Belg. J. Zool. - Volume 128 (1998) - issue 2 - pages 189-200 - Brussels 1998

Received: 10 June 1998

SPERM MORPHOLOGY OF THE DIPODID RODENTS (JERBOAS) COMMON IN EGYPT

ADEL A. BASYOUNY SHAHIN AND MOHAMMED H. IBRAHEEM
Department of Zoology, Faculty of Science, Minia University,
P.O. Box 61519, El-Minia, Egypt
e-mail: rumenia@enstinet.eg.net

Abstract. Sperm morphology of the jerboas *Allactaga* and *Jaculus* species common in Egypt was described by light and transmission electron microscopy. Two morphs of spermatozoa were observed among these dipodids. One type observed in the smaller jerboa, *A. tetradactyla*, has a paddle-shaped long head, long tail, and the connecting piece of tail inserts off-centre at the base of the sperm head. The other form found in both lesser jerboas, *Jaculus jaculus* subspecies and large jerboa, *Jaculus orientalis orientalis*, has a pear-shaped short head, relatively short tail, and the connecting piece of the tail attaches midbasally to the lower concave surface of the sperm head. In both types, the sperm has nearly the same internal organization and the head is symmetrical, bilaterally flattened, lacks any traces of hooks or processes, and is capped by a massive symmetrical apical acrosomal segment. Accordingly, it was concluded that they are part of one evolutionary radiation and the « symmetrical head-short tail » sperm type represents the ancestral type for dipodid rodents. Moreover, it was shown that the dipodids share many of their sperm features with muroids. Hence, it was suggested that the dipodids during their evolution have formed a clade that has been branched off either from Muroidea or Myomorpha. Of course this association needs more further studies which are under consideration.

Key Words: Sperm, morphology, ultrastructure, Dipodidae, rodents, Jerboas, *Allactaga tetradactyla*, *Jaculus* spec.

INTRODUCTION

Observations on sperm morphology from most species of mammals have indicated that although nearly all eutherian spermatozoa have the same basic design, the morphology of the head of the mature spermatozoon varies markedly between, and occasionally within, the various mammalian orders. It is generally spatulate, paddle-shaped or pear-shaped, but in most murid rodents it is hook-shaped with the anterior region of the nucleus surrounded by an elaborate acrosome and an extension of the subacrosomal cytoskeleton as a perforatorium (RETZIUS, 1909; FRIEND, 1936; BISHOP & AUSTIN, 1957; FAWCETT, 1970; FAWCETT *et al.*, 1971; BREED & YONG, 1986; BEDFORD & HOSKINS, 1990; BREED & MUSSER, 1991; BREED & APLIN, 1994; EDDY & O'BRIEN, 1994; BASKEVICH & LAVRENCHENKO, 1995; LAVRENCHENKO & BASKEVICH, 1996; BREED, 1991, 1995a, b, 1997). The degree of variation in sperm head shape related to functional requirements is still unknown. However, as appeared from studies on different mammalian groups, the patterns of similarity and difference in sperm head morphology can be indicative of interspecific or intergeneric relationships (LINZEY & LAYNE, 1974; HARDING *et al.*, 1979, 1982; TEMPLE-SMITH, 1987; HARDING & APLING, 1990; BREED & APLIN, 1994).

Since recent studies on the spermatozoal morphology of murid rodents from certain continents have indicated a considerable range of morphological types in comparison with those occurring elsewhere (BREED & SARAFIS, 1979; BREED, 1980, 1983, 1984a, b; BASKEVICH & LAVRENCHENKO, 1995; LAVRENCHENKO & BASKEVICH, 1996), it became possible to use the sperm morphology data to evaluate the taxonomic and phylogenetic relationships and to support the conclusions arrived at from karyotypic and electrophoretic studies (BAVERSTOCK *et al.*, 1981; BREED & YONG, 1986; BREED & MUSSER, 1991; BREED & APLIN, 1994; BREED, 1991, 1995a, b, 1997).

The dipodids, jerboas, in Egypt were classified into two genera: *Allactaga* Cuvier, 1836 and *Jaculus* Erxleben, 1777 (OSBORN & HELMY, 1980). The *Allactaga* has one species, *A. tetradactyla* (small jerboa), while the *Jaculus* includes two species, *J. orientalis* (greater jerboa) and *J. jaculus* (lesser jerboa). The latter species, according to OSBORN & HELMY (1980), has four subspecies, *J. j. jaculus*, *J. j. flavillus*, *J. j. schlueteri*, and *J. j. butleri*.

According to ANDERSON (1967), the Dipodoidea likewise Muroidea and Gliroidea were considered as a fairly distinctive group of Myomorpha. However earlier, the Muroidea were considered the nucleus of the Dipodoidea and Gliroidea (SIMPSON, 1945).

Although some ecological, behavioral, anatomical, and physiological information is available on the jerboas, family Dipodidae, (ELLERMAN, 1942; WASSIF, 1960; EL HILALI & VEILLAT, 1975; OSBORN & HELMY, 1980; LAKHDAR-GHAZAL *et al.*, 1992; 1995a, b), there appears to be no further information on the spermatozoa of North-African Dipodidae or those occurring elsewhere. Thus the present study was undertaken to describe the appearance and organization of spermatozoa of the dipodids common in Egypt, and their significance for discrimination between these morphologically similar jerboas.

