

A RE-EXAMINATION OF *MESEMBRIOMYS HIRSUTUS*¹ GOULD 1842 (MURIDAE)

by H. H. FINLAYSON

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SUMMARY

The characters of *Mesembriomys hirsutus* Gould are re-examined with fresh material. Detailed evidence of its arboreal specializatum is presented. The validity of the insular form *M. hirsutus melvillensis* Hayman is confirmed. Some aspects of the living animal, of skull and dentition, manus and pes, are illustrated.

I owe to the kindness of my friend and former student, Wilfred Bateman, Esq., now of the Commonwealth Administration in Port Darwin, a magnificent living specimen of this great tree rat of Northern Australia, which though formerly much collected and written upon taxonomically, is still very imperfectly known.

The specimen was caught by blacks near Garden Point, Melville Island, where it is still plentiful and it occurs also on the adjoining Bathurst Island across the mile-wide Apsley Strait. Formerly it was a common animal in suitably forested country over much of the Northern Territory as far south as Daly Waters, but in recent years its numbers have declined and in many of the localities of the Daly River sector, where Knut Dahl found it plentiful in 1894-95, it seems now to be a rarity. It occurs also on Cape York Peninsula, Queensland. Dahl recorded the aboriginal names Nunjala, Dombot and Kalambo for the species and the last of these is still in use by mixed Tchingilli and Mudburra blacks at Daly Waters, though it is 20 years since the animal was seen by them there. Mr. Bateman also supplies the names Intamunga and Puturamucka as being used on Melville Island. About 60 specimens have been listed in overseas collections, but it is much less well represented in Australian museums.

The animal was flown to me from Port Darwin and the air lift of 2,000 miles, spanning a considerable climatic gap, terminated in unusually cold weather in an Adelaide spring (August) which continued for much of the period of captivity. Although it was provided with artificial warmth and much thought taken for its comfort in roomy quarters, it remained extremely secretive and could only be momentarily glimpsed by torch light. When denied its

¹ The specific name *hirsutus* was consistently used for the species through all the changes in its generic designation from *Mus hirsutus* of Gould 1842, through *Hapalotis*, *Conilurus*, *Annomys* to *Mesembriomys*, and in the definition of its three subspecies. In recent years it has been superseded by *gouldii* of Gray 1843 on the grounds of its pre-occupation by *Mus hirsutus* of Elliot 1839. The animal so named by Elliot is now known as *Colundu ellioti* Gray 1837 (vide Ellerman) and belongs to an Oriental genus whose species cannot possibly be confused with those of the Australian *Mesembriomys*. In view of these facts and of its unambiguous use for 90 years in all the formative contributions to the knowledge of the animal, there would seem to be a strong case for the conservation of *hirsutus* in *Mesembriomys*. This would make possible the continued use of *gouldii* in *Notomys*, as is done as late as 1951 by Tate.

nesting box occasionally for observation it repulsed all advances with implacable ferocity and was a difficult subject for photography, so that the attempt to gain some insight into its habits and peculiarities was largely nugatory. Dahl (1897) writes of its irritability and savage temper in the wild and the severity of its biting, and the blacks I interrogated at Daly Waters in 1953, who formerly took it by hand from hollow trees, also spoke feelingly of what they called its "cheekiness". In its frequent rages, the captive displayed considerable vocal powers of a kind quite different from the squealing and piping of more normal forms, such as *Rattus*, *Pseudomys*, *Gyomys* and *Mus*, raising its voice progressively into a sort of whirring machine-like crescendo, not unlike some of the *Phalangeridae*, such as *Petaurus breviceps*. There was no difficulty in keeping it nourished as it ate very freely of sugared biscuits of several sorts (a taste evidently inculcated by the air hostess, as his box was strewn with them on arrival), of bananas and other soft fruits and of mixed grain, but showed no interest in green vegetation nor flesh foods. Dahl records that the chief food of the species in the Daly River districts is the fruit of the local *Pandanus odoratissimus*, but the stomach of one of those examined below, which was taken on the Stewart River in North Queensland, was crammed with a gritty mass in which the shell of a fresh water mussel appeared to be the chief constituent. When examined after three months' detention, the Garden Point animal was found to be in excellent condition, weighing 670 g. and showing a smooth, well-groomed coat; no external parasites were noted. Ellerman (1941) records a life span of more than four years in captivity in London.

In checking over the characters of the species, I have used for comparison eight other specimens in the South Australian Museum representing all three of the areas from which the described geographic forms have come. Six of these were collected for the Museum in 1913-14 by Mr. W. P. Dodd, whose itinerary in the field was planned during the directorate of Sir Edward Stirling and two are donations from Mr. P. Foelsche, formerly stationed at Port Darwin. The account which follows is based primarily on my freshly chloroformed captive, which is a young adult male, and four additional examples from Melville Island, and thus represents the form *M. hirsutus melvillensis* Hayman 1936; where subspecific uniformity is departed from, it is noted in the text, and an appraisal of the validity of the described forms, as far as the material permits, is appended later.

EXTERNAL CHARACTERS

Form stout, with sturdy arms and shoulders and thick neck; the hind quarters are considerably larger than the fore, but not greatly exaggerated.

