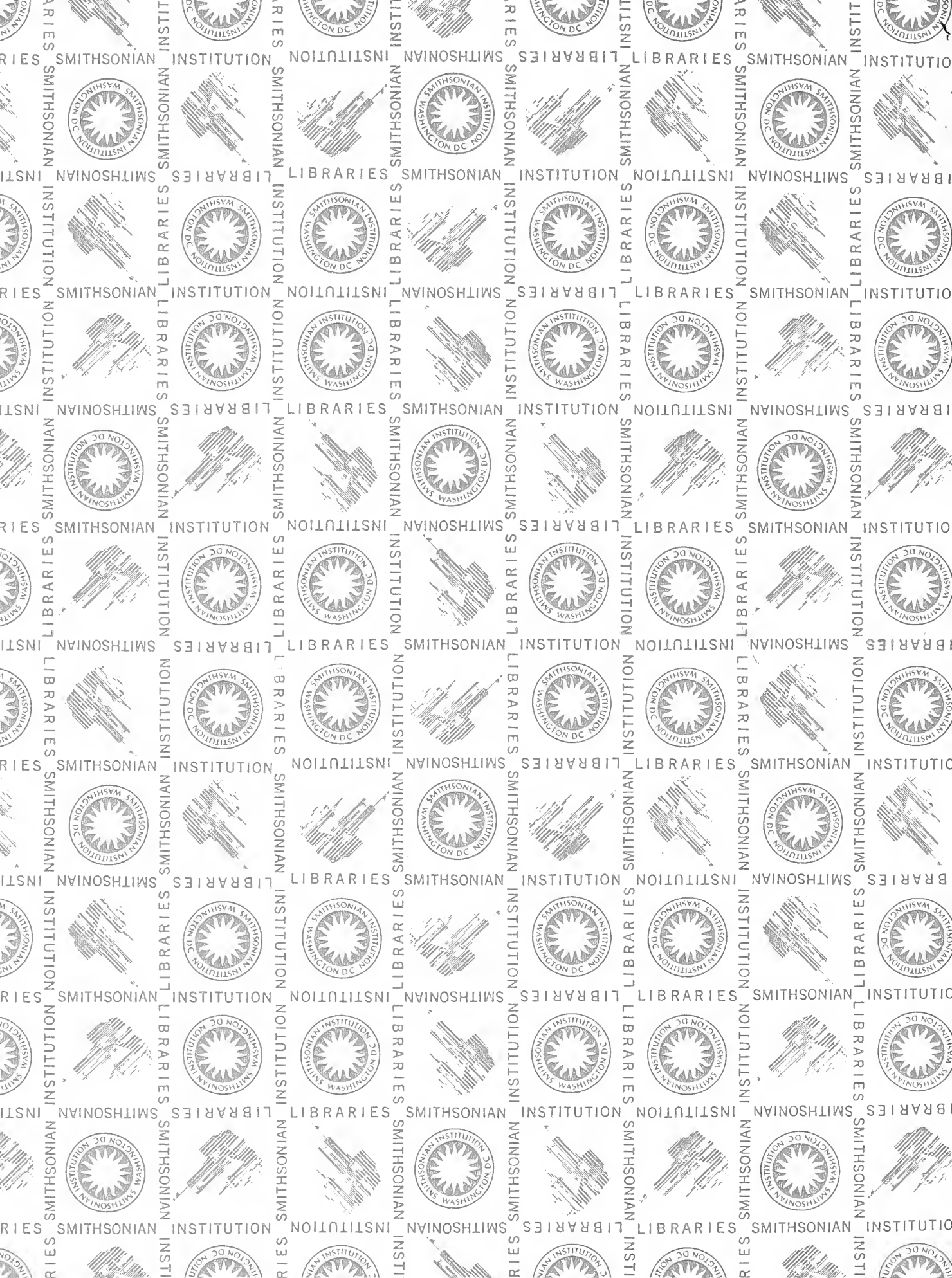
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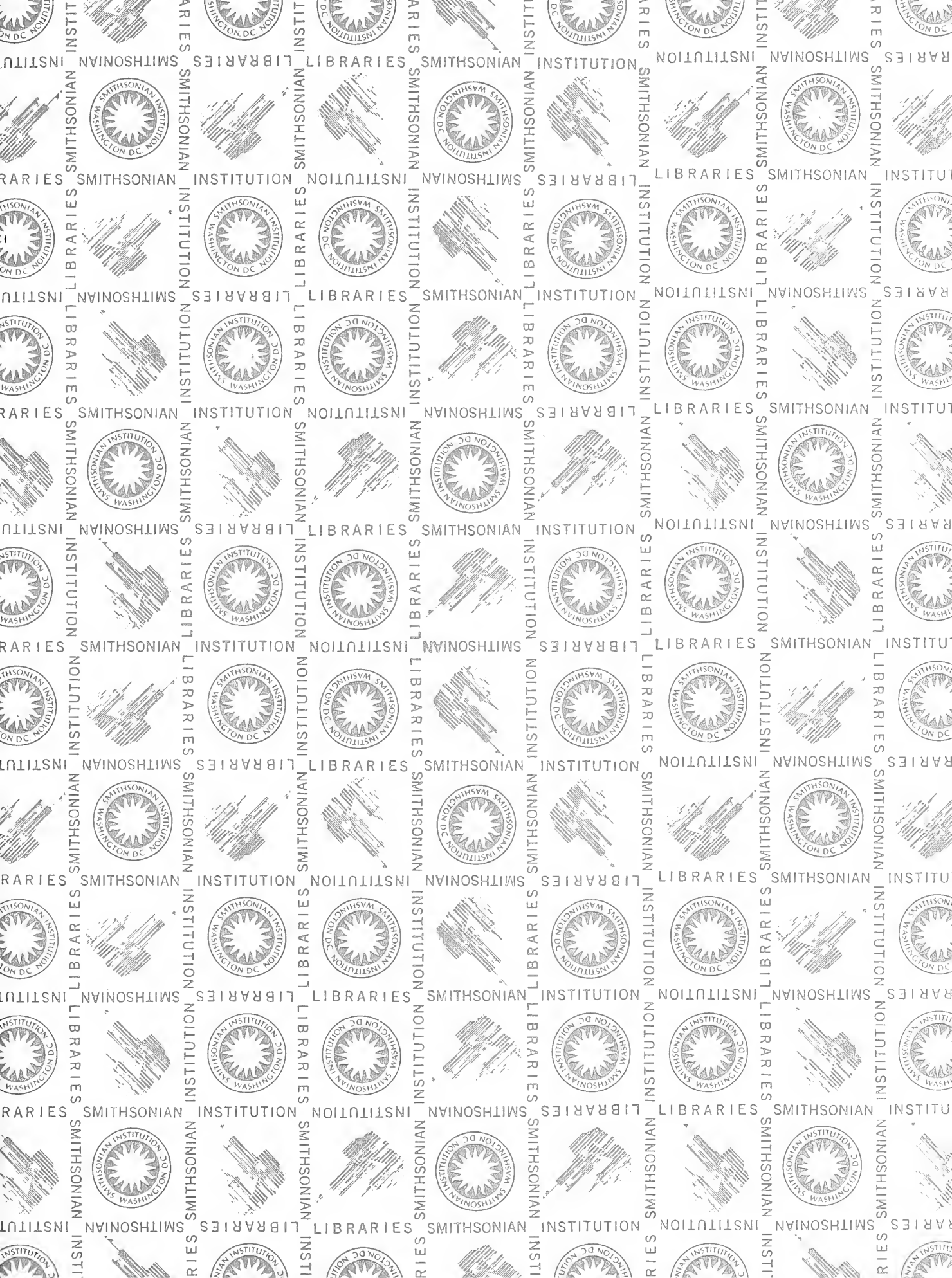
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ROBERT J. RAIKOW
Research Associate, Section of Birds,
Carnegie Museum of Natural History, and
Department of Biological Sciences,
University of Pittsburgh, Pittsburgh, Pennsylvania 15260

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CONTENTS

ABSTRACT

The gross morphology of the forelimb and hindlimb muscles was studied in approximately 100 species of songbirds, and analyzed cladistically to construct a phylogeny of the New World nine-primaried oscines. Methods and problems of phylogenetic analysis are discussed, and the rationale for the proposed phylogeny is presented. It is suggested that the Parulidae are the most primitive family of the group, the Thraupidae somewhat more advanced, and the Fringillidae and their descendents the most highly derived. The Icteridae may be the sister group of the Emberizinae, with *Spiza* as a link. The Drepanididae arose from the Carduelinae. The position of various problematic genera is discussed.

INTRODUCTION

This is a study of the evolutionary relationships in a large assemblage of songbirds, the New World nine-primaried oscines. The relationships among passerine birds continue to be unclear despite many studies attempting to unravel the pattern of their affinities. This is because of the large number of species, genera, and families involved, the general lack of distinctive characters defining specific groups, the tendency of groups to intergrade, and the high frequency of parallel and convergent similarities, especially in the suborder Oscines (Passeres). These problems are apparent in the confused taxonomic situation. On the one hand there has been a tendency to combine great numbers of species into large and unwieldy families, as in the treatment of the broadly defined Muscicapidae and Emberizidae of the Check-list of Birds of the World. On the other hand many small (often monotypic) families have been created for forms whose relationships to larger groups are undetermined, such as the Tersinidae, Catamblyrhynchidae, and Zeledoniidae. The family names used herein are those of Wetmore (1960) unless otherwise stated. If any sense is to be made of the oscine problem, the first task will have to be to cluster the large families into groups of apparently related forms, and then to analyze these groups individually. Affinity in this case should be based on evolutionary rather than purely phenetic relationships, that is, superfamilial assemblages should be hypothesized to be monophyletic. If the hypothesis of monophyly withstands scrutiny, the next step should be to analyze evolutionary relationships *within* each assemblage, that is, to develop a phylogeny of the families involved. In the course of this process an attempt should be made to determine to which large family each small family has its closest relationships, so that they may be combined where possible, and the number of families reduced. Once the phylogeny of several such assemblages has been determined, then the phylogenetic relationships between them may be analyzed, and gradually an overall phylogeny of the suborder Oscines can be constructed. Any attempt to work out relationships within the whole suborder by individual family comparisons is probably doomed to failure because of the complexity of the situation and the number of families involved.

This paper reports the results of an attempt to analyze the relationships within one large suprafamilial assemblage of the suborder Oscines. The New World nine-primaried oscines have traditionally been regarded as some sort of "natural" group, although various authors have differed on which families should be included, as well as on the rank to be given various groups. For the purpose of analysis I have included all of the groups that various authors have considered part of the assemblage. These are the Vireonidae (including the Vireolaniidae and Cyclarhidae), Parulidae, Zeledoniidae, Thraupidae, Coerebidae, Tersinidae, Catamblyrhychidae, Fringillidae (including the Emberizinae, Cardinalinae, and Carduelinae), Icteridae, and Drepanididae. Together these comprise a significant number of species, approximately 955, which amounts to roughly 11% of living species of birds, 19% of living species of passeriformes, and 24% of living species of oscines.

Problems of Phylogeny Construction

In any analysis of the evolutionary history of a group of organisms, several problems must be overcome, and the first is to choose a method of analysis. Assuming that evolution really has occurred, there must be a true phylogeny of the taxa under study, but we have no sure way to know what this is, or whether we have found it. In practice, then, a phylogeny is a hypothesis that may be presented for subsequent corroboration or refutation. Any method of analysis may be used to hypothesize a phylogeny. Many workers have constructed

branching diagrams (dendrograms) that they hypothesize to be phylogenies on the basis of shared similarities. In current terminology this would be termed a phenetic method, whether done by traditional methods of clustering taxa by resemblance, or by modern computer techniques. A more rigorous approach is advocated by followers of the cladistic school, who construct dendrograms by clustering "sister groups" on the basis of shared derived character states (synapomorphies) only. The differences between the phenetic and cladistic philosophies have engendered much vigorous and often rancorous discussion, though one has the impression that the philosophical differences are greater than the results that the two methods produce. It appears to me that both approaches represent extremes to which practical students need not limit themselves, and I expect that some intermediate position, containing contributions from both camps, will probably become the standard approach in the coming years. In the present study I will use mainly the cladistic method of analysis, but where this falters I will not hesitate to employ more traditional approaches. I see no justification for ignoring information that cannot be forced into a cladistic mold. While one good synapomorphy may be better than many "similarities," several solid similarities are still probably better in suggesting relationships than a trivial or contrived synapomorphy.

Once cladistics has been chosen as the principal method of phylogeny construction, several other problems arise: (1) It must be established that the taxon under analysis is monophyletic; (2) A sufficient number of characters must be found whose primitive/derived polarity can be determined with confidence; (3) Character conflicts must be resolved; (4) A consistent philosophy of evolutionary probabilities must be maintained. These points will be discussed individually.

(1) One could probably do a cladistic analysis of any collection of taxa, but unless the group can be shown to be probably monophyletic, there is little reason to suppose that the result represents a true phylogeny. To demonstrate monophyly, the most convincing arguments are demonstrations that the taxa comprising the group share one or more synapomorphies. If this is done, the existence of phenetic similarities will strengthen the hypothesis of monophyly. A hypothesis based on such similarities alone, however, is less convincing.

My analysis is based mainly on new information from the limb muscles, but first I will review other kinds of information to establish the likelihood that the New World nine-primaried assemblage is indeed monophyletic. Nevertheless, at the outset the hypothesis of monophyly should be presented as such, and after the analysis of new data is completed, this hypothesis should be reexamined to see whether the new information supports or refutes it. If it is supported, then the hypothesis of monophyly is strengthened, the proposed phylogeny may be taken as reasonable, and the whole exercise is justified. If it is refuted, then the major result of the study may be to show that a group formerly considered monophyletic or "natural" is not so, leading to the necessity for a reevaluation of its relationships.

(2) One of the greatest problems in cladistic analysis is finding a sufficient number of characters that can be analyzed to determine primitive to derived polarities. The more characters available, the greater the number of branching points that can be placed in a proposed phylogeny. Also, the validity of branching points is increased if more than one character shift can be indicated at each, especially if they are not parts of a single adaptive complex. The lower the categorical level of the group being analyzed, the more difficult it is to find many characters useful in analysis. The New World nine-primaried oscines are a particularly difficult group in this respect because they differ little in major features, while at the same time having undergone an enormous amount of speciation.

(3) Character conflicts arise when different characters indicate different branching patterns. Some characters must, therefore, have arisen independently in different lineages by convergence, parallelism, or evolutionary reversals, giving rise to false synapomorphies. This is especially troublesome in the lower taxonomic categories with groups that share a similar genetic background, and when the character states themselves are of a relatively simple nature, such as losses of structures or minor structural modifications. Although we may realize that these conflicts can result from recognized biological processes, in many specific cases it will be difficult or impossible to determine which alternative branching pattern is most likely to reflect the actual evolutionary history of the group. In such cases the expedient solution is to adopt the simplest pattern, or to attempt to correlate different characters so as to arrive at a reasonable solution. I emphasize strongly that it is impractical to expect that any phylogeny will be without some character

conflicts, but if it is recognized that these situations arise through ordinary biological processes, one need not refrain from developing a phylogenetic hypothesis that reflects the best fit available with the data at hand.

(4) In phylogenetic analysis, as in any branch of science, there may be a tendency to lose sight of the overall problem when confronted with a mass of individual data. In cladistics the problem is to maintain an overview of the whole evolutionary picture while dealing with many individual character phylogenies. In analyzing the New World nine-primaried oscines I will adhere to a model of evolution that postulates (a) that new major adaptations arise by the gradual modification of preexisting states, and (b) that the development of a new major adaptive feature may be followed by extensive radiation into specialized subdivisions of the new adaptive zone. Thus, in developing a phylogeny of these birds, I will hypothesize that the major family and subfamily groups represent secondary radiations in new adaptive zones associated primarily with feeding specializations. This hypothesis will be tested by comparing the correlation between feeding adaptations and modifications of the locomotor apparatus.

Monophyly of the New World Nine-Primaried Oscines

This group is generally but uncritically regarded as monophyletic, an idea based mainly on several lines of evidence that I will review below. Some of this evidence can be interpreted in terms of primitive and derived character states, even though it may previously have been presented in more traditional phenetic terms, and such evidences give the most convincing arguments in favor of monophyly. Other evidences cannot be interpreted in this way, and must be considered only in terms of general similarity. I do not agree with those who believe that such data are of no use in phylogenetic analysis. Such information may not be helpful in determining the exact pattern of branching points in a phylogeny, but it does indicate genetic similarity between taxa and can at least be used to support hypotheses about clusters of related forms within a larger group. The purpose of this section is not to analyze relationships *within* the New World nine-primaried complex, but to examine the likelihood that the group as a whole is monophyletic, which is a necessary precondition for a cladistic analysis of its subgroups. This hypothesis of monophyly will be reexamined after the limb muscle data have been analyzed to see whether the new information will corroborate or refute the idea of monophyly. It will be seen that neither earlier studies nor the present investigation support the inclusion of the Vireonidae in the New World nine-primaried oscine assemblage. Nevertheless, they are included here because they have traditionally been grouped with this assemblage.

Number of primaries.—The number of primary feathers varies among birds, but is usually constant within a family. The number may be reduced (or occasionally increased) among flightless forms, but in flying birds it varies from 10 to 12. In passeriformes the number is 10, but the tenth (outermost) primary is sometimes reduced to a vestige, and such birds are referred to as nine-primaried (Van Tyne and Berger, 1976:127–129). In all, this suggests that the nine-primaried condition among passerines is a derived state, and that a "functional" tenth primary is primitive.

Most of the New World nine-primaried oscines have only a vestigial tenth primary, except for some of the vireonids (*Cyclarhis, Vireolanius*, and some vireos, Mayr and Amadon, 1951:27). There are several other nine-primaried oscine families as well, such as the Zosteropidae, Hirundinidae, Alaudidae, and Motacillidae. These families do not appear to be closely related to the New World nine-primaried oscines, however, and most probably acquired a reduced tenth primary independently of them. Thus, except for the vireonids, the New World nine-primaried oscine assemblage is linked by this condition, which may be reasonably interpreted as a synapomorphy supporting the hypothesis that the group is monophyletic.

Pneumatic fossa.—A well-developed second pneumatic fossa of the humerus is a derived condition, whereas the primitive state is the presence of only one fossa (Bock, 1962:437). The derived state occurs in several oscine families, some of which are not closely related, suggesting parallel evolution of this state. Bock (1962:432) pointed out that the New World nine-primaried oscines ". . . appear to be the only larger subgroup within the oscines, that is rather uniform in having a fully developed condition." Again, the Vireonidae are an exception, having ". . . only the beginnings of the second fossa" (Bock, 1962:432). A few genera of Icteridae also have only a small second fossa, but because their familial position is unquestioned, this is best interpreted as a case of secondary reduction.

Tongue apparatus.—In a study of the skeleton and certain muscles of the tongue of songbirds, George (1962, 1968) found two correlated differences between the New World nine-primaried oscines and other families. The basihyale, an unpaired bone forming part of the central axis of the tongue skeleton, is laterally flattened in the Coerebidae, Drepanididae, Parulidae (except *Peucedramus*), Icteridae, Catamblyrhynchidae, Thraupidae, and in the cardueline, cardinaline, and emberizine finches. In 20 other oscine families, including the vireonids, cyclarhids, vireolaniids, and Tersinidae, it is cylindrical rather than flattened in cross section. There is a related variation in the hyoglossus obliquus muscle (which George termed the hypoglossus posterior). This muscle arises from the posterior processes of the paraglossalia, passing transversely beneath the basihyale without inserting on it (condition A) in most families examined. However, it is partly or completely attached to the basihyale (condition B) in the New World nine-primaried oscines except for the Cyclarhidae, Vireonidae, and *Peucedramus* (not determined for *Vireolanius* or *Tersina*). The cylindrical basihyale always occurs together with the unattached muscle (condition A) except in swallows (cylindrical and B), whereas in the Certhiidae a compressed basihyale also occurs with condition B. Because neither swallows nor creepers are closely related to the New World nine-primaried oscines, these exceptions need not concern us. The correlation of the compressed basihyale with the attached hyoglossus obliquus suggests a functional relationship, so these two characters will be regarded as a single complex character. The fact that the New World nine-primaried assemblage as a whole stands apart from many other oscine families in this character argues, at least on phenetic grounds, that they form a related group.

This suggestion would be greatly strengthened if it could be shown that the tongue condition in the New World nine-primaried oscines is a derived state. George (1962, Table 1) recognized two character states for the hyoglossus obliquus as already noted—A (not inserted on the basihyale), and B (inserted on the basihyale). This is a simplification, however, as there are variations in condition B. George recorded three variations, as shown in his figs. 5B–D and 6B–D. One is a condition peculiar to the Hirundinidae, which need not concern us. The condition shown in Figs. 5C and 6C has some fibers inserting on the basihyale, while a deeper layer passes beneath the bone. The condition shown in Figs. 5D and 6D has all fibers inserting on the basihyale, with none passing beneath it. There is some confusion in interpreting George's explanation because in his Table 1 he lists only the conditions A and B noted above, whereas in the text he notes conditions A (as in Table 1), B (as in the Hirundinidae, corresponding to Figs. 5B and 6B), and C (corresponding to Figs. 5C, D and 6C, D). Thus several variants are combined under condition B of Table 1, and it is not apparent which variant occurs in any given species having this general condition B.

These variations may be interpreted as stages in a morphocline. Either the hyoglossus obliquus is primitively attached to the basihyale, and is progressively losing this connection in some forms, or alternatively it is primitively not attached and is progressing to an inserted state. Which is the most likely direction of evolutionary change?

I believe that the condition in the New World nine-primaried oscines, with the hyoglossus obliquus attached to a flattened basihyale, is the derived state for the following reasons: (1) The cylindrical basihyale with no muscle insertion occurs in Alaudidae, Corvidae, Paridae, Sittidae, Chamaeidae, Cinclidae, Troglodytidae, Mimidae, Turdidae, Sylviidae, Motacillidae, Dulidae, Bombycillidae, Ptilogonatidae, Laniidae, Cyclarhidae, and Vireolaniidae (George, 1962, Table 1). These groups represent a great variety of different adaptive types with many different feeding specializations. It would seem most likely that the occurrence of the same structural conditions in all these different groups would be due to inheritance from a common ancestor, with the different condition in the New World nine-primaried oscines being related to some specialization in early members of this group. George (1962) argues that it is a specialization for more firmly attaching the movable tongue to the hyoid skeleton. (2) George (1962:27) notes that in the development of "*Setophaga picta*" (=*Myioborus pictus*) (Parulidae) from the nestling to the fledgling stage, the developing basihyale becomes progressively more flattened. Possibly this ontogenetic change parallels a phylogenetic change in the shape of the bone from a primitive to a derived state. As with any criteria for determining morphocline polarity, these are not without uncertainty, but on the whole it appears more likely than not that the condition of the tongue apparatus in the New World nine-primaried oscines is derived relative to the condition in oscines generally.

Egg-white proteins.—Sibley (1970) studied rela-

tionships among passerine birds by electrophoresis of egg-white proteins. The New World nine-primaried oscines were found to have similar electrophoretic patterns, even to the point where some groups generally recognized as families were virtually indistinguishable. Data of this sort cannot be analyzed cladistically because the direction of evolutionary change of the protein molecules is not known; indeed differences in molecular structure are only indirectly estimated by the procedure. This is because the technique does not examine molecular structure directly, but only electrophoretic mobility, which has a close but imperfect correlation with molecular structure as coded in the genes. Therefore, as Sibley (1970:21) makes clear, what is measured is "genetic relatedness," not genealogy. Nevertheless, this information is useful in the present context since I am concerned not only with cladistic genealogy, but also with the nature and amount of evolutionary change in evolving lineages between branching points. The close similarity in proteins indicates a close similarity in the genes coding for their production, and by any philosophy this is a strong indication that the various members of the New World nine-primaried oscine assemblage share a common genetic background. This strongly supports the idea of monophyly of the assemblage, even though it does not contribute to an analysis of its phylogenetic branching pattern.

Distribution and adaptive diversity.—The New World nine-primaried oscines occur mainly in the New World as their name implies; the exceptions are probably offshoots from this center of distribution and presumed origin. The coherence of the group suggests that the various families are interrelated as parts of a single adaptive radiation in the New World, and that the family groups correspond roughly to major adaptive niches based mainly on feeding specializations. Thus the Parulidae are mainly insectivorous; the Thraupidae, rather omnivorous but with a strong reliance on fruits; the Emberizinae may be characterized as mainly terrestrial foragers on relatively small seeds; the Carduelinae are mainly arboreal feeders on larger seeds; the Icteridae are marked by a specialized biomechanical system involving forceful jaw gaping into crevices, for opening fruits, and so forth. The Drepanididae are a special case; founded by a cardueline ancestor (Raikow, 1977*b*), the family radiated into an unusually wide variety of feeding niches in the absence of ecological competitors.

Sibley (1970:107) warns against overreliance on feeding specializations; the possibility of convergence provides a danger of classifying feeding niches rather than organisms. Nevertheless, there is also a possibility that useful taxonomic characters may be needlessly shunned by the fear that if adaptive, they are subject to convergence. Some organisms must be similar because of ancestry rather than convergence, and I think it probable that the major families of New World nine-primaried oscines represent the products of secondary radiations, arising when an ancestor entered a new adaptive zone. In the present case this idea is generally supported by the anatomy of the limb muscles as discussed below; this is important because these muscles are not part of the adaptive complex of the feeding mechanism.

These New World families often appear to be ecological equivalents of unrelated Old World families that have independently radiated into similar broadly-defined adaptive niches. Thus, for example, the Parulidae correspond to the Sylviidae, and the "New World finches" (Emberizinae and Cardinalinae) to the Ploceidae and Estrildidae. The Carduelinae, however, are widely distributed and ecologically diverse in both areas, and especially in the Old World. The Icteridae correspond to the Sturnidae.

In general, then, the cohesive assemblage of New World nine-primaried oscines presents a picture of distribution and specialization that is most reasonably interpreted as resulting from an evolutionary radiation into various broad feeding niches, with secondary radiations within each adaptive zone, and paralleling a separate pattern of similar radiations among other taxa in the Old World. This picture supports the idea that the group is monophyletic.

Pterylosis.—The unity of the nine-primaried New World oscine group is also attested to by the pterylosis. According to Mary H. Clench (personal communication) "aside from the distinctive pattern found in vireos (including *Cyclarhis* and *Vireolanius*) the body pterylosis of the New World nine-primaried oscines is relatively uniform. Minor differences in tract geometry and numbers of feathers may serve to group some genera, or to indicate certain family divisions, but the overall similarity of the pterylosis of this assemblage is striking."

Indistinct boundaries.—Although the New World nine-primaried oscines are usually classified in several separate families, the boundaries between them are often indistinct and arbitrary, many genera

being intermediate between the typical members of different families. This indicates that the group is cohesive and closely interrelated. Indeed, some authors have suggested merging them into a small number of families in the light of these difficulties. For example Sibley (1970) reduced the assemblage (excluding the vireonids) to a single family Fringillidae, with three subfamilies and nine tribes.

In the preceding discussion the hypothesis that the New World nine-primaried oscine assemblage (possibly excluding the Vireonidae) is monophyletic has been supported by various lines of evidence. Some of these, including the number of primaries, the pneumatic fossa of the humerus, and the tongue apparatus, appear to be derived character states grouping these taxa apart from other oscines. Other evidences, including the indistinct boundaries between families, the egg-white proteins, the pterylosis, and the geographic distribution and pattern of adaptive diversity, are not readily interpretable in cladistic terms, but nevertheless offer supporting evidence in favor of the theory of monophyly. Individually, each type of evidence generates a certain degree of confidence in the hypothesis; taken together they reinforce each other to further strengthen the hypothesis.

MATERIALS AND METHODS

Dissection

The forelimb and hindlimb muscles were dissected in nearly 100 species of songbirds (listed in Tables 2 and 3). Dissection was carried out under a stereomicroscope at magnifications of 6× to 25×, and the muscles were stained with iodine (Bock and Shear, 1972) to render fiber arrangement more visible. Detailed descriptions of the muscles were prepared for a reference species, *Loxops virens*, and are presented elsewhere (Raikow, 1976, 1977*a*). In the present study the muscles in each species are compared to those of *L. virens* and only the differences are noted. Drawings were made with a camera lucida attachment to the microscope.

Berger (1969) reviewed the variations in passerine appendicular muscles. He listed various muscles for which knowledge of structure and variation is uncertain or ambiguous. In the following account further information will be provided to clarify these problems with regard to the groups studied herein.

Nomenclature

The nomenclature of avian myology has a long and confusing history. Many workers have applied different names to the same muscle and the same name to different muscles. Some have occasionally attempted to stabilize the nomenclature for groups of muscles, but with only partial success. Most recently Berger (George and Berger, 1966) presented a standardized nomenclature for the entire avian muscular system. In the present study I have made some changes from that system to conform with a new system of names being developed by the International Committee of Avian Anatomical Nomenclature for publication as the *Nomina Anatomica Avium* (N.A.A.), which is intended to stabilize avian anatomical nomenclature in all branches of avian biology. The names for muscles used herein are those tentatively adopted for the N.A.A. at the time this is written. Synonyms with the nomenclature of Berger are given in my previous papers (Raikow, 1976, 1977*a*).

Determination of Primitive and Derived States

There are no certain methods for determining the direction or polarity of evolutionary change in an evolving character, but several criteria have become generally accepted as being reasonably reliable. The most common is out-group comparison. If a character varies within a group, and one of the variants also occurs in a related outside group, then the character state that occurs in both groups is considered primitive within the group being studied. Another method is in-group comparison. Within the group under study, the primitive state is considered likely to be that which is distributed among a variety of different subgroups. Ross (1974) and Kluge (1977) discuss the rationales underlying these and other methods of determination. Out-group comparisons are the principal method used in this study to determine character states, while in-group comparisons are used occasionally. I have tried to explain in the text the basis for each individual determination so that its validity may be examined. This practice is not always followed by students of cladistics.

For doing out-group comparisons it is important to choose taxa that are appropriate for comparison to the in-group. The general opinion is that proper out-groups should be of about the same categorical level as the in-group, and closely related to it so as to minimize the chances of convergence. Ideally an out-group should be the sister group of the in-group, but in practice this may be impossible to carry out because the sister group is not known. The practical approach is to choose groups that appear to be closely related to the in-group even though their precise cladistic relationships are unknown. In this study I have chosen certain likely out-groups for examination and have considered in addition the literature on more distant relatives. Thus, the muscle variations in birds generally are first examined, with particular emphasis on passerines (information summarized by George and Berger, 1966). To this I have added new observations on limb muscles from unpublished studies now underway in my laboratory. Clench and Austin (1974) summarized the ideas of various workers on the relationships of passerines as expressed in linear arrangements, and this has aided me in choosing groups for comparison. In their own arrangement the Nectariniidae, Estrildidae, and Ploceidae are grouped with the New World nine-primaried oscines, along with a few other families, so I have included a nectariniid in my dissections, and also have used the extensive observations of Bentz (1976) on the Ploceidae and Estrildidae. No principally New World oscine family appears close to the New World nine-primaried oscines, and in the Old World, many families are either highly specialized

(for example, Paradisaeidae, Hirundinidae) or are small or of limited distribution (for example, Artamidae, Irenidae) and, therefore, seem to be unlikely candidates for a sister-group relationship with the New World nine-primaried oscines. I have, therefore, concentrated my dissections on a small group of relatively unspecialized, mainly insectivorous, and evolutionarily successful Old World forms in the Sylviidae. These appear, rather intuitively, to lie near the origin of the New World nine-primaried oscines. My dissections of the limb muscles of these groups, and the work of Bentz (1976) on the ploceid-estrildid complex confirm that these groups are close to the New World types because their limb muscles in general are very similar. I also included some thrushes and mimids as examples of somewhat more distant but not highly specialized forms. Altogether I believe that this collection of out-groups gives a good idea of the ancestral muscle forms in the general group from which the New World nine-primaried assemblage arose. It is in any event the best solution to the problem of out-group selection that available information and materials permitted.

MUSCLES OF THE FORELIMB

Detailed descriptions and illustrations of the forelimb muscles in a reference species, *Loxops virens*, were given previously (Raikow, 1977*a*). In the following section only variations from these conditions are given; where no variations are noted, the condition in all forms studied was as described for *Loxops*.

M. latissimus dorsi.—This muscle has two separate parts in most birds, and sometimes also includes cutaneous slips that are not considered in this study. Of the two main parts, pars cranialis occurs in all forms studied here. Pars caudalis is a parallel-fibered, strap-shaped muscle that arises from the neural spines of the dorsal vertebrae caudal to the origin of pars cranialis. It passes craniolaterally to insert on the humerus deep to the insertion of pars cranialis. Pars caudalis is present in many nonpasserine orders as well as some families of passerines (George and Berger, 1966:293; Berger, 1969:220; Table 2) and, therefore, its absence in passeriformes is considered due to loss and is a derived state.

Pars caudalis occurs consistently in the Vireonidae, where it is present in all genera (Table 2). This supports the theory that the several genera are closely related, and set apart from the remainder of the assemblage. Among the Parulidae pars caudalis occurs only in *Peucedramus*, which supports the idea that the genus is misplaced in this family. Pars caudalis also occurs in a few species of Thraupidae and Icteridae, in some cases on one side of the body only (Table 1). This peculiar distribution could represent either the retention of a primitive state or its secondary reappearance (Raikow and Borecky, manuscript), but in view of its pattern of correlation with other myological characteristics, the latter explanation is more probable.

M. tensor propatagialis.—A scapular tendon (Raikow, 1977*a*) occurs in all members of the New World nine-primaried oscines (Fig. 1) except the Vireonidae. It was also found in some Turdidae and Mimidae, but not other out-groups (Table 2). Its presence in the New World nine-primaried oscines may be primitive, or the structure could have arisen independently in the other forms. There is no compelling evidence allowing a choice of these alternatives. At any rate its absence does distinguish the Vireonidae from the other families.

M. deltoideus major.—In most forms the caudal head inserts fleshy. In *Psarocolius* (Icteridae) it narrows distally and inserts by a stout tendon. This appears to be an autapomorphic state in this genus only.

M. deltoideus minor.—This muscle arises from the pectoral girdle and inserts on the head of the humerus. In most cases the origin is from the scapula only, but sometimes there is also an origin from the adjacent coracoid. In the latter case the coracoidal origin may form a somewhat separate head, or a single continuous belly may be present. Because I suspect that the separation of the two heads may be an

Table 1.—*Occurrence of M. latissimus dorsi caudalis in some species of Thraupidae and Icteridae.*[1]

Species	No. of specimens	Left side	Right side
Thraupidae			
Thraupis virens	7	+	+
Thraupis palmarum	2	+	+
Thraupis palmarum	1	−	+
Thraupis cyanocephala	3	−	−
Icteridae			
Cacicus cela	1	+	+
Cacicus cela	1	+	−
Cacicus haemorrhous	1	−	−
Psarocolius angustifrons	1	+	+
Psarocolius decumanus	1	−	−

[1] + = muscle present; − = muscle absent.

Table 2.—*Major variations in pectoral musculature. For each muscle, the character states and character phylogenies are as follows: M. latissimus dorsi pars caudalis: + = present (primitive), − = absent (derived); M. tensor propatagialis, scapular tendon: + = present, − = absent (polarity undetermined); M. deltoideus minor, coracoidal head: + = present (derived), − = absent (primitive); M. coracobrachialis cranialis, + = well developed (primitive), ± = vestigial (derived), − = absent (further derived); M. pronator profundus: 1 = single belly (primitive), 2 = 2 bellies (derived); M. flexor digitorum profundus: 1 = belly wide (primitive), 2 = belly narrow (derived).*

Species	M. latissimus dorsi pars caudalis	M. tensor propatagialis scapular tendon	M. deltoideus minor, coracoidal head	M. coraco-brachialis cranialis	M. pronator profundus	M. flexor digitorum profundus
			Sylviidae			
Sylvia atricapilla	−	−	+	±	1	1
Apalis flavida	+	−	−	±	1	1
Orthotomus atrogularis	+	−	+	±	1	1
Regulus satrapa	−	?	−	±	1	1
			Ploceidae/Estrildidae			
Grouped data on 41 genera from Bentz (1976). No. of genera indicated in parentheses	+(29) −(12)	−(41)	+(4) −(37)	+(2) −(39)	1(32) 2(8)	?
			Turdidae			
Turdus migratorius	+	?	−	±	1	2
Sialia sialis	−	+	−	−	1	2
Catharus ustulatus	+	+	−	−	2	2
			Mimidae			
Dumetella carolinensis	+	+	−	±	2	1
			Nectariniidae			
Nectarinia sperata	+	?	−	−	1	?
			Vireonidae			
Vireo olivaceus	+	−	−	+	1	1
Vireo pallans	+	−	−	+	1	1
Hylophilus poicilotis	+	−	−	±	1	1
Cyclarhis gujanensis	+	−	−	±	1	1
Vireolanius pulchellus	+	−	−	+	1	1
			Parulidae			
Dendroica coronata	−	+	−	−	2	1
Geothlypis semiflava	−	+	−	−	1	1
Icteria virens	−	+	+	−	2	1
Mniotilta varia	−	+	−	−	2	1
Myioborus miniatus	−	?	−	−	2	1
Oporornis tolmei	−	+	−	−	2	1
Peucedramus taeniatus	+	+	−	−	1	1
Seiurus aurocapillus	−	+	+	−	2	1
Wilsonia pusilla	−	+	−	−	2	1
Basileuterus rufifrons	−	+	−	−	1	1
			Zeledoniidae			
Zeledonia coronata	−	+	−	+	1	1
			Thraupidae			
Sericossypha albocristata	−	?	−	±	1	1
Rhodinocichla rosea	−	+	+	±	1	1
Euphonia laniirostris	−	+	−	±	1	1
Tangara cyanicollis	−	+	−	±	1	1
Piranga ludoviciana	−	+	−	±	2	1
Rhamphocelus passerini	−	+	−	−	2	1

Table 2.—(*Continued*)

Species	M. latissimus dorsi pars caudalis	M. tensor propatagialis scapular tendon	M. deltoideus minor, coracoidal head	M. coraco-brachialis cranialis	M. pronator profundus	M. flexor digitorum profundus
Thraupis virens	+	+	−	±	2	1
Tachyphonus rufus	−	+	−	±	2	1
Urothraupis stolzmanni	−	+	−	±	1–2	1
Nephelornis oneilli	−	+	−	±	1–2	1
			Tersinidae			
Tersina viridis	−	+	−	±	1	2
			Coerebidae			
Conirostrum speciosum	−	+	−	±	2	1
Coereba flaveola	−	+	−	?	2	1
Dacnis cayana	−	+	−	±	2	1
Diglossa barbitula	−	+	−	±	2	1
Cyanerpes cyaneus	−	+	−	?	2	1
Chlorophanes spiza	−	+	−	?	2	1
Euneornis campestris	−	+	−	±	2	1
			Catamblyrhynchidae			
Catamblyrhynchus diadema	−	+	−	+	2	1
			Fringillidae:Emberizinae			
Aimophila ruficauda	−	+	+	−	1	1
Arremonops conirostris	−	+	+	±	2	1
Calcarius lapponicus	−	+	+	−	2	1
Chlorura chlorura	−	+	+	−	2	1
Emberiza flaviventris	−	+	−	±	2	1
Geospiza fuliginosa	−	+	−	±	2	1
Junco hyemalis	−	+	+	±	2	1
Loxigilla portoricensis	−	?	−	±	2	1
Passerella iliaca	−	?	+	±	2	1
Plectrophenax nivalis	−	+	+	±	2	1
Zonotrichia capensis	−	+	+	−	2	1
			Fringillidae:Cardinalinae			
Passerina cyanea	−	+	−	±	2	1
Pheucticus ludovicianus	−	+	+	±	2	1
Cardinalis cardinalis	−	+	+	±	2	1
Saltator maximus	−	+	−	+	2	1
Guiraca caerulea	−	+	−	±	2	1
			Fringillidae:Carduelinae			
Leucosticte australis	−	+	+	?	?	1
Leucosticte tephrocotis	−	+	+	±	2	1
Carpodacus cassini	−	+	−	?	2	1
Pinicola enucleator	−	+	+	±	2	1
Serinus mozambicus	?	+	?	?	?	1
Serinus serinus	−	+	+	±	2	1
Carduelis carduelis	−	+	+	?	2	1
Chloris chloris	−	+	+	±	2	1
Hesperiphona vespertina	−	+	+	±	2	1
Loxia curvirostra	−	+	+	±	2	1
Pyrrhula pyrrhula	−	+	+	±	2	1
Carduelis pinus	−	+	+	±	2	1
Fringilla coelebs	−	+	−	±	2	1

Table 2.—(*Continued*)

Species	M. latissimus dorsi pars caudalis	M. tensor propatagialis scapular tendon	M. deltoideus minor, coracoidal head	M. coraco-brachialis cranialis	M. pronator profundus	M. flexor digitorum profundus
			Drepanididae			
Hemignathus procerus	−	+	+	−	2	1
Hemignathus wilsoni	−	?	+	?	2	1
Paroreomyza maculata bairdi	−	?	+	±	2	1
Loxops virens wilsoni	−	+	+	±	2	1
Psittirostra cantans cantans	−	+	+	±	2	1
Psittirostra cantans ultima	−	+	+	?	2	1
Psittirostra psittacea	−	+	+	±	2	1
Himatione sanguinea	−	+	+	?	2	1
Vestiaria coccinea	−	+	+	±	2	1
Palmeria dolei	−	+	+	±	2	1
			Icteridae			
Cacicus cela	+	+	−	±	1	2
Cassiculus melanicterus	−	+	−	±	2	2
Dolichonyx oryzivorus	−	+	+	±	2	2
Psarocolius decumanus	−	+	−	±	1	2
Quiscalus quiscula	−	+	+	±	2	2
Spiza americana	−	+	+	±	2	2
Sturnella magna	−	+	+	±	2	2
Sturnella neglecta	−	+	?	?	?	2
Agelaius phoeniceus	−	+	+	±	2	2
Icterus parisorum	−	+	−	±	2	2
Molothrus ater	−	+	+	±	2	2

artifact resulting from manipulation, I have not distinguished these variants. The significant variation in this muscle, therefore, is the presence or absence of a coracoidal head. I have described and illustrated this variation previously (Raikow, 1977*b*). A coracoidal head is absent in most out-groups and in most New World nine-primaried oscines, including the generally primitive Vireonidae and most Parulidae. For these reasons its absence is considered primitive and its presence derived in the assemblage under investigation.

The only groups in which a coracoidal head is virtually universal are the Carduelinae and Drepanididae, which argues for their close relationship (Raikow, 1977*b*). In the Parulidae it occurs only in *Icteria*, whose position in the family is uncertain, and in *Seiurus*, which is also aberrant in some hindlimb muscles. Among the Emberizinae the coracoidal head is absent only in a few genera. In the Thraupidae the coracoidal head is absent, but the scapular head is relatively slender, which is apparently also a derived state. In *Saltator* and *Catamblyrhynchus* the muscle is also slender, supporting their connection to this family. On the other hand, the peculiar *Rhodinocichla*, which is currently included in the Thraupidae with uncertainty, possesses a coracoidal head. See Table 2.

M. coracobrachialis cranialis.—This is a small (ca. 3-mm long) parallel-fibered muscle of the shoulder. It arises from the cranial surface of the head of the coracoid and inserts on the humerus between the articular surface and the pectoralis insertion. The muscle is buried in the tissue of the coracohumeral joint capsule, which must be dissected away to reveal the tiny belly (Fig. 2). It is well developed in *Vireo* and *Vireolanius*, but in *Hylophilus* and *Cyclarhis* it is pale in color and takes up little or no stain as compared to normal muscles. It arises by a well-defined tendon, but the belly is soft and difficult to separate from surrounding connective tissue, though slightly more dense than the latter. This appears to be a degenerate condition, with perhaps an absence or poor development of muscle fibers, which may be partly or mostly replaced by connective tissue. This would have to be determined by histological examination. In any event I term this condition vestigial, as it appears to represent a stage leading to complete loss. The muscle is well developed in *Zeledonia*,

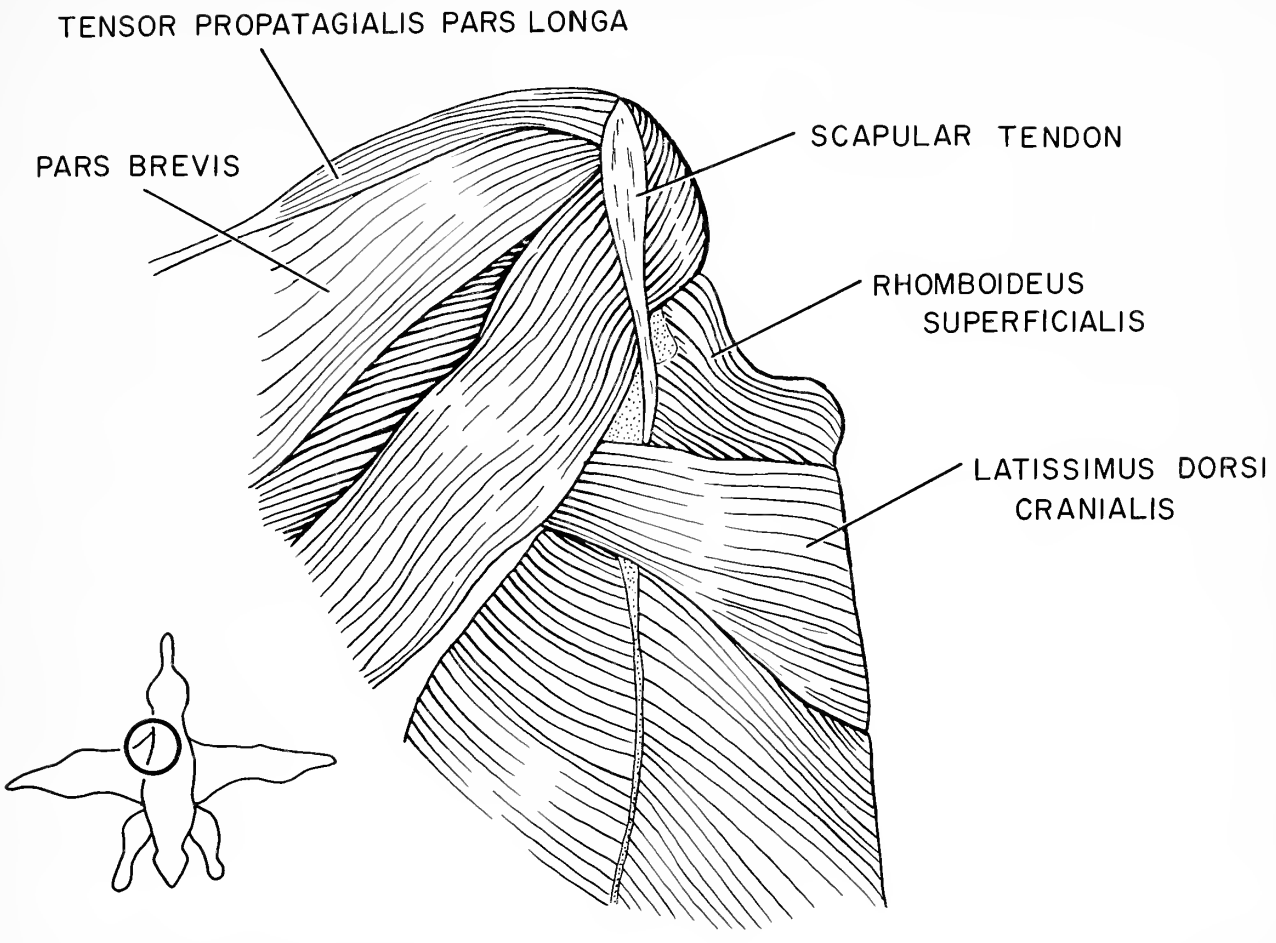

Fig. 1.—Dorsal view of the superficial muscles of the shoulder in *Hesperiphona vespertina* showing the scapular tendon passing from the origin of the two parts of M. tensor propatagialis to the dorsal surface of the scapula.

staining deeply. It is apparently absent in Parulidae, where I could find no trace. It is present in *Saltator* and *Catamblyrhynchus*. Otherwise it is demonstrable in most other forms as a vestige, or not at all, especially in smaller species.

This muscle is present in many nonpasserine orders (George and Berger, 1966:313–315); hence its reduction and loss are a derived trend in the group studied. Its relative retention in *Zeledonia* and *Catamblyrhynchus* set these forms apart as primitive offshoots of the Parulidae and Thraupidae, respectively, with which they are currently associated.

M. serratus superficialis.—In *Catamblyrhynchus* the caudal head of pars cranialis is wider than usual, arising not only from the first true rib (and its uncinate process) but also from the second true rib. Pars costohumeralis generally arises from the third true rib, but from the fourth in *Tangara* and *Tersina*.

M. rhomboideus superficialis.—In most cases this muscle inserts only on the scapula, but in a few cases the area of insertion is extended cranially so that a few fascicles also insert on the clavicle. This insertion is on the medial surface of the head of the clavicle and the shaft just distal to the head. It occurs in *Sialia, Nectarinia,* and to a small extent in *Quiscalus*. In *Zonotrichia, Chlorura,* and *Emberiza*, in contrast, the muscle is shorter, its anterior extreme ending about 2 mm short of the clavicle.

M. serratus profundus.—In most cases the cranial head arises by two slips, one each from the penultimate and antepenultimate cervical vertebrae. An origin from only the penultimate vertebra was found in *Wilsonia, Loxops*, and *Himatione*.

M. expansor secondariorum.—In *Rhodinocichla* this inserts only on the proximal two secondaries, rather than three as in most species.

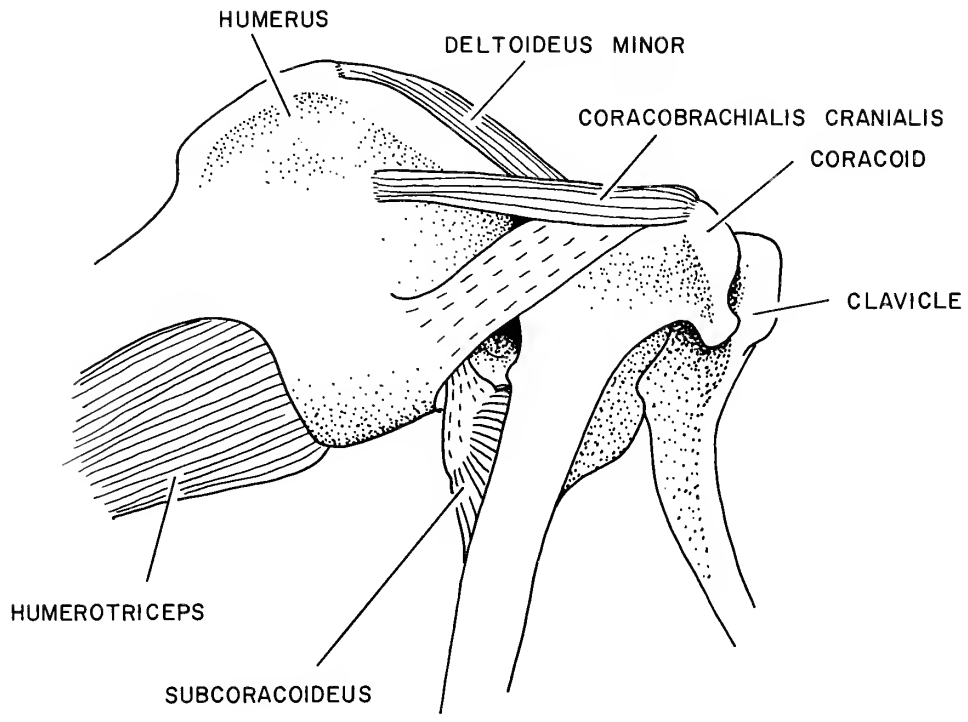

Fig. 2.—Deep shoulder muscles in *Vireolanius pulchellus* showing the well-developed coracobrachialis cranialis muscle.

M. pronator profundus.—As noted by Berger (1969:221), this muscle arises in part by a tendon from the humerus and in part fleshy from the adjacent humeroulnar pulley. These two parts tend to form separate bellies, but there is a distinct variation in the degree of separation in the bellies (Fig. 3). In Type 1 the two parts are adjacent and more or less fused together, so that the belly is essentially single, flat, and fan shaped. It spreads out to an essentially continuous line of insertion along the radius. In Type 2, however, the two bellies become separated. The proximal belly inserts proximally on the radius by a flat aponeurosis, while the distal belly inserts more distally on the radius by a narrow tendon that arises along its cranial surface. Between these two bellies there stretches a very thin connective tissue membrane that may represent a vestige of the formerly continuous tendon of insertion, but has no mechanical strength in this form, and indeed may merely be derived from fascia. The effect of this change is to make two distinct muscular bellies rather than one, presumably with a capability of acting more independently of each other in contraction, and thus increasing the functional versatility of the pronator profundus.

In their review of this muscle, George and Berger (1966:346–347) did not mention a separation of this muscle into two bellies in nonpasserine birds. Most other passerines studied have Type 1, but a few have Type 2. This suggests that the separation into two bellies (Type 2) is a derived state in passerines, probably arising several times (Table 2).

M. flexor digitorum profundus.—In all Icteridae examined (including *Spiza*) this muscle narrows distally so that its caudal margin does not overlie the distal part of the belly of the underlying M. ulnometacarpalis ventralis (Fig. 4). A similar condition was seen only in *Tersina*, among the New World nine-primaried oscines (Table 2).

M. extensor digitorum communis.—In *Tersina* the belly is longer than usual, extending nearly the entire length of the ulna.

M. interosseus dorsalis.—In *Zeledonia* the belly was lacking, the fine tendon being anchored in connective tissue. In *Catamblyrhynchus* the belly is reduced to a tiny vestige, the tendon still being present.

M. ulnimetacarpalis ventralis.—This muscle arises from the ulna, and may have one or two moderately separate heads. The two-headed condition may simply represent a v-shaped origin of the single bel-

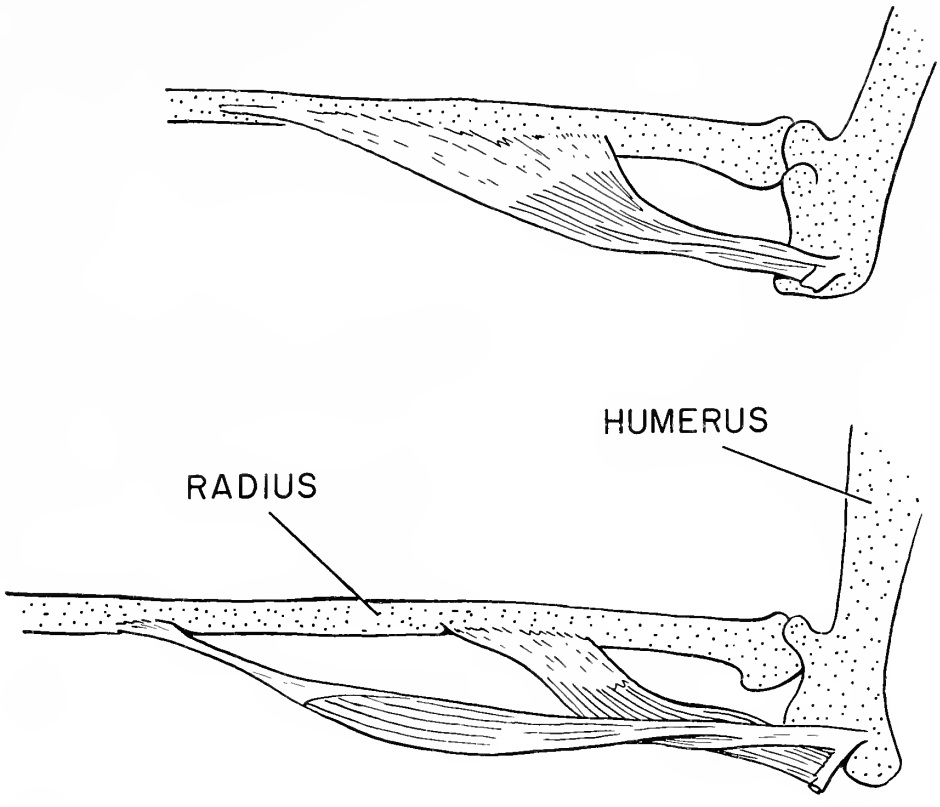

Fig. 3.—Variation in M. pronator profundus. Above, the primitive Type 1 with a continuous belly, shown in *Vireo olivaceous*. Below, the derived Type 2 with separate bellies, shown in *Dolichonyx oryzivorus*.

ly, however, distinctly separate heads being unusual. Most forms studied have the v-shaped origin, but some members of most families have the single condition, which occurs most consistently in the Drepanididae. Although Berger (1968:221) suggested that this variation might prove taxonomically useful, the extent of intergradation and apparently random distribution make it of no value in the present study.

MUSCLES OF THE HINDLIMB

Detailed descriptions and illustrations of the hindlimb muscles have been given previously (Raikow, 1976) for the reference species *Loxops virens*. In the following section I report variations in some of these muscles; where no variations are noted, the muscle in all forms examined was like that in *L. virens*. There are also some comments related to muscle variations in passerines generally, which will add to the review given by Berger (1969).

M. iliotibialis lateralis.—In some passerines the postacetabular portion of the muscle is absent (Berger, 1969:221) but both pre- and postacetabular portions were present in the New World nine-primaried oscines. Stallcup (1954:165) reported that in *Vireo* the muscle lacks a central aponeurotic portion found in other forms, but I found it present and identical to the condition in the other species, including some that Stallcup also dissected. In *Sericossypha* a small part of the dorsal fleshy part is absent between the pre- and postacetabular parts, and reaching as far distally as the distal central aponeurosis of the muscle.

M. femorotibialis externus.—No differences were noted. Berger (1969:221) reported a deep distal head in some passerines, which I also described in *L. virens*. Because Berger did not name these divisions,

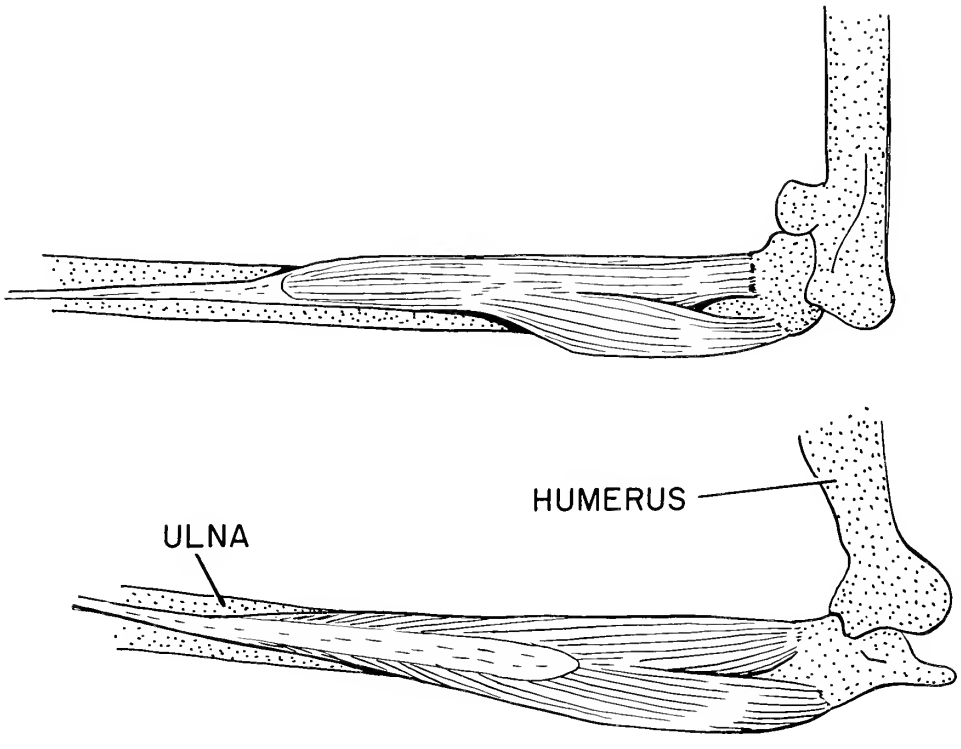

Fig. 4.—Variation in M. flexor digitorum profundus. Above, the derived state with narrowed distal portion of the belly, shown in *Spiza americana*. Below, the primitive state in *Sericossypha albocristata*.

I propose the terms pars proximalis (the superficial part) and pars distalis (the deep, distal head). Stallcup (1954) did not describe pars distalis, but apparently overlooked it as I found it in many species that he studied. I also found it in *Hirundo* (it was not mentioned by Gaunt, 1969), and in some Sturnidae, Mimidae, Corvidae, Turdidae, Alaudidae, Paridae, and Nectariniidae. The division of M. femortibialis externus into proximal and distal heads is probably common in passerines but has been overlooked by most workers.

M. pubo-ischiofemoralis.—Gaunt (1969) found that pars cranialis and pars caudalis are fused together in the Hirundinidae, but they are separate in the forms studied here. Stallcup (1954:168) claimed that the origin is modified in *Vireo*, but I could not find any difference from the other forms examined.

M. obturatorius lateralis.—This muscle has distinct dorsal and ventral bellies (Fig. 5). Pars ventralis is present in all forms studied, but pars dorsalis is absent in some. Because it occurs in many groups of birds, its absence in some genera of the families studied herein is undoubtedly due to loss and is derived. When present, pars dorsalis varies in size. I term it small when the area of origin is not caudal to the obturator foramen; medium when the origin lies between the obturator foramen and the midpoint of the ilioischiatic fenestra; and large when the origin lies caudal to this point. Pars dorsalis is large in most families studied herein, and in most of the out-groups as well. Thus its reduction in size in the Carduelinae and Drepanididae must be a derived state, and one that supports the theory (Raikow, 1977*b*) that these families are sister groups. Reduction continues to a point of complete loss in some cardueline genera. The pars dorsalis is also independently lost in a few genera of families where it is otherwise well developed (Table 3). Bentz (1976) found a similar tendency toward loss in the Old World finches.

M. gastrocnemius.—This muscle has three separate bellies with a common tendon of insertion. Pars externa and pars intermedia do not vary, but pars interna is highly variable and of some taxonomic use (Fig. 6). Pars interna is the most superficial muscle on the medial surface of the crus, arising by two distinct heads. The superficial head arises in part from the inner cnemial crest of the tibiotarsus, while a band of fibers (the patellar band) may extend around

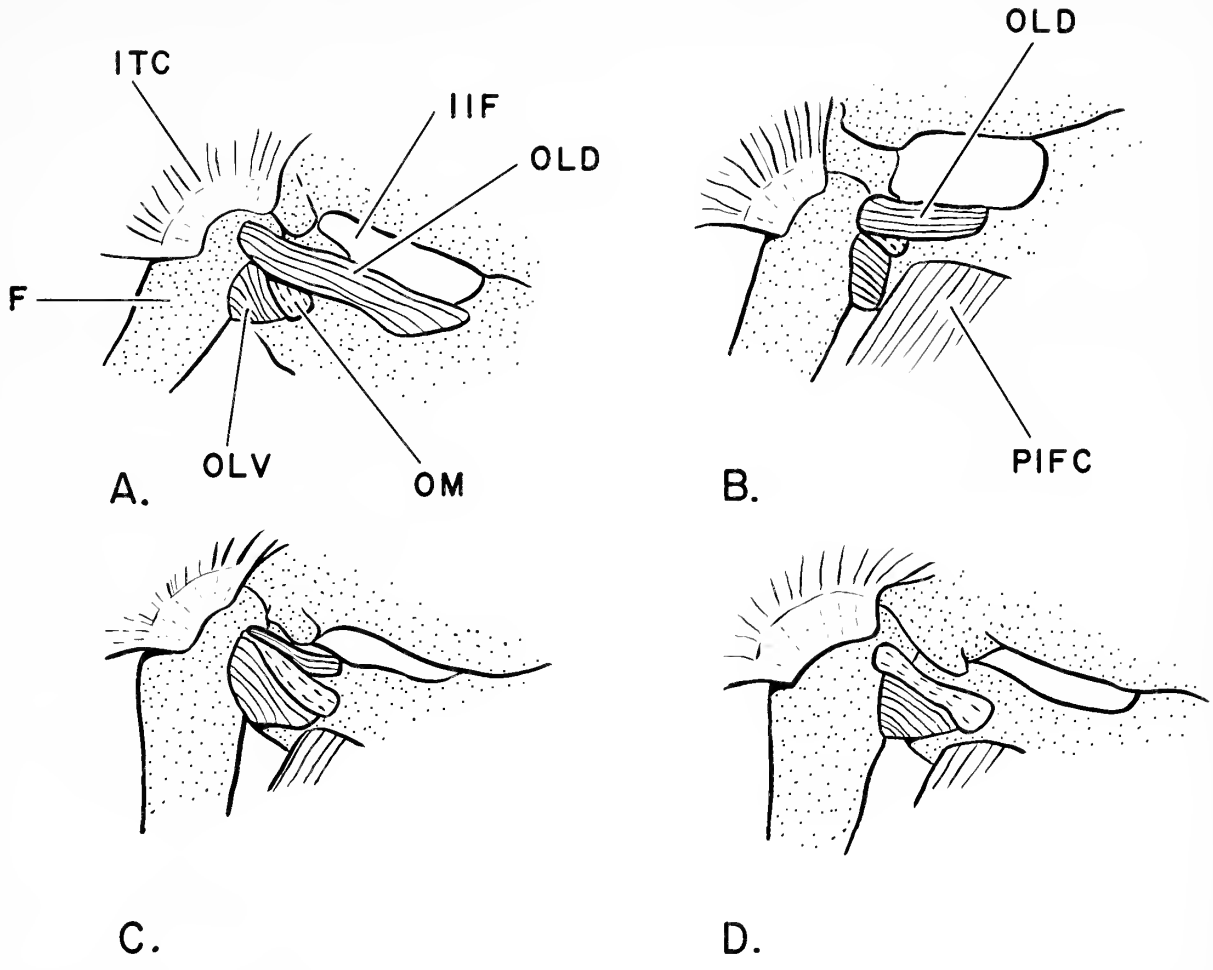

Fig. 5.—Deep muscles of the hip in four species of New-World, nine-primaried oscines, showing variation in the size and occurrence of M. obturatorius lateralis pars dorsalis. A) *Cyanerpes cyaneus*, showing muscle of large size; B) *Loxops virens wilsoni*, showing muscle of medium to large size; C) *Pinicola enucleator*, showing muscle of small size; D) *Hesperiphona vespertina*, showing muscle absent. Abbreviations: F, femur; IIF, ilio-ischiatic fenestra; ITC, M. iliotrochanterichus caudalis; OLD, M. obturatorius lateralis pars dorsalis; OLV, M. obturatorius lateralis pars ventralis; OM, tendon of M. obturatorius medialis; PIFC, M. pubo-ischiofemoralis pars cranialis.

the knee, arising from the patellar tendon. The deep head of pars interna arises from the medial surface of the head of the tibiotarsus. The two heads fuse and the common belly extends caudally. Stallcup (1954) noted some variation in pars interna, but a more detailed classification of this variation is given here. In Type 1 the superficial head is present, including a patellar band. In Type 2 the superficial head is present but lacks a patellar band. In Type 3 the superficial head is absent. In forms having Type 1 the relative size of the patellar band varies. This is expressed in Table 3 as the percentage of the distance between the patellar crest and the patella which the origin of the patellar band covers (Fig. 7). This variation is only of occasional usefulness, but variation in the Types 1 through 3 is more valuable taxonomically. The three types appear to be stages in a morphocline. I believe that Type 1 is the ancestral state in the New World nine-primaried oscines because of out-group comparisons (Table 3), because it is the most common condition within the group, and because it occurs in families (for example, Parulidae) generally considered on other grounds to be primitive within the assemblage.

The derived state, loss of the patellar band, occurs in some cardinalines and thraupids, most carduelines, and all icterids. If this were considered a synapomorphy, however, it would conflict with oth-

Table 3.—*Major variations in pelvic musculature. For each muscle, the character states and character phylogenies are as follows: M. gastrocnemius pars interna: 1 = superficial head present, including patellar band (primitive), 2 = superficial head present but patellar band absent (derived), 3 = superficial head absent (further derived); Patellar band: decimal value = width of band as % of distance between patella and patellar crest (polarity undetermined); M. obturatorius lateralis pars dorsalis: − = absent (derived), size classes defined in text (polarity undetermined); M. plantaris: + = present (primitive), − = absent (derived); M. peroneus brevis tibial head: − = absent (primitive), ± = partially developed (derived), + = fully developed (further derived); M. flexor digitorum longus: ABB (primitive), other patterns (derived).*

Species	M. gastrocnemius pars interna	Patellar band	M. obturatorius lateralis pars dorsalis	M. plantaris	M. peroneus brevis tibial head	M. flexor digitorum longus
			Sylviidae			
Sylvia atricapilla	1	0.95	lge.	+	−	ABB
Apalis flavida	1	0.80	lge.	+	−	ABB
Orthotomus atrogularis	1	1.00	lge.	+	−	ABB
Regulus satrapa	1	0.60	lge.	−	+	ABB
			Plocidae/Estrildidae			
Grouped data on 41 genera from Bentz (1976). No. of genera indicated in parentheses. Some genera have more than one condition in different species.	1(7) 2(30) 3(8)	0–1.00	−(26) sml.(10) med.(5) lge.(3)	+(37) −(4)	−(41)	ABB(37) ABC(3) AAA(1)
			Turdidae			
Turdus migratorius	1	0.50	lge.	+	−	ABB
Sialia sialis	1	0.50	lge.	+	−	ABB
Catharus ustulatus	1	0.80	lge.	+	−	ABB
			Mimidae			
Dumetella carolinensis	1	1.00	lge.	+	−	ABB
			Nectariniidae			
Nectarinia sperata	1	0.50	lge.	+	−	AAB
			Vireonidae			
Vireo olivaceus	1	0.70	med.	+	−	AAB
Vireo pallens	1	0.90	lge.	+	−	AAB
Hylophilus poicilotis	1	0.80	med.	+	−	AAB
Cyclarhis gujanensis	1	0.30	med.	+	−	AAB
Vireolanius pulchellus	1	1.00	sml.	+	−	AAB
			Parulidae			
Dendroica coronata	1	0.70	med.	+	−	ABB
Geothylpis semiflava	1	0.50	lge.	+	−	ABB
Icteria virens	1	0.90	med.	+	−	ABB
Mniotilta varia	1	0.80	med.	+	−	ABB
Myioborus miniatus	1	0.80	med.	+	−	ABB
Oporornis tolmei	1	0.90	med.	+	−	ABB
Peucedramus taeniatus	1	0.90	lge.	+	−	ABB
Seiurus aurocapillus	1	0.90	−	+	+	ABB
Wilsonia pusilla	1	1.00	med.	+	−	ABB
Basileuteurus rufifrons	1	1.00	med.	+	−	ABB
			Zeledoniidae			
Zeledonia coronata	1	1.00	med.	+	−	ABB
			Thraupidae			
Sericossypha albocristata	2	−	med.–lge.	+	±	ACB
Rhodinocichla rosea	1	0.60	lge.	+	−	CBB
Euphonia laniirostris	1	0.50	med.	+	−	ABB
Tangara cyanicollis	1	0.60	med.	+	±	ABB
Piranga ludoviciana	2	−	med.	+	−	ABB

Table 3.—(*Continued*)

Species	M. gastrocnemius pars interna	Patellar band	M. obturatorius lateralis pars dorsalis	M. plantaris	M. peroneus brevis tibial head	M. flexor digitorum longus
Rhamphocelus passerini	2	–	med.	+	–	ABB
Thraupis virens	2	–	lge.	+	–	ABB
Tachyphonus rufus	3	–	lge.	+	–	ABB
Urothraupis stolzmanni	1	0.80	lge.	+	±	ABA
Nephelornis oneilli	1	0.80	lge.	+	±	ABB
			Tersinidae			
Tersina viridis	3	–	med.	+	–	ACB
			Coerebidae			
Conirostrum speciosum	1	0.40	med.	+	–	ABB
Coereba flaveola	1	1.00	lge.	+	±	ABB
Dacnis cayana	1	0.40	med.	+	–	ABB
Diglossa barbitula	1	1.00	lge.	–	–	ABB
Cyanerpes cyaneus	3	–	lge.	–	–	ABB
Chlorophanes spiza	1	0.30	lge.	+	–	ACB
Euneornis campestris	1	0.80	lge.	+	–	ABB
			Catamblyrhynchidae			
Catamblyrhynchus diadema	1	1.00	lge.	–	–	ABA
			Fringillidae:Emberizinae			
Aimophila ruficauda	1	0.60	lge.	+	–	ABB
Arremonops conirostris	1	1.00	med.	+	–	ABB
Calcarius lapponicus	1	0.70	med.	+	–	BBB
Chlorura chlorura	1	1.00	?	+	–	ABB
Emberiza flaviventris	1	0.40	lge.	+	–	?
Geospiza fuliginosa	1	1.00	lge.	+	–	ABB
Junco hyemalis	1	1.00	lge.	+	–	BBB
Loxigilla portoricensis	1	0.60	lge.	+	–	ABB
Passerella iliaca	1	0.80	lge.	+	–	BBB
Plectrophenax nivalis	1	0.30	lge.	+	–	?
Zonotrichia capensis	1	0.70	med.	+	–	ABB
			Fringillidae:Cardinalinae			
Passerina cyanea	2	–	lge.	+	–	ABB
Pheucticus ludovicianus	3	–	lge.	+	–	ABB
Cardinalis cardinalis	1	0.25	lge.	+	–	ABB
Saltator maximus	1	0.25	sml.	+	–	ABB
Guiraca caerulea	2	–	lge.	+	–	AAB
			Fringillidae:Carduelinae			
Leucosticte australis	1	0.70	sml.	+	–	BBB
Leucosticte tephrocotis	1	0.60	–	+	–	ABB
Carpodacus cassini	2	–	sml.	–	–	ABB
Pinicola enucleator	2	–	sml.	+	–	ABB
Serinus mozambicus	2	–	med.	+	±	ABB
Serinus serinus	2	–	sml.	–	±	?
Carduelis carduelis	3	–	med.	–	+	ABB
Chloris chloris	3	–	–	+	+	ABB
Hesperiphona vespertina	3	–	–	+	–	ABC
Loxia curvirostris	3	–	sml.	–	+	ABB
Pyrrhula pyrrhula	3	–	–	+*	+	ABB
Carduelis pinus	3	–	sml.	–	+	ABB
Fringilla coelebs	3	–	sml.	+	–	ABB

Table 3.—(*Continued*)

Species	M. gastrocnemius pars interna	Patellar band	M. obturatorius laterialis pars dorsalis	M. plantaris	M. peroneus brevis tibial head	M. flexor digitorum longus
			Drepanididae			
Hemignathus procerus	1	0.75	med.	+	+	ABB
Hemignathus wilsoni	1	0.60	sml.	+	+	ABB
Paroreomyza maculata bairdi	1	0.60	sml.	+	+	ABB
Loxops virens wilsoni	1	0.75	med.	–	+	ABB
Psittirostra cantans cantans	1	0.50	sml.	+	+	ABA
Psittirostra cantans ultima	1	0.50	sml.	+	+	ABA
Psittirostra psittacea	1	0.40	sml.	+	+	ABB
Himatione sanguinea	1	0.60	med.	–	+	ABB
Vestiaria coccinea	1	0.70	sml.	–	+	ABB
Palmeria dolei	1	0.75	med.	–	+	ABA
Ciridops anna	1	>0.50	med.	?	?	?
			Icteridae			
Cacicus cela	2	–	lge.	+	–	ABA
Cassiculus melanicterus	2	–	med.	+	–	ABB
Dolichonyx oryzivorus	2	–	med.	+	–	ABB
Psarocolius decumanus	2	–	lge.	+	–	ABB
Quiscalus quiscula	2	–	lge.	+	–	ABB
Spiza americana	2	–	med.	+	–	ABB
Sturnella magna	2	–	–	+	–	ABA
Sturnella neglecta	2	–	?	+	?	?
Agelaius phoeniceus	3	–	lge.	+	–	ABA
Icterus parisorum	3	–	med.	+	–	ABB
Molothrus ater	3	–	med.	+	–	ABB

* Reduced.

er data as discussed below, so most probably the loss of the patellar band has occurred independently in these three groups.

M. peroneus brevis.—This muscle shows an important variation not previously described in birds. In most forms studied it arises from the fibula alone, or also the adjacent tibial shaft. In some, however, there is also a fleshy origin from the caudal margin of the lateral cnemial crest, just caudal to the origin of the tibial head of M. tibialis cranialis. This *tibial head* passes distad superficial to the femoral head of the tibialis cranialis, and joins the usual fibular head to form a single belly. I have illustrated this muscle and discussed its mode of origin elsewhere (Raikow, 1977*b*). Its occurrence is listed in Table 3. Because it does not occur in other birds so far as known, and because it is found here in the carduelines and drepanidids, two groups of advanced position in the New World nine-primaried assemblage, the presence of a tibial head is clearly derived and argues for a sister-group relationship of these two families (Raikow, 1977*b*). A partial or complete tibial head was also found in a few other genera (Table 3) where it presumably arose independently.

M. flexor perforatus digiti II.—In *Rhodinocichla rosea* the muscle was distinct, having a small secondary head originating from the surface of M. flexor hallucis longus, and joining the main head along its medial border. This condition was not observed in any other form. Berger (1969:222) reported that the tendon of insertion in this muscle is not perforated by the tendons of M. flexor perforans et perforatus digiti II or M. flexor digitorum longus in various passerines. Stallcup (1954:171) claimed that it is so perforated in the species he studied. I believe that in all the species I studied the tendon is not perforated, and that Stallcup made an error in interpretation. It appears from his description of the insertion, when compared to observation of specimens, that what he considered a sheathlike termination of the tendon of M. flexor perforatus digiti II is actually the tendon sheath of the first phalanx. Although this is in contact with the tendon of M. flexor perforatus digiti II at its insertion, the sheath

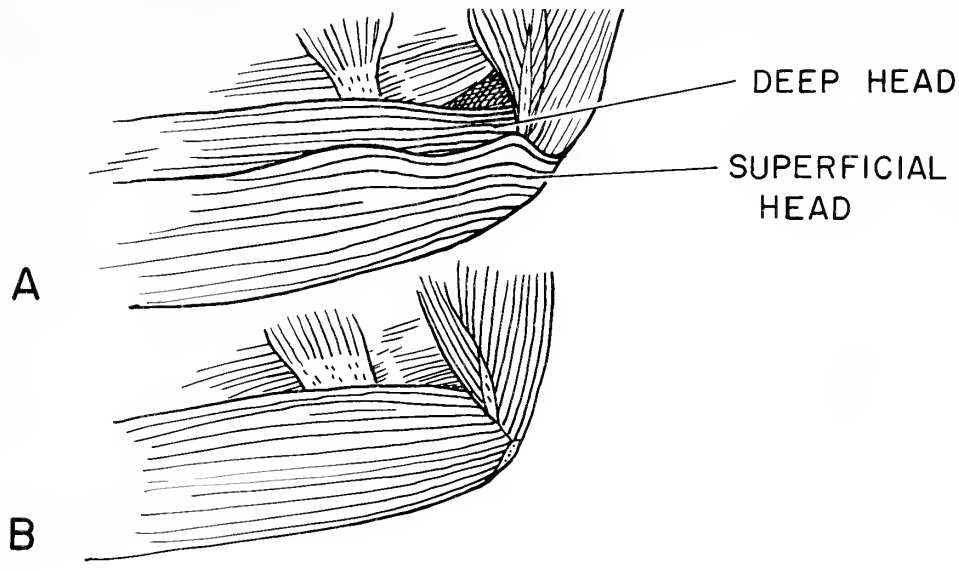

Fig. 6.—Medial view of the knee area showing variation in M. gastrocnemius pars interna. A) *Sericossypha albocristata*, showing the superficial head present as in Types 1 and 2. B) *Icterus parisorum*, showing Type 3 with the superficial head lacking.

itself should not be considered part of that tendon. Such a sheath covers all the flexor tendons on the plantar surface of each phalanx of every digit. Stallcup (1954:171) stated that this muscle is not in contact with M. flexor hallucis longus in *Vireo*, but I found that it is in such contact as in the other species studied.

M. plantaris.—This muscle is designated by the letter F in muscle formulae, and until recently was considered present in all passerines. However, Gaunt (1969) found it absent in most Hirundinidae, and Bentz (1976) in some estrildids. I also found it absent in some New World nine-primaried oscines (Table 3). Because M. plantaris is present in many passerine and nonpasserine families, its absence here is considered a derived state due to loss.

M. flexor hallucis longus.—Berger (1969:22) noted that the muscle may have one, two, or three heads of origin in passerines. Stallcup (1954:174) reported the lateral head absent in *Vireo*, but I found it present. According to Stallcup (1954) the usual origin is by two heads, but Berger found three heads in *Agelaius* (George and Berger, 1966:443) and *Dendroica* (Berger, 1968:613). My findings agree with Berger's descriptions, and it appears that Stallcup failed to distinguish between the intermediate and medial heads described by Berger.

M. flexor digitorum longus.—There is a third, femoral head of origin in some birds. Among the forms included in this study, a femoral head was found only in the tanager *Sericossypha*, arising from the lateral condyle of the femur and passing caudad to join the fibular head. The tendon of this muscle divides into three branches inserting on the three anterior digits. Variations in this pattern of insertion (Fig. 8; Table 3) are sufficiently constant in recognized groups to be useful in this study. The usual pattern in the New World nine-primaried oscines is ABB (letter designations are shown in Fig. 8), the main exception being the Vireonidae with AAB. In other families there are occasional variations, usually involving the addition of delicate accessory vincula, but only in the Vireonidae is the variation consistent. It is difficult to determine the polarity of this character as the structural changes involved are minor, but out-group comparisons (Table 3) suggest that ABB is probably primitive.

M. flexor hallucis brevis.—In the Vireonidae this muscle is greatly enlarged and somewhat bipennate in structure, while in most groups it is quite small (or even apparently absent) and appears to be narrowly fan-shaped (Fig. 9). This sets the Vireonidae apart from the New World nine-primaried oscines, and also clusters the four genera of the Vireonidae, attesting to the unity of the group. The large size is probably a derived specialization of the Vireonidae as it did not occur in other groups studied.

M. extensor hallucis longus.—This muscle con-

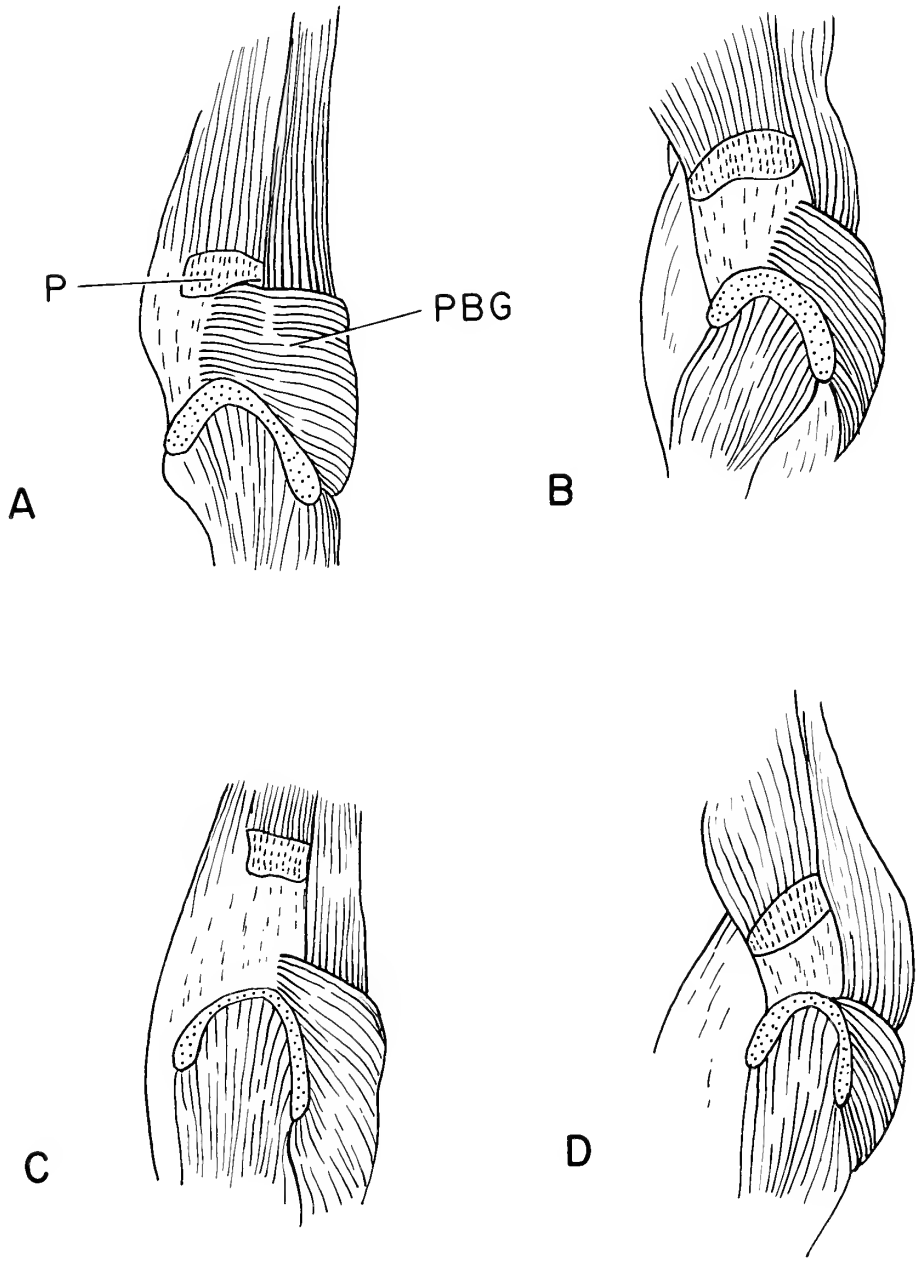

Fig. 7.—Cranial view of the knee in four species showing variation in the size and occurrence of the patellar band of M. gastrocnemius pars interna. A) *Coereba flaveola*, Type 1, patellar band size 1.00; B) *Leucosticte tephrocotis*, Type 1, patellar band size 0.60; C) *Saltator maximus*, Type 1, patellar band size 0.25; D) *Carpodacus cassini*, Type 2, patellar band absent. See text for explanation. Abbreviations: P, patella; PBG, patellar band of M. gastrocnemius.

sists of proximal and distal heads. The proximal head is as described by Berger (1968). A distal head has been described in a few nonpasserine birds (George and Berger, 1966:454–455), but apparently has not previously been found in passerines. It can be demonstrated only under high magnification (25×) and with the iodine stain. It is a fan-shaped muscle about 3 mm long, and arises from the medial surface of the distal end of the shaft of the tarsometatarsus just proximal to the first metatarsal. It passes distad alongside the tendon of the proximal head and inserts into the joint capsule between metatarsal I and the proximal phalanx of the hallux (Fig. 9).

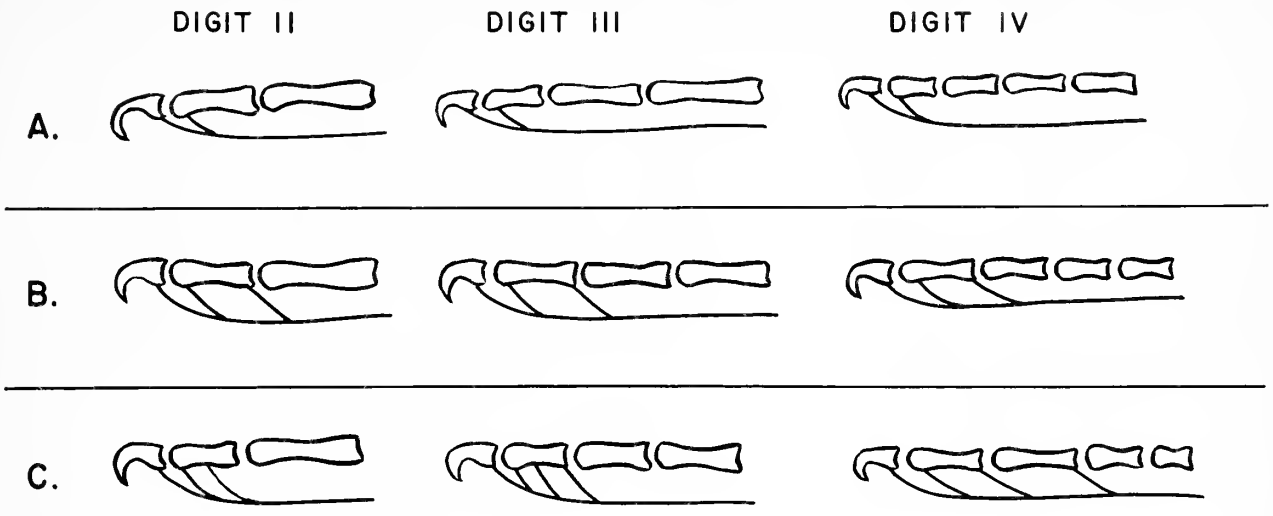

Fig. 8.—Diagram showing the patterns of insertion of the three branches of M. flexor digitorum longus on digits II, III, and IV. The formula for insertions can be determined from this diagram. For example, ABB, the most common pattern, means that digit II has the form shown in line A, whereas digits III and IV have the forms shown in line B.

The proximal head shows little variation except that in the vireonid group it is relatively larger compared to the other forms studied. This enlargement is not as striking as the enlargement of M. flexor hallucis brevis in the same group, but is perhaps related to it as part of an adaptation for increased strength in movement of the hallux.

M. lumbricalis.—Stallcup (1954) described this muscle in the forms he studied, but Berger (1966, 1968) did not find it in *Agelaius* or *Dendroica*. I found the muscle to be universally present in the forms studied here. It is small and strap-shaped, and lies deep in the plantar surface of the foot. It arises from the tendon of M. flexor digitorum longus just proximal to the point at which that tendon trifurcates, and inserts on the joint pullies of digits III and IV. No variation was observed. The muscle is very easily stretched, suggesting that in passerines it may be partly or completely converted to an elastic ligament, but this would have to be determined histologically.

CHARACTERIZATION OF TAXA

Vireonidae

The genera *Vireo, Hylophilus, Cyclarhis*, and *Vireolanius* are often included in one family (Mayr and Amadon, 1951; Blake, 1968), but the latter two are sometimes placed in separate families near the Laniidae (Wetmore, 1960). In terms of limb muscles, the four genera are generally primitive in most characters that vary significantly in the New World nine-primaried oscines, but also show some unique derived character states (Tables 3 and 4). The superficial head of M. gastrocnemius pars interna is more clearly separate from the deep head than in the other families. The insertion pattern of M. flexor digitorum longus is AAB compared to the usual ABB pattern of other families. M. flexor hallucis brevis is greatly enlarged in all four genera; in no other family does it approach this size, and indeed is often so small as to be difficult to identify. These are interpreted as derived states. The tensor propatagialis scapular anchor is absent in the vireonids, but present in the other families. I cannot determine whether this is a derived state, but at least it does separate the vireonids from the other groups. M. coracobrachialis cranialis is well developed in *Vireo* and *Vireolanius*, but is reduced in *Hylophilus* and *Cyclarhis*, the latter being a derived state shared with most of the assemblage. This could mean that reduction of the muscle occurred independently in the vireonid radiation and the other families, or that the vireonid genera with reduction are closer to the

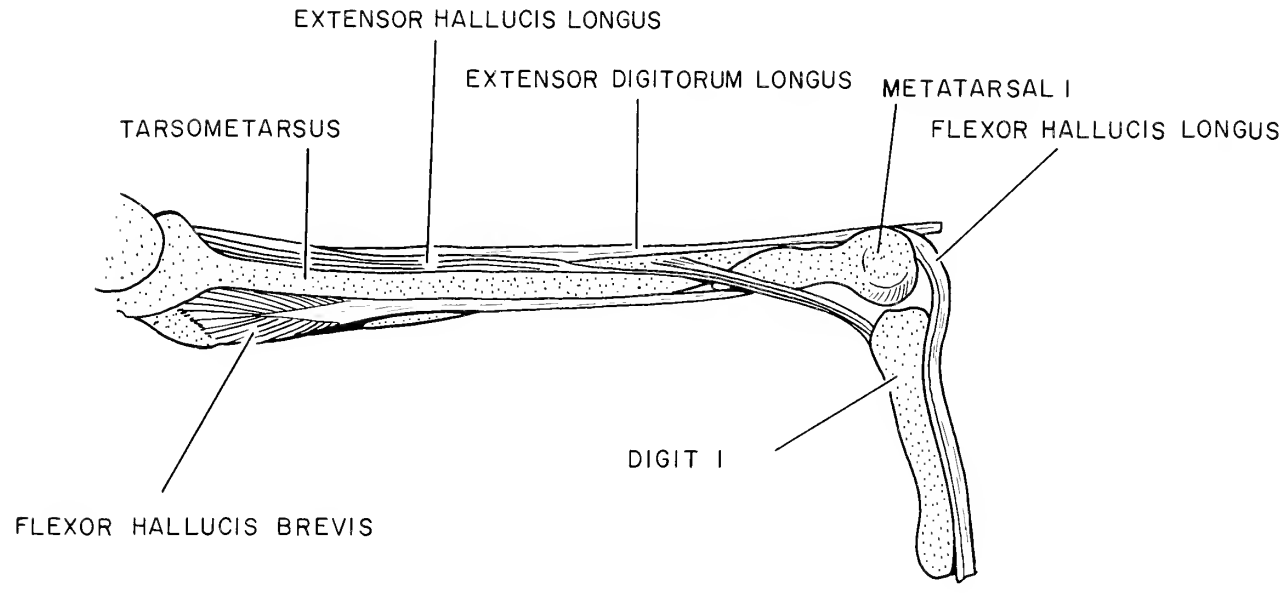

Fig. 9.—Muscles of the tarsometatarsus in *Vireolanius pulchellus*, showing the well-developed flexor hallucis brevis characteristic of the Vireonidae.

origin of the remainder of the assemblage. The latissimus dorsi pars caudalis is present in all vireonids, but otherwise almost always absent in the nine-primaried groups.

Are *Cyclarhis* and *Vireolanius* closely related to *Vireo* and *Hylophilus*, and should one family or three be recognized? The derived conditions of Mm. gastrocnemius pars interna, flexor digitorum longus, flexor hallucis brevis, and perhaps tensor propatagialis tend to cluster these genera apart from the other families, and indicate that the group as a whole is monophyletic. Retention of M. latissimus dorsi pars caudalis supports this, though less strongly as it is a shared primitive character. Furthermore, these genera lack various derived states of several muscles that occur in many nine-primaried families, such as those of Mm. gastrocnemius, obturatorius lateralis, plantaris, and peroneus brevis. They are, therefore, clearly related, and a single family is desirable to emphasize both their closeness to each other, and their distinctiveness from the remainder of the assemblage.

A second question concerns the possible relationship of the Vireonidae to the shrikes (Laniidae). Early workers suggested a close relationship, though this is now usually regarded as unlikely, and based mainly on the convergent development of a "toothed" bill. I dissected a typical shrike (*Lanius vittatus*: Laniinae) and a bush shrike (*Telophorus dohertyi*: Malaconotinae) for comparison. Table 4 shows that the two shrikes are unlike one another, and indeed they represent subfamilies that some workers consider unrelated. This is a separate problem, however. With respect to the vireonids, the main emphasis should be placed on *Lanius* as representative of the "true" shrikes, to which a vireonid relationship is presumably suggested. Table 4 shows little support for this idea. The derived conditions of Mm. gastrocnemius, flexor digitorum longus, and flexor hallucis longus possessed by the vireonids are lacking in the shrikes. The shrikes have a reduced flexor perforatus digiti III that is not seen in the vireonids. *Lanius* has a large femoral head of origin on M. flexor digitorum longus, which is lacking in the vireonids. The only character shared by the shrikes and vireonids is the retention of M. latissimus dorsi pars caudalis, a primitive character state in the passeriformes. In short, the myological evidence fails to support the idea of a close vireonid-laniid relationship.

Parulidae

Except for certain genera that appear to be either aberrant or misplaced in this family, and which are discussed separately below, most of the wood warblers examined are myologically similar to each other and generally primitive in their appendicular musculature. They are similar to the Emberizinae,

Table 4.—*Myological comparisons of the Vireonidae with other taxa.*

Taxa	M. gastrocnemius pars interna, superficial head	M. flexor digitorum longus femoral head	M. flexor digitorum longus insertion	M. flexor perforatus digiti 3	M. flexor hallucis brevis	M. latissimus dorsi caudalis
Vireo	Separate	–	AAB	Normal	Large	+
Hylophilus	Separate	–	AAB	Normal	Large	+
Cyclarhis	Separate	–	AAB	Normal	Large	+
Vireolanius	Separate	–	AAB	Normal	Large	+
Lanius	Partly fused	+	AAA	Reduced	Small	+
Telophorus	Partly fused	–	ABB	Reduced	Medium	+
New World, nine-primaried oscines	Partly fused or lost	–	ABB[1]	Normal	Small	–[2]

[1] The few exceptions (Table 3) do not affect the distinction between this group and the Vireonidae.
[2] Occasionally present (Tables 1 and 2).

although their muscles are often less robust than those of the latter group, which may reflect their more actively arboreal habits and frequently smaller body size. The latissimus dorsi caudalis has been lost, a derived state, whereas the deltoideus minor coracoidal origin is absent, which is a primitive condition in the New World nine-primaried oscine assemblage. M. coracobrachialis cranialis appears to have been entirely lost, as I could not find even a vestige in these forms, though one generally remains in other groups (Table 2). It is possible, however, that some trace of this muscle does remain but was not detected because of the small size of most species. The pronator profundus has the derived condition of two bellies (Type 2) except in *Geothlypis* and *Basileuterus*. This important character state difference suggests that Lowery and Monroe (1968) erred in combining *Oporornis* and *Geothlypis*. M. flexor digitorum profundus, however, is invariably primitive. In the hindlimb the typical parulids are primitive in all the variable muscles described herein, altogether this places the family low on an evolutionary scale within the nine-primaried assemblage.

Seiurus is distinct in several features. In the forelimb of *S. aurocapillus* M. deltoideus minor possesses an origin from the coracoid, which is lacking in typical parulids, as well as in *S. motacilla* and *S. noveboracensis*. In the hindlimb the obturatorius lateralis pars dorsalis is absent (a derived state), except in *S. motacilla*. Most unusual is the presence of a tibial head of M. peroneus brevis. Such a head occurs in other families, but its form here is different. Instead of arising independently from the lateral cnemial crest, it arises from that area in common with the tibial head of M. tibialis cranialis. This indicates that its occurrence here is an independently derived state, and is not homologous with the condition in the cardueline/drepanidid group. It was found in *S. aurocapillus* (two specimens) and *S. motacilla* (one specimen), but not in *S. noveboracensis* (one specimen). The significance of these peculiarities is unknown. Possibly they link *Seiurus* with some unanalyzed oscine family. Alternatively *Seiurus* may indeed be a parulid, whose peculiarities are in some way functionally related to its locomotor habits, as it is much more terrestrial than other parulids. This appears reasonable because *Seiurus* has hybridized with *Dendroica* (Short and Robbins, 1967).

Icteria is larger than other parulids and has been thought not to belong to this family (Ficken and Ficken, 1962; Eisenmann, 1962*a*; Clark, 1974), but its pelvic muscles are like those of typical parulids. In the forelimb, however, M. deltoideus minor arises in part from the coracoid, a derived condition otherwise found only in some *Seiurus* among the parulids dissected.

Peucedramus is another genus whose placement in the Parulidae has been questioned. George (1962, 1968) suggested that it may be more closely related to the Sylviidae. Its pelvic musculature is like that of typical parulids, but so is that of the Sylviidae examined for the most part (Table 3). In the forelimb M. latissimus dorsi caudalis is retained, which links it more with the Sylviidae than the Parulidae. Likewise, *Peucedramus* has a Type 1 (primitive) pronator profundus as in the Sylviidae, rather than

the Type 2 found in most (but not all) typical parulids. These data are consistent with George's hypothesis of a sylviid relationship.

Zeledonia coronata, the Wrenthrush, was formerly thought to be related to the Turdidae, but Sibley (1968, 1970) studied the egg-white proteins and concluded that it properly belongs among the New World nine-primaried oscines, and probably closest to the Parulidae. Ames (1975) reported that thrushes have a derived condition of the syringeal muscles that is lacking in *Zeledonia*. Hunt (1971) presented life history evidence supporting placement of *Zeledonia* in the New World nine-primaried assemblage. In the thrushes that I examined M. obturatorius lateralis pars dorsalis is very large, arising from the entire ventral margin of the ilioischiadic fenestra as well as its caudal margin. In *Zeledonia* and the nine-primaried types it arises only from the ventral margin of the fenestra, not the caudal margin. In the general structure of hindlimb muscles *Zeledonia* is typical of the more primitive New World nine-primaried oscines, such as the Parulidae (Table 3). Its large patellar band resembles that of *Basileuterus*, a parulid genus to which relationship of *Zeledonia* has been suggested (Hunt, 1971). In the forelimb *Zeledonia* lacks the latissimus dorsi caudalis as do the parulids. This muscle was present in two of the three turdids examined (Table 2). The flexor digitorum profundus in *Zeledonia* is Type 1 as in the Parulidae, whereas in the Turdidae examined it is Type 2. The most peculiar condition in *Zeledonia* is that the coracobrachialis cranialis is large and stains like a muscle, which is a primitive condition. In both the Parulidae and Turdidae examined this muscle is either reduced to a vestige or lost. Thus, in most respects, the limb myology of *Zeledonia* is similar to that of the Parulidae, but differs from that of the Turdidae.

Compared to the genera of Parulidae dissected, *Zeledonia* is most similar to *Basileuterus*. Both have a maximally developed (1.00) patellar band, which is smaller in the other genera examined except *Wilsonia*. Both also have a Type 1 (primitive) pronator profundus, whereas most other genera (except *Geothlypis*) have a Type 2. (*Peucedramus* also has Type 1, but as discussed above, is probably not a parulid.) These similarities may be significant because Hunt (1971) showed life history similarities of *Zeledonia* and *Basileuterus*, and the two genera also have a similar dorsal coloration and nasal operculum, though these could be convergent (Sibley, 1968). Thus, the results of the present study support the hypothesis that *Zeledonia* is not a thrush, but is a member of the New World nine-primaried oscines, close to the Parulidae and perhaps especially to *Basileuterus*.

Thraupidae

This family is a classic example of taxonomic confusion resulting from the variety of plumages, sizes, and feeding adaptations that it exhibits (Storer, 1969). The problem is not eased by reducing the group to subfamily status as some have advocated. Not only are relationships within the family difficult, but the affinity of the thraupids to the cardinal finches, parulids, and other groups are also problematical. A number of genera seem to connect the more typical tanagers to one or another of these other groups, and the allocation of these genera forms an additional difficulty. I have dissected only a few of the many tanagers, but even this small sample shows considerable diversity in appendicular muscles. My analysis will not begin to solve the problems surrounding this group, but should contribute to their eventual resolution.

In the forelimb M. latissimus dorsi caudalis is generally absent, but was found either bilaterally or unilaterally in some species of *Thraupis* (Tables 1 and 2). The presence of this muscle is inconsistent with the apparent phylogenetic position of the family (see below), and as in the case of its presence in some Icteridae (see discussion under that family) I suspect that its appearance here may be a case of the reestablishment of a previously lost muscle. The coracoidal head of the deltoideus minor (derived) was found only in the aberrant genus *Rhodinocichla*; it was absent in all the more typical tanagers examined. Indeed, in these other forms the scapular portion of the muscle was invariably rather slender compared to its form in other families. The pronator profundus occurs in both primitive and derived states (Table 2).

In the hindlimb (Table 3) both primitive and derived states of the gastrocnemius were found, but otherwise the musculature is generally primitive.

Euphonia and *Tangara* are myologically the most primitive forms studied, with their Type 1 pronator profundus and Type 1 gastrocnemius pars interna. These muscles in the other typical thraupids examined are more highly derived.

Nephelornis oneilli, a new genus and species of nine-primaried oscine, was recently described from Peru (Lowery and Tallman, 1976). *N. oneilli* is a rather nondescript, moderately thin-billed species

Table 5.—*Myological comparisons of* Nephelornis *with other taxa.*

Muscle	*Nephelornis*	*Urothraupis*	Parulidae	Thraupidae	Emberizinae
Gastrocnemius	Type 1	Type 1	Type 1*	Types 1*, 2, 3	Type 1*
Gastrocnemius, patellar band	0.80	0.80	0.50–1.00*	0.50–0.60	0.40–1.00*
Obturatorius lateralis p. dorsalis	Lge.	Lge.	Med. (1 Lge.)	Med., Lge.*	Lge.* (most)
Flexor digitorum longus	ABB	ABA	ABB*	ABB* (most)	ABB*, BBB
Peroneus brevis	±	±	−(1+)	−(few±)*	−
Pronator profundus	1–2	1–2	2* (few 1)	1, 2*	2* (one 1)
Deltoideus minor coracoidal head	−	−	−*(2+)	−*	+(3−)
Deltoideus minor	narrow	narrow	wider	narrow*	wider

* Indicates correspondence with *Nephelornis*.

living in highland cloud forests. Lowery and Tallman (1976) were unable to determine in which family it should be placed. Walter J. Bock examined the jaw and tongue muscles and confirmed that *Nephelornis* is a primitive member of the nine-primaried group (cited in Lowery and Tallman, 1976) but left the question of family position open. The hindlimb myology suggests that *Nephelornis* is closely related to *Urothraupis*, which has been placed in the Thraupidae as recently as 1969 (Storer, 1969), but has been transferred to the Emberizinae by Paynter (1970) without explanation. Relevant comparisons are given in Tables 2, 3, and 5.

The gastrocnemius pars interna is of the primitive type (Type 1) with a relatively wide (0.80) patellar band, in both *Nephelornis* and *Urothraupis*. This falls within the range of variation in Parulidae and Emberizinae. Most Thraupidae have a more derived condition (Type 2 or 3) but *Tangara* and *Euphonia* have the primitive state. M. obturatorius lateralis pars dorsalis is large in *Nephelornis* and *Urothraupis* as in many thraupids and most emberizines. The insertion pattern of the flexor digitorum longus is ABB in *Nephelornis*, and ABA in *Urothraupis*, which is the only notable difference between the limb muscles of the two genera. ABB is the primitive and usual condition in the New World nine-primaried oscines, and ABA and other variants are rare and show no pattern, so the condition in *Urothraupis* is probably significant only at the generic level.

One possibly significant feature is found in M. peroneus brevis. In both *Nephelornis* and *Urothraupis* there is a small band of fibers arising from the ligament to the head of the tibiotarsus. As noted (Raikow 1977*b*) this is probably an early stage in the development of a tibial head to the muscle. A rudiment such as this was also seen in *Tangara*, *Coereba*, and *Sericossypha*.

In the forelimb the pronator profundus is intermediate in form between the primitive Type 1 and the derived Type 2, but closer to the latter. The deltoideus minor in both genera lacks a coracoidal head, which is a primitive state, whereas most emberizines possess one, as do a few parulids but no thraupids. Furthermore it is rather slender in these two genera, thus resembling the condition in thraupids. The latter is a rather subjective character, however.

It is apparent that the limb muscles do not provide sufficient information to definitely ally *Nephelornis* with any given family. However, they do show the following points: (1) *Nephelornis* is nearly identical in limb musculature with *Urothraupis*; it is not as similar to any other genus examined. (2) *Nephelornis* (and *Urothraupis*) are clearly very primitive members of the New World nine-primaried assemblage, close to the base of the Thraupidae and Emberizinae. (3) In Table 5 I have marked with an asterisk the families to which each muscle indicates a probable close relationship. There are five similarities to the Parulidae, five to the Emberizinae, and seven to the Thraupidae. The latter include the probably significant similarities in the peroneus brevis and deltoideus minor. (4) The other families in the assemblage are more highly derived in various characters and are, therefore, of no concern to this problem.

The bill of *Nephelornis* is rather slender, and the jaws show little deflection, which suggests little if

any adaptation for seed-eating. Lowery and Tallman (1976) reported that it fed mainly on insects, and found no seeds in stomachs examined. This suggests that it is more primitive in feeding habits than typical emberizines, though it is clear that more investigation of both its feeding habits and feeding mechanism are needed.

There is thus a conflict of evidence concerning familial position. The limb myology favors inclusion of *Nephelornis* and *Urothraupis* in the Thraupidae. This family is traditionally regarded as being characterized by fruit-eating in addition to insectivory. I have no information on the food of *Urothraupis* and the few data on *Nephelornis* suggest a concentration on insects, along with a small amount of plant material.

On the basis of the foregoing discussion I conclude that *Nephelornis* is a very primitive member of the New World nine-primaried oscine assemblage, and that it is little modified from the primitive basal stock from which the early Thraupidae and Emberizinae arose. *Nephelornis* is thus of interest because it more closely approaches this hypothetical ancestor than any other genus examined, except *Urothraupis*. On the basis of limb musculature alone, I would hesitate to separate the genera. I suggest on the basis of present knowledge that for the purpose of classification *Nephelornis* be considered a very primitive member of the Thraupidae, and that *Urothraupis* be returned to this family, adjacent to *Nephelornis*.

Rhodinocichla has been placed in various families but no solution has been entirely satisfactory. Skutch (1962) argued on the basis of behavior that its affinities lie with the Mimidae, whereas Eisenmann (1962*b*) concluded mainly from morphology that it is a tanager; this was supported by Clark (1974). A study of the limb myology only confuses the picture more. The latissimus dorsi caudalis is absent as in most tanagers, whereas in *Dumetella* it is present. The deltoideus minor has a coracoidal head, unlike either *Dumetella* or thraupids. The pronator profundus in *Rhodinocichla* is the Type 1, whereas in *Dumetella* it is Type 2. Both types occur among Thraupidae, but Type 1 was found only in a few forms. These data tend to support the thraupid theory rather than the mimid theory, but the limited evidence is hardly convincing. The problem is complicated because *Rhodinocichla* has several unique myological conditions that are not found in either the Mimidae or Thraupidae. The flexor digitorum longus has a CBB insertion pattern (Fig. 8), which I found in no other form examined. The expansor secondariorum inserts only on two secondaries, rather than the usual three. The flexor perforatus digiti II has a secondary head as described above, which is not found in any other form dissected. The limb myology, then, shows *Rhodinocichla* to be even more distinctive than previously supposed, but does not help in determining in which family it should be placed. For the present it is most practical to retain *Rhodinocichla* in the Thraupidae until other evidence suggests an alternative.

Sericossypha is the most myologically aberrant tanager dissected, with its centrally reduced iliotibialis lateralis, and well-developed femoral head of M. flexor digitorum longus, both unique conditions in the New World nine-primaried oscines studied. It also has a partial tibial head to M. peroneus brevis, and unusually large Mm. flexor hallucis brevis and extensor hallucis longus. This pattern of peculiar features does not resemble any other form studied, and so its relationships remain obscure.

Catamblyrhynchus is a distinctive genus of uncertain affinities, sometimes being placed in the Thraupidae and sometimes in a family Catamblyrhynchidae. The interosseus dorsalis is vestigial, an autapomorphic character that does not assist in determining the relationships of the genus. The coracobrachialis cranialis is well developed, a primitive condition. The deltoideus minor, which lacks a coracoidal head, is slender as in the Thraupidae.

The pelvic musculature is primitive with respect to Mm. gastrocnemius, obturator lateralis, and peroneus brevis. The ABA insertion pattern of the flexor digitorum longus does not occur in thraupids, but was found in several other families as a variant, and probably has no significance. The absence of the plantaris is a derived state. Altogether, the limb myology places *Catamblyrhynchus* within the nine-primaried assemblage as a relatively primitive, but in some ways distinct form, lying close to the parulid/emberizine/thraupid group. The robustness and length of the shank muscles, however, set it apart from the Parulidae. The bill, although superficially finchlike, differs in detail from that of true finches. The tip of the bill is abruptly squared off when seen from above, and there are peculiar grooves running forward from the nostril on either side. Furthermore there is hardly any indication of an angled commissure, as is typical of finches. All this suggests that the resemblance of the bill is a superficial

case of convergence, and does not indicate that *Catamblyrhynchus* is a modified emberizine, as suggested by Paynter (1970).

On the basis of these observations my inclination is to regard *Catamblyrhynchus* as most probably an early offshoot of the Thraupidae, and to regard it taxonomically as rather distinct within that family. I do not advocate giving it full family status as that obscures its probable affinity with the Thraupidae.

The Swallow Tanager, *Tersina viridis*, is unusual because of its flycatching behavior. It is sometimes included in the Thraupidae, and sometimes placed in a monotypic family Tersinidae. *Tersina* was found to have a few unusual myological characteristics. M. serratus superficialis pars costohumeralis arises from the fourth true rib, rather than the third as in most species studied. M. flexor digitorum profundus narrows distally rather as in Icteridae (Type 2), though the similarity must certainly be convergent. M. extensor digitorum communis has an elongated belly. The flexor digitorum longus has an ACB insertion pattern, rather than the usual ABB. Otherwise the myological conditions fall within the usual range of variation in the Thraupidae (Tables 2 and 3). The several distinctive conditions in the forelimb could possibly represent modifications somehow related to flycatching.

Coerebidae

This family was long maintained for a group of nectar-feeding genera though it was recognized that some were close to the Parulidae and some to the Thraupidae. Following Beecher (1951*a*) *Coereba* and *Conirostrum* (including *Ateleodacnis*) are now generally placed in the Parulidae, and *Cyanerpes, Diglossa, Dacnis, Chlorophanes, Euneornis, Hemidacnis, Iridophanes, Xenodacnis,* and *Oreomanes* in the Thraupidae. It is generally believed that nectar feeding arose at least twice and perhaps several times independently in this assemblage. I have dissected the first seven of the above 11 genera. There are some variations, but no derived specializations that would cluster the genera into a separate family. *Coereba* and *Conirostrum* fit easily into the range of variation in the Parulidae, being more like typical wood warblers than are such aberrant forms as *Seiurus* and even *Icteria*. The only peculiarity is a small partial tibial head of the peroneus brevis in *Coereba*, a feature that occurs in some members of several other groups.

The Thraupidae have more limb muscle variation than do the Parulidae, but again the related "coerebid" genera fit easily among them. All have the derived state of the pronator profundus, while both primitive and derived forms occur among the Thraupidae. *Dacnis, Diglossa, Chlorophanes,* and *Euneornis* retain the patellar band of the gastrocnemius, whereas in *Cyanerpes* and several typical tanagers it is lost. The essential coherence of this group is further attested by the successful hybridization of such diverse genera as *Cyanerpes* and *Tangara* (Delacour, 1972).

Emberizinae

The emberizine finches show great uniformity in their appendicular musculature. They are similar to the Parulidae except that their muscles tend to be heavier and the shank muscles tend to extend farther along the length of the tibiotarsus than in the wood warblers. In the forelimb the latissimus dorsi caudalis is absent, M. coracobrachialis cranialis is vestigial or lost, and with one exception the pronator profundus is of the derived type. The emberizines agree with the parulids in these derived states, and also share the primitive condition of M. flexor digitorum profundus. However, unlike typical parulids the deltoideus minor has in most cases an expanded area of origin from the coracoid, a derived state.

In the hindlimb all forms studied have the primitive state in Mm. gastrocnemius, obturatorius lateralis, plantaris, and peroneus brevis. The patellar band and the dorsal head of M. obturatorius lateralis are both large, showing no trends toward reduction. However, the emberizine finches are generally primitive and show little variation in their appendicular muscles.

Cardinalinae

The cardinal finches show a small amount of myological diversity in both limbs. The deltoideus minor coracoidal head may be present or absent. *Saltator* has a well-developed coracobrachialis cranialis, a muscle that is reduced to a vestige in most forms studied. In the hindlimb the gastrocnemius pars interna varies from the most primitive to the most derived conditions. As a whole, this group cannot be distinctly separated from either the emberizine finches or the tanagers on the basis of limb myology.

Icteridae

The Icteridae are of particular interest because the family has undergone a considerable adaptive radiation in feeding specializations and related behavior (Beecher, 1951*b*; Lowther, 1975). It includes both terrestrial and arboreal types ranging from smaller, short-billed genera like *Spiza*, *Dolichonyx*, and *Molothrus* that closely resemble emberizine finches, to large long-billed arboreal foragers like *Cacicus* and *Psarocolius*.

In the forelimb the Icteridae show a modification of the flexor digitorum profundus in which the caudal border of the muscle is narrowed (Fig. 4). Though this is not a profound modification, it is found without exception in all forms examined, and this consistency suggests that it is a reliable character useful in defining the family. The pronator profundus and deltoideus minor show the derived state in most forms, but are primitive in a few.

The occurrence of M. latissimus dorsi pars caudalis in a few icterids is especially intriguing (Table 1). This muscle occurs consistently only in the Vireonidae (Table 2). Its presence in a few members of an otherwise advanced group is difficult to explain. Possibly the muscle was retained in the history of the group, and was lost independently in many lineages, including most of the icterids, but I believe it possible that its presence here may be an example of a reestablished condition. In other words, the muscle (or rather its expression in the phenotype) may have been lost early in the evolution of the nine-primaried assemblage, but the genetic information for its production could have been retained and later reactivated in a few forms. This is suggested by the distribution of the muscle in the Icteridae (Table 2). It occurs in some species of a genus, and not in others; it may even occur on one side of the body only in some specimens. This suggests an easily perturbed genetic mechanism controlling its appearance. A similar phenomenon was also found in some Thraupidae. The reappearance of "lost" ancestral muscles in birds is discussed elsewhere (Raikow, 1975; Raikow and Borecky, in preparation).

The muscles of the hindlimb are similar to those of the emberizines except that the patellar band of the gastrocnemius pars interna is always absent (Type 2 or 3), a derived condition whereas in the emberizines it is Type 1.

Spiza requires special mention because of its controversial taxonomic status. Sibley (1970) and Tordoff (1954) placed it among the cardinaline (richmondenine) finches, whereas Sushkin (1925) considered it intermediate between the Emberizinae and Icteridae and arbitrarily placed it in the former group for convenience. Beecher (1951*b*) considered it an icterid on the basis of jaw muscles and the horny palate. The forelimb myology tends to support the icterid theory. *Spiza* has a Type 2 flexor digitorum profundus as in the Icteridae, whereas the Cardinalinae have a Type 1 muscle.

In *Sturnella* the forelimb is typically icterid, but the hindlimb is distinctive in several ways. The dorsal head of the obturatorius lateralis is absent, unlike all other genera studied, where it is relatively large. The aponeurosis of origin of M. adductor femoris pars caudalis is very short. The superficial head of M. gastrocnemius pars interna is very well developed and separate for most of its length from the deep head. The tendon of M. flexor perforans et perforatus digiti III is ossified in the shank and tarsus, and the tendon of M. peroneus longus is ossified from the belly to its bifurcation near the tibial cartilage. The lateral head of M. flexor hallucis longus arises about 3 mm proximal to the iliofibularis insertion, whereas in other forms it arises just distal to this insertion. The intermediate and medial heads of M. flexor hallucis longus are not clearly separable. The significance of these variations is unknown, but perhaps they are functionally related to the terrestrial habits of this form. In this regard it may be significant that in *Dolichonyx*, another terrestrial genus, the gastrocnemius pars interna has a form similar to that in *Sturnella*.

Carduelinae

The cardueline finches show little variation in the forelimb musculature but a great deal in the hindlimb. The only variation found in the forelimb is in M. deltoideus minor—most forms possess a coracoidal head (derived state) but it is lacking in *Fringilla* and in *Carpodacus cassini* and *C. purpureus* (but was present in *C. mexicanus*). This suggests that its absence in the latter genus, which on the basis of its pelvic myology is a fairly advanced member of the family, is probably due to secondary loss in some species. Its absence in *Fringilla*, however, is probably primitive, as is discussed below.

There is considerable diversity in the hindlimb muscles (Table 3). M. gastrocnemius pars interna shows a complete range of structure from the most primitive through the most derived conditions. The dorsal head of M. obturatorius lateralis is present in some forms, and absent in others. When present,

however, it is of medium or (usually) small size, showing a general trend throughout the family for reduction and loss of the muscle. The tibial head of M. peroneus brevis may be absent, partially developed, or completely developed. M. plantaris may be present or absent. Furthermore, the diversity is increased by the several combinations of variations found in different species. This diversity characterizes the Carduelinae as a progressive and rapidly evolving group.

There are several taxonomic problems involving the Carduelinae to which the present study can contribute useful insights. First, are the carduelines more closely allied with the Old World finches (Ploceidae and Estrildidae) or the New World finches (Emberizinae and Cardinalinae)? Tordoff (1954) argued on the basis of palatal osteology that the group is unrelated to the latter and placed it as a subfamily of the Ploceidae, but few workers have supported this. Bentz (1976) described the limb myology of the Ploceidae and Estrilididae and some of his findings are briefly summarized in Tables 2 and 3. Many of the Old World forms retain the latissimus dorsi pars caudalis, which is totally absent in the carduelines. Bentz did not find the tensor propatagialis scapular tendon in his study, whereas it is always present in the Carduelinae. The deltoideus minor lacks a coracoidal head in most Ploceidae/Estrilididae, but is almost universally present in the Carduelinae. The pronator profundus is Type 1 in all ploceids and most estrildids, but is Type 2 in all carduelines. The peroneus brevis has a tibial head in many carduelines, but never in the Ploceidae or Estrildidae. Altogether, the limb myology supports the theory that the Carduelinae are part of the New World nine-primaried oscine assemblage and are not closely related to the ploceid/estrildid complex.

A second problem is the relationship of the Carduelinae to the genus *Fringilla*. Sibley (1970:100–103) reviewed this problem in detail. Bock (1960:476) suggested that *Fringilla* is intermediate between the Emberizinae and the Carduelinae, and the limb muscle data are consistent with this view. The deltoideus minor lacks a coracoidal head in *Fringilla*, a primitive state found in a few emberizines (Table 2), but only in some species of one of the cardueline genera studied. The gastrocnemius pars interna shows a derived state in *Fringilla*, like most carduelines rather than emberizines, but in other respects its limb myology is generally primitive. In terms of pelvic muscle structure *Leucosticte* is even more primitive than *Fringilla*, as it is the only cardueline retaining the Type 1 gastrocnemius pars interna. *Leucosticte* also has a relatively primitive tongue structure, more like that of some emberizines than that of the more advanced carduelines (Raikow, 1977*b*). Tordoff (1954) showed that in the carduelines the head of the humerus is relatively broader than in the emberizines, but that this trait was least developed in *Leucosticte*. These considerations suggest that *Leucosticte* rather than *Fringilla* might be better regarded as the most primitive of the cardueline genera investigated.

Finally, there has been much discussion of the relationship of the Carduelinae and the Drepanididae. The drepanidid genus *Psittirostra* is anatomically essentially a cardueline, and the two families appear to be sister groups. This is discussed further below.

Drepanididae

The history of drepanidid classification was reviewed by Sibley (1970:104). Early workers placed the different genera in several families, allying the finchlike *Psittirostra* with the Fringillidae, and the nectar-feeding forms with Old World nectar-feeders (Dicaeidae and Meliphagidae). Later they were recognized as constituting a single assemblage despite their diversity. Some workers were impressed by the nectar-feeding adaptations of many Drepanidids and supposed their ancestors to be either the Coerebidae or Thraupidae. Others have been more impressed by similarities between the finch-billed Drepanididae and the cardueline finches. Beecher (1953) found similarities in the jaw muscles between the groups. Sushkin (1929) allied the Drepanididae and Carduelinae on the basis of the bill, skull, and horny palate. Bock (1960) suggested that the Carduelinae lack specialized features that would preclude their ancestry of the Drepanididae, and that they have a tendency to wander erratically in flocks, a habit that might be expected in a colonizing group.

The pelvic musculature of the Drepanididae is relatively uniform (Table 3), including both subfamilies. This reinforces the idea that the family is derived from a single founding species. The M. gastrocnemius pars interna in all forms studied is Type 1, the most primitive sort. Among the Carduelinae only *Leucosticte* shows this condition; all other genera examined have derived conditions 2 or 3 for this character. The dorsal head of M. obturatorius lateralis is present in all forms; again this is the

ancestral state, whereas both conditions occur among carduelines. The plantaris muscle is present (primitive state) in most Drepanididae, but absent (derived state) in three species; the Carduelinae also include both conditions. Of greatest significance is the M. peroneus brevis. In all Drepanididae examined this muscle has a fully developed tibial head. As noted above, this is a derived character state of infrequent occurrence. The only other New World, nine-primaried group that regularly shows this character state is the Carduelinae, where it occurs in a majority of genera. These observations suggest strongly that the Carduelinae are the closest relatives of the Drepanididae.

The carduelines have evolved considerably since the time that they split off from the ancestral Drepanididae. The derived state of M. gastrocnemius pars interna must have arisen after this separation. The ancestral state was retained in the Drepanididae, but only the genus *Leucosticte* among the forms studied still shows it in the Carduelinae; other genera have progressed to more derived states. Partly on the basis of the evidence cited above I feel that the Drepanididae are best regarded as an offshoot of a fairly primitive cardueline species, though one in which the tibial head of M. peroneus brevis had already developed. They have remained relatively conservative in their pelvic myology while radiating spectacularly in their feeding apparatus. The Carduelinae in contrast have radiated more in their pelvic musculature since the separation of the two lineages, but less so in their feeding apparatus. A more detailed analysis of the drepanidid-cardueline relationship is presented elsewhere (Raikow 1977*b*).

A PHYLOGENY OF THE NEW WORLD NINE-PRIMARIED OSCINES

I will now present a phylogeny of the New World nine-primaried oscines as a hypothesis of the pattern of ancestral relationships in the group to the degree that present information makes possible. This model phylogeny is based on the idea that the major groups are the products of adaptive radiations into discrete adaptive zones defined mainly in terms of feeding specializations, and involving the structure of the feeding apparatus, the methods of foraging, and the types of foods taken. Many writers have suggested that feeding specializations are "adaptive" and hence poor indicators of relationships because of the supposed ease with which divergent groups may come to resemble each other through convergence. Thus "bill shape," formerly an important taxonomic character, is now in disrepute. These criticisms are valid only insofar as comparison is superficial and limited to simple structures, but, if a whole adaptive complex is examined in some detail, it should be possible to recognize convergence in most cases. This can be tested by comparing the feeding system with information from other sources, such as the limb muscles studied herein. The present classification of the New World nine-primaried oscines is to a great extent based on feeding adaptations, so the present analysis is an attempt to see whether this concept is a valid model for a theory of phylogenetic relationships within the group.

This type of evolutionary pattern has been discussed by various workers including Schaefer (1976), Mayr (1976), and Bock (1965). Basically, it is suggested that an evolving lineage may enter a new adaptive zone by developing a new structural and behavioral specialization that allows it to exploit the environment in a manner not highly competitive with other organisms. This could involve the use of a new kind of food, or the ability to feed in places formerly unreachable. When this happens, the way is open for an extensive radiation of the pioneering group into a variety of specialized subzones of the general adaptive zone. For example, once a mechanism was developed for cracking hard-shelled seeds, specializations could occur in the relative size of the bill, in bill shape, in the mechanics of jaw action, in the structure of the tongue, and in the locomotor apparatus, making possible a radiation into specific feeding niches defined by the size and hardness of the seeds taken, the substrate on which foraging occurs, and so forth.

Fig. 10 is a cladogram representing the phylogeny of the New World nine-primaried oscines analyzed at the generic level for most of the forms dissected in the present study. Especially uncertain relationships are indicated as dotted lines; some of these show alternative possibilities. This phylogeny is not intended as a final solution to the problem of relationships among the birds studied; rather it is a hy-

pothesis representing what I consider to be the most reasonable interpretation of the information available at the present time. It is presented as a framework for discussion of the possible history of the New World nine-primaried oscines and to point out specific problem areas where further research is particularly needed.

We must first deal with the problem of the Vireonidae. Sibley (1970:170) reviewed the taxonomic history of this family; the general opinion today is that the family Vireonidae is related to the New World nine-primaried oscines, but is somewhat set apart from the other families. The remainder of the group is clustered by a collection of synapomorphies and corroborating noncladistic data that exclude the Vireonidae. Both in the characteristics reviewed earlier, and in the limb muscle structure reported herein, the Vireonidae do not appear to be part of this otherwise monophyletic group. They share none of the evolutionary trends in limb muscle structure seen in the other families. In addition, they have several derived states not found in the other families, including the separation of the superficial head of M. gastrocnemius pars interna, the enlargement of flexor hallucis brevis, and the flexor digitorum longus insertion. Furthermore they lack the tensor propatagialis scapular anchor and retain the latissimus dorsi caudalis. Except for Beecher's (1953) belief that the jaw muscles show an ancestral relationship to the Parulidae, there is no compelling evidence, and most importantly, no shared derived character states that group the Vireonidae with the other New World nine-primaried oscines. Therefore, it must be concluded that the Vireonidae have at most only a distant phylogenetic link to this group, and should not be included within it.

Cluster 1

With the exclusion of the Vireonidae, the remainder of the New World nine-primaried assemblage clearly appears monophyletic on the basis of apparent synapomorphies (reduced tenth primary, pneumatic fossa of humerus, compressed basihyale with attached hyoglossus obliquus, and loss of latissimus dorsi caudalis) supported by noncladistic evidences (egg-white proteins, pterylosis, and pattern of adaptive diversity) as discussed in detail above.

The Parulidae are in general the most primitive group of this assemblage on the basis of their limb muscles, although a few genera depart from the typical condition of the family in certain muscles. This general condition is correlated with the widely held idea that purely insectivorous habits are more primitive than feeding on plants. *Dendroica, Mniotilta, Oporornis, Myioborus,* and *Wilsonia* are "typical" wood warblers showing the derived state of M. pronator profundus (1a), but not separable from each other by any characters analyzed herein. *Geothlypis* and *Basileuterus* are similar except for possession (presumably retention) of the primitive state of M. pronator profundus. *Zeledonia* is very primitive myologically, even to the retention of a well-developed M. coracobrachialis cranialis. It is placed beside *Basileuterus*, with which it possibly has a relatively recent common ancestor as discussed above. The reduction of its flight mechanism is autapomorphous (1b).

The "coerebid-parulids" *Coereba* and *Conirostrum* are essentially typical parulids in their limb muscles. They are clustered here (1c) because they share nectar-feeding adaptations. It is uncertain whether this is really a synapomorphy; quite possibly they evolved this specialization independently and do not share a nectar-feeding common ancestor. Limb myology cannot resolve this problem, but a study of the feeding apparatus might possibly do so.

Seiurus and *Icteria* are clustered by the common possession of a coracoidal origin of M. deltoideus minor (1d). However, each is so distinctive (1e, 1f, and discussion above) that I consider it doubtful that they are closely related; more likely they evolved this derived state independently, especially because it only occurs in one of the three genera of *Seiurus* examined. Their placement here is very speculative, and mainly serves to point out the need for additional studies of their relationships.

Nephelornis and *Urothraupis* are morphologically similar to each other, but their exact position remains uncertain pending further studies. However, they are myologically primitive and must lie somewhere close to the position shown, near the border of the Parulidae and Thraupidae.

Cluster 2

The Parulidae are almost entirely insectivorous, whereas the emberizine, cardinaline, and carduline finches eat seeds as well, as do the more primitive members of the highly diversified Icteridae and Drepanididae. This provides a spectrum of feeding specializations in the New World nine-primaried assemblage; the problem has been to determine which is the primitive end of the spectrum (for ex-

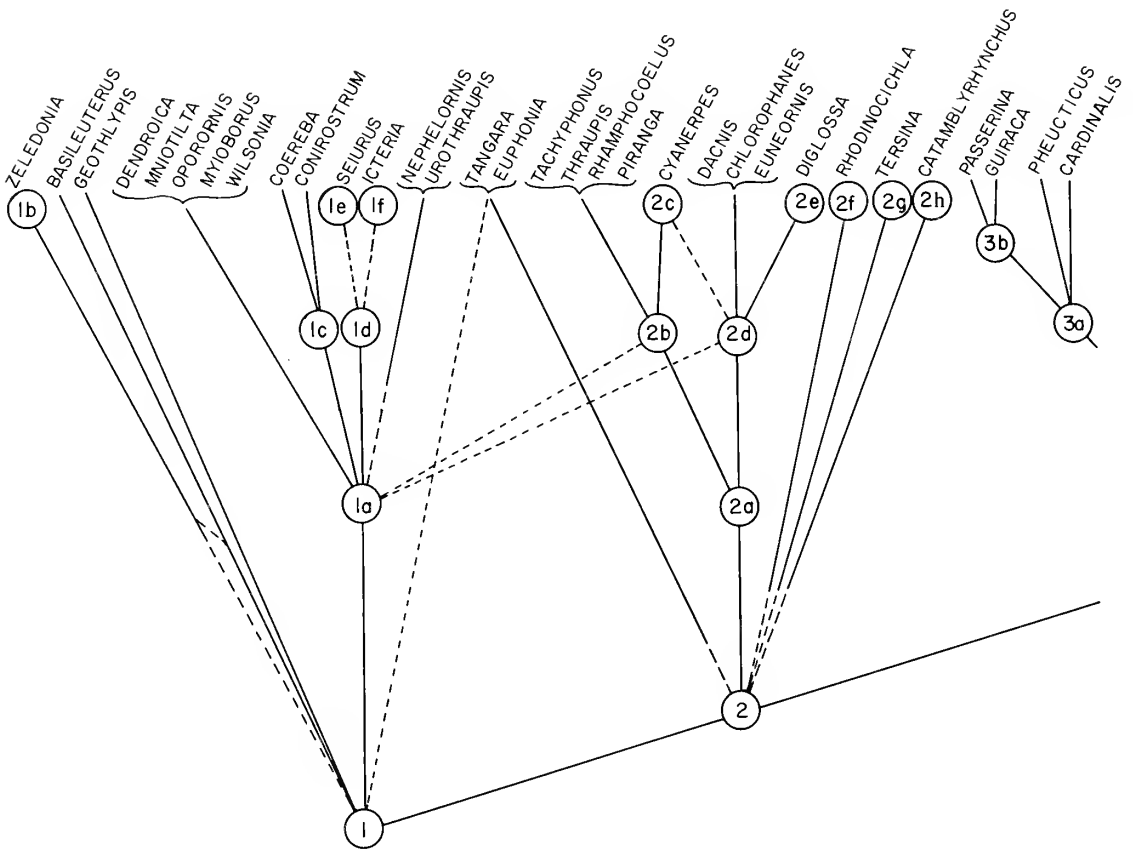

Fig. 10A.—A cladogram suggesting phylogenetic relationships in the New World nine-primaried oscines. Numbers in circles designate presumed shared derived character states. See text for discussion. 1. Reduced tenth primary; fully developed pneumatic fossa; compressed basihyale with attached hyoglossus obliquus; latissimus dorsi caudalis lost. Supportive noncladistic data: egg-white protein similarities; indistinct family boundaries; pattern of adaptive diversity; pterylography. 1a. Type 2 pronator profundus. 1b. Reduction of wings and near loss of flight. 1c. Nectar feeding. 1d. Deltoideus minor coracoidal head added. 1e. Peroneus brevis tibial head added; obturatorius lateralis dorsalis lost. 1f. Large size; deltoideus minor coracoidal origin. 2. Feeding on fruits added to insectivory; bill heavier but lacking pronounced deflection. 2a. Type 2 pronator profundus. 2b. Patellar band of gastrocnemius lost. 2c. Plantaris lost; nectar feeding. 2d. Nectar feeding. 2e. Plantaris lost. 2f. Flexor digitorum longus type CBB; deltoideus minor coracoidal head added; flexor perforatus digiti 2 extra head added. 2g. Serratus superficialis from 4th rib; flexor digitorum profundus type 2; flexor digitorum longus ACB; wide bill and flycatching. 2h. Interosseus dorsalis vestigial; coracobrachialis cranialis well developed; flexor digitorum longus ABA; plantaris lost. 3. Bill shorter and deeper, with pronounced deflection; seeds eaten, nutcracker method; deltoideus minor coracoidal head added. 3a. Bill still heavier; feed on larger percentage of seeds and often larger seeds, fewer insects. 3b. Patellar band of gastrocnemius lost.

ample, Mayr, 1955:34). The limb muscle data analyzed herein provide a solution to this problem; as most workers have suspected at least intuitively, the seed-eating habit is a derived specialization as shown by its correlation with limb muscle evolution. However, seed-eating is a highly specialized condition requiring extreme structural modifications of the feeding apparatus, and it is unlikely that it evolved suddenly in insectivorous forms. More likely birds first began eating the softer tissues of fruits, and gradually moved up to the harder seeds. Fruit-eating is a likely intermediate stage in the evolution of herbivorous habits, and thus the Thraupidae appear to represent a probably intermediate stage between purely insectivorous types (Parulidae) and the advanced granivores. The Thraupidae are a diverse group, some members being quite thin-billed and difficult to separate from the Parulidae, others being more intermediate, and still others closely approaching the cardinaline and ember-

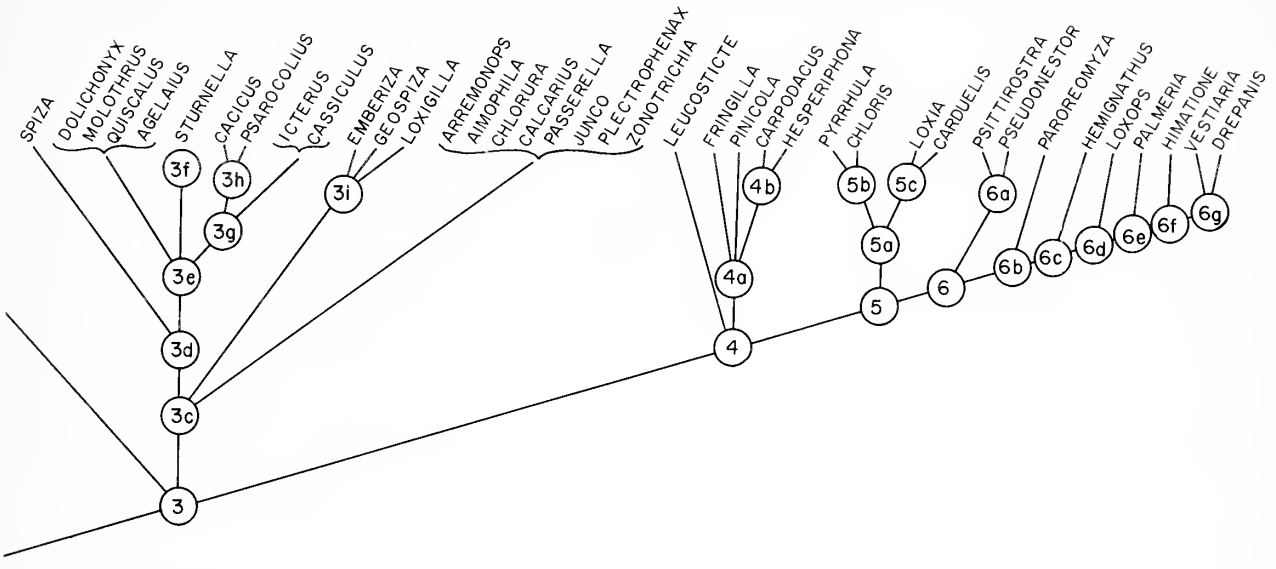

Fig. 10B.—3c. Ground-foraging habits, sometimes with double-scratch method. 3d. Patellar band of gastrocnemius lost; flexor digitorum profundus Type 2. 3e. Rictal bristles reduced or lost. 3f. Obturatorius lateralis dorsalis lost. 3g. Primarily arboreal habits. 3h. Pronator profundus Type 1. 3i. Deltoideus minor coracoidal origin lost. 4. Bill heavier, with vise method of seed cracking; obturatorius lateralis dorsalis reduced. 4a. Patellar band of gastrocnemius lost. 4b. Plantaris lost. 5. Peroneus brevis tibial head added. 5a. Patellar band lost. 5b. Obturatorius lateralis dorsalis lost. 5c. Plantaris lost. 6. Colonization of Hawaiian Islands. Supportive noncladistic data: near uniformity of limb muscles throughout family. 6a. Bill enlarged with increased overlap of upper mandible. 6b. Bill, tongue, and nares elongated. 6c. Tubular tongue; enlargement of nasal operculum with convex margin. 6d. Plantaris lost. 6e. Nasal operculum larger and more flattened; plumage harder and less fluffy. 6f. Nasal operculum still larger, anterior notch added; primaries truncate. 6g. Bill elongated and decurved.

izine finches. Thus the family seems to contain genera representing various stages in the evolution of the seed-eating types. In their limb myology the thraupids are generally rather primitive, but various genera differ in the possession of several derived conditions. More than any other family, this one is difficult to characterize as monophyletic, because the Thraupidae are not clustered by any important synapomorphies. The best solution, which I recognize as very imperfect, is to regard the Thraupidae as probably representing more a structural/behavioral grade than a monophyletic taxon, and to place it in this position as being more highly derived than the Parulidae but more primitive than those families with clear specializations for seed cracking. The following discussion and conclusions are rather tentative because I have studied only a small extent of the range of diversity that occurs in the Thraupidae. Many more genera must be examined in order to clarify the problems in this group.

Point (2) indicates the development of herbivorous habits and in correlation, a heavier bill. The forms radiating from point (2) constitute the heterogeneous thraupid assemblage, plus the ancestral lineage of the seedeaters. *Tangara* and *Euphonia* are the most primitive genera in limb myology; their Type 1 pronator profundus is more primitive than even the typical parulid condition. If we assume that the evolution of herbivory in addition to insectivory occurred only once, so that the thraupid assemblage is monophyletic in the strictest sense, then these genera will arise as shown from point (2) in Fig. 10. This assumption is certainly parsimonious, but is also very simplistic and probably false. On the basis of their primitive limb myology these two genera could also have arisen earlier within the primitive insectivorous ancestry of the assemblage, as shown by the alternative pathway leading from point (1). In this case they would have developed herbivorous adaptations independently of other Thraupidae. Here is a case where a study of the feeding mechanism could prove helpful.

Tachyphonus, *Thraupis*, *Rhamphocoelus*, and *Piranga* are "typical" tanagers and essentially alike in limb myology. They share synapomorphous states of M. pronator profundus (2a) and M. gas-

trocnemius (2b). *Cyanerpes* has these features plus the loss of M. plantaris and the addition of nectar feeding (2c). Again, this group is part of the radiation of a monophyletic Thraupidae if we hold to the assumption of a single origin of herbivory. However, if we do not insist on this, then the genera arising from (2b) could, on the basis of limb myology, also have arisen from point (1a) instead, as shown by the dotted line in Fig. 10.

The "coerebid-thraupids" *Dacnis*, *Chlorophanes*, and *Ennerornis* are similar in limb myology; *Diglossa* has an additional derived state in the loss of M. plantaris (2e). These forms are clustered on the basis of a presumed common origin of nectar-feeding adaptations (2d). As with *Coereba* and *Conirostrum* in the Parulidae, this is an expedient, parsimonious, and tentative placement pending future analysis of the feeding mechanism. Again, these forms could arise via (1a) rather than (2a) if the assumption of monophyletic herbivory is not held to, as shown in Fig. 10. If *Cyanerpes* is also hypothesized as part of a single radiation of nectar-feeding forms, then its loss of the patellar band (2b) must have occurred independently.

As discussed earlier, *Rhodinocichla*, *Tersina*, and *Catamblyrhynchus* lie within the thraupid assemblage, but on the basis of limb myology these traditionally problematic forms remain troublesome (2f, 2g, 2h).

The depiction of the thraupid radiation arising from a single point (2) implying a single common ancestor for the group is undoubtedly a gross oversimplification. It appears intuitively likely that several lineages independently developed herbivorous feeding adaptations, as suggested by the alternative phylogenies shown in Fig. 10. Only a few thraupid genera were dissected in this study, and the true phylogeny of the group must be far more complex than that shown here. The limited analysis of limb myology has not solved this problem, but it has clearly shown that the analysis of the limb muscles can support a hypothesis of a polyphyletic family Thraupidae.

Cluster 3

These groups are clustered by a feeding apparatus adapted for cracking seeds. Exceptions are some icterids and drepanidids with feeding mechanisms otherwise specialized, but which are clearly derived within their families, the more primitive members of which possess the seed-eating adaptations. This adaptation is presumably derived by further specialization from the principally fruit-eating Thraupidae. Bock (1960) analyzed the functional anatomy of the feeding mechanism. The emberizines show a relatively modest development of this system, and feed on relatively smaller seeds, using a biomechanical system that Bock termed the "nutcracker" method. Cardinalines use the same method, but have larger bills and eat larger seeds.

This group is also clustered by possession of a derived character state in a wing muscle, the presence of a coracoidal head to M. deltoideus minor. There are a few exceptions, however. A few genera of most of these families have the primitive state, and a few parulids and one (presumed) thraupid have the derived state (Table 2). Nevertheless, nearly all parulids and thraupids are primitive, and nearly all the remainder are derived in this character. This is an example of the type of character conflicts that were disucssed earlier, and because they are few, I think it probable that cluster 3 is correctly grouped by this synapomorphy. Thus cluster 3 is grouped by two independent characters (seed-eating adaptations and coracoidal head of the deltoideus minor).

Three lineages are shown arising from this branching point, though strict cladistic methodology demands only dichotomous branches. In order to resolve this it would be necessary to demonstrate some synapomorphy clustering two of the three branches, but I do not know of one.

The Cardinalinae resemble the Thraupidae in their colorful plumages and arboreal habits, but in their enlarged bills and habit of eating larger seeds (3a) appear to be more highly derived in feeding specializations than the emberizines. There is some variation in limb muscles (3b) but as only a few genera were dissected, the range of variation in the group is not well known.

The Emberizinae and Icteridae share a specialized ground foraging technique with both structural and behavioral aspects (3c). The other taxa in this assemblage are highly arboreal and seldom forage to any extent in open terrestrial habitats. They are also characterized in general by brightly colored, conspicuous plumages, at least in males. The emberizines in contrast are more terrestrial in foraging habits, and less brightly colored. Their plumages emphasize browns, grays, blacks, and sometimes yellows, and their backs are commonly streaked with brown and gray. Presumably this is associated with their ground foraging habits by making them less conspicuous to predators. The Icteridae appear

to have been derived from the emberizines through such forms as *Spiza*, *Dolichonyx*, and *Molothrus*, which resemble them in bill form and habits. Furthermore, many emberizines forage with a specialized type of movement, the bilateral scratch, in which they jump first forward and then backward with both legs simultaneously, scratching the substrate on the second jump to scatter surface litter and reveal food. At least two icterid genera, *Molothrus* and *Agelaius*, are known to use a similar foraging technique (Greenlaw, 1976).

The emberizines are very uniform in limb myology and most genera are inseparable on this basis. *Geospiza*, *Emberiza*, and *Loxigilla* lack the coracoidal origin of M. deltoideus minor. This could be either a primitive state or a derived (secondarily primitive) condition. I have chosen the second alternative as shown in Fig. 10 (3i) because they so closely resemble the other emberizines in general, but the matter is uncertain. In view of the wide geographic separation between these genera, it is likely that this derived state arose independently in the three groups, so that cluster 3i may well be a false synapomorphy.

The Icteridae are clustered by two derived states, the loss of the patellar band and the Type 2 flexor digitorum profundus (3d). In most icterids the rictal bristles are either vestigial or completely lost (3e) as noted by Ridgway (1902:169). However, I have observed that the rictal bristles are well developed in *Spiza*, which myologically is allied with the Icteridae (3d). This supports the idea that *Spiza* is a primitive icterid, and a link to the emberizines.

The assumption of (3c), that ground-foraging is a synapomorphy of the Icteridae and Emberizinae, is contradicted by the arboreal habits of some icterids (3g) and the primitive Type 1 pronator profundus of a few (3h). If this suggestion is correct, then the apparently primitive states of cluster (3g) are presumably due to evolutionary reversal. The conflict is clearly unsettled, but I have chosen as most probable the scheme shown in Fig. 10 because (1) *Spiza* is so clearly an intermediate form between the two groups, and (2) the grossly enlarged bill of most genera in cluster (3g) is highly specialized and most certainly derived within this assemblage.

Cluster 4

This group includes the cardueline finches and the Drepanididae. The carduelines and the drepanidid genus *Psittirostra* are seedeaters that possess a more specialized biomechanical seed-cracking system than that found in the emberizines and cardinalines. This was studied by Bock (1960), who termed it the "vise" method. It includes a stronger skull ossification, a restriction of the mobility of the upper jaw, and other features, and is thought to have evolved from the less specialized "nutcracker" system of the other members of cluster (3). It must be noted, however, that Bock's concept of "nutcracker" and "vise" systems of jaw biomechanics has been questioned (Zusi, 1961). The carduelines and drepanidids are also clustered by the reduction in size (leading in some cases to complete loss) of a hip muscle, M. obturatorius lateralis dorsalis.

Despite their diversity, the Carduelinae appear to be a coherent group on the basis of various structural and behavioral features (see Tordoff, 1954) as well as the presence of the vise method of seed cracking, and so the parsimonious suggestion that the group is monophyletic is a reasonable one. For this reason they are shown as having arisen from a single lineage (Fig. 10).

Several cardueline genera appear relatively primitive by the absence of a derived state, the tibial head of M. peroneus brevis. In terms of limb myology *Leucosticte* is the most primitive cardueline studied (4); the structure of the tongue also supports this view (Raikow, 1977*b*). Several other genera are more advanced in limb myology (4a, 4b).

Cluster 5

The development of the tibial head of M. peroneus brevis, a derived state, occurs in several other genera (cluster 5), which may be further clustered on other myological synapomorphies (5a, 5b, 5c). There is a character conflict in that the plantaris was apparently lost twice (at least) in the carduelines (4b, 5c), but the arrangement shown here is the most reasonable one given the distribution of the tibial head of the peroneus brevis.

Cluster 6

The derivation of the Drepanididae is treated in considerable detail elsewhere (Raikow, 1977*b*) and therefore will be considered here only briefly. It is difficult to demonstrate by strictly cladistic methods that the family Drepanididae is monophyletic; because of their incredible diversity, resulting from their adaptive radiation, they do not all share any clear-cut derived character states not also found among the Carduelinae. The argument for monophyly is based instead on the geographical restric-

tion to the Hawaiian Islands, the morphological intergradation between distinct adaptive types, and the remarkable uniformity of their limb muscles (Raikow, 1976, 1977*a*, 1977*b*).

Psittirostra is a finch-billed, seed-eating genus, whereas the other genera have bills adapted to a variety of feeding specializations. *Psittirostra* is clearly the most primitive drepanidid genus, little modified from the cardueline ancestor that founded the family. A phylogeny of the genera of the Drepanididae is shown in Fig. 10 for the sake of completeness, but as I have analyzed it in detail elsewhere (Raikow, 1977*b*), I will not do so here.

PROPOSED CLASSIFICATION

Because of the diverse philosophies of classification now current, it is desirable to explain briefly the basis for a proposed classification. The school of phylogenetic systematics based on the ideas of Hennig includes both a methodology for reconstructing phylogenies, and a technique for constructing classifications based on those phylogenies. I accept the first but reject the second. Thus, although my phylogeny was derived by mostly Hennigian methods, my proposed classification is not.

In the Hennigian or cladistic method of classification the hierarchy of taxonomic categories is based directly on the branching pattern of the cladogram without regard to the nature or degree of evolutionary change (which may be quite variable) occurring between branching points. In a group of any size this will result in a large number of categories and of named taxa. The resulting classification is so complex and unwieldy as to be wholly impractical. Consider, for example, the classification of mammals proposed by McKenna (1975). This includes the categories (in alphabetical order) class, cohort, grandorder, infraclass, infraorder, legion, magnorder, mirorder, order, parvorder, subclass, sublegion, supercohort, superlegion, and superorder. These are just the categories; the named taxa are much more numerous. The method does have the advantage that one can specify any monophyletic group in the cladogram by name. However, this can also be done more simply by referring to the group by the number of the branching point from which it arises. For instance, in referring to the group containing the Drepanididae plus those carduelines possessing the peroneus brevis tibial head (Fig. 10), one could specify, say, the "infrasupercohort Carduelоidida," but it is simpler (dare I say more parsimonious?) merely to say "cluster 5."

I also reject Hennigian classification because it is redundant, being merely verbal restatement of the cladogram. I prefer a classification in which evolutionary changes are considered, so that each taxon is characterized by some adaptive or other peculiarity that sets it apart from other taxa. If we are to have both phylogenies and classifications, why not let them serve different purposes? Critics claim that this results in subjectivity because different workers, given the same data, might produce different classifications. This may be true, but I see no fault in it. Different workers can emphasize the events that they consider to have been of the greatest biological significance in the history of the group. Mayr (1974) has effectively criticized cladistic classification, so I will not belabor the point further.

For most families I have not suggested subfamilies because I consider the basis for them to be uncertain or ambiguous. Future studies of intergeneric relationships may make subdivision of more families possible. My classification is not greatly different from those generally in use at the present time, as the limb myology has, in general, confirmed previous ideas of relationships. Several small families, such as the Cyclarhidae, Vireolaniidae, Tersinidae, and Catamblyrhynchidae, listed by Wetmore (1960), are not recognized because I have included their genera in other families of which they appear to be aberrant members. Inclusion of *Fringilla* with the cardueline finches unfortunately necessitates the use of the name Fringillinae for the combined group, although I would have preferred to retain the name Carduelinae.

Each family recognized appears to be a coherent group. The Vireonidae includes *Cyclarhis* and *Vireolanius* because of their anatomical similarity, as pointed out by several other authors. The Parulidae are essentially arboreal insectivores, with occasional lines specializing in different directions, as with *Seiurus* and the nectar-feeders. The Thraupidae are essentially arboreal fruit and insect eaters. This family is still the least understood, and may by polyphyletic, but recognition of a single family is the most practical course on the basis of our present

understanding. The Fringillidae are seed-eaters. The Cardinalinae are basically heavy-billed types using the nutcracker method of seed breaking, and with colorful plumages. The Emberizinae are essentially smaller-billed nutcracker types, with emphasis on ground foraging. The Fringillinae (Carduelinae) are mainly short-legged, arboreal seedeaters with a heavy bill, using the vise method of seed cracking. The Icteridae, despite their considerable diversity, are marked by a specialized bill-gaping feeding mechanism. The line between Fringillinae and Drepanididae is vague and admittedly arbitrary. However, I feel that the Hawaiian Honeycreepers merit family rank because they are unquestionably the product of a single adaptive radiation in a geographic region where no other members of the assemblage occur naturally.

The sequence of families given here is, in my opinion, the most reasonable solution to the problem of expressing a multidimensional branching pattern in a linear order. In any linear sequence of the families of oscines, the sequence from the Parulidae onward should be kept intact, with no other families interposed. This follows from the monophyly of the group. The position of the Vireonidae, however, remains problematical because their affinities are still obscure.

Proposed Classification:

Vireonidae

Parulidae
Thraupidae
Fringillidae
  Cardinalinae
  Emberizinae
  Fringillinae
Drepanididae
Icteridae

CONCLUSIONS

1. The hypothesis that the New World nine-primaried oscines form a monophyletic group is supported by the comparative anatomy of the limb muscles for all groups except the Vireonidae. For all other groups the muscles show a common general pattern with a series of gradual evolutionary changes consistent with a scheme of adaptive radiation presented in a phylogenetic hypothesis.
2. The Vireonidae do not share derived character states with the other groups and cannot be included with them in a single phylogeny. The shrike-vireos and peppershrikes share unique derived states with the vireos, and it is recommended that all be included in a single family whose monophyletic nature is indicated by their synapomorphies.
3. The limb myology indicates that the Parulidae are a primitive but fairly cohesive group which is probably monophyletic. This conclusion is based more on the general similarity of most genera than on the existence of any clear-cut synapomorphies. The "coerebid" genera *Coereba* and *Conirostrum* are included. *Peucedramus* does not fit into this family but probably belongs with the Sylviidae. *Icteria* and *Seiurus* are aberrant in limb muscles but the significance of this is uncertain. *Zeledonia* is myologically primitive, and may reasonably be included in the Parulidae near *Basileuterus*.
4. The Thraupidae are myologically heterogeneous and may be polyphyletic. *Nephelornis* and *Urothraupis* are very similar and relatively primitive. Their exact position is uncertain but is at the parulid/thraupid border. It is somewhat arbitrarily suggested that they be placed in the Thraupidae. The "coerebid" tanagers fit easily within the Thraupidae, but the question of their monophyly as nectar feeders is unsettled. *Rhodinocichla*, *Tersina*, and *Catamblyrhynchus* are best treated as aberrant thraupids whose intergeneric affinities are obscure.
5. The Emberizinae and Icteridae may be sister-groups on the basis of terrestrial foraging habits and techniques. The limb myology is consistent with the hypotheses that both are monophyletic groups. *Spiza* is a primitive icterid close to the Emberizinae. The orioles, caciques, and oropendolas are secondarily arboreal.
6. The Cardinalinae are somewhat diverse in limb myology and their phylogenetic position is probably close to the emberizine/icterid group.
7. The Carduelinae are diverse in limb myology, with *Leucosticte* and *Fringilla* being relatively primitive within the group. The hypothesis of monophyly is supported by a derived jaw mech-

anism and a pattern of derived limb muscle features.

8. The Drepanididae are almost certainly monophyletic as indicated by geographical distribution and morphological intergradation. They arose from a single cardueline founder species.
9. Based on the foregoing phylogenetic study, the general taxonomic recommendation arising from this investigation follows from a belief that the family category should be used for grouping rather than separating forms, and that families with one or a very few genera should be avoided as much as possible. For the most part I will not suggest subfamily groups because I consider the basis for most to be uncertain or ambiguous.

Proposed Classification:

Vireonidae

Parulidae
Thraupidae
Fringillidae
  Cardinalinae
  Emberizinae
  Fringillinae
Drepanididae
Icteridae

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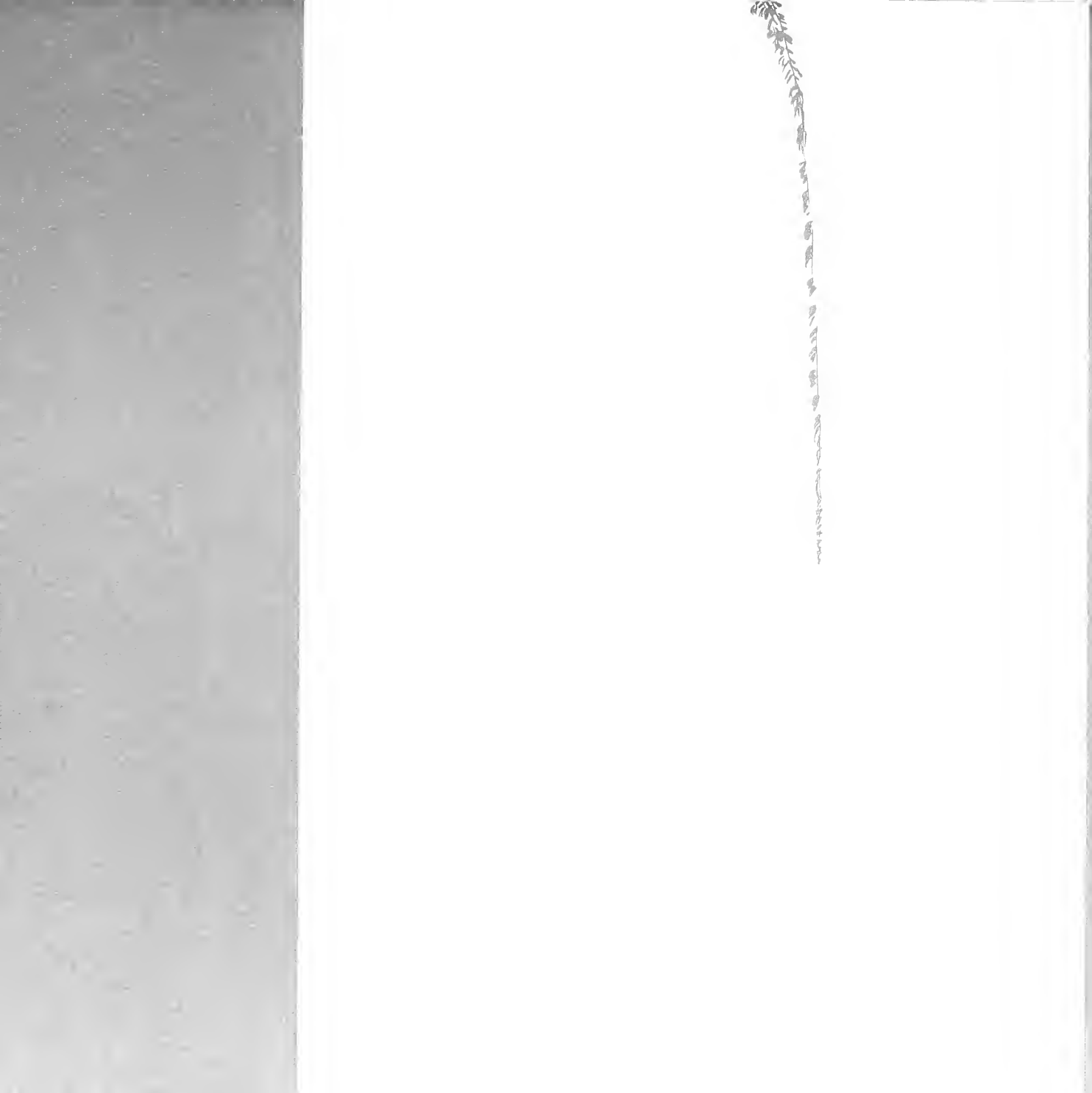

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DAVID S BERMAN
Assistant Curator, Section of Vertebrate Fossils

JOHN S. McINTOSH
Wesleyan University, Middletown, Connecticut 06457

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ABSTRACT

Evidence is presented to show that 1) *Apatosaurus* probably possessed a *Diplodocus*-like, rather than *Camarasaurus*-like, skull, and 2) *Apatosaurus* and *Diplodocus* are closely related and well separated from *Camarasaurus*. A *Diplodocus*-like skull attributed to *Apatosaurus* by W. J. Holland over a half century ago is described for the first time. A cranium and a pair of quadrates that are very similar to those of *Diplodocus* are also described and shown probably to belong to *Apatosaurus*. Inaccuracies and omissions in previous descriptions of the skull of *Diplodocus* have necessitated a redescription of much of its external features and braincase. Differences between the skull attributed here to *Apatosaurus* and that of *Diplodocus* are of a subtle proportional and structural nature. Comparisons of the postcranial skeletons of the Jurassic *Apatosaurus*, *Diplodocus*, and *Camarasaurus* demonstrate that the former two genera share a large number of significant features and are quite distinct from the latter.

Apatosaurus and *Diplodocus*, along with the Jurassic *Barosaurus*, *Cetiosauriscus*, *Mamenchisaurus*, and *Dicraeosaurus* and the Cretaceous *Nemegtosaurus*, should be grouped under Diplodocidae Marsh, 1884.

INTRODUCTION

Of the six well-established sauropod genera from the Upper Jurassic Morrison Formation of North America, *Brachiosaurus*, *Haplocanthosaurus*, and *Barosaurus* are rare and the latter two incompletely known. The other three, *Camarasaurus*, (=*Morosaurus*, =*Uintasaurus*), *Apatosaurus* (=*Brontosaurus*), and *Diplodocus* are common and well known. The last three genera were described a century ago on small but diagnostic portions of skeletons (Cope, 1877*a*; Marsh, 1877*b*, 1878*a*). Although large collections of numerous isolated elements and some partial skeletons of *Camarasaurus*, *Apatosaurus*, and *Diplodocus* were made during the next quarter century, adding greatly to the knowledge of these genera, significant misinterpretations concerning their morphology and relationships arose. Despite detailed descriptions (Gilmore, 1925, 1936; Hatcher, 1901*a*, 1903*b*; Holland, 1906) of excellent specimens of all three genera even after this period, some of the misinterpretations were so entrenched in the literature that they persist today. The misunderstandings discussed here regard two important aspects of the morphology and relationships of *Apatosaurus*. First, since the original restorations of "*Brontosaurus*" published by Marsh (1883, 1891), the skull of *Apatosaurus* has been incorrectly depicted as being *Camarasaurus*-like and the alternative suggestion presented by Holland (1915*a*) and supported here, that it is *Diplodocus*-like, has been almost totally ignored. Second, *Apatosaurus* has been falsely viewed as more closely related to *Camarasaurus* than to *Diplodocus*, despite the fact that descriptions of their postcranial skeletons demonstrate just the opposite.

In an earlier review of the nature of the skull of *Apatosaurus*, we (McIntosh and Berman, 1975) discussed the controversy raised by Holland (1915*a*, 1924), who refuted Marsh's (1883, 1891) use of probable *Camarasaurus* skulls in his restorations of *Apatosaurus*, pointing out that the skulls were not found directly, or even closely, associated with postcranial skeletons of this genus. Holland argued that the skull of *Apatosaurus* is probably like that of *Diplodocus*. His opinion was based almost solely on a very large *Diplodocus*-like skull that was very closely associated with two nearly perfectly preserved postcranial skeletons of *Apatosaurus* in the quarry at what is now Dinosaur National Monument near Jensen, Utah. This skull was never described by Holland and his assertion was almost totally disregarded, because it ran counter to the then well-established view that *Apatosaurus* is structurally more similar and more closely related to *Camarasaurus* than to *Diplodocus*; this skull is described here for the first time. A pair of quadrates and the greater portion of a cranium that are nearly indistinguishable from those of *Diplodocus* are also described as probably belonging to *Apatosaurus*. These elements were found near Morrison, Colorado, by Marsh's collectors in 1877 and evidence is presented that suggests that they belong to the holotype of *A. ajax*. Previous descriptions of the skull of *Diplodocus* are inaccurate and incomplete, necessitating a redescription of most of its external features and braincase. A comparison of the postcranial skeletons of the three common, Morrison Formation sauropods confirms that *Apatosaurus* and *Diplodocus* are very similar and are distinct from *Camarasaurus*.

The close resemblance of the skull and postcranial skeleton of *Apatosaurus* to those of *Diplodocus* clearly indicates that *Apatosaurus* is more closely

related to *Diplodocus* than to *Camarasaurus*. *Apatosaurus* and *Diplodocus*, along with five lesser known genera, *Barosaurus*, *Cetiosauriscus*, *Mamenchisaurus*, *Dicraeosaurus*, and *Nemegtosaurus*, are grouped under Diplodocidae Marsh, 1884, for the first time.

ABBREVIATIONS

AMNH, CM, USNM, and YPM refer to collections at the American Museum of Natural History, the Carnegie Museum of Natural History, the National Museum of Natural History, and the Yale Peabody Museum, respectively.

Abbreviations used in figures are as follows:

aca	canal for anterior cerebral artery
Bo	basioccipital
bpp	basipterygoid process
Bs	basisphenoid
ca	crista antotica
cp	crista proötica
Eo	exoccipital
F	frontal
gr pn	groove for palatine branch of facial nerve
ica	foramen for internal carotid artery
J	jugal
jv	foramen for jugular vein
L	lacrimal
Ls	laterosphenoid
M	maxilla
mpa	canal for median palatine artery
N	nasal
Op	opisthotic
Os	orbitosphenoid
P	parietal
pa	foramen for palatine artery
pao	preantorbital opening
Pf	prefrontal
pf	posttemporal fenestra
Pm	premaxilla
pn	foramen for palatine branch of facial nerve
Po	postorbital
Pr	proötic
Ps	parasphenoid
Pt	pterygoid
Q	quadrate
Qj	quadratojugal
So	supraoccipital
Sq	squamosal
s-Sq	sutural surface for squamosal
I–XII	foramina for cranial nerves

HISTORICAL REVIEW

Previous Collections and Descriptions

In order to understand fully and, therefore, hopefully, to resolve remaining areas of confusion concerning the morphology of *Apatosaurus* and its relationships to other sauropods, particularly to *Camarasaurus* and *Diplodocus*, it is necessary to give a detailed chronicle of the circumstances and events surrounding the collecting and description of those specimens pertinent to this topic.

In July, 1877, Marsh (1877*a*) described a large incomplete sauropod sacrum (YPM 1835) as *Titanosaurus montanus*, which was found by Arthur Lakes and H. C. Beckwith at what was later designated as YPM quarry 1 north of Morrison, Colorado (Ostrum and McIntosh, 1966). As Lydekker (1877) had used the same generic name several months earlier in describing two caudals and a chevron of a different species of sauropod, *Titanosaurus indicus*, Marsh (1877*b*) altered the name of his Morrison specimen to *Atlantosaurus montanus* in December of the same year. Farther on in the same publication Marsh also described a second sauropod sacrum and vertebrae as representing a new genus, *Apatosaurus ajax*. This specimen, also discovered by Lakes in another quarry near Morrison, later designated YPM quarry 10, had originally been sent to E. D. Cope for identification. However, when Marsh purchased the specimen from Lakes, Cope sent it to the Yale Peabody Museum at Lake's request. Marsh kept accurate records of his collections and an accession number was placed on all fossils arriving at the museum as the boxes containing them were unpacked. Later, when the bones were identified and studied, they were given a catalogue number. The *Apatosaurus* sacrum from YPM quarry 10 which originally had been sent to Cope, was included as part of accession no. 993 and was later catalogued as YPM 1860. Lakes was to make a number of additional shipments from a total of 11 separate quarries at Morrison. In the shipments that followed from quarry 10 there was a very large femur that was attributed by Marsh (1878*a*) to a new species of *Atlantosaurus*, *A. immanis*, and

was later catalogued as YPM 1840. The numerous shipments from Morrison included many more elements from quarry 10. By 1883 the Morrison collections had been prepared and it was evident that the material from quarry 10 belonged to two very large skeletons. The smaller of the two, which included the *Apatosaurus ajax* sacrum YPM 1860, was from a dark clay layer that imparted a black color to it. The larger skeleton, which included the *Atlantosaurus immanis* femur YPM 1840, came from a light colored sandstone immediately overlying the clay layer and its elements are light colored. S. W. Williston, who, as Marsh's assistant, sorted out the bones of these two specimens in 1883, noted in a memorandum to Marsh their close similarity and believed them to belong to the same species.

Included in the shipments from Morrison were cranial materials that have a direct bearing on the controversy about the nature of the skull of *Apatosaurus*. The second Morrison shipment sent by Lakes and B. F. Mudge in 1877 and assigned accession no. 1002 contained material from quarries 1, 8, and 10. Among this material was the greater part of a cranium on which was originally marked only the accession number. The importance of this specimen was apparently not realized at the time of its receipt, because the box number, which would have indicated from which of the three quarries it came, was not recorded on the cranium. In sorting out the collections from Morrison, Williston assigned the cranium to the "*Atlantosaurus immanis*" specimen, indicating that he believed it was found in quarry 10. Marsh (1896) later figured the cranium as *Atlantosaurus montanus*, which would appear to indicate that he believed it to be from quarry 1. The cranium, as will be shown in a later section, is *Diplodocus*-like in structure and its quarry origin is, therefore, of great importance. Adding to the confusion, when the quarry 10 material was catalogued the number YPM 1860 was placed on not only the bones of the holotype of *Apatosaurus ajax*, but also on those of "*Atlantosaurus immanis*." It is not known why, when or by whom this was done. Also from quarry 10 at Morrison was a pair of very large *Diplodocus*-like quadrates. Although the catalogue number YPM 1860 is marked on both, only the left one bears the accession no. 1052 and the box no. 53, which definitely identifies its origin as quarry 10. The quadrates, therefore, provide important evidence on the nature of the skull of *Apatosaurus*.

In the summer of 1879 two of Marsh's foremost collectors, W. H. Reed and E. G. Ashley, discovered the major portions of two very large sauropod skeletons in the same stratum of two adjacent quarries at Como Bluff, Wyoming. These were described by Marsh as two species of a new genus, *Brontosaurus*. The more perfect skeleton, YPM 1980 from Como Bluff quarry 10 (to date, one of the most complete sauropod skeletons ever found), he described (1879*a*) as the holotype of the type species *Brontosaurus excelsus*, whereas the other, YPM 1981, from Como Bluff quarry 11, he described (1881) as the type of *B. amplus*. YPM 1980 lacked the skull, first few cervicals, posterior half of the tail, ulna, and all the bones of both the manus and pes except the astragalus; YPM 1981 possessed only one bone not represented in YPM 1980, the second metacarpal. In 1883 Marsh published a restoration of *B. excelsus*, the first for any sauropod dinosaur. Though his restoration was quite good overall, it contained numerous errors, most of which depicted "*Brontosaurus*" as having *Camarasaurus*-like features. The feet were incorrectly restored with a full complement of phalanges and, in *Camarasaurus* fashion, two proximal carpals and tarsals were attributed to "*Brontosaurus*"; *Apatosaurus* has only one each of these elements, the astragalus and "scapholunar." The crushed ulna and manus used in Marsh's restoration belonged to a partial skeleton of a large adult *Camarasaurus*, YPM 4633, from YPM Como Bluff quarry 1A. Detailed drawings of these elements, which were prepared for Marsh for a proposed sauropod monograph, have been reproduced by Ostrom and McIntosh (1966). The narrow, elongated metacarpals and the slender ulna of YPM 4633 are in sharp contrast to the short, stout metacarpals and the extremely robust ulna of *Apatosaurus*. When YPM 1980 was mounted at the Yale Peabody Museum the ulna and manus of YPM 4633 were used to complete the skeleton. Marsh was unaware of the correct number of cervical and caudal vertebrae of "*Brontosaurus*" and restored the neck and tail after "*Morosaurus*," that is, *Camarasaurus*, with too few vertebrae. The neck was shown as having only 12 vertebrae as in *Camarasaurus*, rather than the correct number of 15. Marsh also did not know that "*Brontosaurus*" had a long, "whip-lash" tail, containing as many as 82 vertebrae, almost twice the number found in *Camarasaurus*. Most importantly, for the missing skull of his restoration of YPM 1980 Marsh used a large, incomplete *Camarasuarus*-like skull, YPM 1911, from YPM Como Bluff quarry 13,

located about 4 mi from and in a stratum distinctly lower than that of YPM quarry 10 from which came "*B.*" *excelsus* (Ostrom and McIntosh, 1966). Quarry 13 had yielded four partial skeletons of *Camarasaurus*, including the type of "*Morosaurus*" *lentus* (YPM 1910), and a quadratojugal and caudal centrum of *Diplodocus,* but no identifiable remains of *Apatosaurus*. The skull YPM 1911 consists of premaxillae, maxillae, lacrimals, vomers, dentaries, loose teeth, and some fragments; its massive jaws and spatulate teeth are prominent *Camarasaurus* features. In 1891 Marsh published a revised reconstruction of "*Brontosaurus,*" which was in some ways less accurate than his first (Riggs, 1903*a*). Although he added a thirteenth vertebra to the cervical series, he also increased the number of dorsals from the correct 10 to 14, which is closer to the 12 possessed by *Camarasaurus*. In his second restoration Marsh used a different skull, USNM 5730, from YPM-USNM Canyon City quarry 1 at Garden Park, Colorado. It is about the same size as the skull YPM 1911 but somewhat more complete, consisting of maxillae, premaxillae, squamosal, dentaries, cranium, and perhaps a quadrate. USNM 5730 also has the distinctive massive jaws and spatulate teeth of *Camarasaurus*. The skull was found isolated from other skeletal materials in quarry 1, representing as many as five or six sauropod genera. Although *Apatosaurus* was one of those genera present, quarry maps indicate no reason to believe that the skull was associated with any remains of this genus.

Most, if not all, of the vast collections of sauropods made by the American Museum of Natural History from 1897 to 1905 at Bone Cabin quarry, Como Bluff, and nearby localities in southeastern Wyoming, belonged to the three common genera of the Morrison Formation. A partial skeleton of *Apatosaurus* from Como Bluff was described by Osborn (1898) as *Camarasaurus* and, although not explicitly stated, he strongly implied that *Camarasaurus* and "*Brontosaurus*" were very closely related, if not synonymous. The greater part of the collections from Bone Cabin quarry consisted of limbs, feet, and tail segments. The feet were sometimes articulated with the limbs, but more often not. For unknown reasons the numerous undersized limbs were separated out as "*Morosaurus,*" the large robust limbs as "*Brontosaurus*" and the large slender limbs as *Diplodocus;* these assignments caused problems. The robust hindlimb bones of *Camarasaurus* are very similar to those of *Apatosaurus* and some of the large hindlimb elements of the former were assigned to the latter. Also resulting in misidentifications, the forelimb bones of *Camarasaurus* are slender and the radius and ulna, in particular, resemble those of *Diplodocus*. Further, it was not known that the metacarpals of *Camarasaurus* were much longer and more slender than those of *Diplodocus*. Important to the discussion here was the misidentification of a right radius, ulna and manus of *Camarasaurus* AMNH 965 from Bone Cabin quarry. Osborn (1904) originally described the manus correctly as "*Morosaurus*" but apparently reconsidered his identification about a year later when he sent a cast of it to the Carnegie Museum in response to their request for a manus to complete the *Diplodocus* being mounted there. A reduced model of the manus was not only used in the Carnegie Museum exhibit, but also in 10 casts of the entire skeleton sent to museums throughout the world. Osborn also sent photographs of AMNH 965 to Abel, who not only published them (1910) as the manus of *Diplodocus,* but also used them in his restoration of this genus. Forelimbs of *Diplodocus* and forefeet of *Camarasaurus* from Bone Cabin quarry were also mistakenly associated as composite specimens of *Diplodocus* and sent by the American Museum of Natural History to a number of museums throughout the world.

In the early 1900s numerous important discoveries were made that revealed errors in Marsh's (1883, 1891) restorations of *Apatosaurus*. Most significantly, these discoveries not only removed some of the erroneous resemblances between *Camarasaurus* and *Apatosaurus* that were suggested by Marsh's restorations of the latter, but also disclosed some important features shared by *Apatosaurus* and *Diplodocus*. Hatcher (1901*b*, 1902) described the forelimb and, more importantly, the forefoot of *Apatosaurus* correctly, using associated material, CM 563, now mounted at the University of Wyoming, Laramie. Hatcher, however, failed to notice that the forefeet of *Apatosaurus* and *Diplodocus* are much closer in structure than either is to that of *Camarasaurus*. Riggs (1903*b*) not only showed that *Brontosaurus* is a junior synonym of *Apatosaurus,* but also demonstrated that *Apatosaurus* possesses 10 dorsal vertebrae, that the number of sacral vertebrae of sauropods is not a valid generic character as Marsh believed, and that the chevrons of the midcaudals of *Apatosaurus* are *Diplodocus*-like in having fore and aft distal processes. Undoubtedly, the most important event with regard to this dis-

cussion here was the discovery in 1909 by Earl Douglass of the Carnegie Museum of the well-known, richly fossiliferous, dinosaur quarry at what is now Dinosaur National Monument, near Jensen, Utah. The first specimen discovered and excavated from this quarry, known then as Carnegie quarry, was important not only in being the most complete *Apatosaurus* skeleton ever found, but in having a large skull closely associated with it. In 1915 Holland (1915*b*) not only described the postcranial skeleton, CM 3018, as a new species, *A. louisae*, but, on the basis of the skull associated with it, he (1915*a*) also challenged Marsh's (1883, 1891) original identifications of the skull of "*Brontosaurus*." The type of *A. louisae*, which was designated field no. 1, was found (Fig. 1) largely articulated, but with the trunk, neck and forelimb somewhat displaced. A second, almost as complete and articulated skeleton of this species, field no. 40, lay beside CM 3018 and, although an adult specimen, was 15 to 20% smaller than the type; this specimen is now at the Los Angeles County Museum. Lying beside cervicals 12 and 13 of field no. 40 and about 4 m from the atlas of CM 3018 was a large *Diplodocus*-like skull without mandibles, CM 11162. Though the posterior portion of a medium-sized *Diplodocus* skeleton (field no. 60) lay only about 3 m from the skull CM 11162 (Fig. 1), their size difference precludes any possibility that they were associated. Noting the close proximity of the skull CM 11162 to the skeleton CM 3018, their position in the same layer and the exact fit of the occipital condyle of the skull into the articular cup of the atlas of CM 3018, Holland (1915*a*:274) concluded that the *Diplodocus*-like skull represented the true skull of *Apatosaurus*, stating that "Had nothing in the past been written in reference to the structure of the skull of *Brontosaurus* the conclusion would naturally and almost inevitably have been reached that this skull belongs to the skeleton the remainder of which has been recovered." However, when the skeleton of *A. louisae* CM 3018 was mounted at the Carnegie Museum, Holland considered using this skull but refrained from doing so apparently at the insistence of Osborn (Holland, 1915*a*) and, instead, the skeleton stood headless for more than 20 years (Gilmore, 1936). After Holland's death in 1932 a cast of the *Camarasaurus* skull CM 12020 was used to complete the mount. This large, incomplete skull was collected at Carnegie quarry as part of field no. 240, which included the greater part of an adult *Camarasaurus* skeleton, and originally both the skull and postcranial skeleton received the same catalogue number, CM 11393. There is no reason to believe that the skull and postcranial skeleton did not belong to the same individual and, further, no *Apatosaurus* material was found nearby to suggest that the skull might pertain to this genus. It is also important to mention here that Holland (1915*a*) described a second feature of *Apatosaurus* that further helps to substantiate its closeness in structure to *Diplodocus*, the presence of a "whip-lash" type of tail. This structure was clearly documented not only in *A. louisae* CM 3018, but in a medium-sized specimen, CM 3378, found isolated at the far western end of Carnegie quarry and consisting of a vertebral column complete and articulated from the mid-cervical region to the eighty-second caudal.

Three other specimens found closely associated at Carnegie quarry (Fig. 1) are pertinent to this discussion. A partial skeleton, field no. 24, of a small, juvenile *Apatosaurus*, CM 3390, was found lying near the cervicals of *A. louisae* CM 3018. CM 3390 consists of the complete dorsal vertebral series, sacrum, caudals 1–12, left pelvic bones, right ischium, and a few ribs. Earl Douglass, who directed the Carnegie quarry excavation, estimated its total length to be about 5 m. Most interesting, however, in the records of the collection from the quarry Douglass states that "About 20 feet east of here [field no. 24], ten or more connected cervicals of a small dinosaur (field no. 37) were found, also the anterior portion of a small jaw with pencil-like teeth (field no. 35). I worked out nos. 24 and 37 later when in the museum in Pittsburg and this confirmed the surmise that these belonged to the same individual." If these three specimens belonged to the same individual, then the *Diplodocus*-like teeth of the jaw provides additional evidence on the nature of the skull of *Apatosaurus*.

Carnegie quarry has also been important in yielding excellent skulls of *Diplodocus;* two of these are relied on heavily in redescribing the skull of *Diplodocus* in a later section. The complete and uncrushed skull and mandible CM 11161 was discovered beside the anterior caudals of the nearly complete vertebral column of the medium-sized *Apatosaurus* CM 3378 found isolated at the far western end of the quarry. Earl Douglass viewed this association as evidence that *Apatosaurus* possessed a *Diplodocus*-like skull (McIntosh and Berman, 1975). The skull, however, was the basis of Holland's (1924) description of the skull of *Diplodocus*. The palate and lower jaw of CM 11161 were

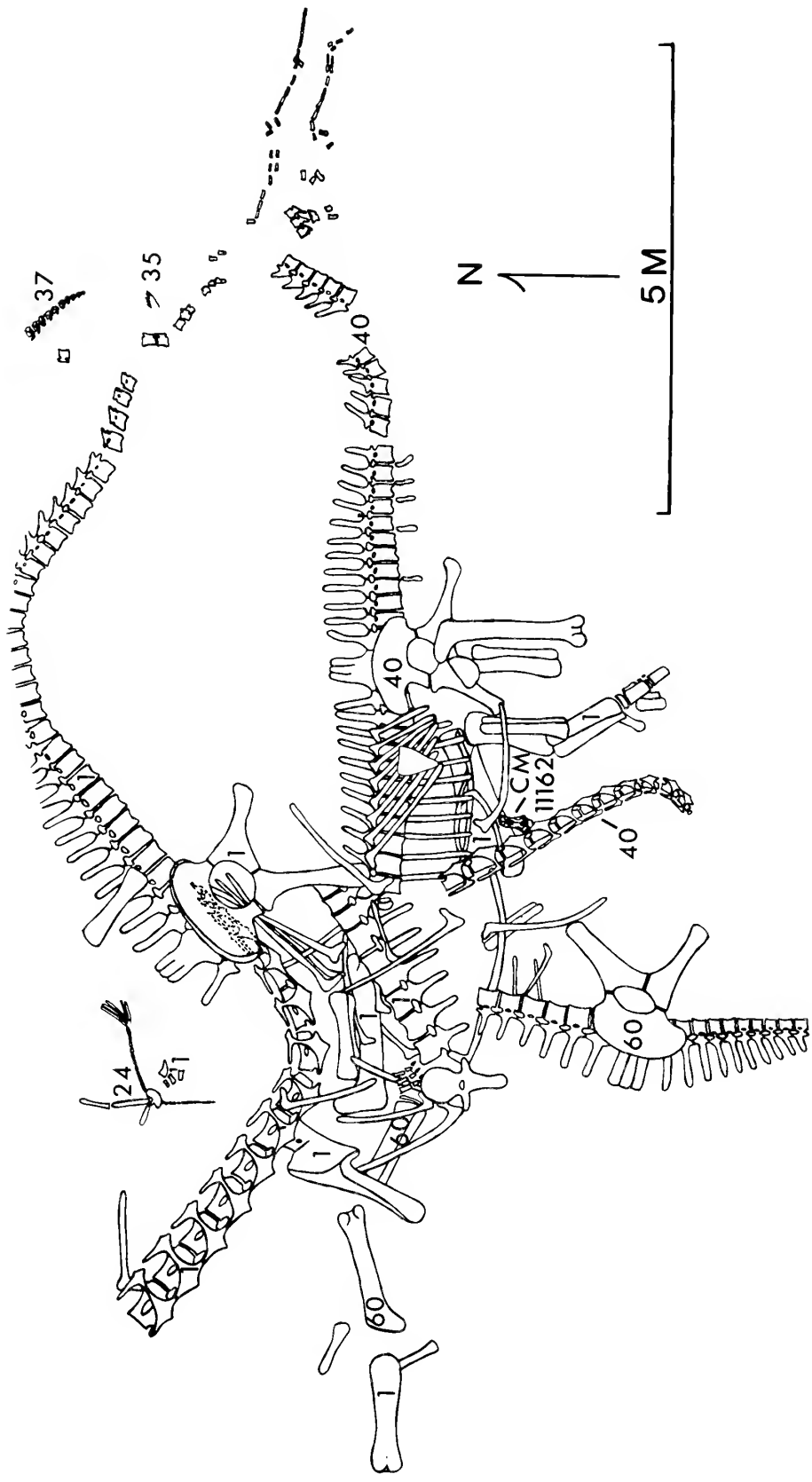

Fig. 1.—Relative quarry positions of various sauropod specimens discussed in text from Dinosaur National Monument. Redrawn from quarry map on file at Carnegie Museum of Natural History showing specimens removed from quarry by that institution. Field nos. 1 and 40, postcranial skeletons of type of *Apatosaurus louisae*, CM 3018, and specimen now at the Los Angeles County Museum; CM 11162, skull very probably belonging to field no. 1 or 40; field no. 60, postcranial skeleton of *Diplodocus;* field no. 24, portion of postcranial skeleton of a juvenile *Apatosaurus* (CM 3390), field no. 37, series of cervical vertebrae, and field no. 35, anterior portion of small jaw with *Diplodocus*-like teeth, probably belonging to one individual of *Apatosaurus*.

recently redescribed (McIntosh and Berman, 1975). CM 3452, consisting of skull, mandible, and the first six cervicals in articulation, is a very important specimen in that it is the only instance in which a *Diplodocus* skull has been found articulated with postcranial elements. This specimen was sketchily illustrated and briefly referred to a few times by Holland (1924) in his description of the skull of *Diplodocus*. Some of its disarticulated palatal bones were recently described (McIntosh and Berman, 1975).

Discussion

Numerous factors can be attributed to the origin of the false notions that *Apatosaurus* possessed a *Camarasaurus*-like skull and was more closely related to *Camarasaurus* than to *Diplodocus*. Not least among these is that the first descriptions of *Apatosaurus* Marsh (1877*b*) and *Camarasaurus* Cope (1877*a*) were based on only very small portions of the type skeletons, were very brief, and were without illustrations. The reason for this was the Cope-Marsh feud at that time (Romer, 1964). In their zeal to be first in describing the large sauropods of North America, Marsh and Cope rushed out descriptions on the first few elements of the type skeletons they received from their collectors, even though the greater portions of the skeletons were still being excavated. During the next year and a half, as more material was collected and prepared, these descriptions were only slightly amplified (Cope, 1877*c*, 1878*a*; Marsh, 1879*b*), including figures of a few bones of both genera, but neither genus received the description it merited. Thereafter, both genera were largely ignored. Marsh's (1878*b*, 1879*a*) descriptions of two new sauropods, *Morosaurus* and *Brontosaurus,* further complicated the picture. Both genera were based on good material and were described in detail with many excellent illustrations. However, of the half dozen or more partial skeletons Marsh had identified as *Morosaurus,* all were juveniles or subadults and were considerably smaller than the two large skeletons of *Brontosaurus* he had. As a result, the few adults *Camarasaurus* specimens he had were apparently misidentified as *Brontosaurus* because of their large size. Had he realized that "*Monosaurus*" attained the same size as "*Brontosaurus,*" he might not have used the large *Camarasaurus*-like skulls YPM 1911 and USNM 5730, and the ulna and manus of the partial skeleton of the adult *Camarasaurus* YPM 4633 in his (1883, 1891) restorations of *Brontosaurus*. Although YPM 1911 and USNM 5730 represent individuals much larger than any of the specimens in Marsh's collection, which he recognized as *Morosaurus,* they are not too large when compared with the type skeleton of *C. supremus* described by Cope (1877*a*), for which he did not report any skull parts (portions of the skull, including upper and lower jaws with teeth, were later described by Osborn and Mook, 1921). It can also be pointed out that Marsh never indicated his use of referred specimens, seemingly selected on purely conjectural grounds, to complete his restorations of *Brontosaurus*. This practice undoubtedly helped to perpetuate many of the misconceptions about the structure of *Apatosaurus*. Adding to the confusion, in 1898 Osborn described a "*Brontosaurus*" skeleton as *Camarasaurus,* apparently believing the two genera to be synonymous. Even after a thorough study of the type of *Camarasaurus* by Osborn and Mook (1921) showed it to be a senior synonym of *Morosaurus*, the erroneous concept of a close relationship between *Camarasaurus* and *Apatosaurus* persisted. This was due largely to 1) the recognition that the skeletons of *Apatosaurus* and *Camarasaurus* are very robustly constructed and their hindlimbs are nearly indistinguishable, whereas the skeleton of *Diplodocus* is very slender in structure and its hindlimbs are easily identified and 2) the continued acceptance of the false notion that *Apatosaurus* possessed a *Camarasaurus*-like skull. It is remarkable that Holland's claim that *Apatosaurus* possessed a *Diplodocus*-like skull continued to fail to receive serious consideration even after accurate restorations of the postcranial skeletons of *Apatosaurus* (Gilmore, 1936), *Camarasaurus* (Gilmore, 1925) and *Diplodocus* (Hatcher, 1901*a*, 1903*b*; Holland, 1906) became available. Despite the fact that even a cursory comparison of their postcranial skeletons, excepting their hindlimbs, shows that *Apatosaurus* is not only quite distinct from *Camarasaurus,* but shares a great number of significant features with *Diplodocus*, such observations have, to date, not been made.

Examination of the type skeletons of *Apatosaurus ajax* YPM 1860 and *Atlantosaurus immanis* YPM 1840, the only postcranial specimens from YPM quarry 10 at Morrison, Colorado, substantiates Williston's observation that they belong to the same species and the latter is considered to be a junior synonym of *A. ajax*. The pair of *Diplodocus*-like quadrates from YPM quarry 10 are identical in size, color and morphological detail, leaving almost

no doubt they belong to the same individual. Further, their black color suggests that they belong to the identically colored skeleton YPM 1860, rather than to the light colored skeleton YPM 1840. The greater portion of cranium contained in the shipment of specimens Marsh received from Lakes and Mudge in 1877 from the Morrison quarries 1, 8, and 10 is also *Diplodocus*-like and is also thought to belong to YPM 1860. If the cranium is from quarry 10, as Williston must have thought in assigning it to *Atlantosaurus immanis* YPM 1840, then it probably belongs to YPM 1860, because both have the same black coloring. It is also important to point out that the quadrates and the partial cranium are of the appropriate sizes to have belonged not only to the same animal, but to a skeleton the size of YPM 1860 or YPM 1840. The other possible, but far less likely, origin of the cranium is YPM quarry 1, as Marsh (1896) apparently thought when describing it as *Atlantosaurus montanus*. In addition to the type sacrum YPM 1835 of *A. montanus,* YPM quarry 1 has yielded *Camarasaurus*-like vertebrae. Examination of the sacrum YPM 1835 reveals that it is too fragmentary to permit generic identification and it could conceivably belong to either *Apatosaurus, Diplodocus,* or *Camarasaurus,* which have been found at the 11 quarries at Morrison. It is not unlikely, however, that either Williston or Marsh may have obtained more precise locality information for the cranium from Lakes or Mudge well after it arrived at the Yale Peabody Museum and that this was never recorded in the catalogues. The cranium now bears the catalogue number YPM 1860, but we do not know when, by whom, or on what basis it was given this number. It is possible that this was done at the same time that this number was placed on the bones of both the type of *Apatosaurus ajax* and "*Atlantosaurus immanis*" (=*A. ajax*) YPM 1840. White (1958), on the basis of the catalogue number YPM 1860 on the cranium, quite reasonably assumed that it was part of the type of *A. ajax* and that Marsh (1896) had a *lapsus calami* in describing it as *Altantosaurus montanus*. Further, White considered the cranium to closely resemble that of *Camarasaurus* and, therefore, to provide evidence of a close relationship between *Apatosaurus* and *Camarasaurus*. It is surprising that White appears not to have been aware of the pair of quadrates from YPM quarry 10; had he examined them, he surely would have immediately recognized their *Diplodocus*-like structure and so might have noticed the *Diplodocus*-like nature of the cranium. White also mentioned that parts of both pterygoids, which embrace the recesses basipterygoideus, are present with the cranium. We found one of these elements but were unable to either confirm or give an alternative to his identification.

The probable *Apatosaurus* skull CM 11162 has never been described and only a small portion of it has been illustrated. In a discussion of tooth replacement in *Diplodocus,* Holland (1924:Fig. 5) illustrated a small part of the anterior end of the right maxilla, where, due to the loss of surface bone, the replacement pattern is clearly seen. Additional preparation of CM 11162 has revealed considerable plaster restoration. Further, the Carnegie Museum of Natural History collections include a plaster cast of the skull in its restored state and it is suspected that the restoration and cast were done at the request of Holland, who (1915*a*:277) stated that at times he was inclined to mount it on the postcranial skeleton of *A. louisae* CM 3018 on exhibit at Carnegie Museum. After a thorough review of all the evidence we (McIntosh and Berman, 1975) concurred with Holland that the skull CM 11162 probably represents *Apatosaurus,* if not the type of *A. louisae*.

SKULL OF *DIPLODOCUS*

The skull here described as probably belonging to *Apatosaurus*, CM 11162, is so close to that of *Diplodocus* in structure that the problem of distinguishing between them is difficult. In light of this problem, comparisons using previous descriptions of skulls of *Diplodocus* are made somewhat tenuous, because these skulls were found isolated, leaving some doubt as to their identification. Most importantly, previous descriptions of the skull of *Diplodocus* are incomplete and contain numerous inaccuracies. The *Diplodocus* skull CM 3452 from Dinosaur National Monument is, therefore, emphasized here, because it represents the only known direct association of skull and postcranial skeleton of this genus. In Holland's (1924:Pl. XL, fig. 2) illustration of this specimen only the damaged and partially disarticulated right side of the skull is shown. Further preparation reveals that the left

side, occiput, and roof of the skull are nearly perfectly preserved. The essentially complete and uncrushed skull CM 11161 is here considered to represent *Diplodocus* even though it was found closely associated with the nearly complete vertebral column of *Apatosaurus* CM 3378 isolated at the far western end of Dinosaur National Monument quarry. This assignment is justified by the common possession of characters of CM 11161 and the unquestionable *Diplodocus* skull CM 3452 that are not seen in the probable *Apatosaurus* skull CM 11162. An excellently preserved cranium, CM 26552 from Dinosaur National Monument, on which our description of the braincase of *Diplodocus* mainly rests, is assigned to this genus on the same grounds; CM 26552 has not been previously described. Similarly, the posterior portions of the skulls CM 662 used by Holland (1906) and AMNH 694 by Osborn (1912) to describe the braincase of *Diplodocus* exhibit a closer resemblance to CM 3452 than to CM 11162. The skulls USNM 2672 and USNM 2673 used by Marsh (1884, 1896) and AMNH 969 used in part by Holland (1906, 1924) in reconstructions of the skull of *Diplodocus* are also tentatively accepted as belonging to this genus.

External Features

The shape and proportions of the skull of *Diplodocus* have been accurately reconstructed by Marsh (1884, 1896; see also Ostrom and McIntosh, 1966) and Holland (1906, 1924); in some details these aspects of Marsh's reconstructions are more exact. One apparent error in Marsh's restorations of the shape of the skull, however, should be noted. In his dorsal views of the skull the steeply pitched, lateral surface below the larger, posterior, antorbital opening is incorrectly shown as being broadly bowed laterally, rather than flat. Whereas Marsh's restorations omit some of the sutures and inaccurately show the courses of a few, Holland's not only incorrectly show the extent of many of the bones, but erroneously depict the presence of others, such as a supraorbital and postfrontal. Most of the errors in the literature that pertain to the external features of the skull of *Diplodocus* concern the sutural pattern of the posterior half of the skull; the description that follows is mainly intended to resolve this confusion. Most of this information is readily visible in Figs. 2 and 3.

In dorsal view the cranial roof is dominated by the broad, flat frontals. They contact the fused parietals posteriorly in a nearly straight, transverse suture that extends laterally to nearly the upper end of the supratemporal fossa; at this point the frontal-parietal contact continues a short distance as it turns abruptly anteriorly to skirt the upper end of the fossa. Lateral to the frontal-parietal suture the frontal is drawn outward into a transversely oriented, nearly vertical wing that extends ventrally to contact on its posterior surface a dorsal, medially expanded process of the postorbital; the plane of their contact is oriented obliquely anteroventrally in sagittal section. The anterior surface of the lateral wing of the frontal forms the posterodorsal portion of the orbital border and wall. The posterior surface of the frontal wing is extensively overlapped by the postorbital and their surface line of contact extends outward and downward along the anterodorsal margin of the supratemporal fossa so that the frontal makes little or no contribution to the fossa wall. Seen from above the frontal portion of the orbital rim is deeply concave. The nasal-frontal suture is sinuous and extends laterally, meeting the prefrontal a short distance posterior to its medialmost level of projection. The anterolateral corner of the frontal is deeply incised by the narrowly triangular, posteromedially directed, posterior half of the prefrontal. The fused parietals are narrowly exposed on the skull roof, where they taper somewhat as they extend toward the supratemporal fossa. A vertically oriented, lateral wing of the parietal, forming the posterior wall of the supratemporal fossa, has an extensive occipital exposure. The lateral wing of the parietal is triangular in cross-section and thins toward its outer edge, which in occipital view is greatly expanded dorsolaterally into a smooth, broadly convex border.

