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Morphological Characteristics of Sperm in the Korean Striped Field Mouse, *Apodemus agrarius coreae*: Possible Role of Sperm Neck in the Movement of Sperm Head

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To investigate the movement of sperm head and the role of sperm neck in forward sperm motility in the Korean striped field mouse, *Apodemus agrarius coreae*, the morphological characteristics of the cauda epididymal spermatozoa were examined by light microscopy and scanning and transmission electron microscopy. Spermatozoa of *A. agrarius coreae* were characterized by the conspicuous shape of the acrosome and the long tail compared with those of other rodents. Total length of the sperm was 133 μm. The sperm head had a curved falciform shape. The head was 8.0 μm in length, and about 4.0 μm in width. The shape of acrosome had an opener-like form. The sperm tail (125 μm) consisted of four major segments: neck (0.5 μm), middle piece (29.5 μm), and principal piece plus the end piece (95 μm). The outer dense fibers were arranged in a horseshoe fashion, and No. 1, 5, 6, and 9 of the outer dense fibers were larger than the others. The mitochondrial bundles of middle piece were composed of a pair of arms, which surrounded the axone of the middle piece by the 45° angled helical structure. The total number of mitochondrial gyres was 188. In particular, the microfilament structures existed in plasma membrane of the sperm, which was adjacent to the acrosomal region on the nuclear membrane. The segmented columns were surrounded by microfilament structures, and the microfilament bundles were adjacent to the outer membrane of the first mitochondria of middle piece. This study presents for the first time the existence of microfilament structures within the plasma membrane of sperm which is located from the adjacent acrosome region to the connecting piece in sperm neck of Korean striped field mouse, *Apodemus agrarius coreae*. The present result suggests that the constriction and extension of microfilament in sperm neck as well as the wave-movement of sperm tail may play a role in the movement of sperm head.

Generally, the mammalian spermatozoon consists of two major parts, the head and the tail. The tail is subdivided into four segments; neck, middle piece, principle piece and end piece.

Among the mammalian sperm components, the neck has been well known as the most structually complex region of the spermatozoon (Fawcett and Phillips, 1969; Fawcett, 1970; Guraya, 1987). It is usually defined as the part of the spermatozoon between the base of the nucleus and the first gyre of the mitochondrial helix (Fawcett and Phillips, 1969; Zamboni and Stefanini, 1971).

Since the capitulum and the striated column have developed in contact with the centrioles in the neck region of spermatozoa (Fawcett and Phillips, 1969; Woolley and Fawcett, 1973), it is a common component of mature spermatozoa in all mammalian species. However, the physiological functions of each structural component of the sperm neck in a forward sperm motility are not yet fully understood.

The aim of the present study is to investigate the relationship between the movement of sperm head and the role of sperm neck by sperm motility in the Korean striped field mouse (*Apodemus agrarius coreae*). This is based on the morphological characteristics of the cauda epididymal spermatozoa from eight Korean striped field mice. *Apodemus agrarius coreae* belonging to the family Murinae, genus *Apodemus*, were examined by light microscopy and scanning and transmission electron microscopy.

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Table 1. Comparison of morphological characteristics of the spermatozoa in the Korean striped field mouse, *Apodemus agrarius coreae*

Head (μm)				Acrosome shape	Tail (μm)					Authors
L	W	Nl	Shape		Tl	Nc	Mp	Pp+Ep	NoMg	
8.0±0.07	–	–	F	–	–	–	24.8±0.14	–	–	Yang et al. (1991)
8.0	4.0	7.4	F	O-lf	125.0	0.5	29.5	95	188	Present studies

F, falciform; L, length; Mp, middle piece; Nc, neck length; Nl, nuclear length; NoMg, the total number of mitochondrial gyres; O-lf, opener-like form; Pp + Ep, principal piece plus end piece; Tl, total length; W, width.

Materials and Methods

Eight adult specimens of the Korean striped field mouse *Apodemus agrarius coreae*, 32-35 g in weight, were used in the present study. All samples were captured in Kyungnam province.

For light microscopy, epididymal spermatozoa of two adult male mice were flushed from the cauda epididymis, smeared on slide glass after being left alone at room temperature for 5 min., and washed in 0.1 M Milloing's buffer (pH 7.4). They were then fixed in 3%-glutaraldehyde (Milloing's buffer, pH 7.4) and dehydrated in a graded series of ethanol for 10 min, respectively. These samples were observed without staining under the light microscopy.

In using scanning electron microscopy, the samples smeared on the slide glass were fixed and dehydrated as light microscopic methods, and coated with gold, and observed under Akashi SX-40 scanning electron microscope at 15 kV.

For transmission electron microscopy, under ether anaesthesia, the cauda epididymis of six mice were excised surgically, cut into smaller pieces and prefixed in 3% glutaraldehyde (0.1 M Milloing's buffer, pH 7.4) for 4 h. Following fixation, the tissues were washed in the corresponding buffer, postfixed in 1.33%-osmium tetroxide in the same buffer for 2 h, and dehydrated in a graded series of ethanol and embedded in Epon 812. Thin sections (60-90 nm) were stained with uranyl acetate and lead citrate, and examined with a H-600 (Hitachi) transmission electron microscope at 75 kV.