The head (Plate 2 and Plate 3, Fig. A) large and deep, with a strongly protuberant rhinarium and labia well developed but not pouted as in *Leporillus*. At a point one-third of the distance from the rhinarium to anterior canthus of the eye, there is a dent in the profile, the remaining curvature to the crown being moderately convex. The eye is large, black and very brilliant and is surrounded by an area of almost nude epidermis, which in turn is conspicuously ringed by a narrow band of jet black hair; the upper eye lashes are fairly well developed reaching 4 mm. in length. The ear is large, thick in substance, rather narrow and with its maximum breadth below the midpoint; it is carried well away from the head and conspicuously pricked. The epidermis of its inner surface is dusky brown with bluish pink areas showing through on the conch and the margins almost black; processes of the conch are well marked and the

tragal notch deep and undivided. The cephalic *vibrissae* are strongly developed and entirely black except for the interramals which are paler at the tip. The mystacial set reach 100 mm. as a maximum, the supraorbitals 38 mm.; and the genals, two of which spring from a very strongly developed papilla, 35 mm. The postoral group was not traced in adults of the Melville Island lot, but in a subadult all-black bristles on this site reached 14 mm. and in an adult female of *M.h. rattoides*, 20 mm.; the submentals reach 12 mm. and the interramals 23 mm.

The general physiognomy is distinctive and in some features sciuroid rather than murine.

The *manus* is variably developed, but is usually large in respect to the general size of the animal, and sometimes much stouter than in the example figured (Pl. 3, Fig. C). The length from base of metacarpal pads to apical pad, excluding claw, reaches 30 mm. in adults, the breadth from base of digit 5, 14 mm., yielding a breadth/length ratio of 0.47; the 3rd digit, 13 mm., and its nail 8 mm.; in two examples of the typical race in which the manus is very heavy the breadth rises to 16 mm. and the value of B/L to 0.53 as maxima. The digital formula is the normal $3 > 4 > 2 > 5 > 1$, but the pollex is unusually large and apparently functional and provided with a broad, blunt, projecting sheath-like nail; the claws of the other digits varying much in length from individual to individual, but always stout and strongly curved and unusually deep dorso-ventrally at the base: pale yellowish in colour, but slightly darkened along the dorsal curve.

The general palmar surface is lightly creased, not noticeably punctate and in life its colour is a pale slightly bluish pink with the pads and digital ridges strongly contrasted in blackish brown. The palmar aspect of the digits is quite hairless, and the ridges prominent, entire and unusually numerous; 8 or 9 on D3 and D4, but reaching 11 in one subadult of the typical race—the highest count noted on an Australian murid. The metacarpal pads are broad and obtusely oval and greatly exceed the interdigitals in area; the outer (hypothemar) much larger than the inner, which has its long axis inclined laterad towards the pollex and its distal margins well raised above the base. The lateral interdigitals are subtriangular or inverted heart-shaped, with a strongly developed satellite pad at the base of the outer, and the median pad a broad inverted pyriform; the size sequence for area is outer metacarpal $>$ inner metacarpal $>$ 3rd interdigital $>$ 1st $>$ 2nd. The palmar pads are strongly striated, the apical pads of the digits, feebly so.

The *pes* (Plate 3, Fig. B) has numerous well-marked peculiarities. Its dimensions vary, but yield several maxima which exceed all other Australian murids, except possibly the species of *Uromys*. In plantar aspect it tapers strongly from a broad interdigital area to a nude strongly constricted heel; its relative size is large, attaining in the largest examples 25 p.c. of the head and body length and a maximum breadth/length ratio of 0.30; the 3rd digit reaches 16 mm. and its nail 9.5 mm. (11 mm. in one example of *M.h. rattoides*). The digital formula is $4 > 3 > 2 > 5 \geq 1$, but the disproportion between the lateral and median digits is much less than that which prevails in the majority of Australian species, both the hallux and D.5 being longer in their phalanges and at the same time their bases are brought into a more anterior position on the pes, by longer metatarsals supporting them. Thus the apical pad of the hallux, which in most Australian species lies far below the level of the base of D.2, here reaches to its posterior third, and similarly that of D.5 to the anterior third

of D.4. The digital ridges are strongly developed and clear cut and are entire except posteriorly, where some obscure bifurcation may be seen; all show more or less distinctly the novel feature of antero-posterior striation, but there is no scalation; they are numerous, ranging from 9-11 on the median digits in the Melville Island material and to 14 in a subadult of the typical race, which (like that of the manus) is the highest count I have obtained in an Australian rat. The claws are still stronger than in the manus and almost equally curved, and slightly darker in colour.

The plantar surface generally is soft and plump, markedly punctate, but with the creasing reduced to a minimum; the colour in life as in the manus, but with the differential darkening of the pads and digital ridges carried still further. The disposition of the *interdigital pads* is unusually symmetrical owing to the above peculiarity of the lateral digits; they are of but moderate size, but very sharply defined and well raised above cingulum-like structures, which also have margins almost as well defined as the pads which surmount them, in contrast to the rather amorphous folds of integument usually found in that site. The lateral pair are somewhat kidney shaped; the inner (I.D.1) with two rather ill-defined accessory pads at its postero-external corner and the outer (I.D.4) with a single well-defined satellite at the middle of its postero-lateral margin, and a vestige of another anterior to it; the 2nd inter-digital is obtusely oval and the 3rd inverted pyriform, and the size sequence (area) is approx. $1 = 4 > 2 = 3$.

The *metatarsal pads* are remarkably elaborated. The inner pad takes the form of a shallow crescent- or boomerang-shaped structure, concave outwards and with an overall length of 19 mm. and average width of about 2 mm., expanding to 3.5 mm. at the club-shaped upper extremity. In the example figured (Pl. 3, Fig. B) there is a well-marked antero-internal process reaching out into the centre of the sole towards a corresponding process of the opposite pad—this feature, however, is absent or only very weakly indicated in the other eight examples examined. The outer metatarsal pad is of enormous length and when undivided may span two-thirds of the interval between the heel and the 4th interdigital; it runs an almost straight line course parallel to the margin of the foot and has a maximum length of 28 mm. and average width of 2.5 mm., expanding to 4.5 mm. at the anterior extremity. It is constricted at several points in its length and in most examples splits up at these necks into a chain of from two to four separate elements with low gaps between, but entire and divided pads may occur on opposite feet of the same animal. All pads are strongly striated at right angles to their long axes, except the apicals, which are concentrically engraved.

