3. The specific relations of Rattus tiomanicus (Miller)

By LORD MEDWAY

and

B. L. LIM

INTRODUCTION

RATS OF THE subgenus Rattus are endemic on many of the islands off the coast of Malaya. In most cases each population is recognisably distinct from other island forms, and from related rats on the Malayan mainland. Many island forms have been described, including R. tiomanicus (Miller) the ecology of which has already been discussed (Medway, this Bulletin, p. 20). On the mainland three ecologically separated forms occur (Chasen, 1933), namely, the Malaysian House Rat, diardii11 Jentink, the Malaysian Field Rat, jalorensis Bonhote, and the Ricefield Rat, argentiventer Robinson and Kloss. These three, together with all island forms, were listed by Chasen (1940) as subspecies of R. rattus (Linn.) However, Harrison (1961) has surveyed the distribution of these and related rats throughout Eurasia and adjacent regions, and has suggested that the three forms are best regarded as distinct species of Rattus, "each of which is a commensal with man, which have been separately introduced into Malaysia, and which have not yet wholly occupied the area" (Harrison, 1961: 23). Independently, Dhaliwal (1962 & 1963) has undertaken a detailed morphological comparison of series of jalorensis and diardii from two Malaysian localities, and has shown statistically that the two taxa are distinguished by differences of species rank. Both Harrison (1961) and Dhaliwal (1962) have also noted that several of the island forms are little differentiated from R. jalorensis, and are better considered races of this species rather than of R. rattus.

On the other hand, on Singapore Island (where argentiventer is unknown) jalorensis occurs only in a very restricted area, probably having been absent until recently (Searle and Dhaliwal, 1961). On the Malayan mainland, in localities where they are sympatric, jalorensis, argentiventer and diardii are separated by habitat preference; but if one or more is absent, the remaining species characteristically expands to occupy the vacant niches (Harrison, 1957). Similarly in Singapore diardii occurs in a wide range of habitats, including not only houses but also field and fringe habitats that on the mainland are occupied by jalorensis (Dhaliwal, 1961).

R. argentiventer is the more highly specialised rat, and its distribution is limited by its relatively stringent ecological demands. But it is clear that either of the more adaptable diardii or jalorensis may occur on islands, and that in the absence of competition either may exploit an equally wide range of habitats. Consequently the ecology of an island form is no indication of its taxonomic relations.

It appears from the distribution of *jalorensis* on Singapore Island that the species has entered only recently. By inference, the narrow sea barrier of the Straits of Johore had hitherto effectively prevented the spread of this rat. R. jalorensis is probably the older commensal rat in mainland S.E. Asia and diardii a more

The emended spelling diardi is preferable to the original diardii, (which was used by Chasen, loc. cit.), see the International Code of Zoological Nomenclature (1961 edition). Article 31, Article 32 (c), and Appendix D (III) 16 (b).

recent introduction (Harrison, 1957). But the case of Singapore Island stresses that it is not possible to assume on theoretical grounds that an island form such as tiomanicus is a race of the more ancient species. In fact it is clear that under modern conditions the cosmopolitan diardii is better equipped than jalorensis to

cross the relatively broad sea barrier.

It is characteristic of island situations of this sort, where one of two closely related and normally exclusive species is absent, that the population of the species that is represented should be intermediate in character (e.g., also among Muridae, Cranbrook, 1957). This is true of *tiomanicus*, and it is by no means clear on superficial inspection to which species this island rat should be ascribed. In the present contribution we have attempted to assess the specific relations of *tiomanicus* by detailed comparison of morphological characters.

MATERIALS

Measurements of tiomanicus are taken from a series of 28 adults of both sexes collected by us from the main island; we have also included 9 adults of both sexes from P. Tulai. For diardii and jalorensis, where we have not made use of Dhaliwal's published measurements, our figures are based on a series of 17 diardii and 18 jalorensis, adults of both sexes, collected from Selangor.

The preserved material is divided among the collections of the Institute for

Medical Research and the Department of Zoology, University of Malaya.

