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Sperm Morphology of Murid Rodents from Malaysia and its Possible Phylogenetic Significance

W. G. BREED[1] AND H. S. YONG[2]

ABSTRACT

The morphology of spermatozoa from rodents of peninsular Malaysia was investigated with the light microscope. The sperm had a long tapering head and long tail in four species of *Rattus,* two species of *Leopoldamys,* and in single species of *Berylmys* and *Sundamys.* Sperm head morphology of the three species of *Niviventer* varied, but in two of them it was generally similar to that of *Rattus.* By contrast, the sperm head was broader and the tail much shorter in the three species of *Maxomys* and in single species of *Chiropodomys* and *Hapalomys.* Highly divergent forms of spermatozoa occurred in *Pithecheir, Lenothrix canus,* and *Bandicota bengalensis.* No species were found in which the sperm head had two extra ventral hooks as occurs in most of the Australian Hydromyinae. The possible phylogenetic implications of these findings are briefly discussed.

INTRODUCTION

The early taxonomic investigations of the murid rodents of peninsular Malaysia indicated the presence of three monotypic genera, *Chiropodomys, Hapalomys,* and *Pithecheir,* and two species of *Bandicota* and *Mus.* All the other species were originally placed within the genus *Rattus* in which several subgenera were proposed (Chasen, 1940; Ellerman, 1949; Ellerman and Morrison-Scott, 1955; Medway, 1978; Medway and Yong, 1976; Chan et al., 1979). Subsequent karyotypic and electrophoretic studies emphasized the distinctiveness of some of the subgenera within the *Rattus* group (Yong, 1969; Chan et al., 1978, 1979) the extent of the divergence between some of the subgenera being as great

[1] Senior Lecturer, Department of Anatomy, The University of Adelaide, Adelaide, South Australia 5001.
[2] Professor, Department of Zoology, University of Malaya, Kuala Lumpur.

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as that between different genera of North American rodents (Chan et al., 1979). More recently Musser et al. (1979), Musser (1981), and Musser and Newcomb (1983) reexamined the skins, skulls, and dental morphology of these species and elevated some subgenera and named and described new genera. *Maxomys* (with *M. whiteheadi, M. inas, M. rajah,* and *M. surifer*), *Leopoldamys* (with *L. sabanus* and *L. edwardsi*), *Berylmys* (with *B. bowersii*), and *Sundamys* (with *S. muelleri*) are among the genera that concern us here. Musser and colleagues retained *R. argentiventer, R. tiomanicus, R. annandalei,* and *R. exulans* in *Rattus.* This latter terminology will be used in the present study.

Although some information is available on the reproductive biology of the female of some of these species (for example, see Harrison, 1955), very little data have been gathered on any aspect of the reproductive biology of the male; and there appears to be no information on the spermatozoa. Since recent studies on spermatozoal morphology of the Australian murids have indicated a considerable range of morphological types (Breed and Sarafis, 1979; Breed, 1983, 1984b), and phylogenetic conclusions based on these data have supported some of the conclusions previously arrived at using karyotypic and electrophoretic information (Baverstock et al., 1977a, 1977b, 1981), knowledge of this character in Malaysian murids might provide further insight into their relationships. In addition, as the origin of the Australian murids is unknown and as most of the species have spermatozoa with a complex apomorphic character (Breed, 1984b), a study of spermatozoa from Southeast Asian murids might shed some light on the origin of the Australian groups. The present study thus describes the appearance of spermatozoa from most of the murids on Peninsular Malaysia under light microscopy. The results are considered in relation to phylogenetic conclusions based on other data.