The *tail* is very long and flexible, but gives no external evidence of prehensile functions; its length ranges in the Melville Island material from 108-128 p.c., but reaches 150 p.c. of the head and body length in one example from Arnhem Land; it tapers gently and uniformly to the small horny spur which forms its apex. The *scrotum* in the captive male is conspicuous and well distended to accommodate enlarged testes in November, but the condition was not checked satisfactorily in wild caught examples. The *mammæ* are abdomino-inguinial only; $0-2 = 4$; in a subadult female of the typical race, they were large; the posterior about 5 mm. from the base of the genital tubercle and the anterior 11 mm. from the posterior.

EXTERNAL DIMENSIONS

Some external dimensions of nine examples are summarized in the table below. Number 4 was measured in the flesh shortly after death; number 5 is a filled skin, and the rest are alcohol preserved.

	ARNHEM LAND			MELVILLE ISLAND					NORTH QUEENS- LAND
	Young Adult ♂	Sub- ad. ♂	Sub- ad. ♀	Young Adult ♂	Adult ?	Sub- ad. ♂	Sub- ad. ♂	Adult ♀	Adult ♀
	1	2	3	4	5	6	7	8	9
Head and Body	300	210	200	284	268	205	228	297	315
Tail: length	277	286	300	363	310	ca.	ca.	ca.	ca.
Tail: $\frac{1}{2}$ H and B	inc.	136	150	128	115	ca.	108	ca.	ca.
White of Tail	—	73	85	80	82	—	—	80	107
Pes: length	67	62	62	71	64	59	58	62	64
Ear	36	36	36	38 × 18	—	ca.	31	33	35
Rhinarium to eye	35	30	28	36	—	ca.	28	28	35
Eye to ear	23	20	18	24	—	ca.	19	18	22
						ca.			

PELAGE

The type on which Hayman (1936) based his description of the pelage of *M. hirsutus melvillensis* was an animal kept in captivity in London. Although in good agreement with the material now examined, it has been thought well to supplement it in some particulars by the following observations made upon field skins of animals killed in the wild as well as on the Garden Point specimen kept in captivity here.

Coat comparatively harsh and thin; mid-dorsally there are three series. (1) An underfur of 14 mm. not slaty nor plumbeous as is usual, but very dark grey or blackish (about Ridgway's fuscous black) and not, or very obscurely, annulated. (2) Stouter hairs of 23 mm. concolorous with the underfur in the basal half, which is followed by a 5 mm. band of warm buff, and the extreme tip, black. (3) All black guard hairs to 42 mm. The general colour of the dorsum is a coarse grizzle of black and buff, paler on the nape and forequarters, but rapidly darkening to almost black on the mid-dorsum and rump, through a great increase in the number and length of the guards. A small area on the nape and prescapular area is more richly coloured than the rest, the subterminal band here being an orange buff, near Ridgway's ochraceous tawny.

The ventrum is shorter furred, and with the basal colour paler than on the dorsum, but still drab rather than plumbeous (about hair brown). The underfur of 10 mm. is overlain by a second series reaching 18 mm. with a terminal band of pale buff, and lightly sprinkled with all black hairs. The basal drab shows through strongly and the general effect is of a dull buffy grizzled grey which occupies all the ventrum and extends on to the anterior

lateral surface as well. Except for the darker scrotum, the whole ventrum is very uniform. There is a narrow nude area in advance of the genital tubercle and the narrow posterior extremities of the scrotum are also nude and with the epidermis nearly black.

Crown of head, cheeks and neck grizzled like the lower foreback. Lips, rhinal and mystacial area and a ring round the eyes jet black and the muzzle also much darkened though finely grizzled. Ears densely furred jet black on the whole external surface and on the interior margins, and strongly contrasted with the crown. Outer aspect of forelimb darker than the adjacent lateral surface and becoming increasingly so distally until carpus, metacarpus and digits of manus are jet black, with no lighter markings. Hind limb also darker externally than the adjacent body surface and becoming glossy jet black on tarsus, metatarsus and digits with a similar absence of variegation. The tail strongly haired on all surfaces, largely obscuring the scales which are 8 per cm. proximally and 6 per cm. mid-dorsally, where the hairs are 5 scales long. It is jet black on all surfaces except for a variable apical portion which becomes abruptly greyish white and lengthens progressively on all surfaces to a terminal pencil of 40 mm. ca.

The Garden Point specimen, after three months captivity in Adelaide, was found to be in a different moult phase from the above, the three components of the much shorter coat averaging mid-dorsally 9, 16 and 27 mm. respectively. The coat was glossy and even but on the posterior back showed a heavily grizzled replacement coat mingling with the fuscus underfur. The second series in the London type, with a length of 35-40 mm., is much longer than in any of the local material.

THE SKULL AND DENTITION

The cranial and dental characters of the species were briefly diagnosed by Thomas (1906, 1909) and dealt with in more detail by Ellerman (1941) and Tate (1951), sometimes with conflicting results. The following notes at species level covering some additional points, are based on the skull of the Garden Point specimen, together with that of a young adult ♂ from Arnhem Land at the same stage, and a much younger male skull with unworn molars from the same area.

