	17	75.0 (4-11)	±2.35	6- 8	3-13

DISCUSSION

This study indicates that in the fisher the adult class consists of all animals more than 1 year of age and that all animals of both sexes less than 1 year are sexually immature. Females older than 1 year normally are carrying unimplanted blastocysts throughout the year except during active pregnancy in late winter. The fisher, then, differs from all other American mustelids studied in this regard except the wolverine. The weasels, *Mustela erminea* and *M. frenata*, are similar in that the males reach sexual maturity in 1 year; but the females breed during their first summer and thus produce young at the age of 1 year (Wright 1963:83–84). In the marten, males also apparently reach sexual maturity in 1 year, but females may not breed until they are 2 years old, and thus two year-classes of immature females may be found in wild populations (Jonkel and Weckwerth 1963: 95–96). This has made further refinement of Marshall's (1951) original study of marten quite difficult.

In the female otter it appears that sexual maturity is delayed another year beyond that in the fisher and that there are two age-classes of immature otters (Hamilton and Eadie 1964:245). In the badger the same type of situation prevails as in the fisher except that some females breed precociously during their first summer and such females would produce litters at the age of 1 year, whereas most badgers produce their first litters at the age of 2 years (Wright 1966:42). Only in the wolverine (*Gulo gulo*) does it appear that a reproductive cycle like that of the fisher is found; but owing to a small sample of animals of the former species, the matter of age at sexual maturity is somewhat in doubt.

The recovery of the marten in Maine has been much slower than in the fisher (Coulter 1959) although both species originally occurred sympatrically in much the same habitat. The present study indicates that the potential rate of reproduction in the fisher is higher than in the marten. A large sample of winter-caught marten is not available from Maine, but such material was obtained from Montana. Wright (1963: 79) indicates that corpora lutea counts averaged 3.02 in a sample of 44 trapper-caught marten. The present study showed 3.28 for the fisher. Perhaps of greater significance, though, is the fact that some female martens (in Glacier National Park) (Jonkel and Weckwerth 1963) do not produce litters for the first time until they are 3 years old.

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GROWTH, DEVELOPMENT, AND WING LOADING IN THE EVENING BAT, *NYCTICEIUS HUMERALIS* (RAFINESQUE)

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ABSTRACT.—Selected aspects of growth and development of young evening bats are presented and summarized. In addition, information on wing loading and development of flight in known-age animals is given. Data regarding growth, development, and wing loading of *Nycticeius humeralis* and information that is available for some other species of bats are compared and discussed.

Few observations have been made previously on growth and development of bats, and such information has been frequently incidental to other studies of natural history or reproduction. Ryberg (1947), while presenting data on parasites and natural history of bats, made some mention of growth and development of young. Considerable information on growth and development of two North American bats has been contributed by Pearson *et al.* (1952) and Orr (1954). Some observations of young and early growth and development of *Nycticeius humeralis* were noted by Gates (1941). In general, reproduction of bats has been summarized by Cockrum (1955) and Asdell (1964).

To my knowledge, no information has been made available with regard to wing loading of *Nycticeius humeralis.* Vaughan (1959), while presenting data on aerodynamic considerations of three species of bats, provided a survey of important earlier works. More recently, limited information on flight of some North American bats has been contributed by Struhsaker (1961), Davis and Cockrum (1964), Hayward and Davis (1964), Vaughan (1966), and others.

The purpose of this report is to present information on growth and development and to discuss briefly some aspects of wing loading of *Nycticeius humeralis.*

MATERIALS AND METHODS

This report is based upon observations of 28 young of 14 litters born in captivity to females netted at Clear Springs, Homochitta State Park, Franklin County, Mississippi. The adults were captured between 11:30 PM and 4:30 AM on 9 and 10 May 1965.

Pregnant bats were weighed periodically prior to parturition; following birth of the young, weights and measurements of all bats were taken regularly. The growth and development of three litters were followed in detail and the animals were measured daily. The remaining animals were measured each 3- or 5-day period. Because the bats were not anesthetized, it was not always possible to obtain relaxed individuals for measuring.

As a result of these methods, some discrepancies in the measurements of individuals from one date to another are evident in the data. Measurements that were taken include total length, length of tail, length of foot, length of ear from notch, length of forearm, and length of fifth finger. All measurements were taken with a Vernier caliper.

At regular intervals of age of the animals, wings were outlined for the analysis of surface areas utilized in flight. For the purposes of measuring wing loading, I have followed the assumption of Vaughan (1959) that the wings extend through the body and I have computed the wing loadings in lb per sq ft.

Pregnant females and females with young were housed in one-quart cardboard cans with screen tops. Following the weaning of the young, each female and her offspring were housed in one-half gallon cardboard cans with screen tops. Cardboard cans containing bats were stored on the sides. The animals were maintained at room temperatures and provided a daily diet of larvae of *Tenebrio molitor* and water with Theragran (Squibb Therapeutic Formula Vitamin) added. Feeding, watering, and handling of the bats were started at about the same time every day, usually between 3:30 and 5:30 PM.

For purposes of identification, adult bats were banded. Young animals were toe clipped soon after birth, but were banded when adult size was attained.

Some animals were sacrificed at various stages of development and then cleared and stained or were preserved either in fluid or as dried specimens.

RESULTS

Birth of young.—The females gave birth to the young within 15 to 26 days after capture. The births recorded herein occurred on 25 May (two litters), 26 May (one litter), 29 May (two litters), 30 May (five litters), 31 May (two litters), 2 June (one litter), and 4 June (one litter). Fourteen adult females gave birth to 12 females and 16 males. This ratio of sexes (0.75 to 1.00) was similar to the ratio (0.736 to 1.00) reported by Hooper (1939). Asdell (1964) reported two young as the usual number per litter and stated that birth occurred in late May.

All births observed were by breech presentation and the times recorded for births were from 3 to 114 minutes. With the exception of two litters that were born at about 9:00 and 10:45 AM, all litters were dropped between 1:00 and 4:00 PM.

During parturition all females moved to the bottoms of the containers. Females ate the placentae and umbilical cords and licked the young very soon after birth. Placentae were eaten first, then umbilical cords were eaten to within 2 or 3 mm of the naval area. Some of the females hung head up on the screening of the containers while eating the placental materials, but then turned head down and licked the young thoroughly. Placentae and umbilical cords were eaten and the young were licked usually within 35 to 70 minutes after delivery.

In every case observed, the young found and grasped the nipples of the adult within a short time, usually 5 to 8 min following birth. The young were aided often by the adult in climbing to the mammary glands. The young were oriented in the same direction as the adult. The plagiopatagium and uropatagium of the female enveloped the young. The young bats held firmly to the nipples of the females and had to be removed forcibly for measuring.

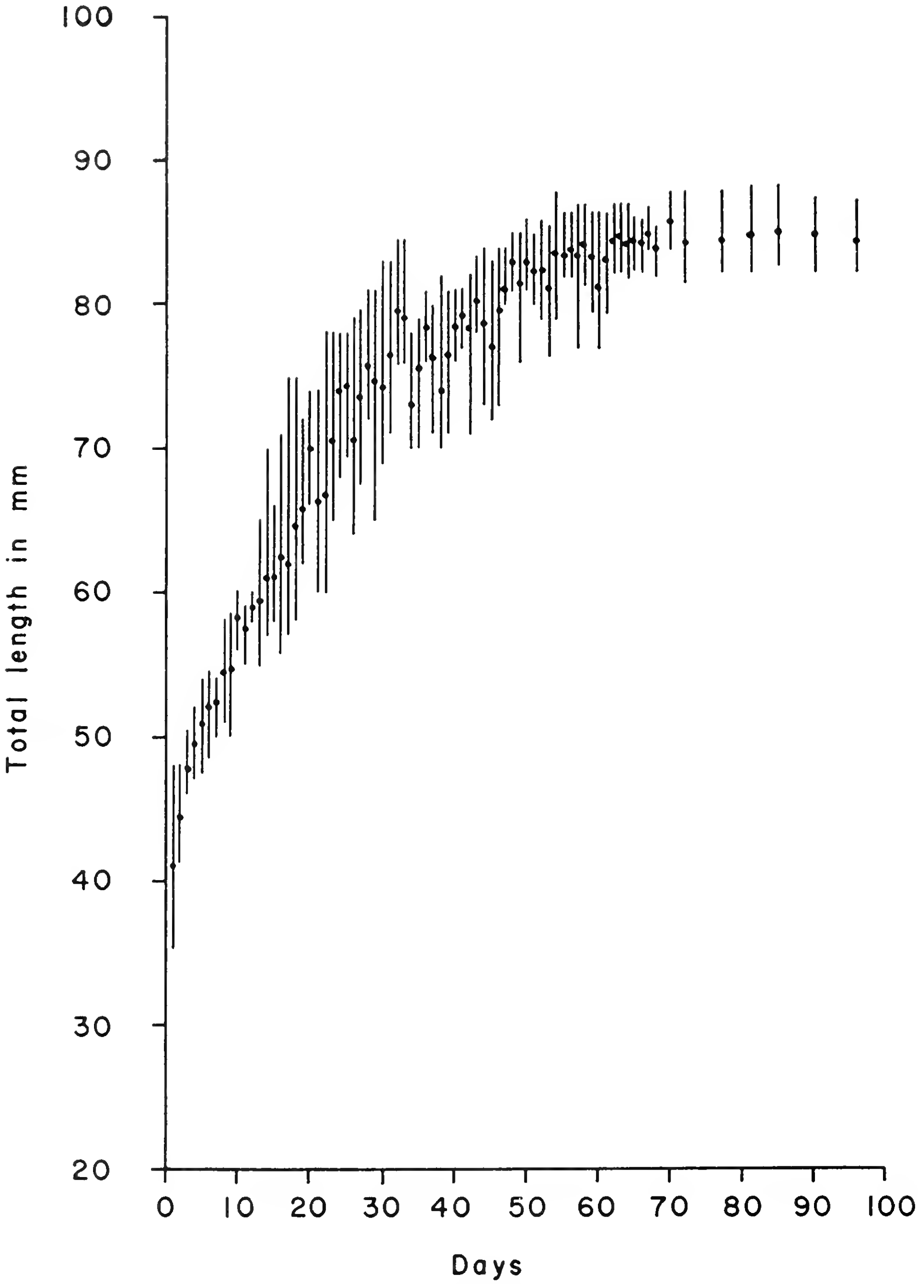

FIG. 1.—Total lengths of young *Nycticeius humeralis*. Dots represent the arithmetic means and lines represent the ranges of measurements.

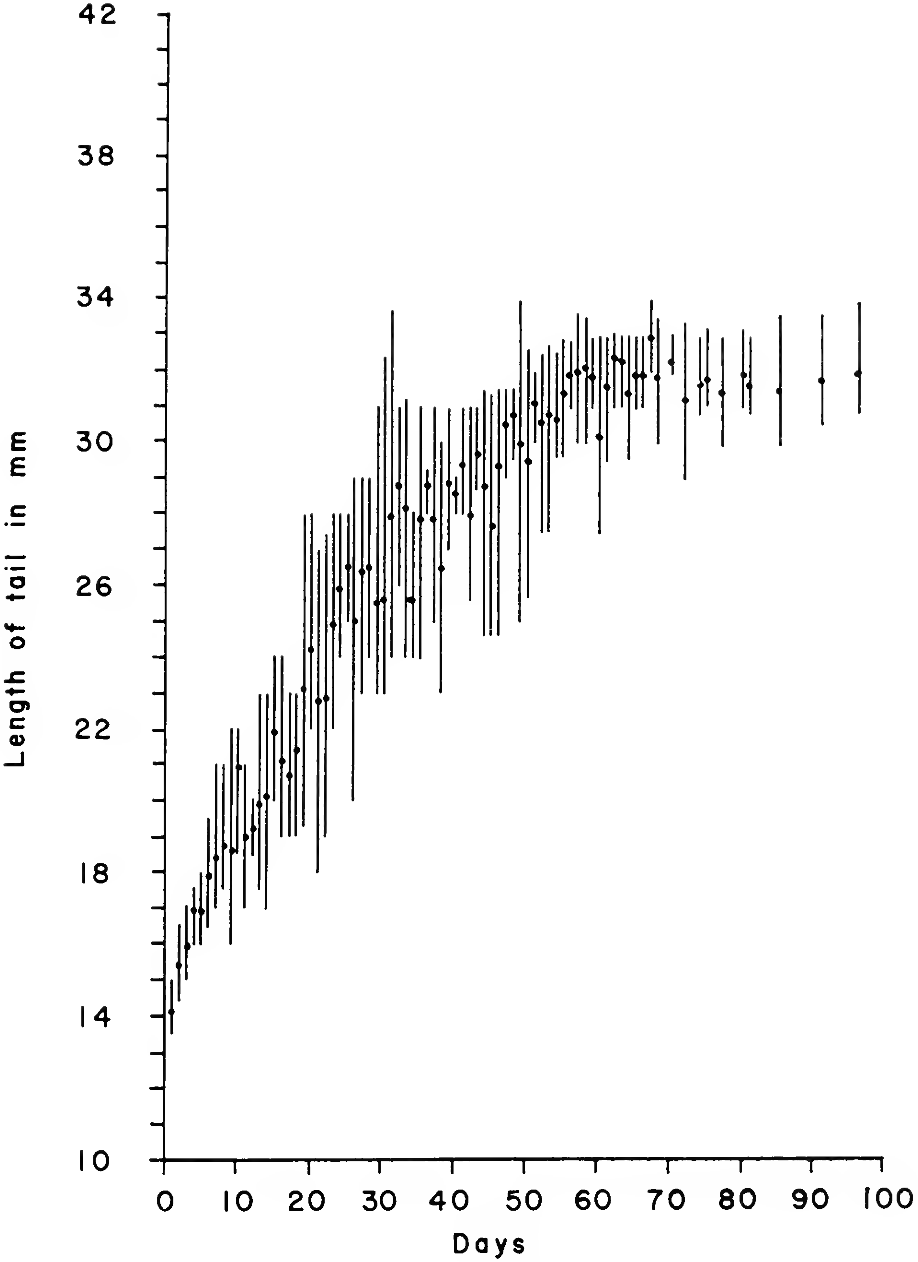

FIG. 2.—Tail lengths of young evening bats. Dots represent the arithmetic means and lines represent the ranges of measurements.

Table 1.—*Correlation of age and various aspects of growth and development of young evening bats.*

Age in weeks	Attached to nipples	Remain under adult most of the time	Body furred completely	Extend wings and flutter when thrown into the air	Glide or parachute when thrown into the air	Fly when thrown into the air or take off from shelf	Negotiate turns and avoid obstacles	Land head down on wall or ceiling	Eat larvae of meal-worms and drink water	Cease to nurse completely
1	×	×								
2	×	×	×	×						
3		×	×	×	×	×	×	×		
4						×	×	×		
5									×	
6									×	×
7									×	×
8										×
9										×

In addition, the feet and first fingers were utilized for clinging to the fur of the adults.

Skin and pelage.—Young bats examined within 1 hr after birth were pink with smooth, soft skin. Vicera were seen through the skin of the abdomen. There was slight dark pigmentation on the feet, membranes, tips of the pinnae, and lips. Only a few hairs were present on the feet and on the dorsum of the head and shoulders. Some vibrissae were evident on the swollen glandular areas of the lips.

When about 6 hr old, the young had more pigmentation on the dorsal sides of the back and head than at birth. Pigmentation became evident on the venter at approximately 18 hr of age. Within 24 hr the dorsum was pigmented heavily and the venter was pigmented except for a small abdominal area that appeared rather opaque. The skin was very wrinkled and had the appearance of being hard and dry, but was soft and pliable to the touch.

In the 2-day-old young, a few hairs appeared on the dorsum at the base of the uropatagium. The hairs and vibrissae on the feet and lips were noticeably stiffened.

At 3 days of age a small patch of hair became noticeable on the dorsum over the scapulae.

By the 4th day, pelage was seen on the dorsum over the scapulae, on the rump, and along the flanks. At this age, fur was first apparent on the venter at the base of the uropatagium and in the pectoral region.

At 5 days of age, fur was present on the dorsum across the scapular region to the flanks and extended onto the rump. At this time the fur was short, soft, and gray in color.

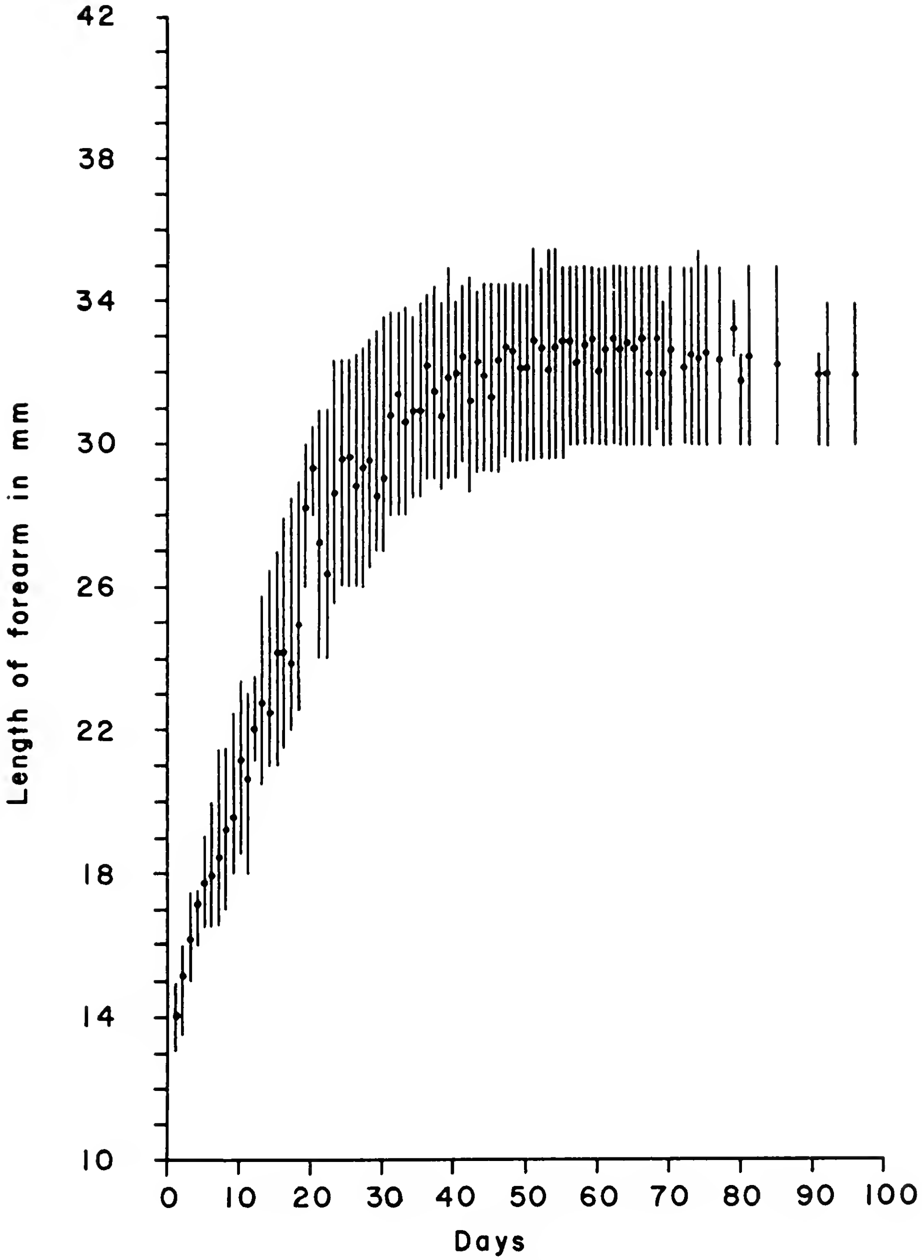

FIG. 3.—Forearm lengths of young *Nycticeius humeralis*. Dots represent the arithmetic means and lines represent the ranges of measurements.

On the 6th day, soft gray hairs covered most of the dorsum, and, except for a bare abdominal region, much of the venter. The feet were well furred.

At 7 days of age, the hairs on the dorsum, in the scapular region, appeared longer and darker than the rest of the general pelage.

At 8 to 9 days of age, the young were furred completely with grayish black hairs on the dorsum with long, dark fur over the scapulae. In contrast to the dorsum, the venter was grayish white in color.

The aforementioned general appearance of the pelage remained until the young were approximately 30 days of age. At this time the hair became burnished slightly with brown at the tips, perhaps due to wearing of the ends of the hairs. Young bats were not observed to undergo molt during the course of this study. At the time the young bats reached about 80 to 95 days of age, the parent females molted; the pelages of young and adults were similar in appearance.

Eyes, ears, and vocalization.—At birth the lids of the eyes were sealed, but the line of fusion was very evident. At 18 to 24 hr following birth, the eyes opened. At this age, the young would jump and scamper about in response to the flash of light from a photographic strobe.

Young examined soon after birth had pinnae that were folded over. When the young were 24 to 36 hr old, the pinnae were unfolded and held erect.

The young bats were vocal almost immediately after birth. The utterances of weak "squeaks" or "chirps" seemingly were continuous for about 10 days. After this time, bats made vocal sounds only when disturbed or handled.

Dentition.—The complete number of deciduous teeth in young *Nycticeius humeralis* is expressed by the formula i 2/3, c 1/1, p 2/2 = 22. Examination of newly-born young revealed that all of the deciduous teeth were erupted at birth. The deciduous teeth have two accessory cusps, one on either side of the main central cusp. In general, each cusp is in the shape of a hook and is curved backward and inward toward the mouth. The highest degree of development of curved, hook-shaped cusps is on the incisors. The cusps of the canines are hooked noticeably, but some premolars have relatively poorly developed accessory cusps that appear as small bumps rather than hooks. Hooked cusps are more highly developed in 2- and 7-day old young than in young 1 day of age.

The complete number of permanent teeth is expressed by the formula i 1/3, c 1/1, p 1/2, m 3/3 = 30. In specimens of young 2 days old that were cleared and stained, the crowns of the permanent teeth are clearly visible in a position internal to the deciduous teeth. In specimens of young 7 days old, the permanent canines have penetrated through the gums and crowns of the other teeth are seen at the gum line just beneath the surface. In the order of appearance of permanent dentition, the canines become apparent first, followed in eruption by the incisors, premolars, and molars. At 4 weeks of age, the permanent teeth are generally in place; the third molars may not be in place fully, but the crowns are apparent well above the gum lines.

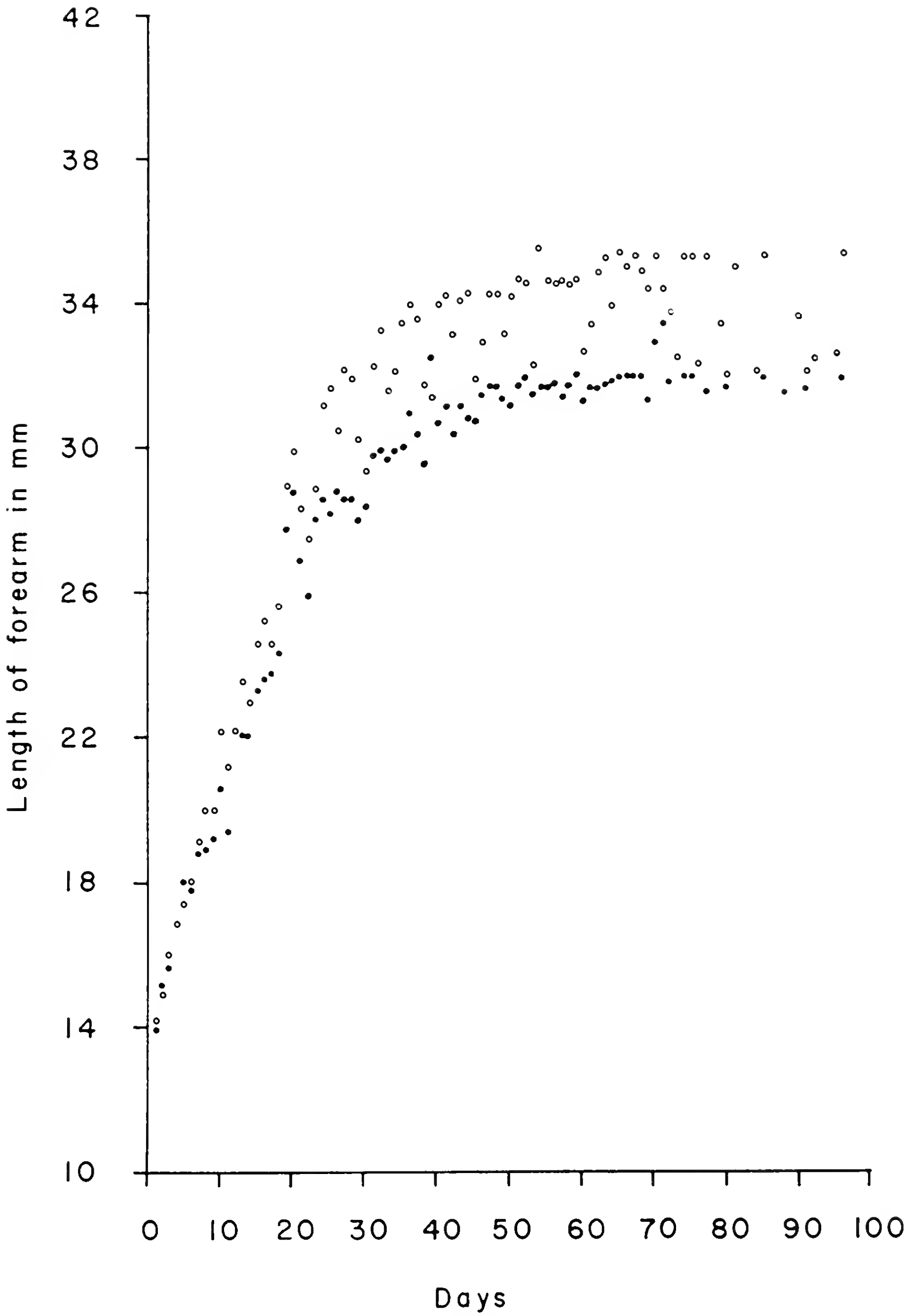

FIG. 4.—Forearm lengths of known-age evening bats. The open circles represent the arithmetic means of measurements for females; the dots represent the arithmetic means of measurements for males.

Digits.—The digits of the hind limb were separated at birth and the claws were well developed and pigmented. Young bats at birth had feet nearly equal in size to the feet of adults.

The first finger of the forelimb was developed very well at birth and thumbs of young were similar in size to thumbs of adults. Measurements of the length of the first finger of young and adults were 5.5 to 6.2 mm.

The remaining digits of the forelimb were developed to a lesser degree in young than in adults. In the young less than 15 days of age, the distal portion of the forelimb was less developed than the proximal part of the wing; digits two to five were shorter in length than the forearm. In adults, the lengths of digits two to five were 18 to 61% greater than the length of the forearm.

Flight of young.—In an attempt to determine the exact age when the young bats could fly, four young were thrown into the air each day when the adults were fed; four young and adults were housed in containers placed on a shelf 4.6 ft from the floor and the tops of the containers were taken off at feeding time; the remaining young and adults were cared for in the manner mentioned previously. When the young bats 10 to 14 days of age were thrown into the air, the wings were extended and fluttered, but the animals simply fell to the floor, sometimes without righting themselves. When the bats were 15 days of age, the fifth fingers were flexed and the bats would right themselves and then glide or "parachute" to the floor. At 18 days of age, bats thrown into the air flew 10 to 12 ft, but would hit a wall or the ceiling and flutter down to a flat surface such as the floor or a desk or would hang head up on a wall. At 19 days of age, one young bat housed on the aforementioned shelf emerged and flew across the room. When the young were 20 to 21 days old, they were observed to negotiate turns, land, and hang head down from walls and ceilings of the room. All of the young animals, including those with no practice previously, could fly short distances (10 to 12 ft) at 21 days of age, and all could fly well, turn, and land head down on the walls or ceilings at 23 days of age.

All observations of flight were made in a room that measured 18 by 15 ft with a partial corner partition separating an area about 8 by 8 ft. The young bats could fly and avoid obstacles well in these spaces.

Behavior of young and adults.—The young evening bats seemed weak and uncoordinated at birth. Although the babies attached themselves firmly to the parent, young 1 day of age seemed rather helpless when separated from the adult. At 1 day of age, the young could crawl about only feebly and were unable to right themselves when placed on the dorsum on a flat surface.

By 3 days of age the young could crawl about very well and could right themselves quickly. In part, these abilities may be a reflection of the aforementioned unfolding of the pinnae at this time.

For nearly the first 2 weeks of age the young were attached to the nipples of the adults almost constantly and remained enveloped by the membranes of the adults. With the exception of a few occasions when a young bat was

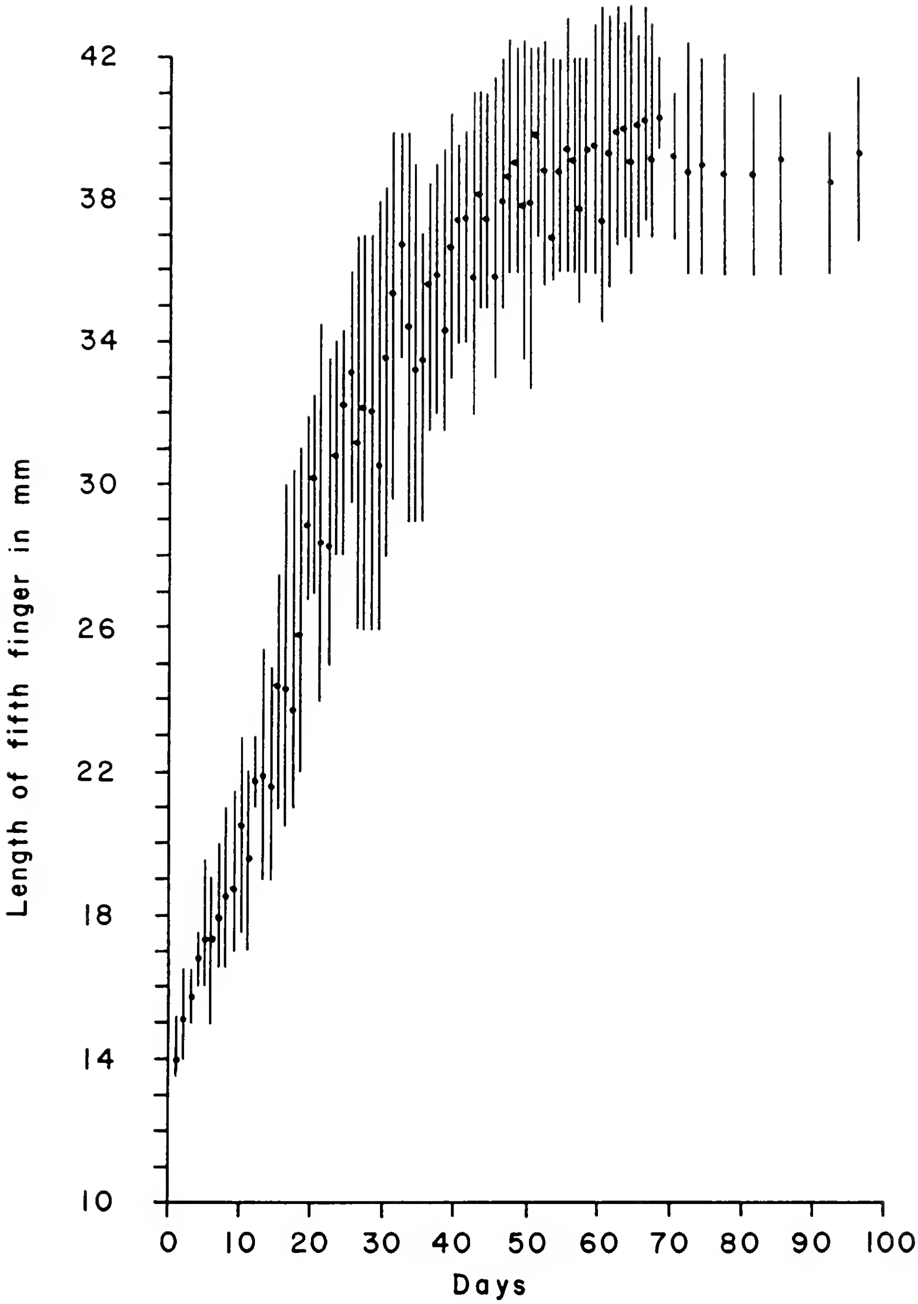

FIG. 5.—Fifth-finger lengths of young *Nycticeius humeralis*. Dots represent the arithmetic means and lines represent the ranges of measurements.

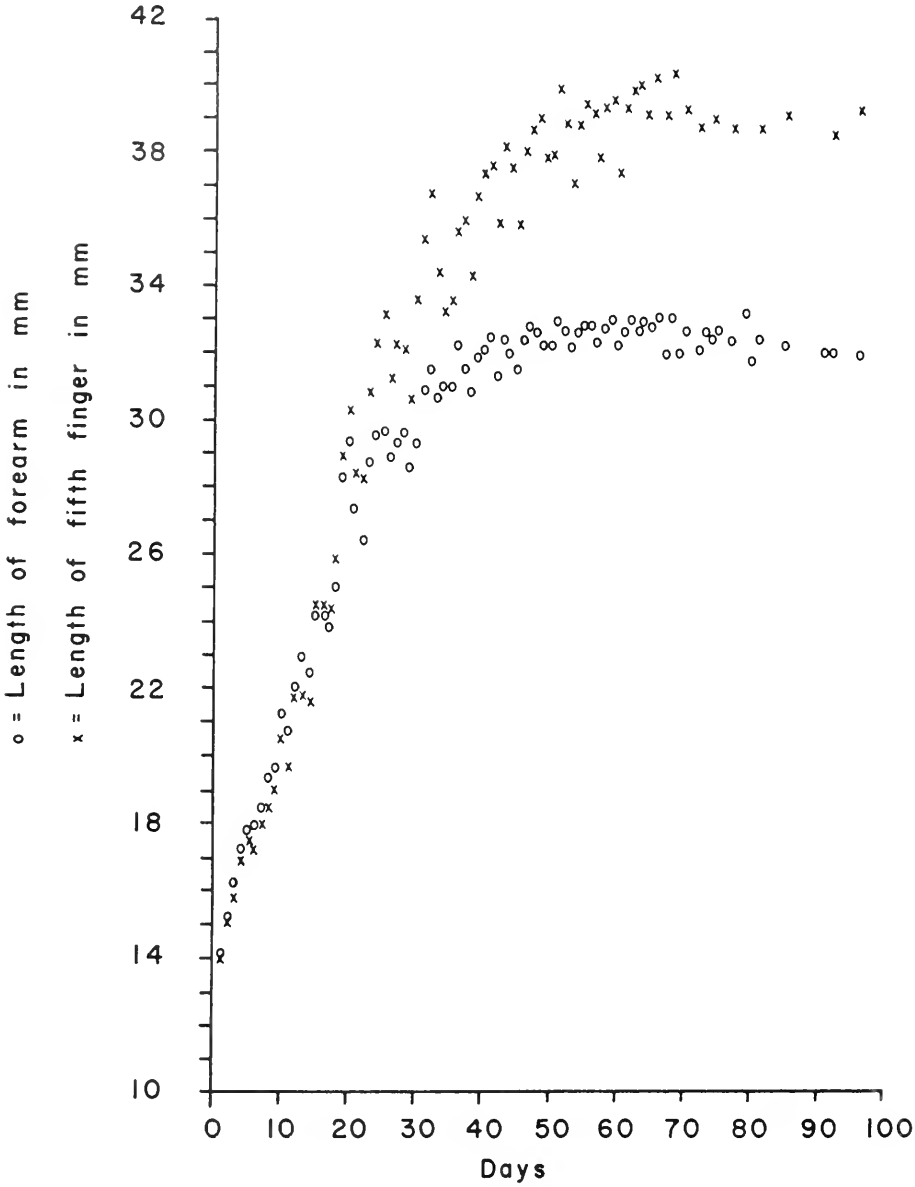

FIG. 6.—Relationships of forearm lengths and fifth-finger lengths of *Nycticeius humeralis*. Open circles represent arithmetic means of measurements of forearm lengths; crosses represent arithmetic means of measurements of fifth-finger lengths.

observed uncovered, the young did not leave the close association with the parent and move about in the containers until about 3 weeks of age. After this time, young scampered frequently about the cages, but hung adjacent to the female when at rest.

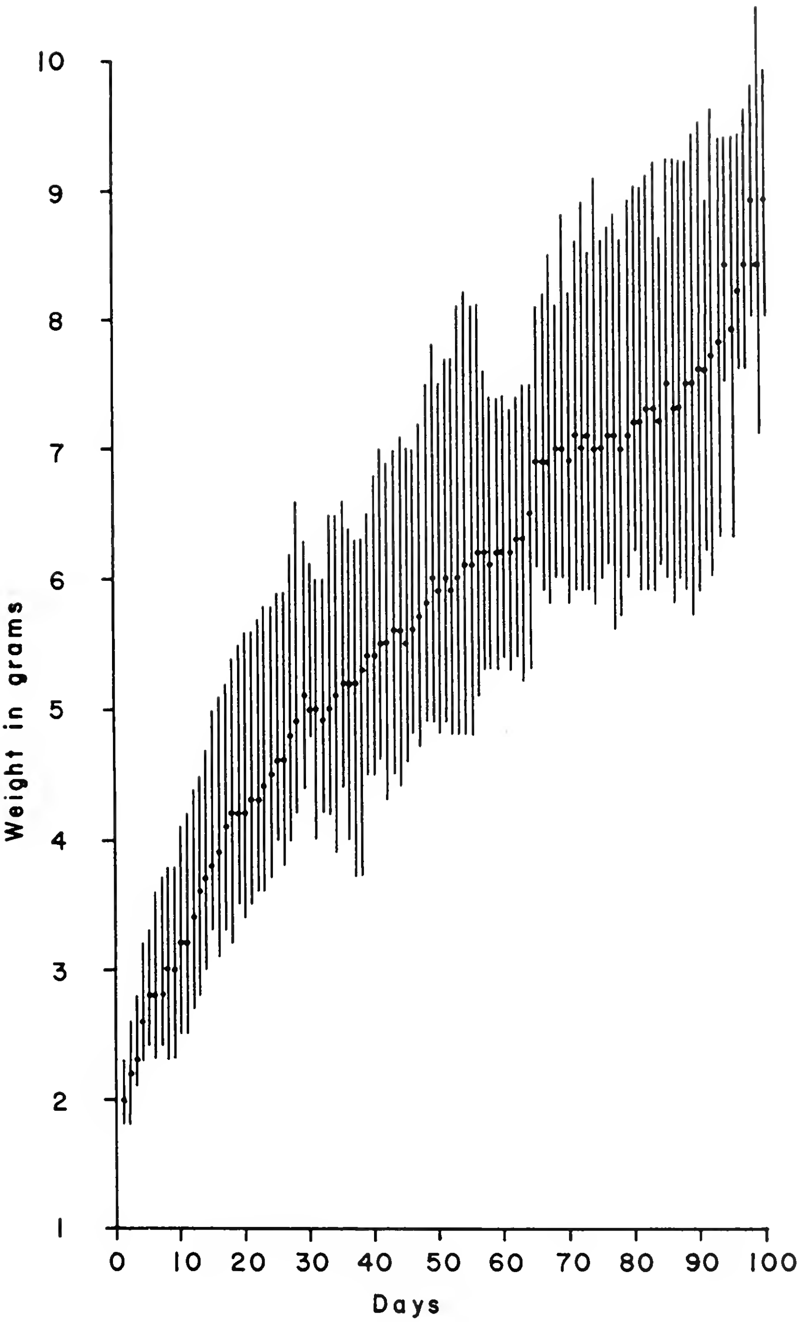

FIG. 7.—Weights of young bats. Dots represent the arithmetic means and lines represent the ranges of weights.

TABLE 2.—*The relationships of wing loading, proportions of the forearm and fifth finger, and total body weight of known-age* Nycticeius humeralis.

Age in days	Weight in g	Wing loading in lb/sq ft	Length of forearm/ length of fifth finger	Size of sample
1	2.0	0.5365	1.00	11
2	2.2	0.4067	0.99	11
4	2.6	0.4523	1.02	7
5	2.8	0.3765	1.02	8
8	3.0	0.3300	1.04	11
12	3.4	0.2500	1.02	19
15	3.8	0.2500	0.99	23
18	4.2	0.2433	0.97	23
35	5.2	0.2375	0.93	23
43	5.6	0.2220	0.85	22
60	6.2	0.2079	0.85	19
73	7.1	0.1921	0.85	19
97	8.4	0.2261	0.83	5

As mentioned previously, the young were highly vocal for the first 10 days following birth, but then made vocal sounds only when disturbed or handled. During these observations, the adults emitted sounds only when disturbed, handled, or sometimes when offered food.

Some definite specificities of adults for their young were noted. As long as the young bats were returned to the same nipples from which they were taken, no female refused to accept the young after they had been removed from the mother and measured or handled otherwise. On several occasions attempts were made to get adult females to accept nursing young from other females; all such efforts failed. The adults would bite and move away from the strange young. One young bat that was allowed to become attached to the nipple of a restrained female was attacked and thrown from her when the adult was released. This same adult accepted her own young a few minutes later. Litters and females could not be mixed successfully until nursing ceased. The refusal of adult females to accept other young may be a reflection of the manner in which the animals were maintained in relative isolation from other young and adults. Gates (1941) reported that he detected no specificity with regard to nursing young and adult females when the young and adults no longer remained together during periods of feeding.

The young first showed an interest in food and water at approximately 3 weeks of age, when they appeared to smell and lick items of food (portions of mealworm larvae) held before them. Early interests of young in water included considerable licking of the end of a water-filled dropper. At the age of 4 weeks, young bats were taking water from a dropper and eating small mealworms that were presented with forceps.

Throughout the course of this study, the adults were given mealworms from forceps and water was administered from a dropper. In only two cases

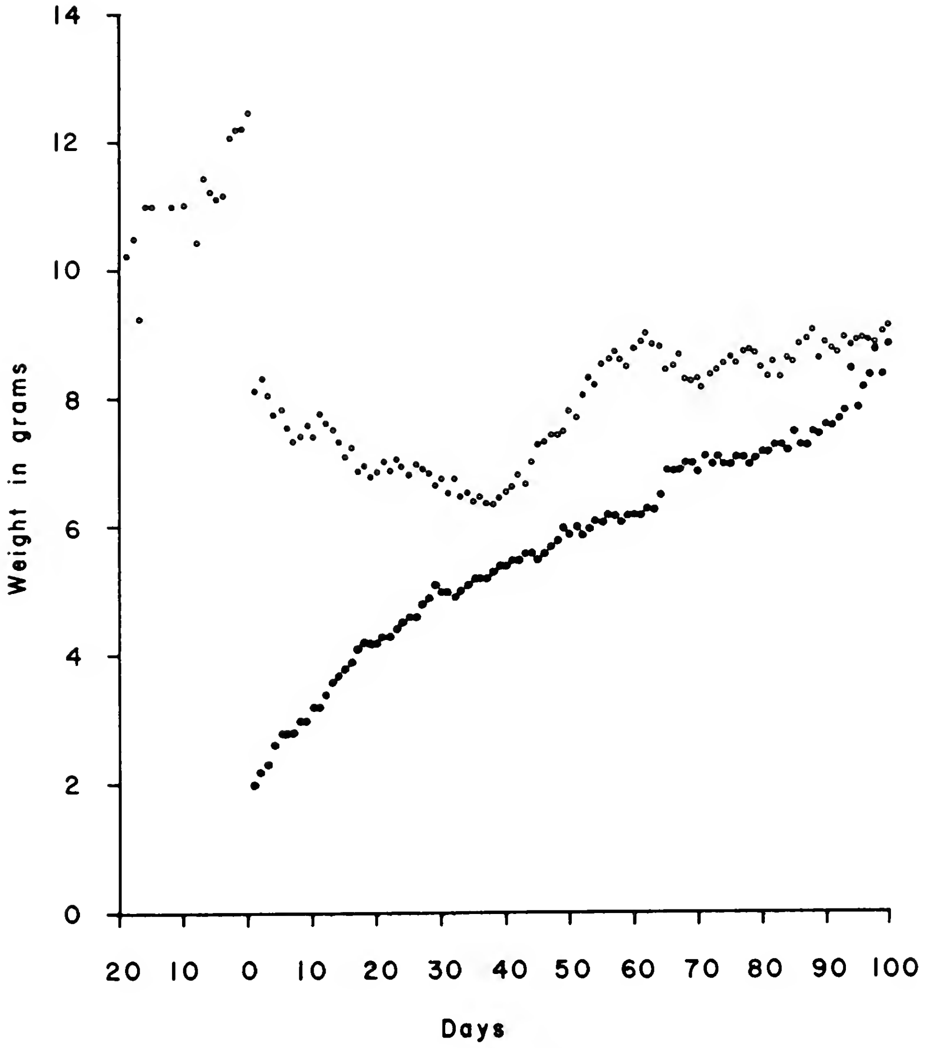

FIG. 8.—Weights of *Nycticeius humeralis.* Open circles represent arithmetic means of weights of adults and dots represent the arithmetic means of weights of young.

did individuals become accustomed to picking up and eating mealworms that were not presented by hand. In general, the bats made little effort to fly or move about while being fed and it was possible to feed four to six animals at one time. One adult crawled about almost continually while being fed. The young reared by this female behaved in similar fashion during the periods of feeding.

Some animals began eating immediately when food was offered; others simply held a food item in the mouth for a short time. During this time the

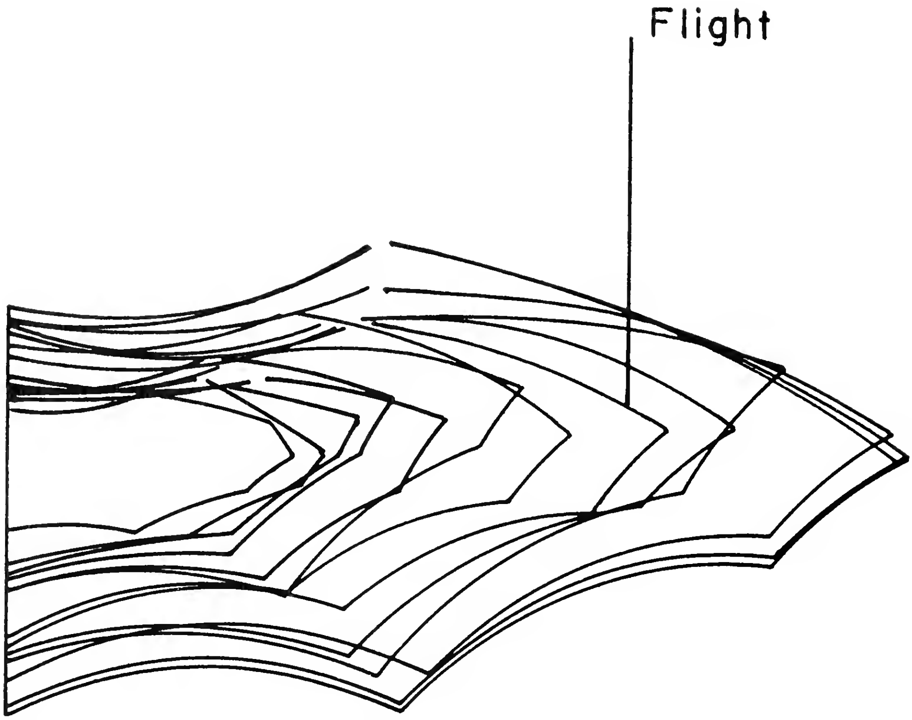

FIG. 9.—Actual outlines of a wing of a young *Nycticeius humeralis* of known age. Wing outlines were made when the bat was 1, 2, 4, 5, 8, 12, 15, 18, 35, 43, 60, 73, and 97 days of age.

animals exhibited considerable shivering, presumably while the body temperature was increased.

Growth.—Information relating to growth and development of young *Nycticeius humeralis* given herein is based upon bats born and reared in captivity. No malformations of any kind were noted and all animals seemed normal, but it is possible that under laboratory conditions the rate of growth and development may not have been normal.

Data regarding growth and development of young bats are presented in Tables 1 and 2 and Figs. 1–9. Because the length of the first finger and length of foot of newborn bats were noted to increase little between birth and adulthood, those measurements are not depicted graphically.

At 45 to 50 days of age, total length, length of tail, and length of fifth finger of young bats were of adult proportions and little growth occurred thereafter (Figs. 1, 2, and 5). Length of forearm, on the other hand, was of adult proportions when the bats were about 30 days of age (Figs. 3 and 4) and little growth occurred at later ages. Some sexual dimorphism of the length of the forearm was noted (Fig. 4). The smaller size of the forearm of males became apparent when the animals were about 20 days of age. Pearson, Koford, and Pearson (1952) found a similar situation in their studies of growth of *Plecotus townsendii.* In young bats, the proportional relationships of the length of the forearm and the length of the fifth finger (Table 2 and Fig. 6) are correlated with flight and are discussed later with regard to flight.

Weights of young bats were noted to increase rather constantly throughout the period of study (Figs. 7 and 8). Some activities of the bats, such as the development of the ability for flight and the acceptance of mealworms and water are reflected in the weights of the young. The gradual cessation of nursing and lactation seemingly is reflected more vividly in the weights of the adults (Fig. 8) than in the weights of young during the same period of time.

Growth, development, and relative surface area of the wings of bats of known ages are depicted in Fig. 9. The data presented indicate a gradual increase in surface area of the wing with the development of a wing of adult proportions at the age of 60 to 97 days; surface area is stabilized with the cessation of growth.

At the age when young bats first began to fly, several changes in the wings were apparent for the first time. The length of the fifth finger was greater than the length of the forearm (Table 2 and Fig. 6) and the distal portion of the wing, that area from the apex of the wing to the first and fifth fingers, was nearly equal in surface area to the proximal portion of the wing, that region between the body and the first and fifth fingers (Fig. 9). In addition, there was a change in the ratio of body weight to surface area of the wing (Table 2).

Discussion

Data on various aspects of growth and development of some species of North American vespertilionids have been presented by Pearson *et al.* (1952), Orr (1954), and others. The availibility of these data permits a general comparison of the rates of growth and development of *Nycticeius humeralis* with those of *Plecotus townsendii* and *Antrozous pallidus.*

The development of fur over the entire body of young evening bats was completed by 8 to 9 days of age. Short gray hair covered the bodies of *Plecotus* 4 days old and scanty fur was evident on the bodies of *Antrozous* at 10 days of age.

The eyes of young *Nycticeius* were opened at the age of 18 to 24 hr, but eyes of young *Plecotus* and *Antrozous* were not opened until the age of 7 to 10 days. Pinnae of young *Nycticeius* were erected after 2 to 3 days of age; pinnae of the two other species were erected after 7 days of age. Vocalization was noted almost immediately following birth of *Nycticeius* and was evident within a few hours after birth of *Plecotus.*

The complete set of deciduous teeth of *Nycticeius* was present at birth and these teeth were grown out fully by 7 days of age. Orr (1954) found the deciduous premolars lacking in newborn *Antrozous,* but noted that the deciduous teeth were grown out fully by the second week of age. In *Nycticeius*, all of the permanent teeth were erupted at an age of 4 weeks, and in *Antrozous*, permanent teeth were erupted at an age of 5 weeks.

The forearm in young *Nycticeius* was of adult proportions at 30 days of age, but the forearm in young *Plecotus* reached adult size at 21 days of age.

Comparisons of the rates of growth and development of the young of *Nycticeius humeralis*, *Plecotus townsendii*, and *Antrozous pallidus*, indicate that young *Nycticeius* exhibit more rapid growth and development and are perhaps more precocious than young of the other species.

On the basis of the data presented in this report, it seems that young *Nycticeius humeralis*, prior to 18 days of age, simply lack adequate surface areas of wing membranes to support the weight of the body in flight. For information with regard to surface areas of flight membranes and body weights of bats, see Vaughan (1959 and 1966) and Struhsaker (1961). In addition to the relationships of surface areas and weights, other factors of growth and development must have considerable bearing on the abilities of young bats to fly. For example, both lift and power for flight of young bats must be highly dependent upon the development of the ventral thoracic flight muscles as well as development of the musculature of the entire forelimb. For a discussion of surface areas of flight membranes and volumes of flight muscles in relation to total volumes of the body, see Struhsaker (1961), and for descriptions and discussions of flight muscles, see Vaughan (1959 and 1966). It was noted that after the forearm of the bats observed during this study reached maximum length (at about 30 days) there was an increase in diameter of this portion of the forelimb. This increase in diameter of the forearm was noticed especially at the proximal portion and was due apparently to growth and development of the muscles that are located in this region.

Sexual dimorphism in the surface area of wings was not detected, but some dimorphism in the length of the forearm was noted (Fig. 4). The slightly greater length of the forearm in females implies that perhaps females may be capable of supporting a slightly greater load in flight than males.

At 18 to 21 days of age when young bats were capable of flight for the first time, the relationships of the surface areas of the wings to the total weights of the animals (Table 2) perhaps were indicative of the optimal wing loading for flight in the species of bat considered herein. If this were true, an indication of maximum weight-carrying capacity of these bats could be obtained by comparing the wing loadings of bats capable of first flight with wing loadings of mature animals. It is of interest that none of the young bats were capable of flight unless the wing loading was less than 0.250 lb per sq ft (Table 2). Young bats may be capable of flight with the optimal wing loading for the species, but probably would lack the coordinations and skills of flight that were developed in the adults, thus more mature bats probably have the ability to carry extra weight at least for brief periods of time. The achievement of the relationship of surface area versus weight was correlated closely with the relative growth rate of the forearm and fifth finger (Table 2 and Fig. 6). Wing loading of adult animals (73 and 97 days of age) varied from 0.1921 to 0.2261 lb per sq ft. On the basis of these aforementioned data, it can be suggested that, allowing for reasonable amounts of variation, adult animals with a weight of 9 to 11 g would have a wing loading not far removed from the postulated maximum of about 0.2500 lb per sq ft.

According to Gates (1941), weight of two females prior to parturition was 11.6 g each. Some of the females observed in this study weighed as much as 14 g (the average was slightly more than 12 g) prior to parturition, but these animals were kept in confined situations. At the time of capture, 20 days before parturition, average weight of females was slightly more than 10 g (Fig. 8). Because weights of newborn bats recorded during this study were greater than weights of young bats given by Gates (1941), it is suggested that the young and females kept in captivity may have weighed more, due to overfeeding, than animals living in natural conditions.

Bats have been reported to carry various weight loads in addition to the normal weight of the body (Davis and Cockrum, 1964). The weight carrying capacity of individuals of any given species of bats undoubtedly is important with regard to the relationships between adult females and the young, and may be reflected in the behavior of adults prior to and following parturition. As noted earlier in this report (Table 1), young *Nycticeius humeralis* remained associated closely with the parents for nearly 3 weeks. This relationship may be a reflection of the methods of housing the animals during these observations. Gates (1941) suggested that the young remained with the adult for less than 10 days and he implied that this is a reflection of the weight carrying capacity of the adults. Hamilton (1943) mentioned that nursing female *Nycticeius* probably do not carry the young while foraging for food. The relationships of weights, surface areas of flight membranes, and related abilities of flight of the animals may be reflected in the selection of sites for roosting by adults both prior to and following birth of the young.

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A COMPARATIVE STUDY OF GROWTH AND DEVELOPMENT OF THE KANGAROO RATS, *DIPODOMYS DESERTI* STEPHENS AND *DIPODOMYS MERRIAMI* MEARNS

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During a recent study of sexual behavior and reproduction of the kangaroo rats, *Dipodomys deserti* and *Dipodomys merriami,* a comparison of growth and development of closely related sympatric species reared under identical laboratory conditions was possible. Litters born in the laboratory were carefully examined and measured from birth to maturity.

Although growth in other genera of mammals has been carefully studied, few instances of breeding in the genus *Dipodomys* have been recorded and limited growth data are available. The solitary nature of the animals prevents laboratory breeding under ordinary conditions. Animals confined in restricted space engage in fighting which usually results in the death of one or both of them. Chew and Butterworth (3) published an analysis of growth and development of Merriam's kangaroo rat, *D. merriami* in which the senior author was successful in laboratory breedings of this species. The scattered literature on growth and development in the genus *Dipodomys* is summarized in their paper.

Materials and Methods

A total of 32 laboratory animals representing 8 *D. deserti* litters and 4 *D. merriami* litters that were the direct progeny of wild parents were used in this study. Seven of the 8 litters of *D. deserti* were the products of laboratory breedings, the first recorded instances for this particular species. The other litters were from pregnant females captured in the field and brought back to the laboratory for observation and which subsequently produced young.

The parent animals were all obtained from one locality at the western edge of the Mojave Desert near the base of Alpine Butte located approximately 16 miles northeast of Palmdale in Los Angeles

County, California. The altitude of the collecting area was approximately 1000 meters (3261 feet).

The captive animals were placed in two large breeding cages measuring 3 by 4 meters at the University of Southern California. A partition separated the two cages and sand and desert soil up to several inches in depth was spread on the floor. Animals were allowed to run in these cages without restriction. Nesting sites consisting of glass bottles, empty cardboard mailing tubes and cardboard boxes were provided. One pair of each species was placed in each cage. Instances of breeding in *D. deserti* occurred in these cages. Animals were fed rolled oats and sunflower seeds. Lettuce was provided and water was also made available. An excess amount of food material was always available.

All animals were measured from birth and the measurements were continued daily or at frequent intervals until adult sizes were attained. Standard measurements of total length, tail length, hind foot length, ear (from the notch) length, and body weight were taken. Measurements were analyzed as in Brody (2) and values were plotted on a semilogarithmic scale against age on the arithmetic scale. Linear segments of such a plot indicate periods when growth increments are constant percentages of previous sizes. From these linear sections instantaneous growth rates were calculated as:

$$K = \frac{\ln m_2 - \ln m_1}{t_2 - t_1}$$

The value of *K* is the instantaneous percentage rate of growth for the unit of time in which t_2 and t_1 are expressed. Ln m_2 and ln m_1 are natural logarithms of the measurements made at t_1 and t_2.

Observations and Discussion

General Development. The general pattern of development in *D. deserti* is similar to that described by Chew and Butterworth (3) for *D. merriami.* The desert kangaroo rat is born hairless and has a thin, pink, wrinkled, transparent integument. Viscera are apparent through the skin of the venter and sutures and blood vessels on the skull are visible. The snout area containing the vibrissa sheaths appear to be swollen and are richly vascular. The yellowish-brown vibrissae are about 6 millimeters long at birth, but lengthen to 13 mm. in 5 days and

23 mm. by 15 days. The adult length of 72 mm. is attained by 90 days.

Black pigmentation appears about 5 days after birth. The pigmentation begins on the dorsum and top of the head. A faint dorsal tail stripe is present. The end of the tail is unpigmented for 10 mm. and then a black ring circles the entire tail for about 7 mm. The black area extends on the dorsal side of the tail for about 30 mm. and shades out to a pale gray color. The entire ventral surface of the tail is white except for the small black area near the tip. The feet and venter are white. The site of the dermal gland shows as a light depression just posterior to the scapulae. It darkens by 15 days, begins to lighten by 19 days and is covered with hair by 21 days. The head is sufficiently pigmented by 7 days so that the dorsal cranial sutures and blood vessels are no longer visible. By 21 days the mammae have become very distinct. The insides of the thighs and the venter, in general, are sparsely haired until about 15 days. By 21 days the animal is fully furred and the color pattern of the young is now similar to that of the adult. The young appear darker than the parents, however.

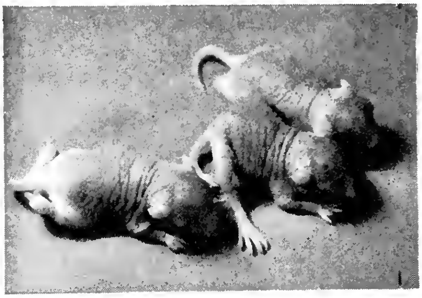
The pelage of *D. merriami* is a darker yellowish-buff than that of *D. deserti,* the white tail stripe is wider than the dark tail stripe, and the terminal tuft is brown. Dark whisker patches are distinct in *D. merriami* but are absent in *D. deserti.* Juvenile *D. merriami* are completely furred by 15 days. Developmental stages are shown in Figures 1 to 6.

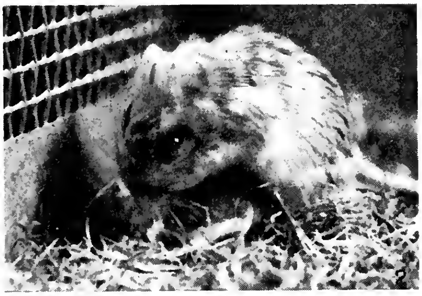
The pinnae of the ears, closed at birth, and only two mm. in length gradually open from 9 to 15 days. The length of time until opening varies with different litters. The ears are fully opened by 15 days in *D. deserti* and by 10 days in *D. merriami.*

The nails are soft at birth and gradually become hard by 15 days in both species.

The incisor teeth appear later in *D. deserti* than in *D. merriami.* They break through the gums at about 2 days in the latter (Chew and Butterworth, 3) while they do not appear until about 9 days in the former. Teeth are white at first but gradually darken to yellow. By 25 days the teeth of *D. deserti* are strong enough to pierce the skin of man.

Eye development is summarized in Figure 7 for various species of kangaroo rats. In my laboratory, individuals of *D. deserti* had their eyes open as follows: 3 on the 15th day; 3 on the 16th day and 6 on





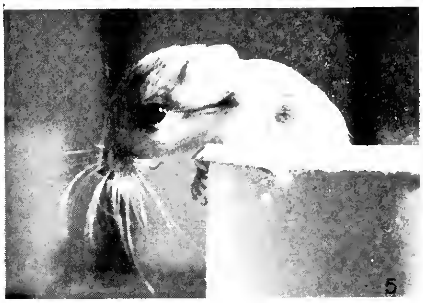


FIGURE 1

Dipodomys deserti, 3 days old. Note absence of hair and the relative sizes of the feet. Both eyes and ears are tightly closed.

FIGURE 2

Dipodomys merriami, a mother nursing her young.

FIGURE 3

Dipodomys deserti, 10 days old. A litter of 5. Note the white tail tip, one of the distinguishing features of this species.

FIGURE 4

Dipodomys merriami, 11 days old. A litter of 3.

FIGURE 5

Dipodomys deserti, 16 days old. From the same litter as pictured in Figure 3.

FIGURE 6

Dipodomys merriami, 16 days old

the 17th day. *D. merriami* had their eyes open between the 11th and 15th days.

Species	Days after birth that eyes open	Reference
Dipodomys deserti	15–17	Butterworth
D. deserti	16	Rush (8)
D. merriami	11	Butterworth
D. merriami	11–15	Chew and Butterworth (3)
D. merriami	21	Doran (5)
D. merriami	by third week	Reynolds (7)
D. heermanni	12–15	Fitch (6)
D. heermanni	14–16	Tappe (9)
D. nitratoides	13–14	Culbertson (4)
D. spectabilis	14	Bailey (1)

FIGURE 7
Eye development in various species of kangaroo rats.

A comparison of general development in the two species in this study is shown in Figure 8.

	Days after birth	
	D. deserti	*D. merriami*
Eyes open	11–17	11–15
Ears open	9–15	8–10
Incisor teeth erupt	7–10	2–8
Solid food eaten	15	13
Solid feces first noted	15	17
Nails harden	12–15	12–15
Sand used for cleaning pelage	17	13–15
Well haired	11–15	14
Weaned	15–25	17–22
Mammae first visible	21	11
Drumming with feet first noted	33	—

FIGURE 8
Comparison of sequences of general development of *Dipodomys deserti* and *Dipodomys merriami*. Selected features based on 8 litters of *D. deserti* and 4 litters of *D. merriami*.

Growth Analyses: A comparison of weight increases in *D. deserti* and *D. merriami* is shown in Figures 9 and 10. Weights become constant at adult levels of approximately 145 grams in *D. deserti* and 40 grams in *D. merriami*. An analysis indicates that early growth is rapid in *D. merriami* and continues more slowly toward the maximum weight. At 10 days *D. deserti* had reached 16 per cent of its total adult weight while *D. merriami* had attained 26 per cent of its adult weight. At 30 days the two species had reached approximately half their maximum weight, 47 per cent in *D. deserti* and 53 per cent in *D. merriami*. At

	15 days		20 days		30 days		50 days		90 days	
	D.d.	D.m.	D.d.	D.m.	D.d.	D.m.	D.d.	D.m.	D.d.	D.m.
Total length	47	54	55	70	72	80	83	95	97	99
Tail length	39	47	50	61	73	81	91	97	93	99
Foot length	70	82	80	87	82	95	96	99	100	100
Ear length	63	63	67	82	78	90	81	95	88	99
Weight	27	35	33	43	47	53	75	64	91	78

FIGURE 9

Percentages of growth toward maturity completed at indicated intervals in *D. deserti* and *D. merriami.*

50 days *D. deserti* had reached 75 per cent of its adult weight while *D. merriami* had only attained 64 per cent. At this point *D. merriami* lagged behind and then very slowly approached the maximum weight. At 90 days *D. deserti* had attained 91 per cent of its weight while in *D. merriami* only 78 per cent had been reached. In the later phases of growth *D. merriami* gained weight more slowly than *D. deserti.* Both attained full adult average weights by 150 to 180 days.

In total length (Figures 9 and 11) *D. merriami* grew more rapidly than *D. deserti* throughout the growth period. Maximum adult lengths are difficult to measure but approximate adult dimensions are attained by 90 days.

The tail of *D. merriami* (Figures 9 and 11) grew faster than that of *D. deserti* during the developmental period. After 90 days *D. merriami* had little tail growth while *D. deserti* continued to increase its tail length by 7 per cent.

The foot (Figures 9 and 12), which was already well developed at birth, grew fastest of all. At 15 days *D. deserti* had a foot 70 per cent of adult size while *D. merriami* had attained 82 per cent of the adult foot size. Both species attained maximum foot size between 50 and 90 days.

The ear (Figures 9 and 12) grew rapidly in both species, that of *D. merriami* faster than that of *D. deserti.* The ear was approximately fully grown by 90 days in *D. merriami* but continued to grow slowly in *D. deserti.*

Size of the litter (Figure 13) made little difference on increases in weight of *D. deserti.* Litters containing 2, 3, 4, and 5 individuals were compared and showed very little variation in weight changes. Apparently all individuals in the respective litters received sufficient food both by nursing and individually after weaning. Litters of *D. merriami* were not numerous enough to permit these observations.

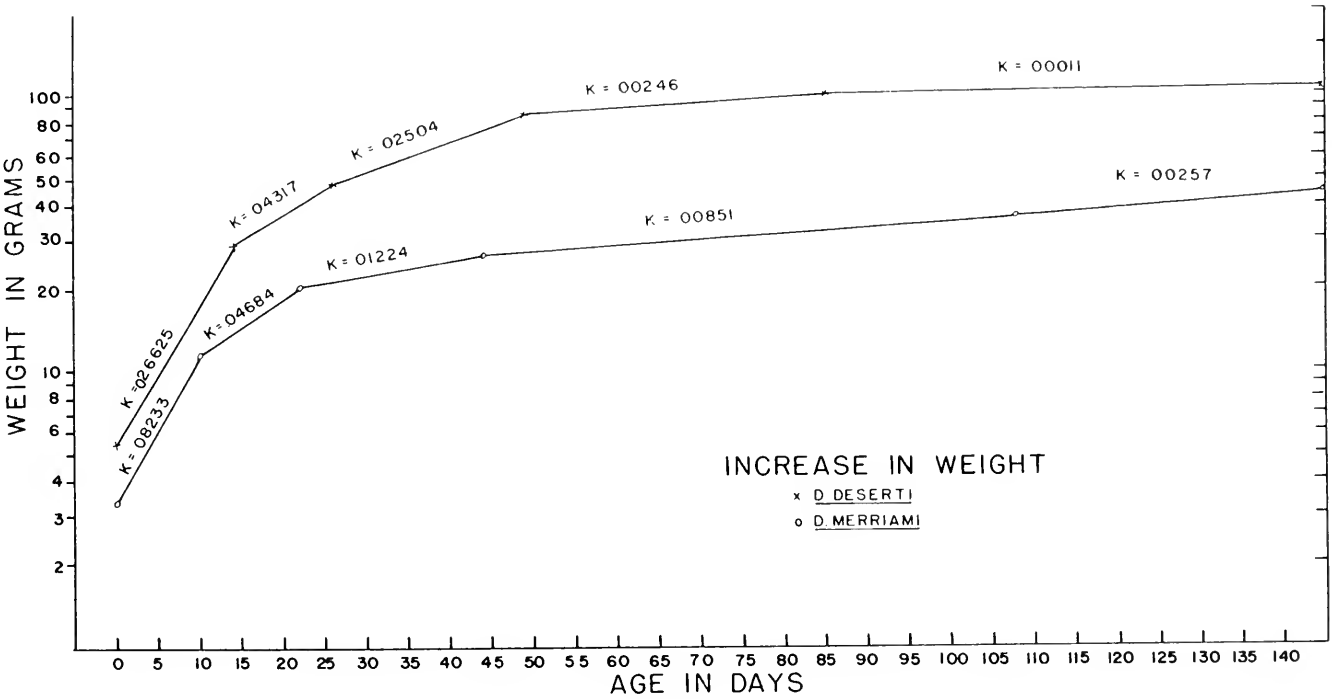


FIGURE 10

A comparison of weight increases during the growth of *D. deserti* and *D. merriami*, semilogarithmic plot; the value times 100 equals the percentage of increase per day during a particular growth phase. The *K* values above the segments of the plot are instantaneous growth rates. Weights are means of 12 litters of animals.

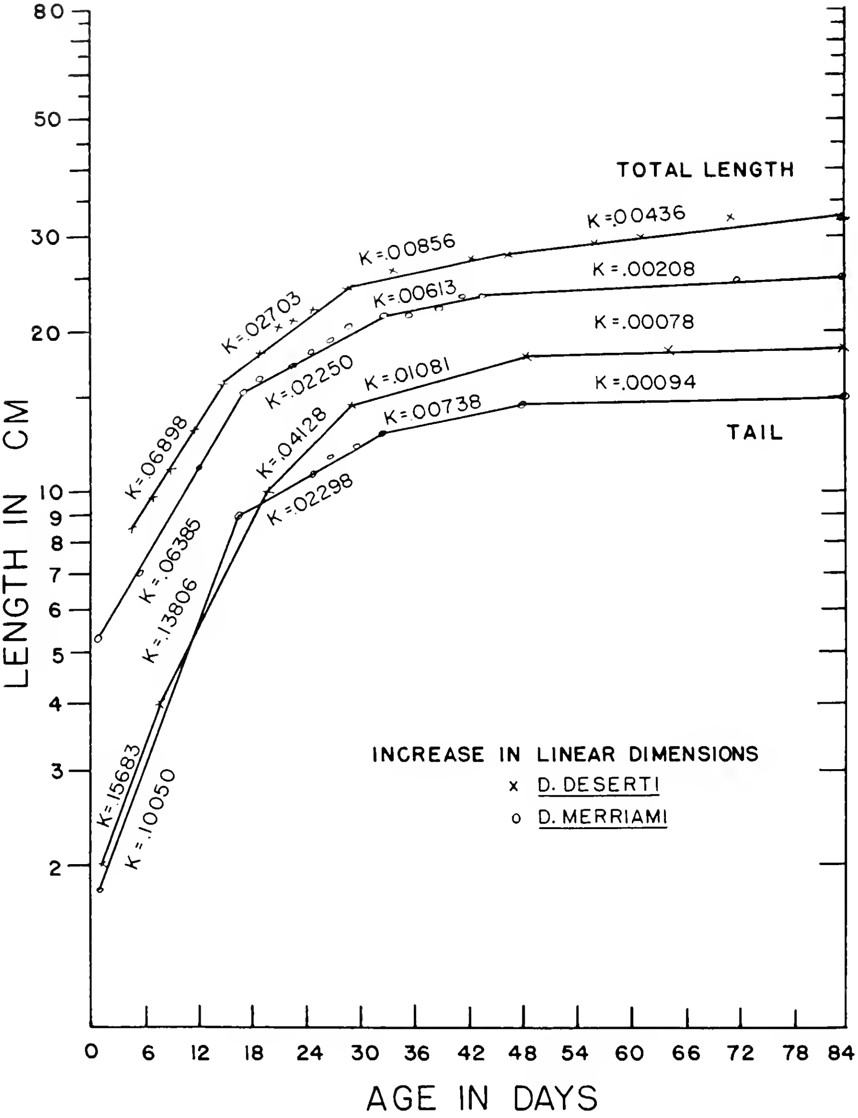


FIGURE 11
A composite graph showing increase in linear dimensions of total length and tail length in *D. deserti* and *D. merriami,* semilogarithmic plot.

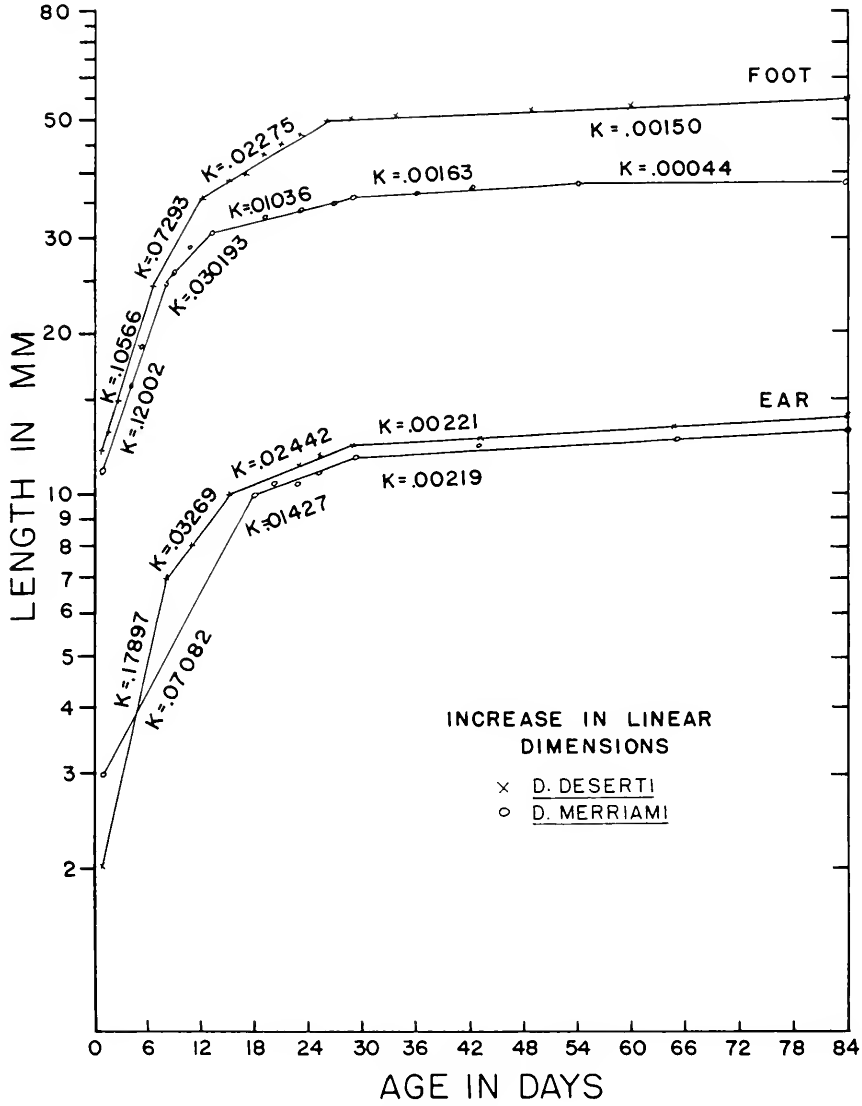


FIGURE 12

A composite graph showing increase in linear dimensions of foot length and ear length of *D. deserti* and *D. merriami*, semilogarithmic plot.

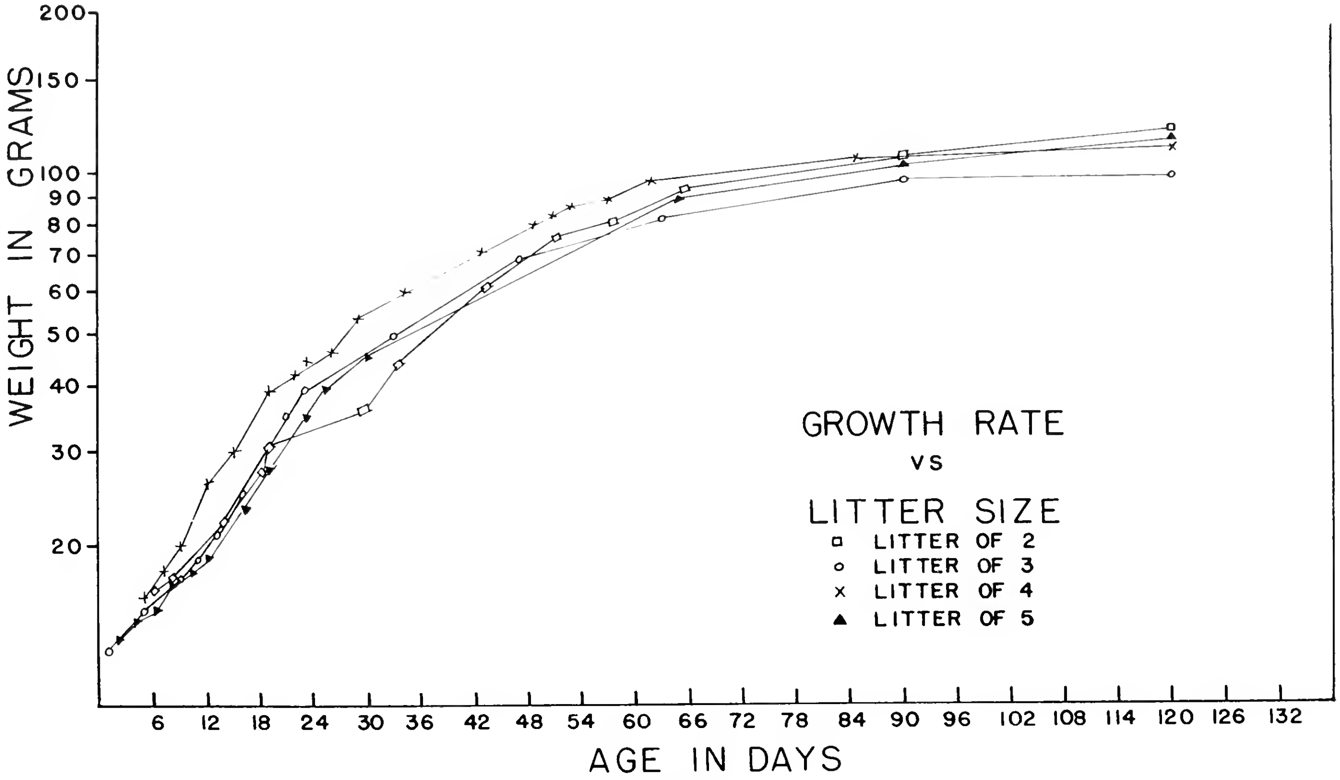


FIGURE 13
Growth rate versus litter size in *D. deserti* semilogarithmic plot. Measurements are means for each litter.

The differential rates of growth during development in the two species of kangaroo rats is significant. The smaller *D. merriami* matures more rapidly than the larger *D. deserti.* The development of various body parts in growing juveniles of *D. merriami* demonstrates more rapid growth and an earlier maturity than *D. deserti.* The precocious growth, especially during early development, brings *D. merriami* to an earlier seasonal reproductive potential than *D. deserti* and may allow for an earlier dispersion. Rapid development may be one contributing factor for the larger geographical range of Merriam's kangaroo rat.

SUMMARY AND CONCLUSIONS

The growth and development of two sympatric species of kangaroo rats is discussed, utilizing data from 8 litters of *D. deserti* and 4 litters of *D. merriami* reared under identical laboratory conditions. General development and sequences of hair acquisition are described. Animals of both species were completely furred by 15 days. Their pelages were darker than those of their parents.

The ears, which were closed at birth, opened in 15 days in *D. deserti* and in 10 days in *D. merriami.* The nails hardened by 15 days in both species and the teeth erupted after 5 days in *D. merriami* and in 8 days in *D. deserti.* The teeth were white at first but gradually darkened to a shade of yellow. Eyes opened at about 16 days in *D. deserti* and from 11 to 15 days in *D. merriami.*

Instantaneous growth rates were calculated for various measurements, such as weight, total length, tail length, foot length, and ear length. Both species of kangaroo rats attained average adult weights from 150 to 180 days. Each species reached approximately one-half of its adult weight by 30 days. Early growth was rapid in *D. merriami* but continued more slowly toward maximum weight. *D. deserti* attained maximum adult weight at a slightly earlier age than *D. merriami.* In total length, *D. merriami* grew more rapidly than *D. deserti* throughout the growth period. Both grew to approximately adult lengths by 90 days. The tail of *D. merriami* grew faster than that of *D. deserti* during development. After 90 days *D. merriami* had little tail growth while the tail of *D. deserti* continued to increase slowly in length. The foot showed the fastest development. By 15 days *D. deserti* had 70 per cent of its adult size while *D. merriami* had attained 82 per cent of its adult size. Both species attained maximum size between 50 and

90 days. The ear of *D. merriami* grew slightly faster than that of *D. deserti*. Ears were almost completely grown to adult size in *D. merriami* by 90 days. They continued to grow slowly in *D. deserti*. Size of litter made no appreciable difference in growth rates.

The precocious early development of *D. merriami* may partly explain its larger geographical range.

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Article IX.—CRANIAL VARIATIONS IN NEOTOMA MICROPUS DUE TO GROWTH AND INDIVIDUAL DIFFERENTIATION.

By J. A. Allen.

Plate IV.

In view of the stress naturally, and very properly, laid upon the importance of cranial characters in the discrimination of species in groups of closely-allied forms, it seems desirable to ascertain the character and amount of change in not only the general form of the skull but in the form of its separate bones due to growth, and also to determine the amount and kind of individual variation that may be expected to occur in skulls unquestionably of the same species. Having of late had occasion to examine a large amount of material relating to the genus *Neotoma*, the subject has been forcibly brought to my attention, and some of the results of a careful examination of a large series of skulls pertaining to several species of this genus are here presented. No attempt is made to treat the subject exhaustively, only a few special points being here presented.

As is well known to all experienced workers in mammalogy, the general contour of the brain-case, the relative size and form of individual bones, notably the interparietal, and the condition of the supraorbital and other ridges for muscular attachment, alter materially after the animal reaches sexual maturity; the deposition of osseus matter, the closing of sutures, the building out of crests and rugosities continuing throughout life, so that a skull of a very old animal may differ notably from that of an individual of the same species in middle life, and this latter from one just reaching sexual maturity.

The Museum has at present a large series of specimens of *Neotoma micropus* Baird, including ages ranging from nursling young to very old adults. They are mainly from three localities in the eastern coast district of Texas, namely, Brownsville, Corpus Christi, and Rockport. In order to avoid any complications that might arise through geographic variation, only the specimens from Rockport and Corpus Christi—localities less than twenty-five miles apart, and similar in physical conditions—are here considered. There is not the slightest reason for questioning their conspecific relationship. The series selected to illustrate variations due to age are, with one exception, from Rockport; those figured to show individual variation are all from Corpus Christi.

Variations due to Age.

General Contour.—The variation in the general form of the skull resulting from growth is due mainly to the lengthening of the several skull segments without a corresponding relative increase in the breadth of the skull. Hence in the young skull, in comparison with an adult skull of the same species, the brain-case is disproportionately large in comparison with the anteorbital and basal portions of the skull. This is well shown in Plate IV, and in the subjoined table of measurements of three

Measurements and Ratios showing Cranial Variations due to Age in *Neotoma micropus*.

	No. 5834, ♀ juv.	Ratio[1]	No. 4480, ♂ juv.	Ratio[1]	No. 4478, ♂ very old.	Ratio[1]
Occipito-nasal length	31	100	41	100	53	100
Length of nasals	10	32.3	14.5	35.4	22	41.5
Length of frontals	13	42	15	36.6	18	34
Length of parietals on median line	5	19.4	6	14.6	8	15
Greatest length of parietals	12	39	15	36.6	16	30.2
Length of interparietal	4.5	14.5	5.5	13.4	7	13.2
Length of brain-case	14	45.2	17	41.5	21	39.6
Greatest rostral breadth	5.5	17.7	6.3	15.4	6.5	12.3
Least interorbital breadth	6	19.4	6	14.6	6	11.3
Breadth of brain-case	16	51.6	19.5	45	20	38
Breadth of interparietal	11	35.5	10	24.4	7.5	14.2
Greatest zygomatic breadth	20?	64.6	23	56.1	30	56.6
Depth of skull at middle of palate	8	26	11	26.8	15	28.5
Depth of skull at front of basisphenoid	11	35.5	12	29.3	14	26.4
Length of tooth-row (crown surface)	8[2]	25.8	8	19.5	9	17
Length of incisive foramina	6	19.3	8.5	20.7	11.5	21.7
Width of incisive foramina	3	9.7	3	7.3	3.5	6.6
Length of palatal floor	5	16.1	7	17	7	13.2

[1] Ratio to occipito-nasal length.
[2] From No. 4482, ♀ juv., in which the last molar has just come into use.

specimens of *N. micropus* from Rockport, Texas. No. 5834, ♀ juv., is a nursling so young that the last molar is still wholly enclosed in the jaw;[1] No. 4480, ♂ juv., though not quite full-grown, would pass as a 'young adult'; No. 4478, ♂ ad., is a very old male, with the teeth well worn down, and the fangs visible at the alveolar border. Other specimens in the series furnish a complete series of gradations between the two extremes (Nos. 5834 and 4478).

In general contour (Figs. 1–11, Pl. IV), the young skull, in comparison with adults, is much more convex in dorsal outline,[2] very broad posteriorly, and very narrow anteriorly. In comparing the relative length of the several skull segments the occipito-nasal length is taken as the basis, and the skulls will be referred to as *A* (=No. 5834), *B* (=No. 4480), and *C* (=No. 4478).

Rostral Segment.—In *A* the ratio of the rostral segment to the total length is 32.3 per cent.; in *B*, 35.4; in *C*, 41.5—giving a rapid *increase* in the ratio with age.

Frontal Segment.—In *A* the ratio of the frontal segment—*i. e.*, the distance between the naso-frontal and fronto-parietal sutures—to the total length is 42 per cent.; in *B*, 36.6; in *C*, 34—a considerable *decrease* in the ratio with age.

Parietal Segment.—In *A* the ratio of the parietal segment—*i. e.*, the distance from the latero-anterior angle of the parietal bone on either side to the occipito-parietal suture—to the total length is 39 per cent.; in *B*, 36.6; in *C*, 30.2—again a rapid decrease in the ratio.

Brain-case.—The length of the brain-case in *A* is 51.6 per cent. of the total length of the skull; in *B*, 45; in *C*, 38.

In each case the change in ratio is due to the disproportionate growth of the rostral portion of the skull. Thus in *A* the nasals have a length of only 10 mm.; in *B* they have increased to 14.5 mm., and in *C* to 22 mm., while the total occipito-nasal length of

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[1] The length of the tooth-row given in the table is taken from an older specimen (No. 4482, ♀ juv.), in which the last molar has reached the level of the others and is just beginning to show traces of wear.

[2] In Figs. 10 and 11 it should be noted that the greater flatness of the skull interorbitally, as compared with Fig. 6, is masked by the raised supraorbital borders in the older skulls when viewed in profile.

the skull has increased only from 31 mm. in *A* to 53 mm. in *C*. In other words, the nasal bones have increased in length 120 per cent., while the total length has increased only 77 per cent.

Transverse Breadth.—In respect to the breadth of the skull the variations with growth are much less than in its length. Thus the greatest diameter of the rostrum varies only from 5.5 mm. in *A* to 6.5 in *C*—an increase of about 20 per cent. in the breadth of the rostrum, against an increase of 120 per cent. in its length. The interorbital breadth remains nearly constant, being 6 mm. in all three of the skulls here compared. The width of the brain-case shows an increase of 25 per cent. against an increase in the total length of the skull of 77 per cent. The zygomatic breadth shows an increase of about 50 per cent., due almost wholly to the thickening and increased convexity of the zygomatic arches.

Vertical Depth.—In respect to the depth of the skull, the variations with age prove especially interesting, although only such as would be expected from the facts already given. For present purposes the depth of the skull is taken at two points, namely, (*a*) at the middle of the palatal region, and (*b*) at the posterior border of the basisphenoid (basisphenoid-basioccipital suture). The palatal depth increases markedly with age, correlatively with the growth of the rostrum ; the basisphenoidal depth changes but slightly after the molars have attained to functional development. Thus in *A* the basisphenoidal depth is 11 mm. ; in *B*, 12 mm. ; in *C*, 14 mm.—an increase of about 28 per cent. The palatal depth in *A* is 8 mm. ; in *B*, 11 mm. ; in *C*, 15 mm.—an increase of nearly 88 per cent.

Tooth-row.—The length of the upper tooth-row varies about 12 per cent., due almost wholly to the wearing down of the teeth, the length of the crown surface being much less, in slightly worn teeth, than the length taken at the alveolar border.

Interparietal.—The interparietal shows surprising modification with age, both as to size and form, but especially in respect to the latter. At early stages, as in *A*, this bone is more or less crescentic in shape, with the transverse diameter more than twice the antero-posterior diameter. Thus in *A* the two diameters are respectively 11 and 4.5 mm.; in *B*, 10 and 5.5 mm.; in *C*, 7.5 and 7 mm. In other words, the short, broad, convex sub-crescentic interparietal in *A* becomes transformed in *C* into a squarish, flat bone in which the two diameters are nearly equal, instead of the transverse being twice as great as the antero-posterior, as in *A*. This would be almost incredible were not the proof so abundantly furnished by the material in hand, where every stage of transition is shown. (Figs. 1–8, Pl. IV.) This change is coincident with the development of the raised supra-orbital borders and their prolongation backward as ridges to the parieto-occipital suture, and the flattening of the whole dorsal aspect of the post-rostral portion of the skull. In old age these ridges become confluent with the lateral edges of the interparietal which has now lost its postero-lateral moieties, partly apparently by absorption and partly by their being overgrown by the mediad posterior angle of the parietals. A sharp thin ridge for muscular attachment also extends back from the posterior base of the zygomatic arch. The interparietal at the same time develops a more or less prominent median angular projection at its posterior border, confluent with the median ridge of the supraoccipital. The contrast between these conditions, obtaining only in very old skulls, and their almost entire absence in skulls which have just reached sexual maturity, is strikingly great.

Supraoccipital.—The supraoccipital changes from a posteriorly convex, thin lamina of bone, in early life, to a thick, nearly vertical plate, with a strongly-developed median ridge produced into an angular spine at its superior border, and with a lateral ridge on either side about midway between the median line and its lateral borders; these lateral ridges also each develop an angular rugosity or process about midway their length. The superior border is also produced into an incipient occipital crest.

Basioccipital.—The basioccipital becomes greatly altered by growth, as in fact is the case with the whole postpalatal region. In comparing stages *A* and *C* it is found that the distance across the occipital condyles increases only about 15 per cent., while the breadth of the anterior border increases 100 per cent., and the length about 50 per cent. (Figs. 12-14, Pl. IV.)

Basisphenoid.—The basisphenoid doubles in length, and its anterior third becomes differentiated into a narrow projecting neck. The presphenoid at stage *A* is nearly hidden by the palatal floor. (Figs. 12-14, Pl. IV.)

Postpalatal Region as a whole.—This doubles its length with an increase in breadth of only about 50 per cent. At stage *A* the postpalatal border terminates slightly behind the posterior edge of M.2 ; in stage 3 it holds very nearly the same position. The distance between the postpalatal border and the front border of the auditory bullæ, compared with the total length of the skull, is as 1 to 9 in *A*, and as 1 to 5 in *C*. In *A* the pterygoid hamuli reach the second fourth of the bullæ ; in *C* they terminate slightly in advance of the bullæ. The bullæ themselves in *A* are more obliquely placed than in *C*, in relation to the axis of the skull, and are quite differently shaped. Also the form of the foramen magnum has undergone much change. These points are all well shown in Figs. 12-14 of the accompanying plate.

Incisive Foramina.—Consequent upon the growth of the rostral portion of the skull, the incisive foramina undergo marked change in form, and somewhat in position, as regards both their anterior and posterior borders. In the stage designated as *A* they are short and broad, and extend relatively further both anteriorly and posteriorly than in stage *B* or *C*, their anterior border being nearer the base of the incisors, and their posterior border being carried back to or slightly behind the front border of the first molar. Thus in *A* the length of the incisive foramina is 6 mm., with a maximum breadth of 3 mm., while in *C* the dimensions are respectively 11.5 and 3.5 mm.—a great increase in length with only slight increase in breadth. At the same time the anterior border is considerably further from the base of the incisors, and the posterior border is slightly in advance, instead of slightly behind, the front border of the molars.

Spheno-palatine Vacuities.—In adults of *Neotoma micropus*, as in other species of the 'round-tailed' section of the genus, there is a long, broad vacuity on each side of the presphenoid and anterior third of the basisphenoid, which Dr. Merriam has recently named[1] the '*spheno-palatine vacuities*,' and he has also called attention to the fact that they are not present in some forms of the 'bushy-tailed' section of the genus. It is therefore of interest in the present connection to note that these vacuities are absent at stage *A*, and are only partially developed at later stages (Figs. 12-14, Pl. IV). My attention was called to the matter by finding several nearly fully-grown skulls from Texas and northeastern Mexico with these vacuities either quite absent or represented by an exceedingly narrow slit, while I could find no differences in the skins or in other cranial characters that gave the slightest hint that the animals were not referable to *N. micropus*. Further examination of young skulls of undoubted *N. micropus* from Rockport and Corpus Christi, Texas, showed that the closed condition was in this species a feature of juvenility. It is thus of interest to find that a feature which proves to be merely a character of immaturity (and quite inconstant as well) in *N. micropus* is a permanent condition in *N. cinerea occidentalis*.[2]

In the development of these vacuities it appears that as the presphenoid increases in length it becomes reduced in width; at the same time, as the skull broadens, the edges of the ascending wings of the palatine bones become slightly incised. There is, however, much individual variation in this respect, as will be shown later.

Molars.—When the molars first cut the gum they have nearly the entire crown-surface capped with enamel. Very soon, even before the tooth has attained its full height, the enamel begins to disappear from the centers of the enamel loops, the capping remaining longer over the narrower loops than over the broader ones; it quickly disappears from all as soon as the crown-surface becomes subject to wear. In stage *A*, in which only M. 1 and M. 2 have appeared, and are less than one-third grown, the enamel walls of the loops nearly meet over the dentinal areas—quite meeting over the narrower portions, especially in the case of the middle transverse loop of each tooth. Some time before the age represented by *B* is reached, the crown-surface is worn to an

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[1] Proc. Biol. Soc. Wash., VIII, p. 112, July, 1893.

[2] Unfortunately the outline figures here given (Figs. 12-15, Pl. IV,) fail to show clearly the points at issue.

even plane; the tooth has reached its normal length, but the fluting of the sides still extends to the alveolar border. As attrition goes on, with the advance of the animal in age, the crown-surface wears down, and the neck of the tooth appears above the alveolar border, till, especially in the upper molars, the fluted terminal and the smooth basal portions are of nearly equal extent; but in old age (as in *C*) the smooth basal portion is the longer and the division of the root into fangs is clearly shown. With this wearing down the tooth increases somewhat in both width and length, but the pattern of the enamel folds undergoes but slight change until nearly the whole crown is worn away, except that the angles become gradually more rounded.

Résumé.—As already stated the change with age in the general form of the skull is due to the relatively disproportionate increase in length of the pre- over the post-orbital region, and the same disproportionate increase of the basal region as compared with the frontoparietal elements. In the first case the rostrum becomes relatively greatly produced; in the second the basioccipital and adjoining parts become so greatly enlarged as to change the entire aspect of the basal region of the skull. Thus the occipital condyles, which in *A* terminate slightly in advance of the most convex portion of the supraoccipital, and are crowded up very close to the bullæ, form in *C* the most posterior part of the skull, with a considerable interval between them and the bullæ. (Figs. 12–14, Pl. IV.)

INDIVIDUAL VARIATION.

In comparing a large series of skulls of the same species it quickly becomes apparent that no element of even the adult skull is constant, either as to form or relative size. There is also much variation in the size of skulls of the same sex and approximately the same age.

Variation in Size.—Thus in *Neotoma micropus*, from the same locality, there are dwarfs and giants. While the females average smaller than the males, size is by no means a safe criterion of sex. Thus two old females, not appreciably different in age, from Corpus Christi, Texas, vary as follows: No. 2948, total length 51 mm., zygomatic breadth 26 mm.; the corresponding dimensions in No. 2955 are 45 mm. and 24 mm. These are merely the extremes of a series of six specimens; with a much larger series doubtless the difference would be considerably increased. A series of six old males, from the same locality and indistinguishable as to age, vary as follows: No. 2952, total length 50.5 mm., zygomatic breadth 27 mm.; the corresponding dimensions in No. 2956 are 45 mm. and 25 mm.

Nasals and ascending branches of the Premaxillæ.—Ordinarily in *N. micropus* the nasals terminate in a gradually narrowed evenly rounded point, a little less than 2 mm. in front of the posterior termination of the ascending branches of the premaxillæ. The distance between the points of termination of the nasals and premaxillæ, however, frequently varies between 1.5 and 2.5 mm.; more rarely from 1 to 3 mm. These extremes each occur in the ratio of about 10 per cent. of the whole, while probably 60 per cent. would not vary much from the normal average of about 2 mm. (See Figs. 1–8 and 16, 17, Pl. IV.)

The nasals, as already said, usually terminate in an evenly rounded point, but in several of the 50 skulls of *N. micropus* before me their posterior border forms a double point, *each* nasal terminating in a distinctly rounded point; in one or two the posterior border is squarely truncate; in others it is irregularly uneven. The ascending branches of the premaxillæ usually terminate in an obtusely V-shaped point, with a uniformly even outline, their breadth, however, being subject to variation; in some specimens they terminate in a brush of irregular spiculæ. (Figs. 1–8 and 16, 17, Pl. IV.)

Frontals.—The posterior border of the frontals is subject to great irregularity, varying from a nearly transverse line (rounded slightly at the outer corners) to a gentle, rather even convexity, and thence to an acute angle, involving the whole posterior border. It is difficult to decide what outline is the most frequent, though the tendency seems to be greatest toward a well-pronounced rather even convexity. Figures 1–8 and 18, 19, Plate V, well show the variation in the position and direction of the fronto-parietal suture.

Parietals.—The anterior outline of the parietals of course conforms to the posterior outline of the frontals, and must be equally variable. It hence follows that their length on the median line is also variable. Their posterior border is also subject to much variation in consequence of the great diversity in the form of the interparietal.

Interparietal.—In middle-aged specimens the interparietal tends strongly to a quadrate form, varying from quadrate to diamond shape, through a more or less marked median angular extension of both its anterior and posterior borders, and occasionally of its lateral borders as well. Often it forms a quadrate figure, in which each of its four sides is slightly convex ; again the corners are so much rounded, and the lateral breadth so much in excess of the antero-posterior, as to give a lozenge-shaped figure. In other cases it is distinctly shield-shaped ; in others it is hexagonal. In size the variation is fully 50 per cent. of what may be regarded as the average dimensions. These remarks have strict reference to fully adult specimens, and as nearly as can be judged these variations are not at all due to differences of age, which, as already shown, has so great an influence upon the size and form of this exceedingly variable element of the skull.[1] (Figs. 20–23, Pl. IV. Compare also the interparietal, as shown in Figs. 1–8.)

Ventral aspect.—The ventral aspect of the skull presents numerous points of variability, only a few of which will be here mentioned. The palate varies more or less in breadth, and especially in the development of the anterior palatal spine, which is sometimes slight, and sometimes so strongly produced anteriorly as to touch the vomer. The postpalatal border may be evenly concave, or present a slight median process. The presphenoid is very variable in size, being often an exceedingly slender rod of bone, and at other times very stout, the variation in thickness being nearly or quite 100 per cent. The anterior third of the basisphenoid shares in the same variability. As the

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[1] As regards variation with age in the form of the interparietal, *Neotoma micropus* is only an example of what doubtless prevails throughout the genus, and even in many other genera as well. Yet in adult animals the form of this bone seems, as a rule, to be sufficiently constant to be of more or less taxonomic value. Thus in the *N. cinerea* group it may be said to be normally quadrate ; in the *N. fuscipes* group it is quite constantly shield-shaped. In *N. floridana*, however, and in the *N. mexicana* group, it seems to be nearly or quite as variable as in *N. micropus*, both as to size and shape.

ascending borders of the palatals are also variable in respect to the extent of their development, it follows that there is, even among adults, a wide range of variation in the size of the spheno-palatine vacuities.

Teeth.—Aside from differences due to age and attrition, the teeth vary in size to a considerable extent among individuals strictly comparable as to sex and age, some having a much heavier dental armature than others. But more particularly noteworthy in this connection is the variation in the color of the teeth, which seems strongly a matter of individuality. Although Dr. Merriam has recently placed *N. micropus* in his "*Neotoma leucodon* group,"[1] which has, among other alleged characters, "color of teeth white or nearly white," the teeth in *N. micropus* average blacker than in any other species of the genus known to me. Were this all it might be considered that *N. micropus* was erroneously referred to the '*leucodon* group'; but unfortunately the range of individual variation in the color of the teeth in the large series at hand covers also the whole range of variation for the genus. Thus in some instances the molar teeth are intensely black from base to crown, while the crown-surface itself is strongly blackish, even the enamel loops, as well as the enclosed dentine being tinged with blackish; in other cases the teeth are merely slightly tinged with brownish near the base and at the bottom of the sulci. These extremes are connected by a series of very gradual intergradations. In other words, among hundreds of skulls of *Neotoma*, those with the blackest teeth occur in *N. micropus*, as well as those in which the teeth are practically white.

In the suckling young the teeth are pure white; before M.3 has come to wear, M.1 and M.2 have become more or less blackened; in young adults, and in middle aged specimens, the teeth are often intensely black; in old specimens, with the teeth much worn, the teeth average lighter than in the younger individuals. There is, however, a wide range of variation in the color of the teeth in specimens of corresponding age, whether old or young. The black coloring consists to a large extent of a

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[1] Proc. Biol. Soc. Wash., IX, p. 118, July 2, 1894.

superficial incrustation which tends to scale off in flakes in the prepared skull, and its absence apparently may be due sometimes to removal in the process of cleaning the skull for the cabinet. In other words, the blackness is to some extent an accidental or pathological condition, due probably more or less to the particular character of the food or to the health of the animal.

General Remarks.

The bearing of what has been stated above respecting variations in the form of the skull and of its principal elements due to age is of course obvious, the inference being that in animals which have reached sexual maturity variations due wholly to growth, in passing through adolescence to senility, may readily be mistaken, when working with very small series or with single specimens, for differences of subspecific or even specific importance. Not only do the individual bones vary in their outlines and proportions and in relative size, but the skull varies as a whole in its relative dimensions, including depth as well as length and breadth. There is beside this a wide range of purely individual variation, affecting every character that can be used in a diagnostic sense. Thus in a series of fifty skulls of *Neotoma micropus* it would be easy to select extremes, of even individual variation, that depart so widely from the average, in one or more characters, as to deceive even an expert, on considering these alone, into the belief that they must represent very distinct species ; yet in the present instance the proof that such is not the case is overwhelming. In *N. micropus* the coloration is remarkably constant, for a member of this genus, at all seasons and ages, so that the case is less complicated than it would be in many other species of the group, where the color of the pelage varies radically with season and age.

Personal criticism is not the purpose of the present paper, and it was not my intention at the outset to refer specifically to the work of any of my *confrères*. Since its preparation was begun, however, its *raison d'être* has perhaps been emphasized by the publication of two brochures of 'preliminary descriptions' of species and subspecies of the genus *Neotoma*, numbering altogether 10 species and 8 subspecies, which added to the 22 species and subspecies previously standing practically unchallenged, makes, at the present writing, a total of 40 forms of the genus *Neotoma*. Of these no less than 26 have been described within the last nine months.[1] Without the material before me used by the original describers of these forms it would be presumptive to give an opinion respecting the merits of many of them. While the greater part may have some real basis, it is evident that others are almost unquestionably synonyms of previously-described forms, judging by 'topotypes' in this Museum, the brief diagnoses accompanying the names affording in these cases no characters that are in the least degree distinctive.

The genus *Neotoma* was chosen for treatment in this connection in preference to some other almost solely by chance, as the facts of variation above presented are not at all exceptional. In fact the common muskrat (*Fiber zibethicus*) would have shown a still more striking case of variability, as would also various species of many other genera. Yet describers of new species are constantly laying stress upon cranial differences that have not necessarily the slightest specific or even subspecific importance; and, so far as can be judged from their descriptions, they are entirely unconscious that such can be the case.

On the other hand, it is equally certain that such alleged characters may have the value assigned them; since it is now a well known fact that the extremes of purely individual variation in any character, external or internal, may exceed in amount the average differences that serve to satisfactorily distinguish not only well-marked subspecies, but even forms that are unquestionably specifically distinct. Hence it must often happen that the determination of the status of a species or subspecies originally described from one or two specimens, in groups especially susceptible to variation, must depend upon the subsequent examination of a large amount of material bearing upon this and its closely-related forms.

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[1] For a list of the species and subspecies of *Neotoma* described prior to July 6, 1894, see Abstr. Proc. Linn. Soc. New York, No. 6, pp. 34, 35, July, 1894.

EXPLANATION OF PLATE IV.

Figures all Natural size.

Neotoma micropus *Baird.* Showing cranial variations due to age and individualism. (Unless otherwise stated, the specimens are from Rockport, Texas.)

Figs. 1–8. Dorsal aspect of skull, showing gradual change in form with age, and especially in the form and relative size of the interparietal. Fig. 1, No. 5834, ♀ juv. (suckling). Fig. 2, No. 2975, ♀ juv. (nearly sexually adult), Corpus Christi, Texas. Fig. 3, No. 5841, ♀ ad. Fig. 4, No. 4480, ♂ ad. Fig. 5, No. 2958, ♂ ad., Corpus Christi. Fig. 6, No. 4479, ♂ ad. Fig. 7, No. 4477, ♀ ad. Fig. 8, No. 4478, ♂ ad.

Figs. 9–11. Skull in profile, to show change of form with growth. Fig. 9, No. 5834, ♀ juv. (nursling). Fig. 10, No. 4480, ♂ ad. (rather young). Fig. 11, No. 4478, ♂ ad. (very old).

