ORIGIN OF THE KAIBAB SQUIRREL

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Abstract

Since its origin, the Grand Canyon of the Colorado River has provided an effective barrier, isolating the Kaibab squirrels on the north rim from the Abert squirrels on the south rim. The differences in these squirrels have been used as a classical example of the role of geographical isolation in evolution. This paper examines the differences in the two populations and describes the nature and extent of the isolating mechanism. It then evaluates the applicability of the violations of restrictions of the Hardy-Weinberg equilibrium population. The study concludes that the Kaibab squirrel populations should be an ideal test group for assessing the extent of changing gene frequencies across the uniformitarian time scale claimed for the formation of the Grand Canyon. Evidence is presented showing violations of all of the Hardy-Weinberg restrictions for an equilibrium population but with only minute differences between the two populations. This does not correlate well with the standard explanation for the time of formation of the isolation barrier. It is suggested that these data provide indirect evidence for a very recent origin of the Grand Canyon.

Key Words: *Sciurus aberti*, Kaibab squirrel, Grand Canyon, Geographical isolation, Hardy-Weinberg equilibrium.

Introduction

The Grand Canyon of the Colorado River is of interest to creationists, not only because of its geological features, but also because it represents what is probably the world's most sharply delineated barrier to terrestrial animal movement. Here, the Colorado River separates the Kaibab Plateau on the north from the Coconino Plateau on the south by the largest canyon on earth. The Grand Canyon, 5,000 feet deep and from 12 to 15 miles in width, encompasses most of its 200 mile length by nearly vertical walls of rock.

The natural history and management of the tassel-eared squirrel *(Sciurus aberti)* has generated considerable interest in recent years, resulting in the publication of a bibliography of 175 entries.[1] This animal is widely distributed throughout the Ponderosa Pine forests of the southwest. Because of specific needs for the cones and terminal buds of the Ponderosa as a food source, these squirrels, like the forest they inhabit, are characterized by a discontinuous distribution.[2] See Figure 1 for a map of present distribution.

In northern Arizona the Grand Canyon of the Colorado acts as a barrier separating the two populations of these squirrels. The population north of the canyon (Kaibab squirrel) is confined to the Kaibab Plateau (see Figure 2 for a map showing place names used in this paper), an area 60 miles long and 35 miles wide, ranging from 8,000 feet in elevation upward to about 9,200 feet (see Rasmussen, reference 3, for a detailed analysis of the biotic communities of the area). The population south of the Grand Canyon (Abert squirrel) is found not only in higher areas of the Coconino Plateau, but also in an arc southward into central Arizona, eastward into New Mexico, and northward into the Colorado Rockies. There are also several isolated populations in Mexico.

Because of differences in color between the two populations separated by the Grand Canyon, evolutionists have used this feature as ". . . a classical example of the role of geographical isolation in evolution."[4] See reference 5 for use in college textbooks. The purpose of this paper is to survey the biology of the tassel-eared squirrel, examine the actual differences between the two populations, evaluate the nature and extent of the Grand Canyon as an isolation barrier, and explore the reasons why they should have undergone extensive differentiation if violations of the restrictions of the Hardy-Weinberg equilibrium population are valid.

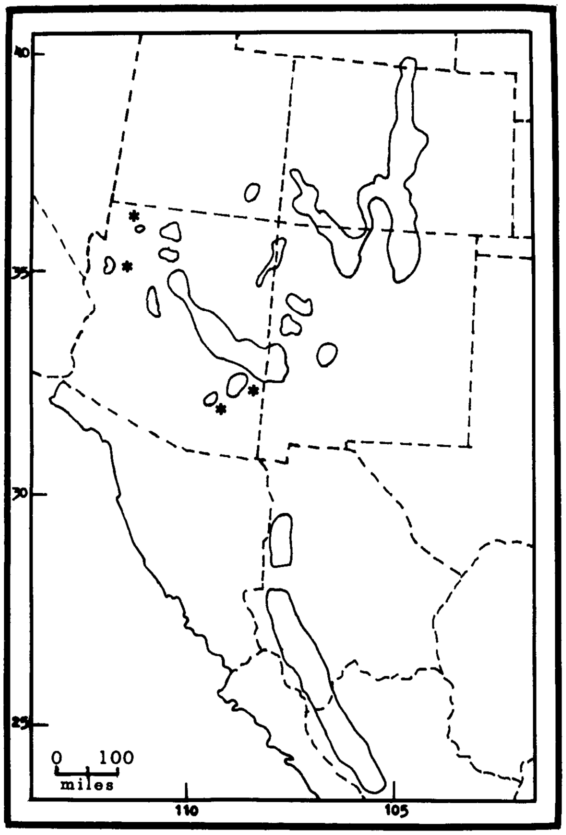

Figure 1. Distribution map of Tassel-eared squirrels. This map has been compiled from a number of sources with adjustments made from personal observations and known distributions of Ponderosa Pine to which the squirrel is confined. Starred areas indicate localities where present populations are thought or are known to have been introduced by man.