MATERIAL AND METHODS

Live adult males of three species and four subspecies of jerboas belonging to two genera common in Egypt were collected during the period of sexual activity (May-June) from the following localities:

- *Allactaga tetradactyla* Lichtenstein, 1823 (Four-toed or small jerboa), n = 4: Mersa Matruh.
- *Jaculus jaculus jaculus* Linnaeus, 1758 (lesser jerboa with orangish back and black tail band incomplete on the underside), n = 5: El-Faiyum,
- *Jaculus jaculus flavillus* Setzer, 1955 (lesser jerboa with brownish back, hind foot length less than 63 mm and ear length more than 23 mm), n = 5: Sidi Barrani,
- *Jaculus jaculus schlueteri* Nehring, 1901 (lesser jerboa with brownish back, hind foot length more than 63 mm and ear length more than 23 mm), n = 5: Ismailia,

- *Jaculus jaculus butleri* Thomas, 1922 (lesser jerboa with brownish back and ear length less than 23 mm), n = 5 : Red Sea area,
- *Jaculus orientalis orientalis* Erxleben, 1777 (Greater jerboa), n = 5 : Mersa Matruh.

The animals were killed in the laboratory and the testes and epididymides were dissected out. Small pieces of cauda epididymides were immediately fixed for about 1½ hr in 3% glutaraldehyde made up in 0.1 M phosphate buffer (pH 7.4) for transmission electron microscopy (TEM). After fixation the samples were washed several times in 0.1 M cacodylate buffer (pH 7.4) and fixed in 1% osmium tetroxide for 1-1½ hr, then rinsed again in buffer, dehydrated by passing through a series of ethanols and embedded in epoxy resin. Thick plastic sections (1 µm) were cut, stained with toluidine blue and when appropriate regions were found, ultrathin sections were obtained and stained with lead citrate and uranyl nitrate. The sections were subsequently observed with JEOL JEM-100CX II and photomicrographs were taken.

In addition, sperm samples from all individuals of each species were also prepared for light microscopy (LM) by extruding the contents from caudae epididymides on a watch glass that contained 3% buffered glutaraldehyde. After fixation, drops of the solution with cellular material were placed on microscope slides. After placing a coverslip on each slide, the spermatozoa were observed under phase contrast optics and photographed with x 100 objective.

Measurements of spermatozoa from each species were taken with an ocular micrometer slide at x 100 magnification. The approximate lengths of the head, midpiece and tail as well as breadth of the head and midpiece were measured as described by Breed & Aplin (1994). The combined length of the principal and end pieces of the tail was taken because they are indistinguishable from each other under the light microscope.

RESULTS

The terminology used for describing orientation of the sperm head and morphology of the head and tail follows Breed (1983, 1984a, b) and Flaherty & Breed (1983). However, the terminology of the planes of sections through the sperm follows Breed (1995a, b).

Two major sperm types were observed among the jerboas examined depending on the shape of the head and site of the tail insertion into the head. One type (Fig. 1b) has a paddle-shaped head, a broad face (6.0 µm wide) and a connecting piece of tail that inserts off-centre at the basal concave surface of the sperm head. The other type (Figs 2a; 3a) has a pear-shaped head, a relatively narrow face (4.0 µm wide) and a connecting piece of tail that attaches to the midbasal concave surface of the sperm head. In both forms, the sperm head appears symmetrical, bilaterally flattened, lacks any traces of hooks or processes, and narrows a little toward the connecting piece of the tail. The acrosome is large and massive; it is symmetrical with an apical segment forming a cap above the bilaterally flattened nucleus and a thin equatorial segment extending along part of the lateral nuclear surfaces, caudal to which is the postacrosomal dense lamina. There is an invagination of the inner acrosomal membrane, into which the subacrosomal cytoskeleton or perforatorium projects, as a midline apical ridge over the convex nuclear surface. The midpiece is readily distinguishable from the principal piece of the tail. The ultrastructural organization of the sperm tail resembles that of other rodents.

Furthermore, differences in the dimensions of sperm head and tail among the species studied are considerable (Table 1) and are as follows.

