BULLETIN

OF THE

FLORIDA STATE MUSEUM

BIOLOGICAL SCIENCES

Volume 12 Number 1

VARIATION AND EVOLUTION OF GULF COAST POPULATIONS OF BEACH MICE, PEROMYSCUS POLIONOTUS

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Gainesville
1968

VARIATION AND EVOLUTION OF GULF COAST POPULATIONS OF BEACH MICE, PEROMYSCUS POLIONOTUS.

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SYNOPSIS: Inadequate taxonomic research has resulted in misinterpretation of the course of evolution in these beach mice. Five new subspecies are here described. Pelage patterns are described and in the case of the three primary hair-tip rump patterns, preliminary results of laboratory breeding experiments are given, along with a model based on four postulated genes. Basal-hair melanin patterns appear to be under separate control from the hair-tip xanthophyll pigment patterns. Disharmonious interactions between two presumed phylogenetic lines with different hair-base patterns are described and discussed. Zonal variance in width of dorsal body pigment in certain specimens is attributed to epigenetic interaction during molt and an approximate molt sequence is given. Variations in color, relative paleness, and body dimensions are also discussed. Polymorphism occurs in some subspecies.

Several of the pelage pattern traits that characterize different beach mouse populations have been discovered also in occasional specimens of *P. maniculatus*, and it is believed that many, if not all of the genes responsible for pigment reduction in intensity and extensity in the beach mice, were already present before the species came in contact with the beach dune habitat. Evolutionary sequences are discussed and certain partial reproductive barriers are noted. The species appears to be in process of splitting into two species along a line initiated by a topographical barrier during the Yarmouth interglacial stage of the Pleistocene. The two ends of a circular overlap appear to be sympatric, and a partial break in the middle of the chain of subspecies is also manifest.

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Bowen, W. Wedgwood. 1968. Variation and evolution of Gulf Coast populations of beach mice, *Peromyscus polionotus*. Bull. Florida State Mus., vol. 12, No. 1, pp. 91.

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INTRODUCTION

Along the Gulf coast of Alabama and Florida from Mobile Bay east to Cape San Blas, and on the Atlantic coast from Jacksonville south to Palm Beach, the dunes are inhabited by small fossorial mice of relatively pale coloration. They are subspecifically related to the Old Field Mouse, *Peromyscus polionotus*, a dark form that ranges throughout most of Alabama, Georgia, extreme northern Florida and the southern part of South Carolina. In the intervening coastal plain the mice are intermediate between the two extremes. Over much of the coast where the dunes have been bulldozed away, and inland where the land has been cleared for reforestation, these mice are now extinct or rapidly becoming so.

The palest form, inhabiting the almost pure white dunes of Santa Rosa Island on the northern Gulf Coast, was first described by A. H. Howell (1920) and named *Peromyscus leucocephalus.* The greater degree of cryptic paleness in this form (in contrast to the somewhat darker mice living on other beaches of equally white dunes), he conjectured, offered "a striking illustration of the effect of isolation in perpetuating color variations, and in the case of the Alabama representative of *albifrons* the inadequacy of a peculiar environment apart from isolation to produce similar changes."

Sumner (1926), who was then engaged in pioneer studies to determine whether or not geographic color variation was genetically controlled, became interested in this case. His findings (1929, 1930) have been widely discussed and quoted in evolutionary literature (e.g. Mayr, 1942, 1954, 1963; Huxley, 1943; Haldane, 1948; Ford, 1954, 1960, 1964). In Sumner's time the systematics of the species, especially along the Gulf Coast, had not been adequately studied and Sumner's conclusions were consequently based in large measure on misinterpretations. The first major purpose of the present paper is thus to clarify the taxonomy of the Gulf Coast subspecies and so to lay a foundation for a thorough re-examination of the course of differentiation in these mice.

After collecting population samples on Santa Rosa Island and the adjacent beaches to west and east, Sumner (1929) next ran a line of trapping stations inland at approximately 20 mile intervals, and found what appeared to be a cline terminating in an abrupt change from pale to dark some 40 miles inland. This he interpreted as the result of gene flow extending inland from the beach populations. Evidently he was not aware of the fact that between his coastal stations and his first inland trapping station at Crystal Lake an extensive swamp (the Devil's Swamp) poses an effective barrier between the two populations. Furthermore, for the past hundred years (10,400 ± mouse generations) another barrier to gene flow has existed, created by the intracoastal ship canal. It was the discovery of these barriers that first led to the present investigation. Later it was found that the line of abrupt change from pale to dark mice coincided with the highest (Okefenokee) Pleistocene shoreline (MacNeil, 1950).

Four extensive field trips have been made to collect specimens and acquire first-hand knowledge of the topography and ecology of the region. Breeding stocks as well as museum specimens were obtained, and laboratory crosses have been made between a number of beach and inland forms. More than 2500 mice have been reared, and the genetic control of certain pigment traits is now well enough understood to attempt correlation with the systematic conclusions. Due consideration has been given to former changes in coastline, both Pleistocene (as mapped by MacNeil, 1950) and Recent as revealed by early maps.

Soil characteristics play an important role in determining the distribution of these fossorial mice. Poorly drained soils and those underlain by hard-pan constitute barriers. *Peromyscus polionotus* inhabits the more loamy soils of the interior, whereas *P.p. subgriseus* occurs chiefly in sandhill scrub areas above the level of the highest Pleistocene marine encroachment. In sandy areas of scrub and pine/turkey-oak between the 150 foot contour, which approximates this level of greatest inundation, and the present coastline, live four subspecies that are intermediate between the darker inland forms and and the present-day beach mice. These are here considered remnants of former (Pleistocene) beach mice. The intensely white, shifting sand of the present-day dune coastlines constitutes an entirely different, and in many respects a very hostile environment (Fig. 1, A, B) to which the mice have become adapted.

The northern Gulf Coast area presents a checkerboard pattern of mouse distribution, with these soil differences forming the horizontal lines. The several rivers that flow from north to south divide the area vertically and isolate the watersheds on which the mice live. The outer coastline is isolated from the mainland more or less completely by lagoons, swamps, tidal marshes, and flatwood areas of hardpan. It is also broken into segments by the inlets to the several large bays. But these distribution barriers are not absolute; sections of sand peninsulas may from time to time be cut off by storms and translocated by wind and current action (Fig. 1, C) from one side of a bay to the other. Several such cases are documented by early historic maps, and the possibility of mice being transplanted in this manner is demonstrated by the existence of a thriving population on Ono Island which was, until about 90 years ago, a peninsula on the west side of Perdido Bay. This island now appears to be in the process of joining onto the east side of the bay where a distinctly different mouse population exists. Such transplants and exchanges have no doubt occurred many times in the past.

Selection pressures favoring reduction and dilution of pelage pig-

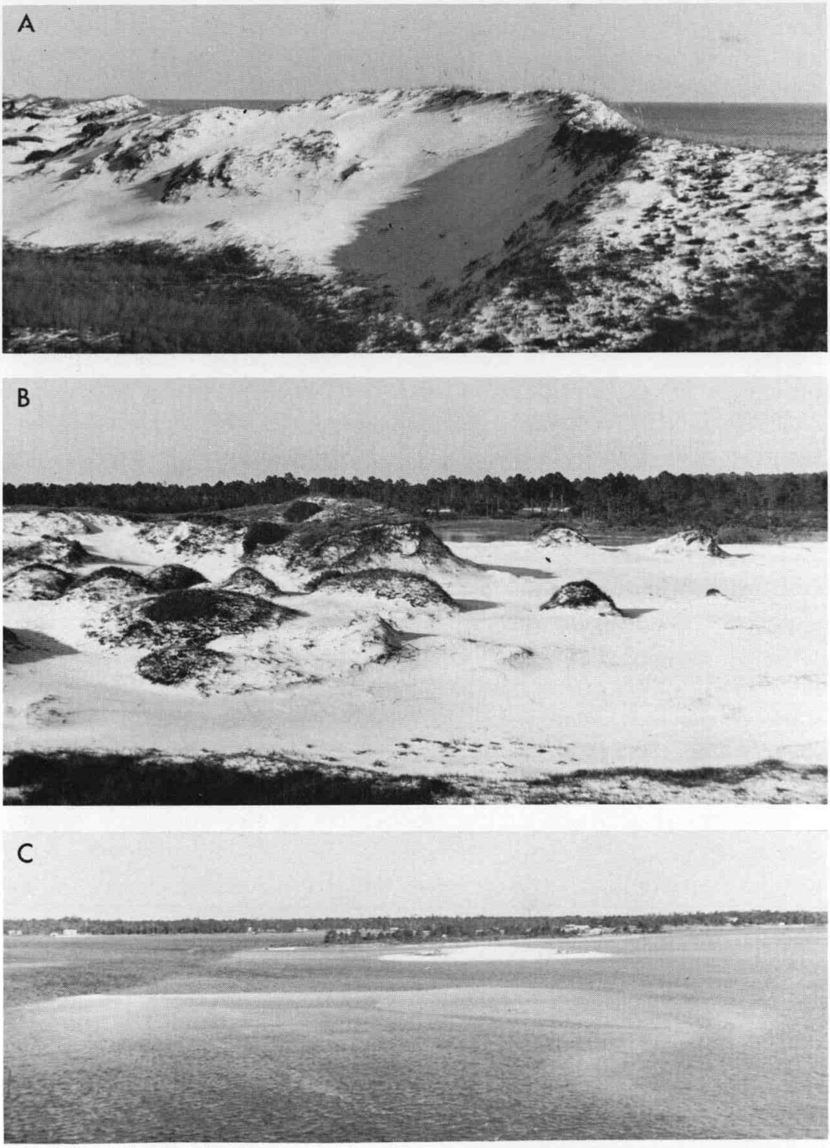

FIGURE 1. Typical beach mouse habitats. Eastern Lake, Walton Co., Florida. (A) Frontal dune ridge and (B) blowout area photographed from the same spot. Portions of Silver Bluff dunes are seen among the trees in the background. (C) Sand bars forming near the mouth of Perdido Bay.

ment have probably been strong and constant ever since these mice first invaded the coastal dunes, but there have been several advances and retreats of the sea (MacNeil, 1950). Beach mouse populations stranded inland by a retreating shore line must soon become subjected to reversed selection pressure for life on a darker substrate of fallen leaves. The transformation of an active coastal dune with sparse vegetation into a scrub where the ground is largely covered by fallen leaves can be visualized on many parts of the present coast where outer bars shelter former dune ridges (Fig. 2).

Such instances are usually only local phenomena affecting mouse populations here and there. The almost incredibly slow rate of marine retreat during periods of glaciation can best be visualized by comparing the Silver Bluff and Recent shore lines. According to MacNeil (1950), the "Silver Bluff age might be tentatively correlated with the so-called 'climatic optimum' of glacial geologists, botanists, and zoologists, a period of about 6,000 to 4,000 years ago when the climate was appreciably warmer than now. For many reasons it is regarded as the peak of the Recent interglacial stage." No great distance separates the two shore lines as is shown in photograph B, figure 1, which was taken from the top of the present outer dune ridge and shows a portion of Silver Bluff dunes among the trees in the background. At other points the two shore lines are even closer and in some places they coincide, as they do some 5 miles east of where the photograph was taken. Here the mice must have been present continuously, with selection still favoring reduced pigmentation.

The fate of a beach mouse population at the time of a marine encroachment is less easily envisaged. Undoubtedly a slowly rising water table would tend to increase the size of, and eventually inundate, the marshy areas that lie back of the frontal dunes (Fig. 1, A and B; see also beach profiles in Kurz, 1942). The mice would thus be isolated and finally eliminated as the frontal dunes became submerged. Those stranded pockets below the highest level of the new shore line would also perish, but others above this line would remain to colonize the new beaches. No selection pressures favoring pigment reduction would have occurred, as the pattern of lagoon formation behind the dunes must have been repeated constantly throughout the encroachment period. The new beach would thus be colonized by former beach mice that had subsequently been subjected to selection pressures associated with a scrub type of habitat.

The assumption that the beach populations, adapted as they are to a highly specialized and rather hostile environment, could have

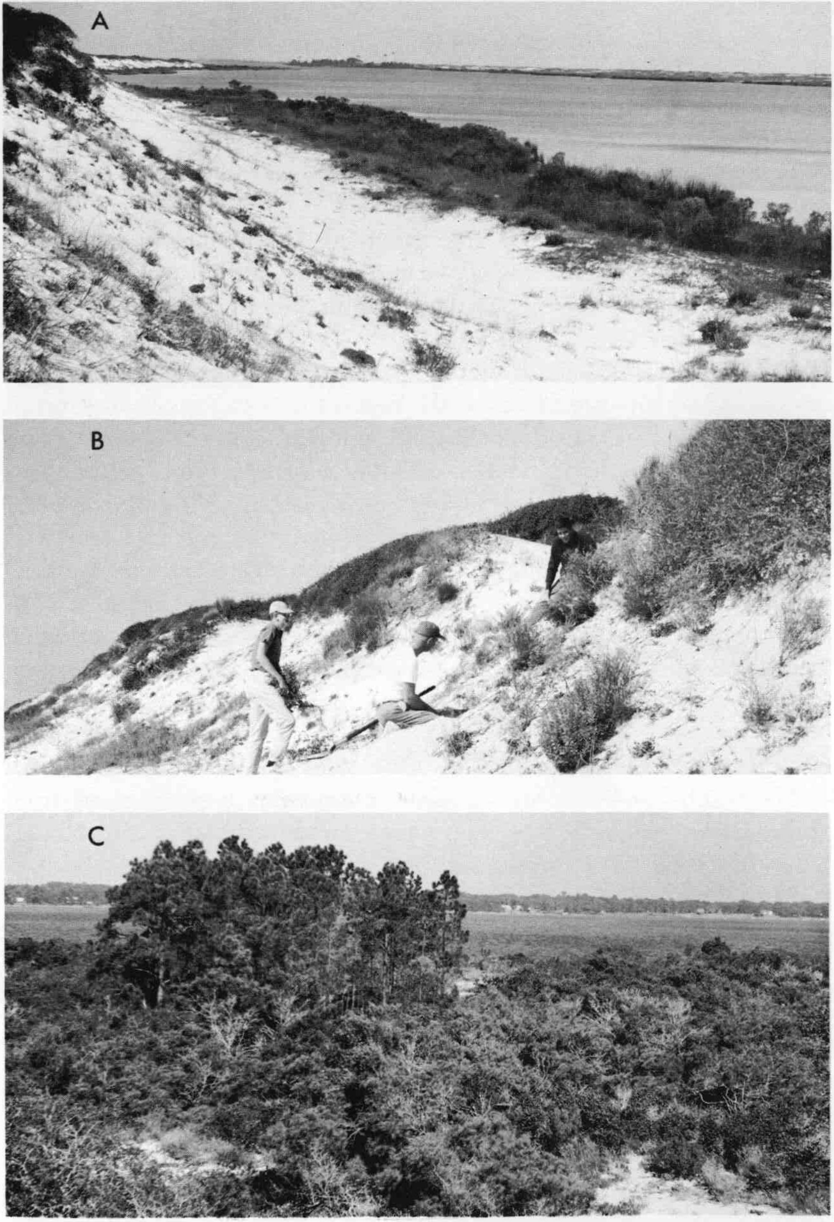

Figure 2. Transformation of beach habitat. Ono Island, Baldwin Co. Alabama. (A) Lagoon with marshy shoreline, resulting from sheltering action of outer sand peninsula (Florida Point), seen in distance. (B) Scrub vegetation invading the frontal dune ridge, with field party digging at mouse hole. (C) Scrub, with occasional sandy patches on inland (north) side of island.

acquired the capacity to overcome the opposing pressures of the inland populations, long adapted to scrub environments, cannot be valid. Evidence from the present study points to the reverse, and this is particularly noticeable in the beach population with which Sumner worked. Here, as will be described later, fertility appears to be greatly reduced, and only absence of competition can explain the success of these mice. (*Sigmodon* inhabits the marshy areas of these shore lines and so does not compete with *Peromyscus*). Throughout the various beach populations are numerous indications of reduced overall fitness.

Sumner (1929) formulated his hypothesis of opposing population pressures and superior fitness of the beach forms to explain the abrupt transition from pale to dark mice 40 miles inland. Pleistocene shore lines in this area had not been identified at that time, but now it can be seen that this line of sudden change coincides with the inner shore line of a large bay that existed during the Yarmouth interglacial stage (Fig. 30, D). A difference in soil types also exists and a partial reproductive barrier (as yet unconfirmed, see below) may exist at this point. As the present studies do not support the supposed cline below this line, the slate must be wiped clean and a fresh start made toward understanding the course of subspeciation in these mice.

MATERIALS AND METHODS

The results and conclusions here presented are synthesized from three approaches, field work, systematic museum studies, and laboratory crosses between various subspecies.

Field work: Emphasis here was placed on acquiring first-hand knowledge of the topography and ecology of as much of the range of the species as possible. Specimens were collected both by trapping ("museum specials" and Sherman live traps) and by digging mice out of their holes in the daytime. Four field trips were made as follows:

2 October to 6 November 1950
17 November to 29 November 1951
8 October to 24 November 1961
12 September to 21 December 1962

The first trip was devoted mainly to a study of the area previously investigated by Sumner (1926, 1929), and was followed by a quick swing through peninsular Florida, with 2 days along the Atlantic coast.

The second trip extended the Gulf coast study to Baldwin County, Alabama, and supplemented the study of beach mouse distribution along the Atlantic coast. On the third trip 32 days were devoted to further studies of the northern Gulf coast from Baldwin Co., Alabama, east to the Apalachee Bay region, and north to Crestview, Marianna, and Quincy; the remaining 15 days were then devoted to comparative studies of topographical and ecological conditions in pensinsular Florida, including the ranges of all three Atlantic coast subspecies. Headquarters for the fourth trip was the Florida State Museum, from which trips were made in all directions to check and amplify the information and conclusions drawn during the three previous trips. A total of 31 days was spent in the northern Gulf Coast region, and 9 days on the Atlantic coast; the remaining period was devoted to visiting various inland localities in peninsular Florida and to museum studies at Gainesville.

On all four trips different routes were taken through Georgia and South Carolina in order to see as much as possible of the habitats of the inland forms, and some trapping was done en route. Parts at least of the ranges of all the subspecies were thus visited and a grand total of 92 days was spent in the area of chief concern to the present study. Conventional museum specimens were collected during the 1950-51 trips; on the 1961 trip the specimens were frozen in a portable refrigerator and taken back to Hanover, N. H. for preparation.

On this trip the first live breeding stocks were collected and shipped back by air express. All specimens collected in 1962 were shipped back alive. For consultation in the field on all these trips, maps of soils, vegetation, Pleistocene shore lines, geological features, and coastal topography were previously prepared in the map library of Dartmouth College and plotted on large scale county maps issued by the Florida State Road Department. U.S. Geological Survey topographic maps (1:250,000 scale, as well as a number of the more detailed 1/31680, and the 7½-minute series) were also used.

Museum studies: A total of 1254 specimens was examined in the course of the systematic part of this project. Most of this material was obtained through loans (see appendix). Two visits were made to study the great amount of material in the U.S. National Museum, Washington, D. C. Standard taxonomic procedures have been followed in respect to size variation, in which reliance must be placed on measurements taken by collectors at the time of preparation. Head-body measurements were obtained by subtracting tail length from total length. Only ear length measurements that were clearly taken from the tip to the notch have been used. Skull measurements, including those of previously described subspecies (not included here) were all taken in the usual manner by the author.

In order to avoid *nomina nuda* and the cumbersome use of locality descriptions (many of the mouse population ranges have no single local name) descriptions of new subspecies have been moved forward of the sections dealing with phenotype pattern characters and their variation. Certain letter symbols for the several natural pelage patterns are thus used in advance of their full discussion. However, by referring to the illustrations in figures 5. 10, 20, and 21 the reader should have no difficulty in interpreting the visible patterns of the several new subspecies.

Color measurements of all but one of the Gulf coast subspecies were taken with a Bausch and Lomb spectronic-20 colorimeter with reflectance attachment. This instrument provides numerical values for dominant wave length (analogous to the concept of hue), purity of color (chroma or degree of saturation), and brightness (total amount of reflected light).

Ridgway's color standards have long been used in descriptive taxonomy, but they depend to a great extent on the acuity of visual discrimination of the individual worker. Often the same species or subspecies may be described differently by different authors, as in the following four subspecies of *P. polionotus:*

polionotus–"uniform brownish fawn" in unworn pelage and "between fawn and cinnamon" in worn pelage (Osgood, 1909); "olive brown" (Sumner, 1926).

subgriseus–"between wood-brown and cinnamon" (Chapman, 1893); "between Avellaneous and Vinaceous buff" (Schwartz, 1954).

rhoadsi–"fawn color" shading towards "orange buff" (Bangs, 1898); "rather dark ochraceous buff . . . sparingly mixed with dusky" (Osgood, 1909).

leucocephalus–"light drab" (Howell, 1920); "wood brown" or "light drab" (Sumner, 1926).

Average color measurements of these same sub-species are given below; they may serve as reference standards for comparing the new forms described (see also figure 25):

	Number of specimens measured	Dominant wave-length	Purity of color	Reflectance (paleness)
polionotus	45	576.5 mμ	9.2	15.5
subgriseus	39	586.0 mμ	20.0	15.6
rhoadsi	28	582.0 mμ	16.5	18.5
leucocephalus	37	557.0 mμ	11.0	33.0

Special jigs were made to hold flat skins in a manner permitting a pin-pointing of the spot to be measured, as well as to exclude external light. Conventional filled museum skins are not easily measured by this instrument, and no flat skins of *peninsularis* were available. Two sets of measurements were taken for each specimen, one along the mid-dorsal stripe in the mid-body region, the other lateral to it and midway between the dorsal stripe and the outer margin of the dorsolateral pigment area. In each case 10 individual readings were taken at different wave lengths and reduced by means of a special "trichromatic coefficient computing form for illuminant C" (provided with the instrument) to determine the three component values, x, y and Y. The Y value provides an index of reflectance at all wave lengths and is therefore an indicator of relative paleness, regardless of color. The x and y values must be plotted on a chromaticity diagram to determine the dominant wave length and the purity of color.

The process is a lengthy one which has not yet been completed for all the 2500 specimens, captured and laboratory bred. The value Y (reflectance), however, has now been determined for all the specimens and, for the purpose of this report, about 20 specimens of each wild-caught subspecies were picked at random, their individual wavelength readings averaged, and average values thus determined for dominant wave length and purity (Fig. 25).

A description of this instrument and its application to systematic studies has been published by Selander *et al* (1964).

Breeding experiments: Slightly more than 2500 mice were raised in captivity, chiefly to find possible traits that might furnish clues to relationships between the various subspecies and so aid and supplement the conclusions drawn from taxonomic studies. Breeding stocks were obtained from the following localities:

1. Vicinity of Pensacola, Florida (Fig. 3, A).
2. Gainesville, and Ocala National Forest, Florida (Fig. 3, B).
3. Vicinity of DeFuniak Springs, Florida (Fig. 3, C).
4. Beaches of Baldwin Co., Alabama, including Ono Island (Fig. 3, E).
5. Beach section between Perdido and Pensacola Bays (Fig. 3, F).
6. Santa Rosa Island, western end and central region near the Navarre bridge (Fig. 3, G).
7. Beach section between Choctawhatchee and St. Andrew Bays (Fig. 3, I).
8. Vicinity of the Archbold Research Laboratory at Hikoria, Florida (Fig. 3, K2).

Efforts to collect live specimens from areas D, H, and J (Fig. 3) were unsuccessful.

Crosses were made with more or less success, between all these stocks. Mated pairs were kept in cages measuring 8"x9"x11" and litters were removed usually before, or soon after, the next litter was born. Because of their social nature, solitary individuals or pairs tend to be less active and do not thrive so well as family groups. A detachable nesting box with sliding door fastened by hooks and eyes to each cage permitted easy cleaning of the main cage. Food consisted of sunflower seeds, vegetables (cabbage, lettuce, apple peel, etc.) and ordinary dog chow pellets. (Dawson's (1965) higher fertility rate may perhaps be the result of his use of "Mouse Breeder Chow."). A colony of about 400 was maintained for 4 years, half being fed one night, and the other half the next night; all water bottles were checked each day.

Some phenotype traits were visible in the live specimens, others could be observed only by examining the prepared flat skins under magnification. Because of the size of the colony and time limitations, anaesthetization of individuals was not feasible, and several preliminary tabulations were needed before a decision to close down the experiments could be made. The phasing out has been in progress for some time and the colony is now, at the time of writing (June 1966) down to six cages and three actively breeding pairs. Complete results cannot, therefore, be presented now. Also, as the genetic results are being studied in collaboration with George B. Saul 2nd., Dartmouth College (now at Middlebury College), they are to be published separately under joint authorship.

This poses a dilemma because much of the discussion and some of the conclusions presented here are based, in part at least, on the results of the preliminary genetic analyses. The latest of these, however, is complete enough to give confidence of their general reliability, although the counts may be expected to differ slightly when the final tabulation is made. To withold publication of this systematic-evolutionary study until after the genetic results are presented is undesirable and, indeed, the systematic conclusions constitute a necessary foundation for discussion of the genetic results. Although the genetic results must be taken largely on trust for the time being, some indication of the evidence derived from these laboratory experiments is shown by the latest preliminary results of crosses involving the three primary hair-tip rump patterns included here, together with a model in which the effect of three autosomal dominant genes is postulated, and a fourth recessive gene superimposed upon the system is included. Other phenotypes are more involved, due chiefly to the greater number of presumed loci, but in the case of head pattern traits a somewhat similar model involving seven loci has been constructed as a working hypothesis.

The rump pattern traits have been particularly helpful in tracing gene flow and furnishing clues to subspecific relationships. Were it not for the fact that two different genotypes produce phenotypes that are visually indistinguishable, it might be possible to discuss the evolutionary aspects here without recourse to these preliminary genetic results. But as the hypothesized system permits the concealment of traits and as the discovery of the presence of the factor for "tapered rump" in an inland population is crucial to the evolutionary discussion, this compromise procedure is necessary.

TAXONOMY

Prior to Osgood's (1909) revision of the genus *Peromyscus*, *P. polionotus* was unrecorded from Alabama and northwest Florida. Osgood described 13 specimens W. E. Clyde Todd collected at Whitfield, Walton Co., Florida in 1903 as a new subspecies, *P.p. albifrons*, and 6 additional specimens A. H. Howell collected at Bon Secour, Baldwin Co., Alabama, in 1908 allowed him to define the range of this new form as "coast of western Florida and Alabama." Osgood's manuscript was evidently in press when he received the latter specimens (*vide* his footnote), and considerable doubt now exists as to whether the two samples were adequately compared.

During the present study six of the original topotypic series were compared with a number of specimens from the Alabama coast, including Howell's Bon Secour examples. The two populations are clearly not the same. The Alabama population lacks the diagnostic median nose-stripe and is distinctly paler and grayer than the topotypical *albifrons*. It also has a significantly larger hind foot. Other populations heretofore included in the range of *albifrons* (Schwartz, 1954; Hall and Kelson, 1959) also differ in various ways.

The beach population between Perdido Bay and Pensacola Bay, for instance, differs markedly in pelage pattern as well as being paler. The populations east of the Choctawhatchee River, which were studied intensively and mistakenly identified as *albifrons* by Sumner (1929, 1930), Blair (1944), and Hayne (1950) differ in many respects from true *albifrons*. Indeed, as will be shown later, there appears to be a partial reproductive barrier between these and the true *albifrons* population. Re-examination of the taxonomy of all the Gulf Coast forms is thus a necessary preliminary to further study of evolutionary changes within the species.

P. polionotus albifrons Osgood

The confusion caused by identifying the Alabama beach mice with *albifrons,* and later the inclusion of the populations east of the Choctawhatchee drainage system, has been compounded more recently by a further eastward extension of the range of so-called "albifrons" (Schwartz, 1954; Hall and Kelson, 1959). Mice from the Flint-Chattahoochee-Apalachicola basin, as well as those from Marianna, Sills and Daleville (recorded as *P.p. polionotus* by Hayne, 1950), and eastward to the Quincy region are now being included in the range of *albifrons.* These are in reality more like *subgriseus,* but they intergrade with *rhoadsi* and other forms where the ranges meet (Fig. 3). The Flint-Chattahoochee basin was a large bay during the Yarmouth interglacial stage and its present population is the result of subsequent invasion by primarily *subgriseus* stocks. The distinctly orange color of Daleville, Marianna, and Graceville specimens (Fig. 25) agrees with that of *subgriseus* from peninsular Florida, rather than with the yellow color of *albifrons* and *polionotus.* The Sills sample approaches *rhoadsi* in its more yellow-orange color. All the mice east of the Chipola River must therefore be excluded from further consideration of the so-called *"albifrons"* assemblage.

