Morphological variation in the testes and accessory sex organs of Australian rodents in the genera *Pseudomys* and *Notomys*

W. G. Breed

Department of Anatomy and Histology, University of Adelaide, Adelaide, South Australia 5001

Summary. The relative size and histology of the testes of sexually active adult *Pseudomys* and *Notomys* differed markedly between species. Average weight of testes (as % of body wt) ranged from about 3% in *P. australis* and *P. nanus* to about 0.15% in most *Notomys*. In the testes of most species, interstitial tissue was relatively sparse, but in *P. apodemoides*, *P. delicatulus* and *P. hermannsburgensis* it was abundant and consisted of a mass of lipid-rich epithelioid Leydig cells. Seminiferous tubule diameters were similar in all species, but epididymides ranged from about 500 mg in weight (about 1% body wt) in *P. australis* to about 20 mg (about 0.05% body wt) in most *Notomys*. Likewise numbers of spermatozoa in the paired cauda epididymidis ranged from about 500×10^6 in *P. australis* and *P. nanus* to about 2×10^6 in 3 of 4 *Notomys* species.

Introduction

In Australia there are two related genera of relatively small native rodents, the *Pseudomys* or 'mouse-like' species and the *Notomys* or hopping mice (F. Muridae), but there is little information on the anatomy or histology of the testes and accessory sex glands of most of these species. Taylor & Horner (1970, 1972) found large scrotal testes, with histology similar to that of *Rattus*, in *Pseudomys gracilicaudatus* and *P. hermannsburgensis*, but in reproductively active *P. delicatulus* small testes with extensive interstitial tissue were observed. Taylor & Horner (1972) also concluded that the male accessory sex glands of *P. gracilicaudatus* and *P. shortridgei* were similar to those of the laboratory rat, except for the apparent absence of coagulating glands. By contrast, 3 of 4 species of *Notomys* have extremely small testes and an arrangement of the male accessory sex glands in which the ventral prostate is the only large gland found (Breed, 1980, 1981a). The present study was therefore carried out to investigate more extensively the interspecific variation in testes, epididymides, seminal vesicles, coagulating glands and ventral prostates in all available *Pseudomys* and *Notomys* species.

Materials and Methods

Many of the Australian non-*Rattus* rodents are rare and/or sparsely distributed and few species are bred routinely in captivity. In the present study, some of the animals used were laboratory bred adults, of known age, maintained singly or with an adult female in a controlled laboratory environment of 14-h light, 10-h dark and at a regulated temperature of about 23°C (see Table 1). Others were wild-caught individuals that had then been kept in the controlled laboratory environment or

had been killed at the time of capture and stored in 70% alcohol in the South Australian Museum (S.A.M.) mammal collection. In the latter case data were only analysed if pregnant and/or oestrous females had also been collected at the same time. For origin of many of these animals see Morrissey & Breed (1982).

Preparation of material

Animals were anaesthetized with pentobarbitone sodium (Nembutal) or halothane (Fluothane). From some, one testis was removed, immediately immersed in 3% glutaraldehyde/formaldehyde made up in 0.05 M-phosphate or cacodylate buffer, pH 7.4, and weighed. As initial observations indicated similar testis size on both sides, the weight of the one testis was doubled to give the approximate weight of the testes for the animal. Other individuals were perfused with the same fixative through the left ventricle. Testes were subsequently post-fixed in osmium tetroxide and embedded in Spurr's resin; 0.5–1 μ m plastic sections were cut on an ultramicrotome and stained with toluidene blue in borate buffer. The sections were observed with $\times 10$ objective on a Wild, semi-automatic, sampling microscope containing a Weibel graticule to determine the approximate relative volume of interstitial tissue by a standard point counting procedure (Weibel, Kistler & Scherle, 1966): an average of 277 points were counted for each specimen. Subsequently, diameters were determined of at least 4 seminiferous tubules cut in cross-section from each testis. Reproductive tracts were also removed and immersed in buffered formaldehyde. Subsequently, seminal vesicles, coagulating and ventral prostate glands were dissected out and weighed.