Results

The morphological characteristics and relationship between the movement of sperm head and the role of sperm neck by forward sperm motility in the Korean striped field mouse are described (Figs. 1-10) and the dimensions of the spermatozoa are summarized in Table 1.

Sperm head

The sperm head of *A. agrarius coreae* took on a curved falciform shape (Figs. 1, 2, and 3). The sperm head was 8.0 μm in length, whose posterior 7.4 μm was occupied by a nucleus, about 4.0 μm in width (Table 1). The shape of acrosome had an opener-like form (Fig. 3A-C; double arrows, 9B).

The nucleus and acrosome were separated by the apical body (Figs. 8A, B (Insect), and 9B) which was sharply pointed towards the convex surface of the sperm cell. Microfilament structures existed in the plasma membrane of sperm, which were adjacent to the acrosomal region of the nuclear membrane (Figs. 3B; arrowheads, 4).

Sperm neck

The major components of the neck region were composed of the basal plate (Figs. 3B, 4, and 9C), the capitulum, poximal centriole and remnants of distal centriole (Fig. 4).

The basal plate, which was the most anterior component of the neck, was a band of electron dense material that occupies, and conforms to the shape of the implantation fossa (Fig. 4; arrowheads, 9C).

The segmented columns were surrounded by microfilament structures, and the microfilament bundles were adjacent to outer membrane of first mitochondria of the middle piece (Figs. 4, and 9C). The proximal centriole laid immediately below the capitulum in the surrounding segmented columns. It laid in the long trans-

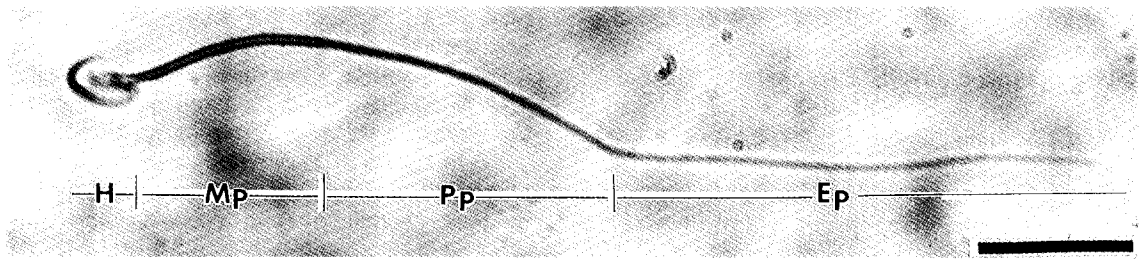

Fig. 1. Light micrograph of the mature spermatozoon in the cauda epididymis of *Apodemus agrarius coreae*. H, head; Ep, end piece; Mp, middle piece; Pp, principal piece. Scale bar=20 μm.

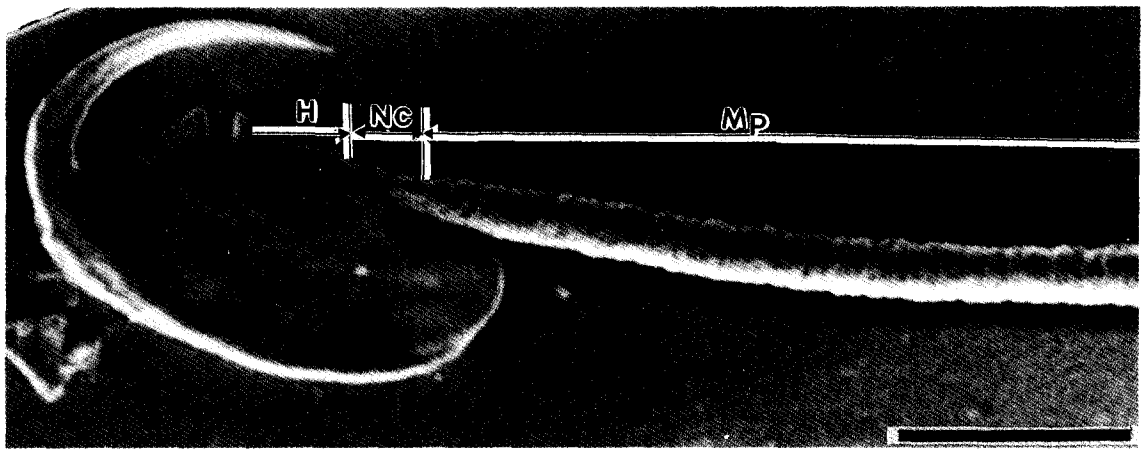

Fig. 2. Scanning electron micrograph showing external features of the mature spermatozoon. Note that the sperm head had the curved falciform shape. H, head; Mp, middle piece; Nc, neck. Scale bar=4 μm.