This leaves the following six areas, all of which are at least partially isolated, and each is inhabited by mice that differ from the others in pigment patterns, color, and body dimensions. Some are monomorphic, others polymorphic:

1. the Yellow-Shoal-Alaqua watershed (Fig. 3, D);
2. the Alaqua-Choctawhatchee watershed (Fig. 3, C);
3. the Choctawhatchee-Chipola watershed (Fig. 3, J);
4. the beach dunes between St. Andrew Bay and Choctawhatchee Bay (Fig. 3, I);
5. the dunes between Pensacola and Perdido Bays (Fig. 3, F);
6. the dunes between Perdido and Mobile Bays (Fig. 3, E).

Whitfield, the type locality of *albifrons,* no longer exists as a hamlet. The name is forgotten by most of the inhabitants of the nearby village of Portland, which is situated only 2 miles to the north at the head of Alaqua Bayou. Search of the area on the west side of the Bayou to its mouth where Whitfield stood revealed only poorly drained soils quite unsuited to the species. To the east of Alaqua Bayou, a few miles east of Portland, some dry sandy areas were located and signs of mice were seen, but time did not permit digging or trapping there.

Later, after returning to New Hampshire, a request was made to borrow some of the topotypical series in the Carnegie Museum. In reply, Kenneth Doutt informed me that he had shown my letter describing my failure to obtain specimens to W. E. Clyde Todd who had collected the original series, and who then informed him that all the specimens were taken in the sandy area *east* of Alaqua Bayou and not on the west side where Whitfield was located. This places the type locality of *albifrons* within the Alaqua-Choctawhatchee watershed (area 2, above) and the designation should be changed to read as follows:

AMENDED TYPE LOCALITY: Approximately 4 miles northeast of Whitfield, Walton Co., Florida, in a dry sandy area east of Alaqua Bayou.

P.p. albifrons Osgood is characterized by head pattern D (Fig. 20) and rump pattern S (Fig. 5). In color it approaches *polionotus* in being distinctly of a yellow hue, but more pure and somewhat paler (Fig. 25). Average color measurements are: dominant wave length, 578 mμ; purity value, 15.2; reflectance (paleness), 17.0. This last value is intermediate between *subgriseus* and *rhoadsi*, but differs from both in its yellower, less orange hue. Contrary to Osgood's statement that the "hairs of the underparts [are] white to roots or very slightly plumbeous at bases", all the specimens here examined have gray hair bases, but these are often very pale and difficult to see in a conventional stuffed skin. Flat skins, folded to reveal the entire length of the hairs under magnification, always show at least some dilute basal-hair pigment in this race (Fig. 11, ALB 1043). In size and relative proportions (Figs. 26 and 27) *albifrons* is almost exactly like *subgriseus*, including the small ears which differentiate the latter from *polionotus*.

This subspecies is monomorphic, except that occasional specimens from the De Funiak Springs area lack the narrow median white nose stripe and/or the square rump pattern. This can be explained on the basis of intergradation with *polionotus* whose range abuts immediately to the north. A single specimen in the U.S. National Museum (number 263748), labeled Crestview, agrees closely with this subspecies and serves to indicate that the range of *albifrons* extends westward along the high sandy ridge north of the Alaqua and Shoal drainage systems (Fig. 3, C). The remaining five populations differ from this form and from each other and may be designated as follows:

P. polionotus griseobracatus new subspecies

Holotype: U.S. Nat. Mus. 308957; ♀ adult, 20 miles west of Ft. Walton (= about 5 miles west of Navarre, Santa Rosa County) Florida, April 1955, E. V. Komarek. Skull and jaws in good condition.

Diagnosis: Similar to *P.p. albifrons* but of a purer, more yellow-orange hue, and with slightly longer hind feet and significantly larger ears (Fig. 27). Dimorphic in respect to head pattern; about two thirds of the specimens examined have head patterns C and one-third D (Fig. 20). Almost identical in color with *rhoadsi,* local population K3 (Figs. 3 and 25), but differing in having rump pattern S, not P (Fig. 5). Average dominant wave length, 580.7; purity value, 23.5; reflectance, 17.5. Basal-hair pattern U-3 (Fig. 10); venter very pale, almost white in some specimens; tail-stripe incomplete (up to ¾ the length in some specimens) and often very dilute. Mid-dorsal stripe moderately well-defined. Head-body and tail length similar to *albifrons* and *subgriseus* (Fig. 26).

CRANIAL MEASUREMENTS

	Type	Ten-Specimens	
		range	mean
Occipito-nasal	22.7	21.7 - 23.1	22.52
Basilar	17.1	16.2 - 17.9	17.25
Post-palatal	8.1	7.8 - 8.6	8.32
Incisive foramen	4.5	4.5 - 4.9	4.65
Maxil. tooth-row	3.1	2.9 - 3.4	3.09
Zygomatic breadth	11.7	11.7 - 12.5	11.98
Cranial breadth	10.4	9.6 - 10.5	10.00
Inter-orbital breadth	3.6	3.6 - 4.0	3.78
Cranial height	8.5	7.4 - 8.7	7.85

Distribution: Known only from the inner coast line of Santa Rosa Sound, from Pensacola Bay to the northwest shore of Choctawhatchee Bay (Fig. 3, D). Extending probably throughout the Yellow-Shoal-Alaqua watershed, which is a restricted military zone from which specimens are not available.

Etymoloy: Grise (ML) gray, bracat (L) wearing trousers, in allusion to the pale gray hind legs.

P. polionotus ammobates new subspecies

Holotype: UF 8520; ♀ adult, sand bar *west* of Perdido Inlet (Alabama Point), Baldwin County, Alabama, 23 October, 1961, W. W.

Bowen. Skull and jaws in good condition, excepting a small gap in the left zygomatic arch.

Diagnosis: Paler and grayer than *albifrons* and *griseobracatus;* venter pure white; hind foot averaging larger than in *griseobracatus* and significantly larger than in *albifrons;* ear intermediate in length between the two (Fig. 27). Dimorphic in respect to head pattern (Fig. 20, B and C) and rump (Fig. 5, P and S): basal-hair pattern as in figures 10 and 11, U-4. Similar in color to *leucocephalus,* but much darker and less pure; near to *polionotus,* but much paler (Fig. 25). Dominant wave length, 575.2; purity, 9.0; reflectance, 20.5. Tail stripe incomplete (up to ¾ the length); mid-dorsal stripe indistinct. Similar in size to *albifrons* and *griseobracatus,* but tail averaging longer (Fig. 26.)

CRANIAL MEASUREMENTS

	Type	Ten Specimens	
		range	mean
Occipito-nasal	22.6	21.0 - 22.9	22.30
Basilar	17.4	17.3 - 18.1	17.83
Post-palatal	8.2	7.4 - 8.5	8.16
Incisive foramen	4.6	4.5 - 5.2	4.72
Maxil. tooth-row	2.9	2.7 - 3.5	3.10
Zygomatic breadth	12.0	11.2 - 12.4	11.68
Cranial breadth	10.3	10.2 - 10.7	10.43
Inter-orbital breadth	3.6	3.6 - 4.0	3.89
Cranial height	8.6	8.1 - 9.1	8.51

Distribution: Coastal dunes between Mobile Bay and Perdido Bay; also Ono Island at the mouth of Perdido Bay, Alabama (Fig. 3, E).

Etymology: Ammo (G) sand, bates (G) one that haunts.

P. polionotus trissyllepsis new subspecies

Holotype: UF 8521; ♀ adult, sand bar *east* of Perdido Inlet (Florida Point), Baldwin County, Alabama, 22 October, 1961, W. W. Bowen. Skull and jaws in good condition.

Diagnosis: Paler than *ammobates* and differing in pelage pattern from all other subspecies. Similar to *albifrons* in color but much paler (Fig. 25); the mean reflectance value falling within the range of *leucocephalus* (Fig. 7). Average dominant wave length 576.5; purity value 14.6; reflectance 23.5. Dimorphic for head patterns H and I (Fig. 21) and rump patterns S and S + T superimposed (Figs. 5 and 24). Basal-hair pattern as in figure 10, W (see also Fig. 12, T 21);

tail-stripe absent; mid-dorsal stripe indistinct; venter pure white. Similar in size to *ammobates* but averaging slightly smaller (Fig. 26 and 27).

CRANIAL MEASUREMENTS

	Type	Ten Specimens	
		range	mean
Occipito-nasal	22.6	20.6 - 23.2	22.11
Basilar	17.0	16.0 - 17.9	16.85
Post-palatal	8.6	7.5 - 8.6	7.97
Incisive foramen	4.9	3.9 - 4.9	4.49
Maxil. tooth-row	3.2	2.8 - 3.2	3.00
Zygomatic breadth	11.6	10.9 - 11.9	11.52
Cranial breadth	10.2	9.6 - 10.9	10.20
Inter-orbital breadth	4.0	3.8 - 4.0	3.89
Cranial height	8.6	8.2 - 8.9	8.48

Distribution: Coastal dunes between Perdido Bay and Pensacola Bay, Alabama and Florida (Fig. 3, F).

Etymology: Tri (L) three, syllepsis (G) put together, in allusion to its postulated trihybrid origin.

P. polionotus allophrys new subspecies

Holotype: UF 8522; ♂ adult, coastal dunes near Morrison Lake, Walton County, Florida (= about 10 miles east of Destin), 4 October, 1962, W. W. Bowen. Skull and trunk skeleton in good condition. Representative of morph 4 of this polymorphic race. Captured alive as a young adult and laboratory-bred for some time before being killed at age 15+ months.

Paratype 1: UF 8523; ♂ adult, laboratory-bred from wild-caught parents taken at same time and place as the holotype. Killed 3 April, age 6 months. Skull and trunk skeleton in good condition. Representative of morph 3.

Paratype 2: UF 8524; ♀ adult, laboratory-bred from wild-caught parents taken at same time and place as the holotype. Killed 18 April, 1964, age 8.5 months. Skull and trunk skeleton in good condition. Representative of morph 2.

Paratype 3: UF 8525; ♂ adult, captured alive at the type locality in trap adjacent to that which secured the holotype (same locality and date). Kept in laboratory for 18 months (infertile). Skull and trunk skeleton in good condition. Representative of morph 1.

Diagnosis: Polymorphic in respect to head and rump patterns, width of dorsal pigment and color. *Morph 1:* similar to *rhoadsi,* but averaging more pure orange, and slightly paler (Fig. 25 and Fig. 7); head pattern B (Fig. 20; Fig. 23, ALL 588); rump pattern P (Fig. 5); width of dorsal pigment as in *rhoadsi* (Fig. 7). Dominant wave-length 583.5; purity 19.1; reflectance 20.8 (Figs. 25 and 28). *Morph 2:* similar to morph 1, but with head pattern D (Fig. 20); rump pattern either P, S, or intermediate (half-pointed) and dorsal pigment width averaging slightly narrower (Fig. 7). Averaging more yellow and purer in color (Fig. 28). Dominant wave length 581.0; purity 20.9; reflectance 21.1. *Morph 3:* similar to morph 2, but with a full, or nearly full, white nose (Fig. 23, ALL 1893). Head pattern E (Fig. 21); rump pattern S (Fig. 5), occasionally half pointed; dorsal pigment width averaging distinctly narrower than in morph 1 (Fig. 7). More yellowish than morphs 1 and 2 (Fig. 28). Dominant wave length 579.2; purity 19.2; reflectance 20.5. *Morph 4:* similar to morph 3, but with the face white to the eyebrows (Fig. 23, ALL 1924). Head pattern F (Fig. 21); rump pattern S (Fig. 5); dorsal pigment width relatively narrow and largely within the range of *leucocephalus* (Fig. 7). Distinctly more yellow than the other morphs. Dominant wave length 576; purity 20.7; reflectance 20.7. *All morphs:* basal-hair pattern V (Figs. 10 and 12); tail stripe variable; present and usually full-length in morph 1 and absent in morph 4; head-body length averaging slightly more than in *rhoadsi,* but tail significantly longer (Fig. 26); hind foot averaging larger and ear significantly longer (Fig. 27).

CRANIAL MEASUREMENTS

	Holotype	23 Specimens (all morphs)	
		range	mean
Occipito-nasal	23.7	21.7 - 23.9	22.26
Basilar	18.0	16.0 - 18.5	17.12
Post-palatal	8.4	7.5 - 8.8	8.06
Incisive foramen	4.8	3.9 - 4.9	4.46
Maxil. tooth-row	3.2	2.8 - 3.1	2.95
Zygomatic breadth	12.3	10.9 - 12.3	11.60
Cranial breadth	10.3	9.7 - 10.9	10.39
Inter-orbital breadth	4.0	3.5 - 4.0	3.91
Cranial height	8.6	7.9 - 9.0	8.42

Distribution: Coastal dunes between Choctawhatchee Bay and St. Andrew Bay, Florida (Fig. 3, I).

Etymology: All (G) differing, ophrys (G) eyebrows, in allusion to head pattern polymorphism.

P. polionotus sumneri new subspecies

Holotype: UF 8526; ♂ adult, Merial Lake, Bay County, Florida, 11 November, 1950, W. W. Bowen. Skull and jaws in good condition, excepting slight damage to right bulla and small gap in left zygomatic arch. Representative of morph 2.

Diagnosis: Trimorphic; morphs 1, 2 and 3 similar in pattern to those in *allophrys*, morph 4 absent as far as is known. Darker and less variable in color than *allophrys* (Fig. 28). Dominant wave length 580.0 (morph 3) to 582.0 (morph 1); purity 18.1 (morph 3) to 20.6 (morph 1); reflectance 19.2 (morph 3) to 19.8 (morph 2). Significantly smaller in all dimensions than *allophrys* except female ear length, which is nearly significant, Figs. 26 and 27). Hind foot averaging smaller than in all other inland forms, and significantly smaller than in all the beach forms.

CRANIAL MEASUREMENTS

	Type	25 Specimens	
		range	mean
Occipito-nasal	21.8	21.0 - 22.7	21.78
Basilar	16.9	16.2 - 17.5	16.91
Post-palatal	8.0	7.8 - 8.6	8.12
Incisive foramen	4.7	4.5 - 4.7	4.54
Maxil. tooth-row	2.9	2.8 - 3.0	2.90
Zygomatic breadth	11.8	10.7 - 12.0	11.41
Cranial breadth	—	9.5 - 10.6	10.11
Inter-orbital breadth	3.8	3.5 - 3.9	3.77
Cranial height	8.3	8.0 - 8.3	8.16

Distribution: Dry sandy areas of the Choctawhatchee-Chipola watershed (Fig. 3, J).

Etymology: Honoring Francis B. Sumner, pioneer student of the genetic basis of color variation in natural populations of mice.

VARIATION AND PREDATION

The striking relationship between soil color and pelage color has focussed attention on these mice. Most investigators concede, or imply, that predator selection is the causative factor, but no experimental proof of this exists. Dice's (1947) experiments with darker and paler subspecies of *P. maniculatus*, caged with owls as predators showed a significant selective advantage in those mice whose pelage color most nearly matched the background. In the case of these beach mice an even more rigorous selection pressure may be assumed be-

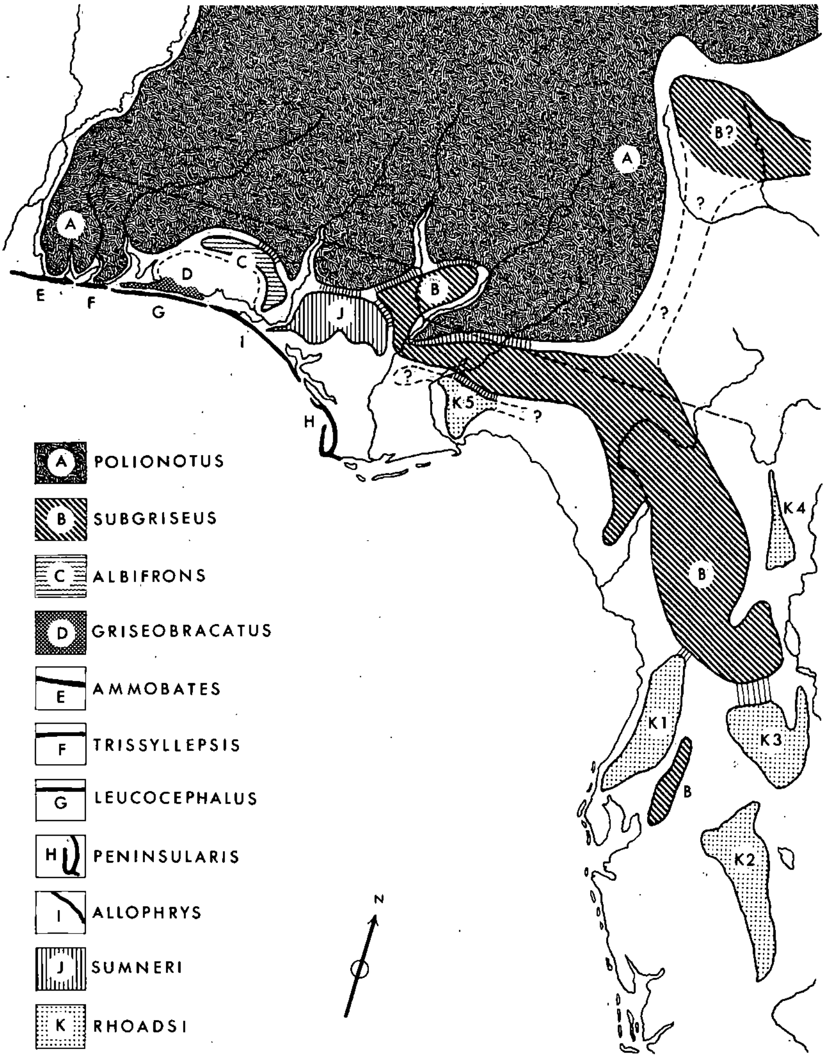

FIGURE 3. Distribution of Gulf Coast subspecies.

cause of the intense whiteness of the beach dunes. But the beach forms show a considerable amount of variation in cryptic paleness that cannot be explained on the basis of gene flow and isolation, as was thought by Howell and Sumner.

Much useful information on the ecology, behavior and population dynamics of this species has been published (Sumner and Karol, 1929;

Hayne, 1936; Rand and Host, 1942; Blair, 1951; and others), but beyond listings of probable predators, virtually nothing is known about predation and mortality rates in this species. A female is capable of producing 80 or more young under laboratory conditions, and litters are born regularly at approximate 26 day intervals, so the attrition rate must be very high. Blair (1948) records the average life-span to be less than 5 months in *P. maniculatus*, and only a few live the full potential of 3 or more years.

Seasonal fluctuation in population size appears to be great, as is indicated by the following note furnished by James N. Layne, then at Cornell University: "We trapped two nights [between 27 March and 4 April] on Santa Rosa, at the west end near the entrance to Fort Pickens State Park. In 252 trap nights with live traps and 100 traps with museum specials, we took 27 *polionotus*–. They were really swarming in the area. At first we had the impression that they were most abundant on the dunes just behind the beach, but we later took them in almost all the habitat types in the open sand areas. They were even in the rather dense grassy plots that contained runways, clippings and burrows of *Sigmodon*. One of our party went out at night with a headlamp and found it quite easy to observe the beach mice in their activities. Some were seen within 50 feet of a home. Tracks were everywhere, and there were almost no sea oat heads left. This was in great contrast to what I found in January when I came through this area. At that time there was a tremendous crop of sea oats. I trapped only one night then, about two miles east of Fort Walton Beach. I took only one *polionotus* in 25 live traps and saw relatively little sign."

During periods of food scarcity starvation must take a large toll, but at other seasons predation is the most potent factor controlling population size. The crucial question is whether, and to what extent predation is selective. The feral house cat is becoming an increasing factor in the reduction of beach populations. During the present field work (1950-1961) this became so apparent that in the later years we avoided trapping wherever we found cat tracks.

On one stretch of beach cat tracks were abundant for nearly a mile on either side of a lonely closed cottage. Not a single mouse track or hole was discovered within the 2-mile stretch, which had become a virtual barrier to gene flow within the already shrinking range of this closed population. Not all the instances observed were as drastic as this, and in one place mouse tracks and cat tracks were seen to converge on the entrance to a hole in a rotten log stranded on the

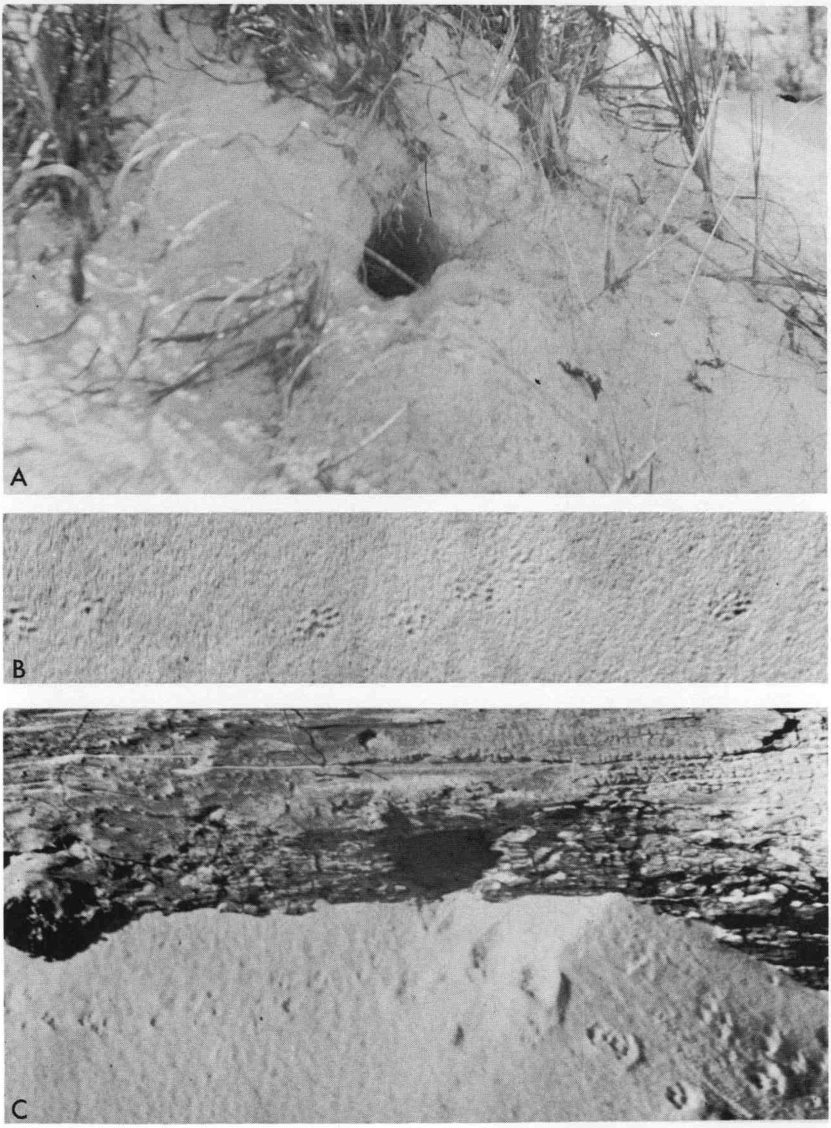

FIGURE 4. Mouse hole excavated by a weasel (*Mustela frenata*?), as identified by tracks (B). Mouse tracks (C, left) and cat tracks (right) leading to a hole in a stranded log, into which the mouse evidently escaped.

sand (Fig. 4, C). Here the mouse clearly had escaped, but on the whole all indications point to the imminent threat of extinction by heavy cat predation on top of the natural balance maintained by native predators.

Once after trapping a mouse near the entrance to its hole, I returned with camera that afternoon only to find that the hole had been enlarged to a diameter of some 3 inches or more. Weasel tracks (*Mustela frenata?*) were discovered leading to the spot (Fig. 4, A and B). I had noted similar large holes on previous occasions, and now their origin was clear. At other times I have seen snake trails leading into mouse holes but how the plug the mice construct is circumvented is not known. Observations on captive mice indicate that their daytime sleep is so very deep that the silent entry of a snake into the nest chamber could wipe out most if not all of a mouse family. But such predation cannot be selective.

The actions of a weasel enlarging the hole, on the other hand, would be more likely to awaken the mice. which could then escape through their preformed escape tunnel. Perhaps a litter might be captured, but if it happened to be suckling at the time, the young clinging tenaciously to the mother's teats would be dragged to safety (as I have often seen when digging out mouse holes). In either event differential survival would not occur, except possibly in favor of those young that attach themselves most firmly to the mother's teats, and the tenacity with which the young do cling while nursing provides circumstantial evidence of predation by digging.

In the case of larger predators such as skunks and raccons, the disturbances created by their digging would most likely awaken the mice soon enough for them to break out before the predator's vision was obscured by the tunnel wall. Pursuit might then occur and the differential values in cryptic variation come into play. No records of predators capturing foraging mice have been noted, but tracks are soon obliterated in the shifting sand of the dunes. Mice might be expected to be particularly vulnerable to predatory attack during such foraging trips, but perhaps even more critical is the moment when the mouse emerges from its hole, as a lurking predator could then surprise and capture it. Laboratory observations indicate that these mice cautiously sniff the air with only the tip of the nose above ground, before emerging. Later the face is exposed as far as the eyes, and only after these tests by scent and sight will their bodies emerge. A white nose, or face, matching the white rim of the hole could thus be of great selective value, and the significant trend toward white faces in these beach mice might be so explained.

Conversely the rump and tail are the last portions to be seen by a pursuing predator as a mouse tries to escape down its hole, which might explain the trend toward reduced pigment in these areas. A mouse blocked from a hole will run for the nearest vegetative cover, which is seldom far away (Figs. 1 and 2). Hiding thus at the base of a tuft of grass or other vegetation, they are exceedingly difficult to see, as I have noted many times when digging their holes. Complete elimination of pigment would undoubtedly destroy this cryptic effect by nullifying counter-shading and the disruptive camouflage of a bicolor pattern.

In *leucocephalus,* where dorsal body pigment is reduced to less than 50 per cent of the girth, counter-shading cannot be effective, and this must be particularly so in the occasional examples where pigment is eliminated except for the mid-dorsal stripe (Fig. 18, number 208). Here a dazzling effect might be produced by the white dorsum in contrast to the shaded venter and pigmented dorsal stripe. Such a condition may well produce a disruptive pattern under strong light, and the sudden change as the mouse reaches the shade of a clump of grass would aid in its concealment. This could be comparable to insects that display conspicuous markings in flight and cryptic patterns when at rest. The fact that these mice are nocturnal and usually inactive on moonlit nights might seem to negate this hypothesis, but a mouse being chased from its hole by a digging predator in the daytime or on a moonlit night might produce such a dazzling effect.

The dune habitats of the beach mice are not uniform; numerous microhabitat differences occur within the range of a given population. In photographs A and B (Fig. 1), for example, which were taken from the same spot in nearly opposite directions, the grassy foreground of B is part of the same area shown in the lower left in A. But the dune formations and their vegetation are dissimilar. The dunes in the blowout area, B, are held together by the matted roots of scrubby oaks (mostly *Quercus geminata* Small) which make it virtually impossible to dig out the holes. The dense micro-jungle above the ground also provides abundant food (at certain seasons at least) and excellent cover which would insure safety from predatory attack.

In contrast, the frontal dunes, A, are easily dug and provide only sparse cover for concealment. Food is more plentiful and varied here, which probably accounts for the greater number of holes. On this particular beach the *allophrys* population is quadrimorphic and possibly the microhabitat differences help maintain the polymorphic balance, but the number of specimens captured in the two areas was not large enough to detect a difference.

Inland in scrub areas that were formerly Pleistocene beaches, selection pressures have been reversed by the presence of a carpet of fallen leaves and the mixing of clay particles in the sand. Here a correlation between pelage color and leafy substrate might be expected rather than the soil color that Hayne (1950) measured. Actually large patches of more or less exposed sand may be found, especially in turkey oak-longleaf pine habitats, and mouse tracks are often seen within these areas as well as along sand roads that traverse the region. Pelage color, if selectively determined, would therefore reflect a compromise between the colors of the two substrates.

PELAGE PATTERNS

Hair pigment in this species is of the usual banded (agouti) type, and genetic control of the gray (melanin) hair-base pattern appears to be independent of that of the colored (xanthophyll) hair-tips. Reduction of total pigmented area in the beach populations is not simply a general restriction, as Sumner (1929) evidently assumed when he measured the total pigment area by planimeter regardless of shape or pattern. Nor has support been found in the present genetic studies for Blair's (1944) hypothesis of a major gene for white cheek (Wc) and five "grades of reduction of pigmented area."