From some of the non-perfused animals, epididymal weights were determined and spermatozoa were counted in the caput plus corpus and cauda epididymidis. For this, the tissue was placed in 0.5–3 ml saline (9 g NaCl/l) to which had been added a little hyaluronidase. The tissue was macerated, and 0.01 ml sperm suspension was diluted to 0.1 or 1.0 ml with 10% formalin for counting in a haemocytometer. The final figure was adjusted after taking into account the initial dilution. If sperm counts were not performed, a small piece of vas deferens or cauda epididymidis was removed and its contents were either squeezed onto a microscope slide flooded with 3% buffered glutaraldehyde/formaldehyde or into a watch glass containing saline. An animal was considered sexually mature if abundant, intact spermatozoa of normal appearance were found. Only testes from such animals were sectioned and analysed in the present study. Reproductive organs of the wild-caught animals that had been preserved in 70% alcohol in the South Australian Museum were also dissected out and weighed. None of the latter tissue was used for histology.

Results

Testicular weights

The paired testicular weights of the *Pseudomys* individuals were generally consistent within species in spite of the material being derived from several sources and being exposed to different fixatives for varying periods of time. The values ranged from about 0.3 to 4.0% relative to body weight for the various species (Table 1). In animals from 3 of 4 *Notomys* species studied, testes were invariably very small and usually did not exceed 0.2% body weight regardless of the age or history of the animals but that of the fourth species was about 0.6% body weight (Table 1).

Testicular histology

Full spermatogenesis and various germ cell associations could always be seen regardless of relative testicular size. Seminiferous tubules showed only little variation between species and were usually between 200 and 240 μ m in diameter (see Table 2).

Table 1. Absolute and relative testes weights in adult male *Pseudomys* and *Notomys*

Species	Age (months)	No.	Body wt (g)*	Wt of testes (mg)*	Relative testicular wt (mean and range)
<i>Pseudomys apodemoides</i>	4-8	3	31 ± 11	141 ± 24	0.5 (0.3-0.7)
	+	5	22 ± 7	113 ± 18	0.5 (0.3-0.7)
	++	1	21	143	0.7
<i>P. australis</i>	4-5	5	55 ± 5	1853 ± 254	3.4 (2.5-4.2)
	6-9	5	63 ± 5	2155 ± 127	3.5 (3.0-4.0)
	13-20	4	59 ± 9	2242 ± 129	3.8 (3.4-4.9)
<i>P. delicatulus</i>	17	1	8	50	0.6
	+	4	9 ± 0.6	43 ± 2	0.5 (0.4-0.5)
<i>P. desertor</i>	+	2	39 ± 1	558 ± 82	1.4, 1.5
<i>P. gracilicaudatus</i>	+	2	105 ± 17	1084 ± 78	1.1, 0.9
<i>P. hermannsburgensis</i>	9	1	12	133	1.1
	+	3	18 ± 6	163 ± 54	0.9 (0.7-1.1)
	++	10	15 ± 1.5	128 ± 27	0.9 (0.6-1.3)
<i>P. nanus</i>	5-6	4	70 ± 16	1782 ± 588	2.5 (1.8-3.6)
	19-22	2	78 ± 12	1874 ± 47	2.0, 2.9
<i>P. novaehollandiae</i>	+	2	19 ± 3	71 ± 9	0.3, 0.4
<i>P. shortridgei</i>	+	3	78 ± 15	345 ± 53	0.4 (0.3-0.5)
<i>Notomys alexis</i>	3-4	7	30 ± 6	41 ± 11	0.13 (0.10-0.21)
	6-9	6	28 ± 2	43 ± 6	0.15 (0.11-0.20)
	19-25	5	34 ± 6	50 ± 12	0.14 (0.10-0.19)
	++	7	31 ± 4	36 ± 7	0.12 (0.11-0.14)
<i>N. mitchelli</i>	6-7	4	34 ± 7	74 ± 10	0.21 (0.16-0.26)
	11-16	6	39 ± 7	62 ± 11	0.16 (0.11-0.19)
	++	6	45 ± 6	57 ± 18	0.13 (0.09-0.20)
<i>N. fuscus</i>	+	1	44	67	0.15
<i>N. cervinus</i>	+	2	33 ± 1	198 ± 28	0.64, 0.53

* Values are mean ± s.d.

+ Wild-caught individuals maintained in the laboratory for at least 5 months.

++ Wild-caught individuals killed in the field; pregnant or oestrous females also present in field sample at the same time.

