

Palatal ridges as an epigenetic marker in *Rattus rattus* and *Rattus exulans* populations

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Abstract

Palatal ridges of 240 roof rats (*Rattus rattus*), 236 Polynesian rats (*Rattus exulans*) from the Enewetak Atoll, Marshall Islands, and 22 roof rats (*R. rattus*) from the Galápagos Islands were examined to test the feasibility of using these characteristic patterns as an epigenetic marker to separate rat populations. The "mean divergence" was calculated for seven major palatal ridge characters.

Large homogeneous rat samples from Enewetak Atoll, served as "indicator" populations for determining the strength of this technique. It was concluded that this statistic reflected theoretical assumption of similarity between neighboring islet populations and greater distinctiveness of populations farther apart. It was further hypothesized that deformations of diastemal ridges found in some Polynesian rat populations might be due to radiation effects and that founder effect is present on two small islets of the Galápagos Islands.

Introduction

Nonmetrical, or discontinuous, characters, such as the absence or presence of such skeletal variants as accessory foramina or sutures, have been applied to describe variations at the population level (BROTHWELL 1958; BERRY 1963, 1964, 1968, 1970; BERRY and SEARLE 1963; BERRY and BERRY 1967; PATTON et al. 1975). Epigenetic variants, which are expressions of genes affecting development, can reflect heritable differences among populations (BERRY and BERRY 1967). Application of these techniques to rodent populations has been made by BERRY (1964, 1970), GRÜNEBERG et al. (1966), and PATTON et al. (1975). Island populations are especially amenable to this approach because of their separation and confinement.

A rather unfamiliar example of such an epigenetic feature in rodents is the palatal ridge (Rugae palatinae) pattern. Palatal ridges, a peculiar mammalian feature, received early anatomic attention (CUVIER 1845; MILNE-EDWARDS 1860; GEGENBAUR 1878; HARRISON 1888; KOLENATI 1860; ROBIN 1881; LINTON 1905; RETZIUS 1906; ANDERSEN 1912). More recently EISENTRAUT (1969, 1975a, b) incorporated palatal ridge features into identification criteria and in phylogenetic considerations of West African Murids and Sciurids. EISENTRAUT provided detailed descriptions, including numerous figures of palatal ridge morphology in about 530 species of 117 mammalian families. MARSHALL (1972) also attempted to use palatal ridges in the difficult task of classifying Asian rodents.

EISENTRAUT (1969, 1976) pointed out that the morphology of palatal ridges may become a useful taxonomic and phylogenetic aid, although his results did not meet such expectations fully. Interspecific and intraspecific variations are great, and overlapping of pattern requires analysis of large samples.

A detailed description of intra- and interspecific variation in palatal ridges of over 500 Norway rats (*Rattus norvegicus*) from 26 major U.S. cities, 52 rice-field rats (*R. argentiventer*) and a few specimens of less common rodents (*R. everetti*, *R. adustus*, *R. losea*) from tropical Asia is given by TEMME (1977). He attempted also to assess the validity of palatal ridges of *Rattus* as a taxonomic aid and described variations on the population level. This paper deals with epigenetic variation of populations of roof rats (*R. rattus*) and Polynesian rats (*R. exulans*) from Enewetak Atoll, Marshall Islands and *R. rattus* from the Galápagos Islands.

Material and methods

Specimens of roof rats ($n = 240$) and Polynesian rats ($n = 236$) were caught in single trapping episodes on several islets at Enewetak Atoll (Fig. 1) in March 1977. Two samples of *R. rattus* were obtained in January 1977 from the two islets Eden ($n = 10$) and Sombrero Chino ($n = 12$) of the Galápagos Islands (Fig. 2). The animals were decapitated and their heads preserved in 10% formalin. Later the heads were boiled in water and the flesh removed superficially; the palatal ridges remained in the skull.

