

Ultrastructure of Spermatozoa in Urodela and Primitive Anura (Amphibia) with Phylogenetic Considerations

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ABSTRACT

The ultrastructure of spermatozoa in urodeles and primitive anurans was examined and compared. The spermatozoa of urodeles are characterized by seven plesiomorphies in subacrosomal cone, endonuclear canal, perforatorium, ring, marginal filament, undulating membrane and tail axis. Most primitive anuran spermatozoa have no marginal filament, subacrosomal cone and ring structure with the exception of having the subacrosomal cone in *Ascaphus* and the ring in *Discoglossus* as compared with those of urodeles. Persistence of the subacrosomal cone and the ring structure is typical in most urodeles and is further linked with the primitive anurans. Therefore, these characters are regarded as symplesiomorphies in urodeles and primitive anurans. The organization of sperm tail, endonuclear canal and perforatorium indicates a close phylogenetic relationship between urodeles and the primitive anurans.

Key words: Urodeles, anurans, spermatozoa, ultrastructure, phylogeny

INTRODUCTION

Amphibia consist of three orders: Apoda, Urodela and Anura. There has been considerable debate among the three orders in terms of their relationships. The commonly held position is that Urodela and Anura are sister groups. This close relationship of Urodela and Anura is sustained by morphological data, mainly osteological features (Inger, 1967; Hillis, 1991). However, the soft anatomy characters among morphological data support the view that Urodela and Apoda are closer related than either are to Anura (Trueb and Cloutier, 1991). In addition discrepancies in the evaluation of the morphological data, comparative molecular analysis makes the solution of

relationship among the three orders still difficult (Larson and Wilson, 1989).

Although the evolution of the spermatozoon has been considerably studied in the animal kingdom, the different evolutionary tendencies have been chiefly exposed among invertebrates and particularly in the arthropod phylum (Franzen, 1970; Baccettii, 1979; Jamieson, 1987; Lee and Lee, 1992; Jamieson et al., 1993). Fish show great spermatid diversity among vertebrates and the different evolutionary tendencies that characterize arthropods are also formed (Mattei, 1988). Further, anurans of the amphibians have the evolutionary tendencies at comparative spermatology level (Lee and Jamieson, 1992; Jamieson et al., 1993; Kwon and Lee, 1995). Jamieson et al. (1993) have worked these aspects and have considered the phylogenetic significance of sperm morphology in amphibians.

The ultrastructure of amphibian spermatozoa has been described in urodeles (Baker, 1962, 1963; Barker and Biesele, 1967; Barker and Baker, 1969; Kim et al., 1995; Picheral, 1979) and anurans (Burgos and Fawcett, 1956; Sandoz, 1973, 1974; Furieri, 1975; Bernardini et al., 1986; Asa and Phillips, 1988; Kwon and Lee, 1992; Bao et al., 1991; Reed and Stanley, 1972; Lee and Jamieson, 1992; Jamieson et al., 1993). Recently Kwon and Lee (1995) compared ultrastructure of anuran spermatozoa. They described that primitive anuran spermatozoa of Ascaphidae and Discoglossidae are characterized by the endonuclear canal, the perforatorium, the subacrosomal cone and the ring structure. The main evolutionary tendencies in anurans based on ultrastructural characteristics of spermatozoa are the disappearance of the subacrosomal cone and the endonuclear canal of primitive anurans in the other anuran groups, and the disappearance of the perforatorium and the axial rod in higher anuran group. These characters show most of the common feature of urodeles. The sum of spermatozoal characteristics substantiated the hypothesis of a high affinity between urodeles and primitive anurans.

The purpose of this paper is to examine the ultrastructural characteristics of spermatozoa in *Hynobius leechii* and *Bombina orientalis* and to compare it to those of other groups of urodeles and primitive anurans. The results are also discussed with regard to the phylogenetic relationships within the urodeles and of the urodeles with the primitive anurans.

MATERIALS AND METHODS

The amphibian species from which spermatozoal ultrastructure is examined are listed in Table 1, with references to the species on which research has been published.