The skull is stout and densely ossified. The general form in dorsal aspect is narrow, with the maximum zygomatic breadth less than half the greatest length (0.44-0.48), zygomatic arch with the maximum width either median or posterior in adults and the combined outline a narrow oval somewhat flattened at the sides and in the young skull slightly concave; the anterior root of the zygoma, though massive, has little lateral development, dropping rapidly below the dorsal level. Rostrum heavy and broad, the nasals with little posterior taper and the least width at the nasofrontal suture about 28 p.c. of the length. Preorbital fossa medium in size, rather narrow from above and with the outer wall slanting inwards rather markedly. Anterior frontal region unusually broad and inflated and infringing on the orbits so that the lacrymals, which are small and rugose, are deeply imbedded between the frontals and the zygoma root and scarcely project into the orbit at all. Interorbital region strongly concave as noted by Ellerman, a distinct depression extending to or beyond the coronal suture. Brain case much longer than wide and with feebly developed temporal crests following the rather sharply angulated parieto-squamosal suture to the supraorbital ridges, which in the Melville Is. example especially, are sharp and

slightly overhanging. Interparietal as given by Collett (1897); a large, broad sharply angulated element.

In lateral aspect the most conspicuous feature is the sharp division of the dorsal profile into two distinct planes meeting in an angle of ca. 155° , the junction being slightly in advance of M^1 and marking the maximum depth of the skull. The anterior margin of the zygomatic plate has a convex but somewhat sloping shoulder without spine and its lower course is variably pitched and may be the seat of racial difference (*infra*). The tympanic annulus is large, and has prominent thickened margins and the lingulate process of the squamosal overlying the petrous temporal and mastoid is developed to remarkable strength and is a conspicuous object above and behind the meatus.

The anterior palatal foramina are variable as to breadth, overall shape, position of septal suture and posterior extension—in the latter particular they fall short of the molar rows by half the length of M^1 in the Melville Island skull and almost reach them in the immature Arnhem Land specimen. Two minute (? nasopalatine) foramina are constantly developed in the premaxillae, anterior to the incisive canals and within 2 mm. of the alveolar border; they are evidently homologous with those which in *Leporillus* coalesce to form a single median aperture at the same site. The palate has been described in contradictory terms by Ellerman and Tate; in the present material, at its narrowest point between the first molars, I find that its breadth compared with that of M^1 varies from 1.7 in the heavy toothed Arnhem Land skulls to 2.1 in that of Melville Island; so measured, the palate is certainly not narrow therefore, and might be described as broad in relation to the majority of Australian species; the median spur on its posterior margin may be strongly developed or almost suppressed. The pterygoid plates are also very strongly developed and terminate bluntly without hamular processes. The bullae fall short of the molar rows in length, and in so large a skull, are relatively small. A very conspicuous feature in the palatal aspect of the skull is the great width of the mesopterygoid fossa—half as great again as that of the ectopterygoid.

The mandible is massive, has a straight inferior border and comparatively slight emargination of the posterior border above the angle; the coronoid is distinctly developed though much reduced, its relative size about as in *Mustacomys fuscus* and *Leporillus jonesi*. Within the Zyzomyid group of genera, the relative development of the coronoid appears to follow the sequence *Zyzomys* > *Laomys* > *Mesembriomys* > *Conilurus*.

The upper incisors are very large teeth with a variable angle; the Melville Island example being less opisthodent than those from Arnhem Land; in the former also the incisors are notched almost as in *Mus musculus*. In the molars the cingulum of M^1 is large and prominent anteriorly, but the accessory cusps, two or more of which are usually claimed for the dentition, are either absent or very small and imperfect and could not justly be compared with the *Leggadina* condition. The buccal cusps vary from skull to skull and sometimes on the two sides of the same skull; T.3 of M^1 although small is generally quite distinct and separate, but T.6 and T.9 are almost absorbed by the median cusp. In M^2 an interesting feature in one of the mainland skulls is a very distinct though minute T.3 as in *Apodemus* and *Acomys* of the Palaearctic; it is also feebly indicated in the Melville Island individual. In the latter also (on one side only) a supplementary cusplet is crowded in between T.1 and T.4 giving the appearance of a duplication of the former. In M^3 the postero-internal cusp T.7 is well developed in the two Arnhem Land skulls (which therefore have the full antero-posterior complement of nine lingual cusps), but is absent in

the Melville Island example. The cusp formula of the upper molars, using the Miller notation is:—

$$M^1 \begin{cases} T.1 : T.2 : T.3 \\ T.4 : T.5 : T.6 \\ T.7 : T.8 : (T.9)^1 \end{cases} \quad M^2 \begin{cases} T.1 : X : X \text{ or } (T.3) \\ T.4 : T.5 : T.6 \\ T.7 : T.8 : (T.9) \end{cases} \quad M^3 \begin{cases} T.1 : X : X \\ T.4 : T.5 : T.6 \\ X \text{ or } T.7 : T.8 : X \end{cases}$$

¹ () = greatly reduced.

In the lower molars the posterior median supplementary cusp is strongly developed in M_1 and M_2 and feebly indicated also on M_3 . In the Melville Island specimen an anterior supplementary cusp also appears on the first lamina of M_1 in a median site between the two main elements — again as in *Apodemus*. Johnson (1952) has recorded the occurrence of supernumary upper cheek teeth in this species.