HAIR-TIP RUMP PATTERNS

Extension of pigment down the hind legs is characteristic of the genus. This "pointed-rump" condition (Fig. 5, P) is found in *polionotus, subgriseus, rhoadsi* and morphs 1 of *sumneri* and *allophrys.* A "square-rump" phenotype (S) is characteristic of *albifrons, griseobracatus, ammobates* and the polymorphic forms *sumneri, allophrys,* and *peninsularis.* A "tapered-rump" phenotype (T) occurs only in *leucocephalus* and one morph of *peninsularis.*

These three patterns do not always occur in pure form. A half-pointed condition, varying from almost full pointed to nearly square may be found in some specimens of *albifrons, griseobracatus, ammobates, allophrys* and *sumneri.* Similarly, specimens showing the tapered pattern superimposed upon the square pattern, as in a double exposed photograph, occur in many *leucocephalus* specimens. This "double image" phenotype also occurs in approximately 50 percent of the *trissyllepsis* population (Fig. 24, A), but strangely it has not been seen in *peninsularis,* where square and tapered rumps appear to maintain separate identities. The tapered-rump phenotype is not found in *allophrys* (with one exception) and the square rump has been found only once in *leucocephalus.*

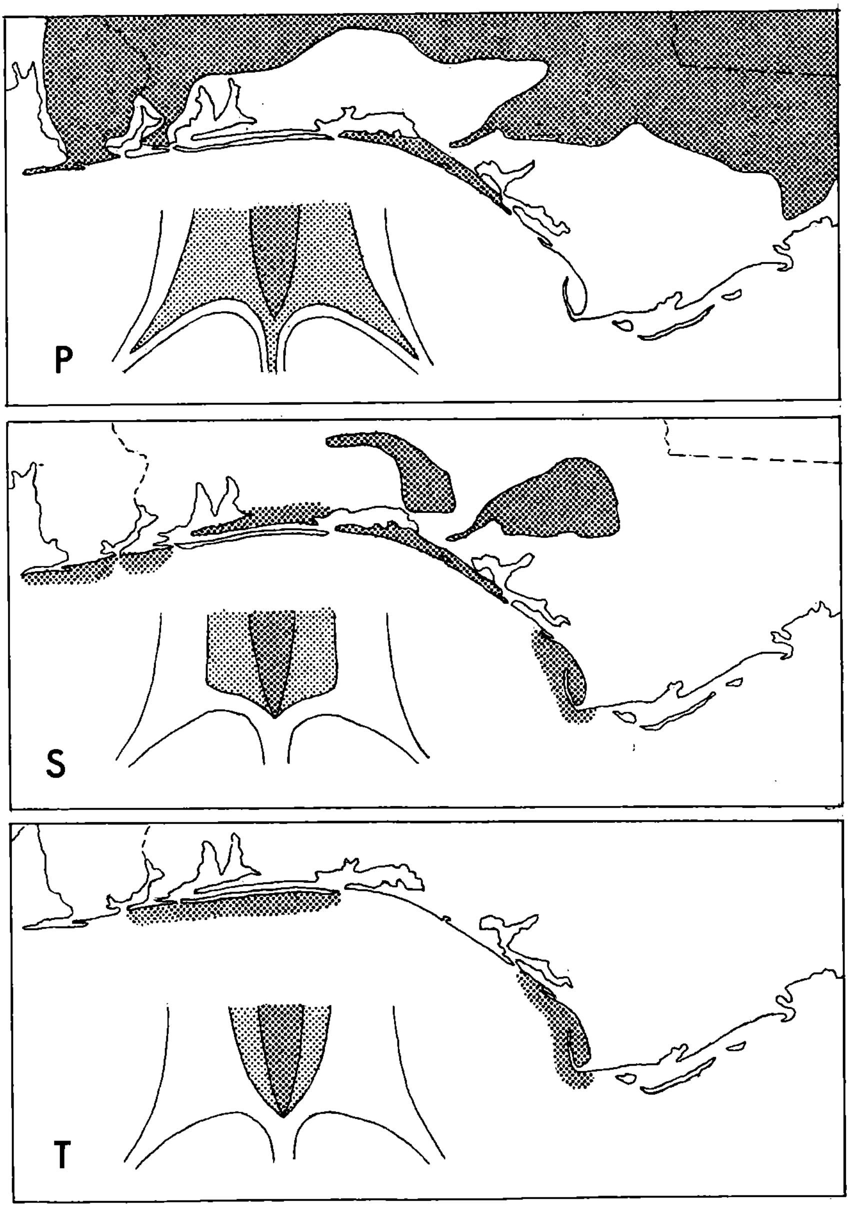

FIGURE 5. Hair-tip rump patterns and their primary distribution.

Each of the primary rump patterns breeds true, but since none of the wild populations is entirely pure, many matings give mixed results. Thus a pair of square-rumped *allophrys* produced a ratio of 14 square:5 double image, indicating that the tapered-rump factor can be concealed in this population. These rump characters have proved most useful by permitting one to see what phenotypic patterns are in each specimen, and thus what the phenotypic variation is in each population. From this, on the basis of a model here proposed, what genes are present in the populations and how the populations may be related genetically and evolutionarily can be deduced. Three autosomal dominant genes are proposed for the three primary rump phenotypes. Thus, the effects of genes P-, S- and T- are postulated as pointed rump, square rump and tapered rump. Superimposed on this system is Q,q; the effect of qq is believed to be a reinforcement of PP, making it epistatic to SS and TT. In effect, this seems to be a homeostatic mechanism that resists change from the presumed ancestral pointed rump phenotype.

The results of the laboratory crosses suggest that the intermediate patterns "half-pointed" and "double image" are the effects of "balance" between the postulated genes P- and S- (giving the half-pointed phenotype) and S- and T- (giving the double image phenotype). The intermediate "balanced" effect of P- and T- appears to be indistinguishable from the square rump phenotype (S-). When P is heterozygous, the effect of qq seems to be that of raising the effect of P to the equivalent of homozygous dominance. Thus PpSsttQ- is "half-pointed", whereas PpSsttqq is fully pointed. Similarly PpSSTTQ- would be the double image phenotype, whereas PpSSTTqq would be square rump phenotype. The following possible gene combinations are postulated for the five rump phenotypes. The recessive genotypes (ppssttQ- and ppssttqq) are believed to be generally inviable, as will be discussed later.

Phenotype	*Possible gene combinations*
Pointed rump	PPssttQ-, PPssTtQ-, PpssttQ-, PPSsttQ-, PPSsTtQ-, PPssttqq, PPssTtqq, PPssTTqq, Ppssttqq, PpssTtqq, PPSsttqq, PPSsTtqq, PPSsTTqq, PpSsttqq, PpSsTtqq, PPSSttqq, PPSSTtqq.
Half-pointed rump	PpSsttQ-, PPSSttQ-, PPSSTtQ-, PpSSttqq, PpSSTtqq, PPSSTTqq(?)
Square rump	PPssTTQ-, PpssTtQ-, PPSsTTQ-, PpSsTtQ-, ppSsttQ-, PPSSTTQ-, PpSSttQ-, PpSSTtQ-, ppSSttQ-, ppSSTtQ-, PpssTTqq, PpSsTTqq, ppSsttqq, PpSSTTqq, ppSSttqq, ppSSTtqq,
Double image rump	ppSsTtQ-, PpSSTTQ-, ppSSTTQ-, ppSsTtqq, ppSSTTqq.

Tapered rump ....PpssTTQ-, ppssTtQ-, ppssTTQ-, PpSsTTQ-, ppSsTTQ-, ppssTtqq, ppssTTqq, ppSsTTqq.

Results of the preliminary analyses are as follows:—

Pointed (P—) x *pointed* (P—), 10 matings, gave 114 pointed (P—).

Square (S—) *x square* (S—), 1 mating, gave 17 square (S—).

Tapered (T—) x *tapered* (T—), 4 matings, gave 48 tapered (T—).

Pointed (PPsstt) x *tapered* (ppssTT), 3 matings, gave 49 square (PpssTt), indistinguishable from square (ppSStt).

Square (ppSStt) x *tapered* (ppssTT), 1 mating, gave 18 double image (ppSsTt).

Square (ppSStt) x *pointed* (PPsstt); the expected result of all half-pointed (PpSstt) was not observed owing probably to the presence of qq.

The results of crosses where the postulated gene qq is present are given in table I. In some other crosses the results do not conform to the model. The explanation of this is not forthcoming. Perhaps another gene must be postulated, but more likely the odd ratios are caused by temporal fluctuations in epigentic interaction during molt, as will be discussed later. These nonconforming results are as follows:

Pointed x double image: one mating gave 1 half-pointed to 12 square to 2 double image; one mating gave 1 pointed to 7 square; four matings gave 15 pointed to 4 half-pointed to 12 square to 11 double image; two matings gave 26 pointed to 3 half-pointed to 25 square to 2 double image to 2 tapered.

Pointed x *tapered:* two matings gave 32 double image; one mating gave 6 square to 5 double image; one mating gave 20 square to 6 double image; one mating gave 4 square to 4 double image to 1 tapered.

Half-pointed x *square*: two matings gave 4 pointed to 8 half-pointed to 34 square to 4 double image; two matings gave 17 square to 6 double image; one mating gave 5 half-pointed to 28 square; two matings gave 1 pointed to 7 half-pointed to 34 square to 14 double image; two matings gave 4 half-pointed to 13 square to 15 double image to 2 tapered.

Notwithstanding these unexplained results, which may indicate that the proposed model should be modified, the results of the breeding experiments demonstrate the value of such experiments as a means of detecting hidden traits in the various populations. The tapered-rump phenotype, for example, is found only along the present coastline (Fig. 5, T) and the systematic studies suggested that it was probably of recent mutational origin. But a mated pair of *albifrons* from De Funiak Springs produced 2 double image rumps in 12 sibs, and as the arguments against gene flow inland from the coast (see above) are applicable here, we must conclude that gene T is of much older origin and is possibly present throughout the species. The peculiar geographic interpolation of *allophrys* (pointed and square rumps) between *leucocephalus* (tapered rump) and *peninsularis* (square and tapered rumps) is also explained in these experiments by the high frequency of P in the *allophrys* population.

Table 1. COMPARISON OF EXPECTED WITH OBSERVED FREQUENCIES OF OFFSPRING RESULTING FROM MATINGS OF KNOWN GENOTYPES.

MATINGS (number)	EXPECTED					OBSERVED				
	Pointed	Half-pointed	Square	Double-image	Tapered	Po	H-p	Sq	D-i	Ta
Pointed x pointed										
PPSSttqq x PpssttQQ (1)	1PPSsttQq	1 PpSsttQq	-	-	-	29	31	-	-	-
PPSsTtQQ x PPSSttqq (2)	1 PPSsttQq	1 PPSSTtQq	-	-	-					
PPssttQQ x PpSsttqq (1)	1 PPSsttQq 1 PPssttQq 1 PpssttQq	1 PpSsttQq	-	-	-	14	6	-	-	-
Pointed x half-pointed										
PpssttQQ x PpSSttqq (7)	1 PPSsttQq	2 PpSsttQq	1 ppSsttQq	-	-	40	78	36	-	-
PPSsttqq x PPSSttQq (2)	1 PPSsttQq 2 PPS-ttqq	1 PPSSttQq	-	-	-	23	7	-	-	-
PPSSttqq x PPSSttQQ (4)	-	1 PPSSttQq	-	-	-	-	38	-	-	-
PPssttQ- x PPSSttQ- (2)	1 PPSsttQ-	-	-	-	-	26	-	-	-	-
PPSsttQ- x PPSSttQ- (8)	1 PPSsttQ-	1 PPSSttQ-	-	-	-	74	76	-	-	-
PpssttQ- x PpSsttQ- (3)	1 PPSsttQ- 1 PPssttQ- 2 PpssttQ-	2 PpSsttQ-	1 ppSsttQ- *	-	-	22	14	11	-	-
Pointed x square										
PPSSTtqq x ppSSTtQQ (1)	-	-	1 PpSSttQq 2 PpSSTtQq	1 PpSSTTQq	-	-	-	10	2	-
PpSsttqq x ppSsttQq (4)	1 PpssttQq 1 Ppssttqq 2 PpSsttqq	2 PpSsttQq 1 PpSSttqq	1 PpSSttQq 1 ppSSttQq 1 ppSSttqq 2 ppSsttQq 2 ppSsttqq *	-	-	32	26	51	-	-
PPSsttqq x ppSsttQQ (2)	1 PpssttQq	2 PpSsttQq	1 PpSSttQq	-	-	6	16	8	-	-
PPssTtqq x ppSSTtQq (1)	1 PpSsttqq	2 PpSsTtqq 1 PpSsttQq	2 PpSsTtQq 1 PpSsTTqq	-	1 PpSsTTQq	2	4	4	-	1
PPSsTtqq x ppSSTtQq (1)	1 PpSsttqq	1 PpSsttQq 2 PpSSTtqq 2 PpSsTtqq 1 PpSSttqq 1 PPSSTTqq	1 PpSSTTQq 2 PpSSTtQq 2 PpSsTtQq 1 PpSSttQq 1 PpSsTTqq	-	1 PpSsTTQq	4	23	24	-	2
Pointed x double image										
PPSSttqq x ppSSTTQq (2)	-	1 PpSSTtqq	1 PpSSTtQq	-	-	-	14	19	-	-
PPSSttqq x ppSSTTQQ (1)	-	-	1 PpSSTtQq	-	-	-	-	6	-	-

MATINGS (number)	EXPECTED					OBSERVED				
	Pointed	Half-pointed	Square	Double-image	Tapered	Po	H-p	Sq	D-i	Ta
Pointed x tapered										
PPSSttqq x ppssTtQQ (1)	-	1 PpSsttQq	1 PpSsTtQq	-	-	-	4	6	-	-
Half-pointed x half-pointed										
PPSSttQq x PpSSttqq (3)	1 PPSSttqq	1 PPSSttQq 1 PpSSttqq	1 PpSSttQq	-	-	21	46	24	-	-
PPSSttQq x PPSSttQq (1)	1 PPSSttqq	3 PPSSttQ-	-	-	-	3	7	-	-	-
PPSSttQ- x PPSSttQ- (4)	-	1 PPSSttQ-	-	-	-	-	49	-	-	-
PpSsttQ- x PpSsttQ- (1)	2 PPSsttQ- 1 PPssttQ- 2 PpssttQ-	1 PPSSttQ- 4 PpSsttQ-	2 PpSSttQ- 1 ppSSttQ- 2 ppSsttQ- *		-	5	3	4	-	-
Half-pointed x square										
PPSSttQ- x PpSSttQ- (4)	-	1 PPSSttQ-	1 PpSSttQ-	-	-	-	52	56	-	-
Half-pointed x tapered										
PPSSttQ- x ppssTTQ- (2)	-	-	1 PpSsTtQ-	-	-	-	-	15	-	-
PPSSTtQ- x ppssTTQ- (1)	-	-	1 PpSsTtQ-	1 PpSsTTQ-	-	-	-	7	5	-
Square x square										
PpSSttQ- x PpSSttQ- (1)	-	1 PPSSttQ-	2 PpSSttQ- 1 ppSSttQ-	-	-	-	4	10	-	-
ppSSTtQ- x ppSSTtQ- (1)	-	-	2 ppSSTtQ- 1 ppSSttQ-	1 ppSSTTQ-	-	-	-	14	5	-
Square x double image										
ppSSTtQ- x ppSSTTQ- (3)	-	-	1 ppSSTtQ-	1 ppSSTTQ-	-	-	-	31	28	-
PpSSTtQ- x PpSSTTQ- (1)	-	1 PPSSTtQ-	1 PPSSTTQ- 2 PpSSTtQ- 1 ppSSTtQ-	2 PpSSTTQ- 1 ppSSTTQ-	-	-	2	7	7	-
Double image x tapered										
ppSSTTQ- x ppSsTTQ- (3)	-	-	-	1 ppSSTTQ-	1 ppSsTTQ-	-	-	-	33	31
ppSSTTQ- x ppssTTQ- (2)	-	-	-	-	1 ppSsTTQ-	-	-	-	-	22
ppSsTtQ- x ppssTtQ- (1)	-	-	1 ppSsttQ-	2 ppSsTtQ-	1 ppSsTTQ- 1 ppssTTQ- 2 ppssTtQ-*	-	-	2	5	8

* The triple recessive (ppsstt--) is believed to be usually inviable - see text.

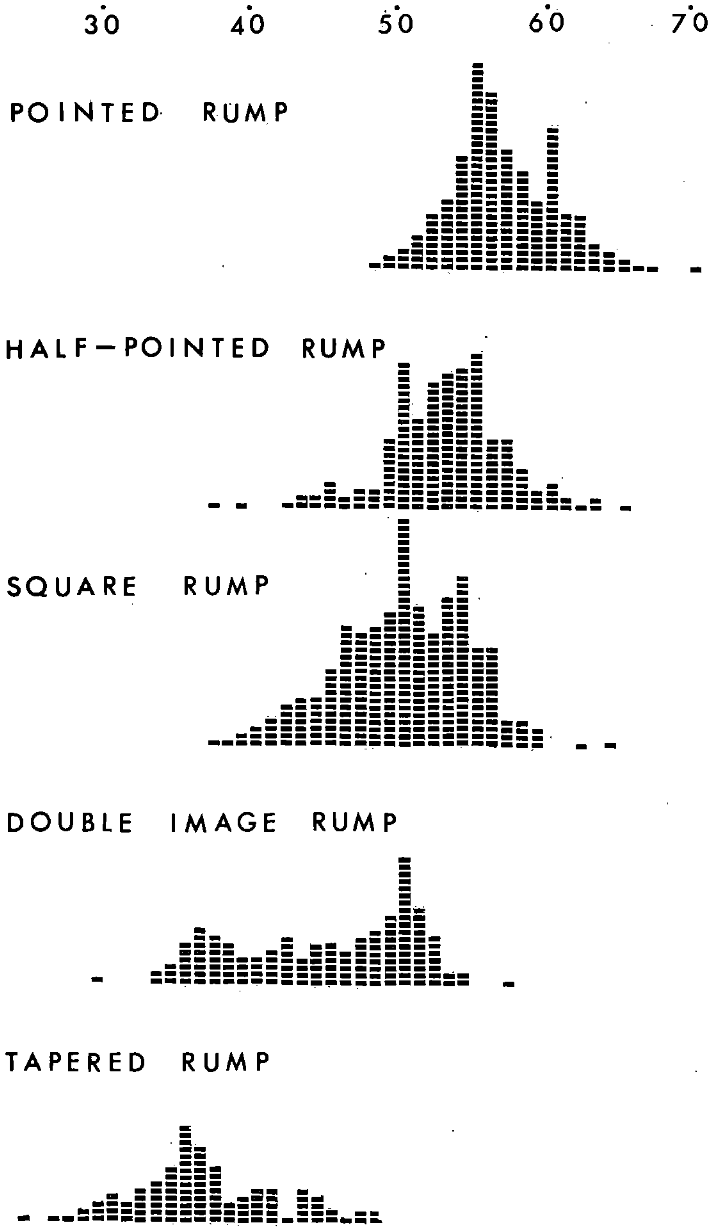

FIGURE 6. Width of hair-tip dorsal pigment in relation to rump patterns. To neutralize differences in stretching the skins, the measurements are expressed as percentages of total girth. Each solid rectangle represents two specimens. The skins were classified according to visible phenotypes, but many were probably genotypically impure. Square rump includes both genotypes S- and P-T-.

WIDTH OF DORSAL HAIR-TIP PIGMENT

As measured on the flat skins and expressed as percentages of total girth to compensate for unequal stretching in the skins, width of dorsal pigment is seen to be related to the three rump pattern traits (Fig. 6). This suggests that the action of the three postulated genes, P, S, and T, extends forward as far as the neck. When dorsal pigment width is plotted according to populations rather than by rump patterns (Fig. 7), subspecies *rhoadsi, sumneri,* and *allophrys* morph 1 agree fairly closely with *polionotus* and *subgriseus.* These populations (with the

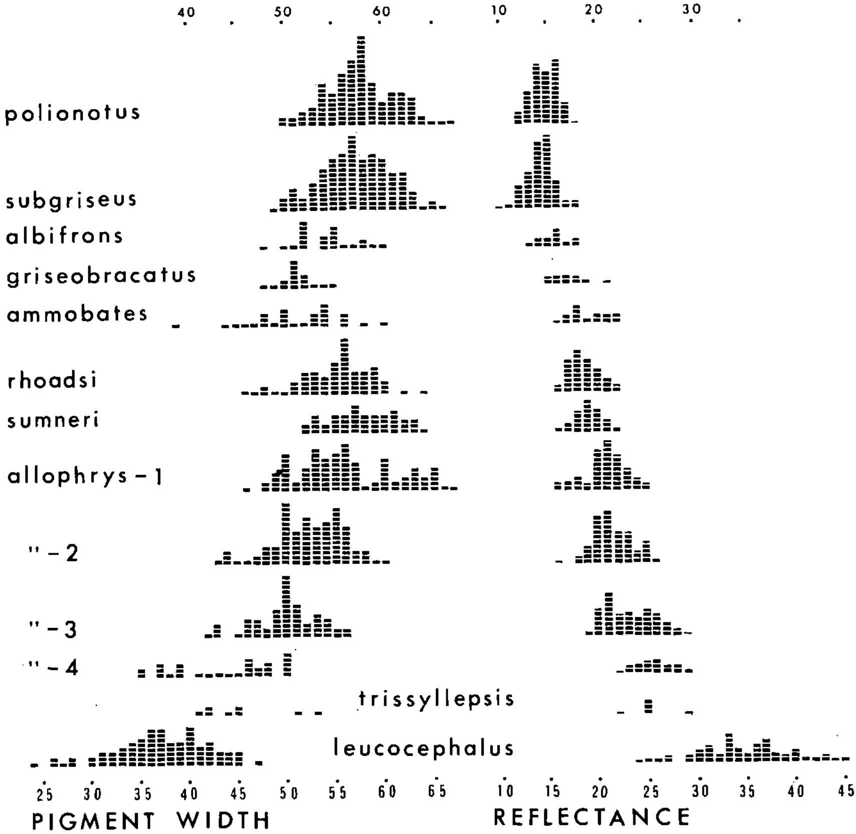

FIGURE 7. Hair-tip pigment width (left) and reflectance (paleness) in Gulf Coast subspecies. Pigment width is expressed as a percentage of total girth in the midriff zone; each solid rectangle represents one specimen. The four morphs of *allophrys* are plotted separately. Reflectance measurements were taken midway between the dorsal stripe and the outer pigment margin in the midriff zone; each solid rectangle represents two specimens.

exception of morphs 2 and 3 of *sumneri*) have pointed rump patterns. Subspecies *albifrons, griseobracatus, ammobates,* and morphs 2 and 3 of *allophrys* (in which square rump pattern predominates) all have slightly narrower dorsal pigment width. Morph 4 of *allophrys* approaches the narrower width of *leucocephalus,* and here the results of the breeding experiments show a fairly high frequency of gene T hidden in *allophrys* morph 4. Similarly, in *trissyllepsis,* where about half the specimens examined (museum skins as well as the flat skins measured) have the double image rump pattern, the dorsal pigment width averages somewhere within the lower range of *leucocephalus.*

Reflectance (paleness) also seems related to dorsal pigment width (Fig. 7). Thus the three genes act to reduce body pigment both in intensity and extensity. To some extent this conclusion concurs with Sumner's (1930) findings, but not in respect to head patterns, where other genes appear to be involved. The trend toward paleness and reduced body hair-tip pigment area in the coastal races seems, therefore, to be correlated with the presence and frequency of genes S and T (visible or hidden) in these populations.

A very puzzling feature of these hair-tip body patterns is the occurrence of occasional specimens having different width of dorsal pigment in different zones (Fig. 8). Specimen RSR 1570, for example, has wider pigment in the midriff (M) and iliac (I) zones than in the rump (R) and scapular (S) regions. Specimen LPP 530* is rather similar, but has a double image rump instead of the pointed rump of 1570. Specimen ALL 372 shows a narrow neck (N) zone combined with half-pointed rump, whereas LPS 158 has a wide neck zone and tapered rump. These zonal peculiarities (which appear occasionally in wild specimens as well as in laboratory-bred mice) were believed at first to indicate separate gene control for the rump area, but a more probable explanation will be discussed after similar zonal peculiarities in basal-hair pigment patterns have been described.

With this tentative establishment of identity between body pigment widths and the three rump patterns, consideration may now be given to the recessive phenotype for all three rump traits. This, as stated in the footnote to Table I, is believed to be usually inviable at, or shortly after birth. According to the proposed model, this triple recessive condition was to be expected in four of the crosses made,

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*Letters in front of specimen numbers indicate stocks, thus LPP is a *leucocephalus* x *polionotus* F1 backcrossed to a *polionotus;* LPS is a backcross to *subgriseus.* Letter R stands for *rhoadsi* and ALL distinguishes *allophrys* from *albifrons* (ALB) and *ammobates* (AM), etc.

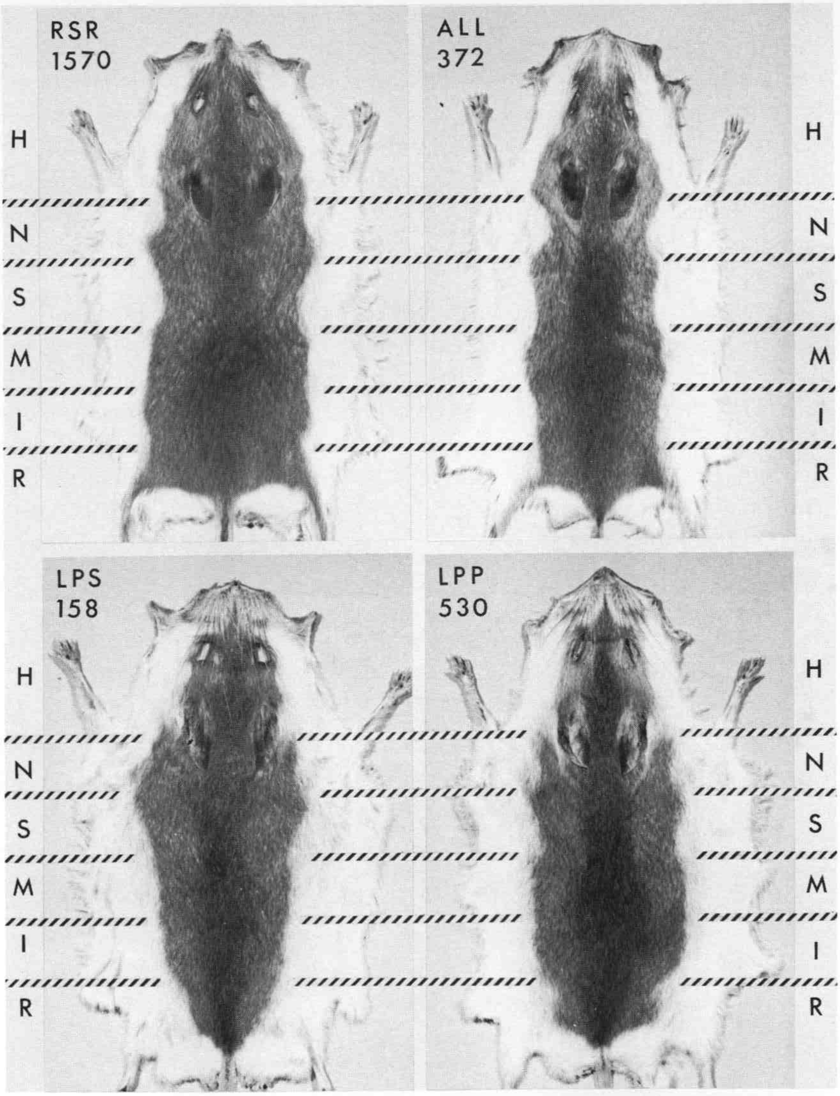

FIGURE 8. Zonal variation in hair-tip dorsal pigment. Head (H), neck (N), scapular (S), midriff (M), iliac (I) and rump (R).

and in two of these the numbers of progeny were large enough to justify this assumption. Natal and/or post-natal deaths did, in fact, occur in all these matings, but since similar mortality occurs in other litters, no conclusions can be drawn from this. In one case, however, (one of the half-pointed x half-pointed crosses designated by an asterisk in Table I) a partly grown specimen was recovered that is believed to represent this condition. This was a young *allophrys* (Fig. 9, number 1927), undergoing postjuvenal molt, which was found one morning on the floor of its cage badly mauled and dying. It had been noted earlier that this animal was constantly scratching its rump and biting its tail. A sib of a previous litter had been similiarly mauled and killed, but at that time the death was attributed merely to fighting and the badly mauled skin was not preserved, nor was the pigment pattern minutely examined.

The head pattern of *allophrys* 1927 is normal, but the dorso-lateral body pigment is restricted, irregular, and "blotchy". Of the 16 progeny born of this mating, 12 were normal, 2 died soon after birth, and 2 had skin irritation during post-juvenal molt and died, presumably from attacks by cage-mates. The parents were a second generation of sib-matings from two wild-caught mice taken in adjacent traps on the same night. These could have been related, and so number 1927 had been inbred for two or possibly more generations. Its appearance suggests the absences of a delineating factor to determine where pigment is to be laid down. Such a condition might conceivably result in skin irritation and other deleterious effects at the time of molt.

