Studies on the Spermiogenesis of
Siphonaria laciniosa (Gastropoda, Pulmonata)
from the Gulf of Aqaba

1. Nuclear Changes

Ramsis G. Lutfy and Hameed Al-Hajj

*Department of Biological Sciences, University of Jordan,
Amman, Jordan*

ABSTRACT. The spermiogenesis of *Siphonaria laciniosa* (Gastropoda, Pulmonata) was studied by electron microscopy. Some of the most drastic changes comprising the process of spermiogenesis involve the nucleus which undergoes a series of changes affecting its shape, size, differentiation of various regions of its envelope, and progressive condensation of its chromatin. Active nucleo-cytoplasmic exchange seems to take place in the various phases of the process especially in its early stages. The various shapes acquired by the nucleus are described in detail, and are taken as salient points in the continuous process of spermiogenesis. These stages are: the "urn" stage; the "hammer head" stage; the "hazel-nut" stage; and the "spearhead" stage. Many of the morphological transformation exhibited by the nucleus, especially those of the later phases of spermiogenesis are effected by microtubules.

It is quite evident that the mollusca have achieved remarkable evolutionary success and managed to adapt to a wide spectrum of ecological niches. In doing so they, (among other things) have undergone an enormous diversification in their reproductive processes in order to ensure species survival as well as dispersal. The extensive diversity in structure of molluscan spermatozoons is a reflection of the variation in the physiological demands imposed by widely different fertilization environments. These generalizations are more true for the gastropods than for the other classes of mollusca.

The degree of difference in structural details of the gastropod spermatozoons at the species level, is such that it has been suggested as being significant for taxonomic classification.

The pulmonates have attracted more attention than other gastropod groups insofar as the detailed structure and histochemistry of the spermatozoon are concerned. Among the most important reports are those of Franzén (1957, 1970); Grassé et al. (1956); Rebhun (1957); Gatenby (1960); Barth and Oliveira (1964); Tahmisian (1964); Galangau and Tuzet (1966); Tuzet and Galangau (1967); Anderson and Personne (1967, 1969, 1970a,b&c, 1976); Anderson et al. (1968); Takahashi et al. (1973); Thompson (1973); Takaichi and Dan (1977); Takaichi (1978); Terakado (1981); Atkinson (1982); Azevedo and Corral (1985) and Healy (1986).

The present study is the first of a series that deals with the ultrastructural aspects of the process of spermiogenesis of *Siphonaria laciniosa*, a littoral pulmonate from the Aqaba Gulf.

Materials and Methods

Several specimens of the pulmonate gastropod *Siphonaria laciniosa* were collected monthly for a period of 12 months in the intertidal zone opposite to the Marine Science Station of the Gulf of Aqaba. The ovotestes were dissected out, cut into small pieces and fixed in 2.5% glutaraldehyde buffered with 0.1M sodium cacodylate, at 4°C, for 2 hours. Later, tissues were rinsed with the same buffer several times, and postfixed with cacodylate-buffered 1% OsO_4 for 2 hours. After dehydration in a graded series of acetone, the tissues were infiltrated and embedded in Spurr's medium. Ultra-thin sections (60 nm thick) were cut, collected on naked copper grids and stained with uranyl acetate and lead citrate. Sections were examined in a Zeiss EM 10B electron microscope at 60 KV.

Observations

I. The spermatid just prior to metamorphosis

At this phase, the spermatids are spheroidal, ovoidal or polyhedral according to the degree of crowding. Both cytoplasm and nucleoplasm exhibit lesser electron density than in later phases of metamorphosis (Fig. 1).

The nucleus is spheroidal, and has a fairly distinct nuclear envelope with a surrounding perinuclear space of largely uniform width. The chromatin is scattered all over the nuclear space with some local aggregations of no special pattern. Some of these aggregates lie against the inner nuclear membrane, enhancing the distinctness of the nuclear envelope. Many nuclear pore complexes are discernible.

The endoplasmic reticulum, which is mainly of the smooth type, is weakly represented and in the form of single or double cisternae of variable length. The Golgi apparatus is much less developed than in later stages and appears in the form of typical stacks of smooth-surfaced cisternae constituting almost circular dictyosomes. Judging by the paucity of dense vesicles at the extremities of the cisternae and the trans or maturing face, the organelle is hardly active at this stage (Fig. 1).

There are moderate numbers of spheroidal or oval mitochondria scattered in the perinuclear cytoplasm. In structural detail they resemble the classical configuration. However, many of them show signs of the initial steps of transformation. The mitochondrial crests lose much of their regular relationship to the inner membrane, become swollen at their inner tips and exhibit distinct inner space granules. The intermembrane space also develops local irregularities.

The cytoplasm also contains multivesicular bodies, electron dense bodies of unknown nature and fate, besides some clear vacuoles. Clusters of ribosomes are encountered in different regions of the cytoplasm (Fig. 1).

II. Changes exhibited by the nucleus during spermiogenesis

The changes undergone by the nucleus during spermiogenesis are so conspicuous that the different forms it assumes can be utilized as conventional markers for the various stages of the process as a whole. In the following description, the terms used for each stage are based on the profile of the nucleus in median, anteroposterior section. On this basis 4 distinct stages can be identified, namely: the urn stage; the hammer head stage; the hazel-nut stage and the spearhead stage (text Fig. 1).