TABLE 1

Sperm dimensions of the dipodoid rodents in Egypt. The value given is the largest measurement for each dimension; all values are in micrometers (μm)

Species	*Head*		*Tail*		
	Lenth	*Breadth*	*MP*	*PP+EP*	*Total*
Allactaga tetradactyla	9	6	15(2)	95	110
Jaculus j. jaculus	7	4	8(1)	50	58
Jaculus j. butleri	6	4	7(1)	50	57
Jaculus j. schlueteri	7	4	8(1)	50	58
Jaculus j. flavillus	7	4	8(1)	49	57
Jaculus o. orientalis	8	4	7(1)	46	53

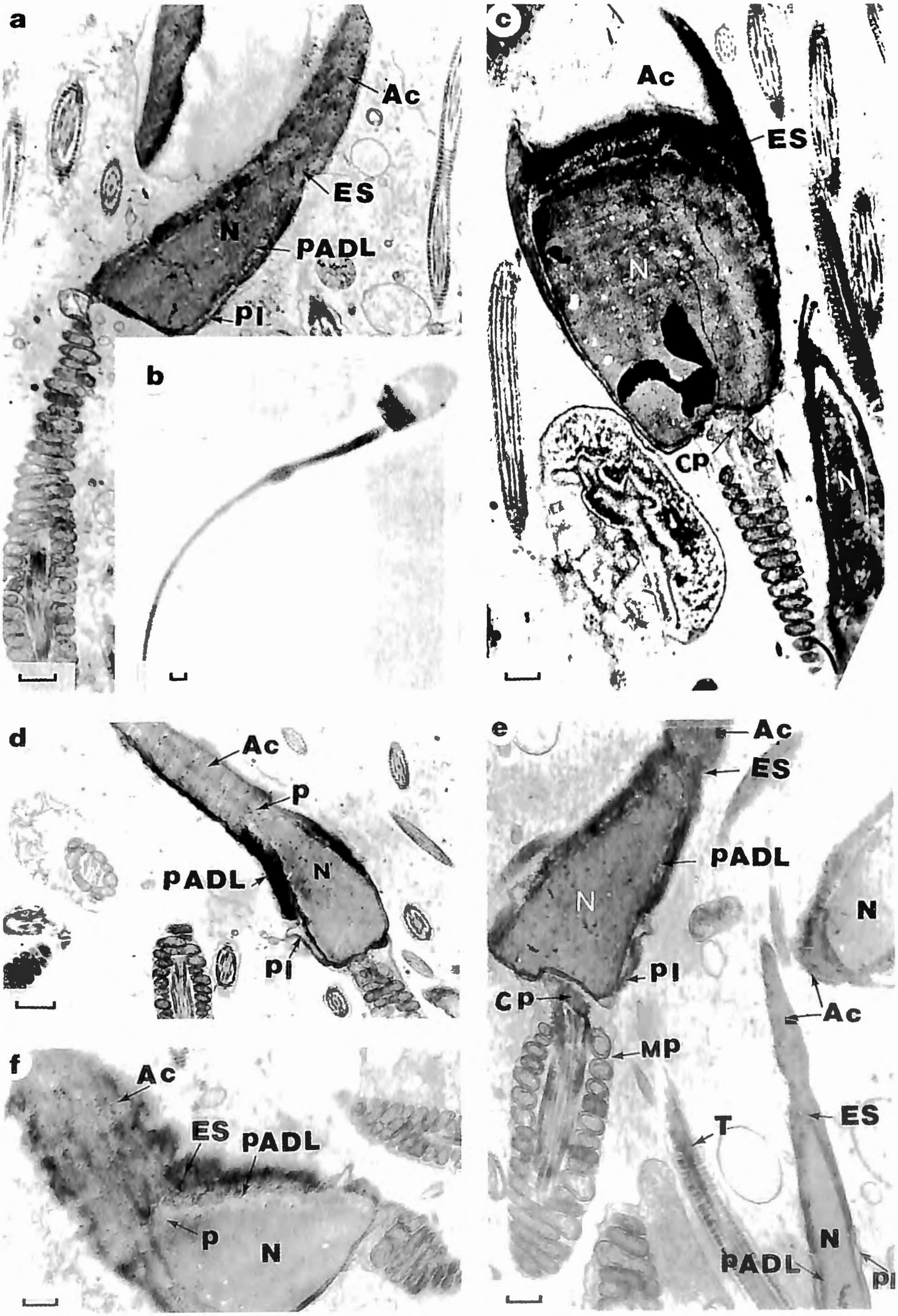
MP= Midpiece length; the value in brackets is the midpiece breadth. PP+EP= Combined length of principal and end pieces.

Allactaga tetradactyla. In *A. tetradactyla*, the sperm is considerably different from those of *Jaculus* species. The head has a paddle-shape (Fig. 1b); it is 9.0 μm long and 6.0 μm wide. The tail is relatively long; it is 110 μm long, of which 15 μm is distinguishable as midpiece. The midpiece is inserted off-centre in a concave surface at the base of the head (Fig. 1b, c, e, f). The acrosome forms a prominent girdle around the posterior nuclear region (Fig. 1b, c).