Testes of *Hynobius leechii* and *Bombina orientalis* were dissected and fixed in 2.5% glutaraldehyde in 0.1 M sodium cacodylate buffer and postfixed in 1% osmium tetroxide in the same buffer. They were then dehydrated in a graded ethanol series and embedded in Epon 812. The samples were sectioned with a Sorvall MT 2-B ultramicrotome and LKB ultramicrotome, stained in 4% aqueous uranyl acetate, poststained with lead citrate, and examined with a Hitachi H-600 electron microscope.

Abbreviations used in the figures

A, acrosome; AR, axial rod; Ax, axoneme; C, centrioles; M, mitochondria; MF, marginal filament; N, nucleus; P, perforatorium; PB, protoplasmic bead; PM, pericentriolar material; R, ring; SC, subacrosomal cone; UM, undulating membrane.

Table 1. Amphibian species from which spermatozoal ultrastructure is examined.

	Sources
Order Urodela	
Family Hynobidae	
<i>Hynobius leechii</i>	Kim et al., 1995
<i>H. nebulosus</i>	Picheral, 1979
Cryptobranchidae	
<i>Cryptobranchus alleganesis</i>	Baker, 1963
Ambystomatidae	
<i>Ambystomata opacum fuscus</i>	Barker and Baker, 1969
Plethodontidae	
<i>Desmognathus fuscus</i>	Lommen, 1970
Amphiumidae	
<i>Amphiuma tridactylum</i>	Baker, 1962; Barker and Biesele, 1967
Salamandridae	
<i>Salamandra salamandra</i>	Picheral, 1979
<i>Triturus palmatus</i>	Picheral, 1979
<i>Pleurodele waltlii</i>	Picheral, 1967, 1971, 1972
Sirenidae	
<i>Pseudobranchius striatus</i>	Austine and Baker, 1964
Order Anura	
Family Ascaphidae	
<i>Ascaphus truei</i>	Jamieson et al., 1993
Discoglossidae	
<i>Discoglossus pictus</i>	Sandoz, 1974
<i>Alytes obstetricians</i>	Furieri, 1975
<i>Bombina variegata</i>	Furieri, 1975
<i>Bombina orientalis</i>	Kwon and Lee, 1992

RESULTS AND DISCUSSION

1) Comparative ultrastructure of the spermatozoa in *Hynobius leechii* and *Bombina orientalis*, and other urodeles and primitive anurans.

Although the spermatozoa of *H. leechii* and *B. orientalis*, show many similar features — an elongated nucleus, a tapering acrosome, a rod-shaped endonuclear perforatorium, an axial rod as main axis, a 9+2 axoneme and an undulating membrane, they possess several characteristics that conform the taxonomic value of comparative spermatology (Table 2).

The spermatozoa of *H. leechii* are 292 μm in total length and those of *B. orientalis* are approximately 43 μm . The chromatin of *B. orientalis* is condensed into large-sized lumps instead of

Table 2. Phylogenetic relationships based on the ultrastructure of amphibian spermatozoa

characters		orders	Urodela					Anura		
		families	Hy	Cr	Am	Sa	Si	As	Di	
		genera	a	b	c	d	e	f	g, h	
PC	clover-shaped acrosome									
	mitochondria around nucleus									
	large axial rod (AR)									
	nuclear ridge						*			
	heterogeneous axial rod			*						
	marginal filament									
	subacrosomal cone									
	ring structure							*		
	perforatorium									
	undulating membrane (UM)									
	axoneme as sperm tail axis									
	endonuclear canal									
	AC	conical acrosome								
		mitochondria related to AR								
small AR										
extention of AR to UM										
uncompact chromatin										

PC, plesiomorphic characters; AC, apomorphic characters; Hy, Hynobiidae; Cr, Cryptobranchidae; Am, Amphiumidae; Sa, Salamandridae; Si, Sirenidae; As, Ascaphidae; Di, Discoglossidae; a, *Hynobius*; b, *Cryptobranchus*; c, *Amphiuma*; d, *Triturus*; e, *Pseudobranchus*; f, *Ascaphus*; g, *Discoglossus*; h, *Bombina*; *, no data.

compacted completely as in *H. leechii* (Figs. 1, 2, 6).