All palatal ridges were examined under a dissecting scope and their configuration classified in accordance with established four attributes for each of the five intermolar ridges. Special attention was given to aberrant ridge patterns. These specimen characteristics often were drawn, and many were photographed. All skulls and their palatal ridges were checked and scored independently five times at different time intervals to ensure maximum

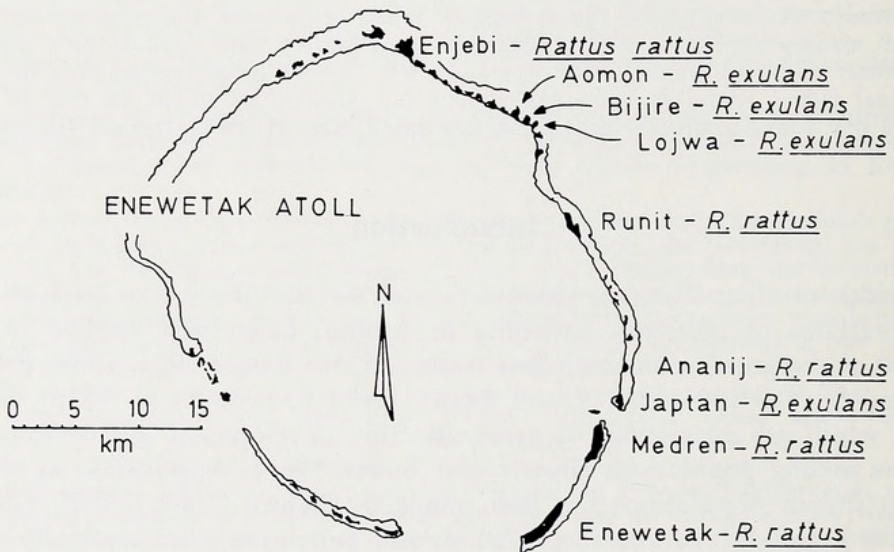


Fig. 1. Islets at Enewetak Atoll, Marshall Islands, on which rat populations were sampled

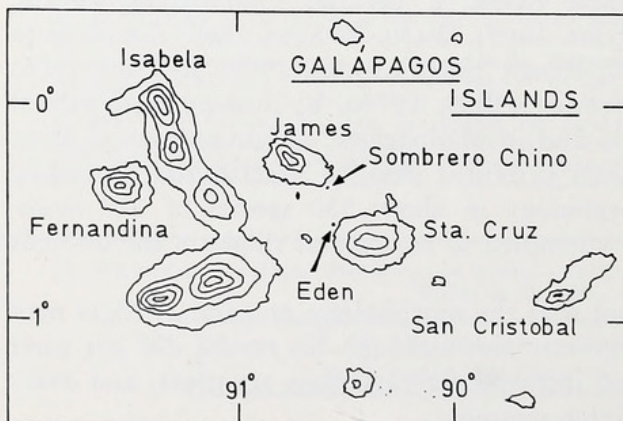


Fig. 2. Localities of roof rat (*R. rattus*) populations in Galápagos Islands sampled

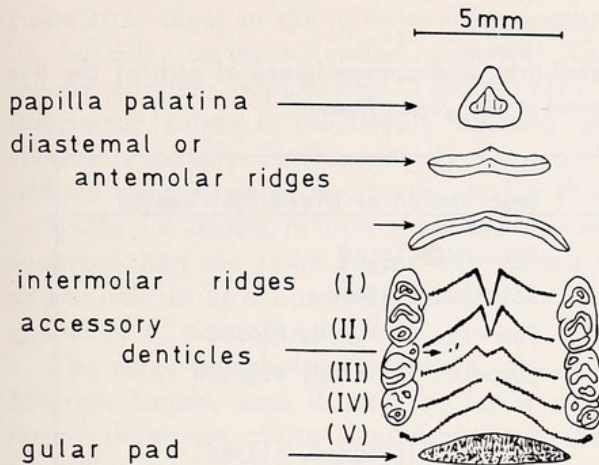


Fig. 3. Nomenclature of palatal ridges. This schematic example shows a typical and regular pattern in a roof rat (*Rattus rattus*)

objectivity in determining features. It could not be claimed that uniformity in scoring could be always achieved by different workers, but one experienced individual achieved consistent results.

Establishing palatal ridge attributes and devising a nomenclature of descriptive and qualitative terms was desirable (Fig. 3). As suggested by BARBEHENN (personal communication), botanical terms, as they are used to describe configurations of leaf margins, seemed to be most appropriate and therefore are introduced here (Table 1). The character statements given here apply to the *Rattus* group but probably could be modified for other mammal orders and genera.