TEM sections through sperm head indicate that the nucleus is bilaterally flattened and has a homogeneous electron-dense material; it is thicker basally and thinner apically. Its anterior two-thirds is capped by the thinner equatorial segment of the acrosome (Fig. 1a, d, e, f). In the anterior region of the sperm head the acrosome forms a thick apical segment with a homogeneous electron-dense matrix over the dorsal convex surface of the nucleus; it presumbly corresponds to the principal segment with the thinner equatorial segment being present posteriorly (Fig. 1a, d, e, f). At the anterior tip of the nucleus there is a very

Legend to the figures (see page 193)

Fig. 1. – Sperm morphology of *Allactaga tetradactyla*. b. Phase-contrast micrograph. a, c-f. TEM micrographs showing sperm ultrastructure. (a) Scale bar = 0.23 μm, x 10 000; (b) Scale bar = 1.33 μm, x 1 350; (c) Scale bar = 0.08 μm, x 17 300; (d) Scale bar = 0.23 μm, x 10 000; (e) Scale bar = 0.13 μm, x 17 000; (f) Scale bar = 0.98 μm, x 14 000. Abbreviations in this and the following plates are: Ac= acrosome; CP= connecting piece of the tail; ES= equatorial segment of the acrosome; MP= midpiece of the tail; N= nucleus; P= perforatorium; Pl= plasmalemma; PADL= postacrosomal dense lamina; T= tail of the sperm.


a
Ac
ES
N
PADL
pl
b
c
Ac
ES
N
CP
N
d
Ac
p
PADL
N
pl
e
Ac
ES
PADL
N
N
pl
CP
Ac
MP
ES
T
N
PADL
pl
f
Ac
ES
PADL
p
N

small accumulation of the subacrosomal material which passes a little down between the outer nuclear envelope and inner acrosomal membrane (Plate 1d). In the posterior region of the sperm head there is a relatively short postacrosomal dense lamina which is tightly bound to overlying plasmalemma (Fig. 1a, d, e, f).

Jaculus species. LM observations of spermatozoa from the two species of *Jaculus, J. jaculus* and *J. orientalis*, indicate marked similarity in form. The head is pear-shaped, i.e., it narrows slightly posteriorly, and the tail attaches to the lower midbasal concave surface of the nucleus (Figs 2a; 3a). The acrosome, in common with that of *A. tetradactyla,* is symmerical; it has a large apical acrosomal segment that forms a cap over much of the head surface. The tail is relatively short. However, variations in the head and tail dimensions occur between the two species (Table 1).

In *J. jaculus* subspecies, the sperm head ranges from 6.0 to 7.0 µm in length and is about 4.0 µm wide. The midpiece is readily distinguishable from the principal piece; it is from 8.0 to 9.0 µm long and 1.0 µm wide. The principal and end pieces combined are from 49.0 to 50.0 µm long.

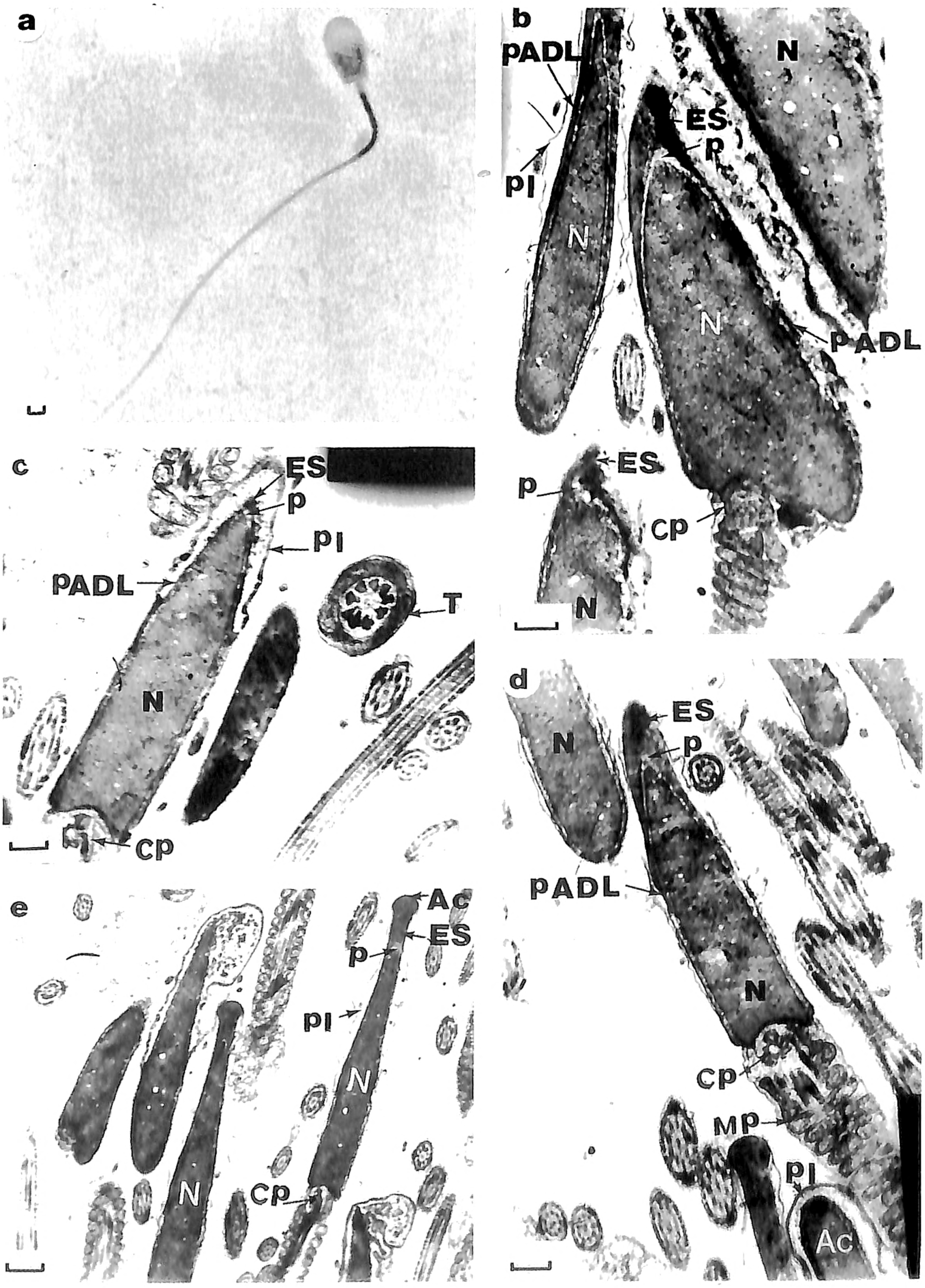
In *J. orientalis*, however, the head is usually longer; being 8.0 µm in length, but in common with *J. jaculus*, it is 4.0 µm in width and has no hooks or processes. The tail measures 53 µm, of which the midpiece is 7.0 µm.