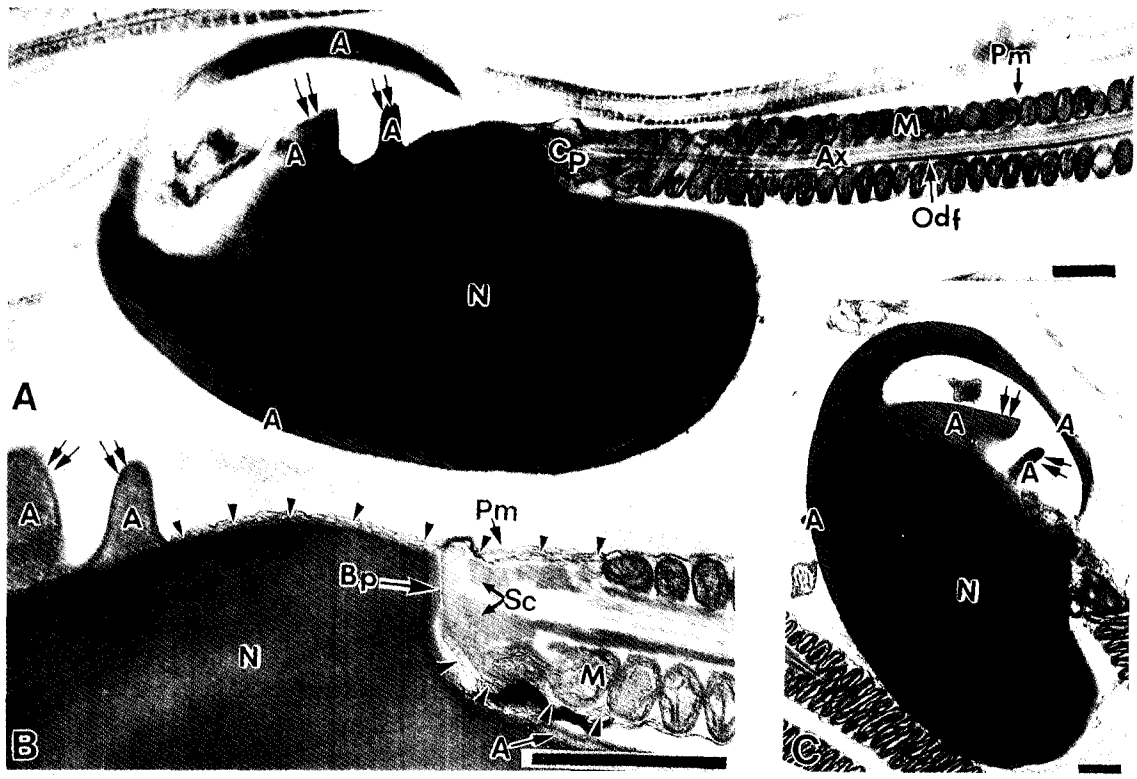

Fig. 3. Electron micrographs showing internal features of the cauda epididymal spermatozoa. Note that the shape of the acrosome had the opener like form (A-C, double arrows) and the microfilament structures (arrowheads) existed in sperm plasma membrane from the acrosomal region on the nuclear membrane to the connecting piece (B). A, acrosome; Ax, axoneme; Bp, basal plate; Cp, connecting piece; M, mitochondria; N, nucleus; Odf, outer dense fiber; Pm, plasma membrane; Sc, segmented column. Scale bar=0.5 μm.

verse axis of the flattened head.

The microfilament structure was twined as a reticular form within the basal plate and the implantation fossa (Figs. 4, arrowheads, and 9C).

Sperm tail

The total length of the sperm tail was 125 μm. The sperm tail consisted of four major segments: neck (0.5 μm), middle piece (29.5 μm), and principal piece plus end piece (95 μm) (Table 1).

The outer dense fibers were arranged in a horseshoe fashion, and No. 1, 5, 6, and 9 of the outer dense fibers were larger than the others (Figs. 6A and 9B). The mitochondrial bundles were composed of a pair of