Statistical analysis

The utilization of large samples from discrete populations in the study of palatal ridges of rodents has not occurred before. A non-metrical approach, utilizing ridge attributes, which could be considered epigenetic characters, was directed at obtaining a measure of divergence, following the procedures applied by BERRY (1963, 1964, 1968) and BERRY (1967).

Each of the five intermolar ridges was classified into four character statements and attributes; dichotomous decisions were made for each ridge. For example, whether the ridges were closed or clefted mid-ventrally was a specific concern for ridges I, II and III; ridges IV and V were scored in accordance with their shape. The presence or absence of accessory denticles and additional ridges also was noted. Each animal was scored for seven data points, and the incidence of each character in each population was determined.

Distinctiveness between two populations was measured by the mean measure of divergence, which is expressed as:

$$\Sigma (\Theta_1 - \Theta_2)^2 - (1/n_1 + 1/n_2)/N$$

where:

Θ = angular transformation of the percentage incidence (p) for any character (in radians) such that $\Theta = \sin^{-1} (1 - 2p)$

n = sample size of the respective population

N = number of characters (= 7) taken

According to BERRY and BERRY (1967), this formula has the advantage over the more common angular transformation ($\Theta = \sin^{-1} \sqrt{p}$ in degrees) in that the variance of Θ in sample of size n is almost $1/n$ independently of the value of n , instead of $820.7/n$.

Because Θ has the variance $1/n$, this formula has the additional property that $\Theta_1 - \Theta_2$ has variance $1/n_1 + 1/n_2 = V$. With one degree of freedom, $(\Theta_1 - \Theta_2)^2/V$ will be approximately distributed as χ^2 and significant at the 0.05 probability level if it is greater than 3 V ; at the 0.01 level, if it is greater than 6 V . An estimate of the standard deviation of the mean measure of divergence is given by the formula:

$$\sqrt{4 (1/n_1 + 1/n_2) \Sigma [(\Theta_1 - \Theta_2)^2 - (1/n_1 + 1/n_2)]/N}$$

The mean measure of divergence is a quantitative expression for all identified characters of the separation of the populations (BERRY 1964; BERRY and BERRY 1967). However, it is understood that those values do not represent actual or absolute relationships between populations, nor can any conclusion be drawn directly from these data. However, BERRY et al. (1967) believe that such measures of divergence more accurately reflect genetic differences than statistics from metrical data.

Table 1

Schematized palatal ridge configurations, attributes, and nomenclature of each of the five intermolar ridges found in the genus *Rattus*

| Designation | Schematized Shape | Description of mid-dorsal wedges |
|-------------|-------------------|----------------------------------|
| IA | | Retused, closed |
| IB | | Retused, clefted |
| IC | | Cuneate, inflexed, closed |
| ID | | Cuneate, inflexed, clefted |
| IIA | | Cuneate, inflexed, closed |
| IIB | | Retused, closed |
| IIC | | Cuneate, inflexed, clefted |
| IID | | Retused, clefted |
| IIIA | | Cuneate, inflexed, closed |
| IIIB | | Cuneate, inflexed, clefted |
| IIIC | | Retused, closed |
| IIID | | Retused, clefted |
| IVA | | Obtused angled, clefted |
| IVB | | Acute angled, clefted |
| IVC | | Obtused angled, closed |
| IVD | | Acute angled, closed |
| VA | | Aristate |
| VB | | Cuspidate |
| VC | | Acute |
| VD | | Acuminate |

Additional features:

| | |
|--|-------------------------------------|
| A) without accessory denticles | B) one or few "accessory denticles" |
| C) one-fourth to one-half of an additional ridge | D) full additional ridge |

Results and discussion

Description of palatal ridges

Although the pattern of palatal ridges in *R. rattus* superficially resemble that of *R. norvegicus* (TEMME 1977), careful comparison reveals differences in some of the ridges. The first intermolar ridge (I) was found not to be retused but cuneately inflexed (99% incidence); of these, 75% were clefted. In *R. rattus* the bilateral

ridge arms taper in the mid-dorsal region as the denticles diminish in size; the edge of the ridge becomes "entire" (smooth). Considerable variation in this cleft exists among different populations (TEMME 1977). Another characteristic of the first three intermolar ridges is the deeply inflexed and elongated wedge. Ridge III in this species is usually less irregularly shaped than in *R. norvegicus*, forming clearly defined wedges, which are mostly smaller than the ones by ridge II.

