A COMPARISON OF CHROMOSOMAL AND PALEONTOLOGICAL EVIDENCES OF EVOLUTION IN RODENTS

A THESIS

IN ZOOLOGY

by

Jean Ann Rosenbaum

Approved

Dean of the Graduate School

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Jean Ann Rosenbaum, B. A.

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A COMPARISON OF CHROMOSOMAL AND PALEONTOLOGICAL EVIDENCES OF EVOLUTION IN RODENTS

I. INTRODUCTION

In order to obtain a more accurate picture of evolution among a group of organisms, it is necessary to coordinate information obtained from the study of various aspects of the group, rather than to postulate an evolutionary trend based upon evidence of a single specific trait. For this reason, a study of the chromosomes of rodents has been undertaken in an effort to corroborate the paleontological findings of A. E. Wood (1935, 1937, 1947) which are based, for the most part, on anatomical comparisons of the fossil skeletons of rodents. By comparing the teeth, jaws, and limb bones of different species, Wood has demonstrated the trend toward "parallel" evolution among rodents, as opposed to "radial" evolution. This parallel evolution is evidently a result of the early acquisition of ever-growing incisors, which consequently has modified the adaptive radiation of the later rodents to a single direction.

The work of Wood will be correlated with certain chromosomal evidence, particularly as it pertains to five families of the order Rodentia: the Heteromyidae, the

Geomyidae, the *Sciuridae*, the *Cricetidae*, and the *Muridae*. Part of the chromosome material has been taken from the research of Dr. J. C. Cross (1931, 1938) of this department, in which he has compared twenty species and subspecies of rodents according to the range in number and variation in morphology of their spermatogonial chromosomes. The results obtained by Cross have been further substantiated by those of Makino (1953), who has established the haploid number of sixteen species of American rodents.

The author has supplemented the limited available material concerning rodent evolution by studying the spermatogonial cells of the pocket gopher, *Cratogeomys castanops perplanus*.

II. MATERIALS AND METHODS

The gopher specimen studied by the author (fig. 10) was trapped in Lubbock, Texas, and brought to the laboratory where it was sacrificed by a blow on the head. The testes were removed immediately and the tissue was fixed in Allen's modification of Bouin's fluid, which had been adjusted for increased altitude according to a method developed by Cross (1951). The tissue was dehydrated with graded alcohols, embedded in paraffin, and sectioned at 10 microns. The testes were stained with crystal violet.

The drawing was made with the aid of a camera lucida at a magnification of approximately 4750 diameters.

III. DISCUSSION

According to Wood (1947) there were originally a number of groups of rodents which arose from a single basic stock and which were forced, by the adaptation of initial gnawing characteristics, to evolve in the same general direction. Differences among the groups may be attributed to the diverse selective effects of various climatic or other environmental factors.

Generally speaking, the limited amount of cytological evidence which is available tends to support this theory. When the diploid chromosome numbers of five families of Rodents are studied, a wide range in number is noted among the groups. Assuming the chromosome number for the basal placental stock to be 48 (Painter), it is postulated that the older families of rodents having a diploid number close to 48 evolved from the basic rodent stock first, while those families having a higher chromosome number appeared as offshoots in a later geological period. The large differences in the number of chromosomes among the rodents, ranging roughly from 40-86, indicate a parallel evolution rather than a radial evolution. If radial evolution were the case, one would expect to find the diploid numbers converging around 48, with perhaps a gradual increase or decrease from this base number. At the present time, no specimens have been found which present evidence for an "adaptive radiation" or a gradual progressive divergence with occasional parallelisms and convergences. Rather, a theory which appears to fit the evidence in a more satisfactory manner is one such as that postulated by Wood, in which these families evolved from the basic rodent stock at different times, and continued to evolve in a parallel manner. Those groups which are more closely related, such as the Heteromyidae and the Geomyidae, exhibit chromosomes which are very similar in number and morphology.

Chart I has been constructed in an effort to show one possible trend of rodent evolution according to both the anatomical traits and the chromosome numbers of these mammals. Since there is no available cytological evidence concerning the Cretaceous, Paleocene, or Eocene rodents, this section of the chart is based on Wood's studies, which show that the rodents probably separated from the basal placental stock not later than the end of the Cretaceous, and that the earliest known rodents occur at the top of the Paleocene. By comparing the different types of zygomasseteric structure, it is possible to conceive of the Eocene rodent, Paramys, as being either the common ancestor or a slightly modified descendant of the stem form of the later rodents.