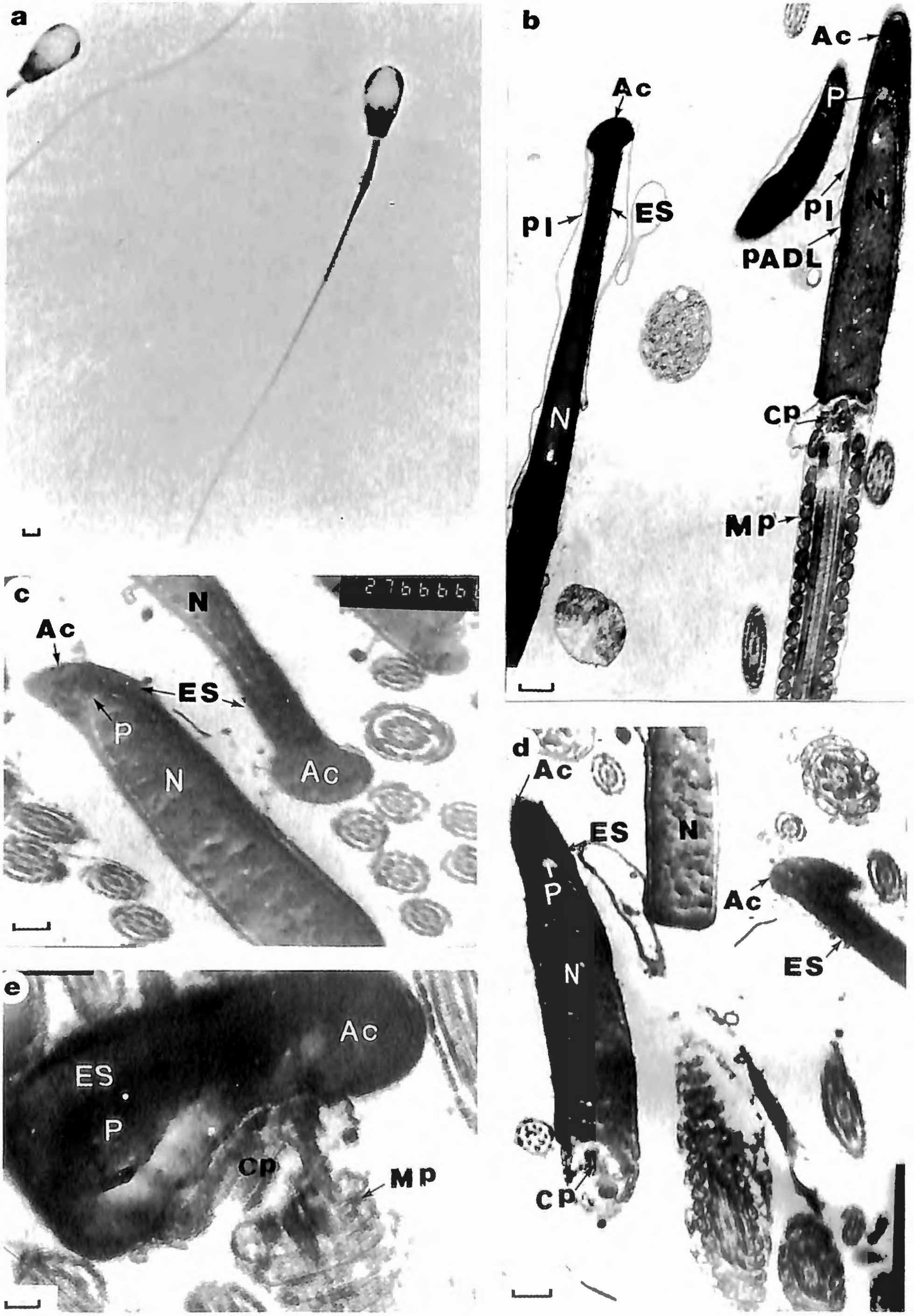
TEM sections through the spermatozoa of *J. jaculus* subspecies as well as *J. orientalis* indicate that the bilaterally flattened head has a homogenous electron-dense nucleus that tapers apically; only one-third of its covex margin is capped by the equatorial segment of the acrosome (Figs 2b, c, d; 3b, c, d). There is a large apical acrosomal segment with a narrower principal segment over the anterior part of the nucleus, posterior to which the equatorial segment passes down over the convex nuclear margin with the postacrosomal dense lamina passing around the posterior caudal margin (Figs 2b, d, e; 3b, c, d). The postacrosomal dense lamina is relatively long in comparison with that present in *A. tetradactyla*, and comes also in direct contact with the plasmalemma. The plasmalemma as in *A. tetradactyla* is wavy over the acrosomal region, but tightly bound to the underlying structures in the postacrosomal region (Figs 2b, c, d; 3b). The acrosomal matrix has a homogeneous electron-dense structure. A moderate subacrosomal space with a less electron-dense material occurs between the inner acrosomal membrane and outer nuclear envelope (Figs 2b, c, d, e; 3b, c, d, e).