The Urn Stage

At this stage the nucleus acquires a subspheroidal shape as a result of a slight reduction of its antero-posterior axis. Furthermore, the nuclear envelope becomes differentiated into 4 distinct zones, namely: apical plate; subapical ring; equatorial zone and basal plate.

a) The basal plate is the most conspicuous of all 4 zones and is formed by condensation of material both of cytoplasmic and nuclear origin directly onto the inner and outer membranes respectively. This results in a 5-layered structure including the perinuclear space which becomes narrow, strictly uniform and loses its electron lucidity (Figs. 3 & 4 and text Fig. II). The basal plate lacks nuclear pores and soon its central area becomes invaginated into the nucleus to form the implantation fossa (Fig. 7). The cytoplasm in the immediate vicinity of the basal plate is relatively rich in ER elements that seem to participate in the production of some of the plate's components.

b) The apical plate caps the nucleus constituting the "lid" of the urn. It is thinner and less extensive than the basal plate but is built up of similar components.

c) The subapical ring: at the periphery of the apical plate, the perinuclear space becomes dilated into a ring constituting the shoulders of the nuclear frame or the "ears" of the urn in vertical section (Figs. 3 & 4 and text Fig. I). In some sections the outer membrane of the subapical ring is folded and continuous with the
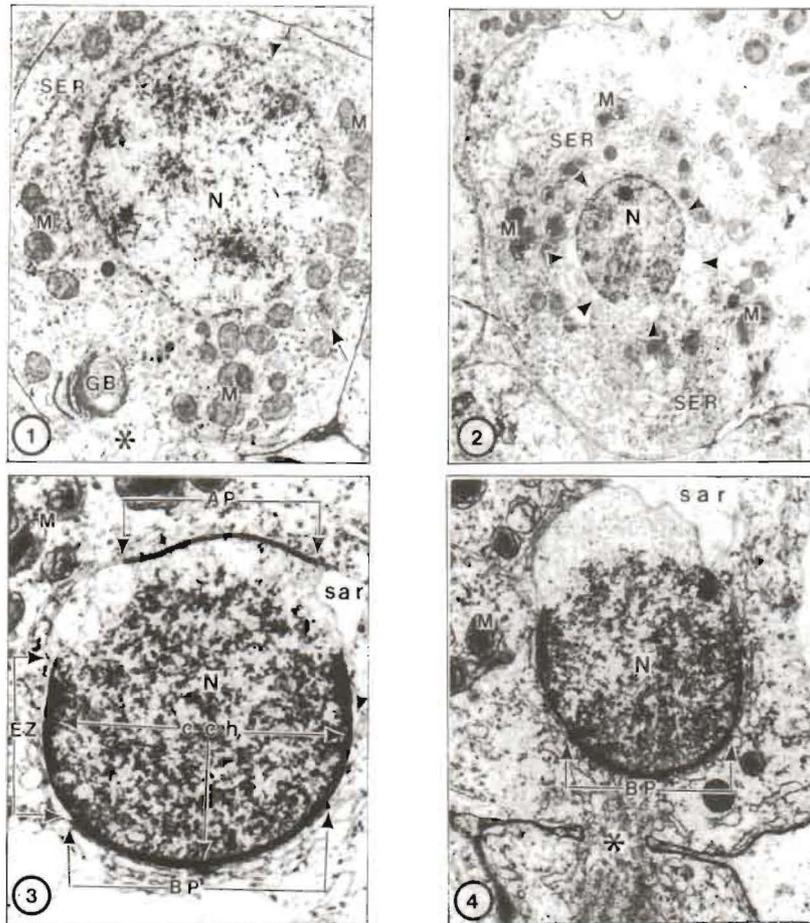

Fig. 1. Early spermatid, showing the undifferentiated nucleus and cytoplasmic organelle;, multivesicular body (arrow); intercellular bridge (asterisk). 9,100 X.

Fig. 2. Spermatid at start of metamorphosis, with the perinuclear space swollen at several points (arrow heads). 7,800 X.

Fig. 3. Urn stage spermatid showing nucleus in median vertical plane; apical and basal plates; subapical ring and perinuclear space in equatorial zone (arrow head). 18,400 X.

Fig. 4. Urn stage spermatid in oblique section passing through basal plate and subapical ring on one side only; intercellular bridge (asterisk). 15,000 X.

adjacent ER elements (Fig. 3). The contents of the subapical ring are largely of an electron lucent nature. Occasionally, however, it may include some flocculent material. In a few cases, the dilation of the perinuclear space was evident at several points around the nuclear circumference (Fig. 2).

d) The equatorial zone of the nuclear envelope constitutes a broad belt between the lower edge of the subapical ring and the upper rim of the basal plate. It shows little differentiation and has a perinuclear space with the normal limited variability in width. Furthermore, there is a higher degree of peripheral chromatin condensation associated with the inner membrane of the envelope in this zone especially between the nuclear pore complexes, which are now exclusive to the equatorial belt (Fig. 3-7).

The variety of configurations exhibited at this stage results from the variation in planes of sectioning as explained by text Fig. I.

Chromatin is slightly more condensed in this stage than it is in the earlier spermatid. The chromatin becomes crowded peripherally just beneath the nuclear envelope where it constitutes a layer thicker in the equatorial zone than in any of the three other zones. The region of the nucleoplasm underlying the apical plate is much poorer in chromatin and thus more electron lucent than elsewhere in the nucleus.