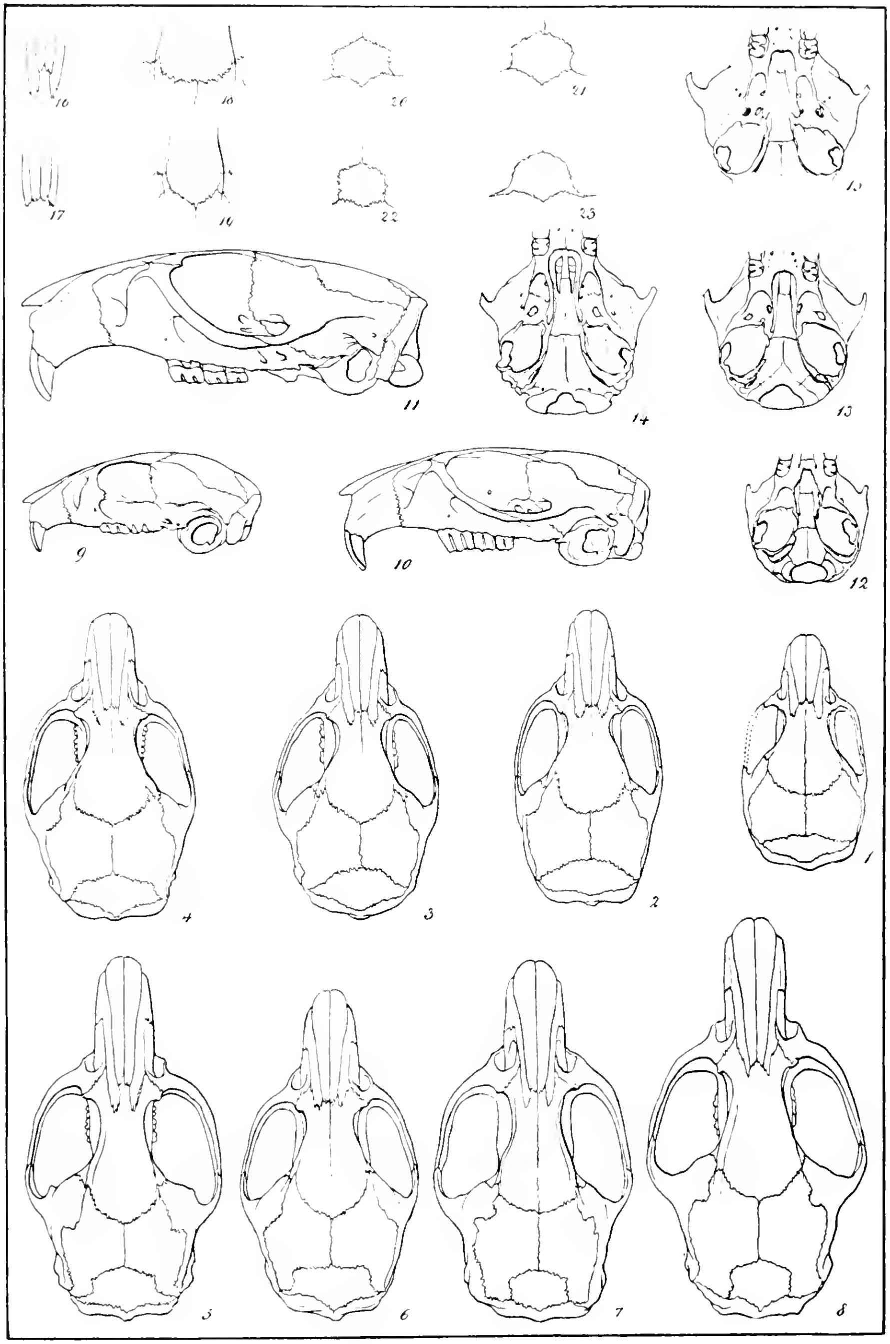
Figs. 12–15. Ventral aspect, showing variations in postpalatal region due to age. Fig. 12, No. 5834, ♀ juv. (nursling). Fig. 13, No. 5841, ♀ ad. (young adult). Fig. 14, No. 2958, Corpus Christi, ♂ ad. (very old). Fig. 15, No. 1456, *Neotoma cinerea occidentalis*, ♂ ad., Ducks, B. C. (for comparison with *N. micropus*).

Figs. 16, 17. To show extremes of individual variation in relative posterior extension of nasals and ascending branches of premaxillæ. Locality, Corpus Christi, Texas. Fig. 16, No. 2958, ♂ ad. Fig. 17, No. 2948, ♀ ad.

Figs. 18, 19. To show extremes of individual variation in posterior border of frontals. Locality, Corpus Christi, Texas. Fig. 18, No. 2949, ♂ ad. Fig. 19, No. 2951, ♂ ad.

Figs. 20–23. To show individual variation in the size and form of the interparietal. Specimens all from Corpus Christi, Texas. Fig. 20, No. 2949, ♂ ad. Fig. 21, No. 2948, ♀ ad. Fig. 22, No. 2952, ♂ ad. Fig. 23, No. 2945, ♀ ad.

Note.—If the Brownsville, Texas, series of specimens had also been included, the range of individual variation would have been considerably increased.



Neotoma micropus.

Figures nat. size.

MATURATIONAL AND SEASONAL MOLTS IN THE GOLDEN MOUSE, *OCHROTOMYS NUTTALLI*

Donald W. Linzey and Alicia V. Linzey

Abstract.—The adult pelage of the golden mouse (*Ochrotomys nuttalli*) is attained by a single maturational molt. Data on the post-juvenile molt were obtained from 96 young golden mice. This molt began on the ventral surface and spread dorsally, meeting in the dorsal midline. It then proceeded anteriorly and posteriorly. The average age at which male golden mice began molting was 36 days, whereas that of females was 38 days. The average duration of molt for the sexes was 29 days and 25 days, respectively. Golden mice undergo two seasonal molts—spring and fall. Data were obtained from 36 mice. The winter pelage was generally much darker than the summer pelage. Both spring and fall molts were more irregular than the post-juvenile molt, and the spring molt tended to be more irregular than the fall molt. Young golden mice born after 1 October and 8 April appeared to combine the post-juvenile and seasonal molt. Hair replacement was more irregular than during the normal post-juvenile molt.

During the course of a study on the ecology and life history of the golden mouse, *Ochrotomys nuttalli nuttalli*, in the Great Smoky Mountains National Park (Linzey, 1966), considerable data were obtained on pelage changes. The limited data presented by Layne (1960) have been the only published information concerning molt in this species.

Maturational Molt

The adult pelage of the golden mouse is attained after a single maturational molt. Data on the post-juvenile molt were obtained from 96 young golden mice. Eighty-four of these mice were raised in captivity. Data from the remaining 12 individuals were obtained from field observations.

The molt from the golden-brown juvenile pelage to the golden-orange adult pelage, although varying in details, followed a definite pattern (Fig. 1). The first indication of the beginning of the dorsal molt was the appearance of new golden fur along the line separating the golden-brown dorsal fur from the white fur of the ventral surface. The replacement of the juvenile pelage progressed dorsally on both sides and met on the dorsal midline forming a continuous band of new fur. The molt then proceeded anteriorly between the ears and onto the head, while posteriorly, it joined the molt proceeding dorsally near the thighs. By this time, new fur had appeared on the sides of the face and just anterior to the ears. The molt along the sides of the body had nearly been completed by this time. The last two areas in which the fur was replaced were the top of the head and the base of the tail. In some individuals, the new fur first appeared just in back of the front leg. It proceeded both posteriorly and dorsally and formed a band of new fur just behind the ears. The molt proceeding posteriorly then covered the remainder of the body.

This pattern of molt generally agrees with that described for *Peromyscus*

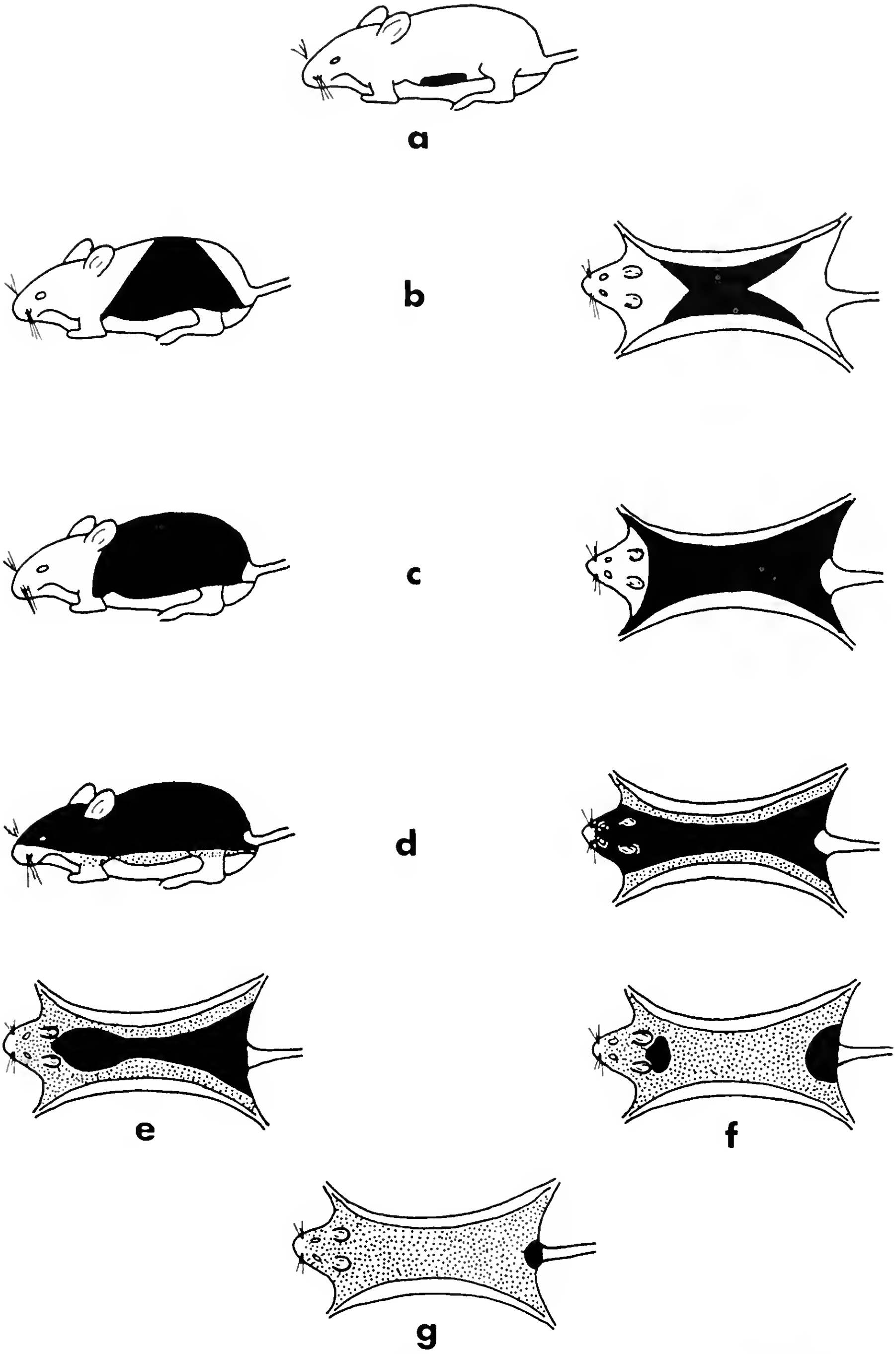


FIG. 1.—Sequence of post-juvenile molt on the dorsum in *Ochrotomys nuttalli*. Shaded portions represent areas of active hair replacement. Stippled areas represent adult pelage.

TABLE 1.—*Duration of post-juvenile molt and average age at beginning and ending of molt in 34 captive golden mice (Range of values in parentheses).*

	Males (15)	Females (19)
Duration	29 days (14–45)	25 days (12–49)
Beginning	36 days (33–42)	38 days (31–47)
Ending	64 days (51–87)	63 days (51–84)

truei (Hoffmeister, 1944), *Peromyscus gossypinus* (Pournelle, 1952) and *Peromyscus boylei* (Brown, 1963). It differs from that reported for *Peromyscus leucopus noveboracensis* (Gottschang, 1956).

Data on the beginning, ending, and duration of the post-juvenile molt on the dorsum in male and female golden mice are compared in Table 1. The average duration of molt for males was slightly longer than for females. The shortest time recorded was between 12 and 14 days, whereas the maximum time required was about 49 days. Approximately 3.5 weeks are required for most *Peromyscus leucopus noveboracensis* to attain their full adult coat according to Gottschang (1956). He recorded a minimum duration of 12 days for captive individuals and 10 days for one wild mouse to undergo the complete molt; the maximum number of days required was about 36.

In the field, animals undergoing various stages of maturational molt were recorded in June (1), July (1), August (2), and December (8). These mice were between 150 mm and 164 mm in total length (mean, 156 mm). In the captive population, male golden mice began molting when their total length was 149 mm, whereas females averaged 146 mm. At the completion of molt, their measurements averaged 163 mm and 160 mm, respectively. From these data, it appears that both wild and captive individuals molted at approximately the same body size, although it is not known whether they were the same age.

The youngest individuals in captivity to begin molting during the current study were 31 days of age. Layne (1960) recorded one young *Ochrotomys* molting at 31 days of age with the molt apparently being complete 10 days later. Molting was in progress in one four week old mouse, while in another of the same age, it had not yet begun (Layne, 1960). Collins (1918) reported that the transition from juvenile to post-juvenile pelage in *Peromyscus* usually began at 6 weeks and was completed about 8 weeks later. The earliest age at which *Peromyscus leucopus noveboracensis* began molting was 38 days (Gottschang, 1956). These were all males. The youngest female to begin molting was 40 days of age. Ninety-five per cent of his mice of both sexes started the pelage change between the ages of 40 and 50 days. Young *Peromyscus gossypinus* began molting when they were between 34 and 40 days of age (Pournelle, 1952).

Gottschang (1956) found that, in general, mice of the same sex in a single litter started molting simultaneously. However, in every case where a difference did occur, he found that the males started to molt first. In the current study, the males in 13 out of 21 litters containing mice of both sexes began molting before the females, whereas the females began molting first in three litters. The initiation of molt was simultaneous in the remaining five litters.

The progression of the ventral molt was studied in seven individuals (four males, three females). The white belly fur was dyed purple by the stain Nyanzol A (20 g per liter of water-hydrogen peroxide mixture in ratio of two to one) and replacement by new hairs was followed. The ventral molt began approximately 2–4 days before the dorsal molt. Hair replacement occurred first in the center of the belly and continued laterally, and then dorsally into the golden fur. Simultaneously, new hair appeared over the entire chest and abdomen. The last areas to acquire new pelage were the throat and the ventral bases of the hind limbs. The ventral molt was complete at about the time that the dorsal molt covered the entire back (Fig. 1).

SEASONAL MOLT

Mice of the genus *Peromyscus* are generally considered to undergo one annul adult molt in autumn (Collins, 1923). However, Osgood (1909) and Brown (1963) recorded two annual molts in *Peromyscus melanotis* and *Peromyscus boylei*, respectively.

Golden mice in the Great Smoky Mountains National Park apparently undergo two annual molts. These take place during the spring (April–June) and fall (October–December). The difference between summer and winter pelage was clearly distinguishable with the unaided eye. The winter pelage was much darker than the usual summer pelage, especially on the mid-dorsum. Osgood (1909) noted that winter specimens of *Peromyscus melanotis* possessed a paler colored pelage, whereas summer specimens were in a dark pelage. The fall molt of *P. boylei* was characterized by the replacement of a bright cinnamon-brown pelage by a more drab, brown winter pelage (Brown, 1963).

Nineteen of 21 adult golden mice in captivity underwent a fall molt between October 20 and December 24. A total of 10 adult golden mice were observed in the wild between December 12–17. Six of these were molting; four already had the winter pelage. The fall molt appeared to be more irregular than the post-juvenile molt. In several animals, it began near the hind leg, covered the rump and then progressed anteriorly to the head. Replacement of the hair was completed first over the posterior half of the body. This separated the two remaining areas of molt—the base of the tail and the head. The replacement of fur at the base of the tail was completed shortly thereafter. The final area of molt was on the head between the ears, and this sometimes required several weeks for completion. This is in contrast to the post-juvenile molt, where the last area of molt in all of the animals was at the base of the tail.

The spring molt must have occurred between 1 April and 15 June. All wild individuals observed between 26 March and 1 April 1964 still retained their winter pelage. By 15 June, all adult golden mice had either already completed their spring molt or were very near completion. Seventy-four per cent (23) of the adult individuals in the captive population molted during the spring. Of those molting, 83% (19) did so between 15 May and 30 June. As in the fall molt, the pattern was irregular. Hair replacement occurred in patches along the sides and across the shoulders, and a simultaneous molt of the entire dorsum took place in only five of 31 individuals (16%). In the cases where this molt was complete, it followed a more regular pattern, with hair replacement occurring last on the nape of the neck.

Gottschang (1956) noted no difference in the onset, progress or length of time required for the pelage change between spring-, summer-, or fall-born litters of *Peromyscus leucopus.* During the current study, however, golden mice born after 1 October and 8 April appeared to combine the post-juvenile molt and seasonal molt. The process of hair replacement was more irregular than during the normal post-juvenile molt. The molt began at a point just behind the front legs, as in the regular post-juvenile molt. It then proceeded dorsally and posteriorly at approximately equal rates. During the combined fall molt (post-juvenile plus fall molt), the replacement of hair at the base of the tail was completed prior to the completion of molt on the head in all cases. In this respect, this combined molt was more similar to the regular seasonal molt than to the regular post-juvenile molt. Upon completion of this molt, the mice had acquired the typical dark winter pelage. However, during the combined spring molt (post-juvenile plus spring molt), hair replacement was completed last at either the tail or head regions.

On the average, those animals born after 1 October began molt at a later age than did those animals born earlier in the breeding season. Males in this group began molting at an average age of 37 days, whereas spring and summer-born males began at 35 days of age. Females born after 1 October began molting at an average age of 43 days, while females born earlier in the season began molting at an average age of 37 days.

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SECTION 4—ECOLOGY AND BEHAVIOR

Ecology and behavior comprise amazingly varied, active, and expanding fields. Probably most current mammalogical publications relate to one or both of these disciplines. Ecology particularly is of special importance to man owing to his increasing awareness of, and concern for, his own environment and such problems as the need to regulate human populations and to reduce pollution of air and water. The papers selected here can suggest to the perspective reader some basic ecological principles that apply to man himself.

A host of topics other than those we were able to include in our selection come to mind when the ecological literature is contemplated—topics such as food habits as learned from stomach contents or droppings, or small mammal populations as censused by various methods (one such method is the study of bones in pellets regurgitated by owls, which are very efficient "mouse traps"). Long term cycles in populations and daily cycles in activity have had their share of ecological work also, but lack of space precludes further discussion of these topics.

A large and well-documented textbook on animal ecology is that by Allee *et al.* (1949). Three books relating to animal populations and factors that may regulate them are by Lack (1954), Andrewartha and Birch (1954), and Wynne-Edwards (1962). Their views differ and are interesting; their examples, however, are largely non-mammalian.

The older term "natural history" is perhaps a broader concept than ecology, but the older naturalists were deeply committed to the types of studies that have come to be called ecological, as well as ethological (a word currently used for studies of behavior). In the latter context, Ewer's (1968) recent book entitled *Ethology of Mammals* is of note to the student interested in a general coverage of the field, and *Maternal Behavior in Mammals* (Rheingold, 1963) also is useful.

Papers reproduced here illustrate concepts such as territoriality and home range (applied to mammals in the paper by Burt), relatively larger studies (note the numbers of specimens mentioned in Frank's paper for example) that provided a firm statistical base and sound quantitative results, and the application of experimental procedures (as in the manipulation of rats in city blocks reported by Davis and Christian or the tests run by McCarley in compartmented cages). The application of newer techniques such as Pearson's traffic counter for mouse runways, the squirrel radio described by Beal, and automatic recording equipment of various types, all have contributed to advances in ecology and ethology. The recent study by Estes and Goddard of the African wild dog will serve to remind the reader that careful observational methods such as were used so effectively by older field naturalists certainly have not been supplanted, but only expanded and supplemented.

Recent field studies dealing with primates have relied heavily on good observational techniques. Schaller's (1963) book on the gorilla is a good example. Other recent workers have studied baboons, chimpanzees, langurs, and other primates in similar ways. A report by Struhsaker (1967), not here reproduced, on vervet monkeys is a good example of a shorter paper on primate behavior in the field.

The short paper, here included, by Miller, written more than 60 years ago, was based on limited data, but reflects a thoughtful and somehow modern way of looking at the problem of bat migration, about which, incidentally, little is known even today.

Ecological problems may be approached at different levels of inclusiveness. For example, the relationships of all species of plants and animals in an entire community may be studied. Such a broad approach to entire ecosystems merges imperceptibly with problems concerning factors that limit distributions, hence to ranges of species and faunal and zoogeographic problems. A short paper by L. R. Dice (1931), not included here, on the relation of mammalian distribution to vegetation types is a classic, for here he adopted the term "Biotic Province" for a major concept that he and others expanded in later American zoogeographic studies. Even an analysis of a few species such as Brown's study of six species of shrews has obvious zoogeographic relevance. At a less inclusive level the ecological relationships of a single species may be studied. This approach is called autecology as opposed to community or synecological studies. If we restrict ourselves further to the environmental relationships of individual animals, we find our studies, again by gradual stages, merge with those that are primarily physiological and behavioral. Physiological techniques also enter directly into the study of ecosystems when energy flow is considered, as often is the case in recent studies. Lyman's paper, reproduced here, on hibernators relates to energy, its sources, and its dissipation. Two noteworthy contributions to the study of hibernation are by Lyman and Dawe (1960) and Kayser (1961); these and other studies are summarized and cited in the textbook by Davis and Golley (1963).

Some of the more important journals that regularly publish contributions relating to ecology and behavior, and of which the serious student should be aware, are ANIMAL BEHAVIOR, BEHAVIOR, ECOLOGICAL MONOGRAPHS, ECOLOGY, JOURNAL OF ANIMAL ECOLOGY, and ZEITSCHRIFT FÜR TIERPSYCHOLOGIE.

MORTALITY PATTERNS IN MAMMALS

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Abstract. Methods of obtaining life table data are outlined and the assumptions implicit in such treatment are defined. Most treatments assume a stationary age distribution, but published methods of testing the stationary nature of a single distribution are invalid. Samples from natural populations tend to be biased in the young age classes and therefore, because it is least affected by bias, the mortality rate curve (q_x) is the most efficient life table series for comparing the pattern of mortality with age in different populations.

A life table and fecundity table are presented for females of the ungulate *Hemitragus jemlahicus*, based on a population sample that was first tested for bias. They give estimates of mean generation length as 5.4 yr, annual mortality rate as 0.25, and mean life expectancy at birth as 3.5 yr.

The life table for *Hemitragus* is compared with those of *Ovis aries*, *O. dalli*, man, *Rattus norvegicus*, *Microtus agrestis*, and *M. orcadensis* to show that despite taxonomic and ecological differences the life tables have common characteristics. This suggests the hypotheses that most mammalian species have life tables of a common form, and that the pattern of age-specific mortality within species assumes an approximately constant form irrespective of the proximate causes of mortality.

INTRODUCTION

Most studies in population ecology include an attempt to determine mortality rates, and in many cases rates are given for each age class. This is no accident. Age-specific mortality rates are usually necessary for calculating reproductive values for each age class, the ages most susceptible to natural selection, the population's rate of increase, mean life expectancy at birth, mean generation length, and the percentage of the population that dies each year. The importance of these statistics in the fields of game management, basic and applied ecology, and population genetics requires no elaboration.

The pattern of changing mortality rates with age is best expressed in the form of a life table. These tables usually present the same information in a variety of ways:

1) Survivorship (l_x) : this series gives the probability at birth of an individual surviving to any age, x (l_x as used here is identical with P_x of Leslie, Venables and Venables 1952). The ages

are most conveniently spaced at regular intervals such that the values refer to survivorship at ages 0, 1, 2 etc. yr, months, or some other convenient interval. The probability at birth of living to birth is obviously unity, but this initial value in the series need not necessarily be set at 1; it is often convenient to multiply it by 1,000 and to increase proportionately the other values in the series. If this is done, survivorship can be redefined as the number of animals in a cohort of 1,000 (or any other number to which the initial value is raised) that survived to each age x. In this way a kl_x series is produced, where k is the constant by which all l_x values in the series are multiplied.

2) Mortality (d_x): the fraction of a cohort that dies during the age interval x, x + 1 is designated d_x. It can be defined in terms of the individual as the probability at birth of dying during the interval x, x + 1. As a means of eliminating decimal points the values are sometimes multiplied by a constant such that the sum of the d_x values equals 1,000. The values can be calculated from the l_x series by

$$d_x = l_x - l_{x+1}$$

3) Mortality rate (q_x): the mortality rate q for the age interval x, x + 1 is termed q_x. It is calculated as the number of animals in the cohort that died during the interval x, x + 1, divided by the number of animals alive at age x. This value is usually expressed as $1{,}000q_x$, the number of animals out of 1,000 alive at age x which died before x + 1.

These are three ways of presenting age-specific mortality. Several other methods are available—e.g. survival rate (p_x), life expectancy (e_x) and probability of death (Q_x)—but these devices only present in a different way the information already contained in each of the three series previously defined. In this paper only the l_x, d_x and q_x series will be considered.

METHODS OF OBTAINING MORTALITY DATA

Life tables may be constructed from data collected in several ways. Direct methods:

1) Recording the ages at death of a large number of animals born at the same time. The frequencies of ages at death form a kd_x series.

2) Recording the number of animals in the original cohort still alive at various ages. The frequencies from a kl_x series.

Approximate methods:

3) Recording the ages at death of animals marked at birth but whose births were not coeval. The frequencies form a kd_x series.

4) Recording ages at death of a representative sample by ageing carcasses from a population that has assumed a stationary age distribution. Small fluctuations in density will not greatly affect the results if these fluctuations have an average wave length considerably shorter than the period over which the carcasses accumulated. The frequencies form a kd_x series.

5) Recording a sample of ages at death from a population with a stationary age distribution, where the specimens were killed by a catastrophic event (avalanche, flood, etc.) that removed and fixed an unbiased sample of ages in a living population. In some circumstances (outlined later) the age frequencies can be treated as a kl_x series.

6) The census of ages in a living population, or a sample of it, where the population has assumed a stationary age distribution. Whether the specimens are obtained alive by trapping or are killed by unselective shooting, the resultant frequencies are a sample of ages in a living population and form a kl_x series in certain circumstances.

Methods 1 to 3 are generally used in studies of small mammals while methods 4 to 6 are more commonly used for large mammals.

TESTS FOR STATIONARY AGE DISTRIBUTION

Five methods have been suggested for determining whether the age structure of a sample is consistent with its having been drawn from a stationary age distribution:

a) Comparison of the "mean mortality rate," calculated from the age distribution of the sample, with the proportion represented by the first age class (Kurtén 1953, p. 51).

b) Comparison of the annual female fecundity of a female sample with the sample number multiplied by the life expectancy at birth, the latter statistic being estimated from the age structure (Quick 1963, p. 210).

c) Calculation of instantaneous birth rates and death rates, respectively, from a sample of the population's age distribution and a sample of ages at death (Hughes 1965).

d) Comparison of the age distribution with a prejudged notion of what a stationary age distribution should be like (Breakey 1963).

e) Examination of the "l_x" and "d_x" series, calculated from the sampled age distribution, for evidence of a common trend (Quick 1963, p. 204).

Methods a to c are tautological because they assume the sampled age distribution is either a kl_x or kd_x series; method d assumes the form of the life table, and e makes use of both assumptions.

These ways of judging the stationary nature of a population are invalid. But I intend something more general than the simple statement that these five methods do not test what they are supposed to test. Given no information other than a single age distribution, it is theoretically impossible to prove that the distribution is from a stationary population unless one begins from the assumption that the population's survival curve is of a particular form. If such an assumption is made, the life table constructed from the age frequencies provides no more information than was contained in the original premise.

MORTALITY SAMPLES AND AGE STRUCTURE SAMPLES

Methods 4 to 6 for compiling life tables are valid only when the data are drawn from a stationary age distribution. This distribution results when a population does not change in size and where the age structure of the population is constant with time. The concept has developed from demographic research on man and is useful for species which, like man, have no seasonally restricted period of births.

Populations that have a restricted season of births present difficulties of treatment, some of which have been discussed by Leslie and Ranson (1940). Very few mammals breed at the same rate throughout the year, and the stationary age distribution must be redefined if it is to include seasonal breeders. For species with one restricted breeding season each year, a stationary population can be defined as one that does not vary either in numbers or age structure at successive points in time spaced at intervals of 1 yr. The stationary age distribution can then be defined for such populations as the distribution of ages at a given time of the year. Thus there will be an infinite number of different age distributions according to the time of census, other than in the exceptional case of a population having a constant rate of mortality throughout life.

The distribution of ages in a stationary population forms a kl_x series only when all births for the year occur at an instant of time and the sample is taken at that instant. This is obviously impossible, but the situation is approximated when births occur over a small fraction of the year. If a population has a restricted season of births, the age structure can be sampled over this period and at the same time the number of live births produced by a hypothetical cohort can be calculated from the number of females either pregnant or suckling young. In this way a set of data closely approximating a kl_x series can be obtained.

If an age distribution is sampled halfway between breeding seasons, it cannot be presented as a kl_x series with x represented as integral ages in years. With such a sample (making the usual assumptions of stability and lack of bias) neither l_x nor d_x can be established, but q_x values can be calculated for each age interval $x + \frac{1}{2}$, $x + 1\frac{1}{2}$. The age frequencies from a population with a continuous rate of breeding are exactly analogous; they do not form a kl_x series but can be treated as a series of the form

$$k\ (l_x + l_{x+1})\ /2$$

This series does not allow calculation of l_x values from birth unless the mortality rate between birth and the midpoint of the first age interval is known.

Because a sample consists of dead animals, its age frequencies do not necessarily form a mortality series. The kd_x series is obtained only when the sample represents the frequencies of ages at death in a stationary population. Many published samples treated as if they formed a kd_x series are not appropriate to this form of analysis. For instance, if the animals were obtained by shooting which was unselective with respect to age, the sample gives the age structure of the living population at that time; that the animals were killed to get these data is irrelevant. Hence unbiased shooting samples survivorship, not mortality, and an age structure so obtained can be treated as a kl_x series if all other necessary assumptions obtain. Similarly, groups of animals killed by avalanches, fires, or floods—catastrophic events that preserve a sample of the age frequencies of animals during life—do not provide information amenable to kd_x treatment.

A sample may include both l_x and d_x components. For instance, it could consist of a number of dead animals, some of which have been unselectively shot, whereas the deaths of others are attributable to "natural" mortality. Or it could be formed by a herd of animals killed by an avalanche in an area where carcasses of animals that died "naturally" were also present. In both these cases d_x and l_x data are confounded and these heterogeneous samples of ages at death can be treated neither as kd_x nor kl_x series.

Even if a sample of ages at death were not heterogeneous in this sense, it might still give misleading information. If, for instance, carcasses attributable to "natural" mortality were collected only on the winter range of a population, the age frequencies of this sample would provide ages at death which reflected the mortality pattern during only part of the year. But the d_x series gives the proportion of deaths over contiguous periods of the life span and must reflect all mortality during each of these periods.

It has been stressed that the frequencies of ages in life or of ages at death provide life-table information only when they are drawn from a population with a stationary age distribution. This age distribution should not be confused with the stable distribution. When a population increases at a constant rate and where survivorship and fecundity rates are constant, the age distribution eventually assumes a stable form (Lotka 1907 a, b; Sharpe and Lotka 1911). Slobodkin (1962, p. 49) gives a simple explanation as to why this is so. A stable age distribution does not form a kl_x series except when the rate of increase is zero, the season of births is restricted, and the sample is taken at this time. Hence the stationary age distribution is a special case of the stable age distribution.

The Relative Usefulness of the l_x, d_x and q_x Series

Most published life tables for wild mammals have been constructed either from age frequencies obtained by shooting to give a kl_x series, or by determining the ages at death of animals found dead, thereby producing a kd_x series. Unfortunately, both these methods are almost invariably subject to bias in that the frequency of the first-year class is not representative. Dead immature animals, especially those dying soon after birth, tend to decay faster than the adults, so that they are underrepresented in the count of carcasses. The ratio of juveniles to adults in a shot sample is usually biased because the two age classes have different susceptibilities to hunting. With such a bias established or suspected, the life table is best presented in a form that minimizes this bias. An error in the frequency of the first age class results in distortions of each l_x and d_x value below it in the series, but q_x values are independent of frequencies in younger age classes. By definition, q is the ratio of those dying during an age interval to those alive at the beginning of the interval. At age y the value of q is given by

$$q_y = d_y/l_y$$

but

$$d_y = l_y - l_{y+1}$$

therefore

$$q_y = (l_y - l_{y+1})/l_y \ .$$

Thus the value of q_y is not directly dependent on absolute values of l_x but on the differences between successive values. If the l_x series is calculated from age frequencies in which the initial frequency is inaccurate, each l_x value will be distorted. However, the difference between any two, divided by the first, will remain constant irrespective of the magnitude of error above them in the series. Thus a q_x value is independent of all but two survivorship age frequencies and can be calculated directly from these frequencies (f_x) by

$$q_x = (f_x - f_{x+1})/f_x$$

if the previously discussed conditions are met.

The calculation of q from frequencies of ages at death is slightly more complex:

by definition $q_y = d_y/l_y$

but $l_y = \sum_{x=0}^{\infty} d_x - \sum_{x=0}^{y-1} d_x$

therefore $q_y = d_y/(\sum_{x=0}^{\infty} d_x - \sum_{x=0}^{y-1} d_x)$

$$= d_y/\sum_{x=y}^{\infty} d_x$$

but the frequencies of ages at death (f'_x) are themselves a kd_x series and so $q_y = f'_y/\sum_{x=y}^{\infty} f'_x$.

Thus the value of q at any age is independent of frequencies of the younger age classes. Although the calculated value of q for the first age class may be wrong, this error does not affect the q_x values for the older age classes.

The q_x series has other advantages over the l_x and d_x series for presenting the pattern of mortality with age. It shows rates of mortality directly, whereas this rate is illustrated in a graph of the l_x series (the series most often used when comparing species) only by the slope of the curve.

A Life Table for the Thar, *Hemitragus jemlahicus*

The Himalayan thar is a hollow-horned ungulate introduced into New Zealand in 1904 (Donne 1924) and which now occupies 2,000 miles^2 of mountainous country in the South Island. Thar were liberated at Mount Cook and have since spread mostly north and south along the Southern Alps. They are still spreading at a rate of about 1.1 miles a year (Caughley 1963) and so the populations farthest from the point of liberation have been established only recently and have not yet had time to increase greatly in numbers. Closer to the site of liberation the density is higher (correlated with the greater length of time that animals have been established there), and around the point of liberation itself there is evidence that the population has decreased (Anderson and Henderson 1961).

The growth rings on its horns are laid down in each winter of life other than the first (Caughley 1965), thereby allowing the accurate ageing of specimens. An age structure was calculated from a sample of 623 females older than 1 yr shot in the Godley and Macaulay Valleys between November 1963 and February 1964. Preliminary work on behavior indicates that there is very little dispersal of females into or out of this region, both because the females have distinct home ranges and because there are few ice-free passes linking the valley heads.

As these data illustrate problems presented by most mammals, and because the life table has not been published previously, the methods of treatment will be outlined in some detail.

Is the population stationary?

Although it is impossible to determine the stationary nature of a population by examining the age structure of a single sample, even when rates of fecundity are known, in some circumstances a series of age structures will give the required information. This fact is here utilized to investigate the stability of this population.

The sample was taken about halfway between the point of liberation and the edge of the range. It is this region between increasing and decreasing populations where one would expect to find a stationary population. The animals came into the Godley Valley from the southwest and presumably colonized this side of the valley before crossing the 2 miles of river bed to the northeast side. This pattern of establishment is deduced from that in the Rakaia Valley, at the present edge of the breeding range, where thar bred for at least 5 yr on the south side of the valley before colonizing the north side. Having colonized the northeast side of the Godley Valley, the thar would then cross the Sibald Range to enter the Macaulay Valley, which is a further 6 miles northeast. The sample can therefore be divided into three subsamples corresponding to the different periods of time that the animals have been present in the three areas. A 10 × 3 contingency test for differences between the three age distributions of females 1 yr of age or older gave no indication that the three subpopulations differed in age structure ($\chi^2 = 22.34$; $P = 0.2$).

This information can be interpreted in two ways: either the three subpopulations are neither increasing nor decreasing and hence are likely to have stationary age distributions, or the subpopulations could be increasing at the same rate, in which case they could have identical stable age distributions. The second alternative carries a corollary that the subpopulations would have different densities because they have been increasing for differing periods of time. But an analysis of the three densities gives no indication that they differ (Table I). This result necessitates the rejection of the second alternative.

TABLE I. Relative densities of thar in three zones

Zone	Number females autopsied	Mean density index[a]	Standard error
Godley Valley south........	258	2.19	0.56
Godley Valley north........	240	1.67	0.53
Macaulay Valley...........	115	2.66	0.69

$F_{2,56}$ for densities between valleys = 1.74, not significant

[a] Density indices were calculated as the number of females other than kids recorded as autopsied in a zone each day, divided by the number of shooters hunting in the zone on that day.

The above evidence suggesting that the sample was drawn from a stationary age distribution is supported to some extent by observation. When I first passed through the area in 1957, I saw about as many thar per day as in 1963-64. J. A. Anderson, a man who has taken an interest in the thar of this region, writes that the numbers of thar in 1956 were about the same as in 1964 (Anderson, pers. comm.). These are subjective evaluations and for that reason cannot by themselves be given much weight, but they support independent evidence that the population is stationary or nearly so.

Is the sample biased?

A sample of the age structure of a population can be biased in several ways. The most obvious source of bias is behavioral or range differences between males and females. For instance, should males tend to occupy terrain which is more difficult to hunt over than that used by females, they would be underrepresented in a sample obtained by hunting. During the summer thar range in three main kinds of groups: one consists of females, juveniles and kids, a second consists of young males and the third of mature males. The task of sampling these three groupings in the same proportions as they occur throughout the area is complicated by their preferences for terrain that differs in slope, altitude and exposure. Consequently the attempt to take an unbiased sample of both males and females was abandoned and the hunting was directed towards sampling only the nanny-kid herds in an attempt to take a representative sample of females. The following analysis is restricted to females.

Although bias attributable to differences in behavior between sexes can be eliminated by the simple contrivance of ignoring one sex, some age classes of females may be more susceptible than others to shooting. To test for such a difference, females other than kids were divided into two groups: those from herds in which some members were aware of the presence of the shooter before he fired, and those from herds which were undisturbed before shooting commenced. If any age group is particularly wary its members should occur more often in the "disturbed" category than is the case for other age groups. But a χ^2 test ($\chi^2 = 7.28$, df $= 9$, $P = 0.6$) revealed no significant difference between the age structures of the two categories.

The sample was next divided into those females shot at ranges less than 200 yards and those shot out of this range. If animals in a given age class are more easily stalked than the others, they will tend to be shot at closer ranges. Alternatively, animals which present small targets may be underrepresented in the sample of those shot at ranges over 200 yards. This is certainly true of kids, which are difficult to see, let alone to shoot, at ranges in excess of 200 yards. The kids have therefore not been included in the analysis because their underrepresentation in the sample is an acknowledged fact, but for older females there is no difference between the age structures of the two groups divided by range which is not explainable as sampling variation ($\chi^2 = 9.68$, df $= 9$, $P = 0.4$). This is not to imply that no bias exists—the yearling class for instance could well be underrepresented beyond 200 yards—but that no bias could be detected from a sample of this size.

The taking of a completely representative sample from a natural population of mammals is probably a practical impossibility, and I make no claim that this sample of thar is free of bias, but as bias cannot be detected from the data, I assume it is slight.

Construction of the life table

The shooting yielded 623 females 1 yr old or older, aged by growth rings on the horns. As the sampling period spanned the season of births, a frequency for age 0 cannot be calculated directly from the number of kids shot because early in the period the majority had not been born. In any case, the percentage of kids in the sample is biased.

The numbers of females at each age are shown in Table II, column 2. Although the ages are given only to integral years each class contains animals between ages x yr — ½ month and x yr + 2½ months. Variance owing to the spread of the kidding season is not included in this range, but the season has a standard deviation of only 15 days (Caughley 1965).

Up to an age of 12 yr (beyond this age the values dropped below 5 and were not treated) the frequencies were smoothed according to the formula

$$\log y = 1.9673 + 0.0246x - 0.01036\,x^2,$$

where y is the frequency and x the age. The linear and quadratic terms significantly reduced

TABLE II. Life table and fecundity table for the thar *Hemitragus jemlahicus* (females only)

1	2	3	4	5	6	7
Age in years x	Frequency in sample	Adjusted frequency	No. female live births per female at age x m_x	$1{,}000\ l_x$	$1{,}000\ d_x$	$1{,}000\ q_x$
0	—	205[a]	0.000	1,000	533	533
1	94	95.83	0.005	467	6	13
2	97	94.43	0.135	461	28	61
3	107	88.69	0.440	433	46	106
4	68	79.41	0.420	387	56	145
5	70	67.81	0.465	331	62	187
6	47	55.20	0.425	269	60	223
7	37	42.85	0.460	209	54	258
8	35	31.71	0.485	155	46	297
9	24	22.37	0.500	109	36	330
10	16	15.04	0.500	73	26	356
11	11	9.64	0.470	47	18	382
12	6	5.90		29		
13	3		0.350			
14	4					
15	3					
16	0					
17	1					

[a] Calculated from adjusted frequencies of females other than kids (column 3) and m_x values (column 4).

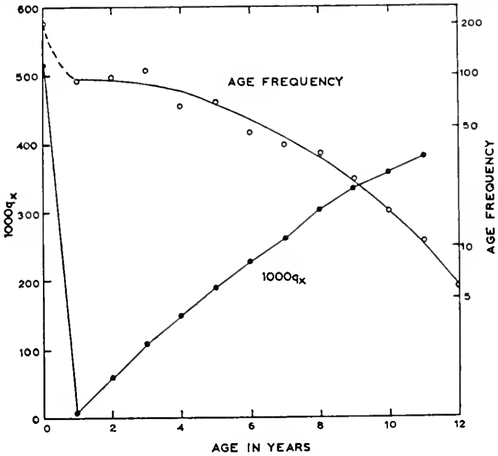

FIG. 1. Age frequencies, plotted on a logarithmic scale, of a sample of female thar, with a curve fitted to the values from ages 1 to 12 yr, and the mortality rate per 1,000 for each age interval of 1 yr ($1{,}000q_x$) plotted against the start of the interval.

variance around the regression, but reduction by the addition of a cubic term was not significant at the 0.05 level. There are biological reasons for suspecting that the cubic term would have given a significant reduction of variance had the sample been larger, but for the purposes of this study its inclusion in the equation would add very little. The improved fit brought about by the quadratic term indicates that the rate of mortality increases with age. Whether the rate of this rate also increases, is left open. The computed curve closely fitted the observed data (Fig. 1) and should greatly reduce the noise resulting from sampling variation, the differential effect on mortality of different seasons, and the minor heterogeneities which, although not detectable, are almost certain to be present. The equation is used to give adjusted frequencies in Table II, column 3.

The frequency of births can now be estimated from the observed mean number of female kids produced per female at each age. These are shown in column 4. They were calculated as the number of females at each age either carrying a foetus or lactating, divided by the number of females of that age which were shot. These values were then halved because the sex ratio of late foetuses and kids did not differ significantly from 1:1 (93 ♂♂ : 97 ♀♀). The method is open to a number of objections: it assumes that all kids were born alive, that all females neither pregnant nor lactating were barren for that season, and that twinning did not occur. The first assumption, if false, would give rise to a positive bias, and the second and third to a negative bias. However, the ratio of females older than 2 yr that were either pregnant or lactating to those neither pregnant nor lactating did not differ significantly between the periods November to December and January to February ($\chi^2 = 0.79$, $P = 0.4$), suggesting that still births and mortality immediately after birth were not common enough to bias the calculation seriously. Errors are unlikely to be introduced by temporarily barren females suckling yearlings, because no female shot in November that was either barren (as judged by the state of the uterus) or pregnant was lactating. Errors resulting from the production of twins will be very small; we found no evidence of twinning in this area.

The products of each pair of values in columns 3 and 4 (Table II) were summed to give an estimate of the potential number of female kids produced by the females in the sample. This value of 205 is entered at the head of column 3. The adjusted age frequencies in column 3 were each multiplied by 4.878 to give the $1{,}000l_x$ survivorship values in column 5. The mortality series (column 6) and mortality-rate series (column 7) were calculated from these.

Conclusions

Figure 1 shows the mortality rate of females in this thar population up to an age of 12 yr. Had the sample been larger the graph could have been extended to an age of 17 yr or more, but this would have little practical value for the calculation of population statistics because less than 3% of females in the population were older than 12 yr.

The pattern of mortality with age can be divided into two parts—a juvenile phase characterized by a high rate of mortality, followed by a postjuvenile phase in which the rate of mortality is initially low but rises at an approximately constant rate with age.

Table II gives both the l_x and m_x series, and these two sets of values provide most of the information needed to describe the dynamics of the population. Assuming that these two series are accurate, the following statistics can be derived: generation length (i.e. mean lapse of time between a female's date of birth and the mean date of birth of her offspring), T:

$$T = \frac{\Sigma l_x m_x x}{\Sigma l_x m_x} = 5.4 \text{ yr;}$$

mean rate of mortality for all age groups, $\bar{q}_x$:

$$\bar{q}_x = 1/\Sigma l_x = 0.25 \text{ per female per annum;}$$

life expectancy at birth, e_0:

$$e_0 = \Sigma\, l_x - \tfrac{1}{2} = 3.5 \text{ yr.}$$

The last two statistics can also be expressed conveniently in terms of the mortality series by

$$\bar{q}_x = 1/\Sigma\ (x+1)\ d_x$$

and

$$e_0 = \frac{\Sigma\ (2x+1)\ d_x}{2}.$$

The relationship of the two is given by

$$\bar{q}_x = 2/(2e_0+1).$$

Life Tables for Other Mammals

The difficulty of comparing the mortality patterns of animals that differ greatly in life span can be readily appreciated. To solve this problem, Deevey (1947) proposed the percentage deviation from mean length of life as an appropriate scale, thereby allowing direct comparison of the life tables of, say, a mammal and an invertebrate. For such comparisons this scale is obviously useful, but for mammals where the greatest difference in mortality rates may be at the juvenile stage the scale often obscures similarities.

By way of illustration, Figure 2 shows $1{,}000q_x$ curves for two model populations which differ only in the mortality rate of the first age class. When the values are graphed on a scale of percentage deviation from mean length of life the close similarity of the two sets of data is no longer apparent. Thus the use of Deevey's scale for comparing mortality patterns in mammals might result in a loss rather than a gain of information. In this paper, absolute age has been retained as a scale in comparing life tables of different species, although this scale has its own limitations.

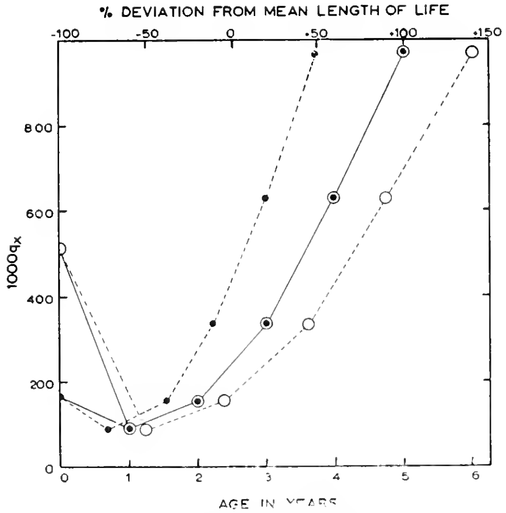

Fig. 2. The mortality rate per 1,000 for each year of life for two model populations that differ only in the degree of first-year mortality. These $1{,}000q_x$ values are each graphed on two time scales: absolute age in years (continuous lines) and percentage deviation from mean life expectancy (broken lines).

Domestic sheep, Ovis aries.—Between 1954 and 1959, Hickey (1960) recorded the ages at death of 83,113 females on selected farms in the North Island of New Zealand. He constructed a q_x table from age 1½ yr by "dividing the number of deaths which have occurred in each year of age by the number 'exposed to risk' [of death] at the same age." An age interval of 1 yr was chosen and the age series 1½, 2½, 3½ etc. was used in preference to integral ages.

The q_x series conformed very closely to the regression: $\log q_x = 0.156x + 0.24$, enabling him in a subsequent paper (Hickey 1963) to present the interpolated q_x values at integral ages. He also calculated q for the first year of life from a knowledge of the number of lambs dying before 1 yr of age out of 85,309 (sexes pooled) born alive.

These data probably provide the most accurate life table for any mammal. The $1{,}000q_x$ curve is graphed in Figure 3.

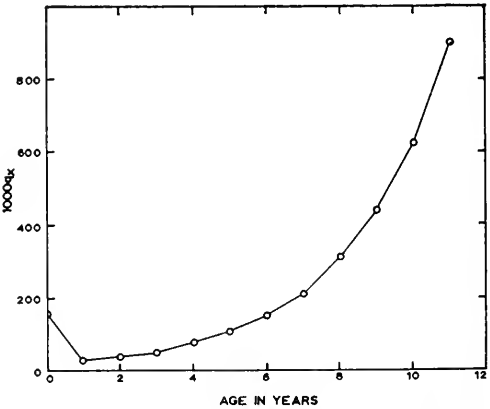

Fig. 3. Domestic sheep: mortality rate per 1,000 for each age interval of 1 yr ($1{,}000q_x$), plotted against the start of the interval. Data from Hickey (1963).

Dall sheep, Ovis dalli.—During his study on the wolves of Mount McKinley National Park, Murie (1944) aged carcasses of dall sheep he found dead, their ages at death being established from the growth rings on the horns. This sample can be divided into those that died before 1937 and those that died between 1937 and 1941. The former sample was used by Deevey (1947) to construct the life table presented in his classic paper on mortality in natural populations. Kurtén (1953) constructed a life table from the same data, but corrected the underrepresentation of first-year animals resulting from the relatively greater perishability of their skulls by assuming that adult females produce 1 lamb per annum from about their second birthday. Taber and Dasmann (1957) constructed life tables for both males and females from the sample of animals dying between 1937 and 1941, and adjusted both the 0 to 1- and 1 to 2-year age frequencies on the assumption that a female produces her first lamb at about her third birthday and another lamb each year thereafter, that the sex ratio at birth is unity and that the loss of yearlings is not more than 10%.

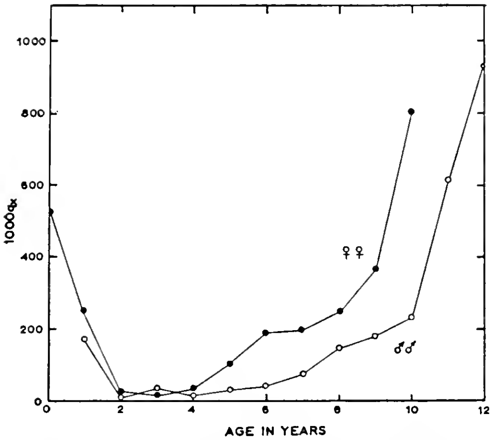

FIG. 4. Dall sheep: mortality rate per 1,000 for each age interval of 1 yr ($1{,}000q_x$), plotted against the start of the interval. Data from Murie (1944).

Figure 4 shows a version of this table constructed from the pre-1937 sample. The mortality of the first year class has been adjusted by assuming that the sex ratio at birth is unity, that 50% of females produce their first kids at their second birthday and that thereafter 90% produce kids each year. The figure of 50% fecundity at age 2 is borrowed from Woodgerd's (1964) study on the closely related *Ovis canadensis*, and the subsequent 90% fecundity is based on Murie's (1944) statement that twins are extremely rare. To allow for temporarily or permanently barren animals, 10% is subtracted from the potential fecundity.

This life table must be taken as an approximation. As Deevey (1947) has pointed out, the pre-1937 and 1937–41 samples differ significantly in age structure. The obvious conclusion is that the mortality rate by age was changing before and during the period of study. Consequently the age structure of the sample is likely to be only an approximation of the kd_x series. Furthermore, the q_x values for age 1 yr are likely to have been biased by differential perishability of skulls, but no arbitrary adjustment has been made.

Man.—Most of the life tables available for man show that males have a higher rate of mortality than females. However, Macdonell's (1913) tables for ancient Rome, Hispania and Lusitania suggest that this might not always have been so and that in some circumstance the reverse can be true.

A $1{,}000q_x$ curve for Caucasian males and females in the United States between 1939 and 1941 is shown in Figure 5. The values are taken from Dublin, Lotka, and Spiegelman (1949).

Rat, Rattus norvegicus.—Wiesner and Sheard (1935) gave the ages at death of 1,456 females of the albino rat (Wistar strain) in a laboratory population. Their table begins at an age of 31 days, but Leslie et al. (1952) calculate from Wiesner and Sheard's data that the probability of dying between birth and 31 days was 0.316. Figure 6 gives a q_x curve constructed from these data.

Short-tailed vole, Microtus agrestis.—The ages at death of 85 males and 34 females were reported by Leslie and Ranson (1940) from a laboratory population of voles kept at the Bureau of Animal Population, Oxford. Frequencies for both sexes were pooled and the data were smoothed by the formula $f_x = f_0 \, e^{-bx^2}$ where f is the frequency of animals alive age x, and b is a constant. The computed curve closely fitted the data ($P = 0.5$ to 0.7). Figure 6 shows the $1{,}000q_x$ curve derived from the authors' sixth table.

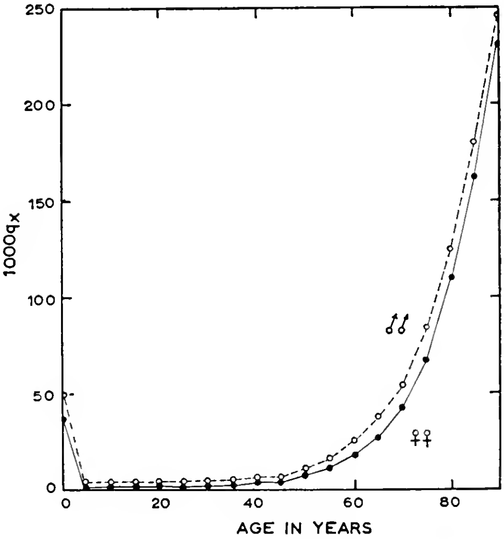

FIG. 5. Man in U.S.: mortality rate per 1,000 per year of age ($1{,}000q_x$). Data from Dublin et al. (1949).

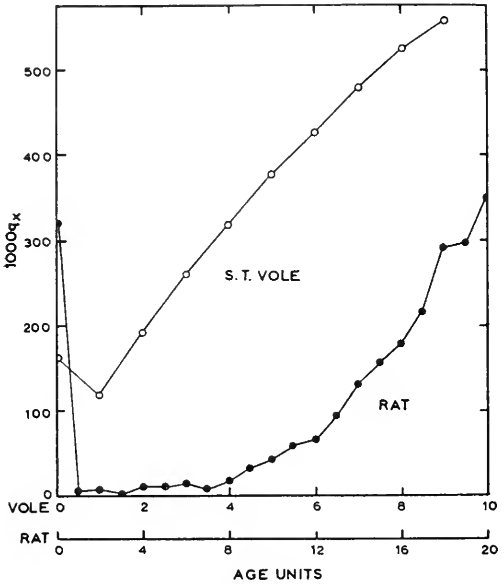

FIG. 6. Short-tailed voles and rats: mortality rate per 1,000 for each age interval ($1{,}000q_x$), plotted against the start of the interval. Age interval is 56 days for voles and 50 days for rats. Rat data from Wiesner and Sheard (1935); vole data from Leslie and Ranson (1940).

The pooling of mortality data from both sexes is strictly valid only when the two q_x series are not significantly different. Studies on differential mortality between sexes are few, but those available for man (Dublin et al. 1949, and other authors), dall sheep (Taber and Dasmann 1957, and this paper), the pocket gopher (Howard and Childs 1959) and Orkney vole (Leslie et al. 1955) suggest that although mortality rates certainly differ between sexes, the trends of these age-specific rates tend to be parallel. Consequently, this life table for voles, although based on presumably heterogeneous data, is probably quite adequate for revealing the gross pattern of mortality with age.

Orkney vole, Microtus orcadensis.—Leslie et al. (1955) gave a life table for both males and females in captivity from a base age of 9 weeks. In addition they gave the probability at birth of surviving to ages 3, 6, and 9 weeks, but did not differentiate sexes over this period. The q_x curve given here (Fig. 7) was constructed by calculating survivorship series for both males and females from these data, drawing trend lines through the points, and interpolating values at intervals of 8 weeks.

Proposed life tables not accepted

In the Discussion section of this paper the life tables discussed previously are examined in an attempt to generalize their form. Only a small proportion of published life tables are dealt with, and any generalization from these could be interpreted as an artefact resulting from selection of evidence.

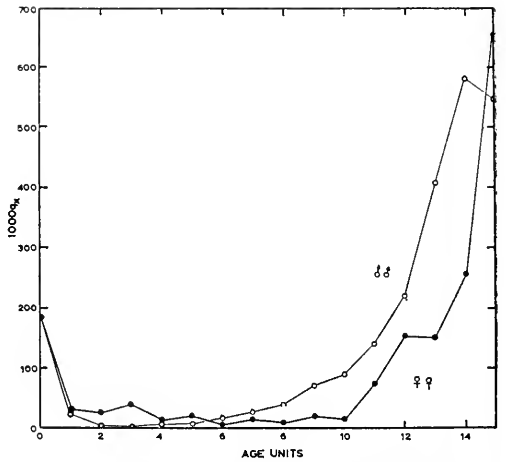

FIG. 7. Orkney vole: mortality rate per 1,000 for each age interval of 56 days ($1{,}000q_x$), plotted against the start of the interval. Data from Leslie et al. (1955).

To provide the reader with the information necessary for reaching an independent conclusion, the published life tables not selected for comparison are listed below with the reason for their rejection. Only those including all juvenile age classes are cited. These tables are rejected only for present purposes because comparison of mortality patterns between species demands a fairly high level of accuracy for individual tables. The inclusion of a table in this section does not necessarily imply that it is completely inaccurate and of no practical value.

Tables based on inadequate data (i.e. less than 50 ages at death or 150 ages of living animals): *Odocoileus hemionus* (Taber and Dasmann 1957), *Ovis canadensis* (Woodgerd 1964);

Probable sampling bias: *Lepus americanus* (Green and Evans 1940), *Rupicapra rupicapra* (Kurtén 1953), fossil accumulations (Kurtén 1953, 1958; Van Valen 1964), *Balaenoptera physalus* (Laws 1962);

Age structure analyzed as a kd_x series: *Sylvilagus floridanus* (Lord 1961), *Odocoileus virginianus* and *Capreolus capreolus* (Quick 1963);

Death and emigration confounded: *Peromyscus maniculatus* (Howard 1949), *Capreolus capreolus* (Taber and Dasmann 1957, Quick 1963);

Sample taken between breeding seasons: *Odocoileus virginianus* (Quick 1963);

Form of life table, or significant portion of it, based largely on assumption: *Callorhinus ursinus* (Kenyon and Scheffer 1954), *Myotis mystacinus* (Sluiter, van Heerdt, and Bezem 1956), *Cervus elaphus* (Taber and Dasmann 1957), *Rhinolophus hipposideros, Myotis emarginatus,* and *Myotis daubentonii* (Bezem, Sluiter, and van Heerdt 1960), *Halichoerus grypus* (Hewer 1963, 1964);

Sample from a nonstationary population: *Sylvilagus floridanus* (Lord 1961);

Inadequate aging: *Gorgon taurinus* (Talbot and Talbot 1963);

Confounding of l_x and d_x data: *Rangifer arcticus* (Banfield 1955).

DISCUSSION

The most striking feature of the q_x curves of species accepted for comparison is their similarity. Each curve can be divided into two components: a juvenile phase where the rate of mortality is initially high but rapidly decreases, followed by a postjuvenile phase characterized by an initially low but steadily increasing rate of mortality. The seven species compared in this paper all produced q_x curves of this "U" or fish-hook shape, suggesting that most mammals share a relationship of this form between mortality rate and age. This conclusion, if false, can be invalidated by a few more life tables from other species. It can be tested most critically by reexamining some of the species for which life tables, although published, were not accepted in this paper. Those most suitable are species that can be adequately sampled, and accurately aged by growth rings on the horns or growth layers in the teeth (chamois, Rocky Mountain sheep, and several species of deer), or those small mammals that can be marked at birth and subsequently recaptured.

High juvenile mortality, characterizing the first phase of the q_x curve, has been reported also for several mammals for which complete life tables have not yet been calculated (e.g. for *Oryctolagus cuniculus* (Tyndale-Biscoe and Williams 1955, Stodart and Myers 1964), *Gorgon taurinus* (Talbot and Talbot 1963), *Cervus elaphus* (Riney 1956) and *Oreamnos americanus* (Brandborg 1955). Kurtén (1953, p. 88) generalized this phenomenon by stating that "the initial dip [in the survivorship curve] is a constitutional character in sexually reproducing forms at least . . .". This phase of mortality is highly variable in degree but not in form. Taber and Dasmann (1957) and Bourlière (1959) have emphasized the danger of considering a life table of a population in given circumstances as a typical of all populations of that species. Different conditions of life tend to affect life tables, and the greatest differences between populations of a species are likely to be found at the juvenile stage. For example, the rate of juvenile mortality in red deer (Riney 1956) and in man differ greatly between populations of the same species.

The second phase—the increase in the rate of mortality throughout life—is common also to the seven species compared in this paper. However, although the increase itself is common to them, the pattern of this increase is not. Mortality rates have a logarithmic relationship to age in domestic sheep and to a less marked extent in the rat, the Orkney vole, and the dall sheep, whereas the relationship for the thar and the short-tailed vole appears to be approximately arithmetic. However, this difference may prove to be only an artefact resulting from the smoothing carried out on the data from these two species.

Despite these differences, the characteristics common to the various q_x curves dominate any comparison made between them. The similarities are all the more striking when measured against the ecological and taxonomic differences between species. Taxonomically, the seven species represent three separate orders (Primates, Rodentia, and Artiodactyla), and ecologically they comprise laboratory populations (rats and voles), natural populations (thar, dall sheep and man) and an artificial population (domestic sheep). The agents of mortality which acted on these populations must have been quite diverse. Murie (1944) reported that most of the dall sheep in the sample had been killed by wolves; most mortality in the thar population is considered to result from starvation and exposure in the winter; mortality of domestic sheep seems to be largely a result of disease, physiological degeneration, and possibly iodine deficiency in the lambs (Hickey 1963); whereas the deaths in the laboratory populations of voles and rats may be due to inadequate parental care and cannibalism of the juveniles, and perhaps disease and physiological degeneration in the adults. These differences suggest that the q_x curve of a population may assume the same form under the influence of various mortality agents, even though the absolute rate of mortality of a given age class is not the same in all circumstances. This hypothesis is worth testing because it implies that the susceptibility to mortality of an age class, relative to that of other age classes, is not strongly specific to any particular agent of mortality. A critical test would be to compare the life tables of two stationary populations of the same species, where only one population is subjected to predation.

Although no attempt is made here to explain the observed mortality pattern in terms of evolutionary processes, an investigation of this sort could be informative. A promising line of attack, for instance, would be an investigation of what appears to be a high inverse correlation between the mortality rate at a given age and the contribution of an animal of this age to the gene pool of the next generation. Fisher (1930) gives a formula for the latter statistic.

Bodenheimer (1958) divided expectation of life into "physiological longevity" ("that life duration which a healthy individual may expect to live under optimum environment conditions until dying of senescence") and "ecological longevity" (the duration of life under natural conditions). This study suggests that such a division is inexpedient because no clear distinction can be made between the effect on mortality rates of physiological degeneration and of ecological influences.

It is customary to classify life tables according to the three hypothetical patterns of mortality given by Pearl and Miner (1935). These patterns can be characterized as: 1) a constant rate of mortality throughout life, 2) low mortality throughout most of the life span, the rate rising abruptly at old age, and 3) initial high mortality followed by a low rate of mortality. Pearl (1940) emphasizes that the three patterns are conceptual models having no necessary empirical reality, but a few subsequent writers have treated them as laws which all populations must obey. None of these models fit the mortality patterns of the seven species discussed in this paper although Pearl's (1940) later modification of the system provides two additional models (high–low–high mortality rate and low–high–low mortality rate), the first of which is an adequate approximation to these data. For mammals at least, the simple threefold classification of mortality patterns is both confusing and misleading. The five-fold classification allows greater scope; but do we yet know enough about mortality patterns in mammals to justify the construction of any system of classification?

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THE CAUSALITY OF MICROTINE CYCLES IN GERMANY

(Second Preliminary Research Report)

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Hitherto the phenomenon of cycles has not been a subject of detailed research in central Europe, so one could have the impression that cycles of extreme degree do not exist in the temperate zones of this continent (and this is often asserted, indeed); but this is not the case. The central European rodents not only exhibit irregular population fluctuations, but some of them also show regular cycles of an intensity and a strict periodicity not inferior to those of the cyclic animals in the arctic zone. Primarily, there are large plague districts of *Microtus arvalis* Pallas in Germany and her neighbouring countries which can be followed back at least to the fifteenth century. Recently, these plague districts have increased because of cultivation measures, especially the drainage of moist lowlands and fens, which create optimal biotopes for the voles (Frank, 1953c, 1955, 1956b). Besides, particularly since the end of the last war, *Microtus agrestis* L. caused heavy damage in the forest plantations, as it did in Great Britain, and it did so in a decidedly cyclic manner (Frank, 1952). Systematic research on the causality of these cycles was started by the author in 1951 at first with main emphasis on *M. arvalis*. Besides detailed publications, a first preliminary report was given in 1954 (Frank, 1954b). In the meantime, many new results have been collected—in laboratory populations of more than 10,000 animals and in outdoor-cage populations, as well as in wild populations involving 1,150 individually marked animals. This paper summarizes the present state of the work, including as-yet-unpublished material. I am much indebted to Frances Hamerstrom, Plainfield (Wis.), and to Robert Rausch, Anchorage (Alaska) for critically revising my English rough copy, and also for inducing me to adjust my ecological terms to American usage and to formulate some passages more precisely.

The main emphasis on cyclic work formerly was mostly placed on the attempt to get to the bottom of the causality of cycles by analysing and explaining the periodicity from phenological data, often with speculation on cosmic causalities before having explored all terrestrial events and influences. In contrast, the German researches were concentrated on the observation and analysis of the internal events occurring in cyclic populations and on the environmental factors influencing them. Naturally, we are not able to solve all problems connected with microtine cycles in so short a time, but I dare say many partial solutions have now been attained. When assembled, they already show a rough picture of the cyclic structure established on a foundation of facts containing few elements of a speculative or hypothetical nature. In this way the cyclic phenomenon presents itself—as do other biological problems—as an interaction between biological events and environmental factors of a particularly complicated structure, depending on several factor-groups and many individual factors.

POPULATION INCREASE

First, population increase results from three factor-groups—the "reproductive potential" of the cyclic species, the "carrying capacity" of the environment, and that which I call in German "Verdichtungspotential" (Frank, 1954b), in English "condensation potential" of the cyclic species.

Reproductive Potential

This first factor-group is based on age at maturity, litter size, litter succession, and length of the reproductive season. Working with a captive population of more than 10,000 laboratory-reared animals (Frank, 1956a) and individually marked wild populations of *M. arvalis* (yet unpublished), my findings concerning this point had most remarkable results. *M. arvalis* distinguishes itself by having a pronounced suckling-maturity. The young females, which suckle until the seventeenth day, already show a perforated vagina from the eleventh day on and are mated by old males from the thirteenth day on. Correspondingly, the earliest litters were dropped by a wild female 33 days old and by a captive female 34 days old (pregnancy lasts 19-21 days, on an average 20 days). Indeed under natural conditions, a high proportion of the young females mate in the maternal home range before being weaned or immediately after being weaned.[1] But this happens only in the spring and summer; the females born during and after September for the most part do not reach sexual maturity in the same year. In the autumn the young generally show a slower growth rate than in the spring and summer, when an astonishing growth rate is evident. At the age of about 40 days a pregnant female can weigh up to 34g., and the males of this age also may be as heavy as very old animals. Every analysis of vole populations for age classification based on weight classification, therefore, must lead to serious errors, and conclusions based on them are subject to question (Frank and Zimmerman, 1957).

Besides age at maturity, reproductive potential is based on litter size and litter succession. Litter size depends upon inheritance, upon age and size of the female, and upon season (Frank, 1956a), and is modified by several environmental influences; in particular, quality and quantity of food are of decisive importance. In *M. arvalis* maximum litter size is 12; in one case Reichstein (1957) found 13 embryos. Under optimal conditions postpartum mating is usual, so that one litter follows another every 20 days. The maximum number of litters produced by one female in my laboratory-reared population of more than 10,000 animals has been 33, with 127 young and an average litter size of 3.85. Under optimal food and climatic conditions in spring and summer, the average litter size in wild populations can amount to 7 young. Concerning reproductive efficiency, *M. arvalis* represents a maximum among all mammals hitherto investigated. In captive females the litter weight amounts to 53.2 per cent of the mother's weight (both measured immediately after birth), while in other mammals, for instance some other rodents and pygmy dogs, it is only one-third (Frank, 1956a).

Length of the reproductive season, a further factor influencing reproductive potential, continues from February or March to October or November, but under favourable conditions, for example in cornricks, reproduction goes on through the winter (Stein, 1953a; Frank, 1954b). On the whole, *M. arvalis,* and probably *M. agrestis,* both showing pronounced cycles, possess an uncommon reproductive potential attainable under the optimal environmental conditions presented in the plague districts.

Carrying Capacity of Environment

Whether or not this high reproductive potential causes a violent population increase depends on the second factor-group, the carrying capacity of the environment. In other words, it depends on whether or not the environment can support a high population. The individual factors influencing this are especially food, cover, sunlight, good overwintering places, and ground-water level (but in the case of *M. arvalis* not the nature and humidity of the soil). Also it is striking that all plague districts of *M. arvalis,* although they lie in very different geological formations (lowlands, marshes, fens, loam steppes, lower mountain regions, etc.), show very similar characteristics in the structure of their landscape. They always represent large, open, monotonous, and uniform biotopes with extremely scant cover of trees and bushes, which we call "cultivation steppes" caused by human activity in the once-wooded or marshy central European country. Extremely severe and regular plagues of *M. arvalis* occur only in such biotopes, evidently representing the ecological optimum for this species; in districts miscellaneously covered by varied biotopes

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[1] Early maturity of females seems to be a general feature of the genus *Microtus* because I found mating females 20 days old also in *M. oeconomus* (Frank and Zimmermann, 1956). As far as I know suckling-maturity among other mammals has hitherto been established only for *Mustela erminea* L. (Müller, 1954).

and higher proportions of woods, trees, and bushes, only moderate fluctuations are visible. Doubtless these circumstances represent certain parallels to the opinion of Dymond (1947), that the uniformity of the arctic biotopes favours the amplitude of cycles. This further shows that not only the climate but also the structure of environment is important for the origin of regular cycles, which indeed are observable in the temperate zones where there are corresponding environmental conditions. The abundance and the cycles of *M. arvalis* are also influenced by the economic use of the country. Extensive agricultural use favours plagues, intensive use prevents plagues. On grazing land a low stock of cattle and an extensive pasturing favours plagues, while high stocks of cattle and intensive pasturing prevent plagues (Frank, 1956b).

Thus, in central Europe, the cycles of *M. arvalis* are "released" by human cultivation. This enables us to stop the development of plagues by an ecological and economic reorganisation of the plague districts. Based on this example the author has postulated the introduction of the more effective "ecological plague control" for crop protection, rather than the usual chemical pest control by poisons and biological control by encouragement of enemies and parasites (Frank, 1956b). In principle, the same is valid for *M. agrestis,* which shows regular fluctuations only in former woodland where the trees have been felled or new plantations of trees are laid out, and the bare plains are covered with large grass jungles, evidently representing the ecological optimum for this species (Frank, 1952, 1954b). In any case true cycles appear only under optimal environmental conditions permitting both the realization of the high reproductive potential and the establishment of the descendants produced by this potential: in other words, where a high carrying capacity is present. On this point our conclusions probably come near to some of the ideas expressed by Paul Errington.

Condensation Potential

The degree of the population increase depends decisively on the third factor-group: the condensation potential, which consists of certain behaviour mechanisms that enable many cyclic species to live at an uncommonly high population density. Before describing these behaviour mechanisms I must explain the new term "condensation potential" (Frank, 1954b). It is based on all intraspecific and especially social behaviour that favours the increase of density. Normally the condensation potential is limited by intrinsic behaviour, especially by territoriality, to a "saturation point" which is approximately adapted to the carrying capacity of the environment. It seems to be a feature of many cyclic species that they show particular social behaviour that abolishes the normal limits, and enables them, under optimal environmental conditions, to exceed the saturation point so far that the carrying capacity of the environment is greatly exceeded, and simultaneously population regulation by crash, mass emigration, or other drastic mechanisms becomes necessary and inevitable. In *M. arvalis* the condensation potential concerns: reduction of the home ranges, social communities of the females, and diminution or elimination of males. These points seem worth stressing as aspects of cycle research that further the understanding of this phenomenon and of population dynamics in general (Frank, 1954b, 1956a).

Fundamentally the European microtines are territorial animals; this we have demonstrated in the laboratory (Frank, 1953a, 1956a) as well as in individually marked wild populations. Females occupy a range around their burrows where they tolerate no stranger of their species. Females tolerate a strange male in their home ranges only when they are in heat and even then the male must fight to approach. With the exception of the short period of heat, all strangers of either sex are driven away. This home range has a diameter of 10-20 meters during the reproductive season. Males inhabit an irregular larger range, wandering from female to female to mate those that are in heat. They are only intolerant of strange males of mature age. Recently we found that in spring and summer the young males without exception disappear from their mother's territory and its surroundings after becoming mature, and the old males mating the resident females are all strangers, having immigrated from other places. This would tend to prevent inbreeding. In contrast, the young females settle in the immediate vicinity of their mother's home range, or sometimes within it. When space becomes scarce, the size of the home ranges can be reduced. This also gives the voles a considerable condensation potential (Frank, 1953a).

In contrast to the territorial behaviour that causes intraspecific demarcation and guarantees the individual space and food needed for life and reproduction, the following mechanisms favour life in social communities and also high density. In the first place we have the "mother-family," consisting of the female and her suckling young, sometimes also her unmated subadult offspring. But this is not typical of spring and summer when, for the most part, the weaned young, particularly the males, leave the maternal home range. "Great families" arise every autumn, for the last two to three litters of the year remain in the maternal home range (because the female does not drive them out), and constitute the overwintering community (Frank, 1954a). This lightens existence in the cold season when stress is great; all live together in a single, thickly lined nest, the many small individuals form a greater thermal unit, and the loss of heat and energy is significantly reduced. Freezing weather and heavy precipitation reduce the activity of the voles, which remain in their nests and eat the food stores they have brought in during autumn. Nevertheless, the size of the home ranges and the radius of activity of the voles is importantly enlarged during winter (about four or five times larger than the summer home range), probably because of both the greater number of the inhabitants (overwintering community instead of the female and her last litter in summer), and because of the shortage of available food requiring a larger feeding area for these herbivorous animals. In the peak years the impossibility of such an enlargement of activity radius, caused by population density, might contribute much to intensify competition for food and to bring on a crash situation. In spring the overwintering communities dissolve by scattering.

Furthermore, a behaviour mechanism of highest importance is involved in the nest communities of the females (Frank, 1953a). Increasingly with population condensation, the young females remain together, occupy a common territory, and bring up their litters in a single nest by means of social breeding care. Generally they remain together for the rest of their lives, and if they change their home range because of disturbance, etc., they move as a community, often with their young also. The nest community can consist of 2-4 (perhaps 5) sisters, and sometimes of their mother too. The decisive influence of this behaviour upon the population dynamic is that it enables these primarily territorial animals to live in an abnormally high density. In this way not only more females can live in the same space, but also a correspondingly greater number of young can be produced and brought up. Doubtless this particular social behaviour of *M. arvalis* explains the uncommon population density and the outright explosive population increase in plague centres, i.e., those parts of the plague districts ecologically most favourable and first occupied by the voles.

In contrast to the females, the mature males cannot draw so near to one another because they generally display rivalry (except as members of a family or of an overwintering community). During population increase in a given space, the number of old males remains the same, while that of the mature females rapidly increases. Progressing with population condensation, a considerable elimination of mature males occurs (Frank, 1953a, 1954a, 1954b; Stein, 1953b). This reduction is also evident from the pellets of owls (Becker, 1954), and thus not caused by selective predation (on the males), but by intraspecific competition (among the males). In spring and summer the weaned young males, without exception, leave their birthplaces, probably because of an innate drive after maturing. They must look for a new home range and come up against all other males they meet. Whether their number diminishes by killing each other or merely by driving each other away requires further observations. A large number of the wild males show injuries, especially bites in the region of the hindquarters, and lost tails, caused by intraspecific fighting; however, these injuries might have been acquired from resident females as well as from other males.

Thus we see that the intraspecific, especially social, behaviour of the animals is of great importance to all population-dynamic events. Further research is needed on this point, especially in other cyclic species, to find out whether similar or other condensation mechanisms are prevalent.

POPULATION DECLINE

What causes the population decline of *M. arvalis*? The life span of the little microtines is naturally short. Periods of crises and losses seem to be: (1) becoming acquainted with the maternal home range first, in which there is danger if strange neighbours are encountered; (2) the period of spreading after weaning, which involves heavier losses in the males than in the females; and (3) the winter season, which normally diminishes the population up to 50 per cent or more (Frank, 1954b). The animals of my marked wild populations never survived two winters, and the markedly old individuals almost all succumb to the stresses of the first winter months. Not only those individuals that have survived a winter die, but also those born in spring and summer that had reproduced suffer mortality. Their body weight gradually diminishes throughout the autumn, and their body reserves are nearly consumed by then. In contrast, the young animals born in the autumn increase in weight and lose only a little in the beginning of winter; then their weight is maintained during the winter months (mostly about 12-18g.) and mounts again quickly in early spring. While the period of spreading causes heavier losses among males, winter mortality strikes more females because they are mostly somewhat smaller and weaker (Frank, 1954b). Nevertheless, mortality effects a real selection by eliminating the less fit individuals. After the winter period, the surviving population consists nearly exclusively of autumn-born animals that had remained sexually immature until spring. The older voles, already having participated in reproduction during the last year, have vanished with only few exceptions.

Winter mortality can be so great, particularly in extremely severe winters, that the population declines to a minimum level by a gradual die-off of most individuals; but this happens only when population density is not high enough to produce a regular crash. However, the physiological mechanism of this gradual die-off seems to be similar to that of the regular crash, and to be based on the endocrine system also (see below). In this way, the stress of such a severe winter can injure the survivors of the gradual die-off (and also of a regular crash) so much that a remarkable subsequent mortality occurs among them during spring. They do not mount in weight and can hardly bring up their young, which therefore show heavy mortality. This has already been pointed out by Chitty (1952, 1955) and in every way confirmed also by my own researches in outdoor cages (Frank, 1954a) as well as by research on wild populations of *M. arvalis* and *M. agrestis* (as yet unpublished). Therefore, vole populations always have a difficult and slow start toward recovery after severe winters and after crashes. Predation plays only a very small part, because predators are not at all numerous in the plague districts, having been kept down both by the unfavourable, monotonous and coverless biotope and by human persecution (Frank, 1954b, 1955, 1956b).

In the peak years characterized by overcrowding, the regulation of microtine population density by no means shows itself as mass emigration as with the lemmings (*Lemmus lemmus* L.), for we observed movement of individuals only, more commonly in the males than in the females. As previously stated, the latter are generally inclined to settle in the neighbourhood of their birthplaces as long as they are able to find places unoccupied by other females. But space finally becomes scarce (in spite of and after reduction of the size of the home ranges) and competition among females increases. Reproduction is then gradually restricted (Frank, 1953a, 1954a). The degree of embryonal resorptions, infertility, and mortality of young all mount quickly, but population density can no longer be regulated by these; the carrying capacity of the environment has already been greatly exceeded. For this reason regulation must be performed by a more effective mechanism: the crash. Our investigations could not produce any evidence for the hypothesis that epizootic diseases or parasites cause the crash, although our material was examined by many specialists (Frank, 1953b). An explanation was only possible on the basis of Christian's (1950) important idea that the "shock disease" of the varying hare (*Lepus americanus* Erx.), discovered by Green and Larson (1938), seems to be an appearance of the general adaptation syndrome of Selye (1946).

First I must say that the crash symptoms in *M. arvalis* are the same as in *L. americanus*: lethargy, convulsions, liver degeneration, enlargement of the adrenals and hypoglycemia, and moreover (not mentioned by Green and Larson) marked decline in body temperature long before death, and behavioural changes such as crowding and cannibalism. The last represents an important chance for survival of the fitter individuals by making use of the carcasses of their dead companions as food reserves during the period of general deficiency or shortage of vegetable food already used up by the overcrowded population (Frank, 1953b). Not only have we found these symptoms experimentally in outdoor cages where vole populations were kept overcrowded and showed drastic crashes, but we were also able to produce crash symptoms by artificial hypoglycemia induced by insulin injections; conversely, the symptoms could be suspended, temporarily at least, by injection of grape sugar (Frank, 1953b).

We get the impression that condensation and crowding favour competition and cause a state of psychological excitement being transformed by the pituitary-adrenocortical system into a physical stress. This, acutely combined with the stress of food shortage, produces a "readiness" for crash, whether the real releasing of the crash is caused by an increase in the force of these stresses, or, in nature, largely by additional meteorological stresses, such as periods of cold or precipitation. On the whole, a situation with several stress-producing components ultimately produces the resulting "crash" either when all stress factors jointly reach a critical point or value, or when a new stress is superimposed on the already stressed adreno-pituitary system.

In my opinion, our results confirm the basic trends of ideas presented by Christian's (*op. cit.*) important working hypothesis, but my results differ in one essential point. Christian supposes that the crash, the readiness for which is brought about by several stresses, is ultimately caused and released by the additional stress of the activation of gonads happening in the early spring. But I never found any enlargement of testes and uteri in crashing wild populations. Also in my experimentally induced crashes of outdoor-cage populations, activation of gonads was certainly not in play. I am therefore convinced that gonadotrophic demands are not involved in the crash phenomenon, in *Microtus* at least. In my conception the ultimate trigger, producing the crash of vole populations, is an additional stress of meteorological events, particularly frost periods. I believe that this conception explains better than Christian's the sudden advent of a crash within a few days. The stress of gonadotrophic demands would be extended over longer time and would operate in very different moments upon the single animal. In contrast, the meteorological stress caused by the intrusion of frost periods acts equally and suddenly upon all individuals and makes more easily understandable the suddenness of the crash.

Nevertheless, gonadotrophic activation might play an essential role, indeed, in the subsequent mortality occurring in spring among the survivors from crashes and gradual winter die-offs, which was discovered by Chitty (*op. cit.*) and also found in the vole populations investigated by the author (see above). In this case, gonadotrophic activation presents a true additional stress upon the endocrinological system, as Christian has supposed.

I must emphasize that this conception is based on investigations in vole populations only. In any event, it now seems to be certain that the adreno-pituitary system has decisive importance in intraspecific regulatory events occurring in vertebrate populations. Further research is needed to complete and deepen our knowledge of this important point, and to find out in what manner and with which different effects this psycho-physiological mechanism is operating and which environmental factors are acting upon them, in voles as well as in other rodents and vertebrates generally.

THE PERIODICITY OF CYCLES

Many workers on the periodicity of cycles (recently again Siivonen and Koskimies, 1955) attempt to connect this problem with cosmic factors before having explored all terrestrial environmental factors possibly influencing it. But nearly all such work on this subject generally seems to suffer from the fact that the phenological data, particularly the meteorological conditions, are not brought into relationship as the most important environmental factors acting upon cyclic populations. Favoured by the extremely equalized temperate climate in the Gulf Stream neighbourhood of northwestern Germany, Maercks (1954) has been able to evaluate the interaction between the cycles of *M. arvalis* and meteorological events over a period of 39 years, based on the five-day median values of temperature, quantity and frequency of precipitation, and duration of sunshine. Therefore the cyclic events take place in a rather "pure culture" generally little influenced by extreme changes in weather conditions, which—if they occurred —could easily be analysed regarding their effects on the cyclic events. Maercks found a clear and strict microtine-cycle periodicity of three years from peak to peak, obviously caused by the reproductive and condensation potential of the species and the carrying capacity of its environment. Under optimal environmental conditions *M. arvalis* is able to replenish a plague district within three years so completely that the carrying capacity is exceeded and natural regulation by crash must occur. Every population has its own autonomous periodicity, and in other spheres (other species or other environment, or both) there will be other frequencies of the periodicity (Frank, 1954b). Dymond (1947) has already suggested that animals with a high and constant reproductive potential may be able to populate deficiently buffered[2] biotopes of optimal and constant ecological conditions at regularly occurring intervals to an unbearable density.

As to the influence of meteorological conditions, Maercks (*ibid.*) found frequent quantitative oscillations in the degree of the peak population density and plague damage, but few temporal mutations of the periodicity itself. The former are caused by changes of rainfall and duration of sunshine, for example, while the latter are all reducible to uncommon and extreme deviations in weather conditions, especially in winter. In the 39 years investigated by Maercks, the three-year periodicity has undergone three mutations, which led to the following conclusions: (1) A particularly mild winter prolongs the plague over a two-year period, and therefore the cyclic interval extends to four years, because the expected crash does not happen but comes a year later; (2) an extremely long and severe winter cuts off the population increase by causing a gradual die-off or a precocious crash and forcing a new start of population increase.

In both cases the cycle periodicity suffers a shifting of phase by one year (or more perhaps in other cases). This shifting, indeed, is a point in the cycle phenomenon that has caused considerable difficulty to cycle workers, who have almost established a periodicity of 3 1/3 years. But this was unsatisfactory because the cyclic periodicity is based (in my opinion at least) on the reproductive season's being fixed by the astronomical year. Every biological periodicity extended over several years might also present whole numbers corresponding to the whole numbers of years. This difficulty is removed by the shifting of phase caused by meteorological deviations that occur in every climate; the phase shift easily explains the fact that animal cycles never show a symmetrical periodicity over a long period of time but always show a few exceptions or deviations from the prevailing equal periodicity (three years in the case of *Microtus arvalis*).

Also the striking conformity in the periodicity of different cyclic populations and plague districts, independent of and isolated from each other, is produced by meteorological conditions prevailing equally over a large region (Frank, 1954b). For example, an uncommon and extremely severe winter will simultaneously throw back all populations influenced by it (each having its own autonomous periodicity previously), to a new (and common) starting point. Nevertheless, some populations exposed to special environmental conditions can show a different periodicity, most commonly because favourable overwintering conditions have counterbalanced unfavourable meteorological conditions.

SUMMARY

The results of recent work on microtine cycles occurring in Germany enable us to understand this phenomenon as an interaction between biotic and environmental factors only, and without aid of any hypothetical explanation by extraterrestrial "cosmic" factors. It may be supposed that the causality of other animal cycles will find a similarly "natural" explanation after being explored as intensively as the cycles of *Microtus arvalis* in Germany. Although these

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[2] These are biotopes with a scarcity of natural counterpowers to the species in question, as enemies, competition by other species, limit of food and habitats, or other unfavourable ecological conditions.

are indeed "released" by human cultivation measures, which have produced optimal biotopes and thus the ecological base of cycles, the biotic causalities and laws of these cycles must be the same as those prevailing in cycles occurring in natural districts not influenced by man.

Concerning *M. arvalis* the population increase is based on: (1) a high reproductive potential based on (a) extremely early maturity and mating (in females often before being weaned), (b) high reproductive efficiency (litter weights to 53.2 per cent of the mother's weight), (c) large litter size (maximum 12-13, average in wild populations about 7 young), (d) rapid litter succession (pregnancy about 20 days, post-partum mating normal), and (e) extended season of reproduction (sometimes throughout winter); (2) a high carrying capacity of the environment under the optimal ecological conditions of the plague districts, based on food, cover, ground-water level, sunlight, overwintering places, and last but not least on the uniform structure of the landscape; and (3) a high "condensation potential" based on behaviour, particularly social mechanisms concerning (a) reducible home-range size during population increase, formation of (b) "great families" and (c) overwintering communities, (d) communal nesting of females, and (e) elimination of males. On the whole, these factors sufficiently explain the outright explosive increase and the uncommon density of microtine populations in German plague districts.

Because this rapid population increase cannot be regulated by normal mortality and dispersal, more efficient regulatory mechanisms are called into play. When the supportable density of population is approached, restriction of reproduction and accelerated individual emigration take place, but these are not enough to keep the population within the limits set by the carrying capacity of the environment. When supportable density is exceeded, crash, caused by shock disease, occurs in the following winter. Psychological stresses (such as crowding and competition) and physical stresses (such as food shortage) produce a "readiness" for crash, but the real trigger is largely the additional meteorological stress of winter. Three years are ordinarily required to reach this point, hence an autonomous and strict 3-year periodicity exists. The seldom-occurring deviations ("shifting of phase") are caused only by uncommon meteorological conditions. Unusually severe winters synchronize the periodicity of isolated populations over large districts.

On the whole, cycles take place where the high biotic potential of the species is fully realizable in the optimal biotopes of plague or other cyclic districts. It seems remarkable that this disproportion is not balanced by selection. Cycles have undoubtedly gone on from time immemorial, and the quick succession of generations of voles should have favoured such an adaption in a relatively short time.

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TERRITORIALITY AND HOME RANGE CONCEPTS AS APPLIED TO MAMMALS

By William Henry Burt

TERRITORIALITY

The behavioristic trait manifested by a display of property ownership—a defense of certain positions or things—reaches its highest development in the human species. Man considers it his inherent right to own property either as an individual or as a member of a society or both. Further, he is ever ready to protect that property against aggressors, even to the extent at times of sacrificing his own life if necessary. That this behavioristic pattern is not peculiar to man, but is a fundamental characteristic of animals in general, has been shown for diverse animal groups. (For an excellent historical account and summary on territoriality, with fairly complete bibliography, the reader is referred to a paper by Mrs. Nice, 1941). It does not necessarily follow that this trait is found in all animals, nor that it is developed to the same degree in those that are known to possess it, but its wide distribution among the vertebrates (see Evans, L. T., 1938, for reptiles), and even in some of the invertebrates, lends support to the theory that it is a basic characteristic of animals and that the potentialities are there whether the particular animal in question displays the characteristic. Heape (1931, p. 74) went so far as to say:

"Thus, although the matter is often an intricate one, and the rights of territory somewhat involved, there can, I think, be no question that territorial rights are established rights amongst the majority of species of animals. There can be no doubt that the desire for acquisition of a definite territorial area, the determination to hold it by fighting if necessary, and the recognition of individual as well as tribal territorial rights by others, are dominant characteristics in all animals. In fact, it may be held that the recognition of territorial rights, one of the most significant attributes of civilization, was not evolved by man, but has ever been an inherent factor in the life history of all animals."

Undoubtedly significant is the fact that the more we study the detailed behavior of animals, the larger is the list of kinds known to display some sort of territoriality. There have been many definitions to describe the territory of different animals under varying circumstances. The best and simplest of these, in my mind, is by Noble (1939); "territory is any defended area." Noble's definition may be modified to fit any special case, yet it is all-inclusive and to the point. Territory should not be confused with "home range"—an entirely different concept that will be treated more fully later.

The territoriality concept is not a new one (see Nice, 1941). It has been only in the last twenty years, however, that it has been developed and brought to the front as an important biological phenomenon in the lower animals. Howard's book "Territory in Bird Life" (1920) stimulated a large group of workers, chiefly in the field of ornithology, and there has hardly been a bird life-history study since that has not touched on this phase of their behavior.

In the field of mammals, much less critical work has been done, but many of the older naturalists certainly were aware of this behavior pattern even though they did not speak of it in modern terms. Hearne (1795) apparently was thinking of property rights (territoriality) when he wrote about the beaver as follows: "I have seen a large beaver house built in a small island, that had near a dozen houses under one roof; and, two or three of these only excepted, none of them had any communication with each other but by water. As there were beavers enough to inhabit each apartment, it is more than probable that each family knew its own, and always entered at their own door without having any

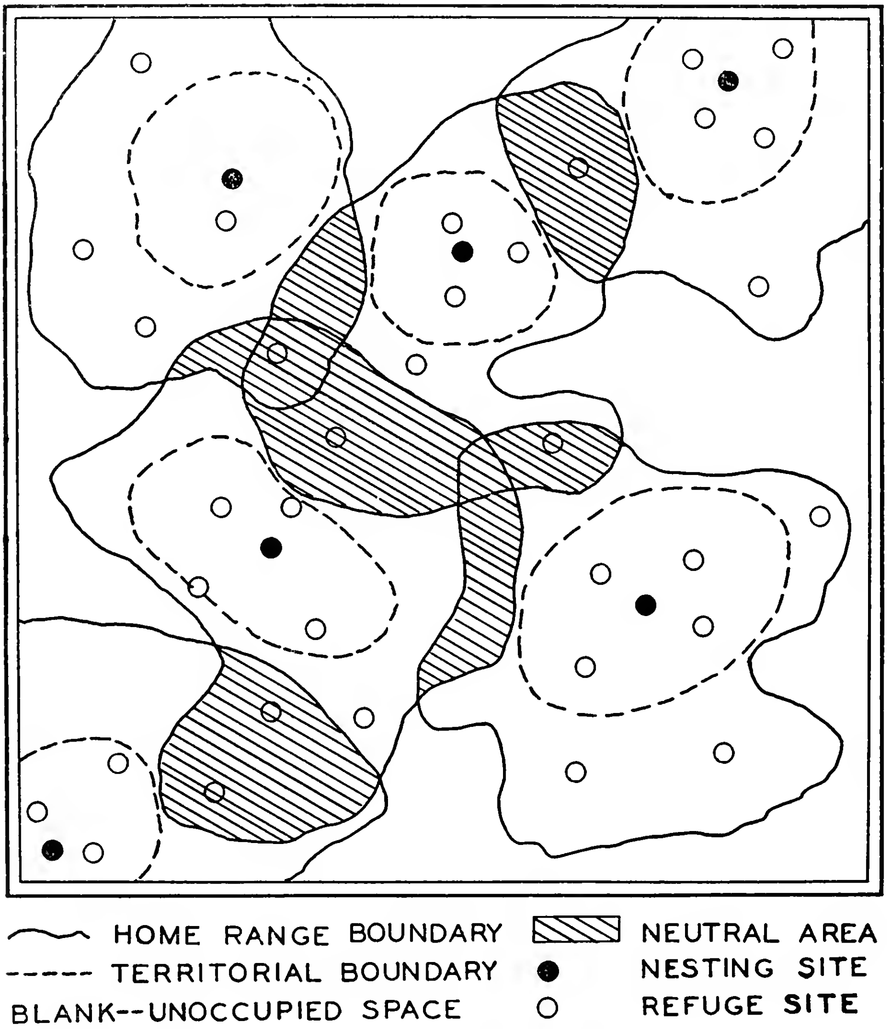

Fig. 1. Theoretical quadrat with six occupants of the same species and sex, showing territory and home range concepts as presented in text.

further connection with their neighbors than a friendly intercourse" (in Morgan, 1868, pp. 308–309). Morgan (*op. cit.*, pp. 134–135), also writing of the beaver, made the following observation; "a beaver family consists of a male and female, and their offspring of the first and second years, or, more properly, under two years old. . . . When the first litter attains the age of two years, and in the third summer after their birth, they are sent out from the parent lodge." Morgan's observation was later confirmed by Bradt (1938). The works of Seton are replete with instances in the lives of different animals that indicate territorial behavior. In the introduction to his "Lives" Seton (1909) states "In the idea of a home region is the germ of territorial rights." Heape (1931) devotes an entire chapter to "territory." Although he uses the term more loosely than I propose to, (he includes home ranges of individuals and feeding ranges of tribes or colonies of animals), he carries through his work the idea of defense of an area either by an individual or a group of individuals. Not only this, but he draws heavily on the literature in various fields to support his thesis. Although the evidence set forth by Seton, Heape, and other early naturalists is of a general nature, mostly garnered from reports by others, it cannot be brushed aside in a casual manner. The old time naturalists were good observers, and, even though their techniques were not as refined as those of present day biologists, there is much truth in what they wrote.

A few fairly recent published observations on specific mammals serve to strengthen many of the general statements made by earlier workers. In speaking of the red squirrel (*Tamiasciurus*), Klugh (1927, p. 28) writes; "The sense of ownership seems to be well developed. Both of the squirrels which have made the maple in my garden their headquarters apparently regarded this tree as their private property, and drove away other squirrels which came into it. It is quite likely that in this case it was not the tree, but the stores that were arranged about it, which they were defending." Clarke (1939) made similar observations on the same species. In raising wild mice of the genus *Peromyscus* in the laboratory, Dice (1929, p. 124) found that "when mice are placed together for mating or to conserve cage space it sometimes happens that fighting takes place, especially at first, and sometimes a mouse is killed. . . . Nearly always the mouse at home in the cage will attack the presumed intruder." Further on he states, "However, when the young are first born, the male, or any other female in the same cage, is driven out of the nest by the mother, who fiercely protects her young." Similarly, Grange (1932, pp. 4–5) noted that snowshoe hares (*Lepus americanus*) in captivity "showed a definite partiality for certain spots and corners to which they became accustomed" and that "the female would not allow the male in her territory (cage) during late pregnancy and the males themselves were quarrelsome during the breeding season."

Errington (1939) has found what he terms "intraspecific strife" in wild muskrats (*Ondatra*). Much fighting takes place when marshes become overcrowded, especially in fall and winter during readjustment of populations. "But when invader meets resident in the tunnel system of one of [the] last lodges to be used in a dry marsh, conflict may be indeed savage." Gordon (1936) observed definite territories in the western red squirrels (*Tamiasciurus fremonti* and *T. douglasii*) during their food gathering activities. He also performed a neat experiment with marked golden mantled squirrels (*Citellus lateralis chysodeirus*) by placing an abundance of food at the home of a female. This food supply attracted others of the same species. To quote Gordon: "she did her best to drive away the others. Some of her sallies were only short, but others were long and tortuous. There were rather definite limits, usually not more than 100 feet from the pile, beyond which she would not extend her pursuit. In spite of the vigor and the number of her chases (one day she made nearly 60 in about 6 hours) she never succeeded in keeping the other animals away." This individual was overpowered by numbers, but, nevertheless, she was using all her strength to defend her own log pile. To my knowledge, this is the best observation to have been published on territorial behavior in mammals. I have observed a similar situation (Burt, 1940, p. 45) in the eastern chipmunk (*Tamias*). An old female was watched fairly closely during two summers. Having marked her, I was certain of her identity. "Although other chipmunks often invaded her territory, she invariably drove them away [if she happened to be present at the time]. Her protected area was about fifty yards in radius; beyond this fifty-yard limit around her nesting site she was not concerned. Her foraging range (*i.e.*, home range) was considerably greater than the protected area (territory) and occasionally extended 100 or more yards from her nest site." From live trapping experiments, plotting the positions of capture of individuals on a map of the area covered, I interpreted (*op. cit.*, p. 28) the results to mean that there was territorial behavior in the white-footed mouse (*Peromyscus leucopus*), a nocturnal form. When the ranges of the various individuals were plotted on a map, I found that "the area of each of the breeding females is separate—that although areas sometimes adjoin one another, they seldom overlap." Carpenter (1942) writes thus: "The organized groups of every type of monkey or ape which has been adequately observed in its native habitat, have been found to possess territories and to defend these ranges from all other groups of the same species." In reporting on his work on the meadow vole (*Microtus pennsylvanicus*), Blair (1940, pp. 154–155) made the statement "It seems evident that there is some factor that tends to make the females occupy ranges that are in part exclusive; . . . . Possibly there is an antagonism between the females, particularly during the breeding season, but the available evidence does not indicate to me that they have definite territories which they defend against all trespassers. It seems highly probable that most mammalian females attempt to drive away intruders from the close vicinity of their nests containing young, *but this does not constitute territoriality in the sense that the term has been used* by Howard (1920), Nice (1937), and others *in reference to the breeding territories of birds.*" (Ital. mine.) To quote Howard (1920, pp. 192–193): "But the Guillemot is generally surrounded by other Guillemots, and the birds are often so densely packed along the ledges that there is scarcely standing room, so it seems, for all of them. Nevertheless the isolation of the individual is, in a sense, just as complete as that of the individual Bunting, for each one is just as vigilant in resisting intrusion upon its few square feet as the Bunting is in guarding its many square yards, so that the evidence seems to show that that part of the inherited nature which is the basis of the territory is much the same in both species." Blair, in a later paper (1942, p. 31), writing of *Peromyscus maniculatus gracilis*, states: "The calculated home ranges of all sex and age classes broadly overlapped one another. Thus there was no occupation of exclusive home ranges by breeding females. . . . That individual woodland deer-mice are highly tolerant of one another is indicated by the foregoing discussion of overlapping home ranges of all sex and age classes." Reporting on an extensive field study of the opossum, Lay (1942, p. 149) states that "The ranges of individual opossums overlapped so frequently that no discernible tendency towards establishment of individual territories could be detected. On the contrary, tracks rarely showed that two or more opossums traveled together." It seems quite evident that both Blair and Lay are considering the home range as synonymous with the territory when in fact they are two quite distinct concepts. Further, there is no concrete evidence in either of the above papers for or against territoriality in the species they studied. It is to be expected that the territory of each and every individual will be trespassed sooner or later regardless of how vigilant the occupant of that territory might be.

It is not intended here to give a complete list of works on territorial behavior. The bibliographies in the works cited above lead to a great mass of literature on the subject. The point I wish to emphasice is that nearly all who have critically studied the behavior of wild mammals have found this behavioristic trait inherent in the species with which they worked. Also, it should be stressed, there are two fundamental types of territoriality in mammals—one concerns breeding and rearing of young, the other food and shelter. These two may be further subdivided to fit special cases. Mrs. Nice (1941) gives six major types of territories for birds. Our knowledge of territoriality in mammals is yet too limited, it seems to me, to build an elaborate classification of types. Some day we may catch up with the ornithologists.

HOME RANGE

The home range concept is, in my opinion, entirely different from, although associated with, the territoriality concept. The two terms have been used so loosely, as synonyms in many instances, that I propose to dwell briefly on them here. My latest Webster's dictionary (published in 1938), although satisfactory in most respects, does not list "home range," so I find no help there. Seton (1909) used the term extensively in his "Lives" where he explains it as follows: "No wild animal roams at random over the country: each has a home region, even if it has not an actual home. The size of this home region corresponds somewhat with the size of the animal. Flesh-eaters as a class have a larger home region than herb-eaters." I believe Seton was thinking of the adult animal when he wrote the above. We know that young adolescent animals often do a bit of wandering in search of a home region. During this time they do not have a home, nor, as I consider it, a home range. It is only after they establish themselves, normally for the remainder of their lives, unless disturbed, that one can rightfully speak of the home range. Even then I would restrict the home range to that area traversed by the individual in its normal activities of food gathering, mating, and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered as in part of the home range. The home range need not cover the same area during the life of the individual. Often animals will move from one area to another, thereby abandoning the old home range and setting up a new one. Migratory animals have different home ranges in summer and winter—the migratory route is not considered part of the home range of the animal. The size of the home range may vary with sex, possibly age, and season. Population density also may influence the size of the home range and cause it to coincide more closely with the size of the territory. Home ranges of different individuals may, and do, overlap. This area of overlap is neutral range and does not constitute part of the more restricted territory of animals possessing this attribute. Home ranges are rarely, if ever, in convenient geometric designs. Many home ranges probably are somewhat ameboid in outline, and to connect the outlying points gives a false impression of the actual area covered. Not only that, it may indicate a larger range than really exists. A calculated home range based on trapping records, therefore, is no more than a convenient index to size. Overlapping of home ranges, based on these calculated areas, thus may at times be exaggerated. From trapping records alone, territory may be indicated, if concentrations of points of capture segregate out, but it cannot be demonstrated without question. If the occupant of an area is in a trap, it is not in a position to defend that area. It is only by direct observation that one can be absolutely certain of territoriality.

Home range then is the area, usually around a home site, over which the animal normally travels in search of food. Territory is the protected part of the home range, be it the entire home range or only the nest. Every kind of mammal may be said to have a home range, stationary or shifting. Only those that protect some part of the home range, by fighting or agressive gestures, from others of their kind, during some phase of their lives, may be said to have territories.

SIGNIFICANCE OF BEHAVIORISTIC STUDIES

I think it will be evident that more critical studies in the behavior of wild animals are needed. We are now spending thousands of dollars each year in an attempt to manage some of our wild creatures, especially game species. How can we manage any species until we know its fundamental behavior pattern? What good is there in releasing a thousand animals in an area large enough to support but fifty? Each animal must have so much living room in addition to other essentials of life. The amount of living room may vary somewhat, but for a given species it probably is within certain definable limits. This has all been said before by eminent students of wildlife, but many of us learn only by repetition. May this serve to drive the point home once more.

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MIGRATION OF BATS ON CAPE COD, MASSACHUSETTS.

BAT migration has received little attention. Various writers have made vague reference to the fact that certain bats are found in winter at localities where they are not known to breed, but no detailed account of the migratory movements of any species has yet been published. The only special paper on the subject that I have seen is by Dr. C. Hart Merriam,* who clearly establishes the fact that two North American bats migrate. The data on which this conclusion rests are as follows: The hoary bat, one of the migratory species, is not known to breed south of the Canadian fauna. In the Adirondack region it appears about the middle of May and disappears early in October. During the autumn and winter it has been taken in South Carolina (Georgetown, January 19th), Georgia (Savannah, February 6th), and on the Bermudas† ('autumn'). As the writer remarks, these facts may be fairly regarded as conclusive evidence of migration. The evidence of the migratory habits of the silver-haired bat rests chiefly on the animal's periodical appearance in spring and fall at the lighthouse on Mount Desert Rock, thirty miles off the coast of Maine. This species has also been observed on the Bermudas.

In August and September, 1890 and 1891, I had the opportunity to watch the appearance and disappearance of three species of bats at a locality where none could be found during the breeding season. Highland Light, the place where my observations were made, is situated near the edge of one of the highest points in the series of steep bluffs of glacial deposit which form the outer side of Cape Cod, Massachusetts. The light, which is less than ten miles from the northern extremity of the cape, is separated from the mainland toward the east and northeast by from twenty-five to fifty miles of water. The bluff on which it stands rises abruptly from the beach to a height of one hundred and fifty feet. I found the bats for the most part flying along the face of this bluff, where they fed on the myriads of insects blown there by the prevailing southwest winds. They chiefly frequented the middle and upper heights and seldom flew over the beach at the foot of the bluff or over the level ground about the lighthouse. I do not know where the animals spent the day, as careful search in old buildings, under the overhanging edge of the bluff, and in deserted bank swallow holes, failed to reveal their hiding places. It is possible that they found shelter in the dense, stunted, oak scrub with which the bluff is in many places crowned, but of this I have no evidence. I hope that the observations given below may again call the attention of field naturalists to a subject which presents many difficult and interesting problems.

ATALAPHA NOVEBORACENSIS* (RED BAT).

August 21, 1890. The first bats of the season were seen this evening. There were

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*Trans. Royal Soc. Canada V (1887), Section V, p. 85, 1888.

† I may add that I have a bat of this species, killed at Brownsville, Texas, on October 22d.

*With bat nomenclature in its present unsettled state it is well to use the names adopted by Dr.

only two, and I could not positively identify them, but they were probably red bats.

August 25, 1890. An adult male taken.

August 28, 1890. Two seen.

August 29, 1890. The evening was too chilly for many bats to be on the wing. A few *A. noveboracensis* seen and two taken.

August 30, 1890. Six or eight *A. noveboracensis* seen and three taken. The evening was warm and bats flew much more freely than on the 29th.

August 31, 1890. A chilly evening again, and only two bats seen, both *A. noveboracensis*.

September 2, 1890. A few red bats seen and two taken.

September 5, 1890. I was not at Highland Light this evening, but Mr. W. M. Small reported a heavy flight of bats. He shot five, all *A. noveboracensis.*

September 8, 1890. Heavy fog, so that no bats could be seen, if any were moving along the face of the bluff. Three or four red bats flew about the light house tower during the first half of the night, feeding on insects attracted by the light. They flew mostly below the level of the deck which encircles the tower about six feet below the lantern and never approached the light itself.

September 12, 1890. A single red bat shot this evening.

After this date I watched for bats on several consecutive evenings. As I saw no more I concluded that the migration had ended.

August 25, 1891. Fourteen *Atalapha noveboracensis*, the first bats of the season, seen this evening. They were flying both north and south.

August 26, 1891. Evening very foggy. A red bat which flew about the lighthouse was the only one seen.

August 27, 1891. Half a dozen red bats seen and one taken.

August 28, 1891. Four red bats seen. All flew toward the south.

August 30, 1891. A red bat caught in a house near the edge of the bluff.

September 2, 1891. Eight or ten seen and three taken. The movement this evening was mostly, though not wholly, from north to south.

September 3, 1891. Six seen and three taken.

September 5, 1891. Evening cold and misty. No bats moving.

September 7 and 8, 1891. A few bats seen each evening, but none taken. All appeared to be this species.

September 10, 1891. One red bat shot.

September 11, 1891. One seen.

September 12, 1891. One killed. About a dozen bats seen, but how many were of this species, and how many *Lasionycteris noctivagans* I could not determine.