With the evolution of the Myomorphs (*Muridae* and *Cricetidae*) and the Sciuromorphs (*Sciuridae*, *Heteromyidae*, and *Geomyidae*) in the Oligocene, cytological evidence in the form of the diploid chromosome number is available.

As was mentioned previously, this theory of the evolutionary trend is based on the assumption that the rodents with a chromosome number close to 48 (basal placental stock) evolved first, while those with higher diploid numbers appeared later. If this hypothesis is correct, then it is necessary to assume that the higher chromosome numbers arose as a result of the fragmentation of the original base number of the chromosomes, rather than the fusion of chromosomes which would result in just the opposite case. Actually it is impossible to show whether fragmentation or fusion has played the major role in altering the numbers.

According to Cross (1931) there is strong evidence of fragmentation among species of the *Cricetidae*. Three species of *Peromyscus* show 48 chromosomes, while there are 48 and 52 chromosomes in two subspecies of *P. maniculatus*. Cross states that 48 is probably the base number of the genus, and that the deep constrictions which are observed in *P. maniculatus gambeli* with 48 chromosomes (fig. 1) may be a step toward the formation of *P. maniculatus hollesteri*, which exhibits 52 chromosomes (fig. 2).

Furthermore, *hollesteri* does not have the medium-sized constricted elements, but shows more small chromosomes than *gambeli*.

There are, of course, several other phenomena which could account for an addition or reduction of the chromosome number. However, evidence indicates that for various reasons these factors are not as likely to be responsible for the change in number as fragmentation or fusion. Polyploidy would be one such possibility, but Painter points out that this condition is relatively rare in animals since it would result in a disruption of the sex-determining mechanism and the formation of a sterile animal. Hybridization and non-disjunction also appear very unlikely since a large amount of sterility usually occurs in both cases.

Assuming then that the base number is 48, and that those forms having a smaller chromosome number are the more primitive forms, it is postulated that, of the five families studied, the *Muridae* and the *Cricetidae* were the earliest to evolve from the basic rodent stock. The *Muridae* are the Old World mice and rats, and Cross (1931) has demonstrated that the diploid chromosome number of *Rattus rattus alexandrinus* (fig. 3) is 40; the chromosomal evidence thus indicates that the *Muridae* evolved before the *Cricetidae*, which exhibits an average chromosome number of 50.. Although Wood (1937) agrees that both the *Muridae* and the *Cricetidae* evolved from the basic stock during the Oligocene, he points out that the *Cricetidae* appear to be more primitive than the *Muridae*; evidence for this statement is based on a comparison of the patterns of rodent cheek teeth. The *Cricetidae* exhibit a five-cusped pattern arranged in this manner : · : in addition to a series of connecting crests. He feels that this pattern may represent the basic pattern from which the cheek teeth pattern of the *Muridae* has been derived.

The *Sciuridae* (squirrels) also arose from the parent rodent stock during the Oligocene. Their range in chromosome number and morphology is much more striking than that of the two preceding families. The southern grey squirrel (Sciurus carolinensis carolinensis) shows 48 pairs of chromosomes (fig. 4), with 15 V- or J-shaped pairs and slightly more than half that number of relatively small rods; there are no very small dots. On the other hand, *Sciurus niger rufiventer* or western fox squirrel (fig. 5) has a diploid number of 62. This genus exhibits only eight pairs of large V- and J-shaped elements; these spermatogonial cells also reveal a number of comparatively small rods and dots, as contrasted with the grey squirrel. This difference may be explained by fragmentation, provided that the grey squirrel is regarded as the more primitive.

The chromosomes of the flying squirrel *Glaucomys volans volans* (fig. 6) are quite different in their morphological characteristics from the other squirrels. Of the 52 chromosomes, no V-shaped were visible, and there appeared to be only one pair of J-shaped chromosomes; the other chromosomes are rod-like.

For the purposes of indicating a possible location on the evolutionary chart I, the avarage chromosome number for the *Sciuridae* has been taken as 60.