Materials and Methods

Live adult males of 14 species were obtained from the following sources or localities:

Rattus tiomanicus (n = 4), *Sundamys muelleri* (n = 1), and *Berylmys bowersii* (n = 3): Fraser's Hill and Ulu Lepah, Pahang.
Rattus argentiventer (n = 2): Parit Buntar.
Rattus exulans (n = 3): donated by Institute for Medical Research, Kuala Lumpur.
Leopoldamys sabanus (n = 4): Ulu Lepah and Ulu Gombak, Selangor.
Leopoldamys edwardsi (n = 2): Fraser's Hill.
Chiropodomys gliroides (n = 1): Bagan Datok, Selangor.
Maxomys inas (n = 2): Fraser's Hill.
Maxomys whiteheadi (n = 1): Ulu Gombak.
Niviventer rapit (n = 2): Cameron Highlands.
Niviventer bukit (n = 1) and *M. surifer* (n = 2): Kedah.
Bandicota bengalensis (n = 1): Penang.

The animals were killed in the laboratory and sperm smears were prepared for light microscopy by placing a suspension of spermatozoa on a microscope slide flooded with 0.1 M buffered glutaraldehyde.

Spermatozoa for light microscopy from *Niviventer cremoriventer* (n = 2) and *Hapalomys longicaudatus* (n = 1) were obtained from animals that had been preserved in 70 percent alcohol at the Museum in the Department of Zoology, University of Malaya. A sperm smear of *Pithecheir,* which had been air-dried and stained with nigrosin and eosin, was donated by the Institute for Medical Research, Kuala Lumpur. Epididymides and testes were taken from two *Lenothrix canus* that had been collected in the Subang Forest Reserve, Selangor, and kept at the American Museum of Natural History.

Smears were observed under phase contrast and photographed under phase contrast or Nomarski optics. Approximate lengths of the sperm head, midpiece, and principal and end pieces were determined where possible. Sperm head length was measured from the base of the postacrosomal region to the top of the curvature of the hook, whereas breadth was determined from the dorsal to ventral surface at the point where the connecting piece joins to the sperm head. The length of hook, when present, was taken from the ventral surface of the sperm head to the apical extremity of the hook. Measurements were made with an ocular micrometer at ×1000 magnification, and carried out on fixed material with a phase contrast microscope. Use of the terms