September 13, 1891. About a dozen bats seen. Two of these were certainly red bats.

After this date I watched for bats on consecutive evenings for more than a week. As I saw none I finally gave up the search.

ATALAPHA CINEREA (HOARY BAT).

August 26, 1890. One *Atalapha cinerea*, the only bat seen, shot this evening.

August 28, 1890. Two hoary bats taken, and at least two, and probably four, others seen.

Harrison Allen in his latest Monograph of the Bats of North America (1893), although many of these will require revision.

August 30, 1890. Two taken and two others seen.

September 2, 1890. Only two seen. Both taken.

No more hoary bats seen during 1890.

August 25, 1891. A single *Atalapha cinerea* seen flying south along the face of the bluff this evening.

September 2, 1891. One seen flying north.

September 12, 1891. An adult male shot—the last of the season.

At Highland Light I found the hoary bat less active and irregular in its movements than the red bat. Its large and comparatively steady flight made it easier to shoot than either of the two smaller species with which it was associated. It began to fly immediately after sunset. In the Adirondacks Dr. C. Hart Merriam found the hoary bat a late flyer, and an exceeding difficult animal to kill on account of its swift, irregular motions.* It is possible that while on Cape Cod the animal modifies its habits on account of the unusual surroundings in which it finds itself. The fatigue of a long migration might also have an appreciable effect on a bat's activity.

LASIONYCTERIS NOCTIVAGANS (SILVER-HAIRED BAT).

September 1, 1890. One silver-haired bat taken.

September 2, 1890. Four taken and perhaps a dozen others seen.

The silver-haired bat was not seen again during 1890.

September 10, 1891. Three shot and probably half a dozen others seen. They were mostly flying north.

September 11, 1891. Two shot and four or five more seen.

September 12, 1891. About a dozen bats seen. Some were without doubt this species, but just what proportion I could not tell.

While September 12th is the latest date at which I have seen *Lasionycteris noctivagans* at Highland Light, I have a specimen killed there by Mr. W. M. Small on October 28, 1889.

GERRIT S. MILLER, JR.

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* Trans. Linn. Soc New York, II, p. 78–83. 1884.

ECOLOGICAL DISTRIBUTION OF SIX SPECIES OF SHREWS AND COMPARISON OF SAMPLING METHODS IN THE CENTRAL ROCKY MOUNTAINS

Larry N. Brown

Abstract.—The ecological distribution of six species of shrews was studied using sunken cans in 14 montane and intermontane habitats in southern Wyoming. The vagrant shrew (*Sorex vagrans*) and masked shrew (*Sorex cinereus*) were cosmopolitan in distribution. *Sorex cinereus* was slightly more abundant in moist plant communities, whereas *Sorex vagrans* predominated in slightly drier communities. Merriam's shrew (*Sorex merriami*) occurred only in arid portions of the plains and foothills, and in short-grass prairie was the only shrew taken. The water shrew (*Sorex palustris*) occurred only along or near cold mountain streams and ponds. The dwarf shrew (*Sorex nanus*) and pigmy shrew (*Microsorex hoyi*) occupied restricted mountain habitats. The dwarf shrew was abundant in rocky locations in both alpine and subalpine plant communities; the pigmy shrew was taken only in peat-moss bogs in the spruce–fir zone. A comparison of snap traps and sunken cans as methods of collecting shrews revealed that snap traps failed to demonstrate the presence of *Sorex nanus* and *Microsorex hoyi* in areas where they were abundant. Also, densities of *Sorex vagrans* and *Sorex cinereus* indicated by snap traps were considerably below those indicated by sunken cans.

The habitat preferences and ecological distribution of the six species of shrews found in the Central Rocky Mountains have not been extensively studied. Only scattered references to the ecological distribution of shrews in the Rocky Mountains occur in the literature (Cary, 1911; Warren, 1942; Negas and Findley, 1959; and Spencer and Pettus, 1966). No thorough study dealing with Wyoming shrews has been reported.

The species studied were the masked shrew (*Sorex cinereus*), the vagrant shrew (*Sorex vagrans*), the dwarf shrew (*Sorex nanus*), the Merriam's shrew (*Sorex merriami*), the water shrew (*Sorex palustris*), and the pigmy shrew (*Microsorex hoyi*). Information was collected on the ecological distribution of these species in southern Wyoming in terms of type of plant cover and proximity of water. Data on the indicated abundance of shrews using two different trapping methods were also compiled.

Materials and Methods

The Medicine Bow Mountains and Laramie Basin area of southern Wyoming have a wide range of plant communities, which occur at altitudes of from 7000 to 12,000 ft. The eight montane and intermontane plant communities selected for sampling were cottonwood–willow, short-grass prairie, sagebrush, mountain mahogany, aspen, lodgepole pine, spruce–fir and alpine tundra. Brief descriptions of the sampled areas in Albany County, Wyoming, are as follows:

1. *Cottonwood–willow*.—7160 ft; 10 miles SW Laramie, along Big Laramie River. Dominants: *Populus angustifolia*, *Salix* sp. Several grasses (*Poa*, *Agropyron*, *Carex*) present in understory.

2. *Short-grass prairie.*—7180 ft; ½ mile E Laramie. Dominants: *Bouteloua gracilis, Buchloë dactyloides.* Numerous forbs (*Eriogonum, Gaura, Phlox*) also represented.

3. *Sagebrush.*—7220 ft; 20 miles N Laramie. Dominants: *Artemisia tridentata, Purshia tridentata.* Several grasses (*Poa, Koeleria,* and *Agropyron*) abundant in open spaces between shrubs.

4. *Mountain mahogany.*—7250 ft; 1 mile E Laramie. Dominant: *Cercocarpus montanus.* Present: *Symphoricarpos, Artemisia, Amelanchier,* as well as several grasses and forbs.

5. *Aspen.*—8205 ft; ⅜ mile NW Centennial. Dominant: *Populus tremuloides.* A dense understory of grasses (*Poa, Agropyron*) and scattered shrubs (*Acer, Rosa,* and *Berberis*).

6. *Lodgepole pine.*—9300 ft; 5 miles W Centennial. Dominant: *Pinus contorta.* Understory of scattered forbs (*Lupinus, Antennaria,* etc.) and small trees (*Abies, Juniperus,* and *Picea*).

7. *Spruce–fir.*—9630 ft; 7 miles W Centennial. Dominants: *Picea engelmanni, Abies lasiocarpa.* Several shrubs (*Ribes, Rosa, Vaccinium, Berberis*) common in understory.

8. *Alpine tundra.*—10,470 ft; 5 miles W University of Wyoming Science Camp. Dominants: *Artemisia scopulorum, Silene acaulis, Poa alpina, Trifolium* sp., *Salix* sp.

A more detailed description of most communities in the Front Range of the Rocky Mountains is found in Marr (1961).

Moist bogs or marshes interrupted the uniformity of four of the above plant communities, specifically the aspen, lodgepole pine, spruce–fir, and alpine tundra. Therefore, to compare shrew populations in adjacent wet and dry situations, a bog or marsh near each original sampling station was trapped (sampling sites were 500–1000 ft apart). Brief descriptions of these wet plant communities are as follows:

1. *Bog in alpine tundra.*—10,460 ft; 5 miles W University of Wyoming Summer Science Camp. Dominants: sedges (*Carex* sp.), dwarfed willows (*Salix* sp.) around small, shallow pond.

2. *Bog in spruce–fir.*—9620 ft; 7 miles W Centennial. Dominants: sedges (*Carex* sp.), horsetails (*Equisetum* sp.), willows (*Salix* sp.), sphagnum moss (*Sphagnum* sp.).

3. *Bog in lodgepole pine.*—9295 ft; 5 miles W Centennial. Dominants: willow (*Salix* sp.), alder (*Alnus tenuifolia*), sedges (*Carex* sp.). Small pond of open water at edge of bog.

4. *Bog in aspen.*—8200 ft; ¼ mile W Centennial. Dominants: willow (*Salix* sp.), alder (*Alnus tenuifolia*), aspen (*Populus tremuloides*), sedges (*Carex* sp.), horsetails (*Equisetum* sp.). Two beaver ponds adjacent to the area.

To check the preference of certain shrews for rocky areas, two extensive rockslides were sampled at different elevations. One of these was a subalpine rockslide at 8480 ft elevation (3 miles NW Centennial) in an ecotone area of lodgepole pine, aspen, and sagebrush. The other trapping station was in a vast alpine rockslide above tree line at 10,600 ft elevation. Thus, 14 locations were sampled.

Shrews were trapped in pit-fall traps made of one-gallon tin cans. These were buried in the ground with the mouth of each can just below the ground's surface. A grid with an interval of 30 ft was used in placing these traps. Each sampling plot consisted of 25 cans arranged in five rows having five cans each.

In areas with a high water table, it was necessary to punch holes in the bottom or sides of each can. This allowed water to enter the can to equalize pressure and prevent the can from being forced up out of the ground. To catch shrews in such localities, it was desirable that the top of the water table be at least an inch or so below ground surface. High water tables in several bogs required that cans be placed on a slight elevation or hummock nearest each grid intersect.

The sinking of cans in rockslides was accomplished by removing rocks by hand until a pit into the interior of the slide was created. Wedged rocks and large boulders usually limited the depth of each excavation to three to five feet. Each can was then placed at the deepest point and fist-sized rocks were used to rebuild the substrate almost up to the lip of

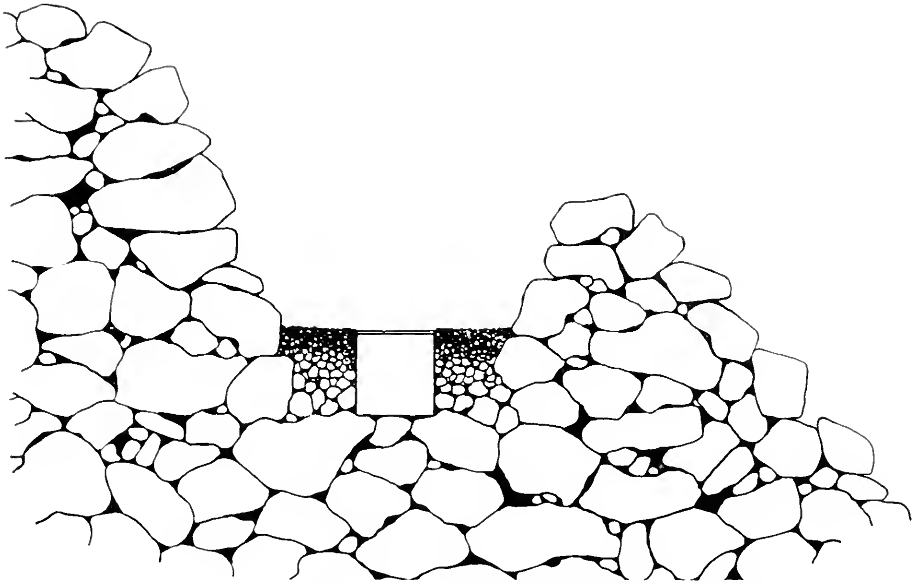

FIG. 1.—Diagrammatic representation of placement of pitfall traps (gallon cans) in study of rockslide habitats in mountain locations.

the can. Then gravel was used to build a pavement to the lip of the can (Fig. 1). If only larger, fist-sized rocks were placed around each can, sufficient spaces remained adjacent to the mouth to constitute a barrier for access by the shrews.

Between 30 May and 3 June 1966, 350 can traps were set out at the 14 locations. Cans were checked on alternate days for slightly more than 3 months. The total number of shrews by species taken per habitat was determined for the total sampling period.

In September 1966, a direct comparison of two methods of collecting shrews was made involving standard mouse-sized snap traps and the sunken cans. A snap trap was baited and set adjacent to each can in the sampling grid of the subalpine rockslide and the spruce-fir bog. Both sets of traps were checked once daily for 12 days. The bait for the snap traps consisted of a mixture of peanut butter, bacon grease, rolled oats, and chopped raisins.

RESULTS AND DISCUSSION

Following the placement of cans in various plant communities no shrews were captured in any plot for a period of 10 to 14 days. After this period, shrews appeared in the cans with regularity throughout the remainder of the summer; this suggested that all shrews avoided the areas where cans were placed until they became accustomed to the change.

Table 1 summarizes the relative abundance of five species of shrews at the various sampling stations. The masked shrew (*Sorex cinereus*) and vagrant shrew (*Sorex vagrans*) were the most cosmopolitan in distribution, being represented in all the habitats sampled except short-grass prairie. These species were always taken together, but in varying densities that appeared to correlate with moisture conditions. *Sorex cinereus* was generally more abundant than S. *vagrans* in the moist bog localities regardless of altitude. *Sorex vagrans* had

TABLE 1.—*Ecological distribution and relative abundance of five species of shrews in relation to various habitats in the Medicine Bow Mountains and Laramie Basin of Wyoming, summer 1966.*

Habitat and elevation		*Sorex cinereus*	*Sorex vagrans*	*Sorex nanus*	*Sorex merriami*	*Microsorex hoyi*	Total collected
Cottonwood–willow	(7160)	2	14	0	0	0	16
Short-grass prairie	(7180)	0	0	0	3	0	3
Sagebrush	(7220)	4	11	0	3	0	18
Mountain mahogany	(7250)	2	6	0	2	0	10
Aspen	(8205)	5	16	0	0	0	21
Bog in aspen	(8200)	28	12	0	0	0	40
Subalpine rockslide	(8480)	11	20	25	0	0	56
Lodgepole pine	(9300)	6	16	0	0	0	22
Bog in lodgepole	(9295)	29	11	0	0	0	40
Spruce–fir	(9630)	8	18	0	0	0	26
Bog in spruce–fir	(9620)	32	15	0	0	6	53
Alpine tundra	(10,470)	4	8	2	0	0	14
Alpine willow bog	(10,460)	9	5	0	0	0	14
Alpine rockslide	(10,600)	3	9	21	0	0	33

higher population densities in the mesic communities that were paired with the bogs (aspen, lodgepole pine, spruce–fir, and alpine tundra). The vagrant shrew was likewise slightly more abundant than S. *cinereus* in the other mesic situations sampled such as rockslides, sagebrush, mountain mahogany, and cottonwood–willow communities. These findings are in disagreement with those of Clothier (1955), who reported that S. *vagrans* was always more numerous in Montana than S. *cinereus* regardless of habitat. My results confirm the findings of Getz (1961) that S. *cinereus* is abundant in moist or standing-water situations, and the findings of Hoffmann and Taber (1960) that S. *vagrans* is present at high altitudes as well as low.

The dwarf shrew, which is generally considered by mammalogists to be rare, was abundant in two restricted habitats and was present at a third. It was more numerous than S. *vagrans* by a slight margin (25 S. *nanus* as compared to 20 S. *vagrans*) in the subalpine rockslide and was by far the predominant shrew in the alpine rockslide (21 animals out of 33). *Sorex nanus* was also represented in the alpine tundra plot by two animals taken near a rock outcrop. This represents an altitudinal range extending from 8480 to 10,600 ft and including several types of montane plant communities. Since rockslides extend continuously from 10,600 to 12,000 ft in the Medicine Bow Range, there is little doubt the species reaches that altitude in this habitat. All dwarf shrews were captured at considerable distances from water, suggesting they may be somewhat adapted to dry situations.

The preference of S. *nanus* for rocky areas in the mountains was first suggested by Hoffmann and Taber (1960), who collected several in polygonal rock fields on the Beartooth Plateau. They have been recorded in a variety of other montane habitats by Schellbach (1948), Clothier (1957), and Bradshaw (1961). Spencer and Pettus (1966) reported S. *nanus* was abundant in an open clear-cut area of spruce–fir forest. They did not mention the presence or absence of rocks.

Sorex merriami was trapped in three plant communities that were represented only at lower elevations in southern Wyoming. These habitats were short-grass prairie, sagebrush, and mountain mahogany. None of these habitats occurred higher than the mountain foothills (7500 ft). These three plots produced only eight Merriam's shrews for the whole summer, indicating that population levels in the areas sampled were not high. In the short-grass prairie plot, S. *merriami* was the only species of shrew present; in the low foothills, where sagebrush and mountain mahogany communities were sampled, they were present in low numbers with S. *vagrans* and S. *cinereus*. The only Merriam's shrew previously taken in southeastern Wyoming was reported by Mickey and Steele (1947), from short-grass prairie near Laramie. In Washington, Johnson and Clanton (1954) found that this species preferred the sagebrush–bunch grass community, where individuals were taken in the tunnels of the sagebrush vole (*Lagurus curtatus*). Hoffmann (1955) likewise collected S. *merriami* in sagebrush in California. One of the few records of occurrence of the species in mountain mahogany was that of Hoffmeister (1956) in Owl Creek Canyon in northeastern Colorado, about 40 miles south of the present study area.

In southeastern Wyoming, S. *merriami* occurred in the driest habitats and generally at lower elevations than did other species. Merriam's shrew was taken with *Lagurus curtatus* in the sagebrush and short-grass prairie area, but this vole was absent from the mountain mahogany community.

The pigmy shrew (*Microsorex hoyi*) was not known to occur in Wyoming until it was taken in 1963 in the Medicine Bow Range (Brown, 1966). A disjunct population occurs in southern Wyoming and adjacent northern Colorado and is more than 500 miles south of the nearest locality in Montana where the species has been reported (Hall and Kelson, 1959). In the course of the present study, pigmy shrews were captured at one sampling station, in the spruce–fir bog at 9620 ft elevation. Here *Microsorex* was encountered only around the periphery of the bog in an area dominated by a deep, spongy mat of sphagnum moss. In the strip of sphagnum, they were taken in equal numbers with S. *cinereus* and in greater numbers than S. *vagrans*. Spencer and Pettus (1966), in their study of a single bog area west of Fort Collins, Colorado, reported that the pigmy shrew was most abundant in the transition area between the bog and the surrounding spruce–fir forest. This is in agreement with my findings.

The habitat preferences of *Microsorex* in the other parts of its range seem to be rather broad, including heavy woods, clearings, and pastures in both wet and dry situations (Burt, 1957). However, Jackson (1961) and Buchner (1966) noted that in Wisconsin and Canada the species occasionally is found in cold sphagnum or tamarack bogs. In the MacDonald Range of northwestern Mon-

TABLE 2.—*Comparison of trapping results for shrews using snap traps and sunken cans for 12 days at two locations in the Medicine Bow Mountains, Wyoming.*

	Subalpine rockslide		Spruce–fir bog	
Species	Snap traps	Sunken cans	Snap traps	Sunken cans
Sorex vagrans	2	4	2	3
Sorex cinereus	1	2	4	9
Sorex nanus	0	6	0	0
Microsorex hoyi	0	0	0	2
Totals	3	12	6	14

tana, Conaway (personal communication) captured *Microsorex* in dry areas of clearcut forest having a dense ground cover. The relict population located in the central Rockies may have a broader habitat specificity than indicated by the present study.

The water shrew (*Sorex palustris*) is too large to be retained in gallon cans unless there is some water present. Water shrews were taken in partially flooded cans in habitats ranging from the alpine willow bog at 10,470 ft elevation down to the willow–alder bog in the aspen community at 8200 ft elevation. The species was never trapped at a distance greater than 100 ft from a mountain stream or pond.

The total samples of shrews at each location were compared, and two types of habitats were found to support especially high densities of shrews. The most productive habitats were rockslide areas and marshy or boggy areas, both of which have high invertebrate populations that can serve as a readily available food supply. The least productive trapping plot for shrews was located in shortgrass prairie. This may have been due to the scarcity of suitable cover or to a relative scarcity of invertebrates.

A comparison of the number and species of shrews collected utilizing equal numbers of snap traps and cans is presented in Table 2. In 300 trap-nights using snap traps, three shrews of two species were collected at the subalpine rock slide. The sunken cans produced four times as many shrews during the same period and three species were represented. Six S. *nanus* were taken in cans while none appeared in adjacent snap traps, suggesting that the species readily avoids traps and therefore gives the appearance of being rare.

Twenty-five sunken cans produced slightly more than twice as many shrews (14 animals) than did 25 snap traps (six animals) in the bog in the spruce–fir community during the 12-day period. Again, S. *vagrans* and S. *cinereus* were taken in both snap traps and cans, but *Microsorex* was captured only in cans. Even for the two "common" species, higher numbers were recorded for the can traps.

These and other trapping results indicate that S. *nanus*, S. *merriami*, and *Microsorex hoyi* are seldom captured in snap traps even when all are abundant. *Sorex vagrans*, S. *cinereus*, and S. *palustris* were readily captured in snap traps, but data provided by pitfall traps suggest that densities calculated for these species on the basis of snap-trap catches may be consistently too low. MacLeod and Lethiecq (1963) presented similar data when comparing these trapping methods for S. *cinereus* in Newfoundland.

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CHANGES IN NORWAY RAT POPULATIONS INDUCED BY INTRODUCTION OF RATS

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The introduction of aliens into an existing population of mammals may be followed by unexpected effects that relate to social structure and population composition. These effects were studied by introducing alien rats into stationary and increasing populations of rats in city blocks. This work is part of a continuing study of the mechanisms of change in vertebrate populations using Norway rats (*Rattus norvegicus*) in residential areas in Baltimore as experimental animals (Davis, 1953). These rats inhabit back yards, basements, and garages and feed on garbage. The human sanitary conditions in general are poor and remain unchanged for months at a time, so that the food supply of the rats has only slight seasonal variations. Other environmental conditions are similarly subject to little change for many months at a time. The constancy of these factors permits experiments on populations in a relatively stable environment. Finally, the population of rats in each block is essentially discrete and isolated, as rats rarely travel from one block to another (*see* Davis, 1953, for references).

METHODS AND PROCEDURES

The procedures followed to study the effects of introducing strange rats into a population consisted of taking some rats from a stationary or increasing population in one block and introducing them into a comparable population in another block and observing the resulting changes in the second population. The status (stationary or increasing) of the population was determined by estimates at bimonthly intervals for more than a year. Blocks that appeared to be either stationary or increasing were selected in October and monthly estimates made. From this group 4 stationary and 4 increasing populations were chosen. To get a base line for adrenal weights, six rats of one sex, weighing over 200 grams each, were removed from each block during the first experimental week (week 1). Alien rats were then introduced into each block during the third week, and at the same time native rats were removed from the increasing populations. The details of these removals and introductions are contained in tables 2 and 3. Estimates were made during the sixth and eighth weeks, each followed by the removal of a small sample of rats for adrenal weights. The adrenal weights were expressed for each sample as the mean per cent of standard reference values (Christian and Davis, 1955). The rats to be introduced into a population were individually marked by toe-clipping prior to introduction, whereas the native rats were not marked. The details of the history of each population were complicated by the impossibility of introducing exactly the same number of rats into each block on exactly the same days, and the numerical population size also differed in each block.

A discussion of the likelihood of error is desirable when it is claimed that two populations differ in number, since the detection of changes is fundamental to the conclusions derived from these introductions. Some aspects of the census method were discussed by Brown, *et al.* (1955). However, the basic problem is that, even with trapping, the true number of rats in a block is not known. Nevertheless, a check on the validity of estimation can be made by comparing estimates before and after a trapping program. Suppose that an estimate of N_1 rats is first obtained, subsequently T rats are removed and a second estimate of N_2 rats is made. Obviously N_1 should equal $T + N_2$. A figure for percentage of error can be given as $\frac{N_1 - (T + N_2)}{N_1}$. For example, if the estimate for a block is 151 rats and then 81 are removed by trapping and an estimate of 63 is made, then $\frac{151 - (81 + 63)}{151} = 4.6$ per cent. Other procedures could be used such as $\frac{T - (N_1 - N_2)}{T}$ or $\frac{N_1 - T - N_2}{N_1 - T}$. The first procedure is preferred because it bases the calculations on N_1, which is the estimate that was used to determine the status of the block. A total of 50 populations was available to determine the extent of error. Each had been trapped during the past 6 years, and an estimate had been made before trapping and another within a month after cessation of trapping. Naturally, some changes can occur during the intervening month, but for practical reasons it is usually not possible to make an estimate promptly after the cessation of trapping. These blocks contained 3,707 rats by the estimates (N_1) and 1,502 were trapped. The number of rats per block varied from 15 to 182. The distribution of errors is given in Table 1. The percentage of error was independent of the number of rats in the population. From these differences the standard error of the difference can be calculated to be 10.7 per cent. This value can be used as an indication of the errors to be expected in estimates of population changes in blocks. For example, from Table 2 it is seen that the estimate (block 150128) before introduction was 116 and after was 89. The percentage difference is 23.3 which when divided by 10.7 gives a ratio of 2.2. This difference appears to be statistically significant.

TABLE 1. — DISTRIBUTION OF DIFFERENCES AMONG ESTIMATES

Per cent Error*	Blocks Positive	Blocks Negative	Total
0–9	13	6	19
10–19	6	11	17
20–29	4	4	8
30–39	2	3	5
40–49	1	0	1
Totals	26	24	50

* $\frac{N_1 - (T + N_2)}{N_1}$

RESULTS AND DISCUSSION

The histories of the populations are given by blocks in tables 2 and 3 and figures 1, 2, and 3. The terms "replacement" and "supplement" require clarification for this discussion. We mean by replacement that approximately the same number of rats was introduced as was removed. Supplement means that many more alien rats were introduced than were removed. A quantitative percentage might have been used to distinguish these two terms, but it would have been rather meaningless because (1) the size of the individual rats varies considerably, and (2) immediate mortality is probably high. Therefore, we really do not know the actual number of rats that produced the results. Another factor is that births and deaths are normally high in any population of rats. The average monthly death rate is about 20 per cent for stationary rat populations; therefore, their birth rate is also about 20 per cent. Comparable mortality and birth rates for increasing populations are prob-

TABLE 2. — RESULTS OF INTRODUCTION OF RATS INTO STATIONARY POPULATIONS

Block number	140338		140344		140118		150128	
Zero week is	Dec. 16		Dec. 16		Feb. 9		Feb. 9	
	Week	Rats	W	R	W	R	W	R
Population	−20	62	−20	30	−19	105	−18	122
Population	−13	42	−13	32	−11	98	−10	118
Population	− 5	40	− 5	38	− 6	87	− 6	120
Population	0	49	0	35	0	100	0	116
Rats removed	1	6M	1	6F	1	6F	1	6M
Rats introduced	3	10M	3	8F	2-6	23F	2-6	27M
Rats removed	—	—	—	—	—	—	—	—
Population	6	45	6	44	6	76	7	89
Rats removed	6	6M	6	6F	6	6F	7	6M
Population	8	56	8	23	11	63	10	86
Rats removed	8	22	8	12	11	27	10	36
	Week	Index[1]	W	1	W	1	W	1
Adrenal size	1	83.0	1	91.8	1	93.4	1	79.2
	6	84.1	6	85.3	6	90.4	7	71.4
	8	88.0	8	102.4	11	68.4	10	73.6

[1] Mean of the individual per cent of appropriate reference value for the sex and size of the rat.

ably about 15 per cent and 25 per cent per month respectively. It is unwise, under these circumstances, to attempt a precise measurement of numerical differences in the numbers of rats used.

The population estimates (Table 2) in the two replacement blocks 6 weeks after the introduction of rats showed (Fig. 1) that block 140338 was not significantly different from the previous estimate, while block 140344 had apparently increased (P is about .04). While the apparent difference in results in these 2 blocks might be due to sex (the females less disturbing) or to numbers (fewer introduced into 140344), no interpretation will be attempted for the reasons cited above. The two supplemented blocks declined significantly (P is about .04 for each) (Fig. 1).

We recognize that the replacement pair of populations was done in December 1953, and the supplemented pair in February 1954, and that differences might be due to some seasonal aspect. However, the only known seasonal change, an increase in breeding from December to February, would produce the opposite result.

Population growth ceased in all four increasing populations following the replacement of native with alien rats (figs. 2, 3,). In no block was the difference statistically significant. It apparently made no difference whether the sex of the introduced rats

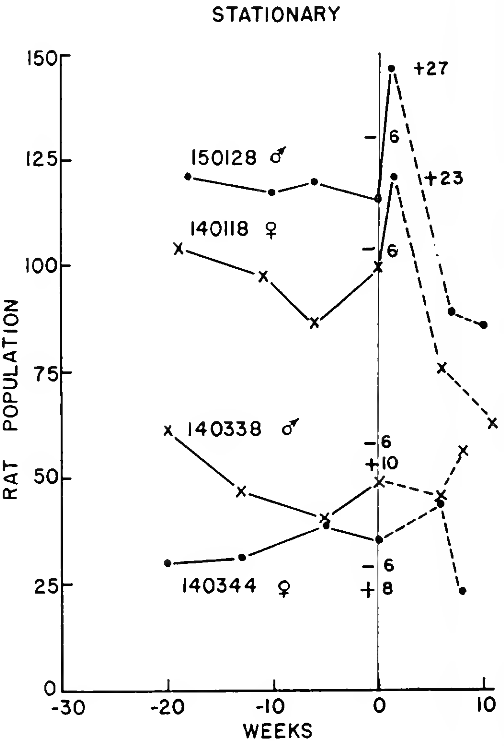

FIG. 1. The changes in four stationary populations for 20 weeks before introduction of rats (at 0 time) and about 10 weeks after. The number added is indicated by a plus sign, the number removed by a minus sign.

TABLE 3. — RESULTS OF INTRODUCTION OF RATS INTO INCREASING POPULATIONS

Block number	140111		140134		140201		140222	
Zero week is	Dec. 16		Dec. 16		Feb. 9		Feb. 9	
	Week	Rats	W	R	W	R	W	R
Population	–20	110	–20	80	–25	86	–20	57
Population	–13	118	–13	88	–16	100	–14	62
Population	– 5	133	– 4	115	– 8	105	– 5	95
Population	0	150	0	140	0	135	0	90
Rats removed	1	6F	1	6F	1	6M	1	6M
Rats introduced	3	22F	3	28F	3	18M	3	20M
Rats removed	3	28F	3	22F	3	20M	3	18M
Population	6	167	6	130	6	130	6	85
Rats removed	7	6F	7	6F	7	6M	7	6M
Population	10	152	10	130	10	130	10	70
Rats removed	10	48	10	73	10	57	10	24
	Week	Index[1]	W	I	W	I	W	I
	1	92.1	1	91.5	1	104.4	1	93.8
Adrenal size	7	93.8	7	102.8	7	85.3	7	99.1
	10	101.5	10	90.4	10	91.1	10	84.6

[1] Mean of the individual per cent of appropriate reference value for the sex and size of the rat.

was male or female. The population from block 140222 (Fig. 2) may have become stationary just prior to the introduction of aliens, but the high rate of reproduction (4/6 mature females were pregnant) suggests that the population was increasing. The population in block 140111 increased numerically after the introduction, but the difference between the two estimates is within the error of estimate and does not indicate a change in population. It appears that introducing a number of alien rats may halt the growth of increasing populations.

The reader may have noticed that the total number of rats removed from the four increasing blocks was about 5 per cent greater than the number introduced, so that the rats in these populations were not replaced in the strict arithmetic sense of the word. However, considering the previously mentioned birth and mortality factors, it is not desirable to be more precise. All aspects considered, it is likely that the four increasing populations were somewhat reduced following replacement procedures. The four blocks (taken together) increased by 173 rats in the 20 weeks preceding replacement, so that they might have been expected to have had 600 rats 10 weeks after replacement instead of the observed 482, although the rate of increase would decline as the population increased.

On several occasions episodes have been noted that appear to be explainable on the basis of introduction or actual immigration. In January 1946, about 60 rats were released in a block in one night as part of an experi-

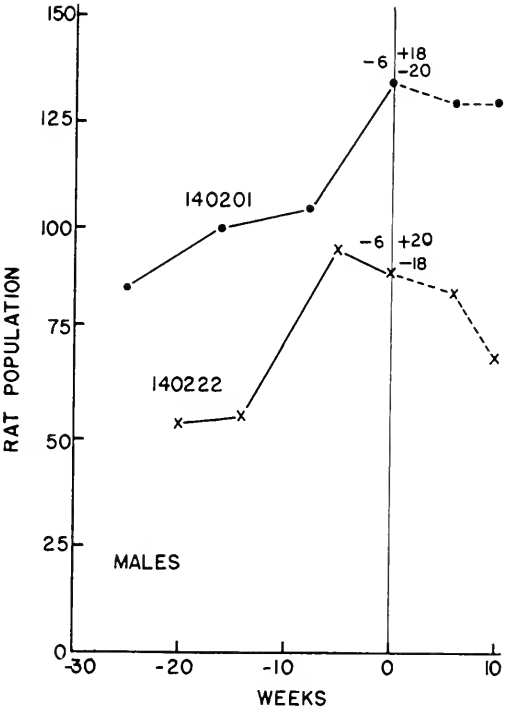

FIG. 2. The changes in two increasing blocks before and after the introduction of males (symbols as in Fig. 1.)

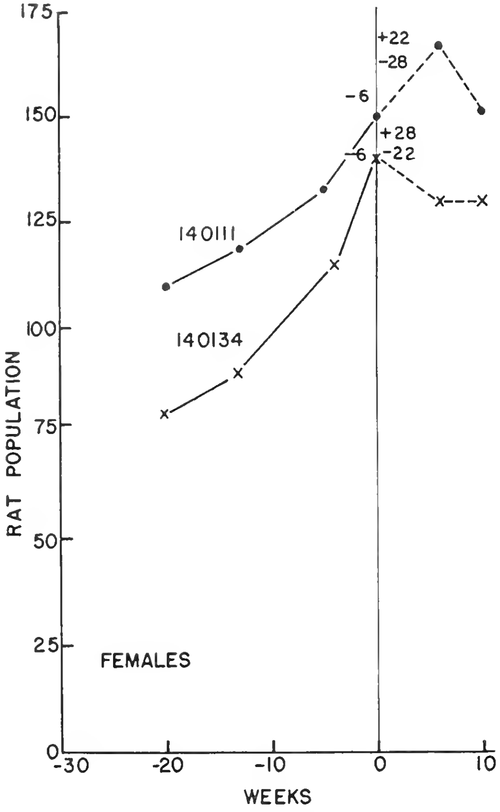

Fig. 3. The changes in two increasing blocks before and after the introduction of females (symbols as in Fig. 1.)

ment on "homing" ability in rats. The block originally contained about 100 rats but within 3 weeks there were so few rats left in the block that the project was stopped. Calhoun (1948) noticed the same result when he introduced rats into blocks. These episodes, as well as miscellaneous observations, stimulated a test in 1947 of the idea that the introduction of rats into a population would result in its decline. Accordingly, rats were introduced over a period of 4 months into two populations that had just reached a level judged to be stationary (Davis, 1949). The introduction of 90 rats in one block and 101 in the other was accompanied by declines of about 25 per cent and of 40 per cent respectively. The populations increased after the introductions ended.

The present experiments suggest that the introduction of large numbers of rats into a population disrupts the population mechanisms in some way that causes the populations either to decline in numbers or stop growing.

The decrease is due in part to a decline in reproduction. Data are not available for the period immediately after introduction, as it is not feasible to follow the population changes and simultaneously to collect a number of rats for reproductive data. However, the large sample of rats collected from the blocks 8 to 11 weeks after introduction had a high reproductive rate (Table 4) and a low lactation rate. One would conclude from these data that the number of pregnancies was low immediately after the introduction. Only about 25 per cent of the females were lactating at 10 weeks, whereas normally about 40 per cent of the females of these rats are lactating (Davis, 1953). The high prevalence of pregnancy presumably resulted from their more or less simultaneous recovery from the effects of introduction. The decreases in rat populations obviously may have been due largely to mortality and movement, but data on this aspect are impossible to obtain under these conditions.

TABLE 4. — REPRODUCTIVE RECORDS OF LOCAL RATS CAPTURED 8-11 WEEKS AFTER ARTIFICIAL IMMIGRATION OF RATS INTO BLOCKS

Population status	Number Mature Females	Per cent Pregnant	Mean Number Embryos	Per cent Lactating
Increasing	85	33.0	10.38	20.0
Stationary	66	31.8	9.63	28.8

Previous experiments have shown that the weight of the adrenal glands in rats responds to changes in population. An increase in adrenal weight parallels increases in population; the artificial reduction of a population also results in a decrease in adrenal weight (Christian, 1954; Christian and Davis, 1955). The adrenal responses of the two sexes are parallel (*ibid.*). Experiments have indicated that changes in adrenal weight in response to changes in population result primarily from changes in cortical mass (Christian, 1955a, 1955b, 1956). To examine these problems, the adrenals of the rats from each block were removed and weighed. The observed adrenal weight for each rat was compared with a standard reference weight for the appropriate sex and size (length of head and body) of rat (Christian and Davis, 1955), and expressed as a per cent of the reference value. These percentages for the rats from each sample were averaged and the means are recorded at the bottom of tables 2 and 3. We have used the mean value of a given sample as the unit of measurement for comparing adrenal weight with population size (Christian, 1954; Christian and Davis, 1955).

The results indicate that, in the replacement stationary blocks (140338 and 140344), there was a small increase in adrenal weight after 8 weeks, while the populations apparently remained practically unchanged (tables 2 and 3, Fig. 1).

A mean decline in population size, paralleled by a decrease in adrenal weight in at least one of the two blocks, followed the addition of a large number of alien rats to stationary populations (blocks 140118 and 150128). The adrenal weights probably reflect largely the final results of population manipulation rather than the immediate effects, as the adrenal samples were obtained several weeks after the introductions or estimates. Therefore, the changes in adrenal weight probably reflect overall population changes rather than any immediate social strife resulting from the introductions. An experiment to collect samples a few days after the introductions is in progress and may show an increase in adrenal weight.

The adrenal glands of rats from the increasing blocks showed no consistent change, although population growth terminated (Table 3, figures 2 and 3). The replacement of rats in increasing populations had little effect on the adrenal weights of rats examined 10 weeks later.

The results reported here may be applicable to certain stocking programs. A routine part of many game-management programs has been the introduction of a number of animals into an area with the expressed hope of increasing the population either directly or eventually by reproduction. Indeed, such stocking has often been considered a panacea for all hunting problems. The present results, using rats as experimental animals, show that the disruption of a population following an introduction may actually produce a decline under certain conditions. Evidently the introduction of a number of animals may have disastrous results when a population is above the halfway point on a growth curve.

SUMMARY

Wild Norway rats (*Rattus norvegicus*) were introduced from one city block to another to simulate immigration. The population changes were determined by frequent estimates for about 20 weeks before introduction and 8 to 11 weeks thereafter. From two blocks with stationary rat populations, some rats were removed and then replaced by aliens. The populations remained stationary. In two blocks about four times as many rats were introduced as were removed. The populations declined about 25 per cent. In four blocks with increasing populations about one-fourth of each population was removed and replaced by alien rats from other blocks. The increase halted.

The reproductive rate 8 to 11 weeks after the introduction was normal for an increasing population, but the lactation rate was low, indicating that the decline in population growth was due in part to a decreased reproductive rate, and that the population was back to normal pregnancy rate in two months. The adrenal weights were also essentially normal for the population level two months after introduction.

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A TRAFFIC SURVEY OF *MICROTUS-REITHRODONTOMYS* RUNWAYS

By Oliver P. Pearson

Patient observation of the comings and goings of individual birds has long been one of the most rewarding activities of ornithologists. The development in recent years of inexpensive electronic flash photographic equipment has made it possible and practical for mammalogists to make similar studies on this aspect of the natural history of secretive small mammals. The report that follows is based on photographic recordings of the vertebrate traffic in mouse runways over a period of 19 months. Species, direction of travel, time, temperature and relative humidity were recorded for each passage. In addition, many animals in the area were live-trapped and marked to make it possible to recognize individuals using the runways.

THE APPARATUS

Two recorders were used. Each consisted of an instrument shelter and a camera shelter. Each instrument shelter was a glass-fronted, white box containing an electric clock with a sweep second hand, a ruler for measuring the size of photographed individuals, a dial thermometer and a Serdex membrane hygrometer. The ends of the box were louvered to provide circulation of air as in a standard weather station. This box was placed along one side of the runway, across from the camera shelter, so that the instruments were visible in each photograph (Plate I). The camera shelter was a glass-fronted, weatherproof box containing a 16-mm. motion picture camera synchronized to an electronic flash unit. In one of the recorders the camera was actuated by a counterweighted treadle placed in the mouse runway immediately in front of the instrument shelter (Plate I, bottom). An animal passing along the runway depressed the treadle, thereby closing an electrical circuit through a mercury-dip switch. This activated a solenoid that pulled a shutter-release pin so arranged that the camera made a single exposure. The electronic flash fired while the shutter was open. This synchronization was easily accomplished by having the film-advance claw close the flash contact. The camera would repeat exposures as rapidly as the treadle could be depressed, but at night about three seconds were required for the flash unit to recharge sufficiently to give adequate light for the next exposure.

The other recorder was actuated by a photoelectric cell instead of by a treadle. A beam of deep red light shone from the camera shelter across the runway and was reflected back from a small mirror in the instrument shelter to a photoelectric unit in the camera shelter. When an animal interrupted the light beam, the photoelectric unit activated a solenoid that caused the camera to make a single exposure, as in the other recorder.

To avoid the possibility of frightening the animals it would be desirable to use infra-red–sensitive film and infra-red light, but standard electronic flash tubes emit so little energy in the infra-red that this is not practical. Instead, I used 18 layers of red cellophane over the flash tube and reflector to give a deep red flash of light. Wild mice, like many laboratory rodents, are probably insensitive to deep red light. I found no evidence that the flash, which lasts for only 1/1000th of a second, frightened the mice. A muffled clunk made by the mechanism also seemed not to alarm the mice unduly.

When the camera diaphragm was set to give the proper exposure at night, daytime pictures were overexposed, since the shutter speed was considerably slower than 1/30th of a second. To reduce the daytime exposure, a red filter was put on the camera lens. The filter did not affect night exposures because red light from the flash passed the red filter with little loss. In addition, on one of the cameras the opening in the rotary shutter was reduced to give a shorter exposure.

Both recorders function on 110-volt alternating current. The treadle-actuated one could be adapted to operate from batteries. The units continue to record until the motion picture camera runs down or runs out of film. One winding serves for several hundred pictures. The film record can be studied directly by projecting the film strip without making prints.

The camera shelter and instrument shelter had overhanging eaves to prevent condensation of frost and dew on the windows. A small blackened light bulb was also kept burning in the camera shelter to raise the temperature enough to retard fogging on the glass. Animals were encouraged to stay in their usual runway by a picket fence made of twigs or slender wires. No bait was used.

A few individual animals could be recognized in the pictures by scars or molt patterns, but most had to be live-trapped and marked. Using eartags and fur-clipping I was able to mark distinctively (Plate I, bottom) all of the mice captured at any one station. The clipping remained visible for days or months depending upon the time of the next molt.

The apparatus produces photographic records such as those shown in the lower pictures in Plate I. These can be transposed into some form as Fig. 2.

THE STUDY AREA

The study centered around a grassy-weedy patch surrounding a brush pile in Orinda, Contra Costa County, California (Plate I). The runways wound through a 20 × 20-foot patch of tall weeds (*Artemisia vulgaris, Hemizonia* sp. and *Rumex crispus*) and under the brush pile. The weeds were surrounded by and somewhat intermixed with annual grasses. Oaks and other trees, as well as a house and planting, were 50 feet away.

Summer climate in this region is warm and sunny with official mean daily maximum temperatures rising above 80°F. in late summer. Official temperatures occasionally reach 100°, and temperatures in the small instrument shelters used in this study sometimes exceeded this. Nights in summer are usually clear and with the mean daily minimum temperature below 52° in each month. About 27 inches of rain fall in the winter and there is frost on most clear nights. The mean daily maximum temperature in January, the coldest month, is 54°, and the mean daily minimum 31°.

PROCEDURE

I placed the first recorder in operation on January 29, 1956, and the second on October 19, 1956. Except for occasional periods of malfunction and a few periods when I was away they continued to record until the end of the study on September 10, 1957. Approximately 778 recorder-days or 111 recorder-weeks of information were thus obtained. The monthly distribution of records was as follows: January, 54 days; February, 70; March, 90; April, 80; May, 84; June, 67; July, 52; August, 88; September, 48; October, 33; November, 52; and December, 60.

The recorders were placed at what appeared to be frequently used *Microtus* runways, usually situated on opposite sides of the weedy patch 20 to 30 feet apart. For one period of four months one of the recorders was placed at a similar weedy patch 70 yards away. Early in the study it was discovered that a neighbor's Siamese cat sometimes crouched on the camera shelter waiting for mice to pass along the exposed runway in front of the instrument shelter. Consequently, a 2½-foot fence of 2-inch-mesh wire netting was set up enclosing most of the weedy patch. This prevented further predation by cats at the center of the study area, although cats continued to hunt outside of the fence a few yards away from the recorders. The only other tampering with predation was the removal of two garter snakes on April 11, 1957.

RESULTS

Traffic in individual runways.—The recorders were operated at eighteen different stations. At seven of these apparently busy runways a traffic volume higher than a few passages per day never developed, and so the recorders were moved within two weeks. Perhaps the mice originally using these runways had abandoned them or had been killed shortly before a recorder was moved to their runway, or perhaps the disturbance of placing a recorder caused the mice to divert their activities to other runways. At the other eleven stations a satisfactory volume of traffic was maintained for three to more than twenty weeks. A station was abandoned and the recorder moved when the traffic had decreased to a few passages per day. Subsequently, I found that even this little activity does not indicate that the mice are going to abandon the runway, for on several occasions traffic in a runway dropped this low and then climbed again to high levels. At one recorder the total number of passages in consecutive weeks was 183, 84, 26, 75 and 203. The runway represented in Fig. 1 was one of those used most consistently, but even it shows marked daily and weekly fluctuations. It is probable that after a few weeks of disuse during the season when grass and weeds are growing rapidly, a runway would not be reopened, but during the rest of the year an abandoned runway remains more or less passable and probably more attractive to mice than the surrounding terrain.

Figure 1 summarizes the traffic in one of the busiest runways. On the first night there were an unusual number of records of harvest mice whose curiosity may have been aroused by the apparatus. Obviously they were not frightened away. After a short time traffic increased to a high level and remained high until the middle of November, when passages by *Microtus* decreased sharply. During the week before the decrease, seven marked individuals provided most of the *Microtus* traffic. One of these individuals, an infrequent passerby, disappeared at the time of the decrease, but the other six remained nearby for at least another week and continued to pass occasionally. Those *Microtus* that disappeared later were replaced by others so that even the infrequent passages in late November and early December were being provided by seven marked individuals. The decrease of *Microtus* traffic was caused, therefore, not by deaths but by a change in runway preference. Several of these same individuals were using another runway 20 feet away in mid-January, February and March.

Three to six marked *Reithrodontomys*, depending upon the date, were providing most of the harvest-mouse traffic in the runway represented in Fig. 1. The average number of passages per day of animals of all kinds was eighteen. In the ten other most successful runways, the average number of passages per day ranged from two to nineteen.

Figure 2 gives a detailed accounting of the traffic at a single recording station for six days. One can judge from this figure the kind of information (excluding

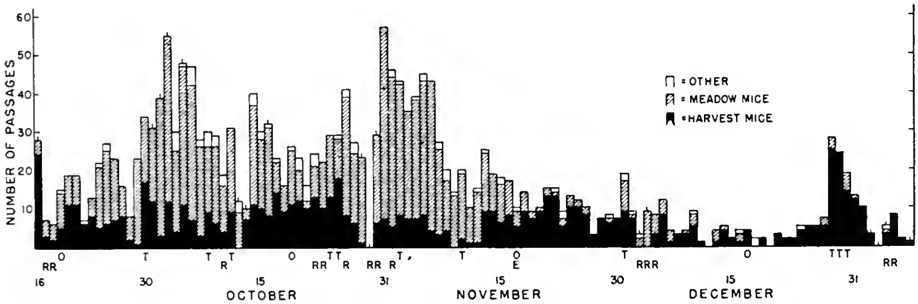

FIG. 1.—Traffic volume along one runway for 16 weeks. Meaning of symbols under the base line: *T*= live-trapping carried out for part of this day; *O*= full moon; *E*= total eclipse of the moon; *R*= rain. Columns surmounted by a vertical line represent days for which the recording was incomplete; the heights of the various segments of these columns should be considered minimum values.

temperatures and humidities) obtained with the recorders and can at the same time catch a revealing glimpse of an aspect of the biology of small mammals that has heretofore been revealed inadequately by trapping and other techniques. It may be seen that the mouse traffic was provided by one female and two male harvest mice and by three male, three female, and one or more unidentified meadow mice; together they gave between 15 and 24 passages each day. No individual passed more than eight times in one day. One harvest mouse (R2) seemed to spend the day to the left and to make a single excursion

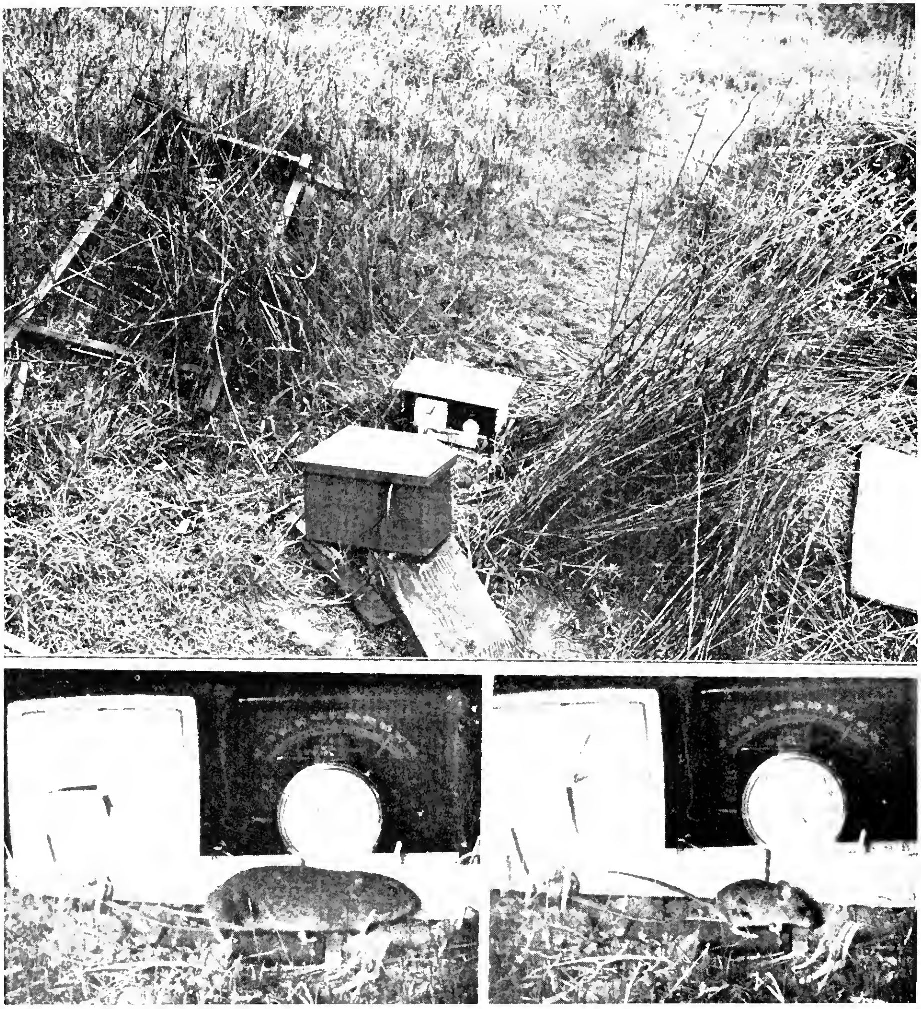

PLATE I

Top: Camera shelter (foreground) and instrument shelter in position at a mouse runway on the study area. Bottom: The kind of records obtained with the recorder; *left*—a meadow mouse marked by clipping two strips of fur on the hips; *right*—a marked harvest mouse crossing the treadle.

to the right each night. Harvest mice first appeared in the evening between 6:37 and 7:22 and none passed after 6:26 in the morning. Five or six *Microtus* passed within a few hours (February 24), and there was nightly near-coincidence of *Reithrodontomys* and *Microtus*.

Traffic in all runways combined.—During the 111 recorder-weeks, the following passages of animals were photographed:

Meadow mouse, *Microtus californicus*	6,077
Harvest mouse, *Reithrodontomys megalotis*	1,753
Bird (see following account)	382
Brush rabbit, *Sylvilagus bachmani*	94
Shrew, *Sorex ornatus*	56
Peromyscus (see following account)	39
Fence lizard, *Sceloporus occidentalis*	33
Garter snake, *Thamnophis* sp.	17
Salamander (see following account)	11
Alligator lizard, *Gerrhonotus* sp.	10
House cat, *Felis domesticus*	6
Newt, *Taricha* sp.	5
Pocket gopher, *Thomomys bottae*	3
Gopher snake, *Pituophis catenifer*	3
Mole cricket, *Stenopelmatus* sp.	2
Ground squirrel, *Citellus beecheyi*	1
Weasel, *Mustela frenata*	1
King snake, *Lampropeltis getulus*	1
Racer, *Coluber constrictor*	1
TOTAL	8,495

On the basis of trapping results in this and in similar habitat nearby, large numbers of meadow mice and harvest mice were expected. The recording of at least 26 other species in the runways came as a pleasant surprise. Whereas all of these species would be expected to record their presence eventually, some of them are rarely seen or trapped near this location. After living five years on the study area, after doing considerable field work nearby, and after checking the recorders twice each day during the study, I have not yet seen a weasel or a ground squirrel within at least a mile of the study area. Weasels could easily escape detection, but large, diurnal ground squirrels must be very rare. The single individual recorded on August 31 may have been a young squirrel emigrating from some distant colony. Noteworthy absences were those of wood rats (*Neotoma fuscipes*), moles (*Scapanus latimanus*), and probably California mice (*Peromyscus californicus*), all of which were common within 100 feet of the recorders. An opossum (*Didelphis marsupialis*) was seen a few feet from one of the recorders but did not appear on the films. No house mice (*Mus musculus*) were detected in the photographs, although it is possible that some passages of *Mus* were listed as of *Reithrodontomys.* House mice were caught occasionally in houses nearby and in a field near a poultry house 200 yards away, but none was caught during frequent live-trapping near the recorders.

The total of 8,495 passages of animals gives an average of 11 passages per day in each runway. A patient, non-selective predator waiting for a single catch at runways such as these could expect, theoretically, a reward each 2.2 hours. The mean weight of animal per passage was about 31 grams, which would yield approximately 40 calories of food. This much each 2.2 hours would be more than enough to support an active mammal the size of a fox.

Meadow mouse.—The 6,077 *Microtus* passages were distributed throughout the day and night as shown in Fig. 3 (above). The hours of above-ground activity, however, were quite different in winter than in summer, so Fig. 3 is only a year-around average somewhat biased by the fact that more *Microtus* were recorded in the spring than in the other seasons. A more detailed analysis of the *Microtus* data will be given in a later report. By marking as many of the mice as possible, it was found that usually four or more individual *Microtus* were using each runway but rarely more than ten. On some occasions more than 60 *Microtus* passages were recorded at a single point in 24 hours.

Harvest mouse.—Harvest mice were almost entirely nocturnal (Fig. 3, center). They not only used the *Microtus* runways, but their passages were frequently intermixed with those of *Microtus* (Fig. 2). On fourteen occasions the two species passed within 60 seconds of each other, and on one occasion

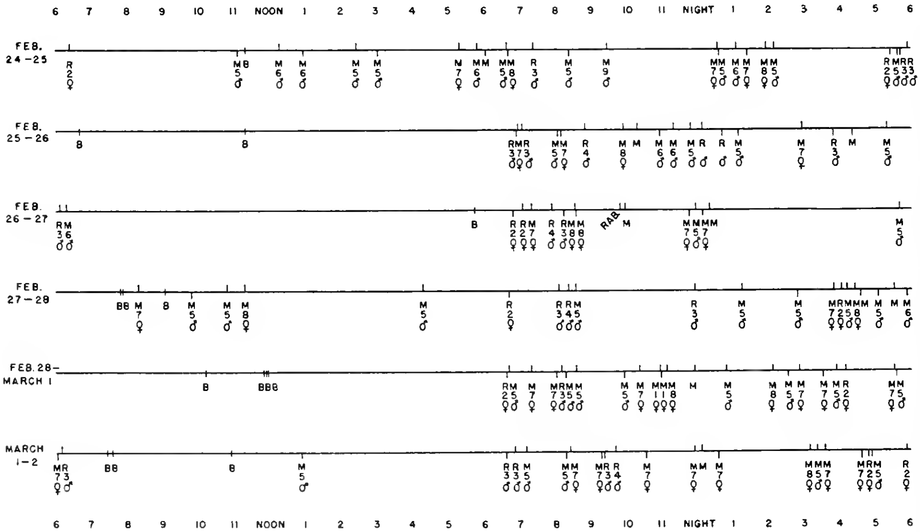

FIG. 2.—A sample record of the total traffic in a single runway over a period of six days. Marks above the base lines indicate passages from right to left, and marks below the base line passages from left to right. *R* represents *Reithrodontomys*; *M*, *Microtus*; *B*, bird (includes brown towhee, wren-tit, and song sparrow); and *RAB*, brush rabbit. Most of the mice are further identified by number and sex.

a 4-month-old male *Microtus* and a 5-month-old male *Reithrodontomys* appeared in the same photograph.

The history of one runway indicates that traffic by *Reithrodontomys* alone does not keep a *Microtus* runway open. One or more *Microtus* passed almost daily along this runway during February. At the end of the month the *Microtus* disappeared and two *Reithrodontomys* became active in the same runway. Despite an average of 3.3 passages per day by *Reithrodontomys* throughout March and up to mid-April, grass and weed seedlings grew up

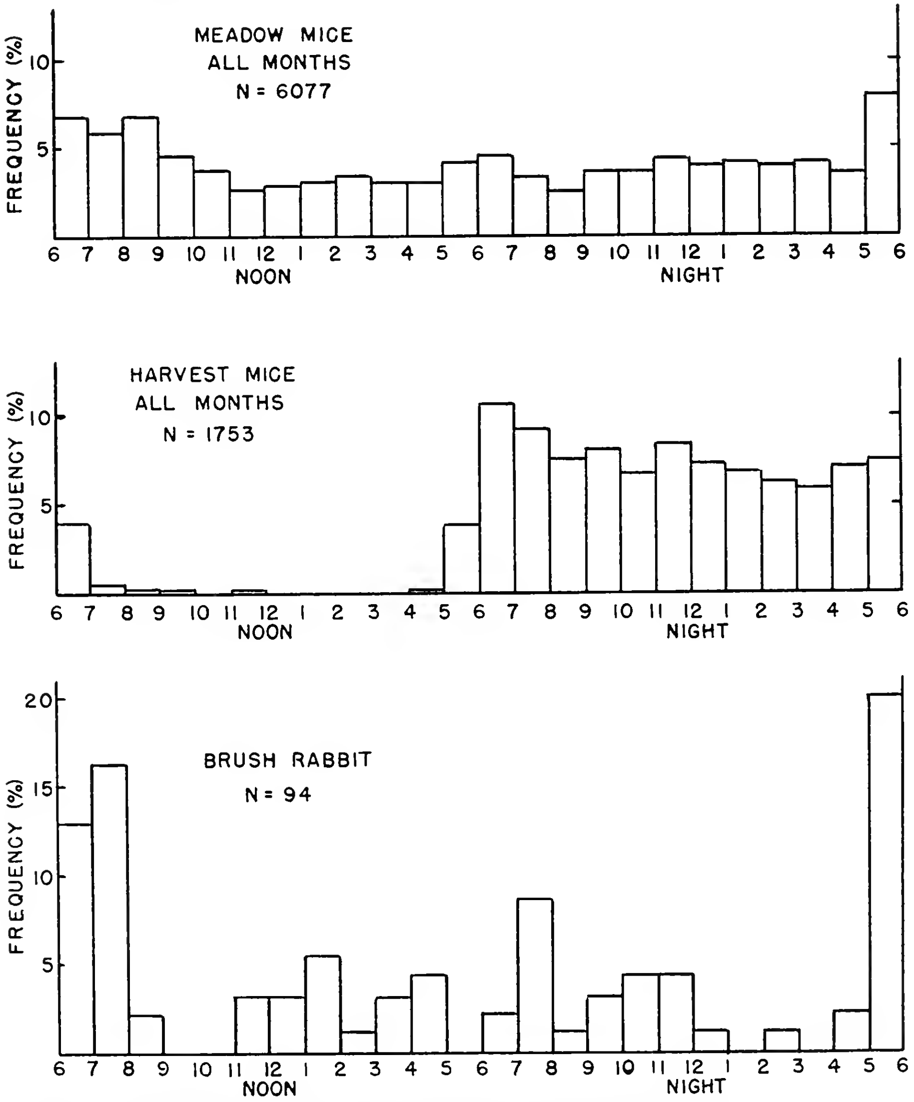

FIG. 3.—Distribution by hours of 6,077 passages of meadow mice (above); 1,753 passages of harvest mice (center); and 94 passages of brush rabbits (below).

in the runway and it began to look unused. By the end of April almost all traffic had ceased.

The *Reithrodontomys* data will be analyzed in a later report.

Birds.—Of the 382 bird records, at least 255 were of sparrows (at least 122 song sparrow; the remainder mostly fox sparrow, white-crowned sparrow and golden-crowned sparrow). Other birds recognized were wren-tit, wren, brown towhee and thrush. On several occasions birds, especially song sparrows, battled their reflections in the window of the instrument shelter. This caused long series of exposures. Each series was counted as a single passage. If the bird stopped for a minute or more and then returned to the battle, this was counted as another passage. All bird records were during daylight hours.

On three occasions a sparrow and an adult *Microtus* appeared in the same photograph. On one of these occurrences a song sparrow was battling its reflection when an adult, lactating *Microtus* came along the runway. The sparrow retreated about 12 inches toward the camera shelter and, as soon as the mouse had passed, returned to the runway.

Brush rabbit.—All except four of the records of brush rabbits were in June and July of 1957, a season when these animals, especially young ones, were abundant. Figure 3 (below) shows that they were most active in the early morning.

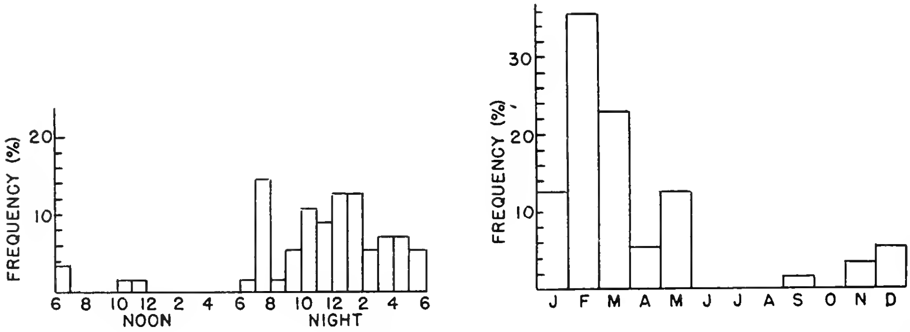

Fig. 4.—Distribution by hours of 56 passages of shrews (left) and distribution by months of 56 passages of shrews (right).

Shrew.—The dry, weedy habitat chosen was not favorable for shrews, and they were near the minimum weight necessary to depress the treadle of one of the recorders, so that some may have passed along the runway without making a record. The shrews were highly nocturnal (Fig. 4, left) and avoided the surface runways during the dry summer months (Fig. 4, right). Since captive specimens of *Sorex* are rarely inactive for more than one hour (Morrison, Amer. Midl. Nat., 57: 493, 1957), the scarcity of records in the daytime probably means only that the shrews were not moving above ground at this time. They may have been foraging along gopher, mole and *Microtus* tunnels during the daytime.

A shrew was marked on March 4, a few inches from one of the recorders. It was captured 15 feet away on May 30 and 5 feet farther away on June 23. It passed along the study runway five times in the 16-week interval between first and last capture: on March 13, 27, 31, and April 17, and possibly on April 10 (markings obscured). Another shrew was recorded on March 27. Unless baited traps attract shrews from a considerable distance, or the recorder repels them, a trapper setting traps in this runway for a few nights would have had small chance of recording the presence of this individual which apparently was nearby for at least 16 weeks.

Not a single shrew was recorded during the dry summer months of June, July and August. Nevertheless, on July 8 when I was checking the photoelectric recorder at 5:55 AM, a shrew emerged completely from a small hole in

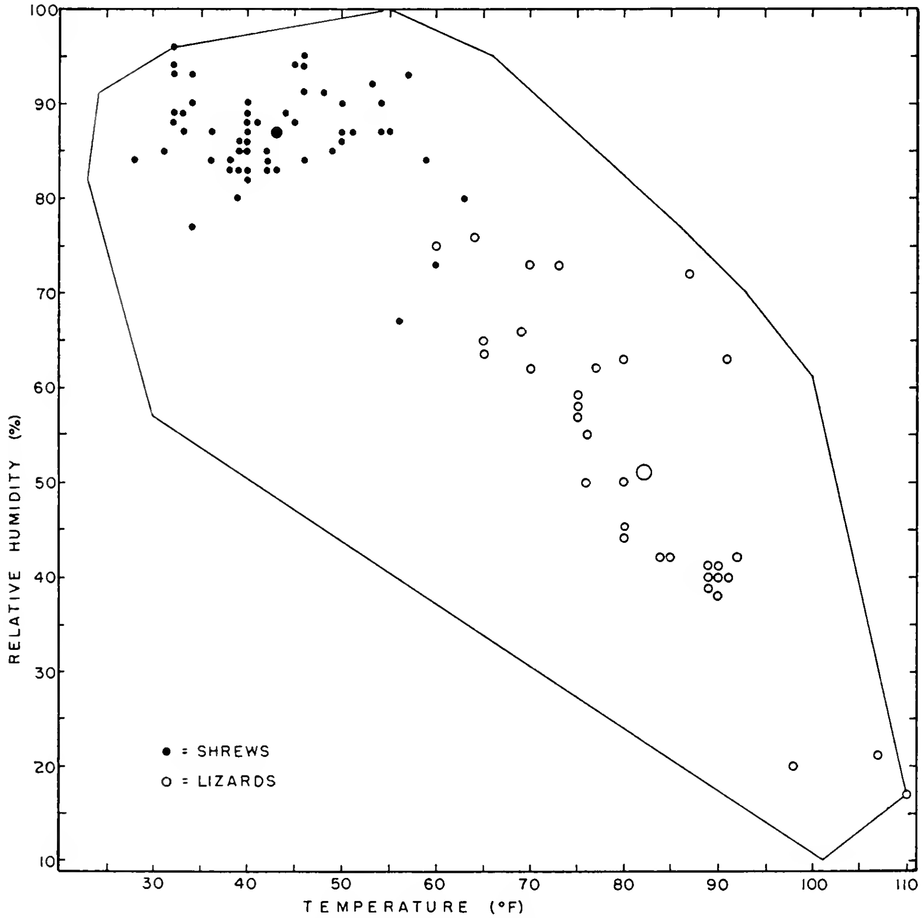

FIG. 5.—A comparison of the temperatures and humidities encountered by shrews and fence lizards in the runways. The larger circles show the position of the mean for each species. The large polygon encloses the range of temperatures and humidities available to the animals during the study.

the ground a few inches from the instrument shelter, twitched his nose rapidly for a few seconds, and retreated down the same hole. The air temperature was 54° and the relative humidity 78 per cent—normal for this season. Obviously shrews were present on the study area during some or all of the summer months but were not frequenting the surface runways.

Figure 5 shows the temperatures and relative humidities encountered above ground by the shrews on the study area compared with the total range of temperatures and humidities recorded throughout the study. By their nocturnal, winter-time activity shrews encountered the coldest, most humid conditions available in the region. In contrast, the similarly small, insectivorous fence lizards existing in the same habitat managed by their own behavioral patterns to encounter a totally different climate (Fig. 5). The mean of the temperatures recorded at the times of lizard passages was 39° warmer than that recorded for shrew passages, and relative humidity was 36 per cent lower.

This activity pattern of shrews differs from that reported by Clothier (Jour. Mamm., 36: 214–226, 1955) for *Sorex vagrans* in Montana. He found shrews there to be active "both day and night and throughout the year, even during extremely bad weather." It is important to understand, however, that he collected in damp areas near water, where the shrews may not have had to modify their activity to avoid desiccation. Extremely bad weather, for a shrew, is hot dry weather.

Peromyscus.—Peromyscus truei was abundant in brushy places and in houses nearby; *P. maniculatus* was scarce. Some of the *Peromyscus* records were clearly of *truei* and some may have been of *maniculatus*, but many could not be identified with certainty. No adult *P. californicus* was recognized although a few young ones may have passed and been listed as *truei*. All passages of *Peromyscus* were at night.

Salamander.—The record includes passages by both *Ensatina escholtzii* and *Aneides lugubris*. They were recorded in October, November, March and April. By being nocturnal and by avoiding the dry season, they encountered in these autumn and spring months about the same microclimate as shrews, but were recorded neither in the winter months nor at temperatures below 39°. A third species, *Batrachoceps attenuatus*, was common in the study area but is so small that it could not be expected to actuate either of the recorders. One *Batrachoceps* electrocuted itself underneath the treadle but has not been included in the records.

Comparison of traps and recorders.—The combination of live-trapping and photographing revealed a failure of small mammals to move between runways only a few feet apart. On several occasions meadow mice and harvest mice were live-trapped a few feet from one of the recorders, were released at the same place, and were recaptured a week or more later not more than a few feet away, yet during the intervening time they failed to pass the recorder. Conversely, some individual mice repeatedly recorded themselves on the films yet could never be induced to enter any of a large number of live traps placed in the same runway and in nearby runways. It is obvious that all mice present do not use all of the active runways close to their home, and it is also obvious that neither the recorders nor traps give a complete accounting of the mice present.

SUMMARY

A motion-picture camera synchronized to an electronic flash unit was used to record the passage of animals along meadow-mouse runways and to record the temperature, relative humidity and time at which they passed. More than 26 species used the runways during 111 weeks of recording. Meadow mice, harvest mice, sparrows, brush rabbits and shrews passed most frequently. The average traffic per day in each runway was 11 passages; on some days there were more than 60 passages. Rarely more than ten meadow mice or six harvest mice used a runway in any one period. Meadow mice and harvest mice used the same runways simultaneously. Traffic by harvest mice alone did not keep the runways open.

Meadow mice were active during the day and night; harvest mice were strongly nocturnal. Brush rabbits were active primarily early in the morning. Almost all shrews were recorded at night and in the winter months. Consequently, they encountered the coldest, most humid conditions available to them. In contrast, the similarly small, insectivorous fence lizards encountered a microclimate that was 39° warmer and 36 per cent less humid.

Neither traps nor recorders accounted for all the individuals living nearby.

Museum of Vertebrate Zoology, Berkeley, California. Received October 29, 1957.

PREY SELECTION AND HUNTING BEHAVIOR OF THE AFRICAN WILD DOG[1]

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Abstract: African wild dog (*Lycaon pictus*) predation was observed in Ngorongoro Crater, Tanzania, between September, 1964, and July, 1965, when packs were in residence. The original pack of 21 dogs remained only 4 months, but 7 and then 6 members of the group reappeared in the Crater at irregular intervals. The ratio of males:females was disproportionately high, and the single bitch in the small pack had a litter of 9 in which there was only one female. The pack functions primarily as a hunting unit, cooperating closely in killing and mutual defense, subordinating individual to group activity, with strong discipline during the chase and unusually amicable relations between members. A regular leader selected and ran down the prey, but there was no other sign of a rank hierarchy. Fights are very rare. A Greeting ceremony based on infantile begging functions to promote pack harmony, and appeasement behavior substitutes for aggression when dogs are competing over meat. Wild dogs hunt primarily by sight and by daylight. The pack often approaches herds of prey within several hundred yards, but the particular quarry is selected only after the chase begins. They do not run in relays as commonly supposed. The leader can overtake the fleetest game usually within 2 miles. While the others lag behind, one or two dogs maintain intervals of 100 yards or more behind the leader, in positions to intercept the quarry if it circles or begins to dodge. As soon as small prey is caught, the pack pulls it apart; large game is worried from the rear until it falls from exhaustion and shock. Of 50 kills observed, Thomson's gazelles (*Gazella thomsonii*) made up 54 percent, newborn and juvenile wildebeest (*Connochaetes taurinus*) 36 percent, Grant's gazelles (*Gazella granti*) 8 percent, and kongoni (*Alcelaphus buselaphus cokei*) 2 percent. The dogs hunted regularly in early morning and late afternoon, with a success rate per chase of over 85 percent and a mean time of only 25 minutes between starting an activity cycle to capturing prey. Both large and small packs generally killed in each hunting cycle, so large packs make more efficient use of their prey resource. Reactions of prey species depend on the behavior of the wild dogs, and disturbance to game was far less than has been represented. Adult wildebeest and zebra (*Equus burchelli*) showed little fear of the dogs. Territorial male Thomson's gazelles, which made up 67 percent of the kills of this species, and females with concealed fawns, were most vulnerable. The spotted hyena (*Crocuta crocuta*) is a serious competitor capable of driving small packs from their kills. A minimum of 4–6 dogs is needed to function effectively as a pack. It is concluded that the wild dog is not the most wantonly destructive and disruptive African predator, that it is an interesting, valuable species now possibly endangered, and should be strictly protected, particularly where the small and medium-sized antelopes have increased at an alarming rate.

The habits of the African wild dog or Cape hunting dog (*Lycaon pictus*) have been described, sometimes luridly, in most books about African wildlife. Accounts by such famous hunters and naturalists as Selous (1881), Vaughan-Kirby (1899), and Percival (1924), repeated and embellished by other authors, have created the popular image of a wanton killer, more destructive and disruptive to game than any other African predator.

Because of its bad reputation, the wild dog was relentlessly destroyed in African parks and game reserves for many years. In Kruger National Park, for instance, it was shot on sight from early in the present century up until 1930 as part of an overall policy to keep predators down. In Rhodesia's Wankie National Park some 300 wild dogs were killed by gun and poison between 1930 and 1958.

Acceptance of modern concepts of wildlife management has finally brought an end to the indiscriminate destruction of wild dogs and other predators in most, if not all, African national parks. There is now

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[1] Field work supported by the National Geographic Society; also by grants from the New York Explorers Club and the Tanzania Ministry of Agriculture, Forests and Wild Life.

a general awareness among game wardens of the predator's role in regulating populations, which perhaps began with Stevenson-Hamilton (1947), Warden of Kruger Park for almost 30 years, who related the alarming increase of impala (*Aepyceros melampus*) to the disappearance of the park's formerly large wild dog packs.

While the wild dog has benefited from more enlightened concepts of game management, its reputation, still based on popular writings and myth, remains unchanged. But recent scientific investigations indicate that a new and less-prejudiced evaluation of this species is long overdue. Kühme (1965) has studied the social behavior and family life at the den of a pack with young whelps on the Serengeti Plains, Tanzania. We have observed prey selection and hunting behavior in a free-ranging pack of adults and juveniles in nearby Ngorongoro Crater, a caldera with a floor area of 104 square miles that supports a resident population of around 25,000 common plains herbivores. The two studies together throw quite a different light on the habits, character, and predator–prey relationships of this highly interesting species.

We are indebted to Dr. B. Foster of the Royal College, Nairobi, and to G. C. Roberts of the Crater Lodge for reporting four kills and one kill respectively, that they witnessed in the Crater; also to Professors W. C. Dilger, O. H. Hewitt, and H. E. Evans of Cornell University for critical readings of the manuscript. Nomenclature follows Haltenorth (1963) for artiodactyls, and Mackworth-Praed and Grant (1957) for birds.

METHODS

Most observations were made from a vehicle; we each had a Land Rover and usually operated independently. The wild dogs, like many other African predators in sanctuaries, paid very little attention to cars and could be watched undisturbed from within 30 yards or less. It was also feasible to keep pace with the pack during chases over the central Crater floor, either driving parallel to the leader at a distance of 100–200 yards or following behind and to one side so as not to get in the way of other pack members. To locate the pack initially, we often drove to an observation point on a hill and scanned the Crater with binoculars and a 20-power binocular telescope. When the pack was moving it could often be spotted at a distance of over 5 miles, and a number of chases and kills were clearly observed from a hilltop through the telescope.

RESULTS

Pack Composition

The pack that first entered Ngorongoro Crater in September, 1964, contained 21 animals, including 8 adult males, 4 adult females, and 9 juveniles. They remained more or less continually in residence through December, then disappeared and were presumed to have left the Crater. One juvenile female had died of unknown causes. During January, 1965, seven members of the same pack, 4 males, 1 female, and 2 juvenile males, reappeared; after a lapse of 5 months, apparently the same animals, minus one male, again took up residence, and have been observed off and on up to the present writing. In March, 1966, the female whelped but died 5 weeks later, leaving 8 male and 1 female pups. They were brought up by the 5 males, who fed them by regurgitation until they were old enough to run with the pack. However, the female and 4 male pups died, leaving an all-male pack of 9 in August, 1966.

While an all-male pack must be exceptional, there is other evidence to suggest that a high proportion of males may be common in this species. The pack Kühme studied consisted of 6 adult males and 2 adult females, which had 11 and 4 pups respectively, sex unreported. During 2–3 years of shooting in Kruger National Park, the ratio of males was 6 : 4, despite an attempt to select females (Stevenson-Hamilton 1947). We have no explanation to offer for the discrepancy, but if it is real and not normal, it might help explain the reported decline of wild dogs during recent years in many parts of Africa.

Social Organization

Leadership and Rank Hierarchy.—In the full pack of 21 and in the pack of 7, the same adult male was consistently the leader; he usually led the pack on the hunt, selected the prey, and ran it down. In the pack of 6, from which the above male was absent, the adult female was the leader. One of the males filled the position after her death.

Apart from the position of leader, we saw no indication of a rank order. Kühme concluded there was no hierarchy in the pack he observed, nor even a leader. The equality of pack members may partly explain the singularly amicable relations typical of the species. On the other hand, competition for food and females could easily lead to aggression; yet neither Kühme nor we ever saw a fight.

Food Solicitation and Appeasement Behavior.—Overt aggression and fighting are minimized through ritualized appeasement behavior derived from infantile food begging. Begging and appeasement appear in almost every contact between individuals, and particularly in situations where aggression would be most likely to occur—for instance, when animals are competing over a kill. However, we cannot comment on sexual competition, having seen none; we observed sexual behavior on only two occasions, when one male mounted another repeatedly as the latter was feeding at a kill. Kühme also saw very little sexual behavior. When two animals were competing for the same piece of meat, each would try to burrow beneath the other, its forequarters and head flat to the ground and hindquarters raised, tail arched and sometimes wagging. The ears were flattened to the head and the lips drawn back in a "grin," while each gave excited twittering calls. As Kühme observed (p. 516), the dogs "tried to outdo each other in submissiveness."

In this way juveniles and even subadults manage to monopolize kills in competition with adults. The young thus enjoy a privileged position in the pack. Pups at the den successfully solicit any adult to regurgitate food by poking their noses into the corner of the adult's mouth, sometimes licking and even biting at the lips. Since all pack members contribute to feeding and protection of the young, the mother is not essential to their survival after the first few weeks.

Greeting Ceremony.—Whenever the pack became active after a rest period, and particularly if two parts of the pack were reunited after being separated, the members engaged in a Greeting ceremony (Fig. 1), in which face-licking and poking the nose into the corner of the mouth played a prominent part. The ceremony thus appears to be ritualized food solicitation; the fact that Kühme actually saw regurgitation elicited by begging adults supports this interpretation. The Greeting ceremony in the wolf (*Canis lupus*), in which one takes another's face in its jaws, may have the same derivation.

As a prelude to greeting, dogs typically adopted the Stalking attitude (Fig. 2), with the head and neck held horizontally, shoulders and back hunched, and the tail usually

Fig. 1. Greeting ceremony.

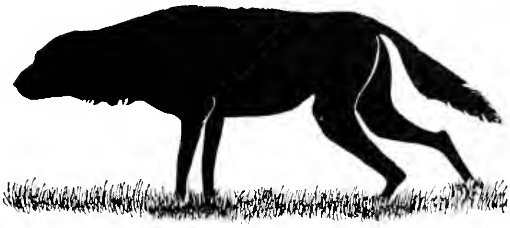

Fig. 2. The Stalking attitude, here displayed by the pack leader while approaching a herd of gazelles.

hanging. Kühme (p. 512) interprets this posture as inhibited aggression; the same attitude is adopted when approaching potential prey and competitors of other species. The Stalking posture changed to greeting when dogs got close. In greeting-solicitation, as they licked each other's lips and poked the nose into the corner of the mouth, one or both crouched low, with head, rump, and tail raised stiffly (Fig. 1). Except for the raised head, this resembles the submissive posture displayed when two dogs are competing over food. The Greeting ceremony was also frequently performed while two dogs trotted or ran side by side.

Vocal Communication.—Although Percival (1924), Stevenson-Hamilton (1947), Maberly (1962), Kühme (1965), and others have given good descriptions of wild dog calls, the function of the calls has often been misinterpreted. This applies particularly to two of the three most frequently heard calls (Nos. 1 and 3):

1. *Contact call*—a repeated, bell-like "hoo." Often called the Hunting call, it has nothing to do with hunting as such, but is given only when members of a pack are separated. Though a soft and musical sound, it carries well for 2 or more miles. When members of the Ngorongoro pack were missing, an imitation of the Contact call would bring the rest to their feet, whereas there was at best only a mild reaction to imitations when the full pack was assembled.

2. *Alarm bark*—a deep, gruff bark, often combined with growling, given when startled or frightened. A good imitation near a resting pack elicited an immediate startled reaction.

3. *Twittering*—a high-pitched, birdlike twitter or chatter. The most characteristic and unusual vocalization, it expresses a high level of excitement. It is given in the prelude to the hunt, while making a kill, in mobbing hyenas or a pack member, and by dogs competing over food. Its primary function is evidently to stimulate and concert pack action. Kühme described this call (*Schnattern*) only in the context of the Greeting ceremony (p. 513).

Besides these vocalizations, whining may be heard during appeasement behavior and when pups are begging, and members of the pack sometimes yelp like hounds when close on the heels of their prey. Kühme (p. 500) further distinguishes an Enticing call (*Locken*) given by adults calling the young out of the den, and a Lamenting call (*Klage*) given by pups when deserted.

Olfactory and Visual Communication.—Wild dogs hunt primarily by sight and by daylight. We never saw them track prey by scent. Though they evidently have a good nose and may well use it for tracking in bush country, olfaction in this species seems to have a primarily intraspecific significance.

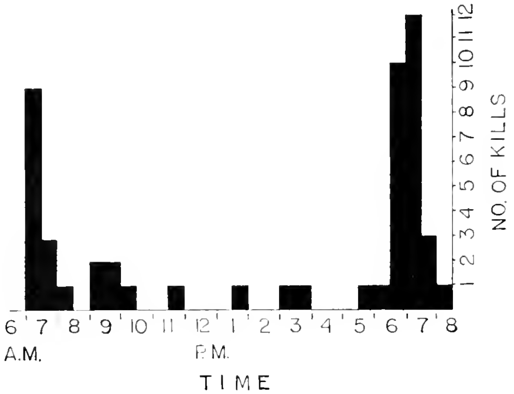

Fig. 3. Time distribution of 50 wild dog kills.

Wild dogs are renowned for their peculiarly strong, and to many humans disgusting, odor, which may emanate from anal glands but seems to come from the whole body. Sniffing under the tail, responsive urination and defecation are socially important activities. But the main role of the strong body odor may be to permit high-speed tracking of the pack by members that have lost visual contact. Lagging members seen running on the track taken by the rest of the pack sometimes appeared to be using their noses. Similarly, the white tail tip probably helps maintain visual contact in bush country, high grass, and under crepuscular conditions; in a species notable for every possible color variation, a white-tipped tail is the most constant and conspicuous mark.

Daily Activity Pattern

The Ngorongoro pack had two well-defined hunting periods each day (Fig. 3). That this periodicity is characteristic of the species may be inferred from Kühme's observations (p. 511), and from Stevenson-Hamilton's (1947) observations in Kruger National Park. In nine recorded instances, though, the Ngorongoro dogs killed between 8:30 AM and 3:30 PM, well outside the normal periods. Failure to kill during the regular hunting cycle is the likeliest explanation; it was more usual, however, for the pack then to wait until the following regular period. Wild dogs will also hunt on moonlight nights, as Stevenson-Hamilton noted. When the Crater dogs had not killed before dusk, the hunt was sometimes prolonged. The latest kill we recorded was at 7:32 PM, when it was fully dark.

Since they are capable of functioning as a pack and of hunting successfully after dark, the fact that wild dogs are so strongly diurnal may seem puzzling. But it may be explained by the fact that they hunt mainly by sight; it would be much more difficult to locate prey and single out a quarry at night. As to the regularity and brevity of their hunting cycles in early morning and late afternoon, this is partly a measure of their hunting efficiency, discussed below. Also, of course, these are the times in the day when diurnal animals, particularly herbivores, are most active and most approachable.

Apart from a certain amount of play and other social activities shortly before starting to hunt and immediately after feeding, pack members were usually active only while actually hunting. At other times they could often be found resting near or in the same place where they had settled after the morning or evening kill. When resting, pack members customarily lay touching in close groups (Fig. 4). Generally speaking, the pack became active between 5:30 and 6:15 PM, and in the morning within ½ hour of dawn, remaining active for 1–2 hours. But where game is less plentiful than it is in Ngorongoro, and a pack must range more widely (Stevenson-Hamilton gives a range of at least 1,500 square miles for a Transvaal pack whose movements were reported over a period of years), a good deal of time between and during hunts must be spent in travel.

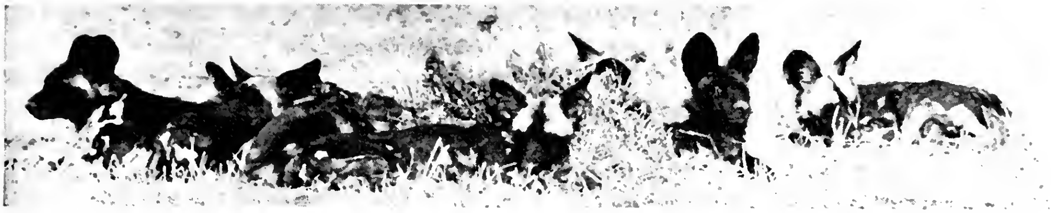

Fig. 4. Part of a resting pack, lying typically close together.

Hunting Behavior

Prelude to the Hunt.—Periods of activity were initiated by the actions of one or a few dogs apparently more restless than the others; rarely did the whole pack arise spontaneously at the start of an activity cycle. Typically, one dog would get up and run to a nearby group, nose the others and tumble among them until they responded. Within a few minutes the whole pack would usually become active. But if, as sometimes happened, the majority failed to respond to the urging of a few, then all would settle down to rest again. Sometimes, after a brief bout of general activity, the whole pack would lie down once more, even if it was past the usual time of hunting.

During the first 5 or 10 minutes after rousing, the pack members sniffed, urinated, defecated, greeted, and romped together. Play and chasing tended to become progressively wilder and reached a climax when the whole pack milled together in a circle and gave the twittering call in unison. As soon as this melee broke up, the pack usually set off on the hunt. Kühme (p. 522) interprets this performance (specifically the Greeting ceremony) as "a daily repeated final rehearsal for the behavior at the kill," wherein mutual dependence and friendliness are reinforced by symbolic begging, thus enabling the dogs to share the kill amicably. While this may be one function, the progressive buildup of excitement before hunting looked to us like nothing so much as a "pep rally," that served to bring the whole pack to hunting pitch. The behavior of domestic dogs urging one another to set off on a chase is somewhat similar.

The Mobbing Response.—During the milling preparatory to hunting, we sometimes saw what appeared to be incipient mobbing action toward a pack member, when up to half a dozen dogs would gang up on one, tumble and roll it but without actually biting it. Intensive play between two or three animals usually preceded and seemed to trigger a mobbing reaction in other members, who signaled their intentions by approaching in the Stalking posture. Percival (1924:48) reports seeing a pack mob and kill a wild dog he had wounded. The occurrence of "play" mobbing suggests that it could indeed become serious when an animal is maimed. On the other hand, sick and crippled pack members are often not molested: one very sick-looking old male in the large pack trailed behind the others for over a month before recovering, and though he kept usually a little apart, was tolerated at kills.

It is significant that basically the same mobbing behavior, at high intensity, is displayed when wild dogs kill large prey and when they harass spotted hyenas, their most serious competitor. It seems very likely, in fact, that mobbing is an innate response which governs pack action in hunting, killing, and mutual defense. It is perhaps the key to pack behavior in all animals that display it. That mobbing appears in play and can be released by a conspecific which is wounded or otherwise transformed from its normal self, supports the hypothesis that it is an innate response. It is also noteworthy that a wild dog removed from its pack apparently makes little effort to defend itself against attack. Selous (in Bryden 1936:24) reported that a wild dog caught by a pack of hounds shammed death and then escaped when he was about to skin it.

Hunting Technique.—Sometimes the pack would set off on the hunt at a run and chase the first suitable prey that was sighted. More often, there was an interval of 10–20 minutes during which the dogs trotted along, played together, and engaged in individual exploratory activity, stopping to sniff at a hole or a tuft of grass, then running to catch up with the rest. At this stage, when the hunt had started but before any common objective had been determined, individuals might forage for themselves. The observer would suddenly notice that a dog was carrying part of a gazelle fawn or a young hare (*Lepus capensis*), that must have been simply grabbed as it lay in concealment. Once during a moonlight hunt by a small pack that visited the Crater in 1963, individual dogs were seen to pick up at least two gazelle fawns and one springhare (*Pedetes surdaster*), a strictly nocturnal rodent, within ½ hour. Concealed small game such as this is apparently not hunted by the pack in concert.

Preparatory to the chase, there was frequently a preliminary stalking phase during which the pack approached herds of game at a deliberate walk, in the Stalking attitude (Fig. 2). The dogs appeared to be attempting to get as close as possible without alarming the game, and certainly the flight distances were much less than when the pack appeared running. The chase was launched the moment the game broke into flight. But game that began running at more than 300 yards was generally not pursued. As far as we could tell, the prey animal was never singled out until after the pack, or at any rate the leader(s), had broken into a run.

In the pack of 21, juveniles and some adults usually lagged far behind, and often caught up 5–10 minutes after the kill was made. In the small pack, however, commonly all kept together and spread out on a front during the stalking phase. When all started running on a front, sometimes more than one dog picked out a quarry from the fleeing herd, whereupon the pack might split, some following one dog, the rest another. Kühme (p. 527) considered this the normal pattern and noted that often each animal acted for itself in selecting a quarry before all combined on a common goal. In this way the slowest prey tended to be selected. Selection by this method was exceptional for the Ngorongoro pack, which had a definite leader; as a rule the lead dog made the choice and the rest of the pack fell in behind him. Nor did it appear that any effort was made to single out the slowest prey, although that would be difficult to observe clearly.

Again as a general rule, no attempt was made to carry out a concealed stalk, which would in any case be practically impossible by daylight on the short-grass steppe. But on one occasion the pack of six made use of a tall stand of grass to get near a group of Thomson's gazelles. On another hunt the pack apparently took advantage of a slight elevation in the expectation of surprising any game that might be out of sight on the far side. They moved deliberately up the slope, then broke into a run and swept at full speed over the crest on a broad front—but without finding any quarry that time.

When the leader had selected one of a fleeing herd, he immediately set out to run it down, usually backed up by one or two other adults who maintained intervals of 100 yards or more behind him, but might be left much further behind in a long chase. The rest of the pack lagged up to a mile in the rear. Discipline during the chase was so remarkable among all pack members that even gazelles which bounded right between them and the quarry were generally ignored. The average chase lasted 3–5 minutes and covered 1–2 miles. At top speed a wild dog can perhaps exceed 35 mph, and can sustain a pace of about 30 mph for several miles. Once when a chase had begun but no single quarry had yet been selected, a male in the pack of 21 broke away and proceeded to make a 5-mile circular sweep quite by itself, turning on bursts of speed when gazelles bounded off before him, but without ever singling one out. His average speed, as determined by pacing him in a vehicle, was approximately 20 mph.

In descriptions of wild dog hunting methods, much has been made of their intelligent cooperation in "cutting corners" on their prey, and particularly of their relay running, with fresh dogs taking the place of tired leaders. We concur that there is a basis for the first idea, but we saw no evidence whatever to support the contention that wild dogs run in relays. The truth is that wild dogs have no need to hunt in relays. The lead dog has ample endurance, if not the speed, to overtake probably any antelope, of which gazelles are among the fleetest. The fact that other members of the pack are able to cut corners on the prey is at least partly accounted for by the prey's tendency to circle instead of fleeing in a straight line. As explained later, some prey animals have a greater tendency than others of their species to do this. Of course, once overtaken, even a quarry that has been running straight is forced to start dodging if it is to avoid being caught straightaway. Thus a dog running not too far behind the leader is well placed to cut corners when the quarry changes course, and it frequently happened that one of the followers made the capture. Most game, after a hard chase of a mile or two, was too exhausted by the time it began dodging to have any real chance of evading its pursuers.

Killing and Eating.—Wild dogs killed small game like Thomson's gazelles with amazing dispatch. Once overtaken, a gazelle was either thrown to the ground or simply bowled over, whereupon all nearby dogs fell on it instantly. Grabbing it from all sides and pulling against one another so strongly that the body was suspended between them, they then literally tore it apart (Fig. 5). It happened so quickly that it was never possible to come up to a kill before the prey had been dismembered. If it didn't go down at once, dogs began tearing out chunks while it was still struggling on its feet. We once saw a three-quarter term fetus torn from a Thomson's gazelle within seconds of the time it was overtaken and before it went down. As Kühme observed, there is no specific killing bite as in felids (Leyhausen 1965). When dealing with larger prey such as juvenile wildebeest and notably a female kongoni, the dogs slashed and tore at the hind legs, flanks, and belly—always from the rear and never from in front—until the animal fell from sheer exhaustion and shock. They then very often began eating it alive while it was still sitting up (Fig. 6). Self-defense on the part of a prey was never once observed; the kongoni, for example, did little more than stand with head high while the dogs cut it to ribbons, looking less the victim than the witness of its own execution.

In eating, the dogs began in the stomach cavity, after first opening up the belly, and proceeded from inside out. Entrance was

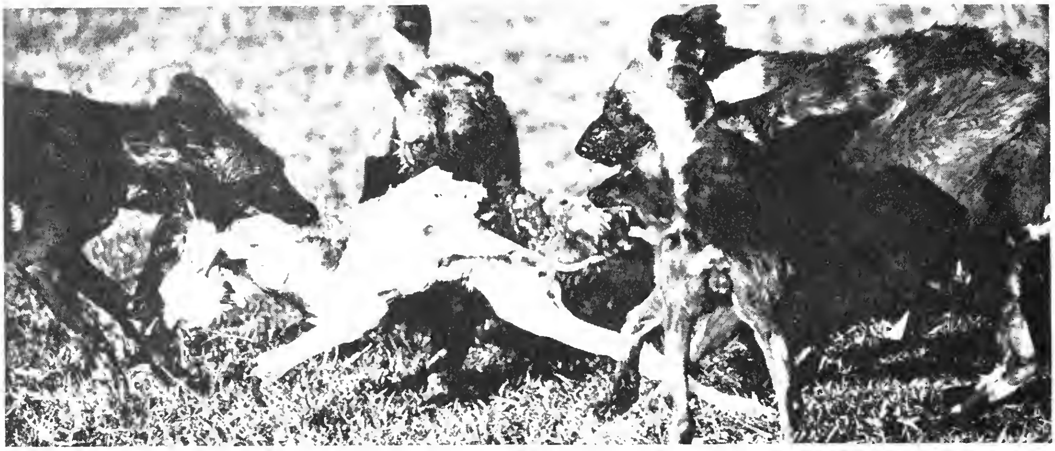

Fig. 5. The pack tearing apart a young gnu calf.

also effected through the anus by animals unable to win a place in the stomach cavity. While several dogs forced their heads inside and ripped out the internal organs, others quickly enlarged the opening in struggling for position. This resulted in skinning out the carcass, leaving the skin still attached to the head, which was seldom touched. Apart from these, the backbone and the leg bones, very little of a Thomson's gazelle would remain at the end of 10 minutes. In the pack of 21, if only part had managed to eat their fill, sometimes the rest went off to hunt again before the carcass was cleaned. They proceeded to chase and pull down another gazelle within as little as 5 minutes from the time of the previous kill, to be joined shortly by the other dogs. As each animal became satisfied it withdrew a little from the kill and joined others to rest, play, or gnaw at a bone it had taken along. Sometimes the pack stayed at the scene until the next hunting period; more often it withdrew to a nearby stream or waterhole and settled down there. Kühme never saw wild dogs drink. The Ngorongoro pack drank, though irregularly, before hunting and after eating.

Selection of Prey and Frequency of Kills

Table 1 summarizes prey selection by species, sex, and age in 50 recorded kills. The 11 wildebeest calves were all taken in January during the peak calving season, when the pack of seven dogs apparently specialized on them; only kills of calves were seen by us or reported by Crater visitors in this month. Thus the percentage of calves in the total gives a biased picture of prey selection during the rest of the year. With new calves excluded, the adjusted percentages, based on 39 kills, are as follows:

Thomson's gazelles	69 percent
Juvenile wildebeest	18 percent
Grant's gazelles	10 percent
Kongoni	one kill

Wright (1960:9) records a similar preponderance of Thomson's gazelles in 10

Fig. 6. Dogs begin eating a yearling-class gnu while it is still alive, but evidently in a state of deep shock.

Table 1. Prey selection by species, sex, and age in 50 kills of the African wild dog.

PREY SPECIES	TOTAL NO.	ADULT MALES	ADULT FEMALES	JUVENILE–SUBADULT	YOUNG*	PERCENT OF TOTAL KILLS
Thomson's gazelle	27	18	6	2	1	54
Wildebeest	18	0	0	7	11	36
Grant's gazelle	4	1	1	2	0	8
Kongoni	1	0	1	0	0	2

* Less than 6 months old.

kills on the Serengeti Plains (7 Thomson's gazelles, 1 wildebeest, 1 impala, and 1 reedbuck [*Redunca redunca*]), and notes that it is the staple diet of wild dogs in the Serengeti. Kühme also observed that wild dogs prey mainly on *Gazella thomsonii* and *G. granti*, and young wildebeest in the Serengeti.

In terms of actual preference, information from the Serengeti, where the Thomson's gazelle is by far the most numerous herbivore, is far less revealing than the figures from the Crater, where this species occurs in relatively small numbers. The status of the principal ungulates in Ngorongoro, based on an aerial count by Turner and Watson (1964), on two ground counts of the gazelles by the authors in collaboration with the Mweka College of Wildlife Management, and on our ground counts of the less numerous species, is as follows:

Wildebeest	14,000
Zebra	5,000
Thomson's gazelle	3,500
Grant's gazelle	1,500
Eland (*Taurotragus oryx*)	350
Waterbuck (*Kobus defassa*)	150
Kongoni	100
Reedbuck	100 (?)

The evidence suggests, then, that Thomson's gazelle is the preferred prey of the wild dog in East African steppe–savanna. In the miambo woodland (Brown 1965) that extends from mid-Tanzania into South Africa, where gazelles are not found, the main prey may be impala, followed by other medium- to small-sized antelopes and the young of large antelopes. In Kruger Park, for example, of 88 identified wild dog kills, 85 percent were impala (Bourliere 1963). Stevenson-Hamilton listed other prey as reedbuck, bushbuck (*Tragelaphus scriptus*), duiker (*Sylvicapra grimmia* and *Cephalophus* spp.), and steinbok (*Raphicerus campestris*), also female waterbuck and kudu (*Tragelaphus strepsiceros*) when pressed by hunger. In Wankie Park, wardens' reports indicate a considerable toll of young kudu, eland, sable (*Hippotragus niger*), and tsessebe (*Damaliscus lunatus*). Instances where adult female and even adult male kudu were pulled down by wild dogs are also cited.

Bourliere states (1963:21) that "Carnivores actually only prey upon herbivores of about the same size and weight." While this generalization is open to dispute, it applies well enough to East African wild dogs preying on Thomson's gazelles. Where the main prey is impala, reedbuck, etc. that weigh in the 100–150 lb class, weight and size may be double or triple that of the wild dog. But the wild dogs of the East African steppe–savanna are smaller (also darker, with more black and less tan and white) than their counterparts in Central and South African woodland (Fig. 7). The average weight of the animals we have seen in East Africa would not exceed 40 lb; the members of a pack seen in Wankie Park, by comparison, looked to be a good 3 inches taller and 20 lb heavier. This consistent geographic size variation may be adapted to size of the principal prey species; specifi-

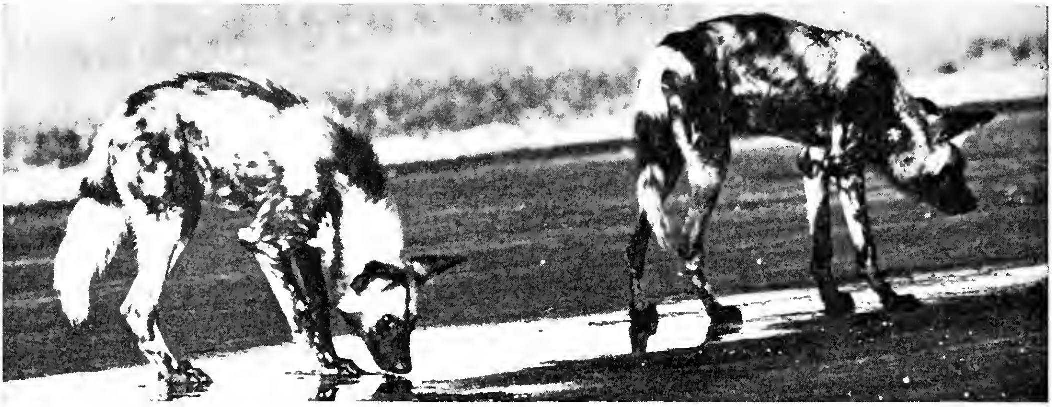

Fig. 7. Two specimens of the larger, lighter-colored wild dog of southern Africa, photographed in Wankie National Park.

cally, wild dogs of the East African plains may be smaller as the result of specialization on Thomson's gazelle.

Kill Frequency.—Because of the difficulty of locating and relocating a free-ranging pack, our data for consecutive hunting periods are inadequate for defining the average kill frequency and average food intake per animal per day. Even when the pack was observed during the two daily hunting periods, it was rarely certain that it had not killed before, after, or between these periods. Nonetheless, because this type of information is badly needed, data covering consecutive hunting periods are presented in Table 2 as a rough average of kill frequency and meat available per animal per day.

The average frequency of two kills per day derived from the data for consecutive hunting periods agrees with our general observation that the pack usually killed during each period. To demonstrate this, on 28 hunts the pack performed as follows:

Chases	Kills	Failures	Did not chase
29	25	4	5

This indicates a success rate per chase of over 85 percent. As a further indication of efficiency in locating and running down prey where game is plentiful, on eight occasions when the dogs were watched from the moment they left their resting place to the moment they killed, the mean time was only 25 minutes, with a range of 15–45 minutes. On five other occasions the pack failed to hunt seriously during the normal period; this was offset in the above figures by five periods during which the dogs chased and killed twice. The possibility that hunting activity and success might be reduced after having killed larger or more than one of the usual prey is not borne out by the six instances when the pack was observed during the next hunting period: in four cases the pack killed again. There are some grounds for asserting, then, that wild dogs kill twice daily regardless of what their prey may be. Certainly they do not feed more than once from the same kill, at least not in Ngorongoro Crater, where the numerous scavengers dispose of all leftovers in very short order.

Meat Available per Animal per Day.—The amount of meat available per wild dog per day works out at roughly 6 lb, assuming that 40 percent of the prey animal consists of inedible or unpalatable bone, skin, and stomach contents. Wright's (1960) calculation of 0.15 lb of food per day per pound

Table 2. Kill frequency and meat available per dog per day, based on observations of consecutive hunting cycles.

DATE	PREY	EST. WT. (LB)	NO. IN PACK	AVAILABLE* MEAT/DOG	MEAT/DOG/DAY
1964					
Sept. 30	Juvenile wildebeest	125	21	3.6	3.6
Oct. 1	Thomson's gazelle (adult M)	60	21	1.7	
	" " (adult F)	40	21	1.1	2.8
Nov. 11	Thomson's gazelle (adult F, including fetus)	50	21	1.4	
	2 Thomson's gazelles (adult F)	80	21	2.2	3.6
Nov. 12	Thomson's gazelle (adult M)	60	21	1.7	
	Kongoni (adult F)	250	21	7.4	9.1
Nov. 27	2 Thomson's gazelles (adult M)	120	21	3.4	
	Thomson's gazelle (subadult M)	50	21	1.4	4.8
Nov. 28	Grant's gazelle (subadult F)	90	21	2.6	
	Thomson's gazelle (adult M)	60	21	1.7	4.3
Dec. 5 (PM)	2 Thomson's gazelles (adult M)	120	12	6.0	
to					
Dec. 7 (AM)	Thomson's gazelle (juv. M)	40	21	1.1	3.5
1965					
Jan. 17 (PM) to Jan. 19 (AM)	4 wildebeest calves	180	7	15.5	7.8
July 16	2 Thomson's gazelles (adult M)	120	6	12.0	12.0

Kill frequency = 2 kills/day.
Meat available per dog per day: combined average = 6 lb; for pack of 21 = 4.5 lb; for pack of 7–6 = 9 lb.

* Available meat is based on 60 percent of carcass weight.

of dog also works out to 6 lb per day if the average weight of a dog is taken as 40 lb, but his figures are based on the total weight of the prey. In either case, two to three times as much food per day is available to wild dogs as is given to domesticated dogs of the same size. However, the number of dogs in the pack is an important factor. When there were 21 dogs, the amount of meat available per day was less than 5 lb per animal; in the pack of 7 and 6, each animal had approximately twice as much available meat. Since the small packs killed at the same rate, large packs are undoubtedly less wasteful.

Reactions of Prey Species

The reactions of game depended on the behavior of the wild dog pack. When the pack was at rest, all game would graze unconcernedly within 150 yards. When the dogs were walking or trotting, potential prey would stand until approached within 350–250 yards, or less if the pack was not headed directly toward them. When stalked, gazelles often stood watching until the pack came within 300–200 yards. But when the pack was running, gazelles, and wildebeest herds containing young, often acted alarmed at a distance of 500 yards, although again, individual animals not directly in the approach line might let the pack go by as close as 150 yards.

Gazelles.—The moment a running wild dog pack appeared on the plain, both gazelle species immediately reacted by performing the stiff-legged bounding display, with tail raised and white rump patch flashing, called Stotting or Pronking. Undoubtedly a warning signal, it spread wave-like in advance of the pack. Apparently in response to the Stotting, practically every gazelle in sight fled the immediate vicinity.

Adaptive as the warning display may seem, it nonetheless appears to have its drawbacks; for even after being singled out by the pack, every gazelle began the run for its life by Stotting, and appeared to lose precious ground in the process. Many have argued that the Stotting gait is nearly or quite as fast as a gallop, at any rate deceptively slow. But time and again we have watched the lead dog closing the gap until the quarry settled to its full running gait, when it was capable of making slightly better speed than its pursuer for the first half mile or so. It is therefore hard to see any advantage to the individual in Stotting when chased, since individuals that made no display at all might be thought to have a better chance of surviving and reproducing. On theoretical grounds, then, it has to be assumed that the Stotting display offers an individual selective advantage which simply remains to be determined. Nor is this type of display confined to the gazelles: during the aforementioned kongoni chase, all six members of the herd began Stotting when the wild dog pack first headed in their direction, and the victim continued to Stot for some time after being singled out.

Table 1 shows that 67 percent of the Thomson's gazelles killed were adult males. This is evidently the result of territorial behavior. Because of attachment to territory, probably coupled with inhibition about trespassing on the grounds of neighboring rivals, territorial males tend to be the last to flee from danger. Moreover they show a greater tendency to circle back toward home, and these two traits together make them more vulnerable to wild dog predation than other members of the population. The same tendencies are displayed by females with young, concealed fawns, making them also more vulnerable.