Ridge IV occurs in two versions. The obtused angled and clefted form is more common than the acute angled and clefted one. Ridge form IV_C is rare and found so far only in two Enewetak specimens. The fifth ridge (V) configuration is similar to that of *R. norvegicus*.

The ridge morphology of the *R. rattus* samples from the Enewetak Atoll islets Medren, Enjebi, and Runit (the latter two being major sites in the nuclear test series) shows no major deviation from the basic *Rattus* pattern. The population from Enewetak islet of the Atoll is distinguished by the acuminate form (V_D) of the fifth ridge. This ridge resembles closely the type found on Galápagos islet of the Sombrero Chino.

The most distinctive character of the Galápagos island populations is the shape of ridge V. In the homogeneous sample from islet Eden, the aristate ridge does not reach ridge IV (Fig. 4). In the Sombrero Chino sample of 12 specimens, however, the more acuminate ends of ridge V extend into the mid-dorsal field of ridge IV. Another distinguishing feature of these two populations is the pelage. All rats from Eden show the traditional "alexandrinus" pelage, whereas the specimens from Sombrero Chino are entirely of the "frugivorous" coloration (D. CLARK, personal communication).

The palatal ridges of the Polynesian rat show also the characteristic *Rattus* configurations. All 236 specimens of four populations from the Enewetak Atoll, considered as the subspecies *R. e. exulans* (JOHNSON 1962), have the first type of ridge I_D, the cuneately inflexed, clefted form. The samples revealed another character of high incidence — the two arms of ridge IV inflexed so as to form another W-shape in the center. Reduced variation is found in ridge V; more than 90% of these ridges

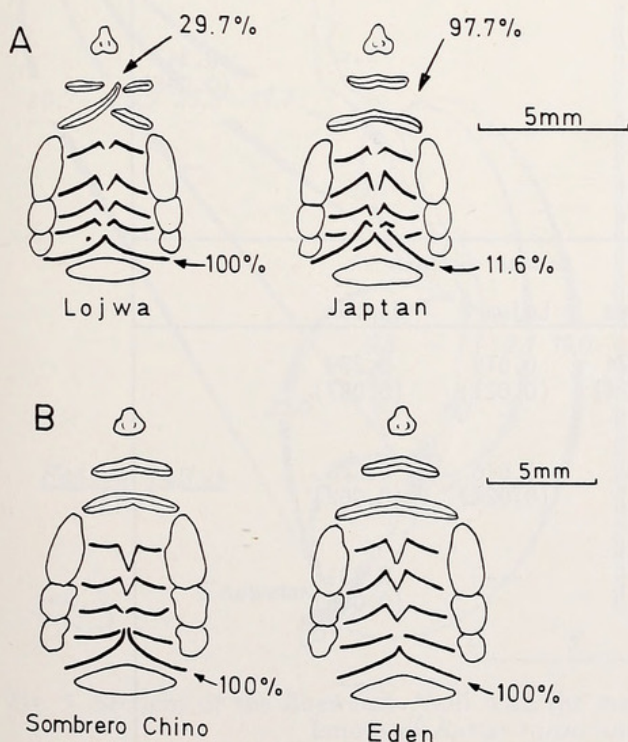


Fig. 4. A: Diastemal ridge deformation in *R. exulans*. On the three neighboring Enewetak islets Aomon, Bijire and Lojwa the frequency of this deformation is relatively high: 12.5%, 12.7% and 29.7%. On the islet Japtan, about 20 km apart, the frequency of this deformation is lower. A new aberration of the intermolar ridges (IV) and (V) is found (11.6%). — B: Ridge divergence between two *R. rattus* populations. On the Galápagos islet Sombrero Chino, the fusion of the ridges (IV) and (V) is consistently found, whereas on the islet Eden the ridge (V) remains below ridge (IV) in all animals examined

are of the type V_C , more or less acutely shaped. Accessory denticles are present in this species in varying frequencies and are confined to the interridge space between ridges IV and V.