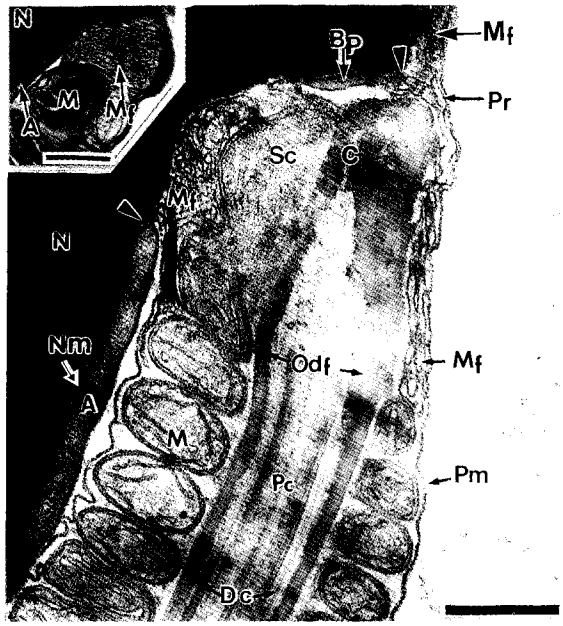

Fig. 4. Electron micrograph showing sperm head, connecting piece and middle piece of the flagellum. The basal plate was adherent to the envelope, defining the implantation fossa (arrowheads) and forming the site of attachment of the flagellum to the sperm head. The proximal centriole laid immediately below the capitulum in the surrounding segmented columns. It laid in the long transverse axis of the flattened head. The microfilament structures is twined as a reticular form within the basal plate between the segmented columns (Inset). Note that the microfilament structures exited to the plasma membrane of sperm from posterior portion of the nucleus to the portion of beginning of middle piece. The segmented columns of connecting piece was surrounded by a reticular microfilament. A, acrosome; Bp, basal plate; C, capitulum; Dc, distal centriole; M, mitochondria; Mf, microfilament; N, nucleus; Nm, nuclear membrane; Odf, outer dense fiber; Pc, proximal centriole; Pm, plasma membrane; Pr, posterior ring; Sc, segmented column. Scale bars=0.2 μm.

arms (Figs. 6A and 9A (a, b)), and surrounded the axone of the middle piece like the thread of a screw with an angle of approximately 45° (Figs. 7 and 9D).

The total number of mitochondrial gyres were 188 (Table 1). The end of the middle piece was marked by the annulus (Figs. 5B, 7, and 9D), a thin dense ring to which the flagellar membrane was firmly adhered.

Discussion

The formation of the spermatid's head in mammals is deeply modified during the maturation phase and takes its definitive shape only at the last step of spermiation (Lalli and Clermont, 1981). Accordingly, the mammalian spermatozoa undergo a complex set of changes along the epididymal transit, in a process known as sperm maturation which takes place gradually from head to cauda of the epididymis (Rodrígues and Bustos-Obregón, 1994).

The mophological features of acrosome formation during spermiogenesis have been throughly analysed with use of the periodic acid-Schiff staining technique by Leblond and Clermont (1952).

The nucleus and acrosome are separated by the

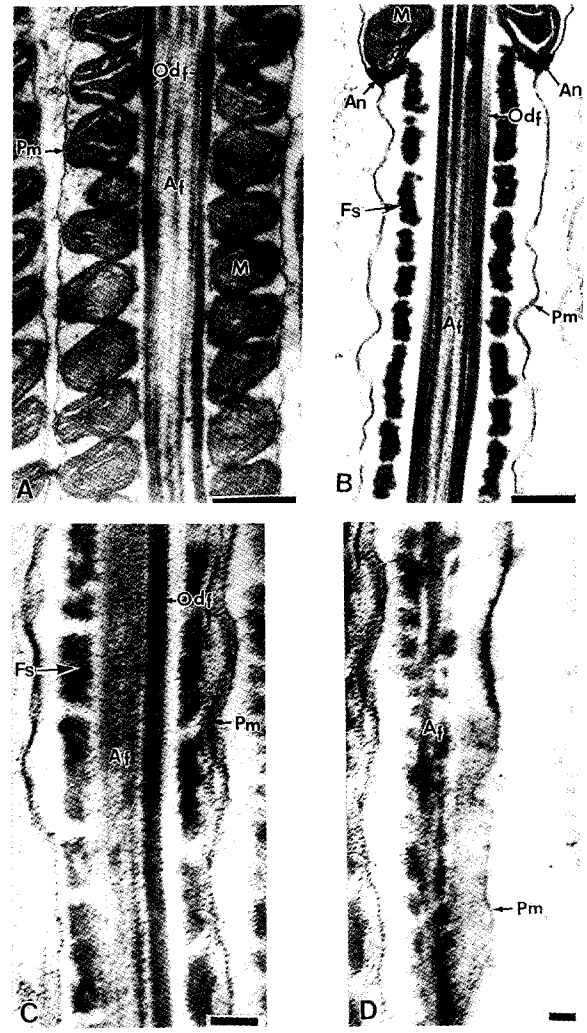

Fig. 5. Electron micrographs of longitudinal section of the middle piece, principal piece and end piece. The mitochondria was arranged at the sides of axoneme regularly (A), and the annulus had appeared at the end of mitochondria (B). The outer dense fiber was seen at the middle and principle piece (C) but it was not seen at the end piece (D). Af, axial filament; An, annulus; Fs, fibrous sheath; M, mitochondria; Odf, outer dense fiber; Pm, plasma membrane. Scale bars=0.2 μm.

perforatorium or subacrosomal material (Bacetti, 1979). According to this present study, the nucleus occupied most of the sperm head, and the form of the sperm head, like that of the most other rodents, were shaped like a falciform and flattened when seen in surface view (Fig. 3A-C).