Wildebeest.—Adult wildebeest, especially territorial bulls, show little fear of wild dogs, which is a good indication that they have little reason to fear them under normal circumstances (Fig. 8). While even territorial males will get out of the way of a running pack, they rarely leave their grounds, but merely trot to one side and turn to stare as the pack goes by. Bulls not infrequently act aggressively toward walking or trotting dogs, and may even make a short charge if the dogs give ground. In Rhodesia we have seen a pack of the larger variety of wild dogs chased by females and yearlings of the blue wildebeest (*C. t. taurinus*) which is also larger and perhaps generally more aggressive than the Western white-bearded gnu. But like zebras, all wildebeest will on occasion follow behind walking or trotting dogs, apparently motivated by curiosity, just as they will gather to stare at and follow lions (*Panthera leo*).

In hunting wildebeest, wild dogs are obviously highly selective. Having walked in the Stalking attitude to within several hundred yards or less and then run into the midst of a large concentration, the pack splits up and works through it, approaching one gnu after another only to turn away if it proves adult. Meanwhile the wildebeest mill and run in all directions, without ever making any effort to form a defensive ring —even when young calves are present. A defensive ring has been reported in some of the wild dog literature. Kühme (p. 528) observed something of the sort in large Serengeti concentrations, though they did not form any regular ring but simply crowded together in a milling mass. Individual females, on the other hand, defend their calves after being overtaken in flight. Against a pack, however, one wildebeest cannot put up any effective defense; while it confronts one or two, the rest go around and seize the calf.

Zebra.—The only other herbivore whose

Fig. 8. Adults, and even a yearling gnu (4th from left) show little fear of running wild dogs, though they ran out of the way immediately after the picture was taken. The quarry is a young calf, visible as a light spot in the upper left.

reactions to wild dogs we observed in detail, zebras are the least concerned about them, and do not hesitate to attack dogs that come too close. Wild dogs on their part rarely stand up to them. Since the members of a harem would probably cooperate with the herd stallion to defend the foals, it would appear that wild-dog predation on zebra is quite rare.

Relations with Other Predators and Scavengers

Vultures.—Since wild dogs customarily kill in early morning and late afternoon, the larger vultures, the white-backed (*Pseudogyps africanus*), Rüppells griffon (*Gyps rüppelli*), and lappet-faced (*Torgos tracheliotus*), whose activities are largely regulated by the presence or absence of thermal updrafts, benefit rather little from their predation. Large vultures were more likely to appear at afternoon than morning kills. But the two smallest species, the hooded and Egyptian vultures (*Necrosyrtes monachus* and *Neophron perenopterus*), were regularly to be found at wild-dog kills, a good hour before other scavengers were even airborne. In addition to these vultures, other regularly encountered scavengers included the tawny eagle (*Aquila rapax*) and the kite (*Milvus migrans*), while the uncommon white-headed vulture (*Trigonoceps occipitalis*), the bateleur eagle (*Terathopius ecaudatus*), and Cape rook (*Corvus capensis*) showed up infrequently.

On several occasions hooded vultures were seen following a chase and landing before the prey had even been pulled down, shortly after full daylight. Aside from gleaning bits and pieces around the kill, vultures had to wait until the dogs left before they could feed on the carcass. But the kite successfully stole small pieces from the dogs by swooping, grabbing, and mounting again to eat on the wing. Although young animals sometimes stalked and ran at vultures that approached close to the kill, the dogs were generally tolerant toward avian scavengers.

Jackals.—The Asiatic jackal (*Canis aureus*) was seen more frequently at kills than the black-backed jackal (*C. mesomelas*). Since the latter seemed to predominate at nocturnal kills by lions or hyenas, it may be that one is more nocturnal and one more diurnal in its habits. Also, the Asiatic jackal tended to behave more boldly and aggressively at kills. It would move closer to a feeding pack of dogs and take advantage of any opportunity to steal meat. When threatened by a dog, a little 15-lb jackal, coat fluffed, head down, and snarling, would stand its ground and snap ferociously if the dog continued to advance. Although it was pure bluff that quickly ended in flight if a dog attacked in earnest, it proved a surprisingly effective intimidation display in most encounters. But on the whole, wild dogs behaved almost as tolerantly toward jackals as toward vultures.

Spotted Hyenas.—Spotted hyenas, on the other hand, seriously compete with the dogs for their kills, attempting to play a commensal role against active resistance. In a place like the Crater, with an exceptionally large hyena population for such a small area, numbering some 420 adults (Kruuk 1966:1258), it is probably safe to say that wild dogs hunting singly or in twos and threes would very frequently lose their kills to hyenas, since this happened occasionally even to the pack of 21.

Hyenas actually stayed near the resting pack for hours at a time, evidently waiting for a hunt to begin. It was not unusual to see one or more of them slowly approach a group of dogs, then crawl to within a few yards and lie gazing at them intently, as though urging them to get started. Often several would wander between resting groups, sniffing the ground, consuming any stools they found, and coming dangerously close, to stand staring with their short tails twitching—a sign of nervousness. Kühme (p. 534) reports an instance in which a hyena even touched a resting wild dog's face, meanwhile "whining friendly." Such boldness, particularly near the time when the pack was becoming active, often triggered the Mobbing response.

Hyenas, which weigh up to 150 lb, would be more than a match for wild dogs if they had the same pack (mobbing) instinct. Lacking it, they are nearly defenseless against a wild dog pack. With three to a dozen dogs worrying its hindquarters, the best a hyena can do is to squat down and snap ineffectively over its shoulder, while voicing loud roars and growls. On rare occasions a hard-pressed one would simply lie down and give up; a hyena we once saw crowded by a persistently curious group of juvenile wildebeest did the same thing. The spotted hyena seems on the whole to be notably timid by nature, as may be judged from the fact that mothers will often not even defend their offspring. Yet they are driven by hunger to take incredible and sometimes fatal risks.

Often, as under the above circumstances, they provoked attack by their own rashness. But in other cases the dogs seemed to go out of their way to harry hyenas encountered during the early stages of a hunt. Those unwary enough to let the pack get close could still usually get off entirely by cowering down and lying still. But those that stayed until the pack was close and then ran away were inviting pursuit and a good mauling. At the same time, hyenas following behind the pack were generally ignored. On one notable occasion, the pack of 21 took it in turns to mob the hyenas it happened upon in a denning area inhabited by more than 30 adults and cubs, many of which were foregathered as usual prior to the evening foraging. What was most surprising was that none, on this or any other occasion, attempted to take refuge underground. When hard-pressed, even half-grown pups bolted into nearby dense streamside vegetation, where the dogs did not follow. But presumably young pups were hidden in the dens, since one lactating female was reluctant to quit the immediate vicinity. She was repeatedly mobbed. Set upon by five or six dogs at a time, she would maintain a squatting defense as long as she could bear it, then break free to race for the nearest hole. Instead of going down it or backing into it, she threw herself into cup-shaped depressions next to the holes, which may or may not have been excavated by the hyenas themselves (territorial wildebeest also dig these depressions by pawing and horning the earth). In these she lay flat and tried to defend herself from the dogs, to whom only her back and head were exposed, while keeping up a steady volume of roars, growls, and staccato chuckles. Eventually she also took refuge in the bushes. Neither this hyena nor the next, which the dogs turned on its back and mauled for 2 minutes, bore any visible wounds. In fact, we have never known the dogs to kill or even seriously injure one. Either hyenas have exceedingly tough hides or else wild dogs are less in earnest about mobbing them than might appear.

Yet the degree to which hyenas are able to capitalize on wild-dog predation for their own benefit would justify a deep antagonism. They frequently drive away the last dogs on a kill unless the rest of the pack remains close by, and are quite capable of taking meat away from one or two dogs only a few yards removed from a kill where the rest are feeding. A more extraordinary example of this exploitation is the way hyenas take advantage of the wild dog's hunting technique: in the final moments of a chase, when only one or a few dogs are close to the quarry, hyenas have an opportunity to appropriate it before the rest of the pack arrives (Fig. 9). They attempted this with considerable regularity in the Crater, and we succeeded in recording one instance on film. In some cases it was a matter of chance that hyenas were near enough the scene of the capture to dash in at the decisive moment; in others up to three or four actually took part in the chase from the beginning. Though not as fast as the dogs, they were able to be in a position to intercept the quarry if it doubled back, or to grab it away from the dog(s) as soon as it was caught. When only two or three of them were on hand, the dogs hesitated to launch an immediate counterattack, particularly if more than one hyena was involved. But usually other pack members quickly appeared, joined together to mob the hyenas, and forced them to surrender the kill.

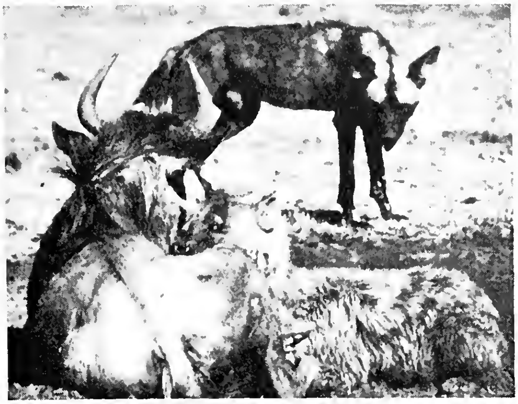
Fig. 9. Hyenas appropriate a wild dog prey and begin eating it alive, while one of two dogs that caught it looks on, panting heavily from the chase. Hyena in foreground is half-grown. As shown in Fig. 6, the dogs reclaimed their prey when the rest of the pack arrived.

But sometimes the dogs were defeated by sheer numbers. Once when the leader of the pack of 21 had pulled down a juvenile wildebeest in a hyena denning area, some 40 hyenas closed in on the kill before the others could gather. Apparently intimidated by so many competitors, the dogs revenged themselves by mobbing stragglers, punishing them savagely. Twenty minutes later, while they were ranging for new prey, the hyenas pulled down an adult female wildebeest on their own, quite near the first kill. Their clamor drew the dogs back to the scene. But they did nothing this time but look on—there were now 60 hyenas!

CONCLUSIONS

Pack Function

Hunting is undoubtedly the primary function of the free-ranging pack. Wild-dog behavior is highly specialized and adapted for pack life by dint of the equal and exceptionally friendly relations between individuals, subordination of individual to group activity, discipline during the chase, and close cooperation in killing prey and mutual defense. It may, in fact, be seriously questioned whether a single wild dog could survive for long on its own. As demonstrated by the successful rearing of a litter after the mother died, feeding and protection of the young is another important pack function. The main selective advantages of the pack hunting unit may be summarized as follows:

1. Increased probability of success through cooperation, hence better opportunity to eat regularly at less cost in individual effort
2. More efficient utilization of food resources
3. Less disturbance of prey populations than would result if each animal hunted individually
4. Mutual protection against competitors (spotted hyenas) and possible predators (hyena, leopard [*Panthera pardus*], and lion)
5. The provision of food for infants at the den and the adults that remain with them when the pack is hunting, and for juveniles and sick or old adults unable to kill for themselves.

Effective Pack Size

We have presented evidence, though admittedly tentative, that large packs utilize prey resources more efficiently than small packs, with less waste. Competition from hyenas, where they are numerous, must exert a strong selective pressure in favor of large packs as well as for close cooperation at kills. While the observed tendency for small packs to keep closer together in the chase and at kills would tend to compensate somewhat for low numbers, there must be a minimum below which competition from hyenas, and reduced hunting and killing capability, would become a serious handicap. From our observations of both large and small packs, four to six would seem close to the minimum effective unit.

We believe that wherever wild dogs are reduced to such small packs, their ability to survive and reproduce may be endangered. This is not taking into account the possibility of a differential birth or mortality rate that results in a low ratio of females. If it represents a pathological condition, this alone could mean that the species is in serious trouble; a prompt investigation of reproduction and neonatal mortality is called for to find out to what extent an abnormally low percentage of females may be responsible for the apparent decline of the species in many parts of Africa.

Prey Relations

It seems clear that wild dogs are highly selective in the species they prey upon, specializing in East African steppe–savanna on Thomson's gazelles, and on wildebeest calves during the gnu calving season. Considering their selectivity, their rate of killing, and the observed reactions of herbivores to them, it can only be concluded that wild dogs are by no means so wantonly destructive or disruptive to game as is commonly supposed. Kühme reached the same conclusion (p. 528). Indeed, until one comes to realize that plains game simply has no place to hide and no sanctuary where predators cannot follow, it is a recurrent surprise to note how short-lived and localized are disturbances due to predation.

In a prey population as small as that of Thomson's gazelles in Ngorongoro, if one assumes an average annual recruitment rate of roughly 10 percent, predation at the rate of only one a day obviously would reduce the population if maintained over a long period. There was, however, no evidence that the Thomson's gazelle population declined after wild dogs became resident in the Crater; our gazelle censuses in October, 1964, and May, 1965, showed no reduction that could not be accounted for by simple counting errors. Even an actual reduction would have no relevance to the overall situation, as Thomson's gazelles are the most numerous herbivores in their centers of distribution (the steppe–savanna from central Kenya to north-central Tanzania). On the Serengeti Plains, where the gazelle population is estimated at 800,000 and there are probably fewer than 500 wild dogs, predation by this species could have no appreciable effect. Indeed wild dogs are only one of nine predators on the Thomson's gazelle (Wright 1960), and not the most important one at that; jackals, which are numerous and specialize in catching new fawns, are probably the main predators.

Since wild dogs are nowhere numerous and everywhere apparently specialize on the most abundant small to medium-sized antelopes, it can be argued that more, not fewer, of them are needed. The population explosion of impala in Kruger National Park and many other places where wild dog numbers have declined offers convincing evidence. The high percentage of territorial males in wild dog kills of Thomson's gazelles offers a more subtle example of how predation may benefit a prey species: in probably every gregarious, territorial antelope species, there is always a surplus of fit, adult and young-adult males which cannot reproduce for want of enough suitable territories, so that the removal of territorial males by predation is of perhaps major importance in opening up territories for younger and sexually more vigorous males.

In our judgment, the wild dog is an interesting, valuable predator whose continued survival may be endangered. We feel it should be strictly protected by law in all African states where it occurs, and that it should be actively encouraged, if this is possible, in every park and game reserve.

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HOMING BEHAVIOR OF CHIPMUNKS IN CENTRAL NEW YORK

Homing movements ranging from about 150 to 700 yards have been recorded for *Tamias* by Seton (LIFE HISTORIES OF NORTHERN ANIMALS, vol. 1: 341, 1909), Allen (Bull. N. Y. State Mus., 314: 87, 1938), Burt (Misc. Publ. Mus. Zool. Univ. Mich., 45: 45, 1940), and Hamilton (AMERICAN MAMMALS, p. 283, 1939). While engaged in other studies during the summer of 1952, I had the opportunity of making additional observations on the homing behavior of the eastern chipmunk, *Tamias striatus lysieri* (Richardson), on the campus of Cornell University at Ithaca, Tompkins County, New York.

Live-trapping was conducted from July 26 to August 3 in a tract of approximately 3 acres of hemlock and mixed hardwood forest bordering a small artificial lake. A maximum of 12 traps was employed. The chipmunks taken were sexed, aged (subadult or adult), marked by clipping patches of fur on various parts of the body, and transported in a cloth bag to one of six release points. The latter were situated in similar continuous habitat or in an area of campus buildings, lawns, shrubbery, and widely spaced trees adjacent to the woodland. An individual was considered as having homed when it was retaken within 115 feet of the original point of capture. Those chipmunks that returned and were recaptured were immediately released again in a different direction and usually at a greater distance. First releases averaged 675 feet (310–1,160) and second ones, 1,015 feet (500–1,570). Two animals that returned after second removals were liberated for a third time at distances of 1,130 and 2,180 feet. All distances given are calculated from the station where the animal was originally trapped. Since the mean home range size of chipmunks in this vicinity has been calculated as about .28 acre (Yerger, Jour. Mamm., 34: 448–458, 1953), it is assumed that in most, if not all, instances the removal distances involved were great enough to place the animal in unfamiliar territory beyond the boundaries of its normal range of movements.

A total of 18 individuals, consisting of five adult males, four adult females, two subadult males and seven subadult females, were marked and released a total of 29 times through July 30. Animals handled after this date are not included in the treatment of the data, since it is felt that there was insufficient opportunity for them to be retaken following their release. Seven of the chipmunks returned to the vicinity of original capture a total of ten times over distances varying from 430 to 1,200 and averaging 650 feet. In six of the ten returns the animals were retaken in the same trap in which they were initially caught. In two instances individuals were retrapped at stations 20 and 40 feet removed from the one where first taken, and in two others the individuals were recovered at a distance of 115 feet from the original site of capture.

Two adult males returned from 490 and 540 feet in two and three days, respectively, but were not recovered after second removals to 1,060 and 1,150 feet. Two other mature males trapped following their release at 310 and 750 feet had moved in a direction other than that of their original capture. An adult female was found in a trap a day after having been released at 775 feet. She returned a second time from 600 feet in two days. Another adult female was retrapped at the original trap station seven days following her release only 430 feet away. A single subadult male was recaptured in his original location the next day after his initial removal to 750 feet and two days after a second liberation at 1,200 feet. He was not retrapped subsequent to a third relocation 2,180 feet distant. Another young male was captured at a point 380 feet closer to its home area six days after being released 940 feet away. Three subadult females homed successfully. One returned from 580 feet the day after release, another from 650 feet in two days' time, and the third from 490 feet after an interval of five days. None were retaken following second liberations ranging from 940 to 1,570 feet. Two other subadult females were captured 100 and 120 feet closer to their original capture sites the day after having been released at 460 and 450 feet, respectively.

These limited data suggest that homing ability was restricted to rather short distances, only one individual being known to have returned from a point more than 775 feet away. The extent of these movements may be somewhat less than several reported by authors previously mentioned. However, because of the smaller home range size of chipmunks in this area as compared to other habitats in which the animals homed from more distant points, the actual distances moved over strange territory may be fairly comparable. The present results indicate no obvious differences in the proportion of adults and subadults homing nor in the average distance over which individuals in each of these age classes returned. The intervals of one to seven days between releases and recoveries, the relatively short distances involved, and the rather low proportion of returns (38.8 per cent) suggest that the animals may have returned to their home areas through random movements until familiar terrain was encountered. It should be mentioned, however, that the small number of traps employed might have been a factor in the low rate of recovery, since a chipmunk returning to its home region had a lower probability of being recaptured than would have been the case had more traps been present. This might also have tended to increase the apparent time taken to reach the home area following release. On the other hand, the use of a limited number of traps may have been advantageous in that there was less interference by traps with the normal activities and movements of the animals.—JAMES N. LAYNE, *Dept. of Biology, Univ. of Florida, Gainesville.*
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COMPARATIVE ECHOLOCATION BY FISHING BATS

Roderick A. Suthers

Abstract.—The acoustic orientation of two species of fish-catching bats was studied as they negotiated a row of strings or fine wires extending across their flight path. Orientation sounds of *Pizonyx vivesi* consisted of a steep descending FM sweep lasting about 3 msec. *Noctilio leporinus* used 8 to 10 msec pulses composed of an initial nearly constant frequency portion followed by a descending frequency modulation. The echolocation of small wires by *N. leporinus* differed from that of surface fish in that during wire avoidance no nearly constant frequency or entirely FM pulses were emitted, nor was the pulse duration markedly shortened as the barrier was approached. There was extensive temporal overlap at the animal's ear of returning echoes with the emitted cries when the bat was near the barrier—a strong contrast to the apparent careful minimization of such overlap during feeding maneuvers. *Noctilio* increased its average pulse duration about 2 msec when confronted with a barrier of 0.21 mm, as opposed to 0.51 mm, diameter wires. *Pizonyx* detected these wires well before pulse-echo overlap began, but at a shorter range than did *N. leporinus*, suggesting the latter species may have a longer effective range of echolocation.

At least two species of Neotropical bats have independently evolved an ability to capture marine or aquatic organisms. A comparison of the acoustic orientation of these animals is of particular interest in view of their convergent feeding habits yet strikingly different orientation sounds. *Noctilio leporinus* Linnaeus (Noctilionidae) catches fish by occasionally dipping its disproportionately large feet into the water as it flies low over the surface. Very small surface disturbances can be echolocated and play an important role in determining the locations of the dips (Suthers, 1965). Fish caught in this way are transferred to the mouth and eaten. *Pizonyx vivesi* Menegaux (Vespertilionidae) also possesses disproportionately large feet. Much less is known concerning the feeding behavior of this species, though it is reasonable to assume that it uses its feet in a manner similar to *N. leporinus* (but see Reeder and Norris, 1954). Extensive attempts to induce captive *P. vivesi* to catch pieces of shrimp from the surface of a large pool were unsuccessful. The following comparison is therefore based on the ability of these bats to detect small obstacles.

Methods

The experimental animals consisted of two *P. vivesi*, selected as the best flyers of several collected in the Gulf of California, and one *N. leporinus* captured in Trinidad. The research was conducted at the William Beebe Memorial Tropical Research Station of the New York Zoological Society in Trinidad.

The bats were flown in a 4 × 15 m outdoor cage described elsewhere (Suthers, 1965). The test obstacles consisted of a row of strings or wires 2.5 m long which were hung at 55 cm intervals across the middle of the cage. Four sets of obstacles were used: 2 mm diameter strings, 0.51 mm, 0.21 mm, and 0.10 mm diameter wires, respectively. The bats were forced to pass through this barrier in order to fly the length of the cage. Each flight was scored as a *hit* or a *miss* according to whether any part of the animal touched the test obstacles. Movement of the larger wires was easily visible following even gentle contact, but lateral illumination of the barrier was necessary in order to score flights through the row of 0.10 mm wires. The wires were occasionally shifted laterally about 20 cm across the width of the cage in order to reduce the possibility that the bats might learn their location.

An attempt was made to test each animal on two or more sets of obstacles per night, though this was not always possible. Cases in which the bat was making unusually frequent landings or was particularly reluctant to fly are omitted. Also excluded are flights on which the barrier was approached very near the upper ends of the wires, along either wall of the cage, or at an angle to the row of obstacles which was decidedly smaller than 90°. Experiments with *P. vivesi* no. 1 were terminated by its sudden death, which occurred before the 0.10 mm diameter wire was available. Tests with this size wire were therefore performed with a second healthy *Pizonyx*.

A series of flights through the 0.51 mm and 0.21 mm diameter wires was photographed with a 16 mm sound motion picture camera, while simultaneous two-channel tape recordings of the orientation sounds were obtained from microphones placed on opposite sides of the barrier. The position of the flying bat relative to the barrier was calculated by comparing the arrival time of each orientation sound at either microphone and also by matching the image of the bat in each frame of the film with rectified orientation sounds on the optical sound track. Details of these methods and the instrumentation are described elsewhere (Suthers, 1965). The overall frequency response of the recording system was approximately uniform between 15 and 100 kc/sec.

A total of 45 flights by *P. vivesi* and *N. leporinus* was tape recorded and photographed. Sixteen of these were discarded for reasons listed above, or because the bat did not fly on a straight path between the microphones, or because of a poor signal-to-noise ratio on one of the channels. The remaining 29 flights were analyzed and pulse intervals (the silent period from the end of one pulse to the beginning of the next) were plotted against the distance of the bat from the barrier (see Fig. 2). The animal's position was determined to within an accuracy of about ± 10–15 cm at a distance of two meters from the wires and ± 5–10 cm in the immediate region of the wires.

RESULTS AND CONCLUSIONS

Obstacle avoidance scores are given in Table 1. The greater success of *P. vivesi* in avoiding 0.10 mm wires may reflect its shorter maximum wingspan of 40 cm, compared to 50 cm for *N. leporinus*. Audio monitoring of the rectified orientation sounds emitted by these species during their flights indicated

TABLE 1.—*Percent of flights through barrier on which bat missed obstacles spaced at 55 cm intervals. Total number of flights in parentheses. Maximum wingspan of* P. vivesi *is about 40 cm; that of* N. leporinus *is about 50 cm.*

	OBSTACLE DIAMETER (MM)			
Bat	2	0.51	0.21	0.10
Pizonyx vivesi (1)	94% (163)	83% (416)	51% (232)	
Pizonyx vivesi (2)		71% (151)		37% (74)
Noctilio leporinus	91% (207)	76% (203)	60% (217)	20% (55)

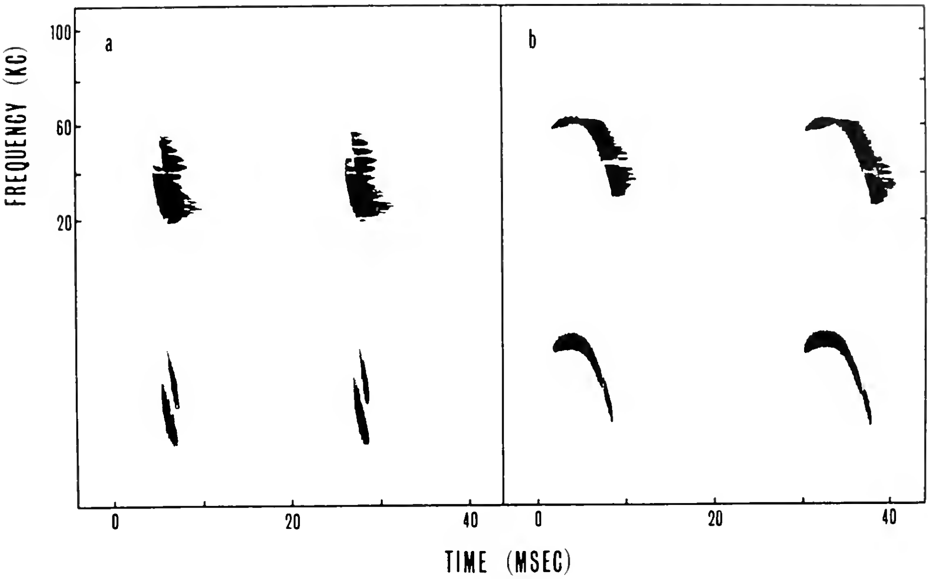

Fig. 1.—Sound spectrographs of orientation sounds emitted by *Pizonyx vivesi* (a) and *Noctilio leporinus* (b) when approaching wire obstacles. A pair of consecutive pulses, reproduced at two different filter settings of the sound spectrograph, is shown for each species. The narrow band filter setting (top) best indicates the frequency spectrum of the cries, whereas pulse duration and temporal relationships are more accurately shown using a wide band filter (bottom).

that approaches to the three larger diameter obstacles were accompanied by increases in the pulse repetition rate, whereas no such increase was noted during approaches to the 0.10 mm wires. This suggests that these latter wires were too small to be detected at an appreciable distance and that tests using them may indicate chance scores.

Tape recordings of flights between 0.51 and 0.21 mm diameter wires showed that these two species used distinctly different kinds of orientation sounds in detecting the obstacles (Fig. 1). When approaching the barrier at a distance of about 2 m, *P. vivesi* emitted ultrasonic pulses with a duration of about 3 msec at a mean repetition rate of 10 to 20 per sec. Each of these was frequency modulated (FM), sweeping downward from about 45 kc/sec to 20 kc/sec and accompanied by a second harmonic. The slightly lower starting frequency (36 kc/sec) reported by Griffin (1958) may be due to the lower sensitivity to high frequencies of microphones available at that time. At a similar distance from the barrier *N. leporinus* produced pulses with a duration of about 8 to 10 msec at comparable repetition rates. These sounds, however, were composed of an initial portion at a nearly constant frequency of about 60 kc/sec followed by an FM sweep down to 30 kc/sec. Neither species made any pronounced change in the frequency structure of its pulses as it approached and negotiated

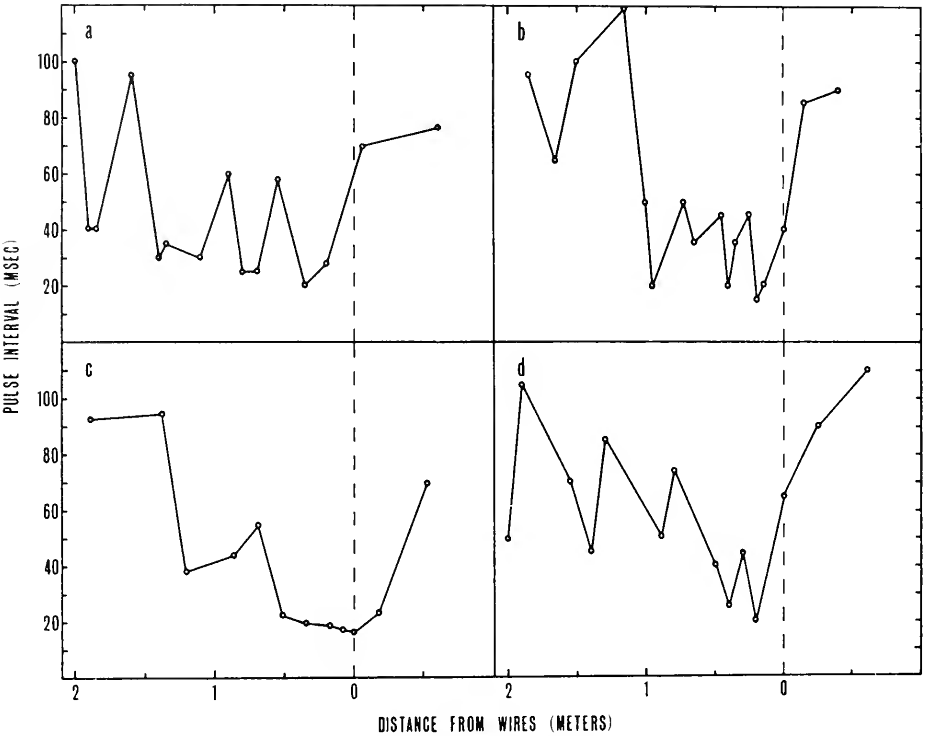

Fig. 2.—Examples of changes in orientation pulse intervals during flights by fishing bats through a barrier of fine wires spaced at 55 cm intervals across their flight path. Each dot represents one orientation sound: (a) *Noctilio leporinus* flying between 0.51 mm diameter wires; (b) *Pizonyx vivesi* flying between 0.51 mm diameter wires; (c) *N. leporinus* flying between 0.21 mm diameter wires; (d) *P. vivesi* flying between 0.21 mm diameter wires. On flights a, b, and d, the bat did not touch the wires. On the flight shown in c the wires were hit by the bat. Vertical dashed line indicates position of the wires.

the barrier. The pulse repetition rate was increased, however, to about 30 or 35 per sec. The use of a single pulse type by *N. leporinus* contrasts with its echolocation during normal cruising and feeding when constant frequency and entirely FM pulses are also employed (Suthers, 1965).

Fig. 2 gives examples of alterations in pulse intervals during one flight by each species through a barrier of 0.51 mm and of 0.21 mm diameter wires. The possible significance of the tendency to alternate long and short pulse intervals during the approach to the barrier is not known. It was not possible to reliably distinguish *hits* from *misses* on the basis of these graphs.

The minimum average distance of detection was estimated by calculating the point at which the bat began to shorten the pulse intervals. *Pizonyx vivesi* and *N. leporinus* must have detected the 0.51 mm wires at an average distance from the barrier of at least 110 and 150 cm, respectively, and the 0.21 mm

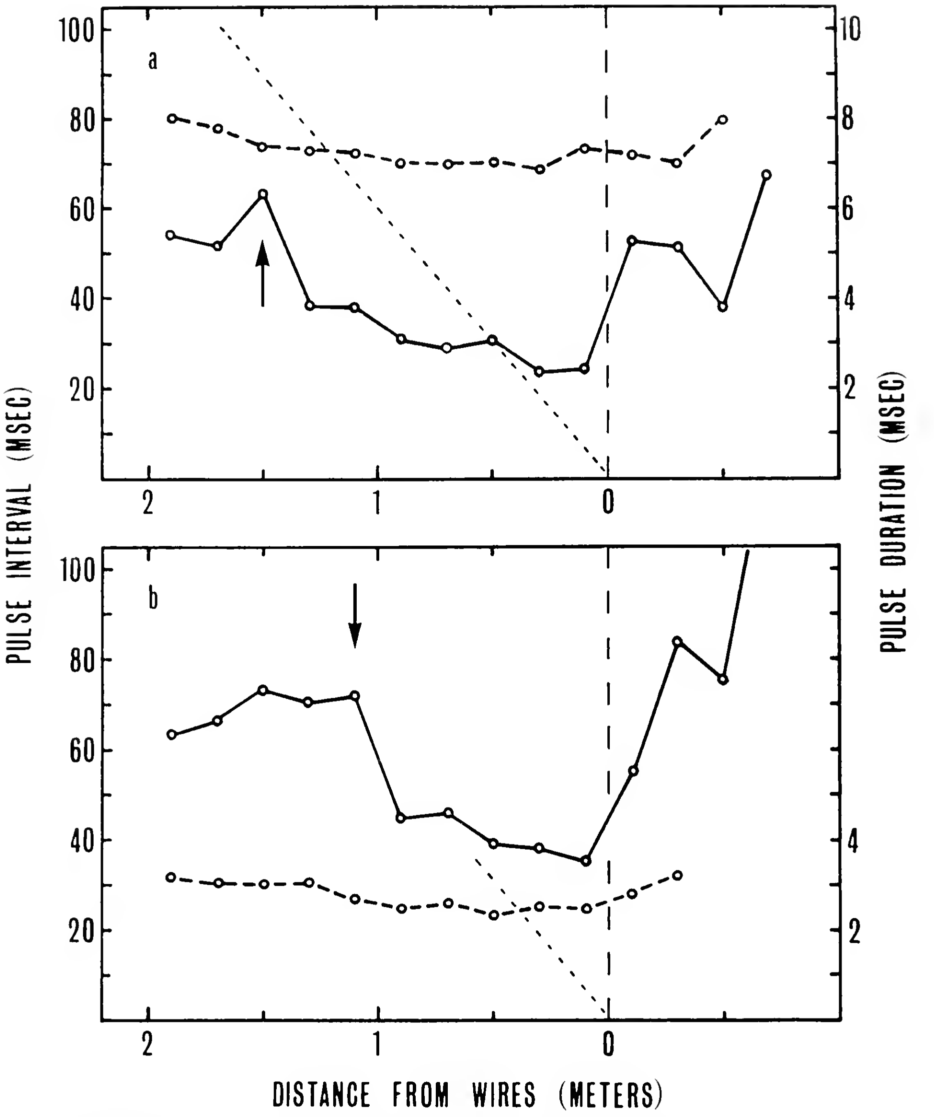

FIG. 3.—Mean pulse intervals (solid line) and mean pulse duration (broken line) of *Noctilio leporinus* (a) and *Pizonyx vivesi* (b) during approaches to the 0.51 mm diameter wires spaced across the flight path at 55 cm intervals. The bat is flying from left to right. Vertical dashed line indicates the position of the wires. Arrows indicate estimated minimum mean distance of detection as judged by progressive shortening of the pulse intervals. Dotted diagonal line shows the distance at which pulse-echo overlap will first occur for any given pulse duration. Echoes from the wires of pulses whose mean duration lies above this line will overlap with the emitted pulse by an average amount equal to their vertical distance above the line. Each point represents the mean interval or duration of pulses emitted in the adjacent ± 10 cm. Intervals for *N. leporinus* are averages of five flights; *P. vivesi* intervals, of seven flights. All pulse durations are averages of three flights.

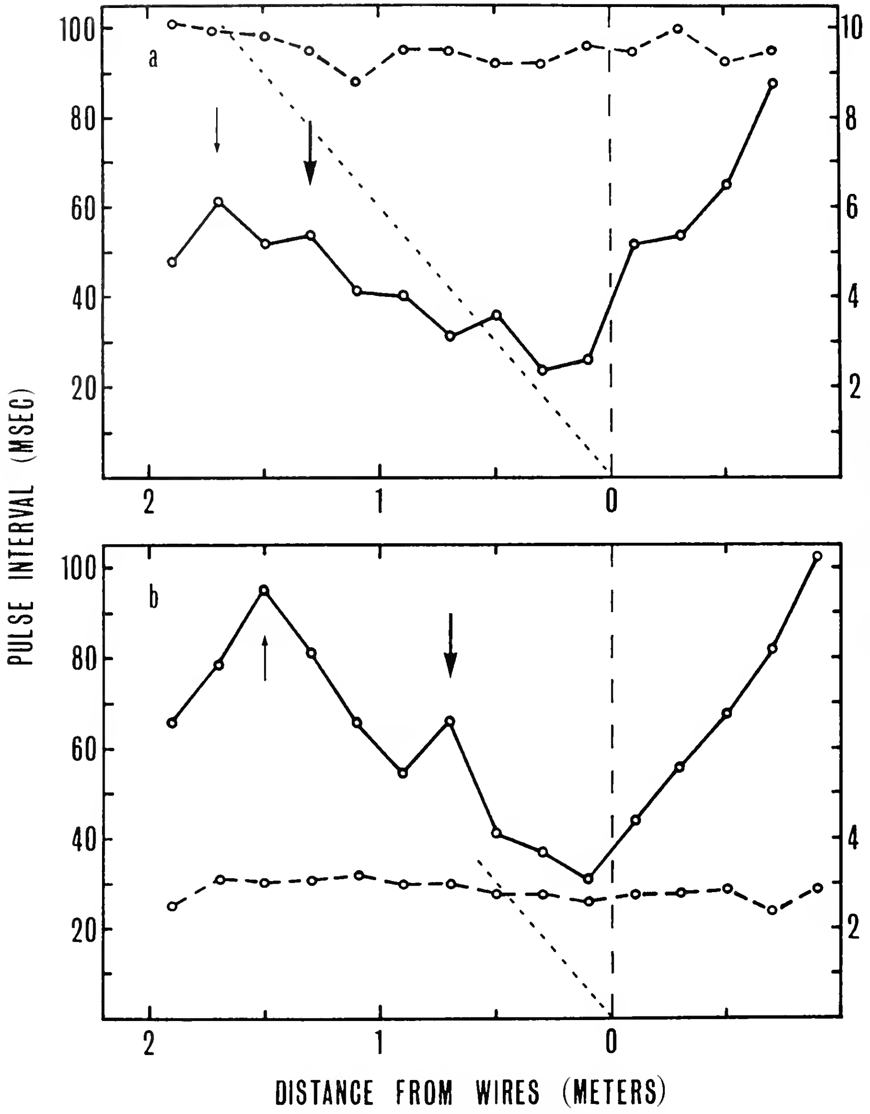

FIG. 4.—Mean pulse intervals (solid line) and mean pulse duration (broken line) of *Noctilio leporinus* (a) and *Pizonyx vivesi* (b) during approaches to the 0.21 mm diameter wires spaced across the flight path at 55 cm intervals. For explanation see legend of Fig. 3. Possible alternate interpretations of the point at which a progressive decrease in pulse intervals first appears are indicated by small arrows. The more conservative estimates denoted by the large arrows have been used in the text. Pulse durations and intervals of *N. leporinus* are averages of 10 flights; those of *P. vivesi* are averages of seven flights.

wires at an average of at least 70 and 130 cm, respectively (Figs. 3 and 4). Pulse durations did not markedly shorten as the barrier was approached. Thus at close ranges the echoes returning from the wires must have overlapped extensively with the emitted pulse. In the case of *N. leporinus* this overlap may have begun on the average when the bat was still 130 and 170 cm from the 0.51 and 0.21 mm wires, respectively (Figs. 3 and 4).

The data do not exclude the possibility that the start of pulse-echo overlap and the start of a progressive reduction in the pulse intervals by *N. leporinus* may occur simultaneously or be closely synchronized. The pulses of *P. vivesi* must have overlapped with their echoes during the last 40 and 50 cm of the approach to the 0.51 and 0.21 mm wires, respectively (Figs. 3 and 4). It seems clear that *P. vivesi* began to decrease its pulse intervals well before the first pulse-echo overlap occurred.

Noctilio leporinus regularly emitted longer pulses when approaching the 0.21 mm wires than when approaching the 0.51 mm wires. The significance of this difference is not known, although it is possible that the earlier initiation of pulse-echo overlap, or the increased duration of overlap at a given distance, when longer pulses are used, in some way facilitated detection of the finer wires. If this is true, however, why is overlap minimized with such apparent care during the detection of small cubes of fish muscle tissue projecting above the water surface (see below)? Since the difference in pulse duration as a function of wire diameter was already present when the bat was two meters from the barrier, either *leporinus* must have determined something about the wire diameter at a distance of more than two meters, or it must have remembered what kind of wires it had to detect and adopted a suitable pulse duration prior to their detection.

Details of the echolocation of *P. vivesi* during feeding are not known. Pulse-echo overlap during wire avoidance by *N. leporinus*, however, contrasts strongly with its apparent careful avoidance during catches of stationary 1 cm^2 cubes of fish muscle tissue projecting above the surface of the water. Pulse lengths under these conditions were progressively shortened as if to avoid pulse-echo overlap until the bat was 30 cm or less from the food (Suthers, 1965). Thus in the case of *N. leporinus*, at least, information concerning the position and nature of small wire obstacles is probably received in the presence of overlap, whereas most of this information regarding potential food must be obtained without such overlap. It has yet to be determined whether or not pulse-echo overlap is actually utilized by the bat.

It has been suggested (Pye, 1960; Kay, 1961) that possible nonlinearities in the ear may allow bats to utilize beat notes arising from pulse-echo overlap as a means of determining distance. Three species of chilonycterine bats have subsequently been found to maintain an overlap during the pursuit and catching of *Drosophila* (Novick, 1963, 1965; Novick and Vaisnys, 1964). *Myotis lucifugus* (Cahlander *et al.*, 1964) and *N. leporinus*, on the other hand, appear to minimize overlap when catching tossed mealworms or fish, respectively.

Should pulse-echo overlap be utilized by *N. leporinus* in determining its distance from the wires, then some basically different method, such as the temporal delay of the returning echo (Hartridge, 1945), must be employed in determining the range of potential food.

Since the constant frequency portion of the Doppler-shifted echo would at first overlap with the FM portion of the call, and later with part of both the constant frequency and FM portions of the call, any resulting beat note would have a complexly varying frequency structure from which it would be difficult for the bat to determine its distance from the barrier.

One would like to know if there is a significant difference in the range of echolocation for these fishing bats. *Noctilio leporinus* emits very loud pulses with a peak-to-peak sound pressure of up to 60 dynes/cm^2 at a distance of 50 cm from the mouth (Griffin and Novick, 1955). The intensity of sounds emitted by *P. vivesi* has not been measured, although the shorter range at which they can be detected on an ultrasonic receiver suggests they are less intense than those of *Noctilio*. *M. lucifugus*, a vespertilionid closely related to *Pizonyx*, can detect 0.46 mm diameter wires at 120 cm and 0.18 mm wires at 90 cm (Grinnell and Griffin, 1958), thus comparing favorably with fishing bats in this respect. Peak-to-peak sound pressures of this species have been measured at 12 dynes/cm^2 at 50 cm (Griffin, 1950). Sound intensity of the emitted pulse, however, is but one of a number of physical and physiological factors which must play important roles in determining the range of such a system for acoustic orientation.

Acknowledgments

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The Intraspecific Social Behavior of Some Cricetine Rodents of the Genus Peromyscus

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Abstract: A three-compartment territorial cage was employed in studying the intraspecific social behavior of *Peromyscus californicus*, *P. eremicus*, *P. crinitus*, and *P. maniculatus*. Two pairs of mice of the same species were allowed to interact for one week following a period of separation from each other in the end compartments. All species showed similar forms of agonistic behavior patterns. The closely related *P. eremicus* and *P. californicus* employed a modified fighting technique involving an attack leap, scuffle, and avoidance leap. The females of *P. crinitus* and *P. californicus* showed a pronounced nest site attachment and defense. Agonistic behavior with the exception of nest defense was confined almost entirely to the males. The aggressivity of *P. eremicus* was the least pronounced. *Peromyscus crinitus* males showed the most agonistic behavior, and *P. californicus* and *P. maniculatus* were intermediate. Pair associations in the territorial boxes were prolonged for *P. californicus* and, to a lesser extent, for *P. crinitus*. The other two species showed a weak pair bonding.

Introduction

In a previous paper (Eisenberg, 1962), the social behavior of *Peromyscus californicus parasiticus* and *P. maniculatus gambelii* was described and contrasted. In the present study the methods used were extended to *P. crinitus stephensi* and *P. eremicus eremicus*. Enough data now exist to present a comparison of all four species.

Peromyscus californicus and *P. eremicus* are closely related (Hooper, 1958) and are included in the Eremicus division of the genus *Peromyscus*. *Peromyscus crinitus* is considered by Hooper to be intermediate between *P. boylei* and *P. maniculatus*, all of which are included within the Maniculatus division.

The individuals of *P. californicus* and *P. maniculatus* used in this study were trapped in the vicinity of Berkeley, Alameda Co., California. They inhabit sympatrically the chaparral areas in west central California, and their ecology has been intensively studied by McCabe and Blanchard (1950).

Peromyscus eremicus and *P. crinitus* inhabit the arid Sonoran life zones of western North America. In general, *P. crinitus* occupies the Upper Sonoran high deserts while *P. eremicus* ranges in the Lower Sonoran zone. The individuals of *P. crinitus* used in this study were trapped in the vicinity of Cottonwood Springs, San Bernardino Co., California. The individuals of *P. eremicus* were all collected around 15 miles west of Borrego Springs in San Diego Co., California. These two species are sympatric over part of their ranges. In general, *P. crinitus* is a rock dweller while *P. eremicus* inhabits the brushy, flat areas of the desert floor. Both *P. californicus* and *P. eremicus* have smaller litters when compared with *P. maniculatus*, while *P. crinitus* has an intermediate average litter size. McCabe and Blanchard report average litter sizes of 1.91 and 5 for *P. californicus* and *P. maniculatus gambelii,* respectively. Hall gives an average litter size of 4 for *P. crinitus,* while Asdell records an average litter size of 3.7 for *P. eremicus.* The maturation and growth of *P. californicus* and *P. maniculatus gambelii* are analyzed in detail by McCabe and Blanchard (1950).

Acknowledgments.—I wish to express my gratitude to Drs. Peter Marler and Seth B. Benson for their valuable criticism of this work. Part of the research was conducted during the tenure of a National Science Foundation Pre-doctoral Fellowship.

METHODS

After the individual behavior patterns had been described for the various species, a series of encounters between two individuals of the sames species was run in order to obtain descriptions of the various postures and activities employed in the social context. Following these preliminary experiments a series of territorial encounters was arranged using two pairs of mice of the same species for each encounter. The territorial boxes were 9 x 26 x 75 inches in size with glass tops, sides, and fronts; the back was of quarter-inch hardware cloth, and the bottom of wood. Each box was divided into three equal compartments by wood partitions. A small opening, 2 x 1 inches, cut in each partition served as a door, and was closed with screen except at the time of experimentation. A pair of animals was placed in each end compartment with food, water, and cotton nesting material, and left for two weeks. The doors between the compartments were then opened and the subsequent behavior of the four individuals was noted for one hour. These observations were made at night using a red light for illumination. The doors were then left open for one week and daily observations at set intervals allowed me to ascertain in which compartment and with whom the animals were dwelling. The specimens were fur-clipped for identification. These experiments were run for all species during the spring, summer, and fall. Five experiments were run with *P. maniculatus* and *P. crinitus,* and six with *P. californicus* and *P. eremicus.* Each experiment was run with a different pair of animals.

AGONISTIC BEHAVIOR PATTERNS

A complete description of the adult behavior patterns for *P. californicus* and *P. maniculatus* is included in a previous publication (Eisenberg, 1962). The adult behavior of *P. eremicus* and *P. crinitus* is very similar. In the present paper only the agonistic patterns which appeared in the encounters will be discussed.

Fighting.—Two animals approach and one or both rush. The animals lock together with their ventral surfaces in contact and roll about, gripping one another very tightly with their fore and hind feet. This is called the *locked fighting* posture. It generally ends either by breaking apart followed by a chase-flight sequence, or when one

TABLE I.—Bouts of the different forms of agonistic behavior during six territorial encounters (*P. californicus*)

Type of encounter	Fighting Modified	Locked	Chase	Upright	Nest defense	Σ	Average/ Encounter
Male to Male	4	17	38	9	0	68	11.3
Male to Female	1	0	4	0	0	5	.8
Female to Male	0	1	5	3	10	19	3.2
Female to Female	0	0	1	1	0	2	.3
Σ	5	18	48	13	10	94	15.6

animal is forced on its back in a defeat posture. *Peromyscus californicus* and *P. eremicus* often employ a *modified fighting* technique where the animals spring at one another, scuffle briefly, and then jump away (cf. Jumping avoidance technique, Eisenberg, 1962).

Chasing.—This is usually confined to the floor of the cage, but small leaps may be employed. During chasing the pursuing animal may bite at the rump or tail of the subordinate.

Upright posturing.—Upright posturing was scored when an animal neither attacked nor fled, but raised its forepaws off the ground and with its body at about 45-90 degrees off the ground either darted its head at or extended its forepaws toward the aggressor. This posture can be broken down into several sub-patterns.

Nest defense.—The animal assumes a crouched upright in the nest and by warding with the forepaws or darting the head repulses the intruder. In *P. maniculatus* and *P. californicus* this movement is often accompanied by an explosive squeak or "chit." *Peromyscus crinitus* has a slightly different nest defense sound in that chits are uttered in bursts of 2 to 20 at a rate of 5-6 per second.

SPECIES COMPARISONS

Tables I through IV summarize the number of bouts of the five major agonistic patterns for each class of interaction (male to male; male to female; female to male; and female to female) for all four species. In general, after the doors were opened the males would

TABLE II.—Bouts of the different forms of agonistic behavior during six territorial encounters (*P. eremicus*)

Type of encounter	Fighting Modified	Locked	Chase	Upright	Nest defense	Σ	Average/ Encounter
Male to Male	12	2	31	1	0	46	7.7
Male to Female	1	0	9	0	0	10	1.7
Female to Male	1	0	4	2	1	8	1.3
Female to Female	2	1	4	0	0	7	1.2
Σ	16	3	48	3	1	71	11.9

TABLE III.—Bouts of the different forms of agonistic behavior during five territorial encounters (*P. maniculatus*)

Type of encounter	Fighting Modified	Fighting Locked	Chase	Upright	Nest defense	Σ	Average Encounter
Male to Male	0	20	24	11	2	57	11.4
Male to Female	0	1	6	3	0	10	2.0
Female to Male	0	0	0	3	2	5	1.0
Female to Female	0	1	0	0	0	1	.2
Σ	0	22	30	17	4	73	14.6

encounter one another and fight. After a variable number of fights the superior male would invade the nest chamber of the subordinate pair. The females were less prone to become involved in fighting, but females of *P. californicus* and *P. crinitus* engaged in a significant amount of nest defense. To a marked extent, males of *P. californicus* and *P. eremicus* employed the modified fighting technique of an attack leap, scuffle, and jumping away. *Peromyscus eremicus* males employed this pattern almost exclusively. *Peromyscus eremicus* showed the lowest number of male-male aggressive bouts per encounter (7.7): *P. californicus* and *P. maniculatus* were intermediate with 11.3 and 11.4 bouts per male-male encounter, respectively. *Peromyscus crinitus* was the highest with an average of 17.0 bouts per encounter. In all species, bouts of chasing comprised the greatest percentage of agonistic behavior. Agonistic behavior involving females was low except for *P. crinitus* and *P. californicus* where nest defense was shown.

By taking notes on the distribution of the animals in the encounter cages on the week following the opening of the doors, it was possible to determine how long a pair remained together and separate from the other pair. *Peromyscus californicus* has a strong tendency to remain paired and separate. *Peromyscus crinitus* exhibits this to a lesser extent and the other two species show a weak pair association. It appears that the pair association results in part from the strong nest defense tendencies by the females of *P. crinitus* and *P. californicus*. The male, whether the winner or loser of the first night's battles, is able to remain with his female while her nest defense mitigates against

TABLE IV.—Bouts of the different forms of agonistic behavior during five territorial encounters (*P. crinitus*)

Type of encounter	Fighting Modified	Fighting Locked	Chase	Upright	Nest defense	Σ	Average Encounter
Male to Male	2	27	50	5	1	85	17.0
Male to Female	0	3	18	0	1	22	4.4
Female to Male	0	..	1	6	36	43	8.6
Female to Female	0	..	1	0	2	3	.6
Σ	2	30	70	11	40	153	30.6

Table V.—Length of time the pairs remained together and separate from the other mice in the territorial experiments

Species	Number of experiments	Average number of days*
P. californicus	6	5.5
P. eremicus	6	1.0
P. crinitus	5	4.4
P. maniculatus	5	.8

* Maximum possible number of days — 7.

the integration of the group. In the experiments with *P. eremicus* and *P. maniculatus,* the winning male and both females generally nested together on the following day. The losing male was gradually assimilated after two or three days.

Table VI portrays the average number of days a pair or a single individual remained in its original nest during the week following the opening of the doors. *Peromyscus californicus* is again appreciably higher. *Peromyscus crinitus* does not demonstrate the same trend even though this species tends to preserve its pair structure. This is probably caused by the extreme aggressiveness of the superior male who displaces the inferior male and his mate. That *P. californicus* can maintain its original nest site may be in part a result of its ability to control the expression of aggressive behavior (Eisenberg, 1962). Although the male *P. californicus* fight readily, they do not persist with overt aggression but soon settle down to a dominance situation in the cage. The males never wound each other seriously by tail and rump bites, and *P. californicus* employs a special mewing cry to inhibit aggressive rushes by a conspecific. The other species seem not to be able to control their agonistic behavior so well. Since *P. eremicus* males fight so little, wounding during the subsequent week was minimal. In only one experiment did a male lose his tail from tail biting. However, *P. maniculatus* and *P. crinitus* males persisted throughout the week in their aggressive chasing and rump and tail biting. In three experiments with *P. crinitus* and two experiments

Table VI.—Consecutive days that a separate or paired animal remained in its original compartment

Species	Number of experiments	Average number of days*
P. californicus	6	5.5
P. eremicus	6	1.3
P. crinitus	5	2.8
P. maniculatus	5	2.0

* Maximum possible number of days — 7.

with *P. maniculatus*, the inferior males lost up to one-half their tails from persistent biting.

In the breeding cages where families of these mice were allowed to reproduce and live together, one could see a reflection of these aggressive trends. *Peromyscus crinitus* is quarrelsome and the females are intolerant during parturition. Serious wounds on the rumps or tails were of common occurrence with this species. *Peromyscus maniculatus* females are more tolerant during parturition and may allow the male to remain with them. However, male-male fights in the breeding cages often resulted in serious rump and tail wounds. *Peromyscus eremicus* females are tolerant and the males fight little among themselves, but at high densities in the breeding cages rump and tail wounds occasionally resulted from male-male and male-female antagonism.

Although *P. californicus* males will fight and the females defend their nests vigorously, the animals in the breeding cages formed stable adult groups with a minimum of wounding. A female would readily permit the male and mature litters to remain with her during parturition.

DISCUSSION

The four species seem to exemplify three types of social organization. *Peromyscus crinitus* seems to be a form having a dispersed social organization with a high male-male antagonism and with separate nesting by females with young. Adult social groupings are probably confined to brief pairings by males and females during the breeding season. This seems quite comparable to the situation exemplified by *P. leucopus* described by Nicholson (1941). *Peromyscus eremicus* and *P. maniculatus gambelii* seem to have a loose type of social structure. Pairing appears to be transient, but males, females, and litters may remain associated in nature for longer periods. This may be comparable to the situation described by Howard (1948) for *P. maniculatus bairdii.*

Peromyscus californicus with its low reproductive potential builds and defends a complex nest and occupies a given area for rather prolonged periods of time (McCabe and Blanchard, 1950). This species may have a prolonged pair bond and if the male and female do not actually nest together through parturition, a male remains in the vicinity of a given female and the litter for several months. This species appears to be developing a social system based on small semipermanent family groups. The ecology of *P. eremicus* and *P. crinitus* is too little known to attempt a correlation between the mode of environmental exploitation and the form of their social organization. *Peromyscus californicus* has probably evolved its tolerance abilities and family formation as a concomitant of its lower reproductive potential and its rather restricted mode of habitat exploitation.

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ETHOLOGICAL ISOLATION IN THE CENOSPECIES *PEROMYSCUS LEUCOPUS*

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Peromyscus leucopus and *P. gossypinus*, constituting the cenospecies *Peromyscus leucopus*, have diverged genetically so that they have different morphological and adaptive norms. Genetic isolation, however, is apparently not complete because interspecific hybridization may occur (Dice, 1937; McCarley, 1954a). The present paper is a report of an ethological mechanism that helps maintain the genetic distinctness of the two species.

Previous studies by Dice (1940), Calhoun (1941), and McCarley (1954b, 1963) showed that *leucopus* and *gossypinus* were generally ecologically separated in areas of sympatric distribution: *leucopus* in upland woods and *gossypinus* in lowland woods. Overlapping frequently occurs, however, during the winter and spring reproductive seasons (McCarley, 1963). Consequently, ecological separation alone would not be adequate to account for the few recorded examples of natural interspecific hybrids in this cenospecies (Howell, 1921; McCarley, 1954a).

Work done by McCarley (1953) and Bradshaw (1957) using the procedures of Blair and Howard (1944) suggested that continued species separation of *leucopus* and *gossypinus* may, in part, depend on ethological, or species discrimination mechanisms. Experiments were begun in 1959 using techniques modified from the procedures of Blair and Howard (1944). These tests utilized three individuals, one male and two females or one female and two males. If males were to be tested, a male was placed in one of the two middle compartments of a four-compartmented cage and was free to move between these two compartments. A *leucopus* female was confined to one end compartment and a *gossypinus* female to the other end compartment. A reciprocal arrangement of mice was used when females were tested. Each combination of three mice was observed daily, usually early in the morning, for not less than 5 nor more than 11 days. Observations were discontinued randomly. If the mouse being tested was observed nesting next to the mouse of its own species, it was recorded as a positive observation, otherwise as a negative observation. Only mice in breeding condition were used. Sympatric mice were from Leon County, Texas. Allopatric *leucopus* were from Bryan and Tillman counties, Oklahoma; allopatric *gossypinus* were from Nacogdoches County, Texas.

The results of these association experiments are summarized in table 1. Sympatric *leucopus* females and *gossypinus* males and females demonstrated a significant positive association with members of their own species of the opposite sex. Sympatric *leucopus* males associated with females of their own species more frequently than with *gossypinus* females but the deviation from the expected was insufficient to produce a significant χ^2 value. Table 1 also presents the results of tests utilizing allopatric stocks of *leucopus* and *gossypinus*. Allopatric mice, in this instance, did not associate with members of their own species significantly more often than with members of the other species. (In the case of allopatric *leucopus* females, five of the six tested showed a preference for individuals of the opposite species.) This suggests that existing isolating mechanisms are being reinforced (Koopman, 1950) in sympatric areas.

McCarley (1963) pointed out that in areas where *leucopus* and *gossypinus* are sympatric, the general restriction of *leucopus* to upland habitats (as opposed to the situation in allopatric

TABLE 1. *Results of discrimination tests using three mice in a four-compartmented cage*

	No. of tests	No. of individuals tested	Positive observations	Negative observations	χ^2 values
Sympatric *leucopus* males	36	19	113	78	3.010
Sympatric *leucopus* females	34	16	330	65	88.000
Sympatric *gossypinus* males	54	18	233	126	15.605
Sympatric *gossypinus* females	20	12	126	46	18.604
Allopatric *leucopus* males	14	7	69	36	4.830
Allopatric *leucopus* females	9	6	25	69	10.297
Allopatric *gossypinus* males	20	10	81	52	2.925
Allopatric *gossypinus* females	12	5	54	64	0.423

areas where *leucopus* occupies both uplands and lowlands) was the result of the presence of *gossypinus* in lowlands. The presence of an ethological mechanism in the form of species discrimination would support this hypothesis.

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ACTIVITY, FOOD CONSUMPTION AND HOARDING IN HIBERNATORS

By Charles P. Lyman

In previous papers it has been emphasized that the phenomenon of hibernation is not precisely the same among all mammals and differs even among various families of rodents. For example, the electroencephalograms of "le spermophile" (probably *Citellus citellus*) and the woodchuck (*Marmota monax*) differ markedly in hibernation and during the process of arousal from that of the golden hamster (*Mesocricetus auratus*) (Kayser, Rohmer and Hiebel, 1951; Chatfield, Lyman and Purpura, 1951; Lyman and Chatfield, 1953). The relatively active electroencephalograms of the deeply hibernating ground squirrel and woodchuck reflect the behavior of these species, for they respond to strong stimuli with uncoordinated muscular movements. The deeply hibernating hamster, on the other hand, is totally inert until the process of arousal is well under way.

Another important difference concerns the nutritional requirements during the hibernating period. Most rodents that hibernate, including the woodchuck and the ground squirrel, become extremely fat before the period of dormancy and apparently live on this fat during hibernation (Kayser, 1950). In contrast, the golden hamster, at least in the laboratory, loses weight when exposed to cold and actually enters hibernation when quite lean (Lyman, 1948). Although *Citellus* *tridecemlineatus* (Howell, 1938) and many other hibernators store some food, storage appears to be of paramount importance in the hamster, for it eats during its periodic arousals from the hibernating state and apparently cannot live throughout the hibernating period if there is no food available (Lyman and Leduc, 1953).

The experiments described below were designed to clarify these differences. The food and water intake and the activity of a series of hamsters and ground squirrels were measured when the animals were kept in a warm environment and compared with the same measurements when the animals were exposed to cold and when they hibernated.

During the course of the experiments it became apparent that hamsters which were denied food for storage did not hibernate as soon as control animals. Therefore, a second experiment was designed to elucidate this point.

MATERIALS AND METHODS

Experiment 1.—A series of nine male hamsters (*Mesocricetus auratus*) between 15 and 20 weeks of age was housed in activity cages equipped with exercise wheels. The rotating wheel of each cage was 36 cm. in diameter and 11.5 cm. wide, and the resting cage measured 38 cm. long by 23 cm. deep by 23 cm. high. The animals were fed ground Purina chow from non-spillable food cups, and water was supplied from non-spillable water containers. Food and water intake and the number of revolutions of the activity wheel were usually measured each day. If very small amounts of water were consumed daily, allowance was made for evaporation from the water container.

The animals were maintained under these conditions for five to nine weeks in the fall of the year in an animal stock room. The environmental temperature was 24 ± 2°C. and the animals were exposed to between eight and nine hours of light daily. At the end of this period the hamsters were moved into a cold room maintained at 5° ± 2°C., which was illuminated daily for eight hours. The measurements were continued under these conditions.

A second series of two female hamsters of 15 weeks of age and two female ground squirrels (*Citellus tridecemlineatus*) over three years of age was housed in individual cages of the same size as the previous experiment. The cages were suspended from springs, and balanced from below by a tambour at each corner. Any major movement of the animal in the cage depressed one or more of the tambours. This was recorded pneumatically by means of a tambour and a stylus on a slowly revolving smoked chart. Food and water intake were measured as in the first experiment, and the animals were exposed to the same environmental conditions. In all experiments, when an animal was observed to be hibernating, a small amount of fine shavings was placed on its back so that, if it moved enough to displace the shavings, this could be noted at the next observation.

Experiment 2.—In order to test the effect of hoarding on hibernation a series of six male and six female hamsters, 15 weeks old, was housed in individual cages supplied with ample shavings in the cold room (5° ± 2°C.). They were fed water *ad libitum* and ground Purina Chow in non-spillable food containers.

Under these conditions the animals were unable to store food, as is their invariable custom if supplied with pellets of compressed food. These animals were observed daily and the day on which they first hiberated was noted.

To provide a controlled comparison with the experimental animals, the records of 373 animals that had been observed during the last few years in this laboratory were used. The use of this large number of animals was employed because it sheds some light on the variations encountered in a large group of animals. These hamsters were housed under conditions identical with the experimental animals in the cold except that they were fed Purina laboratory chow checkers and hence could store their food.

RESULTS

The nine hamsters in the wheel-type activity cages consumed, in the warm room, an average of 7.8 gms. (Standard Deviation 1.7) of Purina Chow each day. Omitting one animal that spilled water in spite of all precautions, the water consumption averaged 11.1 cc. (S.D. 1.2) per day. The animals averaged 7335 revolutions (S.D. 1834) of the wheel each 24 hours. It was apparent that most of the activity took place at night, whether the animals had an exercise wheel or whether the motion of the cage was recorded. There was no clear evidence of regular periodic activity other than the diurnal cycle.

When moved to the cold room, the food intake of the hamsters invariably rose and averaged 12.9 gms. (S.D. 2.3). This rise is statistically highly significant according to the "t" test, for P is less than .01. The water intake rose to 16.3 cc. (S.D. 4.7) per day. This rise is also highly significant in spite of the fact that one animal showed a slight decrease in water intake (from 11.3 to 10.5 cc./day). The hamsters were no more active in the cold than in the warm room as measured by the activity wheels, averaging 7141 revolutions (S.D. 3029) per day. Furthermore, there was no evidence in the tambour records that the animals moved about in their cages to a greater extent when exposed to cold.

Although most of the hamsters provided with activity wheels were kept in the cold room for over a year, only one animal hibernated on and off for 54 days after being in the cold for 44 days. During this period it was observed to be awake on 21 different days and the longest period of continuous hibernation was three days. In contrast, the average period of hibernation, punctuated by brief waking periods, for 19 typical controls was 95.1 days (S.D. 21.7). Furthermore, most hamsters remain continually in the hibernating state for protracted periods, the longest recorded in this laboratory being 21 days.

There was no diminution of exercise or food and water intake in the days just prior to entering the hibernating state. On each awakening the animal ate, drank and ran on the exercise wheel. Considering only the 21 days that the animal was awake, it averaged 4207 revolutions of the wheel, 12.7 gms. of food, and 25 cc. of water per day. This animal averaged 11,646 revolutions of the wheel, 14.8 gms. of food and 21.9 cc. of water per day in the cold room before entering hibernation.

One of the hamsters maintained in the tambour-recording cages hibernated after only 11 days exposure to cold, but the total hibernating period lasted only 18 days during ten days of which the animal was observed to be awake. The period in the cold room before hibernation took place was too short to give a reliable figure, but the food intake increased and the water intake decreased during the 11 days. There was no evidence that food and water intake or exercise decreased in the last few days just prior to hibernation. In the ten days the animal was awake during the hibernating period it averaged 8.4 gms. of food and 10 cc. of water per day. This compares with 8.1 gms. of food and 5.1 cc. of water per day in the eleven days before hibernation.

The hamster in the other tambour-recording cage adopted a peculiar storing habit which spoiled the records of food intake and caused the abandonment of records on this animal, but also led to Experiment 2 of this series. This hamster was able to obtain food from the unspillable food cup by forcing its muzzle into the ground dog chow. Upon lifting its head from the food cup, it removed the crumbs clinging to its vibrissae with its fore paws and transferred them to its cheek pouches. After it had obtained a satisfactory amount of food in this way, it carried it to a far corner of the cage and stored it in the manner observed in hamsters fed solid pellets of food. This animal hibernated on the 72nd day after exposure to cold.

Ground Squirrels.—In the 62 days of observation prior to exposure to cold, ground squirrel no. 1 averaged 7.0 gms. of food per day and 12.2 cc. of water. During this period its weight dropped from 266 gms. to 237 gms. Ground squirrel no. 2 averaged 10.9 gms. of food per day and 22.5 cc. of water, and its weight dropped only from 275 to 267 gms. Both animals were very fat at the start of the experiment.

In sharp contrast to the hamsters, the two ground squirrels hibernated within 24 hours after being exposed to cold. Ground squirrel no. 1 hibernated over a period of 62 days, at the end of which time the animal was moved to the warm room because of its emaciated condition. Of the 62 days, it was observed to have moved enough to displace the shavings on its back on 14 days and was active enough to cause movement of the cage for a total period of 171 hours, or 12 per cent of the time. During the time it was awake it ate a total of 16 gms. of food and drank 87 cc. of water. It lost 111 gms. body weight during the 62 days of the sojourn in the cold.

Ground squirrel no. 2 hibernated over a period of 120 days after which it was moved to the warm room. During this period it was observed to have lost the shavings from its back on 23 days and was active enough to move the cage for a total of 225 hours or 8 per cent of the time. During the time it was awake it ate a total of 6 gms. of food and drank no water. It lost 130 gms. body weight during the 120 days.

Storing Experiment.—The twelve hamsters that were moved to the cold room but not allowed to store food hibernated after an average period of 97.6 days (S.D. 20.4). The earliest hibernation occurred on the 54th day and the latest on the 114th day. The average time before entering hibernation was approximately the same for both sexes. Once in the hibernating state, the animals remained in this condition, with the usual periodic awakening, for a period of about three months. Thus the length of the hibernating period, once started, was not curtailed.

Of the 252 control animals that entered hibernation the average time before the hibernating state occurred was 56.6 days (S.D. 33.2). The shortest period before hibernation occurred after moving to the cold room was three days and the longest was 218 days. On the other hand, 121 animals of the control groups died before entering the hibernating state. The average time when death occurred after moving to the cold room was 71.5 days (S.D. 67.2).

In a statistical comparison between the time of onset of hibernation in the 12 hamsters deprived of storing and the 252 controls that hibernated, P is less than .01. This highly significant difference shows that the ability to store food has a profound effect on the occurrence of hibernation. On the other hand, the data on the other 121 control animals show that in a large population of hamsters in the laboratory, some animals will live in the cold and eventually die without entering hibernation. Therefore it may be more accurate to include the animals that died in the cold with the other control animals. If the total span of life in the cold of these animals is averaged with the total time in the cold before hibernation in other controls, one obtains a figure of 61.4 days (S.D. 47.4). When this figure is compared with the 97.6 days for the experimental animals the difference between the two figures is still found to be highly significant according to the Fisher "t" test ($P < .01$). In other words, the possibility that the marked delay in the onset of hibernation in the non-storing hamsters is due to chance is less than one in 100.

DISCUSSION

The increased food and water intake of hamsters when exposed to cold is typical of mammals that do not hibernate, and is to be expected with the increase of metabolic rate. That the metabolic rate does increase in hamsters when exposed to cold can be seen by comparing the figure 1014 cc. O_2/K/hr. for golden hamsters at 29.6° (Kayser, 1940) or 930 cc. O_2/K/hr. at 30–34°C. (Adolph and Lawrow, 1951) with 2877 cc. O_2/K/hr. at 5°C. (Lyman, 1948). These reactions are in sharp contrast to the almost immediate hibernation and cessation of eating and drinking that took place when the two ground squirrels were exposed to cold. Although ground squirrels do not invariably hibernate within 24 hours after exposure to cold, as Johnson (1930) has amply demonstrated, still the onset of hibernation is usually quite rapid. On the other hand, of the more than 1000 hamsters exposed to cold in this laboratory, the shortest recorded time before hibernation occurred was three days, with most animals far exceeding this figure.

The hibernating phase of the two hamsters recorded here cannot be regarded as typical, because the period was curtailed and the animals awoke more often than is normal. However all indications are that golden hamsters keep up high food and water intake and remain active up to the time they hibernate. Furthermore, the data emphasize that the hamsters will consume considerable nourishment each time they wake from hibernation. Although observations in the wild on the golden hamster are lacking, the European hamster is known to be an inveterate hoarder of food, so much so that the German word "hamster" means to hoard or store in anticipation of need. It is highly probable that hamsters do not have access to water when they are holed up for the winter, and it is reasonable to suspect that metabolic water and water from the stored food are their only sources. The data indicate, however, that the animals will drink a considerable quantity if water is available.

The second experiment demonstrates clearly that the ability to store food has a profound effect on the time of onset of hibernation. Waddell (1951) has shown that noxious conditions such as illuminating the food bin will increase the storage of food by hamsters, and McCleary and Morgan (1946) have demonstrated similar reactions in the rat when it is exposed to cold. The denial of the ability to hoard when stimulated to do so by cold must upset the behavioral pattern of the animal so that the onset of hibernation is delayed, or, in the case of one animal in the cage on tambours, the period of hibernation abnormally shortened. This takes place in spite of the fact that there is obviously ample food obtainable at all times from the food containers.

Again in contrast to the hamsters, the ground squirrels hardly touched food or water while they were exposed to cold and the fast is reflected in the great loss of body weight. This loss of weight bears out the recent work of Kayser (1952) with the European ground squirrel (*Citellus citellus*). He was able to show that the large weight losses observed in animals during the hibernating period were not due to loss of weight during hibernation, but were directly correlated with the amount of time the animals were awake during that period, for the process of arousal and the awake condition consumed a great deal of energy. Thus in ground squirrel no. 1, which was awake a much larger proportion of the time, the weight loss was much faster (1.8 gms./day) than in ground squirrel no. 2 (1.1 gms./day).

Although laboratory experiments can not completely clarify the conditions that occur in the wild, it seems justifiable to draw from these results a sharp distinction between the preparation for hibernation in animals such as the ground squirrel on the one hand, and the hamster on the other. Under stimuli which have yet to be elucidated, the former animals grow extremely fat in the period previous to hibernation. Exposure to cold is then apt to cause almost immediate hiberation. If hibernation does not occur at once, denial of food will hasten it (Johnson, 1930, confirmed in these laboratories). Although the ground squirrel stores food (Howell, 1938), it is apparent that it can survive repeated awakenings with practically no nourishment by utilizing its stored fat. From all indications the woodchuck (*Marmota monax*) is very similar to the ground squirrel, for it becomes extremely obese by fall, and does not even store food in its burrow (Merriam, 1884).

The hamster, on the other hand, apparently makes no physiological preparation for hibernation until actually exposed to cold. Under the stimulus of cold exposure, it stores food and loses weight. If food storage is denied, hibernation is delayed. Food storage is essential for the maintenance of the hamster during the hibernating period, for the energy necessary for the periodic awakening is soon exhausted if the stored food is removed and the animal cannot eat during the periods of activity (Lyman and Leduc, 1953). Unpublished experiments in these laboratories have conclusively shown that, in contrast to the ground squirrel, denial of food or water will never cause hibernation in the hamster, which is precisely what might be expected in view of the importance of stored food. Thus the golden hamster is provided with a check against hibernation before food has been stored, which, under natural conditions, must protect the animal against starvation during the hibernating period.

How the lack of food hoarding can delay hibernation is a problem in itself. Indications are that it is not the only psychic factor which can influence the onset of hibernation, for of the nine animals with activity wheels only one hibernated for a very short period, though all were exposed to cold for over a year. Possibly exercise on activity wheels itself may have an effect on the onset of hibernation. In any event, it is evident that a behavior pattern such as storing can have a profound effect on the onset of hibernation in the hamster. That behavior must be considered along with all the physiological factors when attempting to resolve the cause of hibernation certainly compounds the complexity of the problem.

SUMMARY

In a series of experiments with golden hamsters (*Mesocricetus auratus*) and thirteen-lined ground squirrels (*Citellus tridecemlineatus*) it was found that the former animals did not hibernate at once, but increased their food and water intake when moved to a cold environment, while the amount of exercise taken remained unchanged. In the two hamsters that eventually hibernated there was no decrease of eating, drinking or exercise up to the time of hibernation. The hamsters ate and drank considerable quantities and exercised to some extent on each awakening from hibernation. Hamsters that were prevented from hoarding food showed a marked delay in entering hibernation.

In contrast, the ground squirrels hibernated within 24 hours after exposure to cold. In their periodic wakenings the ground squirrels ate and drank almost nothing and in consequence lost much of their stored fat.

It is concluded that the ground squirrel is stimulated in some unknown way to prepare for hibernation by becoming extremely obese. Exposure to cold brings on hibernation quickly and the animal lives almost exclusively on his stored fat during the hibernating period. The golden hamster, on the other hand, does not fatten prior to hibernation, but is stimulated by cold to store food. This food is used during the periodic arousals in the hibernating period, and without the store the animal would perish. Denial of the ability to hoard causes a delay in the onset of hibernation and thus must provide the animal with a check against premature hibernation that would result in starvation.

Acknowledgement.—This research was supported by a grant under U. S. Air Force Contract AF 33 (038)-18133.

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RADIO TRANSMITTER-COLLARS FOR SQUIRRELS[1]

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Abstract: An adjustable plastic transmitter-collar suitable for the gray squirrel (*Sciurus carolinensis*) and fox squirrel (*Sciurus niger*) was developed. It can be attached at the trap site within 5 min. Placed on 23 squirrels, the transmitter-collar permitted 35–45 days of radio-tracking data to be obtained from each squirrel.

Transmitter-collars have been used successfully on rabbits, hares, and raccoons (Mech et al. 1965). This paper describes a transmitter-collar which was found satisfactory for use on the gray squirrel and fox squirrel. The author believes that this same type of apparatus can be attached to other mammals.

The electronic components for a squirrel transmitter-collar were mounted on a self-locking, 11-inch adjustable plastic hospital ID bracelet (purchased from Aloe, 1831 Olive St., St. Louis, Missouri). The components were then waterproofed with synthetic latex rubber and wrapped with a layer of plastic tape (Fig. 1).

The antenna loop was made the same size on each transmitter-collar; its circumference was measured for a snug fit over the head of the largest anticipated squirrel. The plastic bracelet, not the antenna loop, is the adjustable component of the collar (Fig. 1).

Average weight of the completed transmitter-collars was 0.75 oz. The transmitter battery life averaged 35–45 days, with a range of ¾ to 1¼ miles, as determined by the Drake 2-B receiver and two Hy-Gain 5-element beams.

The behavior of a penned gray squirrel with a transmitter-collar attached during a 2-month observation period appeared normal. The squirrel ate regularly and moved without hindrance. At the end of the test period, the squirrel was in good physical condition and the neck hair was not worn.

In the wild, squirrels were livetrapped in a wooden box trap, and removed from the trap with heavy leather gloves. The activated transmitter-collar was slipped over the head of the squirrel, adjusted to the correct fitting, permanently snap-locked, and the loose end of the collar cut off. The squirrel was ear-tagged and then released. This entire procedure was performed at the trap site by two workers, and required 5 minutes or less.

Between February, 1964, and August, 1966, transmitter-collars were attached to 23 squirrels (6 adult gray males, 11 adult gray females, 4 adult fox males, 1 adult fox female, and 1 juvenile fox male). In 15 cases squirrels were recovered with the transmitter-collar attached. In all but one

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[1] A contribution from Ohio P.-R. Project W-105-R.

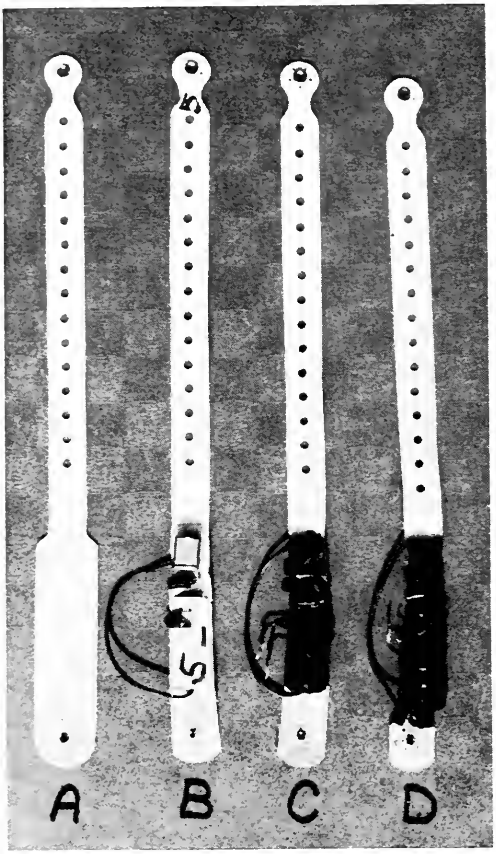

Fig. 1. Construction sequence of transmitter on adjustable plastic hospital ID bracelet.

case, the squirrels appeared in good physical condition. The one exception was an adult male fox squirrel which was retrapped after 1 month of radio-tracking. Its neck had a deep cut, possibly caused by the edge of the collar. The transmitter-collar was removed and the squirrel released. The animal was retrapped 4 months later and a transmitter-collar was attached after examination showed that the neck had completely healed.

There is evidence that the plastic bracelet will break and free the transmitter after the duration of battery life. A gray squirrel was trapped in May, 1965, tagged and released. In August, 1965, this animal was retrapped without the transmitter-collar. Examination of several recovered collars showed that they were brittle after being worn for a month or more.

In three instances collars were chewed, presumably by another squirrel. However, this did not appear to be a serious problem.

The transmitter-collar described meets the requirements for continued study by radio telemetry of squirrel behavior in southeastern Ohio forests.

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SECTION 5—PALEONTOLOGY AND EVOLUTION

If there be one unifying principle that pervades all of biology, it is that of evolution. Not only is this evident in consideration of the papers here reproduced (which range from one that deals in part with intrapopulational variation up to those concerned with higher taxonomic categories), but it also is evident in the contents of virtually all other papers chosen for inclusion in this anthology. The few selections in this section, then, provide but a glance at some aspects of mammalian evolution.

Linked inseparably with the evolutionary process is the fossil record, which is unusually good for some groups of mammals and provides much of the raw data for phylogenetic considerations. For papers relating to paleontology, we have chosen one on a local fauna (Hibbard), one (Wilson) that alludes to the importance of sound geographic and stratigraphic data and that ties in with the historic record, one (Radinsky) that deals with evolution and early radiation of perissodactyls, and two on rodents, one a classic early paper by Miller and Gidley in which the major groups of that extremely complex order are outlined, and the other a modern treatment of the same problem by Wood (see also Wood, 1959). The study by Guthrie compares evolutionary change in molar teeth, using both fossil and Recent species of *Microtus*, and thus stresses the on-going evolutionary process. The short paper by Reed clearly presents an interesting problem arising from attempts to classify some early relatives of man.

The essay by Durrant and Hansen places biogeography in the evolutionary framework. Some of the species of ground squirrels mentioned by them are treated also in the serum protein analysis of Nadler and Hughes included in Section 1. The paper by Jansky is interesting because it provides an excellent example of evolutionary trends in features other than those directly related to "hard anatomy."

The literature of mammalian evolutionary and paleontological studies is widely scattered. Aside from the journals and bibliographic sources mentioned in the Introduction, the interested student should consult EVOLUTION, a quarterly journal published by the Society for the Study of Evolution, and the JOURNAL OF PALEONTOLOGY. He should also be aware of the *Bibliography of Fossil Vertebrates, 1959-1963,* compiled by Camp *et al.* (as well as earlier volumes in the same series) and the News Bulletin of the Society of Vertebrate Paleontology.

Romer's textbook, *Vertebrate Paleontology* (1966) and Simpson's (1945) *The Principles of Classification and a Classification of Mammals* are especially recommended as sources of considerable information on the fossil history and evolution of mammals, and we would be remiss not to mention also Zittel's 1891-93) classic *Handbuch der Palaeontologie* (volume 4, Mammalia). Three substantial longer papers on systematics and evolution of special groups are Shotwell's (1958) study of aplodontid and mylagaulid rodents, Dawson's (1958) review of Tertiary leporids, and Black's (1963) report on the Tertiary sciurids of North America. Extensive paleofaunal studies of note are many;

those by Hibbard (1950) on the Rexroad Formation from Kansas and by Wilson (1960) on Miocene mammals from northeastern Colorado serve as excellent examples.

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THE GENERIC ALLOCATION OF THE HOMINID SPECIES HABILIS AS A PROBLEM IN SYSTEMATICS

CHARLES A. REED

THE recent controversial discussion, in *Current Anthropology* (Oct. 1965) and elsewhere, concerning the correct generic placement of the Lower Pleistocene hominid species *habilis* (Leakey, Tobias, and Napier, 1964), depends for its solution upon which one of two kinds of philosophy of systematics is followed. None of the participants in the discussion have emphasized this particular aspect of the issues, but an understanding of these concepts is basic to both argument and solution.

If one is impressed with the phylogenetic approach to the study of fossils, stressing the implications of those evolutionary innovations found in them which place a particular group at the beginning of a new evolutionary line, leading in time to new adaptive possibilities, then the classification will be vertical ('classification by clade'). Utilizing this approach to zoological systematics the investigator will emphasize the importance of the new evolutionary direction (the new adaptive plateau being approached), by placing his fossils in the taxon with the advanced forms derived from them. Leakey, Tobias, and Napier did exactly this when they placed the population *habilis*, from Bed I of Olduvai Gorge, Tanzania, in the genus *Homo* (Fig. 1).

The alternate approach to systematics is "classification by grade," wherein the investigator emphasizes in his taxonomic system, as he emphasizes in his own thinking about the material, the greater or lesser degree of morphological likenesses between two populations which have essentially reached, at the generic or specific levels, a considerable similarity. Obviously, the individuals of *habilis* are anatomically more similar to individuals of *Australopithecus africanus* that they are to ourselves as *Homo sapiens*, or even to individuals of the mid-Pleistocene taxon *H. erectus*. Robinson (1965a, b) and separately Howell (1965), seeing clearly this essential anatomical similarity between *africanus* and *habilis*, wish to emphasize what to them is a clear closeness of biological relationship by placing the two populations together in the same genus, *Australopithecus* in this instance.*

The issues involved have roots deep in the history of post-Darwinian systematics, particularly as practised by palaeontologists. Simpson (1961) has summarized the problems with a suggestion for a solution which attempts (although in my opinion not

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* The mentioning of two genera, but only two, as comprising the known Quaternary hominids is done on the basis of the general usage of the authors involved in the controversy presently being considered, and with the view that *Paranthropus* is probably best considered as a sub-genus of *Australopithecus*. We must not forget, however, that Mayr (1950) advocated that all Quaternary hominids be included in *Homo*, a practice followed only intermittently thereafter but espoused in at least two recent textbooks (Brace and Montagu, 1965; Buettner-Janusch, 1966). There is also another possible point of view, the one that *habilis* be included within *Homo erectus*, probably as a subspecies, although Tobias (1965b) has indicated that on the basis of present evidence this is a conclusion with which he could not agree.

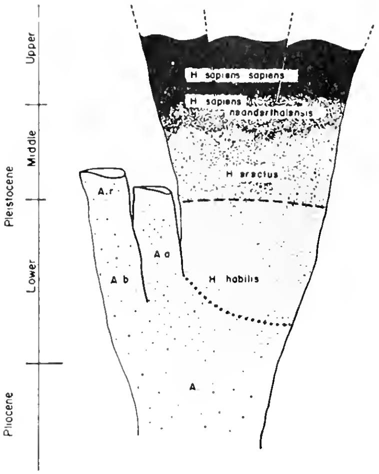

Fig. 1: Phylogeny and classification of the Family Hominidae, as presently understood (after Tobias, 1965a). The dotted line represents the boundary in time and between the taxa Homo **and** Australopithecus **as conceived on the basis of classification by clade; the dashed line represents the same concepts on the basis of classification by grade.**

successfully) to combine the two approaches. An earlier paper by myself (Reed 1960), as based on publications listed in its bibliography, states these particular issues in a shorter article and also points out the logical consequences of accepting either system, that "by clades" or the contrasting one, "by grades."

Neither system is necessarily correct, nor either wrong; they simply are based on two different, and in my opinion mutually exclusive, approaches to the systematic organization of biological populations in a time-continuum. For this reason, systematics remains an art and is not a science, depending upon the opinion of trained investigators for decisions which eventually are or are not followed by larger numbers of people who are interested in the fossils and the phylogeny, but have neither the time nor training to study the materials in detail.

Our problems with the systematics emerge irrevocably from the pattern of a continuous flow of genes, generation by generation, and from the occasional divisions of a population's gene pool into separate evolutionary streams.

The vertical type of classification based on clades is possible only if a population has proved its survival value by becoming the ancestral type of a new lineage, and if we have found a good record of these happenings. Thus if the population *habilis* had become extinct during the period of the formation of Bed I at Olduvai Gorge, its evolutionary potential would be unrecognizable and its remains would most certainly be classified with *Australopithecus* by whatever subsequent intelligent being was doing the paleontology. The *Homo*-ness of *habilis* lies in those characters which we can recognize as being important in initiating the lineage *Homo* only because we have a record of that lineage. Until, however, we had as complete a record of that lineage as we finally now have, systematics by clade was not possible.

A bit of an analogy, involving non-hominid lineages with which we are not personally involved, may help to clarify the principles. Thus the phylogenies of two super-families, those of the horses (Equoidea) and of the tapirs (Tapiroidea), diverged early in the Eocene. The first-known individual fossils of each of these two super-families are extremely similar, but each—to the eye of the expert—indicates its affinities to its known descendants by what might appear to be, but is not, a trifle of dental pattern (Radinsky, 1963). Where the fossil record is as complete as with these perissodactyls, the solution of the systematic problems has typically been to include in different clades (families or super-families) different populations which on the basis of similarity of anatomical form would be grouped at the grade level as closely related genera or as species in the same genus. If, at this Eocene level of evolution, one of these ancestral groups, such as *Hyracotherium* (ancestral to all later "horses" *sensu lato*), had become extinct, no palaeontologist would be capable of recognizing its potential "horse-ness" and *Hyracotherium* would today be classified as a primitive tapir. Conversely, if *Homogalax*, the earliest of the tapiroid line, had become extinct without issue, undoubtedly it would today be classified as an Eocene equid.

In general, as the gaps in the fossil record of any lineage have been filled, the tendency has been, often without any realization of the philosophy of the systematics involved, to shift from a horizontal (grade) type of classification to the vertical (clade) type, and the recent flurry of published opinions as to the formal position of the species *habilis* illustrated a repetition of this historical pattern. Tobias (1965c) has stated that there is general agreement as to the meaning of the morphological data and the validity of the evolutionary position of the fossils included in the population *habilis* from Bed I at Olduvai Gorge; if precedent has any value as a guide, we may safely assume that *habilis* will remain in *Homo*.

In general, the Primates have been classified on the principle of grades, typical of groups with an incomplete fossil record and thus lacking well-defined lineages. As more fossils are found and the phyletic pattern becomes clearer, various parts of the suborder (grade) Prosimii will become continuous with at least two lineages (platyrrhine and catarrhine) of the suborder (grade) Anthropoidea, and slowly the present pattern of the systematics will change.

Exactly this sort of change, to the surprise of some, is what is occurring in the Hominidae, due to the filling of the gaps priorly existing between the groups called Australopithecinae and Homininae. We should realize also that, as now defined, the names applied to extinct populations of *Homo* remain as grade concepts, as has already been stated clearly by Tobias and von Koenigswald (1964). Thus, if and when human fossils are found to fill the near-void now existing between the latest *erectus* and the earliest acknowledged neandertals, the whole present taxonomic scheme will necessarily be changed from the horizontal to the vertical. Perhaps that agonizing reappraisal will be easier then—as indeed I hope it will be now at the *habilis* level—if we realize that it is inevitable.

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MICROTUS PENNSYLVANICUS (ORD) FROM THE HAY SPRINGS LOCAL FAUNA OF NEBRASKA

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Abstract—*Microtus pennsylvanicus* (Ord), the meadow vole, a member of the present fauna of Nebraska, is known from fossil remains in the American Museum of Natural History, which were taken with the Hay Springs local fauna of Sheridan County, Nebraska. On the basis of known Pleistocene faunas, the Hay Springs mammals are post-Pearlette ash in age. The fauna appears to be equivalent to those that lived during the late Illinoian and Sangamon.

The occurrence of *Microtus* in the Hay Springs local fauna of Nebraska has long been known (Matthew, 1918, p. 227; Hay, 1924, p. 305; Osborn, 1942, p. 1010). In the spring of 1944 while studying the holotypes of *Ondatra nebracensis* (Hollister) and *Capromeryx furcifer* Matthew, I examined a lower jaw of *Microtus* from the Hay Springs fauna which led to my statement (Colbert, et al., 1948, p. 625) regarding the occurrence of this vole in that fauna. Through the courtesy of Dr. G. G. Simpson I have been given permission to study and figure these specimens.

In the American Museum of Natural History collection there are parts of three lower jaws and two left upper incisors from the Hay Springs, Nebraska locality, collected by the American Museum Expedition of 1897.

Specimen AMNH 2711 is part of a left lower jaw with the incisor, M_1 and M_2. M_1 consists of a posterior loop, six alternating triangles and an anterior loop. The sixth alternating triangle opens into the anterior loop (Text-fig. 1B). M_2 consists of a posterior loop and four closed alternating triangles. Enamel is lacking on the anterior face of

M_1, the labial and lingual sides of the posterior loop of M_1 and the anterior face of M_2. The posterior loop of M_2 has an interrupted enamel pattern. A narrow dentine tract on the labial and lingual sides of the loop extends from the occlusal surface to the base of the tooth. The anteroposterior length of the occlusal surface of M_1 and M_2 is 5.3 mm.

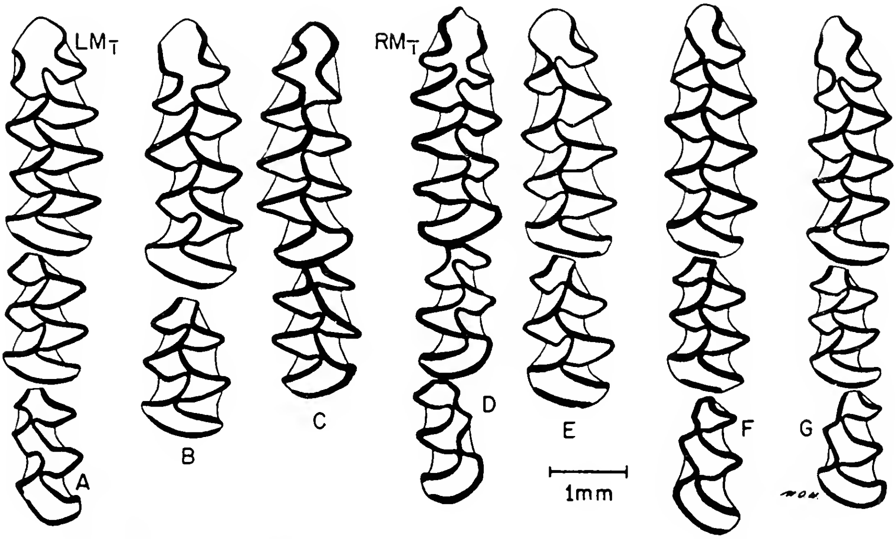
A fragmentary right lower jaw, AMNH 2712, contains part of the incisor, M_1 and M_2. The occlusal dental pattern is similar to that of the previous specimen, except that the sixth alternating triangle opens more widely into the anterior loop (Text-fig. 1C). The anteroposterior occlusal length of M_1–M_2 is 5.0 mm.

Specimen AMNH 2713 is a right lower jaw with an incisor and M_1–M_3. The occlusal pattern is like that of the other two specimens. M_3 consists of a posterior loop with the first and second alternating triangles broadly confluent. The third is closed off from the fourth triangle (Text-fig. 1D). The anteroposterior occlusal length of M_1 and M_2 is 4.75 mm.; that of M_1–M_3 is 6.5 mm. Dentine occurs in the reentrant angles of the teeth and is as well developed as in recent specimens. A deep pit occurs between M_3 and the ascending ramus as in Recent specimens of *Microtus pennsylvanicus*. The general shape of the lower jaw is like that of other fossil and Recent specimens of this species.

The two left upper incisors, AMNH 2714, are the size and shape of those of the Recent species.

The original American Museum label carries the name *Arvicola ?agrestis* but on the back of the label is written, "A note from O. P. Hay says: Not *A. agrestis*—an European species. Probably *Microtus pennsylvanicus*. O. P. H." At what time O. P. Hay made this identification is unknown but it must have been after the publication of his 1924 paper.

The number of closed alternating triangles of M_1 vary (5 to 6) in both Recent and fossil specimens. Text-fig. 1E is an occlusal view from a specimen, Univ. Michigan 31773, taken with the Berends local fauna of Oklahoma. Text-fig. 1F is an occlusal view of a specimen, Univ. Michigan 29333, from the Jinglebob local fauna. Both of these specmens have an M_1 with six closed alternating



TEXT-FIG. *1*—*Microtus pennsylvanicus* (Ord), occlusal views of lower dentitions. All ×10. Drawings by Michael O. Woodburne. *A*, UMMZ 30048, left M_1–M_3, Recent specimen. *B*, AMNH 2711, left M_1 and M_2, Hay Springs local fauna. *C*, AMNH 2712, right M_1 and M_2, Hay Springs local fauna. *D*, AMNH 2713, right M_1–M_3, Hay Springs local fauna. *E*, UMMP 31773, left M_1–M_2, Berends local fauna. *F*, UMMP 29333, left M_1–M_3, Jinglebob local fauna. *G*, UMMZ 30013, left M_1–M_3, Recent specimen.

triangles posterior to the anterior loop. The two Text-figs. 1A and 1G of Recent specimens in the Museum of Zoology, University of Michigan, are given for comparison with the fossil occlusal patterns.

Age of the Hay Springs local fauna.—A stratigraphic control is lacking on this fauna since it appears that the exact location of the quarry or quarries is unknown. Matthew (1902, p. 317) gives the location as a bonebed near the Niobrara River, not far from Hay Springs.

O. P. Hay (1924, p. 304) makes the following statement regarding the location:

> Many species of fossil vertebrates have been taken on Niobrara River, near a place now known as Old Grayson, not far from the present town of Grayson, from excavations known in the literature as the "Hay Springs quarry." The locality is said to be along a ravine about a mile away from the Niobrara River, and south of it.

Schultz & Stout (1948, p. 564) make the following remark regarding this early locality:

> The American Museum of Natural History expeditions of 1893, 1897, and 1916 conducted minor quarry operations south of Hay Springs, but the exact locations of these quarries cannot now be determined.

A succession of Pleistocene faunas, for which there is a stratigraphic control, is known from Meade County, Kansas and Beaver County, Oklahoma (Hibbard, 1956, p. 146. fig. 1).

The earliest remains of *Microtus* in the Plains region are known from the Crooked Creek formation (Hibbard, 1949). This formation is tentatively considered as having been deposited during Kansan and Yarmouth time. The basal part of this formation consists of sand and gravel (Stump Arroyo member) which rests unconformably upon the Meade formation. The following fossils have been taken from the Stump Arroyo member (Hibbard, 1951) in Clark and Meade counties: *Megalonyx* sp., *Stegomastodon* sp., *Stegomastodon mirificus* (Leidy), *Nannippus phlegon* Hay and *Plesippus* cf. *P. simplicidens* (Cope). So far *Equus* s.s. and *Mammuthus* have never been taken from this sand and gravel. They are known from later deposits of this region (Hibbard, 1953). Above this sand and gravel member occurs sandy silt, silt, clay, Pearlette ash, clay, silt and sandy silt which is overlain by massive caliche. Two faunas are known from these deposits. The older, the Cudahy fauna, occurs in the base of the Pearlette ash and the underlying silts, and is considered as latest Kansan in age. Frye, Swineford, & Leonard (1948) and Frye & Leonard (1952) have shown that the Cudahy molluscan fauna from the base and just below the Pearlette ash is the same in Nebraska and Kansas. It is therefore evident that the mammalian fauna should be the same in Kansas as in Nebraska except for a few more northern forms that may occur in the fauna in Nebraska. It is in this fauna that the remains of *Microtus* and other microtines are found. The species of *Microtus* that have been taken in this fauna are extinct. The small muskrat (*Ondatra kansasensis* Hibbard) occurring in this fauna is not as advanced or as large as *Ondatra nebracensis* (Hollister) from the Hay Springs fauna. The Hay Springs muskrat is also more advanced than the small *Ondatra hiatidens* (Cope) from the Port Kennedy Cave fauna of Pennsylvania (Hibbard, 1955).

The younger Borchers fauna occurring in the Crooked Creek formation is found above the Pearlette ash and is tentatively considered as Yarmouth in age. The two microtines known from this fauna are *Synaptomys landesi* Hibbard, and a small muskrat-like vole, not as advanced as the older *Ondatra kansasensis*.

The earliest occurrence of *Microtus pennsylvanicus* in the Plains region south of Nebraska is in the Illinoian Berends local fauna of Oklahoma and the Sangamon Jinglebob fauna of Kansas. It is well known from Wisconsin faunas. It should be noted that this vole which is now a common member of our northern North American fauna is unknown from the Port Kennedy Cave and Cumberland Cave local faunas of northeastern United States. All evidence at the present time points to a rather late arrival of this form in our North American fauna.

In Kansas the remains of *Microtus pennsylvanicus*, *Paramylodon harlani* (Owen) (see Stock, 1925, p. 120); *Mammuthus imperator* (Leidy), *Capromeryx furcifer* Matthew, and *Equus niobrarensis* Hay are known only from deposits that are post-Pearlette ash in age. Rinker (1949) commented on the resemblance of the Hay Springs fauna to the Cragin Quarry fauna and its equivalents in Kansas.

The Hay Springs local fauna of Matthew (1918) and Hay (1924) is post-Pearlette ash in age (late Kansan). All faunal evidence points to a late Illinoian and Sangamon age. In this paper the assignment of Pleistocene subages to the faunas and deposits in the nonglaciated Plains region is tentative.

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TYPE LOCALITIES OF COPE'S CRETACEOUS MAMMALS

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ABSTRACT

It is generally stated in paleontological literature that J. L. Wortman found the types of two species of Late Cretaceous mammals in unknown parts of South Dakota. These species, subsequently described and named by E. D. Cope, are **Meniscoessus conquistus** (probably the first Cretaceous mammal to be found and described), and **Thalaeodon padanicus**. They are the only Cretaceous mammals of published record from the state.

Review of some neglected sources of information leads to the conclusion that: (1) the type of **Meniscoessus conquistus** came from Dakota Territory, but not necessarily from South Dakota, and (2) E. D. Cope, rather than Wortman, found the type of **Thlaeodon padanicus**, and this specimen came from Hell Creek beds along the Grand River approximately four miles southeast of Black Horse.

E. D. Cope named and described two genera of Cretaceous mammals: these were the multituberculate *Meniscoessus* in 1882, and the marsupial *Thlaeodon* in 1892, with type species *M. conquistus* and *T. padanicus* respectively. Cope credited J. L. Wortman with the discovery of *Meniscoessus conquistus,* but said nothing about the type locality. In his description of *Thlaeodon padanicus,* he said nothing about either the discoverer or the place of discovery, except to state that the upper and lower jaws were found about one hundred feet apart, but probably pertained to a single individual. At a considerably later time, G. G. Simpson (1929) and others have stated that the type specimens of both *M. conquistus* and *T. padanicus* were found by Wortman in the "Laramie" [Lance] of South Dakota, but that no other locality data were available.

The Museum of Geology of the South Dakota School of Mines and Technology has been exploring the Hell Creek (Late Cretaceous) of South Dakota for mammals.[1] In an attempt to gain clues as to where Wortman might have found his specimens, I searched such literature as was available to me with care. As a result, I have reached tentative conclusions at variance with those of Simpson.

In respect to *Meniscoessus conquistus* not much can be said with assurance. A note by Wortman (1885, p. 296) states that Hill (Russell?) and Wortman found the type in the summer of 1883 (*sic,* but

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surely 1882) in Dakota. Because the division of the Territory into the present states of North and South Dakota did not take place until 1889, the question arises as to how it is known that the locality was in what is now South Dakota if nothing is known about the details of the locality. The only slight clue I can uncover is that a year after Wortman's finding of *Meniscoessus,* Cope, himself, was exploring the Cretaceous of the Dakota Territory. In a letter to his wife dated August 28, 1883 (Osborn, p. 306), and written at what is seemingly now Medora, North Dakota, he says in describing local outcrops: "This is the formation from which Wortman got the *Meniscoessus.*" This sentence can be taken literally as simply that the specimen came from Cope's Laramie Formation, or with more license that he meant these are the outcrops from which the specimen came. In the same letter, he wrote that he planned to go 30 miles south where the "badlands are said to be exceptionally bad." If he were following Wortman's footsteps at this point, he would have been approximately 45 miles north of the state line. After proceeding this far south along the Little Missouri, Cope went southeastward to White Buttes before turning back to Medora. White Buttes was his closest approach to South Dakota on this trip of several days, and he was then still about 30 miles from South Dakota. It may be that in the general area bounded by Medora, Marmath, and Bowman, North Dakota, Wortman found the type of *Meniscoessus,* but even if he did not, it is highly uncertain that the discovery was made in the South Dakota of today. As a matter of fact, most of the outcrops south of the state line for some miles may be somewhat too high in the geologic section for *Meniscoessus.*

In respect to the type locality of *Thlaeodon padanicus,* there are several bits of evidence suggesting (1) that Cope rather than Wortman found the specimen, and (2) that it was in fact found in South Dakota along the south bank of the Grand River southeast of Black Horse. These lines of evidence are itemized below.

1. Nowhere in the account published in 1892 in the American Naturalist does Cope credit Wortman with discovery of *Thlaeodon padanicus.*

2. The Indian name for the Grand River is Padani, and hence the specific name *T. padanicus* is a broad hint as to locality.

3. In the year of its discovery, Cope prospected along the Grand River. Wortman was also in South Dakota, but was occupied by collecting in the Big Badlands to the south, and such Cretaceous collections as he made seemed to have been in the Lance Creek area of Wyoming. In any case, even before the summer of 1892, he had left the employ of Cope, and was working for the American Museum of Natural History.

4. In a letter to his wife dated July 17, 1892 (Osborn, p. 431), Cope says, "We made noon camp on the bank of Grand R. and then climbed the bluffs on the S. side leaving the Rock Creek and this subagency to the N. We followed this high land, driving through the Grass, sometimes with, sometimes without trail. We had great distance views, fine air, and plenty of flowers. During the afternoon we crossed Five (*sic,* for Fire) Steel Creek, which comes in from the South. As evening approached thunderclouds arose in the W. and I began to think of camp. Oscar however drove on, and the Sioux boy kept ahead. As it grew late we turned down a low hill to the left and climbed a low bench at the foot of an opposite hill. I saw a low bare bank and lying around white objects. I told Oscar to let me get out, as I thought I saw bones. Sure enough the ground was covered with fragments of Dinosaurs, small and large, soon we found water and stopped for camp." ingly thought; see 1931, p. 415).

5. In the letter above-mentioned (Osborn, p. 443), Cope states his results as, "In the 3 days I collected I got 21 species of vertebrates, of which 3 are fishes, and all the rest reptiles except one mammal. This is a fine thing, the most valuable I procured, and new as to species at least; and it throws important light on systematic questions." This mammalian specimen is not otherwise accounted for in collections if it is not the type specimen of *T. padanicus* (as H. F. Osborn seem-

Reference to a geological map (Firesteel Creek Quadrangle, South Dakota State Geological Survey) shows that the closest exposures from whence these bones could come after the Firesteel crossing is in the vicinity of section 25, T. 20N, R. 22E, or sections 29 and 30, T. 20N, R. 23E. A good skeleton of *Anatosaurus* in the Museum of Geology collections is from the southwest corner of the SW¼ of section 25, T. 20N, R. 21E. The type of *Thlaeodon padanicus* surely came from somewhere in the area of these localities.

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THE ADAPTIVE RADIATION OF THE PHENACODONTID CONDYLARTHS AND THE ORIGIN OF THE PERISSODACTYLA[1]

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The mammalian order Condylarthra includes a heterogeneous assemblage of small- to medium-sized archaic omnivores and herbivores. Most families in the order flourished in the Paleocene and became extinct early in the Eocene. A few lineages, however, developed crucial adaptations which led to their emergence as new orders of mammals, one of which was the Perissodactyla. The origin of the Perissodactyla is better documented than that of any other order of mammals and provides an excellent opportunity to study the emergence of a major taxon.

Dental evidence indicates that perissodactyls were derived from the condylarth family Phenacodontidae. To view in proper perspective the evolutionary changes which led to the origin of the Perissodactyla, it will be necessary to survey the adaptive radiation of the Phenacodontidae.

The oldest true phenacodontid condylarth, *Tetraclaenodon*, first appears in faunas of middle Paleocene age, and by the beginning of the late Paleocene appears to have radiated into three main groups, represented respectively by *Phenacodus*, *Ectocion*, and an as yet unknown proto-perissodactyl. Forms transitional between *Tetraclaenodon* and *Phenacodus* (primitive species of *Phenacodus*), and between *Tetraclaenodon* and *Ectocion* (the genus *Gidleyina*) are known, but no intermediates between *Tetraclaenodon* and the most primitive known perissodactyl, the early Eocene genus *Hyracotherium*, have yet been found. However, *Tetraclaenodon* is the most advanced form which is still unspecialized enough to have given rise to *Hyracotherium*. (The occurrence of incipient mesostyles in a small number of *Tetraclaenodon* specimens does not preclude this possibility; the alternative hypothesis, that proto-perissodactyls and *Tetraclaenodon* were independently derived from a still more primitive common ancestor, requires an additional complicating factor—an independent acquisition of molar hypocones by perissodactyls and phenacodontids.) Thus, in the absence of evidence to the contrary, *Tetraclaenodon* may be considered directly ancestral to perissodactyls. The major morphological changes involved in the evolution of the *Tetraclaenodon* stock into *Phenacodus*, *Ectocion*, and *Hyracotherium*, fall into two functional categories, one concerned with mastication and the other with locomotion.