The Enewetak Atoll Polynesian rat samples have a high incidence of aberrantly shaped diastemal ridges. The arms of the often-divided diastemal ridges point either upward or downward and extend between each other (Fig. 4). A local peculiarity are the deformations between both intermolar ridges IV and V found in the Japtan Islet sample (Fig. 4).

Palatal ridges as an epigenetic marker

The discovery of the distinctiveness of the two populations of the Galápagos islets of Eden and Sombrero Chino, based solely on palatal ridges and corresponding differences in coat color, gave the study of palatal ridges impetus. BERRY (1963, 1964) pre-

Table 2

Mean measure of divergence between geographically separated rat populations from the Marshall Island (Enewetak Atoll)

The figures in parentheses are estimates of the standard deviation. (All values = $P < 0.01$)

| <i>Rattus rattus</i> | | | | | |
|-----------------------|----|------------------|------------------|------------------|------------------|
| Islets | n | Runit | Ananij | Medren | Enewetak |
| Enjebi | 44 | 0.177 (0.065) | 0.255 (0.080) | 0.265 (0.075) | 0.397 (0.111) |
| Runit | 50 | --- | 0.135 (0.056) | 0.021 (0.021) | 0.190 (0.076) |
| Ananij | 46 | | --- | 0.096 (0.045) | 0.314 (0.099) |
| Medren | 69 | | | --- | 0.347 (0.096) |
| Enewetak | 31 | | | | --- |
| <i>Rattus exulans</i> | | | | | |
| Islets | n | Bijire | Lojwa | Japtan | |
| Aomon | 40 | 0.024 (0.024) | 0.015 (0.021) | 0.209 (0.067) | |
| Bijire | 55 | --- | 0.026 (0.024) | 0.228 (0.062) | |
| Lojwa | 55 | | --- | 0.131 (0.048) | |
| Japtan | 86 | | | --- | |

viously had shown that it is possible to detect genetic variation in island populations, especially with the use of nonmetrical character variants. Calculation of the mean measure of divergence provides an analytical tool for comparisons of populations.

To test the presence or absence of any correlation between the different ridge variants, the correlation coefficient (tetrachoric r) was calculated between 7 variants of 500 specimens, using the method refined by JENKINS (1955). Except for the ridge pairs I and III in *R. rattus* and ridge pair II and III in *R. exulans*, no strong correlations between configurations were found. It appears that these correlations are partly due to the characteristic clefted forms of these ridges in the two species. The virtual absence of strong correlations between ridges made it possible to sum all individual measures of divergence and calculate their means without the necessity to perform complicated corrections.

The homogeneous samples of *R. rattus* and *R. exulans* from islets of Enewetak Atoll serve ideally as "indicator populations" to test the validity of palatal ridges as an epigenetic trait and to test the strength of the mean measure of divergence for these characters. Specimens of both species, allopatrically distributed over the islets of the Atoll, have been obtained from neighboring islets, which permits some geneflow possibilities, and from others far enough apart to disrupt intermovements. Similarities in ridge configurations are quite obvious by superficial inspection of the samples from neighboring populations, whereas islets farther apart show a higher degree of deviation. This is also reflected by the mean "measure of divergence" (Table 2, Fig. 5).