The acrosome is conical in its cross section, clover-shaped from the anterior end to a third of the way down, and then rounded till the posterior end in *H. leechii* (Figs. 3, 5), while that of *B. orientalis* shows cone shape truncated at the anterior end and in cross section, round all along the acrosome (Figs. 4, 6).

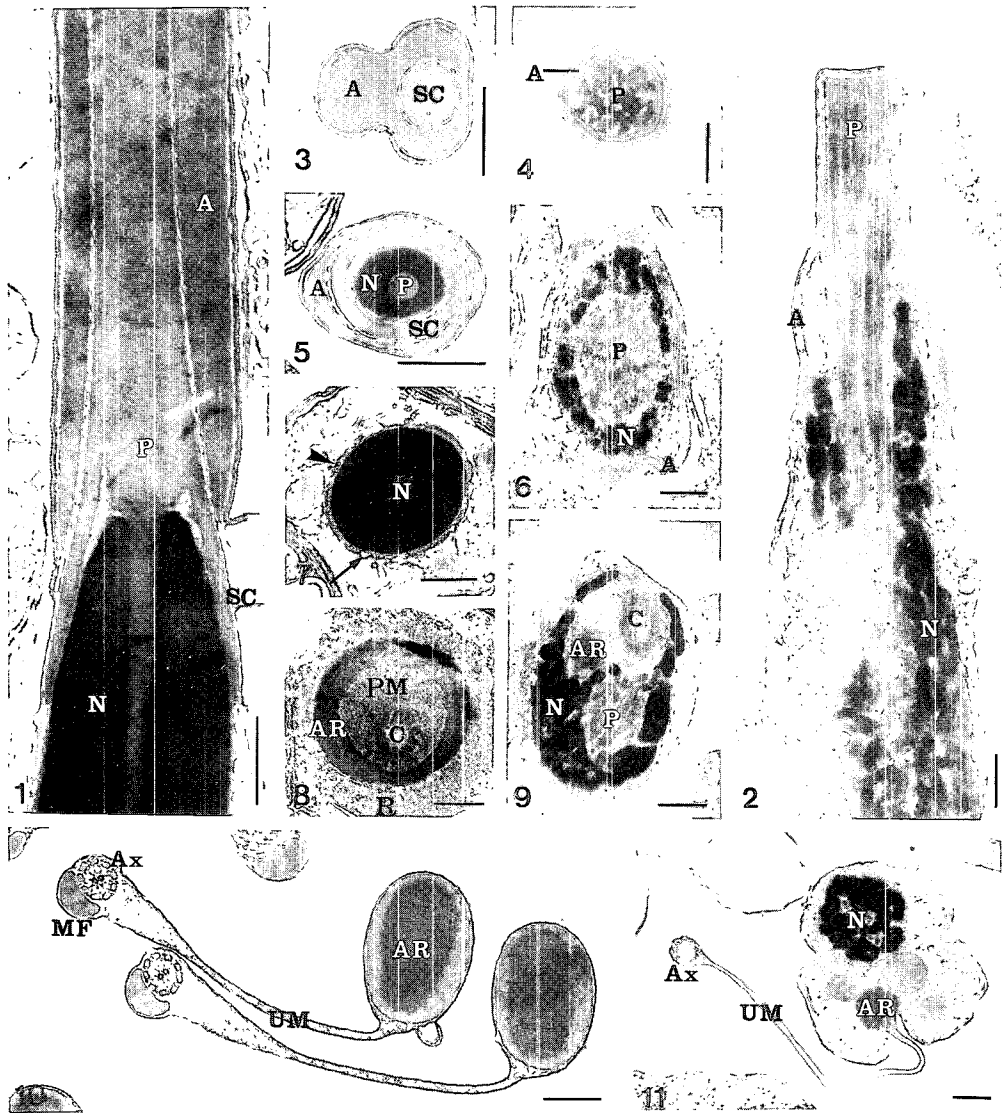
The nuclear ridge is developed and located around the chromatin in *H. leechii* (Fig. 7), whereas it is not observed in *B. orientalis* (Fig. 6). The nuclear ridge is subdivided into several bundles around the nuclear membrane. This aspects have been reported in *Hynobius nebulosus*, *Euproctus asper* and *Salamandra salamandra* (Picheral, 1979). In *Pleurodele waltlii* (Picheral, 1971) and *Ambystoma opacum* (Sever and Kloepfer, 1993), the nuclear ridge is composed of minute tubular subunits packed closely together and located in the one side of chromatin. In *Triturus palmatus* it is surrounded around chromatin and is also developed in the area of chromatin (Picheral, 1979). The nuclear ridge has been also described in many urodeles with the variation of its shape and position. The nuclear ridge which characterizes the nucleus of spermatozoa of urodeles is not observed in anurans.