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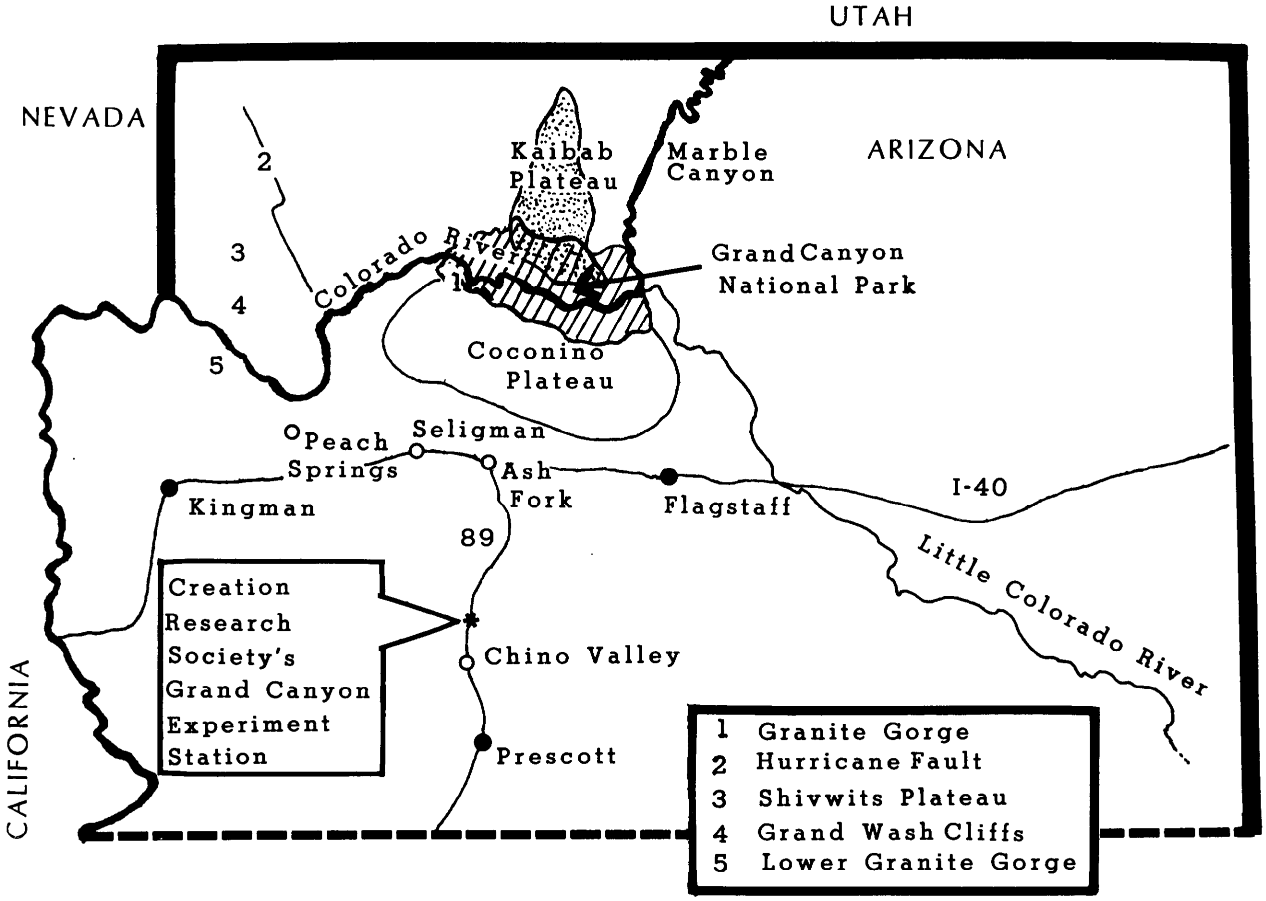

Figure 2. Map of the Grand Canyon region and vicinity showing place names mentioned in the text.

Finally, I will attempt to show that tassel-eared squirrel distribution and limited morphological differences provide direct evidence of extremely limited intraspecific changes and indirect evidence for a recent origin of the Grand Canyon as an isolating mechanism.

Abert Color Description

In general, the main color features of the typical Abert squirrel include a dark-colored tail, white belly and steel-gray body. More specifically, the body possesses a steel-gray color resulting from hairs which are black at the base and midsection, but white or tan-colored at the tip. A rufous-brown spot of variable size is found on the back, usually extending three-quarters of the way across and running from the shoulder blade to near the base of the tail. There is much variability however. The rufous spot on the back is due to hairs which are black at the base but reddish brown at the tips. However, some hairs in this region are black to the tip. Thus, the characteristic color results from intermingling of different hair-tip colors.

The tail is gray on the dorsal side across four-fifths of the width and nearly to the tip. The lateral edges are white (see Figure 3). The gray color derives from each individual hair having repeating black and white regions. A dark lateral line extends from the lateral foreleg, along the lateral stomach area to about the hip region; but again much variability exists here. This lateral line usually varies from 10 to 20 mm. in width with considerable variation in length.

The belly tends to be nearly pure white in most specimens with the color extending to about the tip of the tail on the ventral side and along the lateral edge of the dorsal side. White coloration also extends to the ventral and lateral chin areas, ventral forelegs, and dorsal front and rear feet. Dark hair is found in the pubic area, and the base of the ear is brown.

Kaibab Color Description

The Kaibab is considered to be the most handsome of all North American squirrels. (See Hall's "White Tails and Yellow Pines"[6] for a delightfully written popular account of this animal.) Its unique white tail flashes its presence as it jumps from limb to limb or attempts to conceal itself by flattening against the top of a high branch.

A more careful examination of typical individual animals reveals the white tail is streaked with a central line of dark hairs, especially on the dorsal surface. Except for the nearly pure-black belly and the white tail, the Kaibab appears similar to the Abert in all other respects.

Abert and Kaibab Color Variations

The animals sampled in the present study were all specimens found in the research collection of the Grand Canyon National Park. Most of the animals were obtained from road kills within the park itself. Thus the two groups may not represent the full range of variations possessed by the tassel-eared squirrel in Northern Arizona. For example, the variations seen

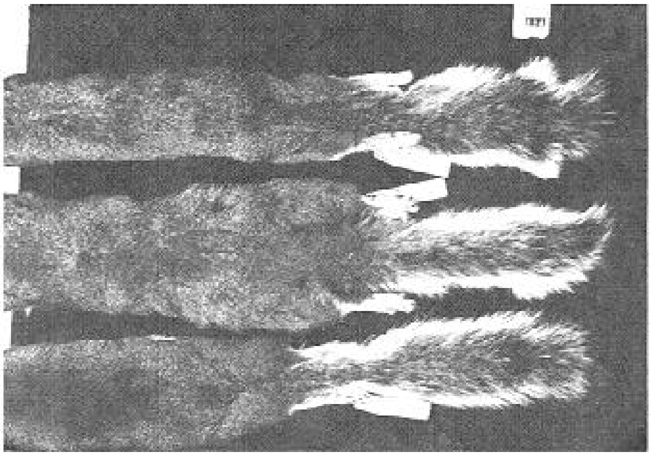

Figure 3. Photographs of typical Abert squirrel tails. Even though Abert tails are usually described as black and appear this way at a distance, these museum specimens show that a significant number of white hairs are present, especially along the lateral edges.

within the Kaibabs which I was able to examine may display only a limited amount of the variation seen within the total populations, since the animals were sampled from within the Grand Canyon National Park which makes up only a small part of their entire range. Body and tail color variations are tabulated in Table I and displayed in photographs in Figures 3 through 6.

Coloration within the Abert squirrel populations tends to be quite variable. This has been noted by Ramey and Nash[7] for populations along the Colorado front range. In their view of the tassel-eared squirrels, Hoffmeister and Diersing[8] indicate that coat color polymorphism is so common in this group that "Analyses were made without using color because of its variability within species of tree squirrels." They go on to state "Because of the variability of color and the absence of a correlation of color with other morphological features, color is not considered an important taxonomic feature." This would appear to be an approach not totally acceptable to all taxonomists. Numerical taxonomists in particular assign values to characteristics without any weighting factors.[9] While Abert squirrel tails in the Grand Canyon National Park Study Collection tend to be quite uniform in coloration (see Figure 3, but note from Table I, nine percent show a slight tendency toward banding), Kaibab squirrel tails show a considerable range (see Figure 4). These vary from almost pure white (except for the median area) to significant darkening (18 percent), approaching but not reaching the level of coloration seen in the Abert only.