The Hammer Head Stage

Further reduction of the antero-posterior axis confers upon the nucleus a distinctly discoidal shape. The apical plate constitutes the upper surface of the nuclear disc, with the acrosome pedestal in its center, while the basal plate constitutes the lower surface of the disc, with the deeper implantation fossa in its center (Figs. 9 & 10). The equatorial zone of the urn stage is now restricted to the peripheral ring of the nuclear disc, and it still exhibits a few nuclear pores and a distinct somewhat irregular perinuclear space. The upper and lower rims of the peripheral ring are angular, and the upper rim is occasionally turned inwards (Figs. 9 & 10).

As the axoneme extends backwards from the centriolar complex in the implantation fossa, vertical sections present hammer head and handle configurations (Fig. 10); hence the designation.

The apical plate is now thicker, but still fuzzier than the basal plate, and there are signs of higher protein synthesis activity in its proximity as evidenced by the presence of ER elements nearby. Such activity seems to have ceased near the basal plate (Figs. 9 & 10).

(i)   (ii)   (iii)   (iv)
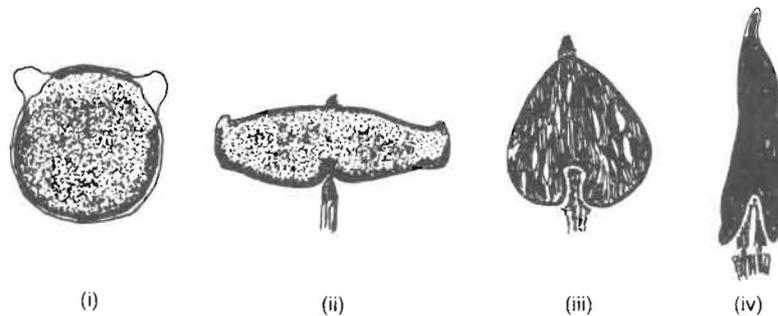
Text Fig. I. Diagrammatic representation of the four distict morphological stages in nuclear transformation utilized here as markers of *S. Laciniosa* spermiogenesis.

(i) Urn stage; (ii) hammer head stage; (iii) hazel-nut stage; (iv) spearhead stage.
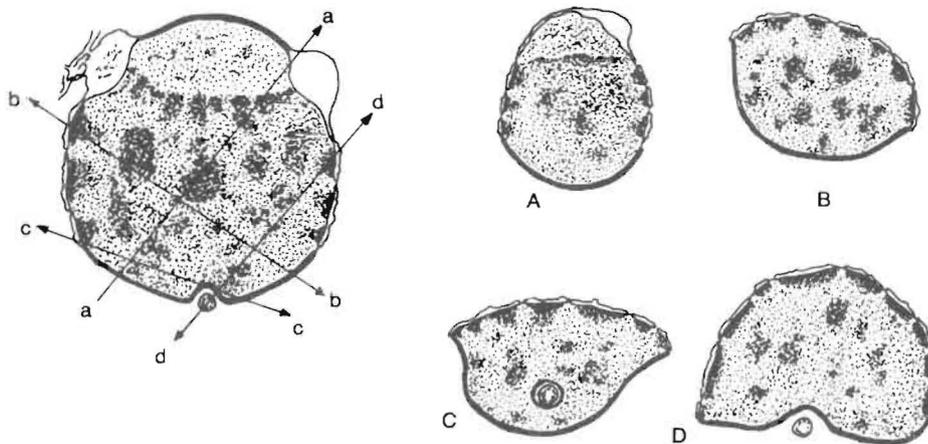

Text Fig. II. Semidiagrammatic representation of the urn stage nucleus and the various configurations it may show according to plane of section (a−a = A; b−b = B; c−c = C; d−d = D).

Chromatin condensation is more advanced. It is evidently a polarized process, starting at the basal plate and proceeding towards the apical one. Thus, beaded chromatin filaments arise in association with the basal plate, extend through the middle and upper zones of the discoidal nucleus, but, in many instances stop short of the apical plate. At the inner corners of the upper and lower edges of the nuclear disc, some of the chromatin filaments extend obliquely from the basal plate to the equatorial zone (Fig. 11).