Table 2. Testicular histology of *Pseudomys* and *Notomys*

Species	No.	Relative vol. occupied by interstitial tissue (%)*	Diam. of seminiferous tubules (µm)†
<i>P. apodemoides</i>	7	29.0 (21-37)	231 ± 17
<i>P. australis</i>	6	4.9 (3-7)	232 ± 15
<i>P. delicatulus</i>	3	27.8 (24-36)	204 ± 24
<i>P. desertor</i>	2	5.4 (5-6)	197 ± 32
<i>P. hermannsburgensis</i>	5	17.9 (11-23)	226 ± 20
<i>P. nanus</i>	5	4.4 (4-6)	241 ± 15
<i>P. novaehollandiae</i>	2	7.0 (6-8)	184 ± 10
<i>P. shortridgei</i>	3	4.2 (2-6)	201 ± 13
<i>N. alexis</i>	7	8.9 (5-13)	203 ± 13
<i>N. mitchelli</i>	4	11.9 (8-17)	206 ± 13
<i>N. fuscus</i>	2	14.4 (12-16)	217 ± 3
<i>N. cervinus</i>	2	14.9 (14-16)	221 ± 4

* Mean (range).

† Mean ± s.d.

Intraspecific variation in testicular histology was minimal at the time of death, irrespective of the age or history of the animals, but there were large interspecific differences. In *P. nanus* (Pl. 1, Figs 1 & 2), *P. australis*, *P. desertor*, *P. novaehollandiae* (Pl. 1, Fig. 3) and *P. shortridgei* (Pl. 1, Fig. 4) the interstitial tissue was relatively sparse and its relative volume did not exceed 8% (see also Table 2). A few Leydig cells were usually clustered around capillaries, while lymphatic channels were often seen between the Leydig cells and the myoid layer surrounding the tubules (Pl. 1, Figs 2 & 4). A continuous parietal endothelium lay close to the myoid cells. The surface of the Leydig cells that abutted the lymphatic space often had long microvilli.

In the testes of the other *Pseudomys* examined, the interstitial tissue was invariably much more abundant. In *P. hermannsburgensis* (Pl. 1, Figs 5 & 6) its relative volume was 11 to 23%, whereas in wild-caught and laboratory bred *P. delicatulus* (Pl. 2, Figs 7 and 8) and *P. apodemoides* (Pl. 2, Figs 9 & 10) it was 21–37% of the total testicular volume (see Table 2). In these 3 species there was invariably a mass of lipid-rich epithelioid Leydig cells. Some were binuclear, but, in most, a single more or less central nucleus and often a prominent nucleolus was visible (Pl. 2, Figs 8 & 10). Occasional blood channels were evident, but lymphatics were generally rare or non-existent.

In *Notomys* the relative volume of interstitial tissue varied but, on average, was about 10% (Table 2; Pl. 2, Fig. 11). Most of this tissue was composed of lipid-rich Leydig cells (Pl. 2, Fig. 12). Blood channels could usually be seen amongst each group of Leydig cells and lymphatic channels were sometimes present near the tubules.

Epididymal weights and number of spermatozoa

Total weight of the epididymides ($\pm$ s.d.) was 28 ± 6 mg ($n = 3$) in *P. apodemoides*, 552 ± 56 mg ($n = 6$) in *P. australis*, 23 ± 10 mg ($n = 8$) in *P. hermannsburgensis*, 102 mg ($n = 1$) in *P. shortridgei*, 18 ± 4 mg ($n = 8$) in *N. alexis*, 27 ± 10 mg ($n = 6$) in *N. mitchelli*, 20 mg ($n = 1$) in *N. fuscus* and 58 mg ($n = 1$) in *N. cervinus*.

Spermatozoa were invariably more numerous in the cauda than in the caput plus corpus epididymidis and the number present in the excurrent ducts correlated, in general, with the relative size of the epididymides and testes (Table 3).

PLATE 1

Fig. 1. Testis from *Pseudomys nanus* showing relatively sparse interstitial tissue (IT) between the seminiferous tubules (ST). $\times 225$.

Fig. 2. Interstitial tissue between 3 adjacent seminiferous tubules from *P. nanus* showing small blood vessels (BV) lacking blood cells due to perfusion, surrounded by a group of Leydig cells. Lymphatic spaces (LS) occur close to the tubules around which a myoid cell layer (MC) occurs. SC = Sertoli cell nucleus or abnormal spermatogonium, St = spermatids. $\times 2250$.

Fig. 3. Testes from *P. novaehollandiae* are relatively small and there is sparse interstitial tissue (IT) between the tubules (ST). $\times 225$.