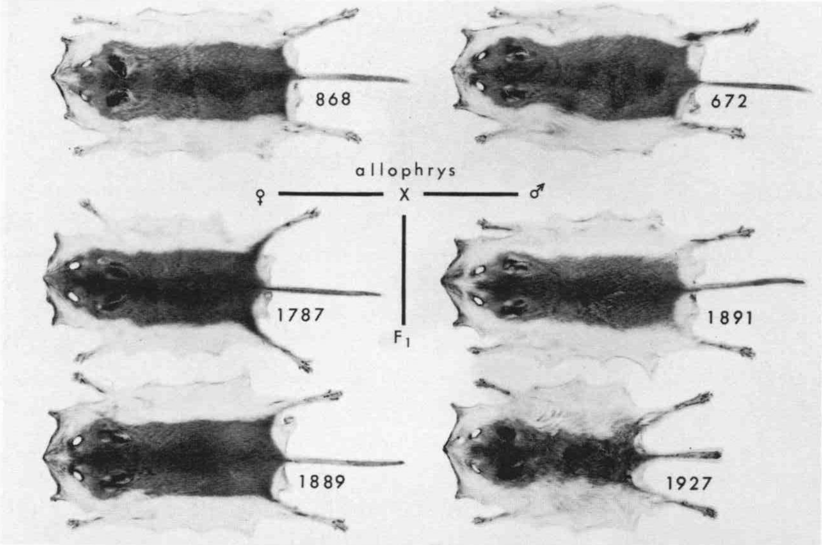

FIGURE 9. Inbred *allophrys* mating with defective pelage pattern (1927), believed to be recessive for body pattern-delineating genes.

HAIR-BASE PATTERNS.

Genetic control of basal hair melanin pigment patterns appears to be distinct from that of the yellow-orange pigments in the hair tips. Close study of the basal patterns is rendered difficult, not only by

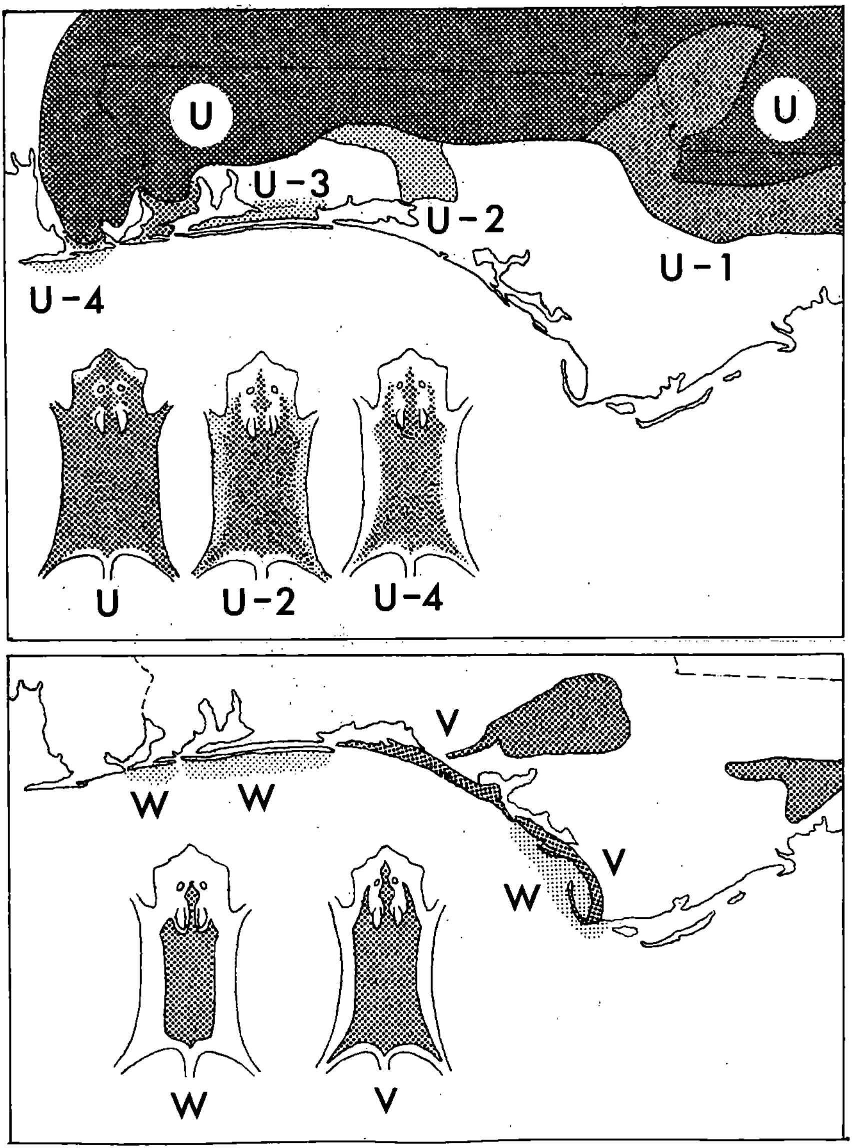

FIGURE 10. Hair-base pigment patterns and their primary distribution.

the fact that they are largely hidden by the hair-tip patterns, but also because of an apparent antagonistic interaction between at least two of the genes. Three general patterns (Fig. 10, U, V, W) can be distinguished, but the case is further confused by the fact that U ranges through at least five grades, from dark venter (U) to white venter (U-4). The latter is nearly, or completely, indistinguishable from pat-

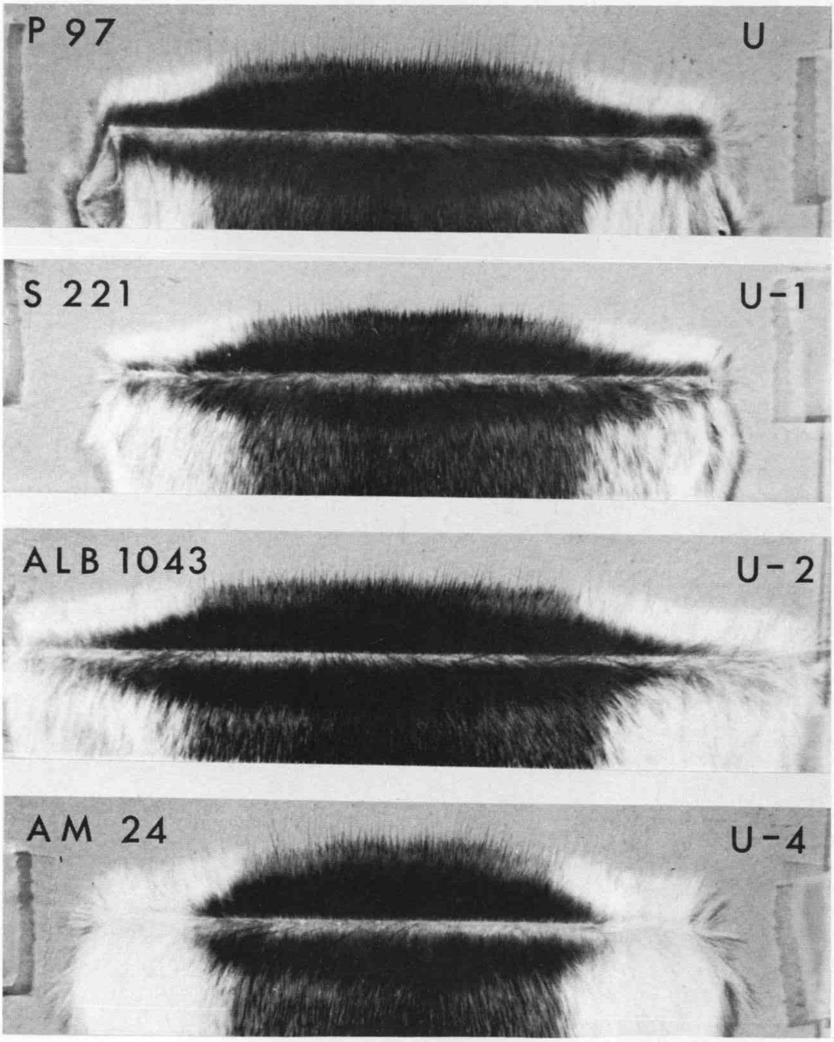

FIGURE 11. Hair-base pigment restriction in the U to U-4 series. Skins folded to show pelage pattern contour.

tern V. Thus, the white venter pattern of *ammobates* is genetically different from that of *rhoadsi, sumneri,* and *allophrys.* When crossed with *polionotus* (pattern U) or *subgriseus* (U-1), *ammobates* (U-4) interacts in a quantitative type of inheritance whereas *rhoadsi* (V) exhibits disharmonious symptoms of pelage development when crossed with individuals of the U series.

The gradient of reduction of ventral hair-base pigment is illustrated in figure 11. These photographs were obtained by folding the skins transversely in the mid-body region and pressing the folded area between two 3x1 inch microscope slides held together with plastic adhesive tape. Because this process mars the specimen to some extent (c.f. Fig. 19) *griseobracatus* (U-3) is not included, as all available skins were borrowed from other institutions. The V pattern is very similar to pattern U-4, but the outer margin (ventrad) tapers and fades out in the latter whereas in the former it ends more abruptly (c.f. Figs. 11, AM 24 and 12, R211). These differences are so slight, however, that the two cannot always be differentiated visually.

The ventrad margin of pattern W terminates abruptly (Fig. 12, L 249, T 21). Occasional specimens of *allophrys* show a condition where the margin tapers, as in V, but shows also a more abrupt termination of darker pigment superimposed upon it (Fig. 12, ALL 752). This is interpreted as a combination of V and W, which seems to indicate some degree of compatibility. Crosses between *rhoadsi* (pattern V) and *polionotus* or *subgriseus* (pattern series U), on the other hand, usually result in molt disturbances and hair abnormalities in the progeny (Fig. 13). Specimen RP 126 is a typical case in which a line corresponding to the margin of pattern V can be seen. In the folded skin along line A the antagonistic interaction of U and V is seen to produce weak hair development. This often occurs as a "fault line" with complete suppression of hair growth (Fig. 16).

Specimen RPR 1020 illustrates a less pronounced case of molt abnormality confined chiefly to the neck and scapular regions (c.f. fold-lines B and C). This indicates a zonal type of control comparable with that of the hair-tip body patterns. A pronounced fault line is seen in the neck zone in specimen RS 586 (Fig. 14), whose pelage is otherwise fairly normal. A similar fault line seen less distinctly in ALL 594 seems to indicate the presence of the U series genes in occasional individuals of this pure stock. RPR 388 shows a very pronounced molt disturbance in the neck and scapular zones, whereas in RPR 517 the abnormal pelage is confined chiefly to the scapular and midriff zones. The transverse line between the midriff and iliac zones is a molt line, the posterior pelage being juvenal.

That these fault lines and zonal differences of pelage abnormalities are not related to such lines of active molt is shown in RPR 388,

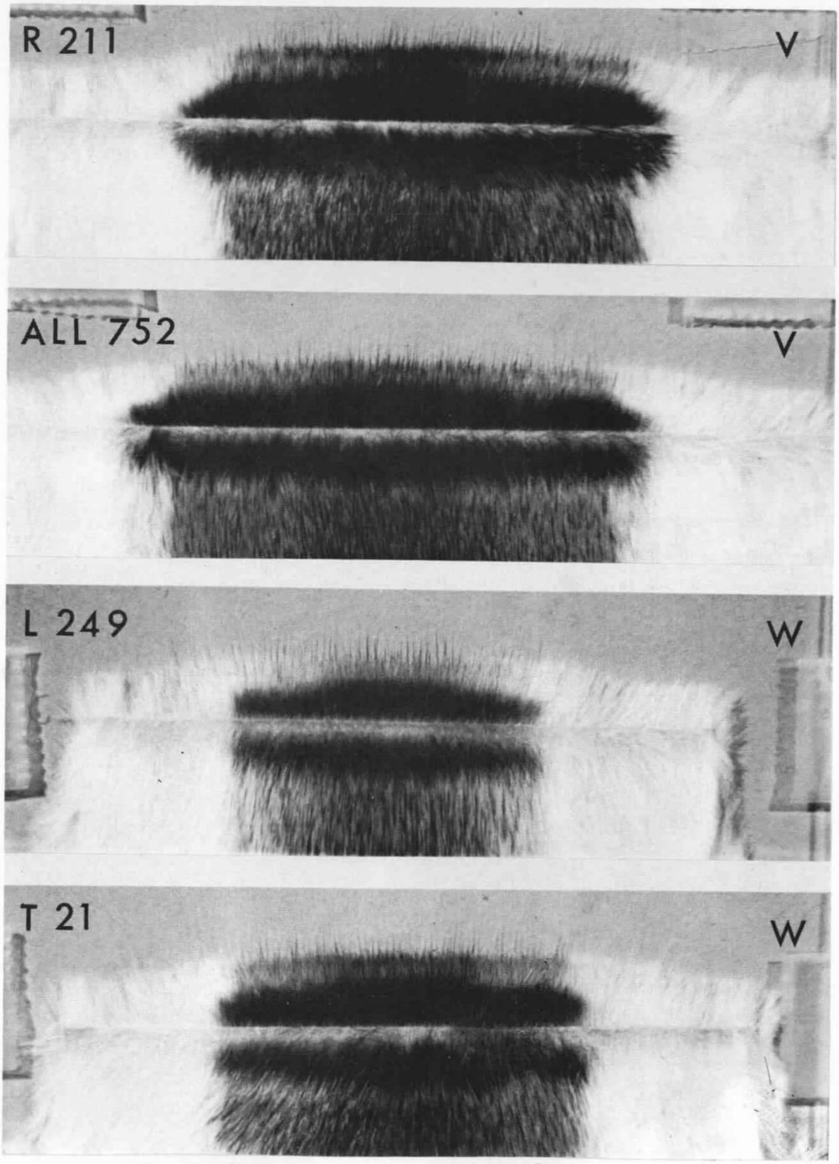

FIGURE 12. Hair-base pigment patterns V and W.

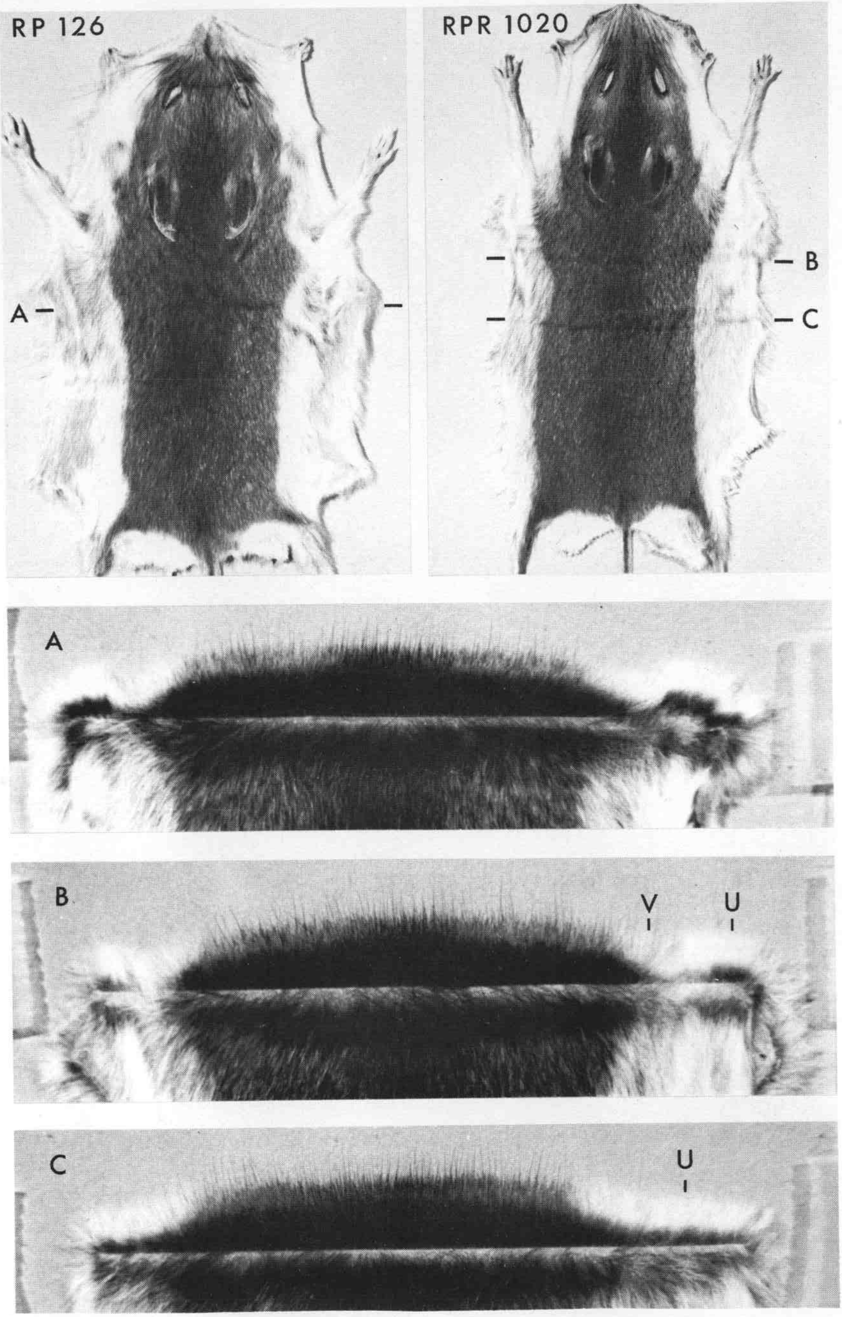

FIGURE 13. Disharmonious interaction of hair-base pattern traits U and V in *rhoadsi* x *polionotus* crosses.

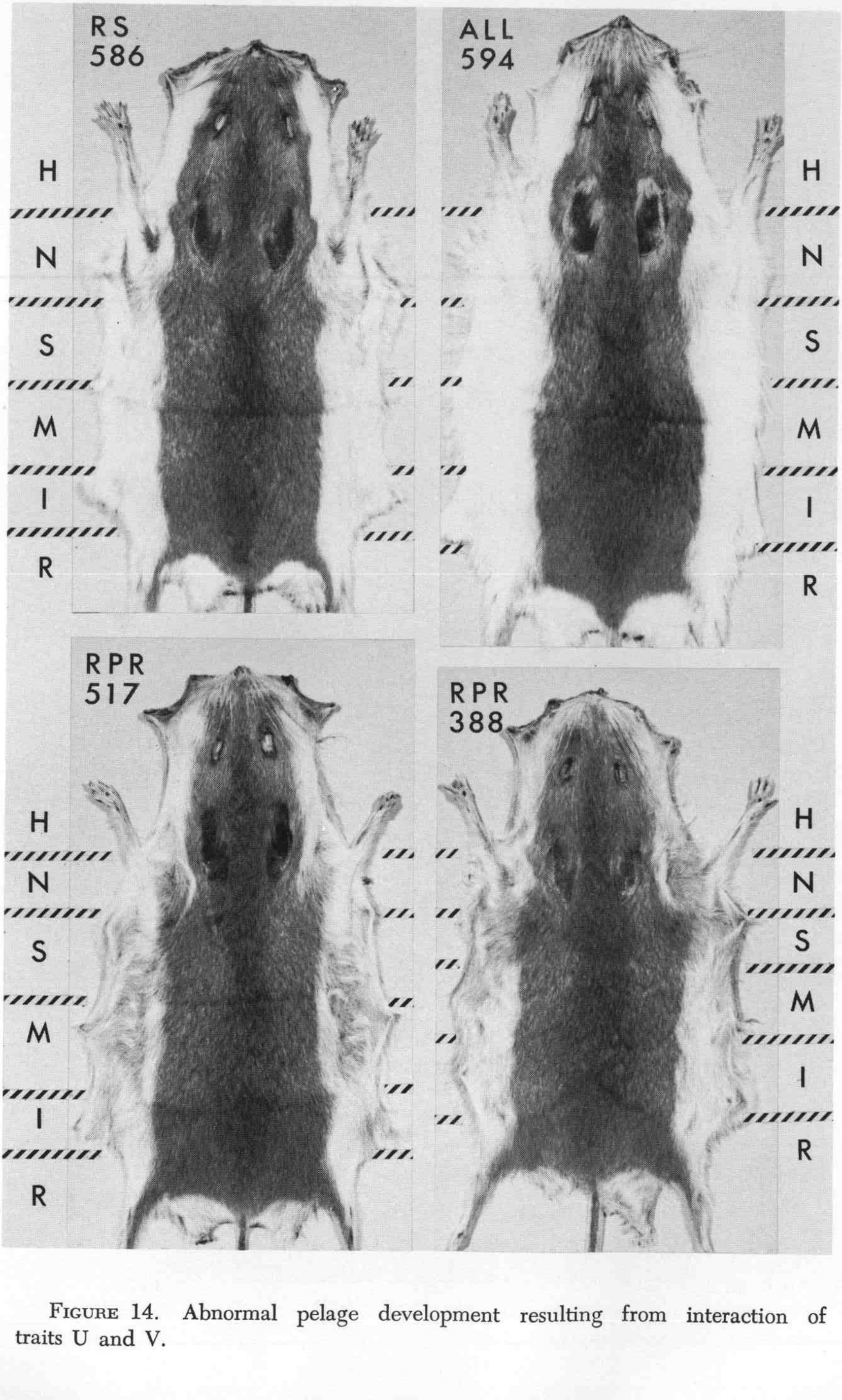

FIGURE 14. Abnormal pelage development resulting from interaction of traits U and V.

which was molting when killed at age 54 days. Normally at that age postjuvenal molt is completed, as was the case for all the sibs that showed no pelage abnormalities. A crescent-shaped area of active molt, as indicated by a dark area on the internal side of the skin, is seen in the iliac-rump area (Fig. 15, left). Two smaller molt areas occur in the neck region, but these are paler and appear to be drying up. Traces of three molt areas are only just visible in the head area; they appear to be last remnants of former molt activity.

Anterior to the crescent-shaped area of active molt the hair is developed normally up through the scapular zone. Beyond this it is defective with patches of normal-appearing postjuvenal pelage interspersed with patches of juvenal hair. The rump shows typical juvenal pelage. No correlation is to be seen between this molt pattern and the fault lines, some of which occur within the area of normal hair development while others cut across its boundary. In the neck zone

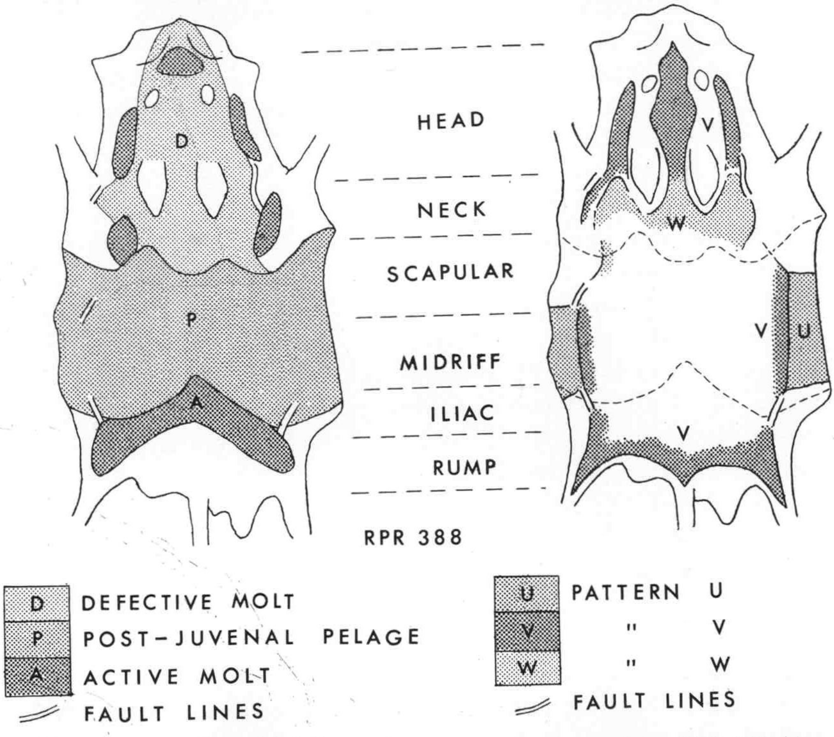

Figure 15. Molt and hair-base pigment patterns in specimen RPR 388 (See photograph, figure 14). Note the presence of traits U, V, and W in different body zones.

two fault lines coincide with the boundary between the dorsal area of defective molt and the ventral area which is almost completely devoid of hair.

These lines coincide also with the margin of the V-pattern, as is the case with the fault lines in the body area as well (Fig. 15, right). A further noteworthy point is that fault lines occur only between adjacent zones with differing interactions. Thus, in the midriff zone both phenotypes U and V occur together, and U spreads slightly beyond the midriff zone and into the iliac area where the fault lines occur. In the neck zone pattern W appears and spreads somewhat into the scapular zone on the right side. Where it meets the V pattern lateral to the ear, a fault line occurs.

The presence of pattern W in this stock can be explained by the fact that the *polionotus* involved came from the area southwest of Pensacola where a temporary sand bar bridged the lagoon that isolates *trissyllepsis* from the mainland *polionotus* population briefly about 1882 (see list of maps, p. ......), and it is interesting to find evidence of the lingering effects of this gene exchange.

The appearance of such overlaps between one zone and another can be seen in many other skins, but demonstrating it photographically is not easy. In specimen RPR 517 (Fig. 14) the white-tipped hairs within the V pattern are weakly developed in the scapular and midriff zones, but hair-development is strong in the area of overlap and shows up as two more distinctly white patches on either side of the hair-tip pigment pattern.

The above examples of molt irregularities and pelage deficiencies are all rather extreme cases that would probably not survive under natural conditions. But instances of fault lines and other minor pelage abnormalities can be found in wild-caught mice, especially in the areas where the ranges of *subgriseus* and *rhoadsi* approach one another. Specimens taken in the Ocala National Forest, for example, frequently show fault lines (Fig. 16, S 257), and in the area to the south where the ranges of *subgriseus* and *rhoadsi* meet such cases are even more frequent.

In this area where *rhoadsi* population K3 (Fig. 3) interbreeds with *subgriseus* to the north, some unusual features are exhibited. Instead of a blending type of intergradation, as is usually the case where two subspecies meet, the mice here tend to be either white-bellied or gray-bellied, and the proportions change from north to south. This gives the appearance of a more or less clear-cut segregation and no specimens with marked pelage abnormalities have been found.

Apparently the very abnormal specimens are being eliminated by selection, and thus a partial barrier to gene flow is in effect. No such barrier was anticipated when the laboratory crosses were planned, and no special effort was made to cross these two subspecies, but the records show that in seven attempts, only one mating was successful.

This mating lasted 15 weeks and though it should have had five litters in that time, it produced only one litter of four. This raises the possibility that some degree of infertility, or pre-natal inviability, exists between these two subspecies. It may be noted that Watson (1942) recorded greatly reduced fertility in crosses between *rhoadsi* and four subspecies of *P. maniculatus*, all of which are gray-bellied, presumably pattern U. In my laboratory experiments however, I encountered no special difficulty in crossing *rhoadsi* with a *polionotus* stock from the Pensacola area, but this is not pure *polionotus*, as noted above, and as infertility was not being tested, only four pairings were made, two of which were successful.

Subspecies *allophrys*, which is believed to have evolved from a *rhoadsi*-like ancestor (see later discussion) also seems to show reduced interfertility with other subspecies. As the laboratory experiments

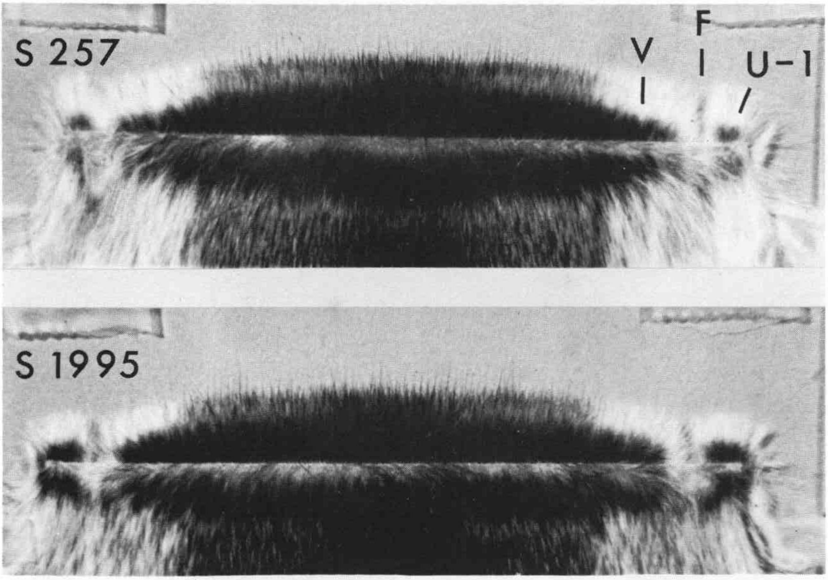

FIGURE 16. Fault lines (F) of hair development in *subgriseus* pure stocks, indicating antagonistic interaction of traits U-1 and V.

in this study were directed toward analyzing the polymorphism in this *allophrys* stock, relatively few out-crosses to other subspecies were attempted and the results are inconclusive. No breeding stock of *sumneri* was collected, and so no information is available regarding this subspecies, which is also believed to have been derived from a *rhoadsi* stock. Sumner and Blair did not differentiate these forms and so no conclusions can be drawn from their results, except that infertility is not entirely precluded.