In the mammalian sperm head components, the acrosome undergoes a profound modification or breakdown (acrosome reaction) shortly before the spermatozoa penetrate the eggs (Austin and Bishop, 1958; Bedford, 1968). Oko et al. (1976) have reported that the bovine sperm head was divided into two major regions: the anterior acrosomal area and the posterior postnuclear-cap area. The former is characterized by the presence of the acrosome, and the thinner posterior

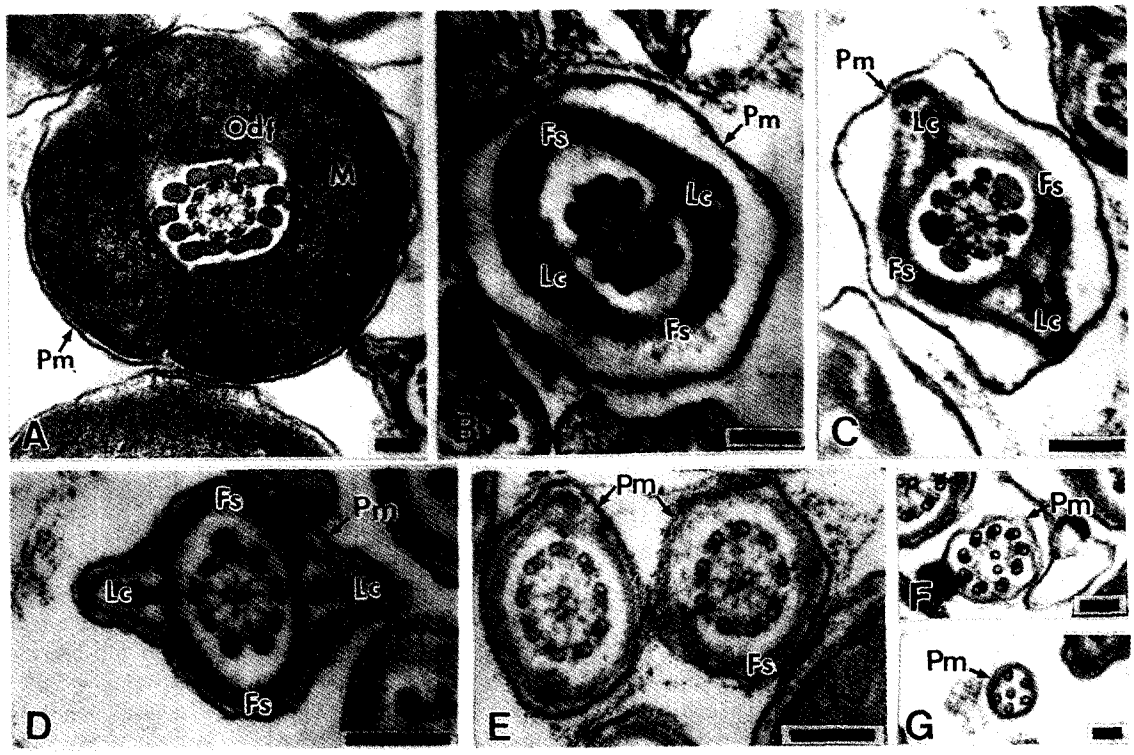

Fig. 6. Electron micrographs of the cross section of sperm tail at various levels. The outer dense fibers were arranged in a horseshoe fashion, and No. 1, 5, 6, and 9 of the outer dense fibers were larger than the others. The mitochondrial bundles of the middle piece were composed of a pair of arms (A). The fibrous sheaths and longitudinal columns was seen the principal piece (B-D). The outer dense fiber was not seen in the first portion of the end piece (E). The fibrous sheaths and longitudinal columns are not seen at the mid or end portion of the end piece (F) and (G). Fs, fibrous sheath; Lc, longitudinal column; M, mitochondria; Odf, outer dense fiber; Pm, plasma membrane. Scale bars=0.2 μm.

region of the acrosome is called the equatorial segment (Saacke and Almquist, 1964). Saacke and Marshall (1968) show that the acrosome of bull spermatozoa

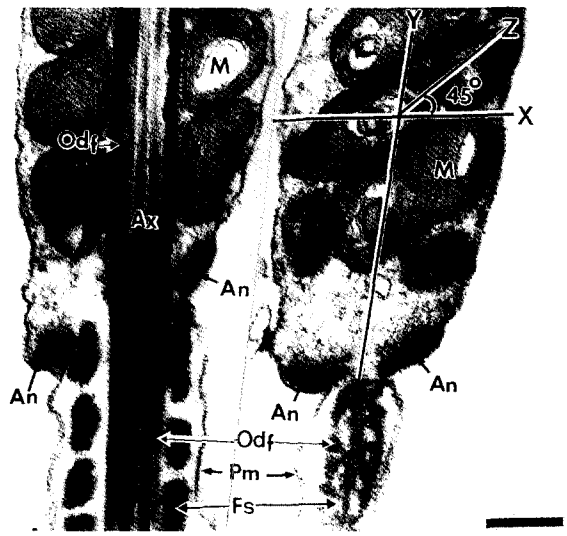

Fig. 7. Electron micrograph of the longitudinal section of the sperm tail. Note that the axoneme of the middle piece was surrounded by mitochindria of a pair of arms, and the mitochondria bundles surround the axone of the middle piece by the 45° angled helical structure. An, annulus; Ax, axoneme; Fs, fibrous sheath; M, mitochondria; Odf, outer dense fiber; Pm, plasma membrane. Scale bar=0.5 μm.

can be clearly divided into two regions, namely the anteriorly located, enlarged region and posteriorly located, thin region. The latter was called equiatorial segment.

