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疣荔枝螺精子的超微结构

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摘要: 应用透射电镜技术研究了疣荔枝螺精子的超微结构。成熟精子由头部与尾部组成。头部由顶体和核构成, 顶体细长锥状; 核呈长圆筒状, 核内沟从核后端中央向前伸至核的近前端, 位于核近前端的核内沟顶端有一单个中心粒形成的基体, 由基体向后发出"9+ 2"结构的轴丝贯穿整个精子。尾部分中段、主段和末段, 中段"9+ 2"结构外包丝状线粒体螺旋环绕形成的线粒体鞘; 主段线粒体鞘消失, "9+ 2"结构外包糖元颗粒鞘; 末段仅"9+ 2"轴丝结构外包质膜。比较了疣荔枝螺与前鳃亚纲其它动物精子结构的异同, 进一步证明了顶体的有无及其形态、精核的长短与形态、尾部线粒体的形态与数目及其排列方式、糖元颗粒鞘结构的有无等是前鳃亚纲动物精子结构比较研究的主要内容。

关键词: 前鳃亚纲; 疣荔枝螺; 精子; 超微结构; 进化
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Ultrastructure of spermatozoon of *Purpura clavigera* K ster

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Abstract: Ultrastructure of mature spermatozoon of *Purpura clavigera* K ster was observed by transmission electron microscopy. The mature spermatozoon contains two parts: head and tail. The head comprised an acrosome and a nucleus. The slim-cone shaped acrosome is about 2 μm in length. The content in the acrosome is homogeneous and highly electron-densed. The morphology of subacrosomal space which is filled with highly electron-densed materials is similar to the shape of acrosome. The cylinder nucleus is about 16 μm in length. The content of the nucleus is highly densed. The nucleus is homogeneous. The endonuclear channel extends to the front part of nucleus from caudal nucleus. The inner diameter of the endonuclear channel is about 0.2 μm. The basal body is formed by a single centriole which is located at the apex of endonuclear channel. The "9+ 2" arrangement of axoneme emitting from basal body run through the whole sperm. The tail is composed of mid-piece, principal piece and end piece. The chondriosomal mantle which is formed by filar mitochondria enwraps the "9+ 2" arrangement in the middle piece. The thickness of every mitochondrial gyration is about 0.1 μm . The distance between gyration is equidistant. No chondriosomal mantle exists in the principal piece, only glycogen particle mantle surrounds axoneme. In the end piece, only plasma membrane surrounds the axoneme. The similarities and differences of the sperm ultruastructure between *Purpura clavigera* K ster and other Prosobranchia including Archaeogastropoda, Mesogastropoda and Neogastropoda are discussed. The evolving trend of Prosobranchia sperm can be seen obviously by comparing the structure. The sperm structure of Prosobranchia changes from "primitive type" which was found in Archaeogastropoda to "modified type", the latter were found in Mesogastropoda and Neogastropoda. The head of Archaeogastropoda sperm that undergoes external fertilization tapers. The rear part of the nucleus has a posterior nuclear pocket. The proximal and distal centrioles are located in posterior nuclear pocket. The distal contrioles emits axoneme and finally forms the tail. The simple tail contains a short mid-piece and

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a slim end piece. Several mitochondria enwrap centriole in middle piece. In the end piece, only plasma membrane surrounds the axoneme. The head of sperm in Mesogastropoda and Neogastropoda animals which undergoes internal fertilization is slim. The tail is composed of middle piece, principal piece and end piece. The chondriosomal mantle which is prolonged and originated from mitochondria surrounds the axoneme. In the principal piece, the "9+2" axoneme was surrounded by glycogen particles. The ultrastructure of the end piece is the same as Archaeogastropoda animals. Chondriosomal mantle is formed to cumulate more energy and the glycogen particle mantle can supply more energy. The formation of chondriosomal mantle and glycogen particle mantle in the sperm tail meets the energy requirement for the internal fertilization, and it also shows us an important morphological feature during the sperm evolution. *Purpura clavigera* sperm ranks higher evolutionary status in Prosobranchia than other species. The following aspects should be considered when we pursue Prosobranchia species evolution: The existence or not of acrosome, the fine feature of acrosome, the shape and the length of nucleus, the number, morphology and the arrangement of mitochondria in the mid-piece, and the existence or not of glycogen particle mantle. The comparative study on representative species sperm structure in different order, family, genus of Prosobranchia can help us in revealing the evolutionary trend of Prosobranchia, and also in analysing the evolutionary relationship of different order, family, genus and species.