Only one mating of *allophrys* x *rhoadsi* was made, which raised two normal litters. Out of seven attempts to mate *allophrys* with *subgriseus* only one was successful, and here only two litters were born in a period long enough to have produced four. All other attempts to outcross this subspecies failed, as follows: *allophrys* x *polionotus*, 2; x *albifrons*, 5; x *leucocephalus*, 11. In the last case two pregnancies at least, occurred but the females (both *allophrys*) died during parturition. In one of these putrification was too advanced for an autopsy, but in the other, which was discovered a short while before death, a putrifying spot was noted on the skin of the right abdominal wall before death. This female had given birth to four young, which were dead when found. Autopsy revealed two more embryos, that in the left uterine horn appearing quite normal. The embryo in the right horn, lying directly below the putrid spot on the skin, was in an advanced state of putrification, and had obviously caused the death of the mother. Two similar cases of parturient mortality occurred in attempts (all unsuccessful) to cross *rhoadsi* with *leucocephalus*.

These results, inconclusive though they are, do seem to point to a partial reproductive barrier between the *rhoadsi*, *sumneri* (?), *allophrys* group on the one hand and the *polionotus*, *subgriseus*, *albifrons*, *leucocephalus* series on the other. Whether this is related to the observed incompatibility of the genes for U and V, in some pleiotropic way or whether it is the result of divergent genotypes that have been isolated since early Pleistocene, is not known. Probably the disharmony between patterns U and V is but one symptom of this dichotomy, which is discussed further below. The "certain amount of reproductive isolation" between *P. polionotus leucocephalus* and *P. maniculatus blandus* Liu (1953) reported cannot be related to this problem in the way that Watson's results appear to be.

EPIGENETIC MOLT INTERACTIONS

The zonal differences in body pigment width described above in both basal and hair-tip patterns are quite puzzling. If, as seems probable, the effects of the genes for rump patterns extend forward to include the body area, then what causes the pigment width to vary from one body zone to another in some specimens? The answer seems to lie in the time lag between beginning and ending of molt. The many examples of delayed and/or arrested molt in the hair-base pigment patterns show that the phenomenon is associated with molt (Figs. 14, 15). Evidently some temporal variance in epigenetic interactions must occur during molt and, as different body areas molt at different times, the effect of one or another gene might be expressed accordingly (Fig. 17). As stated earlier, the interaction of the three postulated hair-tip rump pattern genes appears to be a matter of balance, and so they might conceivably be weighted one way or another from time to time.

Storer, Evans, and Palmer (1944, Fig. 10) describe molt as starting in the lateral midbody region of *Peromyscus maniculatus* and spreading forward and backward along the lateral line first, and then upward to the mid-dorsal region. Collins (1918, Figs. 1, 2 and 3) states that "the new pelage of *P. maniculatus* first appears on the throat near the angle of the jaw, or rarely on the anterior surface of the forelimb along the lateral line." In his diagrams he indicates four regions on which molt proceeds more or less independently, face, occiput, body, and rump. In *P. leucopus,* Gottschang (1956, Fig. 1) indicates molt starting along the lateral line in the iliac region and spreading forward and backward along this line to join with a second focal point in the neck region and a third under the eyes. The mid-dorsal region is indicated as the last to be molted.

Golley, Morgan and Carmon (1966, Fig. 1) show molt patterns of *P. polionotus* at 5-day intervals, the first postjuvenal stage being at 25 days of age. In the present study most of the specimens were killed at about 60 days or more, when normal postjuvenal molt is usually completed, but a limited number were sacrificed at earlier ages to determine molt patterns and sequences. Earliest signs of postjuvenal molt were found in some specimens killed when 23 days old. Here faint traces of pigment deposition on the under surface of the skin are manifest along the dorsal side of the lateral line in the neck and scapular areas (Fig. 17, A). In all the age groups examined the stages of molt progress were rather variable, and the sequence illustrated in Fig. 17 is therefore somewhat of a composite. At 25 days of age some specimens showed patches of dark skin pigmentation in the neck and scapular zones as well as initiation of pigment deposition in the midriff zone (Fig. 17, B), others were more advanced (C). At about this time dark pigment begins to appear also on the ventral side of the lateral line in the neck and scapular zones.

The 25-day stage of Golley *et al.* (1966, Fig. 1) corresponds to a stage between B and C in figure 17. Usually by 30 days first signs of pigment appear in the rump area, and the ventral molt is well under

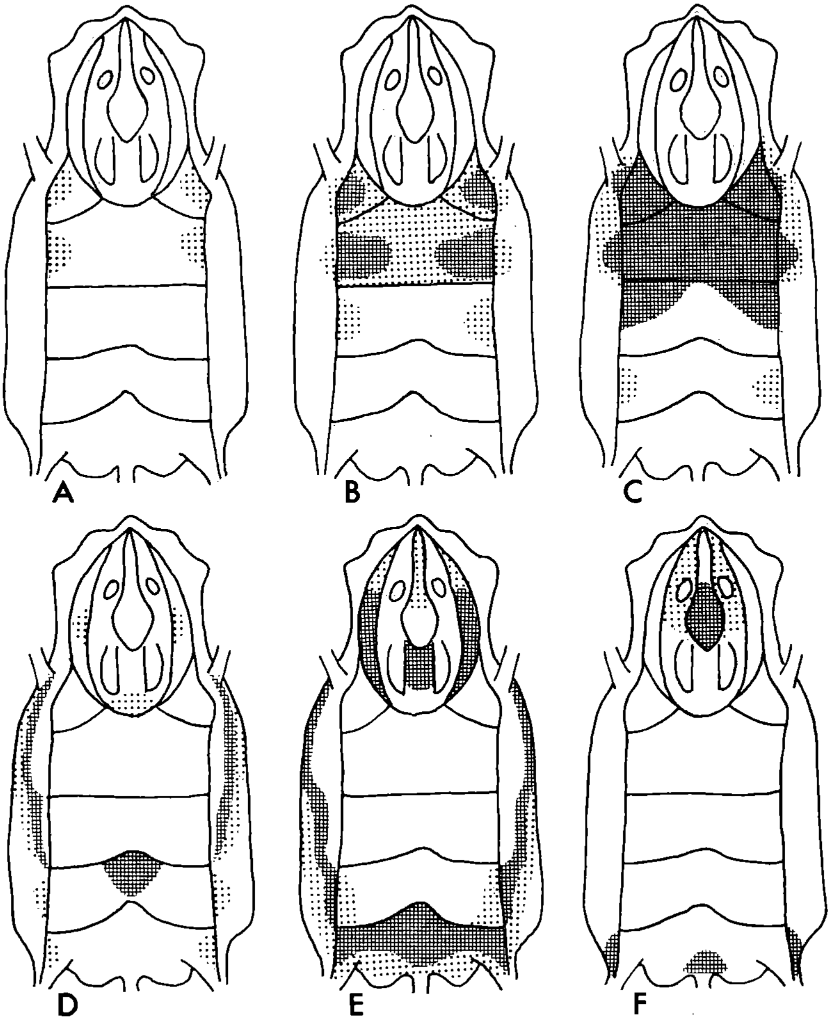

FIGURE 17. Areas of independent molt and molt sequence as indicated by pigment seen on the undersides of the skins. Heavy pigment indicates active molt, light pigment may indicate either beginning or ending of molt. Differentiation of the latter (not shown) was determined by pelage examination.

way in the neck and scapular zones (Fig. 17, D). Head molt also begins at about this age. At 35 days the rump is usually undergoing active molt, as is also the head, and ventral molt is often complete, or nearly so, in the anterior body region (Fig. 17 E). This stage

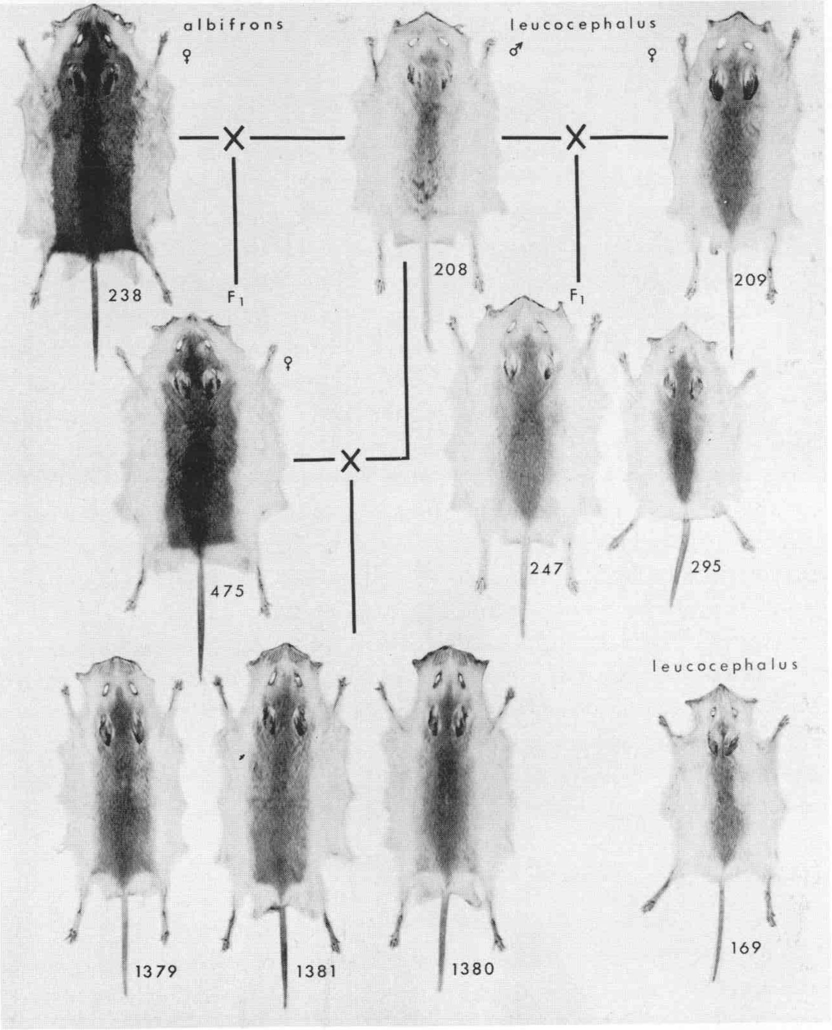

FIGURE 18. Dorsolateral hair-tip pigment suppression in *leucocephalus*, leaving only the mid-dorsal stripe fully pigmented. Specimens 208 (complete suppression), 209 (normal) and 169 (anterior suppression) are wild-caught. Wild-caught animals similar to 295 (posterior suppression) have also been observed. Photograph by Barbara B. Loeffler.

corresponds to the similarly aged stage shown by Golley *et al.* Head molt sequences have not been worked out fully, but in general the two molt regions (occiput and nose) indicated by Collins (1918) correspond to similar areas identified in the present study. A third focal point midway between and slightly ventral to the eyes and ears (Fig. 17, D) is also recognized. This appears to correspond to an arrow shown in figure 1 of Collins (l.c.).

Dorso-lateral Hair-tip Pigment Suppression

In occasional specimens of *leucocephalus* only the mid-dorsal stripe is fully pigmented. In others this pigment suppression is limited to one or more of the body zones (Fig. 18, specimens 208, 295 and 169, and Fig. 19). At first this absence of all three rump phenotypes was thought to signify recessiveness. Male 208, with no dorsolateral hair-tip pigment, was first mated to a fully pigmented female (209) and a litter of six was obtained, two of which had suppressed pigment in the posterior body area (c.f. 295). This male was then mated to a female *albifrons* (Fig. 18 specimen 238) with pointed rump, and five square-rumped Fl were obtained. This is the expectation for a cross of pointed x tapered, and had the male been recessive all the Fl should have had pointed rumps. One of the Fl was then backcrossed to her father. Two litters were born, but only one (of four) survived: one had a half-pointed rump (1379), two were square-rumped and one was a double image phenotype (1380).

As no other successful matings were achieved, no conclusions can be drawn. However the existence of these individuals with reduced pigment is worth noting, for as suggested earlier, they may have some survival advantage. Examination of hair profiles on folded skins (Fig. 19, A) shows that hair-tip pigment is suppressed or diluted rather than entirely eliminated in these cases.

Hair-tip Head Patterns

The natural head patterns of the various subspecies (Figs. 20 and 21) are not unit characters, but are composed of various combinations and interactions of several unit pattern elements. This can be clearly seen in figure 21, where H combines C and G; I combines C, F and G; and J combines F and G. Closer study reveals some six such unit elements which are shown in Fig. 22. They may be distinguished from the natural patterns by the lettering AE, BE, CE, etc. A and AE largely coincide; the absence of element AE in patterns H, I and J reveals the posterior limit of head pattern genetic control. Pattern G is thus shown to be the absence, or suppression, of all six unit elements.

These unit elements may occur superimposed, one upon the others as in figure 23, specimen RPR 595, which shows element CE as a

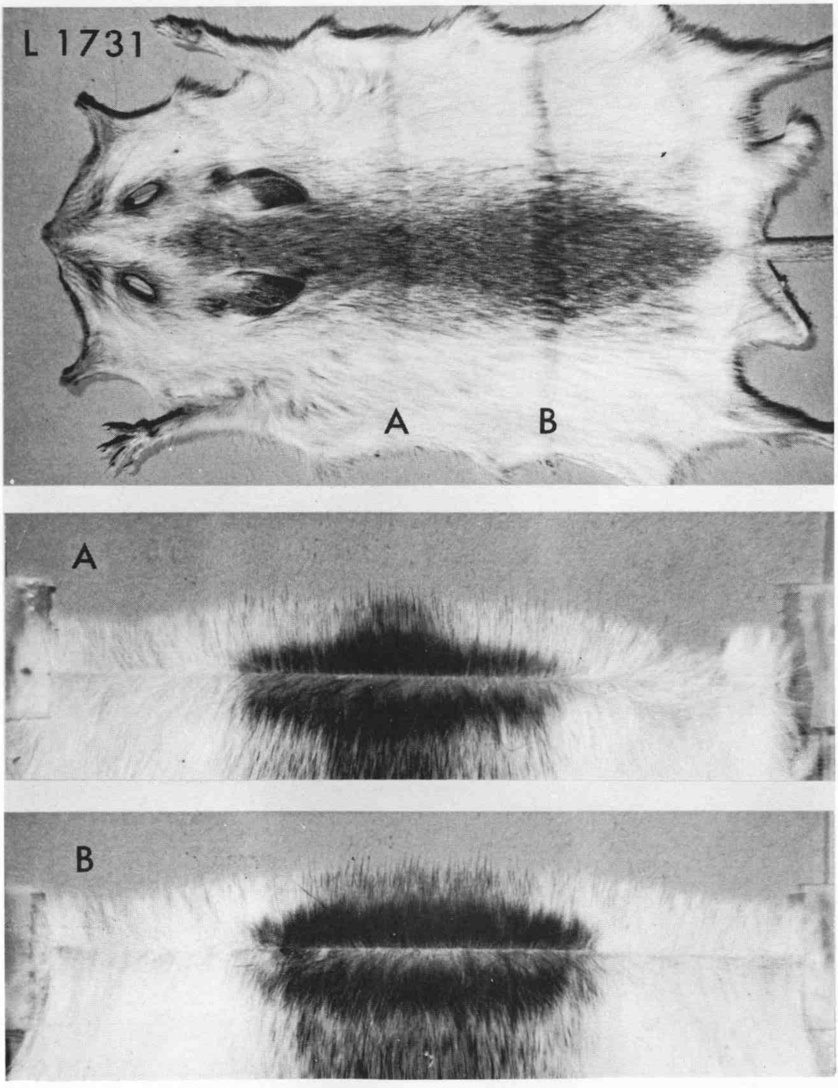

FIGURE 19. Dorsolateral hair-tip pigment suppression in *leucocephalus*. The hair profile along fold line A indicates that pigment is reduced rather than eliminated entirely.

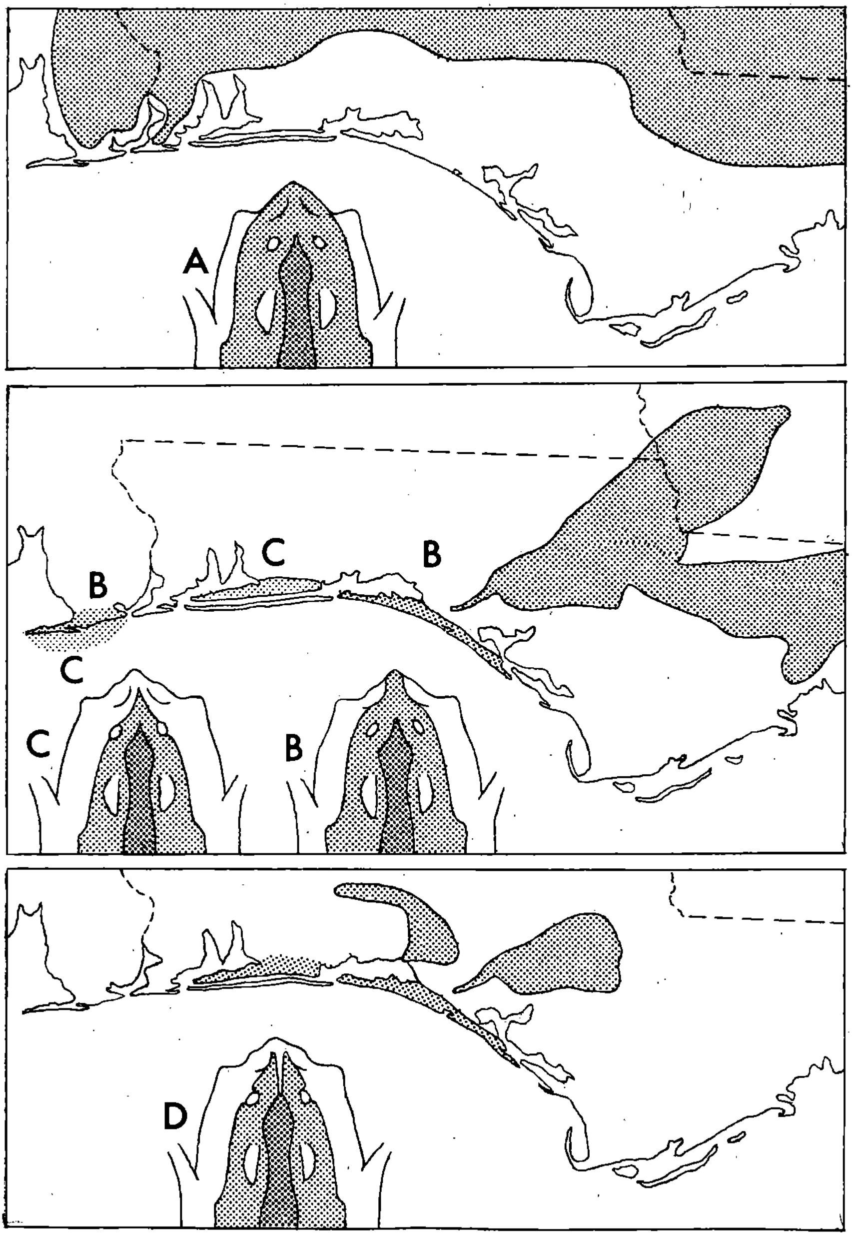

FIGURE 20. Hair-tip head patterns and their primary distribution.

darker area within the area of AE in the nose region. Often they show mosaic interactions, as in RP 134, where pigment extends onto the left labial area (AE) but not the right (BE). The pattern margin between the eyes and ears of this specimen corresponds to element

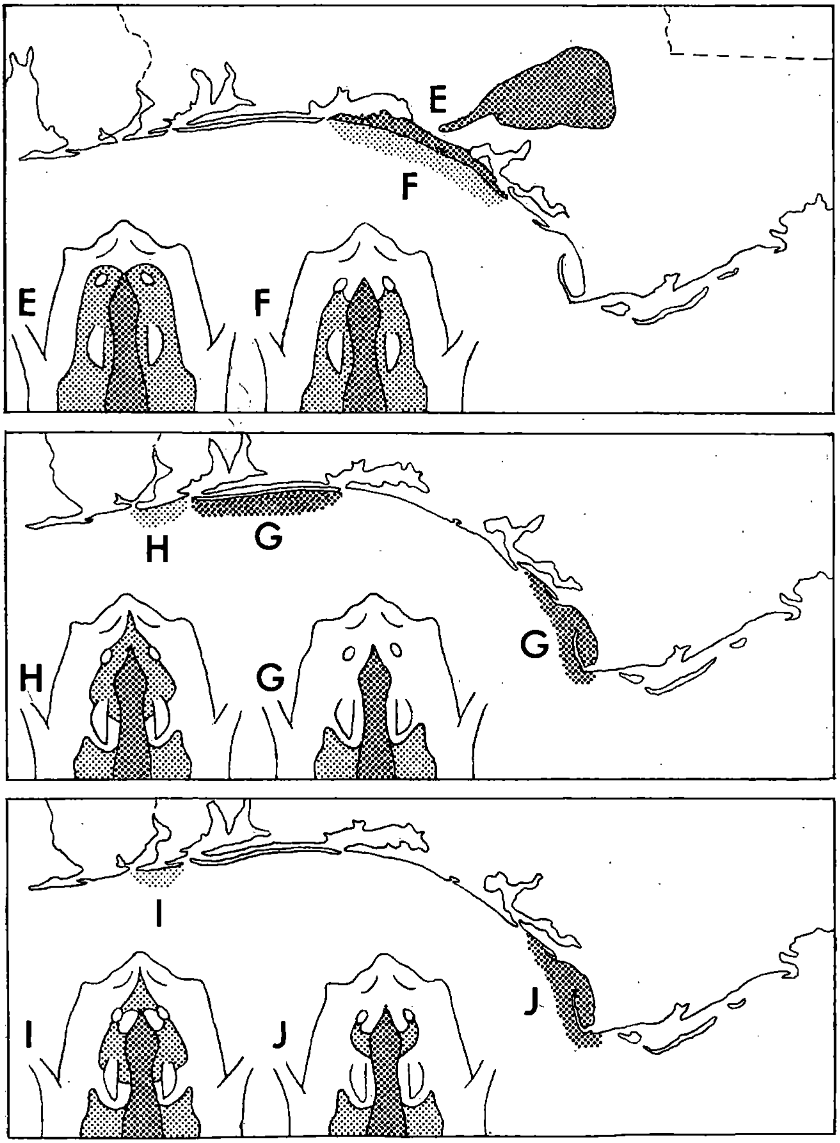

FIGURE 21. Hair-tip head patterns (continued)

CE. Specimen RP 113 shows a mosaic of elements BE and CE, as is seen in the pigment below the left eye (BE), but not the right (CE). These examples are laboratory crosses chosen for photographic clarity, but similar instances can be found among wild-caught specimens.

Parenthetically the supposed major gene for white-cheek (Blair, 1944) may be discussed at this point. Three of the six unit-elements, CE, DE, and FE are white-cheeked, and pattern G (Fig. 21) also lacks pigment below the eye. Blair started with a mixed stock of *leucocephalus* crossed with what he called "albifrons" (= *allophrys*, *sumneri*, or both). Both the latter carry element DE, and the former also may carry FE. Pattern G of *leucocephalus* seems to be the result of a suppressor gene that conceals the head unit-elements more or less completely, but elements CE, DE and FE can often be detected in this form.

Blair's "*leucocephalus*" stock, obtained from this mixture and selected for "minimum extent of pigmented hairs" must certainly have carried the genes for all these unit elements: indeed, his photograph (Fig. 1) clearly shows the white brow-spots indicative of element FE. The similarity of head pattern between his specimen and the examples of *trissyllepsis* shown here in Fig. 24, A and B is quite apparent. Laboratory crosses indicate this pattern is a combination of elements CE and FE. As all the genes for unit elements without pigment below

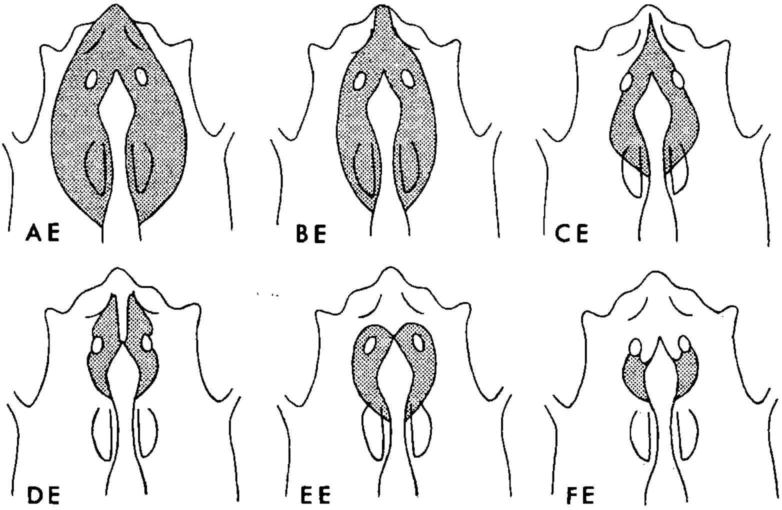

FIGURE 22. Hair-tip head pattern unit elements

the eye were probably present in Blair's stock, it is not surprising that white cheeks showed up as a common denominator in the results of his crosses with *P. maniculatus.*

Once the interactions between these unit headpattern factors are understood, identification of the various phenotype unit elements

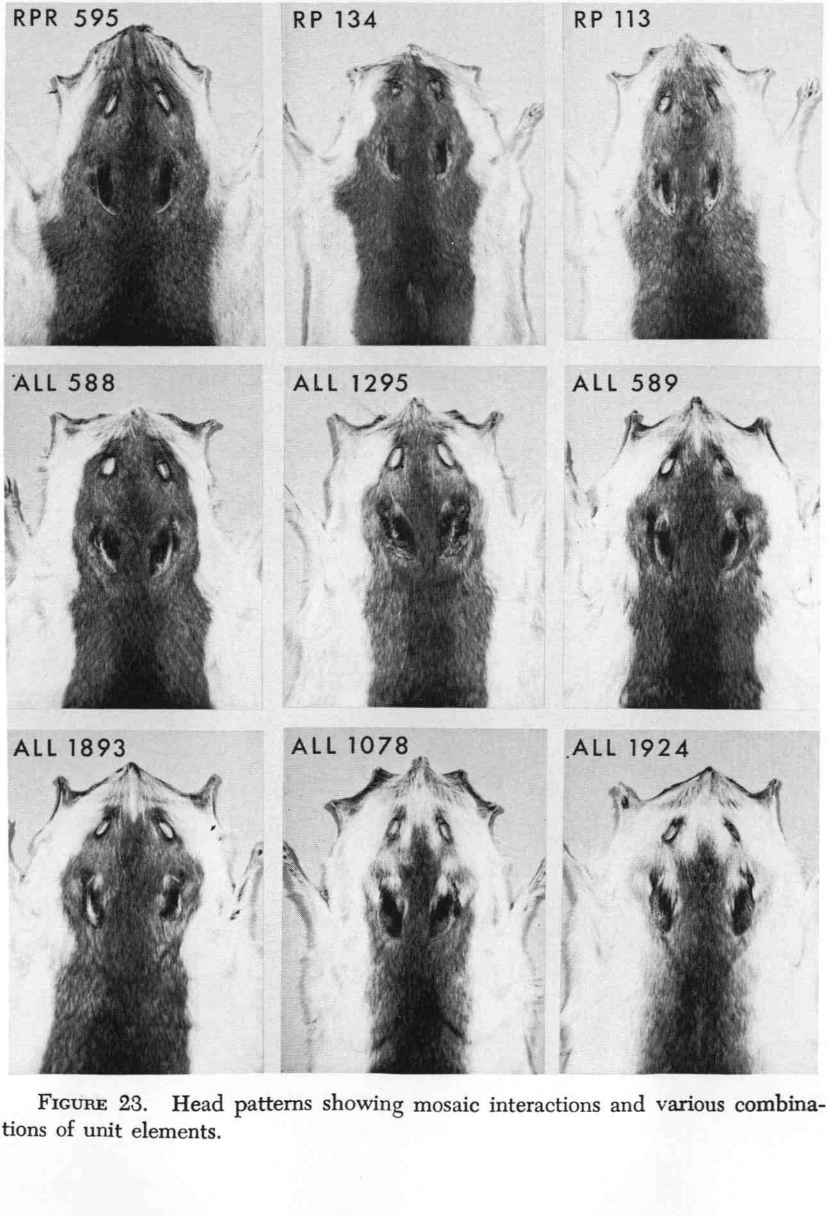

FIGURE 23. Head patterns showing mosaic interactions and various combinations of unit elements.