Fig. 4. Interstitial tissue from *P. shortridgei* is sparse and made up of few Leydig cells (LC) surrounding blood vessels (BV) between seminiferous tubules. $\times 2250$.

Fig. 5. Testis from *P. hermannsburgensis* has much interstitial tissue (IT) between the seminiferous tubules (ST). Blood vessels (BV) lack cells due to perfusion. $\times 225$.

Fig. 6. Interstitial tissue from *P. hermannsburgensis* is composed of abundant Leydig cells (LC) with numerous lipid droplets. There are occasional blood vessels (BV), but few lymphatic spaces. $\times 4500$.

(Facing p. 610)

Table 3. Numbers of spermatozoa in the epididymides in several species of *Pseudomys* and *Notomys*

Species	Age (months)	No.	No. of spermatozoa ($\times 10^6$) in:	
			Caput + corpus	Cauda
<i>Pseudomys apodemoides</i>	—	4*	3 ± 1	10 ± 2
<i>P. australis</i>	5-7	3	68 ± 21	387 ± 33
	8-9	5	73 ± 22	514 ± 86
	13-18	3	93 ± 5	483 ± 24
<i>P. hermannsburgensis</i>	—	1	11	20
<i>P. nanus</i>	—	6	94 ± 28	387 ± 153
<i>P. shortridgei</i>	—	2	—†	51 ± 30
<i>Notomys alexis</i>	3-5	7	0.5 ± 0.3	1.3 ± 0.6
	6-9	6	0.7 ± 0.3	2.3 ± 1.4
	19-28	5	0.9 ± 0.1	2.6 ± 0.7
<i>N. mitchelli</i>	—	4	1.8 ± 1.6	1.8 ± 0.5
<i>N. fuscus</i>	—	1	1.6	2.0
<i>N. cervinus</i>	—	1	10.9	21.4

Values are mean $\pm$ s.d. for 2 epididymides per animal.

* 2 wild caught animals were 6 months old.

† Not recorded.

Accessory sex gland weights

P. australis and *P. nanus* had relatively large seminal vesicles and coagulating glands but small ventral prostate glands (Table 4). In the other *Pseudomys* species the seminal vesicles and coagulating glands were generally slightly smaller relative to body weights. In most of these species ventral prostate glands were also small, except in the two *P. novaehollandiae* in which relatively large glands occurred. In three *Notomys* species a markedly different arrangement of accessory glands occurred: the seminal vesicles and coagulating glands were minute and did not exceed 3 mm in length in *N. alexis* and 5 mm in *N. mitchelli*, but relatively large ventral prostate glands were present (see Table

PLATE 2

Fig. 7. Testis from *P. delicatulus* has very extensive interstitial tissue (IT) between seminiferous tubules (ST). $\times 225$.

Fig. 8. Interstitial tissue from *P. delicatulus* is composed of abundant, lipid-rich, Leydig cells (LC) with spherical central nuclei and often a prominent nucleolus. Occasional blood vessels (BV) here shown as small arteriole occurred, but lymphatics were rare. $\times 1800$.

Fig. 9. Testes from *P. apodemoides* also has very extensive interstitial tissue (IT) occurring between the seminiferous tubules (ST). $\times 225$.

Fig. 10. Interstitial tissue from *P. apodemoides* is composed of a mass of epithelioid lipid rich Leydig cells (LC) between the seminiferous tubules (ST), blood vessels (BV) like that shown here, occurred only occasionally. $\times 1800$.

Fig. 11. Testis from *Notomys alexis* is extremely small. There is variable amount of interstitial tissue (IT) between the seminiferous tubules (ST). $\times 225$.

Fig. 12. Interstitial tissue of *N. alexis* is often composed of fairly abundant Leydig cells (LC) amongst which small blood vessels (BV), and occasional lymphatic spaces, usually lying close to the myoid cell layer, occur. SC = Sertoli cell, ST = seminiferous tubule. $\times 2250$.