In CM 3452 the intersection of the median union of the frontals with the fused parietals is well preserved and, as Holland (1924) pointed out, a parietal opening is absent. Holland also noted the absence of such an opening in the *Diplodocus* skull CM 662, but claimed that a medial opening was present in the parietal region of the skull roof of the probable *Diplodocus* skulls CM 11161, AMNH 969, USNM 2672 and USNM 2673, and the probable *Apatosaurus* skull CM 11162. We can find no evidence that this opening existed in these specimens. Though in none of the specimens illustrated here can the presence of a midline suture of the nasals be verified, it is assumed that Marsh (1884, 1896) and Holland (1906, 1924) were correct in describing the nasals as paired. The paired nasals form the posterior margin of the narial opening; each is slightly concave

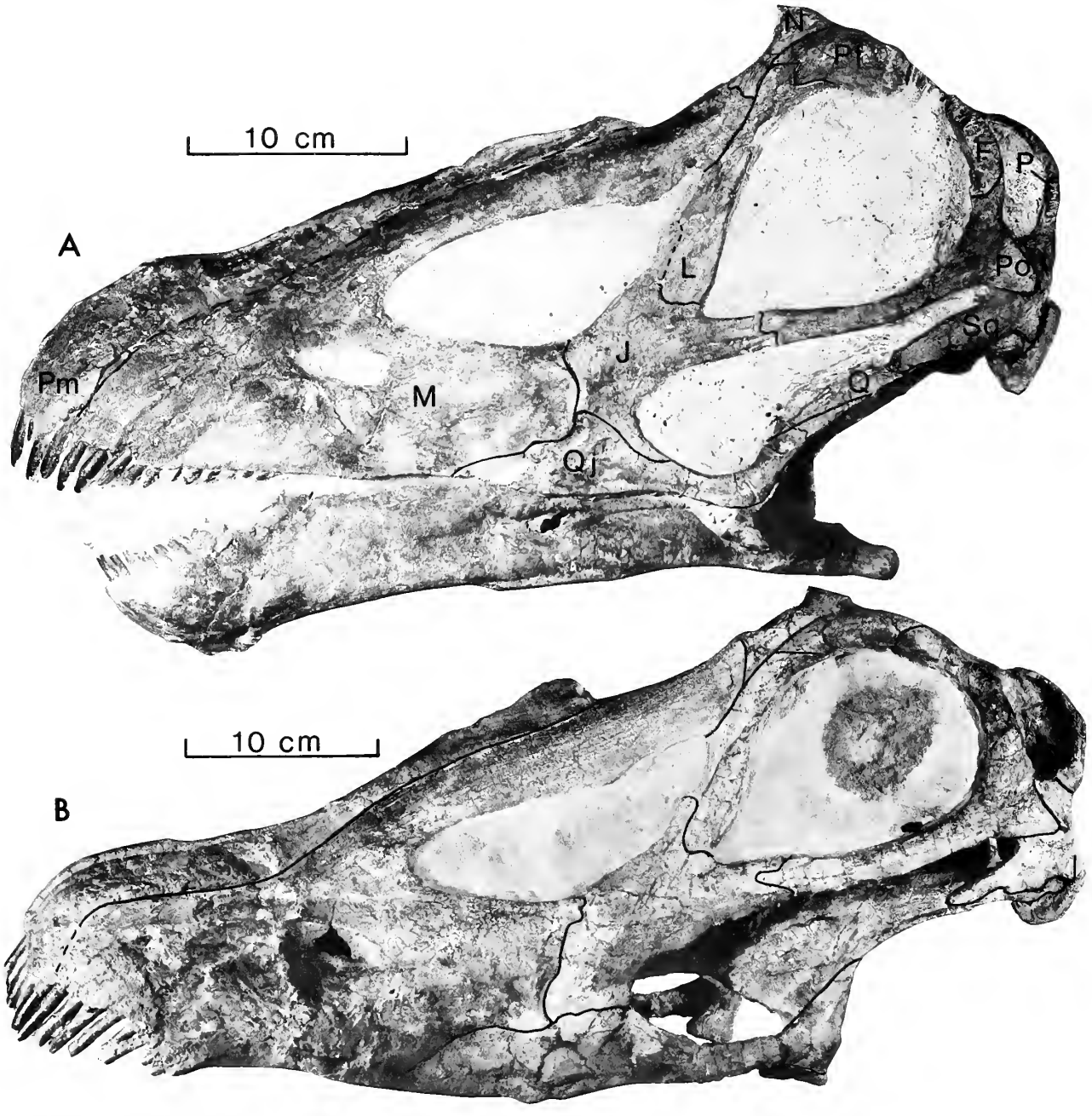

Fig. 2.—Skulls of *Diplodocus*. A, CM 3452, and B, CM 11161.

along this border, so that together they project somewhat forward into the narial opening along the midline. Laterally the nasal continues anteroventrally as a narrow, strip-like process that contacts the anterior half of the medial border of the prefrontal while bounding the posterolateral border of the narial opening. The anterior end of this process in CM 11161 is strongly beveled anteroventrally to form a short, sharply pointed lappet of bone that overlaps the upper end of the ascending process of the maxilla and contacts the anterior margin of the upper end of the lacrimal. The anteroventral pro-

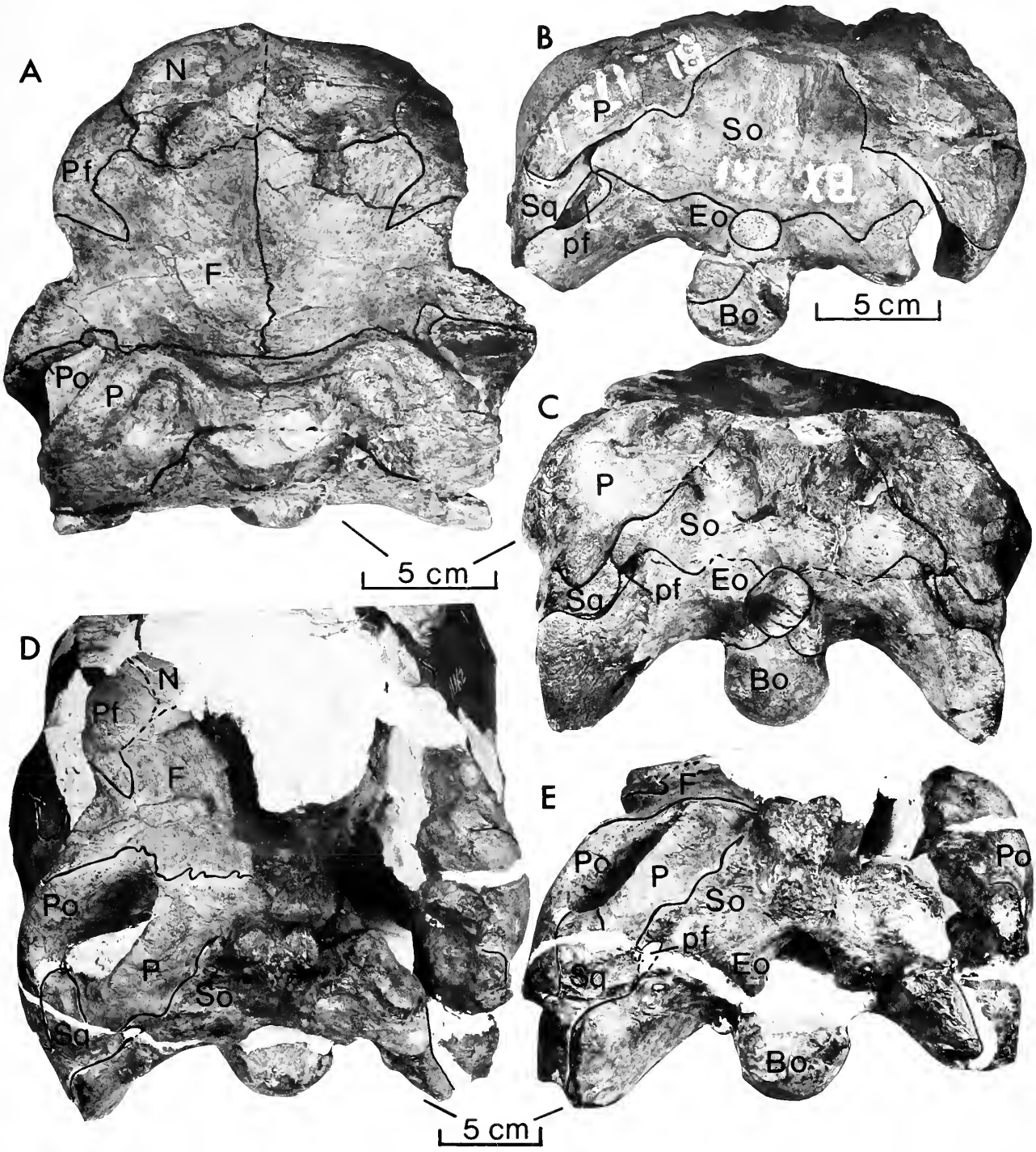

Fig. 3.—A, cranial roof, and C, occipital views of *Diplodocus* skull CM 3452. B, occipital view of *Diplodocus* braincase CM 26552. D, cranial roof, and E, occipital views of probable *Apatosaurus* skull CM 11162.

cess of the left nasal of CM 3452 appears to differ from that of CM 11161 by terminating in a border that is normal to its long axis.

The prefrontal enters the anterodorsal margin of the orbit and in lateral view its sharply pointed anterior end wedges between the nasal and lacrimal. In CM 11161 the prefrontal-lacrimal suture extends directly posteromedially across the dorsal wall of

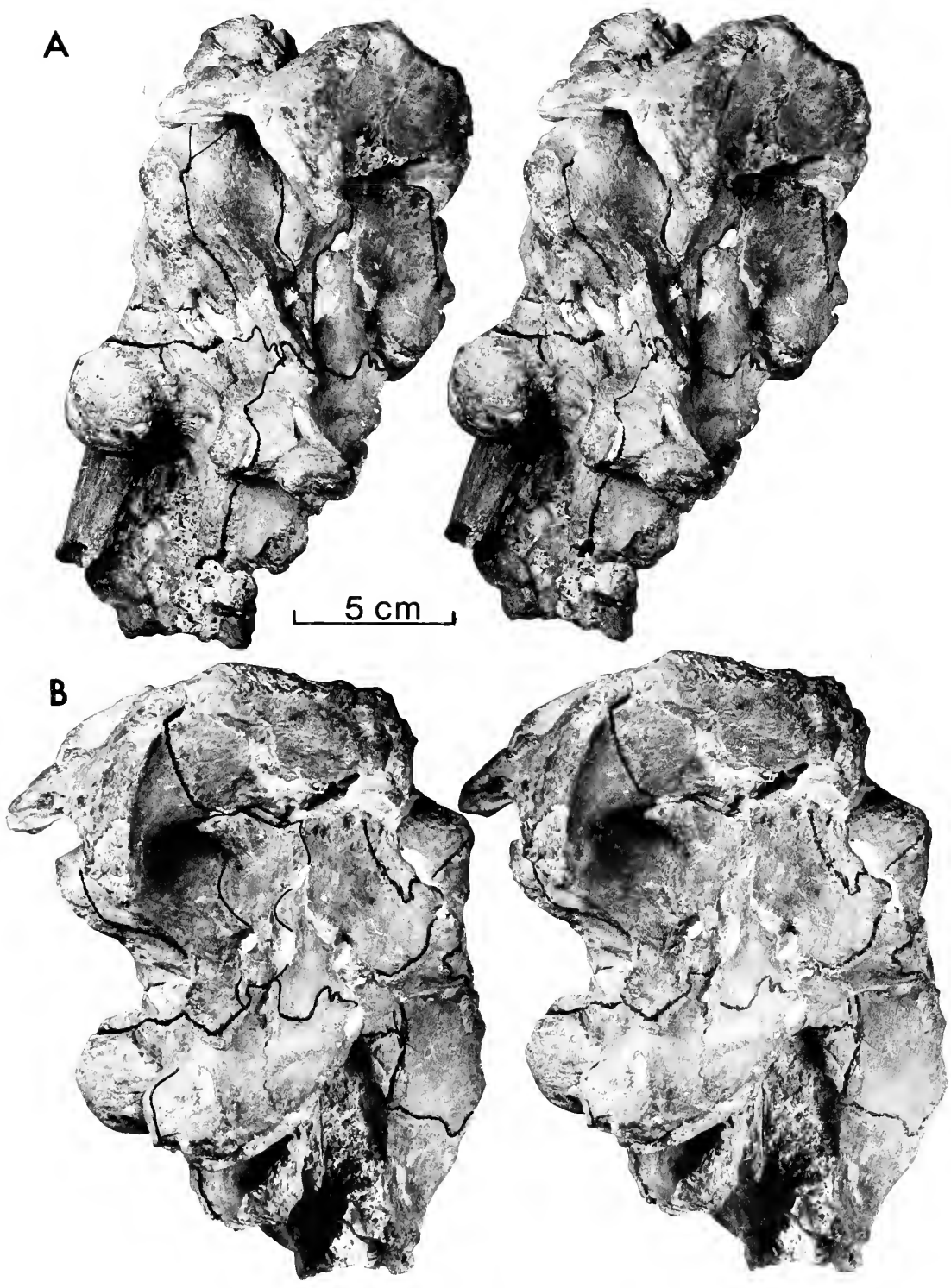

Fig. 4.—A, ventrolateral, and B, anterolateral stereo views of *Diplodocus* braincase CM 26552. Structural features indicated in Fig. 6.

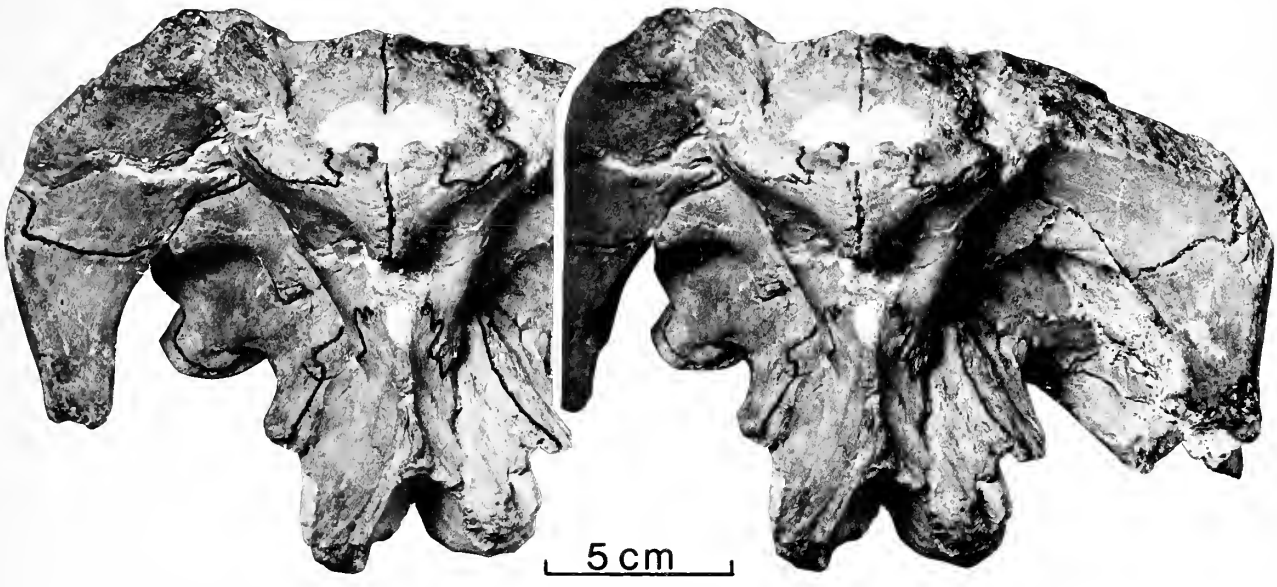

Fig. 5.—Anterior stereo view of *Diplodocus* braincase CM 26552. Structural features indicated in Fig. 6.

the orbit, whereas in CM 3452 there is a sharply angular jog in this suture. The jugal makes a small contribution to the anterior end of the ventral margin of the orbit. From the anteroventral corner of the orbit the jugal-lacrimal suture, best preserved in CM 11161, runs a short distance anteriorly, then swings abruptly dorsally, forming the posterior border of a narrow, dorsal process of the jugal, as it extends for a somewhat longer distance to reach the antorbital opening. The bluntly rounded, distal end of the dorsal process of the jugal, incomplete in the skulls CM 11161 and CM 3452 but well illustrated in the restorations by Marsh (1884, 1896; see also Ostrom and McIntosh, 1966) and Holland (1906), projects a short distance dorsally and slightly anteriorly into the posterior corner of the antorbital opening. The dorsal process of the jugal and a broadly convex expansion of the ventral margin of the ascending process of the maxilla opposite this process greatly constrict the antorbital opening. Sutural contacts of the jugal with the maxilla and quadratojugal are accurately depicted in the restorations by Marsh and Holland and are well preserved in CM 3452.

The postorbital is basically triradiate in shape. A thick, medially expanded, dorsal blade forms the anterior wall of the supratemporal fossa and contacts the parietal in a nearly vertical suture on the medial wall of the fossa. In lateral view the postorbital-frontal suture extends obliquely across the posterolateral edge of the orbit at about its midheight, then turns sharply ventromedially across the posterior wall of the orbit (Figs. 4–6). Thus the postorbital forms the ventral half of the posterior orbital wall. A short, broadly triangular, posterior process of the postorbital overlaps the squamosal. A third, greatly attenuated, anterior process of the postorbital bounds almost the entire ventral margin of the orbit; its suture with the jugal is clearly preserved in CM 3452 and its essentially vertical orientation is in marked contrast with the nearly horizontal contact depicted in previous accounts. In CM 11161 this suture is not well defined and the anterior process of the postorbital appears to have a wedge-shaped, overlapping contact with the jugal. The squamosal can also be described as consisting of basically three processes, all emanating from the posteroventral corner of the lateral side of the skull. A narrow, dorsomedially directed, occipital process of the squamosal is described in detail below. The narrow, ventral border of the supratemporal fossa is bounded by an anterodorsal process of the squamosal that is interposed between the distal end of the lateral wing of the parietal and the superior border of the posterior process of the postorbital. A third, tongue-like process is directed anteroventrally along the lateral margin of the proximal end of the quadrate. The proximal head of the quadrate, which fits into a shallow concavity on the ventral surface of the squamosal, is narrowly exposed by

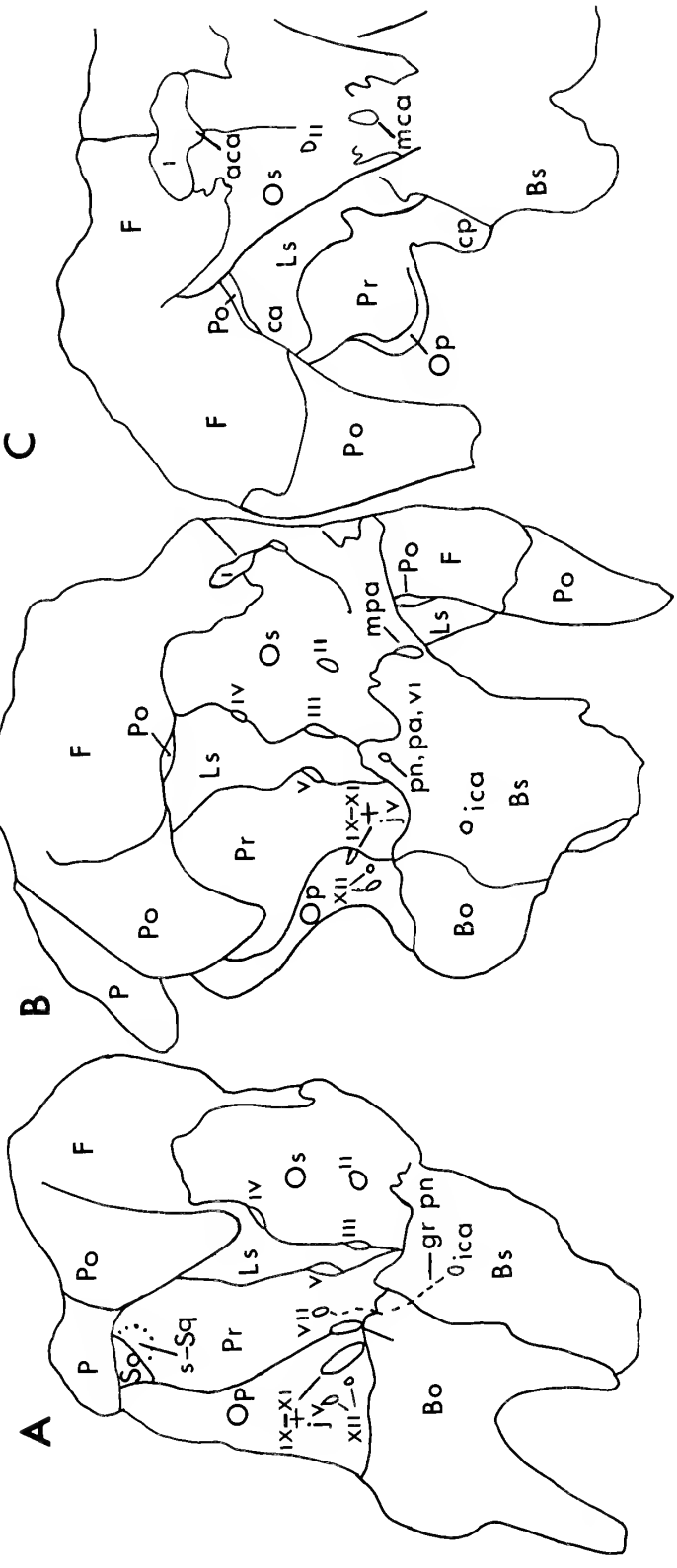

Fig. 6.—A, B, C, outline sketches of views of *Diplodocus* braincase CM 26552 of Figs. 4 and 5 with major structural features indicated.

a concave notch at the posterior end of the ventral margin of the quadrate process of the squamosal. The upper half of the anterior surface of the flared, distal end of the paroccipital process abuts against a narrow, slightly concave recess on the posteromedial edge of the squamosal below its occipital process and also buttresses the head of the quadrate; the lower half of the anterior margin of the flared end of the paroccipital process is free of contact. The posterior end of the quadratojugal has an extensive, overlapping contact with the lateral surface of the distal end of the quadrate. The ventral margin of the quadratojugal curves very slightly ventrally as it crosses the quadrate only a short distance above its distal end; the quadratojugal then turns dorsally for a considerable length, where it terminates by smoothly tapering toward the posterior margin of the quadrate. Although the quadratojugal and the squamosal closely approach each other along the lateral margin of the quadrate, they do not meet.

Braincase

The first detailed description of the braincase of *Diplodocus* was given by Holland (1906) and was based on a well-preserved posterior portion of skull, CM 662 (now at Houston Museum of Natural Science). A critique of this paper was published by Hay (1908), who challenged many of Holland's determinations of the bones and foramina. In particular, he pointed out that the supraoccipital occupies a much larger area than that assigned to it by Holland, and that Holland's failure to recognize the presence of the proötic was the basis of many of his errors. Both interpretations, however, contain a great number of significant errors. Osborn (1912) presented an illustration of the braincase of AMNH 694 in sagittal section, which accurately depicts the internal positions of most of the cranial foramina. However, in this figure and in one other, showing the same specimen in frontal view, he not only omitted the sutures of almost all of the bones, but also incorrectly indicated the extent of others. Von Huene (1914) gave a rough sketch of the lateral aspect of the braincase of the same specimen used in Holland's (1906) study. Though most of the foramina are indicated and correctly identified, his essentially diagrammatic illustration does not show some of the cranial sutures. In Marsh's restorations of the skull of *Diplodocus* (1884, 1896; see also Ostrom and McIntosh, 1966) no attempt was made to denote the bones of the occiput. Finally, in a reconstruction by Marsh of the skull in midsagittal section, published for the first time by us (McIntosh and Berman, 1975), the braincase is depicted in only a general way. Figs. 3–6 may largely take the place of a detailed description of the braincase.

The occiput (Fig. 3), whose shape and general features are best preserved in CM 3452, is of typical sauropod form. The occiput is subrectangular in outline and is formed by the basioccipital, exoccipitals, supraoccipital, fused parietals, and a small process of the squamosal. In none of the specimens (CM 26552, CM 11161, and CM 3452) has it been possible to trace the suture between the exoccipital and the opisthotic; thus these two elements became completely fused early. It is assumed, however, that a large but undetermined portion of this compound element exposed on the occiput and the part which encloses the two openings for cranial nerve XII at the extreme posteroventral corner of the lateral wall of the braincase represent the greater part of the surface extent of the original exoccipital. The original opisthotic, bounded by the exoccipital posteriorly and the proötic anteriorly, undoubtedly included the narrow span between the foramen for cranial nerves IX–XI and the fenestra ovalis and then presumably extended dorsolaterally as a flattened process that covered the anterior surface of the exoccipital in the paroccipital process. The exoccipital bounds the lateral wall of the foramen magnum, is separated from its mate in the roof of the foramen magnum by the supraoccipital and in the floor by the basioccipital, and makes a small contribution to the dorsolateral surface of the occipital condyle and its articular surface. Only in CM 26552 is the supraoccipital-exoccipital suture clearly preserved. The exoccipital extends directly outward from the foramen magnum, making contact with the supraoccipital above in a broadly undulating suture that laterally reaches the dorsal margin of the small posttemporal fossa. At the level of the upper end of the posttemporal fossa the exoccipital-opisthotic complex bends downward to form a broad paroccipital process, constricting in breadth somewhat as it bounds the medial side of the posttemporal fossa, then expanding again distally where it contacts the squamosal and quadrate. A hook-like process at the ventrolateral corner of the supraoccipital forms the dorsolateral margin of the posttemporal fossa. The remainder of the lateral border of the fossa is completed by a narrow, occipital process of the squamosal. It enters the occiput by extending medially between the ventrolateral corner

of the lateral, occipital wing of the parietal and the dorsal margin of the expanded end of the paroccipital process, then turns upward along the ventromedial side of the parietal to meet the hook-like process of the supraoccipital. From this point the occipital process of the squamosal continues a very short distance, still in contact with the parietal but in front of the hook-like process of the supraoccipital; the end of the occipital process of the squamosal contacts a small area on the superior edge of the anterolateral face of the proötic (Fig. 3).

In ventrolateral view the exoccipital pedicle is triangular, widening toward its ventral contact with the basioccipital where it encloses three foramina and bounds the posterior wall of a fourth. The most posterior of these openings is oval and carried the posterior branch of cranial nerve XII. Immediately anterior to this is a very small, round opening presumably for an anterior branch of the same nerve. The largest and most anterior foramen enclosed by the opisthotic is elongate (about 17 mm high and about 4 mm wide), is inclined posterodorsally, and faces somewhat posteroventrally; often referred to as the jugular foramen, it presumably transmitted nerves IX–XI and probably the jugular vein. Anterior to the jugular foramen the narrow fenestra ovalis opens on the boundary between the opisthotic and proötic. The proötic, an extensive element, is surrounded by the opisthotic and supraoccipital behind, the basioccipital and basisphenoid below, the laterosphenoid in front, and the parietal above. The proötic is tightly sutured to all of these elements except the laterosphenoid and parietal, with which it has abutment contacts. Exposed mainly as a broad, flat plate that faces anterolaterally, the proötic extends only slightly onto the anterior surface of the proximal end of the paroccipital process. Below the level of its contribution to the paroccipital process the proötic is deeply exposed posteriorly, forming a narrow, laterally projecting lamina of bone that extends downward to the ventralmost point of contact of this bone with the basisphenoid. The lateral edge of the lamina is deeply emarginated into a smooth, broad, concave arc; the lamina forms the body of the crista proötica. The lower portion of the proötic encloses one foramen and impinges on two others. Posteriorly it forms the anterior border of the fenestra ovalis. From the dorsal border of this opening two shallow, parallel grooves of nearly equal dimensions, one on either side of the proötic-opisthotic suture, extend posterolaterally to about where the suture between them turns abruptly upward across the anterior face of the proximal end of the paroccipital process. Directly anterior to the fenestra ovalis the posterior face of the crista proötica is perforated by a small round foramen for the VII nerve. A large, subcircular exit for nerve V, measuring about 8 mm in diameter, is positioned on the boundary between the proötic and laterosphenoid and at the same level as the facial nerve opening.

The laterosphenoid is a narrow, wing-like structure that is principally exposed as a flat, anterolaterally facing surface. It is strongly sutured to the basisphenoid below, but has an abutment contact with the proötic behind, the orbitosphenoid in front and the postorbital above. A short distance above its narrow contact with the basisphenoid the laterosphenoid forms the anterior margin of the trigeminal foramen and the posterior margin of the oculomotor foramen; the latter foramen is about 11 mm high and about 4 mm wide. A smooth, concave notch in the laterosphenoid margin of the trigeminal foramen probably allowed the forward passage of the ophthalmic branch of nerve V. Extending downward from the ventral border of the trigeminal foramen along the lateropehnsoid-orbitosphenoid contact is a deep channel that probably carried the maxillary and mandibular branches of this nerve. An ovate foramen for the trochlear nerve, measuring approximately 7 mm high and 4 mm wide, opens on the laterosphenoid-orbitosphenoid suture dorsal to the oculomotor foramen. As the laterosphenoid extends above the level of the trigeminal foramen it expands outward to form a thick, laterally arching lamina of bone, the crista antotica. The convex dorsal edge of the crista antotica fits into a shallow, concave channel on the ventromedial edge of that part of the postorbital forming the anterior wall of the supratemporal fossa. In anterior view of the braincase the lateral wing of the frontal, which forms the posterodorsal wall of the orbit, nearly hides from view the laterosphenoid-postorbital contact. The lateral wing of the frontal tapers to a thin edge toward the ventromedial margin of the posterodorsal wall of the orbit and does not make substantial contact with the laterosphenoid. The orbitosphenoid, which forms the anteriormost component of the lateral wall of the braincase, may possibly include some portion of the presphenoid. Its posterior portion, which forms the anterior margins of the openings for nerves III and IV, is in the form of a stout vertical pillar whose expanded ends have a digitating suture with the frontal above and

the fused basisphenoid-parasphenoid below. A short, thick process projects posteriorly from about mid-length along its posterior margin to separate the oculomotor and trochlear foramina. Immediately anterior to the oculomotor foramen and close to the midsagittal plane is a large, anterolaterally directed opening for the optic nerve, measuring about 8 mm high and 5 mm wide. At the level of the optic foramen the orbitosphenoid extends forward a short distance as it converges on the midline to unite with its mate. Dorsally the united orbitosphenoids form the ventral borders of the very large, nearly coalesced canals for the olfactory tracts, whereas ventrally they extend in front of and a short distance below the optic foramina to contact the basiparasphenoid complex; the portion of the paired orbitosphenoids forming the anteromedial borders of the optic foramina is nearly missing in CM 26552, but is well preserved in CM 11161 (not shown here). Small, blunt processes on the orbitosphenoid margins of the olfactory canals, one on either side of the midline suture, form a small cleft through which probably passed the anterior cerebral artery, a branch of the internal carotid artery. A short distance anterior to the orbitosphenoid in CM 11161 are fragments of a thin vertical plate of bone (not shown here) oriented on the midsagittal plane of the skull, which may represent remnants of the presphenoid portion of the interorbital septum.

The basioccipital appears to form the greater part of the articular surface of the condyle. The condyle is convex posteriorly and ventrally, and flattened dorsally. The long axis of the condyle is oriented at about a right angle to a plane passing through the jaw margins, indicating that the head was tilted at about a right angle to the neck. Between the condyle and the basal tubercles the inferior face of the basioccipital arches anterodorsally, then curves smoothly downward and slightly backward to form the caudal halves of the basal tubercles. The tubercles diverge slightly ventrolaterally and their posterior surfaces are separated by a deep furrow. Forming the cranial floor anterior to the basioccipital is the basisphenoid; it is completely fused with the parasphenoid, which is principally represented by the parasphenoidal rostrum. The parasphenoidal rostrum is broken off at its base in CM 26552 but is well exhibited in CM 11161 (Fig. 8). The basisphenoid forms the anterior halves of the basal tubercles, the long, slender, anterolaterally directed basipterygoid processes (broken off at their bases in CM 26552) and the inferior margin of the crista proötica. There is a deep, smooth spheroidal depression between the bases of the basipterygoid processes; this depression is bounded anterolaterally by a narrow, ridge-like projection along the anteroventral surface of the proximal third of the basipterygoid process which merges with the ventral edge of the narrow, blade-like parasphenoidal rostrum. Above the basipterygoid processes the lateral walls of the basisphenoid converge anteromedially to become smoothly continuous with the rostrum. The entrance for the internal carotid artery and the palatine branch of the facial nerve into the basicranium, via the vidian canal, is in its normal location on the ventrolateral surface of the basisphenoid between the inferior border of the crista proötica and the base of the pterygoid process. The vidian canal begins at the upper end of an approximately 5-mm-wide groove that extends a short distance anteroventrally onto the base of the basipterygoid process. A faint groove, extending ventrally from the lower rim of the facial foramen to a smooth notch in the dorsal edge of the vidian canal (Fig. 4), presumably traces the course of the palatine branch of the facial nerve. Directly below the foramina for cranial nerves III and V is a small, round opening for the exit of the palatine branch of the carotid artery, the palatine branch of the facial nerve and probably the abducens nerve. On the midline of the basiparasphenoid complex and immediately above the dorsal edge of the adjoining rostrum is a narrow, vertical opening that probably transmitted the paired, median palatine branches of the carotid arteries.

PROBABLE SKULL OF *APATOSAURUS*

Description of Skull CM 11162

The large skull CM 11162 that was closely associated with the postcranial skeletons of *Apatosaurus louisae* field no. 1 (type, CM 3018) and *Apatosaurus* field no. 40 at Carnegie quarry (Fig. 1) and presumed to belong to one of these specimens, conforms closely to the skull of *Diplodocus*, despite some postmortem distortion. The skull is missing the lower jaw and has been variably crushed dorsoventrally (Fig. 7); though the right side of the

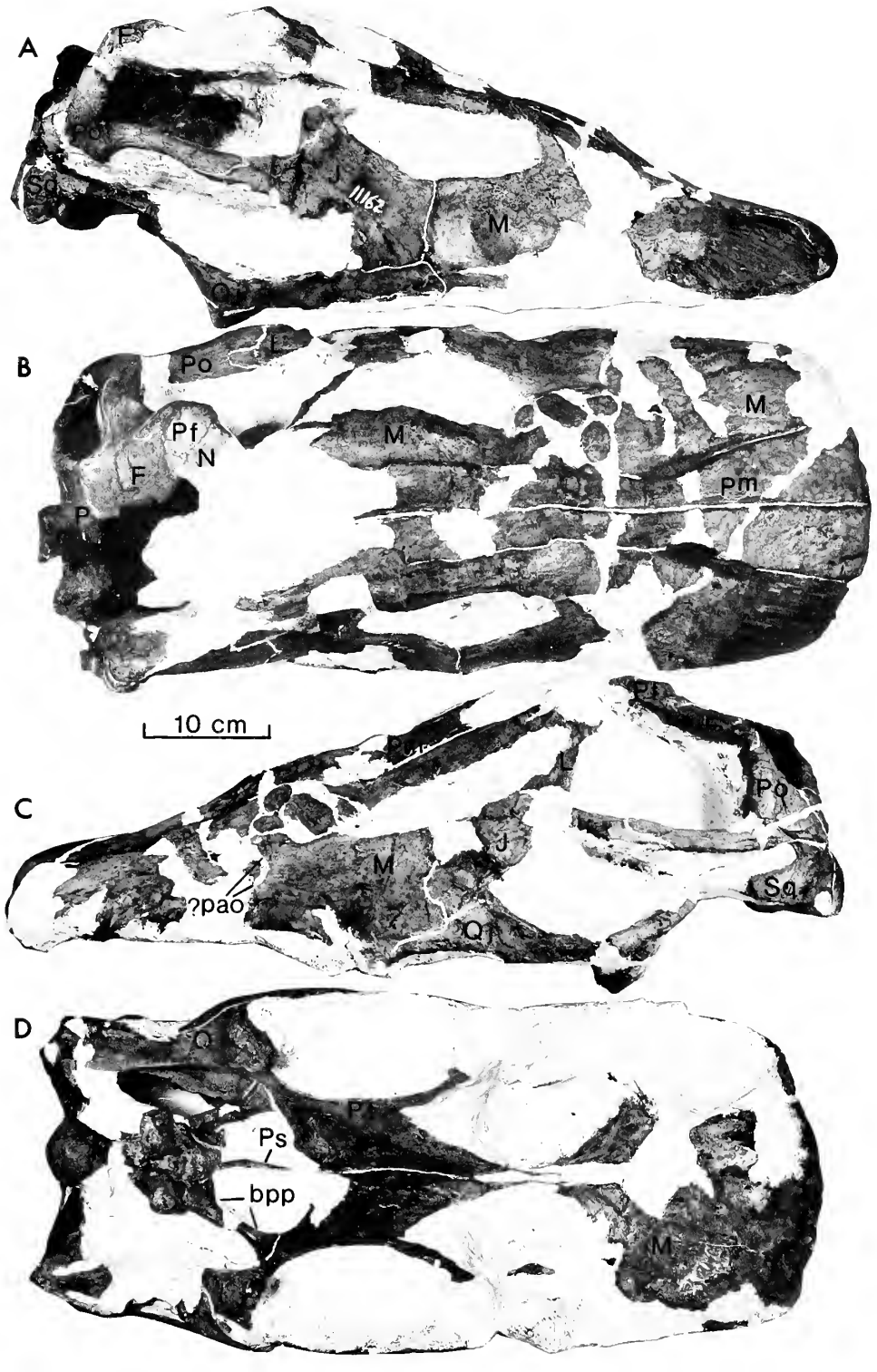

Fig. 7.—A, right lateral, B, dorsal, C, left lateral, and D, ventral views of probable *Apatosaurus* skull CM 11162.

skull has retained, for the most part, its proper pitch, the left side has undergone flattening, giving it a broader appearance, especially in the snout region. Distortion and incomplete preservation make impossible determination of the exact outlines of all the major skull openings except for the left supratemporal fossa. However, there is no structural evidence that they differed in any important way from those in *Diplodocus*; this is certainly true of the supratemporal fossa. Skull dimensions of CM 11162 are given in Table 1. In lateral view the angles subtended between the meeting of the projections of the occipital plane with a plane passing through the ventral margins of the maxillae, the occipital plane with the cranial roof, and the cranial roof with the dorsal margin of the snout are about 75, 120, and 140 degrees, respectively. A restoration of CM 11162 in lateral view is given in Fig. 8.

The incompletely preserved external dermal bones of CM 11162 do not differ greatly from those of *Diplodocus*. The premaxillae are well preserved and show that each possessed four or five functional teeth, represented by their bases. The maxillae are fairly well represented except for two important structures. The upper ends of their ascending processes have been lost, so their sutural relationships with the nasals and lacrimals are indeterminate. Also, it is not certain if the smaller, more anterior of the two antorbital openings of the maxilla that is characteristic of *Diplodocus* is present. The posterior rim of the preantorbital opening of the left maxilla is hesitantly identified in Fig. 7C; its position would approximate that in *Diplodocus*. A small, isolated fragment of bone lies in what would be the position of this opening. A tooth count is possible for only the right maxilla, where it is based on replacement teeth, or in most instances their impressions, which have been exposed by the loss of surface bone of the maxilla; the right maxilla may have held as many as 12 or 13 functional teeth. The teeth of CM 11162 are identical to the very slender, cylindrical teeth of *Diplodocus*. The jugal and quadratojugal, best preserved on the right side of the skull, show their boundaries with each other and the maxilla. The distal end of the dorsal process of the right jugal projects into the antorbital opening as in *Diplodocus*. Remnants of the lacrimals remain. The contacts of the left postorbital are clear except for that with the parietal, which in *Diplodocus* extends vertically down the innermost level of the supratemporal fossa wall. The right squamosal is fragmentary; the left is nearly complete except for the loss of the distal end of its anteroventrally directed quadrate process and has suffered little distortion, exhibiting the same basic relationships with is bordering elements as in *Diplodocus*.

Table 1.—*Measurements (in mm) of skulls assigned here to* Diplodocus *and* Apatosaurus. *1, skull length, measured from snout tip to posterior margin of occipital condyle; 2, skull width, measured at ventralmost level of quadrates; 3, greatest length of quadrate, measured through shaft; 4, skull length to quadrate length ratio; 5, length to distal width ratio of quadrate.*

Taxa and catalog numbers	Measurements				
	1	2	3	4	5
Diplodocus					
CM 11161	515	178	185	.36	.20
CM 3452	440	—	167	.38	.19
USNM 2672	550	190	183	.33	.22
USNM 2673	600	—	215	.36	.22
Apatosaurus					
CM 11162	650	280	185	.28	.30

All that remains of the cranial roof (Fig. 3D) is the greater part of the left side. The left parietal is nearly complete, missing only a small portion of its medial boundary; the other sutural boundaries of the left parietal are distinct except for the dorsomedial end of its contact with the supraoccipital on the occiput and its contact with the postorbital. Approximately a fourth of the left frontal is lost along its medial border. The preserved portion of its posterior suture with the parietal and postorbital is distinct and rather dentate for about the medial half of its length; the orbital margin of the frontal exhibits the same concave emargination seen in *Diplodocus*. Also as in *Diplodocus*, the triangular, posterior half of the prefrontal penetrates deeply posteromedially into the anterolateral corner of the frontal. The posterior two thirds of the prefrontal projection into the frontal is well defined, but its anteromedial contact with the frontal and nasal is hesitantly traced. The anterior portion of the prefrontal is absent. Only a short, narrow strip of the nasal is preserved along the medial border of the prefrontal; its contact with the frontal is not clear.

The somewhat abraded occiput (Fig. 3E) is nearly intact on the left side, whereas the greater part of the right side is absent. Only the supraoccipital-exoccipital suture of the occiput cannot be found. The median, nuchal crest on the supraoccipital above the foramen magnum is strongly developed. The small, left posttemporal fossa is clearly visible and is identical to that of *Diplodocus* in outline and in the way its borders are formed. The articular surface of the occipital condyle is hemispherical except

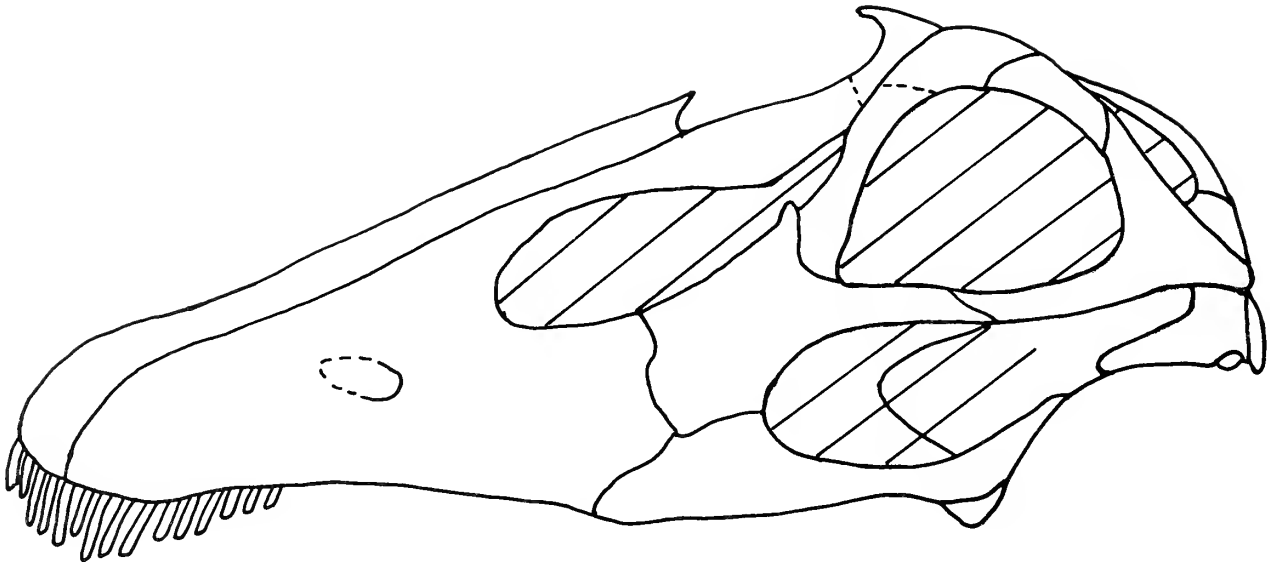

Fig. 8.— Restoration of probable *Apatosaurus* skull CM 11162.

for its flat, even possibly slightly concave, dorsal margin. The axis of the condyle is directed posteroventrally at about 120 degrees from the long axis of the skull; this angle may have been exaggerated by dorsoventral crushing. A widely open fracture that extends across the floor of the foramen magnum, giving this otherwise round opening a vertically elongate appearance, continues outward and slightly upward through the posterior process of the postorbital on the lateral side of the skull. The basicranium (Fig. 7D) contains a number of major and minor fractures along some of which there has been displacement. Except for proportional differences discussed below, the basicranium of CM 11162 exhibits no marked structural differences from that of *Diplodocus*.

With the exception of proportional differences, the partially preserved palate of CM 11162 (Fig. 7D) exhibits no noticeable departures from that described (McIntosh and Berman, 1975) for *Diplodocus*. The pterygoids are essentially complete, undistorted and, as in *Diplodocus,* form a midventral, dihedral angle between them of about 60 degrees. The palatines, which presumably would have occupied the acute angle formed between the narrow, transverse process and the anterior process of the pterygoids, are absent. Both vomers are lost, but they undoubtedly occupied the same position as those in *Diplodocus* (McIntosh and Berman, 1975); there the flat, narrowly triangular vomers articulate with the lateral surface of the broadly concave, anteroventral portion of the pterygoid borders for most of their length and their anterior ends are clasped together at the midline by broad, medially directed processes of the maxillae. The maxillary processes are well preserved in CM 11162 and the medial gap between them, which held the anterior ends of the vomers, is somewhat wider than normal due to the dorsoventral flattening of the snout. Both ectopterygoids appear to be absent, although they may be buried in the remaining matrix. The right quadrate is essentially complete, undistorted and in its proper orientation, whereas the left is badly crushed and missing a large central section.

Comparison of CM 11162 with *Diplodocus*

Though the incomplete preservation of the skull CM 11162 eliminates many opportunities for detailed comparisons, this skull is obviously very close to that of *Diplodocus*. Comparisons between CM 11162 and *Diplodocus* skull CM 3452 and those skulls very likely belonging to *Diplodocus* have revealed a number of subtle proportional and structural differences. Some of these differences, however, have to be evaluated with caution because they may be the result of postmortem distortion of CM 11162. It will also be noticed that the obviously

greater general robustness of CM 11162 is a fundamental aspect of many of the features used below to contrast it with the skull of *Diplodocus*.

In lateral view the occiput of the probable *Apatosaurus* skull CM 11162 slopes anterodorsally at an angle of about 75 degrees to the horizontal passing through the ventral margins of the maxillae as compared to its right angle orientation in *Diplodocus* (Fig. 2); differences they exhibit in the angles subtended between the occipital plane and the cranial roof, and the cranial roof and the snout are too small to be safely considered as diagnostic. In CM 11162 the axis of the occipital condyle is inclined posteroventrally at an angle of about 120 degrees to the long axis of the skull in contrast to its approximately right angle orientation in *Diplodocus;* the larger angle of the former, however, may be partly due to crushing. The triangular, posterior process of the postorbital of CM 11162 differs from that of *Diplodocus* in being more broadly developed and in extending to a level posterior to the supratemporal fossa. In the probable *Apatosaurus* skull there is also a greater vertical development of the squamosal below the posterior process of the postorbital, which has resulted in a corresponding lengthening of its posterior contact with the distal end of the paroccipital process; the quadrate process of the squamosal is also proportionally broader in CM 11162 than in *Diplodocus*.

Differences are also seen in the occipital views of the skulls (Fig. 3). In this aspect CM 11162 appears rather dome-shaped in outline, whereas the skull of *Diplodocus* CM 3452 is subrectangular in outline; this difference can be attributed mainly to development of the lateral, occipital wing of the parietal. In *Diplodocus* its free, superior border arches smoothly and rather strongly dorsolaterally, completely hiding the supratemporal fossa from occipital view. The lateral wing of the parietal in CM 11162 is much narrower and its nearly straight, ventrolaterally sloping, free border allows the supratemporal fossa to be partially seen in occipital view. Further, in CM 11162 the distal end of the parietal wing does not encroach as greatly upon the squamosal as in *Diplodocus* and, as a result, in the former the dorsolateral process of the squamosal, which forms the ventral border of the supratemporal fossa, is wider and the contact between the occipital process of the squamosal and the occipital wing of the parietal is considerably shorter. In *Diplodocus* the lateral surface of the skull below the supratemporal fossa meets the occiput in a sharp, right angle corner, whereas in CM 11162 this intersection is somewhat rounded. As a consequence, the probable *Apatosaurus* skull can also be distinguished from that of *Diplodocus* by its greater exposure of the squamosal and its partial exposure of the posterior process of the postorbital in occipital view. In *Diplodocus* all that can be seen of the squamosal in this view is its narrow, occipital process. In addition to this process in CM 11162, the anterodorsal process of the squamosal and a wide margin along its posterior contact with the flared, distal end of the paroccipital process are also clearly visible in occipital view.

The most marked proportional differences between CM 11162 and the skull of *Diplodocus* CM 11161 are in the palate, quadrate, and braincase (Fig. 9). Though proportionally the lengths of their braincases, measured from the back of the condyle to either the base or the tip of the paraphenoid rostrum, are very similar, the basipterygoid process of CM 11162 is shorter and stouter, and the condyle is much more massive. In CM 11162 there is a marked flaring of the distal end of the basipterygoid process, whereas in CM 11161 there is only a slight swelling. In these features of the braincase the *Diplodocus* skulls CM 3452 and CM 11161 are identical. The quadrate of CM 11162 is proportionally shorter and more massive at its distal end than in CM 11161, CM 3452, USNM 2672, and USNM 2673 (Table 1). A proportionally shorter quadrate in CM 11162 is reflected in a more posterior position of its contact with the quadratojugal than in CM 11161. Although the lengths of these contacts along the posterior borders of the quadrates of both specimens are proportionally very similar, if not equal, the posterior margin of the quadratojugal in CM 11162 is at a level slightly anterior to the median union of the basipterygoid processes, whereas in CM 11161 it is considerably posterior to this level. In this feature the *Diplodocus* skull CM 3452 is identical to CM 11161. In palatal view the angle formed between the basipterygoid processes in CM 11162 is about 60 degrees, whereas it is about 40 degrees in CM 11161. As a result, the end of the basipterygoid process in CM 11162 is brought closer through a horizontal plane to the distal end of the quadrate. The basipterygoid process and the quadrate are also brought closer together in CM 11162 because the medial surface at the distal end of its quadrate does not curve slightly laterally as in CM 11161. In CM 3452 the angle between the basipterygoid processes is about 35 degrees and the medial

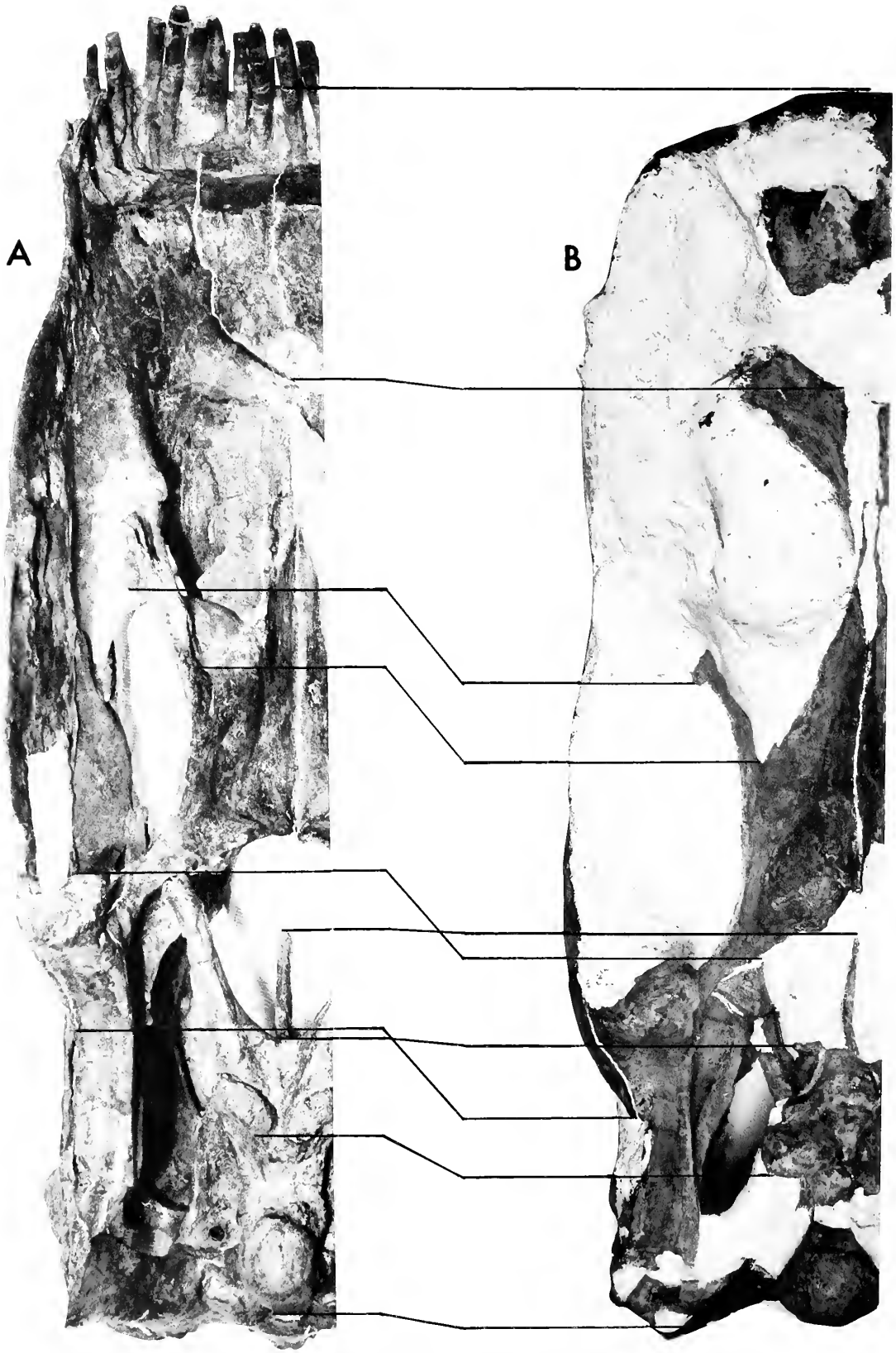

Fig. 9.—Palatal views of skulls of A, *Diplodocus* CM 11161, and B, probable *Apatosaurus* CM 11162 reduced to same size in order to demonstrate proportional differences. Horizontal lines connect identical topographical points.

surface of the quadrate also curves slightly laterally at its distal end. As a result of the proportionally shorter postpterygoid structures in CM 11162, its pterygoid occupies the more posterior position in the skull than that in CM 11161. At the level occupied by the vomers there is a disproportionate, longitudinal lengthening of the palate in CM 11162 over that of CM 11161 to the extent that, anterior to this level none of their palatal structures shows any appreciable differences in anteroposterior position.

Holland (1915*a*) stated that maxillary teeth of CM 11162 did not insert vertical to the jaw line as in *Diplodocus*, but were more or less procumbent; we cannot find any evidence to support this observation. Further, our earlier observation (McIntosh and Berman, 1975) that the probable *Apatosaurus* skull CM 11162 may differ from *Diplodocus* in the reduced size and more anterior position of the foremost antorbital opening also cannot be verified with further preparation.

Additional Evidence on the Skull of *Apatosaurus*

A pair of quadrates and the greater part of a cranium were found by Marsh's collectors at Morrison, Colorado, which provide additional evidence, though circumstantial, that the skull of *Apatosaurus* was *Diplodocus*-like in structure. The catalogue number YPM 1860, which both quadrates bear, is very likely their correct assignment. In reviewing the ambiguities surrounding the locality data of the cranium, it was concluded that there is not only strong reason to believe that it came from YPM quarry 10, but that it also belongs to the type of *A. ajax,* YPM 1860. Both the quadrates and the cranium represent a skull larger than any skull heretofore identified as *Diplodocus* and are also slightly larger than the presumed *Apatosaurus* skull CM 11162.

The left quadrate from Morrison (Fig. 10) is complete except for the thin, anteriorly directed plate of bone on whose medial surface the pterygoid articulated, the right quadrate is missing not only the pterygoid process, but also a little over 20% of the upper, proximal end of its main shaft. The quadrates are not only near duplicates of those of *Diplodocus* and the probable *Apatosaurus* skull CM 11162, but are readily distinguishable from those of *Camarasaurus*. White's (1958) detailed description and illustration of the quadrate of *Camarasaurus*, as well as the excellent illustrations of this bone given by Ostrom and McIntosh (1966, Pl. 4), make a close comparison here between the quadrate of this genus and the quadrates YPM 1860 unnecessary. Viewed laterally the posterior margin of the quadrate shaft curves smoothly and gently anteroventrally and has a greatest length of about 21 cm. In anteroposterior length the distal end of the shaft, measuring 3.8 cm, does not greatly exceed the proximal end, which measures 2.8 cm. The lower half of the shaft is expanded into a strongly ridged, articular surface for the posterior end of the quadratojugal; the upper, narrowly tapering end of this sutural scar extends slightly onto the posterior surface of the shaft. That part of the quadratojugal, which articulated with the quadrate, was undoubtedly like that in *Diplodocus* and the probable *Apatosaurus* skull CM 11162 in its shape and sutural relationship with the quadrate. Beginning at the anterodorsal margin of the shaft, a deep channel extends a considerable distance ventrally as it curves gradually onto and across the lateral surface of the shaft; the channel certainly held the same narrow, quadrate process of the squamosal seen in skulls of *Diplodocus* and in CM 11162. Further, the course of the channel indicates that a small portion of the lateral surface of the proximal end of the quadrate was exposed at the posterior end of the ventral margin of the quadrate process of the squamosal as in *Diplodocus*. In posterior view, the quadrate appears club-shaped. From the greatest width of about 4.8 cm near its distal, lower end, it gradually narrows dorsally to about 1.5 cm at a point approximately three fourths its height, then widens slightly to about 2.0 cm. The lower, wider portion of the posterior surface is very slightly concave except along the distal margin of the shaft, where it is moderately convex; above this region the posterior surface becomes flat and remains so until near the proximal end of the shaft, becoming here a pronounced ridge. For most of its length the medial surface of the shaft consists of a strongly developed ridge; dorsally the ridge merges with the nearly flat, narrow, proximal end of the shaft. Only the base of the anteriorly projecting pterygoid process is preserved, but the general outline and orientation of the process can be largely deduced from its remaining margins. Anterior view of the quadrate reveals the base of the pterygoid process as a rather thin plate that is broadly bowed laterally. The base of the process is thinnest at mid-height, thickening only somewhat dorsally, but greatly thickening ventrally. Below the pterygoid process the

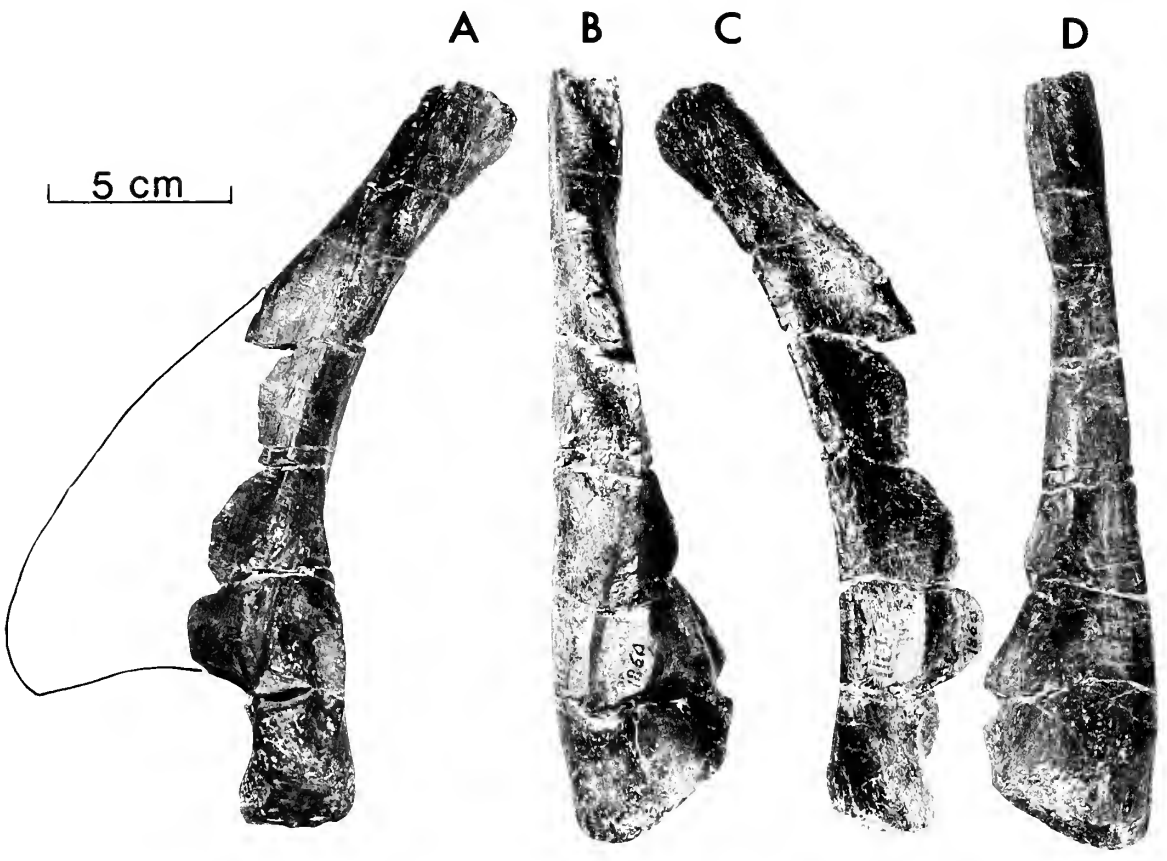

Fig. 10.—A, lateral, B, anterior, C, medial, and D, posterior views of left quadrate probably belonging to the holotype of *Apatosaurus ajax* YPM 1860. Missing anterior pterygoid process indicated in A. Distal end toward bottom.

anterior surface of the shaft is excavated into a shallow depression, giving the articular surface a kidney-shaped outline. In anterior view the condylar surface slopes ventromedially.

In Marsh's (1896) description of the cranium from Morrison, Colorado, as "*Atlantosaurus montanus*" the only feature he commented on was a so-called pituitary canal leading from the brain cavity down through the base of the skull. The cranium was illustrated by Marsh (1896:274, Pl. XV) in posterior and ventral views only and with just a few of the sutures and foramina indicated; further preparation has revealed almost all of these features clearly (Fig. 11). The only major portions of the occiput not represented are the distal end and superior margin of the lateral, occipital wing of the parietal, and the occipital process of the squamosal that forms the lateral border of the posttemporal fossa. Only the left side of the cranial roof is present but this includes most of the parietal and frontal, and the posterior third of the prefrontal. The parietal-frontal juncture has been destroyed, separating the cranial roof from the principal portion of the cranium; these have been reunited in what is thought to be their correct relative position. The more complete left cranial wall includes the exoccipital-opisthotic complex, proötic, laterosphenoid, and the base of the orbitosphenoid. Of the cranial floor elements, the basioccipital is complete, the basisphenoid lacks mainly the basipterygoid processes and the parasphenoidal rostrum is broken off at its base. The occipital condyle is as in *Diplodocus* in its shape and orientation and the skull must have been directed at nearly a right angle to the neck. The basioccipital-basisphenoid suture is not detectable. Two features of the cranial roof clearly distinguish the cranium from that of *Camarasaurus* and give it a distinctly *Diplodocus*-like character: 1) the posterior end of the prefrontal is triangular and projects posteromedially into the anterolateral corner of the frontal, and 2) a moderately deep, concave emargination of the orbital margin of the frontal occurs

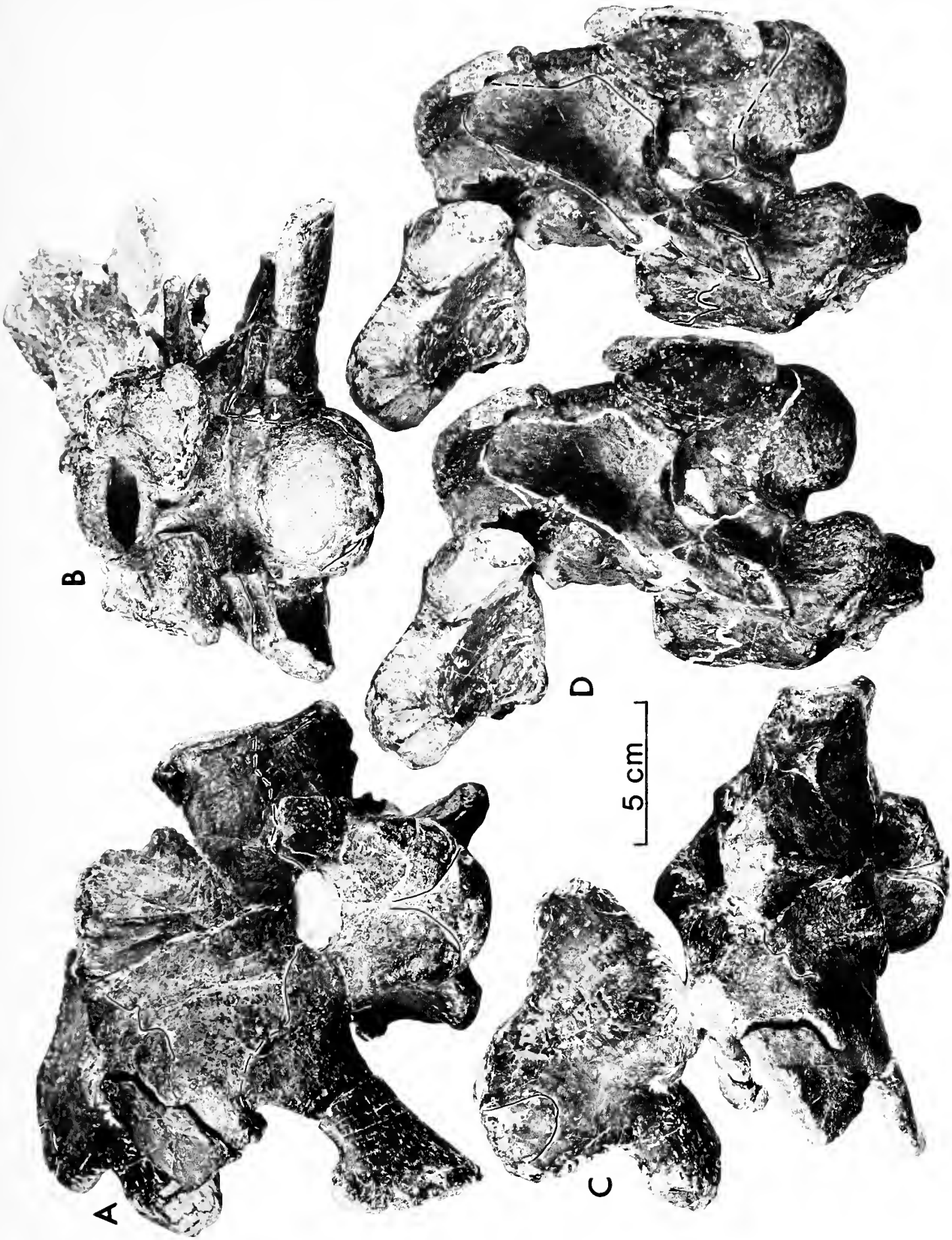

Fig. 11.—A. posterior, B. ventral, C. dorsal, and D. left lateral (stereo pair) views of braincase probably belonging to holotype of *Apatosaurus ajax* YPM 1860.

at a level just behind the posterior end of the prefrontal. Both these features are present in the probable *Apatosaurus* skull CM 11162. Only a few minor differences between the Morrison cranium and that of *Diplodocus* can be noted. Small proportional differences, such as the greater size of the condyle and basal tubercles, are to be expected in the Morrison cranium because of the greater robustness of *Apatosaurus* over *Diplodocus*. The proötic-laterosphenoid suture is tightly closed and is not an abutment contact as in *Diplodocus;* this probably indicates a fully grown individual. The transverse opening of the "pituitary canal" between the basal tubercles that was noted by Marsh (1896) is most likely the result of incomplete preservation. The thin cranial floor in this region and the fact that the cranium was glued along a number of breaks that intersect this opening could account for the absence of bone here.

One other piece of evidence suggests that the skull of *Apatosaurus* was like that of *Diplodocus*. Examination of the partial skeletons field nos. 24 (CM 3390) and 37, found about 6 m apart at Dinosaur National Monument (Fig. 1), convinces us that Douglass (see Historical Review) was probably correct in his conclusion that these specimens belong to the same juvenile individual of *Apatosaurus*. Unfortunately, although the anterior portion of a small jaw possessing *Diplodocus*-like teeth (field no. 35) that was noted by Douglass in the collection records as having been found with field no. 37 was prepared at the Carnegie Museum, it cannot be located. If Douglass' observation on the nature of the teeth of the jaw is correct—there is no reason to doubt it—and if the jaw and field specimens nos. 24 and 37 were part of one individual, then it follows that *Apatosaurus* had *Diplodocus*-like teeth, reinforcing our conclusion that the skull of *Apatosaurus* is *Diplodocus*-like.

COMPARISON OF POSTCRANIAL SKELETONS

If *Apatosaurus* possessed a *Diplodocus*-like, rather than a *Camarasaurus*-like, skull, it may be asked how the postcranial skeletons of these three sauropods compare. Comparisons are made possible by detailed accounts of the postcranial skeletons of *Diplodocus* (Osborn, 1899; Hatcher, 1901*a*, 1902; Holland, 1906; Gilmore, 1932), *Apatosaurus* (Gilmore, 1936), and *Camarasaurus* (Gilmore, 1925). The postcranial skeletons of *Apatosaurus* and *Camarasaurus* have been generally considered more similar to each other than to *Diplodocus* because of their much greater robustness. It is in fact difficult to distinguish between isolated hindlimb bones of *Apatosaurus* and *Camarasaurus*, especially if these elements are imperfectly preserved. Excepting this superficial resemblance between *Camarasaurus* and *Apatosaurus*, the postcranial skeletons of *Apatosaurus* and *Diplodocus* share a large number of characters that set them widely apart from *Camarasaurus*. *Diplodocus* and *Apatosaurus*, in contrast to *Camarasaurus*, have relatively very long necks, short trunks, and very long tails, unusual anterior caudal vertebrae and midcaudal chevrons, shorter forelimbs and metacarpals, and reduced number of carpal and tarsal elements.

Vertebral Column

The cervical vertebrae, particularly the posterior ones, are among the most diagnostic bones in the sauropod skeleton. *Apatosaurus* and *Diplodocus* possess 15 cervicals, *Camarasaurus*, 12. In all three genera the neural spines of the posterior cervicals and the anterior dorsals are deeply cleft; in *Apatosaurus* and *Diplodocus* the clefts are V-shaped, whereas those of *Camarasaurus* are more U-shaped. The cervicals of *Apatosaurus* are proportionally shorter and more solidly constructed than those of either *Diplodocus* or *Camarasaurus*. In *Apatosaurus* and *Diplodocus* the cervical ribs are much shorter than in *Camarasaurus* and do not extend beyond the posterior end of the centrum from which they originate, whereas in *Camarasaurus* some cervical ribs, such as the ninth, may reach a length of about two and a half times the length of the centrum. The cervical ribs of *Apatosaurus* are considerably stouter than those of either *Diplodocus* or *Camarasaurus*. *Apatosaurus* and *Diplodocus* have 10 dorsal vertebrae that exhibit similar regional variations. Their anterior dorsal centra are opisthocoelous; posteriorly they are amphiplatyan or amphicoelous. In the shoulder region the neural spines in both are low but rise posteriorly to become very high and slender in the sacral region. *Camarasaurus* has 12 dorsals, all of which are opisthocoelous. The dorsal neural spines exhibit little change in height posteriorly and at the posterior end of the series they are much lower, stouter, and laterally expanded above than in the other two genera.

There are five sacral vertebrae in all three genera. In *Apatosaurus* and *Diplodocus,* the sacral centra and ribs are hollow, the second and third spines are united and there is a tendency for the fourth to unite with the third. In *Camarasaurus* the centra are solid or have much smaller cavities and four or even all five spines may fuse.

The tails in *Apatosaurus* and *Diplodocus* reach enormous lengths, up to 82 caudals in the former and 73 or more in the latter; the caudals of approximately the posterior third of their tails consist essentially of elongated rods that form a "whip-lash" structure. The centra in both are generally amphiplatyan throughout, although there is a tendency, particularly in *Diplodocus,* for the anterior centra to be somewhat procoelous. In both genera the transverse processes in the anterior part of the tail form thin, vertically expanded, wing-like plates that more closely resemble the sacral ribs than the transverse processes of the remainder of the tail. In *Apatosaurus* the first three or four caudals show this development; in *Diplodocus* it occurs in the first 12 or more. In both the caudal spines are very high anteriorly and their distal ends are not expanded transversely. Their anterior caudal chevrons are of normal structure, the laminae of the chevrons being united by a bridge of bone above the haemal canal but joining below the canal to form a simple, laterally flattened spine. The chevrons of the mid-caudal region, however, are unusual in that they lack the bridge of bone above the haemal canal and the laminae do not unite immediately below the canal but at the ends of well-developed anteriorly and posteriorly directed processes that originate at their distal ends. This character is more pronounced in *Diplodocus*. The presence of these unusual mid-caudal chevrons in *Apatosaurus* was not discussed by Gilmore (1936) because only the anterior three chevrons are present in the specimen (CM 3018) studied by him, but he did indicate them in his post-cranial restoration. The "double-arch" type of mid-caudal chevron was, however, briefly noted by Riggs (1903*b*) and shown in his restoration of *Apatosaurus*. In some features the caudals of *Apatosaurus* and *Diplodocus* are distinct. The anterior caudal centra of *Diplodocus* have deep lateral pleurocoels and ventral excavations; the ventral excavations occur well into the midcaudal region. The centra are even more elongated in *Diplodocus* than in *Apatosaurus,* a feature which becomes more pronounced posteriorly, especially in the whip-lash portion of the tail. In *Apatosaurus* the caudal centra are not excavated laterally or ventrally except for possibly the first few, which may have small irregularly placed cavities, and the anterior centra have a blunt, ventral keel. The tail of *Camarasaurus* differs from those of *Apatosaurus* and *Diplodocus* in having only 53 much shorter vertebrae. The transverse processes of even the anteriormost caudals are simple. The anterior neural spines are not unusually high and distally are expanded transversely into ball-like structures. The centra are amphicoelous, unexcavated and without a ventral keel, and the chevrons are unspecialized throughout and almost never enclose the haemal canal above.

Appendicular Skeleton

The marked difference in massiveness of the appendicular skeletons of *Diplodocus* and *Apatosaurus* is more apparent than their similarities. The scapulae are distinct in all three genera. The broad plate, which extends anterodorsally from the base of the scapular blade, is more vertically expanded and the prominent ridge, which divides its external surface into two broad muscle fossae, is less developed and makes a larger angle with the shaft in *Apatosaurus* and *Camarasaurus* than in *Diplodocus*. The upper end of the scapula is greatly expanded in *Camarasaurus,* much less so in *Diplodocus,* and only slightly expanded in *Apatosaurus*. The coracoids are dissimilar in outline in all three, being quadrangular in *Apatosaurus,* roughly triangular in *Camarasaurus,* and intermediate between these two in *Diplodocus*. The ilia in all three genera are similar. The pubes of *Apatosaurus* and *Diplodocus* are relatively slender compared to those of *Camarasaurus*. *Diplodocus* has a pronounced hook-like process for the ambiens muscle on the upper, anterior margin of the pubis; this process is much less prominent in *Apatosaurus* and is nearly absent in *Camarasaurus*. Confusion has occurred through the legend of figure 37 in Gilmore's (1936) description of *Apatosaurus* in which the figured pubis of *Diplodocus carnegiei* CM 94, exhibiting a very prominent ambiens process, is mistakenly identified as *Apatosaurus excelsus* CM 563. The figure given by Hatcher (1903*a*, Pl. IV, Fig. 1) of the pelvis of CM 563 also tends to exaggerate this feature in *Apatosaurus*. The ischium is one of the most diagnostic bones in the sauropod skeleton. In *Apatosaurus* and *Diplodocus* the blades of the ischia are tilted ventromedially and their expanded distal ends contact each other along a wide margin of the ventral borders of their medial surfaces. The more

slender blades of the ischia in *Camarasaurus* are not expanded distally and are twisted along their long axes so that the ends of the blades come to lie in a horizontal plane with their inferior margins contacting each other medially.

Perhaps the most striking and significant feature separating the limbs of *Apatosaurus* and *Diplodocus* from those of *Camarasaurus* is their forelimb to hindlimb length ratio; the humerofemoral length ratio is 2/3 in both *Apatosaurus* and *Diplodocus* and 4/5 in *Camarasaurus*. The forelimb of *Apatosaurus* is robust, rivaled in this feature only by that of the South American *Titanosaurus australis* (von Huene, 1929). Forelimbs of *Camarasaurus* resemble those of *Diplodocus* more nearly in their overall slenderness, although the humerus of *Camarasaurus* is somewhat more robust and the medially projecting process at the upper end of its ulna is also more pronounced. The manus of *Apatosaurus* and *Diplodocus* are similar so far as known. A single carpal bone remains in *Apatosaurus*; the condition in *Diplodocus* is unknown. The metacarpals of *Apatosaurus* are short and robust and in *Diplodocus* they are short but more slender. *Camarasaurus* has two carpals and its metacarpals are very long and slender. The hindlimb bones of *Apatosaurus* and *Camarasaurus* are about equal in their much greater robustness than those of *Diplodocus*. Despite this feature, the hindlimbs of *Apatosaurus* and *Diplodocus* can be distinguished from those of *Camarasaurus*. The femur of *Camarasaurus* has a straight shaft, whereas femora of *Apatosaurus* and particularly of *Diplodocus* exhibit a slight sigmoid curve. In *Camarasaurus* the cnemial crest of the tibia is relatively less pronounced and the muscle scar on the lateral surface of the fibula is much more strongly developed than in the other two genera. The pes of *Apatosaurus* and *Diplodocus* exhibit differences from that of *Camarasaurus*. No calcaneum has yet been found associated with any *Diplodocus* or *Apatosaurus* pes, and, although the question of its existence has not been settled, the evidence strongly suggests that the only tarsal element they possess is an astragalus. In *Camarasaurus* the tarsus consists of an astragalus and a small, spherical calcaneum. The metatarsals of *Apatosaurus* and *Diplodocus* are very similar except that the third and fourth are more slender in the latter. In both, metatarsals III and IV are the longest, the fourth often being slightly longer, and metatarsal I is unusual in having a process on the posteroventral margin of its lateral surface. In *Camarasaurus* metatarsals II and III are equal in length and the longest, and metatarsal I does not possess the above-mentioned process.

RELATIONSHIPS OF *APATOSAURUS*

It has become common practice (Janensch, 1935; Nopcsa, 1930; von Huene, 1948) to divide the Sauropoda into two families primarily on the basis of dentition. Though a variety of family names has been employed, these classifications are in essential agreement in their separation of the broad, spatulate-toothed forms such as *Brachiosaurus* and *Camarasaurus* from the slender-toothed forms such as *Diplodocus*. The long-standing conclusion that *Apatosaurus* had a *Camarasaurus*-like skull and dentition was the major reason for its alliance with the former group. Romer (1956) divided the sauropods into the Brachiosauridae and Titanosauridae; *Apatosaurus* was assigned to the latter family even though Nopcsa (1930) and von Huene (1948) placed it in the former. White (1958), believing he had substantiating evidence that the skull of *Apatosaurus* was *Camarasaurus*-like, recommended the removal of *Apatosaurus* from the Titanosauridae and placement in the subfamily Camarasaurinae of the Brachiosauridae. In a later classification Romer (1966) referred *Apatosaurus* to the Titanosauridae and *Brontosaurus* to the Brachiosauridae even though Riggs (1930*b*) had clearly demonstrated that the latter genus is a junior synonym of the former. It is beyond the scope of this paper to present a revised classification of the sauropods, but we reject the commonly used, two-family division, which artificially associates widely divergent forms.

Apatosaurus and *Diplodocus* are morphologically very similar, and the former is quite different from *Camarasaurus*, to which it has been closely allied by many authors. Equally important, *Apatosaurus* and *Diplodocus* share a suite of characters that can be seen in various combinations in five other less well known sauropod genera—*Barosaurus*, *Cetiosauriscus*, *Mamenchisaurus*, *Dicraeosaurus*, and *Nemegtosaurus*. These genera are judged by us to be very closely related and quite distinct from all other adequately known sauropods and deserving of familial separation. The oldest valid name available for this group is Diplodocidae Marsh (1884).

The only other family names that could be considered, Atlantosauridae (Marsh, 1877*b*) and Amphicoeliidae Cope (1877*b*) are rejected because their type genera are indeterminate. In the case of Atlantosauridae the type genus *Atlantosaurus* (first described as *Titanosaurus* Marsh, 1877*a*) cannot be adequately defined and has to be considered a *nomen dubium*. The type species, *A. montanus*, is based on only an incomplete sacrum (YPM 1835) that cannot be clearly distinguished from those of a number of sauropods, including genera outside the new family grouping proposed here. The adoption of Amphicoeliidae has the same drawback as Atlantosauridae; the type genus cannot be adequately defined. The family was established by Cope (1877*b*) to include two species of a new genus, *Amphicoelias altus*, the type species, and *A. latus;* a third species, *A. fragillimus*, was later added by Cope (1878*b*). In a restudy of these species, all of which are represented by single specimens, Osborn and Mook (1921) concluded that *A. altus* represents a young individual of *Camarasaurus* and suggested that *A. fragillimus* should be provisionally referred to *A. altus;* we are in agreement with these conclusions. Though the type of *A. altus* is referable to the Diplodocidae, as defined below, its incompleteness does not allow it to be distinguished from either *Diplodocus* or *Barosaurus*. *Diplodocus* was first described by Marsh (1878*b*) on the basis of a small, but adequately diagnostic portion of the postcranial skeleton, yet it was not until his later description of the skull (1884) that he considered the genus unique and the type of a new monotypic family, Diplodocidae. Though Marsh (1898) later transferred *Barosaurus* from the Atlantosauridae to the Diplodocidae, subsequent classifications of the sauropods by von Huene (1927*a*, 1927*b*) continued to recognize the latter family as monotypic. In a recent catalogue of the dinosaur genera White (1973), without giving a revised or expanded definition of the family Diplodocidae, included within it a great variety of genera, many of which are too divergent to be grouped together at this taxonomic level.

The availability of the family name Diplodocidae is fortunate because *Diplodocus* is well known and very representative of the new family grouping proposed here, for which we offer the following revised definition.

Diplodocidae, Marsh, 1884

Definition.—SKULL: nares superior in position; quadrate directed anteroventrally; basipterygoid processes elongated; definition of weak, pencil-like teeth. VERTEBRAL COLUMN: midpresacrals exhibit tendency toward "cervicalization" to produce long neck; midpresacral spines cleft; sacral spines very high; anterior caudals with broad, wing-like transverse processes; midcaudal chevrons having distal, fore and aft directed processes; tail consisting of large number of vertebrae, forming a "whip-lash" structure. APPENDICULAR SKELETON: Forelimbs short with a humerofemoral length ratio of 2/3; tarsus and at least in some cases the carpus reduced to single element; distal ends of ischia expanded in vertical plane and contacting each other along a wide, ventral margin of their medial surfaces; process on posteroventral edge of lateral face of metatarsal I; metatarsals III and particularly IV longest.

Remarks.—Although our inclusion of *Apatosaurus* in the Diplodocidae is obvious, assignment of the other genera to this family must be justified. The brief comments that follow are intended to serve this purpose.

The Upper Jurassic *Barosaurus* Marsh, 1890, is structurally very close to *Diplodocus* and is distinguished mainly by its enormously elongated cervical vertebrae and slightly less developed caudal neural arches and spines; its limb elements are scarcely distinguishable from those of *Diplodocus*. In *Barosaurus* cervicalization of the midpresacrals is evident, the anterior caudals have wing-like transverse processes, the midcaudal chevrons possess the *Diplodocus*-like fore and aft processes, the distal ends of the ischia are expanded and contact each other on their ventromedial surfaces, and metatarsal I has a distinct process on the posteroventral edge of its lateral surface.

Cetiosauriscus von Huene (1927*b*) has not previously been associated with the members of the family group proposed here, but a number of characters indicate that this Upper Jurassic genus should be considered a primitive member of the Diplodocidae. Except for several posterior dorsal centra, its presacral vertebrae, which are very diagnostic among the sauropods, are otherwise unknown. The anterior caudals, although incompletely known, appear to possess wing-like transverse processes, the midcaudal chevrons are *Diplodocus*-like in that their distal ends possess fore and aft directed processes and there is a whip-lash development of the tail. The humerofemoral length ratio is 2/3. The calcaneum appears to be absent in the tarsus and the astragalus is the only tarsal element. Metatarsals III and IV are the longest and metatar-

sal I clearly exhibits a process on the posteroventral margin of its lateral surface.

The Upper Jurassic *Mamenchisaurus* Young, 1954, tentatively referred to Diplodocidae, has a long neck with 19 cervicals and there are 11 dorsal vertebrae, which possess cleft neural spines. The length of the tail is unknown, but the midcaudal chevrons possess the distal fore and aft directed processes as in *Diplodocus*. Though the humerus and femur are not known for any one specimen, the humerofemoral length ratio is considered to be a little greater than 2/3 in the type genus. This is based on the fact that the height of the sacral neural spines is relatively somewhat less than in other members of the family and that there exists a direct correlation between the height of the sacral spines and the humerofemoral length ratio. This ratio may vary among specimens referred to this genus and only articulated material will reveal its true value.

Dicraeosaurus Janensch, 1914, is a somewhat puzzling, Upper Jurassic genus and is tentatively referred to this family. The neck is short; the number of both the cervical and dorsal vertebrae is 12. Surprisingly, the dorsal vertebrae do not possess pleurocentral cavities; the skull and teeth, however, are distinctly diplodocid. The neural spines of the presacrals are more deeply cleft than in any other sauropod and the sacral spines are high. The anterior caudals have wing-like, transverse processes and the midcaudal chevrons are *Diplodocus*-like. The distal ends of the ischia are greatly expanded. The forelimb is short, which, along with the high sacral spines, suggests that the humerofemoral length ratio may be close to 2/3.

Finally, the Upper Cretaceous *Nemegtosaurus* Nowinski, 1971, known only by the skull, which is distinctly diplodocid in structure, including the teeth, is referred to Diplodocidae.

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TAKESHI SETOGUCHI
Resident Museum Specialist, Section of Vertebrate Fossils
(permanent address: *Primate Research Institute, Kyoto University, Inuyama City, Aichi 484, Japan*)

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ABSTRACT

Upper Oligocene strata unconformably overlying upper Eocene sediments outcrop along Badwater Creek, in central Wyoming. The fauna from the underlying Eocene sediments has been collected and studied by Carnegie Museum of Natural History since 1962. Late Oligocene mammals were first recognized in the overlying sandy facies during the 1964 field season by field parties of Carnegie Museum.

Intensive collecting and use of screen washing techniques have resulted in the recognition of 26 mammal genera. Most of the fossils recovered are fragmentary, and are generally less than 3 mm in size, which indicates considerable transport of the material. This assemblage of animals is biased by two major factors. First, due to stream sorting, only small teeth and bones were deposited so that larger mammals, which surely lived near the site of deposition at that time, are not represented in the fauna. And second, the local climate was dry and of moderate temperature. This is indicated by the presence of calcic feldspars and gypsum crystals throughout the section. Due to the dry climatic conditions, only land mammals, which were adapted to this ecological situation, could live there and consequently these animals are represented in the present fauna. On the other hand, the animals, which required a more mesic condition, could not have lived there and consequently they are not represented in the fauna. Currently sampled upper Oligocene deposits along Badwater Creek do not preserve the real diversity of late Oligocene mammals.

Due to the less favorable ecological conditions, land micromammals, which lived there in the late Oligocene, were specialized in having higher crowned and more lophate teeth. The evolution of this type of dentition was the result of the adaptation to a more herbaceous diet in a drier climatic situation. Some rodents represented had more hypsodont teeth than did their middle Oligocene counterparts, but they had not yet developed rootless or ever-growing cheek teeth. Near the Oligocene-Miocene boundary, the climate returned to more mesic conditions and these highly specialized rodents, which were adapted to drier conditions, could not have survived and either became extinct or migrated to other areas by the end of the Oligocene.

During the early Miocene, a few rodents migrated into North America from Eurasia. These are not direct descendents of the late Oligocene rodents of North America. All the late Oligocene micromammals of North America have their ancestry in the middle or early Oligocene of North America. Based on the micromammal assemblages, the faunal gap between the late Oligocene and the early Miocene is greater than the one between the middle and late Oligocene in North America.

INTRODUCTION

Since 1962, the Section of Vertebrate Fossils of Carnegie Museum of Natural History has been working Tertiary deposits and collecting vertebrate fossils along Badwater Creek in the northeastern part of the Wind River Basin, Natrona and Fremont counties, central Wyoming. The University of Colorado Museum, the Museum of Natural History of the University of Kansas and The Museum of Texas Tech University cooperated with this work in various ways. A considerable number of vertebrate fossils has been recovered in volcanic rich silts and clay along Badwater Creek. These sediments were thought to be eastern equivalents of the Tepee Trail Formation (Tourtelot, 1957). There is now almost overwhelming evidence that these sediments do not represent the Tepee Trail Formation (Krishtalka and Black, 1975), but until a thorough geologic review of the area can be completed, Tourtelot's usage is followed. The vertebrates recovered from these deposits are primarily of the late Eocene age although other faunal levels are also recognized. Much of the fauna has been described since 1966.

In 1964, a field party from the Carnegie Museum of Natural History discovered a much later faunal level in the tan silts, which unconformably overlie "the Tepee Trail Formation" along Badwater Creek. Recovery of vertebrate fossils from this level was continued by field parties from the University of Kansas in 1971 and from Texas Tech University in 1973 and 1974. As in many other early Cenozoic assemblages, most vertebrates in the later faunal level in Badwater Creek area are represented by fragmentary remains, generally consisting of isolated or loosely associated teeth. More than fifteen hundred identifiable specimens are at hand. These specimens are described below.

The present study is a part of a series of studies of the Badwater fauna. Most of the materials dealt with were collected by me during the field season of 1974, and some by field parties of Carnegie Museum of Natural History and the University of Kansas.

The abbreviations used in this paper are as follows: CM, Carnegie Museum of Natural History; KU, University of Kansas; L, length; W, width; AW, anterior width (width of trigonid); PW, posterior width (width of talonid).

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Dr. Black, and Dr. Mary R. Dawson (Carnegie Museum of Natural History, Pittsburgh) originally suggested this study to me as a significant subject for a doctoral dissertation in vertebrate paleontology, and provided general access to and loan of fossil material in their care.

I am also grateful to them and to the following people for thoughtful and stimulating discussion concerning Tertiary insectivore, rodent, and lagomorph evolution: Dr. John F. Sutton and Dr. Leonard Krishtalka, both at Carnegie Museum of Natural History; Dr. Robert W. Wilson and Dr. Larry D. Martin at the University of Kansas, Lawrence.

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PREVIOUS WORK

The presence of mid- or later Tertiary strata along the Badwater Creek area was recognized as early as 1948. In the 1948 Guidebook for the Third Annual Field Conference of the Society of Vertebrate Paleontology, Tourtelot (p. 66) briefly mentioned a sequence of soft, tan, ashy siltstone with two beds of vitric tuff which occur along Badwater Creek overlying the late Eocene Tepee Trail Formation in Secs. 23 and 24, T39N R89W, Natrona County, Wyoming. He referred to these rocks as "uppermost Eocene or Oligocene (?) and Younger . . . ," and said that the siltstone was remarkably similar to Miocene rocks in other parts of Wyoming but there was "little" break between the Tepee Trail Formation and this siltstone sequence. Later (1957) he referred to this tan siltstone sequence as the upper part of the Hendry Ranch Member of the Tepee Trail Formation. Thus, the Hendry Ranch Member defined by him (1957) includes all the strata, which overlie the Green and Brown Member in the Badwater area.

No fossils were known from these rocks until 1964 when a Carnegie Museum of Natural History field party discovered a vertebrate fauna in the NW ¼, Sec. 24, T39N R89W (locality 19 of Black and Dawson, 1966:303). The tan silt sequence was prospected in 1965 and some two tons of matrix were washed from locality 19 in 1966 by Carnegie Museum of Natural History field parties. Vertebrates recovered from locality 19 were then designated the Cedar Ridge local fauna (Black, 1968:51). When identifiable remains are recovered higher in the section along Badwater Creek, they will be of a later age and therefore the use of the name "Cedar Ridge local fauna" must be restricted to the assemblage found at locality 19. The use of "Badwater local fauna" is restricted to the assemblage found in the Upper Eocene Hendry Ranch Member below the Oligocene strata.

Riedel (1969) recognized an unconformity within Tourtelot's Hendry Ranch Member. Vertebrates at locality 19 are found in the tan tuffaceous siltstones above the unconformity.

Prospecting at locality 19 was continued by field parties from the University of Kansas in 1971 and Texas Tech University in 1973 and 1974. I started work on the geology and paleontology of the Cedar Ridge local fauna after 1974.

Brief accounts of the geology and vertebrate fossils of the Cedar Ridge local fauna are to be found in Black (1968, 1969) and Riedel (1969).

COLLECTING METHODS

All the fossils were collected from one locality. The matrix containing fossils is weakly cemented by carbonate. Normal washing and screening methods are not applicable for this matrix as it is not easily distintegrated because of the cement. I used citric acid to desolve the calcareous cement.

After quarrying, all the matrix was dried and broken down, and the concentrates were then soaked in a weak solution of citric acid (3–5 weight percent). Reaction between the calcareous matter and citric acid lasts almost two days. The matrix was soaked in the citric acid twice to desolve the calcareous cement completely. After dissolving the calcareous cement, normal washing and screening methods were used.

When fossils are soaked in a strong solution of citric acid (for example 25 weight percent) for one day, they are damaged by the acid. I used a weak solution to avoid damaging the fossils.

GENERAL GEOLOGY

The area of the present study is located in the northeastern part of the Wind River Basin along the southern edge of the Big Horn Mountains and the southeastern end of the Owl Creek Mountains in

Natrona County, Wyoming. All the fossil localities along Badwater Creek of both late Eocene and younger age lie to the south of Badwater Creek between the creek and the Cedar Ridge fault.

Love (1939) proposed the name Tepee Trail Formation for a sequence of volcanic tuffs and flows of late Eocene age in the East Fork Basin near the southeast margin of the Absaroka Range. Tourtelot (1948, 1957) applied this name to a sequnce of volcanic-rich sedimentary rocks along the southern margins of the Owl Creek and Big Horn Ranges. He subdivided the Tepee Trail Formation into two members, a lower Green and Brown Member and above this the Hendry Ranch Member. The Hendry Ranch Member defined by Tourtelot (1957) includes all the strata, which overlie the Green and Brown Member in the Badwater area. Black (1968, 1969) reported the discovery of late Oligocene vertebrates from a tan siltstone sequence at the top of the Hendry Ranch Member. During his study of the geology of the Badwater Creek area, Riedel (1969) recognized an unconformity within the Hendry Ranch Member between the gray and buff tuffaceous mudstones from which late Eocene vertebrates were obtained and the tan tuffaceous siltstones and sandstones from which late Oligocene vertebrates were obtained. He proposed to restrict usage of the Hendry Ranch Member to the gray and buff tuffaceous mudstones, especially excluding the tan tuffaceous siltstones and sandstones, which lie unconformably above them. The vertebrates discovered from the latter sediments are dealt with here.

The gray and buff tuffaceous mudstone along Badwater Creek from which late Eocene vertebrates were found has been classified as the Tepee Trail Formation (Tourtelot, 1957). There is now almost overwhelming evidence that these sediments do not represent eastern equivalents of the Tepee Trail Formation. Rather, these volcanic rich silts and clay were probably deposited at the same time as, or somewhat later than, the volcanic conglomerates of the Wiggins Formation, which overlies the Tepee Trail Formation in its type area. This problem is outside the scope of the present study. Because a thorough geologic review of the area has not been completed as yet, I shall continue to follow Tourtelot's usage.

Tentatively, I assign the deposit to the Oligocene strata, which include the tan tuffaceous siltstones and sandstone from which late Oligocene vertebrates were obtained. The best exposures are in NE Sec. 24, T39N R89W where more than 200 ft of strata are exposed and an additional 500 ft are concealed by overlying Quaternary gravel and vegetation. The lower contact here is marked by an angular unconformity of approximately 2 degrees and erosional relief of up to 40 ft. The top of the unit is truncated by erosion throughout the area. The Oligocene strata and the Hendry Ranch Member of the Tepee Trail Formation are down faulted against the Green and Brown Member, or against the Lost Cabin and Lysite Members of the Wind River Formation along the course of Badwater Creek and the Cedar Ridge. This fault, called the Cedar Ridge fault, can be traced roughly from ESE to WNW throughout the area.

A general geologic map of the Badwater Creek area is shown in Fig. 1. A structural cross section near the late Oligocene fossil locality is shown in Fig. 3. Below the unconformity are the gray and buff tuffaceous mudstones of the Hendry Ranch Member of the Tepee Trail Formation. The erosional relief ranges up to 40 ft. The bottom of the relief (the point A in the Fig. 3) represents a stream channel. At the point A, conglomerates of medium pebble size are deposited. The maximum thickness of the conglomerates is 3 cm. The transverse (perpendicular to the stream course) extension of the conglomerates is 7 m or so, and the layer is lenticular. High on the sides of the relief surface at point B, conglomerates are not observed, and here the fine-grained sandstones of the Oligocene strata lie directly on the tuffaceous clay of the Hendry Ranch Member.

The relief is lower to the east of the old stream channel. Here the erosional relief is approximately 10 ft or less. At the point C, about 2 ft above the contact with underlying Hendry Ranch Member is a vitric tuff with a thickness of about 1 m. The tuff is traceable laterally so that it is used as a marker bed. Laterally, it thins and is about 0.5 m above point A. Geochron Laboratories, Inc. used potassium-argon ratios to determine the age of the vitric tuff at point C (Riedel, 1969). This age was given as 34 million years and falls within the lower Oligocene as delimited by Kulp (1961) and Evernden and others (1964). If the age determination is valid, it indicates that these lowest beds were deposited during early Oligocene time.

Above the vitric tuff are siltstones and fine-grained sandstones about 24 m thick. Cross-bedding and truncate bedding are predominant in the fine-grained sandstones. A calcareously cemented lens of siltstone (Loc. 19) is found about 12 m above the

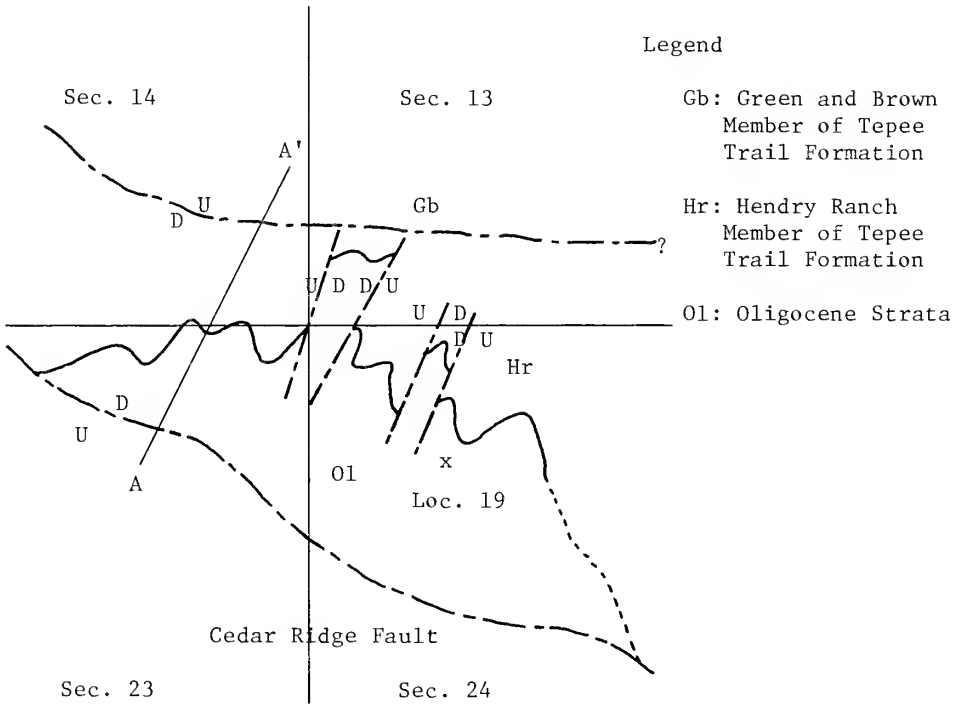

Fig. 1.—Simplified geologic map along Badwater Creek, at Secs. 13, 14, 23, & 24, T39N, R89W, in Natrona County, Wyoming. Scale—1:24,000.

vitric tuff. A number of vertebrate fossils have come from this calcareous lens. Below the lens and above the vitric tuff are predominantly fine-grained sandstones, and the homogeneity of the sequence indicates that no depositional breaks are represented within this sequence of sandstones. The vertebrate fauna is inferred to be of late Oligocene age. The radiometric determination of an age of 34 million years for the vitric tuff does not correlate well with the postulated age of the fauna. Although they are separated stratigraphically by 12 m, I could find no evidence for the presence of a depositional break, or a hiatus between the tuff and the fossiliferous lens. I believe that the potassium-argon age determination is in error and is too old. I can not believe that the section preserved north of the Cedar Ridge fault consists of a thin sequence representing early Oligocene deposition, a long depositional hiatus and then the resumption of deposition in late Oligocene time.

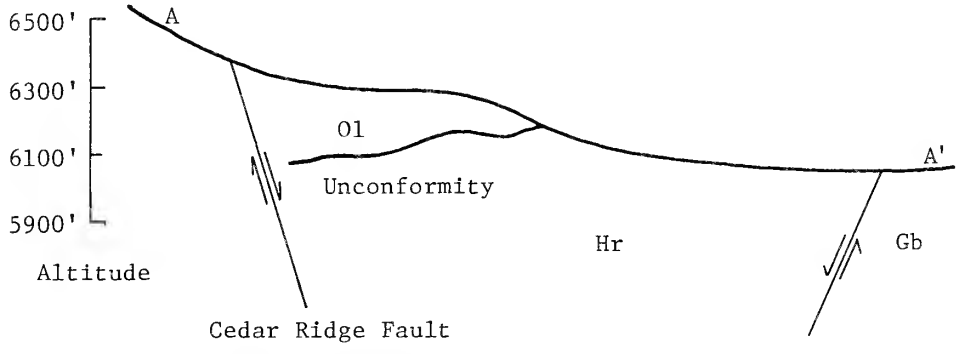

Fig. 2.—Cross section along A-A' shown in the Fig. 1. Horizontal scale—1:8,000. Vertical scale—1:6,000.

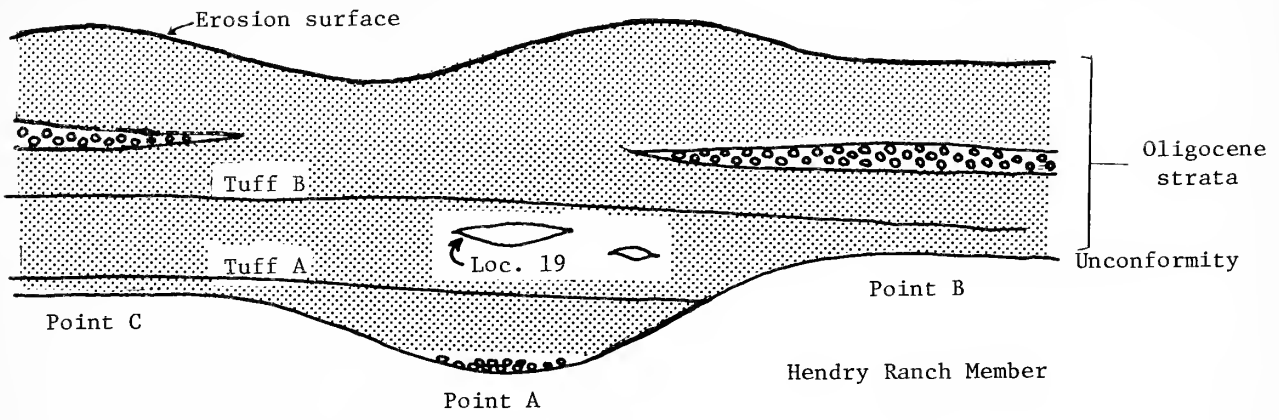

Fig. 3.—Structural cross section near the late Oligocene fossil locality, Loc. 19, at Sec. 24, T39N, R89W, in Natrona County, Wyoming. Horizontal scale—1:5,000. Vertical scale—1:2,000.

A hard gray tuffaceous sandstone lies 1 m above the siltstones and sandstones and can be used as a marker bed. One and one-half m above the sandstone there is a pebble to cobble sized conglomerate. The thickness is about 30 to 40 cm and its distribution is quite wide. The conglomerate represents depostion on a flood plain. The direction of the current at the time of deposition of the conglomerates is determined by the direction of axes of elongated cobbles—from SW to NE. The pebble and cobbles consist of Precambrian gneisses and granites, sandstones and limestones of the Paleozoic, and reworked siltstones of underlying Oligocene strata. The average diameter of the pebbles is 5 cm. Based on the direction of the current, uplift had taken place to the southwest of Badwater Creek. Rapid erosion of Precambrian and Paleozoic rocks and transportation toward the northeast cause the deposition of the conglomerates in Badwater Creek area.

All the strata mentioned above dip gently southward (about 10°).

FAUNAL LIST

The following is the list of the amphibians, reptiles, and mammals identified in the Cedar Ridge local fauna.

Class Amphibia
  Order Urodela
    Family Batrachosauroididae
      ? *Batrachosauroides* sp.
Class Reptilia
  Order Sauria
    Family Iguanidae
      Leiocephalus sp.
Class Mammalia
  Order Marsupicarnivora
    Family Didelphidae
      Peratherium sp. cf. *P. spindleri* Macdonald, 1963
      Nanodelphys new species, unnamed
  Order Insectivora
    Family Leptictidae
      Leptictis sp.
    Family Adapisoricidae
      Ankylodon sp. cf. *A. annectens* Patterson & McGrew, 1937
    Family Geolabididae
      Centetodon sp. cf. *C. marginalis* (Cope, 1974)
    Family Soricidae
      Domnina sp. cf. *D. gradata* Cope, 1873
    Family Talpidae
      Proscalops miocaenus Matthew, 1901
      Oligoscalops ? sp.
    Family Micropternodontidae
      Micropternodus sp.
  Order Rodentia
    Family Aplodontidae
      Prosciurus relictus (Cope, 1973)
      Pelycomys placidus Galbreath, 1953
    Family Eomyidae
      Adjidaumo douglassi Burke, 1934
      Paradjidaumo hypsodus, new species
      Metadjidaumo hendryi, new genus and new species
      Eomyidae, genus indet., Type A
      Eomyidae, genus indet., Type B
    Family Heteromyidae
      Proheteromys sp. cf. *P. nebraskensis* Wood, 1937
      Heliscomys sp. cf. *H. vetus* Cope, 1873

Family Cricetidae
Eumys parvidens Wood, 1937
Eumys elegans Leidy, 1856
Eumys brachyodus Wood, 1937
Eumys sp. cf. *E. planidens* Wilson, 1949
Order Lagomorpha
Family Leporidae
Palaeolagus burkei Wood, 1940
Palaeolagus sp. cf. *P. intermedius* Matthew, 1899
Order Carnivora
Family Canidae
Hesperocyon temnodon (Wortman & Matthew, 1899)
Order Perissodactyla
Family Equidae
Miohippus sp.
Family Hyracodontidae
Hyracodontidae genus indet.
Order Artiodactyla
Family Hypertragulidae
Leptomeryx sp. near *L. evansi* Leidy, 1853
Hypisodus sp. near *H. minimus* (Cope, 1873)

MAMMALIAN TAXA ABSENT FROM THE CEDAR RIDGE LOCAL FAUNA

The Cedar Ridge local fauna is represented by a sufficient number of identifiable specimens to make it worthwhile to consider prominent absences from the known mammalian fauna. A good many forms are absent from the Cedar Ridge local fauna. The reasons for the absence of some taxa, I believe, should be considered from the following two points of view. First, some forms were surely living at the time of deposition in the area where the Cedar Ridge local fauna has been recovered, but for some reasons they were not fossilized there. Second, the other forms could not have lived in the Badwater Creek area so that they are not represented in the present fauna.

The remarkable absence of larger forms, such as ungulates and carnivores, could be explained according to the first reason mentioned above. As I explained in the section of the paleoecological setting of the sites, the climate of the area during the late Oligocene was drier than the middle Oligocene and is thought to have been grassland, steppe to semidesert. This is supported by the presence of gypsum crystals throughout the section. Schultz and Falkenbach concluded that the leptauchine oreodonts (tribe Leptaucheniini) lived in very arid, desert-like regions (Schultz and Falkenbach, 1968:407). They stated (1968:408), "The Leptaucheniini apparently were well adapted to the unfavorable climatic conditions of the late Oligocene and were able to survive in great numbers, but most of the other kinds of oreodonts either became extinct or lived in areas where the climate was more hospitable. Evidently the hyracodont rhinoceroses also had specialized in such a manner as to live in arid desert areas. Most of the other mammals must have found it difficult to survive, and migrated elsewhere, or lived along the banks of small streams that existed in the area at that time. The Leptaucheniini were well adapted for dwelling in deserts. The same was apparently true of the hyracodonts." I think that surely leptauchine oreodonts and hyracodont rhinoceroses were living in the Badwater Creek area during the late Oligocene time. No oreodonts are represented but a few unidentifiable rhinoceros tooth and bone fragments are found in the fauna. The fossils found at Loc. 19 are mostly isolated teeth and jaw fragments. The nature of preservation indicates that teeth and bones were transported some distance after the death of animals and before the time of final burial. Moreover, the size of most teeth and bones found there are less than 3 mm in longest diameter, and specimens over 5 mm are very scarce. This type of preservation indicates that the material deposited were well sorted by stream action. The teeth and bones of larger size are not suitable for distance transport and were not deposited there. By this sorting mechanism, no oreodonts were transported and deposited at the site where the Cedar Ridge local fauna was recovered. The occurrence of *Hypisodus* in this fauna is meaningful. A few teeth referable to *Hypisodus* are found teeth. The size of these teeth is at the upper limit of the size range of teeth found at Loc. 19. The species of *Hypisodus* are the smallest of known artiodactyls, indicating that only the teeth of the size of the smallest artiodactyls could be transported. This is true for perissodactyls and carnivores. Galbreath (1953) reported 10 genera of ungulates and carnivores from the Vista Member of the White River Formation of northeastern Colorado. In the present fauna, only three genera are represented and they are very scarce in comparison with the other smaller forms.

The absence of some insectivores and rodents in

the present fauna must be explained by unfavorable ecological conditions for them in the Badwater Creek area. *Scottinus* has been reported from the late Oligocene in the Great Plains (in Nebraska) but this form was not found in the present fauna. *Leidymys* and *Paciculus* are known from the late Oligocene of Oregon but they are not represented in the Badwater Creek area. Interestingly enough, they did not become extinct at the beginning of Miocene time but they continued to survive into the Miocene in the Rocky Mountain region, that is in Montana, Colorado, and Wyoming. Their ancestral forms are known in the middle Oligocene of the Great Plains. These forms all have lower-crowned teeth and probably lived in a more mesic habitat. Most small mammals in the present fauna have high-crowned teeth or teeth with high, thin cross-lophs. The trend towards higher-crowned teeth is perhaps an adaptation for a typical herbaceous diet in a dry environment. The animals, which required a more mesic habitat, are not represented in the present fauna. Martin (1972) clearly described the evolutionary pattern of cricetid rodents in relation to the climatic changes; the steppe forms became extinct near the Oligocene-Miocene boundary. This extinction may be related to a return of mesic conditions and the subsequent expansion of the genera *Leidymus* and *Paciculus*. This is the most probable explanation as to why *Leidymys, Paciculus,* and *Scottimus* were not represented in the late Oligocene in the Rocky Mountain region but occur there in Miocene time. Oregon, from which *Leidymus* and *Paciculus* are reported in the late Oligocene, was a costal area and was under a milder climatic regime throughout the Tertiary period. *Scottimus* is also supposed to have lived near stream banks during the late Oligocene and becomes abundant once the climate returned to a more mesic condition in the Miocene. The ecological requirements of *Trimylus* and *Domnina* are not certain. *Trimylus* has a more bulbous, less high crowned condition of the teeth (Repenning, 1967) than *Domnina*. The presence of *Domnina* and the absence of *Trimylus* in this fauna seems to be analogous to the presence of rodents with higher-crowned and the absence of those with lower-crowned teeth. The relative abundance of *Eumys planidens*, which has more lophate teeth, may be explained in the same way. All the eomyids and the most of the cricetine *Eumys* species became extinct without leaving any descendants. I believe that pseudotheridomyine rodents known from the Miocene of North America are not descended from the North American Oligocene eomyids but represent immigrants from the Old World. The extinction of many eomyids and cricetids in North America by the end of the Oligocene may be related to a return of mesic conditions as Martin (1972) stated.

The Cedar Ridge local fauna represents a fauna adapted to a drier environment and is biased due to sorting by stream action. For these reasons, a good many forms are absent from the fauna. This leads to the conclusion that currently sampled Whitneyan deposits in the Badwater Creek area do not preserve the real diversity of the late Oligocene mammals.

AGE OF THE STRATA

As noted above, the Oligocene strata lie unconformably above the late Eocene clay. The overlying siltstones and sandstones are of the upper Oligocene age as indicated by the occurrence of the late Oligocene fauna. We obtained the K-Ar age for the Tuff A as 34.3 ± 1.4 m.y. This age falls into the early Oligocene as delimited by Kulp and Evernden. The determination of the age for the tuff does not correlate well with the fauna. I believe that the K-Ar age given is too old. If it is correct, no middle Oligocene strata are represented in the Badwater Creek area.

In the Wind River Basin and surrounding area, epeirogenic uplift began after Eocene time. For the Oligocene of Wyoming, van Houten (1964:71) stated, "Reduced relief resulted in the slow accumulation of stream-laid deposits; however, numerous showers of ash from vents in the Yellowstone-Absaroka volcanic field contributed a substantial amount of sediment. Altered ash that mantled the uplands supplied most of the mud that was spread as an almost continuous sheet on flood plains over much of Wyoming and the adjacent Great Plains." These sediments of the Oligocene consist of the White River Formation in Wyoming and Colorado, or the White River Group of the Great Plains.

The Oligocene strata along Badwater Creek are separated from the Eocene strata by only a modest angular (about 2°) and erosional unconformity. This indicates that no severe orogenic disturbance was represented in this region during the period of time between the time of deposition of the Hendry

Ranch Member and that of the Oligocene strata. I believe that volcanic ash from vents in the Yellowstone-Absaroka volcanic field were deposited in this region, but that these sediments were eroded and the erosion acted on the clay of the Hendry Ranch Member. By late Oligocene time, the drainage system was changed and upper Oligocene strata were deposited along this new drainage system. These sediments were first accumulated as channel fillings and later as flood plains deposits.

Along Badwater Creek, no lower and middle Oligocene strata correlative to the White River Formation are observed. A sequence of sediments of early Oligocene age occurs along Beaver Rim on the southern edge of the Wind River Basin, 50 mi southwest of the Badwater Creek area. The sediments along Beaver Rim are referred to the White River Formation (van Houten, 1964). Once the lower part, at least, of the Oligocene strata of the Badwater Creek were believed to be of the early Oligocene age because of the age of the Tuff A given as 34 m.y. and because the lower Oligocene sequence occurs along Beaver Rim (Black, 1969:45). As I stated before, I could not find any evidence of a break in deposition, or hiatus between Tuff A and the calcareous lens (Loc. 19 of Carnegie Museum of Natural History) from which the late Oligocene vertebrates are obtained.

For these reasons, I consider the potassium-argon age determination is too old. All the sediments were accumulated in the late Oligocene as indicated by the occurrence of vertebrates of the late Oligocene age.

CORRELATION OF THE STRATA

In the Beaver Rim area, the White River Formation is well developed. The thickness of the formation varies locally; the formation reaches its maximum exposed thickness of approximately 650 ft along the Beaver Rim in the vicinity of Cameron Springs and may have been as much as 800 ft thick 2.5 mi north of the divide (van Houten, 1964:55–56). In this area, the White River Formation yields mammalian fossils of early (Chadronian) and possibly of middle (Orellan) Oligocene age. Van Houten (1964:71) concluded that, "There is no clear evidence of deposits of late Oligocene age in the southern part of the Wind River Basin."

The Oligocene strata of the upper Oligocene along Badwater Creek are not directly correlative with the White River Formation in the Beaver Rim area. As far as I know the Vista Member of the White River Formation in Logan County, northeastern Colorado (Galbreath, 1953) and the Whitney Member in Nebraska and South Dakota are the only known deposits, which yields vertebrate fossils of late Oligocene (Whitneyan) age. These beds are composed of massive, tan silt with a highly calcareous zone. The thickness is about 100 ft and the areal extent probably is not large (50 to 75 square mi). The Vista Member can be distinguished faunally and lithologically, but it should be emphasized that the lithologic separation from the (underlying) Cedar Creek Member of the White River Formation is largely arbitrary. Were the fauna not known, the lithologic differences would have no stratigraphic significance.

Although the Vista fauna is scanty, the fossils are individually rare, the late Oligocene Badwater fauna is correlative with the Vista fauna. Lithologically, the well laminated appearance of the Oligocene strata in the Badwater Creek area is quite different from the massive nature of the Vista Member in Colorado. It is not certain whether the upper Oligocene deposits in the Badwater Creek area and in northeastern Colorado accumulated in different structural basins or not, but if they were deposited in different basins, they should be assigned to different formations. This problem is beyond the scope of the present work. Although I believe that the Oligocene strata along Badwater Creek may be assigned to the White River Formation but to a different member, I leave it unnamed until a thorough geologic study of this area is completed.

FAUNAL AGE

The late Oligocene, or Whitneyan, mammalian faunas of North America are not well known. An age determination for a micromammalian assemblage such as the present fauna is complicated by the fact that we have only the haziest idea as to other late Oligocene small mammal faunas. Of some

40 genera of mammals known from the upper part of the Brule Formation in Nebraska, South Dakota, and Colorado, and considered to be late Oligocene in age, only one-fourth are in the "micro" mammal range. Galbreath (1953) described several mammals of the late Oligocene from the Vista Member of the White River Formation of northeastern Colorado. But the Vista fauna is scanty, and the fossils are individually rare.

A late Oligocene age for the present fauna is based upon the following data.

(1) *Marsupials.—Peratherium* and *Nanodelphys* are typically early Tertiary genera ranging from the mid-Eocene to the early Miocene. As far as the specific level is concerned, the species of *Peratherium* and *Nanodelphys* are intermediate between the middle Oligocene and the early Miocene forms. Based on marsupials alone, it is fairly safe to conclude that the age of the fauna is post-middle Oligocene and pre-early Miocene.

(2) *Insectivores.—Ankylodon, Centetodon,* and *Micropternodus* are typically Oligocene genera, although *Centetodon* and *Micropternodus* are known from the early Miocene of Nebraska and Oregon. *Proscalops* and *Domnina* are known from the middle Oligocene for the former and from the late Eocene for the latter into the early Miocene. Of the five genera, one is known only from the Oligocene and four from the mid-Oligocene into the early Miocene. At the specific level, all the species of the present fauna are a little advanced over the middle Oligocene species and are not conspecific with any of the known early Miocene species. This is also suggestive of a late Oligocene, or at least pre-Miocene, age for the fauna.

(3) *Lagomorphs.*—The occurrence of *Palaeolagus intermedius* is not well documented. The other species of *Palaeolagus* is intermediate between *P. burkei* of the middle and late Oligocene and *P. hypsodus* of the earliest Miocene, although it is a little closer to the former. *P. hypsodus* is known from the Gering Formation in Nebraska and Wyoming and from the Sharps Formation of South Dakota both considered to be basal Miocene in age. The present population is not as advanced as this species and would therefore suggest a latest Oligocene age for the fauna.

(4) *Rodents.—Pelycomys* is known from the Oligocene. At the specific level, this form is close to the middle Oligocene species. *Adjidaumo* and *Paradjidaumo* are typically Oligocene genera. At the specific level, *Paradjidaumo* in the present fauna is advanced over the middle Oligocene *Paradjidaumo*. It is suggestive of a post mid-Oligocene age for the fauna. The other eomyids differ from the typical Oligocene *Adjidaumo* and *Paradjidaumo* genera but are certainly closely related to them and show no resemblance to the Miocene *Pseudotheridomys*. *Prosciurus, Heliscomys, Proheteromys,* and *Eumys* are all known from the earliest Miocene but are more typical, abundant, and diverse in the Oligocene. The absence of beavers, mylagaulids, and aplodontids (beside *Prosciurus*) from the present fauna is meaningful. Their absence most probably reflects a different habitat preference. These three rodent families are almost always found in faunas of the early Miocene. They are known from the earliest Miocene of South Dakota, eastern Wyoming, and Nebraska but are unknown from the late Oligocene of these same areas.

PALEOECOLOGICAL SETTING

The Oligocene strata were accumulated as channel-fill. The lower part of the sequence seems to be one of over-filling of the previously eroded valley. Aggradation was greater than erosion. Granites and gneisses, sandstones and limestones, and mud balls from the underlying Hendry Ranch beds are common in the gravel lenses near the base of the unit. As sedimentation proceeded, the previously eroded valley was filled by sediments, and sediments were deposited on a broader flood plain. Well sorted, laminated and truncated sandstones indicate that sedimentation took place in a braided stream situation.

Paleosols are not recognized in the Oligocene strata. Andesine is the most common feldspar throughout the section. In a calcareous lens from which the late Oligocene vertebrates are found, bytownite and probably anorthite are present. X-ray diffraction patterns of the sample from the same calcareous lens also indicate that feldspars preserved are calcic (Hattori, personal communication). The presence of fresh, calcic feldspar indicates that the sediments were not heavily weathered, and the paleoenvironment should have been open land or grassland type with moderate temperature. This conclusion is strengthened by the presence of

gypsum crystals throughout the section. The texture of gypsum crystals is fine to medium grained. They occur in beds with disturbed bedding. This seems to be due to expansion during hydration. Gypsum is usually formed at lower temperatures, whereas anhydrite is precipitated at temperatures above 30° C. The presence of evaporites indicates the climate was rather dry at the time of deposition. This is consistent with other evidence that the climate became progressively drier towards the late Oligocene in the Great Plains (Schultz and Falkenbach, 1968).

The origin of calcareous lenses is uncertain. The siltstones and sandstones are essentially noncalcareous throughout the section. In the Great Plains near the type locality of the Whitney Member, most of the fossils found in the Middle and Upper Whitney sediments are enclosed in clay-siltstone nodules, which are cemented by calcium carbonate, and the nodules must have been formed by the action of ground water (Schultz and Falkenbach, 1968:408). This is not the case for the Oligocene sediments along Badwater Creek. There, calcareous lenses are rare and only two calcareous lenses have been found so far. Both of them are fossiliferous. The non-calcareous nature of the siltstone and sandstone may argue against the process of the formation of the calcareous lenses by the action of ground water. The calcium carbonate may have been accumulated in small playa lakes on the flood plain and vertebrate bones and teeth were transported in these lakes. The vertebrate remains are well preserved because the lenses are resistant to weathering or to stream action. Vertebrate fossils are found only in the calcareous lenses, and are not found in the siltstones and sandstones.

The sedimentary structure through the whole section is predominated by the high degree of sorting, cross-bedding, and truncated bedding. All the sandstones are fine-grained and pebble size grains are observed only in conglomerate layers. The sediments were accumulated under running water with rather low energy. The fossil teeth and bones found at Loc. 19 are isolated and abraded, and the diameter of these are mostly less than 3 mm. No bones in articulation are found. The nature of preservation of the fossils indicates that these teeth and bones were transported some distance before final burial by running water, and due to the energy of running water the materials transported were well sorted. Only a few larger bones were deposited near Loc. 19. This sorting mechanism of stream action greatly influenced the kinds of mammals buried and preserved at Loc. 19. The larger mammals, if they lived near the site of deposition, would have been not easily transported and buried there after their death.

During the middle Oligocene, the White River Formation was developed over a vast area east of the ancestral Rocky Mountains in Wyoming, Colorado, South Dakota, and Nebraska. These deposits are typically flood-plain sediments accumulated under a climatic regime of relatively high precipitation. Toward the end of Oligocene time, apparently precipitation became reduced and the aerial development of the White River Formation also became reduced. The aerial distribution of the late Oligocene sediments is greatly restricted and represented only in a few areas—the Vista Member in Colorado and the Whitney Member in Nebraska and South Dakota of the White River Formation. This restriction was caused by the reduced precipitation and subsequent reduced drainage systems in the Great Plains region. This interpretation is consistent with the climate becoming progressively drier in the late Oligocene (Schultz and Falkenbach, 1968; van Houten, 1964). The vegetation in the late Oligocene must have been of a steppe-type. In relation to the restricted distribution of the late Oligocene sediments, the late Oligocene mammal faunas are not well known except for the one from the type area of the Whitney Member of the White River Formation in Nebraska. The latter fauna is composed mostly of oreodonts.

In the early Miocene, climatic conditions apparently changed again to a period of more precipitation. The Arikaree group in Nebraska was deposited as channels cut through to the underlying middle Oligocene series in most areas. These sediments are mostly of the channel-filling type initially. The extensive development of the lower Miocene series reflects the return of the climate to a more mesic condition with greater precipitation and resultant development, or rejuvenation of drainage systems. The early Miocene must have been considerably more humid and the vegetation more luxuriant.

The climatic and environmental changes near the Oligocene-Miocene boundary caused a great difference in the composition of faunas between the late Oligocene and the early Miocene.

SYSTEMATIC ACCOUNTS

Class Amphibia
Order Urodela
Family Batrachosauroididae Auffenberg, 1958
? **Batrachosauroides** sp.
(Fig. 4)

Referred specimens.—Vertebrae, CM 33649 and uncatalogued specimens.

Locality.—Loc. 19, Badwater Creek, Wyoming.

Age.–Late Oligocene.

Discussion.—The vertebra is amphicoelous. When Taylor and Geese (1943) established a new salamander genus *Batrachosauroides* from the Miocene of Texas, they determined that the vertebrae were amphicoelous and not opisthocoelous. The present specimen may be referred to this genus. Auffenberg (1958:170–171) argued about the genus *Batrachosauroides* and stated that the vertebrae referred to *B. dissimulans* are all strongly opisthocoelous. At present, I cannot evaluate which statement should be more reasonable. Tentatively I followed Taylor and Hesse and I refer the present specimen to that genus.

Class Reptilia
Order Sauria
Family Iguanidae
Leiocephalus sp.
(Fig. 5)

Referred specimens.—Jaws; CM 33650 and uncatalogued specimens.

Locality.—Loc. 19, Badwater Creek, Wyoming.

Age.—Late Oligocene.

Description and discussion.—The pleurodont teeth have tall, slim, and straight-sided shafts, except for a slight flaring toward the crown. The crown is flattened linguobuccally into a narrow tricuspid fan-shaped structure, the central cusp largest. Each side cusp is prominently separated from the main cusp by a wide groove, which fades out at the base of the crown. These grooves lack an associated ridge.

The present form may well be compared with *Leiocephalus* sp. described by Estes (1963:239) from the early Miocene Thomas Farm local fauna of Florida. As in Florida specimens, the grooves on the crown which separate side cusps from the main cusp lack an associated ridge, seen in many such lizard teeth, which extends from the apex of the lateral cusp to the base of the crown.

Class Mammalia
Infraclass Metatheria
Order Marsupicarnivora
Family Didelphidae Gray, 1821
Peratherium sp. cf. **P. spindleri** Macdonald, 1963
(Fig. 6, Table 1)

Referred specimens.—P^3-M^1: CM 17085; M^1-M^4: CM 33404; M^2-M^3: CM 33439; M^1: CM 33404–33438; M^2: CM 33440–33462; M^3: CM 33463–33479; M^4: CM 33541–33544; M_1-M_2: CM 33480; M_2-M_3: CM 17080, CM 33481; M_1: CM 33482–33500; M_2: CM 33501–33520; M_3: CM 33521–33536; M_4: CM 17082, CM 33537–33540.

Locality.—Loc. 19, Badwater Creek, Wyoming.

Age.—Late Oligocene.

Description.—The size of teeth is smaller than that of *Peratherium fugax*. Except for size, the morphology of the present form agrees exactly with that seen in *P. fugax*. On M^1, the metaconule is not well defined. The posterior walls of the protocone and the metacone form a continuous posterior border of the tooth. Stylar cusp C is prominent and relatively high. Unlike *P. knighti*, the buccal border of the crown is concave as in *P. fugax*. In relation to this, stylar cusp C is situated more lingually in the present form and in *P. fugax* than in *P. knighti*. On M^2, the metaconule is prominent and expanded posteriorly. The posterior walls of the protocone and the metacone meet at an angle. The buccal border of the stylar shelf between stylar cusps B and C is concave as in *P. fugax*. On M^3, the concavity of the buccal border of the stylar shelf is more exaggerated than on M^1 and M^2. The metaconule is less prominent than on M^2.

The morphology of lower molars is very similar to that seen in *P. fugax* and *P. knighti*. The buccal cingulum is slightly more prominent than in *P. fugax*, but this character is variable. I cannot find any morphological characters other than size on the lower molars to separate this species from other species of *Peratherium*. On M_3, the paraconid is elongate transversely and the lingual end of it is situated more lingually than in *P. fugax*. Because of this character, the width of M_3 is slightly greater than the corresponding tooth of *P. fugax*. But this character is not always true for all specimens of M_3; some specimens have a normal paraconid. Moreover, this character is seen also in a few specimens of *P. fugax* from the middle Oligocene.

Discussion.—Macdonald (1963) described *P. spindleri* from the lower Miocene of the Wounded Knee Area, South Dakota. The diagnosis of this new species of *Peratherium* given by him (1963:164) is as follows: "of medium size; strongly developed anterior and posterior cingula; labial cingulum continuous." The holotype of *P. spindleri* is significantly smaller than *P. fugax*. The size of the Badwater specimens is intermediate between *P. fugax* and *P. spindleri*. Badwater specimens show a wide range of morphological variation of the development of cingula. On some specimens, the development of cingula is weak so that the anterior cingu-

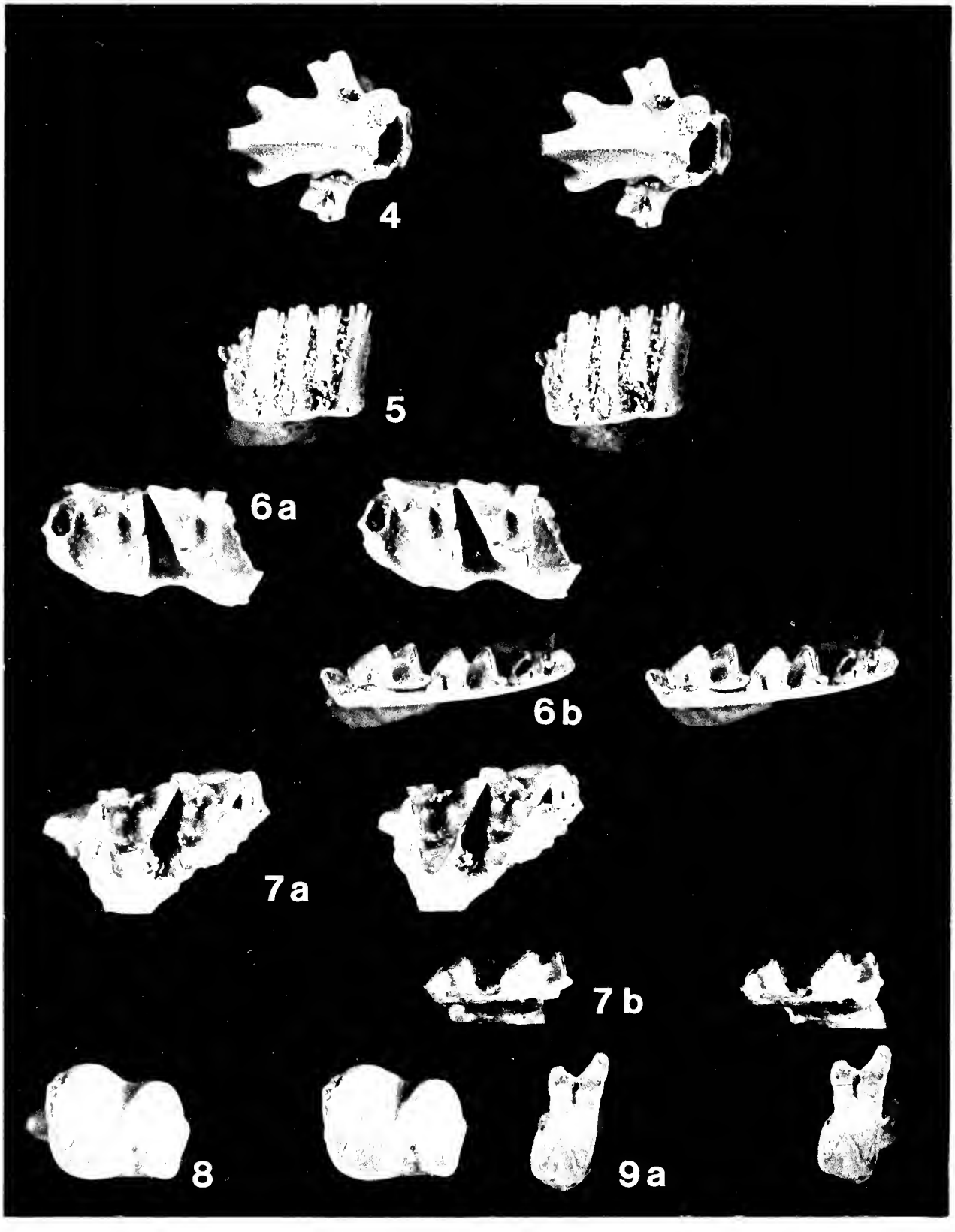
4
5
6a
6b
7a
7b
8
9a

Table 1.—*Dimensions of teeth of* Peratherium *sp. cf.* P. spindleri *and unnamed new species of* Nanodelphys.

Statistics	M^1		M^2		M^3		M^1		M^2		M^3	
	L	W	L	W	L	W	L	W	L	W	L	W
	Peratherium sp. cf. *P. spindleri*											
N	36	36	25	25	19	19	20	20	23	23	17	17
OR	1.62–2.00	1.73–2.22	1.66–2.08	1.81–2.43	1.68–2.09	2.21–2.65	1.66–1.91	0.88–1.12	1.78–2.09	1.00–1.23	1.74–2.07	0.99–1.27
Mean	1.788	1.944	1.836	2.098	1.887	2.433	1.798	1.016	1.925	1.119	2.005	1.181
SD	0.1226	0.1279	0.1175	0.1781	0.1133	0.1403	0.0700	0.0691	0.0876	0.0675	0.1004	0.0870
CV	6.86	6.58	6.40	8.49	6.01	5.77	3.89	6.80	4.55	6.03	5.01	7.37
	Nanodelphys new species											
N	16	16	17	17	18	18	8	8	25	25	24	24
OR	1.18–1.46	1.30–1.77	1.18–1.52	1.48–1.77	1.12–1.32	1.52–1.74	1.20–1.64	0.62–0.81	1.23–1.53	0.67–0.90	1.24–1.47	0.70–0.87
Mean	1.319	1.444	1.355	1.604	1.243	1.612	1.355	0.735	1.348	0.768	1.375	0.796
SD	0.0620	0.1202	0.0787	0.0910	0.0548	0.0683	0.1496	0.0659	0.0679	0.0537	0.0541	0.0456
CV	4.70	8.33	5.81	5.68	4.41	4.24	11.04	8.97	5.04	7.00	3.94	5.73

lum does not unite with the buccal cingulum. On others, the anterior cingulum continues to run posteriorly along the buccal base of the protoconid and unite with the buccal cingulum. The latter character is also seen in a few specimens of *P. fugax* from the middle Oligocene. I do not agree that the greater development of cingula is a good criterion to separate species of *Peratherium*. Size is the only criterion, which separates *P. spindleri* from *P. fugax*.

Nanodelphys new species
(Fig 1., Table 7)

Referred specimens.—M^1-M^2: CM 33549, M^2-M^3 and broken M^4: CM 33600; M^3-M^4: CM 33601; M^1: CM 33602–33616; M^2: CM 33617–33632; M^3: CM 33628, CM 33633–33647; M^4: CM 33648; P_2-P_3: CM 19806; M_2-M_3: CM 19805, CM 33553; M_2-M_4: CM 33554; M_3-M_4: CM 17081, CM 19803, CM 21697; M_1: CM 33545–33552; M_2: CM 19804, CM 33555–33575; M_3: CM 33576–33594; M_4: CM 19802, CM 33595–33598.

Locality.—Loc. 19, Badwater Creek, Wyoming.

Age.—Late Oligocene.

Description.—The general morphology of upper molars resembles that of *N. minutus*. The paracone and the metacone are somewhat more appressed anteroposteriorly. The posterior ridge of the paracone and the anterior ridge of the metacone are more sharp and well defined than in *N. minutus*. These two ridges are as strong as the parastylar or metastylar crests in the present form, whereas in *N. minutus* these ridges are clearly weaker than the parastylar and metastylar crests. This condition indicates that the upper molars of this species of *Nanodelphys* approach the dilambdodont tooth pattern.

In the lower molars, the postcristid and the hypoconulid block the talonid basin posteriorly. The crista obliqua is straight, not concave as in *N. minutus* and the hypoflexid does not excavate the talonid basin bucally as in *N. minutus*. The hypoconulid is displaced more lingually than in *N. minutus* and situated posterior to the entoconid. The postcristid is almost transverse and forms an acute ridge. The hypoconulid is lower than the entoconid but still higher than the talonid basin. The posterior cingulum is very weak and terminates lingually at the base of the hypoconulid. The posterior cingulum does not unite with the occlusal surface of the hypoconulid.

Discussion.—Upper molars of the present form approach the dilambdodont condition. *Nanodelphys minutus* has upper molars with less well-developed dilambdodont tooth pattern, as I discussed elsewhere (Setoguchi, 1975). In animals with dilambdodont upper teeth, the lower molars have a hypoconid with a very sharp buccal angle that occludes with the ectoloph of the upper teeth. These teeth either lack a hypoconulid or have this cusp displaced (Robinson, 1968). In *Nanodelphys minutus* the displacement of the hypoconulid is less emphasized in the lower dentition. The hypoconulid is situated posterobuccal to the entoconid in *N. minutus*. In the present form, the displacement of the hypoconulid is emphasized; this cusp is situated posterior to the entoconid. This condition is very

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Fig. 4.—?*Batrachosauroides* sp. CM 33649, vertebra. ×8. Fig. 5.—*Leiocephalus* sp. CM 33650, jaw with teeth. ×10. Fig. 6.—*Peratherium* sp. cf. *P. spindleri*. a: CM 33439, left M^2-M^3. b: CM 33481, right M_2-M_3. ×8. Fig. 7.—*Nanodelphys* new species, unnamed. a: CM 33600, left M^2-M^3. b: CM 19805, right M_2-M_3. ×10. Fig. 8.—*Leptictis* sp. CM 21676, right M_2. ×8. Fig. 9a.—*Ankylodon* sp. cf. *A. annectens*. CM 33658, right M^2. ×8.

Table 2.—*Dimensions of teeth of* Leptictis *sp. and* Ankylodon *sp. cf.* A. annectens.

Statistics	M^1			M^2			P_4		M_1			M_3		
	L	AW	PW	L	AW	PW	L	W	L	AW	PW	L	AW	PW
							Leptictis sp.							
N				1	1	1								
OR				3.46	2.77	2.34								
							Ankylodon sp. cf. *A. annectens*							
N	1	1	2	1		1	2	2	2	2	2	1	1	1
OR	1.72	3.11	2.57–2.66	0.98		2.08	1.76–1.77	1.26–1.32	1.74–1.85	1.53–1.66	1.47–1.65	1.87	1.57	1.29

similar to the talonid structure of *Peratherium*. But in the lower dentition of *Peratherium*, the hypoconulid forms a horizontal, posteriorly directed ledge directly posterior to the entoconid, and the talonid basin opens posteriorly across the flattened hypoconulid. Moreover, in *Peratherium*, the posterior cingulum is well developed; this cingulum unites lingually to the buccal face of the hypoconulid so that the hypoconulid and the posterior cingulum are a continuous structure. On the other hand, in the present form of *Nanodelphys*, the hypoconulid and the postcristid block the talonid basin posteriorly, and the posterior cingulum does not form a continuous structure with the hypoconulid.

Dr. Larry D. Martin at the University of Kansas (personal communication) informed me that he has several specimens of *Nanodelphys* from the lower Miocene Gering Formation, Nebraska, that are not separable from the present form at the specific level. He has better specimens and he will give the diagnosis of the new species so that I leave the new species unnamed.

Infraclass Eutheria
Order Insectivora
Family Leptictidae Gill, 1872
Leptictis sp.
(Fig. 8, Table 2)

Referred specimens.—M_2: CM 21676.

Locality.—Loc. 19, Badwater Creek, Wyoming.

Age.—Late Oligocene.

Description:—The trigonid is wider transversely than the talonid. The specimen available is worn. Apparently, the paraconid is reduced to crest-like shape and it gives the tooth a more quadrate outline in occlusal view. The apices of the protoconid and metaconid are nearly opposite each other. The hypoconid is stout and the crista obliqua joins to the posterior wall of the trigonid a little buccal to the midpoint of it. The entoconid is small and is situated a little posterior to the hypoconid. Between the metaconid and the entoconid a wide and deep valley opens lingually. On the lingual margin of the floor of the valley, a small cuspule is present.

Discussion.—Only one specimen referable to *Leptictis* is available in the present fauna. *Leptictis* (=*Ictops*) is the most varied and individually the most abundant genus of the family in the White River Oligocene (Scott and Jepsen, 1936:13). *Leptictis* in the present fauna is the youngest occurrence of the genus. But, it is difficult to give the specific identification for this material because the only specimen available is worn.

Family Adapisoricidae (Schlosser, 1887)
Ankylodon sp. cf. **A. annectens** Patterson and McGrew, 1937
(Fig. 9, Table 2)

Referred specimens.—M^1: CM 21675; M^2: CM 17095, CM 33651, CM 33652, CM 33653; M^3: CM 21699; P_4: CM 33654, CM 33655; M_1: CM 33656, CM 33657; M_2: CM 33658; M_3: CM 33659.

Locality.—Loc. 19, Badwater Creek, Wyoming.

Age.—Late Oligocene.

Description.—Material referable to *Ankylodon* is known from the late Eocene to the middle Oligocene. The late Eocene *Ankylodon* is known only from a single M^1, a single M_2, and some fragmentary materials (Krishtalka and Setoguchi, 1975). An excellent, nearly complete palate with complete jaws of both sides is known from the Chadronian. *Ankylodon annectens* (including *A. progressus;* see Krishtalka and Setoguchi, 1975) is known only from the lower dentition.

Like the Chadronian *Ankylodon*, M^2 of the present form is transverse and has a strong hypocone. The paracone is tall and transverse. The metacone is reduced in size and in height when compared with the Chadronian species. The postmetacrista and the metastylar area are also weaker than in the Chadronian form. In relation to these, the posterior wing of the metaconule terminates nearly at the posterior base of the metacone, whereas in the Chadronian specimen the posterior metaconule wing extends along the posterior base of the matacone and joins the posterolingual base of the postmetacrista. The parastylar area expands buccally but it is narrower anteroposteriorly than in the

Table 3.—*Dimensions of teeth of* Centetodon *sp. cf.* C. marginalis *and* Domnina *sp. cf.* D. gradata.

Statistics	P^4		M^1			M^2			P_4		M_1			M_2			M_3		
	L	W	L	AW	PW	L	AW	PW	L	W	L	AW	PW	L	AW	PW	L	AW	PW
Centetodon sp. cf. *C. marginalis*																			
N	1	1		1		1	1	1	2	2				1	1	1	2	2	2
OR	1.69	2.18	—	2.22	—	1.38	2.47	2.27	1.55–1.64	0.88–1.01				1.86	1.21	1.13	1.54–1.66	0.98–1.06	0.80–0.81
Domnina sp. cf. *D. gradata*																			
N	2	2	3	3	3	3	3	3			4	4	4	2	2	2	2	2	2
OR	1.97–1.99	1.98–2.00	1.99–2.08	2.05–2.17	2.15–2.22	1.89–1.97	2.04–2.07	1.80–1.92			2.12–2.20	1.21–1.47	1.31–1.58	1.81–1.96	1.14–1.38	1.16–1.42	1.49–1.52	0.94–0.96	0.80–0.85
Mean			2.043	2.097	2.193	1.920	2.057	1.860			2.170	1.353	1.490						

Chadronian form. In this regard the stylar shelf area is narrower anteroposteriorly than the Chadronian species.

CM 21699 is identified as M^3. The metacone is the only prominent cusp. It is conical and is situated on the middle of the buccal half of the crown. The parastylar area expands anterobuccally but the preparacrista is represented by a weak ridge on the anterobuccal face of the paracone. The stylar shelf is truncated and narrow posteriorly. The metacone is greatly reduced. The protocone forms a triangle with the acute angle lingually. The hypocone is greatly reduced and represented by an enamel crenulation.

P_4 is molariform. It is basially similar in construction with its homologue in *Geolabis*, but is proportionately much shorter and broader. In the Chadronian species of *Ankylodon*, the paraconid is a forward-leaning, short transverse ridge, but it is still a well-defined cusp. In the present form, the paraconid is not a distinct cusp but just an anterior continuation of the anterolingual ridge of the protoconid, which lingually slopes sharply ventrad. The protoconid is taller than the metaconid. The metaconid is elongated lingually so that the protoconid and the metaconid are more widely separated from each other than in the Chadronian species and the Orellan *Ankylodon annectens*. A short weak anterior cingulum is present on the anterior face of the protoconid. The talonid structure agrees exactly with that of the Chadronian species and the Orellan *A. annectens*.

On M_1, the trigonid is a little narrower transversely than the talonid as in the Orellan *A. annectens*, whereas the former is clearly narrower than the latter in the Chadronian form. No cingula are present at all. The metaconid is taller than the protoconid as in the other forms of *Ankylodon*. The talonid is shorter than that in the Orellan *A. annectens* and more so than the Chadronian form. No trace of the hypoconulid is present whereas a rudimentary hypoconulid is clearly present in the Chadronian and the Orellan forms. The entoconid is taller than the hypoconid as in the other forms of *Ankylodon*, but the difference in height between the metaconid and the entoconid is more exaggerated in the present form than in the Orellan form and more so than in the Chadronian form. The notch between the metaconid and the entoconid is deeper than in any other forms of *Ankylodon*.

CM33658 is identified as M_2 because the trigonid is slightly wider transversely than the talonid. No cingula are present. The talonid is narrower anteroposteriorly than in the other members of this genus, and the crista obligua is concave. No trace of the hypoconulid is seen, whereas in the late Eocene form there is a distinct hypoconulid. The notch between the metaconid and the entoconid is also deep, whereas in the late Eocene species the entocristid joins these two cusps and closes the talonid basin lingually.

On M_3, the talonid is narrower transversely than the trigonid. The hypoconulid is present although rudimentary.

Discussion.—The present form is clearly different from the Chadronian species in having a more reduced parastyle and narrower stylar area on the upper molars, more reduced paraconid, no cingulum, deeply separated metaconid and entoconid with the former clearly taller than the latter, and transversely narrower talonid. In these respects, the Orellan *Ankylodon annectens* is intermediate between these two forms. The differences between the present form and the Chadronian species cited above are more clearly exaggerated if my material is compared with the late Eocene form. The present material is more advanced or specialized than either the late Eocene or the Chadronian species. But the distinguishing features listed above, or the morphological differences between the present form and the Orellan *A. annectens*, seem minor and possibly are within the range of usual variation within a species.

Family Geolabididae (McKenna, 1960)

Centetodon sp. cf. **C. marginalis** (Cope, 1874)

(Fig. 10, Table 3)

Referred specimens.—P^4: KU 16606; M^1: CM 33661; M^2: CM 33662; P_3: CM 21673; P_4-M_2: CM 33663; P_4: CM 21674, CM 33664; M_2-M_3: CM 21672, M_3: CM 33665, CM 33666.

Locality.—Loc. 19, Badwater Creek Wyoming.

Age.—Late Oligocene.

Description.—The structure of P^4 closely resembles that in *Centetodon marginalis* and *C. chadronensis* (Lillegraven and McKenna, manuscript). A small anterior lingual cingulum is present on the anterolingual base of the protocone. The width

of this cingulum is almost half that of posterior cingulum. The anterior lingual cingulum is not present on the Chadronian *Cententodon chadronensis,* but on *C. marginalis* a small anterior cingulum is present on the base of the anterior face of the protocone. It is widely separated from the posterior cingulum. On the present form, the anterior lingual cingulum is shifted more lingually and almost united with the posterior cingulum along the base of the lingual face of the protoconid. In this connection, the lingual base of the crown of P^4 is wider anteroposteriorly than in *Centetodon chadronensis* and *C. marginalis*. The posterior cingulum has a slight elevation on the posterolingual base of the protocone and a low, small cingulum runs anteriorly along the lingual base of the protocone. That elevation is more buccal on *C. marginalis* and directly posterior to the protocone on *C. chadronensis*. The lingual root is not bifurcated on the material at hand.

Distinctions in the upper molars between *Centetodon marginalis* and my specimens are minor. A tendency toward a deeper labial emargination of the stylar shelf on M^2 is observed in this form, but the general morphology is essentially the same as in *C. marginalis*.

P_4 is a large semimolariform tooth and its structure is exactly the same as the corresponding tooth of *Centetodon marginalis*. Moreover, there are no really obvious morphological differences on lower molars between *C. marginalis* and the present specimens). The mental foramen is below the posterior root of P_3.

Discussion.—The general morphology of my material is essentially the same as that of *Centetodon marginalis*. The only obvious difference is in the degree of the development of the anterior lingual cingulum on P^4. The anterior lingual cingulum is more developed in the present form than in *C. marginalis*. Lillegraven and McKenna (Manuscript) clearly describe the evolutionary sequence of *Centetodon chadronensis–C. marginalis*. In *C. chadronensis* there is no anterior cingulum on P^4, but a small anterior cingulum is usually present on the base of the anterior face of the protocone in *C. marginalis*. Even in the latter form, the anterior cingulum is widely separated from the posterior cingulum at the lingual margin of the protoconid. In the present form, the anterior cingulum is shifted more lingually and closer to the posterior cingulum. This is just a continuation of the sequence toward better development of the anterior cingulum on P^4 in the *Centetodon chadronensis–C. marginalis* lineage. The present form is surely in this lineage and is descended from the Orellan *C. marginalis*.

A new species of *Centetodon terminalis* will be described by Lillegraven and McKenna (manuscript). The materials referred to the new species were originally discussed by Martin (1972) from the lower Miocene Gering Formation of Nebraska. This form is known only from P_4 and M_1. Morphologically, however, it shows no obvious differences from homologous teeth of *C. marginalis* except for their size. The size of the tooth suggests an animal significantly larger than *Centetodon marginalis* yet smaller than *C. wolffi*. The trends in proportional changes seen in the transition from *C. chadronensis* to *C. marginalis* seem to continue into *C. germinalis*. The size of the present form, which is intermediate between *C. marginalis* and *C. terminalis*, supports this hypothesis.

Family Soricidae (Fischer von Waldheim, 1817)
Domnina sp. cf. **D. gradata** Cope, 1873
(Fig. 11, Table 3)

Referred specimens:—P^4-M^1: CM 33667; CM 21662, CM 33668, CM 33669; M^1: CM 21663, DM 33670, DM 33671, DM 33672; M^2: CM 33673, CM 33674, CM 33675, CM 33676, CM 33677; P_1-P_3, M_1: CM 33678; M_1-M_3: CM 33679; M_1: CM 21664, CM 33680, CM 33681, CM 33682, CM 33683, CM 33684; M_2-M_3: CM 33685; M_2: CM 21665, CM 33686; M_3: CM 33687.

Locality.—Loc. 19, Badwater Creek, Wyoming.

Age.—Late Oligocene.

Description.—P^4 has a tall paracone that tapers posterobuccally to the metastylar tip of the crown. The anterior wall of the paracone is very steep as in the other species of *Domnina*. A low parastyle runs anteriorly from the base of the paracone. The protocone is weak. The hypoconal shelf expands posteriorly, unlike the condition in *Trimylus*.

M^1 lacks an emargination of the posterior border of the crown and the hypoconal shelf expands posteriorly. Accordingly, the crown is quadrate in occlusal view; rather longer than wide, whereas in *Trimylus* M^1 is wider than long. M^2 approaches M^1 in general morphology except for a wider paracone and smaller hypocone. M^2 lacks an emargination of the posterior border of the crown.

P_1 is longer and wider than either P_2 or P_3. Low r molars have a high entocristid, which joins the ento onid to the posterior face of the metaconid and closes the talonid basin lingually. On M_1, the anterior cingulum runs along the ant rior base of the paraconid and along the anterobuccal base of the protoconid. The buccal cingulum runs posteriorly from the buccal base of

→

Fig. 9b–e.—*Ankylodon* sp. cf. *A. annectens* (continued). b: CM 21699, left M^3. c: CM 33654, left P_4. d: CM 33658, right M_2. e: CM 33659, left M_3. ×8. Fig. 10.—*Centetodon* sp. cf. *C. marginalis*. a: KU 16606, left P^4,×8. b: CM 33662, right M^2,×8. c: CM 33663, left P_4-M_2,× 10. d: CM 21672, left M_2-M_3, ×10. Fig. 11.—*Domnina* sp. cf. *D. gradata*. a: CM 33667, left P^4-M^1. b: CM 33673, left M^2. c: CM 33678, left P_1-P_3, M_1. d: CM 33685, left M_2-M_3. ×8. Fig. 12.—*Proscalops miocaenus*. a: CM 33688, left M^1. b: CM 33690, left M^2. c: CM 33694, left M_1. d: CM 33696, left M_2. ×8.

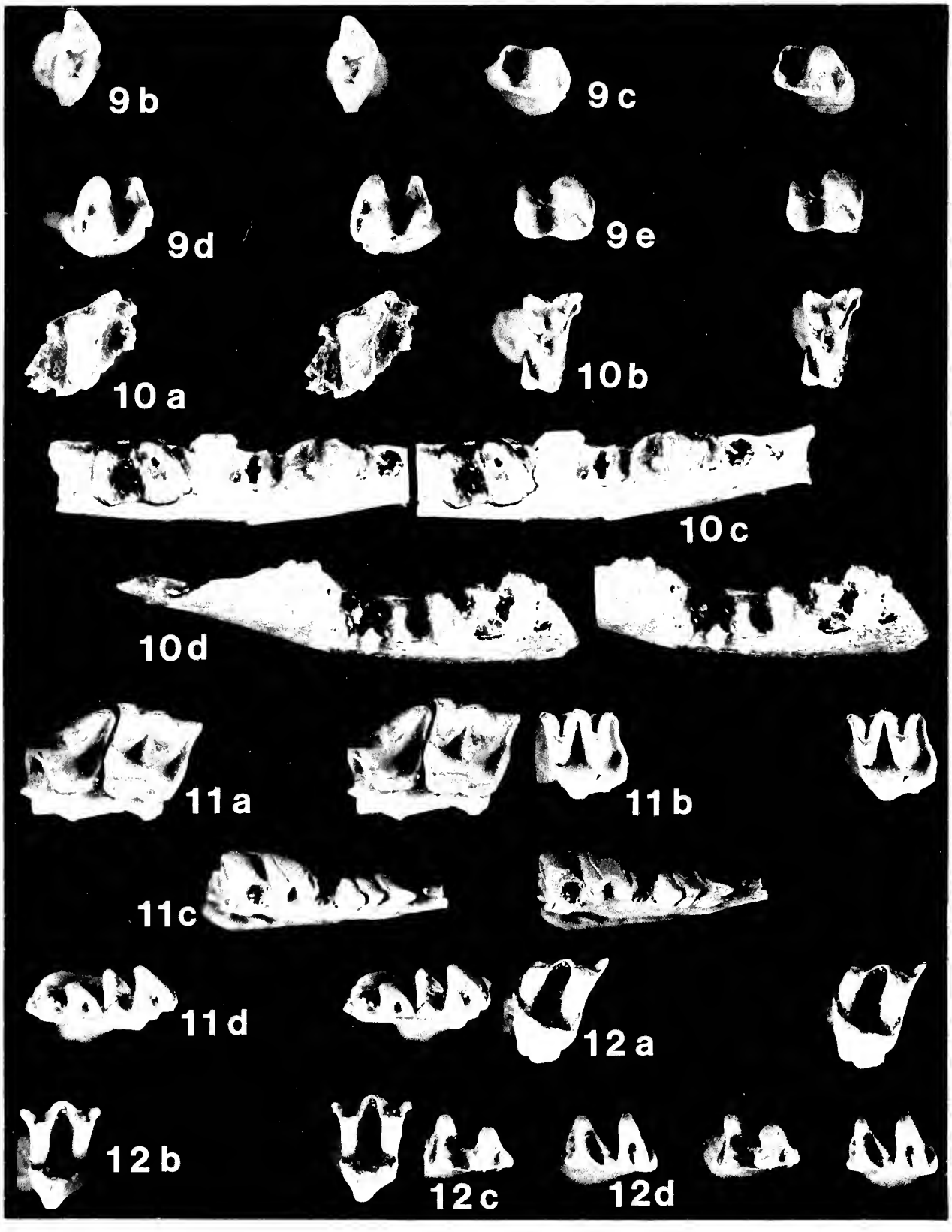
9b
9c
9d
9e
10a
10b
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Table 4.—*Dimensions of teeth of* Proscalops miocaenus, Oligoscalops *? sp., and* Micropternodus *sp.*

Statistics	M^1			M^2			M^3			M_1			M_2			M_3		
	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW
Proscalops miocaenus																		
N	2	2	2	2	2		1	1		4	4	4	1	1	1			
OR	2.02–2.37	1.99–2.05	2.67–2.78	1.76–1.96	2.31*–2.53*		1.41	1.77	—	1.79–2.06 1.905	1.02–1.10 1.075	1.34–1.46 1.405	2.18	1.41	1.30			
Oligoscalops ? sp.																		
N													1	1	1			
OR													1.62	1.17	1.03			
Micropternodus sp.																		
N																	1	
OR																—	1.23	—

* Width at the mesostyle.

the protoconid. On five of the six M_1s, the anterior cingulum does not unite with the buccal cingulum although they are very close together. On one specimen, these cingula are united along the buccal base of the protoconid, although the cingula are very weak there. The labial cingulum is very weak along the buccal base of the hypoconid.

The mental foramen is below the middle of M_1.

Discussion.—Patterson and McGrew (1937) and Repenning (1967) have thoroughly described *Domnina gradata* from the Orellan of Colorado, South Dakota, and Nebraska. In the absence of preserved mandibular condyles or the antemolar dentition, *Domnina,* as well as all other heterosoricines, is best defined by P^4 and M^1 that lack an emargination of the posterior border of the crown and the resultant posterior expansion of the hypoconal shelf. Istead, the posterior margin of P^4 and M^1 of *Domnina* is nearly straight or expands a little posteriorly and the crown is longer than wide, especially on M^1. In relation to the non-bulbous feature of P_4 and M_1 in *Domnina* (in *Trimylus,* lower molars are bulbous), P^4 has a tall paracone and the anterior wall of the cusp is very steep, whereas that in *Trimylus* forms a more gentle slope. Such is the case for P^4 and M^1 in this sample.

The lower molars referred here are very similar to those of *Domnina* and differ from those of *Trimylus* in that a high crest joins the ntoconid to the posterior face of the metaconid and closes the talonid basin lingually. In *Trimylus* a deep notch isolates the entoconid from the metaconid (Repenning, 1967). The anterior cingulum anterobuccal to the protoconid on M_1 is a little more developed than in the Orellan *Domnina gradata.* In the latter form, the buccal cingulum on M_1 is not continuous around the base of the protoconid. In the present form, this feature of the cingula approaches being continuous around the base of the protoconid.

The early Miocene *D. greeni* is not well known. In the original description, Macdonald stated (1963:168), "Labial cingulum on anterior labial face of trigonid only." In the present form, the buccal cingulum buccal to the hypoconid is reduced. The present form may have given rise to *D. greeni.*

Family Talpidae Gray, 1825

Proscalops miocaenus Matthew, 1901

(Fig. 12, Table 4)

Referred specimens.—M^1: CM 33688, CM 33689; M^2: CM 33690, CM 33691; M^3: CM 33692; M_1: CM 21668, CM 33693, CM 33694, CM 33695; M_2: CM 33696.

Locality.—Loc. 19, Badwater Creek, Wyoming.

Age.—Late Oligocene.

Description.—The size of the teeth is close to that of the holotype of *Proscalops miocaenus.* On M^1, the protocone is V-shaped with an apex which is oriented anterolingually. The anterior arm of the protocone runs anterobuccally and soon turns buccally. In continues to run along the anterior face of the paracone and connects to the parastyle. The anterior face of the anterior protocone arm has a small anterior projection at the midpoint between the protocone and the paracone. This small projection is what Reed called the protostyle (Reed, 1961:487). A small, but distinct hypoc ne is present posterior to the protocone. Thus, the lingual portion of the tooth is somewhat broader. The paracone is smaller than the metacone. The former is blade-like running rather posterobuccally, whereas the latter is V-shaped. The posterior arm of the metacone is longer than the anterior arm. The former extends posterobuccally and connects to the metastyle which forms the posterobuccal corner of the crown. Thus, the buccal portion of the crown is truncated an-

teriorly so that the anterior portion is narrower transversely than the posterior one. A small mesostyle is present near the midline on the buccal border of the crown.

On M^2, the anterior arm of the protocone terminates at the base of the anterior face of the paracone. It does not extend buccally beyond the point of the apex of the paracone so that it appears to be shorter anteroposteriorly. As in M^1 a small "protostyle" is present on the anterior arm of the protocone, and a small hypocone is also present posterior to the protocone. The protocone is more acutely V-shaped than in M^1, and the apex is oriented more mesially. The paracone and the metacone are subequal, forming acute V's. The parastyle and the metastyle are also subequal. A robust mesostyle lies on the middle of the buccal border of the crown. Thus, the buccal part of the crown is symmetrical.

M^3 is reduced. The general morphology agrees with that of M^2 although M^3 is smaller than M^2. The portion posterobuccal to the anterior arm of the metacone is completely truncated so that the posterior arm of the metacone and the metastyle are not present. The mesostyle is also reduced in size. The paracone is wider buccally than in M^1.

On M_1, the trigonid is narrower transversely than the talonid. The protoconid is the tallest of the cusps on the trigonid. The protoconid is elongated transversely and forms a V with the apex buccal. The paraconid is the lowest of the trigonid cusps and is situated anterior to the anterior face of the protoconid. The metaconid is situated posterior to the posterior face of the protoconid. Thus, the lingual side of the trigonid is wide anteroposteriorly while the protoconid itself is compressed anteroposteriorly. A rudimentary anterior cingulum is present on the anterobuccal base of the paraconid. The hypoconid is elongated transversely. The crista obliqua extends anterolingually and connects to the posterobuccal corner of the metaconid. The buccal face of the crista obliqua is very steep and the hypoflexid is very deep. The median cingulum is not present between the protoconid and the hypoconid, as in *Mesoscalops*. The entoconid is conical. A transverse ridge unites the hypoconid and entoconid. No entocristid is present between the entoconid and the metaconid so that the talonid basin opens lingually. A rather well-developed posterior cingulum is present on the posterior base of the talonid.

CM 33969 is identified as M_2 of this species. The trigonid is a little wider transversely than the talonid. The lingual part of the trigonid is narrower anteroposteriorly than in M_1. The protoconid is also compressed anteroposteriorly as in M_1, but the paraconid is merely a lingual extension of the anterior arm of the protoconid. The anterior cingulum is wide lingually and descends buccally to the base of the anterior face of the protoconid. The metaconid is elongated anteroposteriorly and has a small notch on its buccal face. The almost transverse posterior arm of the protoconid connects to the midpoint of the elongated metaconid, forming an anterior wall with a notch on the buccal face of the metaconid. The hypoconid is compressed anteroposteriorly. The crista obliqua reaches to the posterobuccal corner of the metaconid, posterior to the notch of the metaconid mentioned above. Thus, the crista obliqua does not connect to the trigonid proper but to the posterior extention of the metaconid. The remainder of the features are almost identical to those of M_1.

Discussion.—The lower molars of the present form do not have a median cingulum between the protoconid and the hypoconid, as do those of *Mesoscalops*. *Oligoscalops* is best defined by P^4 that has a large parastylar area, whereas the corresponding tooth of *Proscalops* lacks a parastylar area. In the present fauna, no materials referable to P^4 are available. In her original description of *Oligoscalops*, Reed stated (Reed, 1961:486–487), "M^1 in *Oligoscalops* is triangular in general outline, with the protocone directed anteriorly. The hypocone is rudimentary, a mere protuberance labial and posterior to the protocone . . . . In *Proscalops miocaenus* the tooth is generally similar, although the hypocone is somewhat better developed and the lingual portion of the tooth therefore somewhat broader. A rudimentary protostyle is present." M^1 of the present form has the small "protostyle," better developed hypocone, and the broader lingual portion of the crown. This form does not belong within the genus *Oligoscalops*. According to Reed (Reed, 1961:487), in *Proscalops tertius* and *P. secundus*, the hypocone is better developed on M^1 than in *P. miocaenus*. The degree of development of the hypocone on M^1 of the present form is close to that in *P. miocaenus*.

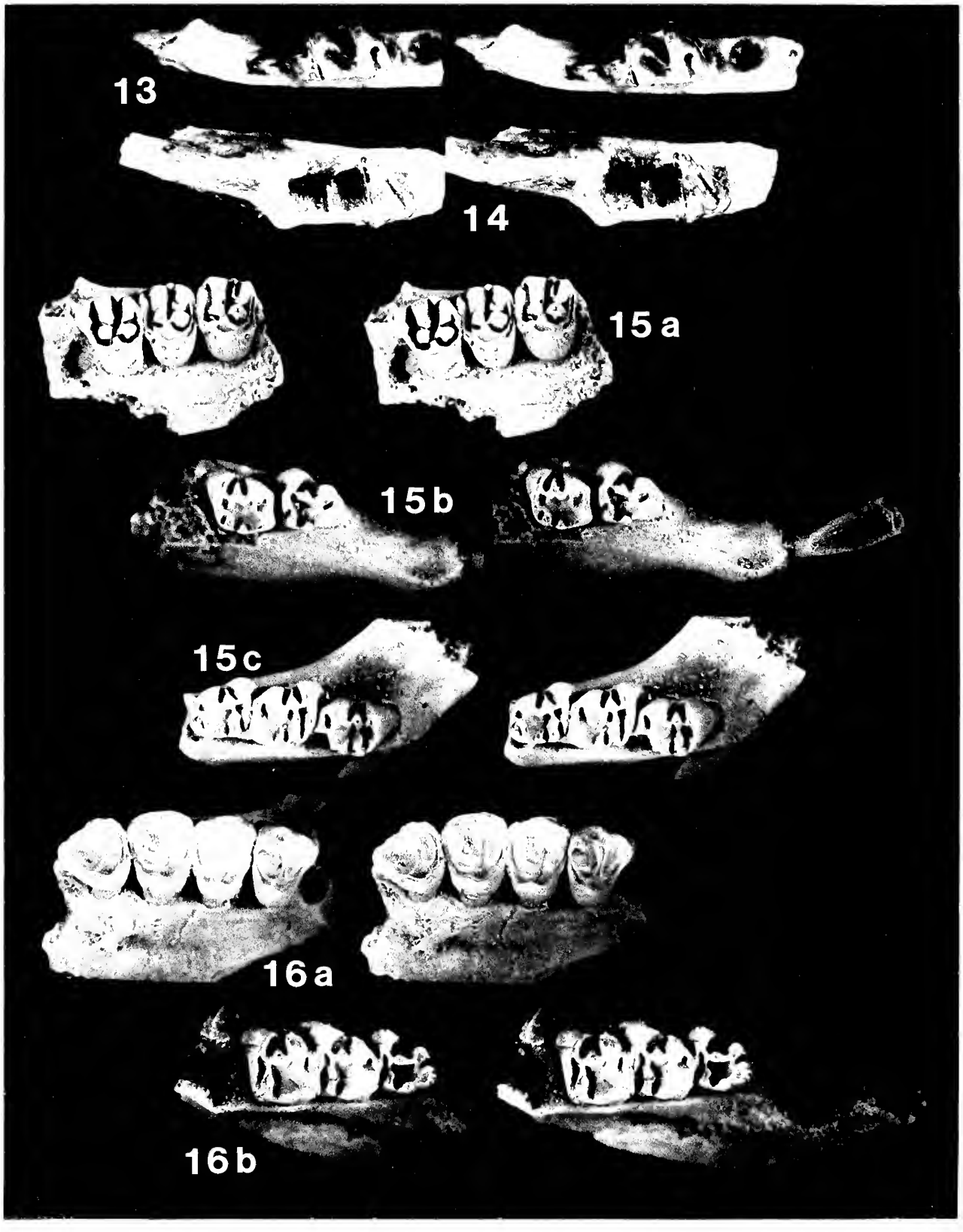
Oligoscalops ? sp.
(Fig. 13, Table 4)

Referred specimen.—CM 17441, a left ramus with M_2.

Locality.—Loc. 19, Badwater Creek Wyoming.

Age.—Late Oligocene.

Description.—M_2 is small. The size of the tooth is smaller than that of *Proscalops miocaenus*. The trigonid is narrow anteroposteriorly. The protoconid is elongated transversely and the paraconid forms a transverse ridge at a slightly worn stage. The paraconid does not reach to the lingual extremity of the base of the trigonid, leaving a shelf lingual to it. On this specimen, the metaconid is broken and only the base of it remains. The base of the metaconid is longer transversely than that of the paraconid reaching the lingual border of the trigonid. A rather broad anterior cingulum is present at the base of the anterior face of the trigonid, and the lingual extension of the cingulum surrounds the anterolingual base of the paraconid and continues to run posteriorly to connect to the anterolingual base of the metaconid. The talonid is a little narrower than the trigonid. The hypoconid is compressed anteroposteriorly. The crista obliqua runs anterolingually and connects to the trigonid at a point one-third of the way from the lingual side on the posterior wall of the trigonid. The hypoflexid is deep. The entoconid is conical and situated on the posterolingual corner of the tooth. A transverse ridge unites the posterior corners of the hypoconid and the entoconid. A small anteroposteriorly elongated metastylid is situated on the lingual border between the metaconid and the entoconid. The metastylid conpletely blocks the talonid basin lingually. The hypoconulid is very low, situated just posterior to the entoconid. The posterior cingulum is rudimentary.


13
14
15a
15b
15c
16a
16b

Discussion.—*Oligoscalops* is smaller than *Proscalops miocaenus*. *Oligoscalops* was established by Reed (1961), and a new species *O. whitmanensis* was regarded as the smallest known member of the Proscalopinae. She gave the diagnosis for the upper dentition of this new form but did not describe the morphology of the lower dentition. The holotype is CM P 25800, partial skull and jaws, but a lower jaw with P_2-M_3, KU 8143 is included in the hypodigm by her. In her discussion, she stated (Reed, 1961:488), "(In the Kansas specimen) In M_1 the talonid is wider than the trigonid, judging from the fragments that remain, and the opposite is true of M_2." In the measurements of the new form, she gave the trigonid and talonid width of M_2 of the Kansas specimen as 1.7 and 2.1 mm, respectively. According to the measurements given by her, the talonid is wider than the trigonid.

Family Micropternodontidae Stirton and Rensberger, 1964

Micropternodus sp.

(Fig. 14, Table 4)

Referred specimen.—Mandible with M_3.

Locality.—Loc. 19, Badwater Creek, Wyoming.

Age.—Late Oligocene.

Description and discussion.—Only one lower jaw with M_3 and the posterior part of the ramus is available. On M_3, the tip of the paraconid and the lingual half of the talonid are broken off. The tooth is somewhat worn. The trigonid is transverse and compressed anteroposteriorly. The metaconid is taller than the protoconid. The protoconid is acutely V-shaped with its apex buccally. The anterior cingulum is developed along the anterior base of the trigonid. This cingulum is narrower buccally, terminates at a point anterior to the protoconid, and does not reach to the buccal face of this cusp. Lingually, the anterior cingulum becomes broader and its lingual extremity reaches to the lingual base of the paraconid. Thus, the cingulum surrounds the anterolingual base of the paraconid. The hypoconid is also V-shaped with its apex buccal. The hypoconid is lower than the protoconid. The crista obliqua does not connect to the protoconid nor to the protolophid; instead, it runs directly anterolingually to connect to the metaconid. This characteristic feature is also seen in M_3 referable to *Micropternodus borealis* where the hypo onid is connected to the metaconid by a crest (Russell, 1960:945). Because of the lingually extended crista obliqua, the hypoflexid is long transversely. The hypoflexid slopes down buccally. Because the lingual portion of the talonid is broken, it is impossible to tell whether or not the hypoconulid is present on M_3.

The coronoid process of the mandible is rather slender. The anterior face of the coronoid process is almost perpendicular to the occlusal plane or leans somewhat anteriorly.

The present form is identified as *Micropternodus* sp. because of the similarity of the talonid structure to that of *M. borealis* of the early Oligocene. The present sample is not sufficient to warrant specific identification.

Order Rodentia

Family Aplodontidae Trouessart, 1897

Prosciurus relictus (Cope, 1873)

(Fig. 15, Table 5)

Referred specimens.—P^3-M^1: CM 33262, P^3-M^3: CM 33261; P^4-M^1: CM 19714, CM 33266; P^4-M^2: CM 33263–33265; P^4-M^3: CM 17078; P^3: CM 33276; DP^4: CM 33268–33275; P^4: CM 17405, CM 17408, CM 17410, CM 33277–33305; M^1-M^2: CM 33267; M^1 or M^2: CM 17406, CM 19793, CM 33306–33379; M^3: CM 17089, CM 17094, CM 33380–33403; P_4-M_1: CM 19791, CM 33122–33124; P_4-M_3: CM 33121; DP_4: CM 33133–33137; P_4: CM 17076, CM 17409, CM 33138–33158; M_1-M_3: CM 33125–33128; M_2M_3: CM 33129–33132; M_1 or M_2: CM 17403, CM 33159–33220; M_3: CM 17077, CM 17404, CM 19794, CM 33221–33260.

Locality.—Loc. 19, Badwater Creek, Wyoming.

Age.—Late Oligocene.

Description.—P^3 is peglike. The apex of the cusp is shifted slightly anteriorly and a small ridge descends posteriorly from the apex.

DP^4 is identified on the basis of its tiny size and the similar tooth structure to that of P^4 referable to this species. In both the parastylar lobe extends anterobuccally and a small, but distinct, cusp is formed on its anterior border. This cusp is lower than the protoconule. The cusp lies lingual to the metacone-paracone line and the distance between the parastylar cusp and the paracone is nearly the same as that between the paracone and the metacone. The transverse valley between the parastylar eusp and the protoloph opens more widely in DP^4 than in P^4. The

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Fig. 13.—*Oligoscalops* ? sp. CM 17441, left M_3. ×10. Fig. 14.—*Micropternodus* sp. CM 17442, left M_3. ×10. Fig. 15.—*Prosciurus relictus*. a: CM 33263, left P^4-M^2. b: CM 19791, left P_4-M_1. c: CM 33126, right M_1-M_3. ×7. Fig. 16.—*Pelycomys placidus*. a: CM 33101, right P^4-M^3. b: CM 19792, left P_4-M_2. ×5.

Table 5.—*Dimensions of teeth of* Prosciurus relictus.

Statistics	DP^4		P^4		M^1		M^2		M^1 or M^2	
	L	W	L	W	L	W	L	W	L	W
N	8	8	25	25	7	7	6	6	43	43
OR	1.48–1.66	1.42–1.73	1.36–1.95	1.63–2.30	1.39–1.62	1.91–2.17	1.44–1.69	1.82–2.14	1.33–1.83	1.64–2.32
Mean	1.554	1.623	1.728	1.943	1.543	2.021	1.567	1.982	1.610	2.000
SD	0.061	0.096	0.150	0.219	0.088	0.111	0.116	0.135	0.114	0.154
CV	3.29	5.92	8.70	11.28	5.72	5.47	7.41	6.83	7.06	7.70

	DP_4			P_4			M_1			M_2			M_1 or M_2		
	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW
N	5	5	5	20	19	20	7	6	7	7	7	7	47	47	47
OR	1.38–1.54	0.85–0.98	1.31–1.48	1.33–1.91	0.88–1.49	1.30–1.97	1.50–1.83	1.36–1.61	1.54–1.80	1.63–1.97	1.46–1.80	1.60–1.95	1.38–1.94	1.25–1.74	1.50–2.07
Mean	1.464	0.914	1.370	1.631	1.186	1.638	1.703	1.480	1.697	1.794	1.624	1.796	1.739	1.514	1.740
SD	0.074	0.054	0.076	0.162	0.165	0.157	0.116	0.097	0.102	0.151	0.132	0.143	0.117	0.118	0.129
CV	5.08	5.92	5.56	9.94	13.88	9.57	6.84	6.58	6.03	8.43	8.14	7.95	6.73	7.77	7.41

floor of the lingual half of the valley is much lower than that between the protoloph and the metaloph. A short ridge descends posterolinguad from the parastylar cusp but no connecting ridge is seen between the parastylar cusp and the protocone so that the valley anterior to the protoloph opens lingually unlike P^4. The structure of the protocone is similar to that of P^4. The protoconule is smaller and lower than the metaconule, and both of them are smaller and lower than the subequal paracone and metacone. The protoloph is low in position and extends almost transversely, and the protoconule is formed on its anterior face between the protocone and the paracone. The paracone is elongated transversely. The metaloph is also low in position and extends posterobuccally so that the valley between the protoloph and the metaloph becomes wider buccally. This valley is rather wide and U-shaped, not V-shaped as in P^4. The metaconule is formed on the posterior face of the metaloph. Both the protoconule and the metaconule are connected to the protocone by weak ridges. No hypocone is formed and the posterior cingulum is weak. The tooth is three rooted; the root underneath the protocone is the largest. This root is elongated trasversely and its buccal margin reaches to the protoconule-metaconule line. The root extends slightly lingually. Two roots are on the buccal base of the tooth. The anterior root is larger and occupies the bases of the parastylar lobe and the anterior half of the paracone. This root is elongated anteroposteriorly and extends anterobuccally. This third root is just underneath the metacone and extends slightly buccally. The cross section of the root is rounded. These three roots are not close together but open widely. This is another reason why these teeth are identified as DP^4.

P^4 and molar structures are almost the same as those described by Galbreath (1953). On all cheek teeth, a single metaconule is present.

The lower jaw is relatively longer than that of *Pelycomys*. The anterior face of the incisor is flat rather than rounded as in *Pelycomys* and the external face is flat as well. The posterior face is rounded and narrow so that the tooth is narrower posteriorly.

DP_4 is also identified on the basis of its tiny size, its similarity to P_4, and widely open roots. The protoconid is lower than the metaconid but is wider anteroposteriorly. Both metalophis I and II are complete although they are low in position, and block the trigonid basin anteriorly and posteriorly. The mesoconid is distinct and as high as the entoconid. The ectolophid is not conspicuous but forms an acute edge between the talonid basin and the valley between the protoconid and the hypoconid. No mesolophid is seen. The hypoconid is at the posterobuccal corner of the tooth and is greatly compressed anteroposteriorly; the anterior face is vertical. The hypoconid is separated from the posterolophid by a deep notch. The posterolophid is a tall, transverse blade high above the bottom of the talonid basin. The entoconid is separated from the posterolophid by a small notch. The hypolophid runs buccally from the entoconid and soon turns posteriorly to unite to the anterior face of the posterolophid. The hypolophid does not extend to the ectolophid. The hypolophid, entoconid, and posterolophid share a common base, which raises high above the bottom of the talonid basin. The mesostylid is inconspicuous, and between it and the entoconid is a deep notch, which runs transversely from the talonid basin. The metastylid crest is not present.

The other cheek teeth are very close to those described by Wood (1937) and discussed by Galbreath (1953).

Discussion.—The Badwater specimens are almost identical to Orellan *Prosciurus relictus*. *Prosciurus* is the best represented of several genera of closely related rodents of the Prosciurinae. The subfamily Prosciurinae has been regarded as a member of the family Ischyromyidae (as that group is defined by Black, 1971:181) or the Paramyidae (Wood, 1955:171; Wood, 1962:226). A slight variation in the classification is presented by Wood (1973), in which the Prosciuridae is considered a separate family.

Recently, Rensberger (1975) transferred the Prosciurinae from the Ischyromyidae or Paramyidae to the Aplodontidae. The aplodontid taxa are segregated as Prosciurinae, Allomynae, and Aplodontinae. I agree with him. Here, *Prosciurus* and *Pelycomys* are treated as members of the Aplodontidae.

Pelycomys placidus Galbreath, 1953
(Fig. 16, Table 6)

Referred specimens.—P^4-M^3: CM 33101; P^4: CM 33102, CM 33103; M^1 or M^2: CM 33104, CM 33105; M^3: CM 33106, CM 33120; P_4-M_2: CM 19792; M_2: CM 17042; M_3: CM 33107, CM 33108.

Locality.—Loc. 19, Badwater Creek, Wyoming.

Age.—Late Oligocene.

Description.—The lower jaw is relatively deeper and shorter than that of *Prosciurus relictus*. The incisor is characterized by greater compression laterally than in *Prosciurus*. The internal face of the incisor is flat, the anterior face is rounded, and the external face is gently curved toward the posterior border of the internal face, as Galbreath (1953) described.

The lower cheek teeth are subtriangular to subrhombic in shape. On P_4, the principal cusps are rounded and large. The trigonid is elongated transversely. The protoconid is tall and somewhat compressed anteroposteriorly. The metaconid is the tallest of the principal cusps. It lies on the anterolingual corner of the tooth. Metalophulid I is absent and the protoconid and the metaconid are separated by a deep notch, which runs anterobuccal from the posterobuccal base of the metaconid. Metalophulid II is very weak but present and unites the protoconid and the metaconid posteriorly. The mesostylid is tiny and low in position. The metastylid crest runs downward and posteriorly from the metaconid, and unites with the mesostylid. The mesoconid is small and rounded. The buccal mesolophid is absent so that a wide valley opens buccally between the protoconid and the hypoconid. The entolophid is a rather wide ridge and descends posteriorly from the posterolingual corner of the protoconid. The ectolophid, posterior to the mesoconid, turns posterobuccal and unites with the lingual corner of the transeversely elongated hypoconid. The hypoconid is stout forming the posterobuccal corner of the tooth. The posterolophid is prominent. It unites with the posterolingual corner of the hypoconid but does not unite with the entoconid. The entoconid is rather small but is a distinct cusp, which is higher than the mesoconid. The hypolophid runs buccally from the entoconid and turns slightly posteriorly and joins the ectolophid between the hypoconid and the mesoconid. The lingual half of the hypolophid is wide and the anterior slope is more gentle than the posterior one so that the basin between the hypolophid and the trigonid becomes narrower transversely. The buccal half of the hypolophid is thin and low. A distinct transverse valley separates the hypolophid from the posterolophid. The entoconid is separated from the mesostylid by a deep notch.

M_1 has a complete metalophulid I, which runs anterad from the protoconid and soon turns linguad. The metalophulid II is also complete but lower than the metalophulid I. A basin is formed on the trigonid between the metalophulids, and the protoconid and the metaconid. The mesoconid has a tiny buccal mesolophid and tends to divide the valley between the protoconid and the hypoconid into two parts. The hypolophid is wider than on P_4 and runs buccally. The buccal ends connects to the ectolophid posterior to the mesoconid; near the buccal end it becomes narrower. The basin between the hypolophid and the trigonid is deeper than on P_4 and the notch which separates the entoconid from the mesostylid is also deeper than in P_4.

M_2 agrees with M_1 in general morphology. The mesoconid is more prominent than in P_4 and M_1. The mesoconid itself divides the valley between the protoconid and the hypoconid into two parts; the posterior part is wider than the anterior part. The ectolophid posterior to the mesoconid runs posteriorly and slightly lingually, and turns posterobuccally. The buccal slope is gentle so that the valley between the mesoconid and the hypoconid is long transversely in an unworn stage but becomes shorter with wear. The posterolophid is also prominent and tends to have a distinct cusp near its union with the hypoconid. The hypolophis is taller than in M_1 and connects to the ectolophid more posteriorly than in M_1. The basin between the hypolophid and the trigonid is more widely open than in P_4 and M_1.

On M_3, the protonid is low but the metaconid is high. Although the metalophulid I is complete, the metalophulid II is incomplete on the metaconid side. The basin between the metalophulids is wider than in M_1 and M_2, and opens posterolinguad. The talonid basin becomes wider and the difference in height between the talonid basin and the trigonid is reduced. The mesoconid is large and divides the valley between the protoconid and the hypoconid into two parts. The hypoconid is massive and its buccal arm extends anteriorly to the protoconid enclosing the large mesoconid buccally. The entoconid is distinct but the hypolophid is weakened. The hypolophid runs posterobuccally making the talonid basin wider. The valley between the posterolophid and the hypolophid is wider and deeper than in the rest of the cheek teeth.

A maxilla and a few isolated teeth are tentatively assigned to this species. The size of these agrees with that of the lower teeth of the species. They are not associated with any lower jaws so that whether or not they are referable to *Pelycomys* remains uncertain, as only lower cheek teeth of *Pelycomys* are known. On P^4, the parastyle is prominent. The protocone is elongated anteroposteriorly. The protoconule and the metaconule are subequal, but only the former connects to the the protocone by the thin protoloph. After heavy wear, the metaconule will unite with the protocone. The posterior crest of the protocone runs posterad and continues to run transversely as the posterior cingulum. Near the union of the posterior crest with the posterior cingulum, a small hypocone is present. The metaloph unites the metacone and the metaconule on their anterior side. A tiny but distinct mesostyle is present between the paracone and the metacone on the buccal border of the tooth.

All the specimens referable to M^1 and M^2 are heavily worn. A parastyle seems to be present on the buccal end of the anterior cingulum. The posterolingual corner of the tooth extends linguad indicting the presence of the hypocone.

M^3 is triangular in shape. The anterior crest of the protocone is heavy. The buccal end of the anterior cingulum has a wide base. The paracone is elongated anteroposteriorly. The protoconule is tiny and situated just between the protocone and the paracone. The protoconule connects to the protocone by a ridge. The basin between the protoloph and the anterior cingulum is wide. Posterior to the protoloph is a broad basin. Only a tiny metaconule is present and it is completely isolated. The posterior crest of the protocone, the posterior cingulum, and the buccal cingulum surround the basin.

Discussion.—The present form differs from *Prosciurus* in having the following morphology: incisors are laterally compressed; on lower cheek teeth, metalophulid II is essentially complete; hypolophulid is well developed and separated from the posterolophid. These are the diagnostic features of *Pelycomys*.

Galbreath (1953) recognized two species of *Pelycomys*—*P. rugosus*, the type species, and *P. planidus*. *P. planidus* differs from *P. rugosus* in having narrower trigonids, better developed mesoconids, and weaker and lower metalophulid II than metalophulids I.

The Badwater specimens are almost identical to *Pelycomys planidus*.

Family Eomyidae Deperet and Douxami, 1902

Adjidaumo douglassi Burke, 1934

(Fig. 17, Table 6)

Referred specimens.—M^1 or M^2: CM 33702, CM 33703; P_4-M_1: CM 33697; P_4: CM 33698; M_1-M_2: CM 33699; M_1: CM 33700; M_2: CM 33701.

Locality.—Loc. 19, Badwater Creek, Wyoming.

Age.—Late Oligocene.

Description and discussion.—The morphology of the mandible is very similar to that of *Adjidaumo minimus*. The mandible is long and slender. The mental foramen lies anterior to P_4 and almost on the dorsal surface of the mandible. The masseteric fossa ends rather acutely below the talonid of P_4. The doral masseteric ridge is stronger than the ventral and rises gently to the ascending ramus, which originates opposite the posterior half of M_2.

The crown pattern of the lower cheek teeth of *A. douglassi* differs from that of *A. minimum* and *A. minutus*. In *A. minimus*, the protoconid and the hypoconid are on the buccal side of the tooth, and the ectolophid also lies on the buccal margin to the midline of the crown. But in the type of *A. douglassi*, the protoconid and the hypoconid lean linguad making the buccal wall of each cusp more gentle and pushing the ectolophid towards the midline of the crown. The difference in morphology of these two types is clearly seen on worn specimens. When worn, the ectolophid in *A. minimus* lies buccally, whereas it in *A. douglassi* lies near the center of the crown. In *A. minimus*, the protoconid and the hypoconid are more stout than in *A. minutus* and *A. douglassi*. M_2 of *A. minutus* is wider than long, whereas M_2 of both *A. minimus* and *A. douglassi* is clearly longer than wide. *A. minutus* is larger than both *A. minimus* and *A. douglassi*, which are essentially of the same size. *A. douglassi* is a direct descendent from *A. minimus* but not via *A. minutus*.

All the specimens in the Badwater fauna are well worn. The P_4 has a narrower trigonid, almost half as wide as the talonid. The ectolophid lies near the midline of the tooth. No indication of the mesolophid is seen.

M_1 and M_2 have essentially the same morphology. M_1 is clearly longer than wide. One specimen of M_1 has a little narrower anterior half than the posterior but another specimen has the same anterior and the posterior width. On M_2, the anterior half is wider than the posterior half on the type of *A. douglassi* and CM 33701. The anterior cingulum is joined to the base of the metaconid and by a short crest to the metalophid where the latter leaves the protoconid. The buccal end of the cingulum is apparently free. These features are also found in *A. minimus*. The mesolophid is short on all the specimens passing half way to the lingual border on M_1 and M_2. The ectolophid lies near the midline of the crown. No M_3s are present in the sample.

The upper dentition of *Adjidaumo* has not been adequately described and figured. Wood (1937:237–238) briefly discussed the morphology of upper molars of this genus but did not figure them. The upper cheek teeth of *Adjidaumo* in the present fauna are identified based primarily on size and the mirror imaged structure of the lower molars referable to *A. douglassi*. Only two heavily worn specimens are identified. Both of them are M^1 or M^2. The anterior

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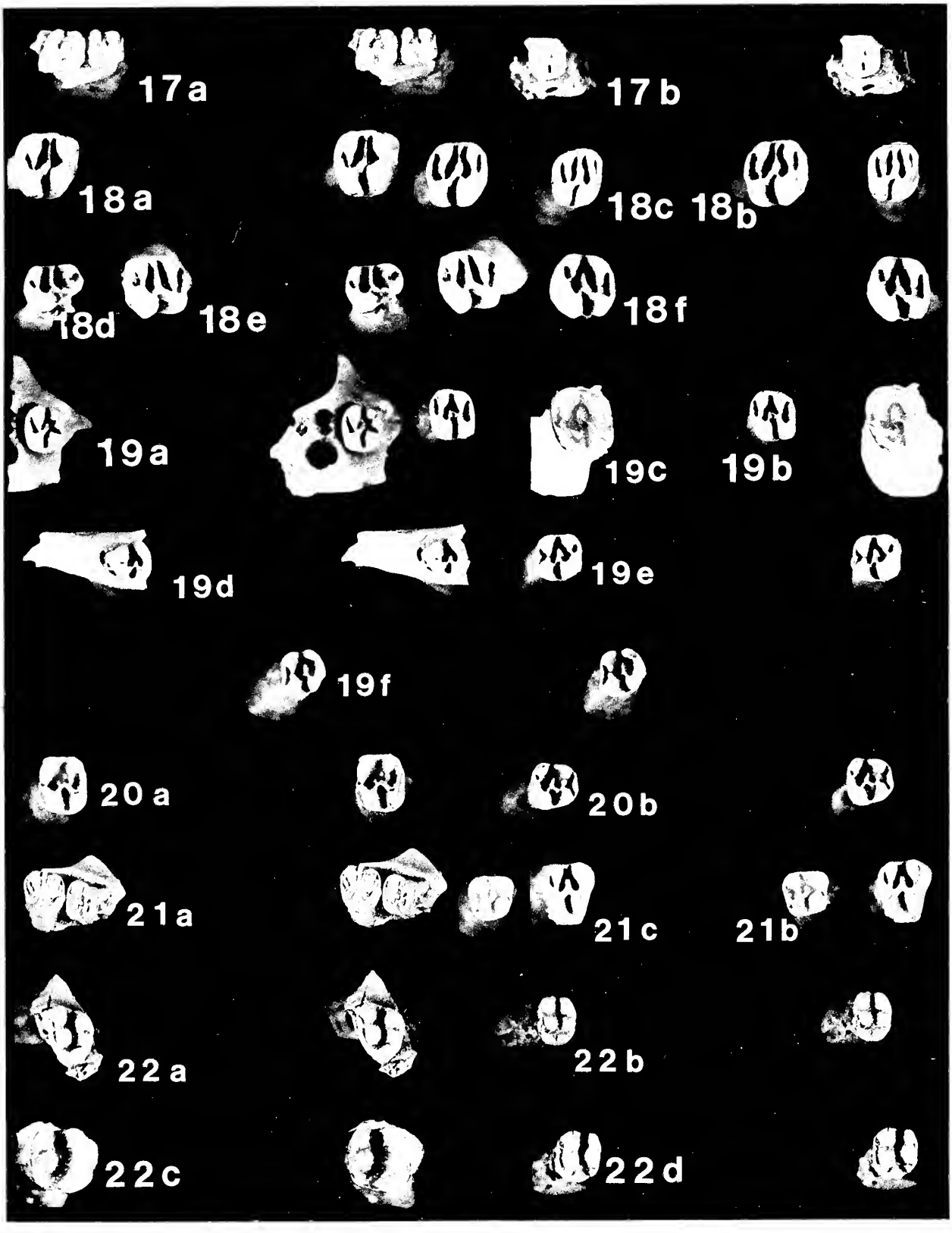
Fig. 17.—*Adjidaumo douglassi*. a: CM 33699, right M_1-M_2. b: CM 33703, left M^1 or M^2. ×8. Fig. 18.—*Paradjidaumo hypsodus*, new species. a: CM 33707, right P^4. b: CM 33704, holotype, right M^1. c: CM 33723, right M^2. d: CM 33732, right P_4. e: CM 33743, right M_1. f: CM 33752, right M_2. ×8. Fig. 19.—*Metadjidaumo hendryi*, new genus and new species. a: CM 33775, right P^4, ×8. b: CM 33780, left M^1, ×8. c: CM 33783, left M^2, ×15. d: CM 33784, left P_4, ×8. e: CM 33786, holotype, left M_1, ×8. f: CM 33808, left M_2, ×8. Fig. 20.—Eomyidae, genus indet., Type A. a: CM 33811, right M^2. b: CM 33812, right M_1. ×8. Fig. 21.—Eomyidae, genus indet., Type B. a: CM 33813, right P^4-M^1. b: CM 33815, right P^4. c: CM 33816, lower molar? ×8. Fig. 22.—*Proheteromys* sp. cf. *P. nebraskensis*. a: CM 33818, left M^1, ×8. b: CM 33846, left M^2, ×8. c: CM 33857, right M^1, ×15. d: CM 33884, left M_2, ×8.


17a
17b
18a
18c
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22d

Table 6.—Dimensions of teeth of *Pelycomys placidus* and *Adjidaumo douglassi*.

Teeth and measurements	*Pelycomys placidus* N	OR	Mean	*Adjidaumo douglassi* N	OR	Mean
P^4						
Length	3	2.13–2.57	2.353			
Width	3	2.30–2.96	2.600			
M^1						
Length	1	2.41				
Width	1	3.09				
M^2						
Length	1	2.49				
Width	1	3.27				
M^1 or M^2						
Length				2	0.87–0.91	
Width				2	0.94–0.97	
M^3						
Length	2	2.62–2.78				
Width	2	2.75–2.88				
P_4						
Length	1	2.72		2	0.78–1.02	
Width				2	0.76–1.05	
Anterior	1	1.90				
Posterior	1	2.56				
M_1						
Length	1	2.47		3	0.91–0.93	0.920
Width				3	0.79–0.88	0.847
Anterior	1	2.21				
Posterior	1	2.86				
M_2						
Length	2	2.51–2.72		2	0.92	
Width				2	0.91–0.95	
Anterior	1	2.10				
Posterior	2	2.66–2.93				
M_3						
Length	2	3.19–3.48				
Width						
Anterior	2	2.64–2.73				

cingulum is restricted on the buccal half of the tooth, whereas the posterior cingulum is well developed. The mesoloph is short and extends only half way to the buccal border. Union of the mesoloph to the metaloph is at almost the midline of the crown. The mesoloph is connected to the protocone.

Paradjidaumo hypsodus, new species
(Fig. 18, Table 7)

Holotype.—CM 33704, isolated right M^1.

Hypodigm.—Type and P^4: CM 33705–33708; M^1: CM 17097, CM 33709–33718; M^2: CM 33719–33730; M^3: CM 33731; P_4: CM 17436, CM 19808, CM 33732–33742; M_1: CM 17437, CM 17440, CM 33743–33743; M_2-M_3: CM 33749; M_2: CM 17433, CM 33750–33762; M_3: CM 33763–33769.

Etymology.—Hypsodont *Paradjidaumo*.

Locality.—Loc. 19, Badwater Creek, Wyoming.

Age.—Late Oligocene.

Diagnosis.—Higher crowned than *P. trilophus*—cusps and lophs (lophids) are higher and valleys are deeper than in any other known species of *Paradjidaumo*.

Description.—The cheek teeth of *Paradjidaumo* are mesodont, showing in relation to other eomyids an increase in the height of the cross lophs and lophids as well as increase in height of cusps (Black, 1965:26). The teeth of the present species are more advanced in this character than are those of *P. trilophus*.

P^4 is essentially molariform. It differs from M^1 and M^2 primarily in the absence of the anterior cingulum. On one specimen (CM 33705), however, a very narrow and shallow scar is present below the lingual end of the paracone on the anterior face of the tooth and the scar is covered anteriorly by a thin, short ridge. This ridge may be a remnant of the anterior cingulum and the scar, a remnant of the anterior valley. The scar is low in position so that it would be obliterated only after considerable wear. On the other specimen (CM 33707), no trace of an anterior cingulum and an anterior valley are seen. The protocone and the paracone are elongated transversely forming elongated blades. The buccal part of the protocone and the lingual part of the paracone run slightly anterad and join together at an angle below the tips of both cusps which are of the same height. The mesoloph reaches across the crown to a tiny mesostyle. The mesocone is well defined situating closer to the protocone than to the hypocone. The anterobuccal corner of the mesocone is very close to the posterobuccal corner of the protocone but apparently they are not connected to each other. This is a situation of the incipient separation of the protocone and the protoloph from the mesoloph as seen in some of the European forms, like *Pseudotheridomys*. The posterior cingulum is well developed but the valley between the metaloph and the posterior cingulum is not deep so that these elements become fused into a single loph with further wear. The base of each cusp is broad as in *P. trilophus* but the tips of these cusps near the unworn crown surface are high above the base and become compressed anteroposteriorly leaving deep valleys between the cusps and the mesoloph. These valleys are deeper than in *P. trilophus*.

M^1 differs slightly from M^2 in crown pattern. The anterior cingulum is distinct on both M^1 and M^2 when the teeth are unworn but restricted to the lingual half of the crown. It quickly merges with the protoloph as wear proce ds. The posterior valley is deeper than the anterior valley so that the former remains distinct somewhat longer but it also eventually fuses with the metaloph, producing the "Omega" pattern as in *P. minor* and *P. trilophus*. The protocone is pushed posterolinguad so that the anterior half of the crown is narrower transversely than the posterior half on M^1. On M^2, both halves are of the same width or the anterior half is a little wider. The mesostyle is tiny but distinct. It is lower than both the paracone and the metacone, and separated from them by notches on M^1. The mesoloph reaches to the mesostyle across the crown surface. On M^2, the mesostyle is more prominent and higher than in M^1, and united to both the paracone and the metacone forming the lingual wall to block the

Table 7.—*Dimensions of teeth of* Paradjidaumo hypsodus, *new species, and* Metadjidaumo hendryi, *new genus and new species.*

Statistics	P^4		M^1		M^2		P_4		M_1		M_2	
	L	W	L	W	L	W	L	W	L	W	L	W
Paradjidaumo hypsodus, new species												
N	4	4	10	10	12	12	10	10	6	6	11	11
OR	1.28–1.58	1.32–1.50	1.17–1.54	1.29–1.88	1.20–1.62	1.34–1.72	1.21–1.60	0.93–1.36	1.29–1.44	1.34–1.51	1.30–1.49	1.40–1.62
Mean	1.432	1.405	1.384	1.519	1.389	1.542	1.387	1.164	1.352	1.415	1.366	1.482
SD			0.140	0.174	0.139	0.120	0.115	0.159	0.050	0.071	0.062	0.066
CV			10.14	11.48	9.98	7.77	8.29	13.70	3.73	5.01	4.53	4.42
Metadjidaumo hendryi, new genus and new species												
N	8	8	6	6	2	2	1	1	12	12	13	13
OR	0.95–1.12	0.96–1.21	0.97–1.07	1.03–1.27	1.04–1.09	1.11–1.13	0.98	0.95	0.96–1.13	0.94–1.15	0.90–1.04	0.94–1.12
Mean	0.970	1.061	1.018	1.175					1.034	1.074	0.991	1.066
SD	0.070	0.084	0.034	0.088					0.066	0.067	0.038	0.053
CV	7.27	7.87	3.31	7.53					6.39	6.22	3.85	5.00

central valley buccally. The buccal corner of the metacone is elongated anteriorly to join the mesostyle so that the metacone and the paracone are closer together on M^2 than on M^1. The central valley is deeper on both M^1 and M^2 than in *P. trilophus* and *P. minor*. The mesocone is not well defined on either M^1 or M^2. The anterior extremity of the anterior arm of the hypocone is very close to the protocone. They are united by a short, thin ridge on M^1, and by a thicker ridge on M^2. This condition, especially of M^1 is close to that of P^4, but no specimens available of M^1 show closer separation of them.