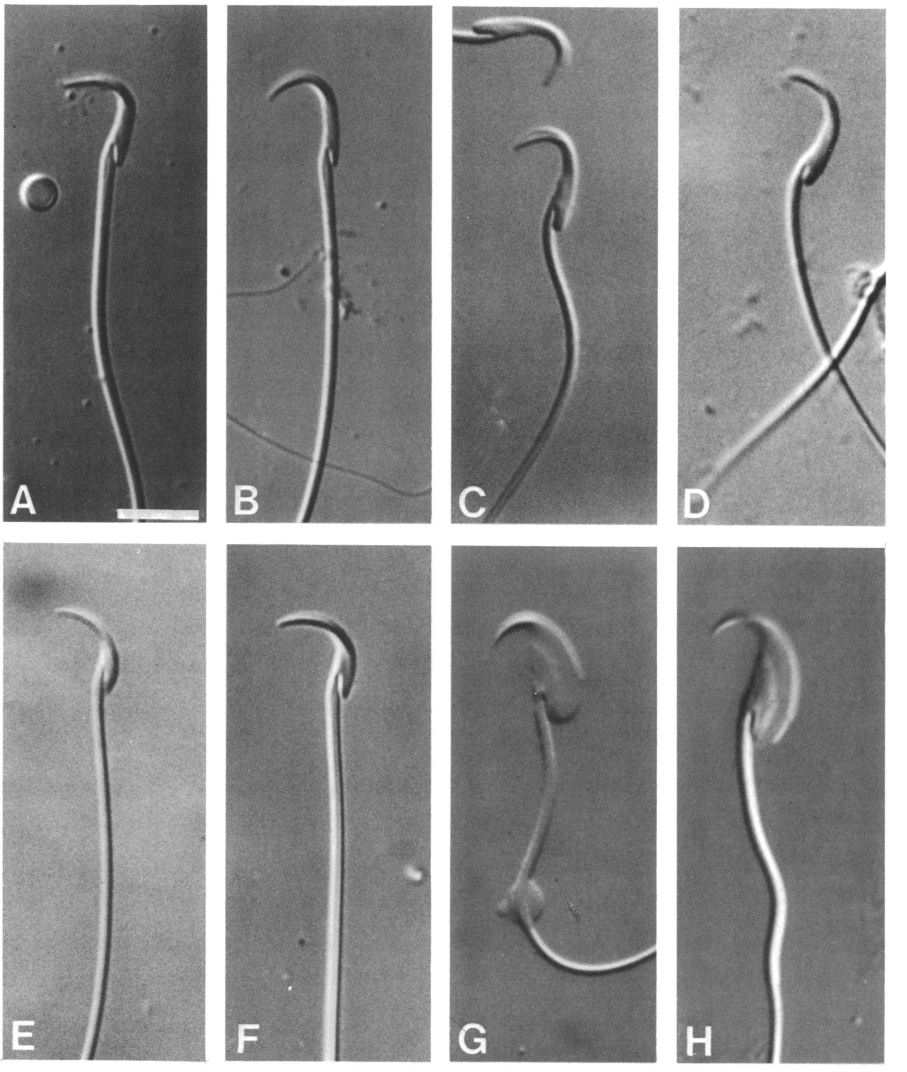

Fig. 1. Nomarski optics light micrographs of spermatozoa from Malaysian rodents. **A,** *Rattus tiomanicus*; **B,** *Rattus exulans*; **C,** *Sundamys muelleri*; **D,** *Berylmys bowersii*; **E,** *Leopoldamys edwardsi*; **F,** *Leopoldamys sabanus*; **G,** *Maxomys whiteheadi*; **H,** *Maxomys inas.* Bar equals 10 μm.

dorsal and *ventral* follows Breed (1983) and Flaherty and Breed (1983).

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RESULTS

Only slight variation in morphology of spermatozoa from any one species was gen-

TABLE 1
Approximate Head and Tail Lengths of Spermatozoa of Various Malaysian Rodents

Taxon	Head length	Midpiece	Principal and end piece	Total tail length
Rattus rattus diardii	11.0	—	—	160
Rattus tiomanicus	10.0	[a]	—	160
Rattus exulans	12.0	[a]	—	164
Rattus argentiventer	11.0	[a]	—	172
Sundamys muelleri	12.0	[a]	—	150
Berylmys bowersii	12.0	[a]	—	175
Leopoldamys sabanus	[b]	[a]	—	170
Leopoldamys edwardsi	[b]	[a]	—	172
Niviventer rapit	12.0	45	85	130
Niviventer bukit	11.5	44	96	140
Niviventer cremoriventer	9.0	35	75	110
Maxomys whiteheadi	12.0	25	100	125
Maxomys inas	13.5	32	107	139
Maxomys surifer	10.5	35	70	105
Chiropodomys gliroides	10.0	22	80	102
Pithecheir parvus	7.5	22	62	84
Hapalomys longicaudatus	12.0	37	72	109
Bandicota bengalensis	11.5	43	95	138
Lenothrix canus	9.0	45	95	140

[a] Junction between mid and principal piece could not be accurately determined.
[b] Head length could not be accurately determined.

erally found, but there were considerable interspecific differences.

In *Rattus exulans* (fig. 1B), *R. tiomanicus* (fig. 1A), *R. rattus diardii, R. argentiventer, Sundamys muelleri* (fig. 1C), and *Berylmys bowersii* (fig. 1D) the head of the spermatozoon was similar and sickle-shaped. It had a length of 10 to 12 μm with the connecting piece lying 2.5 to 3 μm from the base on the ventral surface (table 1). The lateral face was thin, only about 2 μm in breadth; the hook extended 6 to 8 μm from the ventral surface, appearing longest in *R. tiomanicus.*

In the two species of *Leopoldamys* (*L. sabanus,* fig. 1F, and *L. edwardsi,* fig. 1E), the overall sperm head was shaped more like that of a scythe; its total length could not be determined accurately, but the lateral face was about 2 μm in breadth, and the hook extended up to 8 μm from the ventral surface. In these two species of *Leopoldamys,* as well as the species of *Rattus, Sundamys muelleri,* and *Berylmys bowersii,* there was a long (150 μm to 172 μm) sperm tail (table 1). The junction between the mid and principal pieces could not be determined with the light microscope, but the total sperm tail length was somewhat less in *S. muelleri* than in spermatozoa from other species where the differences were only small.