The acrosome is an exocytotic vesicle that overlies the anterior head region of sperm. It contains more than 20 hydrolytic enzymes such as hyaluronidase and acrosin (Yanagimachi, 1981; Eddy, 1988) and presumably unknown proteins. In the morphological changes of the acrosome, Kurohmaru et al. (1994) have demonstrated that the enormous fan-shaped acrosome was completely formed at step 13, and the prominent extension and subsequent shortening and flattening of the acrosome in the musk shrew *Suncus murinus* appears to be unique process to form the enormous fan-shaped acrosome. In the present study, the shape of the acrosome of *Apodemus agrarius coreae* had the opener-like form (Fig. 3; double arrows), and the form of the dorsal part of the head looked as if it were the stream formed by a ship. It suggests that the sperm swings easily in the female reproductive tract.

The neck is the most structually complex region of the spermatozoon (Fawcett and Phillips, 1969; Fawcett, 1970; Guraya, 1987). The capitulum and the striated column are developed in contact with the centrioles, and the function of the sperm neck has been well known in that it may play some role in controlling

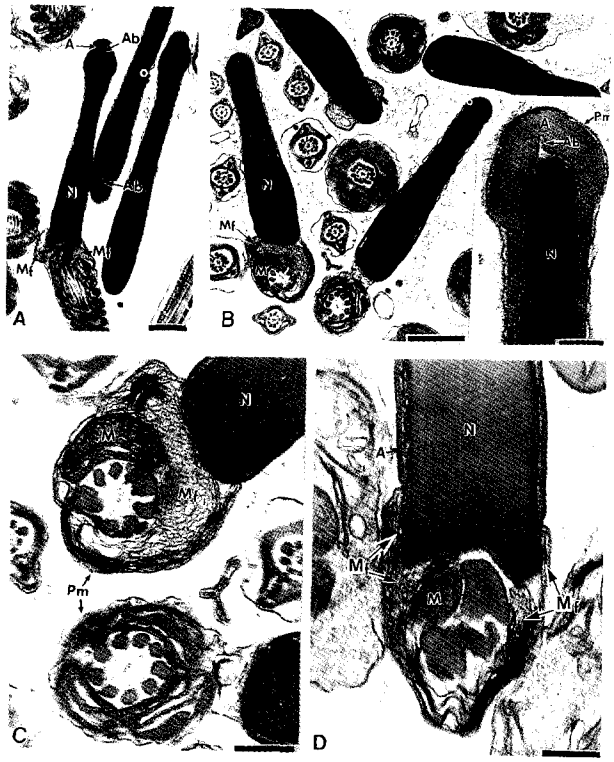

Fig. 8. Electron micrographs of sagittal section of the cauda epididymal sperm. Note that the reticular shaped microfilament structures was seen in the connecting piece (A-D) and the plasma membrane of sperm of the posterior portion of the nucleus (D). The apical body sharply pointed towards the convex surface of the sperm cell (A, B). A, acrosome; Ab, apical body; M, mitochondria; Mf, microfilament; N, nucleus; Pm, plasma membrane. Scale bars=1 μm.

movement of the flagellum by many investigators (Fawcett and Phillips, 1969; Zamboni and Stefanini, 1970, 1971; Woolley and Fawcett, 1973). On the other hand, the capitulum is said to be well-developed in rodent sperm, but to be lacking in humans and monkeys (Zamboni and Stefanini, 1970).

The middle piece formation is characterised by the development of a long distal centriole which determines the length of the midpiece and the distal centriole surrounds a pair of microtubules embedded in a core of dense material (Soley, 1994).

The outer dense fibers are accessory fibres in the spermatozoon. Yang et al. (1991) reported that the outer dense fiber numbers 1, 4, 5, and 9 were larger than other fiber numbers 2, 3, 6, 7, and 8. In the present study, the outer dense fiber numbers 1, 5, 6 and 9 were larger than others, and the outer dense fibers of middle piece arranged in a horseshoe fashion (Figs. 6A and 9A (b)).

Comparison of the forms of the outer dense fiber in Asiatic musk shrew, *Suncus murinus* (Cooper and Bedford, 1976; Green and Dryden, 1976; Koehler, 1977; Phillips and Bedford, 1985; Mōri et al., 1991) and the European common shrew, *Sorex aruneus* (Plöen et al., 1979), all had well-developed satellite fibers found in association with the inner aspect of dense fiber Nos. 5 and 6, but were not observed in *Apodemus agrarius coreae*. Phillips and Bedford (1985) show that the outer dense and satellite fibers help to determine the precise character of the sperm tail beat. Henkel et al. (1994) showed that the outer dense fiber represent up to 30% of the protein portion in human spermatozoa and are involved in sperm progressive motility. If outer dense fibers are missing or developed poorly, spermatozoa are only locally motile.

Sperm motility is a key function in the processs of fertilization as well as the recent development of assisted reproductive technologies and extensive use of sperm movement is important for fertilization (Auger et al., 1994). Phillips (1972) has reported that the motility patterns of mouse spermatozoa were divided into three types: the first type involves an asymmetrical beat which seems to propel the sperm in circular paths, the second type involves rotation of the sperm and appears to allow them to maintain straight paths, and the sperm appears to move by crawling on surfaces in a snakelike manner.