M^3 is the smallest of the upper cheek teeth but the crown elements are not as greatly reduced as in *P. minor*. The protocone and the paracone are the largest cusps and they are joined by a strong protoloph as in *P. minor*, but the protocone lies more anteroposteriorly than in *P. minor*, and the anterior extremity of the protoconal ridge ends more lingually. The anterior cingulum is longer than in *P. minor*. All lophs rise to the same level as the protocone leaving rather deep valleys. On one specimen (CM 33731), the posterior valley is shallow but distinct. On the other, it is represented by a small pit. The mesoloph reaches to the lingual wall. No mesostyle is visible. The central valley anterior to the mesoloph is deeper than the posterior one which, in turn, is deeper than the anterior valley. This molariform morphology of M^3 in the present species is unusual.

P_4 is longer than wide. The crown height is almost the same as in *P. trilophus*. The trigonid is higher than the talonid, but less prominent than in *P. trilophus*. The protocone and the metacone are closely appressed and bounded posteriorly by the thin metalophid. A short anterior cingulum descends sharply from the anterior face of the protoconid to merge into the base of the metaconid. The posterior arm of the protoconid extends posteriad and connects to the mesolophid at right angle. The mesolophid extends transversely to the buccal border of the tooth and there turns anterad at a right angle to connect to the posterior base of the metaconid. The mesoloph is a thin ridge and slightly higher than the lingual wall of the tooth. The hypoconid forms a ridge, which extends more anteroposteriorly than in *P. trilophus*. The talonid is narrower in relation to the crown length to make the tooth longer than in *P. trilophus*. In *P. minor* and *P. trilophus*, a rather broad and deep excavation is present on the buccal wall of the tooth between the protoconid and the hypoconid. In the present species, this pit becomes shallower and narrower, and the excavated rather posteriad on the anterior base of the hypoconid. On some specimens (CM 33732), the central valley posterior to the mesolophid is deeper than the anterior one, but on one specimen (CM 33738) these two are essentially of the same depth.

M_1 is slightly longer than wide, whereas M_2 is rather wider than long. Both M_1 and M_2 are higher crowned than in *P. minor* and *P. trilophus*. Cusps become less prominent than in other species of *Paradjidaumo*. The anterior and posterior cingula, the metalophid, and the hypolophid lie essentially on the same level as the protoconid and the hypoconid, which are no more distinct cones but rather thin, elongated ridges. The metaconid is a sharp-pointed cusp slightly above the level of lophids. The metalophid descends transversely from the peak of the metaconid. Only the metalophid is slightly higher than the remainder of the cross lophids in an unworn stage. The entoconid is a small knob. On M_1, the mesolophid reaches to the lingual border of the tooth on all specimens available but on M_2, some specimens show that the mesolophid ends in the center of the crown. The central valley is deep. On some specimens of M_2, the trigonid is higher than talonid. The anterior cingulum of M_2 is not as closely appressed to the metalophid as in *P. minor*, but on some (CM 33752) the former is appressed to the latter. The posterior cingulum is short and is confined to the lingual quarter of the posterior face of the tooth on M_1 and M_2.

M_3 differs from M_1 and M_2 primarily in the absence of the posterior cingulum. M_3 in *P. minor* and *P. trilophus* have essentially the same crown pattern as M_1 and M_2. But in M^3 of these species of *Paradjidaumo* the crown elements are reduced. In the present species, as far as M_3 is concerned, the same trend is retained. The mesolophid reaches to the entoconid across the crown surface, instead of reaching to the lingual wall between

the metaconid and the entoconid as in M_1 and M_2. The hypolophid forms a posterior wall and is convexed posteriorly. The crown is also higher than that of *P. minor* and *P. trilophus*.

Discussion.—*P. hypsodus* differs from *P. minor* and *P. trilophus* in having more hypsodont teeth. In *P. minor,* the che k teeth are not high crowned, and the paracone and the metacone on the one hand, and the metaconid and the entoconid on the other are elevated high above the cross lophs and lophids. In *P. hypsodus,* however, the lophs, the lophids, and the cusps are elevated to a nearly common plane. The paracone and the metacone on the upper cheek teeth, and the metaconid and the entoconid on the lower teeth rise only slightly above the lophs and the lophid. In relation to the high lophs and lophids, the protocone and the hypocone on the upper teeth become higher, forming elongated ridges elevated to the same plane as the cross lophs. The lower cheek teeth show exactly the same trend. The cheek teeth of *P. hypsodus* are characterized by strong lophs and lophids rather than being cuspidated. This situation is analogous to the tooth character of *Eumys planidens* discussed elsewhere in this article.

The cheek teeth of *Paradjidaumo hypsodus* become higher crowned. Not only the lophs and lophids, but also the cusps become elevated as if elongated ridges were developed on the summit of the original cusps. The base of each elongated cusp is thick and broad showing the cuspidate condition of the ancestral stock to *P. hypsodus*. This condition could easily be derived from the tooth pattern of *P. trilophus*. As for the height of the crown of the cheek teeth, *P. trilophus* is intermediate between *P. minor* and *P. hypsodus*. The crown patterns of these three species of *Paradjidaumo* are essentially the same.

The essentially unreduced morphology of M^3 is worth discussing. Although the posterior cingulum is reduced, M^3 of *P. hypsodus* has all other crown elements, whereas on M^3 of *P. minor* the crown elements are reduced. In the latter, the size is not greatly reduced although it is a little smaller than M^1 and M^2. M^1 and M^2 of *P. hypsodus* have high lophs, and M^3 also follows this trend so that lophs and elongated cusps become emphasized in this species. The reduction of M^3 is a trend in the central stock of *Paradjidaumo* with increased hypsodonty; however, M^3 is modified to emphasize all the molar elements. This kind of rejuvenation is not common in rodent evolution.

Metadjidaumo, new genus

Type species.—*Metadjidaumo hendryi,* new species.

Etymology.—From Greek *metá, met-* after, descent of *Adjidaumo.*

Diagnosis.—Near size of *Adjidaumo minimus* and *A. douglassi;* molars higher crowned than in *A. minimus* and *A. douglassi* with high, thin lophs (lophids); trigonid higher than talonid on M_1 and M_2; no posterior cingulum on M_2.

Metadjidaumo hendryi, new species
(Fig. 19, Table 7)

Holotype.—CM 33786, isolated left M_1.

Hypodigm.—Type and P^4-M^1: CM 33770, CM 33771; P^4: CM 33772–33777; M^1: CM 17435, CM 33778–33780; M^2: CM 33781–33783; P_4: CM 33784; M_1-M_2: CM 33785; M_1: CM 17439, CM 33787–33796; M_2: CM 17438, CM 33797–33808.

Etymology.—For Mr. Jim Hendry, who provided his cabin during field seasons.

Locality.—Loc. 19, Badwater Creek, Wyoming.

Age.—Late Oligocene.

Diagnosis.—Only known species of genus.

Description.—The fourth upper premolar is square-shaped. All the cusps are well developed. Among them the metacone and the hypocone are taller than the paracone and protocone. The anterior half is narrower transversely than the posterior half. There is considerable variation in the morphology of the anterior half of the crown. The protocone is stout and extends anterobuccally leaving a narrow valley between it and the hypocone. The valley runs slightly posterad on CM 33775 as in M^1 or M^2, whereas the protocone is shifted more buccally from the usual position so that the valley between the protocone and the hypocone runs rather anterad on CM 33777. The protoloph is a thick ridge extending anterobuccally from the protocone and joining the paracone at its anterolingual corner. On two specimens, no anterior cingulum is seen. On other specimens, however, a very shallow, compressed pocket is present on the anterior face of the paracone which is bounded anteriorly by what is probably a short anterior cingulum that fades into the anterior face of the paracone. This pit would be obliterated with further wear. The mesocone is well defined on CM 33775. It is half as large as the protocone and is a little lower than the latter. The mesoloph is essentially not present on this specimen. On the other specimens, the mesocone is merely a buccal extension of the anterior arm of the hypocone and quickly merges with the floor of the crown near the posterolingual base of the paracone. On three specimens, the mesocone or a thin ridge, the mesoloph, is connected to the protocone by what may be called the posterior arm of the protocone. On one specimen, the mesocone and the protocone are close together but no connection is seen between these cusps, and on one other specimen, these two cusps are clearly separated from each other. The separation of the protocone from the mesoloph is not common in North American eomyids, but this characteristic feature is commonly seen

in European eomyids. In four specimens, no metastyle is present, but on others the metastyle is present on the buccal border at the posterior base of the paracone. The posterior cingulum is well developed but the posterior valley is shallower than the central valley.

Only two upper jaw fragments, both of which bear P^4 and M^1, are available and M^1 on both is heavily worn. M^1 is clearly wider than long on both specimens. One specimen (CM 33771) has a wider posterior half than anterior, and the other (CM 33770) is nearly square. The valley between the protocone and the hypocone is narrow and long reaching to nearly the center of the crown. The valley runs almost transversely but a little posteriad. The ectoloph or mure lies at the center of the crown on CM 33770 and a little buccal to the midline of the tooth on CM 33771. The mesoloph is short. The buccal halves of the paracone and the metacone are curved posterad and anterad, respectively, so that the central valley becomes narrower buccally. On worn teeth, the lingual three-fourths of the crown is flattened, whereas the buccal one fourth remains a little higher. On CM 33771, the buccal portion of M^1 is not eompletely worn with the buccal wall between the paracone and the metacone unworn although both cusps are worn. This indicates that on M^1 the buccal wall between these two cusps is low and not elevated to block the central valley buccally. This condition is also seen on M^1 of *Paradjidaumo*. On M^2 of *Paradjidaumo,* however, the buccal wall between the paracone and the metastyle, and between the latter and the metacone is elevated nearly to the level of these three cusps so that the central valley is blocked buccally by this wall.

No unworn definite M^1 or unworn M^2 associated with P^4 on the same jaws are available in the present fauna. This makes it difficult to identify M^1 and M^2 of the new genus and species. Isolated M^1 and M^2 are identified on the basis of size and similar morphology with the low buccal wall between the paracone and the metacone for the former and with the high wall between them for the latter.

M^1 and M^2 are of similar size and the erown pattern is essentially the same. The size is very close to *Adjidaumo minimus,* but a little larger. The crown is definitely higher than in *A. minimus* and *A. douglassi*. The ratio of the crown height to the width is nearly 1.0 in the present form, whereas it is clearly below 1.0 in *Adjidaumo douglassi* and is definitely over 1.0 in *Paradjidaumo hypsodus*. The molars emphasize ridges rather than stout cusps. The protocone is elongated sending a thick anterior arm anterobuccally. From the anterobuccal corner of the arm the anterior eingulum extends buccally and reaches to the anterior base of the paracone. The anterior cingulum is restricted to the buccal half of the crown. A short, transverse protoloph unites the anterior arm of the protocone and the transversely elongated paracone. The hypocone projects more lingually than the protocone. The buc al tip of the hypocone is excavated making the posterior valley longer transversely. The anterior arm of the hypocone extends to the center of the crown, and there it turns anterad making what may be called the mur . A short mesoloph runs buccally; it does not reach to the buccal border of the crown. The posterior cingulum is well developed from the tip of the hypocone to the posterior base of the metacone. On some specimens, the union of the protocone and the mesoloph is seen by way of the posterior arm of the protocone, but on some, the connection is by a thin ridge (CM 33780, M^1 and CM 33783, M^2), and almost no connection is seen (CM 33782, M^2), where the mesoloph connected to the anterior arm of the hypocone. No metastyle is seen on any of the specimens.

No lower jaw materials associated with upper jaws are available. The lower molars are identified primarily based on size and the mirror image morphology of the upper molars. P_4 is also identified based on size and the similar morphology to M_1 and M_2.

One lower jaw fragment (CM 33784) has P_4. The diastema is not deep and essentially the same as that of *Adjidaumo*. P_4 is larger than that of *Adjidaumo douglassi* and wider than M_1 of *A. douglassi*. The trigonid is narrower than the talonid. The protoconid and the metaconid are of equal size and are joined posteriorly by a short crest. The anterior valley between the cusps is open. The mesolophid is short and ends half way across the crown. The mesoloph is lower than the ectolophid. No posterior cingulum is present on one specimen (CM 33784) but on the other specimen a small pit is present just posterobuccal to the entoconid and the pit is bounded posteriorly by what is probably a short posterior cingulum that fades into the posterior face of the entoconid.

One lower jaw (CM 33785) has M_1 and M_2. These teeth are well worn. M_1 is clearly longer than wide and a short posterior cingulum is present. M_2 is rather wider than long and has no posterior cingulum. Isolated M_1 and M_2 are identified solely on the basis of this morphology—longer teeth with the posterior cingulum for M_1 and wider teeth without the posterior cingulum for M_2. The following morphology is described based on isolated teeth referable to M_1 and M_2. M_1 differs only slightly from M_2 in crown pattern. The anterior cingulum is distinct on both M_1 and M_2 but unlike *Adjidaumo* it does not connect to the metalophid. The anterior cingulum extends from near the anterior base of the metaconid to the anterobuccal corner of the protoconid. On one specimen (CM 33793, M_1), the anterior cingulum is separated from the protoconid by a small notch, and nearly so on the holotype, CM 33786, also M_1. On the other specimen (CM 33795, M_1), the lingual half of the protoconid is excavated and the anterior cingulum is connected to the protoconid on its anterior side. All the specimens except for one referable to M_2 are worn at least on the trigonid. On this unworn specimen (CM 33808), the morphology of the anterior cingulum is close to CM 33795; connection to the protoconid is as in *Paradjidaumo*. The trigonid is clearly higher than the talonid. The metaconid is the most prominent cusp and a little taller than the protoconid. The entoconid is conical and higher than the hypoconid, but lower than the protoconid. From the protoconid a short ridge descends linguad and meets a short ridge, which also descends buccally from the transversely elongated metaconid. These two ridges are arranged transversely and represent what is called the metalophid. The posterior arm of the protoconid runs posterolinguad and meets the short anterior arm of the hypoconid. The junction lies near the center of the crown. From this junction, the mesolophid extends linguad only half way across the crown. The mesolophid is distinct and higher than in *Adjidaumo minimus* and *A. douglassi*. These three ridges are really lower than the trigonid and a little lower than the hypoconid. The posterior wall of the metaconid is vertical and the central valley is deeper than the anterior valley. A metastylid is not present. The metaconid is rather widely separated from the entoconid. The hypoconid is elongated and the posterior arm of it extends posterolinguad. A short ridge runs posterobuccally from the buccal corner of the entoconid and meets the posterior hypoconid arm at a right an-

gle. From this junction, the posterior cingulum runs posterolinguad but it does not connect to the entoconid so that the posterior valley opens lingually on M_1. The posterior valley is essentially of the same depth as the central valley. On M_2, the hypolophid marks the posterior margin of the crown and is convex posteriorly.

Discussion.—The present form differs from *Adjidaumo* in having higher crowned teeth and from *Paradjidaumo* in having weaker development of the mesoloph and mesolophid. The higher trigonid in this new genus is quite unique among the North American eomyids. I cannot find any form having the higher trigonid on the lower cheek teeth even among the European forms.

Except for the higher trigonid, primitive features characterize the tooth structure of this new form. The weakness of the mesolophs and the mesolophids and the emphasis on the separate cusps are primitive among eomyids, as discussed by Wood (1973). In these respects, *Paradjidaumo* and *Centimanomys* are more specialized in having long mesolophs and mesolophids. *Meliakrouniomys* is also specialized in having bilophate cheek teeth of which each loph is formed of two cusps and accessory structures are very small. *Namatomys* has a peculiar feature having the posterior protoconid arm fused to the base of the metaconid. *Viejadjidaumo* has M_1 with only the hypolophid but without the posterior cingulum. *Yoderimys* has a long lophid, which passes from the center of the anterior cingulum to the center of the metalophid on M_1 and M_2. This removes *Yoderimys* from any close relationship with other eomyids. The narrow trigonid with near fusion of the protoconid and the metaconid on P_4 in *Aulolithomys* is also unique and suggests its isolated position within the family. These rather specialized features make it difficult to believe that any of these genera, *Namatomys, Viejadjidaumo, Meliakrouniomys, Yoderimys, Aulolithomys, Centimanomys,* and *Paradjidaumo,* could give rise to *Metadjidaumo. Adjidaumo* retains the most generalized features of che k tooth structure among North American eomyids.

The most remarkable modification seen in the present form from the original stock is the higher crowned cheek teeth. Although the posterior half becomes a little more highly elevated than in *Adjidaumo,* the anterior half becomes elevated above the posterior half, and the tendency is more emphasized on lower cheek teeth than upper. This gives us the impression that the trigonid becomes higher than the talonid as if these teeth might have been rejuvenated to nearly the tribosphenic condition. This trend took place in correlation with the development of hypsodonty of cheek teeth; the rate of increase in height is higher on the anterior half than the posterior half making the trigonid taller than the talonid on lower cheek teeth. The trend towards hypsodonty is seen also in *Paradjidaumo hypsodus* in the present fauna, but a differ ntial rate for height increase of different parts of a single crown is highly unusual.

The talonid is not as high as the trigonid in the present form. This could mean that the degree of modification on the talonid might not be as great as on the trigonid in the original form. Compared with the talonid structure of *Adjidaumo douglassi,* a great resemblance is seen between the talonid structure in the present form and *A. douglassi.* The hypoconid is elongated sending its posterior arm posterolinguad. A short ridge originates from the buccal corner of the entoconid running posterobuccally and meets the posterior hypoconid arm rather nearer to its posterior end than to the hypocone. From the posterior end of the posterior hypoconid arm, the posterior cingulum runs linguad on M_1. On M_2, the posterior cingulum is reduced on *A. douglassi,* whereas it is gone on the present form. A short posterior protoconid and a short anterior hypoconid arm, and the transverse mesolophid make a triple junction near the center of the crown. The mesolophid is rather short and does not connect to either the metaconid or the entoconid so that two valleys anterior and posterior to the mesoloph join together and run further linguad. The hypoconid itself leans linguad so that the tip of it is situated rather closer to the midline of the crown. *Adjidaumo douglassi* and the present form share the common features listed above. This suggests that they have a common ancestry sometime in the mid-Oligocene. As I show elsewhere in this article, *A. douglassi* is a direct descendent from *A. minimus* of the early Oligocene but not via *A. minutus* of the middle Oligocene. The present form may stand on a side branch from *A. minimus.*

The trigonid structure of *Metadjidaumo* differs from that of *A. douglassi,* even though some similarities are seen. The protoconid is taller than the mesolophid and the ectolophid so that the latter connects to the protoconid on its posterior wall below the tip of this cusp on M_1 of *A. douglassi.* This is also true for M_1 of *Metadjidaumo* although the connection is well below the tip of the protoconid

Table 8.—*Dimensions of teeth of Eomyidae, genera indet., Type A and Type B.*

Statistics	P^4		M^1		M^2		M^1 or M^2		M_1	
	L	W	L	W	L	W	L	W	L	W
Eomyidae, genus indet., Type A										
N			1	1	2	2			1	1
OR			1.27	1.36	1.16–1.21	1.29–1.33			1.07	1.07
Eomyidae, genus indet., Type B										
N	3	3	1	1			2	2		
OR	0.78–1.08	0.92–1.08	0.98	1.08			1.23–1.24	1.23–1.31		
Mean	0.927	0.983								

because it is a greatly elevated cusp. On M_1 of *A. douglassi*, the metaconid has a wider base lingually and the base becomes narrower buccally. A ridge descends buccally but slightly anterad towards the buccal base of the metaconid and meets a short ridge descending linguad from the tip of the protoconid. The junction is well below the tips of the protoconid and the metaconid, and even below the anterior cingulum. These two ridges combined together are what is called the metalophid. This kind of condition may indicate the origin of the metalophid.

The same morphology is seen on M_1 of *Metadjidaumo*, although the metaconid and the protoconid are greatly elevated and share a common base. The elevation takes place almost vertically so that the posterior wall of the metaconid and the protoconid are vertical. The junction of two ridges descending from the tips of the protoconid and the metaconid are a little below the anterior cingulum. The anterior valley is not deep and its floor lies a little below the junction between two ridges just mentioned above. The presence of the rather shallow anterior valley indicates that the whole trigonid becomes elevated from the base of the crown.

The anterior cingulum is well developed and extends along the whole anterior face of molars on both *Adjidaumo douglassi* and *Metadjidoumo*. But here a major difference takes place between these forms. In the holotype of the *A. douglassi*, the anterior cingulum is joined to the anterolingual base of the protoconid, and the buccal part of the former is free but descends buccally joining to the protoconid far below on its anterobuccal base. In the present form, the anterior cingulum does not connect to the metalophid but connects to the protoconid making the anterior valley longer transversely. The protoconid in *A. douglassi* is not as large and prominent when compared with the hypoconid, and on M_1, the trigonid is narrower than the talonid. On the other hand, in the present form, the protoconid is more prominent and stout than the hypoconid, and the trigonid is rather wider than the talonid on M_1 although the tooth itself is longer than wide. The wider trigonid could be associated with the heightening of this part.

Except for the union of the anterior cingulum with the protoconid and the wider trigonid, an overall similarity of crown structure is seen between *A. douglassi* and the present form. The absence of the posterior cingulum on M_2 in the present form should be mentioned. On M_2, the hypolophid forms the posterior border of the crown and the posterior cingulum is not present. This feature is highly specialized for M_2 and not seen commonly in the North America eomyids. *Viejadjidaumo* shows this feature even on M_1. On the holotype of *Adjidaumo douglassi*, the posterior cingulum is more reduced on M_2 than on M_1 because the posterior hypoconid arm extends more linguad on the posterior border of the crown on M_2. The short posterior cingulum runs linguad along the posterior margin of the crown and ends posterior to the entoconid, but does not connect to the latter. The posterior valley is represented by a shallow pocket. If the reduction proceeds, the situation without the posterior cingulum on M_2 will take place.

Eomyidae, genus indet., Type A
(Fig. 20, Table 8)

Referred specimens.—M^1: CM 33809; M^2: CM 33810, CM 33811; M_1: CM 33812.

Locality.—Loc. 19, Badwater Creek, Wyoming.

Age.—Late Oligocene.

Description.—Three isolated upper molars and one lower molar are available. They are low-crowned and of equal size. The determination of upper and lower molars are primarily based on the position of roots; both are three rooted; in upper molars, one anteroposteriorly elongated root is underneath the protocone and the hypocone, and two roots are underneath the paracone and the metacone, respectively; in lower teeth, one transversely elongated root is underneath the hypoconid and the entoconid, or underneath the talonid, and two roots are underneath the protoconid and the metaconid, respectively.

One upper tooth (CM 33809) is longer than wide, probably M^1, and this tooth is heavily worn. All the cusps are well defined and connected by rather thin ridges. The anterior cingulum is represented by a thin ridge, which is thinner than the posterior cingulum and extends along the whole anterior border of the crown. The buccal end of the anterior cingulum is connected to the anterior base of the paracone. A rather thick ridge connects the anterior cingulum with the anterobuccal corner of the protocone. The lingual portion of the anterior cingulum is free. The floor of the anterior valley is unworn as are the floors of the central and the posterior valleys. All three valleys are of equal depth. The base of the protocone is wider anteroposteriorly than the remainder of cusps. The protoloph is curved anteriorly making the anterior valley narrow. The central valley is wide and opens buccally. The mesoloph is not defined clearly. A short and rather thick mure connects the posterobuccal corner of the protocone with the metaloph. The posterior cingulum extends only half way to the buccal border along the posterior margin of the tooth. The posterior valley opens buccally.

Two upper molars are wider than long and are probably M^2s. One of them (CM 33811) is almost unworn. The crown structure is almost the same as the one described just above. The four cusps are stout and rather tall, and all the ridges are thin and low in position; thus the crown pattern emphasizes cusps rather than ridges. The anterior arm of the protocone with a thick base descends from the stout protocone anterobuccally and its anterior extremity connects to the anterior cingulum. A ridge also with a thick base descends almost transversely from the paracone and joins the anterior protocone arm forming the protoloph. The posterior arm of the protocone descends linguad but slightly posterad and near the center of the crown turns posterad to join the anterior arm of the hypocone. The mesoloph is not well defined; two short, thin and low ridges are slightly elevated from the floor of the central valley just buccal to the mure—one is near the anterior end of the mure, and the other is near the middle of it. The buccal border between the paracone and the metacone is slightly elevated but well below the tips of these cusps. The posterior cingulum is rather long and connects to the metacone on its posterior base.

One lower molar (CM 33812) is longer than wide and the trigonid is narrower than the talonid. It is probably M_1. This tooth also emphasizes cusps rather than ridges. The anterior cingulum is well developed extending along the whole width of the tooth. The base of it is rather wide and it is not as close appressed to metalophid. The lingual end of the anterior cingulum is fused to the metaconid at its anterior base. The anterior cingulum does not connect to either the metalophid nor the protoconid so the V-shaped valley extends between the anterior cingulum and the metalophid, and opens buccally. The metaconid and the entoconid are conical and taller than the buccal cusps. The size of the entoconid is reduced compared with that in other eomyids. The metaconid and the entoconid are widely separated. No metastylid is seen. The hypoconid is more stout than the protoconid. The hypolophid is the most prominent of the ridges. The rather weak metalophid connects the protoconid with the metaconid. The ectolophid is also weak and lower in position than both the metalophid and the hypolophid. The mesolophid is short and as weak as the ectolophid. The mesolophid extends linguad only half way to the lingual border and merges to the floor of the central valley posterior to the metaconid. The posterior cingulum is short and restricted to only the lingual quarter of the posterior margin. The posterior valley is represented by a small pocket situated posterolingual to the entoconid.

Discussion.—In size this form is close to *Adjidaumo douglassi* but is a little larger than it. The well developed cusps and weakness of lophs and lophids in the present form are unusual among eomyids. The reduction of the entoconid is seen on M_2 in *Adjidaumo douglassi* as compared to this cusp on M_1 of this species. This, together with the well-developed anterior cingulum indicates the close relationship of this form to *Adjidaumo*. In *Adjidaumo*, lophs and lophids are better developed than in the present form. At present, I cannot find any close relation of this form to any other eomyids.

Eomyidae, genus indet., Type B
(Fig. 21, Table 8)

Referred specimens.—P^4-M^1: CM 33813; P^4: CM 33814, CM 33815; M_1 or M_2: CM 17434, CM 33816.

Locality.—Loc. 19, Badwater Creek, Wyoming.

Age.—Late Oligocene.

Description.—An upper jaw fragment (CM 33813) with P^4 and M^1 is available. Size is close to *Adjidaumo douglassi*. Both teeth are heavily worn but they are higher crowned than in *A. douglassi*. Unlike *Adjidaumo*, the mesoloph is long and reaches across the crown surface to the mesostyle, which is thin and elongated transversely on M^1. Both the paracone and the metacone are elongated transversely and of equal size. The anterior and the posterior cingula are well developed and both are restricted only on the buccal half of the tooth. The anterior cingulum is closely appressed to the protoloph. No lingual portion of the anterior cingulum is seen. The protocone and the hypocone are close together, and the valley between them is narrow running linguad and posterad as well.

The fourth premolar associated with M^1 on the same upper jaw is heavily worn. Two isolated P^4s (CM 33814, CM 33815) are present. A root beneath the paracone of these teeth extends

anterobuccally indicating that the tooth is the first tooth of the cheek tooth series. All the cusps are well defined. The hypocone is the largest and extends more linguad than the protocone so that the posterior half is wider than the anterior half. A short anterior cingulum is present on the buccal quarter of the anterior margin of the tooth. This cingulum does not connect to the paracone. The mesoloph extends only half way across the crown to the buccal border. No mesostyle is present but the buccal border between the paracone and the metacone is slightly elevated. The posterior cingulum is long and connects to the hypocone on its posterobuccal corner making the posterior valley longer transversely. The lingual half is narrower anteroposteriorly than the buccal half.

Two isolated lower molars (CM 17434, CM 33816) are at hand. On both, the buccal half is narrower anteroposteriorly than the lingual half. Both specimens have the well-developed anterior cingulum connecting to the tip of the protoconid. The central valley is deeper than the anterior valley. The lingual wall is elevated with a thick base, but it is below the metaconid and the entoconid. A mesostylid is present on one specimen but not on the other. The mesolophid is well developed reaching to the buccal wall but the connection is below the mesostylid. The posterior cingulum is not present.

Discussion.—The above described specimens are characterized by small size, long mesolophs and mesolophids, narrower lingual half on upper and buccal half on lower teeth, and high-crowned teeth. Some similarities between this form and *Paradjidaumo* are seen—higher-crowned teeth, long mesolophs and mesolophids, and anterior cingulum connecting to the protoconid on the lower molars. The present form is smaller than *Paradjidaumo,* and has a narrower lingual length on the upper and buccal length on the lower teeth. I cannot find any close relatives of this form.

Family Heteromyidae Allen and Chapman, 1893

Heteromyid specimens are reasonably common in the Badwater assemblage, but consist almost entirely of isolated teeth. Only in 13 specimens are two or more cheek-teeth in association. Two species are present. Specimens referable to M^1 are clearly able to be separated into two size categories. One, having greater length and width, emphasizes stronger lophs and deeper transverse valley, and the other, smaller type, is characterized by independent cusps and a shallow transverse valley being essentially the same depth as the anteroposterior valley. The second upper molars are also divisible into two size categories, but the separation is not as clearcut. In the first lower molars, the larger size group usually has stronger lophs and lophids than the smaller.

Proheteromys sp. cf. **P. nebraskensis** Wood, 1937 (Fig. 22, Table 9)

Referred specimens.—M^1: CM 33817–33842; M^2: CM 17423, CM 17426, CM 17427, CM 33843–33856; M_1: CM 17425, CM 33857–33879; M_2: CM 17429, CM 17431, CM 33880–33885.

Locality.—Loc. 19, Badwater Creek, Wyoming.

Age.—Late Oligocene.

Description.—M^1 of this species is considerably larger than that of *Heliscomys* in this fauna. The size of the former is very close to that of *Heliscomys schlaikjeri,* and a little larger than that of *H. tenuiceps.* Morphologically, the present form is very close to *H. schlaikjeri.* As in *H. schlaikjeri,* M^1 is more lophate than are those of the middle Oligocene species of *Heliscomys,* although the principal cusps are still prominent. On most specimens, the protocone and the metacone are of equal size, but the protocone is lower than the paracone even on unworn stage. Several specimens show that whereas the protocone and the hypocone are worn a little, the paracone and the metacone are not worn at all, consequently the paracone becomes much higher than the protocone. The paracone is situated anterobuccal to the protocone so that the tooth is longer and the anterior half of the tooth is considerably wider than the posterior half. The characteristic feature of the anterior half of the tooth being wider is also seen in M_1 of *Heliscomys schlaikjeri,* although Black (1961) did not mention this in his description of his new species. On most specimens, the protocone unites with the paracone only at its base, and these two cusps share a common base, which is raised above the floor of the transverse valley. The notch between the protocone and the paracone is lower than the notch between the hypocone and the metacone. The anterior cingulum is strong and runs linguad from the anterior base of the paracone, but well below the paracone and the protocone. The lingual cingulum exhibits only one large cusp opposite the lingual end of the transverse valley, and shows no evidence of having been divided into two cusps, as in *H. tenuiceps.* This cingular cusp is smaller and lower than the hypocone, but much higher than the anterior cingulum, which unites with the lingual cingular cusp at its anterior base. The cingular cusp connects to the hypocone near its base and the anterior cingulum. The transverse valley is confluent with the valley between the anterior cingulum and the protocone, although the former valley is deeper than the latter, but is blocked by the cingular cusp and the hypocone posterolingually. The hypocone and the metacone are subequal and share a common base, which is high above the floor of the transverse valley. The valley, which separates the metacone from the hypocone, is elongated anteroposteriorly and is blocked posteriorly by the posterior cingulum. The short posterior cingulum runs buccally from the posterobuccal corner of the hypocone to the posterior base of the metacone. With wear, the posterior cingulum is obliterated as in *Heliscomys tenuiceps* and *H. schlaikjeri.*

M^2 of this form is identified based on larger size and more lophate morphology. The morphology of M^2 almost agrees with that of M^1. On M^2, the crown is transverse but the anterior half of the tooth is not greatly wider than the posterior half, even though the former is a little wider than the latter. The paracone and the metacone are closer together than in M^1. The floor of the transverse valley between these buccal cusps is raised so that the valley becomes shallower buccally. The protocone is

Table 9.—*Dimensions of teeth of* Proheteromys *sp. cf.* P. nebraskensis.

Statistics	M^1			M^2			M_1		M_2	
	L	AW	PW	L	AW	PW	L	W	L	W
N	26	26	26	17	17	17	24	24	8	8
OR	1.08–1.27	1.21–1.51	1.09–1.38	0.87–1.00	1.12–1.34	1.08–1.25	1.11–1.30	1.01–1.19	0.96–1.06	1.07–1.20
Mean	1.149	1.416	1.255	0.945	1.210	1.154	1.183	1.117	1.026	1.136
SD	0.050	0.071	0.075	0.038	0.056	0.050	0.047	0.047	0.035	0.047
CV	4.34	5.03	6.01	3.98	4.61	4.35	3.94	4.22	3.37	4.10

lower than the paracone. With wear, the protocone and the hypocone are lowered faster than the paracone and the metacone are. The anterior cingulum is also prominent but lower than the protocone. The lingual cingulum is very thick and tall. No distinct cusps are seen on the lingual cingulum. The lingual cingulum is highest at the point opposite the lingual end of the transverse valley. From there, a ridge descends anterobuccally and is confluent with the anterior cingulum. Posteriorly, the lingual cingulum connects to the hypocone at its lingual base. On one specimen (CM 33844), the lingual cingulum tends to divide into two parts by a small notch, and on one specimen (CM 33846), this cingulum is completely divided into two parts; both parts are conical; the anterior one is small and is anterolingual to the protocone, and the posterior one is larger and is anterolingual to the hypocone. On both specimens (CM 33844, CM 33846), all six cusps are not united by lophs, and the transverse valley and the anteroposterior valley are of the same depth. This situation is very close to that seen in *Heliscomys*.

Lower fourth premolars are not available.

M_1 is square-shaped and somewhat longer than wide. The principal cusps are prominent. Among them, the protoconid and the entoconid are subequal and smaller than both the metaconid and hypoconid. The metaconid is the highest cusp, and the other three cusps are of the same height. After a little wear, the tips of the protoconid and the hypoconid are truncated, whereas the metaconid and the entoconid remain unworn. Then, the difference in height between the buccal cusps and the lingual cusps becomes more emphasized. The differential height in cusps of M_1 is just the mirror image of that of M^1; the buccal cusps are higher than the lingual ones in M_1, whereas the opposite condition holds in M^1. The protoconid and the metaconid share a common base as do the hypoconid and the entoconid. These bases are elevated high above the floor of the transverse valley so that the transverse valley is deeper than the anteroposterior valley. The notch between the protoconid and the metaconid is a little higher than the valley between the anterior cingulum and the protoconid. On most specimens, the anterior cusps do not form a distinct loph. But on several specimens, especially on CM 33859 and CM 33858, the protoconid and the metaconid connect broadly to each other at their base forming the metalophid, although two cusps are still prominent. The anterior cingulum is strong although it is low leaving a transverse valley between it on the one hand and the protoconid and the metaconid on the other. The anterior cingulum connects to the buccal cingulum at the anterobuccal corner of the tooth. No connection between cingula and the protoconid is seen. The protostylid is represented by a thick and elevated ridge, which is merely the posterior continuation of the buccal cingulum. The protostylid is situated posterobuccal to the protoconid. The hypostylid is more conical and of the same height as the protostylid. The hypostylid connects to the hypoconid at its base. Both the protostylid and the hypostylid are significantly lower than the protoconid and the hypoconid. These stylids are widely separated by a valley, which is confluent with the transverse valley. The degree of development of the posterior cingulum varies. On most specimens, the short posterior cingulum runs buccally from the post robuccal corner of the entoconid to the posterior base of the hypoconid. A small cingulum connects the hypostylid with the hypoconid at the posterobuccal corner of the tooth, but this cingulum does not connect to the posterior cingulum between the hypoconid and the entoconid, on most specimens. On some (for example, CM 33874), these two cingula unite with each other and surround the posterobuccal base of the hypoconid.

M_2 of this form is identified based on more lophate morphology. The size of M_2 is not significantly larger than that of *Heliscomys* in this fauna so that the difference in size is not applicable for separation into two groups. M_2 is wider than long. The protoconid is subequal to the metaconid and the hypoconid. The entoconid is the smallest among the principal cusps. The protoconid and the metaconid are transversely elongated and united broadly with each other at their base forming the prominent metalophid. The low entoconid unites with the hypoconid at its base, but the hypolophid is not so strongly lophate as in the metalophid. The anterior cingulum is as in M_1. The protostylid is more conical than on M_1. The hypostylid is significantly lower and smaller than the protostylid. On most specimens, the posterior cingulum is absent, but on one specimen (CM 33884), a rudimentary cingulum runs along the posterior bases of the hypoconid and the entoconid.

The morphology of M_3 varies. The protoconid and the metaconid are subequal but the former is a little higher than the latter. The transverse valley is deep separating the metalophid from the hypolophid. The entoconid is reduced in size. The hypoconid is lower than the anterior cusps. The anterior cingulum is present on most specimens, but weak. The protostylid is a small cusp on the buccal cingulum or absent. The hypostylid is greatly reduced if present, or absent. The transverse valley opens buccally. No posterior cingulum is present on all specimens available.

Discussion.—The upper dentition of this form is very close to that of *Heliscomys schlaikjeri*. The holotype of *H. schlaikjeri* is worn a little so that it is rather difficult to compare it precisely with the present form. The size is almost the same. That the molars are more lophate and the anterior half of M^1

Table 10.—*Dimensions of teeth of* Heliscomys *sp. cf.* H. vetus.

	P^4		M^1			M^2			P_4		M_1		M_2	
Statistics	L	W	L	AW	PW	L	AW	PW	L	W	L	W	L	W
N	27	27	27	27	27	15	15	15	9	9	17	17	15	15
OR	0.64–0.91	0.66–0.93	0.74–0.94	0.96–1.16	0.92–1.11	0.72–0.92	0.89–1.10	0.86–1.07	0.48–0.73	0.52–0.72	0.88–1.07	0.89–1.08	0.85–1.00	0.94–1.14
Mean	0.739	0.807	0.859	1.046	0.990	0.806	0.994	0.961	0.623	0.634	0.970	0.967	0.923	1.004
SD	0.068	0.078	0.053	0.061	0.055	0.062	0.063	0.057	0.073	0.069	0.062	0.062	0.055	0.056
CV	9.17	9.69	6.21	5.86	5.53	7.66	6.29	5.93	11.79	10.87	6.36	6.39	5.94	5.62

is wider than the latter is clearly shared in both forms. I have not found any reason to separate the present form from *H. schlaikjeri*. The present form and *H. schlaikjeri* differ from *H. tenuiceps* of the middle Oligocene in having a wider anterior half of M^1. The size of *H. tenuiceps* is a little smaller than that of both the present form and *H. schlaikjeri*. *Heliscomys tenuiceps* and *H. schlaikjeri*, which are known only from the upper dentition may eventually be removed from the genus. This problem will be discussed below.

The most remarkable feature seen in the upper dentition of the present form is the presence of the smaller protocone than the paracone. The holotype of *H. schlaikjeri* is worn and the protocone unites with the paracone with wear on this specimen. It is impossible to tell whether *H. schlaikjeri* might have had the smaller protocone on M^1 or not. The presence of a small protocone on the upper molars is unusual among heteromyids. The morphology of the smaller protocone on M^1 is reflected in the morphology of M^1, too.

On M_1, the protoconid is smaller than the paraconid. The size and general morphology except for the smaller protoconid are very close to *Proheteromys nebraskensis*. The holotype of *P. nebraskensis* is worn. The paratype established by Wood (1937) is an almost unworn specimen. Wood stated (1937: 215) that "(In *P. nebraskensis*) The protostylid of the molars is separate from the cingulum when unworn, and it far to the rear. The protoconid and metaconid are connected by a cingulum along their anterior margin." All the specimens at hand referable to M_1 have the anterior cingulum, which is clearly separated from the protoconid and the metaconid. On most specimens at hand, the protostylid is connected to the buccal cingulu, but on one specimen (CM 33876), the protostylid is clearly separated from the cingulum. The degree of the development of the anterior cingulum usually varies among heteromyids. I believe the strong or weak development of the anterior cingulum is not a good criterion for separating species.

Although the present form has a small protoconid on M_1, I believe the morphology of the present form is not clearly separable from *Proheteromys nebraskensis*. The present form is best described as *Proheteromys* sp. cf. *P. nebraskensis*. And, I consider *Heliscomys schlaikjeri* to be conspecific with the present form.

Heliscomys sp. cf. **H. vetus** Cope, 1873
(Fig. 23, Table 10)

Referred specimens.—P^4-M^1: CM 17421, CM 33886–33889; P^4-M^2: CM 17091, CM 19879, KU 16626; P^4-M^3: CM 19787; P^4: CM 19790, CM 33890–33906; M^1-M^2: CM 33907; M^1: CM 17092, CM 33908–33923; M^2: CM 33924–33935; P_4-M_2: CM 19786; P_4-M_3: CM 33936; P_4: KU 16627, CM 17432, CM 19788, CM 33937–33940; M_1: CM 17424, CM 33941–33954; M_2-M_3: CM 33955; M_2: CM 17430, CM 33956–33966.

Locality.—Loc. 19, Badwater Creek, Wyoming.

Age.—Late Oligocene.

Description.—Nine upper jaw fragments with P^4 and M^1 are referable to *Heliscomys*. The size, both length and width, varies, even among these specimens. Materials referable to P^4 are not able to be separated into two groups on the basis of size. All the specimens referable to heteromyid P^4 are described below as *Heliscomys*, but surely some of them must be referred to *Proheteromys*. At present, I cannot tell morphological differences between the upper fourth premolars of *Heliscomys* and *Proheteromys* in the Oligocene.

P^4 shows a pattern of a large, anteriorly placed protocone and a three-cusped metaloph. The protocone and the hypocone are subequal and conical on most specimens. The metacone is a little smaller than the hypocone. On several specimens, the protocone is smaller than the hypocone and subequal to the metacone. The degree of the development of the entostyle varies; on some specimens, the entostyle is a small, low cusp; on some, it is a rudimentary cusp on the lingual base of the hypocone; on two specimens (CM 33891, CM 33897), the entostyle is not seen at all and the tooth has three cusps, one on the anterior loph and two cusps on the posterior loph. Galbreath stated (1953:63) that there seems to be a definite correlation between the size of the premolar and the amount of reduction of the entostyle. In the present fauna, no such correlation is seen; the cuspidate ento-

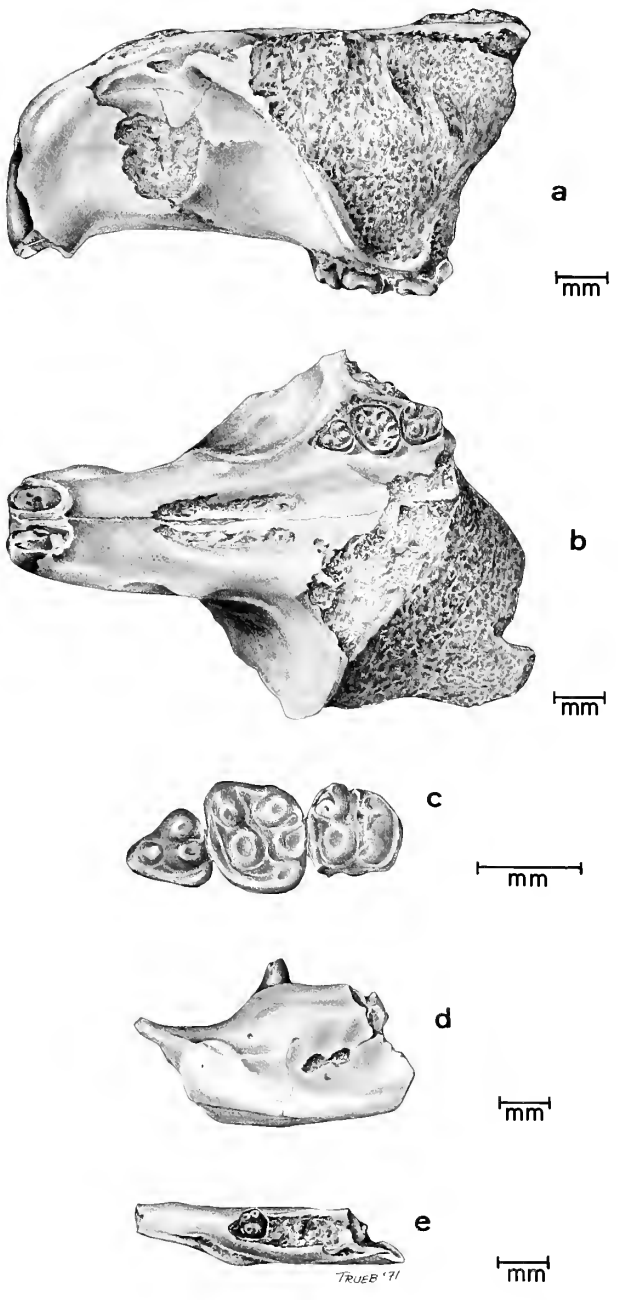


Fig. 23a–e.—*Heliscomys* sp. cf. *H. vetus*. a: KU 16626, skull with left P^4-M^2, lateral view. b: same, ventral view. c: same, crown view of teeth. d: KU 16627, left lower jaw with P_4, lateral view. e: same, crown view.

style is seen on both large and small teeth, and the rudimentary entostyle is also observed on both types. Most specimens show a tendency towards the formation of transverse lophs. The hypocone and the metacone share a common base and the valley separating these cusps is not deep. These two cusps are not discrete and with further wear they lose their individual identity. On one specimen (CM 17091), however, no tendency towards the formation of a loph is seen and the cusps are discrete. Even on this specimen, the entostyle is situated anterolingual to the hypocone as in another specimen. With wear, the metaloph and the entostyle give rise to an incipient J-pattern. The entostyle, if present, does not connect to the protocone. On some specimens, there is a small cusp at the anterobuccal base of the protocone. On others, no cusp is seen there.

The size of M^1 is considerably smaller than that of *Proheteromys*. The morphology of M^1 greatly varies. Some of them are not separable morphologically except by size from the corresponding tooth of *Proheteromys*. The principal cusps are subequal. The transverse valley is a little deeper than the anteroposterior valley. Great morphological variation is seen in the structure of the lingual cingulum. On some specimens (for example, CM 33907), the small but distinct protostyle is present just lingual to the protocone. It is separated from the anterior cingulum by a small notch, and from the entostyle by the transverse valley. In this form, the transverse valley is opened lingually. The entostyle is lingual and a little anterad to the hypocone, and only slightly smaller than the hypocone and the metacone. On one specimen (CM 33918), a small cusp is present at the anterolingual corner of the tooth and posterior to it another smaller cusp is present just linguad to the protocone. The entostyle is rather prominent. These three cusps form the lingual border of the tooth so that the transverse valley is not opened lingually. One specimen (CM 33917) shows the entostyle shifted more anteriorly closer to the small protostyle and it tends to block the transverse valley lingually. On this specimen, the entostyle is separated from the protostyle by a small notch, which lies little above the floor of the transverse valley. On other specimens (CM 33910, CM 33914), the entostyle is shifted further anteriorly just lingual to the transverse valley. From the entostyle, a thick ridge descends anteriorly and is confluent with the anterior cingulum. In this situation, it is impossible to distinguish either a protostyle or entostyle in this ridge. Thus the central valley is completely blocked by this lingual cusp. This morphology agrees exactly with that seen in *Proheteromys*. The protocone is of the same size as the paracone on M^1. Otherwise, morphologically this tooth is not easily separated from the corresponding tooth of *Proheteromys*.

M^2 agrees in most respects with the patterns seen on M^1, and the morphological variation among individuals seems to be reduced. The morphological differences from the pattern seen in M^1 are in the construction of the lingual cingulum and the styles. On M^2 there is a high ridge which closes the transverse valley at the lingual margin. In this ridge it is impossible to distinguish either a protostyle or entostyle. On several specimens (CM 33930, CM 33931, CM 33933), a small notch lingual to the transverse valley divides the lingual cingulum into two portions. The notch is not deep and both parts of the cingulum do not form any cusp. On all specimens, the connection of the lingual cingulum to the hypocone is stronger and at a higher level than is the connection to the anterior cingulum.

The mandible is rather slender. The diastema is short and the diastemal depression is shallow. The anterior end of the masseteric fossa is swollen and makes the jaw appear massive at this point. The mental foramen lies anterior to P_4, and almost on the dorsal surface of the mandible.

Nine specimens referable to heteromyid P_4 are available. They cannot be separated into two groups only based on size. Two jaw fragments with at least P_4 and M_1 are available, of which lower first molars are referable to *Heliscomys*. All the materials

of P_4 in this fauna will be described below as *Heliscomys* but the possibility that some of them should be referred to *Proheteromys* is not ruled out. Eight specimens of P_4 out of nine are quadricuspate. On most specimens, the m taconid, hypoconid, and entoconid are of equal size and height. On some specimens (CM 17432, CM 33938), the metaconid is the smallest and the hypoconid is the largest among these three cusps. Seven specimens out of eight quadriscuspate lower fourth premolars have the tiny protoconid, which is significantly smaller and lower than the metaconid and situated on the anterobuccal corner of the tooth. On six specimens out of these seven, the protoconid is separated by small notches from both the metaconid and the hypoconid. On one specimen (CM 33936), the protoconid is united with the hypoconid by a short ridge, but separated by the anteroposterior valley from the metaconid. On one specimen (CM 33903), the protoconid is much larger than on the other specimens although it is a little smaller than the metaconid. On this specimen, the protoconid is separated from both the metaconid and hypoconid. On all eight specimens there is an indication of a hypoconulid between the hypoconid and entoconid at the posterior margin of the tooth. One specimen (CM 33937) is triscuspate. On this, the metaconid is situated just anterad to the midline between the hypoconid and entoconid. The hypoconid is the largest and the other two cusps are of equal size. No shelf is seen on the anteroexternal corner of the tooth. No indication of a hypoconulid is seen.

The structure of M_1 and M_2 is very close to those of *Heliscomys vetus* described by Galbreath (1953) from the middle Oligocene of Colorado. The pattern of lower molars is that of four well-developed primary cusps more or less bordered on three sides by low cingula, which develop cusps. The teeth are cuspate rather than lophate, but with wear, lophs tend to form. The protostylid is larger than the hypostylid, but smaller and lower than the protoconid. On most specimens, the anterior cingulum is united to the anterolingual angle of the protoconid by a weak crest. The connection of the anterior part of the buccal cingulum to the protostylid varies; these two structures are separated by a notch, or where the cingulum is weak, it may unite to the protostylid without any notch between them. The transverse valley separates the protostylid from the hypostylid. Posterior to the hypostylid the cingulum varies from strong to weak, on some specimens extending across the posterior face of the entoconid and in others fading out on the posterior face of the hypoconid.

M_3 is composed of four well-developed primary cusps. Stylids are reduced. The hypoconid is somewhat reduced and is the smallest of the primary cusps. The anterior cingulum is weak on the face of the metaconid, absent at the midline of the anterior border of the tooth, and stronger on the anterior and buccal faces of the protoconid. The posterior cingulum is greatly reduced; on two specimens, it is absent completely, but on one specimen a small shelf lies on the posterior border between the hypoconid and the entoconid.

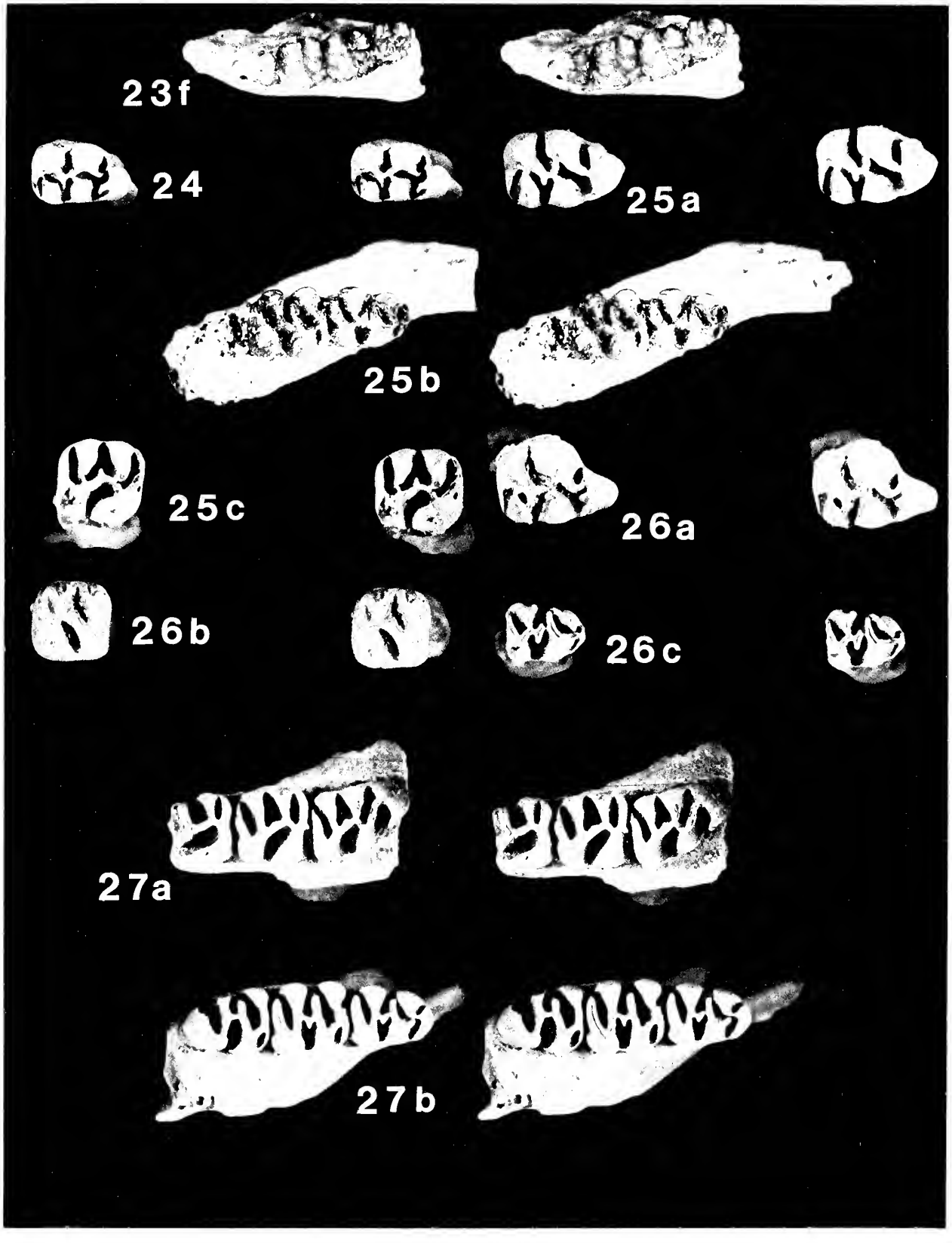
Discussion.—In size these specimens appear to be slightly larger than the mean for the middle Oligocene populations from Colorado discussed by Galbreath (1953:65). However, most of them fall well within the size range given for the Colorado specimens. Also, the structure of the cheek teeth and the variation seen in the present material coincide well with those which are observed in the earlier Colorado populations. The same situation was reported by Black (1965:45) for the early Oligocene population.

It must be noted that the morphological variation observed in the middle Oligocene populations is duplicated in the late Oligocene Badwater fauna, and also in the early Oligocene Pipestone material (Black, 1965); in the late Oligocene Badwater population, the three-cusped condition of P_4 as well as the four-cusped condition are both represented. Both the three-cusped and four-cusped condition persisted from the early Oligocene through the late Oligocene. Wood (1939:560), Wilson (1949*b*:115), Galbreath (1953:65) and Black (1965:45) have all suggested that the four-cusped condition of P_4 was primitive and that the three-cusped condition represented reduction from that more primitive stage. This would certainly seem the most probable evolutionary pattern in *Heliscomys*. In the late Oligocene population, the three-cusped condition is seen on only one specimen out of nine of P_4. Although the sample size is not big enough to determine definitely, it would appear that the selection was favoring the four-cusped condition and the reduction or eventual loss of the protoconid on P_4 was under somewhat strong selective pressure through the Oligocene Epoch. If this were the case, this variation suggests that *Heliscomys* was ancestral to *Proheteromys*.

Affinities of the Oligocene Heteromyids

The Oligocene and the early Miocene heteromyids having the three-cusped P_4 and more cuspidate molars tend to be assigned to *Heliscomys*, and those having the four-cusped P_4 and more lophate molars to *Proheteromys*. The morphological variation seen in P_4 of *Heliscomys vetus* creates a problems for the taxonomic assignment.

Heliscomys vetus has the three-cusped as well as the four-cusped P_4. The difference in morphology of P_4 is not a good criterion any more for the separation of *Heliscomys* from *Proheteromys*. It seems to me that the best criterion for separation of these genera is the degree of development of lophs and lophids on molars; *Proheteromys* is more lophate and *Heliscomys* is more cuspidate. If this is true, *Heliscomys tenuiceps* and *H. schlaikjeri* must be removed from the genus *Heliscomys* and referred to *Proheteromys*, because both forms have clearly lophate crown patterns.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27a
27b

On M_1 of both forms just mentioned, the lingual cingulum is high enough to block the transverse valley lingually. In *Heliscomys vetus*, M_1 has a moderate lingual cingulum having two styles, which are separated from each other by the continuation of the transverse valley. So the transverse valley is open lingually on this form. But the morphology of M_1 of *H. vetus* shows a considerable range of variation as stated in the description. From the "normal" situation of the lingual cingulum, it tends to unite two styles into single style and form a high ridge to block the transverse valley lingually. In an undescribed collection many specimens referable to *Heliscomys vetus* have exactly the same morphological variation. The variant having the strong lingual cingulum with a single style blocking the transverse valley is not easily separated from *Heliscomys tenuiceps* morphologically other than size. *H. tenuiceps* and *H. schlaikjeri* are larger than *H. vetus*. This suggests that *H. vetus* should have given rise to *H. schlaikjeri* via *Proheteromys nebraskensis*-stage in the late Oligocene.

Family Cricetidae Rochebrune, 1883

Eumys parvidens Wood, 1937

(Fig. 24, Table 11)

Referred specimen.—M_1: CM 32939.

Locality.—Loc. 19, Badwater Creek, Wyoming.

Age.—Late Oligocene.

Description.—M_1 is square-shaped, except for the anterocone. The tooth is smaller than that of *Eumys elegans*. The anterocone is large and situated on the buccal side of the tooth. The anterior cingulum is very short and curves posterobuccally; the posterobuccal end connects to the anterior arm of the protocone. A short ridge runs posterobuccally from the summit of the anterocone but does not reach the buccal border of the tooth. No connection between the anterocone and the paracone is seen so that a narrow valley runs buccally between these cusps. The protocone is stout and somewhat elongated anteroposteriorly. The anterior arm of the protocone descends anterobuccally from the anterobuccal corner of the protocone and turns anterolingually connecting to the anterior cingulum. A small valley is seen in front of the protocone. This valley is blocked anterolingually by a thin ridge forming the anterolingual corner of the tooth. The paracone is round and as high as the protocone, which is slightly higher than the anterocone. The paracone is situated buccal to the posterior half of the protocone. The mure is a thin ridge descending posterobuccally from the posterobuccal corner of the protocone turning posterolingually from the lingual extremity of the mesoloph. The protolophule II originates at the posterolingual corner of the paracone and runs lingually but slightly posteriorly. This connects to the mure at the middle of it between the posterobuccal corner of the protocone and the mesoloph. The mesoloph is short but distinct. This merges to the anterior border of the metacone at the midpoint of it so that a narrow valley runs buccally between the paracone and the mesoloph. The hypocone is stout and as high as the protocone forming the posterolingual corner of the tooth. A deep valley runs lingually between the protocone and the hypocone but is blocked lingually by a tiny entostyle. The metacone is somewhat compressed anteroposteriorly, and is situated just posterior to the paracone and buccal to the hypocone. It is almost as high as the paracone. The metalophule II runs almost lingually from the posterolingual corner of the metacone and connects to the body of the stout hypocone. A valley is present between the metacone and the hypocone but blocked by both the mesoloph anteriorly and the metalophule II posteriorly. The posterior cingulum runs buccally behind the metacone and connects to the posterobuccal corner of the metacone so that the valley just behind the metacone does not open buccally. All the ridges are very low.

Discussion.—This taxon is represented by a single tooth. The tooth is characterized by well-defined cusps and low ridges. The structure of the tooth differs from that seen in *Eumys elegans* in having the protocone and the hypocone essentially as high as the paracone and the metacone, anteroposteriorly elongated protocone, and low ridges. These characteristic features are less specialized than those of *Eumys elegans*, which shows more developed ridges. I agree with Wood (1937) who stated, "In general, this form (*E. parvidens*) has a primitive *Eumys* pattern on a small scale."

Eumys elegans Leidy, 1856

(Fig, 25, Table 11)

Referred specimens.—M^1: CM 32918–32921, CM 32940; M^2: CM 32922, CM 32923, CM 33109, CM 33110, CM 33112; M^3: CM 32926–32934; M_1-M_2: CM 17086; M_1: CM 32900–32905, CM 32907, CM 32908, CM 32910, CM 32911, CM 32935, CM 32936; M_2: CM 32912–32917, CM 32937, CM 33113; M_3: CM 32938.

Locality.—Loc. 19, Badwater Creek, Wyoming.

Age.—Late Oligocene.

Description.—On M^1, the anterocone is prominent and triangular in shape, with the apex leaning anteriorly. The anteroloph, or the anterior cingulum forming the base of the trigon of the anterocone, is transverse. The anterior arm of the protocone connects to the anterocone at the midpoint of the base of the triangle in most specimens. The paracone and the metacone are

←

Fig. 23f.—*Heliscomys* sp. cf. *H. vetus* (continued). f: CM 33936, left P_4-M_3. ×15. Fig. 24.—*Eumys parvidens*. CM 32939, left M^1. ×8. Fig. 25.—*Eumys elegans*. a: CM 32919, left M^1. ×8. b: CM 17086, right M_1-M_2. ×6. c: CM 32922, right M^2. ×8. Fig. 26.—*Eumys brachyodus*. a: CM 17412, left M^1. b: CM 32925, left M^2. c: CM 32909, right M_1. ×8. Fig. 27.—*Eumys*. sp. cf. *E. planidens*. a: CM 32941, right M^1-M^3. b: CM 19799, right M_1-M_3. ×8.

Table 11.—*Dimensions of teeth of* Eumys parvidens, Eumys elegans, *and* Eumys brachyodus.

	M^1		M^2		M^3		M_1		M_2		M_3	
Statistics	L	W	L	W	L	W	L	W	L	W	L	W
						Eumys parvidens						
N	1	1										
OR	2.40	1.45										
						Eumys brachyodus						
N	1	1	3	3			2	2				
OR	2.89	1.89	1.82–1.91	1.83–1.93			1.86–2.13	1.41–1.68				
Mean			1.860	1.880								
						Eumys elegans						
N	2	2	3	3	5	5	10	10	7	7	1	1
OR	2.84–2.98	1.70–2.02	2.03–2.07	1.77–2.03	1.44–1.67	1.51–1.80	2.09–2.70	1.51–2.07	2.07–2.31	1.71–2.01	1.96	1.78
Mean			2.050	1.880	1.568	1.660	2.293	1.715	2.186	1.871		
SD							0.171	0.178	0.101	0.111		
CV							7.45	10.37	4.60	5.91		

subequal but the latter is somewhat elongated transversely. Both are slightly taller than the protocone and the hypocone. The protocone is compressed posteriorly so that the posterior wall is vertical, whereas the anterior wall descends gently. From the summit of the protocone two ridges originate—one runs anterobuccally forming the anterior arm of the protocone, and the other runs almost transversely forming the protolophule II and connects to the paracone. The paracone is situated just buccal to the protocone. The mure is very short and runs anteroposteriorly. This connects to the protolophule II near the lingual corner of the paracone. The metaloph is very short but distinct. On most specimens the metaloph is situated between the paracone and the metacone, but on some (for example, CM 32920) it is closely related to the metacone though it does not unite to the latter. The hypocone is stout forming the posterolingual corner of the tooth. The anterior wall of the hypocone descends gently towards the posterior base of the protocone so that the valley between the protocone and the hypocone is very narrow in contrast to the wide valley in *Eumys planidens*. From the summit of the hypocone two ridges originate—one passes anterobuccally forming the anterior arm of the hypocone and the other runs buccally forming the posterior cingulum. The metalophule unites to the anterior arm of the hypocone just anterior to the hypocone. Because of the transversely elongated metacone, the metalophule is very short. All the ridges are rather thick and high above the crown of the tooth but they do not rise to the summits of the cusps.

M^2 is longer than wide. All the cones are compressed anteroposteriorly but are still well defined. The paracone and the metacone are taller than both the protocone and the hypocone. The protocone is elongated posterolingually. The anterior arm of the protocone forms the anterior cingulum so that no lingual part of the anterior arm of the protocone runs posterobuccally. The protolophule II is short and the protolophule I is not present. A narrow valley is present between the paracone and the anterior cingulum. The mure runs anteroposteriorly but is very short. The hypocone is smaller than in M^1. The anterior base of the hypocone extends anterobuccally forming the base of the anterior arm of the hypocone. The valley between the protocone and the hypocone runs posterolingually and is very narrow. This valley becomes deeper lingually. A short mesoloph is present between the paracone and the metacone. The metacone is elongated transversely and the metalophule is but a lingual extention of the metacone. The summit of the hypocone is shifted more lingually than in M^1 so that the valleys between the posterior cingulum and the metacone and the metacone and the mesoloph are longer transversely than in M^1.

M^3 is very small. The protocone extends posteriorly forming the lingual border of the tooth. The paracone is the tallest and the metacone is as high as the protocone. All the ridges rise to almost the same level of the protocone and the paracone. The bases of all the ridges and cusps are broad so that all the valleys between ridges and cusps are rather narrow. The protolophule II runs posteriolingually from the lingual corner of the paracone.

M_1 is long and narrows anteriorly. The anteroconid is elongated transversely and situated on the front of the tooth. The anterior arm of the protoconid runs anterolingually from the summit of the protoconid but soon turns anteriorly and joins the anteroconid just buccal to the midpoint of the tooth. No direct connection between the anteroconid and the metaconid is present on most specimens, but there is considerable variation in morphology; some have no connection of the anterior arm of the protoconid with the anteroconid (CM 32901); some have a connection between the anteroconid and the metaconid (CM 32900). The metaconid and the entoconid are subequal and taller than both the protoconid and the hypoconid. The lingual wall of the metaconid is curved lingually. The anterior and the posterior walls of the metaconid are very steep leaving a sharp crest between them, which forms the metalophulid I. The posterior protoconid arm runs posterolingually and then turns buccally. It connects with the posterior corner of the metaconid so that a basin without outlet is formed between the protoconid and the

metaconid on most specimens. On some specimens (CM 32900), the posterior arm of the protoconid is closely related to the metaconid but does not connect to it. The ectolophid runs almost anteroposteriorly and is lower in position than the posterior arm of the protoconid. The mesolophid is distinct but shorter than the posterior arm of the protoconid on most specimens. On one specimen (CM 32935), the mesolophid is clearly longer than the posterior arm of the protoconid but does not reach the lingual border of the tooth . The hypoconid is stout. The anterior arm of the hypoconid is short. The valley between the protoconid and the hypoconid is broad lingually but becomes narrower buccally. The posterior cingulum does not connect to the entoconid.

M_2 is slightly longer than wide. All the cusps are somewhat compressed anteroposteriorly. The metaconid and the entoconid are taller than the protoconid and the hypoconid. All the ridges rise to almost the same level as the protoconid and the hypoeonid. The anterior cingulum is complete buccally and lingually. The protoconid and the metaconid unite to the anterior cingulum separately. The posterior arm of the protoconid extends posterolingually. On some specimens (CM 32937), it runs between the metaconid and the entoconid, on some (CM 32912) it is closely related to the metaconid but does not reach the lingual border of the tooth, and on some (CM 32914) it reaches nearly the lingual border of the tooth and connects to the metaconid on its posterior base. The lingual portion of the mesolophid is not present. The buccal portion of it is clearly defined but short on most specimens. Some specimens (CM 17086) do not have the buccal portion of the mesolophid. The valley between the protoconid and the hypoconid is excavated posteriorly and narrow buccally. The ectolophid runs almost anteroposteriorly. The hypolophulid I runs transversely but slightly anteriorly. The anterior arm of the hypoconid runs anterolingually from the summit of the hypoconid. The posterior cingulum is strong.

On M_3, the general morphology agrees with that of M_2. The posterior protoconid arm reaches the lingual border of the tooth. The entoconid is greatly reduced. It forms a thin ridge like the posterior arm of the protoconid and runs parallel with the latter. The hypoconid is reduced and the valley between the protoconid and the hypoconid is deep. The posterior cingulum is not as strong as in M_2. The reduced hypoconid and entoconid and the weak posterior cingulum make the tooth narrower posteriorly.

Discussion.—The teeth of this species show a wide range of morphological variation. Based on the variable morphology, I believe, too many species of *Eumys* have been described. The type species of *Eumys* is *E. elegans*. The characteristic features of this species as listed by Wood (1937) are subequal buccal and lingual portions of the anterior cingulum, long posterior arm of the protoconid being free from both the metaconid and the entoconid, no lingual portion and weak buccal portion of the mesolophid, and reduced hypoconulid. Most of the present specimens referable to M_2 show exactly the same features. They surely belong to *E. elegans*.

One specimen (M_1, CM 32935) has a longer mesolophid than the posterior arm of the protoconid. This characteristic feature is seen in the European cricetid, *Cricetodon*. Wood (1937) described a similar form from the Upper Oreodon Beds of Nebraska under the name of *Cricetodon nebraskensis*. The present form is very close to the holotype of *C. nebraskensis* but all the morphology except the long mesolophid agrees with that of *Eumys elegans*. I am not confident to separate this form from *E. elegans*.

Martin (1972) placed *Eumys obliquidens, E. cricetodontoides, E. latidens, E. spokanensis* and *Cricetodon nebraskensis* into the synonomy of *E. elegans*.

Specific characters, especially of M_2, of each named species are summarized as follows: *Eumys obliquidens*—the posterior arm of the protoconid runs posteriomesiad and unites with the entoconid; *E. cricetodontoides*—lingual part of the anterior cingulum is long, posterior arm of the protoconid long but not united with metaconid, mesolophid short but distinct; *E. latidens*—lingual part of the anterior cingulum is half as long as the buccal part, posterior arm of the protoconid is not long and not united with the metaconid, no mesolophid; *E. spokanensis*—lingual portion of the anterior cingulum obsolete, posterior arm of the protoconid closely applied to entoconid, no mesolophid; *Cricetodon nebraskensis*—longer mesolophid than the posterior arm of the protoconid.

When Galbreath (1953) discussed the variation among the eumyine rodents, he stated that presence or absence of cingula are good but strength of development of cingula are poor criteria to evaluate the characters of the teeth. I agree with him. As for the present specimens referable to M_2, the buccal part of anterior cingulum is almost always present and extends along the buccal half of the tooth. Although the lingual part of it is usually present, the degree of development varies; it is long and extends to the lingual margin of the front of the tooth on some specimens, but it is short and half or less as long as the buccal part on the others. The degree of development of the lingual portion of the anterior cingulum used as the key to separate *E. latidens* from *E. cricetodontoides* by White (1954) is of no value. Various degrees of development of the cingulum are seen within the specific variation of *E. elegans*.

On most of the present specimens of M_2, a short buccal portion of the mesolophid is present. On one specimen (CM 17086), a tiny mesoconid is seen on the middle of the ectolophid but the buccal portion of the mesolophid is totally absent. The presence

or absence of short buccal portion of the mesolophid seems to me to be of no great value for taxonomic evaluation for species of *Eumys*.

I do not find any reasons to separate *E. cricetodontoides* from *E. elegans*. As I described above, CM 32912 is an *E. latidens*-type form and CM 32935 is a *Cricetodon nebraskensis*-type form. I believe they are variants of *E. elegans* and I cannot find any reasons to separate them from *E. elegans*. *E. obliquidens* and *E. spokanensis* are characterized by having the posterior protoconid arm closely applied to or united with the entoconid. No specimens in the present fauna show this characteristic feature. Based on the present Badwater Oligocene fauna, I agree with Martin (1972) in part to place *E. cricetodontoides*, *E. latidens*, and *Cricetodon nebraskensis* into the synonymy of *E. elegans*.

Eumys brachyodus Wood, 1937
(Fig. 26, Table 11)

Referred specimens.—M^1: CM 17412; M^2: CM 32924, CM 32925, CM 33096–33098; CM 33111; M^3: CM 33099, CM 33100; M_1: CM 32906, CM 32909.

Locality.—Loc. 19, Badwater Creek, Wyoming.

Age.—Late Oligocene.

Description.—The general morphology of M^1 almost agrees with the corresponding tooth of *Eumys elegans*. The present form differs from *E. elegans* in having a wider crown and the reduced anterocone. The crown is compressed anteroposteriorly. The anterocone is reduced. The anterior arm of the protocone unites with the anteroloph near its lingual margin, and from the summit of the anterocone one short ridge descends posterobuccally but this ridge does not connect to the paracone. The protocone leans buccally so that the protocone occupies the lingual half of the anterior part of the crown. The valley between the protocone and the hypocone is lying transversely and its anterobuccal extremity is very close to the lingual tip of the paracone. That valley extends buccal to the middle of the crown.

M^2 is wider than that of *Eumys elegans*. The width is almost subequal to the length, but on most specimens the length is little greater than the width. On one specimen (CM 32925), the crown is clearly wider than long. The lingual half of the anterior cingulum is not present on all specimens available. The valley between the protocone and the hypocone is long transversely. The mesoloph is very short.

Discussion.—The size of the present form is very close to that of *Eumys elegans*. The teeth of *E. brachyodus* is short and wider than *E. elegans*. Moreover, in *E. brachyodus*, the lingual half of the anterior cingulum is not present and the mesoloph is extremely short on M^2. The present form shows these morphology. The remainder of morphology of *E. brachyodus* is almost exactly the same as *E. elegans*. I believe that *Eumys brachyodus* has a common ancestry with *Eumys elegans*.

Eumys sp. cf. **E. planidens** Wilson, 1949*a*
(Fig. 17, Table 12)

Referred specimens.—M^1-M^2: CM 19795, CM 32943, CM 32944; M^1-M^3: CM 17088, CM 32941; M^1: CM 17413, CM 32946–32980, CM 33061, CM 33093, CM 33095, CM 33114; M^2-M^3: CM 19713, CM 32942, CM 32945; M^2: 33003, CM 33062, CM 33094, CM 33115, CM 33116; M^3: CM 17411, CM 17414, CM 33004–33026; M_1-M_3: CM 19798, CM 1979 ; M_1: CM 17416–17419, CM 33028–33037, CM 33063–33078, CM 33117, CM 33118; M_2: CM 17420, CM 33038–33060, CM 33079–33091, CM 33119.

Locality.—Loc. 19, Badwater Creek, Wyoming.

Age.—Late Oligocene.

Description.—On M^1, the anterocone is large. It is nearly two-thirds as wide as the tooth at the paracone-protocone line. All the cones except the anterocone are compressed anteroposteriorly and together with all the ridges rise to a nearly common plane. All the ridges are thin. The anterior protocone arm runs anterobuccally to reach the anterocone buccal at the midline. Between the anterior protocone arm and the anterior cingulum, a deep valley opens lingually. The posterior protocone arm runs posterobuccally but is short. It connects to the mure and the protolophule buccal to the paracone. Between the paracone and the anterior protocone arm, a valley opens deeply and runs anterobuccally. The protolophule is just a lingual extension of the paracone. No mesocone is seen, but a tiny buccal projection is present on the middle of the mure. The metalophule is also just a lingual extension of the metacone. The protolophule and the metalophule run parallel to each other and open into a wide valley lingually. This valley becomes narrower buccally because of the widened bases of the paracone and the metacone. The hypocone is also compressed anteroposteriorly so that the valley between the protocone and the hypocone is wide and opens lingually. The posterior cingulum located buccally from the hypocone forms a deep valley between it and the metalophule. This valley opens buccally. The tooth is characterized by deep valleys and thin ridges.

On M^2, the protocone is greatly compressed anteroposteriorly forming a high, thin ridge. The length of the protocone is almost half the width of the tooth. The anterior arm is short, half as long as the posterior protocone arm. The anterior arm merges into the buccal part of the anterior cingulum, which reaches to the anterobuccal margin of the tooth. No lingual anterior cingulum is seen. The paracone and the metacone are more compressed anteroposteriorly than on M^1 forming thin ridges running transversely. The valley between the paracone and the metacone opens more widely than on M^1, but is a little narrower buccally. The mure runs posterolingually and is situated in the center of the tooth. The hypocone is also more compressed than on M^1. The valley between the protocone and the hypocone is wide and opens posterolingually. The posterior cingulum runs from the hypocone buccally and slightly posteriorly. This cingulum is short, almost half as long as the metacone-metalophule. This cingulum does not form a wall on a posterobuccal corner of the tooth so that the valley between it and the metacone is wider than on M^1.

On M^3, the lingual portion of the anterior cingulum and the protocone form the anterior border of the tooth. The lingual margin of the protocone extends posteriorly and reaches to nearly the posterolingual corner of the tooth. A hypocone does not occur on this tooth but the ridge correlated to the anterior arm

Table 12.—*Dimensions of teeth of* Eumys *sp. cf.* E. planidens.

Statistics	M^1		M^2		M^3		M_1		M_2		M_3	
	L	W	L	W	L	W	L	W	L	W	L	W
N	16	16	11	1	13	13	16	16	12	12	4	4
OR	2.27–2.96	1.57–2.09	1.86–2.18	1.64–2.18	1.53–1.88	1.68–1.93	1.87–2.35	1.30–1.78	1.85–2.27	1.75–2.08	2.24–2.40	1.74–2.11
Mean	2.734	1.884	1.989	1.957	1.756	1.822	2.156	1.568	2.084	1.942	2.338	1.920
SD	0.176	0.126	0.107	0.132	0.102	0.070	0.153	0.131	0.135	0.105		
CV	6.42	6.69	5.37	6.74	5.80	3.83	7.10	8.33	6.50	5.43		

of the hypocone remains forming a posterior extension of the mure. The valley between the protocone on the one hand, and the mure and the anterior arm of the hypocone on the other, forms a wider, anteroposterior trench. No posterior eingulum is seen. The paracone and the metacone are thinner transversely than on M^2.

M_1 is longer than wide. The anteroconid is elongated transversely. The connections of the anteroconid with the anterior arms of the protoconid and the metaconid vary. On most specimens, the anterior arm of the protoconid runs anterolingually and unites with the anterior arm of the metaeonid, which runs almost transversely. Then the former turns anteriorly and connects to the anteroconid at its midpoint. The buccal part of the anterior cingulum is as long as the lingual part. On some specimens (CM 33029), the anterior arm of the protoconid joins the anteroconid more lingually so that the lingual part of the anterior cingulum is much shorter. Some specimens (CM 19799) show no connection between the anterior arms of the protoconid and the metaconid on an unworn stage, and only the anterior arm of the metaconid connects to the anteroconid on its lingual side so that the lingual part of the anterior cingulum is short. One specimen (CM 17416) shows peculiar features—the anteroconid on its buccal side; the lingual part of the anterior cingulum extends posteriorly and joins the anterior arm of the metaconid; no connection between the anterior arms of the protoconid and the metaconid at all. All the ridges and the anteroconid rise to the same level as the protoconid and the hypoconid. The metaconid and the entoconid are slightly taller than both the protoconid and the hypoconid. The posterior arm of the protoconid extends lingually but does not reach the lingual border of the tooth. This arm connects to the posterior margin of the metaconid at the base. A mesoconid is tiny and has a small buccal projection. No mesolophid is present. The entoconid is triangular in shape. The metalophid II is transverse. The valley between the entoconid and the posterior arm of the protoconid becomes narrower lingually but opens there. The hypoconid is compressed anteroposteriorly and forms a wide valley between it and the protoconid. The valley between them becomes narrower buccally because the buccal margin of the protoconid extends slightly posteriorly. The valley opens buccally. The posterior cingulum runs posterolingually to near the lingual border of the tooth forming a long valley between it and the entoconid. This cingulum does not connect to the entoconid.

M_2 has no lingual part of the anterior cingulum. The anterior wall of the metaconid has a small excavation indicating the original presence of a valley between the metaconid and as ancestral lingual anterior cingulum. The posterior cingulum is prominent. The metaconid is more stout than on M_1 but more compressed anteroposteriorly. The protoconid is also compressed. The posterior arm of the protoconid runs almost buccally. The base of that arm reaches to the lingual border of the tooth but does not connect to the metaconid so that the valley between it and the metaconid opens lingually. The mesoconid is small and has a buccal projection as in M_1. No mesolophid is present. The metalophid II is also transverse. The valley between the hypoconid and the protoconid is wide, but is blocked buccally by a small, thin ridge.

In M_3, the buccal part of the anterior cingulum is shorter than in M_2. No lingual part of the anterior cingulum is present. The posterior arm of the protoconid is short and the hypoconid is smaller than in M_2. No buccal projection on the mesoconid is seen. The valley between the protoconid and the hypoconid is wide and opens buccally. The posterior cingulum is prominent.

Discussion.—A new species of *Eumys, E. planidens,* was established on the basis of a single specimen (Univ. Colo. No 19810, a left ramus of mandible with M_2-M_3) by Wilson in 1949. Galbreath (1953) reported two additional lower jaws with M_1-M_3. The diagnostic features seen in the molars are ridges and cusps of grinding surface of cheek teeth rising to a nearly common plane. The specimens at hand show exactly the same characteristic features as the holotype of *E. planidens.*

The anteroposteriorly compressed cusps and thin ridges are characteristic of *E. planidens* and are not seen in any other species of *Eumys* described. Galbreath once stated that *E. planidens* may eventually be removed from the genus (Galbreath, 1953:74). Martin (1972) followed this argument and established a new genus for "*Eumys*" *planidens.* This should be published in the near future.

Three specimens of *Eumys planidens* have been reported. Galbreath (1953) described the morphological variation seen in the anteroconid of M_1. The present Badwater specimens show a greater variation than he recognized. He also mentioned an interesting variation seen in M_3 as follows: "In them, the posterior protoconid arm does not extend transversely beyond the mesoconid crest, whereas the type specimen has this arm extending to the internal

border." (His mesoconid crest must be called the entoconid crest, because no mesoconid or mesolophid is present at all on M_3.) On M_3 of the holotype of this species, the internal border between the internal extremities of the metaconid and the entoconid is concave internally making the posterior arm of the protoconid shorter than the entoconid crest even if this posterior arm extends to the internal border. But on the holotype, the grinding surface of this posterior arm is shorter than that of the entoconid crest so that this arm does not extend beyond the mesoconid crest. The base of the protoconid posterior arm extends to the lingual border so that the base of it is longer than the grinding surface. This situation is rather close to that in Galbreath's specimens.

Wilson (1949) stated in the description of the holotype that on M_2 and on M_3 the posterior arm of the protoconid is closely related to the metaconid. On M_3, the posterior arm of the protoconid runs linguad between the metaconid and the entoconid but slightly closer to the metaconid so that the valley betwe n the metaconid and the protoconid posterior arm is narro er than the valley between the latter and the entoconid. Even so the posterior arm of the protoconid does not unite with the metaconid. On M_2 of the holotype, the posterior arm of the protoconid is connected to the metaconid and the basin between the metalophid and the anterior arm of the protoconid on the one hand and the posterior arm of it on the other hand is blocked completely. Galbreath (1953) gave the description of the posterior arm of the protoconid as follows: the posterior protoconid arm is long and free, but closer to the metaconid than the entoconid. The Badwater specimens of M_2 show variation in length of the posterior protoconid arm; on more specimens, it runs between the metaconid and the entoconid, closer to the former but free and does not reach to the lingual border of the to th; on some (CM 33045 and 33053) it nearly reaches to the lingual border. Most specimens have no metastylid but on one specimen (CM 33048) a tiny but distinct metastylid is seen on the lingual border just linguad to the posterior protoconid arm, which does not extend to the lingual border of the tooth.

On M_2 of the holotype, the entoconid and the hypolophulid lingual to its union with the ectolophid form a straight transverse ridge but the hypolophulid buccal to the ectolophid (= the anterior arm of the hypoconid) runs posterobuccally forming a thin ridge. So these two ridges join with an angle at their union with the ectolophid. On the Badwater specimens, these two ridges form a straight line without an angle making a straight transverse hypolophulid.

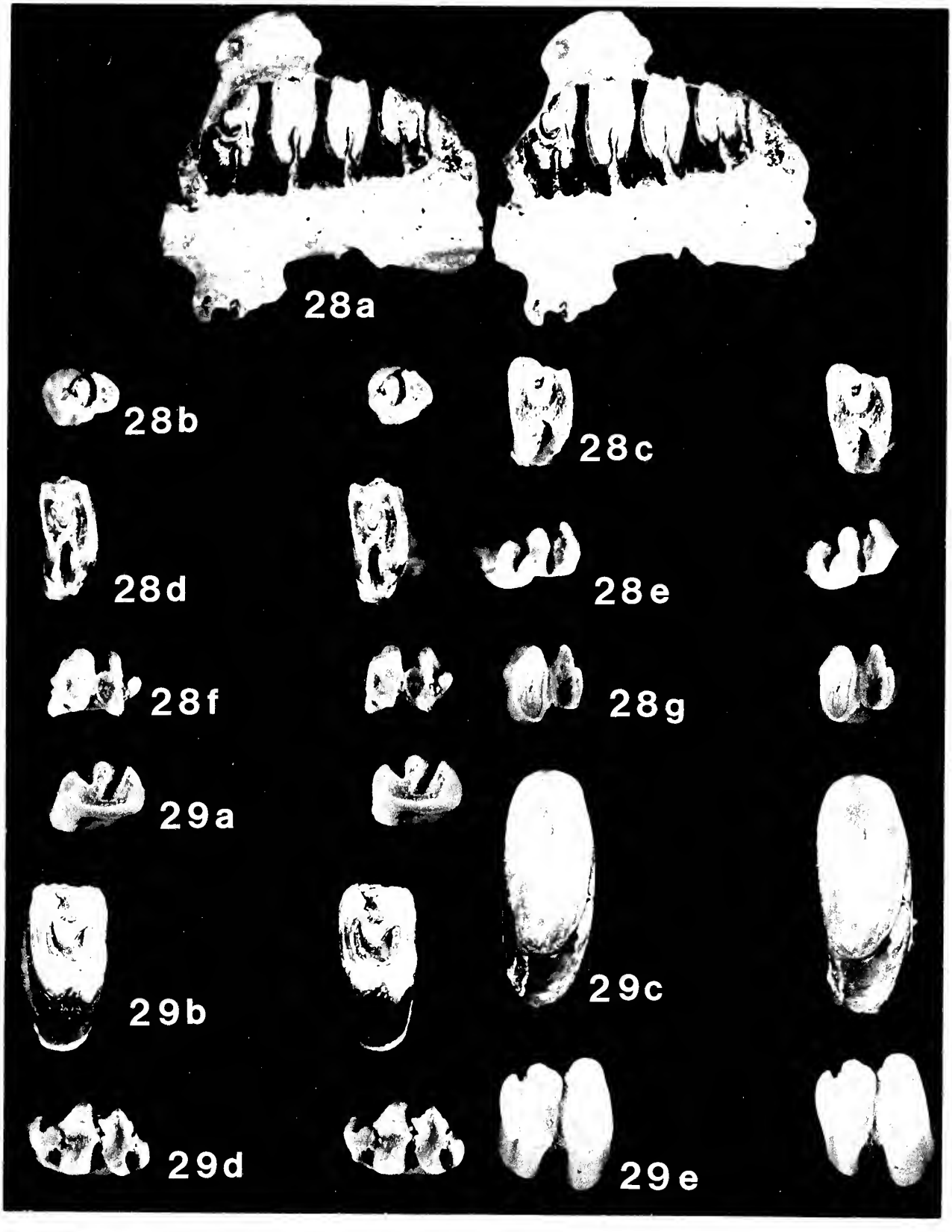
Carnegie Museum of Natural History has a few undescribed specimens referable to *Eumys planidens* from Toadstool Park, Nebraska, Orellan, or the middle Oligocene in age. On some of the referable M_2s, the posterior arm of the protoconid does not connect to the metaconid even if the former is close to the latter. This condition is rather close to the Badwater specimens. On all teeth from the Toadstool Park referable to M_2, the hypolophulid lingual to the ectolophid joins the anterior arm of hypoconid at an angle as seen in the holotype. In all the species of *Eumys* except for *"Eumys" planidens*, the hypolophulid lingual to the ectolophid joins to the hypoconid anterior arm at an angle so that the situation seen in the holotype of *E. planidens* is close to the generalized forms of *Eumys* species. Although there is a considerable time span between the middle to the late Oligocene, the present forms are best described as *Eumys* sp. cf. *Eumys planidens*.

Order Lagomorpha
Family Leporidae Gray, 1821
Palaeolagus burkei Wood, 1940
(Fig. 28, Table 13)

Referred specimens.—skull: CM 33967; DP^2: CM 33968–33977; DP^3: CM 17075, CM 33978–33998; P^3-P^4: CM 34035, CM 34036; P^3-M^2: CM 34037; P^3: CM 33999–34008; DP^4 and P^4: KU 16631; DP^4: CM 34009–34029; P^4: CM 19712, CM 34030–34034; M^1: CM 18267, CM 34038–34042; M^2: CM 34043–34050; DP_3: CM 34051–34059; P_3: CM 18269, CM 34060–34077; DP_4: CM 34078–34093; P_4: CM 34094–34100; M_1: CM 17075, CM 34101–34103.

→

Fig. 28.—*Palaeolagus burkei*. a: CM 39037, left P^3-M^2, ×5. b: CM 38968, right DP^2, ×8. c: CM 38980, right DP^3, ×8. d: CM 39011, right DP^4, ×8. e: CM 39051, right DP_3, ×8. f: CM 39081, right DP_4, ×8. g: CM 39101, right M_1, ×8. Fig. 29.—*Palaeolagus* sp. cf. *P. intermedius*. a: CM 39105, right DP^2. b: CM 39107, left DP^4. c: CM 39108, right M^1. d: CM 39109, right DP_2. e: CM 39110, right M_2. ×8.


28a
28b
28c
28d
28e
28f
28g
29a
29b
29c
29d
29e

Locality.—Loc. 19, Badwater Creek, Wyoming.

Age.—Late Oligocene.

Description.—The skull is flat. The braincase is not inflated. The plane of the palate is not bent on the basicranial axis, and the angle between the plane of the palate and the basicranial axis is small. The snout is very narrow and slender.

On DP^2, the tooth has two anterior re-entrants; one is on the anterobuccal corner of the tooth and crosses one-third or one-fourth of the occlusal surface; the other is situated lingual to the midline of the tooth and crosses almost two-thirds of the occlusal surface. The latter re-entrant persists to the base of the tooth whereas the former does not extend to the base of the tooth and will be obliterated in an earlier stage of wear. A small and shallow posterolingual re-entrant is observed, which will also be obliterated with wear. The enamel is well developed lingually and is reduced buccally.

Several specimens are identified as DP^3. In these, the tooth has buccal roots. An isolated crescent is present between the central and lingual lobes. The anterior extension of the crescent is longer transversely than the posterior one. The enamel is thicker anteriorly than posteriorly. Cement is weakly developed.

The anterior loph of P^3 is narrower transversely than the posterior loph. Following moderate wear, the tooth has an internal, straight walled hypostria crossing about one-third of the occlusal surface. A J-shaped crescent has a connection to the anterobuccal side of the tooth. Following further wear, the hypostria becomes shortened and the crescent completely worn away.

Several deciduous upper fourth premolars are recognized. One of them (KU 16631) is a DP^4 with unerupted permanent P^4 underneath. These two teeth were carefully separated. DP^4 has buccal roots, but they are short and weak. The anterior loph is a little narrower transversely than the posterior loph. An isolated crescent which is concave buccally is retained between the central and lingual lobes. Another small, circular crescent is present just inside and a little buccal to the convex crescent just mentioned above. These crescents will be obliterated with further wear. On most specimens, the hypostria are straight-walled, but on some specimens (for example KU 16631) the posterior wall is crenulated. The enamel is well developed on its anterior and lingual sides, reduced on the buccal side, and absent on the posterior side and on the posterobuccal corner of the tooth.

On an unworn specimen of P^4 (KU 16631), the anterior loph is slightly narrower than the posterior loph. The crown is square-shaped but will be elongated transversely with wear. The central lake is elongated anteroposteriorly but does not have a connection to the anterobuccal side of the tooth. The hypostria is straight-walled but at an unworn stage the anterior and posterior walls meet with an angle nearly 90°. With wear the hypostria becomes narrower. The enamel is thicker anteriorly than posteriorly. The buccal wall is formed by thin enamel, but with further wear the enamel becomes absent.

When worn, P^4, M^1, and M^2 resemble one another in pattern. The crescent is completely worn away. In occlusal view each of these teeth has an internal, straight-walled hypostria crossing nearly one-half of the occlusal surface. The teeth become narrower transversely from P^4 to M^2.

On DP^3, there are three main lobes. The central lobe is the tallest when unworn. The posterior lobe is the widest transversely. The enamel is developed on the anterior face of the anterior lobe and the posterior face of the central lobe. No separation by an enamel and between the anterior and the central lobes is seen even when unworn. The posterior lobe is completely surrounded by enamel when unworn. With slight wear, the anterior and the central lobes unite together forming a single lobe clearly separated from the posterior lobe. With further wear, anterior lobe and the posterior lobe unite, first in the middle of the tooth and next on the lingual side, leaving a small enamel lake on the lingual side of the tooth. The small lake will be lost with further wear.

P_3 has only two lobes. The talonid is wider transversely than the trigonid. After wear the internal re-entrant between the trigonid and talonid is retained. A shallow groove is present on the anterobuccal corner of the trigonid. This groove runs all the way down to the base of the tooth.

On DP_4, the tooth has two main lobes and a small accessory one. The anterior lobe is the trigonid and the second one is the talonid. The small accessory lobe is the hypoconulid. On unworn teeth, the hypoconulid is separated by enamel from the trigonid but soon they unite and the hypoconulid will be obliterated. The union of the trigonid and the talonid is solely by cement as in P_4.

P_4, M_1, and M_2 resemble one another in pattern. No unworn specimens referable to P_4 are available. Worn specimens have only two lobes. One specimen (KU 16630) has an almost unworn DP_4 and unworn M_1 *in situ* in the same individual. The unworn specimen of M_1 has a tiny hypoconulid posterior to the talonid. The hypoconulid is smaller than the corresponding cusp on DP_4 and is especially narrower transversely. This cusp on M_1 will be obliterated with further wear. Although no unworn materials of P_4 are known, I assume that P_4 has the hypoconulid posterior to the talonid when unworn, because DP_4 and M_1 have a clear hypoconulid before wear.

M_3 consists of two small lobes of which the posterior one is the smallest.

Discussion.—The present form is directly comparable to the materials described by Wood (1940) and Dawson (1958). On P_2, although shallow, the anterior re-entrant is persistent to the base of the tooth. This characteristic feature is seen in *Palaeolagus burkei*, but not seen in *P. hypsodus*. In this respect, the present form is closer to *P. burkei* than to *P. hypsodus*.

Palaeolagus sp. cf. **P. intermedius** Matthew, 1899
(Fig. 29, Table 13)

Referred specimens.—DP^2: CM 34104–34106; DP^4: CM 34107; M^1: CM 34108; DP^3: CM 34109; M_2: CM 34110.

Locality.—Loc. 19, Badwater Creek, Wyoming.

Age.—Late Oligocene.

Description.—These teeth are larger than those of *Palaeolagus burkei*. A DP^2 is tentatively referred to this species. The tooth has two anterior re-entrants; one is on the anterobuccal corner of the tooth, and the other is just lingual to the midline of the tooth and crosses almost two-thirds of the occlusal surface. The latter re-entrant is persistent to the base of the tooth. The enamel is well developed posteriorly and lingually but reduced buccally.

The material referable to DP^4 is larger than the corresponding

Table 13.—*Dimensions of teeth of* Palaeolagus burki *and* Palaeolagus *sp. cf.* P. intermedius.

Palaeolagus burkei

	DP^2		DP^3			P^3			DP^4			P^4			M^1			M^2		
	L	W	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW
N	4	4	5	5	5	5	5	5	6	6	6	4	4	4	4	4	4	4	4	4
OR	1.40–1.60	0.98–1.13	1.23–1.50	1.52–1.76	1.98–2.30	1.49–1.67	1.50–1.93	1.99–2.85	1.30–1.56	1.86–2.49	1.74–2.43	1.39–1.82	1.74–2.96	1.87–3.09	1.46–1.65	2.43–2.83	2.67–3.03	1.21–1.41	2.14–2.53	1.93–2.24
Mean	1.540	1.035	1.402	1.658	2.116	1.568	1.776	2.432	1.400	2.103	2.067	1.600	2.353	2.450	1.550	2.610	2.813	1.303	2.273	2.010

	DP_3		P_3			DP_4			P_4			M_1			M_2		
	L	W	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW
N	4	4	4	4	4	4	4	4	4	4	4	4	4	4			
OR	2.08–2.30	1.30–1.79	1.85–2.21	1.25–1.51	1.56–1.83	1.63–2.12	1.44–1.56	1.42–1.57	1.68–1.88	1.77–1.96	1.46–1.68	1.79–1.87	1.55–1.91	1.34–1.60			
Mean	2.165	1.610	2.005	1.350	1.695	1.833	1.518	1.498	1.783	1.890	1.568	1.838	1.743	1.480			

Palaeolagus sp. cf. *P. intermedius*

	DP^2		DP^3			P^3			DP^4			P^4			M^1			M^2		
	L	W	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW
N	3	3							1	1	1				1	1				
OR	1.91–2.20	1.29–1.42							1.98	2.62	2.84				2.22	4.30	—			
Mean	2.067	1.340																		

	DP_3			P_3			DP_4			P_4			M_1			M_2		
	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW
N	1	1	1													1	1	1
OR	3.00	1.85	1.65													2.79	2.37	2.16

tooth of *P. burkei*. The general morphology agrees with that of *P. burkei*.

The upper molars are also larger than those of *P. burkei*. The hypostria is shallower than in *P. burkei*, and on worn specimens the hypostria almost vanishes. Only a shallow groove remains on the posterolingual face of the tooth.

On DP^3, there are three lobes and a small accessory one. The anterior three lobes resemble those seen in DP_3 of *P. burkei*. The accessory one is half as wide transversely as the posterior lobe. The morphology of the remainder of the crown agrees with that seen in *P. burkei*.

Discussion—Based on its larger size and the shallow hypostria, these specimens are referred to *P. intermedius*.

Order Carnivora
Family Canidae Gray, 1821

Hesperocyon temnodon (Wortman and Matthew, 1899)
(Fig. 30, Table 14)

Referred specimen.—CM 21678.

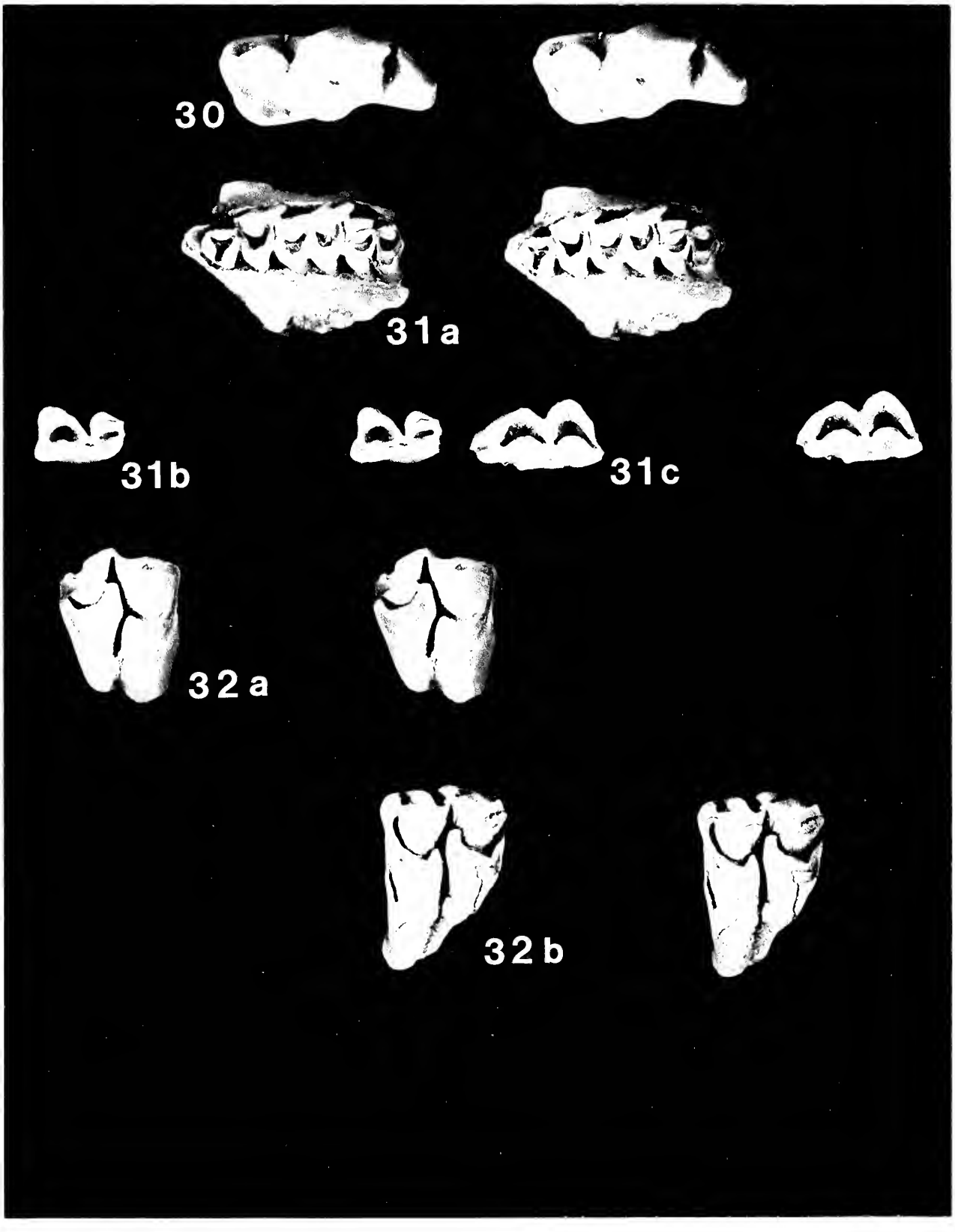
Locality.—Loc. 19, Badwater Creek, Wyoming.

Age.—Late Oligocene.

Discussion.—Only one specimen referable to this species is available. Matthew (1901:357) referred a specimen from the *Leptauchenia* zone in Logan County, northeastern Colorado, to this species, but he did not describe the specimen. Galbreath

Table 14.—*Dimension of teeth of* Hesperocyon temnodon *and* Leptomeryx *sp. near* L. evansi.

Statistics	M^1			M^2			M_1		
	L	AW	PW	L	AW	PW	L	AW	PW
Hesperocyon temnodon									
N							1	1	1
OR							9.88	4.25	4.16
Leptomeryx sp. near *L. evansi*									
N	1	1	—	1	1	1	—	—	—
OR	5.62	6.29	—	8.69	8.69	8.21	—	—	—


30
31a
31b
31c
32a
32b

(1953:76) cited Matthews but also did not describe the material. *H. temnodon* was originally established by Wortman and Matthew (1899:130) as *Cynodictis temnodon* based on an upper dentition. Macdonald (1963:202) listed the characteristics of M_1 of *Hesperocyon* as: entoconid present; one or two enteroconids; deeply basined talonid; talonid closed posteriorly. The present specimen shows this morphology. In size it is smaller than *H. leptodus*. Tentatively, the present specimen is referred to *H. temnodon*.

Order Perissodactyla
Family Equidae Gray, 1821
Miohippus sp.

Referred specimen.—Astragalus: CM 21679.

Locality.—Loc. 19, Badwater Creek, Wyoming.

Age.—Late Oligocene.

Discussion.—An astragalus is the only equid specimen available. The size of the astragalus is clearly larger than that of *Mesohoppus* and a little larger than that of *Miohippus equiceps* described and figured by Osborn (1918:324). No teeth referable to this genus are available. The specific identification is difficult.

Family Hyracodontidae Cope, 1879
Hyracodontidae genus indet.

Referred specimens.—Tooth and limb bone fragments: uncatalogued.

Locality.—Loc. 19, Badwater Creek, Wyoming.

Age.—Late Oligocene.

Discussion.—Small fragments of teeth and limb bones of hyracodont rhinoceros have been found, but nothing is generically determinable.

Order Artiodactyla
Family Hypertragulidae Cope, 1879
Leptomeryx sp. near **L. evansi** Leidy, 1853
(Fig. 32, Table 14)

Referred specimens.—P^3: CM 21694; M^1: CM 21695; M^2: CM 21696; M_1: CM 21693.

Locality.—Loc. 19, Badwater Creek, Wyoming.

Age.—Late Oligocene.

Discussion.—The materials at hand are too incomplete for specific identification. The size is very close to or a little larger than that of *Leptomeryx evansi*. The tooth morphology is almost exactly the same. CM 21696 is a second upper molar where the buccal face of the metacone is not completely flattened but a small ridge runs vertically on the middle of the surface. This part of the enamel is slightly thickened so that the buccal face of the metacone is rather convex buccally. On most specimens of *L. evansi* which I examined the buccal face of the metacone is flat or slightly concaved.

Leptomeryx is a typically Oligocene genus. Scott (1940:537) stated, "It (=*Leptomeryx*) is one of the commoner fossils of the lower Brule (Oreodon Beds) and is much less frequently found in the upper Brule, or the Chadron. It persisted through the John Day and into the lower Miocene (Gering stage)." Occurrences of *Leptomeryx* from the lower Miocene were reported by Macdonald (1963:233) from western South Dakota and Martin (1972) from western Nebraska. The materials referrable to *Leptomeryx* reported by them are again too fragmentary to warrant specific identification.

Hypisodus sp. near **H. minimus** (Cope, 1873)
(Fig. 31)

Referred specimens.—M^1-M^3: CM 21682; M^1: CM 34111, CM 34112; M^2: CM 21684, CM 21687, CM 34113; P_3: CM 21688; M_1: CM 21683, CM 21685, CM 21686, CM 21690, M_2: CM 21689.

Locality.—Loc. 19, Badwater Creek, Wyoming.

Age.—Late Oligocene.

Description.—The size of the present form is a little larger than that of the holotype of *Hypisodus minimus*. A similar form has been reported by Scott (1940:535) from "the Uppermost Brule" of eastern Nebraska and by Galbreath (his Form B, Galbreath, 1953:91) from the Vista Member of the White River Formation of northeastern Colorado. On specimens of the present form, the upper molars have a weak buccal style, or a median rib on the anteroexternal crescent of Scott (1940:525) so that the vertical valley between the style and the parastyle is very shallow. But on a few specimens (CM 39111, M^1 and CM 21684, M^2), the upper molars have a fairly well-developed buccal style on the buccal face of the paracone so that the valley between it and the parastyle is fairly deep. The degree of the depth of that valley also depends on the orientation of the parastyle. On the specimens having a shallow valley, the parastyle projects rather anteriorly whereas the parastyle extends more anterobuccally on molars having a deeper valley. Thus, the degree of weakness of the buccal style on the buccal face of the paracone and the depth of the valley have a fairly wide range of variation.

Discussion.—*Hypisodus* has been thought to be restricted to the Oligocene. Martin (1972), however,

←

Fig. 30.—*Hesperocyon temnodon*. CM 21678, left M_1. ×4. Fig. 31.—*Hypisodus* sp. near *H. minimus*. a: CM 21682, right M^1-M^3. b: CM 21685, right M_1. c: CM 21689, right M_2. ×4. Fig. 32.—*Leptomeryx* sp. near *L. evansi*. a: CM 21695, right M^1. b: CM 21696, left M^2. ×4.

reported an occurrence of *Hypisodus* from the lower Miocene Gering formation of western Nebraska. His form is larger than any other known species of *Hypisodus*. He stated that the labial styles are low and flattened. As stated above, based on the present samples at hand, the degree of development of styles varies from specimen to specimen. Size seems to be the only criterion for separating species of *Hypisodus*.

SUMMARY AND CONCLUSIONS

Besides a few lower vertebrates, only small mammals have been recovered from the upper Oligocene sediments along Badwater Creek. The preserved fauna of the Cedar Ridge local fauna is greatly biased by two major factors, which are wholly independent of each other; first, due to stream action, only small teeth and bones were transported and deposited at Loc. 19 so that larger mammals, which surely lived near the site of deposition during the late Oligocene are not represented in the fauna; second, due to drier climatic conditions along Badwater Creek in late Oligocene time, only land animals, which were adapted to such kind of ecological conditions, could live there and consequently these animals are represented in the fauna, whereas the animals, which required more mesic conditions, could not have lived there and therefore they are not represented in that fauna.

The drier climatic condition along Badwater Creek in the late Oligocene is indicated by the presence of calcic feldspars and evaporites throughout the section. These were formed under a climatic regime with moderate temperatures. Although no botanical evidence has been recovered, the environmental situation is thought to be of a grassland, steppe to semidesert type with low precipitation and moderate temperature.

Due to unfavorable ecological conditions, land micromammals, which lived there during late Oligocene time, were specialized in having higher crowned and more lophate teeth. This was the result of adaptation to a more herbaceous diet in drier climatic conditions. Some of the rodents represented had more hypsodont teeth than in their middle Oligocene counterparts, but they have never developed rootless or everygrowing cheek teeth.

Among rodents, many specialized eomyids are the most common constituents of the Cedar Ridge local fauna. Eomyids appear to have had their major North American radiation during the early Oligocene. Wilson (1949:112) pointed out that the tooth pattern in eomyids is similar to, although not identical with, the cricetodont pattern. As Black (1963:41) has stated, it is quite possible that members of the Eomyidae occupied many of the same habitats that were later filled by the cricetids. Only a few cricetids are at present known from the early Oligocene when the major radiation of the Eomyidae took place (Clark, et al., 1964). It seems possible that many of the early Oligocene eomyids such as *Yoderimys*, *Centimanomys*, *Namatomys*, and *Aulolithomys* were replaced by the more highly specialized cricetids during Chadronian time. Eomyids became abundant and varied in the late Oligocene perhaps through adaptation to drier climatic conditions and more open environmental situations. Eumyine cricetids are abundant in the Orellan and by the Arikareean, a number of cricetid types are known. Most of them, however, required more mesic conditions and surely lived under a more hospitable climate in present Oregon and Nebraska. Among cricetid rodents, *Leidymys*, *Paciculus*, and *Scottimus* are known from the late Oligocene of Oregon and Nebraska, but they are not represented in the Cedar Ridge local fauna. Highly specialized eomyids and also a few highly specialized cricetids coexisted in the Badwater Creek area during the late Oligocene time.

Near the Oligocene-Miocene boundary, the environment returned to a more mesic condition with considerable precipitation. In relation to the climatic changes, the highly specialized eomyids and cricetids, which were adapted to drier conditions, could not survive and most of them became extinct by the end of the Oligocene. Subsequently, cricetids represented by *Leiydyms*, *Paciculus*, and *Scottimus* expanded during the Miocene.

An eomyine genus, *Pseudotheridomys*, is represented in the North American early Miocene by *P. hesperus* (Wilson, 1960) from the Martin Canyon Quarry A fauna. This species, however, is closely related to European forms and evidently represents an early Miocene immigration into the New World. Thus, most of the North American Oligocene eomyids became extinct by the end of the Oligocene and a few forms could have survived into Miocene time.

It is worth discussing whether any new forms

migrated into North America from some other center of radiation during the Oligocene. Based on the study of the late Eocene Badwater local fauna, Black, (1967:63) stated, "Many groups that made their first appearances in the late Eocene may represent immigrants from other areas and thus were not present in earlier North American faunas." I agree with his conclusion. Thus, many groups represent immigrants into North America from other areas in the late Eocene. Now we have to consider whether any forms represent immigrants during the Oligocene.

The eomyids were probably descended from members of the Sciuravidae (Black, 1965:42), sometime during the latter half of the Eocene, but their ancestors are not known as yet. The number and diversity of eomyids now known from the early Oligocene would seem to indicate either a much greater late Eocene radiation in North America than has been recognized to date or a considerable immigration into western North America in the latest Eocene from some other center of radiation. Only *Adjidaumo* and *Paradjidaumo* persist into the middle Oligocene and, by the end of the Oligocene a number of specialized eomyids have evolved from the ancestral stocks of *Adjidaumo* and *Paradjidaumo*. The major Old World eomyid radiation evidently took place during the Aquitanian and Burdigalian (early to middle Miocene). As far as the North American eomyids are concerned, they evolved within the North American continent and they did not receive any new comers from outside North America although the possibility of an immigration from North America to Europe can not be ruled out. After the climate returned to a more hospitable condition in the late early Miocene, some European eomyids, for example, *Pseudotheridomys* (Wilson, 1960) and *Eomys* (Lindsay, 1974), migrated into North America. These forms are not descendents of the North American Oligocene eomyids.

The origin of the Cricetidae is not certain. It seems likely that the cricetids along with many other rodent families may be derived from late Eocene sciuravids. The North American Cricetidae are already abundant in the lowermost Orellan (Martin, 1972) in Nebraska. They are very close to certain Eurasian cricetids, notably *Eucricetodon* and *Pseudocricetodon,* and it seems likely that there was an exchange of cricetids between North America and Eurasia in the Chadronian (early Oligocene). As the place of the origin of the cricetids is unknown, the direction of this exchange is not clear; however, it seems likely that it took place soon after the probable time of origin of the Cricetidae in the late Eocene. But, once the basal stocks of the cricetids had been established in North America sometimes during the early Oligocene, they evolved in North America and it seems likely that the cricetids replaced eomyids in large part during the middle Oligocene. *Cricetodon* has been described from the Upper Oreodon Beds (middle Oligocene) of Nebraska by Wood (1937:256). *Cricetodon* is a European genus and if the material described by Wood is referable to *Cricetodon,* it must represent an immigration from Europe into North America during the middle Oligocene. Close examination, however, shows that having the mesolophid longer than the posterior arm of the protoconid on M_1 and M_2 is seen not only in *Cricetodon,* as Wood believed, but in some other forms of North American cricetids as well, especially *Eumys elegans*. The material described by Wood thus does not represent an immigrant from Europe, but should be regarded as a variant of the North American *Eumys*-complex. All the North American late Oligocene cricetids have their ancestry in the middle Oligocene of North America (Martin, 1972).

The other rodents and insectivores in the Cedar Ridge local fauna have their ancestry in the middle and even in the early Oligocene of North America. Thus, the late Oligocene mammal fauna represented by the Cedar Ridge local fauna has a close relationship to the middle Oligocene faunas of North America and no great faunal gap between them is recognized. Because most of the "typical" North American Oligocene eomyids and some cricetids became extinct by the end of Oligocene and some forms migrated into North America during the Miocene, a more distinct faunal gap is recognized between the late Oligocene and the early Miocene faunas than between the middle and the late Oligocene faunas.

The rodent families Castoridae (beavers), Mylagaulidae (mylagaulids), and Aplodontidae (aplodontids besides *Prosciurus* and *Pelycomys*) are almost always found in faunas of the early Miocene of North America. They are totally absent from the Cedar Ridge local fauna and this makes the faunal distinction clearer, between the late Oligocene and the early Miocene faunas.

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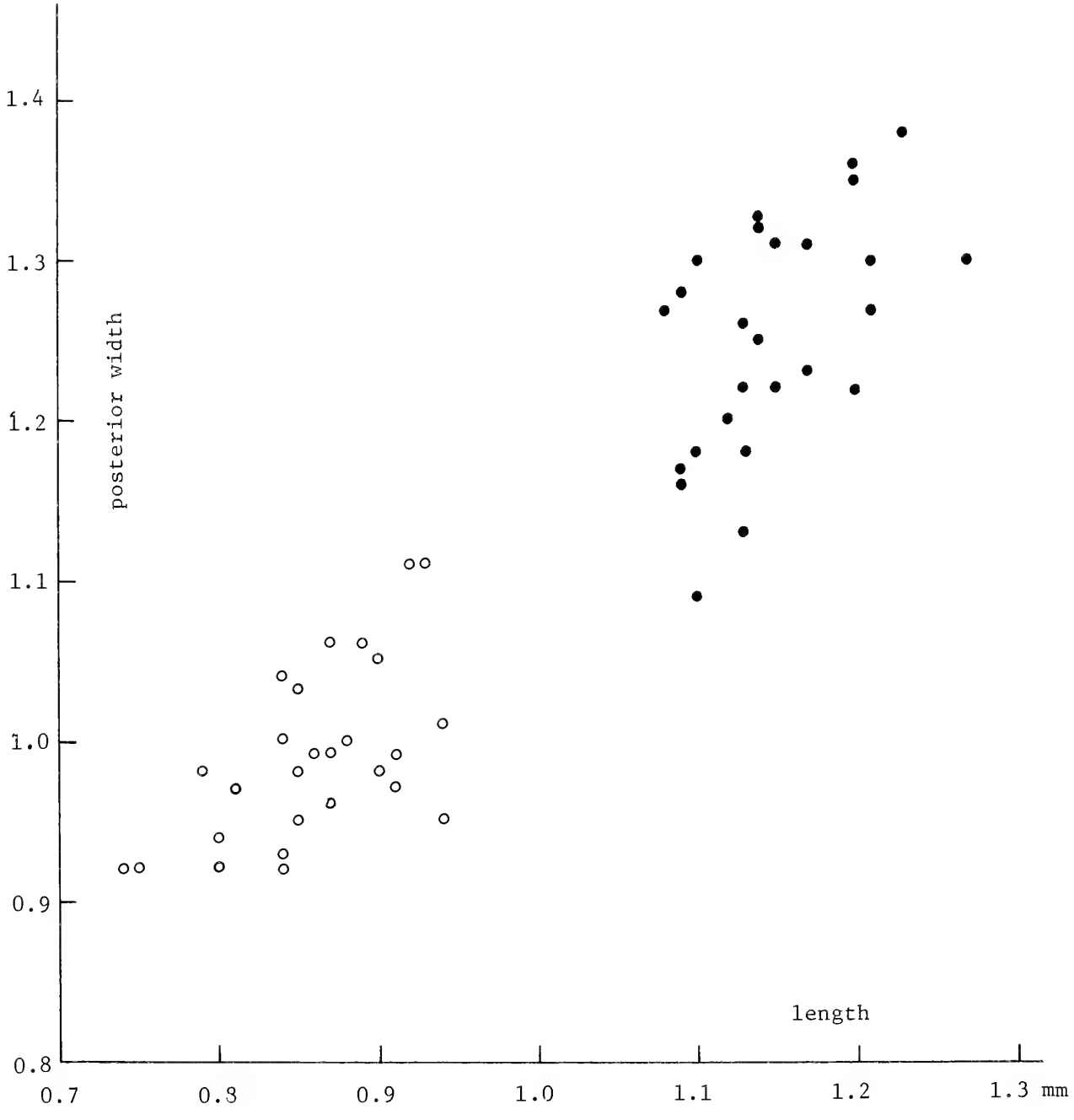
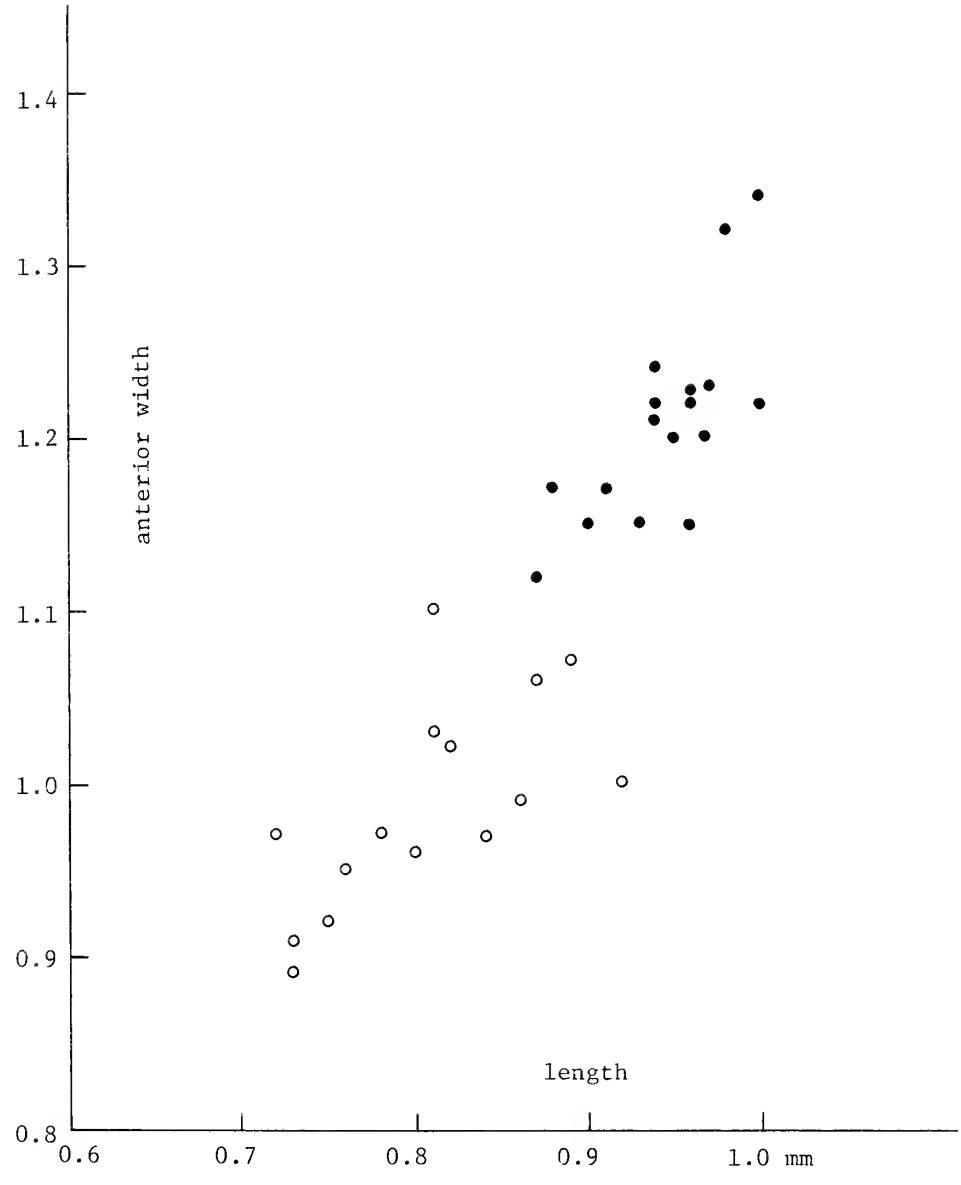
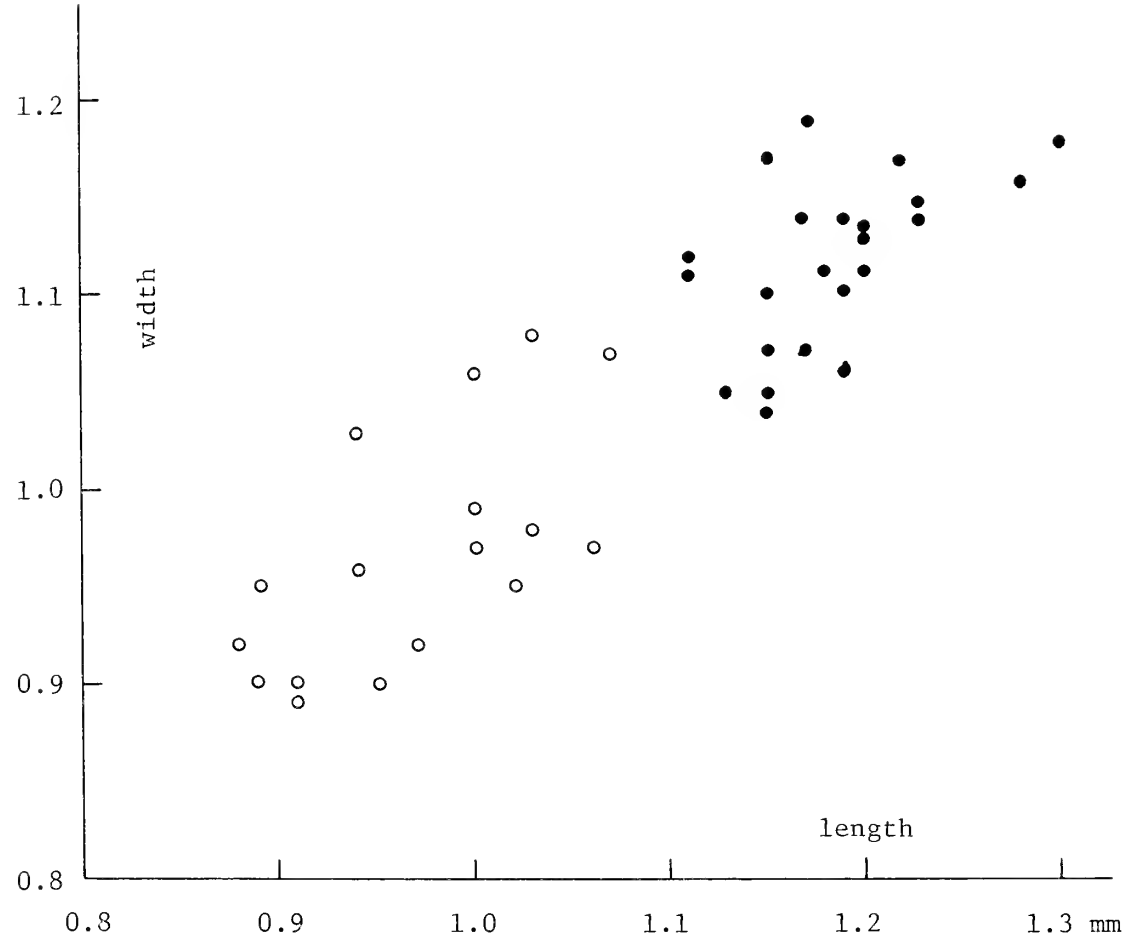


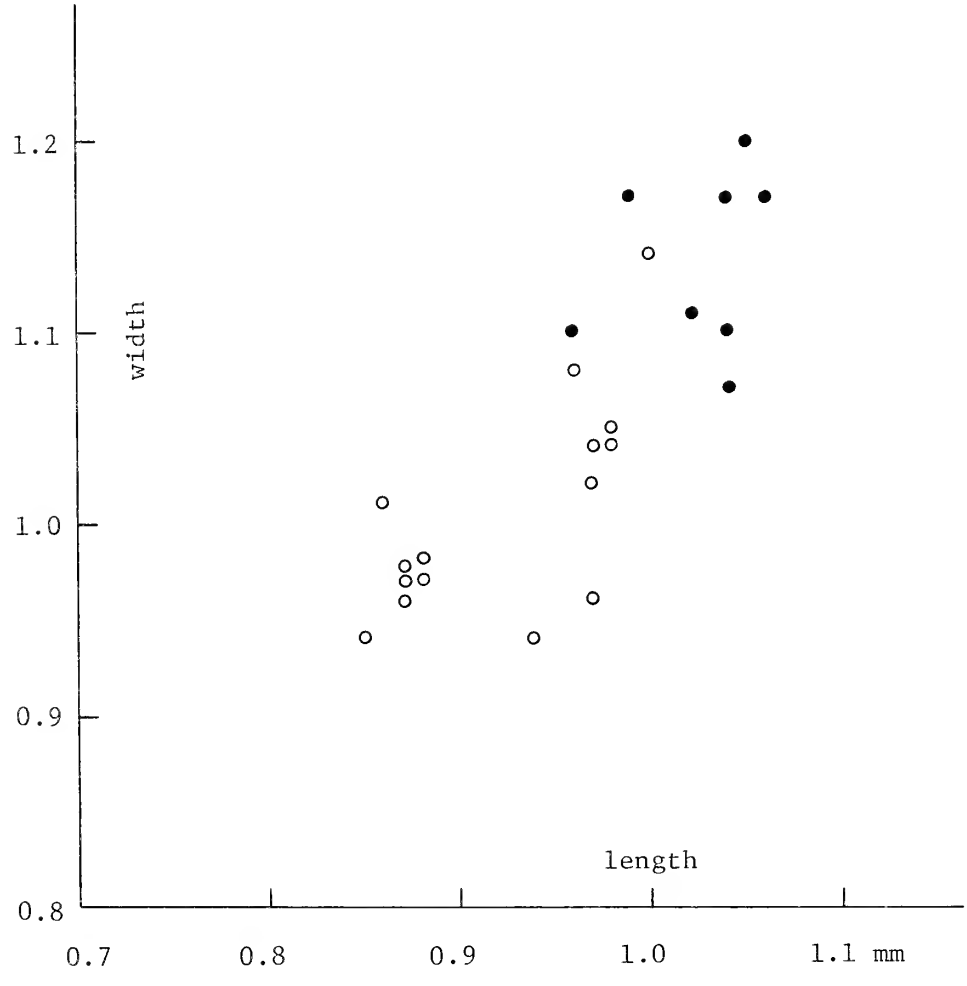
Appendix A.—Size-frequency graph of M^1 of heteromyids. Closed circles, *Proheteromys;* open circles, *Heliscomys*.



Appendix B.—Size-frequency graph of M^2 of heteromyids. Closed circles, *Proheteromys;* open circles, *Heliscomys.*



Appendix C.—Size-frequency graph of M_1 of heteromyids. Closed circles, *Proheteromys;* open circles, *Heliscomys.*



Appendix D.—Size-frequency graph of M_2 of heteromyids. Closed circles, *Proheteromys;* open circles, *Heliscomys*.

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DANIEL F. WILLIAMS
Post-doctoral Fellow, Section of Mammals
(permanent address: Department of Biological Sciences, California State College–Stanislaus, Turlock, California 95380)

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CONTENTS

ABSTRACT

Geographic variation in *Perognathus apache* Merriam and the systematic relationships of *P. fasciatus* Wied-Neuwied and *P. flavescens* Merriam with *P. apache* were investigated. Most geographic variation was attributable to a relatively few climatic and geographic factors. A strong north-south size cline, with small mice in the warmer, southern latitudes and large mice in the colder, northern latitudes was observed. The posterior cranial region became progressively more constricted with increasing size, and the length of the tail increased at a rate faster than the length of the head and body. Body size was inversely correlated with mean annual temperature, size of the auditory bullae was inversely correlated with mean annual precipitation, and the size of the rostrum increased with increasing aridity. A color index, relative darkness, was highly correlated with mean annual precipitation. These patterns of variation were as predicted by principles of ecogeographic variation, except for length of the tail, which increased with increasing latitude and decreasing mean annual temperature. It is hypothesized that the tail is important for maintaining balance while foraging, and that as size increases, relative tail length increases to maintain proper balance.

Populations of *P. apache* and *P. flavescens* were found to have identical karyotypes and to be closely similar in structure. *Perognathus apache* is considered to be conspecific with *P. flavescens*. Four intermountain races of the plains pocket mouse are recognized—*P. flavescens apache, P. f. caryi* Goldman, *P. f. melanotis* Osgood, and *P. f. relictus* Goldman. The race *P. f. cleomophila* Goldman is a junior synonym of *P. f. apache*, and the race *P. f. gypsi* Dice is a junior synonym of *P. f. melanotis*.

INTRODUCTION

The Apache pocket mouse is a small, sand-inhabiting, desert-adapted rodent belonging to the genus *Perognathus* of the family Heteromyidae. It occurs on the intermountain plateaus from Chihuahua northward into the Uintah Basin of Utah and Colorado, ranging from the upper Pecos and Rio Grande valleys in the east to near San Francisco Peaks and the Grand Canyon in the west (Fig. 1). *Perognathus apache* was described by C. H. Merriam (1889) in the first revision of *Peroguathus*. The holotype was collected near Keam's Canyon, Navajo Co., Arizona. Merriam considered *P. apache* to be most similar to *P. inoruatus* Merriam, 1889, from the Central Valley of California. Osgood (1900), in the only other revision of *Perognathus*, named an additional race of the Apache pocket mouse, *P. a. melanotis* from Casas Grandes, Chihuahua. He thought that *P. apache* was closely related only to *P. callistus* Osgood, 1900 (=*P. fasciatus callistus*). He remarked on the resemblance between *P. apache* and *P. inornatus* (*P. inoruatus* Merriam, 1889 = *P. longimembris* of Osgood, 1900), but considered the great distance between their ranges to belie a close relationship. Goldman (1918) subsequently described two additional subspecies of Apache pocket mice, *P. a. cleomophila* from the black lava sands near Flagstaff, Arizona, and *P. a. caryi* from the Grand River Valley of Garfield Co., Colorado. Next, Dice (1929) described a new species of pocket mouse, *P. gypsi*, from the White Sands of the Tularosa Basin, New Mexico. Benson (1933*a*) later arranged this nearly white form as a subspecies of *P. apache*. Finally, Goldman (1938) named a subspecies, *P. a. relictus*, which occurs on the Great Sand Dunes of the San Luis Valley of Colorado.

Prior to the initiation of this study, *P. apache* was allied with four other species in the *fasciatus* group (Osgood, 1900), including *P. fasciatus* Wied-Neuwied, 1838, *P. flavescens* Merriam, 1889, *P. flavus* Baird, 1855, and *P. merriami* Allen, 1892. *Perognathus apache* was generally regarded as being most closely related to *P. fasciatus* of the northern Great Plains (Fig. 1). Harris (1965) proposed that *P. apache* was conspecific with *P. fasciatus*. *Perognathus fasciatus* was also thought to be closely related to *P. flavescens* of the central and southern Great Plains (Fig. 1). In fact, Merriam (1889) originally described *flavescens* as a subspecies of *P. fasciatus*. Osgood (1900) elevated *P. flavescens* to specific status, noting that both forms occurred at the Rosebud Indian Agency, South Dakota, without apparent hybridization. The two species are now known to be sympatric over a broad area (Fig. 1). Osgood (1900) believed that *P. flavescens* was possibly conspecific with *P. merriami*, and suggested that intergradation might occur through *P. copei* Rhoads, 1893 (=*P. flavescens copei*), which he regarded as being synonymous with *P. flavescens*. Blair (1954) also thought that *P. flavescens* and *P. merriami* were closely related, and proposed that the two forms diverged from a common ancestor during Wisconsin or post-Wisconsin changes in the distribution of grasslands in the southern Great Plains. Earlier, Blair and Miller (1949) noted a close resemblance between *P. flavus* and *P. merriami*, as had other workers (Osgood, 1900; Bailey, 1932). Patton (1967) demonstrated a close similarity be-

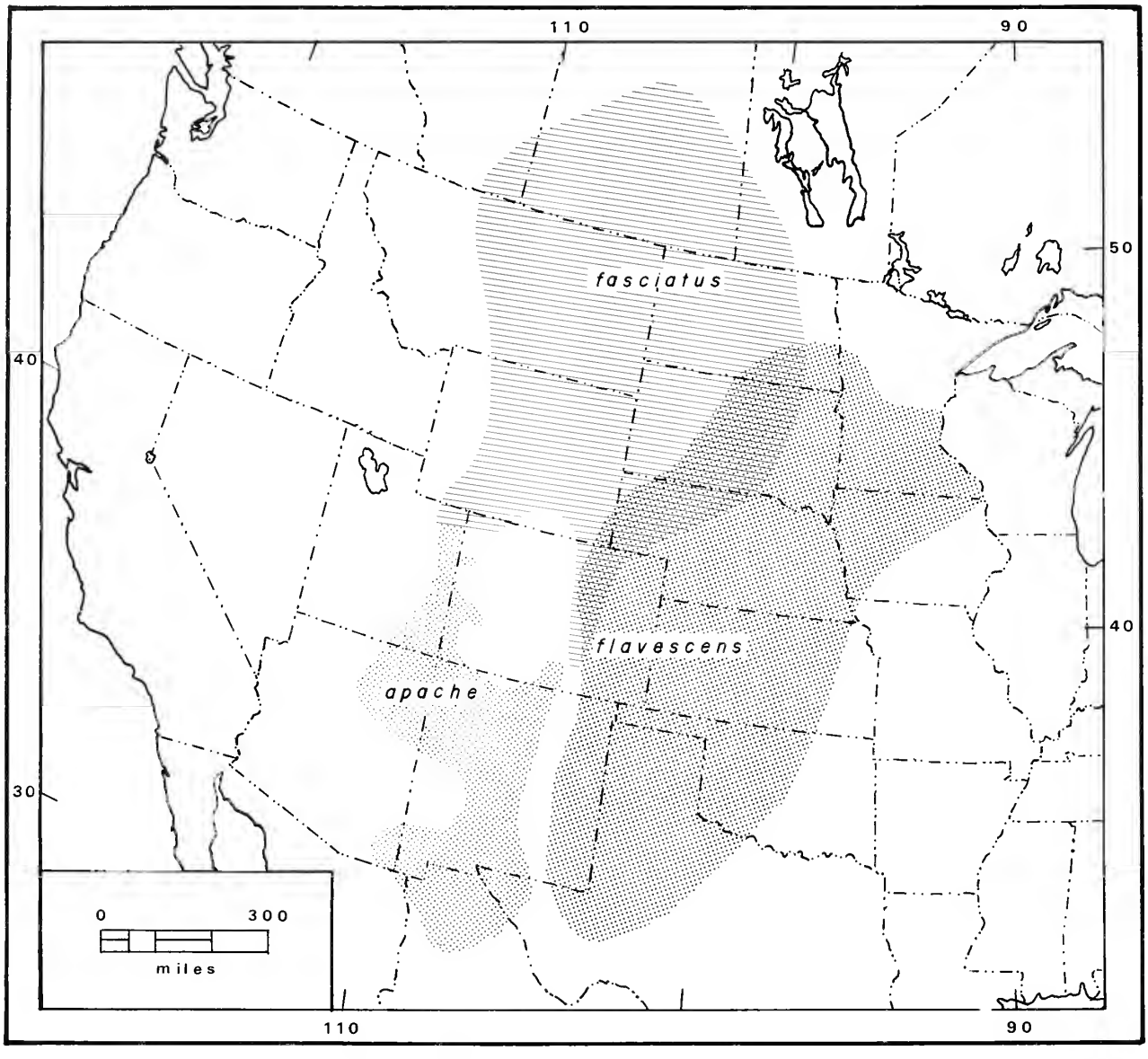

Fig. 1.—Distribution of *Perognathus fasciatus* species group.

tween the karyotypes of *P. flavus* and *P. merriami*, and noted that these taxa differ in chromosome structure from *P. amplus* Osgood, 1900, *P. longimembris* (Couse, 1875), and *P. parvus* (Peale, 1848). Wilson (1973) later reported that *P. merriami* was conspecific with *P. flavus*.

I undertook studies of *Perognathus* in order to clarify the specific status of *P. apache* and to define the interspecific relationships of the species of the *fasciatus* group. In another paper (Williams, 1978), using chromosome structure, I demonstrated that *P. flavus merriami* is only distantly related to *P. flavescens*, and redefined Osgood's (1900) species groups, limiting membership in the *fasciatus* group to *P. fasciatus*, *P. flavescens*, and *P. apache*. These latter three species have nearly identical karyotypes, and are widely divergent in chromosome structure to other members of the subgenus *Perognathus*. In that paper, I proposed a model for the evolution of the species groups of the subgenus *Perognathus*. When I initiated these studies, Dr. Robert Packard had undertaken a review of the geographic variation in the plains pocket mouse, *P. flavescens*. For this reason, I have made no attempt

to review the systematics of that species. A systematic review of *P. fasciatus* is under study, and will be reported elsewhere. This paper presents an analysis of the geographic variation of the Apache pocket mouse, and explores its relationships to *P. flavescens* and *P. fasciatus*.

METHODS AND ACKNOWLEDGMENTS

I conducted field studies during the warmer months (generally May through September) of 1967 through 1970. I visited most of the known collecting localities of *P. apache* to examine adjacent localities for habitat continuity, and to collect specimens for morphologic and karyotypic studies. Generally, I set between 200 and 300 traps per night, relocated the traps each night, and usually checked and removed animals from the traps one or two times after dark. Except for the summer months of 1967, when I set both Museum Special snap traps and Sherman live traps, I set only Sherman traps (primarily the small, 5 by 6.4 by 16.5 cm size). Trapping results during 1967 suggested that moonlight severely curtailed surface activity of Apache pocket mice; thus, in subsequent years most field work was done when there was little or no moonlight. Nearly all trapping was done in areas that had either yielded specimens of *P. apache* previously, or where the habitat seemed favorable for this species. Most collecting activities were conducted in peripheral areas of the range of *P. apache*. Most traps were set in favorable habitats (primarily loose, sandy soils with sparse vegetation), but some traps (generally 45 to 100) were nearly always set in adjacent areas with harder-packed soils and in areas with denser vegetation. In addition to trapping, I also searched for pocket mice by lantern light for 1 to 4 h after dark on most evenings.

Preparations of metaphase chromosomes were secured from 53 specimens, representing all of the subspecies of *P. apache*, three subspecies of *P. fasciatus*, and *P. flavescens copei* (see lists of specimens examined). The methods and a comparative karyological treatment of the species of the subgenus *Perognathus* are given elsewhere (Williams, 1978). Only data pertinent to the present study will be discussed here.

Thirty morphometric characters were utilized (Table 1). Dial calipers were used to measure the cranial traits depicted in Fig. 2. Dental measurements were taken with an ocular micrometer in a dissecting microscope. All dental measurements were taken from occlusal view, and represent greatest length and greatest width of the teeth. Standard external measurements were as recorded on specimen tags. For specimens I prepared, length of ear and length of hind foot were taken with vernier calipers. Because many early collectors did not measure the ear, most of the multivariate analyses did not include this character.

Color was analyzed subjectively. Two color parameters were scored for each skin with adult pelage. Two individuals were selected as color standards and were assigned a numerical value for each parameter. One, darkness, is the degree of darkness produced by the relative number of black-tipped hairs on the dorsal and lateral surfaces. The other, richness, is the quality of the color produced by yellowish pigments in the terminal or subterminal bands of the dorsal and lateral hairs. This parameter ranges from white (no pigment) through a rich yellowish-orange, closest to Ochraceous-Orange or Ochraceous-Tawny (all capitalized colors are from Ridgway, 1912). Specimen MSB 17848 from 5 mi N, 6 mi E Newcomb, San Juan County, New Mexico, was the lighter, less rich color standard, and was assigned values of 2 for both darkness and richness. Specimen MSB 12598 from 4 mi N, 2 mi W Estrella, McKinley County, New Mexico, was assigned values of 4 for both darkness and richness. All other specimens of *P. apache* and *P. flavescens* were compared with the two standards. If an individual had less of a blackish overwash than the 2 standard, it was assigned a value of 1 for darkness; if it appeared to have the same amount as the 2 standard, it received a score of 2. Specimens intermediate to the standards were assigned values of 3, and those darker than 4 were given scores of 5. Specimens without black-tipped hairs received a score of 0 for darkness. Richness was quantified independently and in the same manner. The dominant wavelength of the yellowish color did not appear to vary in the samples of *P. apache* and *P. flavescens*, but the concentration of the pigment varied from none (white, with a value of 0) to high (dark Ochraceous-Tawny, with a value of 5). Because both darkness and richness contribute to an appearance that varies from light (much reflected light) to dark (little reflected light), combining these indices

Table 1.—*Morphometric traits utilized on this study. Measurements are in mm.*

No.	Trait	Abbreviation	Decimal recorded
1.	Total length	TOTL	1.00
2.	Length of tail	TL	1.00
3.	Length of head and body	HBL	1.00
4.	Length of hind foot	HFL	1.00
5.	Length of ear	EL	0.10
6.	Tail/head and body ratio	TL/HBL	—
7.	Greatest length of skull	GLS	0.05
8.	Occipitonasal length	ONL	0.05
9.	Interorbital breadth	IOB	0.05
10.	Length of maxillary toothrow (alveolar)	MXTL	0.05
11.	Width across maxillary toothrow	WMXT	0.05
12.	Bullar length	BL	0.05
13.	Width across bullae	BW	0.05
14.	Length of interparietal	IPL	0.05
15.	Width of interparietals	IPW	0.05
16.	Length of nasal	NL	0.05
17.	Width of nasals	NW	0.05
18.	Width of rostrum	RW	0.05
19.	Least interbullar distance	LID	0.05
20.	Length of mandibular toothrow	MNTL	0.05
21.	Length of P_4	P_4L	0.03
22.	Width of P_4	P_4W	0.03
23.	Length of M_3	M_3L	0.03
24.	Width of M_3	M_3W	0.03
25.	Length of articular process	LAP	0.05
26.	Width of P^4	P^4W	0.03
27.	Width of M^1	M^1W	0.03
28.	Width of M^3	M^3W	0.03
29.	Length of M_1	M_1L	0.03
30.	Width of M_1	M_1W	0.03

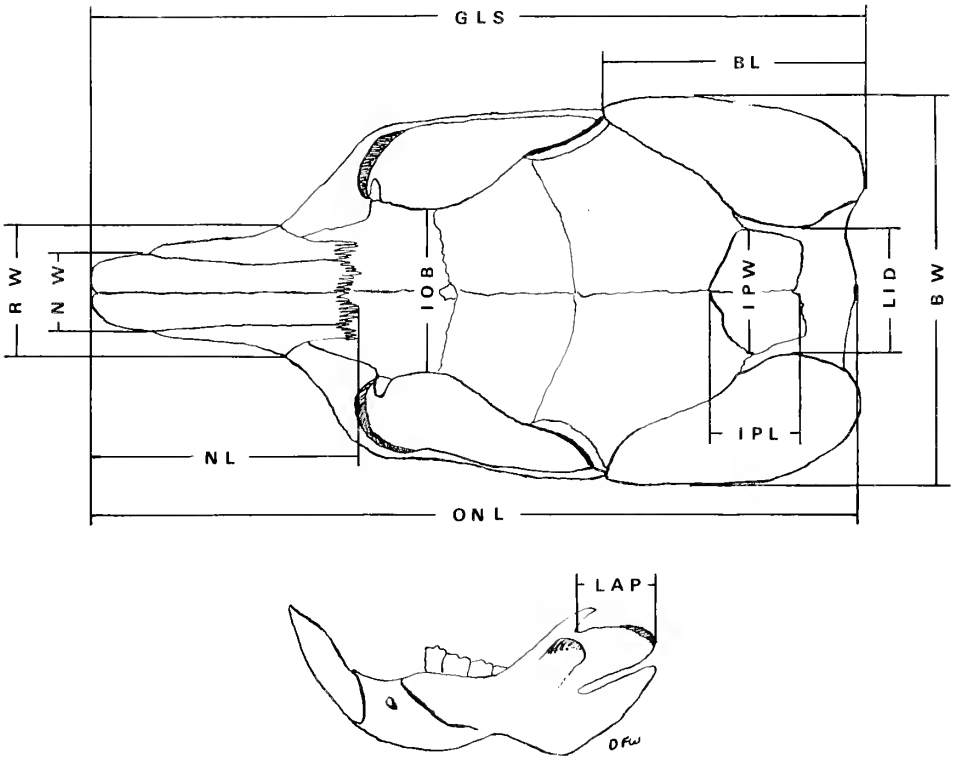

Fig. 2.—Cranial measurements used in this study. Measurements are identified in Table 1. Alveolar length of maxillary toothrow and length of mandibular toothrow are now shown.

expresses the relative darkness of the specimens. Animals with large numbers of black-tipped hairs (for example, a score of 5 for darkness), and with little yellowish pigment (a score of 1 for richness) would score the same relative darkness (6) as a mouse intermediate for darkness (3) and richness (3). Samples of *P. fasciatus* were not compared with the color standards because that species has a qualitative difference in the yellowish pigment. Because these color data were ordinal, and because color was much more variable than were the morphometric traits, these data were not used in the multivariate analyses.

Climatic and geographic data were obtained from the 1960 Ten Year State Summaries of Climatic Data, U.S. Weather Bureau. Where elevation or latitude of the collecting localities differed from the nearest weather stations, these data were obtained from the 1970 editions of Sectional Aeronautical Charts. The climatic and geographic variables used were mean duration of the frost-free period (growing season), mean annual precipitation, mean annual temperature, mean July minimum temperature, elevation, latitude, elevation adjusted for latitude (latitude × 350 + elevation), and a climatic severity index, calculated by dividing the elevation adjusted for latitude by the growing season.

Specimens were sorted into five age classes on the basis of dental characters. Individuals with deciduous upper premolars, and with no evidence of the permanent premolars, were assigned to Age Class 1 (Fig. 3). Individuals with deciduous premolars, and with permanent premolars clearly visible beneath the eroded roots of the deciduous teeth comprised Age Class 2. The permanent P^4 was not at occlusal level and its cusps were unworn for individuals of Age Class 3. Individuals of Age Class 4 had the P^4 at occlusal level and there was moderate wear on the cusps of P^4, M^1, and M^2. The P^4 cusps of Age Class 5 individuals were worn to where at least the metaloph cusps were obliterated.

For statistical analyses, Age Classes 1 and 2 were grouped as juveniles. Individuals of Age Class 3 (subadults) were treated separately, and individuals of Age Classes 4 and 5 (adults) were grouped together. Statistical comparisons were made between juveniles, subadults, and adults from the four localities with the largest samples (Uintah Basin, San Juan Basin, Painted Desert, and Rio Grande Valley). Male and female adults of these samples were also compared.

Standard univariate statistics included mean, variance, standard deviation, standard error of the mean, range, and coefficient of variation, and were computed by a program in the Biomedical Computer Programs series (BMD, Dixon, 1976), or by a program developed by me (DFW). The sums of squares simultaneous testing procedure (SS-STP, Gabriel, 1964) was performed using the UNIVAR program. This program employs a single-classification analysis of variance to test for differences between or among means ($P \leq 0.05$), and is used to determine maximally nonsignificant subsets. Student's *t*-tests were two-tailed, and were performed using both pooled and separate variance estimates (BMD), or separate variance estimates only (DFW).

Factor analysis (BMD08M) utilized matrices of correlation for factor extraction. The diagonal elements in the matrices of correlation were not altered, and intial communality estimates were the maximum absolute row values. Analyses included both or-

thogonally rotated and unrotated factor matrices (Dixon, 1976). Because the unrotated factor matrix met the main requirements of simple structure (Wallace and Bader, 1967) and because I found that the rotated matrix could not be as easily interpreted in a biological context, only the unrotated matrix is presented.

Stepwise discriminant function analysis and canonical analysis (BMD07M) are techniques that define and separate groups and identify unknown specimens. The program performs a multiple discriminant analysis in a stepwise manner, selecting the variable entered by finding the variable with the greatest F value. The F value for inclusion was set at 0.01, and the F value for deletion was set at 0.005. Canonical coefficients are derived by multiplying the coefficient of each discriminant function by the mean of each corresponding variable. The program also classifies individuals, placing them with the group that they are nearest to on the discriminant functions.

The MINT programs are a package of numerical taxonomic routines (Rohlf, 1971). Data were standardized for all of the analyses by the MINT programs. Phenograms were constructed by the unweighted pair-group method using arithmetic averages (UPGMA, Sneath and Sokal, 1973). The coefficients of similarity were derived from a Q-mode correlation analysis. Coefficients of taxonomic distance are average Euclidean distances. The principal components were extracted from a matrix of correlation. A seven-centroid solution to the distance matrix was computed using the K-Centroid program (MINT). This program partitions a set of OTU's into a specific number of groups, such that the sum of the taxonomic distances of each OTU to its closest centroid is a minimum. The potential centroids are limited to the OTU's present in the data set (Rohlf, 1971).

Preliminary groupings of samples were made only for immediately adjacent localities (less than 15 to 20 km distance) that were ecologically similar and continuous. Then, if no significant differences were found between localities that were both similar and continuous ecologically, they were combined. This process resulted in four samples of *P. fasciatus,* two samples of *P. flavescens,* and 15 samples of *P. apache* that were utilized in the univariate and multivariate analyses. A few specimens from scattered localities, such as along the lower San Juan River in Utah and near Navajo Mountain in Arizona, were not included in the morphometric analyses. The specimens examined are listed in the systematic accounts. The geographic localities for all samples are shown in Fig. 4. The number and name codes for these samples are as follows: 1—*P. f. fasciatus;* 2—*P. f. olivaceogriseus;* 3—*P. f. litus;* 4—*P. f. callistus;* 5—*P. apache,* Uintah Basin; 6—*P. apache,* Moab; 7—*P. apache,* Painted Desert; 8—*P. apache,* Flagstaff; 9—*P. apache,* Gallup; 10—*P. apache,* San Juan Basin; 11—*P. apache,* Canyon Largo; 12—*P. apache,* Estrella; 13—*P. apache,* San Luis Valley; 14—*P. apache,* Santa Fe; 15—*P. apache,* Rio Grande Valley; 16—*P. apache,* San Augustine Plains; 17—*P. apache,* Gran Quivira; 18—*P. apache,* White Sands; 19—*P. apache,* Deming Plains; 20—*P. flavescens copei;* 21—*P. f. flavescens.*

The following institutions provided specimens for this study. The abbreviations preceding the institutions are used in the accounts to identify the disposition of specimens. Addresses and curators in charge of the collections can be obtained from Choate and Genoways (1975). Specimens of institutions marked with an asterisk were not included in the statistical analyses. All were, however, measured and checked for conformity with the conclusions based on the statistical results.

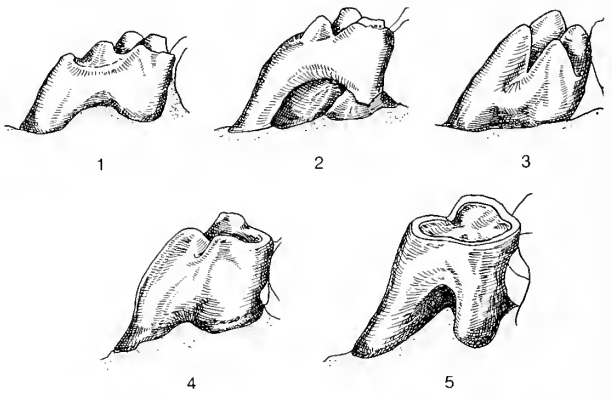

Fig. 3.—Labial view of right upper fourth premolars, representing age classes 1 through 5. 1 and 2 = deciduous premolars; 3, 4, and 5 = permanent premolars.

AMNH—American Museum of Natural History, New York.
BS—Biological Survey Collections, National Fish and Wildlife Laboratory, Washington, D.C.
CAS—California Academy of Sciences.*
CM—Carnegie Museum of Natural History, Pennsylvania.
DCBML—U.S. Bureau of Sport Fisheries and Wildlife, Ft. Collins, Colorado.
ENMU—Eastern New Mexico University.
FMNH—Field Museum of Natural History, Illinois.*
KSU—Kansas State University.*
KU—University of Kansas, Museum of Natural History.
LACM—Los Angeles County Museum, California.
MALB—University of Texas, El Paso, Museum of Arid Land Biology.
MMNH—University of Minnesota, James Ford Bell Museum of Natural History.*
MNA—Museum of Northern Arizona.*
MSB—Museum of Southwestern Biology, University of New Mexico.
MVZ—University of California, Berkeley, Museum of Vertebrate Zoology.
MWU—Midwestern University, Texas.*
NMSU—New Mexico State University.
SIUC—Southern Illinois University.*
TCWC—Texas Cooperative Wildlife Collections, Texas A&M University.*
UA—University of Arizona.
UCM—University of Colorado Museum.
UIMNH—University of Illinois, Museum of Natural History.*
UMMZ—University of Michigan, Museum of Zoology.*
UNSM—University of Nebraska, State Museum.*
UU—University of Utah.
VMKSC—Kearney State College, Vertebrate Museum, Nebraska.*

Acknowledgments

This study was initiated at the University of New Mexico in conjunction with a Master's thesis entitled "The geographic variation of the Apache pocket mouse in New Mexico," and

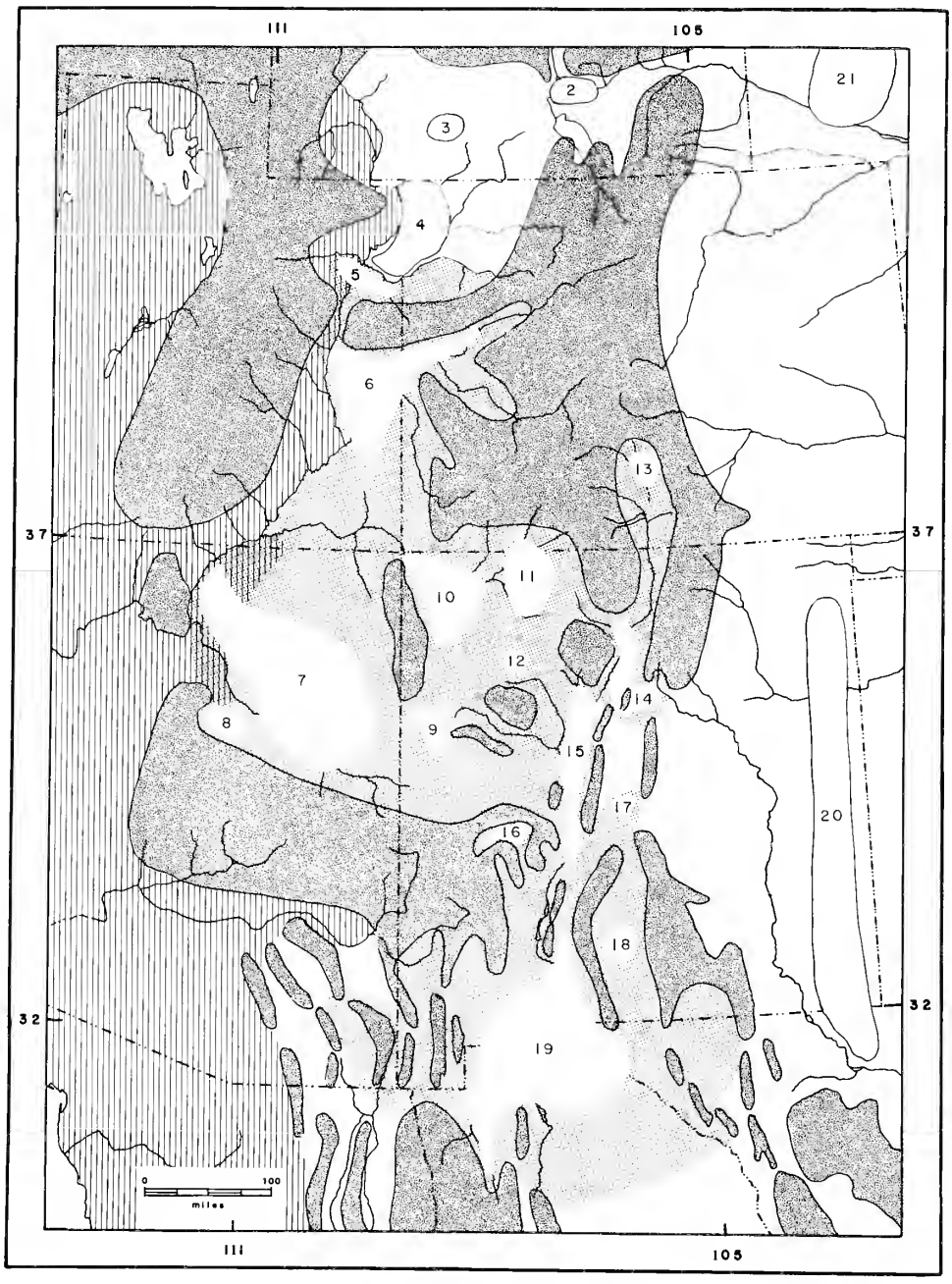

Fig. 4.—Map showing distribution of *Perognathus apache* samples used in the statistical analyses. Numbered, white areas within the lightly stippled area represent the positions of the *P. apache* samples (as defined in the text and in Table 7). Numbered areas aurrounded by unshaded areas represent samples of *P. fasciatus* (2–4) and *P. flavescens* (20, 21). Line-shaded areas represent the combined ranges of the *P. longimembris* and *P. parvus* species groups. The lightly stippled area represents the range of *P. apache*. Darkly shaded areas represent mountainous regions that may serve as barriers to the dispersal of *P. fasciatus* group pocket mice.

grew into a Ph.D. dissertation, "The systematics and evolution of the *Perognathus fasciatus* group of pocket mice." After the completion of that phase, the project lay dormant for nearly seven years. A sabbatical leave from California State College, Stanislaus and a research appointment at the Carnegie Museum of Natural History provided the time and resources to bring this project to completion. This report is based upon a portion of the data gathered for my dissertation. Most of the analyses are new and I have examined about 200 additional specimens that were previously unavailable.

Table 2.—*Summary of trapping results. The total number of traps set varies for the different species, as only traps set within their ranges are counted.*

Target species and associates	Traps set	Captures				Substrate	
		By traps	%	By hand	Total	Sand	Other
Perognathus apache	12,296	128	1.0	20	148	118	30
Perognathus flavus	10,261	198	1.9	40	238	28	210
Perognathus parvus	565	28	5.0	0	28	0	28
Perognathus penicillatus	3,629	31	0.9	0	31	25	6
Perognathus amplus	280	16	5.7	0	16	0	16
Perognathus intermedius	870	1	0.1	0	1	0	1
Dipodomys ordii	12,296	833	6.7	13	846	602	244
Dipodomys merriami	5,240	375	7.2	0	375	297	78
Peromyscus spp.	12,296	287	2.3	0	287	183	104
Onychomys spp.	12,296	264	2.1	3	267	213	51
Reithrodontomys spp.	12,296	24	0.2	0	24	20	4
Other nocturnal species	12,296	34	0.3	5	39	26	13
Diurnal species	12,296	10	0.1	0	10	8	2
Perognathus fasciatus	2,095	48	1.7	0	48	32	16
Perognathus parvus	150	1	0.6	0	1	0	1
Dipodomys ordii	2,095	133	6.3	0	133	84	49
Peromyscus maniculatus	2,095	340	16.2	0	340	276	64
Onychomys leucogaster	2,095	15	0.7	0	15	13	2
Reithrodontomys spp.	2,095	4	0.2	0	4	3	1
Other nocturnal species	2,095	7	0.3	0	7	0	7
Diurnal species	2,095	15	0.7	0	15	8	7
Perognathus flavescens	1,229	11	0.9	0	11	11	0
Perognathus flavus	1,229	1	0.1	0	1	0	1
Dipodomys ordii	1,229	200	16.3	0	200	200	0
Dipodomys merriami	869	5	0.6	0	5	0	5
Peromyscus maniculatus	1,229	21	1.7	0	21	21	0
Onychomys leucogaster	1,229	28	2.3	0	28	28	0

The University of New Mexico provided financial assistance in the form of assistantships and an NDEA Title IV fellowship. I am grateful for that assistance, and for the equipment and facilities furnished by the University. Dr. Arthur H. Harris laid the groundwork for this study with his collection of Apache pocket mice and his investigation into their relationship with the olive-backed pocket mouse. Dr. James S. Findley suggested the original project, and gave advice and encouragement along the way. Several of my fellow students aided my studies. Kenneth Andersen, Hal Black, Gwen Britt, Michael Bogan, Jay Druecker, Kenneth Geluso, and Don Wilson were particularly helpful. California State College, Stanislaus paid a portion of my travel expenses incurred in examining holotypes. The Carnegie Museum of Natural History furnished computer time at Carnegie-Mellon University. Teresa Bona typed the manuscript, and Nancy Perkins drew Figs. 3 and 6. Suzanne Braun and Hugh H. Genoways have been especially helpful in editing drafts of this report. James L. Patton and Robert E. Martin critically reviewed a draft of this paper, and offered several suggestions for improving it. A special note of appreciation is extended to these persons and to the many curators and curatorial assistants who made specimens available for study.

RESULTS AND DISCUSSION

Distribution and Habitat

A summary of the relevant capture data is presented in Table 2. A total of 522 individuals of *Perognathus* was captured, representing 16.5% of the small mammals taken. A majority of traps were set in sandy areas, and no attempt was made to sample all habitats or to sample different habitats equally. The small traps undoubtedly reduced the catch of larger species, including *Dipodomys*. Even so, kangaroo rats were captured from six to 16 times more frequently than were *fasciatus* group pocket mice. The silky pocket mouse, *P. flavus*, was captured twice as often as *P. apache*, despite a trapping regimen that was designed to maximize the catch of *P. apache*.

Apache pocket mice are usually limited to loose,

sandy soils and dunes with a sparse vegetational cover. I often captured them on sand dunes, several hundred feet from the nearest vegetation. One exception was in the Unitah Basin of Utah, where I found *P. apache* to be common and widespread on a variety of substrates. In the Navajo Reservoir area of northwestern New Mexico, Harris (1963) captured two specimens on fine-textured soils. Some specimens from adjacent areas in Colorado may have come from similar habitats. Twice, in northwestern New Mexico and southeastern Utah, I took single specimens on hard-packed, fine-textured soils along arroyos. In both cases, I captured several specimens in adjacent, sandy areas.

The geographic distribution of *P. apache* is shown in Fig. 4. Apache pocket mice are most numerous in steppe-grassland associations between 5,000 and 7,500 ft in elevation. Common plant associates are sagebrush (*Artemisia*), saltbush (*Atriplex*), mormon tea (*Ephedra*), snakeweed (*Gutierrezia*), juniper (*Juniperus*), rice grass (*Oryzopsis*), tumbleweed (*Salsola*), yucca (*Yucca*), and rabbit bush (*Chrysothamnos*). *P. apache* ranges from Lower Sonoran mesquite associations through lower Transition pinyon-juniper associations. It is recorded as occurring in the yellow-pine zone in the Gallina Mountains of New Mexico (Bailey, 1932). That locality is actually a stabilized dune system at the northeastern edge of the San Augustine Plains, where scattered yellow pines (*Pinus ponderosa*) extend onto an old dune system that abuts against the mountains. I, and others, have also taken *P. apache* among scattered yellow pines in the vicinity of Winona, east of Flagstaff, Arizona. There, mice were captured on lava sands among rabbit bush, sagebrush, and juniper, with scattered yellow pines growing mostly along the bases and slopes of cinder buttes and on rocky outcrops. In both areas yellow pines occur at lower and drier elevations than normal due to local edaphic factors. *P. apache* is not known to occur in typical yellow-pine forests.

Apache pocket mice may be prevented from spreading farther to the west by competition with *P. amplus*, *P. longimembris*, and *P. parvus*. There is very marginal sympatry between *P. apache* and *P. amplus* along the western edge of the range of *P. apache* in northern Arizona (Fig. 4). According to Benson (1933*b*), *P. amplus* is restricted to sand habitats in that area. In contrast, I found *P. amplus* common on rocky slopes and gravelly soils. Around Navajo Mountain, Utah, *P. longimembris* has been taken with *P. apache* (Benson, 1935). It seems likely that Apache pocket mice are prevented from occupying areas west of the Colorado River in southern Utah by competition with *P. longimembris* and *P. parvus* (Fig. 4).

South of Socorro Co., New Mexico, in the southern portion of its range (Fig. 4), *P. apache* appears to be confined to sandy hummocks and dunes in mesquite (*Prosopis*) associations. At these lower, warmer elevations, *P. apache* is very rarely captured. Here, and farther north in New Mexico and Arizona, *P. flavus* is generally most numerous on both fine-textured and gravelly soils with moderate vegetational cover. In the southern portion of the range of *P. apache*, the desert pocket mouse, *P. penicillatus*, is common in sandy areas and on creosote flats with sparse vegetational cover. Competition with *P. penicillatus* may be a major reason for the relative scarcity of *P. apache* there.

The silky pocket mouse (*P. flavus*) does not occur much farther north than the San Juan River in southeastern Utah and southwestern Colorado. North of the range of *P. flavus*, *P. apache* has been more frequently captured on non-sand substrates. This suggests that competition with *P. flavus* may generally limit *P. apache* to sandy substrates. In this regard, I found *P. flavus* to be common on loose sand soils in most areas where no *P. apache* were captured, and I caught *P. flavus* in the same trap lines as *P. apache* at just four localities.

The geographic range of *P. apache* was found to terminate at the White and Duchesne rivers in the Uintah Basin of Utah and Colorado (Fig. 5). I captured 22 *P. apache* at a single locality north of the White River (1.5 mi E Ouray). The mice were taken on hard-packed, sand-gravel conglomerate soil. There is a bridge across the White River within a kilometer of this site, and individuals may have recently colonized the north bank of the White River via the bridge. About 2 km east of this collecting site (also north of the White River), I trapped for two nights in a sand dune area extending over about 100 hectares, but caught no pocket mice. The olive-backed pocket mouse, *P. fasciatus*, was captured at several localities north of the White River, north and east of the site where I captured *P. apache* (Fig. 5). Most *P. fasciatus* were taken in sandy areas, although one was captured on a rocky slope. I did not find them to be common at any site in the Uintah Basin.

Perognathus apache and *P. fasciatus* occur in

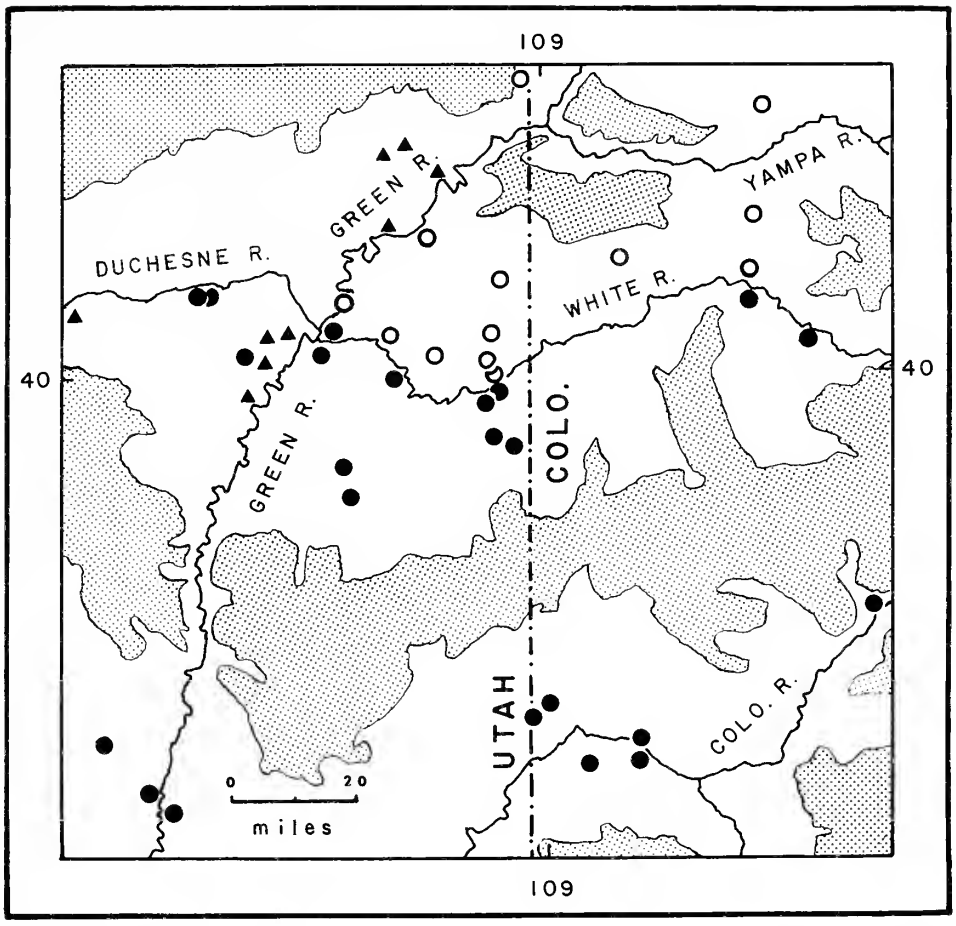

Fig. 5.—Map of northeastern Utah and northwestern Colorado, showing the distribution of three species of pocket mice. Triangles = *Perognathus parvus;* closed circles = *P. apache;* open circles = *P. fasciatus.* The shaded areas represent mountains and plateaus over 7,500 ft in elevation.

similar habitats and are nearly the same size, and it is possible that competitive exclusion limits their ranges along a line formed by the White and Duchesne rivers. Certainly the rivers are not barriers to these pocket mice, as they are shallow, and meander through broad floodplains near their confluence with the Green River. The geographic ranges of both species may be limited on the west by competition with *P. parvus* (Fig. 5). In areas where I caught *P. parvus,* they seemed to be common on all types of substrates, including slopes and level areas. There appear to be no physical barriers to the spread of *P. parvus* to the east.

All three species may be recent arrivals to the Uintah Basin, possibly within historic times. Wells (1970*a*, 1970*b*) presents evidence that both *Pinus ponderosa* and *Juniperus scopulorum* were widely distributed over the now treeless, arid Laramie Basin from at least 5,600 years B.P. to 200 years B.P. He states that the hypsithermal period (from 9,000 to 2,500 years ago) was a time of higher temperatures and greater moisture. The drastic reduction of woodlands over the past several centuries may constitute the first climatically induced episode of treelessness in the area in post-Wisconsin time, and may have allowed the recent spread of these species into the Uintah Basin.

The major habitat of Apache pocket mice extends more or less continuously from the Tavaputs Plateau of eastern Utah and adjacent Colorado southward into the Painted Desert of Arizona and the San Juan Basin of New Mexico, and southeastward into the Rio Grande Valley (Fig. 4). Most other inhabited areas are smaller, are found at higher elevations, and are more or less isolated by very narrow corridors of intermittent habitat along water

courses. Populations appear to be isolated by wide stretches of unfavorable habitat in a few areas (for example, the Uintah Basin, San Luis Valley, San Augustine Plains, and Willcox Playa).

The Uintah Basin is bounded on the south by the high, east-west oriented Tavaputs Plateau (Fig. 5). Most of the plateau is over 8,000 ft. On its southern front the plateau rises abruptly, as along the Book and Roan Cliffs, and in some places is nearly 2,000 ft higher than the land to the south. On its northern side, the plateau slopes more gradually into the Uintah Basin. Sheer cliffs and steep rocky slopes on the south provide no sandy habitat for Apache pocket mice, and only a few large drainage channels cut sharply into the plateau. In Colorado, the plateau does not stand out in such bold relief, and it is possible that Apache pocket mice crossed the plateau via passes, such as that north of Rifle. More likely, however, *P. apache* colonized the Uintah Basin via the Green River Canyon through the plateau (Fig. 5). This is a narrow, precipitous route, and one that is likely to be breached only rarely.

The Rio Grande Valley abruptly narrows south of Socorro, New Mexico, and the river, from near Val Verde to near Las Cruces, flows through a narrow channel along the western front of a series of low mountains (Fig. 4). A southward drop in elevation occurs near Socorro, and creosote (*Larrea*) associations replace the more northern steppe-grasslands. Near this locality, a biotic transition occurs, and the ranges of several species characteristic of the southern desert associations end (for example, *Perognathus penicillatus, Geomys arenarius,* and *Peromyscus eremicus,* Findley et al., 1975). To the east, the Jornada Del Muerto (a broad, north-south valley) extends without interruption from the Deming Plains to near Val Verde. Sandy, mesquite-dominated hummocks are scattered throughout the Jornada, with creosote being found on hard-packed, fine-textured soils and on the gravelly slopes. Elevation increases gradually to the north, where the Jornada is partially blocked by a large lava flow. Sandy habitat continues intermittently northeastward in the direction of Gran Quivira, and elevation increases more rapidly. The Gran Quivira site is in a juniper association, where sands have accumulated at the base of some low hills.

The San Augustine Plains are connected on the southwest by a large drainage channel with intermittent sandy spots along its banks (Fig. 4). On the western and northwestern perimeters mountains and low hills and stretches of rocky soils probably form a barrier to dispersal and intermingling with the Rio Grande Valley population. Only low hills form the boundaries of the San Augustine Plains to the northwest, and population interchanges in the direction of Gallup and the Painted Desert are probable.

There are no significant physiographic barriers between the ranges of *P. flavescens* and *P. apache,* and their populations may be in contact at a few points. The plains pocket mouse (*P. flavescens*) may be distributed all along the Pecos River Valley, and Apache pocket mice have been collected in the upper Pecos River Valley (Fig. 4). The two populations may contact each other on the plains north of Gran Quivira, although there is a stretch of hard, rocky, limestone soils between the Pecos Valley and the Gran Quivira site. However, the most likely contact zone is in the Trans-Pecos region. Neither species is known from a fairly wide area (Fig. 4), but it is likely that Apache pocket mice occur eastward to the sands along the salt lakes west of the Guadalupe Mountains. This Trans-Pecos gap is no greater than several other gaps between known populations. That Apache pocket mice are found at nearly every sandy site within their range suggests that they have the ability to disperse through areas not suitable for supporting permanent populations. Even in areas where they are relatively abundant and widespread, such as the San Juan Basin, they are discontinuously distributed, as loose, sandy soil is a minor habitat of spotty occurrence.

Intrapopulation Variation

Adults averaged significantly larger than subadults in most characters, and larger than juveniles in all traits except the dimensions of the permanent teeth. Consequently, juveniles and subadults were excluded from interpopulation comparisons.

There were no significant differences between the sexes of adults in the morphometric characters for the Albuquerque sample (39 males, 31 females) and the Painted Desert sample (35 males, 27 females). Females of the Uintah Basin sample (28 males, 33 females) averaged significantly larger in length of the interparietal and length of P_4. Males of the White Sands sample (28 males, 26 females) averaged significantly larger than females in bullar length, width across the bullae, and in width of M_3. All of the significant differences were relatively slight (1 to 3%) and could be due to normal sampling errors. Because of the small number of differences,

Table 3.—*Premolar cusp numbers and bullae apposition in* fasciatus *group samples.*

Sample	P^4 cusps				P_4 cusps				Bullae meet	
	1	2	4	5	2	3	4	5	Yes	No
1. *Perognathus fasciatus fasciatus*			12				12			12
2. *Perognathus fasciatus olivaceogriseus*			21			1	18			21
3. *Perognathus fasciatus litus*			19				19			18
4. *Perognathus fasciatus callistus*			31				31			31
5. *Perognathus apache* Uintah Basin		3	59	1		7	61		1	63
6. *Perognathus apache* Moab			30			1	27		1	25
7. *Perognathus apache* Painted Desert			66	1		2	66		6	55
8. *Perognathus apache* Flagstaff			36			3	34		3	30
9. *Perognathus apache* Gallup			5			2	4			6
10. *Perognathus apache* San Juan Basin			30	2		1	27	1	3	32
11. *Perognathus apache* Canyon Largo			24	5		2	23		3	27
12. *Perognathus apache* Estrella			12	3		1	13			14
13. *Perognathus apache* San Luis Valley			20			4	16			16
14. *Perognathus apache* Santa Fe			25	3		1	27		2	22
15. *Perognathus apache* Rio Grande Valley			53	18		1	54		14	57
16. *Perognathus apache* San Augustine			19			1	14			17
17. *Perognathus apache* Gran Quivira			15			1	14		2	12
18. *Perognathus apache* White Sands	1	1	52	2	7	16	28	3	7	40
19. *Perognathus apache* Deming Plains			16			2	14		4	12
20. *Perognathus flavescens copei*			14	2		2	14		5	12
Total	1	4	511	37	7	58	518	4	49	491
%	0.0	0.7	92.0	6.7	1.2	9.9	88.3	0.7	9.1	90.9

and because there was no pattern or consistency to the differences, I decided that the advantages of pooling the sexes for intersample comparisons outweighed the possible disadvantages. There were no significant differences between the sexes in the color indices. Thus, all intersample univariate and multivariate comparisons were made using pooled samples of both sexes.

Essentially no individual variation was noted in external morphology (other than normal meristic and color differences) in *P. apache*, *P. fasciatus*, or *P. flavescens*. Only a single specimen was found that lacked black-tipped guard hairs (MVZ 55716 from Keam's Canyon, Navajo Co., Arizona). This condition must be regarded as a rare anomaly.

Some authors (for example, Blair et al., 1957) have stated that the auditory bullae are in contact (apposed) ventrally, and have used this feature as a taxonomic character for *P. apache*. For adults, I noted if the bullae were in contact (Table 3). None of the specimens of *P. fasciatus* had bullae in apposition, whereas approximately 10% of the *P. apache* and *P. flavescens* samples had apposed bullae. The Rio Grande Valley sample exhibited a significantly greater than expected number of individuals with bullae in contact, whereas the Uintah Basin sample exhibited significantly fewer individuals than expected. Populations with relatively large bullae had a higher proportion of bullae in apposition than those with relatively small bullae, such as the Uintah Basin sample. In any case, this character is not useful as a taxonomic trait.

Several departures from the typical cusp patterns of the upper and lower fourth premolars were noted (Table 3). The normal pattern of the upper premolar consists of four major cusps, an anterior protocone (comprising the protoloph), and a three-cusped metaloph, consisting of a metacone, hypocone, and hypostyle (Fig. 6A). In about 7% of the individuals a prominent accessory cusp, representing either a paracone or a protostyle, was present on the P^4 (Fig. 6B, C, D, and F). In four individuals, the metaloph was compressed laterally, and the metaloph cusps were united into a single structure, giving the tooth a bicuspid appearance (Fig. 6E). The P^4 of one individual was unicusped (Fig. 6G).

The typical lower premolar has four prominent cusps on two transverse lophs. The anterior protolophid consists of a protoconid and protostylid, and the posterior metalophid consists of a metaconid and hypoconid (Fig. 6H). The most common departure from the normal condition was the union

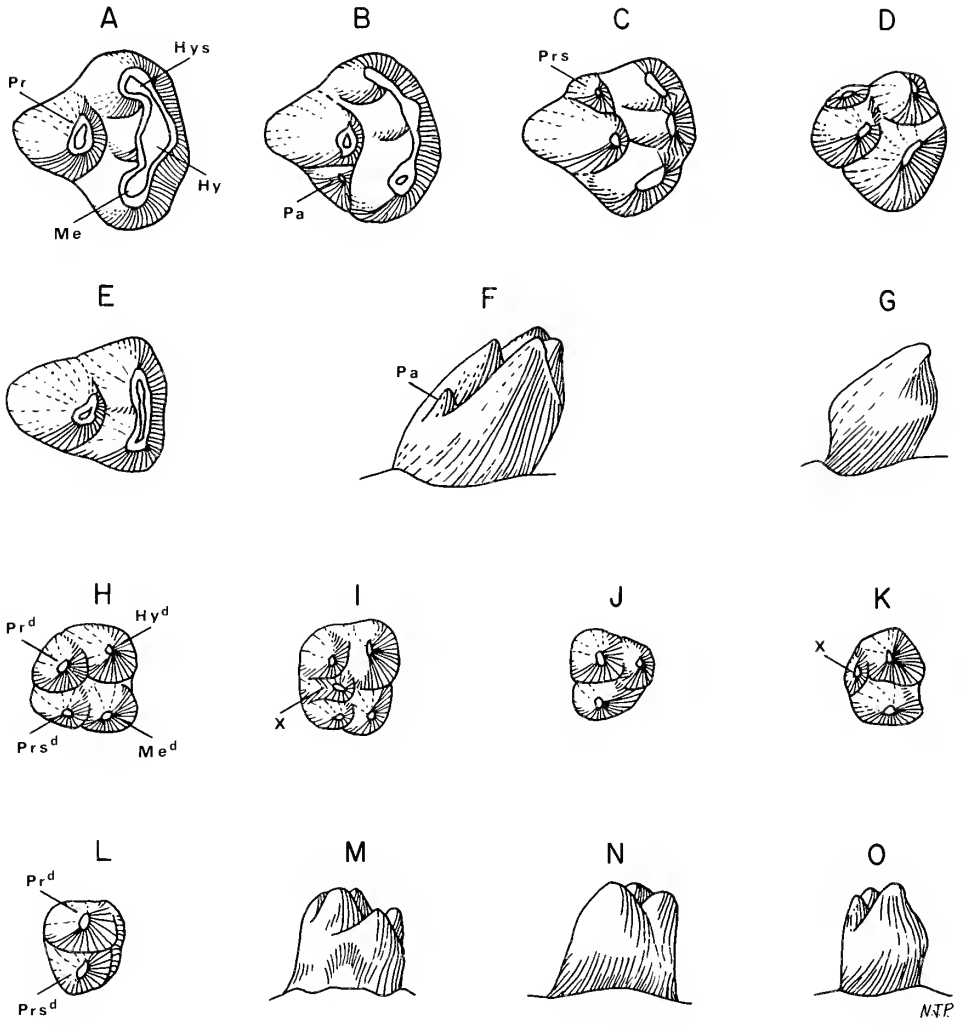

Fig. 6.—Cusp patterns and some anomalies observed in the upper and lower permanent fouth premolars of *Perognathus fasciatus* group pocket mice. A–E = occlusal views of right P^4; F and G = labial views of right P^4; H–L = occlusal views of left P_4; M–O = labial views of left P_4. A and H represent normal cusp patterns; B, C, D, F, I, K, M, and O depict teeth with accessory cusps; D, E, G, J, K, L, N, and O depict teeth with cusp deletions; B and F, I and M, J and N, and K and O each represent two views of similar anomalies. Hy = hypocone; Hy^d = hypoconid; Hys = hypostyle; Me = metacone; Me^d = metaconid; Pa = paracone; Pr = protocone; Pr^d = protoconid; Prs = protostyle; Prs^d = protostylid; X = accessory cusp of uncertain homology.

of the protostylid and metaconid into a single cusp (Fig. 6J and N). Also common was the loss of one or two of the cusps. Generally, this loss involved the cusps on the metalophid (Fig. 6K, L, and O), but in a few instances cusps on the protolophid were absent (not figured). An extra cusp of uncertain homology was noted in a few individuals (Fig. 6I, K, M, and O). Although some samples of *P. apache* exhibited a disproportionate number of cusp anomalies (for example, the White Sands and Rio Grande samples), and the samples of *P. fasciatus* exhibited fewer than expected anomalies, no obvious geographic pattern could be discerned.

Interpopulation Variation

Karyology

The karyotypes of *P. apache*, *P. flavescens*, and *P. fasciatus* are very similar (Table 4), and widely divergent from those of other members of the subgenus *Perognathus* (Williams, 1978). A typical karyotype of *P. apache* is presented in Fig 7. The

X chromosomes of this individual (Fig. 7) were differentially contracted, a condition noted frequently in the cells of females. Other karyotypes of *P. fasciatus, P. flavescens,* and *P. apache* are figured in Williams (1978). The chromosomes of *P. flavescens copei* were identical in gross structure to all *P. apache* samples except that from near Nueva Casas Grandes, Chihuahua. This latter population differed in having a submetacentric X, and in having a pair of small biarmed autosomes. This small autosome pair appears to be homologous to the small acrocentric pair with the secondary constriction found in the other karyotypes (the pair on the right in the bottom row in Fig. 7). A single pericentric inversion can account for this difference. The karyotype of *P. fasciatus* differed from the others in having acrocentric sex chromosomes.

The nature of the karyotypic variation in the *fasciatus* group is not easy to interpret phyletically. According to one model of karyotypic evolution in the subgenus *Perognathus* (Williams, 1978), the autosomal karyotype represented by *P. fasciatus, P. flavescens,* and most *P. apache* is primitive, and the karyotype of the Casas Grandes sample is derived. The differences are slight, however, and from one to three arm additions or pericentric inversions could convert any of the karyotypes into any of the others. The submetacentric X and the acrocentric Y have been regarded as primitive for *Perognathus* (Patton, 1969; Williams, 1978), but none of these karyotypes exhibits that combination of sex chromosome structure. The identical appearance of the chromosomes of *P. flavescens* and typical *P. apache* sets them apart from *P. fasciatus* and the Casas Grandes sample of *P. apache,* but the importance of these differences has not been established.

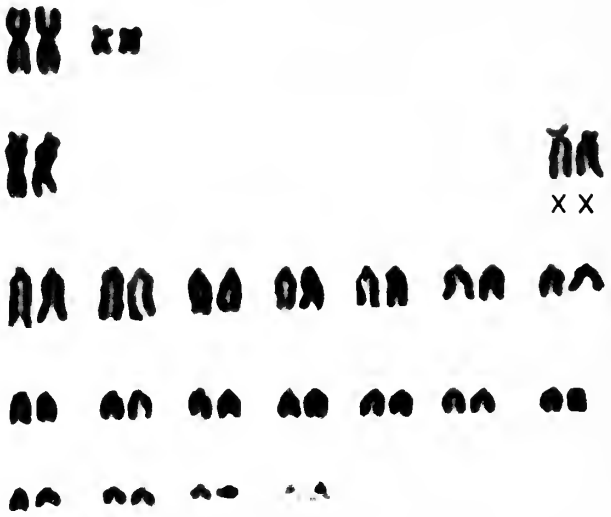

Fig. 7.—Representative karyotype of *Perognathus apache*. Female *P. a. gypsi* from Walker Ranch, White Sands National Monument, Otero Co., New Mexico.

Morphometric Variation

The statistical summaries of the standard univariate analyses are given in Table 5. Coefficients of correlation between the morphometric traits, based upon the 21 sample means, are presented in Table 6. The number of significant correlations was high, and only width of interparietals and least interbullar distance exhibited significant negative correlations with the other characters. These two traits were highly correlated ($r = 0.91$), and either expresses the degree of posterior constriction of the braincase. Some traits (TL/HBL, IPL, IPW, RW, and LID) exhibited relatively low numbers of significant correlations.

A factor analysis of the matrix of correlation demonstrated that only nine factors accounted for

Table 4.—*Chromosome characteristics of* fasciatus *group pocket mice. BA = biarmed; UA = uniarmed.*

Species	♂	♀	2N	FN	Autosome pairs BA	Autosome pairs UA	X	Y
P. fasciatus olivaceogriseus	1	1	44	48	3	18	A	A
P. fasciatus litus	1	1	44	48	3	18	A	A
P. fasciatus callistus	3	2	44	48	3	18	A	A
P. flavescens copei	5	2	44	48	3	18	ST	ST
P. apache apache	7	9	44	48	3	18	ST	ST
P. apache caryi	7	6	44	48	3	18	ST	ST
P. apache cleomophila	1	–	44	48	3	18	ST	ST
P. apache gypsi	–	1	44	48	3	18	ST	—
P. apache relictus	2	1	44	48	3	18	ST	ST
P. apache melanotis	3	1	44	50	4	17	SM	ST

Table 5.—*Standard statistics for samples of* Perognathus fasciatus, P. apache, *and* P. flavescens.

Trait	N	M	SE	CV	Range Minimum	Range Maximum	N	M	SE	CV	Range Minimum	Range Maximum
			1. *P. f. fasciatus*						2. *P. f. olivaceogriseus*			
1	11	135.7	2.269	5.54	123.0	147.0	15	133.1	1.099	3.20	126.0	142.0
2	11	62.6	1.410	7.46	57.0	70.0	15	62.7	0.720	4.45	59.0	68.0
3	11	73.1	1.504	6.82	65.0	80.0	15	70.4	0.974	5.36	65.0	81.0
4	11	17.4	0.338	6.45	16.0	19.0	15	16.7	0.157	3.63	15.7	18.0
5	11	7.5	0.157	6.92	7.0	8.0	15	7.1	0.134	7.37	6.0	8.0
6	11	0.859	0.023	8.72	0.738	0.971	15	0.894	0.016	6.92	0.738	0.985
7	8	22.60	0.208	2.59	21.65	23.50	15	22.17	0.104	1.89	21.25	22.80
8	8	22.60	0.208	2.59	21.65	23.50	15	22.14	0.101	1.77	21.25	22.75
9	10	4.88	0.063	4.08	4.55	5.20	15	4.95	0.041	3.24	4.65	5.20
10	10	3.22	0.041	4.01	3.05	3.40	15	3.12	0.032	3.96	2.95	3.35
11	8	4.41	0.063	4.04	4.05	4.70	15	4.33	0.030	2.71	4.00	4.50
12	9	7.69	0.094	3.68	7.35	8.20	15	7.60	0.086	4.39	7.00	8.05
13	8	11.92	0.082	1.96	11.45	12.20	15	11.71	0.075	2.54	11.15	12.10
14	10	2.62	0.054	6.55	2.30	2.90	15	2.63	0.062	9.18	2.30	3.00
15	10	4.69	0.104	6.99	4.25	5.20	15	4.75	0.048	3.89	4.35	5.00
16	10	8.22	0.112	4.30	7.65	8.65	15	8.20	0.073	3.45	7.55	8.65
17	10	2.21	0.028	3.94	2.10	2.35	15	2.15	0.016	2.97	2.05	2.30
18	10	3.68	0.060	5.16	3.35	3.90	15	3.74	0.041	4.30	3.40	4.00
19	8	4.80	0.052	3.04	4.65	5.10	15	4.58	0.071	6.00	4.10	5.00
20	10	2.80	0.022	2.50	2.70	2.90	15	2.78	0.024	3.38	2.60	2.95
21	11	0.63	0.007	3.51	0.61	0.68	15	0.62	0.006	3.65	0.58	0.65
22	11	0.67	0.011	5.32	0.61	0.74	15	0.67	0.010	5.60	0.61	0.71
23	10	0.62	0.006	3.29	0.58	0.65	15	0.61	0.008	4.85	0.58	0.65
24	10	0.73	0.014	5.89	0.68	0.81	15	0.72	0.010	5.26	0.68	0.81
25	11	2.76	0.070	8.24	2.40	3.05	15	2.75	0.033	4.60	2.40	2.90
26	11	0.98	0.010	3.39	0.90	1.03	15	1.00	0.014	5.31	0.90	1.10
27	11	1.10	0.022	6.58	1.00	1.23	15	1.09	0.015	5.27	0.97	1.19
28	10	0.71	0.013	5.82	0.65	0.77	15	0.70	0.009	4.96	0.65	0.77
29	11	0.86	0.014	5.48	0.81	0.97	15	0.86	0.008	3.70	0.81	0.90
30	11	0.98	0.008	2.69	0.94	1.00	15	0.97	0.006	2.34	0.94	1.03

90% of the total variance, and that the first five factors accounted for 85.1% of the variance (Table 7). Each of the traits except length and width of the interparietals and least interbullar distance showed high positive loading on Factor I, which is a general size factor. The posterior cranial region become more constricted with increasing size, as demonstrated by the negative loading of interparietal dimensions and least interbullar distance on Factor I.

Factor II, which accounts for 15.6% of the total variance, showed high positive values for width of interparietals, least interbullar distance, width of P_4, and width of M^3. Traits with high negative values were least interorbital breadth, length of M_1, and length of hind foot. Factor II was most strongly influenced by traits expressing the postcranial constriction.

Factor III, accounting for 5.7% of the total variance, showed a high positive value only for length of interparietal. Width of interparietals also also exhibited positive loading for Factor III, whereas length of tail exhibited negative loading. Samples with high positive scores for Factor III had relatively long interparietals and short tails. Factor IV accounted for 4.2% of the total variance and was loaded most strongly by length of articular process. Factor V, accounting for 3.5% of the total variance, had high loading on the TL/HBL ratio. Negative loading on length of head and body and positive loading on length of tail also reflect this "tail factor." Samples with high factor scores for Factor V had relatively long tails. Beyond Factor V, the individual factors accounted for relatively little of the variance.

The factor scores of the first three factors, for each of the samples, are plotted in Fig. 8. Note that *P. fasciatus* samples are most distinctive in terms of Factor II, having wide interparietals and narrow

Table 5.—*Continued.*

Trait	N	M	SE	CV	Range Minimum	Range Maximum	N	M	SE	CV	Range Minimum	Range Maximum
			3. *P. f. litus*						4. *P. f. callistus*			
1	27	139.8	0.824	3.06	134.0	149.0	18	134.3	1.249	3.95	123.0	146.0
2	27	66.9	0.536	4.16	61.0	75.0	18	63.3	1.105	7.41	53.0	70.0
3	27	72.9	0.531	3.78	69.0	80.0	18	71.0	0.925	5.53	63.0	78.0
4	27	17.7	0.099	2.89	16.9	19.0	18	18.0	0.164	3.88	17.0	19.0
5	27	6.9	0.093	6.98	6.1	7.9	18	6.8	0.200	12.47	5.0	8.0
6	27	0.919	0.009	5.02	0.813	1.029	18	0.894	0.022	10.58	0.739	1.079
7	27	23.23	0.118	2.64	22.15	24.80	17	23.00	0.111	1.98	21.95	24.00
8	27	23.07	0.111	2.50	22.10	24.55	17	22.85	0.102	1.85	21.90	23.70
9	27	5.13	0.026	2.65	4.95	5.40	18	5.18	0.028	2.34	5.00	5.40
10	27	3.27	0.019	3.03	3.05	3.50	18	3.18	0.026	3.50	3.00	3.40
11	27	4.45	0.022	2.69	4.15	5.65	18	4.44	0.027	2.65	4.20	4.60
12	27	8.60	0.056	3.39	8.00	9.35	18	8.48	0.062	3.11	7.90	8.90
13	27	12.90	0.072	2.81	12.20	13.85	18	12.71	0.081	2.62	12.10	13.35
14	27	2.63	0.040	8.01	2.25	3.15	18	2.78	0.057	8.67	2.25	3.35
15	27	4.50	0.072	8.36	3.85	5.15	18	4.56	0.054	5.19	4.15	5.15
16	27	8.55	0.051	3.11	7.95	9.10	17	8.30	0.072	3.58	7.75	8.85
17	27	2.33	0.021	4.69	2.10	2.55	17	2.23	0.029	5.30	2.05	2.45
18	27	3.71	0.027	3.76	3.50	4.00	18	3.64	0.024	2.81	3.45	3.85
19	27	4.37	0.077	9.13	3.55	5.30	18	4.39	0.080	7.78	3.65	5.05
20	27	2.84	0.014	2.69	2.65	2.95	16	2.82	0.026	3.65	2.60	3.00
21	27	0.66	0.006	4.75	0.61	0.71	14	0.64	0.004	2.37	0.61	0.65
22	27	0.69	0.005	4.15	0.65	0.77	14	0.67	0.013	7.10	0.61	0.74
23	27	0.60	0.007	5.71	0.55	0.68	14	0.62	0.008	5.07	0.58	0.68
24	27	0.74	0.007	5.01	0.65	0.81	14	0.72	0.006	3.25	0.68	0.74
25	27	2.89	0.025	4.57	2.53	3.20	14	2.86	0.037	4.87	2.67	3.13
26	27	1.03	0.008	3.90	0.97	1.10	14	1.00	0.008	2.95	0.97	1.03
27	27	1.10	0.009	4.06	1.00	1.19	14	1.10	0.012	3.95	1.03	1.16
28	27	0.71	0.008	6.18	0.61	0.81	14	0.73	0.012	5.94	0.68	0.81
29	27	0.91	0.010	5.92	0.81	1.00	14	0.88	0.009	3.91	0.84	0.94
30	27	0.95	0.007	3.98	0.87	1.00	14	0.96	0.015	5.81	0.81	1.03

interorbital regions. The *P. flavescens* samples are most notable in their highly negative scores for Factor I and high positive scores for Factor III. They are small in size (Factor I), with relatively short tails and with broad interparietals (Factor III). Of the *P. apache* samples, the northern ones are, perhaps, the most unique, being large, with long tails and narrow crania (Factor I). This is, of course, a simplification of the geographic variation in the morphometric traits (Table 5), but most of the variation (77.4%) is accounted for in these three factors, and the factors are most strongly influenced by suites of related characters.