MASTICATION

Dentition

The main changes involved in the evolution of the phenacodontid dentition occur in the molar teeth. The molars of *Tetraclaenodon* (see Fig. 1) are low-crowned, with low, obtuse cusps. The first and second upper molars are advanced over the primitive tritubercular molar pattern by the addition of a fourth main cusp, the hypocone. There are two relatively large intermediate cuspules, the protoconule and metaconule, and broad anterior and posterior cingula. The third upper molar is smaller than the second and lacks a hypocone. In the lower molars the paraconid has been reduced, leaving two main anterior cusps, the protoconid and metaconid, and a prominent anterior ridge, the paralophid. There are

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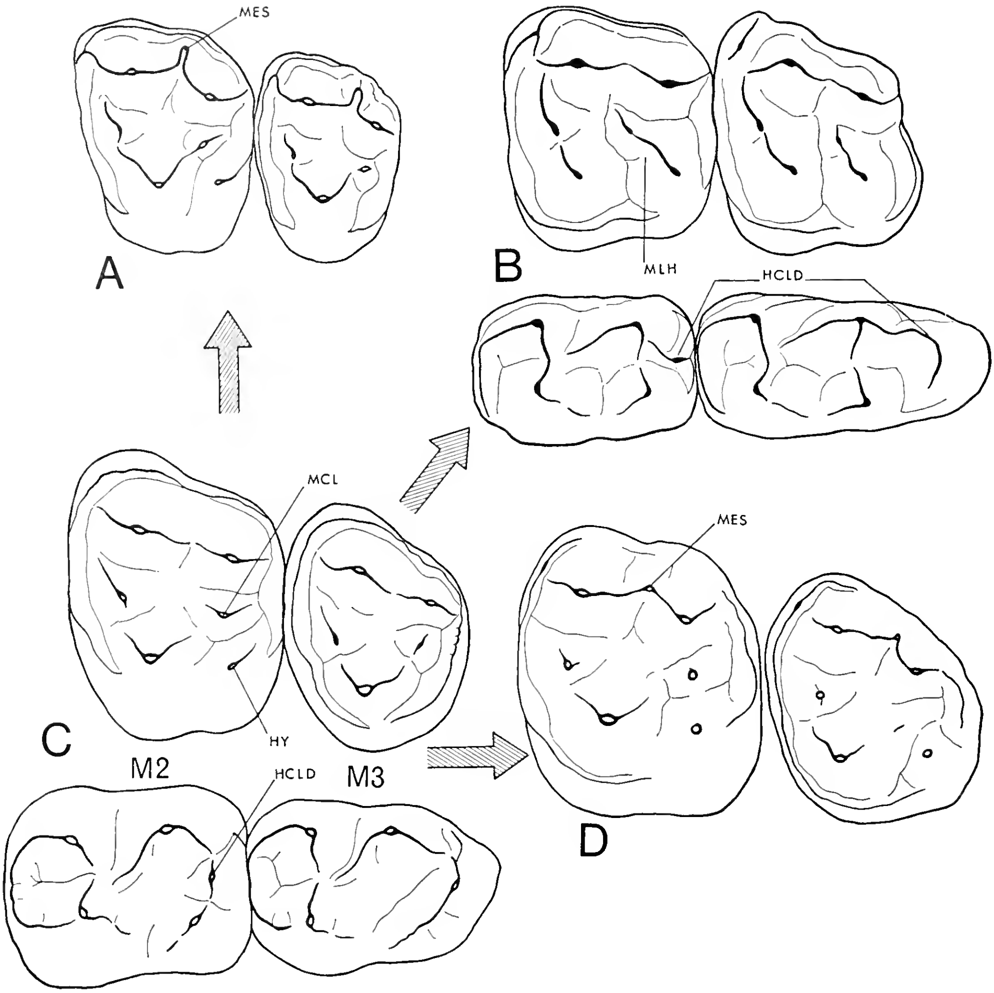

FIG. 1. Second and third molars of A. *Ectocion*, B. *Hyracotherium*, C. *Tetraclaenodon*, and D. *Phenacodus*. Lower molars of *Ectocion* and *Phenaodus* have the same basic cusp pattern as is seen in *Tetraclaenodon* and are therefore omitted. All about × 3. Abbreviations: HY, hypocone; HCLD, hypoconulid; MCL, metaconule; MES, mesostyle; MLH, metaloph.

three posterior cusps, a large hypoconid and slightly smaller entoconid and hypoconulid. The third lower molar is narrower posteriorly than the second. The wear facets on the molars of *Tetraclaenodon* suggest that both crushing and shearing occurred in mastication, with the emphasis apparently on crushing.

The teeth of *Phenacodus* are very similar to those of *Tetraclaenodon*, having low, obtuse cusps and ridges. The main differences are the development of a small mesostyle on the upper molars and the enlargement of the posterior cingulum into a hypocone on the third upper molar. The upper molars are relatively long (anteroposteriorly) and narrow. As in *Tetraclaenodon*, the broad low cusps are more adapted for crushing than shearing. The addition of a hypocone on the third upper molar increases the surface area available for chewing. The mesostyle is not large enough to add significantly to the ectoloph area.

In molars of *Ectocion* the cusps are relatively higher and more acute and the ridges connecting cusps are more prominent than in *Tetraclaenodon* or *Phenacodus*. The ectoloph is higher relative to the lingual cusps and is folded into a prominent mesostyle. The upper molars are relatively short and wide. The third upper molar does not develop a hypocone. On the lower molars the paraconid is lost and the paralophid no longer extends to the metaconid (as it does in *Phenacodus*). The high, narrow cusps and ridges provide steep occlusal surfaces, indicating relatively more shear and less crushing than occurred in *Tetraclaenodon* or *Phenacodus*. The prominent mesostyle increases the length of ectoloph available for vertical shear against the labial sides of ridges on the lower molars.

The molars of *Hyracotherium*, like those of *Ectocion*, have relatively higher and more acute cusps and ridges than do those of *Tetraclaenodon* or *Phenacodus*. However, *Hyracotherium* is even more advanced in this respect than is *Ectocion*, for the crests connecting cusps are better developed. An important modification in cusp pattern has been brought about by the loss of the protcone-metaconule connection, an anterior shift of the metaconule and the development of a hypocone-metaconule crest. These changes result in a cusp pattern with two oblique tranverse crests (an anterior protoloph and posterior metaloph) separated by a lingually open valley. Correlated with the changes in upper molar pattern, in the lower molars the hypoconulid has been posteriorly displaced, leaving the posterior sides of the hypoconid and equally large entoconid clear for shear against the anterior side of the metaloph above. Another new feature in the dentition of *Hyracotherium* is the enlargement of the third molars. In *Hyracotherium* the upper third molar has a hypocone and is as large as the second molar. The third lower molar is larger than the second, owing to the great enlargement of the hypoconulid. (In the first and second lower molars the hypoconulid is reduced.) However, even excluding the enlarged hypoconulid, the third lower molar is still as large as the second. Finally, the lower molars of *Hyracotherium* are narrower relative to the uppers than is the case in the phenacodontids.

The changes in cusp pattern and tooth proportions in evolution from *Tetraclaenodon* to *Hyracotherium* indicate an increase in the amount of shearing (especially along transverse crests) and a corresponding decrease in the amount of crushing in mastication. A shift toward increased shearing also occurred in *Ectocion*, but in that genus the emphasis was on vertical ectoloph shear. The enlargement of the third molars in *Hyracotherium* provided greater occlusal surface and could have been brought about simply by a slight posterior shift of the molarization field. The greatly enlarged hypoconulid of the third lower molar served the function in occlusion of a paralophid and presumably developed in correlation with the molarization (and enlargement) of the posterior half of the upper third molar. The relatively narrower lower molars of *Hyracotherium* required a greater degree of transverse jaw movement for complete occlusion with the uppers than was necessary in *Tetraclaenodon*.

Jaw Musculature

The structure of the lower jaw, known for *Phenacodus*, *Ectocion*, and *Hyracotherium* (see Fig. 2), provides information on the relative proportions of the main components of the jaw musculature. In mandibles of *Hyracotherium* the coronoid process is relatively smaller and the angle relatively larger than in *Phenacodus* or *Ectocion*. In addition, the posterior border of the angle is thicker and more heavily scarred (from insertions of the external masseter and internal pterygoid muscles) in *Hyracotherium*. These differences suggest that the masseter and internal pterygoid muscles were relatively

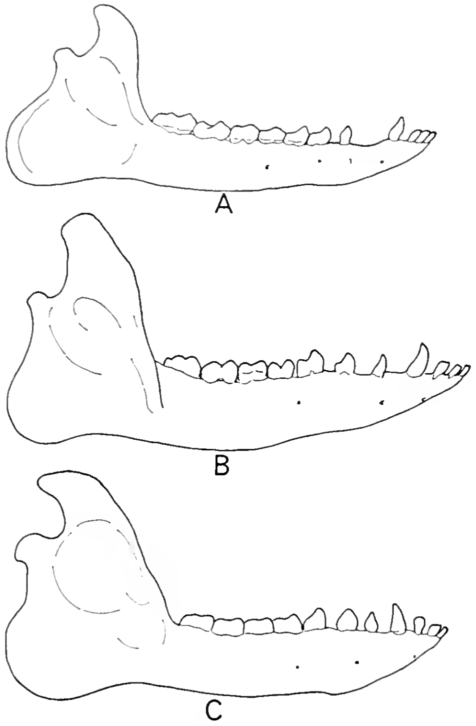

FIG. 2. Lower jaws of A. *Hyracotherium* (after Simpson, 1952), × ½; B. *Ectocion* (Yale Peabody Mus. no. 21211), × ⅔; C. *Phenacodus* (Princeton Univ. no. 14864), × ⅓. All in lateral view.

larger, and the temporalis, which inserts on the coronoid process, relatively smaller in *Hyracotherium* than in the phenacodontids.

In living ungulate herbivores the masseter-pterygoid complex is larger than the temporalis, while in carnivores the opposite is true (Becht, 1953, p. 522; Schumacher, 1961, pp. 143, 180). In carnivores, jaw movement is almost entirely confined to adduction, for which the temporalis is well suited, but in ungulates and many other herbivores transverse movement is important in mastication, and for transverse movement the deep part of the masseter and the internal pterygoid are more efficient than the temporalis (Smith and Savage, 1959, p. 297). Thus the relatively larger masseter and internal pterygoid musculature indicated by the jaw structure of *Hyracotherium* suggests increased specialization for lateral jaw movement in mastication. This specialization of the jaw musculature correlates with the narrower lower molars and predominance of transverse shear indicated by the molar cusp patterns of *Hyracotherium*.

LOCOMOTION

Much of the postcranial skeleton is known for *Hyracotherium*, *Phenacodus* and, to a lesser degree, *Tetraclaenodon*, but that of *Ectocion* is largely unknown. Therefore the following discussion of locomotory adaptions will deal mainly with the first three genera.

Vertebral Column

Slijper (1946, p. 103) pointed out that with decreasing mobility of the vertebral column in ungulates the longissimus dorsi shifts its insertion posteriorly from lumbar to sacral vertebrae and consequently the neural spines of the lumbar vertebrae become less cranially, and even caudally, inclined. In *Phenacodus copei* (Amer. Mus. Nat. Hist. no. 4378) the lumbar neural spines are inclined cranially about 15 degrees from vertical. Kitts (1956, p. 21) states that the neural spine of the last lumbar vertebra of *Hyracotherium* is less cranialy inclined than that of *Phenacodus*. No specimen of *Hyracotherium* available to me preserves lumbar neural spines, but in *Heptodon posticus*, an early Eocene tapiroid similar in morphology to *Hyracotherium*, the neural spine of the last lumbar vertebrae (Mus. Comp. Zool. no. 17670) is inclined cranially about five degrees from vertical. This difference from the condition in *Phenacodus* suggests that the vertebral column in early perissodactyls was somewhat less flexible than that of *Phenacodus*.

Kitts (1956, p. 20) states that the zygapophyses of the lumbar vertebrae of *Hyracotherium* are embracing, but his illustration (*loc. cit.*, fig. 3) shows what appears to be a relatively flat prezygapophysis, similar to the condition in *Phenacodus*.

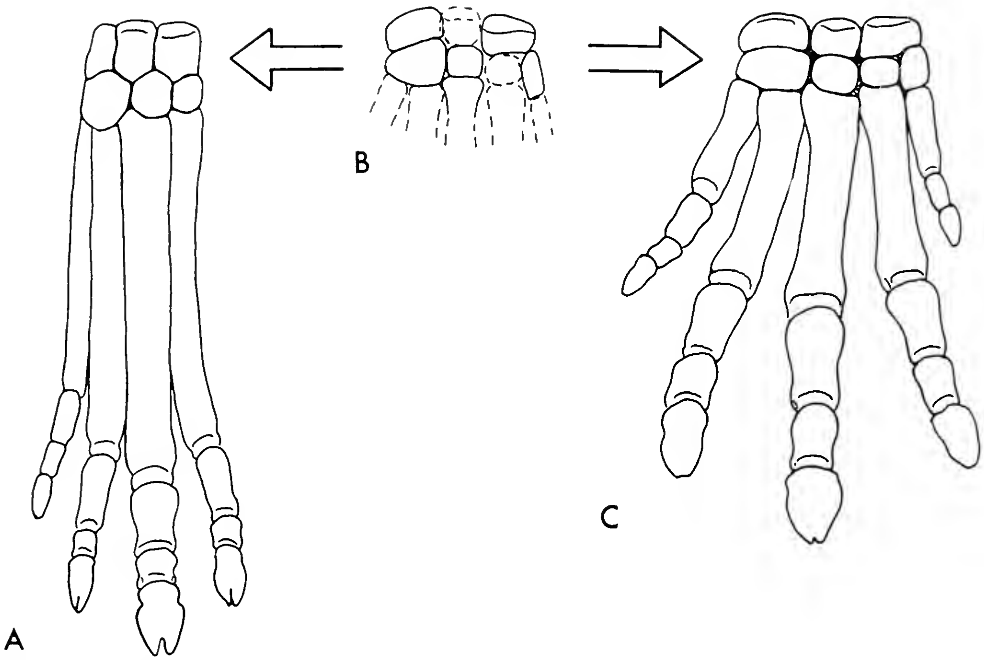

FIG. 3. Front feet of A. *Hyracotherium* (composite from Kitts, 1957, and Osborn, 1929, fig. 700), × ⅔; B. *Tetraclaenodon* (composite from AMNH nos. 2468 and 2547a), × 1; C. *Phenacodus* (AMNH no. 2961), × ⅓.

Forelimb

In *Tetraclaenodon* the humerus has a prominent deltoid crest, with the deltoid tubercle located on the distal half of the shaft, and a large medial epicondyle, with an entepicondylar foramen. The proximal end of the radius is about twice as wide as it is deep (anteroposteriorly) and articulates with the ulna along a wide flat facet, indicating loss of the ability to supinate. The carpus (see Fig. 3) is relatively low and wide, and has been called "alternating"; that is, in dorsal view the scaphoid rests partly on the magnum and the lunar partly on the unciform. The amount of overlap, however, is slight. Facets on the distal row of carpals indicate that there were five digits; except for the proximal head of the third metacarpal, the metacarpus is unknown.

The humerus, radius, and ulna of *Phenacodus* are similar to those of *Tetraclaenodon*, except that the deltoid crest of the humerus is slightly weaker and the deltoid tubercle is higher on the shaft. The carpus of *Phenacodus* has been described as being of the serial type, i.e., with the scaphoid resting solely on the trapezoid and trapezium, and the lunar only on the magnum. This arrangement occurs in the large species of *Phenacodus*, *P. primaevus*, but in the small species *P. copei* (AMNH no. 16125), the lunar overlaps the unciform to about the same degree (which is very little) as in *Tetraclaenodon*.

The less prominent deltoid crest and higher deltoid tubercle suggest that the forelimb of *Phenacodus* was relatively less powerful but perhaps capable of more rapid movement than that of *Tetraclaenodon*. The small medial displacement of the lunar and scaphoid, resulting in loss of the lunar-unciform and scaphoid-magnum articulations in large species of *Phenacodus*, suggests a slight increase in importance of the ulna in weight support.

The forelimb of *Hyracotherium* differs from that of *Tetraclaenodon* in the following features: humerus with shorter and less prominent deltoid crest and more proximally located deltoid tubercle, greatly reduced medial epicondyle (with consequent loss of the entepicondylar foramen), and sharper intercondyloid ridge (= capitulum); radiohumeral index of about 1.0 compared to 0.8 in *Tetraclaenodon* and *Phenacodus*, ulna with narrower, less massive, more symmetrical olecranon; carpus relatively higher and narrower, with more extensive articulations between elements; cuneiform smaller and scaphoid displaced laterally to extensively overlap unciform and magnum, respectively; unciform, magnum, and scaphoid with larger posterior tuberosities; first digit lost and trapezium reduced to a tiny nubbin; remaining metacarpals relatively longer and thinner (the ratio of the length of the third metacarpal to the humerus is 1 : 2 compared to about 1 : 3 in *Phenacodus* and probably also *Tetraclaenodon*); fifth metacarpal relatively smaller.

All of these differences indicate increased specialization for running in *Hyracotherium*. The elongation of distal limb segments (radius and metacarpals) and reduction of lateral digits increases the length of stride and makes the limb a more effective lever. The reduction of the medial epicondyle probably correlates with the decreased importance of the pronator teres (which originates on that epicondyle), for the manus is fixed in a permanently pronated position, and may also correlate with the decrease in importance of the ulna as a weight-bearing element of the forearm. The latter change is indicated by the reduction in size of the cuneiform and lateral displacement of the lunar and scaphoid, which increases the relative size of the area of manus under the radius. The alternating arrangement of the carpals and more compact carpus make the wrist less flexible but better for resisting stresses. The larger posterior tuberosities on several of the carpals indicate more powerful flexor musculature. The sharper intercondyloid ridge on the humerus restricts lateral movement at the elbow joint. The weaker deltoid crest, higher deltoid tubercle, and narrower and less asymmetrical olecranon are features associated with increased cursoriality. Thus, in a complex of features, the forelimb of *Hyracotherium* is more specialized for running than is that of *Tetraclaenodon* or *Phenacodus*.

Hind Limb

In *Tetraclaenodon* the greater trochanter of the femur is only slightly higher than the head, the lesser trochanter is very weak, and the third trochanter is large and located about two-fifths of the way down the shaft. The cnemial crest of the tibia is relatively large and extends about halfway down the shaft, the grooves for the astragalus are broad and very shallow, and the medial malleolus and distal end of the fibula (lateral malleolus) are large and massive. The astragalus has a relatively flat, low, and wide trochlea with a foramen, a relatively long neck, and a dorsoventrally flattened, convex head. The posterior astragalocalcaneal articulation is only slightly rounded. The calcaneum has a large peroneal tubercle and the ectocuneiform a large plantar process. The pes is pentadactyl, with the lateral toes slightly reduced (see Fig. 4).

The hind limb of *Phenacodus* is similar to that of *Tetraclaenodon*, differing in the following features: femur with larger lesser trochanter; tibia with weaker cnemial crest, smaller medial malleolus, and slightly deeper grooves for astragalus; fibula relatively slimmer, with smaller distal end; astragalus with a slightly relatively higher, narrower, and more deeply grooved trochlea, a slightly more curved posterior astragalocalcaneal facet, no astragalar foramen, and a deeper (dorsoplantarly) head; first and fifth metatarsals slightly more reduced.

The enlarged lesser trochanter of the femur suggests a stronger iliopsoas, an adductor of the femur. The reduction of the cnemial crest suggests reduced power

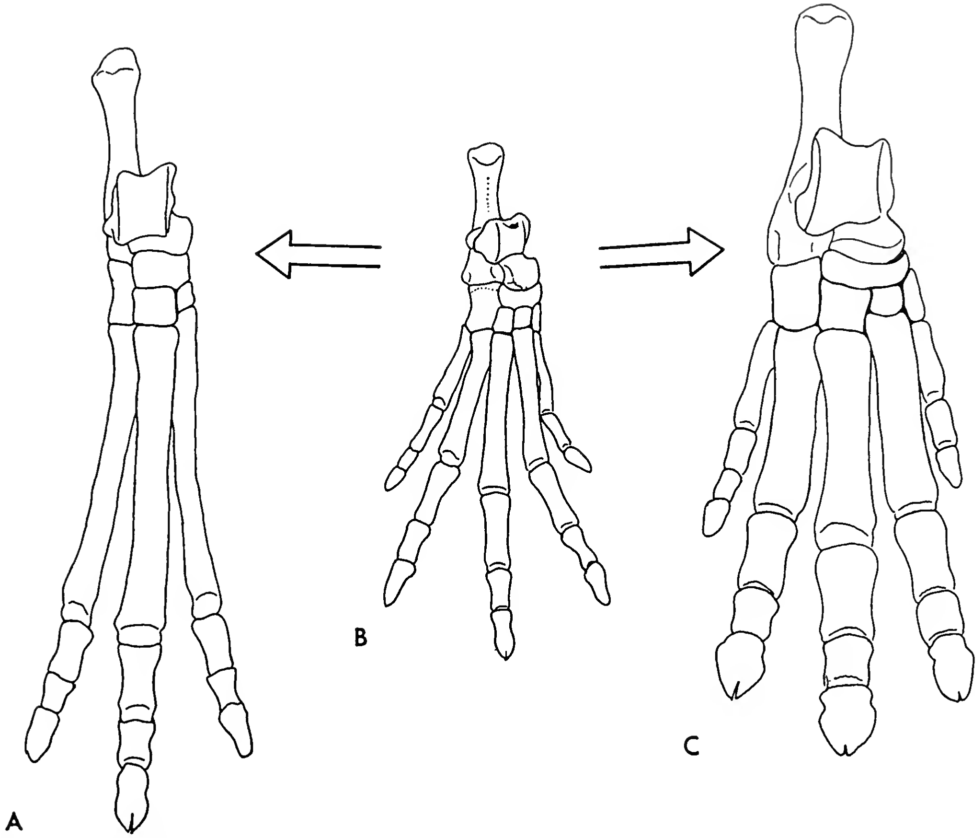

FIG. 4. Hind feet of A. *Hyracotherium* (from Kitts, 1956), × ½; B. *Tetraclaenodon* (from Matthew, 1897), × ½; C. *Phenacodus* (AMNH no. 293), × ⅓.

but increased speed in the hind limb. The more deeply grooved astragalar trochlea helps restrict lateral movement at the upper ankle joint and reduces the necessity for large lateral and medial malleoli. The loss of the astragalar foramen allows a slightly greater arc of rotation of the astragalus on the tibia. The more curved posterior astragalocalcaneal facet and deeper astragalar head may be related to a more digitigrade posture, which is suggested by the reduction of the lateral toes. In all of these features the hind limb of *Phenacodus* is slightly more specialized for running than is that of *Tetraclaenodon*.

The hind limb of *Ectocion* is known only from an astragalus and part of a calcaneum (AMNH no. 16127). The astragalus (see Fig. 5) differs from that of *Tetraclaenodon* in having a slightly higher and narrower tibial trochlea with a slightly deeper groove and no astragalar foramen, a more anteriorly directed posterior calcaneal facet, a wider neck with a high anteroposteriorly oriented ridge at the dorsolateral corner, and a slightly flatter and deeper navicular facet. The high dorsolateral ridge probably marks the attachment of a strong lateral astragalocalcaneal ligament, which suggests restriction of rotation between astragalus and calcaneum. This interpretation is supported by the less oblique posterior calcaneal facet and the flatter head (the latter indicates less movement between astragalus and navicular). These features suggest a slight

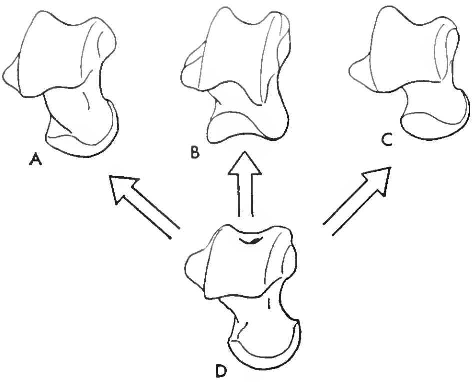

Fig. 5. Astragali of A. *Ectocion* (AMNH no. 16127), B. *Hyracotherium*, C. *Phenacodus*, D. *Tetraclaenodon*. Not to scale.

loss of freedom for lateral movement in the tarsus of *Ectocion* compared with the condition in *Tetraclaenodon*. The anterior end of the calcaneum is as wide in *Ectocion* as in *Tetraclaenodon*, suggesting that the pes of *Ectocion* was pentadactyl.

The hind limb of *Hyracotherium* differs from that of *Tetraclaenodon* in the same features mentioned for *Phenacodus*, but to a greater degree and with additional modifications. The latter include: femur with higher greater trochanter and more proximally located third trochanter; cnemial crest of tibia does not extend as far distally; first and fifth digits lost and remaining metatarsals relatively longer (length of third metatarsal/femur = 0.50 in *Hyracotherium* compared to 0.35 in the phenacodontids); tarsus relatively narrower and more compact, and astragalus, calcaneum, and navicular modified to eliminate the possibility of lateral movement of the foot.

The higher greater trochanter (which provides better leverage for the gluteal muscles, important abductors of the femur), more proximally located third trochanter, shorter cnemial crest, and longer metatarsals, plus the modifications noted in *Phenacodus*, are cursorial specializations of *Hyracotherium* which occur also in other running mammals. The loss of the first and fifth toes and the great elongation of the remaining metatarsals are not unusual cursorial adaptations in later forms but are extremely progressive features for an early Eocene mammal. They require a compact, relatively rigid tarsus and it is in modifications of the tarsus to provide a stable ankle joint that *Hyracotherium* was unique.

The interpretation of tarsal mechanics in extinct animals is necessarily limited by lack of knowledge of the tarsal ligaments, for the ligaments may be as important as the bone articulations in restricting movement. Thus the degree of tarsal movement inferred from the bones alone represents the maximum amount possible and in life the actual amount of movement may have been considerably less.

The configurations of the tarsal articulations in *Tetraclaenodon* suggest that lateral movements of the foot (eversion and inversion) were possible, resulting from a combination of rotation at the lower ankle joint (between astragalus and calcaneum) and transverse tarsal joint (between astragalus and navicular). The posterior astragalocalcaneal articulation is only gently curved and the astragalonavicular articulation resembles a shallow ball-and-socket joint. In *Hyracotherium* the posterior astragalocalcaneal articulation is bent into a right angle and is more vertically oriented, restricting rotation at the lower ankle joint, and the astragalonavicular articulation is saddle-shaped (with the distal end of the astragalus concave mediolaterally), allowing a small amount of dorsoplantar rotation but no lateral movement. The saddle-shaped astragalonavicular articulation is unique to the Perissodactyla and a diagnostic feature of the order.

The redistribution of weight necessitated by the loss of the lateral toes and relative enlargement of the middle digit in *Hyracotherium* is reflected in the narrower, more compact tarsus, in which the cuboid and calcaneum are narrower (the peroneal tubercle of the calcaneum is lost), the neck of the astragalus shorter, wider, and deeper, and the head more closely appressed to the calcaneum, and the entocuneiform reoriented so that the vestigial first metatarsal is located behind the ectocuneiform and third metatarsal where it serves as attachment for deep flexor muscles and as a brace for the tarsus (Radinsky, 1963). The plantar process of the ectocuneiform is lost, its function apparently having been usurped by the reoriented vestige of the first metatarsal. Thus virtually the whole tarsus of *Hyracotherium* was remodeled to provide the stability required by the loss of lateral toes and great elongation of the metatarsus. Versatility was sacrificed for increased efficiency in running.

DISCUSSION

Absolute dating of the early Tertiary (Evernden *et al.*, 1964) indicates that evolution from *Tetraclaenodon* to *Hyracotherium* took place in less than five million years. Considering the magnitude of the morphological changes involved, the speed of that transition indicates a considerably higher rate of evolution in late Paleocene proto-perissodactyls than occurred during most of the subsequent 55 million years of perissodactyl evolution. This fact, coupled with the evidence of a major adaptive radiation of perissodactyls at the beginning of the Eocene, suggests that the origin of the Perissodactyla coincided with a shift to a new adaptive level.

The two major areas of specialization of the earliest perissodactyls, as far as the paleontological evidence indicates, are in mastication and locomotion, and there is evidence of experimentation among the condylarths in both of these fields. The dentition of *Phenacodus* is essentially a conservative continuation of the basic *Tetraclaenodon* pattern, while that of *Ectocion* is specialized for vertical shear. The molars of *Ectocion* are more specialized for vertical shear than are those of *Hyracotherium*, but are less specialized for transverse shear. In the closely related meniscotheriid condylarths, *Meniscotherium* has teeth which are more specialized for vertical shear than those of *Hyracotherium* and at least as specialized, although in a somewhat different way, for transverse shear. The specialization for transverse shear is also reflected in the mandible of *Meniscotherium*, which has a relatively large angular process and small coronoid process. This experimentation in dentition among condylarths suggests that a variety of ecological niches for medium-sized browsers was open at the beginning of the late Paleocene.

Phenacodus, *Ectocion*, and *Meniscotherium* appear to have been only slightly more specialized for running than was *Tetraclaenodon*, although the astragalus of *Ectocion* suggests that lateral movement at the ankle joint may have been restricted by ligaments. In *Hyracotherium*, however, a radical and unique remodeling of the ankle joint prevented lateral movement and made possible a precocious elongation of the metatarsals and reduction of the lateral digits. Other specializations for running are evident in the forelimb of *Hyracotherium*.

During the early Eocene perissodactyls underwent an extensive radiation while phenacodontid and meniscotheriid condylarths became extinct. Since the meniscotheriid dentition was at least as specialized for shear as was that of *Hyracotherium* it would seem that the masticatory specialization was less important for the success of the Perissodactyla than the adaptations for running. The early perissodactyls were considerably more specialized for running than were the contemporary predators, while the condylarths were not. It is surely no coincidence that the other major order of medium-sized to large herbivores, the Artiodactyla, appeared at the same time as the Perissodactyla, with their main adaptive feature a cursorial modification of the ankle joint (see Schaeffer, 1947). Thus it would seem that predator pressure, resulting in a major cursorial specialization, was the critical selective force involved in the origin of the Perissodactyla. Unfortunately there is no direct evidence of the ecological factors involved, for the faunas in which the condylarth-perissodactyl transition took place have not yet been discovered. The absence of perissodactyls in known late Paleocene faunas and their sudden appearance in abundance at the beginning of the Eocene suggests migration from an unknown area. Thus early perissodactyls may have originated isolated from, and perhaps under different selective pressures than, other descendant lineages of the middle Paleocene *Tetraclaenodon* stock.

SUMMARY

The middle Paleocene phenacodontid condylarth genus *Tetraclaenodon* gave rise to three late Paleocene groups, represented by *Phenacodus*, *Ectocion*, and an as yet unknown proto-perissodactyl. The main morphological changes indicated by the fossil evidence of this evolutionary radiation are specializations for mastication and locomotion. Molars of *Phenacodus* are very similar to those of *Tetraclaenodon*, with low broad cusps apparently mainly adapted for crushing. Teeth of *Ectocion* have prominent W-shaped ectolophs, an adaptation for vertical shear, while molars of *Hyracotherium*, the most primitive known perissodactyl, are specialized for both vertical and transverse shear. *Phenacodus* and *Ectocion* show little specialization for running over the primitive ambulatory condition of *Tetraclaenodon*, but the limbs of *Hyracotherium* display major cursorial modifications, including a unique remodeling of the ankle which prevented lateral movement at that joint and made possible a precocious elongation and narrowing of the metatarsus.

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ZOOLOGY.—*Synopsis of the supergeneric groups of Rodents.*[1] GERRIT S. MILLER, JR., and JAMES W. GIDLEY, U. S. National Museum.

Work on the taxonomy of the Rodents, living and extinct, has occupied much of our time during the past four years. This paper contains a brief synopsis of the results.

The classification which we have adopted is based on the following conception of the evolutionary course followed by the order during its development. This course has been mainly conditioned by the mechanical problem of strengthening a chewing apparatus in which the unusually important cutting function of the incisors is strongly contrasted with the grinding function of the cheekteeth; the highest degree of efficiency to be given always to the incisors and in most instances to the cheekteeth as well. The problem has been solved by five sequences of correlated changes in the masseter muscle and the bones to which this muscle is attached. All of these sequences could originate from the structures present in a generalized mammal, but there is no evidence that any rodent during its development has passed from one to another. The groups characterized by the various sequences are therefore natural. We have treated them as superfamilies: the *Sciuroidae*, *Myoidae*, *Dipodoidae*, *Bathyergoidae*, and *Hystricoidae*. Of the secondary problems the most conspicuous has been the strengthening of the cheekteeth. These teeth, however unlike their structure in extreme instances may appear, have all been developed from some primitive, low-crowned, tritubercular type not essentially different

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[1] Published by permission of the Secretary of the Smithsonian Institution.

from that present in the Eocene *Paramyidae* and in living species of *Sciurus.* During the adjustment of the cheekteeth to increasingly heavy fore-and-aft grinding motion, a process which has taken place in most members of the order, the crown height has been augmented, while the original tubercles and lophs have been made more efficient by (a) increase in complexity, and (b) conversion into transverse ridges and specialized enamel plates, usually with reduction in the number of elements present. In each superfamily the characteristic modifications in the muscles and skull were begun in connection with the development of the incisors. Mechanical improvement of the cheekteeth came later. All rodent teeth have been developed from an essentially uniform original type under the influence of practically identical mechanical forces. Parallelism in highly specialized dental structures between genera and species which are not closely related is therefore frequent enough to be one of the noticeable peculiarities of the order. The history of development extends so far into the past that the essential features of structure are modernized in the oldest known Eocene rodents. No extinct member of the order has yet been found which can be regarded as ancestral to any considerable number of subsequent forms.

The order *Rodentia* may be defined as follows: Terrestrial and fossorial (occasionally arboreal or semiaquatic) placental mammals with both brain and placentation generalized in type; feet unguiculate; elbow joint always permitting free rotary motion of forearm; fibula never articulating with calcaneum; masseter muscle highly specialized, divided into three or more distinct portions having slightly different functions; cecum without spiral fold; dental formula not known to exceed i $\frac{1}{1}$, c $\frac{0}{0}$ pm $\frac{2}{1}$, m $\frac{3}{3}$ = 22 permanent teeth; incisors scalpriform, growing from persistent pulp, the enamel of the upper tooth not extending to posterior surface; distance between mandibular and maxillary toothrows approximately equal, both pairs of rows capable of partial or complete opposition at the same time, the primary motion of the lower jaw in mastication longitudinal or oblique.

Superfamily SCIUROIDAE

Masseter lateralis superficialis with anterior head distinct, this portion of the muscle not attached to any part of the zygoma except occasionally to a point at extreme base of zygomatic plate; zygomatic plate tilted upward, usually broad, with its superior border always above lower margin of infraorbital foramen. Infraorbital foramen inferior, transmittng nerve only; masseter lateralis passing obliquely upward to superior border of rostrum, always to exclusion of masseter medialis.

THREE-CUSPED SERIES

Teeth becoming hypsodont on the basis of a tritubercular structure.

Family SCIURIDAE

Skull never truly fossorial; infraorbital foramen with outer wall usually though not always forming a distinct canal, its orifice protected from muscular action by the presence, at or near its lower border, of an outgrowth for attachment of masseter lateralis superficialis; frontal with decurved postorbital process; cheekteeth brachydont or unilaterally hypsodont, the fundamental tritubercular plan usually (probably always) evident in functional adult teeth that have not undergone considerable wear; external form suited to arboreal or terrestrial life.

The *Sciuridae* of authors.

Subfamily *Sciurinae.*—Orbital region normal, the middle of orbit in front of middle of skull (except in genera with greatly elongated rostrum), the lachrymal bone above or in front of anterior extremity of toothrow, the zygomatic plate not especially emarginate below, the postorbital process indicating an evident boundary between orbit and temporal fossa; no parachute membrane.

The entire family except the members of the two following groups; Oligocene to Recent; Northern Hemisphere, South America, continental Africa.

Subfamily *Nannosciurinae.*—Like the *Sciurinae* but orbital region abnormal, the middle of orbit behind middle of skull (rostrum short), the lachrymal bone above middle of toothrow, the zygomatic plate conspicuously emarginate below, the postorbital process not indicating an evident boundary between large orbit and much reduced temporal fossa.

Nannosciurus of the Malay region, *Myosciurus* of West Africa, and *Sciurillus* of South America (the last not seen); Recent.

Subfamily *Pteromyinae.*—Like the *Sciurinae* but with a well developed parachute membrane present.

The Flying-squirrels; Middle Miocene to Recent; Northern Hemisphere.

Family GEOMYIDAE

Skull fossorial; zygoma robust; infraorbital foramen always at end of a long canal, its orifice protected from muscle pressure by countersinking in an oblique sulcus; frontal without postorbital process; cheekteeth evenly hypsodont or in their extreme development ever-growing, the fundamental tritubercular plan lost in functional adult teeth, the first and second molars of adult consisting of either one or two simple loops. External form in living members of the group highly modified for underground life.

Subfamily *Entoptychinae.*—Angular portion of mandible mostly below alveolar level; cheekteeth rooted, the enamel pattern of first and second molars consisting of two simple loops joined at protomere.[2]
Entoptychus; North American Oligocene.

Subfamily *Geomyinae.*—Angular portion of mandible mostly above alveolar level; cheekteeth ever-growing, the first and second adult molar consisting each of a simple prism, with an enamel plate always present on anterior surface in upper teeth and on posterior surface of lower teeth.
North American pocket gophers; Miocene to Recent.

Family Heteromyidae

Essential characters as in the *Geomyidae* but skull not fossorial; zygoma slender; orifice of infraorbital canal protected from muscle pressure by countersinking in a vacuity which extends transversely through rostrum; external form murine or saltatorial.
North American pocket-mice and kangaroo-rats; Middle Oligocene (*Heliscomys*) to Recent.

FOUR-CUSPED SERIES

Teeth becoming hypsodont on the basis of a quadritubercular structure.

Family Adjidaumidae

Zygomasseteric structure[3] and infraorbital canal as in the *Sciuridae;* cheekteeth $\frac{4}{4}$, slightly hypsodont, the enamel pattern unmodified heptamerous.[4]
Adjidaumo; North American Middle Oligocene.

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[2] Protomere = inner side of maxillary cheekteeth and outer side of mandibular cheekteeth.

Paramere = outer side of maxillary cheekteeth and inner side of mandibular cheekteeth.

[3] Zygomasseteric structure = the combined and correlated structures of the masseter muscle and of the skull in the region at which the muscle takes its origin.

[4] Heptamerous pattern = the enamel pattern of a flat-crowned cheektooth in which each of seven original tubercles is represented by a loop (two on the protomere, five on the paramere).

Family EUTYPOMYIDAE

Like the *Adjidaumidae* but with cheekteeth somewhat more hypsodont and the heptamerous enamel pattern complicated by the development of a considerable number of secondary closed loops which appear in partially worn teeth as an aggregation of minute enamel lakes covering nearly entire surface of crown.

Eutypomys; North American Middle Oligocene.

Family CHALICOMYIDAE

Like the *Adjidaumidae* but cheekteeth strongly hypsodont and enamel pattern reduced-heptamerous (sometimes paralleling that of the *Hystricidae*) becoming rapidly simplified as the crowns wear away; skull occasionally fossorial; no postorbital process on frontal; no pit-like depression in basioccipital region.

Chalicomys (= *Steneofiber*) and related genera, European Miocene and Pliocene; *Trogontherium,* European Pliocene and Pleistocene; *Palaeocastor, Eucastor* and related genera, North American Upper Oligocene and Lower Pliocene.

Family CASTORIDAE

Skull with rostrum broadened and deepened and braincase narrowed; basioccipital region with conspicuous pit-like depression; cheekteeth not ever-growing but so excessively hypsodont that the slightly reduced-heptamerous pattern (parallel: *Myocastor*) changes little with age and rarely if ever wears out; external form highy modified for aquatic life; caudal vertebrae flattened.

Castor; Lower Pliocene to Recent; Northern Hemisphere.

Family CASTOROIDIDAE

Zygomasseteric structure modified by the passage of the shaft of the incisor below the infraorbital foramen instead of above it, the ridge formed by the tooth dividing the area of masseteric origin on side of rostrum into two planes; posterior nares divided horizontally by the median fusing of palatine bones over roots of cheekteeth; teeth ever-growing, the enamel pattern a series of 5–7 parallel transverse ridges (parallel: *Dinomyidae*).

Castoroides; North American Pleistocene.

Superfamily MUROIDAE

Zygomasseteric structure as in the *Sciuroidae* except: Infraorbital foramen superior in whole or in part, entered or traversed by muscle as well as nerve; masseter lateralis seldom reaching superior border of rostrum, and never doing this to exclusion of masseter medialis.

THREE-CUSPED SERIES

Modifications of teeth based on an underlying tritubercular structure.

Family MUSCARDINIDAE

Skull with no striking modifications of general form; zygomatic root. much as in the *Sciuridae* except that its anterior face is nearly vertical instead of strongly oblique, and the infraorbital foramen extends above median level of orbit, receiving or transmitting a strand of muscle as well as the nerve; no postorbital processes; auditory bullae large, globular, rounded in front; cheekteeth $\frac{4}{4}$, brachydont (in *Leithia* subhypsodont), the enamel pattern reduced-hexamerous in forms with basin-shaped crowns, passing to a system of parellel transverse ridges in those with flat crowns (parallel: *Graphiuridae*); external form showing a combination of murine and sciurine features.

Eliomys, Dyromys, Glis, Muscardinus, Leithia; Old World Middle Miocene to Recent.

FOUR-CUSPED SERIES

Modifications of teeth based on an underlying quadritubercular structure.

Family ISCHYROMYIDAE

General characters of the skull as in the *Muscardinidae;* teeth $\frac{5}{4}$, moderately hypsodont, rooted, the fundamental structure quadritubercular, the enamel pattern in worn teeth reduced-heptamerous.

Ischyromys; North American Middle Oligocene.

Family CRICETIDAE

Fundamental zygomasseteric structure as in the *Muscardinidae* and *Ischyromyidae*, but infraorbital foramen usually enlarged and specialized, consisting of a rounded upper portion for transmission of muscle and a narrow lower portion for transmission of nerve, the zygomatic root developed into a broad, oblique plate; skull varying excessively in form, but always without postorbital process on the frontal; checkteeth $\frac{3}{3}$, the crown structure showing all stages from brachydont to ever-growing, the fundamental structure quadritubercular, the enamel pattern varying from simple heptamerism to excessive specialization, the tubercles in the maxillary teeth always presenting a longitudinally biserial arrangement and never developing a functional third series on lingual side of crown; external form murine or fossorial.

Subfamily *Cricetinae*.—Skull without special modification, the zygomasseteric structure as usual in the family, the squamosal not developing a postorbital ridge or process; molars rooted, their crowns varying gradually from tubercular and brachydont to flat-crowned and strongly hypsodont, when in the latter condition the prisms not opposite (compare *Gerbillinae*) and the posterior termination of m^1 and m^2 not angular (compare *Microtinae*).

The *Cricetinae, Sigmodontinae, Neotominae,* and *Nesomyinae* of authors; Oligocene to Recent; continental region of the world; Madagascar.

Subfamily *Gerbillinae.*—Auditory bullae and entire posterior portion of skull enlarged; teeth subhypsodont or hypsodont, flat-crowned in adults, with opposite prisms, these tending to form transverse ridges joined at median line, or, in their extreme development, to separate into plates; external form saltatorial.
The *Gerbillinae* of authors; Recent only, unless *Trilophomys* from the Pliocene of France is a member of the group; Asia and Africa.

Subfamily *Microtinae.*—Like the more hypsodont members of the subfamily *Cricetinae* but cheekteeth often growing from a persistent pulp, the enamel pattern always consisting of (at least partially) alternating triangles, the posterior termination of m^1 and m^2 never rounded; squamosal with distinct postorbital ridge or process.
The *Microtinae* of authors; Miocene to Recent; Northern Hemisphere.

Subfamily *Lophiomyinae.*—Like the *Cricetinae* with tubercular, slightly hypsodont teeth, but skull with temporal fossa bridged by a plate formed of laminae arising from the jugal, frontal, and parietal, a structure not known to occur elsewhere among rodents.
Lophiomys; Recent; Africa.

Family PLATACANTHOMYIDAE

Like the *Cricetidae* but zygomasseteric structure unusual, the infraorbital foramen of normal cricetine form, but zygomatic plate much narrowed, and masseter lateralis profundus extending its line of attachment along upper zygomatic border to side of rostrum above foramen; cheekteeth subhypsodont, the enamel pattern a modified heptamerous with tendency to form parallel oblique cross-ridges (parallel: *Muscardinidae*).
Platacanthomys and *Typhlomys;* Recent; Southern Asia.

Family RHIZOMYIDAE

Like the *Cricetidae* but zygomasseteric structure unusual, the infraorbital foramen with neural portion reduced or obliterated by partial or entire fusion of zygomatic plate with side of rostrum; skull and external form fossorial.

Subfamily *Tachyoryctinae.*—Infraorbital foramen with neural portion reduced to an inconspicuous notch by fusion of the broad zygomatic plate with side of rostrum (outline of plate below foramen usually visible); skull strongly fossorial; cheekteeth closed at base but extremely hypsodont, the enamel pattern not changing in character during adult life; enamel pattern in adult consisting of 2–3 parallel curved cross-ridges (the concave surface directed backward and outward in upper teeth, forward and inward in lower teeth; parallel: *Protechimys*); reduced-heptamerism evident in unworn enamel cap; external form modified, though not excessively, for underground life.
Tachyoryctes; Recent; Africa.

Subfamily *Rhizomyinae.*—Like the *Tachyoryctinae* but peculiarities of infraorbital region carried farther, the neural notch being obliterated and the foramen appearing as a small orifice confined to upper surface of zygomatic root; teeth moderately hypsodont, the enamel pattern obviously heptamerous or reduced-heptamerous and changing rapidly during adult life.

Rhizomys and related genera; Pliocene to Recent; southern Asia.

Subfamily *Braminae.*—Like the *Rhizomyinae* but cheekteeth with definitely prismatic structure.

Bramus; Pleistocene; northern Africa (not seen).

Family Spalacidae

Like the *Cricetidae* but zygomasseteric structure unusual, the zygomatic plate narrowed and turned downward to a nearly horizontal position, thus doing away with the separate neural portion of the opening by a process the exact opposite to that bringing about a similar result in some of the *Rhizomyidae;* skull excessively fossorial, the lambdoid crest carried forward to level of zygomatic root.

Subfamiy *Myospalacinae.*—Mandible scarcely movable at symphysis, a large post-symphyseal buttress early developed; cheekteeth growing from persistent pulps, the crowns elongated, the enamel pattern consisting of alternating triangles, the posterior termination of m^1 and m^2 rounded.

Myospalax; Recent; Asia.

Subfamily *Spalacinae.*—Mandible movable at symphysis throughout life; cheekteeth moderately hypsodont, rooted, subterete, the pattern reduced-heptamerous, changing rapidly with wear; skull with the characters of the family carried to such an extreme as to make it the most fossorial type known among rodents.

Spalax, Recent. *Prospalax,* Upper Pliocene, and an undescribed genus from the upper Oligocene; eastern Mediterranean Region, and southern Europe.

Family Muridae

Skull as in the typical *Cricetidae*; cheekteeth $\frac{3}{3}$, the upper teeth with a functional row of tubercles on lingual side of crown internal to the protocone and hypocone, these tubercles entering conspicuously into the plan of modification of the crowns.

Subfamily *Dendromyinae.*—Upper cheekteeth with triserial arrangement not fully developed; manus with only 3 functional digits.

The *Dendromyinae* of authors; Recent; Africa.

Subfamily *Murinae.*—Upper cheekteeth with fully developed triserial arrangement of tubercles always evident, though frequently varying from the symmetrical plan; crowns brachydont or slightly hypsodont; manus normal.

The *Murinae* of authors; Upper Miocene to Recent; Old World, except Madagascar.

Subfamily *Phloeomyinae*.—Upper cheekteeth with triserial arrangement of elements obscured by flattening out of each trio of tubercles to form a simple, detached, transverse lamina (parallel: *Diplomys*); crowns moderately hypsodont; braincase relatively small and auditory bullae reduced; external form heavy, arboreal.

Phloeomys; Recent; Philippine Islands.

Subfamily *Otomyinae*.—Upper cheekteeth with same modification as in the *Phloeomyinae*, but m^3 tending to become the dominant tooth in the series, its size always greater than that of m^2, and its elements usually reduplicated; external form heavy, terrestrial.

Otomys; Recent; Africa.

Subfamily *Hydromyinae*.—Upper cheekteeth with triserial arrangement obscured by suppression of tubercles of outer series; m^3 vestigial.

The *Hydromyinae* of authors; Recent; Australian Region.

Superfamily DIPODOIDAE

Masseter lateralis superficialis with anterior head not distinct, this portion of the muscle attaching along a considerable area on anterior border of zygoma; zygomatic plate nearly horizontal, always narrow and completely beneath infraorbital foramen. Angular portion of mandible not distorted outward at base to permit free passage of a branch of the masseter lateralis, its general direction not parallel with zygoma.

THREE-CUSPED SERIES

Modifications of teeth based on an underlying tritubercular structure, the hypocone when present not entering into the essential mechanical scheme of the crown.

A.—*Skull with no special pecularities except that the auditory bullae appear to be imperfect or absent (perhaps merely reduced as in* Phloeomys); *infraorbital foramen not transmitting muscle; cheekteeth brachydont or subhyposodont, their structure essentially as in the less modified Sciuridae.*

Family PARAMYIDAE

Rostrum and braincase approximately equal in width, infraorbital foramen very small, not visible in lateral view of the skull; cheekteeth $\frac{5}{4}$, the upper molars obviously and simply tritubercular in general plan, the hypocone, when present, appearing as a supplement to the original structure of the tooth.

Paramys, *Mysops*, *Prosciurus*, and related genera; North American Lower Eocene to Middle Oligocene.

B.—*Skull and teeth as in the Paramyids except that the auditory bullae are well developed, the infraorbital foramen is enlarged to transmit a small strand of muscle, and the cheekteeth are flattened.*

Family GRAPHIURIDAE

Cheekteeth $\frac{4}{4}$, brachydont, crowns wider than long, basin-shaped with small tubercles and low ridges (parallel: *Muscardinidae*); skull with no special peculiarities, the braincase much wider than rostrum; auditory bullae globular; external form muscardinine.

Graphiurus; Recent; Africa.

C.—*Skull fossorial (except perhaps in the Allomyidae); infraorbital foramen not transmitting muscle; auditory bullae well-developed; cheekteeth brachydont, hypsodont, or ever-growing; modification of crowns based on a structure including well developed protoconule and metaconule, and conspicuously trenchant outer commissures.*

Family ALLOMYIDAE

Cheekteeth $\frac{5}{4}$, brachydont or moderately hypsodont, the tritubercular structure of upper teeth evident in unworn crowns; protoconule and metaconule large; functional cusps in m^1 and m^2; mesostyle appearing in hypsodont forms as a conspicuous median rib on outer surface of crown (parallel: *Pseudosciuridae*).

Allomys, *Haplomys*,[5] *Meniscomys*, *Mylagaulodon;* North American Upper Oligocene and Miocene.

Family APLODONTIIDAE

Like the *Allomyidae* but the skull greatly widened posteriorly, the auditory bullae flask-shaped with neck directed horizontally outward; cheekteeth growing from persistent pulp, the unworn caps showing evident pattern of the *Allomys*-type, this soon wearing away and leaving a simple enamel ring; paramere with conspicuous vertical ridge.

Aplodontia; Pleistocene and Recent; *Liodontia*,[6] Miocene; western North America.

Family CYLINDRODONTIDAE

Skull fossorial with braincase slightly wider than rostrum; cheekteeth $\frac{4}{4}$, subterete, excessively hypsodont but not growing from persistent pulp, the enamel pattern in considerably worn upper teeth consisting of an outer ring and a central lake.

Cylindrodon; North American Lower Oligocene. Position of group doubtful.

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[5] New genus, type *Meniscomys liolophus* Cope.

[6] New genus, type *Aplodontia alexandrae* Furlong.

FOUR-CUSPED SERIES

Modifications of teeth based on an underlying quadritubercular structure, the hypocone always entering into the essential mechanical scheme of the crown.

A.—*Skull not specially modified; upper molars with large protoconule and metaconule, and conspicuously trenchant outer commissures, their structure paralleling that of the Allomyidae in the three-cusped series.*

Family PSEUDOSCIURIDAE

Skull essentially as in the *Sciuravidae* but with larger infraorbital foramen which may have transmitted a strand of muscle.
Pseudosciurus; European Oligocene.

B.—*Skull excessively fossorial; occipital region obliquely truncate, with lambdoid crest moved forward nearly to level of zygomatic root; frontal with short postorbital process; bony horn-cores present on rostrum in two genera, absent in a third; cheekteeth highly modified from a normal heptamerous structure, the grinding function of toothrow in adult almost completely taken over by the greatly enlarged fourth premolar.*

Family MYLAGAULIDAE

General structure of skull much as in the *Aplodontiidae;* cheekteeth $\frac{4}{4}$ or $\frac{2}{3}$; a reduced-heptamerous pattern evident in slightly worn crowns, but this giving place with wear to a system of narrow longitudinal and oblique lakes; molars relatively small, soon crowded out by the premolar, an excessively hypsodont, laterally compressed tooth, closed at the base, and rapidly increasing in crown length from the unworn surface downward. Skeleton highly modified for underground life.
Mylagaulus, Ceratogaulus, and *Epigaulus;* North American Miocene and Pliocene.

C.—*Skull without special peculiarities; infraorbital foramen moderate or very large, transmitting both muscle and nerve; cheekteeth subhypsodont or brachydont, their modifications based on a heptamerous structure in which the ridges are narrow and the reentrant spaces wide (parallels:* Funisciurus, *Erethizontidae); external form glirine or pteromyine; under side of tail with scaly outgrowths near base.*

Family ANOMALURIDAE

Skull with moderate infraorbital foramen; lower zygomatic root at level immediately in front of anterior cheektooth; anterior point of masseteric insertion on mandible beneath hinder part of m_1; no discrepancy between size of incisors and molars; cheekteeth subhypsodont, their crowns flat, longer than wide; external form pteromyine.
Anomalurus; Recent; Africa.

Family IDIURIDAE

Like the *Anomaluridae* but skull with infraorbital foramen greatly enlarged, the lower zygomatic root nearer to incisor than to anterior cheektooth; anterior point of masseteric insertion on mandible in front of pm^4; incisors excessively heavy; cheekteeth weak, extremely brachydont, their crowns flat, wider than long.

Subfamily *Idiurinae.*—Flying membrane present; cheekteeth with two complete median transverse ridges.
Idiurus; Recent; Africa.

Subfamily *Zenkerellinae*—Flying-membrane absent; cheekteeth with one complete median transverse ridge.
Zenkerella; Recent; Africa.

D.—*Skull without striking peculiarities other than a tendency to assume a form characterized by broad braincase, large auditory parts, and weak rostrum (parallels; Gerbillinae, Octodontinae); infraorbital foramen transmitting muscle in all members of the group in which the skull is known except probably* Sciuravus; *cheekteeth varying from brachydont to evergrowing, their modifications based on a heptamerous structure in which the ridges are wide and the reentrant spaces narrow.*

Family SCIURAVIDAE

Infraorbital foramen small, but visible in lateral view of skull, probably transmitting nerve only; cheekteeth $\frac{5}{4}$, brachydont; the structure of the upper molars obviously and simply quadritubercular.
Sciuravus; North American Middle Eocene.

Family ZAPODIDAE

Infraorbital foramen large, transmitting muscle as well as nerve; cheekteeth varying in number from $\frac{5}{4}$ in the earlier members of the group to $\frac{3}{3}$ in the most advanced; the quadritubercular crown structure usually though not always much modified; metatarsals not reduced or fused.

Subfamily *Theridomyinae.*—The earlier, less modified members of the family: pm^4 a large, functional tooth; crowns of cheekteeth varying from brachydont and simply quadritubercular (*Sciuroides*) to hypsodont and much reduced heptamerous (*Issiodoromys;* parallel: *Eocardia*).
The *Theridomyidae* of authors; European Lower Eocene to Miocene.

Subfamily *Sicistinae.*—Cheekteeth brachydont, $\frac{4}{3}$, distinctly quadrituberculate, the enamel of moderately worn upper molars with a simple heptamerous pattern; external form murine, the hind legs and feet not lengthened.
Sicista, Recent, Eurasia; *? Eomys*, European Upper Eocene.

Subfamily *Zapodinae.*—Cheekteeth subhypsodont, $\frac{4}{3}$ or $\frac{3}{3}$, flat crowned, the enamel pattern of the upper molars heptamerous, slightly or considerably modified; external form saltatorial, the hind legs and feet lengthened.
Eozapus, Recent, China; *Zapus, Napaeozapus,* Pleistocene and Recent, North America.

Family Dipodidae

Like the *Zapodidae* but with the inner and outer metatarsals reduced or absent and the three median fused to form a canon bone; cheekteeth hypsodont, the heptamerous enamel pattern undergoing modifications most of which are parallel to those taking place in the teeth of the *Cricetidae* and in the hystricine families.

Subfamily *Protoptychinae.*—Upper cheekteeth 4, moderately hypsodont; pm^4 a large, functional tooth; skull with relatively broad rostrum and narrow braincase.
Protoptychus;[7] North American Upper Eocene.

Subfamily *Dipodinae.*—Cheekteeth $\frac{4}{3}$ or $\frac{3}{3}$, strongly hypsodont; pm^4 vestigial; skull with relatively narrow rostrum and broad braincase.
The *Dipodidae* of authors who recognize the *Zapodidae* as a distinct family; Pleistocene and Recent; Eurasia and northern Africa.

Family Ctenodactylidae

Cheekteeth growing from a persistent pulp, the adult pattern reduced to a simple ring infolded on one or both sides (parallel: *Octodontinae*); external form fossorial.
Ctenodactylus and related genera from the Mediterranean region; Pliocene to Recent.

Family Pedetidae

Cheekteeth subterete, growing from a persistent pulp; all trace of the original crown structure lost, the unworn enamel cap transversely cleft, the adult pattern consisting of a narrow median infold from the paramere extending nearly across to opposite side; external form conspicuously saltatorial, but median metatarsals showing no tendency to become reduced or fused.
Pedetes; Recent; Africa.

Superfamily BATHYERGOIDAE

Zygomasseteric structure as in the *Dipodoidae* except: Angular portion of mandible distorted outward to allow passage of a specialized and

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[7] While *Protoptychus* is a true dipodid with few primitive characters its exact position is not clear. It may prove to be a member of the *Theridomyinae*; but for the present we prefer to place it in the *Dipodidae* on account of its resemblance to the recent genus *Euchoreutes.*

enlarged distal anterior limb of the masseter lateralis superficialis, its general direction parallel with zygoma. Masseter medialis arising from upper margin of orbit and not passing through small infraorbital foramen.

Family Bathyergidae

Skull and external form with conspicuous fossorial adaptations. Cheekteeth extremely hypsodont, though not ever-growing; enamel pattern in adult a ring with or without a reentrant fold on one or each side (parallel: *Octodontinae*); number of cheekteeth ranging from $\frac{2}{2}$ to $\frac{6}{6}$. (In the genus, *Heliophobius*, with the greatest number of teeth there are never more than $\frac{5}{4}$ functional at one time; the apparent addition of one tooth in the upper jaw and two in the lower jaw to the maximum rodent formula is probably due to a specialized condition of the milk dentition.)

The *Bathyergidae* of authors; Recent; Africa.

Superfamily HYSTRICOIDAE

Zygomasseteric structure as in the *Bathyergoidae* except: Masseter medialis arising from side of rostrum and passing through large infraorbital foramen.

LATERALIS SERIES

Masseter lateralis the chief agent in modifying form of outer side of mandible; an oblique ridge extending forward from lower border of angular process usually present for attachment of this muscle.

A.—*Lachrymal bone small, forming no important part of zygomatic root, its lower portion confined within orbit; lachyrmal canal closed in front of orbit.*

Family Hystricidae

Skull with no special peculiarities other than a tendency (most pronounced in the genus *Hystrix*) to inflation of the rostral and frontal regions; mandibular rami rather freely movable at symphysis; angular process deep, neither produced backward conspicuously behind articular level nor folded inward along lower margin; cheekteeth $\frac{4}{4}$, their enamel pattern slightly removed from the simple heptamerous type, the reentrant folds narrow and not angular.

Old World porcupines; Upper Miocene to Recent.

Subfamily *Hystricinae*.—Base of upper zygomatic root over a point decidedly behind the anterior extremity of toothrow; cheekteeth strongly hypsodont, closed at base but without definite roots; sacral vertebrae 4.

Hystrix, *Acanthion*, *Thecurus*; Africa, southern Asia, and Malay region.

Subfamily *Atherurinae.*—Base of upper zygomatic root over anterior extremity of toothrow; cheekteeth subhypsodont, with well developed roots; sacral vertebrae 3.

Atherurus, Trichys: Recent; Malay region.

Family ERETHIZONTIDAE

Like the *Hystricidae* but: Mandibular rami with conspicuous post-symphyseal buttresses which prevent movement at the symphysis; lower border of angular process folded inward; cheekteeth subhypsodont, flat crowned, with reduced-heptamerous enamel pattern characterized by narrow ridges and wide reentrant spaces, the spaces on the paramere tending to become transformed into pits (parallels: *Funisciurus, Anomaluridae*). Upper zygomatic root over anterior part of toothrow; feet noticeably modified for arboreal life.

New World porcupines except *Chaetomys:* Oligocene to Recent. Oligocene of Egypt?[8] Extinct South American genera: *Asteromys, Eosteiromys, Parasteiromys, Steiromys.*

Family ECHIMYIDAE

Like the *Erethizontidae* but lower border of angular process usually with no evident infolding, feet usually not modified for arboreal life, and adult cheekteeth with narrow reentrant folds; cheekteeth varying from brachydont to ever-growing, the structure when hypsodont not multilaminar.

Subfamily *Echimyinae.*—Fossorial specialization usually absent; skull and cheekteeth showing great variety of form; enamel pattern not simplified to a ring with an infold on one or each side.

Tropical America; Miocene to Recent. Spiny-rats (provisionally including *Chaetomys*), Hutias (*Capromys, Plagiodontia*), etc.; also many extinct genera, among them *Acaremys, Boromys, Brotomys, Colpostemma, Eocardia* (parallel: *Issiodoromys*), *Eoctodon, Graphimys, Gyrignophus, Haplostropha, Heteropsomys, Homopsomys, Isolobodon, Prospaniomys, Protadelphomys, Protacaremys, Sciamys, Scleromys, Spaniomys, Stichomys, Strophostephanus, Tribodon.* It is probable that this group needs subdividing.

Subfamily *Octodontinae.*—Fossorial specialization usually present; cheekteeth, except in earliest known genera, with enamel pattern completely simplified to a ring with an infold on one or each side (parallel: *Ctenodactylidae*).

South America; Oligocene to Recent. Recent genera: *Ctenomys, Octodon, Octodontomys, Spalacopus.* Among the fossil genera are: *Cephalomys, Dicoelophorus, Eucoelophorus, Litodontomys, Neophanomys, Palaeoctodon, Phtoramys, Pithanotomys, Plataëomys, Scotomys.*

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[8] The genera *Phiomys* and *Metaphiomys*, based on lower jaws and teeth, have no characters by which they can at present be referred to any other family.

Family PETROMYIDAE

In general resembling the *Octodontinae* but crown of each cheektooth margined by two elevations on the protomere, these elevations probably resulting from the unusual obliquity at which the teeth appear to be set. The teeth are rooted, strongly hypsodont; the enamel pattern consists of two transverse lobes united by a median isthmus, the outer edges of the lobes becoming joined in the upper teeth when worn. No specimens examined.[9] Recognized as a family by Tullberg, partly on whose authority we continue to treat it as distinct. The characters of the teeth indicate important mechanical peculiarities of the chewing apparatus. The enamel pattern appears to be of a type which could be directly derived from that present in the relatively low-crowned molars of *Erethizon* and the Oligocene African *Phiomys*.

Petromys, South Africa: Recent.

Family MYOCASTORIDAE

In general like the *Erethizontidae* but upper zygomatic root over middle of toothrow, and cheekteeth with structure paralleling that present in *Castor;* lateral process of paroccipital large, projecting freely above base of greatly elongated paroccipital process; in living species external form modified for aquatic life.

Myocastor and related fossil genera; South America; Miocene to Recent.

Family THRYONOMYIDAE

Like the *Myocastoridae* but cheekteeth with structure paralleling that present in some of the *Echimyinae,* and lateral process of paroccipital small, closely applied to base of moderately large paroccipital process; external form not modified for aquatic life.

Thryonomys; Africa; Recent.

Family DINOMYIDAE

Like the *Echimyidae* but cheekteeth combining a multilaminar structure with excessive hyposodonty (parallel: *Castoroides*); so far as known the external form is robust, terrestrial.

South America and the Greater Antilles; Miocene to Recent. Includes the living *Dinomys* and the extinct genera *Amblyrhiza, Briaromys, Discolomys, Elasmodontomys, Gyriabrus, Megamys, Neoepiblema, Olenopsis, Potamarchus, Tetrastylus.*

Family CUNICULIDAE

Not essentially different from the *Dinomyidae;* but the jugal and part of the maxillary are expanded to form a conspicuous cheekplate, the surface of this becoming excessively rugose in adult; cheekteeth strongly

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[9] Mr. Oldfield Thomas has kindly sent us photographs of a skull in the British Museum (No. 4.2.3.98).

hypsodont, but enamel structure not completely multilaminar; external form robust, terrestrial.

Cuniculus (="*Coelogenys*"); Tropical America; Pleistocene and Recent.

Family Heptaxodontidae

First tooth of maxillary series mechanically dominant, cheekteeth apparently reduced to $\frac{2}{2}$, conditions not known elsewhere in the *Hystricoidae*, and indicating zygomasseteric development along a line different from that followed elsewhere in the group; enamel structure multilaminar with reduplication in the anterior tooth; diagnostic cranial characters unknown.

Heptaxodon; Porto Rico; Pleistocene? The genus *Morenia* from the South American Miocene may be a second member of the family; it is at present known from isolated teeth only.

B.—*Lachrymal bone large, usually forming an important part of zygomatic root, its lower portion extending forward out of orbit to a level in front of anterior margin of infraorbital foramen; some part of lachrymal canal open on side of rostrum in front of orbit.*

Family Dasyproctidae

Skull generalized in structure, closely resembling that of the less specialized *Hystricidae;* cheekteeth hypsodont but with a nearly unmodified heptamerous structure, paralleling that in the *Hystricidae;* external form cursorial, the legs lengthened, the digits 5–3.[10]

The *Dasyproctidae* of authors with *Cuniculus* removed and *Neoreomys* added; South and Middle America; Miocene to Recent.

Family Chinchillidae

Cheekteeth with heptamerous structure excessively modified, the enamel pattern consisting of parallel transverse laminae (parallel: *Dinomyidae*); mandible with no sharply defined ridge for attachment of masseter lateralis; external form saltatorial.

South America; Miocene to Recent. Living genera: *Chinchilla, Lagostomus, Viscaccia.* Extinct genera: *Euphilus, Perimys, Pliolagostomus, Prolagostomus, Scotaëumys, Sphaeromys.*

Family Abrocomidae

Like the *Chinchillidae* but cheekteeth with deep reentrant angles on both sides, and mandible with sharply defined ridge for attachment of masseter lateralis; external form not saltatorial.

Abrocoma; South America; Pliocene to Recent.

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[10] The feet of *Neoreomys* are imperfectly known, but there appears to be nothing in the structure of the parts which have been described that indicates the presence of more than three digits in the hind foot.

MEDIALIS SERIES

Masseter medialis the chief agent in modifying form of outer side of mandible; a conspicuous horizontal ridge for the attachment of this muscle present on side of mandible slightly below alveolar level.

Family Caviidae

Posterior cheektooth both above and below without reduplication of elements, the general character of the toothrow normal.

The *Caviidae* of authors with *Hydrochoerus* and its allies removed; South America; Miocene to Recent. Extinct genera: *Anchimys*, *Neoprocavia*, *Orthomyctera*, *Palaeocavia*, *Phugatherium*, *Procardiotherium*.

Family Hydrochoeridae

Posterior cheektooth both above and below with conspicuous reduplication of elements, the general character of the toothrow thus rendered abnormal.

Hydrochoerus and its extinct allies *Plexochoerus*, *Prohydrochoerus* and *Protohydrochoerus;* perhaps *Cardiomys*, *Caviodon* (=*Diocartherium*) and *Cardiotherium* also; South America, Miocene to Recent; southeastern United States, Pleistocene.

GRADES AND CLADES AMONG RODENTS

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As has been pointed out many times, the rodents are the most abundant and successful mammalian order. Their evolution has been channeled into a single major direction by the development, as an initial modification, of ever-growing, gnawing incisors, with associated changes in skull and jaw muscles. Subsequent evolution has involved a great deal of parallelism within the order, making it very difficult to disentangle the convergent and parallel changes from those that are truly indicative of phyletic relationship. The similarity in complexity of the evolutionary pathways among rodents to those among actinopterygians, and particularly teleosts, has also been pointed out.

Work by various authors has indicated that the evolution of the actinopterygians consists of the sequential attainment of a series of morphological stages, or grades (as in Huxley, 1958), each of which has been derived from the preceding one several independent times by a series of parallel trends. The classification of actinopts at the supraordinal level involves a series of taxa that are currently agreed to represent such polyphyletic grades rather than monophyletic units or clades (Schaeffer, 1956, p. 202).

The rodents were, classically, divided into three suborders on the basis of the structure of the jaw musculature and associated osteological differences—the Sciuromorpha, Myomorpha, and Hystricomorpha (Simpson, 1945). All recently proposed classifications of the order (Lavocat, 1956; Schaub, 1958, p. 691–694; Simpson, 1959; and Wood, 1955a and 1959), adopt the multiplicity of major groups postulated by Miller and Gidley (1918) or Winge (1924), and agree that the three classic suborders are not monophyletic clades, but rather, taken as a whole, represent a grade that is an advance over the primitive rodent grade. The classic suborders represent alternative expressions of an advanced rodent grade, and may well have been achieved approximately simultaneously. The various clades within the order are still not clearly recognizable, and much work remains to be done before rodent cladal classification is stabilized to everyone's satisfaction, though considerable progress is being made.

There is no direct evidence as to the type of jaw muscles in the still unknown ancestral rodents that lived during the Paleocene. However, Edgeworth (1935, pp. 73–75), in discussing the primitive mammalian jaw musculature, indicates that a major part of it consists of an embryological single muscle mass, divisible into the *Temporalis*, *Zygomaticomandibularis*, and *Masseter*. The *Zygomaticomandibularis* is usually divided into anterior and posterior portions by the masseteric nerve. The masseter may be single or be divisible into two or more layers, with no clear indications as to which is the primitive condition.

Among students of rodent anatomy there have been many varying interpretations of the jaw musculature. Usually, the *Zygomaticomandibularis* has been considered to be part of the masseter (*Masseter medialis* of Tullberg, 1899, pp. 61–62; *Masseter profundus* of Howell, 1932, pp. 410–411), but sometimes it is treated as a separate muscle (Lubosch, 1938, p. 1068; Müller, 1933, pp. 14–24). The two parts of the masseter of Edgeworth are the *Masseter lateralis superficialis* and *Masseter lateralis profundus* of Tullberg, or the *Masseter superficialis* and *Masseter major* of Howell. Lubosch (1938, fig. 930) and Müller (pp. 19–20) also consider the anterointernal portion of what is usually called the masseter to be a distinct muscle, the *Maxillomandibularis.*

In the following discussion, the masseter is considered to consist of three parts—the *Masseter superficialis*, arising from the anterior end of the zygoma or the side of the snout and inserting on the ventral border of the angle (= *Masseter lateralis superficialis*); the *Masseter lateralis*, arising from most of the length of the lateral surface of the zygoma and inserting on the ventral part of the angular process (= *Masseter lateralis profundus*; *Masseter major*); and the *Masseter medialis*, arising from the medial side of the zygoma, whence it has sometimes spread to the medial wall of the orbit or forward through the infraorbital foramen, and inserting on the dorsal portion of the masseteric fossa of the jaw (= *Masseter profundus*; *Zygomaticomandibularis*; *Maxillomandibularis*). These are illustrated in Figs. 1–4.

The separation of evolutionary grades among the rodents can best be done on the basis of: (1) the incisor pattern and structure; (2) the structure of the jaw muscles and the associated areas of the skull and jaws; and (3) the general pattern and height of crown of the cheek teeth. These can be used as general clues to evolutionary grades throughout the order. The discussion below will largely be limited to these sets of criteria. On the other hand, the separation and identification of the clades must involve the use of all available data, and must not select one set of structures as the most critical one, with other criteria neglected.

Grade One—Protrogomorph Radiation

The initial recorded rodent radiation, known from the Eocene but presumably having gotten well started in the later Paleocene, involved animals that had already acquired the basic gnawing adaptations.

The incisors were ever-growing, with the enamel limited to an anterior band, giving the perpetual chisel-edge that characterizes the Rodentia. The upper incisor was recurved, the worn surface being nearly vertical, and the lower incisor acted against it by moving upward and forward. The enamel cap had extended around the edges of the incisor, on both medial and lateral faces, to brace it better against the stresses of gnawing. The incisor enamel is of constant distribution on the incisor cross section, once the animal reached its adult size. Histologically, the incisor enamel in the Eocene members of the group is of the type called pauciserial by Korvenkontio (1934, p. 97, and fig. 1), in which the enamel is made up of irregular bands, ranging from a single row of enamel prisms, to as many as three or four rows of prisms. A change to the uniserial type of enamel (*op. cit.*, p. 130) has taken place in members of this radiation by the Oligocene.

As in all known rodents, there were no pre- or postglenoid processes, the glenoid fossa being elongate and slightly inclined from rear to front, so that the jaw could be moved backward bringing the cheek teeth into occlusion, or forward bringing the incisors together and separating the cheek teeth, vertically.

The dental formula had been reduced to the most primitive that is still found in living rodents. namely I^1_1, C^0_0, P^2_1, M^3_3. The cheek teeth were low-crowned and cuspidate in the earliest family (Paramyidae) or higher crowned and crested in derived families (Ischyromyidae, Sciuravidae), but were always based on a pattern of no more than four transverse crests. Occasional Eocene forms plus most later ones had hypsodont or even ever-growing cheek teeth (Cylindrodontidae, Aplodontoidea). Locomotion was largely scampering (or arboreal scampering), though some derivatives of this group had developed burrowing locomotion (Cylindrodontidae, Mylagualidae), and some may have been saltatorial (Protoptychidae).

The angle of the lower jaw was essentially in the same vertical plane as the rest of the jaw, as is usual among mammals. Specifically, it is usually in the plane of the incisive alveolus (sciurogna-

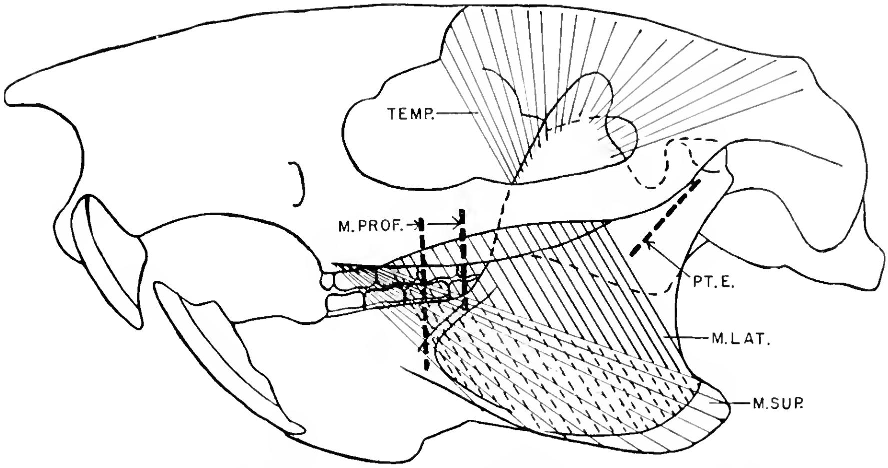

FIG. 1. Skull of the Eocene protrogomorph *Ischyrotomus*, with the jaw musculature restored, × 1. Abbreviations: M. LAT.—*Masseter lateralis*, dashed portions lying beneath *Masseter superficialis*; M. PROF.—dashed lines indicating the course of the *Masseter profundus*; M. SUP.—*Masseter superficialis*; PT. E.—dashed line indicating course of *Pterygoideus externus*; TEMP.—*Temporalis*.

thous), though occasionally (*Reithroparamys*—Wood, 1962, fig. 41E) it has shifted to a position just laterad of the alveolus (incipiently hystricognathous).

The chief components of the jaw musculature were the temporal, the pterygoid, and the masseter. All showed a certain amount of differentiation (Fig. 1). In a form such as *Ischyrotomus*, the temporal was a large, fan-shaped muscle, arising in a semicircle from the frontal and parietal, and inserting on the coronoid process. Although the anterior fibers had a forward component and the posterior ones a backward component, its primary function was to raise the jaw, which pivoted about the condyle. The internal pterygoid, arising on the inner side of the pterygoid fossa and inserting on the inner surface of the angle (Wood, 1962, fig. 69B), pulled the jaw toward the midline as well as closing it. The external pterygoid (Fig. 1 PTE) arose on the external pterygoid process and inserted on the medial surface of the condyle. It helped to pull the jaw mesiad, but very largely served to slide the condyle forward and ventrad, along the glenoid cavity, to disengage the cheek teeth and bring the incisor tips into contact. The jaw was moved back again by the combined action of the temporal and the digastric.

In *Ischyrotomus* the areas of origin and insertion of the *Masseter superficialis*, *M. lateralis*, and *M. medialis* are readily separable (Fig. 1). The *Masseter medialis* arose from the medial surface of the zygoma and inserted on the dorsal surface of the masseteric fossa of the lower jaw. It pulled the jaw nearly straight upward. There was the beginning of a differentiation of this muscle into two portions, the anterior inserting on the masseteric tuberosity by a separate tendon. It seems probable that these parts were separated by the masseteric nerve. The *Masseter lateralis* arose from a fossa extending most of the length of the zygoma, and occupying the ventral third of the arch. It inserted over much of the lateral surface of the angle, and pulled the lower jaw laterally, upward, and slightly forward. The most superficial of the three divisions of the masseter was the *Masseter superficialis*, which arose from the masseteric fossa on the base of the maxillary portion of the zygoma, immediately laterad of the upper premolars, and inserted along the ventral margin of the jaw all the way to the angle.

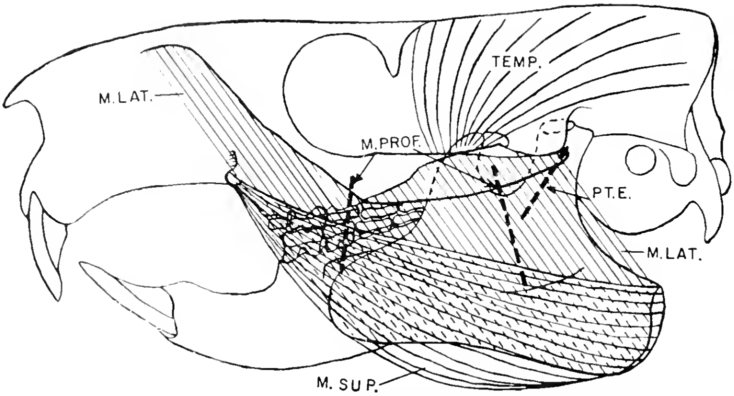

FIG. 2. Skull of the sciuromorphous sciurid *Marmota*, × 1. Abbreviations as for Fig. 1.

It was the major element in pulling the lower jaw forward, and hence in gnawing.

The functional activity of the jaws was composed of three parts (Becht, 1953, p. 515). A vertical or transverse movement, with the condyle toward the posterior end of the glenoid cavity, was used in the chewing activities of the cheek teeth. This would have involved the use of the main part of the temporal, the two inner parts of the masseter, and the internal pterygoid, and is the usual mammalian chewing activity. If the condyle were moved forward to the anterior end of the sloping glenoid cavity, the cheek teeth would be disengaged, and the same combination of muscles plus the *Masseter superficialis* would provide the motion of the lower incisor against the upper, resulting in gnawing. The third component, the shift from the first position to the second, would be brought about by the anterior portion of the temporal, the external pterygoid, and the *Messeter superficialis*; the reverse by the posterior portion of the temporal and the digastric.

The members of this grade include nearly all of the pre-Oligocene rodents of North America and Asia and some of those of Europe (none being known from the rest of the world). Several lines survive into the Oligocene or early Miocene, and the Aplodontoidea occur from the Oligocene to the present, mostly in North America, although some aplodontids are present in Palaearctica. This grade seems to include forms so related that they may be considered to be a clade, the Suborder Protrogomorpha.

Grade Two—Second Radiation

Gnawing in the method outlined above was effective and presumably more efficient than that of the multituberculates or any of the other gnawing groups that were competing with the rodents in the Eocene. But the gradual filling of the available niches resulted in greater intra-ordinal competition and increased selective value for more efficient use of the incisors, which was brought about by a series of changes involving the muscles of mastication, the skull structure, the incisors, and the cheek teeth.

The modifications of the masseter muscle and the concomitant skull changes were the most prominent alterations leading to Grade Two. These changes involved either the *Masseter lateralis* or the *Masseter medialis* or both, the *Masseter superficialis* remaining essentially unchanged.

The *Masseter lateralis* may shift forward and upward, behind and median to the origin of the *Masseter superficialis*, onto the front of the zygomatic arch (Fig. 2). The shift was beginning in the ischyromyids *Titanotheriomys* (Wood, 1937, pp. 194–195, pl. 27, fig. 1, 1a, 1b) and *Ischy-*

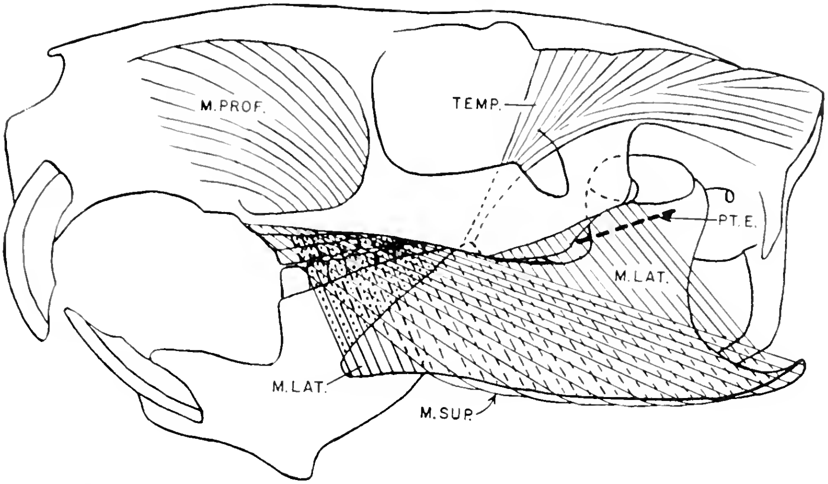

FIG. 3. Skull of the hystricomorphous caviomorph *Myocastor*, × 1. Abbreviations as for Fig. 1. Ventral part of *M. profundus* dotted.

romys troxelli (*op. cit.*, p. 191; Burt and Wood, 1960, p. 958), where the muscle was below, instead of lateral to, the infraorbital foramen. This process continued, with the muscle origin moving forward and upward along the anterior face of the zygoma, passing lateral and dorsal to the infraorbital foramen, eventually reaching almost to the top of the snout and forward onto the premaxillary. This pattern characterizes the sciuromorphous rodents—the Sciuridae, Castoroidea, and Geomyoidea. This shift of origin has changed the direction of pull of the anterior part of the *Masseter lateralis* by 30 to 60°, so that it essentially parallels the *Masseter superficialis*, greatly strengthening the forward component of masseteric action (Fig. 2).

In other rodents, the anterior part of the *Masseter medialis* has spread from the inner surface of the zygoma (or, perhaps, from the medial margin of the orbit) forward through the enlarged infraorbital foramen onto the snout (Fig. 3). In extreme cases, its origin extends as far forward as the premaxilla, almost reaching the posterior end of the external nares (*Hydrochoerus, Pedetes, Thryonomys*). This gives an almost horizontal resultant to the contraction of this muscle, and strongly augments the horizontal action of the *Masseter superficialis*. This pattern characterizes the hystricomorphous rodents—the Caviomorpha; the Dipodoidea, Theridomyoidea, and Thryonomyoidea; and the Anomaluridae, Ctenodactylidae, Hystricidae, and Pedetidae.

The Bathyergidae have developed perhaps the most massive masseters of any of the rodents, although there seems to have been very little shifting of the muscles (Tullberg, 1899, p. 78). The *Masseter medialis* has a broad expanse on the median side of the orbit (perhaps associated with the reduction of the eyes) and is confluent with the anterior end of the *Temporalis* (Tullberg, *op. cit.*, p. 75, and pl. 2, figs. 8–10, 17–18). In most members of the family, no part of the *Masseter medialis* passes through the small infraorbital foramen, but in *Cryptomys* (= *Georychus coecutiens*, Tullberg, 1899, p. 79) a small portion just edges through the foramen (*op. cit.*, pl. 2, fig. 17). Landry (1957, pp. 66–67) has argued that the small size of the infraorbital foramen and the limited forward extent of the *Masseter medialis* are secondary modifications of a hystricomorphous pattern, and that, in spite of their differences, this family is relatively

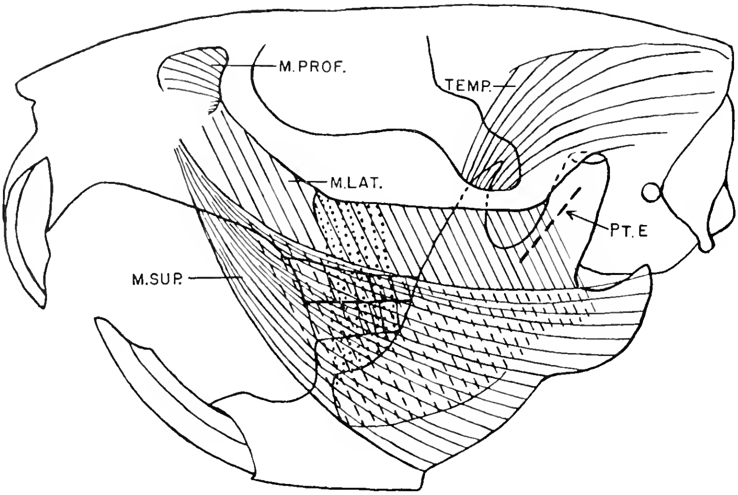

FIG. 4. Skull of the myomorphous cricetid *Ondatra*, × 1.5. Abbreviations as for Fig. 1. Ventral part of *M. profundus* dotted.

closely related to the Hystricidae. Most authors would not accept this conclusion. Since the earliest known bathyergids, from the Miocene of Kenya, were essentially identical in masseteric structure to living forms (Lavocat, 1962, p. 292), it is impossible to be certain of the direction of evolutionary change in this group. However, the *Masseter lateralis* seems to be in the process of spreading forward and upward onto the anterior side of the snout. This, together with the enlarged expanse of the *Masseter medialis* on the mesial side of the orbit, seem to be jaw muscle migrations sufficient to place these forms in Grade Two.

The expansion of the *Masseter medialis* onto the medial as well as lateral side of the orbit in bathyergids (Tullberg, 1899, pl. 2) and in *Castor* (*op. cit.*, pl. 22, fig. 9), putting it in an ideal position to expand through the infraorbital foramen if that opening were large enough, was probably a structural antecedent of the hystricomorphous pattern. Whether or not it indicates any close relationship between these forms and any histricomorphous rodents is arguable.

Finally, in the myomorphous rodents, both the *Masseter lateralis* and the *Masseter medialis* have migrated, combining the features of the sciuromorphous and hystricomorphous groups (Fig. 4). This pattern characterizes the Muroidea, Spalacoidea, and Gliroidea. Such a type of masseter gives the greatest anteroposterior component of any of the types of rodent jaw musculature, with the possible exception of the paca (*Cuniculus*). It is perhaps not a coincidence that this pattern is found in the Muroidea, the most successful and cosmopolitan of all rodents.

At the same time that these changes in the masseter were occurring, the temporal muscle withdrew in most forms from the anterior area where it originated in *Ischyrotomus*, and is restricted in its origin to areas behind the tip of the coronoid process. In such forms it serves to raise the lower jaw and close the mouth or joins with the digastric and part of the *Masseter medialis* to move the jaw backward. However, the temporal keeps its anterior area of origin in the Bathyergidae and in some of the Rhizomyidae. Whether the conditions in these two families are primitive or secondary is unknown. The reduction of the temporal muscle continued in many rodents, especially those with enlarged auditory bullae (Howell, 1932, p. 411), so that in some it eventually became reduced to an exceedingly minute slip (Tullberg, 1899, pl. 9, figs. 8–9, *Ctenodactylus*; pl. 10, figs. 8–9, *Pedetes*; pl. 12, *Dipus* and *Alactaga*; and pl. 23, figs. 18–20, *Dipodomys*).

All of the sciuromorphous and myomorphous rodents and a number of the hystricomorphous ones (Theridomyoidea, Anomaluridae, Ctenodactylidae, and Pedetidae) have an angular process of the sciurognathous type, with the angle in the plane of the incisive alveolus. This is undoubtedly the primitive condition. In the other hystricomorphous rodents, the angle has shifted until it arises quite markedly laterad of the incisor. This would make the *Masseter lateralis* and *M. superficialis* more nearly vertical. This hystricognathous arrangement is fully developed in the earliest known (early Oligocene) members of the South American subordinal clade Caviomorpha (Wood and Patterson, 1959, p. 289) and of the African clade Thryonomyoidea (Wood, MS. 1), as well as in the Hystricidae, apparently of south Asiatic origin (Lavocat, 1962, pp. 292–293), and in the Bathyergidae.

Associated with these changes in the jaw muscles, but not necessarily occurring at precisely the same time, nor necessarily functionally correlated, there have been changes in the incisors, involving both their angulation and their histology. The lower incisors have usually become arcs of larger circles, so that they are more nearly horizontal, with the tips moving anteroposteriorly against the upper incisors. The upper incisors have tended to become either larger or smaller arcs, so that the tips tend to point either forward (true usually of burrowing forms), or slightly backward as is true of most living rodents. The former of these adjustments increases the ability to use the incisors as digging implements, with a corresponding increase in the rate of growth of the incisors, which reaches almost 0.5 cm per week in the lower incisors of geomyids (Manaro, 1959). The second change brings the enamel blades of the upper and lower incisors more nearly into direct opposition than was true in Grade One.

Changes also took place in the histology of the incisor enamel. The pauciserial type has been modified, in members of Grade Two, in two different directions. In the uniserial type (Korvenkontio, 1934, p. 227), the lamellae are regular, and made up of one row of prisms each, with the prisms oriented in opposite directions in successive lamellae. This pattern is found in the Sciuridae, Castoridae, Geomyoidea, Gliridae, Muroidea, Spalacidae, Dipodoidea, and Anomaluridae among members of Grade Two, and in *Aplodontia*, *Meniscomys*, and *Ischyromys* among the members of Grade One (Korvenkotio, 1934, table on pp. 116–123).

The situation among the Theridomyoidea is most instructive. In the middle Eocene to Oligocene Pseudosciuridae, which are fully hystricomorphous in the infraorbital structure, the incisors are still pauciserial. The same is true of the more primitive members of the Theridomyidae, such as *Theridomys*. In more advanced theridomyids, there is a complete transition to the uniserial type of enamel. In *Issiodoromys* [=*Nesokerodon*] *minor*, Korvenkontio describes the enamel as "pauci-uniserial" (*op. cit.*, p. 116). He further describes that of *Protechimys gracilis* as pauciserial, and that of *Archaeomys laurillardi* as uniserial. These two forms are currently recognized as being two species of *Archaeomys* (Schaub, 1958, figs. 48–49). So in the Theridomyoidea, the transition from Grade One to Grade Two has occurred later in the incisor enamel than it did in the jaw musculature, the two apparently being completely independent.

A different type of enamel modification occurs in what Korvenkontio (*op. cit.*, p. 130) calls the multiserial type. Here each lamella is formed of four to seven identically oriented rows of prisms, the lamellae lying at an angle of about 45° to the surface of the enamel. Successive lamellae have the prisms oriented in opposite directions (Korvenkontio, 1934, pl. 8, figs. 3, 5, 7). This occurs in the Caviomorpha, and the Bathyergidae, Ctenodactylidae, Hystricidae, and Pedetidae.

Finally, there are likely to be differences in cheek-tooth formula or pattern associated with the change to Grade Two from Grade One. Primitively, the rodent cheek-tooth formula was P^2_1 and M^3_3, although some members of Grade One have lost P^3. This tooth has been preserved today only in *Aplodontia* and among the Sciuridae. In many rodents (most Caviomorpha, Anomaluridae, Castoroidea, Ctenodactylidae, Geomyoidea, Gliroidea, Hystricidae, and probably Pedetidae), P^4_4 have been retained. In such caviomorphs as the Echimyidae (Friant, 1936) and Capromyidae (Wood and Patterson, 1959, p. 324) and in the living African Thryonomyoidea (Wood, 1962, p. 316–317), the permanent premolars have been suppressed and the deciduous premolars are retained throughout life. This may also be true for the Pedetidae (Wood, MS. 2). According to Schaub (1958, p. 678), the reverse of this process occurs, with the elimination of the deciduous tooth in many hystricomorphous forms. Finally, the Muroidea and Spalacoidea have lost all the premolars and the Dipodoidea have almost reached this stage.

In summary, in Grade Two, there is a tendency to reduce the length of the tooth row, probably an adaptation permitting greater contrast between the gnawing and chewing activities, and therefore greater specialization in each. Usually, the loss of these teeth occurred at times when there are still gaps in the paleontological history of the groups. However, the loss of P^3 occurs within the known history of the Eomyidae (Wood, 1955b) and Gliridae (Schaub, 1958, figs. 201, 203), and the presence of P^4 is variable in living members of the Dipodidae (Schaub, 1958, p. 792).

Although the loss of cheek teeth brought about greater specialization of gnawing and chewing activities, it may have interfered with the functional activities of chewing, since in almost all members of Grade Two there has been a tendency secondarily to elongate the cheek teeth by developing an additional transverse crest (mesoloph or mesolophid) in the middle of the teeth, making them five-crested in contrast to the four-crested pattern found in Grade One. This five-crested stage seems certainly to have developed independently in many lines, and therefore is no better than any other single criterion in determining the phylogenetic relationships (clades) among the rodents.

The changes in the jaw musculature look as though they are indicative of genetic relationships (i.e., clades), and were so used by most authors as far back as Brandt (1855) or even earlier, until fairly recently, giving three suborders of rodents, the Sciuromorpha, Hystricomorpha, and Myomorpha (see Simpson, 1945).

However, the use of other criteria for rodent classification complicated this apparently simple pattern. Tullberg (1899), for example, showed that rodents could be divided into two groups on the basis of the way in which the angle of the lower jaw originated—the Sciuragnathi, in which the angle arises in the plane of the alveolus of the lower incisor, and the Hystricognathi, in which it arises lateral to this plane. The hystricognathous forms include only those that are more or less hystricomorphous, whereas the sciurognathous ones may be sciuromorphous, myomorphous or hystricomorphous.

With an increase in the detailed studies of rodent paleontology since 1920, the chance that any of the three Brandtian suborders represents a clade has become progressively smaller, and students of fossil rodents have universally abandoned them at present.

The Sciuromorpha may be considered to be typical. The sciuromorphous condition was achieved by the squirrels (Sciuridae) in a transition, which is as yet not completely documented but that seems very probable, from a mid-Eocene paramyid such as *Uriscus* (Wood, 1962, p. 247;

Black, 1963, p. 229). A similar trend, not carried so far, is seen in the Oligocene ischyromyids, *Titanotheriomys* (Wood, 1937, pp. 194–195) and some species of *Ischyromys* (Burt and Wood, 1960, p. 958). These forms could not be in the ancestry of the squirrels, as their cheek-tooth pattern is much more advanced than is that of the squirrels.

The sciuromorphous Geomyoidea (including the extinct Eomyidae as well as the Geomyidae and Heteromyidae) seem to have many fundamental similarities especially in the basicranium (Wilson, 1949, pp. 42–48; Galbreath, 1961, pp. 226–230), to the myomorphous Muroidea (Muridae, Cricetidae), and have probably come from a common source. Whether this source was a sciuromorphous form, among some of whose descendants the *Masseter medialis* shifted forward, or whether it was a protrogomorphous form, and one group of descendants shifted the *Masseter lateralis* alone and the other shifted both branches of the muscle simultaneously, is completely unknown. It seems rather probable, however, that the Geomyoidea and the Muroidea are descended from some member of Grade One that would be included among the Sciuravidae. The jaw mechanism of the beavers (Castoridae) and their Oligocene to Miocene relatives, the Eutypomyidae, is almost identical to that of the squirrels, except for the expansion of the *Masseter medialis* onto the median side of the orbit. At present there is no evidence as to the pre-beaver ancestry of this group. The tooth structure of the Castoroidea is completely different from that of any of the other sciuromorphous rodents, which has led Schaub to include them, with the Theridomyoidea and Hystricoidea, in his Infraorder Palaeotrogomorpha (1958, p. 694). This association seems unnatural. It is possible that there is a special relationship of the beavers with either the ischyromyids or the sciurids, although the presence of five-crested teeth in both upper and lower jaws of the beavers makes this seem very unlikely.

The evidence that masseteric structure represents a grade is equally clear among the hystricomorphous rodents. These include the Old World porcupines (Hystricidae); the African Oligocene to Recent Thryonomyoidea (Cane Rats, Rock Rats, and Phiomyidae); the isolated African families Anomaluridae, Bathyergidae, Ctenodactylidae, and Pedetidae; the European Eocene to Oligocene Theridomyoidea; the South American Caviomorpha; and, as already indicated, the Dipodoidea. The lines of descent of most of these groups are either not clear or are unknown. The South American forms are a natural unit, the Suborder Caviomorpha of Wood and Patterson (1959, p. 289) or the Infraorder Nototrogomorpha of Schaub (1958, p. 720). It seems certain that these rodents have evolved in isolation in South America since the late Eocene or early Oligocene, when at least some members of the group were fully hystricomorphous and all were hystricognathous, and that they have had no connections with any other hystricomorphous forms during that period. On the basis of the available evidence, the most reasonable explanation for them is that they represent derivatives of a North American Grade One stock, that managed to reach South America by island hopping during the late Eocene, either via Middle America (Simpson, 1950, p. 375; Wood, 1962, p. 248; Wood and Patterson, 1959, p. 401–406), or via the West Indies (Landry, 1957, p. 91, who believed that these were hystricomorphs from the Old World; Wood, 1949, p. 47). The African Thryonomyoidea are clearly derived from the Oligocene to Miocene Phiomyidae (Lavocat, 1962, p. 289), whose Oligocene members (Wood, MS. 1) show no signs of relationship with any other group of hystricomorphous rodents, and can only (at present) be considered as an independent line derived from unknown protrogomorphs. The Hystricidae (all that seems to be left of the old Hystricomorpha) seem to have had a south Asiatic origin and differentiation, whence they spread, in the late Miocene or early Pliocene, to Europe and Africa. The Bathyergoidea are, unfortunately, very poorly known as fossils, though they occur in the African Miocene (Lavocat, 1962, p. 290). Certain Mongolian Oligocene fossils that have sometimes been referred to this family (Matthew and Granger, 1923, p. 2–5; Landry, 1957, pp. 72–73) have generally been agreed probably to be late members of the Grade One Cylindrodontidae.

The other hystricomorphous groups are all sciurognathous. The Dipodoidea (Dipodidae, Zapodidae) are extremely close to the cricetids in tooth pattern—so close, in fact, that many Miocene and Pliocene zapodids were originally referred to the Cricetidae (Schaub, 1930, pp. 616–617, 627–629; Wood, 1935b, *Schaubeumys*; Hall, 1930, *Macrognathomys*). The skeletal and myological differences between the Muroidea and Dipodoidea also seem to be relatively minor, and the Dipodoidea almost certainly belong to the same clade as do the Muroidea and Geomyoidea, which may be called the suborder Myomorpha.

The Theridomyoidea are an Eocene–Oligocene group, not known outside of Europe. The earliest members of the superfamily are close to the Paramyidae in cheek-tooth structure (Wood, 1962, p. 170) and in enamel histology (Korvenkontio, 1934, pp. 96–97), but are already fully hystricomorphous. It was long customary to consider them ancestral to the Caviomorpha, with the descendants, among other things, becoming hystricognathous. This interpretation is easily read into Schaub's classification, although he specifically states that current knowledge is not adequate to demonstrate such a relationship (1958, p. 693). But the closest resemblances to the theridomyoid tooth pattern are *not* found in the earliest caviomorphs as should be the case if they were genetically related (Wood and Patterson, 1959, pp. 400–401). Current work makes it equally improbable that there is a theridomyoid–thryonomyoid relationship (Wood, MS. 1). The earliest known Anomaluridae are from the Miocene of Africa. There is no good evidence indicating relationship between them and any other group of rodents. It is conceivable that they are related to the Theridomyoidea, but there is no real evidence for such a relationship. The Ctenodactylidae, now exclusively African, have been shown by Bohlin (1946, pp. 75–146) to be abundant in the Oligocene of central Asia, and are known from Africa only since the late Miocene (Lavocat, 1962, p. 289). Work in progress (Dawson, 1964) rather strongly suggests an independent derivation of this family within central Asia from members of Grade One, though the jaw muscle transitions have not been worked out.

Finally, the Pedetidae are in many ways the most isolated of all rodents. They have lived in Africa since the Miocene (Stromer, 1926, pp. 128–134; MacInnes, 1957), and have a tooth pattern which is only very slightly reminiscent of that of any other rodents. They probably (with no evidence) represent an independent derivation from members of Grade One (Wood, MS. 2).

Schaub (various sources, especially 1958) completely abandoned the use of the zygomasseteric structure or that of the angle, in the subordinal classification of rodents, and relied only on the cheek-tooth pattern. He argued extensively (1958, p. 684, 691–694) that either the five-crested pattern ("plan *Theridomys*") originated only once, in the Theridomyoidea, and that all other five-crested forms are descended from them, or that his suborder Pentalophodonta, including these forms, is a natural group (clade) in that it contains those forms, and only those forms, that have achieved a five-crested pattern as a result of parallelism. As he stated (*op. cit.*, p. 693), our current knowledge of the detailed phylogeny of the rodents is still inadequate to permit us to make positive statements of the exact ancestry of most of the families of what are here included in Grade Two. Schaub further stated: "Il me parait aussi évident que l'idée de ce plan fondamental qui nous permet de révéler sinon tous, mais presque tous les parallélismes, peut servir comme base utilisable de la classification, tandis qu'on ne peut pas placer la même confiance dans celles qui s'appuie sur les structures zygo-massétériques et la configuration de l'angle mandibulaire" (*op. cit.*, p. 693).

The current conclusion of most students of fossil rodents is that there is no simple key to separating clades from grades within this complex order, and that no one set of criteria (tooth patterns, zygomasseteric structure, type of angle, fusion of ear ossicles, incisor histology, etc.) may be relied upon. Parallelisms and convergences are so abundant that only an analysis of all possible criteria can give reliable evidences of cladal unity (Lavocat, 1962, p. 288).

From the analysis of the features that are used to separate members of Grade Two from those of Grade One (jaw musculature; angle of the jaw; incisor position; incisor histology; cheek-tooth formula and pattern), it seems quite clear that these features evolved independently of each other. Hystricomorphous forms can be either hystricognathous or sciurognathous; any clade of Grade Two can include forms with high-crowned, as well as low-crowned, cheek teeth; and the changes in incisor histology seem to have taken place independently of all the others. This situation is not surprising and should not cause insurmountable difficulties in classification. It merely emphasizes that the grades must not be interpreted as clades, and that a key, based on grade characters, may be useful but is still only a key.

Grade Three—Hypsodonty and Pattern Modification

The third grade in rodent evolution is not as clear-cut as are the first two. It is represented by those members of Grades One or Two that have developed extremely hypsodont or ever-growing cheek teeth. These have developed independently many times, in almost all clades of rodents, as adaptations to grazing or burrowing modes of living. Among protrogomorphs, the burrowing cylindrodonts, the perhaps steppe-living protoptychids, the aplodontids and the mylagaulids all become very hypsodont. There is a definite trend toward hypsodonty in burrowing squirrels (*Cynomys*) and in some of the Old World ground squirrels. The burrowing geomyids and the desert-living saltatorial heteromyids have ever-growing cheek teeth. Extremely high crowns also characterize most of the Caviomorpha except for the New World porcupines (Erethizontidae); the Thryonomyoidea, the Bathyergidae, Ctenodactylidae, and Pedetidae in Africa; the Spalacidae and Rhizomyidae; the Castoridae; and the Microtinae among the Cricetidae.

Perhaps the suppression of the premolars and retention of the deciduous teeth, discussed above, are also features of this grade. On theoretical grounds, it would seem that a good explanation might be that the wear of the cheek teeth was so rapid that selection for increase of height of dP_4^4 was very strong, resulting in teeth that would last, proportionately, as long as in low-crowned ancestral forms. A long-growing tooth of this sort would be capable of increasing its horizontal dimensions, thus eliminating the primary adaptive reason for the replacement of deciduous teeth by permanent ones—the fact that the baby jaws were not big enough for adult-sized teeth. However, in the only case where the details of the suppression of P_4^4 by retained dP_4^4 are known (Phiomyidae, Wood, MS. 1), this change is taking place in animals some of which are still low-crowned while others are, at most, mesodont.

Two types of ever-growing teeth have developed among rodents. Usually, there has been growth of the pattern-bearing portion of the crown, so that the pattern is preserved with wear—at least in considerable part. This has resulted in cheek teeth that lose the details of cusp arrangement early in life, but in which a characteristic pattern is quickly achieved, and retained for the rest of the animal's lifetime. Such patterns are found in most caviomorphs, the Thryonomyoidea, the Theridomyidae, Bathyergidae, Ctenodactylidae, Pedetidae, Rhizomyidae, Castoridae, Spalacidae, and Microtinae.

In some rodents, however, there is little or no growth of the pattern-bearing portion of the crown, but rather a strong unilateral hypsodonty of the basal part of the crown. This arrangement usually results in the reduction of the enamel to one or a few transverse plates on each tooth, alternating with dentine (or occasionally cement) prisms. Such pattern developments are most characteristically developed in the Geomyidae (Merriam, 1895; Wood, 1936) and Heteromyidae (Wood, 1935a). Similar developments are present in Mongolian Oligocene cylindrodonts (Schaub, 1958, fig. 156), in several cases among caviomorphs (Wood and Patterson, 1959, p. 333 *et seq.*; figs. 9A, 14C, 16B, 23A), and in advanced theridomyids (Schaub, 1958, figs. 45, 49, 51, and 55).

The tendency to elongate the cheek teeth, discussed above under Grade Two, has been continued in a considerable number of forms by developments at the front end of the anterior cheek teeth (the anterocone and anteroconid), or by additions at the rear of the last tooth. The former is especially characteristic of the Microtinae, the latter of the Hydrochoeridae.

There can be no possible doubt that these high-crowned or ever-growing cheek teeth have been acquired independently in the various clades that are involved.

Grade Zero—The Basic Level

The evidence suggests that the Paleocene rodent differentiation was based on a distinctly more primitive level of gnawing ability than that seen in later forms. This radiation, while essentially hypothetical, can be fairly well characterized, and is here called Grade Zero.