The endonuclear canal and the perforatorium are common structure of urodelan sperm and also characteristics of sperm in many amniotes and sarcopterygian fish (Jamieson, 1991). The endonuclear canal is more developed in *H. leechii* than in *B. orientalis* and it is occupied by the perforatorium (Figs. 1, 2, 5, 6). Among anurans they are reported only in primitive anurans; *Ascaphus* (Jamieson et al., 1993), *Discoglossus* (Sandoz, 1974), *Bombina* and *Alytes* (Furieri, 1975). Their presence in *Ascaphus* and discoglossid sperms of anurans shows the close relationship with urodeles and is symplesiomorphic. Thus, the absence of their structures from other anurans can be interpreted as a synapomorphy.

The subacrosomal space of *H. leechii* contains the subacrosomal rod running along the inner acrosomal membrane (Figs. 1, 3) but no subacrosomal rod in *B. orientalis* (Figs. 2, 4). Also the subacrosomal space of *B. orientalis* is conical and smaller than in *H. leechii*. The subacrosomal cone is present in the spermatozoa of urodeles (Baker, 1962, 1963; Picheral, 1967, 1972, 1979; Barker and Biesele, 1967), but it is not described in any other anuran examined excepting *Ascaphus*. Its presence in *Ascaphus* gives support for placement of this taxon at the base of the anurans which has been proposed by other workers on the basis of macromorphological character (Hillis, 1991) and r-RNA sequence (Hedges et al., 1990). This cone thus appears to be also plesiomorphic condition in amphibians.

The neck region of *H. leechii* consists of two centrioles, the pericentriolar material, the proximal portion of axial rod and the granular ring structure (Fig. 8). In *B. orientalis* it contains the centriole and the anterior portion of axial rod and is located in the lateral surface of the nucleus surrounded by a longitudinal depression (Figs. 9, 11). There are no ring and pericentriolar material in *B. orientalis* unlike *H. leechii* (Figs. 8, 9).

The ring structure is a typical feature of urodelan sperm. It shows the differences in its position and composition among taxa. The ring consists of granules and is not elongated to middle piece in *Hynobius* (Picheral, 1979; Barker and Baker, 1969) and *Cryptobranchus* (Barker and Baker, 1969). The lamellar ring elongates down the length of the middle piece in *Desmognathus* (Lommen, 1970) and *Amphiuma* (Barker and Biesele, 1967). The ring of the proximal granular and distal lamellar



Figs. 1-11. Longitudinal and transverse sections at different levels of the spermatozoa of *Hynobius leechii* (1, 3, 5, 7, 8, 10) and *Bombina orientalis* (2, 4, 6, 9, 11). Scale bar = 0.3 μ m. 1-6: Longitudinal (1,2) and transverse sections (3-6) of the anterior head, showing the acrosome and the perforatorium. Note the subacrosomal cone (1,3) and the outer trifoliate acrosome (3) in *H. leechii*. 7: Tranverse section of the anterior nucleus showing the nuclear ridge area (arrowhead) containing many bundles of minute tubules and the chromatin area in *H. leechii*. Note that the nuclear membrane (arrow) surrounds the nuclear ridge area. 8-9: Transverse sections of the neck showing the relationship of the ring (8), axial rod and perforatorium (9). Note the ring surrounding the neck region in *H. leechii* (8). 10-11: Transverse sections of the anterior part of tail showing the axial rod, the undulating membrane and the axoneme. Note the marginal filament related to the axoneme in *H. leechii* (10), and the mitochondria adjacent to axial rod in *B. orientalis* (11).

structure also elongates to middle piece in higher urodeles (Werner, 1969; Picheral, 1979). The size of the ring reduces in Hynobiidae and Cryptobranchidae in contrast to those in other urodeles. The

ring structure is not reported in any other anurans excepting *Discoglossus* (Sandoz, 1974).