The following figures give in turn some *skull dimensions* of the young adult male from Garden Point, Melville Island; a young adult male at the same growth stage from the Northern Territory mainland, and a much younger male from the same area. Greatest length, 62.8, 63.0, 58.0; basal length, 56.7, 57.4, 50.7; zygomatic breadth, 30.2, 28.8, 26.0; interorbital breadth, 10.2, 10.5, 9.3; nasals length, 26.3, 25.1, 22.2; nasals greatest breadth, 7.3, 7.0, 6.7; palatal length, 37.0, 37.0, 33.4; anterior palatal foramina, length, 11.6, 11.9, 11.8; ditto, breadth, 4.2, 3.4, 4.0; bulla length, 9.1, 8.8, 8.9; Ms^{1-3} , 11.1, 11.3, 11.6.

SKELETAL CHARACTERS

The disarticulated skeleton of the Garden Point specimen gives the following data. Vertebrae; cervical 7; thoracic 13; lumbar 7; sacral 2; caudal 35. Possibly the element here reckoned as the first caudal would be fused to the true sacrals in later life, but there would not be four sacrals as is frequent in *rattus*. The mesosternum has 5 segments. Scapula, max. length, 36.5; ditto, max. breadth, 17.5; clavicle, length, 18.3; humerus, length, 43.0; ditto, distal breadth, 10.5; radius, length, 38.7; ditto, max. distal breadth, 4.9; ulna, length, 47.8; ulna, max. breadth (coronoid), 5.5; femur, length, 56.5; ditto, distal (inter condylar), breadth, 11.6; tibia, length, 65.4; ditto, proximal breadth (medial aspect), 11.0; maximum, combined tibio-fibular breadth, 12.5; fibula, greatest proximal breadth, 7.2; ilio-ischial length of 1 pelvic ramus, 59.4; ilium breadth ditto, 11.0; ischial breadth, ditto, 18.5.

SUBSPECIFIC DIFFERENTIATION

Two subspecies have been distinguished from the primary form of Arnhem Land, by reference to differences in such characters as general pelage colour, markings of the manus and pes, pes length, extent of white on the tail, and the relative development of the zygomatic plate in the skull, etc. Although the species is represented by considerable series in more than one European Museum, no detailed analysis of characters has so far been attempted, and until this is done and the normal range of variation in a homopatric group is determined, the real status of the described forms must remain to some extent uncertain. The material here reviewed is not sufficient to explore this field adequately, but the following comments may contribute to a partial clarification.

1. *Mesembriomys hirsutus hirsutus* Gould, 1842.

Three specimens only have been available and none is accurately localized; there is contributory evidence, however, that all three are almost certainly from Arnhem Land or the Daly River drainage of the Northern Territory.

Published dimensions might be taken to indicate that this form is larger than *M.h. melvillensis* and with a relatively longer tail, but this may be due in part at least to the lack of aged males of the latter for comparison. The data available, however, is too heterogeneous and scanty to permit of reliable deductions on this head at present.

The body form and limbs in the three examined here are somewhat stouter than in the Melville Island examples, the manus in particular being thick and heavy and with shorter claws and interdigital pads and there is a tendency for higher counts in the digital ridges, one subadult carrying 11 on D3 of the manus and 14 on D4 of the pes. The two complete tails are relatively longer than in the other examples — 136 to 150 p.c. of the head and body length as compared with a range of 108-125 p.c. in similarly immature *melvillensis*, but previously published figures do not indicate any significant difference in the tail length of adults.

The pelage in all three is less harsh and more profuse than in the island form and the general colour much paler especially on the outer aspect of the limbs. The ventral fur is creamy white to base without trace of darker ticking. The dorsum of the pes (Pl. 3, Fig. D) is strikingly variegated with blotches of cream and black in all three specimens and this is apparently almost invariably the case as there seems to be no specific record to the contrary in the literature of the 50-odd examples which have been noted. Gould's plate, however (1857), which is presumably drawn from the second specimen from Port Essington (since the type skin lacked feet) appears to have the dorsum of the feet all black. The dorsum of the manus also carries markings though less conspicuous and generally confined to a cream or buff area along the outer margin of the metacarpus and some white fringing bristles at the apical pads of the digits.

2. *Mesembriomys hirsutus melvillensis* Hayman, 1936.

This appears to me to be a well-founded and even strongly differentiated insular race. Its distinctions lie chiefly in pelage characters, and Hayman based his excellent description on four examples, three of which were living at the time in the Zoological Gardens, London; the five additional specimens from Melville Island here examined are in good accord with his findings and well contrasted with both the above primary form from the Northern Territory mainland and that of Cape York Peninsula. It is a somewhat slimmer animal than *M.h. hirsutus* and with a rather harsher coat and a distinctly atrate colour scheme, which affects the head and external aspect of the limbs differentially so that they are thrown into contrast with the lighter sides and foreback. The ears are more densely furred externally and are uniformly jet black, as are also the dorsal surfaces of manus and pes, the characteristic markings of the animal from the adjacent mainland being quite suppressed. The ventral surface is quite different in appearance from that of the latter, being dark grey at the base and buffy grey externally and with a distinct admixture of all black hairs so that the general colour is a rather dark grizzled drab like the sides and totally different from the all-cream ventrum of the primary race.

Dimensions given by Hayman for the type, which is a male at about the same developmental stage as No. 4 of the table (*supra*), agree as to head and body and tail, but his pes length is lower (63 c.f. 71); Tate's remeasurement of the type, however, corrects this to 68. The local material gives widely different values for pes length in the adult ♂ and ♀ (71 c.f. 62), which is not foreshadowed in the other two groups, and is probably an individual rather than a sexual peculiarity. The ear measurement of 44 for the type is higher than in

any of the four taken here from the tragal notch (44 c.f. 38 max.), but the method of measurement may be different.