The mean measure of divergence clearly demonstrates a relatedness of the three

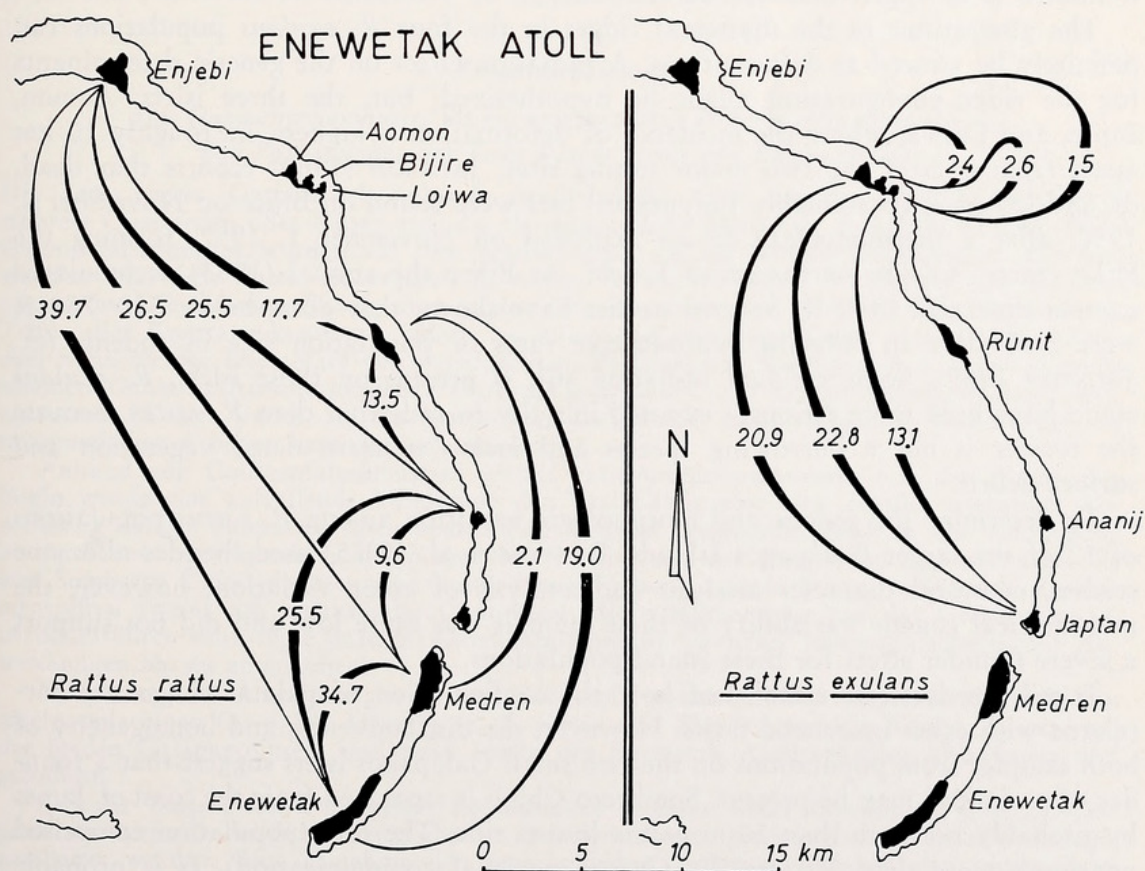


Fig. 5. Sections of the Enewetak Atoll with the mean measure of divergence ($\times 100$) populations of *Rattus rattus* and *Rattus exulans*

R. exulans populations on the three neighboring islets of Aomon, Bijire, and Lojwa. Gene flow probably has occurred, since the islets have been connected by a bridge and a causeway, respectively, for more than two decades. The increasing distinctiveness of Enewetak Atoll rat populations of both species with increasing geographical distance is apparent and shows a relatively good correlation *R. rattus*, $r = 0.5174$; *R. exulans*, $r = 0.9481$).

Additional evidence for this conclusion is given by the almost identical incidence of diastemal ridge deformations in *R. exulans* on the three neighboring islets Aomon, Bijire, and Lojwa; this decreased to only 2.3% on Japtan, which lies roughly 20 km apart in the south (Fig. 4).

Strong evidence of founder effect, as found on the two Galápagos islets, is not apparent in the Enewetak Atoll populations; but a reduction of variation definitely occurred. It is assumed, based on conversations with Enewetak people, that prior to 1946 only Polynesian rats were present at Enewetak Atoll and that roof rats were introduced during post-World War II activities. As of now, both rat species live allopatrically on the islets; the Polynesian rats are found only on the more mesic, and the roof rats on the more disturbed and xeric islets.

At Enewetak Atoll the islets Enjebi and Runit were the major sites of nuclear testing and were exposed to heavy radiation between 1948 and 1958 (JACKSON and CARPENTER 1967). In *R. rattus* populations from both islets no major deviants were found in the palatal ridges. GEORGE SACHER (personal communication) has determined that this species is unusually resistant to the effects of X-radiation. Roof rats on the islet Runit, however, have exhibited an increasing prevalence of black pelage coloration over the past 15 years, likely evidence of genetic drift in this population estimated to be approximately 500 animals.