In the 94 museum specimens examined, considerably more abdominal color variation was seen in the Aberts than in the Kaibabs. Abert abdominal coloration in some specimens was almost pure black while it was nearly white in the majority of cases. Kaibab squirrel abdominal colors varied from pure black to a significant number of white hairs seen along the mid-ventral region. In no case, however, did the light color approach that seen on the typical Abert. In addition, Aberts show considerable variation in brown tufts at the base of the ear and extent of the lateral line (see Table I).

Nevertheless, the similarities between certain Aberts and Kaibabs are striking, This is illustrated by the fact that Hall[10] refers to some of the squirrels on the north rim as "Abert-like Kaibabs." In my examination of the Abert specimens in the Grand Canyon National Park Study Collection, I noted a drawer of animals marked "Kaibab-like Aberts." While the average color characteristics for Kaibabs and Aberts show significant differences,[11] it is possible to pick "outliers" in each population that are very similar in coat color. Thus the "Kaibab-like Aberts" on the south rim show very close resemblances to the "Abert-like Kaibabs" on the north rim. Confirmation of rumored reports of white-tailed Aberts in the upper Beaver Creek drainage basin in the Coconino National Forest would be highly significant in establishing additional similarities between "outliers" in the two populations.

Taxonomic Status

The Kaibab squirrel was first reported by Merriam in 1904[12] and classified as *Sciurus kaibabensis* in contrast to *Sciurus aberti* for the rest of the population throughout the southwest. This classification has recently been modified however. Cockrum[13] has attributed subspecies standing to the Kaibabs. The important work of Hoffmeister and Diersing[14] using principal component analysis and numerical taxonomic methods based on morphological measurements of 244 animals from 20 different localities seeks to clarify the situation. Based on the results of this study they conclude:

> We are convinced there are five recognizable subspecies of *S. aberti*, but we have hedged with *kaibabensis. S. kaibabensis* is separable primarily on color-pattern, and this color and color pattern separation from other subspecies is complete at above 95 percent. Therefore, we hesitantly recognize *S.a. kaibabensis* as our sixth subgroup (subspecies).

In his monumental work *A Field Study of the Kaibab Squirrel in Grand Canyon National Park* representing over a decade of observations, Hall[15] accepts this classification; even though as mentioned previously, he uses the Kaibab situation as "a classic example of the role of geographical isolation in evolution." Thus, at

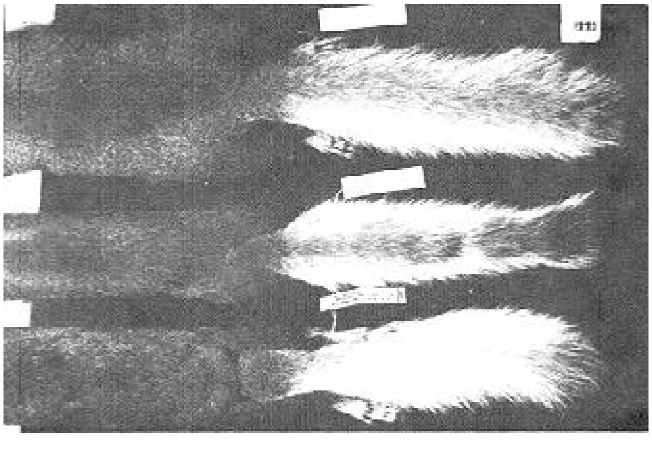

Figure 4. Photograph of Kaibab squirrel tails. The lower specimen displays the typical nearly pure white tail while the other two examples show significant presence of dark hairs centrally.

Table I
Comparisons of Body Color Variations Within and Across Abert and Kaibab Groups of Tassel-eared Squirrels

Characteristic	Abert (%)	Kaibab (%)
1. Small brown patch on back, less than ½ length of body and less than ½ width of back.	12	6
2. Extensive dorsal brown patch extending at least nearly full length of body and extending over edge of hips.	21	30
3. Slight tendency toward tail banding.	9	0
4. Brown tufts at base of ears.	51	0
5. Narrow or short and indistinct lateral line.	16	0*
6. At least some black mottling on belly.	30**	100

This table is based on examination of 94 squirrels, 67 Aberts and 17 Kaibabs. *71% show thick (up to 30mm) black lateral line which appears as an extension of black on belly. **One Abert shows very extensive black on belly. Of particular interest is the normal variation seen within the Abert squirrels, presumably the parent population for the isolated Kaibab population.

the time of writing, it appears that the accepted technical name for the Kaibab squirrel is *Sciurus aberti kaibabensis*, the name reflecting subspecies classification for the squirrel.

The work by Hoffmeister and Diersing merits further attention. The following discussion requires critical examination of several of the figures from their paper, and thus presupposes that their work is in hand for evaluation by the reader who wishes to pursue this critique in detail.

Of special importance is their Figure 3 (locality clusters projected on the first two principal components) and Figure 4 (dendrogram depicting phenetic similarities among locality clusters.) Based on the data presented in these two figures, it is of interest to note the remarkable similarities obtained for the Kaibab and the Abert squirrels. Hoffmeister's and Diersing's own analysis of the displayed data, however, appears to be somewhat inaccurate in one aspect. They claim:

> As with principal component analysis, this Numtax (computer program for numerical taxonomy) analysis indicates that the squirrels from the Kaibab Plateau . . . are most like squirrels from the Coconino Plateau. . . .[16]

While this is valid for the Numtax data presented in their Figure 4, it appears at variance with the principal component data displayed in their Figure 3. Kaibab squirrels in their work are shown to be more similar to Abert squirrels found south of the Coconino plateau on the central Mogollon Plateau. The locality cluster which is the most similar to Coconino Plateau Abert squirrels is found along the northern Arizona-New Mexico border.

In addition, Hoffmeister and Diersing's categorizing the Kaibab squirrel as a subspecies is somewhat puzzling. In their Figure 4 the level of statistical significance for the dimensionless similarity index is set at above 0.527 (the lower the number the greater the similarity). Examination of this Figure, however, indicates that the branching point for Kaibabs and south rim Aberts is barely above the 0.260 level. Only two other sets of locality clusters (out of 17 displayed here) show lower values (i.e. higher degrees of similarity). There are 13 branching points for the other locality cluster which show more divergence from each other than for the Kaibab-Abert complex. Of these, only five achieve statistical significance. Based on this data they accept five clear subspecies but equivocate on "*kaibabensis.*" If coat color is ignored, as they have chosen to do, then there is no objective data forming a basis for separating the Kaibab squirrels from the Abert squirrels, even at the subspecies level. If the data do not support this taxonomic scheme, we must ask why it is that they are nevertheless assigned to a subspecies different from their south rim relatives. One wonders if it is not the evolutionary presupposition that is the controlling factor, demanding significant changes across time for isolated populations—changes which the data do not support.