Legend to the figures (see pages 195-196)

Fig. 2. – Sperm morphology of *Jaculus jaculus jaculus* (as example of *Jaculus jaculus* subspecies). a. Phase-contrast micrograph. b-e. TEM sections through the sperm showing sperm ultrastructure. (a) Scale bar = 1.33 µm, x 1 350; (b) Scale bar = 0.15 µm, x 20 000; (c) Scale bar = 0.15 µm, x 20 000; (d) Scale bar = 0.15 µm, x 20 000; (e) Scale bar = 0.33 µm, x 10 000.

Fig. 3. – Sperm morphology of Jaculus orientalis orientalis. a. Phase-contrast micrograph. b-e. TEM micrographs showing sperm ultrastructure. (a) Scale bar=1.33 µm, x 1 350; (b) Scale bar = 0.20 µm, x 20 300; (c) Scale bar = 0.13 µm, x 27 000; (d) Scale bar = 0.15 µm, x 20 000; (e) Scale bar = 0.06 µm, x 40 000.


a
b
PADL
pl
N
ES
p
N
N
PADL
ES
p
Cp
N
c
ES
p
pl
PADL
T
N
Cp
d
N
ES
p
PADL
N
Cp
MP
pl
Ac
e
Ac
ES
p
pl
N
N
Cp


a
b
Ac
P
Pl
ES
N
PADL
CP
Mp
c
Ac
ES
P
N
d
Ac
ES
P
N
CP
e
ES
P
Ac
Cp
Mp

DISCUSSION

Two spermatozoal types were observed among the dipodids examined. The first is found in *A. tetradactyla* and typified by a paddle-shaped long head, long tail, and the connecting piece of tail inserts eccentric or off-centre at the lower concave surface of the head. The second type is found in both *J. jaculus* subspecies and *J. orientalis* and characterized by a pear-shaped short head, and short tail that attaches at the lower midbasal region of the head. These two morphs may be alternations of a single morphological type; the plesiomorphic type (BREED & MUSSER, 1991). In both cases the sperm head is bilaterally flattened and symmetrical with a basally attached, and relatively short, sperm tail.

ROLDAN *et al.* (1992) concluded from the wide distribution among myomorph and perhaps caviomorph rodents of the plesiomorphic sperm head that lacks an apical hook and is associated with a shorter tail, that it represents the ancestral condition for Rodentia as a whole and is basal to each of the major radiations within Myomorpha. Moreover, they further postulated that the elongate falciform head form was apomorphic and had evolved on a number of different occasions within the Muroidea.

Generally, the considerable heterogeneity in sperm head morphology does not show any obvious adaptive significance, *i. e.*, not to be related to ecology or life history and may have evolved by random genetic drift (AUSTIN, 1976; BREED & YONG, 1986). Accordingly, sperm morphology may be a useful independent character for gleaning information about the genealogical relationships when considered in relation to other morphological, biochemical, and karyotypic data (BREED & YONG, 1986). The site of attachment of the sperm tail to the head and the occurrence of the subacrosomal cytoskeleton or perforatorium beneath the acrosome vary markedly between rodents (BREED & YONG, 1986; BREED & MUSSER, 1991; BREED, 1991, 1995a, b). As described by BREED (1995b), the falciform sperm nucleus is always associated with a highly developed cytoskeleton, presence of a perforatorium, asymmetrical acrosome, and a relatively long tail that usually attaches to the lower concave surface of the sperm head. Conversely, a more symmetrical nucleus is accompanied by a simpler structural organization of the cytoskeleton, sometimes a relatively short tail that attaches basally, and a more symmetrical acrosome. An interpretation of this association of morphological traits is still obscure, although BREED (1995b) suggested that the occurrence of highly developed and elaborate cytoskeletal structures and long sperm tails of the falciform-shaped sperms may be adaptations for chromatin protection needed during the physical thrust of the sperm through the zona pellucida. On the other hand, spermatozoa with a poorly developed cytoskeleton, partly condensed chromatin, and large acrosome, as described by BREED (1995b) and observed in the present study, may occur where a large hole is digested in the zona as a result of the release of acrosomal contents without need for any physical thrust.