Among middle Eocene and later rodents, the incisors universally have an enamel cap that covers the entire front face, and that curves around onto the buccal and lingual sides of the tooth for a short distance, serving to lock the enamel firmly onto the dentine. Among some of the earliest rodents of the Family Paramyidae, however, the locked-on pattern of enamel had not been achieved and the enamel merely forms a strip extending across most (but not all) of the width of the front edge of the tooth. As a result, there would have been danger of chipping or breaking off pieces of the enamel strip. This pattern shows up well in the late Paleocene *Paramys atavus* (Wood, 1962, fig. 21 B, C), and is also suggested in many individual specimens of several early Eocene paramyids, which seem to represent the last remnants of this Paleocene radiation. The early development of the *Leptotomus* incisor pattern, with the enamel extending over a very large part of the tooth, may also be derived from such a basic condition.

While there is no evidence one way or the other, it would seem entirely possible that the rodents of Grade Zero had a complete enamel cap on the unworn incisors, as did the multituberculates, and had merely achieved extreme unilateral hypsodonty. At some unknown time during the Paleocene, the rodents achieved a level where the incisors, including the enamel strip, became ever growing. Since the few known late Paleocene rodent incisors are all fragments, it cannot be determined when this condition was reached, though these incisor fragments seem to belong to ever-growing teeth similar (in this respect) to those of Grade One. This suggests that this type of tooth began to be acquired not later than middle Paleocene.

In the early rodents or their immediate precursors there was a reduction from the primitive placental formula of $I^3_3\ C^1_1\ P^4_4\ M^3_3$ to that characteristic of the early Eocene Paramyidae, $I^1_1\ C^0_0\ P^2_1\ M^3_3$. This almost certainly had taken place well before the end of the Paleocene, and presumably had begun before the enlargement of the incisors was completed.

The difference between the jaw musculature of Grade One (Fig. 1) and that of primitive mammals was presumably not very great, if Edgeworth's figures (1935, fig. 692a, b, p. 459) of the musculature of *Dasyurus* are any criterion. Here the *Masseter superficialis* has the same anteroposterior alignment as in *Ischyrotomus*, and the *Masseter lateralis* and *Masseter medialis* (*Masseter profundus* and *Zygomatico-mandibularis* of Edgeworth) have an almost vertical alignment. Thus, the *Dasyurus* pattern of jaw musculature seems preadaptive for the beginnings of gnawing rodents, and therefore probably is essentially what was found in Grade Zero.

The skull structure of Paleocene rodents is completely unknown. But it seems probable that the development of free anteroposterior movement of the condyle of the lower jaw occurred *pari passu* with the development of extremely hypsodont to ever-growing incisors and the reduction of the dental formula discussed above, and that the structure of the condyle and glenoid fossa, of the incisors, of the cheek teeth and of the jaw muscles evolved as a unit complex.

Discussion

The analysis of rodent morphological evolution, given above, involves the interpretation of the classical suborders, the Sciuromorpha, Myomorpha, and Hystricomorpha, as representing alternative expressions of a major and a secondary adaptive level in the order, here called Grade Two and Grade Three. In all cases, they seem clearly *not* to be clades. The Protrogomorpha, as defined by Wood (1959, p. 170) are a closer approach to being both a clade and a grade. This suborder does not quite coincide with a grade because some members, while not having achieved any of the specializations of Grade Two, have reached a level of dental complexity that is here considered indicative of Grade Three. Whether the Protrogomorpha, as here delimited, can be considered to represent a clade, is perhaps arguable. Certainly the Ischyromyoidea are a clade. Certainly the Aplodontoidea are derived from them, but most authors consider that the same is true of all the other rodents as well. However, the Protrogomorpha, as here defined, are related forms that have structural features in common, permitting the group to be satisfactorily defined.

Black has recently (1963, pp. 126–128) argued that the Sciuridae, because of their primitive dentition, should be returned to the Protrogomorpha, where Wood once included them (1955a). The suborder could then be defined as members of Grade One plus certain groups that had not gone very far in evolving into Grades Two or Three. It seems better, however, for the present to use the break between Grade One and Grade Two as a fundamental division in rodent classification, and hence to eliminate the Sciuridae from the Protrogomorpha. A major reason why Black considers that the squirrels can no longer be separated from the members of Grade One is that *Miosciurus* and *Protosciurus*, from the early Miocene, have zygomasseteric structures that have not fully achieved the sciuromorphous pattern. However, his description (1963, pp. 136, 140) and figures (*op. cit.*, pls. 3, 6) show that the masseter had already begun its migration in these forms, so that, technically, they belong to what is here called Grade Two. Naturally, there had to have been a transition from Grade One to Grade Two, and the transitional forms would be hard to place with exactitude, but it seems best to consider all the known Sciuridae as members of Grade Two.

The rest of the cladal classification of rodents must still remain largely as indicated by Simpson (1959) and Wood (1959, p. 172). The main changes that are required at the present time involve certain African rodents. The Phiomyidae are clearly not Protrogomorpha, but are hystricomorphous forms ancestral to the Thryonomyoidea, to which superfamily they should be referred. There seems to be even less justification than formerly (Wood, 1955a) for placing the Hystricidae close to any other known families.

All the available evidence suggests that the level of Grade Two has been achieved many times independently. Instead of the three suborders that were formerly recognized, it seems better to recognize at least eleven clades that have independently passed from Grade One to Grade Two. Which of these should be considered suborders and which merely families or superfamilies is, for the moment, largely a matter of convenience (Simpson, 1959; Wood, 1959).

A cladal classification of rodents, based on current knowledge, is as follows:

- Order Rodentia
  - Suborder Protrogomorpha
    - Superfamily Ischyromyoidea
      - Paramyidae, Sciuravidae, Cylindrodontidae, Protoptychidae, and Ischyromyidae
    - Superfamily Aplodontoidea
      - Mylagaulidae and Aplodontidae
  - Suborder Caviomorpha
    - Superfamily Octodontoidea
      - Octodontidae, Echimyidae, Ctenomyidae, Abrocomidae, and Capromyidae
    - Superfamily Chinchilloidea
      - Chinchillidae, Dasyproctidae (incl. Cephalomyidae), Cuniculidae, Heptaxodontidae, and Dinomyidae
    - Superfamily Cavioidea
      - Eocardiidae, Caviidae, and Hydrochoeridae
    - Superfamily Erethizontoidea
      - Erethizontidae
  - Suborder Myomorpha
    - Superfamily Muroidea
      - Cricetidae (incl. Melissiodontidae Schaub) and Muridae (incl. Gerbillidae Stehlin and Schaub)
    - Superfamily Geomyoidea
      - Geomyidae, Heteromyidae, and Eomyidae
    - Superfamily Dipodoidea
      - Dipodidae and Zapodidae
    - Superfamily Spalacoidea
      - Spalacidae and Rhizomyidae
    - Superfamily Gliroidea
      - Gliridae and Seleveniidae
  - Clades not in suborders:
    - Family Sciuridae (incl. Eupetauridae Schaub and Iomyidae Schaub)
    - Superfamily Castoroidea
      - Castoridae and Eutypomyidae
    - Superfamily Theridomyoidea
      - Pseudosciuridae and Theridomyidae
    - Family Ctenodactylidae (incl. Tataromyidae Bohlin)
    - Family Anomaluridae
    - Family Pedetidae
    - Family Hystricidae
    - Superfamily Thryonomyoidea
      - Phiomyidae (incl. Diamantomyidae Schaub), Thryonomyidae, and Petromuridae
    - Family Bathyergidae

The Family Pellegriniidae of Schaub is based on a single species of completely unknown affinities, which should not be considered a family until more is known about it.

SUMMARY

Rodent evolution can be envisioned as involving three relatively clear-cut evolutionary levels, here called Grades One, Two, and Three. The first involves well-developed gnawing animals, with a primitive mammalian jaw musculature. Grade Two includes those animals that have modified the jaw musculature in one of several ways that formerly were used as the basis for rodent subordinal classification. There were also changes in the dentition, especially in the development of cheek teeth with five transverse crests, rather than ones with no more than four crests as in Grade One. Changes occurred in numerous other parts of the skeleton and dentition, although these were probably not correlated with each other. Grade Three includes those rodents with very high-crowned or even ever-growing cheek teeth, in which there is sometimes the same type of limitation of the enamel that occurred during the Paleocene on the incisors. Grade Three also includes forms in which there has been a marked secondary increase in the length of the cheek teeth. A hypothetical Grade Zero is imagined for the rodents of the second half of the Paleocene.

Only Grade One comes close to approximating a clade. The Protrogomorpha, as here defined, include the members of Grade One and some forms that have

reached Grade Three without going through Grade Two. The cladal classification of the rodents still requires the recognition of numerous independent lines, showing no evidence of interrelationship later than in members of Grade One. Only two or possibly three clades can be recognized that require units larger than the superfamily—the Protrogomorpha, the Caviomorpha, and perhaps the Myomorpha. The other rodents fall into nine familial or superfamilial clades.

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A discussion of the similarities and differences between rodent and teleost evolution prompted Schaeffer to make the oral suggestion that an analysis of evolutionary grades and clades among rodents would be very useful to students of the evolution of other groups. This has led to the preparation of the present review. This study was assisted by grants from the National Science Foundation and from the Marsh Fund of the National Academy of Sciences.

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Distribution Patterns and Phylogeny of Some Western Ground Squirrels

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IT IS well known that many kinds of mammals attain their distributional limits in the intermontane West. In Utah in particular many species reach their limits, and along the margins of the ranges, many small populations have developed under semi-isolation into recognizable subspecies in relatively short periods of time. We have been making a detailed study of ground squirrels of the subgenus *Citellus* (Oken) for the past several years. The study of taxonomy and speciation has to date been largely restricted to data concerning the morphological features of the animals. While plotting the ranges of these species, and studying competition between different species at the interphases of their ranges, we have made many observations which lead us to believe that a significant supplement to the morphological data may be obtained by field studies of the distribution and ecology of related species under intense competition. Within the given genus, what are the relationships as indicated between degrees of allopatry and sympatry? What does competition indicate about the rate of differentiation and selection?

The ground squirrels of North America belong to the genus *Citellus* and are divided into eight subgenera. The group here reported upon is that of the shorttailed ground squirrels of the subgenus *Citellus* (Oken). We are not concerned at present with all the species of this subgenus, but only with the following: *C. armatus, C. beldingi, C. richardsoni, C. columbianus,* and *C. townsendii* and its allies. Generally speaking *C. armatus* is a northern species that attains its southern limits in Utah; *C. beldingi* is a northwestern species that attains its southeastern limits in Utah, in the extreme northwestern part of the state; *C. richardsoni* is a northern and eastern species that has its southern limits in Colorado and Utah and its western limits in Nevada; *C. columbianus* is also a northern species that extends as far south as southcentral Idaho; and *C. townsendii* and its allies are western and northern animals that extend as far east as central Utah (Fig. 1).

Students of these shorttailed ground squirrels are familiar with the fact that within their ranges they occupy several types of habitats ranging from dry hillsides to lush, moist meadows. Members of all of the aforementioned species apparently prefer moist, lush meadows when they are available. Within the ranges of the several species of this subgenus, members of each species always occupy a wider variety of habitats if that species is the only representative of the subgenus present.

Intraspecific competition appears to be of lesser degree than does interspecific competition. We have noted that where the ranges of *C. richardsoni* and *C. armatus* come into contact in Rich and Daggett counties, Utah, each species occupies a narrower variety of habitats than it would if it occurred there alone. At these localities, where the ranges of the two come into contact, colonies of *C. richardsoni* occupy the dry, open areas between stands of sagebrush and greasewood, while those of *C. armatus* occupy the grassy meadows. It is noteworthy that at this zone of contact between the ranges of these two species, the competition is extreme; the burrows and feeding areas of the animals of one species being in some instances but a

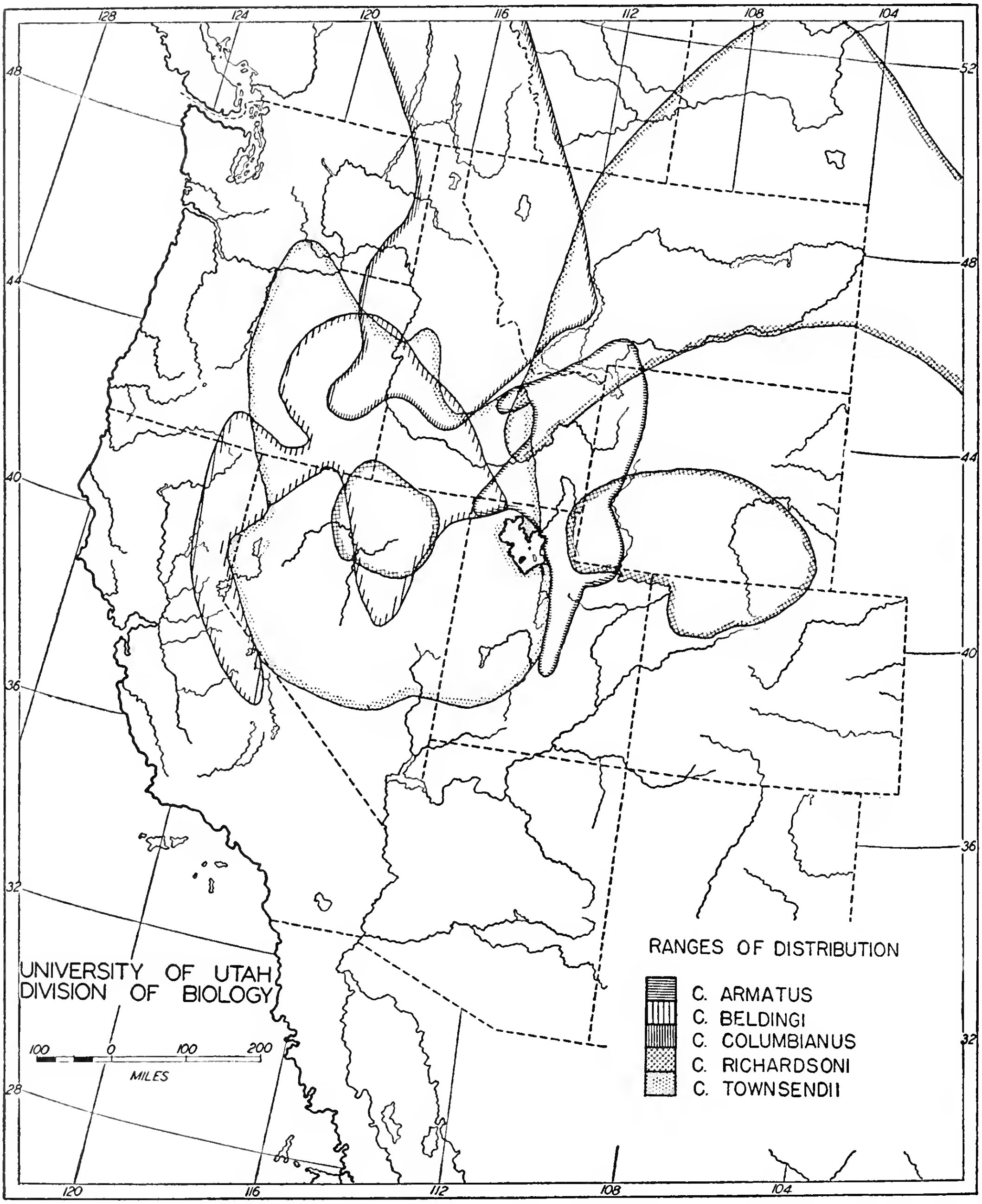

FIG. 1. Distribution of the species of the subgenus *Citellus* (Oken) in the intermontane region of western U. S.

few feet from those of the other. Back from the zone of contact between the ranges of these two species, we noted that where animals of only one of the two species occurred, they lived in both the wet and dry situations, indicating that they could live successfully in either wet meadows or dry, barren ground as long as members of the competing species were not present.

In Colorado, Warren (1942, p. 124) reported colonies of *C. richardsoni* as occurring in high mountains, and that in some instances they had crossed over passes at 11,000 feet to become established in the heads of drainages on the other side of the mountains. Since members of a competitive species do not occur in these mountains in Colorado, colonies of *C. richardsoni* were able to establish themselves there. In the western part of the Bridger Basin the ranges of *C. armatus* and *C. richardsoni* overlap. Where both are found together here, they are ecologically displaced as previously noted. Each lives, however, in wet, moist areas and also in dry, semiarid areas in the Bridger Basin, except where colonies of the two co-exist. In Idaho, Davis (1939, pp. 171–180) reported the same relative ecological distribution for colonies of *C. armatus* and *C. richardsoni* as we have noted, and commented that they both occupy the same types of habitats; but he did not indicate whether or not the animals of the two species are ecologically displaced when they occur together. We suspect that they are. Apparently ground squirrels belonging to *C. richardsoni* are better adapted to dry soils than are those of *C. armatus,* but since both are known to survive in the same range of ecological habitats, it is competition that limits their ranges where they meet. In the Grouse Creek area of northwestern Utah, where colonies of *C. armatus* and *C. beldingi* come into contact with each other, we noted that the animals of *C. armatus* occupied the dry localities, while those belonging to *C. beldingi* occupied the wet meadows. In Idaho, Davis (1939, pp. 169–172) reported that animals of these two species occupy the same habitats, and that the ranges of the two species overlapped there, but he did not note whether or not they were ecologically displaced, although he found them in separate colonies in the same field. He did state that animals of both species prefer moist meadows, although both will live in dry areas, and this is in agreement with our findings in Utah. Apparently animals of *C. armatus* are better adapted to dry situations than are those of *C. beldingi.*

In Utah, we have not found colonies of *C. townsendi* in close proximity to those of *C. armatus* and *C. beldingi,* but we have found them about a mile apart. Our observations indicate that in these localities, ground squirrels of the species *C. townsendii* lived in extremely dry habitats, drier than any found for the other two aforementioned species. In Idaho, however, north of the Snake River in Jerome County, we did find animals of *C. townsendii* living on the dry soils while the adjacent meadow was occupied by animals of *C. beldingi.* We noted animals of *C. beldingi* also on dry soils, but only in the absence of *C. townsendii.* It is evident that animals belonging to the species *C. townsendii* are remarkably well adapted to life in extremely dry areas.

Hall (1946, p. 290) reported that wherever *C. beldingi* and *C. townsendii* were found together in Nevada, the Belding ground squirrel occupied the meadowland, and colonies of *C. townsendii* lived on the sagebrush-covered benches. He further commented on the fact that both of these kinds of ground squirrels prefer moist situations, but he did not comment on what happens where the ranges of *C. richardsoni* and *C. townsendii* overlap.

To date, the Belding ground squirrel has not been taken north of the Snake River in Idaho. We found both the Columbian and Belding ground squirrels north of the river. In this region, they both occurred in the moist meadows. We did not have an opportunity to observe them in the same locality, but we are of the opinion that where their ranges overlap, the Belding ground squirrel will be found to occupy the moist habitats, while the Columbian will be found in the drier situations.

Phylogenetic Interpretation

Since all members of this subgenus are of generally northern occurrence, attaining their southern limits in the western states, and since all prefer moist habitats where available, it would seem that the adaptational feature essential to increasing the range to the southward would be the ability to take over more xerophytic situations. From our observations on competition between the several species, we align them with reference to this adaptation in the following order: first, *C. townsendii* is able to outcompete any other for arid places; next is *C. richardsoni,* followed by *C. armatus,* then *C. columbianus,* and finally by *C. beldingi* which is the least adapted to dry conditions. These observations are somewhat borne out by studies on the areas of occurrence. It is axiomatic in the study of mammals that the subspecies of a species are all allopatric. Therefore, within limits, it would appear within a genus or subgenus, that the greater the amount of allopatry between the full species the younger the genus. Moreover, the greater the amount of sympatry between species of the genus, the greater the divergence between the species, hence the older the genus. The subgenus in question has some sympatry, but in general is markedly polymorphic and allopatric. Some species are totally allopatric with reference to other species; some have only a minor degree of overlap of ranges and in only one case are the ranges markedly sympatric. The ranges of *C. townsendii* and *C. beldingi* are sympatric to a large extent, and the animals are markedly distinct in both morphological and ecological characteristics. The ranges of *C. beldingi* and *C. armatus* are practically allopatric and the animals are quite similar in both morphology and ecological tolerances. With the exception of the subspecies *C. r. nevadensis,* the ranges of the species *C. beldingi* and *C. richardsoni* are totally allopatric. The subspecies *C. r. nevadensis* is a relict and is on the way out. Its range is sympatric with both *C. beldingi* and *C. townsendii.* The former outcompetes it for the wet situations while the latter does the same with reference to the dry ecological situations. In comparing the ranges of each species with all others, it is apparent that there is a correlation between the degree of overlap of the ranges, the morphological relationships and the ecological tolerances of the animals of the species in question.

From the above data on interspecific competition, and from our study of the degree of sympatry and allopatry of the ranges of these species, we would formulate a phylogeny of the members reported upon in this subgenus in the following manner: *C. townsendii* is the most divergent, next *C. richardsoni,* then *C. armatus,* with *C. columbianus* and *C. beldingi* being more conservative and closer to the ancestral type. Furthermore, these conclusions are in keeping with the known history of animals of this region with reference to the happenings of Pleistocene and post-Pleistocene time.

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VARIABILITY IN CHARACTERS UNDERGOING RAPID EVOLUTION, AN ANALYSIS OF *MICROTUS* MOLARS

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Information amassed by animal breeders has aided considerably the understanding of the genetic changes that accompany phenotypic population changes through time. In spite of genetic inferences from these artificial selection experiments, there are few studies of genetic and phenotypic changes in characters evolving under natural conditions. Because of the scarcity of statistically adequate series of fossils and the incompleteness of knowledge of phylogenetic patterns, the contributions of paleontology to the understanding of evolutionary dynamics have been far below its potential. However, as phylogenies become better known and series are emphasized rather than types, it is increasingly possible to study the detailed behavior of evolving characters. Findings of these studies, in turn, permit a more critical evaluation of our theoretical models.

One of the critical areas of evolutionary research is the behavior of the intrapopulational variation of a character when it is undergoing change. An understanding of the changes in genetic variation as the population moves from one mean to another is central to any investigation involving evolutionary mechanics. Lerner (1955) listed as one of the significant landmarks of population genetics the discovery of the great genetic reserves in natural populations, yet this high potential genetic variation is usually associated with relatively low phenotypic variation. According to our present concepts, sustained intensive directional selection would decrease and eventually exhaust this residual store of genetic variance. In reality the situation is never brought to this extreme since evolution, even at its most rapid pace, is slow compared to changes produced by artificial selection. However, the problem of the elimination of genetic variance does have meaning at its intermediate stages. It is the assumption of many evolutionary thinkers that as the population responds to the pressures of directional selection the genetic and phenotypic variation immediately decreases, discouraging further evolutionary changes proportionally. The findings of this study lead me to take issue with this assumption.

Empirical documentation supporting a reduction of phenotypic variation in evolving populations has been discussed by Simpson (1953) and Bader (1955), although, in their material, the decreases in phenotypic variation were slight. Since evolutionary change in both cases was taking place at only a moderate pace, an examination of a more rapidly evolving group would theoretically provide greater clarification as the interrelationships would be accentuated by the more intense selection pressures exerted over a shorter period of time. This study is an examination of such a rapidly evolving group. The variation of a suite of evolving characters has been compared to the variation of their more stable homologues.

One of the best examples of rapid evolution documented in the mammalian record has been chosen for this investigation. The setting for this rapid radiation is the late Pliocene and Pleistocene, a time of major ecological upsets, rapid introduction of new habitats, periodic invasions of new territory, and novel associations of faunas. The microtine rodents changed so rapidly during this time that they are used as one of the better markers for correlation of the Pleistocene stages (Hibbard, 1959). Microtines are well represented in the fossil record, and as a result of their generally high population densities, where present, fossils are usually abundant. The microtines have undergone a major adaptive shift from the seed–fruit diet of the typical cricetine to a bark–grass diet. This change has been accompanied by a characteristic increase in the complexity of the dentition, which is the most durable portion of a mammal and also the part most frequently preserved. The microtines have developed in this short period of time a tooth complexity comparable to that which the Equidae achieved throughout the entire Tertiary. Bader (1955) suggested about two million years as the average duration of a species of oreodont. This length of time would be too conservative for genera of microtines.

Preliminary studies indicated that the teeth and the areas of the particular teeth which are undergoing phylogenetic change (more variable interspecifically and intergenerically) are also those which are more variable intraspecifically and intrapopulationally. Two abundant species of *Microtus* that represent two minor grades of tooth complexity were selected, the extinct *M. paroperarius* from the Kansan glaciation and the recent species *M. pennsylvanicus*, first known from the Illinoian.

It should be emphasized that, unlike studies of fossil material which compared the variation between rapidly and slowly evolving lines for a variety of characters, this study was a comparison of characters within populations. The variation of tooth characters that are undergoing rapid evolution was compared with the variation of their serial homologues which are maintaining a fundamentally stable morphology. The hypothesis examined was that highly variable characters are not *ipso facto* vestigial. Quite the contrary, some of these characters have recently been, or are yet being, subjected to directional positive selection. Stated in another way, characters undergoing directional selection do not exhibit the expected phenotypic trend toward homogeneity; rather, they retain the same magnitude of variation or even increase that magnitude. A correlate of this statement is that those characters which are more variable between groups at a lower taxonomic level are also more variable within these groups.

As it is difficult to speak of selection intensity in wild populations, a phylogenetic unidirectional change in a mean will be equated in the ensuing discussions with selection response. This implied association does not necessarily follow since migration, inbreeding, and distortion of the gene pool due to random fluctuations alone may also cause a movement of the population mean. In the case of the microtine tooth variations, these exceptions to the assumption are probably not involved. The tooth evolution follows a syndrome of related adaptive changes of which increased tooth complexity is but one facet. According to our present knowledge, only selection can be held responsible for directional change of this type and magnitude.

EVOLUTION OF MICROTINE MOLARS

Most of the radiations involving grazing mammals began in the Miocene with the formation of the temperate and boreal grasslands. For some unknown reason the microtine radiation, involving a dietary shift from the fruiting part of the plant to the vegetative part, lagged until the late Pliocene. As in many other radiations involving the exploitation of a coarser diet, the low-crowned tuberculate teeth changed into complex high-crowned prismatic teeth to compensate for the increased rate of attrition.

The microtine molar crown consists of a wide enamel loop at one end with alternating left and right triangles following. These triangle-like extensions are termed *salient angles* and the troughs between are the *re-entrant angles* (Fig. 1). The crown pattern of the upper molars is oriented posteriorly (the loop on the anterior part of the tooth) while the crown pattern of the lower molars is just the reverse. Except for this reversal the tooth pattern of the uppers and lowers is fundamentally the same so that M^2 has approximately the same shape as M_2 except that the loop of

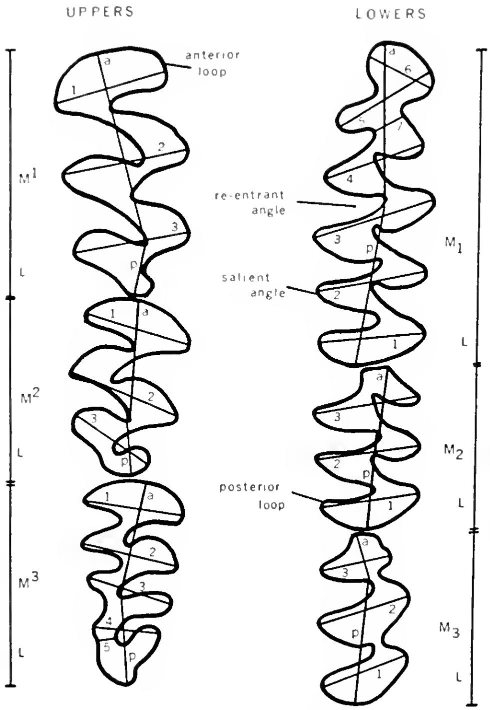

FIG. 1. A pictorial representation of the 42 measurements taken on the upper and lower teeth in two species of *Microtus*. Width measurements are numbered serially from the loop. Anterior and posterior lengths of each tooth are designated by (a) and (p) respectively, and the entire length of each tooth by (L).

the former is anterior and that of the latter posterior. In the upper molars the enamel border of the salient angles is convex on the anterior edge and concave on the posterior; in the lower teeth the pattern is reversed. Moving the teeth anterior–posteriorly produces a self-sharpening system of opposed shearing blades.

Microtine molars have become more complex by the addition of salient angles and in the more advanced forms the teeth are quite elaborate. Phylogenetically the uppers add on to the posterior margins of the teeth and the lowers to the anterior. As a consequence, the posterior margin of M^3 and the anterior margin of M_1 are the most variable between taxa. There have been numerous changes in all of the molar crowns although M^1, M_2, and M_3 are more constant than any of the other teeth. M_3 does vary in form intergenerically; perhaps this is a result of the position of the incisor root as it arcs past M_3. In some genera the incisor passes between M_3 and the two anterior molars and in other genera it does not. The addition of triangles is accomplished in M^3 and M_1, as illustrated in Fig. 2, by an increased penetration of the re-entrant angles in the trefoil or the primordium at the variable end of the tooth. In the other molars the addition of triangles is accomplished by a lateral pinching off, phylogenetically speaking, of a bud from the last triangle (see M^2 in Fig. 2). M^3 and M_1 maintain a labile primordium at the changing end, whereas this analogous area in the other molars abuts against the stable loop of the following tooth and cannot maintain such a variable structure, but has to resort to the use of the last salient angle if new angles are to be added.

The addition of salient angles has taken place throughout the late Pliocene and Pleistocene, but it would be naive to consider the whole subfamily as being constantly driven unidirectionally by a bombardment of selection pressures toward a new adaptive peak. Some groups within the subfamily have become stabilized intermediates between the two adaptive extremes. There is almost a whole generic continuum, even in the living forms, from the simple crushing bunodont dentition to a complex continuously growing hypsodont type. Within the various lines of descent there have been irregular increases in the rate of acquiring tooth complexity. Also there has been a varied differential between lines in the attainment of complex hypsodont molars. Microtine evolution is comparable to the evolution of horse cheek teeth through the Tertiary, where the more progressive grazers were often flanked by browsing groups with dentition of an ancestral pattern.

It is not intended to be implied that the teeth are the only or even the major characters undergoing change. Emphasis has been put on dentition in this treatment as

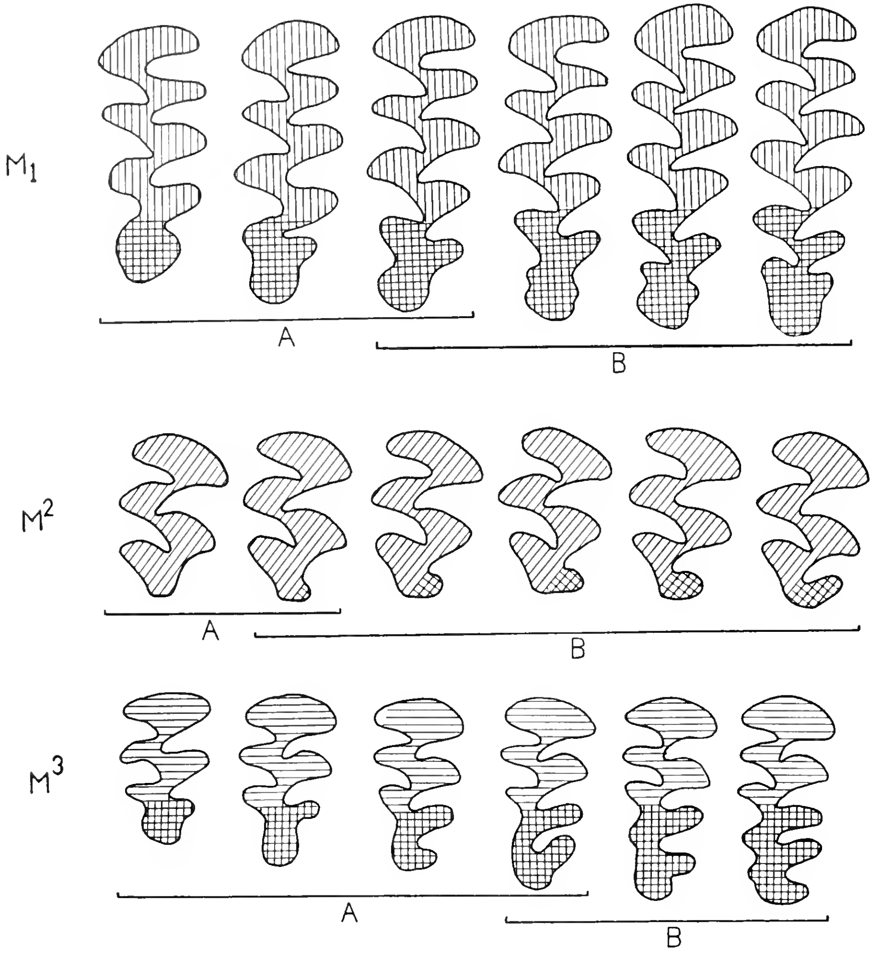

FIG. 2. A semischematic illustration of the extent of tooth crown variations found in the two species of *Microtus*: (A) *M. paroperarius*, (B) *M. pennsylvanicus*. The relatively stable areas are marked with parallel lines, and the variable areas are cross-hatched (see Fig. 1 for orientation).

it is one of the few characters which is consistently preserved in the fossil record. Although character choice in the fossil microtines is limited by default, it would have been difficult to have found a more suitable index of adaptive change.

METHODS, MATERIALS, AND MEASUREMENTS

Samples of multiple series were used in this study to investigate the horizontal (intraspecific) and vertical (phylogenetic) species uniformity of the differential tooth variations. The main comparison is of individual variation within each series and not between series. The material is treated as four samples. The first sample represents the extinct *M. paroperarius*, which occurs only as a fossil. Samples two, three, and four are of the Recent meadow vole, *M. pennsylvanicus*. Sample two is one series with the sexes combined and the last two samples are another series with the sexes treated separately. These two species probably represent one evolutionary line; at least *M. pennsylvanicus* had to pass through the morphological stage represented by *M. paroperarius*.

The series of *M. paroperarius* was obtained from the collections of the University of Kansas Museum of Natural History. This species was first described by Hibbard (1944) and was considered in more detail, including a qualitative analysis of the intrapopulational variation, by Paulson (1961). The sample was collected by Hibbard from several localities in Meade County, Kansas. These localities all belong to the Cudahy Fauna, which lies just below the Pearlette ash, a petrographically distinct volcanic ash. The Pearlette ash is a widespread Pleistocene marker of the non-glaciated areas in central and western North America and serves to delineate a contemporaneous fauna over a considerable territory. Hibbard (1944) considers the Cudahy Fauna to be late Kansan in age.

It was necessary to use teeth from several localities in order that a statistically adequate sample could be acquired. The series of *M. paroperarius* was taken as a not-too-serious deviation from an approximated population sample since the localities were all within one county and stratigraphically contemporaneous.

M. paroperarius is represented by single teeth, although a few remained attached to mandible fragments. The majority of the teeth came from K. U. localities 10 and 17, but a small number were from Locality No. 20. The individual tooth morphology was so characteristic that the individual molars could be easily identified as to upper or lower first, second, or third molars and separated as to left or right. The sexes were not distinguishable. The measurements of the left and right teeth were combined to increase the sample size. There was a positive correlation between the frequency of the teeth in the collection and their size. M_3 was the smallest and most fragile tooth and M_1 was the largest. There were fewer M_3's than any other tooth in the sample (31) and the M_1's were the most numerous (58). This numerical disparity could have been due either to the fact that a more robust structure would better survive preservation or that, as fossils, a larger individual fragment would be more likely to be detected than a smaller one.

The second sample, of the Recent *M. pennsylvanicus*, was obtained from the Carnegie Museum collections through the Chicago Museum of Natural History. This sample was originally collected from the Pymatuning Swamp, Crawford County, Pennsylvania, an area 15 miles long by three miles wide. Goin (1943) included a qualitative review of the M^3 variations of this sample and discussed the locality in more detail. Fifty individuals were used, 25 males and 25 females. The sexes in sample two were combined as in the first sample (*M. paroperarius*). The teeth in the second sample, unlike those of *M. paroperarius*, were all in place in the jaws.

Samples three and four are, respectively, males and females of *M. pennsylvanicus*. There were 40 males and 42 females. This series was borrowed from the University of Michigan Museum of Zoology and was originally collected near the city of Lyndhurst, Ohio. The sexes were treated separately to eliminate the variable of sexual dimorphism and to see what changes this dimorphism brought about in the patterns of tooth variations.

In this study I treated the teeth as prismatic structures with no ontogenetic variation. This assumption is true for all practical purposes once the individual has passed the early juvenile age. Juveniles can be culled from *Microtus* samples by the criteria of overall small skull size, lack of suture closure, and lack of parallel-sided molars. The molars continue to grow throughout the life of the adult individual, maintaining an almost constant crown pattern.

I treated the tooth crown as if it were a two-dimensional surface. This procedure is also not precisely correct. The upper tooth-row surface wears to a slight convex profile and the lower conforms to this with a concave profile of the same magnitude. The mean of the greatest distance that the arc deviates from a straight line, intersecting the terminal ends of the arc, is 0.25 mm or 0.041 of the distance of the straight line. From the lateral view the teeth are also curved; the M^1_1's have their concave sides anterior and M^3_3's posterior. The M^2_2's have only a slight curvature. In most of the teeth there is a dorsoventral twist, so *Microtus* molars may be considered in form as segments of a broad helix.

The teeth of this genus are quite small, the whole tooth-row being only about 6 mm long in *M. pennsylvanicus*. To cope with the problem of measuring teeth of this size in detail, photographs of the tooth crown of the individual teeth in *M. paroperarius*, and of the whole tooth-row in *M. pennsylvanicus*, were taken through a dissecting microscope. The crown was first oriented at right angles to the ocular, then the camera was mounted and brought into focus. All pictures were taken through the same ocular at the same magnification. These were then enlarged and developed under the same conditions, including film, paper, and enlarger magnification. A note on the technique (Guthrie, in preparation) includes approximations of the errors in the technique at the various steps.

The measurements were then taken from the pictures with a dial micrometer reading to the nearest 0.1 mm. With the picture enlargement of 31.8×, this resulted in measurements to the nearest 3.3 microns. The measurements were quite repeatable. The exterior edge of the enamel was used in all measurements. Pictures of both left and right sides were taken of *M. pennsylvanicus*. The side with the picture of highest contrast was used, and, if there was any question, measurements were taken on both sides. Rarely was there a break or crack on both sides so that no measurement could be taken.

Measurements were made as illustrated in Fig. 1. The measurements on the whole were well defined. The only possible exceptions were the anterior part of M_1 and the posterior part of M^3. However, this is a function of their variability in form. Several measurements were used on the anterior part of M_1 and posterior part of M^3, but no one expresses adequately the variation in shape.

The width measurements for each tooth are numbered serially from the loop. Consequently, the uppers are numbered from anterior to posterior and the lowers from posterior to anterior. The total length is designated by L and the anterior and posterior lengths by a and p, respectively. Forty-two measurements were taken on each individual, 20 measurements on the uppers and 22 on the lowers.

Discussion of Molar Variations

The variation in M_1, M^2, and M^3 is represented in Fig. 2. The teeth viewed from left to right depict the nature and extent of the shape variations present in these samples. In reality, this variation does not fall into discrete classes as portrayed in Fig. 2; rather, each tooth in the figure represents a point along the variation continuum. The most variable portions are cross-hatched to facilitate the comparisons. Notice that in M_1 the rounded primordium on the lower part, actually the anterior part of the tooth, is utilized to construct new salient angles by the penetration of reentrant angles into its lateral margins.

In the M^2 a new salient angle is formed by the budding off of the extreme posterior part of the crown, and varies in these samples all the way from absence to almost the size of the other salient angles. *M. paroperarius* has only a slight suggestion of this bud in some individuals, with most not having it at all. In *M. pennsylvanicus* this rudimentary stage is present only at a low frequency, most of the individuals having a well-developed salient angle.

The cross-hatched area in the posterior portion of the M^3 behaves differently than the cross-hatched area in the M_1. M^3 increases its number of salient angles phylogenetically by dropping a bud posteriorly

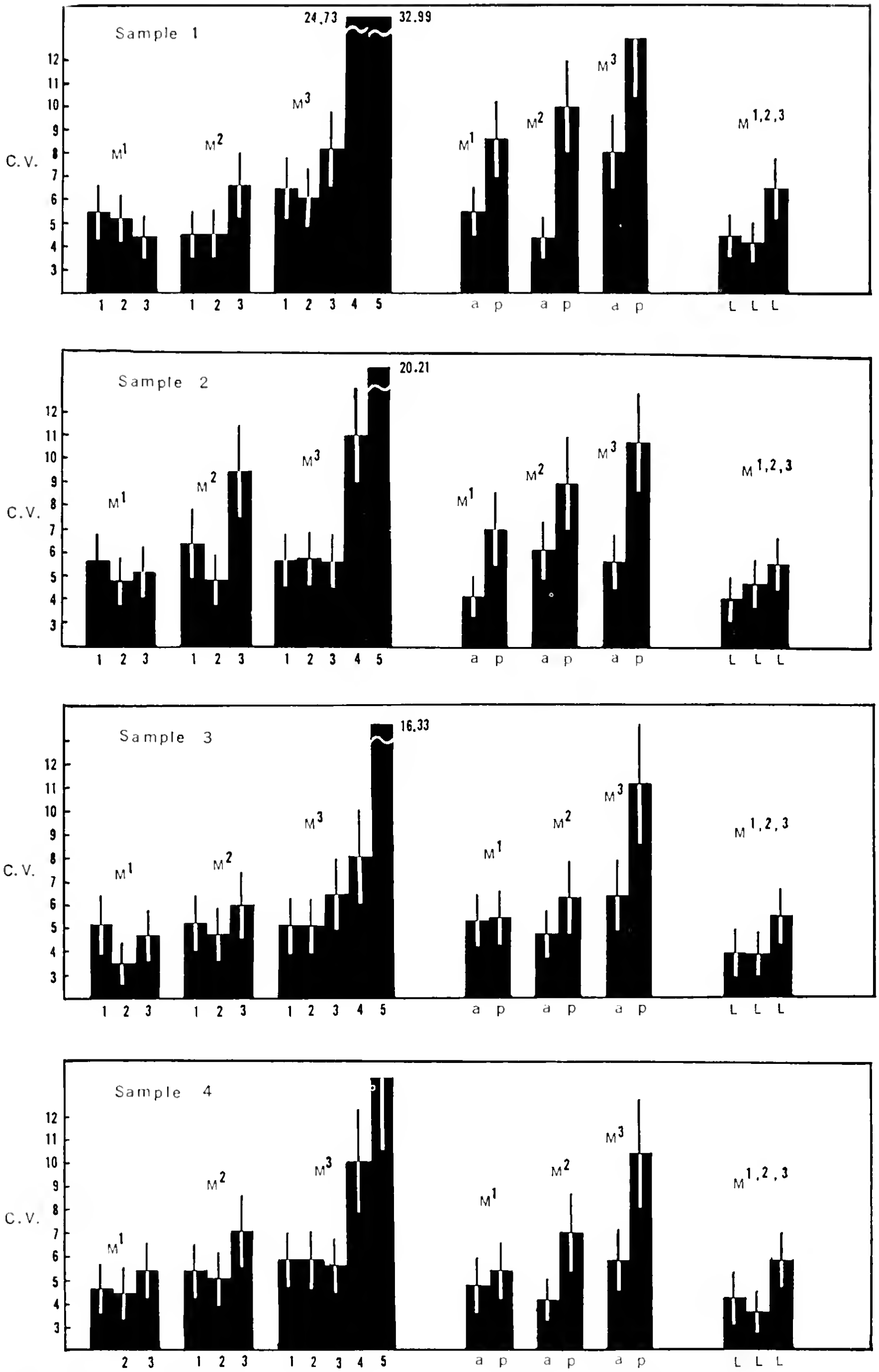

Fig. 3. Coefficients of variation (C.V.) of the upper molars of *M. paroperarius* (sample 1) and *M. pennsylvanicus* (samples 2–4); samples are identified in text. The tongue inserts are equal to two standard errors in each direction. The measurements at the base of each histogram correspond to those in Fig. 1.

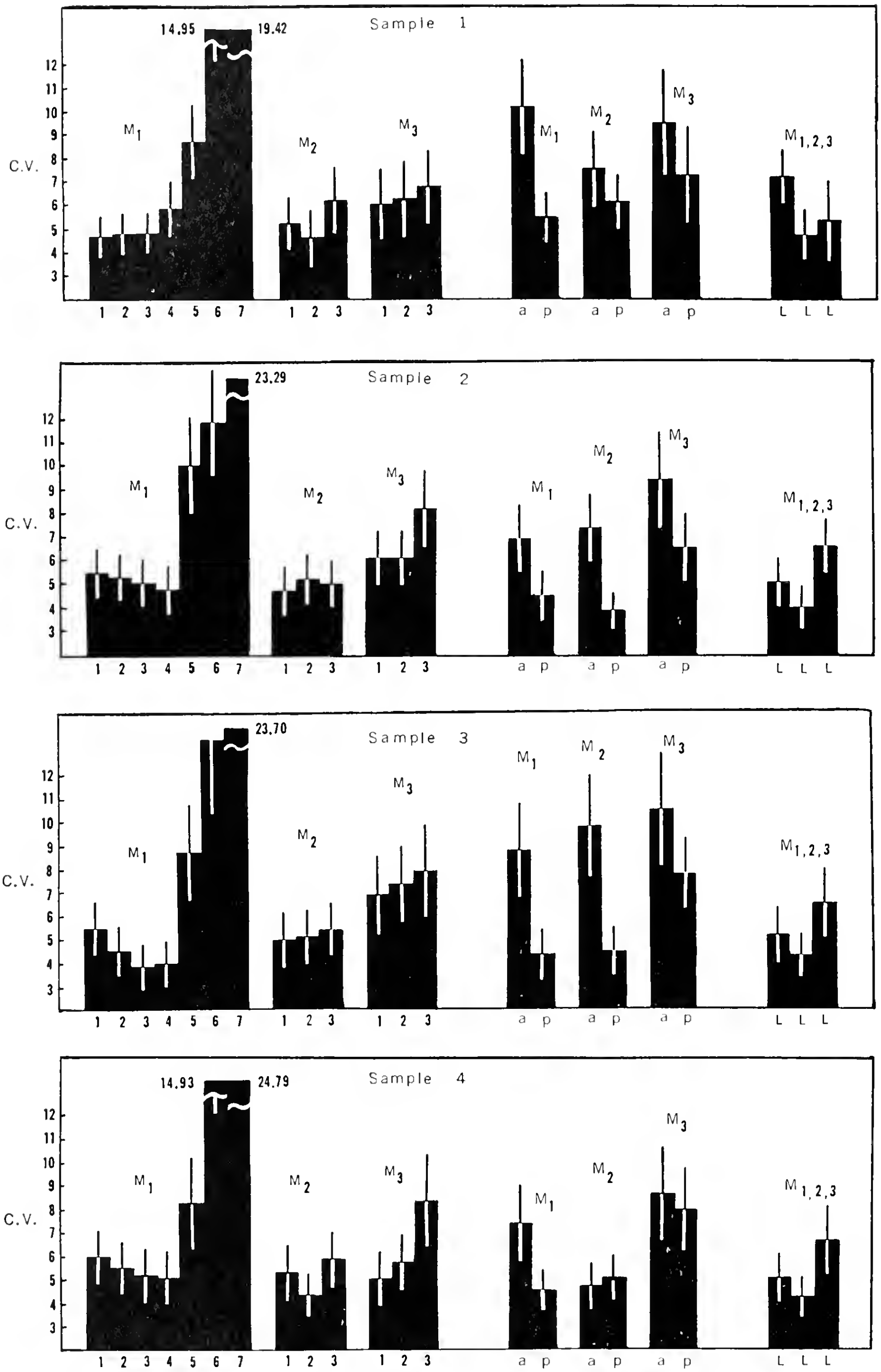

FIG. 4. Coefficients of variation (C.V.) of the lower molars of *M. paroperarius* (sample 1) and *M. pennsylvanicus* (samples 2–4); samples are identified in text. The tongue inserts are equal to two standard errors in each direction. The measurements at the base of each histogram correspond to those in Fig. 1.

and enlarging it lingually. However, on the labial side, the penetration of the re-entrant angles and the outgrowth of the salient angles act in a manner much the same as in the M_1. There is very little difference in principle in the mode of addition of salient angles in any of these teeth, only slight variations in detail.

These cross-hatched areas are the ones that vary most between species. For example, the M^3 tooth pattern at the extreme right in Fig. 2 is present in only one individual in the samples of *M. pennsylvanicus*, but is the most common tooth pattern in *M. chrotorrhinus*. Komarek (1932) reports a specimen of *M. chrotorrhinus* which has one less angle in the M^3 than usual. This specimen would correspond to the most common *M. pennsylvanicus* pattern. In addition to *M. pennsylvanicus*, several other species of *Microtus* have hints of the posteriolingual bud on the M^2, and in *M. californicus* it is of creditable magnitude (Hooper and Hart, 1962). A further discussion of the intrageneric variations in *Microtus* is given by Hooper and Hart in the preceding reference.

There is some overlap in shape between the fossil *M. paroperarius* and the recent *M. pennsylvanicus*. Referring to Fig. 2, in M_1 the third pattern from the left, in M^2 the second, and in M^3 the fourth are common to both species. However, it must be kept in mind that the discrete patterns illustrated here are only chosen points along a continuum.

The 42 different measurements are represented by histograms in Figs. 3 and 4. The most striking pattern is the high variation in the width measurements in the anterior part of M_1 and the posterior part of M^3. Although this varies slightly in magnitude between samples, the general pattern is much the same. The width measurements of M^1 have relatively low coefficients of variation, all under six. The M^2 width measurements also have relatively low coefficients of variation. The width measurement number three of M^2, which includes the incipient angle, has a larger coefficient of variation than any of the other width measurements of either M^1 or M^2. This is the incipient angle which is predominantly present in *M. pennsylvanicus* and expressed in some individuals of *M. paroperarius* as a rudimentary bump.

In every case in the upper molars the anterior length is less variable than the posterior length, Fig. 3, (a) and (p) respectively. In the case of M^1 in samples three and four, which represent males and females from one series, the difference between (a) and (p) is not outstanding. The difference between the coefficients of variation of the anterior and posterior length is greatest in M^3, which has no overlap at two standard errors in either direction. The entire length measurements (L) of M^1 and M^2 appear to have about the same magnitude of variation. The length measurement of M^3 has a larger variation in all cases than either M^1 or M^2. It will be remembered that the upper molars add to the tooth complexity from the posterior margins. From the findings here it may also be stated that these phylogenetically variable posterior areas of the uppers have the greater intrapopulational variability.

The uniformity of the four samples would seem to increase with the order in which they are listed, as there are progressively fewer collecting restrictions imposed. The fossil *M. paroperarius* sample was taken from several localities and with some temporal variation involved. The second sample, of *M. pennsylvanicus*, was taken over a wider territory than samples three and four, which were collected near a small city. Since there is a high interpopulational variation in *M. pennsylvanicus*, even within the same subspecies (Snyder, 1954), the difference in uniformity of the collecting restrictions might be thought to affect the relative amount of within-sample variation. With but one or two exceptions, the measurements did not show this expected variational gradient between samples. There also proved to be no pattern differences of appreciable magnitude between the two sexes of *M. pennsylvanicus*.

In the uppers the measurements of *M. paroperarius* tend to be more variable than the samples of *M. pennsylvanicus*, especially the posterior part of M^3 where the coefficient of variation is about double, at least in the width measurements. In the width measurements of the phylogenetically more stable teeth M^1 and M^2 there is no notable difference in magnitude between *M. paroperarius* and *M. pennsylvanicus*.

The M^2 widths have a relatively low to moderate variation, with a coefficient of variation of about six or less, and no outstanding pattern within the tooth. M_3 width measurements tend to be more variable than those of the M_2 with the anterior width measurements having the greater variation. The coefficients of variation are very large in the anterior part of M_1 (note width measurements five, six, and seven). Another peculiarity of M_1 in *M. pennsylvanicus* is that the width measurements in the midsection of this tooth are less variable than either the anterior or posterior ones. Some of the other teeth show this to a minor degree (note M^1 and M^2). In the lowers the anterior length measurements (a) are more variable than the posterior length (p) in every case except the M_2 of sample four. Unlike the uppers, the lowers add on to the anterior margins of the teeth, and we may conclude from the coefficients of variation in Fig. 4 that these anterior areas of the lower molars also have the greatest variation.

In both the posterior lengths (p) and the whole lengths (L) there is a trend toward greater variation in an anterior to posterior direction in both the uppers and lowers. This is not so well marked in the anterior length (a) measurements.

Of the measurements of the entire tooth length, the length (L) of M_3 is the most variable in *M. pennsylvanicus* while the length (L) of M^1 is the most variable in *M. paroperarius*. This is a case where the patterns produced by the length variations (L) are somewhat misleading. In *M. pennsylvanicus* M^3 is the upper tooth with the most variation, which both the width and the length measurements suggest. M_1, on the other hand, is the most variable tooth in form among the lowers. This is evident in the width measurements but does not show up in the length (L) measurements of *M. pennsylvanicus*. Although M_1 is the most variable lower tooth it has developed a long stable posterior area which dampens the variations occurring at the anterior part of the tooth, thereby producing a deceptively low coefficient of variation for the entire tooth length. This effect is not present to the same degree in the M_1 of *M. paroperarius* (see Fig. 2). At this early phylogenetic stage the tooth has a relatively smaller stable posterior section.

M_3 has a relatively higher variability than the other phylogenetically more stable teeth M^1, M^2, and M_2. It is the one tooth that crosses over the incisor root and has a limited role in adding to the crown complexity of the tooth-row, and may even be in a state of reduction in this particular genus. In some other genera of microtines, *Dicrostonyx* for example, the incisor root does not cross over in this fashion and the M_3 has developed a more complex crown pattern. Also, it is not reduced in size laterally as it is in *Microtus*. These facts suggest that the peculiar relationship of M_3 to the incisor places some limitations on its potential for increased complexity.

In many of the cricetines both the upper and lower third molars have undergone considerable reduction; this is not the case in *Microtus*. Some individuals of *M. pennsylvanicus* have a longer M^3 than M^1.

In summary then, a quantification in these two species of the molar variability reveals an overall pattern of higher variation in the posterior parts of the upper molars and the anterior parts of the lowers. The greatest amount of variation is present in the anterior end of M_1 and the posterior end of M^3. A direct positive correspondence exists between those areas of the teeth which are changing phylogenetically and those which exhibit a greater magnitude of variation.

SUPPORTING EVIDENCE

The significance of a positive association between the rapidly evolving tooth characters and a relatively high variability in *Microtus* is dependent upon its general applicability. This may be either a special case or an expression of a more general phenomenon. The following is a presentation of evidence supporting its more general nature.

In the microtines this association is not limited to the *M. paroperarius–pennsylvanicus* line, but rather it is a common feature of the whole group. *Dicrostonyx* has the most complex crown pattern of the subfamily. *D. torquatus*, the species represented in the second phase of the last glaciation (Zeuner, 1958), has a variable expression of new salient angles on the posterior margin of M^1 and M^2 and the anterior margin of M_2 and M_3. These salient angles are highly variable in their occurrence, grading to complete absence in some individuals. The characteristic species of the last glaciation, phase one (early Wisconsin), was *D. henseli*, which did not possess the salient angle or bud as did *D. torquatus*. This bud seems to be a nascent character developing through the last glacial age. *D. groenlandicus*, a recent species, has this character present in all individuals. *D. hudsonius*, a species with a distribution presently limited to the Hudson Peninsula, is a living relict representative of the *D. henseli* tooth pattern of the early part of the last glaciation. *D. torquatus* exists as the modern Old World collared lemming. Thus there is a chronological and geographical representation of the stages of development of this salient angle. The fossil *D. henseli* and the recent *D. hudsonius* do not have the salient angle. *D. torquatus*, both modern and fossil, has a varied expression of the salient angle from absent to fully present (Hinton, 1926). In populations of *D. groenlandicus* all individuals have it. Some taxonomists give these forms only subspecific status; however, the principle dealt with here remains valid.

Kurtén (1959) suggested that the average rate of mammalian evolution during the Pleistocene was relatively higher than during the Tertiary. His analysis of the variability in several rapidly evolving groups, widely separated taxonomically, revealed an increase in the coefficient of variation in more lines than a decrease. Although his study did not deal in detail with the specific characters which are changing (he used an average of several measurements), it did serve to illustrate that rapidly evolving populations do not all tend toward morphological uniformity. On the contrary, it suggested the opposite. Wright, in the discussion at the end of Kurtén's paper, proposed that recombination is responsible for this amplification of potential variability.

Skinner and Kaisen (1947) noted that while there are few diagnostic patterns in the evolution of *Bison* cheek teeth, there is a general trend toward the molarization of P_4. The metastylid and median labial root of the P_4 increase in frequency through time. In early fossil *Bison* these characters are virtually absent and in modern ones almost universally present. The increases in the complexity of P_4 seem to have occurred over a relatively short period of time during the late Pleistocene. Since these evolving areas range from absent to fully developed in some populations during this period of incipiency, the variability is greater than that of the analogous areas of neighboring teeth.

Simpson (1937) discussed a sample of 33 Eocene notoungulates, *Henricosbornia lophodonta*, which he considered to be from one population, since their variation is normally distributed and they are from the same horizon and locality. These were originally described by Ameghino as belonging to 17 species, seven genera, and three families, principally on the basis of the variation present in the upper third molar. The variations present within this primitive form are characteristic of later species, genera, and families with which Ameghino was familiar. Here is an example of a considerable amount of variation in one population, the elements of which are later characteristic of higher taxa. It would be consistent with the evidence to assume that the tooth is undergoing evolutionary change in a manner which contributes to the types characteristic of later higher taxa.

Hooper's (1957) study of the dentition of *Peromyscus* gives supporting evidence to the main thesis proposed here of rapid evolution being accompanied by high phenotypic variation. A series of *P. maniculatus* from Distrito Federal, Mexico, for example, has highly variable molars. The mesoloph and mesostyle patterns found in this one series resemble the common patterns of the other 17 species of *Peromyscus* studied. In other words, the mesostyle and mesoloph patterns observed in 17 species of *Peromyscus* are also seen in this single series. *P. maniculatus* is first known from the Wisconsin age and has expanded its distribution over a considerable part of North America. It is considered to be one of the "younger" species of *Peromyscus* (King, 1961), and therefore has recently undergone evolutionary change at the species level.

The occurrence of the crochet in horse teeth is another example of an incipient character that is highly variable in the same population (Simpson, 1953; Stirton, 1940). The acquisition of this plication is one of the first features in a general trend toward increased tooth complexity. The crochet, an anastomosing ridge between metaloph and protoloph, shows up in the *Miohippus–Parahippus* line. It is also present in some species of *Archeohippus* and sometimes in the milk teeth of *Hypohippus* (Stirton, 1940). The incipient crochet juts out as a peninsula or pier from the metaconular part of the metaloph toward the protoloph. The degree of its development is extremely variable, from absence to a small spur extending halfway across, to a complete connection between the two lophs. The crochet varies both in frequency and extent between populations and within them, occurring in its various stages of representation in individuals of the same species at one locality.

Butler (1952), speaking of the molarization of premolars in Eocene horses, stated that the metaconule evolving in the premolars is most variable at the intermediate stages of molarization.

Wood's (1962) discussion of the tooth cusp variations in the early paramyid rodents showed that the hypocone is added to the tooth by two basically different means. In some forms it is derived from an enlargement of the posterointernal cingulum; in others it originates as a division of the protocone. Wood attributed these two distinctly different means of achieving fundamentally the same end product to a general selection toward the development of a posterointernal cusp irrespective of the nature of its origin. The addition of the fourth cusp, hypocone, is a common phenomenon in many lines during this part of the Tertiary, and seems to be correlated with the exploitation of more demanding food substances. Wood stated, "There is no question but that all of these variants may occur within a single genus and sometimes within a single species." Here again, when a directional selection pressure is being applied, more phenotypic variation is exhibited in the incipient than in the non-incipient cusps.

The lower third premolar is used to characterize various genera of fossil rabbits. Hibbard (1963) observed much variation within a primitive rabbit genus, *Nekrolagus*, and found at a low frequency a pattern of the P_3 that is characteristic of modern genera. The common tooth pattern of *Nekrolagus* is also found at a very low frequency in some modern genera. This comparative study documents a chronological frequency change in which the early fossil populations have the incipient characters represented at a low frequency and the modern populations at a high frequency. Here is another case in which there is a high variation associated with incipient characters, and the axis of this variation is parallel to phylogenetic change.

Another opportunity to try the hypothesis is on the results of artificial selection experiments. If the hypothesis does approximate the real condition, the character that is artificially selected for or against should behave in a manner similar to the evolving characters that have just been discussed. That is, characters undergoing artificial selection could be expected not to experience a decrease in their phenotypic variation, but to maintain or even increase the variation.

MacArthur (1949) selected for large and small size in mice using the weight at 60 days as a measure of size. In the unselected control the coefficient of variation was 11.1. However, in the strain selected for large size it was 12.8, and in the small line 14.3.

Falconer (1955) also selected for large and small size in mice using the sixth week weight as a measure of size. He stated, "The phenotypic variability, also, does not reflect the expected decline of genetic variance, and in addition reveals a striking and unexpected change in the small line." He further reported that the large line showed a slight increase in variation over the whole course of the experiment, although it remained relatively low compared to the variation of the small line. The coefficient of variation in the small line increased to about double the original value between the seventh and ninth generations and remained at this high level. The realized heritability remained substantially constant up to the point at which response ceased. This phenomenon, he suggested, was due to the release of genetic variation through recombination.

In their selection experiments for wing length in *Drosophila*, Reeve and Robertson (1953) found that the coefficients of variation at the twentieth to seventy-ninth generations were all below two in the unselected strain and all two or above in the selected strain. The strain selected for long wings showed an increase of about 50 per cent in total variance. They attributed this entirely to an increase in additive genetic variance, which rose about two and one-half times, while the absolute amount of other genetic variance remained about the same. This led them to suppose that selection for long wing length would be far more effective in the selected than in the unselected stock.

Clayton and Robertson (1957), selecting for low and high bristle number in *Drosophila*, concluded that "Selection had by no means led to uniformity, but in some cases even magnified the total variation."

Robertson (1955) selected for thorax length in three stocks of *Drosophila* with about the same initial amount of variation. The coefficient of variation in the small lines increased immediately in the first generations and was higher than the control in all three lines, although there were between-strain differences in the pattern of increase in variation. In the large lines the variation fluctuated around that of the control stock. Thus, in the large strains the changes in response to selection occurred without appreciable change in the coefficient of variation, while the variation of the small line increased.

Although the changes in variation accompanying selection response in these experiments do not behave in a completely uniform manner, they do maintain and usually increase the initial magnitude of variation. Thus, evidence supporting the association between directional selection and a constant or increased variation is found both in rapidly evolving groups and in artificial selection experiments in which the degree of variational change has been recorded.

The Theory and Model

The most frequently employed explanation for an inordinate amount of variation is vestigiality. In such a case the characters under consideration are not becoming more complex phylogenetically but are decreasing in pattern complexity. Morphological characters which are in the process of reduction or elimination exhibit more variation than do their more functional homologues. This high correlation between vestigial and highly variable characters no doubt influenced Hinton (1926) to believe the microtines to be, in tooth form, degenerate descendants of the multituberculates and consequently undergoing reduction in tooth complexity. However, there is a time gap in the fossil record of some 35 million years between the multituberculates and microtines. The concept of the vestigial nature of microtine teeth has been perpetuated by some mammalogists (Goin, 1943; Hall and Kelson, 1959). But the position that microtines did not arise from a cricetine stock and have not undergone a general increase in tooth complexity is untenable. Not only does the fossil record support an increase in microtine tooth complexity, but there is an almost complete continuum of recent intermediate forms between the Microtinae and Cricetinae. Vestigiality can be discounted as an explanation of the variation differential in the other examples as well, as these characters are also increasing in complexity.

Lately, much attention has been given to the loss of buffering capacity against environmental stress as the genome tends toward homozygosity (Lerner, 1954). Since directional selection reduces the amount of individual heterozygosity, the loss of buffering would result in a greater magnitude of individual deviation from the mean, increasing the phenotypic variation of that population. This process may be the cardinal factor involved in an explanation of the phenomenon of an increase in variation accompanying directional selection. However, there is some discouraging evidence against an explanation of this nature. (1) The increase of phenotypic variation becomes evident early in artificial selection (Robertson, 1955) before an appreciable amount of genetic variance could have been lost by selection. (2) A character in which selection has considerably altered the mean can often be returned with little difficulty to the original mean by reversed selection. This reversal could not take place if the population had reached a relatively homozygous level for that particular character. (3) A correlate of the latter is that often a substantial heritable component is still present after the mean has been considerably altered by selection (Lerner, 1958). (4) Bader (1962) showed that, in tooth form, inbred mice exhibit slightly less phenotypic variation than wild populations; and the outcrossed heterozygote is less variable than either. (5) If the tooth variation discussed here in *Microtus* is non-genetic, it is difficult to explain the phylogenetic increase in tooth complexity, since the most important cause of evolutionary change is selection acting upon heritable variation. From some preliminary crosses of microtines (Steven, 1953; Zimmermann, 1952), it does seem that these variations are heritable. In at least one species of *Microtus* (*M. arvalis*) there is also a geographic cline in the frequency of tooth complexity. The variations were classed into two discrete types (simple or complex); the frequency of "complex" ranges from five per cent to 95 per cent in the cline from northern to southern Europe (Zimmermann, 1935).

The accumulated evidence from breeding experiments suggests, contrary to the "wild type" or normality concept, that there is considerable heterozygosity underlying the relatively coherent facade of the phenotype. The variation expressed in the phenotype is only a fraction of the total possible variation present (Mather, 1956). There is a diversity of opinion as to the mechanisms involved in the maintenance of this large amount of potential variability. The position that the balanced additive factors maintain the stored variability has much evidence in its favor in terms of its general applicability to evolution at the intrapopulational level. Stated in more detail, this position asserts that there exist balanced systems of linked heterozygous polygenes structurally associated and maintained by selection and perhaps also by decreased recombination.

Delayed responses to selection are best accounted for on the basis of genetic linkage. A rather common phenomenon in experimental breeding is for a selected strain to reach a plateau of response only to have it resume progress after a period of relaxation of the selection pressures. The most plausible explanation of this phenomenon is linkage disassociation; the various elements are unable to segregate out immediately because of linkage restrictions (Mather, 1949). The ineffectiveness of experiments to reduce the variation by selection for intermediates (Lerner's type II selection, Lerner, 1958; Falconer, 1957), and the ineffectiveness of selection for the extremes to alter the variation (type III selection, Falconer and Robertson, 1956) both suggest that the additive genetic material resides in balanced linkage groups.

Structural change, which often inhibits crossing over, may establish an isolation of segments of the chromosome where crossing over is likely to occur only with configurations of that same type; however, the general importance of this mechanism is still not clear. As well as promoting these devices that inhibit recombination, selection can operate directly to maintain these blocks intact (Lerner, 1958) and this is probably the most important mechanism. Carson (1959) reports that most natural inversions are heterotic when removed from nature to the laboratory culture, and that strains derived from a single pair of wild flies retain with extreme tenacity most of their initial inversion variability.

The advantages of a system of balanced linkage groups are multiple. The population can maintain a high degree of heterozygosity in many individuals without the rigorous selection required if these elements were segregating at random. The close linkage association also serves as a buffer against random fluctuations away from the optimum. And perhaps most important, it holds genetic material in reserve, thereby maintaining an evolutionary plasticity.

There is evidence that integrated chromosome segments are important in the association or correlation of continuously distributed characters, and that they behave in a manner similar to single independent genes acting pleiotropically. To resolve or disassociate the correlation of two characters by selection would produce strong evidence for linkage. Such disassociation has been accomplished (Mather and Harrison, 1949; Mather, 1956). Correlation due to pleiotropy is, of course, more resistent to evolutionary change than the more labile system of linkage groups. Linkage groups can originate or be disposed of by the selection for various recombination and structural patterns. It would be a slow process for the population to await a new mutation at one locus which acted upon the desired characters in exactly the right magnitude.

Selection can maintain a frequency of balanced genetic material within each chromosomal block or "internally" at levels that insure a considerable proportion of "relationally" balanced, or heterozygous, individuals in the population. As long as this block remains intact it will carry reserves of variability which may be released and made available for segregation by crossing over. With selection against the crossovers, this residual genetic variability can be maintained (Lerner, 1958). In order to maintain the internally balanced linked groups a selection intensity would be required equivalent to the frequency of crossovers which deviate from the balanced configuration (Falconer, 1960).

The increase in variation of evolving characters may be further enhanced when an interbreeding population experiences the stress of two selective optima. This condition would occur in most evolutionary changes when the group is partially exploiting two adaptive zones. Thus, a character in transition may be expected to experience some reduction in stabilizing selection along its axis of change.

The high variation usually associated with vestigiality can also be accounted for in the context of this theory. A vestigial character is in essence an evolving character, as reduction plays a great part in evolutionary change. According to the explanation given for the greater amount of variation in evolving characters, the stored variability is maintained in a linked system by stabilizing selection. When this balance is altered by directional selection, the variability is released. Due to its decreasing functional role, the variation of a vestigial character would also be compounded by a decrease in stabilizing selection.

Carson (1955), in his discussion of the genetic composition of marginal populations, surmised that, since the marginal populations contain fewer inversions than central populations, the more stringent selection on the periphery is against the heterotic groups which predominate in the central population. These findings are in agreement with the idea expounded here, that directional selection away from the mean is selection for the breakdown of present linkage configurations. Carson further reported that when strong artificial selection was applied to both marginal and central population lines, the marginal lines showed the greater initial response. This difference would exist if the genetic material has been made available for segregation in the marginal populations by the breakdown of the linkage groups.

Reeve and Robertson (1953), selecting for wing length in *Drosophila*, found that the selected strain showed an increase in additive genetic variance of 250 per cent, all other genetic variance remaining about the same. They further suggest that selection for long wing length would be more effective in the selected than in the unselected stock. Robertson (1955) states: "Selection generally leads to an increase in variance which appears to be largely due to the increased effects of genetic segregation and this constitutes an aid to selection progress."

This release of additive genetic variation provides a mechanism whereby directional selection, in continuously distributed polygenic systems, increases its own resolving power. Selection against the mean and its present balance situation is selecting against the present linkage configurations, which results in a breakdown of these integrated units. The genetic components are then released and made available for novel segregants hitherto unavailable. The consequence of this is an increase in phenotypic variation, which is heritable in an additive fashion. As the amount of variation is a determining factor of the effectiveness of selection, in conjunction with selection intensity and heritability, further selection gains are facilitated.

To set up a simple visual model of this theory let us suppose, as is expressed in Fig. 5, that there is a series of loci with alleles acting in an additive fashion either to the left or right of the mean. Loci a, b, c, and d control the size of character X and e, f, g, and h control Y. The contribution of each allele is specified. Further, suppose these are balanced "internally" and "relationally," with an equal frequency of each linkage group. The mean will be considered as zero with the deviations from it in both positive and negative directions. A stabilizing selection for the mean would cull out deviants, the crossovers, from this configuration. The genetic material present is potentially able to produce an individual representative of any point in the figure, but this particular linkage configuration limits the phenotypes to a coherent cluster around the mean. The broken circle represents a variation of two standard deviations from the mean, if each locus were acting individually with an equal frequency of each allele. The linked configuration, however, would produce a population with a lower variation, expressed here at two standard deviations by the solid inner circle.

If a new adaptive optimum ($\bar{X}_2$) were created with a consequent directional selection of moderate magnitude exerted on the distribution, the linkage groups would be selected against by a selection for the crossovers in the direction of the new adaptive optimum, resulting in a partial breakdown of the coherent phenotype.

A structural association of the loci controlling the two characters (Fig. 6) would result in their correlation. The points all fall along the diagonal axis between +2

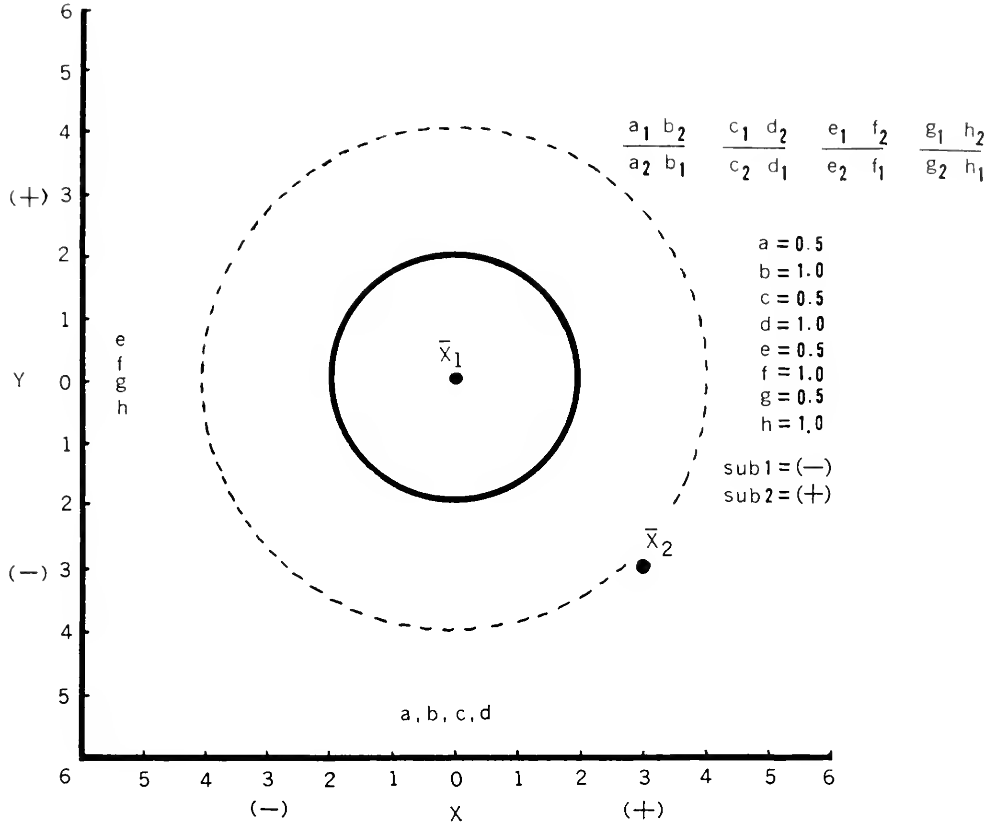

FIG. 5. An elementary model of the non-correlated case of two characters X and Y, where low phenotypic variation is maintained by selection for the linkage configuration represented in the upper right. With equal frequencies of each linkage group the variation of the population, at two standard deviations, would be circumscribed by the solid circle. The dashed line represents the same loci with no linkage. Selection for $\bar{X}_2$ would increase the variation as the linkage configuration would be selected against.

and −2 units, as shown by the ellipse. If one were to think in terms of the major axis of variation as size, this provides a relatively constant individual shape throughout a population in which the individuals are varying in size. As in Fig. 5 it will be noted that an imposed directional selection will produce an increase in variation. Even directional selection parallel with the main axis of size will increase the variation. The greatest increase in variation, however, would be produced by a selection pressure at right angles to the principal axis of variation, toward $\bar{X}_2$, which would be selection for shape changes. The long-term effect of this type of selection would be twofold: (1) an increase in phenotypic variation, and (2) a decrease in the correlation of characters X and Y. Unlike the situation in Fig. 5, if a selection pressure is exerted on only one character (perpendicular to the scale of the other), the second character is also initially affected. However, it is an inherent mechanism of the model that the linkage which provides the correlation of the characters will be selected against when only one character is subjected to directional selection. This system then would further contribute to evolutionary plasticity.

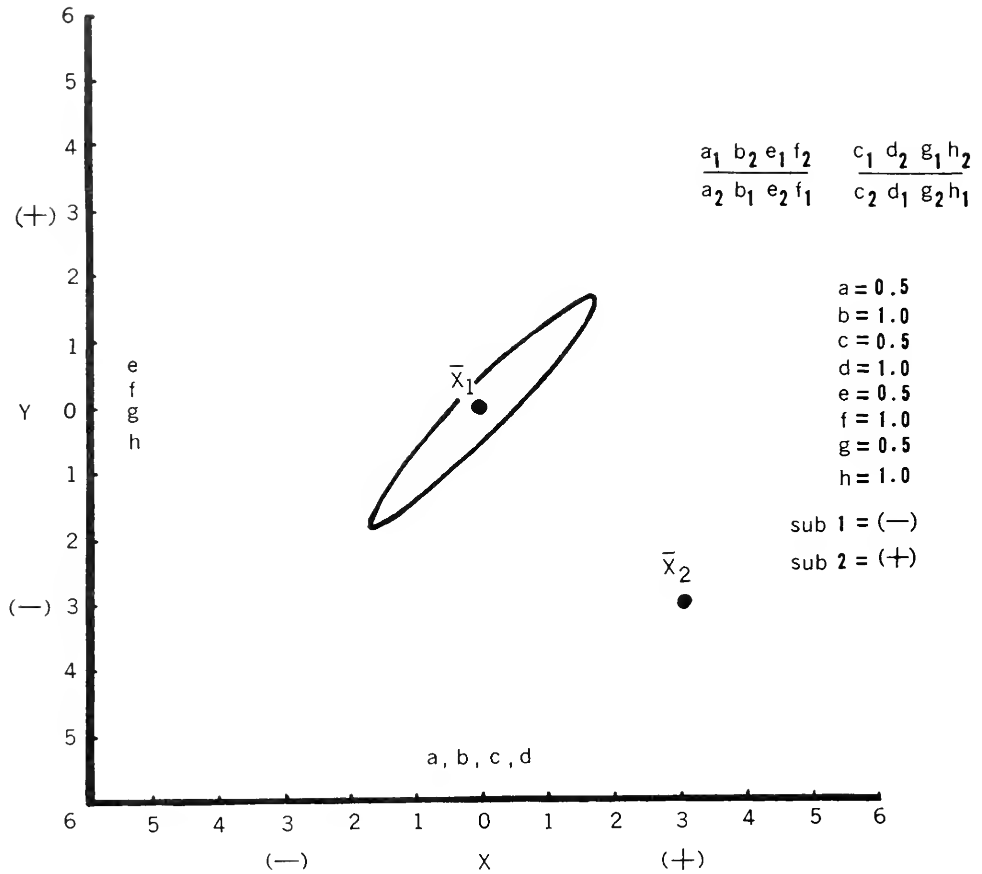

FIG. 6. Same as Fig. 5 except that characters X and Y are now correlated due to the linkage association. This new linkage configuration maintains a coherence differentially on the size and shape axes. Selection toward $\bar{X}_2$ would considerably increase the variation along the shape axis.

I do not wish to imply that the theory expressed here accounts for all the various behavior exhibited by residual genetic variation. Rather, I have investigated one aspect, the association of directional selection and the maintenance or increase of the initial phenotypic variation, and have hopefully offered a plausible explanation, which will be further explored soon by breeding experiments with *Microtus*.

Summary

This is a study of the intrapopulational variability present in the dentition of two species of *Microtus*, and the more general questions arising from it. The central thesis is that quantitative characters undergoing rapid evolution do not show the decline in phenotypic variation predicted by our present evolutionary concepts. On the contrary, the variation is maintained and usually increased.

Of the two species used, the fossil species is thought to be ancestral to the modern meadow vole; thus the study materials comprise an evolutionary line with two grades of tooth complexity represented. In the molar crowns of both species, the areas which are changing phylogenetically are those which vary most within the population. Evidence from other sources in which characters are undergoing directional selection, both evolutionary and artificial, suggests that a greater variation in characters undergoing directional selection is a general condition.

A theory to account for association between rapidly evolving characters and a relatively higher amount of phenotypic variation is that the coherence of the population around the mean is due to balanced heterozygous linkage groups and that with the application of directional selection this organization is partially broken down. The genetic variation is then released and made available for recombination. The relatively high variability associated with vestigial characters is also fitted into the context of the theory. The theory suggests that directional selection on continuously distributed characters increases its own effectiveness.

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Evolutionary adaptations of temperature regulation in mammals[1]

By L. Jansky

Eingang des Ms. 25. 10. 1966

Generally speaking, adaptations may take place either during individual life of animals (acclimations and acclimatizations), or they may be specific to certain species (evolutionary adaptations) (Hart 1963b). They may be realized by different mechanisms with different degree of efficiency, however the aim of all adaptations is essentially the same — to reduce the dependence of animals on environmental conditions and thus to increase their ecological emancipation. The study of physiological mechanisms of adaptations is therefore of great ecological importance since it helps us to elucidate physiological processes influencing limits of distribution of different species and having a profound effect on the quality or density of animal populations. The comparison of individual and evolutionary adaptations permits us to trace the evolutionary progressive physiological processes and to contribute to the problems of phylogeny.

In lowered temperatures mammels tend to lose heat. Theoretically, they can prevent hypothermia either by increasing heat production in the body or by reducing heat loss from the body to the environment. Heat production is realized by shivering; heat conservation may be manifested by reducing the body surface, by improving its insulation qualities and by decreasing the body—air temperature gradient according to formula:

$$H = K \frac{T_B - T_A}{I} \quad (1) \qquad (\text{Hart, 1963b})$$

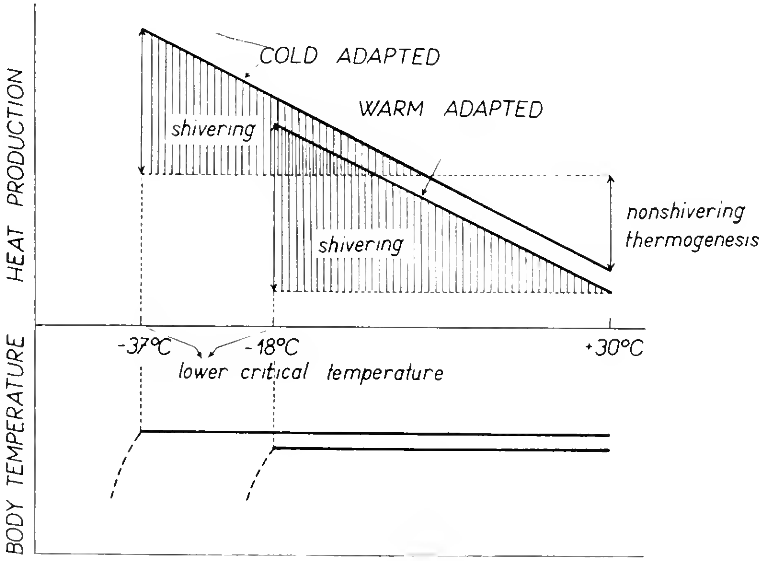

Fig. 1. Scheme of heat production of rats adapted to warm (30° C) and cold (5° C) environments. According to Hart & Jansky, 1963

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[1] Presented at the 40th meeting of the German Mammalogical Society in Amsterdam.

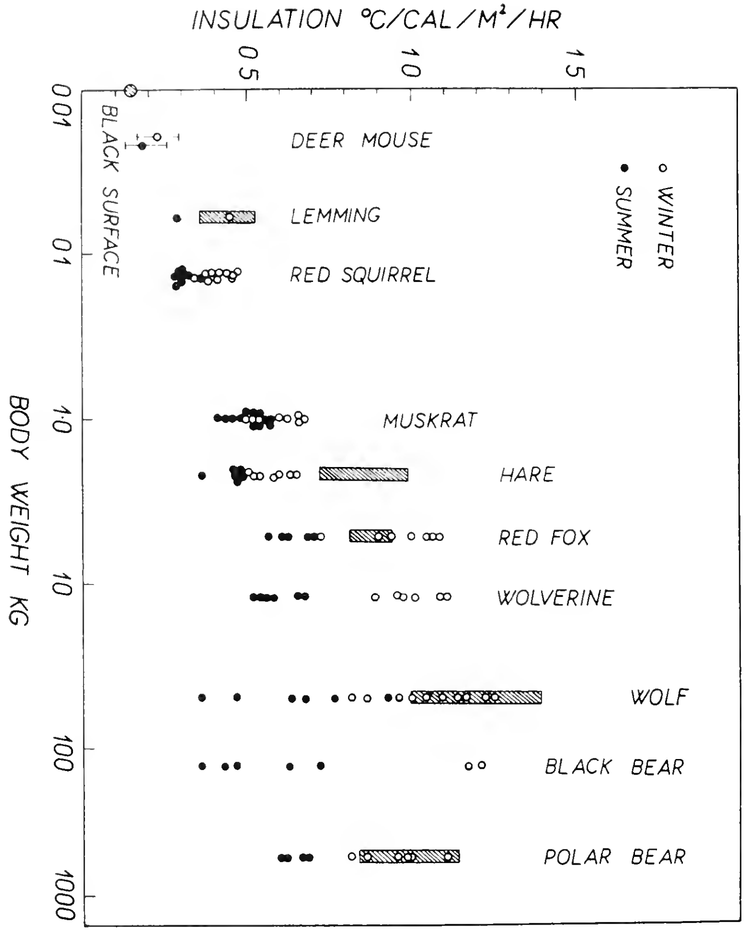

Fig. 2. Seasonal changes in fur insulation in various mammals (HART, 1956)

(H = heat production, K = a constant representing the body surface area, T_B = body temperature, T_A = air temperature, I = insulation qualities of the body surface.)

Similary, the adaptations of temperature regulation to cold can be realized either by increasing the capacity of heat production or by mechanisms leading to reduction of heat loss from the body. The adaptation to cold appears as a shift of the lowest temperature limit animals can survive (lower critical temperature).

In our earlier work we have shown that the individual adaptations are manifested predominantly by an increased capacity of heat production owing to the development of a new thermogenetic mechanism — called nonshivering thermogenesis (HART, JANSKY 1963). Physiological background of this phenomenon consists in an acquired sensitivity of muscular tissue to thermogenetic action of noradrenaline liberated from sympathetic nervous endings (HSIEH, CARLSON 1957). Nonshivering thermogenesis potentiates heat production from shivering and in rats shifts the lower critical temperature for about 20° C (from —18° C down to — 37° C; Fig. 1).

Mechanisms controlling heat loss by changes in body surface area or by changes in body-air temperature gradient are not common in individual adaptations. On the other hand it is well known, that certain species can improve body insulation in winter season. However, this phenomenon becomes functionally justified only in animals of greater size (size of fox and larger; Fig. 2. Hart 1956).

The individual adjustments with the aid of nonshivering thermogenesis are encountered both in acclimations under laboratory conditions and in seasonal acclimatizations induced in the same species under natural conditions. They are undoubtelly very efficient and biologically important. On the other hand, from the ecological point of view, they have also their negative side. The increased heat production results in higher demands for energy restitution in the body, which is attained in cold adapted animals by an increased food consumption. As a result, individuals adjusted this way become more dependent on the quantity and availability of food and they are forced to use more effort to provide it. The reduced dependence of animals on temperature factors is thus substituted by increased dependence on food factors.

Contrary to individual adaptations, in evolutionary adaptations mechanisms leading to the reduction of the heat loss are greatly emphasized. Their importance consists in the fact that they save energy for the organism and have lower demands to its restitution in the body. This fact is obviously evolutionary very important — in the processes of phylogeny there occurs natural selection of those individuals that are less impeded by the lack of food, often occuring in nature.

Evolutionary adaptations are realized in the first place by an increased insulation of the body cover (fur, Fig. 3). This adjustment, typical for arctic animals, can reduce the heat loss so efficiently, that even considerably reduced ambient temperatures (down to — 50° C) do not result in an increased heat production in larger animals. (Fig. 4; Scholander et al. 1950a, b). The same role plays a thick layer of subcutaneous fat which appears in some mammals, such as seal and swine. The insulation qualities of this fat layer can be increased by an active restriction of the blood flow to this area. This results in superficial hypothermia, which also efficiently prevents the heat loss (Irving 1956). Animals endowed with superficial hypothermia have normal thermogenetic abilities. However, compared to the species from tropical regions with little insulation and to arctic species with great surface insulation they show a reduced sensitivity of afferent sensory input to temperature stimuli (Fig. 5).

A tendency to reduce heat loss by reduction of the body surface area may be considered as another type of evolutionary adaptations. This phenomenon occurs in animals living permanently in cold climate, which are generally larger and have shorter body appendages than animals from tropical zone (Bergmann's and Allen's rules). Both the validity and the physiological significance of these rules have been recently questionend by several workers, however.

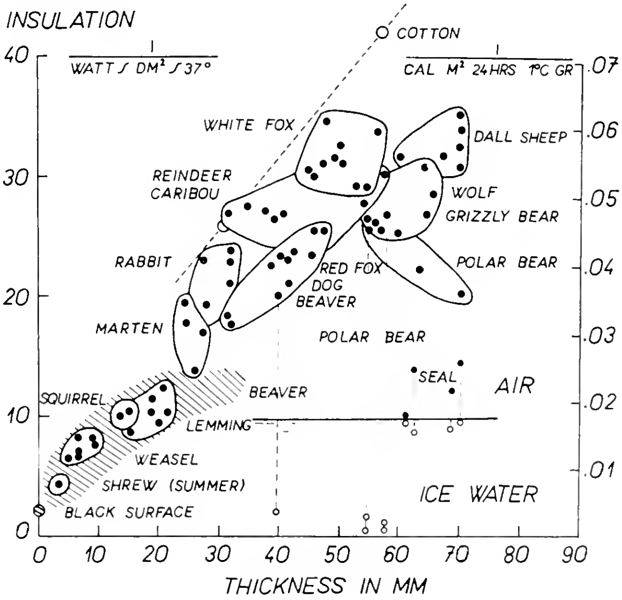

Fig. 3. Insulation in relation to winter fur thickness in arctic and tropical mammals (Scholander et all., 1950 b)

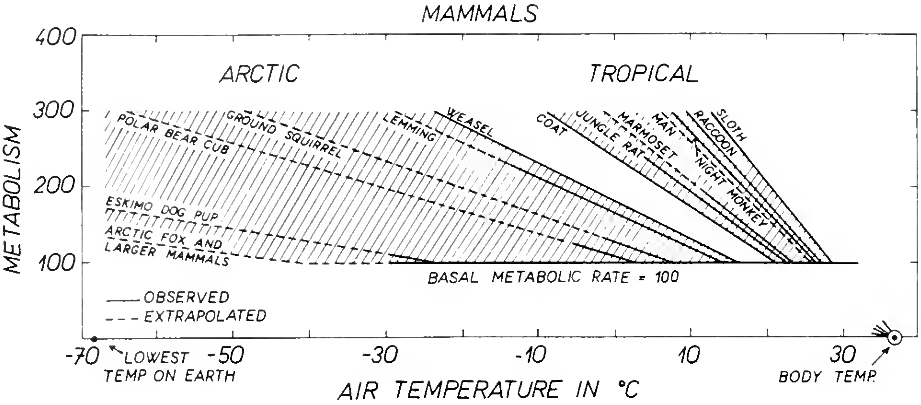

Fig. 4. The effect of environmental temperature on metabolism of arctic and tropical mammals (Scholander et all., 1950 a)

The reduction of heat loss by changing the body-air temperature gradient can be realized either by active choice of higher environmental temperature or by considerable lowering of body temperature.

It is generally recognized that the active choice of the environmental temperature occurs by seasonal migrations and by changes in patterns of daily activity. It was found that different species of voles and shrews transfer the peak of daily activity to warmer part of the day in a cold weather (Jansky & Hanák 1959).

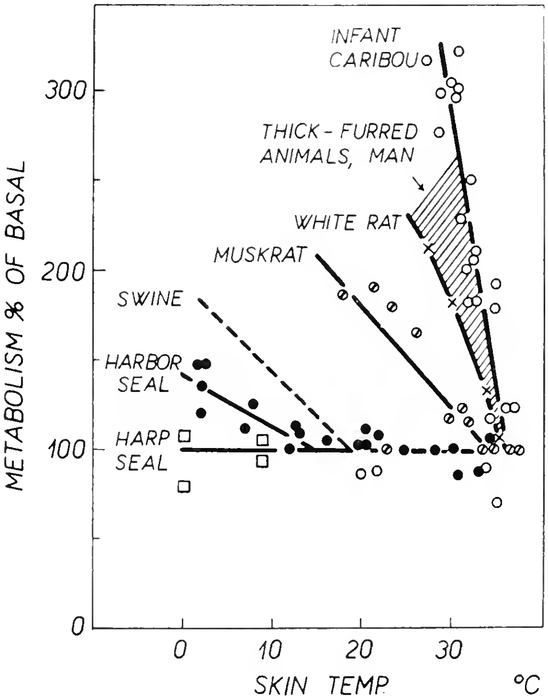

Fig. 5. Heat production as a function of skin temperature under fur of the back for a series of mammals (Hart, 1963 a)

The mechanisms leading to reduction of body-air temperature gradient by lowering of body temperature are especially developed in hibernators. According to the latest view hibernation is not considered as a lack of temperature regulation rather as a special adaptation of thermogenetic processes. There are two reasons for that: first, hibernators have the same capacity of heat production as other hemeotherms of similar size (see Jansky, 1965) and second, the entering, the arousal and the deep hibernation are under remarkably precise physiological control (see Lyman, 1963).

This indicates a leading role of central nervous system in controlling hibernation, which is adapted to hypothermal conditions and it is functional at all levels of body temperature. This adaption has certainly its metabolic background, however only little is known about this phenomenon so far.

The control of entering into hibernation is realized by the active inhibition of shivering heat production by signals from subcortical centres of the brain. Simultaneously with the decrease in shivering an active inhibition of the activity of the sympathetic nervous system also takes place, which is manifested by the reduction of heart rate and by vasodilatation. These changes facilitate the lowering of body temperature of animals which is realized successively in the form of "undulating" cooling so the organism can slowly prepare to hypothermia (Fig. 6). Nervous control of hibernation persists in deep hypothermia as evident from the sensitivity to thermal and other stimuli. The arousal from hibernation is equally an active process, very efficiently controlled, so that organism can produce a great amount of heat in minimum of time. The coordination of thermogenetic processes depends also on the activity of nervous centres. Characteristic of awakening is the preponderence of sympathetic nervous system, leading to vasoconstriction and to an increase in heart rate. The main source of heat in awakening is again constituted by shivering. However, nonshivering heat production was also found during arousal and also the rapidly beating heart, working against a high pressure, may contribute a certain amount of heat.

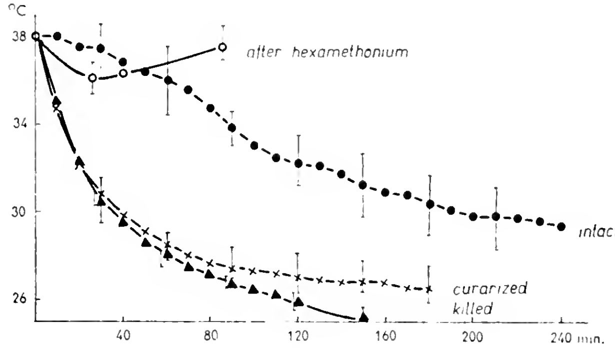

Fig. 6. Changes in body temperature of the bat *Myotis myotis* during entering hibernation (Jansky, Hájek, 1961)

Summary

On the basis of all mentioned data we conclude that the adaptations of temperature regulation to cold may be realized either by an increased ability to produce heat or by reducing the heat loss. While the individual adaptations are manifested chiefly metabolically as evident from an increased capacity of heat production, the inherited adaptations are realized mainly by mechanisms leading to the heat loss reduction (e. g. increased insulation by fur or by superficial hypothermia, reduction of body surface area, active choice of environmental temperature and lowering the body temperature). The control of the mentioned adjustments consists in the changes in function of the central and sympathetic nervous systems inducing changes in intensity of the energy metabolism (individual adaptations), changes in the plasticity of vasomotor mechanisms and in heat production of hibernators during entering into and awakening from hibernation (evolutionary adaptations). Morphologically based adjustments (improvement of insulation by fur) appearing in both evolutionary and individual adaptations forms the connecting link between both types of adaptations.

Zusammenfassung

Aus allen erwähnten Daten folgern wir, daß die Adaptationen der Temperaturregulierung bei Kälte entweder durch die erhöhte Wärmeproduktion oder durch die Verringerung des Wärmeverlustes erreicht werden. Während die individuellen Adaptationen hauptsächlich metabolischer Art sind, was durch die erhöhte Kapazität der Wärmeproduktion in Erscheinung tritt, findet man erbliche Adaptationen zumeist in Form von Mechanismen, die eine Verringerung des Wärmeverlustes bewirken (z. B. erhöhte Isolierung durch das Fell oder durch oberflächliche

Hypothermie, Verringerung der Körperoberfläche, aktive Wahl der Umgebungstemperatur und Absinken der Körpertemperatur). Die Steuerung der erwähnten Anpassungen beruht auf Veränderungen in der Funktion des zentralen und des sympathischen Nervensystems, welche Veränderungen in der Intensität des Energiestoffwechsels (individuelle Adaptationen) hervorrufen, weiterhin Veränderungen in der Plastizität der vasomotorischen Mechanismen und in der Wärmeproduktion von Winterschläfern beim Einritt in den Winterschlaf und beim Erwachen (evolutive Adaptationen). Morphologische Adaptationen (Verbesserung der Isolierung durch das Fell), die sowohl als evolutive und auch als individuelle Adaptationen vorkommen, stellen die Verbindung zwischen beiden Typen der Adaptation her.

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SECTION 6—ZOOGEOGRAPHY AND FAUNAL STUDIES

Studies of faunas, both of local areas and of broad regions, have contributed substantially to the literature in mammalogy. From the earliest contributions to the present, papers and books dealing with faunistics have included much information on systematics, ecology, distribution, ethology, and reproduction, among other topics. The sobriquet "natural historian" implied an interest in all these fields and more.

Darlington's (1957) book *Zoogeography* and Udvardy's (1969) *Dynamic Zoogeography* are the best single sources of general information on the subject; Hesse *et al.* (1937) is a substantial and still useful earlier reference. Insular biogeography was aptly dealt with by Carlquist (1965) and in a more mathematically-oriented way by MacArthur and Wilson (1967). Matthew's (1939) *Climate and Evolution* and Dice's (1952) *Natural Communities* are but two of the other general treatises that should be called to the attention of the beginning student.

Among the major faunal catalogues are Allen (1939) for Africa, Ellerman and Morrison-Scott (1951) for the Palearctic Region, Miller and Kellogg (1955) and Hall and Kelson (1959) for North America, Cabrera (1958, 1961) for South America, and Troughton (1965) for Australia. At the regional or provincial level, Kuroda's (1940) treatment of Japanese mammals, Laurie and Hill (1954) on New Guinea and the Celebes, and Peterson's (1966) *The Mammals of Eastern Canada* are good examples as are many of the state lists published for North America (e.g., DeKay, 1842; Miller, 1899; Hall, 1946; Jackson, 1961; Baker and Greer, 1962; Jones, 1964), of which Hall's *Mammals of Nevada* stands out in completeness of coverage from most points of view. In terms of smaller geographic areas, Harper (1927) on the Okefinokee Swamp, Johnson *et al.* (1948) on the Providence Mountains of California, Anderson (1961) on the Mesa Verde of Colorado, and Foster's (1965) study of the Queen Charlotte Islands illustrate that substantial information can be gleaned from the study of a geographically restricted fauna. These papers as well as several reproduced here certainly indicate that the serious student of faunistics must be as broadly trained as any student in the discipline of mammalogy.

Because of the sustained interest in faunal studies over the years, it was inevitable that certain "rules," "laws," and "systems"—directed at overall explanations for natural phenomena associated with distribution and variation—would emerge. These have been of two basic sorts, various "ecological rules" such as those proposed by Allen, Bergmann, and Gloger, and the biogeographic systems proposed on a world-wide scale by Wallace and others and applied more specifically to North America by Merriam (Life-zones), Shelford (Biomes), and Dice (Biotic Provinces). Space does not permit the reproduction of the lengthy papers dealing with these subjects, but a short contribution by Dice, which is included, serves to introduce the reader to this aspect of mammalian zoogeography.

Other selections for this section deal with zoogeographic problems related to Pleistocene, sub-fossil, and Recent faunas (Guilday, Koopman and Martin, and Findley and Anderson). One paper concerns a local fauna (Jones and

Lawlor) but also includes information relevant to other sections of this anthology. The essay by Davies covers an entire order (or suborder according to many other authors) of mammals, whereas the short paper by Davis deals with the relationship of soil types and altitude to the distribution of a single species in a restricted area. The final paper is a statistical treatment by Hagmeier of distributional patterns on a continental basis. This analysis is based on data compiled in one of the faunal catalogues (Hall and Kelson) cited above.

THE CANADIAN BIOTIC PROVINCE WITH SPECIAL REFERENCE TO THE MAMMALS

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In eastern North America many zoogeographers recognize six life zones, all assumed to be transcontinental in extent and named, respectively, Arctic (or Arctic-alpine), Hudsonian, Canadian, Transition, Upper Austral, and Lower Austral (Merriam, '98: 18–53). The Alleghanian, Carolinian, and Austroriparian faunas are the eastern portions, respectively, of the Transition, Upper Austral, and Lower Austral life zones. In addition, some zoogeographers recognize a Tropical region which covers the southern part of Florida.

Ecologists, on the contrary, divide eastern North America somewhat differently. Shelford, Jones, and Dice ('26: 60–73) recognized here the Arctic Tundra, Northern Coniferous Forest, Mixed Coniferous and Deciduous Forest, Deciduous Forest, and Southeastern Coniferous Forest biotic areas. Weaver and Clements ('29, frontis) divide the eastern part of the continent among the Tundra, Boreal Forest, Lake Forest, Deciduous Forest, and Tropical climaxes.

There is rather general agreement among biogeographers on the importance of the Tundra (Arctic) and Boreal Forest (Hudsonian) divisions. Also most students of distribution would accept the Southeastern Coniferous Forest (Austroriparian) as at least a minor unit. On the other hand, there is little agreement on the biogeographical division of the remaining middle portion of eastern North America.

In order to examine the several biotic provinces of northeastern North America I drove by automobile in the summer of 1936 through considerable parts of eastern Canada and of the northeastern United States. The observations made on this trip and a subsequent study of the available descriptions of the vegetation and faunas of the area have convinced me that the so-called Canadian and Alleghanian faunas are only different aspects of the same ecological complex. The name Canadian is more descriptive of this complex than is the name Alleghanian, and, therefore, the term Canadian biotic province is here adopted for that part of northeastern North America in which

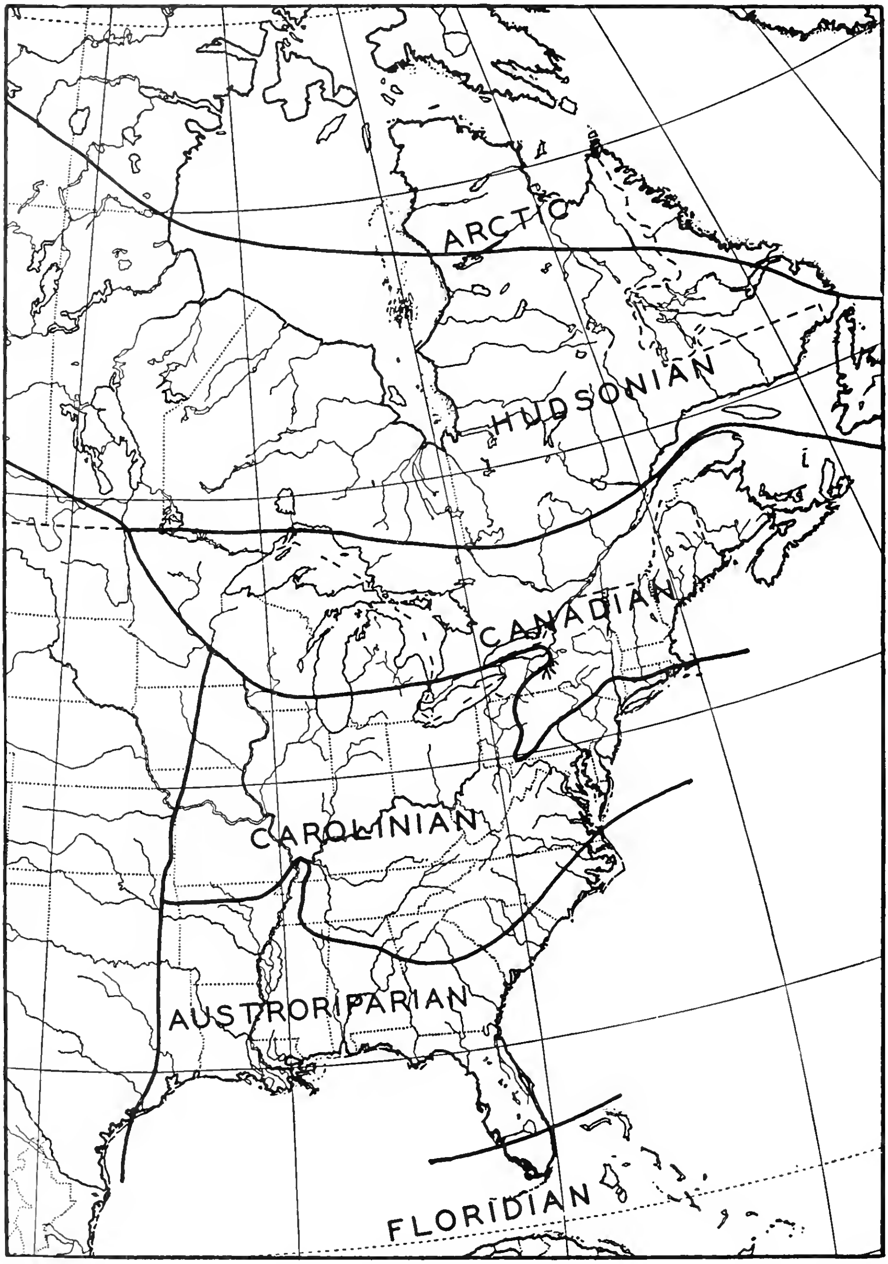

FIG. 1. Map of eastern North America showing the distribution of the several biotic provinces.

hardwoods form the climax and conifers of several kinds form several types of subclimaxes. A biotic province is, according to my definition, a major biogeographic division of a continent, characterized by the biotic communities which compose it.

The Canadian biotic province as here recognized (fig. 1) covers much of southern Quebec, including the Gaspé Peninsula, and all of New Brunswick, Nova Scotia, and the adjacent islands. It extends southward to include much of New England, most of New York state, and the mountainous parts of Pennsylvania. It covers Michigan and Wisconsin, except their southern parts; the northeastern half of Minnesota; and all of southern Ontario, except along Lake Erie. The province is in my interpretation not transcontinental, although there are some similarities between its biota and that of the western mountains.

An excellent description of the vegetation of the Canadian biotic province has been given by Nichols ('35: 403–422) under the designation Hemlock—white pine—northern hardwood region. Nichols, however, includes the southern Appalachian Mountains in his region, while I consider it better to include these mountains in the Carolinian biotic province, by which they are surrounded.

The western end of the northern boundary of the Canadian province should in my opinion be placed a little north of the position given by Nichols ('35, fig. 4), so as to include all the important stands of sugar maple, white pine, and Norway (red) pine (see Howe and Dymond, '26: 288–291). An unpublished study of the plant ecology of Isle Royale by Clair A. Brown shows that there are considerable stands of sugar maple forest on this island, which lies in the northern part of Lake Superior. The northernmost important stands of sugar maple and white pine observed by me along the road between North Bay and Cobalt, Ontario, were about 50 miles north of North Bay, on the rocky ridges of the Timagami Provincial Forest.

A second-growth forest of white spruce and pine was studied at James Lake, 11 miles south of Latchford, or about 66 miles by road north of North Bay. This forest was growing on moderately high rolling rocky hills, and the soil, while often thin, contained much humus. White birch was the most common tree, and balsam fir, black ash, and aspen were numerous. There were a few small white and Norway pines, and a few of a species of poplar with long leaves. A maple (*Acer spicatum*) was the most common shrub. Signs of snowshoe hare were numerous, and red squirrels and chipmunks (*Tamias*) were seen. Ten red-backed voles (*Clethrionomys gafferi gafferi* and 1 deer-mouse (*Peromyscus maniculatus gracilis*) were trapped on a short trap-line. This situation obviously is transitional between the Hudsonian and Canadian provinces.