The tail of *H. leechii* consists of marginal filament, axoneme, axial rod and undulating membrane (Fig. 10), while in *B. orientalis* it contains no marginal filament. The marginal filament of *H. leechii* is located near the axonemal doublet no. 8 opposite to the axial rod as in most urodeles.

The tail is generally located behind the nucleus in many taxa. The prenuclear implantation of the flagellum at the lateral surface of the nucleus in *Bombina* is a notable difference from postnuclear implantation in many taxa. This aspect has been observed in *Alytes* (Furieri, 1975) among other anurans and has been also known only from *Pseudobranchus* in urodeles, which have two flagella and two undulating membrane (Austin and Baker, 1964). The occurrence of a prenuclear implantation of flagellum in the spermatozoa of *Bombina*, *Alytes* and *Pseudobranchus* is an independent development. The axoneme is usually oriented in the main axis of the sperm in most species. But in urodeles and primitive anurans, *Ascaphus*, *Bombina* and *Discoglossus* it is positioned laterally to the main axis which is the axial rod. This lateral axoneme should be considered as symplesiomorphy in urodeles and primitive anurans. The axial rod is quite large in its size in primitive urodeles, *Hynobius* and *Cryptobranchus*, while it is very reduced in higher groups of urodeles and primitive anurans, and disappears in higher groups of anurans.

The mitochondria gathered in a semicircle adjacent only to the axial rod in *Bombina* have been also observed in *Ascaphus* of primitive anurans and most urodeles (Baker, 1962, 1963; Barker and Biesele, 1967). Lee and Jamieson (1992) suggested that in myobatrachids the location of the mitochondria adjacent only to the axial rod is plesiomorphic, as compared with the mitochondria surrounding the axial rod observed in the higher anurans. In *Hynobius* and *Cryptobranchus*, the mitochondria are not positioned around the flagellum but only located within the protoplasmic bead observed around the nucleus. This arrangement has described in fish (Mattei, 1988) and nemertean (Afzelius, 1971). This should be considered as plesiomorphic character in urodeles. The above two species are positioned in the most primitive position among urodeles. Diagrams summarizing cross sections through spermatozoa of representative families of amphibians are illustrated in Figs. 12-13.

2) Phylogenetic relationships within the urodeles and of the urodeles with the primitive anurans based on the spermatozoal ultrastructure.

Hynobiidae and Cryptobranchidae spermatozoa show similar aspects in the structure and composition of ring and the location of mitochondria. The short and granular ring and the mitochondria located around nucleus are not observed in other urodeles and anurans. They seem to be plesiomorphic in urodeles. Therefore, the above two families may be the most primitive position in urodeles. This coincides with the morphological and karyological data (Morescalchi, 1973) in that Hynobiidae and Cryptobranchidae are the primitive families of urodeles and are closely related.

Plethodontidae and Amphiumidae are characterized by common features such as the presentation of the lamellar and elongated ring. According to the data of comparative spermatology, these two families belong to the intermediated position between the primitive group of urodeles, Hynobiidae-Cryptobranchidae, and the advanced group which agrees with the classification opinion (Duellman and Trueb, 1994). But this result disagrees with the opinion of Larson and Wilson (1989) that the Plethodontidae are placed at the base of urodeles.