On the other hand, Mohri and Yanagimachi (1980) have reported the sperm motility in the hamster testis and epididymides: the testis and caput epididymis are virtually immotile, while cauda epididymal and ejaculated spermatozoa are capable of active progressive movement. And, the capacitated and activated spermatozoa have very vigorous motility characterized by whiplash-like beating of their flagella. According to Ishijima et al. (1994), the motive force to propel a spermatozoa is mainly due to the bends in the cell body, and the spermatozoa reverse the direction of their swimming as a result of a change in the direction of bend propagation.

The dynein arms of the peripheral doublets of axonema play a major role in controlling the flagellar movement (Sugrue et al., 1991). Nevertheless, it is possible that the neck region might play a minor role in controlling the tilt toward the right or left side during the rotating and proceeding movement of mature sperm. The mechanisms of control and modulation of sperm motility still remain unknown.

A spiral proceeding movement of the sperm fagellum has been observed in rodent spermatozoon, but the role of sperm neck to effect on the sperm head motion is not understood.

Nevertheless, in the present study, the microfilament structures existed in plasma a membrane of the sperm, which is adjacent to the acrosomal region on the nuclear membrane and the adjacent outer membrane of the first mitochondria of the middle piece (Figs. 3B, and 4). The segmented columns were surrounded by microfilament structures. These structures twined around as a reticular form under the basal plate within implantation fossa (Fig. 4 and Inset).

In conclusion, the presence of microfilament structures within the plasma membrane of the sperm contributes