In the three species of *Niviventer* there was interspecific variability in sperm head morphology. The sperm head of *N. rapit* (fig. 2C) and *N. bukit* (fig. 2D) was 11 to 12 μm long and about 2 μm broad. In the former species the hook usually curved more caudad, extending 5 to 6 μm from the ventral surface. Spermatozoa of *N. cremoriventer* (fig. 2B) had a head length of only 9 μm, whereas the lateral face was about 3 μm in breadth. In these three species, the sperm tail was shorter than in *Rattus,* ranging from 110 to 140 μm.

Spermatozoa of the three species of *Maxomys* also showed interspecific differences. In none of the species were the sperm similar in morphology to those of *Rattus, Leopoldamys, Berylmys, Sundamys,* or *Niviventer,* as all had a sperm head with a broader lateral face. The spermatozoa of *M. whiteheadi* (fig. 1G) were about 12 μm long with the connecting piece 3.5 μm from the caudal surface (table 1). The width of the lateral face was between 5.0 and 5.5 μm, and hook length about 4.5 μm. In *M. surifer* (fig. 2A) the sperm

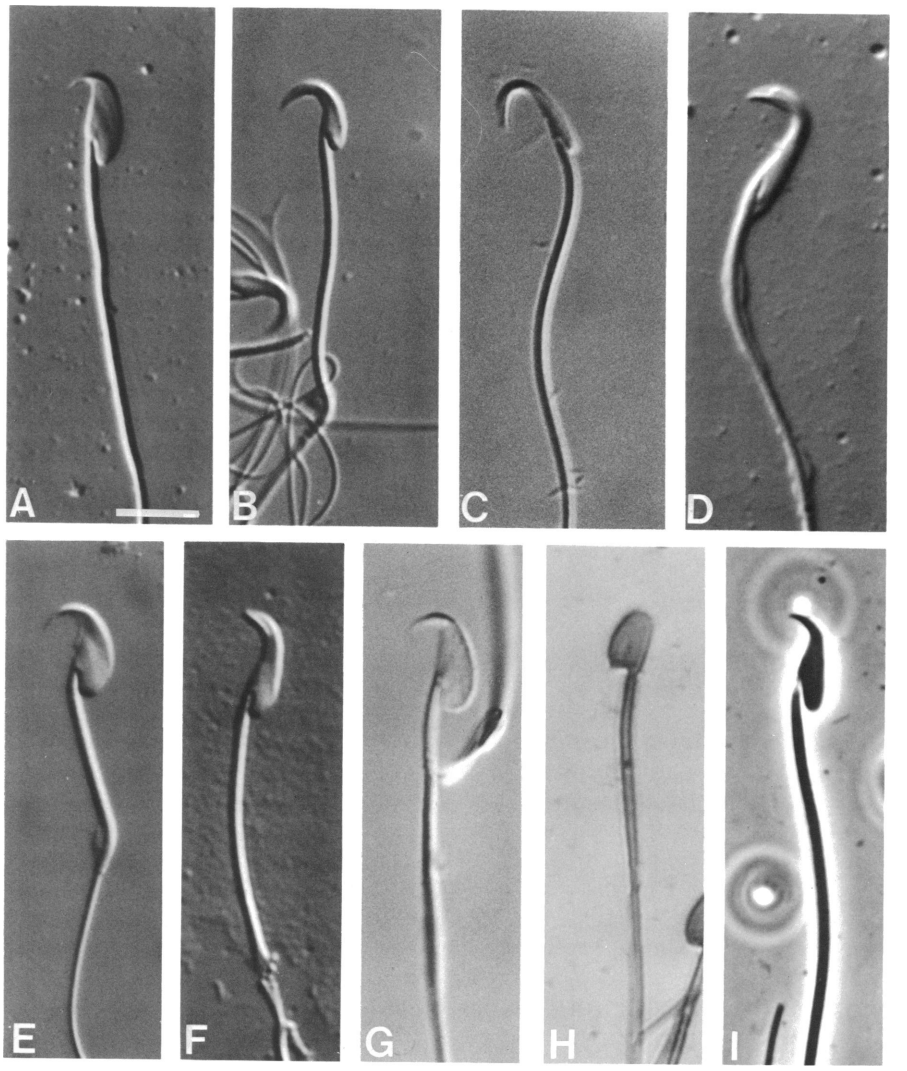

Fig. 2. Nomarski optics (A–G), bright field (H), and phase contrast (I) light micrographs of spermatozoa from Malaysian rodents. **A,** *Maxomys surifer*; **B,** *Niviventer cremoriventer*; **C,** *Niviventer rapit*; **D,** *Niviventer bukit*; **E,** *Chiropodomys gliroides*; **F,** *Bandicota bengalensis*; **G,** *Hapalomys longicaudatus*; **H,** *Pithecheir parvus*; **I,** *Lenothrix canus.* Bar equals 10 μm.

head was generally smaller (length about 10.5 μm, width 3.5 μm), and the hook extended only 2.0 to 2.5 μm from the ventral surface. In *M. inas* (fig. 1H), the sperm head was considerably larger and the hook longer. In all species of *Maxomys* the length of the sperm tail, in particular that of the midpiece, was relatively short.

The general shape of the sperm head of *Chiropodomys gliroides* (fig. 2E) was similar to that of laboratory *Mus* in having a hook about 5 μm long, head length of about 10 μm, and breadth of lateral face of 5 μm. The connecting piece was 3.5 μm from the caudal part of the sperm head, and midpiece length was about 22 μm. In *Hapalomys longicaudatus* (fig. 2G) the head shape of the spermatozoon was similar to that of *M. whiteheadi* and *M. inas,* but the hook was only about 3 μm. The lateral face was about 5.0 μm wide in the region of the connecting piece, which was inserted 2.5 μm from the caudal part of the

sperm head. Also no ventral spur was seen, as is clearly evident on the sperm head of *C. gliroides.*