Key words: Prosobranchia; *Purpura clavigera* K ster; spermatozoon; ultrastructure; evolution

动物精子的形态结构与受精过程密切相关。在物种进化过程中,动物的精子结构能显示亲缘关系很近的物种的种间差异。因此,精子结构是衡量物种间亲缘关系的一个重要指标[1];对精子结构的比较研究已经和研究精子中重要蛋白功能的异同一样,成为进化生物学研究的重要手段[2-4]。在软体动物中,探讨精子形态结构在物种的分类、亲缘关系分析及系统进化上的意义已有一些报道[2,5-7]。腹足纲前鳃亚纲(Prosobranchia)软体动物的精子结构变化多样,现有的研究表明,该亚纲物种的精子依受精方式的不同,可分为适应于体外受精的原始型和适应于体内受精的修饰型两类[8,9]。迄今未见对前鳃亚纲疣荔枝螺(*Purpura davigera* K ster)精子超微结构及其与相近物种比较研究的报道。疣荔枝螺属新腹足目(Neogastropoda)、骨螺科(Muricidae),生活于岩相潮间带中、下潮区,我国沿海均有分布,是人们喜食的经济贝类之一。本文报道了疣荔枝螺精子的超微结构,并与腹足纲前鳃亚纲其它物种精子形态进行了比较,并提出了前鳃亚纲动物精子结构用于比较研究的重要指标。

1 材料与方法

实验用疣荔枝螺于2003年7月采自浙江象山沿海的潮间带。样品采集后立即带回宁波大学实验室。挑选活力好的个体进行解剖,取得成熟雄贝精巢中的精液,用0.1 mol·L^{-1}、pH 7.4的磷酸缓冲液配制的2.5%戊二醛(4℃)固定1 h,然后,用1%锇酸(4℃)后固定1 h。乙醇梯度浓度脱水,Spurr氏低粘度包埋剂渗透、包埋,Leica ultracut超薄切片机切片,醋酸铀及柠檬酸铅双重染色,JEM-1230型透射电镜观察并拍照。

2 结果与分析

疣荔枝螺精子属鞭毛型,结构上可分为头部(head)和尾部(tail)两部分,整个精子包被在质膜内。

2.1 头部

精子头部由顶体(acrosome)和精核(nucleus)组成。

顶体 位于核的前端,纵切面观为一细长的锥体,长约2 μm,近核端的基部与核同宽,向顶端渐细(图版Ⅰ-1,2);顶体的外周由质膜包被;顶体中央有一伸达顶体顶端的腔隙,称之为顶体下腔(subacrosomal space),顶体下腔的近核端最宽,向顶端渐窄;顶体内部物质分布均匀,电子密度较高;顶体下腔中也充满电子密度较高的物质(图版Ⅰ-1,2,3)。顶体基部与核前端连接紧密。顶体的斜切面观呈尖削状(图版Ⅰ-3,4,5)。

精核 呈细长圆筒状,长约16 μm,前端直径约0.35 μm,后端直径约0.5 μm,核质致密,电子密度高,核膜平整,核膜外由质膜包被,质膜呈微波纹状,与核膜间留有电子密度透亮的间隙。核内沟从核后端中央向前伸至核的近前端;核内沟的前、中、后段直径基本相同,约0.2 μm;位于核近前端的核内沟顶端有一单个中心粒形成的基体,由基体向后发出"9+2"结构的轴丝贯穿整个精子,轴丝与核之间有一电子密度低的间隙(图版Ⅰ-4,5,6,7;图版Ⅱ-4)。