It is my contention that the data support the idea that the south rim Aberts and the north rim Kaibabs form, for all practical purposes, one continuous population because of the minute differences. It is only the

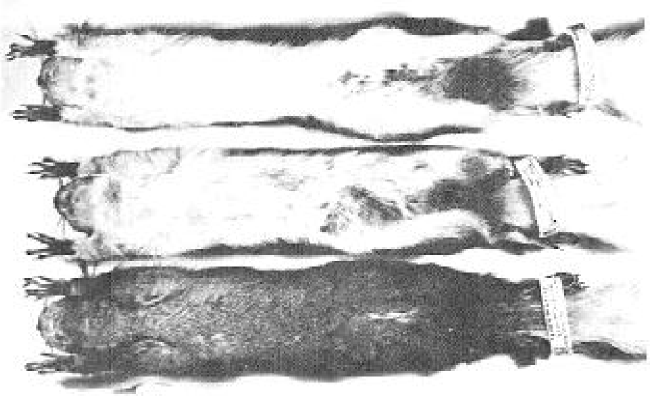

Figure 5. Photograph of Abert squirrel abdomens. The lower specimen displays the usual white belly while the top specimen displays an almost pure-black belly. The middle specimen is intermediate in abdominal coloration.

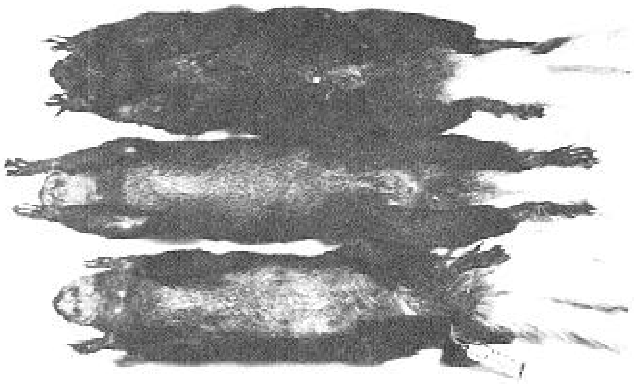

Figure 6. Photograph of Kaibab squirrel abdomens. The lower specimen displays the usual dark belly while the top specimen displays the lighter colored form. The middle specimen is intermediate in belly coloration.

recent origin of the Grand Canyon which now separates these two similar populations. Our own data (unpublished observations) based on 28 measurements from the skulls of each of 10 individuals, are in agreement with Hoffmeister and Diersing who also suggest "The sample from the Kaibab Plateau . . . and the sample from the Coconino Plateau . . . differ little from each other. . . ."[17]

Grand Canyon Climatology

Although located only a short distance apart and characterized by similar flora and fauna, the two rims of the canyon present strikingly different climatological environments for the two squirrel populations. Even more striking is the difference in weather features between the floor of the canyon at Phantom Ranch and either rim. The extent of these differences in precipitation, temperature, and humidity are shown in Table II and displayed graphically in Figures 7 and 8.

Table II

Summary of Climatological Data from the Grand Canyon South Rim, Phantom Ranch(bottom of canyon at Colorado River) and North Rim

	G.C.N.P. S. Rim 6950 ft.	Phantom Ranch 2570 ft.	Bright Angel N. Rim 8400 ft.
1. Yearly temperature mean (°F)	48.8	69.2	44.0
2. Mean daily maximum temperature (°F)	62.5	81.8	56.1
3. Mean daily minimum temperature (°F)	35.1	56.5	31.8
4. Highest recorded temperature (°F)	98	120	91
5. Lowest recorded temperature (°F)	–16	–9	–25
6. Mean frost free days	148	331	101
7. Yearly mean precipitation in inches	14.46	8.39	22.78
8. Yearly mean inches of snow, sleet, and hail	64.9	0.2	128.7

These data are derived from *Climatological Data,* U.S. Department of Commerce. Means are reported for the period from 1941 to 1970. Extremes for south rim and north rim are reported for 1931 to 1972. Extremes for Phantom Ranch are reported for 1935 to 1972. Calculated statistical deviations from mean values are not available.

These data, based on observation periods ranging from 29 to 41 years[18] indicate dramatic differences in weather patterns across the width of the Grand Canyon. In the author's own experience it is quite possible to start an early morning descent from the south rim in mid-winter surrounded by a howling snowstorm, only to meet upward-bound hikers who report moderate temperatures, sunshine, and no precipitation at the bottom. Thus, any small terrestrial mammal accustomed to the high, cool woodlands which attempts to traverse the canyon would find itself in a hostile environment at the bottom.

Furthermore, this warmer, more xeric climate of the lower canyon extends far up the north wall. As the sun warms the north side, the heated air rises and curls back over the north rim. This produces a zonal suppression-type situation where semi-desert plants such as the cliff rose, various cacti, yucca, and agave grow in a strip a few dozen meters wide separated by only a few more dozen meters from the Ponderosa pine forest[19]. Thus, even in the possibly more mesic and cooler climates of past millennia (see reference 20 for details), the north wall heating effect would have presented a xeric environment for vegetation which might have otherwise occupied the lower reaches of the canyon.

Age of the Grand Canyon

Of major interest in evaluating the isolation of Kaibab squirrels on the north rim is the time factor involved. It is clear from an examination of the pertinent literature that the evolutionary explanation for the history of the Colorado River in the vicinity of the Grand Canyon has not crystallized and seems unlikely to do so for the foreseeable future. Hunt[21] refers to this as "the grand problem of the Colorado, the age of the Grand Canyon."

This problem appears to arise in large part because of the unquestioning acceptance of certain widely divergent radiometric dates associated with various parts of the Grand Canyon area . For example, some investigators believe[22] the lower end of the Canyon is geologically young based on a 10.6 million year age from radiometrically inferred dates of the Fortification Basalt Member of the Muddy Creek formation which sets the upper limit. They also suggest the lower age limit is set by the 2.6 million year date estimated for basalt at Sandy Point which overlies gravels deposited by the Colorado River. Further upstream at the upper end of Lower Granite Gorge, an abandoned canyon breaches the southeast wall of the Grand Canyon and presumably represents the ancient but now abandoned course for the Colorado River flowing south and west through the Kingman area and back into its present course below Needles, California. Debris now filling this canyon has been estimated at 18.2 million years. The stretch of the Colorado upstream from the Grand Canyon is thought to be 30 to 40 million years old.[23]

A number of interesting hypotheses have been put forward in an attempt to harmonize the geography of the area with the inferred radiometric dates and various geological features of the area.[24-26] Some of these are as follows:

1. "The precocious gully" hypothesis. This view suggests that the course of the Colorado River above the Grand Canyon has always been essentially as it is today. However, in earlier times it flowed out through the Little Colorado in reverse from the latter river's present flow. Thus moving southward through the Little Colorado, it eventually emptied into the Rio Grand. In more recent times, a smaller river eroding its headlands eastward breached the ancient drainage course of the Colorado and captured the drainage system by river piracy. Hunt [27] has criticized this view, suggesting it was improbable for what must have then been a very minor river with very limited drainage basin to capture a river the size and volume of the original Colorado.