Tests for significant differences between samples, using the SS-STP routine, resulted in a large number of superfluous comparisons between samples that are widely separated geographically. Therefore, only a summary of the comparisons between samples in geographic proximity is presented (Table 8). The comparisons were limited to samples of populations that are neighbors and, potentially, can exchange genes. The results of the SS-STP comparisons are illustrated in Fig. 9. To simplify the picture, some of the less likely comparisons were omitted from Fig. 9, but are given in Table 8. Note that the *P. fasciatus* samples (1–4) exhibited high numbers of significant differences with adjacent samples of *P. flavescens* (21) and *P. apache* (5). These were not the highest numbers of significant differences, but because these populations are sympatric, or, in the case of *P. apache*, in close proximity, reproductive isolation is suggested. Of the *P. apache* samples, numbers 5, 6, 10, 12, 15, 16 or 17, and 19 form a chain of populations with few significant differences, extending from northern Utah to Chihuahua (Fig. 9). Most other samples peripheral to this chain are connected by only one or a few routes. For example, the Painted Desert and Flag-

Table 5.—*Continued.*

Trait	N	M	SE	CV	Range		N	M	SE	CV	Range	
					Minimum	Maximum					Minimum	Maximum
		5. *P. apache* Uintah Basin						6. *P. apache* Moab				
1	60	140.7	0.717	3.94	128.0	155.0	27	137.4	1.078	4.07	123.0	146.0
2	60	68.3	0.489	5.55	52.0	74.0	27	66.7	0.817	6.36	59.0	73.0
3	61	72.5	0.646	6.97	61.0	87.0	27	70.7	0.636	4.68	64.0	78.0
4	61	18.2	0.095	4.08	16.7	20.0	27	18.5	0.233	6.56	15.0	21.0
5	60	7.0	0.064	7.05	6.0	8.0	24	6.7	0.107	7.79	6.0	8.0
6	60	0.949	0.012	9.67	0.667	1.147	27	0.946	0.013	7.37	0.815	1.078
7	60	23.92	0.076	2.44	22.85	25.50	23	23.53	0.133	2.71	22.30	24.60
8	59	23.74	0.075	2.42	22.55	25.30	21	23.33	0.127	2.49	22.05	24.25
9	61	5.36	0.023	3.36	5.00	5.70	25	5.26	0.030	2.85	5.00	5.60
10	61	3.30	0.015	3.61	3.05	3.55	27	3.27	0.048	7.64	2.35	3.75
11	61	4.58	0.017	2.83	4.35	4.90	26	4.51	0.028	3.19	4.15	4.75
12	61	8.80	0.038	3.36	8.30	9.45	26	8.51	0.051	3.08	7.85	9.05
13	61	13.08	0.042	2.50	12.45	14.00	24	12.81	0.058	2.24	12.30	13.25
14	61	3.22	0.028	6.71	2.80	3.65	26	3.14	0.037	5.95	2.80	3.50
15	61	4.35	0.034	6.07	3.75	4.95	26	4.39	0.085	9.92	3.80	5.25
16	60	8.74	0.044	3.92	8.00	9.50	25	8.54	0.075	4.38	7.90	9.25
17	60	2.23	0.014	4.90	2.00	2.50	25	2.30	0.024	5.33	2.00	2.60
18	61	3.85	0.019	3.88	3.60	4.20	26	3.79	0.043	5.79	3.45	4.30
19	61	3.94	0.027	5.27	3.50	4.35	25	4.05	0.069	8.49	3.55	4.60
20	60	2.95	0.011	2.88	2.70	3.10	27	2.93	0.019	3.39	2.70	3.10
21	60	0.65	0.004	4.91	0.58	0.71	27	0.63	0.007	6.26	0.52	0.68
22	60	0.66	0.004	4.23	0.61	0.71	27	0.64	0.008	6.75	0.58	0.71
23	60	0.64	0.004	4.74	0.58	0.71	27	0.64	0.006	5.28	0.58	0.71
24	60	0.75	0.005	4.61	0.68	0.84	27	0.74	0.009	6.36	0.65	0.81
25	60	2.84	0.022	6.00	2.53	3.27	27	2.96	0.038	6.65	2.67	3.40
26	61	1.05	0.005	4.00	0.94	1.16	27	1.03	0.006	3.05	1.00	1.10
27	61	1.22	0.005	3.37	1.13	1.32	27	1.20	0.009	3.98	1.10	1.29
28	61	0.72	0.005	5.70	0.61	0.77	26	0.69	0.008	6.20	0.61	0.77
29	60	0.96	0.005	3.60	0.84	1.06	27	0.99	0.007	3.91	0.94	1.06
30	60	1.01	0.005	4.11	0.94	1.13	27	1.01	0.010	5.28	0.87	1.13

staff samples were closely similar, and appear to be linked with the others along an avenue to the east, in the direction of the Gallup sample (Fig. 9). The Canyon Largo sample from higher juniper and pinyon-juniper associations (11), was very distinct from the adjacent San Juan Basin sample (10) from a lower, sage-grassland habitat. The Canyon Largo sample was more similar to the Santa Fe (14) and Estrella samples (12) from ecologically similar areas.

The Rio Grande Valley sample (15) was very different from the adjacent Deming Plains sample (19), and they appear to be linked only by an indirect route through the Gran Quivira (17) or San Augustine Plains sample (16). Mice typical of the Rio Grande Valley sample were found from the Rio Salado, north of Albuquerque, southward to where the Valley narrows near Val Verde, New Mexico. No Apache pocket mice are known from between Val Verde and Las Cruces in the Rio Grande Valley. I have, however, collected a few Apache pocket mice, typical of the Deming Plains population, as far north as Engle in the Jornada del Muerto.

Only two significant differences were found between the Deming Plains sample of *P. apache* and *P. flavescens copei* (Table 8, Fig. 9). Other populations of the Apache pocket mouse in proximity to *P. flavescens* were quite distinct from *flavescens*, with from seven to 16 significant differences. These were no greater than the differences among some samples of Apache pocket mice, however. Of the potential avenues of gene exchange between Apache and plains pocket mice, the Trans-Pecos route seems most likely on the basis of the univariate analyses (Fig. 9).

Even though the Uintah Basin appears to be isolated, samples of the Apache pocket mice occupying the Basin were essentially the same as samples

Table 5.—*Continued.*

Trait	N	M	SE	CV	Range		N	M	SE	CV	Range	
					Minimum	Maximum					Minimum	Maximum
		7. *P. apache* Painted Desert						8. *P. apache* Flagstaff				
1	52	133.1	0.987	5.26	119.0	156.0	32	132.2	1.098	4.69	120.0	145.0
2	52	64.1	0.595	6.64	50.0	73.0	32	63.4	0.598	5.34	58.0	73.0
3	54	69.3	0.750	7.78	61.0	89.0	32	68.8	0.724	5.95	58.0	77.0
4	54	18.5	0.119	4.97	17.0	21.0	32	19.1	0.137	4.05	17.5	20.5
5	28	6.1	0.067	8.15	6.0	7.0	7	6.4	0.190	7.86	6.0	7.0
6	52	0.929	0.012	9.49	0.714	1.076	32	0.918	0.011	6.73	0.824	1.086
7	49	22.60	0.090	2.90	21.30	24.35	31	22.60	0.156	3.83	21.10	24.55
8	49	22.42	0.089	2.89	21.25	23.95	32	22.50	0.149	3.73	21.00	24.50
9	51	5.14	0.022	3.07	4.75	5.55	32	5.25	0.039	4.18	4.80	5.70
10	55	3.19	0.022	5.07	2.95	3.85	32	3.19	0.028	4.99	2.85	3.60
11	53	4.37	0.021	3.58	4.05	4.65	32	4.29	0.029	3.83	3.95	4.60
12	54	8.37	0.049	4.41	7.50	9.35	32	7.97	0.071	5.02	7.25	8.60
13	49	12.58	0.059	3.29	11.65	13.35	31	12.25	0.076	3.49	11.60	13.15
14	54	2.87	0.032	8.01	2.20	3.30	32	2.88	0.041	8.02	2.35	3.40
15	54	3.94	0.040	7.26	3.30	4.65	32	3.92	0.073	10.50	2.80	4.70
16	53	7.94	0.048	4.55	7.10	8.95	32	8.15	0.070	4.87	7.40	9.25
17	51	2.26	0.016	5.30	2.05	2.55	32	2.32	0.024	5.94	2.10	2.60
18	55	3.68	0.023	4.61	3.35	4.15	32	3.69	0.028	4.24	3.40	4.00
19	53	3.90	0.034	6.06	3.45	4.45	31	3.87	0.057	8.21	3.10	4.40
20	55	2.79	0.014	2.07	2.60	3.05	32	2.76	0.021	4.13	2.50	3.05
21	55	0.58	0.006	7.33	0.48	0.65	32	0.59	0.008	7.64	0.48	0.68
22	55	0.62	0.006	6.94	0.55	0.74	32	0.60	0.007	6.43	0.55	0.68
23	55	0.61	0.005	6.17	0.55	0.68	32	0.61	0.007	6.68	0.52	0.68
24	55	0.70	0.006	6.90	0.61	0.81	32	0.70	0.008	6.25	0.61	0.81
25	54	2.80	0.002	5.80	2.33	3.20	32	2.86	0.030	5.99	2.53	3.27
26	55	0.99	0.006	4.68	0.87	1.10	32	0.97	0.007	4.36	0.87	1.03
27	55	1.10	0.008	5.63	0.94	1.26	32	1.10	0.011	5.56	0.97	1.23
28	54	0.65	0.006	7.41	0.55	0.81	32	0.66	0.008	7.33	0.55	0.81
29	55	0.93	0.007	5.35	0.81	1.06	32	0.95	0.009	5.31	0.84	1.06
30	53	0.96	0.007	5.34	0.84	1.13	32	0.94	0.009	5.41	0.84	1.03

of populations from farther south in Utah and Colorado. On the other hand, the San Luis Valley population of south-central Colorado appeared to be relatively isolated and well differentiated from its neighbors. Samples of the Painted Desert and Flagstaff populations were quite different from those from adjacent areas to the north and east. The lower San Juan River and Chuska Mountains appear to be effective barriers to gene exchange between these populations (Fig. 4).

The most apparent geographic pattern to the morphometric variation in Apache pocket mice was a strong north-south size cline. This is best seen in the main chain of populations extending from north to south. Occipitonasal length is representative of size and well illustrates this cline (Fig. 10). A correlation analysis between the morphometric characters and the climatic and geographic variables showed the size cline to be highly significant (Table 9, Fig. 11). Latitude showed 23 significant positive correlations with the morphometric traits, of which 21 were highly significant (Table 9). The climatic severity index, growing season, and mean July minimum temperature were not significantly correlated with any of the morphometric traits. Mean annual temperature was negatively correlated with body size (TOTL and HBL). Latitude was, however, more highly correlated with size than the variables expressing environmental temperature. It is probable that these variables do not adequately express the complexities of the yearly climatic cycle or the temperature factors affecting these pocket mice. Apache pocket mice do vary in size as predicted by Bergman's principle, and it is most likely that relative heat loss is an important factor in determining size in these populations. These mice store seeds, become hypothermic at low ambient temperatures and in times of food deprivation, and are generally

Table 5.—*Continued.*

Trait	N	M	SE	CV	Range		N	M	SE	CV	Range	
					Minimum	Maximum					Minimum	Maximum
		9. *P. apache* Gallup						10. *P. apache* San Juan Basin				
1	8	131.5	2.062	4.43	124.0	139.0	32	137.8	1.093	4.49	127.0	151.0
2	8	61.9	1.187	5.42	58.0	69.0	32	67.3	0.511	4.29	62.0	72.0
3	8	69.6	1.557	6.33	63.0	76.0	32	70.4	0.747	6.00	63.0	80.0
4	8	18.3	0.164	2.53	18.0	19.0	32	19.5	0.105	3.06	18.0	20.0
5	0	—	—	—	—	—	32	6.8	0.050	4.19	6.0	7.0
6	8	0.891	0.025	7.85	0.815	0.985	32	0.958	0.009	5.20	0.858	1.078
7	5	22.54	0.206	2.05	22.00	23.00	32	23.34	0.135	3.27	21.30	24.70
8	6	22.41	0.183	2.00	21.80	23.00	32	23.14	0.128	3.12	21.10	24.60
9	6	5.16	0.077	3.65	4.90	5.35	32	5.29	0.033	3.55	4.90	5.65
10	6	3.29	0.042	3.10	3.10	3.35	32	3.42	0.025	4.09	3.15	3.75
11	6	4.37	0.031	1.72	4.30	4.45	32	4.40	0.019	2.41	4.20	4.60
12	5	8.17	0.087	2.35	7.90	8.40	32	8.42	0.067	4.45	7.60	9.25
13	6	12.51	0.073	1.55	12.25	12.80	32	12.71	0.062	2.81	12.05	13.70
14	6	3.19	0.104	8.01	2.80	3.45	32	3.07	0.047	2.65	3.70	8.76
15	6	4.07	0.077	4.64	3.75	4.25	32	4.05	0.057	8.02	3.50	4.75
16	6	8.14	0.104	3.14	7.80	8.50	32	8.46	0.075	5.01	7.60	9.25
17	6	2.26	0.047	5.13	2.10	2.40	30	2.38	0.026	5.88	1.90	2.60
18	6	3.71	0.108	7.16	3.40	4.00	32	3.85	0.034	5.00	3.50	4.30
19	6	4.01	0.030	1.83	3.90	4.10	32	3.92	0.043	6.26	3.35	4.40
20	7	2.88	0.031	2.81	2.75	3.00	32	2.97	0.017	3.31	2.75	3.15
21	7	0.62	0.011	4.70	0.58	0.65	32	0.62	0.007	6.65	0.55	0.71
22	7	0.63	0.011	4.53	0.61	0.68	32	0.65	0.008	6.98	0.58	0.77
23	7	0.63	0.009	4.02	0.58	0.65	32	0.64	0.007	5.88	0.58	0.74
24	7	0.73	0.018	6.70	0.68	0.81	32	0.75	0.009	7.10	0.68	0.87
25	7	2.77	0.095	9.09	2.27	3.00	32	2.93	0.027	5.28	2.60	3.33
26	5	0.99	0.012	2.72	0.97	1.03	32	1.05	0.008	4.49	0.97	1.13
27	5	1.13	0.016	3.11	1.10	1.16	32	1.18	0.007	3.17	1.10	1.26
28	4	0.68	0.022	6.73	0.61	0.71	32	0.69	0.007	6.01	0.61	0.77
29	7	0.99	0.010	2.45	0.97	1.03	32	0.99	0.007	4.08	0.94	1.10
30	7	0.99	0.013	3.62	0.94	1.03	32	1.01	0.009	4.84	0.90	1.13

inactive on the surface during inclement weather (personal observations); so it would, perhaps, be naive to expect a simple relationship between size and mean annual temperature.

Another factor that is possibly working in concert with temperature in selecting for size is differential resource allocation. In the southern portion of their range, Apache pocket mice are sympatric with another sand-dwelling species, *P. penicillatus*. The desert pocket mouse has about the same body size as the northern populations of *P. apache* (HBL = 70–75 mm), but is about 13% larger than the sympatric population of *P. apache*. Mares and Williams (1977) presented experimental evidence suggesting that the differences in body size among several heteromyid granivores determines, in part, the sizes of the seeds gathered. They also showed that larger species were able to gather a greater size array of seeds. Thus, within limits, larger body size should be advantageous for most species. Competition between *P. apache* and *P. penicillatus* could select for mice with well-differentiated body sizes, and could be partly responsible for the small size of southern populations of *P. apache*. North of the range of *P. penicillatus*, the lack of competition with that species may permit selection for larger body size in *P. apache*. North of the San Juan River, the absence of competition with sympatric congeners and cooler ambient temperatures may both be important factors in the selection for even larger body size in Apache pocket mice.

The size of the auditory bullae (BL, BW) and interorbital breadth exhibited significant negative correlations with mean annual precipitation (Table 9, Fig. 12). These traits were positively correlated with latitude, although latitude and mean annual

Table 5.—*Continued.*

Trait	N	M	SE	CV	Range Minimum	Range Maximum	N	M	SE	CV	Range Minimum	Range Maximum
		11. *P. apache* Canyon Largo						12. *P. apache* Estrella				
1	25	132.9	1.171	4.48	120.0	143.0	13	137.4	1.146	3.01	131.0	144.0
2	25	63.6	0.716	5.63	55.0	71.0	13	67.6	0.738	3.94	62.0	72.0
3	26	69.0	0.860	6.35	57.0	75.0	13	69.8	0.856	4.42	64.0	75.0
4	26	17.8	0.126	3.61	16.7	19.3	13	19.3	0.166	3.11	18.5	20.5
5	26	6.6	0.062	4.76	6.1	7.2	13	6.7	0.104	5.64	6.0	7.0
6	25	0.922	0.015	8.25	0.733	1.105	13	0.970	0.015	5.74	0.837	1.045
7	24	22.57	0.162	3.53	21.35	24.10	13	23.05	0.161	2.53	22.25	23.80
8	25	22.41	0.151	3.37	21.30	24.00	13	22.87	0.168	2.63	22.00	23.70
9	26	5.13	0.034	3.46	4.75	5.50	13	5.22	0.051	3.53	5.00	5.50
10	26	3.26	0.034	5.26	2.85	3.50	13	3.34	0.024	3.20	3.50	2.67
11	26	4.32	0.027	3.22	4.10	4.65	13	4.36	0.038	3.18	4.15	4.65
12	24	7.97	0.065	4.02	7.45	8.55	13	8.30	0.038	4.25	7.65	8.80
13	25	12.27	0.080	3.34	11.65	13.20	13	12.75	0.096	2.59	12.10	13.25
14	26	2.81	0.043	7.84	2.30	3.20	13	2.89	0.059	7.45	2.60	3.30
15	26	3.96	0.045	5.87	3.60	4.45	13	4.09	0.069	6.06	3.55	4.45
16	25	8.08	0.071	4.42	7.55	9.00	13	8.27	0.107	4.67	7.60	8.80
17	25	2.23	0.030	6.83	1.85	2.40	13	2.31	0.039	6.13	2.10	2.50
18	26	3.68	0.039	5.39	3.35	4.10	13	3.79	0.045	4.32	3.55	4.10
19	26	3.85	0.054	7.20	3.40	4.30	13	3.96	0.064	5.83	3.50	4.25
20	25	2.85	0.030	5.30	2.55	3.15	13	2.93	0.033	4.04	2.80	3.15
21	25	0.59	0.011	9.14	0.52	0.68	13	0.63	0.008	4.49	0.58	0.68
22	25	0.63	0.008	6.75	0.55	0.71	13	0.64	0.011	6.30	0.58	0.74
23	25	0.63	0.008	6.48	0.55	0.68	13	0.62	0.011	6.58	0.55	0.68
24	25	0.74	0.009	6.34	0.65	0.84	13	0.74	0.013	6.40	0.68	0.84
25	24	2.88	0.036	6.13	2.67	3.20	13	2.90	0.017	4.36	2.67	3.13
26	26	1.01	0.011	5.70	0.94	1.13	13	1.02	0.013	4.78	0.97	1.10
27	26	1.13	0.010	4.58	1.00	1.19	13	1.14	0.014	4.38	1.03	1.19
28	26	0.68	0.007	5.29	0.61	0.74	13	0.67	0.011	6.11	0.58	0.74
29	25	0.95	0.010	5.43	0.81	1.03	13	0.97	0.009	3.60	0.90	1.03
30	25	0.98	0.011	5.84	0.87	1.10	13	0.99	0.011	3.90	0.90	1.03

precipitation were not correlated (Table 10). Relative bullar size appears to be related to two independent factors, the general size factor and the amount of environmental moisture. These two factors were not correlated, and their associations with bullar and interorbital size were conflicting. Variation in the size of the auditory bullae is in agreement with the commonly observed ecogeographic principle of animals from drier climates having larger sound sensing organs that their relatives from moister climates. The rostrum (NL, NW, RW, IOB) was wider and longer in samples from the more arid localities, but only interorbital breadth showed a significant negative correlation with mean annual precipitation. This association is as one would expect if these mice are adapted to decrease pulmonary water loss in drier climates. The strong size cline, however, partially masked these associations.

Tail size did not exhibit a significant negative correlation with mean annual temperature, contrary to the prediciton of Allen's principle. Rather, the TL/HBL ratio increased with increasing latitude (r = 0.60), with increasing body size (r with HBL = 0.68) and with head size (r with ONL = 0.72). This suggests that some factor or factors are selecting for increasingly longer tails with increasing body size. I have observed these mice in bipedal stances while foraging, and a longer tail could be necessary to counterbalance a larger body. The relationship between head size and tail length is shown in Fig. 13.

The significant associations between length of interparietal and elevation, and between certain dental measurements (P^4W and M_1L; Table 9) and elevation adjusted for latitude have no obvious explanations. Perhaps they are spurious correla-

Table 5.—*Continued.*

Trait	N	M	SE	CV	Range		N	M	SE	CV	Range	
					Minimum	Maximum					Minimum	Maximum
		13. *P. apache* San Luis Valley						14. *P. apache* Santa Fe				
1	17	136.3	1.288	3.90	123.0	144.0	24	136.2	1.325	4.81	118.0	145.0
2	17	67.2	0.671	4.11	60.0	71.0	24	65.0	0.797	6.01	56.0	70.0
3	17	69.1	0.813	4.85	63.0	76.0	26	70.2	0.797	5.78	62.0	80.0
4	17	18.6	0.139	3.09	18.0	20.0	26	18.2	0.141	3.95	16.5	20.0
5	15	6.7	0.152	8.86	6.0	8.0	11	6.6	0.187	9.38	5.8	7.8
6	17	0.972	0.011	4.58	0.882	1.031	24	0.927	0.013	7.15	0.802	1.060
7	13	22.41	0.186	3.00	21.00	23.60	22	22.46	0.136	2.85	21.25	24.20
8	15	22.39	0.162	2.80	21.00	23.55	21	22.40	0.138	2.82	21.25	23.90
9	16	5.37	0.045	3.39	5.00	5.65	24	5.10	0.034	3.27	4.80	5.40
10	17	3.12	0.030	3.97	2.90	3.35	26	3.24	0.024	3.80	3.00	3.55
11	16	4.21	0.029	2.78	3.95	4.35	25	4.34	0.030	3.50	4.10	4.60
12	14	7.86	0.074	3.52	7.30	8.30	25	7.73	0.066	4.27	7.00	8.45
13	15	12.14	0.080	2.58	11.60	12.50	23	12.17	0.087	3.38	11.55	13.55
14	16	2.63	0.048	7.30	2.35	3.00	24	2.81	0.059	10.25	2.35	3.55
15	16	3.83	0.065	6.81	3.35	4.50	24	4.06	0.078	9.44	3.25	4.90
16	16	7.79	0.098	5.02	7.15	8.40	25	8.07	0.064	4.02	7.35	8.65
17	15	2.25	0.027	4.70	2.05	2.35	24	2.24	0.028	6.16	1.95	2.50
18	15	3.75	0.041	4.29	3.45	3.95	25	3.74	0.038	5.13	3.35	4.10
19	15	3.99	0.052	5.01	3.65	4.40	24	4.15	0.056	6.63	3.75	4.75
20	16	2.76	0.027	3.93	2.55	2.90	27	2.81	0.017	3.24	2.65	2.95
21	16	0.57	0.010	7.27	0.48	0.65	27	0.61	0.006	5.32	0.55	0.68
22	16	0.59	0.006	4.38	0.55	0.65	27	0.64	0.006	5.05	0.58	0.71
23	16	0.61	0.007	4.71	0.55	0.65	27	0.61	0.007	5.65	0.55	0.68
24	16	0.71	0.009	5.12	0.68	0.81	27	0.73	0.007	5.19	0.65	0.81
25	16	2.78	0.021	6.36	2.40	3.07	27	2.73	0.030	5.75	2.40	3.00
26	16	0.86	0.008	3.66	0.81	0.90	26	0.97	0.011	5.93	0.89	1.06
27	16	1.02	0.010	3.77	0.97	1.10	26	1.11	0.010	4.80	1.00	1.19
28	16	0.63	0.008	5.22	0.58	0.71	26	0.65	0.008	6.19	0.55	0.74
29	16	0.95	0.008	3.26	0.90	1.00	27	0.95	0.007	3.67	0.87	1.00
30	16	0.94	0.009	3.73	0.90	1.03	27	0.97	0.008	4.34	0.90	1.06

tions, or perhaps they are somehow affected by available moisture which increases with increasing elevation.

Color Variation

Color was more variable geographically than were the morphometric traits, and consequently, I did not group samples as much for the analysis of color. Table 11 lists the means for the color indices of samples of *P. apache* and *P. flavescens*. In general, an increase in darkness was accompanied by an increase in richness ($r = 0.52$). Notable exceptions were seen in samples from unusually light or dark colored soils. The Uintah Basin sample had a relatively large number of black-tipped guard hairs (darkness), but the yellowish color (richness) was quite pale. Soils in that region are very pale-tannish or grayish in color. The White Sands sample was also exceptional in that yellowish pigment was absent in most adults (most young mice in juvenile pelage had a very pale yellowish tinge). Their basic color was white, overlain by a normal number of black-tipped hairs, presenting a neutral, grayish appearance. The gypsum dunes upon which these mice were collected are white. Samples from reddish sands, such as those near Caprock and Tolar were darker and more orange-colored than those from tanner soils.

A correlation analysis between the color parameters and the climatic and geographic variables is given in Table 10. The color indices were all highly correlated with mean annual precipitation, and richness and relative darkness were correlated with elevation (elevation and mean annual precipitaion were highly correlated). The relative darkness index is plotted against mean annual precipitation in

Table 5.—*Continued.*

Trait	N	M	SE	CV	Range		N	M	SE	CV	Range	
					Minimum	Maximum					Minimum	Maximum
		15. *P. apache* Rio Grande Valley						16. *P. apache* San Augustine Plains				
1	66	133.8	0.762	4.77	119.0	151.0	17	128.8	1.651	5.28	117.0	145.0
2	66	63.1	0.565	7.32	50.0	78.0	17	60.2	1.034	7.08	51.0	68.0
3	68	70.9	0.506	6.00	58.0	80.0	17	68.6	0.955	5.74	64.0	77.0
4	68	18.6	0.100	4.62	17.0	20.0	17	18.1	0.157	3.59	17.3	19.5
5	67	6.6	0.067	8.39	5.0	8.0	14	6.6	0.093	5.34	6.1	7.1
6	66	0.892	0.011	9.64	0.734	1.121	17	0.879	0.015	7.08	0.708	0.984
7	63	22.88	0.087	3.14	21.00	24.45	15	22.30	0.131	2.27	21.75	23.60
8	63	22.81	0.085	3.06	21.00	24.15	15	22.20	0.124	2.16	21.65	23.45
9	68	5.24	0.026	4.12	4.65	5.75	17	5.09	0.053	4.32	4.75	5.60
10	69	3.27	0.017	4.41	3.00	3.60	17	3.15	0.029	3.83	2.95	3.35
11	68	4.36	0.016	3.14	4.05	4.65	17	4.28	0.025	2.38	4.05	4.45
12	64	8.10	0.045	4.60	7.30	8.95	16	7.97	0.073	3.68	7.50	8.40
13	64	12.34	0.059	3.79	11.35	13.40	17	12.24	0.089	2.97	11.60	12.90
14	68	2.87	0.027	7.80	2.35	3.35	17	2.81	0.060	8.79	2.40	3.35
15	68	4.07	0.039	7.93	3.45	5.00	17	4.09	0.081	8.17	3.50	4.65
16	65	8.28	0.046	4.51	7.35	9.15	15	7.95	0.072	3.49	7.60	8.55
17	66	2.28	0.020	7.02	1.95	2.80	16	2.14	0.022	4.11	2.00	2.30
18	68	3.78	0.028	6.20	3.30	4.25	17	3.71	0.047	5.31	3.50	4.15
19	68	3.99	0.040	8.19	2.65	5.10	17	4.00	0.079	8.11	3.45	4.50
20	69	2.85	0.013	3.85	2.60	3.20	17	2.74	0.025	3.81	2.55	2.90
21	69	0.58	0.005	6.91	0.52	0.71	17	0.58	0.010	6.80	0.52	0.65
22	69	0.64	0.004	6.03	0.58	0.71	17	0.60	0.009	5.81	0.55	0.68
23	69	0.61	0.004	5.88	0.52	0.71	17	0.60	0.009	6.07	0.52	0.68
24	69	0.73	0.005	5.41	0.61	0.81	17	0.71	0.011	6.37	0.65	0.84
25	69	2.82	0.010	6.05	2.40	3.27	17	2.73	0.016	4.95	2.40	2.93
26	69	0.98	0.006	5.01	0.84	1.10	17	0.93	0.011	4.65	0.87	1.03
27	69	1.19	0.006	4.43	1.03	1.23	17	1.11	0.012	4.46	0.97	1.16
28	69	0.66	0.004	5.42	0.58	0.74	17	0.65	0.008	4.79	0.61	0.71
29	69	0.97	0.004	3.74	0.87	1.03	17	0.91	0.010	4.60	0.81	0.97
30	69	0.98	0.004	3.59	0.90	1.06	17	0.95	0.008	3.62	0.90	1.03

Fig. 14. Here too, notable exceptions to the relationship between darkness and the amount of precipitation are explained by unusually colored sands. For example, the White Sands sample was lighter than would be expected on the basis of precipitation, and the sample from near Flagstaff was darker than expected. This latter sample came from an area with a relatively high amount of precipitation, and with soils composed of black, volcanic cinders. Samples from dark, reddish sands were also darker than expected on the basis of precipitation.

With two independent color parameters, individuals of the populations can be selected to closely match the color of the substrate. The yellowish-orange pigment varies in concentration to approximate the color of the sands, which are generally some shade of tan or reddish, although both white (gypsum crystals) and black (volcanic cinders) soils occur within the range of *P. apache*. The number of black-tipped hairs seems most important in determining the overall darkness or lightness of the mice. Within limits, the actual color of the substrate appears to be less important in determining darkness, especially relative darkness, than is the amount of precipitation. Precipitation does not directly determine soil color, although it is a well-known phenomenon that soils tend to be darker colored in areas of higher precipitation, due to higher humus contents. The sandy soils upon which these mice are found have very little organic matter and essentially no surface litter, and vegetation consists mostly of small, annual forbs. The perennials that occur are generally widely scattered. The amount of vegetational cover is primarily dependent upon the amount of moisture available during the growing season of small annuals. Within the range of *P.*

Table 5.—*Continued.*

Trait	N	M	SE	CV	Range		N	M	SE	CV	Range	
					Minimum	Maximum					Minimum	Maximum
		17. *P. apache* Gran Quivira						18. *P. apache* White Sands				
1	13	130.5	1.651	4.56	120.0	139.0	51	128.7	0.677	3.76	120.0	140.0
2	13	62.4	1.010	5.83	57.0	69.0	51	62.2	0.456	5.23	56.0	68.0
3	15	68.6	0.979	5.53	63.0	74.0	54	66.2	0.448	4.98	60.0	73.0
4	15	17.6	0.114	2.56	16.7	18.1	54	18.3	0.103	4.13	16.0	20.0
5	10	6.5	0.139	6.72	6.1	7.5	48	6.5	0.072	7.67	6.0	7.5
6	13	0.898	0.020	8.10	0.783	1.063	51	0.939	0.009	6.71	0.828	1.097
7	11	22.30	0.087	1.30	21.90	22.80	52	22.47	0.073	2.35	21.35	23.80
8	12	22.28	0.087	1.36	21.85	22.75	47	22.40	0.071	2.16	21.30	23.75
9	13	5.10	0.037	2.59	4.85	5.25	54	5.17	0.023	3.30	4.50	5.45
10	15	3.14	0.062	1.98	3.00	3.25	53	3.12	0.017	4.06	2.90	3.40
11	15	4.30	0.032	2.88	4.10	4.60	54	4.21	0.015	2.67	3.85	4.45
12	15	8.05	0.085	4.10	7.35	8.50	51	8.21	0.042	3.61	7.55	8.85
13	14	12.30	0.080	2.49	11.65	12.85	48	12.40	0.042	2.39	11.65	13.00
14	14	2.73	0.050	6.84	2.35	3.05	52	2.91	0.029	7.13	2.55	3.50
15	14	4.06	0.088	8.09	3.40	4.65	52	3.94	0.035	6.40	3.15	4.35
16	13	7.94	0.057	2.57	7.60	8.25	54	8.00	0.045	4.15	7.40	8.80
17	13	2.20	0.029	4.67	2.00	2.35	53	2.21	0.018	5.78	1.90	2.55
18	14	3.83	0.038	3.71	3.60	4.00	54	3.83	0.020	3.93	3.45	4.15
19	14	4.00	0.064	5.96	3.60	4.50	51	3.76	0.035	6.64	3.10	4.15
20	14	2.80	0.017	2.32	2.70	2.85	49	2.78	0.015	3.72	2.55	3.10
21	15	0.60	0.009	5.51	0.58	0.68	48	0.56	0.007	8.59	0.48	0.68
22	15	0.64	0.009	5.57	0.61	0.79	49	0.60	0.006	7.05	0.52	0.68
23	14	0.61	0.006	3.86	0.58	0.65	49	0.62	0.005	5.72	0.55	0.71
24	14	0.72	0.007	3.61	0.68	0.77	49	0.72	0.005	5.18	0.65	0.81
25	15	2.77	0.028	3.94	2.53	3.00	49	2.67	0.009	4.83	2.40	2.93
26	15	0.97	0.011	4.54	0.90	1.03	49	0.94	0.011	8.29	0.55	1.06
27	15	1.10	0.013	4.58	1.03	1.19	49	1.06	0.006	4.36	0.97	1.23
28	15	0.65	0.008	5.02	0.58	0.71	49	0.63	0.005	5.32	0.58	0.71
29	15	0.94	0.009	3.78	0.87	1.00	49	0.92	0.006	4.43	0.87	1.00
30	15	0.97	0.012	5.19	0.87	1.06	49	0.94	0.006	4.68	0.87	1.06

apache, the growth of annuals generally occurs from June through August. Sands receiving higher amounts of moisture will have a more lush vegetational cover, and appear darker (due both to the plant cover, seen from above, and the shadows cast on the sand by vegetation). The highly significant correlation between mean annual precipitation and relative darkness is, I believe, attributable to this phenomenon, with predation being the ultimate factor determining the color of the mice.

There was no apparent geographic continuity to the observed color variation (Fig. 15), although there was a predictable pattern. Higher elevations receive more precipitation ($r = 0.60$) and have lower temperatures ($r = 0.73$), hence more moisture is available for plant growth. Samples of Apache pocket mice from higher areas such as Flagstaff, Coventry, Navajo Reservoir, Canyada Larga, San Luis Valley, Pecos, San Augustine Plains, Gran Quivira, and Casas Grandes were correspondingly dark (Table 11, Fig. 15). Color variation was very localized, and no broad pattern emerged from this analysis that would support the current arrangement of subspecies.

Color variation in *P. apache* and *P. flavescens* was similar and the same pigments appeared to be involved. *P. fasciatus* is colored differently and one can readily distinguish sympatric specimens of *P. fasciatus* and *P. flavescens* from the Great Plains by their color differences. *P. fasciatus* is darker dorsally, with an "olive" tone. The yellowish color bands of the dorsal hairs are much narrower in *P. fasciatus* and the dark-grayish basal bands show on the surface and contribute to the darker, olive tone. *P. flavescens* has a more orange lateral line. In the Uintah Basin, both *P. fasciatus* and *P. apache* have

Table 5.—*Continued.*

Trait	N	M	SE	CV	Range		N	M	SE	CV	Range	
					Minimum	Maximum					Minimum	Maximum
		19. *P. apache* Deming Plains						20. *P. flavescens copei*				
1	23	124.8	1.320	5.07	113.0	134.0	17	122.1	1.257	4.24	112.0	129.0
2	23	58.2	0.868	7.16	50.0	65.0	17	56.4	0.753	6.56	50.0	61.0
3	25	66.6	0.714	5.36	57.0	73.0	17	65.7	0.817	5.13	61.0	72.0
4	26	17.6	0.193	5.61	15.0	19.0	17	16.7	0.145	3.58	15.9	17.9
5	23	6.6	0.086	6.27	6.0	7.1	17	6.6	0.129	8.07	5.8	7.6
6	23	0.874	0.014	7.85	0.725	1.000	17	0.859	0.013	6.28	0.754	0.938
7	21	21.94	0.130	2.70	20.45	22.95	16	21.23	0.179	3.37	19.65	22.25
8	22	21.83	0.117	2.50	20.45	22.65	17	21.19	0.160	3.11	19.65	22.10
9	24	5.12	0.032	3.07	4.90	5.40	17	5.16	0.064	5.12	4.60	5.60
10	23	3.07	0.027	4.16	2.85	3.30	17	3.04	0.028	3.73	2.85	3.20
11	23	4.25	0.027	3.07	4.00	4.50	17	4.16	0.043	4.25	3.90	4.50
12	21	7.94	0.084	4.84	7.25	8.70	16	7.48	0.089	4.80	6.85	8.00
13	22	12.10	0.074	2.89	11.60	13.00	16	11.79	0.116	3.88	11.00	12.85
14	24	2.83	0.049	8.52	2.40	3.25	17	3.06	0.077	10.37	2.35	3.40
15	24	4.06	0.069	8.27	3.15	4.65	17	4.44	0.084	7.82	3.75	5.00
16	24	7.81	0.060	3.75	7.25	8.35	16	7.70	0.094	4.89	6.85	8.15
17	23	2.24	0.020	4.32	2.00	2.35	16	2.16	0.048	8.87	1.70	2.40
18	23	3.63	0.045	6.53	3.35	4.25	17	3.70	0.038	4.29	3.40	3.95
19	23	3.95	0.078	9.52	2.85	4.85	17	4.31	0.074	7.08	3.80	4.85
20	17	2.67	0.023	3.63	2.45	2.80	15	2.62	0.028	4.13	2.50	2.95
21	17	0.56	0.009	6.75	0.52	0.65	15	0.57	0.009	6.30	0.48	0.61
22	17	0.59	0.008	5.66	0.52	0.65	15	0.59	0.007	4.91	0.52	0.65
23	17	0.58	0.008	6.22	0.48	0.65	15	0.57	0.011	7.68	0.48	0.65
24	17	0.70	0.008	4.65	0.65	0.77	15	0.67	0.012	7.08	0.61	0.74
25	17	2.66	0.033	5.16	2.40	2.87	15	2.77	0.048	6.68	2.40	3.07
26	17	0.93	0.010	4.35	0.87	1.00	15	0.93	0.009	3.88	0.84	0.97
27	17	1.07	0.009	3.52	1.00	1.13	15	1.04	0.011	4.01	0.97	1.13
28	17	0.64	0.010	6.26	0.58	0.71	15	0.62	0.012	7.61	0.55	0.68
29	17	0.94	0.009	4.21	0.84	1.00	15	0.87	0.015	6.62	0.81	0.97
30	17	0.95	0.011	5.09	0.84	1.03	15	0.90	0.012	5.05	0.81	0.97

about the same degree of relative darkness, but *P. apache* has a pale yellowish-orange (Light Ochraceous-Buff) color, and *P. fasciatus* has a pale olive-yellow color (near Cream-Buff or Chamois). I have found these color differences to be reliable for distinguishing these taxa.

Multivariate Analyses

The matrix of taxonomic distances is presented in Table 12. The least similar samples have the largest distance coefficients. These data are summarized in the phenogram of Fig. 16. Note four main clusters, a *P. fasciatus* cluster (samples 1–4), a *P. apache* cluster encompassing the southern and western samples (samples 7 through 13, in descending order in Fig. 16), a *P. apache* cluster of northern samples (samples 5, 6, 10, and 12), and a *P. flavescens* cluster (samples 20 and 21). Two principal deficiencies in the phenogram are apparent. All samples had an equal chance of being linked regardless of their geographic positions, and in clustering samples, many of the intersample relationships were simply lost. The coefficient of cophenetic correlation (derived from a distance-cophenetic matrix comparison) is a measure of the amount of information lost in the phenogram. This value (0.77) falls near the lower end of the range reported by Sneath and Sokal (1973). The phenogram is weakest in adequately portraying relationships at the more distant levels. Placing the distance values in their geographic context (Fig. 17) corrects some of these deficiencies and alters the interpretations derived from the phenogram. The sample of *P. f. copei* was about equally similar to the Deming Plains sample and to *P. f. flavescens*. Samples of Apache and olive-backed pocket mice from the Uintah Basin were

Table 5.—*Continued.*

Trait	N	M	SE	CV	Range	
					Minimum	Maximum
			21. *P. f. flavescens*			
1	10	121.7	1.453	3.78	114.0	128.0
2	10	58.7	1.350	7.27	52.0	65.0
3	11	62.7	0.702	3.71	60.0	66.0
4	11	16.8	0.122	2.41	16.0	17.0
5	11	6.5	0.157	7.98	6.0	7.0
6	10	0.931	0.026	8.23	0.839	1.083
7	8	21.39	0.120	1.59	20.90	21.85
8	8	21.39	0.120	1.59	20.90	21.85
9	9	4.99	0.042	2.52	4.85	5.20
10	10	3.02	0.038	3.99	2.85	3.25
11	9	4.21	0.034	2.41	4.10	4.40
12	9	6.98	0.095	4.07	6.45	7.35
13	9	11.46	0.102	2.76	10.95	11.90
14	9	3.01	0.044	4.43	2.90	3.35
15	9	5.01	0.074	4.42	4.75	5.40
16	9	7.53	0.078	3.11	7.10	7.80
17	8	2.22	0.028	3.60	2.10	2.30
18	9	3.72	0.034	2.78	3.60	3.90
19	8	4.92	0.117	6.71	4.15	5.20
20	5	2.64	0.024	2.07	2.60	2.70
21	6	0.52	0.013	6.08	0.48	0.58
22	6	0.60	0.014	5.67	0.55	0.65
23	6	0.57	0.013	5.51	0.55	0.61
24	6	0.67	0.018	6.61	0.61	0.74
25	6	2.74	0.020	1.82	2.67	2.80
26	6	0.92	0.023	6.11	0.87	1.03
27	6	1.04	0.018	4.22	1.00	1.10
28	5	0.63	0.030	10.58	0.55	0.71
29	6	0.85	0.007	1.96	0.84	0.87
30	6	0.90	0.019	5.29	0.84	0.97

distant phenetically, as were samples of the olive-backed and plains pocket mice. The relatively small distances linking neighboring samples 5, 6, 10, 12, 15, and 17 reinforce the previous interpretation that these samples represent a more or less continuous population. Peripheral populations in Arizona (7 and 8), the San Luis Valley (13), and the San Augustine Plains (16) showed high similarity to only one or two other samples (see Table 12 for coefficients of distance not depicted in Fig. 17). The Gran Quivira sample (17) was about equally distant to the Rio Grande Valley (15) and White Sands (18) samples. Gene exchange between the White Sands and Gran Quivira populations is not too likely today, but this route may have only recently been blocked. Large lava flows, of fairly recent age, and upland rocky terrain constrict the Tularosa Valley north of the White Sands, and any movement along this route would be through non-sand habitats.

A matrix of similarity, based upon the Q-mode correlation analysis, is given in Table 13, summarized in the phenogram of Fig. 18, and the data placed in a geographic context in Fig. 19. The higher the similarity values, the greater the similarity between samples. Note in the phenogram (Fig. 18) a *P. fasciatus* cluster (samples 1–4), a cluster including *P. flavescens* and a set of neighboring samples of Apache pocket mice (samples 9, 16, 19, 20, and 21), and a *P. apache* cluster. Those closely linked samples (that is, 1 and 2, 3 and 4, 5 and 6, 7 and 8, 10 and 12, and 20 and 21) are ones that are geographic neighbors and were shown to be closely similar in the other analyses. Otherwise, these two phenograms do not appear to be too similar (Figs. 16 and 18). A matrix comparison between the matrices of distance and similarity showed only an approximate 50% ($r = -0.51$) correspondence. They differed most in the linkages of the more dissimilar

Table 6.—*Interpopulation matrix of correlation between morphometric traits. The numbers of the traits correspond to those in Table 1. Degrees of freedom = 19.*

Traits	1	2	3	4	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
1	—																											
2	.85	—																										
3	.84	.68	—																									
4	.56	.71	.25	—																								
6	.44	.70	−.10	.63	—																							
7	.89	.69	.76	.61	.37	—																						
8	.90	.72	.78	.59	.35	.99	—																					
9	.40	.42	.15	.67	.48	.54	.52	—																				
10	.80	.71	.66	.69	.38	.81	.80	.37	—																			
11	.78	.56	.71	.35	.30	.86	.85	.24	.72	—																		
12	.69	.57	.55	.61	.37	.86	.84	.61	.66	.74	—																	
13	.72	.59	.56	.64	.39	.89	.86	.64	.73	.74	.97	—																
14	−.06	−.09	−.19	.26	.20	.23	.20	.49	.24	.24	.27	.34	—															
15	−.17	−.34	.02	−.69	−.36	−.16	−.14	−.51	−.28	.11	−.36	−.34	−.02	—														
16	.83	.55	.81	.40	.17	.93	.93	.36	.78	.87	.77	.78	.21	.06	—													
17	.51	.56	.36	.65	.32	.59	.57	.50	.66	.35	.47	.56	.21	−.22	.50	—												
18	.32	.24	.20	.26	.21	.43	.45	.41	.35	.15	.26	.32	.33	−.06	.39	.27	—											
19	−.22	−.33	.00	−.70	−.41	−.35	−.32	−.68	−.35	−.07	−.58	−.55	−.30	.91	−.16	−.26	−.23	—										
20	.84	.77	.63	.67	.51	.89	.88	.46	.92	.80	.76	.79	.31	−.24	.83	.53	.45	−.40	—									
21	.81	.56	.83	.25	.12	.74	.74	.13	.73	.82	.64	.64	−.05	.08	.85	.30	.15	−.01	.74	—								
22	.72	.49	.77	.05	.06	.64	.65	−.12	.63	.79	.47	.47	−.16	.32	.78	.23	.11	.26	.65	.91	—							
23	.76	.69	.58	.62	.44	.81	.81	.39	.76	.69	.68	.67	.23	−.33	.71	.42	.37	−.43	.88	.59	.50	—						
24	.81	.71	.66	.52	.42	.78	.77	.22	.85	.74	.64	.64	.01	−.29	.76	.32	.28	−.36	.88	.77	.70	.82	—					
25	.61	.57	.46	.46	.31	.67	.65	.52	.62	.58	.56	.61	.32	.04	.65	.65	.23	−.15	.65	.50	.43	.47	.37	—				
26	.63	.47	.56	.30	.23	.73	.70	.08	.79	.84	.62	.64	.25	.10	.82	.42	.22	−.09	.79	.79	.79	.64	.73	.57	—			
27	.63	.48	.50	.49	.35	.78	.76	.34	.81	.85	.67	.70	.49	−.11	.79	.38	.35	−.33	.86	.68	.56	.74	.76	.55	.87	—		
28	.68	.42	.72	.09	.07	.68	.68	−.05	.57	.84	.53	.49	−.07	.33	.79	.20	−.04	.22	.63	.85	.91	.57	.67	.46	.77	.60	—	
29	.47	.55	.22	.79	.50	.55	.53	.67	.69	.35	.56	.61	.40	−.73	.38	.56	.35	−.79	.68	.26	.02	.64	.58	.35	.34	.62	.00	—
30	.76	.60	.67	.52	.30	.80	.79	.25	.86	.79	.63	.64	.21	−.23	.78	.37	.38	−.34	.91	.75	.64	.85	.90	.43	.78	.89	.64	.66

Table 7.—*Factor scores for the first five factors extracted from a matrix of correlation.*

Sample	Factors				
	I	II	III	IV	V
1. *Perognathus fasciatus fasciatus*	−0.26180	2.47176	−0.78360	1.84415	−1.12312
2. *Perognathus fasciatus olivaceogriseus*	−0.48409	2.26763	−0.08344	0.27492	0.59393
3. *Perognathus fasciatus litus*	0.80838	1.51588	−0.74339	2.45487	−0.47299
4. *Perognathus fasciatus callistus*	0.62812	1.01588	−0.12778	1.29386	0.14666
5. *Perognathus apache* Uintah Basin	1.59702	0.57906	2.17739	−1.32724	−2.18045
6. *Perognathus apache* Moab	1.49471	−0.40347	1.05894	1.69595	2.39596
7. *Perognathus apache* Painted Desert	−0.07471	−0.66931	0.14526	0.58163	−0.56386
8. *Perognathus apache* Flagstaff	−0.34763	−0.78385	0.17254	0.83553	−1.47170
9. *Perognathus apache* Gallup	0.22867	0.16594	1.83041	−1.58717	−1.32679
10. *Perognathus apache* San Juan Basin	1.67000	−1.20200	−0.83880	1.01375	2.61925
11. *Perognathus apache* Canyon Largo	0.18009	−0.16779	−0.23676	−1.55194	−0.52558
12. *Perognathus apache* Estrella	0.84708	−0.03241	1.18789	−1.13915	−1.20545
13. *Perognathus apache* San Luis Valley	−0.56873	−1.38406	−1.44469	2.01622	−0.42079
14. *Perognathus apache* Santa Fe	0.44337	−0.62562	−1.69960	0.36607	1.25001
15. *Perognathus apache* Rio Grande Valley	0.34882	0.06618	0.81357	−0.12503	−0.64501
16. *Perognathus apache* San Agustine Plains	−0.64491	−0.50534	−0.73553	1.38297	0.32324
17. *Perognathus apache* Gran Quivira	−0.44968	−0.03960	−1.05570	−1.90546	−1.56102
18. *Perognathus apache* White Sands	−0.56426	−1.18087	0.05141	−0.42458	−0.13820
19. *Perognathus apache* Deming Plains	1.15288	0.61484	0.05253	1.77366	1.43557
20. *Perognathus flavescens copei*	−1.94565	−0.30397	1.28590	0.31711	−0.02803
21. *Perognathus flavescens flavescens*	−2.25961	0.70574	1.81326	0.86707	2.04352
Cumulative % of total variance	56.1	71.7	77.4	81.6	85.1

samples. The shortcomings noted for the distance phenogram are also apparent in the similarity phenogram. Namely, much information was lost (the coefficient of cophenetic correlation is 0.73), and the geographic relationships were obscured. The same overall pattern of intersample relationships are apparent in the similarity map of Fig. 19 as was shown in the distance map (Fig. 17). Samples 5, 6, 10, 12, 15, and 17 form a geographic chain, with sample 15 being the weakest link between the more northern and more southern populations. Peripheral populations exhibited much the same relationships to other samples as were shown on the distance map. Some differences stand out, such as the Canyon Largo sample (11), which was most similar to the San Juan Basin sample (10), and was particularly dissimilar to the Santa Fe sample (14). The Painted Desert sample (7) showed little similarity to the San Augustine Plains sample (16), and was more similar to the San Juan Basin sample in this analysis than in previous ones. The Deming Plains sample (19) was most similar to *P. f. copei* (20), but *copei* was much closer to *P. f. flavescens* (21) than to the Deming Plains sample.

The differences in computational procedures account for much of the disparity between these distance and similarity analyses. Taxonomic distance is a measure of the Euclidean distance separating the samples arrayed, in this case, in 29 dimensional hyperspace. The closer two samples are, the more similar they will be in both size and proportions of all 29 characters. Q-mode correlation analysis, on the other hand, measures the correspondence between the columns (samples) in a matrix of 29 rows. If two samples differ in size, but have the same body proportions, they would have a similarity value of 1.0. Samples could be significantly different in the size of all traits and have relatively large distance values, yet exhibit similar proportions and have high similarity values. Conversely, samples with no significant differences in size (for example, samples 11 and 14), but which differ proportionately ($Q - r = 0.07$), appear to be quite close phenetically ($d = 0.59$). Samples that are shown to be quite similar by both procedures are probably closely related.

A principal components analysis of the matrix of correlation yielded results very similar to the other factor analysis, and reinforced the conclusions of the other multivariate analyses. The first five principal components accounted for 89.6% of the total variance. The scores for the first three principal

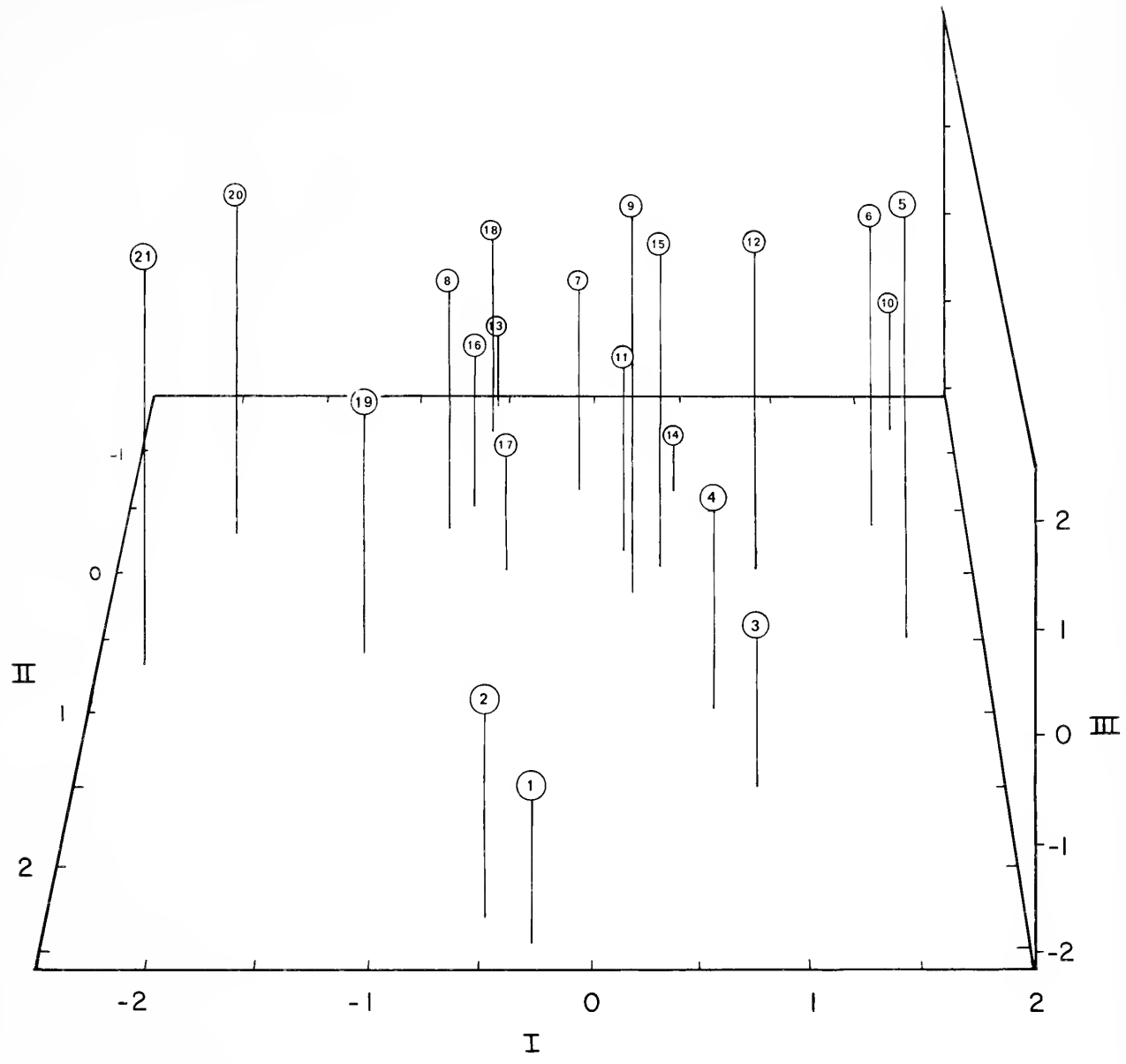

Fig. 8.—Three-dimensional plot of first three factors, extracted from the matrix of correlation, for samples of the *Perognathus fasciatus* species group. The sample codes are defined in the text and Table 7, and are shown in Fig. 4.

components for each of the samples are plotted in Fig. 20. Component I accounted for 58.3% of the total variance, and is the size component. Only width of interparietals and least interbullar distance were loaded negatively on component I. Component II, accounting for 16.8% of the variance, exhibited highest negative loading on traits expressing the constriction of the postcranial region (IPW, LID) and the width of P_4. Traits with high positive loading were length of hind foot, skull length (ONL) and length of M_1. Component III was most highly loaded by traits measuring external dimensions (TOTL, TL, HBL with positive coefficients), and bullar inflation (BW with a negative coefficient). Note, by comparing Figs. 8 and 20, that the principal components and factor analyses yielded similar results, except that the images are rotated on the horizontal axis. There are other minor differences

Table 8.—*Summary of SS-STP analysis between geographically adjacent samples. Refer to Table 7, the text, or Figs. 4 or 9 for an explanation of sample codes. + = significant difference; − = nonsignificant difference.*

	Traits																													
Samples	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	Total
1–2	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	0
1–21	+	−	+	−	+	−	+	+	−	+	+	−	−	+	−	+	−	−	−	−	+	+	−	+	−	−	−	+	−	+	14
2–3	+	+	−	−	−	−	+	+	−	+	−	+	+	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	8
2–4	−	−	−	−	−	−	−	−	−	−	−	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	2
2–20	+	+	+	−	+	−	−	−	−	−	−	−	−	+	−	+	−	−	−	−	−	+	−	−	−	+	−	+	−	−	9
2–21	+	−	+	−	+	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	+	+	−	−	−	+	−	+	−	−	8
3–4	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	0
3–5	−	−	−	−	−	−	−	−	+	−	−	−	−	+	−	−	−	−	+	+	−	−	−	−	−	−	+	−	+	+	7
4–5	−	−	−	−	−	−	+	+	−	−	−	−	−	+	−	−	−	+	+	+	−	−	−	−	−	−	+	−	+	+	9
5–6	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	1
6–7	−	−	−	−	−	−	+	+	−	−	−	−	−	+	+	+	−	−	−	+	−	−	−	−	−	−	+	−	+	−	8
6–10	−	−	−	+	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	2
6–11	−	−	−	−	−	−	+	+	−	−	+	+	+	+	+	+	−	−	−	−	−	−	−	−	−	−	+	−	−	−	9
7–8	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	1
7–9	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	1
7–10	−	−	−	+	−	−	+	+	−	+	−	−	−	−	−	+	−	+	−	+	+	−	+	−	−	+	+	+	+	+	14
8–9	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	1
8–16	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	2
9–10	−	+	−	+	−	+	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	5
9–12	−	+	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	2
9–15	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	1
9–16	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	+	−	−	−	−	−	+	−	−	+	−	4
10–11	−	−	−	+	−	−	+	+	−	−	−	+	+	+	−	−	+	+	−	+	−	−	−	−	−	−	−	−	−	−	9
10–12	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	1
11–12	−	−	−	+	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	2
11–14	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	0
12–14	−	−	−	+	−	−	−	−	−	−	−	+	+	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	4
12–15	−	+	−	−	−	+	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	3
13–14	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	+	+	−	−	−	4
14–15	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	0
14–17	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	0
14–20	+	+	+	+	−	−	+	+	−	+	+	−	−	−	+	−	−	−	−	+	−	+	−	+	−	+	+	−	+	+	16
15–16	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	1
15–17	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	2
15–18	−	−	+	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	+	+	−	−	−	−	+	−	+	−	6
15–19	+	+	−	+	−	−	+	+	−	+	−	−	−	−	−	+	−	−	−	+	−	+	−	−	−	−	−	−	−	−	9
16–19	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	0
17–18	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	1
17–19	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	+	−	−	−	−	−	−	−	−	2
17–20	+	−	−	−	−	−	−	+	−	−	−	+	−	−	+	−	−	−	−	+	−	−	−	−	−	+	−	−	+	−	7
18–19	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	1
18–20	−	+	−	+	−	+	+	+	−	−	−	+	+	−	+	−	−	−	+	+	−	−	+	−	−	−	−	−	+	−	12
19–20	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	2
20–21	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	1

(the factor analysis was based upon the unstandardized data of a 30 characters matrix, whereas the principal components analysis utilized standardized data in a 29 characters matrix), but the differences seem relatively trivial. Note in Fig. 20 that the Apache and plains pocket mice samples differed mostly in size (Component I). The olive-backed pocket mice differed from the others in having small bullae, short skulls, unconstricted crania, small feet, large lower premolars, and short lower first molars. The San Luis Valley sample was the most distinctive of the Apache pocket mice, having short tails and wide crania (Component III), but paralleled the White Sands sample in Components I and II.

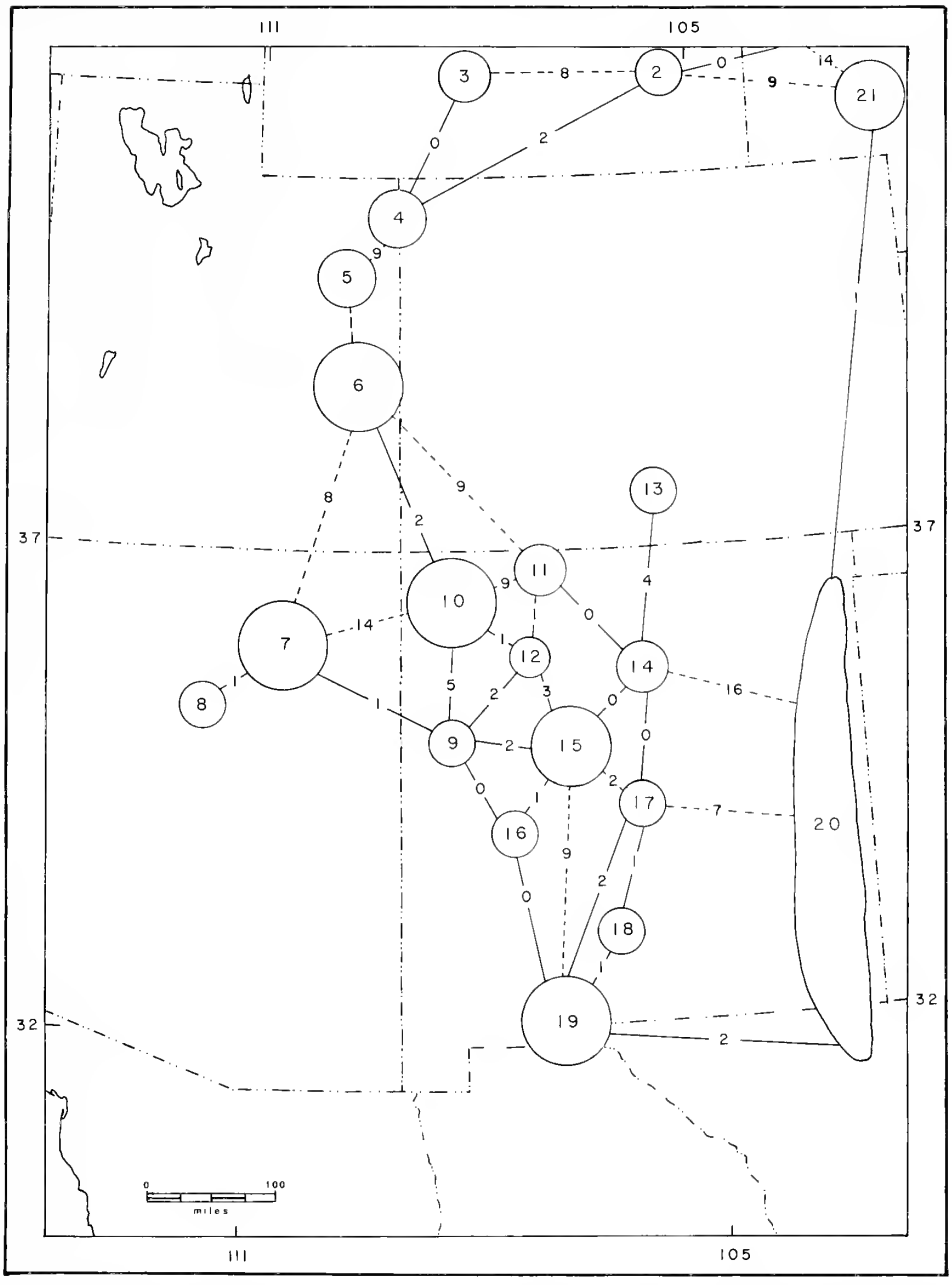

Fig. 9.—Map depicting the number of significant differences between adjacent samples of the *Perognathus fasciatus* species group, based upon the SS-STP analysis. The lines extending northward from samples 2 and 21 represent intersample comparisons with sample 1 (*P. f. fasciatus* from parts of North and South Dakota). The geographic positions of the samples are only approximations. Solid lines represent most likely routes of gene exchanges, and broken lines represent unlikely routes of gene exchange, based upon the number of significant differences between samples.

The lines in Fig. 20 connect samples sharing the same centroid. Seven centroids extracted from the distance matrix and the distances of each sample to its closest centroid are shown in Fig. 21. This summary technique resulted in a much more satisfactory geographic grouping of samples than was the case with the phenograms. Only one sample (13) was erroneously placed with a nonneighboring sample. The San Luis Valley sample was closest to the Painted Desert sample, as shown in the centroid

Table 9.—*Coefficients of correlation between morphometric traits, color indices, and climatic and geographic variables for samples of* P. apache. *DI = darkness; RI = richness; RDI = relative darkness; AEL = elevation adjusted for latitude; CS = climatic severity index; EL = elevation; GS = growing season; Lat = latitude; MJT = mean July minimum temperature; MP = mean annual precipitation; MT = mean annual temperature. Refer to Table 1 for a list of traits. The degrees of freedom for the morphometric traits and the color indices are 14 and 33, respectively.*

Trait	CS	LAT	EL	GS	MT	MP	MJT	AEL
1	.40	.84**	.18	−.34	−.54*	−.31	−.42	−.01
2	.34	.65**	.21	−.25	−.39	−.29	−.26	−.13
3	.36	.68**	.27	−.33	−.53*	−.11	−.44	.16
4	.35	.39	.17	−.29	−.36	−.29	−.27	.01
6	.19	.60**	−.04	−.12	−.25	−.40	−.14	−.20
7	.19	.75**	−.12	−.19	−.31	−.40	−.28	.18
8	.21	.75**	−.10	−.21	−.34	−.39	−.30	.14
9	.26	.60**	−.19	−.21	−.34	−.50*	−.26	−.47
10	.29	.61**	.06	−.33	−.30	−.15	−.23	.38
11	−.07	.78**	−.23	.08	−.17	−.27	−.11	.39
12	−.08	.58*	−.37	.07	−.04	−.58*	−.07	.20
13	.07	.66**	−.23	−.09	−.19	−.50*	−.20	.26
14	−.26	.33	−.58*	.14	.15	−.26	.13	.33
15	−.31	.17	−.47	.22	.19	−.09	.20	.29
16	.09	.69**	−.25	−.15	−.22	−.26	−.18	.36
17	.21	.29	.04	−.18	−.16	−.13	−.07	.04
18	.15	.28	−.12	−.28	−.19	−.37	−.18	−.02
19	−.04	−.12	.16	.03	−.06	.29	.04	−.01
20	.21	.72**	−.08	−.22	−.27	−.32	−.22	.27
21	.16	.72**	−.02	−.18	−.34	−.10	−.24	.39
22	.10	.67**	.00	−.14	−.25	−.07	−.17	.48
23	.23	.69**	−.06	−.26	−.29	−.20	−.30	.12
24	.18	.63**	−.04	−.21	−.22	−.16	−.18	.30
25	.25	.63**	−.08	−.22	−.23	−.17	−.17	.13
26	−.05	.56*	−.25	−.02	−.01	−.07	.01	.67**
27	−.03	.69**	−.26	−.02	−.12	−.17	−.08	.54*
28	.12	.77**	−.17	−.14	−.25	−.14	−.23	.39
29	.21	.60**	.05	−.15	−.27	−.13	−.20	.08
30	.11	.67**	−.08	−.12	−.20	−.21	−.16	.37
DI	—	.13	.28	—	−.36*	.50**	—	.31
RI	—	−.14	.45**	—	−.23	.64**	—	.30
RDI	—	−.04	.43**	—	−.31	.66**	—	.34

* $P \leq 0.05$; ** $P \leq 0.01$.

analysis, but was next most distant to the Santa Fe sample (Table 12, or Fig. 17), with which it has its only geographic affinities.

Discriminant function and canonical analysis provided a technique whereby individuals of each sample could be tested for phenetic fidelity to their populations, and the distances between individuals could be measured. As only individuals with complete data could be utilized, length of ear was excluded, and some of the smaller samples were either submitted for classification only or were combined with other samples. Table 14 is a classification matrix, based upon the squared Mahalanobius distance of individuals from the nearest group means on the discriminant functions. The samples listed in the columns of Table 14 were those utilized in computing the discriminant functions and F statistics. Samples in the rows without a corresponding column were submitted for classification only. Note that only one *P. fasciatus* was misclassified as a *P. flavescens*, and that only three Apache pocket mice were closest to *P. fasciatus*. Three Apache pocket mice were placed with the plains pocket mice, and two plains pocket mice were classified as Apache pocket mice. Overall, the individuals showed relatively high group fidelity, and misclassifications were most between neighboring groups. Samples showing relatively little misclassification were the San Luis Valley, the Uintah Basin, Moab, and the *P. fasciatus* samples.

Table 10.—*Coefficients of correlation between climatic and geographic variables. The abbreviations are defined in Table 9. Degrees of freedom = 14.*

	CS	LAT	EL	GS	MT	MP	MJT	AEL
CS	—							
LAT	.33	—						
EL	.75**	.01	—					
GS	−.96**	−.28	−.65**	—				
MT	−.89**	−.52*	−.74**	.83**	—			
MP	.21	−.23	.46	−.24	−.22	—		
MJT	−.90**	−.42	−.72**	.87**	.96**	−.26	—	
AEL	−.25	−.07	−.10	.14	.23	.35	.17	—

* $P \leq 0.05$; ** $P \leq 0.01$.

Table 15 lists the group means of the first five canonical variables and their cumulative proportions of the total dispersion. Twelve canonical variables accounted for 100% of the dispersion, although variables beyond the third individually accounted for relatively little. The sample means of the first two canonical variables are plotted in Fig. 22. The encircled areas correspond to the distribution of the 457 individual cases. There was considerable overlap within the samples of *P. fasciatus*, *P. apache*, and *P. flavescens*, and between samples of *P. apache* and *P. flavescens*, but essentially none between *P. fasciatus* and the other taxa. A single specimen of *P. apache* from the Moab sample overlapped the position of the *P. fasciatus* sample (Fig. 22). The overlap between *P. apache* and *P. flavescens* included numerous specimens from several samples of both taxa. Note that the uppermost sample of *P. apache* (5) is from the Uintah Basin, and that the spatial relationships of the *P. apache* samples in Fig. 22 are nearly the same as their geographic relationships (see, for example, Fig. 21). The *P. fasciatus* samples, starting on the right side of Fig. 22, are distributed from northeast to southwest. Starting on the lower left side of the *P. flavescens* samples, individuals are distributed from southwest to northeast. With only a little distortion, Fig. 22 could be placed over a map, and the geographic positions of the samples would nearly correspond to their positions on canonical variates I and II. The space in the middle of the samples would fit over the Rocky Mountains in Colorado and New Mexico.

CONCLUSIONS

In summarizing the patterns of structural variation, it must be emphasized that the latitudinal size cline in the Apache pocket mouse populations is the dominant trend. Apache pocket mice are larger in colder and more northern areas. With increasing size the posterior cranial region becomes progressively more constricted and the length of the tail increases at a rate faster than the length of the head and body. Imposed upon the general size cline are significant relationships between relative amounts of moisture and bullar and rostral sizes. Generally, these skull parts increase with increasing body size, but the rates of increase are apparently also influenced by the amount of available moisture. Small mice from drier areas have as large or larger bullae than larger mice from moister sites. Rostral size increases at a slower rate with increasing moisture. Color is strongly associated with a combination of climatic and local edaphic soil factors that together determine relative substrate darkness. In general, mice from higher, moister elevations or latitudes are darker than those from lower, drier climes. This relationship is modified by unusually light or dark colored sands.

Apache pocket mice are primarily limited to loose sands and this habitat type is relatively uncommon and discontinuously distributed. Therefore, most populations are probably small and well isolated from their neighbors. Under such circumstances, populations can quickly evolve according to the dictates of local selective forces. This undoubtedly explains the great amount of local variation in color, and the relatively great degree of morphometric variation over short distances. Several peripheral populations have apparently evolved along parallel paths, due to similar selective forces. Most of these

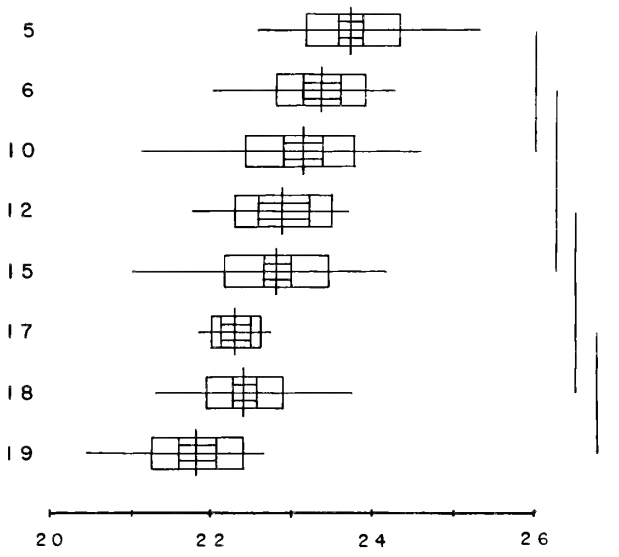

Fig. 10.—North-south variation in occipitonasal length for adjacent samples of *Perognathus apache*. Samples are arranged from north to south. Vertically arrayed numbers are sample codes (see Fig. 9). The scale is in mm. Horizontal lines depict the sample ranges; the vertical lines mark the sample means; the outer rectangles encompass ±1 SD from the mean; the inner rectangles encompass ±2 SE from the mean; and the vertical lines on the right side of the diagram connect nonsignificant subsets, based upon the SS-STP analysis.

Table 11.—*Mean values for color indices of samples of* Perognathus apache *and* P. flavescens. *Sample numbers are as defined in the text and shown in Fig. 4. Within samples, localities are arranged from north to south, as shown in Fig. 15. DI = darkness; RI = richness; RDI = relative darkness (darkness + richness).*

Locality	Sample	DI	RI	RDI
Uintah Basin, UT	5	3.9	2.1	6.0
Fruita-Rifle, CO	6	4.7	2.2	6.8
Green River (city), UT	6	3.8	1.2	5.0
Dewey-Castle Valley, UT	6	4.0	4.7	8.7
Moab, UT	6	4.4	4.5	8.9
Coventry, CO	–	4.0	5.0	9.0
Navajo Mtn, UT-Page, AZ	–	3.8	4.3	8.2
Tuba City, AZ	7	3.2	3.4	6.6
Oraibi, AZ	7	2.5	2.6	5.1
Keam's Canyon, AZ	7	2.9	3.4	6.3
Zuni Well, AZ	7	4.0	4.0	8.0
Holbrook-Winslow, AZ	7	2.4	2.8	5.2
Flagstaff-Winona, AZ	8	4.7	5.0	9.7
Gallup, NM	9	3.7	4.0	7.7
El Morro, NM	9	3.0	5.0	8.0
Chaco Wash, NM	10	2.5	2.3	4.8
Navajo Reservoir, CO, NM	11	4.7	5.0	9.7
Canyon Largo, NM	11	3.0	2.5	5.5
Canyada Larga, NM	11	4.3	4.3	8.6
Estrella, NM	12	3.2	3.0	6.2
San Luis Valley, CO	13	4.7	3.8	8.5
Espanola, NM	14	3.4	3.0	6.5
Santa Fe, NM	14	4.1	3.9	8.0
Pecos, NM	14	4.7	4.1	8.8
Albuquerque, NM	15	3.0	2.5	5.5
Socorro, NM	15	3.1	3.3	6.5
San Augustine Plains, NM	16	4.8	4.0	8.8
Gran Quivira, NM	17	4.3	4.2	8.5
White Sands, NM	18	2.6	0.2	2.8
Engle, NM	19	4.3	3.6	7.9
Las Cruces, NM	19	4.0	3.4	7.4
El Paso, TX	19	4.0	4.0	8.0
Samalayucca, CH	19	2.7	2.3	5.0
Casas Grandes, CH	19	4.1	4.5	8.6
Willcox, AZ	—	3.0	3.2	6.2
Clayton, NM	20	2.0	3.0	5.0
Logan, NM	20	3.7	3.8	7.5
Tolar, NM	20	3.9	4.6	8.5
Caprock (Mescalero Sands), NM	20	4.0	4.5	8.5
Jal-Carlsbad, NM	20	3.3	3.2	6.5
Mentone, TX	20	3.0	4.0	7.0

populations live in higher, moister areas, although there are some parallel developments in populations from drier sites too.

Plains pocket mice, in contrast, are less variable over much greater distances. The same trends in variation are apparent, but are not nearly so dramatic. Plains pocket mice from the drier southern and western portions of their geographic range have larger bullae and slightly more constricted crania and larger rostra than the more mesic-adapted northern and eastern populations. The relatively uniform topography and the gradually changing climatic patterns of the Great Plains have resulted in selection for a more uniform and gradually varying population.

Populations of the olive-backed pocket mouse exhibit a similar pattern of geographic variation in relationship to changing climatic patterns. Some structural convergence with *P. apache* can be seen in populations that approach the range of the Apache pocket mouse (see Fig. 20). A size cline in the *P. fasciatus* samples runs from northeast (small mice) to southwest (larger mice). This does not defy Bergman's principle, as elevational increases and corresponding temperature decreases occur from northeast to southwest. Along the same transect, aridity increases from northeast to southwest, and there is a corresponding increase in the relative bullar and rostral sizes, and color becomes progressively lighter.

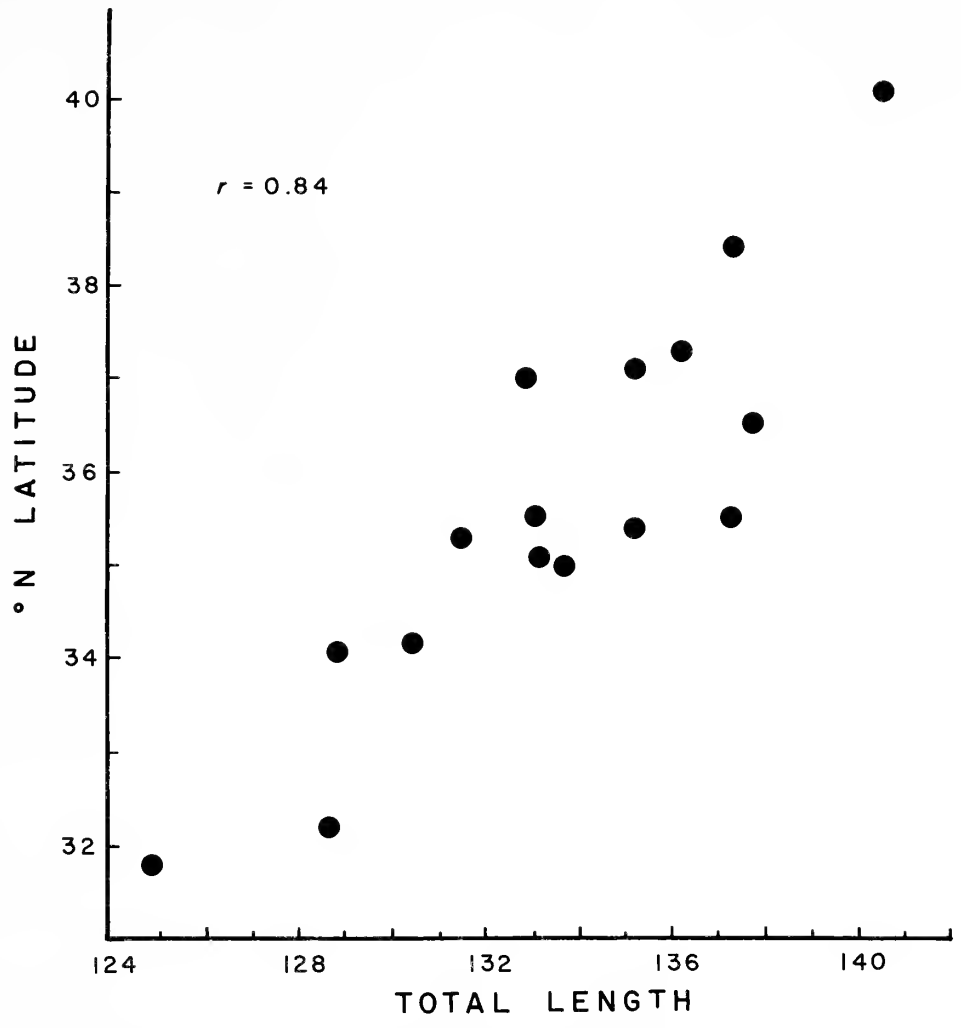

Fig. 11.—Two dimensional plot, depicting geographic variation in total length (in mm) of samples of *Perognathus apache*, $P < 0.001$.

Speciation

Only two major taxonomic units are apparent from the data presented in this study. One unit, *P. fasciatus,* is the more northern and shows adaptations for life in a cooler, moister environment. It is relatively dark colored and large bodied, with a short tail, small bullae, narrow interorbital region, and an unconstricted cranium. The more southern unit, represented by Apache and plains pocket mice, exhibits adaptations for life in a warmer and drier climate. The Great Plains populations are lighter colored and smaller bodied, with relatively larger bullae than *P. fasciatus*. The intermountain plateau populations are much more variable, as should be expected from the great amount of topographic and climatic variability within their range. The variability of the mice follows a predictable course, with temperature and moisture factors, and, perhaps, competition from congeners determining to a great degree the size and shape of individuals in each population.

I envision that these two units arose from a parent population which was widely distributed in the Great Plains and intermountain plateaus. Adaptation to local environmental conditions was probably similar to that exhibited by extant populations. The events leading to speciation may have been initiated as late as the last interglacial period (Sangamon), although speciation at an earlier time seems equally feasible. At the close of of the interglacial period,

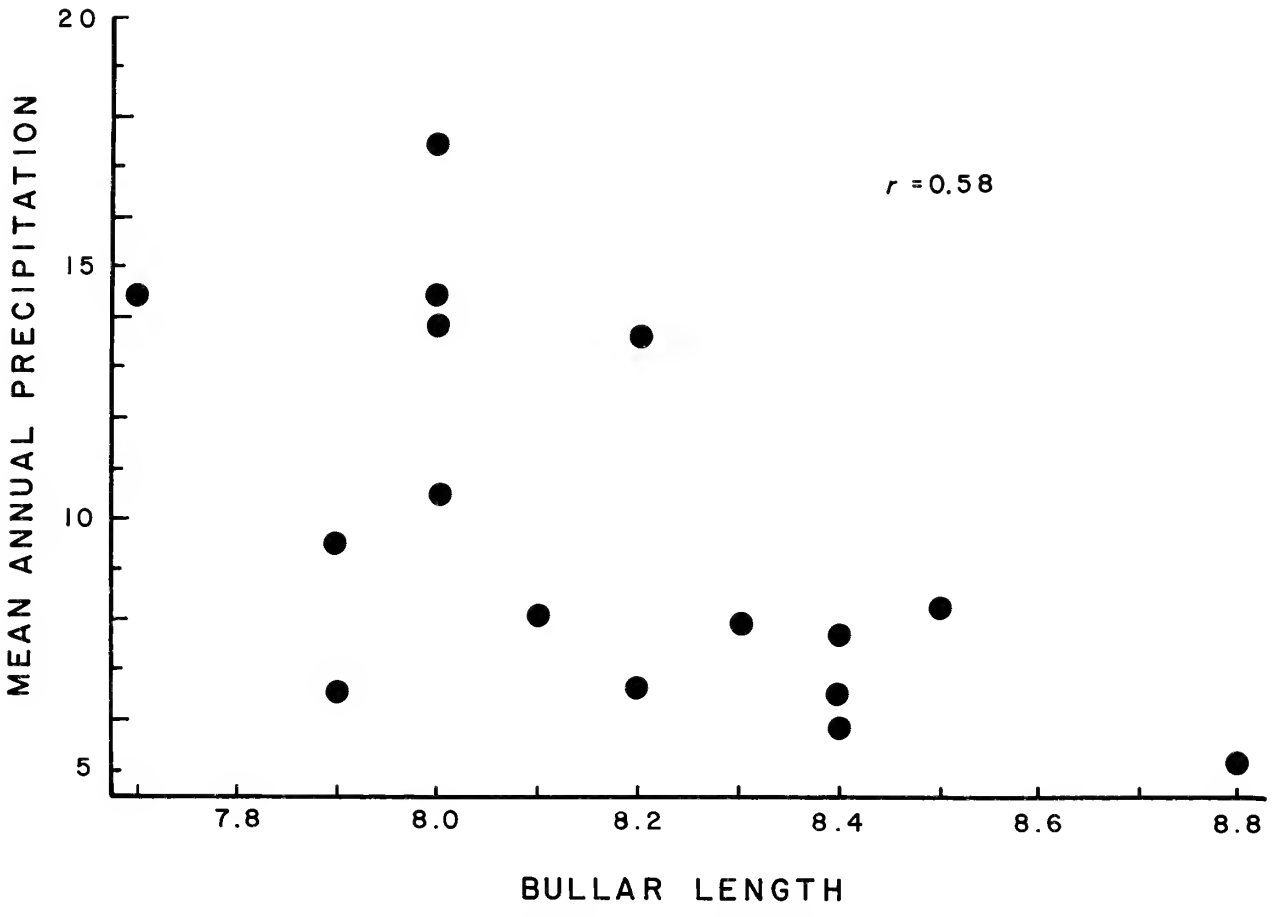

Fig. 12.—Two-dimensional plot, depicting relationship between bullar size (in mm) and mean annual precipitation (in inches), of samples of *Perognathus apache*. $P < 0.05$.

the southward advance of glacial conditions, including the increasingly cooler and wetter climate in the Southwest, caused a southward contraction of the range of the ancestral form. At the height of the glacial pluvial period the population was fragmented into a Chihuahuan Plateau unit and a Southern Plains unit. The most likely barrier separating these populations was the mountains and highlands that transect the Trans-Pecos area of Texas and eastern Chihuahua, and which are continuous with the mountain axis extending southward from the main Rocky Mountain mass.

According to Wells (1970*a*), much of the southern Great Plains region was an open yellow pine-sagebrush parkland during the Wisconsin pluvial period, which is the same type of habitat occupied by some *P. fasciatus* populations today. Northern sagebrush-grassland species, such as *Lagurus curtatus*, have been found in late Pleistocene cave deposits of southeastern New Mexico (Harris, 1970). This supports the hypothesis that a northern plains grassland fauna occupied this region during the Wisconsin pluvial maximum. West of the highland barrier, the other population was isolated in more arid, grassland or desert conditions. Wells (1970*b*) stated that he found no indication that treeless grassland shifted southward into the now arid Chihuahuan Desert during the Wisconsin glacial. Much of the slightly higher plateau regions in this area were vegetated with semiarid grasslands and pinyon-juniper woodlands, habitats that support the denser populations of Apache pocket mice today.

In isolation, these populations, which were already adapted to different environments diverged even more and speciation occurred. The Great Plains isolate was adapted to conditions essentially

Table 12.—*Matrix of taxonomic distance coefficients (average Euclidean distances) for samples of* Perognathus fasciatus, P. apache, *and* P. flavescens. *Refer to Fig. 17, Table 7, or the text for an explanation of the sample codes.*

Sample	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1	0.000																				
2	0.571	0.000																			
3	1.136	1.325	0.000																		
4	0.894	1.026	0.693	0.000																	
5	1.849	1.955	1.286	1.363	0.000																
6	1.669	1.775	1.119	1.182	0.678	0.000															
7	1.319	1.276	1.228	0.943	1.611	1.263	0.000														
8	1.452	1.415	1.343	1.094	1.723	1.318	0.477	0.000													
9	1.266	1.319	1.244	0.970	1.285	1.000	0.764	0.860	0.000												
10	1.860	1.974	1.266	1.437	0.943	0.599	1.383	1.362	1.115	0.000											
11	1.174	1.150	1.149	0.907	1.474	1.113	0.628	0.727	0.632	1.220	0.000										
12	1.555	1.607	1.008	1.121	1.116	0.714	0.931	0.967	0.897	0.599	0.849	0.000									
13	1.747	1.600	1.717	1.530	2.125	1.786	0.958	0.971	1.399	1.807	1.184	1.348	0.000								
14	1.074	1.067	1.101	0.952	1.460	1.144	0.621	0.686	0.659	1.226	0.591	0.808	0.976	0.000							
15	1.217	1.260	1.047	0.929	1.283	0.986	0.682	0.670	0.586	1.042	0.615	0.707	1.148	0.431	0.000						
16	1.207	1.034	1.578	1.161	1.960	1.723	0.750	0.867	1.012	1.876	0.896	1.437	1.091	0.835	0.934	0.000					
17	1.158	0.958	1.331	1.068	1.695	1.439	0.691	0.833	0.857	1.550	0.719	1.135	1.029	0.613	0.695	0.579	0.000				
18	1.634	1.424	1.738	1.450	1.916	1.677	0.820	0.881	1.098	1.725	1.038	1.335	0.905	0.928	1.018	0.761	0.709	0.000			
19	1.555	1.370	1.919	1.516	2.367	2.090	1.013	1.039	1.311	2.218	1.248	1.803	1.231	1.224	1.303	0.641	0.976	0.963	0.000		
20	1.879	1.560	2.344	1.938	2.820	2.555	1.599	1.587	1.844	2.719	1.783	2.301	1.680	1.710	1.833	1.134	1.415	1.453	0.909	0.000	
21	1.958	1.629	2.499	2.141	3.032	2.716	1.852	1.851	2.131	2.872	2.024	2.465	1.865	1.920	2.114	1.520	1.711	1.692	1.332	0.894	0.000

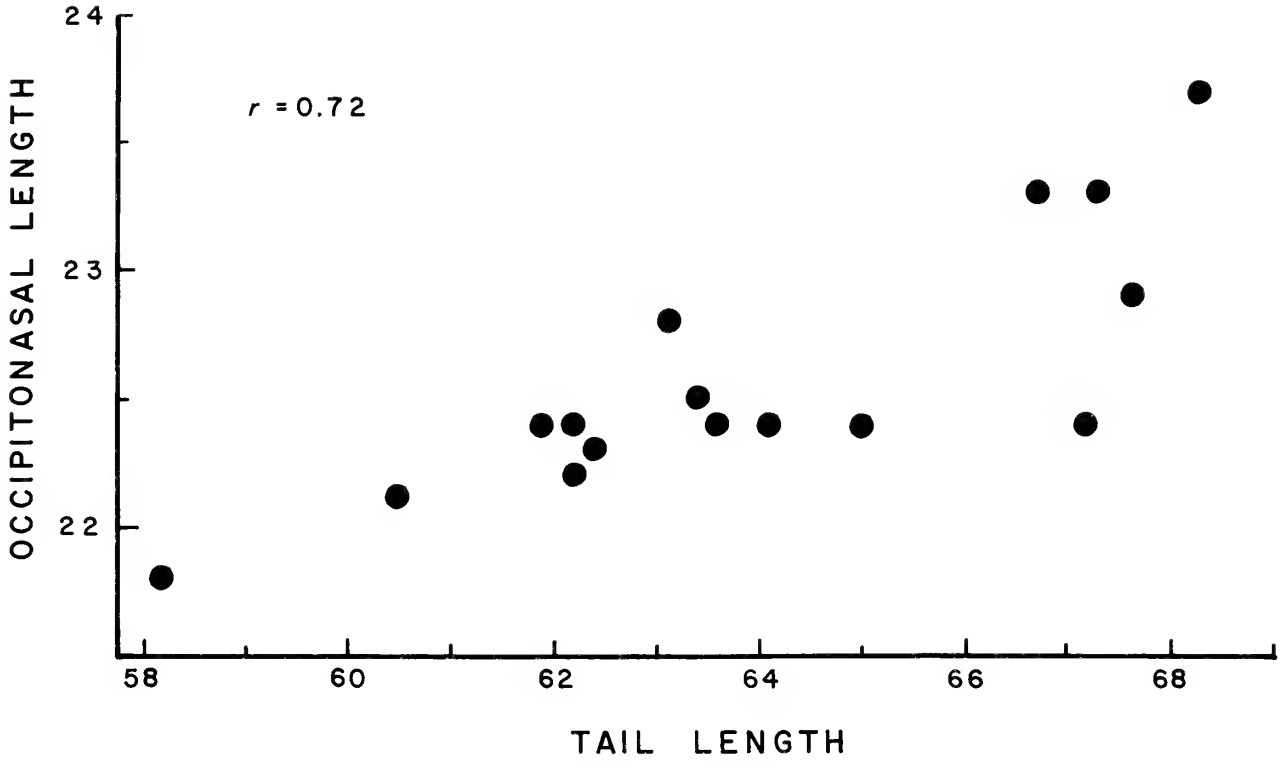

Fig. 13.—Two-dimensional plot, showing relationship between occipitonasal length and length of tail (both in mm), of samples of *Perognathus apache*. $P < 0.01$.

the same as *P. fasciatus* lives under today. The Chihuahuan Desert isolate was adapted to the more arid conditions extant in much of the intermountain region. With the wane of pluvial conditions and the disappearance of woodlands from the central grasslands, both populations began to expand northward. The Rocky Mountain axis of New Mexico and Colorado remained a barrier to pocket mice for some time, and probably prevented contact between the two northward expanding populations. Part of the Chihuahuan isolate's population spread northward as conditions became suitable, but part also remained in place and became progressively more adapted to warmer and more xeric conditions. In time, the Trans-Pecos barrier fell and the Chihuahuan isolate spread onto the southern Great Plains. There, it probably contacted relictual populations of *P. fasciatus*. Perhaps competition with the more xeric adapted *P. flavescens*, coupled with increasingly xeric conditions in the southern Great Plains, hastened the retreat of *P. fasciatus* to the north. Some populations, instead, retreated to higher elevations along the southern Rocky Mountain front of Colorado, such as near La Veta, Silver Cliff, and Colorado Springs, where relict populations are found today. Perhaps others will be found along the Sangre de Cristo range in northern New Mexico. Apache pocket mice pushed northward through the intermountain basins, finally arriving in the Uintah Basin. Olive-backed pocket mice moved into the Uintah Basin from the northeast as forests retreated and conditions became suitable. Primary contact by individuals of these populations is though to be taking place now.

Taxonomic Conclusions

All evidence points to the specific status of *P. fasciatus*. Its different karyotype (which can be used to document interspecific hybrids), different color, and high number of morphometric differences with adjacent populations of Apache and plains pocket mice suggest reproductive isolation. If, as I believe, Apache and olive-backed pocket mice are now making contact for the first time, it is possible that hybridization may occur. However, it seems unlikely that introgression of genes be-

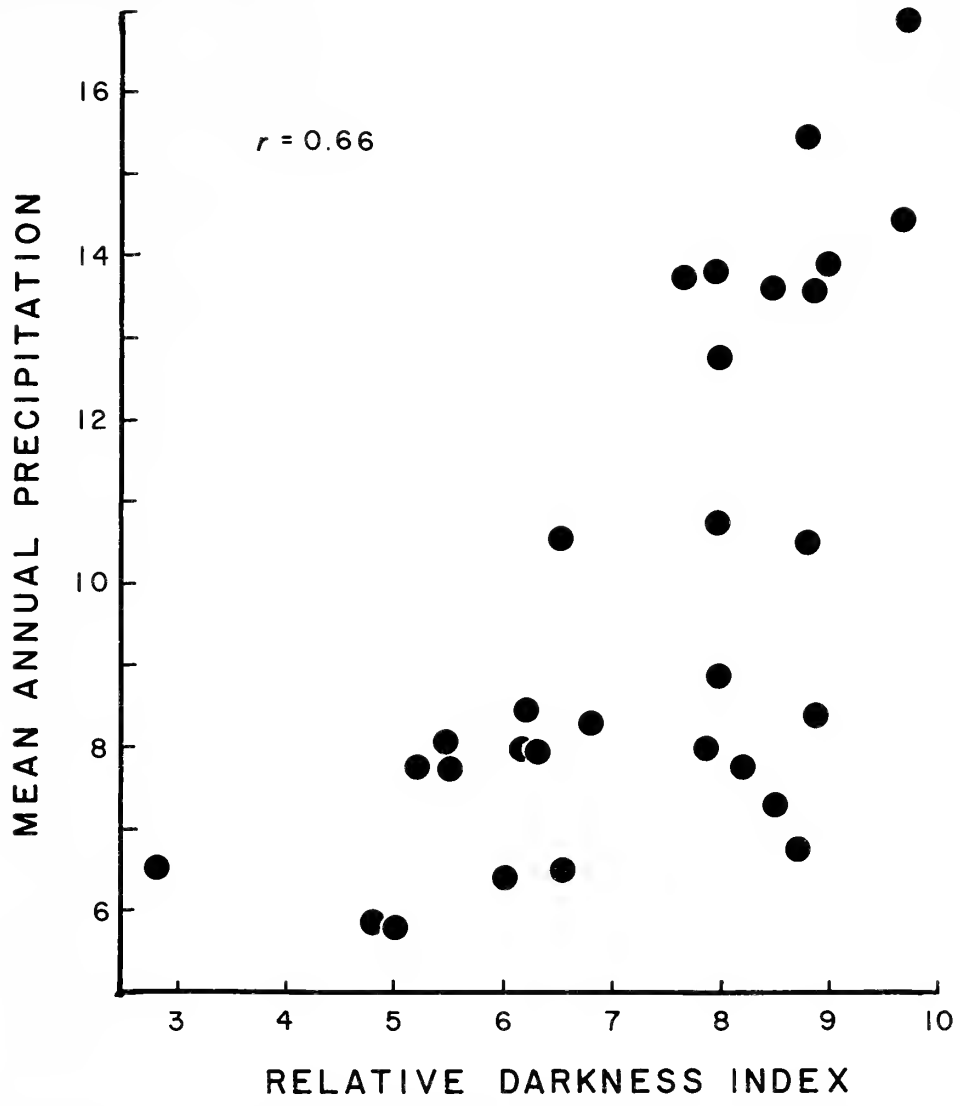

Fig. 14.—Two-dimensional plot, showing relationship between relative darkness index and mean annual precipitation (in inches), of samples of *Perognathus apache*. $P < 0.001$.

tween their populations would occur. This situation warrants further monitoring. Sympatry, without apparent hybridization between olive-backed and plains pocket mice, is widespread in the Great Plains, and confirms their specific integrity in that area.

The evidence suggests that the Apache and plains pocket mice are conspecific. Common color patterns and the close phenetic similarity (including chromosome structure) between adjacent samples point to a close relationship. Greater differences are found between some Apache pocket mouse samples than between *P. f. copei* and the Deming Plains sample of *P. apache*. The approximate 200-km hiatus between nearest collecting localities of the two populations may seem large, but is no greater than some others. The Trans-Pecos gap may be narrowed considerably by additional field work. Both taxa are rarely collected in the southern parts of their ranges, and in my experience, repeated trapping is often necessary to collect one or a few specimens.

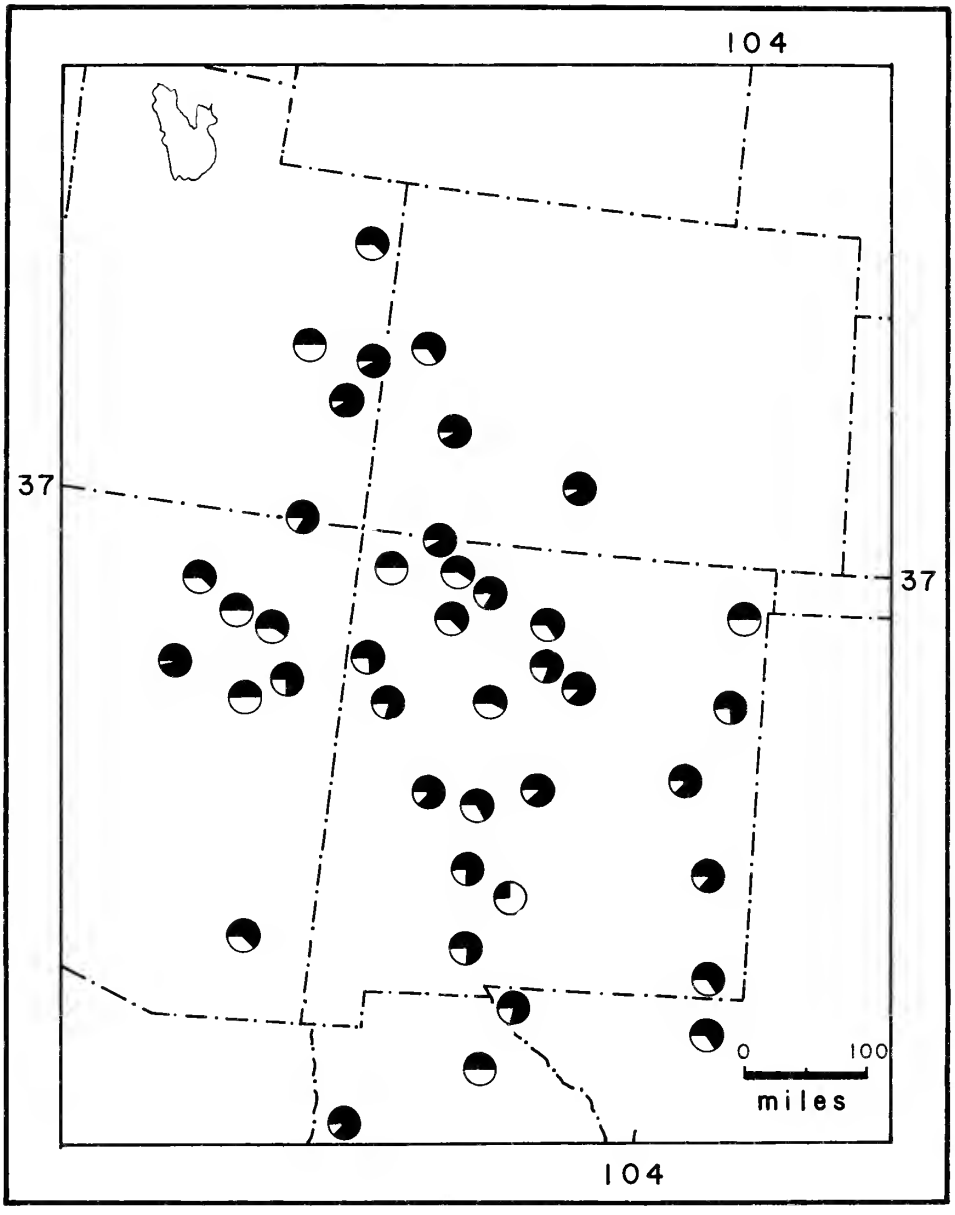

Fig. 15.—Geographic variation in the relative darkness index for samples of *Perognathus apache* and *P. flavescens*. The degree of darkening of the circles represents the relative darkness of the samples. Refer to Table 11 for identification of the samples.

Perognathus flavescens and *P. apache* were named by Merriam (1889), who published their descriptions simultaneously in the same paper. As the first reviser, I have chosen *Perognathus flavescens* as the species name because it has precedence of position (p. 11 versus p. 14, Merriam, 1889), and, more importantly, because the epithet *flavescens* will best ensure stability and universality of nomenclature. In this regard, *apache* appears to be a misspelling of apeches (Greek: discordant, noisy, quarrelsome), probably originating through the French variant, apache (a gangster or thug of Paris).

Fitting the named subspecies of Apache pocket mice into the observed pattern of geographic variation is not too difficult. But, from the original subspecies descriptions, it is clear that most were based primarily on color differences. Paradoxically, the holotypes of *cleomophila, caryi, relictus,* and *melanotis* are very similar in color, all being darker and richer than the holotype of *apache*. To recog-

Table 13.—*Matrix of similarity coefficients for samples of* Perognathus fasciatus, P. apache, *and* P. flavescens. *Refer to Fig. 19, Table 7, or the text for an explanation of sample codes.*

Sample-	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1	1.000																				
2	0.869	1.000																			
3	0.526	0.413	1.000																		
4	0.584	0.468	0.712	1.000																	
5	–0.150	–0.090	–0.068	0.094	1.000																
6	–0.418	–0.432	–0.268	–0.189	0.516	1.000															
7	–0.515	–0.669	–0.048	–0.053	0.025	0.361	1.000														
8	–0.616	–0.760	–0.216	–0.270	–0.264	0.267	0.576	1.000													
9	–0.153	–0.312	–0.443	–0.186	0.257	0.290	0.099	0.029	1.000												
10	–0.561	–0.623	–0.304	–0.549	0.090	0.463	0.361	0.550	0.313	1.000											
11	–0.070	–0.139	–0.025	–0.032	0.115	0.464	0.160	0.108	0.350	0.501	1.000										
12	–0.548	–0.563	–0.060	–0.438	–0.089	0.271	0.501	0.495	–0.053	0.778	0.397	1.000									
13	–0.487	–0.441	–0.208	–0.383	–0.331	–0.123	0.292	0.490	–0.358	0.183	–0.093	0.433	1.000								
14	0.059	–0.045	–0.138	–0.484	–0.183	–0.155	–0.065	0.046	0.058	0.195	0.069	0.281	0.415	1.000							
15	–0.260	–0.458	–0.122	–0.380	0.185	0.171	0.119	0.327	0.267	0.530	0.141	0.339	0.117	0.414	1.000						
16	0.066	0.010	–0.293	0.049	0.343	–0.065	–0.116	–0.277	0.208	–0.284	–0.175	–0.251	–0.178	–0.040	0.176	1.000					
17	–0.067	0.141	–0.135	–0.320	0.194	–0.025	–0.270	–0.424	–0.029	0.106	–0.052	0.068	0.031	0.115	0.220	0.169	1.000				
18	–0.634	–0.480	–0.569	–0.588	0.177	0.074	0.201	0.176	0.071	0.337	–0.158	0.280	0.443	0.068	0.087	0.139	0.339	1.000			
19	–0.262	–0.360	–0.291	–0.096	–0.078	–0.087	0.173	0.247	0.392	–0.142	–0.267	–0.293	–0.038	–0.273	0.092	0.205	–0.248	0.110	1.000		
20	–0.060	0.128	–0.228	–0.043	–0.218	–0.268	–0.336	–0.115	–0.032	–0.476	–0.522	–0.497	–0.189	–0.305	–0.293	0.119	–0.073	–0.100	0.343	1.000	
21	0.129	0.324	–0.187	–0.090	–0.477	–0.354	–0.320	–0.172	–0.312	–0.464	–0.485	–0.414	–0.071	–0.227	–0.572	–0.150	–0.183	–0.039	0.167	0.723	1.000

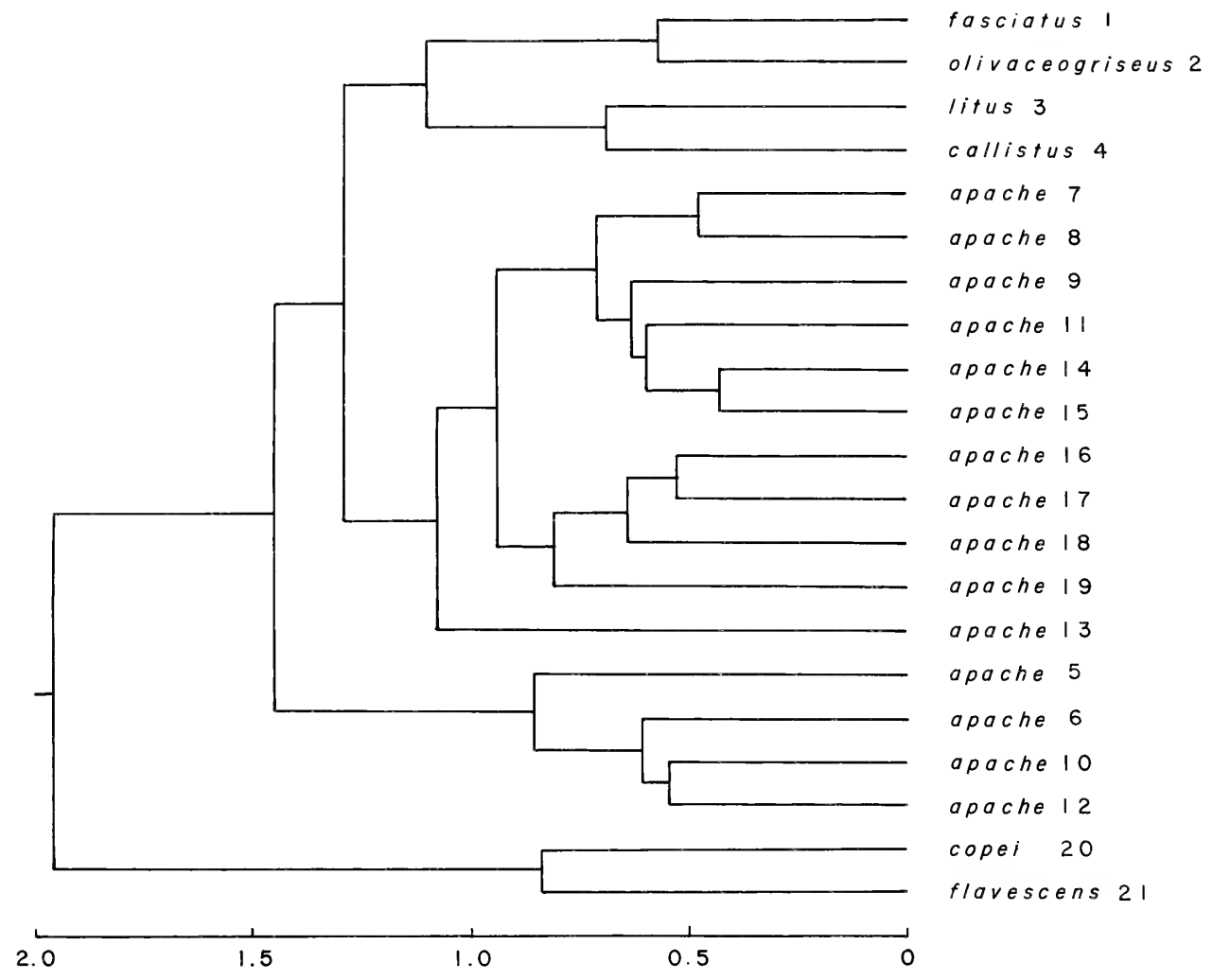

Fig. 16.—Phenogram, based upon taxonomic distances, of samples of the *Perognathus fasciatus* species group. Refer to Fig. 17 or the text for an explanation of sample codes. Grouping was by the unweighted pair-group method using arithmetic averages. The coefficient of cophenetic correlation was 0.77.

nize these and all of the other unique populations (each sample is unique) would require naming a number of new taxa. A more conservative approach seems to be required.

Mice from near Flagstaff differ from *P. flavescens apache* from the lower, drier Painted Desert areas only in color, and even color is quite variable among samples from those areas (Fig. 15). I can see no reason to recognize more than a single subspecies from northeastern Arizona, and regard *P. f. cleomophila* as a junior synonym of *P. f. apache*. The name *P. f. apache* applies only to populations from northern Arizona (Fig. 23) and Utah south of the San Juan River. The southern samples of Apache pocket mice (Fig. 23) comprise a recognizable morphologic unit that is about equally similar to *P. f. copei* and the more northern populations of Apache pocket mice. These samples represent populations previously known as *P. a. apache* (samples 16, 17, and parts of 19), *P. a. melanotis* (part of 19), and *P. a. gypsi* (18). The name *P. flavescens melanotis* is the senior unoccupied name, and *P. f. gypsi* is considered to be a junior synonym. The San Luis Valley sample is divergent structurally, and the name *P. flavescens relictus* is retained for this population. The remaining samples (Fig. 23), extending southeastward from the Uintah Basin through the northwestern quarter of New Mexico, vary clinally in size, but exhibit sufficient morphologic and geographic continutity to make any taxonomic separation highly arbitrary. The name *P. flavescens caryi* applies to these populations.

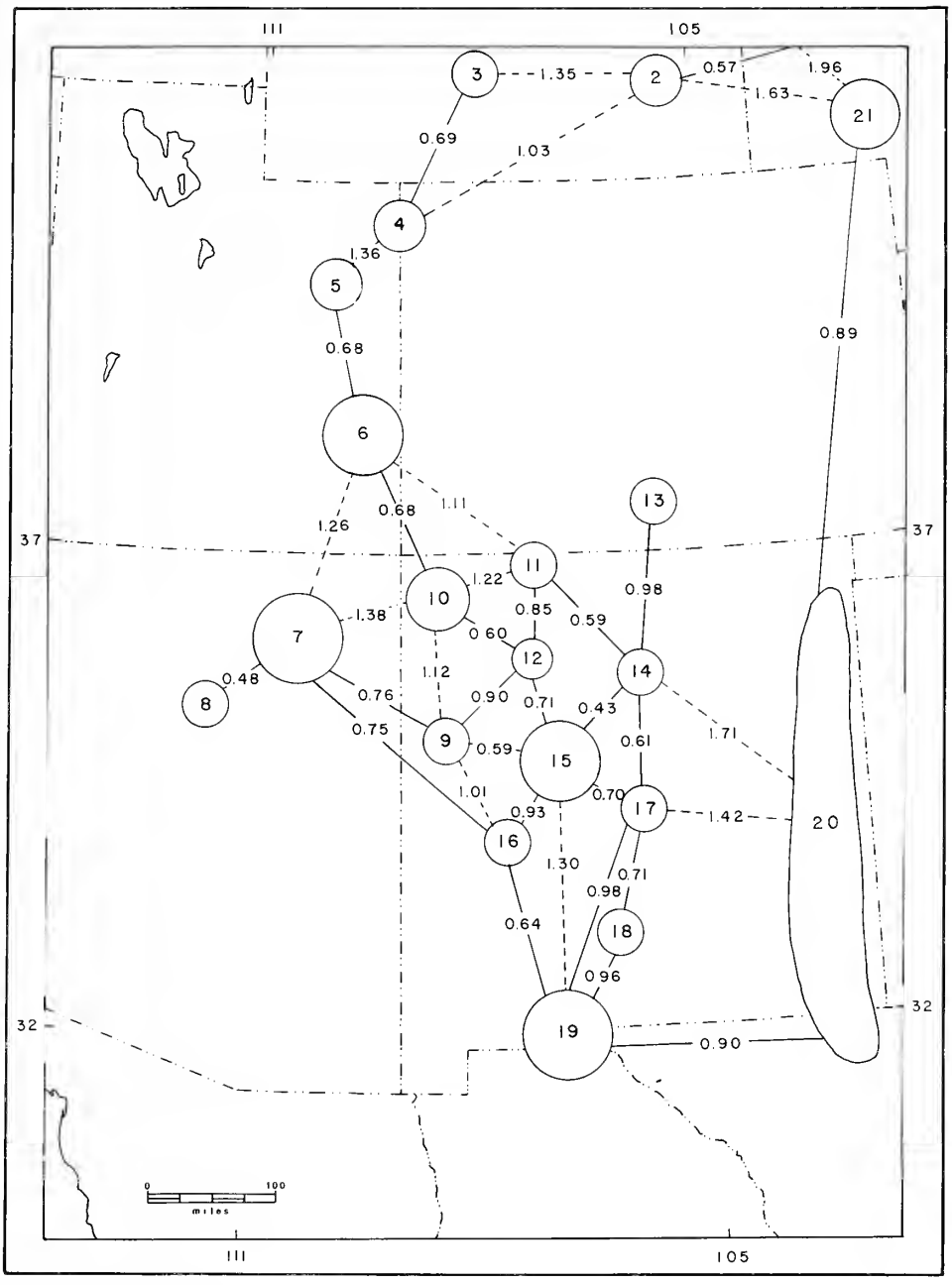

Fig. 17.—Map showing taxonomic distances between adjacent samples of the *Perognathus fasciatus* species group. Lines extending northward from samples 2 and 21 represent intersample comparisons with sample 1. Broken lines connect samples with distance values greater than 1.0. The geographic positions of the samples are only approximations.

SYSTEMATIC ACCOUNTS

Perognathus flavescens apache Meriam, 1889

1889. *Perognathus apache* Merriam, N. Amer. Fauna, 1:14, 25 October.

1918. *Perognathus apache cleomophila* Goldman, Proc. Biol. Soc. Washington, 31:23, 16 May; holotype from Winona, 6,400 ft, Coconino Co., Arizona.

Holotype.—Adult male (age class 5), skin and skull, BS 4253/4984, from near Keam's Canyon, Navajo Co., Arizona; obtained on 22 May 1888 by Jere Sullivan. Skin in good condition; skull in fair condition, bullae damaged.

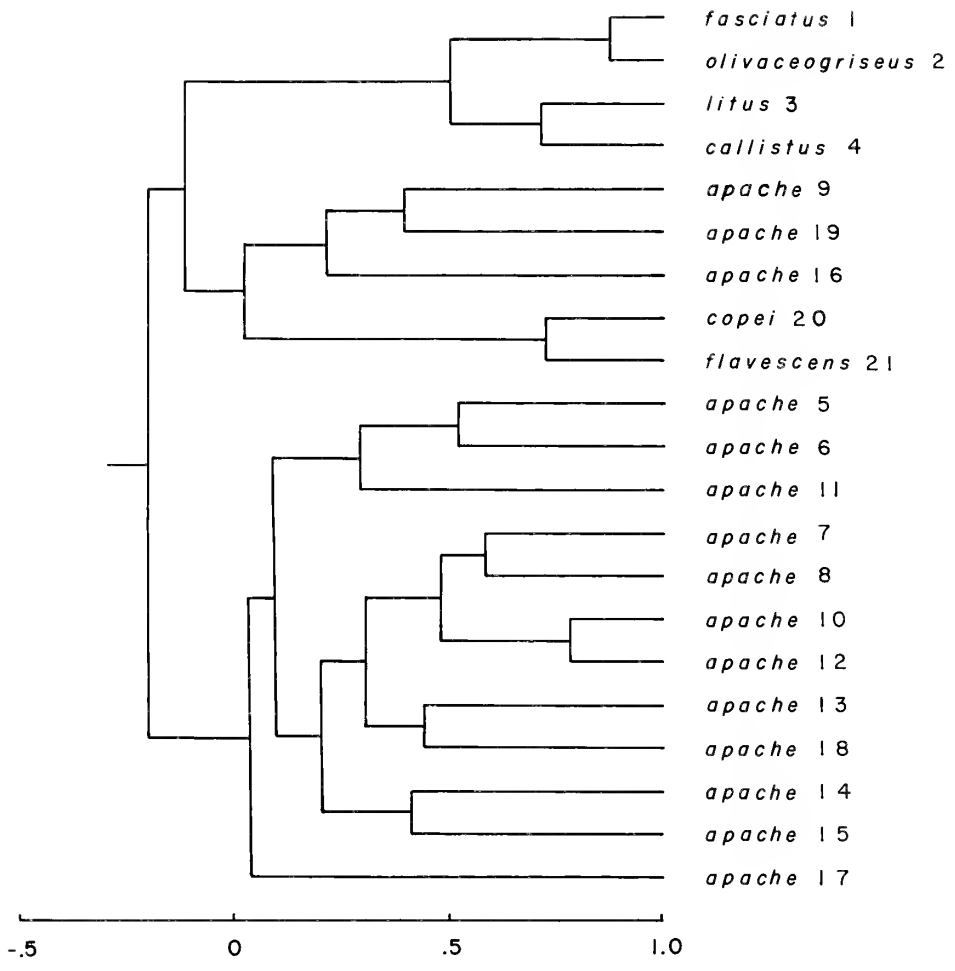

Fig. 18.—Phenogram, based upon coefficients of similarity, of samples of the *Perognathus fasciatus* species group. Refer to Fig. 19 or the text for an explanation of sample codes. The coefficient of cophenetic correlation was 0.73.

Measurements of holotype.—Total length, 140; length of tail, 68; length of hind foot, 18.5 (all external measurements from Merriam, 1889; measurements not recorded on skin tag); occipitonasal length, 24.05; interorbital breadth, 5.10; alveolar length of maxillary toothrow, 3.20; width across maxillary toothrow, 4.60; bullar length, 8.45; length of interparietal, 2.50; width of interparietals, 3.75; length of nasal, 8.70; width of nasals, 2.45; width of rostrum, 4.65; least interbullar distance, 4.00; length of mandibular toothrow, 2.90.

Distribution.—Sandy areas in semiarid grasslands and pinyon-juniper woodlands in northeastern Arizona, north and east of the Mogollon rim, west of the Chuska Mountains, and east of the Coconino Plateau, northward into southeastern Utah east of the Colorado River and south of the San Juan River (Fig. 23).

Diagnosis.—See Table 5, samples 7 and 8, for measurements. Size medium, feet relatively large, ears relatively small. Skull with interparietals very narrow, bullae large, nasals short, rostrum narrow, and interbullar region constricted. Color variable (Table 11, Fig. 15), from lighter and yellower than average, as near Holbrook and Oraibi, to much darker and oranger than average, as near Flagstaff.

Comparisons.—Distinguishable from *P. amplus* and *P. longimembris* by its shorter, nonpenicillate tail and slightly stiffer pelage (length of tail averages greater than 114% of length of head and body in sympatric *P. amplus* and *P. longimembris*, and less

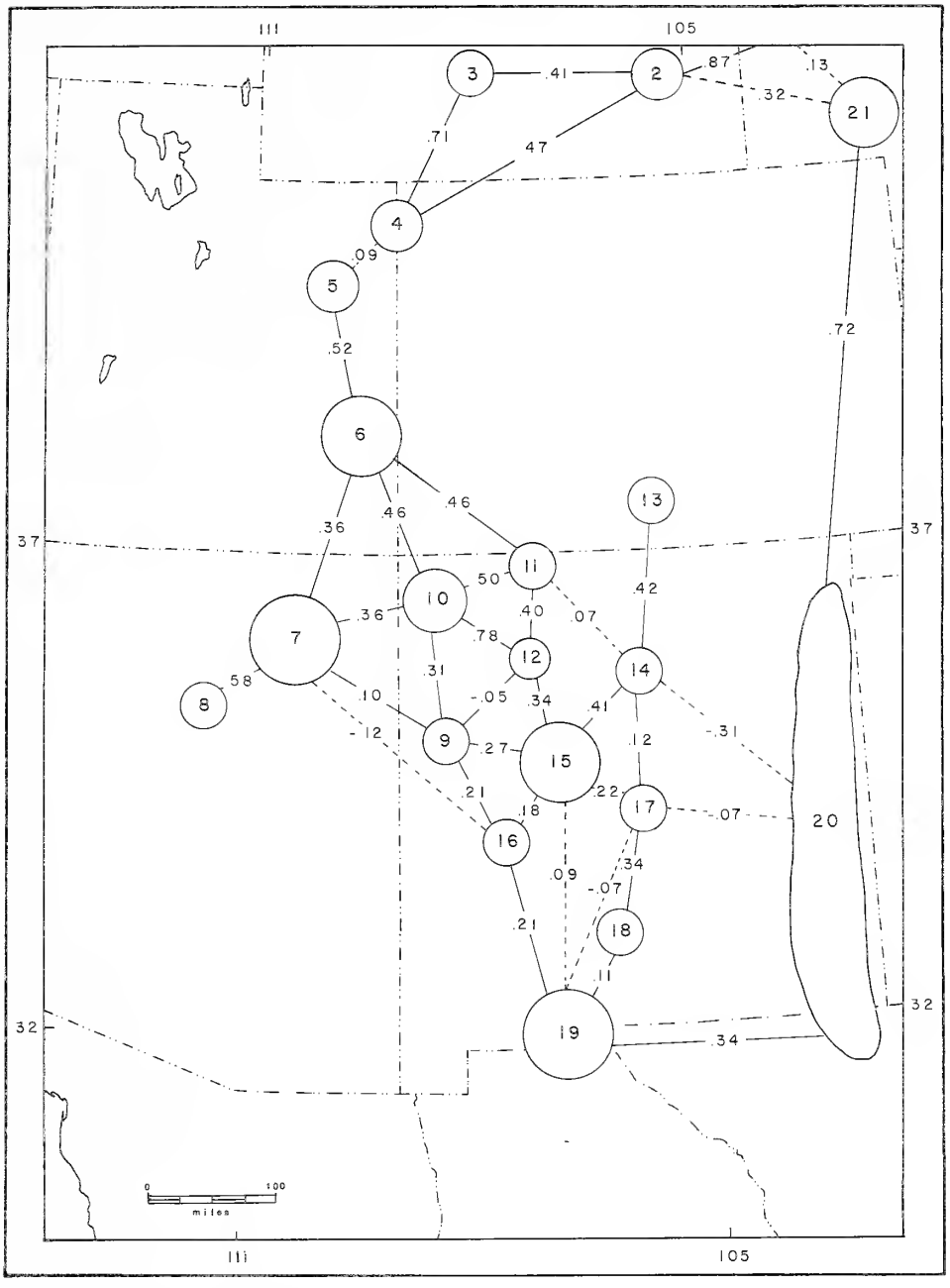

Fig. 19.—Map showing coefficients of similarity between adjacent *Perognathus fasciatus* species group samples. Lines extending northward from samples 2 and 21 represent intersample comparisons with sample 1. Broken lines connect samples with similarity values of less than 0.1, and samples of sympatric species. The geographic positions of the samples are only approximations.

than 95% in *P. f. apache*). Body size about 18% larger than sympatric *P. flavus*, with a relatively longer tail (length of tail averages 86% of length of head and body in *P. flavus*) and with smaller postauricular spots that contrast less with dorsal color. Skull about 11% longer than that of *P. flavus*, with relatively smaller bullae (length of bullae averages 40% of occipitonasal length in *P. flavus*, and 37% in *P. f. apache*), and wider interorbital region (interorbital breadth averages greater than 5.1 mm in *P. f. apache* and less than 4.5 mm in *P. flavus*). Size somewhat smaller than adjacent *P. f. caryi* popu-

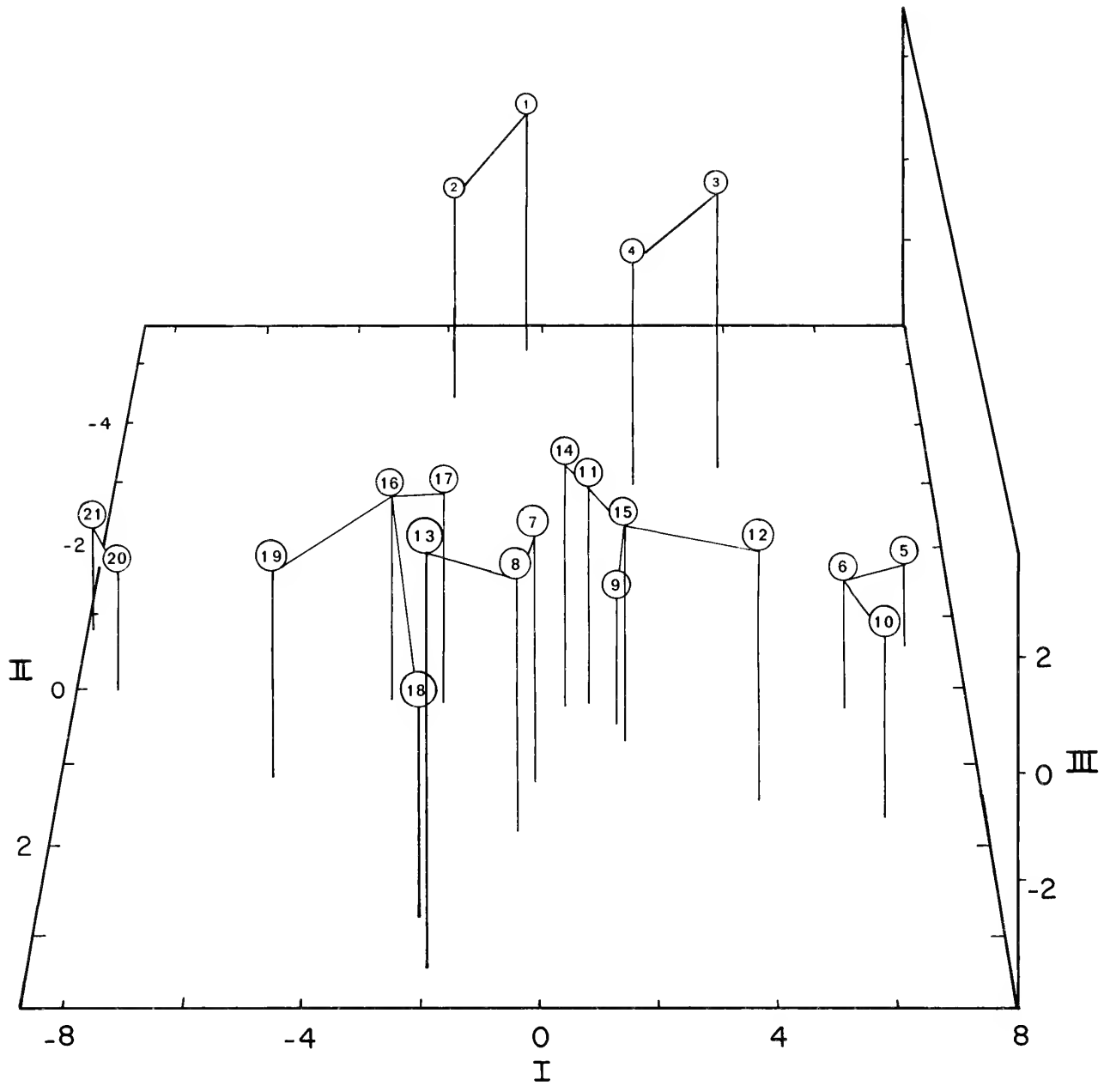

Fig. 20.—Three-dimensional plot of the first three principal components, derived from the matrix of similarity, for samples of the *P. fasciatus* species group. Lines between samples connect samples sharing the same centroid. The sample codes are defined in the text and in Table 7.

lations, with shorter skull, smaller interparietal dimensions, and smaller teeth (Tables 5 and 8). Size larger than *P. f. melanotis*, with relatively longer tail and shorter nasals.

Remarks.—The type locality was listed as Apache Co. by Merriam (1889), but is actually in Navajo Co. The holotype averaged larger in most dimensions than typical specimens of *P. f. apache*, but was within the range of measurements for the Keam's Canyon sample. *P. f. apache* populations averaged largest in measurements in the north, near the San Juan River, and smallest in the south. Spec-

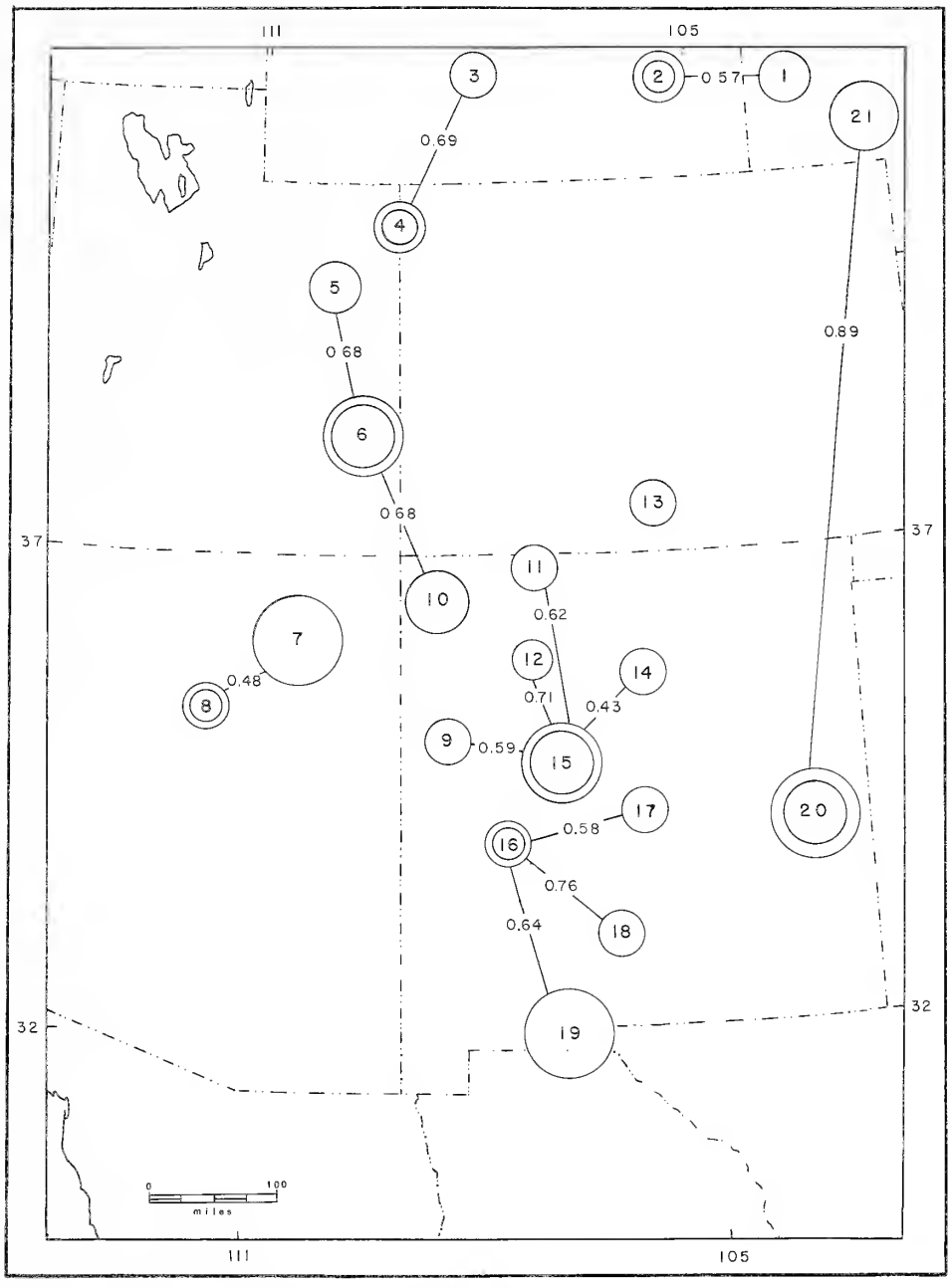

Fig. 21.—Map showing the geographic positions of the samples belonging to the seven centroids extracted from the matrix of taxonomic distances. Concentric circles depict the centroid samples. Sample 13 was placed with the Arizona samples (centroid 8).

imens from southern Utah and adjacent Arizona are somewhat intermediate to *P. a. caryi* from northwestern New Mexico, and their populations are probably continuous in the Four Corners area. Specimens from near Holbrook and Adamana approach *P. f. caryi* of the Gallup sample in size and proportions and are somewhat similar to *P. f. melanotis* from the San Augustine Plains. Cockrum (1960) assigned two specimens from 3 and 2 mi W Wupatki, Coconino Co., Arizona, to *P. a. cleomophila*. These specimens represent *P. amplus cineris* Benson, 1933.

Table 14.—*Matrix of classification, based upon the discriminant functions of 29 morphometric traits. Values indicate the number of individuals classified into each group. See text for further explanation.*

	Classification groups											
Samples	2	3	5	6	7	8	10	13	15	18	19	20
1. *Perognathus fasciatus fasciatus*	7	—	—	—	—	—	—	—	—	—	—	—
2. *Perognathus fasciatus olivaceogriseus*	15	—	—	—	—	—	—	—	—	—	—	—
3. *Perognathus fasciatus callistus* and *litus*	—	40	—	—	—	—	—	—	—	—	—	1
5. *Perognathus apache* Uintah Basin	—	—	53	2	1	—	1	—	—	—	—	—
6. *Perognathus apache* Moab	—	—	1	17	1	—	1	—	—	—	—	—
7. *Perognathus apache* Painted Desert	—	1	—	—	28	1	2	—	2	6	1	—
8. *Perognathus apache* Flagstaff	—	—	—	—	1	23	1	—	2	1	2	1
9. *Perognathus apache* Gallup	—	—	—	—	1	1	1	—	—	—	—	—
10. *Perognathus apache* San Juan Basin	—	—	1	4	2	1	21	—	1	—	—	—
11. *Perognathus apache* Canyon Largo	—	1	—	4	—	3	3	—	5	—	4	1
12. *Perognathus apache* Estrella	—	—	—	1	3	2	5	—	2	—	—	—
13. *Perognathus apache* San Luis Valley	—	—	—	—	—	—	—	13	—	—	—	—
14. *Perognathus apache* Santa Fe	1	—	—	—	1	3	1	2	7	—	1	—
15. *Perognathus apache* Rio Grande Valley	—	—	—	—	3	4	6	1	36	3	4	—
17. *Perognathus apache* Gran Quivira	—	—	—	—	—	—	—	—	3	1	5	—
18. *Perognathus apache* White Sands	—	—	—	—	2	1	1	—	1	31	1	—
19. *Perognathus apache* Deming and San Augustine	—	—	—	—	1	4	—	—	1	1	23	1
20. *Perognathus flavescens* and *P. f. copei*	—	—	—	—	—	—	—	—	—	1	1	13

Records of occurrence.—Specimens examined, 187, distributed as follows: ARIZONA. *Apache Co.:* Four Corners, 1 (UIMNH); Chin Lee, 5,600 ft, 3 (BS); Zuni Well, 7.5 mi N Adamana, 5,337 ft, 1 (MVZ). *Coconino Co.:* 2 mi S Endische Spring, Navajo Mountain, 3 (MVZ), 1 (TCWC); 5 mi S Navajo Mountain, 1 (MVZ); Page, 1 (UIMNH); 0.5 mi NW Page, 1 (UIMNH); 0.5 mi S Page, 7 (UIMNH); Salt River Project, Navajo Generating Plant Site, Page, 4,520 ft, 4 (MNA); 6 mi SE Page, 1 (MNA); 19 mi SW Page (hwy. 189), 1 (UIMNH); 2 mi N, 1 mi E Bitter Springs, 3 (UIMNH); Cedar Ridge, 6,000 ft, 1 (MVZ); 3 mi above mouth, Cedar Ranch Wash, 3 (BS); Tuba City, Painted Desert, 1 (BS), 1 (MVZ); Moa Ave, 1 (BS), 10 (MVZ); Moenkopi Wash, 12 mi above mouth, 4,500 ft, 3 (BS); 2.5 mi S, 2 mi E Moenkopi, 5,050 ft, 6 (UIMNH); 2.5 mi SE Moenkopi, 4,900 ft, 4 (UIMNH); 5 mi S, 2 mi E Moenkopi, 5,500 ft, 4 (UIMNH); 5 mi N Cameron, 1 (UIMNH); 4.5 mi N Cameron, 1 (UIMNH); 3 mi S Visitor Center, Wupatki National Monument, 5,000 ft, 4 (MNA), 1 (UIMNH); 4 mi W Winona, 1

Table 15.—*Mean scores for canonical variables for samples of* Perognathus fasciatus, P. apache, *and* P. flavescens.

	Canonical variables				
Samples	I	II	III	IV	V
1. *Perognathus fasciatus fasciatus*	−1.667	−4.449	2.163	−0.400	1.074
2. *Perognathus fasciatus olivaceogriseus*	−1.772	−4.215	1.878	−0.244	2.057
3. *Perognathus fasciatus callistus* and *litus*	−2.802	−2.722	−1.040	0.841	−0.733
5. *Perognathus apache* Uintah Basin	−3.107	1.489	0.207	−0.852	−0.428
6. *Perognathus apache* Moab	−1.607	1.439	0.908	0.372	0.235
7. *Perognathus apache* Painted Desert	0.745	0.594	−1.648	0.329	0.115
8. *Perognathus apache* Flagstaff	2.094	0.160	0.659	0.854	−0.190
9. *Perognathus apache* Gallup	0.883	1.267	0.389	0.888	0.265
10. *Perognathus apache* San Juan Basin	0.283	1.668	0.601	1.960	0.373
11. *Perognathus apache* Canyon Largo	0.740	−0.147	0.361	0.708	0.357
12. *Perognathus apache* Estrella	0.642	0.787	−0.057	1.396	−0.283
13. *Perognathus apache* San Luis Valley	3.942	−1.416	0.954	−1.057	−2.710
14. *Perognathus apache* Santa Fe	1.411	−0.816	1.272	0.066	−0.259
15. *Perognathus apache* Rio Grande Valley	1.188	−0.062	0.756	−0.184	−0.139
17. *Perognathus apache* Gran Quivira	0.680	−1.056	−0.205	−1.020	0.493
18. *Perognathus apache* White Sands	1.636	0.459	−0.953	−0.724	1.049
19. *Perognathus apache* Deming and San Augustine	1.284	−0.516	−0.290	−1.244	0.555
20. *Perognathus flavescens copei* and *P. f. flavescens*	0.897	−1.881	0.357	−0.614	1.461
Cumulative % of total dispersion	39.75	64.21	73.49	81.83	88.82

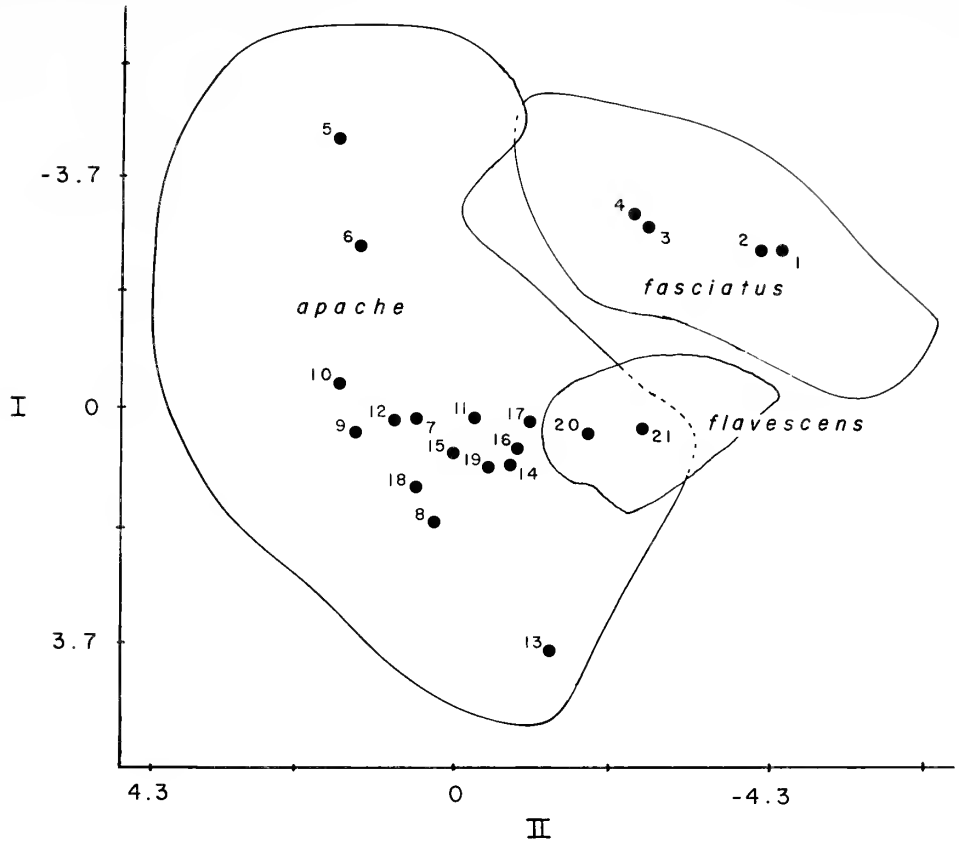

Fig. 22.—Two-dimensional plot of the first two canonical variables for individuals of the *P. fasciatus* species group. Circles mark the positions of the sample means, whereas the lines encompass the distribution of the individual cases for each taxon. To prevent visual confusion, the positions of the individual cases are not shown. Refer to the text or Table 7 for an explanation of the sample codes.

+ chromosomes (MSB); 3 mi NW Winona, 6,400 ft, 27 (BS); Winona, 6,400 ft, 7 (MVZ); Grand Falls, Little Colorado River, 2 (UCM); 1 mi SE Grand Falls, 1 (MVZ); 30 mi NE Flagstaff, 1 (BS); 9 mi E Flagstaff, 1 (BS); Walnut, 5 mi from Turkey Tank, 4 (BS). *Navajo Co.:* 11 mi N Kayenta, 4 (UIMNH); 4.5 mi N, 1 mi E Kayenta, 2 (UIMNH); 1 mi E Kayenta, 5 (UIMNH); Dogoszhi Biko Canyon, mouth of Water Lily Canyon, 11 (MNA); Keam's Canyon, 7 (BS), 20 (MVZ), 8 (UIMNH); Oraibi, 6,000 ft, 7 (BS), 5 (MVZ); Holbrook, 2 (BS); 0.5 mi S, 3 mi E Holbrook, 1 (UIMNH); Winslow, Painted Desert, 5,326 ft, 1 (BS), 3 (UMMZ); 2 mi N, 2 mi E Winslow, 1 (UIMNH); 2 mi E Winslow, Little Colorado River, 1 (BS); Winslow, N side river, 1 (BS). UTAH. *San Juan Co.:* Navajo Mountain Trading Post, 5 mi SE Navajo Mountain, 1 (MVZ).

Additional records.—ARIZONA. *Apache Co.:* Canyon de Chelley (Cockrum, 1960). *Coconino Co.:* Tappan Spring, 4,500 ft (Cockrum, 1960). *Navajo Co.:* Walpi (Cockrum, 1960).

Perognathus flavescens caryi Goldman, 1918

1918. *Perognathus apache caryi* Goldman, Proc. Biol. Soc. Washington, 31:24, 16 May.

Holotype.—Adult male (age class 4), skin and skull, BS 148206, from 8 mi W Rifle, Garfield Co., Colorado; obtained on 4 October 1906 by M. Cary. Both skin and skull in good condition.

Measurements of holotype.—Total length, 154; length of tail, 73; length of hind foot, 21; occipitonasal length, 25.15; interorbital breadth, 5.60; alveolar length of maxillary toothrow, 3.50; width across maxillary toothrows, 4.65; bullar length, 9.00; width across bullae, 13.40; length of interparietal, 3.35; width of interparietals, 4.15; length of nasal, 9.30; width of nasals, 2.30; width of rostrum, 4.35; least interbullar distance, 4.20; length of mandibular toothrow, 3.15.

Distribution.—Usually in sandy areas in semiarid grasslands and pinyon-juniper associations, from near Val Verde in the Rio Grande Valley, northward to at least the Rio Chama; and from the upper Pecos Valley and the Rio Grande Valley westward to Gallup and the Chuska Mountains, all in New Mexico; northward from the Four Corners area through western Colorado and eastern Utah into the

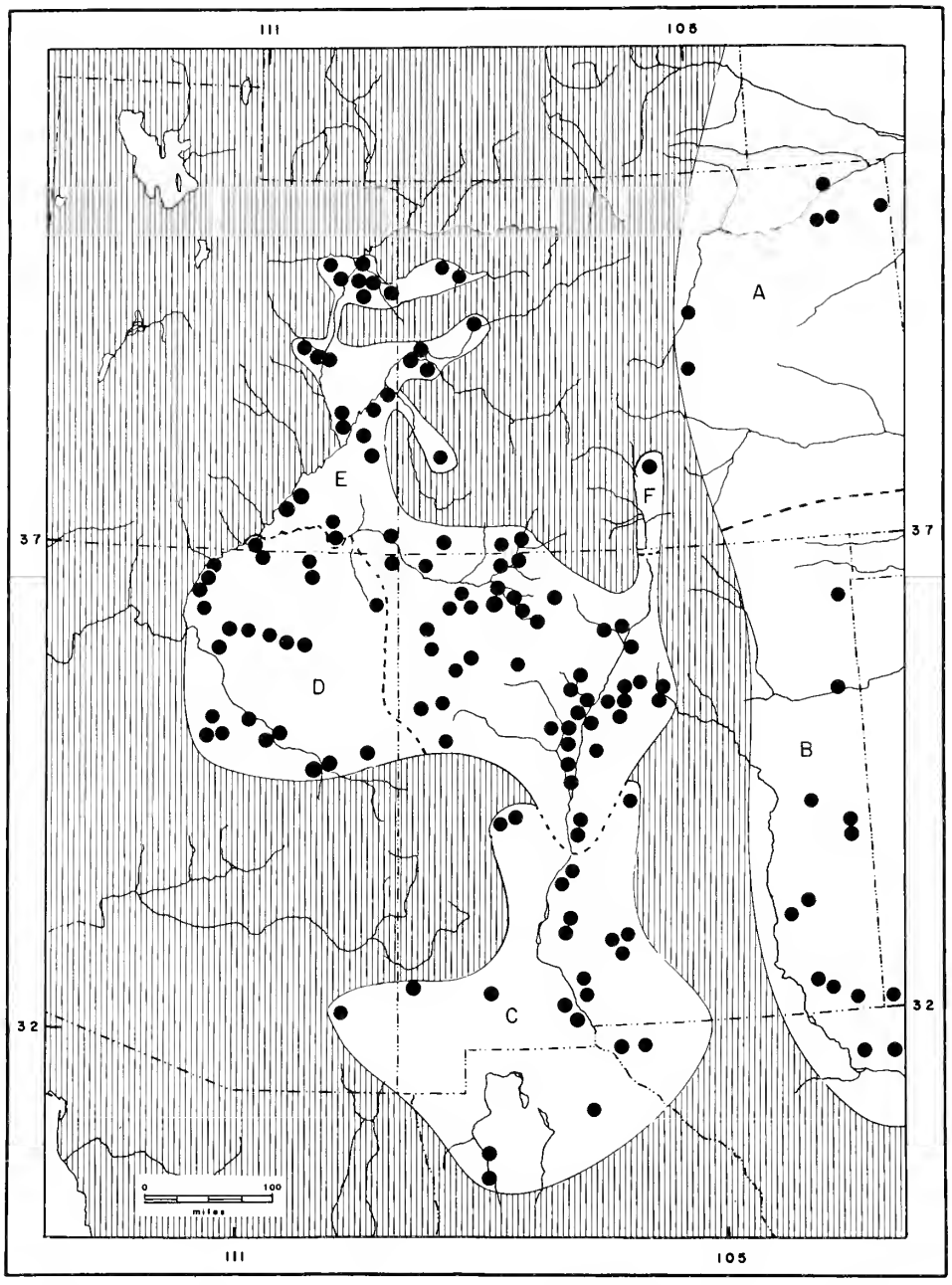

Fig. 23.—Map showing geographic range of the intermountain races of *Perognathus flavescens*, and portions of the ranges of two of the Great Plains races. Circles represent localities from which specimens were examined. To prevent crowding, single circles represent two or more localities that partially overlapped on the map. A = *P. f. flavescens;* B = *P. f. copei;* C = *P. f. melanotis;* D = *P. f. apache;* E = *P. f. caryi;* F = *P. f. relictus*.

Uintah Basin, at least to the Duchesne and White rivers. Not known from west of the Colorado and Green rivers south of the city of Green River (Fig. 23).

Diagnosis.—See Table 5, samples 5, 6, 9, 10, 11, 12, 14, and 15, for measurements. Size of most characters averaging from medium to large, and varying clinally, being largest in the north (sample 5) and smallest in the southeast (sample 14). Skull with relatively constricted interbullar region and with narrow interparietals. Color variable, lightest and palest in the San Juan Basin and near Green

River, Utah, and darkest and richest at higher elevations (Table 11, Fig. 15).

Comparisons.—See account of *P. f. apache* for remarks on distinguishing *P. flavus*. Size smaller and with a relatively shorter, nonpenicillate tail than *P. parvus; P. parvus* is generally tannish-gray or tannish colored (not yellowish-orange), and has less contrasting postauricular spots than *P. flavescens;* occipitonasal length less than 25.5 mm in *P. flavescens,* but greater than 26.5 mm in *P. parvus*. Differs from *P. fasciatus callistus* in larger size, relatively longer tail, and yellowish-orange, rather than olive-yellow, lateral line; interparietal of *P. f. caryi* longer, rostrum wider and interbullar region narrower than *P. f. callistus;* mandibular toothrow longer, M^1 wider, and M_1 larger in *P. f. caryi*. Skull larger, but interorbital region narrower and interparietals larger than *P. f. relictus;* premolars and molars larger than *P. f. relictus*. Size larger and tail relatively longer than *P. f. melanotis;* skull longer and interparietals shorter and narrower than *P. f. melanotis*.

Remarks.—This is the most variable of the intermountain races of *P. flavescens*. The dominant trend is the north-south size cline. Specimens from Gallup are somewhat intermediate to *P. f. apache* and also show some similarity to *P. f. melanotis* from the San Augustine Plains. The Uintah Basin population is found on a variety of substrates, but most others appear to be limited to loose sands. Durrant (1952) thought that the Uintah Basin population represented an undescribed subspecies. Size averages slightly larger in the Uintah Basin population, but it is, overall, similar to *P. f. caryi* from south of the Tavaputs Plateau, and subspecific recognition does not seem warranted.

A specimen from San Antonio Mountains, N Tres Piedras, Rio Arriba Co., New Mexico, listed as this species by Findley et al. (1975), is *P. flavus*.

Records of occurrence.—Specimens examined, 448, distributed as follows: Colorado. *Garfield Co.:* 7 mi W Rifle, 2 (BS); 8 mi W Rifle, 2 (MVZ). *La Plata Co.:* 9 mi S Ignacio, 1 (UU). *Mesa Co.:* Sieber Ranch, Little Dolores Creek, 1 (UCM); 0.25 mi E Colorado National Monument, 1 (DCBML); 0.5 mi E Grand Junction Entrance Station, Colorado National Monument, 2 (UCM); Fruita, 1 (BS); Badger Wash, 8 (DCBML); State Line, 1 (MVZ). *Montezuma Co.:* Morfield Mesa, Mesa Verde National Park, 2 (KU). *Montrose Co.:* Coventry, 1 (BS); Bedrock, 3 (UCM). *Rio Blanco Co.:* 17 mi W Meeker, 1 (DCBML); 7 mi N, 19 mi E Rangely, 2 (DCBML). New Mexico. *Bernalillo Co.:* 2 mi N Albuquerque, 2 (MSB); West Mesa, W Albuquerque near Lava Flow, 1 (MSB); 2 mi N, 5.5 mi W Albuquerque, 2 (MSB); 2.5 mi N, 6 mi W Albuquerque, 2 (MSB); 5 mi W Albuquerque, 3 (MSB); W Albuquerque, E side Rio Puerco Valley, S U.S. 66, 2 (MSB); 18 mi W Albuquerque, Puerco Valley, 3 (MSB); 14 mi W Albuquerque, 24 (MSB), 2 + chromosomes (MSB); 16 mi W Albuquerque, 2 (UIMNH); 4.8 mi N, 14 mi W Albuquerque, 1 (MSB); 14.7 mi N, 3 mi E Suwanne, 2 (MSB); 2.5 mi S, 7.5 mi E Suwanne, 3 (MSB); 0.25 mi S, 10.2 mi W Isleta, 12 (MSB); 2.2 mi S, 10.5 mi W Isleta, 1 (MSB). *McKinley Co.:* Gallup, 3 (BS); Wingate, 4 (BS); 3 mi N, 2 mi W Estrella, 7 (MSB); 4 mi N, 2 mi W Estrella, 8 (MSB); 3 mi N Crownpoint, 1 (MSB). *Rio Arriba Co.:* Stinking Springs Lake (Burford Lake), 1 (BS); 10 mi W Lindrith along Canyada Larga, 4 (MSB); River mile 165, River Island, San Juan River, 1 (UU); River mile 166, San Juan River, 1 (UU); Rio Ojo Caliente, 1.5 mi E, 1 mi N Chili, 2 (MSB); Espanola, 9 (BS); 5 mi E Abiquiu, 1 (BS); 3.5 mi S junction U.S. 285 and N.M. 30, on 30, T20N, R8E, 1 (MSB). *Sandoval Co.:* 5 mi S, 3 mi E Domingo, 2 (MSB); San Felipe Indian Reservation, sec. 2, T13N, R5E, 1 (MSB); Jemez, 1 (BS); 0.25 mi S, 1 mi W San Ysidro, 1 (MSB); 6 mi S, 4.5 mi W San Ysidro, 9 (MSB); 1 mi SW Santa Ana Pueblo, 2 (MSB), 4 (CM), 12 + chromosomes (MSB); 4.5 mi N, 14 mi W Alameda, 6 (MSB). *San Juan Co.:* Chaco Wash, 6 mi E, 14 mi S Shiprock, 43 (MSB); Newcomb, 5 mi N, 6 mi E, 1 (MSB); Newcomb, 1 (MSB); Gallego Canyon, 7.5 mi S, 5 mi E Farmington, 1 (MSB); Gallego Canyon, 7.5 mi S, 4 mi E Farmington, 1 (MSB); 7 mi S, 6 mi W Bloomfield, sec. 4, T27N, R12W, 2 (MSB); 13 mi S, 11 mi E Farmington, 3 (MSB); 3 mi S, 3 mi E Farmington, 2 (MSB); 10 mi S, 7 mi E Farmington, 1 (MSB); 16 mi S, 1 mi W Farmington, sec. 17, T26N, R13W, 2 (MSB); upper Benito Canyon, 1 (UU); Lucero Place, sec. 17, T31N, R7W, 1 (MSB); Pine River Road, sec. 9, T31N, R7W, 1 (MSB); Canyon Largo, sec. 22, T29N, R9W, 7 (MSB); 3 mi S, 3 mi E Blanco, 1 (MSB); Canyon Largo at Fresno Canyon, sec. 33, T28N, R8W, 27 (MSB); 0.5 mi ESE Four Corners boundary marker, 2 (MSB); 5.5 mi N, 1.5 mi W Waterflow, 1 (MSB); El Huerfano, 0.5 mi SE base, 1 (MSB); Chaco Canyon National Monument, 2 (MSB). *San Miguel Co.:* Pecos, 4 (BS); 3 mi S Pecos, 13 (BS). *Santa Fe Co.:* Rio Tesuque, sec. 14, T18N, R9E, 1 (MSB); NW Santa Fe Airport, 2 mi W Sewage Disposal Plant, 1 (MSB); Santa Fe, 1 (BS); Galisteo Creek, 1 mi E U.S. 85, sec. 31, T15N, R7E, 1 (MSB); 1 mi W Cerillos on Galisteo Creek, 1 (MSB); Galisteo Creek, 1 mi E Galisteo R.R. Station, sec. 26, T14N, R8E, 1 (MSB); Glorieta, 2 (BS); San Pedro, 1 (BS). *Socorro Co.:* 1 mi N Pope, 2 mi S Lava Mesa, 1 + chromosomes (MSB); Lava Mesa, 2 mi SE San Marcial, 1 (MVZ); 0.5 mi S, 2 mi W Bernardo, 2 (MSB); 4 mi E Escondida, 2 (MSB); 2 mi N, 4.5 mi E Socorro, 3 (MSB); Lava Mesa, S of Clyde, 1 (MBZ). *Valencia Co.:* 2 mi E Valencia, 1 + chromosomes (MSB); 1.5 mi S, 5 mi W Los Lunas, 1 (MSB); 2 mi S, 8.5 mi W Los Lunas, 4 (MSB); 2 mi W Los Chavez, 2 (MSB); 7 mi W Belen, 1 (MSB); Zuni Mountains, 2.5 mi E El Moro, 1 (LACM). Utah. *Duchesne Co.:* S Myton Bench, 3 mi SE Myton, 3 (UU); Myton Bench, 5 mi SE Myton, 16 (UU). *Emery Co.:* 16 mi NW Green River, 1 (CM); Gunnison Valley, W side Green River, 7.6 mi N Green River (city), 4,200 ft, 2 (UU). *Grand Co.:* Castle Valley, 10 mi NE Moab, 5,000 ft, 5 (UU); Castle Valley, 8 mi NE Moab, 1 (UU); 1 mi E Green River (city), 4,080 ft, 8 (UU); 1 mi SE Dewey Bridge, S side Colorado River, 4,500 ft, 1 (UU); 3 mi SE Dewey, S side River, 4,810 ft, 1 (UU); 4 mi SE Dewey, 5,000 ft, 1 (UU); Big Flat, sec. 21, T26N, R19E, 6,000 ft, 2 (UCM). *San Juan Co.:* S end Gray's Pasture, sec. 32, T27S, R19E, 5,960 ft, 7 (UCM); Willow Flat, sec. 6, T28S, R19E, 6,040 ft, 4 (UCM); sec. 5, T27S, R19E, 6,050 ft, 1 (UCM); NE Corner Gray's Pasture, sec. 22, T26S, R19E, 6,000 ft, 1 (UCM); Chester Canyon at Beef Basin Rd.,

sec. 7, T31S, R19E, 5,280 ft, 7 (UCM); W of Squaw Butte, sec. 25, T30S, R19E, 5,040 ft, 3 (UCM); S of Squaw Butte, sec. 30, T30S, R20E, 5,040 ft, 2 (UCM); SW Cave Spring, sec. 29–30, T30S, R20E, 5,000 ft, 4 (UCM); Canyon Lands National Park, sec. 15, T27S, R19E, 5,900 ft, 1 (MMNH); Dry Valley (=Hatch Crossing, about 30 mi N Monticello), 1 (BS); 1 mi S Kern Spring, 5 + chromosomes (MSB); Highway 160, 25 mi N Monticello, 6,100 ft, 1 (UU); Bluff, 4,400 ft, 1 (MVZ); 1 mi N Bluff, 4,500 ft, 1 (UU); Noland's Ranch, San Juan River, 1 (BS); Johns Canyon, 5,150 ft, 1 (UU); 119 mi N Lee's Ferry, 3 (UU); 121 mi N Lee's Ferry, 2 (UU); 142 mi N Lee's Ferry, 2 (UU). *Uintah Co.:* Evacuation Creek, 2 mi S White River, 1 (MSB), 2 + chromosomes (MSB); S shore White River, 3 mi S Bonanza, 1 (MSB), 1 + chromosomes (MSB); Evacuation Wash, 4 mi NE Rainbow, 5,600 ft, 3 (UU); 2 mi NE Rainbow, 5,800 ft, 2 (UU); Brown's Corral, 20 mi S Ouray, 6,250 ft, 4 (UU); Willow Creek, 25 mi S Ouray, 5,250 ft, 2 (UU); White River, 2 mi W upper White River Crossing, 14 mi N Dragon, 5,000 ft, 1 (UU); confluence of Green and White rivers, 1 mi S Ouray, 4,654 ft, 2 (UU); 2 mi S Ouray, 4,800 ft, 2 (UU); 1.5 mi S, 1 mi E Ouray, 7 (MSB); 2 + chromosomes (MSB); 1.5 mi E Ouray, N White River, 20 (MSB), 2 + chromosomes (MSB); Pariette Bench, 4,700 ft, 6 mi SW Ouray, W Green River, 1 (CM).

Additional records.—COLORADO. *Mesa Co.:* 0.25 mi W Red Canyon Overlook, Colorado National Monument, 6,400 ft; 0.25 mi SE East Entrance Ranger Station (Armstrong, 1972). NEW MEXICO. *Valencia Co.:* near Laguna (Bailey, 1932). UTAH. *San Juan Co.:* 0.5 mi N Bluff, 4,400 ft (Durrant, 1952); River View (Durrant, 1952).

Perognathus flavescens relictus Goldman, 1938

1938. *Perognathus apache relictus* Goldman, J. Mamm., 19:495, 14 November.

Holotype.—Adult male (age class 4), skin and skull, BS 150768, from Medano Ranch, 15 mi NE Mosca, Alamosa Co., Colorado; obtained on 2 November 1907 by M. Cary. Both skin and skull in good condition.

Measurements of holotype.—Total length, 137; length of tail, 68; length of hind foot, 19.0; occipitonasal length, 22.70; interorbital breadth, 5.45; alveolar length of maxillary toothrow, 3.15; width across maxillary toothrows, 4.20; bullar length, 8.00; width across bullae, 12.40; length of interparietal, 3.10; width of interparietals, 3.75; length of nasal, 7.90; width of nasals, 2.35; width of rostrum, 3.60; least interbullar distance, 4.00; length of mandibular toothrow, 2.80.

Distribution.—Sandy areas in arid grassland associations in and around the Great Sand Dunes of the San Luis Valley, Colorado (Fig. 23).

Diagnosis.—See Table 5, sample 13, for measurements. Size medium, with tail relatively longer than other populations. Skull with broadest interorbital region, short nasals, and shortest and narrowest interparietals; bullae relatively small, molariform, teeth relatively narrow, expecially premolars and M^1. Color dark and rich (Table 11, Fig. 15).

Comparisons.—See account of *P. f. apache* for remarks on distinguishing *P. flavus*. Skull smaller, interorbital region wider, and interparietals smaller than *P. f. caryi*. Size generally larger, interorbital region much wider, and interparietals shorter and narrower than *P. f. melanotis*.

Remarks.—Goldman (1938) assigned all of the relatively dark-colored specimens of Apache pocket mice from New Mexico, including those from Gran Quivira, Santa Fe, Pecos, Glorieta, and Burford Lake to *P. a. relictus*. The Gran Quivira specimens are referred to *P. f. melanotis*, and the Pecos, Santa Fe, Glorieta, and Burford Lake specimens are assigned to *P. f. caryi*.

Records of occurrence.—Specimens examined, 26, distributed as follows: COLORADO. *Alamosa Co.:* 1.4 mi N, 9.6 mi E Mosca, 2 (MSB); 1.4 mi N, 11 mi E Mosca, 1 + chromosomes (MSB); Medano Ranch, 15 mi NE Mosca, 1 (BS), 2 (MVZ), 7 (UCM); Great Sand Dunes National Monument, 1.6 mi NE Headquarters Medano Springs Ranch, 11 (MVZ); 3 mi S Great Sand Dunes National Monument, 1 (MVZ).

Additional records.—COLORADO. *Alamosa Co.:* Great Sand Dunes National Monument (Armstrong, 1972).

Perognathus flavescens melanotis Osgood, 1900

1900. *Perognathus apache melanotis* Osgood, N. Amer. Fauna, 18:27, 20 September.

1929. *Perognathus gypsi* Dice, Occas. Papers Mus. Zool., Univ. Michigan, 203:1, 19 June; holotype from White Sands, 12 mi SW Alamogordo, Otero Co., New Mexico.

1933. *Perognathus apache gypsi*, Benson, Univ. California Publ. Zool., 40:26, 13 June.

Holotype.—Adult female (age class 5), skin and skull, BS 97416, from Casas Grandes, Chihuahua; obtained on 21 May 1899 by E. A. Goldman. Both skin and skull in good condition.

Measurements of holotype.—Total length, 133; length of tail, 65; length of hind foot, 19.5; occipitonasal length, 22.20; interorbital breadth, 5.10; alveolar length of maxillary toothrow, 2.85; width across maxillary toothrows, 4.20; bullar length, 7.60; width across bullae, 11.75; length of interparietal, 2.60; width of interparietals, 3.95; length of nasal, 8.25; width of nasals, 2.25; width of rostrum, 3.65; least interbullar distance, 4.20; length of mandibular toothrow, 2.70.

Distribution.—Sandy areas in desert and grassland associations from Gran Quivira and the San Augustine Plains, New Mexico, southward to the Samalayucca Sands and Casas Grandes, Chihua-

hua; and extending west from El Paso Co., Texas to Willcox Playa, Arizona (Fig. 23).

Diagnosis.—See Table 5, samples 16, 17, 18, and 19 for measurements. Size small in most dimensions, with relatively short tail. Size varies altitudinally and latitudinally, being largest in the higher, northern populations and smallest in the Deming Plains and Jornada del Muerto populations. Skull short, but with relatively large bullae; interparietals not noticeably broadened. Color extremely variable geographically, from white with a grayish overwash (White Sands) to relatively dark and rich (Jornada del Muerto and Casas Grandes, Table 11 and Fig. 15).

Comparisons.—More similar in size and proportions to *P. flavus* than the more northern populations of *P. flavescens*. Interorbital breadth 4.9 mm or greater in *P. f. melanotis*, and 4.7 mm or less in *P. flavus;* posterior cranial region more constricted and bullae more inflated in *P. flavus,* least interbullar distance averages 2.90 mm in *P. flavus* and 3.95 mm in *P. f. melanotis*. See account of *P. f. apache* for additional remarks on distinguishing *P. flavus*. *P. f. melanotis* differs from *P. f. copei* in larger size; the skull of *P. f. melanotis* has a narrower interorbital region, the interparietals are shorter and narrower, the interbullar region is more constricted, and the articular process of the mandible is shorter than in *P. f. copei*.

Remarks.—The San Augustine Plains and Gran Quivira populations approach the Rio Grande Valley population of *P. f. caryi* in most characters. Members of the White Sands population have relatively large feet, inflated bullae, and wide rostra, and approach *P. f. copei* in having wide interorbital regions and long interparietals. The individuals from Willcox Playa were too few to adequately assess their morphologic features. However, other than a slight color difference (Table 12), that sample did not appear to be materially different from specimens from near Lordsburg and from Casas Grandes. Bailey (1932) allied all of the relatively dark-colored samples of Apache pocket mice from New Mexico, including those from Pecos, Santa Fe, Glorieta, Burford Lake, and Gran Quivira with the holotype of *P. a. melanotis* from Casas Grandes, but assigned specimens from Deming to *P. a. apache*. Goldman (1938) later assigned the dark-colored specimens from New Mexico to *P. a. relictus,* restricted *P. a. melanotis* to the holotype, and retained the Deming specimens under *P. a. apache*. These latter specimens (BS collection) were dug from a burrow, and are too young to show any characteristics useful for distinguishing subspecies.

Records of occurrence.—Specimens examined, 148, distributed as follows: ARIZONA. *Cochise Co.:* 3 mi SE Willcox, 4,163 ft, 5 (MVZ). NEW MEXICO. *Catron Co.:* 15 mi S, 15 mi W Magdalena, 1 (DCBML). *Doña Ana Co.:* 6 mi W La Mesa, 1 (ENMU); 7 mi N, 2 mi E Las Cruces, 1 (UA); 6 mi E Las Cruces, 1 (NMSU); 13 mi SW Las Cruces, 1 (NMSU). *Hildago Co.:* 11 mi N, 10 mi W Lordsburg, 1 (ENMU). *Luna Co.:* Deming, 3 (BS). *Otero Co.:* White Sands, 10 mi SW Tularosa, 5 (MVZ); Quartz Sands, 14 mi SW Tularosa, 4,100 ft, 18 (MVZ); White Sands, 12 mi W Alamogordo, 8 (MVZ); White Sands, 18 mi W Alamogordo, 4 (AMNH), 5 (MVZ); 15 mi SW Alamogordo, 1 (LACM); White Sands, 18 mi SW Alamogordo, 32 (MVZ); White Sands, 1 (LACM), 2 (UMMZ); Walker Ranch, White Sands National Monument, 1 + chromosomes (MSB); Interior of White Sands, 3 (UMMZ). *Sierra Co.:* 1 mi N, 4.5 mi E Engle, 1 (MSB); 1 mi S, 5.4 mi E Engle, 3 + chromosomes (MSB). *Socorro Co.:* Mesa Jumanes, southern portions, 1 (BS); Mesa Jumanes, Ruins of Gran Quivira, 1 (BS); Gran Quivira National Monument, T1S, R8E, 13 (MSB); San Augustine Plains, 12 mi E, 10 mi S Datil, 1 (MSB); San Augustine Plains, sec. 28–29, T2S, R7W, 13 (MSB); San Augustine Plains, 12 mi NW Monica Spring, 4 (BS); Gallina Mountains, 2 (BS). TEXAS. *El Paso Co.:* 7.5 mi E City Hall, El Paso, 1 (KU); 19.4 mi E El Paso, 1 + chromosomes (MSB); 2.5 mi N Ysleta, 10 (UIMNH); 3 mi E Ysleta, 1 (MALB). CHIHUAHUA. 1 mi E Samalayucca, 1 (MVZ); 2.5 mi S, 2 mi W Samalayucca, 1 (KU); 10 mi SE Zaragosa, 1 (KU); Rio Casas Grandes, 9 mi N Nueva Casas Grandes, 1 (MSB); 1 mi E Rio Casas Grandes, 10 mi N Nueva Casas Grandes, 4 + chromosomes (MSB).

OTHER SPECIMENS EXAMINED

Perognathus fasciatus fasciatus.—Specimens examined, 33, distributed as follows: MONTANA. *Roosevelt Co.:* 9 mi SE Baineville, 4 (UMMZ). NORTH DAKOTA. *Billings Co.:* 1 mi S, 1 mi W Medora, 2,300 ft, 10 (KU). *Burleigh Co.:* 9 mi E Bismark, 5 (UMMZ). *Kidder Co.:* 6 mi W Steele, 6 (UMMZ). *Pembina Co.:* Weeks Farm, sec. 36, T160N, R56W, 1 (MSB). *Stutsman Co.:* 7 mi N Jamestown, 1 (UMMZ); 14 mi W Jamestown, 4 (UMMZ). SOUTH DAKOTA. *Todd Co.:* 15 mi W Mission, 1 (MSB). *Walworth Co.:* Molstad Lake Park, 1 (KU); Swan Creek, 13 mi S Selby, 1,600 ft, 1 (KU). NEBRASKA. *Cherry Co.:* Sparks, 1 (UMMZ); Ft. Niobrara Game Reserve, 1 (UNSM).

Perognathus fasciatus olivaceogriseus.—Specimens examined, 44, distributed as follows: MONTANA. *Carter Co.:* Ekalaka Hills, 4.5 mi S, 1 mi E Ekalaka, (MMNH). NEBRASKA. *Banner Co.:* 10 mi S, 2.5 mi E Gering, 3 (VMKSC). *Dawes Co.:* 1 mi SW Chadron, 1 (UNSM). *Sioux Co.:* 5.5 mi W Crawford, 6 (UNSM); 6 mi W Crawford, 1 (UNSM); Glenn, 1 (UNSM); 3 mi N Glenn, 2 (UNSM); 3.5 mi N, 1 mi E Glenn, 3 (UNSM); 8 mi W Ft. Robinson, 1 (UNSM). SOUTH DAKOTA. *Jackson Co.:* 7 mi SW Kadoka, 1 (MMNH). WYOMING. *Carbon Co.:* 1 mi E Ft. Steele, 13 (MSB), 2 + chromosomes (MSB). *Converse Co.:* Van Tassel Creek, 1 (CM). *Johnson Co.:* 2 mi S, 6.5 mi W Buffalo, 5,620 ft, 3 (KU). *Sheridan Co.:* 5 mi NE Clearmont, 3,900 ft, 1 (KU).

Perognathus fasciatus infraluteus.—Specimens examined, 7, distributed as follows: COLORADO. *El Paso Co.:* Air Force Academy, 10 mi N Colorado Springs, 4 (CAS); 6 mi N, 1 mi W Colorado Springs, 2 (UIMNH). *Huerfano Co.:* 4 mi S LaVeta, 7,000 ft, 1 (KU).

Perognathus fasciatus litus.—Specimens examined, 31, distributed as follows: WYOMING. *Natrona Co.:* 5 mi W Independence Rock, 6,000 ft, 4 (KU). *Sweetwater Co.:* 25.4 mi N Table Rock, 25 (MSB), 2 + chromosomes (MSB).

Perognathus fasciatus callistus.—Specimens examined, 30, distributed as follows: COLORADO. *Moffatt Co.:* N Bank Yampa River, 5 mi NW Cross Mountain, 1 (CM). *Rio Blanco Co.:* 16 mi W Meeker, 3 mi up Scenery Gulch (N of White River), 1 (CM). UTAH. *Dagget Co.:* 0.5 mi SW Clay Basin Camp, 6,300 ft, 2 (UU); Bridgeport, 1 (UU). *Uintah Co.:* West Rim, Dead Man Bench, opposite Leota Flats (W of Green River), 2 (CM); E Green River, 3 mi S Jensen, 1 (CM); 4.6 mi N Bonanza, 1 (MSB), 3 + chromosomes (MSB); Bonanza, 1 (UU); 1 mi S, 1.5 mi E Bonanza, 1 + chromosomes (MSB); 13.4 mi E Ouray, 1 + chromosomes (MSB). WYOMING. *Sweetwater Co.:* Kinney Ranch, 6,900 ft, 21 mi S Bitter Creek, 6 (KU); Kinney Ranch, 21 mi S Bitter Creek, 7,100 ft, 2 (MVZ); Kinney Ranch, sec. 8, T15N, R98W, 23 mi SW Bitter Creek, 1 (MVZ); Shell Creek, 25 mi S Bitter Creek, 5 (CM); Blacks Fork, opposite mouth, 5,930 ft, 1 (UU).

Perognathus flavescens flavescens.—Specimens examined, 90, distributed as follows: COLORADO. *Adams Co.:* Barr, 1 (UCM). *El Paso Co.:* Sandy Gulch, 2 mi E center Colorado Springs, 6,000 ft, 1 (UCM). *Washington Co.:* Akron, 5 (UMMZ); 8 mi W Akron, 1 (UMMZ). *Yuma Co.:* N of Wray, 2 (UCM). NEBRASKA. *Antelope Co.:* Clearwater, 1 (UMMZ); Neligh, 1 (MVZ), 1 (UNSM). *Banner Co.:* 10 mi S, 2.5 mi E Gering, 4 (VMKSC). *Cherry Co.:* Hackberry Lake, Valentine National Wildlife Refuge, 2 (KU), 18 (UMMZ); 4 mi E Valentine, 1 (KU); 2 mi E Valentine, 1 (KU); Kennedy, 5 (MVZ), 1 (UMMZ); 4 mi S Kennedy, 1 (UNSM); 2 mi E Kennedy, 3 (KU); 4 mi E Kennedy, 2 (KU); 18 mi NW Kennedy, 1 (UNSM); Niobrara River, 10 mi S Cody, 1 (UNSM); 11.5 mi S, 0.5 mi W Nenzel, 3,000 ft, 1 (VMKSC). *Custer Co.:* 1 mi S, 2 mi W Broken Bow, 2 (VMKSC). *Garden Co.:* Crescent Lake National Wildlife Refuge Headquarters, sec, 29, T21N, R44W, 3 (VMKSC); 0.75 mi E Crescent Lake National Wildlife Refuge Headquarters, sec. 29, T21N, R44W, 1 (VMKSC); 3 mi SE Crescent Lake National Wildlife Refuge Headquarters, 4 (VMKSC); 5 mi S Crescent Lake National Wildlife Refuge Headquarters, 1 (VMKSC). *Hooker Co.:* Kelso, 7 (UMMZ). *Kearney Co.:* 10 mi N, 1 mi E Axtell, 6 (VMKSC); 5 mi S, 2 mi E Kearney, 6 (VMKSC); Doby Town, 5 mi S, 3 mi E Kearney, 1 (VMKSC). *Keith Co.:* N side Kingsley Reservoir, 1 (UNSM). *Lincoln Co.:* 1 mi N Brady, 1 (UNSM); 2.5 mi N, 4.5 mi E North Platte, 1 (VMKSC). *Sheridan Co.:* 14 mi W Lakeside, 1 (MVZ). *Thomas Co.:* Halsey National Forest, 1 (VMKSC).

Perognathus flavescens perniger.—Specimens examined, 22, distributed as follows: IOWA. *Freemont Co.:* Randolph, 1 (UNSM). MINNESOTA. *Sherburne Co.:* Elk River, 1 (UCM), 5 (MVZ); Sand Dune State Park, 3 (MMNH); 6 mi E St. Cloud, 5 (UMMZ). SOUTH DAKOTA. *Bon Homme Co.:* 0.3 mi N, 0.3 mi E Springfield, 2 (MSB). *Clay Co.:* 1.5 mi N Vermillion, 3 (MSB); 1 mi W Vermillion, 1 (MSB); 3.5 mi N, 0.5 mi E Meckling, 1 (MSB).

Perognathus flavescens cockrumi.—Specimens examined, 5, distributed as follows: KANSAS. *Barber Co.:* 2 mi N, 2 mi W Sharon, 2 (SIUC). *Geary Co.:* Junction City, 1 (UCM). *Harvey Co.:* Section N of Harvey Co. Park, 2 (KSU).

Perognathus flavescens copei.—Specimens examined, 54, distributed as follows: NEW MEXICO. *Chaves Co.:* 3 mi N, 9 mi W Caprock, 4 (MSB), 3 + chromosomes (MSB); 7 mi E Hagerman, 1 (MSB). *Eddy Co.:* 1 mi N, 26.5 mi E Carlsbad, 2 (ENMU). *Lea Co.:* 29 mi E Carlsbad, 1 (ENMU); 3 mi S, 29 mi E Carlsbad, 2 (ENMU); 2.5 mi S, 31 mi E Carlsbad, 1 (ENMU); 7 mi N, 15 mi W Jal, 2 (MSB). *Quay Co.:* 2 mi S, 0.5 mi E Logan, 1 (MSB). *Roosevelt Co.:* 3.3 mi S Tolar, 3 + chromosomes (MSB); 3.25 mi N, 1 mi E Portales, 1 (ENMU); 9 mi S Portales, 1 (ENMU); 4.5 mi S, 3 mi W Portales, 1 (ENMU). *Union Co.:* Perico Creek, 4 mi S Clayton, 3 (MSB). OKLAHOMA. *Woods Co.:* Waynoka, 10 (UMMZ). TEXAS. *Andrews Co.:* 14 mi S Andrews, 3 (UMMZ). *Haskell Co.:* 7 mi SW Rochester, 1 (MWU). *Hemphill Co.:* Gene Howe Refuge, 5 mi NE Canadian, 1 (TCWC). *Loving Co.:* 11 mi E Mentone, 1 + chromosomes (MSB). *Roberts Co.:* 6 mi N Miami, 4 (MWU); 7 mi N Miami, 1 (MWU). *Scurry Co.:* 4 mi SW Snyder, 4 (MWU). *Ward Co.:* 4 mi NE Monahans, 1 (UIMNH). *Wheeler Co.:* 1 mi W Mobeetie, 2 (MVZ).

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JOHN E. GUILDAY
Associate Curator, Section of Vertebrate Fossils

HAROLD W. HAMILTON
Research Associate, Section of Vertebrate Fossils

ELAINE ANDERSON
730 Magnolia Street, Denver, Colorado 80220

PAUL W. PARMALEE
Department of Anthropology, University of Tennessee, Knoxville, 37916

with contributions by

CHARLES H. FAULKNER
Department of Anthropology, University of Tennessee, Knoxville 37916 (Archaeology)

FREDERICK C. HILL
Department of Biology, Bloomsburg State College, Bloomsburg, Pennsylvania 17815 (Fish)

GEORGE H. VAN DAM
The Museum, Michigan State University, East Lansing, Michigan 48823 (Amphibians and Reptiles)

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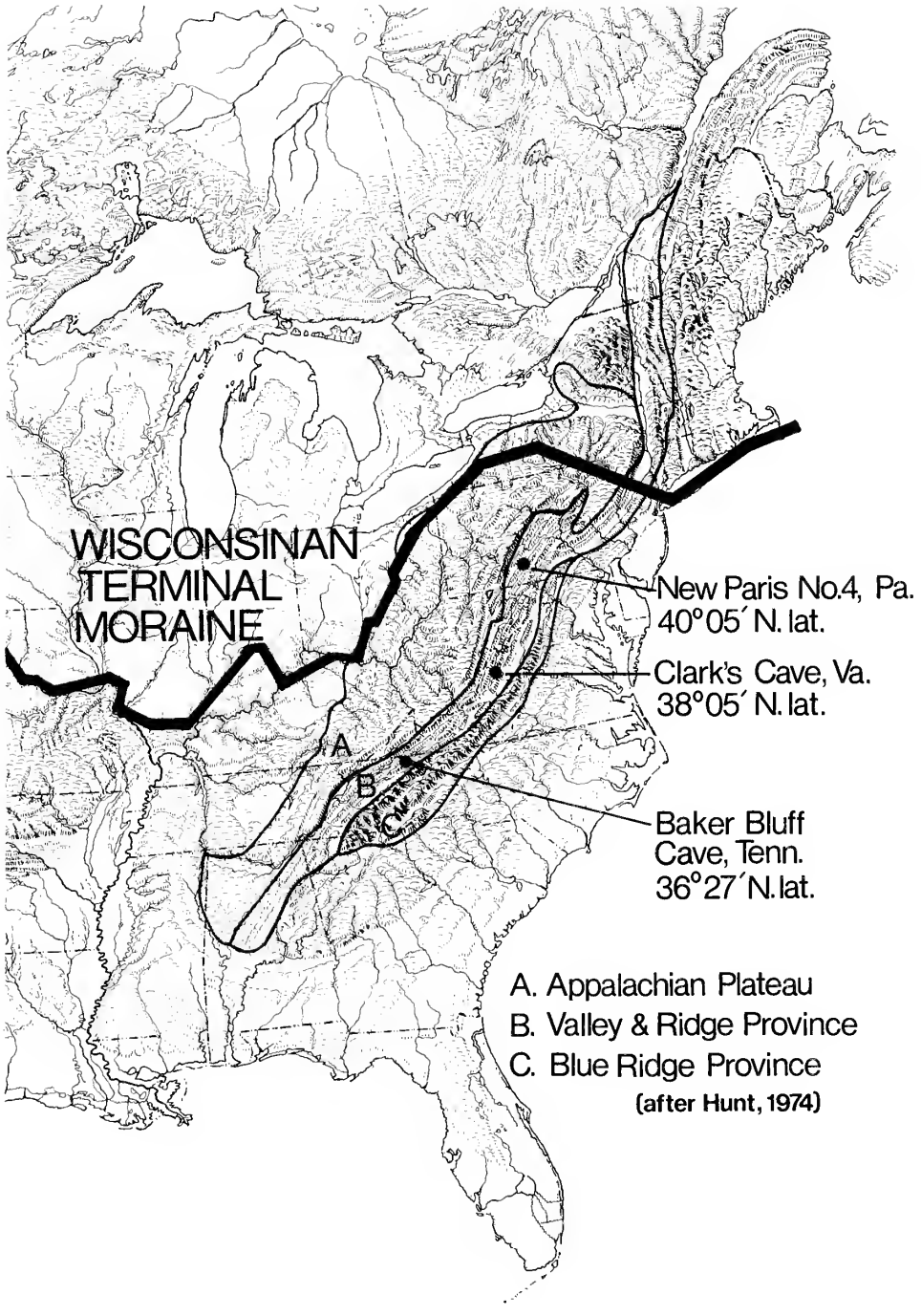

Fig. 1.—Location of three late Pleistocene cave paleofaunas, eastern USA (Base map Erwin Raisz, 1954).

ABSTRACT

Late Pleistocene remains of 180 taxa of vertebrates and invertebrates are reported from a 3 m (10 ft) column of fissure-fill, Baker Bluff Cave, Sullivan County, Tennessee, USA. Radiocarbon dates suggest deposition began about 19,100 years ago. Accompanying faunal sequence indicates a transition from cool-temperate in the lower levels to boreal open woodland in the upper levels. The Pleistocene/Holocene transition was not recorded. Evidence of human occupation from Early Archaic, 8,000 to 9,000 years BP, to the Historic period was present in the top 90 cm (3 ft) of the deposit. Pollen analysis was negative.

Six mammalian taxa are extinct—*Dasypus bellus, Castoroides ohioensis, Felis onca* cf. *augusta, Sangamona fugitiva, Platygonus compressus,* and *Tapirus* cf. *veroensis*; 16.6% of mammalian taxa are found only north or west of the site today; 15% have retreated to higher elevations. Evidence for the contemporaneity of two size classes of *Blarina brevicauda* is presented. One bird, cf. *Pica pica,* no longer occurs in the eastern U.S. The fauna is composed of eastern temperate, midwestern grassland, and boreal forest species, many now allopatric in distribution. No mammals of southerly distribution were present.

A 500 km north-south transect of the Ridge and Valley province comparing late Pleistocene and Recent mammal faunas indicates a steeper faunal gradient under current environmental conditions, but the late Pleistocene mammalian fauna was more boreal in character and richer in species, suggesting cooler but more equable conditions.

INTRODUCTION

The Site

Baker Bluff Cave, 13 km southeast of Kingsport, Sullivan County, is in northeastern Tennessee, 64 km west of the North Carolina border and 11 km south of the Virginia border (Fig. 1). It is perched high on a precipitous bluff overlooking the South Fork Holston River, a tributary of the Tennessee River, 5 km northwest, downstream from the junction of the South Fork Holston and Watauga Rivers, latitude 36°27′30″N, longitude 82°28′W, Boone Dam quadrangle U.S.G.S. 7½′ topographic map.

The cave is 90 m above the west bank of the river on the eastern face of Ayers Ridge, locally known as Baker Bluff, at an altitude of 450 m (Fig. 2). The cave is little more than a single large chamber approximately 10 m long and 3.6 m wide in vertically-bedded Cambrian dolomite. Prior to all excavations the cave floor was within 130 cm of the ceiling and the cave was little more than a crawlway (Figs. 3–4).

The regional landscape today is one of timbered ridges and rolling farmlands. The site lies near the southern end of the Ridge and Valley physiographic province (Atwood, 1940) and is in the Carolinian biotic province (Dice, 1943). At the time of European colonization an oak/chestnut (*Quercus/Castanea*) dominant, mixed mesophytic, closed-canopy woodland covered the land, interspersed with river meadows and sometimes extensive Indian clearings and fields in the major river valleys. Annual precipitation at Knoxville, 140 km SW of the site, is 119 cm (46.85 in); average temperature ranges from 4.6°C (40.3°F) in January to 25.5°C (77.9°F) in July; average last frost 30 March; average first frost 2 November, with a growing season of 217 days. Rainfall is prevalent throughout the year with a slight increase during spring and summer. Snow cover is light and rarely lingers (USDA Yearbook, 1941).

Excavation

The top 3 ft of cave deposit was excavated by private collectors S. D. Dean, Jr., Robert Wilson, and Larry Gardner in 1968, while searching for Indian artifacts. They guided Hamilton to the site 1 September 1969, and on the basis of a caribou *Rangifer tarandus* premolar from the original excavation it was decided to sample the site to a depth beyond that of their excavations. Excavation was recorded in feet and inches.

Dean, Wilson, and Gardner divided the cave floor into six 3 ft squares and excavated to a depth of 3 ft, in 6-inch levels. They saved Indian artifacts, large bone fragments, and the larger land snails. We were able to examine color slides of the archaeological material. Bones and snails were donated by Dean to Carnegie Museum of Natural History. Between 15–23 August 1970, Hamilton and party excavated an irregular shaft 4 ft by 3 ft by 7 ft deep. It began at the base of the Dean excavation 3 ft below the original floor of the cave and extended to the limits of fossiliferous matrix approximately 10 ft below the original cave floor.

A description of the surficial deposits is not now possible. A rim-fire .22 cartridge case, a scorched opossum vertebra indicating at least one fire, and Indian cultural material to a depth of 3 ft suggested considerable disturbance. This disturbed material was described to us as "dark organic to dark brownish-red at the 3-foot level." Below the level of the Dean excavation the matrix changed abruptly in character. Directly in the present entrance and slightly behind it, was a plug of dry, coarsely indurated, light yellow-tan "cave clay," possibly the back-slope of a former entrance cone built by slope-wash at a time when the entrance was more extended. No inclusions other than modern tree roots were noted. Directly behind this non-fossiliferous deposit and extending down 10 ft from the original cave floor was a dark red-brown to yellow partially indurated matrix rich in bone fragments, snails, and hackberry seeds. Frost-spalled dolomite fragments and an occasional broken speleothem occurred at all levels but increased slightly in number with depth. There were no obvious stratigraphic changes in color or texture. No evidence of water action or river

Fig. 2.—Baker Bluff (Ayers Ridge), 13 km SE Kingsport, Sullivan County, Tennessee. South Fork Holston River, flowing to the right, in middle foreground. Arrow points to concealed entrance of Baker Bluff Cave. Hamilton photograph.

pebbles was noted. As the excavation proceeded sterile cave fill encroached from the cave side of the deposit and at 10 ft the fossiliferous material pinched out. Little, if any, is believed to be left *in situ* at the site.

Preservation at all levels was chemically good but mechanically poor. Large mammals were represented by isolated teeth or heavily rodent-gnawed bone fragments. Thousands of complete or fragmentary small vertebrate bones were recovered, but no skeletons were found in articulation. Skulls of woodrats (*Neotoma*) were occasionally complete. Mammal identifications are based mostly upon isolated teeth or mandible fragments containing teeth. All bird remains were fragmentary. Snake vertebrae survived better than most bone because of their small size and compact structure. Gastropod remains were often complete at all levels and probably represented individuals that died *in situ*.

The site throughout its history was a nesting area for rodents,

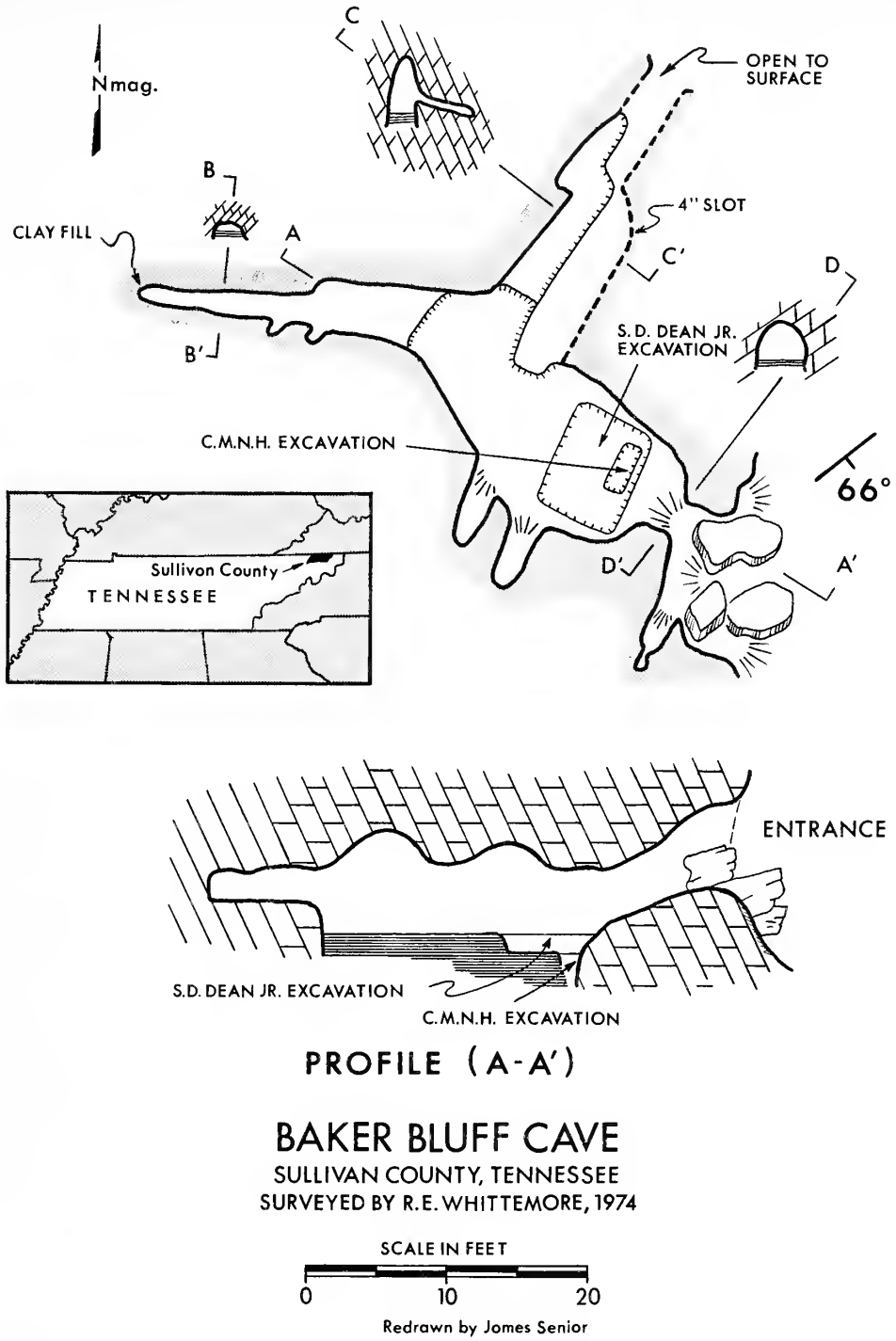

Fig. 3.—Survey plan of Baker Bluff Cave, Sullivan County, Tennessee, showing location of excavations.

primarily *Neotoma* and *Peromyscus*. Unlike rodent middens in the arid West (Wells, 1976; King and Van Devender, 1977) where plants remains are well preserved, most plant tissues and pollen had decayed in this humid eastern environment, leaving a lag deposit of bones, teeth, snails, and hackberry (*Celtis*) seeds. Woodrats were probably responsible for the large mammal remains—isolated teeth and heavily-gnawed bone fragments. Raptors, primarily owls, were responsible for the bulk of the small vertebrates in the deposit. All gastropods and some *Neotoma* probably died *in situ*, and the site may have served as a hibernaculum or shelter

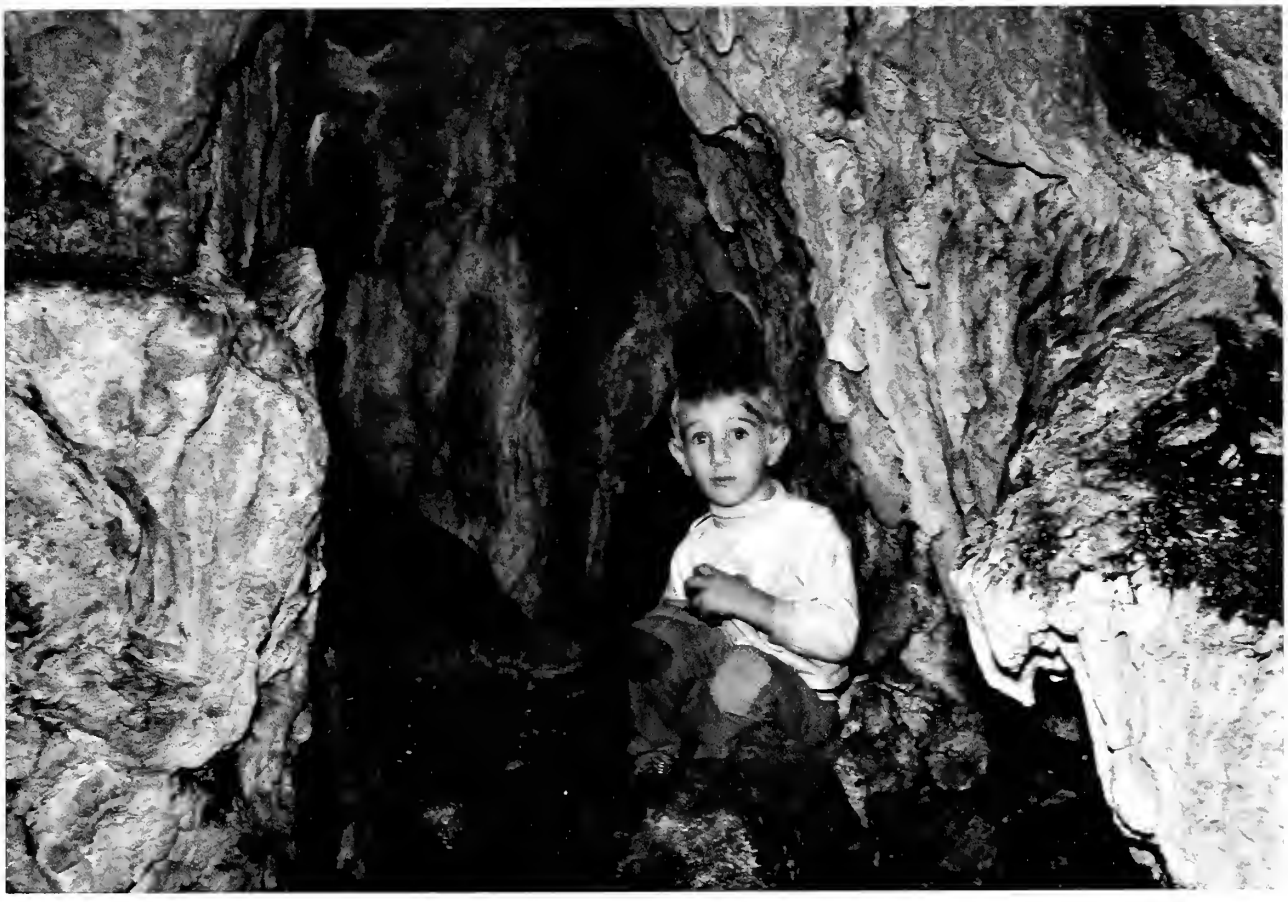

Fig. 4.—Allen Hamilton sitting on original cave floor level, view facing NW taken from entrance of Baker Bluff Cave, Sullivan County, Tennessee. Note edge of CMNH excavation at his feet. Hamilton photograph.

for snakes. Bones of a variety of Recent mammals from the upper 3 ft of the deposit were, in part, introduced by Indians as aboriginal food items.

Procedure

Matrix from each 1 ft level was dry-screened through a ¼ in. (5 mm) grid, and water-screened at the New Paris, Pennsylvania, field laboratory through 1 mm window screening to recover the finer fraction. It is felt that recovery of all fossil materials greater than 1 mm in diameter was total. Specimens are catalogued by stratigraphic levels in the Section of Vertebrate Fossils, Carnegie Museum of Natural History. Minimum number of individuals (MNI) was estimated for each level by counting the commonest replicable element for a given species, usually, but not always, teeth. Summing MNI by stratigraphic levels often results in a larger site total than if specimens from all levels were pooled before calculating MNI. This is true of large mammals represented by widely scattered identifiable elements, deer teeth, for instance, but not necessarily true of small vertebrates and invertebrates, which are either not as highly fragmented or whose MNI is based upon one specific element, such as the M_1, in the case of the small rodents.

Measurements less than 1 cm were taken with a Spencer Cycloptic stereoscopic microscope using an ocular grid at 10×. Larger measurements were taken with a dial micrometer calibrated to 0.1 mm.

Abbreviations in this paper are: BP—before present; CM and CMNH—Carnegie Museum of Natural History; MNI—minimum number of individuals. Dental abbreviations are: I—incisor; C—canine; P—premolar; M—molar; d preceding tooth—deciduous. Tooth position indicated by super- and subscripts. Sites repeatedly referred to throughout the text are: Natural Chimneys, Virginia (Guilday, 1962); New Paris No. 4, Pennsylvania (Guilday et al., 1964); Robinson Cave, Tennessee (Guilday et al., 1969); Welsh Cave, Kentucky (Guilday et al., 1971); and Clark's Cave, Virginia (Guilday et al., 1977).