In conclusion, the present data on sperm morphology demonstrate that the two species *J. jaculus* and *J. orientalis* are more similar to each other than either of them to *A. tetradactyla*. However, the similarity of the internal structural organization of sperm in these three dipodids suggest very strongly that they are part of one evolutionary radiation and this « symmetrical head-short tail » sperm type represents the ancestral condition for dipodid rodents. Moreover, the dipodids in Egypt have many of muroid sperm features.

Therefore, they are not so apart from muroid rodents and may form a clade that is either an offshoot of Muroidea (SIMPSON, 1945) or may have branched off from the Myomorpha (ANDERSON, 1967). Furthermore, sperm morphology provides good taxonomic evidence for discrimination between these externally similar jerboas.

ACKNOWLEDGMENTS

We thank Prof. Dr. M. A. Ramadan, department of zoology, faculty of science, Minia university, for his critical and helpful comments on the manuscript, Mr. H. A. El-Azm, central laboratory of university, for technical assistance, and Mr. A. H. Toulba for collecting the specimens.

REFERENCES

ANDERSON, S. (1967) – Introduction to the rodents. In: *Recent mammals of the world: a synopsis of families.* ANDERSON, S. & J.K. JONES, Jr. (Eds.). New York: Ronald Press Co., 206-209.

AUSTIN, C.R. (1976) – Specialization of gametes. In: *The evolution of reproduction.* Cambridge Univ. Press, **6**: 149-182.

BASKEVICH, M.I. & L.A. LAVRENCHENKO (1995) – On the morphology of spermatozoa in some African murines (Rodentia, Muridae): the taxonomic and phylogenetic aspects. *J. Zool. Syst. Evol. Research*, **33**: 9-16.

BAVERSTOCK, P.R., C.H.S. WATTS, M. ADAMS & S.R. COLE (1981) – Relationships among Australian rodents (Muridae). *Aust. J. Zool.*, **29**: 289-303.

BEDFORD, J.M. & D.D. HOSKINS (1990) – The spermatozoon: morphology, physiology and biochemistry. In: MARSHALL's *physiology of reproduction. The male reproductive system.* LAMMING, G.E. (Ed.). London: Churchill Livingstone, **2**: 379-568.

BISHOP, M.W.H. & C.R. AUSTIN (1957) – Mammalian spermatozoa. *Endeavour*, **16**: 137-150.

BREED, W.G. (1980) – Further observations on spermatozoal morphology and male reproductive tract anatomy of *Pseudomys* and *Notomys* (Mammalia: Rodentia). *Trans. R. Soc. S. Aust.*, **104**: 51-5.

BREED, W.G. (1983) – Variation in sperm morphology in the Australian rodent genus *Pseudomys* (Muridae). *Cell Tissue Res.*, **229**: 611-625.

BREED, W.G. (1984a) – Sperm morphology of New Guinea rodents-phylogenetic implications. *Aust. Mammal Soc. Bull.*, **8** (2): 101 pp.

BREED, W.G. (1984b) – Sperm head structure in the *Hydromyinae* (Rodentia: Muridae): a further evolutionary development of the subacrosomal space in mammals. *Gamete Res.*, **10**: 31-44.

BREED, W.G. (1991) – Variation in sperm head morphology of the Murinae (Family Muridae): some taxonomic implications. In: *Comparative spermatology: 20 years after.* BACCETTI, B. (Ed.). New York: Raven Press: 937-939.

BREED, W.G. (1993) – Novel organization of the spermatozoon in two species of murid rodents from southern Asia. *J. Reprod. Fert.*, **99**: 149-158.

BREED, W.G. (1995a) – Variation in sperm head morphology of Muroid rodents of Africa: phylogenetic Implications. In: *Advances in spermatozoal phylogeny and Taxonomy.* JAMIESON, B.G.M., J. AUSIO & J.-L. JUSTINE (Eds.). Paris: Mém. Mus. natn. Hist. nat., **166**: 409-420.

BREED, W.G. (1995b) – Spermatozoa of murid rodents from Africa: morphological diversity and evolutionary trends. *J. Zool. Lond.*, **237**: 625-651.

BREED, W.G. (1997) – Evolution of the spermatozoon in Australian rodents. *Aust. J. Zool.*, **45** : 459-478.

BREED, W.G. & K. APLIN (1994) – Sperm morphology of murid rodents from New Guinea and the Solomon Islands : phylogenetic implications. *Aust. J. Zool.*, **43** : 17-30.

BREED, W.G. & G.G. MUSSER (1991) – Sulawesi and Philippine rodents (Muridae) : a survey of spermatozoal morphology and its significance for phylogenetic inference. *Am. Mus. Novit.*, **3003** : 1-15.

BREED, W.G. & V. SARAFIS (1979) – On the phylogenetic significance of spermatozoal morphology and male reproductive tract anatomy in Australian rodents. *Trans. R. Soc. S. Aust.*, **103** : 127-139.