2.2 尾部

尾部是精子的最长部分,从结构上可明显地区分为中段(middle piece)、主段(principal piece)及

末段(end piece)。

中段连接于核的后端, 横切面直径与核后端基本同宽, 由线粒体形成的鞘(chondriosomal mantle)包绕在轴丝外, 线粒体呈丝状、螺旋环绕轴丝, 每一螺层厚约 0.1 μm, 各螺层间并非紧贴, 而留有一等距的间隙, 线粒体鞘与轴丝间也留有电子密度透亮的间隙; 线粒体的嵴难看清, 但双层外膜仍清楚, 内部基质丰富; 线粒体鞘的外周由微波纹状质膜包被, 其间有一间隙(图版 I-7, 8; 图版 II-1, 3, 5)。

中段之后是主段, 线粒体鞘消失, "9+ 2" 结构的轴丝外由颗粒状物质形成的 9 束纵行的间隔等距的粗纤维环绕, 最外层为质膜(图版 I-9; 图版 II-2, 6); 从横切面可见 9 组颗粒状物质由轴丝向外辐射状排列, 每组与轴丝的 9 组微管一一对应, 这些颗粒状物质在台湾东风螺(*Babylonia formosae*)[10] 及中国圆田螺(*Cipangopaludina chinensis*)[11] 精子中也存在, 并被证实为糖元颗粒(glycogen particles), 因此, 9 束纵行的粗纤维也可称之为糖元颗粒鞘; 随着主段接近末段, 糖元颗粒鞘缩小(图版 II-7), 至末段糖元颗粒鞘消失, 只留下"9+ 2"轴丝结构外包质膜(图版 II-8, 9)。

3　讨论

3.1　疣荔枝螺精子与前鳃亚纲其它物种精子结构比较

软体动物的精子根据形态与受精方式的不同可大体划分为"原始型(primitive type)"和"修饰型(modified type)"两类。前者属于体外受精的种类, 如双壳纲与掘足纲的精子属此类型[8]; 后者属于体内受精的种类, 如腹足纲中的后鳃亚纲和肺螺亚纲、以及头足纲的精子属此类型[9]。在腹足纲的前鳃亚纲中, 两种类型精子都存在, 原始腹足目的种类营体外受精, 精子属原始型[2,6,12], 其特点是精子头部呈锥形, 中段短、无线粒体鞘结构; 而中腹足目与新腹足目的种类营体内受精, 精子属修饰型, 其特点是精子头部呈线状, 中段加长、有线粒体鞘结构[10,11,13]。疣荔枝螺属新腹足目、骨螺科、体内受精, 精子由头部及尾部两部分组成, 头部呈线状, 尾部结构复杂化, 分中段、主段与末段, 中段由螺旋线粒体鞘围绕轴丝, 主段轴丝外包糖元颗粒鞘, 从精子的结构特征及受精方式看属修饰型精子。Hodgson 和 Bernard[2] 报道的帽贝科 16 种帽贝的精子形态, 都呈典型的原始型, 其顶体呈大小、高低不同的圆锥形, 核为圆柱状或瓶状或三角形, 中段 3~ 4 个线粒体平面型环绕于近端与远端中心粒周围, 中段之后是细长的"9+ 2"轴丝结构外包质膜的尾鞭。此外, 笠贝科的笠贝(*Acmaea testudinalis*)、马蹄螺科的丽口螺(*Calliostoma militare*)与驼峰螺(*Gibbula cineraria*)等种类的精子形态也均属典型的原始型[14]。柯才焕等[6] 对鲍科杂色鲍(*Haliotis diversicolor supertexta*)、盘鲍(*H. discus discus*)、皱纹盘鲍(*H. discus hannai*)精子超微结构的比较研究, 发现杂色鲍精子呈典型的原始型; 而盘鲍和皱纹盘鲍的精子, 从中段和尾鞭特征看属原始型, 但头部却呈改进型的线状, 而非原始型的锥型, 带有原始型和改进型的双重特点, 是一种过渡类型, 据此推论盘鲍和皱纹盘鲍在分类地位上比杂色鲍高等。将本研究中的疣荔枝螺精子与上述原始腹足目动物精子的形态结构相比较后发现, 疣荔枝螺精子与已知原始腹足目动物精子在头部与尾部结构上均存在很大差异, 主要体现在: ①疣荔枝螺精子头部呈线形, 核后端开口深凹至核前端形成核内沟, 中心粒(也称基体)一个, 位于核内沟的顶端, 由此发出轴丝贯穿整个精子; 原始腹足目的帽贝[2], 笠贝、丽口螺及驼峰螺等种类精子[14] 头部呈锥形或纺锤形, 而非线状, 核后端具有一浅的凹窝即核后窝, 近端与远端中心粒位于核后窝处; ②疣荔枝螺精子尾部从结构上可明显地分为中段、主段及末段, 具线粒体鞘(中段)及糖元颗粒鞘(主段)结构; 而上述原始腹足目动物精子尾部只具中段与末段, 中段具线粒体环, 但未形成线粒体鞘, 无糖元颗粒鞘结构。疣荔枝螺精子头部呈线形、尾部具线粒体鞘及糖元颗粒鞘结构, 具备了典型修饰型精子的结构特征。