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PREHISTORIC CULTURAL MATERIAL

CHARLES H. FAULKNER

Eleven chipped stone artifacts were found in the top 3 ft of the cave fill by Dean, Wilson, and Gardner. Whether this represents the total lithic assemblage is not known, because no chipping debris from tool manufacturing was included in this collection. It is likely that some debitage was present but was not saved by the excavators. The excavators reported no features, pottery or charcoal in the upper fill, which would imply that the cave was occupied for extremely short periods of time. Food bone fragments are discussed elsewhere. One partially charred caudal vertebra of an opossum from the 0–6 in. level suggests at least one fire.

Unfortunately, the chipped stone artifacts were not available for the writer to examine, and their description in this report is based on the examination of color prints and slides of fair quality. The excavators reported that the artifacts were originally typed by James Cambron. The writer concurs with some of Cambron's identifications but disagrees with others. Based on the various limitations of this study, any conclusions should be considered tentative.

The excavated area was laid out in a 3 ft grid. At least six "squares" were excavated, presumably all to the 3 ft level. The earth was removed in arbitrary 0.5 ft cuts and the provenience of the artifacts was given by square number and level.

Two artifacts came from the deepest level (2.5 ft–3.0 ft). These are a side-notched bifurcated base projectile point (Fig. 5c) and a small stemmed biface with an asymmetrical blade (Fig. 5g), the latter being tentatively identified as a knife. Both artifacts are made from a dark gray or black chert. All of the artifacts except one appear to be made from this material. Although it is impossible to positively identify this chert in the photographs, it is probably the so-called "black flint" which occurs as small nodules in the shaley limestones of the eastern Tennessee Valley. This material ranges in color from black to opaque gray (Kellberg, 1963).

The projectile point was identified by Cambron as a *LeCroy* type (Kneberg, 1956). While the bifurcated base of the specimen would certainly seem to place it into the cluster of Early Archaic bifurcated base projectile points that have been reported in the Appalachian uplands from Tennessee to West Virginia, the artifact does not really conform to the classic *LeCroy* type and if anything, might be more like the *St. Albans Side Notched* (Broyles, 1966). However, given the method of analysis, no specific type name should be assigned to this artifact. It can only be identified as an Early Archaic projectile point, probably dating between 6,000–7,000 B.C. in the Eastern Tennessee Valley. The depth of occurrence would seem to substantiate this early placement.

The 2.0 ft–2.5 ft level produced four artifacts from three squares. These include two artifacts identified as projectile points. One of these projectile points (Fig. 5d) had been classified as a *Brewerton Side Notched* (Ritchie, 1961). While this artifact could fall within the range of this Northeastern type, the Brewerton series of projectile points have never been identified in the upper Tennessee Valley. The artifact also appears to resemble the bifurcated base type recovered in the lowest level. While the depth of recovery could indicate it is another Early Archaic artifact, the most prudent conclusion is that it is sim-

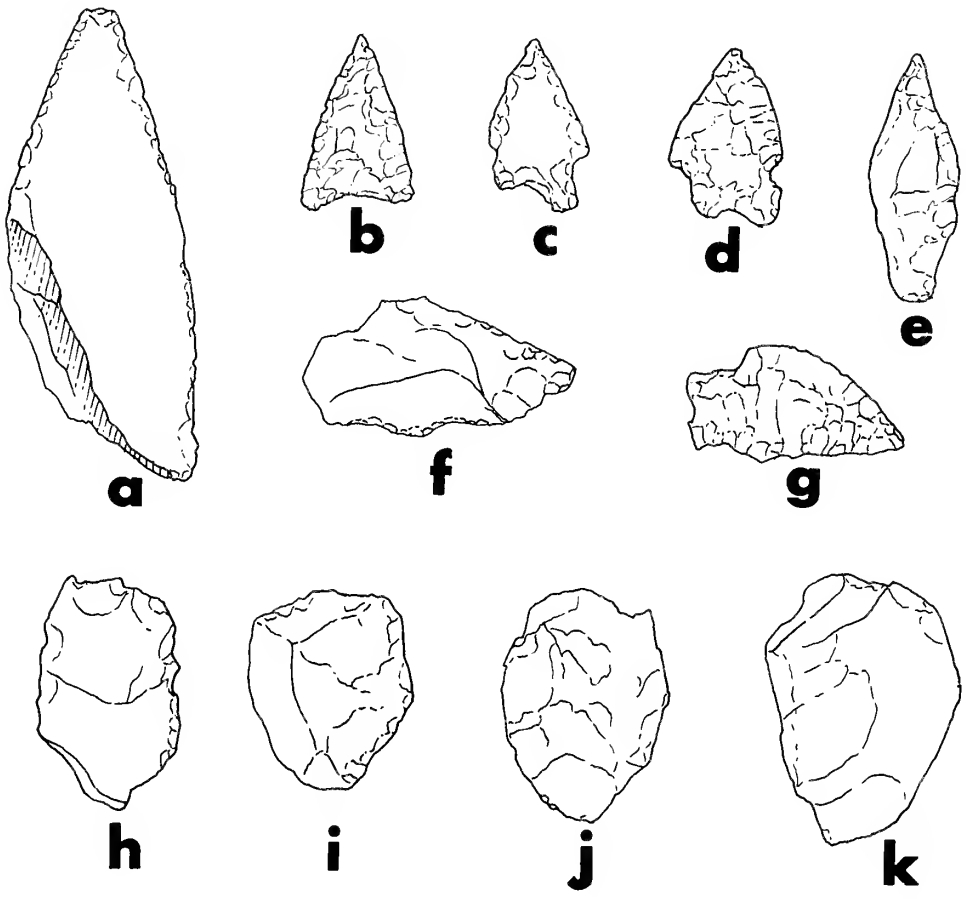

Fig. 5.—Flaked stone artifacts from 0–3 ft level of Baker Bluff Cave, Sullivan County, Tennessee, S. D. Dean, Jr., and R. Wilson private collection. a) Quartzite projectile point "Savannah River type"; b) "Madison" projectile point; c) "LeRoy" projectile point; d) "Brewerton" projectile point; e) "Mt. Fork" projectile point (typology provided by Dean, see Faulkner discussion this paper); f) side-scraper; g) Archaic stemmed curved knife; h) uniface scraper; i–k) oval scrapers. Drawing by E. Hansen from photographs supplied by Dean.

ply an Archaic type. The other projectile point from this level (Fig. 5e) was identified as a *Mountain Fork* which is considered to date from the Middle to Late Woodland periods in Alabama (Cambron and Hulse, 1964). While this spike-shaped artifact may generally conform to the *Mountain Fork* type, the present writer would not place it into any named type and would assign it to an Archaic horizon in the cave. The apparently retouched blade could also indicate this was a specialized tool type such as a perforator.

Two additional implements were recovered in this level. These were previously identified as an "oval" scraper (Fig. 5j) and a uniface scraper (Fig. 5h). The writer will have to assume the latter was actually examined since the lack of retouch on the ventral surface of the flake is not apparent in the photograph. Because the writer did not examine these tools it is impossible to assign a definite function to them although their crude shape suggests they were probably used for generalized scraping or cutting tasks.

No projectile points were found in the 1.5 ft–2.0 ft level. Artifacts from this level have been identified as a side scraper and two oval scrapers. The former (Fig. 5f) appears to be simply a utilized flake, whereas the latter two crude implements (Fig. 5i and Fig. 5k) seem to exhibit bifacial flaking and retouched edges.

Only two additional artifacts were recovered in the top 1.5 ft of the cave floor. Both occurred above the 1 ft level. A stemless triangular projectile point which Cambron identified as a *Madison* type (Scully, 1951) was found in the 0.5 ft–1.0 ft level (Fig. 5b). Although the shape generally conforms to this type, the thickness and incurvate base is more reminiscent of such Early-Middle Woodland types in the upper Tennessee Valley as the *Greenville* and *Nolichucky*

(Kneberg, 1957). In any case, this is certainly a Woodland artifact. The other worked piece is the distal end of a large biface made of quartzite (Fig. 5a). Although it is possible this is a large broken Late Archaic projectile point or knife such as the *Appalachian Stemmed* (Kneberg, 1957) or *Savannah River Stemmed* (Coe, 1964), the fragmentary nature of this artifact precludes such a precise identification. It was found in the 0.0 ft–0.5 ft level of the cave floor.

The 11 artifacts described above indicate Baker Bluff Cave was periodically occupied by several different prehistoric Indian groups. The presence of projectile points, scraping and cutting tools, and food bone fragments indicate they probably used it as a short-term hunting and butchering station. Because the artifacts were not examined by the writer, a precise typology is impossible. It is also probable that they do not represent all of the human derived material deposited there. If this is a representative collection, however, and the tentative typology from the photographs is reasonably accurate, Baker Bluff Cave was first occupied by prehistoric Indians during the Early Archaic period, between 6,000–7,000 B.C. The cave continued to be utilized intermittently through the Late Archaic and Early Woodland periods. There is no evidence that it was occupied by Indians during the late prehistoric or historic periods. Perhaps the change in subsistence and settlement systems during these periods, or more likely the filling of the cave to within 4 ft of the ceiling, finally caused the Indians to abandon it as a temporary camping site.

Table 1.—*Faunal list Baker Bluff Cave, Sullivan County, Tennessee. Superscript*[1] *= extinct;* [2] *= no longer present at site; ? = no observation; * = present but not tallied; MNI = minimum number of individuals.*

Taxon	Depth in feet from surface								MNI
	0–3	3–4	4–5	5–6	6–7	7–8	8–9	9–10	
Mollusca Class Gastropoda (snails) (identified by L. Hubricht)									
Helicinidae									
Helicina orbiculata (Say)	?	—	—	—	1	—	—	—	1
Hedersonia occulta (Say)	?	2	1	1	5	4	4	5	22
Cionellidae									
Cionella lubrica (Muller)	?	—	4	4	5	2	6	9	30
Valloniidae									
Vallonia parvula (Sterki)	?	1	—	—	—	—	—	1	2
Pupillidae									
Gastrocopta armifera (Say)	?	1	3	4	3	—	1	2	14
Gastrocopta contracta (Say)	?	—	—	—	—	—	—	1	1
Gastrocopta corticaria (Say)	?	—	2	—	—	—	1	—	3
Strobilopsidae									
Strobilops labyrinthica (Say)	?	2	—	—	7	—	8	6	23
Succineidae									
Succinea ovalis (Say)	?	—	—	—	—	2	2	—	4
Catinella sp.	?	1	—	1	—	—	—	—	2
Endodontidae									
Anguispira alternata (Say)	?	—	—	—	2	—	1	—	3
Anguispira strongylodes (Pfeiffer)	143	37	45	40	25	7	7	11	315
Discus patulus (Lesh.)	?	2	5	8	6	2	5	3	31
Discus bryanti (Harper)	?	—	1	—	8	4	11	3	27
Discus catskillensis (Pilsbry)	?	4	9	13	—	—	—	3	29
Helicodiscus multidens (Hubricht)	?	3	3	13	7	—	5	4	35
Helicodiscus parallelus (Say)	?	3	—	5	—	—	—	1	9
Helicodiscus singleyanus (Pilsbry)	?	13	4	3	13	—	4	8	45
Helicodiscus inermis (H. B. Baker)	?	200	75	75	150	50	200	50	800

Table 1.—*Continued.*

Taxon	Depth in feet from surface 0–3	3–4	4–5	5–6	6–7	7–8	8–9	9–10	MNI
Zonitidae									
Glyphyalinia wheatleyi (Bland)	?	—	—	5	2	—	1	1	9
Glyphyalinia lewisiana (Clapp)	?	16	19	50	9	2	8	15	119
Glyphyalinia caroliniensis (Ckll.)	?	2	2	3	2	—	—	—	9
Glyphyalinia solida (H. B. Baker)	?	—	—	—	—	—	2	3	5
Mesomphix capnodes (W.G.B.)	6	3	—	1	9	2	1	—	22
Paravitrea multidentata (Binney)	?	—	—	—	—	—	—	2	2
Paravitrea tridens Pilsbry	?	3	10	3	1	—	—	1	18
Paravitrea blarina (Hubricht)	?	1	—	2	—	—	1	—	4
Hawaiia minuscula (Binney)	?	16	14	35	16	—	14	25	120
Euconulus fulvus (Muller)	?	—	—	1	—	—	—	1	2
Gastrodonta interna fonticula (Wurtz)	?	—	—	—	1	—	3	2	6
Ventridens pilsbryi (Hubricht)	?	—	—	—	3	4	6	5	18
Ventridens coelaxis (Pilsbry)	?	—	—	2	2	—	3	2	9
Ventridens demissus (Binney)	?	—	1	—	1	—	—	—	2
Zonitoides arboreus (Say)	?	5	13	7	2	1	2	5	35
Haplotrematidae									
Haplotrema concavum (Say)	?	1	—	2	—	—	1	—	4
Polygyridae									
Polygyra plicata (Say)	?	1	—	12	11	—	1	3	28
Stenotrema spinosum (Lea)	?	—	—	1	2	—	—	1	4
Stenotrema stenotrema (Pfeiffer)	?	—	3	6	1	—	1	2	13
Stenotrema, undescribed species	?	1	—	1	1	1	4	3	11
Stenotrema fraternum fasciatum (Pilsbry)[2]	?	—	—	—	1	—	2	—	3
Mesodon clausus clausus (Say)	?	1	—	1	1	—	—	—	3
Mesodon elevatus (Say)	?	1	—	1	1	—	—	—	3
Mesodon appressus (Say)	422	26	41	33	35	2	9	9	577
Mesodon inflectus (Say)	20	1	—	3	1	3	—	1	29
Mesodon rugeli (Shutt.) small	?	1	—	9	6	1	—	3	20
Mesodon rugeli large	?	—	1	—	2	—	—	—	3
Triodopsis tridentata (Say)	3	—	—	4	17	2	3	1	30
Triodopsis tridentata tenneseensis (Walker)	3	—	—	—	—	—	—	—	3
Triodopsis vulgata (Pilsbry)	?	1	1	1	—	1	—	—	4
Triodopsis denotata (Fer.)	1	—	—	1	1	—	—	—	3
Triodopsis albolabris (Say)	48	3	1	4	2	2	—	3	63
Allogona profunda (Say)	?	3	—	2	2	—	—	1	8
Amnicolidae									
Pomatiopsis lapidaria (Say)	?	—	1	—	—	1	7	1	10
Pomatiopsis cincinnatiensis (Lea)	?	—	—	—	1	—	—	—	1
Pleroceridae									
Io fluviatilus	1	—	—	—	—	—	—	—	1
Class Bivalvia (freshwater mussels)									
Unionidae, sp.	3	—	—	—	—	—	—	—	3
Vertebrata Class Pisces (identified by F. Hill) Order Semionotiformes									
Lepisosteidae									
Lepisosteus sp.—gar	?	—	—	*	—	—	—	—	*
Order Salmoniformes									
Esocidae									
Esox sp.—pike or pickerel	?	*	—	*	—	—	—	—	*

Table 1.—*Continued.*

Taxon	Depth in feet from surface								MNI
	0–3	3–4	4–5	5–6	6–7	7–8	8–9	9–10	
Order Cypriniformes									
Cyprinidae—Cyprinids, unidentified minnows	*	*	*	*	*	*	—	*	*
Catostomidae									
Catostomus commersoni—white sucker	?	—	—	*	*	—	—	—	*
Hypentelium nigricans—northern hog sucker	?	—	—	*	—	—	—	—	*
Moxostoma carinatum—river redhorse	?	—	—	—	*	—	—	—	*
Moxostoma cf. *duquesnei*—black redhorse	?	—	—	*	—	—	—	—	*
Moxostoma erythrurum—golden redhorse	?	*	*	*	—	—	—	—	*
Moxostoma sp.—redhorse, unidentified	?	*	*	*	*	*	*	*	*
Order Siluriformes									
Ictaluridae									
Ictalurus punctatus—channel catfish	?	—	—	*	*	—	—	—	*
Ictalurus sp.—catfish, unidentified	?	—	*	—	—	—	—	—	*
Noturus sp.—madtom or stonecat	?	—	*	—	—	—	—	*	*
Order Perciformes									
Centrarchidae									
Ambloplites rupestris—rock bass	?	*	*	—	—	—	*	—	*
Micropterus dolomieui—smallmouth bass	?	—	—	*	—	—	—	—	*
Micropterus sp.—bass, unidentified	?	—	*	—	—	—	—	—	*
Percidae									
Stizostedion canadense—sauger	?	*	—	—	—	—	—	—	*
Stizostedion sp.	?	*	*	*	*	—	*	—	*
Sciaenidae									
Aplodinotus grunniens—freshwater drum	?	*	*	*	*	*	*	*	*
Class Amphibia (identified by G. Van Dam) Order Anura									
Bufonidae									
Bufo americanus—American toad	?	12	24	10	7	2	2	3	60
Bufo w. fowleri—Fowler's toad	?	3	3	1	—	—	—	—	7
Bufo sp.—toad	?	4	15	4	1	1	2	—	27
Hylidae									
Hyla sp.—tree frog	?	1	—	—	—	—	—	—	1
Ranidae									
Rana sylvatica—wood frog	?	5	6	8	3	—	—	2	24
Rana catesbeiana—bullfrog	?	—	1	—	—	—	—	—	1
Rana sp.	?	3	2	2	1	—	1	—	9
Order Urodela									
Ambystomatidae									
Ambystoma opacum—marbled salamander	?	—	1	1	1	—	1	—	4
Ambystoma maculatum—spotted salamander	?	—	1	1	1	—	—	—	3
Ambystoma sp.	?	1	1	1	1	1	1	1	7
Proteidae									
Necturus maculosus—mudpuppy	?	1	1	1	1	1	1	—	6
Cryptobranchidae									
Cryptobranchus alleganiensis—hellbender	?	1	1	1	1	1	—	1	6
Plethodontidae									
Desmognathus sp.—dusky salamander	?	1	1	1	1	1	1	—	6

Table 1.—*Continued.*

Taxon	Depth in feet from surface 0–3	3–4	4–5	5–6	6–7	7–8	8–9	9–10	MNI
Class Reptilia (identified by G. Van Dam) Order Testudines									
Emydidae									
Graptemys geographica—map turtle	?	—	1	—	—	—	—	—	1
Order Squamata									
Scincidae									
Eumeces fasciatus—five-lined skink	?	1	1	—	1	—	—	—	3
Viperidae									
Crotalus horridus—timber rattlesnake	1	1	1	1	1	1	1	1	8
Colubridae									
Heterodon platyrhinos—eastern hognose snake	?	—	—	1	1	—	1	—	3
Diadophis punctatus—ringneck snake	?	1	1	1	—	—	—	—	3
Carphophus amoenus—worm snake	?	1	1	—	—	—	—	—	2
Coluber or *Masticophis* sp.—racer or coachwhip	?	—	1	1	1	1	1	—	5
Lampropeltis triangulum—eastern milksnake	?	1	1	1	1	1	1	—	6
Lampropeltis getulus—kingsnake	?	1	1	1	—	—	1	—	4
Elaphe sp.—rat snake	?	—	—	—	1	—	—	—	1
Natrix sipedon—water snake	?	1	1	1	—	—	—	—	3
Natrix sp.	?	—	—	—	1	—	—	—	1
Thamnophis sirtalus—garter snake	?	1	1	1	1	—	—	—	4
Thamnophis sauritus—ribbon snake	?	1	1	—	—	—	1	—	3
Thamnophis sp.	?	1	1	1	1	—	1	1	6
Class Aves (identified by P. Parmalee) Order Podicipediformes									
Podicipedidae sp.—grebes	?	—	1	—	—	—	—	—	1
Order Anseriformes									
Anatidae									
cf. *Anas crecca*—green-winged teal	?	1	—	—	—	—	—	—	1
Anas sp.—duck	?	1	1	1	—	—	—	—	3
Mergus sp.—merganser	?	—	1	—	—	—	—	—	1
Lophodytes cucullatus—hooded merganser	?	1	1	1	—	—	—	1	4
Order Falconiformes									
Accipitridae									
Accipiter gentilus—goshawk	?	—	—	—	—	1	—	—	1
Accipitridae sp.—hawk	?	—	2	1	—	—	—	—	3
Falconidae									
Falco sparverius—kestrel	?	1	1	1	—	—	—	—	3
Order Galliformes									
Tetraonidae									
cf. *Bonasa umbellus*—ruffed grouse	4	3	2	2	—	—	—	—	11
Tetraonidae sp.—grouse	?	1	6	—	1	—	1	1	9
Meleagrididae									
Meleagris gallopavo—turkey	1	—	—	1	—	—	—	—	2
Phasianidae									
Gallus gallus—chicken	1	—	—	—	—	—	—	—	1

Table 1.—*Continued.*

Taxon	Depth in feet from surface								MNI
	0–3	3–4	4–5	5–6	6–7	7–8	8–9	9–10	
Order Charadriiformes									
Charadriidae									
cf. *Arenaria interpres*—ruddy turnstone	?	—	—	—	1	—	—	—	1
Scolopacidae									
Philohela minor—woodcock	?	2	1	—	—	—	—		3
Capella gallinago—common snipe	?	1	—	—	—	—	—	—	1
cf. *Actitis macularia*—spotted sandpiper	?	—	1	—	—	—	—	—	1
Scolopacidae spp.	?	—	6	6	1	—	—	—	13
Laridae									
Larus sp.—gull	?	1	—	—	—	—	—	—	1
Order Columbiformes									
Columbidae									
Ectopistes migratorius—passenger pigeon	8	10	23	11	5	1	1	1	60
Order Strigiformes									
Strigidae									
Bubo virginianus—great horned owl	?	—	1	—	—	—	—	—	1
Otus asio—screech owl	*	—	—	—	—	—	—	—	1
Order Caprimulgiformes									
Caprimulgidae									
cf. *Chordeiles minor*—common nighthawk	?	1	—	—	—	—	—	—	1
Order Apodiformes									
Apodidae									
Chaetura pelagica—chimney swift	?	—	—	—	—	—	—	1	1
Order Coraciiformes									
Alcedinidae									
Megaceryle alcyon—kingfisher	?	1	1	2	—	—	—	—	4
Order Piciformes									
Picidae									
Colaptes auratus—common flicker	?	1	1	1	2	—	—	—	5
Picidae sp.	?	2	1	—	—	1	—	—	4
Order Passeriformes									
Tyrannidae									
Empidonax sp.—flycatcher	?	1	—	—	—	—	—	—	1
Hirundinidae									
Petrochelidon pyrrhonota—cliff swallow	?	—	—	—	—	1	—	—	1
Corvidae									
Cyanocitta cristata—blue jay	?	1	—	—	1	—	—	—	2
cf. *Pica pica*—black-billed magpie	?	—	—	—	1	—	—	—	1
Turdidae									
cf. *Turdus migratorius*—robin	?	—	1	—	—	—	—	—	1
Parulidae sp.—warblers	?	—	—	—	1	—	—	—	1
Icteridae									
cf. *Agelaius phoeniceus*—red-winged blackbird	?	1	—	—	—	—	—	—	1
Fringillidae sp.—sparrow	?	—	1	—	—	—	—	—	1
Passeriformes sp.	?	6	4	4	3	—	1	3	21

Table 1.—*Continued.*

Taxon	Depth in feet from surface 0–3	3–4	4–5	5–6	6–7	7–8	8–9	9–10	MNI
Class Mammalia (identified by J. Guilday and E. Anderson)									
Order Marsupialia									
Didelphidae									
Didelphis virginiana—Virginia opossum	1	—	—	—	—	—	—	—	1
Order Insectivora									
Soricidae									
Blarina brevicauda—short-tailed shrew	?	15	20	40	31	6	24	13	149
Cryptotis parva—least shrew	?	1	2	—	—	—	—	—	3
Microsorex hoyi[2]—pygmy shrew	?	2	5	2	—	—	—	—	9
Sorex arcticus[2]—arctic shrew	?	1	1	1	—	—	—	—	3
Sorex cinereus—masked shrew	?	9	19	16	5	—	2	2	53
Sorex dispar[2]—rock shrew	?	4	3	2	—	—	—	—	9
Sorex fumeus—smoky shrew	?	2	6	6	6	1	—	1	22
Sorex fumeus or *arcticus*	?	—	4	5	3	—	—	—	12
Sorex cinereus or *dispar*	?	—	11	5	2	—	—	—	18
Talpidae									
Condylura cristata—star-nosed mole	?	1	2	—	—	—	—	—	3
Scalopus aquaticus—eastern mole	1	1	1	3	1	2	2	1	12
Parascalops breweri—hairy-tailed mole	1	2	2	4	3	1	3	1	17
Order Chiroptera									
Vespertilionidae									
Myotis sp.—little brown bats	?	3	4	6	3	—	1	1	18
Pipistrellus subflavus—eastern pipistrelle	?	—	2	1	1	—	1	2	7
Eptesicus fuscus—big brown bat	?	2	3	9	2	1	1	1	19
Nycticeius humeralis—evening bat	?	—	—	—	—	—	1	—	1
Plecotus sp.—big-eared bats	?	—	—	1	—	—	—	—	1
Order Edentata									
Dasypodidae									
Dasypus bellus[1]—"beautiful" armadillo	?	*	*	*	*	—	*	—	1
Order Lagomorpha									
Leporidae									
Sylviagus or *Lepus*—rabbits or hares	*	11	20	22	17	7	10	8	95
Order Rodentia									
Sciuridae									
Tamias striatus—eastern chipmunk	?	3	2	9	4	1	5	3	27
Eutamias minimus[2]—least chipmunk	?	1	2	—	—	—	—	—	3
Marmota monax—woodchuck	1	3	6	5	2	1	3	2	23
Spermophilus tridecemlineatus[2]—thirteen-lined ground squirrel	1	4	10	8	2	1	1	1	28
Sciurus carolinensis—gray squirrel	1	—	2	4	3	1	3	3	17
Tamiasciurus hudsonicus—red squirrel	1	3	6	3	2	1	1	1	18
Glaucomys volans—southern flying squirrel	1	—	1	1	—	—	2	2	7
Glaucomys sabrinus[2]—northern flying squirrel	?	3	5	3	1	1	—	—	13
Castoridae									
Castor canadensis—beaver	—	—	1	—	1	—	1	—	3
Castoroides ohioensis[1]—giant beaver	1	—	—	—	—	—	—	—	1
Cricetidae									
Peromyscus maniculatus or *P. leucopus*—white-footed mice	?	8	26	24	18	2	8	8	94
Neotoma floridana—eastern woodrat	*	23	62	52	46	13	31	33	260

Table 1.—*Continued.*

Taxon	Depth in feet from surface								MNI
	0–3	3–4	4–5	5–6	6–7	7–8	8–9	9–10	
Arvicolidae									
Clethrionomys gapperi[2]—southern red-backed vole	?	32	70	43	7	—	1	6	159
Phenacomys intermedius[2]—heather vole	?	12	31	15	5	—	—	1	64
Microtus chrotorrhinus[2]—rock vole	?	7	18	7	4	—	1	—	37
Microtus pennsylvanicus—meadow vole	?	18	35	22	3	1	1	4	84
M. chrotorrhinus or *pennsylvanicus* (total figure includes identified *M. chrotorrhinus* and *M. pennsylvanicus*)	?	58	62	42	10	2	4	8	186
Microtus xanthognathus[2]—yellow-cheeked vole	?	1	1	1	1	—	—	—	4
Microtus pinetorum and/or *M. ochrogaster*—woodland vole and/or prairie vole	?	28	81	93	37	5	17	21	282
Ondatra zibethicus—muskrat	*	2	1	—	1	—	—	—	4
Synaptomys cooperi—southern bog lemming	?	27	71	43	15	3	17	15	191
Synaptomys borealis[2]—northern bog lemming	?	2	3	3	3	—	1	—	12
Zapodidae									
Zapus hudsonius—meadow jumping mouse	?	—	1	1	—	—	—	—	2
Napaeozapus insignis[2]—woodland jumping mouse	?	1	1	1	1	—	—	—	4
Erethizontidae									
Erethizon dorsatum[2]—porcupine	?	1	1	1	—	—	—	—	3
Order Carnivora									
Canidae									
Vulpes vulpes—red fox	?	—	—	1	1	—	—	1	3
Urocyon cinereoargenteus—gray fox	*	—	—	—	—	—	—	—	1
Ursidae									
Ursus americanus—black bear	*	1	1	—	—	—	—	1	4
Procyonidae									
Procyon lotor—raccoon	*	—	—	1	1	—	1	1	5
Mustelidae									
Martes americana[2]—marten	?	2	1	—	—	—	—	1	4
Martes pennanti[2]—fisher	?	(1)		—	—	—	—	—	1
Mustela nivalis—least weasel	?	1	2	1	—	—	—	—	4
Mustela frenata—long-tailed weasel	?	—	1	2	—	—	2	1	6
Taxidea taxus[2]—badger	—	—	—	depth unknown		—	—	—	1
Spilogale putorius—eastern spotted skunk	?	1	—	—	1	—	1	1	4
Mephitis mephitis—striped skunk	*	—	—	—	—	—	—	—	1
Felidae									
Felis onca—jaguar	?	—	—	—	—	—	—	1	1
Order Artiodactyla									
Tayassuidae									
Platygonus compressus[1]—flat-headed peccary	?	—	—	—	1	—	—	1	2
Cervidae.									
Cervus elaphus[2]—elk	*	—	—	1	—	—	—	—	2
Odocoileus virginianus—white-tailed deer	*	*	*	*	*	*	*	*	10
cf. *Sangamona fugitiva*[1]—"fugitive" deer	*	—	1	—	—	—	—	—	1
Rangifer tarandus[2]—caribou	*	—	1	—	1	—	—	—	2
Order Perissodactyla									
Tapiridae									
Tapirus cf. *veroensis*[1]—tapir	?	—	1	—	—	—	—	—	1

FLORA

Botanical specimens were not saved from the upper 0–3 ft levels of the deposit, but two fragmentary hickory nuts (*Carya* sp.) were present in the Dean/Wilson collection from the top few inches of the cave floor and are undoubtedly Recent.

A total of 1,071 hackberry seeds (*Celtis* sp.) were identified from the deposit. Many more were originally present but so pulverized that they could not be counted. Thirty-two percent were puncture-gnawed by small rodents, probably *Peromyscus*. Seed counts by stratigraphic level, beginning at the 3–4 ft level, were 31, 73, 320, 359, 73, 94, and 121 at the 9–10 ft level. A stratigraphic increase in abundance is suggested by the relative numbers of hackberry seeds compared to small rodents (Arvicolidae). Applying the formula, *Celtis* seeds ÷ by Arvicolidae MNI × 100, a change in frequency with depth is noted: 3–4 ft level = .19; 4–5 ft level = .23; 5–6 ft level = 1.33; 6–7 ft level = 4.60; 7–10 ft level = 2.82. Hackberry seeds increased in relative abundance in the lower levels of the deposit. There are two possible explanations for this. The greater relative abundance of hackberry in the lower levels may be due to the climatic shift indicated by the small mammals of the deposit, a shift from relatively temperate in the lower levels, favoring *Celtis*, to more boreal conditions in the upper levels. Or the reason may simply be due to a change in the activity level of the raptors responsible for the small mammals in the deposit. It is possible that rodent midden activity, and its accompanying seed caching predominated in the lower levels of the deposit while rodent activity decreased and raptor activity increased in the upper levels of the deposit, which may have been either a secondary effect of climatic change or due simply to the configuration of the deposit.

Pollen analysis was attempted, with negative results, on seven samples from various stratigraphic levels, by Robert Thompson, Laboratory of Paleoenvironmental Studies, Department of Geosciences, University of Arizona, Tucson; four samples utilizing zinc bromide density separation, three samples using hydrofluoric acid. The lack of fossil pollen in this indurated, yellow-brown, basic (pH—7.6–7.7) cave sediment was not unexpected and is unfortunately consistent with results of other Appalachian cave or talus deposits, such as the Meadowcroft Rockshelter, Pennsylvania, and Trout Cave, West Virginia. Apparently, unless pollen is deposited in a subaqueous or other oxygen deficient environment it is soon destroyed in the humid East. Pollen was well-preserved in the late Pleistocene fissure fill of New Paris No. 4, Pennsylvania, due to a rapid rate of deposition in a water-saturated colloidal clay matrix, which served as an impervious shield effectively sealing all accumulating organic inclusions from the atmosphere.

FISH REMAINS

FREDERICK C. HILL

Seventeen taxa of fishes represented by 147 identifiable bones and at least 13 species were identified from the Baker Bluff Cave faunal sequence (Tables 1 and 2). Numerous pharyngeal arches of Cyprinidae have not been studied. Fish are catalogued under CM 30228.

The species recovered from the seven levels at Baker Bluff could be found coexisting in a moderate gradient, medium order river. Only *Catostomus commersoni* is characteristically found in intermittent streams, but it also occurs in larger streams or rivers. Most of these species, including *Aplodinotus grunniens, Moxostoma erythrurum, M. carinatum, Micropterus dolomieui, Ambloplites rupestris, Esox* sp., and *Lepisosteus* sp. are typically found in pools. The presence of riffles between pools is evidenced by young *Ictalurus punctatus*, none of which exceed 16 cm total length (Table 3), and *Micropterus dolomieui*. Nearly all species prefer water with a moderate to swift current although some, such as *Lepisosteus* sp., *Aplodinotus grunniens, Moxostoma erythrurum*, and possibly the *Noturus* sp. are better adapted to slower currents. Six of the species, including *Hypentelium nigricans, Catostomus commersoni, Moxostoma* cf. *duquesnei, M. carinatum, Ambloplites rupestris*, and *Micropterus dolomieui* are best adapted to clear streams, whereas *Moxostoma erythrurum, Aplodinotus grunniens, Ictalurus punctatus*, and *Stizostedion canadense* tolerate varying degrees of turbidity. Thus, one

Table 2.—*Total number of fish bones identified from levels 3–4 ft through 9–10 ft, Baker Bluff Cave, Tennessee. ? = no observation; * = present, not tallied.*

Taxon	Stratigraphic levels							
	0–3	3–4	4–5	5–6	6–7	7–8	8–9	9–10
Hypentelium nigricans (Lesueur)	?	—	—	2	—	—	—	—
Catostomus commersoni (Lacepede)	?	—	—	1	1	—	—	—
Moxostoma cf. *duquesnei* (Lesueur)	?	—	—	1	—	—	—	—
Moxostoma erythrurum (Rafinesque)	?	1	2	1	—	—	—	—
Moxostoma carinatum (Cope)	?	—	—	—	1	—	—	—
Catostomidae sp.	*	—	—	—	—	—	—	—
Aplodinotus grunniens Rafinesque	?	3	5	9	10	8	30	16
Ictalurus punctatus (Rafinesque)	?	—	—	5	1	—	—	—
Noturus sp. Rafinesque	?	1	—	—	—	—	—	3
Stizostedion canadense (Smith)	?	1	—	—	—	—	—	—
Ambloplites rupestris (Rafinesque)	?	2	2	—	—	—	1	—
Micropterus dolomieui Lacepede	?	—	—	1	—	—	—	—
Lepisosteus sp. Lacepede	?	—	—	3	—	—	—	—
Moxostoma sp. Rafinesque	*	9	6	3	1	—	1	—
Stizostedion sp. Rafinesque	?	1	6	1	2	—	1	—
Ictalurus sp. Rafinesque	*	—	1	—	—	—	—	—
Micropterus sp. Lacepede	?	—	1	—	—	—	—	—
Cyprinidae sp.	?	17	46	25	6	2	—	4
Esox sp. Linnaeus	?	1	—	1	—	—	—	—
Total		36	69	53	22	10	33	23

would expect to find these species coexisting in various habitats within a small section of a stream near Baker Bluff.

The estimated sizes (Table 3) of the various fishes suggests that, for the most part, small predators were responsible for their presence in the cave. *Stizostedion canadense* was the largest fish recorded, 50 cm T.L. A single *Ictalurus punctatus* was the smallest fish, only 4 cm T.L. *Moxostoma* identifications were based upon either dentaries or pharyngeal arch teeth. All of the elements from small *Moxostoma* were assigned only to the generic level because of the difficulty encountered in making species identifications. No fish of unusual size were recorded.

The small sample size precludes the recognition of any subtle changes in this ichthyofauna. The greatest number of individuals and taxa appear in the upper 6 ft of the deposit.

AMPHIBIANS AND REPTILES

GEORGE HENRY VAN DAM

The Baker Bluff Cave faunal sequence includes at least five species of urodeles, five species of anurans, one species of turtle, one species of lizard, and 11 species of snakes.

Class Amphibia—Amphibians
Order Urodela—Salamanders
Family Ambystomatidae—mole salamanders

Vertebral centrum amphicoelous, weakly constricted ventrally, without spine produced from its posteroventral surface; neural spine obsolete and single throughout (Holman, 1962).

Ambystoma opacum (Gravenhorst)—marbled salamander

Material.—CM 29754–29757. 2 precaudal vertebrae (4–5 ft); 1 precaudal vertebra (5–6 ft); 5 precaudal vertebrae (6–7 ft); 1 pre-caudal vertebra (8–9 ft).

Remarks.—The Ambystomatidae can be divided into major groups using vertebral ratios—(1) the length of the centrum divided by its width at the anterior end, and (2) the combined zygapophyseal width divided by the zygapophyseal length (Tihen, 1958). Tihen noted that in the *A. maculatum* group and in the subgenus *Linguaelapsus* (at least in the

Table 3.—*Estimated live total length (in cm) of Baker Bluff fish.*

Taxon	Total length in centimeters																							
	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32	34	36	38	40	42	44	46	48	50
Ictalurus punctatus	2	2	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ictalurus sp.	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Moxostoma sp.	—	—	—	2	1	—	1	1	1	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
Ambloplites rupestris	—	—	—	1	—	1	1	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Noturus sp.	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Catostomus commersoni	—	—	—	—	—	—	—	1	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—
Stizostedion sp.	—	—	—	—	—	—	—	—	1	—	—	—	1	—	—	1	—	—	—	—	—	—	—	—
Micropterus dolomieui	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Micropterus sp.	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—
Hypentelium nigricans	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—
Moxostoma erythrurum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	2	—	—	—
Stizostedion canadense	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1

posterior part of the trunk) the postzygapophyses extends as far, usually farther posteriorly, than does the neural arch.

In my examination of the material, I used the length of the centrum divided by its width at the anterior end for species determination.

Ambystoma maculatum (Shaw)—spotted salamander

Material.—CM 29758–29760. 6 precaudal vertebrae (4–5 ft); 3 precaudal vertebrae (5–6 ft); 4 precaudal vertebrae (6–7 ft).

Remarks.—Material was assigned to *A. maculatum* based on criteria discussed under *A. opacum*.

Ambystoma sp. indet.

Material.—CM 29761–29767. 3 precaudal vertebrae (3–4 ft); 15 precaudal vertebrae (4–5 ft); 7 precaudal vertebrae (5–6 ft); 7 precaudal vertebrae (6–7 ft); 3 precaudal vertebrae (7–8 ft); 7 precaudal vertebrae (8–9 ft); 1 precaudal vertebra (9–10 ft).

Remarks.—Material which was too fragmentary for measurement or those whose ratios fell within the ranges of both *A. maculatum* and *A. opacum* were assigned to genus only.

Some specimens referred to *Ambystoma* species exhibited the back-swept neural arch characteristic of *A. tigrinum* as pointed out by Holman (1969), but these could not be assigned to species because anterior thoracic vertebrae of *A. maculatum* and *A. opacum* have this characteristic. Conant (1975) states that *Ambystoma opacum* occurs in a variety of habitats, ranging from moist, sandy areas to dry hillsides. *A. maculatum* is occasionally found (from spring to autumn) beneath stones or boards.

Family Proteidae—Mudpuppies

Specimens were assigned to the Proteidae by comparison with Recent specimens and using criteria of Holman (1968) who noted that their vertebrae are amphicoelous and the transverse processes are undivided.

Necturus maculosus (Rafinesque)—mudpuppy

Material.—CM 29768–29773. 15 precaudal vertebrae (3–4 ft); 22 precaudal and 2 caudal vertebrae (4–5 ft); 5 precaudal vertebrae (5–6 ft); 3 precaudal vertebrae (6–7 ft); 5 precaudal vertebrae (7–8 ft); 3 precaudal vertebrae (8–9 ft).

Remarks.—The fossils were indistinguishable from Recent *N. maculosus*. *Necturus maculosus* habitats include lakes, ponds, rivers, streams, and other permanent bodies of water (Conant, 1975).

Family Cryptobranchidae—Hellbenders

Cryptobranchus alleganiensis (Daudin)—hellbender

Material.—CM 29774–29779. 30 precaudal, 3 caudal vertebrae, and 1 right dentary (3–4 ft); 73 precaudal vertebrae and 2 vomers (4–5 ft); 33 precaudal vertebrae (5–6 ft); 9 precaudal vertebrae (6–7 ft); 1 precaudal vertebra (7–8 ft); 4 precaudal vertebrae (9–10 ft).

Remarks.—Meszoely (1967) gave characteristics for the identification of *Cryptobranchus*—deeply amphicoelous cotyles, circular in outline; centrum relatively short in respect to the diameter of the cotyle; ventral surface of the centrum rounded without keel or processes; large lateral fossa anteriad to the base of the transverse process; very large size. In addition, Holman (1968) notes that the transverse processes are undivided.

Due to the fragmentary nature of much of the material I found it sometimes difficult to separate vertebrae of *Cryptobranchus alleganiensis* and *Necturus maculosus*. I have found the following criteria useful in differentiating these two: in *C. alleganiensis* the sides of the centrum are more sculp-

tured than in *N. maculosus*; in *C. alleganiensis* the upper transverse process is heavy and cylindrical in shape (*N. maculosus* has a very wing-like upper transverse process); *C. alleganiensis* has the articular facets of the transverse processes exhibiting a single opening, whereas in *N. maculosus* there are usually two distinct openings. *C. alleganiensis* is always found in rivers and larger streams where water is running and ample shelter is available in the form of large rocks, snags, or debris (Conant, 1975).

Family Plethodontidae—Plethodontid Salamanders

Desmognathus sp. indet.—dusky salamanders

Material.—CM 29780–29785. 22 vertebrae (3–4 ft); 158 vertebrae (4–5 ft); 95 vertebrae (5–6 ft); 81 vertebrae (6–7 ft); 19 vertebrae (7–8 ft); 21 vertebrae (8–9 ft).

Remarks.—These specimens have been assigned to *Desmognathus* based on descriptions by Soler (1950) who states that their vertebrae are opisthocoelous and have pointed processes arising from the dorsal surfaces of the postzygapophyses. I am unable to carry the identification any further due to lack of Recent comparative material.

Desmognathus fuscus, D. quadramaculatus, D. monticola, and *D. wrighti* are all present in northeastern Tennessee today and it is not unlikely that all four are present in the collection. *Desmognathus fuscus* occurs in brooks, near springs, and in seepage areas along edges of small woodland streams where stones, chunks of wood, and miscellaneous debris provide ample shelter both for the salamanders and for their food. *D. quadramaculatus* is abundant in boulder-strewn brooks and also found near waterfalls or other places where cold water drips or flows. *D. monticola* prefers a habitat of cool, well-shaded ravines and banks of mountain brooks. *D. wrighti* is today a resident chiefly of high spruce-fir forests and lives under moss and bark on rotting logs or beneath rotting wood or litter on the forest floor near seepage areas (Conant, 1975).

Order Anura—Frogs and Toads
Family Bufonidae—Bufonid Toads

Fossil *Bufo* may be identified by the following characteristics (Holman, 1962): ilium with dorsal blade absent; dorsal prominence produced dorsally, well developed, grooved or irregular in shape; sacral vertebrae procoelus, with one anterior and two posterior condyles; sacrum free from urostyle, its diapophyses moderately expanded.

Bufo americanus Holbrook—American toad

Material.—CM 29786–29792. 12 right, 7 left ilia (3–4 ft); 17 right, 24 left ilia (4–5 ft); 10 right, 10 left ilia (5–6 ft); 3 right, 7 left ilia (6–7 ft); 2 right ilia (7–8 ft); 2 right ilia (8–9 ft); 3 left ilia (9–10 ft).

Remarks.—The ilium of *Bufo woodhousei fowleri* has the base of the dorsal protuberance narrower than in equal-sized *B. americanus* (Holman, 1967). Habitats include shallow bodies of water in which to breed (temporary pools or ditches or shallow portions of streams, for example), possess shelter in the form of hiding places where there is some moisture, and harbor an abundant food supply of insects and other invertebrates (Conant, 1975).

Bufo woodhousei fowleri Girard—Fowler's toad

Material.—CM 29793–29795. 3 right ilia (3–4 ft); 2 right, 3 left ilia (4–5 ft); 1 left ilium (5–6 ft).

Remarks.—Assignment of material to *Bufo w. fowleri* was based on criteria given in the discussion of *B. americanus*. *Bufo w. fowleri* occurs chiefly in sandy areas, along shores of lakes or in river valleys (Conant, 1975).

Bufo sp. indet.

Material.—CM 29796–29801. 2 left ilia, 4 sacral vertebrae (3–4 ft); 3 right, 2 left ilia, 15 sacral vertebrae, 10 frontoparietals (4–5 ft); 4 sacral vertebrae, 6 frontoparietals (5–6 ft); 2 frontoparietals (6–7 ft); 1 sacral vertebra, 1 frontoparietal (7–8 ft); 2 sacral vertebrae, 2 frontoparietals (8–9 ft).

Remarks.—Ilia were assigned to *Bufo* sp. when the anterior or posterior portions of the prominence were missing, thus making it impossible to examine the prominence-protuberance relationship, or when the boundaries of the dorsal protuberance were not clearly defined within the prominence. Tihen (1962) pointed out that the frontoparietal is the most reliable single element for identification of the greatest number of New World *Bufo*. I could not find any distinct differences between the frontoparietals of *B. americanus* and *B. w. fowleri*.

Family Hylidae—Hylid Frogs

Hyla sp. indet.—tree frog

Material.—CM 29802. 1 left ilium (3–4 ft).

Remarks.—Specimen is assigned to the genus *Hyla* based on characters given by Holman (1962)—ilium with dorsal blade absent; dorsal prominence produced dorsolaterally, well developed, usually round and smooth.

The bone is too fragmentary for specific identification, but in comparison with Recent material, it

most closely resembles *Hyla chrysoscelis* and *H. versicolor* in the shape of the dorsal prominence.

Family Ranidae—Ranid Frogs

Ilium with dorsal blade well developed and arising anterior to dorsal prominence, without lateral deflection, and with a deep notch between it and dorsal acetabular expansion (Holman, 1962).

Rana sylvatica LeConte—wood frog

Material.—CM 29803–29807. 5 right, 4 left ilia (3–4 ft); 6 right, 6 left ilia (4–5 ft); 8 right, 3 left ilia (5–6 ft); 1 right, 3 left ilia (6–7 ft); 2 left ilia (9–10 ft).

Remarks.—Assignment to *Rana sylvatica* is based on Holman (1967) who noted that *Rana palustris, R. pipiens,* and *R. sylvatica* may be distinguished from *R. catesbeiana* and *R. clamitans* in that the posterodorsal border of the ilial shaft slopes more gently into the dorsal acetabular expansion in the former group than in the latter. The prominence for the origin of the vastus externus head of the triceps femoris muscles is larger, less produced, and less roughened in *R. pipiens* and *R. palustris* than it is in *R. sylvatica*. Based on these criteria, the specimens are assigned to *R. sylvatica*.

In examination of nine Recent specimens of *R. sylvatica* and two of *R. palustris,* the above characteristics hold in separating the two species. *Rana sylvatica* is usually encountered in or near moist wooded areas, but it often wanders considerable distances from water (Conant, 1975).

Rana catesbeiana Shaw—bullfrog

Material.—CM 29808. 1 left ilium (4–5 ft).

Remarks.—This specimen is assigned to *Rana catesbeiana* on the basis of characters discussed above and the observation of Tihen (1954) that *R. catesbeiana* ilia appear to be highly sculptured. *R. catesbeiana* is an aquatic frog that prefers larger bodies of water than most other frogs. It is a resident of lakes, ponds, bogs, and sluggish portions of streams (Conant, 1975).

Rana sp. indet.

Material.—CM 29809–29813. 3 sacral vertebrae (3–4 ft); 2 sacral vertebrae (4–5 ft); 2 sacral vertebrae (5–6 ft); 1 sacral vertebrae (6–7 ft); 1 sacral vertebra (8–9 ft).

Remarks.—These vertebrae have the diplasiocoelous condition with cylindrical rather than expanded diapophyses (Holman, 1962) and more closely resemble those of *R. sylvatica* in the shape of the neural canal and in their small size.

Class Reptilia—Reptiles
Order Testudines—Turtles
Family Emydidae—Pond Turtles

Graptemys geographica (Le Sueur)—map turtle

Material.—CM 29814. 1 proneural bone (4–5 ft).

Remarks.—Material is assigned to *G. geographica* based on the shape, location of shield impressions, and surface sculpturing compared to Recent material. *Graptemys geographica* occurs in large bodies of water, prefering rivers to creeks, and lakes rather than ponds (Conant, 1975).

Order Squamata—Snakes and Lizards
Suborder Sauria—Lizards
Family Scincidae—Skinks

Eumeces fasciatus (Linnaeus)—five-lined skink

Material.—CM 29815–29817. 1 precaudal vertebra (3–4 ft); 3 precaudal vertebrae (4–5 ft); 1 precaudal vertebra (6–7 ft).

Remarks.—*E. fasciatus* has a more backswept neural spine than *E. laticeps. Eumeces fasciatus* lives in rock piles and decaying debris in or near woods. The habitat is usually damp (Conant, 1975).

Suborder Serpentes—Snakes
Family Viperidae—Vipers

Crotalus horridus Linnaeus—timber rattlesnake

Material.—CM 29818–29824. 27 vertebrae (3–4 ft); 50 vertebrae (4–5 ft); 27 vertebrae (5–6 ft); 9 vertebrae (6–7 ft); 4 vertebrae (7–8 ft); 2 vertebrae (8–9 ft); 2 vertebrae (9–10 ft).

Remarks.—Holman (1963) provides characters, which can be used to differentiate *Crotalus* from *Agkistrodon.* In *Agkistrodon* a distinct pit usually occurs on either side of the cotyle of the centrum. Each of these pits contains one moderately large fossa. In *Crotalus* the distinct pits are usually absent and the one or more fossae that occur on either side of the cotyle of the centrum are minute. In addition, *Crotalus horridus* has a lower neural spine than either *C. adamanteus* or *Agkistrodon piscivorus* (Holman, 1967). The material most closely resembles *Crotalus horridus* in these characters. *Crotalus horridus* lives in timbered terrain; usually it is common in second-growth timber where rodents abound (Conant, 1975).

Family Colubridae—Colubrid Snakes
Subfamily Xenodontinae

Members of this subfamily lack hypapophyses on their lumbar vertebrae and have depressed vertebral neural arches and wide vertebral hemal keels (Holman, 1973*b*).

Heterodon platyrhinos Latreille—eastern hognose snake

Material.—CM 29825–29827. 1 precaudal vertebra (5–6 ft); 1 precaudal vertebra (6–7 ft); 1 precaudal vertebra (8–9 ft).

Remarks.—The genus *Heterodon* Latreille may be diagnosed by the following strong characters: hypapophyses absent; vertebrae wider than long through zygapophyses; neural arch flat; neural spine longer than high, usually thickened dorsally with its anterior and posterior borders concave; prezygapophyseal processes large, pointed or truncated; epizygapophyseal spines absent; hemal keel very broad and indistinct on many thoracic vertebrae (Holman, 1962).

In addition, Holman (1963) was able to differentiate between *H. platyrhinos* and *H. nasicus* in that in the former, the anterior zygapophyseal faces are more elongate, and in dorsal view, their anterior margins are much flatter than in the latter species. This material compares closest to the characteristics of *H. platyrhinos*. The eastern hognose snake is usually found in sandy areas (Conant, 1975).

Subfamily Colubrinae

Colubrinae never bear lumbar hypapophyses as do species in the subfamily Natricine, and they lack the combination of the depressed neural arch and the very wide hemal keel of the Xenodontinae (Holman, 1973*b*).

Diadophis punctatus (Linnaeus)—ringneck snake

Material.—CM 29828–29830. 26 precaudal vertebrae (3–4 ft); 19 precaudal vertebrae (4–5 ft); 6 precaudal vertebrae (5–6 ft).

Remarks.—Holman (1967) provides the following characters by which to distinguish the vertebrae of *Diadophis punctatus* from *Carphophis amoenus*: the neural spine is higher, thicker, and usually with more of a posterior overhang in the former than in the latter species. The Baker Bluff Cave fossils more closely resemble those of *D. punctatus*.

Diadophis punctatus is a woodland snake, usually most common in cutover areas that include an abundance of hiding places such as under stones, logs, bark slabs, or in rotting wood. Rocky, wooded hillsides are also favored (Conant, 1975).

Carphophis amoenus (Say)—worm snake

Material.—CM 29831–29832. 16 precaudal vertebrae (3–4 ft); 7 precaudal vertebrae (4–5 ft).

Remarks.—Fossils are assigned to *C. amoenus* based on criteria discussed under *Diadophis punctatus*. *Carphophis amoenus* is partial to moist earth and disappears deep underground in dry weather (Conant, 1975).

Coluber or **Masticophis** Linnaeus—racer or coachwhip

Material.—CM 29833–29837. 1 precaudal vertebra (4–5 ft); 3 precaudal vertebrae (5–6 ft); 7 precaudal vertebrae (6–7 ft); 1 precaudal vertebra (7–8 ft); 3 precaudal vertebrae (8–9 ft).

Remarks.—Holman (1962) characterizes the lumbar vertebrae for the genus *Coluber* as follows: hypapophyses absent; vertebrae longer than wide through zygapophyses; neural arch vaulted; neural spine about as high as long, thin, and delicate, not beveled anteriorly; epizygapophyseal spines usually well developed; hemal keel narrow throughout.

The vertebrae of *Coluber*, *Masticophis*, and *Opheodrys* are elongate and the neural spine is thin and delicate. But vertebrae of the former two genera are larger, the neural spine is higher, and a well-developed epizygapophyseal spine is almost always present. The fossils resemble the characters of the former two genera in this respect. Based on the present geographic ranges of *Masticophis* and *Coluber* it would appear that the fossils represent *Coluber*, but I am unable to separate the two genera on vertebral remains.

Lampropeltis Fitzinger

Remarks.—The vertebrae of *Pituophis*, *Elaphe*, and *Lampropeltis* are very similar but have been separated on the basis of characters described by Holman (1965). *Pituophis* is distinct from the other two genera in having a higher neural spine with an indented edge. The genera *Elaphe* and *Lampropeltis* can be separated by the more depressed neural arch of the latter.

Lampropeltis triangulum (Lacepede)—eastern milksnake

Material.—CM 29838–29843. 8 precaudal vertebrae (3–4 ft); 33 precaudal vertebrae (4–5 ft); 11 precaudal vertebrae (5–6 ft); 5 precaudal vertebrae (6–7 ft); 1 precaudal vertebra (7–8 ft); 3 precaudal vertebrae (8–9 ft).

Remarks.—Fossils are assigned to *L. triangulum* because the vertebrae possess lower neural spines than those of *L. getulus*. Also, *L. getulus* vertebrae are quite robust with thick neural spines and neural arches; the hemal keels and subcentral ridges are usually quite strong with the valleys between them quite deep (Holman, 1965).

Lampropeltis getulus (Linnaeus)—kingsnake

Material.—CM 29844–29848. 1 precaudal vertebra (3–4 ft); 2 precaudal vertebrae (4–5 ft); 6 precaudal vertebrae (5–6 ft); 2 precaudal vertebrae (8–9 ft); 2 precaudal vertebrae (9–10 ft).

Remarks.—The fossils have been assigned to *L. getulus* based on criteria discussed under *L. triangulum*. *L. getulus* occurs regionally but has not been recorded in the immediate area. It is possible that Recent *L. getulus* may be collected in the area in the future.

Elaphe sp. indet.—rat snake

Material.—CM 29849. 3 precaudal vertebrae (6–7 ft).

Remarks.—These specimens are assigned to the genus *Elaphe* sp. indet. because they have a more vaulted neural arch than *Lampropeltis* but a less vaulted arch than *Pituophis* (Holman, 1973*a*). In addition, *Pituophis* exhibits strongly developed epizygapophyseal spines, which are lacking in the fossils (Auffenberg, 1963). The material is too fragmentary to assign to species.

Subfamily Natricine

Material is assigned to the subfamily Natricine on characters given by Holman (1973*b*)—hypapophyses on their lumbar vertebrae—and by Auffenberg (1965)—epizygapophyseal spines are usually present.

Natrix sipedon (Linnaeus)—water snake

Material.—CM 29850–29852. 2 precaudal vertebrae (3–4 ft); 1 precaudal vertebra (4–5 ft); 3 precaudal vertebrae (5–6 ft).

Remarks.—In general, *Thamnophis* vertebrae are elongate when viewed from above, whereas *Natrix* vertebrae are almost square (Brattstrom, 1967). *Natrix* vertebrae tend to have higher neural spines (Holman, 1962).

Natrix septemvittata and *N. sipedon* occur in the area today. *N. septemvittata* possesses a long, low neural spine and *N. sipedon* possesses a much higher one (Auffenberg, 1963). The fossils resemble the latter species in this respect.

Natrix sp. indet.

Material.—CM 29853. 1 precaudal vertebra (5–6 ft).

Remarks.—The fossil is too fragmentary for specific identification but the genus was determined using criteria discussed under *Natrix sipedon*.

Thamnophis sauritus (Linnaeus)—ribbon snake

Material.—CM 29854–29856. 1 precaudal vertebra (3–4 ft); 5 precaudal vertebrae (4–5 ft); 1 precaudal vertebra (8–9 ft).

Remarks.—Criteria for assignment to *Thamnophis* was discussed under *Natrix sipedon*. In *T. sauritus* the accessory processes are oblique to the longitudinal axis of the centrum; in *T. sirtalis* they are at right angles (Holman, 1962).

Thamnophis sirtalis (Linnaeus)—garter snake

Material.—CM 29857–29860. 11 precaudal vertebrae (3–4 ft); 6 precaudal vertebrae (4–5 ft); 2 precaudal vertebrae (5–6 ft); 1 precaudal vertebra (6–7 ft).

Remarks.—The fossils were assigned to *T. sirtalis* based on criteria discussed under *T. sauritus*.

Thamnophis sp. indet.

Material.—CM 29861–29866. 16 precaudal vertebrae (3–4 ft); 20 precaudal vertebrae (4–5 ft); 3 precaudal vertebrae (5–6 ft); 2 precaudal vertebrae (6–7 ft); 1 precaudal vertebra (8–9 ft); 1 precaudal vertebra (9–10 ft).

Remarks.—The material was too fragmentary for specific identification but could be assigned to genus based on characters discussed under *Natrix sipedon*.

Discussion

All species of reptiles and amphibians from the Baker Bluff Cave local fauna, as far as can be determined, live in the area today. Only *Lampropeltis getulus*, which occurs regionally, is not found in the immediate area.

Perhaps the most striking thing about the herpetofauna is that there is nothing that strongly indicates that the climate or topography was any different then than it is today in northeastern Tennessee. Minimum numbers of individuals from each level (Table 1) show no discernible trends in the herpetofauna to indicate that climatic or ecological conditions changed markedly from approximately 20,000 years BP to approximately 600 years BP (but see Faunal Summary).

The Baker Bluff Cave herpetofauna exhibits many similarities to the late Pleistocene herpetofauna from Ladds Quarry, Georgia (Holman, 1967). At least 10 species, mostly snakes, from the Ladds Quarry site are also present at Baker Bluff Cave.

The Baker Bluff Cave herpetofauna is indicative of four major ecological preferences: a permanent aquatic habitat based on the evidence of *Rana catesbeiana* and *Graptemys geographica*; a marsh-stream border situation indicated by the water snakes *Natrix* and *Thamnophis* and the toad *Bufo. w. fowleri*; an open, sandy area indicated by *Heterodon platyrhinos*; and a moist woodland habitat

where the majority of the identified Colubrinae, *Crotalus horridus*, *Ambystoma opacum*, and *A. maculatum* probably occurred.

The diversity of habitats exhibited by the herpetofauna suggests that the fossil remains were probably deposited by raptors.

AVES—BIRDS

Material.—CM 29725, 30176–30181, 30227, 30787–30789. MNI = 169.

Remarks.—The majority of bird remains were fragmentary and represent prey items of raptorial birds. Approximately 30 species were identified (Table 1), 23% of all vertebrate species from the deposit. One hundred sixty-nine individuals were represented, 7% of the combined numbers of individual birds and mammals from the deposit; this figure closely approximates the 5% at the Clark's Cave, Virginia, local fauna, another riverside raptor roost.

The riverbluff location of the site is reflected in the numerous remains of aquatic and semiaquatic species—grebe, ducks, mergansers, sandpipers, turnstone, gull, kingfisher—30% of the recovered avian species, a figure again comparable to the 26% from the Clark's Cave, Virginia, deposit.

Despite the variety of birds, only grouse Tetraonidae and passenger pigeon, *Ectopistes migratorius*, were present in any appreciable numbers. These two taxa accounted for 48% of all individual birds from the site, a figure identical to that of the Clark's Cave deposit avifauna, reflecting the collecting bias of raptors. However the two sites did differ significantly in the relative numbers of grouse (all species) and passenger pigeons. Grouse accounted for 34% of all birds at Clark's Cave, but only 12% at Baker Bluff Cave. Passenger pigeon, on the other hand, accounted for only 14% of all birds at Clark's Cave, but a high 36% at Baker Bluff, almost a direct reversal in relative numbers. Both sites are late Pleistocene in age, lie in a similar physiographic setting, and both contain boreal elements. It is probable that the higher number of passenger pigeon remains at Baker Bluff Cave, 2° south of Clark's Cave, is due to the site's lower latitude and therefore greater relative freedom from boreal periglacial conditions. Spruce grouse (*Canachites*), sharp-tailed grouse (*Pedioecetes*), and ptarmigan (*Lagopus*) were recovered from Clark's Cave in addition to ruffed grouse (*Bonasa*), the only tetraonid there today; only the ruffed grouse is definitely recorded from Baker Bluff Cave. However, the distal end of a left tibiotarsus from the 6–7 ft level (CM 30810) may possibly be sharp-tailed grouse (*Pedioecetes phasianellus*).

One bird of western affinities, the black-billed magpie (*Pica pica* Linnaeus), is tentatively identified from the Baker Bluff Cave deposit. The determination is based on a right scapula from the 6–7 ft level (CM 30181). The black-billed magpie in North America is found from southern Alaska to northern New Mexico and east to Kansas. It occurs east casually to Ontario and western Quebec in the north and to the Mississippi River in the south, with occasional strays reported as far east as South Carolina and Florida (A.O.U. Checklist 1957:376). Assuming that the Baker Bluff Cave specimen was from a resident bird, its presence at the site would complement that of other western or midwestern forms from the deposit such as the thirteened-lined ground squirrel (*Spermophilus tridecemlineatus*) and the badger (*Taxidea taxus*). The magpie has also been reported from the late Pleistocene raptor deposit at Natural Chimneys, Virginia (a complete humerus, Wetmore, 1962). All other species of birds from the site are of wide geographical distribution and are either common migrants or residents of the area today.

Chicken (*Gallus gallus*) remains were found within the upper 2 ft of the deposit by Dean and Wilson and are Recent in origin.

MAMMALIA—MAMMALS

Order Marsupialia—Marsupials
Family Didelphidae—American Opossums
Didelphis virginiana Linnaeus—Virginia opossum

Material.—Dean/Wilson collection: 6 vertebrae, 1 right jugal.

Remarks.—The opossum was not a member of the Pleistocene component at Baker Bluff Cave. The six vertebrae and one skull fragment were recovered from the top 2 ft of the deposit in an archaeological context. Four of the vertebrae were

Table 4.—*Measurements (in mm) of* Sorex cinereus *Kerr.*

Locality	Anteroposterior crown length P_4-M_3				
	Mean	OR	SD	CV	N
Recent					
Pennsylvania*	3.69	3.6–3.9	.07	1.89	20
Late Pleistocene					
New Paris No. 4, Pennsylvania*	3.90	3.7–4.3	.16	4.09	29
Clark's Cave, Virginia*	3.98	3.6–4.4	.13	3.40	35
Robinson Cave, Tennessee**	3.90	3.6–4.5	—	—	18
Baker Bluff Cave, Tennessee	3.97	3.78–4.36	.06	1.51	28

* From Guilday et al., 1977.
** From Guilday et al. 1969.

recovered from a depth of less than 6 in. One of the latter, a caudal vertebra, was charred, the only indication of fire in the cave.

Didelphis is common in the Pleistocene of Florida, from Irvingtonian and Rancholabrean sites (Webb, 1974), and has been reported from the Pleistocene of Georgia (Ray, 1967). It has not been found in Pleistocene sites farther north, but extended its range northward following the Wisconsinan glacial recession. Opossum remains are common in late prehistoric archaeological sites as far north as west-central West Virginia (Guilday, 1971). The spread of *D. virginiana* into Pennsylvania and points north was apparently associated with ecological changes brought on by European settlement of the country (Guilday, 1958).

Order Insectivora—Insectivores
Family Soricidae—Shrews

Sorex arcticus Kerr—Arctic shrew

Material.—CM 29959–29961. 3 partial left mandibles. MNI = 3.

Sorex cinereus Kerr—masked shrew

Material.—CM 29962–29967. 52 left, 41 right mandibles; 4 maxillae. MNI = 53.

Sorex dispar Batchelder—rock shrew

Material.—CM 29968–29970. 7 left, 4 right mandibles. MNI = 9.

Sorex fumeus Miller—smoky shrew

Material.—CM 29971–29976. 10 left, 21 right mandibles; 3 left, 1 right maxillae. MNI = 22.

Sorex sp., large (**S. arcticus** or **S. fumeus**)

Material.—CM 29977–29979. 10 left, 11 right mandibles. MNI = 12.

Sorex sp., small (**S. cinereus** or **S. dispar**)

Material.—CM 29980–29983. 13 left, 20 right mandibles. MNI = 20.

Microsorex hoyi (Baird)—pygmy shrew

Material.—CM 29956–29958. 6 left, 7 right mandibles; 2 partial skulls. MNI = 9.

Cryptotis parva (Say)—least shrew

Material.—CM 29954–29955. 3 right mandibles. MNI = 3.

Blarina brevicauda (Say)—short-tailed shrew

Material.—CM 29746–29753. 130 left, 130 right mandibles; partial skulls, maxillae, isolated teeth. MNI = 149.

Remarks.—Seven species of shrews were identified from the deposit. Three of these live in the area today. *Blarina brevicauda* and *Cryptotis parva* are common; *Sorex fumeus* and *Sorex longirostris* (the latter apparently not represented in the cave fauna) are uncommon (Smith et al., 1974).

The four species of shrews from the deposit not represented in the modern fauna (*Sorex cinereus, S. dispar, S. arcticus, Microsorex hoyi*) are now confined either to higher latitudes or to higher altitudes in the Great Smoky Mountains east of the site.

There is a change in the relative frequency of various soricids at successive stratigraphic levels in the deposit (Fig. 11) which suggests environmental changes during deposition. Those species requiring cooler conditions, *S. arcticus, S. dispar,* and *Microsorex hoyi,* were confined to the upper 2 ft of the undisturbed sequence. Only *Blarina brevicauda, Sorex fumeus,* and *Sorex cinereus* occurred at all levels. *Sorex cinereus* does not occur at the site today but is present at higher elevations in the Great Smoky Mountains at the same latitude.

Table 5.—*Measurements (in mm)* Microsorex hoyi *(Baird), Baker Bluff Cave, Tennessee.*

Measurement	Mean	OR	N
Length of palate	—	5.0–5.2	2
Maxillary width	—	3.7–4.1	2
P^4-M^3	—	3.4–3.6	2
M^1-M^3	2.4	—	1
Total length, mandible with incisor	8.0	7.9–8.2	3
Total length, dentary	6.2	6.1–6.2	3
Height, ascending ramus	2.8	2.7–2.9	7
P_4-M_3	3.5	3.4–3.6	6
M_1-M_3	2.9	2.7–3.0	8

Given the fragmentary nature of the collection the southeastern shrew, *S. longirostris*, may be represented in the referred *S. cinereus* material from the deposit. The entire cave collection is identified as *S.* cf. *cinereus*, however, because the mandibles average larger than Recent Pennsylvania specimens and are comparable in size to late Pleistocene material from New Paris No. 4 and Clark's Cave (Table 4). Mandibular measurements show no stratigraphic size shifts which suggest the absence of the smaller *S. longirostris* in the lower levels of the deposit where boreal conditions were apparently less intense. The third unicuspid was larger than the fourth, a character distinguishing *S. cinereus* from *S. longirostris*, in the one example complete enough for observation (CM 29964, 6 ft level). The presence of *S. cinereus* in the lower more temperate levels of the deposit suggests that climatic conditions at the time of lower-level deposition, although milder than upper-level conditions that supported a larger number of boreal species, was cooler than at present. Remains of *Clethrionomys gapperi* and one *Phenacomys intermedius* from the lowest level support this conclusion.

The presence of *Cryptotis parva*, a temperate species, in the upper levels seems anomalous in the boreal context suggested by the associated fauna. However it has also been reported from the late Wisconsinan Robinson Cave, Tennessee, and Eagle Cave, West Virginia, local faunas, both of which suggest cooler conditions, so it may have persisted in the richer boreal/temperate faunal mix of the late Wisconsinan periglacial environment. The least shrew was not present in either the New Paris No. 4, Pennsylvania, or the Clark's Cave, Virginia, soricid faunas, however, and its late Wisconsinan distribution is yet to be determined. The three mandibles from the upper levels of Baker Bluff Cave may have filtered down from Recent levels through undetected oblique deposition or animal burrowing.

The absence of the water shrew, *Sorex palustris*, a semiaquatic soricine of boreal affinities, was unexpected. Its remains have been recovered from the late Pleistocene Robinson Cave deposit, 256 km west of Baker Bluff. But *S. palustris* remains are rare in eastern late Pleistocene deposits (New Paris No. 4, 0.9%; Clark's Cave, 3%; Robinson Cave, 0.8% of all soricids) and their absence from the Baker Bluff fauna may be a matter of chance.

The *Blarina brevicauda* collection from Baker Bluff Cave (Figs. 6 and 7) presents an interesting picture of the coexistence of two size-forms throughout a portion of the depositional time span, confirming a concept developed by Graham and Semken (1976). *Blarina brevicauda*, the most common shrew in temperate eastern North America today, is also the commonest soricid at all levels in the Baker Bluff deposit. Its remains comprise 41.6% of all shrews from the 3 ft level, increasing relatively (but not actually) to a high of 87.7% at the lowest cave level as a result of the lessening numbers of *Sorex*, *Microsorex*, and *Cryptotis* (Fig. 11).

There are two forms of *Blarina brevicauda* present in the Baker Bluff Cave deposit (Fig. 6). A small form, comparable in size to the modern mid-Appalachian *B. b. kirtlandi*, occurred at all levels; in the lower 3 ft of the deposit it was the only form represented. However, the upper level sample (3 to 7 ft) is bimodal, with modal values of P_4-M_3 of 5.92 mm (*B. b.* cf. *kirtlandi*) and 6.59 mm. The latter value is comparable to *B. b.* cf. *brevicauda* from the late Pleistocene Clark's Cave deposit (6.56 mm), somewhat larger than that of modern Minnesota specimens of *B. b. brevicauda* (6.29 mm, N = 20, Guilday et al., 1977).

An additional expression of variability is the spread of the observed range expressed as the percent of increase from the smallest to the largest values. That figure, for the upper levels of the deposit, is 21.4%, comparable to the bimodal samples from the New Paris Sinkhole No. 4, Pennsylvania, 20% and Meyer Cave, Illinois, 25%. In the lower levels the figure shrinks to 11.1%, a figure comparable to the unimodal Clark's Cave sample.

A small form of short-tailed shrew, comparable in size to modern mid-Appalachian material, occurred at the earliest level represented at Baker Bluff. At the 6–7 ft level, however, an influx of larger stock took place and both forms apparently

BLARINA BREVICAUDA (SAY) MEASURMENTS (IN MM) P_4-M_3, M_1-M_3, RECENT NORTHEASTERN TENNESSEE AND BAKER BLUFF CAVE, TENNESSEE. HISTOGRAMS ARRANGED BY STRATIGRAPHIC LEVELS.

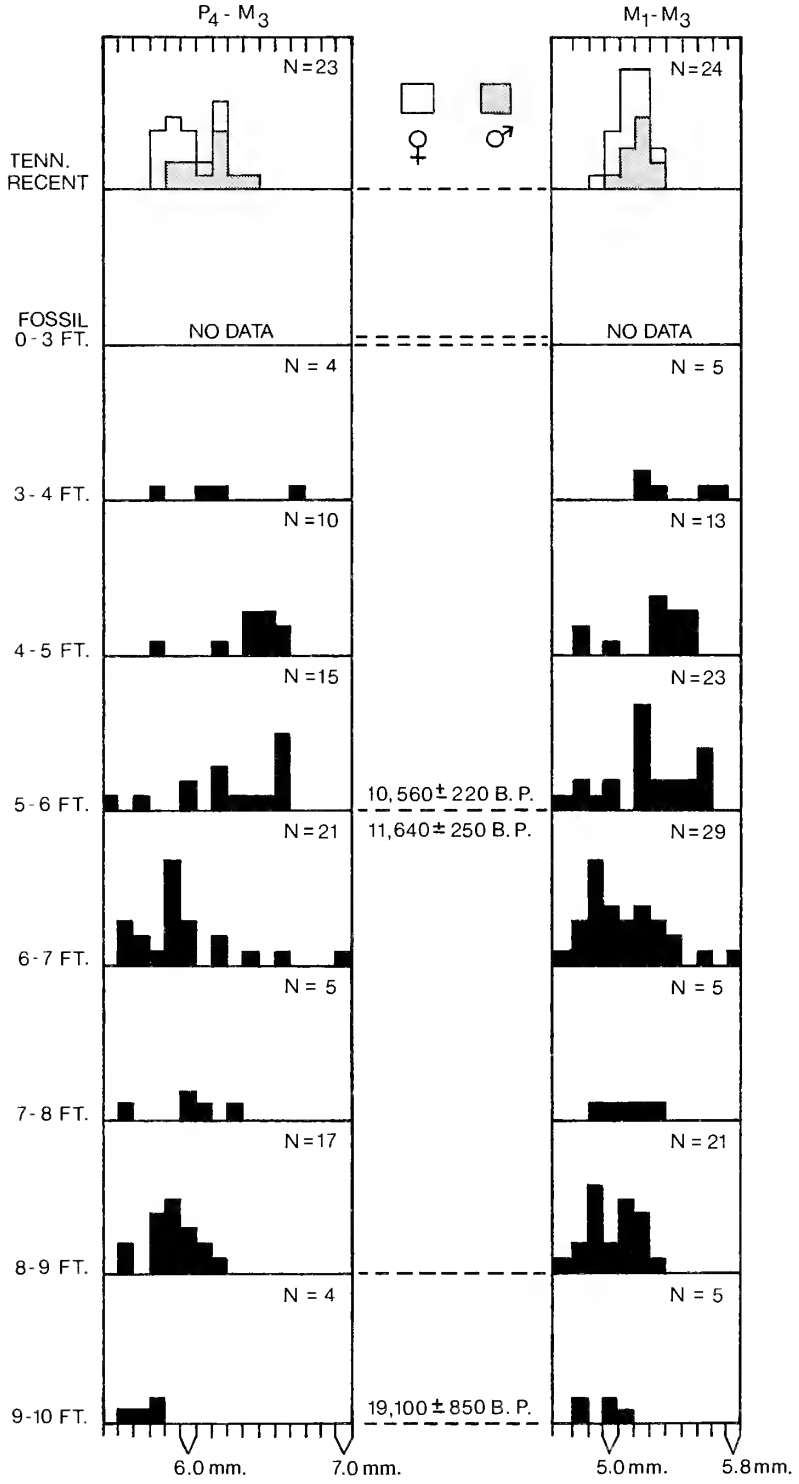

Fig. 6.—Histograms of mandibular measurements, *Blarina brevicauda* (Say), arranged by stratigraphic levels illustrating presence of two size groups, corresponding to Recent *B. b. kirtlandi* (smaller) and *B. b. brevicauda* (larger), Baker Bluff Cave, Sullivan County, Tennessee.

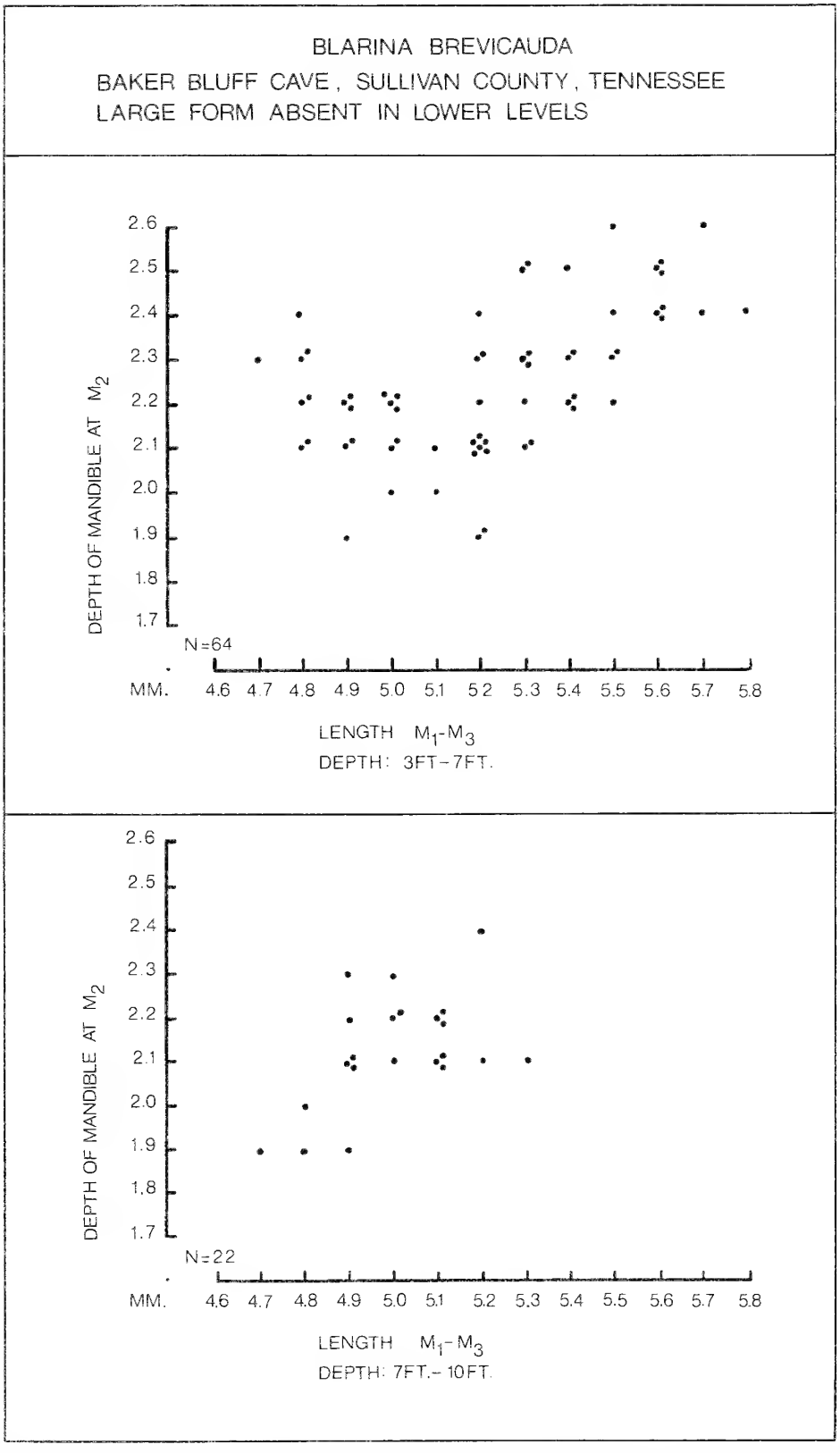

Fig. 7.—Scatter diagrams of mandibular measurements *Blarina brevicauda* (Say), Baker Bluff Cave, Sullivan County, Tennessee. Compare with Fig. 6.

existed in the area during the 3–7 ft depositional period. The top 3 ft of the deposit was destroyed and with it the Pleistocene/Holocene transition. The influx of the larger, presumably northern *B. b.* cf. *brevicauda* at the 6–7 ft level coincides with an increase in relative numbers of boreal voles. Climatic change is inferred at this point and it would appear that both forms of *Blarina* were coexisting in the area during an episode that was cooler than lower level times when only the smaller form existed at the site.

Graham and Semken (1976:443) speculate that "Sympatry of these phena [size-forms] during the Pleistocene suggested a more equable climate existed during glacial times than at present and that sympatric phena of *Blarina* coexisted in partitioned niches that presently are not defined. Post-glacial continental climates subsequently divided the . . . phena into their existing parapatric distributions." They suggest that "Coexistence of these phena in the same deposit without apparent interbreeding suggest a specific rather than a subspecific relationship." This assumes that there were no ecological barriers. *B. b. brevicauda* and *B. b. kirtlandi*, the modern equivalents of two of these late Pleistocene phena, and so identified by Graham and Semken, are currently considered to be subspecies. Current studies underway by J. R. Choate and H. H. Genoways on the evolution of *Blarina* may clarify the situation.

Family Talpidae—Moles

Condylura cristata (Linnaeus)—star-nosed mole

Material.—CM 30149–30150. 3 humeri. MNI = 3.

Scalopus aquaticus (Linnaeus)—eastern mole

Material.—CM 30151–30157. 3 humeri, 5 mandibles, skull fragments and isolated molars. MNI = 12.

Parascalops breweri (Bachman)—hairy-tailed mole

Material.—CM 30158–30165. 14 humeri, 15 mandibles, assorted limb bones, skull fragments and isolated molars. MNI = 17.

Remarks.—The eastern mole, *Scalopus aquaticus*, is common in the area today. The hairy-tailed mole, *Parascalops breweri*, has been reported from Bristol, Sullivan County, 50 km NE of the site in the Ridge and Valley province (Smith et al., 1974), and may occur at or near the site. The star-nosed mole, *Condylura cristata*, does not occur in the Ridge and Valley province at this latitude but does occur east of the site in the Great Smoky Mountains. This species is the most demanding in its ecological requirements, preferring boggy or mucky areas. It is a relatively weak burrower and often semiaquatic in its habits. Remains of the star-nosed mole were confined to the upper 3–5 ft levels.

Moles accounted for 1.6% of all mammals from the site. They were also scarce, 0.9% of the fauna, in the Clark's Cave local fauna, 307 km NE of Baker Bluff. Both accumulations are old raptor roosts, so the selection bias was much the same at both sites. But the relative percentages of the three species of talpids were quite different. The *Condylura/Scalopus/Parascalops* composition of the Baker Bluff Cave mole fauna (all levels combined) was 9%-54%-37%. At Clark's Cave it was 50%-4%-46%. The striking difference between the relative numbers of *Condylura* and *Scalopus* suggests that some factor other than relative availability to raptors was responsible for the discrepancy. The topography of the two sites is much the same but there is some evidence that the Cowpasture River valley, in which Clark's Cave is located, may have been relatively wetter (number and variety of ranids and semiaquatic birds) so that the high number of *Condylura* at that site can be attributed to local ecological factors.

At the latitude of Baker Bluff, *Condylura* and *Parascalops* are at the southern limits of their modern ranges. The fact that *Parascalops* was the commonest of the three species in the deposit is in accordance with the overall boreal aspect of the recovered fauna. *Parascalops breweri* has also been recorded from Robinson Cave, Overton County, Tennessee, 256 km west of Baker Bluff, well south of its present mid-continental range.

Order Chiroptera—Bats

Family Vespertilionidae—Evening Bats

Myotis sp. Kaup—little brown bats

Material.—CM 30143–30148. Partial mandibles and maxillae. MNI = 18.

Pipistrellus subflavus (F. Cuvier)—eastern pipistrelle

Material.—CM 30136. Partial mandibles; maxilla. MNI = 7.

Eptesicus fuscus (Palisot de Beauvois)—big brown bat

Material.—CM 30138–30142. Partial mandibles; maxilla; partial skull; isolated teeth. MNI = 19.

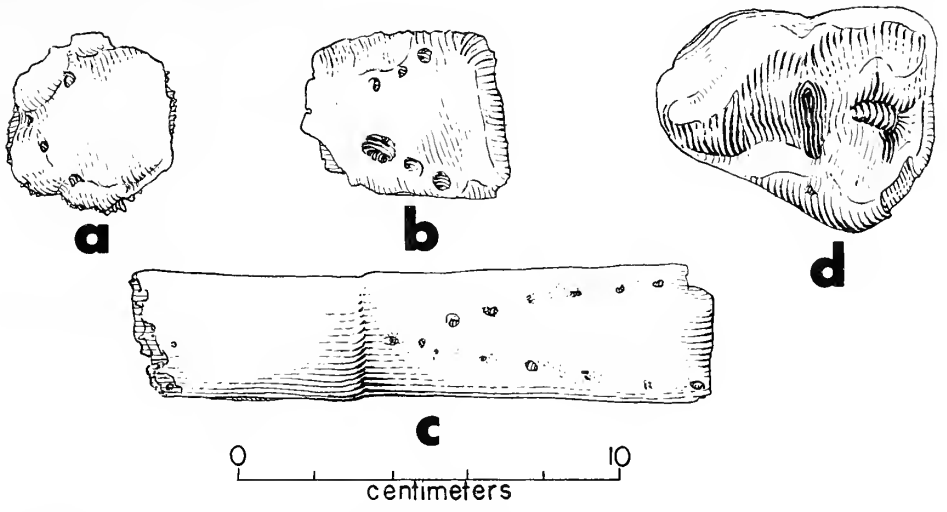

Fig. 8.—*Dasypus bellus* Simpson, dermal scutes: a) CM 29524; b) CM 29536; c) CM 29531. *Tapirus* cf. *veroensis* Sellards: d) CM 29522, left P^1, occlusal view, anterior to left. Baker Bluff Cave, Sullivan County, Tennessee.

cf. **Nycticeius humeralis** (Rafinesque)—evening bat

Material.—CM 30137. Partial mandible. MNI = 1.

Plecotus sp. E. Geoffroy Saint Hilaire—big-eared bat

Material.—CM 30143. Partial mandible. MNI = 1.

Remarks.—Baker Bluff Cave is too small and exposed to support a large bat colony and there is no other cave in the immediate vicinity capable of doing so. Bat remains were relatively uncommon, only 46 individuals, or 2.4%, of the total mammalian assemblage. By way of contrast bats accounted for 36% of the mammalian assemblage from Clark's Cave, Virginia, and 74% from Robinson Cave, Tennessee. The high number of bats from the Clark's Cave local fauna was due to raptor predation on a nearby cave colony; the bulk of the Robinson Cave bat remains (87% *Eptesicus fuscus*) resulted from natural mortality of the resident bat colony.

The big brown bat (*Eptesicus fuscus*) was the commonest bat from the Baker Bluff fossil fauna—19 individuals, 41% of all bats. This is a reflection of the shallowness of the cave, a condition differentially favoring this large hardy species.

Although at least 18 little brown bats (*Myotis* spp.) were present, only 11 mandibles were complete enough to measure. At least two size classes were represented. The alveolar length C-M_3 of two specimens measured 5.3 mm and 5.5 mm. Nine additional mandibles measured C-M_3 as follows: 6.2; 6.3; 6.4; 6.5; 6.5; 6.5; 6.7; 6.8 mm. The smaller group lies within the modern *M. leibii/austroriparius/sodalis/lucifugus* size range, the larger series within the modern *M. keenii/grisescens* range (Guilday et al., 1977, Fig. 16).

All species of bats recovered from the site are found in Tennessee today (Graves and Harvey, 1974). Only *Plecotus rafinesquii* has been reported from the state today, although a relict colony of *P. townsendii*, the western big-eared bat, in the central Appalachians northeast of the site (Handley, 1959), implies a former range continuum that may have included eastern Tennessee. The Baker Bluff specimen, a partial mandible, cannot be identified to species.

Order Edentata—Edentates
Family Dasypodidae—Armadillos
Dasypus bellus Simpson—"beautiful" armadillo

Material.—CM 29506, 29515, 29523, 29524, 29531, 29535, 29536. 15 fragmentary scutes (Fig. 8). MNI = 1.

Remarks.—Fifteen fragmentary dermal scutes were recovered, scattered throughout the deposit, but no other skeletal remains of this extinct armadillo were recognized (Fig. 8). This is due to the poor condition of all large bones from the deposit and the characteristic appearance of even fragmentary armadillo scutes. Armadillo remains are found

in Appalachian late Pleistocene sites as far north as West Virginia (Guilday and McCrady, 1966). Its presence in such sites is an indication of milder winter extremes despite the presence of so many boreal forms in the deposit. Armadillo remains have also been reported from Robinson Cave, Overton County, Tennessee.

Order Lagomorpha—Rabbits, Hares, and Pikas
Family Leporidae—Rabbits and Hares
Sylvilagus, sp. and/or **Lepus**, sp.—cottontail rabbit or snowshoe hare

Material.—CM 30007–30013. Isolated teeth, fragmentary maxillae, fragmentary mandibles. MNI = 95.

Remarks.—Leporid remains were common at all stratigraphic levels (Table 1). Preservation was so poor that identification beyond family level was not feasible and minimum number of individuals is based on counts of isolated teeth.

At least three species may be represented—*Sylvilagus floridanus*, the eastern cottontail, *Sylvilagus transitionalis*, the New England cottontail, and *Lepus americanus*, the snowshoe hare. The Baker Bluff leporid sample consists of remains of medium-sized animals, of *S. floridanus/transitionalis* size, too small for the Recent Appalachian subspecies of snowshoe hare, *L. a. virginianus*. But in the light of the presence of other northern forms in the deposit, a small late Pleistocene form of snowshoe hare may be present (see Guilday et al., 1964, for discussion of size relationships). Kellogg (1939) reports hearsay evidence of snowshoe hare from the Great Smokies in eastern Tennessee.

S. floridanus is the only leporid now in the cave area. *S. transitionalis*, a species more characteristic of a northern hardwood forest situation, has been taken as far soutn as northeastern Alabama (Howell, 1921) and its distribution prior to colonial deforestation may have included the cave area. *S. aquaticus*, the swamp rabbit, occurs in swampy situations along the Mississippi and Tennessee river valleys, farther west in the state (Kellogg, 1939), but the fossil remains are too small to be those of *S. aquaticus*.

Minimum number of individuals was based upon upper incisors and upper second premolars per level. Crown width of 138 upper incisors produced a unimodal curve skewed to the left with a high coefficient of variation—16.12. Based upon this measurement a single size-population with a large relative percentage of juvenile animals is most probable.

Order Rodentia—Rodents
Family Sciuridae—Squirrels
Tamias striatus (Linnaeus)—eastern chipmunk

Material.—CM 30083–30096. 3 left, 4 right partial maxillae, 11 left, 9 right partial mandibles: 25 M^1 or M^2, 1 M^3, 2 P^4, 57 M_1 or M_2, 4 M_3. MNI = 27.

Remarks.—Remains of the eastern chipmunk, 19.8% of all sciurids, were exceeded only by those of the thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*).

Measurements (Table 6) indicate that the Baker Bluff *T. striatus* were large-sized individuals, with a P_4-M_3 length averaging 10% larger than modern Pennsylvania material and some 6% larger than *T. s. pipilans*, the largest living subspecies. But the Baker Bluff sample averages 11% smaller in length of P_4-M_3 than the one extant mandible of the large extinct *T. aristus* from the Pleistocene of Georgia (USNM 23321, Ray, 1965). The largest of the Baker Bluff measurements, however, is only 2% smaller than that of *T. aristus*. We are dealing with small samples (seven measurements from Baker Bluff, one of *T. aristus*) and additional material may demonstrate a size-continuum. More material is needed to show whether *T. aristus* is a valid species or one based upon very large specimens of a large late Pleistocene form of *T. striatus*. Ray (1965) discusses this possibility and we concur with his opinions.

T. striatus increases in body size with decreasing latitude today, a condition which apparently held in late Pleistocene times as well even though all late Pleistocene *T. striatus* appear to have been larger than modern counterparts in the same latitude. Measurements P_4-M_3 of late Pleistocene material show a size increase from Pennsylvania through Virgina and Tennessee (Table 6).

The eastern chipmunk, a woodland form, and the thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*), a prairie form, were both common in the Baker Bluff local fauna, suggesting a regional mosaic of prairie and woodland. Numbers of the thirteen-lined ground squirrel diminished with increasing depth in the deposit while those of the eastern chipmunk remained relatively constant. This suggests that woodland was present throughout depositional times, although other evidence from the site suggests that the percent of woodland to grassland varied.

Eutamias cf. **minimus** (Bachman)—least chipmunk

Material.—CM 30114–30115. 2 left M_1 or M_2; CM 30116, partial left mandible with P_4-M_3. MNI = 3.

Table 6.—*Measurements (in mm) of* Tamias striatus *(Linnaeus) and* Tamias aristus *Ray.*

Sample data	Mean	OR	SD	CV	N
		Alveolar length P_4-M_3			
Recent					
Tamias striatus					
Pennsylvania*	6.58	6.20–6.98	.24	3.64	17
New Paris No. 2, Pennsylvania (1,875 years B.P.)	6.28	5.80–6.80	.18	2.86	114
*Tamias striatus pipilans***	6.76	6.30–7.40	.30	4.40	19
Late Pleistocene					
Tamias striatus					
Baker Bluff, Tennessee	7.24	6.79–7.95	—	—	7
Robinson Cave, Tennessee	7.50	7.30–7.80	—	—	2
Clark's Cave, Virginia***	6.81	6.50–7.30	.21	3.08	28
Hartman's Cave, Pennsylvania**	6.90	6.20–7.70	.42	6.11	9
New Paris No. 4, Pennsylvania	6.74	6.30–7.10	.20	2.96	30
*Tamias aristus***	8.10	—	—	—	1
		Occlusal length M_1			
Recent					
Tamias striatus					
Pennsylvania*	1.47	1.30–1.50	.05	3.49	16
*Tamias striatus pipilans***	1.58	1.49–1.67	—	—	2
Late Pleistocene					
Tamias striatus					
Baker Bluff, Tennessee	1.61	1.50–1.70	.06	3.88	13
Ladds, Georgia**	1.54	1.49–1.60	—	—	2
Tamias aristus					
Ladds, Georgia**	2.12	—	—	—	1
		Occlusal width M_1			
Recent					
Tamias striatus					
Pennsylvania*	1.61	1.45–1.75	.09	5.33	16
*Tamias striatus pipilans***	1.71	1.70–1.73	—	—	2
Late Pleistocene					
Tamias striatus					
Baker Bluff, Tennessee	1.71	1.50–1.80	.07	4.48	13
Ladds, Georgia**	1.73	1.73–1.74	—	—	2
Tamias aristus					
Ladds, Georgia**	2.29	—	—	—	1
		Occlusal length M_2			
Recent					
Tamias striatus					
Pennsylvania*	1.63	1.45–1.75	.08	4.88	16
*Tamias striatus pipilans***	1.89	1.81–1.91	—	—	2
Late Pleistocene					
Tamias striatus					
Baker Bluff, Tennessee	1.68	1.45–1.84	—	—	16
Ladds, Georgia**	1.86	1.82–1.90	—	—	2
Tamias aristus					
Ladds, Georgia**	2.42	—	—	—	1
		Occlusal width M_2			
Recent					
Tamias striatus					
Pennsylvania*	1.70	1.55–1.75	.07	4.11	16
*Tamias striatus pipilans***	1.89	1.82–1.96	—	—	2

Table 6.—*Continued.*

Sample data	Mean	OR	SD	CV	N
Late Pleistocene					
Tamias striatus					
Baker Bluff, Tennessee	1.86	1.64–1.94	—	—	16
Ladds, Georgia**	1.79	1.78–1.81	—	—	2
Tamias aristus					
Ladds, Georgia**	2.53	—	—	—	1
	Occlusal length M_1 or M_2				
Late Pleistocene					
Tamias striatus					
Baker Bluff, Tennessee	1.62'	1.45–1.84	.14	8.66	45
	Occlusal width M_1 or M_2				
Late Pleistocene					
Tamias striatus					
Baker Bluff, Tennessee	1.68	1.45–2.03	.13	7.70	46
	Alveolar length P^4-M^3				
Recent					
*Tamias striatus pipilans***	6.55	6.50–6.60	—	—	2
Late Pleistocene					
Tamias striatus					
Baker Bluff, Tennessee	6.30	—	—	—	1
*Tamias aristus***	7.25	—	—	—	1
	Occlusal length M^1				
Late Pleistocene					
Tamias striatus					
Baker Bluff, Tennessee	1.55	1.40–1.50	—	—	4
	Occlusal width M^1				
Late Pleistocene					
Tamias striatus					
Baker Bluff, Tennessee	1.86	1.80–1.90	—	—	4
	Occlusal length M^2				
Late Pleistocene					
Tamias striatus					
Baker Bluff, Tennessee	1.50	—	—	—	3
	Occlusal width M^2				
Late Pleistocene					
Tamias striatus					
Baker Bluff, Tennessee	1.90	1.80–2.00	—	—	3
	Occlusal length M^1 or M^2				
Late Pleistocene					
Tamias striatus					
Baker Bluff, Tennessee	1.66	1.40–1.80	.11	6.36	24
	Occlusal width M^1 or M^2				
Late Pleistocene					
Tamias striatus					
Baker Bluff, Tennessee	1.89	1.60–2.10	.12	6.15	24

* CMNH Recent mammal collection: 25091, 25104, 25105, 25107, 25109–25116, 25118, 25120, 25123, 25124, 25132.
** Ray, 1965.
*** Guilday et al., 1977.

Remarks.—The least chipmunk occurs today in the American West and subarctic western Canada east to Lake Superior, Lake Huron, and southwestern Hudson Bay, where it prefers open to brushy coniferous forest situations (Banfield, 1974). Remains have been reported from two other late Pleistocene cave deposits in the Appalachians, Back Creek Cave No. 2 and Clark's Cave, Virginia. Baker Bluff Cave marks the southernmost record for the least chipmunk in eastern North America.

Rare in the deposit, and confined to the upper 3–6 ft levels, presence of the least chipmunk in conjunction with high numbers of *Spermophilus tridecemlineatus* from those levels suggests an open, predominantly coniferous parkland environment. Measurements of CM 30116 are as follows: P_4-M_3, 5.2 mm; P_4, .97 mm × .97 mm; M_1, 1.3 mm × 1.4 mm; M_2, 1.4 × 1.4 mm; M_3, 1.5 × 1.4 mm.

Marmota monax (Linnaeus)—woodchuck

Material.—CM 30166–30173. 3 skull fragments; 3 left, 1 right mandibles; 15 upper incisors; 8 dP^4; 12 P^3; 16 P^4; 22 M^1 or M^2; 1 M^2; 17 M^3; 14 lower incisors; 7 dP_4; 8 P_4; 26 M_1 or M_2; 1 M_1; 16 M_3. MNI = 23.

Remarks.—Remains of this large hibernating ground squirrel are present in all Holocene and Pleistocene Appalachian cave deposits of any size, and they are common in the Baker Bluff fauna—at least 23 individuals, based upon dentitions, 17% of all sciurids from the site.

Most of the remains may represent individuals who died of natural causes as the deposit is within a few meters of the present entrance. All but juvenile woodchucks are too large for most raptors and their diurnal habits protect them from owls. The extent to which woodchuck remains may build up in cave deposits is dramatically illustrated by the early Holocene fissure, Meyer Cave, Illinois (Parmalee, 1967). At least 597 individuals were present in that deposit, 82% of all sciurids.

Woodchuck burrowing in such a small deposit as Baker Bluff Cave may have affected stratigraphic integrity, but there is no field evidence for this.

Spermophilus tridecemlineatus (Mitchell)—thirteen-lined ground squirrel

Material.—CM 30073–30082. 1 left, 3 right partial maxillae; 5 left, 2 right partial mandibles; 2 dP^4; 1 P^3; 24 P^4; 2 M^1; 3 M^2; 33 M^1 or M^2; 10 M^3; 7 P_4; 2 M_1; 36 M_1 or M_2; 22 M_3. MNI = 28.

Remarks.—The thirteen-lined ground squirrel, *Spermophilus tridecemlineatus*, was the commonest squirrel, 20% of all sciurids, from the deposit. This is a high figure for an eastern late Pleistocene cave fauna compared with 9.6% New Paris No. 4, Pennsylvania, 4.3% Clark's Cave, Virginia, and 7.6% of the sciurids from Robinson Cave, Tennessee.

The thirteen-lined ground squirrel is a prairie species, occurring in the American Midlands from Wyoming to western Ohio and from Manitoba to Texas (Hall and Kelson, 1959). It does not now live in the forested East. It is not found south of the Ohio River except in those few instances where it has been introduced locally by man (Doutt et al., 1973). However during at least late Wisconsinan times it was distributed throughout the mid-Appalachian region. It has been reported from cave sites in Pennsylvania, West Virginia, Virginia, Kentucky, and Tennessee (Guilday et al., 1977). The presence of thirteen-lined ground squirrels at such sites, in association with boreal woodland mammals, suggests a mixed woodland/grassland ecotype. At Welsh Cave, Kentucky, 268 km NW of Baker Bluff Cave, ^{14}C dated 12,950 ± 950 BP, *S. tridecemlineatus* dominated the small mammal fauna, and, other than a single red squirrel (*Tamiasciurus hudsonicus*), was the only sciurid from the site. It was found with remains of *Taxidea taxus*, *Ursus arctos*, *Mammuthus*, and *Equus*, as well as with boreal forest rodents and insectivores, suggesting a prairie parkland periglacial environment in what is now a region of deciduous forest.

The relative percent of thirteen-lined ground squirrel to chipmunk (*Tamias striatus*) is instructive. Both are diurnal, conspicuous ground squirrels of comparable size; both are susceptible to predation by raptors. They occupy separate ecological niches, however. *S. tridecemlineatus* is a prairie form, whereas *T. striatus* inhabits woodland or forest edge. Their changing relative numbers, stratigraphically or geographically, should provide a relative index to the type of ground cover present at the time of deposition.

S. tridecemlineatus comprised 23% of the ground squirrels (*Spermophilus*, *Tamias*) from New Paris No. 4, Pennsylvania, 17% from Clark's Cave, Virginia, 33% from Robinson Cave, Tennessee, 51% at Baker Bluff Cave, and 100% from Welsh Cave, Kentucky. It is apparent that variation in the *Spermophilus/Tamias* ratio does occur but not enough paleofaunas have been analyzed to recognize any geographic pattern that might reflect paleoenvironmental trends. The data now at hand suggest that *Spermophilus* is relatively more common in south-

Table 7.—*Measurements (in mm) of* Spermophilus tridecemlineatus, *Baker Bluff Cave, Tennessee.*

Mean	OR	SD	CV	N	Mean	OR	SD	CV	N
	Occlusal length M^1					Occlusal width M^1			
1.64	1.40–1.70	—	—	5	2.30	2.10–2.40	—	—	5
	Occlusal length M^2					Occlusal width M^2			
1.69	1.50–1.80	—	—	7	2.30	2.00–2.40	—	—	7
	Occlusal length M^1 or M^2					Occlusal width M^1 or M^2			
1.67	1.40–1.80	.13	7.68	24	2.20	1.70–2.40	.16	7.30	24
	Occlusal length M_1					Occlusal width M_1			
1.55	1.40–1.60	—	—	5	1.92	1.84–1.94	—	—	5
	Occlusal length M_2					Occlusal width M_2			
1.68	1.40–1.80	—	—	3	2.16	1.90–2.30	—	—	3
	Occlusal length M_1 or M_2					Occlusal width M_1 or M_2			
1.60	1.40–1.80	.13	8.69	20	1.98	1.50–2.10	.17	8.57	20
	Alveolar length P_4-M_3								
8.60	—	—	—	1					

ern (Tennessee) and western (Kentucky) late Pleistocene sites.

There is a stratigraphic change in the ground squirrel fauna from Baker Bluff Cave itself (Fig. 12). At levels 0–7 ft *S. tridecemlineatus* was the dominant species—58.1%. In the lower levels, 7–10 ft, the relative numbers of *S. tridecemlineatus* and *Tamias striatus* shifted and *T. striatus* became the dominant species—66%. This suggests a trend toward a denser woodland in the lower levels, an impression heightened by an accompanying shift in the relative numbers of large tree squirrels; the temperate deciduous forest *Sciurus* became common in the lower levels. In the upper levels of the deposit it was partially replaced by the red squirrel (*Tamiasciurus hudsonicus*), a coniferous/northern hardwood species that does not require as dense a forest habitat.

Spermophilus (*Ictomys*) sp. has been reported from Haile XIV A, a Sangamonian/Wisconsinan fissure site in Florida, accompanied by a predominantly xeric fauna. No northern species were noted. It was suggested that either *S. tridecemlineatus* or *S. mexicanus* might be represented and that they represented a western element in this Florida fauna (Martin, 1974). Northern species dominate all of the eastern late Wisconsinan faunas studied so far from the mid-Appalachians. The accompanying *Spermophilus* from these sites is believed to be the northern *S. tridecemlineatus*, which ranges north to Manitoba today, rather than *S. mexicanus*, which ranges only as far north as Texas and northern Mexico. Both species are larger than *S. spilosoma* (Table 7).

Sciurus carolinensis Gmelin—gray squirrel

Material.—CM 30106–30113. 1 right mandible with P_4-M_3; 1 left maxilla with P^3-P^4; 1 right dP^4; 4 left, 2 right P^4; 19 left, 12 right M^1 or M^2; 9 left, 4 right M^3; 3 P_4; 12 left, 9 right M_1 or M_2; 4 left, 2 right M_3. MNI = 17.

Remarks.—The gray squirrel and the larger fox squirrel (*Sciurus niger*) occur in the area at the present time. *S. niger* may have been present in the fossil deposit, but there is no indication of it. A right mandible from the Dean/Wilson collection (CM 30106) agrees in size with *S. carolinensis*, and a maxilla (CM 30107) bears the diagnostic P^3. The remainder of the collection, 81 isolated premolars and molars, are referred to *S. carolinensis* on the basis of their size and the lack of any apparent bimodality (Table 8).

Gray squirrel remains in the deposit became more common relative to those of red squirrel, *Tamiasciurus hudsonicus*, with increasing depth (Fig. 12). In the upper levels, 0–7 ft, the percentage of *Sciurus*

Table 8.—*Length and width of molars (in mm) of* Sciurus *cf.* carolinensis *Gmelin, Baker Bluff Cave, Sullivan Co., Tennessee.*

Measurements	Mean	OR	SD	CV	N
Crown length M^1 or M^2	2.49	2.10–2.70	.15	6.02	26
Crown length M_1 or M_2	2.54	2.30–2.80	.20	7.87	18
Crown width M^1 or M^2	2.81	2.40–3.10	.16	5.69	26
Crown width M_1 or M_2	2.75	2.50–2.90	.13	4.69	16

Table 9.—*Measurements (in mm) of* Tamiasciurus hudsonicus *(Erxleben).*

Age and locality	Mean	OR	SD	CV	N
		Occlusal length P_4-M_3			
Recent					
Pennsylvania*	7.39	6.80–7.80	—	—	33
Natishquan River, Quebec*, and Hamilton River, Labrador*	7.66	7.30–8.00	—	—	20
Hudson Bay, Quebec*	7.84	7.60–8.20	—	—	15
Moorhead, Minnesota*	7.92	7.20–8.50	—	—	11
Aklavik NWT, Seward, Alaska*	8.20	8.00–8.40	—	—	9
Late Pleistocene					
New Paris No. 4, Pennsylvania*	8.20	8.00–8.30	—	—	4
		Alveolar length P_4-M_3			
Late Pleistocene					
Clark's Cave, Virginia*	8.68	8.15–9.20	0.30	3.46	20
Baker Bluff Cave, Tennessee	8.48	8.24–8.73	—	—	4
Robinson Cave, Tennessee**	8.70	8.65–8.70	—	—	2
		Occlusal length M_1 or M_2			
Late Pleistocene					
Baker Bluff Cave, Tennessee	2.01	1.84–2.32	0.12	5.85	30
		Occlusal width M_1 or M_2			
Late Pleistocene					
Baker Bluff Cave, Tennessee	2.21	1.94–2.72	0.21	9.51	29
		Occlusal length M^1 or M^2			
Late Pleistocene					
Baker Bluff Cave, Tennessee	1.95	1.64–2.32	0.14	7.16	31
		Occlusal width M^1 or M^2			
Late Pleistocene					
Baker Bluff Cave, Tenn.	2.36	2.04–2.72	0.16	7.85	30

* Measurements from Guilday et al., 1977.
** Measurements from Guilday et al., 1969.

to *Tamiasciurus* was 40%, but increased to 70% in levels 7–10 ft. The gray squirrel is a more temperate species and its relative increase in numbers with depth suggests a more temperate environment during lower-level depositional times. The presence of gray squirrel throughout the stratigraphic column is a reflection of the low latitude of the cave and its distance from periglacial effects. *S. carolinensis* was scarce at Clark's Cave, Virginia, 2° latitude father north, where the percentage of *S. carolinensis* to *T. hudsonicus* was only 1.1%. Two degrees farther north of Clark's Cave, at New Paris No. 4, Pennsylvania, only *T. hudsonicus* was present.

Martin and Webb (1974) point out that *S. niger* is absent from all but late Pleistocene/early Holocene deposits in Florida. They believe that *S. niger* dates back only 8,000 years in Florida and speculate that it may have been a northern invader. The apparent absence of *S. niger* from Baker Bluff Cave in eastern Tennessee during the late Pleistocene does not bear this out. Undated *S. niger* remains, two complete skulls covered with thin layers of flowstone (CM 8050–8051), were recovered from Robinson Cave in northcentral Tennessee (Guilday et al., 1969).

Tamiasciurus hudsonicus (Erxleben)—red squirrel

Material.—CM 30097–30105. 2 incisors; 4 P^4; 38 M^1 or M^2; 8 M^3; 1 P_4; 34 M_1 or M_2; 10 M_3; 2 left, 4 right partial mandibles; 1 humerus. MNI = 18.

Remarks.—A form of red squirrel larger than *T. h. loquax,* the subspecies now occupying the southern and central Appalachians, but similar in size to red squirrels from other Appalachian cave deposits of late Pleistocene age (New Paris No. 4, Clark's

Cave) is indicated by dental and mandibular measurements (Table 9).

The red squirrel does not occur in the area, nor in the state, outside of the Great Smokies where it occurs in spruce/fir/hemlock situations above 1,000 m (Kellogg, 1939; Smith et al., 1974).

Remains of both gray squirrel (*Sciurus carolinensis*) and red squirrel were present at all levels in the deposit, but red squirrel was relatively more common in the upper levels, reinforcing the ecological shift indicated by the presence of other boreal forms in those same upper levels (Fig. 12).

Only 18 individuals were indicated from the site, 13% of all sciurids. This is one-half of the relative number of red squirrel represented from the Clark's Cave local fauna, 307 km NE. But, if we include numbers of both *Sciurus* and *Tamiasciurus* from Baker Bluff Cave, the aggregate percentage of large diurnal tree squirrels is about the same at both sites.

The percentage of large diurnal tree squirrels (*Sciurus*, *Tamiasciurus*) relative to small diurnal ground squirrels (*Tamias*, *Eutamias*, *Spermophilus*) differs from the two sites (38% arboreal, Baker Bluff Cave, 47% arboreal, Clark's Cave, Virginia). Assuming that the squirrels from both sites were raptor prey, then raptors at Clark's Cave captured a larger proportion of arboreal squirrels, suggesting that forest cover was denser at Clark's Cave during depositional times than it was at Baker Bluff Cave.

At Baker Bluff Cave the percentage of diurnal ground squirrels relative to that of diurnal arboreal squirrels dropped somewhat in the lower levels from 70% in levels 3–7 ft to 55% in levels 7–10 ft, suggesting a denser forest cover in lower level depositional times. The fact that red squirrel also became relatively less common in the lower levels suggests a warmer deciduous woodland situation.

Genus **Glaucomys** Thomas—flying squirrels

Glaucomys sabrinus (Shaw)—northern flying squirrel

Material.—CM 30117–30128. 6 left, 2 right partial mandibles; 2 right maxillae, 67 isolated molars and premolars. MNI = 13.

Glaucomys volans (Linnaeus)—southern flying squirrel

Material.—CM 30130, 30132–30135. 2 left, 1 right partial maxillae; 5 M^1 or M^2; 5 M_1 or M_2. MNI = 7.

Glaucomys, sp. (cf. **sabrinus** or **volans**)

Material.—CM 30129, 30131. 2 partial maxillae; 1 P^4; 2 M^1 or M^2.

Remarks.—Flying squirrels comprised 15% of all sciurids in the Baker Bluff deposit (19% at New Paris No. 4, Pennsylvania, 43% at Clark's Cave, Virginia, 46% at Robinson Cave, Tennessee, 63% at Natural Chimneys, Virginia) a relatively low figure for an Appalachian cave deposit, reflecting the greater relative abundance of remains of the thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*).

Glaucomys volans is common throughout the state today. *Glaucomys sabrinus* is a boreal species of the Hudsonian/Canadian Zone coniferous forests whose range extends south in the Appalachian highlands at ever increasing elevations. It is present in the Great Smoky Mountains east and south of the site at elevations over 900 m higher than Baker Bluff in hardwood-coniferous woodlands. *Glaucomys sabrinus* accounted for 65% of the Baker Bluff flying squirrels. Its presence in decreasing relative numbers in the site with depth is in accordance with other internal evidence suggesting a cooling of the environment during mid- and late-depositional times at the site.

Measurements of the fossil material (Table 10) indicate a form of *Glaucomys sabrinus* larger than present day eastern races but comparable in size to modern northern and western material and to late Pleistocene specimens from other Appalachian cave deposits (Guilday et al., 1977). *Glaucomys volans* also averaged larger in dental dimensions during the late Pleistocene in the Appalachians, but the Baker Bluff specimens, referred to *G. volans*, were insufficient for valid size inferences to be drawn. *G. volans* has been reported from numerous Pleistocene sites in Florida extending back to the Sangamonian interglacial (Webb, 1974), but Baker Bluff Cave and Robinson Cave, Tennessee, are the most southern Pleistocene stations for *Glaucomys sabrinus*.

The ratio of remains of nocturnal flying squirrels (*Glaucomys*) to those of the diurnal chipmunk (*Tamias*) in a fossil bone sample give some indication of the relative importance of owls in its formation. The percent of *Glaucomys* to *Tamias* at Baker Bluff Cave was a low 42%, suggesting that nocturnal predators such as owls played a lesser role at Baker Bluff Cave in building the fossil assemblage than at Clark's Cave (66%), Robinson Cave (66%), and Natural Chimneys (82%). The New Paris No. 4 deposit (38%) was a fissure pitfall where no owl activity was involved and the low percent of *Glaucomys* to *Tamias* reflects this. On

Table 10.—*Measurements (in mm) of* Glaucomys *Thomas.*

Age and locality	Mean	OR	SD	CV	N
		Alveolar length P^3-M^3			
Pleistocene, Baker Bluff Cave, Tennessee					
Glaucomys cf. *sabrinus*	8.15	—	—	—	1
Glaucomys cf. *volans*	6.68	—	—	—	1
		Alveolar length P_4-M_3			
Recent, Pennsylvania*					
Glaucomys sabrinus (Shaw)	7.19	6.80–7.60	.17	2.36	18
Pleistocene					
Glaucomys cf. *sabrinus*					
New Paris No. 4, Pennsylvania	7.70	7.60–8.10	—	—	3
Natural Chimneys, Virginia	7.80	7.30–8.40	—	—	14
Clark's Cave, Virginia	8.00	7.60–8.60	.01	1.19	30
Robinson Cave, Tennessee	7.80	7.00–8.70	—	—	8
Baker Bluff, Tennessee	7.90	7.70–8.40	—	—	7
		Anteroposterior crown length M_1 and M_2			
Recent, Pennsylvania					
Glaucomys volans (Linnaeus)**	1.57	1.45–1.75	.10	6.83	34
Glaucomys sabrinus (Shaw)*	1.69	1.45–1.94	.13	7.65	36
Pleistocene, Baker Bluff Cave, Tennessee	1.65	1.45–2.01	—	—	29
		Crown width M_1 and M_2			
Recent, Pennsylvania					
Glaucomys volans (Linnaeus)**	1.71	1.55–1.94	.12	6.99	34
Glaucomys sabrinus (Shaw)*	1.81	1.65–2.13	.15	8.26	36
Pleistocene, Baker Bluff Cave, Tennessee	1.97	1.69–2.42	—	—	29

* CMNH Recent mammal collection: 31603, 31604, 31606, 31607, 31609–31611, 36392, 36394–36402, 37134.
** CMNH Recent mammal collection: 34318–34325, 34327–34329, 34332, 34333, 34335–34337, 34382, 34383.

the face of it, this percentage suggests that owls were of relatively little importance in amassing the fossil deposit at Baker Bluff Cave. But a more likely possibility, strengthened by high numbers of thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*) and the presence of badger (*Taxidea taxus*), both open country forms, in the deposit is that the country was not as densely forested, a situation differentially favoring the chipmunk (*Tamias*).

Family Castoridae—Beavers

Castoroides ohioensis Foster—giant beaver

Material.—CM 24680. 1 M^1 or M^2 (illustrated in Parmalee et al., 1976). MNI = 1.

Remarks.—A single molar of the extinct giant beaver was recovered prior to the CMNH excavation by Bob Wilson and S. D. Dean, Jr., 36 to 72 in. inside the entrance, and 36 to 72 in. from the north wall at a depth of 1.5 to 2 ft, in what appears to have been the Holocene level. The molar probably belongs to the underlying late Pleistocene fauna, and the upper levels (0–3 ft) represent a chronological mix due to human disturbance. This tooth may have represented a woodrat hoard-object. *Castoroides* has been reported from an unnamed cave along the Clinch River, near Oak Ridge, Roane County, Tennessee (Parmalee et al., 1976).

Castor canadensis Kuhl—beaver

Material.—CM 30062–30064. 4 isolated molars. MNI = 3.

Remarks.—The stratigraphic distribution of these isolated teeth has no significance. Beaver were probably present throughout the depositional sequence. Lt. Henry Timberlake, in December 1761, specifically noted the abundance of beaver along the Holston River in what is now Sullivan County (Williams, 1927, in Kellogg, 1939). Smith et al. (1974) mention sporadic reports of their presence in the county today.

Family Cricetidae—New World Rats and Mice

Peromyscus, sp.—white-footed mouse [either **P.** cf. **maniculatus** (Wagner) and/or **P.** cf. **leucopus** (Rafinesque)]

Material.—CM 29994–30000. maxillae, mandibles, isolated molars. MNI = 94.

Remarks.—White-footed mouse remains were common in all levels from 3–10 ft in the deposit (Table 1). They were undoubtedly present in the upper 0–3 ft of the deposit, but small vertebrate remains were not recovered by the original excavators. *Peromyscus leucopus* and *P. maniculatus* are common in the cave area at the present time. The golden mouse (*Ochrotomys nuttali*), close to *Peromyscus* in dental morphology, has also been recorded (Phillips and Richmond, 1971; Smith et al., 1974).

M_1 morphologies, typical of *P. maniculatus* and *P. leucopus* (see Guilday et al., 1977:59, for criteria), were noted, but no stratigraphic percents were calculated due to the low frequency of recovered M_1's.

Alveolar length of M_1-M_3 of 90 mandibles averaged 3.59 mm (OR = 3.2 to 4.2 mm). This is 0.19 mm larger than the mean of 48 mandibles of a mixed *P. leucopus-P. maniculatus* sample from the late Pleistocene Clark's Cave, Virginia, deposit (Guilday et al., 1977). Some examples measured 0.5 mm larger than the largest Clark's Cave specimen. This suggests that *Ochrotomys nuttalli* may be present in the Baker Bluff Cave collection, but no molars of *O. nuttalli* morphology were noted.

A bimodal curve of M_1-M_3 alveolar length with modes at 3.4 mm and 3.7 mm suggests that the smaller *P.* cf. *maniculatus* comprised about one-third of the total sample (stratigraphic levels combined) and the larger *P.* cf. *leucopus* about two-thirds of the population sample. Frequencies ran in 0.1 mm increments of increasing size—2, 13, 15, 7, 13, 17, 9, 6, 5, 2, 1.

Neotoma floridana (Ord)—eastern woodrat

Material.—CM 24686–24692. partial crania, mandibles, isolated molars. MNI = 260.

Remarks.—The woodrat was the commonest mammal represented at all stratigraphic levels of the deposit, with the exception of voles of the genus *Microtus*. Most of the remains are, we believe, those of rats that died a "natural" death in this woodrat midden/raptor roost accumulation. This is suggested by the excellent preservation of some of the skulls compared with those of other species of small mammals, and by the high numbers of *Neotoma* remains, 18% of all rodents from the deposit. By way of contrast, woodrats accounted for only 2% of all rodents from the large, late Pleistocene raptor roost deposit at Clark's Cave, Virginia, in a similar physiographic setting.

Woodrats are common in cliff and cave habitats throughout the Ridge and Valley province but do not persist in settled areas, perhaps because they cannot compete with introduced black and/or Norway rats (*Rattus*). Smith et al. (1974) do not record *Neotoma* from Sullivan County, and characterize its distributional status as uncertain. They were probably widespread in suitable habitats at least until European settlement of the area.

Woodrats were responsible for most of the isolated teeth and bones of large mammals in the deposit. Scavenged items are a common constituent of modern woodrat middens, an expression of the animal's well-known gathering and hoarding propensities.

Family Arvicolidae—Voles

Clethrionomys gapperi (Vigors)—red-backed vole

Material.—CM 24462–24466, 24655–24661. 132 left, 153 right mandibles and/or M_1. MNI = 159.

Remarks.—Red-backed vole remains were common in the deposit at all levels, 17.6% of all voles. However, the relative frequency of *Clethrionomys* remains varied stratigraphically (Fig. 13) from over 25% of all voles in the upper levels to less than 10% in the lower levels.

The species no longer occurs at the site or in the Ridge and Valley province of eastern Tennessee. It does occur as the dominant woodland vole in northern hardwood/coniferous woodlands at that latitude east of the Ridge and Valley province in the higher elevations of the Great Smoky Mountains. Smith et al. (1974) reported it as relatively common above 660 m in Unicoi County, Tennessee. Howell and Conaway (1952) trapped a specimen in the Cumberland Mountains, about 232 km WSW of Baker Bluff Cave, in an "overgrown jumble of rocks in a growth of rhododendron and hemlock." This is the first Recent record of *Clethrionomys* from the Cumberland Plateau of Tennessee, although Barbour and Davis (1974) record it from the Cumberland Plateau of eastern Kentucky (Big Black Mountain) above 680 m elevation in northern hardwood situ-

ations. But in the Ridge and Valley province of Tennessee today *Clethrionomys* is replaced by the woodland vole, *Microtus pinetorum*.

Clethrionomys has been reported from at least two other late Pleistocene Tennessee sites situated beyond its present range—Carrier Quarry Cave, Sullivan County, 10% of all voles (CM 30216–30223; vole MNI = 212), and Robinson Cave, Overton County, 14% of all voles (Guilday et al., 1969; vole MNI = 227).

The relative decrease in numbers of *Clethrionomys* with increasing depth at Baker Bluff is in accord with the decrease of all other species of boreal affinities in the lower levels of the deposit and suggests a change from boreal to temperate conditions with depth.

Phenacomys intermedius Merriam—heather vole

Material.—CM 24467–24470, 24662–24666. 45 left, 57 right M_1; 142 additional molars. MNI = 64.

Remarks.—The heather vole occurs throughout the boreal forest of northern North America, but is no longer found in the Appalachians south of the St. Lawrence estuary. Although usually present in mid-Appalachian late Pleistocene vole faunas from Pennsylvania south to Tennessee, and in some midwestern and western deposits of Wisconsinan age (Guilday and Parmalee, 1972) it is usually the rarest species of vole encountered. Comparative percentages relative to all voles are as follows: 3.8%, New Paris No. 4, Pennsylvania; 3.6%, Natural Chimneys, Virginia; 1.6%, Clark's Cave, Virginia; 5.6%, Carrier Quarry Cave, Tennessee; 7.1%, Baker Bluff Cave.

Phenacomys remains were recovered from all levels in the deposit but diminished with depth from a high of 10% of all voles at the 3–4 ft level to a low of 1.1% at the 7–10 ft level (Fig. 13).

The habitat requirements of the heather vole, within the context of boreal forest, vary from "dry, open coniferous forests . . . with an understory of heaths" to "borders of forest and in moist mossy meadows" (Banfield, 1974:193). Their present absence from the closed-canopy northern hardwood/coniferous forests of the northern Appalachians suggests more open woodland during late Wisconsinan times in the periglacial Appalachians.

Phenacomys intermedius and *Clethrionomys gapperi* were present throughout the deposit. Both are woodland voles and their relative numbers in a given Appalachian cave deposit are usually positively correlated. But *Phenacomys* appears to be unusually abundant in two Tennessee paleofaunas studied to date. Percentages of *Phenacomys* relative to *Clethrionomys* at various Appalachian sites are as follows: 15%, New Paris No. 4, Pennsylvania; 17.5%, Natural Chimneys, Virginia; 10%, Clark's Cave, Virginia; 28.7%, Baker Bluff Cave, Tennessee; 35.3%, Carrier Quarry Cave, Tennessee. The comparative abundance of the heather vole in these two Tennessee sites, at what must have been at or near the southern limit of their Wisconsinan range expansion, is puzzling.

Microtus chrotorrhinus (Miller)—rock vole

Material.—CM 24483–24486, 24643–24747. 29 left, 25 right M^3; associated molars and partial palates. MNI = 37. (Adjusted MNI = 57, see *Microtus pennsylvanicus* account for explanation).

Remarks.—The rock vole no longer occurs at the site. This is the rarest Appalachian *Microtus* and occurs sporadically in the mountains to the east. Linzey and Linzey (1971) record the species above 800 m in the Great Smoky Mountain National Park, usually in talus or under mossy logs and rocks in high humid forest, much the same habitat as the red-backed vole *Clethrionomys gapperi*.

The rock vole was present at all levels in the deposit, but it was relatively more abundant in the upper levels (Fig. 13) and accounted for only 6.3% of all voles. Their numbers relative to those of the meadow vole (*Microtus pennsylvanicus*) were high, 30.6%, reinforcing the impression of a cool forest habitat. This percent was virtually identical with that of Clark's Cave, 30.7%, suggesting that conditions for *Microtus chrotorrhinus* were equally favorable at both sites. These figures differ markedly, however, from those of the Carrier Quarry Cave, 24 km east of Baker Bluff (CMNH collections). At that site *Microtus chrotorrhinus* formed 5.2% of the vole fauna but 10% of the *M. chrotorrhinus/M. pennsylvanicus* sample, only a third of the figure for Clark's and Baker Bluff caves. The interpretation of such varying percentiles must await the analysis of other paleofaunas.

Microtus pennsylvanicus (Ord)—meadow vole

Material.—CM 24478–24482, 24636–24642. 61 left, 65 right M^2; 72 left, 65 right M^3; isolated molars and fragmentary palates. MNI = 84; adjusted MNI = 129.

Remarks.—The meadow vole is common in suitable moist grassy habitat in the immediate area (Phillips and Richmond, 1971; Smith et al., 1974), but is here at the southwestern edge of its eastern

North American range (Hall and Kelson, 1959). It is absent from west Tennessee (Severinghaus and Beasley, 1973). During late Pleistocene times its range extended much farther south, however. Webb (1974) records the meadow vole from at least four late Pleistocene sites in Florida.

Microtus pennsylvanicus was the commonest vole at Baker Bluff Cave from the 3–4 ft level, but decreased rapidly in relative abundance with depth, from 25% of all voles at the 3–4 ft level to 9.8% at the 7–10 ft level where it ran a poor third in relative numbers of voles, exceeded by three times as many *Synaptomys cooperi* and four times as many *M. pinetorum* and/or *M. ochrogaster* (Fig. 13). The decreasing abundance of *M. pennsylvanicus* with depth suggests drier conditions at the lower cave levels. This species prefers moist grasslands, although they may occur as forest enclaves.

Meadow vole remains accounted for 14.3% of all voles from the site (Fig. 16), a relatively low figure compared with that of Clark's Cave, Virginia, 32%, and New Paris No. 4, Pennsylvania, 30%. But this overall figure of 14.3% of all voles does not take into account the marked stratigraphic change from common in the upper levels of the site to scarce in the lower older levels. Thus it would be misleading to interpret the low relative number of *M. pennsylvanicus* from Baker Bluff Cave as due solely to the more southerly geographic location of the site. The meadow vole accounted for a high 31% of all voles from Robinson Cave, Tennessee (N = 227, Guilday et al., 1969), and an even higher 48% at Carrier Quarry Cave, Tennessee, only 24 km away (N = 212, CMNH collections) and just as far south as Baker Bluff. Both Robinson Cave and Carrier Quarry Cave lack some species of boreal affinity that were recovered at Baker Bluff Cave, *M. xanthognathus* for example, and probably postdate the site.

It is obvious that relative numbers of *M. pennsylvanicus* varied markedly from site to site, as well as stratigraphically, at Baker Bluff. But more data are necessary. We are at that unfortunate stage of too much data for simplistic explanations to suffice and too little to resolve the picture.

The adjusted minimum numbers of *M. pennsylvanicus* and *M. chrotorrhinus* were derived by dividing the minimum numbers of voles identified as either *M. pennsylvanicus* or *M. chrotorrhinus* on the basis of recovered M_1's (the commonest elements recovered) into two groups based on the percentage of the specifically identified M^3. This diagnostic tooth is smaller than the M_1, hence not as often recovered from fossil deposits due to its greater chance of destruction. This resulted in an adjusted increase in the minimum numbers of both species and made their numbers a truer relative approximation to the minimum numbers of other species of voles recovered from the site based on M_1 counts.

Microtus xanthognathus (Leach)—yellow-cheeked vole

Material.—CM 24487–24490. 4 left, 1 right mandible; partial skull; left maxilla; left M^3. MNI = 4.

Remarks.—The yellow-cheeked vole is now found in the Hudsonian Life Zone of Alaska and northern Canada. Remains at Baker Bluff are confined to the upper levels of the deposit (Table 1, Fig. 13), suggesting at least marginal boreal conditions during the deposition of the upper cave levels.

The former occurrence of the yellow-cheeked vole in North American periglacial sites of Wisconsinan age is well documented (Guilday and Bender, 1960; Hallberg et al., 1974). It was a common vole in sites of this age in the central Ridge and Valley province where its remains were encountered by the hundreds in such sites as Clark's Cave or New Paris No. 4, where it dominated the vole faunas. At Baker Bluff Cave, however, only four individuals were recovered, 0.4% of the minimum number of all voles, and the animal was probably at or near the southern limits of its maximum Wisconsinan range extension (Fig. 16). Two other Sullivan County sites have produced boreal voles, Carrier Quarry Cave and Guy Wilson Cave (CMNH collections), but *Microtus xanthognathus* was not present. These sites may not, however, have been contemporaneous with the Baker Bluff deposit.

Microtus xanthognathus has been recorded slightly farther south in the American Midlands during late Wisconsinan times, 36°N, Peccary Cave, Arkansas (Hallberg et al., 1974). Dental measurements are given in Table 11 and Fig. 9.

Microtus pinetorum (Le Conte)—woodland vole and/or
Microtus ochrogaster (Wagner)—prairie vole

Material.—CM 24471–24477, 24648–24654. 241 left, 254 right mandibles or M_1. MNI = 282.

Remarks.—The woodland vole (*Microtus pinetorum*) is widely distributed throughout Tennessee and is the commonest vole at the site today (Phillips and Richmond, 1971). *Microtus ochrogaster* does not occur in East Tennessee east of the Cumberland Plateau, but is common in grassy situations in west-

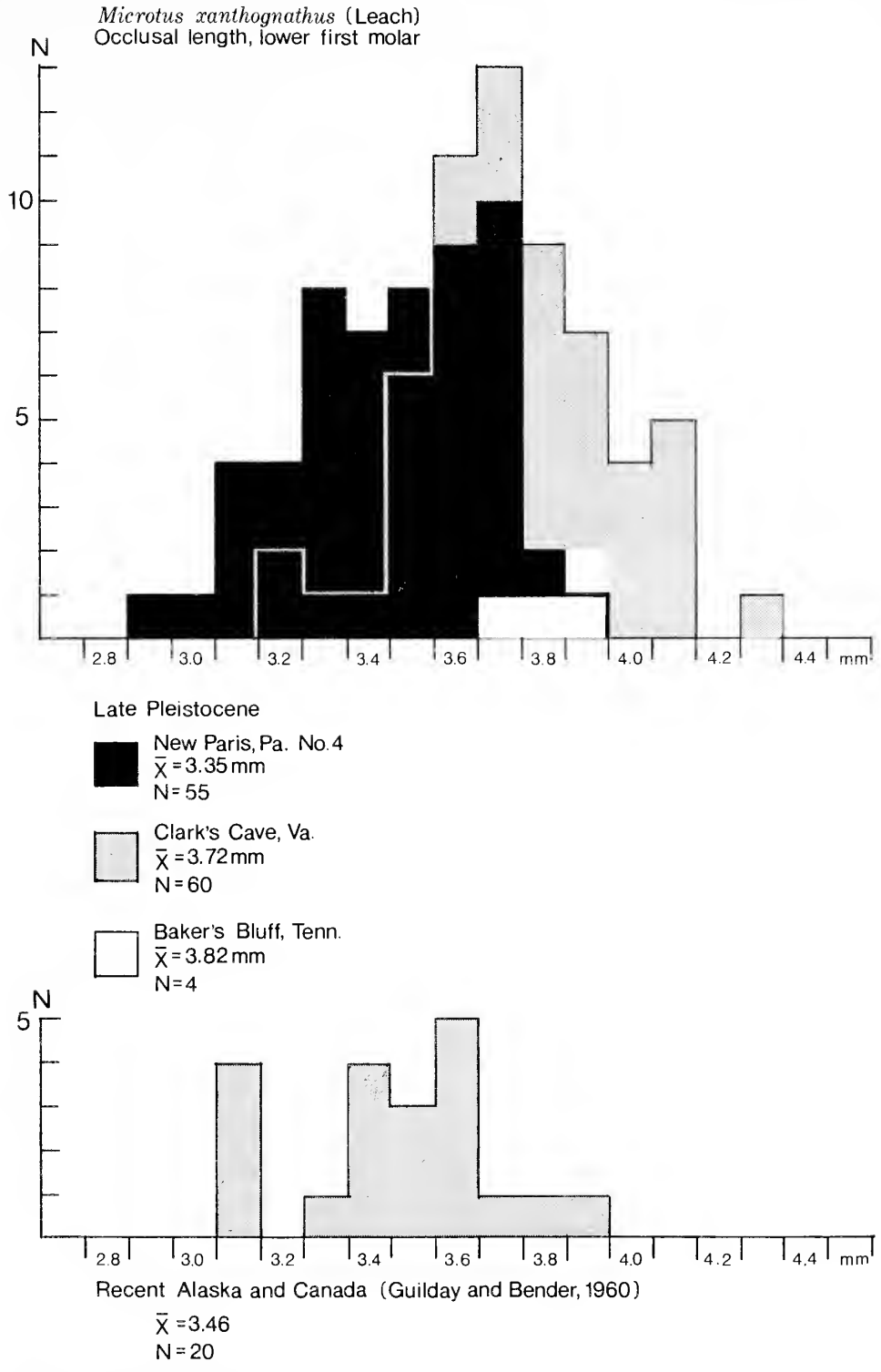

Fig. 9.—Histograms of length M_1 (in mm) *Microtus xanthognathus* (Leach), various localities.

Table 11.—*Measurements (in mm) of* Microtus xanthognathus *(Leach), various Pleistocene localities.*

Locality	Mean	OR	SD	CV	N	CMNH catalog nos.
		Occlusal length M_1				
New Paris No. 4, Pennsylvania	3.35	2.90–3.90	.22	6.34	55	6750, 6845, 6873, 6885,6930, 7150, 7171, 7179, 7185, 7192
Clark's Cave, Virginia	3.72	3.20–4.30	.215	5.78	60	24522
Baker Bluff Cave, Tennessee	3.80	3.70–3.90	—	—	4	24487–24488
		Occlusal width M_1				
New Paris No. 4, Pennsylvania	1.24	0.97–1.45	.11	8.74	56	as above
Clark's Cave, Virginia	1.29	1.07–1.46	.09	7.23	60	as above
Baker Bluff Cave, Tennessee	1.20	1.00–1.36	—	—	5	as above

central Tennessee (Phillips and Richmond, 1971; Barbour and Davis, 1974). In East Tennessee today, the meadow vole *M. pennsylvanicus* occupies the meadow, old-field niche to the exclusion of *M. ochrogaster* (Smith et al., 1974).

We do not trust our ability to differentiate *M. pinetorum* from *M. ochrogaster* on dental characters alone, the only criteria that can be used on the Baker Bluff Cave specimens. The difficulty lies in the amount of variation, individual and geographic, which cannot be satisfactorily assessed without a comprehensive study. Either or both species may be present in the deposit. We suspect both in the light of the presence of such western species as the thirteen-lined ground squirrel, least chipmunk, badger, and probably the black-billed magpie in the deposit.

M. pinetorum and/or *M. ochrogaster* accounted for 31% of the voles from the deposit. The relative numbers varied stratigraphically, increasing from 17.5% at the 3–4 ft level, to 45% at the 6–10 ft level (Fig. 13). Both are temperate species, their modern ranges stopping short of the boreal forest; *M. pinetorum* at 45°N and *M. ochrogaster* at 53°N, in the Central Plains (Hall and Kelson, 1959). No matter which of the two species is present in the Baker Bluff Cave collection, their decreasing relative numbers in the upper cave levels agrees well with the relative decrease of other temperate species from those same levels.

Relative numbers of *M. pinetorum* and/or *M. ochrogaster*, compared with those of other voles, fluctuate in late Pleistocene Ridge and Valley sites—0.9% at New Paris No. 4; 8% at Clark's Cave; 31% at Baker Bluff Cave (Fig. 16). The high figure from Baker Bluff Cave is due to its lower latitude or to an influx of *M. ochrogaster*, or both. Relative numbers of *M. pinetorum* to *M. ochrogaster* from eastern cave sites, and from the various stratigraphic levels at Baker Bluff Cave itself, might supply information about the relative abundance of deciduous woodland (*M. pinetorum*) and grassland (*M. ochrogaster*) during depositional times. Unfortunately "the state of the art" does not permit unequivocal identification from the dentition alone.

Ondatra zibethicus (Linnaeus)—muskrat

Material.—CM 30068–30070. 2 partial palates; partial left mandible; 6 isolated molars. MNI = 4.

Remarks.—Muskrat remains were scarce in the deposit, 0.4% of all arvicolids. They were also uncommon at the extensive Clark's Cave deposit, 0.2%. Both sites are primarily owl-roost deposits located beside rivers, but the low number of muskrats is probably due to predator bias. Adults are too large for many birds of prey and are protected by their semiaquatic habits.

Synaptomys cooperi Baird—southern bog lemming

Material.—CM 24448–24463, 24667–24673. 185 left, 168 right partial mandibles and/or M_1; 1 partial palate. MNI = 191.

Remarks.—Rare and local in the area today and indeed throughout most of its range, the southern bog lemming occurs here at the extreme southern edge of its range. Smith et al. (1974) record a specimen from the South Holston Dam, elevation 485 m within a few km of the site. Recent specimens are also known from Morristown, Hamblen County, 75 km SW of Baker Bluff Cave (University of Tennessee, Knoxville, collections). The southern bog lemming is seldom taken by modern trapping methods throughout the Appalachian area. They accounted for only 5.5% of all voles (N = 1,367) collected from central Pennsylvania (Gifford and Whitebread, 1951; Roslund, 1951). These results may be biased by both trapping methods and modern land usages, but at the Sheep Rockshelter, Pennsylvania, a prehistoric owl-roost deposit in the

Table 12.—*Measurements (in mm) of* Synaptomys cooperi *and* S. australis, *occlusal length* M_1.

Locality	Mean	OR	SD	CV	N
	Synaptomys cooperi Baird				
Pennsylvania, Recent*	2.48 ± .038	2.1–2.7	0.19	7.66	25
New Paris No. Pennsylvania, late Pleistocene	2.41 ± .020	2.3–2.5	0.09	3.73	20
Clark's Cave, Virginia, late Pleistocene	2.40 ± .019	2.2–2.7	0.11	4.75	33
Natural Chimneys, Virginia, late Pleistocene	2.39 ± .013	2.2–2.5	0.05	2.92	14
Robinson Cave, Tennessee, late Pleistocene	2.65 ± .014	2.3–2.9	0.122	4.61	71
Baker Bluff Cave, Tennessee, late Pleistocene	2.53 ± .007	2.2–2.8	0.13	5.21	265
Carrier Quarry Cave, Tennessee, late Pleistocene	2.55 ± .018	2.2–2.8	0.13	5.10	48
	Synaptomys australis Simpson				
Florida, CMNH collection	3.5	3.3–3.9	—	—	7

* Guilday et al., 1977:68.
** Guilday et al., 1969:57.

same area (Guilday and Parmalee, 1965) *S. cooperi* remains comprised only 7% of the voles suggesting that it was a relatively uncommon animal even prior to colonial deforestation. *Synaptomys cooperi* is also uncommon in late Wisconsinan sites from Pennsylvania and Virginia (Fig. 16), where it is usually outnumbered by remains of the northern bog lemming *S. borealis*.

Yet, surprisingly, *Synaptomys cooperi* was one of the commonest small mammals represented in the deposit at all stratigraphic levels, and in three other late Wisconsinan sites from Tennessee—Guy Wilson Cave and Carrier Quarry Cave, Sullivan County; Robinson Cave, Overton County. In the highest undisturbed level at Baker Bluff Cave, *Synaptomys cooperi* accounted for 17% of all vole remains and increased to a high of 34% in the lower 3 ft of the deposit (Fig. 13).

In addition to being more common in the area during late Wisconsinan times, *Synaptomys cooperi* remains are larger than those of modern eastern North American specimens (Table 12). There is a significant size difference between the small late Pleistocene specimens from Pennsylvania and Virginia, which average smaller in dental dimensions than Recent Pennsylvania specimens of *S. c. cooperi,* and M_1's from three Tennessee Pleistocene sites. M_1's from Baker Bluff Cave, Carrier Quarry Cave, and Robinson Cave average larger than both Recent and more northerly late Pleistocene specimens. *Synaptomys cooperi* today becomes larger with decreasing latitude, as does the Pleistocene material. This suggests there may be a yet-undemonstrated size continuum between *S. cooperi* and the large extinct *S. australis* from the Pleistocene of Florida. At present there is a size gap between the two populations, but there is also a geographic gap in Alabama and Georgia between the southern range limits of Pleistocene *S. cooperi* and the northern range limits of *S. australis* from which specimens have yet to be collected.

Synaptomys borealis (Richardson)—northern bog lemming

Material.—CM 24454–24458, 24674–24676. 10 left, 9 right partial mandibles and/or M_1. MNI = 12.

Remarks.—Remains of the northern bog lemming were scarce in the deposit, 1.3% of all voles, and largely confined to the upper stratigraphic levels (Fig. 13). This species no longer occurs in the central or southern Appalachian region. Its present range includes the coniferous forest and taiga of Canada and Alaska south to Minnesota and the White Mountains of New Hampshire, some 1,200 km northeast of Baker Bluff Cave.

The southeastern portion of the range of *S. borealis* overlaps the northern portion of the range of *S. cooperi* (Hall and Kelson, 1959). Both species are usually present in late Wisconsinan cave deposits from Pennsylvania to Tennessee. *S. borealis* is never a common species relative to other voles in such deposits, however, and becomes rarer with decreasing latitude (Fig. 16). Relative numbers of *S. borealis* to *S. cooperi* also change with latitude in late Wisconsinan Appalachian sites (Table 13). Sullivan County, Tennessee, marks the southern limit of its known late Pleistocene range.

Family Zapodidae—Jumping Mice

Zapus hudsonius (Zimmerman)—meadow jumping mouse

Material.—CM 30001–30002. 1 left, 2 right mandibles with M_1. 1 left M_1. MNI = 3.

Remarks.—Sparingly present in the upper levels

Table 13.—*Relative abundance of* Synaptomys cooperi *Baird and* Synaptomys borealis *(Richardson) in various late Wisconsinan Appalachian cave deposits, CMNH collections.*

Site	Latitude	MNI voles	% *Synaptomys cooperi*	% *Synaptomys borealis*	% *S. borealis* to all *Synaptomys*
New Paris No. 4, Pennsylvania	40°05′N.	1,212	1.32	5.8	82.0
Natural Chimneys, Virginia	38°22′N.	323	4.62	1.07	19.0
Clark's Cave, Virginia	38°05′N.	2,060	1.11	3.0	73.0
Carrier Quarry Cave, Tennessee	36°29′N.	212	14.60	—	—
Baker Bluff Cave, Tennessee	36°27′N.	899	21.24	1.3	5.9
Robinson Cave, Tennessee	36°17′N.	227	14.80	0.4	2.0

of the deposit (Table 1), remains of the meadow jumping mouse were not as common as those of the woodland jumping mouse. Both species were absent from the lower levels of the deposit which, in conjunction with other stratigraphic species shifts in the deposit, suggests more mesic conditions in the upper levels.

Zapus hudsonius has not been reported from the Ridge and Valley section of eastern Tennessee today, but it does occur farther east in the Great Smoky Mountains (Smith et al., 1974). It has been reported from low elevations farther west in the state, however (Severinghaus and Beasley, 1973), so it may occur near the cave at the present time. Remains of at least four individuals were recovered from the late Pleistocene deposits of Robinson Cave, Overton County, northcentral Tennessee. Length of M_1-M_3, one mandible, was 3.8 mm. Length of M_1, four specimens, was 1.4, 1.4, 1,4, 1.5 mm. Comparable measurements from the Robinson Cave deposit: M_1-M_3 = 3.5 mm; length M_1 = 1.2, 1.4, 1.55 mm.

Napaeozapus insignis (Miller)—woodland jumping mouse

Material.—CM 30003–30006. 3 maxillae; 2 mandibles; 2 isolated molars. MNI = 4.

Remarks.—Remains of the woodland jumping mouse in the upper levels of the deposits, from 3–7 ft depths, suggest a cooler more mesic environment than that of the lower-level fauna or the Recent local mammal fauna. At the latitude of Baker Bluff Cave the woodland jumping mouse occurs in the Great Smoky Mountains to the east, at altitudes of 760 m or more, in cool Transition or Canadian Zone hardwood/coniferous forests (Smith et al., 1974). Remains of *Napaeozapus insignis,* considerably south of their modern range, have also been reported from the late Pleistocene deposits of Robinson Cave, Tennessee, 256 km west of Baker Bluff, in association with other small mammals. Their presence at these sites suggests a cooler environment.

Dental measurements (Table 14) suggest that late Pleistocene *Napaeozapus insignis* from Robinson and Baker Bluff caves, Tennessee, were somewhat smaller than individuals from more northerly late Pleistocene deposits such as Clark's Cave, Virginia, and New Paris No. 4, Pennsylvania, thus paralleling the present day increase in size with increasing latitude (Wrigley, 1972).

Family Erethizontidae—Porcupines

Erethizon dorsatum (Linnaeus)—porcupine

Material.—CM 30065–30067. 5 isolated molars, 3 isolated premolars. MNI = 3.

Remarks.—Porcupine remains were confined to the upper levels of the deposit (Table 1). The animal

Table 14.—*Crown length (in mm)* M_1, Napaeozapus insignis *(Miller).*

Locality and age	Mean	OR	SD	CV	N
Recent					
Quebec, Ontario (CMNH collections)	1.6	1.6–1.6	—	—	3
Pennsylvania (CMNH collections)	1.6	1.5–1.8	.04	2.5	20
Late Pleistocene					
New Paris No. 4, Pennsylvania	1.8	1.7–2.1	.09	5.0	11
Clark's Cave, Virginia	1.7	1.6–1.9	—	—	27
Robinson Cave, Tennessee	1.7	1.6–1.8	.09	5.01	13
Baker Bluff Cave, Tennessee	1.66	1.6–1.8	—	—	3

is not a member of the Recent fauna of Tennessee, or of the southern Appalachians, but its remains have been recovered from caves and archaeological sites in central Tennessee, northern Alabama, and Georgia. These sites range in age from late Pleistocene to an estimated 3,000 to 5,000 years old (summarized in Corgan, 1976:11). But Bogan (1976) states that no remains of porcupines have been recovered from archaeological sites in East Tennessee. The porcupine has a predilection for rocky situations and may have survived in karst areas later than it might otherwise have during late Pleistocene climatic adjustments. Given the above fossil record its presence at Baker Bluff was expected and may not be of any climatic significance.

Order Carnivora—Carnivores
Family Canidae—Wolves and Foxes
Urocyon cinereoargenteus (Schreber)—gray fox

Material.—Dean/Wilson collection. Square 1, 0–6 in. Left humerus, immature. MNI = 1.

Vulpes vulpes Linnaeus—red fox

Material.—CM 29525, 29534, 29546. C_1; left M^2; right M_1; unassigned premolar. MNI = 3.

Remarks.—Remains of the gray fox were confined to the superficial Recent strata. Red fox remains were found only in the Pleistocene levels (Table 1).

Both red and gray fox are present in East Tennessee today. The red fox is not as common as the gray and prefers less heavily timbered areas (Smith et al., 1974). Kellogg (1939) speculates that the red fox may not have been native to the state. Evidence derived from analysis of mammal bones from pre-Columbian Indian garbage bears this out. Only gray fox remains occur in late prehistoric archaeological sites from Pennsylvania on south in eastern North America. The red fox appears to have been absent from the eastern forests south of New York state during most of Holocene times and extended its range to the south as Colonial deforestation resulted in copse-woodland, more to its liking. Red foxes have also been extensively stocked in the Southeast.

The presence of the red fox in the Pleistocene levels of Baker Bluff Cave does not contradict this picture. The presence of both boreal and steppe forms in the paleofauna suggest a more open, cooler environment compared to present day conditions and the red fox appears to have spread as far south as Florida, during at least the late Pleistocene, under the influence of expanding periglacial conditions. Pleistocene *Vulpes* remains have also been reported from Natural Chimneys, Virginia, and Vero Beach and Melbourne, Florida (Ray, 1958). With the waning of glacial conditions in post-Wisconsinan times the eastern range of the red fox contracted to the north, as far as archaeological evidence shows, to about the Pennsylvania-New York border, only to expand again within historic times under the influence of environmental changes brought on not by climatic shifts but by human land-use practices.

Family Ursidae—Bears
Ursus americanus Pallas—black bear

Material.—CM 29500, 29504–29505, 29512–29513, 29516–29518, 29545. 2 C^1; 1 C_1; 1 P^4; 1 M^2; 1 M_2; 2 M_3; 1 unassigned premolar. MNI = 4.

Remarks.—Black bear was represented by isolated teeth and a partial ulna. Teeth are comparable in size to those of Recent northeastern black bear (Table 15). These isolated elements undoubtedly represent woodrat detritus. Black bear remains are among the commonest of Appalachian cave finds.

Family Procyonidae—Procyonid Carnivores
Procyon lotor (Linnaeus)—raccoon

Material.—CM 29526, 29532, 29537, 29544. Isolated molars and premolars. MNI = 5.

Remarks.—Isolated raccoon teeth occurred at five different levels of the deposit, ranging from the surface material to the deepest 9–10 ft level. It is common in the area today and was probably so throughout the depositional history of the deposit.

Family Mustelidae—Mustelid Carnivores
Martes americana (Turton)—pine marten

Material.—CM 29509–29510, 29519, 29542. Right mandible with P_3-P_4, 2 M_1, 2 M_2, 1 M^1. MNI = 4.

Martes pennanti (Erxleben)—fisher

Material.—CM 29514. Right mandible with P_2; M_1. MNI = 1.

Mustela nivalis Linnaeus—least weasel

Material.—CM 29508, 29521, 29529. Right mandible with M_1M_2; left mandible with M_1; left M_1; 2 C; 2 P^4. MNI = 4.

Mustela frenata Lichtenstein—long-tailed weasel

Material.—CM 29507, 29520, 29527–29528, 29538–29539, 29541. Partial mandibles, isolated molars. MNI = 6.

Table 15.—Ursus americanus *Pallas, crown length and width (in mm)* M_2.

Locality	Age	OR length	OR width	N
East Tennessee, males Parmalee et al., in press	Recent	20.5–22.7	11.9–14.1	6
West Virginia archaeological sites, 46Pu31 and 46Fa7	Recent (1600 A.D.)	17.7–31.1	10.7–13.3	17
Baker Bluff Cave, Tennessee, CM 29517	Rancholabrean	18.7	11.5	1
Baker Bluff Cave, Tennessee, CM 29518	Rancholabrean	17.3	12.7	1

Mephitis mephitis (Schreber)—striped skunk

Material.—CM 29503. Right maxilla with P^3-P^4. MNI = 1.

Spilogale putorius (Linnaeus)—eastern spotted skunk

Material.—CM 29511, 29533, 29540, 29543. Partial mandible, isolated molars. MNI = 3.

Taxidea taxus (Schreber)—badger

Material.—CM 29549. I^3. MNI = 1.

Remarks.—Seven species of mustelids have been reported from East Tennessee within Recent times—fisher; striped skunk; spotted skunk; least weasel; long-tailed weasel; mink (*Mustela vison*); otter (*Lutra canadensis*) (Kellogg, 1939; Howell and Conaway, 1952; Smith et al., 1974). With the exception of the mink and the otter, both semiaquatic, all Recent species were also present in the Baker Bluff Cave local fauna. Carnivore remains are scarce in raptor deposits, their numbers, usually in inverse proportion to their size, reflecting not their relative abundance during life but the inability of raptors to handle such aggressive animals. Isolated teeth or bones of the larger species may have been introduced into the deposit piecemeal by woodrats.

Striped skunk remains were confined to the disturbed top strata and spotted skunk remains to the lower late Pleistocene levels, but this distribution may be fortuitous.

The pine marten (*Martes americana*) is no longer found as far south nor the badger (*Taxidea taxus*) as far east as Tennessee. Within historic times the pine marten occurred only as far south as central Pennsylvania, 5° north of Baker Bluff Cave and its presence complements the large boreal element present in the paleofauna. Pine marten remains have also been reported from Robinson Cave, Overton County, Tennessee, and it is frequently found in mid-Appalachian late Pleistocene cave faunas (Guilday et al., 1977).

This is the first record of badger from the Pleistocene of Tennessee. Unfortunately its site provenience is unknown. Badger remains are known from late Pleistocene sites east and south of their present prairie range at Welsh Cave, Kentucky, Bootlegger Sink, Pennsylvania, and Baker Bluff Cave, Tennessee (CMNH collections). At all three sites the thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*), another western to midwestern grassland species, was also present, indicating an eastern spread of the modified steppe biota, at least in early post-Wisconsinan times. Pre-Wisconsinan, perhaps late Kansan, badgers have also been reported from two eastern cave deposits, Fort Kennedy Cave, Pennsylvania (Cope, 1899), and Cumberland Cave, Maryland (Gidley and Gazin, 1938).

Family Felidae—Cats

Felis onca Linnaeus—jaguar

Material.—CM 29547. P_4. MNI = 1.

Remarks.—Jaguar remains are common in Tennessee caves. Guilday and McGinnis (1972) list specimens from five cave sites in the state. There are no historic records and the Baker Bluff tooth from the lowest cave level is referred to *F. o. augusta*, the extinct late Pleistocene subspecies.

Order Artiodactyla—Even-toed Ungulates

Family Tayassuidae—Peccaries

Platygonus compressus Le Conte—flat-headed peccary

Material.—CM 29548, partial upper molar. CM 30229, LdP_2. MNI = 2.

Remarks.—These two molars, from an adult and a piglet, may have been introduced by rodents. Corgan (1976) records *Platygonus* from four Tennessee sites, two of them, Worley Cave and Guy Wilson Cave, in Sullivan County. Remains of at least 16 animals with a ^{14}C date of 19,700 ± 700 yr BP (I-4163) were recovered from Guy Wilson Cave (CM 20042, 20043, 20083–20101). This extinct species is common in late Pleistocene Appalachian sites.

Table 16.—*Anteroposterior length (in mm) teeth of* Odocoileus virginianus *(Zimmerman), Baker Bluff Cave, Tennessee, late Pleistocene; Eschelman Site, Pennsylvania (36 La 12), early historic; and Chota Site, Tennessee (40 Mr 2), early historic.*

Tooth	Locality	Mean	OR	SD	CV	N
dP^3	Baker Bluff Cave	14.0	—	—	—	1
dP^4	Baker Bluff Cave	11.5	11.0–12.0	—	—	2
dP_2	Baker Bluff Cave	7.8	7.0–9.0	—	—	5
dP_3	Baker Bluff Cave	9.7	9.0–11.0	—	—	8
dP_4	Baker Bluff Cave	15.7	15.0–17.0	—	—	4
P^2	Baker Bluff Cave	11.4	10.0–12.0	—	—	5
	Eschelman Site	11.9	11.0–13.0	—	—	25
P^3	Baker Bluff Cave	9.0	8.0–10.0	—	—	3
	Eschelman Site	10.5	9.0–12.0	—	—	29
$M^{1,2,3}$	Baker Bluff Cave	13.9	12.0–15.0	—	—	15
	Eschelman Site	14.6	12.0–16.0	—	—	80
P_2	Baker Bluff Cave	8.2	7.0–9.0	—	—	9
	Eschelman Site	9.1	7.0–10.0	—	—	20
P_3	Baker Bluff Cave	10.8	10.0–12.0	—	—	5
	Eschelman Site	11.4	10.0–13.0	—	—	23
P_4	Baker Bluff Cave	11.0	10.0–13.0	—	—	10
	Eschelman Site	11.7	10.0–13.0	—	—	25
M_1 or M_2	Baker Bluff Cave	13.4	12.0–16.0	—	—	22
	Eschelman Site	14.5	12.0–17.0	—	—	53
M_3	Baker Bluff Cave	19.1	18.0–23.0	—	—	8
	Eschelman Site	20.7	19.0–24.0	—	—	26
	Chota Site	19.4	17.0–22.3	1.18	6.06	49

Family Cervidae—Deer
cf. **Cervus elaphus** Erxleben—elk

Material.—CM 29530, unerupted right M_3; CM 30226, left dP^3 (0–3 ft, Dean collection). MNI = 1.

Remarks.—Identification of CM 29530 is based primarily on size and is tentative because the tooth appears to be congenitally deformed. A normal cervid M_3 is trilobed. The posterior lobe is reduced in *Rangifer* but is prominent in other cervids. It may rarely be absent in *Odocoileus* (Guilday, 1961). The third lobe is reduced to a low cingulum in CM 29530. The external valley between the anterior and central lobe appears cramped compared with *Rangifer* or normal *Cervus elaphus* specimens. The ectostylid is absent. Size as in *Cervus elaphus*.

Elk are not present in Tennessee today, but in pre-Colonial times were common and their remains occur in Holocene archaeofaunas as far south as North Alabama (Barkalow, 1972).

Odocoileus virginianus (Zimmerman)—white-tailed deer

Material.—CM 30051–30057. 1 dP^3, 2 dP^4, 5 dp_2, 8 dP_3, 4 dP_4, 5 P^2, 1 P^2 or P^3, 3 P^3, 2 P^3 or P^4, 9 M^1, 2 M^1 or M^2, 2 M^2, 2 M^3, 2 M^1, M^2 or M^3, 10 P_2, 6 P_3, 9 P_4, 13 M_1, 11 M_2, 1 M_1 or M_2, 8 M_3, 3 incisors. MNI = see discussion below.

Remarks.—The Baker Bluff Cave white-tailed deer, at all levels, were the same size as their Recent Tennessee counterparts. Molar teeth agreed in size with historic archaeological specimens from a Cherokee Indian village site (Chota Site, 40 MR 2, Monroe County, Tennessee, Table 16). This is interesting and somewhat surprising considering the presence of boreal small mammals in the upper levels of the deposit. Modern deer become larger with increasing latitude (Doutt, no date) and one might have expected the Baker Bluff deer to have been larger than Recent local deer as a reflection of more boreal conditions. But compared with archaeological deer dentitions from only as far north as Pennsylvania (Eschelman Site, 36 LA 12), Guilday et al., 1962), Baker Bluff Cave deer are smaller in all dental dimensions by 4.8% in the upper molars and 7.6% in the lower molars (Table 16). This is also true of Pennsylvania versus Tennessee archaeological material and points up the necessity for using local comparative material if valid comparisons are to be made between Pleistocene and Recent *Odocoileus*.

If the size of northern white-tailed deer today is correlated with environment, then the size of the Baker Bluff Cave specimens do not suggest boreal conditions at the site. Although the deposit extends throughout the late Pleistocene and early Holocene and environmental change during that period is evident throughout the stratigraphic column there was

no correlation between dental dimensions of deer and depth in the deposit.

Some measure of the stratigraphic dispersal of large mammal elements in the deposit may be gained from the fact that by lumping isolated teeth from all levels, a minimum of only five adult deer and five fawns could be accounted for, but if analyzed by stratigraphic level with no reference to levels above or below, 14 adults and seven fawns were represented when levels were totaled. A broken premolar from the 8–9 ft level fit a similar fragment from the 9–10 ft level. As with all large mammals remains in the deposit, deer bones and teeth probably accumulated by sporadic woodrat caching with a greater loss of stratigraphic integrity compared to the small vertebrate, owl-deposited, debris.

cf. **Sangamona fugitiva** Hay—"fugitive" deer

Material.—CM 29501, P^4; CM 30060, left P_3. MNI = 1.

Remarks.—The P^4 was compared with the referred dentition from Frankstown Cave, Pennsylvania (CM 11044). Upper premolars of *Sangamona* are much larger relative to the molars than are those of *Odocoileus*, and there is little likelihood of confusing them with white-tailed deer on size alone. They are, however, about the size of premolars of the large *Rangifer* from the deposit. As noted by Hay (1920) the weak buccal ribbing of *Sangamona* cheek teeth appears to be definitive. The P_3, identical in cusp conformation with *Cervus* or *Odocoileus*, was referred to *Sangamona* because of its intermediate size. It differs from a P_3 of *Rangifer* in cusp conformation.

Remains of this deer have been reported from two other Tennessee localities—the type locality, Whitesburg, Hamblen County (Hay, 1920), and Robinson Cave in Overton County (Guilday et al., 1969).

Measurements of P^4 are (CM 29501), length 14.0, width 15.8 mm; P_3 (CM 30060), width 9.6 mm.

Rangifer tarandus Linnaeus—caribou

Material.—CM 24588. Left P_4 (Fig 10). CM 24681, 29502, 30058, 30061. Left P^3 or P^4; right P_2, P_4, M_2. CM 30274. Partial left humerus. MNI = 2.

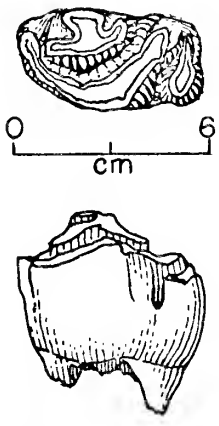

Fig. 10.—*Rangifer tarandus* Linnaeus, CM 24588, left P_4, occlusal and labial views, anterior to left, Baker Bluff Cave, Sullivan County, Tennessee.

Remarks.—One P_4, CM 24681, was found by S. D. Dean, Jr., in the upper 1 ft of the Baker Bluff Cave deposit mixed with Indian cultural refuse, but was probably displaced from the underlying Pleistocene levels by human activity. The occurrence of caribou from this and two other Tennessee cave deposits, Beartown Cave and Guy Wilson Cave, also in Sullivan County, is discussed and specimens figured in Guilday et al. (1975). This marks the southernmost North American extension of the genus *Rangifer*.

Order Perissodactyla—Odd-toed Ungulates
Family Tapiridae—Tapirs
Tapirus cf. **veroensis** Sellards—Vero tapir

Material.—CM 29522. Left P^1 (Fig. 8). MNI = 1.

Remarks.—The crown length of 18.7 mm and crown width of 15.5 mm of this isolated premolar lie within the range of *T. veroensis* Sellards, smaller than the mid-Pleistocene *T. copei* Simpson, as presented by Lundelius and Slaughter (1976). Tapirs are common Pleistocene fossils in eastern cave deposits from Pennsylvania south to Florida. Corgan (1976) records remains from nine other East Tennessee caves.

FAUNAL SUMMARY

The Baker Bluff Cave faunal sequence consists of at least 180 species of vertebrates and invertebrates—3 freshwater snails, 50 land snails, 1 mussel, 14 fish, 10 amphibians, 13 reptiles, 29 birds, and 60 species of mammals. About 2,600 individual molluscs and 2,305 vertebrates were present.

Mammals accounted for 82.8% of all individual vertebrates, birds 7.2%, amphibians 6.9%, reptiles

2.3%, and fish .67%. Fish are underestimated because of the difficulty of estimating minimum numbers of individuals from fragmentary material.

Forty-six of the 50 species of land snails still occur in the area. According to Leslie Hubricht, one species of *Stenotrema* is undescribed and has not yet been found alive. Three other land snails do not occur at the site today—*Hendersonia occulta*, present in central Tennessee; *Discus catskillensis*, a montane form reaching its southern limits in Highland County, Virginia; and *Stenotrema fraternum fasciatum*, a montane form. All other invertebrates are present in the area today.

All identified species of fish, amphibians, and reptiles still occur regionally.

Two birds, cf. *Pica pica* and *Ectopistes migratorius*, and 10 species of mammals no longer occur in the southern Appalachian area—*Sorex arcticus*, *Eutamias minimus*, *Spermophilus tridecemlineatus*, *Phenacomys intermedius*, *Microtus xanthognathus*, *Synaptomys borealis*, *Erethizon dorsatum*, *Martes americana*, *Taxidea taxus*, and *Rangifer tarandus*. Nine species of mammals occur today only at higher elevations in the southern Appalachians—*Microsorex hoyi*, *Sorex cinereus*, *Sorex dispar*, *Condylura cristata*, *Tamiasciurus hudsonicus*, *Glaucomys sabrinus*, *Clethrionomys gapperi*, *Microtus chrotorrhinus*, and *Napaeozapus insignis*. Four species were represented by forms larger than those now inhabiting the area—*Blarina brevicauda*, *Tamias striatus*, *Glaucomys volans*, and *Synaptomys cooperi*. Six taxa are extinct—*Dasypus bellus*, *Castoroides ohioensis*, *Felis onca* cf. *augusta*, *Sangamona fugitiva*, *Platygonus compressus*, and *Tapirus* cf. *veroensis*.

In summary, 29 taxa of mammals, 48% of the 60 mammalian taxa from the site, differed in some fashion from the modern mammalian fauna. Ten percent are extinct; 16.6% are found only north or west of the site in either a boreal forest or a temperate grassland habitat today; 15% have retreated to higher elevations in the southern Appalachians; and an additional 6.6% have decreased in bodily size at least locally since depositional times. No taxa of southern distribution such as *Sigmodon*, *Ochrotomys*, *Reithrodontomys*, or *Oryzomys* were present in the deposit, although each of these four rodent genera occur at or near the site today (Smith et al., 1974).

Faunal Analysis—Stratigraphic Change

There is a marked change in faunal composition between the upper and lower levels of the site (Figs. 11, 12, and 13). Those species of small mammals found in cooler regions today, either at higher latitudes in Canadian/Hudsonian zone situations or at higher altitudes in the southern Appalachians, were relatively more abundant in the upper levels of the deposit.

Stratigraphic analysis begins at the 3 ft level (3 ft from the original cave floor surface prior to the Dean excavation). All stratigraphic levels are arbitrary. Natural stratigraphic levels were either not present or were not noticed under the awkward excavating conditions. Remains of large mammals were not considered. They are present in such small numbers that statistical comparison is not feasible and their presence in the deposit is probably due to capricious woodrat scavenging.

Remains of small mammals were numerous at every level. These animals were probably collected by raptors hunting the local countryside with regularity and, unlike the sparse large mammal material, their presence, absence, or relative abundance up and down the stratigraphic column takes on interpretative significance. Minimum numbers used for stratigraphic analysis were, in the case of shrews and voles, based upon minimum numbers of individuals derived from tooth or mandible counts. In the case of the squirrels (*Marmota* omitted), numbers of M^1's and M^2's of each species were combined per level in order to increase sample sizes and lessen the effect of random fluctuations.

Results of the analysis of shrew, squirrel, and vole remains tell a consistent complementary story.

There were seven species of shrews recovered from the deposit. Only three, *Blarina brevicauda*, *Sorex cinereus*, and *Sorex fumeus*, occurred at all stratigraphic levels (Fig. 11). Two additional species of *Sorex* occurred sparingly in the upper 3–5 ft levels, *S. arcticus*, a boreal woodland species no longer found in the Appalachians, and *S. dispar*, a woodland rock-talus species found at higher elevations in the mountains east of the site. Two other shrews were also present sparingly in the upper levels, *Microsorex hoyi*, of boreal affinities and not a member of the Recent fauna of the state, and *Cryptotis parva*, a temperate grassland/old-field species. Long-tailed shrews, genus *Sorex*, were commonest in the upper stratigraphic levels, 63% of all shrews, twice as prevalent as *Blarina brevicauda*, the common temperate/woodland shrew of the Baker Bluff area today.

Blarina brevicauda increased in numbers with depth while shrews of the genera *Sorex*, *Microsorex*, and *Cryptotis* became relatively scarce or dis-

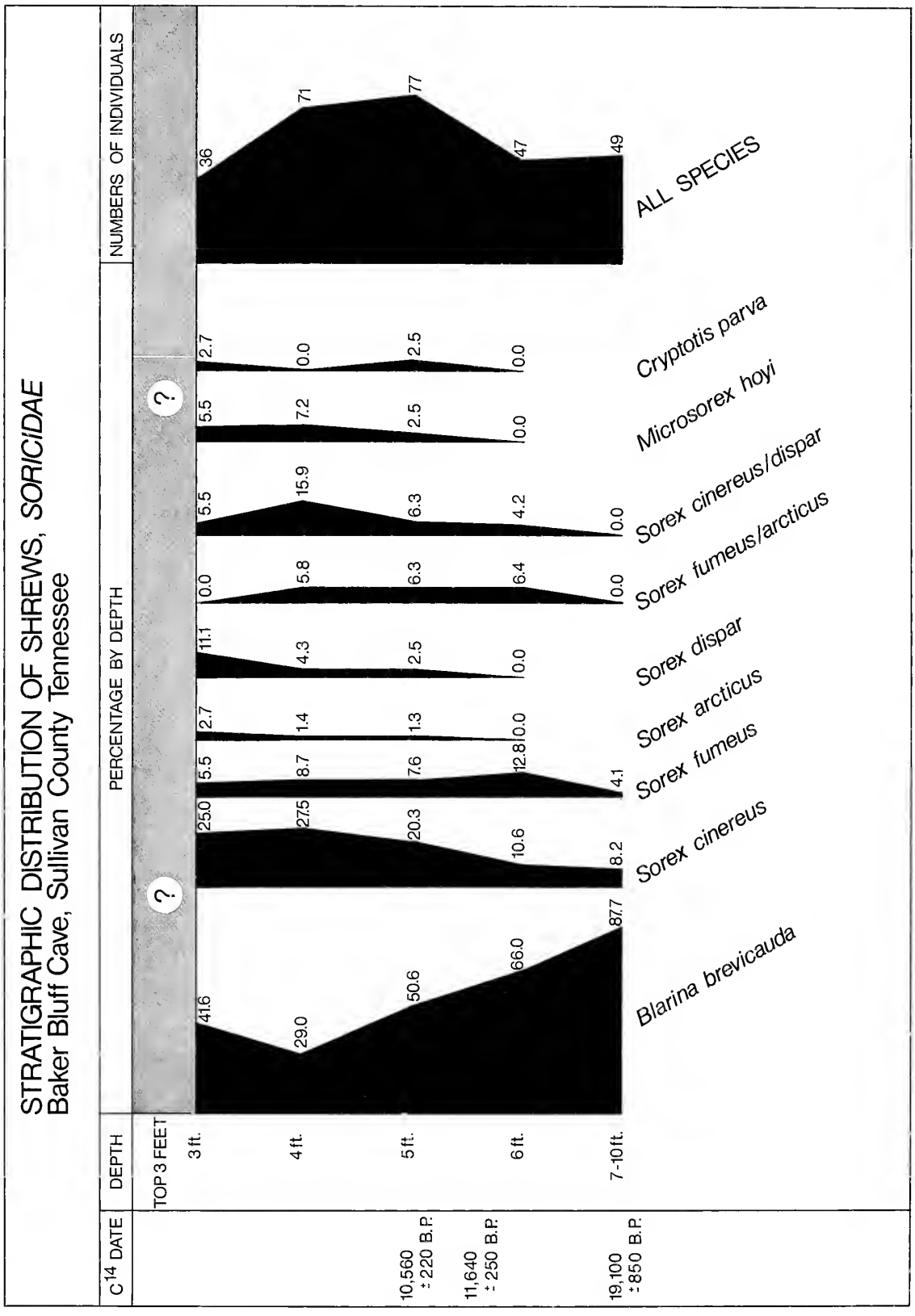

Fig. 11.—Shrews, Family Soricidae. Stratigraphic distribution, Baker Bluff Cave, Sullivan County, Tennessee.

appeared from the stratigraphic column. An interesting infraspecific situation occurs in *Blarina brevicauda* from the deposit. The upper cave levels contained two distinct sizes, a smaller form similar to *B. b. kirtlandi,* the subspecies currently found in the area, and a larger form similar to the large northern race, *B. b. brevicauda* of the Minnesota/Wisconsin area and also to the large *Blarina* from late Pleistocene sites farther north in the Ridge and Valley province, New Paris No. 4, Pennsylvania, and Clark's Cave, Virginia.

The increase in numbers and variety of soricine shrews and the influx of a northern form of *Blarina* in the upper levels of the deposit suggest a transition to cooler boreal forest conditions in the upper levels that would support shrews now confined to higher altitudes or latitudes.

Paralleling the stratigraphic behavior of the voles and shrews from the deposit, numbers of boreal sciurids, *Tamiasciurus hudsonicus* and *Glaucomys sabrinus,* increased in the upper levels (Fig. 12), whereas relative numbers of temperate species, *Sciurus carolinensis, Glaucomys volans,* and *Tamias striatus* increased with depth. The red squirrel (*Tamiasciurus hudsonicus*) and the northern flying squirrel (*Glaucomys sabrinus*) are characteristic of the northern hardwood/boreal coniferous forest belt of North America. The gray squirrel (*Sciurus carolinensis*) and the southern flying squirrel (*Glaucomys volans*) are temperate deciduous-forest forms common in the Baker Bluff area today. Numbers of the thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*), a midwestern prairie form today, increased dramatically from 2.2% in the lowest levels of the deposit to over 30% in the upper levels where it was the commonest species of sciurid. This reinforces a suggested change from closed to open-canopy forest in the upper levels of the deposit and is reflected by the correlated increase in numbers of the meadow vole (*Microtus pennsylvanicus*). The least chipmunk (*Eutamias minimus*), confined to the upper levels of the Baker Bluff deposit, also suggests a boreal parkland.

Much the same picture of stratigraphic change from cool temperate-woodland to boreal forest conditions of some sort is suggested by the voles from the deposit (Fig. 13). All boreal forest species decrease in relative numbers with depth, *Clethrionomys gapperi, Phenacomys intermedius, Microtus chrotorrhinus. Microtus xanthognathus,* a boreal taiga species today, is confined to the upper levels of the deposit. Remains of *Synaptomys borealis,* rare in this southern site, occurred throughout the stratigraphic column but become rarer relative to numbers of the temperate *S. cooperi,* with increasing depth. Only temperate species *Synaptomys cooperi* and voles of the subgenera *Pitymys* or *Pedomys,* increased in numbers with depth, and they did so markedly. A cooling trend as one ascends the stratigraphic column is suggested. A change in the woodland to grassland ratio is also suggested by a rise in relative numbers with decreasing depth of *Microtus pennsylvanicus,* a moist-grassland species, an observation reinforced by the stratigraphic distribution of the Sciuridae.

Detailed ecological reconstruction is obscured by the complicated topography of the area and the southern location of the site. While it has undergone considerable Pleistocene and post-Pleistocene change, it has done so under relatively benign conditions. Water has been available throughout its Quaternary history so that climatic changes cannot be as closely monitored by accompanying biotic changes as they can in the arid (today) West where organisms exist under more confining strictures.

Nevertheless a definite change from temperate to boreal small mammal species is noted at Baker Bluff Cave as one ascends the stratigraphic column. But the presence of such boreal species as *Synaptomys borealis* and *Phenacomys intermedius* in the lowest cave levels suggests that the lower level climatic episode was cooler than that of the Sullivan County area today.

DATING AND CORRELATIONS

Carbon-14 dates from the CMNH excavations at Baker Bluff Cave are as follows: 555 ± 185 years, BP, bone apatite, GX-3369, 4–5 ft level; 10,560 ± 220 years BP, bone apatite, GX-3370a, 6–7 ft level; 11,640 ± 250 years BP, bone collagen, GX-3370b, 6–7 ft level; 19,100 ± 850 years BP, bone apatite, GX-3495, 9–10 ft level. All dates were run on uncharred bone fragments selected from each level at

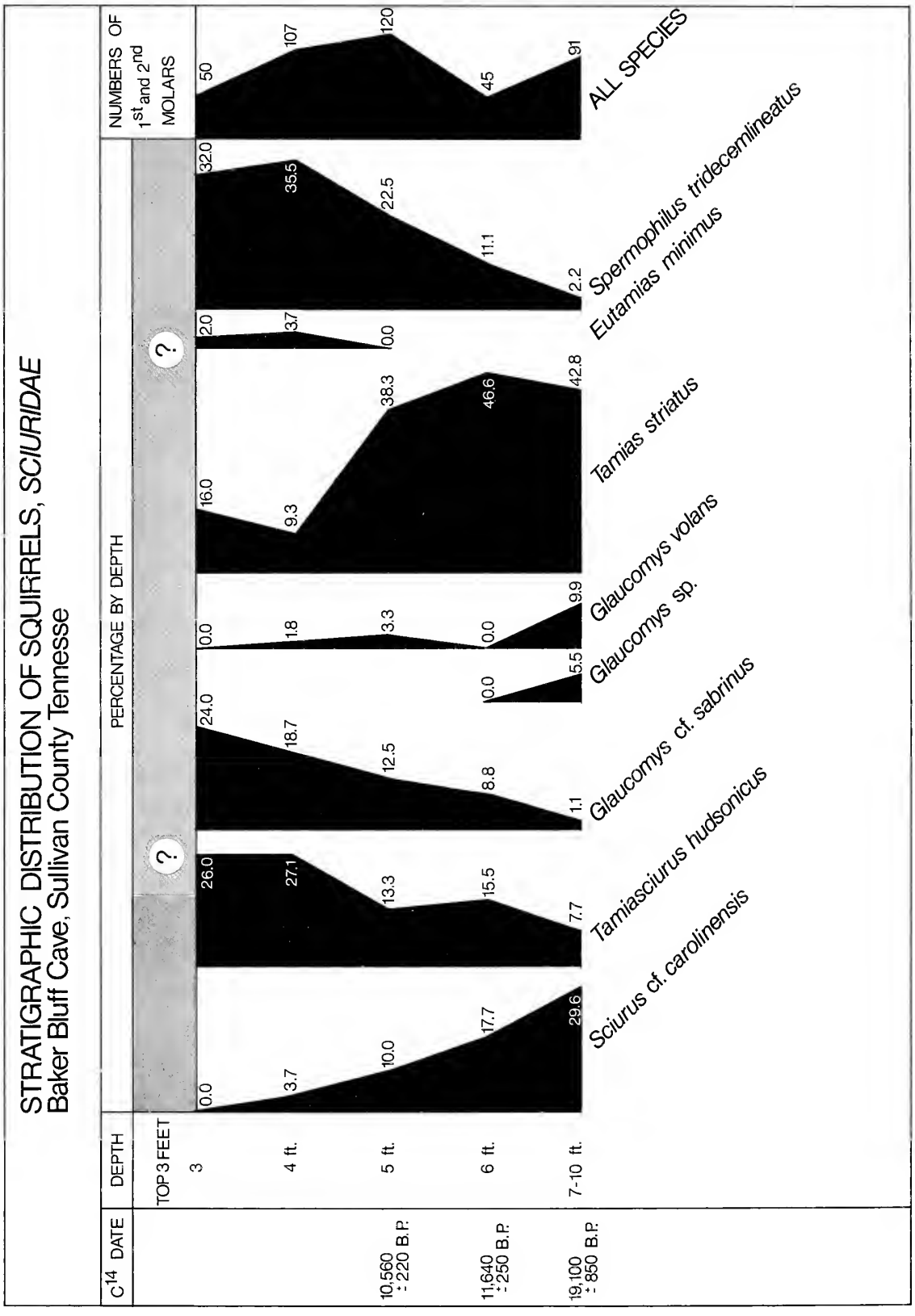

Fig. 12.—Squirrels, Family Sciuridae (*Marmota monax* omitted). Stratigraphic distribution, Baker Bluff Cave, Sullivan County, Tennessee.

random. Surface contamination may be present due to modern plant roots occurring throughout the deposit and perhaps from rodent burrowing. This is suggested by the relatively late date at the 4–5 ft level. Dates below 6 ft indicate a late Wisconsinan sequence.

The basal date of 19,100 ± 850 years BP suggests that infilling began in full-glacial times. The faunal interpretation indicates a transition from cool-temperate to boreal as deposition proceeded. This suggests that deposition occurred during the recovery phase of an interstadial. Alexsis Dreimanis, University of Western Ontario (personal communication), tentatively suggests that deposition at Baker Bluff Cave may have begun during the Connersville Interstadial, from 22,000 years BP to slightly less than 21,000 years BP. During this time the Laurentide ice mass retreated from its maximum boundary some 40 to 100 km over a broad front in Indiana and Ohio and the climate was apparently less severe. "The presence of spruce wood and even 'forest bed' in the Connersville interstadial silts suggests that open woodland probably reoccupied the area deglaciated during this interstade, and the climate was not too rigorous" (Dreimanis, 1977:74). It is possible that the more temperate conditions suggested by the lower level paleofauna at Baker Bluff Cave may record this interstadial or the influence of its later stages as climatic deterioration began again. The depositional sequence may record the transition from interstadial to renewed glacial conditions. Pollen studies from Quicksand and Bob Black Ponds, Bartow County, Georgia, 34°19′30″N, 310 km SW of the cave in the Ridge and Valley province, do not seem to indicate any interstadial oscillations after 22,900–20,100 years BP. Rather, a *Pinus-Picea* full-glacial boreal pollen assemblage followed in early postglacial times by a *Quercus*-dominated flora superseded by a modern *Pinus*-dominant woodland (Watts, 1970), is indicated.

It remains to be seen whether short-term interstadial oscillations produced relatively large-scale biotic adjustments as far south as Tennessee. The faunal change recorded in the Baker Bluff Cave deposits suggests that they might, assuming that the accompanying ^{14}C dates are correct. Watts' data suggest that they do not. The presence of tree roots throughout the excavation may cast doubt as to the validity of the dates. They may be too young and the deposit may represent a time interval prior to the full Wisconsinan maximum when climatic conditions were worsening.

THE RIDGE AND VALLEY PROVINCE FAUNAL GRADIENT

Three late Pleistocene cave deposits, New Paris No. 4, Pennsylvania, Clark's Cave, Virginia, and Baker Bluff Cave, Tennessee, lie along a 550 km transit of the Ridge and Valley physiographic province, 150 km, 340 km and 370 km respectively southeast of the terminal Wisconsinan moraines (Fig. 1). Sites and morainal lines trend northeast/southwest so that the distance differential south of the maximum continental glaciation is less than their actual distances apart. The three sites are spaced approximately two degrees of latitude from each other and extend from 40°N to 36°30′N. The maximum southern limit of the Laurentide Ice Sheet was approximately 39°N in the central lowlands of Illinois, Indiana, and western Ohio (Flint, 1971).

The sites lie in the unglaciated portion of the Ridge and Valley province (= Valley and Ridge province of Hunt, 1974), a narrow belt of long even-crested NE/SW trending parallel ridges and intermontane valleys formed of folded Paleozoic rocks 80 to 120 km wide lying between the Appalachian Plateau (Allegheny Plateau to the north, Cumberland Plateau to the south) and the higher pre-Cambrian Great Smoky Mountain/Blue Ridge/South Mountain range on its eastern boundary. Ridgetop elevations average 480 m, valley floors 360 m. The central portion of the Ridge and Valley province lies in the rainshadow of the Appalachian Plateau. This is especially marked in its central portion and has produced mildly xeric "shale barrens" that occur along the crest of low shale hills on the valley floors from southern Pennsylvania south to southern Virginia (Keener, 1970) and support several plant endemics of midwestern and coastal plain affinities. The drop in precipitation may be as much as 25–35 cm just east of the plateau at New Paris No. 4, Pennsylvania; it is also apparent at the latitude of Clark's Cave, Virginia, but is hardly evident as far south as Baker Bluff, Tennessee.

The topography of the Ridge and Valley province is such that a number of long parallel sheltered val-

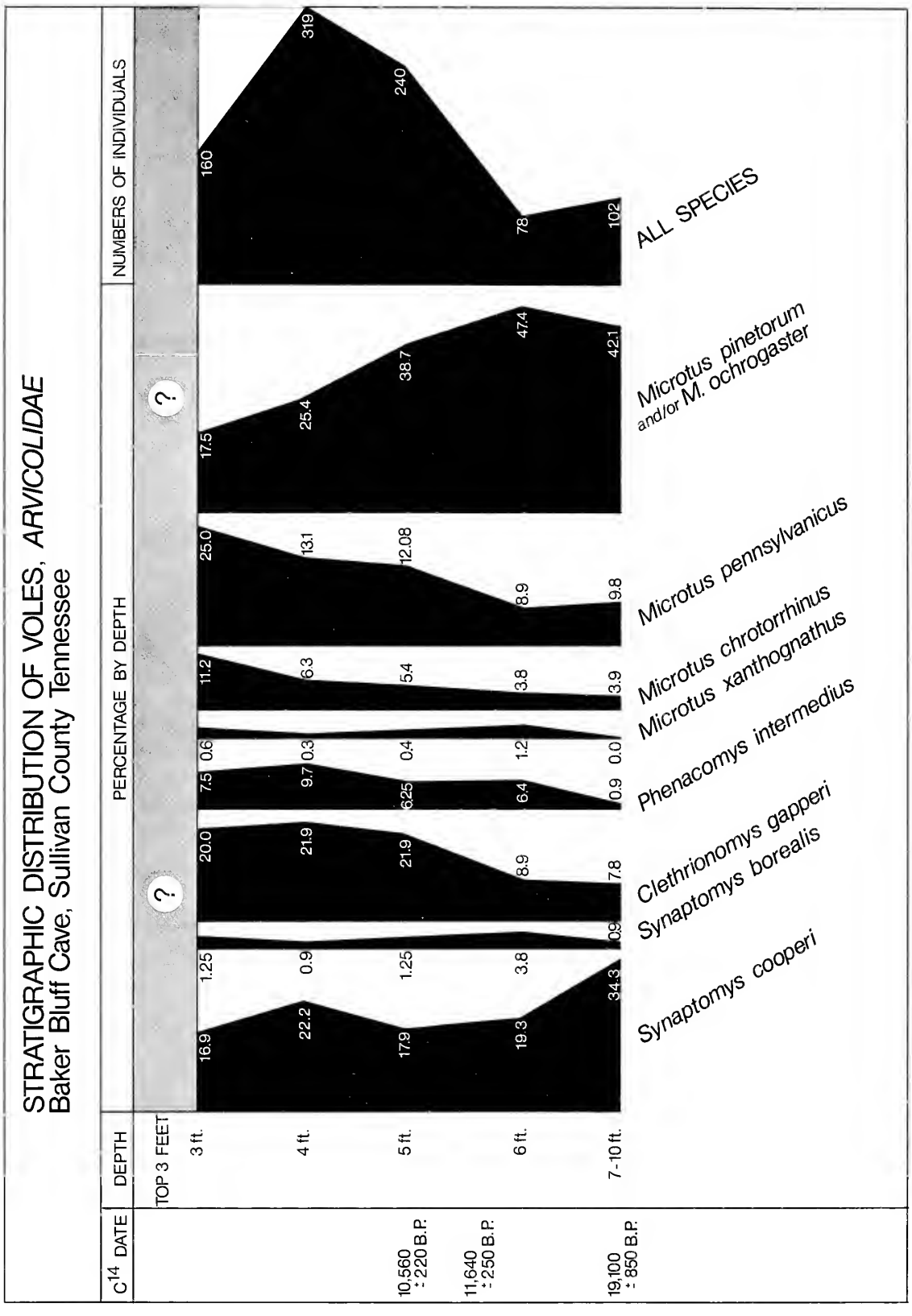

Fig. 13.—Voles, Family Arvicolidae (*Ondatra zibethicus* omitted). Stratigraphic distribution, Baker Bluff Cave, Sullivan County, Tennessee.

leys lead south or southwest from the former continental glacial margin directly into the southland unencumbered by any topographic obstacles for over 1,300 km. These long conduits, walled by ridges, should have furnished ideal migratory routes for northern late Pleistocene megafauna. They could also have provided relatively sheltered lanes for the northern penetration of tapir or armadillo into the central Appalachians.

The three sites are all late Wisconsinan or early Holocene but may not be exactly contemporaneous. New Paris No. 4, Pennsylvania, was a 10-m sinkhole fissure choked with colluvium, clay, and bones with a pollen profile indicative of an open *Picea/Pinus* cf. *banksiana* woodland and a ^{14}C date of 11,300 ± 1,000 years BP. Infilling was relatively rapid and the site data is interpreted as representing a transition from an open to a closed boreal woodland. Remains of 2,430 individual mammals were recovered.

Clark's Cave, Virginia, 243 km to the south of New Paris No. 4, was an extinct raptor roost at the mouth of a large cave. Its precise age is unknown, probably late Wisconsinan. Remains of 4,343 individual mammals were recovered.

Baker Bluff Cave, Tennessee, 307 km south of Clark's Cave, 550 km south of New Paris No. 4, was a 3-m stratified fissure fill just inside the antechamber of a small cave. Radiocarbon dating suggests that deposition began at about 19,000 years BP and the fauna records a transition from cool/temperate deciduous/coniferous woodland to boreal coniferous parkland. The top 1 m of the deposit was disturbed by both an aboriginal occupation and modern private excavations, so that evidence of the Pleistocene/Holocene transition was destroyed and late Pleistocene and Holocene material was intermingled. Remains of 1,909 individual mammals were recovered.

On the basis of ^{14}C dates the mid-levels of the Baker Bluff deposit, 10,560 to 11,640 years BP are contemporaneous with the New Paris No. 4 deposit. The Clark's Cave deposit is no younger than the late Wisconsinan/early Holocene faunal change about 10,000 years BP.

All three sites contain boreal, mid-continental, and eastern temperate elements in their respective paleofaunas. They demonstrate a faunal gradient both quantitatively and qualitatively in the direction boreal to temperate, from north to south. Only small mammals, shrews (Soricidae), squirrels (Sciuridae), and voles (Arvicolidae) are analyzed because of their abundance in each of the three sites (Figs. 14, 15, 16).

It is difficult to obtain a modern faunal equivalent for comparison. Most modern mammal collections are not heavily concentrated but reflect the regional ecology, agricultural lands, and multiple-growth woodlands, so that the relative numbers of small mammals do not represent the primeval climax fauna under the present climatic regime. Data are presented, however, for 1,447 soricids, 407 sciurids, and 1,367 arvicolids in the CMNH mammal collections from the Ridge and Valley section of central Pennsylvania—39°43′N to 42°N (Gifford and Whitebread, 1951; Roslund, 1951). Forest cover within the area today varies from 19% to 98% with a 22 county average of 61%. Collecting was concentrated in woodlands, forest edge, and meadowlands. Derived percentages of small mammals do not approximate those of primeval times but do accurately represent the present picture.

Small mammals at New Paris No. 4 were concentrated by tumbling into a funnel-shaped fissure opening; those at Clark's Cave and Baker Bluff by the hunting activities of birds of prey. The former site represents a local sample; the latter two microfaunas were drawn from a larger collecting area. Owls are opportunistic feeders, taking small vertebrates as they are encountered, but may differ in their habitat preferences. Some, the barn owl (*Tyto alba*) or the short-eared owl (*Asio flammeus*), hunt open country; others, such as the long-eared owl (*Asio otus*), prefer woodland and thicket.

Despite these obvious sources of bias and the fact that the data for New Paris No. 4 and Baker Bluff Cave represent pooled strata, comparative analysis does indicate some trends. As one progresses from north to south, New Paris No. 4, Pennsylvania, to Clark's Cave, Virginia, to Baker Bluff, Tennessee, the respective paleofaunas become progressively less boreal. Species of northern affinities either disappear from some faunas (collared lemming, *Dicrostonyx hudsonius*), or are present in diminishing numbers, whereas temperate species increase in relative numbers from north to south. Although boreal species are found at all three sites, the most southern of the paleofaunas, Baker Bluff Cave, most closely resembles the modern Pennsylvania temperate small mammal fauna.

Some few species did not follow this boreal to temperate gradient. The heather vole (*Phenacomys intermedius*) and the least chipmunk (*Eutamias minimus*) increased in relative numbers with dimin-

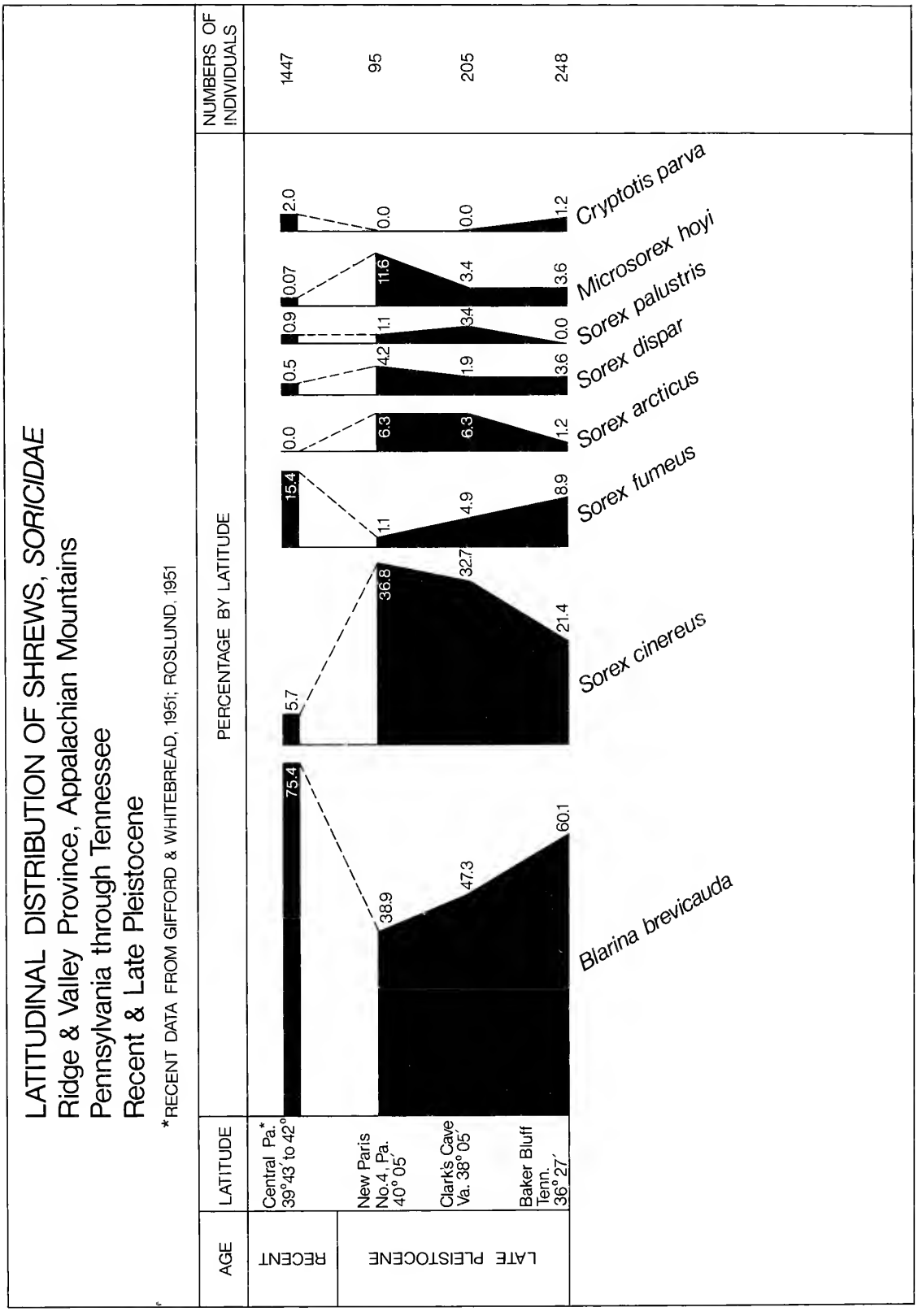

Fig. 14.—Shrews, Family Soricidae, late Pleistocene and Recent relative faunal composition, various sites, Ridge and Valley province, eastern USA.

ishing latitude. The number of *Eutamias* at any one site, however, is so low that relative numbers are meaningless, but the unexpected increase in *Phenacomys* to 7.1% of the Baker Bluff Cave vole fauna appears to have been a real event. It is supported by similar large relative numbers of *Phenacomys* (5.6% of all voles) from Carrier Quarry Cave, also in Sullivan County, Tennessee. One interesting lump of cave breccia from Carrier Quarry Cave (CM 30217) contains an incomplete but uncrushed skull of *Phenacomys* with associated mandibles and a partial skull of either *Microtus pinetorum* or *M. ochrogaster* in direct association, indicating contemporaneity of these now allopatric boreal and temperate voles. The relative increase of *Phenacomys* at Baker Bluff Cave may be associated with a marked increase in numbers of the midcontinental thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*) and the relative absence of small mammals typical of mesic environments such as soricine shrews and the meadow vole (*Microtus pennsylvanicus*).

The voles furnish the most striking evidence of the boreal affinities of these three late Pleistocene Ridge and Valley paleofaunas relative to the fauna of the Recent Appalachian area. Five species currently live in the area (Fig. 16, central Pennsylvania; *Ondatra* omitted from analysis), but nine species were present at New Paris No. 4, and at least eight at both Clark's Cave and Baker Bluff Cave. The minimum number of individual voles of species still extant in the area constituted 62% of the New Paris No. 4 fauna (51% of that contributed by just two species, *Clethrionomys gapperi* and *Microtus pennsylvanicus*, both of northern affinities). At Clark's Cave this figure increased to 70% of the vole fauna, and at Baker Bluff Cave 91% of the number of individual voles were of species still extant at that latitude (of which *Clethrionomys gapperi* and *Microtus pennsylvanicus* comprised only 34%). Thus, although all three faunas contained the same large complement of vole species (only *Dicrostonyx hudsonius* dropping out of the Virginia and Tennessee sites), the percentage of boreal to temperate species, in terms of individual animals, dropped an 8% from New Paris No. 4 to Clark's Cave, and an additional 21% from Clark's Cave to Baker Bluff.

The situation in the case of the shrews is different and reflects primarily altitudinal rather than latitudinal range shifts. There are seven species now in the mid- and southern Appalachian area. There were seven species at both New Paris No. 4 and Clark's Cave, with an additional eighth at Baker Bluff Cave (Fig. 14). Different species were involved, however. *Cryptotis parva*, a temperate field form, now present at all three localities, did not occur in either the New Paris No. 4 or the Clark's Cave paleofaunas, but the arctic shrew (*Sorex arcticus*), a boreal forest form, was added to the fauna of all three sites. There was an increase from north to south of blarinine shrews (*Blarina, Cryptotis*). But all soricine shrews (*Sorex, Microsorex*), with the exception of the smoky shrew *S. fumeus*, decreased in relative numbers with decreasing latitude. *S. fumeus* is the commonest soricine in the Appalachians today, with the broadest regional environmental tolerance and might be considered the most temperate of those species of *Sorex* identified from the three sites. Changing proportions of blarinine to soricine shrews from the three paleofaunas are New Paris No. 4, 39%; Clark's Cave, 47%; and Baker Bluff Cave, 61%.

Species of sciurids also increased slightly to the south (Fig. 15). Six species of squirrels (*Marmota* omitted from analysis) are present in the area today. Five species were present at New Paris No. 4 and seven at both Clark's and Baker Bluff caves. The additional two, *Eutamias minimus* and *Spermophilus tridecemlineatus*, are of midwestern affinities; *E. minimus* favoring central and western boreal woodlands and *S. tridecemlineatus* grasslands.