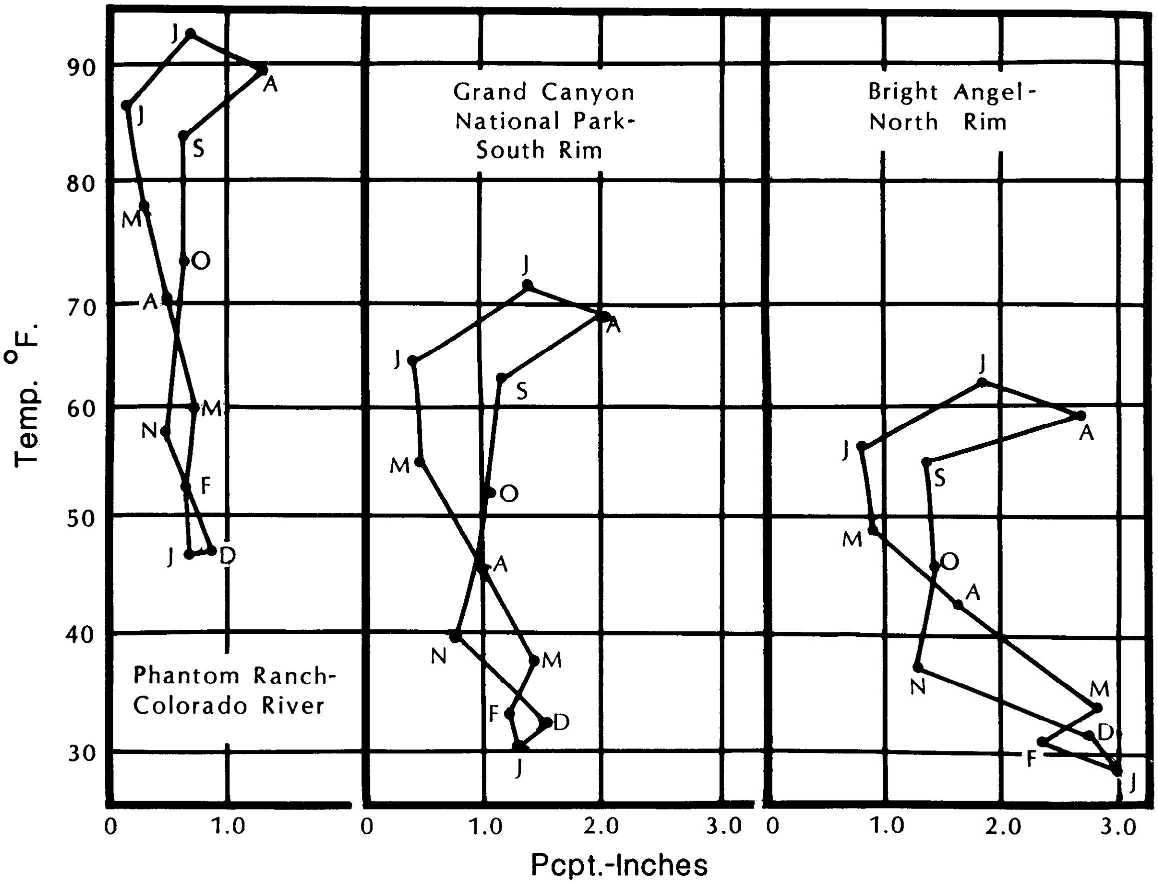

Figure 7. Climographs relating precipitation to temperature for three weather stations located in the Grand Canyon and on adjacent rims. Locations are the same as for stations for data from Table II. Means are derived from data reported for the period of 1941-1970. Abbreviations at data points represent months of the year.

2. "Precocious cave" hypothesis. This view put forward by Hunt suggests that the Little Colorado River never reversed directions, but in fact carried large quantities of water from a large mountainous region to the southeast which has since largely disappeared, having been faulted off the edge of the Colorado Plateau. To the west of the Grand Canyon, the Colorado River turned south (instead of its present northward course toward the Hurricane Fault) and drained through the ancient basin at Kingman, Arizona. This route was eventually blocked by volcanics or uplifts forcing the river into lakes and vast underground caves in the cavernous late Paleozoic limestone which plunges down a 1,000 foot syncline to the northwest towards the Grand Wash Cliffs. Dissolution and collapse of these caves opened the way for the present course of the River in that vicinity.

3. "Anti-gravity waterfall" hypothesis. Surely named tongue in cheek, this view holds that the ancestral river left the Colorado Plateau north and east of the Shivwits Plateau. To do so, Hunt points out,[28] would require that the stream flow up and out of the Grand Canyon and on to the rim of the higher adjacent plateau through a reversed waterfall!

An additional radiometrically inferred age for the Canyon is derived from the volcanic flows which at one point substantially blocked the flow of the Colorado. Radiometric values for these flows suggest the canyon was within 50 feet of its present depth 1.8 million years ago.[29] McKee,[30] however, believed that the canyon itself is between seven and nine million years of age. Matthews[31] suggests seven million years. It is clear that no current evolutionary explanation has found universal acceptance among the geology experts on the area.

We are thus left in a bit of a quandary when trying to arrive at an evolutionarily inferred age for the isolation of the Kaibab from the Abert squirrel population. Given differences of opinion regarding the process of formation of the canyon, the dates assigned to the dissection of the Coconino-Kaibab Plateau by the Colorado River must vary widely from one authority to another. For the sake of simplicity and to be on the conservative side, I will arbitrarily work with a value of two million years. Even the Colorado River itself without a major canyon would provide a significant isolation barrier for the squirrels. Furthermore, given present rates of mass wastage, landslides, and other factors working to enlarge the canyon, a uniformitarian approach would appear to demand as much elbowroom as possible for present processes to have created a canyon five thousand feet deep and 10 to 15 miles across. Thus a two million year figure must be a minimum for significant isolation of the two populations, if one accepts evolutionary time scales.

In view of this postulated time span of separation, it is instructive to look at the forces for change which may be operating on the Kaibab squirrels within this framework.