The aberrations in the diastemal ridges in the four *R. exulans* populations can definitely be viewed as deformations. A radiation effect on the genetic determinants for the ridge configuration might be hypothesized; but, the three islets, Aomon, Bijire, and Lojwa, where the incidence of deformation is highest, lie roughly 10 km apart from each of the two major testing sites. JACKSON (1969) reports that dead, ill, and lethargic (presumably Polynesian) rats were found on Bijire on November 8, 1952, after a thermonuclear device exploded on November 1, 1952, forming the Mike crater, 4.8 km northwest of Enjebi. At Bijire the annual (1953) accumulated gamma dose was 1440 R. Several studies have shown that doses below 500–750 R were ineffective in reducing reproductive rates or population size in rodents (cf. JACKSON 1969). Some residual radiation still is present on those islets. *R. exulans* could have been more seriously exposed initially to radiation than *R. rattus*, because the former is not a burrowing species and makes nests in dense vegetation and surface debris.

To determine the genetic and morphologic variation among *R. rattus* populations of 12 of the larger Galápagos Islands, PATTON et al. (1975) used, besides allozyme studies, mensural character analysis and analysis of color variation; however, the non-metrical genetic variability of these animals was quite low and did not support a severe founder effect for these island populations.

It still needs to be established how the configuration of palatal ridges are correlated with other epigenetic traits. However, the distinctiveness and homogeneity of both samples from populations on the two small Galápagos islets suggest that a founder effect indeed may be present. Sombrero Chino is separated from the coast of James by probably no more than 30 m at the lowest tide. The total population comprised not much more than 30 rats (D. CLARK, personal communication). It is probable that a few rats colonized this islet on their own. *R. rattus* was already on James (Isla Santiago) on DARWIN'S visit in 1835 (LACK 1947; PATTON et al. 1975). Islet

Eden lies northeast of Sta. Cruz, separated by a narrow channel approximately 60 to 120 m wide. It is possible that Eden was colonized from Sta. Cruz, on which most of the rats are also of the "alexandrine" coloration (D. CLARK, personal communication). The estimated population on Eden may be only about 100 rats. There is no likelihood of rats moving between Eden and Sombrero Chino.

Conclusively, it can be said that the mean measure of divergence is applicable to the presence and absence of certain ridge characters and detects satisfactorily relative differences between populations. Because palatal ridges basically are genetically controlled, it would probably be best to see them as a composite and treat them statistically in that manner. If individual ridges and their incidences of variations are compared among populations, often statistical significance is determined.

The question still remains whether the incidence of an individual variant (in one ridge), even if it is formally significant, is all that meaningful. Slight disadvantages, associated with the measure of divergence, by summing up all the differences of all variants and averaging them, are fully discussed by BERRY (1963), BERRY and BERRY (1967). Too little is known so far about the genetic determination of the palatal ridges. Whether they can be regarded as a pleiotropic manifestation of allelomorphs, as BERRY (1964) established for his skeletal variants, is not clear. The trivial morphological characters of the palatal ridges may well be used as markers to trace, in part, the genetic divergence among different, well-separated rodent populations.

Acknowledgements

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Zusammenfassung

*Das Gaumenfaltenmuster als ein epigenetisches Differenzierungsmerkmal von Populationen der Taxa *Rattus rattus* und *Rattus exulans**

Die den „harten Gaumen“ bedeckende Epithelschicht weist bei den meisten Säugetieren mehrere Querleisten oder Falten auf, die als epigenetische Merkmale aufgefaßt werden. Diese Gaumenfaltenmuster wurden auf ihre Brauchbarkeit als ein Bestimmungsmerkmal nah verwandter Muriden: *Rattus norvegicus*, *R. rattus*, *R. argentiventer*, *R. exulans* und *R. losea* untersucht. Die Gattung *Rattus* zeigt in den Grundmustern eine ziemliche Übereinstimmung. Trotz aller Konstanz kommt es jedoch zu inner- und zwischenartlichen Variationen, besonders wenn wenige Exemplare von verschiedenen Populationen vorliegen. Aus diesem Grunde scheinen Gaumenfaltenmuster dieser Gattung nicht allein als Artbestimmungsmerkmal auszureichen, können jedoch als ein wertvolles, zusätzliches morphologisches Kennzeichen zu taxonomischen Arbeiten herangezogen werden.