BREED, W.G. & H.S. YONG (1986) – Sperm morphology of murid rodents from Malaysia and its possible phylogenetic significance. *Am. Mus. Novit.*, **2856** : 1-12.

EDDY, E.M. & D.A. O'BRIEN (1994) – The spermatozoon. In : *The physiology of reproduction*, 2nd edn. KNOBIL, E. & J.D. NEILL (Eds). New York : Raven Press : 29-77.

EL HILALI, M. & J.P. VEILLAT (1975) – Jaculus orientalis : A true hibernator. Mammal., **39** : 402-404.

ELLERMAN, J.R. (1942) – Families and genera of living rodents. *Brit. Mus. Nat. Hist.* London, **2** :1-690.

FAWCETT, D.W. (1970) – A comparative view of sperm ultrastructure. *Biol. reprod.*, (Suppl.) **2** : 90-127.

FAWCETT, D.W., W.A. ANDERSON & P.M. PHILLIPS (1971) – Morphogenetic factors influencing the shape of the sperm head. *Devl. Biol.*, 28 : 220-251.

FIAHERTY, S.P. & W.G. BREED (1983) – The sperm head of the plains mouse *Pseudomys australis* : ultrastructure and effect of chemical treatments. *Gamete Res.*, **8** : 231-244.

FRIEND, G.F. (1936) – The sperms of British Muridae. *Q. J. microsc. Sci.*, **78** : 419-443.

HARDING, H.R. & K.P. APLIN (1990) – Phylogenetic affinities of the koala (Phascolarctidae ; Marsupialia) : a reassessment of the spermatological evidence. In : *Biology of the koala*. LEE A.K., HANDASYDE, K.A. & G.D. SANSON (Eds.). Sydney : Surrey Beatty : 1-31.

HARDING, H.R., F.N. CARRICK & D.C. SHOREY (1979) – Special features of sperm structure and function in marsupials. In : *The spermatozoon*. FAWCETT, D.W. & J.M. BEDFORD (Eds.). Urban and Schwarzenberg : Baltimore : 289-303.

HARDING, H.R., P.A. WOOLLEY, D.C. SOREY & F.N. CARRICK (1982) – Sperm ultrastructure, spermiogenesis, phylogenetic implications. In : *Carnivorous marsupials*. ARCHER, M. (Ed.). Sydney : R. Zool. Soc. New South Wales, **2** : 659-673.

LAKHDAR-GHAZAL, N., M. DUBOIS-DAUPHIN, M.L.H.J. HERMES, R.M. BUIJS, W.A. BENGELLOUN & P. PÉVET (1995a) – Vasopressin in the brain of a desert hibernator, the jerboa (*Jaculus orientalis*) : Presence of sexual dimorphism and seasonal variation. *J. Comp. Neurol.*, **358** : 499-517.

LAKHDAR-GHAZAL, N., A. KALSBEEK & P. PÉVET (1992) – Sexual differences and seasonal variations in vasoactive intestinal peptide immunoreactivity in the suprachiasmatic nucleus of jerboa (*Jaculus orientalis*). *Neurosci. Lett.*, **144** : 29-33.

LAKHDAR-GHAZAL, N., R. OUKOUCHOUD & P. PÉVET (1995b) – Seasonal variation in NPY immunoreactivity in the suprachiasmatic nucleus of the jerboa (*jaculus orientalis*), a desert hibernator. *Neurosci. Lett.*, **193** : 49-52.

LAVRENCHENKO, L.A. & M.I. BASKEVICH (1996) – Variation of generative system structure in some species of the genus *Mastomys* Thomas, 1915 (Rodentia, Muridae). Mammalia, **60** : 277-288.

LINZEY, A.V. & J.N. LAYNE (1974) – Comparative morphology of spermatozoa of the rodent genus *Peromyscus* (Muridae). *Am. Mus. Nov.*, **2532** : 1-20.

OSBORN, D.J. & I. HELMY (1980) – The contemporary land mammals of Egypt (including Sinai). – *Fieldiana Zool.* No. 5 : 579 pp.

RETZIUS, G. (1909) – Spermatozoa of mammals. Biol. Unters., (NF) **14** : 163-178.

ROLDAN, E.R.S., M. GOMENDIO & A.D., VITULLO (1992) – The evolution of eutherian spermatozoa and underlying selective forces : female selection and sperm competition. *Biol. Rev.*, **67** : 551-593.

SIMPSON, G.G. (1945) – The principles of classification and a classification of mammals. – *Bull. Am. Mus. Nat. His.* New York, **85** : 1-350.

TEMPLE-SMITH, P.D. (1987) – Sperm structure and marsupial phylogeny. In : *Possums and Opossums : studies in evolution.* ARCHER, M. (Ed.). Sydney : R. Zool. Soc. New South Wales, **1** : 172-194.

WASSIF, K. (1960) – Studies on the osteology of Egyptian Jerboas. – *Bull. Zool. Soc. Egypt*, **15** (29) : 71- 92.