The Hazel-Nut Stage

At this stage the nucleus is in the form of a short cone, with the maximum diameter about the level of the tip of the implantation fossa. It presents a hazel-nut
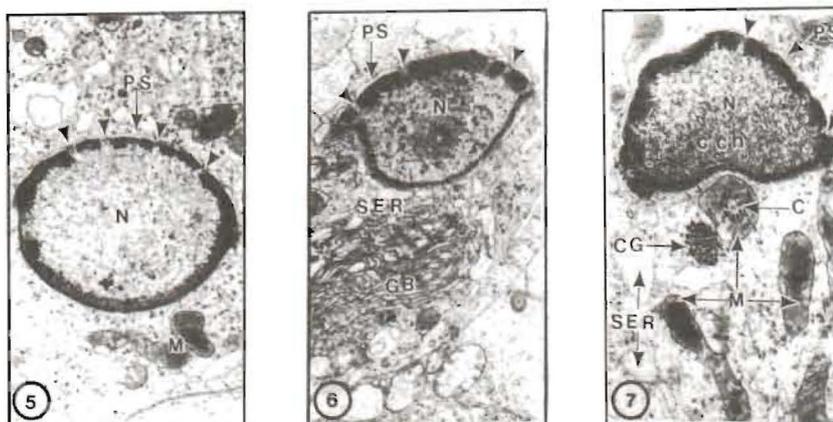
Figs. 5-7. Parts of urn stage spermatids showing nuclei sectioned in different directions (refer to text figure II for interpretation). Arrow heads point to numerous nuclear pore complexes in the equatorial zone. Fig. 5, 12,300 X; Fig. 6, 11,400 X; Fig. 7, 19,100 X.
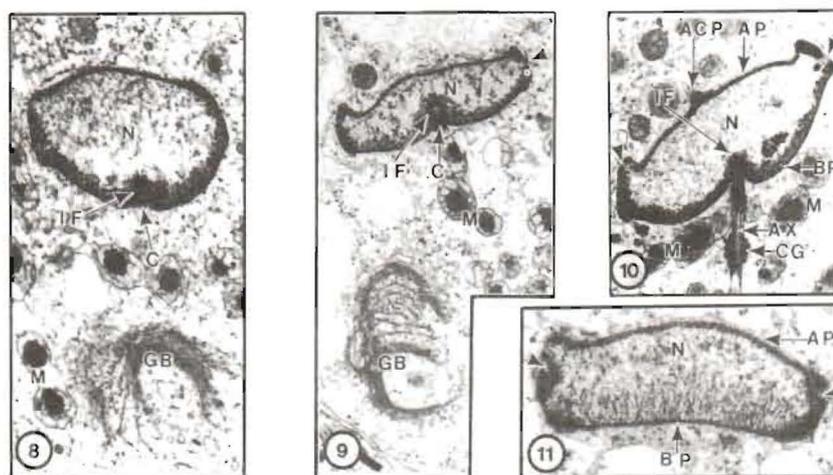
Figs. 8-11. Parts of hammer head stage spermatids, showing some nuclear pore complexes (arrow heads) at the circumference of the discoidal nucleus. Fig. 8, 12,800 X;, Fig. 9, 9,800 X; Fig. 10, 14,500 X; Fig. 11, 20,100 X.

form in median longitudinal section. Thus, during this and the following stages, the anteroposterior axis of the nucleus undergoes progressive lengthening, reversing its trend in the previous stages.

The nuclear envelope complex is thicker and denser now and its region involved in the implantation fossa is more distinct than elsewhere over the nuclear

periphery. There are only a few interruptions in this solid-looking covering confined to the region roughly corresponding to the previous equatorial zone (Figs. 12-14), where chromatin-poor electron lucent nuclear areas seem to communicate with the surrounding cytoplasm.

The beaded chromatin fibers are thicker and are closely packed into groups with narrow spaces intervening more or less logitudinally. These are occasionally wider and may harbour sparse granules. The groups of chromatin fibers are aligned mainly in a direction extending from the basal plate upward towards the nuclear coat at the sides and apex of the nucleus, and are more crowded and denser at the former than at the latter regions.

The acrosome is quite conspicuous at the tip of the nuclear cone, resting on the acrosome pedestal (Figs. 12 & 13). The plasma membrane of the spermatid is either seen approaching the acrosome from above or is already in contact with it (Figs. 13 & 14). In intimate relation with the plasma membrane and closely parallel to it over most of its surface, is the Sertoli cell plasma membrane. At slightly later phases, desmosomes can be seen holding the two plasma membranes together (Figs. 15 & 16).

The centriole complex has, by this stage, acquired an elaborate organization, and presents various configurations depending on the plane of sectioning.

The main bulk of spermatid cytoplasm is now being sloughed and is accumulating at more posterior levels of the already long axoneme. However, a small amount of clear cytoplasm still surrounds the nucleus; it contains a few mitochondria, some vacuoles and very few membranous elements. Numerous microtubules are present in close proximity to the nuclear surface, and must obviously play a role in shaping the nucleus at this and later stages.

The Spearhead Stage

The nucleus acquires this form by further elongation of its antero-posterior axis and reduction of its maximal diameter. Concomitantly, the chromatin undergoes further condensation and the cell membrane becomes draped over most of the nucleus, with hardly any intervening cytoplasm. The main agents in this phase of nuclear morphology change are the microtubules clearly evident encircling the nucleus in both longitudinal and cross sections (Figs. 19-25).