Comparison of the dimensions of the three skulls here examined with those already published, suggests that there are few, if any, valid differences between the Melville Island and Arnhem Land forms. Considerably higher values have been recorded for the latter, but this is very likely due to age differences as no aged *melvillensis* skull has yet been examined. It is possible that the molar rows may be shorter in the latter (11.1-11.4 c.f. 11.3-12) and individual molars a little narrower. Tate's claim of a difference in the bulla does not stand. In non-metrical points, Hayman's opinion that there is a difference in the slope of the free margin of the zygomatic plate, seems to be confirmed and it should also be mentioned that the arching of the profile is much steeper in the Garden Point skull than in the two Arnhem Land examples. In both these latter also, the parieto-squamosal suture shows an abrupt angle of re-entrance into the squamosal, near the posterior root of the zygoma, which is much less developed in the island example. Several other minor differences are noted (*supra*), but it is unlikely that these have a geographical basis.

I am at a loss to understand Tate's statement that "the type differs little from other races" — the general level of distinction of *melvillensis* from *hirsutus* is distinctly higher than that generally accepted as justifying a trinomial in Muridae and appears to be maintained with satisfactory constancy in the nine specimens now examined. Moreover, the factor of complete geographical isolation and the considerable differential gradient attained across so small a water gap as Clarence Strait, are, as Hayman suggested, additional reasons for accepting it as a valid form.

The status of the Bathurst Island representative, separated by the still narrower Apsley Strait, remains to be determined.

3. *Mesembriomys hirsutus rattoides* Thomas, 1924.

Thomas founded this name on three specimens from Cape York Peninsula of Queensland, which were more or less intermediate between *M.h. hirsutus* and *M.h. melvillensis* in ventral pelage, being grey at base and greyish white rather than cream externally. He also considered that the foot was longer in Queensland than in Arnhem Land. Tate (1951) on re-examining the type, described the ventral fur as light grey basally and yellowish externally, which considerably reduces the distinction in this feature. He also found marked differences in pelage due to moult phase in additional specimens taken at the Pascoe River and Port Stewart in 1948, but confirmed the longer pes. It is to be noted in the latter connection, however, that the range in *M.h. melvillensis* reaches the maximum for *rattoides* (71 mm.). Hayman (1936) states that both all black and variegated feet occur in the three *rattoides* in the British Museum, but Tate does not discuss this feature in his four additional examples. His skull measurements suggest that the anterior palatal foramina average longer in *rattoides* than in *hirsutus*.

A single specimen, an adult ♀ in alcohol, collected by W. P. Dodd in 1914 on the Stewart River of the Pacific Coast of Cape York Peninsula, Queensland, has been examined for external and pelage characters only. The general coloration is nearer *M.h. hirsutus* than *M.h. melvillensis*, though the ventral pelage is intermediate and possibly somewhat nearer the latter. The ears in this specimen are nearly nude, the dorsum of manus and pes quite black, and the foot length low (64 mm.). No skull of *rattoides* has been examined here and there is no comment by Tate on his new material apart from dimensions; these might indicate that it has the largest skull of the three forms.

With this degree of overlapping it is impossible at present to assess the standing of *rattoides*, though clearly it is much less distinct from typical *hirsutus* than from *melvillensis*. There is a probability that in recent times at least the Arnhem Land and Queensland populations have been isolated; the characteristic northern Eucalyptus savannah woodland, which seems to be the chief habitat of the mainland forms is interrupted by a zone of treeless Mitchell grass downs towards the southern shore of the Gulf of Carpentaria.

ADAPTIVE MODIFICATIONS

It is remarkable that the arboreal adaptations of *Mesembriomys*, particularly in the pes, have found scant mention in the definition of the genus, but have been ousted and overlain by traditional and quite erroneous views of its terrestrial saltatory or Jerboa-like modifications.

On emergence from the early omnibus "genus" *Mus*, the two species of *Mesembriomys* were lumped with many others which are now considered very diverse, in the almost equally omnibus but purely Australian genus, *Hapalotis* of Lichtenstein, in which enlarged hind limbs, modified feet, lengthened ears and long and tufted tail were considered to indicate adaptive analogy to the Jerboas of the Old World. Analysis of this complex of species, chiefly by Oldfield Thomas, had by 1909 split Lichtenstein's *Hapalotis* into the two groups of currently accepted genera, *Zyzomys*, *Laomys*, *Conilurus sensu stricto*, and *Mesembriomys* on the one hand and *Leporillus* and *Notomys* on the other. The saltatory element in the original complex is now seen to be isolated in *Notomys* alone, but recognition of this fact was long delayed and as late as 1914 the species of *Mesembriomys* are still described in Brehm's Tierleben as "Australischen springratten" with "namentlich aber verlängerten hinter beinen".

The first references of Gould and Gray contained no mention of the habits of the animal and Gilbert, who forwarded the type to London, if he had information on this head, evidently did not transmit it. In 1871 Gerrard Krefft in Sydney, who appears to have had very sound views on the field relations of many Australian mammals, published a list of Australian rats with a broad classification into four categories, based on what was known locally of their habits. In this scheme he divided *Hapalotis* into two sections, "The Tree Rats representing the Squirrels in Australia" and the "Jerboa Rats". His allocation of some of the species to the first group would not meet with acceptance now, but *Mesembriomys hirsutus* was correctly placed there as "The Great Hapalotis or Tree Rat of North Australia". Krefft, I believe, never worked personally in the habitats of the species, but evidently had access to information on it, derived from Strange or Macgillivray or other early collectors in the North. In 1897, Knut Dahl published an excellent first-hand account of both species of *Mesembriomys* in which the tree haunting habits of *hirsutus* and its ability as a climber were well documented for the first time. These two contributions on the natural history of the animal, as noted above, made no impact on the classifications which were worked out in London, which followed severely theoretical lines, and it was not till 1951 that the arboreal character of the genus was plainly stated by Tate.