In *Bandicota bengalensis* the sperm head differed. It had a short, broad hook that tended to form an obtuse angle with the rest of the sperm head (fig. 2F). In *Lenothrix canus* (fig. 2I) the hook on the sperm head again often formed an obtuse angle, but it was very different in shape and tapered apically. Finally, the spermatozoa from *Pithecheir parvus* (fig. 2H) were highly divergent in having no apical hook. These sperm heads had a rounded, apical border and were only 7.5 μm long. There was an eccentric, basal insertion of the connecting piece, these being the only spermatozoa where the connecting piece was not inserted on the ventral surface and no apical hook occurred.

DISCUSSION

The mammalian spermatozoon is a highly specialized cell designed for transmission of the haploid male genome to the female oocyte. The same basic structural components are present in all mammalian species, but their size and shape vary considerably. The nucleus is usually the largest component of the sperm head and it contains highly condensed chromatin arranged in a species-specific manner; it is capped by an acrosome which covers the anterior pole. Factors that determine overall sperm head shape are not known, but it generally reflects that of the nucleus. In most mammalian species the head shape is ovoid or spatulate, but in murid rodents there is usually an apical hook which is composed of nuclear, subacrosomal, and acrosomal material (Friend, 1936; Austin and Bishop, 1958; Fawcett, 1970). However, in many of the Australian murids two extra ventral hooks which are composed largely of an extension of the subacrosomal space are also present (Breed and Sarafis, 1979; Breed, 1983, 1984b; Flaherty and Breed, 1983). Among murid rodents there is considerable variation in the length of the hook(s), size and shape of the sperm head, and length of the various components of the tail; spermatozoa of a few species totally lack hooks (Friend, 1936; Breed, 1983). Such variation in sperm head morphology does not show any obvious adaptive significance and may have evolved by random genetic drift (Austin, 1976). As sperm morphology appears not to be related to ecology or life history, it may be a useful independent character for gleaning information about the genealogical relationships when considered in relation to other morphological, biochemical, and karyotypic data. Among myomorph rodents, this character has been used in phylogenetic studies of members of the Sigmodontinae (Linzey and Layne, 1974), Australian muridae (Breed and Sarafis, 1979), and Heteromyidae (Hafner and Hafner, 1983). In this study the structure of spermatozoa has been considered in an attempt to gain some insight into relationships among Malaysian murids.