中腹足目、田螺科动物中国圆田螺[11] 精子头部虽无顶体, 但精核呈螺旋状, 中段螺旋状线粒体围绕在轴丝外, 尾段轴丝外有糖元颗粒鞘包绕, 精子结构特征属修饰型, 与本研究的疣荔枝螺精子相比, 尾部形态结构较为相似, 但头部形态结构完全不同。滨螺科滨螺(*Littorina sitkana*)[15] 精子尾部的线粒体拉长, 但不螺旋化, 与疣荔枝螺精子尾部螺旋状线粒体不同。

新腹足目、蛾螺科动物台湾东风螺(*Babylonia formosae*)[10] 精子顶体呈倒"U"字形(长为 0.93~

1.38 μm), 顶体下腔中有顶体棒结构, 核长圆筒状(长 8.5 μm), 核内沟仅在核的后方; 中段线粒体已演化为线粒体鞘; 主段最长, 轴丝的外围有 9 组颗粒状物质包绕, 系糖元颗粒鞘, 精子结构特征属典型的修饰型。与本研究的疣荔枝螺精子相比, 顶体与精核的结构差异明显, 精子头部的长度约为疣荔枝螺的 1/2。骨螺科动物脉红螺(*Rapana venosa*)[16] 精子头部似弹头状, 顶体不发达, 核呈倒"U"字的袋状(长 3~5 μm), 核后端中央向前内陷至核的前端, 由单个基体向后延伸出轴丝, 中段由丝状线粒体形成的鞘包围在轴丝外, 主段轴丝外包 9 束粗纤维、即糖元颗粒鞘包绕。可见, 脉红螺与疣荔枝螺虽属同一科不同属, 精子结构特征都属修饰型, 两物种精子尾部结构较为相似, 但精子头部长度与形态结构差异很大。

从以上比较中发现前鳃亚纲精子结构演化有明显的由原始腹足目的原始型向中腹足目及新腹足目的修饰型演变的渐趋。体外受精的原始腹足类精子中段短, 几个囊状线粒体平面型环绕于中心粒的周围, 无线粒体鞘结构[2,6,12]; 而营体内受精的中腹足目与新腹足目的种类精子中段的线粒体拉长, 演化为线粒体鞘结构[10,11,13,16], 中段之后出现了糖元颗粒鞘结构。线粒体是精子运动的供能者, 线粒体鞘的形成能蓄积更多的能量, 糖原颗粒鞘的出现说明供能物质的增多, 满足了精子在雌性生殖道中长时间运动的需要。可以认为, 精子尾部线粒体鞘及糖元颗粒鞘的形成, 是对体内生殖方式的一种适应, 也是腹足纲前鳃亚纲动物原始型精子向修饰型演变的重要结构依据。疣荔枝螺精子结构复杂, 显示在前鳃亚纲中处于较高等的进化地位。