Squirrels can be divided into two groups—arboreal (*Sciurus, Tamiasciurus, Glaucomys*) and terrestrial (*Tamias, Eutamias, Spermophilus*). Arboreal species were commonest at Clark's Cave, Virginia, 69% of all sciurids. At New Paris No. 4, Pennsylvania, they comprised only 53% (50% of this *Tamiasciurus hudsonicus* and *Glaucomys sabrinus*, the only two arboreal sciurids in the North American boreal forests), suggesting a more open boreal woodland. Relative numbers of arboreal to terrestrial squirrels were lowest at Baker Bluff Cave, 47% of the sciurid fauna, again suggesting an open woodland. But, although arboreal squirrels in general declined in importance at Baker Bluff Cave, one temperate species, *Sciurus carolinensis*, nonetheless increased from 0% at New Paris No. 4, to 3% at Clark's Cave, to 13% of all squirrels at Baker Bluff Cave. This suggests a sequential change in forest composition in the Ridge and Valley province north to south from a predominantly open boreal forest at New Paris No. 4, Pennsylvania, to a denser boreal woodland cover at Clark's Cave, Virginia,

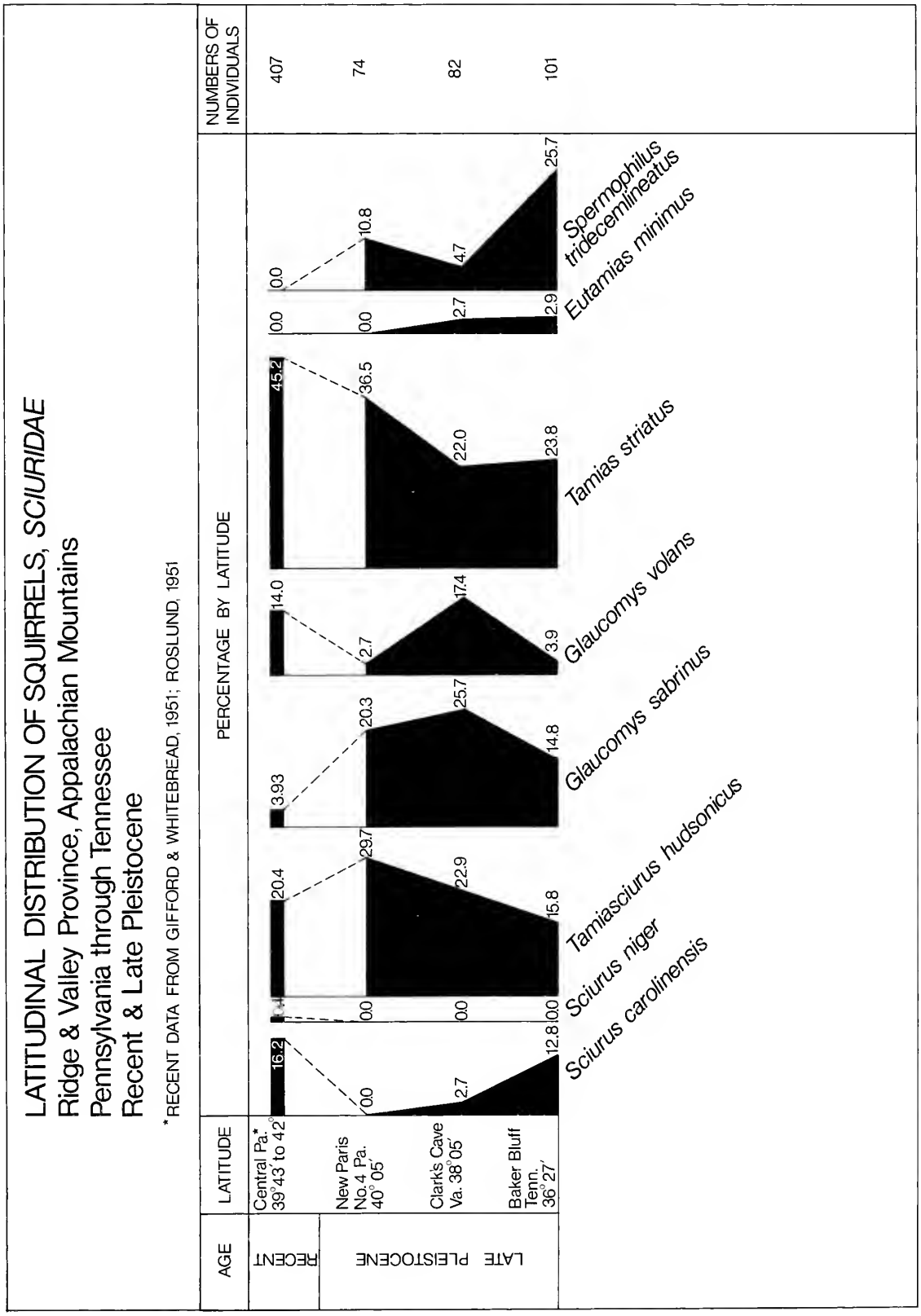

Fig. 15.—Squirrels, Family Sciuridae (*Marmota monax* omitted), late Pleistocene and Recent relative faunal composition, various sites, Ridge and Valley province, eastern USA.

to a mixed coniferous deciduous woodland at the latitude of Baker Bluff Cave, Tennessee. That all three sites were open to at least some extent is implied by the widespread late Pleistocene distribution of the thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*) in eastern North American periglacial sites from Kentucky to eastern Pennsylvania, south to at least Tennessee (Guilday et al., 1977). Its numbers were high (26% of all sciurids) at Baker Bluff Cave, where it was the commonest squirrel in the deposit, representing a distinct grasslands element.

Paleoenvironmental inferences based upon these few fossil faunas cannot be refined until additional sites are discovered and studied. But the analysis suggests that the effects of glacial cooling during the Wisconsinan glaciation profoundly affected mammalian distributions and, by inference, that of the entire biota in the Ridge and Valley province at least as far south as Tennessee. It also demonstrates the contemporaneity of both temperate and boreal species in these paleofaunas and the lack of any southern forms (except several extinct species, *Tapirus* cf. *veroensis, Dasypus bellus,* whose ecological requirements we do not know). There were no species in the Baker Bluff faunal sequence of southern affinities, which are at or near the northern edge of their modern distribution in the central Appalachians. So that while a more equitable climate is suggested, one that would allow presently allopatric boreal and temperate species to coexist, the mean climate must have been cooler.

The faunal gradient in late Wisconsinan times must have steepened south of Baker Bluff, Tennessee. Of the many boreal forms from that site only *Microtus pennsylvanicus, Erethizon dorsatum,* and *Vulpes vulpes* penetrated as far south as Florida (Webb, 1974). Ridge and Valley karst areas extend both north and south of the sites discussed here so that the late Pleistocene faunal gradient can be extended and refined by future work.

Ladds Quarry paleofauna, Bartow County, Georgia, 34°09′N, 84°50′W, 320 km SW of Baker Bluff Cave, just east of the Ridge and Valley province and south of the Great Smoky Mountains, at an altitude of about 300 m, also presents a mixture of presently allopatric species—a northern element, wood turtle (*Clemmys insculpta*), spruce grouse (*Canachites canadensis*), masked shrew (*Sorex cinereus*), fisher (*Martes pennanti*), New England cottontail (*Sylvilagus transitionalis*), southern bog lemming (*Synaptomys cooperi*); a southern faunal element which does not occur at late Pleistocene sites farther north, southern toad (*Bufo terrestris*), opossum (*Didelphis virginianus*), rice rat (*Oryzomys palustris*), cotton rat (*Sigmodon hispidus*), round-tailed muskrat (*Neofiber alleni*), hog-nosed skunk (*Conepatus leuconotus*), and ? jaguarundi (*Felis* (?) *Herpailurus*) (Holman, 1976; Ray, 1967; Wetmore, 1967).

With the exception of the spruce grouse, which reaches its present southern Appalachian limits in the Adirondack Mountains of New York, 44°N, and the wood turtle, which reaches its southern limit in northern Virginia, 39°N, the other species of northern affinities were broadly distributed throughout the Appalachian area in Historic times near the latitude of Ladds Quarry. Unfortunately the age of the site is not known, or even if it is a synchronous local fauna (see discussions in Ray, 1965, and Lipps and Ray, 1967). The presence of *Peromyscus cumberlandensis,* a species otherwise known only from two Irvingtonian age sites in the Appalachians (the type locality Cumberland Cave, Maryland, Guilday and Handley, 1967; Trout Cave, West Virginia, CMNH collections; and absent to date from all Appalachian sites of Wisconsinan age or later), in conjunction with *Platygonus compressus,* a Wisconsinan peccary, suggests that the Ladds Quarry paleofauna may in fact be heterochronic. Remains of *Neofiber alleni,* the Recent round-tailed muskrat, a Wisconsinan to Recent species, now confined to Florida and southern Georgia, 31°N, 640 km south of the Ladds Quarry paleofauna, suggests a Wisconsinan date and milder winter temperatures (Ray, 1965; Frazier, 1977). But spruce (*Picea*) pollen, indicative of a cooler environment has also been recorded from the site (Benninghoff and Stephenson, 1967).

If the Ladds Quarry paleofauna proves to be contemporaneous with the late Wisconsinan Baker Bluff Cave faunal sequence it demonstrates a steepening of the faunal gradient south of Baker Bluff Cave. As Ray pointed out, the problem can only be resolved by further fieldwork.

A comparison of the late Wisconsinan faunal gradient of the Ridge and Valley province with that of today shows significant differences. Based upon Recent small mammal ecological requirements the late Pleistocene gradient, Pennsylvania to Tennessee, was in the direction "boreal" to "temperate." Today the same gradient runs "temperate" to "austral." This reflects the regional postglacial rise in mean temperature.

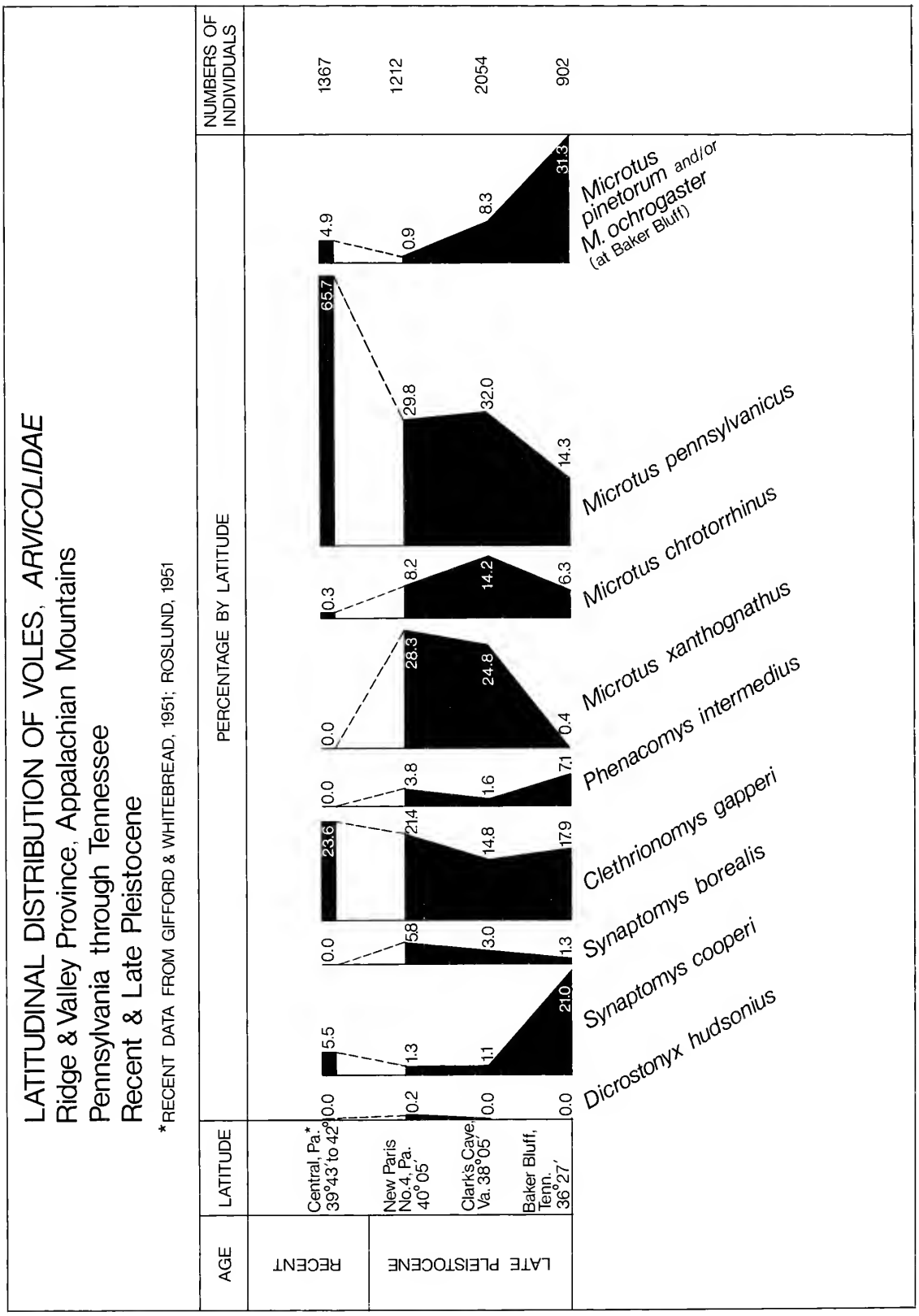

Fig. 16.—Voles, Family Arvicolidae (*Ondatra zibethicus* omitted), late Pleistocene and Recent relative faunal composition, various sites, Ridge and Valley province, eastern USA.

Perhaps the most significant fact to be drawn from the present study is that the faunal gradient is more extreme today than it was under late glacial conditions although different combinations of species are involved. This is best illustrated by comparing the two gradient sets of small rodents—cricetids, arvicolids, and zapodids. In south-central Pennsylvania, at the gradient's northern end, there are today 10 species of native small rodents (*Peromyscus leucopus, Peromyscus maniculatus, Neotoma floridana, Clethrionomys gapperi, Synaptomys cooperi, Microtus pennsylvanicus, Microtus pinetorum, Ondatra zibethicus, Zapus hudsonius,* and *Napaeozapus insignis;* Gifford and Whitebread, 1951). All but two, *Napaeozapus insignis* and *Clethrionomys gapperi,* occur throughout the gradient transect in the Ridge and Valley province south to East Tennessee. At its southern terminus at Baker Bluff Cave, 12 species of small rodents have been reported (*Reithrodontomys humulis, Oryzomys palustris, Peromyscus leucopus, Peromyscus maniculatus, Ochrotomys nuttalli, Sigmodon hispidus, Neotoma floridana, Microtus pennsylvanicus, Microtus pinetorum, Ondatra zibethicus, Synaptomys cooperi,* and *Zapus hudsonius;* Smith et al., 1974, Hall and Kelson, 1959). Four of these, *Reithrodontomys, Ochrotomys, Sigmodon,* and *Oryzomys,* do not range as far north as south-central Pennsylvania today. In other words, six out of a total of 14 species involved have restricted ranges within the transit (two reach their southern limits, four their northern limits); 43% of the small rodent fauna in the modern faunal gradient were involved in range termination.

During the late Pleistocene 15 species of small rodents were identified from the northern end of the gradient (New Paris No. 4, Pennsylvania) and 14 from its southern limit (Baker Bluff Cave, Tennessee). Only one species *Dicrostonyx hudsonius,* present at New Paris No. 4, failed to occur throughout the gradient, although there were changes in abundance of other species from north to south. There were no northern range terminations. Only 7% of the late Pleistocene small rodent fauna (one species) was involved in range terminations, contrasted with 43% in the modern faunal gradient.

A comparison of these two Ridge and Valley faunal gradients indicates that environmental conditions during late Pleistocene times were definitely boreal in character but more equable than today throughout the transect. This reinforces the concept of Pleistocene climatic equability developed primarily from Great Plains fossil faunas by the late C. W. Hibbard and others since the 1960s. Graham (1976) suggests that the increasing continental climate of the postglacial (heightened seasonality) accentuated climatic gradients, narrowed ecotones, and established the present diversities and distributional patterns. The Baker Bluff Cave faunal sequence and other Ridge and Valley late Pleistocene faunas bear out this concept.

FAMILY COMPOSITION OF THREE RIDGE AND VALLEY MAMMALIAN PALEOFAUNAS

Representatives of 20 mammalian families have been recovered from three large late Pleistocene cave faunas in the Ridge and Valley province—New Paris No. 4, Clark's Cave, and Baker Bluff Cave (Table 17). Dasypodidae, Tayassuidae, and Tapiridae represented by extinct species, no longer occur in the Appalachian region. The opossum sole representative of the Didelphidae, has not been found in a Pleistocene context in any Ridge and Valley site, although it is common in the area today. The Baker Bluff Cave record is based on bones of a Recent animal from the surface deposits.

Small mammals, marmot size or less, predominate in these faunas where they form 99% of all individual mammals from New Paris No. 4, 99% from Clark's Cave, and 96% from Baker Bluff Cave. The large numbers of small mammals reflects raptor bias at Clark's Cave and Baker Bluff Cave, both owl-roost deposits, and at New Paris No. 4 inadvertent trapping of unwary animals tumbling into a funnel-shaped sinkhole.

Bats, Vespertilionidae, fluctuated dramatically from a high of 42% MNI at New Paris No. 4, representing natural mortality of the resident bat colony, to 36% MNI at Clark's Cave, due to selective predation by raptors at a large cave system entrance, to a low of 2.4% MNI at Baker Bluff Cave, attributable to a low resident bat population in that unsuitably small cave.

Small rodents of the families Cricetidae, Arvicolidae, and Zapodidae formed the largest portion of each fauna; 50% at New Paris No. 4, 54.5%,

Table 17.—*Mammalian composition of three Appalachian cave deposits based upon minimum number of individuals (MNI).*

Family	Common name	New Paris No. 4, Pennsylvania (MNI = 2,957)	Clark's Cave, Virginia (MNI = 4,343)	Baker Bluff Cave, Tennessee (MNI = 1,910)
Didelphidae	opossums	—	—	.05%
Soricidae	shrews	3.61%	5.30%	14.55%
Talpidae	moles	.10%	.59%	1.67%
Vespertilionidae	evening bats	41.76%	35.78%	2.40%
Dasypodidae	armadillos	—	—	.05%
Leporidae	rabbits and hares	1.75%	.55%	4.97%
Sciuridae	squirrels	2.80%	2.69%	7.12%
Castoridae	beavers	—	—	.20%
Cricetidae	New World rats and mice	8.04%	6.26%	18.53%
Arvicolidae	voles	41.02%	47.43%	47.22%
Zapodidae	jumping mice	.57%	.85%	.30%
Erethizontidae	porcupines	.10%	.02%	.15%
Canidae	wolves and foxes	—	.02%	.20%
Ursidae	bears	—	.02%	.20%
Procyonidae	raccoons	—	.02%	.26%
Mustelidae	weasels, otters, etc.	.16%	.36%	1.09%
Felidae	cats	—	—	.05%
Tayassuidae	peccaries	.03%	—	.05%
Cervidae	deer	—	.04%	.78%
Tapiridae	tapirs	—	—	.05%
		99.94%	99.91%	99.89%

Clark's Cave, and 66% at Baker Bluff Cave. Insectivores, Soricidae and Talpidae, formed a low 4% MNI at New Paris No. 4, and 6% MNI at Clark's Cave, but a much higher 16% at Baker Bluff Cave, a mathematical artifact caused primarily by the low percentage of bats from the latter site. If bats had been eliminated from consideration at New Paris No. 4 and Clark's Cave, insectivores would have constituted a larger percentage of those faunas. The percent of small rodents to shrews is actually much the same at all three sites, about the same as that of the Baker Bluff Cave local fauna.

Carnivore remains—Canidae, Ursidae, Procyonidae, Mustelidae, Felidae—are rare in raptor sites. Only weasels, genus *Mustela,* appear with some consistency; their small size makes them vulnerable to predation. The almost total absence of carnivores from the sinkhole fauna of New Paris No. 4 is due to the small size of the fissure, the alertness and agility of most carnivores, and the absence of skunks (*Mephitis*) from that boreal fauna. (Skunks, because of their myopic, terrestrial habits, are common in Holocene sinkhole faunas in the New Paris area, Guilday and Bender, 1958.) The slightly larger percentage of large mammal remains at Baker Bluff Cave, Tennessee, all represented by isolated teeth or bone fragments, is due to woodrat scavenging. None of these sites present true cross-sections of the paleofaunas they sample. However, they may fairly approximate the relative abundance of small mammals present in the samples areas that can be profitably compared with other local faunas where the depositional and recovery factors are similar.

Relative percents at these three sites were based upon recovery procedures using screens of both 5-mm and 1-mm grid size for specimen recovery. The sites had not been exposed to selective processes such as weathering, water-sorting, or differential chemical decomposition, and are all primary deposits. As a result postdepositional disruption was minimal and specimen recovery thorough. These factors could drastically affect relative faunal composition and should be kept in mind when comparing fossil faunas.

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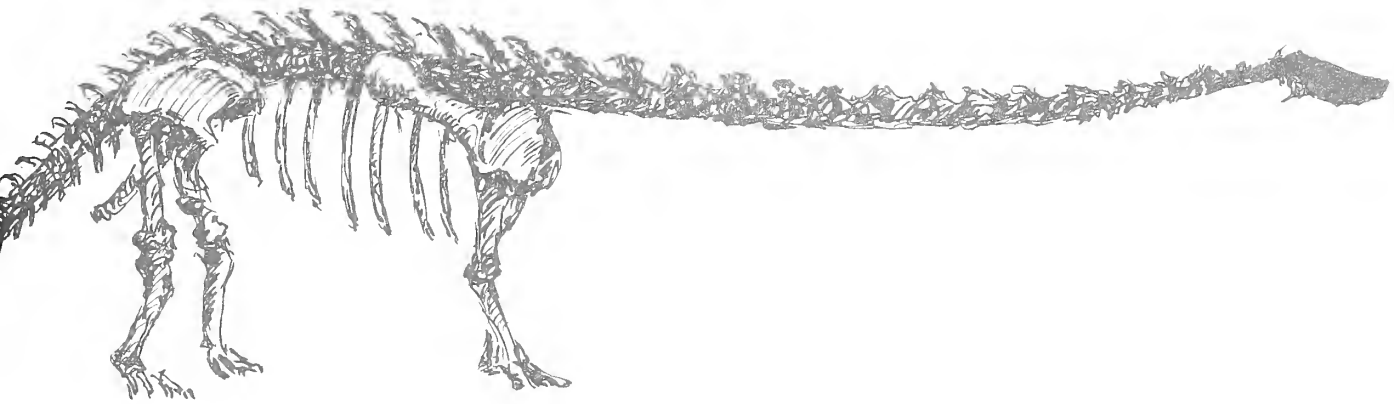

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PIERRE SWANEPOEL AND HUGH H. GENOWAYS

NUMBER 12

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PIERRE SWANEPOEL
Resident Museum Specialist, Section of Mammals
(permanent address: Kaffrarian Museum, King William's Town, 5600, Republic of South Africa)

HUGH H. GENOWAYS
Curator, Section of Mammals

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ABSTRACT

Nongeographic and geographic variation have been analyzed in the genus *Brachyphylla*, which belongs to the Antillean endemic subfamily Phyllonycterinae of the family Phyllostomatidae. Males were found to be generally larger than females; therefore, the sexes were analyzed separately for geographic variation. External measurements except length of forearm were found to display a high degree of individual variation. They were not used in subsequent analyses. Of cranial measurements, greatest length of skull and condylobasal length showed the least individual variation, whereas palatal length, postorbital breadth (in samples from west of the Mona Passage only), and rostral width at canines showed relatively high coefficients of variation. Variation in color was found not to follow any geographic pattern.

Two species—*Brachyphylla cavernarum* and *B. nana*—were recognized in the genus. *B. cavernarum* occurs on Puerto Rico, the Virgin Islands, and the Lesser Antilles as far south as St. Vincent. Three subspecies are recognized. Populations of large bats occur on St. Croix in the Virgin Islands and the Lesser Antilles as far south as St. Vincent. The smallest individuals occur only on the island of Barbados. Populations of bats of intermediate size, described herein as a new subspecies, occur on Puerto Rico and most of the Virgin Islands. *Brachyphylla nana* is a monotypic species occurring on Cuba, Isle of Pines, Grand Cayman, Middle Caicos, and Hispaniola and as a sub-Recent fossil on Jamaica.

INTRODUCTION

Bats of the genus *Brachyphylla* belong to the subfamily Phyllonycterinae. This subfamily, which is endemic to the West Indies, belongs to the family Phyllostomatidae, the New World leaf-nosed bats. Members of the genus *Brachyphylla* occur throughout most of the Greater and Lesser Antilles south to St. Vincent and Barbados, and in the Bahamas on Middle Caicos Island. The genus is known on Jamaica only from fossil material.

The genus *Brachyphylla* was erected by Gray in 1834 to include the new species *B. cavernarum*. Gray (1838) placed the genus in the tribe Phyllostomina of the family Vespertilionidae. Gervais (1855–1856) placed the genus in the tribe Stenodermina, which subsequently was recognized as the subfamily Stenoderminae of the family Phyllostomatidae. In 1866, Gray erected the tribe Brachyphyllina with *Brachyphylla* as the sole genus. Later, Dobson (1878) included *Brachyphylla* in his group Stenodermata but stated that it was the most closely related of all known genera of phyllostomatids to the desmodontines. McDaniel (1976) in his study of the brain anatomy also thought that *Brachyphylla* was most closely allied to the Desmodontinae or possibly the Stenoderminae. H. Allen (1898) placed *Brachyphylla* in the subfamily Glossophaginae, but separated it in a group termed Brachyphyllina along with *Phyllonycteris* and *Erophylla*. Miller (1898) in describing *Reithronycteris* followed this arrangement but clearly allied *Reithronycteris* with *Brachyphylla*, *Phyllonycteris*, and *Erophylla*. Miller later changed his opinion and stated that he (Miller, 1907) could detect no indication that *Brachyphylla* was a phyllonycterine and placed it in the subfamily Stenoderminae. Here it remained until Silva-Taboada and Pine (1969) presented evidence based on osteology, behavioral characteristics, and host-parasite specificity for considering *Brachyphylla* a member of the subfamily Phyllonycterinae. Slaughter (1970) reflected on the similarity between this genus and *Sturnira* and thought it possible that these two genera, in addition to the glossophagines and stenodermines were related to some unknown common ancestor, and concluded that the dentition offers no evidence that *Brachyphylla* is any more closely related to the stenodermines than *Sturnira*. It should be pointed out, however, that *Sturnira* is now included in the Stenoderminae by most authorities.

In erecting the genus *Brachyphylla*, Gray (1834) described *cavernarum* from St. Vincent as the first species. Subsequently three additional species have been described, *nana* by Miller (1902*a*) from Cuba, *minor* by Miller (1913) from Barbados, and *pumila* by Miller (1918) from Haiti. Koopman (1968) presented evidence for considering *minor* a subspecies of *cavernarum*. Varona (1974) without presenting any evidence recognized only one species, *cavernarum*, with all other previously recognized species as subspecies thereof. Jones and Carter (1976) and Silva-Taboada (1976) recognized two species, *cavernarum* and *nana*, with *minor* as a subspecies of the former and *pumila* of the latter. Buden (1977) studying geographic variation in Greater Antillean populations agreed with Varona's (1974) arrangement.

The systematics of *Brachyphylla* remained virtually unstudied except for description of species until Koopman's work in 1968. Since that time, four additional papers have appeared dealing with this subject (Varona, 1974; Jones and Carter, 1976; Silva-Taboada, 1976; Buden, 1977). These authors have

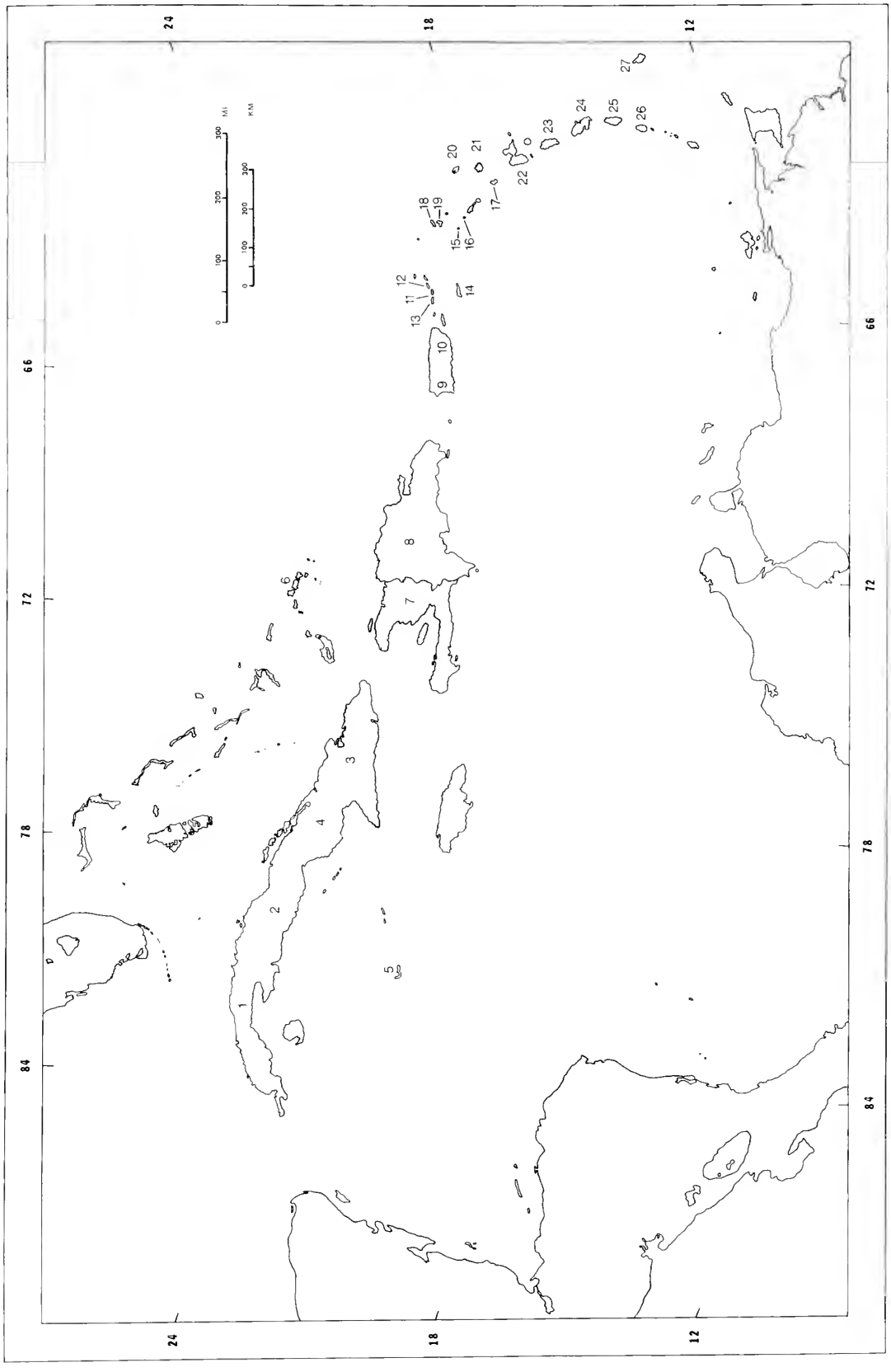

Fig. 1.—Geographic areas included in samples of *Brachyphylla*. See text for localities included in each sample.

not agreed as to how many species to recognize in the genus nor have they examined in detail variation throughout the geographic range of the genus. We have assessed herein inter- and intraspecific relationships in the genus using both univariate and multivariate analyses. We examined samples from throughout the range of the genus including fossil material from Jamaica. The results of these studies are presented below.

MATERIALS AND METHODS

In the course of this study, 648 specimens were examined. Most of these consisted of either standard museum skins and skulls or specimens preserved in fluid with skulls removed. In addition skull only, skin only, or complete fluid-preserved specimens were examined. All holotypes were examined by the authors. Individuals were judged to be adults if the phalangeal epiphyses were completely fused. Specimens consisting of a skull only were considered to be adult if the cranial sutures were well ossified.

External measurements were obtained from labels of specimens prepared as standard museum skins, except for length of forearm, which was taken with dial calipers on the dried skins and fluid-preserved specimens. This measurement was taken from the posteriormost projection of the olecranon process (elbow) to the anteriormost projecting point of the wrist with the wing flexed.

Definitions of cranial measurements are given below. All measurements are given in millimeters.

Greatest length of skull.—Greatest distance from the anteriormost projection of the incisors to the posterior portion of the occipital bone.

Condylobasal length.—Greatest distance from the anterior part of the premaxillae (not including the incisors) to the posteriormost part of the occipital condyles.

Palatal length.—Greatest distance from the posterior edge of the anterior palatal foramen to the anteriormost edge of the palate.

Depth of braincase.—Skull was placed on a microscope slide and the least distance measured from the dorsalmost portion of the skull to the ventralmost part of the slide, thereafter, the thickness of the slide was subtracted from this value.

Zygomatic breadth.—Greatest width across zygomatic arches, measured at right angles to the longitudinal axis of cranium.

Breadth of braincase.—Greatest width across braincase, measured at right angles to the long axis of the cranium.

Mastoid breadth.—Greatest width across mastoid processes, measured at right angles to the long axis of the cranium.

Postorbital breadth.—Least width across postorbital constriction, measured at right angles to the long axis of the cranium.

Length of maxillary toothrow.—Least distance from the lip of the posterior alveolus of M^3 to the anterior lip of the alveolus of the canine.

Rostral width at canines.—Least width across rostrum immediately posterior to the canines.

Breadth across upper molars.—Least distance measured at right angles to long axis of the cranium from labial side of the crowns of one maxillary toothrow to the labial side of the other toothrow.

Mandibular length.—Least distance measured from the mandibular symphysis (not including the incisors) to the midpoint of a line connecting the articular processes of the right and left mandible.

All adult speeimens from throughout the geographic range of *Brachyphylla* were grouped into 26 samples for males and 25 for females as follows (see also Fig. 1): *sample 1*—Habana Province, Cuba; *sample 2*—Las Villas Province, Cuba; *sample 3*—Oriente Province, Cuba; *sample 4*—Camagüey Province, Cuba; *sample 5*—Grand Cayman; *sample 6*—Middle Caicos, Bahamas; *sample 7*—Haiti; *sample 8*—Dominican Republic; *sample 9*—western Puerto Rico (Adjuntas, Guanica, Utuado); *sample 10*—eastern Puerto Rico (Comerio, Corozal, San Juan, El Verde, Pueblo Viejo, Trujillo Alto); *sample 11*—St. John, Virgin Islands; *sample 12*—Norman, Virgin Islands; *sample 13*—St. Thomas, Virgin Islands; *sample 14*—St. Croix, Virgin Islands; *sample 15*—Saba; *sample 16*—St. Eustatius; *sample 17*—Montserrat; *sample 18*—Anguilla; *sample 19*—St. Martin; *sample 20*—Barbuda; *sample 21*—Antigua; *sample 22*—Guadeloupe; *sample 23*—Dominica; *sample 24*—Martinique; *sample 25*—St. Lucia; *sample 26*—St. Vincent; *sample 27*—Barbados.

Selected measurements were also taken from fragmented *Brachyphylla* Pleistocene or sub-Recent fossil material from Jamaica. In order to compare these measurements to extant material similar measurements were also taken from adult specimens from the selected localities including both *Brachyphylla cavernarum* and *B. nana*. These were grouped into seven samples as follows: *sample a*—Cuba (five males, five females); *sample b*—Middle Caicos (five males, five females); *sample c*—Dominican Republic (five males, five females); *sample d*—Jamaica (fossils); *sample e*—Puerto Rico (five males, five females); *sample f*—St. John (five males, two females); *sample g*—Norman (five males, five females). The following measurements were taken from this material: *palatal length*—as for extant material; *rostral width at canines*—as for extant material; *length of maxillary toothrow*—as for extant material; *interorbital breadth*—least distance across interorbital region measured at right angles to the long axis of the cranium; *height of coronoid process*—least distance from a line connecting the angular process and ventral surface of the mandible to the dorsalmost point of the coronoid process; *width of articular process*—least width across the articular process; *mandible breadth at M_3*—least breadth of mandible at level of M_3; *length of mandibular toothrow*—least distance from posterior lip of alveolus of M_3 to anterior lip of alveolus of canine.

Dried skins examined in the study were assigned to one of the five color standards. The five specimens used for the color standards and a description of their color as as follows: 1) TTU 22761 (male)—Haiti, Dept. du Sud, 1 km S, 1 km E Lebrun, on the dorsum base of hair white, pattern blackish gray; 2) MCZ 21430 (male)—Martinique, on dorsum base of hair white, pattern blackish brown; 3) AS 5531 (female)—Puerto Rico, 17.7 km NE Utuado, on dorsum base of hair white, pattern grayish brown sometimes with buffish tint; 4) TTU 20975 (female)—Guadeloupe, Grande-Terre, 1 km N, 1 km W St. François, on dorsum base of hair white, pattern dark brown with a very faint reddish tint; 5) AS 5126 (male)—Barbados, St. Thomas Parish, Cole's Cave, on dorsum base of hair white with yellowish tint, pattern dark brown with generally more of a buffy tint than color standard 3.

Statistical analyses were performed on an IBM 370 computer at Texas Tech University. Univariate analyses of individual variation, secondary sexual variation, and geographic variation were performed using the UNIVAR program, developed and introduced by Power (1970). Standard statistics (mean, range, standard deviation, standard error, variance, and coefficient of variation) are generated by this program. In the event of two or more groups

being compared, a single-classification analysis of variance (ANOVA) to test for significant differences between or among means is employed. Sums of Squares Simultaneous Test Procedure (SSSTP) (Gabriel, 1964) was used to determine maximally nonsignificant subsets, if means were found to be significantly different. See also Smith (1972) for an overview of these statistical methods.

Some of the multivariate analyses were performed using the Numerical Taxonomy System (NT-SYS) package developed by F. J. Rohlf, R. Bartcher, and J. Kishpaugh at the University of Kansas. The samples (OTUs) were grouped localities discussed above, and the values for each character were means for the measurements. Matrices of Pearson's product-moment correlation and phenetic distance coefficients were derived. Cluster analyses were conducted using UPGMA (unweighted pair group method using arithmetic averages) on the correlation and distance matrices, and phenograms were generated for both. Only distance phenograms were used because they gave higher coefficients of cophenetic correlation than the correlation phenograms. These phenograms give a two-dimensional multivariate view of the data with characters unweighted. The first three principal components were then extracted from a matrix of correlation among characters and three-dimensional projections of the samples onto the first three principal components were made. This provides a three-dimensional view of the data with unweighted characters. For the theory and use of these tests see Sokal and Sneath (1963), Schnell (1970), Atchley (1970), Choate (1970), Genoways and Jones (1971), Smith (1972), Genoways (1973), and Sneath and Sokal (1973).

Other multivariate analyses performed involved use of the Statistical Analysis System (SAS) package developed by Barr and Goodnight (Service, 1972). Individual specimens, and not series of means as in NT-SYS, were used in these analyses. Specimens with missing data could not be used, consequently sample sizes for SAS analyses were substantially reduced in some cases. To determine the degree of divergence among samples, a multivariate analysis of variance (MANOVA) and canonical analysis were performed. Canonical analysis of the data provides weighted combinations of the characters, which maximize the distinction among groups. This analysis extracts characteristic roots and vectors and computes mean canonical variates for each sample. Additional orthogonal axes are constructed, which extract the next best combination of characters, emphasizing those with the least within sample and greatest among-sample variation, hence, providing the next best combination of characters to discriminate among samples. Each eigenvalue and its corresponding canonical variate represents an identifiable fraction of the total variation. Sample means and individuals were plotted on those canonical variates, which account for the greatest fraction of total variation. The relative importance of each original variable (character) to a particular canonical variate was computed by multiplying the vector variable coefficient by the mean value of the dependent variable, summing all variable values for a particular vector, and then computing the percent of relative importance of each variable per vector. These techniques have recently been used in the study of mammals by Schmidly and Hendricks (1976), Yates and Schmidly (1977), and Yates et al. (1978).

NON-GEOGRAPHIC VARIATION

Three kinds of nongeographic variation—variation with age, secondary sexual variation, and individual variation—are discussed in the following section.

Variation with Age

One external and 12 cranial measurements of one non-adult male from Oriente Province, Cuba, and one non-adult female from Martinique are respectively, as follows: length of forearm, —, 56.8; greatest length of skull, 26.0, 28.6; condylobasal length, 23.3, 26.0; palatal length, 7.9, 9.9; braincase depth, 11.1, 11.5; zygomatic breadth, 13.5, 15.1; breadth of braincase, 11.8, 11.7; mastoid breadth, 12.8, 13.3; postorbital breadth, 6.3, 5.9; length of maxillary toothrow, 8.9, 9.8; rostral width at canines, 6.5, 6.4; breadth across upper molars, 9.4, 10.2; mandibular length, —, 16.8.

Comparing measurements of the subadult male from Oriente Province, Cuba, with those of adult males (1–4) from Cuba (Table 1) shows that there is overlap in only four measurements (breadth of braincase, mastoid breadth, postorbital breadth, rostral width at canines). A similar comparison between the subadult and adult females from Martinique (24) shows no overlap in measurements tested (Table 1). Only adult specimens (phalangeal epiphyses completely fused) were used in the study of geographic variation.

Secondary Sexual Variation

External and cranial measurements of adult males from each sample were tested against those of adult females utilizing single classification ANOVA. This was done in order to establish if any significant differences in size exist between the sexes. The results are shown in Table 1.

In samples from west of the Mona Passage, males proved to be significantly ($P < 0.05$) larger than females in two measurements (greatest length of skull, zygomatic breadth) in specimens from Habana Province, Cuba (sample 1); in one measurement (length of hind foot) in specimens from Las Villas Province, Cuba (sample 2), and in two measurements (length of hind foot, postorbital breadth) in specimens from the Dominican Republic (sample 8). On the other hand, females were found to be significantly larger than males in one measurement (length of ear) in specimens from Las Villas Province (sample 2).

In samples from east of the Mona Passage, males

Table 1.—*Geographic variation and secondary sexual variation in external and cranial measurements of* B. nana *(seven samples of males, and eight samples of females) and* B. cavernarum *(19 samples of males and 17 samples of females). Statistics given are number, mean, two standard errors, range, coefficient of variation, F_s value. Means for males and females that are significantly different at $P < 0.05$ are marked with an asterisk. See text for key to sample numbers.*

Sample no.	Male				Female				
	N	$\bar{X} \pm 2$ SE	Range	CV	N	$\bar{X} \pm 2$ SE	Range	CV	F_s
				Brachyphylla nana					
				Total length					
1	2	79.0 ± 2.00	78–80	1.8	1	75.0			
2	2	87.5 ± 9.00	83–92	7.3	4	84.0 ± 4.90	80–90	5.8	4.581
3	1	95.0			2	93.5 ± 7.0	90–97	5.3	
4	2	82.5 ± 5.0	80–85	4.3	1	81.0			
7	1	80.0			1	79.0			
8	26	72.0 ± 1.28	65–78	4.5	25	73.8 ± 1.74	67–84	5.9	2.68
				Length of hind foot					
1	2	16.5 ± 1.0	16–17	4.3	1	16.0			
2	8	19.5 ± 0.38	19–20	2.7	4	18.0 ± 1.16	17–19	6.4	20.0*
3	1	21.0			2	21.5 ± 3.0	20–23	9.9	
4	2	18.0	18		1	19.0			
5					1	17.0			
7	1	19.0			1	19.0			
8	26	16.0 ± 0.43	13–18	6.8	25	15.3 ± 0.53	12–17	8.6	4.043*
				Length of ear					
1	2	20.0	20		1	19.0			
2	9	17.2 ± 1.04	16–21	9.1	4	21.5 ± 1.30	20–23	6.0	33.639*
3	1	21.0			2	23.0 ± 6.00	20–26	18.4	
4	2	21.0	21		1	21.0			
5					1	21.0			
6	7	20.7 ± 0.37	20–21	2.4	12	20.3 ± 0.05	19–21	4.3	1.674
7	1	19.0			1	20.0			
8	25	19.7 ± 0.55	17–22	7.0	25	19.8 ± 0.52	17–22	6.5	0.101
				Length of forearm					
1	13	59.2 ± 1.34	53.0–61.4	4.1	9	58.1 ± 0.81	56.3–59.8	2.1	1.361
2	13	58.8 ± 0.80	56.8–61.3	2.5	7	58.7 ± 1.08	57.0–61.0	2.4	0.030
3	5	59.0 ± 2.02	55.2–61.0	3.8	2	60.3 ± 0.20	60.2–60.4	0.2	0.558
4	2	55.3 ± 1.00	54.8–55.8	1.3	1	57.7			
5					1	60.2			
6	7	56.2 ± 1.81	51.5–58.3	4.3	12	56.7 ± 0.59	54.6–58.5	1.8	0.375
7	1	58.9			4	58.7 ± 0.65	57.9–59.5	1.1	
8	35	56.7 ± 0.50	53.5–59.1	2.6	29	57.2 ± 0.56	54.1–60.3	2.6	1.424
				Greatest length of skull					
1	12	28.7 ± 0.28	27.6–29.4	1.7	9	28.2 ± 0.42	27.1–29.0	2.2	4.547*
2	11	28.4 ± 0.30	27.5–29.2	1.7	7	28.4 ± 0.28	27.7–28.8	1.3	0.039
3	7	28.3 ± 0.29	27.5–28.6	1.3	3	28.5 ± 0.50	28.0–28.8	1.5	0.553
4	2	28.8 ± 0.50	28.5–29.0	1.2	1	27.4			
5					1	28.9			
6	7	28.7 ± 0.43	28.0–29.4	2.0	12	28.9 ± 0.27	28.4–29.8	1.6	0.568
7	1	28.3			4	28.6 ± 0.40	28.2–29.1	1.4	
8	34	28.3 ± 0.18	27.2–29.3	1.8	33	28.2 ± 0.18	27.1–29.0	1.8	0.639
				Condylobasal length					
1	12	25.5 ± 0.29	24.5–26.2	2.0	7	25.3 ± 0.47	24.4–26.3	2.4	0.631
2	13	25.3 ± 0.23	24.7–26.0	1.7	7	25.4 ± 0.35	24.8–25.9	1.8	0.205
3	7	25.0 ± 0.23	24.6–25.5	1.2	3	25.3 ± 0.70	24.6–25.7	2.4	0.829
4	2	25.4 ± 0.20	25.3–25.5	0.6	1	24.4			
5					1	25.6			
6	6	25.4 ± 0.43	24.5–25.9	2.1	12	25.3 ± 0.23	24.7–26.0	1.6	0.280
7	1	24.9			4	25.2 ± 0.46	24.7–25.8	1.8	
8	35	24.9 ± 0.16	23.7–25.7	1.9	32	24.8 ± 0.17	23.7–25.7	2.0	1.220

Table 1.—*Continued.*

Sample no.	Male				Female				
	N	$\bar{X} \pm 2$ SE	Range	CV	N	$\bar{X} \pm 2$ SE	Range	CV	F_s
				Palatal length					
1	11	9.3 ± 0.23	8.7–9.9	4.1	8	9.3 ± 0.26	8.7–9.9	4.0	0.005
2	13	9.1 ± 0.12	8.7–9.4	2.3	7	9.1 ± 0.27	8.7–9.6	4.0	0.0
3	7	9.2 ± 0.24	9.0–9.9	3.4	3	9.5 ± 0.24	9.3–9.7	2.2	1.23
4	2	9.3 ± 0.10	9.2–9.3	0.8	1	9.0			
5					1	9.4			
6	7	9.8 ± 0.28	9.0–10.1	3.8	12	9.5 ± 0.19	8.9–10.0	3.5	1.685
7	1	9.4			4	9.6 ± 0.44	9.2–10.1	4.6	
8	36	9.5 ± 0.13	8.7–10.4	4.0	33	9.4 ± 0.18	8.5–10.6	5.4	1.386
				Depth of braincase					
1	12	11.9 ± 0.15	11.5–12.2	2.2	8	11.8 ± 0.20	11.4–12.1	2.5	0.454
2	12	11.9 ± 0.17	11.4–12.3	2.5	7	12.0 ± 0.16	11.7–12.2	1.8	0.226
3	5	11.7 ± 0.35	11.3–12.1	3.3	3	11.7 ± 0.29	11.5–12.0	2.1	0.044
4	2	12.0	12.0		1	11.7			
5					1	11.9			
6	6	12.3 ± 0.29	11.6–12.6	2.9	12	12.2 ± 0.13	11.8–12.5	1.8	0.126
7	1	11.9			4	12.3 ± 0.22	12.1–12.6	1.8	
8	32	11.9 ± 0.12	11.3–12.8	2.9	31	11.9 ± 0.12	11.3–12.6	2.9	0.261
				Zygomatic breadth					
1	10	15.2 ± 0.10	14.9–15.4	1.1	7	14.9 ± 0.11	14.7–15.1	1.0	17.704*
2	13	15.2 ± 0.21	14.5–16.0	2.5	7	15.3 ± 0.25	14.9–15.9	2.2	0.572
3	6	15.1 ± 0.41	14.4–15.7	3.3	4	14.9 ± 0.69	14.0–15.5	4.6	0.390
4	2	15.1 ± 0.10	15.0–15.1	0.5	1	14.8			
5					1	15.1			
6	7	15.1 ± 0.26	14.6–15.6	2.3	12	15.3 ± 0.17	14.7–15.7	2.0	1.094
7	1	14.7			5	15.1 ± 0.37	14.6–15.5	2.7	
8	34	14.8 ± 0.12	14.2–15.5	2.3	30	14.8 ± 0.15	14.0–15.4	2.8	0.000
				Breadth of braincase					
1	13	11.9 ± 0.19	11.0–12.4	2.9	9	11.8 ± 0.21	11.4–12.2	2.6	0.166
2	13	11.8 ± 0.14	11.4–12.4	2.1	7	11.7 ± 0.17	11.3–12.0	1.9	0.000
3	7	11.8 ± 0.25	11.4–12.3	2.9	4	11.8 ± 0.33	11.4–12.2	2.8	0.007
4	2	12.0 ± 0.20	11.9–12.1	1.2	1	11.7			
5					1	11.7			
6	6	11.8 ± 0.13	11.6–12.0	1.4	12	11.9 ± 0.10	11.5–12.1	1.5	0.612
7	1	11.2			5	11.8 ± 0.20	11.5–12.1	2.0	
8	37	11.8 ± 0.09	11.2–12.3	2.2	30	11.7 ± 0.09	11.2–12.2	2.2	0.182
				Mastoid breadth					
1	12	13.5 ± 0.19	12.9–14.0	2.5	7	13.2 ± 0.16	12.8–13.4	1.6	3.492
2	13	13.7 ± 0.16	13.1–14.1	2.1	7	13.4 ± 0.27	12.9–13.9	2.7	3.553
3	7	13.3 ± 0.33	12.7–14.0	3.2	4	13.4 ± 0.30	13.1–13.7	2.2	0.100
4	2	13.8 ± 0.40	13.6–14.0	2.0	1	13.1			
5					1	13.8			
6	5	13.6 ± 0.16	13.4–13.8	1.3	12	13.7 ± 0.14	13.2–14.0	1.8	0.146
7	1	13.7			5	13.1 ± 0.30	12.8–13.5	2.6	
8	34	13.4 ± 0.13	12.9–14.4	2.9	31	13.3 ± 0.12	12.8–13.9	2.5	0.263
				Postorbital breadth					
1	12	6.2 ± 0.18	5.7–6.8	5.1	9	6.1 ± 0.15	5.8–6.5	3.7	0.283
2	13	6.1 ± 0.11	5.9–6.6	3.4	7	6.2 ± 0.11	6.0–6.4	2.4	1.028
3	7	6.0 ± 0.30	5.6–6.6	6.7	4	6.1 ± 0.27	5.7–6.3	4.4	0.251
4	2	6.2 ± 0.10	6.1–6.2	1.4	1	6.2			
5					1	6.0			
6	7	6.2 ± 0.08	6.1–6.4	1.7	12	6.1 ± 0.12	5.7–6.6	3.5	1.510
7	1	6.1			5	6.3 ± 0.11	6.1–6.4	2.1	
8	38	6.4 ± 0.06	6.0–7.0	3.0	33	6.2 ± 0.05	6.0–6.5	2.5	13.688*

Table 1.—*Continued.*

Sample no.	Male				Female				F_s
	N	$\bar{X} \pm 2$ SE	Range	CV	N	$\bar{X} \pm 2$ SE	Range	CV	
				Length of maxillary toothrow					
1	13	9.5 ± 0.11	9.1–9.8	2.1	9	9.5 ± 0.14	9.2–9.8	2.2	0.017
2	11	9.4 ± 0.11	9.2–9.8	2.0	7	9.3 ± 0.20	8.8–9.6	2.8	1.828
3	7	9.3 ± 0.15	9.0–9.6	2.1	4	9.4 ± 0.16	9.2–9.6	1.7	1.207
4	2	9.1	9.1		1	9.0			
5					1	9.4			
6	7	9.5 ± 0.16	9.3–9.8	2.2	11	9.5 ± 0.12	9.2–9.9	2.2	0.488
7	1	9.4			5	9.3 ± 0.22	8.9–9.5	2.7	
8	34	9.4 ± 0.06	9.0–9.8	2.0	25	9.4 ± 0.07	9.0–9.7	1.8	0.00
				Rostral width at canines					
1	12	6.6 ± 0.10	6.3–6.9	2.7	9	6.6 ± 0.20	5.9–7.0	4.4	0.031
2	12	6.6 ± 0.10	6.3–6.9	2.7	7	6.7 ± 0.23	6.0–6.9	4.5	0.047
3	7	6.5 ± 0.20	6.1–6.9	4.1	2	6.7 ± 0.10	6.6–6.7	1.1	0.365
4	2	6.7 ± 0.20	6.6–6.8	2.1	1	6.7			
5					1	6.7			
6	7	6.5 ± 0.15	6.2–6.8	3.1	11	6.3 ± 0.16	5.9–6.8	4.2	2.413
7	1	5.9			4	6.2 ± 0.20	5.9–6.3	3.2	
8	37	6.2 ± 0.08	5.6–6.7	3.7	29	6.1 ± 0.08	5.8–6.7	3.5	2.755
				Breadth across upper molars					
1	12	10.5 ± 0.09	10.2–10.6	1.4	9	10.3 ± 0.23	9.8–10.8	3.4	1.087
2	11	10.4 ± 0.11	10.1–10.6	1.7	7	10.4 ± 0.33	9.6–10.8	4.2	0.000
3	7	10.2 ± 0.24	9.8–10.6	3.0	4	10.2 ± 0.33	9.8–10.6	3.2	0.010
4	2	10.3 ± 0.20	10.2–10.4	1.4	1	10.3			
5					1	10.5			
6	7	10.2 ± 0.12	10.0–10.4	1.6	12	10.3 ± 0.08	10.1–10.5	1.3	2.229
7	1	9.4			4	10.1 ± 0.13	9.9–10.2	1.2	
8	36	9.9 ± 0.07	9.5–10.4	2.2	26	10.0 ± 0.10	9.6–10.5	2.6	0.610
				Mandibular length					
1	10	17.4 ± 0.20	16.7–17.8	1.9	6	17.2 ± 0.29	16.8–17.8	2.0	0.602
2	13	17.5 ± 0.22	16.7–17.9	2.2	7	17.5 ± 0.32	16.8–17.9	2.4	0.072
3	6	17.2 ± 0.41	16.7–18.1	2.9	1	17.5			
4	2	17.6 ± 0.90	17.1–18.0	3.6	1	16.9			
5					1	17.4			
6	7	17.3 ± 0.27	16.8–17.8	2.1	12	17.1 ± 0.24	16.4–17.7	2.4	1.054
7	1	17.9			4	17.6 ± 0.46	17.1–18.2	2.6	
8	35	17.3 ± 0.13	16.3–18.2	2.2	28	17.3 ± 0.14	16.5–18.1	2.1	0.030
				Brachyphylla cavernarum					
				Total length					
9	8	86.6 ± 3.33	79–92	5.4	11	88.9 ± 1.9	84–95	3.5	1.614
10	23	92.5 ± 3.4	82–118	8.9	19	96.7 ± 4.4	84–115	9.8	2.377
11	52	94.0 ± 1.21	84–104	4.6	7	89.1 ± 3.8	82–95	5.6	7.298*
12	33	92.3 ± 1.76	88–103	5.5	19	93.3 ± 1.9	86–102	4.5	0.543
13	1	95.0							
14	2	93.5 ± 7.0	90–97	5.3	2	96.5 ± 10.1	91–102	8.1	2.212
18	9	90.2 ± 2.0	85–95	3.3					
19	1	90.0			2	102.0 ± 2.0	101–103	1.4	
22	3	90.3 ± 2.4	88–92	2.3	2	90.5 ± 1.00	90–91	0.8	0.012
23	8	91.1 ± 2.99	87–98	4.6	4	88.3 ± 0.50	88–89	0.6	1.756
24	10	91.6 ± 1.41	89–95	2.4	19	89.6 ± 1.57	86–93	2.6	3.786
25	2	94.5 ± 1.0	94–95	0.7					
26	2	84.5 ± 9.0	80–89	7.5	1	90.0			
27	3	91.0 ± 1.15	90–92	1.1	8	90.6 ± 1.85	86–94	2.9	0.056

Table 1.—*Continued.*

Sample no.	Male				Female				
	N	$\bar{X} \pm 2$ SE	Range	CV	N	$\bar{X} \pm 2$ SE	Range	CV	F_s
Length of hind foot									
9	8	20.4 ± 1.60	16–23	11.1	11	21.0 ± 1.24	17–23	9.8	0.396
10	22	21.4 ± 0.41	16–23	6.5	19	21.9 ± 0.30	15–23	6.0	4.165*
11	52	22.4 ± 0.23	19–25	3.8	7	21.6 ± 0.74	20–23	4.5	5.537*
12	33	21.5 ± 0.52	18–24	6.9	19	22.1 ± 0.43	20–23	4.2	2.194
13	1	23.0							
14	2	20.0	20		2	19.5 ± 1.00	19–20	3.6	3.00
18	9	22.6 ± 0.35	22–23	2.3					
19	1	23.0			2	23.0	23		
22	3	21.3 ± 0.67	21–22	2.7	2	21.5 ± 1.00	21–22	3.3	0.086
23	8	22.5 ± 0.53	21–23	3.4	4	22.5 ± 1.0	21–23	4.4	0.000
24	10	20.3 ± 0.85	18–22	6.6	9	19.1 ± 1.39	17–23	10.9	2.232
25	2	21.5 ± 1.00	21–22	3.3					
26	2	21.5 ± 3.0	20–23	9.9					
27	3	20.7 ± 1.33	20–22	5.6	8	21.1 ± 0.7	20–23	4.7	0.431
Length of ear									
9	8	21.3 ± 0.73	20–23	4.9	11	20.9 ± 0.87	19–23	6.9	0.323
11	43	22.0 ± 0.26	20–26	3.8	5	23.4 ± 0.49	23–24	2.3	3.146
12	33	22.4 ± 0.38	20–24	4.9	19	22.8 ± 0.41	21–24	3.9	2.002
14	2	21.0	21		2	20.5 ± 1.00	20–21	3.4	3.000
21	1	21.0							
22	3	21.0 ± 3.06	18–23	12.6	2	24.0	24		
23	8	23.0 ± 0.53	22–24	3.3	4	22.3 ± 0.5	22–23	2.3	3.158
24	5	20.2 ± 1.47	19–23	8.1	6	19.7 ± 0.67	18–20	4.2	0.492
25	2	21.0	21						
26	2	23.0	23						
27	3	22.7 ± 0.67	22–23	2.6	8	22.4 ± 0.37	22–23	2.3	0.664
Length of forearm									
9	8	64.0 ± 1.19	60.7–65.4	2.6	11	65.1 ± 1.10	60.4–67.0	2.8	1.734
10	61	65.0 ± 0.47	61.6–69.4	2.8	24	65.0 ± 0.77	60.3–68.2	2.9	0.128
11	38	63.3 ± 0.59	60.0–66.4	2.9	7	63.3 ± 1.41	60.9–65.7	2.9	0.000
12	18	62.5 ± 0.87	60.0–66.1	3.0	8	62.8 ± 1.31	60.0–65.5	3.0	0.127
13	1	64.3							
14	6	64.1 ± 1.61	60.2–65.5	3.1	8	65.6 ± 0.49	64.5–66.8	1.1	4.019
15	6	65.6 ± 2.07	61.6–68.7	3.9	5	65.7 ± 2.28	62.0–68.0	3.9	0.002
16	3	65.3 ± 2.05	63.9–67.3	2.7					
17	1	65.2			2	63.9 ± 0.60	63.6–64.2	0.7	
18	9	65.7 ± 1.18	62.3–67.4	2.7					
19	6	65.4 ± 0.10	65.3–65.6	0.2	5	65.2 ± 0.44	64.5–65.9	0.8	9.940*
20	4	65.4 ± 0.78	64.4–66.3	1.2	3	67.3 ± 2.60	65.9–69.9	3.3	2.578
21	6	66.6 ± 0.90	65.3–67.9	1.6	5	67.6 ± 0.96	65.8–68.4	1.6	2.131
22	19	65.6 ± 0.69	63.0–68.9	2.3	13	65.4 ± 0.85	63.1–68.8	2.3	0.081
23	9	63.9 ± 0.93	62.3–65.7	2.2	7	64.6 ± 2.09	60.4–67.6	4.3	0.495
24	10	65.0 ± 1.88	59.6–68.1	4.6	9	66.8 ± 1.34	64.4–71.1	3.0	2.408
25	10	65.0 ± 0.59	62.9–66.5	1.4	5	65.5 ± 1.41	63.0–66.7	2.4	0.526
26	5	64.6 ± 0.40	61.8–65.5	2.4	6	65.2 ± 0.81	64.3–66.8	1.5	0.555
27	6	61.0 ± 1.06	59.2–63.1	2.1	12	61.1 ± 0.53	59.3–62.4	1.5	0.056
Greatest length of skull									
9	9	31.4 ± 0.31	30.5–32.0	1.5	11	31.3 ± 0.29	30.6–31.8	1.5	0.000
10	66	31.7 ± 0.15	30.5–33.0	1.9	27	31.4 ± 0.20	30.3–32.1	1.6	4.681*
11	48	31.4 ± 0.17	30.1–32.7	1.8	5	31.5 ± 0.71	30.6–32.7	2.5	0.098
12	26	31.6 ± 0.25	30.2–32.9	2.0	8	31.0 ± 0.49	30.2–32.2	2.3	4.309*
13	1	32.0							

Table 1.—*Continued.*

Sample no.	Male				Female				F_s
	N	$\bar{X} \pm 2$ SE	Range	CV	N	$\bar{X} \pm 2$ SE	Range	CV	
14	6	32.2 ± 0.30	31.7–32.6	1.1	8	32.3 ± 0.30	31.6–32.7	1.3	0.192
15	6	32.1 ± 0.54	31.4–33.0	2.1	5	31.6 ± 0.43	31.0–32.3	1.5	2.036
16	3	32.3 ± 0.41	31.9–32.6	1.1					
17	1	32.2			3	31.7 ± 0.81	31.0–32.4	2.2	
18	8	32.1 ± 0.31	31.5–32.8	1.4	1	32.4			
19	8	32.1 ± 0.41	31.3–33.0	1.8	8	31.6 ± 0.29	31.2–32.2	1.3	3.233
20	4	32.4 ± 0.14	32.2–32.5	0.4	7	32.0 ± 0.45	31.1–32.8	1.8	1.976
21	9	31.9 ± 0.26	31.2–32.5	1.2	8	31.9 ± 0.23	31.5–32.5	1.0	0.000
22	18	32.0 ± 0.26	30.9–32.8	1.7	13	31.6 ± 0.38	30.4–32.4	2.2	3.621
23	8	31.9 ± 0.40	31.2–32.8	1.8	8	31.9 ± 0.15	31.6–32.2	0.6	0.129
24	10	32.2 ± 0.19	31.8–32.8	0.9	9	31.7 ± 0.40	30.6–32.3	1.9	6.208*
25	10	31.9 ± 0.32	31.0–32.5	1.6	7	32.1 ± 0.51	30.7–32.7	2.1	0.654
26	5	31.9 ± 0.48	31.3–32.7	1.7	8	32.2 ± 0.36	31.7–33.3	1.6	0.505
27	7	30.5 ± 0.36	30.0–31.2	1.5	11	30.5 ± 0.24	29.6–30.9	1.3	0.043
					Condylobasal length				
9	8	28.0 ± 0.34	27.2–28.5	1.7	11	27.8 ± 0.29	27.2–28.4	1.7	0.580
10	63	28.1 ± 0.13	26.4–29.5	1.9	24	28.0 ± 0.21	27.2–29.0	1.9	0.438
11	49	28.2 ± 0.13	27.2–29.1	1.7	5	27.9 ± 0.65	26.8–28.7	2.6	1.402
12	27	28.2 ± 0.21	27.3–30.0	1.9	8	28.0 ± 0.24	27.3–28.3	1.2	1.280
13	1	28.4							
14	6	28.6 ± 0.39	27.8–29.0	1.7	9	28.5 ± 0.31	28.0–29.4	1.6	0.070
15	6	28.6 ± 0.48	27.9–29.3	2.1	5	28.0 ± 0.39	27.6–28.6	1.6	4.073
16	3	28.8 ± 0.37	28.4–29.0	1.1					
17	1	29.0			3	28.2 ± 0.58	27.7–28.7	1.8	
18	8	28.5 ± 0.30	27.9–29.0	1.5	1	28.8			
19	8	28.7 ± 0.53	27.7–29.8	2.6	7	28.4 ± 0.21	28.1–28.7	1.0	0.929
20	4	29.2 ± 0.26	28.8–29.4	0.9	4	28.2 ± 0.69	27.4–28.9	2.5	6.892*
21	8	28.5 ± 0.14	28.2–28.7	0.7	8	28.3 ± 0.29	27.6–28.9	1.5	1.811
22	19	28.4 ± 0.24	27.1–29.0	1.9	13	28.1 ± 0.34	26.8–29.0	2.2	1.479
23	8	28.6 ± 0.33	27.9–29.4	1.6	7	28.4 ± 0.16	28.1–28.7	0.7	0.941
24	9	28.5 ± 0.24	28.0–29.0	1.3	9	28.2 ± 0.25	27.6–28.6	1.3	4.330
25	9	28.6 ± 0.34	27.9–29.2	1.8	7	28.6 ± 0.48	27.6–29.4	2.2	0.000
26	4	28.6 ± 0.54	28.0–29.3	1.9	8	28.4 ± 0.24	28.0–29.0	1.2	1.032
27	7	27.1 ± 0.40	26.3–27.7	1.9	12	27.0 ± 0.26	26.3–27.6	1.6	0.086
					Palatal length				
9	9	11.7 ± 0.24	11.3–12.2	3.1	11	11.6 ± 0.25	10.8–12.1	3.6	0.808
10	67	11.7 ± 0.10	10.8–12.6	3.4	27	11.5 ± 0.18	10.8–12.6	4.1	1.445
11	51	12.0 ± 0.13	11.0–12.9	3.9	6	11.3 ± 0.52	10.5–12.4	5.6	9.496*
12	31	12.1 ± 0.17	11.2–12.9	4.0	16	12.0 ± 0.24	11.0–12.7	4.0	1.101
13	1	11.8							
14	6	12.6 ± 0.28	12.3–13.1	2.7	8	12.2 ± 0.39	11.3–13.0	4.5	3.033
15	6	12.2 ± 0.53	11.5–12.9	5.3	5	11.8 ± 0.33	11.4–12.4	3.1	1.026
16	3	12.5 ± 0.58	12.0–13.0	4.0					
17	1	11.9			3	11.6 ± 0.35	11.3–11.9	2.6	
18	8	12.4 ± 0.15	12.1–12.8	1.7	1	12.2			
19	8	12.3 ± 0.34	11.5–12.8	4.0	8	12.0 ± 0.39	11.1–13.0	4.5	0.675
20	4	12.4 ± 0.26	12.0–12.6	2.1	7	12.2 ± 0.40	11.6–13.0	4.4	0.499
21	9	12.1 ± 0.30	11.4–12.7	3.7	7	12.0 ± 0.44	11.1–12.6	4.8	0.055
22	19	11.9 ± 0.27	10.6–12.8	5.0	13	11.9 ± 0.26	11.2–12.7	4.0	0.013
23	9	11.9 ± 0.23	11.5–12.5	2.9	8	12.2 ± 0.23	11.8–12.7	2.7	2.163
24	9	12.0 ± 0.25	11.3–12.3	3.1	9	11.8 ± 0.23	11.3–12.4	3.0	1.712
25	10	12.2 ± 0.28	11.6–12.7	3.7	4	12.5 ± 0.45	12.1–13.1	3.6	0.410
26	5	11.9 ± 0.33	11.4–12.3	3.1	8	11.8 ± 0.12	11.5–12.0	1.4	0.958
27	7	11.4 ± 0.39	10.7–12.0	4.5	12	11.6 ± 0.32	10.7–12.3	4.8	0.449

Table 1.—*Continued.*

Sample no.	Male				Female				F_s
	N	$\bar{X} \pm 2$ SE	Range	CV	N	$\bar{X} \pm 2$ SE	Range	CV	
				Depth of braincase					
9	8	13.4 ± 0.17	13.1–13.7	1.8	11	13.2 ± 0.20	12.5–13.7	2.6	0.993
10	65	13.4 ± 0.10	12.5–13.9	3.0	25	13.1 ± 0.13	12.4–13.6	2.5	12.368*
11	50	13.3 ± 0.10	12.4–13.9	2.6	5	13.1 ± 0.33	12.5–13.4	2.8	0.796
12	29	13.3 ± 0.13	12.3–13.9	2.6	8	13.2 ± 0.26	12.7–13.6	2.8	1.103
13	1	13.8							
14	6	13.6 ± 0.38	13.0–14.3	3.4	9	13.6 ± 0.20	13.3–14.1	2.2	0.048
15	6	13.5 ± 0.24	13.0–13.8	2.2	5	13.2 ± 0.19	13.0–13.5	1.6	2.072
16	3	13.7 ± 0.18	13.5–13.8	1.1					
17	1	12.9			3	13.1 ± 0.18	12.9–13.2	1.2	
18	8	13.4 ± 0.21	13.0–13.7	2.2	1	13.1			
19	7	13.8 ± 0.37	13.0–14.4	3.6	8	13.4 ± 0.20	13.0–13.7	2.1	2.655
20	4	13.2 ± 0.35	12.8–13.6	2.7	5	13.2 ± 0.38	12.7–13.7	3.2	0.000
21	9	13.2 ± 0.24	12.3–13.5	2.7	8	13.2 ± 0.22	12.9–13.7	2.3	0.179
22	18	13.4 ± 0.19	12.4–13.9	2.9	13	13.2 ± 0.21	12.4–13.7	2.9	3.730
23	8	13.3 ± 0.28	12.6–13.9	3.0	7	13.3 ± 0.13	13.0–13.5	1.3	0.058
24	10	13.5 ± 0.15	13.1–13.9	1.7	9	13.2 ± 0.28	12.7–13.8	3.2	4.673*
25	8	13.4 ± 0.19	13.1–13.9	2.1	7	13.4 ± 0.22	13.0–13.9	2.1	0.028
26	4	13.3 ± 0.30	12.9–13.5	2.3	7	13.1 ± 0.26	12.7–13.6	2.7	0.422
27	6	13.1 ± 0.08	13.0–13.2	0.8	12	12.7 ± 0.18	12.2–13.3	2.4	6.921*
				Zygomatic breadth					
9	7	17.0 ± 0.34	16.4–17.6	2.6	11	17.0 ± 0.21	16.5–17.7	2.0	0.026
10	65	17.2 ± 0.11	15.8–18.1	2.6	26	17.0 ± 0.17	16.0–17.7	2.5	5.041*
11	47	17.2 ± 0.13	16.5–18.0	2.5	6	16.7 ± 0.42	15.9–17.2	3.1	6.857*
12	29	17.2 ± 0.12	16.7–17.8	2.0	12	17.1 ± 0.29	16.2–18.0	2.9	0.104
13	1	17.1							
14	4	17.5 ± 0.19	17.2–17.6	1.1	7	17.5 ± 0.37	16.5–17.9	2.8	0.019
15	6	17.4 ± 0.27	16.8–17.8	1.9	5	17.1 ± 0.28	16.8–17.6	1.8	1.573
16	3	17.7 ± 0.37	17.5–18.1	1.8					
17	1	17.2			3	17.0 ± 0.07	16.9–17.0	0.3	
18	8	17.5 ± 0.24	17.0–18.0	1.9	1	17.5			
19	7	17.5 ± 0.29	17.0–18.2	2.2	7	17.3 ± 0.28	16.8–17.9	2.1	1.136
20	4	17.4 ± 0.35	16.9–17.7	2.0	7	17.1 ± 0.31	16.5–17.6	2.4	1.822
21	9	17.5 ± 0.17	17.0–17.9	1.4	8	17.2 ± 0.22	16.5–17.4	1.8	5.436*
22	18	17.4 ± 0.25	16.0–18.2	3.0	11	17.3 ± 0.30	16.6–18.3	2.9	0.088
23	8	17.4 ± 0.21	17.0–17.9	1.7	7	17.5 ± 0.25	17.0–18.0	1.9	0.548
24	10	17.7 ± 0.20	17.2–18.2	1.8	8	17.0 ± 0.36	16.3–17.5	3.0	13.149*
25	9	17.3 ± 0.18	16.6–17.6	1.6	7	17.5 ± 0.26	17.0–17.8	2.0	1.560
26	3	17.1 ± 0.64	16.5–17.6	3.2	8	17.3 ± 0.29	16.8–17.8	2.3	0.376
27	8	16.5 ± 0.13	16.2–16.7	1.1	10	16.5 ± 0.23	16.0–17.2	2.2	0.262
				Breadth of braincase					
9	9	12.6 ± 0.10	12.4–12.9	1.2	11	12.6 ± 0.16	12.2–13.1	2.1	0.005
10	66	12.8 ± 0.07	12.3–13.6	2.2	28	12.5 ± 0.11	11.9–12.9	2.2	19.992*
11	51	12.8 ± 0.07	12.3–13.2	1.8	7	12.6 ± 0.12	12.4–12.8	1.3	3.242
12	29	12.7 ± 0.08	12.3–13.3	1.7	11	12.6 ± 0.17	12.3–13.1	2.2	1.761
13	1	13.0							
14	6	13.0 ± 0.15	12.8–13.3	1.4	9	13.0 ± 0.23	12.4–13.4	2.7	0.000
15	6	13.0 ± 0.15	12.8–13.3	1.4	5	12.8 ± 0.13	12.6–13.0	1.2	3.924
16	3	13.1 ± 0.13	13.0–13.2	0.9					
17	1	12.6			3	12.7 ± 0.07	12.6–12.7	0.5	
18	8	12.8 ± 0.22	12.4–13.4	2.5	1	13.0			
19	8	12.9 ± 0.18	12.5–13.2	2.0	8	12.8 ± 0.16	12.4–13.1	1.8	0.683
20	4	12.9 ± 0.21	12.6–13.1	1.6	6	12.8 ± 0.15	12.6–13.0	1.5	0.151
21	9	12.8 ± 0.17	12.5–13.3	2.0	8	12.8 ± 0.12	12.5–13.0	1.3	0.562
22	19	12.7 ± 0.13	12.3–13.1	2.2	13	12.7 ± 0.16	12.4–13.3	2.3	0.332
23	9	12.9 ± 0.26	12.2–13.3	3.0	7	12.7 ± 0.19	12.2–12.9	2.0	1.407

Table 1.—*Continued.*

Sample no.	Male				Female				
	N	$\bar{X} \pm 2$ SE	Range	CV	N	$\bar{X} \pm 2$ SE	Range	CV	F_s
24	10	13.1 ± 0.14	12.7–13.4	1.7	10	12.7 ± 0.20	12.1–13.0	2.5	13.807*
25	10	12.9 ± 0.13	12.6–13.2	1.6	7	12.8 ± 0.19	12.4–13.2	2.0	0.647
26	5	12.9 ± 0.23	12.5–13.2	2.0	8	12.8 ± 0.21	12.4–13.2	2.3	0.423
27	8	12.4 ± 0.11	12.2–12.7	1.3	12	12.3 ± 0.15	11.9–12.7	2.2	2.039
				Mastoid breadth					
9	8	14.8 ± 0.26	14.2–15.4	2.5	11	14.6 ± 0.21	14.2–15.4	2.4	0.995
10	65	15.0 ± 0.08	14.1–15.7	2.1	24	14.6 ± 0.11	14.1–15.1	1.8	24.343*
11	46	14.8 ± 0.10	14.0–15.3	2.2	5	14.4 ± 0.27	14.0–14.8	2.1	4.320*
12	27	14.8 ± 0.12	14.2–15.4	2.2	7	14.6 ± 0.32	14.1–15.2	2.9	1.237
13	1	14.6							
14	6	15.1 ± 0.19	14.9–15.5	1.6	9	14.9 ± 0.29	14.3–15.5	2.9	0.465
15	6	15.0 ± 0.33	14.4–15.6	2.7	5	14.5 ± 0.37	14.0–14.9	2.8	3.472
16	3	15.1 ± 0.47	14.7–15.5	2.7					
17	1	14.9			3	14.3 ± 0.41	14.0–14.7	2.5	
18	8	14.9 ± 0.17	14.5–15.3	1.6					
19	8	15.0 ± 0.25	14.5–15.6	2.4	8	14.9 ± 0.17	14.5–15.3	1.6	0.432
20	4	15.0 ± 0.44	14.6–15.6	3.0	5	14.6 ± 0.33	14.1–15.1	2.5	2.105
21	9	14.9 ± 0.11	14.6–15.1	1.1	8	14.7 ± 0.25	14.2–15.3	2.4	2.319
22	18	14.9 ± 0.17	14.1–15.5	2.4	13	14.7 ± 0.22	14.1–15.5	2.7	2.025
23	8	15.0 ± 0.16	14.7–15.4	1.5	6	14.8 ± 0.15	14.5–15.9	1.3	5.846*
24	10	15.0 ± 0.15	14.7–15.5	1.6	9	14.6 ± 0.31	14.0–15.4	3.2	6.294*
25	9	15.0 ± 0.18	14.5–15.4	1.8	7	14.8 ± 0.30	14.1–15.4	2.7	0.448
26	3	14.7 ± 0.12	14.6–14.8	0.7	8	14.7 ± 0.18	14.4–15.0	1.7	0.000
27	7	14.4 ± 0.27	13.7–14.8	2.5	12	14.1 ± 0.17	13.7–14.6	2.0	4.007
				Postorbital breadth					
9	8	6.5 ± 0.11	6.3–6.7	2.3	11	6.4 ± 0.10	6.1–6.6	2.5	0.359
10	67	6.5 ± 0.04	6.0–6.8	2.4	28	6.5 ± 0.08	6.1–6.8	3.2	2.127
11	53	6.4 ± 0.06	5.8–6.9	3.2	7	6.5 ± 0.11	6.2–6.7	2.3	2.254
12	31	6.3 ± 0.07	5.9–6.8	3.0	15	6.3 ± 0.08	6.0–6.6	2.6	0.280
13	1	6.5							
14	6	6.4 ± 0.11	6.2–6.6	2.1	9	6.4 ± 0.10	6.2–6.6	2.4	0.078
15	6	6.4 ± 0.11	6.3–6.6	2.1	5	6.2 ± 0.15	6.0–6.4	2.6	3.330
16	3	6.4 ± 0.18	6.3–6.6	2.4					
17	1	6.2			3	6.2 ± 0.07	6.1–6.2	0.9	
18	9	6.4 ± 0.12	6.2–6.7	2.7	1	6.5			
19	8	6.4 ± 0.17	6.1–6.9	3.8	8	6.3 ± 0.13	6.0–6.5	2.9	0.211
20	4	6.1 ± 0.17	5.9–6.3	2.8	7	6.2 ± 0.11	6.0–6.4	2.4	1.404
21	9	6.3 ± 0.13	6.0–6.6	3.1	8	6.3 ± 0.09	6.0–6.4	2.1	0.111
22	19	6.5 ± 0.08	6.2–6.9	2.6	13	6.3 ± 0.09	6.1–6.6	2.5	5.361*
23	8	6.3 ± 0.08	6.1–6.4	1.9	8	6.3 ± 0.08	6.2–6.5	1.7	1.762
24	10	6.4 ± 0.07	6.2–6.5	1.7	10	6.4 ± 0.11	6.1–6.6	2.8	0.102
25	11	6.3 ± 0.07	6.1–6.5	1.9	6	6.3 ± 0.15	6.1–6.6	2.8	0.133
26	5	6.4 ± 0.09	6.3–6.5	1.6	8	6.4 ± 0.12	6.2–6.7	2.6	0.202
27	8	6.3 ± 0.15	6.1–6.6	3.5	12	6.2 ± 0.10	5.8–6.5	2.8	2.179
				Length of maxillary toothrow					
9	9	10.6 ± 0.13	10.3–10.9	1.9	11	10.7 ± 0.15	10.1–11.0	2.3	0.650
10	62	10.7 ± 0.05	10.1–11.1	1.9	24	10.7 ± 0.08	10.4–11.0	1.8	0.661
11	38	10.8 ± 0.06	10.3–11.2	1.9	7	10.7 ± 0.20	10.4–11.1	2.5	0.347
12	22	10.7 ± 0.10	10.3–11.1	2.2	11	10.7 ± 0.06	10.5–10.8	0.9	0.148
13	1	10.7							
14	6	11.0 ± 0.10	10.8–11.1	1.1	8	10.9 ± 0.21	10.5–11.3	2.8	0.887
15	6	10.9 ± 0.16	10.6–11.1	1.8	5	11.0 ± 0.24	10.6–11.2	2.4	0.479
16	3	11.1 ± 0.18	11.0–11.3	1.4					
17	1	11.0			3	11.0 ± 0.44	10.6–11.3	3.4	
18	9	11.0 ± 0.24	10.6–11.6	3.3	1	11.5			

Table 1.—*Continued.*

Sample no.	Male				Female				
	N	$\bar{X} \pm 2$ SE	Range	CV	N	$\bar{X} \pm 2$ SE	Range	CV	F_s
19	6	10.9 ± 0.10	10.7–11.0	1.1	5	10.8 ± 0.15	10.7–11.0	1.5	1.129
20	4	11.3 ± 0.14	11.2–11.5	1.3	7	11.1 ± 0.20	10.6–11.4	2.4	1.900
21	9	11.0 ± 0.11	10.7–11.2	1.5	8	11.0 ± 0.14	10.5–11.1	1.8	0.877
22	19	11.0 ± 0.11	10.6–11.6	2.1	13	10.9 ± 0.13	10.6–11.4	2.1	2.659
23	9	11.0 ± 0.06	10.9–11.2	0.9	8	11.0 ± 0.12	10.8–11.2	1.6	0.000
24	10	11.1 ± 0.12	10.7–11.3	1.7	9	10.9 ± 0.10	10.6–11.1	1.4	7.159*
25	11	11.0 ± 0.12	10.7–11.3	1.8	8	11.1 ± 0.13	10.7–11.2	1.7	0.026
26	4	10.9 ± 0.30	10.5–11.2	2.7	8	11.0 ± 0.15	10.8–11.4	1.9	0.355
27	8	10.6 ± 0.14	10.3–10.9	1.9	12	10.5 ± 0.13	10.0–10.8	2.1	0.173
				Rostral width at canines					
9	9	7.2 ± 0.11	7.1–7.6	2.3	11	7.1 ± 0.08	6.8–7.3	1.9	1.995
10	67	7.2 ± 0.06	6.5–7.6	3.4	28	7.1 ± 0.08	6.5–7.4	3.0	9.096*
11	52	7.3 ± 0.07	6.6–7.7	3.4	7	7.0 ± 0.21	6.6–7.4	3.9	7.397*
12	30	7.3 ± 0.08	6.8–7.8	2.9	14	7.2 ± 0.08	6.9–7.5	2.2	4.375*
13	1	7.4							
14	6	7.3 ± 0.12	7.2–7.6	2.1	8	7.2 ± 0.14	7.0–7.6	2.8	0.962
15	6	7.2 ± 0.26	6.8–7.7	4.4	5	7.2 ± 0.21	6.8–7.4	3.2	0.052
16	3	7.3 ± 0.18	7.1–7.4	2.1					
17	1	6.8			3	7.4 ± 0.57	6.8–7.7	6.7	
18	8	7.3 ± 0.19	7.0–7.8	3.6	1	7.4			
19	8	7.5 ± 0.24	7.0–8.1	4.5	8	7.2 ± 0.16	6.8–7.4	3.0	2.491
20	4	7.6 ± 0.05	7.6–7.7	0.6	7	7.1 ± 0.12	6.9–7.3	2.3	37.664*
21	9	7.3 ± 0.14	7.0–7.6	2.8	8	7.2 ± 0.18	6.8–7.6	3.5	0.448
22	18	7.4 ± 0.13	6.7–7.8	3.8	13	7.2 ± 0.09	6.9–7.4	2.4	3.884
23	9	7.4 ± 0.23	6.8–7.9	4.6	8	7.2 ± 0.13	7.0–7.5	2.4	2.337
24	9	7.4 ± 0.15	7.1–7.8	3.0	9	7.1 ± 0.15	6.7–7.5	3.1	11.422*
25	11	7.4 ± 0.12	7.0–7.5	2.6	7	7.3 ± 0.08	7.2–7.5	1.5	0.233
26	5	7.4 ± 0.20	7.1–7.7	3.1	8	7.2 ± 0.12	7.0–7.4	2.3	2.392
27	8	6.9 ± 0.15	6.6–7.2	3.0	12	6.7 ± 0.14	6.3–7.0	3.6	2.070
				Breadth across upper molars					
9	9	11.5 ± 0.28	10.9–12.2	3.7	11	11.5 ± 0.10	11.2–11.7	1.5	0.244
10	66	11.5 ± 0.07	10.8–12.1	2.6	27	11.5 ± 0.11	10.9–12.1	2.4	0.558
11	50	11.6 ± 0.09	10.9–12.3	2.7	7	11.2 ± 0.22	10.8–11.7	2.6	7.009*
12	26	11.5 ± 0.11	11.0–12.1	2.5	14	11.7 ± 0.15	11.2–12.2	2.4	2.569
13	1	11.7							
14	5	11.7 ± 0.29	11.2–12.0	2.7	8	11.8 ± 0.19	11.4–12.2	2.3	0.046
15	6	11.7 ± 0.27	11.2–12.2	2.8	5	11.7 ± 0.46	11.2–12.4	4.4	0.015
16	3	11.7 ± 0.18	11.6–11.9	1.3					
17	1	11.1			3	11.9 ± 0.27	11.6–12.0	1.9	
18	9	11.8 ± 0.21	11.4–12.3	2.7	1	12.2			
19	6	11.8 ± 0.34	11.4–12.4	3.5	7	11.6 ± 0.25	11.0–12.0	2.8	0.439
20	4	12.0 ± 0.06	11.9–12.0	0.5	7	11.5 ± 0.18	11.2–11.9	2.1	11.128*
21	9	11.8 ± 0.16	11.6–12.2	2.0	8	11.8 ± 0.28	10.9–12.1	3.3	0.130
22	19	11.8 ± 0.15	11.0–12.3	2.8	13	11.7 ± 0.19	11.2–12.2	2.9	0.276
23	9	11.8 ± 0.18	11.3–12.2	2.2	8	11.8 ± 0.20	11.3–12.1	2.3	0.000
24	10	12.0 ± 0.19	11.5–12.4	2.5	10	11.6 ± 0.14	11.2–12.0	1.9	10.770*
25	10	11.7 ± 0.12	11.3–12.0	1.7	7	11.9 ± 0.11	11.8–12.2	1.2	7.171*
26	5	11.7 ± 0.19	11.6–12.1	1.8	8	11.7 ± 0.23	11.2–12.2	2.8	0.006
27	8	11.1 ± 0.15	10.9–11.5	1.9	11	11.2 ± 0.19	10.8–11.9	2.9	0.576
				Mandibular length					
9	8	19.9 ± 0.26	19.3–20.3	1.9	11	19.9 ± 0.24	19.3–20.4	2.0	0.053
10	63	19.9 ± 0.10	19.0–20.9	2.1	26	19.9 ± 0.18	19.1–20.9	2.3	0.105
11	45	20.3 ± 0.10	19.6–21.0	1.7	7	20.1 ± 0.26	19.7–20.5	1.7	2.069
12	26	20.2 ± 0.21	19.4–20.8	2.7	10	20.1 ± 0.26	19.4–20.8	2.1	0.945
13	1	20.1							

Table 1.—*Continued.*

Sample no.	Male				Female				F_s
	N	$\bar{X} \pm 2$ SE	Range	CV	N	$\bar{X} \pm 2$ SE	Range	CV	
14	4	20.6 ± 0.38	20.0–20.8	1.8	9	20.3 ± 0.19	20.0–20.7	1.4	2.328
15	6	20.6 ± 0.31	20.3–21.1	1.8	5	20.0 ± 0.54	19.4–20.6	3.0	3.938
16	3	20.5 ± 0.20	20.4–20.7	0.8					
17	1	20.8			2	20.0 ± 0.60	19.7–20.3	2.1	
18	9	20.6 ± 0.34	20.0–21.5	2.5	1	21.1			
19	7	20.7 ± 0.39	20.0–21.3	2.5	7	20.4 ± 0.26	19.9–21.0	1.7	1.520
20	4	20.7 ± 0.49	20.1–21.3	2.4	7	20.6 ± 0.34	19.8–21.0	2.2	0.184
21	7	20.4 ± 0.29	19.8–20.9	1.9	8	20.4 ± 0.21	19.9–20.8	1.5	0.000
22	19	20.5 ± 0.16	19.7–21.0	1.7	12	20.4 ± 0.28	19.5–21.0	2.4	0.809
23	8	20.5 ± 0.19	20.1–20.9	1.3	7	20.4 ± 0.17	19.9–20.5	1.1	0.875
24	9	20.8 ± 0.13	20.5–21.1	0.9	7	20.3 ± 0.26	19.8–20.8	1.7	14.000*
25	9	20.6 ± 0.27	19.8–21.1	1.9	6	20.5 ± 0.26	20.0–20.9	1.5	0.429
26	4	20.7 ± 0.47	20.2–21.3	2.3	8	20.7 ± 0.34	19.9–21.3	2.3	0.000
27	7	19.5 ± 0.30	18.9–20.0	2.0	11	19.7 ± 0.20	19.1–20.3	1.7	1.781

proved to be significantly larger than females in the following measurements from localities shown in parentheses: total length (St. John, 11); length of hind foot (St. John, 11); length of forearm (St. Martin, 19); greatest length of skull (eastern Puerto Rico, 10; Norman Island, 12; Martinique, 24); condylobasal length (Barbuda, 20); palatal length (St. John, 11); braincase depth (eastern Puerto Rico, 10; Martinique, 24; Barbados, 27); zygomatic breadth (eastern Puerto Rico, 10; St. John, 11; Dominica, 23; Martinique, 24); breadth of braincase (eastern Puerto Rico, 10; Martinique, 24); mastoid breadth (eastern Puerto Rico, 10; St. John, 11; Dominica, 23; Martinique, 24); postorbital breadth (Guadeloupe, 22); length of maxillary toothrow (Martinique, 24); rostral width at canines (eastern Puerto Rico, 10; St. John Island, 11; Norman Island, 12; Barbuda, 20; Martinique, 24); breadth across upper molars (St. John Island, 11; Barbuda, 20; Martinique, 24); mandibular length (Martinique, 24).

Although males exceeded females significantly in size in all 16 measurements except length of ear from one or more localities, females proved to be significantly larger than males in length of hind foot in the sample from eastern Puerto Rico (10), and in breadth across upper molars in specimens from St. Lucia (25).

Samples showing males to be significantly larger than females in more than one character include eastern Puerto Rico, St. John Island, Norman Island, Barbuda, and Martinique. With the exception of the sample from Barbuda, all these correspond to fairly large samples. However, Guadeloupe, also represented by a large (males 19, females 13) sample, showed significant differences in males over females only in postorbital breadth.

Forearm measurements, which because of loading in pregnant females, might be expected to be greater in females than males, average longer in females than males in 11 of 15 samples, but never significantly. In two samples the sexes have the same average length of forearm. In specimens from St. Martin, length of forearm in males was significantly longer than that of females.

Conclusions.—In general, males are larger than females in the genus *Brachyphylla*. Therefore, in all subsequent analyses, where size was involved, males and females were treated separately.

Individual Variation

In samples from west of the Mona Passage, external measurements, excluding length of forearm, were found to vary much more (CV, 1.8 to 18.4) than forearm and cranial measurements (CV, 0.2 to 6.7) (Table 1).

Of forearm and cranial measurements, palatal length (CV, 0.8 to 5.4), rostral width at canines (CV, 1.1 to 4.5), and postorbital breadth (CV, 1.4 to 6.7) showed the highest individual variation, whereas greatest length of skull (CV, 1.2 to 2.2) and condylobasal length (CV, 0.6 to 2.4) showed the least.

In samples from east of the Mona Passage, variation in external measurements (excluding length of forearm) was again found to be higher (CV, 0.6 to 12.6) than in forearm and cranial measurements (CV, 0.2 to 6.7). Of the latter, palatal length showed the most variation (CV, 1.4 to 5.6) and greatest length

of skull (CV, 0.4 to 2.5) and condylobasal length (CV, 0.7 to 2.6) the least. Rostral width at canines also showed relatively high coefficients of variation (CV, 0.6 to 6.7).

Conclusions.—From both east and west of the Mona Passage, external measurements taken from the skin tags proved to be highly variable. As pointed out by Sumner (1927), external measurements can be expected to vary more because of the fact that these were usually taken by various collectors under different circumstances. Because of missing data and high individual variation, total length, length of hind foot, and length of ear were excluded from subsequent analyses.

SPECIFIC RELATIONSHIPS

Because of the discordance in the literature (see Introduction) concerning the specific relationships within the genus, both univariate and multivariate analyses were employed to compare the geographic samples. Standard statistics for samples of males and females from geographic samples are given in Table 1.

Univariate Analyses

The SS-STP analyses revealed geographic samples west of the Mona Passage (samples 1 to 8) grouped in one subset, differing significantly from all other samples in the following cranial measurements: greatest length of skull (females); condylobasal length (males and females); palatal length (males); zygomatic width (males and females); length of maxillary toothrow (females); breadth across upper molars (females); mandibular length (males). The results of these analyses for condylobasal length and mastoid breadth are shown in Table 2. This division corresponds to the specific division in the genus as recently suggested by Silva-Taboada (1976) in which he recognized two species, *B. nana* from west of the Mona Passage and *B. cavernarum* from the remainder of the geographic distribution of the genus.

Characters that showed wide overlap of subsets were depth of braincase (males) and postorbital breadth (males and females). The remainder of the characters all tend to show basically a break across the Mona Passage, with varying numbers of overlapping subsets.

Multivariate Analyses

Distance phenograms for both males and females generated with the NT-SYS program package are illustrated in Fig. 2. In addition, a map (Fig. 3), including values for both sexes, presents appropriate distance coefficients between the connected samples; in most cases, distance coefficients have been given only for contiguous samples. The first three principal components extracted from the principal component analyses are shown for males and females (Fig. 4).

The distance phenograms for both male (cophenetic correlation value, 0.975) and female (cophenetic correlation value, 0.965) *Brachyphylla* clearly show two major groups. In both cases the upper cluster corresponds to samples west of the Mona Passage (Cuba, 1 to 4; Grand Cayman, 5; Middle Caicos, 6; and Hispaniola, 7 and 8), whereas the lower cluster corresponds to samples east of the passage (Puerto Rico, 9 and 10; Virgin Islands, 11 to 14; and the Lesser Antilles, 15 to 27). Distance coefficients on the map also clearly show this break across the Mona Passage with values of 1.96 for males and 2.04 for females. On the other hand, these values between contiguous samples west of the passage, and between similar samples to the east of it are less than 1.00, except between St. Lucia and Barbados where it is 1.03 in the females.

The amount of phenetic variation explained by the first three principal components, for males and females, respectively, was 90.6% and 91.3%, 5.1% and 4.6%, and 2.1% and 1.7% (total, males, 97.8%; females, 97.6%). Results of factor analyses showing characters influencing the first three components for both males and females are given in Table 3. The high percentage of variation explained by the first component in both males and females reveals that size is the major factor separating the two groups in the principal component analyses. From the factor analysis it can be seen that on the first component, postorbital width is not weighted heavily (males 0.643 and females 0.677) in separating the groups, whereas all the other characters contribute heavily (above 0.900). Postorbital breadth (Component II) and rostral width at canines (Component III) influence the other components most heavily.

Examination of three-dimensional plots reveals basically the same pattern as the distance phenograms for both sexes. Samples on the left of the plot are the same samples that were found in the upper cluster of the phenograms, which are the samples

Table 2.—*Results of two SS-STP analyses (condylobasal length and mastoid breadth) of geographic variation in* Brachyphylla nana *and* B. cavernarum. *Vertical lines to the right of each set of means connect maximally nonsignificant subsets at the 0.05 level. See text for key to sample numbers.*

Males			Females		
Sample number	Means	Results SS-STP	Sample number	Means	Results SS-STP
		Condylobasal length			
20	29.2		25	28.6	
16	28.8		14	28.5	
19	28.7		19	28.4	
26	28.6		23	28.4	
14	28.6		26	28.4	
15	28.6		21	28.3	
25	28.6		17	28.2	
23	28.6		24	28.2	
24	28.5		20	28.2	
21	28.5		22	28.1	
18	28.5		10	28.0	
22	28.4		15	28.0	
11	28.2		12	28.0	
12	28.2		11	27.9	
10	28.1		9	27.8	
9	28.0		27	27.0	
27	27.1		2	25.4	
1	25.5		3	25.3	
4	25.4		6	25.3	
6	25.4		1	25.3	
2	25.3		7	25.2	
3	25.0		8	24.8	
8	24.9				
		Mastoid breadth			
16	15.1		14	14.9	
14	15.1		19	14.9	
24	15.0		25	14.8	
23	15.0		23	14.8	
19	15.0		21	14.7	
15	15.0		26	14.7	
10	15.0		22	14.7	
25	15.0		10	14.6	
20	15.0		24	14.6	
18	14.9		12	14.6	
21	14.9		9	14.6	
22	14.9		20	14.6	
9	14.8		15	14.5	
12	14.8		11	14.4	
11	14.8		17	14.3	
26	14.7		27	14.1	
27	14.4		6	13.7	
4	13.8		2	13.4	
2	13.7		3	13.4	
6	13.6		8	13.3	
1	13.5		1	13.2	
8	13.4		7	13.1	
3	13.3				

from west of the Mona Passage. Samples on the right of the plot correspond to all samples east of the passage. Sample 27 (Barbados) is somewhat separated from the cluster of samples on the right, and corresponds to the presently recognized subspecies *B. c. minor*.

In both male and female *Brachyphylla*, multivariate analysis of variance (MANOVA) showed that there were significant ($P < 0.0001$) morphological differences among samples for all characters in the following statistical tests (Hotelling-Lawley's Trace, Pillai's Trace, Wilks' Criterion, and Roy's Maximum Root Criterion).

Two-dimensional plots of the samples onto the first two canonical variates based on a matrix of variance-covariance among one external and 12 cranial characters are presented for 26 male samples in Fig. 5 and for 24 female samples in Fig. 6. The amount (percentage) of phenetic variation represented in the first three canonical variates for male and female *Brachyphylla*, respectively, was 87.1 and 76.9 for variate I, 4.2 and 7.5 for variate II, and 3.2 and 4.5 for variate III. Combined the first three canonical variates express 94.5% in males and 88.9% in females. In both males and females it took all 13 canonical variates to explain all the variation. The relative contributions of each character to the first three canonical variates in males and females are given in Table 4.

Examination of the two-dimensional plots of the samples of both males and females reveals two distinct groups well separated on the first variate. Samples of the population east of the Mona Passage are grouped in the cluster at the top and those from west of the passage in the cluster at the bottom. In both males and females, length of maxillary toothrow (males 23.5, females 15.7) and mandibular length (males 15.4, females 20.2) contributed the heaviest toward separating the two groups on the first variate. Other characters that contributed more than 10% on the first variate include breadth across upper molars in males, and condylobasal length in females. The following characters in males contributed more than 10% on the second variate, condylobasal length, palatal length, depth of braincase, postorbital breadth, and rostral width at canines, and on the third variate, forearm length, greatest length of skull, postorbital breadth, and mandibular length; and in females on the second variate, greatest length of skull, condylobasal length, and rostral width at canines, and on the third variate, greatest length of skull and mandibular length.

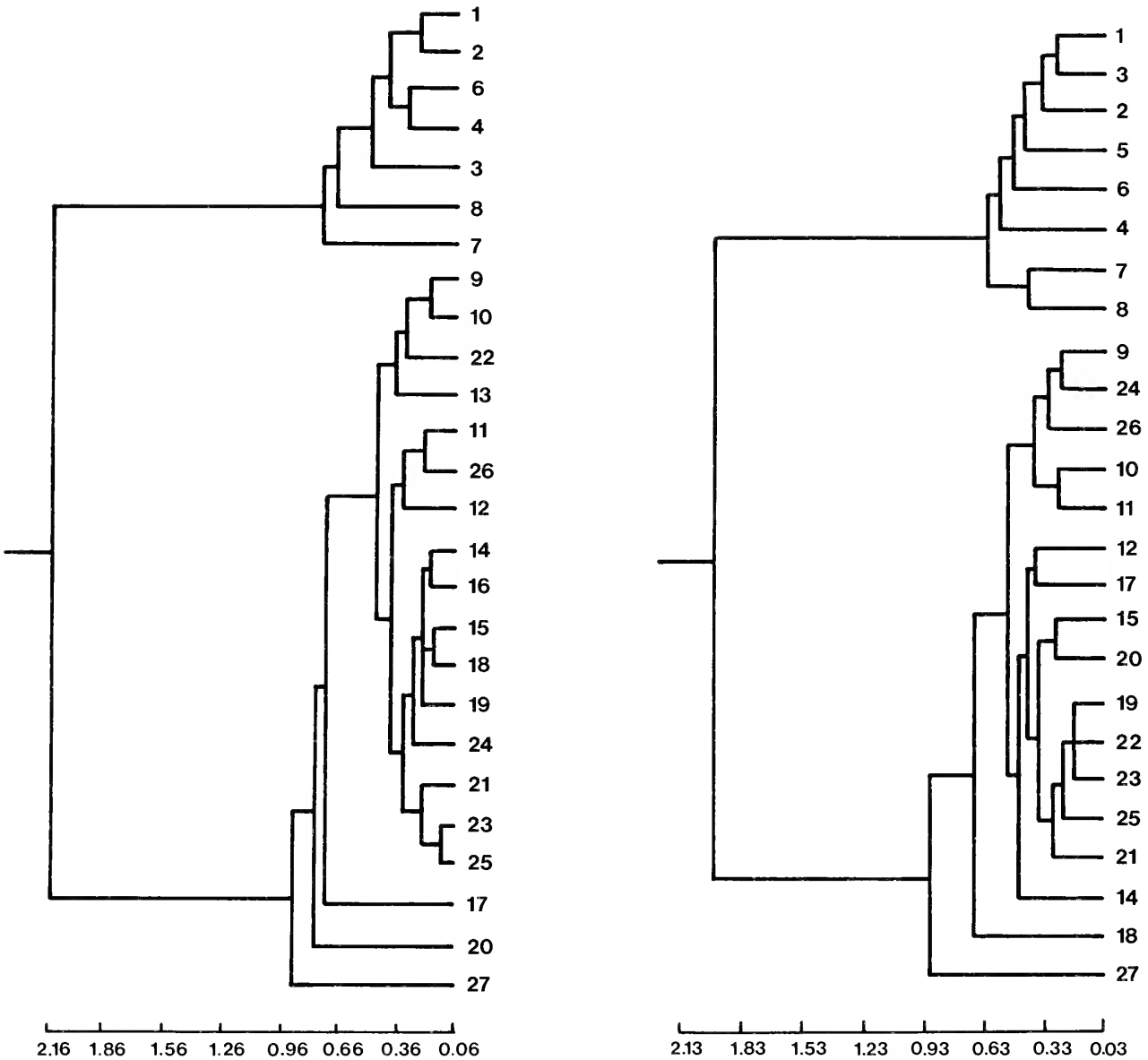

Fig. 2.—Phenograms of numbered samples (see Fig. 1 and text) of *Brachyphylla* (males left, females right) computed from distance matrices based on standardized characters and clustered by unweighted pair-group method using arithmetic averages (UPGMA). The cophenetic correlation coefficient for males is 0.975 and for females 0.965.

The SAS canonical variate analyses, therefore, closely correspond to the NT-SYS cluster analysis and the principal component analysis in separating the two groups.

Variation in Color

Color in the genus *Brachyphylla* does not exhibit a great deal of variation. Typically the hair is white to yellowish white at the base with the tips darker in some areas on the dorsum. These darker areas, which vary in size, occur as a distinct patch on top of the head and neck and a V-shaped mantle starting approximately at the shoulders and meeting posteriorly in the middle of the dorsum. The flanks are ususally lighter colored. The darker areas may be blackish gray, blackish brown, grayish brown, or dark brown in color.

In 38 skins from Cuba, 47% correspond to color standard 5, whereas nearly an equal proportion (37%) are comparable to color standard 3 (see Ma-

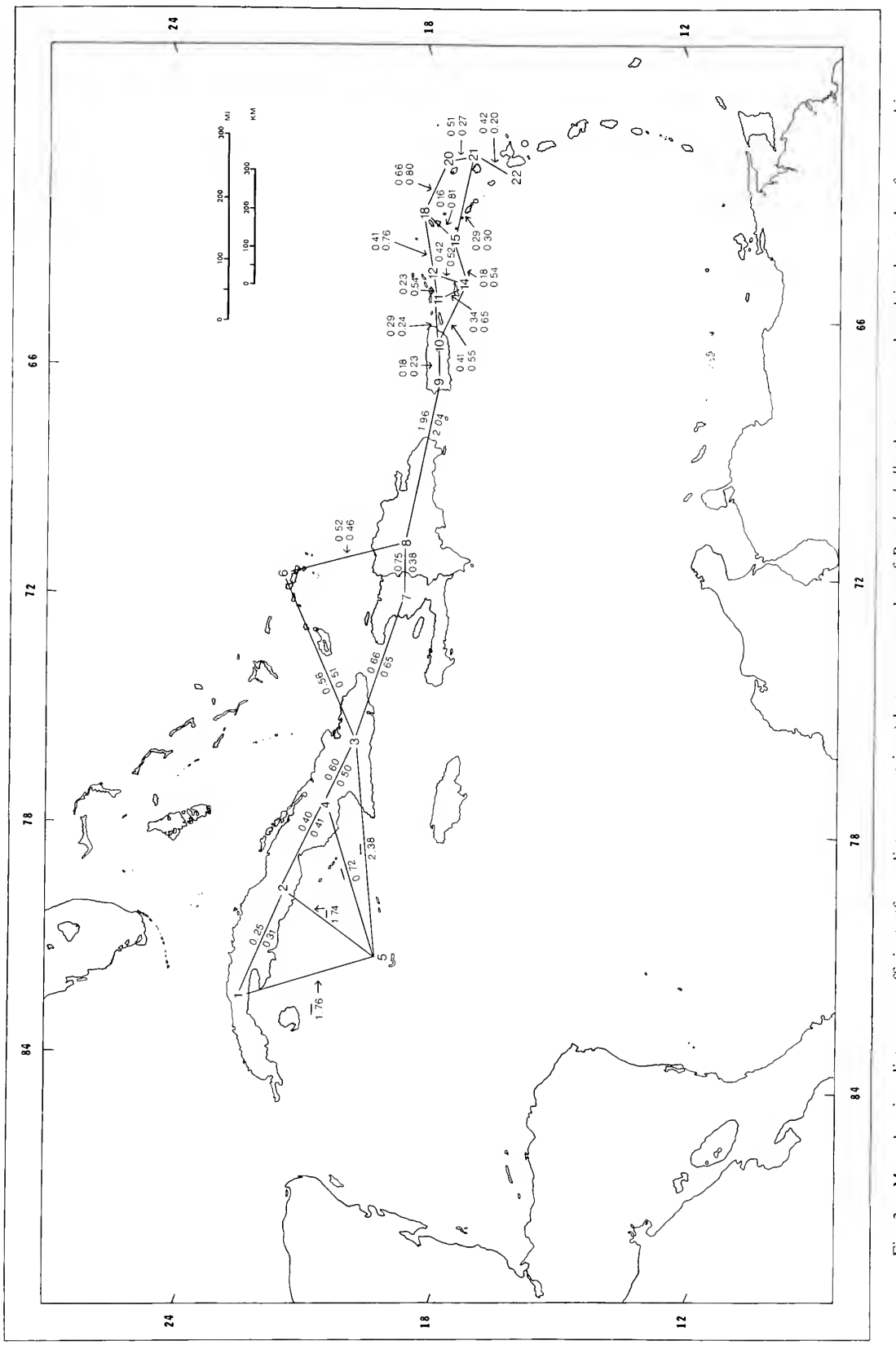

Fig. 3.—Map showing distance coefficients (from distance matrices) between samples of *Brachyphylla* that were analyzed in the study of geographic variation. The upper coefficients are for males and the lower for females. See Fig. 1 and text for key to samples.

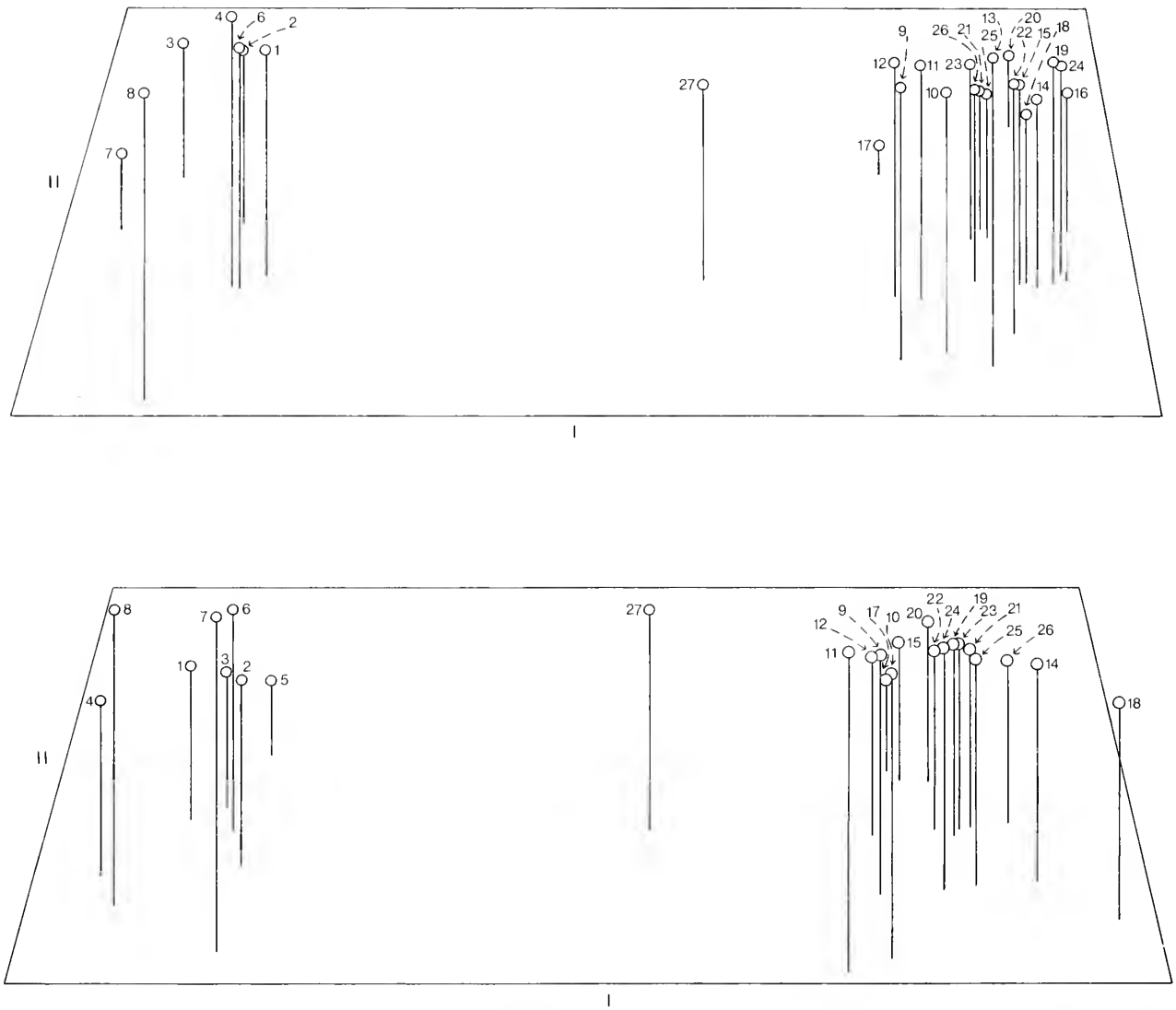

Fig. 4.—Three-dimensional projections of samples of *Brachyphylla* (males above, females below) onto the first three principal components based on matrices of correlation among one external and 12 cranial measurements. Components I and II are indicated in the figure and component III is represented by height. See Fig. 1 and text for key to samples.

terials and Methods). Therefore, the majority have the base of the hair white to yellowish white with the tips of the hair in the dorsal V-pattern varying from grayish brown to dark brown with varying shades of buff. The dark brown specimens having a yellowish tint, all from the Albert Schwartz Collection, have a more washed-out appearance than the color standard 5. Other specimens (16%) from Cuba were blackish brown (color standard 2).

Of 56 skins examined from Hispaniola, 63% have hair white at the base with blackish gray tips (color standard 1). However, there is also a large percentage (35%) that are grayish brown colored, sometimes tinted buffish (color standard 3), which corresponds in color to all specimens examined from Middle Caicos (19) and Grand Cayman (1).

From Puerto Rico, 57 skins were examined. Of these, 42% were blackish brown (color standard 2) in color; however, nearly an equal number (35%) were grayish brown, some with a buffy tint (color standard 3). The remainder consisted of 18% blackish gray specimens (color standard 1), and 5% yellowish dark brown specimens (color standard 5). The latter specimens are mostly from the Albert Schwartz Collection. The majority (54%) of the 41 bats from St. John Island are blackish brown in col-

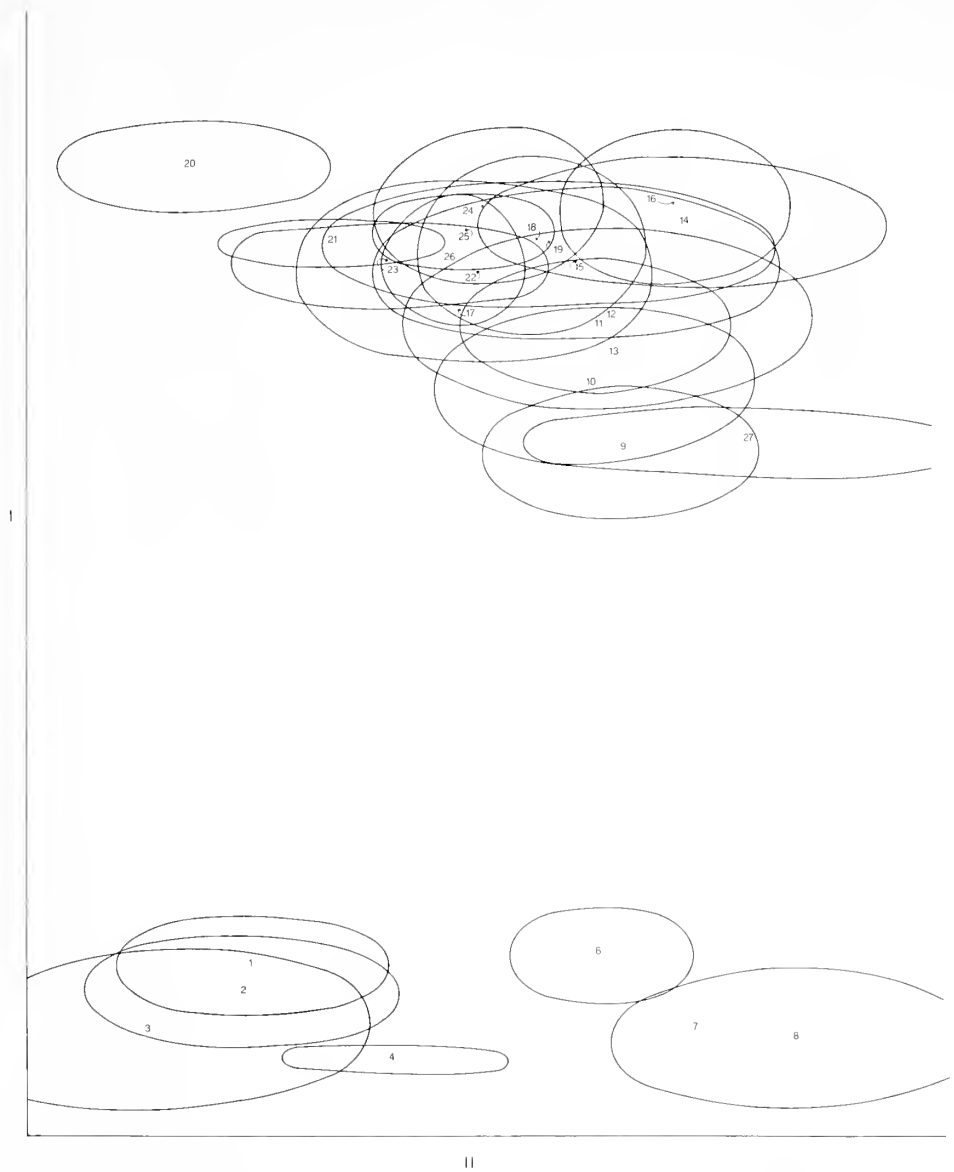

Fig. 5.—Two-dimensional projection of male samples (mean and one standard deviation) of *Brachyphylla* onto the first two canonical variates based on a matrix of variance-covariance among one external and 12 cranial measurements. See Fig. 1 and text for key to samples.

or (color standard 2). The remainder varied from grayish brown (34%) (color standard 3) to dark brown (12%), tinted buff or reddish (color standard 4). Over 30 specimens from Norman Island were found to be molting and were excluded from color analysis. Of the 26 remaining skins that were studied, 46% were found to be grayish brown (some with a buffish tint) (color standard 3), 35% blackish brown (color standard 2), 15% dark brown with a reddish tint (color standard 4), and 4% blackish gray (color standard 1). All specimens from St. Thomas (1), St. Croix (4), Anguilla (9), St. Martin (16), and Antigua (1) were blackish brown in color (color standard 2).

Of the seven specimens examined from Guadeloupe, three were blackish gray (color standard 1), two dark brown (color standard 4), one grayish brown (color standard 3), and one dark yellowish brown (color standard 5). Ten of 12 bats from Dominica were blackish brown colored (color standard 2); the remaining two were grayish brown (color standard 3). Of nine specimens from Martinique,

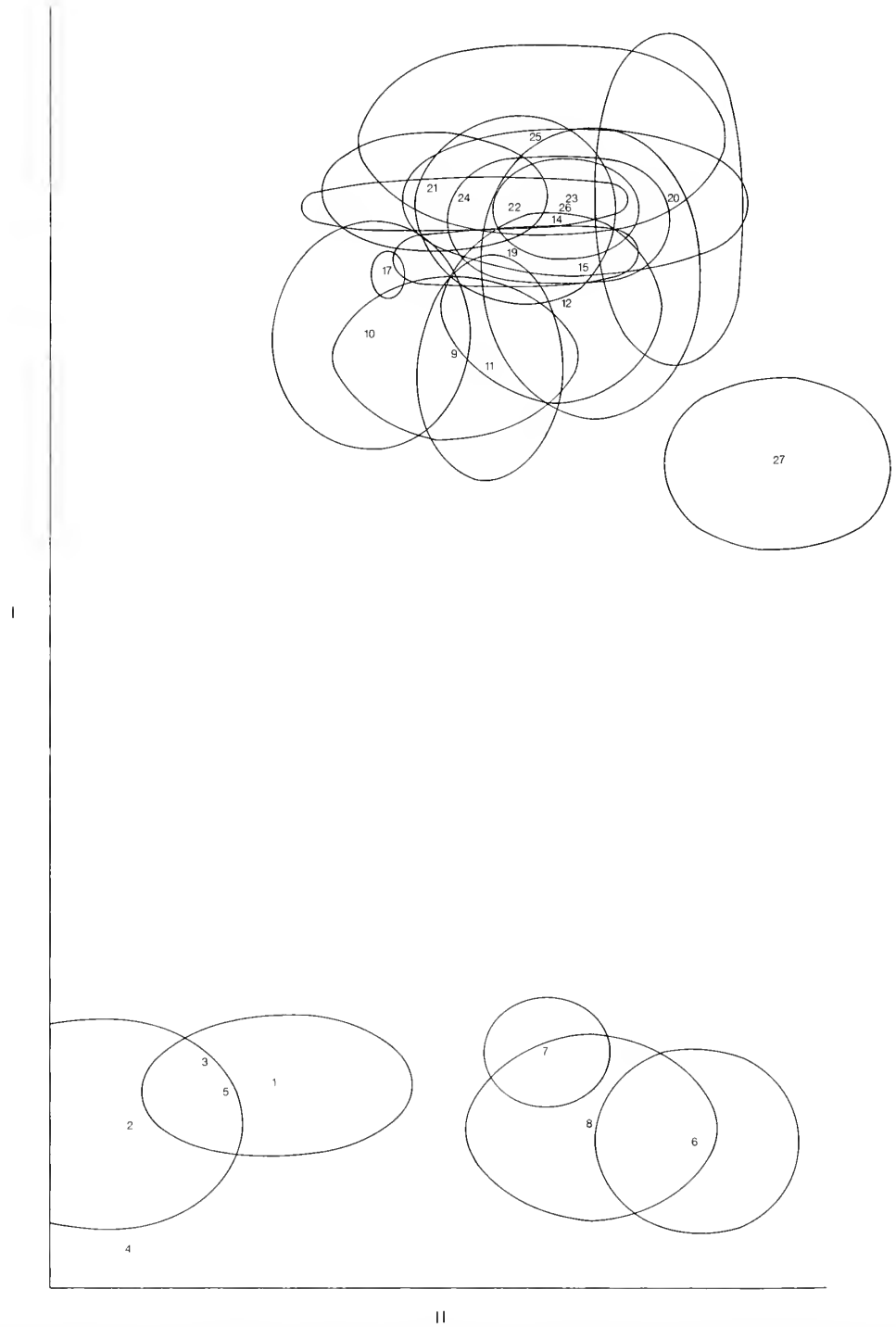

Fig. 6.—Two-dimensional projection of female samples (mean and one standard deviation) of *Brachyphylla* onto the first two canonical variates based on a matrix of variance-covariance among one external and 12 cranial measurements. See Fig. 1 and text for key to samples.

six were blackish brown (color standard 2) and three yellowish dark brown (color standard 5). All three specimens from St. Vincent were blackish gray (color standard 1). Coat color in most (nine of 14) specimens from Barbados have the base of the hair yellowish white with the tips of the hair dark brown and tinted buffy (color standard 5). All (nine) of these specimens are from the Albert Schwartz

Table 3.—*Factor matrix from correlation among 13 characters of* Brachyphylla *studied, showing characters influencing the first three components.*

Characters	Males			Females		
	Component I	Component II	Component III	Component I	Component II	Component III
Length of forearm	0.940	0.125	−0.163	0.947	0.084	−0.020
Greatest length of skull	0.993	0.058	−0.049	0.991	0.017	0.069
Condylobasal length	0.987	0.108	−0.040	0.996	0.030	0.002
Palatal length	0.983	0.034	−0.089	0.981	0.052	0.129
Depth of braincase	0.967	−0.162	−0.002	0.969	−0.051	0.156
Zygomatic breadth	0.994	0.055	−0.004	0.993	0.019	0.031
Breadth of braincase	0.972	−0.025	0.173	0.988	−0.015	0.037
Mastoid breadth	0.978	0.050	−0.097	0.975	0.041	0.036
Postorbital breadth	0.643	−0.760	−0.063	0.677	−0.728	−0.107
Length of maxillary toothrow	0.979	0.113	−0.100	0.985	0.049	0.046
Rostral width at canines	0.933	0.027	0.343	0.905	0.184	−0.377
Breadth across upper molars	0.972	0.026	0.210	0.979	0.099	−0.108
Mandibular length	0.980	0.092	−0.128	0.990	−0.020	0.042

Collection. Other material from Barbados have the base of the hair white with blackish gray tips (color standard 1) in two specimens, and grayish brown with a buffish tint (color standard 3) in three others.

There is little variation in color in bats of this genus. All have the same basic pattern of color. The variation that is present is in color of the tips, which varies from grayish brown to blackish gray, and in

Table 4.—*Eigenvalues of canonical variates showing the percentage influence among 13 characters of* Brachyphylla. *Eigenvalues shown represent the normalized vector coefficient of each character.*

Characters	Vector I		Vector II		Vector III	
	Eigenvalue	Percent influence	Eigenvalue	Percent influence	Eigenvalue	Percent influence
			Males			
Length of forearm	0.0072	4.8	−0.0088	6.3	−0.0264	15.8
Greatest length of skull	−0.0204	6.8	−0.0032	1.0	−0.0411	12.2
Condylobasal length	−0.0199	6.0	−0.0479	14.5	−0.0307	8.2
Palatal length	0.0408	5.0	0.1000	12.4	0.0613	6.7
Depth of braincase	0.0319	4.6	0.0884	12.6	0.0289	3.7
Zygomatic breadth	0.0095	1.9	−0.0386	7.1	−0.0435	7.1
Breadth of braincase	0.0665	9.1	0.0380	5.3	−0.0050	0.6
Mastoid breadth	−0.0148	2.4	0.0130	2.1	−0.0262	3.7
Postorbital breadth	−0.0995	6.9	0.2331	16.4	−0.2212	13.6
Length of maxillary toothrow	0.2049	23.5	−0.0121	1.4	−0.0051	0.5
Rostral width at canines	−0.0376	3.0	−0.1400	10.9	0.0440	3.0
Breadth across upper molars	0.0883	10.8	−0.0482	5.9	−0.0089	1.0
Mandibular length	0.0716	15.4	0.0192	4.1	0.1275	24.1
			Females			
Length of forearm	0.0151	9.2	−0.0325	8.4	0.0088	2.6
Greatest length of skull	0.0197	6.0	0.1546	19.2	−0.1887	27.0
Condylobasal length	−0.0415	11.1	−0.2381	26.2	−0.0696	8.9
Palatal length	0.0486	5.3	0.0965	4.3	0.0566	3.0
Depth of braincase	−0.0233	2.9	0.0737	3.9	0.1341	7.4
Zygomatic breadth	0.0467	7.6	0.0990	6.6	−0.0830	6.4
Breadth of braincase	−0.0278	3.4	0.0006	0.1	−0.0909	5.3
Mastoid breadth	−0.0361	5.0	0.0257	1.5	−0.0385	2.6
Postorbital breadth	0.0662	4.1	−0.2989	7.7	0.1967	5.8
Length of maxillary toothrow	0.1551	15.7	0.2197	9.3	−0.0719	3.5
Rostral width at canines	−0.0189	1.3	−0.3608	10.1	−0.0120	0.4
Breadth across upper molars	0.0757	8.3	−0.0546	2.5	0.0280	1.5
Mandibular length	0.1067	20.2	0.0051	0.4	0.2836	25.6

the bases of the hair, which vary from whitish to reddish and yellowish white. Some authors (Goodwin, 1933; Sanborn, 1941; Buden, 1977) believed that variation in color in *Brachyphylla* followed a geographic pattern. Basically, they felt that the underfur of specimens from Hispaniola was more distinctly white than in specimens from Cuba, Puerto Rico, and Lesser Antilles. They also stated that the tips of the hair were more conspicuously pale brown with reddish or yellowish tones compared to specimens from the remainder of the geographic range of the genus.

We have not been able to detect these differences in the material that we have studied. Specimens on Cuba were mostly grayish brown to dark brown with a buffy or reddish tint but some specimens lacked this tint. The same was true for the underfur, which had a reddish or buffy tint in most individuals but in some it was white. Most of the specimens from Hispaniola corresponded to color standard 1 but 35% matched with color standard 3 as did 37% from Cuba.

On Puerto Rico, Norman Island, and Guadeloupe, specimens matched four of the five color standards, indicating that color variation on these islands nearly spans that found in the entire genus. Specimens from St. John Island and Barbados, recognized as a distinct subspecies, corresponded to three of the color standards.

We have not been able to detect any geographic trends in this variation in color. There appears to be little variation in color and what variation is present can nearly be spanned by individuals from a single island.

Taxonomic Conclusions

We interpret the univariate and multivariate analyses as revealing that the genus *Brachyphylla* represents two species, *Brachyphylla nana* from Cuba, Grand Cayman, Middle Caicos, and Hispaniola, and *B. cavernarum* from Puerto Rico, Virgin Islands, and the Lesser Antilles as far south as St. Vincent and Barbados. The latter species is clearly the larger of the two; the range of some measurements of *B. cavernarum* not overlapping those of *B. nana* in some characters.

It is also worthy of note that no species of parasites are known to be common to both *B. cavernarum* and *B. nana*. However, within *nana*, Cuba and the Dominican Republic share one species of the genus *Trichobius* and within *cavernarum* Guadeloupe and Martinique share a species of *Ornithodoros* (Webb and Loomis, 1977). *B. cavernarum* and *B. nana* do share the streblid genus *Trichobius*, but host different species.

Buden (1977), considering these two species to be conspecific, argued that the size differences between the two allopatric taxa are nearly matched by those found among Middle American populations of *Artibeus jamaicensis*, which were treated as subspecies by Davis (1970). However, these differences are in fact more comparable to size differences seen between *A. jamaicensis* and *A. lituratus* in Central America.

A further argument presented by Buden (1977) for recognizing only one species is that there are no differences in the standard karyotypes of the two taxa. However, when considering the fact that, for example, species included in *Artibeus*, *Sturnira*, *Vampyrops*, and *Myotis* show no intrageneric variation in chromosomal complements (Baker, 1973; Bickham, 1976), this argument is of little value. It should also be pointed out that *Erophylla bombifrons* and *Phyllonycteris poeyi*, both endemic West Indian phyllonycterines, have identical karyotypes (Baker and Lopez, 1970; Nagorsen and Peterson, 1975) to *Brachyphylla*, but no one has considered even placing them in the same genus.

Throughout the remainder of this study, we have considered the genus *Brachyphylla* to be composed of two species—*B. cavernarum* and *B. nana*.

SYSTEMATIC ACCOUNTS

Genus **Brachyphylla**

1834. *Brachyphylla* Gray, Proc. Zool. Soc. London, pp. 122–123, 12 March.

Type species.—*Brachyphylla cavernarum* Gray.

Definition

Resembles the other phyllonycterines externally in all respects except for having a more stocky build with a shorter snout; lower lip with median groove

ridged by papillae; nodular ridges on chiropatagium; calcar absent; five lumbar vertebrae, fifth lacking neural spine; skull relatively long, narrow; upper incisors markedly different in size and shape, inner one large, higher than long, recurved, outer one rounded, minute, flat-crowned; anterior upper premolar minute; posterior upper premolar high and short; crowns of upper and lower molars heavily wrinkled; first lower molar with distinct posterointernal cusp, differing markedly from last premolar; interpterygoid space not extending forward as a palatal emargination; nasal region without emargination; ears small, separate; nose-leaf rudimentary; tail very short if present and wholly enclosed by interfemoral membrane. Dentition, I,2/2; C,1/1; P,2/2; M,3/3 = 32, karyotype 2N = 32, FN = 60.

Ecology

Brachyphylla occupies most of the islands in the Greater and Lesser Antilles. A notable exception is Jamaica from where it is known only from Pleistocene or sub-Recent fossil material. These bats are primarily cave dwelling but have been recorded from an old sugar factory by Bond and Seaman (1958), from an underground unused sugar house by Koopman (1975), and from a large well by Nellis and Ehle (1977). For the observations on roosting sites of *Brachyphylla*, see Allen (1911), Barbour (1945), Goodwin (1933), Gundlach (1877), Miller (1902*b*, 1913), and Nellis and Ehle (1977). The microclimate in the caves inhabited by this bat varies from relatively hot, humid, and stable on Cuba (Silva-Taboada and Pine, 1969) to relatively cool, not too humid, and less stable on Middle Caicos (Buden, 1977).

The diet of *B. cavernarum* is pollen, fruit, and insects (Bond and Seaman, 1958; Nellis, 1971; Gardner, 1977; Nellis and Ehle, 1977) and that of *B. nana* is fruit, pollen, nectar, and insects (Silva-Taboada and Pine, 1969; Gardner, 1977). Indications are that *B. cavernarum* is a good thermoregulator (McManus and Nellis, 1972). Nellis and Ehle (1977), however, noted that the body temperature of the young, in contrast to adults, seemed to be lowered during sleep.

Only ectoparasites have been reported from the genus *Brachyphylla* (Silva-Taboada and Pine, 1969; Ubelaker et al., 1977; Webb and Loomis, 1977). Webb and Loomis (1977) summarized the ectoparasites known to be found on *Brachyphylla nana* (six species of five genera) and *B. cavernarum* (six species of five genera). No species of parasites are common between *nana* and *cavernarum*. However, two genera, *Ornithodoros* (Argasidae) and *Trichobius* (Steblidae), have been found on both. Two species of *Ornithodoros* have been found on *nana* from Cuba and one on *cavernarum* from Guadeloupe and Martinique. One species of *Trichobius* has been found on each *nana* and *cavernarum*. The same species of *Trichobius* known from Cuba was found also on these bats from the Dominican Republic.

Brachyphylla cavernarum

Distribution

This species occurs on Puerto Rico, the Virgin Islands, and down the Lesser Antillean chain as far as St. Vincent and Barbados.

Diagnosis

Distinguished by large external and cranial size. Various other cranial and dental characteristics suggested in the literature to separate the two species appear to be attributable to individual, age, and secondary sexual variation.

Comparisons

The two species, which occur allopatrically, can be readily distinguished. *Brachyphylla cavernarum* is larger than *Brachyphylla nana*, especially in cranial measurements (Table 1). In length of maxillary toothrow and mandibular length, there is no overlap in measurements between the two species. No overlap in measurements between males of the two species is present in palatal length, breadth across upper molars, greatest length of skull, and condylobasal length. In the latter two characters, overlap of measurements in females occurs only between the sample of *B. cavernarum* from Barbados in the southern Lesser Antilles and samples of *B. nana* in the Greater Antilles.

Geographic Variation

Standard statistics for males and females from geographic samples (9 to 27, Fig. 1) are given in Table 1.

Univariate Analyses

External measurements.—Because of missing data and consequent small or non-existing samples, external measurements, with the exception of forearm length, were not subjected to SS-STP analysis.

Variation in length of forearm for *Brachyphylla cavernarum* shows the population from Barbados

(27) to have the shortest forearm of all samples for both sexes, and those from St. John (11) and Norman (12) islands to be the next smallest-sized. The range of forearm length in males from Barbados does overlap, to a certain extent, with most other populations, except St. Eustatius (16), St. Martin (19), Barbuda (20), and Antigua (21). This was not the case in females where overlap was found only with samples from Puerto Rico (9, 10), St. John (11), Norman (12), Saba (15), and Dominica (23). Males and females from Antigua (21) had on the average the longest forearms for the species. No clinal variation in forearm length was apparent.

Cranial measurements.—The 12 cranial measurements analyzed are discussed below in three groups—1) five measurements dealing with length of the skull (greatest length of skull, condylobasal length, palatal length, length of maxillary toothrow, and mandibular length); 2) six measurements dealing with breadth of the skull (zygomatic breadth, breadth of braincase, mastoid breadth, postorbital breadth, rostral width at canines, breadth across upper molars); 3) one measurement dealing with depth of the skull (depth of braincase).

Geographic variation in greatest length of skull for *Brachyphylla cavernarum* also shows, as for forearm length, the population from Barbados (27) to be the smallest in size. The range of this measurement in the Barbados population was clearly lower than that found in samples from the remainder of the geographic range of the species. The male Barbados sample showed range overlap in greatest length of skull only with samples from St. Lucia (25), Dominica (23), Guadeloupe (22), Antigua (21), Puerto Rico (9, 10), St. John (11), and Norman (12) and females showed overlap only with samples from St. Lucia (25), Martinique (24), Guadeloupe (22), Puerto Rico (9, 10), St. John (11), and Norman (12). In both sexes there was no overlap in this measurement between the Barbados sample and the nearest population, St. Vincent (26). However, in both sexes overlap was found between measurements of specimens from Barbados and the next to the nearest population, St. Lucia (25). In both sexes, the two samples from Puerto Rico (9, 10) are grouped with those from St. John (11) and Norman (12), being the next four smallest-sized samples. These four areas are, however, at the opposite end of the geographic range of the species from Barbados. The one specimen examined from St. Thomas has a greater skull length than the means observed for the four samples discussed above (9 to 12), but it falls within the range of observed measurement in these samples and because of its geographic position, it is thought to be grouped best with the samples from Puerto Rico, St. John, and Norman. The one male specimen examined from Montserrat (17) corresponds in greatest length of skull to surrounding localities. The sample of males from Barbuda (20) has the largest mean for this character. The one female specimen examined from Anguilla (18) was larger in greatest length of skull than the means of all other samples and above the upper range of this measurement in some samples. The population of females from St. Croix (14) had the longest skull. As in forearm length, no geographic cline in this measurement was apparent. In both sexes, samples from Barbados, Puerto Rico, and the Virgin Islands, although overlapping, tend to be grouped in subsets showing a break with the others.

Variation in condylobasal length of *Brachyphylla cavernarum* follows basically the pattern of variation found in greatest length of skull.

Palatal length displays a pattern of variation somewhat different from the two previous measurements of length. In males the sample from Barbados (27) is again the smallest with the next smallest two being the samples from Puerto Rico (9, 10). However, the palate in the samples from St. John (11) and Norman (12) is relatively much longer. In females this is only true for the sample from Norman (12). The one from St. John (11) is in fact the smallest in size of all samples. The only other measurement in which the population from Barbados (27) was not the smallest is in postorbital breadth for males. The mean palatal length for females from Saba (15) falls between those of Puerto Rico and St. John on the one hand and Norman on the other. Fairly broad overlap in palatal length was found between the different samples of the species. This is also evident from the SS-STP analyses where four broadly overlapping subsets in males and three in females are evident.

Variation in length of maxillary toothrow is essentially the same as for greatest length of skull. However, a somewhat broader overlap of subsets occurs.

The pattern of variation displayed in mandibular length is essentially the same as for greatest length of skull. However, the four subsets in which the female sample means fall overlap much more extensively than in greatest length of skull. The means of the female samples from Saba (15) and Montser-

rat (17) fall among the means of the populations from Puerto Rico (9, 10), St. John (11), and Norman (12).

The pattern of variation displayed in zygomatic breadth of *Brachyphylla cavernarum* is essentially the same as for greatest length of skull. However, in the males the population from St. Vincent (26) falls within the grouping of populations from Puerto Rico (9, 10), St. John (11), and Norman (12), whereas in greatest length of skull it was just slightly longer than the means of these populations. In females, samples from Martinique (24) and Montserrat (17) displayed a relatively narrow zygomatic breadth, falling within the range of means exhibited by the populations from Puerto Rico, St. John, and Norman. Because of broadly overlapping subsets in females, this could be due to random variation. In males, there is less overlap and an indication of a break between the Virgin Islands and the Lesser Antilles is evident as it was for both sexes in greatest length of skull. The samples from Barbados (27) again averaged the smallest in size for the species.

Variation in breadth of braincase is essentially as in greatest length of skull, with somewhat wider overlap of subsets. It also differs in that the male sample from Guadeloupe (22) displays a relatively narrower breadth of braincase.

Variation in mastoid breadth, judged by the broadly overlapping subsets displayed in SS-STP analysis, could perhaps be explained mainly by random variation. However, the population from Barbados (27) still had the narrowest braincase, and the populations from Puerto Rico, St. John, and Norman still tend to group together exhibiting relatively narrow braincases. In males, the one sample from Puerto Rico (10) exhibited a relatively wide braincase.

Variation in postorbital breadth reveals that the populations from Puerto Rico (9, 10), St. John (11), and Norman (12) have a relatively broad postorbital region, falling among the samples with the largest means. The male sample from Barbuda (20) displays the narrowest postorbital breadth of all samples. The female Barbuda (20) sample also averaged relatively narrow for the species but the Barbados (27) population averaged the narrowest. Fairly widely overlapping subsets in both sexes indicate that little variation is present.

The pattern of variation displayed by rostral width at canines shows very much the same pattern observed in most of the characters studied. Specimens from Barbados (27) have the narrowest rostrum with those from Puerto Rico (9, 10), St. John (11), and Norman (12) being relatively narrow as well. The males from Barbuda (20) have the broadest rostrum, whereas in the females from Barbuda (20) it is relatively much narrower, grouping with the smallest-sized samples.

Variation in width across upper molars follows that of rostral width at canines. Four broadly overlapping subsets are exhibited in both sexes.

Variation in depth of braincase shows little geographic variation, exhibiting only two broadly overlapping subsets in both sexes. The samples of both sexes from Barbados (27) still have the shallowest braincase but the Barbuda (20) samples of both males and females also have a relatively shallow braincase in contrast to the situation in most other characters where this sample averaged relatively large-sized.

Multivariate Analyses

Distance phenograms for both males and females generated with the NT-SYS program package are illustrated in Fig. 7. In addition a map (Fig. 8), including values for both sexes, shows the appropriate distance coefficients between the connected samples; in most cases distance coefficients have been given only for contiguous samples. The first three principal components extracted from the principal component analysis are shown for both males and females in Fig. 9. A factor matrix from correlation among one external and 12 cranial measurements for both sexes is given in Table 5. Two-dimensional plots of the first two variates in a canonical variate analysis generated with the Statistical Analysis System (SAS) package are illustrated for males in Fig. 10 and females in Fig. 11. The relative contribution of each original variable to a particular canonical variable is shown in Table 6.

The distance phenogram (cophenetic correlation coefficient, 0.910) for male *Brachyphylla cavernarum* shows the samples falling into five major groups. The first cluster contains samples from Puerto Rico (9, 10), St. John (11), Norman (12), and St. Thomas (13). Specimens from samples in this cluster are of medium size. The second group includes samples from St. Croix (14), Saba (15), St. Eustatius (16), Anguilla (18), St. Martin (19), Antigua (21), Guadeloupe (22), Dominica (23), Martinique (24), St. Lucia (25), and St. Vincent (26). Although this cluster could be divided into two subclusters, the groupings would not be logical on

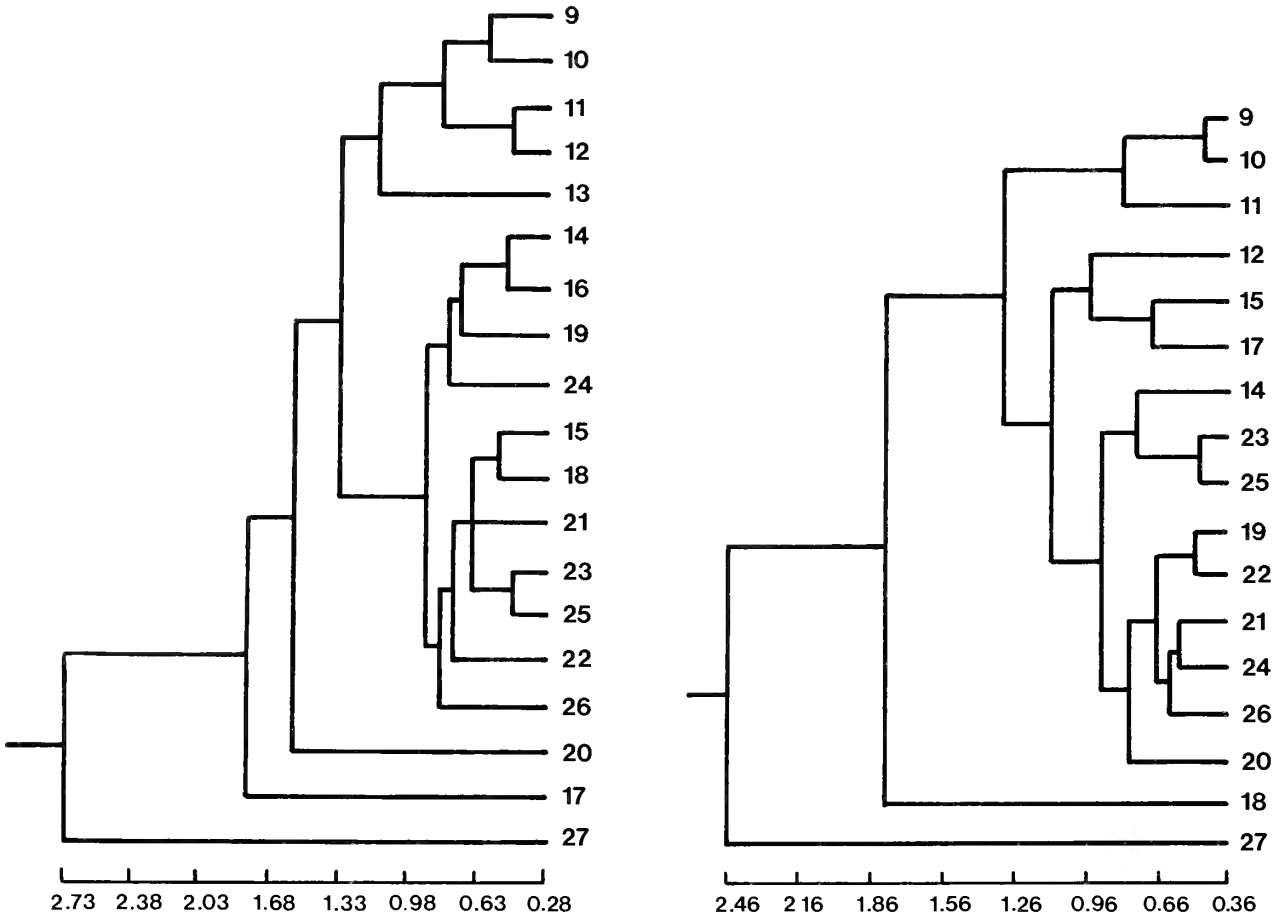

Fig. 7.—Phenograms of numbered samples (see Fig. 1 and text) of *Brachyphylla cavernarum* (males left, females right) computed from distance matrices based on standardized characters and clustered by unweighted pair-group method using arithmetic averages (UPGMA). The cophenetic correlation coefficient for males is 0.910 and for females 0.864.

geographical grounds. Groups 3, 4, and 5 include one sample each—Barbuda (20), Montserrat (17), and Barbados (27). The sample of four specimens from Barbuda is large-sized with a relatively narrow postorbital region and shallow braincase. The one specimen from Montserrat (17) is characterized by a long skull that is relatively narrow and shallow. The sample from Barbados consistently averaged among the smallest in size for the species.

The distance phenogram (cophenetic correlation coefficient 0.864) for female *B. cavernarum* reveals the samples falling into five groups. The first cluster consists of samples from Puerto Rico (9, 10) and St. John (11). The second cluster contains samples from Norman (12), Saba (15), and Montserrat (17). The third cluster consists of the following samples: St. Croix (14), St. Martin (19), Barbuda (20), Antigua (21), Guadeloupe (22), Dominica (23), Martinique (24), St. Lucia (25), St. Vincent (26). This cluster could be divided into two subclusters but again this would not be logical on geographic grounds. The fourth and fifth clusters each consist of only one sample each, Anguilla (18) and Barbados (27). The sample from Anguilla consists of only one specimen, which is characterized by a large skull with a relatively shallow braincase. The sample from Barbados, as in the males, is the smallest-sized population within the species.

In both sexes samples from Puerto Rico (9, 10), and St. John (11), group in the one cluster. However, in the case of the males, the sample from Norman (12) is also contained in this cluster, whereas in the females it groups with another cluster, which has no counterpart in the males. This might be indicative of some past gene flow among populations

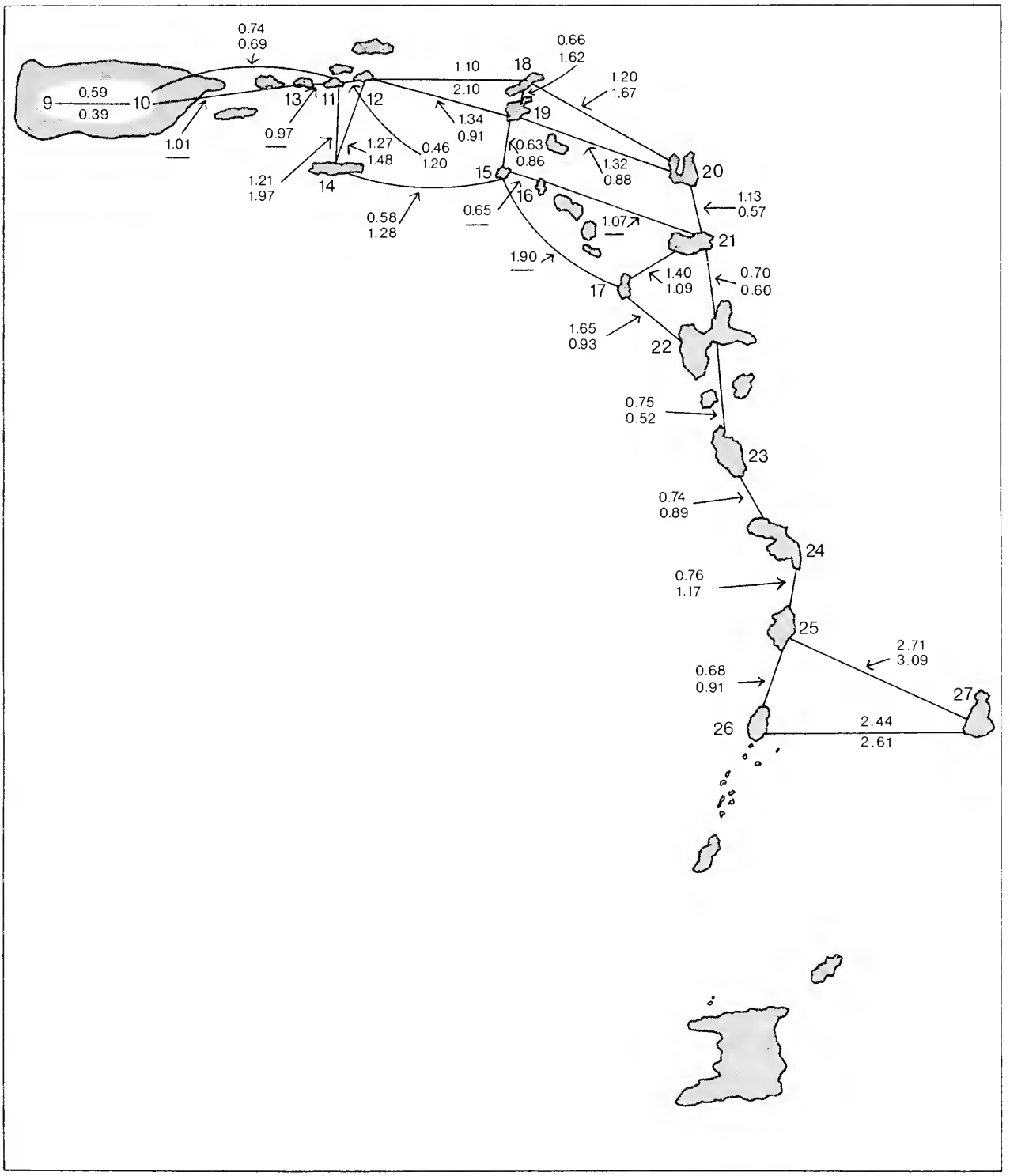

Fig. 8.—Map showing distance coefficients (from distance matrices) between samples of *Brachyphylla cavernarum* that were analyzed in the study of geographic variation. The upper coefficients are for males and the lower for females. See Fig. 1 and text for key to samples.

Table 5.—*Factor matrix from correlation among 13 characters of* B. cavernarum *studied, showing characters influencing the first three components.*

Characters	Males			Females		
	Component I	Component II	Component III	Component I	Component II	Component III
Length of forearm	0.772	−0.063	−0.341	0.679	−0.069	0.123
Greatest length of skull	0.938	−0.095	−0.178	0.915	−0.136	−0.110
Condylobasal length	0.880	−0.321	−0.064	0.970	−0.116	−0.025
Palatal length	0.826	−0.062	0.005	0.762	0.407	0.247
Depth of braincase	0.409	0.836	−0.068	0.702	−0.078	0.655
Zygomatic breadth	0.930	0.070	−0.150	0.932	0.058	0.186
Breadth of braincase	0.812	0.374	0.049	0.931	−0.009	0.011
Mastoid breadth	0.823	−0.067	−0.276	0.880	−0.248	0.242
Postorbital breadth	−0.121	0.855	−0.405	0.181	−0.949	−0.134
Length of maxillary toothrow	0.839	−0.416	0.156	0.854	0.154	−0.454
Rostral width at canines	0.652	0.414	0.575	0.826	0.106	−0.185
Breadth across upper molars	0.800	0.332	0.398	0.845	0.230	−0.257
Mandibular length	0.854	−0.313	−0.043	0.855	−0.047	−0.258

from Puerto Rico through the Virgin Islands to the remainder of the Lesser Antilles. The population from St. Croix (14), geographically intermediate between the two areas but fairly well isolated from the remainder of the Virgin Islands by a deep channel, do not seem to be instrumental in the relationship. The distinct cluster formed by four male specimens from Barbuda is not matched in the sample of seven females.

The amount of phenetic variation represented in the first three principal components for male and female *Brachyphylla cavernarum*, respectively, was 60.1 and 67.0 for component I, 17.3 and 9.7 for component II, and 7.2 and 7.7 for component III. From the factor analysis it can be seen that in males the first and most important component is heavily influenced by general size; however, depth of braincase showed a relatively low positive value and postorbital breadth a low negative value. This negative influence of postorbital breadth corresponds to what we have seen in the univariate analysis, where this measurement tended to become narrower when others became larger. Component II is influenced by depth of braincase and postorbital breadth. Component III is negatively influenced by length of forearm and postorbital breadth and positively by rostral width at canines and breadth across upper molars. In females, component I is heavily influenced by all characters except postorbital breadth, although not negatively so as in males. Component II is negatively influenced by postorbital breadth. Component III is positively influenced by depth of braincase and negatively by length of maxillary toothrow.

Examination of the three-dimensional plot of the male samples reveals a pattern similar to that of the distance phenogram, whereas in the plot of the female samples the two analyses differ in some ways. The sample of females from Norman (12) clustering in the distance phenogram with samples from Saba (15) and Montserrat (17), appears in the three-dimensional plot to be closer to samples from Puerto Rico (9, 10). Samples from St. Croix (14) and St. Lucia (25) form a distinct cluster in the three-dimensional plot but this is not evident in the distance phenogram. In both the distance phenogram and principal component analysis the samples from Anguilla (18) and Barbados (27) form their own clusters.

In both male and female *Brachyphylla cavernarum*, a MANOVA showed that there were significant ($P < 0.0001$) morphological differences among samples in all four statistical tests (Hotelling-Lawley's Trace, Pillai's Trace, Wilks' Criterion, and Roy's Maximum Root Criterion) utilized. Among individual measurements only depth of braincase in males showed no significant differences among samples. In the univariate analysis of depth of braincase, two broadly overlapping subsets resulted from the SS-STP analysis in both males and females, also suggesting little variation in this measurement between different samples of *Brachyphylla cavernarum*.

The amount (percentage) of phenetic variation represented in the first three canonical variates for male and female *Brachyphylla cavernarum*, respectively, was 53.7 and 33.0 for variate I, 15.1 and 23.1 for variate II, and 8.3 and 15.0 for variate III. Com-

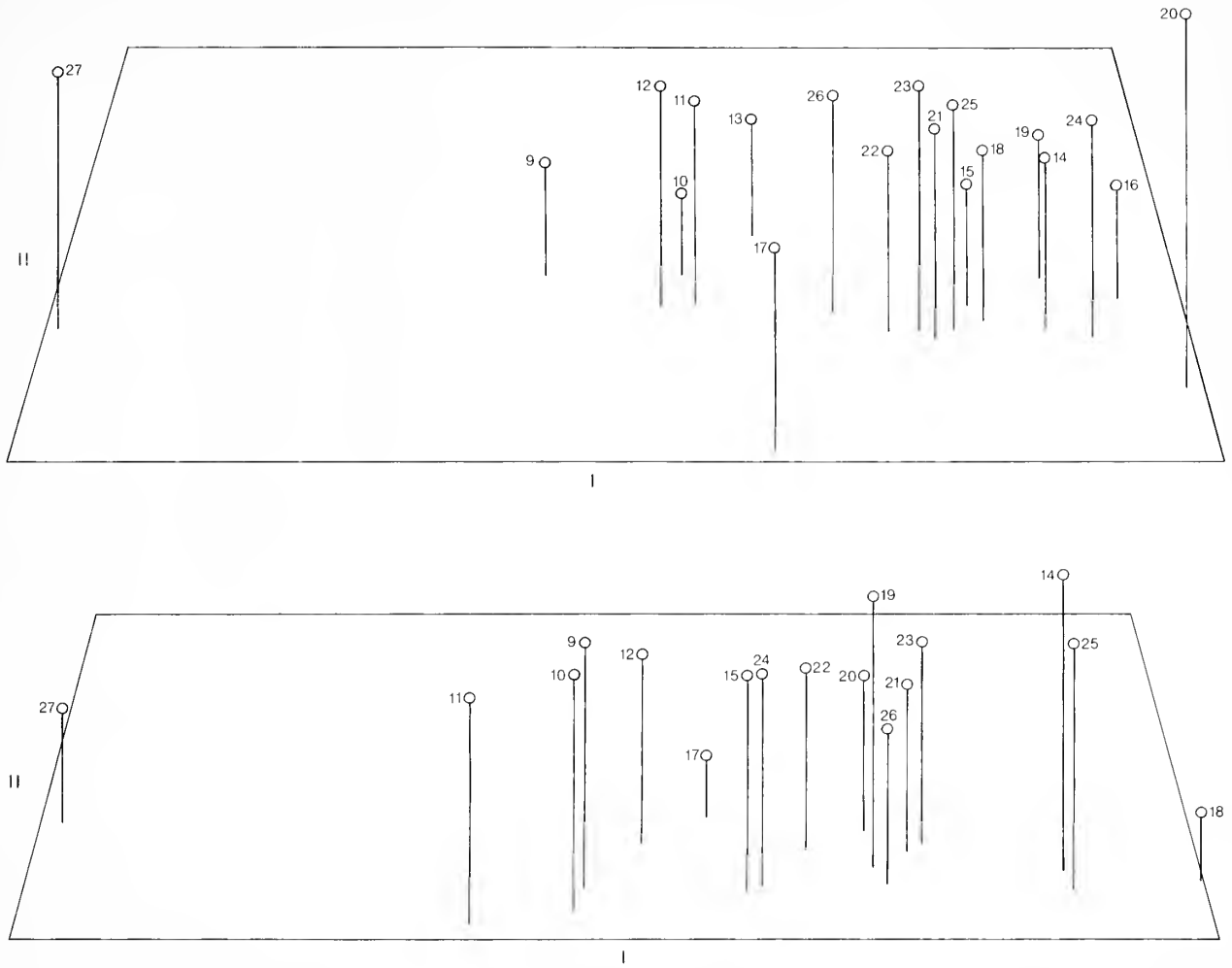

Fig. 9.—Three-dimensional projections of samples of *Brachyphylla cavernarum* (males above, females below) onto the first three principal components based on matrices of correlation among one external and 12 cranial measurements. Components I and II are indicated in the figure and component III is represented by height. See Fig. 1 and text for key to samples.

bined these variates express 77.1% in males and 71.1% in females. In both males and females it took all 13 canonical variates to explain all the variation. The relative contributions of each character to the first three canonical variates in males and females are given in Table 6.

Separation on the first variate in males is heavily (10%) influenced by greatest length of skull, postorbital breadth, length of maxillary toothrow, and mandibular length, and in females by condylobasal length and mandibular length. The second variate in males is heavily (10%) influenced by length of forearm, greatest length of skull, length of maxillary toothrow, and mandibular length, and in females by condylobasal length, length of maxillary toothrow, and rostral width at canines. The third variate in males was most heavily influenced (10%) by condylobasal length, breadth of braincase, and mandibular length. In females length of forearm, condylobasal length, zygomatic breadth, and length of maxillary toothrow contributed more than 10% to the separation of the samples on the third variate.

Examination of the two-dimensional canonical variate plot of the 19 male samples generally reveals a pattern of variation similar to that found in the distance phenogram and principal component analysis. On the first variate, three groups are evident. The one at the top consists of only one sample (Barbuda, 20), one at the bottom consists of the Puerto Rican samples (9, 10), and the main group in the middle includes all other samples, including the one specimen from Montserrat (17), which in both the

Table 6.—*Eigenvalues of canonical variates showing the percentage influence among 13 characters of* B. cavernarum. *Eigenvalues shown represent the normalized vector coefficient of each character.*

Character	Vector I		Vector II		Vector III	
	Eigenvalue	Percent influence	Eigenvalue	Percent influence	Eigenvalue	Percent influence
			Males			
Length of forearm	−0.0066	2.3	0.0285	11.2	0.0136	4.3
Greatest length of skull	−0.0642	10.3	0.0929	17.7	0.0360	5.9
Condylobasal length	−0.0351	5.0	−0.0293	4.9	−0.2016	29.3
Palatal length	0.0117	0.7	−0.0897	6.5	0.0126	0.8
Depth of braincase	0.0303	2.0	−0.1117	9.0	0.0535	3.6
Zygomatic breadth	−0.0218	2.0	0.0594	6.1	0.0151	1.3
Breadth of braincase	0.0926	6.0	0.0140	1.1	−0.1604	10.5
Mastoid breadth	−0.0897	6.9	0.0038	0.4	−0.0586	4.5
Postorbital breadth	−0.4782	15.5	0.1109	4.2	0.1826	6.0
Length of maxillary toothrow	0.3126	29.9	0.2143	24.1	−0.0534	3.1
Rostral width at canines	0.0187	0.7	0.0359	1.6	−0.0762	2.9
Breadth across upper molars	0.0421	2.5	0.0289	2.0	0.1257	7.5
Mandibular length	0.1587	16.3	−0.0933	11.3	0.1751	18.2
			Females			
Length of forearm	0.0362	8.6	0.0264	4.8	0.0363	11.5
Greatest length of skull	−0.0152	1.7	0.0998	9.0	0.0348	5.5
Condylobasal length	0.2787	28.9	−0.3084	24.5	−0.1641	22.7
Palatal length	−0.0976	4.3	0.1219	4.1	−0.1068	6.3
Depth of braincase	−0.1637	8.0	0.0329	1.3	−0.0750	4.1
Zygomatic breadth	−0.0618	3.9	0.0987	4.8	−0.1677	14.2
Breadth of braincase	0.1207	5.7	0.2673	9.6	0.0933	5.8
Mastoid breadth	0.0732	4.0	−0.1189	4.9	0.0205	1.5
Postorbital breadth	0.2399	5.7	−0.4875	8.8	0.0208	0.6
Length of maxillary toothrow	−0.0988	4.0	0.3853	11.8	0.3602	19.2
Rostral width at canines	0.3576	9.4	−0.0586	11.9	−0.0147	0.5
Breadth across upper molars	−0.0425	1.8	0.0085	0.3	−0.0165	0.9
Mandibular length	−0.1880	14.0	−0.0728	4.2	−0.0625	6.2

distance phenogram and principal component analysis is clearly separated from the other samples. On the second variate the population from Barbados (27) is well separated, showing one standard deviation overlap only with the samples from St. John (11) and Norman (12). The sample from St. John (11) is somewhat removed on the first variate from the middle cluster and shows some overlap with the western Puerto Rican sample (9) at the bottom. The Norman population (12) falls between the Barbados sample (27), and the main cluster of samples. At the right of the plot, the sample from Antigua (21) shows some separation from the main cluster on the second variate.

Examination of the two-dimensional canonical variate plot of 16 female samples onto the first two variates reveals a pattern of variation generally similar to that found in the distance phenogram and the principal component analyses. Two main groups of samples are evident on the first variate. The one at the bottom consists of only one sample (Barbados, 27) and the group at the top contains the remainder of the samples. The eastern Puerto Rican (10), St. John (11), and Norman (12) populations are clearly separated from the main cluster on the second variate. None of these three sample means are included within a one standard deviation range of any of the other samples nor do their ranges (1 SD) include means of any other samples. The western Puerto Rican sample (9) overlaps extensively with the main cluster, whereas a clear separation from the main cluster and a grouping with eastern Puerto Rico (10), St. John (11), and Norman (12) is illustrated in the distance phenogram and principal component analyses. The sample of two specimens from Montserrat (17) forms a subgroup somewhat removed from the main group on the first variate to the top of the plot and overlaps with the one standard deviation range of the samples from Martinique (24) and St. Lucia (25). At the right of the plot, a sub-

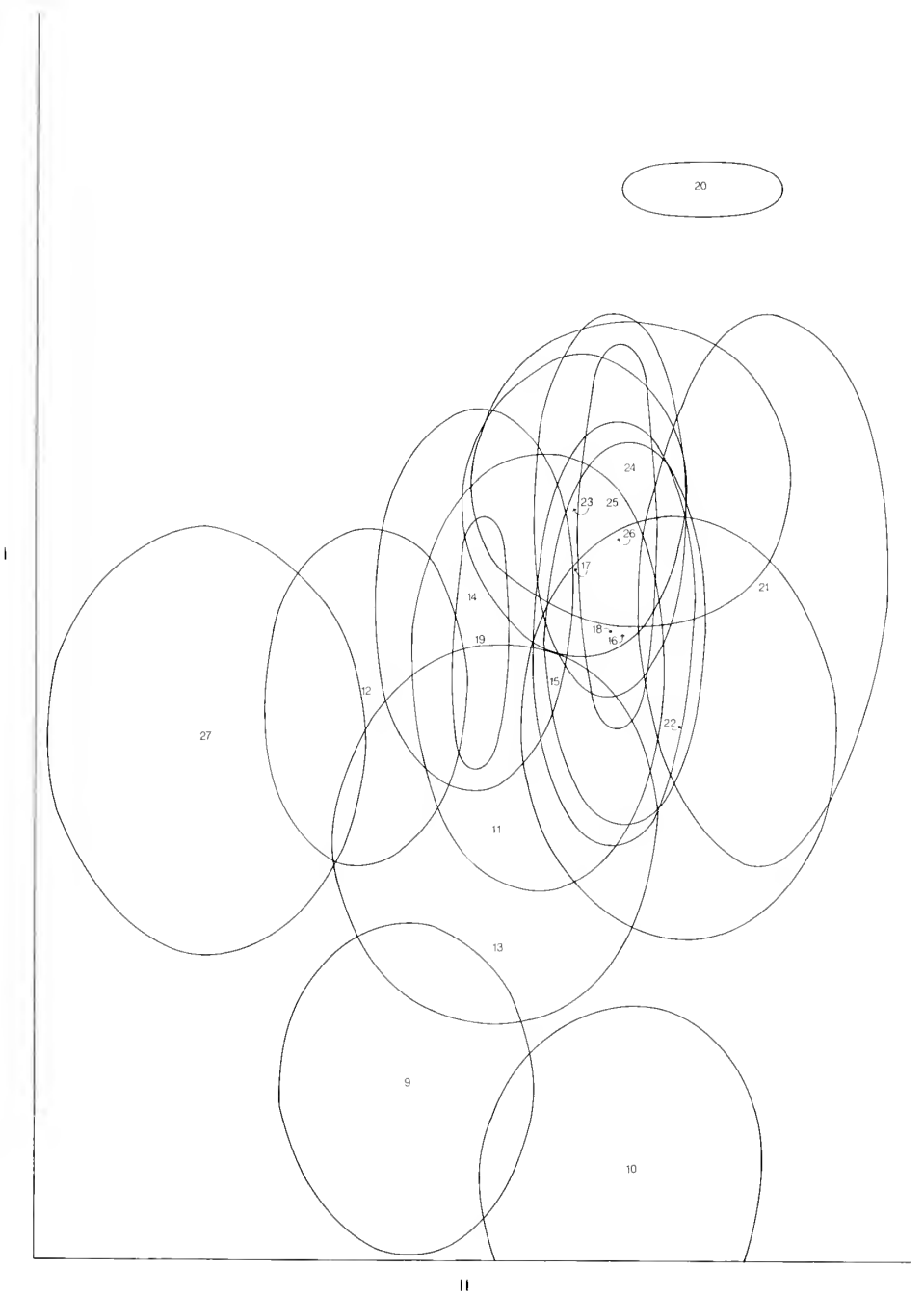

Fig. 10.—Two-dimensional projection of male samples (mean and one standard deviation) of *Brachyphylla cavernarum* onto the first two canonical variates based on a matrix of variance-covariance among one external and 12 cranial measurements. See Fig. 1 and text for key to samples.

group separated on the first variate, with no counterpart in the other multivariate analyses, is formed by samples 15 (Saba) and 20 (Barbuda). The means of these two samples fall outside the one standard deviation range of all other samples.

Taxonomic Conclusions

Based upon our assessment of geographic variation in *Brachyphylla cavernarum*, we believe there are three identifiable populations. The smallest individuals in the species, and phenetically the most

Fig. 11.—Two-dimensional projection of female samples (mean and one standard deviation) of *Brachyphylla cavernarum* onto the first two canonical variates based on a matrix of variance-covariance among one external and 12 cranial measurements. See Fig. 1 and text for key to samples.

distinct, occur on Barbados and the name *Brachyphylla cavernarum minor* Miller, 1913, applies to them. The nominate subspecies, *Brachyphylla cavernarum cavernarum*, representing the largest individuals of the species, occurs on St. Croix in the Virgin Islands and Anguilla southward through the Lesser Antilles to St. Vincent. A third subspecies, which is characterized by intermediate size and is

described herein as new, occurs on Puerto Rico and most of the Virgin Islands (St. John, Norman, and St. Thomas excluding St. Croix). This subspecies is not distinguished by any one single character but its overall size as measured in multivariate analyses indicates that 80% to 90% of the individuals in this population are distinguishable from Lesser Antillean populations. The population from Barbuda may represent a phenetically identifiable population and, therefore, may represent a separately evolving lineage. However, because our data are inconclusive, we have thought it best not to recognize this population for the time being.

Brachyphylla cavernarum cavernarum Gray, 1834

1834. *Brachyphylla cavernarum* Gray, Proc. Zool. Soc. London, p. 123, 12 March.

Lectotype.—Adult male, in alcohol with skull not removed, BMNH 77.2746, from St. Vincent, Lesser Antilles, obtained by L. Guilding.

Measurements of lectotype.—Length of forearm, 65.5.

Distribution.—Known from St. Croix in the Virgin Islands and Anguilla southward through the Lesser Antilles to St. Vincent.

Comparisons.—The nominate subspecies can be distinguished from *minor* and *intermedia* by its larger overall size (see also Comparisons under *B. c. intermedia*).

Remarks.—*Brachyphylla cavernarum cavernarum* is a large-sized subspecies potentially in contact with the medium-sized *B. c. intermedia* in the north on the Virgin Islands and Puerto Rico, and to the southeast with the small-sized *B. c. minor* from Barbados. The only indication of possible past contact between *cavernarum* and *intermedia* was the grouping of samples of females from Norman Island, Saba, and Montserrat in the female distance phenogram. There is no evidence for intergradation between these two subspecies through the population on St. Croix. This population is clearly related to *B. c. cavernarum*.

If there is intergradation between *cavernarum* and *minor*, it is probably through the population to the northwest of Barbados on St. Lucia rather than the population to the west on St. Vincent. In greatest length of skull (both sexes), condylobasal length (females), breadth across upper molars (males), and mandibular length (males) there was no overlap in the range of measurements between populations on Barbados and St. Vincent; however, there was overlap in both sexes between Barbados and St. Lucia populations.

In the original description Gray listed two cotypes, a male and a female, from St. Vincent. Gray (1838) again stated that this species is known only from St. Vincent. In listing the mammalian specimens present in the collection of the British Museum, Gray (1843) indicated that at that time an additional specimen from Cuba, presented by W. S. MacLeay, was in the collection. From the above it is clear to us that this female specimen from Cuba was not available to Gray when he described *B. cavernarum*. Therefore, Dobson (1878) incorrectly listed this specimen from Cuba as the holotype. Dobson does list a male from St. Vincent and a female from the "West Indies," which may represent the cotypes.

The female paralectotype mentioned by Gray (1834) could not be located in the British Museum (Natural History) collection. The specimen presumably has been destroyed or was exchanged with another institution sometime in the past. However, according to John Edwards Hill (*in litt.*, 16 November 1977) "There are in the collections male and female specimens of *B. cavernarum* BM(NH) 7.1.1. 701-702, that came here from the collection of R. F. Tomes. The documentation indicates that Tomes obtained these from the Zoological Society of London and there is every probability that these, too, are from the original series. Both are in good condition: the male is BM(NH) 7.1.1. 701, the female BM(NH) 7.1.1. 702."

Specimens examined (206).—St. Croix: Sion Hill, 11 (AMNH); no specific locality, 6 (4 AMNH, 2 AS). Saba: Bat hole near Land Point, 2 (RMNH); Ladderberg, 6 (RMNH); Windwardside, 1 (AMNH); no specific locality, 2 (RMNH). St. Eustatius: rim of The Quill, 2 (AMNH); no specific locality, 1 (MCZ). Montserrat: no specific locality, 5 (USNM). St. Martin: Lowlands, 16 (AMNH).Barbuda: no specific locality, 12 (USNM). Anguilla: Island Harbor, Fountain Cave, 7 (AMNH); Valley, 3 (AMNH). Antigua: 1 mi E English Harbor, 1 (KU); St. Paul Parish, 2 (FMNH); no specific locality, 17 (3 BMNH, 14 USNM). Guadeloupe: 2 km S, 2 km E Baie-Mahault, Basse-Terre, 1 (TTU); 2 km N Baillif, Basse-Terre, 1 (TTU); 1 km S Basse-Terre, Basse-Terre, 1 (TTU); 1 km S, 4 km W Vernou, Basse-Terre, 1 (TTU); 1 km W Vernou, Basse-Terre, 1 (TTU); 1 km N, 1 km W St. François, Grand-Terre, 27 (TTU); no specific locality, 1 (MCZ). Dominica: Clarke Hall Estate, 100 ft, St. Joseph Parish, 10 (KU); 6 mi NE Roseau, St. Paul Parish, 2 (AS); no specific locality, 6 (1 AS, 5 USNM). Martinique: Bellefontaine, 2 (AMNH); Casé Pilote, 5 (AMNH); 6 km E La Trinité, 4 (AMNH); no specific locality, 9 (1 AMNH, 8 MCZ). St. Lucia: no specific locality, 20 (USNM). St. Vincent: Clifton Hill, 400 ft, St. George Parish, 2 (KU); Kingstown, 150 ft, St. George Parish, 1 (KU), no specific locality, 18 (3 BMNH, 15 USNM).

Brachyphylla cavernarum intermedia, new subspecies

Holotype.—Adult female, skin, skull, and skeleton, CM 44707; from 1 mi W Corozal, Puerto Rico; obtained by R. J. Baker on 22 July 1969, original no. 1375. Skin, skull, and body skeleton in good condition.

Paratypes.—Two adult males and one adult female, skin, skull, and skeleton, TTU 9819, CM 44708, and TTU 9820; from 1 mi W Corozal, Puerto Rico; obtained by R. J. Baker on 21 July 1969, original nos. S. L. Williams 319, 321, and 320, respectively. Skins, skulls, and body skeletons in good condition.

Measurements.—External and cranial measurements of the holotype and paratypes, respectively, were as follows: total length, 86, 93, 87, 91; length of hind foot, 18, 17, 16, 15; length of ear, 20, 22, 21, 21; length of forearm, 66.5, 66.6, 66.5, 68.0; greatest length of skull, 32.1, 32.1, 32.7, 32.0; condylobasal length, 28.9, 28.4, 28.9, 28.6; palatal length, 12.0, 12.4, 11.8, 11.7; depth of braincase, 13.7, 13.6, 13.8, 13.6; zygomatic breadth, 17.6, 17.5, 17.4, 17.5; breadth of braincase, 12.6, 12.6, 12.9, 12.7; mastoid breadth, 15.0 15.0, 14.9, 14.9; postorbital breadth, 6.5, 6.4, 6.6, 6.6; length of maxillary toothrow, 10.8, 10.8, 10.7, 10.7; rostral width at canines, 7.1, 7.2, 7.5, 7.0; width across upper molars, 12.1, 11.6, 11.8, 11.5; mandibular length, 20.5, 20.5, —, 20.3.

Distribution.—Puerto Rico and Virgin Islands (excluding St. Croix).

Comparisons.—*Brachyphylla cavernarum intermedia* is distinguished from *Brachyphylla cavernarum cavernarum* by its smaller cranial size. From *B. c. minor*, with which it is not potentially in contact, *B. c. intermedia* differs in being larger, both externally and cranially (see Tables 1 and 2). Specimens herein referred to *B. c. intermedia* previously have been reported as *B. c. cavernarum*. No overlap was found in sample means of either sex among *intermedia*, *cavernarum*, and *minor* in one measurement (range of means in *intermedia*, *cavernarum*, and *minor*, respectively)—greatest length of skull (males, 31.4–31.7, 31.9–32.4, 30.5; females, 31.0–31.5, 31.6–32.3, 30.5). In length of maxillary toothrow (males, 10.6–10.8, 10.9–11.3, 10.6; females 10.7, 10.8–11.1, 10.5) overlap was observed in sample means of males of *minor* and *intermedia* only. Overlap in sample means of only one of the sexes among the three subspecies is present in condylobasal length (males, 28.0–28.2, 28.4–29.2, 27.1; females, 27.8–28.0, 28.0–28.6, 27.0), breadth of braincase (males, 12.6–12.8, 12.7–13.1, 12.4; females, 12.5–12.6, 12.7–13.0, 12.3), breadth across upper molars (males, 11.5–11.6, 11.7–12.0, 11.1; females, 11.2–11.7, 11.5–11.9, 11.2), and mandibular length (males, 19.9–20.3, 20.4–20.8, 19.5; females, 19.9–20.1, 20.0–20.7, 19.2).

Remarks.—In our opinion, there are populations of three distinct sizes in *Brachyphylla cavernarum*. The populations on Puerto Rico and most of the Virgin Islands are intermediate in size between the large *B. c. cavernarum* of St. Croix and the Lesser Antilles as far south as St. Vincent and the small-sized population of *B. c. minor*, which is restricted to Barbados. This new taxon, *B. c. intermedia*, is potentially in contact with *B. nana* on the west and *B. c. cavernarum* on the east.

Although *B. c. intermedia* is smaller than *B. c. cavernarum*, it is still distinctly larger than *B. nana* (range of greatest length of skull, male, 30.5–33.0, female, 30.3–32.1 in Puerto Rican samples as compared with 27.2–29.3 and 27.1–29.1 in Hispaniolan samples, see also Table 1). We have seen no evidence to indicate intergradation or hybridization between these taxa. See account of *B. c. cavernarum* for possible intergradation with that taxon and the status of the population on St. Croix.

Coloration in *intermedia* is generally blackish brown, or grayish brown tinted buff, whereas *cavernarum* is mostly blackish brown, with a few grayish brown individuals being found.

Choate and Birney (1968) reported on sub-Recent fossil material from Puerto Rico. The only measurements they took that are comparable to ours in the way they were taken are zygomatic breadth, breadth of braincase, and height of coronoid. In both zygomatic breadth and breadth of braincase, ranges of measurements of Recent material encompass those of the sub-Recent material and the means are very close. However, in the sub-Recent material, height of coronoid process ranged lower in addition to averaging smaller. Anthony (1925) after comparing and measuring fossil and Recent *Brachyphylla* from Puerto Rico could find "no differences worthy of mention." We consider the sub-Recent as belonging to the new subspecies.

Specimens examined (233).—Puerto Rico: 1.5 km N, 13.5 km E Adjuntas, 1 (LSU); Iglesia de la Mora Comerio, 11 (USNM); 1 mi Corozal, 48 (2 CM, 46 TTU); El Verde Field Station, 2 (TTU); 5 km E Guanica, 1 (LSU); 7.5 km E Guanica, 12 (AS); Pueblo Viejo, 13 (9 AMNH, 4 USNM); Cueva de Fari, San Juan, 7 (UMMZ); Trujillo Alto, 4 (AMNH); La Cueva de Mollfulleda, Trujillo Alto, 13 (USNM); 17.7 km NE Utuado, 7

(AS). St. John: Cruz Bay, 4 (AMNH); Lameshur, 14 (AMNH); ½ mi S, ⅖ mi W Lameshur, 42 (40 KU, 2 TCWC). Norman: west end, 53 (15 AMNH, 36 KU, 2 TCWC). St. Thomas: Botany Bay, 1 (AMNH).

Brachyphylla cavernarum minor Miller, 1913

1913. *Brachyphylla minor* Miller, Proc. Biol. Soc. Washington, 26:32, 8 February.
1968. *Brachyphylla cavernarum minor*, Koopman, Amer. Mus. Novit., 2333:5, 19 July.

Holotype.—Adult female in alcohol with skull removed, USNM 101,528, from Cole's Cave, St. Thomas Parish, Barbados, Lesser Antilles, obtained by P. McDonough on 14 June 1899.

Measurements of holotype.—Total length, 78; length of forearm, 61.5; condylobasal length, 26.3; palatal length, 10.8; depth of braincase, 12.6; zygomatic breadth, 15.8; breadth of braincase, 12.0; mastoid breadth, 13.8; postorbital breadth, 6.1; length of maxillary toothrow, 10.3; rostral width at canines, 6.4; width across upper molars, 11.0.

Distribution.—This subspecies is restricted to Barbados, Lesser Antilles.

Comparisons.—Size small for the species cranially; averaging the smallest-sized sample of *B. cavernarum* in all characters except palatal length for females and postorbital breadth in males.

Remarks.—*Brachyphylla cavernarum minor* is well differentiated and is potentially in contact only with *B. c. cavernarum* and can be distinguished from it by its generally shorter forearm and smaller-sized cranium (see also Comparisons under *B. c. intermedia*). *Brachyphylla c. minor* from Barbados shows no overlap in measurements with both its nearest neighbors, St. Vincent (26) and St. Lucia (25) in condylobasal length (males) and forearm length (females), and no overlap with St. Vincent (26) only, in the following characters: greatest length of skull (males and females); condylobasal length (females); breadth across upper molars (males); and mandibular length (males) (see Table 1).

This taxon was considered to be a distinct species until Koopman (1968) reviewed its status. He presented evidence, and our study supports his findings, that this taxon is distinct but only at the subspecific level. The isolation of the island of Barbados to the east of the main chain of the Lesser Antilles undoubtedly has provided the isolation necessary for the genetic differentiation of this population to occur.

Most of the bats from Barbados have hair yellowish white at the base with dark buffy tinted tips. All these specimens are Albert Schwartz Field Series material and as in the case of the Cuban material from this collection might have been exposed to some bleaching. Other material from Barbados have base of hair white with blackish gray tips, or grayish brown with a buffish tint.

Specimens examined (24).—Barbados: Brighton, 250 ft, St. George Parish, 3 (KU); Cole's Cave, St. Thomas Parish, 6 (5 AMNH, 1 USNM); St. Thomas Parish, 1 (USNM); no specific locality, 14 (11 AS, 1 BMNH, 2 FMNH).

Brachyphylla nana

Distribution

This species occurs on Cuba, Isle of Pines (Varona, 1974), Grand Cayman, Hispaniola, Middle Caicos, and as a Pleistocene or sub-Recent fossil on Jamaica.

Diagnosis

See account for *Brachyphylla cavernarum*.

Comparisons

See account for *Brachyphylla cavernarum*.

Geographic Variation

Univariate Analyses

Standard statistics for geographic samples of *Brachyphylla nana* (samples 1–8, Fig. 1) are given in Table 1.

External measurements.—As in *Brachyphylla cavernarum*, because of missing data and consequent small or nonexisting samples, external measurements except length of forearm, were not subjected to ANOVA and SS-STP analyses. However, in spite of small sample sizes, it is apparent that the sample from the Dominican Republic (8) is relatively smaller sized than the others at least in total length.

Length of forearm of the samples from Middle Caicos (6) and the Dominican Republic (8) is relatively short for the species in both males and females. The small sample size available from the Haitian (7) population makes meaningful conclusions difficult concerning the relationship between the Haitian and Dominican Republic populations. In males, the SS-STP analysis shows that the three samples from Cuba (1, 2, 3) fall in one subset, differing significantly from the second subset, which includes samples from the Dominican Republic (8), Middle Caicos (6), and Cuba (Camagüey, 4). Sample 4 consists of only two specimens and their fore-

arm measurements appear to fall within the normal variation of most Cuban samples. Females do not exhibit such a clearcut break in the SS-STP analysis. Although no clinal trend exists in males from Cuba (1–3), there appears to be an increase in size from the small-sized specimens in Habana Province (1) eastward to Oriente Province (3) in females.

Cranial measurements.—The 12 cranial measurements analyzed are discussed below in three groups—1) five measurements dealing with length of the skull (greatest length of skull, condylobasal length, palatal length, length of maxillary toothrow, mandibular length); 2) six measurements dealing with breadth of the skull (zygomatic breadth, breadth of braincase, mastoid breadth, postorbital breadth, rostral width at canines, breadth across upper molars); 3) one measurement dealing with depth of skull (depth of braincase).

Geographic variation in greatest length of skull for *Brachyphylla nana* males shows no significant differences among the seven samples tested, as revealed by an ANOVA. In females the values for greatest length of skull fall into two broadly overlapping subsets. In both sexes the population from the Dominican Republic (8) has a relatively short skull and the one from Middle Caicos (6) a relatively long one. Female samples from Cuba (1–3) show a clinal trend similar to length of forearm, but male samples follow a reverse trend. The two males from Camagüey Province (4) average large for the species. The one female available from this locality is among the smallest for females in the species.

Variation in condylobasal length in *Brachyphylla nana* follows the pattern of variation for greatest length of skull. In this character, however, the females from Cuba (1, 2, 3) do not show any clinal variation, whereas the males do.

Palatal length displays a pattern of variation differing from the previous two cranial measurements. Male samples from the Dominican Republic (8) and Middle Caicos (6) have on the average the longest palate for the species. Although no significant differences were detected among the samples of females with an analysis of variance test, the Dominican Republic (8) and Middle Caicos (6) samples have on the average relatively long palates for the species. The clinal trend among samples from Cuba (1, 2, 3) is not observed in this character.

There is no significant variation in length of maxillary toothrow in both males and females.

No significant variation in mandibular length is displayed. Although differences among samples could be ascribed to random variation, Middle Caicos (6) and Dominican (8) populations tend to have relatively short mandibles.

Variation in zygomatic breadth essentially follows the pattern of variation for greatest length of skull and condylobasal length. However, no clinal variation is present.

No significant differences in breadth of braincase were detected among samples of both males and females of *B. nana* with analysis of variance tests. There were only slight differences (range of 0.2) among samples in both sexes.

No significant differences in mastoid breadth were detected among samples of males, whereas in females two overlapping subsets were present. In both sexes, it was found that the Dominican Republic (8) population clearly averages narrower than did the Middle Caicos population.

Variation in postorbital breadth for males, falling into two overlapping subsets, shows the Dominican Republic (8) population characterized by a relatively broad postorbital region and those from Cuba (1, 2, 3) and Middle Caicos (6) by relatively narrow postorbital regions. No significant differences were detected among the samples of females.

Rostral width at canines displays a pattern of variation in which the population from the Dominican Republic (8) averages the narrowest and those from Cuba (1, 2, 3) relatively wide, whereas the Middle Caicos (6) population is of intermediate size. In males the means fall into two slightly overlapping subsets. The Dominican Republic (8) and Middle Caicos (6) samples are in one subset and all other samples in the second subset. Overlap between the two occurs only in the Caicos sample. Females fall into four overlapping subsets.

The pattern of variation present in breadth across upper molars for males is essentially the same as that found in both sexes for rostral width at canines. The pattern of variation in breadth across upper molars in females differs in that the mean for females from Middle Caicos is closer in size to those of the Cuban samples than to the Dominican Republic one. The clinal variation found in some measurments for Cuban males is also found in breadth across upper molars.

Variation in depth of braincase in both sexes shows the Middle Caicos (6) population characterized by a relatively deep braincase, and the Cuban and Dominican Republic populations by a relatively shallow braincase. The four female specimens from Haiti have relatively deep braincases.

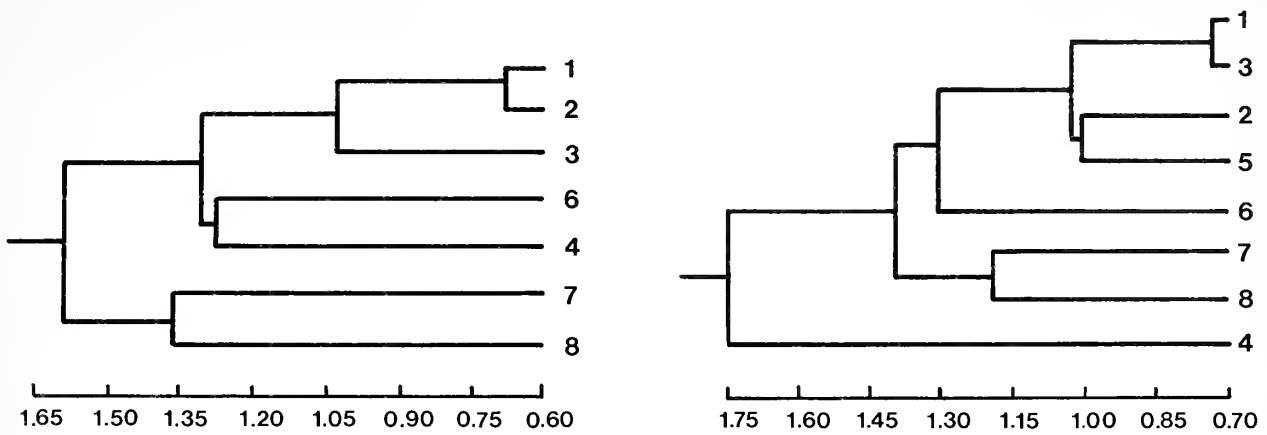

Fig. 12.—Phenograms of numbered samples (see Fig. 1 and text) of *Brachyphylla nana* (males left, females right) computed from distance matrices based on standardized characters and clustered by unweighted pair-group method using arithmetic averages (UPGMA). The cophenetic correlation coefficient for males is 0.808 and for females 0.831.

Multivariate Analyses

Distance phenograms for both males and females, generated with the NT-SYS program package, are given in Fig. 12. In addition a map (Fig. 13), including values for both sexes, shows the appropriate distance coefficients between the connected samples; in most cases distance coefficients have been given only for contiguous samples. The first three principal components extracted from the principal component analysis are shown three-dimensionally for both males and females in Fig. 14. A factor matrix from correlation among one external and 12 cranial measurements in both males and females are given in Table 7. Two-dimensional plots of the first two variates in a canonical analysis generated with the Statistical Analysis System (SAS) package are illustrated for males in Fig. 15 and for females in Fig. 16. The relative contribution of each character to the first three canonical variates is shown in Table 8.

The distance phenogram (cophenetic correlation coefficient, 0.808) for male *Brachyphylla nana* shows the samples falling into three major groups. The first cluster contains three samples from Cuba (1, 2, 3). The second cluster contains the samples from Middle Caicos (6), and Camagüey Province, Cuba (4). The two samples in the latter cluster are phenetically quite distinct. The Camagüey sample (4) consists of only two specimens and, as seen in the univariate analysis, they are medium to large sized except in length of forearm and length of maxillary toothrow where they averaged the smallest. The third cluster consists of two phenetically quite

Table 7.—*Factor matrix from correlation among 13 characters of* Brachyphylla nana *studied, showing characters influencing the first three components.*

Characters	Males			Females		
	Component I	Component II	Component III	Component I	Component II	Component III
Length of forearm	0.316	−0.752	0.047	−0.562	−0.395	0.697
Greatest length of skull	−0.813	0.375	0.277	0.983	0.125	−0.012
Condylobasal length	−0.909	0.160	0.163	0.937	−0.221	0.136
Palatal length	0.073	0.832	−0.426	0.651	0.596	0.156
Depth of braincase	−0.346	0.858	−0.048	0.479	−0.659	−0.168
Zygomatic breadth	−0.889	−0.349	0.093	0.694	−0.058	−0.271
Breadth of braincase	−0.921	−0.113	−0.214	0.485	−0.421	−0.477
Mastoid breadth	−0.181	0.461	0.829	0.730	−0.337	−0.319
Postorbital breadth	0.010	0.617	−0.446	−0.490	0.639	0.268
Length of maxillary toothrow	0.172	0.085	−0.503	0.753	0.215	−0.114
Rostral width at canines	−0.968	−0.209	0.002	−0.013	−0.944	0.107
Breadth across upper molars	−0.930	−0.291	−0.156	0.358	−0.807	−0.251
Mandibular length	0.421	0.237	0.843	0.556	0.200	0.771

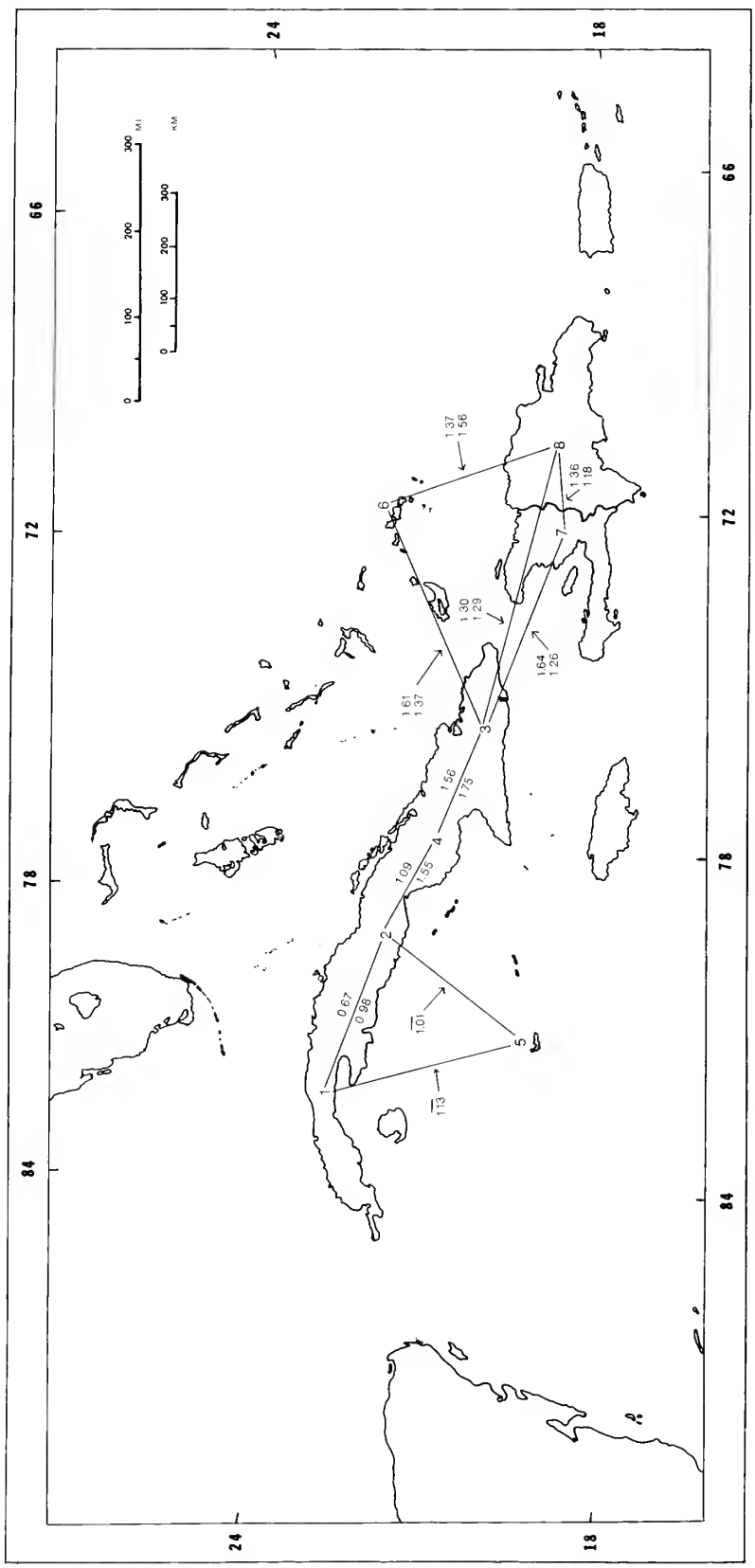

Fig. 13.—Map showing distance coefficients (from distance matrices) between samples of *Brachyphylla nana* that were analyzed in the study of geographic variation. The upper coefficients are for males and the lower for females. See Fig. 1 and text for key to samples.

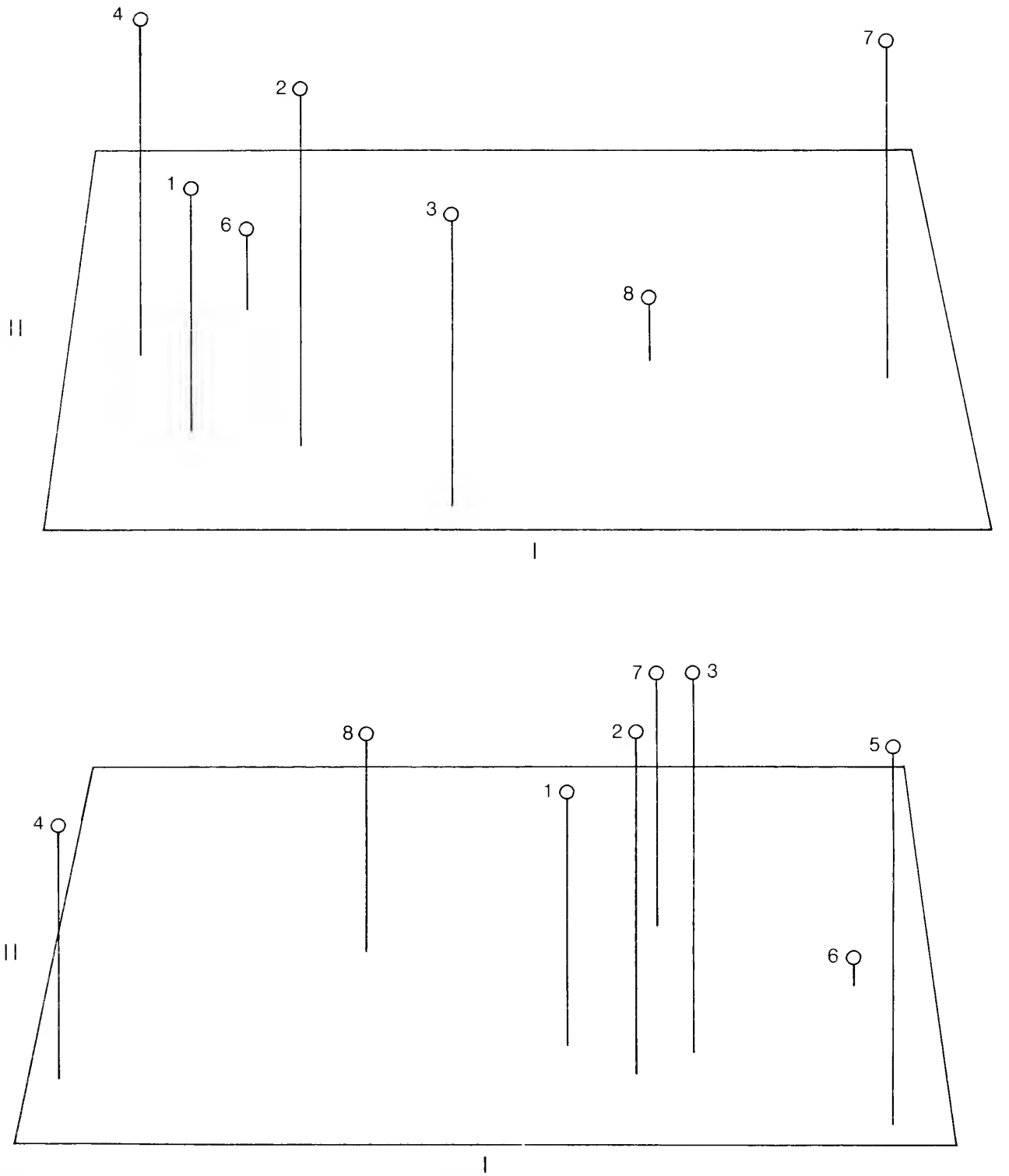

Fig. 14.—Three-dimensional projections of samples of *Brachyphylla nana* (males above, females below) onto the first three principal components based on matrices of correlation among one external and 12 cranial measurements. Components I and II are indicated in the figure and eomponent III is represented by height. See Fig. 1 and text for key to samples.

distinct samples, Haiti (7) and the Dominican Republic (8). The sample from Haiti (7) consists of only one specimen, which varies from relatively small to large in the different measurements taken.