COMPARISON OF CHARACTERS

EXTERNAL CHARACTERS

The dorsal pelage of *R. jalorensis* is brown, and relatively sleek with only a slight admixture of soft spines; the venter is white to greyish white. The dorsal pelage of *R. r. diardii* is also brown, but is coarser and harsher; the venter on the mainland is usually brownish grey, but among the population on Singapore Island varies in colour from this shade through grey to nearly white. Dhaliwal (1963), by microscopic study of the hair types, has shown that auchenes and zigzags of the ventral pelage are always unpigmented in *jalorensis*, and always pigmented in even the palest *diardii* and in hybrids between the two forms. Topotypes of *tiomanicus* resemble *jalorensis* dorsally, but ventrally vary like *diardii* from brownish grey through grey to greyish white; both auchenes and zigzags of the venter may be pigmented. The population on Tulai is distinguished by a pure white venter.

Where the two forms are sympatric, diardii and jalorensis are also readily distinguished by measurement. In Table 1 the principal dimensions in the flesh of two populations of diardii and jalorensis (from Dhaliwal, 1962) and of our series from Tioman and Tulai are compared. The mean head and body length of tiomanicus topotypes is within the total range of variation of jalorensis from the two localities; it is also not significantly different from the mean head and body length of Singapore diardii. The mean head and body length of the series from Tulai is larger, although not significantly larger than that of Singapore jalorensis. In both series the tail is generally longer than the head and body, a charac-

teristic of diardii rather than of jalorensis (mean $\frac{T}{HB}\%$ is 101.5 \pm 1.3% for

tiomanicus topotypes, $106.5 \pm 2.1\%$ for the Tulai series). The hind feet are intermediate in length. The ear is within the range of variation of diardii, and significantly larger than the ear of jalorensis.

TABLE 1

Principal measurements of diardii, tiomanicus and jalorensis, in mm given as means ± S.E. of mean. Figures for diardii (Singapore and Selangor) from Dhaliwal (1962).

					dlardii (Singapore)	diardii (Selangor)	tiomanicus (Tioman)	Tulai rat	Jalorensis (Selangor)	jalorensis (Singapore)
Head and body	dy	\$	*		184,4±1.7	170.8±3.1	170.8±2.0	178.3±2.8	167.7±1.3	176,9±2.6
Tail		*	**	40	186.9±1.9	180.5±4.2	174.1 ± 2.1	189.3±5.4	160.6±1.3	158.8 ± 4.3
Hind foot	7	*	#/	53.	35.2±0.2	35.0±0.4	33,3±0,2	34.4 ± 0.1	31.7±0.2	32.7±0.3
Ear	•	*	:	613	20,4±0.2	21.3±0.3	20.7±0.1	20.6±1.0	19,4±0.1	19.8±0.3
Occipitonasal length of skull	l length o	f skull	*	*	41.5±0.2	41.6±0.3	41.9±0.9	41.3±0.1	40,2±0,4	40,6±0,9
Length of right anterior palatatal fo	ht anteric	or palatatal	foramen	4	7.7±0.05	7.7 ± 0.1	6.8±0.1	7.0±0.7	6.8 ±0.05	7,1±0,1
Maxillary toothrow	othrow	=11		i.	7.1±0.05	7.1 ± 0.04	6.7 ±0.04	6.6±0.1	6.8+0.04	6.7+0.05

The hindfoot of diardii as well as being absolutely longer is also proportionately longer than the hindfoot of jalorensis; in this character tiomanicus is again intermediate. The proportions length of hind foot: length of head and body, expressed as the mean of the percentages \pm S.E., are as follows: diardii (Selangor) 19.8 \pm 1.3%, jalorensis (Selangor) 18.8 \pm 0.8%, tiomanicus (topotypes) 19.5 \pm 0.6%, from P. Tulai 19.3 \pm 0.2%.

SKULL CHARACTERS

Skull measurements are also given in Table 1. It is seen that the skull of tiomanicus is larger, in occipitonasal length comparable to diardii and not jalorensis. On the other hand certain important features of the skull, notably the small anterior palatal foramen and the short toothrow, are closely compatible with

jalorensis, and significantly different from diardii of all localities.

Dhaliwal (1962) has suggested that the foramen magnum of jalorensis tends to be more ventrally placed than that of diardii. Any significant difference in this character between the two taxa should be revealed by the ratio basal length: occipitonasal length, where basal length is measured from the anterior margin of the foramen magnum. We have analysed both this ratio from measurements of diardii and jalorensis from Selangor, and the ratio condylobasal length: occipitonasal length, from Dhaliwal's original measurements of his series from Singapore and Selangor. We find that there is wide individual variation within both taxa, without significant difference between the means. We conclude that this character cannot be used to distinguish between the species.