Table 4. Absolute and relative accessory sex gland weights of *Pseudomys* and *Notomys*

Species	No.	Seminal vesicles (mg)	Coagulating glands (mg)	Ventral prostate (mg)
<i>P. apodemoides</i>	7	142 ± 38 (0.3-0.6)	18 ± 3 (0.05-0.11)*	12 ± 3 (0.02-0.09)*
<i>P. australis</i>	13	865 ± 191 (1.0-1.7)	272 ± 79 (0.22-0.54)	90 ± 30 (0.09-0.18)
<i>P. delicatulus</i>	3	32 ± 2 (0.3-0.4)	18 (0.2)†	10 (0.1)†
<i>P. desertor</i>	1	202 (0.5)	56 (0.1)	22 (0.04)
<i>P. hermannsburgensis</i>	7	122 ± 42 (0.4-0.9)	22 ± 12 (0.05-0.13)	48 ± 10 (~0.2)
<i>P. nanus</i>	6	694 ± 98 (0.6-1.2)	257 ± 79 (0.2-0.6)	97 ± 30 (0.1-0.2)
<i>P. novaehollandiae</i>	2	86 ± 2 (0.4, 0.6)	32 ± 0 (0.1, 0.2)	65 ± 21 (0.3, 0.4)
<i>P. shortridgei</i>	2	222 ± 96 (0.1, 0.4)	60 ± 34 (0.11, 0.03)	20 ± 4 (0.01, 0.03)
<i>N. alexis</i>	12	—‡	—‡	105 ± 38 (0.2-0.6)
<i>N. mitchelli</i>	8	—‡	—‡	174 ± 64 (0.2-0.6)
<i>N. fuscus</i>	1	—‡	—‡	90 (0.2)
<i>N. cervinus</i>	2	182 ± 52 (0.7, 0.4)	25 ± 5 (0.08, 0.06)	106 ± 3 (0.3, 0.3)

Values are mean ± s.d. with range of relative weights expressed as % body weight in parentheses.

* Determined for 4/7 animals.

† Determined for 1/3 animals.

‡ Rudimentary.

4), by contrast in *N. cervinus* there were both large seminal vesicles and coagulating glands similar to those in *Pseudomys*.

Discussion

The testes of all the animals investigated had large canalised seminiferous tubules with all stages of spermatogenesis indicating sexual maturity. Nevertheless, within these species of Australian rodents there are considerable differences in relative testicular size and histology, epididymal weight, and number of spermatozoa present. In some *Pseudomys* (e.g. *P. australis*) there are very large testes, sparse interstitial tissue and very large sperm stores. Others, e.g. *P. delicatulus*, *P. hermannsburgensis* and *P. apodemoides*, have small or medium-sized testes with much interstitial tissue made up of abundant Leydig cells and fairly low sperm stores, whereas 3 out of 4 *Notomys* have minute testes and extremely low sperm stores.

Interspecific variation in amount and organization of the testicular interstitial tissue has been shown for at least two other mammalian groups (see Fawcett, Neaves & Flores, 1973; Setchell, 1977) but abundant interstitial tissue in rodents has been documented for only one other species, the naked mole rat, *Heterocephalus glaber* (Fawcett *et al.*, 1973).

Harcourt, Harvey, Larson & Short (1981) have shown that, in primates, relative testicular size correlates with the breeding system. In multimale breeding groups there were relatively larger testes, and Harcourt *et al.* (1981) suggested that such trends might also occur in other mammalian orders. Amongst the Australian rodents *P. australis* probably occurs in groups, has a social hierarchy (Watts & Aslin, 1981), and sexual dimorphism of body weight (Smith, Watts & Crichton, 1972), suggesting a polygynous mating system. By contrast, *P. desertor* individuals probably occur in isolation except at the time of mating, whereas *P. shortridgei* may form pair bonds and thus could be monogamous (Happold, 1976). In *P. apodemoides* there is relatively little aggression between males when placed together and, in the wild, more than one reproductively active adult of each sex is sometimes found in the one burrow system. A promiscuous mating strategy has thus been suggested (Happold, 1976; Cockburn, 1981). *N. alexis* also breeds communally in the wild. In the laboratory, no pair bonding is evident but a high degree of cohesion occurs between all animals kept together in the same group. No social order between cohabiting males is apparent, and when a female comes into oestrus she is followed by several males until one achieves intromission or ejaculation (Happold, 1976). A promiscuous reproductive strategy also seems likely for this species. Thus within

these Australian rodents the information presently available suggests a possible relationship between relative testicular size and breeding system; amongst the species that tend to occur communally, the smallest testes are present in those that probably exhibit the lowest levels of intermale aggression.