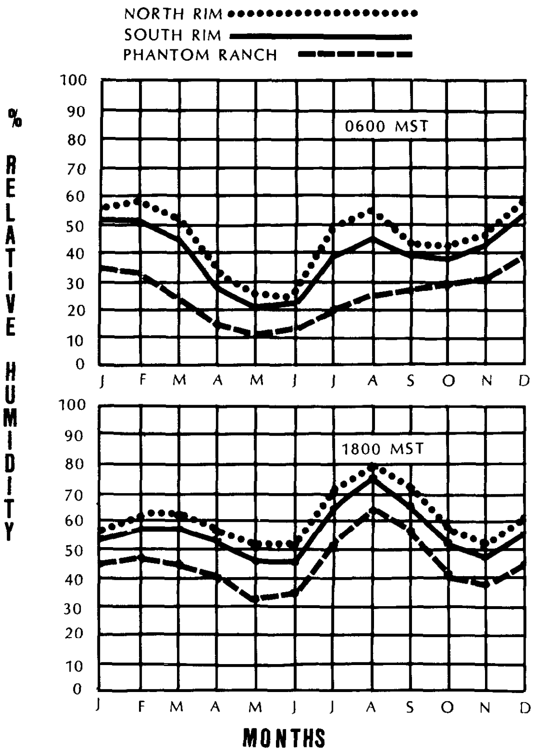

Figure 8. Estimated monthly mean relative humidity readings at 0600 mountain standard time (MST) and 1800 MST for three weather stations located in the Grand Canyon and on adjacent rims. Locations are the same as for data from Table II. Means are derived from data reported for the period of 1941-1970.

Hardy-Weinberg Law, Equilibrium Populations and the Forces of Change

Most discussions of the supposed process of evolution center about exceptions to the restrictions necessary for the Hardy-Weinberg equilibrium population. For example, Stansfield[32] in his widely-used textbook, attaches such importance to this concept in his chapter on the subject that he states: "This chapter is extremely important because it sets the stage for a thorough understanding of the remainder of this book" (nearly 300 pages). Volpe[33] suggests "An understanding of the Hardy-Weinberg equilibrium provides a basis for recognizing the forces that permit evolutionary change." In view of the importance attached to the Hardy-Weinberg equilibrium concept by evolutionists, it is instructive to consider this idea, the conditions under which it fails to apply, the implications of this failure, and finally, how the whole concept relates to the Kaibab squirrel situation.

The quantitative aspects of the Hardy-Weinberg equilibrium are covered in almost any standard text on evolution. The paper by Howe and Davis[34] presents a thorough creationist evaluation in the larger context of natural selection. In general the Hardy-Weinberg equilibrium population is a group of interbreeding organisms which have a stable gene frequency throughout the population from one generation to the next. This fixity of gene frequency in space and time results in a static gene pool (defined as all genetic information distributed among an interbreeding group of individuals). This hypothetical population of organisms can only exist under one unique and highly restricted set of conditions. Stansfield[35] presents 10 of these restrictions and their implications:

1. The population is composed of a very large number of sexually reproducing diploid individuals (theoretically infinitely large).
2. Mating is completely at random, including selfing in random amount; this implies that each gamete of one sex has an equal chance of uniting with any gamete of the opposite sex.
3. Both alleles are adaptively neutral, i.e., there is no selection for or against either allele; all genotypes have equal viability and leave progeny directly in proportion to their respective frequencies.
4. The population is closed; no immigration into, nor emigration from the population is allowed.
5. Mutation from one allelic state to another is disallowed.
6. Generation overlap does not exist.
7. All members of the population are of equivalent reproductive age.
8. Meiosis is completely normal so that chance is the only factor operative in gametogenesis and segregation of alleles into functional gametes.
9. Gene frequencies are identical in males and females of the population.
10. Parents make equal contributions to the heredity of their offspring.

He goes on to explain the significance of these restrictions:

> As long as a population conforms to these restrictions: neither the allelic frequencies of the gene pool nor the genotypic distribution of the population would change from one generation to the next. The population is said to be in *genetic equilibrium,* Violation of any of the restrictions on the Hardy-Weinberg model would produce a change in the gene pool (evolution). Since it is virtually impossible for any natural population to conform to all the Hardy-Weinberg restrictions (e.g. no population is infinitely large, completely random mating probably never exists, mutations cannot be prevented, etc.) evolution is almost inevitable.

Howe and Davis[36] note the significance of the Hardy-Weinberg equilibrium population as follows:

> The evolutionist uses this stable base from which to launch an argument for change within gene pools. He asserts that the assumptions listed are important precisely *because* they are impossible to attain in actual populations. For this reason he views the Hardy-Weinberg equation as describing a hypothetical null set or 'non-evolving" population to which real populations may be compared.

Does the Kaibab Squirrel Population Satisfy the Requirements of an Equilibrium Population?

The extent to which the Kaibab squirrels violate the tight restrictions of the Hardy-Weinberg model should give us some insight into the rate at which the population is changing across time. Thus, if the population conforms to all of the restrictions we should expect a stable gene pool, even across immense expanses of time. On the other hand, if any of the restrictions are violated we should expect to see progressive changes; and the extent of these changes should at least be roughly correlated with the time involved and the degree of restriction violation. Therefore, let us now consider the available information relating to each of the hypothetical restrictions:

1. Population is composed of a very large number of sexually-reproducing diploid individuals (theoretically infinitely large). Considerable concern has been attached to the Kaibab squirrel population size in recent years. National Forest Service personnel have derived a number of population estimates for the Kaibab squirrel based on various sources. These data are presented in Table III. Here it is seen that in the last 19 years, estimates range from a low of 10,000 to a high of 27,000 individuals. It should be noted that it is extremely difficult to secure accurate population number estimates from small, secretive, free-ranging mammals. Thus, these yearly values do not necessarily reflect population crashes and blooms. On the other hand, there is at least subjective and anecdotal evidence, as well as research data suggesting that population numbers do vary widely over time.

Table III
Estimated Number of Existing Kaibab Squirrels for the Years Indicated

Year	Estimated Number of Kaibab Squirrels
1965	10,000 +
1966	15,000 - 16,000
1968	18,000 +
1970	22,000 +
1974	18,000 - 20,000
1975	22,000 +
1977	25,000 +
1978	27,000 +
1979	18,000 +
1980	20,000 +
1981	22,000 +

Perhaps the mean value for the indicated years can serve as a working number. Thus, the total population for the Kaibab squirrel averaged over the last several decades appears to be a bit over 20,000, though Hall[37] thinks the present number may be lower than in previous times due to decrease in forest vigor. Thus the population of Kaibab squirrels is clearly not 'theoretically infinitely large.'

2. Mating is completely at random, including selfing in random amount. It is highly unlikely that any squirrel is capable of self-fertilization. In addition, given the extent of the Kaibab plateau and the limited range of an individual squirrel (well under 100 acres),[38] mating must be much more likely with members of the population in the vicinity than with those located at some distance. On a higher level of resolution, the squirrels are not even locally evenly distributed, preferring certain select trees over all others. Recent evidence[39] suggests this is due to the chemical composition of trees. Thus, with an erratic distribution pattern throughout the Kaibab Plateau, mating cannot be completely at random.