There is one other important skull character that cannot be reduced to metrical terms. This is the degree of development of the supraorbital ridges, which are more pronounced in diardii than in jalorensis (Dhaliwal, 1962). We find that in diardii these ridges extend forward distinctly to the base of the zygomatic arch on the jugal, whereas in jalorensis they terminate at a point posterior to the posterior suture of the jugal behind the base of the zygomatic arch. Using this character we are able to pick out skulls of diardii and jalorensis from mixed collections with very few mistakes. In this character too, the skull of tiomanicus is not intermediate but is decidedly of the jalorensis type, readily distinguished from that of diardii.

DISCUSSION

In Table 2, the principal characters of R. tiomanicus are summarised, and the relations that they suggest are indicated. It is seen that there is a predominance of characters indicating affinity with jalorensis. Moreover three of these characters relate to the anatomy and proportions of the skull rather than to absolute size. Discussion of the mammalian fauna of Tioman (Medway, this Bulletin, p. 24) has already shown that the endemic subspecies of rats and other rodents on the island may be distinguished from their mainland congeners by appreciable variations both in pelage coloration and in body size and proportion (particularly in the length of the tail). By inference, affinities indicated by characters of this nature are significant only at the subspecific level, and are not reliable indicators of specific relationship.

We therefore attach considerably more importance to the three skull characters listed, all of which are noted by Dhaliwal (1962: 258) among the essential differences between jalorensis and diardii. On the basis of these characters, we suggest that tiomanicus should be regarded as conspecific with jalorensis rather than with

diardii12.

^{12.} Attempts to produce hybrids with other forms were not successful. Sixteen tiomanicus were brought back from the island and paired as follows: 4 with jalorensis, 4 with diardii, and 8 with jarak Bonhote, the form endemic on P. Jarak in the Straits of Malacca, which has crossed freely with jalorensis in captivity at the I.M.R. We have no evidence of fertile matings from any of these pairs.

TABLE 2

Affinities of the principal characters of topotypical tiomanicus (measurements in mm.) Resembling Intermediate Resembling diardii ialorensis Ventral pelage grey-brown to pale grey; auchenes and zigzags both pigmented Dorsal pelage relatively sleek. Tail generally greater than Mean head and body 100%HB length 170.8 ± 2.0 Mean hindfoot length 33.3 ± 0.2 Mean ear length 20.7±0.1 Occipitonasal length of skull Length of anterior palatal foramem 6.8±0.1

 41.9 ± 0.9

Length of maxillary toothrow 6.7 ± 0.04 . Supraorbital ridges relatively weekly developed,

The variation in ventral coloration is probably related to habit (cf. Harrison, 1961). The venter of the house and town dwelling diardii of mainland Malaya is greyish brown, but on Singapore Island where this form occupies a wide range including field and fringe habitats, the ventral coloration is very variable, from greyish brown to pale grey (Dhaliwal, 1963). Conversely tiomanicus, although apparently descended from a white-bellied form, shows considerable darkening in ventral coloration in accordance with its range of habitats including close commensal situations. On P. Tulai only the field habitat is available, and the rat population is, like mainland jalorensis, white bellied. The rat of Tulai is significantly larger than jalorensis and is as distinct as many of the island forms that have been described as separate subspecies. Its affinity with tiomanicus and jalorensis is again indicated by the skull characters discussed.

The name tiomanicus dates from 20th August, 1900 (Proc. Wash. Acad. Sci., 2: 209), and is in fact the oldest name available for the pale-bellied field rats of Malaysia. The name tiomanicus was used by Sody (1941) to designate this group, although subsequent authors have preferred to preserve the epithet ialorensis. It is an unfortunate result of the international rules of nomenclature that the older name, albeit applied only to an island population, must take precedence, so that the name jalorensis is superceded as specific epithet for the Malaysian Field Rat.

Harrison (1961) has discussed the white-bellied forms occurring outside this region. From India the oldest name available appears to be brunneusculus Hodgson 1845; this in turn is antedated by frugivorus Rafinesque 1814, the white-bellied form of the Mediterranean region (Ellerman and Morrison-Scott, 1951). However, in view of the obvious plasticity of the group, the demonstrated unreliability of ecology as a taxonomic indicator, and the probable relationship between ecology and ventral coloration, we hesitate to suggest that these may all be conspecific. We do not have material available to assess the wider relations of the tiomanicus group, but we suggest that the most profitable approach is likely to be based on the features of skull anatomy discussed above, rather than on other morphological characters.

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