The significance of the moderately enlarged hind limb (in contradistinction to elongation and narrowing of the pes) which is found more or less developed in most of the six genera named above, is evidently not adaptive in the narrow and immediate sense, since it occurs alike in arboreal, cursorial, truly saltatory and rock-haunting forms of Australian murids and in monodelphia, in groups as different in habits as Leporidae and Sciuridae. Gray early recognised this peculiarity of the larger members of "*Hapalotis*" and coined the not altogether

inappropriate name of "Rabbit Rats" for them, though it has been suggested that the ear form also had its influence in this. In the evolution of the generic concept of *Mesembriomys* it plays a diminishing part and the above statement in Brehm's Tierleben may be contrasted with that of Thomas in 1909, "form normal" — or of Longman, 1916 — "legs not markedly unequal". Justification for the latter may be obtained by expressing the length of the humerus plus ulna-radius as a percentage of that of femur plus tibia, thus obtaining an approximate intermembral index which gives an estimate of the relative development of the fore and hind limb, *sans manus* and *pes*. In *Mesembriomys hirsutus* this is 75, *Leporillus jonesi* 73, *Rattus lutreola* 78, *R. rattus alexandrinus* 79, *Oryctolagus cuniculus* 77, and *Lepus europaeus* 85.

The *pes* was thought by Thomas (1909) to be long and narrow; a mistake corrected by Ellerman in 1941 and again by Tate in 1951. Its length in relation to that of head and body (max. 25 p.c.) is certainly high when compared with most Australian *Rattus* species, but is closely approached in this by several non-saltatory forms such as *Cyromys apodemoides* 25 p.c., *Leporillus conditor* and *apicalis* 24 p.c., and *Laomys pedunculatus* and *Rattus greyi* 22 p.c., and falls much below its value in saltatory *Notomys*, which in the five species measured ranges from 32-35 p.c. The hallmark of the saltatory *pes*, moreover, is in the low breadth/length ratio, which in the above *Notomys* spp. has the range 9-12 (11) p.c. as against the remarkably high value of 24-30 (26) p.c. in *Mesembriomys hirsutus* vars. Metrical support of terrestrial saltatory specialization is therefore lacking. Tate claimed as "scansorial" modifications, chiefly the width of the metatarsal segment of the foot and the large size and strong curvature of the claws. In view of what is now well established as to the habits and habitats of the animal, this wide term may give place to one of narrower connotation, and most of the features of the *pes* listed below may be regarded as evidence of arboreal adaptation, analogous to those found in other groups of tree-climbers, and including very likely, the modified type of arboreal "saltation" from branch to branch, frequent in such forms.

1. *The relatively great length of the hallux and of D5 and their more anterior position on the pes.* The former of these two conditions was recognised by Ellerman and the latter is also valid. Whether these features are to be regarded as specializations *de novo*, or rather as a retention of primitive conditions may be debated, but they certainly run counter to the trend in most Australian terrestrial genera, which (especially in subdesert areas) show a progressive reduction in the size of the lateral digits with a markedly posterior position on the *pes*, culminating in the extreme condition of *Notomys*, which is inescapably specialized.

The disposition of Ds, 1 and 5 on the *pes* of *M. hirsutus* is similar to that in some arboreal species of the Austro-Pacific genera *Cyromys* and *Uromys*, but whether it is accompanied in life by an increase in the range of lateral movements of these digits, there is no evidence to show.

2. *High value of the breadth/length ratio of the foot.* This trend in a general way is parallel to the above, the nearest analogues amongst Australian forms being species of *Melomys* and *Uromys*, with *Notomys* again providing the opposite extreme. *Laomys pedunculatus* and some *Rattus* spp. (e.g. *lutreola*), which are not usually suspected of arboreal habits, offer partial exceptions and have very high B/L values; *Laomys*, however, may be scansorial in the sense of rock climbing.

3. *Increased size, strength and curvature of the nails of the digits.* This is a strongly marked feature shown also in the manus, and equalled by few, if any, Australian species.

4. *Increase in the number, area, and effectiveness of the plantar structures involved in frictional contact.* This is the most obvious, if not the most significant, modification of the member. It is shown in the rubber-like consistence and punctation of the general plantar surface; in the prominence and multiplication of the digital ridges and their striation; in the height and sharp sculpturing of the interdigital pads; and particularly in the enormous development of the metatarsal pads, which (especially in the outer of the two) is probably unique in Australian muridae and recalls the condition of some of the arboreal Dasyuridae.

The tail, as mentioned (*supra*), gives no evidence of prehensile powers, but it may be recalled that the long terminally tufted tail in general is by no means exclusive to terrestrial saltators like the Jerboas, but is strongly developed in such typical arboreal animals as the Tree Shrews (*Tupaia*) and *Tarsius*.

In some particulars the modifications listed above may fall short of what is found in some Austro-Pacific muridae and are certainly much inferior to those of the perfected arboreal forms of the Oriental region, such as *Haeromys* and *Chiromyscus*. Nevertheless, they probably entitle *Mesembriomys hirsutus* (in spite of the Jerboa myth) to rank at least equally with the tree-living species of *Uromys* and *Melomys*, as an Australian arboreal product.