The transition between the Canadian and Hudsonian provinces is in some places rather abrupt. On the northern margins of their ranges the sugar maple, yellow birch, and white pine occur only in the most favorable habitats and a slight change in topography or soil may make it impossible for these Canadian province species to exist.

As an example of a fairly abrupt transition I submit herewith two logs of the vegetation observed in the summer of 1936 along the highway in two parts of northern Ontario. The distance each type of forest was traversed by the highway was determined by readings of the automobile mileage meter at each change in vegetation. The figures given cannot be assumed to be a dependable measure of the proportionate occurrence of the several vegetation types in the two regions, because the highway undoubtedly avoids the steeper rocky slopes and at least the more widespread of the bogs. Nevertheless, the figures do give a general indication of the relative abundance of the several ecologic types in the two situations.

The stretch of highway logged in the Canadian province extends from 10 miles north of North Bay, Ontario, to a point 10 miles further north. The road here crosses a number of rocky ridges, and the general exposure is to the south. In the 10 miles of the log 72 per cent is dominated by forests of sugar maple, yellow birch, and white pine. Bogs, in which black spruce was most conspicuous, cover 22 per cent of the distance. In these bogs there occur also some balsam fir and some tamarack. Burns and badly mixed vegetation cover 6 per cent of the recorded distance. Much of the maple forest along the highway has been logged, and part of both the upland forest and of the bogs has been burned.

For contrast, there is available the log of the dominant vegetation along the highway from Cochrane south nearly to Swastika, a distance of 94.7 miles, all in the Hudsonian province. The black spruce type of vegetation formed the original cover for 49 per cent of this distance. Much of this black spruce occurs in lowland bogs called muskegs, and these muskegs are especially extensive on the nearly flat plain near Cochrane. A few balsam firs occur with the black spruce at least as far north as Cochrane, and in the better drained situations the white spruce also occurs. Sphagnum forms a heavy mat under the spruces and Labrador tea is a characteristic low shrub. Near Cochrane the black spruce type of bog vegetation is not restricted to low and undrained situations, but extends also over the lower hills. Another important type of vegetation between Cochrane and Swastika is the jack pine forest, which covers 11 per cent of the log. This forest type is restricted to sandy areas. Associated with the jack pine are frequently the aspen, the black and the white spruces, and less commonly the white birch. Blueberries are a characteristic low shrub. Fires have been frequent in this region and 26 per cent of the distance between the two cities is dominated by aspen. Mixed types of vegetation of various sorts, including arbor vitae, black spruce, alder, willow, aspen, balsam fir, white spruce, jack pine, and white birch made up 11 per cent of the vegetation. Clearings in which the original type of vegetation could not be determined from the road cover 3 per cent of the distance.

Although the sections of highway described above in the Canadian and Hudsonian provinces, respectively, are only about 150 miles apart at their nearest approach, there are very obvious differences in their vegetation. In the Hudsonian province near Cochrane the sugar maple, yellow birch, and white pine type of forest characteristic of the Canadian province is absent, while the spruce bog is the most extensive community. Climatic differences related to latitude are probably in large part responsible for these dissimilarities in vegetation. However, the soil characters of the two regions are very different and these variations in soil greatly affect the vegetation.

The rocky ridges 10 to 20 miles north of North Bay are probably at nearly the northern limit of the forest of sugar maple, yellow birch, and white pine, and it is doubtful if this type of forest could exist at Cochrane even on rocky slopes. On the other hand, the general lack of jack pine along the highway near North Bay is obviously due to the absence of sandy soil in this area, for jack pine forest is an important vegetation type on sandy soils much further south.

North of Quebec sugar maples occur on the southern slopes of the mountains of the Laurentides National Park, but, so far as could be seen on a hasty drive through this park, all the higher parts of the mountains are dominated by spruce forest (see also Fuller and Marie-Victorin, '26: 295–296). On the northern slopes of these mountains, toward Lake St. John, sugar maples reappear, and numbers of these trees were noted near Abbeyville. The position of the boundary between the Hudsonian and Canadian in this region must therefore be drawn somewhat arbitrarily.

The tip of the Gaspé Peninsula has been excluded by Nichols from the Hemlock region (Canadian province). It is true that the high interior parts of the peninsula would be expected to be dominated by spruce forests. However, along the northeastern Gaspé coast, on crossing a ridge several hundred feet high between the villages of Chloridorme and Gaspé, I noted the occurrence of a few white pines and sugar maples, along with fir, spruce, arborvitae, aspen, white birch, and mountain ash. Several kinds of mammals reach their northern limits in the Gaspé peninsula, and probably occur over most of the peninsula. It therefore is much simpler for the mammalogist if all the peninsula is included in the same province. I have for this reason drawn the northern boundary of the Canadian province down the middle of the Bay of St. Lawrence.

The southern boundary of the Canadian province in the Appalachian Mountains is difficult to place, because isolated areas of northern type forests and fauna recur on the Appalachian Mountains south as far as North Carolina and Tennessee. I have here arbitrarily drawn the southern boundary of the Canadian province at the southern border of the state of Pennsylvania. It is, however, quite possible that a more natural division between the northern and southern Appalachian Mountains may occur somewhere in West Virginia.

The climax vegetation of the Canadian province is a hardwood forest, in which the sugar maple (*Acer saccharum*) and yellow birch (*Betula lutea*) are the most characteristic trees. The eastern white pine (*Pinus strobus*) and the eastern hemlock (*Tsuga canadensis*) occur frequently. The beech (*Fagus grandifolia*) is also characteristic, except that it does not occur in the extreme western part of the province. Numerous other trees and many shrubs are characteristic. The Canadian province therefore corresponds closely to the "northern hardwood forest" of some foresters (Frothingham, '15: 1–7).

The pines (*Pinus strobus, P. resinosa,* and *P. divaricata*), often growing in a pure stand of one species, are in many places an important subclimax stage in the Canadian province. The pine forests nearly always occupy sandy or gravelly soil. On some very poor sandy soils the pine forest may persist indefinitely as an edaphic climax, for in such situations insufficient humus may accumulate ever to make the site suitable for a hardwood forest. On good soil the pines are usually quickly succeeded and shaded out by hardwoods, although the white pine often persists in the climax forest. Some of the white pine trees in the climax forest may be relicts of an earlier pine stage, persisting by reason of their height, but some probably spring up from time to time in openings in the forest produced by the fall of large trees.

In poorly drained situations in the Canadian province, many areas are covered by bogs and swamps in which there occur varying mixtures of balsam fir (*Abies balsamea*), black spruce (*Picea mariana*), white spruce (*Picea canadensis*), northern white cedar (*Thuja occidentalis*), and tamarack (*Larix laricina*), with occasional hardwoods such as black ash and red maple. As pointed out by Nichols ('35: 411–412) these bogs and swamps "closely resemble the climatic climax of the northern conifer forest region," which here is called the Hudsonian province.

Following fires in the forest of the Canadian province there often springs up a first forest of aspen (*Populus tremuloides* and *P. grandidentata*) or of white birch (*Betula papyrifera*). The aspens and birches are usually followed by pines.

In northern Michigan, if hardwood forest on clay soil is destroyed by fire, there may be no complete succession through aspens and pines, but at least in some situations the hardwood forest regenerates directly after a brushy stage, and the aspen and pines stages are omitted.

Sandy soils and also poorly drained situations occur over nearly the whole area of the Canadian province, alternating irregularly with good soils and with well drained situations. In some districts hundreds or thousands of square miles may be covered mostly with sandy soil, with accompanying pine forests. In other places equal areas of poorly drained soil may support forests of spruces and firs. Nevertheless, on the better soils throughout this whole area the northern hardwood type of forest natively formed the characteristic vegetation, and it certainly is the ultimate climax for the climate. The firs and pines which have been assumed to distinguish the

Alleghanian biota from the Canadian biota are actually successional stages which mostly are characteristic only of certain soil types. These soil types and their accompanying coniferous vegetation recur throughout most of the area which has been called Alleghanian as well as over the area previously assigned to the Canadian.

Spruce forests occur on the upper parts of mountains and in lowland bogs over most of the Canadian province and also even in parts of the Carolinian province. The fauna and flora of these isolated spruce habitats resemble in part the fauna and flora of the Hudsonian province. Nevertheless, it is futile to attempt to mark on the map every local spruce habitat. In my opinion it is better to treat these isolated habitats as minor communities of the province in which they occur. Actually these isolated spruce communities are never exactly like the major communities of the Hudsonian province, which they resemble superficially, for most or all of the larger Hudsonian mammals are missing.

No attempt will here be made to consider all of the kinds of animals which are characteristic of the Canadian biotic province. In this report I shall confine my attention entirely to the mammals, the group of animals with which I am most familiar. However, it is known that some other classes of land vertebrates and some kinds of invertebrates also are restricted in distribution by some of the same ecological barriers as are the mammals.

In making up the lists of mammals I have followed in general the nomenclature of Miller ('24). For data on the distribution of the several species I have used such revisions as are available, chiefly in the valuable North American Fauna series prepared by the United States Biological Survey. Unfortunately, many species and genera have not been recently revised and the distribution of some species has never been adequately mapped. For records of the distribution of many of the ungulates and larger carnivores I have depended chiefly upon the maps presented by Seton ('29).

The following species of mammals range over most or all of the Canadian province as I have defined it: *Condylura cristata* (Star-nosed mole), *Sorex cinereus* (Masked shrew), *Sorex palustris* (Water shrew), *Microsorex hoyi* (Pigmy shrew), *Blarina brevicauda* (Short-tailed shrew), *Myotis lucifugus* (Little brown bat), *Myotis keenii* (Little brown bat), *Lasionycteris noctivagans* (Silver-haired bat), *Eptesicus fuscus* (Large brown bat), *Lasiurus borealis* (Red bat), *Ursus americanus* (Black bear), *Procyon lotor* (Raccoon), *Martes americana* (Marten), *Martes pennanti* (Fisher), *Mustela vison* (Mink), *Mustela cicognanii* (Short-tailed weasel), *Mustela frenata* (Long-tailed weasel), *Gulo luscus* (Wolverine), *Lutra canadensis* (Otter), *Mephitis mephitis* (Striped skunk), *Vulpes fulva* (Red fox), *Canis lycaon* (Timber wolf), *Lynx canadensis* (Canada lynx), *Marmota monax* (Woodchuck), *Tamias striatus* (Chipmunk), *Sciurus hudsonicus* (Chickaree), *Glaucomys sabrinus* (Flying-squirrel), *Castor canadensis* (Beaver), *Peromyscus maniculatus* (Deer-mouse), *Synaptomys cooperi* (Bog-lemming), *Clethrionomys* *gapperi* (Red-backed vole), *Microtus pennsylvanicus* (Meadow-vole), *Ondatra zibethica* (Muskrat), *Zapus hudsonius* (Meadow jumping-mouse), *Napaeozapus insignis* (Woodland jumping-mouse), *Erethizon dorsatum* (Porcupine), *Lepus americanus* (Snowshoe hare), *Odocoileus virginianus* (White-tailed deer), *Alces americana* (Moose).

Of these species the masked-shrew, silver-haired bat, black-bear, fisher, mink, otter, red-fox, wolf, chickaree, beaver, deer-mouse, meadow-vole, muskrat, and meadow jumping-mouse (*Zapus*) ranged natively over most or all of the Hudsonian of eastern Canada as well as over the Canadian, and all of them also extended into biotic provinces south of the Canadian. These then are wide-ranging forms which extend beyond the Canadian province on both sides.

A few species which are mainly of more northern distribution ranged south natively into the northern part of the Canadian. These are the Arctic shrew (*Sorex arcticus*), wolverine, northern lemming-vole (*Synaptomys borealis*), heather-vole (*Phenacomys ungava*), and caribou (*Rangifer caribou*). Most of these forms are rare in the Canadian and for the larger forms the original southward distribution in eastern North America is not well known. However, probably none of them originally extended as far south as the southern boundary of the Canadian province.

Species which ranged natively over most of the Hudsonian of eastern Canada and which in eastern North America reached their southern limits near the southern border of the Canadian as here mapped are the marten, short-tailed weasel, Canada lynx, northern flying-squirrel (*Glaucomys sabrinus*), red-backed vole, porcupine, and snowshoe hare.

The moose seems to have been the only form which was limited in its southward distribution in eastern North America by the southern border of the Canadian province as here mapped, and which also ranged into the southern part only of the Hudsonian province.

The pigmy-shrew (*Microsorex*) is rare and its distribution not well known. Although it seems to occur mostly in the Hudsonian and Canadian provinces it also occurs in other areas to the southward and westward.

The hoary bat (*Lasiurus cinerea*) occurs in the Canadian province, and is at least in part a migrant, breeding farther north as well as farther south.

Species which range from districts south of the Canadian province north across the whole Canadian and into the southern part of the Hudsonian province are the little brown bat (*Myotis lucifugus*), striped skunk, and woodchuck.

Species of more southern distribution which reach their northern limits at or close to the northern boundary of the Canadian province are the short-tailed shrew, little brown bat (*Myotis keenii*), large brown bat, red-bat, raccoon, long-tailed weasel, chipmunk (*Tamias*), Lemming-vole (*Synaptomys cooperi*), and white-tailed deer. The deer is now extending its range further northward.

Species which mainly are of more southern distribution but which natively ranged into some of the southern parts of the Canadian province are the mole (*Scalopus aquaticus*), pipistrelle (*Pipistrellus subflavus*), gray-fox (*Urocyon cinereoargenteus*), cougar (*Felis couguar*), bob-cat (*Lynx rufus*), gray-squirrel (*Sciurus carolinensis*), fox-squirrel (*Sciurus niger*), flying-squirrel (*Glaucomys volans*), wood-mouse (*Peromyscus leucopus*), American elk (*Cervus canadensis*), and bison (*Bison bison*). In southern Michigan the mole, fox-squirrel, and wood-mouse were probably originally mostly absent from the Canadian province, but with the clearing of the forests they have extended their ranges some distance into the province. The bob-cat has in Michigan in historic time greatly extended its range northward.

The star-nosed mole and woodland jumping-mouse (*Napaeozapus*) cover most of the area of the Canadian province and both extend south in suitable habitats along the Appalachian Mountains. In addition both also extend slightly beyond the limits of the province in other directions.

Several species of mammals occupy part only of the Canadian province and also range south into the Carolinian province along the Appalachian Mountains. These are the hairy-tailed mole (*Parascalops breweri*), smoky-shrew (*Sorex fumeus*), another shrew (*Sorex dispar*), woodrat (*Neotoma pennsylvanica*), rock-vole (*Microtus chrotorrhinus*), and New England cottontail (*Sylvilagus transitionalis*).

Several species which are mostly more western in distribution range into the western parts of the Canadian province. These are the least-weasel (*Mustela rixosa*), badger (*Taxidea taxus*), coyote (*Canis latrans*), western chipmunk (*Eutamias minimus*), and cottontail (*Sylvilagus floridanus*). Of these the coyote has within recent time considerably extended its range eastward. The cottontail seems not to have originally occurred in the Canadian province, but in recent years it has spread northward in Michigan and eastward in Wisconsin well into the province.

The Gaspé shrew (*Sorex gaspensis*) seems to be the only species of mammal restricted to the Canadian province, but this species occurs only in the Gaspé region, so that it is not characteristic of all the province.

Certain subspecies of mammals are largely limited to the Canadian province, but no one subspecies which is restricted to the Canadian completely covers the whole province. In *Sorex palustris* the two subspecies *albibarbis* and *gloveralleni* are largely confined to the northeastern part of the Canadian province and the subspecies *hydrobadistes* largely to the western part of the province. In *Peromyscus maniculatus* the subspecies *abietorum* covers largely the eastern part of the province, *gracilis* the western part, while the subspecies *nubiterrae* extends from the south somewhat into the province in Pennsylvania and possibly in southern New York. In *Synaptomys cooperi* the subspecies *cooperi* covers practically the Canadian area, but it extends in places slightly south of the boundaries of the province.

It is shown by the above discussion that several of the mammals which occur in the Canadian province are wide-ranging species which occupy biotic provinces both to the north and to the south of the Canadian. A number of the mammals of the Canadian biotic province are species which are characteristic of the eastern deciduous forests, and some of these species reach their northern limits at the northern edge of the province where the deciduous forests terminate. A few others extend still further north into the Hudsonian province or completely across it. Several species of mammals found in the Canadian province are characteristic of the northern spruce forests (Hudsonian province) and a few of these species reach their southern limits at or near the southern border of the Canadian province. No species of mammal which ranges over all or over most of the Canadian province seems to be restricted to that province. However, a few subspecies or groups of related subspecies are restricted fairly closely to the limits of the province.

In its mammalian fauna the Canadian biotic province is characterized by the intermingling of species which are abundant in the eastern deciduous forest with those which are abundant in the northern spruce forests. This is what would be expected from the fact that the important mammalian habitats of the Canadian province are predominantly of two types, hardwood forest and conifer swamp and bog. It is true that in the Canadian province there is a considerable occurrence of pine forest, which is largely absent from the Hudsonian province, and which, at least in the interior, is mostly absent from the Carolinian province. However, the pine forests have a very sparse population of mammals, and no form of mammal seems to be restricted to the northern pine forest habitat.

The assemblage of mammalian species ranging over most of the Canadian province is different from the assemblages of species living in either of the adjacent provinces. This is true in spite of the fact that no species or subspecies of mammal which ranges over all the province is restricted to it. It is believed, therefore, that the Canadian biotic province as described above forms a natural biogeographical unit for the mammals as well as for the vegetation.

If a faunal area is to be recognized between the Hudsonian and the Canadian provinces as here described it will have to be cut off from the southern part of the Hudsonian, from the northern part of the Canadian, or made up of parts of both provinces.

All of the mammals listed above as occupying only the southern part of the Hudsonian of eastern Canada range far to the southward and all of them extend into the Carolinian province, except the fisher, flying-squirrel (*Glaucomys sabrinus*), and moose, which stop at the northern boundary of the Carolinian. None of these forms, therefore, could be made the basis for a subdivision of the Hudsonian of eastern Canada into two longitudinal belts, the southern of which might be called the Canadian.

Of the forms of more northern distribution which range south into the northern part of the Canadian as here delimited, the Arctic-shrew is rare and has a discontinuous distribution in this area; the original range of the wolverine in this area is questionable and the species is now extirpated; the northern lemming-vole occurs only in the most eastern part of the area; the heather-vole extends into only the extreme northern edge of the Canadian; and the caribou was probably nomadic and erratic in occurrence as it is now in other parts of its range. It is evident that no division of the Canadian to form also an Alleghanian fauna can be made on the basis of the distribution of these forms.

A small number of forms of southern distribution extend their range into the southern part of the Canadian as I have mapped it. Of these it is questionable if the eastern mole (*Scalopus aquaticus*), pipistrelle, southern flying-squirrel (*Glaucomys volans*), mole-mouse, or bison ever natively extended far into the province. The fox-squirrel is absent from the eastern part of the province. The cougar, elk, and bison are now absent from the region, and the gray-fox has been nearly or completely extirpated in Michigan. On the other hand the eastern-mole, bob-cat, fox-squirrel, wood-mouse, prairie deer-mouse and Mearns cottontail are extending their ranges northward in Michigan until they now occupy a considerably larger part of the Canadian than they did at the time the region was first settled. It would therefore seem inadvisable to base any major faunal area on the distribution of these species.

The Canadian province, as I have described it, is not especially well marked by its mammalian species, and to establish two faunal divisions in this area instead of one, would mean that each of the two would not only have no characteristic species of mammals, but that only a few forms would reach their limits at or near the presumed faunal boundaries.

Two biotic districts, an eastern and a western, can be recognized as subdivisions of the Canadian biotic province. The red spruce (*Picea rubra*) which occurs over the eastern part of the Canadian and which also extends southward along the Appalachian Mountains, is absent from the western part of the province (Nichols, '35, fig. 5F). The beech is more widespread in the province than the red spruce, but it is absent from western Michigan, western Wisconsin, and Minnesota (Transeau, '35, fig. 12). The Gaspé shrew which occurs locally in the eastern part of the Canadian province, is absent from the western part. Several species of prairie mammals, as already mentioned, invade the western part of the Canadian, but do not occur in the eastern part. Further, the water-shrew, woodchuck, chipmunk, deer-mouse, snowshoe hare, and perhaps other species of mammals are represented by different subspecies in the eastern and western parts, respectively, of the province.

New Brunswick does not greatly differ, however, from northern Michigan, either in its vegetation or in its mammalian fauna. There is no sharp transition at any place between an eastern and western district of the Canadian province, and it is impossible to suggest, with the present lack of detailed information, where the boundary between the two districts should be placed.

SUMMARY

A detailed consideration of the vegetation and of mammalian distribution in eastern North America shows that the so-called Canadian and Alleghanian faunas are only different aspects of the same major ecologic complex. They are therefore here combined under the name Canadian biotic province.

The Canadian biotic province is characterized by a hardwood climatic climax in which the hemlock and white pine frequently occur. Pines of several species constitute an important subclimax, or edaphic climax, on sandy and gravelly soils. In poorly drained situations spruces of several species, balsam fir, arbor vitae, and tamarack form another subclimax or group of subclimaxes.

No species or subspecies of mammal which occurs all over the Canadian province is limited to the province. Nevertheless, the assemblage of species living in the province is different from the assemblages living in the adjacent provinces. Furthermore, a number of species of mammals reach their distributional limits at or near the northern or southern boundaries of the province.

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PLEISTOCENE ZOOGEOGRAPHY OF THE LEMMING, *DICROSTONYX*[1]

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The collared lemmings, genus *Dicrostonyx* Gloger, are currently divided into two subgenera. *Misothermus* Hensel contains a single species, *D. hudsonius* Pallas, isolated on the tundra of northern and coastal Ungava from all other *Dicrostonyx* (see fig. 1). The subgenus *Dicrostonyx* Gloger contains the remaining species of the genus, *D. torquatus* Pallas of the palaearctic, *D. groenlandicus* (Traill) of the nearctic, and *D. exsul* G. M. Allen confined to St. Lawrence Island in the Bering Straits. The *torquatus-groenlandicus-exsul* species group may be conspecific as intimated by Ellerman and Morrison-Scott (1951, p. 653). It is clear that they are more closely related to one another than to the isolated *D. hudsonius.*

In the absence of any fossil record and interpreting on the basis of modern geographical distribution alone, one might argue that the differentiation of *D. hudsonius* dated from the Wisconsin glaciation; that as the ice front and its presumed periglacial tundra belt shrank to the north, the eastern segment of the retreating lemming population was cut off by Hudson Bay. The bay eventually cut the Canadian tundra into an eastern and a western component, each with its distinctive form of collared lemming. This does not appear to be the case, however.

The inaccuracy of this interpretation is shown by the fossil record. The one record from the North American Pleistocene, fragmentary skulls and mandibles of at least four individuals from Sinkhole no. 4, New Paris, Pennsylvania (Guilday and Doutt, 1961), is that of typical *Misothermus* (for characters, see Miller, 1898; Hinton, 1926; Hall and Kelson, 1959), indistinguishable from the modern *D. hudsonius.* Carbon particles taken from a position five feet higher in the sinkhole matrix were dated at 11,300 ± 1,000 years (Yale Univ. lab. no. 727). The age of the lemming remains is somewhat in excess of this. The *Misothermus* dental pattern was fixed prior to the Wisconsin recession and the formation of present Hudson Bay.

There have been two species of collared lemmings described from the palaearctic Pleistocene. *Dicrostonyx gulielmi* Sandford based upon cranial material from Hutton Cave, Somersetshire, England, is a late Pleistocene form of the living *D. torquatus,* and may be conspecific with it (see Kowalski, 1959, p. 229). It is a common Eurasian Pleistocene fossil.

The second Old World fossil form, *D. henseli* Hinton, described from cranial material from a fissure deposit at Ightham, Kent, England, appears to be a typical *Misothermus* (see the description by Hinton, 1926, p. 163). *D.* (*Misothermus*) *henseli* has been recorded from the Pleistocene of England, Ireland, Jersey, France, and Germany (Hinton, 1926; Brunner, various papers); *D.* (*Dicrostonyx*) *torquatus* (or *gulielmi*), from the Pleistocene of England, Ireland, France, Poland, Czechoslovakia (Hinton, 1926; Kowalski, 1959; Fejfar, 1961). This by no means exhausts the list of Old World Pleistocene *Dicrostonyx* localities. But enough has been cited to indicate a geographical and possibly a chronological overlap between the two species. Both forms were recovered by Hinton from Merlin's Cave, Wye Valley, Herefordshire, England (22 *D. gulielmi* skulls, 4 *D. henseli*) and at Langwith Cave, Derbeyshire (1 *D. gulielmi,* 2 or 3 *D. henseli*). Brunner recorded *D. henseli* from

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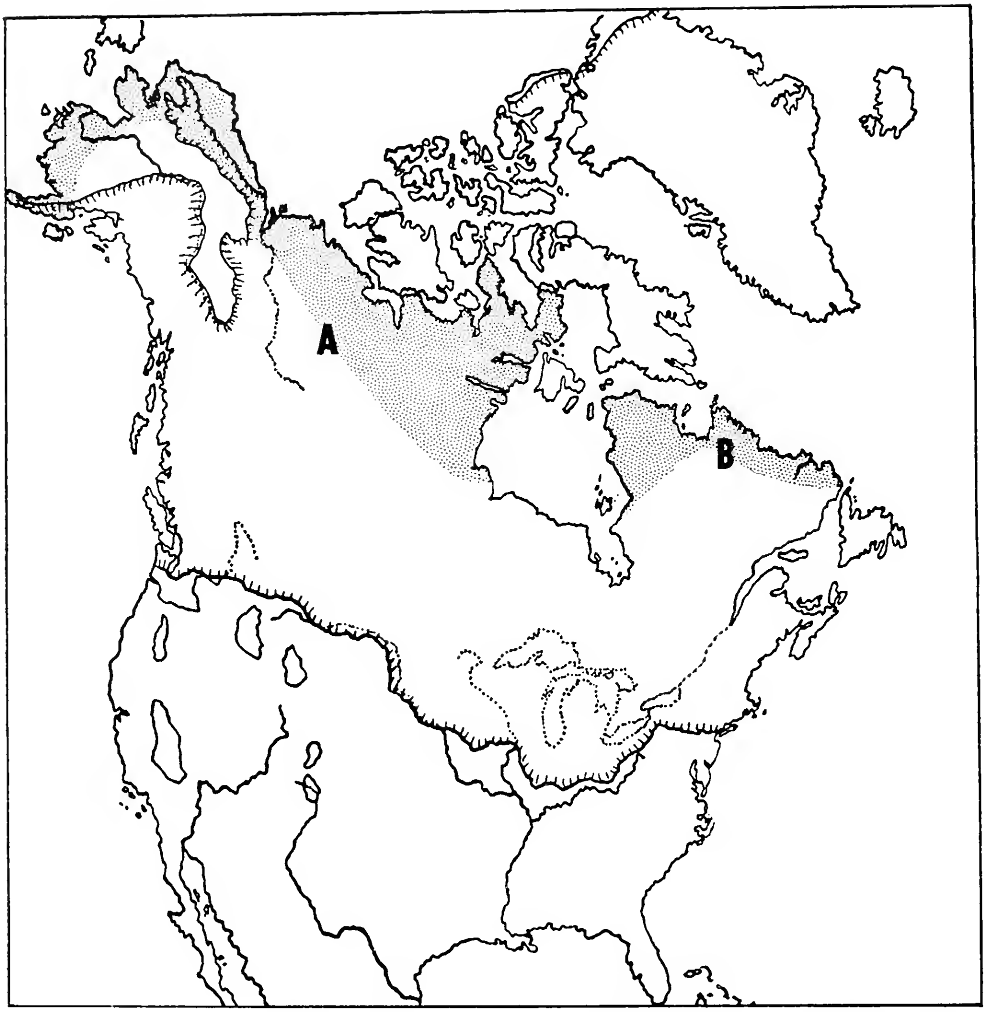

FIG. 1. Outline map of North America, showing approximate limit of continental glaciation. A. Mainland modern distribution of the subgenus *Dicrostonyx* in America. B. Modern distribution of the subgenus *Misothermus*.

thirteen Bavarian cave deposits. In one, the Markgrabenhöhle, Brunner (1952c, p. 465) reported that 25% of the mandibles resembled *D. gulielmi* in possessing a small anteroexternal vestigial angle on M_3, "eine deutliche aüssere Schmeltzfalte." Many uncorrelated fissure, cave, and terrace deposits are involved, however. And while they are all middle to late Pleistocene in age, their sequential position within that time span has not been established with any degree of confidence.

The facts at hand seem to indicate that two forms of the genus *Dicrostonyx* inhabited Eurasia and perhaps North America during the Pleistocene, and that one of them survives as a postglacial relict, isolated in the tundra of Ungava (fig. 2). The pre-Wisconsin origin of the *Misothermus* dental pattern is demonstrated by fossil forms in both continents.

If we assume, as does Hinton (1926), that *Misothermus* is not a true phylogenetic category but that *D. henseli* and *D. hud-*

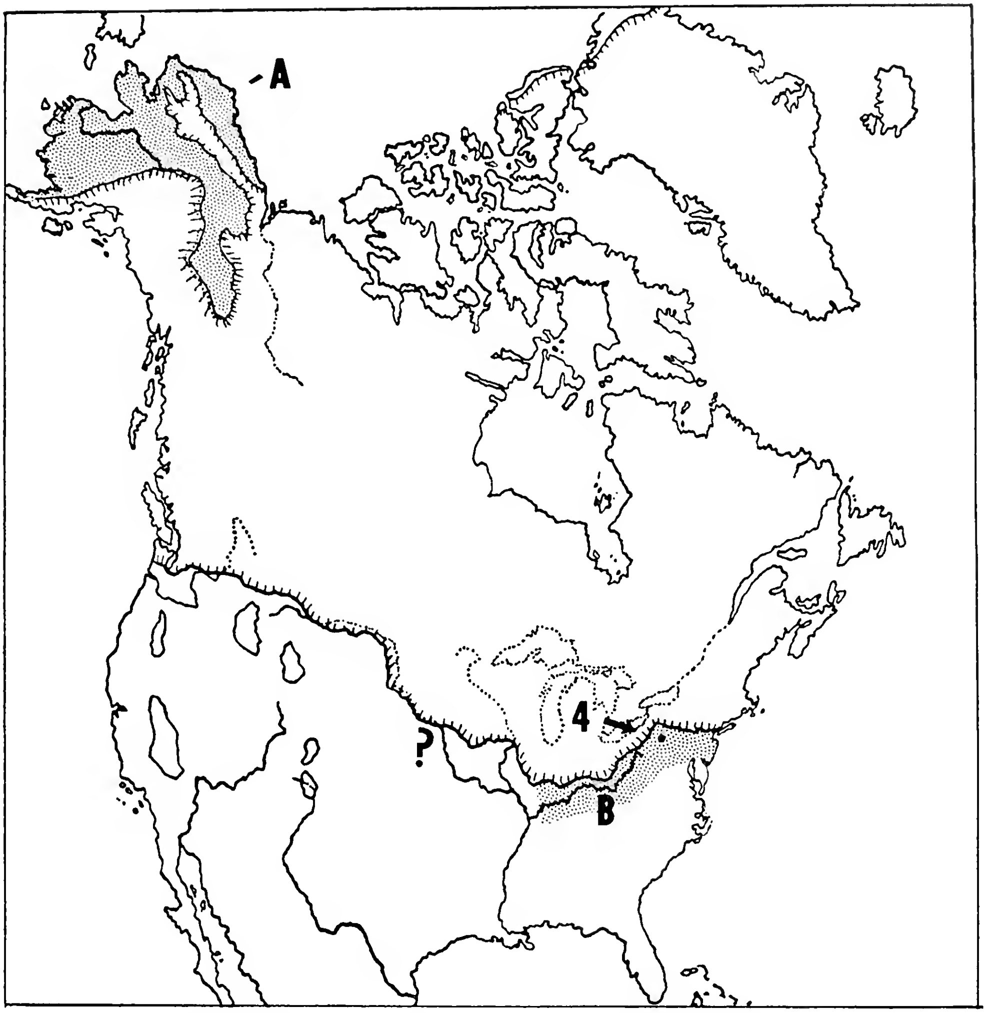

FIG. 2. Postulated distribution of *Dicrostonyx* (A) and *Misothermus* (B) in North America at Wisconsin glacial maximum. Note site of Sinkhole no. 4, New Paris, Bedford County, Pennsylvania. Hachures indicate approximate limit of continental glaciation.

sonius are of independent origin from *Dicrostonyx* proper, we are faced with the apparent coincidence that a form (*henseli*) was replaced by modern *Dicrostonyx* in the Old World while its morphological equivalent, *D. hudsonius,* which ranged as far south as central Pennsylvania during late Wisconsin times, survives today only where it is completely isolated from all contact with the Eurasian-Western Nearctic *Dicrostonyx*.

Both *D. henseli* and *D. hudsonius* appear to have been completely or partially replaced by true *Dicrostonyx.* Is it possible that modern *D. hudsonius* (or some form of *Misothermus*) at one time ranged throughout the holarctic, and that it was replaced during late Pleistocene times by lemmings of the subgenus *Dicrostonyx,* first in the Old World, later in the New; this latter replacement occurring sometime after the post-Wisconsin formation of Hudson Bay and the division of the mainland North

American tundra into an eastern and a western component?

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SUMMARY

The modern distribution of *Dicrostonyx hudsonius* Pallas (confined to the tundra of Ungava) is believed, on the basis of the fossil record, to be a relict of a former holarctic pre-Wisconsin distribution.

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SUBFOSSIL MAMMALS FROM THE GÓMEZ FARÍAS REGION AND THE TROPICAL GRADIENT OF EASTERN MEXICO

By Karl F. Koopman and Paul S. Martin

In the spring of 1953 Byron E. Harrell and P. S. Martin collected superficial animal remains at three cave localities in the Sierra Madre Oriental of southwestern Tamaulipas. Locally, the mountains are sufficiently humid to support small, isolated patches of Cloud Forest and Tropical Evergreen Forest (Martin, 1958). At this latitude, 23° north, these two tropical plant formations appear to reach their limit. In recent years four faunal papers on mammals of southern Tamaulipas have appeared, each reporting certain tropical species unknown at higher latitudes (Baker, 1951; Goodwin, 1954; Hooper, 1953; de la Torre, 1954). Southern Tamaulipas appears to be of primary significance in the Gulf lowlands faunal gradient, a system extending from southern Veracruz to southern Texas. In the lowlands of eastern Mexico many of the dominant tropical American taxa reach their range limits. We seek to define the northeastern section of this gradient with regard to tropical mammal faunas, to relate it to shifts in vegetation and to indicate the relative importance of the Gómez Farías region as a faunal terminus. The Gómez Farías region is defined as the area from 22°48′ to 23°30′ north latitude and 99° to 99°30′ west longitude, or approximately the rectangle enclosed by the towns of Llera, Jaumave, Ocampo and Limon.

In establishing the presence of eight species known in the Gómez Farías region only from the skeletal remains, and in extending the altitudinal or ecological ranges of others, the present collection supplements previous reports. It indicates the value of using owl pellet deposits as a cross check on standard trapping technique.

DESCRIPTION OF DEPOSITS

Cretaceous limestones comprising the precipitous east slope of the Sierra Madre Oriental near the village of Gómez Farías are severely folded. Under torrential summer rains they have eroded into very rough karst terrain with virtually no surface drainage. Caves and sink holes, a characteristic of karst, are a common feature. Most do not appear to be inhabited by bats or owls. Of those that are, the constant high humidity and frequent flushing from percolating rainwater apparently prevent accumulation of deep bone or guano deposits. Large bat colonies numbering thousands of individuals occur in Tropical Deciduous Forest in the Canyon of the Río Boquilla, 8 km. southwest of Chamal, and in a guano cavern at El Abra, 8 km. northeast of Antiguo Morelos. However, no colonies of similar size have been found in the more humid portions of the Gómez Farías region.

Of approximately thirty caves and sink holes explored near Gómez Farías, material from three is represented in our collection. All occur in the mountains west of the village of Gómez Farías, latitude 29°03′ north, longitude 99°09′ west, and within 16 km. of each other (see Table 1). The following information will serve to characterize them:

1. Paraiso. Aserradero del Paraiso is the name of a small sawmill located in Tropical Evergreen Forest 13 km. north-northwest of Chamal. A narrow ravine about 1 km. south of the sawmill harbors several caves, including a deep, wet grotto with permanent water. On the sloping floor of a small

TABLE 1.—*Mammals from cave deposits in the Gómez Farías region (numbers refer to anterior skull parts identified)*

	PARAISO	RANCHO DEL CIELO	INFERNO
Distance from Gómez Farías:	13 km. SW	6 km. NW	7 km. W
Elevation in meters:	420	1050	1320
Vegetation type:	Tropical Evergreen Forest	Cloud Forest	Cloud Forest
Didelphis marsupialis	—	—	1
Marmosa mexicana	—	—	18
Cryptotis pergracilis	3		
Cryptotis mexicana	—	1	10
Chilonycteris parnellii	1		
Enchisthenes harti	—	—	1
Artibeus cinereus	—	3	
Centurio senex	—	—	1
Eptesicus fuscus	1		
Lasiurus cinereus	—	—	1
Antrozous pallidus	1		
Sylvilagus floridanus	1		
Glaucomys volans	1	1	12
Liomys irroratus	1		
Reithrodontomys mexicanus	—	2	5
Reithrodontomys megalotis	—	—	1
Baiomys taylori	1		
Peromyscus boylei	—	1	17
Peromyscus pectoralis	—	—	2
Peromyscus ochraventer	—	—	7
Oryzomys alfaroi	3	—	5
Sigmodon hispidus	29		
Neotoma angustapalata	9	1	17
Total identifications	51	9	98

dry cave on the west wall of this ravine many scattered (apparently water-transported) small bones were found.

2. Rancho del Cielo. A small sink and cave several hundred meters east of this important Cloud Forest collecting locality contained a few bat remains and fresh owl pellets.

3. Inferno (also designated Infernillo). A rather large cave adjacent to an abandoned sawmill of this name is located in upper Cloud Forest roughly 2 km. south of the mill settlement called La Gloria. Abundant pellet remains were found on a dislodged boulder just inside the cave mouth.

All the caves are surrounded by heavy forest, much of it recently lumbered. Jagged, shrub-covered or almost bare karst ridges and pinnacles confine the areas of tall forest to valleys, pockets and gentle slopes. A more complete description of the Gómez Farías region is in preparation (Martin, 1958).

Although the barn owl, *Tyto alba*, occurs in a very large cavern at El Abra north of Antiguo Morelos, the only raptor definitely known to roost in caves in the Gómez Farías region is the wood owl, *Ciccaba virgata.* While it is possible that certain non-volant mammals died from other causes, all skeletal remains of these, and perhaps even some of the bats, can be ascribed to *Ciccaba.*

Cave records do not make ideal locality data, especially when information on ecological or altitudinal distribution is sought. We assume that the forest types and the elevation in the immediate vicinity of each cave represent the habitat in which the owls fed, but this is by no means certain. The hunting range and nocturnal movements of *Ciccaba* are unknown.

There is no stratigraphic evidence for assuming that any material is older than very recent. Limestone deposit on certain bones may represent the concretion of a single rainy season.

SYSTEMATIC TREATMENT OF THE MAMMALS

We emphasize first that only a fraction of the mammalian and none of the bird bones have been identified. Very little attempt has been made to identify any of the post-cranial elements, and in the case of the cricetine rodents only the best of cranial material could be identified with any confidence. Particular difficulty was encountered with lower jaws of cricetines, even when teeth were present. As a result, determinations in this group are considered less reliable than in the others. In particular this applies to the *Peromyscus–Baiomys–Reithrodontomys* group of genera, in which not only specific but also good generic characteristics were hard to find in most of the material. Size, molar form, palatal morphology and shape of the zygomatic plate were found to provide the most useful taxonomic characters in this subfamily.

In many cases a closely adhering limestone drip deposit was present and was sometimes difficult to remove without damaging the underlying bone. No attempt has been made to identify subspecies. In our opinion the theoretical requirements of population sampling and measurement, as employed in subspecific identification, are not met in any but perhaps the best fossil material. For the following species determinations Koopman alone is responsible.

Didelphis marsupialis.—Inferno: one rostral fragment of a young individual. Previously recorded from Gómez Farías (Hooper, 1953).

Marmosa mexicana.—Inferno: three rostral fragments and 15 mandibles. On the basis of dentition, these are clearly opossums, but of the Middle American genera of Didelphidae, all but *Marmosa* are much too large. Of the four species of this genus occurring north of Panama, all but *M. mexicana* differ from the subfossil material either in larger size or greater development of a precondylar crest on the outer side of the mandible. The species has not previously been recorded north of Jalapa, Veracruz.

Cryptotis pergracilis.—Paraiso: one rostrum and two mandibles. Restriction to the family Soricidae and the genus *Cryptotis* may be made on the basis of dentition. In eastern Mexico north of the Isthmus of Tehuantepec (states of Tamaulipas, San Luis Potosí, Hidalgo, Puebla and Veracruz) the following six species of *Cryptotis* are known: *C. parva, C. pergracilis, C. obscura, C. micrura, C. mexicana* and *C. nelsoni.* All except *C. parva* and *C. pergracilis* may be ruled out on the basis of larger size. While clear-cut cranial differences between the latter two species appear to be absent, the eastern race of *pergracilis, C. p. pueblensis,* has a somewhat deeper nasal emargination of the rostrum than the southwestern race of *parva, C. p. berlandieri.* Though slightly broken anteriorly, the subfossil rostrum appears to have a nasal emargination somewhat closer to that of *C. pergracilis pueblensis* than to that of the two Tamaulipan specimens of *C. parva berlandieri* recorded by Goodwin (1954). However, no direct comparison of the Paraiso specimens with *C. pergracilis pueblensis* was made, but only with a sketch. Unfortunately our material seems inadequate to solve the problem of specific status, i.e., are *C. parva* and *C. pergracilis* sympatric in southern Tamaulipas, do they integrade through a narrow hybrid zone, or is there a more complex arrangement?

The northernmost previous record of *C. pergracilis* is Platanito in San Luis Potosí.

Cryptotis mexicana.—Inferno: six rostra, four mandibles, and three humeri; Rancho del Cielo: one rostrum. Specimens were trapped at the latter locality (Goodwin, 1954).

Chilonycteris parnellii.—Paraiso: one mandible. Goodwin (1954) records a series from El Pachon. As Koopman (1955) has pointed out, the mainland *C. rubiginosa* and the West Indian *C. parnellii* are almost certainly conspecific. Since Koopman believed that *C. parnellii* Gray had several months priority over *C. rubiginosa* Wagner, the combined species was called *C. parnellii.* De la Torre (1955) has shown that this is not the case and, finding no way of determining which name was published first, recommended: "In the absence of conclusive evidence, the better known and more widely used name *rubiginosa* should be retained."

Unfortunately, if there is no clear priority, the law of the first reviser would seem to hold, in this case the first to use one of the two names to include both forms, i.e., Koopman (1955). It is not legally possible to withdraw from this position. Therefore it appears that *C. parnellii* must stand as the name assigned to both mainland and West Indian large *Chilonycteris.*

The question of nomenclature should not obscure the more significant taxonomic conclusion that a single species is involved.

Artibeus cinereus.—Rancho del Cielo: two partial skulls, one lower jaw. De la Torre has also recorded this species from Rancho del Cielo.

Enchisthenes harti.—Inferno: one partial skull. The short broad rostrum and characteristic molar pattern rule out all American bats outside the Stenoderminae. Of the Middle American stenodermines, only *Uroderma bilobatum, Vampyrops helleri* and *Enchisthenes harti* agree with the Inferno skull in size and dental formula (i^2 o^1 p^2 m^3). Both *Uroderma* and *Vampyrops,* however, have rostra considerably longer than that of the subfossil skull. On the other hand, there is close resemblance to skulls of *Enchisthenes* from Honduras and Ecuador. De la Torre (1955) has recently summarized the known records, specimens from Ciudad Guzman in Jalisco being the closest to Tamaulipas geographically. Four other localities extend the distribution south to Trinidad and Ecuador.

Centurio senex.—Inferno: one rostrum. Of all the North and Middle American bats, only *Centurio senex* agrees with the subfossil skull in dental formula (i^2 c^1 p^2 m^3) and in the palate being more than twice as wide as it is long. The Inferno rostrum resembles a skull of *Centurio senex* in all important respects. De la Torre (1954) recorded a single specimen from Pano Ayuctle.

Eptesicus fuscus.—Paraiso: one mandible. Several characters of this bone immediately narrow the field considerably. These are mandibular length, tooth size, dental formula (i_3 c_1 p_2 m_3), molar pattern and height of the coronoid process. This leaves us with only two North and Middle American species, *Eptesicus fuscus* and *Dasypterus intermedius.* Of these, *Dasypterus* may be ruled out on the basis of its more robust mandibular ramus. Comparison of the Paraiso mandible with *Eptesicus fuscus* reveals no important differences. I have been able to find no other records of this bat in Tamaulipas, the nearest localities being Río Ramos in Nuevo León to the west (Davis, 1944) and Cañada Grande in San Luis Potosí to the southwest (Dalquest, 1953). Good series from Tamaulipas, if they could be obtained, should show integradation between *E. f. fuscus* and *E. f. miradorensis.*

Lasiurus cinereus.—Inferno: one nearly complete skull. All other species of North and Middle American bats may easily be excluded from consideration on the basis of size, rostral shape and dental formula (i^1 c^1 p^2 m^3). It matches *L. cinereus* closely. Since this bat is migratory, it is impossible to say whether this individual belonged to a resident population or was merely a winter visitor. The nearest previous records are Matamoros in northern Tamaulipas (Miller, 1897) and El Salto in eastern San Luis Potosí (Dalquest, 1953).

Antrozous pallidus.—Paraiso: one partial lower jaw. Mandible and tooth size, molar pattern and dental formula ($i_2\ c_1\ p_2\ m_3$) rule out all North and Middle American bats except *Promops centralis* and *Antrozous*. *Promops* may be excluded by the quite different appearance of the labial surface of the coronoid region. Of the two species of *Antrozous* recognized by Orr (1954), *A. bunkeri* is distinctly larger than the Paraiso mandible. *A. pallidus* resembles it in all respects. The University of Michigan Museum of Zoology has six specimens from Tula, which were mentioned by Orr (1954).

Sylvilagus floridanus.—Paraiso: one maxillary fragment of a young individual. Goodwin (1954) records the species from Gómez Farías, Pano Ayuctle and Chamal.

Glaucomys volans.—Inferno: two palatal fragments, ten mandibles; Rancho del Cielo: one mandible; Paraiso: one mandible. From the dental formula ($i_1\ c_0^0\ p_1^2\ m_3^3$) these specimens are clearly referable to the Sciuridae, of which all northeastern Mexican species except *Eutamias bulleri, E. dorsalis* and *Glaucomys volans* are clearly too large. In *Eutamias,* however, the mandible is much less deep than in the Tamaulipas material. The latter bears a convincing resemblance to *G. volans.* The nearest locality from which the species had previously been obtained is Santa Barbarita in San Luis Potosí (Dalquest, 1953).

Liomys irroratus.—Paraiso: one maxillary fragment. Goodwin (1954) records a series from Pano Ayuctle.

Oryzomys alfaroi.—Inferno: four maxillary fragments, one partial skull; Paraiso: three mandibles. Goodwin (1954) and Hooper (1953) have each recorded the species from Rancho del Cielo.

R. (*Reithrodontomys*) *megalotis.*—Inferno: one partial skull. Identification of this fragment is tentative. The species has already been recorded from Rancho del Cielo by both Goodwin (1954) and Hooper (1953).

R. (*Aporodon*) *mexicanus.*—Inferno: five partial skulls; Rancho del Cielo: two partial skulls. The species has been recorded previously from Rancho del Cielo by Goodwin (1954) and Hooper (1953).

Peromyscus boylei.—Inferno: two partial skulls, 15 maxillaries; Rancho del Cielo: one mandible. The species is recorded by Goodwin (1954) from both Rancho del Cielo and Rancho Viejo.

Peromyscus pectoralis.—Inferno: one partial skull, one maxillary. It has been recorded by Goodwin (1954) from both La Joya de Salas and 2 km. west of El Carrizo.

Peromyscus ochraventer.—Inferno: one partial skull, six maxillaries. The species has been recorded from Rancho del Cielo by both Goodwin (1954) and Hooper (1953).

Baiomys taylori.—Paraiso: one mandible. Goodwin (1954) and Hooper (1953) have recorded it from Pano Ayuctle.

Sigmodon hispidus.—Paraiso: one rostral half, ten maxillaries, two premaxillaries, three braincase elements, 16 mandibles. The species has been recorded from Pano Ayuctle by Goodwin (1954) and Hooper (1953).

Neotoma angustapalata.—Inferno: four partial rostra, five maxillaries, eight mandibles; Rancho del Cielo: one maxillary; Paraiso: one maxillary fragment, two premaxillaries, six mandibles. There is also a great deal of additional *Neotoma* material from Inferno that probably belongs here, but which has not been specifically identified. Both Goodwin (1954) and Hooper (1953) list specimens from Rancho del Cielo and El Pachon although, as Hooper points out, the precise status of *N. angustapalata* and its various southern Tamaulipas populations is far from clear. At the present time this name appears to be something of a "catch-all." It is felt, however, that a revision should be based on entire specimens rather than on skeletal fragments.

FAUNAL COMPARISONS AND THE STATUS OF GLAUCOMYS

The identifications summarized in Table 1 represent total number of anterior skull elements and *not* total number of individuals, which may be somewhat less. Although such data do not lend themselves to close quantitative inspection, we feel that the faunas sampled near Inferno and Paraiso reveal important differences. Two quite different habitats, Cloud Forest and Tropical Evergreen Forest, are represented. It would be surprising if the faunas were qualitatively similar. *Peromyscus*, the dominant genus comprising 27 per cent of the Inferno deposits, is unrepresented at Paraiso. In turn, *Sigmodon*, which comprises 57 per cent of the material obtained at Paraiso, is absent from Inferno. Such a discrepancy may reflect an ecological shift in the dominant cricetine form. Other rather common species which appeared only in the Cloud Forest caves include: *Marmosa mexicana* (18%), *Cryptotis mexicana* (10%) and *Reithrodontomys mexicanus* (5%). One genus, *Neotoma*, occurs at both localities with a relatively constant frequency, 17–18 per cent.

Within the Gómez Farías region the following are known only from their skeletal remains: *Marmosa mexicana, Cryptotis pergracilis, Chilonycteris parnellii, Enchisthenes harti, Eptesicus fuscus, Lasiurus cinereus, Antrozous pallidus* and *Glaucomys volans*. Presence of the latter is perhaps of greatest interest. In Middle America flying squirrels are very poorly known, presumably the result of their nocturnal and arboreal habits rather than an inherent scarcity. We are aware of ten other locality records between Chihuahua and Honduras, each represented by one or two specimens. In the Gómez Farías region remains of *Glaucomys* appeared at each cave locality, suggesting a general range through humid forest, both Cloud Forest and Tropical Evergreen Forest, between 420 and 1,320 meters. To our knowledge *Glaucomys* has not previously been collected in lowland tropical forests (below 1,000 meters).

THE LOWLAND TROPICAL GRADIENT IN EASTERN MEXICO

We might imagine a lowland tropical fauna to decline with increasing latitude at a rather regular rate. However, in reality the environment and fauna undergo a series of discrete changes, stepwise (see Fig. 1). In eastern Mexico four major tropical lowland vegetation types are represented. From south to north they terminate in the following sequence: Rainforest, Tropical Evergreen Forest, Tropical Deciduous Forest and Thorn Forest (Leopold, 1950). Each terminus is marked by a steepening of the faunal gradient.

In defining the lowland tropical fauna we have excluded those genera with distributional centers in temperate montane habitats or of limited lowland tropical ranges, e.g., *Idionycteris, Neotoma, Sciurus, Sigmodon* and *Baiomys.* On the other hand, some of the species selected may range into montane habitats or reach temperate latitudes, such as *Marmosa mexicana* and *Didelphis marsupialis.* In general the species listed in Table 2 are of wide distribution in lowland tropical America. Although they occupy tropical environments of the Mexican escarpment and coastal plain, we exclude *Baiomys* and *Sigmodon* because their phylogeny indicates a north temperate origin and in the case of *Baiomys* because it does not range extensively into Central America. Clearly the question of "tropicality" can be vexing. As one might expect the bats have much more extensive ranges than the small terrestrial mammals. The faunas of Trinidad and southern Tamaulipas share 18 species of bats, but none of rodents.

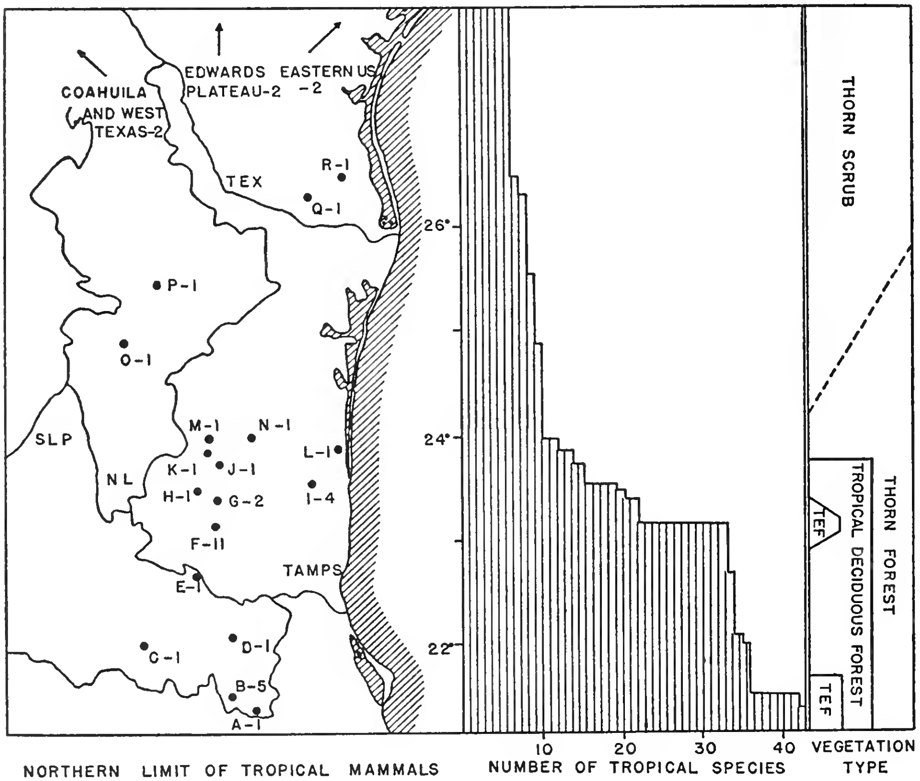

FIG. 1.—Relationship between lowland tropical mammals and latitude in northeastern Mexico. Known range limits for 43 species listed in Table 2 are shown on the map. Major vegetation types are indicated at the right. Tropical Evergreen Forest is abbreviated to TEF.

The general relationship between vegetation, latitude and tropical fauna is shown on Fig. 1. In southern Tamaulipas a rapid "thinning" of tropical forms is evident. Between 23° and 24° north latitude the following 17 genera find their range limits: *Philander, Marmosa, Chilonycteris, Pteronotus, Micronycteris, Macrotus, Glossophaga, Sturnira, Artibeus, Enchisthenes, Centurio, Natalus, Rhogeesa, Molossus, Heterogeomys, Eira* and *Mazama.* At this latitude (24° north) the Tropical Deciduous Forest, well developed and widespread east of the Sierra de Tamaulipas and the Sierra Madre Oriental, disappears. Small, perhaps relict, stands of Cloud Forest and Tropical Evergreen Forest in the Gómez Farías region also enrich the environmental opportunity for tropical mammals. However, these habitats, especially the Tropical Evergreen Forest, are more extensive in southeastern San Luis Potosí and northern Veracruz.

In this region seven genera terminate: *Carollia, Tamandua, Coendou, Cuniculus, Potos, Galictis* and *Ateles.* Although the vegetation near Xilitla, San Luis Potosí, has been designated as Rainforest, it seems preferable to reserve that term for the more luxuriant forests of southern Veracruz with their short dry season. Lowland tropical forests near Xilitla appear taller and richer than those of southern Tamaulipas; however, the area has suffered a long history of intensive Huastecan agriculture. Almost certainly the primeval fauna of southeastern San Luis Potosí included a larger number of tropical genera at their northern limit.

While we have not attempted to represent tropical distributions and plant formations south of San Luis Potosí, the following genera or subgenera approach their northern limit in southern Veracruz: *Caluromys, Vampyrum, Rhynchiscus, Centronycteris, Mimon, Chrotopterus, Hylonycteris, Chiroderma, Alouatta, Tylomys, Dasyprocta, Tayassu, Tapirella* and *Jentinkia.* Is there a relationship between these and the northern limit of Rainforest (see Leopold, 1950)?

Extending from central Tamaulipas northward to Nuevo León and southern Texas is a rather barren Thorn Forest and Thorn Scrub. Gradually these arid habitats lose their tropical character as the Rio Grande Valley is approached. By comparison with plant formations to the south, this environment is poor in tropical fauna. The shift from tropical to temperate thorn scrub involves no sharp faunal boundary among the mammals. *Oryzomys couesi* and *Liomys irroratus* are among the forms reaching southern Texas. At this latitude the herpetological fauna includes such tropical genera as *Coniophanes, Drymobius, Leptodeira, Smilisca* and *Hypopacus.* However, among the reptiles and amphibians, as well as the mammals, the greatest reduction in tropical fauna is found in southern Tamaulipas (Martin, 1958).

DISCUSSION

Although our analysis in confined to eastern Mexico, some interesting comparisons can be made with the tropical biota of the Pacific Coast. Arid tropical vegetation and the genera *Macrotus, Balantiopteryx, Chilonycteris, Pteronotus, Mormoops, Glossophaga, Desmodus, Natalus, Rhogeesa* and *Nasua* extend far-

TABLE 2.—*Northern limits of neotropical mammals*

LOCALITY AND APPROX. ELEV.	REFERENCE	SPECIES PRESENT
San Luis Potosí:		
A. Tamazunchale, 120 m.	Dalquest, 1953	1. *Tamandua tetradactyla*
B. Xilitla and vicinity 630–1350 m.	Dalquest, 1953	2. *Sturnira ludovici* 3. *Coendou mexicanum* 4. *Cuniculus paca* 5. *Potos flavus* 6. *Galictis canaster*
C. Río Verde, 990 m.	Dalquest, 1953	7. *Molossus major*
D. Valles, 75 m.	Koopman, 1956	8. *Balantiopteryx plicata*
E. El Salto, 660 m.	Dalquest, 1953	9. *Carollia perspicillata*
Tamaulipas:		
F. Rancho del Cielo and vicinity, 1000–1320 m.	Goodwin, 1954 Hooper, 1953 present report	10. *Marmosa mexicana* 11. *Enchisthenes harti* 12. *Oryzomys alfaroi* 13. *Reithrodontomys (Aporodon) mexicanus* 14. *Mazama americana*
Pano Ayuctle, 100 m.	Goodwin, 1954 Hooper, 1953 de la Torre, 1954	15. *Micronycteris megalotis* 16. *Sturnira lilium* 17. *Artibeus jamaicensis* 18. *A. lituratus* 19. *A. cinereus* 20. *Eira barbara*
G. 2 km. W of El Carrizo, 800 m.	Baker, 1951	21. *Philander opossum* 22. *Heterogeomys hispidus*
H. Jaumave, 730 m.	UMMZ specimens	23. *Macrotus mexicanus*
I. 10–16 mi. WSW Piedra, 400 m.	Anderson, 1956	24. *Chilonycteris parnellii* 25. *Glossophaga soricina* 26. *Centurio senex* 27. *Natalus mexicanus*
J. 2 mi. S Victoria, 400 m.	Davis, 1951	28. *Molossus rufus*
K. 30 km. NW Victoria, 1000 m.	Málaga-Alba, 1954	29. *Diphylla ecaudata*
L. La Pesca, 10 m.	Anderson, 1956	30. *Rhogeesa tumida*
M. Rancho Santa Rosa, 260 m.	Anderson, 1956	31. *Pteronotus davyi*
N. 8 mi. SW Padilla, 100 m.	Lawrence, 1947	32. *Oryzomys melanotis*
Nuevo León:		
O. 25 km. SW Linares, 700 m.	Málaga-Alba, 1954	32. *Desmodus rotundus*
P. 20 mi. NW General Teran, 300 m.	Hooper, 1947	33. *Oryzomys fulvescens*
Texas:		
Q. Hidalgo Co., 60 m.	Blair, 1952*b*	34. *Oryzomys couesi*
R. Raymondville, 30 m.	Blair, 1952*b*	35. *Liomys irroratus*

TABLE 2.—*Continued*

LOCALITY AND APPROX. ELEV.	REFERENCE	SPECIES PRESENT
Coahuila and West Texas:	Baker, 1956	36. *Choeronycteris mexicana*
	Miller and Kellogg, 1955	37. *Leptonycteris nivalis*
Edwards Plateau, Texas:	Blair, 1952*a*	38. *Mormoops megalophylla*
	Blair, 1952*b*	39. *Nasua narica*
Eastern United States:	Miller and Kellogg, 1955	40. *Dasypus novemcinctus*
		41. *Didelphis marsupialis*

ther north on the western side. On the other hand the humid tropical fauna and plant formations, e.g., Cloud Forest, Tropical Evergreen Forest and Rainforest, are absent or poorly represented on the Pacific slope north of Chiapas. As a general rule for those species or vicariant species occurring on both sides of Mexico, the arid tropical forms range farther north on the west, and the humid tropical forms farther north on the eastern side. This pattern is evident also in the distribution of lowland tropical birds, reptiles, insects, etc.

Other than noting a rather close "fit," it is beyond our purpose to explore the causal relationship between formation and fauna. In brief our conclusions may be summarized as follows:

1. The decline of the tropical fauna in eastern Mexico corresponds with the vegetation gradient.
2. Where the vegetation gradient steepens and a plant formation is lost, one finds a variety of tropical animals at their range limits.
3. In southern Tamaulipas the northern limit of many tropical mammals corresponds roughly to the boundary of Tropical Deciduous Forest. Contributing to the rich tropical fauna of the Gómez Farías region are relict outposts of Tropical Evergreen Forest and Cloud Forest.
4. The problem of establishing a Nearctic-Neotropical faunal boundary in eastern Mexico can be approached realistically in terms of steps in an environmental gradient.

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ZOOGEOGRAPHY OF THE MONTANE MAMMALS OF COLORADO

By James S. Findley and Sydney Anderson

In Colorado the distribution of montane or boreal habitats is at present closely associated with the local climate produced by the mountains. Peculiarities of this habitat are high precipitation, both in winter and summer, cool temperatures, a continuous water supply and a coniferous forest. Certain mammals are more or less restricted in geographic range, in this part of the continent, to the mountains.

In Pleistocene time the distribution of boreal habitat and hence of boreal mammals has undoubtedly fluctuated widely with the advances and retreats of continental and alpine glaciers. The contemporary pattern of distribution is, at least in part, a result of the most recent major glacial advance and retreat which took place in the Wisconsinan Age. It seems probable to us that most contemporary subspecies have differentiated in late Pleistocene time; otherwise the frequent correspondence of their ranges with current topographical and ecological features, which stem from late Pleistocene events in many cases, seems inexplicable. In the western United States the Boreal Zone is found at higher and higher elevations as one proceeds southward until it is scattered on isolated mountain peaks. The presence of isolated populations of boreal mammals on some of these mountains is evidence of a former displacement southward and downward in altitude of the Boreal Zone in a glacial age, presumably the Wisconsin, and subsequent elevation of the Boreal Zone in altitude and latitude in an ensuing interglacial interval, presumably the Recent. These southern, marginal populations would have been the first to become isolated with the retreat of the ice.

The separation of boreal habitat in the mountains of Colorado from boreal habitat in the Uinta and Wasatch Mountains of Utah and the mountains of northwestern Wyoming is probably of later origin than is the isolation of the southern boreal "islands." We have studied the boreal mammals of Colorado in their relation to those of Utah and northwestern Wyoming. These mammals may be grouped according to the pattern of their variation and distribution as follows:

Group I.—Rare, extinct, or insufficiently known to use in this study: *Alces americana*, *Ovis canadensis*, *Lepus americanus*, *Sylvilagus nuttallii*, *Phenacomys intermedius*, *Mustela erminea*, and *Gulo luscus*.

Group II.—Occurring only north and west of the barrier formed by the Wyoming Basin and the Green River (Fig. 1): *Eutamias amoenus*, *Glaucomys sabrinus*, *Microtus richardsoni*, and *Martes pennanti*.

Group III.—Occurring only southeast of the above mentioned barrier: *Sciurus aberti*.

Group IV.—Occurring in the mountains of northwestern Wyoming and the mountains of Colorado as a single subspecies; this group includes eight of fifteen species that occur on both sides of the barrier shown in Figure 1: *Sorex cinereus*, *Sorex vagrans*, *Sorex palustris*, *Clethrionomys gapperi*, *Microtus montanus*, *Microtus longicaudus*, *Zapus princeps*, and *Erethizon dorsatum*.

Group V.—Occurring in the mountains north of the Wyoming Basin and the mountains southeast of the basin, but as different subspecies: *Martes americana*,

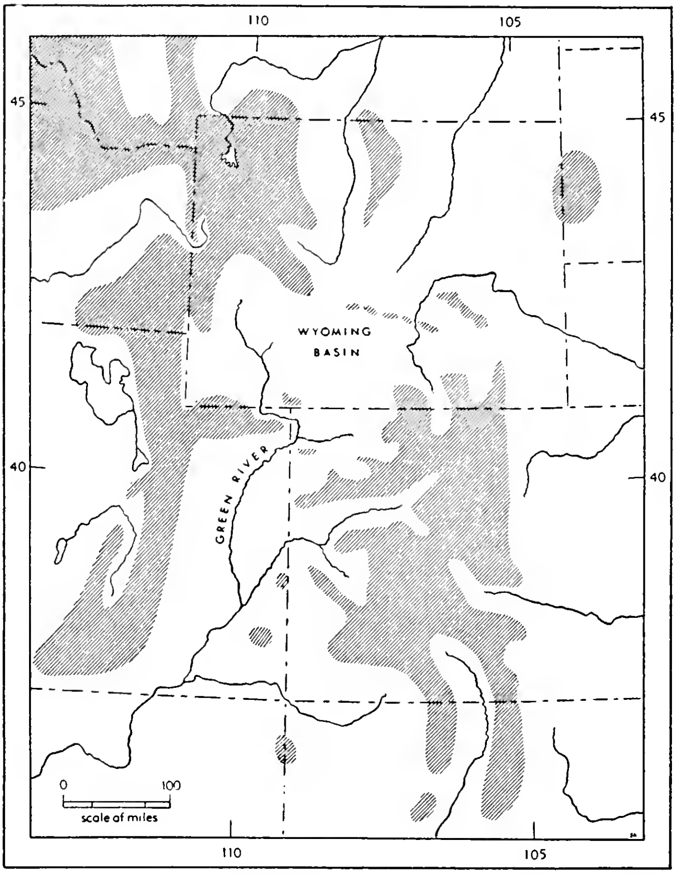

FIG. 1.—The distribution of the Boreal Zone (diagonally lined) in Wyoming, Colorado, and Utah. The major barrier (consisting of the Wyoming Basin and the Green River) separating the boreal habitat in Colorado from the mountains of Utah and northwestern Wyoming is shown.

Marmota flaviventris, *Citellus lateralis*, *Eutamias umbrinus*, *Tamiasciurus hudsonicus*, *Microtus pennsylvanicus*, and *Ochotona princeps*.

In Figure 1 we have mapped the distribution of boreal habitat and the barrier discussed. We note that the arboreal species, namely, the two tree squirrels, the flying squirrel, the marten, and the fisher, occur either on one side of the barrier only or else have distinct northern and southeastern subspecies. The other species that occur only on one side of the barrier or that have separate subspecies on the north side and on the southeast side of the Wyoming Basin are: *Marmota flaviventris*, *Ochotona princeps*, *Microtus richardsoni*, *Microtus pennsylvanicus*, *Citellus lateralis*, and two species of *Eutamias*. The species named immediately above and the arboreal species (in comparison to the next group of species to be discussed) seem to be relatively restricted in the range of habitats that they utilize. The pattern in the chipmunks is complicated by other species of less montane chipmunks whose presence may act as a biological barrier. The red squirrel, the marten, and the golden-mantled ground squirrel have populations in Colorado and northern Utah that are alike and differ from corresponding populations on the northern side of the Wyoming Basin.

The species that have a single subspecies occurring on both the north side and the southeast side of the Wyoming Basin are as follows: three species of shrews, three microtines, the jumping mouse, and the porcupine. The porcupine is a ubiquitous creature, prone to wander. The other seven species are small mammals which may migrate by way of narrow avenues found along streamcourses where the water draining from montane areas supports growths of brush, scrub willow, and grasses and sedges. Furthermore, these species do not seem to be dependent upon forests or forest-edge communities. If the montane mammals here dealt with are arranged in order of their decreasing dependence upon montane conditions it is seen that those kinds appearing early in the list are those that occur only on one side of the barrier shown in Figure 1 or those that have distinct northern and southeastern subspecies (that is, belong in Group V). Those that appear later in such a list are in general those that are subspecifically the same north and southeast of the Wyoming Basin (Group IV). It might be concluded that montane meadow and streamside habitats connected the southern and central Rockies across the Wyoming Basin long after they ceased to be connected by continuous forests. The red-backed mouse, *Clethrionomys*, is restricted to the forested areas of the mountains more than the other species. Investigation of the most recent work on *Clethrionomys* (Cockrum and Fitch, Univ. Kansas Publ., Mus. Nat. Hist., 5: 283, 1952), reveals that these authors regarded northwestern Wyoming and the Bighorn Mountains as centers of incipient subspecies. Judging by their comments on *C. gapperi galei* and on *C. g. uintaensis* in Utah we feel that the four populations, (1) in the Uinta Mountains, (2) in northwestern Wyoming, (3) in the Bighorn Mountains, and (4) in northern Colorado, are differentiated from one another and might be regarded equally well as one or as four subspecies. The latter supposition would place them in Group V and would obviate the seeming inconsistency.

On the basis of the information presented above it seems that: (1) The ranges of montane species are correlated with their dependence upon special habitats; the more dependent species are more restricted in range, both locally and regionally. (2) The more dependent, and therefore relatively restricted, species show more differentiation on opposite sides of the Wyoming Basin than the species that are less restricted. (3) The closest affinities of the boreal mammals in the Rocky Mountains of Colorado are with the boreal mammals of the Uinta Mountains across the Green River Canyon rather than with those of the central Rocky Mountains to the north of the Wyoming Basin. (4) The discontinuity in the boreal forest produced by the erosion of the Green River Canyon has become important as a barrier to montane mammals later than the discontinuity caused by the desiccation of the Wyoming Basin.

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Mammals from Isla Cozumel, Mexico, With Description of a New Species of Harvest Mouse

BY

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Isla Cozumel, or Cozumel Island, lies in the Gulf of Mexico approximately 16 kilometers off the east coast of the Yucatan Peninsula. Administratively, the island is attached to the Mexican Territory of Quintana Roo. The strait that separates Cozumel from the mainland reaches a depth of more than 300 meters, and the current in the strait is swift. The island itself is approximately 45 kilometers long (northeast-southwest) and averages about 14 kilometers wide. "It is composed of limestone and its greatest elevation is about 10 meters above the sea" (Paynter, 1955:8). Vegetationally, Cozumel supports mostly scrubby deciduous forest and mangrove swamps.

From August 7 to 11, 1962, a field party from the Museum of Natural History of The University of Kansas collected vertebrate animals in the vicinity of San Miguel on the west coast of Cozumel. The present report concerns the mammals obtained or observed by the party, among which are several species previously unreported from the island. One of these is a new harvest mouse of the genus *Reithrodontomys* that is named and described beyond. Mention is made also of species previously reported from Cozumel, especially by Hall and Kelson (1959), Koopman (1959), Merriam (1901), and Thomas (1888).

Field operations on Cozumel were supported by funds made available through a contract (DA-49-193-MD-2215) between the U. S. Army's Medical Research and Development Command and The University of Kansas.

Didelphis marsupialis cozumelae Merriam, 1901.—Ten specimens (91428-37), including six pouch young, were taken 3½ km. N San Miguel, where opossums were seen nightly at a garbage dump. The female that carried the six young was obtained on August 8; the young weighed an average of 18.4 (17.6-19.5) grams.

We tentatively retain the subspecific name *cozumelae* for the insular opossums. Comparison of our material with specimens of *D. m. yucatanensis* from the adjacent mainland fails to support Merriam's (1901:102) contention that the two differ in certain cranial features or that *cozumelae* is the larger in size of body. The tail does, however, average shorter in relation to length of body than in specimens from the mainland, and the white tip on the tail is noticeably shorter (one-half to two-thirds as long).

Selected measurements of an adult male and the largest available female (the one with young) are, respectively: total length, 770, 633; length of tail, 319, 300; length of hind foot, 60, 53; length of ear, 54, 52; greatest length of skull, 115.1, 90.7; zygomatic breadth, 63.5, 45.2; palatal length, 65.7, 54.8; length of M1-M4, 19.5, 17.9.

Micronycteris megalotis mexicana Miller, 1898.—Our only specimen (91539), a female in juvenal pelage and with unfused phalangeal epiphyses, was taken in a mist net stretched between two palm trees adjacent to the cottage in which we stayed. Goldman (1951:443) earlier listed this species from Cozumel under the name *Macrotus pygmaeus*.

Artibeus jamaicensis yucatanicus J. A. Allen, 1904.—Judging from our experience, this species is the commonest of the bats occurring on Cozumel. Eighteen individuals were collected as follows: 4 km. N San Miguel, 6 (91724-29); 3½ km. N San Miguel, 12 (91730-40, 91781). All specimens taken were netted, either along small roads through the scrubby forest or among coconut palms adjacent to residences near the beach. Five of 11 females obtained were lactating; the testes of one male measured 10 mm. Several authors previously have reported this bat from the island.

Artibeus lituratus palmarum Allen and Chapman, 1897.—One specimen (91780), a male having testes measuring 6 mm., was netted along with several individuals of *A. jamaicensis* among coconut palms 3½ km. N San Miguel. This species has not been reported previously from Cozumel.

Artibeus phaeotis phaeotis (Miller, 1902).—A male and two females of this small fruit-eating bat were trapped in mist nets stretched across a narrow road in the forest 4 km. N (91790) and 3½ km. N (91791-92) San Miguel. Each of the females carried a single embryo (23 and 25 mm. crown-rump). Although this species long has been known from the Yucatan Peninsula, it was not formerly known from Cozumel.

Previous authors (Hershkovitz, 1949:449, Dalquest, 1953:64, and Davis, 1958:164, among others) have regarded *A. p. phaeotis* (type locality, Chichén-Itzá, Yucatán) as a subspecies of *Artibeus cinereus*. Apparently none of the authors who thus treated *phaeotis* examined the holotype, which actually is identical with the species later described by Andersen (1906:422) as *Artibeus turpis* (type locality, Teapa, Tabasco). Therefore, *A. p. phaeotis* replaces *A. t. turpis* as the correct name for the bat of the Caribbean lowlands of southern Mexico and adjacent areas that is characterized by its small size, relatively broad and naked uropatagium, and short, up-turned rostrum. The slightly smaller subspecies of Pacific coastal areas (see Davis, 1958:163) henceforth should bear the name *Artibeus phaeotis nanus*.

We are grateful to Dr. C. O. Handley, Jr., of the U. S. National Museum, who currently is revising the genus *Artibeus*, for allowing one of us (Jones) to examine the holotype of *phaeotis*. Our attention first was drawn to this matter when we discovered that all individuals of small *Artibeus* in our collection from the Yucatan Peninsula resembled "*turpis*," which was not reported from there, rather than "*cinereus*," which was said to occur there.

Measurements of the male and two females are, respectively: total length, 57, 54, 58; length of hind foot, 12, 10, 11; length of ear, 14, 16, 17; length of forearm, 38.2, 38.3, 40.8; greatest length of skull, 19.6, 19.1, 19.3; zygomatic breadth, 11.5, 11.7, 11.7; length of maxillary tooth-row, 6.0, 5.8, 5.9.

Natalus stramineus saturatus Dalquest and Hall, 1949.—This species, previously unreported from the island, is represented in the U. S. National Museum by 32 specimens in alcohol from San Miguel.

Oryzomys palustris cozumelae Merriam, 1901.—Rice rats were abundant in tangled, second-growth brush and vines. Thirty-six specimens were collected from 3 km. N (92185-86) and 3½ km. N (92168-84, 92187-203) San Miguel. A female obtained on August 8 carried three embryos that measured 15 mm. (crown-rump) and our sample contains many two-thirds to three-fourths grown young.

Up to now, *O. p. cozumelae* has been regarded as a distinct species, although its close relationship with *O. palustris* of the adjacent mainland has been recognized (see Goldman, 1918:43). None of the specimens among our material are as large as the holotype of *cozumelae*, but a number fall within the range of variation cited for adults by Goldman (*loc. cit.*). When our specimens were compared with individuals of *O. p. couesi* from the Yucatan Peninsula, we found that *cozumelae* differed noticeably only in being larger externally; cranially, *couesi* and *cozumelae* differ only in minor details (for example, the skull of *cozumelae* averages slightly larger, is less arched over the orbits, and has heavier teeth and larger nasals), and the latter averages only slightly darker than mainland specimens. Furthermore, adults of *cozumelae* do not exceed in external size individuals from several of the named populations of *O. palustris*. For all these reasons, and because *cozumelae* long has been recognized as only an insular relative of *palustris*, we employ the name *Oryzomys palustris cozumelae* for it. We feel the relationships of the insular population are best reflected by such usage.

Reithrodontomys spectabilis new species

Holotype.—Adult male, skin and skull, no. 92294 Museum of Natural History, The University of Kansas, from 2½ km. N San Miguel, Isla Cozumel, Quintana Roo; obtained by Ticul Alvarez on August 8, 1962 (original no. 848).

Distribution.—Known only from Cozumel Island.

Diagnosis.—Size large both externally and cranially (see measurements); tail long in relation to head and body (134-148 per cent in adults), scantily haired; pelage short and relatively sparse; upper parts brownish ochraceous over-all, brighter ochraceous on sides; underparts grayish white, the individual hairs white terminally and plumbeous basally; pinkish buff pectoral spot sometimes present; tail dark brown above, only slightly paler below; braincase relatively flattened and uninflated; zygomatic arches broad and strong; rostrum relatively short and broad; mesopterygoid fossa broad; auditory bullae large but only moderately inflated; incisive foramina rarely reaching level of M1; teeth large; first and second molars typical of the subgenus *Aporodon* in having well developed mesolophs(ids) and mesostyles(ids); third lower molar essentially a smaller replica of first two; baculum long (9.5 and 10.9 mm. in two adult males), slender, curved dorsally at the distal end, broadly arrow-shaped basally (width of base 1.1 and 1.2 mm. in the two adult bacula studied), possibly largest among members of genus. The skull and teeth are illustrated in Figure 1.

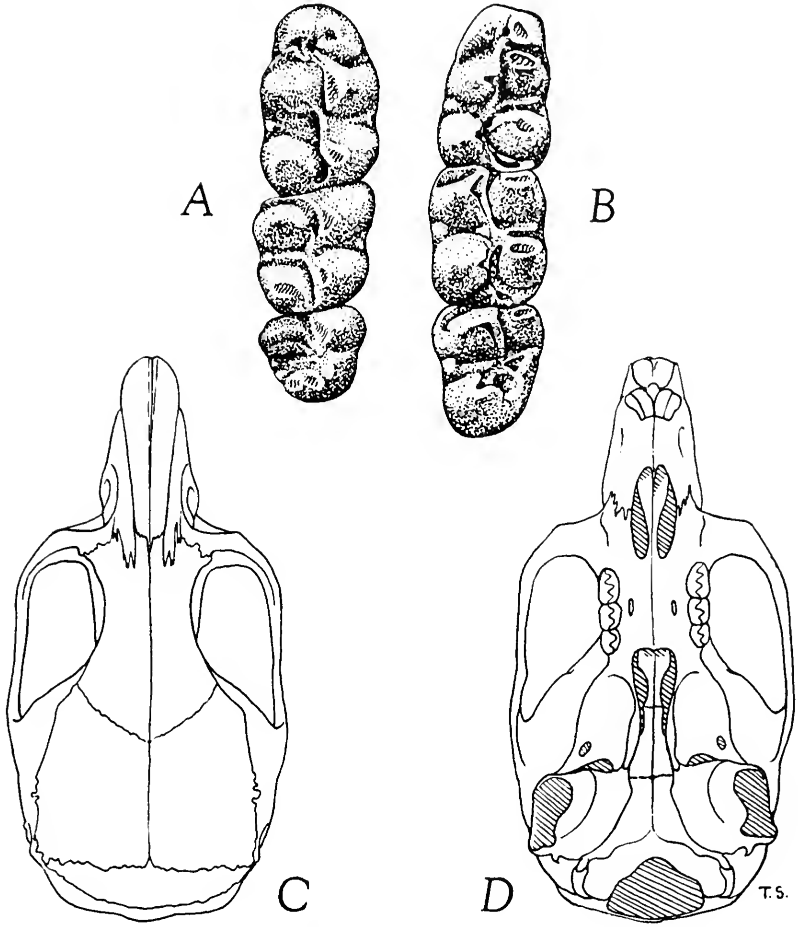

FIG. 1. Skull and teeth of *Reithrodontomys spectabilis.* Right upper (A) and left lower (B) molars of KU 92293 (× 15), and dorsal (C) and ventral (D) views of skull of holotype, KU 92294 (× 3). T. H. Swearingen made the drawings from photographs by J. F. Downhower.

Measurements.—External and cranial measurements of the holotype followed by average and (in parentheses) extreme measurements of eight specimens (four males and four females, including the type) are: total length, 216, 213.8 (205-221); length of tail, 124, 125.7 (121-132); length of hind foot, 22, 21.3 (20-22); weight (in grams), 20.6, 20.2 (18.1-21.4); greatest length of skull, 24.7, 25.2 (24.6-26.2); zygomatic breadth, 12.2, 12.3 (11.8-12.7); interorbital breadth, 3.7, 3.7 (3.5-3.9); breadth of braincase, 11.2, 11.2 (11.0-11.5); depth of skull, 8.5, 9.0 (8.5-9.4); length of rostrum, 8.8, 9.0 (8.7-9.8); breadth of rostrum, 4.1, 4.2 (3.9-4.5); length of incisive foramen, 4.4, 4.5 (4.4-4.8); breadth of mesopterygoid fossa, 1.7, 1.7 (1.5-1.8); length of palatal bridge, 3.9, 4.0 (3.8-4.3); alveolar length of maxillary tooth-row, 3.8, 3.8 (3.7-3.9); alveolar length of mandibular tooth-row, 3.4, 3.5 (3.4-3.7).

Comparisons.—The new species is a member of the subgenus *Aporodon* and is allied to *Reithrodontomys mexicanus* and *R. gracilis* of the *R. mexicanus* species group. It is the largest member of the *mexicanus* group as defined by Hooper (1952) and among the largest species of the genus *Reithrodontomys.*

Of the two kinds to which it appears most closely related, the new species resembles *R. gracilis* of the adjacent mainland of the Yucatan Peninsula to a somewhat greater degree than *R. mexicanus,* known nearest Cozumel Island from the highlands of Guatemala and Honduras. In comparison with *gracilis, R. spectabilis* is immediately recognized by its much larger size (total length averaging 213.8 in adult *spectabilis* but only 175.7 in six adult *R. g. gracilis* from the Yucatan Peninsula, length of hind foot 21.3 and 17.8, greatest length of skull 24.7 and 21.9, zygomatic breadth 12.2 and 10.8), generally darker coloration, and in having a massive skull with broader, heavier zygomatic arches. *R. spectabilis* resembles *R. gracilis* (in contrast to *R. mexicanus*) in that the dark tarsal stripe does not extend onto the hind foot and in having a flattened and relatively uninflated braincase, incisive foramina that rarely reach the level of M1, and in other general features of the cranium. The breadth and depth of the braincase are even less, relative to length of the skull, than in *gracilis*—the breadth averages 44.6 per cent of the greatest length of skull (47.5 in *gracilis* studied), and the depth of skull averages 35.9 in relation to length (36.9 in *gracilis*).

R. spectabilis resembles *R. mexicanus* more than *R. gracilis* in size (measurements of *mexicanus* studied—subspecies *howelli* and *orinus*—are intermediate between those of *spectabilis* and *gracilis*) and to some extent in general coloration. Cranially, aside from averaging smaller, *mexicanus* can be distinguished most easily from *spectabilis* by its proportionately broader and deeper braincase.

Because of its resemblance in many features to the smaller *R. gracilis,* we assume that the precursors of *R. spectabilis* reached Cozumel from the adjacent mainland of the Yucatan Peninsula. The magnitude of the differences between the two species suggests, to us at least, that they have been separated for a relatively long time, since at least late Pleistocene.

Remarks.—Some of the harvest mice from Cozumel Island were trapped in tangled, second-growth vines and brush adjacent to (beachward from) scrub forest; *Oryzomys palustris cozumelae* was abundant in this same habitat. Other individuals were taken in forest in traps set at the bases of trees and along a stone wall. One specimen was caught by hand at night as it climbed in the branches of a small tree, indicating that the Cozumel harvest mouse is at least partly arboreal in habits.

Our sample contains several juvenal and subadult specimens. One female, trapped on August 9, had been recently lactating, but no other females evidenced gross reproductive activity. The testes of two adult males measured 13 and 14 mm.

Specimens examined, 16, as follows: 2½ km. N San Miguel, 3 (92294-96); 3½ km. N San Miguel, 13 (92281-93).

Peromyscus leucopus cozumelae Merriam, 1901.—Six white-footed mice were trapped along trails in scrub forest or in places marginal between forest and second-growth brush. Our specimens are from 3½ km. N (92417-21) and 2½ km. N (92422) San Miguel. A female obtained on August 11 was lactating.

P. l. cozumelae differs from the subspecies of the mainland of the Yucatan Peninsula (*P. l. castaneus*) in being larger, both externally and cranially, and in having heavier teeth. The two kinds closely resemble each other in color.

Dasyprocta punctata yucatanica Goldman, 1913.—According to Merriam (1901:100), *D. punctata* was introduced on Cozumel "shortly before" the visit of Nelson and Goldman to the island in 1901. Goldman actually observed an individual in the forest near San Miguel. Natives reported to us that agoutis still occur on the island.

Agouti paca subsp.—On the morning of August 11, William E. Duellman observed a paca along a trail through the forest approximately 4 km. N San Miguel. We queried local residents concerning the status of this large rodent on the island and, while aware of its presence, they had no knowledge of whether or not it had been introduced.

Urocyon cinereoargenteus subsp.—We did not obtain specimens of the gray fox, but local residents reported its occurrence to us. Earlier, Merriam (1901:99) wrote of this species on Cozumel as follows: "The only mammal heard of [by Nelson and Goldman] which was not secured is a small Gray Fox (*Urocyon*) reported by natives as rather rare, but more common on the eastern and southern parts of the island. From the accounts it agrees with the Raccoon, Nasua, and Peccary in being much smaller than the mainland species."

Procyon pygmaeus Merriam, 1901.—A subadult male raccoon (92565) was shot on August 8 from a coconut palm situated along the beach 3½ km. N San Miguel. Two other individuals were seen in the same tree and the three may have been from the same family group. Our specimen differs in cranial features from raccoons of the Yucatan Peninsula (*P. lotor shufeldti*) in ways described by Goldman (1950:76-77), and we follow Goldman in preserving specific recognition for *pygmaeus*. It is perhaps worthy of note that our specimen has a distinct "interparietal" bone approximately 13 mm. long by 8 mm. wide, at the juncture of the parietal and frontal bones.

Nasua nelsoni Merriam, 1901.—According to local residents, coatis are common in the vicinity of San Miguel. Several were seen at night and in early morning by our party. One (92570), an adult female with well-developed teats (probably recently lactating), was obtained 3½ km. N San Miguel.

We retain *N. nelsoni* as a full species because it differs so strikingly in size from the coati (*Nasua narica yucatanica*) of the adjacent mainland. Measurements of our specimen, followed in parentheses by measurements of an adult female of *yucatanica* from 7 km. N and 51 km. E Escárcega, Campeche, are as follows: total length, 741 (990); length of tail, 332 (485); length of hind foot, 76 (99); length of ear, 35 (40); greatest length of skull, 103.4 (118.6); zygomatic breadth, 50.3 (58.3); interorbital constriction, 20.4 (24.5); palatal length, 62.7 (72.9); breadth of braincase, 38.3 (42.0); alveolar length M1-M3, 16.6 (19.9). Aside from its over-all smaller size, the skull of *nelsoni* is notable for its more delicate construction and distinctly smaller bullae when compared with *N. n. yucatanica*.

Trichechus manatus manatus Linnaeus, 1758.—Local residents reported that manatees were observed occasionally along the west coast of the island and that they were common in the bays and lagoons on the adjacent coast of Quintana Roo.

Tayassu tajacu nanus Merriam, 1901.—The collared peccary of Cozumel was described as a subspecies distinct from that on the adjacent mainland of Yucatan (*T. t. angulatus*) on the basis of smaller size and blacker nose and chin. Subsequently, Hershkovitz (1951:567) noted that the species had been introduced on the island from the adjacent mainland (see also de Vos *et al.*, 1956:176) and suggested that the small size claimed for *nanus* resulted from heavy hunting pressure, which did not allow animals to attain adult size. Additional specimens are needed before Hershkovitz's interesting hypothesis can be tested. Natives on Cozumel reported the collared peccary as common and intensively hunted.

Mammals Reportedly Collected on Cozumel by G. F. Gaumer

George F. Gaumer, well-known naturalist who lived for many years on the Yucatan Peninsula, reported himself, or sent to others, a number of mammals alleged to have come from the island of Cozumel. Some of these probably originated from the island but others seemingly did not, as discussed below.

Oldfield Thomas (1888), in the first technical paper dealing with mammals from Cozumel, reported five species that were collected by Gaumer and communicated to Thomas by Salvin and Godman. These five were *Didelphis marsupialis, Pteronotus parnellii, Artibeus jamaicensis, Tadarida laticaudata,* and "*Nasua nasica.*" The opossum, Jamaican fruit-eating bat, and coati (in the form of the small *Nasua nelsoni*) subsequently have been found to be common on the island. No other records of the two remaining bats, *Pteronotus* and *Tadarida*, have been forthcoming, but each is widespread on the adjacent Yucatan Peninsula and we do not doubt that each occurs on Cozumel.

In his "Monografía de los mamíferos de Yucatán," Gaumer (1917:117) reported the presence of the Yucatan deer mouse, *Peromyscus yucatanicus*, on the island. He did not, however, record *Peromyscus leucopus* from Cozumel and Koopman (1959:237) concluded that Gaumer confused the two species. We are inclined to agree with Koopman, because insofar as we know *P. yucatanicus* does not occur on the island. Gaumer (*op. cit.*:63) also recorded the white-lipped peccary (as "*Dicotyles labiatus*") from Cozumel but this, too, seems to be in error.

By far the most perplexing collection of mammals relating to Cozumel is a lot of specimens acquired from Gaumer by the Museum of Natural History in the early 1900's. Many of these specimens were cited by Hall and Kelson (1959) and all species represented were listed by Koopman (1959). The holotype and paratypes of *Mimon cozumelae* Goldman (1914) were among the specimens in this collection. Aside from *M. cozumelae*, species represented (and their catalogue numbers) are: *Micronycteris megalotis mexicana* (1659-60); *Glossophaga soricina leachii* (1655-58); *Artibeus jamaicensis yucatanicus* (1641-42); *Centurio senex* (1669-70); *Lasiurus borealis teliotis* (1655); *Plecotus* (possibly *mexicanus*) (1658); *Molossus ater nigricans* (1663-64); *Ateles geoffroyi yucatanensis* (885); *Tamandua tetradactyla mexicana* (869-872, 880); *Heterogeomys hispidus yucatanensis* (1370); *Nasua narica yucatanica* (876-77, 1599-1600); *Galictis allamandi canaster* (873); and *Tayassu* sp. (875—said to be *T. t. nanus*, probably solely on supposed geographic grounds, but specimen not now to be found).

Most of the labels that now accompany the above-listed specimens are not the original labels of Gaumer, and, in any event, bear no additional information that could support or refute the contention that the specimens actually came from Cozumel. Many other specimens received at the same time are labeled simply as from "Yucatan." Some of the specimens said to be from Cozumel obviously did not come from there as shown below and there is a strong possibility that others did not. Perhaps few or none of the specimens actually originated on the island.

Of the eight bats, only two (*A. jamaicensis* and *M. megalotis*) have been obtained on Cozumel by other collectors. One, *Plecotus*, seems likely not to occur there (see also Koopman, 1959:237). The remaining five (*Mimon, Glossophaga, Centurio, Lasiurus,* and *Molossus*) are widespread in Middle America and each is known from the adjacent mainland. We took *G. soricina* on the much smaller Isla Mujeres that lies to the north of Cozumel. There is a strong possibility that all five species actually occur on Cozumel and that additional collecting will establish their presence on the island. We are especially hopeful of this development with reference to *Mimon cozumelae*.

With reference to the six strictly terrestrial kinds, we doubt that any save *Tayassu* occurs on the island. The major habitat, scrub forest, doubtfully would support tamanduas or monkeys (although the latter might have been introduced) and neither was reported to us by local residents (nor was the grison mentioned). We especially questioned natives about the occurrence of pocket gophers but they assured us that "tuzas" were not present. All four coatis, formerly labeled "*Nasua nelsoni,*" are unquestionably the much larger *N. narica yucatanica* that occurs only on the adjacent mainland.

Zoogeography

As Koopman (1959) pointed out, the zoogeographic relationships of Cozumel, at least with respect to mammals, are undoubtedly with the adjacent mainland, not with the Antilles. Even though the strait that separates Cozumel from the mainland of Quintana Roo is deep, and the current in it strong, we suppose that most of the mammals that occur on the island reached it by "rafting" across the strait or possibly from the mainland to the south of Cozumel. At a time of maximal glaciation, because of a lowering of the sea level, the strait would have been reduced to approximately half its present width, theoretically making "rafting" much easier than now, especially if favorable winds prevailed. At least three of the mammals that currently inhabit the island are known or suspected to have been introduced by man.

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RELATION OF SIZE OF POCKET GOPHERS TO SOIL AND ALTITUDE

By William B. Davis

While working out the distribution and taxonomy of pocket gophers in southern Idaho, I became interested in the problem of correlation of size with soil conditions and altitude. I do not claim to have settled a problem; in fact, I intend merely to point out one that, to me, warrants further study.

The specimens and field notes on which this discussion is based are contained in the Museum of Vertebrate Zoology, Berkeley, California. I wish to thank the officials of that museum for the many privileges extended me; also, to acknowledge the generous assistance of Messrs. David Johnson and D. Tillotson in supplying additional specimens and information.

Pocket gophers, especially the males, tend to increase in size with age. The ultimate size attained appears to be correlated directly with the type of soil inhabited, and indirectly with altitude. At high elevations where the soil usually is shallow and rocky, or at lower elevations where the same general environmental conditions prevail, races and individuals of the same species tend to be small. In places of this kind the skulls of males and females often are indistinguishable; they are smooth and lack ridges. They are juvenile in character and in many respects appear not to have developed beyond the subadult state of forms living under better environmental conditions. If one compare individuals from poorer soils (for pocket gophers) with others from progressively better and deeper ones, the size of both sexes is found generally to increase, males more so than females. Under optimum conditions the actual weight of the skulls may average two or even three times that of individuals that live amid adverse conditions. In the deeper soils sexual dimorphism is evident and the skulls of both sexes are angular in outline and have well developed sagittal, lambdoidal, and temporal ridges.

This general reduction in size at higher altitude is illustrated by specimens from near Pocatello, Idaho. There the species *Thomomys quadratus* occurs altitudinally from 4400 feet on the floor of Portneuf Valley to over 7000 feet in the Bannock Mountains. Individuals taken from the valley are considerably larger than those from higher altitudes. The skulls are massive, prognathous, angular, and ridged, the males much larger than the females. Individuals taken at progressively higher altitudes are smaller, the skulls tend to be less angular and ridged, as well as less prognathous, and the degree of sexual dimorphism is reduced. Taking the product of three dimensions of the skull, basilar length, zygomatic breadth, and palatofrontal depth, as an index of size, the following results were obtained:

	Males	*Females*	*Difference*
4500 feet	1295 (3)*	1035 (3)	260
5000 feet	1360 (4)	930 (3)	430
5800 feet	1060 (2)	880 (2)	180
6300 feet	920 (6)	840 (6)	80
7000 feet	920 (2)	850 (1)	70

* Number of specimens averaged.

Certain discrepancies are evident in the comparisons. Males from 5000 feet are larger than those from 4500 feet; the female from 7000 feet is larger than those from 6300 feet. These exceptions do not invalidate the general principle because age differences in the males and too few specimens in the females probably account for the deviations from the expected size. A reduction in length of body, length of hind foot, and length of tail accompanies a reduction in "volume" of the skull.

Similar results were obtained in a study of another species in another locality. *Thomomys bottae* occurs on the floor of Monitor Valley, Nevada, at an altitude of 6900 feet, and also on the adjacent Toquima Mountains, which rise to over 10,000 feet. Individuals taken at altitudes ranging from 9000 to 10,000 feet on the mountain are considerably smaller than those from the valley; specimens from Meadow Creek Canyon, at 8000 feet on the east side of the mountain, are intermediate in size. Sexual dimorphism is pronounced in specimens from the valley; it is slight in specimens from above 9000 feet. These facts are evident from the following tabulation.

	Males	*Females*	*Difference*
6900 feet	1775 (6)	1250 (6)	525
8000 feet	1320 (2)	1060 (2)	260
9000 to 10000 feet	1060 (5)	920 (2)	140

Similarly, specimens of *Thomomys bottae* taken at different elevations on Mt. Moriah in eastern Nevada and western Utah exhibit the same trend. Skulls of specimens from 5000 feet elevation are much larger than those from high on the mountain. Between the two extremes the skulls are intermediate, grading, as evidenced below, from large, with pronounced sexual dimorphism, at the bottom, to small at the top, with little difference between males and females.

	Males	*Females*	*Difference*
5000 feet	1664 (3)	1221 (5)	443
5400 feet	1268 (2)	1085 (3)	183
6000 feet	1177 (2)	—	—
6700 feet	—	1001 (2)	—
9100 feet	1139 (3)	994 (6)	45
9800 feet	1086 (1)	1009 (1)	77
11400 feet	—	971 (2)	—

Again, certain discrepancies appear, but the gradation is clearly evident.

Aside from consistently smaller size, specimens of both *quadratus* and *bottae* from the higher altitudes are but little different from those at low levels. The most significant difference is found in the relatively shorter rostrum in specimens from high altitudes. This I interpret as an expression of arrested development. Numerous studies have shown that the rostrum in subadult pocket gophers is consistently relatively, as well as actually, shorter than in adults.

Gradation from large to small size is found in every area studied in the Great Basin where *one species occupies both the valley floor and the adjacent mountain.* Because of this, it becomes increasingly difficult to reconcile present practices in taxonomy with the situation as it actually exists. The tendency of certain students to assign all the populations of pocket gophers occurring on different, isolated mountain tops to one subspecies and those occurring in the lowlands to another defeats the purpose of systematics. To me, it is illogical to assume that the several alpine populations are closely related *inter se* and genetically different, as a unit, from the populations of the same species occurring in the valleys. Nor does it seem logical to assume that the populations of a species in two valleys, separated by a high mountain range on which small individuals of the same species occur, are genetically related *inter se* and at the same time genetically distinct from the smaller alpine individuals.

Various authors have referred the alpine populations of pocket gophers in southern Idaho to *Thomomys uinta* or *Thomomys quadratus uinta* and those in the lowlands to *Thomomys bridgeri* or *Thomomys quadratus bridgeri.* In doing this the topography and geologic history of the area probably were not considered. In this region the mountains certainly are older than the genus *Thomomys* and consequently we cannot assume that populations now restricted to alpine areas once occupied a continuous range that subsequently was disrupted by geologic changes. Nor can we assume that the population of large pocket gophers moved in and usurped the lowland portions of a range once occupied by the smaller animals. Such an assumption would necessitate a divergence of the two at a time earlier than that suggested by cranial characters. Furthermore, it would necessitate a migration of the large individuals *over* high passes in order to explain their present distribution in southern Idaho.

In interpreting the past history of *Thomomys quadratus* in southeastern Idaho I have assumed that during the Pleistocene most of the mountains were glaciated and the lower valleys under water, so that intermediate altitudes alone were available to pocket gophers. It is well known that the yearly increase of a successful species is greater than the carrying capacity of the area occupied, and that as a result of population pressure every available niche is sought out and occupied. As the glaciers receded and the lakes decreased in extent, additional territory became available both above and below the former range. This new territory was occupied by the surplus of the yearly increase. Those gophers that moved down hill encountered deeper and richer soils and consequently could grow larger without handicap. Those that moved uphill found conditions progressively more adverse; the soil was shallower and rockier and plant food less abundant, although sufficient to maintain life. Only individuals with small bodies could survive amid such conditions. Whether size *per se* be heritable or due to ontogenetic processes is not of prime importance to the question at issue because the end result—size—in either instance is the limiting factor in shallow soil. Ultimately, from a population of pocket gophers of medium size, both the mountains and the lowlands became populated, the former by small individuals, the latter by large ones. The parent stock probably remained at intermediate levels.

Such an interpretation explains many facts of distribution. Each high mountain in southern Idaho harbors a population of dwarfed individuals, in each valley the gophers are large, and at middle altitudes, of intermediate size. The alpine populations, even on isolated mountain tops, resemble one another more than they do those in the valleys, yet it is difficult to conceive of them as being subspecifically related *inter se* and at the same time subspecifically distinct from those at lower elevations. The similar cranial characters of the two extremes, the gradation from large size to small, and the topography and geologic history of the region, point toward the conclusion that the alpine and lowland forms are of the same subspecies. This applies also to the two localities in Nevada whence specimens were examined.

The only other logical method I see of treating these alpine populations is to *name each one of them*, a practice that would lead to confusion and ridicule, yet one that is followed by some students.

We should be more cautious in our designation of new races. All too little attention has been given to the study of the effect of environment upon the size of animals. If environmental conditions produce a condition of arrested development, should animals exhibiting this condition be recognized by name? Whether pocket gophers from alpine areas would increase in size if transplanted to better soil at lower elevations, or whether they would retain their identity, is not known. An experiment designed to test this point would be well worth while.

SUMMARY

1. In each of three localities in southern Idaho and the Great Basin where *the same species* of pocket gopher inhabits both the lowlands and the adjacent mountain, a gradation from large, sexually dimorphic individuals, at lower elevations where the soil is deeper, to small individuals with little, if any, sexual dimorphism, at higher elevations where the soil is shallower, is exhibited.

2. Since the same trend occurs at each of three widely separated localities,

it seems logical to conclude that the gradient is a true one; also that the populations at the two extremes of such a gradient are not worthy of recognition by separate names.

3. The possibility of this gradient occurring in other localities should merit careful consideration in systematic work with *Thomomys* so that the formal naming of populations not worthy of recognition by name will be avoided.

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THE PINNIPEDIA: AN ESSAY IN ZOOGEOGRAPHY*

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STUDIES that seek to explain the present distribution of animal forms must draw on a wide and varied field of evidence. Some of the evidence, notably that provided by the paleontologists, is direct and generally capable of reliable interpretation; but rarely, except for some groups of land mammals, is the fossil evidence sufficient. More commonly, paleontology can provide only the framework, perhaps one or two major clues, or even just a tiny piece of the whole picture. The most successful ventures into the field of historical zoogeography have been made by paleomammalogists who have studied particularly the groups living in relatively large numbers in habitats where sedimentation is most rapid. Thus the historical geography of such plains-dwelling groups as the horses and the elephants is comparatively well known, but forms that inhabit mountains, forests, or seas are represented only fragmentarily in the fossil record. For these latter groups other evidence must be invoked, and it is provided by the taxonomy, physiology, ecology, and distribution of the existing forms. This evidence, although easier to accumulate, is not capable of such reliable interpretation as that provided by paleontology, but it must always be explained and often provides the only clues available.

A third, more nebulous, category of evidence derives from our knowledge of past climates and past distributions of land and sea. At present, however, this knowledge is so uncertain that it is clearly dangerous to place too much reliance on it; at the same time, it should not be disregarded, since it can often indicate possibilities and probabilities and provide a set of limits within which the correct solution to any given problem may be found.

Finally, it is necessary to keep in mind present trends of thought in the fields of genetics and evolution, because, although there is anything but unanimity of opinion within these fields, the most generally accepted concepts will have an important bearing on possible zoogeographical conclusions.

Individual bits of evidence culled from all four sources—paleontological, neozoological, paleogeographical, and evolutionary—may often appear

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tenuous and circumstantial by themselves, but if they are placed together to make a unified picture, each one supporting others, the probability of their correctness, and the correctness of the whole picture, is much increased.

The present essay examines an order of marine carnivorous mammals, the Pinnipedia, which is divided by taxonomists into three families: the seals (Phocidae), the sea lions (Otariidae), and the walruses (Odobenidae).[1] The order is comparatively poorly represented in the fossil record, and paleontologists have hesitated to discuss its distributional history. Published discussions of pinniped geography have been by neozoologists, who based their findings on the taxonomy and distribution of existing forms, and such a limitation of the field of evidence has led to some conclusions that are doubtful and even demonstrably wrong. For instance, Von Boetticher[2] followed Sclater[3] in postulating a southern origin for the sea lions and a spread from south to north, though the fossil evidence alone makes this highly unlikely.

The present study attempts to use evidence from as many fields as possible, and, although it lacks the firm basis of paleontological data that would be desirable, it does seem to provide the only theory of pinniped origin and spread that is fully tenable in the light of the facts as they are known at present.

The evidence of existing distribution is summarized on a series of maps that, together with a series published previously,[4] represent an attempt to map the distribution of all pinniped forms.[5] The fossil evidence was gathered together in 1922 by Kellogg,[6] but his work is now out of date in some respects and must be supplemented from a rather scattered literature.

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[1] The fossil *Semantor* was placed in a fourth family by G. G. Simpson: The Principles of Classification and a Classification of Mammals, *Bull. Amer. Museum of Nat. Hist.*, Vol. 85, 1945, pp. 1–350, but this animal was almost certainly a mustelid (see E. Thenius: Über die systematische und phylogenetische Stellung der Genera *Promeles* und *Semantor*, *Sitzungsber. Öster. Akad. der Wiss. in Wien*, Vol. 158, 1949, pp. 323–336).

[2] H. von Boetticher: Die geographische Verbreitung der Robben, *Zeitschr. für Säugetierkunde*, Vol. 9, 1934, pp. 359–368.

[3] P. L. Sclater: On the Distribution of Marine Mammals, *Proc. Zool. Soc. of London*, 1897, pp. 349–359.

[4] J. L. Davies: Pleistocene Geography and the Distribution of Northern Pinnipeds, *Ecology*, Vol. 39, 1958, pp. 97–113.

[5] The scientific nomenclature used here corresponds with that of Simpson (*op. cit.* [see footnote 1 above]) except that Sivertsen (Erling Sivertsen: A Survey of the Eared Seals (Family Otariidae) with Remarks on the Antarctic Seals Collected by M/K "Norvegia" in 1928–1929, *Scientific Results of the Norwegian Antarctic Expeditions No. 36,* Det Norske Videnskaps-Akademi i Oslo, 1954) has been followed in separating the Australian sea lion as *Neophoca* and including in that genus Hooker's sea lion, formerly known as *Phocarctos,* which Simpson makes a synonym of *Otaria*

[6] Remington Kellogg: Pinnipeds from Miocene and Pleistocene Deposits of California, *Univ. of California Publs., Bull. Dept. of Geol. Sciences,* Vol. 13, No. 4, 1922.