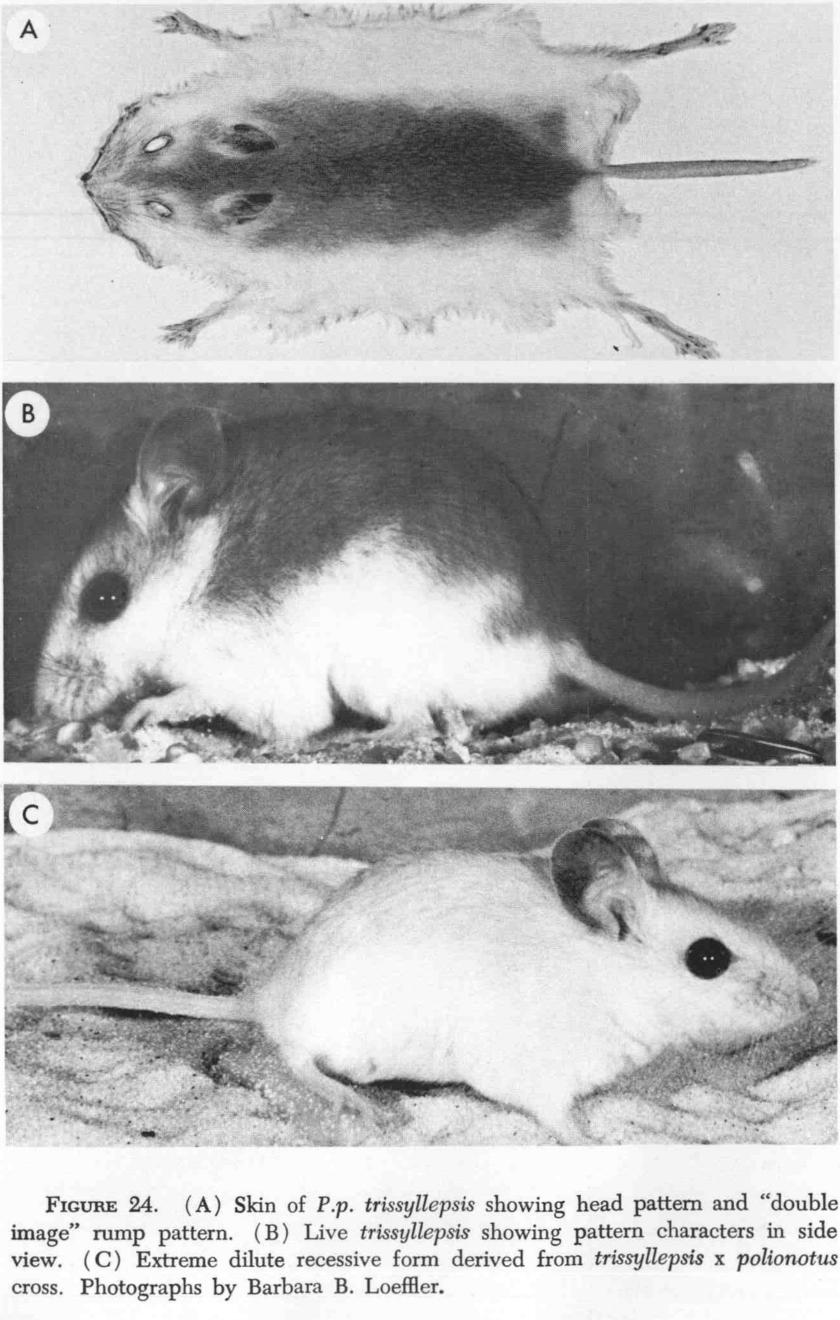

FIGURE 24. (A) Skin of *P.p. trissyllepsis* showing head pattern and "double image" rump pattern. (B) Live *trissyllepsis* showing pattern characters in side view. (C) Extreme dilute recessive form derived from *trissyllepsis* x *polionotus* cross. Photographs by Barbara B. Loeffler.

that comprise the total head pattern can usually be made. Specimen ALL 588 (Fig. 23), for instance, is element BE with AE showing only in the area posterior to the ears. Even when a pattern element is largely suppressed by the combined action of other genes, its presence can usually be detected by faint traces, such as the slight indication of a white line (DE) on the nose tip of ALL 1295. In this specimen unit elements AE and BE are clearly represented and their combined effect is to conceal the white nose line partially. In the adjacent skin (ALL 589) unit element DE dominates the pattern, but AE, BE and FE are also present.

Element FE can usually be detected by the presence of pale or white brow-spots, as well as by pale or white areas at the anterior ear bases. When combined with DE these latter are intensified (c.f. ALL 1078 and ALL 1924). Element EE usually shows pale areas lateral to the ear bases, as shown in varying intensity in the three specimens in the bottom row of figure 23. Absence or low potency of elements AE and/or BE will result in a white collar extending to the posterior ear base, as in figure 24, A and B, and figure 8, LPP 530.

In addition to the six unit elements illustrated in figure 22, two other head patterns have been identified. In one pigment is suppressed nearly, though not entirely; it is found only in the *leucocephalus* population, as previously mentioned. In the other melanin pigment only is suppressed in the area anterior to a transverse line midway between the eyes and the ears. This produces a pinkish-yellow facial color, as the xanthophyll pigments are not affected. Of widespread distribution (it occurs also in some specimens of *P. maniculatus*), it shows no predominance in any one of the Gulf Coast subspecies. In the Atlantic coast form *niveiventris*, however, it is invariably present and probably has selective advantage, for many of those beaches are pinkish-yellow from shell particles. This case is extralimital to the present study and has not been examined closely.

COLOR VARIATION

As mentioned under materials and methods, color measurements have not yet been completed for all the laboratory-bred specimens. Averages of random samples are shown in figure 25, and some preliminary studies have been made that suggest some segregation may occur at specific wave lengths. Little more can be said until all the specimens have been measured. Reflectance measurements (Y factor), now completed, appear to show some correlation with dorsal pigment

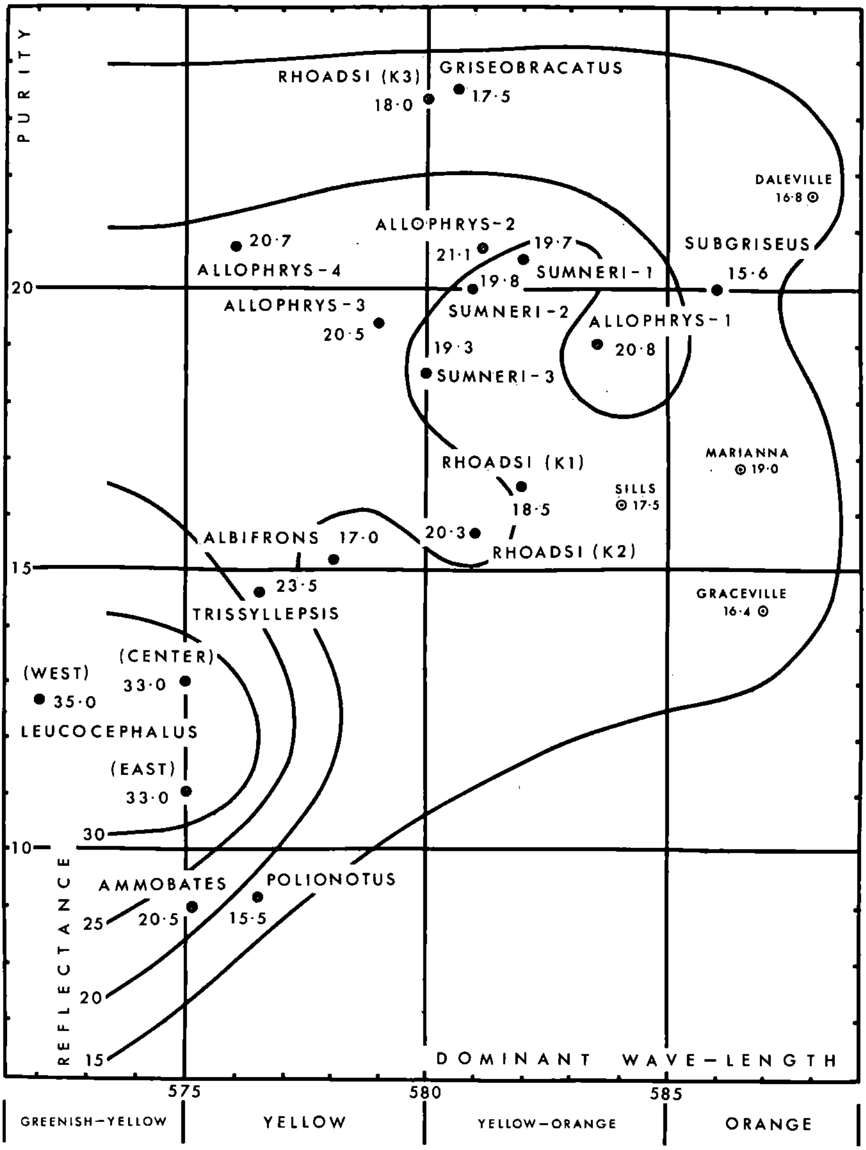

FIGURE 25. Color measurements of samples of various subspecies. Purity of color (ordinate) plotted against dominant wave length (abcissa), with reflectance written in and separated by curvilinear contour lines. Certain population samples, previously identified as *albifrons,* are included to show their closer relationship to *subgriseus.*

width (Fig. 7), the palest population (*leucocephalus*) having also the narrowest pigment. There are also some indications (see above) that dorsal pigment width may be an expression of the genes controlling the three rump pattern traits, and so reflectance (paleness) may also be under the same gene control.

In the case of *allophrys,* where pigment width and reflectance measurements are given separately for the four morphs, a possible correlation with certain head pattern elements is also seen. Morph 1, with the widest and darkest body pigment, is characterized by head pattern B (Fig. 20), whereas morph 4 has head pattern F. Morphs 2 and 3 are characterized by head patterns D and E respectively, but as traces of element FE (Fig. 22) are often found in these morphs, their intermediacy in pigment width and paleness may be due to this, rather than to any correlation with elements DE and EE.

The apparent cline Sumner (1929) records in increasing intensity and extensity of pigment inland from the coast must be disregarded for two reasons: 1) his collecting stations included three subspecies, *allophrys* (shore), *sumneri* (Crystal Lake) and *polionotus* (Chipley). The Round Lake station is within the area of intergradation according to material studied here, and so Sumner had only one sample of each subspecies. 2) the relative proportions of the morphs within each sample is unknown, and random differences could easily affect the results.

Hayne (1950) added another collecting station (Seminole Hills) in his re-study of the subject, but his sample from there was nearer in color to that from Round Lake than to the Crystal Lake sample. The reason for this was probably due to differences in the composition of the two samples. Morph 3 of *sumneri* has an average purity value of a little over 18 as against 20.5 for morph 1 in the measurements taken here (Fig. 28). A larger proportion of one or the other morph in either sample could thus easily affect the reading for red, green, and blue-violet in his results.

No color analysis has yet been made, other than the obtaining of average random sample readings as shown in figure 25. In one or two instances where mice of strikingly different color (to the eye) were mated, the results have been examined casually. These appear to relate to differences in purity rather than in dominant wave length. Here the question may be raised as to whether the purity readings represent actual differences in color saturation or are due to the relative number of black-tipped hairs dispersed within the area of color-tipped hairs. We do not yet know whether these black-tipped hairs, including guard-hairs, are under the same genetic control as the hair-base patterns or are controlled separately. Microscopic examination points generally to a larger proportion of black-tipped hairs in specimens showing lower purity readings, but not always. Subspecies *ammobates,* for example, is distinctly grayish to the eye, and reflectance colorimeter readings show low values for both purity and dominant wave length. But when the skin is folded and examined (Fig. 11, AM 24), far fewer black-tipped hairs are seen than in *rhoadsi, allophrys* or *trissyllepsis* (Fig. 12), all of which give higher purity readings. Also while *polionotus* and *ammobates* show a great difference in numbers of black-tipped hairs (Fig. 11), they give virtually the same purity value reading. Purity of color may therefore be the result of one or the other, or both of these factors.

SIZE VARIATION

Standard body measurements given in figures 26 and 27 show no very significant adaptive trends. *P.p. leucocephalus* from the eastern part of its range averages slightly larger in head-body length than all other Gulf Coast subspecies, and the population from the western end averages smaller than all the others. The range of variation of the two is wide and shows considerable overlap, but when the sexes are compared individually the rectangles giving twice the standard error on either side of the means do not overlap. Tail length averages slightly longer in the beach populations (Fig. 26, five bottom subspecies) than in the inland forms, but what adaptive significance this might have is not clear. *P.p. allophrys* has the longest tail and differs significantly (statistically) from *sumneri* in this respect.

A trend toward larger hind feet in the beach forms may possibly be correlated with locomotion and digging in loose sand. The difference in this respect between *polionotus* and *subgriseus* on the one hand and all the beach forms except *allophrys* and *trissyllepsis*, on the other, is statistically significant, according to the criterion of no overlap of twice the standard error on either side of the means (Dice and Leraas, 1936). An interchange between *trissyllepsis* and *polionotus* is known to have occurred about 120 years ago, which possibly may explain the smaller feet of *trissyllepsis.* The difference in foot size between *sumneri* and *allophrys* is significant and as (discussed below) the latter is believed to have been derived from the former in fairly recent times, the intermediate foot size of *allophrys* may reflect a stage in evolutionary change.

Ear length shows a great deal of variation that clearly is not correlated with environment. Differences between many of the subspecies are statistically significant, as between *subgriseus* and *polionotus, griseobracatus, sumneri, allophrys* and the eastern population of *leucocephalus*. The males of the western population of *leucocephalus* have significantly smaller ears than those from the eastern part of the range, but the females differ less. Also noteworthy is the variability of sexual dimorphism between the several subspecies, some having larger ears in the males, others in the females, and in the case of *leucocephalus* the dimorphism is reversed in the two populations.

Cranial measurements have been taken so far only for relatively small samples of the several subspecies and, excepting the new forms described above, are not included here. No very significant differences have been detected, other than a general size relationship between skull size and head-body length as might be expected.

POLYMORPHISM

"It will be realized . . . that any polymorphism, be it transient or balanced, must be built up and maintained by selective forces. These . . . turn out to be far more powerful in a state of nature than was supposed twenty years ago, while the existence of such genetically controlled diversity must itself be a sensitive indicator of changes in contending advantages and disadvantages involved, or in the spread of a gene. The existence of polymorphism therefore always advertises a situation of importance, and is especially well suited to detecting evolution in progress" (Ford, 1964).

Considering the many investigators who have worked with *P. polionotus* in the field, museum, and laboratory, the absence of any mention of polymorphism is indeed surprising. Sumner (1926, 1929) stated, on more than one occasion, that the white nose of "albifrons" is not constant, but he was referring to two distinct polymorphic populations, neither of which is *albifrons*. Furthermore he mistook the white nose trait (Fig. 21, E) for the diagnostic narrow median white nose stripe of *albifrons* (Fig. 20, D). Osgood's (1909) original description clearly defines this character, and examination of some of the original specimens in the present study confirms it. Trait D alone is characteristic of the monomorphic *albifrons* (a few marginal specimens near the range of *polionotus* lack it), whereas east of the Choctawhatchee drainage system this trait is found as one morph only in two distinct polymorphic populations.

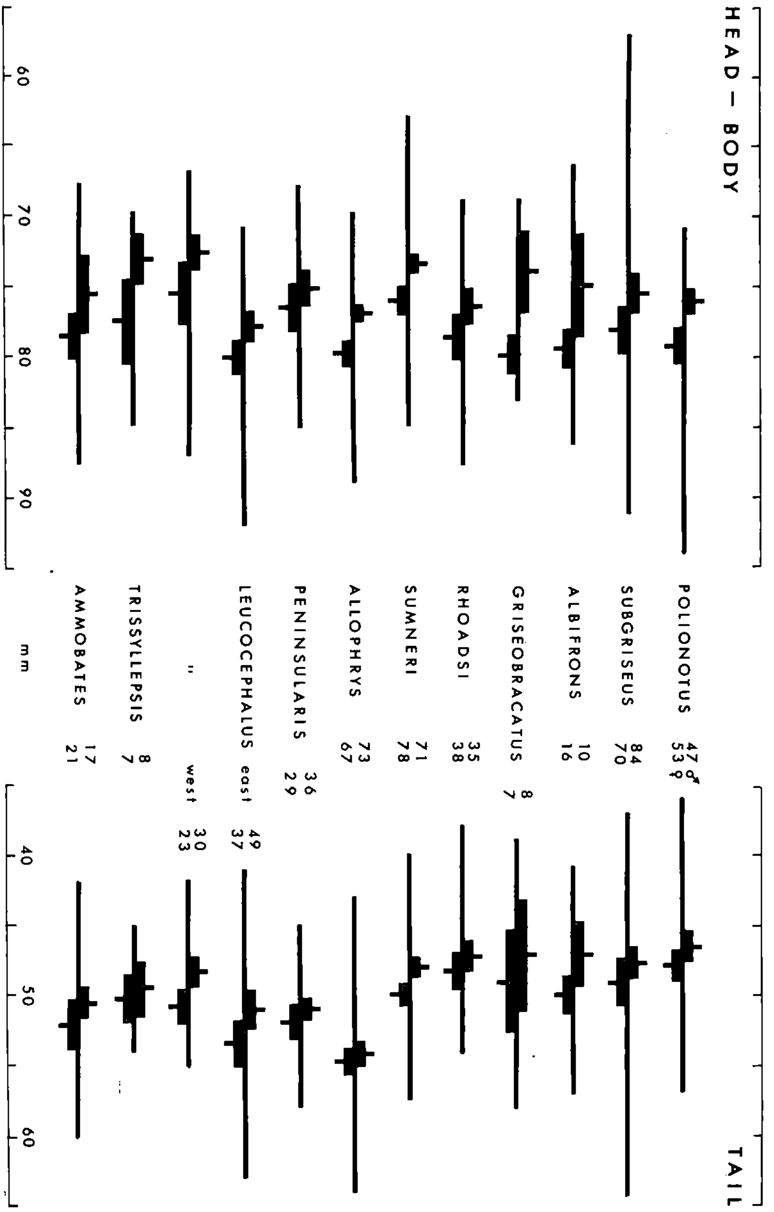

FIGURE 26. Head-body and tail measurements. Horizontal lines indicate range, short vertical lines means (males above, females below) and solid rectangles give twice the standard errors on either side of the means. Sizes of samples indicated. The top six subspecies occur inland, the bottom five are beach dune inhabitants.

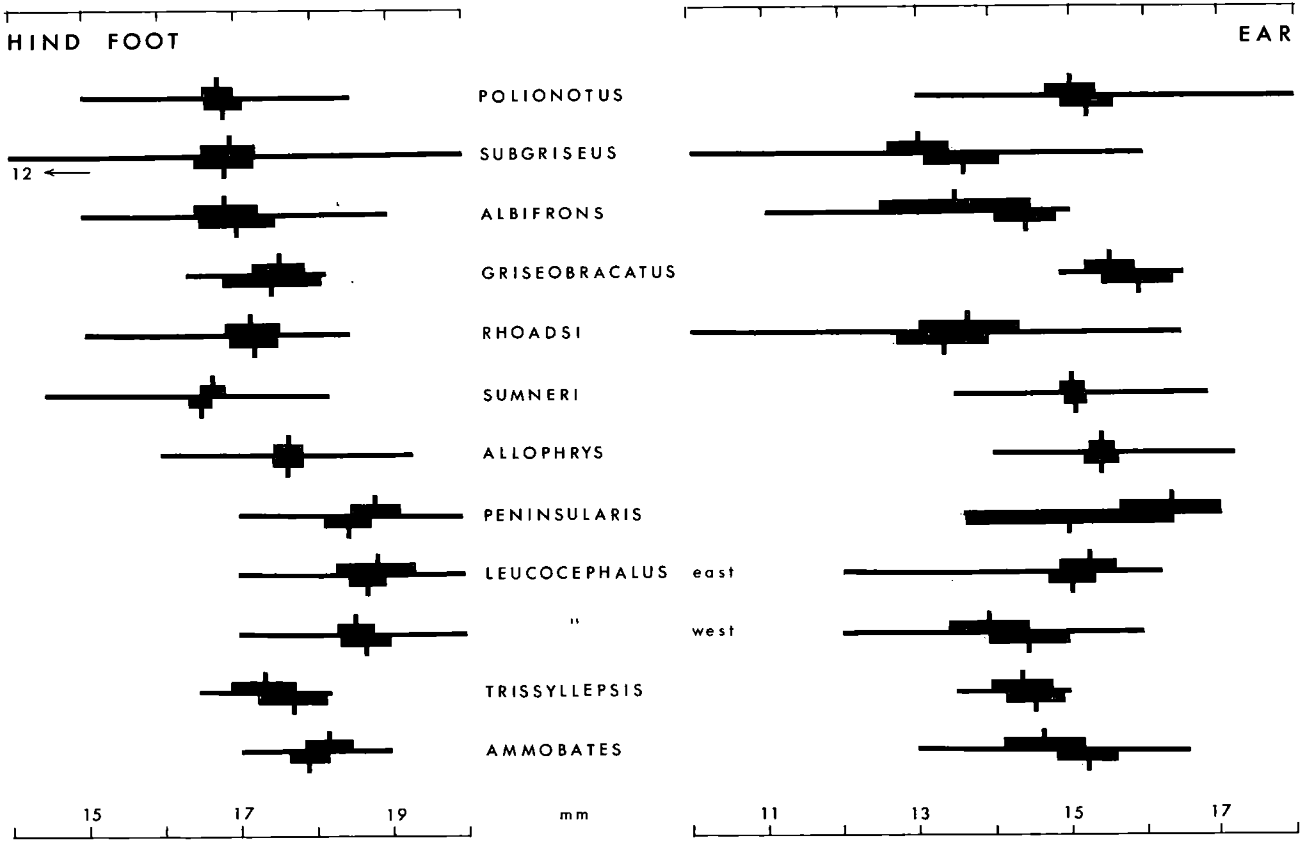

FIGURE 27. Hind foot and ear measurements. For explanation see figure 26.

Of the many polymorphisms in this species, *sumneri* and *allophrys* provide the most conspicuous examples, but others are no less interesting. Square rump and pointed rump traits (Fig. 5) both occur, for instance, in the *ammobates* population. Cryptically the less extensively pigmented square rump should have selective advantages on the white beach, but the two traits occur in nearly equal proportions. The gene for pointed rump must, therefore, give some pleiotropic advantage that maintains the balance. Originally some gene flow must have occurred between this form and *polionotus* which extends to the inner coast line in this part of Alabama, but this contact has been virtually severed during the last hundred years by the intracoastal ship canal.

The *trissyllepsis* population is divided about equally between head patterns H and I (Fig. 21) and these are composed of unit element CE with or without FE. The latter seems to show some correlation with the narrower dorsal pigment width, paler coloration, and square rump, and so would be selectively favored, but the unit element CE masks the advantages of the white face. The gene for CE must therefore impart some quality of fitness that maintains the polymorphic balance. The gene for square rump is present throughout this population, but a fairly large proportion of these mice also have the tapered rump pattern superimposed (Fig. 24, A, B). The reduced pigment area of the latter pattern must carry a selective premium that the square rump pattern largely cancels out, and it must therefore contribute in some way to fitness.

This "double image" rump pattern appears also in a few *leucocephalus* specimens, but it is diluted by another gene or genes. Whatever contribution the gene for square rump makes toward fitness, its visible effects seem largely overridden by the radically different *leucocephalus* genotype. The same applies to the various head pattern elements that show up faintly in some examples of this subspecies. Here we may be dealing with a case of transient polymorphism and a long-range study is desirable. Fortunately this island subspecies is not quite so threatened by extinction as are most of the other races, as nearly a third of its range is protected from real estate development by state parks and military installations.

The genes that suppress or further dilute dorsolateral hair-tip pigment in occasional *leucocephalus* specimens (see above) may also represent the initial stages of a transient polymorphism leading eventually to a disruptive type of concealment, as suggested earlier under variation and predation. The frequency of these examples, with pattern restricted to the mid-dorsal stripe, does not seem high, yet not so low as to be accounted for by recurrent mutation. Contrary to prevailing concepts, the *leucocephalus* population is far from uniform; indeed, it is perhaps the most variable of all the subspecies. This may be due to the presence of dilution genes which suppress or nearly suppress the visible phenotypes of other pattern genes. In this way beneficial effects of pleiotropic genes might be retained without their disadvantageous qualities.

On the other hand, the almost linear character of the range of *leucocephalus* must surely restrict gene flow and so promote diversification. Blair (1951) shows that the home range of a female of this subspecies may extend as much as 1500 feet in its greatest dimension. In at least two places the island narrows to about 500 feet in width, and so the population may be broken into several partially isolated subpopulations. This may explain the extraordinary differences in size and color between the inhabitants of the western third and the remainder of the population.

Polymorphism in *sumneri* and *allophrys* is considered together as the latter form is believed to have been derived from the former. Head pattern morphs 1, 2, and 3 are the same in both, but morph 4 is present only in the coastal subspecies. A degree of correlation exists between head pattern B and pointed rump; likewise head patterns E and F (Fig. 21) seem correlated with square rump. Head pattern D (Fig. 20) may be associated with either pointed or square rump, but more usually with the pointed. Earlier in these studies it was thought that the narrow white nose line of pattern D might represent the heterozygous expression of a gene for white nose (pattern E) and the polymorphism could be explained on the basis of heterozygous advantage in respect to morphs 1, 2, and 3. This is clearly not so.

Both nose traits may be seen combined in various degrees in many specimens (c.f. Fig. 23, ALL 589, ALL 1893, ALL 1078; Fig. 9, P1 and F1 generations). Also, if element DE (Fig. 22) were heterozygous, then occasional examples of head pattern E should occur in *albifrons* which, however, is monomorphic. The polymorphisms of *sumneri* and *allophrys* appear thus to be the results of interactions of the same pattern genes, balanced differently by contrasting selection pressures, brought about by substrates of white sand and darker sand covered largely by dead leaves. Available samples of wild-caught specimens are too small to permit broad conclusions, but 87 *allophrys* and 106 *sumneri* gave the following percentage frequencies:

	morph 1	morph 2	morph 3	morph 4
allophrys	35%	20%	25%	20%
sumneri	37%	60%	3%	–

The small proportion of morph 3 in *sumneri* is consistent with an assumed disadvantage that a less extensively pigmented face and rump might have on a relatively dark background. The absence of morph 4 from this population might also be attributed to selective elimination, and in fact some evidence (see below) suggests that the gene for white face may be concealed in some of the inland dark races. This is not to say that the gene for white face (unit element FE, fig. 22) is presently concealed in the *sumneri* population. Concealment of this gene in *polionotus* and *subgriseus*, if proved, may be due to a masking factor that would have been eliminated had *sumneri* been quadrimorphic when it inhabited white sand in Pleistocene times.

The four morphs of *allophrys* differ also in color, morph 1 being yellow orange (583.5 mμ) morph 4 yellow (576.0 mμ), and morphs 2 and 3 intermediate (Fig. 28). Morph 2 of *sumneri* gave the same reading as that for *allophrys* (581.0 mμ) but morphs 1 and 3 are more divergent in *allophrys* than in *sumneri*. The two populations are quite distinct in respect to reflectance (paleness). This suggests that selection pressures are acting differently in the two populations, that of the white dunes favoring paleness regardless of color, that of the inland yellowish pink sand with fallen leaves favoring the relatively narrow wave-length band of 580 to 582 mμ.

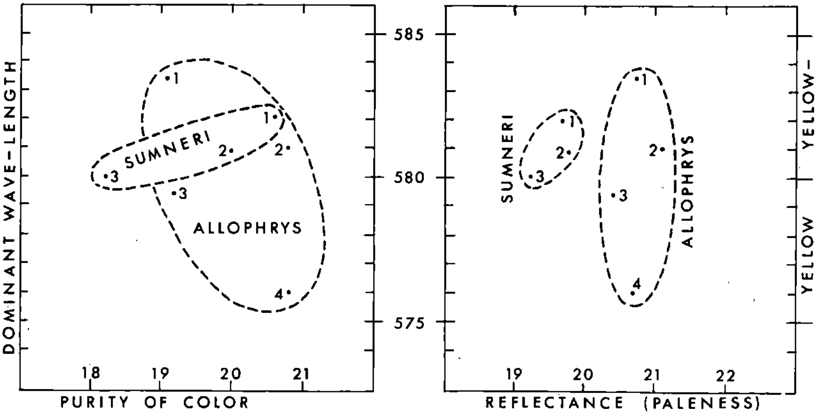

FIGURE 28. Color measurements of *sumneri* and *allophrys*. The morphs are indicated by numerals.