The chromatin is now in the form of lamellae that extend mainly in a radial direction and become progressively more crowded, greatly reducing any interven-ting electron lucent spaces. Some of the lamellae are straight while others follow wavy courses. Groups of such lamellae may together constitute "whirl-pool"
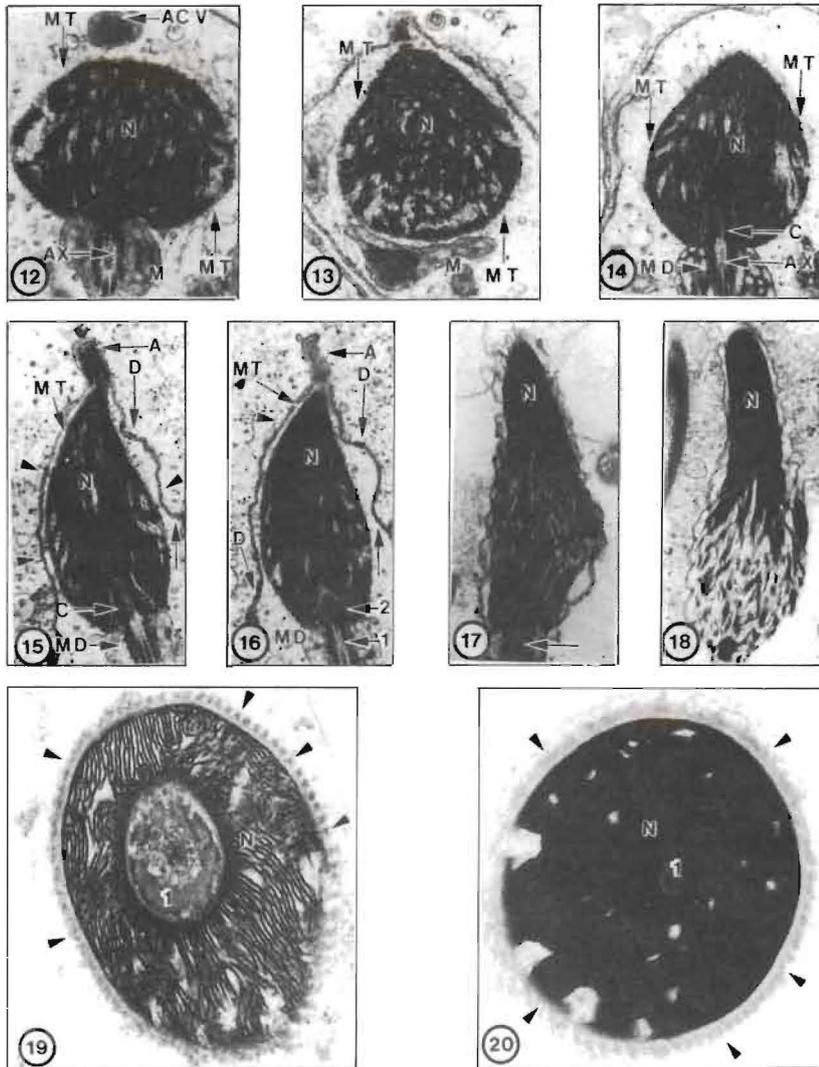
Figs. 12-14. Spermatids in the hazel-nut stage with nuclei cut in median longitudinal plane. Fig. 12, 19,200 X; Fig. 13, 17,600 X; Fig. 14, 16,800 X.

Figs. 15 & 16. Parts of early spearhead spermatids, showing nuclei in L.S.; acrosomes; Sertoli cell plasma membrane (arrow heads), spermatid plasma membrane (arrows), centriole, (1) & coarse granules, (2). Fig. 15, 15,800 X; Fig. 16, 15,600 X.

Figs. 17 & 18. Parts of spearhead spermatids showing phases in chromatin condensation. Fig. 17, 21,400 X; Fig. 18, 41,800 X.

Figs. 19 & 20. T.S. of posterior regions of spearhead spermatids showing phases in chromatin condensation; parts of centriolar complex (1); microtubules (arrow heads) and peristing nucleocytoplasmic points of communications. Fig. 19, 44,600 X; Fig. 20, 25,500 X.

patterns, with some of them running parallel to the nuclear circumference (Fig. 19). Eventually the chromatin of the spearhead nucleus appears highly and homogeneously electron dense (Figs. 21-25).

Furthermore, the nucleus undergoes spiral twisting under the influence of microtubules that appear in close association with the nuclear surface. This spiralization extends to the tip of the nucleus and is evidenced by several helical keels or ridges. The spiral arrangement of microtubules produces those keels as well as larger superimposed humps on the nuclear surface (Fig. 21).

Discussion

The present investigation on *Siphonaria laciniosa* reveals that the sperm of this Aqaba Gulf pulmonate snail conforms to the ultrastructural organization characteristic of the "modified" sperm type established by earlier workers (Franzen 1955; Thompson 1973; Anderson & Personne 1976). The sperm of this snail possesses all the basic features associated with euthyneuran spermatozoa, namely: acrosome composed of an apical vesicle and acrosomal pedestal; helically shaped nucleus and middle piece; complex mitochondrial derivative with at least one enclosed glycogen helix and axoneme associated with nine coarse fibers showing periodic banding proximally.

Apart from such general features, the sperm of *S. laciniosa* bears close resemblance in one aspect or another to those of other pulmonates whether basommatophoran, like *Siphonaria algesirae* (Azevedo & Corral, 1985) and *Physa acuta* (Terakado, 1981) or stylommatophoran like *Onchidium damellii* (Healy, 1986).

The nuclear changes during spermiogenesis are quite drastic. Apart from the considerable reduction in size, the changes involve: (a) morphological transformations; (b) differential regional specializations of the nuclear envelope, and (c) chromatin condensation.