3.2 前鳃亚纲动物精子结构的比较研究参数

通过对疣荔枝螺精子与前鳃亚纲其它物种精子结构的比较, 我们初步认为前鳃亚纲动物精子的下列结构可以作为精子结构比较研究的参数: (1) 顶体, 包括顶体的有无及其外形(短扁或者尖长), 顶体下腔的形态结构; (2) 精核, 包括精核长短及形态, 核前端凹窝或核后端凹窝的有无, 核后窝是否向前深凹入形成核内沟等; (3) 尾部, 包括线粒体的形态(囊状或丝状)与数目、以及排列方式(平面型、螺旋型或非螺旋型), 糖元颗粒鞘结构的有无, 中心粒单个还是双个等。从这些方面对前鳃亚纲各目不同科、属的代表种的精子结构进行比较研究, 从中能了解前鳃亚纲动物的精子结构的进化趋向, 分析各目、科、属及种间的演化关系。

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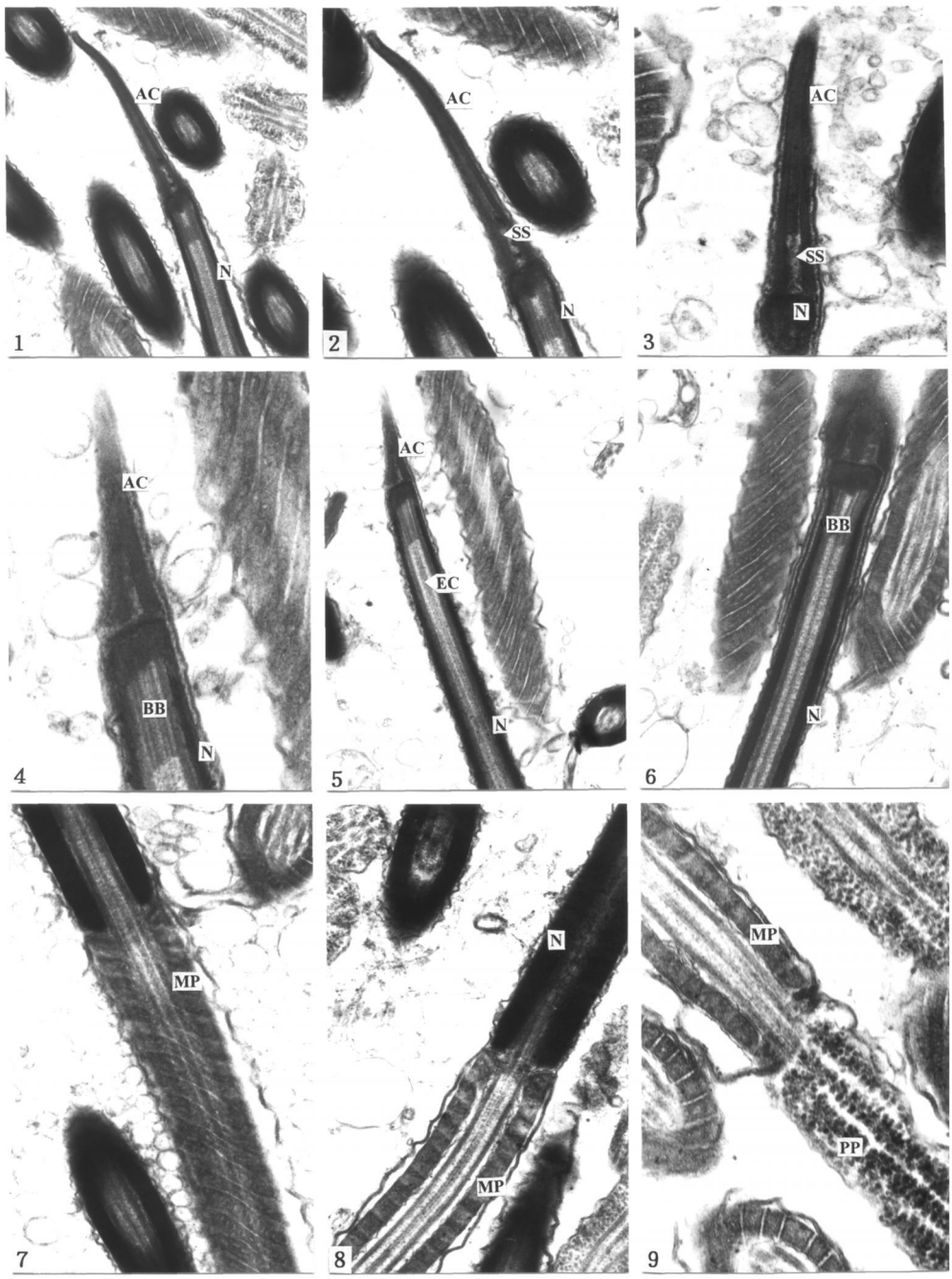