Salamandridae have common features such as superimposed and elongated ring, large neck piece

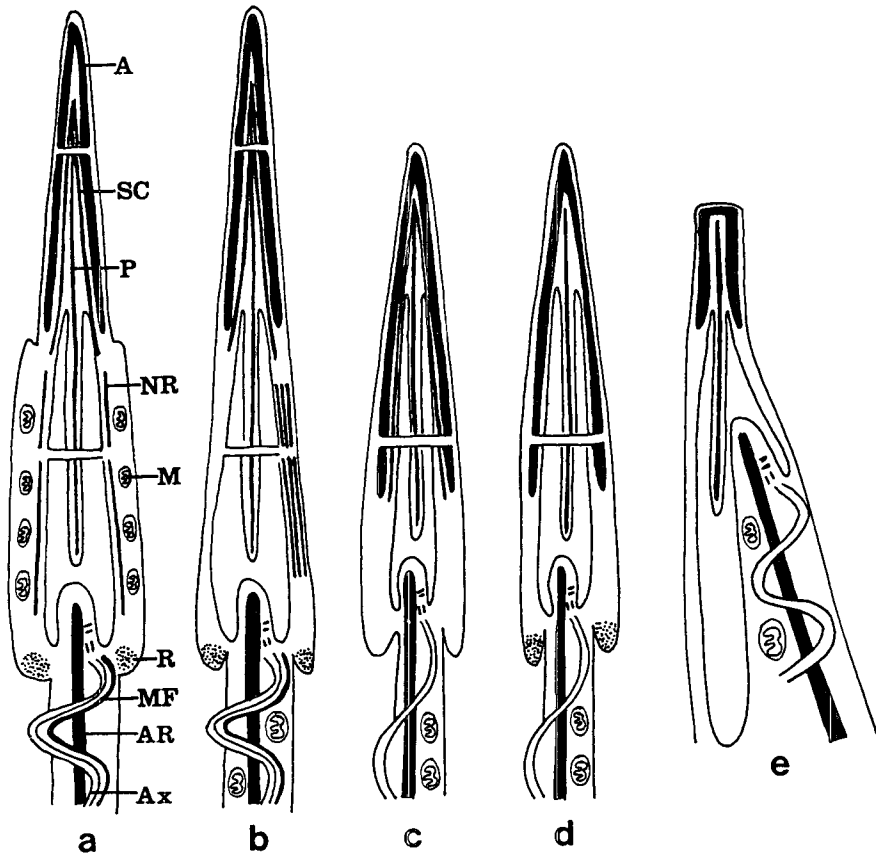
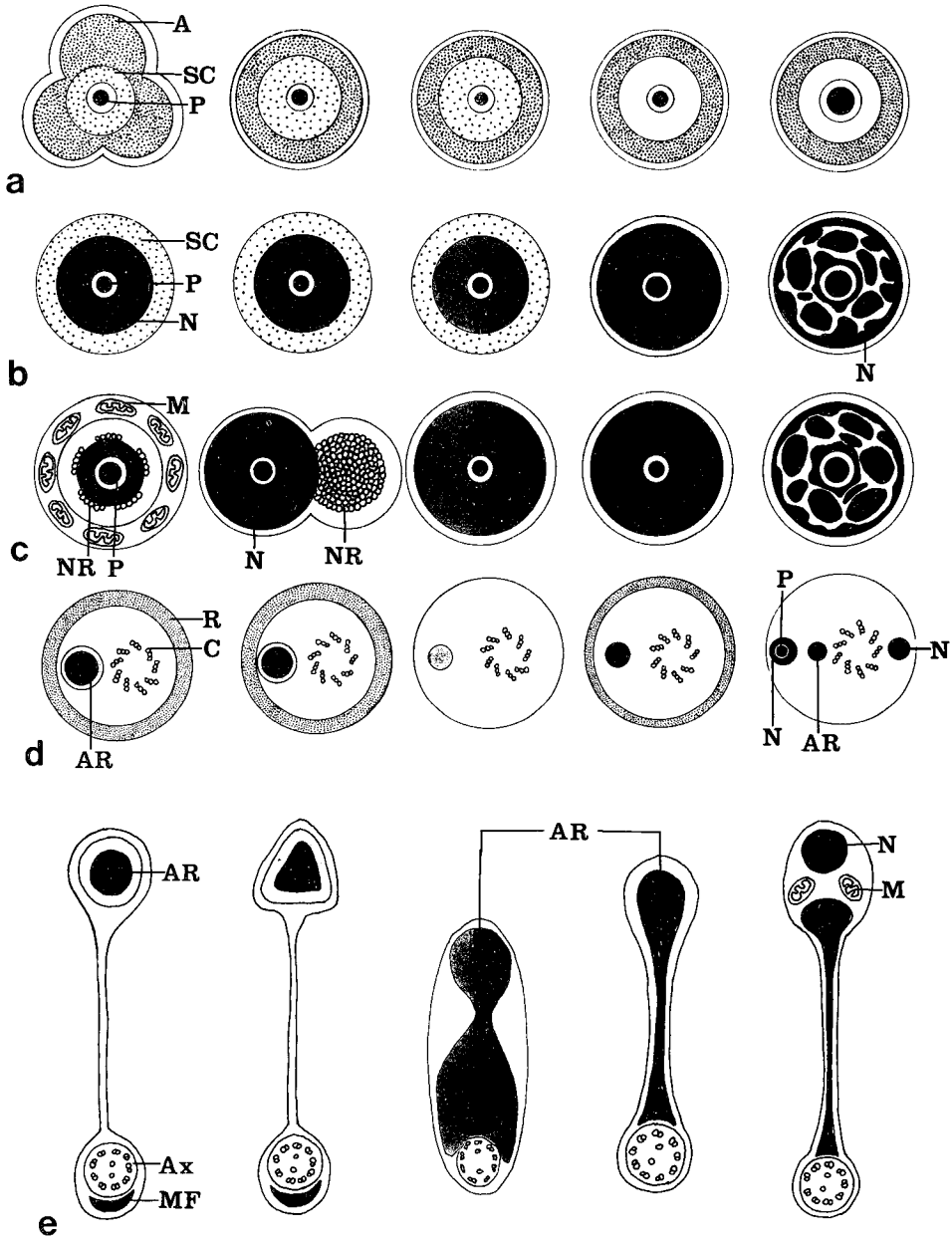