The distance phenogram (cophenetic correlation coefficient, 0.831) for female *Brachyphylla nana* shows the samples falling into four major groups. The first cluster contains samples from Cuba (1, 2, 3) and Grand Cayman (5). The second cluster consists of only one sample, Middle Caicos (6). The third cluster contains the samples from Hispaniola (7, 8). The fourth cluster consists of the sample from Camagüey Province, Cuba (4), and represents a single specimen. This specimen (4) is characterized by a relatively small skull, but its values fall within the range of at least one other Cuban sample.

The distance phenograms of both males and females essentially show the same picture. Samples from Cuba tend to cluster together with the exception of the sample from Camagüey Province (4). Although distantly, the Haitian sample clusters with that from the Dominican Republic. Both male and female distance phenograms show the Middle Caicos samples clustering closer to the Cuban than the Hispaniolan samples, although only distantly so.

The amount (percentage) of phenetic variation represented in the first three principal components for male and female *Brachyphylla nana*, respectively, was 41.5 and 40.8 for component I, 23.7 and 25.7 for component II, and 17.1 and 13.3 for component III. Combined these first three components express 82.3% in males and 79.8% in females. From the factor analysis, it can be seen that characters influencing the different components differ between sexes. In males the first component is heavily negatively influenced by the following characters: greatest length of skull, condylobasal length, zygomatic breadth, breadth of braincase, rostral width at canines, and breadth across upper molars. In females the first component is most heavily influenced positively by greatest length of skull and condylobasal length. In males the second component is heavily positively weighted for palatal length, depth of braincase, and postorbital breadth and negatively for length of forearm. In females a heavy negative weighting was found on component II for rostral width at canines and breadth across upper molars. The third component in males is heavily positively influenced by mastoid breadth and mandibular length. In females the third component is weighted (positive) for length of forearm and mandibular length.

Examination of the three-dimensional plot of the male samples reveals a pattern more or less similar to that of the distance phenogram. The Dominican Republic (8) and the Haitian (7) samples grouped in the lower cluster of the phenogram are shown on the right in the three-dimensional plot, differing from each other on the first and third components. The Middle Caicos (6) and Cuban samples (1, 2, 4) are arranged on the right of the plot with the Oriente Province, Cuba (3) sample falling nearly midway between the samples from the Dominican Republic (8) and Las Villas Province, Cuba (2). This seems to correspond to the conclusion reached in the univariate analysis, where the Cuban samples (1, 2, 3) displayed clinal variation in some measurements, becoming progressively smaller from west to east, with the population from Oriente Province (3) generally approaching the Dominican Republic sample (8) in size.

Examination of the three-dimensional plot of the female samples reveals a pattern with some basic differences from the distance phenogram. The Camagüey Province sample (Cuba, 4) on the left in the three-dimensional plot corresponds to the lower cluster in the distance phenogram. The Dominican Republic sample (8), well removed from sample 4 (Camagüey Province) to the left and the other Cuban (1, 2, 3) and Haitian (7) samples to the right is however, grouped with the Haitian sample (7) in the distance phenogram. The Haitian sample is separated from samples 1, 2, and 3 (Cuba) only on the second component. Therefore, it differs mostly in shape rather than size from the Cuban material. The one specimen from Grand Cayman (5) is grouped with the Cuban (1, 2, 3) populations in the phenogram. It is, however, well separated on the first component in the principal component analysis from these populations. The Grand Cayman specimen is close to the Middle Caicos population on the first component but well separated on the second and third components, suggesting a difference in shape rather than size between the two.

In both male and female *Brachyphylla nana*, multivariate analysis of variance (MANOVA) showed that there were significant ($P < 0.00001$) morphological differences among samples in all four statistical tests (Hotelling-Lawley's Trace, Pillai's Trace, Wilks' Criterion, and Roy's Maximum Root Criterion) utilized. In males the following individual measurements, however, failed to show significant differences among samples: greatest length of skull, breadth of braincase, mastoid breadth, and mandib-

Table 8.—*Eigenvalues of canonical variates showing the percentage influence among 13 characters of* Brachyphylla nana.

Character	Vector I		Vector II		Vector III	
	Eigenvalue	Percent influence	Eigenvalue	Percent influence	Eigenvalue	Percent influence
			Males			
Length of forearm	−0.0354	7.5	0.0767	12.8	−0.0803	14.5
Greatest length of skull	0.0274	2.6	−0.0738	6.1	0.0983	8.4
Condylobasal length	−0.2065	17.7	−0.0125	0.9	0.1004	7.6
Palatal length	0.2340	7.4	−0.1406	3.8	0.0260	0.7
Depth of braincase	−0.0240	1.0	−0.1344	4.6	0.1664	6.0
Zygomatic breadth	−0.0500	2.6	0.2355	10.2	−0.0987	4.5
Breadth of braincase	−0.0825	3.3	0.1709	5.8	−0.2042	7.2
Mastoid breadth	0.0612	2.8	−0.2066	8.1	0.1980	8.1
Postorbital breadth	0.5387	11.5	0.2337	4.2	−0.1181	2.2
Length of maxillary toothrow	0.4703	15.1	0.7122	19.3	0.6221	17.7
Rostral width at canines	−0.2343	5.1	−0.6273	11.6	−0.2832	5.5
Breadth across upper molars	−0.5052	17.5	0.1961	5.7	0.5698	17.5
Mandibular length	−0.0983	6.9	−0.1384	6.9	−0.2081	10.9
			Females			
Length of forearm	−0.1055	11.8	0.0530	6.3	−0.0009	0.2
Greatest length of skull	0.4319	24.0	−0.0344	2.0	0.1146	8.7
Condylobasal length	−0.0382	1.9	−0.5990	30.8	0.0328	2.2
Palatal length	0.0723	1.3	0.1991	3.8	−0.1424	3.6
Depth of braincase	0.1318	3.1	0.1387	3.4	0.4349	13.9
Zygomatic breadth	−0.0100	0.3	−0.4200	13.0	0.3237	13.0
Breadth of braincase	0.2782	6.4	0.1611	3.9	−0.1780	5.6
Mastoid breadth	0.3047	8.0	0.4157	11.4	−0.6531	23.3
Postorbital breadth	−0.9303	11.3	−0.0250	0.3	0.4387	7.2
Length of maxillary toothrow	0.1762	3.2	0.3551	6.8	0.1089	2.7
Rostral width at canines	−0.7437	9.2	0.1798	2.3	−0.3533	5.9
Breadth across upper molars	−0.2416	4.8	−0.2189	4.6	−0.3170	8.5
Mandibular length	−0.4332	14.7	0.3225	11.4	0.1131	5.2

ular length. These measurements as well as length of maxillary toothrow revealed no significant differences among samples in the univariate analysis. In females, condylobasal length, palatal length, breadth of braincase, mastoid breadth, postorbital breadth, length of maxillary toothrow, and mandibular length showed no significant differences among samples in the MANOVA. In the univariate analysis palatal length, breadth of braincase, postorbital breadth, length of maxillary toothrow, and mandibular length also showed no significant difference among samples.

The amount (percentage) of phenetic variation represented in the first three canonical variates for male and female *Brachyphylla nana*, respectively, was 68.5 and 66.4 for variate I, and 12.7 and 20.0 for variate II, and 12.1 and 7.1 for variate III. Combined these three canonical variates express 93.3% in males and 93.7% in females. In males all the variation was explained by the first five canonical variates, whereas in females it was expressed in the first four canonical variates.

In males the following characters contribute more than 10% to variate I in distinguishing among samples: condylobasal length, postorbital breadth, length of maxillary toothrow, and breadth across upper molars; more than 10% to variate II: length of forearm, zygomatic breadth, length of maxillary toothrow, and rostral width at canines; and more than 10% to variate III: length of forearm, length of maxillary toothrow, width across upper molars, and mandibular length. In females, characters contributing more than 10% to variate I are length of forearm, greatest length of skull, postorbital breadth, mandibular length, in variate II, condylobasal length, zygomatic breadth, mastoid breadth, and mandibular length, and in variate III, depth of braincase, zygomatic breadth, and mastoid breadth.

Examination of the two-dimensional canonical variate plot of the male samples reveals the following pattern of variation. Samples from Middle Caicos (6) and Hispaniola (7, 8) are grouped together and are clearly separated from the Cuban samples (1, 2, 3, 4) on the first variate. These two major

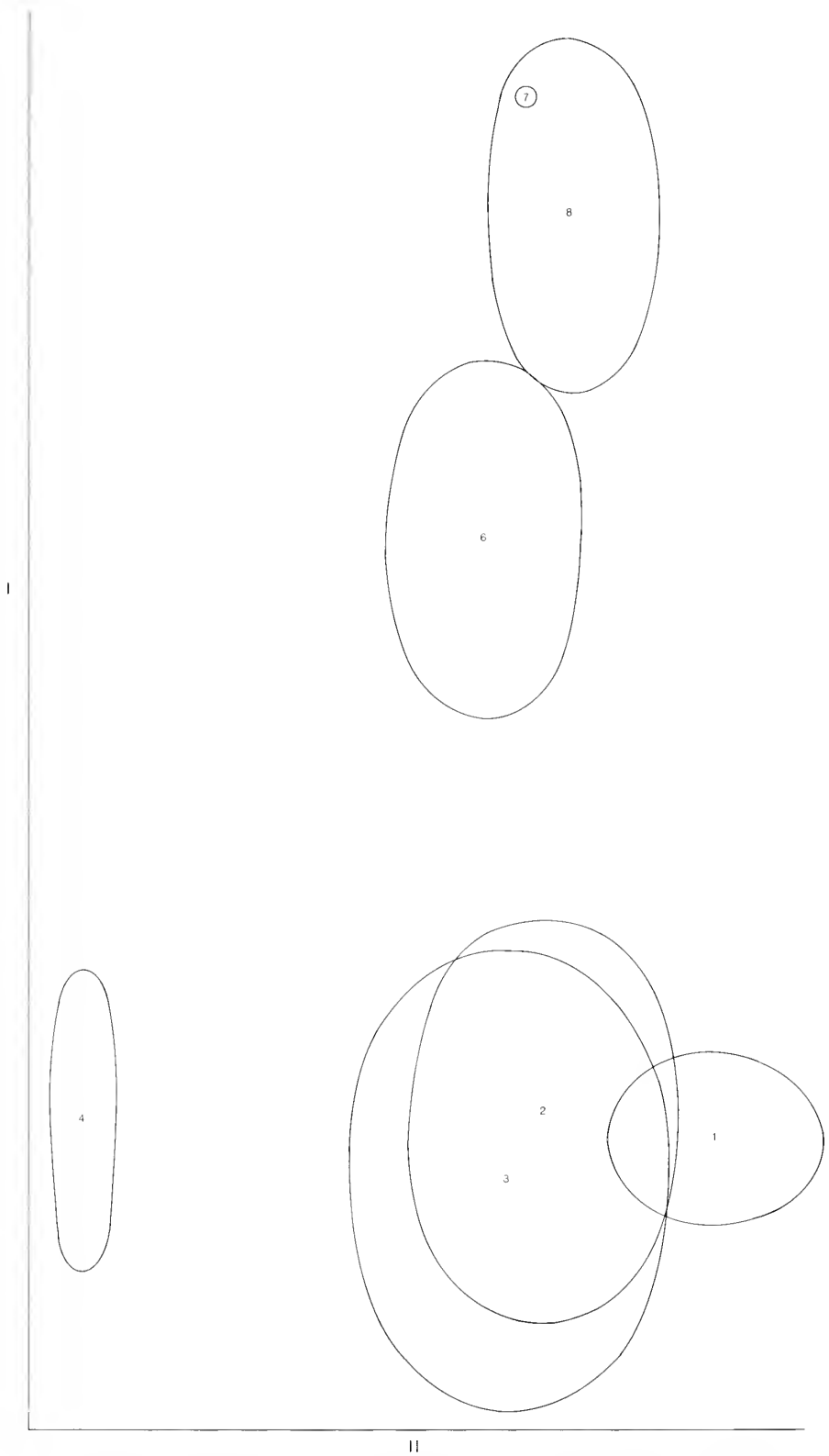

Fig. 15.—Two-dimensional projection of male samples (mean and one standard deviation) of *Brachyphylla nana* onto the first two canonical variates based on a matrix of variance-covariance among one external and 12 cranial measurements. See Fig. 1 and text for key to samples.

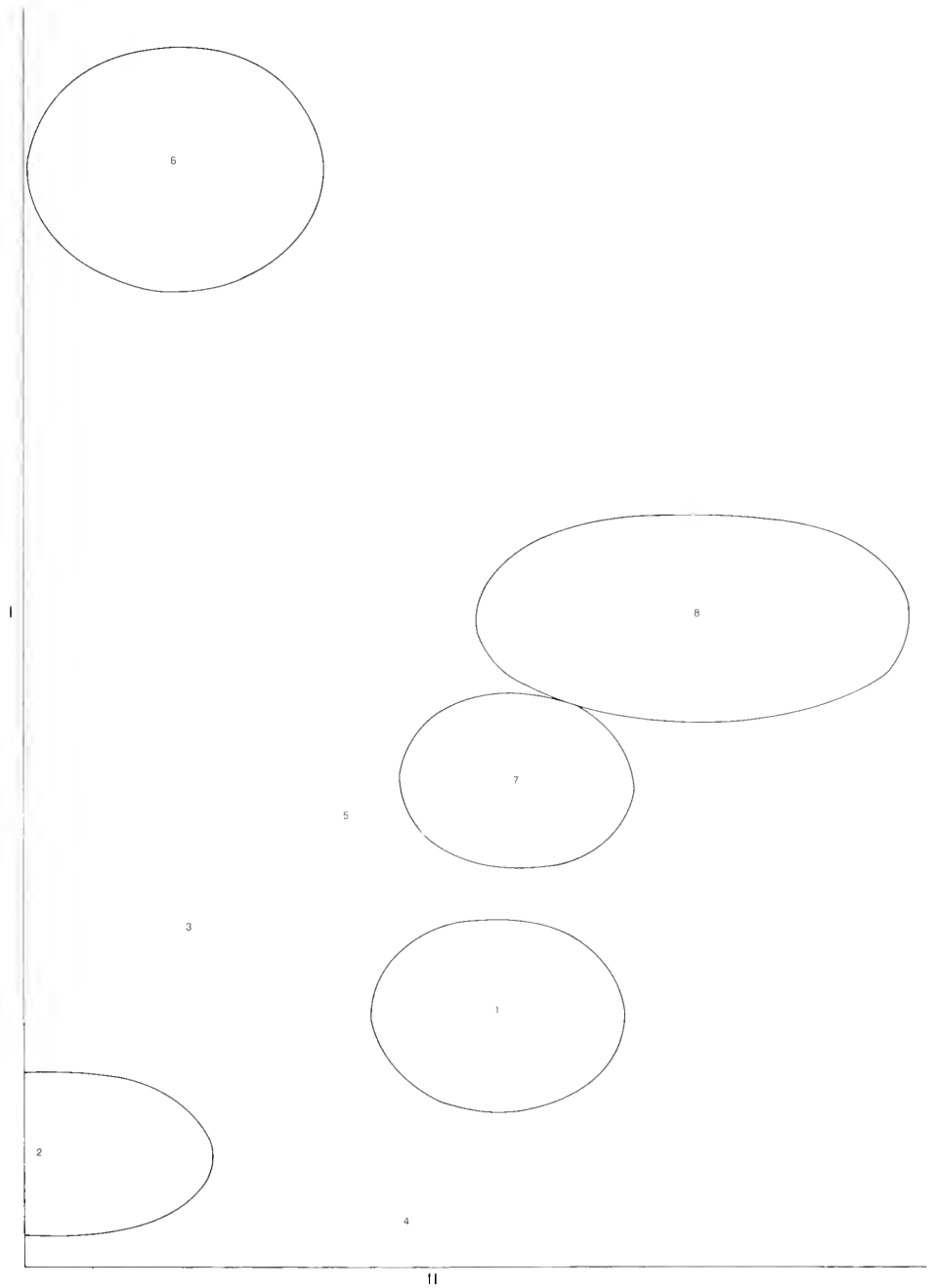

Fig. 16.—Two-dimensional projection of female samples (mean and one standard deviation) of *Brachyphylla nana* onto the first two canonical variates based on a matrix of variance-covariance among one external and 12 cranial measurements. See Fig. 1 and text for key to samples.

groups show no one standard deviation overlap on the first variate. The Cuban group, however, shows overlap between samples 1, 2, and 3, but these are clearly separated from sample 4 on the second variate. The canonical variate analysis shows some basic differences when compared to the principal component analysis. In the principal component analysis the Hispaniolan (7, 8) samples are also separated from the Cuban samples on the first component. However, the Middle Caicos (6) sample is grouped with Cuban material, although differing from these samples on the second and third component. Therefore, in the case of the distance phenogram and principal component analysis the sam-

Table 9.—*Geographic variation in eight cranial measurements of six samples of Recent, and one of Pleistocene or sub-Recent fossil material of* Brachyphylla. *See text for key to samples.*

Sample	N	Mean ± 2 SE	Range	CV
		Palatal length		
a	10	9.3 ± 0.23	8.9–9.9	3.8
b	10	9.5 ± 0.25	8.9–10.0	4.2
c	10	9.5 ± 0.26	9.0–10.2	4.4
d	1	10.1		
e	10	11.8 ± 0.24	10.9–12.2	3.3
f	7	11.8 ± 0.42	11.1–12.8	4.7
g	10	11.9 ± 0.36	11.0–12.8	4.8
		Rostral width at canines		
a	10	6.6 ± 0.11	6.3–6.8	2.6
b	10	6.4 ± 0.17	5.9–6.8	4.3
c	10	6.2 ± 0.15	5.8–6.5	3.8
d	1	6.6		
e	10	7.2 ± 0.13	6.8–7.6	2.9
f	7	7.2 ± 0.21	6.8–7.5	3.9
g	10	7.2 ± 0.09	7.1–7.5	2.0
		Length of maxillary toothrow		
a	10	9.4 ± 0.16	9.0–9.8	2.7
b	10	9.5 ± 0.15	9.2–9.9	2.6
c	10	9.5 ± 0.07	9.3–9.6	1.1
d	1	9.6		
e	10	10.7 ± 0.18	10.1–11.0	2.7
f	7	10.7 ± 0.12	10.4–10.9	1.5
g	10	10.7 ± 0.10	10.5–11.0	1.5
		Interorbital breadth		
a	10	7.8 ± 0.15	7.4–8.1	3.0
b	10	8.4 ± 0.11	8.2–8.7	2.0
c	10	8.1 ± 0.15	7.7–8.6	2.9
d	3	7.7 ± 2.0	7.4–7.8	2.2
e	10	9.0 ± 0.10	8.9–9.4	1.7
f	7	8.6 ± 0.13	8.4–8.9	2.0
g	10	8.5 ± 0.11	8.3–8.9	2.1
		Height of coronoid process		
a	10	7.3 ± 0.14	7.0–7.8	3.1
b	10	7.4 ± 0.12	7.1–7.7	2.5
c	10	7.3 ± 0.13	7.0–7.7	2.9
d	3	7.6 ± 0.14	7.5–7.7	1.5
e	10	9.0 ± 0.15	8.5–9.4	2.6
f	7	9.1 ± 0.18	8.8–9.5	2.6
g	10	9.0 ± 0.18	8.5–9.5	3.1
		Width of articular process		
a	10	2.6 ± 0.12	2.3–2.9	7.5
b	10	2.9 ± 0.06	2.7–3.0	3.3
c	10	2.5 ± 0.10	2.3–2.8	5.9
d	4	2.4 ± 0.18	2.3–2.7	7.9
e	10	3.3 ± 0.12	2.9–3.5	5.6
f	7	3.2 ± 0.12	3.0–3.5	5.0
g	10	3.2 ± 0.10	2.8–3.3	5.2
		Breadth of mandible at M_3		
a	10	1.2 ± 0.05	1.1–1.3	6.7
b	10	1.2 ± 0.03	1.2–1.3	3.9
c	10	1.1 ± 0.04	1.0–1.2	5.6
d	7	1.3 ± 0.06	1.2–1.4	6.9
e	10	1.4 ± 0.04	1.3–1.5	4.9
f	7	1.5 ± 0.04	1.4–1.6	3.8
g	10	1.5 ± 0.04	1.4–1.6	4.8
		Length of mandibular toothrow		
a	10	9.8 ± 0.10	9.5–9.9	1.7
b	10	10.0 ± 0.16	9.6–10.4	2.5
c	10	10.0 ± 0.09	9.7–10.1	1.4
d	2	10.2 ± 0.30	10.0–10.3	2.1
e	10	11.0 ± 0.17	10.5–11.4	2.5
f	7	10.9 ± 0.13	10.7–11.2	1.6
g	10	10.9 ± 0.08	10.7–11.1	1.2

ple from Middle Caicos is placed closer to the Cuban populations, whereas in the canonical analysis it is grouped with the Hispaniolan populations.

In females the two-dimensional canonical variate plot of the samples onto the first two variates shows the Middle Caicos (6) population to be well separated on the first variate and to some extent on the second, from both the Cuban and Hispaniolan populations. Cuban and Hispaniolan samples are closer to each other than either is to the Middle Caicos sample. Therefore, all multivariate analyses of female samples show the Middle Caicos sample to be well separated from the others. In the canonical analysis the Hispaniolan material is grouped with the Cuban material, whereas in both the cluster and principal component analyses they are separated.

Taxonomic Conclusions

Based upon our study of geographic variation in *Brachyphylla nana*, we have chosen to consider it a monotypic species. In five measurements for males and seven measurements for females, either the ANOVA or MANOVA was non-significant. In four of the 13 measurements for the samples of *B. nana* either the ANOVA or MANOVA was non-significant for both sexes, whereas a total of eight were non-significant for at least one sex. The results of the multivariate analyses were inconsistent.

There appears to be very little morphometric variation among our samples of *B. nana*. The range of this variation is, in many cases, encompassed by the four samples from Cuba. Other cranial features used to distinguish *B. nana* and *B. pumila* prove to be inconsistent when large samples are examined. Therefore, we believe the best course of action to follow is to consider *Brachyphylla nana* as being a monotypic species.

Status of Fossil Specimens

The genus *Brachyphylla* is known only as a Pleistocene or sub-Recent fossil from the island of Jamaica. This material was assigned to *B. pumila* by Koopman and Williams (1951). We have taken the opportunity to re-examine this material and to compare it with the two species that we have recognized. Standard statistics from geographic samples listed in Materials and Methods are given in Table 9.

All characters of Pleistocene or sub-Recent fossil material studied with the exception of interorbital breadth showed basically the same pattern of geographic variation. In all cases the fossils grouped with populations that we consider to be *B. nana*. The populations of *Brachyphylla* from Puerto Rico (sample e), St. John (f), and Norman (g) were usually grouped into a subset or subsets significantly different from those populations from Cuba (a), Middle Caicos (b), and Dominican Republic (c). Of the eight measurements, four (rostral width at canines, interorbital breadth, width of articular process, and width of mandible at M_3) showed overlap between the two main areas. The Pleistocene or sub-Recent fossil material generally averaged larger than the Recent material from Cuba, Middle Caicos, and Dominican Republic, but falls within the range of variation displayed by the Recent material. In only two measurements (width of articular process and interorbital breadth) did the Jamaican material average less than the Recent material from Cuba, Middle Caicos, and Dominican Republic. Only in breadth of mandible at M_3 did the Jamaican material show any overlap with the ranges of measurements obtained from specimens from Puerto Rico, St. John, and Norman. Interorbital width in *Brachyphylla* displayed a great deal of geographic variation. Individual variation as indicated by coefficients of variation show width of articular process and breadth of mandible at M_3 to be the most variable.

The cluster, principal components, and canonical variate analyses of these samples reveal the same basic picture. We have illustrated the principal components analysis as being typical.

The first two principal components extracted from the principal component analysis for three *B. nana*, one fossil, and three *B. cavernarum* samples are shown two-dimensionally in Fig. 17. The amount of phenetic variation represented in the first three components was 90.2 for component I, 0.08 for component II, and 0.02 for component III. From the factor analysis (not tabled) it was obvious that the first component is heavily influenced by all characters. Both the second and third components are not notably influenced by any character.

Examination of the two-dimensional plot of the first two principal components reveals two groups of samples. The cluster on the right consists of samples from Puerto Rico, St. John, and Norman; the one on the left contains samples from Cuba, Middle Caicos, Dominican Republic, and Jamaica. The latter group contains the smaller specimens as clearly revealed by the univariate analysis.

Although the Jamaican fossil material tends to be somewhat larger than the Recent material from Cuba, Middle Caicos, and Dominican Republic, it clearly has its relationship to these populations. Decision on whether the bats in the sub-Recent population were actually somewhat larger than in the Recent population or not, must await the discovery of further fossil material. However, we do not believe that the differences noted in the current material warrant taxonomic recognition. Therefore, we assign the Jamaican Pleistocene or sub-Recent fossils to *Brachyphylla nana*.

Brachyphylla nana Miller, 1902

1902. *Brachyphylla nana* Miller, Proc. Acad. Nat. Sci. Philadelphia, 54:509, 12 September.
1918. *Brachyphylla pumila* Miller, Proc. Biol. Soc. Washington, 31:39, 16 May; holotype from Pont de Baisc, Haiti.
1974. *Brachyphylla cavernarum nana*, Varona, Acad. Cien. Cuba, p. 27.
1974. *Brachyphylla cavernarum pumila*, Varona, Acad. Cien. Cuba, p. 27.
1976. *Brachyphylla nana nana*, Jones and Carter, Spec. Publ. Mus., Texas Tech Univ., 10:30, 25 June.
1976. *Brachyphylla nana pumila*, Jones and Carter, Spec. Publ. Mus., Texas Tech Univ., 10:30, 25 June.

Holotype.—Skull of an unsexed adult recovered from owl pellets, USNM 103,828 from El Guama, Cuba, obtained by William Palmer and J. H. Riley on 10 March 1900; original no. 108.

Measurements of holotype.—Condylobasal length, 24.9; palatal length, 8.7; zygomatic breadth, 14.6; braincase breadth, 11.3; postorbital breadth, 5.9; rostral width at canines, 6.4.

Distribution.—This species is known from Cuba, Isle of Pines (Varona, 1974), Grand Cayman, Middle Caicos, Hispaniola, and as a Pleistocene or sub-Recent fossil from Jamaica.

Comparisons.—See Specific Relationships.

Remarks.—Populations described as *pumila* and *nana* were long considered distinct species and most recent authors have considered them to be

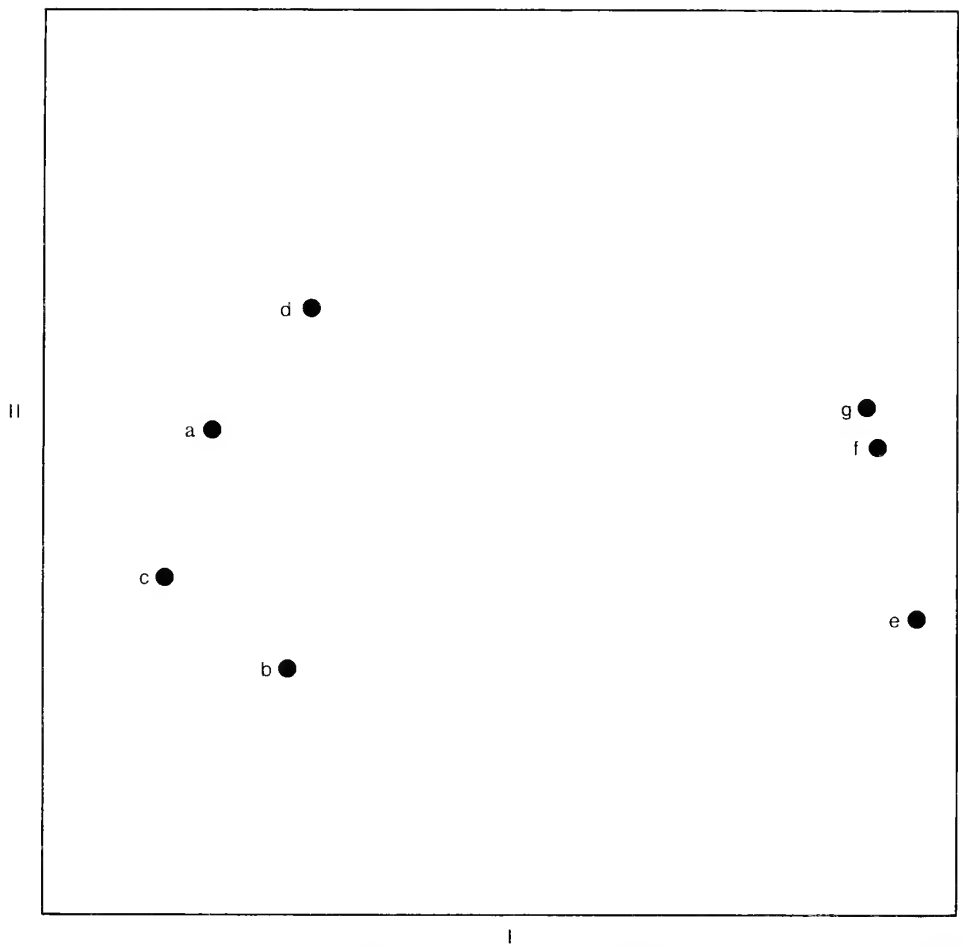

Fig. 17.—Two-dimensional projection of seven samples (six Recent and one Pleistocene or sub-Recent) of *Brachyphylla* onto the first two principal components. See text for key to samples.

distinct at least at the subspecific level (see Silva-Taboada, 1976; Jones and Carter, 1976). However, based upon our analyses and studies, we cannot support this distinction. The populations do not differ much in size and Cuban populations encompass most of the range of variation observed. Various dental and cranial characters, such as difference in size and morphology of M^1 (Miller, 1918), a broader rostrum and palate and larger molars in *B. pumila* (Miller, 1929), shape of interpterygoid fossa (Goodwin, 1933), and depth of pit between orbit and antorbital foramen (Koopman and Williams, 1951), have been used to distinguish these taxa. We have examined these characters in the large series available to us. These characters were found to be individually variable or nonexistent. Buden (1977) found *nana* to have a deeper and more robust zygomatic arch than *pumila*; however, we are unable to appreciate this character in our material.

Dorsal pelage coloration does not appear to separate taxa either. Individuals corresponding to color standard 3 were found in relatively high numbers on all islands—Cuba, 37%; Hispaniola, 35%; Middle Caicos, 100%; Grand Cayman, 100%. The majority of the specimens (63%) from Hispaniola are slightly darker than the majority of material (47%) from Cuba being a blackish gray (standard 1) as compared to dark brown (standard 5). However, in view of the only slight differences in color found throughout this genus and fairly broad overlap between all island populations of *B. nana*, we see no reason based upon color to consider this taxon to be polytypic.

Two recent authors, Varona (1974) and Buden (1977), have recognized *nana* and *pumila* as distinct subspecies but placed them in *B. cavernarum* and considered the genus to be monotypic. Buden (1977) claimed that "differences in size among these

allopatric populations is nearly matched by those found among Middle American populations of *Artibeus jamaicensis* that are treated as subspecies by Davis (1970).'' We disagree with this conclusion based upon our studies. *Brachyphylla cavernarum* and *B. nana* differ considerably in size; there is no overlap between these two species in six of 12 cranial measurements taken. In our opinion, these differences more nearly resemble those found between sympatric populations of the Middle American species *Artibeus jamaicensis* and *A. lituratus*. We, therefore, believe that the differences observed between these allopatric populations of *Brachyphylla* are best represented by considering them to be distinct species.

Brachyphylla nana is known on the island of Jamaica only as a Pleistocene or sub-Recent fossil (Koopman and Williams, 1951). Based upon the reconstruction of the fossil bat faunas by Williams (1952), *B. nana* occurred in about the middle of the known record for bats on the island but no time frame is possible. It was contemporary with members of the genera *Ariteus*, *Mormoops*, *Phyllonycteris*, *Erophylla*, *Monophyllus*, and *Macrotus*, but had disappeared before *Artibeus* appeared in the fossil record. Although it is tempting to theorize some sort of competition to account for the extinction of *Brachyphylla* on Jamaica, the reasons must be far more complex because almost identical faunas occur today on Cuba and Hispaniola, but *Brachyphylla* has survived there (Baker and Genoways, 1978).

Specimens examined (185).—Cuba: 12 mi E Moron, Camagüey Province, 3 (AS); Cueva de los Indios, Habana Province, 6 (1 AS, 5 MCZ); Cueva del Indio, 3 mi E Tapaste, Habana Province, 12 (AMNH); Cueva de Costilla San Jose de las Lajas, Habana Province, 3 (TCWC); 4 mi S San Jose de las Lajas, Habana Province, 2 (AMNH); 9 km SW San Jose de las Lajas, Habana Province, 8 (AS); Cantabria Cave, Hormiguero, Las Villas Province, 11 (1 KU, 10 UMMZ); Cantabria Cave, 14 km NE Cienfuegos, Las Villas Province, 4 (ROM); Finca de Morales, 8 mi NW Trinidad, Las Villas Province, 5 (AS); Guatanama, Oriente Province, 3 (USNM); Los Angeles, Oriente Province, 1 (MCZ); Santiago, Oriente Province, 3 (FMNH); Santiago de Cuba, Oriente Province, 7 (3 AMNH, 4 FMNH); Cueva de la Cantera, Siboney, 14 km SE Santiago de Cuba, Oriente Province, 2 (ROM); El Guama, Pinar del Rio Province, 1 (USNM). Grand Cayman: Old Man Bay, 1 (LSU). Dominican Republic: Cueva no. 2 Los Patos, Barahona Province, 47 (1 AMNH, 1 FMNH, 43 PSNH, 1 TCWC, 1 USNM); Upper Los Patos Cave, Barahona Province, 8 (4 AMNH, 4 PSNH); Los Patos, Barahona Province, 1 (ROM); Cueva Wunker, 19.3 km W La Romana, La Romana Province, 6 (PSNH); Sosúa, Puerta Plata Province, 7 (AS); Cueva el Limón, Samana, Samana Province, 3 (PSNH); Cueva de Sierra de Agua San Cristobal, Samana Province, 2 (ROM). Caicos Islands: Conch Bar, Middle Caicos, 19 (LSU). Haiti: Daiquini [=Diquini], 3 (2 BMNH, 1 FMNH); 1 km S, 1 km E Lebrun, Department du Sud, 4 (TTU); Port de Paix, 1 (USNM). Jamaica: Dairy Cave, Dry Harbor [=Discovery Bay], St. Ann Parish, 12 (AMNH).

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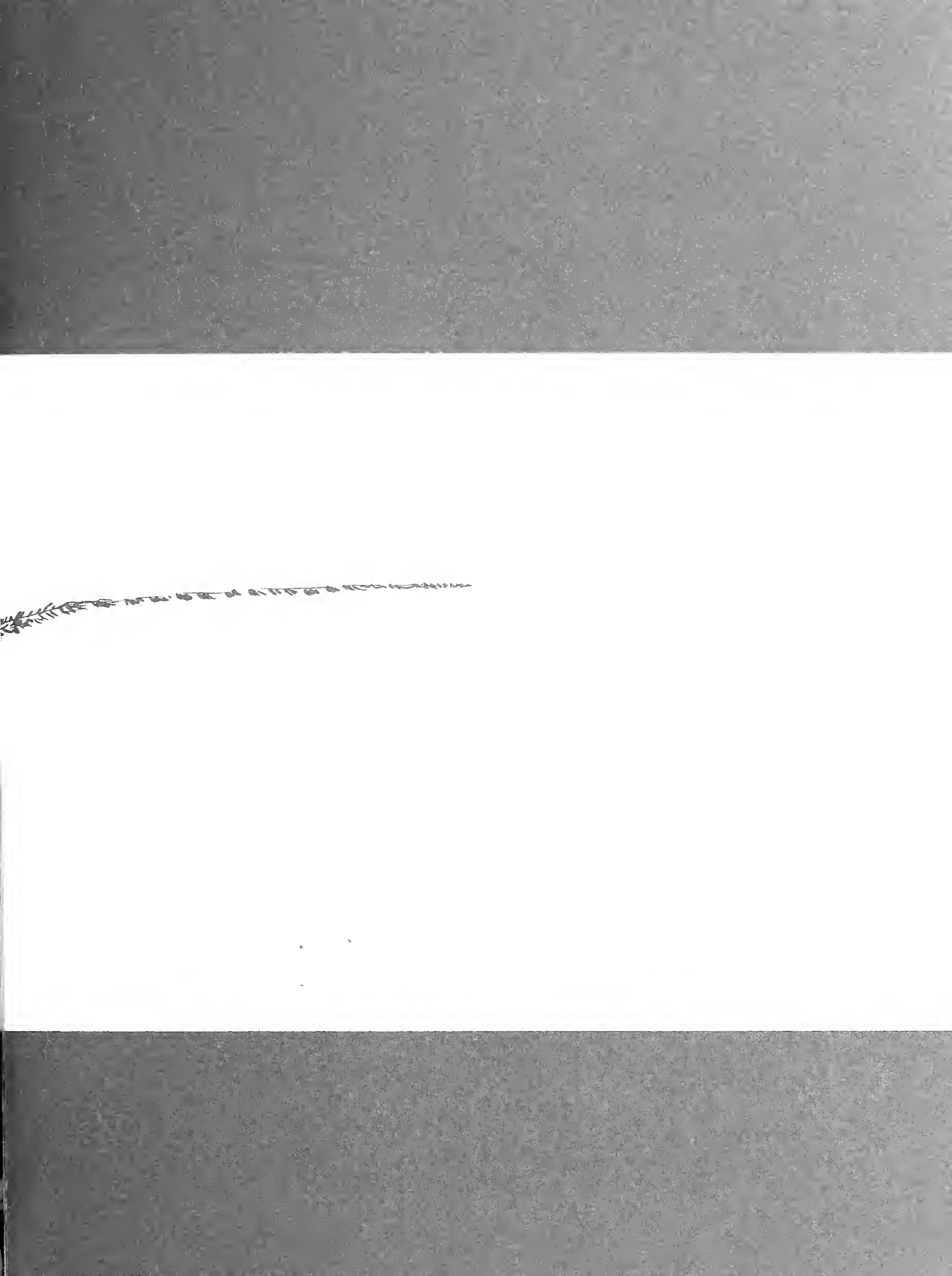

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Edited by

JEFFREY H. SCHWARTZ
Research Associate, Section of Vertebrate Fossils, and Department of Anthropology, University of Pittsburgh, Pennsylvania 15260

HAROLD B. ROLLINS
Department of Earth and Planetary Sciences, University of Pittsburgh, Pittsburgh, Pennsylvania 15260

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CONTENTS

PREFACE

During the academic years 1976–1977, the University of Pittsburgh and the Carnegie Museum of Natural History jointly sponsored two colloquia series dealing with aspects of evolution, "Models and Methodologies in Evolutionary Theory."

The first year's participants were:

Niles Eldredge, The American Museum of Natural History;
Steven Jay Gould, The Museum of Comparative Zoology, Harvard University;
David M. Raup, University of Rochester;
Thomas J. M. Schopf, University of Chicago;
Eugene S. Gaffney, The American Museum of Natural History.

Those of the second series were:

Albert A. Bartlett, University of Colorado;
Robert J. Baker, Texas Tech University;
Walter J. Bock, Columbia University;
Steven M. Stanley, Johns-Hopkins University;
Leonard Radinsky, University of Chicago.

Each participant presented two formal talks and five also submitted original manuscripts for publication. The latter include three papers on approaches to evolutionary theory (Eldredge, Bock, and Baker); one discussing the evolutionary consequences of preservational biases of the fossil record (Raup); and another dealing with philosophy and methodology in phylogeny reconstruction, in this case the origin of Tetrapoda (Gaffney).

We are indebted to Dr. Craig C. Black, Director, Carnegie Museum of Natural History, and the Provost's Office, University of Pittsburgh, for generously funding these colloquia and providing the necessary facilities and equipment. Among the many of both institutions who helped to make these colloquia successful, we wish to especially thank Dr. R. Raikow and Mr. J. Harper (University of Pittsburgh) and Drs. M. Dawson, H. Genoways and L. Krishtalka (Carnegie Museum of Natural History). In addition, we wish to acknowledge the editorial assistance of Ms. G. LoAlbo.

Jeffrey H. Schwartz
Harold B. Rollins

ALTERNATIVE APPROACHES TO EVOLUTIONARY THEORY

NILES ELDREDGE

Department of Invertebrates, The American Museum of Natural History,
Central Park West at 79th Street, New York, New York 10024

INTRODUCTION

To most North Americans who have ever thought about evolution at all, there is only one "evolutionary theory"—"neo-darwinism." We look askance upon other sets of explanations of evolution, such as the various versions of saltationism, much in the way that Judaeo-Christian tradition views devotion to any but the One God. My purpose here is not to espouse pagan alternatives to orthodox darwinism, but rather to develop the theme that neo-darwinian theory is not at all as monolithic as we might suppose. Rather, *all* evolutionary thinking, darwinian and non-darwinian, pre- and post-1859, has been beset by a curious duality, which has effectively hindered a truly integrated theory of any guise from emerging.

Evolution can be viewed in two basic ways. If evolution is "descent with modification" (Darwin, 1859:171) or "change in the genotype of a population" (Dobzhansky, 1951:21), then we must ask how that change occurs. What are the mechanisms? Whether we are discussing genes, their phenotypic expression, physiology, or behavior, variation and factors of heritability lie at the core of the problem. Thus, any standard text properly devotes much of its space to genetics, and mutation, recombination, natural selection and related concepts weigh heavily in our theories of evolutionary mechanics.

Darwin (1859) also gave us our other basic way of looking at evolution—the "origin of species." We see around us today perhaps as many as two million discrete species. If we assume, as seems reasonable, that species are real entities in nature, their origins must be explained, and because species are aggregates of populations, which are themselves aggregates of individuals, the mechanics of speciation do not seem immediately reducible to the principles of genetics (see for example, Avise and Ayala, 1975). Thus, standard texts also devote a good deal of space to speciation.

No one would argue that we can have an evolutionary theory without either one of these two components. A theory is simply incomplete if it lacks either a set of statements concerning (1) changes in genes and their expression or (2) the origins of new species. The problem with neo-darwinian theory today is not that it lacks one or the other of these components, but that they have as yet to be successfully fully integrated.

This problem comes into focus more sharply if we first generalize these two aspects of the evolutionary process. The first aspect can be labelled the "transformational approach"; under this approach, the central question in evolution is: how do genes and their products become modified in the evolutionary process? How are karyotypes, behavior, pelage colors, hormones, and so on, modified by the evolutionary process?

In darwinian theory, natural selection is the key concept of the transformational approach, and evolutionary adaptation seems to be the prime focus of most of the research conducted from this point of view. Trends, adaptive radiations, rates of morphologic change, and even the origin of taxa of higher categorical rank (which superficially sounds as though it belongs under the "taxic approach") are examples of the kinds of evolutionary topics typically addressed by paleontologists and others. These problems are almost entirely defined in terms of the central issue of the transformational approach: how are these particular biochemical, cytological, anatomical, physiological, and behavioral traits changed in evolution? An adaptive radiation, for example, is viewed as a problem of divergent anatomical specializations among a series of related organisms, rather than as a spectrum of discrete species occupying a diverse array of ecological niches. The emphasis in this approach on morphologic (*sensu lato*) change inevitably results in the entire disregarding of taxa in the analysis. And thus we have, particularly in the literatures of genetics and paleontology, a large corpus of statements pertaining to the nature of the evolutionary process which almost completely ignores the existence of taxa and the problem of their origins.

Concern for species and other taxa under the transformational approach is limited to use of Lin-

naean names to refer to complexes of anatomical (or genetic, physiologic, and others) traits. Indeed, most adherents of this approach implicitly or explicitly deny the "reality" of species as discrete entities in nature. For if species are not considered as real, discrete entities, the problem of their origin may of course be safely ignored, and we need not be concerned with integrating speciation theory with the concerns of genetic and morphologic transformation. This attitude is especially prevalent in paleontology and takes several guises. The more obvious, transparent version of the "non-reality" of species is well developed in Shaw (1969) whose main point concerning species is that they are neither operationally nor objectively recognizable, hence can be considered in this sense not to exist. Having thus done away with species as something to be concerned with, Shaw is then at liberty to develop a strategy for analyzing phylogenetic lineages (for the express purpose of correlating rock sequences) which pays no attention to component taxa, but instead focuses on correlation of particular character states.

For a far more subtle rejection of species as objects of central interest in evolutionary theory, consider the work of Simpson (for example, 1944, 1951, 1953). Simpson (for example, 1951) does not reject outright the reality of species[1]. But he does deny their discreteness, as in his rejection of the "genetical definition" of species in favor of a concept of species in evolutionary time: "An evolutionary species is a lineage (an ancestral-descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies." (Simpson, 1961:153, modified slightly from Simpson, 1951:289). Thus, though any lineage may, obviously, have a definite beginning and a definite end (that is, "extinct without issue" as opposed to "extinction by transformation"—see Simpson, 1974:14 for an example of the use of these concepts), the door is purposely left open for anything from negligible to vast amounts of morphological or genetical transformation within the indefinite time segment of this lineage. This is a rather elusive concept of the species, though it may be the best we can have. It is apparent that Simpson's sincere attempt to formulate a more "evolutionary" concept of "species" stemmed from the historical consensus—by no means restricted to paleontology—which views evolution solely as change through time of genes and their products. Such change is construed as an almost inevitable consequence of the mere passage of time. And, of course, this is a reflection of the transformational approach. Simpson's definition, however different in intent from Shaw's (1969) explicit rejection of species, has the identical effect of removing the necessity of considering the origin of species when we confront the tempos and modes of evolution. In one guise or another, the transformational approach to evolution ignores species and hence is under no obligation to integrate speciation theory into the paradigm. If species are not real, or are at best arbitrarily delineated segments of lineages, speciation can safely be viewed as a useful adjunct to evolutionary theory, which merely tells us how new lineages get going in the first place. But the nearly total neglect of speciation by paleontologists and others wedded to the transformational approach can only imply that the truly interesting and meaningful evolutionary phenomena take place subsequent to the origin of a lineage (*sensu* Simpson, as cited above).

The second, or "taxic" approach, looks at evolution the other way around. Under this view, the central issue is: how do new taxa (usually species) originate? A fundamental assumption under this approach, of course, is that, at some level, aggregates of individuals (populations, perhaps species) are actual and discrete entities in nature, with their own roles in the economy of nature.

Speciation is the basic evolutionary model under the taxic approach. There are many particular models of speciation in the neo-darwinian literature (see Bush, 1975, for a useful review, as well as a stimulating advocacy of sympatric speciation). If fault can be found with the taxic approach, it is simply that its adherents have tended to limit themselves to the topic of speciation. But those who work primarily under the taxic approach have, from

[1] The argument about the "reality" of taxa of different categorical rank is an old and interesting one. As may be anticipated, all possible views have been taken from time to time. Thus Simpson (1953:350) has rejected the idea expressed by Willis (1940) and others who claim that kingdoms appear first, followed by phyla, classes, and so forth; in terms of actual evolutionary mechanics, to nearly everyone's evident satisfaction, the evolutionary process goes on at the within- and among-population level. We inductively assume this to have been the case since life began. In this sense, genera and taxa of even higher categorical rank simply do not exist in the same sense as do species and populations. Ghiselin (1974) has recently stated this most cogently, insisting that species are individuals, not classes, and have a specifiable economic role in nature not possessed by taxa of higher categorical rank (which he calls "classes"). Inasmuch as it is populations, rather than species, which are economically integrated into ecosystems, it is perhaps preferable to bestow the quality of "reality" on them rather than species; others would prefer individuals. In any case, a counter-argument has recently appeared among the phylogenetic systematists (for example, Bonde, 1974:567). In this view, all monophyletic groups, of whatever rank, are equally real, presumably in the sense that they are all defined and recognized in the same fashion. Though there is an appealing quality to this argument, considerations of ecological integration cause me to favor the view that populations, and perhaps species, are endowed with an aspect of "reality" not shared by taxa of higher categorical rank.

time to time, addressed the same variety of topics studied under the transformational approach, and have shown, with varying degrees of success, how the same problems may be addressed through the taxic approach.

The crucial point here is that, under the taxic approach, the key concepts of adaptation and selection, as well as the remainder of the principles of population genetics, have not been lost sight of in speciation theory. Rather, no matter how unsatisfyingly and incompletely, they have been integrated with speciation theory. Thus, all the mechanisms invoked under the transformational approach (except some of the fanciful, nonexistent ones, such as "orthogenesis") are very much a part of both the problems addressed and the mechanisms invoked under the taxic approach. The reverse is simply not true—for the transformational approach to operate, at least to date, a prime requisite has been either the outright denial of the existence ("reality") of species or denial of their discreteness, to the extent that the problem of their origin can safely be viewed as a special case, or at most as a small part of the general problem. Because both speciation theory and genetic mechanisms are required in a complete theory, we are justified in rejecting *a priori* any segment of evolutionary theory as at best incomplete, and at worst irrelevant, if it does not contain elements of both. The taxic approach, thus far, at least, offers the only promise of complete integration—under the taxic approach, we are free to investigate mode and degree of genetic and morphologic change in the context of speciation. Under the transformational approach we must ignore the origin of species and view them as *a posteriori* products of the mind of the systematist who uses the results of evolution (genetic and morphologic change) to recognize, name, and pigeon-hole taxa. It must still be shown, however, that the same questions raised under the transformational approach can effectively be attacked under the taxic approach.

It is possible to examine the various subdisciplines of evolutionary biology (genetics, ecology, systematics, and paleontology—this list is perhaps not all-inclusive; certainly there is a large amount of overlap among these four semiarbitrarily delineated fields) and assess the relative degrees to which each of the two approaches has contributed to past and present theoretical work. Certainly elements of both appear in each of these disciplines. For true integration we must take genetics and see how it looks in the context of speciation (see Ayala, 1975, for a valuable review), look at ecological controls of speciation and of the resultant patterns of species diversity, and then turn to systematics and paleontology to look at patterns of taxic evolution in time as well as in space. Only then shall we be effectively translating the genuine problems posed under the transformational approach into the realistic terms of the taxic approach. The remainder of this paper treats just one of the disciplines—paleontology—and restates in taxic terms a single example of an evolutionary problem traditionally formulated and addressed in terms of the transformational approach. But the basic view expressed can be applied to any branch of evolutionary biology and to any problem usually expressed in terms of the transformational approach.

PALEONTOLOGICAL APPROACH TO EVOLUTIONARY THEORY

By the very nature of its materials, paleontology can have nothing direct to say about evolutionary mechanisms. Using fossils, we cannot study mutation, recombination, and selection with any degree of practicality, and certainly these and related concepts would never have come from paleontology. Likewise our modern concepts of speciation, while perhaps less difficult to apply to paleontogical data, do not emerge as self-evident precepts when one examines data on the fossil record. Both these aspects of evolutionary theory are quite difficult to relate hypothetico-deductively to the fossil record. Thus, the relationship between paleontology and evolutionary theory has been mostly a matter of application of neontological concepts to paleontological data and it is indeed difficult to identify any coherent segment of evolutionary theory, no matter how broadly construed, as having originated in paleontology.

In an evolutionary context, paleontologists have always had the option of looking at the fossil record, in either or both of two ways—(1) distributions in space and time of discrete taxa, which differ among themselves to a greater or lesser extent, and (2) distributions in space and time of different states of morphological characters assumed to be evolving. The post-1859 history of paleontology reveals a nearly total dedication to the transformational ap-

proach as opposed to the taxic approach to evolutionary problems. Waagen's (1869:185 ff) study of the evolution of "*Ammonites subradiatus*," in which he coined the expression "mutation," is an early exception to this generalization. As pointed out by Simpson (1942:48; 1953:81) Waagen's "mutations" were actually discrete taxa, an early example of the taxic approach to evolutionary studies in paleontology. But the preponderance of subsequent studies in evolutionary theory fall clearly into the transformational camp—to cite but a few outstanding examples, consider Rowe (1899) on Cretaceous echinoids, Carruthers (1910) on Carboniferous corals, Trueman (1922) on Jurassic oysters, and Brinkmann (1929) on Jurassic ammonites. This work culminated in the general syntheses of Simpson (1944, 1953), who integrated paleontological data and concepts with many of the evolutionary concepts of the rest of the "modern synthesis"—with the notable exception of speciation theory.

We might well wonder why paleontology remained on the whole oblivious to the taxic view of the evolutionary process when other areas of biology—particularly ecology and systematics—early on become aware of the problem of diversity posed by the existence of discrete taxa. The works of Wagner (1869) and Romanes (for example, 1886) (cited by Mayr, 1963) were early forerunners of the works of Mayr (for example, 1942, 1963), which remain the most complete and thorough statements of the taxic view of the evolutionary process in the English language[2]. But only in relatively recent years has the basic thrust of paleontological evolutionary thought begun to switch over to the taxic approach. This change is symbolized by the titles and contents of the two most recent book-length treatments of evolution by paleontologists—Valentine's (1973) "Evolutionary Paleoecology of the Marine Biosphere" and Boucot's (1975) "Evolution and Extinction Rate Controls." To both of these authors, evolution consists essentially of the origin, maintenance, and degradation of diversity—a purely taxic approach to evolution. There is indeed little in common between these two books on the one hand, and those of Simpson (especially 1944 and 1953) on the other. Many of the issues Simpson raised and discussed so ably under the transformational approach are given short shrift by Boucot (1975) and Valentine (1973)—including origin of taxa of higher categorical rank, trends, adaptive radiations, morphologic evolutionary rates (usually considered "macroevolutionary" topics—Simpson's "major features") as well as microevolutionary problems centering around species. Inasmuch as evolution seems to be more than merely the origin, maintenance, and degradation of diversity, we should continue to look for a fuller integration of the issues that Simpson and other paleontologists have addressed under the transformational approach, with the basically taxic/ecological approach advocated by Valentine, Boucot, and a host of other contributors to the recent paleontological literature.

AN EXAMPLE: MORPHOLOGIC RATES OF EVOLUTION AND THE TAXIC APPROACH

Simpson (1944:3) defined "rate of evolution . . . as amount of morphological change relative to a standard," and paid relatively less attention to taxonomic rates. In 1953, Simpson made more explicit the distinction between morphologic and taxonomic evolutionary rates and expanded his discussion of the latter. Boucot (1975) in contrast, used the expression "evolutionary rate" solely to mean taxonomic rate (specifically, rate of origin of new brachiopod genera) and this corresponds only to the taxonomic frequency rate subdivision of Simpson's (1953:10) category of taxonomic rates. In the voluminous literature on evolutionary rates, it is usually unclear precisely what kind of evolutionary rate is intended—"genomic" (see Schopf et al., 1975, for a discussion of this type of evolutionary rate and its relationship to paleontology), morphologic, or taxonomic. Although Simpson (1944, 1953) was

[2] Lesch (1975) has reviewed the work of Romanes and other evolutionary biologists of the latter half of the nineteenth century who stressed the importance of isolation in the speciation process. That a distinction between the transformational and taxic approaches was evident to Romanes is well illustrated by Lesch, who quotes Romanes (1886:347): "it (i.e., natural selection) is not, strictly speaking, a theory of the origin of species: it is a theory of the origin—or rather of the cumulative development—of adaptations, whether these be morphological, physiological, or psychological, and whether they occur in species only, or likewise in genera, families, orders and classes." Lesch (1975:487) then elucidates: "In other words, while the theory of natural selection has succeeded in accounting for the great central fact of adaptation in nature, it had failed to give a complete explanation of the special phenomena associated with species formation, in particular the splitting up of a single species into two or more distinct species." This issue is an old one in evolutionary biology!

There are, of course, exceptions to the generalization that paleontologists have remained oblivious to the taxic approach. For example, J. M. Clarke (1913:17 ff.), citing the works of Wallace, Wagner, and Jordan, was clearly thinking in "taxic" terms in his analysis of the role of geographic isolation in the development of the Devonian faunas of the southern hemisphere. But such examples are few and far between, and constitute only a muted counterpoint to the main theme of "transformationism" in paleontological research over the past 100 years.

correct in separating these various kinds of rates and asserting the unique interest attached to each, the tendency not to distinguish among them implies that the fundamental problems underlying such investigations are interrelated, if not identical.

Degree, hence rate, of genetic change has long been known not to be invariably closely correlated with morphologic change. The existence of sibling species (for example, *Drosophila persimilis* and *D. pseudobscura*—see Dobzhansky, 1951:267) when compared with the rampant variation within a single species (for example, *Homo sapiens*) suffices to dramatize this long-known point, as does the recent demonstration (King and Wilson, 1975) of the close genetic similarity between *Pan troglodytes* and *Homo sapiens*, two species which appear to us to be so different. Similarly this point is directly related to degree, hence rate, of morphological change versus speciation rates; a highly speciose group (such as most drosophilid faunas, perhaps excepting Hawaii—see Hardy, 1970:451) may remain morphologically rather uniform, or produce a broad spectrum of morphologically distinctive species (as in African cichlid fish of the genus *Haplochromis*—see Fryer and Iles, 1969). Finally, degree, hence rate, of genetic change is not clearly related to speciation rate (Avise and Ayala, 1975). These various sorts of rates are "decoupled" (*sensu* Stanley, 1975) to some extent, and it is legitimate to investigate each separately.

When we turn to a specific problem involving rates and examine the hypotheses proposed to explain it, the distinction between the transformational approach and the taxic approach becomes relevant. For example, bradytelic lines—defined by Simpson (1953:113) as "low rates" or "arrested evolution"—imply, above all, extremely low rates of morphological evolution over a considerable span of time—usually at least 100 million years. Most studies of bradytelic lines have focused on the question: what are the factors governing this observed slow rate of morphological transformation? The difficulty in applying a purely hypothetico-deductive approach to evolutionary paleontology is nicely exemplified in the set of explanations devised by paleontologists (and others) to explain bradytely. Simpson (1953:319 ff., see also p. 303 ff) summarizes many of them ably, himself believing that bradytelic lines are qualitatively (as well as quantitatively) different from moderate and fast rates, and concluding (1953:334) "bradytelic lines are merely the residuum of a process that regularly reduces the percentage of unchanged groups but that stops short of reduction to zero . . . ."

There seem to be three general "transformation" sets of explanations of bradytely. First, lack of sufficient genetic variability (for a variety of reasons) has been cited (see Selander et al., 1970, and references cited therein) as a major factor. If genetic varibility be the raw stuff of evolution, lack of such variability might be construed as an impediment to change. But Selander et al. (1970) have shown that *Limulus polyphemus*, a surviving member of a classically bradytelic lineage discussed more thoroughly below, is about as polymorphic at a sample of its loci as most other organisms. A second set of explanations involves selection; for example, Simpson (1953:331) asserts that bradytelic lines are not subject to intense (directional) selection pressures, but rather are always under intense stabilizing (centripetal) selection pressure. The final general kind of explanation of bradytely involves adaptation per se—organisms have persisted essentially unchanged because their adaptations were successful, their habitats persisted, their niches remained recognizably the same, hence so did they. This argument is appealing, but amounts to a tautological restatement of the problem—it essentially says that organisms have persisted because they have persisted. There seems to be few avenues to test most of these hypotheses directly.

Fig. 1, taken from Westoll (1949: Fig. 11), is a typical bradytelic curve for rate of character loss within Dipnoi (following an early tachytelic period), compared with the actual number of dipnoan genera given by Romer (1966). The curves are similar:[3] where there is a high rate of morphological change, there tend to be more taxa recognized by systematists. This poses an important conundrum: do lineages undergoing a relatively high rate of morphological transformation appear to be more taxically diverse simply because their greater morphological variety allows us to recognize more taxa within them? Or is it the other way around—are lineages, which exhibit relatively greater amounts of morphologic change, more taxically diverse because they have a higher rate of speciation? If the former is true there is no compelling reason to consider

[3] Raup and Gould (1974) have illustrated the pitfalls of concocting evolutionary explanations for spindle diagrams of diversity and the lesson is directly applicable to the interpretation of these taxonomic frequency and survivorship curves. Eldredge (1978: Fig. 10) has recently presented a curve of trilobite family diversity which is geometrically very similar to that for Dipnoi (Fig. 1b) and Limulicina (Fig. 2) presented here. Trilobites, as a group, were by no stretch of the imagination bradytelic. Thus, low diversity, on the species or at most the generic level, must be an added element to the very definition of bradytely—see Eldredge, 1975, for a further discussion.

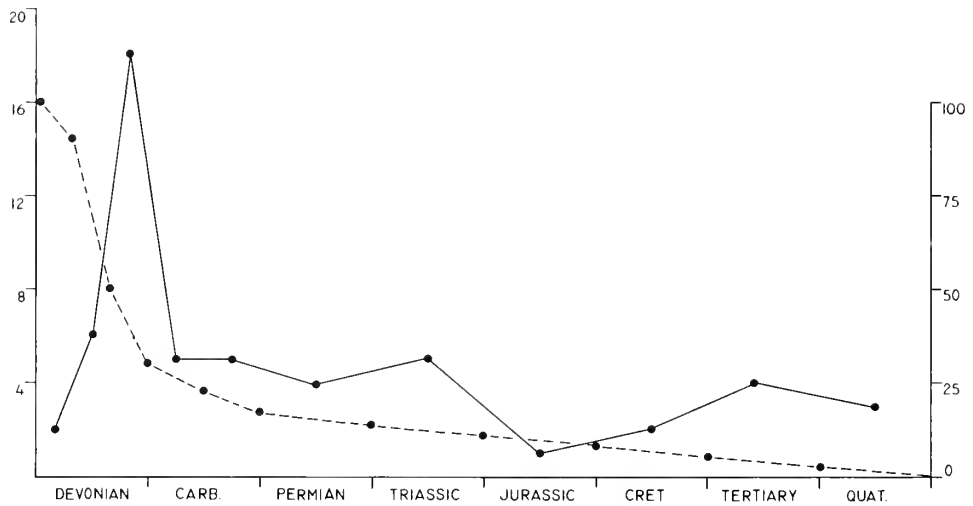

Fig. 1.—Comparison of Westoll's "graph showing rate of loss of characters [for entire body] of the ancestral type during evolution of Dipnoi" (dashed line with scale on right; redrawn from Westoll, 1949: Fig. 11) with a tabulation of dipnoan generic diversity through time tabulated from Romer (1966; solid line with numbers of genera on left). Both diversity and rate of morphological evolution were initially high ("tachytelic"). The bradytelic phase, comprising some 87% of the total history of the group (345 of 395 million years) is accompanied by a greatly reduced but apparently stabilized generic diversity. Compare with Fig. 2.

arguments other than the sort listed above to explain differential rates of morphological change. In that case, it would appear that the problem of bradytely has been exhausted and we are left with a number of narrative, essentially inductive explanatory generalizations (not all mutually exclusive) with which we must be content. However, if we examine the alternative hypothesis, that morphological evolutionary rates reflect, however indirectly, speciation rates, the problem of bradytely takes on an entirely different guise and perhaps admits to a more compelling narrative explanation, and possibly to a more rigorously hypothetico-deductively based investigation.

Fisher's (1975*b*) recent detailed study of the evolution and functional morphology of xiphosurans provides a comprehensive review of the diversity and morphological evolution of the infraorder Limulicina from the Middle Devonian through the Recent. Fig. 2, based on data from Fisher (1975*b*) graphs the approximate number of valid species extant during some part of each third of the various geologic periods. Fisher (1975*a*, 1975*b*) has demonstrated that the classic view of virtually total stasis in limuline evolution has been overstated. For example, Fisher (1975*b*) convincingly shows that the Carboniferous Euproopacea attained full fusion of the opisthosomal segments independently from the true Limulacea. This interpretation is contrary to conventional interpretations (or assumptions) most recently advocated by Eldredge (1974*a*) who cited opisthosomal fusion as a synapomorphy linking the two groups. Fisher (1975*a*) also established actual differences in shape (that is, not just size) of various prosomal and opisthosomal features which bespeak rather more profound differences in behavior among genera of Limulacea. In spite of the enumeration of a large number of morphological differences among the 23 genera and approximately 45 species of living and fossil Limulicina that Fisher has documented, this infraorder remains a typical example of a bradytelic lineage. Fisher (1975*b*) accepts four living species of Limulicina as valid—*Limulus polyphemus*, *Carcinoscorpio rotundatus*, *Tachypleus gigas*, and *Tachypleus tridentatus*. Inspection of Fig. 2 reveals that this low diversity has been characteristic of the infraorder from the Lower Permian through the Recent. The fact that Recent diversity is so similar to the known diversity during this interval suggests that the fossil record is a fairly accurate reflection of the actual diversity, though of course we must expect it to be an underestimation. Thus, this bradytelic lineage is characterized by relatively little morphologic diversity, low rate of morphologic change, and low taxic (species) diversity for all but the earliest phase of the evolution of the Limulicina.

Bradytelic lineages thus exist and their existence remains to be explained. What follows, first, is an attempt to supplant the inductive narratives, which

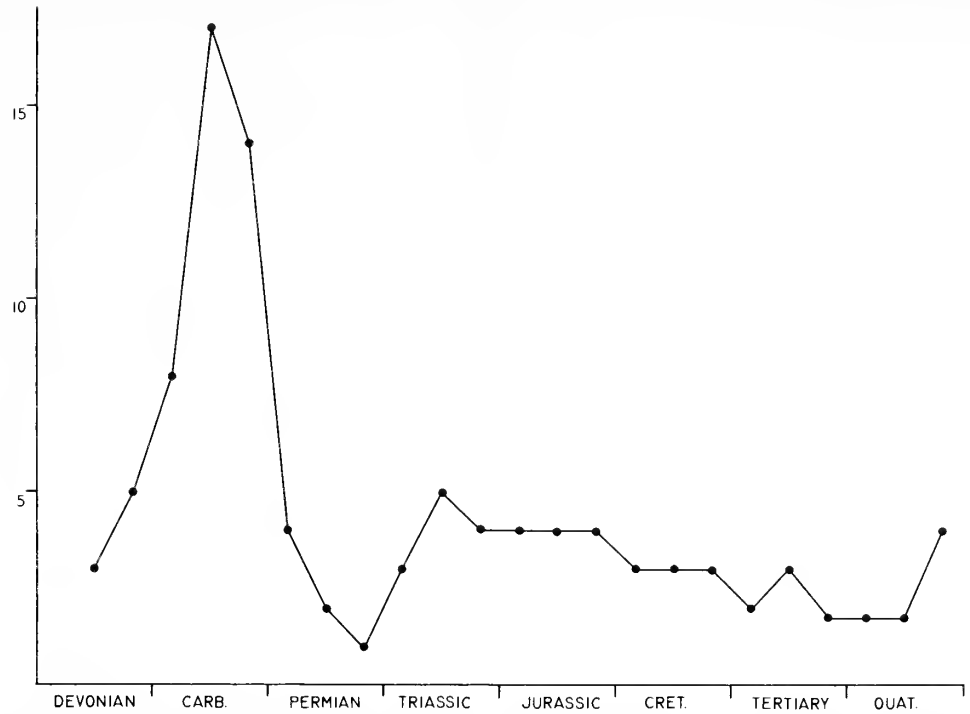

Fig. 2.—Species diversity of Limulicina through time, based on analysis and compilation by Fisher (1975*b*).

approach the problem from a purely transformational standpoint by framing a narrative in the context of taxic evolution. This inductive narrative is then presented as an hypothesis, the components and testability of which will be considered immediately following its presentation.

Assume that very low rates of morphological change are generally correlated with low taxic diversity and that very high rates are correspondingly correlated with high taxic diversity. Counter-examples to these generalizations are easily found; for example, Cambrian echinoderms exhibit substantial morphologic diversity but little taxic diversity (see Sprinkle, 1976 and references therein), whereas North American minnows are speciose and morphologically uniform (Avise and Ayala, 1975, 1976). Nevertheless, insofar as bradytelic lineages are concerned, low rate of morphologic change is correlated with low taxic diversity—compare, for instance, rhynchocephalians versus other diapsid "reptiles," coelacanths and lungfish versus Actinopterygii, Monoplacophora versus Gastropoda, as well as Xiphosura versus both Crustacea and Trilobita.

Inasmuch as the problem of bradytely is being recast in terms of the taxic approach, we consider the possibility that low speciation rates determine the low observed rate of morphologic change, rather than asserting that the low rate of morphologic change results in such little morphologic diversity that systematists do not, or cannot, recognize many discrete taxa. There is the third possibility—that the correlation may be fortuitous and thus low rates of morphologic change may in no way be dependent upon low rates of speciation.

But since we are stating a problem in taxic evolution, we might inquire if there might be a causal connection between speciation rate and degree of morphological change in the evolutionary process. Under orthodox darwinian notions of the significance of evolutionary morphological change, we assume that such change is generally adaptive—morphology is related to ecological niche occupation and exploitation. Similarly, species diversity is related to ecological niche occupation and exploitation, an area of intense investigation among contemporary ecologists, and a theme developed prominently in the recent paleontological literature, notably by Valentine (1973 and elsewhere) and by Bretsky and colleagues (for example, 1970). In view of these relationships, niche theory holds promise for shedding light on aspects (including rates) of the

relationship between the evolution of morphology and the evolution of diversity.

How might this work? Organisms can be characterized on a sliding scale of eurytopy-stenotopy as a means of describing specific aspects of an organism's utilization or tolerance of a given habitat parameter. I use these terms explicitly to refer to relative degrees or breadth of such utilization or tolerance, and not as a measure, for example, of the range of specifiable habitats a species may be found in. The concept of eurytopy-stenotopy is largely qualitative and evaluations are generally subjective, though many physiological parameters are easily quantifiable (for example, Bradshaw, 1961, on relative temperature and salinity tolerances of six species of benthonic foraminiferans). There is a further important caveat in such considerations—a species may be stenotopic in one respect, and eurytopic in another; furthermore a species may be stenotopic in one part of its range, life cycle, or season (for example, rely on a single food resource) while quite eurytopic under other conditions. Yet it appears to be valid to distinguish between "basically" eurytopic species (*Limulus polyphemus* being an excellent example) and stenotopes (for example species of *Haplochromis* cited above), in terms of a comparison of feeding and locomotory behavior and ranges of physiological tolerance. To be useful, such comparisons should be made between closely related organisms in comparable environments.

Stenotopic organisms, almost by definition, are specialists narrowly adapted when compared to their closest analogs. Although there would seem to be a limit to resource subdivision (but see Flessa and Levinton, 1975), stenotopes are those species which exploit only a small portion of the resource space theoretically available to species of their general kind. Eurytopes, in contrast, are broadly adapted generalists. Most paleontologists (for example, Bretsky and Lorenz, 1970) have emphasized the implication of these alternative adaptive strategies in terms of ability to survive extinction events. But it might be asked how these different strategies came about in the first place and came to be maintained in the second place.

There are three major possible outcomes to the onset of sympatry of two closely related species (see Mayr, 1963:81, for a discussion): competitive exclusion, hybridization, and accommodation. Accommodation between two species with initially overlapping niches is typically accomplished through resource subdivision, which frequently results from intensification of specializations already begun prior to sympatry—an accentuation of differences already latent in the allopatric state (Eldredge, 1974*b*). Accommodation amounts to a *de facto* generalization of the typical response of stenotopes to interspecific competition—that is, there frequently ensues a further division of resources. Most closely related sympatric species are rather narrowly adapted organisms. Therefore we may hypothesize that stenotopy increases the probability of survival of new species budded off essentially by accidents of changing geography. On the average, taxic diversity has to be higher among stenotopes. Furthermore, ecological specialization also implies, on the average, that behavioral differences among species will ultimately show up as anatomical specializations. Therefore morphological change itself will be more common and more apparent among stenotopes. Because successful speciation will be more common, morphological change should accumulate more rapidly within stenotopic lineages. Again, African cichlids of the genus *Haplochromis* seem to fit this scenario well, and much of the narrative model corresponds very closely to specific conclusions reached by Fryer and Iles (1969) in their analysis of these fish.

The opposite should be true of eurytopes. Eurytopes are generalized in behavior and physiology, and therefore have relatively unspecialized somatic organizations. Eurytopes, furthermore, tend to be far-flung (Jackson, 1974) and tend not to occur sympatrically with closely related species (for example, the largely allopatric distribution of the relatively few species of the eurytopic cichlid *Tilapia* compared with the great amount of sympatry among *Haplochromis* species; Fryer and Iles, 1969)—presumptive evidence that eurytopes competitively exclude, far more often than they accommodate, closely related species. The data pertaining to limuline evolution also fit these generalizations quite closely. It would thus appear that speciation rates within eurytopic lineages are automatically dampened by their ecological strategy, and, as a corollary, morphological change will be retarded. Remembering that rate of morphological change is not directly or fully correlated with speciation rates, it is further relevant that when successful speciation events do take place within eurytopic lineages, the new species themselves tend to be eurytopic, hence remain morphologically unspecialized. Jackson (1974) reaches much the same conclusions for somewhat different reasons.

We may summarize the above inductive narrative

as a single hypothesis with several component subhypotheses, all of which were contained in the narrative as assumptions. Thus the single hypothesis is rapid rates of morphologic change are correlated with rapid speciation rates; slow rates of morphologic change are correlated with low speciation rates[4]. Correlation is statistical, and a value of R = 1 is not expected; nor, of course, is the narrative held to be true if this initial hypothesis is rejected. But it may be falsified, though not by pointing to a single counter example (for example, Cambrian echinoderms as cited above), as inviolate laws seem impossible to find in evolutionary biology.

Boucot (1975) has recently amassed an enormous amount of data on mid-Paleozoic brachiopods, concluding that eurytopic genera[5] have relatively long stratigraphic ranges, whereas stenotopes (endemics) have relatively short stratigraphic ranges. The former evolves more slowly than the latter. Boucot's data are taxa, that is, aggregates of individuals that Boucot and many others had previously defined on the basis of observed morphological similarities and differences. Thus, in an important way, Boucot has thoroughly confounded morphological and taxic evolutionary rates—the issue he confronts is rate of morphological change, but the data he uses are of generic diversity, and thus we have in a real sense an independent test of the hypothesis above. Based on Boucot's presentation of the brachiopod data, rapid rates of morphological change are indeed highly correlated with more speciose groups, whereas slower rates of morphological change are highly correlated with less speciose groups. Because the interval of time is the same for all groups examined, "more speciose" means "speciating at a higher rate." Boucot (1975 and manuscript) does not seek a purely taxic (speciational) explanation for the correlation he reports, but his data do serve to corroborate this first hypothesis—a further warning that a large if not infinite number of narratives can be concocted for any given set of observations.

Insofar as the specifics of the competition model are concerned, the above inductive argument is only as good as prior theoretical analysis of empirical data already performed by others. Bock (1970, 1972) has utilized competition theory extensively in his analysis of the adaptive radiation of the Hawaiian honeycreepers and other groups. Bock specifically invokes (divergent) character displacement, which results from sympatric interactions among closely related (hence initially similarly adapted) species, to provide the selection force for the direction of morphological change (and specialization) that his prior analysis of relationships revealed. Studies of competitive interaction involving niche subdivision and divergent character displacement are legion, though their interpretation remains arguable (see Grant, 1972, for a recent review of the literature and a skeptical view of the success of the concept; Eldredge, 1974*b*, summarizes the meager paleontological literature on this subject). The studies by Bock and others tend to corroborate the notion that significant amounts of morphological change take place in conjunction with species interactions. But they tell us nothing about the taxic and morphologic stasis hypothesized to take place when competition results in mutual exclusion.

Stanley (1973) in a lucid paper has utilized competition theory to explain the disparity in taxic rate of evolution of mammals *vis à vis* marine bivales. He concluded that, on the whole, sessile bivales are less competitive *inter se* than are mammals[6]. The argument is appealing. To test the hypothesis advocated here, that eurytopic/stenotopic ecological strategies are the prime determinant of a given species' reaction to sympatric competition with a close relative, it would be more germane to compare relatively faster and more slowly evolving lineages within both the mammals and clams. But for the most part, the model developed herein is closely similar to Stanley's model linking differential rates of taxic evolution with interspecific competition.

How, in fact, do we test the hypothesis—eurytopes react to competition by exclusion, whereas stenotopes tend to subdivide niches (hence interact and undergo divergent character displacement as per above hypothesis)? There are several ways—the first being the familiar demonstration of correlation. Fryer and Iles (1969) reach precisely these conclusions upon comparison of the distributions, morphology, and behavior of the cichlid taxa they

[4] Stanley (1975:647) has recently graphed the same data on Dipnoi presented here, and has briefly discussed bradytelic rates. He argues that "groups of taxa that have survived at consistently low diversities over long periods of time should exhibit very little evolutionary change," and that in fact living fossils provide a test of the general validity of the "rectangular model" of evolution. Thus our hypotheses on bradytely are identical, apparently because a preference for the taxic approach immediately leads to such a notion. I stop short of citing this coincidence (Eldredge, 1975; Stanley, 1975) as corroboration of the hypothesis itself.

[5] Boucot's criterion for determining eurytopy-stenotopy is basically the relative breadth of geographic distribution of a genus. This criterion was explicitly rejected earlier in this paper, as specialists may be widely distributed and generalists decidedly less so, all according to the distribution of their habitats. Yet the correlation Boucot relies upon seems real enough and, in any case, no other criterion for judging eurytopy-stenotopy with fossils comes readily to mind.

[6] Van Valen (1976) has taken issue with Stanley's evidence, arguments, and conclusion that there is relatively little interspecific competition among clams.

studied. In a way the hypothesis merely generalizes an empirical observation long known to ecologists and systematists. A further test of the hypothesis that eurytopes tend to mutual exclusion upon the onset of sympatric competition could be gained from mathematical modelling, particularly via simulation. Studies of this kind specifically addressed to this issue have yet to be performed.

Implicit in the inductive model linking morphological rate of evolution with speciation rates, is the notion that morphological change in evolution is largely effected through speciation. This may be stated in another way—we may test the hypothesis that, once established, species tend not to exhibit much morphological change cumulatively (over time) though they would of course be expected to display geographic variation as well as the effects of sympatric interaction with closely related species should this ever occur. Avise and Ayala (1975) recently tested the rival hypotheses that genetic change within a lineage is correlated with (1) amount of speciation, and (2) time (duration of the lineage). Their results were ambiguous, but if anything favored (2). Vuilleumier (1969) has documented allopatric divergence among closely related species of Andean birds, indicating that phyletic evolution is a real possibility. Given time, selection as well as random sampling effects from generation to generation are expected and observed to lead to cumulative changes in both genotype and phenotype within species[7].

But it is still of interest to investigate the relative importance of phyletic morphological change within a species versus the importance of speciation in effecting that change (via a non-random sampling of the parent species genotype/phenotype and post-speciational interspecific interactions more than any "genetic revolution" that might be imagined to take place at the "moment" of speciation). How do we test the relative contribution of these two factors in effecting morphological change?

Close analysis of low-level (ca. species) taxa in the fossil record may be used to arbitrate the discussion. But the situation is not at all straightforward. Gingerich (1974, 1976) concludes that phyletic change in morphological features is the rule, not the exception within lineages of ancestor-descendant population samples. His procedure is straightforward—select a series of stratigraphically closely spaced samples of specimens which, by prior analysis, are thought to belong to a monophyletic assemblage. Select one or more morphological features and simply document what happens to them up the stratigraphic section. Some characters exhibit change, others do not. Gingerich (1974, 1976) has found that the surface area of M_1 of several different Eocene mammalian taxa exhibit gradual, progressive change (see Gould and Eldredge, 1977, for a specific critique of Gingerich's methodology). Graphing the changes against stratigraphic position, Gingerich then simply encircles segments of lineages most clearly linked continuously, and names taxa on the basis of these clusters. Morphology evolves inexorably, and we chop it up to name taxa. Evolution is phyletic.

Eldredge and Gould (1972) and Eldredge and Tattersall (1975) have argued that the first step in paleontological systematics is to recognize basic taxa. Citing examples from trilobites, gastropods, and hominids, they contend that it is possible to recognize and diagnose species at any one point in time, to distinguish such taxa from others living sympatrically (including synchronically, of course) as well as allopatrically and/or allochronically. It is possible to specify in what respects those species differ among each other and, in most cases, those species-specific *differentia* are found in other samples, be they older, younger, or elsewhere. In other words, species are real entities with both geographic and stratigraphic distributions (few species are known from but a single bedding plane). Temporally, there is no significant change in these species-specific *differentia*—after all, it is this very continuity, which allows us to recognize a species in more than one place at more than one time. Other morphological features within the stratigraphic distribution of a species—features which were not cited as *differentia*—often *do* show sequential change within the history of that species. They conclude that species are distinguished both spatially and temporally by virtue of a number of specifiable attributes, which tend *not* to change inexorably as time goes by. Most morphological change is found to be among-species, hence associated with speciation. Stanley (1975) has called this the "rectangular" model of evolution.

Gingerich's entire methodology, hence conclusion, springs from the transformational approach, whereas those of Eldredge and Gould (1972) and

[7] It should be noted that the relatively speciose lineage (North American minnows) investigated by Avise and Ayala (1975, 1976) is morphologically uniform. We may still hypothesize that relatively greater amounts of genetic change, when observed, are strongly correlated with relatively high rates of speciation, in common with the hypothesis above linking morphological rates with speciation rates.

Eldredge and Tattersall (1975) derive from the taxic approach. The disagreement among these authors is ultimately derived from starkly different ways of looking at the evolutionary process. The problem lies more in the fundamental assumptions rather than in faulty logic on either part within the framework of the chosen approach. Thus I would conclude that the patterns of morphological change both within and among species in the fossil record provides a crucial test of species stability through time, and thus tends strongly to corroborate the inductive narrative above on evolutionary rates. In the framework of the taxic approach, this may be so. But as long as we retain these two alternative approaches to evolutionary theory, we shall continue to argue issues from different premises, and we may confidently expect to get nowhere.

SUMMARY AND CONCLUSIONS

1) A complete evolutionary theory requires the presence of two distinct components—(a) a theory of mechanics to explain genetic, morphologic, and behavioral change, and (b) a theory pertaining to the origin of species.

2) Many of the classic areas of investigation, especially in paleontology and genetics, emphasize the aspect of evolutionary mechanics (the "transformational" approach) to the point of near exclusion of consideration of the origin of taxa (the "taxic" approach).

3) Integration of the two approaches is best effected by considering the issues of the transformational approach as a subset of those of the taxic approach. This amounts to saying that taxa evolve, not individual organisms or parts thereof.

4) The problem of bradytely ("arrested evolution") is chosen as an example of a topic in evolutionary biology nearly always stated and investigated purely in terms of the "transformational" approach. Previous hypotheses (actually inductive narratives) proposed to explain bradytely include (a) lack of available variability, (b) lack of directional selection and/or presence of strong "centripetal" or "stabilizing" selection, and (c) retention of original adaptation in conjunction with habitat persistence.

5) Restated in taxic terms, a narrative explanation for bradytely is proposed:

a) Bradytelic lineages are characterized by low diversity for the greatest part of their temporal persistence. Therefore, there is a problem in deciding whether diversity is low simply as a result of there being little morphological diversity for a systematist to use to recognize and name taxa, or whether morphological diversity is low because there has been relatively little speciation within the lineage. The narrative proposed under the taxic approach poses the latter possibility.

b) Taxonomic, morphologic, and genetic evolutionary rates are "decoupled" to a significant extent.

c) However, there is evidence that lineages exhibiting truly low rates of morphologic change have low taxic diversity, and that lineages characterized by high rates of morphologic change have high taxic diversity.

d) Eurytopic organisms (ecologic generalists) react to competition with close relatives largely by mutual exclusion, whereas stenotopes tend toward accommodation by specialization and partitioning of resource space.

e) Thus stenotopes have a higher probability of successful speciation and thus behavioral specializations ultimately are expressed in terms of anatomical modifications. Speciation rates of eurytopes are dampened by their ecological strategy and thus their relatively generalized behavior and physiology leads to retention of relatively primitive phenotypes.

6) Several ways of testing the component hypotheses of the narrative are suggested. The problem remains difficult to attack in an hypothetico-deductive manner. Correlation between different parameters (for example, between low rate of morphologic change and low taxic diversity; between degree of sympatric occurrence among congeneric stenotopes versus congeneric eurytopes, and others) offers a means of rejection, though not a particularly strong source for corroboration.

7) Many of the controversies in contemporary evolutionary biology stem not so much from the relative merits of the logic or data used in arguing a particular point of view, but rather from funda-

mentally different approaches taken by the investigators. The current controversy in paleontology over the relative importance of phyletic evolution versus speciation is an excellent case in point. Most adherents of the view that evolution is essentially phyletic see evolution primarily as the cumulative change of gene content, frequency, and expression. The fundamental assumption of the opponents of this view appears to be that evolution is quintessentially the origin of new taxa (species). Thus the two opposing views (that is, on the relative importance of phyletic evolution versus speciation) are not sufficiently comparable to allow rejection of one in favor of the other. The argument is, in the end, over which approach to evolutionary theory is the more appropriate. The taxic approach seems the superior of the two because of its capacity for subsuming the transformational approach. The converse does not appear to be true.

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THE SYNTHETIC EXPLANATION OF MACROEVOLUTIONARY CHANGE—A REDUCTIONISTIC APPROACH

WALTER J. BOCK

Department of Biological Sciences, Columbia University, New York, New York 10027, and
Department of Ornithology, American Museum of Natural History, New York, New York 10024

INTRODUCTION

Formulation of the synthetic theory of evolution began in the early 1930's with the high hopes of explaining all evolutionary phenomena with a single unified theory. Many of the hopes of these evolutionary biologists were realized, some more than they had dared to believe possible. Other facets of evolutionary theory, once considered incontestably established, were subsequently questioned. Yet the single aspect of evolutionary biology that eluded attempts for successful and convincing explanation is macroevolution—the appearance and subsequent specialization of distinctive new features and taxa. Advocates of the synthetic theory assumed, largely as untested conviction, that major evolutionary changes were simply the consequence of many small modifications and that these large changes would be understood if the microevolutionary events were fully comprehended. Although I believe that this assumption is correct and will advocate it in this paper, one of the major failures of the synthetic theory has been to provide a detailed and coherent explanation of macroevolution based on the known principles of microevolution. In spite of the beliefs of the advocates of the synthetic theory, macroevolution has not been reduced successfully to microevolution.

Because of this failure of the synthetic theory, two major explanations have been advocated for major evolutionary modifications. One is the reductionistic theory as mentioned above and which will be advocated herein. The other stems from the period of idealistic morphology of the second half of the nineteenth century with strong pre-Darwinian roots, and can be termed as the quantum or saltation theory. Differences between these two conflicting theories, as well as the confusing complex of ideas associated with macroevolutionary explanation, are demonstrated by two recent textbooks of evolution published by the same house. Dobzhansky et al. (1977) advocate strongly the synthetic view with a firm statement that macroevolutionary change must be adaptive throughout. Grant (1977) leans strongly toward the quantum theory of major evolutionary change although he rejects extreme versions of saltation. Yet both texts rely heavily on the ideas of Simpson (1944, 1953) and both cite my analysis (Bock, 1970) of the evolution of the Hawaiian honeycreepers (Drepanididae) as an example of adaptive radiation.

I would like, in this paper, to provide a detailed reductionistic explanation of macroevolution within the tradition of the synthetic theory. An important part of this analysis will be an examination of the role of the species and of speciation in this explanation. At this point, I would like to acknowledge my debt to my teacher and mentor Ernst Mayr whose name is usually associated with the species concept and speciation, but who has done more to establish the foundations of an explanation of macroevolutionary phenomena than any other living evolutionist.

LIMITS OF MACROEVOLUTION

Before a causal theory of macroevolution can be postulated, it is necessary to establish the limits of this type of evolutionary change and to distinguish it from microevolutionary phenomena. Unfortunately no definite boundary can be drawn between macro- and microevolutionary changes; I believe that the two grade smoothly into one another. Yet even when no sharp demarkation can be established between two concepts or phenomena, such as night and day, frequently the two may be easily recognized. Hence, by microevolutionary change, I mean those modifications of the level studied by population geneticists and by animal and plant breeders. These would be differences of the degree that distinguish populations and subspecies of the same species or that distinguish congeneric species.

Microevolutionary events are ones amenable to experimentation and direct observation. Macroevolutionary changes are those modifications of the level studied by comparative anatomists and paleontologists. They would be differences of the degree that separate families, orders, and groups of higher categorical rank. Differences between genera are usually considered to be at the lower end of the scale of major evolutionary change. The origin of a distinctive new feature, such as the vertebrate eye or the mammalian jaw articulation, or the radical modification of an existing feature, such as the evolution of the tetrapod limb from a crossopterygian fin or the avian wing from a reptilian forelimb, would all be major changes. Macroevolutionary changes are usually not open to experimentation or direct observation, although some of the results of animal and plant breeding, for example, the fancy breeds of goldfish and the diverse breeds of dogs, surely must be regarded as major modifications.

I do not want to accept any level as the demarcation between micro- and macroevolution in a hard and fast way. Successful development of the reductionistic explanation of major evolutionary change is not dependent upon any particular limit between these two degrees of evolutionary change. More important is the continuum between these facets of evolutionary change and the fact that examples of the two types overlap rather broadly.

REDUCTIONISM

One of the central arguments about theories of the mechanisms of macroevolution is whether they are reducible to mechanisms of microevolution. Stanley (1975) states that macroevolution is not reducible to microevolution and I claim that it is. This is one of the fundamental distinctions between quantum and synthetic theories of major evolutionary change. A consequence of these two positions is that in the reductionistic synthetic approach, no mechanisms of evolutionary change need be proposed other than those needed to explain microevolutionary events. In the nonreductionistic quantum approach, at least one additional mechanism of evolutionary change unique to macroevolutionary events must be postulated over and above those needed to explain the microevolutionary phenomena. The additional major evolutionary mechanism(s) must first be postulated and then tested somehow by observations. Moreover, it must be shown that these unique macroevolutionary mechanisms are really not reducible to known microevolutionary mechanisms.

Before this conflict on the reduction of major evolutionary explanation can be solved, it is necessary to clarify the meaning and usage of the concept of reduction of scientific theories. I accept the approach to reductionism advocated by Ernest Nagel (1961; Chapter 11). Reductionism can be interscience or intrascience; we are here concerned with an intrascience reductionism because we remain within the limits of evolutionary biology. The question is whether a large change in evolution is simply the consequence of a cumulative series of small changes and hence explainable by the mechanisms governing the small changes, or whether the large change involves at least one step different from the microevolutionary changes. If the former is correct, then the explanation must include consideration of levels of organization, which is intimately associated with the concept of reductionism.

Nagel argues that reduction of theories to be successful must follow a rigid set of rules. Both the theory to be reduced and the reducing theory must be carefully stated. It is not sufficient to claim that macroevolutionary explanation can or cannot be reduced to microevolutionary explanation. One must state the details of macroevolution—the theory to be reduced—and the details of microevolutionary explanation—the reducing theory. Hence the statements by many advocates of the synthetic theory that major evolutionary change can be explained by the mechanisms of microevolution is correct, but grossly inadequate. Such a statement can neither be defended or argued against because of its vagueness.

The second point mentioned by Nagel is that all phenomena explained by the reduced theory must be explained by the reducing theory for a successful reduction. If there are any phenomena that were explained by the reduced theory that cannot be explained by the reducing theory, then some additional theory is needed and the reduction is not successful. Nagel goes on to argue that for strong reduction all parts of the reduced theory must be

derivable from the reducing theory. This requirement is not essential for weak reduction.

The usefulness of reduction of theories is a matter quite apart from whether a particular theory is reducible to another. It is generally accepted that reduction will be useful if the reducing theory can explain many phenomena other than those covered by the reduced theory and if the outcome of the reduction is a more generalized theory uniting many aspects of the particular science or sciences.

Reductionism, especially intrascience reductionism, is closely associated with levels of organization and with the question of the emergence of new properties with increasing levels of organization. It is not clear whether the contrast of microevolution and macroevolution fits into the typical pattern of hierarchical organization, but it does fit many of the characteristics of this pattern. Nagel shows that the common statement that the "whole is greater than the sum of its parts" is dependent upon knowing how to add the component parts and whether the details of organization must be included in the addition.

In consideration of whether macroevolutionary explanation is reducible to microevolutionary mechanisms, an important factor is how the individual small steps are added together to obtain a single major change. It is obvious that this addition must be done in a particular manner. The small steps cannot be added randomly or together in a single unit. Rather they must be added sequentially in a chronological series. Thus, the change at any point in time sets the stage for the next change and so forth. Features that arise or are modified at one point in time provide the foundation for the next evolutionary change in features. Macroevolution is thus not just a summation of many small changes, but a sequential summation of many small changes added together in their exact chronological series.

Special care will be given below to stating precisely and completely macroevolutionary explanation as the theory to be reduced and microevolutionary explanation as the reducing theory. Moreover, care will be given to providing reference to the observational and experimental bases used to test the microevolutionary explanation. Attention will also be given to the proper sequential summation of the small changes that add up to a major evolutionary modification. Lack of attention to these facets of reductionism in the past has been a major failure on the part of advocates of the synthetic theory as well as of the quantum theory of macroevolution.

THEORIES AND THEIR TESTING

To be successful, theories or explanation of major evolutionary change must satisfy two major requirements. They must provide a causal explanation of the phenomena associated with large scale modifications and they must be testable against observations. I would like to consider each in turn.

A theory explaining macroevolutionary change, be it the origin and specialization of new features or the adaptive radiation of a new taxon, is a causal explanation similar to theories of speciation, adaptive modification, generation of new genetical variation, and others. Although the time period involved with major changes and hence in the explanation may be great, covering tens of thousands or even millions of years, the theory is not a historical explanation. I am not concerned with analyzing and explaining the evolutionary aspects of a particular feature or of a particular taxon. Rather, I wish to present a causal explanation of macroevolution, which can be used in historical explanations of individual cases.

The fact that a causal explanation of macroevolution includes a sequential analysis of steps does not make it a historical analysis. Numerous other causal explanations, for example, geographical speciation, depend upon a sequence of events arranged in proper chronological order.

The second point is that any successful causal explanation of macroevolution, being a scientific theory, must be tested against experiments and observations. Formulation of any explanation brings with it the obligation of demonstrating how the theory is to be tested and if possible to provide some tests. Development of an explanation that depends upon a vague or untestable mechanism weakens that theory considerably. Perhaps the greatest weakness of past attempts to provide explanations, be they synthetic or quantum, of macroevolution has been the failure to formulate convincing testing procedures. Procedures are frequently proposed to test theories of macroevolution, but upon close scrutiny, these tests prove to be inadequate. An

example is the tests of the theory of punctuated equilibria by the fossil record (Gould and Eldredge, 1977: 120). The nature of the fossil record, especially the scale of resolution of time and geographic distribution, is simply inadequate to distinguish between punctuated equilibria and conflicting theories.

Testing of macroevolutionary theories depends upon formulating a proper argument-chain of predications, secondary theories, and connecting links, and finally the experiments and observations serving as empirical tests. It is generally accepted that theories of major evolutionary change cannot be tested directly against experiments and observation. This is generally valid, but we may have far more evidence available from experimental work and from observations of animal and plant breeders than generally suspected.

Special care will be given to outlining the procedures for testing the synthetic theory of macroevolution. The steps in the argument-chain, the secondary hypotheses, the basic links, and the final observations will all be clarified. What types of observations that can and cannot be used to test this explanation will be pointed out.

CONFLICTING EXPLANATIONS OF MACROEVOLUTION

Introduction

Numerous theories have been advocated to explain the phenomena of major evolutionary modifications. All of these need not be discussed because most have not attracted much attention. I will concentrate only upon the two major sets, which are in direct conflict with each other. Although considerable variation exists between the individual theories included in each of these sets, the basic agreements are more important. The first set is that of quantum theories, which are characterized by advocating a single-step jump or saltation at some point in the major change. The evolutionary mechanism involved in this jump is one other than adaptive change under the control of natural selection arising from the external environment. The second set is that of synthetic theories in which the explanation of major changes is reduced to mechanisms acting on the microevolutionary level. These theories exclude any distinctive saltations, do not invoke any special mechanisms of evolutionary change other than those operating at the microevolutionary level, and depend upon adaptive change throughout. All change is under the control of selection arising from the external environment.

Quantum Theories

I will discuss only those quantum theories advocated since the origins of the synthetic theory of evolution in the early 1930's. However, it should be emphasized that the history of ideas of quantum evolutionary changes date back to the period of idealistic morphology in the second half of the nineteenth century and have their roots in pre-Darwinian typology.

By a quantum theory, I mean one that depends upon a single saltation of a magnitude greater than the evolutionary change observed in microevolutionary modifications as studied by animal and plant breeders and by populations geneticists. The mechanism controlling this saltatory jump is either a nonselective one (not natural selection arising from the external environment) or a type of selection distinctive from natural selection. Frequently these theories depend upon the existence of a threshold or of a selective bottleneck.

The concept of typogenesis or typostrophism of Schindewolf (1936, 1950:206) is a clear consequence of the concepts of typology and the idea of "bauplan" of groups developed directly from the concepts of idealistic morphology (Bock and von Wahlert, 1963; Reif, 1975). This theory depends upon the concept that the characteristics of a taxon are expressed in its bauplan or type, that a type boundary delimits a group and that a distinct gap separates the bauplan of one group from that of another. Hence the evolutionary change from one bauplan to another must be a jump over this gap—over the type boundary of one group to that of another. This change must be of a different type than the evolutionary change within the limits of a bauplan. Otherwise there could not have been a type jump. The saltation is not an adaptive change controlled by selection; it is left as a vague evolutionary mechanism.

A similar theory is offered by Goldschmidt (1940:184–395). He argues that the small genetical changes studied by geneticists are insufficient to result in a major change even if many are added together. Rather he suggests that the large changes

result from the occurrence of systemic mutations (=macromutations) leading to a new type of organism that is adapted to a new set of environmental conditions. These organisms resulting from systemic mutations have been dubbed "hopeful monsters" by other workers. The role of selection in Goldschmidt's theory is vague. He says (p. 396) that accumulation of micromutants by selection has been "ruled out," and that selection can act on the new form after the systemic mutation. But he nowhere discusses the magnitude of the modifications resulting from the systemic mutations and what are the environmental changes that can act as selection. In the absence of details on this point, it cannot be assumed that the selection discussed by Goldschmidt corresponds to selection acting on microgenetical changes or that it can be related to environments in the real world. It is interesting that Goldschmidt cites the Drepanididae (1940:214–215) as an example supporting his concept of macromutation by systemic mutations, but omits many of the details of geographic variation in species as well as possible intermediate stages represented by extant species.

The concept of "quantum evolution" was developed by Simpson (1944:206–217) and has been widely cited as the synthetic theory explanation of macroevolution in sharp contrast to ideas of typogenesis and systemic mutations. However, careful reading of Simpson's text reveals that his concepts are basically more similar to those of earlier saltatory theories than to a reductionary synthetic explanation of macroevolution. Quantum evolution depends upon a shift of a phyletic lineage through "discontinuities or essentially instable ecological zones" that lie between major adaptive zones. The start of quantum evolution is an inadaptive phase when the lineage enters the discontinuity. Exactly what is meant by "an inadaptive phase," how long it exists and whether selection is acting during this period is not clear. The only conclusion that can be reached is that selection is not acting during the "inadaptive phase" otherwise this phase can not be so considered. The instable ecological zone is regarded as a threshold through which the phyletic lineage must pass quickly or become extinct. These ideas are repeated by Simpson in his later book (1953:389–393) but with some changes. He says that "populations making a quantum shift do not lose adaptation" and "that the direction of the change is adaptive" (p. 391) but later says that "No intermediate stage persisted, because intermediate stages were less efficient (i.e., *relatively* inadaptive)" (p. 392). If these shifts were fully adaptive, then it is not clear what is the distinction between quantum evolution and regular phyletic evolution.

The concept of quantum evolution as expressed by Simpson involves a period where selection is not acting, depends upon passing over a threshold in the intermediate unstable ecological zone, and involves (always?) a key mutation. These expressions sound very similar to the concepts of Schinderwolf and of Goldschmidt in spite of differences in wording. Many of the concepts, such as the inadaptive phase and the ecologically unstable zone, are left vague and unconnected to natural phenomena. Quantum evolution is discussed as an evolutionary mechanism, yet it is not tested nor are testing procedures clearly indicated.

The concept of punctuated equilibria was postulated by Eldredge (1971) and developed more fully by Eldredge and Gould (1972) and discussed again by Gould and Eldredge (1977, see for references to other papers). They wished to examine the concept of slow evolutionary rates as the primary mode of evolution and to introduce the concept of allopatric speciation into paleontological thinking. Certainly the role of speciation has been neglected (although not totally) in discussions of macroevolutionary change and clearly many, probably most, major evolutionary modifications are more rapid than believed by many workers. These concepts were already discussed by Simpson (1944, 1953) and were a central part of my earlier analysis (Bock, 1970) of the role of microevolutionary events in macroevolution. Unfortunately, in the formulation of their concept of punctuated equilibria, Eldredge and Gould shifted from considering whether slow changes were the only or predominate mode of phyletic change to discussing mechanisms of evolutionary change. The result was a series of assertions which makes their concept one of quantum evolution and hence unacceptable.

The major problem is that the concept of phyletic gradualism (the term for slow uniform rate of evolutionary change) has been synonymized for phyletic evolution. This is shown in Eldredge (1971:156–157) and clearly in Eldredge and Gould (1972:87–90; by the equating of Kellogg's [1975] discussion of phyletic evolution with phyletic gradualism, pp. 126–128; and by their statement in the abstract "If, as we predict, the punctuational tempo is prevalent, then speciation—not phyletic evolution—must be the dominant mode of evolution." p. 115). Part of

this problem may arise from a combination of their considerations of phyletic speciation, multiplication of species (geographic speciation) and phyletic evolution (1972) where discussions of phyletic evolution and phyletic speciation appear to be interwoven. The consequence is that when they argue against (to the point of denying) phyletic gradualism as a dominant mode of evolution, they do the same for phyletic evolution.

The outcome of this confusion of two concepts, which are completely independent of one another, is that they must reject the synthetic (reductionistic) explanation of macroevolution (for example, Gould and Eldredge, 1977:139–145). They accept the argument of Stanley (1975), which is developed directly from their concept of punctuated equilibrium. Stanley proposes a "rectangular model" for major evolutionary change in which the speciation shifts are regarded to be absolutely different from the evolutionary changes between successive speciations. He introduces a new evolutionary mechanism "species selection," which is not described in sufficient detail and for which no procedures are provided for testing. Stanley states in his discussion (1975:650) that "The reductionist view that evolution can ultimately be understood in terms of genetics and molecular biology is clearly in error. We must turn not to population genetic studies of established species, but to studies of speciation and extinction in order to decipher the higher-level process that governs the general course of evolution."

Thus, the concept of punctuated equilibria can be summarized as major evolutionary changes that are the consequence of a series of speciation, not phyletic evolution, in which the mechanism of species selection is important. Further, the explanation of these macroevolutionary changes cannot be reduced to the evolutionary mechanisms operating at the microevolutionary level. Illustration of this change by a rectangular diagram underscores the quantum nature of this explanation. Further, Gould (1977*a*, 1977*b*, 1977*c*) clearly relates the ideas advocated in punctuated equilibria with Goldschmidt's concept of systemic mutations.

A curious approach to quantum evolution has been developed as an outcome of mathematical topological theory of catastrophe (Thom, 1975; Dobson, 1975; Zeeman, 1976; Dobson and Hallan, 1977) developed by Rene Thom. Sussmann (1976) has presented arguments against the implications of this theory as developed in the above cited papers, and Kolata (1977) has commented on this development (see also letters to the editor, 1977, Science, 196:1268–1270). This explanation can be discounted at this time because the possible evolutionary correlations to the mathematical theory have not been worked out, but it is of interest because it demonstrates how attractive the idea of quantum evolutionary steps is to many workers.

Frazzetta (1970, 1975) discussed major evolutionary change from the viewpoint of a functional morphologist, one of the few to do so. Although he does not deny the possibility of major changes resulting from a series of small evolutionary modifications, he believes that macroevolution can also occur by other processes, possibly by the appearance of systemic mutations as advocated by Goldschmidt. Many of the points discussed by Frazzetta, such as the need to examine interactions between structures and the importance of somatic modifications (= physiological adaptation), are important and have been ignored by most evolutionists. As stressed by Frazzetta, analysis of evolutionary modification of morphological systems is far more complicated than appreciated by most workers advocating macroevolutionary explanation. Yet I am not convinced that he presents a compelling argument why all macroevolutionary explanation cannot be reduced to microevolutionary explanation, albeit the microevolutionary explanation will be more complex than usually assumed.

A central issue in several recent quantum theories of macroevolution is rapid speciation in which most of the evolutionary change takes place prior to the complete development of intrinsic isolating mechanisms and the sympatry of the newly appeared species. This factor is critical, for example, to the theory of punctuated equilibria. Carson's (1975) ideas on the genetics of speciation have been cited in this connection. He argues that "microevolutionary events that lead to adaptations, however, do not appear to yield new species as a necessary or even a directly correlated consequence of the adaptation process" (p. 83). Carson suggests that the genetical system of a species is divided into two parts, the open and the closed. The open system responds readily to selection and is the portion of the genotype that has been studied by geneticists. The closed system is not affected by selection under usual conditions and does not yield easily to Mendelian analysis. Under normal circumstances, gene flow does not affect the closed system. Rather, the closed system is modified during speciation with a forced reorganization of the closed variability sys-

tem by a series of catastrophic stochastic genetic events. This occurs during a period when selection is not acting with a resulting population flush and crash (see his Fig. 2, p. 89). After the crash, a few founder individuals are left from which the new population is generated under natural selection.

Carson is vague on the possible duration of this period of no selection nor does he give reasons to justify the existence of such periods. He does not postulate any new evolutionary mechanisms as the stochastic genetic events occur by known mechanisms of crossing over and other types of genetic recombination. Yet he is vague on why such events cannot take place during periods of normal selection. Because it includes a period of no selection, Carson's concept of speciation belongs to the class of quantum theories and has to be so used (for example, Gould and Eldredge, 1977).

The major difficulty with the theory proposed by Carson is that he does not stipulate how the concept of the closed variability system and the mechanism of its change can be tested by empirical observations. Also, the procedures by which this concept can be tested are difficult to envision because of the stipulation that the closed genetic system is not affected by selection during normal conditions, but changes only during speciation and because of the claim that speciation occurs only as a result of an alteration in the closed genetic system. These interlocking claims form a closed circularity devoid of any means of test by independent observation.

Non-Darwinian evolution as postulated by King and Jukes (1969) and other workers has been invoked by advocates of quantum explanation of macroevolution. Although the theory of non-Darwinian evolution is not a quantum theory, it shares with these theories the notion of a mechanism directing evolutionary modification that is nonselective. Unfortunately, details of the causal mechanism for this nonselective change have been left vague and certainly have not been tested. Other workers in biochemical evolution (for example, Goodman et al., 1975; Goodman, 1976) have argued against the claim of non-Darwinian evolution and state that evolutionary changes in proteins can be explained by selection.

Another theory which does not belong to the class of quantum theories, but should be mentioned here is that of internal selection (Stebbins, 1974:123; Gutmann, 1977:645; Dullemeijer, 1974; Dullemeijer and Barel, 1977). This concept can be interpreted as a form of selection arising from the internal environment of the organism separately and independently of natural selection arising from the external environment. Such a concept has not been clearly formulated nor properly tested. Moreover, the interpretation of a selection independent of natural selection arising from the external environment may not be the intent of Gutmann (personal communication) and possibly not of the other workers. Rather, the concept of internal selection refers to the interrelationships and interactions between features of an individual organism, including all of the mechanisms that serve to keep these features in proper functional balance with one another as required in a viable organism. The various mechanisms on internal adjustment of somatic features and their role in evolution have been considered by few workers (for example, Bock and von Wahlert, 1965; Frazzetta, 1975; Gutmann, 1977) but it is clear that these factors are of prime significance to major evolutionary modification. It is incorrect, however, to term these mechanisms of internal adjustment as internal selection or to imply that these mechanisms are not under the control of natural selection.

Although the emphasis and the mechanisms differ in the above cited and other quantum explanations of macroevolution, the same thread of ideas runs through all. Most important is that they involve a jump or discontinuity at some point, usually during the presympatric phase of speciation, in which a break occurs in the adaptive modification of features and hence of the population. This break coincides with a period in which natural selection resulting from the interaction of the external environment with the organism is not operating. The length of this period is not specified. Often evolutionary modification during this saltation is claimed to be under the control of a nonselective evolutionary mechanism, but this mechanism is not outlined clearly and/or not tested against empirical observations.

These theories fail, in my opinion, for several reasons. The major one is that the needed evolutionary mechanism is not described clearly, or tested; sometimes the indicated mechanism appears incapable of proper testing. Support for the claimed period of no selection is not provided. Although most advocates of quantum theories claim, often tacitly, that macroevolution cannot be reduced to microevolutionary mechanisms, they do not provide the needed support for this claim. To say that macroevolution is or is not reducible to microevolution is not sufficient; the claim must be documented. Most

of the quantum theories do not consider the need to decompose major evolutionary changes into a proper chronological sequence of steps and to show how these individual steps are summarized; rather the component parts of a macroevolutionary modification, if considered at all, are usually treated in some unordered fashion. Lastly, macroevolution usually involves modifications of structural features of organisms. Yet most of the discussions of quantum changes exclude consideration of the total biology of these structural features, for example, functional and ecological morphology, and the details of the complex interactions involved in the internal adjustment of somatic features.

Synthetic Theories

The synthetic or reductionistic explanation of macroevolutionary change is based on the postulate that all major evolutionary modifications in features and taxa are fully understandable in terms of evolutionary mechanisms at the microevolutionary level. No new causal evolutionary mechanisms are needed. Large scale modifications are adaptive throughout in that the entire shift is under the control of natural selection arising from the external environment and acting on individuals of the evolving population. Thus, evolutionary phenomena, from the smallest to the largest changes, can be explained by the same unified theory of evolution. This is the basic belief of many evolutionary biologists since the early 1930's, but close reading of most authors reveals that their statements were unsupported statements—articles of faith. Quite probably these repeated unsatisfactory explanations provided the impetus for repeated formulation of alternative, usually quantum, theories.

Macroevolutionary modifications in features and in taxa are those of a general magnitude characterized by difference, expressed taxonomically, of the generic level or higher. Thus, the appearance of a new bone, a new articulation, feathers or hair, modifications in the feeding apparatus to permit taking of different food and many others, would all be major evolutionary changes. As stated earlier, the minimum level of major evolutionary modification is not essential to the discussion. Most workers would place it at a level of difference greater than that observed between genera, others use a level greater than that between species, and still others would accept species level differences as the minimum macroevolutionary change. The synthetic argument to be developed below could be applied equally well whatever level is accepted.

Explanation of all macroevolutionary phenomena is fully reducible, in the strictest sense, to the known mechanisms of evolutionary change at the microevolutionary level. To be specific, these microevolutionary mechanisms are:

a) Those of phyletic evolution, which are two mechanisms acting simultaneously (that is, every generation) and are namely—the production of genetically based phenotypic variation and natural selection arising from the interaction between the organism and the external environment. These are the mechanisms of evolutionary change in populations, which have been studied by populational geneticists (for example, Dobzhansky, 1970, and earlier) and by animal and plant breeders. These are the evolutionary mechanisms that can be tested directly by experiments and by direct observations of known phyletic changes, for example, the history of breeds of dogs, pigeons, goldfish, wheat, corn and a host of other forms of domesticated plants and animals.

b) The mechanisms of speciation—the multiplication of species—as discussed by Mayr (1942, 1963) and many other workers.

Clearly, much disagreement exists on many aspects of these evolutionary mechanisms and it would be necessary to specify exactly which concept one accepts. There are, for example, a number of concepts of geographical speciation (for example, Carson's concept of the closed variability system and its alteration during speciation), which I do not accept. Much argument exists on the extent and role of gene flow. But these disagreements do not affect the claim about reduction of macroevolutionary explanation made above.

Proper explanation of macroevolution events depends upon correct chronological summation of the individual small modification. If this summation is not done properly, then the remainder of the explanation will dissipate.

I must emphasize that macroevolution is viewed as a sequence of microevolutionary events, not as a sequence of species level changes. The latter implies a distinction between evolution at the species level and evolution above the species level or transspecific evolution which I reject. Such a distinction would suggest that phyletic evolution would transcend the species boundary, which is erroneous (see below). The term "transspecific evolution" should be dropped.

The entire period of major change is adaptive,

being under the control of natural selection at all times. No periods of inadaptiveness exist nor do any periods exist in which natural selection does not operate. However, the synthetic theory does not specify that all evolutionary change of all individual features must be adaptive. Clearly nonadaptive evolutionary modifications of individual features occur as a result of pleiotrophic relationships between features. Such change may be quite common and indeed is responsible for the evolution of a whole class of features, namely the evolution of intrinsic isolating mechanisms. The only exceptions to the generalization that phyletic evolution of a single lineage must be adaptive (under the control of natural selection) are those modifications associated with founders as proposed by Mayr (1942). However, these changes would be of minor magnitude and would soon come under the control of natural selection. It is improbable to a vanishing degree that the whole or a major part of the phenotypic shift in a macroevolutionary change results from genetic drift.

The synthetic theory does not specify rates of evolutionary change. Certainly there is no upper limit on the rate of change other than that imposed by no rates of microevolutionary modification. And these rates of change can vary with periods of rapid modification intermeshed with periods of low change. Almost certainly rates of major change can be far faster than generally believed and the rates during the origin and early development of a major feature or new taxon are rapid, followed by much slower rates, but these ideas are not new, having been expressed by Simpson (1944). Nor am I in disagreement with the ideas of Eldredge and Gould on rates of evolutionary change expressed in their concept of punctuated equilibria. Arguments on rates of macroevolutionary change are independent to a large degree of the mechanisms of change responsible for these rates.

SPECIES AND PHYLETIC LINEAGES

The species and its evolution is central to the dispute between the several major theories of macroevolution. I will consider only species in sexually reproducing organisms and accept the biological species concept as advocated by Mayr (1942, 1963:19). A *species* is composed of groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups. The reproductive gap between species is central and related to preservation of coadaptive complexes of genes. Thus, the species is a genetical unit and an ecological unit with its members forming a reproductive community that shares a common environment. Intrinsic isolating mechanisms serve to preserve the integrity of each species with respect to other sympatric species.

The species concept is most objective as a nondimensional rather than a multidimensional concept (Mayr, 1963:17–19). Thus, sympatric species are most objective with clear-cut limits and separations from one another. As one progresses geographically and chronologically further and further away from a single point, the species distinctiveness becomes more and more vague. Hence, sympatric species are distinct, but allopatric forms become increasingly indistinct with the extreme case being ring species in which the two terminal forms overlap and coexist as species without interbreeding. The unity of the species, which is held together by a common gene pool (and gene flow) and by a similar ecological interrelationship, breaks down as the populations are separated by greater and greater geographical distances and more and more ecogeographical barriers (Fig. 1). A similar breakdown occurs in the unity of the species as one traces it chronologically, generation by generation both forwards and backwards, from a particular point in time. A species comprised of a series of interbreeding populations today is simply not the same as its ancestor 100 generations ago.

The biological species concept is a nondimensional one, but is often applied multidimensionally over a broader geographical space and over a longer temporal period for practical purposes. Thus, I reject the concept of phyletic species except for practical uses in paleontology. The use of the species concept by most phylogenetic systematists as the phyletic segment from one speciation (splitting point) to the next is simply not the same as the biological species concept.

A *phyletic lineage* is the temporal continuum formed by a species (a group of actually or potentially interbreeding populations) reproducing itself generation by generation through time (Fig. 2). A phyletic lineage may remain as a single lineage over long periods of time or it may split into two or more

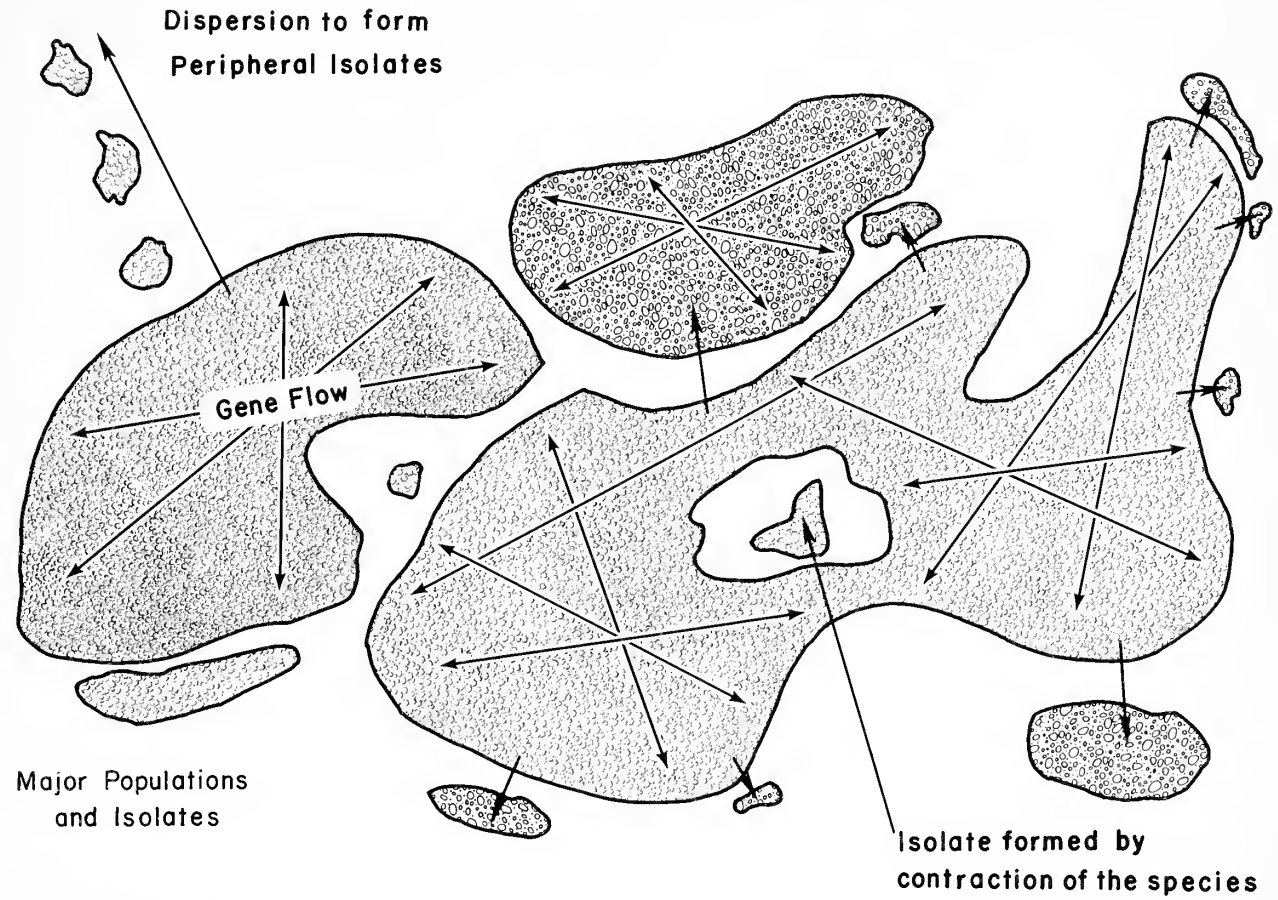

Fig. 1.—Schematic diagram to illustrate the geographic range of a species with several large main populations and a number of small isolates. Some of the peripheral populations were formed by dispersion (indicated by arrows) and perhaps developed from a few founder individuals. Other populations resulted from contraction of the species. Gene flow within populations is indicated by the criss-crossing arrows.

different lineages (= speciate) from time to time. The phenotypic characteristics of the members of a phyletic lineage may remain the same for long periods of time or they may change with respect to time (= phyletic evolution). In any case, whether the phyletic lineage remains single or splits or whether it remains unchanged or modifies through time, no species limits exist between any temporal segments of a phyletic lineage. No matter how much phyletic evolution occurs in a phyletic lineage and no matter how different ancestral and descendent populations may appear, no species boundaries will be crossed as one traces a phyletic lineage; hence, transspecific evolution has not occurred.

A cross-section of a phyletic lineage at any point in time is a species. However, cross-sections of the same phyletic lineage at different points in time are not different species nor are they the same species. These are simply different cross-sections of the same phyletic lineage at different times; one would be ancestral to the chronologically later one.

The phyletic lineage is what is usually implied when the term phyletic species is used. I advocate the former term because it avoids confusion with the concept of species and because the relationship between the phyletic lineage and the species is clear.

Because the biological species concept is a non-dimensional one, it is not possible to speak of the age of a species, or of the origin of a species, or of the life and death of a species. It is meaningless to speak of evolution within the limits of a species and to contrast this mode of evolution with transspecific evolution or with evolution beyond the bounds of a species.

MECHANISMS OF EVOLUTIONARY CHANGE

It is possible to speak of many different types of evolutionary change and to formulate many mechanisms of evolution. These certainly exist and must be detailed if we are to comprehend the full scope of evolutionary biology. Yet it is possible to summarize all evolutionary change into two major types and to correlate these with the concepts of the phyletic lineage and of the species just discussed.

Phyletic Evolution

Phyletic evolution is change in a phyletic lineage with respect to time (Fig. 2). No mention should be made of a minimum time limit because this would become arbitrary. Thus phyletic evolution could be the change seen from one generation to the next. Only modifications that occur in an individual during its lifetime should be excluded from evolutionary change. Phyletic evolution does not have to be specified as hereditary change because this would preclude labeling many modifications (for example, those observed in the fossil record) as evolutionary because it would not be possible to demonstrate that they are hereditary.

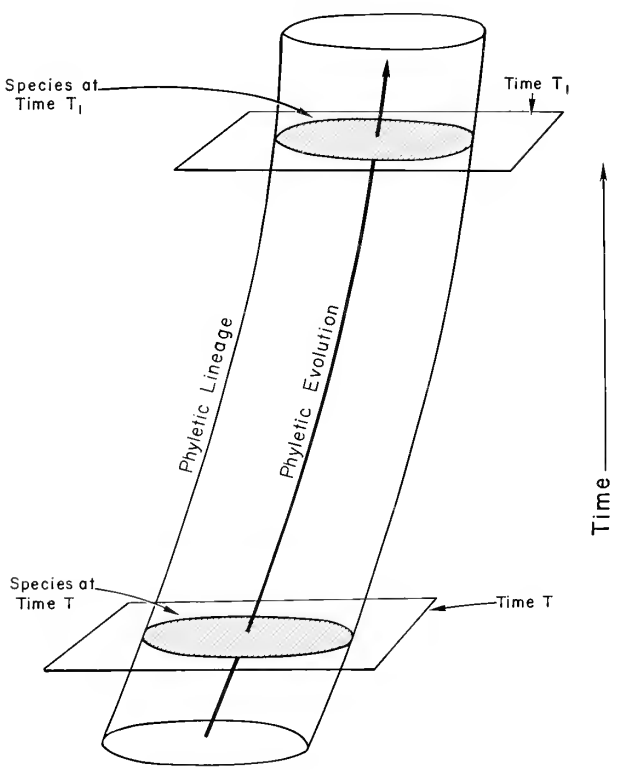

Fig. 2.—Schematic diagram to illustrate the concept of a phyletic lineage, which is a species reproducing itself generation after generation through time. Change in the species with respect to time is phyletic evolution. A cross-section through the phyletic lineage at any point in time is a species. Cross-sections at different points in time are neither the same species nor different species (no species boundary separates them) but simply different cross-sections of the same phyletic lineage.

In phyletic evolution, a descendent cross-section of a phyletic lineage would differ from an ancestral cross-section. Phyletic evolution can occur without speciation (splitting of the phyletic lineage) and, at least in theory, it would be possible to have drastic modification in the characteristics of members of a phyletic lineage by phyletic evolution without any speciation.

The mechanisms by which phyletic evolution occur can be summarized into two types—namely: a) the formation of genetically based phenotypic variation generation by generation; and, b) the action of natural selection arising from the interaction between the individual organisms and their external environment.

The formation of genetically based phenotypic variations is the accidental or chance based factor in phyletic evolution (Mayr, 1962). This genetically based individual variation in a population results from a number of mechanisms of which genetical recombination of all types (crossing-over, inversion, translocation, segregation) is the most important. These are the mechanisms which produce genetic combinations from the existing genetic material in the gene pool. Gene flow is the next most important mechanism, but far less important than recombination. It results in new genetic material in the population, but not new genetic material in the species. Mutations are the least important source for the production of generation by generation genetic variation; it is the source of new genetic material in the phyletic lineage.

Natural selection is the design factor in evolution and results from the interaction of individual organisms with their external environment. I am here concerned with the *mechanism* of natural selection not with its *result* of changes in gene frequencies in the gene pool (the usual definition of natural selection in population genetics). Selection can only result from the action of the external environment on the individual. It cannot arise from the "internal environment" or from the "genetic environment" nor can one speak about a distinct and separate form of "internal selection." Natural selection acts only on the phenotypes of individual organisms and

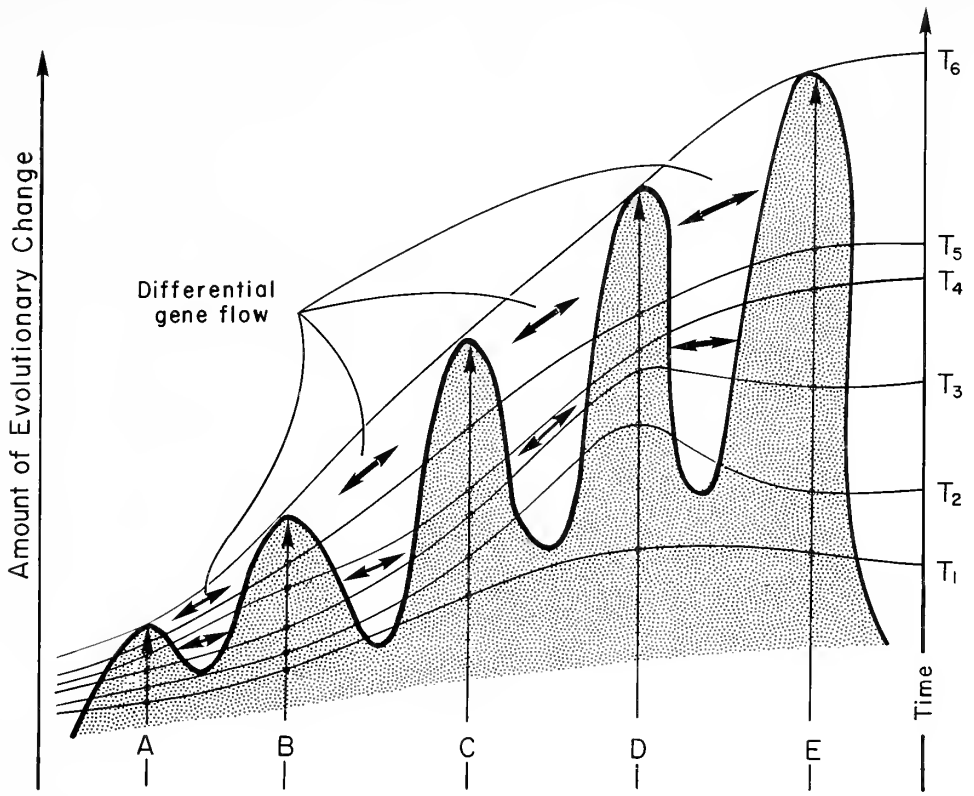

Fig. 3.—Schematic diagram to illustrate that populations of the same species can undergo different amounts of phyletic evolution (indicated by the differential points on the vertical arrows) during the same time period.

can distinguish only between varying phenotypes. The concept of selection is closely associated with that of adaptation (see below).

Both mechanisms of the production of genetically based phenotypic variation and of natural selection are required to have phyletic evolution. Both operate generation by generation and only in the present. Evolutionary change is the result of a chronological summation of the generation by generation simultaneous action of these mechanisms, not an average over a long period. Both mechanisms must be considered simultaneously as the creative mechanism of evolution, neither one or the other is sufficient by itself.

The rate of phyletic evolutionary change depends upon the combined action of these two factors. Rapid evolution cannot occur by mechanisms producing genetically based phenotypic variation alone or by strong directional selection by itself. Of special interest in explanation of macroevolution is the source of the needed directional selection.

It is possible to have varying rates of phyletic evolution in different populations of the same species (Fig. 3). The result will be variation in the amount of evolution in the sublineages of the same phyletic lineage.

Speciation

Speciation is the multiplication of species or the splitting of an original phyletic lineage into two or more lineages (Fig. 4). Speciation can only occur with the accompanying phyletic evolution in, at least, one of the two separated phyletic lineages. The essential aspect of speciation is the mechanism whereby intrinsic isolating mechanisms evolve in the two newly split lineages at a time when members of the two lineages would still be able to interbreed with one another.

Speciation, as I will use it, is only the multiplication of species. It is not phyletic speciation, which is a misnomer for phyletic evolution.

One of the major sources of confusion is: What is the fundamental aspect of the mechanism of speciation? Most workers are not clear about this and have confused many aspects of phyletic evolution in the notion of speciation. Is it the evolution of

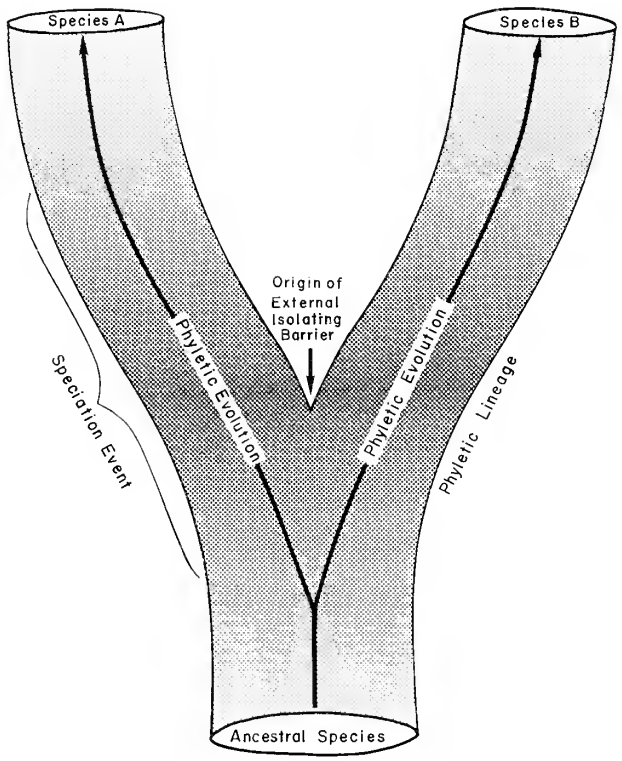

Fig. 4.—Schematic diagram to illustrate the relationship between speciation (splitting of a phyletic lineage into two lineages) and phyletic evolution. Speciation requires the presence of an external isolating barrier and of phyletic evolution in at least one lineage. Species A and B are distinct and separate from one another, but each is not different from the ancestral species common to both phyletic lineages.

intrinsic isolating mechanism? Is it the evolution of ecological, behavioral, and other differences between species that permit them to coexist? Is it the evolution of genetic differences that distinguish species? Moreover, most workers are not clear about the onset and about the completion of the speciation mechanism. Is speciation over when the two newly evolved species become sympatric without gene flow between them? Or does speciation continue for some time after the new species become sympatric?

I will accept the view that the essential characteristic of speciation is the evolution of intrinsic isolating mechanisms and of the ecological, behavioral, and other differences that permit the newly evolved species to coexist ecologically and without interbreeding. Clearly, speciation involves phyletic evolution, but I do not regard phyletic evolution as synonymous with speciation. Moreover, it is clear that the pattern and rate of phyletic evolution may differ in a small peripheral isolate as compared to a large central population or in a small isolate formed by a few founder individuals as compared to one formed by remnants left by a contracting species (Mayr, 1954), but these factors are aspects of phyletic evolution contributing to speciation, not speciation itself. Failure to separate these evolutionary mechanisms and to specify exactly what is meant by speciation has led to much confusion in macroevolutionary explanation.

The onset of speciation frequently occurs prior to the appearance of the external ecogeographical barrier and continues long after this barrier disappears and the two species are able to reinvade each others' range and coexist sympatrically (Fig. 5). Thus, I will separate speciation into two portions—the allopatric period and the neosympatric period.

Populations of a species may start to diverge before the appearance of an external barrier that splits the phyletic lineage into two separate sublineages. Hence at the onset of the allopatric phase of speciation the two sublineages may or may not be different from one another. The ecogeographical barrier (I will consider only allopatric or geographic speciation) splits the original single phyletic lineage into two and prevents members of the two sublineages from interbreeding during a period in which they could do so. The geographical barrier prevents gene flow between the two populations representing the split phyletic lineages. During the allopatric phase, the two populations will undergo separate phyletic evolution and will start to diverge from one another because each lineage is under the control of a different pattern of formation of genetically based phenotypical variation and of natural selection (Fig. 6). The rate of change in each population will depend upon a number of factors, including the size of the population, whether it was founded by a few individuals, and the nature of the environment and hence selection. Intrinsic isolating mechanisms may evolve during this period. If so, these isolating mechanisms appear fortuitously, both in their nature and time of appearance, as a pleiotrophic consequence of other evolutionary changes. Evolution of intrinsic isolating mechanisms is not under the control of selection favoring the evolution of isolating mechanisms.

During the allopatric phase of speciation, a certain and quite variable amount of divergence occurs between the two lineages. Generally, the amount of evolutionary divergence that occurs during this period is a minor amount of the total divergence between two sympatric and fully evolved species.

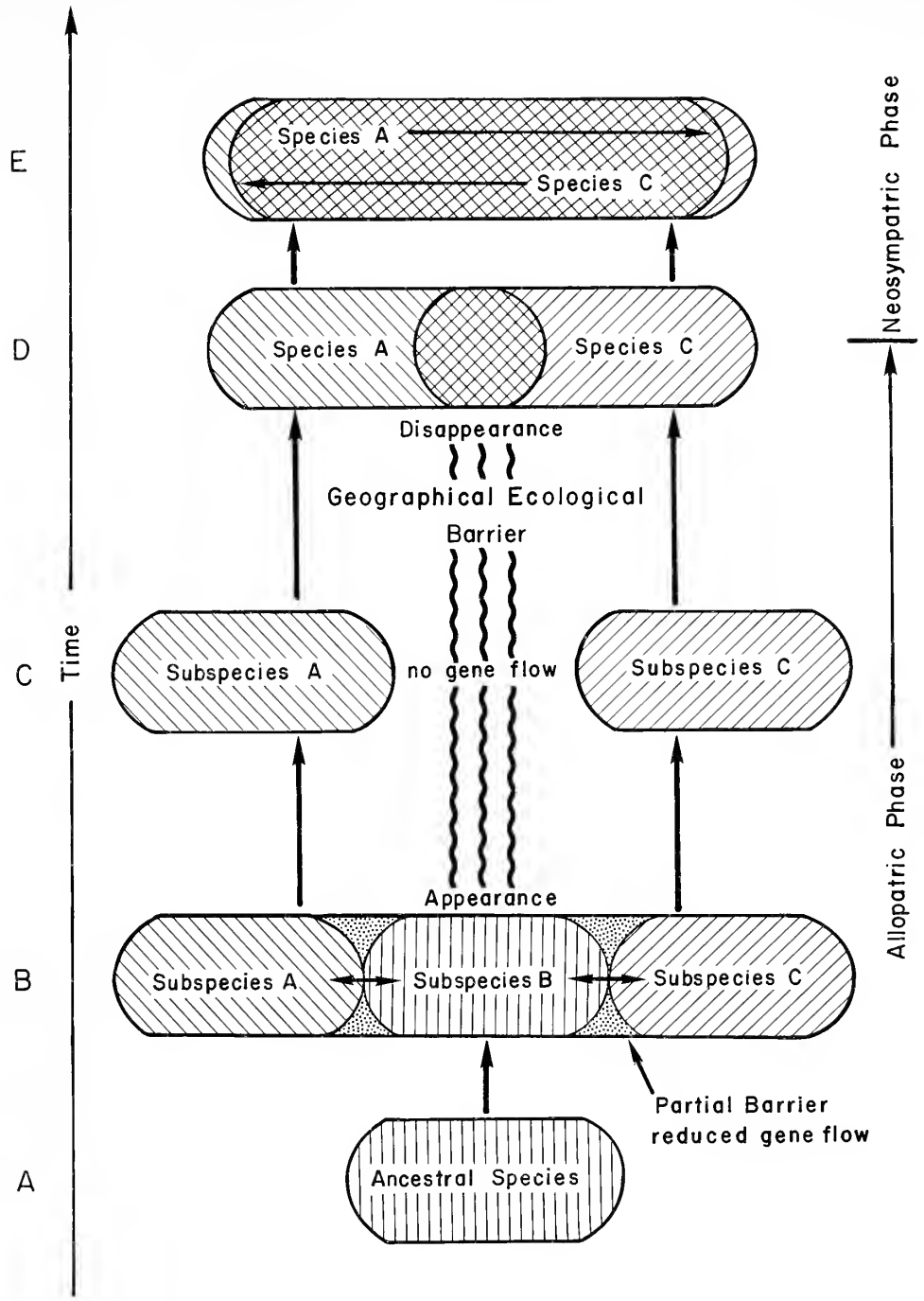

Fig. 5.—Schematic diagram to show the relationships of populations during speciation. The ancestral population (A) may have a period of subspeciation (B) before the appearance of a geographical-ecological barrier that separates two populations (C); this is the start of the allopatric phase of speciation. At this time no gene flow exists between the isolated populations (A and C). After the external barrier disappears, the two species are able to reinvade the geographic range of each other and to coexist if intrinsic isolating mechanisms exist (D); this is the start of the neosympatric phase of speciation. If sufficient ecological differences evolve between the species, geographic overlap can continue until the two species are broadly sympatric (E).

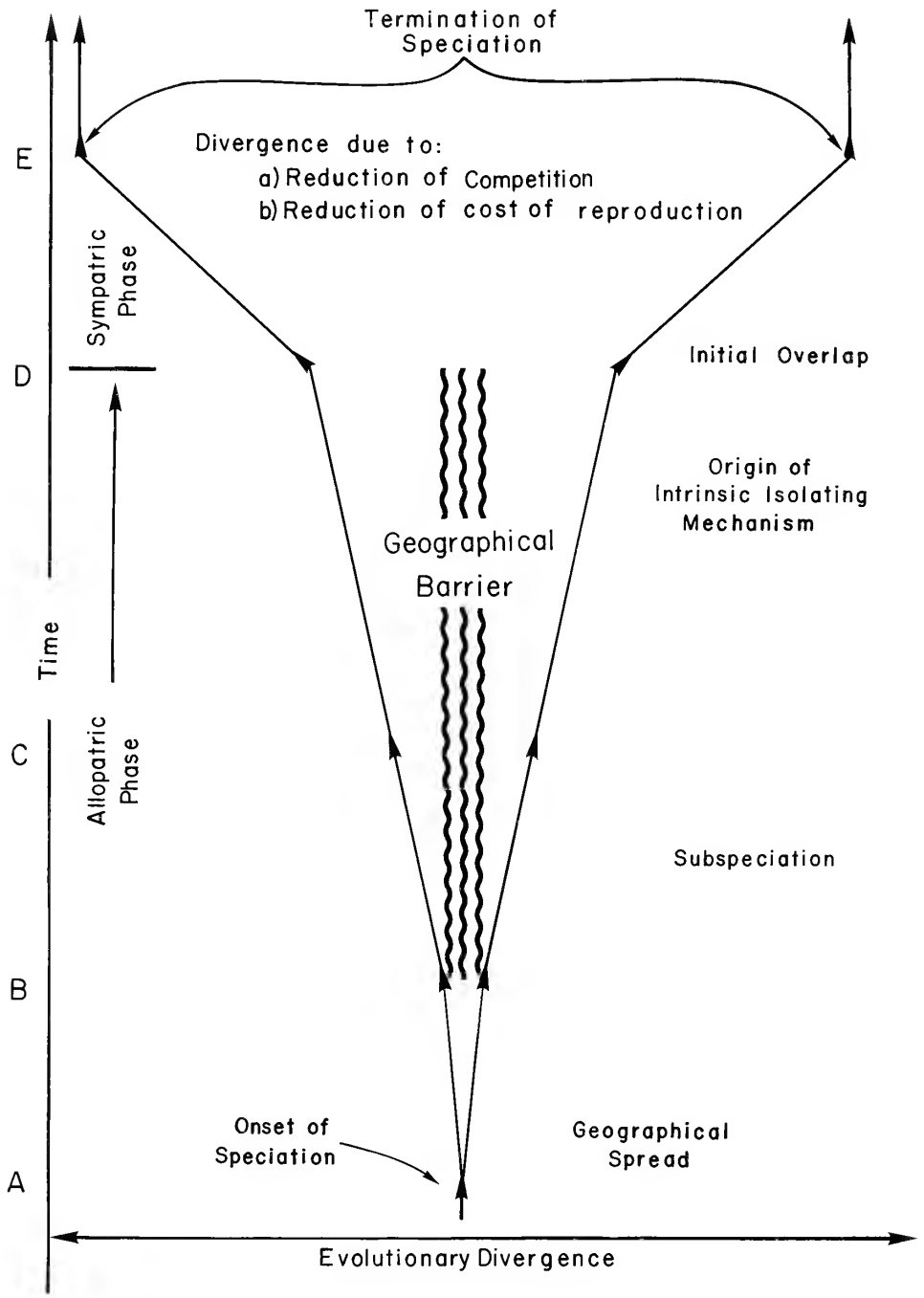

Fig. 6.—Schematic diagram to show divergence of the two phyletic lineages during speciation. The stages indicated by letters along the left edge correspond to those in Fig. 5. Rates of evolutionary change and resulting divergence are low during the period of subspeciation and somewhat higher during the allopatric phase after the appearance of the geographical ecological barrier. The rate of divergence increases sharply after the geographic barrier disappears and the two species become sympatric. Selection forcing the divergence during the sympatric phase arises from exclusionary species interactions between the two species. Speciation comes to an end when this period of rapid divergence terminates.

When the geographical barrier disappears, the two populations can expand their range and become sympatric as species if two conditions are met. The first is that the intrinsic isolating mechanisms evolved during the allopatric phase are 100% effective. This means that there is no gene flow between the two forms even if there is some hybridization. The second is that the two forms are sufficiently different ecologically that they are able to coexist. They need not be completely different or even largely different ecologically. All that is essential is that they differ somewhat so that each can invade the range of the other.

At the time of the breakdown of the external geographic barrier and the establishment of the initial overlap between the two species, the allopatric period ends and the sympatric or neosympatric period begins. This is not the end of the speciation process although most evolutionary biologists end their discussion at this point. For example, Mayr (1963) has almost no discussion of the events during the neosympatric period of speciation, which leaves a major gap between the genetics and ecology of speciation and the role of the species in transspecific evolution in his treatment of species and their evolution.

After the two newly evolved species become sympatric, they are able to interact with one another and thereby exert strong mutual selection on one another. The exclusionary species interaction (Bock, 1972) of the now sympatric species are of two types, namely (a) ecological competition, and (b) reproductive interference. The first type of interaction results from the fact that newly evolved sister species are frequently similar ecologically and still share many parts of their environment (see Lack, 1944, 1947, and elsewhere). The resulting competition will result in mutual selection on both species, which generally results in divergence of the feeding and other structures associated with the ecological competition. The second type of interaction results from the nature of the intrinsic isolating mechanism. When the two species overlap geographically, they must have 100% efficient intrinsic isolating mechanisms or else gene flow will commence between the two forms, which will lead to a breakdown of the distinctiveness of the two species. (I reject the notion that the isolating mechanisms can be less than 100% effective and that selection during the neosympatric period can improve these isolating mechanisms from less than 100% to 100% effective.) Yet intrinsic isolating mechanisms can be 100% effective and vary greatly in their reproductive cost. By reproduction cost, I mean the percentage of a particular breeding period that an individual wastes because it attempts to breed with a member of another species. Such a wastage of time will reduce the number of offspring that individual could have. If one examines the classification of isolating mechanisms presented by Mayr (1963:92), these mechanisms are arranged from high reproductive cost at the bottom of the list (F_1 hybrid zygote fully viable, but sterile) to low reproductive cost at the top (seasonal, habitat, and ethological isolation). Selection will favor isolating mechanisms of lower reproductive cost; hence during the neosympatric period selection arising from species interaction would select for new isolating mechanisms of lower reproductive cost than those existing at the time of initial sympatry. Although this selection is for isolating mechanisms, it is not to improve the efficiency of the isolating mechanism but to reduce reproductive cost. Evolution is from an isolating mechanism that is 100% effective but has high reproductive cost to one that is 100% effective but has low reproductive cost. There has been no improvement in the isolating mechanism, but in reproductive cost. This selection will favor the evolution of courtship displays, more elaborate species-specific recognition characters (color, horns, plumes, song, and others) and temporal separation of breeding seasons.

Features acted upon by the mutual selection from the two species under exclusionary species interaction will diverge rapidly and considerably. These are often features associated with feeding (ecological competition) and with species specific recognition (reproductive cost). They are generally those features which distinguish sympatric species most readily especially in contrast to allopatric, closely related species. Selection arising from these exclusionary interactions are frequently the strongest known natural selection and presumably cause the most rapid evolutionary change. I have postulated (Bock, 1972) that most of the divergence between sister species results from the mutual selection arising from exclusionary species interaction during the neosympatric period of speciation. This is after the two sister species are able to reinvade each other's range after the breakdown of the geographic barrier and after the perfection of the intrinsic isolating mechanism (100% effective). This assertion is in direct variance with that made in some quantum theories (for example, rectilinear model of macro-

evolution) which assumes that the major change occurs prior to the breakdown of the external barrier and the onset of sympatry of the sister species. It can be tested by comparing the amount of divergence observed between allopatric sister species and fully sympatric sister species in closely related taxa (that is, members of the same genus or closely related genera). A rough survey of such species in birds supports the hypothesis that most evolutionary divergence between sister species takes place during the sympatric portion of speciation.

Speciation would be terminated when the exclusionary species interaction and the resultant mutual selection force between the sister species approaches the zero level. Quite possibly one or both of the phyletic lineages of these sister species could have split again and entered a new cycle of speciation before the termination of the original cycle.

Speciation and Macroevolution

Macroevolution is simply a large amount of phyletic evolutionary change. It is a summation of a number of microevolutionary phyletic events, often in a relatively short time. Speciation, per se, has nothing to do with major evolutionary change if one regards speciation as the mechanisms permitting the multiplication of species—evolution of intrinsic isolating mechanisms. Yet the phenomenon of speciation, especially repeated speciations, is an important factor in macroevolution because the selection forces arising from species interactions during the neosympatric phase of speciation is an important driving force in macroevolution (Bock, 1970, 1972). Thus the relationship between speciation and macroevolution or the role of the species in macroevolution is that a major driving force for macroevolutionary evolution comes from the selection forces arising from the exclusionary species interactions between sister species during the neosympatric phase of speciation (as well as between other sympatric species). Another important driving force is coevolutionary interactions for which repeated speciations are less important. Thus, the more speciations (repeated cycles of speciation) and the more species which interact, both exclusionary and coevolutionary, the stronger and the longer in time will be the driving directional selection force required for the phyletic evolution that will result in a major evolutionary change.

Although this assertion may sound like that of punctuated equilibria or rectilinear evolution, it is very different. In the punctuated equilibria model, macroevolution is regarded to be the consequence of a repeated series of speciations. That speciation is *the* essential evolutionary mechanism. Phyletic evolution, which is synonymized with phyletic gradualism, is regarded to be insignificant to the point of being nonexistent. In the punctuated equilibria model, most of the change is assumed to occur during the allopatric period of speciation. In the synthetic model advocated here, most of the change is postulated to occur during the neosympatric period (plus the change resulting from coevolutionary interaction which occurs continuously).

Unity of the Genotype

At this point a digression must be followed to consider the concept of the genotype and of the gene pool of the species as discussed by Mayr (1963:263–296, and elsewhere). Closely associated with this concept is that of genetic revolution (Mayr, 1954, 1959, 1963). The basic concept is the cohesion of the genotype of the individual and of the gene pool of the species. The adaptive value of individual genes is not an absolute intrinsic property of each gene, but is dependent upon "coadaptive" interaction between the gene and the remainder of the genotype. The adaptive value of the gene varies according to the genotype. Cohesion of the gene pool of a population or the interbreeding populations of a species is dependent upon the multiple patterns of gene flow throughout the species (Mayr, 1954, 1959, 1963). It is the phenomenon of gene flow that is the critical factor. It should be noted that many recent evolutionists reject gene flow as an important evolutionary factor, including some workers who accept fully Mayr's concept of genetic revolution.

Mayr argues that elimination of gene flow resulting from isolation of a population will have a great effect on the consequence of selection on that population because the genes affected by selection are acting against a different genetical background and will have a different adaptive value. The effect of the disruptive effect of isolation will be greatest for a new population established by a few founder individuals. It would be next greatest for a small isolate resulting from the appearance of a barrier that cut it off from the remainder of the species. This frequently happens when the range of the species shrinks leaving isolates in pockets of favorable habitat. The effect is smallest for a species with a large range that was divided into two subequal segments. In such examples, divergence would be slowest, but

it would still occur as shown by the many examples of eastern and western species or well-marked subspecies of North American forest birds (for example, *Colaptes, Contopus, Cyanocitta, Dendroica, Oporornis, Icterus, Pheucticus, Passerina*—Mayr and Short, 1970).

Mayr stresses the importance of selection acting on the genetical modification resulting from the disruption of the gene flow. He argues that the consequence of selection acting on genes whose adaptive value has been altered because of the changed genetical background may result in a major change which he termed a genetical revolution. Such alteration in adaptive value of genes would be greatest in populations originating from a few founders. Carson's (1975) model has similar elements in that he includes a population crash that results in a few founder individuals from which the subsequent populations originate. In Mayr's model the founders are considered as individuals that have invaded a new area. Problems exist with the concept of genetic revolution because other workers have deemphasized the importance of selection and have argued that speciation must be associated with a genetical modification without the action of selection. The general notion is that this genetical revolution has occurred completely during the allopatric phase of speciation prior to the reestablishment of sympatry. This implies that evolutionary change as expressed in the phenotype would have occurred prior to the reestablishment of sympatry of the sister species.

The concept of the unity of the genotype and of the gene pool, the concept of variable adaptive value of genes depending upon the genotypic background, and the concept of genetic revolution are all sound and are supported by a considerable mass of observations. However, a number of aspects of genetic revolution and its bearing on macroevolution have not been discussed by Mayr or by other workers who have accepted these ideas in their development of quantum theories.

One of the most important is what are the types of phenotypic features that are usually affected by genetical revolutions. Are these parts of the feeding apparatus, the locomotory system, or external features which may be associated with species-specific recognition characters? To be sure, many examples of distinctive subspecies or allopatric species exist whose evolution is well explained by the concept of genetic revolution. But the features that have been modified are usually not features characteristic of major evolutionary change. What is needed at this point are surveys of the features affected by genetic revolutions, not only of taxa that support this concept.

The second problem is that Mayr quite rightly argues that his concept of genetical revolution places emphasis on the essential and central role of natural selection which is too often ignored. Mayr points out that the genetically based phenotypic variation in the founder population available for selection differs greatly from that in the main population because of the disruption of gene flow. What is not discussed is the source of this selection and the time at which this selection acts. Clearly, in many examples, this selection has acted during the allopatric period of speciation because the taxa being compared are still allopatric. But, one must examine the features modified and consider the possible environmental source of the selection. Disruption of gene flow and evolutionary change during the allopatric period may provide the needed genetically based phenotypic variation for the change during the sympatric phase. Selection may arise largely from species interactions, both exclusionary (from forms other than the sister species) and coevolutionary, during the allopatric period as noted by Mayr (1954) who points out that particularly the biotic environment of an isolate may differ from the rest of the species. Nothing in the concepts of disruption of gene flow and of genetical revolution as advocated by Mayr would conflict with the concept that the major selection forces arise from species interactions and that most of this selection acts during the sympatric phase of speciation after the intrinsic isolating mechanisms are completely effective.

COMPARISON

Most of the testing of models of macroevolutionary explanation is by comparison and interpretation of characteristics of different forms. Moreover, one of the important conceptual steps in the synthetic model is dependent upon proper interpretation of comparison and the extrapolation from one type of comparison to another. This conceptual step is not limited to the synthetic model, but exists in all ex-

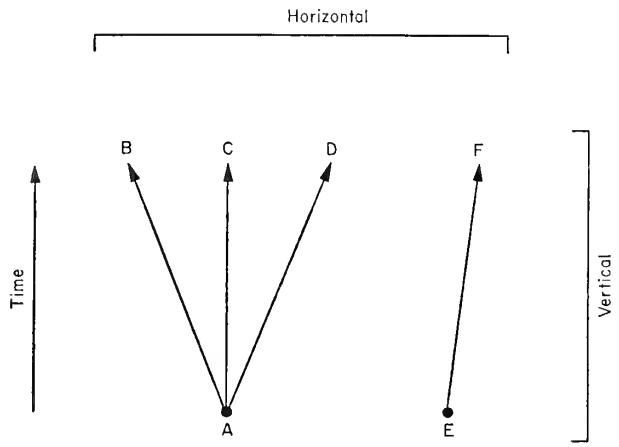

Fig. 7.—Schematic diagram to show the difference between horizontal comparisons and vertical comparisons. Vertical comparisons are those between members of the same phyletic lineage, for example, between A and B, or A and C, or A and D, or E and F, along the time axis. Horizontal comparisons are those between members of different phyletic lineages, for example, between members of lineages A–B, A–C, A–D, and E–F, no matter if the forms being compared are or are not at the same time level (taken from Bock, 1967:Fig. 1).

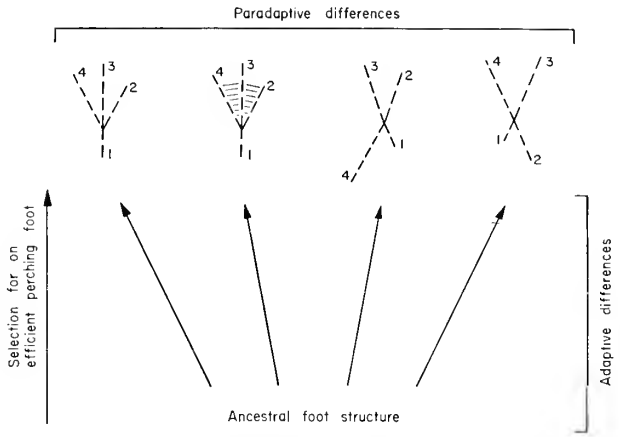

Fig. 8.—Schematic diagram to show the pattern of multiple pathways of evolution of perching feet in birds. Evolution of the four different arrangements of the toes from the ancestral configuration was under the control of the same selection force for a more efficient perching foot. Differences observed in vertical comparisons are adaptive, whereas horizontal differences are paradaptive with respect to the selection force controlling the evolution of these adaptations (taken from Bock, 1967:Fig. 2).

planatory models of macroevolution. Little discussion exists on principles of biological comparison, especially on the theoretical level; I will refer mainly to comments in my earlier papers (Bock, 1967, 1969, 1977).

Not all comparisons in biology are the same and the interpretations reached on the basis of a particular comparison cannot be extrapolated simply to all others. Not all comparisons are between members of different species, excluding the case of comparison between conspecific individuals. Although comparisons can be made for many diverse purposes and with many goals in mind, they can be divided into two major categories—horizontal and vertical (Fig. 7). This dichotomy does not exhaust the possible classifications of types of comparison; it is one that is of particular relevance to the development of macroevolutionary theories.

Horizontal comparisons are those across phyletic lineages—between members of different phyletic lineages and hence, between members of different species. They can be between species at the same point in time or at different points in time so long as they are between different phyletic lineages. Comparisons between conspecific individuals at the same time period would be horizontal.

Vertical comparisons are those within a phyletic lineage—between members of the same phyletic lineage at different points in time. These are comparisons between ancestral and descendent cross-sections of the same phyletic lineage and hence, are not between different species.

It is not possible to extrapolate simply from horizontal comparisons to vertical comparisons. Horizontal similarities are not the same as vertical similarities and horizontal differences are not equal to vertical differences. The origins of these two types of similarities and of these two types of differences may be quite different and hence will require diverse explanations. For example, differences observed in a horizontal classification may have nothing to do with adaptation and are designated as paradaptive (Bock, 1967; and see below) yet the vertical difference in each phyletic lineage may be adaptive. The conclusion offered earlier that the evolution of features is not adaptive if their horizontal differences are not adaptive is simply in error.

The difficulties in extrapolating interpretations from a horizontal to a vertical comparison and vice versa is the consequence of the simultaneous action of two evolutionary mechanisms in phyletic evolution. These are, of course, the production of genetically based phenotypic variation, which is chance-based, and the action of natural selection, which is a design mechanism. These mechanisms act in the phyletic evolution of every lineage. Hence, given

the existence of a particular selection force acting on a species, it is not possible to predict the future course of phyletic evolution and the resulting adaptation, if any, because it is not possible to predict the outcome of the chance-based genetical mechanisms.

The concept of multiple pathways of evolution (or adaption) stems directly from the action of these two evolutionary mechanisms and their consequences as interpreted in horizontal and vertical comparisons (Bock, 1959; Bock and deW. Miller, 1959). Different adaptive answers (Fig. 8) may appear and evolve in several lineages under the control of the same selection force as shown by the evolution of different perching foot types in birds (Bock and deW. Miller, 1959). Associated with this idea is the concept of paradaptation (Bock, 1967). Paradaptive differences are ones between different multiple adaptive answers and are the consequence of the chance-based genetical mechanisms (Fig. 8).

The conceptual step, which will be necessary in the development of the synthetic explanation of macroevolution, is to formulate a (pseudo)phylogeny of steps leading to a major change using horizontal comparisons of closely related forms (for example, congeneric species) and to interpret the differences as adaptive steps. Then this horizontal sequence must be transposed to a vertical sequence which is the key conceptual step. This is one that is difficult to support by empirical observations as one requires known phylogenies (that is, those of domesticated animals and plants). Moreover, it is a conceptual step that falls in the realm of a link or bridge between theories. A worker is free to reject or accept it. However, if rejected, then much of the basis for developing and testing explanatory models, both quantum and synthetic, of macroevolutionary change is eliminated.

In developing the synthetic model and in discussing supporting examples, I will give particular attention to this conceptual jump between horizontal and vertical comparisons.

ADAPTATION

The key to all explanatory models of macroevolution is the concept of biological adaptation. What is an adaptation and how are individual adaptations ascertained? How do adaptive features evolve? What is meant by adaptive evolution of features and by adaptive evolution of a population under the overall notion of adaptive phyletic evolution? Is the adaptive evolution involved in the origin of a new major feature or of a new major taxon (adaptive radiation) different qualitatively from adaptive evolution on the microlevel?

The concept of biological adaptation has always been used to designate features of an organism, which operate well in the particular environment of that organism. Hence wings of most birds are adaptations for aerial flight, whereas the wings of penguins are adaptations for underwater flight. The concept of adaptation long predates ideas of biological evolution and indeed the attempt to provide a scientific explanation for adaptation led to the formulation by Darwin of the concept of organic evolution by natural selection. An adaptation is a feature of the organism. Individual features or complexes of features are adapted to particular components of the organism's environment. It is almost of no interest to inquire whether a whole organism is adapted to its environment—it must be, otherwise it would be dead. The questions of interest are what is the adaptive significance of individual features and how each adapted feature contributes to the survival or to the fitness of the organism.

An adaptation is, thus, a feature of the organism, which interacts operationally with some factor of its environment so that the individual survives and reproduces. Stress is placed on the organism surviving as an individual because it cannot otherwise reproduce. However, adaptations cannot be judged only with respect to survival of the individual; it must survive and reproduce. Adaptations must be judged with respect to a particular environment and always on a probability basis with respect to present (and possibly past) environmental conditions, but never against future factors. The environment is the external environment, be it biotic or physical. Hence the concept of adaptation is defined and individual adaptations are judged with respect to selection forces arising from the external environment and acting on the organism. Adaptation does not designate operational relationships between parts of the organism or an operational relationship of a feature to the "internal environment." Notions such as "the internal environment," or "the genetical environment," or "internal selection" are misleading to the extreme and should be abandoned. Mus-

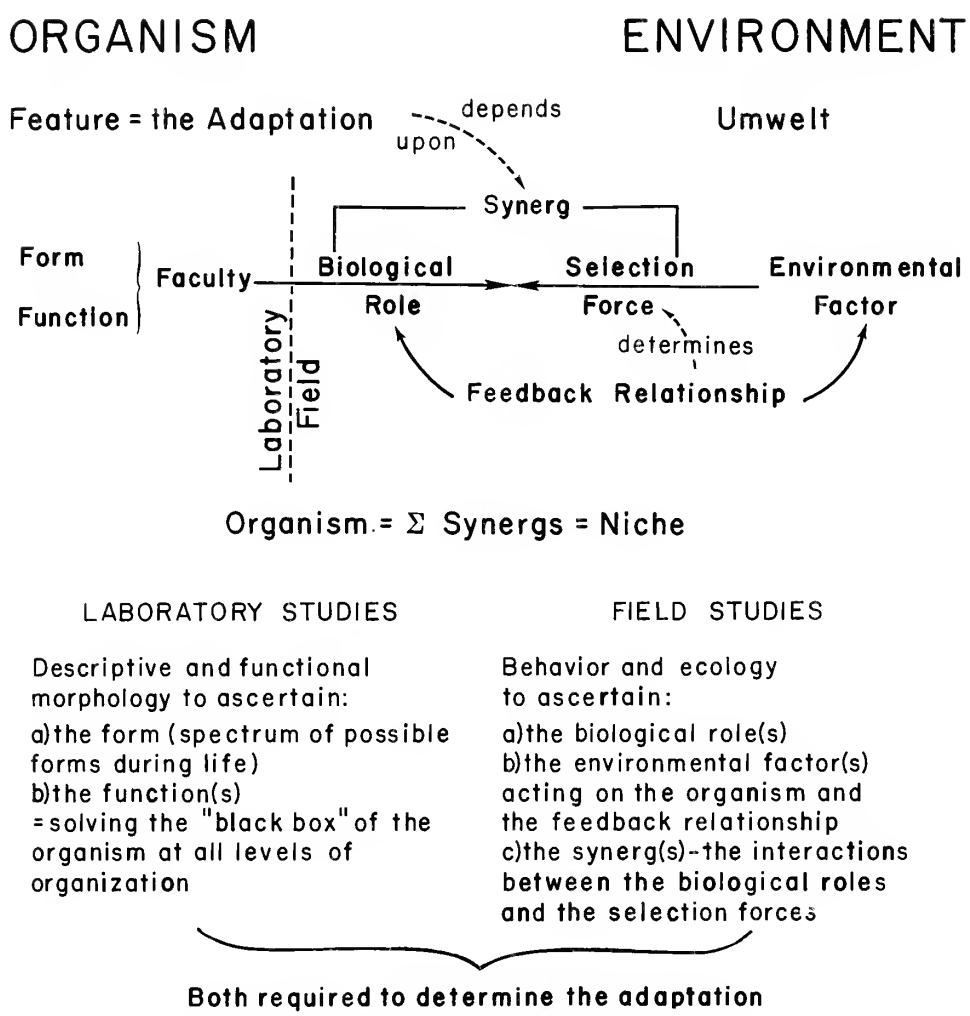

Fig. 9.—Simplified scheme illustrating the laboratory and field studies required for the direct analytic determination of an adaptation. The adaptation is the feature and is reflected in the details of its form-function complex or faculty. The existence of an adaptation is dependent on the existence of a synergical interaction between a biological role of the feature and a selection force. No synerg means no adaptation. A feature may represent a single adaptation or a number of adaptations depending on the number of synergical relationships between the feature and the umwelt of the organism. In the latter case, the form of the feature and hence its functions (that is, the properties of the adaptation) may represent a compromise between conflicting selection forces. Additional investigation is needed to measure the degree or the goodness of the adaptation (taken from Bock, 1978:Fig. 1).

cles are not adapted to bones, but these anatomical systems are integrated ones that are adapted to selective forces arising from the external environment. A clear distinction must be made between the concept of mutual adjustment of features, which is critical to the adaptiveness of features, and the vague notions of adaptation to internal or genetical environments.

The concept of adaptation is not the same as survival of the species (especially over a longer period of time) or the same as fitness. These are different evolutionary concepts; the synonymy of adaptation to either one or both of these other ideas has lead to great confusion in the elucidation of these evolutionary concepts. Rather the concept of adaptation is related to these other concepts in that the adaptiveness of features contributes to the fitness of individuals and to the survival of the species. What is needed are more accurate measures of adaptation so that the contribution of individual adaptations to fitness or to survival can be judged more precisely.

Adaptations, being features, are parts of the phenotype of the individual. Genes, per se, are not ad-

aptations. Genes can be said to be adaptive or to have adaptive value if they contribute to the ontogenetic development of an adaptive feature.

Each adaptation must be determined individually by direct analysis; the comparative approach is invalid for determining adaptations (Bock, 1977). Comparisons can be made only after the individual adaptations had been established. Recognition of adaptations depends upon careful separation and delimitation of properties of features and of the relationships between the environment and the organism. I will rely upon the set of ideas advocated earlier by von Wahlert and myself under the heading of "Adaptation and the form-function complex" (Bock and von Wahlert, 1965). The relationships between these concepts are illustrated in Fig. 9.

Feature

The adaptation is a part, trait or feature of the organism; the feature can be defined (Bock and von Wahlert, 1965:271) as: *a feature is any part or attribute of an organism if it stands as the subject in a sentence descriptive of that organism.* Thus a feature can be any part of the organism, its delimitation depending only upon the interests of the investigator. A feature can be any attribute of the organism, be it a behavioral, physiological, or biochemical trait; it need not automatically be an anatomical structure. Moreover features can be taken from any level of organization within the organism, for example, a muscle cell, or a muscle, or a muscle-bone system, and so forth; the consequences of these levels of organization must always be recognized.

Form

The form of a feature is those properties of material composition, configuration, and appearance that are generally grouped together under the heading of its morphology. It may be defined formally (Bock and von Wahlert, p. 272) as: *in any sentence describing a feature of an organism, its form would be the class of predicates of material composition, and the arrangement, shape, configuration, and appearance of these materials at all necessary levels of organization; these predicates need not make any special reference to the normal environment of the organism.* It must be emphasized that a particular feature in an individual usually does not have a single form as commonly believed by morphologists. Most features modify over the life of the individual; some change irreversibly, some reversibly. Teeth wear and feathers become frayed. Or the shape of flight feathers alter according to the air pressure impinging upon them. The feature may modify slowly under the action of particular stimuli (the phenomenon of physiological adaptation, Bock and von Wahlert, 1965:284–285, which is synonymous with somatic change, Bateson, 1963), such as the change in bone structure under the influence of mechanical stresses. Or the feature may change its form quickly and reversibly as they are used. Muscles may undergo radical changes in their form during each contraction cycle, the lens of the vertebrate eye may undergo change in its curvature, the size of the stomach modifies during the course of a large meal; these possible modifications in form must always be noted. Thus, one cannot assume that a feature has a single form as shown by the specimen lying on the dissection table, but that it possess a spectrum of form, which may change by wear or other environmental forces, or slowly by physiological adaptation, or rapidly by physiological action, or any combination of these mechanisms.

Function

The concept of function is a most controversial one and the following definition is not accepted by many biologists. Most problems arise because the term function is used for at least two quite separate and distinct concepts—that of function (as used herein) and that of biological role. It is not possible to discuss the concept of biological adaptations meaningfully unless these two concepts are carefully distinguished regardless of the names used to designate them. Unfortunately most workers continue to confuse and interchange these concepts by using function as a single broad term covering both. It is essential to separate the concepts of function and of biological role, and to use the terms consistently; I advocate, but do not insist on the concepts and terms as defined below. However, I do insist on a separate and consistent usage whatever terms are used.

Basically the function of a feature is its action or how it works. It is that aspect of a feature studied by physiologists and functional morphologists. It may be defined formally (Bock and von Wahlert, 1965:274) as: *in any sentence describing a feature of an organism, its functions would be that class of predicates which include all physical and chemical properties arising from its form (that is, material composition and arrangement thereof), including all properties arising from increased levels of or-*

ganization; these predicates need not make any special reference to the normal environment of the organism. The properties of function are, in this definition, absolutely bound to the properties of form via chemical and physical laws. A feature will have numerous functions, which may include many never used by that organism. Functions may be classified into utilized and nonutilized ones depending upon whether they are associated with biological roles of that feature.

Although this definition of function may appear awkward to many evolutionary biologists, it has many advantages in addition to being nonambiguous. It is close to the idea of function used by many or most physiologists, biochemists, and other "functional biologists." It frees the concept of function from all associations with teleology or teleonomy (Bock and von Wahlert, 1965:274). It forces the biologist to consider all possible functions of a feature, often revealing several unsuspected ones. And it provides a clearer understanding of some evolutionary concepts such as preadaptation (that is, the source of the "new functions" at this period of "functional change") and such as the correlation between change in form and in function during evolution (that is, they must change hand in hand—it is the biological role via the behavior that generally changes before the form of the feature).

It must be emphasized that care must be exercised in the application of a number of evolutionary statements if the above definition of function is accepted. Most of the statements in the morphological and the evolutionary literature use "function" in a broader or vaguer sense, and hence the statements may no longer be correct with this narrower concept of function. Each of these evolutionary statements or principles must be checked to ascertain its validity with this more restrictive definition of function.

Faculty

The two classes of properties of a feature are its forms and its functions. It is valuable to have a term by which they can be discussed together—the form-function complex or the faculty—because it is this form-function complex of the feature, which determines its adaptive significance, not the form alone or the function alone. The form-function complex or faculty of the feature may be defined (Bock and von Wahlert, 1965:276) as: *a faculty is defined as the combination of the form and one of the functions of a feature.* An expanded definition can be formed by combining the above definitions of form and of function.

The feature will have as many faculties as combinations of the form and the several functions. If the form varies during the life of the organism, with the correlated change in functions, then the faculties will also vary. A feature may have faculties that are not used by the organism during its normal life; utilized faculties are those that have a biological role and interact with a selection force. The faculty is the unit acted upon by natural selection and is the aspect of the feature that is adapted to the environment. Because a feature usually has a number of faculties, which interact with different selection forces, the final adaptation—the final form and functions of the feature—is frequently a compromise.

Biological Role

The biological role is how the organism uses the faculty and hence the feature in the course of its life history; the use may be active or passive. The biological role may be defined (Bock and von Wahlert, 1965:278) as: *in any sentence describing a feature of an organism, its biological roles would be that class of predicates which include all actions or uses of the faculties (the form-function complexes) of the feature by the organism in the course of its life history; these predicates must make explicative reference to the normal environment of the organism.* Essential to the description of a biological role is observation of the organism living freely in its natural environment. A biological role cannot be determined by observations made in the laboratory or under other artificial conditions. Studies by functional morphologists, no matter how detailed or how carefully done, cannot elucidate biological roles so long as this work is done in the laboratory.

Functions can be ascertained from the form of a feature if one knows the causal relationships between the form and the function as dictated by the chemical and physical laws. Hence it is possible to ascertain the function of features by a comparison of the forms, that is, the function of a feature can be obtained from a knowledge of its form. The causal relationships between the faculty (or the form) of a feature and its biological roles is much looser so that it is usually not possible to ascertain the biological role of a feature by comparison or by a knowledge of the form. Hence determination of biological roles is especially difficult in fossils or in

Recent organisms whose life histories are not known.

Statements that the function of a feature cannot be ascertained from a knowledge of its form refer to the biological role, not function, according to the above definitions. Statements about "functionless features" refer to those features that do not possess any biological roles. It is possible, at least theoretically, for a feature to lack biological roles as in the case of a feature, which evolved as a pleiotrophic consequence of some other feature or in the case of a vestigial feature. However, it is not possible to have functionless features because the existence of a form of a feature automatically implies the existence of some functions under the definitions advocated herein.

The study of the biological role(s) of a feature is a definite behavioral-ecological analysis. The leg of a mammal may have locomotion among its several functions, with parameters of speed, rates of fatigue, and so forth, but its biological roles may vary from catching prey or escaping from a predator to migration or courtship display. Large mucus secreting salivary glands are found in a number of birds with a function of the mucus being that of a glue—to stick objects together. However, the biological roles vary from feeding by trapping insects on the tongue in woodpeckers, to nest construction in swifts and some swallows, and to food storage during winter months in the Gray Jays (*Perisoreus*).

Environment

The environment of an organism includes all physical factors and biotic factors impinging on it, the latter being various types of species interactions (Bock, 1972), which appear to provide the largest and the most severe part of the total selection on the organism (see also Darwin, 1859:487–488). All of the environmental factors, which could possibly be utilized by the organism, or, which could possibly act on that organism, comprise the umgebung; it is the sum of the environmental factors generally called the habitat. The umgebung may be recognized without the actual presence of the organism although some knowledge of the features and the life history of the organism is needed to judge the suitability of the habitat.

Those factors of the environment, which are actually being used by the organism, or, which are actually acting on it, comprise the umwelt or the species-specific habitat. The umwelt can be ascertained only in the presence of the organism living naturally in its environment. The umwelt is a subgroup of the environmental factors comprising the umgebung. The umwelt, being the species-specific habitat, changes as the species evolves (the causal relationships are reversed, however) and disappears when the species becomes extinct. Environmental factors are not, however, restricted to the umwelt of a single species. A water hole on the African veld may be used by a number of species. All tetrapods and many other organisms use atmospheric oxygen which is common to the umwelt of all these species.

The factors of the umwelt are designated as the niche by many biologists; I prefer to use this term for the total interaction between the organism and its umwelt (see below).

The definition of natural selection is difficult because a complete definition should include the mechanism by which the environment acts and the result of this environmental action (Bock and von Wahlert, 1965:291). Geneticists have stressed the latter in defining selection as the non-random differential reproduction of genotypes (a result definition). Without gainsaying the importance of this aspect in the definition of selection, I wish to concentrate on the mechanism because I am concerned with the causal interrelationships between the environment and the organism. Thus, the mechanism of natural selection is an interaction between the umwelt of the organism and the phenotype of that organism. The environment places demands on the organism with which it must cope if the organism is to continue to survive as an individual. An individual selection force is the action of a single environmental factor of the umwelt on the phenotype of the individual (that is, on a feature) through a particular biological role of a faculty of that feature. A selection force can act simultaneously on biological roles of several features. The nature of a selection force is not determined automatically by the umwelt factor, but depends upon the umwelt factor and how the organism reacts to that factor. A feedback relationship exists between the factor of the umwelt and the biological role of the faculty (von Wahlert, 1965; Bock and von Wahlert, 1965:282) which determines the final nature of the selection force. Because of the active contribution of the organism through a particular biological role and the factor of the umwelt in creating the exact selection force, this link is called a synerg to indicate the actual working together of the organism and the environment (see von Wahlert, 1973, and elsewhere).

The *synerg* may be defined (Bock and von Wahlert, 1965:281) as *the link between the organism and its umwelt formed by one selection force of an environmental factor of the umwelt and one biological role of a faculty*. Although this definition uses the selection force as the environmental side of this link, it must be remembered that the feedback mechanism of this interaction extends from the organism beyond the selection force to the environmental factor itself. Most selection forces and most biological roles participate in more than one interaction, and hence each may take part in the formation of a number of different synergs of the organism.

The synergs in which an organism partakes in its interaction with the umwelt must be maintained if the organism is to survive as an individual. The sum of all the synergs can be defined as the niche (Bock and von Wahlert, 1965:282). Thus the *niche* may be defined as *the total relationship between the whole organism and its complete umwelt*. The niche is the relationships between the organism and the umwelt—not the total environmental factors of the umwelt—and cannot be recognized without the presence of the organism. No organism means no niche. The niche changes as the species evolves and disappears if the species becomes extinct. Empty niches do not exist. The logical and useful extension of this concept is that the niche is the species. After all, a species is not just the object we can see and describe, but it is the total complex of interactions of this object with its umwelt. The niche, being the total of synergs, describes the total selection of the umwelt on the organism.

Changes in a selection force (or in the total selection) are associated with changes in the synerg (or the niche) and may be associated with modification in the environmental factors of the umwelt, but they need not be. It is possible to have modifications in synergs and hence the niche as the result of the organism reacting differently to the same factor of the umwelt and thus modifying the resulting selection (see von Wahlert, 1961, 1965, 1973; Bock and von Wahlert, 1965:282). Hence adaptations may evolve in response to new selection forces acting on the organisms, but these new selection forces do not have to be coupled with new or different environmental factors of the umwelt.

Adaptation

The concept of biological adaptation has always designated the phenomenon of the organism being well suited to (that is, able to cope with) the demands of its environment. Adaptation has been used in several senses (Bock and von Wahlert, 1965:282–285)—universal adaptation, physiological (= functional or somatic) adaptations, and evolutionary adaptation; I will be concerned only with the last. Evolutionary adaptation connotes both a state of being and a process, but the distinction between the two is usually clear. As a state of being, it makes sense only to speak of individual features of an organism as adaptations; to designate a whole organism or a population as an adaptation is without useful meaning.

Adaptation, both the state of being and the process, must always be stated with respect to a particular environmental factor of the umwelt. Moreover, the feature is not adapted to the environmental factor but to the selection force resulting from the feedback interaction between the organism and umwelt factor. Hence adaptation must be defined and must be judged with respect to definitely delimited selection forces. (Adaptations are often judged with respect to definitely delimited umwelt factors which is not quite correct, but is sufficiently accurate for most studies.)

An adaptation is a feature of an organism that has at least one biological role interacting with a selection force—it forms a synerg. *An adaptation, the state of being,* can be defined as *a feature having properties of form and function which permits the organism to maintain successfully the synerg between a biological role of that feature and a previously stated selection force*. Note that the selection force must be given prior to the statement of the adaptation. By successful, I mean that the individual organism survives as an individual and reproduces to leave progeny in the next generation. Adaptations must be judged on a probability basis and against present (and possibly past) environmental conditions, never against future factors. Success is a relative term and some measure of success or of the relative degree of goodness of the adaptation is needed. Bock and von Wahlert (1965:286–287) suggested that the degree of adaptation could be judged by a measure of the amount of energy required by the organism to maintain the synerg—a sort of efficiency judgment. This is not an optimizing concept of adaptation similar to that advocated by many evolutionary biologists and ecologists. Hence *the degree of adaptation, the state of being,* is defined as *the amount of energy required by the organism to maintain successfully*

the synerg of the stated adaptation with a lower energy requirement indicating a better degree of adaptation. Thus the degree of adaptation is inversely related to the energy required to maintain the synerg. It must be noted that the degree of adaptation is judged for a stated adaptation and that the adaptations are determined relative to a stated selection force. Energy requirements must always be given in terms of calories—gm-wt^{-1} to compensate for different body sizes especially in comparative studies. The adaptiveness of different individuals, either of the same or of different species, can be compared but must be judged against the same selection force. This definition of the degree of adaptation is must useful for comparisons between closely related species and decreases in its usefulness as the degree of evolutionary relationship increases.

Energy utilization can also be used to indicate adaptive change as a feature requiring less energy would be better adapted. Thus *adaptation, the process,* is defined as *any evolutionary change in the form-function complex which reduces the amount of energy required by the organism to maintain successfully the synerg of the stated adaptation.*

The use of energy requirement to maintain the synerg as the measurement of the degree of adaptation is at least theoretically possible for any adaptation, and could be done at present for most structures of the skeletomuscular system, for example. The value of an independent measure of the degree of adaptation is that the adaptation can be measured independently of other evolutionary concepts such as fitness of the individual or survival of the species. If adaptation can be measured independently, then the contribution of the adaptiveness of a feature to the fitness of an individual or to the survival of the species can be ascertained. Questions, such as if an individual possesses a better adapted feature, will it have a greater fitness?, and how close is the correlation between the degree of adaptation and fitness?, can be answered only with an independent measure of the degree of adaptation.

Certain problems exist in the use of energy requirements to measure the degree of adaptation because this measure does not work in all cases. It is possible to provide examples in the skeletomuscular system in which one particular form-function complex is better adapted than another even though it would require more energy. Or to show examples of adaptive changes in a form-function complex that requires more energy. A simple example would be the length of muscle fibers within a muscle—longer fibers are needed if the muscle must shorten over a greater distance. Hence, if the selection force demands that the structure, for example, the tongue of a woodpecker, be moved over a longer distance, then a longer fibered muscle would be better adapted. However, a longer fibered muscle would require more energy when it contracts and shortens. In some cases, especially those adaptations associated with feeding, these difficulties could be overcome by regarding the degree of adaptation in terms of the energy acquired by the organism compared to the energy required; indeed such a measure is used by some ecologists. However, such a ratio would not work for all features and additional analysis is needed to develop a more comprehensive measure of the degree of adaptation. It does seem justified, however, to use the inverse relationship between energy requirement and the degree of adaptation in the large number of cases where it appears applicable. The ratio of energy obtained to energy cost can be used for judging the degree of adaptation associated with feeding. However in other cases some objective system of measure is needed to judge the benefit to the organism to be used in ratios of benefit obtained to energy cost for ascertaining the degree of adaptation.

Determination of Adaptations

Analysis of the form-function complex and its synergistic relationship to the environment makes it clear that a wide range of biological studies is needed for the determination of particular adaptations (Bock, 1978). None of these studies can be omitted and none can be done superficially. Adaptations can be ascertained only by direct analysis of the particular feature and its environment. Comparative studies are not valid for determining adaptations (Bock, 1977) as such methods depend upon causal laws explaining the correlations between environmental factors and adaptations. Such laws do not exist because the particulars of specific adaptations depend in part on their past history, and features with a partial historical, and hence chance-based, explanation cannot be explained by causal laws. Most morphological studies present a detailed anatomy and, more frequently in recent years, a good functional analysis of features but fail to include any observations of biological roles or of ecological factors. On the other hand, many ecological-physiological studies present thor-

ough investigations of ecological and physiological factors and show what the adaptation must do, but stop short of identifying a particular feature as the adaptation and demonstrating its properties of form and function.

A wide range of laboratory and field studies are needed to demonstrate a particular adaptation as indicated in Fig. 9. Few complete studies of adaptations are available in spite of the great increase in functional morphological studies and of ecological investigations over the past quarter-century. The needed work can scarcely be carried out by a single investigator because of the extremely broad training required to undertake all facets of adaptational analysis. The most feasible approach appears to be by informal, flexible small teams which divide the work between laboratory analysis of descriptive and functional morphology and field investigations of biological roles and ecological factors (Bock, 1978). Information from both partners is needed to ascertain the nature of the synerg and of the adaptation. The project should be integrated from the onset with continuous feedback between the laboratory and the field work to permit follow-up on clues provided by different facets of the study. Details on problems associated with the analysis of adaptations can be found in Bock and von Wahlert (1965), Bock (1974, 1978), and in papers cited therein.

A special problem exists in studies of adaptation and of adaptive evolution in fossil organisms although the same exists for recent organisms which have not or cannot easily be studied in the field. Most evolutionary biologists believe that analysis of fossils provides the best basis to test explanatory models of macroevolution and the best examples of adaptive evolutionary change because of the time element available in the fossil record. Although it is clearly possible to test many aspects of organic evolution with observations from the fossil record, I doubt that it is possible to test concepts of adaptive evolutionary change with observations from the fossil record. The difficulty lies in ascertaining the adaptiveness of features observed in fossils which must be done prior to any comparisons made to test ideas of adaptive change. Determination of adaptations cannot be made with comparative methods and the necessary details of the environments of fossil organisms cannot be observed. If concepts of adaptive evolutionary modifications cannot be tested against observations from the fossil record, then it is doubtful that explanatory models of macroevolutionary change can be tested against fossil evidence. If this is true, it has serious consequences for the necessity of testing all facets of evolutionary theory against empirical observations because a major segment of evolutionary theory may be difficult to test.

Adaptation and Natural Selection

The concept of adaptation is intimately connected with the conception of natural selection. Adaptive changes can only occur under the action of selection. Hence an adaptive evolutionary change of a feature is one under the control of natural selection and an adaptive evolutionary change of a population would be one in which a feature is changing adaptively, that is, under the control of selection. It must be emphasized that not all evolutionary changes are adaptive nor must all adaptive changes be genetical changes. Many features can evolve nonadaptively, and even change considerably, as pleiotrophic byproducts of other adaptive evolutionary changes. Not all evolutionary changes in features must be adaptive. Intrinsic isolating mechanisms constitute a whole class of important evolutionary features whose evolution is nonadaptive (actually paradaptive). Almost all phyletic evolutionary modifications are adaptive, being under the control of selection. The only possible exception might be changes resulting from genetic drift (for example, associated with a few founder individuals), but these changes are almost always minor in terms of amount of phenotypic modifications and would soon be once again under the control of selection. Yet there is no reason to postulate that the occurrence of genetic drift means that selection is not operating because these two mechanisms are independent of one another. Genetic drift is simply one of the mechanisms whereby the genetically based phenotypic variation of a population is produced and made available for selection. It is highly doubtful that a nonadaptive change resulting from genetic drift would be freed of selection for more than a few generations if that long. Mechanisms of non-Darwinian evolution have not been supported by empirical observations.

Natural selection has been defined in many ways. The standard definition used in population genetics is *nonrandom differential reproduction of genes*. This is a *result* definition which describes the consequences of the action of certain causal mechanisms given particular initial conditions. Yet many evolutionary biologists use this definition *as if it is*

a causal selective mechanism. They include as selection (a causal mechanism) any phenomena that may result in nonrandom differential reproduction of genes. Care must be taken to distinguish such phenomena, for example, selection of genes because of an altered genetical environment, from causal selective mechanisms which are restricted to synergical relationships between the external environment and the organism. Some uses of selection in quantum explanations of macroevolution, for example, species selection and internal selection, appear to be the result definition applied as a causal mechanism; these must be checked carefully. Any uses of natural selection other than as a causal mechanism arising from a synergical relationship between the external environment and the organism should be rejected. I will use selection only in this sense in developing an explanatory model of macroevolution.

Paradaptation

The concept of paradaptation was introduced to describe those aspects of a feature or those differences between features which are not associated with natural selection (Bock, 1967). Adaptive differences and aspects of features are associated with selection. However, evolutionary change is the result of the simultaneous action of two evolutionary mechanisms—the production of genetically based phenotypic variation and the action of natural selection. And not all differences and aspects of features can be described as adaptive. Those, which are under the control of genetical mechanisms, can be termed paradaptive because they are "besides adaptation," not being under the control of selection. The concept of paradaptation calls attention to the role of genetical mechanisms in evolution as the concept of adaptation calls attention to the role of environmental mechanisms. Because evolution is the consequence of the dual action of both mechanisms, features are simultaneously paradaptive and adaptive. They are adapted only if favored by selection (Fig. 8).

Preadaptation

A long standing dilemma in the adaptive explanation of the origin and further specialization of new features is how features could evolve under the control of natural selection when they first appeared and were too rudimentary to have any selective advantage. The argument has been offered that features could have a selective advantage when still very poorly developed and when their function and biological roles are not obvious. And, after all, extremely small selective advantages are amenable to selection and can be the basis of extensive change. But such arguments have never been convincing. The solution to this dilemma appears to lie in the concept of preadaptation (see Bock, 1959; Bock and von Wahlert, 1965:292).

Preadaptation refers to features that have acquired the necessary properties to be adaptive to a particular environmental demand before that demand and associated selection force has acted on the feature (Fig. 10). The concept of preadaptation has been associated with the notion of a change in functions ever since its proposal by Dohrn in 1875 (see Bock, 1959:200–201), yet it is clear that this use of function is in the meaning of biological role (Bock and von Wahlert, 1965:292). The definition of preadaptation advocated by Bock and von Wahlert (1965:292) is: *a feature is said to be preadapted for a new adaptation when its present form and functions permit the appearance of a new biological role and establishment of a new synergical relationship with the environment whenever the selection force for the new adaptation should arise.*

Evolution of a feature to the preadapted state is under the control of selection forces associated with the existing biological roles of the feature. Or it may be as a pleiotrophic byproduct of some other adaptive change. There is no reason to assume that evolution of a feature to a preadapted stage needs to be nonadaptive. Needless to say, the acquisition of any particular preadapted form by a structure is strictly fortuitous. Whenever a feature has reached the necessary preadapted stage, it is available to interact with the new selection force, establish a synerg, and become a new adaptation. The selection force may have been in existence and acting on the population before the preadapted stage is reached, or it may come into being after the structure reached the preadapted level. Evolutionary change from the preadapted stage to the adapted stage does not involve a change in form or functions, only the acquiring of a new biological role by the feature; hence, it is a nonhereditary evolutionary change. Preadaptation is frequently associated with a non-utilized function of the feature. The new adaptation may be a relatively poor one and usually requires considerable postadaptive change to develop a more perfect correlation between the biological role and the selection force—a synerg requiring less energy.

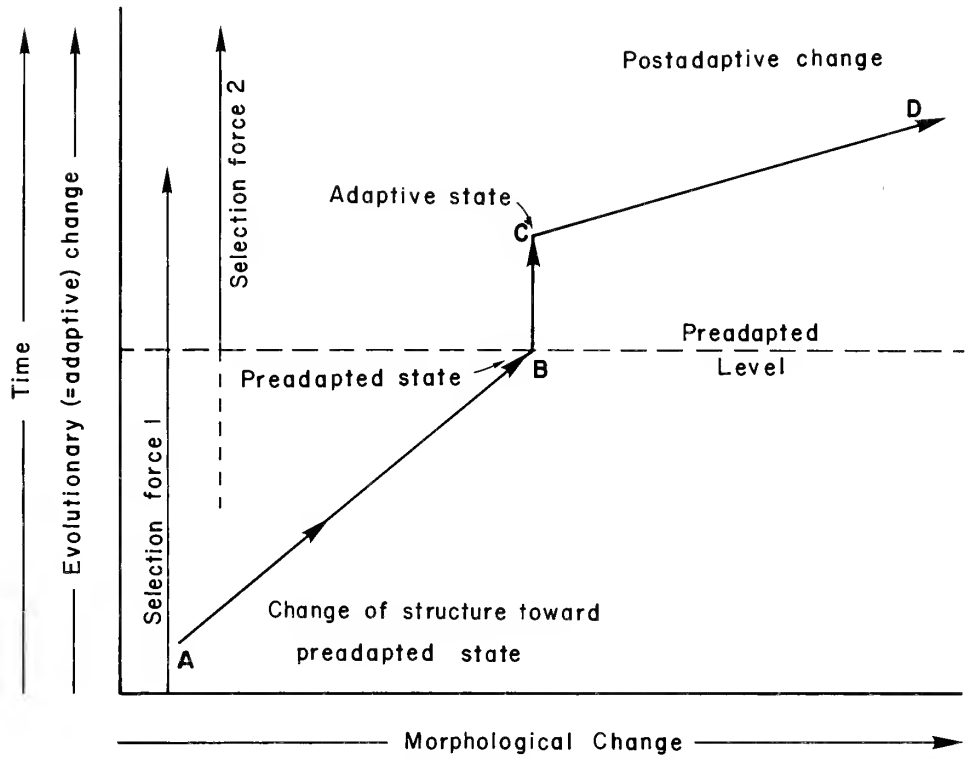

Fig. 10.—Schematic diagram to show the evolution of a new adaptation via a preadapted stage. The horizontal axis indicates morphological change. Time and evolutionary change are shown along the vertical axis. Evolution of the feature to the preadapted state (B) is under the control of selection force 1. When selection force 2 forms a new synerg with the feature at B, the feature shifts to a new adaptive state (C) from which it can undergo a period of postadaptive change toward D (taken from Bock, 1959:Fig. 5).

The origin of new features via a preadapted stage solves the dilemma of the selective value of the new feature at a time when it is too poorly developed to have the needed function and biological roles. Evolution of the feature up to the preadapted level occurs under the action of the old selection forces, not the new selection force associated with the new adaptation.

The notion of preadaptation has a second advantage in that it solves the dilemma of the necessary perfection of adaptations (Frazzetta, 1975), for example, the biomechanical interaction of skeletomuscular systems, during their origin and early evolution when they are not sufficiently developed. I accept the notion that features can be far less than well-integrated, perfected systems and can still be adapted. A period of postadaptive specialization usually follows the appearance of any new adaptation. Yet, some degree of perfection as discussed by Frazzetta (1975) is required which is achieved by the preadapted step.

A SYNTHETIC MODEL FOR MACROEVOLUTIONARY EXPLANATION

The proposed synthetic model to explain macroevolutionary modification must have a number of properties to be a fully reductionistic one. The model must permit adaptive change throughout with selection acting on the evolving population at all times. No jumps or discontinuities of a level greater than those observed between successive generations of the same phyletic lineage can exist. The possible sources of the needed directional selection must be identified. Only those evolutionary mechanisms known to operate on the microevolutionary level can be used; no special macroevolutionary mechanisms are permitted. These mechanisms are those of speciation (=splitting of phyletic lineages)

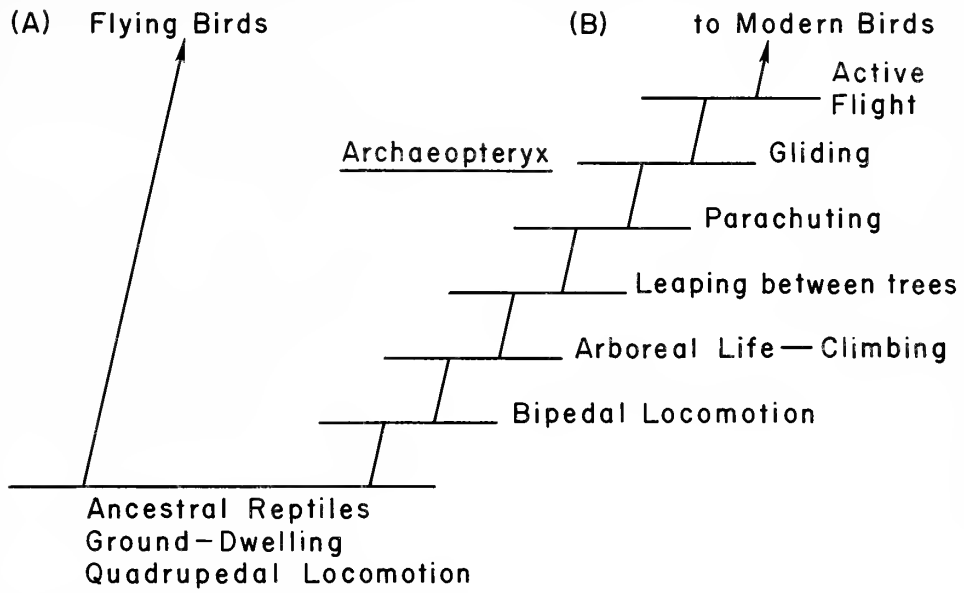

Fig. 11.—Schematic diagrams contrasting two different models of steps in the origin of new taxa. (A) A single-step change from ground-dwelling reptiles to flying birds; the selection forces responsible for this change are associated with flight. (B) A series of stepwise evolutionary changes from reptiles to modern birds; only the major levels have been included. In this model, a series of selection forces are responsible for the total change; each set of forces is associated with the corresponding level of change (taken from Bock, 1965:Fig. 1).

and, most importantly, those of phyletic microevolution. The latter mechanisms are those which have been tested against observations resulting from experiments of population geneticists and from the work of animal and plant breeders. The mechanisms of speciation and of adaptive phyletic evolution (plus pleiotrophic byproducts) discussed above are sufficient for all macroevolutionary explanation. Changes on the microlevel must be summed properly to achieve the major evolutionary modification. This summation must be an exact chronological one with evolutionary events at one point in time setting the stage for those at the next step in the sequence. The critical conceptual transformation in the model is that from a horizontal to a vertical comparison or vice versa depending on how the explanation is being developed. If a sequence of adaptive vertical steps is postulated for phyletic evolution within a single lineage, it can be tested, with extremely rare exceptions, only against a series of observations made in a horizontal comparison across many different phyletic lineages. Although the differences observed in the pseudophylogeny comprised of the steps in the horizontal comparisons may have other than an adaptive explanation, they must be assumed to be adaptive so long as this assumption is a reasonable one.

Model for Major Adaptive Shift

The first step is to develop an overall model which provides the framework for the whole explanation and the basis to focus discussion on the crucial points. The model to be used is one I advocated earlier (Bock, 1965) using the evolution of birds as the example. Although the model will be discussed in terms of the evolutionary origin of a new major taxon—the class Aves—it is equally suitable for explanation of the evolution of a single feature.

Any change from the ancestral to the descendent group involves a sequential series of many steps, each representing an intermediate stage between the old and the new adaptive zones (Fig. 11B). The notion of a single step between the ancestral and descendent groups (Fig. 11A) is not supported by any positive observations. The major difference between these contrasting models is that only one set of selection forces is involved in the one step model while a sequence of different selection forces is involved in the multiple step model. The steps must be in proper chronological order with evolutionary modifications at one step setting the stage for the changes at the next. Each step in the series may include preadaptations and perhaps key innovations as well as a period of postadaptational adjustment. During the postadaptational period, the newly

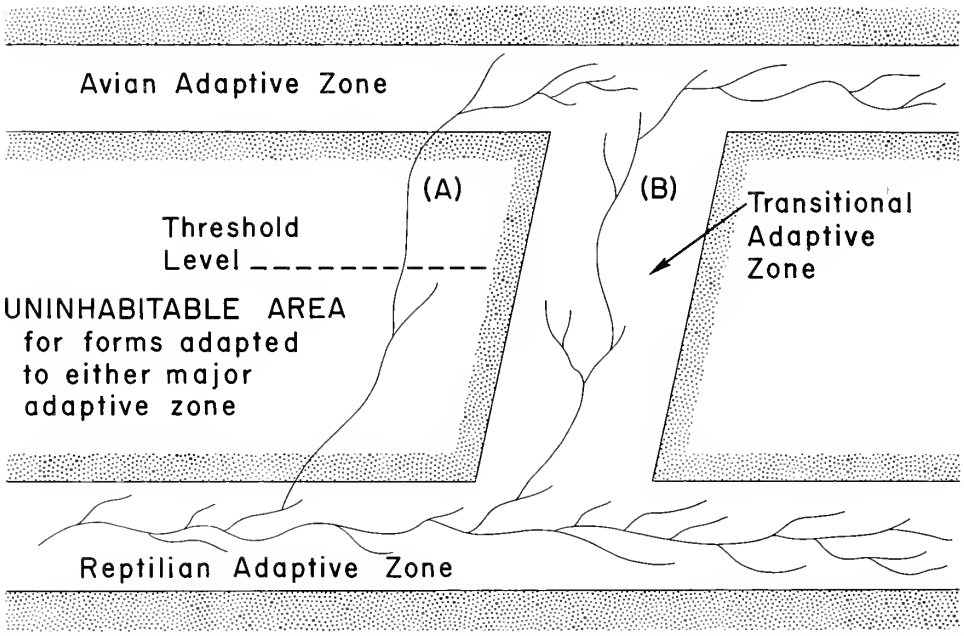

Fig. 12.—Schematic diagrams contrasting two different models of crossing from one major adaptive zone to another. (A) The phyletic lineage must cross an ecologically unstable region which may be considered as a threshold. (B) The phyletic lineage crosses from one major adaptive zone to another through a transitional adaptive zone. In these models, the region between the major adaptive zones is regarded as uninhabitable for organisms adapted to either major adaptive zone (taken from Bock, 1965:Fig. 2).

evolved features are integrated with earlier changes so that the resulting adaptations are dependent on the entire complex of interdependent features. The individuals of the evolving population are always integrated wholes adapted to their environment. Changes appearing at each level in the sequence are dependent on those features that had evolved at previous levels. Thus, flight with an aerodyanamic surface formed by elongated strengthened feathers attached to the posterior edge of the forelimb is dependent upon the earlier evolution of feathers.

In the evolution of flying birds from terrestrial reptiles, the steps would include bipedal locomotion, climbing, leaping, parachuting, gliding and finally active flight. Various features of the ancestral reptiles would have evolved at different times and at different rates in response to the selection forces associated with each step; these changes would occur in a very definite sequence depending upon the features, their somatic interactions and mechanisms of internal adjustment, and the organisms. The resulting pattern of change is stepwise or mosaic evolution (de Beer, 1954). Discussion of the details of mosaic evolutionary change in the evolution of birds is beyond the scope of this paper. Suffice it to say, *Archaeopteryx* exhibits a mosaic of characters, some very reptilian, a few as fully developed as those in modern birds and others at various intermediate stages.

The evolution of each new major feature or modification must be subdivided in like fashion into a series of steps as has been done for the avian feather by Regal (1975).