The morphology of spermatozoa of *Rattus rattus, R. norvegicus* (for example, see Friend, 1936), Australian *Rattus* (Breed and Sarafis, 1979), and *Rattus* from Papua New Guinea (including members of the subgenus *Stenomys*; Breed, 1984a) have a fairly long, sickle-shaped sperm head and long sperm tail. The present study has shown that Malaysian species (*R. tiomanicus, R. argentiventer,* as well as *R. exulans* and *R. r. diardii*) have a similar sperm head morphology. The sperm head was also similar in *Sundamys muelleri* and *Berylmys bowersii* although, in the former species, the length of the sperm tail was significantly shorter than in the other species. Both *Sundamys* and *Berylmys* share a number of derived morphological characters with *Rattus* (Musser and Newcomb, 1983) although they are quite distinct in many of their cranial and dental features. Characteristics of their spermatozoa are consistent with the view that these two genera have evolved from a common ancestor that also gave rise to *Rattus.*

The morphology of spermatozoa in many species of the other three genera, recently split off from *Rattus* by Musser et al. (1979), Musser (1981), and Musser and Newcomb (1983), showed some distinctive features. In the two species of *Leopoldamys* the spermatozoa, unlike those discussed above, had a head tending to be more scythe- than sickle-shaped. No other Malaysian rodent had this sperm head shape. Both *Niviventer* and *Maxomys* exhibited interspecific differences in sperm morphology. In the former genus, spermatozoa of *N. bukit* and *N. rapit* were *Rattus*-

like (except for the shorter sperm tail). In contrast, the sperm head of *N. cremoriventer* was considerably shorter and had a broader lateral face. Using a classical phenetic analysis of nine biochemical markers, Chan et al. (1979) also found *cremoriventer* to be the most divergent of the three species of *Niviventer.*

None of the three species of *Maxomys* had spermatozoa like those of *Rattus*; the sperm heads had a considerably broader lateral face, especially those of *M. whiteheadi* and *M. inas. Maxomys surifer* had a smaller sperm head and a shorter hook than the last two species. Misonne (1969) grouped *whiteheadi* (and *rajah*) with *sabanus* and *edwardsi* in the subgenus *Leopoldamys* but, on the basis of karyotypic and electrophoretic data, Yong (1969) and Chan et al. (1978) considered these groups quite distinct, a conclusion also reached by Musser et al. (1979) and Musser and Newcomb (1983) on reanalysis of skin, skull, and dental characters. Sperm morphology clearly supports these latter conclusions, at least for the Malaysian species. However, preliminary observations on the spermatozoa of *M. bartelsii* (Breed and Yong, unpublished) and three species of *Maxomys* from Sulawesi (Breed and Musser, in prep.) indicate that in these species sperm morphology differs considerably from that of congeners occurring on the Malay peninsula.

Musser and Newcomb (1983) noted that *Maxomys* and *Mus* shared similar molar derivations and they found that members of both genera also had elongated feet with relatively small and low plantar pads. The spermatozoa of these animals also show some similarities. Such similarities in several independently evolved, and possibly derived, characters could be of phylogenetic significance. Musser et al. (1979) also found some similarity in morphology of *Maxomys* and *Melomys* that they considered to be due to convergence. This conclusion is supported by the spermatozoa of species in these genera: *Melomys* has a sperm head with two extra ventral hooks—an apomorphic character shared with most of the other Hydromyinae (Breed, 1984b).