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EXPLANATION OF PLATES

PLATE 1

- Fig. A. Dorsal aspect of the skull of a young adult ♂ of *Mesembriomys hirsutus melvillensis* from Garden Point, Melville Island, Northern Territory of Australia (x 1.1).
 Fig. B. Lateral aspect¹ of the same (x 1.1).

¹ The lower profile of the bulla figured is modified by a malformation; normally it is less flattened than as shown.

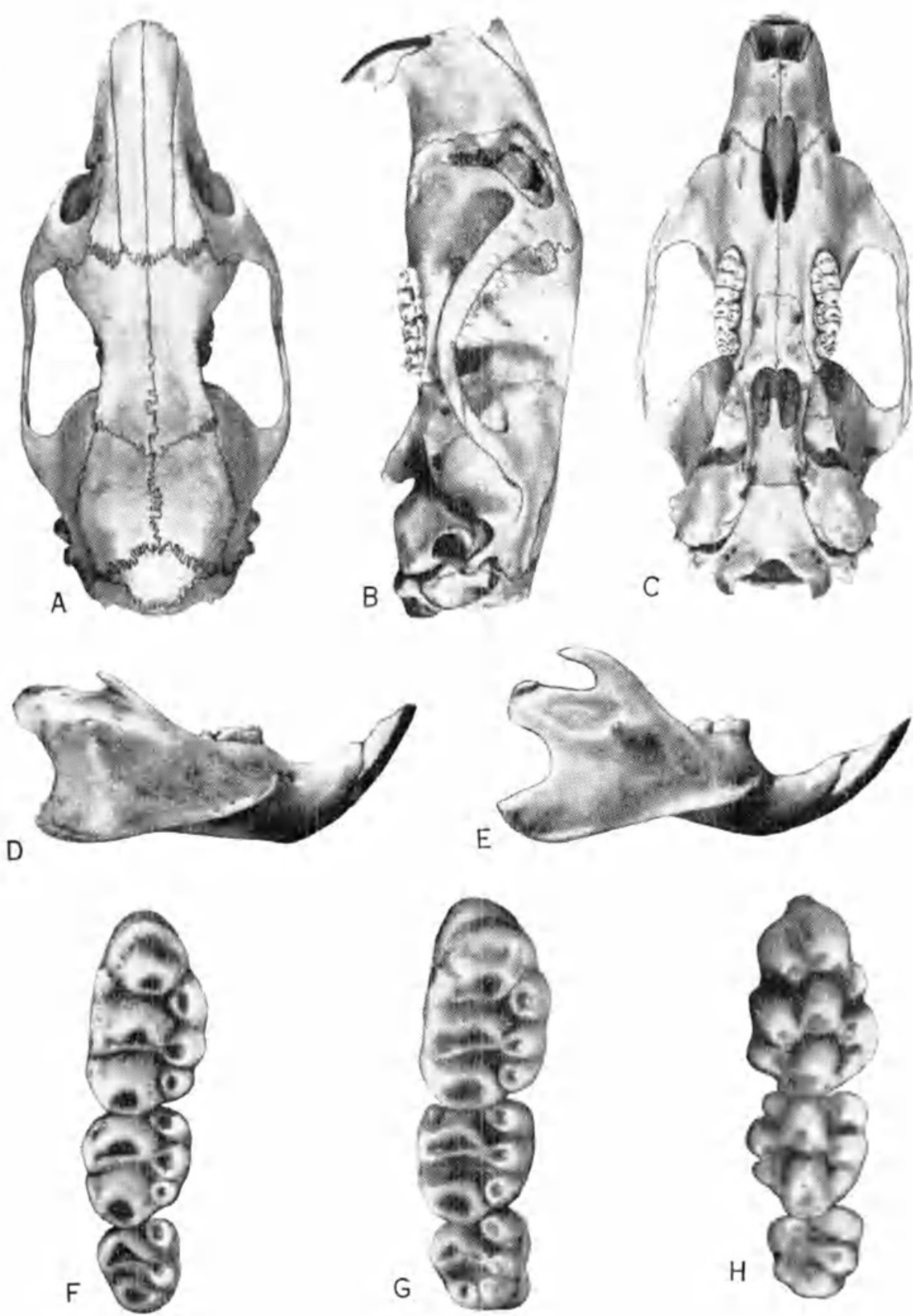
- Fig. C. Palatal aspect of the same ($\times 1.1$).
- Fig. D. Buccal aspect of the mandible of a young adult ♂ of *Mesembriomys hirsutus hirsutus* from the mainland of the Northern Territory of Australia ($\times 1.3$).
- Fig. E. Ditto, in an adult ♂ of *Rattus norvegicus* Erxl. for comparison with Fig. D ($\times 1.6$).
- Fig. F. Occlusal aspect of slightly worn right upper molars of the above example of *Mesembriomys hirsutus melvillensis* ($\times 5.0$).
- Fig. G. Ditto, in the above example of *Mesembriomys hirsutus hirsutus* showing the full complement of 9 lingual cusps and T3 on M2 ($\times 5.0$).
- Fig. H. Ditto, in an adult ♂ of *Apodemus sylvaticus* Linn. for comparison with Fig. G ($\times 14.0$).

PLATE 2

The above example of *Mesembriomys hirsutus melvillensis* in captivity in Adelaide ($\times 0.30$ ca.).

PLATE 3

- Fig. A. Ditto ($\times 0.27$ ca.).
- Fig. B. Plantar aspect of right pes of the same ($\times 1.0$ ca.).
- Fig. C. Palmar aspect of right manus of same ($\times 1.9$ ca.).
- Fig. D. Dorsal aspect of right pes of the above example of *Mesembriomys hirsutus hirsutus* ($\times 1.5$ ca.).









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