The first indications of establishment of nuclear polarity is the appearance of the apical and basal plates through the addition of electron dense material to the nuclear envelope on the anterior and posterior faces of the nucleus; thus is laid down the anteroposterior axis of the nucleus and the direction of arrangement of chromatin. The center of the apical plate will be the seat of the acrosomal pedestal, while the central part of the basal plate becomes invaginated forming the bell-shaped and relatively shallow implantation fossa that accomodates the centriole and its associated structures.
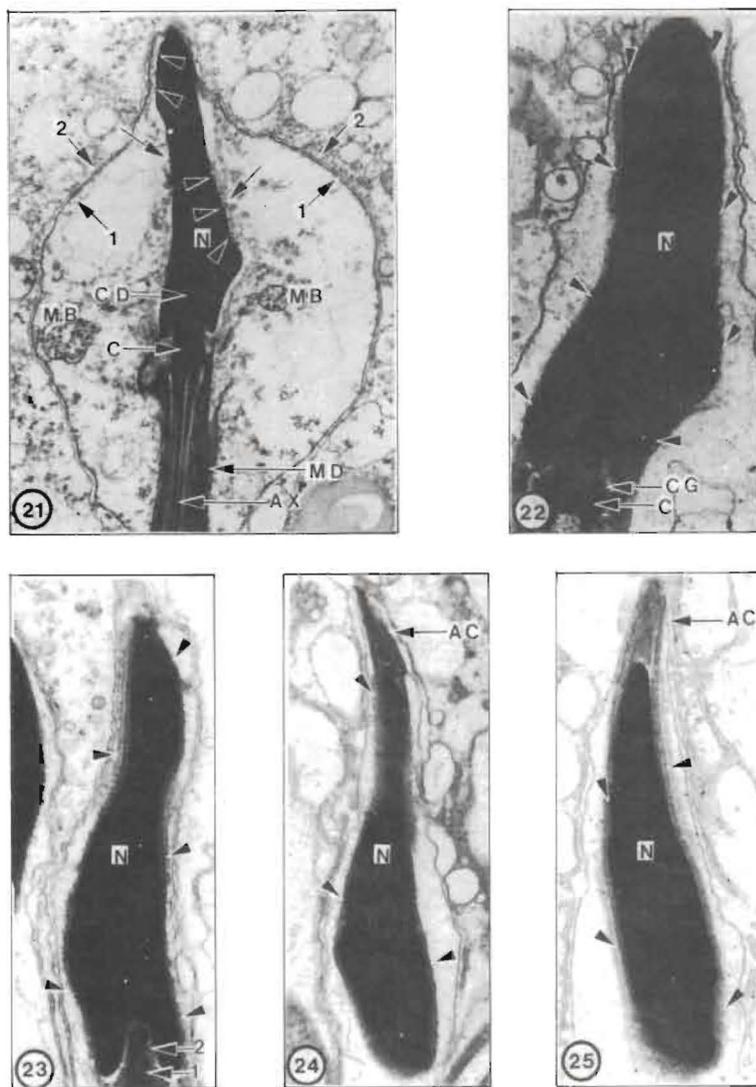
Fig. 21. Shows anterior and posterior keels (arrow heads) indicating nuclear spiralization; associated microtubules (arrows); spermatid plasma membrane (1); Sertoli cell plasma membrane (2). 17,300 X.

Fig. 22. Slightly oblique section showing microtubules (arrow heads) cut in longitudinal, oblique or transverse sections; centriolar complex; associated coarse granules. 29,500 X.

Figs. 23-25. Slightly oblique (23) & median L.S. (24 & 25) spearhead stage spermatids showing microtubules mostly in L.S. (arrow heads) and acrosome pedestals. Fig. 23, 39,200 X; Fig. 24, 19,800 X; Fig. 25, 27,500 X.

Basal and apical plates were reported in gastropods first by Rebhun (1957) and later by Terakado (1976 & 1981), and Takaichi (1978). They have been reported also in spermatids of other invertebrates (Potswald 1967; Reger 1969) as well as some vertebrates (Stanley, 1971).

The swelling of the perinuclear space along a circular band lying just below the rim of the apical plate constitutes the subapical ring which contains mostly clear fluid that, in all probability, seeps from the nucleoplasm. This fluid may eventually make its way to the intracisternal spaces of the ER, which still shows discrete connections with the nuclear envelope in this area.

In the urn stage, the only area of the nuclear envelope that retains nuclear pores is the equatorial zone. Presumably, through these pores more nuclear fluid passes to the surrounding cytoplasm, thus contributing to the progressive condensation of the nucleoplasm. Such nucleocytoplasmic communication seems to last well into the later phases of spermiogenesis albeit at much more limited levels.

The critical phases of chromatin condensation start subsequent to the establishment of the apical and basal plates. Groups of beaded chromatin fibers become attached first to the basal plate and later, at their other ends, to the apical plate extending between the two plates. The forces directly influencing the nuclear change from the spheroidal to the discoidal forms (urn to hammer head stages) are by no means clear. As far as could be discerned no microtubules are associated with the nucleo-cytoplasmic interface at this stage. We suggest that the attachment of chromatin fiber bundles to both basal and apical plates and their possible subsequent shortening would bring the two plates closer to each other and thus help press the nucleus into the discoidal form. This would be greatly assisted by the concomitant maximum loss of fluid from nucleus to cytoplasm through the subapical ring and the nuclear pores of the equatorial zone.

The later phases of nuclear condensation are clearly under the influence of microtubules which make their appearance in close association with the nuclear surface in the hazel-nut and spearhead stages. The microtubules are also influential in the spiralization of both nucleus and middle piece. This spiralization is evident near the posterior end of the nucleus where it produces about four keels, and extends to a point close to the tip of the sperm where four more keels are evident.

Thus spermiogenesis in *Siphonaria laciniosa* bears resemblance to that of several other pulmonates, and it can conveniently be staged by clear-cut morphological markers presented mainly by certain nuclear peculiarities..