The surprisingly high frequency of morph 2 in the *sumneri* population (60%) may thus be the result of selective favoring, as its mean coincides with the presumed average substrate color, whereas only the lower part of the range of the morph 1 group is thus favored. The narrow and relatively inconspicuous white nose stripe of morph 2 can hardly be of much selective disadvantage. In morph 3 selection should favor the more yellow-orange individuals, but here the white nose and more restricted body pigment may also be disadvantageous. The color range of morph 4 presumably falls below the selective range in the inland population and, in any case, the white face and restricted body pigment would act adversely. Thus may be explained the absence of morph 4 (had it been present originally) and the low frequency of morph 3 in *sumneri.*

In purity of color, morphs 2 and 3 of *sumneri* averaged lower readings than those of *allophrys.* This suggests, perhaps, that selection acts in favor of low purity in the darker inland substrate, but in the case of morph 1 the situation is reversed. Perhaps some correlation exists between dominant wave-length and purity, in which case it might be assumed that the selection against the more yellow-orange individuals of morph 1 automatically eliminates those with higher purity.

The approximate equal frequencies of the four morphs in the *allophrys* beach population is very surprising in view of the rather marked pattern differences between them. The white face of morph 4 and the white nose of morph 3 must surely be of cyptic advantage, as suggested earlier. Also the narrower dorsal body pigment (Fig. 7) and square rumps of these two morphs should show selective favoring, but the two more extensively pigmented morphs predominated by 5 per cent. Therefore some quality of superior fitness that counteracts their cryptic disadvantages must be associated with these more extensive patterns.

The absence of the tapered rump character in the *allophrys* population and its presence in the beach populations on either side can be explained by the presence of the gene for pointed rump in that race. The gene for tapered rump, as already stated, interacts with that for pointed rump to give a square rump phenotype. The presence of the tapered rump gene in *allophrys* has been detected in the laboratory experiments. In the *peninsularis* population we have two morphs, one characterized by tapered rump and white head as in *leucocephalus,* the other square rumped and with head pattern J (Fig. 21). No indications of interaction of the two rump pattern genes to give the "double image" pattern (as in *trissyllepsis*) have been found. Unfortunately efforts to secure breeding stocks of this subspecies were unsuccessful.

ORIGIN OF PATTERN TRAITS

Sumner (1928) described a mutant form of *P. maniculatus* in which a "grizzled" and occasionally almost white pelage appears usually after the age of 6 months or more. As young adults these mice are normal in color and pattern and in some cases the grizzling appears as early as at age 2 months. He classified them into eight arbitrary grades and remarked that "the condition in the more pronounced of these grizzled mice, of the *P. maniculatus* series, bears a considerable resemblance to that of certain individuals of a Florida race, *P. polionotus albifrons* in which the dorsal surface of the snout and the top of the head, as far back as the eyes are white." He was referring, of course, to *allophrys* morph 4, not *albifrons*, but the similarity does exist.

The possibility of homology between the two was ruled out by the delayed appearance of the grizzled traits, which are manifest from the time that hair starts to grow in *P. polionotus allophrys*. This conclusion was accepted when the present study was being started, and Sumner's grizzled mutant was put aside as irrelevant. Later when an extremely pale mutant form (Fig. 24, C) appeared, its similarity to Sumner's grade 8 was recalled. By this time the several head pattern unit elements in the beach mice had been studied in some detail. On rereading Sumner's paper the extraordinary similarities in details of head patterns, as shown in his photograph, suggested much more than a superficial resemblance caused by a generalized type of pigment restriction.

Sumner's grade 8 not only bears so striking a resemblance to my extreme dilute that the two can be distinguished only by size and body proportions, but many of the head pattern unit elements found in *P. polionotus* can be distinguished in his photograph of the grizzled *maniculatus* stock. Receipt of a skin of a *maniculatus* mutant resembling Sumner's "grizzled" from R. R. Huestis, University of Oregon, has further strengthened the growing conviction that homology does indeed exist, despite the delayed appearance of the head pattern phenotypes in both Sumner's and Huestis's mutants. The apparently recessive gene for the extreme dilute form appearing in my stock may be widespread in the *polionotus* species, as is suggested by Dice's

(1934) record of a blackeyed white *P.p. polionotus* from Georgia. His description fits, except that it makes no mention of gray basal hair, but this is often so dilute as to be easily overlooked. Also the fact that the specimen is preserved in alcohol may have made it hard to see.

Examined under a lens, specimen number 2 in Sumner's photograph shows clearly a mosaic interaction of the genes for unit elements BE and CE, not unlike examples to be found in *polionotus* specimens (Fig. 23, top row). Even asymmetric pigment below the eyes is shown. Specimen number 3 in Sumner's photograph resembles very closely the head patterns of ALL 1078 and ALL 1924 (Fig. 23). These represent the interactions of unit elements DE, EE and FE, but the *maniculatus* specimen lacks the white spots around the ears, possibly because of the presence of AE. Sumner's specimen number 5 suggests the presence of the gene for square rump; it also bears a strong resemblance to the dorso-lateral hair-tip pigment suppression seen in the posterior body region of some *leucocephalus* specimens (Fig. 18, number 295). In the latter case perhaps the square rump may be due to the basal-hair pattern W (Fig. 10) rather than to the gene for hair-tip square rump, or both may be present, gene S being largely suppressed by a dilution gene.

With these remarkable similarities revealed, a close examination of a museum series of *Peromyscus* study skins showed several instances of head pattern traits characteristic of *polionotus* beach mice in the *maniculatus* series, but not in the other species (Fig. 29). A white forehead spot or blaze, perhaps comparable with the white forelock in man, was also found in both *maniculatus* and *leucopus,* and this has now appeared in the *polionotus* laboratory stock. Thus many, if not all the pattern genes characterizing the beach mice may have been already present in the *P. maniculatus* stock from which *P. polionotus* evolved. But how then is the delayed appearance of the "grizzled" condition to be explained?

Sumner regarded this condition as being the result of genes that *produced* the grizzled effect only in later life. If however the genes for his several grizzled grades are in fact the same pattern genes as in the beach mice, then they must be present but masked in the early stages of life. Thus *P. maniculatus* must possess some factor, perhaps metabolic, that affects pigment production in pelage during molt and prevents these pattern genes appearing in early life. All sorts of genes could thus be hidden and passed on without revealing their effects visibly as the average life-span is less than 5 months (Blair, 1948) and only a few mice live the full potential life-span of 3 or more years. Such a mechanism also allows the few survivors beyond the average

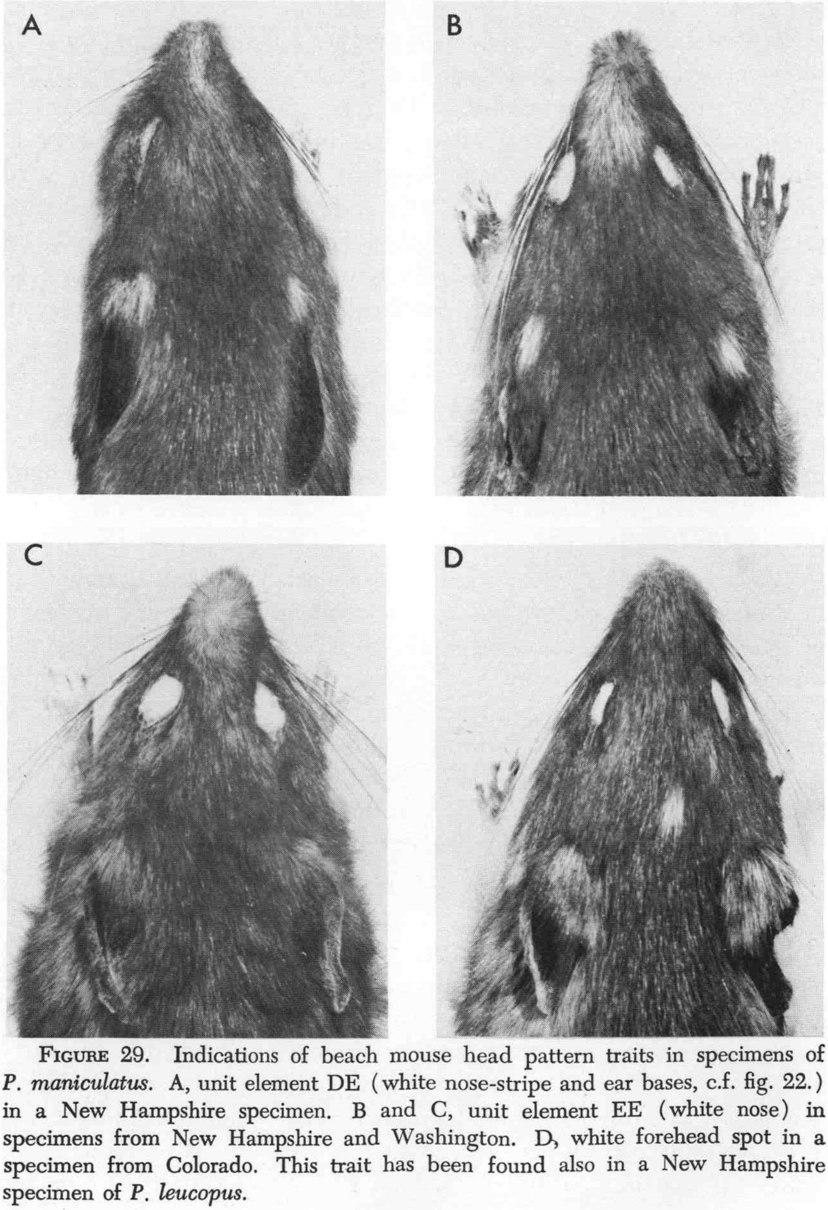

FIGURE 29. Indications of beach mouse head pattern traits in specimens of *P. maniculatus*. A, unit element DE (white nose-stripe and ear bases, c.f. fig. 22.) in a New Hampshire specimen. B and C, unit element EE (white nose) in specimens from New Hampshire and Washington. D, white forehead spot in a specimen from Colorado. This trait has been found also in a New Hampshire specimen of *P. leucopus*.

life-span to test out on changing environments whatever hidden genes they may happen to carry. Most would be eliminated, of course, but in unusual circumstances, such as a new coastline in contact with their habitat, some might reveal traits beneficial to an invasion of the new environment.

As the hidden traits appear anywhere from 2 to 6 months or more after birth, such individuals would still be capable of much reproduction and their offspring would have selective favor. Also selection would favor the earliest revelation of the hidden beneficial traits. Eventually this could lead to elimination of the delaying factor, as appears to be the case in the present-day beach mice. Instead of having to postulate a series of mutations occurring at different times on different beaches, we can view the process of beach mouse subspeciation as the random accumulation of various combinations of previously hidden traits on different beaches isolated by time and space. Some of these might be beneficial, others less so, and still others harmful. Selection would determine their fate and the course of further differentiation.

Evolutionary Sequences

The probability that *P. polionotus* evolved out of a *P. maniculatus* stock is hardly to be questioned. Osgood (1909) pointed out the close similarity between *P.p. polionotus* and *P. maniculatus pallescens* of Texas, and partly because of this Blair (1950) postulated a corridor of access along the Gulf Coast. "An ecological barrier now separates the two coastal-plain populations" he writes, "for the forests and coastal marshlands now occupying the coastal plain eastward from eastern Texas are avoided by both species." Granting that this may be so in Texas and Louisiana, the complete absence of records of occurrence of *P. polionotus* from the apparently quite suitable part of Alabama west of Mobile Bay and the Alabama River cannot be explained by this hypothesis.

The western limit of the range of *P. polionotus* is clearly defined by the barrier formed by marshes and poorly drained soils bordering the Alabama River (Fig. 3), and these extend northward to join the sticky soils of the "black belt" of central Alabama. Had the species evolved from an eastward extension of *maniculatus* stock in Texas, the suitable habitats in western Alabama would surely be occupied today. Another point of immigration must therefore be sought, logically from the north. But here forests populated by the woodland form *P.m. nubi-*

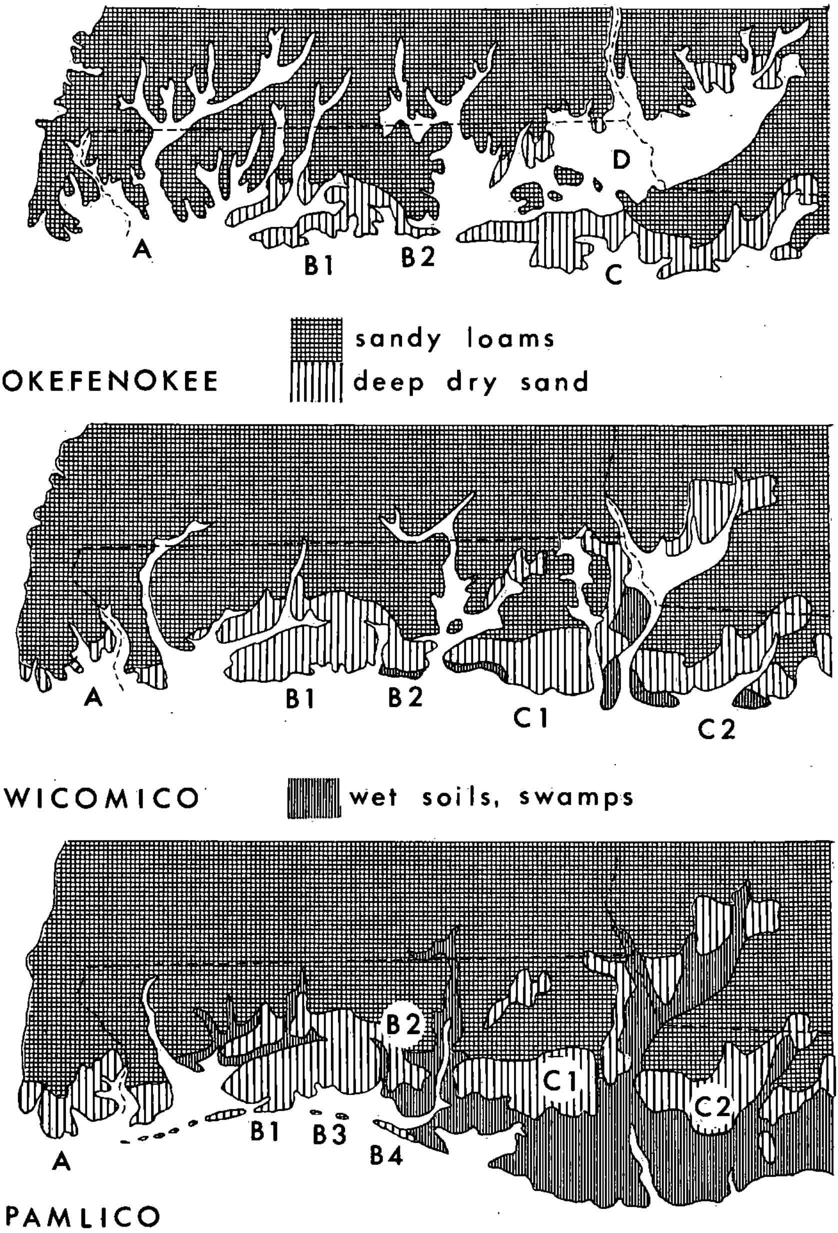

FIGURE 30. Pleistocene shorelines and distribution of sandy soils.

terrae, intervene, and *polionotus* is clearly derived from a grassland form. In recent times deforestation by man has allowed the grassland form *bairdii* to spread into areas once occupied by woodland races. This suggests the possibility that at some temporary dry period in pre-Pleistocene times a grassy corridor could have been formed through which the ancestral *polionotus* stock could have passed.

However this may have been, apparently *P. polionotus* had already evolved in its present range, and the sandhill form *subgriseus* had become differentiated before the sea rose to form the Okefenokee shore line of the Yarmouth interglacial stage. The slightly darker subspecies *colemani*, which ranges from northern Alabama through northern Georgia to northwestern South Carolina (Hall and Kelson, 1959, map, p. 626) may represent the ancestral stock. The Okefenokee shore line corresponds approximately to the present 150 foot contour (MacNeil, 1950). Bays and estuaries must have extended back into areas that are now Alabama and Georgia, cutting the coast into isolated segments (Fig. 30, top map). A large embayment (D) filling the Choctawhatchee-Chipola-Chattahooche-Flint basins (see Hubbell, Laessle, and Dickinson, 1956.), appears to have played a very important role in the subspeciation of these mice. The strongly sloping terrain at this level would have accentuated the isolating effects of these bays. East of the area of the present study, the land mass of peninsular Florida was reduced to an archipelago (Laessle, 1958, fig. 3).

From Mobile Bay eastward to the Blackwater drainage system in Santa Rosa County, Florida (Fig. 30, A), sandhill areas were inundated and the form *subgriseus*, adapted to Longleaf-pine/Turkey-oak Associations (Laessle, 1958), was eliminated. The extension of the range of the subspecies *polionotus* to the present inner coastline here, where sandy areas more suited to the requirements of *subgriseus* now occur, indicates this. (For much unpublished information on the soils of this Gulf Coast region I am indebted to Moray Harrell, U.S. Soil Conservation Service, who was then mapping the soils of this region. Farther eastward at B and C (Fig. 30), the new shoreline was in contact with the sandy areas populated by *subgriseus*, and it was here that the beach invasions are believed to have first occurred (Fig. 31).

The ecological differences are great between the sandy-loam habitat of subspecies *polionotus* with its fairly luxurient vegetative cover and the dry, sparsely-vegetated, dune environment of the beach mice, especially in view of the species' fossorial habits. Subspecies *polionotus* probably never was able to make the adjustment, and all the beach mice are here believed to have descended from a sandhill form similar, if not identical, with the present *subgriseus.* The beaches in contact with these sandhill habitats were split into two segments by the mouth of the great embayment referred to above (Fig. 30, top map, B and C). The gorges of the present Chipola and Apalachicola rivers are believed to have been cut by impounded waters at the time of marine retreat following the Yarmouth interglacial stage (c.f. Fig. 30, top and middle maps). The area now populated by *sumneri* was thus continuous at first with that now populated by *rhoadsi* (Fig. 3, J and K5).

Invasion of these beaches by sandhill mice gave rise to the *rhoadsi* form, characterized chiefly by the white ventral pattern V (Fig. 10). Whether this occurred by mutation or whether the gene for this trait was already hidden in the parental stock is not known. Nor is it known at what points along these beaches the mutation, or mutations, may have occurred. Any one or several of the numerous islands may have been involved, and the trait must have spread widely during the ensuing marine retreat. The incompatibilities between this genotype and that with the series of additive genes giving rise to the U-4 white ventral phenotype suggest that the V pattern arose by mutation instead of being already present in *subgriseus,* which belongs to the incompatible U series.

On the west side of the isolating barrier the embayment created, a different phylogenetic line started, or rather continued, as *subgriseus* was already modified to the U-1 stage. Invasions of the beaches at B (Fig. 30, top map) fostered the establishment of the U-2 stage of pigment reduction. For some reason, probably chance, the gene for head pattern unit element DE became established, and accumulated to a high frequency, on the small peninsula B-2, which was isolated by a bay that filled the present Alaqua drainage system. This gave rise to the *albifrons* population, which shares the square rumped hair-tip pattern characteristic of all the beach mice in area B. When the sea retreated at the close of this stage, pockets of these beach mice were stranded inland, and at the same time that portion of the *rhoadsi* stock destined to become *sumneri* was cut off by the Chipola and Apalachicola gorges (Fig. 31, H).

The next marine encroachment gave rise to the Wicomico shore line during the Sangamon interglacial stage at an approximate elevation of 100 feet. At this lower level sandy areas remained exposed in area A (Fig. 30) but as *subgriseus*-type mice had been eliminated

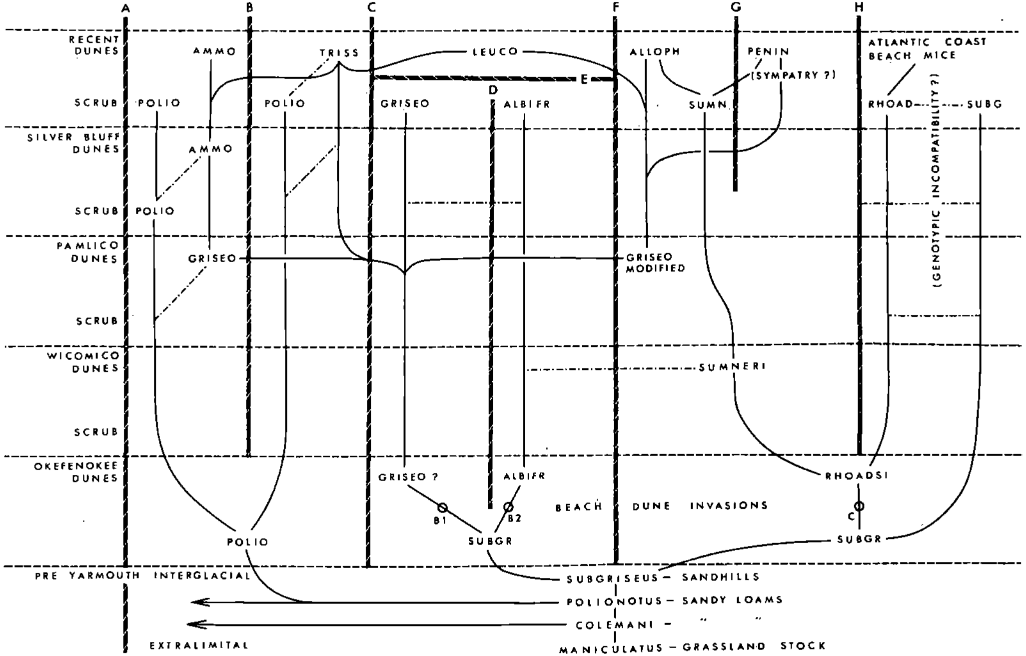

FIGURE 31. Evolution of beach mice as here postulated. Heavy, diagonally broken lines represent major barriers separating watersheds on which the several phylogenetic lines evolved during Pleistocene and Recent times. First invasions of beach dunes during the Yarmouth interglacial stage are indicated by circles, lettered to correspond with Fig. 30. Secondary contacts with probable gene exchanges are indicated by dotted-dashed lines. The major barriers are: A, Alabama-Mobile drainage system; B, Perdido drainage system; C, Pensacola-Yellow-Shoal drainage system; D, Alaqua drainage system; E, Santa Rosa Sound; F, Choctawhatchee drainage system; G, St. Andrew Bay; H, Apalachicola-Chipola drainage system, which separates the peninsular and Atlantic coast subspecies.

previously, no beach invasions occurred. Mice of *polionotus* stock may have spread into these unoccupied habitats at this or a later stage, but they were still incapable of invading the open beach dunes. Thus in this section, the absence of competition with *subgriseus* permitted the range of *polionotus* to extend down below the level of the Okefenokee shore line, whereas elsewhere its range is confined to the high country above that line.

Because the Wicomico shore line was some 50 feet below the Okefenokee shore line, the stranded beach mice of the former coast were now able to invade the new beach dunes where further adaptive modifications could occur. But now, because the territory was less sharply sloping, marshes began to form, especially at the mouths of bays, thus limiting the chances of beach invasions as at B2 and C2 (Fig. 30). This would not necessarily preclude the formation of sand bars on the seaward side of the marshes, just as is happening in various parts of the coast today. Also the entrances to the bays were now shallower, and opportunities for mouse transplants became possible. In some such manner the *albifrons* traits of white nose-line and square rump are believed to have been transferred to the now-isolated *rhoadsi* population at C1.

The basal-hair trait U-2 must also have been introduced by such a transplant, and genetic disharmonies probably occurred until the gene for U-2 was finally eliminated. At the same time part of this population, now dimorphic, had invaded the beaches again, and the gene for head-pattern element EE (Fig. 22) began to accumulate, giving rise to a trimorphism. *Albifrons* in area B2 was now cut off from the open beaches, and no further adaptive trends toward concealment for beach dune habitation occurred. The beach population of area B1 during this stage is unknown, for this region is now a restricted military zone from which no specimens are available.

The Pamlico shore line, which was formed during a mid-Wisconsin glacial recession, is only 25 to 35 feet above present sea level. Because of the flatter terrain much of the coast was marshy, as can be determined by peat in the soils. The *albifrons, sumneri* and *rhoadsi* populations (Fig. 30, B2, C1 and C2) were now out of contact with active beach dune formation, and selection pressures must have gradually changed in favor of concealment on a leafy substrate over a pinkish-yellow sand. At this stage *griseobracatus* probably became much as it is today (head patterns C and D, Fig. 20; rump pattern S, Fig. 5; basal-hair pattern, U-3, Fig. 10). Sandbars may have formed frequently in the shallow bays, thus permitting transplants of segments of mouse populations. In this way traits C, S, and U-3 were probably carried onto the beaches at A (Fig. 30), where they came into contact with the *polionotus* traits A, P and U that had extended down these watersheds without invading the beach dunes (Fig. 31).

The absence of any indication of the gene for head pattern element DE in the *ammobates* population suggests that its presence in *griseobracatus* may be the result of gene flow out of *albifrons* more recently. *Ammobates* appears to have evolved out of this mixture of *griseobracatus* and *polionotus* under selection pressures exerted during this and Recent times. The similarly mixed stock on the beaches between Perdido and Pensacola Bays gave rise to the *trissyllepsis* population later, as discussed below.

At the mouth of the Choctawhatchee estuary a new sandy beach began to form below the marshy shore at B4 (Fig. 30) and from time to time sandbars may have connected this with two islands of red sandy loam (B3) that lay athwart the mouth of the bay to the west. Similar junctions between these islands and the coast at B1 must also have occurred. In this manner at this time, or possibly later when the sea was retreating at the close of the Pamlico stage, the new beach at B4 became populated by mice of *griseobracatus* stock, and these in turn gave rise to the form *peninsularis* by spreading eastward during the succeeding Silver Bluff stage (Fig. 32).

One of the two morphs of *peninsularis* is similar in pattern (white head and tapered rump) to *leucocephalus* but much darker. The latter owes its paleness to dilution genes which must therefore be absent in the former. Santa Rosa Island is of very recent (post-Silver Bluff) formation, and therefore *leucocephalus* must have been derived from the same stock as *peninsularis*, but at a much later date (Fig. 31). The logical point of origin of this stock seems to be the beaches at B3, whose Pamlico population cannot be related to the *sumneri* population at C1, because not only did a marshy barrier intervene, but there also seems to be a genetic incompatibility between the two phylogenetic lines. The ancestral stock of both *leucocephalus* and *peninsularis* must therefore be sought in the original *griseobracatus* population at B1. The more recent interposition of *allophrys* between their ranges is considered later.

For some reason not understood, *griseobracatus* underwent little adaptive modification during the three successive interglacial stages of exposure to dune conditions. The sudden appearance of a radically different cryptic pattern in the isolated subpopulation at B3 is therefore remarkable. Unfortunately efforts to secure breeding stocks of

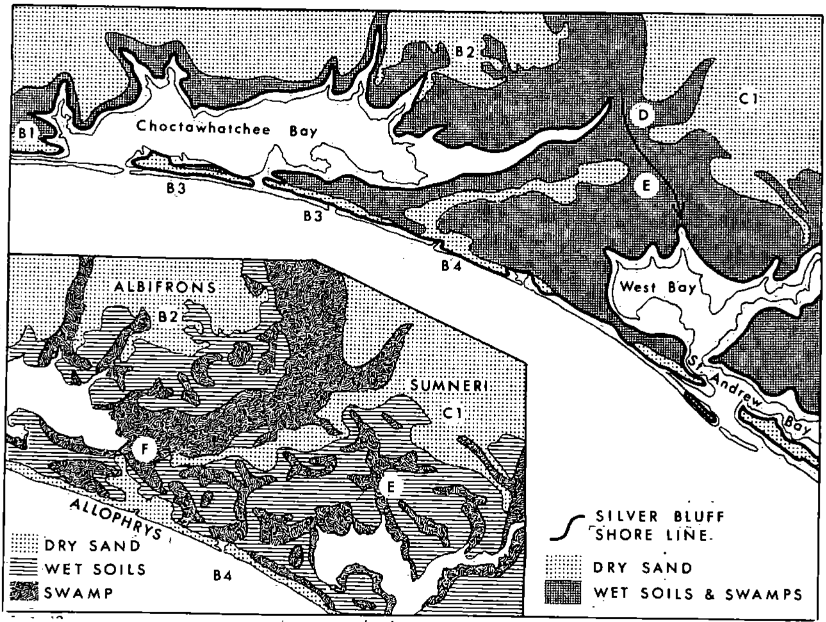

FIGURE 32. Silver Bluff and present coastline between Choctawhatchee and St. Andrews Bays, showing soil characters.

both *griseobracatus* and *peninsularis* failed and so no clues to this problem are at hand. The white head and tapered rump patterns may have appeared by mutation, or their factors may have been already present and masked.