3. Both alleles are adaptively neutral, i.e., there is no selection. This must hold for all genes within the gene pool. Stansfield[40] questions if any characteristic can be adaptively neutral. Patterson[41] asserts that even if some characteristics were adaptively neutral, it would be impossible to recognize them or their effects. He suggests:

> The fact that some attribute of an organism appears useless to us is no guarantee that it is so. Investigations of apparently useless features has shown that some do, after all, have survival value. And while it may be possible to show that a certain feature has survival value and is subject to selection, it is never possible to show that a feature has no such value, and is selectively neutral: we may not have looked carefully or closely enough.

Many other evolutionists reject the concept (for example, see Dobzhansky, reference 42). This situation is therefore similar to attempts to demonstrate the existence of vestigial organs (see reference 43 for a review of a paper relating to this problem).

Furthermore, when one compares the climates faced by the Kaibab and Abert squirrels, it would appear that a number of alleles which should be adaptive for the environment of the Abert population would be less than optimal for the Kaibab population which faces quite different environmental challenges as previously discussed.

In addition, the characteristic coloration of the Kaibab squirrel presents some interesting problems, particularly if one assumes that natural selection is adapting it to its new and climatologically-different home on the north rim. Hall[44] discusses a number of possible adaptive roles for Kaibab body coloration. Two of these views and his objections are summarized as follows:

1) *White tail Cryptic Value.* However, squirrels run with tails extended, thus still making the dark body an easy target. It often rests with tail extended, thus not concealing the dark body. The tail is still white in the summer thus making it even more visible than the Abert.

2) *Signalling to other members of the Species.* But this involves primarily the ventral surface of the tail which is light in both groups.

In my own experience, location of eight Kaibab squirrels in a few hours was greatly facilitated by the presence of the white tail which could be seen through rather dense foliage even when the rest of the squirrel was not visible. Hall concludes that none of the proposals attempting to explain the presence of the white tail in the Kaibab are adequate.

Finally, the wide range of coat color polymorphism seen in the Kaibab (see Figures 3-6 and Table I) suggests that not all patterns can be adaptively neutral or of equal adaptive value.

4. The Population is closed. At the present time this restriction does appear to hold rather firmly. The unique geographical location of the Kaibab Plateau with desert on three sides and the Grand Canyon on the fourth side does appear to be a rather insurmount-

able barrier to immigration and emigration, particularly since the tassel-eared squirrels are restricted to the high altitude Ponderosa Pine forests. On the other hand, if one holds a uniformitarian approach to the origin of the Grand Canyon rather than a catastrophic origin, one must assume a rather gradual development of the canyon, which in its earlier years would have provided, at best, a partial barrier to the movements of squirrels. Thus while this restriction now holds rather tightly, it apparently did not always do so. In addition, there are several sub-populations of Kaibab squirrels which are only partially isolated from the main population. The squirrels living on the Powell Plateau which is an extension of the Kaibab Plateau would be an example of this.

5. Mutation is disallowed. The albino form of the Kaibab is surely the ultimate result of a point mutation. Since mutations are considered random changes in the genetic material, it can hardly be denied that all parts of the genome are subject to this process. To disallow mutations in the Kaibab squirrel would be to undermine great sections of modern genetics. Thus it is clear the Kaibabs do not conform to this restriction.

6-7. Generation overlap does not exist and all members of the population are of equivalent reproductive age. However, the maximum verified age of tassel-eared squirrels is nine years with an average adult life span of three to four years.[45] Any female can produce a number of litters in a life time, thus necessitating generation overlap and ruling out equivalent reproductive age for all members of the population.

8. Meiosis is completely normal. Meiotic aberrations have been well studied and are clearly wide spread throughout the plant and animal kingdoms. While we are unaware of any specific data on this subject relating to the tassel-eared squirrels, it would be astounding, indeed, to find that they had escaped this particular vagary of reproductive problems.

9-10. Gene frequencies are identical in males and females and parents make equal contributions to the heredity of offspring. Not only is this restriction generally unlikely in any population, but also the presence of sex chromosomes of necessity lead to a violation of these restrictions. Since the male chromosome is much smaller than the female, this feature alone would demand that male and female contribution to the genome of the offspring are by their very nature unequal. These restrictions must also fail the test of credibility.

Of the 10 restrictions mandatory for an equilibrium population and gene pool stability from generation to generation, at least eight of them clearly fail the test of credibility and supporting data. One (closed population) must have been violated in the early isolation of the population if the evolutionary scenario based on uniformitarianism is correct. The probability for the validity of the final restriction (meiosis is completely normal) is vanishingly small.

Thus, by the above criteria necessary for the equilibrium population, it is obvious that the Kaibab squirrels have had no hope of genetic stability during their existence; i.e., by the standard definition, they should be "evolving" and doing so at a rather rapid rate. If this is the case we must ask why it is that the differences between Kaibab and Abert squirrels are so little in evidence.

Origin of the Tassel-eared Squirrels in Northern Arizona

How then does one account for the Abert-Kaibab complex from a creationist perspective? To attempt to answer this question we now present a model which is somewhat speculative but nevertheless plausible, being, we believe, faithful to the objective data in hand. The reader will note that the model is *not* in harmony with the dates *inferred* from radiometric procedures and based on uniformitarian assumptions and presuppositions. Critiques of radiometrically based inferred dates have been numerous in creationist literature and will not be repeated here. The interested reader is referred to such important works as Slusher[46] and Whitcomb and Morris[47] for analysis of these problems.

A model should be in harmony with the objective data and sufficiently general to encompass the uncertainties of that data. It should also be sufficiently specific to provide a testable model for future research. Thus the model presented here is a preliminary attempt to meet these guidelines.

The model should consider at least the following features of the tassel-eared squirrel situation in the Southwest:

1. High degree of variability in Abert coat color.
2. Presence of Abert squirrels on the south rim and the distinctively (though not uniformly) colored Kaibab on the north rim.
3. Presence of Kaibab-like Aberts on the south rim.
4. Presence of Abert-like Kaibabs on the north rim.
5. The Grand Canyon as a highly effective isolating mechanism throughout most of its life.

The proposed model is displayed in Figure 9. It is suggested that the original colonizing squirrels, perhaps having few predators and having considerable available habitat, rapidly established themselves in the cool, relatively moist high altitude Ponderosa Pine forests in Northern Arizona and other similar areas of the Southwest. Increasing temperatures and decreasing moisture began to take its toll on the lower altitude Ponderosa Pines. Therefore, in many instances, local populations of Abert squirrels were cut off from their neighbors by the disappearing Pine forests of the valleys. Thus local, higher altitude, Ponderosa Pine forests became isolated islands of vegetation, providing concomitant isolation for local populations of Abert squirrels whose habitat is restricted to these Ponderosa leys. Thus local, higher altitude Ponderosa Pine forests apparently was well underway before the Aberts could establish themselves in the more remote areas since many present areas of suitable habitat are devoid of the squirrel.