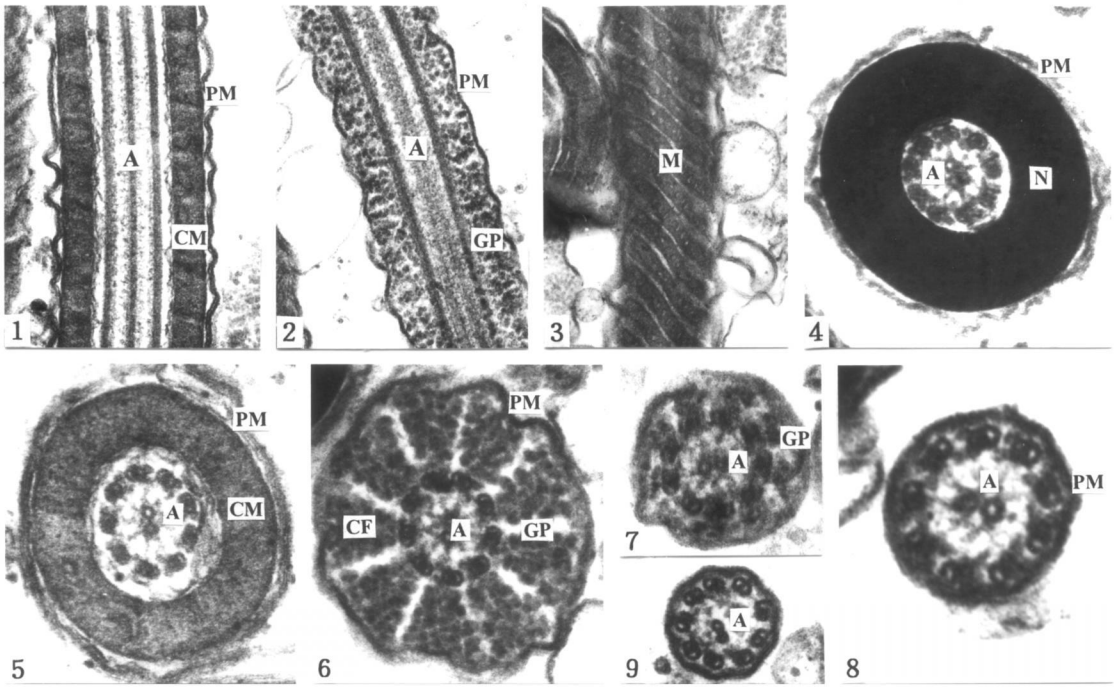
图版Ⅰ　**Plate Ⅰ**

1. 精子头部纵切面, 示顶体及核, × 15 000; 2. 精子顶体纵切面, 示顶体及其下腔, × 22 000; 3. 精子顶体斜切面, 示顶体及顶体下腔, × 30 000; 4. 精子头部斜切面, 示顶体及核前端基体, × 40 000; 5. 精子头部纵切面, 示顶体、核及核内沟, × 22000; 6. 精核前段纵切面, 示基体及轴丝, × 25 000; 7. 精子纵切面, 示核与中段的连接, × 30 000; 8. 精子纵切面, 示核与中段, × 30 000; 9. 精子纵切面, 示中段与主段的连接, × 40 000