Abbreviations Used in the Figures

A	acrosome
ACV	acrosome vesicle
AP	apical plate
AX	axoneme
BP	basal plate
C	centriole
cch	condensed chromatin
CG	coarse granules
D	desmosome
EZ	equatorial zone
GB	Golgi body
IF	implantation fossa
M	mitochondria
MB	multivesicular body
MD	mitochondrial derivative
MT	microtubules
N	nucleus
PS	perinuclear space
sar	subapical ring
SC	Sertoli cell
SER	smooth endoplasmic reticulum

References

Anderson, W.A. and Personne, P. (1967) The fine structure of the neck region of spermatozoa of *Helix aspersa*. *J. Microscopie*, **6**: 1033-1042.

Anderson, W.A., Personne, P. and André, J. (1968) Chemical compartmentalization in *Helix* spermatozoa. *J. Microscopie*, **7**: 367-390.

Anderson, W.A. and Personne, P. (1969) Structure and histochemistry of the basal body derivative, neck and axoneme of spermatozoa of *Helix aspersa*. *J. Microscopie*, **8**: 87-96.

Anderson, W.A. and Personne, P. (1970a) The localization of glycogen in the spermatozoa of various invertebrate and vertebrate species. *J. Cell. Biol.*, **44**: 29-51.

Anderson, W.A. and Personne, P. (1970b) Recent cytochemical studies on the metabolism and function of some invertebrate and vertebrate spermatozoa. *In:* **B. Bacetti** (ed.), *Comparative Spermatology*, Academic Press, N.Y. 431-450 pp.

Anderson, W.A. and Personne, P. (1970c) The cytochemical localization of glycolytic and oxidative enzymes within mitochondria of spermatozoa of some pulmonate gastropods. *J. Histochem. Cytochem.*, **18**: 783-793.

Anderson, W.A. and Personne, P. (1976) The molluscan spermatozoon: dynamic aspects of its structure and function. *Amer. Zool.*, **16**: 293-313.

Atkinson, J.W. (1982) An ultrastructual analysis of the mature spermatozoon of *Anguispira alternata* (Say) (Pulmonata, Stylommatophora). *J. Morph.*, **173**: 249-257.

Azevedo, C. and Corral, L. (1985) The fine structure of the spermatozoa of *Siphonaria algesirae* (Gastropoda, Pulmonata). *J. Morph.*, **186**: 107-117.

Barth, R. and Oliveira, F.B. (1964) Submicroscopic structure of the sperm flagellum of *Triatoma infestans* and *Australorbis glabratus*. *An. Acad. bras. Cl.*, **36**: 559-564.

Bayne, Ch. J. (1970) Organization of the spermatozoon of *Agriolimax reticulatus*, the grey field slug (Pulmonata, Stylommatophora). *Z. Zellforsch.*, **103**: 75-89.

Franzén, A. (1956) On spermiogenesis, morphology of spermatozoon, and biology of fertilization among invertebrates. *Zool. Bidr, Uppsala*, **31**: 355-482.

Franzén, A. (1970) Phylogenetic aspects of the morphology of the spermatozoa and spermiogenesis. *In:* B. Baccetti (ed.) *Comparative spermatology*, Academic Press, N.Y., 29-46 pp.

Galangau, V. and Tuzet, O. (1966) Cou et présence des formations de nature ergastoplasmique dans les spermatides de *Milax gagates* Drap. (Gastéropode Pulmoné). *C.R. Acad. Sci.* (Paris) **D262**: 2364-2366.

Gatenby, J.B. (1960) Notes on the gametogenesis of a pulmonate mollusc. An electron microscope study. *La Cellule*, **60**: 289-300.

Grassé, P.O., Carasso, N. and Favard, P. (1956) Les ultrastructures cellulaires au cours de la spermiogenése de l'Escargot (*Helix pomatia* L): Evolution des chromosomes, du chondriomes, de l'appareil de Golgi, etc. *Ann. Sci. Nat. Zool.*, **18**: 339-380.

Healy, J.M. (1986) Electron microscopic observations on the spermatozoa of a marine 'pulmonate' slug, *Onchidium damellii* (Gastropoda, Onchidiacea). *J. Submicrosc. Cytol.*, **18**(3): 578-594.

Personne, P. and Anderson, W.A. (1969) Compartimentage des activités enzymatiques dans le spermatozoide de certains Mollusques Gastéropodes. I. Localisation des deshydrogenases. *J. Cell. Sci.*, **4**: 693-707.

Personne, P. and Anderson, W.A. (1970) Localization mitochondriale d'enzymes liées au metabolisme du glycogène dans le spermatozoide de l'escargot. *J. Cell. Biol.* **44**: 20-28.

Postwald, H.E. (1967) An electron microscope study of spermiogenesis in *Spirorbis (Lacospira) mörchi* Levinsen (Polychaeta). *Z. Zellforsch.* **83**: 231-248.

Rebhun, L.I. (1957) Nuclear changes during spermiogenesis in a pulmonate snail. *J. Biophys. Biochem. Cytol.* **3**(4): 509-531.

Stanley, H.P. (1971) Fine structure of spermiogenesis in the elasmobranch fish *Squalus suckleyi.* 1. Acrosome formation, nuclear elongation and differentiation of midpiece axis. *J. Ultrastruct. Res.* **36**: 86-102.