Functional significance of each morphological change and feasible biological roles must be discussed together with possible environments and selection forces. Thus, feathers may have a number of functions, two of which are temperature regulation and providing an aerodynamic surface. Each could be associated with biological roles having a synergistic relationship with a selection force that could have been responsible for its origin. Choice of temperature regulation as the most reasonable function associated with the origin of feathers is based on a number of considerations involving the biology of the whole organism, not just the feathers. Yet, this does not solve questions of the biological roles of temperature regulation, the environmental factors and the exact nature of the selection force. A decision that selection forces associated with arboreal life were central to much of the evolution of birds from reptiles does not mean that the transi-

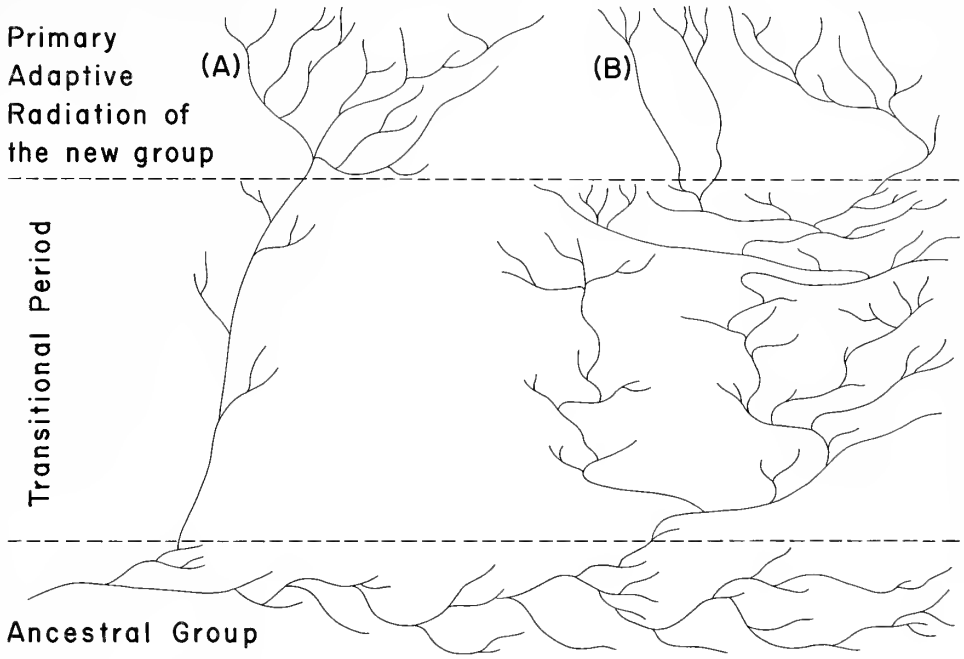

Fig. 13.—Schematic diagrams contrasting two different models of the number of phyletic lineages involved in the origin of a new group of organisms. (A) A single phyletic lineage with a few insignificant side branches leads to the new group. The primary adaptive radiation stems from this single line after the basic features of the new group have evolved. (B) Several phyletic lineages with successive series of adaptive radiations lead to the new group. Several different lineages may contribute to the primary adaptive radiation of the new taxon. The second model emphasizes that evolution of a new taxon involves successive series of adaptive radiations with a number of coexisting phyletic lineages at any point in time rather than a single lineage (taken from Bock, 1965:Fig. 3).

tional protoaves lived only in trees. It is entirely possible for these animals to spend part of their life on the ground as active bipedal predators and part of their time in the trees as a place to rest and to reproduce, that is, incubate their eggs and raise their young in a nest placed in a tree.

The pattern of selection forces acting during the period of a major evolutionary change and the nature of the intermediate environmental zone are crucial for the general model.

Adaptive Zones

The concept of adaptive zones or adaptive peaks has proven to be quite useful except for the ambiguous "regions" between the adaptive zones. Simpson (1953:201–202, and elsewhere) regards these intermediate areas as "discontinuities or essentially unstable ecological zones" that must be crossed when a group evolves toward another adaptive zone and new higher taxon (Fig. 12A). This concept gave rise to the notion that the phyletic lineage is in an inadaptive phase of evolution while passing through this region. Selection is regarded to be severe and the population in the intermediate area is evolving rapidly compared to selection and rates of evolution in the normal adaptive zones. The discontinuity between the two adaptive zones has been described as a threshold level that the evolving population must surmount. If it fails to do so, it either falls back to the old adaptive zone or becomes extinct.

No real evidence supports the concept of unstable areas between adaptive zones which can be regarded as uninhabitable areas for the organisms in either neighboring adaptive zones.

Crossing from one adaptive zone to another is via a transitional zone that extends between the two major zones (Fig. 12B). These transitional zones may be temporary, appearing and disappearing as ecological conditions change. However, some transitional zones may remain in existence for extremely long periods of geological time and others may be as permanent as the major adaptive zones. The last may be the most frequent. A population in a transitional zone is fully adaptive to the ecological conditions there and does not experience selection forces of greater magnitude than those operating in the major adaptive zone. The only difference may be that the selection in the transitional zone may be

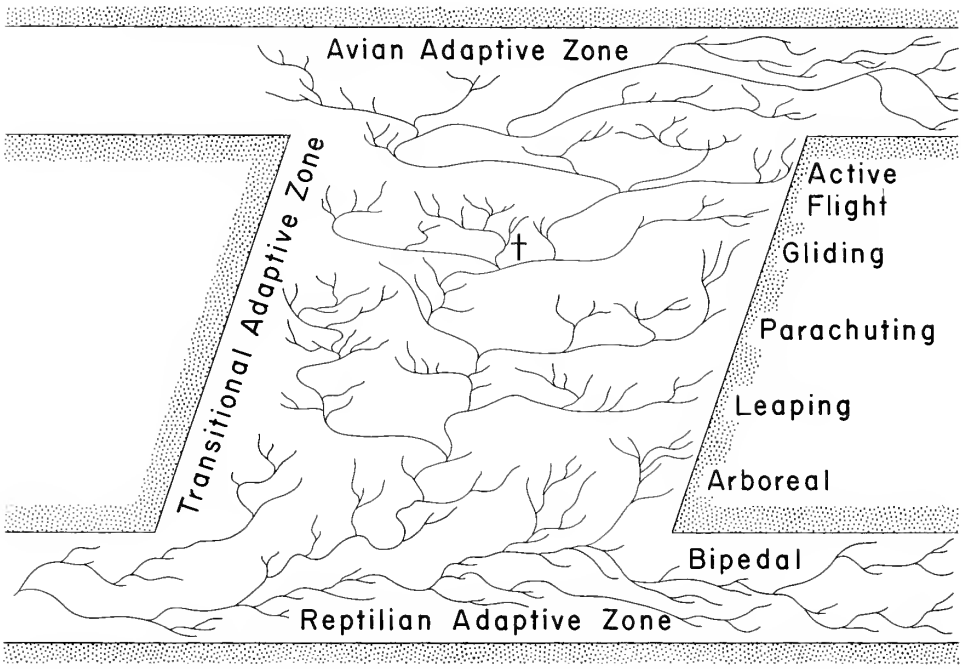

Fig. 14.—A composite model for the adaptive origin of a new group of organisms, in this case the evolution of birds from reptiles. The successive radiations seen in the transitional adaptive zone form a pattern of stepwise evolutionary levels indicated on the side of the transitional zone. The approximate position of *Archaeopteryx* is indicated by a cross (†). Relative widths of the major and transitional zones, sizes of the various radiations and relative times are not shown to correct proportions (taken from Bock, 1965:Fig. 4).

more strongly directional than that in the adaptive zone.

Number of Lineages

It has generally been assumed that a single phyletic lineage, or a small number at most, are involved in the origin of a new taxon (Fig. 13A). This concept developed because of the small number of fossils available to trace the change from one group to another. In the average case, scarcely enough fossils exist to fill the gaps in a single phyletic lineage. But the small number of known fossils associated with the origin of any group is probably a consequence of the speed of the change compared with the "time intervals" of the fossil record.

Although little supporting evidence is available, it seems reasonable to assume that several to many phyletic lines are involved in major evolutionary changes and that a series of small radiations are present throughout the transitional period (Fig. 13B). These small radiations replace one another and may correspond to the sequential stages shown in Fig. 11B. This is the pattern shown by the evolution of mammals from the therapsids and by the evolution of horses. It is not in conflict with any positive paleontological data and is in close agreement with the concepts of mosaic evolution and of transitional adaptive zones and with the pattern of diversification shown by recent groups of organisms.

One difference between these two concepts is that in the single lineage model, adaptive radiation occurs after the lineage enters the new adaptive zone and is suggested to be a mode of evolutionary change different from that responsible for the origin of the group. In the multiple lineage model, adaptive radiations occur during the entire transitional period with perhaps the only difference being one of magnitude of the radiations—those in the major adaptive zones being larger.

The Combined Model

The model for the sequence of events involved in the origin of new groups is simply a combination of the several models shown in the previous figures (Figs. 11B, 12B, and 13B). The composite model is illustrated in Fig. 14 by the evolution of birds.

The ancestral group evolves through time but remains within its adaptive zone. New adaptive radiations occur and new forms appear. These refill the zone again and again to replace the lineages that

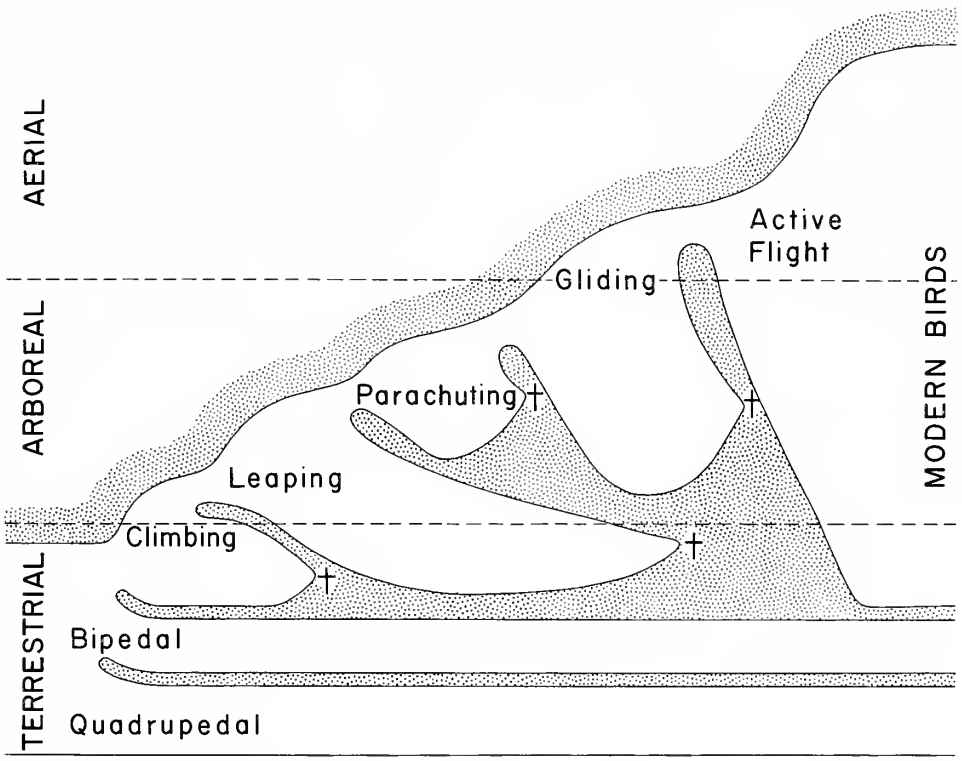

Fig. 15.—A schematic model showing a possible pattern of radiations of the different stages in the evolution of birds through three major adaptive zones—terrestrial, arboreal, and aerial. Sizes and durations of the radiations and the times of extinction are strictly hypothetical. Blank areas inside the stippling are successive adaptive levels. It may be seen that each successive radiation and resulting adaptive radiation did not remove the descendent forms from competition with their ancestors. This model suggests that the radiation at any level would probably continue as long as it did not give use to a higher (better adapted) level (taken from Bock, 1965:Fig. 5).

have died out, but the basic organization of the group remains the same, just as the zone remains the same. The mechanism for the adaptive radiations involves preadaptations, key innovations, postadaptational change, and others as outlined above. The size of the group expands and shrinks as the zone becomes wider and narrower.

The start of evolution toward a new group begins with radiation into an intermediate zone. These radiations continue as long as the intermediate zone continues to exist, and are under the control of the same evolutionary mechanisms that acted earlier in the ancestral adaptive zone. Similar patterns of preadaptations, key innovations and postadaptation occur with the only difference being directional selection acting on the lineages in the transitional zone. The appearance of a new adaptive zone depends to a great extent on the features that appeared, by chance, in the intermediate group. A number of arboreal and even gliding lines appeared in the reptiles, but only one—that leading to birds—possessed the adaptations permitting successful invasion of the new (aerial) zone. Yet, the ecological habitat of open air had existed long before birds evolved.

Extinction of earlier radiations in transition is not because of the nature of the transitional ecological zone but because of the appearance of later radiations (Figs. 15 and 16). As these subsequent radiations appear, the later forms often inhabit the same ecological zones and thereby compete with members of the earlier radiations. If the changes leading to modern birds are shown against three major adaptive zones—terrestrial, arboreal, and aerial—it can be appreciated that members of later radiations are not removed from competition with those of earlier radiations. Species that can leap between trees are still arboreal and will compete with those arboreal species that can only climb. Leaping from tree to tree would be a definite advantage. Later species that could parachute and still later ones that could glide are still arboreal dwellers, but have decided advantages over those that are only able to leap from tree to tree. Competition

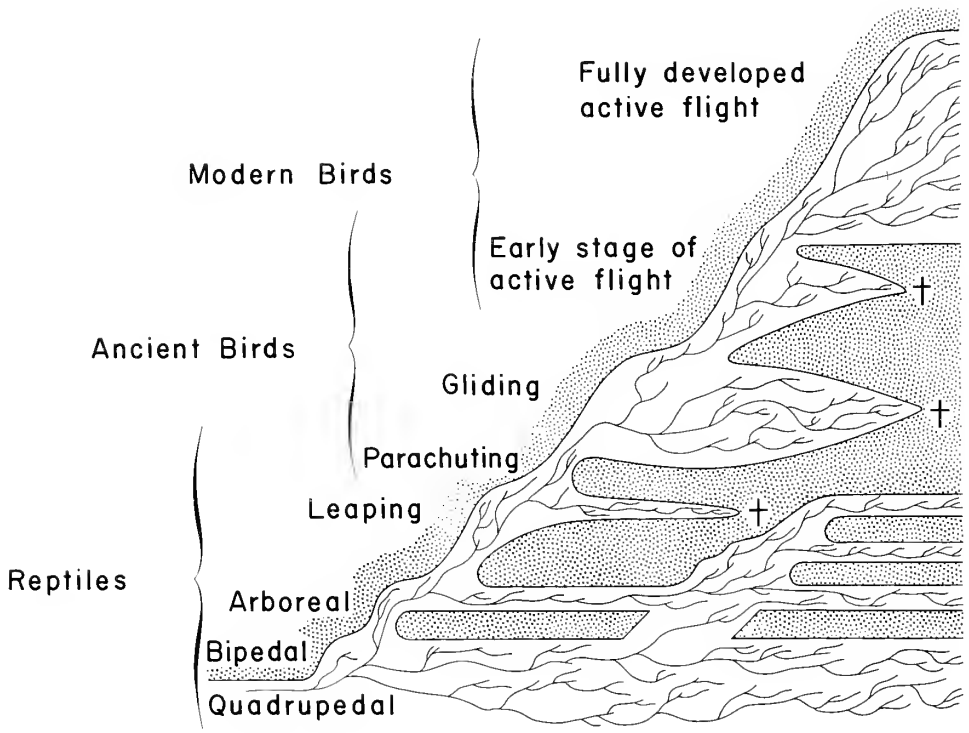

Fig. 16.—A schematic model showing the different stages in the evolution of birds through successive taxonomic groups—reptiles, ancient birds, and modern birds. The possibilities of transitional zones appearing several times and of their continued existence, for example, at the arboreal and leaping levels, are emphasized in this model. Moreover, the model illustrates the severe selection pressure exerted by flying birds on other arboreal groups that may be evolving fully developed aerial adaptations (taken from Bock, 1965:Fig. 6).

between members of different radiations and the usual extinction of the earlier radiations produces the distinct gaps seen between most major taxa. And it may be a significant factor in the usual lack of fossil record of transitions between major groups.

Selectional Sources

Adaptive evolutionary change requires strong directional selection acting over a long period of time. Not even advocates of quantum theories deny this requirement as they rely heavily on selection for much of macroevolution even if a saltation or a period of no selection is included. Moreover, the directional selection must be able to explain the pattern of mosaic evolution that is characteristic of major evolutionary modifications. Thus, directional selection must not only be strong and continuous for a long period of time, but the individual selection forces must act at different times and at varying rates during the intermediate period.

Most workers have not attempted to identify the source of the needed directional selection or assume it to be from the physical environment or from obvious factors as food, shelter, locomotion, and others. I advocated first in 1970 and more fully in 1972*a* that the major source of directional selection pushing a major evolutionary change came from species interactions of all types (see Darwin 1859:487–488). Advocating selection from species interactions as the driving selection for macroevolution does not gainsay the continued action of selection from the physical factors of the environment. These exist and control the evolution of many features of the organism. Selection from species interactions overlies these other selection forces and is almost always the major part of selection responsible for major change. I do not want to leave the impression that selection from species interactions is not important in microevolutionary events, in speciation and in continued evolution within the limits of a taxon remaining in its major adaptive zone. Such selection is also very important there as it is a major component of the total selection acting on all species.

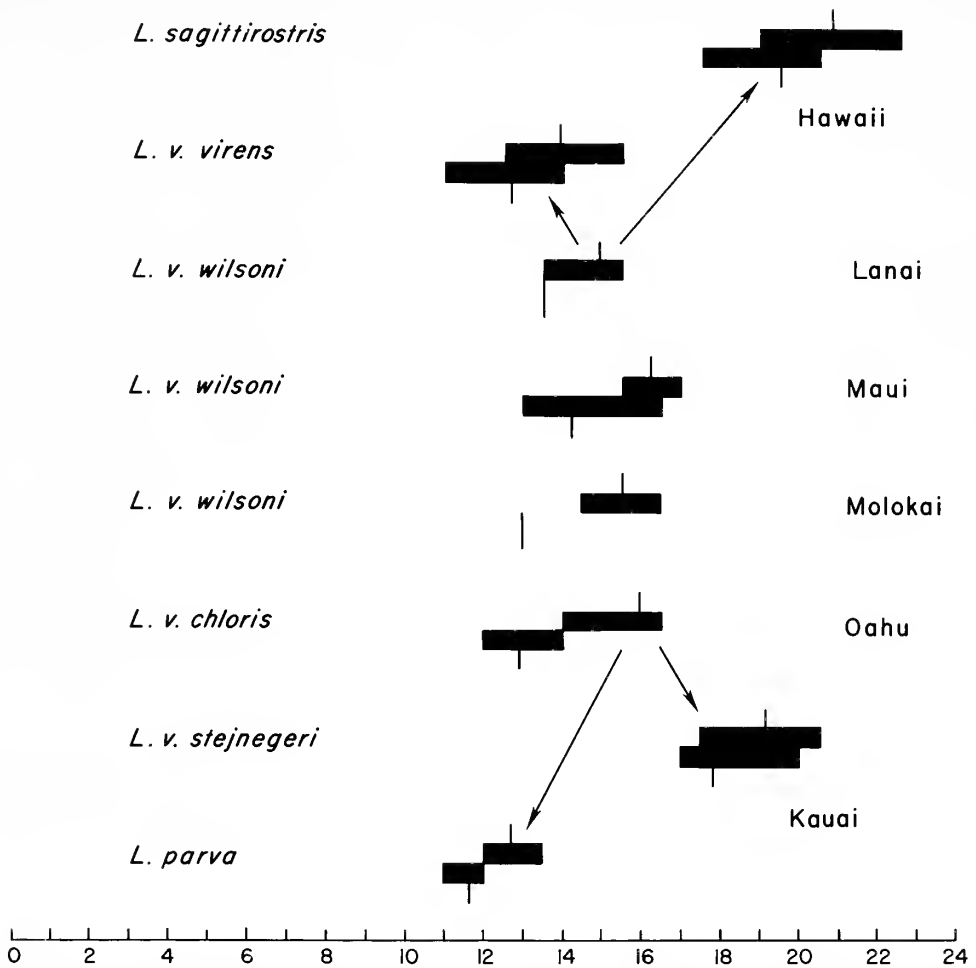

Fig. 17.—Bill length (culmen in mm) of the *Loxops virens* complex to show geographic variation and displacement); data taken from Amadon (1950). Range is indicated by the solid bar, the mean by the vertical line, males shown by the upper bar and females by the lower (taken from Bock, 1970:Fig. 4).

Species interactions can be classified into two major categories—namely, (a) *exclusionary* interactions, including ecological competition and reproductive efficiency (reduction of reproductive cost by improving means of species recognition and other types of intrinsic isolating mechanisms of low reproductive cost); and (b) *coevolutionary* interactions, including predator-prey, parasite-host, and flower-pollinator relationships and all other sorts of symbiotic associations.

Species interactions and the resulting directional selection force are dependent on the coexistence of the interacting species and will result in modification of at least one and usually all of the interacting species. Selection is mutual because each of the interacting species exerts selection on the other; unidirectional selection is extremely rare if it occurs at all. The two types of species interactions are different in their mode of action, in the mode and strength of selection, and in the pattern of evolutionary change of the interacting species. Other than the broadest generalizations that species interactions result in mutual selection and that the strength and complexity of the selection increases with the number of interacting species, no generalizations can be offered on the mechanism of the interaction, the nature of the resulting selection and the pattern of the evolutionary change.

Exclusionary species interactions include ecological features associated with competition and/or ethological features (and all other intrinsic isolating mechanisms) associated with reduction of reproductive wastage (Bock, 1970:706) in pairs of species that are already reproductively isolated. Each

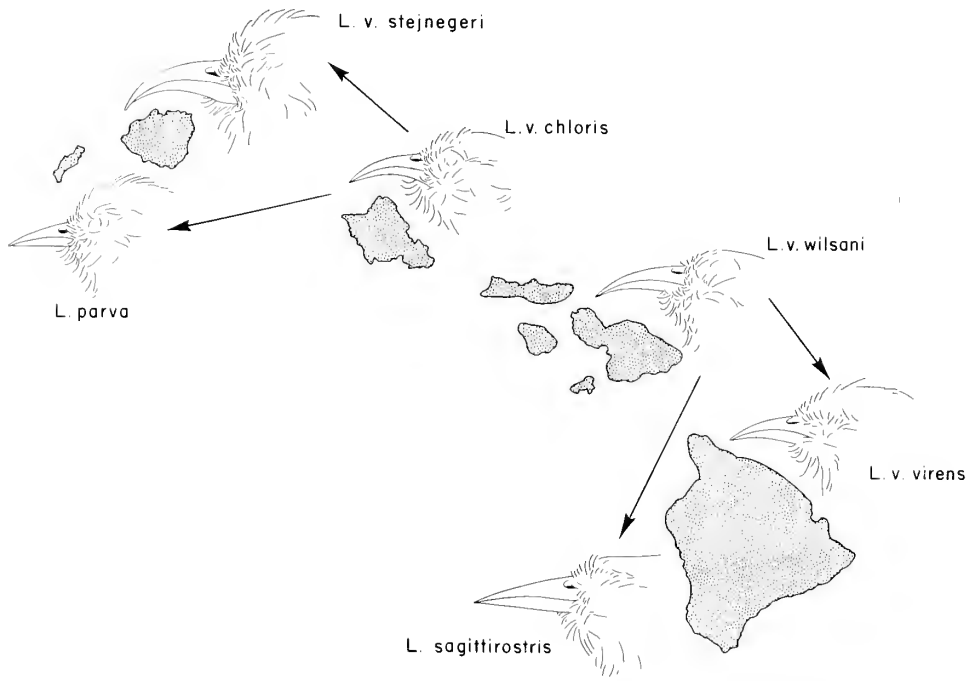

Fig. 18.—Double invasion and character displacement in bill length and shape in the *Loxops virens* complex on Kauai (*v. stejnegeri* and *parva*) and on Hawaii (*v. virens* and *sagittirostris*) to illustrate the consequence of exclusionary species interaction. See Fig. 17 for details in displacement of bill length (taken from Bock, 1970:Fig. 5).

species will exert selection on the other with possible evolutionary consequences ranging from the extinction of one species to character divergence in both (Lack, 1944, 1947). Exclusionary species interactions are usually most intense between two newly evolved sister species during the sympatric phase of speciation, but may be strong between very distantly related species. The introduction of trout into New Zealand resulted in serious decline in the native Blue Duck (*Hymenolaimus malacorhynchos*) because of competition for the same food—aquatic insect larvae (Kear and Burton, 1971). In the Hawaiian honeycreepers (Drepanididae) exclusionary species interactions occurred between sister species (for example, between *Loxops v. virens* and *Loxops sagittirostris* on Hawaii and between *Loxops v. stejnegeri* and *Loxops pava* on Kauai; see Figs. 17 and 18; Bock, 1970:711) and between closely related genera (for example, between *Loxops v. stejnegeri, Hemignathus lucidus hanapepe,* and *Hemignathus procerus* on the island of Kauai; Bock, 1970:714–715). Lack (1947) provided the classic example of how bill size shifts in the sympatric species of *Geospiza* and *Camarhynchus* (the Darwin's finches) depending on which of the congeneric species are present on each island.

The consequence of exclusionary species interaction of greatest significance for macroevolution is character displacement. The two interacting species will diverge from one another under the action of the mutual selection thereby reducing the degree of interaction and hence the strength of directional selection. Once interaction ceases between the species pair, further divergence will be greatly reduced or cease totally until another cycle of speciation occurs or until another species invades the range of one of the two original species. Selection from exclusionary species interaction is frequently very strong at the onset, but is quickly reduced and is of short duration. It depends upon repeated speciations to maintain a high level of selection.

Coevolutionary species interactions involve a number of different types such as predator-prey relationships, pollinating organisms, and symbioses (Ehrlich and Raven, 1965; Ehrlich, 1970). This category of interaction is characterized by a direct utilization by one member of the species pair of resources of the other. In some cases, both members of the pair use resources of the other species, but generally in quite different ways. The only requirement is that use of at least one member of the spe-

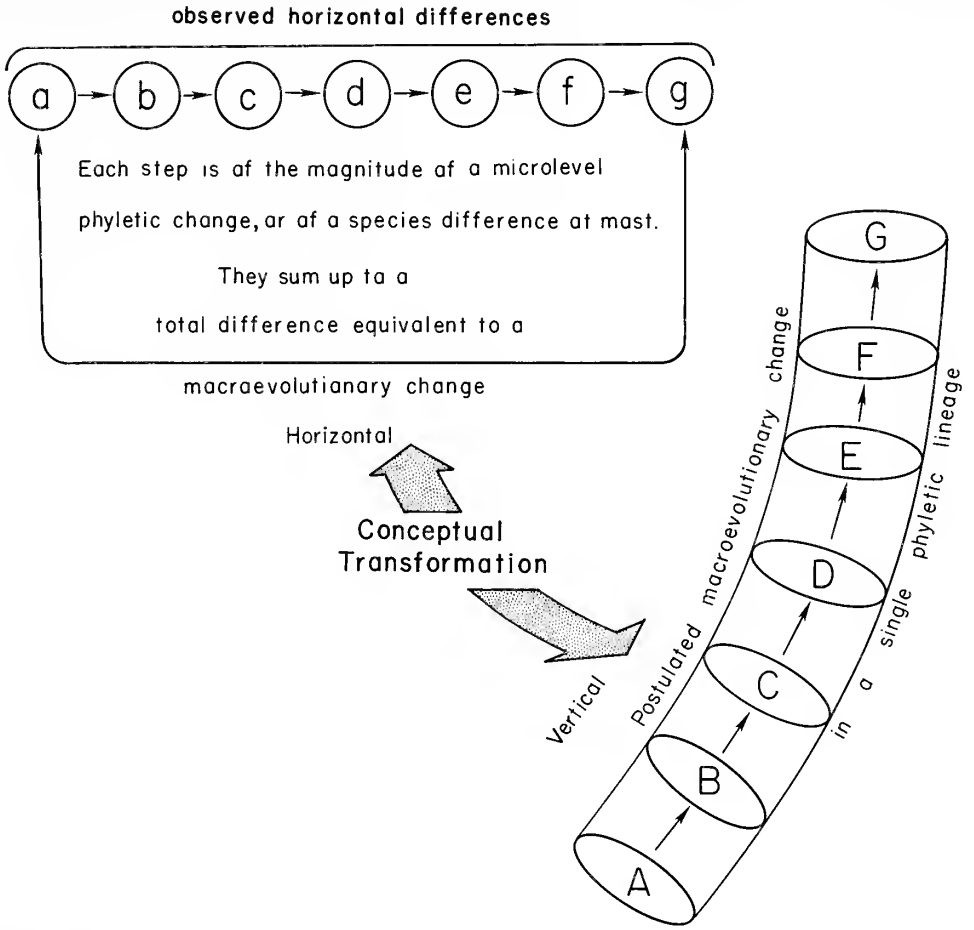

Fig. 19.—Schematic diagram to show the conceptual transformation from a vertical series of changes in a phyletic lineage to an analogous pseudophylogeny of horizontal steps. The horizontal comparison is the sequential species analysis that serves to test the macroevolutionary modification through a successive series of small steps each of which can be explained by the known mechanisms of phyletic microevolution.

cies pair must be advantageous to the other; in symbiosis, both species gain an advantage. In every case, each species exerts selection on the other no matter which one is actively utilizing the other. The result of the mutual selection is modification of one or both species, but this evolutionary change is usually not a divergence as in the case of exclusionary interactions. Generally, both species change with the ensuing modification resulting in only a temporary reduction, if any, of the selection being exerted. The general consequence of coevolutionary interactions is continued evolution of both interacting species as each of the species changes. Coevolutionary interaction is an "arms race" type of evolutionary interaction as each species must continue to evolve to keep abreast of the evolutionary changes of the other. It is not possible to win in coevolutionary interactions except temporarily or in the case of extinction of the other species.

Coevolutionary species interactions probably involve weaker selection than exclusionary interactions, but the strength of selection need not decrease with evolutionary change and the interaction continues for much longer periods of time. Coevolutionary interactions do not depend upon continued speciations and may be especially important in macroevolutionary change of taxonomically isolated species and of single taxa evolving on isolated islands.

An important aspect of selection arising from species interactions is that it modifies as the interacting species evolve under the control of the mu-

tant selection. This would produce the pattern of changing selection forces needed for mosaic evolution.

Both types of species interactions, but especially exclusionary, provide the link between the species and speciation and macroevolutionary change. With increased speciation and greater number of species, more species interactions will occur and with them more directional selection to drive macroevolutionary change. Thus, it is not speciation itself that is essential to macroevolution, but the resulting species interaction and the mutual directional selection that helps to drive macroevolution.

Sequential Species Analysis

The model presented above shows that macroevolution can be explained as adaptive evolutionary change with the major driving directional selection arising from species interactions of all sorts. Yet, the unit changes that comprise a major evolutionary modification do not have to be ones at the microevolutionary level. The model as proposed thus far is completely consistent with the hypothesis that the evolutionary steps are of a larger magnitude than those observed at the microlevel—that is, the hypothesis of quantum jumps. It is possible to postulate a mechanism of quantum evolutionary jumps that is fully adaptive. The concept of systemic mutations proposed by Goldschmidt (1940:206) is consistent with theories of adaptive macroevolution. It is necessary to show that major evolutionary change can be explained fully as a series of sequential changes, each of which is at the level of microevolutionary change as studied by population geneticists and by plant and animal breeders. I discussed the role of sequential species analysis under the heading of microevolutionary sequences (Bock, 1970) and of sequential species analysis (Bock, 1972*b*). The concept of sequential species analysis is that a horizontal comparison of differences between species and subspecies may be postulated to be equivalent to the sequence of microevolutionary steps in a macroevolutionary change. A conceptual transformation must be made between the horizontal comparison of observed differences between species and the postulated macroevolutionary change in a single phyletic lineage (Fig. 19).

The synthetic explanation of macroevolution states that the sequence of modification in a particular phyletic lineage that is large enough to be termed a major evolutionary change can be explained fully by microevolutionary mechanisms. No special evolutionary mechanisms are needed in which case macroevolutionary explanation has been reduced fully to microevolutionary explanation. The macroevolutionary change is the difference between A and G shown in the phyletic lineage in Fig. 19. This change is the result of the chronological series of microevolutionary steps A → B, B → C . . . F → G shown. The populations A B . . . G are successive cross-sections of the phyletic lineage, which are chosen for the purposes of the explanation.

The major evolutionary change to be explained is one of phyletic evolution and hence, it is to be reduced to the mechanisms of phyletic evolution—the formation of genetically based phenotypic variation and natural selection. As change is being traced only along a single phyletic lineage, we are not concerned with the number of lineages that may have split off of the phyletic lineage A–G. Hence, the mechanisms of speciation do not apply at all—they are not part of the needed explanation. *A full reductionistic explanation of macroevolution does not include the mechanisms of speciation.* Speciation, or the splitting of phyletic lineages, results in a multiplication of species. The role of species in macroevolution is they provide mutual species interactions (exclusionary and coevolutionary) and hence mutual selection. The more species existing, the greater will be the selection from the species interactions and the greater will be the driving force of the macroevolutionary change.

Given a macroevolutionary change to be explained with a known starting point and a termination, the first step would be to establish a plausible phylogenetic sequence of changes. If the evolution of a new feature is being analyzed, then the phylogenetic sequence will be of stages associated with this feature. If the evolution of a new major taxon is being examined, then it may be sufficient to limit discussion to the sequence of individual features associated with the origin of the group. Establishment of the phylogenetic sequence depends upon consideration of evolutionary mechanics of individual features, functional and evolutionary interactions of morphological components of functional complexes, organism-environmental interactions, behavior and ecological factors, and whatever else may bear on it. The steps in the sequence should be as small as possible without the total number becoming unreasonably large.

At this point the conceptual transformation must be made from the vertical phylogenetic sequence to a corresponding horizontal series. The species in the horizontal sequence and the differences between adjacent members provide an analogy of the sequence of changes that took place in the phylogenetic lineages. Each step between adjacent members should be of a magnitude and type corresponding to those demonstrated in animal and plant breeding or in experimental work in population genetics. The difference between the ends of the horizontal sequence is assumed to be summation of the small individual differences and to correspond to the macroevolutionary change to be explained.

It must be emphasized that horizontal comparisons are not comparable to vertical ones. Also, it is not possible to equate all horizontal differences or similarities with corresponding vertical differences or similarities. Interpretations reached after a horizontal comparison cannot be automatically extrapolated to vertical comparisons. Yet, the conceptual transformation between a vertical phyletic lineage and a horizontal series of species must be made if one wishes to continue analysis of macroevolution regardless of whether one advocates quantum theories or reductionary theories. This transformation is a scientific hypothesis that must be tested against empirical observations. The nature of the tests is obvious. One must observe actual phylogenies and compare these to corresponding horizontal series. The only phylogenies that are readily available are those from plant and animal breeding. Some of these may not be suitable for tests because of missing information. Examples of tests could be a comparison of the sequence of changes in the history of dog breeding with the types and magnitude of differences between breeds of dogs. Another would be the work done with fruit flies. I will accept that tests can be made of the transformation hypothesis and that these tests will not disprove the hypothesis although I cannot detail any good tests at this time. The actual testing of the transformation hypothesis is of key importance.

If the steps in a phyletic sequence of a macroevolutionary change correspond to an analogous horizontal series and if the observed differences between all adjacent species in the horizontal series are of the magnitude demonstrated in phyletic modifications in plant and animal breeding and in experimental population genetics, then it can be concluded that the modifications along the phyletic lineage are of this magnitude and can be explained by the known microevolutionary mechanisms of phyletic evolution. If the total difference between end members of the horizontal series is the summation of the individual small differences between adjacent species and if this total difference corresponds to a major evolutionary change, then it can be assumed that the major phyletic evolutionary change is the summation of a chronological series of small phyletic modifications. These assumptions can be made because of the possibility of a conceptual transformation between a vertical phyletic sequence and a horizontal "pseudophyletic" series.

If the macroevolutionary modification can be shown to be a summation of a sequence of small steps each of which can be explained by known mechanisms of phyletic microevolution, then the macroevolutionary change is completely explained by these mechanisms of phyletic evolution on the microlevel. No additional mechanisms are required. Macroevolutionary explanation has been reduced to microevolutionary explanation. Thus, phyletic evolutionary change of all magnitudes is explainable with the same set of causal mechanisms which has been one of the long cherished hopes of evolutionary biologists.

Methods of Testing

Scientific theories, hypotheses, and explanatory models are easy to postulate and have little value unless methods are outlined by which they can be tested. And successful testing increases their value. A major failure of most explanatory theories of macroevolution has been the lack of suggestions of how these theories are to be tested or improper testing.

Most workers have attempted to test particular or conflicting sets of macroevolutionary explanations against evidence from the fossil record. Unfortunately, such tests are invalid for several reasons. First, the degree of resolution of geographical distribution of species, including isolates, and of temporal change in the fossil record is simply not fine enough to correspond to microlevel steps in macroevolutionary changes. The necessary level of knowledge of geographical distribution is known only for a few groups of recent organisms, such as birds and mammals, and not even completely for these groups. Important changes for macroevolution can occur in less than 5,000 years and probably in less than 1,000 years. Such time intervals are simply too small to be resolved in the fossil record—they are geologically instantaneous. Second, it is

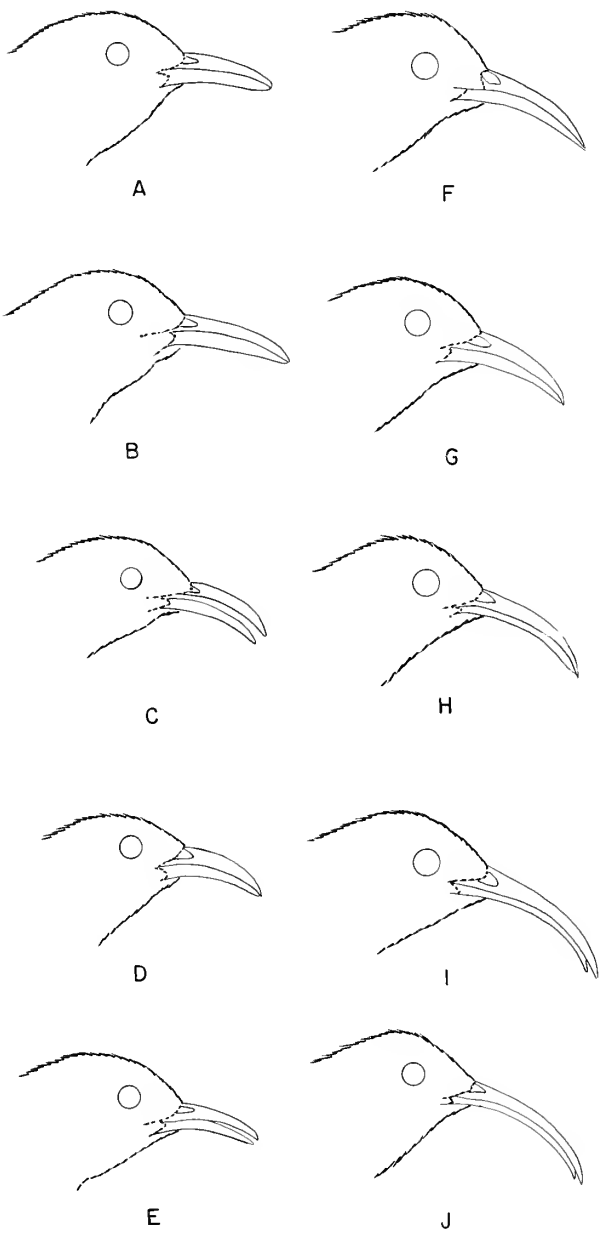

Fig. 20.—Bills of the different species of thrashers (*Toxostoma*) seen in lateral view to show the change in length and in the degree of curvature from the short, straight-billed, *T. rufum* to the heavy curved-billed thrashers. The species are (A) *rufum*, (B) *longirostre*, (C) *guttatum*, (D) *cinereum*, (E) *bendirei*, (F) *ocellatum*, (G) *curvirostre*, (H) *lecontei*, (I) *redivivum*, (J) *dorsale* (taken from Engels, 1940:Fig. 2).

very difficult or impossible to determine the adaptive nature of features in fossils and hence to ascertain actual adaptive change in fossil organisms. It is necessary to turn to observations from Recent organisms to test explanatory models of macroevolutionary change.

The hypothesis to be tested is that macroevolutionary change results from a cumulative summation of chronological small changes along a phyletic lineage and each of these small changes occurs by the known mechanisms of microevolutionary phyletic modification. These vertical phyletic sequences of successive microevolutionary steps can be transformed conceptually to an analogous horizontal series of species in which the difference between adjacent species corresponds to a microevolutionary change and the total difference represents a macroevolutionary modification. The series of horizontal comparisons represents a pseudophylogeny but one analogous to a presumed real phylogeny. The horizontal comparison or sequential species analysis can be undertaken most readily with species-rich genera or groups of closely related genera in which the end forms demonstrate a large difference and which contain enough species to illustrate many stages between the extreme types. The analysis must be a detailed comparison of the descriptive, functional, and ecological morphology of the features involved in the evolutionary change. Unfortunately, these are the types of comparative studies that morphologists have avoided in the past in favor of comparative analyses of large differences in distantly related genera, families, and orders. Relatively few studies are available, which could serve to test the reductionistic model of macroevolution. At this time a request must be made for comparative functional-ecological studies of carefully chosen species-rich genera and genera complexes to obtain observations that would serve to test the reductionistic model. Studies such as those by Webster and Webster (1975, 1977) on the ear of heteromyid mice (kangaroo mice), of Wake and his associates on the plethodontid salamanders of tropical America (see Wake and Lynch, 1976; Lombard and Wake, 1976, 1977) and by Richards and Bock (1973) on the genus *Loxops* (Drepanididae: Aves) are examples of those needed for this testing. I would like to discuss three examples, all from birds, which provide empirical evidence that tests the reductionistic hypothesis.

Engels (1940) reviewed the North American thrashers of the genera *Toxostoma* and *Oreoscoptes* (Passeriformes: Mimidae; these genera are closely related and probably should be considered as congeneric, for example, Mayr and Short, 1970:68). Thrashers are birds of the undergrowth and ground that feed on insects and other small invertebrates, which are found by uncovering the

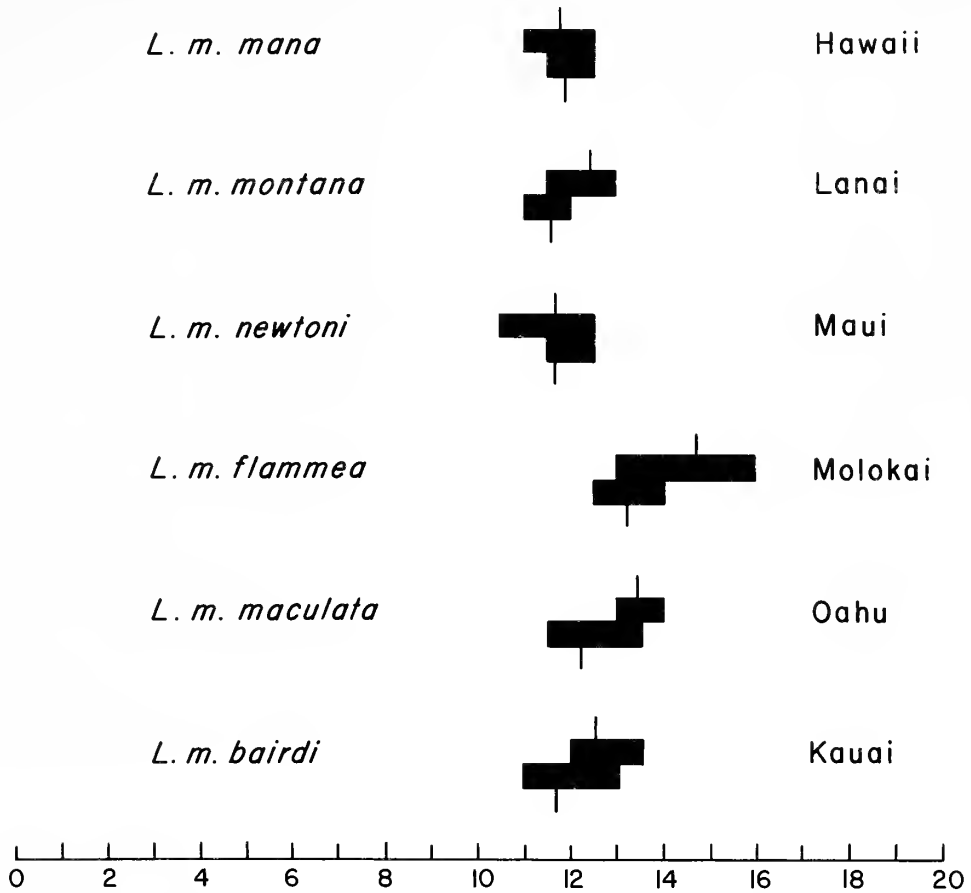

Fig. 21.—Bill length (culmen in mm) of *Loxops maculata* to show pattern of geographic variation; data taken from Amadon (1950). Range is indicated by the sold bar, the mean by the vertical line, males shown by the upper bar and females by the lower (taken from Bock, 1970:Fig. 3).

ground litter with their bills (Fig. 20). Species such as the Sage Thrasher (*Oreoscoptes montanus*, not shown) and the Brown Thrasher (*Toxostoma rufum*) have short, almost straight bills similar to those seen in most other members of the family. A gradual series of increasingly longer and decurved bills are seen in other species of *Toxostoma*. The extreme condition of bill length and curvature is seen in the California Thrasher (*T. redivivum*) and in the Crissal Thrasher (*T. dorsale*) which comprise a superspecies and may be conspecific (Mayr and Short, 1970: 68). Some of the steps in this series are between subspecies or members of a superspecies—for example, the longer and more decurved bill of *longicauda* compared to that of *rufum*.

The curve-billed thrashers use their beak as a pick-ax to dig into the ground and expose their insect prey. The forces involved are considerable judging from the size of the pieces of dirt and the distance they are thrown. Engels describes a suite of morphological changes in the skull and jaw musculature that are associated with the change in bill shape and feeding habits. One of the most obvious is a shift in insertion of a large portion of the M. pterygoideus from a position on the mandible as seen in most passerine birds, including the straight-billed thrashers, to a new position on the base of the braincase in the curve-billed species. The latter is analogous to the structure of the M. pterygoideus seen in the parrots (Psittaciformes). The change in bill structure (and associated internal morphology) and in feeding methods from *Oreoscoptes montanus* to *Toxostoma redivivum* is a major evolutionary change, although at the lower end of the scale, and one which can be clearly demonstrated by a sequential species analysis.

The Hawaiian honeycreepers (Passeriformes:

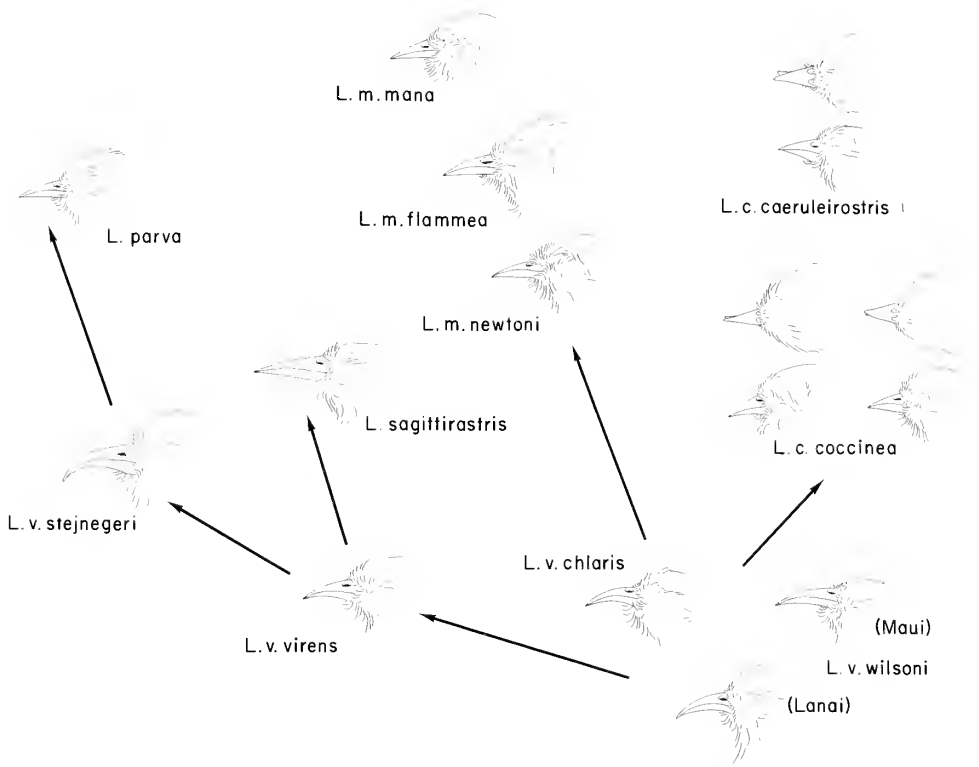

Fig. 22.—Presumed phylogeny of the species of *Loxops* from the ancestral *L. virens*, which stands at the base of the Psittirostrinae. *Loxops* may have evolved from an early member of the Drepanidinae (for example, *Ciridops*) (taken from Bock, 1970:Fig. 6).

Drepanididae) have been a favorite example among evolutionary biologists discussing macroevolution regardless of whether they advocate quantum or reductionistic explanations. They provide an excellent example of a sequential species analysis of a small, but quite diverse adaptive radiation (Bock, 1970) of feeding habits and bill structure. Unfortunately, many of the desired studies of functional and ecological morphology can never be done because of the widespread extinction of species and subspecies and because of the endangered status of a number of the still extant forms.

Several of the widespread species show a pattern of geographic variation from island to island (for example, the *Loxops virens* complex, Fig. 17, and *Loxops maculata*, Fig. 21). Some of the differences between these subspecies are large enough to permit coexistence of the two forms on the same island following invasion should intrinsic isolating mechanisms be fully developed. This had apparently happened in the appearance of *Loxops parva* and *Loxops sagittirostris* at opposite ends of the island chain. A period of exclusionary species interaction and divergence presumably occurred during the neosympatric period. The magnitude of difference observed between the species of the *Loxops virens* complex may be used as a measure of the degree of phyletic evolution on the microlevel in this group. Details of evolutionary change in *Loxops* (Fig. 22) have been presented by Richards and Bock (1973). Most interesting is that a crossed-billed form (*L. coccinea*) had evolved in which the jaw articulation and the jaw muscles have become highly asymmetrical. These species are insect and nectar feeders and include leaf gleaners (*virens*) bark probing creepers (*maculata*), a cross-billed opener of leaf buds and legume pods (*coccinea*), and two deep probing forms (*virens stejnegeri* and *sagittirostris*). Of the last, one is a prober with a decurved bill and the other with a straight bill.

A group of deep bark probers and nectar feeders evolved from a *stejnegeri*-like type, which gave rise to the *Hemignathus* complex (Fig. 23). This group is characterized by an elongated, decurved upper mandible and terminates in the long sickle-billed—*H. obscurus-procerus* superspecies. *Hemignathus wilsoni*, a member of the *lucidus* superspecies, acts like a woodpecker, exposing burrowing insects with

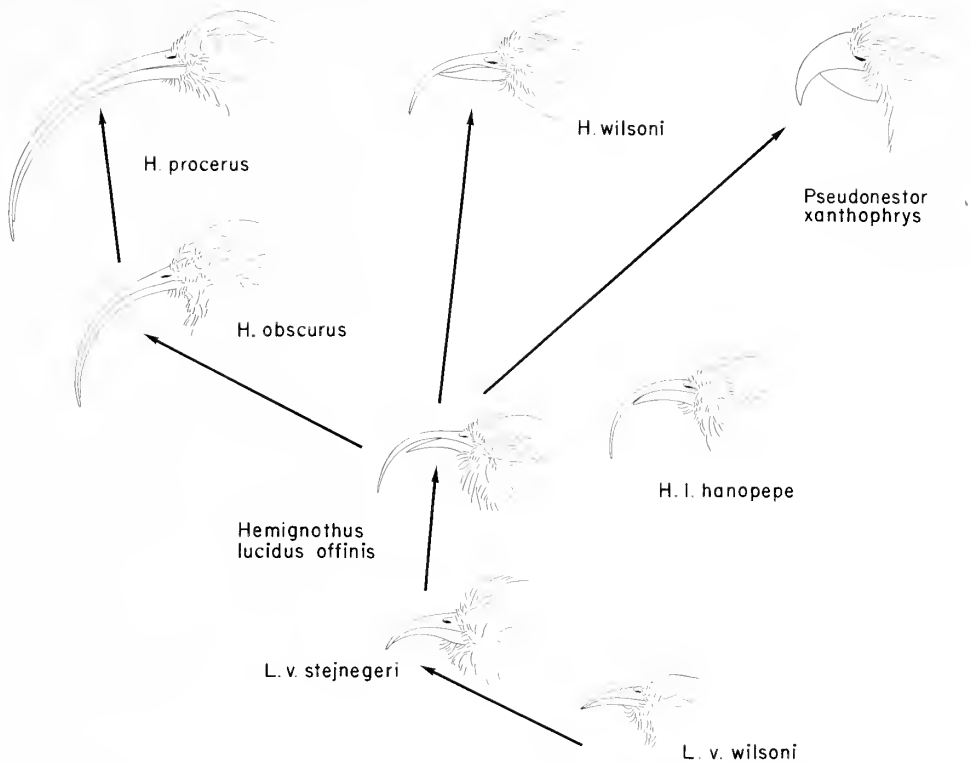

Fig. 23.—Presumed phylogeny of the species of *Hemignathus* and *Pseudonestor* from *L. v. stejnegeri*. The largest-billed members, *L. v. stejnegeri*, *H. l. hanapepe*, and *H. procerus*, of three successive species are sympatric on Kauai and show the consequences of exclusionary species interaction on this island (taken from Bock, 1970:Fig. 7).

its chisel-like mandible and probing for them with its decurved upper jaw. In another line, *Pseudonestor xanthophrys*, burrowing insects are exposed by crushing twigs with a heavy bill, which still has the decurved overshot upper jaw.

The final radiation of the Psittirostrinae arose from a *Pseudonestor*-like form and gave rise to the *Psittirostra* radiation (Fig. 24). This genus is comprised of a group of insect and plant eating forms. It gave rise to the widespread *Psittirostra psittacea* and its geographic representative *P. cantans* of the leeward islands and a radiation of five species of *Psittirostra*, including *psittacea*, on the island of Hawaii. This is probably the largest number of congeneric species of passerine birds found on a single small oceanic island.

Radiation of the second subfamily, the Drepanidinae, involves somewhat larger steps (Fig. 25), but ones not much greater than seen in the Psittirostrinae. These are all insect and nectar eating species.

Thus, the whole adaptive radiation of the Drepanididae can be explained on the basis of a sequential species analysis with the steps being of the magnitude observed between congeneric (for example, *Loxops*) species. Evolutionary change has been from a finch billed-like form, *Ciridops*, to the sickle-billed *Drepanis* in one subfamily and from the thin-billed leaf gleaner, *Loxops virens*, to a cross-billed *Loxops coccinea*, to the sickle-billed *Hemignathus procerus*, and to the heavy finch-billed *Psittirostra kona* in the other subfamily. The sickle-billed species are as specialized as any passerine birds and *Psittirostra kona* is among the heaviest-billed passeriform finches.

The entire radiation of the Drepanididae, which is surely an excellent example of macroevolution, can be explained completely by sequential species analysis. None of the observed steps in the Psittirostrinae are greater than species differences seen in the primitive genus *Loxops* and those in the Drepanidinae are scarcely greater. Anatomical details have been studied in part of this radiation (for example, *Loxops*, Richards and Bock, 1973). The rest remains to be done.

Perhaps the best support for the reductionistic

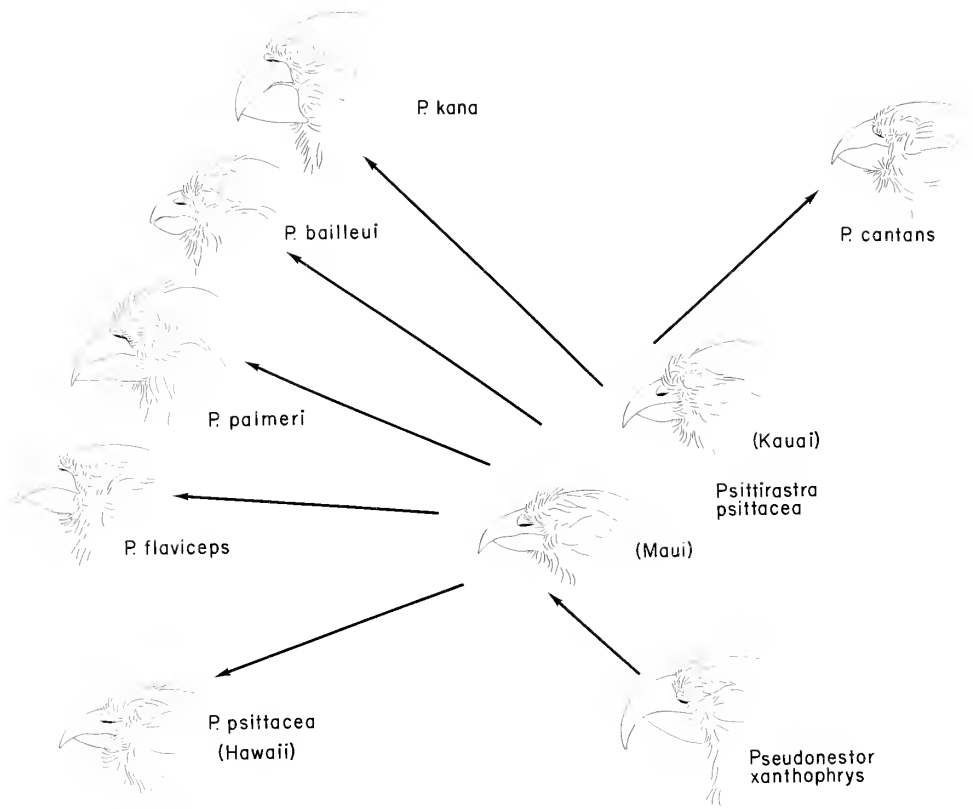

Fig. 24.—Presumed phylogeny of the species of *Psittirostra* from *Pseudonestor*. *Psittirostra contans* is a geographic representative of *P. psittacea* on the leeward islands. The five species, *psittacea, flaviceps, palmeri, bailleui,* and *kona,* are sympatric on Hawaii, but it is not clear whether these are all the result of multiple invasions from Maui or whether some speciated on Hawaii (taken from Bock, 1970:Fig. 8).

model for macroevolutionary change comes from a group of nectar feeding birds, the Australian honeyeaters (Passeriformes: Meliphagidae). Several genera of this family possess a unique articulation of the mandible—the ectethmoid-mandibular articulation in addition to the normal quadrate articulation (Bock and Morioka, 1971). This articulation is best developed in the genus *Melithreptus* (Fig. 26). The mandible has two articulations, one placed far anterior to the other. The ectethmoid articulation serves as a brace for the mandible when the lower jaw is fully adducted. It is analogous to the secondary articulation of the mandible between the internal process of the mandible and base of the braincase seen in many groups of birds (Bock, 1960). Both articulations are excellent analogues of the early stages of the evolution of the mammalian jaw articulation—perhaps the archetype of all major evolutionary changes.

The ectethmoid articulation is well developed and uniform in the seven species of *Melithreptus*. It consists of a distinct process on the mandibular ramus, a fossa in the ventral surface of the ectethmoid, and a definite diarthrosis between these bones. Details of the functional significance and possible biological role of this feature are presented by Bock and Morioka (1971); it appears to be associated with insect feeding with the use of a mucus-coated, sticky tongue. A similar structure is present, but variable in the genus *Manorina,* not closely related to *Melithreptus* within the meliphagids. In this genus, the articulation is absent in *Manorina melanophrys,* is present as a rudiment in *M. melanocephala* and present as a distinct feature, although less well developed than in *Melithreptus,* in *M. flavigula* (Fig. 27) and *M. melanotis,* a pair of sibling species. A rudimentary articulation is present in the New Guinean genus *Ptiloprora* (for example, *P. guisei*) but the distribution of the ectethmoid articulation in this genus is not known with certainty.

Recent observations (Bock, unpublished) fill in

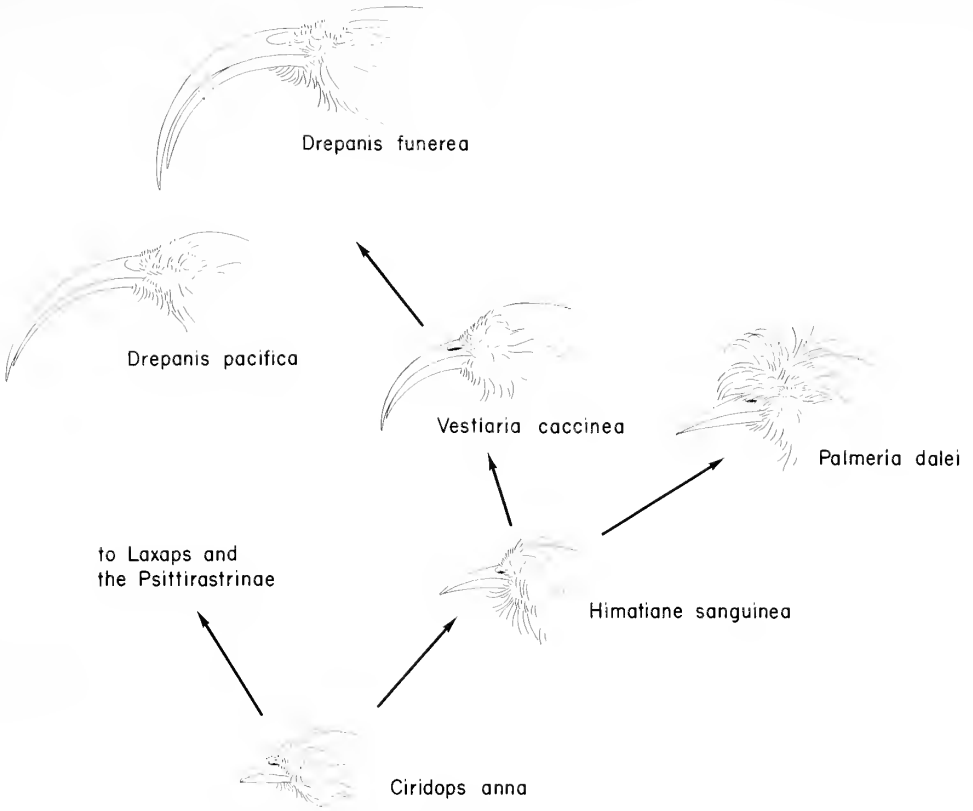

Fig. 25.—Presumed phylogeny of the genera of the Drepanidinae from the ancestral genus *Ciridops*, which may be representative of the founding stock of the Hawaiian honeycreepers (Drepanididae) (taken from Bock, 1970:Fig. 1).

more details of the sequential species analysis illustrating the evolution of the ectethmoid articulation. Two postfledging individuals of *Melithreptus laetior* were examined, which still lack the process suggesting that it arises late in ontogeny. Most interesting is that specimens of local populations of several species of the genus *Meliphaga* (for example, *virescens*, *keartlandi*, *fusca*, *plumula*, *unicolor*, *penicillata*, and *flavescens*) showed that the ectethmoid articulation is present as an individual variation in these populations from completely lacking to an extremely poorly developed rudiment to a definite rudiment as well developed as in *Manorina melanocephala*. Some of these species of

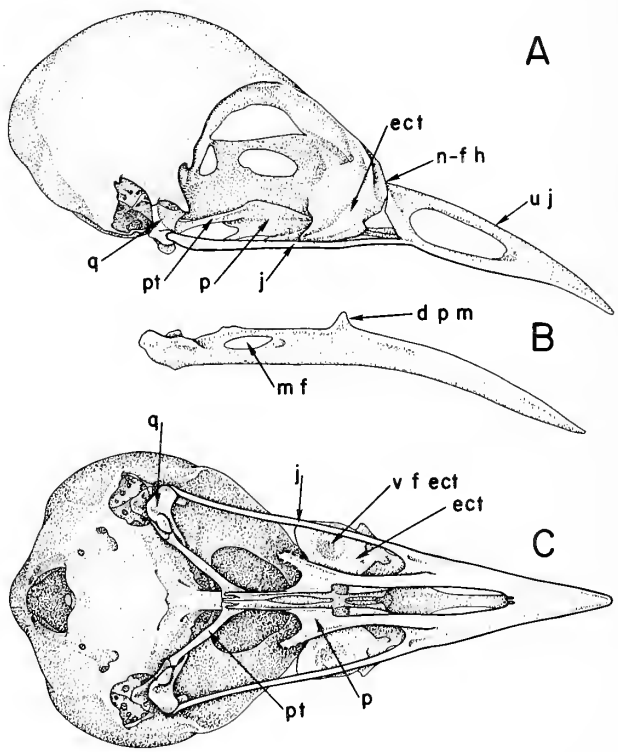

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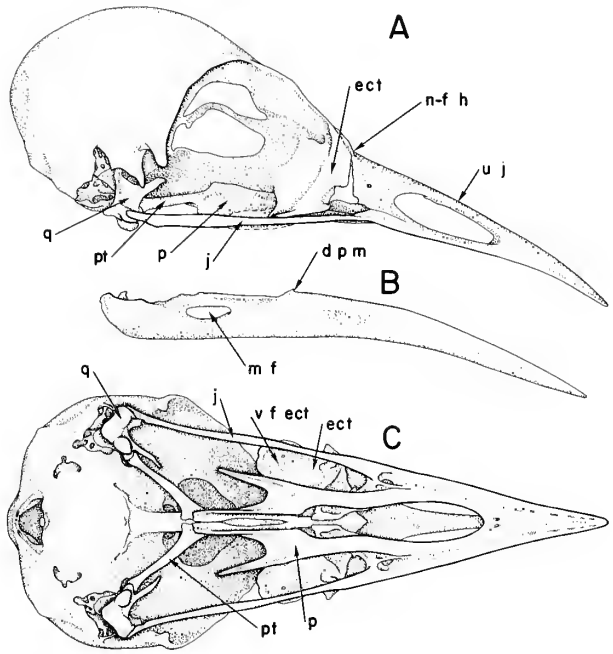
Fig. 26.—Skull and mandible of *Melithreptus albogularis* (USNM 347,693). (A) Lateral view of the skull. (B) Lateral view of the mandible. (C) Ventral view of the skull. The ecethmoid articulation of the mandible is formed by the dorsal process of the mandible (d p m) with the ventral fossa of the ectethmoid (v f ect) (taken from Bock and Morioka, 1971:Fig. 1).



Meliphaga possessing the ectethmoid articulation as an individual variation are widespread throughout Australia.

Thus, the sequential species analysis of the evolution of the ectethmoid-mandibular articulation in the Meliphagidae shows that this feature is absent in most members of the family, that it exists as an individual variant from absent to a definite rudiment in populations of several species of *Meliphaga*, that it varies from being absent in one species of *Manorina*, a rudiment in another species and well developed in two other species but without any great

←

Fig. 27.—Skull and mandible of *Manorina melanotis* (USNM 345,011). (A) Lateral view of the skull. (B) Lateral view of the mandible. (C) Ventral view of the skull. The ectethmoid articulation of the mandible in this genus is less developed than that seen in *Melithreptus* (taken from Bock and Morioka, 1971:Fig. 5).

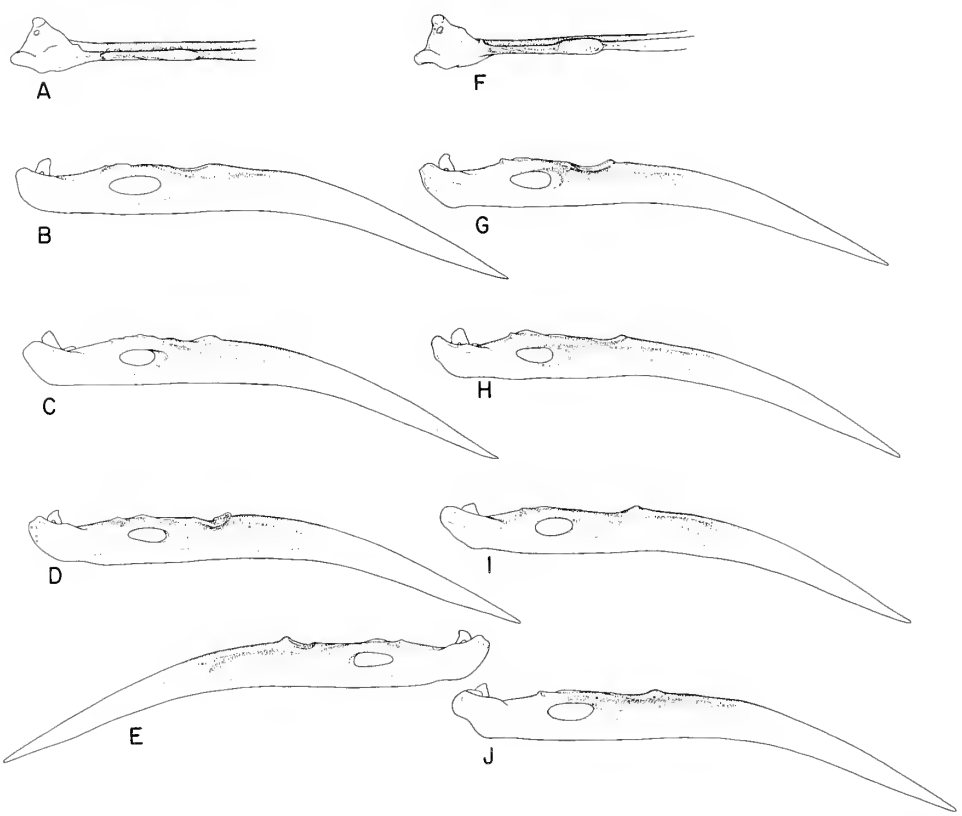


Fig. 28.—Lateral view of the right mandibular rami of a series of seven specimens of *Manorina flavigula* (AMNH uncataloged) to illustrate individual variation in the ectethmoid-mandibular articulation as reflected in the dorsal process of the mandible. Fig. A is the dorsal view of B and Fig. F is the dorsal view of G. Fig. E is the left ramus of the mandible shown in D; the mandible was skewed slightly to the right in this bird. Note the abnormal lip of bone of the dorsal process in Fig. D, which is a result of the bones of the articulation rubbing together incorrectly (taken from Bock and Morioka, 1971:Fig. 8).

variation in any of these species aside from expected individual variation (Fig. 27), and that it is very well developed in all species of *Melithreptus* without any noticable variation between species in spite of the character displacement in feeding habits and bill size of *M. validirostris* and *M. affinis* on Tasmania (Keast, 1968). Moreover, ontogenetic development of this structure is very late in the ontogeny of the individual with no sign of the mandibular process and articulation in adult-sized, fledged young birds.

Thus, the available stages in the horizontal sequential species analysis of the ectethmoid-mandibular articulation provides an analogy to all steps desired in the vertical phyletic evolution of this feature from absent to well developed. All of these stages are taken from species in the same family and some from closely related genera (for example, *Meliphaga* and *Melithreptus*). Many of the morphological details are described with suggestions on the function of this feature (Bock and Morioka, 1971). Only speculations are available on the biological role of this feature and the details of the ecological factors providing selection forces favoring its evolution.

Sufficient variation exists in the structure of the many avian families possessing the secondary (=basitemporal) articulation of the mandible (Bock, 1960) that a similar sequential species analysis could be developed.

In the examples presented, especially for the ectethmoid-mandibular articulation in the Melphagidae, the sequential species analysis provides observations on which to test the hypothesis that macroevolution occurs by successive microevolutionary steps and under the control of the known mechanisms of phyletic microevolutionary change.

CONCLUSIONS

The model of macroevolutionary explanation presented herein argues that all phyletic evolutionary change, small and large, occurs by the action of the same causal evolutionary mechanisms. Macroevolution is simply the consequence of additive microevolutionary change. This explanatory model is silent on rates of these evolutionary changes; presumably, macroevolution occurs at much faster rates than generally supposed. The synthetic or reductionistic model of major evolutionary change is adapted throughout in that selection acts constantly. It can be tested via a conceptual transformation to analogous horizontal sequences which provide suitable pseudophylogenies. These tests can be labelled sequential species analyses.

If macroevolution can be reduced to an additive sequence of microevolutionary steps occurring under the known mechanisms of phyletic evolution, then macroevolution is reduced to microevolution and is fully explained in terms of mechanisms acting on this level. No additional steps, for example, saltation, or additional evolutionary mechanisms are needed for a complete explanation of macroevolution.

Additional studies of sequential species analyses are needed to provide additional tests of the synthetic model of macroevolution and to provide details on the evolution of particular features. These are best done on species-rich genera or groups of closely related genera, and must be comparative studies of descriptive, functional, and ecological morphology. Only after a number of such studies are available from all groups of organisms can we have confidence in the testing of explanatory models of macroevolution.

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CANALIZATION MODEL OF CHROMOSOMAL EVOLUTION

John W. Bickham

Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, Texas 77843

Robert J. Baker

The Museum and Department of Biological Sciences, Texas Tech University, Lubbock, Texas 79409

ABSTRACT

The canalization model implies that the karyotype is a significant aspect in the "adaptive strategy" of an organism and that for each "adaptive zone" there is an optimum karyotype that can be evolved by rearrangements in the karyotype. When an organism invades a new adaptive zone there will be an initial period of karyotypic rearrangement that will continue until the optimum or near optimum karyotype is evolved. After evolution of the optimum karyotype additional evolution will be primarily by genic and morphological mechanisms, not chromosomal rearrangements. An implication of the canalization model is that higher categories are not merely "pigeonholes" that man has created but are real, involving a sequence of orderly events.

INTRODUCTION

The canalization model explains the remarkable difference in patterns of chromosomal variation among different animal groups as a function of the degree to which the optimum karyotype has been achieved for the lineages in an adaptive zone. The taxonomic level at which chromosomal variation occurs will generally be a function of the evolutionary time that a lineage has occupied an adaptive zone. Our model emphasizes the adaptive significance of the karyotype, whereas previous models (White, 1968; Hall, 1973; Wilson et al., 1975) have placed emphasis on chance events that permit chromosomal evolution.

REVIEW OF THE MODELS OF CHROMOSOMAL EVOLUTION IN ANIMALS

Models of Chromosomal Speciation

Cytogenetic studies of Australian flightless morabine grasshoppers by White and colleagues have led to the model of stasipatric speciation (White, 1968, 1974, 1978; White et al., 1967). These animals show a pattern of chromosomal diversity in which virtually every species or race possesses a distinct chromosomal complement, with chromosomal types distributed parapatrically with a slight area of overlap. Hybridization takes place within the zone of overlap, but sterility barriers exist between chromosomally characterized populations. Chance events (genetic drift) or perhaps meiotic drive are responsible for the fixation of chromosomal rearrangements in small, localized demes. These animals have low vagility and a deme may be as small as the number of individuals on a single shrub; therefore, genetic drift is probable. Heterozygotes are thought to be of lower fitness due to meiotic malassortment. If the homozygotes possessing the new arrangement are more fit than the heterozygotes and the parental homozygotes, it can spread into previously unoccupied territory and/or into the territory of the parental population (displacing the parental type) until an equilibrium is reached, with a small zone of overlap at the border of the two populations.

Although White (1968, 1974, 1978) believed the process of stasipatric speciation could take place at the periphery or well within the distributional range of a species, other workers contend that the establishment of chromosomal rearrangements will be restricted to small peripheral populations (Bush, 1975; Key, 1968; Patton, 1969).

Bush (1975) has divided models of speciation into four basic kinds, with chromosomal evolution associated with two—parapatric speciation, which is essentially the stasipatric model of White as ammended by subsequent workers (Bush, 1975; Key, 1968; Patton, 1969), and speciation by the founder effect.

Hall (1973) has proposed a "cascading chromo-

somal speciation" model that is similar to the stasipatric model of White. The cascading model is based on chromosomal variation in a wood crevice inhabiting species of iguanid lizard (*Sceloporus grammicus*) (Hall and Selander, 1973). Like the stasipatric model, Hall envisions chromosomal rearrangements becoming fixed by genetic drift in small, inbred demes, and subsequent range expansion due to competitive advantage. The cascading model differs from other models in that Hall envisions a linear pattern to chromosomal speciation, an apparent rapid nature of chromosomal speciation, and alternative mechanics of contact hybridization.

The above mentioned models possess a common theme. Chromosomal rearrangements act as cytogenetic isolating mechansims that serve to maintain species integrity, because of negative heterosis. Chromosomal rearrangements come to fixation by chance events in small, inbred demes. Thus, animals that speciate in this way are characterized by low vagility or social structure that promotes inbreeding (Arnason, 1972; Bush, 1975). Natural selection plays a positive role in the process only after a population of the new homozygote is established. Selection accounts for subsequent expansion of the range of the new chromosomal type, although none of the above models state precisely why or how the chromosomal alteration gives new species an adaptive advantage.

Significance of Chromosomal Variation

A series of papers by A. C. Wilson and colleagues (Wilson, 1976; Wilson et al., 1974*a*, 1974*b*, 1975; Maxson and Wilson, 1975; Prager and Wilson, 1975) have developed hypotheses to explain the role that chromosomal changes have played in the evolution of organisms. Based on studies of placental mammals and frogs (Wilson et al., 1974*a*, 1974*b*; Maxson and Wilson, 1975) and birds (Prager and Wilson, 1975), they conclude that organismal (morphological) evolution is correlated with chromosomal but not genic evolution. Their reasoning is as follows. Frogs have experienced a slow rate of morphological change, are an old group (150 million years) with over 3,000 species, but consist of only a single order. Placental mammals are a younger group (75 million years) of about 4,600 species and 16–20 orders, which have evolved rapidly at the organismal level. Both groups have evolved at an equal rate on the genic level; however, based on diploid and fundamental number, mammals have experienced considerably more rapid chromosomal evolution. Birds follow the same pattern as frogs (Prager and Wilson, 1975).

Their explanation for this phenomenon is that chromosomal changes are a source of genetic regulatory change. The evidence for this is largely indirect. It is known from genetics of microorganisms that gene regulation can play an important role in the adaptive process (Wilson, 1976). Chromosomal rearrangements can also effect the regulation of structural genes by placing them next to a different set of gene loci, the "position effect" known in *Drosophila* (Bahn, 1971). Wilson and colleagues point out that frogs (Wilson et al., 1974*a*) and birds (Prager and Wilson, 1975) have the ability to form hybrids between species that are considerably more genically distinct than do placental mammals, which they interpret as meaning that chromosomal changes alter the regulatory systems of genes which result in the inability of mammals (which have extensive chromosomal evolution) to form interspecific hybrids. They conclude that genetic regulatory changes are a primary source of the more rapid organismal evolution of mammals.

Wilson et al. (1975) and Bush (1975) suggest that placental mammals have achieved a high degree of inbreeding and small population size due to their social structure. The small population size facilitates fixation of chromosomal rearrangements that are thought to be deleterious in the heterozygous state. Thus, drift is again ascribed as a requisite mechanism for evolution of new chromosomal complements. Frogs, and other lower vertebrates, are presumed to have a lower rate of karyotypic change than placental mammals because they do not have the complex social behavior that produces small deme size (see also Bush et al., 1977).

PATTERNS OF CHROMOSOMAL VARIATION IN DIVERSE GROUPS OF VERTEBRATES

Patterns of chromosomal variation within orders of vertebrates (especially turtles, Order Testudines, and bats, Order Chiroptera) have led us to question the above models as the best explanation of patterns of chromosomal variation in vertebrates. All orders discussed below encompass extensive chromosomal diversity, but the taxonomic levels that exhibit chromosomal stability vary between orders.

Table 1.—*The families and subfamilies of cryptodiran turtles with geological ages, number of species, and chromosomal diversity.*

Group	No. species	Age	2*n* (followed by no. of known species)
Kinosternidae		Oligocene	
Kinosterninae	19		56 (12), Unknown (7)
Staurotypinae	3		54 (3)
Carettochelyidae	1	Eocene	Unknown (1)
Trionychidae		Cretaceous	
Trionychinae	18		52–54 (1), 64 (1), 66 (6), Unknown (10)
Cyclanorbinae	5		66 (1), Unknown (4)
Dermatemyidae	1	Cretaceous	Unknown (1)
Dermochelidae	1	Eocene	Unknown (1)
Cheloniidae	6	Cretaceous	56 (2), 58 (1), Unknown (3)
Chelydridae		Paleocene	
Chelydrinae	3		52 (3)
Platysterninae	1		54 (1)
Emydidae		Paleocene	
Emydinae	37		50 (22), Unknown (15)
Batagurinae	47		50 (2), 52 (12), 56 (1), Unknown (32)
Testudinidae	38	Eocene	52 (6), Unknown (32)
Total	186		

The factor that seems to be correlated with this pattern of stability is the geological age of the group—older groups exhibit chromosomal stability at higher taxonomic levels than is characteristic of younger groups. Some data which support these conclusions follow.

Order Testudines

Chromosomal evolution.—The S-necked turtles, Infraorder Cryptodira of Gaffney (1975), which encompass some 200 species and 10 families, are distributed on all of the major land masses, except Antarctica (albeit marine turtles are the only representatives in Australia), and even on many of the oceanic islands (for example, the tortoises of the Galapagos and Aldabra islands).

Examination of the geological age and the available diploid numbers of the families and subfamilies of Cryptodira (Table 1) reveals karyotypic stability within each family or subfamily. For example, each of the two subfamilies of Kinosternidae is characterized by a single diploid number (Staurotypinae $2n = 54$, Kinosterinae $2n = 56$), the subfamily Emydinae are all $2n = 50$, nearly all trionychids so far studied are $2n = 66$, all testudinids studied are $2n = 52$.

Conservatism in diploid numbers is seen in standard and banded karyotypes. G-band studies of the emydine turtles revealed no variation in karyotypes of the species studied (Bickham and Baker, 1976*a*, 1976*b*). Fig. 1 shows G-banded karyotypes of three morphologically diverse genera of emydines where no karyotypic differences were detected. Karyotypes of the emydid subfamily Batagurinae are more variable ($2n = 50, 52, 56$) than those of the emydines. However, in almost all species the diploid number is 52 with two species being reported as 50, and one species, 56 (this latter species, *Rhinoclemys punctularia*, differs from a $2n = 52$ congener by the addition of some heterochromatic microchromosomes). Comparisons of banded karyotypes between the two subfamilies indicate a high degree of homology (Bickham and Baker, 1976*a*) in that all macrochromosomes of the emydines can be identified in such batagurines as *Sacalia*. *Rhinoclemys* has fewer macrochromosomes and a higher number of microchromosomes, but the macrochromosomes present can be identified in emydines and other batagurines. Banding data for chelydrids, emydids, and kinosternids were compared by Sites et al. (1979) and nearly all of the macrochromosomes appear to have homologues in each of the three families although there appears to be some differences between each. In all testudinids (tortoises) reported in the literature, the diploid number is 52 (Bickham and Baker, 1976*a*, 1976*b*; Stock, 1972), and the karyotypes reported for certain species of *Geochelone* are indistinguishable from those of some $2n = 52$ batagurines (Bickham and Baker, 1976*a*).

The family Kinosternidae is a fairly abundant group restricted to the New World. A single karyotype is known for the entire subfamily Kinosterinae (two genera, *ca.* 20 species, Table 1). The subfamily Staurotypinae is characterized by a different diploid number with several structural karyotypic differences, but all staurotypines have a virtually identical karyotype (Bull et al., 1974). Many of the kinosternid macrochromosomes have homologues in emydids and chelydrids. Fig. 2 is a comparison of the banded karyotypes of a kinosternine and an

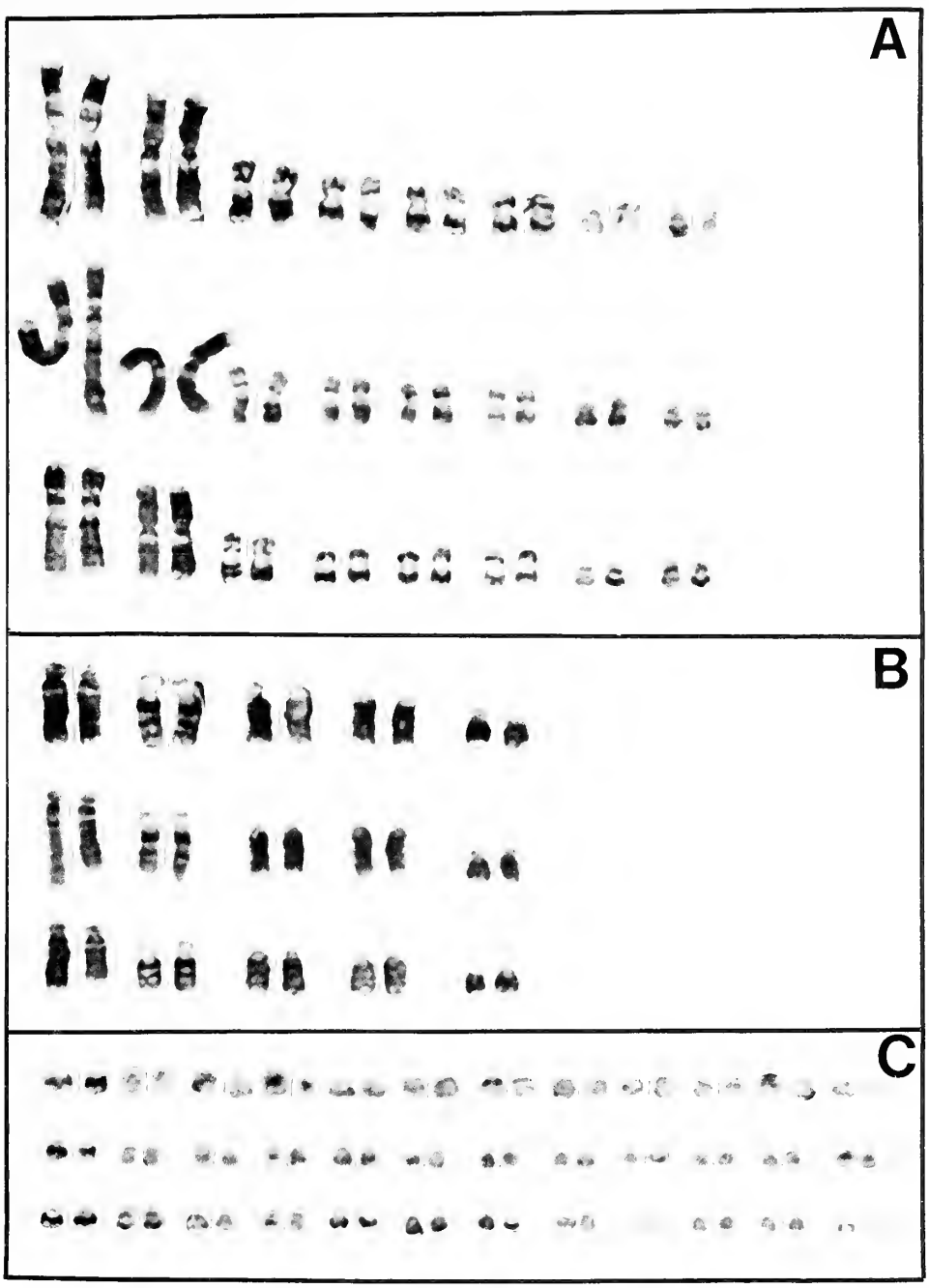

Fig. 1.—G-band comparison of three morphologically diverse genera of emydine turtles to demonstrate karyotypic stability within higher categories of turtles. The chromosomes are arranged into three groups (A, B, C) according to Bickham (1975). The top row in each group is from *Chrysemys decorata*, $2n = 50$; the middle row in each group is from *Graptemys pseudogeographica*, $2n = 50$; the bottom row in each group is from *Terapene carolina*, $2n = 50$. No differences in banding pattern can be detected in the macrochromosomes (groups A and B); the microchromosomes (group C) cannot be reliably identified, but all three species possess 12 pairs.

emydine. Although most of the macrochromosomes appear to be homologous, there are several that have undergone rearrangements since divergence from a common ancestor.

The family Trionychidae is both morphologically and chromosomally quite distinct from the families discussed above. They are characterized by a $2n = 66$ karyotype except for one known exception (Gorman, 1973).

Morphological evolution.—Turtles probably

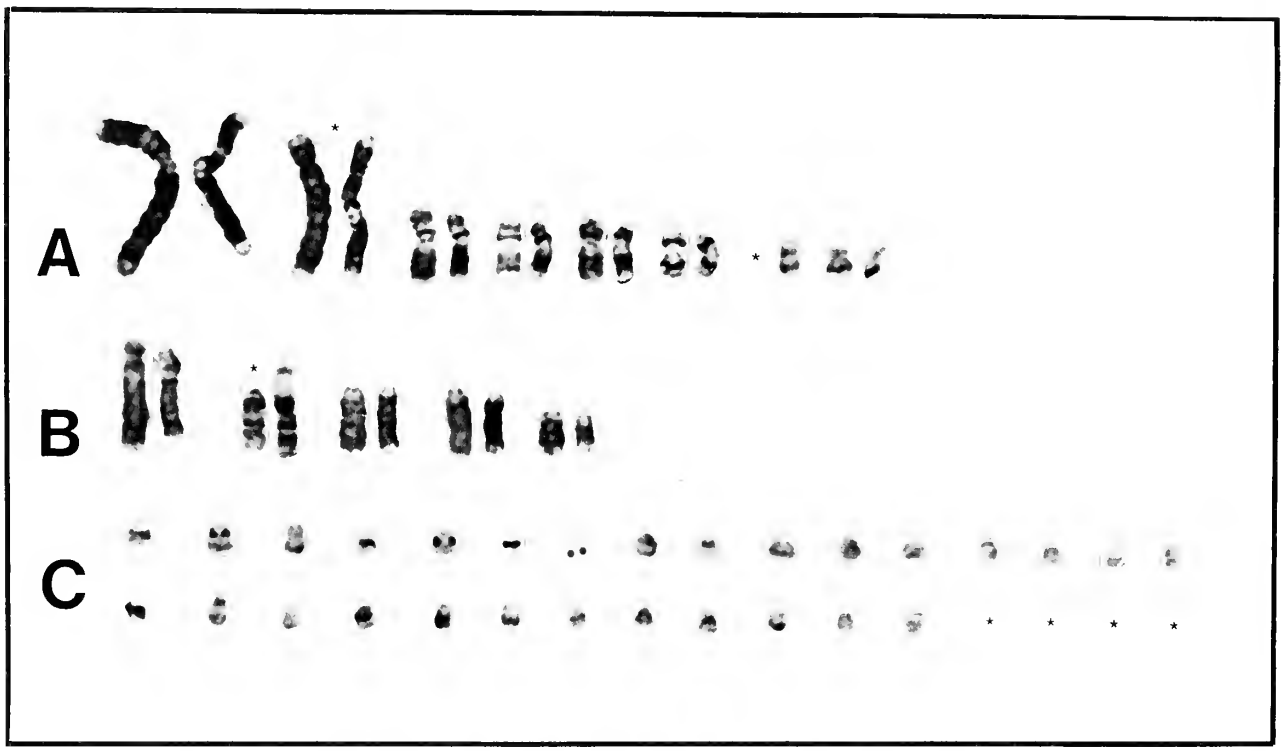

Fig. 2.—G-band comparison of a kinosternid and an emydid turtle to demonstrate the degree of chromosomal homology between higher categories of turtles. In groups A and B the right member of each pair is from *Chrysemys concinna* (Emydidae) $2n = 50$, and the left member is from *Sternotherus minor* (Kinosternidae) $2n = 56$. The microchromosomes (group C) cannot be reliably identified, the top row is from *Sternotherus* and the bottom row is from *Chrysemys*. An asterisk indicates an identifiable chromosomal difference between the two species. The second pair in group A differs in centromere position; the seventh pair in group A differs by the absence of this chromosome from the *Sternotherus* complement. The second pair in Group B is acrocentric in *Sternotherus* and subtelocentric in *Chrysemys*. There are four more pairs of group C microchromosomes in *Sternotherus* than there are in *Chrysemys*.

originated in the lower Triassic and had already undergone a long period of evolution before the two modern groups (pleurodires and cryptodires) first appear in the Jurassic. Cryptodiran families are relatively old (Table 1), ranging from the Dermatemyidae (no chromosomal data) and the Trionychidae from the Cretaceous, to the Kinosternidae from the Oligocene. No family is of a relatively young age.

Although karyotypic data are lacking for over half of the species and even some families of cryptodires, there is a definite pattern to the variation already documented. Higher categories (families and subfamilies) are, for the most part, characterized by a single, almost unvarying karyotype, but each group is distinct from the others. At the lower levels of classification (genus and species) there is almost no variation, which indicates that recent turtles have undergone speciation in the absence of chromosomal rearrangements. However, the differences seen between higher categories indicate that during the origin and establishment of modern families and subfamilies there was a period of chromosomal evolution. This has been followed by morphological diversification within the larger families that was not accompanied by significant amounts of chromosomal evolution. An example of morphological diversification with the absence of chromosome diversity is found in the diverse genera *Graptemys, Chrysemys, Terrapene,* and others in the Emydinae that all have identical karyotypes (Fig. 1). The same pattern is present in other families or subfamilies of turtles.

Order Chiroptera

Our discussion will be limited to the Suborder Microchiroptera, which is nearly worldwide in distribution and encompasses 16 extant families and more than 720 living species. Reviews of bat cytosystematics (Baker, 1970; Capanna and Civitelli,

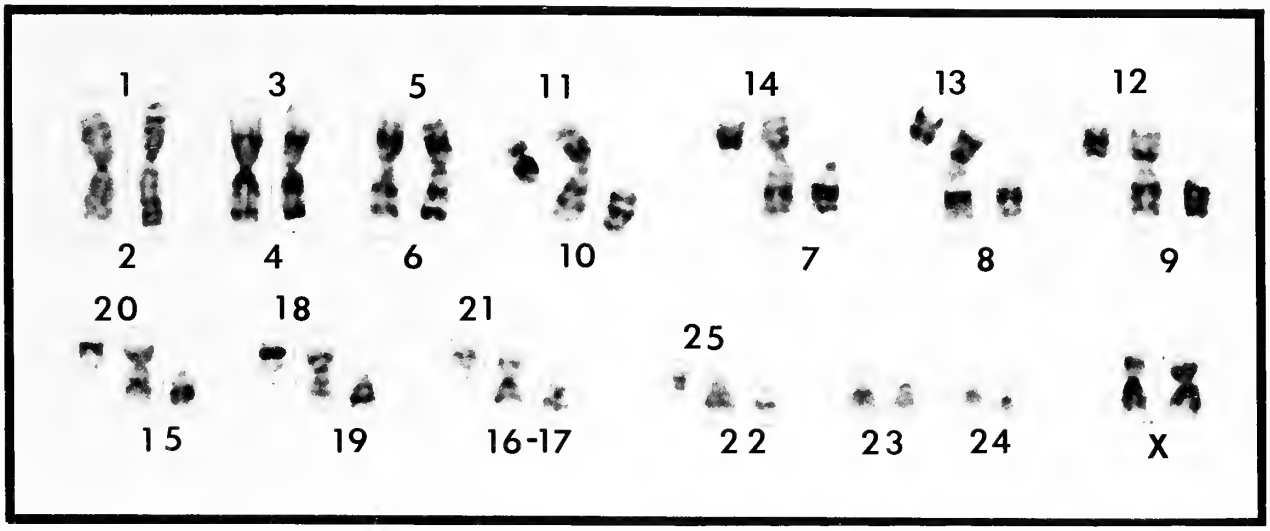

Fig. 3.—G-band comparison of two morphologically distinct genera of vespertilionid bats to demonstrate the degree of chromosomal homology within higher categories of bats. Chromosomal arms are identified and numbered according to Bickham (1979*b*). The left member of the first three pairs is from *Lasiurus borealis* $2n = 28$, the right member is from *Myotis sodalis* $2n = 44$. In the next eight triplets, the biarmed element is from *Lasiurus* and the acrocentric homologues are from *Myotis*. In pairs 23, 24, and X the left member is from *Lasiurus*. Centric fusions account for nearly all of the variation between these species.

1970; Matthey, 1973) are somewhat out of date, but they allow an assessment of the patterns of chromosomal variation in bat evolution.

Vespertilionid chromosomal evolution.—The largest family of bats (287 species, 33 genera, and six subfamilies) has been studied reasonably well for standard and banded karyotypes (Ando et al., 1977; Baker, 1970; Bickham, 1979*a*; Capanna and Civitelli, 1970). Most genera of vespertilionids are characterized by a single diploid number and karyotype; for example, genus *Myotis* (Bickham, 1979*b*) where all species studied possess virtually identical karyotypes with a $2n = 44$. Members of *Eptesicus* studied have $2n = 50$, except one African species (Peterson and Nagorsen, 1975). Members of *Lasiurus* have $2n = 28$ except *L. intermedius* with $2n = 26$. Members of the genus *Plecotus* all have $2n = 32$, as does the closely related genus *Barbastella*.

The two genera of vespertilionids that differ from this pattern of chromosomal stability are *Rhogeesa* ($2n = 30$–44) and *Pipistrellus* ($2n = 26$–44). The differences between genera and within the variable genera can be explained primarily by Robertsonian mechanisms (centric fusion and fission of whole arms), whereas non-Robertsonian rearrangements (such as inversions and reciprocal translocations) are rare (Bickham, 1979*a*; Bickham and Baker, 1977). Thus, the general pattern of chromosomal variation seen within vespertilionids is one of conservatism below the generic level but with nearly all genera differing from one another by Robertsonian variation. Because Robertsonian mechanisms are involved, the basic chromosomal banding pattern is conserved in vespertilionids to the extent that the chromosomal banding sequence of all segments can be identified in such disparate forms as *Myotis* ($2n = 44$) and *Lasiurus* ($2n = 28$) (see Fig. 3).

Phyllostomatid chromosomal evolution.—This family shows a pattern of variation similar to that of the Vespertilionidae. Recent studies (Baker, 1978; Gardner, 1977) reveal that a few genera (that is, *Macrotus, Uroderma, Vampyressa,* and *Micronycteris*) show interspecific or intraspecific variation. Except for these few genera, most of the chromosomal variation in phyllostomatids is at the generic level or higher. Banding studies demonstrate that in most cases homologous elements can be demonstrated among all genera (Baker and Bass, 1979; Baker et al., 1979; Patton and Baker, 1979). With some notable exceptions, intergeneric variation is due to Robertsonian change and G-banding patterns are conserved.

Although diverse genera within the families Vespertilionidae and Phyllostomatidae show considerable banding homology, comparisons made between species from different families may show little banding homology. Fig. 4 shows a banding

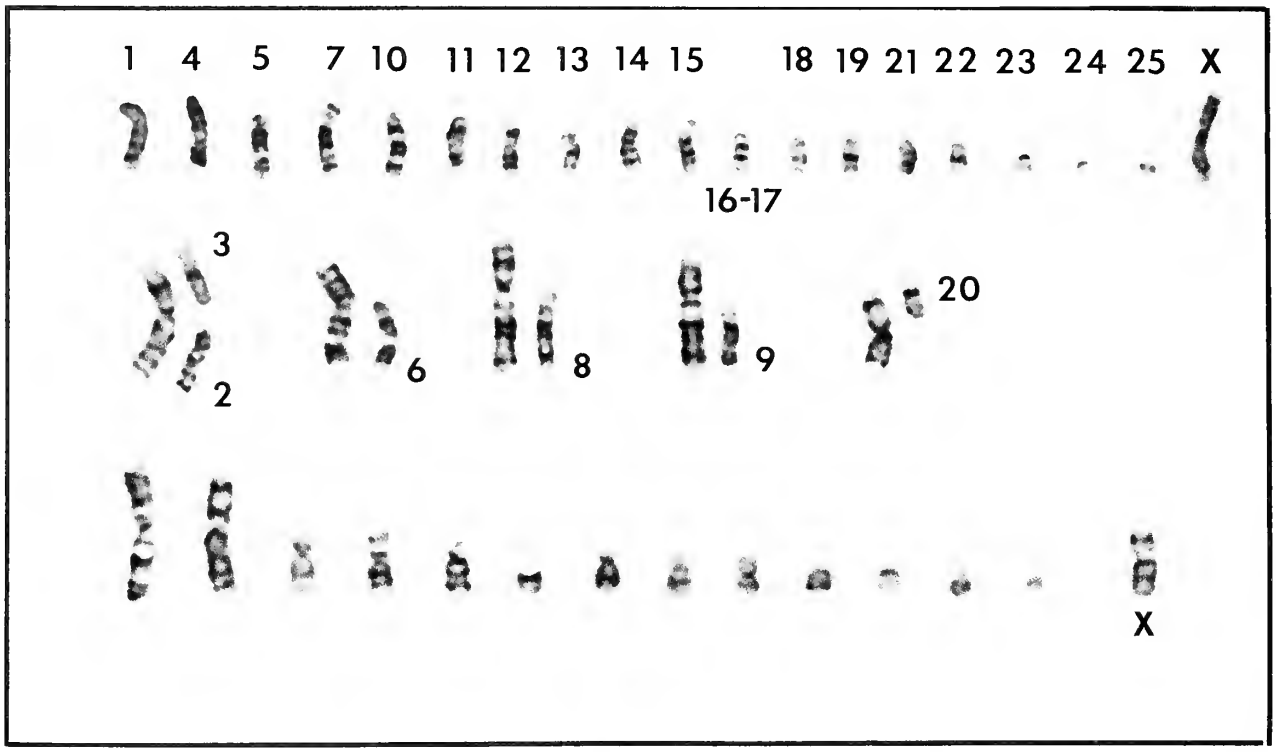

Fig. 4.—G-band comparison of a mormoopid and a vespertilionid bat to show the slight amount of chromosomal homology characteristic of interfamilial comparisons of bats. The top row are chromosomes from *Eptesicus fuscus* (Vespertilionidae) $2n = 50$ that do not show identifiable homologues in *Mormoops blainvilli* (Mormoopidae) $2n = 38$. The middle row are homologous elements identifiable between the two species, the acrocentrics are from *Eptesicus* and the biarmed chromosomes are from *Mormoops*. The bottom row are unpaired elements from *Mormoops*. Of the 24 autosomal arms of *Eptesicus*, only six can be identified in *Mormoops*, a considerable number of non-Robertsonian changes have taken place since the divergence of these two species. The *Eptesicus* chromosomes are numbered according to Bickham (1979*b*).

Table 2.—*The families of microchiropteran bats, with number of species and geological ages.*

Family	No. extant species	Age
Rhinopomatidae	2	Recent
Emballonuridae	44	Upper Eocene–Lower Oligocene
Noctilionidae	2	Recent
Nycteridae	13	Recent
Megadermatidae	5	Upper Eocene–Lower Oligocene
Rhinolophidae	128	Middle Eocene
Phyllostomatidae	120	Miocene
Mormoopidae	8	Pleistocene
Natalidae	4	Pleistocene
Furipteridae	2	Recent
Thyropteridae	2	Recent
Myzopodidae	1	Recent
Vespertilionidae	283	Upper Eocene
Mystacinidae	1	Recent
Molossidae	82	Upper Oligocene
Total	697	

comparison between a vespertilionid and mormoopid. Only six autosomal arms can be identified between the two. Thus, the kinds of rearrangements involved in separating these two families include a sufficient number of non-Robertsonian changes to make arm identification impossible. Few interfamilial homologies can be identified among the families Vespertilionidae, Molossidae, and Phyllostomatidae. An exception is seen in comparisons of Phyllostomatidae, Noctilionidae, and Mormoopidae (Baker and Bass, 1979; Baker et al., 1979; Patton and Baker, 1979). These three families are related at the superfamily level and the mormoopids and phyllostomatids were considered confamilial in the past.

To summarize the general pattern of chromosomal variation in bats, there is a consistent stability below the generic level, considerable variation among genera or closely related groups of genera, remarkable conservatism of banding patterns within

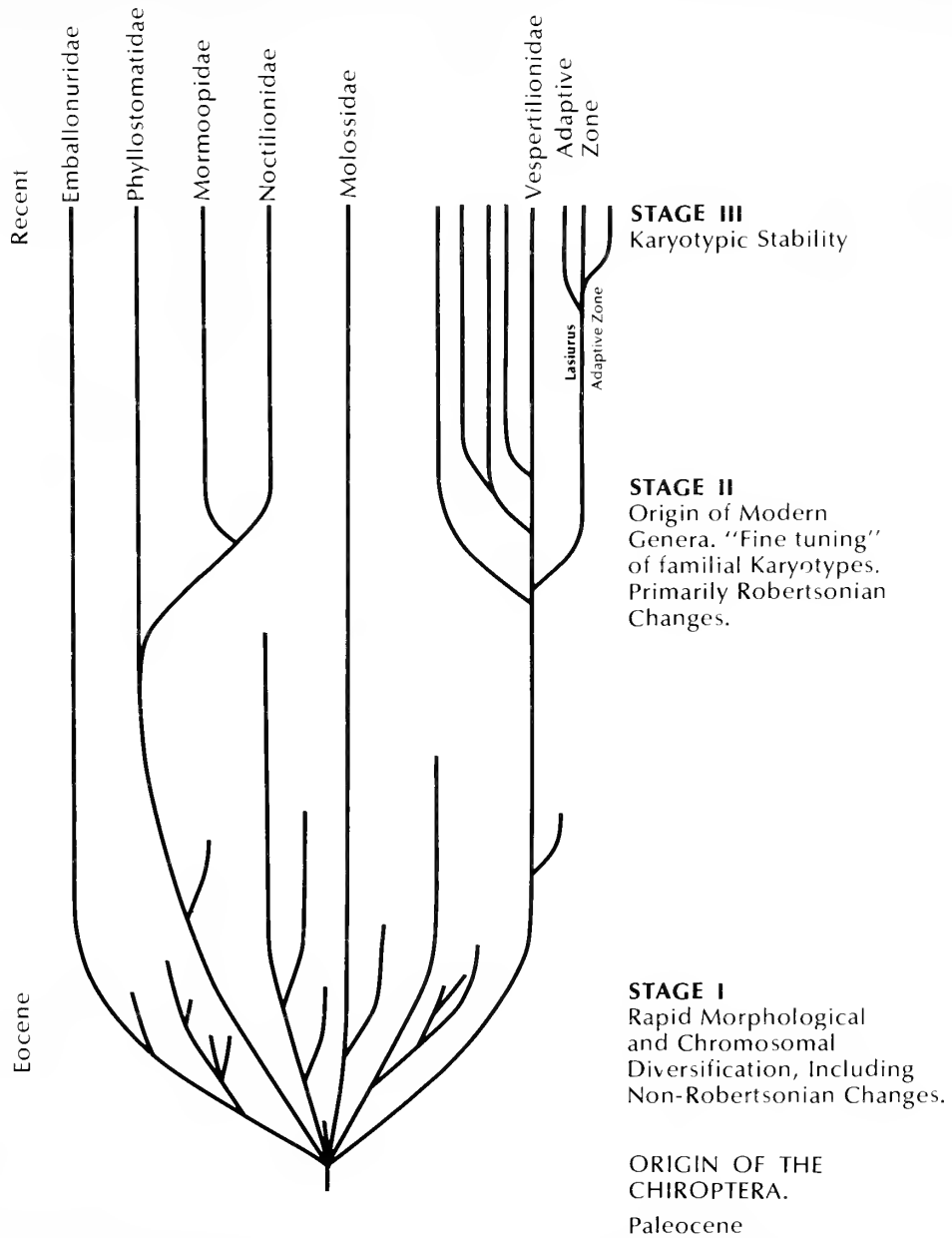

Fig. 5.—Schematic representation of the events characteristic of the canalization model as related to some bat families.

families, but very little homology between many families. It appears that Robertsonian mechanisms are most important within families (that is, have been used to rearrange the karyotypes characteristic of different genera) but non-Robertsonian changes are more important in explaining the karyotypic differences between such families as Phyllostomatidae, Molossidae, and Vespertilionidae.

Morphological evolution.—Bats are thought to have evolved from an arboreal insectivore sometime during the Paleocene (Fig. 5). The fossil record is not as good as for most other mammals, and there are no fossils of any transitional forms. An early Eocene bat, *Icaronycteris index* from Wyoming, is already morphologically highly advanced and, for the most part, a typical bat. Thus, bats apparently underwent a period of rapid development during the Paleocene. By the end of the Eocene many of the modern families (Emballonuridae, Megadermatidae, Rhinolophidae, and Vespertilionidae) were al-

Table 3.—*The families of rodents, with number of species and geological ages.*

Family	No. extant species	Age
Aplodontidae	1	Upper Eocene
Sciuridae	261	Upper Eocene or Lower Oligocene
Octodontidae	8	Lower Oligocene
Echimyidae	43	Lower Oligocene
Ctenomyidae	26	Upper Pliocene
Abrocomidae	2	Middle Pliocene
Capromyidae	11	Middle Pliocene
Chinchillidae	6	Lower Oligocene
Dasyproctidae	11	Lower Oligocene
Dinomyidae	1	Lower Miocene
Caviidae	12	Upper Miocene
Hydrochoeridae	2	Lower Pliocene
Erithozontidae	8	Lower Oligocene
Cricetidae	567	Lower Oligocene
Muridae	457	Lower Miocene
Dipodidae	27	Upper Oligocene
Zapodidae	11	Upper Oligocene
Geomyidae	40	Upper Eocene
Heteromyidae	75	Lower Oligocene
Gliridae	23	Upper Eocene
Spalacidae	3	Lower Pliocene
Rhizomyidae	18	Middle Oligocene
Castoridae	2	Lower Oligocene
Thryonomyidae	6	Lower Miocene
Bathyergidae	22	Pleistocene
Hystricidae	15	Oligocene
Ctenodactylidae	8	Upper Oligocene
Anomaluridae	12	Lower Miocene
Pedetidae	2	Lower Miocene
Total	1,681	

ready present (Table 2). Many of the modern genera are quite old. *Myotis*, for example, first appeared in the Oligocene. It is apparent that bats are an old group, relative to other mammals, but their fossil records are spotty. Thus, values listed in Table 2 may well be an underestimate of the age of most families.

Order Rodentia

Chromosomal evolution.—Rodents have received a major portion of the attention of cytogeneticists compared to other vertebrate orders. Rodents contrast with bats and turtles in the nature of their karyological diversity. Such genera as *Dipodomys, Perognathus, Peromyscus, Sigmodon, Oryzomys, Thomomys, Geomys, Spalax*, and others are all karyotypically diverse and interspecific (and a high level of intraspecific) chromosomal diversity is the rule rather than the exception. Mascarello et al. (1974) demonstrated that comparisons of banded chromosomes between the murid-crecetid complex revealed a considerable homology between distantly related genera. Comparisons made between the more distantly related families Cricetidae and Heteromyidae revealed no homology. This is similar to the pattern of variation at the generic and familial levels in bats.

Morphological evolution.—Rodents originated in the Paleocene (Romer, 1966), as did bats; however, most rodent families are younger than most modern bat families (disregarding those without a fossil record). For example, the large and diverse families Cricetidae and Heteromyidae appear in the lower Oligocene (Table 3), but the Muridae appear in the lower Miocene. Although some of the modern rodent families are as old as bat families (Eocene-Early Oligocene) (Table 3), there has been a considerable diversification and a relatively recent origin (Upper Oligocene, Miocene, Pliocene, and even Pleistocene) for many rodent families. Also, rodents seem to fossilize much better than bats and their fossil records are probably a better estimate of their actual ages than are those of bat families. We conclude that the primary diversification of rodents has been more recent than that of bats and turtles.

THE CANALIZATION MODEL

A major tenet of the canalization model is that the karyotype contributes significantly to the fitness of the individual and that, for a given set of biological parameters faced by an evolving lineage, there is an optimal karyotype. The karyotype, which is a product of selection for arrangement of genes (supergenes, position effect), size and number of linkage groups, centromere position, regulatory function, and others, is an important means of achieving an adaptive phenotype. The model predicts that the role of chromosomal evolution is most rapid immediately after a lineage breaks into a new adaptive zone and the rate becomes slower through time. The model further predicts that chromosomal stability would characterize lineages that have evolved the optimum karyotype for their adaptive

zone (with chromosomal fitness maximized, additional evolution would be by means other than chromosomal). The taxonomic level at which chromosomal stability occurs would be a function of the amount of morphological divergence that had occurred since a lineage had attained its optimal karyotype. In most cases, this would strongly correlate with the amount of time since a lineage had attained its optimum karyotype.

The origin of any higher category is ultimately an ancestral population that achieves an evolutionary breakthrough into a new adaptive zone; the broader the zone, the higher the category (Bock, 1965; Schaeffer, 1976; Mayr, 1963; Simpson, 1959). Problems concerning the origin and development, and the biological reality of higher categories have been addressed by numerous authors (for example, Schaeffer, 1976); however, little discussion has been given to the role of chromosomal evolution in regard to the development of higher categories.

Once the breakthrough is made and the adaptive morphological complex is more or less functional (such as flight in bats and protective shell in turtles), the progenitor will spread and diversify into lineages which become adapted to subdivisions of the zone. This whole process may be relatively rapid, which may explain why there usually are few fossil intermediates between orders (see Bock, 1965 for more thorough discussion of this process). We have divided the process of evolution into a new adaptive zone into three stages (Fig. 5).

Stage I

This stage is characterized by rapid diversification, with members of the radiating group poorly adapted to the new zone either morphologically or karyotypically. Each lineage will generally be characterized by chromosomal changes. Data from bats and turtles suggest that karyotypic evolution in Stage I is often non-Robertsonian rearrangements that serve to radically alter the arrangement of genes and the nature of linkage groups and, hence, the banding patterns of the chromosomes. There is evidence to suggest that chromosomal rearrangements serve to alter genetic regulatory systems and, thus, serve to enhance rapid evolution (Wilson, 1976; Wilson et al., 1974*a*, 1974*b*). During this time there is rapid development of independent lineages within the order, aided by the effects of different gene arrangements. Some of the successful lineages evolve highly adaptive gene arrangements.

Lineages within the order that have evolved a highly adaptive karyotype invade new and distinct subzones of the ordinal level adaptive zones. These subzones are familial level zones and the lineages that achieve these breakthroughs diversify, but in a more restrictive context than when the ordinal zone was invaded.

Stage II

Chromosomal evolution is now much more restricted (canalized). At this stage lineages are characterized by gene arrangements that are reasonably well adapted and, at this point, non-Robertsonian rearrangements (inversions and others) are generally selected against because they serve to break up adaptive linkage groups. Diversification takes place within the family zone and chromosomal evolution proceeds primarily by Robertsonian fusions and fissions, or by non-Robertsonian mechanisms, such as telomere-telomere fusions, that do not markedly alter the gene arrangements and banding patterns. As a result, homologies can be determined between even very ancient and morphologically very distinct genera within a family. This seems to be generally true in reptiles and mammals. We hypothesize that most chromosomal changes that do become established are adaptive, but seem to be a "fine tuning" of the generally adaptive familial karyotype.

Stage III

When the karyotype is essentially optimum, nearly all karyotypic mutations are nonadaptive and the lineage becomes karyotypically "stable." Further evolution and speciation in such a lineage proceeds primarily by means that are not associated with karyotypic change. Thus, in our example in Fig. 5, *Lasiurus* species have virtually identical karyotypes, but are morphologically distinct. As time goes on, further morphological differentiation may become established between the lineages within the *Lasiurus* generic adaptive zone, but few, if any, karyotypic alterations will be selected for. As a result of canalization, the karyotype of *Lasiurus* is adaptive and stable. We envision that as the lineage becomes older, this generic group might evolve sufficient morphological differences to justify it being divided into units with a higher taxonomic rank, as is the case in the karyotypically stable Phyllonycterinae or the Emydinae. Various families of lower vertebrates seem to be karyotypically stable and at the same time quite old (Trionychidae and Emydidae, for example).

Once lineages develop more "optimum" karyo-

types, and some lineages become extinct, new radiations of surviving lines will be accompanied by less chromosomal diversity. This, in part, explains why there are often no species with intermediate karyotypes, for example between the primitive *Myotis* ($2n = 44$) and the highly derived *Lasiurus* ($2n = 28$) (Fig. 3).

The end point of karyotypic evolution in a higher category may take longer in one lineage than another. It is obvious, however, that the older the group, the more likely it is to have already achieved Stage III karyotypic stability and the younger the group the more likely it is to be chromosomally diverse.

In all three stages of the canalization process, some chromosomal alterations with no or little selective value may become established. A greater number of such "neutral" changes will become established in species with a high level of inbreeding and small deme size. However, it is our thesis that such "neutral" or "drift" events play a much less important role than do adaptive changes.

DISCUSSION

Unlike other models, the canalization model emphasizes the adaptive nature of the karyotype and implies that the karyotype is a major component of the "adaptive strategy" of an organism. This model is also based on the assumption that for each "adaptive zone" there is an optimum karyotype that can be evolved by rearrangements in the karyotype of the invader of that zone. Additionally, it should be recognized that most chromosomal evolution is phyletic in that a chromosomal mutation becomes characteristic of a lineage without the production of sister species (our model is not primarily concerned with the role of chromosomal change as an isolating mechanism in the speciation process).

Primary Reason for Chromosomal Diversity

Comparisons of models.—In previous models deme size and inbreeding, as a result of vagility, social structure, and other factors are given as the primary reasons why some species and genera are karyotypically stable, whereas others are highly variable. Previous models predict that taxa with large deme sizes have stable karyotypes with low levels of karyotypic evolution, whereas taxa with small deme sizes have greater variation and high levels of karyotypic evolution (White, 1978; Hall, 1973; Bush, 1975). In the canalization model the amount of chromosomal evolution is a function of the degree to which the optimum karyotype has been achieved for the adaptive zone occupied by the taxa. Assuming that the rate of chromosomal mutation is essentially a constant per individual, then the most important factor in any rearrangement surviving and becoming established is a function of the degree of fitness it confers to its possessor over individuals with the previous karyotype. If the karyotype for a species or a group of species is optimum, then the likelihood of any new karyotype becoming characteristic of the species is essentially zero (unless drift occurs). However, if the karyotype of a group of species is poorly adapted, then a higher percentage of the rearrangements will confer sufficient fitness to result in that karyotype becoming characteristic of the species. In the latter case, speciation will then generally be accompanied by the evolution of distinct karyotypes.

Some indirect data, which indicate that chromosomal types have selective advantages of sufficiently high value to result in the above process, are available (Berry and Baker, 1971; Patton, 1970; Staiger, 1954; Stebbins, 1950). We see no reason to believe chromosomal changes cannot be selected for by natural selection in the same way as any genetic change. Even if such mechanisms as preferential assortment and reduced chiasma frequency are not present, chromosomal changes will occur in populations if a change results in a level of fitness great enough to overcome the disadvantages of the heterozygosity bottleneck. Thus, a new adaptive gene arrangement could quickly become established in even a large Mendelian population.

Chromosomal variation of higher taxonomic levels.—Wilson and colleagues characterize frogs as having small amounts of chromosomal variation, but they possess a 22–44 range of diploid numbers (not counting polyploids). Other orders characterized by Wilson and his colleagues as having conservative rates of chromosomal evolution, such as bats, also possess considerable chromosomal diversity. For instance, in the family Phyllostomati-

dae (Baker, 1978; Gardner, 1977) the diploid number ranges from 14 to 46 and the fundamental number ranges from 20 to 68. Within some subfamilies, the range is also extensive (Phyllostomatinae, $2n$ = 26–46; FN = 20–68; Glossophaginae, $2n$ = 16–32; FN = 24–60; Carolliinae, $2n$ = 20–36; FN = 36–62; Stenoderminae, $2n$ = 14–44; FN = 20–56). If small deme size is a requisite for extensive chromosomal evolution, then to account for the extensive variation at higher taxonomic levels, the breeding structures of the ancestral populations of turtles and bats were radically different than those of modern species.

The canalization model predicts that the longer a taxon has occupied an adaptive zone, the more probable it will be that the taxon will have achieved karyotypic stability and the higher the taxonomic category at which chromosomal stability is found.

This general trend is quite apparent in the tables on rates of chromosome evolution in Bush et al. (1977, Table 1) and Wilson et al. (1975, Table 1). These authors have documented the average age of genera, rate of karyotypic changes, and rate of speciation (Bush et al., 1977, Table 2), for about 10 order level groups of mammals and several lower vertebrate groups. Among the mammals there is an inverse correlation between greater average generic age, and higher rate of chromosomal change and higher rate of speciation. Among the placental mammals, for example, horses, primates, lagomorphs, rodents, and artiodactyls have the highest rates of chromosomal evolution and speciation and are the youngest groups. The insectivores, carnivores, bats, and whales all have lower rates of chromosomal change and speciation and they are also all older than the above-mentioned groups. These data are compatible with the canalization model.

Frogs are a much more ancient group than mammals and have had more time for their karyotypes to become canalized than, say, rodents. The same can be said for turtles and even bats because they are also older than rodents. When turtles, bats, and frogs were younger groups, they underwent a similar period of intense chromosomal evolution now observed in rodents. Turtles are older and more chromosomally stable than bats, and bats are older and more chromosomally stable than rodents. This aspect of the canalization model is in direct contradiction to Wilson et al. (1975) who stated, "However, there is little or no dependence of karyotypic evolution on elapsed time." These authors derive an equation to relate time with chromosomal diversity. Although their data did not show a significant correlation, the average correlation coefficient and average slope were negative, which would be predicted by the canalization model.

Deme size and chromosomal races.—Small deme size, low vagility, and other factors are certainly associated with most well-documented examples of chromosomal races and with one exception, *Uroderma* (Baker et al., 1975; Greenbaum, 1978), these biological features characterize examples of possible speciation by chromosomal mechanisms. Factors that produce high levels of inbreeding (low vagility, social structure, isolated populations, and others) have a strong influence in allowing some types of chromosomal variation to survive. However, most chromosomal races in such taxa will prove ephemeral unless a variant is of sufficient selective advantage to ultimately become characteristic of the species or to allow invasion of a different niche. If the new chromosomal variant has such selective advantage, it will follow the prediction of the canalization model. If it is not highly adaptive, then it will not prove critical to the overall pattern observed in vertebrate evolution. If the karyotype is as adaptive as envisioned in the canalization model, then genetic drift, low deme size, and low vagility may result in prolonging the existence of less fit chromosomal variants by microgeographic isolation from populations possessing a more optimal karyotype.

Bush et al. (1977) and Wilson et al. (1975) hypothesize that the small deme size and rapid chromosomal evolution of mammals results in more rapid speciation. It is undoubtedly true that deme size affects speciation rates to some extent, and perhaps to some extent the number of species in an adaptive zone. However, what is more important is that ancient genera will seem to have lower rates of speciation simply because they are older. When a generic lineage first breaks into its adaptive zone it undergoes a period of relatively rapid speciation until it fills the zone. As time goes on, no increase in the number of species takes place because the zone is full, although there may be a replacement of ancestral species by descendant species that have attained a more "optimum" generic karyotype, characteristic of Stage III evolution. The older the lineage becomes the lower the apparent rate of speciation within that lineage because, to determine that rate, you divide the number of extant species by the age of the group. The point here is that if bats were studied at the same relative age that ro-

dents are today, they probably would have had equivalent rates of chromosomal evolution and speciation.

Is the Nature of Evolution Different for Different Vertebrate Groups?

The canalization model suggests that there is no fundamental difference in the nature of evolution in diverse vertebrate groups. As to why there is more morphological diversity in mammals than in frogs (see *Significance of Chromosomal Variation*, above), Wilson and colleagues compared the amount of morphological diversity between two different taxonomic categories—Class Mammalia and Order Anura. A more appropriate comparison would be a mammalian order (such as Chiroptera or Rodentia) to the frogs or Class Mammalia to Class Amphibia. At this point it becomes evident that a comparison of morphological diversity between frogs and any large mammalian order is essentially of the same magnitude. As to why there is a difference between the ability of frogs and birds versus mammals in producing interspecific hybrids, we feel certain points need to be considered before concluding that altered regulator systems is an important reason that hybrids are not produced in mammals. It is true that mammals do not readily hybridize (relative to frogs and birds), but this is true not only of taxa that differ chromosomally (that might result in regulator gene problems), it is just as true of groups (such as *Myotis*) which have indistinguishable karyotypes (which should not have such developmental problems). The primary reason for the reduced hybridization in mammals is probably more sophisticated behavioral premating isolating mechanisms, not postmating chromosomal mechanisms.

We agree with Wilson and colleagues that structural gene changes occur at or near same rates within the groups and that chromosomal changes affect regulatory systems. But we do not agree that there are different types of evolution at work in these groups. The older groups, such as frogs, experienced their karyotypic revolution during Stage I which occurred long ago, when they first entered their adaptive zone.

How is the Canalization Process Redirected?

It is apparent that the process of karyotypic canalization has been redirected many times during the evolution of the vertebrates; otherwise, everything from fish to mammals would have identical karyotypes. Breaking into a new adaptive zone is what results in some new chromosomal mutations being adaptive, producing the revolution characteristic of Stage I or Stage II, depending on the width of the adaptive zone that is invaded.

Tests of Models

Canalization model.—In order for a model to be most useful, it should be stated in a manner subject to tests of Popperian falsification. Adequate tests of the canalization model primarily include correlating age with chromosomal diversity, and comparing chromosomal banding patterns among higher categories to determine inter- versus intra-higher category variation. Certainly, if it is found that there is not an inverse correlation between age and chromosomal diversity within many groups, this would represent a falsification of the model, and would mean that the canalization model is not of general applicability.

Deme size models.—A valid test of the deme size model would be variation in some nonmammalian old vertebrate group that has considerable variability in deme size. Turtles appear to us to be such a group. Marine turtles and species that inhabit large lakes and extensive river systems undoubtedly have large deme sizes and should show essentially no chromosomal diversity. Other species, such as softshelled turtles (*Trionyx*) and tortoises (Testudinidae) have low vagility, are frequently isolated in small subunits, and should reflect a level of chromosomal variability similar to that observed in mammals with equivalent deme sizes. We feel if the deme size model is to have any credibility it must be demonstrated in some of the vertebrate lineages older than mammals.

Another group that seems to be well suited as a test of the small deme size and canalization models is moles (Talpidae). If the deme size model is correct, highly fossorial, solitary mammals (as some moles are thought to be) would be expected to show a pattern of chromosomal variation similar to that of other fossorial mammals such as pocket gophers and *Spalax*. However, the Insectivora is an old group and the canalization model would predict that their karyotypes should be becoming canalized.

The Nature of Higher Categories

The canalization model suggests that higher categories undergo a series of stages in their development. Categories at or above the ordinal level represent such broad adaptive zones that chromo-

somal homologies cannot be deduced among higher groups, but below the ordinal level homologies can generally be identified. It also appears that there is a difference in the kind of chromosomal rearrangements that take place in Stage I (interfamilial comparisons) and Stage II (intrafamilial comparisons). Thus, the breaking into a ordinal level zone may be associated with a different genetic revolution than is involved in the breaking into a familial or lower level adaptive zone. An implication of the canalization model is that higher categories are real as suggested by Schaeffer (1976). The various categories are not merely "pigeonholes" that man has created, but in fact have evolutionary meaning.

In a communication such as this (as well as those presenting previous models), it is impossible to discuss all aspects of such an extensive process as chromosomal evolution; however, we do believe that there are more than adequate data (some of which are presented above) to justify the consideration of the canalization model as a viable alternative to previous models. It is in this spirit that we present our model.

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BIASES IN THE FOSSIL RECORD OF SPECIES AND GENERA

David M. Raup

Department of Geology, Field Museum of Natural History,
Roosevelt Road at Lake Shore Drive, Chicago, Illinois 60605

INTRODUCTION

Many of the larger scale problems now being investigated by paleoeeologists and evolutionary paleobiologists depend for their solution on having an accurate knowledge of the Phanerozoic history of taxonomic diversity. The problems are exemplified by the following questions. Has the number of species increased steadily since the mid-Paleozoic or was a steady state reached in at least some environmental realms or adaptive zones? Are temporal changes in the numbers of species and higher taxa basically unpredictable because of the complexity of causative factors or are there trends, cycles, or periods of equilibrium that are recognizable and amenable to rigorous analysis? Do geographic patterns of diversity (provincialism, endemism, and others) change in a predictable fashion in response to climatic or tectonic changes? Can the quantitative relationship between number of species and habitable area be applied on a world-wide scale to large evolutionary groups?

Most of these questions have been investigated to some extent in two important books—Valentine's (1973) *Evolutionary Paleoecology of the Marine Biosphere* and Boucot's (1975) *Evolution and Extinction Rate Controls*. In addition, many shorter contributions have explored a few of the questions in detail. For example, Flessa and Imbrie (1973) and Fischer and Arthur (1977) have analyzed diversity data for temporal patterns and cycles. The Fischer and Arthur work is particularly important because it concludes that diversity in pelagic biotas fluctuates with a rhythm of about 32 million years. Sehopf (1974) and Simberloff (1974) have applied the species-area concept to Permo-Triassic changes in family diversity and to the question of mass extinction. Van Valen (1973*a*) applied a probabilistic model (the Red Queen Hypothesis) to the problem of extinction of higher taxa. Many other examples could be cited.

The main shortcoming of these and comparable works is that their basis in empirical data is limited. The published syntheses of distributions of fossil taxa in space and time are generally not adequate to provide truly definitive answers to the questions being asked. The problem is two-fold—first, tabulation of diversity data is an extremely time consuming job and is frought with procedural difficulties (sampling, nomenclatural problems, questionable records, and others) and second, raw data on fossil diversity are misleading because of the distorting effects of systematic biases. The best syntheses of data are those confined to single biologic groups that have been especially well monographed. The more comprehensive tabulations (Harland et al., 1969; Kukalova-Peck, 1973) are at too high a taxonomic level for many interpretive purposes. At the lower taxonomic levels (genus and species), theoretical work has had to rely on published tabulations of intelligent guesses (Easton, 1960; Van Valen, 1973*b*; and a few others). It is at the lower taxonomic levels where evolutionary and ecologic theory is most robust and it is at these levels where interpretive analysis may be most fruitful—given the proper data base.

The purpose of this paper is to evaluate our knowledge of Phanerozoic diversity at the specific and generic levels and to suggest ways of improving the quality of this knowledge. The emphasis will be on the fossil record of invertebrate animals.

SAMPLING CONSIDERATIONS

The fossil record is an exceedingly small sample of past life. The probability of any individual animal being preserved and later found is vanishingly small. It is only because so many individuals have lived in the geologic past that we have as large a fossil record as we do. Because fossilization is a rare event, a group of organisms having even a slight advantage in the preservation process will be vastly over-represented in the record. The fossil record is thus a strongly biased one.

Table 1.—*Numbers of taxa found in a sample from the Arnum formation (Miocene of Denmark) as reported by Sorgenfrei (1958) and rarefaction estimates of the numbers of taxa that would have been found had the sample been smaller. The estimates calculated from rarefaction have been rounded off to the nearest whole number.*

Taxonomic level	Actually found	Predicted for a sample of 500	Predicted for a sample of 100
Phylum	1	1	1
Class	3	3	2
Order	12	9	7
Family	44	24	14
Genus	64	31	17
Species	86	39	19
Specimen	2,954	(500)	(100)

Taxonomic Level

In general, the quality of the fossil sample increases as one moves up the taxonomic scale. This is because higher taxa (excluding monotypic taxa) inevitably contain more individual organisms than lower taxa. All things being equal, a taxon having the most individuals will have the highest probability of becoming part of the fossil record. Table 1 illustrates this relationship with a Miocene assemblage taken from a drill hole in Denmark (data from Sorgenfrei, 1958). The studied part of this assemblage was made up of molluscs and thus only one phylum (Mollusca) was reported. There were 2,954 specimens and any one of them would have sufficed to record the presence of the phylum. There were three classes in the sample (Gastropoda, Bivalvia, and Scaphopoda) but they were present in unequal numbers—only 47 of the 2,954 specimens were scaphopods. Thus, if the sample had been substantially smaller than 2,954, it is likely that the order Scaphopoda would not have appeared. By the same token, it is conceivable that a much larger sample would have yielded specimens of a fourth class. As one goes down through the taxonomic hierarchy, the likelihood of missing taxa increases in a systematic fashion.

The case just considered can be analyzed rigorously by rarefaction techniques (Sanders, 1968; Simberloff, 1972; Raup, 1975). It can be shown in the Danish Miocene case, for instance, that if 500 specimens had been collected, only 39 species and 24 families would have been found rather than the 86 and 44, respectively, that were found. Table 1 shows estimates for other taxonomic levels and other sample sizes.

Table 2.—*Estimates of preservability for a few biologic groups.*

Biologic group	Taxonomic level	Percent of living taxa with a fossil record
Brachiopods	family	100
	genus	77
Echinoids	family	89
	genus	41
Asterozoans	family	51
	genus	5
Bivalves	family	95
calcitic	genus	86
aragonitic	genus	54
freshwater	genus	27
Ostracodes	family	84
	genus	42
Arachnids	genus	2
	species	<1

An important corollary of the relationship just described is that as sample size increases, the ratios of lower to higher taxa increase systematically. In Table 1, there are 1.1 species per genus in the smallest sample and 1.3 species per genus in the largest sample. The number of families per order increases from 2.0 to 3.7, and so on. When sampling starts and only one specimen has been collected, all taxonomic ratios are inevitably 1.0. With increased sampling, the ratios approach their true values.

The most important element of sampling for taxonomic ratios is that the systematic increases just described mimic the temporal sequence usually postulated for an adaptive radiation in evolution.

Because paleontological sampling is nearly always incomplete, our knowledge of past life is much better at high taxonomic levels than at low. At the generic and specific levels, sample size is a factor that cannot be ignored and may actually be the dominant factor in influencing diversity data.

Variation in Preservability

It is a truism that some biologic groups in some habitats are more readily preserved than others. Extremes are easily recognized. Insects, for example, are vastly underrepresented as fossils relative to other groups because they lack hard skeletons and because their terrestrial habitats do not normally yield a good sedimentary record. At the other extreme, heavy shelled, infaunal, marine molluscs enjoy a much higher probability of preservation and thus make up a larger fraction of the record.

One way to quantify variation in preservability is to calculate the percentage of living taxa that have a fossil record. These percentages may be taken as a first approximation of differences in inherent preservability. Table 2 gives the values for a few fossil groups. This approach requires the tacit assumptions that all groups have had constant abundance throughout recent geologic periods and that all originated at the same time. These assumptions are patently false but the results are still valuable as a general guide.

The data in Table 2 show a wide range of values, yet for each group, preservability increases with taxonomic level. It is clear that fossil diversity data at low taxonomic levels should be corrected for preservability. From a statistical standpoint, one hundred fossil echinoid genera represent a considerably higher original diversity than one hundred fossil brachiopod genera. Comprehensive work on a correction system remains to be done, however.

Geographic Factors

The geographic distribution of fossil data is irregular and is influenced by many factors. That the geographic coverage is incomplete is immediately evident when one superimposes the distribution of fossiliferous rocks on a map of the world showing present-day biographic provinces. To cite an extreme case, the sedimentary record of the marine Lower Triassic is available in only a few regions. Africa, South America, and Antarctica are essentially devoid of record and the present oceanic areas are virtually closed to paleontological exploration for rocks of this age. With sampling as sparse as this, several large faunal provinces could easily be missed. The low taxonomic diversity for species and genera of the Lower Triassic may thus be an artifact of sampling.

Also, paleontologic exploration has not proceeded at equal rates in all areas because of variation in the distribution of practitioners. For example, of the fossil species described between 1900 and 1970, 24% were found in the United States. This is slightly more than were found in the combined areas of Central America, South America,, Africa, and Asia (exclusive of USSR) (Raup, 1976*a*). Correction for this factor is nearly impossible because it is difficult to distinguish differences in sampling from real differences in diversity.

Idiosyncratic Variation in Sampling

In spite of the generally poor quality of the sample, the fossil record occasionally yields spectacularly good preservation. Such cases, commonly termed *Lagerstätten,* are scattered in an apparently idiosyncratic fashion throughout the Phanerozoic record. Classic examples include the Solnhofen limestone, the Mazon Creek shale, and the Burgess shale.

The influence of *Lagerstätten* on diversity data varies with taxonomic level. Because these assemblages contain organisms that are normally "unpreservable," they often provide the only occurrences of extinct taxa or the only fossil occurrences of extant taxa. The many "Middle Cambrian to Recent" ranges stemming from the Burgess shale play a significant part in diversity data at the order and class levels. But at the lower taxonomic levels (species and genus), the influence is minor because the total number of taxa involved is a small fraction of the total fossil record.

Cisne (1974) has proposed that the faunal lists for *Lagerstätten* can be used by themselves as a measure of standing diversity. He argued that by concentrating on situations where sampling bias is minimal, a more accurate picture of relative changes in diversity can be achieved. Cisne's suggestion is being implemented in a comprehensive manner at the specific level by Bambach (1975).

THE PULL OF THE RECENT

It has been suggested that the nature of the fossil record and the conventional methods of analyzing it carry built-in factors that make an increase in diversity toward the Recent almost inevitable (Cutbill and Funnel, 1967; Raup, 1972). This effect may be called the "Pull of the Recent." A spectacular example of this is shown in Table 3. Data on ranges of a large sample of Paleozoic genera and subgenera show that most taxa on this level are confined to a single geologic period, as indicated by the high values along the main diagonal in Table 3. For each period, the number of taxa extending into subsequent periods is small and decreases sharply as the range increases. If all the taxa originating in a period are considered as a cohort (the sum of the numbers in the first column constitutes the Cambrian

Table 3.—*Range data for genera and subgenera of invertebrates extracted from the* Treatise on Invertebrate Paleontology. *Table should be read as follows: 1,038 taxa originated and terminated in the Cambrian, 38 taxa originated in the Cambrian and terminated in the Ordovician, and so on.*

Last occurrences	First occurrences					
	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian
Cambrian	1,038	—	—	—	—	—
Ordovician	38	1,439	—	—	—	—
Silurian	7	180	512	—	—	—
Devonian	3	86	173	1,136	—	—
Carboniferous	3	19	20	104	774	—
Permian	3	20	24	59	243	470
Triassic	0	1	2	8	11	15
Jurassic	0	5	2	1	6	2
Cretaceous	0	4	0	6	5	5
Tertiary	0	3	0	1	3	1
Recent	30	25	13	25	24	16

cohort, for example), standard methods of population dynamics can be applied. Such analysis shows that the half-life of genera and subgenera is consistently about 25 million years. But the important feature of the data in Table 3 is the row of numbers at the bottom which records those taxa with fossil-to-Recent ranges. In the case of the Cambrian, the original cohort "decays" in a regular fashion through the Paleozoic—if allowance is made for minor sampling error as the number of survivors becomes small. If the 30 Cambrian-to-Recent ranges are ignored, the Cambrian data produce a reasonable survivorship curve. There is clearly something special about the 30 taxa that reportedly extend to the Recent. The same pattern can be seen throughout the table although the special nature of the fossil-to-Recent taxa becomes blurred as the diagonal converges with the bottom row.

What is special about the Recent taxa in Table 3? One possibility is that there are two fundamentally different kinds of genera—a large number that have a high probability of extinction early in their existence and a much smaller number that for some reason survive indefinitely. Such a discontinuity in survival potential is inconsistent with current evolutionary theory but cannot be ruled out absolutely. A much more likely explanation, however, is that the bottom row in the table is largely an artifact resulting from the Pull of the Recent.

The Pull of the Recent results from the following factors, arranged in descending order of importance:

Table 4.—*Effect of Recent records on inferred diversity in regular echinoids.*

	Number of genera using Recent taxa	Number of genera ignoring Recent taxa	Difference	Percent exaggeration
Pleistocene	47	15	32	213
Pliocene	51	37	14	38
Miocene	51	46	5	11
Oligocene	31	26	5	19
Eocene	54	50	2	4
Paleocene	25	23	2	9

(1) *Sampling Is More Complete in the Recent*

We know (from Table 2, for example) that many taxa are not preserved as fossils. Other taxa are quite readily preserved owing to a favorable combination of skeletal structure and habitat. Between these extremes, there is a continuum of intermediates such that some groups are found as fossils but have only a sparse and incomplete record. In these cases, the geologic range of the individual taxon is usually truncated by nonpreservation. It is unlikely, in fact, that the ends of the actual range will be recorded. But if the taxon is still living, the chances of this fact going undiscovered is remote particularly at generic and higher levels and among biologic groups important in the fossil record. Because sampling is so much better among living organisms, the geologic ranges of extant taxa are unlikely to be truncated at the Recent end. This may be the explanation for the 30 Cambrian-to-Recent taxa in Table 3—that is, point occurrences in the Cambrian combined with the existence of living species yields a long range. If these genera were not still living, most would probably remain as point occurrences or as genera with substantially shorter ranges.

Table 4 shows another example. As part of an earlier study of taxonomic diversity, accurate data on Cenozoic and Recent echinoid ranges were amassed (Raup, 1975). As is conventional, generic ranges were inferred from the stratigraphic distribution of species. For example, a genus having only Eocene and Miocene species was inferred to have existed in the Oligocene even though it was not found in Oligocene rocks. Similarly, a genus having only Eocene and Recent species was inferred to

have existed throughout the Eocene to Recent span. The first column in Table 4 was developed by this method. The second column was constructed in the same way except that information from Recent records was not used. The effect of ignoring Recent records is indicated in the third and fourth columns.

Table 4 shows convincingly that for regular echinoids, at least, the Pull of the Recent produces an exaggeration in fossil diversity that varies from 4% (Eocene) to 213% (Pleistocene). There is a clear trend toward increasing exaggeration as the Recent is approached, as would be expected.

(2) *Misassignment of Fossils to Recent Taxa*

Although hard data are unavailable, it is likely that some fraction of the taxa with long fossil-to-Recent ranges are invalid in the sense that the grouping of species into the higher taxon is in error. This is presumably most common among organisms with simple morphology. Twenty-nine of the thirty Cambrian-to-Recent genera in Table 3 are radiolarians. Although taxonomic procedures vary greatly from group to group, most modern workers probably prefer to assign a fossil species to an extant genus rather than to erect a new genus in cases where morphologic evidence leaves room for doubt.

(3) *Recent Taxa Have More Fully Developed Taxonomy*

Because extant taxa almost always have more known species than extinct taxa and because the array of usable phenetic characters is generally greater, extant higher categories tend to be more finely subdivided than their fossil counterparts. Once this subdivision has been accomplished with living organisms, the subdivisions are more likely to be recognized in the fossil record. For example, the morphology of pedicellariae in living echinoids has proved valuable in the classification of species into higher taxa. Pedicillariae are rarely useful in the fossil record but, I submit, extraordinary efforts are made to recognize the same higher taxa as fossils. Although proof of this effect is elusive, it may have a significant influence in increasing apparent fossil diversity in those taxa that are still extant. And this has the statistical effect of artificially increasing apparent diversity as the Recent is approached.

Discussion

The three elements of the Pull of the Recent are difficult to disentangle. Nevertheless, summary data such as are presented in Table 3 can be used to assess the combined effect of the three elements. In Table 3, there are 133 taxa having Paleozoic-to-Recent ranges (the sum of the bottom row of the table from Cambrian through Permian). The 30 in the Cambrian and the 13 in the Silurian are the most likely to be artifacts of Recent records because they have zeros above them in the table. In the cases of the Ordovician, Devonian, Carboniferous, and Permian, the numbers in the bottom row are dominantly artifactual but may contain a few taxa with legitimately long ranges. Thus, something approaching 133 genera and subgenera are added to the diversity totals for all post-Paleozoic intervals even though they either did not exist or are in the data only because the sampling in the Recent is atypical. With each successive stratigraphic interval, the "load" of artifactual data increases. This effect is most significant in intervals where the generic standing crop is low for other reasons. For example, the standing crop of genera and subgenera for invertebrates in the Triassic, as inferred from ranges, is about 600. Even if only 100 of the 133 taxa referred to above are artifacts of Recent records, the Pull of the Recent is responsible for a 20% exaggeration of Triassic diversity (from 500 to 600)!

Although the quantitative evaluation of the Pull of the Recent is still at a primitive stage, we can look forward to a rigorous assessment when more data along the lines of Tables 3 and 4 have been amassed and analyzed.

EFFECTS OF AVAILABILITY OF FOSSILIFEROUS ROCKS

A bias deserving special attention stems from natural geologic variation in the quantity of sedimentary deposits through geologic time. It has been shown repeatedly that there is an irregular yet consistent increase in volume and map area of sediments through time (Gilluly, 1949, 1969; Higgs, 1949; Gregor, 1970; Blatt and Jones, 1975). That is, the volume and area of rock, *preserved and known,* per million years increases from Precambrian to Recent. The consensus interpretation of this phe-

nomenon is that the increase is due simply to the fact that the younger rocks are least likely to have been eroded, metamorphosed, or covered.

Not surprisingly, the number of fossils (and therefore fossil taxa) is influenced by variation in amount of available rock. Gregory (1955) showed that there is a strong correlation ($r = 0.94$) between apparent generic diversity in vertebrates and the number of principal collecting localities. In fact, he concluded (pp. 598–599) that ". . . accidents of present-day exposure so strongly influence figures on the abundance and diversity of fossils that conclusions as to . . . times of organic diversification should be based upon other types of evidence." Simpson (1960) and Raup (1972) also argued for the biasing effect of variation in quantity of potentially fossiliferous rock although few hard data were available. A recent analysis, however, of about 70,000 species of fossil invertebrates shows that diversity is correlated with both geologic map area and estimated volume of sediments (Raup, 1976*b*). These correlations are statistically significant at the 1% level. Ironically, species diversity is more highly correlated with area and volume than area and volume are with each other. A multiple regression analysis of the same data by Sepkoski (1976) shows that although most of the variation in diversity is caused by sampling, differences in area of shallow seas also play a role. This effect is biologically real but can be seen only after the effects of rock volume and area have been removed.

As one moves up the taxonomic scale, the sampling effects described above decrease in influence. For genera, quantity of fossiliferous rock still has strong effects. Sampling is apparently of minimal importance at the family level and is virtually absent at the order and class levels. Except for classes with very few species or cases where preservability is low, the availability of fossiliferous rocks is adequate to insure a fossil record, which is reasonably free of bias stemming from sample size.

TOWARD BIAS-FREE ESTIMATES

Before accurate diversity curves for species and genera can be constructed, the new data must be filtered to remove the biases discussed in this paper. The two most important factors are the Pull of the Recent and the variation in quantity of fossiliferous rock. These two are important in part because they have the largest effect on diversity data and in part because their effects are time-dependent.

The Pull of the Recent has little if any effect on species diversity because species durations are very short relative to the geologic time scale. For genera, the effects are greatest in the late Mesozoic and Cenozoic. These time intervals contain many genera that are still extant and thus the better sampling in the Recent exerts a pull. The late Mesozoic and Cenozoic also carry a large accumulation of artifactual records of the Cambrian-to-Recent type discussed above in connection with Table 3. To remove these effects rigorously will require more data than are presently available. The data in Table 3 are preliminary and incomplete and Table 4 is based on only one class.

Filtering out the effects of area and volume of sediment is possible, but the results cannot be made bias-free with the data base available now or likely to be available in the near future. The basic problem may be exemplified by the Triassic. Species diversity for the Triassic shows a negative residual with respect to quantity of rock. That is, fewer species are recorded than would be predicted from rock quantity. The problem is that the deficiency could have resulted either from a true drop in number of species or from a surplus of unfossiliferous rock. In the case of the Triassic, the high frequency of terrestrial red beds makes the second alternative a possibility but a definitive answer is not possible at this time.

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TETRAPOD MONOPHYLY: A PHYLOGENETIC ANALYSIS

EUGENE S. GAFFNEY

Department of Vertebrate Paleontology, The American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024, and Department of Geological Sciences, Columbia University, New York, New York

INTRODUCTION

"What we really need is more fossils." This oft-repeated statement usually follows, both in print and in meetings, arguments concerning the relationships of primitive tetrapods. But we do have more fossils; in fact, we have more fossils than ever before and, because of new discoveries and newly prepared "old" specimens, we have over the past fifty years conspicuously enlarged the diversity of extinct forms as well as increased our knowledge of their structure. Yet Panchen (1975:290) writes ". . . the story of the early evolution of tetrapod vertebrae is certainly less simple and less certain than it appeared to be even less than ten years ago . . . ." Although his comment is directed toward one particular morphologic region, I think it characterizes feelings about tetrapod phylogeny in general. For example, Olson (1971:583) in a review of early tetrapod evolution stated ". . . the use of assumed phylogenies as bases for deductions concerning almost all of the problems of tetrapod origins have introduced such a mixture of objective and subjective analyses of data that dispassionate assessments are difficult and too infrequently encountered." Olson lays the blame on "assumed phylogenies" but I will argue here that the general lack of success in developing objective ideas about relationships is due to basic problems in methodology.

Tattersall and Eldredge (1977) analyze a similar situation in studies of hominid evolution. They suggest that ". . . phylogenetic hypotheses can be formulated at three different levels of complexity, each successively further removed from the basic data available" (p. 204). The first, and most objective, is the *cladogram,* a methodology advocated here and explained below. The second level, called *phylogenetic trees* by Nelson (manuscript) and Tattersall and Eldredge (1977) involves the recognition of ancestor-descendant sequences, even though this requires the addition of untestable assumptions and suppositions. The third and least objective type of hypothesis is the *scenario,* which is essentially a tree further encumbered by assumptions and speculations about selective forces, niches, key innovations, radiations, adaptive zones, and other notions that have become the hallmark of explanation couched in the jargon of the Synthetic Theory. The elements of a cladogram are usually implicit in a scenario and might be abstracted from it, but ". . . as things stand, the diverse components of scenarios are seldom separable, and much of the reasoning that goes into their construction is circular: the many elements involved feed back upon each other in an extremely intricate way" (Tattersall and Eldredge, 1977:205). "There is no methodology at all for the formulation of a scenario, with all its varied aspects of evolutionary relationship, time, adaptation, ecology, and so forth. In devising a scenario one is limited only by the bounds of one's imagination and by the credulity of one's audience . . ." (Tattersall and Eldredge, 1977:207).

My own examination of literature on the "fish-amphibian transition" suggests to me that nearly all hypotheses concerning this subject have been formulated at the scenario level with little or no effort to separate adaptive speculation from testable phylogenetic hypotheses. Representative examples of scenarios are Szarski (1962), Schaeffer (1965), and Thomson (1966*a*). This, rather than the use of "assumed phylogenies," is the source of the problem referred to by Olson above (1971:583). It is impossible to choose objectively among contradictory scenarios and the result of difficult and tedious work in exploration for and preparation of fossils is often simply the generation of new scenarios.

It is my feeling that the prominence of scenario creation has had a particularly subtle effect even on critical workers not easily swayed by *ad hoc* hypotheses. For example, Carroll (1969:427), whose work is clearly oriented towards phylogeny reconstruction per se rather than adaptive scenarios of the sort seen in Olson (1966, 1976), nonetheless describes the standard "parallelism scenario" even though he does not accept it: "From our knowledge

of the reptilian-mammalian transition, we know that extensive parallel development of very similar structures and character complexes may occur independently in numerous lineages. It is conceivable that limnoscelids, solenodonsaurids and romeriids evolved independently from a group with the anatomy similar to that of *Gephyrostegus*. Similar selective pressure could produce the reptilian condition in each. In the absence of any evidence to the contrary, solenodonsaurids and limnoscelids may be included as reptiles since they have developed a typically reptilian palatal structure and atlas-axis complex."

This insistence on the *ad hoc* recognition of parallelism or convergence is unfortunate because it requires information that cannot be obtained in an objective system. It would be wonderful to have testable hypotheses of "selection pressure" and "adaptive zones" concerning Devonian tetrapods and to be able to relate these to morphologic parameters. Ideas of this sort must be relegated to the "scenario" level of explanation and should not be used as tests of phylogenies. In fact, the only way to argue for the presence of parallelism or convergence is the demonstration that two alternative phylogenies are still viable after testing. As Cracraft (1972:387) has said: "A judgement of convergence must be based on an *a priori* assumption of relationship. The fact that two taxa . . . might show a number of morphological differences cannot serve as an argument for nonrelationship. The latter can only be proposed once a relationship has been demonstrated between one of these taxa and a third taxon." An argument for parallelism or convergence is simply an argument (often unstated) in favor of one phylogeny over an alternative one.

Another aspect of scenario creation particularly evident in early tetrapod studies is the "derivationist" approach to character distributions. Because of the emphasis on ancestor recognition rather than the testing of monophyletic groups, much effort has been put into how the rhipidistian fin (or vertebral column, skull, or whatever) might be changed into a tetrapod foot. This sort of argument was probably of significance in the early days of evolution versus creation debates when series of recent forms or fossils were arranged with hypothetical intermediates in order to show how changes *might* take place between greatly divergent morphologies. However, this has become an argument for homology of structures, and, therefore, phylogenetic relationship.

I think a more empirical approach, clearly related to a philosophic framework of science within which ideas may be criticized and judged, will lead to greater progress in understanding the history of organisms. Such an approach begins with phylogeny reconstruction of the sort advocated here, but this is not to say that scenarios have no place in paleontology. We will always be interested in mechanisms and processes of change as well as the geometry of it, and even though I see little hope of developing testable hypotheses of this sort in the near future, it is truly impossible to test hypotheses that are not formulated at all.

My intention in this paper is to take two hypotheses that although commonly accepted often create considerable debate, and test them using shared derived characters. In this procedure I hope to point out problem areas and alternative views also worthy of test. I also hope that this treatment will serve as a basis for further studies of tetrapod relationships. It should not be construed that I think this study in any way "settles the question" of tetrapod monophyly nor necessarily provides a complete review of all the characters pertinent to this hypothesis. I have used all the characters that in my opinion are pertinent but this is based primarily on a study of the literature. I hope that new studies of specimens will suggest the use of new characters that can be used to test monophyly of the Tetrapoda.

METHODOLOGY

There are currently a number of competing methods of phylogeny reconstruction, and I have based my choice of method on a particular view of the philosophy of science. Some systematists argue that philosophic discussions are fruitless, a waste of time, and irrelevant; that the interesting and important job is to "do the work." There is a growing feeling among systematists, however, that objective choices can be made but that they are dependent on a basic philosophy of science that sets limits and objectives. A philosophy of science is like any other intellectual subject matter; a certain amount of thoughtful inquiry is essential to its acquisition.

Perhaps the most common view of science, held by both scientists and non-scientists alike, is the Baconian view, or induction. In this philosophy, science is supposed to be a fact gathering operation, which proceeds until a theory or generalization emerges from the accumulations and finally a proving or dem-

onstrating experiment or observation proves the truth of the generalization. It may then take its place in the firmament of acquired knowledge and the seeker of truth moves on to the frontiers of the unknown to gather new data. This process is usually called induction and it has been criticized philosophically at least since Hume's day, and more recently scientists such as Einstein and Medawar (Magee, 1973) have argued that in reality induction does not describe the manner in which the acquisition of knowledge progresses. In phylogeny reconstruction, I am continually impressed by the falseness of the inductive method when workers state that there are not enough fossils to "prove" a phylogeny, or that phylogeny cannot be done because of an "incomplete" fossil record, both required elements of the inductive approach.

One of the primary difficulties with the inductive or Baconian philosophy of science is that it allows or even requires the recognition of truth. Most scientists are too skeptical to accept this, and even though they may use induction, they will argue that their conclusions are expressable only in terms of probability. One conclusion is said to be more probable than the next or with increasingly greater quantities of data, one's conclusions become more probable. But how can "more versus less" probable be dealt with objectively? How can one identify a "more probable" conclusion unless one knows the yardstick of comparison, that is, the "true" conclusion?

The problem, as has been pointed out by philosophers for some time, is that no matter how many observations have been made that are consistent with a generalization, another observation that is inconsistent with the generalization is always possible. In other words, no number of consistent observations can prove the truth of a generalization. An alternative view of science and the acquisition of knowledge is the hypothetico-deductive method, or, as Karl Popper, a noted exponent of this philosophy has characterized it, conjectures and refutations. This philosophy recognizes that although we may have found the truth in our hypotheses and generalizations, we cannot identify it. We can, however, identify hypotheses or ideas that are inconsistent with observations, and this is the focal point of Popper's view of science. Although we can never know when we have found the truth, we do know when we are wrong. In this philosophy, all ideas and explanations in science are advanced as unprovable hypotheses that are intended to be submitted to rigorous attempts at falsification. Falsification may be defined as the result of a test of a hypothesis in which one (or more) of the expectations (predictions) of the hypothesis is shown to be inconsistent with observations. Observation, in this sense, refers to a lower level hypothesis (that is, a more specific or less general hypothesis) that is not itself being questioned or analyzed at this time but that is susceptible to test. Those hypotheses that survive repeated attempts at falsification are the most useful for further work. Nothing, however, is permanently removed from criticism, nor accepted as true.

Karl Popper (1968*a*, 1968*b*; see also Magee, 1973, 1974) has been most responsible for a modern development of the hypothetico-deductive view of science, but the method of advancing ideas or conjectures and then attempting to test them by experiment and observation is an old one. The application of the hypothetico-deductive method to systematics is relatively recent, at least in a formalized explicit sense, although Ghiselin (1969) has argued that it was essentially the method used by Darwin. In any case, some recent systematic work has emphasized the use of the hypothetico-deductive philosophy (Bock, 1973; Bonde, 1974, 1975; Miles, 1973, 1975; Platnick and Gaffney, 1977; Wiley, 1975). Because Wiley (1976) has an excellent review of the method of phylogenetic reconstruction used here, only a short summary is given below.

Hypothesis

The simplest hypothesis of relationship is the statement—two taxa are more closely related to each other than either is to a third. An equivalent statement would be—two taxa have an ancestor in common that neither has in common with a third taxon. Much of the confusion about cladism can be dispelled by understanding this statement of the hypothesis. A three-taxon statement of this sort is best expressed in the form of a diagram, called a cladogram. Cladograms do not indicate the positions of ancestral taxa, even though they may be present, and each line does not necessarily imply the existence of a separate lineage (see Nelson, manuscript; Tattersall and Eldredge, 1977, for cladograms versus trees). A cladogram is meant to be a hypothesis of monophyly and an ancestor and its descendant is just as much a monophyletic group as two descendants from a common ancestor. The recognition of ancestors requires a further set of assumptions that I am not willing to make. In any case, despite the incongruence with tradition, ancestors are not particularly important in phylogeny reconstruction.

Each of the three taxa in the three-taxon hypothesis should be monophyletic. That is, they are not monophyletic by assumption but they should be susceptible to test for monophyly. However, it is not necessary that these tests for individual monophyly of the three taxa be completed before testing the three-taxon statement as a whole. When one of the taxa in a three-taxon statement is hypothesized as being non-monophyletic, it changes the hypothesis, making the original hypothesis logically irrelevant rather than false per se. In any case, it is clear that a hypothesis of relationships, such as the one advanced below for Tetrapoda, that does not include tests for monophyly of its constituent taxa, is less satisfactory than one that does.

Test

The use of cladistic techniques to test hypotheses of monophyly rests on the following basic hypothesis (or axiom, an assumption at this level of hypothesis formation but still subject to falsification; see Popper, 1968*a*, chapter III): strictly monophyletic groups (descendants of a single species) are often characterized by new features (that is, morphology, behavior, ecology, genotype, and others). Conceivably, new species may not have new features but if and when this occurs, I know of no objective criteria that will allow the recognition of new species. The word "new" in the basic hypothesis must be qualified. A new feature in my sense could very well be a character reversal and therefore not "new" in a temporal sense. However, it would still be new to the species in question. This simply means that character reversals are not disqualified, however inconvenient their appearance may be.

If we use the basic hypothesis stated above, we may test a hypothesized monophyletic group for a character[1] or characters in common not found in any other group. Hennig (1966) termed

[1] Throughout this paper I refer to "characters" rather than "character states." As far as I can see all "character states" should be termed "characters" to avoid hypotheses of homology (higher level synapomorphy), which are not required and usually not tested.

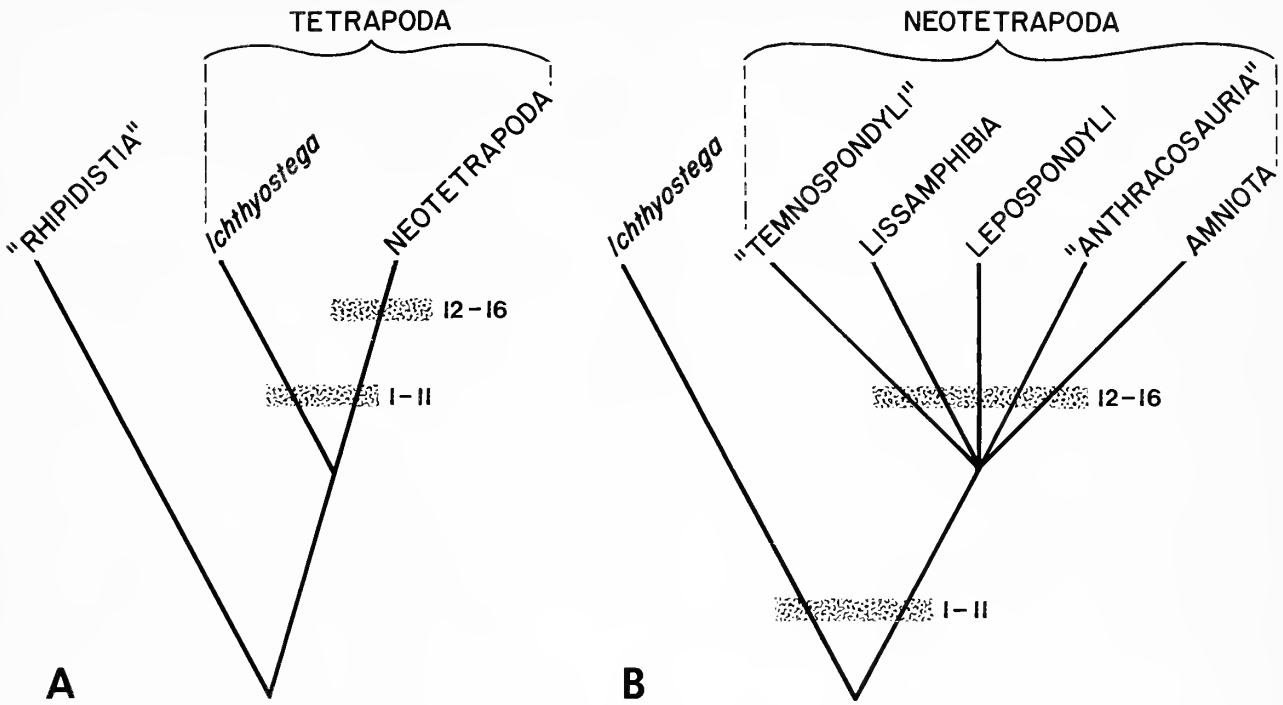

Fig. 1.—Cladograms of the two phylogenetic hypotheses discussed in the text. A) A three-taxon statement of monophyly of the Tetrapoda tested by characters 1–11. B) The statement that Neotetrapoda are monophyletic and consist of an unresolved multichotomy tested by characters 12–16. See text for discussion. Taxa in quotes are not hypothesized as monophyletic (see text under "basic taxa").

such unique or derived characters apomorphous and the common possession of such characters among taxa synapomorphy. In terms of the three-taxon statement, the test for monophyly of two of the three taxa is the presence of the same character in those two taxa but not in any other taxon. This is also called "out-group" comparison; it has been referred to frequently in the systematic literature and has been a prominent feature of systematics for a long time. In theory the out-group consists of all taxa outside the group being tested for monophyly but in practice one usually assumes the correctness of a higher level (more inclusive or more general) hypothesis of relationships and makes comparisons within it. If a character is consistently found within and only within a designated group then the test is consistent with (but does not prove) the hypothesis that the group is monophyletic. In and of itself this test does not mean very much but the important aspect of the test is that a character with the indicated distribution in a three-taxon statement falsifies two of the three alternative hypotheses relating the three taxa in question. This is the strength of the application of the hypothetico-deductive method of phylogeny reconstruction.

Wiley (1975, 1976) has, I think, demonstrated a fundamental relationship in his argument that the criteria used to test homology are the same used to test synapomorphy. For example, when we argue that the forelimb of a frog and the forelimb of a bat are homologous we are actually arguing that at some level (Tetrapoda) both taxa belong to a monophyletic group possessing a forelimb of a particular sort as a synapomorphy. Conversely, an argument proposing the use of forelimb morphology as a derived character testing the monophyletic nature of the tetrapods is also an argument that tetrapod forelimbs are homologous but only at some level of relationship; because as Wiley (1975, 1976) has emphasized, the words "homology" and "synapomorphy" as they are often used are not strictly equivalent. To continue this example, the forelimbs of two mammals would be homologous but not synapomorphous at the level of Mammalia. Homology and synapomorphy are both primarily tests for common ancestry and all of the classical criteria for homology determination, that is, development, topology, and morphology, the basic features of comparative biology, are all tests for monophyly.

The two hypotheses that I am presenting and testing here are diagrammed in Figs. 1 and 2. Fig. 1A shows the first hypothesis in terms of a three-taxon statement which would read as follows: *Ichthyostega* has an ancestor in common with (or is the sister group of) the Neotetrapoda. The non-monophyletic group "Rhipidistia" is indicated as the out-group, but the out-group for the tested characters may be considered as being all nontetrapod vertebrates; I have chosen rhipidistians for specific mention because they are generally the most similar to tetrapods and therefore are best suited for the search for characters presumed to be unique to tetrapods. In other words, if we find a character in rhipidistians (or any other nontetrapod) that is supposed to be a unique feature (derived character or synapomorphy) of tetrapods then this feature no longer can be argued to support the monophyly hypothesis. The first hypothesis (that is, that Tetrapoda is monophyletic) is tested by characters 1–11. The second

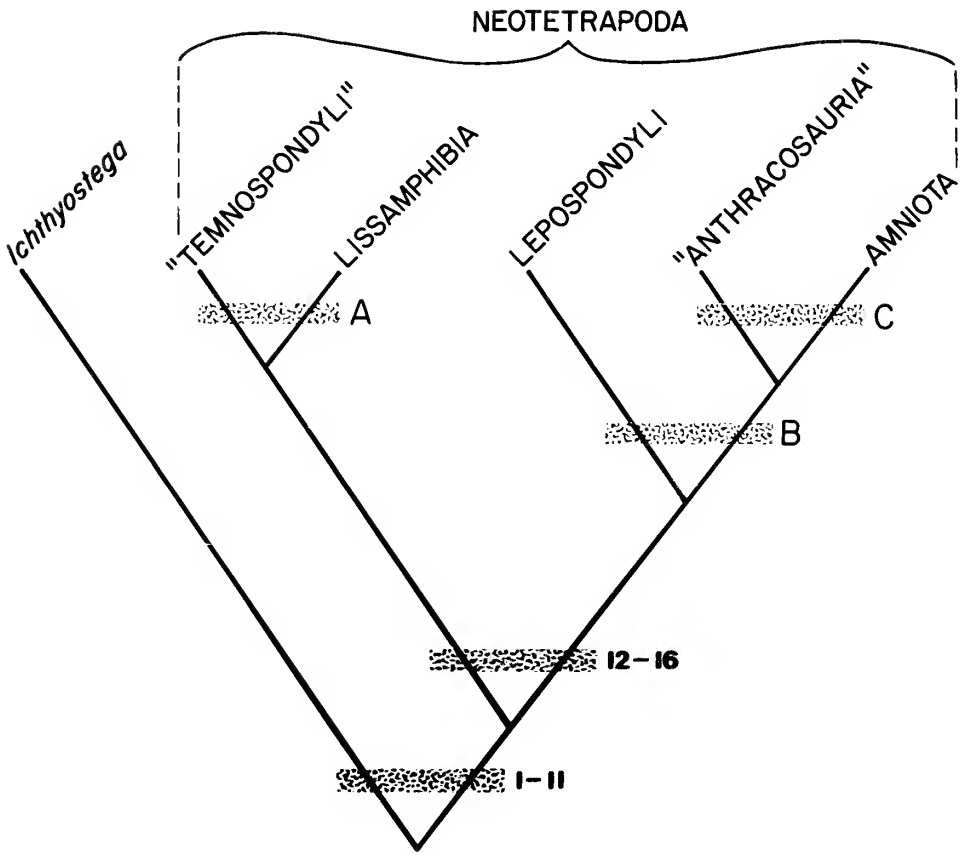

Fig. 2.—One of several possible hypotheses of relationship for the five suggested taxa in Neotetrapoda. This hypothesis is not dealt with in the text but is presented here to suggest future areas of inquiry. Tests would be developed by seeking characters with the distributions A, B, and C.

hypothesis is that the five listed taxa ("Temnospondyli," Lissamphibia, Lepospondyli, "Anthracosauria," and Amniota) constitute a monophyletic group Neotetrapoda. This group is not analyzed in terms of a three-taxon statement because I wish to specify as few hypotheses as possible below this level. Therefore, I use five taxa (termed "basic taxa," see below) in the form of an unresolved multichotomy (Fig. 1B). The outgroup for hypothesizing derived characters (12–16 in Fig. 1) for testing monophyly of Neotetrapoda is *Ichthyostega* plus rhipidistians and other fishes.

I show in Fig. 2 one possible three-taxon analysis of Neotetrapoda but I do not test this phylogeny with characters. In order to do so, derived characters should be sought and their distributions among the taxa determined.

BASIC TAXA

My hypothesis of tetrapod monophyly utilizes seven taxa, for some of which I am accepting hypotheses of monophyly, whereas for others I am not. The important point is that the units involved are all parts of subsidiary hypotheses of relationships that could be tested using shared derived characters. At this time it is not really necessary to examine these hypotheses even in the detail that I have. The few instances where my characters are absent (that is, limbless forms such as aistopods, apodans, snakes) are relatively well tested as tetrapods nonetheless. Rather, I am interested in suggesting areas for future inquiry and in showing what some hypotheses of lower tetrapod relationships look like when presented cladistically, and what some alternative hypotheses might be. I hardly consider this discussion any more than a series of suggestions and I want to emphasize that although I

use these basic taxa hypotheses here, I do not consider any one of them to be particularly well tested at present.

"*Rhipidistia*"

The rhipidistians are here hypothesized as a nonmonophyletic group (hence the quotes) that consists of Choanata (sensu Miles, 1975) minus Tetrapoda (see below). This hypothesis requires that within the rhipidistians there is a monophyletic taxon that is the sister group of the tetrapods, but I am not hypothesizing what this group (or individual species) may be. *Eusthenopteron,* perhaps by virtue of being the best known rhipidistian, is often considered to be the most similar to tetrapods in that it has relatively well-ossified proximal limb elements that can be hypothesized as synapomorphous with tetrapods (Westoll, 1943*b*; Andrews and Westoll, 1970*a,* 1970*b*). However, some poorly known taxa have been reported that have more tetrapod-like features than *Eusthenopteron.* For example, *Elpistostege* (Westoll, 1938), *Hyneria* (Thomson, 1968*b*), and *Eusthenodon* (Jarvik, 1952) have tetrapod-like skull proportions, whereas *Sterropterygion* (Thomson, 1972) and *Sauripterus* (Andrews and Westoll, 1970*b*) have a tetrapod-like forelimb. Therefore I am making my comparisons throughout the Rhipidistia.

I am using here the hypothesis that rhipidistians plus tetrapods form a monophyletic group, the Choanata, as suggested by Miles (1975). The unique presence of internal nares (choanae) is the principal synapomorphy for this group. Dipnoans have a similar structure but this has been strongly disputed as a homologue of the choanae (see references in Panchen, 1967; especially those by Allis, Jarvik and Bertmar), and I am following this hypothesis. Although the coelacanths (Actinistia) have been widely accepted as near relatives of the rhipidistians (for example, Romer, 1966; Moy-Thomas and Miles, 1971; Miles, 1975) there is an alternative hypothesis that is currently gaining favor; this is, that the dipnoans are the sister group to the Choanata rather than the coelacanths (Løvtrup, 1977; Miles, personal communication). Either of these alternatives is satisfactory for my purposes because both require similarities between Recent dipnoans and Recent lissamphibians (that is, autostylic and monimostylic suspension, persistance of the chondrocranium) to be the result of convergence.

Alternatives:

1. Kesteven (1950, and references) presented 57 characters found in common between living dipnoans and living amphibians. He argued that crossopterygians (coelacanths and rhipidistians) lacked these features (to the extent they are determinable) and belonged to a group quite far removed from dipnoans and amphibians. Although to my knowledge a rigorous criticism of Kesteven's characters has not been published, my own examination of them suggests that few would survive a thorough analysis. The "soft" characters, however, could well be consistent with *Latimeria* being the sister group of dipnoans and tetrapods, if only the living groups are considered.

2. Jarvik (1975 and earlier) has argued for some time that urodeles plus porolepiforms are the monophyletic sister group of osteolepiforms plus remaining tetrapods (see Lissamphibia, below, for comments).

Ichthyostega

I am using the hypothesis that the described material of *Ichthyostega* is referable to one strictly monophyletic taxon, either a species or a group of species, that are characterized by the features noted by Jarvik (1952) for the genus *Ichthyostega,* and shown in his figures of the whole animals (Jarvik, 1955: Fig. 11), the skull (1952: Figs. 35, 36), tail (1952: Fig. 6), pelvis (1952: Fig. 5; 1964: Fig. 24), and hind foot (1952: Fig. 5; 1964: Figs. 25, 26). This hypothesis, however, can be criticized. Panchen (1975:634) has said: "Any conclusion about *Ichthyostega,* however, is weakened by the fact that the name may well represent a fauna rather than a taxon." Säve-Söderbergh (1932), when he described the first seven specimens, erected two new genera and five new species for their reception. Jarvik (1952) had a much greater number of specimens at his disposal but (as far as is determinable from the literature) none of the skulls are associated with the postcranial material and much of the postcranial material is disarticulated. In view of the probability that few of Säve-Söderbergh's types will allow the development of adequate diagnoses, it is easy to see why Jarvik's (1952) restorations were identified as *Ichthyostega* sp. Furthermore, Jarvik's description of *Acanthostega* (see below) added to the liklihood of more than one taxon being represented by postcranial material. Therefore, the hypothesis that we are dealing with one monophyletic taxon in "*Ichthyostega* sp." may very well be falsified in the future.

Romer (1947, 1966) and Jarvik (1952) have re-

ferred various forms to the Ichthyostegalia and Panchen (1973) has described a fragmentary specimen with opercular bones. I consider most of these taxa incertae sedis, but they are of sufficient interest to discuss here.

Jarvik (1952) described a new taxon, *Acanthostega*, based on three fragmentary specimens of temporal roofs. His taxon has the lateral lines in canals as in fishes and *Ichthyostega* and a reduced but present preopercular. The palate, snout, and postcranium are unknown. The otic notch is shallow as in *Ichthyostega* but *Acanthostega* is unique among amphibians in having a tabular embayment with a short tabular horn.

Crassigyrinus (Panchen, 1973) has a cheek with bone proportions more rhipidistian-like than occurs in *Ichthyostega*, but its lateral line system is in grooves not canals, a good neotetrapod (see below) character.

Both of these taxa are too incomplete to deal with reasonably in a phylogenetic analysis but they give an intriguing indication of the endless potential for novelties in the fossil record.

Westoll (1938) described *Elpistostege* as a primitive tetrapod, but Thomson (1969) says it is a fish. In any case, it has dermal bone proportions that are now known in both rhipidistians and tetrapods, so that it is no longer of particular interest phylogenetically. Romer (1966) assigned *Otocratia* and the colosteids to the Ichthyostegalia, primarily on the common absence of an intertemporal and the presence of a shallow otic notch, but Panchen (1975) has argued otherwise.

"*Temnospondyls*"

Temnospondyli is a term used by Romer in 1947 to include all labyrinthodonts (including ichthyostegids and stereospondyls) except anthracosaurs. I am using it in the later sense of Romer (1966) so that it excludes ichthyostegids but includes rhachitomes and stereospondyls. In this sense, it would be non-monophyletic under the hypothesis advocated here because it excludes lissamphibians (see below). Romer's (1947) diagnosis of temnospondyls is a list of characters that with few exceptions appear to be primitive for Tetrapoda. In fact, the only one of Romer's characters that might be derived is the four digit manus (Romer, 1947:79). The other characters are found in rhipidistians, *Ichthyostega*, and anthracosaurs. Furthermore, as I am using hypotheses suggested by Bolt (1969) and Estes (1965) that dissorophids are the sister group of Lissamphibia, the temnospondyls of Romer (1966) are paraphyletic unless Lissamphibia are included. The four digit manus would be consistent with a grouping of the temnospondyls and lissamphibians.

Loxommatids (Romer, 1947; Beaumont, 1977) are a good plesiomorphic sister group for remaining temnospondyls (including lissamphibians), which could be hypothesized as monophyletic using palatal vacuities and other features described by Romer (1947). The primitive condition of the vacuities would be the sort seen in *Edops* while the remaining temnospondyls and lissamphibians would possess the more advanced condition.

I know of no alternative hypotheses suggested in the literature, but the available character distributions (forefoot is unknown in loxommatids) would be consistent with loxommatids as the sister group of temnospondyls plus anthracosaurs.

Lissamphibia

I am here using this term in the sense of Parsons and Williams (1963), that is, that urodeles, anurans, and apodans form a strictly monophyletic group. Parsons and Williams' discovery of pedicellate teeth reawakened interest in living amphibians as a strictly monophyletic group. Jurgens (1971) has made a detailed study of the nose and concluded on the basis of specialized characters, that lissamphibians were monophyletic. However, little other work in this direction has been published. As Carroll and Currie (1975) have argued, the really weak point is the relationship of apodans. Apodans are so highly specialized in the loss of limbs and girdles, eye reduction, and skull morphology that few hypotheses about their relationships can be falsified at present. To me, an obvious procedure would be the assessment of primitive characters within apodans via a shared derived character analysis of their phylogeny. Comparison of this with primitive morphotypes of anurans and urodeles should be productive, as Jurgens has shown.

As with most of my other basic taxa, a non-monophyletic Lissamphibia might not affect tetrapod monophyly. If, for example, Carroll and Currie's (1975) hypothesis (see below) is accepted, apodan limblessness is nonetheless considered to be derived for that group and still consistent with tetrapod monophyly.

Among the alternatives to lissamphibian monophyly are the following ideas (restated to make them comparable) that have appeared in the literature.

1. Dipnoans and urodeles form a monophyletic group which is the sister group of rhipidistians and remaining tetrapods. Developed by Säve-Söderbergh (1934) and Holmgren (1933, 1949), criticized by Westoll (1943*a*, 1943*b*, 1943*c*), Schmalhausen (1968), and Thomson (1968*a*). Holmgren's hypothesis was based initially on similarities between the chondrocrania of dipnoans and urodeles and later on limb development.

2. Porolepiforms and urodeles form a monophyletic group that is the sister group of a monophyletic group containing osteolepiforms and remaining tetrapods. Jarvik has argued this hypothesis from 1942 until 1975 (the most recent reference I am aware of) and has changed from using snout and palate characters to many other areas. Nelson (1973) and Bonde (1975) correctly say that there has been no effort to explicitly analyze Jarvik's characters, pro or con, for synapomorphies, and that therefore the criticisms by Szarski (1962), Kulczycki (1960), and Thomson (1962, 1964, 1967*b*, 1968*a*) among others are not particularly telling to his argument. I think, however, that although most of these arguments do not serve as adequate tests of Jarvik's hypothesis, some of them, particularly Thomson (1967*b*, 1968*b*) do serve to dispute Jarvik's homologies and this would be critical to a synapomorphy analysis. And, as Nelson (1973:826) has said: "There is the possibility that his initial conclusions, based on conformity to type, were overextended enough to fatally bias his subsequent argument."

3. Lepospondyls, urodeles, and apodans form a monophyletic group which is the sister group of the remaining tetrapods. Romer (1945, 1947) advanced this hypothesis basing it primarily on patterns of vertebral development. Romer retreated from this position in 1966 following Parsons and Williams' (1963) work.

4. Apodans and microsaurs form a monophyletic group, sister group unspecified (Carroll and Currie, 1975).

5. Apodans are the sister group of the Amniota (Løvtrup, 1977).

6. Microsaurs are the sister group of urodeles plus apodans but excluding anurans (Gregory, 1965).

Lepospondyls

I use this group in their conventional sense (Baird, 1965), that is, consisting of aistopods, nectrideans, and microsaurs (including lysorophids, *Acherontiscus*, and *Trihecaton*). In view of the fact that the initial criterion for the group, holospondyly, is now known to be true only for aistopods and nectrideans (microsaurs have intercentra in a number of genera, Carroll and Currie, 1975; Carroll, 1968) it might seem that there are few characters uniting this group. Nonetheless, lepospondyl monophyly is the most viable hypothesis at present, and the lack of an otic notch, enlarged tabular, and strap-shaped concave occipital condyle might be suggested as shared derived characters.

Although many authors (see Panchen, 1977, and references) have argued that lepospondyls are not a natural group, there have been few arguments presented for alternatives. Thomson and Bossy (1970), however, argue for aistopod-nectridean-anthracosaur monophyly using the tabular-parietal contact. Microsaurs also have this feature and this is actually consistent with lepospondyl-anthracosaur-amniote monophyly (see Fig. 2). Bossy (1976) has used derived characters (accessory apophyses, intravertebral foramina, fused centrum) for a hypothesis of aistopod-nectridean monophyly.

Vaughn (1960, 1962) and others have suggested lepospondyl-amniote monophyly but it is not clear whether or not this would involve remaining lepospondyls as the sister group or not.

In any case, only Carroll's (1967) suggestion that lepospondyls evolved from holospondylous rhipidistians while rhachitomous tetrapods evolved from "rhachitomous" rhipidistians would be inconsistent with my argument of tetrapod monophyly. However, vertebral diversity among Choanata as presently known is great and there are few hypotheses that would be falsified by such distributions because as Panchen (1977, see also for most recent review of this subject) has remarked: ". . . the variety of vertebrae within 'rhipidistia' is so great that . . . almost any theory of the origin of tetrapod vertebrae could be corroborated by a well chosen rhipidistian" (p. 303).

"*Anthracosaurs*"

The anthracosaurs (here used in the sense of Romer, 1966, equals Batrachosauria of Panchen, 1972) are argued to be the nearest known relatives of amniotes in most traditional hypotheses (Carroll, 1969, and other references); that is, they would be the sister group of amniotes, using cladistic terms. Panchen (1972) argued that they are not near relatives of reptiles but are more closely related to temnospondyls. Panchen's (1975) diagnosis of Batrachosauria consists of characters that I would

consider to be primitive for Neotetrapoda with these exceptions: tabular-parietal contact, vomers narrow between internal nares. Both of these characters occur widely in lepospondyls as well as in anthracosaurs and amniotes and could only be considered consistent with monophyly of these three together (as I have suggested in Fig. 2). Panchen (personal communication) has suggested that tooth structure (Panchen, 1970) and a small or absent post-temporal fossa may be synapomorphous for anthracosaurs.

Amniota

My hypothesis of amniote monophyly includes fossils and therefore utilizes preservable characters for tests. Carroll (1970:305) lists a series of nine characters that can be hypothesized as derived for this taxon. Some of them, such as the astragalus, absence of intertemporal, absence of palatal fangs, small or absent intercentra, and no otic notch, occur in microsaurs, but the pterygoid flange is a unique amniote feature. Furthermore, the detailed structure of the temporal region and the sporadic distribution of the astragalus in microsaurs (Carroll and Baird, 1968) suggest that these features are not homologous in both groups.

Monophyly of living amniotes has rarely been questioned but there have been statements of reptilian polyphyly concerning fossil groups (Olson, 1947; Vaughn, 1960).

SHARED DERIVED CHARACTERS TESTING THE MONOPHYLETIC NATURE OF TETRAPODA[2]

1. *Anterior (ethmosphenoid) and posterior (otico-occipital) moieties of braincase intimately united in adult with only a suture persistent (if at all), a distinct fissure as seen in rhipidistians absent, dermal skull roof region overlying braincase united without indication of transverse hinge seen in rhipidistians.*—In rhipidistian fishes and coelacanths the braincase is characteristically separated in the adult into an anterior ethmosphenoid moiety, and a posterior otico-occipital (Moy-Thomas and Miles, 1971) moiety. All tetrapods, with the exception of *Ichthyostega*, show no indication of this division in the adult and the solid braincase is here hypothesized as a derived condition for tetrapods. *Ichthyostega* is reported as having a suture separating the two moieties but it lacks the fissure seen in rhipidistians (Jarvik, 1954; Romer, 1937; Thomson, 1965).

In the dermal skull roof of rhipidistians the braincase articulation is reflected in a distinct transverse fissure between the intertemporal plus parietal and supratemporal plus postparietal. Apparently this fissure acted as part of the intracranial joint (Thomson, 1967*a*). In *Ichthyostega* and other tetrapods the bones on either side of this suture are close together rather than separated. Dipnoans and actinopterygians also have fused braincases but differ from tetrapods in the manner of fusion, elements incorporated, and relative proportions.

2. *Parachordal (otico-occipital) region of skull (area posterior to basipterygoid articulation) longitudinally compact in comparison to rhipidistians.*—The relative proportions of rhipidistian and tetrapod skulls have been one of the classic characters used in discussions of the "fish-amphibian transition." Romer (1937, 1941) first brought attention to this feature in his work on crossopterygians and some version of his figure (1941: Fig. 4) has appeared in almost every discussion of the "transition" (see especially Westoll, 1943*c*: Figs. 3 and 4; Schaeffer, 1965: Fig. 4; Schmalhausen, 1968: Fig. 49). More knowledge of rhipidistians, however, has shown that some rhipidistians (*Eusthenodon,* Jarvik, 1952; *Hyneria,* Thomson, 1968*b*) have parietal and postparietal proportions that are very similar to tetrapods. Furthermore, some tetrapods (*Greererpeton,* Romer, 1969) have very short preorbital lengths, as in rhipidistians. However, information on the braincase of rhipidistians and tetrapods seems to show that the relatively compact parachordal region is derived for tetrapods. Dipnoans lack a compact otico-occipital region and are similar to rhipidistians.

3. *Otic notch.*—*Ichthyostega,* temnospondyls, and anthracosaurs are characterized by an otic

[2] With regard to my use of the terms Choanata, Tetrapoda, and Amniota as monophyletic groups in a system of relationships using rigorous tests, it is interesting to note Romer's comments in 1937 (p. 56): "Säve-Söderbergh . . . has proposed the term Choanata . . . to include these forms [Dipnoans, Crossoperygians] and their tetrapod descendants as part of a phylogenetic scheme of rather unusual character. The term is hardly necessary in any phylogenetic and taxonomic scheme for which there is adequate support, although it is highly useful in a more 'popular' sense, comparable to 'tetrapod,' 'amniote,' etc."

notch, a V-shaped cleft formed at the posterior margin of the skull between the tabular and squamosal. In *Ichthyostega* the notch is shallow in comparison to temnospondyls and anthracosaurs in which it is usually deeper and may have the supratemporal involved as well. *Ichthyostega* also has a preopercular bordering the otic notch, a presumed primitive tetrapod condition. Amniotes and lepospondyls have no otic notch and the primitive condition of the temporal region would be a relatively straight transverse edge. The structure of the transverse edge is different in lepospondyls and amniotes (see Carroll and Baird, 1968: Fig. 11, for what may be suggested as the primitive condition for each group) and a straightforward, most parsimonious hypothesis would be that the features of the temporal region in lepospondyls is synapomorphous for that group and the temporal region of captorhinomorphs is synapomorphous for amniotes, and that an otic notch is synapomorphous at the level of tetrapods and neotetrapods. This is the hypothesis I use here, but the literature is filled with papers that are concerned with various problems in the ear region, particularly with regard to amniotes (see Amer. Zool., 6(3), 1966, for a symposium on the ear region and references). However, I have not been able to find any that propose a serious falsification of the above hypothesis. Most are concerned with developing a derivationist hypothesis involving unknown intermediates (see Parrington, 1958; Panchen, 1975) so that a "labyrinthodont intermediate" (that is, the otic notch being primitive for all tetrapods) is not required in a search for reptilian ancestry.

4. *Single pair of nasals with or without a single median ossification (internasal).*—In rhipidistians multiple median ossifications occur anterior to the frontals and are bordered on either side by multiple pairs of bones. Tetrapods have only a single pair of nasals (sometimes lost or fused) with an internasal primitively, as in *Ichthyostega.*

5. *Stapes.*—It has long been hypothesized, primarily on embryological evidence, that the hyomandibular of fishes is homologous to the stapes in tetrapods (see Goodrich, 1930, and references). This hypothesis of homology is equivalent to the hypothesis that tetrapods and fishes with a hyomandibular form a monophyletic group. At the level of tetrapods unique features of the hyomandibular may be used to test monophyly of that group. The stapes of tetrapods may be characterized as having the following derived features in contrast to the hyomandibular of rhipidistians: a) expanded proximal footplate intimately associated with fenestra ovalis; b) no contact with an ossified operculum; c) distal portion small or unossified; d) overall small size in relation to skull.

The stapes is not described in *Ichthyostega* nor in anthracosaurs (Panchen, 1970) and the discovery of a stapes, particularly in *Ichthyostega,* that differed strongly in these features might seriously weaken the use of this feature. Stapes are reported, although sporadically, in temnospondyls and lepospondyls. Among Lissamphibia, salamanders lack a well-developed stapes and may lack one entirely. Even if the Lissamphibia are not monophyletic, a stapes may by hypothesized as a primitive feature for urodeles.

6. *Fenestra ovalis.*—The fenestra ovalis is a lateral opening of the cavum labyrinthicum and is usually occupied by the footplate of the stapes. Rhipidistians do not have a fenestra ovalis[3], whereas all tetrapods in which the area is known have a fenestra ovalis. The condition for the area is not described in *Ichthyostega,* however, and although I am hypothesizing this as a tetrapod synapomorphy, it may be a neotetrapod synapomorphy.

7. *Carpus, tarsus, and dactyly.*—The presence of fingers in the fore and hind limbs in company with definitive ankle and wrist joints are among the most distinctive tetrapod attributes. Andrews and Westoll (1970*a*) identify tetrapod features in the humerus, radius, and ulna of *Eusthenopteron,* but find no indication of tetrapod features in a more distal position. Holmgren (1949, and earlier) and Jarvik (1965) have disputed presumed homologies between the carpus and digits of urodeles versus other tetrapods by arguing that similarities exist between urodeles and non-tetrapods in the morphology of the carpus and digits. Schmalhausen (1968:252, 255, Fig. 154) and Thomson (1968*a*:294–301, Figs. 8, 9; see also Olson, 1971:594) have developed arguments against using the limb characters of Holmgren and Jarvik by disputing the supposed homologies between urodeles and non-tetrapods. I think these arguments are apt and consistent with my methodology[4] but more importantly both authors use the detailed morphology of temnospondyl and lissamphibian appendages to argue for a common ancestor possessing these features. The characters

[3] Jarvik (1972:210) describes a fenestra ovalis in porolepiforms and osteolepiforms but as far as I can tell the proximalmost portion of the hyomandibular does not fit into any fenestra and the "fenestra ovalis" of Jarvik lies posterior to the hyomandibular.

[4] Even Bonde (1975:309) agrees, saying that Thomson "probably demolishes this very unconvincing argument for 'diphyly.'"

of both authors are not expressed in terms of primitive and derived but the structure of carpus and tarsus in urodeles, *Ichthyostega* (tarsus only), temnospondyls, and amniotes (see Thomson, 1968*a*), as presented by these authors is readily hypothesized as synamorphous for these taxa in comparison with fishes.

Although the primitive number of digits in tetrapods may be disputed, there is rarely any argument about homology of the five known digits. Even Holmgren and Jarvik (above) do not dispute the identification of digits I–V among the tetrapods used in their studies (including urodeles). This is based not only on the position of the digits but also upon their consistent relations to carpal and tarsal elements even when one or more digits are secondarily lost. The absence of fin rays also makes tetrapod limbs distinctive. The combination of all these features results in a series of synapomorphies testing monophyly for Tetrapoda.

The apparently universal presence of four digits in the manus of lissamphibians and temnospondyls may be a synapomorphy uniting these two groups or it may be primitive for all tetrapods. The manus of *Ichthyostega* is not known but the close agreement of the carpus in temnospondyls and anthracosaurs suggests that five fingers in the manus is the primitive tetrapod condition. Also the common, but not universal occurrence of four digits in the manus of lepospondyls weakens the possible use of this as a temnospondyl-lissamphibian synapomorphy.

Howell (1935) and Schaeffer (1941) argue that there is no evidence for more than five digits in the manus and pes and that the prepollex and postminimus do not represent lost digits (Schaeffer, 1941, suggests that calling them pre- and postcarpale would be more accurate).

8. *Pectoral skeleton free from skull; post-temporal, supracleithrum, and anocleithrum absent; scapulocoracoid relatively larger than dermal shoulder girdle elements.*—Andrews and Westoll (1970*a*:219, and following) give a good comparison of this region between *Eusthenopteron* and tetrapods. As in other areas, detailed information on *Ichthyostega* would allow greater precision in comparisons of this sort. These features are universally present in tetrapods (except in the case of the scapulocoracoid, which is absent in some forms, that is, aistopods, apodans, snakes).

9. *Iliac blade of pelvis extends dorsally to level of vertebral column and is attached to vertebral column by an ossified sacral rib (or ribs).*—In *Eusthenopteron* there is no evidence of ossified sacral ribs although Andrews and Westoll (1970*a*) feel that a cartilaginous rib was present. At least one sacral rib and a well-developed iliac blade is present in all tetrapods, again with the exception of limbless forms.

10. ***Well-developed ischiac ramus of pelvis, well-developed pubic symphysis (along with a generally large ventral portion of the pelvis).***—No rhipidistian approaches tetrapods in the development of these pelvic features, and these features are universal among tetrapods with the exception of limbless forms.

11. *Ossified ribs well developed and directed ventrally.*—Ribs are absent in nearly all rhipidistians but are present in *Ichthyostega* and nearly all other tetrapods. *Eusthenopteron* is the only rhipidistian definitely known to have ribs but they are small and dorsally directed. Well-developed and ventrally directed ribs are widespread in actinopterygians but this distribution would be plesiomorphic for this character only if the Choanata were not monophyletic and if the actinopterygians were the sister group of the tetrapods. Ribs also occur in two coelacanths (*Chinlea* and *Diplurus*) but this appears to be autapomorphic for those taxa.

SHARED DERIVED CHARACTERS TESTING THE MONOPHYLETIC NATURE OF THE NEOTETRAPODA

The Neotetrapoda[5] is the group of tetrapods which are the sister group of *Ichthyostega*, that is, temnospondyls, anthracosaurs, lepospondyls, lissamphibians, and amniotes, as characterized here. The five characters listed below are found universally throughout this group and no discussion of character contradictions is needed. They are listed in numerical sequence following the Tetrapoda characters for ease of reference (see Figs. 1, 2).

12. *Persistent notochord excluded from braincase in adult, parachordal (otico-occipital) region formed without significant contribution from notochord.*

13. *Preopercular and opercular (subopercular) ossification absent.*

[5] "Eutetrapoda" might be more appropriate but it has been widely used by Säve-Söderbergh (1934) for a group of tetrapods excluding urodeles and to adopt this might cause confusion.

14. *Median bony fin supports with lepidotrichia absent.*

15. *Lateral line system absent or in grooves, enclosed in bony canals.*

16. *Ethmosphenoid and parachordal (otico-occipital) portions of braincase solidly fused in adult, not separated by suture.*

SUMMARY

The theory of relationships that the Tetrapoda are a strictly monophyletic group (in the sense of Hennig) is tested using the following derived (synapomorphous) characters:

1. Anterior (ethmosphenoid) and posterior (otico-occipital) moieties of braincase intimately united in adult with only a suture persistent (if at all), a distinct fissure as seen in rhipidistians absent, dermal skull roof region overlying braincase united without indication of transverse hinge seen in rhipidistians.

2. Parachordal (otico-occipital) region of skull (area posterior to basipterygoid articulation) longitudinally compact in comparison to rhipidistians.

3. Otic notch.

4. Single pair of nasals with or without a single median ossification (internasal).

5. Stapes.

6. Fenestra ovalis.

7. Carpus, tarsus, and dactyly.

8. Pectoral skeleton free from skull; post-temporal, supracleithrum, and anocleithrum absent; scapulocoracoid relatively larger than dermal shoulder girdle elements.

9. Iliac blade of pelvis extends dorsally to level of vertebral column and is attached to vertebral column by an ossified sacral rib (or ribs).

10. Well-developed ischiac ramus of pelvis, well-developed pubic symphysis (along with a generally large ventral portion of the pelvis).

11. Ribs well developed and directed ventrally.

A second theory of relationships suggests that the Tetrapoda consists of two sister groups, the Devonian tetrapod *Ichthyostega* and the Neotetrapoda. The Neotetrapoda is a term coined here to refer to the group consisting of the Temnospondyli, Lissamphibia, Anthracosauria, Amniota, and Lepospondyli. The following shared derived characters test monophyly of the Neotetrapoda:

12. Persistent notochord excluded from braincase in adult, parachordal (otico-occipital) region formed without significant contribution from notochord.

13. Preopercular and opercular (subopercular) ossifications absent.

14. Median bony fin supports with lepidotrichia absent.

15. Lateral line system absent or in grooves, not enclosed in bony canals.

16. Ethmosphenoid and parachordal (otico-occipital) portions of braincase solidly fused in adult, not separated by suture.

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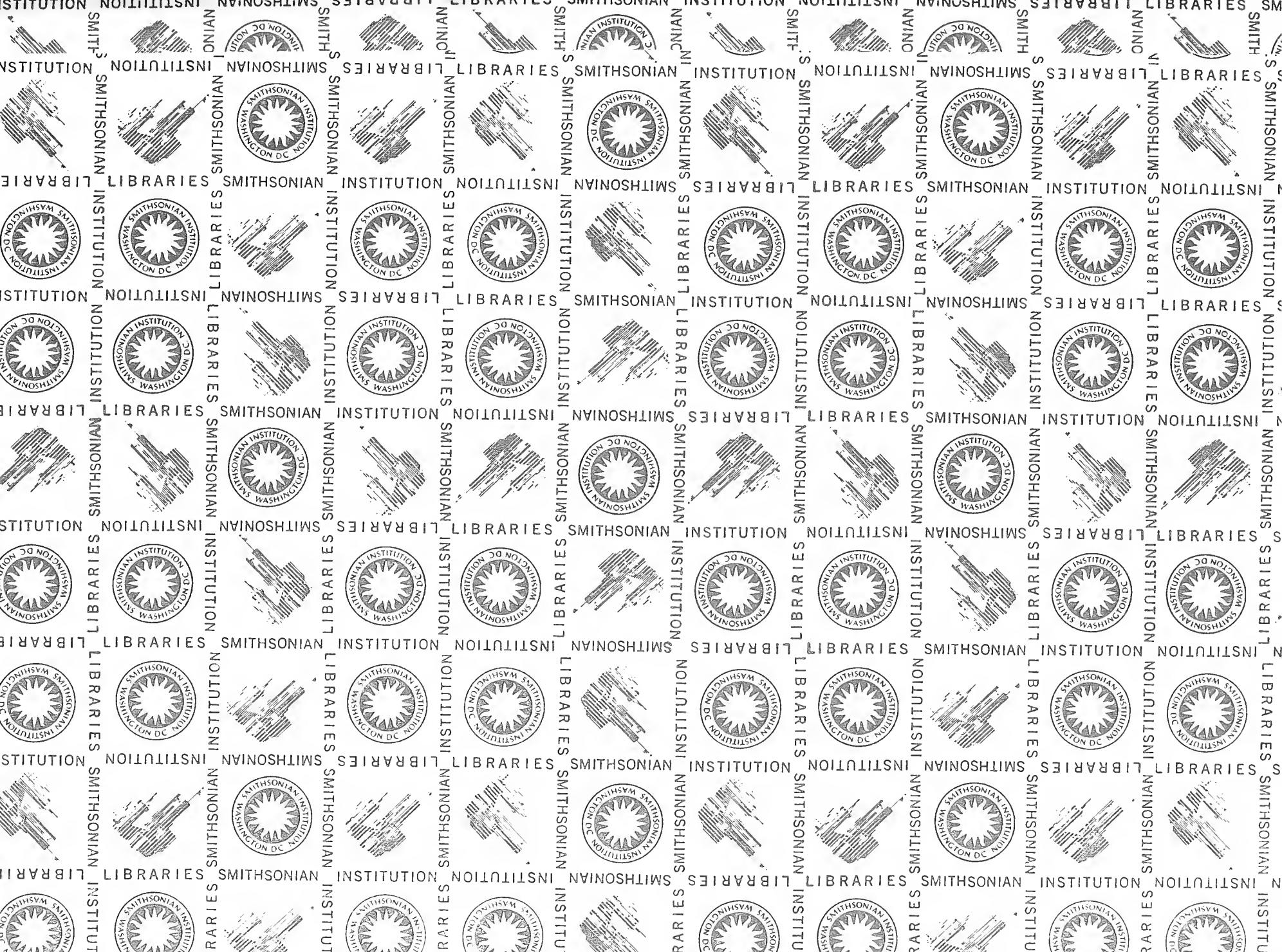
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