A Working Hypothesis

The general argument that will be advanced depends largely on one working hypothesis: The pinnipeds are, and always have been, generally tied to a cold-water environment.

There can be little disagreement with the statement that present-day pinnipeds are cold-water animals and, with a few exceptions, are found where sea temperature does not exceed 20° C. at any time of the year (Fig. 1). The greatest concentrations both of species and of numbers are found in the subarctic North Atlantic and North Pacific and around the fringe of Antarctica. The one major oceanic region from which they are entirely absent is the Indo-Malayan–West Pacific, which is also the only warm-water region with a continuous history as such since the beginning of the Tertiary. In addition, all fossil forms have been recovered from regions where sea temperatures when the deposits were formed lay within prevailing existing tolerances. The distribution of pinnipeds is, and possibly always has been, generally complementary to that of the reef-forming corals, and there is no evidence that they have ever inhabited tropical waters.

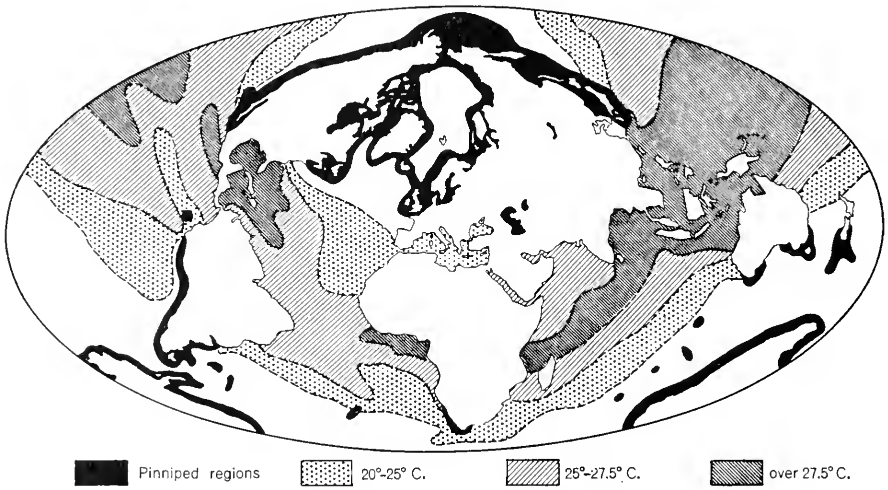

Fig. 1—Pinnipeds and sea temperatures. Distribution of pinnipeds is shown in black; shaded areas indicate warm-month mean sea-surface isotherms. The exceptional genus *Monachus* has been omitted from this map for the sake of clarity, but see Figure 8.

That pinnipeds are physiologically adapted to life in a cold-water environment needs little elaboration. In particular, they have progressed far in the development of insulating hair and blubber and of highly efficient circulatory systems. The upper limit of exterior temperature at which internal temperature regulation becomes difficult is presumably not high, and most, if not all, species experience obvious difficulty in regulating body temperatures while on land.[7]

Physiological adaptation provides evidence that pinnipeds have long frequented cold waters, but it does not provide a reason. The reasons are probably many and include the abundance of available food in the colder high-latitude waters and the virtual absence of competitors. The large carnivorous reptiles and fishes have been and are warm-water forms: it has remained for the homoiothermal seals and whales to exploit the cold-water environment.

ORIGIN OF THE PINNIPEDIA

Pinniped ancestry has long been debated. Separate creodont origin, as suggested by Wortman,[8] now seems most unlikely, and the general consensus would probably be that the pinnipeds are derived from the ancestral dog-bear stock.[9] Recent serological work[10] has indicated a close relationship with the bears, a relationship forecast on morphological grounds by Weber[11] among others. The present study is concerned only with the time and place of pinniped origin, and in order to arrive at reasonable estimates it is not necessary to discuss these arguments at length.

The latest possible time of origin is determined by the earliest fossil pinnipeds, which are sea lions from the lower Miocene of California, and, as these are fairly advanced and diversified forms, the latest probable date must surely be sometime about the middle Oligocene. The earliest possible time of origin is determined by the earliest occurrence of the ancestral group. If the early dog-bear stock is accepted as ancestral, then this date is upper Eocene; if it is necessary to look to the miacid creodonts as ancestors, the date is pushed back into the lower Eocene, and even possibly into the upper Paleocene. Derivation from the "inadaptive" creodonts would push it still farther back in the Paleocene, but this likelihood does not seem to be envisaged today and need not be considered here. The possible extremes are thus upper Paleocene to lower Miocene, and the probable extremes middle

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[7] See, for instance, G. A. Bartholomew and F. Wilke: Body Temperature in the Northern Fur Seal, *Callorhinus ursinus*, *Journ. of Mammalogy*, Vol. 37, 1956, pp. 327–337.

[8] J. L. Wortman: Osteology of *Patriofelis*, a Middle Eocene Creodont, *Bull. Amer. Museum of Nat. Hist.*, Vol. 6, 1894, pp. 129–164.

[9] See, for instance, W. D. Matthew: The Carnivora and Insectivora of the Bridger Basin, Middle Eocene, *Memoirs Amer. Museum of Nat. Hist.*, Vol. 9, 1909, pp. 289–567, references on pp. 413–417; A. S. Romer: Vertebrate Paleontology (Chicago, 1933); and Simpson, *op. cit.* [see footnote 1 above].

[10] C. A. Leone and A. L. Wiens: Comparative Serology of Carnivores, *Journ. of Mammalogy*, Vol. 37, 1956, pp. 11–23.

[11] M. C. W. Weber: Die Säugetiere (Jena, 1909).

Eocene to middle Oligocene. A late Eocene or early Oligocene date is suggested by Simpson,[12] and because of the highly specialized nature of the lower Miocene pinnipeds, Kellogg[13] concluded that the pinniped stock originated no later than the Eocene. Most considerations point, therefore, to the upper Eocene as the likely time of origin.

The place of origin is limited by the distribution of the ancestral group, and whether the ancestral group is canoid, miacid, or creodont, an area somewhere in the Holarctic is inevitable. The Carnivora did not reach Africa until the Oligocene and South America until the Pliocene, and only the dingo has arrived in Australia. To judge by this evidence and by the success of the relatively ancient penguins, the Carnivora have never reached Antarctica. But, although an origin somewhere within the Holarctic seems certain on paleontological grounds, further limitation must be attempted by reference to other considerations. Matthew[14] suggested the Arctic Basin as the most likely place, and the arguments in its favor appear overwhelming. It is centrally placed to provide the fossil and living sea lions of the North Pacific and the fossil and living seals and walruses of the North Atlantic. Its shores have an abundance of shallow waters and wide, long estuaries that would provide the right conditions for a first venture into the marine environment. The Pacific shores are steep and surf-battered, with mountain folds parallel to the coast. This difference between Arctic and Pacific coasts must have continued throughout Cenozoic time and stems from fundamental structural and tectonic differences.

The third major argument in favor of the Arctic Basin as the birthplace of the Pinnipedia hinges on the postulate that they have always been cold-water animals. If the group originated as a cold-water form, it can have originated only in the Arctic, which was the only northern marine region where sea temperatures in the Eocene were comparable with temperatures tolerated by pinnipeds today and by those fossil forms which have so far been discovered. The most satisfactory conclusion, therefore, is that the pinnipeds originated from an ancestral dog-bear stock in the middle or late Eocene Arctic Basin. From the Arctic there was a spread southward during succeeding periods, which was influenced in rate and extent by certain geomorphic and climatic barriers and avenues.

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[12] *Op. cit.* [see footnote 1 above].

[13] *Op. cit.* [see footnote 6 above].

[14] W. D. Matthew: Climate and Evolution (2nd edit.), *Special Publs. New York Acad. of Sci.*, Vol. 1, 1939.

GEOMORPHIC BARRIERS AND AVENUES

Much has been written on problems connected with land mammals and past distributions of land and sea. In a consideration of the pinnipeds the same problems must be faced, but from the opposite direction. Here the primary concern is with the existence or nonexistence of seaways between the Arctic and the North Pacific, between the Arctic and the North Atlantic, and between the Caribbean and the East Pacific. Studies in the geography of land animals have been concerned with the existence of land bridges across these seaways and obviously have an important bearing on the question.

There is general agreement that the two Americas were separated almost continuously from the middle Paleocene to the late Pliocene, and during this time there must have been virtually no obstacle to migration between the Caribbean and the East Pacific.

Simpson[15] has examined in detail paleomammalogical evidence for the existence of a land bridge between North America and Asia and between North America and Europe during the Cenozoic. A transatlantic land bridge may have existed in the Eocene, and possibly even in the Oligocene, but Simpson could find no supporting evidence. The problem remains open, but it seems unlikely that there was any continuous barrier between the Arctic Sea and the North Atlantic at these times. Considerable marine deposition took place throughout Europe during the early Tertiary, and there must have been seas separating Western Europe from the main Eurasian land mass and joining the northern seas with the Tethyan Mediterranean. Ekman[16] mentions a probable connection (Obik) between the Tethys Sea and the Arctic Sea in the Eocene.

Regarding the North American–Asian bridge across present-day Bering Strait, Simpson reaches fairly firm conclusions from the degree of interchange of land-mammal faunas between the two continents. The evidence suggests that there was a land bridge continually, if not continuously, throughout the Tertiary except about the middle Eocene and the middle to late Oligocene. There may also have been a shorter break during the early Pliocene. From this it may be deduced that interchange of sea faunas would have been pronounced at these three times, but it would be wrong to infer that it did not take place at other times. It seems fairly clear that in the million years or so

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[15] G. G. Simpson: Holarctic Mammalian Faunas and Continental Relationships during the Cenozoic, *Bull. Geol. Soc. of America,* Vol. 58, 1947, pp. 613–687.

[16] Sven Ekman: Zoogeography of the Sea (translated from the Swedish by Elizabeth Palmer; London, 1953), p. 96.

of the Pleistocene there was interchange of seal populations through Bering Strait, even though important movements of land mammals took place across it. It is reasonably certain that there was a series of sea-level fluctuations, though Simpson believes the land connection must have been constant in the early Pleistocene, when most of the land movements took place. To a great extent the Pleistocene epoch was exceptional. The rapid fluctuations in sea level that took place then were related to the expansion and contraction of glacier ice, and no reason is known why there should have been similar relatively rapid fluctuations in earlier epochs. The most that can be assumed is that the middle Eocene, the middle and late Oligocene, and perhaps the early Pliocene were times of exceptionally easy movement between the Arctic and the North Pacific. Movements at other times would not have been precluded, but there would have been much less time for them to occur, and they are therefore less likely.

CLIMATIC BARRIERS AND AVENUES

Climatic barriers, though less tangible and potentially less difficult to overcome, are none the less real. If the hypothesis that the pinnipeds have always been cold-water forms is allowed, it follows that the major climatic barrier to their spread would be high sea temperatures. Evidence regarding Cenozoic sea-surface temperatures in the North Pacific has been summarized by Durham.[17] There seems to be no such convenient and documented summary for the North Atlantic, but the general history of its marine fauna during the Cenozoic is outlined by Ekman.[18] Durham's summary shows that in the Eocene the cold-water environment in the North Pacific was of small extent and the February surface isotherm of 20° C. lay somewhere between 50° and 60° N. The August 20° C. isotherm would have been even farther north. During succeeding epochs there was a gradual southward movement of isotherms, so that the cold-water environment expanded progressively until the early Pliocene. There was then a small northward movement, followed by increasing cooling in the Pleistocene.

A similar progressive cooling of the seas took place in the North Atlantic. The tropical faunas of the Eocene gave way to subtropical faunas in the Oligocene, and these in turn were replaced in a mass invasion of northern forms at the beginning of the Miocene. The climatic deterioration extended

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[17] J. W. Durham: Cenozoic Marine Climates of the Pacific Coast, *Bull. Geol. Soc. of America*, Vol. 61, 1950, pp. 1243–1263.

[18] *Op. cit.* [see footnote 16 above].

to the West Indian region, where, according to Ekman,[19] Caribbean temperature "seems to have sunk from 26–27° C. to 19–20°." During the Pliocene, temperatures recovered and tropical faunas reappeared in the West Indies. A similar deterioration and recovery occurred in the Mediterranean region but not to so marked a degree.

Much less is known about fluctuations in sea temperatures in the Southern Hemisphere. The most significant feature here is the corridor formed by the Peru Current, which brings cold water almost to the equator. There is no reason for believing that it was much less effective through the latter half of the Cenozoic at least, and there is clear evidence in the distribution of existing genera and species that the current has served as a route for pinniped migration on at least two occasions.

The conclusions to be drawn from this summary of climatic barriers and avenues are as follows. The cold-water environment, defined for present purposes as that where surface temperature does not exceed 20° C., was of small extent in the Eocene and was virtually limited in the north to the Arctic Basin. In the Oligocene and Miocene it spread considerably, so that by the end of the Miocene it extended south to California and to the Caribbean. Since the Central American isthmus did not exist at this time, there was no land barrier between the cold Caribbean and the cold west-coast waters of South America. There were thus two cold-water routes available, one from the North Atlantic via the Caribbean to Peruvian waters, the other from the North Pacific along the west coasts of the two Americas. Toward the end of the Pliocene, the route from the Atlantic disappeared because of the reinvasion of the Caribbean by tropical waters and the closing of the isthmus. However, the availability of the Pacific route depended only on sea temperatures, and it became usable again on several occasions during the Pleistocene.

FAMILY BEGINNINGS

Despite suggestions to the contrary, it seems unlikely that the pinniped families are of separate origin. There is general agreement that seals diverged from sea lions and walruses at a very early stage and that the split into the latter two families occurred later. The walruses are, in fact, little more than highly specialized sea lions. In all three families the limbs are used for swimming and the tail is vestigial. This suggests that they are descended from an ancestral form in which the tail was too short to develop into an organ of

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[19] *Ibid.*, p. 71.

propulsion, whereas in all other aquatic mammals it is used, in a varying degree, as propeller or rudder or both. The physiological researches of Howell[20] strongly suggest that, doglike, the original pinnipeds used both fore and hind limbs in swimming but that subsequently they split into two groups, one ancestral to the seals, in which use of the hind limbs came to predominate, the other ancestral to the sea lions and walruses, in which the fore limbs were used more and more. All the evidence of present and past distributions points to the Bering land barrier as the place where this split occurred; for no sea lions, either fossil or existing, are known from the Arctic and the North Atlantic, and the only seals reliably recorded from the North Pacific are living forms derived during the Pleistocene from the Arctic and the North Atlantic. If the original split did take place at the Bering barrier, it would have been necessary for the ancestral population to spread from the Arctic to the North Pacific at a time when the barrier was nonexistent, for the barrier to reappear, splitting the population into two, and for it to remain in existence long enough to prevent further contact and interbreeding between the two groups.

The split between sea-lion and walrus ancestors followed after an interval long enough for the Pacific group to acquire the considerable number of characters common to both families. This time, population movement was reversed, and a more northern, bottom-feeding group took advantage of another sinking of the Bering bridge to spread back into the Arctic. A subsequent re-emergence of the land or increasing ecological specialization then cut this group off for an indefinite period, so that it evolved independently into the later walruses, which before the Pleistocene are known only from the Arctic and the North Atlantic.

It is immediately evident that this picture of family origins fits readily into the history of the Bering bridge as deduced by Simpson. The break in the middle Eocene could have been that required for the spread of the original population between Arctic and Pacific. It was followed, according to Simpson, by a strong land connection in the late Eocene and the early Oligocene, which would have allowed time for characters common to sea lions and walruses to develop in the Pacific group, and then by a break in the middle Oligocene, which would have permitted walrus ancestors to move back into the Arctic. However, the bridge did not close strongly again until the early, or perhaps even the middle, Miocene, so that continued separation of ancestral

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[20] A. B. Howell: Contribution to the Comparative Anatomy of the Eared and Earless Seals (Genera *Zalophus* and *Phoca*), *Proc. U. S. Natl. Museum*, Vol. 73, 1928, pp. 1–142.

walruses would be attributable to their increasing adaptation to life in shallow, northern waters. *Prorosmarus,* the earliest known walrus, appears in the upper Miocene of Atlantic North America.

Such a timetable would necessitate a slightly earlier origin for the pinnipeds than might be favored by most, but this seems no insuperable obstacle. A long interval need not have occurred between the first entry into the marine environment and the spread from Arctic to Pacific; an early canoid fissiped ancestry is not incompatible with the sequence of events postulated above.

The Sea Lions (Otariidae)

The earliest sea lions were found in the lower Miocene of Oregon and California. According to the hypothesis of generally continuous association between pinnipeds and cold water, this would be expected, since it was in the Miocene that the requisite low sea temperatures reached California. That pinnipeds are absent from Paleogene formations in California, Oregon, and Washington is not surprising; for if the hypothesis is correct, we can expect to find sea-lion forms older than the extinct *Allodesmus* and *Desmatophoca,* not in the United States, but in Eocene and Oligocene marine deposits of Canada and Alaska. Unfortunately, such deposits are rare and have been little worked.

The cold-water environment spread southward until by the end of the Miocene or the early Pliocene it had reached its greatest extent. By this time a large number of sea-lion types had arisen in the North Pacific; in addition to *Allodesmus* and *Desmatophoca,* the genera *Neotherium, Pithanotaria, Dusignathus, Pontolis, Atopotarus,* and *Pliopedia* have been named. All are now extinct. By this time too the East Pacific cold-water route to the Southern Hemisphere was available. The population groups that spread along this avenue were ancestral to the present-day southern sea lion, *Otaria,* the Australian sea lion, *Neophoca,* and the southern fur seal, *Arctocephalus;* and the earliest known southern member of the family comes from the Pliocene beds of the Paraná in Argentina.[21] It is possible that *Otaria* is derived from the same stock as the northern sea lion, *Eumetopias,* and that *Neophoca* is related to the California sea lion, *Zalophus; Arctocephalus* is usually linked with the northern fur seal, *Callorhinus.* The probable lines of spread of the ancestral forms are well shown by the distribution of the present-day sea lions illustrated in Figure 2. All fossil sea lions have been found within the regions inhabited by existing forms.

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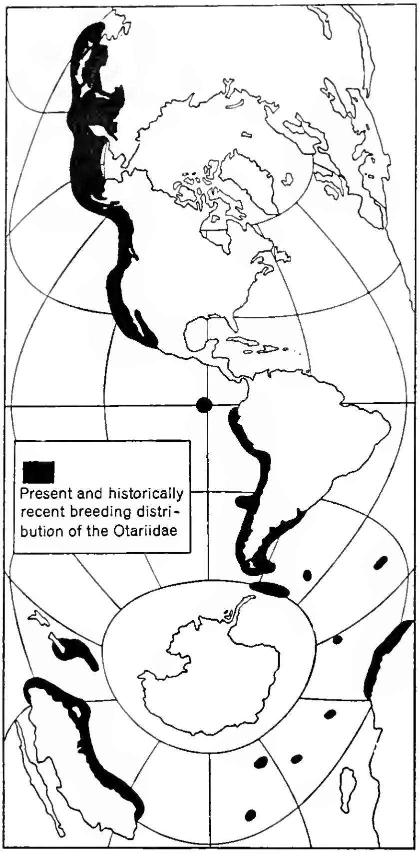
[21] These deposits are listed as Miocene in Kellogg, *op. cit.* [see footnote 6 above], but are now believed to be of Pliocene age and are listed as such in Simpson, The Principles of Classification . . . of Mammals [see footnote 1 above].



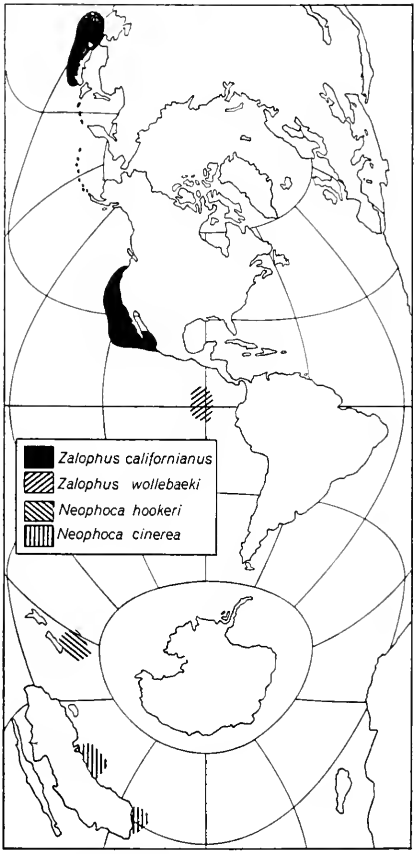
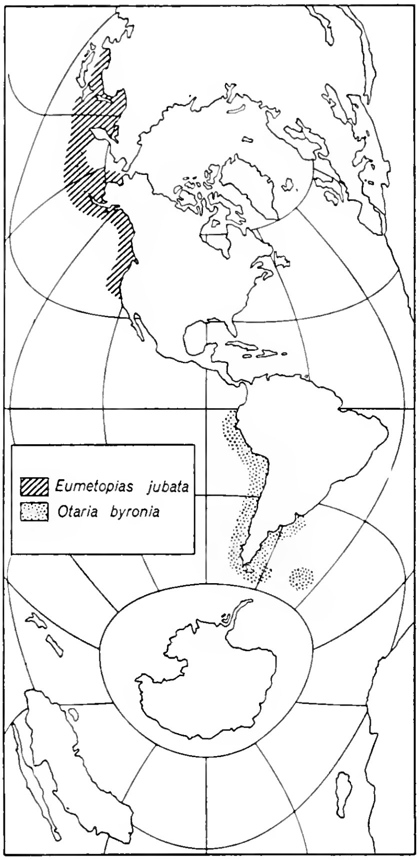


FIG. 2—Distribution of the sea lions (family Otariidae).
FIG. 3—Distribution of the sea-lion genera *Zalophus* and *Neophoca*.

When distributions are examined at the generic instead of the family level, it becomes clear that the East Pacific cold-water route has been used on several occasions; for the species that today occupy sections of this route are not derived from the original populations that spread southward but from newer groups that spread both southward and northward along the route on later occasions. These later occasions can almost certainly be equated with the glacial ages of the Pleistocene. Renewed spread from the north is suggested by the genus *Zalophus,* represented by the California sea lion, which is found as far south as the Tres Marías Islands off the Mexican coast, and by its close relative *Zalophus wollebaeki* of the Galápagos (Fig. 3). Renewed spread from the south is suggested by the distribution of the southern sea lion, *Otaria,* which has spread northward as far as northern Peru (Fig. 4).

The distribution of the southern fur seal, *Arctocephalus,* is particularly



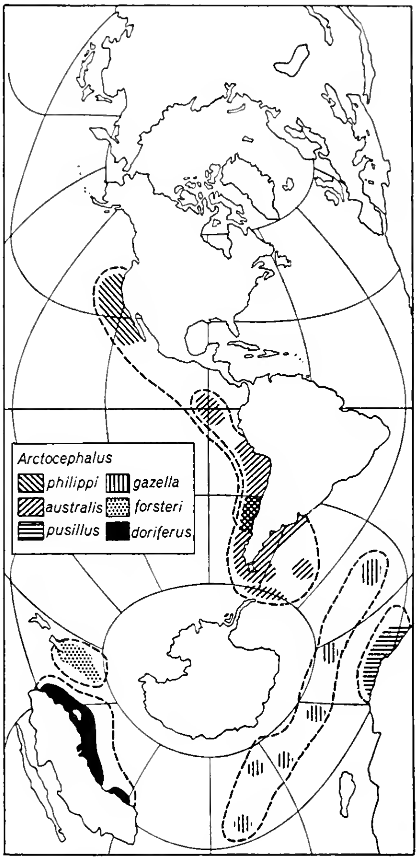


FIG. 4—Distribution of the sea-lion genera *Eumetopias* and *Otaria*.
FIG. 5—Distribution of the southern fur seals, *Arctocephalus*.

interesting, since it indicates at least three transequatorial population movements (Fig. 5). The genus itself is derived by evolution in the Southern Hemisphere from an ancestral stock that spread southward at the time of general movement of the sea-lion family, which is here assigned to the late Miocene or the early Pliocene. It has spread successfully throughout the temperate Southern Hemisphere and has given rise to a series of allopatric species that are a bone of contention among taxonomists. But according to a recent study by King[22] the East Pacific cold-water corridor is inhabited by two species, the ranges of which overlap considerably. They are both recorded from Juan Fernández, off Chile. There seems little doubt that these two sympatric species, *A. philippi* and *A. australis*, are the result of two

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[22] J. E. King: The Otariid Seals of the Pacific Coast of America, *Bull. Brit. Museum* (*Nat. Hist.*): *Zoology*, Vol. 2, 1954, pp. 311–337.

separate movements along the cold-water route. During a glacial age of the Pleistocene an *Arctocephalus* population spread northward to California; during the subsequent interglacial it became cut off and had an opportunity to evolve independently into the *A. philippi* group. In a subsequent glacial it spread south again, while at the same time the main *A. australis* population of South America once more moved north. The two now overlap and presumably have diverged sufficiently to enable them to remain distinct species.

The Walruses (Odobenidae)

Early walruses, *Prorosmarus, Alachtherium,* and *Trichecodon,* were apparently restricted to the North Atlantic, but the fact that they came of an ancestry shared by the sea lions implies that the walruses as a whole originated in the North Pacific or at least in the vicinity of Bering Strait. They first appear in upper Miocene beds of eastern North America, and their gravitation across the Arctic and into the North Atlantic was part of a general movement of marine animals in this direction in mid-Tertiary time that is correlated with a southward expansion of the cold-water habitat. According to Ekman,[23] a considerable part of the North Atlantic Boreal fauna was derived from the North Pacific about this time. The present walrus, *Odobenus,* is also essentially Arctic–North Atlantic in distribution, and its entry into the Bering Sea is almost certainly of Pleistocene date. The distribution of *Odobenus* has been discussed and mapped in an earlier paper.[24]

The Seals (Phocidae)

The Phocidae are the most diverse and well distributed of the pinniped families (Fig. 6), and the members are best adapted to marine life. Ancestral seals were separated from the sea lion–walrus stock at a very early stage, and the initial development of the family undoubtedly took place in the Arctic–North Atlantic region. By the middle Miocene, when the fossil record begins, at least five genera had made their appearance, and two of the present subfamilies, the Phocinae and the Monachinae, were distinguishable. The existing genus *Phoca* was also recognizable. Here, as in the North Pacific, the coincidence is found between the southward extension of the cold-water environment and the sudden appearance of pinnipeds in fossil beds, and here the negative fossil record can be quoted with greater confidence; for the marine Paleogene beds of Europe are much more extensive and better worked

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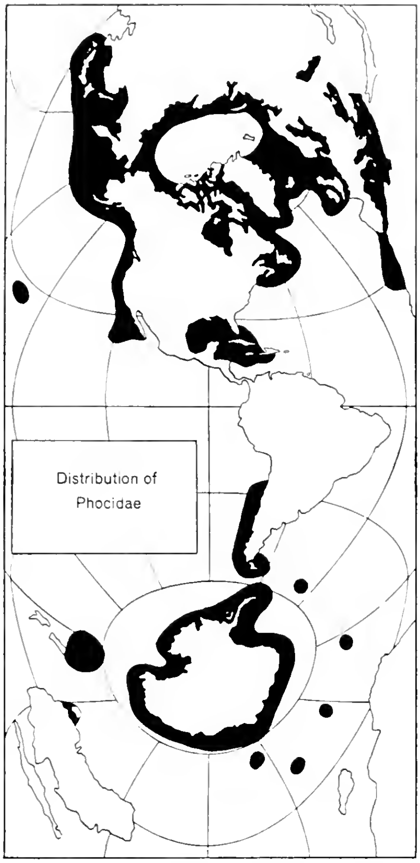
[23] *Op. cit.* [see footnote 16 above], p. 159.

[24] Davies, *op. cit.* [see footnote 4 above].



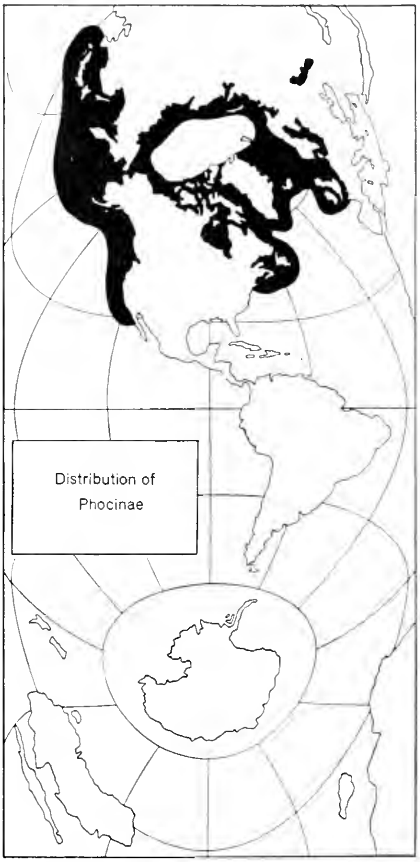


FIG. 6—Distribution of the seals (family Phocidae).
FIG. 7—Distribution of the northern seals (subfamily Phocinae).

than those of North America. There is even more reason, then, for the conclusion that both seals and walruses were confined to the Arctic until the Miocene, when they moved south into the North Atlantic. This southward movement to occupy an expanding environment would have been accompanied by a marked multiplication of forms and of numbers, which would explain the comparative variety of genera and species named from the Miocene and Pliocene of Europe. By the end of the Miocene, three major groups, which today are named as subfamilies, had formed; a fourth subfamily is named from the Pliocene.

THE NORTHERN SEALS (PHOCINAE)

The subfamily Phocinae must always have been the northernmost seal group, since it alone has succeeded in invading the North Pacific across the Arctic and, unlike the other groups, it has no Southern Hemisphere representative. The fossil genera, *Miophoca, Leptophoca, Prophoca, Callophoca, Gryphoca, Platyphoca,* and *Phocanella,* have been described from North Atlantic shores, and the existing genera, *Phoca, Erignathus,* and *Halichoerus,* are North Atlantic and Arctic in distribution, though the first two have recently separated representatives in the North Pacific (Fig. 7).

THE MONK SEALS (MONACHINAE)

The monk seals were well represented in Miocene and Pliocene European waters by species of such now extinct genera as *Monotherium, Paleophoca,* and *Pristiphoca.* The group seems to have been in the van of phocid expansion southward and later in its history to have been particularly characteristic of the Tethyan Mediterranean. Only the ancestors of the present-day *Monachus* survived the constriction and rewarming of the Mediterranean toward the end of the Pliocene, a feat they doubtless accomplished by adapting themselves to the warmer environment. Thus arose the one major exception to the rule of association between pinnipeds and cold water. Indeed, *Monachus* was so successful that, at a time when the Mediterranean was open to the west, it was able to spread across the Atlantic to the Caribbean and enter the Pacific shortly before the Central American isthmus closed toward the end of the Pliocene. Subsequently, the Pacific population was able to spread to the Hawaiian Islands (Fig. 8). There is some possibility that the spread from Caribbean to Pacific took place in the Pleistocene rather than the Pliocene. King,[25] in a recent discussion of the monk seals, points to many characters in which the Caribbean *tropicalis* population is much closer to the Hawaiian *schauinslandi* population than to the Mediterranean *monachus* population. In fact, *schauinslandi* and *tropicalis* appear to be so close anatomically that by analogy with other species it seems doubtful whether they could have been separated since the Pliocene. To meet this objection, King suggests an overland migration across Panama in the Pleistocene, but this seems even more doubtful, and if the transisthmian spread did take place at that time, it is more probably related to a high sea-level stage during an interglacial. However, there seems to be no other evidence to substantiate such a possibility. The *Monachus* westward spread seems to have been an isothermal one, taking place along the northern fringe of tropical waters.

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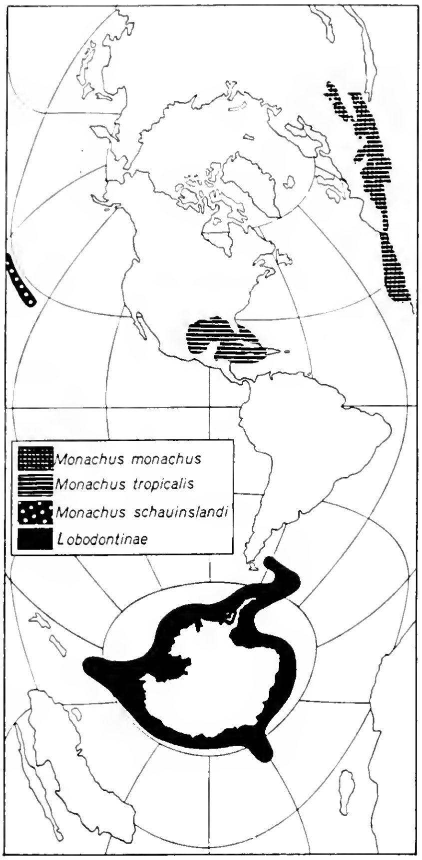
[25] J. E. King: The Monk Seals (Genus *Monachus*), *Bull. Brit. Museum (Nat. Hist.): Zoology,* Vol. 3, 1956, pp. 203–256.



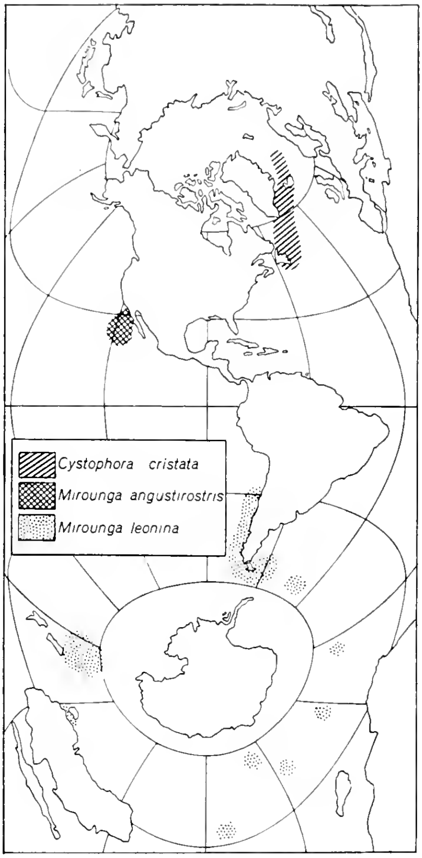


FIG. 8—Distribution of the monk seals and Antarctic seals (subfamilies Monachinae and Lobodontinae).

FIG. 9—Distribution of the bladdernosed seals (subfamily Cystophorinae).

THE ANTARCTIC SEALS (LOBODONTINAE)

The Antarctic seals (Fig. 8) comprise four species, each of which has been placed in a separate genus, though they are probably derived by adaptive radiation from one group. The Weddell seal, *Leptonychotes weddelli,* lives farther south than any other mammal; it keeps breathing holes in the ice and feeds principally on fish and squid. The crabeater seal, *Lobodon carcinophaga,* lives along the edge of the pack ice and feeds on pelagic crustaceans. The leopard seal, *Hydrurga leptonyx,* ranges from the ice edge northward to the subantarctic islands and feeds on fish, penguins, and young seals. The Ross seal, *Ommatophoca rossi,* is little known but seems to be a deep diver, feeding mainly on squid. The four species are thus to some extent separated geographically, and they occupy distinct ecological niches. Their evolutionary divergence has an analogy in the rapid development of the many forms of Australian marsupials from a possible common ancestor that found itself in a continent unpopulated by other mammals. In the case of the Antarctic seals, the nature of this common ancestor can only be inferred from a consideration of anatomical relationships.

In her study of the monk seals, King points to many relationships between the Antarctic seals and the monk seals. There is little doubt that the two groups are much more closely related than either is to any other group. In fact, a few taxonomists include them both in the subfamily Monachinae. The inference to be drawn from this is that the Antarctic seals were derived from a group of ancestral monk seals that spread southward to the Caribbean at the time of sea-water cooling in the Miocene and took advantage of the absence of the isthmian barrier to enter the East Pacific cold-water route to the south. Unfortunately, only one fossil find can be called in evidence on this question of Lobodontinae antecedents. A mandible and some teeth found in late Miocene or early Pliocene beds in Argentina were given the name of *Prionodelphis rovereti* and were later found to belong to a seal. Of these, Kellogg[26] says: "The ornamentation and general configuration of the crowns of these teeth are not unlike those of corresponding teeth of the Recent West Indian Seal, *Monachus tropicalis*. Teeth of this type conceivably might also represent a stage ancestral to that of the Recent Antarctic Weddell seal, *Leptonychotes weddelli*."

THE BLADDERNOSED SEALS (CYSTOPHORINAE)

The bladdernosed seals form much the smallest seal subfamily, being represented only by *Mesotaria* from the Pliocene of Europe and by the living hooded seal, *Cystophora*, of the North Atlantic and the elephant seal, *Mirounga*, of the East Pacific and Subantarctic (Fig. 9). Their derivation from the main seal stock implies origin in the North Atlantic, a conclusion supported by the presence of *Cystophora* and *Mesotaria* in this region. Invasion of the Southern Hemisphere would then have been roughly contemporary with that by the ancestors of the Antarctic seals and would have followed the same Caribbean–East Pacific route. The elephant seals arose subsequently in the Southern Hemisphere, where the existing species, *leonina*, has succeeded in colonizing most of the anti-Boreal zone. It has also reinvaded the Northern

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[26] Remington Kellogg: Tertiary, Quaternary, and Recent Marine Mammals of South America and the West Indies, *Proc. Eighth Amer. Sci. Congr., Washington, 1940*, Vol. 3, Washington, 1942, pp. 445–473; reference on p. 453.

Hemisphere by retracing the ancestral route of dispersal along the west coast of South America. But this later spread must have taken place in a Pleistocene glacial age, and by this time the door into the Caribbean was closed, with the result that the product of the expansion, the group known as *Mirounga angustirostris,* is found in the Lower California region, having been cut off from the main elephant-seal population by the rewarming of the seas.

Rates of Evolution

The postulation that pinnipeds did not enter the Southern Hemisphere until the late Miocene or the early Pliocene will probably meet with the objection that this provides too little time for southern forms to have developed to the extent that they have. But uneven rates of evolution are as marked in the pinnipeds as in other groups of mammals. The existence of clearly defined seals, sea lions, and walruses by the Miocene has long inhibited zoologists from placing the date of pinniped origin as late as might seem desirable on other grounds. It is even more notable that seals of the modern genus *Phoca,* and only slightly distinguishable from the modern species *Phoca vitulina,* are recorded from the Miocene. The evidence, although small in bulk, clearly shows that there was comparatively rapid evolution up to the Miocene but that since then rates have been extremely slow, at least in the Northern Hemisphere.

The general hypothesis of pinniped origin and dispersal advanced here seems to provide a satisfactory explanation for this change in the evolutionary tempo. From what is known or inferred about the evolutionary processes, rates would have been rapid in the early stages when the ancestral pinnipeds were first entering the new marine environment. Equally, the expansion of the cold-water environment from the late Eocene through the Oligocene and Miocene would also have provided conditions for rapid evolution, bringing, as it must have done, great increases in population numbers and in varieties of habitats. But by the end of the Miocene the expansion had come to a halt: all available regions had presumably been occupied and most readily utilized habitats exploited. The one major exception was the Southern Hemisphere. The seal and sea-lion groups that entered southern waters discovered a whole new cold-water environment in which they were able to multiply enormously and to occupy a variety of habitats. A second golden age of pinniped evolution dawned, but one that has lasted a much shorter time than that of the Paleogene in the Northern Hemisphere. As a result, differentiation in the south has reached the generic stage only.

Regional Geography of the Pinnipeds

Sclater[27] proposed marine zoogeographical regions based on the distribution of marine mammals, and Von Boetticher[28] re-examined them with reference to the distribution of the pinnipeds. The usefulness of these regional definitions may be doubted, but it is worth while to review them here in order to summarize some of the conclusions reached in the present study. Figure 10 shows Sclater's regions somewhat modified.

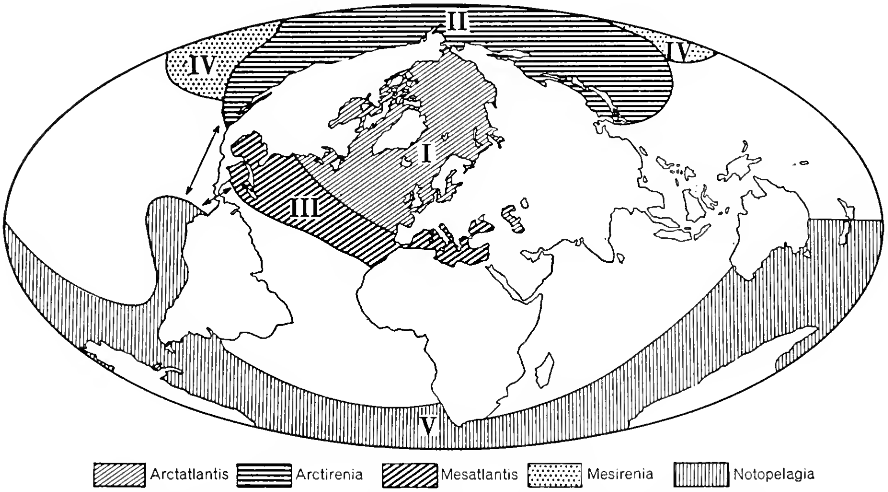

Fig. 10—Pinniped regions: I, Arctatlantis; II, Arctirenia; III, Mesatlantis; IV, Mesirenia; V, Notopelagia. The arrows indicate the two major dispersal routes between the Northern and Southern Hemispheres.

I. *Arctatlantis* extends from Bering Strait across the Arctic to about the August sea-surface isotherm of 20° C. It is the region of development of the seals and walruses, and there is no evidence that the sea lions have ever penetrated it. It is characterized today by the presence of *Halichoerus* and *Cystophora,* which are endemic, and by *Phoca, Erignathus,* and *Odobenus,* which were probably endemic until the Pleistocene.

II. *Arctirenia* extends from Bering Strait south to about the August sea-surface isotherm of 20° C. Here the sea lions developed and still have their headquarters. The walruses must have originated in the extreme north of Arctirenia but early moved into Arctatlantis. Both seals and walruses spread into the northern section of Arctirenia during the Pleistocene; earlier in-

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[27] *Op. cit.* [see footnote 3 above].

[28] *Op. cit.* [see footnote 2 above].

cursions may have occurred but left no trace. The region is characterized by the presence of *Callorhinus* and *Eumetopias,* which are endemic, and by *Zalophus,* which would be endemic if it had not spread to the Galápagos. Comparatively recently, *Phoca, Erignathus,* and *Odobenus* entered from the Arctic and *Arctocephalus* and *Mirounga* spread into the extreme southeast off Lower California.

III. *Mesatlantis* comprises the Mediterranean and Caribbean Seas.

IV. *Mesirenia* consists of the seas around the Hawaiian Islands. Regions III and IV are the home of the relic genus *Monachus,* the only surviving monk seal, which is endemic and the only form that occurs here.

V. *Notopelagia* extends from Antarctica northward to about the February sea-surface isotherm of 20° C. and thus includes the Southern Ocean and the coastal waters of Chile and Peru. All forms—*Lobodon, Ommatophoca, Leptonychotes, Hydrurga, Mirounga, Otaria, Neophoca,* and *Arctocephalus*—are endemic except that *Mirounga* and *Arctocephalus* have partly invaded Arctirenia. All have evolved in the Southern Hemisphere from ancestral groups derived from the north.

A Numerical Analysis of the Distributional Patterns of North American Mammals. II. Re-evaluation of the Provinces

EDWIN M. HAGMEIER

Abstract

In an earlier paper, numerical techniques were developed and used to analyze distribution patterns of the native terrestrial mammals of North America. An error in method is here corrected, indicating that 35 provinces, 13 superprovinces, four subregions, and one region may be recognized. The methods used are relatively objective, quantitative, and suited to computerization.

Introduction

In an earlier paper (Hagmeier and Stults, 1964, hereafter referred to as H & S), quantitative and relatively objective methods were used to demonstrate that (1) the range limits of North American terrestrial mammals are grouped, (2) that as a result it was possible to delimit geographic regions of faunistic homogeneity which were termed mammal provinces, and (3) that such provinces could be useful in the analysis of other zoogeographic phenomena.

This paper is concerned with the recalculation of some of the data of the second item above. It was assumed in our earlier paper (H & S) that several of the large provinces of the northern half of the continent required further analysis. On initiation of this analysis, it became apparent that an error in method had been made which required correction. As a consequence of the correction, the number of North American mammal provinces is here increased from 22 to 35, two of which are of uncertain status.

The general philosophy, methodology, and conclusions reached in our earlier paper (H & S) do not differ from those arrived at here, and the earlier paper should be referred to for accounts of these. The material given here, since it is essentially revisionary, is presented in as brief a form as possible. Because of the changes reported here, the analysis of mammal areas given in H & S (p. 141–146 and Figs. 6c–8d) needs revision, and this revision will form the subject of a future paper. Since submission of our earlier paper (H & S), Simpson (1964) has considered variation in abundance of species of North American mammals in a superior manner, and his work should be referred to for a treatment of the subject.

Derivation of Provinces

In our earlier paper (H & S), the ranges of all 242 species of native terrestrial North American mammals were converted into a model, first by separately computing the percentage of species and genera whose ranges ended within blocks 50 miles by 50 miles throughout the continent (each such value was called Index of Faunistic Change, or IFC), second by plotting species and genus IFCs on maps of North America, and third by fitting isarithms. The species IFC map resulting was given as H & S, Figure 1. Low IFC values indicated faunistic homogeneity, and regions characterized by such values were termed primary areas.

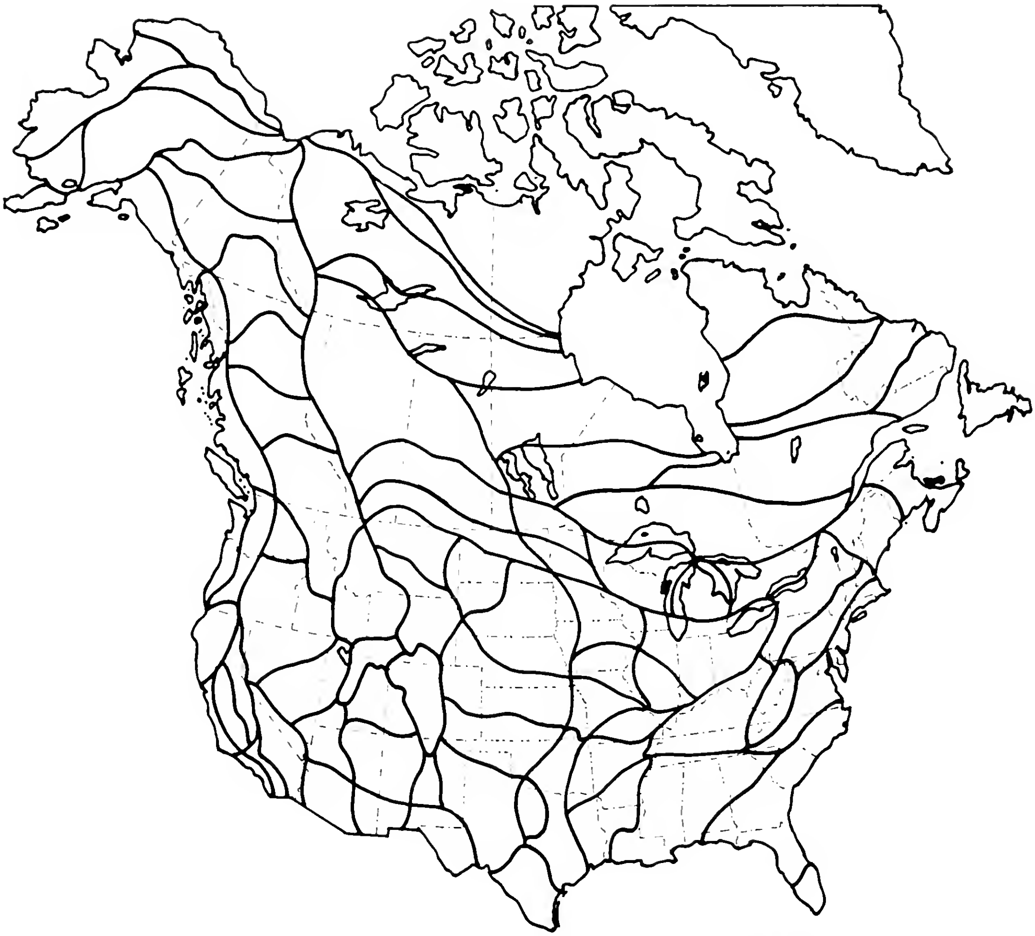


FIG. 1. Eighty-six primary areas derived through examination of IFC Map (H & S, Fig. 1).

Twenty-four of these were identified through examination of IFC maps of both species and genus and species checklists of each were prepared (H & S, Table 2). The percentage of species common to all combinations of pairs of provinces (Coefficients of Community, or CCs, Jaccard, 1902) were then computed. CCs were then subjected to cluster analysis using the weighted pair-group method, and simple averages (Sokal and Sneath, 1963:180–184, 304–312; H & S: 132, 137), and drawn up in the form of a dendrogram (H & S, Fig. 5). Primary areas pooled at a mean CC level lower than 62.5% were termed mammal provinces, those pooling at below 39% were termed mammal superprovinces, those below 22.5%, mammal subregions, those below 8% as mammal regions.

The basis of our error lay in the fact that we attempted to identify only the 24 North American mammal areas corresponding to those described by Kendeigh (1961) in his modification of Dice's (1943) scheme of biotic provinces. This error became apparent only when subsequent analysis of parts of certain of these provinces showed that the parts in some cases merited full province status.

The correction made and reported here

TABLE 1.

	1 Ungavan	2E E. Eskimoan	2W W. Eskimoan	3 Alaskan	4 Aleutian	5 Yukonian	6W W. Hudsonian	6E E. Hudsonian	7E E. Canadian	7W W. Canadian	8 Montanian	9 Coloradan	10 Vancouverian	11 Oregonian	12 Humboldtian	13 Sierran	14 Alleghanian	15 Illinoian	16 Carolinian	17 Kansan	18 Saskatchewanian	19 Balconian	20 Tamaulipan	21 Texan	22 Louisianian	23 Columbian	24 Artemisian	25 Kaibabian	26 Sonoran	27 Yaquinian	28 Mapimian	29 Navahonian	30 Uintian	31 San Matean	32 Mohavian	33 Californian	34 Diablian	35 San Bernardinian
Didelphis marsupialis																	×	×	×	×		×	×	×	×													
Sorex cinereus		×	×	×	×	×	×	×	×	×	×	×	×			×	×	×			×																	
S. longirostris																			×						×													
S. vagrans				×	×	×					×	×	×	×	×	×										×				×		×	×	×		×	×	×
S. nanus												×																					×					
S. palustris									×	×	×	×	×	×		×	×									×							×					
S. bendirei														×	×																							
S. fumeus																	×																					
S. arcticus			×	×	×	×			×	×																												
S. dispar																	×																					
S. trowbridgei														×	×	×																					×	
S. merriami												×									×					×	×	×				×	×	×				
Microsorex hoyi	×					×	×	×	×	×	×						×																					
Blarina brevicauda									×								×	×	×	×					×													
Cryptotis parva																		×	×	×			×	×	×													
Notiosorex crawfordi																		×				×	×					×	×	×	×	×		×	×			×
Neurotrichus gibbsii														×	×																							
Scapanus orarius														×	×																							
S. latimanus															×	×																					×	×
S. townsendii														×																								
Parascalops breweri																	×																					
Scalopus aquaticus																		×	×	×			×	×	×													
Condylura cristata									×								×																					
Dasypus novemcinctus																						×	×	×														
Ochotona collaris						×																																
O. princeps											×	×		×		×																						
Sylvilagus idahoensis																										×	×											
S. bachmani														×	×	×																					×	×
S. palustris																									×													
S. floridanus																	×	×	×	×		×	×	×	×			×	×		×			×				
S. transitionalis																	×																					
S. nuttallii												×				×					×					×	×					×	×					
S. audubonii																×				×	×	×	×				×	×	×	×	×	×	×		×	×	×	×
S. aquaticus																								×	×													

TABLE 1. (*Continued.*)

	1 Ungavan	2E E. Eskimoan	2W W. Eskimoan	3 Alaskan	4 Aleutian	5 Yukonian	6W W. Hudsonian	6E E. Hudsonian	7E E. Canadian	7W W. Canadian	8 Montanian	9 Coloradan	10 Vancouverian	11 Oregonian	12 Humboldtian	13 Sierran	14 Alleghanian	15 Illinoian	16 Carolinian	17 Kansan	18 Saskatchewanian	19 Balconian	20 Tamaulipan	21 Texan	22 Louisianian	23 Columbian	24 Artemesian	25 Kaibabian	26 Sonoran	27 Yaquinian	28 Mapimian	29 Navahonian	30 Uintian	31 San Matean	32 Mohavian	33 Californian	34 Diablian	35 San Bernardinian
Lepus americanus				×		×	×	×	×	×	×	×	×	×		×	×																					
L. arcticus	×	×	×	×	×		×	×																														
L. townsendii												×				×				×	×					×	×						×					
L. californicus															×	×				×		×	×	×		×	×	×	×	×	×	×	×	×	×	×	×	×
L. gaillardi																														×								
L. alleni																													×									
Aplodontia rufa														×	×	×																						
Tamias striatus									×								×	×	×																			
Eutamias alpinus																×																						
E. minimus										×		×				×					×					×	×						×	×				
E. amoenus											×			×	×	×										×												
E. townsendii														×	×	×																						
E. sonomae															×																							
E. merriami																×																					×	×
E. dorsalis																											×	×		×		×						
E. quadrivittatus																																×	×	×				
E. ruficaudus											×																											
E. cinereicollis																																×		×				
E. quadrimaculatus																×																						
E. speciosus																×																						
E. panamintinus																																			×			
E. umbrinus												×														×							×					
Marmota monax						×		×	×	×	×						×	×						×														
M. flaviventris												×				×										×												
M. caligata						×					×		×																									
Ammospermophilus harrisii																												×	×									
A. leucurus																											×				×	×	×	×	×			
Spermophilus townsendii																										×	×											
S. richardsonii												×									×																	
S. armatus												×																										
S. beldingi																×										×												
S. columbianus											×																											
S. undulatus		×	×	×	×	×				×																												
S. tridecemlineatus												×						×		×	×			×										×				

TABLE 1. (*Continued.*)

	Ungavan 1	E. Eskimoan 2E	W. Eskimoan 2W	Alaskan 3	Aleutian 4	Yukonian 5	W. Hudsonian 6W	E. Hudsonian 6E	E. Canadian 7E	W. Canadian 7W	Montanian 8	Coloradan 9	Vancouverian 10	Oregonian 11	Humboldtian 12	Sierran 13	Alleghanian 14	Illinoian 15	Carolinian 16	Kansan 17	Saskatchewanian 18	Balconian 19	Tamaulipan 20	Texan 21	Louisianian 22	Columbian 23	Artemesian 24	Kaibabian 25	Sonoran 26	Yaquinian 27	Mapimian 28	Navahonian 29	Uintian 30	San Matean 31	Mohavian 32	Californian 33	Diablian 34	San Bernardinian 35
S. mexicanus																						×	×								×							
S. spilosoma																				×		×	×							×	×	×		×				
S. franklinii																		×		×																		
S. variegatus																						×					×	×	×	×	×	×	×	×				
S. beecheyi														×	×	×																				×	×	×
S. tereticaudus																													×						×			×
S. mohavensis																																				×		
S. lateralis											×	×			×											×	×					×			×			
Cynomys ludovicianus																				×	×	×								×	×			×				
C. leucurus												×																					×					
C. parvidens																											×											
C. gunnisoni																																×		×				
Sciurus carolinensis																	×	×	×					×	×													
S. griseus														×	×	×																				×	×	
S. aberti												×																×				×						
S. niger																	×	×	×	×			×	×	×													
S. apache																														×								
S. arizonensis																														×		×						
Tamiasciurus hudsonicus				×		×	×	×	×	×	×	×	×				×	×														×	×	×				
T. douglasii														×	×	×																						
Glaucomys volans																	×	×	×					×	×													
G. sabrinus						×			×	×	×	×	×	×	×	×	×																					
Thomomys umbrinus															×	×											×	×		×	×	×	×	×	×	×	×	×
T. talpoides												×		×							×					×							×					
T. bulbivorus														×																								
Geomys bursarius																		×		×		×		×														
G. arenarius																															×							
G. personatus																							×															
G. pinetis																									×													
Cratogeomys castanops																						×									×			×				
Perognathus fasciatus																					×																	
P. flavescens																				×		×																
P. merriami																						×	×								×							
P. flavus																				×		×								×	×	×		×				

TABLE 1. (*Continued.*)

	1 Ungavan	2E E. Eskimoan	2W W. Eskimoan	3 Alaskan	4 Aleutian	5 Yukonian	6W W. Hudsonian	6E E. Hudsonian	7E E. Canadian	7W W. Canadian	8 Montanian	9 Coloradan	10 Vancouverian	11 Oregonian	12 Humboldtian	13 Sierran	14 Alleghanian	15 Illinoian	16 Carolinian	17 Kansan	18 Saskatchewanian	19 Balconian	20 Tamaulipan	21 Texan	22 Louisianian	23 Columbian	24 Artemesian	25 Kaibabian	26 Sonoran	27 Yaquinian	28 Mapimian	29 Navahonian	30 Uintian	31 San Matean	32 Mohavian	33 Californian	34 Diablian	35 San Bernardinian
P. apache																																×	×	×				
P. longimembris																											×								×	×		×
P. amplus																												×	×									
P. inornatus																																				×		
P. parvus																										×	×											
P. formosus																											×								×			
P. baileyi																													×									×
P. hispidus																				×		×	×	×						×	×			×				
P. penicillatus																												×	×	×	×							
P. intermedius																													×	×	×			×				
P. fallax																																						×
P. californicus																×																				×	×	×
P. spinatus																																						×
Microdipodops megacephalus																										×	×											
M. pallidus																											×								×			
Dipodomys ordii																				×	×	×	×			×	×	×		×	×	×	×	×				
D. microps																										×	×											
D. panamintinus																																			×			
D. elephantinus																																					×	
D. agilis																																						×
D. heermanni															×	×																					×	
D. ingens																																				×		×
D. spectabilis																														×	×			×				
D. elator																								×														
D. merriami																												×	×	×	×				×	×		×
D. deserti																													×						×			
Castor canadensis						×	×	×	×	×	×	×	×	×	×		×	×	×	×	×	×	×	×	×	×		×	×	×	×	×	×	×		×		
Oryzomys palustris																			×						×													
Reithrodontomys montanus																				×		×		×						×	×			×				
R. humulis																			×						×													
R. megalotis															×	×				×	×	×				×	×	×	×	×	×	×	×	×	×	×	×	×
R. raviventris																																				×		
R. fulvescens																							×	×					×		×							
Peromyscus crinitus																										×	×	×					×		×			

TABLE 1. (*Continued.*)

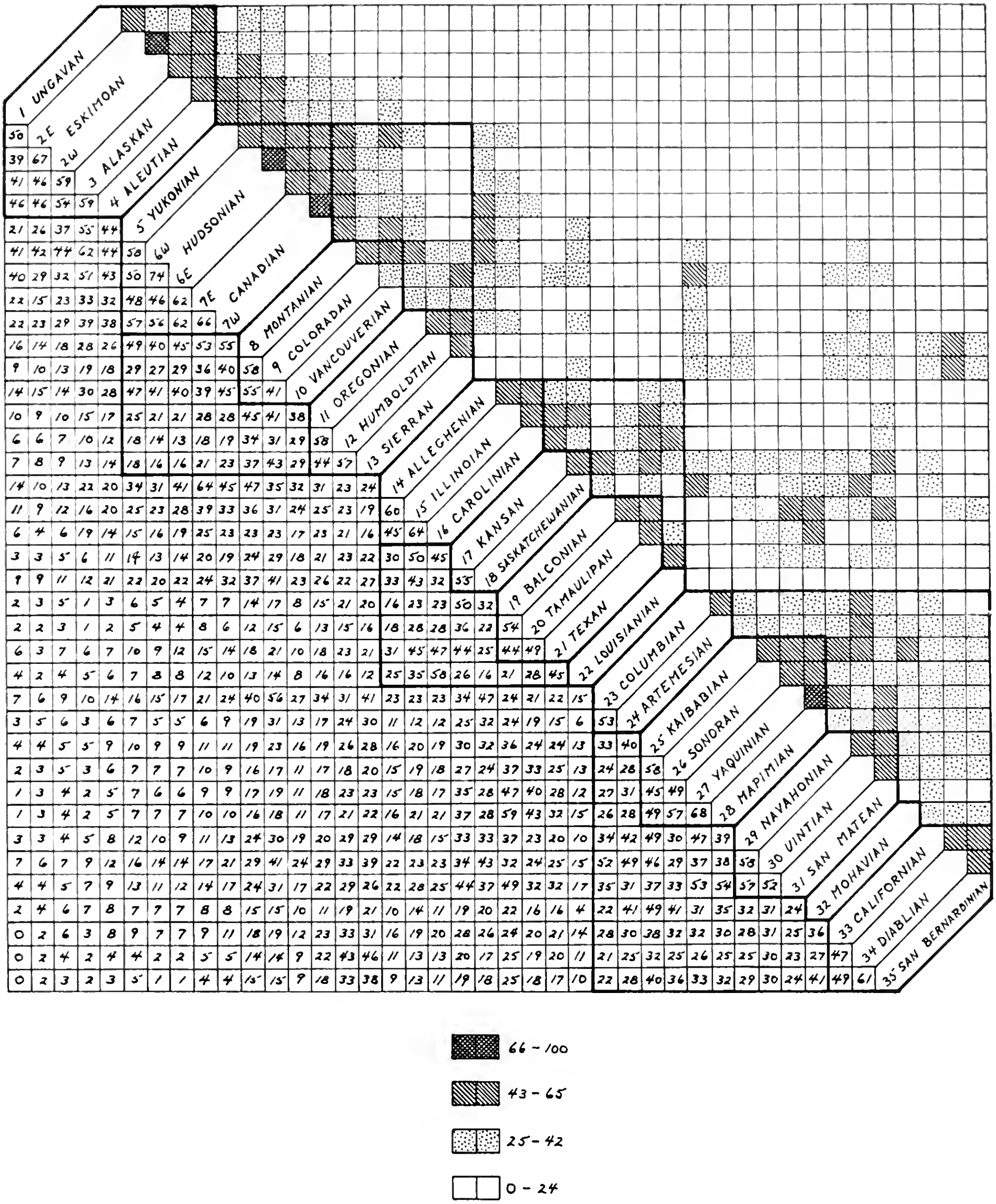
	1 Ungavan	2E E. Eskimoan	2W W. Eskimoan	3 Alaskan	4 Aleutian	5 Yukonian	6W W. Hudsonian	6E E. Hudsonian	7E E. Canadian	7W W. Canadian	8 Montanian	9 Coloradan	10 Vancouverian	11 Oregonian	12 Humboldtian	13 Sierran	14 Alleghanian	15 Illinoian	16 Carolinian	17 Kansan	18 Saskatchewanian	19 Balconian	20 Tamaulipan	21 Texan	22 Louisianian	23 Columbian	24 Artemisian	25 Kaibabian	26 Sonoran	27 Yaquinian	28 Mapimian	29 Navahonian	30 Uintian	31 San Matean	32 Mohavian	33 Californian	34 Diablian	35 San Bernardinian
P. californicus															×																					×	×
P. eremicus																											×	×	×	×				×			×
P. merriami																												×									
P. maniculatus							×	×	×	×	×	×	×	×	×	×	×	×	×	×			×		×	×	×	×	×	×	×	×	×	×	×	×	×	×
P. polionotus																								×												
P. leucopus																×	×	×	×	×	×	×	×						×	×			×				
P. gossypinus																								×												
P. boylei														×	×						×		×				×		×	×	×	×	×	×		×	×
P. pectoralis																					×							×		×							
P. truei														×			×	×	×	×	×		×	×									×				
P. nasutus																													×	×	×	×	×				
P. nuttallii																		×						×												
P. floridanus																								×												
Baiomys taylori																						×							×								
Onchomys leucogaster											×								×	×	×	×			×	×			×		×	×	×				
O. torridus																											×	×	×	×				×	×		×
Sigmodon hispidus																					×	×	×	×				×	×	×							
S. minimus																													×				×				
S. ochrognathus																													×	×							
Neotoma floridana																		×	×				×	×												
N. micropus																					×	×								×			×				
N. albigula																					×						×	×	×	×	×		×				
N. lepida																									×	×	×	×	×	×		×		×	×	×	×
N. stephensi																															×						
N. mexicana																													×	×	×	×	×				
N. fuscipes														×	×																					×	×
N. cinerea										×	×	×	×	×	×					×					×	×	×				×	×					
Clethrionomys rutilus		×	×	×		×	×																															
C. gapperi							×	×	×	×	×					×				×					×								×				
C. occidentalis												×	×	×																							
Phenacomys intermedius						×	×	×	×	×	×		×		×										×												
P. albipes													×																								
P. silvicola													×																								
P. longicaudus													×	×																							

TABLE 1. (*Continued.*)

	Ungavan 1	E. Eskimoan 2E	W. Eskimoan 2W	Alaskan 3	Aleutian 4	Yukonian 5	W. Hudsonian 6W	E. Hudsonian 6E	E. Canadian 7E	W. Canadian 7W	Montanian 8	Coloradan 9	Vancouverian 10	Oregonian 11	Humboldtian 12	Sierran 13	Alleghanian 14	Illinoian 15	Carolinian 16	Kansan 17	Saskatchewanian 18	Balconian 19	Tamaulipan 20	Texan 21	Louisianian 22	Columbian 23	Artemesian 24	Kaibabian 25	Sonoran 26	Yaquinian 27	Mapimian 28	Navahonian 29	Uintian 30	San Matean 31	Mohavian 32	Californian 33	Diablian 34	San Bernardinian 35
Microtus pennsylvanicus						×	×	×	×	×	×	×	×				×	×	×	×	×																	
M. montanus												×				×										×	×											
M. californicus															×	×																				×	×	×
M. townsendii														×																								
M. oeconomus			×	×	×	×																																
M. longicaudus						×					×	×	×	×	×	×										×	×					×	×	×				×
M. mexicanus																														×		×		×				
M. xanthognathus						×	×			×																												
M. chrotorrhinus								×	×								×																					
M. richardsoni											×	×		×																								
M. oregoni														×	×																							
M. miurus				×		×																																
M. ochrogaster																		×		×	×																	
M. pinetorum																		×	×					×														
M. parvulus																									×													
Lagurus curtatus												×									×					×	×											
Neofiber alleni																									×													
Ondatra zibethicus				×	×	×	×	×	×	×	×	×	×	×			×	×	×	×	×					×		×	×		×		×	×	×			
Lemmus trimucronatus		×	×	×		×	×																															
Synaptomys cooperi									×								×	×		×																		
S. borealis				×		×	×	×		×	×		×																									
Dicrostonyx groenlandicus	×	×	×	×	×		×	×																														
Zapus hudsonius					×	×		×	×	×	×						×	×	×	×																		
Z. princeps											×	×	×		×	×					×					×								×				
Z. trinotatus														×	×																							
Napaeozapus insignis									×								×																					
Erethizon dorsatum					×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×					×	×	×	×	×	×	×	×	×	×	×		
Canis latrans			×			×			×		×	×		×	×	×	×	×		×	×	×	×	×		×	×	×	×	×	×	×	×	×	×	×	×	×
C. lupus	×	×	×	×	×	×	×	×	×	×	×	×	×	×		×	×	×	×	×	×	×	×	×		×	×	×	×	×	×	×	×	×	×			
C. niger																							×	×	×													
Alopex lagopus	×	×	×	×			×	×																														
Vulpes fulva	×	×	×	×	×	×	×	×	×	×	×	×		×	×	×	×	×	×					×	×								×	×				
V. velox																				×	×	×					×	×	×	×	×	×		×	×	×		×
Urocyon cinereoargenteus														×	×	×	×	×	×			×	×	×	×		×	×	×	×	×	×	×	×	×	×	×	×
Ursus americanus						×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×				×	×	×	×	×				
U. horribilis		×	×		×	×	×			×	×	×	×	×	×	×				×	×	×				×	×	×	×	×	×	×	×	×	×	×	×	×

TABLE 1. (*Continued.*)

	Ungavan	E. Eskimoan	W. Eskimoan	Alaskan	Aleutian	Yukonian	W. Hudsonian	E. Hudsonian	E. Canadian	W. Canadian	Montanian	Coloradan	Vancouverian	Oregonian	Humboldtian	Sierran	Alleghanian	Illinoian	Carolinian	Kansan	Saskatchewanian	Balconian	Tamaulipan	Texan	Louisianian	Columbian	Artemesian	Kaibabian	Sonoran	Yaquinian	Mapimian	Navahonian	Uintian	San Matean	Mohavian	Californian	Diablian	San Bernardinian
	1	2E	2W	3	4	5	6W	6E	7E	7W	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
Bassariscus astutus															×	×						×	×	×			×	×	×	×	×	×	×	×	×		×	×
Procyon lotor														×	×	×	×	×	×	×	×	×	×	×	×	×		×	×	×	×		×	×		×	×	×
Nasua narica																							×						×	×	×							
Martes americana				×		×	×	×	×	×	×	×	×	×	×	×	×																					
M. pennanti									×	×	×	×	×	×	×	×	×	×																				
Mustela erminea	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×									×	×						×					
M. rixosa	×		×	×	×	×	×	×	×	×	×						×	×																				
M. frenata											×	×		×	×	×	×	×	×	×	×	×	×	×	×	×	×			×	×		×	×		×	×	×
M. nigripes																				×	×	×										×	×	×				
M. vison			×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×			×	×	×										×		
Gulo luscus	×	×		×	×	×	×	×	×	×	×	×	×	×	×	×	×	×			×																	
Taxidea taxus											×	×			×	×		×		×	×	×	×	×		×	×	×	×	×	×	×	×	×	×	×	×	×
Spilogale putorius												×		×	×	×			×	×		×	×	×	×	×	×	×	×	×	×	×	×	×		×	×	×
Mephitis mephitis									×	×	×	×		×	×	×	×	×	×	×	×	×	×	×	×	×		×	×	×	×	×	×	×		×	×	×
M. macroura																													×	×	×							
Conepatus leuconotus																							×						×	×	×			×				
Lutra canadensis	×			×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×			×	×	×		×				×	×	×				
Felis onca																							×				×		×	×				×				
F. concolor											×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
F. pardalis																						×	×	×						×								
F. wiedii																							×															
F. yagouaroundi																							×							×								
Lynx canadensis	×	×	×	×	×	×	×	×	×	×	×	×	×	×			×	×			×					×												
L. rufus											×	×		×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
Tayassu tajacou																						×	×	×					×	×	×							
Cervus canadensis										×	×	×		×	×		×	×	×	×	×					×	×			×		×	×	×		×		
Dama hemionus											×	×	×	×	×	×				×	×	×				×	×	×	×	×	×	×	×	×			×	×
D. virginiana									×		×	×		×			×	×	×	×	×	×	×	×	×	×			×	×	×			×				
Alces alces			×	×		×	×	×	×	×	×	×					×																					
Rangifer tarandus	×	×	×	×	×	×	×	×	×	×	×																											
Antilocapra americana												×				×				×	×	×	×	×		×	×	×	×	×	×	×	×	×	×	×		
Bison bison										×		×						×	×	×	×	×	×	×	×	×					×		×	×				
Oreamnos americanus						×					×		×	×																								
Ovibos moschatus		×	×				×																															
Ovis canadensis											×	×				×					×					×	×	×	×	×	×	×	×		×			×
O. dalli						×																																



	1	2E	2W	3	4	5	6W	6E	7E	7W	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
1 UNGAVAN																																					
2E ESKIMOAN	50																																				
2W	39	67																																			
3 ALASKAN	41	46	59																																		
4 ALEUTIAN	46	46	54	59																																	
5 YUKONIAN	21	26	37	55	44																																
6W HUDSONIAN	41	42	44	62	44	58																															
6E	40	29	32	51	43	50	74																														
7E CANADIAN	22	15	23	33	32	48	46	62																													
7W	22	23	29	39	38	57	56	62	66																												
8 MONTANIAN	16	14	18	28	26	49	40	45	53	55																											
9 COLORADAN	9	10	13	19	18	29	27	29	36	40	58																										
10 VANCOUVERIAN	14	15	14	30	28	47	41	40	39	45	55	41																									
11 OREGONIAN	10	9	10	15	17	25	21	21	28	28	45	41	38																								
12 HUMBOLDTIAN	6	6	7	10	12	18	14	13	18	19	34	31	29	58																							
13 SIERRAN	7	8	9	13	14	18	16	16	21	23	37	43	29	44	57																						
14 ALLEGHENIAN	14	10	13	22	20	34	31	41	64	45	47	35	32	31	23	24																					
15 ILLINOIAN	11	9	12	16	20	25	23	28	39	33	36	31	24	25	23	19	60																				
16 CAROLINIAN	6	4	6	19	14	15	16	19	25	23	23	23	17	23	21	16	45	64																			
17 KANSAN	3	3	5	6	11	14	13	14	20	19	24	29	18	21	23	22	30	50	45																		
18 SASKATCHEWANIAN	9	9	11	12	21	22	20	22	24	32	37	41	23	26	22	27	33	43	32	55																	
19 BALCONIAN	2	3	5	1	3	6	5	4	7	7	14	17	8	15	21	20	16	23	23	50	32																
20 TAMAULIPAN	2	2	3	1	2	5	4	4	8	6	12	15	6	13	15	16	18	28	28	36	22	54															
21 TEXAN	6	3	7	6	7	10	9	12	15	14	18	21	10	18	23	21	31	45	47	44	25	44	49														
22 LOUISIANIAN	4	2	4	5	6	7	8	8	12	10	13	14	8	16	16	12	25	35	58	26	16	21	28	45													
23 COLUMBIAN	7	6	9	10	14	16	15	17	21	24	40	56	27	34	31	41	23	23	23	34	47	24	21	22	15												
24 ARTEMESIAN	3	5	6	3	6	7	5	5	6	9	19	31	13	17	24	30	11	12	12	25	32	24	19	15	6	53											
25 KAIBABIAN	4	4	5	5	9	10	9	9	11	11	19	23	16	19	26	28	16	20	19	30	32	36	24	24	13	33	40										
26 SONORAN	2	3	5	3	6	7	7	7	10	9	16	17	11	17	18	20	15	19	18	27	24	37	33	25	13	24	28	58									
27 YAQUINIAN	1	3	4	2	5	7	6	6	9	9	17	19	11	18	23	23	15	18	17	35	28	47	40	28	12	27	31	45	49								
28 MAPIMIAN	1	3	4	2	5	7	7	7	10	10	16	18	11	17	21	22	16	21	21	37	28	59	43	32	15	26	28	49	57	68							
29 NAVAHONIAN	3	3	4	5	8	12	10	9	11	13	24	30	19	20	29	29	14	18	15	33	33	37	23	20	10	34	42	49	30	47	39						
30 UINTIAN	7	6	7	9	12	16	14	14	17	21	29	41	24	29	33	39	22	23	23	34	43	32	24	25	15	52	49	46	29	37	38	58					
31 SAN MATEAN	4	4	5	7	9	13	11	12	14	17	24	31	17	22	29	26	22	28	25	44	37	49	32	32	17	35	31	37	33	53	54	57	52				
32 MOHAVIAN	2	4	6	7	8	7	7	7	8	8	15	15	10	11	19	21	10	14	11	19	20	22	16	16	4	22	41	49	41	31	35	32	31	24			
33 CALIFORNIAN	0	2	6	3	8	9	7	7	9	11	18	19	12	23	33	31	16	19	20	28	26	24	20	21	14	28	30	38	32	32	30	28	31	25	36		
34 DIABLIAN	0	2	4	2	4	4	2	2	5	5	14	14	9	22	43	46	11	13	13	20	17	25	19	20	11	21	25	32	25	26	25	25	30	23	27	47	
35 SAN BERNARDINIAN	0	2	3	2	3	5	1	1	4	4	15	15	9	18	33	38	9	13	11	19	18	25	18	17	10	22	28	40	36	33	32	29	30	24	41	49	61

FIG. 2. Final trellis or matrix giving Coefficients of Community (percentage of species common to pairs of provinces). Ordering of provinces is that resulting from cluster analysis. Heavy lines outline superprovinces and subregions. The classes of shading shown in the mirror image are determined by the critical mean CC values used to obtain higher categories of areas.

consisted of laying a transparent overlay over the species IFC map (H & S, Fig. 1) and drawing lines through all regions of high IFC value, delimiting ultimately a total of 86 (rather than the original 24) primary areas. The distribution of these is given as Figure 1. The genus IFC map was not used in the corrected analysis.

Subsequent procedure was that of our earlier paper. Species checklists of each of the primary areas were prepared, and CCs were computed and subjected to cluster analysis. Because of the large number of CCs involved (86! = 3,741), calculation of CCs in this and subsequent operations was done by computer.

In our earlier paper (H & S: 137–138), a mammal province was defined as an area with a mean CC of 62.4% or less, when compared to other areas by cluster analysis. This decision was based on the work of Preston (1962), who found that analysis of faunas by means of a "Resemblance Equation" (RE) indicated that values of z (as derived from the RE) of about 0.27 represented the break between faunistic homogeneity and heterogeneity. In our earlier paper we converted z to S (Similarity), where $S = 100\ (1 - z)$, and calculated both S and CC for all items in the matrix. These were compared by regression, giving a slope $b = 1.17 \pm 0.02$. Conversion of Preston's critical z value to S gave an S of 73%, and conversion of the critical value of S to CC equaled 73/1.17 = 62.4%, and hence our use of this value. We did not, however, allow for the effects of statistical error. If this is incorporated, in the form of plus and minus two standard errors (providing limits at the 95% level of probability), the critical CC value falls within the range 60.30–64.60%. As a result, in this and subsequent papers I propose the use of a CC value of 65% as critical for the determination of mammal provinces. This is a conservative standard, and all values lying between 60 and 65% should be considered suspect, and are reported.

The results of cluster analysis were evaluated according to this new standard. Pairs of primary areas with CCs higher than 65% (as determined by actual calculation or by averaging during cluster analysis) were pooled to create secondary areas. The whole process was then repeated. A new species checklist was prepared for each area, CCs were computed and subjected to cluster analysis, and a new dendrogram prepared. Pooling of areas was again done where CC values were higher than 65%. In all, four such sets of sequential operations were carried out. In the final operation, the total number of primary areas had been reduced from 86 to 38 secondary areas, all but three of which had CCs lower than 65% (2E and 2W, 6E and 6W, and 7E and 7W; see Figs. 2 and 3). These three sets of secondary areas were not pooled because they occur over large geographic areas and because I was concerned with their detailed analysis. The 35 secondary areas with CCs less than 65% constitute mammal provinces by the standards used here and are so treated, although two pairs of these fall within the questionable range 60–65% (15 and 16, 34 and 35, see Fig. 4). Figure 2 is the matrix resulting from cluster analysis, showing ordering of provinces and Coefficients of Community between pairs. Figure 3 is a map showing geographic distribution of the provinces, and Figure 4 is a dendrogram delineating the faunistic relationships existing between provinces, as determined by cluster analysis. A species checklist for each of the provinces, as it was used in the final operation, is given as Table 1.

In our earlier paper (H & S), mammal provinces were grouped into the higher categories of superprovinces, subregions, and regions. The method used in deriving these was to draw lines across the dendrograms at suitable CC levels, the choice of CC level being arbitrary but providing what appeared to be a useful classification (H & S: 139–140, 149). I have tried here to make as little change from the original scheme as possible; however, a small number of minor adjustments have been necessary.

The 0–8% CC range of the dendrogram still stands as a level useful for the category

FIG. 3. Final grouping of primary areas into mammal provinces. Broken lines indicate subdivisions of provinces. The approximate relationships of island faunas are also shown.

of region. At this level, one region, the Nearctic is isolated. Subregions in our earlier paper stood between the 20–25% CC range; this is changed here to the 22–27% CC range, and still encompasses four subregions, following Wallace (1876). The category of superprovince was, in the earlier paper, set at a mean CC level of about 39%. The selection of this value was based on conclusions reached by Savage (1960), details of which may be obtained from H & S, p. 139–140. The 39% level would, in the case of the dendrogram used here (Fig. 4) give 11 superprovinces. Several cluster at a level very little higher than this, and I have arbitrarily moved the limit up to about 42.5%, so as to encompass these, giving a total of 13 superprovinces. These decisions

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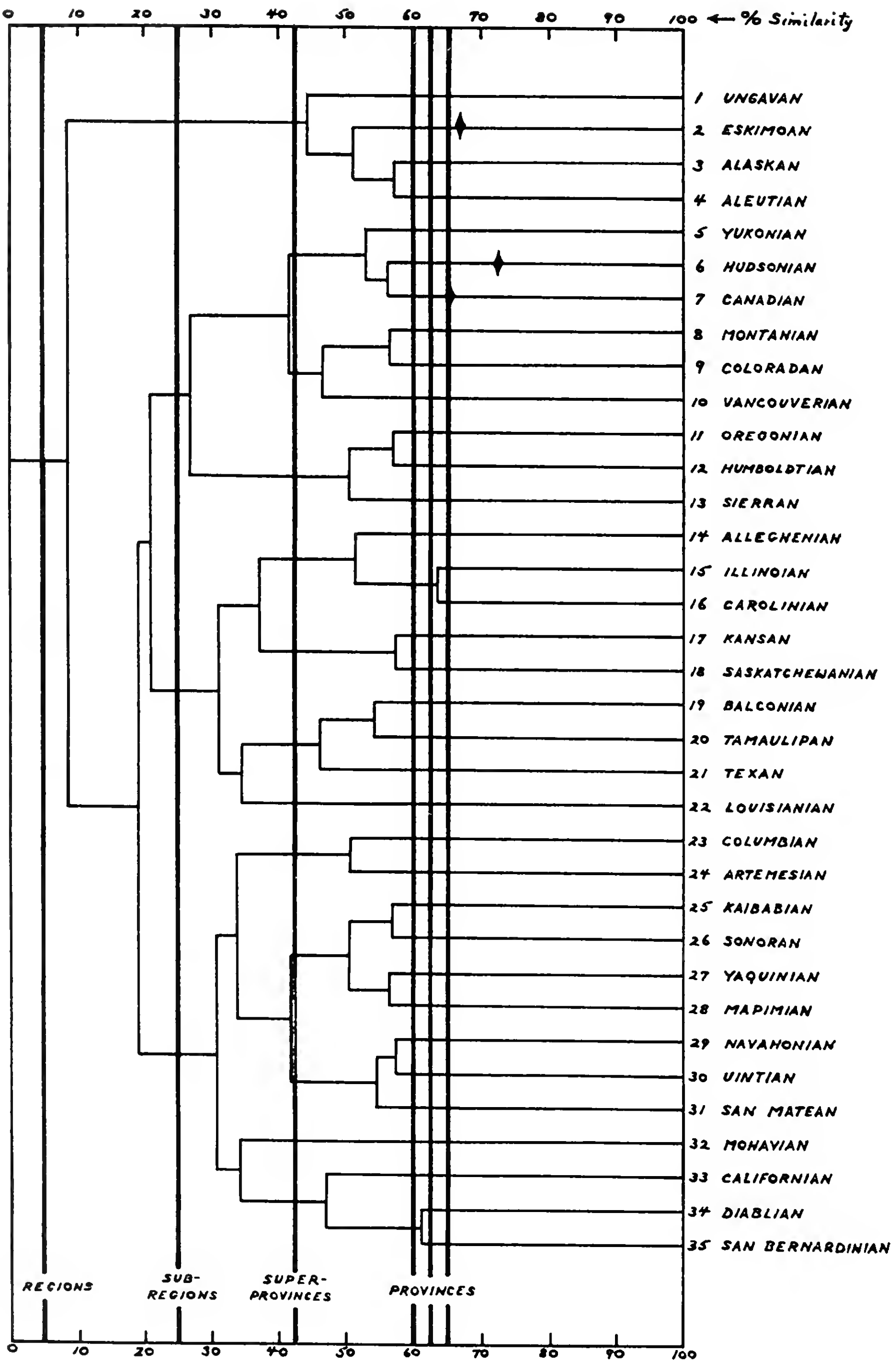
FIG. 4. Final dendrogram showing relationship between provinces. Ordering of provinces and mean Coefficients of Community (CC) are the results of cluster analysis. Solid vertical lines show mean CC levels at which regions, subregions, superprovinces, and provinces segregate. The three vertical lines for provinces represent the mean critical value plus and minus two standard errors. Per cent similarity is mean Coefficient of Community (CC). The "diamonds" of provinces 2, 6, and 7 represent the mean CCs at which the subdivisions of these provinces pool on cluster analysis.


0
10
20
30
40
50
60
70
80
90
100
% Similarity
1 UNGAVAN
2 ESKIMOAN
3 ALASKAN
4 ALEUTIAN
5 YUKONIAN
6 HUDSONIAN
7 CANADIAN
8 MONTANIAN
9 COLORADAN
10 VANCOUVERIAN
11 OREGONIAN
12 HUMBOLDTIAN
13 SIERRAN
14 ALLEGHENIAN
15 ILLINOIAN
16 CAROLINIAN
17 KANSAN
18 SASKATCHEWANIAN
19 BALCONIAN
20 TAMAULIPAN
21 TEXAN
22 LOUISIANIAN
23 COLUMBIAN
24 ARTEMESIAN
25 KAIBABIAN
26 SONORAN
27 YAQUINIAN
28 MAPIMIAN
29 NAVAHONIAN
30 UINTIAN
31 SAN MATEAN
32 MOHAVIAN
33 CALIFORNIAN
34 DIABLIAN
35 SAN BERNARDINIAN
REGIONS
SUB-REGIONS
SUPER-PROVINCES
PROVINCES
0
10
20
30
40
50
60
70
80
90
100

continue to fill the desirable requirements outlined in our earlier paper.

Good single values for each of these hierarchic levels would be: provinces 62.5%, superprovinces 42.5%, subregions 25%, and regions 5%. By this scheme the 35 mammal provinces of North America are grouped into 13 superprovinces, four subregions, and one region. These are named and their distributions mapped on Figures 5a and 5b. They are also blocked out in the matrix (Fig. 2) and marked by lines drawn at appropriate CC levels on the dendrogram (Fig. 4). The problem of nomenclature of mammal areas is discussed subsequently.

The nearest approach to the biotic provinces of Dice (1943), and Kendeigh (1961) through the analysis carried out here, is obtained by fitting a line at about the 54% CC level of the dendrogram. The more intuitive decisions of these workers implies a degree of segregation about 10% lower than the one used here.

Nomenclature and Status of Areas

No changes in the names or status of regions or subregions over those of our earlier paper have resulted from the reanalysis. Because of the increase in numbers of provinces however, minor adjustments in these and in other categories have been obligatory.

As few name changes as possible have been made. Where new names have been applied, an attempt has been made to take them from the literature and to apply them on the basis of priority. Where there has been need to coin names, I have tried to follow the spirit of earlier workers. As an aid to recognition, names of provinces are in the form of adjectives, names of superprovinces in the form of nouns.

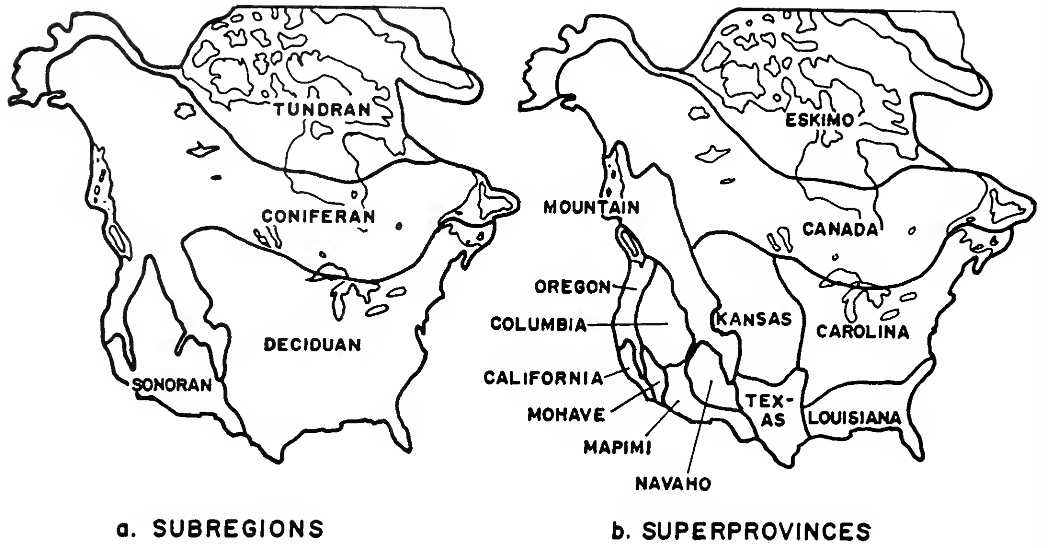
Those cases in which provinces segregate within the doubtful 60–65% CC range, or in which segregation occurs at a level only slightly higher than 65%, are here described. More detailed analyses will doubtless result in some changes in status within these groups.

The following provinces are new and have been named by me: no. 1, Ungavan; no. 12, Humboldtian; no. 25, Kaibabian; no. 30, Uintian; no. 31, San Matean; no. 34, Diablian and no. 35, San Bernardinian. Those provinces that are new but that have been given an older name are, together with the source of the name: no. 3, Alaskan (Allen, 1892); no. 5, Yukonian (Cooper, 1859); no. 10, Vancouverian (Van Dyke, 1939); no. 13, Sierran and no. 23, Columbian (Miller, 1951). The names Saskatchewan and Mapimi are here converted to the adjectival forms, Saskatchewanian, and Mapimian.

The Hudsonian (no. 6) is a new province. The name was formerly applied to the province here termed Canadian (no. 7), and the Canadian of earlier workers is here termed Alleghenian (no. 14), following the precedence set by Cooper (1859), and Allen (1892), after Kendeigh (1954). The Carolinian (16) is a new province. The name was applied to what is here largely represented by the Louisianian province (22), in our earlier paper. Its present application is the correct one, however, by the standards of older workers. The Louisianian should properly be called the Austroriparian, following Dice (1943), Kendeigh (1961), and H & S. Because it has superprovince as well as province status, and requires the nounal form of the same as well as an adjectival one, I have applied Allen's (1892) terminology to it.

Not all provinces segregate clearly. The northern limit of no. 3, the Alaskan, was difficult to locate, it being a region of broad transition. Its mapped limit is relatively arbitrary. The Sitkan province of H & S is here included in the Yukonian (no. 5), and the Vancouverian (no. 10), clustering with the former with a CC of 76%. That part of the Yukonian province made up of the Brooks Range very nearly segregates with a CC of 66%.

The Eskimoan, Hudsonian, and Canadian provinces (nos. 2, 6, and 7) have, for reasons given elsewhere, each been split into eastern and western components. Of these,



a. SUBREGIONS

b. SUPERPROVINCES

FIG. 5, a and b. The distribution of mammal subregions and mammal superprovinces, as determined from the dendrogram.

the Eskimoan components cluster with a CC of 67%, and the Canadian with a CC of 66%. These are nearly critical values, indicating that the components almost merit province status.

The Oregonian (no. 11) almost segregates into western coastal and eastern Cascadian provinces, pooling with a CC of 66%. The Alleghenian (no. 14) segregates from the eastern component of the Canadian (no. 7) with a CC of only 64%, a critical value. It clusters with the Carolina superprovince on analysis, however, and does so with province rating.

The Carolinian (no. 16) is not a clearly defined province and probably should have been pooled with the Illinoian (no. 15), the two clustering with a CC of 64%. The Carolinian is made up of three distinctive geographic components; that east of the Appalachian Mountains clusters with the rest of the province with a CC of 67%, and that of the Ozark Mountains clusters at 66%. Two of these components are distinct enough from the Illinoian that I have provisionally kept the Carolinian as a full province.

The Balconian (no. 19) was incorrectly identified by H & S as part of what is here called the Tamaulipan (no. 20). The Balconian in its present sense stands as a full province.

The Louisianian (no. 22), under the name Austroriparian, was in part identified as the Carolinian by H & S. Its distribution as determined by reanalysis is the more realistic one.

The larger part of the Columbian province (no. 23) was named Artemesian by H & S. The latter term is here applied to a restricted portion of the Columbian as province no. 24. The Palusian of H & S is here pooled with the Columbian, with a CC of 70%.

The Mohavian province (no. 32) presents something of a puzzle. It was not recognized through examination of the IFC map but appeared through scrutiny of individual species maps. Once recognized, however, cluster analysis caused it to segregate out to the extent of meriting superprovince status, and I have accepted it as this. Its geographic limits, however, have been determined subjectively, and they should be considered as suspect.

The Diablian (no. 34) is also of uncertain status, as it clusters with the San Bernardinian (no. 35) with a CC of 61%, a critical value. Because not all of the latter occurs in the area studied, its analysis is incomplete, and for this reason the distinction is provisionally accepted here.

Of superprovinces, the Texas, Columbia, Mapimi, and Mohave are new, and the names Hudson and Austroriparian of H & S are replaced by the names Canada and Louisiana, for reasons given elsewhere.

Insular Faunas

Sixty-four species (27%) of the total mammal fauna occur on the larger islands adjacent to the continent and on the islands of the Great Lakes. Insular faunas were in each case compared with the faunas of several of the nearest mainland provinces by means of the Coefficient of Community and Simpson's Coefficient (SC). The latter is a measure of the percentage of species occurring on an island that also occur in in the mainland province (Simpson, 1943; H & S: 131). Results are given in Table 2.

Most island faunas give a CC much lower than Preston's critical 65% value when compared with the faunas of adjacent mainland provinces (Table 2). Most islands would therefore merit full province status, if this standard were to be applied. The generally low CC obtained, however, is the result of the small size of insular faunas, a bias being introduced as a consequence of it. Simpson's Coefficient is, in these circumstances, a more reliable measure, and I attribute greater significance to it. No critical value of SC is available, however. Because of this, and because there is more interest in similarities than dissimilarities, island faunas have in all cases been named as part of the fauna of the adjacent province to which they show nearest relationship as determined primarily by Simpson's Coefficient.

TABLE 2.

Island	No. of species	Adjacent provinces	CC	SC
Long Island	29	14 Alleghanian	51	93
		16 Carolinian	52	61
Cape Breton	31	14 Alleghanian	55	94
		7E E. Canadian	64	87
Prince Edward Island	29	7E E. Canadian	68	93
		14 Alleghanian	48	90
Anticosti	5	6E E. Hudsonian	17	100
		7E E. Canadian	13	100
		14 Alleghanian	10	100
Newfoundland	12	6E E. Hudsonian	40	100
		7E E. Canadian	28	92
		14 Alleghanian	19	83
Belcher	3	1 Ungavan	25	100
		6E E. Hudsonian	10	100
		7E E. Canadian	3	33
Manitoulin	25	14 Alleghanian	49	100
		7E E. Canadian	62	96
Isle Royale	9	7E E. Canadian	24	100
		14 Alleghanian	18	100
Arctic Archipelago	10	2E E. Eskimoan	67	100
		1 Ungavan	57	80
Kodiak	12	5 Yukonian	33	100
		4 Aleutian	57	92
		3 Alaskan	39	85
Alexander Archipelago	21	10 Vancouverian	61	95
		5 Yukonian	44	90
Queen Charlottes	12	10 Vancouverian	36	92
		5 Yukonian	24	83
Vancouver	22	11 Oregonian	33	83
		10 Vancouverian	54	79

Long Island shows closest relationship to the Alleghenian province (no. 14), not the Carolinian (no. 16), as might have been expected. Cape Breton is nearest to the Alleghenian by Simpson's Coefficient; I have placed it there though it shows a very high CC with the eastern Canadian (64%). Prince Edward Island lies nearest to the eastern Canadian province (no. 7E), which is surprising in the light of its geographic proximity to the Alleghenian. Anticosti is grouped with the eastern Hudsonian (no. 6E), on the basis of its high CC, as is Newfoundland, the latter on the basis of both coefficients. Belcher Island is, because of its CC only, treated as being most closely related to the Ungavan (no. 1). Manitoulin has highest SC with the Alleghenian, highest CC with the eastern Canadian, but because greater weight is given to Simpson's Coefficient, I have grouped it with the Alleghenian. Isle Royale shows closest affinity with the eastern Canadian province.

Of the islands of the west coast, the Alexander Archipelago and the Queen Charlotte Islands show closest relationship to the Vancouvarian (no. 10). Vancouver Island, on the basis of its SC only, is closest to the Oregonian (no. 11).

Kodiak Island has highest CC with the Aleutian (no. 4), but highest SC with the Yukonian (no. 5), and following the policy set previously is considered most closely related to the latter.

Of the Arctic archipelago and Greenland, the following groups of islands have identical faunas: group 1, Baffin, Southampton, and Coats islands; group 2, Somerset Island; group 3, Banks Island; group 4, Greenland, Sverdrup Islands, Borden and Prince Patrick islands; group 5, Victoria, Prince of Wales, Melville, Bathurst, Cornwallis, Devon, and Ellesmere islands. The faunas of these groups of islands, together with those of the Ungavan and eastern Eskimoan provinces (nos. 1 and 2E) were analyzed by first computing Coefficients of Community between them, then subjecting these to cluster analysis, using the methods outlined previously. All of the island groups cluster at a mean level of 61% or higher, falling within the critical range or better. The groups taken together segregate from the eastern Eskimoan with a mean CC of 54% and from the Ungavan with a mean CC of 44%. The equivalent mean SCs are 100% and 85% respectively. As a result I have treated all of the Arctic archipelago and Greenland as part of the eastern component of the Eskimoan province.

A generalized mapping of these relationships is given in Figure 3. It should be noted that the affinities of Cape Breton, Prince Edward and Long islands are indicated incorrectly here.

Discussion

The general conclusions reached as a result of this re-evaluation differ in no way from those obtained through our earlier analysis (H & S; 147–151), and they are not treated further. It is important that the subjectivity of the methods used here be kept in mind however. The sources and attempted controls of these have been discussed in our earlier paper (H & S: 148–149, 151) and include taxonomic errors, distributional errors, choice of point or block for sample; size of sample block, fitting of isarithms, selection of primary areas, choice of coefficient of association, choice of clustering method, and others.

The methods used here are ideally suited to computer techniques. This reanalysis could not in fact have been completed within reasonable time had such techniques not been available. Miller, Parsons, and Kofsky (1960) have described the use of so-called successive scanning mode microdensitometers, which automatically map the densities of films and other kinds of transparencies. Such devices are sold by Beckman and Whitley of San Carlos, California, under the registered trade name of Isodensitracer. The use of such a device on a transparent map showing the distribution of all North American mammals drawn in inks or paints which gave progressively less translucency as additional layers were added, would be ideal in the development of more refined IFC maps.

The IFC map used in this work (H & S, Fig. 1) was based on the computation of the percentage of species whose ranges ended within blocks 50 miles to a side. The absolute value of an IFC is a function of size of block (H & S: 148). I suggest that any future use of IFCs incorporate as subscript to values given, a statement of the area of the block in kilometers. Converting size of block used here to square kilometers gives an area per block of approximately 6,500 square kilometers, and the IFCs used here are symbolized as $\mathrm{IFC}_{6,500}$. Subscripts made up of a statement of length of side of a block rather than area would be less cumbersome. I suspect however that circles may prove more useful than blocks as sampling units, especially if microdensitometers are used, which make the use of area necessary.

Since preparation of our earlier study, a number of similar papers have been drawn to my attention or have been published. Munroe (1956) gave a fine account of the ecologic and zoogeographic features of Canada and an analysis of the insect faunas of the continent. Udvardy (1963) provided an excellent analysis of the bird faunas of North America. His methods differed from ours in that, rather than treating all species simultaneously, he grouped them by type of distribution pattern, and then prepared maps showing numbers of species geographically, by type of pattern. By this method he was able to recognize the presence of 17 primary faunas and 25 secondary ones. The methods used, while different in basic respects from those used here, could easily prove to be more useful.

The following should be added to our earlier summary of coefficients of association (H & S: 131–132). Smith (1960) used the term "Faunistic Relation Factor" (FRF) for the Coefficient of Community, and Huheey (1965) called it a "Divergence Factor" (D), when subtracted from 100. Fager (1965) has devised a new coefficient in the form of $100\ C/\sqrt{n_1 n_2} - \frac{1}{2}\sqrt{n_2}$, where n_1 is less than n_2. Long (1963) gives a review of coefficients and suggests use of an "average resemblance formula" first used by Kulcznski in 1927, and listed in H & S, p. 132.

In our earlier study (H & S: 128–129, 148) we pointed out that our work has been based on Webb's (1950) analysis of the mammals and herpetofauna of Texas and Oklahoma. The work of Ryan (1963) who improved on Webb's technique in analyzing the mammal faunas of Central America was not known to us at the time. Subsequently, Huheey (1965) published an account of further modifications of the technique in the study of the herpetofauna of Illinois. Since the methods used in all of these are related, and because they are similar in principle, their comparison may be of interest, and I have attempted to do this briefly in the account following. Webb's (1950) method was to lay a grid of sample points at 100-mile intervals on a map of the area to be studied, to prepare a species checklist for each sample point, to compute Coefficients of Community between sample points and then plot these, to draw lines connecting CCs of equal value, providing a form of "contour map," and to consider "valleys" with CCs of 75% or more as "biogeographic regions." A key point underlying Webb's analysis lies in the fact that he found CCs computed in a north–south plane to differ statistically from those computed in an east–west plane. Since he found that the east–west data gave most significant results, he accepted these in the preparation of his final map and rejected the north–south data. Webb deserves commendation for being first, to my knowledge, to devise a numerical technique for biogeographic analyses in two dimensions.

Ryan's (1963) analysis used a methodology only slightly different from that of Webb. Because of the unusual shape of the area studied, the grid of one portion of it was made up of points 100 kilometers (about 62 miles) to a side, of a second portion of it, 50 kilometers (about 31 miles) to a side. CCs, called "Similarity Values" by both Webb and Ryan, were calculated for both the north–south and east–west planes, and both sets of data were used in preparation of the final contour maps, so far as I can determine. Ryan called the contour lines "isobiots." It is not clear whether Webb's 75% rule for biogeographic regions was used.

Huheey's (1965) method differed to some degree from the preceding. It was to lay a grid of 20 miles to a side onto the area to be studied. Within each block of the grid a species checklist was prepared. For each of the four sides of all blocks, a Divergence Factor (*D*) was computed, where $D = 100\text{–CC}$; thus *D* is the complement of the Coefficient of Community. Huheey refers to the CC by Smith's (1960) term, "Faunistic Relation Factor," or FRF. The average of the four *D*s for each block was computed, this being the mean *D* for that block. Finally, contour lines called "isometabases" were drawn around mean *D*s of equal value. From the contour map herpetofaunal regions were described.

Webb's and Ryan's methods, it will be observed, are essentially the same, differing only in distance between sample points and planes in which CCs are computed. Huheey's method, and the method used in this and in our earlier study differ considerably, though they seek identical ends through development of contour maps depicting faunistic change. I have been led to understand that still other techniques and refinements of those discussed here are in preparation. For example, Valentine (1965) reported a study of the distribution of northeastern Pacific molluscan distributions using methods similar to those employed in this and in our earlier paper. It is apparent that there is need for a comparative testing of the several methods of analysis presently at hand, using the same basic materials in each. I plan to attempt such a study.

Earlier (H & S: 129), we mentioned a partial testing of Webb's original method on the mammal fauna of North America. In view of the preceding, a brief account of the testing follows: Webb's method was followed exactly, except that the grid of sample points was placed on a northeast–southwest plane, giving better coverage of certain coastal areas. A number of variations in the planes in which CCs were computed were attempted. These variations included: (1) computing and plotting CCs in the northeast–southwest plane only; (2) doing the same in the northwest–southeast plane only; (3) averaging adjacent CCs taken in both planes and plotting these; (4) plotting highest CCs only of pairs computed in both planes. We did not try Ryan's device of plotting all CCs taken in both planes. However, of the variants tested, none gave results that appeared anywhere near reasonable in terms of what we knew generally of the distribution of biogeographic and ecologic zones. The variants used by Ryan and Huheey, however, appear to work well on the basis of their evidence, and my conclusions apply in no way to their results.

No attempt has been made to take into account the effects of altitude on mammal distributions. Dice, in his original study of biotic provinces (1943) described such effects in terms of "life belts" and named a number of these. Kendeigh (1954) on the other hand did not see altitude as a confounding factor in delimitation of biotic provinces. He wrote: "A mountain range may have several life zones represented on it, but only a single biotic province, provided there is a similar tendency for specific or subspecific distinctiveness of the fauna in all the zones. The two concepts therefore have quite different objectives."

I have not been able to decide which of the two views applies in studies of the sort carried out here. It should be realized, however, that the methods employed here are capable of analyzing the effects of altitude on distribution, and segregating altitudinal provinces, if they exist, given distribution maps of sufficient accuracy in the first place. The maps used here failed to show details of vertical distribution, and as a consequence this aspect of the problem has not proven solvable.

An attempt was made to analyze altitudinal distribution in a different way. Each species of mammal was given its life zone distribution, this information being collated from a large number of sources, chiefly certain of the North American Fauna Series. The faunas of each of the life zones within provinces occurring in generally mountainous parts of the continent were treated as primary areas, Coefficients of Community were computed, and the results subjected to cluster analysis. The initial results were unsatisfactory, however, and because of this and because of the circularity of reasoning involved, the method was abandoned.

No attempt has been made to relate the distribution of mammal areas to the distribution of other natural units, either physiographic, climatic, or vegetational, although a comparison of Figure 3 to maps showing the distribution of such features (e.g., Lobeck, 1948; Thornethwaite, 1948; Rowe, 1959; Shantz and Zon, 1923), shows that the relationship is very close.

Summary

1. An earlier study demonstrated that range limits of North American terrestrial mammals were grouped, and that regions of faunistic homogeneity could as a consequence be identified.

2. The method used to identify such regions was to compute percentage of species whose ranges ended in blocks fifty miles on a side (IFCs), and to then fit isarithms. Topographic "valleys" in the map represented regions of faunistic homogeneity, or "primary areas," and for 24 of these, species checklists were prepared. The percentage of species common to pairs of primary areas (CCs) were computed, and the results subjected to cluster analysis, using the method of weighted pair-groups with simple averages. This resulted in a matrix and dendrogram showing relationships and ordering of primary areas. Using a conversion of Preston's Resemblance Equation, a CC of 62.5% was considered critical. Primary areas with a CC lower than this were considered "mammal provinces." By this criterion, 22 mammal provinces grouped into nine superprovinces, four subregions, and one region were recognized.

3. Many more primary areas should have been derived from the IFC map. Starting with 86 primary areas and carrying out four sequential sets of cluster analyses leads to the conclusion that a minimum of from 33 to 35 mammal provinces occur in the continent. These are mapped, named, and briefly described. For statistical reasons, the upper limit of Preston's critical value is raised to a CC of 65%.

4. Higher categories of mammal areas are derived by grouping the provinces on the matrix and dendrogram at appropriate mean CC levels. A mean CC of 42.5% gives 13 superprovinces; a mean CC of 25%, four subregions; a mean CC of 5%, one region (the Nearctic). These are mapped, named, and briefly described. In general, provinces are named as adjectives derived from geographic place-names, superprovinces as nouns. Where possible the names of these and of regions and subregions are taken from the literature on a priority basis.

5. Approximately one-quarter of the mammal species of the continent also occur on nearby continental islands. Island faunas are always smaller than those of the adjacent mainland and always show closest faunistic similarity to nearby provinces.

6. The methods used have the advantage of being relatively objective, repeatable, and well-suited to computer operations. The use of a successive scanning mode microdensitometer may prove useful in the preparation of accurate IFC maps.

7. Accounts of several techniques in biogeographic analysis similar in aim and method to those used here have recently appeared. These are briefly compared. There is need for a critical testing and evaluation of these to determine which provides the best basis for further refinement.

8. While the methods used here are suitable for analyzing the effects of altitudinal zonation on distribution, lack of requisite detail in the distribution maps now available makes such analyses impractical.

9. There appears to be a high degree of correlation between the distribution of mammal areas and other kinds of natural areas.

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