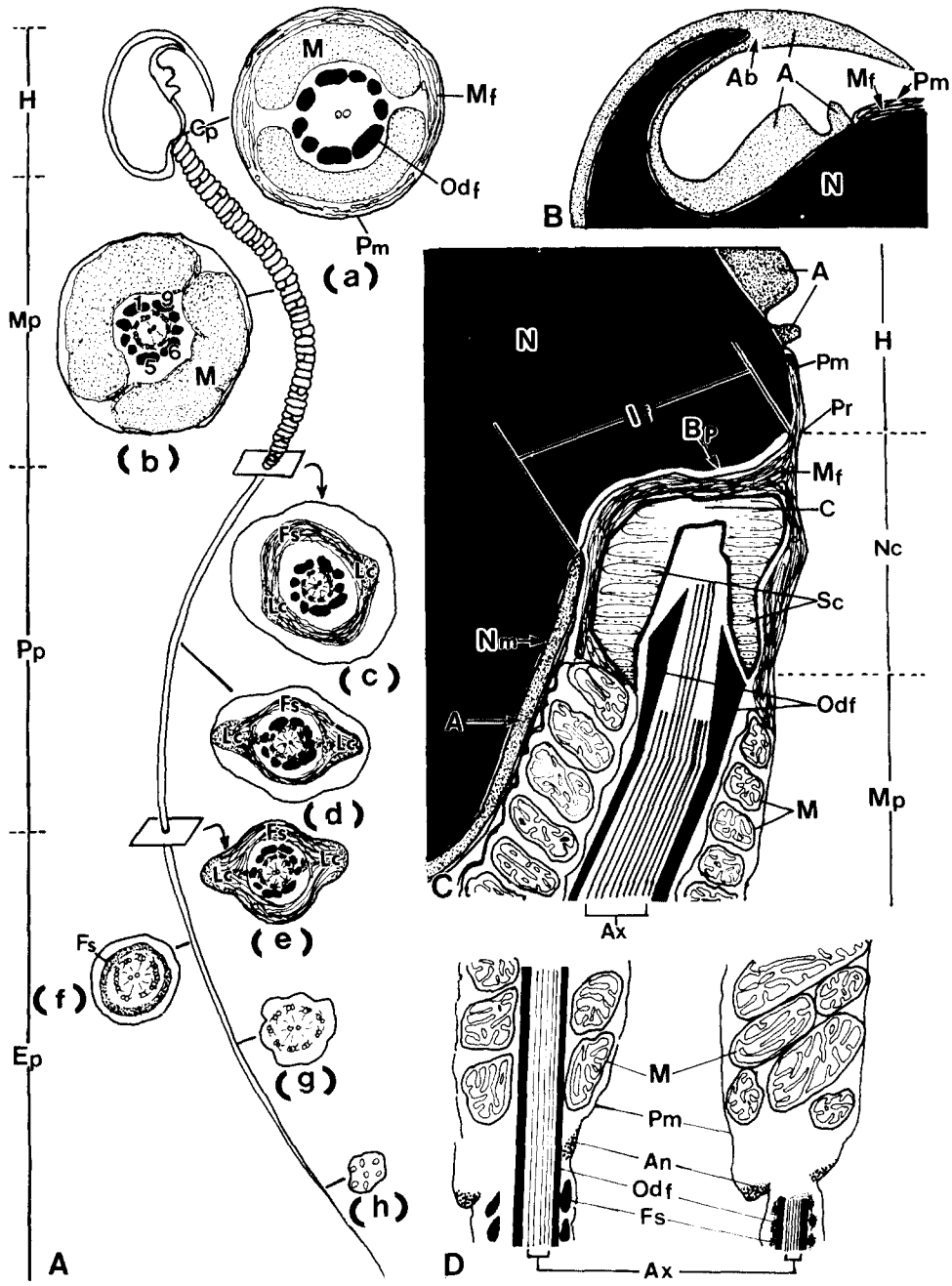

Fig. 9. Diagram demonstrates the variations in shape of components of the head, connecting piece, middle piece, principal piece and end piece of the mature epididymal spermatozoon. The head had the curved falciform shape (A) and (B), and the segmented columns of connecting piece were surrounded by microfilament structures (C). The outer dense fibers of middle piece arranged in a horseshoe fashion. The outer dense fiber number 1, 5, 6, and 9 are larger than others (a). The shape of acrosome on the nucleus had the opener-like form (B). The basal plate is in contact with the segmented columns of the connecting piece (C). The mitochondria was surrounded the axoneme of the middle piece like the thread of a screw with an angle of approximately 45° (D). A, acrosome; Ab, apical body; An, annulus; Ax, axoneme; C, capitulum; Cp, connecting piece; Ep, end piece; Fs, fibrous sheath; H, head; If, implantation fossa; Lc, longitudinal column; M, mitochondria; Mf, microfilament; Mp, middle piece; N, nucleus; Nc, neck; Nm, nuclear membrane; Odf, outer dense fiber; Pm, plasma membrane; Pp, principal piece; Pr, posterior ring; Sc, segmented column.

to the movement of sperm tail in the Korean striped field mice, *Apodemus agrarius coreae.*

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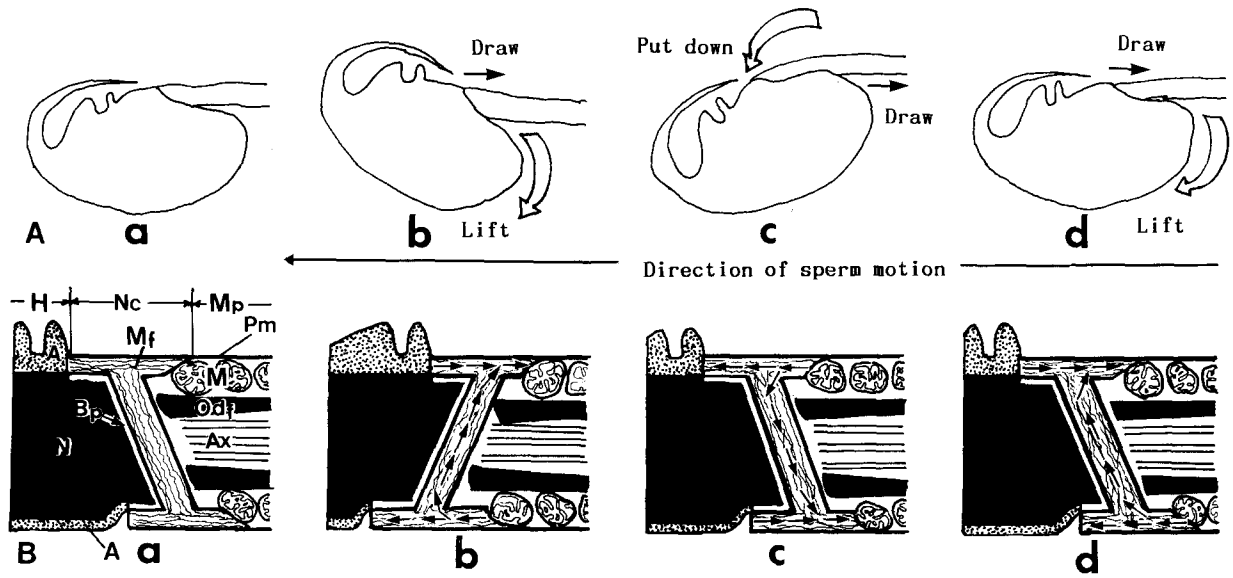

Fig. 10. Diagram demonstrating the model of the relationship between the movement of sperm head and the role of sperm neck by forward sperm motility in the Korean striped field mouse, *Apodemus agrarius coreae*. In the direction of sperm head, the sperm head begin to rise as soon as the upper microfilament bundles of neck get draw from head to tail, and the lower microfilament bundles of neck go forward the nucleus. Immediately, the sperm head begins to fall as soon as the lower ones of neck get drawn from head to tail, and the upper ones go forward to the nucleus relatively. Therefore, up-and-down motion of sperm head is due to constriction and extension of microfilament in plasma membrane of connecting piece by the wave-motion of sperm tail. Non-movement (A, a) and (B, b) and movement (A, b-d) and (B, b-d). A, acrosome; Ax, axoneme; Bp, basal plate; H, head; Mf, microfilament; Mp, middle piece; N, nucleus; Nc, neck; Odf, outer dense fiber; Pm, plasma membrane.

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