Most of the evidence collected by Wood indicating parallel evolution among rodents has been obtained from a study of the two remaining families under consideration - the *Heteromyidae* and the *Geomyidae*.

Chart I shows the *Heteromyidae* (pocket mouse, spiny pocket mouse, and kangaroo rat) evolved to one side as a result of modifications leading to extreme leaping ability; the *Geomyidae* (gopher) branched off to the other side since their burrowing activity enabled them to spend nearly all of their life beneath the ground.

Wood states that the *Heteromyidae* are not closely related to the true rats and mice, but that a comparison of zygomasseteric structures indicates that both the *Heteromyidae* and the *Geomyidae* are more closely related to the *Sciuridae*. Chromosomal evidences also tend to support this theory, since both the kangaroo rat and the pocket gopher have chromosome numbers in the eighties and the *Sciuridae* exhibit the next highest number of 60.

According to Wood (1937), the *Heteromyidae* and the *Geomyidae* were distinct groups as far back as the Oligocene. Since there are no available data concerning the chromosomal characteristics of the primitive ancestors of these two groups, it is necessary to consider first the *Perognathus* (pocket mouse) as being one of the earlier forms for which sufficient cytological evidence can be obtained. Cross (1931) describes the spermatogonia of *Perognathus fallax fallax* (fig. 7) as consisting of 44 chromosomes; there are 7 or 8 pairs of V-, J-, or U-shaped elements, the remainder being rod-like, with a few extremely small dot-like chromosomes. This pocket mouse contains the lowest number of chromosomes of the specimens of *Heteromyidae* which have been studied by the author, and it is therefore considered to have been one of the earlier species to evolve. *Perognathus* illustrates the foundation pattern for the present type of cheek-tooth structure that occurs in the later *Heteromyidae* and *Geomyidae* (Wood, 1937); the four-cusped type of lower premolar exhibited by the pocket mouse is quite primitive and approaches the ancestral conditions.

From the standpoint of chromosome number, *Perognathus* would be an earlier form than Liomys (spiny pocket mouse) which has a diploid number of 58 (Makino). Wood states, however, that the skeleton of Liomys is more primitive than that of Perognathus; in fact when all of the anatomical traits are considered, Liomys is probably the most primitive member of the family. It would perhaps be possible to explain this situation by postulating a fusion of the chromosomes, resulting in a decrease from 58 to 44. Makino (1953) has described the diploid complement of Liomys irroratus (Mexican pocket mouse) as consisting of a pair of small J-shaped chromosomes, in addition to rod-shaped elements of varying sizes. By means of fusion, the rod-shaped chromosomes could join together to form the 7 or 8 pairs of U-, J-, or V-shaped chromosomes described previously in the Perognathus. The question remains a debatable one, however, in view of the stronger evidence which indicates that fragmentation, rather than fusion, has been the prime factor in the evolution of rodents.

The chromosomal data which give rise to the theory that Liomys, with a chromosome number of 58, evolved before Dipodomys, whose chromosomal component is approximately 86, are in accord with the anatomical evidence that the skeleton of Liomys is more primitive than that of Dipodomys. The diploid number of the kangaroo rat (Dipodomys merriami merriami) can only be approximated because of the high number and small size of the chromosomes (fig. 8). Cross feels that the number 86 should be considered the minimum rather than the maximum.

The best evidence showing a correlation between the chromosomal and paleontological evidences for parallel evolution among rodents is exhibited in the kangaroo rat of the Heteromyidae and the pocket gopher of the Geomyidae. Cross (1931) has made a study of the gopher Geomys breviceps breviceps, which reveals the presence of approximately 84 chromosomes (fig. 9). The morphology of the chromosomal elements is very similar to that of the kangaroo rat, and the determination of the exact number is difficult because of the large number and relatively minute size of the chromosomes.

The author has corroborated this work of Cross by studying the spermatogonial cells of the pocket gopher Cratogeomys castanops perplanus, which also exhibits approximately 84 chromosomes. Although Cross describes the Geomys as having several pairs of large J-shaped chromosomes, together with many small rod-shaped ones, the author was able to detect only small rod-shaped chromosomes which were fairly uniform in size and shape in the cells of the Cratogeomys. This discrepancy may be due to the extreme difficulty which was encountered in the attempt to make an accurate study of the metaphase chromosomes.