The Silver Bluff shore line, 8 to 10 feet above present sea level, closely parallels (Fig. 1, B and 32) and in some places coincides with the present coast. Widespread mouse dispersal was probable then, as is the case now. Fluvial sand deposited along the left bank of the Choctawhatchee estuary during the Pamlico stage was now exposed as a narrow dry corridor between the *sumneri* population (C1) and the beach at B4. This must have been interrupted at first by the drainage basin of the present Pine Log Creek (Fig. 32 D), thus allowing time for the eastward extension of *peninsularis* before the wave of *sumneri* migrants reached the beach at B4. Possibly the Choctawhatchee drainage flowed through this gap at some time during the Pamlico stage (Fig. 32, E, arrow). If so, it would have flowed through the swampy area (inset map, E) through which Burnt Mill Creek now flows into West Bay (U.S. Geol. Survey quadrangles: West Bay, 1944 and Red Head, 1945).

Later, this gap was filled by sand brought down by floods in the

Pine Log drainage area (as it is today, Fig. 32, inset map). The gap at F is of later origin, and so a corridor of access was opened for the invasion of *sumneri* stock onto the beach (B4) which was then populated by a modified *griseobracatus* stock. The two phylogenetic lines, isolated since the Yarmouth Interglacial stage, were thus brought together and, judging by laboratory attempts to cross *rhoadsi* and *allophrys* with *leucocephalus*, much genetic disharmony may have resulted. Several of the attempted laboratory crosses resulted in parturient mortality, which suggests a nearly complete reproductive barrier.

The almost total absence of *leucocephalus* traits (similar traits are assumed for the similar morph of *peninsularis*, though not yet tested) within the range of *allophrys* is accounted for by the swamping of the smaller beach population by the larger reservoir of inland *sumneri* stock. In this manner the apparent mutual exclusiveness of head patterns F and G (Fig. 21) and basal-hair patterns V and W (Fig. 10) may have come about. Hair-tip rump pattern T appears to be present at a probable low frequency in the *allophrys* population, but is masked by its interaction with the gene for pointed rump, P. Its reduced frequency may also be due to partial elimination by genetic incompatibility.

The coexistence of two apparent morphs in *peninsularis* with no signs of intermediacy calls for special study. The genes for basal-hair patterns V and W may be partially incompatible, but rump patterns S and T (Fig. 5) combine to give a "double image" which has not been detected in any of the specimens examined. The square-rumped *peninsularis* morph could, of course, represent the interaction of genes P and T, but if this were the case the gene P must have been derived by gene flow from the *allophrys* population. Then why is *peninsularis* phenotypically distinct from *allophrys*? The case is very puzzling, but a possible explanation might be that the *sumneri* stock, which invaded the beaches in sufficient numbers to swamp the *peninsularis*-like population in the area now inhabited by *allophrys*, also spread into the *peninsularis* range to a lesser extent. Here the genetic incompatibility may have resulted in sympatry, and a case of circular overlap is suspected (Fig. 31).

Unfortunately the problem is further confused by the presence of four specimens resembling *allophrys* morph 1 in the original type and topotypic series of *peninsularis*. No such examples have been seen in other museum collections of this subspecies, and as labeling errors are evident in other specimens collected by the Nichols party, these four specimens are suspected to be mislabeled *allophrys*. Proof of this, must rest largely on future intensive field work; meanwhile an element of doubt remains. Actually a small immigration of *allophrys* stock into the *peninsularis* population should not affect the general picture greatly, as its compatibility with the square-rumped *peninsularis* "morph" may be anticipated. The constantly shifting sand bars and islands at the entrance to St. Andrew Bay makes such a transplant highly possible.

The Silver Bluff shore line is considered tentatively (MacNeil, 1950) to represent the peak of the Recent interglacial stage, and Santa Rosa Island has been formed since then (6,000 to 4,000 years ago). Subspecies *leucocephalus* must therefore have been derived from the pre-*peninsularis* stock on beach area B 3 (Fig. 32) some time after Silver Bluff but before the influx of *sumneri* onto the beach. The Silver Bluff beaches at B3 were formed around the two Pamlico islands of red soil (Fig. 30, B3), whose location can be detected today by remnants of the reddish bluffs clearly indicated as navigational landmarks on early maps (Fig. 33). The easternmost of the two islands was already connected to the coast at B4 at the Silver Bluff stage, but the western island was still detached. Its junction appears to have occurred within historical times.

The earliest reliable map of this area is that drawn by Bernard Romans in 1774 (see list of maps consulted). Despite its small scale and relative crudity, this map reveals a surprising degree of accuracy, and the very narrow neck by which the western island is attached can hardly be attributed to lack of information. Moreover, subsequent maps consistently show a progressive broadening of this neck. By 1803 the topography was essentially as it is today. Apparently, therefore, the *griseobracatus*-like pre-*leucocephalus* population on this island, which was evidently joined to the newly formed Santa Rosa Island, remained isolated until not many years before 1774. The closing of this channel resulted in a new channel, which is the present Destin Pass.

This second influx of modified *griseobracatus* must have occurred on the beach at B4 sometime around 1770, thus adding to the genotypic incompatibilities caused by the previous influx from the eastern island. The low fertility observed in the present-day *allophrys* population (see below) may be the result of this mixing of two phylogenetic lines that had evolved separately since early Pleistocene. The gene for head pattern element FE (Fig. 22) common to *leucocephalus*, *allophrys*, and *peninsularis* accumulated probably by chance and selection

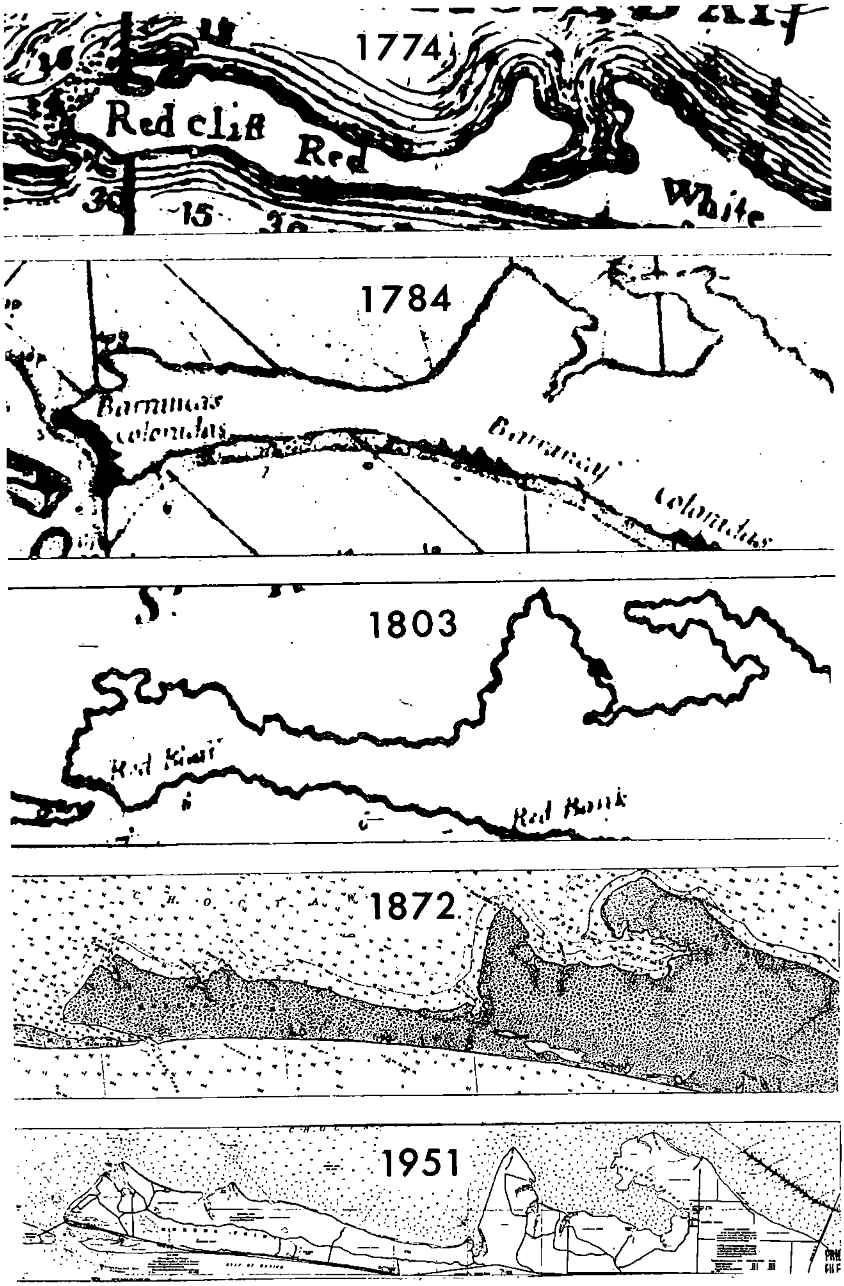

FIGURE 33. Early maps of the Moreno Point area south of Choctawhatchee Bay. For source references see under literature cited.

on these two islands and was subsequently carried into the three populations.

The break in the sandy corridor where the Devil's Swamp (Fig. 32, inset map, F) now isolates *sumneri* from *allophrys* may be of quite recent date. Possibly the hurricane of 1843, which wrought great havoc and changed much of the coastal topography of this northern Gulf Coast region, may have been the agent. Floodwaters of the Choctawhatchee River could have broken through the flat and ineffective barrier during this or some previous period of storm.

As the name implies, *trissyllepsis* is probably the result of mixing of three stocks (*griseobracatus, ammobates,* and *leucocephalus*). The westward spread of *griseobracatus* during the Pamlico stage would have resulted in a beach population of that stock more or less in contact with *polionotus* inland. This may have evolved in the same direction as the adjacent *ammobates*. In any case transplants of the latter form into the area of *trissyllepsis* are known to have occurred in historic times, and undoubtedly similar gene flow occurred in earlier times. Head patterns H and I, double-image rump pattern S+T, and basal-hair pattern W clearly indicate the presence of *leucocephalus* genes in *trissyllepsis*, and its paler coloration is also to be explained in this way. Extensive search among early maps has failed to show any recent contact, and so the *leucocephalus* genes must have been acquired by *trissyllepsis* before 1774. But since *leucocephalus* is of very recent geological origin, this cannot have occurred very long ago.

INCIPIENT SPECIATION

The existence of partial reproductive barriers within the species was wholly unanticipated at the time of the laboratory breeding tests. Therefore no experiments were designed specifically to test this, and the limited data available are incidental to other tests. The first intimation of reproductive incompatibility came with the parturient deaths in *rhoadsi* x *leucocephalus* matings. Similar fatal results in the case of *allophrys* x *leucocephalus* matings were discovered, but their significance was not fully appreciated until after the breeding stocks had been discontinued. Out of 12 attempted crosses between *rhoadsi* and *leucocephalus*, only 1 litter was born alive. In the case of *allophrys* x *leucocephalus* no live progeny was born, and 2 parturient deaths occurred in 11 pairings. The results of attempted matings of *rhoadsi* and *allophrys* to other stocks are as follows:

Crosses	Number of pairings	Successful matings	Litters per 100 days of successful matings	Average litter size	Juvenile mortality %
rhoadsi ♀ x					
polionotus	4	2	2.31	3.93	0.0
subgriseus	7	1	0.92	4.00(?)	0.0
allophrys	2	1	3.36	3.00	0.0
leucocephalus	12	3*	0.93	-*	47.6*
allophrys ♂, ♀ x					
polionotus	2	0	-	-	-
subgriseus	7	1	2.02	4.50	0.0
albifrons	5	0	-	-	-
leucocephalus	11	2*	-	-	100.0*

*Parturient mortality occurred.

Reduced fertility is indicated between *rhoadsi* and *subgriseus, allophrys* and *polionotus, allophrys* and *subgriseus,* and *allophrys* and *albifrons,* in addition to that with *leucocephalus.* As a basis for comparison, the proportion of successful matings of other subspecies is as follows:

Subspecies	Number of pairings	Successful matings	%
polionotus x *polionotus*	27	13	48.1
subgriseus x *subgriseus*	13	6	46.2
albifrons x *albifrons*	15	7	46.7
leucocephalus x *leucocephalus*	31	10	32.3
allophrys x *allophrys*	153	24	15.7

The first three of the above listings suggest that the expected normal number of successful matings, under laboratory conditions, is slightly under 50%. The higher percentage Dawson (1965) obtained is probably to be accounted for on the basis of food (see materials and methods). In *leucocephalus* a somewhat lower fertility rate is noted, and in *allophrys* it is very low. This was noted early in the laboratory experiments and is the chief reason why so few attempts were made to outcross this race. This fact must also be taken into consideration in the interpretation of the results of such outcrosses as were attempted. The explanation of this low fertility is obscure, but it is thought possibly the result of genetic disharmonies caused by the influx of *sumneri* onto this beach which was previously populated by a *peninsularis*-like stock, as suggested above.

James N. Layne has suggested (*in. litt.*) that "the lower fertility of the two beach forms may perhaps also be explained as an adaptive trait involving a reproductive physiology more sensitive to environmental factors—particularly nutrient level. Such an adaptation might better synchronize breeding with food levels, which may be more variable and sporadic on beaches in which vegetative communities are simpler." Such an explanation might well apply to the lower fertility of *leucocephalus* as compared to *polionotus, subgriseus,* and *albifrons,* but can it explain the great difference between *allophrys* and *leucocephalus,* which inhabit adjacent and similar beach environments? According to this hypothesis *allophrys* would be more fully adapted to the beach environment, yet all indications point to its having evolved in very recent times from a secondary contact which, according to laboratory experiments, seemingly leads to deleterious fertility results.

It may therefore be assumed that time has been insufficient for the elimination of the disharmonies in the gene pool caused by mixing of the two stocks derived from separate phylogenetic lines of descent. This is compatible with the hypothesis that the opening of the sandy corridor between the range of *sumneri* and the beaches was of quite recent date, and that the severing of this bridge may have occurred as recently as the 1843 hurricane. The speculation, made above, that *peninsularis* may in reality be two distinct sympatric populations, representing the two ends of a circular overlap, is also consistent (Fig. 31).

The case cannot be left as just another probable example of a circular overlap, as indications of a break appear between *rhoadsi* and *subgriseus* in reduced fertility as well as in the physiological molt disturbances described above. The case appears to be an example of incipient speciation and, as such, demands a great deal of further study. The peculiar all one or all the other type of intergradation between *rhoadsi* and *subgriseus* might easily be interpreted as hybridization, in which two incompatible genotypes lead to selective elimination, and restricted gene flow. Unfortunately most of the specimens from the zone of intergradation (or hybridization) are conventional rounded museum skins which cannot be examined for molt defects and fault lines as readily as can flat skins.

The scanty evidence seems to point to a cleavage developing between the subspecies *polionotus, subgriseus, albifrons, griseobracatus, ammobates, trissyllepsis* and *leucocephalus* on the one hand and *rhoadsi, sumneri* and *allophrys* on the other (see maps, Fig. 3 and 34). The status of *peninsularis* must remain indefinite for the time

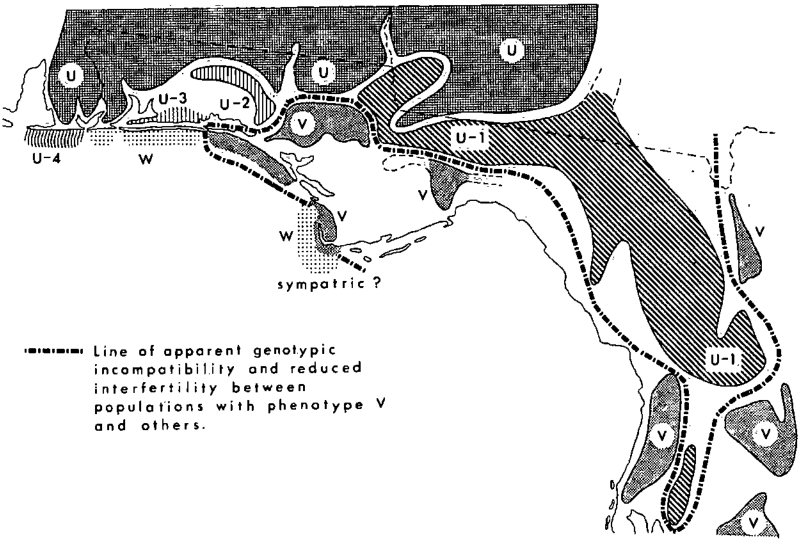

FIGURE 34. Distribution of hair-base phenotypes (cf. Fig. 10) and line of apparent incipient speciation caused by genotypic disharmonies.

being, and in all probability the Atlantic Coast beach forms must be placed with the latter group because on geographical grounds they must have evolved out of *rhoadsi* stock. The present study has been largely exploratory, and much new laboratory experimentation is needed to confirm or deny the several leads that have been uncovered.

The project offers promising scope for future study of evolution in progress. By the time this paper appears in print the writer will have retired to live on the northwest Florida Gulf Coast, where further field studies are anticipated. But laboratory facilities will not be available, and so further pursuit of these aspects must be left to others. An urgency exists, as many of the beach habitats are rapidly being obliterated by the present real estate boom. More than two thirds of the habitat of *allophrys* has thus been destroyed since the first field trip of this particular project was undertaken in 1950. Moreover, the threat of extinction to the mice is not confined to the beaches; large inland tracts of many square miles are constantly being bulldozed of their scrubby oak cover for citrus cultivation, reforestation, and cattle grazing.

ACKNOWLEDGMENTS

For financial assistance grateful acknowledgment is made as follows:

The Henry Clinton Fall Memorial Fund, for field work in 1961.

The Florida State Museum, University of Florida, Gainesville, for field work and museum studies in 1962.

The National Science Foundation (Grant GB. 1621) for genetic experiments and studies of museum materials, 1963-1965.

For loans of specimens, I am indebted to the many curators of collections listed below with their institutions.

For assistance in the field I am indebted to Donald E. Stullken, for generously providing transport in his boat to several otherwise inaccessible localities in the Pensacola area; for much first-hand information about these mice; and for his kindness in searching for early maps in the Pensacola Historical Museum; and to Russell Stullken for assistance in collecting mice in the Pensacola area, and for securing and shipping live stocks of several forms. Also to Carl Schimmel for assistance in collecting specimens in the Pensacola area, to James N. Layne for furnishing live specimens of *rhoadsi*, and for much help given during my stay in Gainesville and later through correspondence, and to Michael Smith for providing breeding stocks of *subgriseus*.

For reading the manuscript and giving helpful criticism I am indebted to Ernst Mayr, Harvard University, L. C. Dunn, Columbia University, James N. Layne, Cornell University, and D. J. McDonald, Dartmouth College.

For advice and help in the genetic part of this project my thanks are extended to George B. Saul, 2nd, Dartmouth College.

For the careful, painstaking work in preparing, measuring, etc. the many hundreds of skins of laboratory-bred mice, my appreciation is extended to my four assistants: Mrs. Susan Tavela, Mrs. Phyllis Levine, Miss Elizabeth Davis, and Mrs. Diane Smith, as well as to those who assisted in more temporary capacities.

And finally for encouragement and help I am deeply grateful to my wife, Katharine Knaebel Bowen.

SPECIMENS EXAMINED

The following list includes all the subspecies occurring on the coastal plain of the Gulf of Mexico. Specimens of the Atlantic coastal races, as well as the inland forms *colemani* and *lucubrans*, were also examined but are not listed here. Mice collected during the present study are identified by the initials WB; others borrowed from other institutions are indicated by initials as follows:

AMNH—American Museum of Natural History, New York, N.Y. Richard G. Van Gelder.

AU—Auburn University, Auburn, Ala. Julian L. Dusi.

CM—Carnegie Museum, Pittsburgh, Pa. Kenneth Doutt.

CNHM—Chicago Natural History Museum, Chicago, Ill. Phillip Hershkovitz.

DMNH—Dayton Museum of Natural History, Dayton, Ohio. E. G. Koestner.

HBS—Private collection of H. B. Sherman, Deland, Fla.
KU—Kansas Museum of Natural History, Lawrence. E. Raymond Hall.
LSU—Louisiana State University Museum of Zoology, Baton Rouge. George H. Lowery, Jr.
MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, Mass. Barbara Lawrence.
PU—Purdue University, Lafayette, Ind. Russell E. Mumford.
UF—University of Florida, Gainesville. James N. Layne.
UG—University of Georgia, Athens. Eugene P. Odum.
UI—University of Illinois Museum of Natural History, Urbana. Donald F. Hoffmeister.
UM—University of Michigan Museum of Zoology, Ann Arbor. William H. Burt.
USNM—United States National Museum, Washington, D.C., including the E. V. Komarek collection on deposit. Charles O. Handley, Jr.

P.p. polionotus: GEORGIA: Screven Co., Hursman's Lake, 10 topotypes (MCZ); Wilkinson Co., Gordon, 2; Jones Co., James, 3; Twiggs Co., Fitzpatric, 4; Crawford Co., Tifton, 8; Dougherty Co., Sycamore, 1 (HBS); Houston Co., Perry, 2 (WB); Dougherty Co., Albany, 1 (UI); Decatur Co., Butter Hill Creek, 1; Seminole Co., Sealy Camp, 1 (UF). ALABAMA: Henry Co., Abbeville, 20 (USNM); Baldwin Co., 5 miles north of Gulf Shores, 4 (AU). FLORIDA: Liberty Co., Rock Bluff, 3; Holmes Co., Ponce De Leon, 1; Escambia Co., Century, 3 (USNM); Washington Co., Chipley, 2 (UM); Gadsden Co., Chattahoochee, 1; Escambia Co., Pensacola, 8 plus many laboratory-bred (WB); Washington Co., Chipley, 2 (KU); Escambia Co., 1 (DMNH), 1 mile south of Pensacola lighthouse, 7 (PU), 15 miles west of Pensacola (Bauer Field), 2 (PU).

P.p. subgriseus: FLORIDA: Alachua Co., Gainesville, 30 topotypes, Archer, 20; Marion Co., Ocala National Forest, 73; Levy Co., Williston, 10; Jackson Co., Sneads, 9 (UF); Alachua Co., Gainesville, 5 topotypes; Marion Co., Ocala National Forest, 17, Silver Springs, 1, Ocala, 11, McIntosh, 8; Gilchrist Co., Fort White, 8, Branford, 4; Dixie Co., Old Town, 2; Madison Co., Lee, 4, Madison, 7, Greenville, 2; Jefferson Co., Aucilla, 1; Gadsden Co., 13, Greensboro, 4 (USNM) Alachua Co., Gainesville, 13 topotypes (CNHM), 10 topotypes (MCZ), 8 topotypes (AMNH), 8 topotypes, Newberry 19; Dixie Co., Eugene, 2; Pasco Co., Dade City, 1; Hillsborough Co., Dug Creek, 8 (HBS).

Near *subgriseus* (?). GEORGIA: Irwin Co., Ocilla, 9 (UF); McIntosh Co., Townsend, 3 (UG).

Intergrades: *polionotus*$\rightleftarrows$*subgriseus*. GEORGIA: Baker Co., Emory Field Station, 1, Ichwaynochaway Creek, 3; Miller Co., Colquitt, 1 (UG); Thomas Co., Boston, 11, Metcalf, 8 (UI), 1 (PU), 2, Thomasville, 14; Grady Co., Beachton, 9, Ochlochnee River, 15 (USNM). ALABAMA: Dale Co., Dalesville, 16 (USNM). FLORIDA: Jackson Co., Marianna, 17 (HBS), 33, Sills, 27 (UM); Holmes Co., Graceville, 9 (UM), 2 (USNM).

P.p. albifrons: FLORIDA: Walton Co., near Whitfield, 6 topotypes (Kenneth Doutt also furnished external measurements of the rest of the original series), (CM), De Funiak Springs, 6 plus laboratory-bred specimens (WB); Okaloosa Co., Crestview, 1 (USNM).

P.p. griseobracatus: FLORIDA: Santa Rosa Co., 20 miles west of Fort Walton, 2, 5 miles east of Pensacola (=Pensacola Shores-Gulf Breeze area), 1; Okaloosa Co., Shalimar, 3 (USNM); Port Dixie Beach (=Shalimar), 7 (UM).

P.p. ammobates: ALABAMA: Baldwin Co., Fort Morgan, 2, Bon Secour (=dunes near Little Lagoon, according to notations on some labels) 6, Orange Beach, 11, Ono Island, 1 (USNM); Gulf Shores, 1 (KU), 8 (UM), Alabama Point, 8 (plus many laboratory-bred), Ono Island, 10 (WB).

P.p. trissyllepsis: ALABAMA: Baldwin Co., Florida Point, 10 (plus others laboratory-bred); FLORIDA: Escambia Co., Gulf Beach, 4, "Foster's Island" (=south side of Big Lagoon) 1 (WB), 1 (USNM).

P.p. leucocephalus: FLORIDA: Okaloosa Co., Santa Rosa Island, opposite Ft. Walton (type locality), 42 (USNM), 35 (UM), 2 (UF), east end, 2 (CNHM), 2 (HBS), 3 (WB), East Pass, 10 (USNM); Escambia Co., Santa Rosa Island, opposite Navarre, 13 (USNM), 28 (UM), 7 plus laboratory-bred stock (WB).

P.p. peninsularis: FLORIDA: Bay Co., St. Andrew's Point (type locality) 10, St. Joseph's Point, 7 (AMNH), 17 (USNM), Port St. Joe, 48, Cape San Blas, 4, Money Bayou, 4 (USNM).

P.p. allophrys: FLORIDA: Walton Co., near Morrison Lake (type locality), 11, plus laboratory-bred stock, Eastern Lake, 3, plus laboratory-bred stock (WB), Seagrove Beach, 1 (USNM); Bay Co., Panama City Beach, 2 (WB), Inlet Bay, 17, St. Andrews State Park, 2 (USNM).

P.p. sumneri: FLORIDA: Washington Co., Crystal Lake, 2 (USNM), 54 (UM); Jackson Co., Round Lake, 2 (WB), 2 (USNM), 22 (UM); Calhoun Co., Clarksville, 15 (USNM); Bay Co., Merial Lake, type locality, 2 (WB); Seminole Hills, 59 (UM). *Intergrades: subgriseus⇄sumneri:* Jackson Co., Kynesville, 3 (WB).

P.p. rhoadsi: FLORIDA: Population K1: Hillsborough Co. (?)[*], head of Anclote River, 1 topotype (MCZ); Hernando Co., Brooksville, 8 (HBS); Citrus Co., Inverness, 6 (USNM), 11 (UF), Citronelle, 1 (MCZ: Population K2: Highlands Co., Childs, 1 (HBS), Hicoria, 11 (UF), 13, (WB), 1 (KU), Sebring, 1 (USNM); Polk Co., Auburndale, 3 (USNM); 1 (UF), Lake Pierce, 7, Green Swamp, 11 (USNM), Laughman, 1 (UF), Frostproof, 3 (HBS): Population K3: Orange Co., Orlando, 1 (USNM), 4 (HBS); Seminole Co., Oviedo, 14 (USNM), Zellwood, 8 (HBS); Population K4: Putnam Co., Interlachen, 1 (UF); Population K5: Leon Co., 5 miles south of Tallahassee, 7; Wakulla Co., Spring Creek, 1, Crawfordville, 6 (USNM), 4 (UI). *Intergrades: subgriseus⇄rhoadsi:* FLORIDA: Liberty Co., Bristol, 1 (USNM); Lake Co., Tavares, 8, Eustis, 10, Okahumpka, 20, Leesburg, 4, Fruitland Park, 2, Emeraldo, 16 (HBS), Howey-in-the-Hills, 1 (USNM).

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[*] The source of the Anclote River is in Pasco County, not Hillsborough. Moreover this river originates in swamps unsuited to the requirements of the species. Possibly the type specimen came from the dry area near Lutz in Hillsborough County, some 10 miles farther south.

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Numbers of the BULLETIN OF THE FLORIDA STATE MUSEUM are published at irregular intervals. Volumes contain about 300 pages and are not necessarily completed in any one calendar year.

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Communications concerning purchase or exchange of the publication and all manuscripts should be addressed to the Managing Editor of the Bulletin, Florida State Museum, Seagle Building, Gainesville, Florida. 32601.

Published April 19, 1968 Price for this issue $1.20