Spermatozoa of *Chiropodomys gliroides* are somewhat similar to those of *Mus* (and thus very different from *Rattus, Berylmys, Sundamys,* and *Leopoldamys*), while those from *Pithecheir* and *Lenothrix canus* are very distinctive and clearly different from each other. The close affinity of *Chiropodomys* to *Micromys* as suggested by Ellerman (1941) and Misonne (1969) is not supported by sperm morphology, and perhaps this genus is related, albeit distantly, to *Mus.* Ellerman (1949) and Ellerman and Morrison-Scott (1955) included *surifer, rajah, inas,* and *whiteheadi* in the same subgenus as *canus* (as *Lenothrix*), a grouping challenged by Yong (1969), Chan et al. (1978), Musser et al. (1979), and Musser (1981). Studies on sperm morphology also clearly do not support this grouping, nor do they support the placing of *canus* with *Rattus.*

Misonne (1969) placed *Lenothrix canus* with *Hapalomys, Pithecheir,* and *Chiropodomys* in the "*Lenothrix-Parapodemus*" division. He considered *Lenothrix,* on the basis of dental features, to be very primitive and suggested that its closest relative on the Malay peninsula might be *Pithecheir.* In addition he stated that it is "clearly" related to the Australian group that includes *Mesembriomys, Pseudomys, Conilurus,* and others. Sperm morphology does not lend support to these suggestions, as the sperm of *Pithecheir* is highly divergent and is the only sperm investigated in the present study that had no apical hook, whereas most of the species of the non-*Rattus* Australian group have the two extra hooks on the sperm head in addition to a dorsal hook, an apomorphic character not shared by *Lenothrix* or any other Malaysian murid.

The two species of *Bandicota* that occur in Malaysia are thought to have been recently introduced or, at least, to be fairly recent immigrants (Musser and Newcomb, 1983). Sperm from only one of these was available for study and it clearly represented a very different morphological type. Because *Bandicota* is not part of the original murid fauna of Malaysia these findings will not be discussed further.

Clearly further work on the sperm morphology of the other species of rodents occurring in the genera investigated must be performed in order to determine whether the present findings apply to the genera as a whole. However, the present study does suggest two main groupings among the species investi-

gated. Group 1 has a long attenuated sperm head and, usually, a long sperm tail; it includes all species of *Rattus,* both species of *Leopoldamys,* and single species of *Sundamys* and *Berylmys.* Two of the species of *Niviventer* also have a similar sperm head morphology. These features are also present in sperm of all Australian and Papua New Guinea *Rattus* as well as in *R. norvegicus.* Group 2 has a sperm head with a broader lateral face and includes all species of *Maxomys, Chiropodomys,* and *Hapalomys.* A ventral spur is present in some and their sperm tails are much shorter than those of *Rattus.* Spermatozoa in this group are more like those of *Mus* (especially those of *Chiropodomys*) and *Apodemus.* Most of the species of murid rodents in Australia, apart from *Rattus,* have a similar basic sperm structure but, in addition, two extra ventral hooks are also present. None of the Malaysian species exhibited this character. Spermatozoa of *Lenothrix, Pithecheir,* and *Bandicota* are all highly divergent and very different from each other.

Whether these findings reflect evolutionary relationships of the Malaysian murids remains to be determined, but some of the conclusions based on sperm morphology agree with those proposed by authors using different sets of characters. A study of sperm morphology of murids occurring in various other biogeographical regions is presently underway (Breed, in prep.), and only when these additional data are analyzed will it be possible to determine which are the ancestral and which the derived forms. It may then be possible to better evaluate the phylogenetic significance of the present findings. In addition, further investigations of the spermatozoa of these animals should also involve transmission electron microscopical observations to determine the more subtle differences in sperm head shape among the various species.

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