The chromosomes of Cratogeomys are represented by fig. 10.

Wood gives many examples of parallel evolution among these two groups: the independant acquisition of upper and lower molars, each consisting of two transverse crests; the trend toward the reduction of the enamel on the buccal and lingual margin of the teeth; the development of rootless teeth; the forward migration of the infra-orbital foramen, impelled by the growth of the masseter, but not separated from the muscle by a crest or ridge, and several other similarities based on skeletal comparisons. The chromosome numbers of 86 in the kangaroo rat and 84 in the pocket gopher appear to this author to be indicative of the trend toward parallel evolution which Wood has observed in the evolution of the rodents.

In conclusion, it is necessary to state that, although the preceding information has afforded a definite correlation between cytological and paleontological evidences, accurate taxonomy should be based for the most part on anatomical comparisons. It is evident that there are many changes which are not observable with the microscope, and for this reason a paleontological study, which has been supplemented with cytological evidence, presents a more satisfactory method of studying the evolutionary trend of the rodents.

IV. SUMMARY

1. A study of the numbers and morphology of the chromosomes of 5 families of *Rodentia* has been made in an effort to compare the chromosomal evidence with the paleontological evidence observed by Wood, which indicates a trend toward parallel evolution.
2. Based on the theory of fragmentation as a method for increasing chromosome numbers, the most primitive forms are those having the lowest diploid numbers.
3. Chromosomal evidence supports the anatomical evidence that the Myomorphs (*Muridae* and *Cricetidae*), with a chromosome range of 40-50, evolved at an earlier stage than the Sciuriomorphs (*Sciuridae*, *Heteromyidae*, and *Geomyidae*), whose chromosomal components range from 60-86.
4. The chromosomal data which best support the theory of parallel evolution among rodents are found by comparing the diploid number of the kangaroo rat (86) with that of the pocket gopher (84).

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EXPLANATION OF FIGURES

Fig. 1. Peromyscus maniculatus gambeli

Fig. 2. Peromyscus maniculatus hollesteri

Fig. 3. Rattus rattus alexandrinus - roof rat

Fig. 4. Sciurus carolinensis carolinensis - grey squirrel

Fig. 5. Sciurus niger rufiventer - western fox squirrel

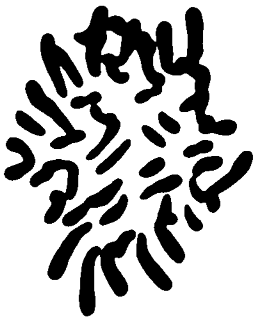
Fig. 6. Glaucomys volans volans - flying squirrel

Fig. 7. Perognathus fallax fallax - pocket mouse

Fig. 8. Dipodomys merriami merriami - kangaroo rat

Fig. 9. Geomys breviceps breviceps - pocket gopher

Fig. 10. Cratogeomys castanops perplanus - pocket gopher



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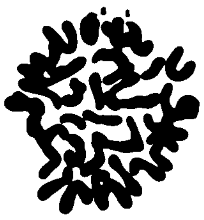

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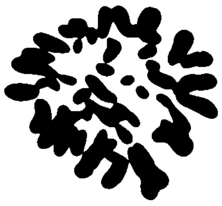

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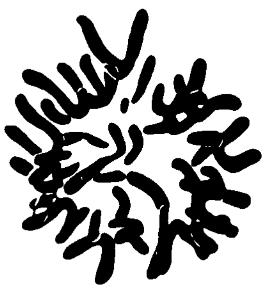

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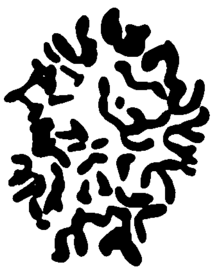

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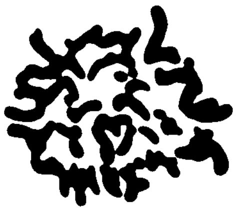

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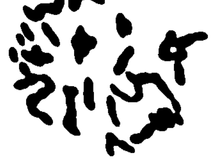