1. Longitudinal section of sperm at head, showing acrosome and nucleus, × 15 000; 2. Longitudinal section of sperm at acrosome, showing acrosome and subacrosomal space, × 22 000; 3. Non-typical longitudinal section of sperm at acrosome, showing acrosome and subacrosomal space, × 30 000; 4. Non-typical longitudinal section of sperm at head, showing acrosome and basal body in the front of nucleus, × 40 000; 5. Longitudinal section of sperm at head, showing acrosome nucleus and endonuclear channel, × 22 000; 6. Longitudinal section of sperm at the forepart of nucleus, showing basal body and axoneme, × 25 000; 7. Longitudinal section of sperm, showing the joint of nucleus and mid-piece, × 30 000; 8. Longitudinal section of sperm, showing nucleus and mid-piece, × 30 000; 9. Longitudinal section of sperm, showing the joint of mid-piece and principal piece, × 40 000

A: 轴丝; AC: 顶体; BB: 基体; CF: 粗纤维; CM: 线粒体鞘; EC: 核内沟; GP: 糖元颗粒; M: 线粒体; MP: 中段; N: 核; PM: 质膜; PP: 主段; SS: 顶体下腔

A: axoneme; AC: acrosome; BB: basal body; CF: coarse fibre; CM: chondriosomal mantle; EC: endonuclear channel; GP: glycogen particles; M: mitochondria; MP: middle piece; N: nucleus; PM: plasma membrane; PP: principal piece; SS: subacrosomal space



图版Ⅱ **Plate Ⅱ**

1. 精子中段纵切面, 示轴丝及线粒体鞘, × 40 000; 2. 精子主段纵切面, 示轴丝及糖元颗粒鞘, × 40 000; 3. 精子中段纵切面, 示螺旋线粒体, × 30 000; 4. 精核横切面, 示核及"9+ 2"结构的轴丝, × 80 000; 5. 精子中段横切面, 示线粒体鞘及"9+ 2"结构的轴丝, × 80 000; 6. 精子主段横切面, 示糖元颗粒鞘及"9+ 2"结构的轴丝, × 80 000; 7. 精子主段末端横切, 示糖元颗粒及"9+ 2"结构的轴丝, × 80 000; 8. 精子末段横切, 示"9+ 2"结构的轴丝, × 80 000; 9. 精子末段横切, 示"9+ 2"结构的轴丝, × 120 000

1. Longitudinal section of sperm at mid-piece, showing axoneme and chondriosomal mantle, × 40 000; 2. Longitudinal section of sperm at principal piece, showing axoneme and glycogen particle mantle, × 40 000; 3. Longitudinal section of sperm at mid-piece, showing spiral mitochondria, × 30 000; 4. Cross sectioo of sperm at nucleus, showing nucleus and the "9+ 2" arrangement of axoneme, × 80 000; 5. Cross section of sperm at mid-piece, showing chondriosomal mantle and the "9+ 2" arrangement of axoneme, × 80 000; 6. Cross section of sperm at principal piece, showing glycogen particle mantle and the "9+ 2" arrangement of axoneme, × 80 000; 7. Cross section of sperm at principal piece, showing glycogen particles and "9+ 2" arrangement of axoneme, × 80 000; 8. Cross section of sperm at end piece, showing the "9+ 2" arrangement of axoneme, × 80 000; 9. Cross section of sperm at end piece, showing the "9+ 2" arrangement of axoneme, × 120 000

A: 轴丝; AC: 顶体; BB: 基体; CF: 粗纤维; CM: 线粒体鞘; EC: 核内沟; GP: 糖元颗粒; M: 线粒体; MP: 中段; N: 核; PM: 质膜; PP: 主段; SS: 顶体下腔

A: axoneme; AC: acrosome; BB: basal body; CF: coarse fibre; CM: chondriosomal mantle; EC: endonuclear channel; GP: glycogen particles; M: mitochondria; MP: middle piece; N: nucleus; PM: plasma membrane; PP: principal piece; SS: subacrosomal space