Anhand von Gaumenfaltenmustern zweier Hausrattenpopulationen von den Galápagosinseln wurde eine auffallende Minderung der Variabilität aber eine deutlich trennende Abweichung einiger Falten zwischen beiden Populationen festgestellt. Auch in der Fellfärbung ist die Trennung erkennbar, indem sämtliche Ratten von der Insel Eden eine schwarze, die von Sombrero Chino dagegen eine braun-graue Färbung zeigen. Dieses auffallende Zusammentreffen zweier sich ergänzender Charaktere, die möglicherweise auf das Gründerprinzip zurückzuführen sind, regte dazu an Gaumenfaltenmuster weiterer Inselpopulationen auf Abweichungen hin zu untersuchen.

Morphologische Abweichungen in den Gaumenfaltenmustern von insgesamt 11 isolierten Inselpopulationen (n = 240 Hausratten, *R. rattus* und 236 Polynesische Ratten, *R. exulans*) der beiden Galápagosinseln und neun Inseln des Enewetak Atolls wurden klassifiziert und tabelliert.

Auf der Basis dieser homogenen Populationen konnten unter Errechnung eines „Divergenzmittelwertes“ deutliche Unterschiede zwischen diesen geographischen Isolaten herausgearbeitet werden. Eine Zunahme der geographischen Isolation zwischen den untersuchten Populationen wird durch höhere Divergenzmittelwerte ausgedrückt. Geringe Unterschiede der Gaumenfaltenmuster dagegen, wie sie zwischen drei *R. exulans* Populationen der Inseln Aomon, Bijire und Lojwa des Enewetak-Atolls bestehen, werden durch niedrigere Divergenz-

mittelwerte aufgezeigt. Diese drei Inseln wurden vor etwa zwei Jahrzehnten mit je einer Brücke und einem Damm miteinander verbunden, wodurch Genaustausch zwischen diesen Populationen möglich wurde.

Eine hochgradige Abnormität der antemolaren Falten der Ratten von den Inseln Aomon, Bijire und Lojwa wird als eine Mutation angesehen, die möglicherweise durch radioaktive Rückstände hervorgerufen wurde. Diese Rattenart war von 1948 bis 1958 den Auswirkungen atomarer Versuchsexplosionen ausgesetzt, die auf den nur etwa 10 km entfernt liegenden Inseln Enjebi und Runit durchgeführt worden waren.

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Some observations on reproduction in *Rattus rattus* (L.) in Rangoon, Burma¹

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Abstract

Observations on the reproduction of *Rattus rattus khyensis*, a white-bellied commensal roof rat common in Rangoon, are described. Breeding activity is seen in all months of the year with no marked seasonal fluctuations. Female *R. r. khyensis* become sexually active at approximately 130 mm head and body length and at 60 g body weight. Prevalence of pregnancy in adult females averaged 33.3 % for the entire 2-years sampling period. Breeding activity as judged by both pregnancy and lactation averaged 52.8 % of all adult females. Litter size was found to be $5.03 \pm .21$ with very little evidence of intrauterine embryo loss. The mammary pattern was determined to be $3 + 3 = 12$, caused by a twinning of the postaxial mammae. The 50 % point for scrotal testes in males occurred at a head and body length of 124 mm and an approximate body weight of 50 g, with sexual activity evident year round.

The high rate of breeding activity is indicative of a population subject to heavy population pressure, predation and stress and a consequent high mortality rate. Similar observations have been noted for *Rattus exulans*, *Bandicota bengalensis* and *Suncus murinus* in Rangoon. Recruitment of young is almost continuous and populations are maintained only by a high degree of breeding activity with little seasonal fluctuation.

Introduction

In Burma, the commensal *Rattus rattus* complex is represented by white-bellied rats (subspecies *khyensis*, *brunneus*, etc.) which are typically found in such places as bamboo clumps, and are secondarily house rats (HARRISON and WOODVILLE 1948;

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