All accessory sex organs, including coagulating glands, were found in all the *Pseudomys* examined, contrary to the previous observations of Taylor & Horner (1972). However, the species with the relatively small testes generally had smaller glands. Although this could indicate lack of full sexual maturity in these animals it seems unlikely, at least for the *P. apodemoides* individuals, as adult wild-caught males were obtained at times when all females were pregnant and/or lactating, and also adult laboratory-bred animals had similar weights. Amongst *Notomys*, *N. cervinus* has a typical murid arrangement of accessory sex glands similar to that of *Pseudomys*, but in the other 3 species the ventral prostate is the only large gland present. Lack of development of the seminal vesicles and coagulating glands appears to preclude the formation of a vaginal plug (Breed, 1981a, b), which has been documented for *N. cervinus* (Crichton, 1974). Why such divergence in the arrangement of the accessory sex glands has evolved between these species remains to be determined, but it is evident that the relative size of the seminal vesicles and coagulating glands in *Notomys* correlates with that of the testes.

I thank Dr P. Baverstock and Dr C. Watts, Institute of Medical and Veterinary Science, Adelaide; Dr B. Fox, Department of Zoology, University of New South Wales, Sydney; Dr S. Morton of East Jabiru, Northern Territory; Mr K. Johnson, Conservation Commission of the Northern Territory, and Mr P. Aitken, South Australian Museum, for some of the animals; Mr C. Leigh, Department of Anatomy for help with the sectioning; Mrs G. Hermanis, Mrs J. Brazier, Mrs B. Sheldon and Mr R. Murphy, Department of Anatomy, for assistance; Dr D. Brooks and Mr J. Thompson for advice on sperm counting procedures; and Dr B. P. Setchell and Dr B. Firth for helpful comments on the manuscript.

References

- Breed, W.G. (1980) Further observations on spermatozoal morphology and male reproductive tract anatomy of *Pseudomys* and *Notomys* species (Mammalia: Rodentia). *Trans. Roy. Soc. S. Aust.* **104**, 51–55.
- Breed, W.G. (1981a) Unusual anatomy of male reproductive tract in *Notomys alexis*. *J. Mammal.* **62**, 373–375.
- Breed, W.G. (1981b) Histology of accessory sex organs and extragonadal sperm reserves in the male hopping mouse *Notomys alexis*. *Arch. And.* **7**, 357–360.
- Cockburn, A. (1981) Population processes of the silky desert mouse *Pseudomys apodemoides* in mature heathlands. *Aust. Wildl. Res.* **8**, 499–514.
- Crichton, E.G. (1974) Aspects of reproduction of the genus *Notomys* (Muridae). *Aust. J. Zool.* **22**, 439–447.
- Fawcett, D.W., Neaves, W.B. & Flores, M.N. (1973) Comparative observations on intertubular lymphatics and the organisation of the interstitial tissue of the mammalian testis. *Biol. Reprod.* **9**, 500–532.
- Happold, M. (1976) Social behaviour of the conilurine rodents (Muridae) of Australia. *Z. Tierpsychol.* **40**, 113–182.
- Harcourt, A.H., Harvey, P.H., Larson, S.G. & Short, R.V. (1981) Testis weight, body weight and breeding systems in primates. *Nature, Lond.* **293**, 55–57.
- Morrissey, B.L. & Breed, W.G. (1982) Variation in external morphology of the glans penis of Australian native rodents. *Aust. J. Zool.* **30**, 495–502.
- Setchell, B.P. (1977) Reproduction in male marsupials. In *The Biology of Marsupials*, pp. 411–457. Eds B. Stonehouse & D. Gilmore. Macmillan, London.
- Smith, J.R., Watts, C.H.S. & Crichton, E.G. (1972) Reproduction in the Australian rodents *Notomys alexis*, and *Pseudomys australis* (Muridae). *Aust. Mamm.* **1**, 1–7.
- Stanley, M. (1971) An ethogram of the hopping mouse, *Notomys alexis*. *Z. Tierpsychol.* **29**, 225–258.
- Taylor, J.M. & Horner, B.E. (1970) Observations on reproduction in *Leggadina* (Rodentia: Muridae). *J. Mammal.* **51**, 10–17.
- Taylor, J.M. & Horner, B.E. (1972) Observations on the reproductive biology of *Pseudomys* (Rodentia: Muridae). *J. Mammal.* **53**, 318–328.
- Watts, C.H.S. & Aslin, H.J. (1981) *The Rodents of Australia*. Angus and Robertson, London.
- Weibel, E.R., Kistler, G.S. & Scherle, W.F. (1966) Practical stereological methods for morphometric cytology. *J. Cell Biol.* **30**, 23–38.

Received 1 March 1982