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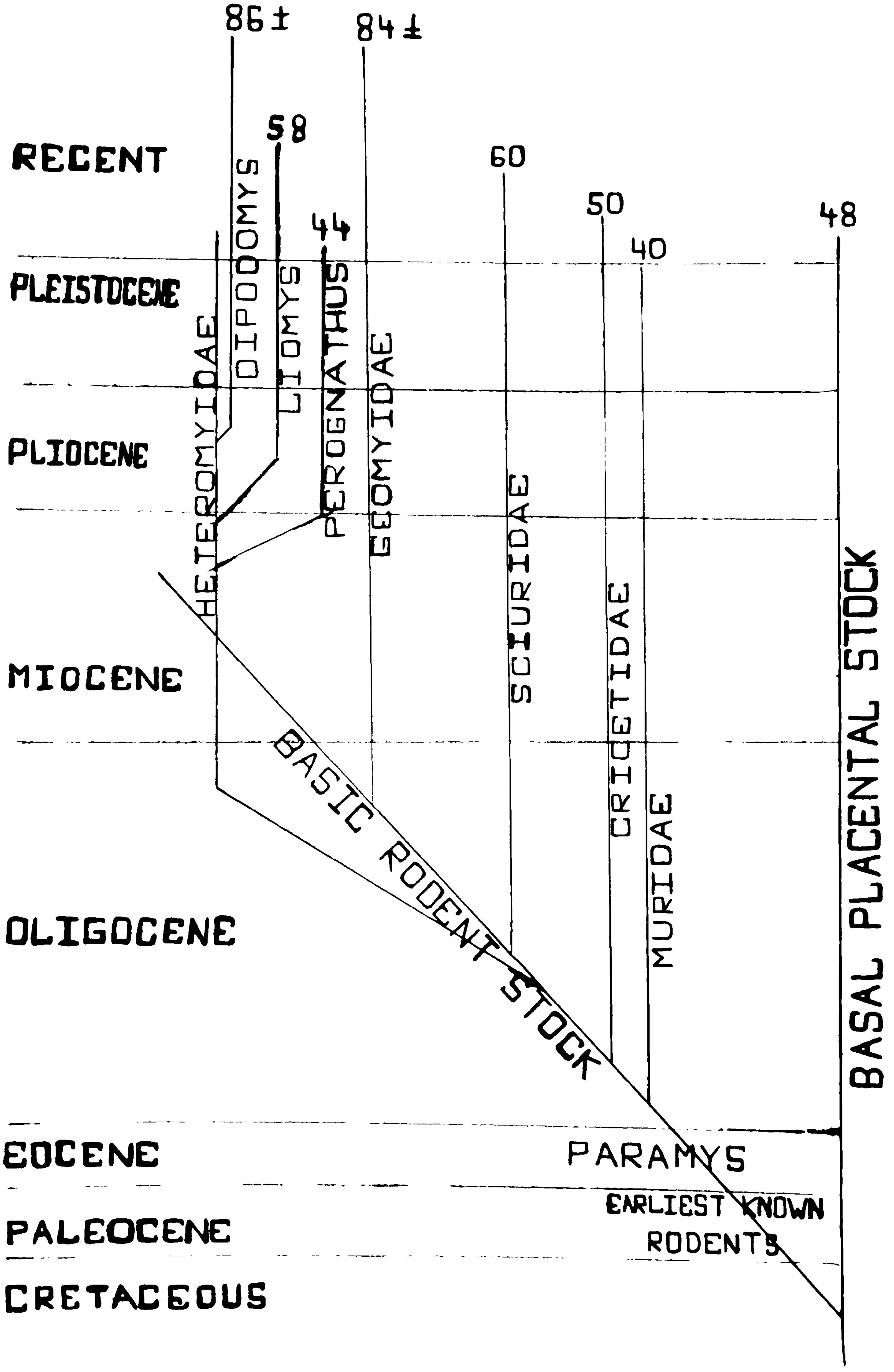
86±
84±
58
60
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44
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RECENT
PLEISTOCENE
PLIOCENE
MIOCENE
OLIGOCENE
EOCENE
PALEOCENE
CRETACEOUS
HETEROMYIDAE
DIPODOMYS
LIOMYS
PEROGNATHUS
GEOMYIDAE
SCIURIDAE
CRICETIDAE
MURIDAE
BASAL PLACENTAL STOCK
BASIC RODENT STOCK
PARAMYS
EARLIEST KNOWN RODENTS

CHART I