Tahmisian, T.N. (1964) On orderly domains of particles associated with cytomembranes during spermatogenesis in *Helix aspersa. Z. Zellforsch.* **64**: 25-31.

Takahashi, Y., Nishimura, Y. and **Yamagishi, N.** (1973) Electron microscopic studies on spermiogenesis of *Limax elevatus* L. *J. Nara Med. Ass.,* **24**: 401-410.

Takaichi, S. (1978) Spermiogenesis in the pulmonate snail, *Euhadra hickonis.* II. Structural changes of the nucleus. *Develop. Growth and Differ.* **20**(4): 301-315.

Takaichi, S. and **Dan, J.C.** (1977) Spermiogenesis in the pulmonate snail, *Euhadra hickonis.* 1. Acrosome formation. *Develop. Growth and Differ.* **19**(1): 3-13.

Terakado, K. (1981) Chromatin arrangement and axis formation in the spermiogenesis of a pulmonate snail. *Develop. Growth and Differ.* **23**(4): 381-399.

Thompson, T.E. (1973) Euthyneuran and other molluscan spermatozoa. Proc. Fourth European Malacological Congress. *Malacologia,* **14**: 167-206.

Tuzet, O. and **Galangau, V.** (1967) Ultrastructure de la "membrane ondulante" *d'Agriolimax agrestis* L. *C.R. Acad. Sci.* (Paris) **D264**: 337-339.

دراسات على تكوين النطف
في حلزون سايفوناريا لاسينيوزا (البطنقدميات ـ الرئويات)
من خليج العقبة
١ ـ التغيـرات النوويـة

رمسيس لطفي و حميد الحاج

قسم العلوم الحياتية ـ كلية العلوم ـ الجامعة الأردنية ـ عمان ـ الأردن

تَتَبَّعَ الكاتبان بواسطة المجهر الالكتروني المرحلة الحـاسمة في تكـوّن النطف في حلزون سايفوناريا لاسينيوزا، وهي مرحلة تحـوّل الخلايـا المنويـة إلى النطف الناضجة والتي تتضمن تغيرات مورفولوجية وفسيولوجية تتنـاول معظم مكونـات الخليـة . ويركّـز المؤلفان في هـذا البحـث على التغـيرات التي تعتـري النـواة، أمـا التغيرات التي تتعـرّض لهـا المكونـات الخلوية الأخـرى فسوف تناقش في نشرات مستقلة .

تعتبر التغيرات التي تتعرّض لها النـواة أثناء تحـوّل الخلايـا المنويـة إلى نطف ناضجة من أبرز معالم تلك العملية ومؤشراتها . وتتم التغيّرات النووية في سلسلة متصلة تتنـاول حجم النواة وشكلهـا وخصائص أخـرى فيها . فـالحجم يتناقص باطراد ليواكب التزايد المطرد في تكثف المادة الكروماتينية . أما من ناحيـة الشكل فإن النواة تتخذ عدة صور في رحلة تحوّلها : فمن الشكل الكروي الذي تتميّـز به نواة الخلية المنوية، تتحوّل النواة إلى شكل «الجرة» ثم تتخذ هيئة «رأس مـطرقة» ثم «بندقة» ثم «رأس رمح» .

والعناصر التي تلعب الدور الأساسي في المراحل المتأخرة في هذه التحوّلات البينة في شكل النـواة هي الأنيبيبات الـدقيقة التي تصطف حول النـواة وتضغط على سطحها بطريق أو بآخر . أما المراحل المبكّرة من التغيرات النووية فيبدو أنها

تأتي عن طريق فقدان كمية وافرة من السائل النووي وكذلك عن طريق الشد الذي تمارسه الألياف الكروماتينية على السطوح الداخلية للغلاف النووي فتعمل على اختزال المسافة بين سقف النواة (الصفيحة القمية) وبين أرضية النواة (الصفيحة القاعدية)، محوّلة أياها من شكل «الجرة» إلى الشكل القرصي (رأس المطرقة) .

وقد تتبّع الكاتبان ما يصيب الغلاف النووي من تحوّلات خلال جميع تلك المراحل، ومساهمة تلك التحوّلات في عمليات التبادل التي تستمر بين السيتوبلازم وبين محتويات النواة حتى طور متأخر من تكوين النطف .

ويطرد تحوّل الكروماتين من خيوط أو ليفات دقيقة مبعثرة في الحيز النووي إلى حزم تمتد بين الصفيحة القمية والصفيحة القاعدية من الغلاف النووي، ثم يتزايد تكثفه باندماج تلك الحزم في صفائح داكنة تشكّل أنماطاً شعاعية أو ثنيات متوازية تفصل بينها فسحات فاهية اللون . ثم يطرد تقارب تلك الصفائح، وينتهي بها الأمر إلى الاندماج . ويؤدي هذا التكثّف الكروماتيني عند اتمامه إلى أن يضفي على النواة لوناً أسود قاتم في تحضيرات المجهر الالكتروني .

ويصف الكاتبان تكوين «حفرة الازدراع» التي يسكنها السنتريول في مركز الصفيحة القاعدية، وكذلك استقرار الحبيبة الأكروسومية في مركز الصفيحة القمية على رأس النواة، واطراد تحوّلها لتكون الأكروسوم نفسه .