Fig. 12. Diagrammatic representation of longitudinal sections of amphibian spermatozoa: a, *Hynobius leechii*; b, *Triturus palmatus*; c, *Ascaphus truei*; d, *Discoglossus pictus*; e, *Bombina orientalis*.

and reduced axial rod. These characters should be considered as apomorphy in urodeles, and therefore they appear in highly differentiated forms. This interpretation perfectly agrees with the karyological data (Morescalchi, 1973).

In anurans Ascaphidae and Discoglossidae are characterized by endonuclear canal, rod-shaped endonuclear perforatorium, axial rod as sperm tail axis, undulating membrane and mitochondria adjacent to only the axial rod. Especially *Ascaphus* and *Discoglossus* have the subacrosomal cone and the ring respectively, and most urodeles have both. These characters show most of the common feature of urodeles. Therefore the characters of these families give some support in placing the taxon at the base of the anurans. One of the clearest conclusions based on comparative spermatology is that the organization of the sperm tail, in addition to the endonuclear canal and perforatorium, indicates a close phylogenetic relationship between the primitive anurans and urodeles. Comparative spermatology thus may be considered as an useful tool in understanding Amphibia.



Hynobius leechii *Triturus palmatus* *Ascaphus truei* *Discoglossus pictus* *Bombina orientalis*

Fig. 13. Diagrammatic representation of transverse sections of amphibian spermatozoa: a, the anterior part of head; b, the middle part of nucleus; c, the posterior part of nucleus; d, the neck region; e, the principal piece of tail.

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적 요

유미류와 하등 무미류 정충의 미세구조를 비교하고 미세구조적 형질에 의한 계통적 관계를 고찰하였다. 대부분의 유미류 정충은 subacrosomal rod, endonuclear canal, perforatorium, ring, marginal filament, 꼬리의 구성과 꼬리의 주축이 axial rod인 7가지 양서류의 원시 공유형질(sympleiomorphies)을 나타내었다. 하등 무미류 정충은 marginal filament가 없으며 subacrosomal rod와 ring의 구조는 단지 *Ascaphus*와 *Discoglossus*의 두 속에서만 각각 보고되었다. 이러한 미세구조적 형질은 유미류와 하등 무미류의 원시 공유형질로 간주되며 두 분류군 사이의 계통적 연속성을 보여준다. 또한 정자 꼬리의 구성, endonuclear canal과 perforatorium의 형성에서도 매우 밀접한 계통적 관계를 보여주었다.