One of the populated Ponderosa Pine forest islands that did contain the Abert squirrel was found in Northern Arizona. Here small numbers of early immigrants made disproportionate contributions to the gene pools of following generations (Founder Principle) and natural calamities (forest fires, severe weather, predation) arbitrarily altered gene frequencies in small populations (Genetic Drift). An occasional mutation, although almost inevitably deleterious, further altered local gene pools. By this time stage two of Figure 9 had been reached. Stage three began with the establish-

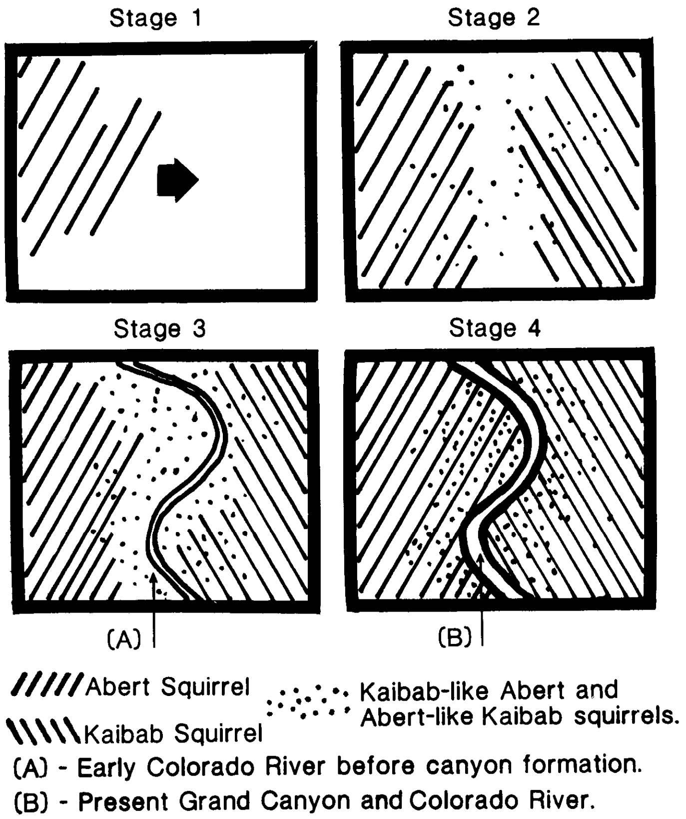

Figure 9. Proposed model for the origin of the Kaibab-Abert complex in the Grand Canyon region. 1. Migration of the Abert squirrel into northern Arizona. 2. Establishment of local sub-populations. 3. Origin of the Colorado River. 4. Development of the Grand Canyon as an effective isolation barrier. Similar pattern exists today.

ment of the Colorado River course through the southern edge of the Colorado Plateau.

Sciurus aberti aberti flourished in the south while *Sciurus aberti kaibabensis* thrived to the north. In between was a hybrid population exhibiting varying degrees of coat polymorphism characteristic of their parent stock. The rapidly developing river course found its way through the center of the mixed intermediate forms and began to deepen its channel, perhaps as the Colorado Plateau uplifted. In a short period of time the river had cut a channel sufficiently deep and wide that it began to curtail free movement of squirrels. As the canyon continued to develop, it provided a highly efficient barrier, keeping the two squirrel populations from sharing gene pools, and thus establishing the populations in essentially the pattern seen today (stage four).

Conclusion

If any group of animals were ever going to undergo significant degrees of evolution from parent stock and obtain resultant speciation, surely the Kaibab squirrel would be one of the more likely candidates. Supposedly isolated from their neighbors for hundreds of thousands of generations over a period of at least several million years, and significantly violating virtually every restriction of the Hardy-Weinberg equilibrium for a non-evolving population, these organisms, even by creationist standards, should have undergone significant and detectable changes. In reality all they show are moderate changes, primarily in two coat color characteristics for part of the population. To make things even worse, this species is known to have a highly variable coat-color polymorphism throughout its range. Thus, even the differences displayed appear to be easily accounted for by several mutations and a slight change in gene frequency for one or two loci, all occurring in a limited period of time.

If an organism such as the Kaibab squirrel is able to escape all but a few minor changes in coat color (and these of dubious survival value) given the supposed immense time of rather complete isolation and violation of the Hardy-Weinberg equilibrium, we must ask wherein lies the fault. Is it in the violation of the Hardy-Weinberg equilibrium concept, or is it in the time alloted for gene pool changes to occur?

The Hardy-Weinberg equilibrium population and associated universal violations of restrictions appears to be reasonably well founded, though perhaps of considerably less importance than demanded by the general theory of evolution. Both theoretically, experimentally, and in natural populations I see no problem with its major features.

This leaves us then with the problem of time. How much time has been allotted for the violations of the Hardy-Weinberg restrictions to work? Perhaps the most logical answer for this, and indeed, for the entire study of geographical isolation of the Kaibab squirrels, is that time has been the limiting factor.

If the above conclusion is correct, then this indirect evidence for time limitation has important consequences not only for the biology of the Grand Canyon area but for the actual formation of the canyon itself. If we are correct in our interpretation of the existing data regarding the Kaibab squirrel, then we have no other choice than to assign a very recent origin to the Grand Canyon of the Colorado and its role as an isolating mechanism for the Kaibab squirrel.

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PERSPECTIVES ON THE ORIGIN OF MITOCHONDRIA

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Abstract

The two main theories of the evolutionary origin of the mitochondria are examined. Evidence that is frequently cited to support each theory is presented to determine how well it supports each. It is concluded that most of the evidence can be fit into either scheme, and that even the best data constitute only circumstantial evidence in favor of any evolutionary origin of mitochondria.

Introduction

In all schemes of the evolutionary advancement of life there is a point where a relatively simple cell must be converted into the more complex cells of which all higher organisms are composed. There are two general theories as to how this division occurred (Figure 1). The autogenous theory claims the cellular organelles arose through a gradual process of compartmentalization of genes and enzymes present in the ancestor. The endosymbiont theory claims the organelles evolved separately from the main part of what is now the eukaryotic cell and became associated with it by being engulfed and then forming a symbiotic relationship.

The debate between the proponents of these theories has been long and sometimes acrimonious with each in turn claiming solid proof of its validity. Consequently many students of origins may find this aspect of the debate between evolutionists confusing and could benefit from a short review outlining the pro and con of these two views. We will limit our discussion to the mitochondrion principally because the authors are more interested in animal cell biology than plant. Some researchers feel the phylogenetic relationship between the plastid and its endosymbiotic ancestor has been established much more firmly than for mitochondria. Those interested in studying this aspect of origins should obtain the review by Gray and Doolittle[1] or the article by Rao et al.[2]

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